CONTEXT DEPENDENCE IN EFFECTS OF NUTRIENT ENRICHMENT ON TROPICAL CORAL REEFS

By

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To my mom, Sheila, who showed me early on that where there is a will there is a way
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Anthropogenic nutrient enrichment of natural systems is rapidly increasing around the world, stimulating fast-growing, weedy species that can elicit a suite of negative effects on foundation species in marine systems. However, despite the magnitude and immediacy of this environmental issue, we understand little of the specific conditions under which nutrient enrichment will control primary producers and, consequently, affect the greater community. In particular, nutrient enrichment can occur: at many different levels, in combination with other anthropogenic stressors, and over vastly different spatial scales and landscapes. Therefore, in my dissertation research, I used field experiments to: 1) examine how the magnitude of nutrient enrichment affects corals (Ch. 2), and 2) test whether nutrient enrichment effects on reef communities depend on other pervasive environmental stressors (Ch. 3). Additionally, I examined the effects of enrichment scale (using mathematical modeling; Ch. 4) and reef habitat configuration (using an observational study and experiment; Ch. 5), on the relative importance of bottom-up (e.g., nutrient enrichment) vs. top-down (e.g., herbivory) effects on primary producers. I found that enrichment effects on primary producers in coral reefs depend strongly on a variety of factors, including the magnitude of
enrichment, the co-occurrence of other prominent environmental stressors, and the scale and landscape over which enrichment takes place. My findings both support (Ch. 3, 5) and refute (Ch. 4) the paradigm in marine systems that herbivores suppress enrichment effects, indicating that while small-scale experiments show herbivore control of enrichment, the mechanisms underlying these effects may fail to operate over more ecologically relevant scales of space and time. Collectively, my findings indicate that the vulnerability of aquatic systems to nutrient enrichment likely depends critically on long-term population dynamics of herbivores.
CHAPTER 1
INTRODUCTION

Many natural systems evolved and persist under nutrient-poor conditions (Elser et al. 2007). However, anthropogenic nutrient enrichment, fueled by rising land and fertilizer use, has recently emerged as a ubiquitous disturbance, increasingly affecting ecosystems around the world (Vitousek et al. 1997, Nixon 2009). In many systems, nutrient enrichment stimulates primary production (Vitousek and Howarth 1991, Elser et al. 2007), which can alter the structure and function of natural communities. In marine systems, including coral reefs (McCook et al. 2001, Smith et al. 2006, Rasher and Hay 2010), seagrass meadows (Burkholder et al. 2007), and kelp forests (Connell et al. 2008), added nutrients can stimulate the growth of weedy benthic algae that can harm foundation species and, consequently, the high biodiversity and ecosystem services they support. While nutrient enrichment poses a rising threat to ecosystems that are vital to humankind (Vitousek et al. 1997, Bellwood et al. 2004, Fabricius 2005, Hughes et al. 2010), a chief challenge in studying enrichment effects lies in the wide diversity of environmental contexts in which enrichment takes place. Below I outline four key factors that could shape enrichment effects.

First, nutrient enrichment can occur over a wide range of magnitudes (Fabricius 2005), which may affect organisms differently. Indeed, nutrients provide nitrogen and phosphorous, which are needed to form both amino acids and nucleic acids and are thus essential to all known life on Earth. While some concentration of nutrients is necessary for an organism to persist, nutrients are also known to become toxic at high levels (Barboza et al. 2009). In tropical coral reefs, direct effects of nutrients on corals are often overlooked, overshadowed by the strong indirect effect of nutrients on corals,
via benthic algae. However, the studies that have tested direct effects of nutrients on coral growth are generally based on two experimental treatments (i.e., low vs. high nutrients) and have yielded qualitatively different conclusions at roughly even frequencies: some studies show negative direct effects of enrichment (Kinsey and Davies 1979, Marubini and Davies 1996, Ferrier-Pages et al. 2000), some positive effects (Atkinson et al. 1995, Koop et al. 2001, Tanaka et al. 2007), and some no effect at all (Davies 1990, Stambler et al. 1991, Koop et al. 2001). This heterogeneity in direct effects of enrichment on corals could be resolved by a nonlinear relationship between coral growth and nutrient enrichment, though such a relationship remains unexplored.

Second, enrichment can co-occur with a variety of other anthropogenic stressors, chief among them in coastal marine systems are sedimentation and overfishing (Jackson et al. 2001, Fabricius 2005). Indeed, nutrient enrichment and sedimentation often occur in combination, resulting from terrestrial runoff that is exacerbated in urbanized coastal areas, in which naturally absorptive soils are covered with less permeable cement (Fabricius 2005). In addition, commercial and recreational fishing pressure can lead to overexploitation of consumers in nearshore ecosystems (Jackson et al. 2001). While the extent to which nutrient enrichment, sedimentation, and overfishing co-occur can vary among systems, interactions among these three dominant stressors remain unknown. Understanding the effects of these three stressors and their potential interactions will be vital to sustainable management of human-altered marine systems.

Third, the spatial scale of enrichment could determine enrichment effects on primary producers by influencing herbivore behavior. Typical enrichment events, fueled
by terrestrial runoff, extend widely over space (e.g., square kilometers to hundreds of square kilometers; Smith et al. 1981, Penna et al. 2004, Paerl et al. 2006, Bell et al. 2014). However, due to logistical and ethical constraints, field enrichment experiments have been historically constrained to scales of manipulation (typically <m²) that are many orders of magnitude smaller than the enrichment events they are intended to represent (Burkepile and Hay 2006, Gruner et al. 2008). This spatial scale discrepancy has broad implications for conclusions from a recent meta-analysis, which indicated that among top-down vs. bottom-up field experiments in marine systems, herbivores generally control effects of enrichment by eating down enriched algae (Burkepile and Hay 2006). The wide movement range of focal herbivores likely allowed herbivores to concentrate in small-scale enriched plots, driving the observed patterns. However, we would expect that this mechanism would increasingly fail to operate as enrichment increased from experimental scales to natural scales. In turn, we remain uncertain about the role herbivores play in enrichment dynamics under realistic scenarios.

Fourth, similar to the spatial scale of enrichment, the spatial context of the landscape may also influence effects of enrichment through the behavior of herbivores. While the relative importance of resources ("bottom-up" effects; Ehrlich and Birch 1967, Osenberg and Mittelbach 1996) versus consumers ("top-down" effects; Hairston et al. 1960, Oksanen et al. 1981, Sih et al. 1985) in structuring communities has long been debated among ecologists, this dynamic may be controlled, in part, by the spatial context (i.e., the type and configuration of surrounding habitat) of a given location. Foraging theory and a variety of terrestrial field studies posit that overall foraging in a resource patch decreases with higher perceived risk of predation by foragers, and
isolation from structural refuge habitat can drive this perceived risk (Brown and Kotler 2004). Conversely, increased densities of resources, resulting from enrichment, provide a greater incentive to forage in a patch (Gilliam and Fraser 1987, Brown and Kotler 2004). These competing demands of safety and food suggest that an interaction may exist between effects of enrichment and effects of habitat isolation on primary producers, via herbivore behavior. Though it remains unexplored, understanding the effect of the spatial context of the landscape on top-down versus bottom-up effects will be particularly important to the management of spatially heterogeneous systems prone to habitat loss and fragmentation, including coral reefs (Bellwood et al. 2004), seagrass meadows (Orth et al. 2006), and kelp forests (Steneck et al. 2002).

In the first two studies of my dissertation, I used field experiments to 1) examine how the magnitude of nutrient enrichment affects corals (Ch. 2), and 2) whether nutrient enrichment effects on reef communities depend on other pervasive environmental stressors (Ch. 3). I also tested the effects of enrichment scale (using mathematical modeling; Ch. 4) and reef habitat configuration across a landscape (using an observational study and experiment; Ch. 5), on the relative importance of bottom-up vs. top-down (e.g., herbivory) effects on primary producers.
CHAPTER 2
UNITY THROUGH NONLINEARITY: A UNIMODAL CORAL-NUTRIENT INTERACTION

Summary

The magnitude and direction of biological effects of environmental disturbances can vary considerably, especially among studies that use presence/absence manipulations. Because non-linearities (e.g., humped relationships) are common in biological systems, this heterogeneity in effects may arise if systems are similar in their responses but specific studies use few (e.g., two) levels, or a narrow range, of a factor. To test whether nonlinearity can explain heterogeneous responses to a common environmental disturbance, I examined the effect of nutrient enrichment on coral growth, which has been previously shown using simple (e.g., 2-level) manipulations to yield positive, negative, or neutral responses. I subjected corals (*Porites*) to a nutrient gradient *in situ* for 28 days. Coral growth rate increased (2.4 fold) then decreased (2.7 fold) with enrichment, returning to near-ambient values at the highest nutrient levels. This unimodal response could explain disparities among past findings and provides a compelling case for using regression designs to understand heterogeneity within ecological interactions.

Background

Nonlinear relationships are ubiquitous in ecology (e.g., Connell 1978, Tilman and Pacala 1993, Bertness and Callaway 1994, Mittelbach et al. 2001, Klemmer et al. 2012). When a relationship is nonlinear, the magnitude, direction, and even the detection of a biological response can depend on the number of levels and range of the independent variable. As a result, multiple studies, each imposing few levels or a narrow range of a factor, may yield conflicting results, owing not to variation in the
underlying nonlinear relationship, but instead to variation in the way the relationship was examined empirically. For example, two-level experiments (e.g., ‘presence vs. absence’, or ‘low vs. high’) characterize the slope of the line between two points, but if the underlying relationship is nonlinear, both the magnitude (i.e., weak vs. strong) and direction (i.e., positive vs. negative) of the observed slope can depend heavily on the relative and absolute positions of the points along the x-axis (Figure 2-1).

Heterogeneity in responses among studies, organisms, and systems, provide the foundation of comparative biology and ecology. Yet a nonlinear response can confuse, or mislead, interpretation of this apparent heterogeneity. For example, past studies on density-area relationships suggested a negative or neutral effect (Connor et al. 2000, Nee and Cotgreave 2002), whereas more recent studies that considered a wider range of areas suggested a unimodal (i.e., ‘hump-shaped’) relationship (Gaston and Matter 2002, Buckley and Roughgarden 2006). Similarly, nonlinearities revealed by ecotoxicologists have helped to resolve heterogeneous and controversial effects of the common pesticide atrazine on rates of amphibian development (Rohr and McCoy 2010). In other systems, monotonic results may be incomplete, as in the case of species richness-productivity relationships: while some works have shown a positive linear relationship (Naeem et al. 1994, Naeem et al. 1996, Tilman 1996), surveys and syntheses that encompass a broader set of conditions, locations and systems suggest these linear interactions are likely portions of an over-arching unimodal relationship (Tilman and Pacala 1993, Leibold et al. 1997, Mittelbach et al. 2001). Generally, the literature has shown that evidence for a linear relationship does not preclude the
existence of nonlinearities, which may be common when responses among studies are heterogeneous (e.g., positive, negative or neutral).

Recently, studies of ‘environmental stressors’ (factors that impose negative effects on organisms), based largely on presence/absence experiments, indicated high variability in the magnitude and direction of both biological responses to stressors and pair-wise stressor interactions (Crain et al. 2008, Darling and Côté 2008, Tylianakis et al. 2008). However, dissimilarities in responses among studies could arise from common, underlying nonlinear relationships (Figure 2-1). Thus, understanding the effects of environmental stressors, which can vary widely in magnitude (Walther et al. 2002), requires that we conduct experiments that include more levels and a wider range of the focal predictor variable (Figure 2-1; Cottingham et al. 2005).

Nutrient availability can vary widely in nature, especially in coastal marine systems, which are subjected to terrestrial runoff, coastal development, localized upwelling, tidal flushing, and internal tidal bores (Vitousek et al. 1997, Leichter et al. 2003, Fabricius 2005). Studies have shown that increasing nutrient availability (hereafter referred to as ‘nutrient enrichment’) can have highly variable effects on reef-forming corals. For example, in a representative collection of studies of nutrient effects on coral growth, there were approximately equal numbers of positive (12 out of 37), negative (12 out of 37), and neutral (13 out of 37) coral growth responses (Table A-1). Previous studies examining the effect of nutrient enrichment on corals have tested few (most often 2) treatment levels, and, as a result, these studies were unable to test for nonlinear responses. Furthermore, previous coral-nutrient studies are difficult to compare directly, due to significant differences in enrichment method and study context.
(Appendix A). Because nutrient enrichment of coral reefs is a growing, worldwide phenomenon, understanding its effect on corals, organisms upon which countless reef creatures depend, remains a fundamental task for reef conservation (Vitousek et al. 1997, Fabricius 2005).

In this study, I investigated the potential for a nonlinear response to explain heterogeneous results in a coral-nutrient system. I imposed a nutrient enrichment gradient \textit{in situ} that elicited a unimodal coral growth response. This novel result potentially unifies disparate findings in the coral-nutrient literature and emphasizes the importance of a regression-based approach as a tool to resolve response heterogeneity and characterize nonlinearities with broad ecological implications.

\textbf{Materials and Methods}

\textbf{Experiment}

This study was conducted in June and July of 2010 at an oligotrophic backreef site off the north shore of Moorea, French Polynesia (17°28’59” S, 149°50’2” W). I studied the response of juvenile colonies of \textit{Porites} (a complex comprised of \textit{Porites lutea} and \textit{Porites lobata}), because of their high local abundance and the global distribution and abundance of this genus (Veron 1995). Colonies of 3-5 cm height were collected near the reef crest just north of the study location and immediately transported in a cooler to the Richard B. Gump South Pacific Research Station. Corals (n=8) were randomly assigned to one of 7 nutrient-enrichment treatments, and each coral was secured to the head of a nylon bolt using Reef Glue® gel (Boston Aqua, USA). Buoyant mass (Davies 1989) was measured the evening of collection, and corals were deployed to the field the following morning. Units were arranged in 8 randomized, complete blocks. To minimize nutrient spillover among treatments, units were separated by 2 m
and arranged in a straight line perpendicular to the unidirectional SSE current that predominates at the study location (Hench et al. 2008).

Each experimental unit was assembled *in situ* using SCUBA by bolting each coral to plastic mesh secured atop the opening of a plastic cup. To deter coral predators, all units were enclosed in galvanized steel cages with 2.5 cm mesh; the large mesh was chosen to minimize caging effects on bulk water flow and coral growth (Burkepile and Hay 2009). Cages were anchored with limestone rocks, and each cage was scrubbed every 2-3 days to reduce fouling. Algae, though present in small quantities, were unable to amass around coral study units, and coral disease was not observed. This allowed me to isolate the direct effect of nutrients on corals without confounding this effect with the stimulation of harmful benthic algae or coral disease (Hallock and Schlager 1986, McCook et al. 2001, Bruno et al. 2003).

I imposed a nutrient-enrichment gradient by adding either 0, 5, 10, 25, 50, 85, or 125 g of Osmocote® (The Scotts Company LLC, USA) slow-release garden fertilizer (19:6:12, N:P:K), packed in fine-mesh nylon pouches (e.g., Burkepile and Hay 2009), to the cup of each experimental unit. These fertilizer treatment levels were chosen based on the volume of the release cup and successful enrichment of benthic algae in this system under similar conditions (Peggy Fong, *pers. comm.*). Fertilizer was added on day one and replaced on day 15 with new fertilizer, providing two 14-day nutrient additions. Nutrient release from fertilizer was expected to reach a maximum early and diminish over time (Peggy Fong, *pers. comm.*), thus these ‘pulses’ of nutrients were meant to resemble coastal enrichment events that are driven by punctuated rainfall and resulting runoff. At the conclusion of each addition, I assessed the amount of fertilizer
that had been released by collecting the remaining fertilizer and drying it at 70°C until a
stable final dry mass was obtained. On the fifth day of the experiment, water-column
samples were collected 1 cm below each coral colony using a 30 mL syringe. Each
sample was immediately run through a 0.45 μm glass fiber filter and frozen until
analysis. These methods were repeated on days 19 and 24, but only for the 25 g and
125 g fertilizer treatments. Samples were analyzed for ammonia (NH₃) and nitrate +
nitrite (NO₃⁻ + NO₂⁻, or NOₓ) concentrations at the University of Florida/IFAS Analytical
Services Laboratories. On the 28th day of the experiment, corals were brought back to
the laboratory, where their final buoyant mass and surface area (using Marsh’s (1970)
foil method) were measured.

**Statistical Modeling**

I compared three models of the relationship between coral growth rate and
nutrient availability using the “nlme” package (Pinheiro 2012) in the program R 2.13.0
(R Development Core Team 2010): 1) a 'no-effect' model (i.e., no slope term, constant
response); 2) a linear model, and 3) a Ricker model (e.g., Brannstrom and Sumpter
2005). I used the Ricker model as a general description of a unimodal relationship:

\[ C = \phi(F + b)e^{-\sigma(F+b)}, \]

where \( C \) is coral growth rate (mg·cm⁻²·d⁻¹), \( \phi \) is the initial slope of the function, \( F \) is the
fertilizer addition (g), \( b \) is the blocking term (thus, \( F + b \) represents the effective nutrient
level), and \( \sigma \) is the scaling exponent. This mixed-effects model allowed each block (with
effects represented by \( b \)) to randomly vary along the nutrient gradient to account for
variation in flow and background nutrient levels (Miller et al. 1999). The linear model
was derived from 1-1 by setting the parameter \( \sigma = 0 \). The 'no-effect' model included a
constant (k) and a blocking term (random effect) only (i.e., $C=k+b$). I used likelihood ratios to test for a significant unimodal pattern in the data, by comparing these three models. To analyze the effect of fertilizer treatment on fertilizer mass loss and water column nutrient concentrations, I used likelihood ratio tests to compare linear and ‘no-effect’ models, each containing a random effect to account for blocking. The code used to run these analyses is included in the Supplement.

Results

Treatment Effectiveness

Loss of fertilizer mass, which provided an integrated measure of treatment efficacy over time, increased linearly with fertilizer treatment during both fertilizer additions: Table 2-1. Water-column nutrient samples provided instantaneous measures of the nutrient environment just below each experimental coral and showed a consistent nutrient increase with fertilizer treatment, an effect that was fairly concordant (i.e., slopes were similar) across sampling days (Table 2-1). Dissolved inorganic nitrogen, NH$_3$+NO$_x$, in the 125 g fertilizer treatment ($5.8 \pm 1.1$ µM, mean ± SE) fell well within observed nutrient levels in degraded reefs associated with coastal development (e.g., Costa et al. 2000) and could occur in less developed systems after significant rainfall events. For example, in Moorea, NO$_x$ levels have been as high as 24 µM at a site just inshore from the study reef (Alldredge 2011). The concentration of nitrates and nitrites (NO$_x$) from the 0 g fertilizer treatment ($0.66 \pm 0.025$ µM) was similar to the ambient levels measured annually from nearby sites (NO$_x$ = $0.57 \pm 0.085$ µM, mean ± SE: Alldredge 2011), suggesting minimal spillover from high- to low-enrichment units. Collectively, these results indicate that fertilizer treatment had a local effect that led to a linear increase in nutrient availability.
Coral Growth Rate

This experiment was intended to measure direct effects of nutrients on coral growth, without indirect effects through benthic algae or disease. As intended, I observed neither encroachment of benthic algae nor incidence of disease, except for one coral from the 125 g fertilizer treatment, which became partially overgrown by filamentous turf algae. This coral was removed from the analysis, but its removal did not qualitatively affect the statistical results. Coral growth rate was demonstrably unimodal with respect to fertilizer treatment (Figure 2-2). The Ricker model (1-1) provided a significantly better fit to the data than either the 'no effect' model (Likelihood ratio = 20.25, \( P = 0.0165 \)) or the linear model (Likelihood ratio = 10.44, \( P = 0.0012 \)). The initial slope (\( \phi = 0.070 \pm 0.016 \); mean ± SE) and scaling exponent (\( \sigma = 0.014 \pm 0.0028 \)) of the Ricker model described a coral growth – nutrient relationship in which growth increased 2.4-fold as nutrients initially increased, peaked, and then declined more gradually (2.7-fold) as nutrients increased further (Figure 2-2).

Discussion

Regression-based approaches can allow us to better understand the nature of ecological processes that yield non-linear effects. This is particularly relevant in the study of “environmental stressors” – factors that act as disturbances to organisms or systems (sensu Darling and Côté 2008). Although we think of stressors as having negative effects, many factors that have been called “stressors” can have effects that vary in magnitude and direction (e.g., nutrient availability, temperature, pH, salinity). In these cases, there exists a qualitative switch point, at which a biological response changes from being positive or neutral to negative. To better understand effects of environmental stressors on biological systems, it is imperative to identify and
characterize the point at which an “environmental factor” becomes an “environmental stressor”. By characterizing switch points and other nonlinearities, regression-based approaches may be useful in resolving heterogeneity among other environmental stressor studies (e.g., Crain et al. 2008, Darling and Côté 2008, Tylianakis et al. 2008).

The unimodal model presented here complements existing theory in nutritional ecology, which posits that the growth rate of an organism is optimized at an intermediate nutrient intake (Figure 2-2; Barboza et al. 2009). Previous studies of coral interactions with zooxanthellae, their endosymbiotic algae (in the genus *Symbiodinium*), may provide a mechanistic explanation for the unimodal pattern observed: when zooxanthellae production is limited by nutrients, nutrient enrichment may increase zooxanthellae photosynthesis and, in turn, increase the amount of carbohydrates transferred to the coral host (Hoegh-Guldberg and Smith 1989, Muller-Parker et al. 1994, Dunn et al. 2012). In contrast, under higher nutrient concentrations, carbon (and not nutrients) may become most limiting. Thus, competition between the zooxanthellae and coral can reduce the amount of carbon provisions to the coral host, depressing coral growth (Dubinsky et al. 1990, Falkowski et al. 1993). Increased expulsion of zooxanthellae by corals and decreased lipid content of coral mucus under elevated nutrients further suggest that zooxanthellae may shift from being mutualists to parasites under certain nutrient scenarios (Stimson and Kinzie 1991). A similar pattern of ‘mutualism to parasitism’ has been observed in plant-mycorrhizal fungus associations (Hoeksema et al. 2010). Further work is needed to clarify how potential mechanisms (e.g., due to zooxanthellae physiology assessed via PAM fluorometry (Schreiber 2004))
or due to changes in coral-microbe interactions (see Dinsdale and Rohwer 2011) may drive unimodality in coral-nutrient interactions.

Nutrient enrichment is among the most common and influential environmental stressors in the world and can have marked effects on the structure and function of communities by increasing primary production, changing abiotic conditions (e.g., light, oxygen availability), and destabilizing systems (von Liebig 1855, Rosenzweig 1971, Vitousek et al. 1997, Smith et al. 1999). While nutrient enrichment can indirectly affect corals by enhancing the growth of competing benthic algae and coral disease (Hallock and Schlager 1986, McCook et al. 2001, Bruno et al. 2003), the direct effect of nutrient enrichment on corals has remained much less clear. The present study shows that nutrient enrichment can have demonstrable, albeit variable, effects on corals, even when effects of benthic algae and pathogens are absent. This suggests that nutrient enrichment can be important on reefs, even when the herbivorous fish community is intact (e.g., protected from fishing) and can control the accumulation of nutrient-stimulated algae. However, to date, most marine reserve designs focus exclusively on fishing restrictions and neglect to consider the effects of land-based nutrient pollution (e.g., Pandolfi et al. 2005).

As nutrient enrichment and other environmental changes are expected to increase in frequency and magnitude with climate change and human population growth (Walther et al. 2002, Fabricius 2005), ecologists must seek to better understand how these changes will affect key organisms and ecosystems. The present study provides new insight regarding this challenge and emphasizes that regression-based approaches are useful for unveiling unifying, though potentially cryptic, ecological relationships.
Table 2-1. Summary of the effectiveness of fertilizer treatments. ‘Addition’ refers to the two phases of fertilizer addition. \(N\) gives the number of replicate units sampled. Slope estimates were extracted from linear mixed effects models. Each likelihood ratio (L. ratio) and associated \(P\)-value was obtained by comparing the linear model to a ‘no effect’ (i.e., constant response) model. Fertilizer loss is based upon the change in dry mass of fertilizer across all treatments; \(\text{NH}_3\) and \(\text{NO}_x\) concentrations are based on water samples collected from all or a subset of treatments.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Addition</th>
<th>Day</th>
<th>(N)</th>
<th>Treatments</th>
<th>Slope</th>
<th>L. ratio</th>
<th>(P)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fertilizer loss (g)</td>
<td>1</td>
<td>1-14</td>
<td>14</td>
<td>All</td>
<td>0.22</td>
<td>47.83</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>15-28</td>
<td>55</td>
<td>All</td>
<td>0.22</td>
<td>267.50</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>(\text{NH}_3) (µM)</td>
<td>1</td>
<td>5</td>
<td>55</td>
<td>All</td>
<td>0.026</td>
<td>38.96</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>19</td>
<td>15</td>
<td>25g, 125g</td>
<td>0.023</td>
<td>1.28</td>
<td>0.26</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>24</td>
<td>15</td>
<td>25g, 125g</td>
<td>0.022</td>
<td>4.35</td>
<td>0.037</td>
</tr>
<tr>
<td>(\text{NO}_x) (µM)</td>
<td>1</td>
<td>5</td>
<td>55</td>
<td>All</td>
<td>0.0067</td>
<td>38.01</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>19</td>
<td>15</td>
<td>25g, 125g</td>
<td>0.0051</td>
<td>0.091</td>
<td>0.76</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>24</td>
<td>15</td>
<td>25g, 125g</td>
<td>0.0056</td>
<td>4.55</td>
<td>0.033</td>
</tr>
</tbody>
</table>
Figure 2-1. Nonlinearities can be cryptic. Conceptual diagram illustrating disparities that can arise when a nonlinear (in this case unimodal) underlying relationship exists, and investigators examine either few levels or a limited range of the predictor variable of interest. Each point on the curve can be thought of as a hypothetical experimental treatment. The line segments show that positive, neutral, or negative effects (lines E1, E2, and E3, respectively) are possible in designs with only a low and a high treatment level (denoted by subscripts L and H, respectively). Even when the number of treatments >2, the use of a narrow range of a predictor variable can yield positive, neutral, or negative effects (labelled as Range 1, 2, and 3, respectively).
Figure 2-2. Coral growth response to enrichment. Coral growth rate across effective nutrient enrichment (fertilizer treatment (g) adjusted by the blocking term; F+b in 2-1) over the full 28-day experiment (each point represents an individual juvenile *Porites* spp. coral colony, N = 55). The unimodal model (black line) was the best fit to the data compared to a 'no effect' (i.e., constant response) model (Likelihood ratio = 20.25, P = 0.0165) and linear model (Likelihood ratio = 10.44, P = 0.0012).
CHAPTER 3
INTERACTIVE EFFECTS OF THREE PERVERSIVE MARINE STRESSORS IN A POST-DISTURBANCE CORAL REEF†

Summary

Ecosystems are commonly affected by natural, episodic disturbances than can abruptly and drastically alter communities. Although it has been showed that resilient ecosystems take time to recover to pre-disturbed states, the extent to which communities in early stages of recovery could be affected by multiple anthropogenic stressors is poorly understood. Pervasive and rising anthropogenic stressors in coastal marine systems that could interactively affect the recovery of these systems following natural disturbances include high sedimentation, nutrient enrichment, and overfishing. Using a 6-month field experiment, we examined the effects of all combinations of these three stressors on benthic communities on simulated post-disturbance reef patches within a system recovering from large-scale natural disturbances (corallivorous seastar outbreak and cyclone). We showed that anthropogenic stressors had interactive effects on the growth and survival of corals as well as the growth of benthic algae, for which we observed a significant three-way stressor interaction. We also showed that stressor effects and interactions were taxon-specific at multiple taxonomic scales. First, our treatments affected corals and algae differently, with some stressor combinations promoting algal growth while depressing coral growth and survival. Second, our

†With co-authors Silvan Goldenberg, Anne Ly Thai Bach, Suzanne Mills and Joachim Claudet
treatments had different effects depending on the functional group of coral species and benthic algae. Synthesis and applications: Our findings suggest that great care should be dedicated towards understanding how human uses interact on ecosystems when management is aimed at fostering resilience. Different combinations of common anthropogenic stressors, either related to sea- or land-based activities, can interactively influence community recovery from disturbance in coral reefs, shifting species compositions within the resulting community, and potentially degrading the nature of the ecosystem services derived from it. Thus, our findings encourage managers of coastal systems to consider in their integrated planning not only interactive effects of prominent anthropogenic stressors driven by stakeholder use but also the temporal context of these co-occurring stressors with respect to episodic natural disturbances

**Background**

Community structure and diversity can change abruptly and drastically due to natural, episodic disturbances, such as fires, storms, disease outbreaks or spikes in consumer production (Dempster 1957, Levin and Paine 1974, Connell 1978, Dimmitt and Ruibal 1980, Lips et al. 2006, Feehan and Scheibling 2014). However, many extant natural systems have continually recovered from natural disturbances; e.g., contemporary coral reefs have persisted for nearly 65 million years, despite intermittent devastation by such large-scale natural disturbances as tropical storms (Hayne and Chappell 2001) and outbreaks of the coral-eating crown-of-thorns seastar, *Acanthaster planci* (Kayal et al. 2012, Leray et al. 2012). Furthermore, a recent synthesis across terrestrial and aquatic systems showed that most systems can fully recover from disturbances on timescales of decades to half centuries (Jones and Schmitz 2009). However, the studies synthesized by Jones and Schmitz (2009) featured systems that
were allowed to recover (or even encouraged to do so, via restoration efforts) in the absence of chronic human-induced disturbances.

Human activities can control levels of biological, physical and chemical properties of natural ecosystems (Foley et al. 2005, Elser et al. 2007), giving rise to ‘anthropogenic stressors’ (hereafter ‘stressors’) that negatively affect organisms or communities. In most systems, multiple stressors co-occur, and recent meta-analyses, based largely on experiments manipulating pairs of stressors, suggest that stressors interact in most stressor combinations (Crain et al. 2008, Darling and Côté 2008). An interaction between factors causes the effect of one factor to change quantitatively or even qualitatively, depending on the level of a second factor. Thus, combined stressor effects can be synergistic and are frequently unpredictable even if we understand each stressor effect in isolation. While it is well established that multiple stressors can degrade ecosystems, the extent to which multiple stressors affect recovering systems, which may be particularly vulnerable to degradation, has rarely been formally explored (Nyström et al. 2000, Hughes et al. 2010). Comparative observational studies in terrestrial and aquatic systems suggest that anthropogenic stressors can inhibit recovery following disturbance (Short and Wyllie-Echeverria 1996, Foster et al. 1999, Chazdon 2003), though field experiments testing these effects are greatly needed.

Coastal marine systems, including coral reefs, seagrass meadows, oyster reefs, and kelp forests, are regularly subjected to meteorological and tidal disturbances and also share a similar set of anthropogenic stressors, dominated by high sedimentation input, nutrient enrichment, and overfishing (Dayton et al. 1992, Jackson et al. 2001, Orth et al. 2006). Land use, including deforestation, urbanization and farming, can
increase the magnitude and frequency of terrestrial runoff events, which deposit sediment into coastal waters (Fabricius 2005). Sedimentation can harm foundation species through inhibition of light, settlement, and gas exchange. Nutrient enrichment, which can also be driven by terrestrial runoff, stimulates the growth of weedy primary producers that can outcompete foundation species for space or light: e.g., kelp: (Connell et al. 2008), seagrasses (McGlathery 2001), and corals (McCook et al. 2001, Smith et al. 2006, Rasher and Hay 2010). Overfishing removes top-down controls on consumers and primary producers, and can result in a loss of foundation species, due to enhanced pressure from consumers or competitors (Jackson et al. 2001, Bulleri et al. 2013).

Despite their ubiquity in coastal marine systems that are also prone to natural disturbances, the effects of different combinations of these stressors on communities following disturbance remain untested.

Through multiple, potentially competing, direct and indirect pathways, sedimentation, nutrient enrichment and overfishing may interactively affect coral reef communities following disturbance (Figure 3-1). Furthermore, life history traits, including growth rate, and morphology could affect susceptibility to inhibition of settlement or early growth due to stressor context (Lenihan et al. 2011). Thus, stressors and their combinations could affect the relative abundance and composition of species, and the relative abundances of functional groups (e.g., corals and algae) in the community following a disturbance.

To assess how recovery of coral reefs can be affected by multiple stressors, we simulated post-disturbance reef habitat patches and subjected these patches to a fully-crossed, three-factor manipulation in situ for six months in a recovering reef system. We
tested for interactive effects of sedimentation, nutrient enrichment and the exclusion of large consumers (those targeted by fishing) on the benthic community, including two distinct morphologies of corals and two algal functional groups: filamentous turf algae and macroalgae. Our study revealed that anthropogenic stressors can have interactive, taxon-specific effects on corals and benthic algae in early post-disturbance coral reefs. Our findings suggest that anthropogenic stressors and interactions thereof can determine the structure of communities recovering from disturbance and may, under certain stressor combinations, inhibit or alter recovery trajectories in coral reefs around the world.

**Materials and Methods**

**Study Site and Experimental Units**

We conducted this study in January-July 2013 at a site within the lagoon of the barrier reef off the north shore of Mo'orea, French Polynesia (17°28'59"S, 149°49'55"W), a system in recovery following two recent, large-scale natural disturbances: a crown-of-thorns seastar (*Acanthaster planci*) outbreak that lasted several years and dissipated in 2010, and cyclone *Oli*, which hit the north shore in February 2010 (Kayal et al. 2012). We selected the thin branching coral *Acropora pulchra* (Brook, 1891) and the more bulbous coral *Porites rus* (Forsskal, 1775) as study species because of their differing growth rate, polyp size, and skeletal morphology (see Figure 3-2), which may affect their susceptibility to stressors (Bulleri et al. 2013). In addition, the genera of these species are common in Mo'orea and they are both globally distributed (Veron 1995). In January 2013, we collected eight coral fragments from each of nine *A. pulchra* and nine *P. rus* colonies at ~1.5-2 m depth near our study site (17°29'15" S, 149°53'18" W) and immediately transported fragments in coolers to the
Richard B. Gump South Pacific Research Station. We mounted each fragment onto hard plastic mesh using epoxy (Splash Zone, Carboline Company, St. Louis, Missouri, USA) and recorded its weight using the buoyant mass technique (Davies 1989).

Two days after collecting corals, we assembled experimental units in situ. Each experimental unit was supported by a concrete block (l x w x h = 25 x 20 x 11 cm), to which we attached one fragment of *A. pulchra* (height = 54 ± 9 mm [mean ± SD]) and one fragment of *P. rus* (height = 30 ± 5 mm), using cable ties woven through plastic bases. We also used pre-cemented set screws and wing nuts to attach to each unit four unglazed terracotta tiles (Figure 3-2), which are commonly used as proxies for reef substratum (Adjeroud et al. 2007, Penin et al. 2010). We arranged experimental units in nine randomized, complete blocks, in which blocks accounted for potential spatial patterns in responses as well as effects due to coral colony of origin (i.e., the eight coral fragments from a given colony were assigned to the same block). To minimize nutrient spillover among treatments (see next subsection), we separated the units of each block by at least 2 m (Wartian 2006) and arranged them in a straight line perpendicular to the unidirectional south-southeast current that predominates at the study site (Hench et al. 2008). Further, a natural channel separating our study location from nearshore waters likely minimized the influence of terrestrial runoff on our study (Alldredge 2012, Alldredge 2013). We placed experimental units among coral habitat patches (within 1 m of hard bottom reef habitat) on sand at 2-3 m depth with the same orientation to the current (Figure 3-2).

**Anthropogenic Stressors Manipulations**

We simulated sedimentation, nutrient enrichment and overfishing over a 6-month period to investigate potential interactive effects of these stressors on coral reef
recovery. First, the ‘high sedimentation’ treatment was chosen to have a sedimentation rate of 212 mg cm\(^{-2}\) day\(^{-1}\): our applied rate (200 mg cm\(^{-2}\) day\(^{-1}\)) + the ambient rate (12 mg cm\(^{-2}\) day\(^{-1}\); Alldredge 2012), because: 1) it greatly exceeds natural (i.e., ‘pristine’) sedimentation rates (Rogers 1990), 2) it falls well within known sedimentation rates affecting various coral reefs (Table B-1), and 3) similar sedimentation rates have been shown to negatively affect or even kill various coral species (Erftemeijer et al. 2012). The high sedimentation treatment was imposed by applying sediment of terrestrial origin to experimental units in multiple, daily pulses over a course of two or three days each week (see Appendix 1 for additional details on sediment collection and application).

Nutrient enrichment was imposed by first placing two PVC tubes, sealed at the bottom and covered by mosquito netting at the top, within the two gaps in cement block supporting each experimental unit (Figure 3-2). We filled each PVC tube in nutrient enriched units with 50 g of Osmocote (The Scotts Company, Marysville, Ohio, USA) slow-release garden fertilizer (N:P:K-ratio = 19:6:12), and this fertilizer was replaced every 4 weeks (Burkepile and Hay 2009). We filled the PVC tubes in unenriched units with sterilized sediment, to prevent colonization by small fishes or invertebrates. We slowly extracted water samples using a 30-mL syringe (Burkepile and Hay 2009) from the bases of coral fragments from 3 complete experimental blocks (24 units) at two times points (4 and 23 days after fertilizer replacement). Each water sample was immediately run through a 0.45-μm glass fiber filter and frozen until analysis for nutrient (nitrate + nitrite) concentrations at the University of Florida/IFAS Analytical Services Laboratories (Gainesville, Florida, USA). These water samples revealed that, as intended, our enrichment procedure achieved a significantly elevated availability of
nutrients (approximately 3-fold) in enriched relative to unenriched units (nitrate + nitrite concentration: $0.448 \pm 0.116$ [mean $\pm$ SE] µM for control vs. $1.24 \pm 0.323$ µM for nutrient-enriched units; Figure B-1). Our control measurements were similar to ambient nitrate + nitrite concentrations measured annually from nearby sites ($0.570 \pm 0.085$ µM; Alldredge 2013).

The absence of large consumers, which would be expected in an overfished reef, was achieved using plastic exclusion cages (diameter = 50 cm, height = 32 cm, mesh = 4 cm). This mesh size was chosen to avoid cage artifacts; previous work have shown that mesh sizes of 2.5 cm do not demonstrably affect current flow or the growth of benthic organisms (Burkepile and Hay 2009). Fouling organisms were brushed off the cages weekly.

We fully crossed two levels (ambient and elevated) of each of the three factors (sediments, nutrients, overfishing), resulting in eight experimental treatments, with one replicate in each of nine replicated blocks for a total of 72 experimental units. At the conclusion of the experiment, we retrieved the corals, obtained their buoyant weights, and visually estimated using the naked eye the % of the surface area of each coral that was alive. We also removed and separated filamentous turf algae and macroalgae from all surfaces of two settlement tiles from each unit, and dried these samples in an oven at $70^\circ$ C until the mass was stable. Lastly, we first removed non-calcified organic matter from the second pair of tiles from each unit by soaking them in a bleach solution. We then used a microscope to count coral polyp skeletons on all surfaces of one of the tiles from each unit; we did not analyze the second tile due to logistical constraints.
We quantified stressor effects and interactions using an ANOVA with seven orthogonal contrasts, comprised of main effects for each of the three factors (sedimentation, nutrient enrichment, and caging), three 2-way interactions, and one 3-way interaction for each response variable. Interactions among factors were calculated based on an additive null model, because this approach is: (1) simple and straightforward (Didham et al. 2007, Brook et al. 2008), (2) generally used in factorial stressor experiments (Crain et al. 2008), and (3) used in multiple stressor applications (Halpern et al. 2008). We also quantified effects of algal biomass on *P. rus* survival with linear models. We conducted statistical analyses of stressor effects and interactions and algal effects using randomization tests based on 10,000 randomly drawn permutations, in which errors were stratified by block, using the lmPerm package (Wheeler 2010) in the program R (Team 2013). This statistical approach is robust across response variables with differing distributions and for which assumptions about parent distributions used in standard parametric tests cannot be meet (e.g., percent live tissue cover of coral fragments).

**Results**

**Settlement to Barren Substrate**

Main effects of sedimentation and caging as well as all interactions were significant for the biomass of newly settled filamentous turf algae, including a significant three-way interaction (Table B-2). This interaction arose because filamentous algae benefited from reduced grazing (due to caging) and further benefitted from increased nutrients when sedimentation was relatively low (Figure 3-3A). Relative to filamentous turf algae, the dry mass of macroalgae was generally lower and exhibited a significant positive effect of caging (*p* < 0.05) and a significant sediment by caging interaction (*p* <
0.05), in which sedimentation had a negative effect in caged units but a positive effect in uncaged units (Figure 3-3B, Table B-2). In contrast to algae, we observed very few coral recruits at the end of our 6-month experiment (23 total recruits, on 20 of 72 settlement tiles), for which we were unable to detect significant treatment effects.

**Coral Fragment Survival and Growth**

We observed responses in survival and growth of coral fragments that differed across treatments and between coral species. First, *A. pulchra* was very sensitive to consumers, suffering complete mortality via consumption (i.e., colonies were completely bitten off down to the base) in all uncaged units in the first week of the study, while all caged colonies achieved 100% survival (i.e., complete live coral tissue cover on each fragment). Conversely, many *P. rus* fragments suffered at least partial mortality of coral tissue. For *P. rus* live tissue cover per colony, we observed a significant interaction between sedimentation and caging (*p < 0.05*), due to negative effects of high sedimentation on uncaged colonies only (Figure 3-4, Table B-2). Our data further revealed a significant negative effect of macroalgal biomass (*p < 0.05*) on live tissue cover of uncaged *P. rus* colonies, while algal effects on caged *P. rus* survival were insignificant (Table B-2). To standardize our coral growth comparisons and to ensure that coral growth was being measured alone (e.g., without either added mass of organisms fouling dead coral skeleton or lost mass due to excavating corallivores), we included only coral fragments that achieved 100% colony survival, which limited our sample size for both coral species (replication was reduced to zero for uncaged *A. pulchra*, while replication was partially, and in one case fully, reduced for *P. rus*). For coral growth, the only significant effect we observed was a positive effect of nutrient
enrichment on the growth of *A. pulchra* (p = 0.022; Figure 3-5A, Table B-2). We observed no significant treatment effects on *P. rus* growth (Figure 3-5B, Table B-2).

**Discussion**

Here, we showed that multiple, pervasive anthropogenic stressors can affect the benthic community on simulated post-disturbance coral reef habitats. We demonstrated that high sedimentation, nutrient enrichment, and low fish abundance (that can result from overfishing) had interactive effects on corals and benthic algae, and certain combinations of these stressors may facilitate increased abundance of algae and decreased cover of coral on coral reefs at early stages of recovery following disturbance. Particularly, filamentous turf algae were stimulated by nutrients in the absence of both large consumers (> 4 cm width or height) and high sedimentation (Figure 3-3A). These results echo previous findings that nutrient enrichment and overfishing can synergistically enhance algal abundance (Burkepile and Hay 2006, Ban et al. 2014) but further indicate that this effect depends on sedimentation load.

Algal functional groups responded differently to multiple stressors. The range of turf algal biomass greatly exceeded that of macroalgae, and while turf algae were quite responsive to different treatment combinations (including a significant 3-way interaction; Figure 3-3A), slower-growing macroalgae were less so, exhibiting only a significant positive response to caging and a caging by sedimentation interaction (Figure 3-3B). This interaction was driven by sedimentation having a negative effect in the absence of large consumers (caged units) but a positive effect in uncaged units. This positive effect could be the result of sedimentation deterring herbivory, by making sediment-fouled algae less attractive (Bellwood and Fulton 2008). Though filamentous turf algae generally predominated over macroalgae in our 6-month experiment, studies suggest
that this pattern will hold for the long term when both herbivore abundance and the level
of sedimentation are low, but that macroalgae will eventually dominate if nutrient
enrichment is also present (Littler et al. 2006).

While we observed minimal coral settlement across treatments, our study may
not have captured commonly episodic coral settlement events, because our timing was
late with respect to coral spawning dates (Adjeroud et al. 2007, Penin et al. 2010).
Nonetheless, algae are known to inhibit coral settlement (Birrell et al. 2005, Kuffner et
al. 2006, Birrell et al. 2008) and our data indicate that barren areas on coral reefs (as
simulated by our study tiles) can become dominated by algae, depending on levels of
sedimentation, nutrient enrichment and fishing. In addition, algal growth was generally
limited by high-sedimentation (Figure 3-3), which can also greatly limit coral recruitment
(Birrell et al. 2005, Jokiel et al. 2014), suggesting that barren areas of reef resulting from
natural disturbances may remain largely unsettled if subjected to high sedimentation
rates (e.g., on the order of 212 mg cm\(^{-2}\) d\(^{-1}\)).

The survival of coral fragments exhibited species-specific responses. First, the
complete and rapid consumption within the first week of all \(A.\) pulchra colonies, by
bioeroding corallivores like triggerfish or puffers (Lenihan et al. 2011), in uncaged
conditions (simulating natural consumer pressure or the absence of overfishing)
suggests that overfishing can, in some cases, alleviate corallivory (Figure 3-5A).
However, it is important to note that our study system is not situated inside the marine
protected areas of Mo'orea and is thus subjected to consistent fishing pressures that
target large piscivores, e.g., grouper, snapper (Leenhardt et al. 2012), potentially
allowing for predator release of many corallivorous fishes (Dulvy et al. 2004, Mumby et
al. 2012, Pinca et al. 2012). Thus, our observed effects might change quantitatively or qualitatively under different ambient fishing scenarios (e.g., species-specific restrictions, a no-take reserve). Conversely, caging and sedimentation interacted for *P. rus* (Figure 3-4), suggesting that negative effects of high sedimentation on the survival of coral fragments may be: (1) enhanced by or, at the levels tested, even contingent upon the presence of consumers (e.g., corallivores), (2) driven by indirect negative effects via sedimentation enhancing the growth of algae in the presence of consumers (see preceding paragraph), and/or (3) driven by indirect positive effects via sedimentation inhibiting the settlement and growth of algae in the absence of consumers (e.g., herbivores; Figure 3-1). Regarding hypothesis (1), sedimentation and corallivory could synergistically reduce coral survival, if corallivore-induced coral tissue damage is less repairable when physically covered by high sedimentation, a mechanism that we are unable to evaluate with our data. On the other hand, our data support hypothesis (2) as a likely contributor to the pattern in *P. rus* survival, which, in uncaged units only, showed a significant negative response to the biomass of macroalgae growing on adjacent settlement tiles. Finally, hypothesis (3) could occur if the direct (and putatively negative) effect of sedimentation is weaker than the indirect positive effect of sedimentation as an inhibitor of algae in the absence of consumers (Figure 3-1), though the relationship between algal biomass on tiles and *P. rus* survival in caged units was insignificant.

In addition to differences in survival, our two species of coral fragments differed in their growth response to treatments. The faster-growing, thin-branching *A. pulchra* showed a significant positive growth response to nutrient enrichment (Figure 3-5A), which had a positive albeit insignificant effect on the growth of *P. rus* (Figure 3-5B).
Nutrient enrichment has been shown to have unimodal effects on coral growth (Gil 2013), with initial positive effects attributed to heightened sugar provisions to corals from the stimulation of their nutrient-limited endosymbiotic algae, zooxanthellae (Hoegh-Guldberg and Smith 1989, Muller-Parker et al. 1994, Dunn et al. 2012). However, nutrient-enhanced coral growth can also result in a reduction in coral skeletal density and thus an increase in susceptibility to breakage (Koop et al. 2001). Sedimentation had insignificant effects on the growth of both coral species, a result supported by recent coral growth assays across a gradient in sedimentation (Jokiel et al. 2014). However, sedimentation in combination with high consumer pressure (i.e., uncaged units) did affect the survival of *P. rus*, for which the coral growth sample size was greatly limited as a consequence (Figure 3-5B). In contrast, the relative resilience of *A. pulchra* fragments to sedimentation was likely driven by their thin, cylindrical morphology, which likely retains less sediment on coral tissue surfaces than the more complex morphology of *P. rus* (see Figure 3-2).

Our findings suggest that at early stages in recovery from disturbances, which can be system-wide if disturbance is severe enough, the emerging coral reef community depends on the combination of sediment, nutrient and fishing pressures on the system. Our work complements recent findings, indicating that under ideal ecological conditions (i.e., near-complete coral cover; no recent disturbance) sedimentation, nutrient enrichment, and reductions in consumer density interactively affect both corals and algae (Muthukrishnan and Fong 2014). Furthermore, our results revealed that effects of multiple, pervasive stressors on the recovery of coral reefs were taxon-specific for both
corals and algae, suggesting that human influences on recovery can lead to shifts in species composition in addition to degradation.

Though the scale of our field experiment was limited by logistical and ethical constraints, our study was indeed nested within and reflective of a system recovering from large-scale natural disturbances (Kayal et al. 2012). Furthermore, other large-scale surveys coincide with our findings that anthropogenic stressors affect the recovery of ecosystems from disturbance. Recently, researchers showed that recovery from a mass, climate-induced coral bleaching event was compromised in coral reefs low in fish density and high in nutrient load, leading to system-wide regime shifts to algal dominance (Graham et al. 2015). Similarly, the failure of seagrass meadows in the Dutch Wadden Sea to recover from disturbance has been attributed to multiple anthropogenic stressors (Short and Wyllie-Echeverria 1996). Fortunately, effects of massive disturbances on ecosystems can be reversed, even rapidly so, as long as systems are given the chance to repair themselves (Jones and Schmitz 2009, Beldade et al. 2015). For example, recent surveys showed a nearly 5-fold increase in coral recruitment 12 years following a mass climactic disturbance event at a highly isolated reef free of most anthropogenic influences (Gilmour et al. 2013). Similarly, a Hawaiian reef destroyed by a hurricane exhibited substantial recovery, following implementation of an offshore sewage disposal system (Grigg 1995).

Our findings, reinforced by long-term monitoring studies, have broad implications for integrated, ecosystem-based management efforts in coastal ecosystems that are globally threatened by diverse anthropogenic stressors. First, our results point to the need for coastal ecosystem managers to consider stakeholder activities (whether sea-
or land-based) that affect levels of sedimentation, nutrient enrichment (e.g., coastal development), or consumer densities (e.g., fishing, habitat loss or fragmentation) when trying to control the abundance of benthic algae. Benthic algae can harm foundation species, including corals, seagrasses, and kelp, and thus remediation of benthic algal blooms is a leading conservation priority for coastal systems worldwide (McCook et al. 2001, McGlathery 2001, Smith et al. 2006, Connell et al. 2008, Rasher and Hay 2010). Furthermore, our findings emphasize the importance of monitoring and remediating sedimentation loads, a potent, highly interactive stressor that has received far less attention than nutrient enrichment or overfishing in coastal studies Figure 3-3 & 3-4 (Orth et al. 2006, Ban et al. 2014). More generally, our study reinforces conclusions from recent meta-analyses: ecosystem managers must recognize the potential for co-occurring stressors to yield effects that are difficult to predict without experimentation, due to stressor interactions, indirect effects, and species-specific responses Figure 3-1 (Crain et al. 2008, Darling and Côté 2008). However, our work extends this recommendation to include the temporal context of stressors, with respect to natural disturbances: ecosystem managers must also consider that interactive effects of stressors can begin molding benthic communities at early, potentially vulnerable, stages following natural disturbances, the timing, frequency and severity of which should be considered in management plans to mitigate anthropogenic stressors and foster resilience. As climate change increases the rate and magnitude of natural disasters (Dilley et al. 2005), and as human population growth increases the magnitude and diversity of anthropogenic stressors (Crain et al. 2008, Darling and Côté 2008), it is increasingly important that we understand and implement management options that
best facilitate ecosystem recovery and thus the maintenance of valuable ecosystem services (Worm et al. 2006, Barbier et al. 2011).

Figures

Figure 3-1. Conceptual diagram, illustrating the nature of direct and indirect effects of stressors on coral. Here we show the nature (black = positive, red or grey = negative) of direct effects, represented by solid arrows with putative mechanism(s) noted, and indirect effects, represented by dotted arrows that manifest through benthic algae (middle left), of sedimentation, nutrient enrichment (e.g., from a sewage outfall) and consumers, which are removed by overfishing (represented by both the herbivorous fish at the top left and the corallivorous fish at the top right), on the settlement, growth and survival of coral.
Figure 3-2. Experimental unit in the field. This includes: A) top-view of a complete unit during the first week of the experiment, and side-views of B) *Acropora pulchra* and C) *Porites rus* fragments 2 months after the start of the experiment.
Figure 3-3. Dry biomass (g) of A) filamentous turf algae, and B) macroalgae, across all treatment combinations (n=9; mean ± SE). Except for the effect of nutrients, all main effects and interactions were significant for the biomass of filamentous turf algae (A), including a significant three-way interaction (results summarized in Table B-2). The biomass of macroalgae (B) was generally lower than that of filamentous turf algae and treatment effects were less explicit. Nonetheless, caging had a significant positive effect on macroalgal biomass (p = 0.021), while there was a significant negative interaction between caging and sedimentation (p = 0.034; results summarized in Table B-2).
Figure 3-4. *Porites rus* survival (% live colony cover) across all treatment combinations (n=9; mean ± SE). There was a significant sediment by caging interaction (p = 0.038), in which sediment had a negative effect in uncaged units but a positive effect in caged units.
Figure 3-5. Coral skeletal growth. Here growth is measured by the change in buoyant mass (g) of A) *Acropora pulchra* in caged treatments and B) *Porites rus* across all treatment combinations (mean ± SE). Coral fragments included in this analysis achieved 100% survival and comprised only a subset of the original 72 units. *A. pulchra* (A) suffered complete mortality due to consumption in all uncaged units, thus growth was measured for caged colonies only (which achieved 100% survival; n=9). For *P. rus* (B), multiple colonies suffered partial or full mortality, and growth was measured for the remaining replicates only; sample sizes for treatments from left to right were: 3, 0, 2, 1, 4, 5, 2, and 4.
CHAPTER 4
SCALE DEPENDENCE IN HERBIVORE CONTROL OF PRIMARY PRODUCERS
FOLLOWING ENRICHMENT†

Summary

Anthropogenic nutrient enrichment stimulates primary production and threatens natural communities worldwide. Herbivores may counteract deleterious effects of enrichment by increasing consumption of primary producers. However, field tests of herbivore control are often done by adding nutrients at small (e.g., sub-meter) scales, while enrichment in real systems often occurs at much larger scales (e.g., kilometers). Therefore, experimental results may be driven by mechanisms that are not relevant at larger scales. Using a mathematical model, we show that herbivores can control primary producer biomass in experiments by concentrating their foraging in small enriched plots; however, at larger, realistic scales, the same mechanism cannot lead to herbivore control of primary producers. Instead, other demographic mechanisms are required, but these are not examined in most field studies (and may not operate in many systems). This mismatch between experiments and natural processes suggests that many ecosystems are less resilient to degradation than previously believed.

Background

Ecologists have long sought to understand how communities are structured and how (or if) consumers (“top-down” effects; Hairston et al. 1960, Oksanen et al. 1981, Sih

†With co-authors Jing Jiao and Craig Osenberg
et al. 1985) and resources ("bottom-up" effects; Ehrlich and Birch 1967, Osenberg and Mittelbach 1996) control this process. This academic debate has pressing, real-world implications, because land and fertilizer use by humans increasingly alter the dynamics of nutrients that limit primary production in both terrestrial and aquatic systems (Vitousek et al. 1997, Elser et al. 2007, Nixon 2009). In aquatic systems, nutrient-stimulated primary production can lead to toxic algal blooms, hypoxia and fish kills (Breitburg et al. 2009). In marine systems, added nutrients can stimulate the growth of algae (Lapointe et al. 1992, Lapointe 1997, Lapointe et al. 2004), which can elicit a suite of negative ecological effects, including declines of corals (McCook et al. 2001, Smith et al. 2006, Rasher and Hay 2010), seagrasses (Burkholder et al. 2007), and kelp (Connell et al. 2008). Indeed, effects of algae on marine systems and associated losses in biodiversity and ecosystem services (e.g., fisheries, storm surge protection) is a critical conservation concern (Vitousek et al. 1997, Bellwood et al. 2004, Fabricius 2005, Hughes et al. 2010).

Field experiments that simultaneously manipulate consumer density (via exclusion designs) and nutrient availability have been used to evaluate the role of consumers in controlling primary producers in the face of eutrophication (Burkepile and Hay 2006, Gruner et al. 2008). Results from these studies suggest that herbivores partially or fully compensate for the deleterious effects of enrichment on algal biomass and thus may facilitate the persistence or recovery of valuable marine ecosystems (Burkepile and Hay 2006). However, in nature, enrichment often occurs at spatial scales that are many orders of magnitude larger than the scale at which field manipulations are conducted. For example, coastal eutrophication due to nutrient...
enrichment has been documented across ~30 km$^2$ off the northeast coast of Italy
(Penna et al. 2004), ~31 km$^2$ of inner Kaneohe Bay, Hawai‘i, USA (Smith et al. 1981),
>100 km$^2$ of both the Chesapeake Bay and Pamlico Sound, USA (Paerl et al. 2006),
and >>100 km$^2$ in the Great Barrier Reef, Australia (Bell et al. 2014). Yet, experiments
are most often conducted at scales smaller than 1 m$^2$ (Burkepile and Hay 2006, Gruner
et al. 2008). This mismatch in scale is well known (Burkepile and Hay 2006), although
the effect of this possible bias has not been explicitly addressed. Thus, we are left
uncertain how the results of small-scale field experiments might inform management of
real ecosystems. Large-scale field manipulations would help, but they are rare and
often unfeasible for both ethical and logistical reasons. Fortunately, consumer-resource
theory frees us from these constraints and allows us to explore how well consumers can
reduce effects of enrichment on primary producers and how these effects depend on
spatial scale.

Traditional models of closed plant-herbivore systems posit that enrichment
increases herbivore population growth, and, consequently, herbivore density. Increased
density of herbivores then drives the abundance of primary producers back to the pre-
for this mechanism has been provided by field experiments in closed systems with rapid
consumer turnover (e.g., zooplankton in lakes: Carpenter and Kitchell 1988, Leibold
1989). However, in many other cases, experiments are conducted in open systems,
with small plots accessible to herbivores that move over much larger spatial scales
(Figure 4-1). In these cases, herbivores can migrate in from surrounding areas,
decoupling local resource dynamics from herbivore dynamics that operate at the
regional scale. Furthermore, a true numerical demographic response by herbivores to enrichment would be unlikely or unimportant in many experiments, because 1) the generation time of the focal herbivore often exceeds the duration of the experiment (Figure C-1), or 2) the offspring produced by local herbivores are dispersed over very large scales, as in many coastal marine systems (Hixon et al. 2002). Thus, the conditions of many field experiments preclude the application of consumer-resource theory developed for closed systems. In contrast, patch or habitat selection models may be more appropriate in these contexts.

Herbivores that are free to move between enriched and unenriched habitats may exhibit an ‘ideal free distribution’ (Fretwell and Lucas 1970), in which herbivores have equal fitnesses in different habitats but their densities across the landscape are heterogeneous, reflecting underlying variation in resource production (Nicotri 1980, Sutherland 1983, Power 1984, Oksanen et al. 1995). In such scenarios, patch-selection by herbivores (i.e., between enriched and unenriched patches) could drive responses of primary producers in top-down vs. bottom-up field experiments, and the magnitude of these responses could depend on the spatial scale of the studies.

We used a mathematical model to evaluate whether the spatial scale of nutrient addition (from small experimental scales to larger, more natural scales) affects the ability of herbivores to control primary producers and thus prevent the deleterious effects of enrichment.

**Model Formulation and Analysis**

We used a mathematical model that simulates typical top-down versus bottom-up field experiments that consist of four treatments: caged plots that exclude herbivores vs. open plots that permit herbivore access crossed with ambient vs. elevated nutrients.
We designated $P_{i,j}$ as the density of the primary producer in the $i^{th}$ nutrient treatment (unenriched = $U$ or enriched = $E$) and the $j^{th}$ herbivore treatment (indicating the presence (+), or absence (−) of herbivores). To examine how increasing the size of experimental plots influences enrichment effects, we made the following assumptions:

The sessile primary producer grew logistically, with its intrinsic growth rate ($r$) and carrying capacity ($K$) greater in enriched vs. unenriched habitat (i.e., $r_E > r_U$ and $K_E > K_U$).

Experimental plots were independent with respect to herbivore or nutrient treatments, i.e., plots were sufficiently separated to prevent the sharing of individual herbivores or nutrients.

Herbivores exhibited an ideal free distribution (Fretwell and Lucas 1970) over uncaged habitat within an area $S_T$, within which a single experimental plot was located. In effect, $S_T$ represents the movement range of the herbivore. Thus, when a plot was uncaged and enriched, herbivore densities could differ between the enriched plot area, $S_E$, and the area of the surrounding, unenriched habitat, $S_{E,\text{out}}$ (Nicotri 1980, Sutherland 1983, Power 1984, Oksanen et al. 1995).

Herbivore density is sufficiently high that when herbivores redistribute themselves following enrichment, some herbivores remain in the unenriched areas surrounding the enrichment plot. As a result, and given Assumptions 2 & 3, the equilibrium densities of primary producers in an enriched plot and the unenriched surrounding habitat within an area $S_T$ will be equivalent in the presence of herbivores: i.e., $P_{E,+}^* = P_{E,+,\text{out}}^*$, where ‘out’ denotes unenriched habitat outside the enriched plot. We later relax this assumption.
Total herbivore abundance ($N_T$) was fixed within an area $S_T$ (i.e., there was no reproduction, mortality, immigration or emigration). In other words, the time scale of the model relative to herbivore generation time matched the short experimental duration that is characteristic of past studies (Figure C-1). Thus, for an unenriched open plot, herbivore density is $H_U = H_T = N_T / S_T$ (and homogeneous throughout $S_T$). In contrast, enriched, open plots create a locally heterogeneous landscape and thus the total herbivore abundance, $N_T$, must be partitioned between the enriched plot and the unenriched habitat that surrounds the plot: i.e., $N_T = S_E H_E + S_{E,\text{out}} H_{E,\text{out}} = S_E H_E + (S_T - S_E) H_{E,\text{out}}$, where $H_E$ and $H_{E,\text{out}}$ are the herbivore densities in the enriched plot and the surrounding unenriched habitat, respectively (and both are >0 due to Assumption 4).

Herbivores had a Type I functional response, i.e., feeding rate increased linearly with the density of food (Holling 1966). The per-capita consumption rate ($\alpha$) was equal for herbivores feeding in enriched and unenriched habitat. (In Appendix D, we show that a Type II functional response yields the same qualitative results, albeit more complex to solve.)

Given these assumptions, in the absence of herbivores (i.e., in caged plots), the equilibrium density of primary producers is set by their carrying capacity:

$$P_{U,\text{eq}} = K_U, \quad \text{and} \quad P_{E,\text{eq}} = K_E. \quad (4-1)$$

In the presence of herbivores, the dynamics of primary producers is set by the balance between logistic growth and herbivore consumption. For unenriched plots accessible to herbivores,

$$\frac{dP_{U,+}}{dt} = r_U P_{U,+} \left(1 - \frac{P_{U,+}}{K_U}\right) - \alpha H_U P_{U,+} , \quad (4-3)$$
and at equilibrium,

\[ P_{U,+}^* = K_U \left( 1 - \frac{\alpha H_U}{r_U} \right). \tag{4-4} \]

For enriched plots accessible to herbivores, we have to consider the dynamics of the enriched plot, as well as the adjacent unenriched habitat, because herbivores can distribute themselves between the two habitats. Thus, we have:

\[ \frac{dP_{E,+}}{dt} = r_E P_{E,+} \left( 1 - \frac{P_{E,+}}{K_E} \right) - \alpha H_E P_{E,+} \quad \text{and} \tag{4-5} \]

\[ \frac{dP_{E,+,\text{out}}}{dt} = r_U P_{E,+,\text{out}} \left( 1 - \frac{P_{E,+,\text{out}}}{K_E} \right) - \alpha H_{E,\text{out}} P_{E,+,\text{out}}. \tag{4-6} \]

Next, we set 4-5 & 4-6 equal to 0 and solve for \( P_{E,+}^* \) and \( P_{E,+,\text{out}}^* \), but based on assumptions of ideal free distribution (i.e., Assumption 4: \( P_{E,+}^* = P_{E,+,\text{out}}^* \)), we can set these solutions equal to one another, and after a few more steps (involving substitutions for \( H_{E,\text{out}} \) and \( H_E \)), we get the final solution:

\[ P_{E,+}^* = \frac{K_E K_U \left( S_T + (S_T - S_E) r_U - \alpha N_T \right)}{S_T K_E r_K U + (S_T - S_E) r_U K_E}. \tag{4-7} \]

From this analytical solution, we see that the equilibrium density of primary producers (\( P_{E,+}^* \)) in uncaged, enriched plots always increases with the spatial scale of enrichment (\( S_E \)):

\[ \frac{\partial P_{E,+}^*}{\partial S_E} = \frac{S_T K_E K_U (K_E - K_U)}{(S_T K_E r_K U + (S_T - S_E) r_U K_E)^2} > 0. \tag{4-8} \]

This result (4-8) was obtained assuming plots were independent (i.e., herbivores could not travel between plots: see Assumption 2 above). If we relax this assumption (e.g., assume that all plots occur within the herbivore’s foraging range), the qualitative result still holds (i.e., \( \frac{\partial P_{E,+}^*}{\partial S_E} > 0 \)).
To quantify the scale dependence of the effect on primary producer biomass, we used results from our model (4-5 through 4-7), analyzed over a range of spatial scales and parameter values, to calculate the effectiveness of herbivores in controlling the enrichment effect on primary producers:

Relative effectiveness of herbivores = \[ 1 - \frac{(P_{E,+} - P_{U,+})}{(P_{E,-} - P_{U,-})}. \]  

(4-9)

This metric describes how well herbivores control the response of primary producers to added nutrients (numerator in second term) relative to the response of primary producers to nutrients in the absence of herbivores (denominator in second term). We then varied experimental plot size (\(S_E\)) to determine its effect on the equilibrium density of primary producers (4-1, 4-2, 4-4, 4-7) and the relative effectiveness of herbivores (4-9).

When the scale of nutrient addition is small relative to the movement range of the herbivore (a ubiquitous characteristic of field experiments: Figure 4-1), the density of primary producers in the enriched plots is low (Figure 4-2a,b), and herbivore control of primary producers (4-9) is very high (Figure 4-2d,e). This is because herbivores move into the enriched plots from surrounding areas in response to localized increases in primary production. Thus, although production increases in the enriched plots, the increased density of the herbivores (via immigration) completely prevents an increase in the density of primary producers (when plots are very small). In contrast, primary producers increase in density (or biomass) in response to enrichment in the absence of herbivores.

However, as the scale of enrichment increases, herbivore density cannot respond to the same degree because of the limited foraging area over which migration...
occurs. As a result, the density of primary producers increases with experimental scale (Figure 4-2a,b,c) and herbivore control decreases (Figure 4-2d,e,f). At very large scales (i.e., as the scale of the experiment approaches the scale of the herbivore's foraging range), the density of primary producers increases to its maximum (Figure 4-2, a-c), and herbivore control is reduced to its minimum (Figure 4-2, d-f). This large scale better matches real-world enrichment scenarios: Figure 4-1 (Smith et al. 1981, Penna et al. 2004, Paerl et al. 2006, Bell et al. 2014).

Although herbivore control of primary producers (4-8) is qualitatively consistent across parameter space, the strength of that control depends upon parameters that govern the dynamics of the system (Figure 4-2). In particular, herbivore control of primary producers is greater when enrichment causes a smaller increase in the intrinsic growth rate ($r$) or a greater increase in the carrying capacity ($K$) of the primary producer, or there is a greater density ($H_f$) or individual feeding rate ($\alpha$) of the herbivore. The effect of increasing $K_E$ is perhaps counterintuitive, but it arises because increased $K_E$ causes the numerator in 4-5 to increase less rapidly than the denominator; i.e., enrichment increases primary producer density more in the absence than in the presence of herbivores.

We derived the above results based on Assumption 4. However, when herbivory is very weak relative to the effect of enrichment on primary producers, the immigration response of herbivores may be insufficient to keep the density of primary producers equal inside and outside of the enriched plot. This happens when all of the herbivores aggregate inside the enriched plot and none remain in the surrounding habitat. Thus, we can substitute $H_E = \frac{N_T}{S_E}$ into 4-5, resolve for the equilibrium and obtain:
\[ P_{E,+}^* = K_E (1 - \frac{\alpha N_T}{r_E S_E}). \] (4-10)

Under this condition, \( \frac{\partial P_{E,+}^*}{\partial S_E} > 0 \): i.e., the previous qualitative result (4-8) still holds.

Indeed, this relaxation of Assumption 4 only reinforces our main finding: enrichment effects increase (and herbivore effects decline) with increasing plot size.

**Discussion**

Here, we provide the first explicit demonstration that the mismatch between the scales of experimental enrichment studies and the scale of herbivore movement (Figure 4-1) can create the (potentially false) perception that herbivores can prevent increased biomass of primary producers: i.e., given the small size of experimental plots, herbivores can aggregate in response to increased food production. However, at larger enrichment scales, which are more indicative of real-world enrichment scenarios (but not field experiments: Figure 4-1), herbivores are less able to control primary producers because the potential immigration response is reduced. This mechanism is similar to that proposed by Englund (1997), in which prey migration into/out of cages could mask effects of predators when experiments were conducted in small plots. As cage size increased, the importance of movement decreased, and the within-plot manipulation (predator presence/absence) became relatively more important in driving observed effects. Our system differed somewhat from Englund’s, however, because the consumer (herbivore) was mobile, but the resource (prey) was sessile. Our quantitative results also echo the conceptual arguments of Van de Koppel et al. (2005) in their general discussion of scale mismatch in consumer-resource interactions. Collectively, these studies indicate that when key players or processes operate at scales that exceed the grain of observation (e.g., plot size; Figure 4-1), results can change significantly (Figure
4-2), simply because observational scales fail to match the natural contexts that they are meant to represent (see Levin 1992).

This mismatch may have important practical implications. For example, top-down vs. bottom-up field experiments in marine systems suggest that mobile herbivores can mitigate, or even prevent, increases in algal biomass following enrichment (Burkepile and Hay 2006). As a result, coral reef managers may conclude that herbivores alone (if they are not over-exploited) can protect marine systems and their associated services from harmful effects of nutrient enrichment (Bellwood et al. 2004, Burkholder et al. 2007, Hughes et al. 2010). However, our results indicate that observed herbivore control of algal biomass in marine systems could be an artifact of the small scale spatial of field experiments relative to the large movement range of dominant herbivores (Figure 4-1 & 4-2).

These experimental biases can be reduced by improving the match between the experimental enrichment and movement patterns of herbivores. For example, systems in which herbivores move over smaller scales (e.g., small-bodied invertebrates) could be studied with less bias. Similarly, increasing the scale of experiments also could reduce the bias (e.g., as in whole lake or watershed experiments: Carpenter and Kitchell 1988, Schindler et al. 2008), but this remains impractical in many systems, or can be difficult or impossible to replicate. Furthermore, alternative experimental approaches also could reduce bias: e.g., inclusion (rather than exclusion) cages (e.g., Silliman and Bertness 2002, Ghedini et al. 2015) would eliminate the influx of consumers into enriched plots. This approach, however, remains impractical for many
systems (e.g., those with large-bodied herbivores) and other potential problems may arise by confining herbivores (e.g., Quinn and Keough 1993).

Spatial scale is just one dimension of the potential problem. Similar challenges, as we have articulated, also exist with respect to the time-scale of experiments, which often are much shorter than the time-scale of population dynamics (Figure C-1). This temporal mismatch probably acts in the opposite direction than the spatial scale mismatch. For example, we would expect herbivore control to increase as their demographic rates change and drive changes in density; i.e., short-term experiments (which preclude demographic responses) likely underestimate potential control of primary producers by herbivores. Thus, the short time-scale and small spatial-scale of experiments could compensate for one another. Because field exclusion studies typically do not allow for population dynamics (e.g., Figure C-1), we did not incorporate population responses into our model. The extent to which the inference provided by our short time-scale model will provide realistic insights about natural systems will depend on the potential for responses in the density of herbivores to enrichment. In natural systems, these considerations include:

- **Dispersal of herbivore offspring**: if offspring are dispersed widely (as they are in many marine systems; Hixon et al. 2002) then the local benefits of enrichment will be less likely to translate into local increases in herbivore density.

- **Trophic complexity**: the numerical response of herbivores to increased primary production depends on the structure of the upper trophic levels: e.g., in a 3-level food chain, increased production results in no change in herbivore density, but instead, an increase in their predator (Oksanen et al. 1981).

- **Interference among herbivores**: higher herbivore interference (e.g., due to competition or territoriality) can cause herbivore populations to grow less at higher herbivore densities (Lamberti et al. 1987), restricting the numerical response to enrichment over timescales that extend well beyond herbivore generation times. However, interference may similarly limit the immigration and recruitment response to enriched patches over experimental time scales.
Feedbacks on consumer behavior and recruitment: herbivory can induce plant defenses (Agrawal 1998) and select for unpalatable or defended plant species (Augustine and McNaughton 1998). Shifts toward less edible plants will reduce herbivory rates as herbivore density increases, and thus limit further increases in herbivore density. Furthermore, nutrients may exacerbate these effects. For example, recent work in coral reefs show that primary producers (i.e., benthic algae) can reach a size at which they become unpalatable to most herbivores (Bellwood et al. 2012, Nyström et al. 2012) and can even reduce herbivore recruitment by producing negative settlement cues and degrading settlement habitat (Paddack et al. 2009, Dixson et al. 2014).

Our study highlights the need for future works to examine numerical responses, both via migration and via population dynamics, in a context that matches data to the scale of interest. Indeed, our results suggest that in many systems herbivores may be less capable of controlling primary producer biomass in natural settings than would be expected based upon small-scale experiments: i.e., when enrichment occurs on the scale of (i.e., on the order of km2; Smith et al. 1981, Penna et al. 2004, Paeerl et al. 2006, Bell et al. 2014) rather than (e.g., typically ≤ m2; Burkepile and Hay 2006, Gruner et al. 2008). Our model may further provide a mechanism to explain observed, long-term phase shifts from coral to algae in enriched coral reefs with intact herbivore communities (Walker and Ormond 1982, Hatcher and Larkum 1983, Ledlie et al. 2007), when such responses are not expected based upon experimental studies (e.g., Burkepile and Hay 2006). Consequently, anthropogenic nutrient enrichment, which continues to increase globally (Vitousek et al. 1997, Nixon 2009), could pose a greater threat to natural ecosystems, particularly coastal marine systems, than we previously believed.
Figure 4-1. Scale discrepancy in previous experiments. Here we compare herbivore movement range to experimental scale of enrichment in previous top-down versus bottom-up field experiments (nutrient addition fully crossed with herbivore exclusion) across systems and taxa (see Appendix C for literature survey methods). The line indicates the 1:1 relationship, and overlapping points were jittered to show all points. The observed ratio of experimental scale to herbivore movement range was miniscule, with a median of $5.2 \times 10^{-6}$. 

**Figure 4-1.** Scale discrepancy in previous experiments. Here we compare herbivore movement range to experimental scale of enrichment in previous top-down versus bottom-up field experiments (nutrient addition fully crossed with herbivore exclusion) across systems and taxa (see Appendix C for literature survey methods). The line indicates the 1:1 relationship, and overlapping points were jittered to show all points. The observed ratio of experimental scale to herbivore movement range was miniscule, with a median of $5.2 \times 10^{-6}$. 

**Ecosystem (taxon)**

- ▲ Coral reef (fish)
- □ Marine: rocky/soft bottom (fish or gastropods)
- □ Freshwater: stream (fish)
- ▲ Wetland (mammals or gastropods)
- ▲ Forest or field (mammals or gastropods)
- ▼ Tundra (mammals)
Figure 4-2. Responses of primary producers and herbivory to enrichment scale. Here, we show the equilibrium density of primary producers in enriched plots with herbivores ($P_{E,+}$ from 4-7; panels a-c) and the relative effectiveness of herbivores in preventing increased density of primary producers in response to enrichment (4-9; panels d-f), as a function of the scale of enrichment relative to the movement range of the herbivore. The y-intercepts of curves in panels a-c indicate the densities of primary producers in unenriched plots with herbivores ($P_{U,+}$ from 4-4). Curves were generated by changing the effect of enrichment on $K$ (a, d) or $r$ (b, e) or altering the herbivore population feeding rate (c, f). Otherwise, default parameter values were: $K_{U}=10$, $K_{E}=40$, $r_{U}=1$, $r_{E}=2$, $\alpha^*N_T=50$. Vertical lines indicate the median scale of enrichment (scaled to herbivores movement range) from field experiments (i.e., $5.2 \times 10^6$; Appendix C). For panels d-f, a response of 1 indicates that herbivores completely prevent an increase in primary producers following enrichment.
CHAPTER 5
RESOURCE DENSITY WEAKENS EFFECTS OF DISTANCE FROM REFUGE ON HERBIVORY IN A CORAL REEF†

Summary

Foraging theory posits that isolation from refuge habitat within a landscape increases perceived predation risk and changes the foraging behavior of prey species at the patch scale. However, effects of refuge isolation on prey foraging behavior may depend on resource-mediated processes like nutrient enrichment, which can increase the density of resources within a patch. We conducted a field survey and experiment in a tropical coral reef to test the effects of isolation from refuge habitat (i.e., reef structures) on herbivory and whether these effects depend on resource density. We found that a wide range of distances from refuge habitat reduced herbivory in attractive resource patches of benthic algae, but higher initial resource densities weakened this effect, causing consumers to accept greater risk to receive greater reward. Furthermore, we observed higher bite rates and larger body sizes of herbivores with greater distance from refuge habitat, responses consistent with higher predation risk. Our results suggest that while the loss and fragmentation of refuge habitat will reduce consumer control of resources, this effect will be less pronounced when patches have greater resource densities, such as patches enriched by nutrients. Our findings reinforce the predominant pattern of consumer control of enrichment effects on marine primary producers at experimental scales.

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Background

To maximize fitness, foragers must balance demands for food and safety from predators (Gilliam and Fraser 1987). Thus, the spatial configuration of structural habitat that provides shelter from predators can affect prey foraging behavior. For example, foraging theory predicts that prey should harvest fewer resources in habitat patches characterized by higher risk of predation (see review by Brown and Kotler 2004). This expectation has been supported empirically in a variety of systems (Brown and Kotler 2004) and suggests that consumer control of resources in a given patch depends on the spatial configuration of the surrounding landscape and weakens with further isolation from structural refuge habitat. However, processes that increase the amount of food available to foragers could cause foragers to accept greater risk of predation when selecting a foraging location.

Nutrient enrichment, driven by terrestrial runoff and exacerbated by coastal urbanization and fertilizer use (Vitousek et al. 1997, Fabricius 2005, Orth et al. 2006), increasingly affects coastal marine systems around the world by stimulating the growth of weedy species of algae (Lapointe et al. 1992, Lapointe 1997, Lapointe 2004). These algae can drive declines of corals (McCook et al. 2001, Smith et al. 2006, Rasher and Hay 2010), seagrasses (Burkholder et al. 2007), and kelp (Connell et al. 2008), and thus algal domination of coastal marine systems is a critical conservation concern (Vitousek et al. 1997, Bellwood et al. 2004, Fabricius 2005, Hughes et al. 2010). Herbivores may counteract enrichment effects on algae, as shown by a meta analysis of field experiments that simultaneously manipulated nutrient availability and herbivore density (via exclusion designs; Burkepile and Hay 2006). However, the spatial extent of enrichment manipulations in these studies (mean ± SE: 0.2 ± 0.03 m²) were many
orders of magnitude smaller than the potential movement ranges of the focal herbivores. For example, among the 15 coral reef studies analyzed by Burkepile and Hay (2006), nutrient manipulations were limited to study plots averaging $0.08 \pm 0.02 \text{ m}^2$, while the potential movement ranges of dominant herbivorous reef fishes have been measured at $7,650 \text{ m}^2$ for Acanthuridae (surgeonfishes, tangs, and unicornfish; Meyer and Holland 2005) and $24,440 \text{ m}^2$ for Scaridae (parrotfish; Welsh and Bellwood 2012). Thus, higher densities of primary producers in small enriched plots likely attracted herbivores from the surrounding landscape. However, this effect could change if enriched plots were located in riskier habitat patches, e.g., those more isolated from structural habitat that provides herbivores with refuge from predators. Consequently, it remains unknown whether mobile herbivores can compensate for enrichment effects on primary producer densities across the spatially heterogeneous landscapes that characterize many coastal marine systems.

In tropical coral reefs, the composition and configuration of habitat can vary tremendously across a landscape (Madin et al. 2011). Reef habitat, built by corals, offers shelter to a multitude of vertebrate and invertebrate taxa, including reef fishes that are dominant herbivores in most healthy reef systems (Bellwood et al. 2004). However, sand flat habitat that comprises the majority of matrix habitat among reef patches in most coral reefs is relatively structure free, providing relatively little refuge for reef organisms. Recent studies suggest that many reef fishes avoid movement into or within open sand flat habitats because of a higher risk of predation (Chapman and Kramer 2000, Meyer et al. 2010, Turgeon et al. 2010). Furthermore, small-scale surveys have verified that patches further away from reef habitat incur lower rates of herbivory by reef
fishes (e.g., Madin et al. 2011). However, effects of nutrient enrichment, which can stimulate attractive resource patches of algae, can provide herbivores with a greater incentive to forage within risky habitat patches (Brown and Kotler 2004). Thus, enrichment effects on algae may counteract the negative effect of isolation from refuge habitat on herbivory. However, the extent to which effects of enrichment moderate the effect of isolation from refuge habitat on herbivore control of algae remains untested (Fabricius 2005, Orth et al. 2006, Connell et al. 2008).

In the following field study, we quantified the relationship between herbivory and isolation from refuge (coral reef habitat) under scenarios that mimic effects of nutrient enrichment. First, we conducted a landscape-scale survey of herbivory, using dense outplanted patches of palatable macroalgae. Second, we conducted a field experiment, testing the effects of five levels of isolation from refuge habitat crossed with two initial densities of algae on loss rates of multiple algal taxa and on traits of foraging herbivores.

**Materials and Methods**

**Study Location**

This study took place in the back reef off of the north shore of the island of Mo'orea, French Polynesia (17°28'59" S, 149°50’2” W). We conducted a survey of herbivory at the landscape scale in the Austral winter of 2011, followed by a field experiment in the Austral winter of 2012.

**Landscape-Scale Herbivory Survey**

We compared herbivory rates across a spatially heterogeneous back reef location, covering an area of ~2,100 m². We used Google Earth imagery and field surveys to select 30 sites that were consistent at the within-patch scale but varied at the
landscape scale (i.e., sites differed in their level of isolation from reef structural habitat). Each site consisted of a mostly-dead *Porites* spp. coral colony, similar in size, benthic composition and depth across sites. We marked each site with a handheld GPS device, which we also used to ground truth our study map. Using Google Earth and ArcGIS software, we quantified isolation at each site by measuring: 1) the distance from each site to the contiguous reef tract to the north (Figure 5-1), and 2) the proportion of the total surface area within either a circular buffer (10, 25, 35, or 50 m radius from the site) or a ring (10-15, 15-25, 25-35, or 35-50 m from the site) centered at each site that was covered by reef structural habitat. We ground-truthed this technique and confirmed its accuracy (Appendix E).

We assessed herbivory rates across study sites by measuring consumption of a standardized amount of outplanted macroalgae of the palatable species *Acanthophora spicifera*, collected from nearby inshore reef locations. We chose this species because it is attractive to a wide range of herbivorous fishes and thus its consumption provides a measure of the relative potential for herbivores to control algae (Littler and Littler 2007). We cut these algae into strands of similar color, thickness, and morphology. We secured the strands upright and held in place at the base by clothespins. 5 cm of each algal thallus protruded from the clothespin. We tied six of these clothespins to each of three nylon strings that we deployed atop each site (18 algal strands per site), anchored on either end using nails buried under coral rubble. At each site, we conducted a single herbivory assay, and we initiated these assays at three sites per day over days of similar weather conditions, taking care to select sites over a range of habitat isolation.
levels for a given day. After 6, 24, 30, and 48 hours, we re-measured each algal strand to the nearest mm to quantify losses in algae due to herbivory.

**Field Experiment**

We used Google Earth imagery and field surveys to select three study locations, each characterized by a distinct interface between habitat dominated by dense, contiguous coral reef structures and relatively structure-free sand flat habitat. At each location, we created two linear arrays, separated by at least 30 m, and each running perpendicular to the reef-sand boundary. Each array consisted of 5 sites, each at a different distance from structural refuge habitat: inside the reef habitat (2 m in from the reef-sand barrier), and 5, 10, 20, and 30 m away from the reef habitat (i.e., in the sand flat habitat). Two weeks prior to our study, we placed a small cinderblock (l × w × h = 25 x 20 x 11 cm; later used for herbivory trials) at each site, to allow fishes to acclimate to the new object.

For our herbivory trials, we used five varieties of benthic algae from two algal functional groups: frondose macroalgae and filamentous algal turf. For macroalgae, we used 4 different species, all native to Mo'orea and easily harvested locally (from nearby backreef locations): *Acanthophora spicifera*, *Amansia rhodanta*, *Asparagopsis taxiformis*, and *Sargassum pacificum*. From our samples, we cut individual algal strands of uniform length and similar characteristics (e.g., color, thickness, straightness, branch density [for *S. pacificum*]). In addition to macroalgae, we used a pneumatic drill to collect circular cores (4-cm diameter) of coral skeleton completely covered in algal turf. To keep samples consistent, we collected these cores from within territories guarded by the farmer fish, *Stegastes nigricans*, which actively maintains dense, homogeneous stands of algal turf (Hata et al. 2002).
For each herbivory trial, we used cable ties and clothespins to attach algae to the cinderblock at each site (see Figure E-2). We secured the base of each strand of macroalgae in the mouth of a clothespin, tied to the cinderblock, allowing for a uniform length of each species of macroalgae to be initially exposed to herbivores. We used cable ties to directly attach cores of algal turf to the cinderblock. At each of the three study locations, we randomly assigned one array to a low algal density treatment and the other array to a high algal density treatment. To impose the low density treatment at a site, we attached one strand of each macroalgal species (exposed length: 5 cm for *A. spicifera, A. rhodantha*, and *A. taxiformis*; 8 cm for *S. pacificum*) and one core of algal turf, while we imposed 4 times that amount for the high density treatment (i.e., 4 strands per macroalgal species and 4 cores of algal turf). To control for effects of algal attachment structures, we kept the amount and configuration of cable ties and clothespins consistent between low and high algal density treatments.

We ran herbivory trials for all 10 treatments at each study location on different days with similar weather conditions (i.e., mostly sunny, low wind). We started each herbivory trial in the late morning (between 930 and 1100 hours), after we attached algae to cinderblocks. We re-measured each strand of macroalgae to the nearest 0.5 cm *in situ* after 4, 24, 28, and 48 hours, to quantify losses due to herbivory. At these same time points, we also assigned one of the following five ordinal categories to each core of algal turf, to quantify loss due to herbivory: 4, no sign of grazing (complete cover of uncropped algal turf; the initial category for all cores); 3, low grazing (e.g., some cropping of turf or small bare area exposed); 2, intermediate grazing (significant cropping of turf and/or larger bare areas exposed); 1, high grazing (all remaining turf
cropped and large bare areas exposed); 0, highest grazing (all turf removed; only bare substrate remains). To control for observer bias, a single observer assigned herbivory categories to all cores of algal turf for a given trial. After the final measurement point for a trial (at 48 hours), we removed all algal turf cores and any remaining macroalgal strands from each cinderblock. After we completed the first herbivory trial for all three study locations, we switched the algal density treatment assigned to each array and conducted a second trial at each study location, yielding 6 replicates for each of 10 treatments (5 distances from structural refuge habitat × 2 initial algal densities).

For each of our three study locations, we randomly selected one of the two arrays to be video recorded for the first 4 hours of both herbivory trials (i.e., we recorded a replicate from both the low and high algal density treatment for each study location). From these video recordings, we extracted multiple metrics regarding the identity and behavior of herbivorous fishes visiting our sites. When we observed a fish taking at least one bite from the cinderblock (i.e., from the algae we attached or from the block itself), we recorded both the number of bites taken and the length of the foraging bout: the time the foraging fish entered the field of view (including the entire cinderblock and ~0.15 m around it, Figure E-2) until it exited the field of view. We also recorded the species and body length of each fish that we observed foraging from one of our sites. To measure fish body length, we took a still frame from the video at a point in which the fish was in a straight orientation, parallel to the screen (i.e., broad side facing the observer). We then used ImageJ software (Rasband 2014), with the clothespins on the cinderblock providing reference lengths, to measure the fish, from the tip of the snout to the edge of the caudal fin.
Statistical Modeling

We used Aikake Information Criterion (AIC) to compare relative fits of models to our data. For the field survey, we measured the relative fit of a null model (intercept only) and a series of models that each contained either a patch-scale or landscape-scale predictor variable. For our field experiment, we compared models with (1) only an intercept term \( y = \beta_0 \) or a term for the effect of trial \( (\beta_{\text{trial}}) \); i.e., our null models, (2) the effect of distance from shelter \( (y = \beta_0/\text{trial} + \beta_{\text{distance}} \cdot \text{distance}) \); (3) the effect of initial algal density \( (y = \beta_0/\text{trial} + \beta_{\text{density}} \cdot \text{density}) \), (4) the effect of distance and the effect of density \( (y = \beta_0/\text{trial} + \beta_{\text{distance}} \cdot \text{distance} + \beta_{\text{density}} \cdot \text{density}) \), or (5) the interaction between distance and density \( (y = \beta_0/\text{trial} + \beta_{\text{distance}} \cdot \text{distance} + \beta_{\text{density}} \cdot \text{density} + \beta_{\text{dist.} \cdot \text{density}} \cdot \text{distance} \cdot \text{density}) \). We fit a stochastic death process model to our algal loss rate data (see Supplement for details). This approach estimated algal loss rates across all four sampling time periods for each site in our study, and it allowed for the high variance in algal loss rate that is characteristic of herbivory assays in coral reefs (Littler and Littler 2007). We tested models that assumed that the rate of algal loss was determined by either a binomial process (algae loss rates \([\mu \cdot m \text{ from F-2}]\) decayed exponentially as the amount of algae was reduced), or a Poisson process (in which algal loss rates were determined at random, independent of the amount of algae). We used the maximum likelihood estimators of our model parameters from the best-fit model to simulate 100 datasets, and we used parametric bootstrapping on these datasets both to verify that our estimators were unbiased and to calculate 95% confidence intervals around the best-fit estimates of \( \mu \) (the loss rate of algae, per unit of algae, per unit of time) across treatments. We then converted estimates of \( \mu \) (units lost per minute) from our best-fit statistical models into patch-level algal loss rates that represent the maximum per-
minute loss rate (i.e., the loss rate in the first minute, in cm·min⁻¹), using the following equations \((m)\) is the initial amount of algae):

\[
\text{algal loss rate from binomial model} = m(1 - e^{-\mu}) \quad (5-1)
\]

\[
\text{algal loss rate from Poisson model} = (1 - e^{-\mu}). \quad (5-2)
\]

We fit linear mixed effects models to our data on the traits of herbivores that we observed visiting our sites, treating site as a random effect (nlme package in R; Pinheiro 2012, Team 2013). We quantified main effects and interactions of our treatments using best-fit models (out of the five basic types described above), determined with \(\Delta\text{AIC}\). We used residual plots to verify that our data met model assumptions of normality and homoscedasticity.

**Results**

**Landscape-Scale Survey**

Distance from contiguous reef habitat was the best predictor of algal loss rate, which was best fit by a binomial model in our landscape-scale survey (\(\Delta\text{AIC: vs. next-best model, -3,611; vs. null model, -7,945; Table G-1}\)); from within the contiguous reef to 298 m away, mean algal loss rate decreased by 83.7\% (mean ±95\% C.I.: from 0.0184 [+0.004,-0.003] to 0.0030 [+0.001,-0.001] cm·sec⁻¹; Figure 5-2). Furthermore, each landscape-scale metric of relative cover of structural refuge habitat in the areas surrounding each site better predicted algal loss rates than each patch-scale metric. We expected this result, because we intentionally constrained the ranges of patch-scale metrics across sites (i.e., to control for patch-level factors).

**Field Experiment: Algal Loss**

The statistical models that best fit our experimental data on algal loss rates showed that the loss rate of *Acanthophora spicifera, Amansia rhodantha, Asparagopsis*
taxiformis, and Sargassum pacificum was significantly affected by our experimental treatments, but one algal turf was not (see model-fitting summary in Table G-2). For each of the four species, however, the best-fit model was not the same, for these four species. For A. spicifera (ΔAIC: vs. next-best model, -3.52; vs. best null, -64.0) and A. taxiformis (ΔAIC: vs. next-best model, -1.04; vs. best null, -13.3) the models with constant per biomass loss rates and the distance*distance interaction performed best (give stats here). For both A. rhodantha and S. pacificum, the model with a constant total loss rate and the main effects of distance and density fit best (A rhodantha: ΔAIC: vs. next-best model, -4.24; vs. best null, -8.09; S. pacificum: ΔAIC: vs. next-best model, -1.55; vs. best null, -142).

We observed pronounced differences in loss rates (cm·min⁻¹) among our macroalgal species; Acanthophora spicifera reached a peak average loss rate (of 1.2 cm·min⁻¹ for the inside-reef [-2 m] treatment) that was more than three times greater than that of the three other macroalgal species combined (Figure 5-3); these rates exceeded those from our field survey (Figure 5-2). Three out of the four macroalgal species (A. spicifera, A. rhodantha, and A. taxiformis) in our experiment exhibited loss rates that declined with distance from reef habitat, while S. pacificum exhibited a slight increase in loss rate with distance from reef habitat. The quadrupled density of algae that we imposed as part of our experimental treatments led to clear increases in algal loss rates only for A. spicifera and S. pacificum, for which mean loss rates increased by a factor of 8.9 (mean ± 95% C.I.: from 0.126 [+0.17, -0.059 ] to 1.12 [+1.3 , -0.58] cm·min⁻¹) and 6.6 (0.029 [+0.017,-0.0032] to 0.20 [+0.21,-0.043] cm·min⁻¹), respectively.

It is important to note that the interaction between the effect of isolation from reef habitat
and initial algal density for *A. spicifera* arose because loss rates declined with distance disproportionately less for high initial algal density patches compared to low initial algal density patches (Fig. 5-3A). This interaction was maintained for loss rates for all four macroalgal species combined (Fig. 5-3E).

**Field Experiment: Herbivores**

Within the 7,200 minutes of footage we analyzed, we observed 578 individual herbivore foraging bouts that encompassed a total of 179.25 minutes. We observed a significant increase in average individual bite rate with both greater distances from reef habitat (0.94 ± 0.07 [mean ± 95% C.I.] to 1.96 ± 0.54 bites·sec⁻¹: mean increase of 208% from -2 [inside the reef] to 30 m, F₁,573 = 31.16, p < 0.0001) and greater initial density of algae (0.93 ± 0.08 to 1.09 ± 0.07 bites·sec⁻¹: mean increase of 21% from low to high density, F₁,573 = 8.84, p = 0.003), though the addition of algal density as a factor did not improve the model fit, relative to the best-fit distance model (Figure 5-4A, Table G-3).

As distance from shelter increased, we observed a significant decrease in total foraging time (966.83 ± 452.51 to 41.17 ± 50.44 seconds: mean decrease of 96%; F₁,24 = 24.35, p < 0.0001) and a significant increase in the body length of foraging herbivorous fishes (13.38 ± 0.43 to 14.40 ± 0.31 cm: mean increase of 7.7%; F₁,574 = 41.08, p < 0.0001; Figure 5-4B,C). The latter effect was most pronounced near the reef edge (5 m distance), where the mean fish body length peaked at 16.08 ± 0.40 cm. Though we observed increases in total foraging time (283.27 ± 228.97 to 433.73 ± 228.08 seconds: mean increase of 53%) and fish body length (14.15 ± 0.43 to 14.59 ± 0.31 cm: mean increase of 3.1%) from our low to high algal density treatments, these effects were not significant.
Discussion

There are many examples in the terrestrial literature of strong effects of landscape context on locally-observed (‘patch-scale’) ecological processes, including water and nutrient cycling (Van de Koppel and Rietkerk 2004, Young et al. 2010), species colonization rates (Burke and Goulet 1998, Bukovinszky et al. 2005), as well as consumer-resource, predator-prey, host-parasitoid, plant-pollinator and competition-facilitation dynamics (Steffan-Dewenter et al. 2002, Orrock et al. 2003, Thies et al. 2003, Thies et al. 2005, Van de Koppel et al. 2006, Kauffman et al. 2007, Tscharntke et al. 2012). Here we show that the relative importance of resource-mediated (i.e., “bottom-up”) versus consumer-mediated (i.e., “top-down”) control of primary producers, which remains hotly debated among ecologists, depends on landscape context in a tropical coral reef. In particular, our study revealed the novel finding that effects of distance from refuge habitat on herbivory depend on initial resource densities: herbivory on greater densities of benthic algae declined with distance from refuge (reef structural habitat), but these declines were disproportionately smaller than those of low-density treatments (Figure 5-3E). This suggests that herbivore control of enrichment effects (i.e., increased algal density) in marine systems, shown in Burkepile and Hay (2006), likely extends to habitat patches isolated from refuge habitat, despite the increase in predation risk for herbivores that visit these patches. Furthermore, our findings indicate that reef fishes balance risk with reward, because they are willing to accept greater risk by foraging more in patches distant from refuge, so long as those patches provide a greater reward in harvested resources.

The background conditions of natural systems could influence the patterns in herbivory that we observed. The initial algal density treatment in our experiment that
took place in a nutrient-poor system (Alldredge 2013) mimicked a pulse of nutrient enrichment (e.g., due to a heavy rainfall event; (Fabricius 2005)), which can increase the density of resources (e.g., algae; Littler and Littler 2007) if background levels of nutrients are low. However, chronic enrichment experienced by many systems can drive long-term increases in the rate of resource growth (e.g., primary production of algae; (Fabricius 2005, Lapointe et al. 2005)). Foraging theory and a variety of supporting empirical works posit that foragers with a greater survivor’s fitness (i.e., the fitness an animal can achieve if it survives; this increases with the animal’s energy state) will accept less risk of predation when foraging (i.e., they have more to lose; Brown 1999). Thus, sustained increases in overall resource availability from chronic enrichment at large spatial scales (i.e., those typically observed in nature; (e.g., Bell et al. 2014) could raise the survivor’s fitness of foragers. Consequently, negative effects of isolation from refuge habitat on herbivory could increase, beyond what we observed in our study (Figure 5-2 and 5-3). However, this could be a transient effect if, over time, herbivore population density increased with enhanced primary production (as would be expected in closed systems with an even number of trophic levels; Oksanen et al. 1981). An increase in the density of the herbivore population could increase competition for resources and, in effect, prevent increases in the survivor’s fitness of herbivores, relative to the pre-enriched system (Oksanen et al. 1981). This scenario may better align with our results, which showed a high degree of risky foraging in patches with higher initial densities of algae (Figure 5-3E). Ultimately, our study provides new insights regarding spatial context dependence of top-down vs. bottom-up control in natural landscapes, but future works should examine the sensitivity of our results to
additional factors, including the temporal/spatial scale, frequency and magnitude of enrichment, as well as the number and relative demographic scales of trophic levels in the system.

Our results on traits of herbivorous fishes foraging from our experimental sites support the conclusion that perceived risk by herbivores drove observed effects of habitat isolation on herbivory. To understand this, let us first consider the costs and benefits of foraging. Optimal foraging theory posits that when an animal chooses to forage, this decision comes with three key costs, including the cost of energy spent on foraging (i.e., metabolic costs, or $C$), the cost of not engaging in an alternative activity, such as mating (i.e., missed opportunity costs, or $MOC$), and finally the cost of being killed by a predator ($P$). Thus, differences in the quitting harvest rate (i.e., when the harvest rate of the forager no longer exceeds the combined costs of foraging, and, thus, the forager leaves a patch; $H$) among patches reflect differences in foraging costs among patches (Brown 1988, Brown and Kotler 2004): $H = C + MOC + P$.

Given that we ran all ten experimental treatments simultaneously in the same general location for a given trial, and given the close proximity of our treatments relative to the wide movement ranges of the visiting herbivorous fishes (e.g., Meyer and Holland 2005, Welsh and Bellwood 2012), it is reasonable to assume that missed opportunity costs and metabolic costs were equivalent among our study sites for a given trial (Brown et al. 2001, Kilpatrick 2003). Our results also showed that: (1) harvest rates were density dependent for the majority of observed herbivory (i.e., the binomial model fit best for the greatly preferred algal species $A. spicifera$ [Figure 5-3A, Table G-1 & G-2], which drove patterns in total algal loss rates [Figure 5-3E]), and (2) foragers
significantly increased their bite rates in patches with higher algal density (Figure 5-4B; Table G-3). These observations are consistent with the assumption that our resource patches offered diminishing returns. Consequently, quitting harvest rates will scale linearly with our recorded metric of individual average bite rate. Thus, the two-fold (1.02 bites·sec⁻¹) increase in individual bite rate we observed between our within-reef (-2 m) patch and our furthest patch from structural refuge habitat (30 m) reflect higher costs of predation, i.e., higher perceived predation risk by herbivores. In addition, we observed a significant, albeit weak, trend toward larger fish body sizes with increased distance from shelter, likely reflecting diminishing risk as fish size increased (Osenberg and Mittelbach 1989, Persson et al. 1996).

We observed that distance from refuge habitat reduced the overall herbivory rate of attractive resource patches of benthic macroalgae in a tropical coral reef (Figure 5-2, 5-3E), but specific herbivory rates differed between our survey and our experiment and among algal taxa within our experiment. First, higher loss rates of A. spicifera in our experiment (Figure 5-3) relative to our survey (Figure 5-2), could be attributed to several factors, including differences in the accessibility/attractiveness of outplanted algae (survey sites atop large coral colonies were potentially more exposed to predators of herbivores), site differences in herbivore or predator density, and/or differences in measurement time points (i.e., algae from surveys were first re-measured at 6 hours, while algae from the experiment were re-measured after 4 hours). Moreover, the increased variance in algal loss rates from our experiment, relative to those from our survey, were likely driven by the demographic stochasticity associated with the much smaller size of outplanted algal patches in our experiment.
A. spicifera, as expected from previous studies (Littler and Littler 2007), was overwhelmingly preferred by herbivores in our experiment (Figure 5-3A). Consequently, the pattern in A. spicifera loss rate largely drove the overall pattern in macroalgal loss rate across treatments and can be thought of as a measure of the relative potential for herbivores to control algae (Littler and Littler 2007, Figure 5-3A,E). The other three macroalgal species in our experiment were consumed at much lower rates and exhibited different patterns across our experimental treatments, including a negative effect of initial algal density on the loss rates of A. rhodantha and A. taxiformis, and a positive effect of distance on the loss rate of S. pacificum. These patterns in the much less preferred algal species could be explained by preferences for different algal species or patch densities among individual (or species of) herbivores that also differ in their propensity to forage away from reef habitat. For example, Hoey and Bellwood (2011) recently showed that some herbivorous fishes prefer relatively open, low-density patches of algae, perhaps because these patches impose less of a visual obstruction to foragers that would benefit from early detection of an approaching predator. In addition, A. spicifera and A. taxiformis loss rates decreased as the amount of each of these species decreased in a patch, while A. rhodantha and S. pacificum exhibited random algal loss rates, independent of the amount of algae available. This further indicates that these species of algae were perceived differently by herbivores, which clearly preferred A. spicifera and may have only incidentally fed on A. rhodantha and S. pacificum. Lastly, we saw no significant effect of either of our experimental factors on loss rates from cores of filamentous algal turf, which could be due, in part, to a high sampling error rate associated with our ordinal category assignments. Together, these results suggest
that in addition to effects on overall algal density, isolation from the structural refuge
habitat of the reef could indirectly affect the species composition of benthic algae, via
herbivore behavior.

Globally, coastal marine systems are experiencing loss and fragmentation of
structural refuge habitat formed by foundation species (e.g., corals, (Bellwood et al.
2004); seagrasses, (Orth et al. 2006); kelp, (Steneck et al. 2002)), due to natural and
anthropogenic factors, including storms, pollution, and overharvesting of consumers
(Jackson et al. 2001, Fabricius 2005). Our study suggests that the loss or fragmentation
of refuge habitat can suppress consumer control of benthic algae, but this effect can
weaken if algal density is higher, e.g., due to bottom-up processes like nutrient
enrichment (Lapointe 1997; Lapointe et al. 2004; Lapointe et al. 1992), providing greater
incentives for foragers. Our results point to protection from overfishing as a key
management strategy to control algal blooms and thus conserve reef systems.
However, our results further stress that to understand the extent to which herbivores
provide protection from actual nutrient enrichment across spatially heterogeneous
landscapes, we must understand how herbivores respond to enrichment over time, at
the population level.
Figure 5-1. Study map. The location of our study sites (open black circles, n = 30) for our landscape-scale field survey, overlaid atop a map that designates each pixel as either sand flat (white) or reef (grey) habitat (created with ArcGIS software). Ten of the 30 study sites were located within the contiguous reef tract to the northwest, and the shoreline ran east-west, just south of the mapped region. We used this map to extract landscape-scale independent variables for our statistical modeling (results summarized in Table G-1).
Figure 5-2. Herbivory across the landscape. Here we show estimated loss rates (mean ±95% confidence intervals) from the best-fit model for *Acanthophora spicifera* over distance from the contiguous reef tract on the north side of the field survey location. Reported values are based on four measures over time of algal loss rate at each of the 30 sites (including 10 sites within the contiguous reef, at 0 distance).
Figure 5-3. Estimated loss rates (mean ±95% confidence intervals) of macroalgae from the best-fit model for each species of macroalgae. This includes: *Acanthophora spicifera* (A), *Amansia rhodantha* (B), *Asparagopsis taxiformis* (C), and *Sargassum pacificum* (D), as well as all algal species combined (E). Our ten experimental treatments included: five distances from the structural refuge habitat of the coral reef (-2 m [inside the reef], 5, 10, 20, and 30 m from the reef edge) crossed with two different initial densities of algae (low [open points] and high [4×low; closed black points]). Grey points represent expected values for the high initial algal density treatment, calculated as 4×the loss rate for the low initial algal density treatment (which differed in algal density by a factor of 4).
Figure 5-4. Traits (mean ±95% confidence intervals) of the foragers (herbivorous reef fishes) we observed at our sites. This included total foraging time (individual bite rate (A), sum of all foraging times per site (B), and body length (C), across our ten experimental treatments: five distances from structural refuge habitat (coral reef: -2 m [inside the reef], 5, 10, 20, and 30 m from the reef edge) crossed with two different densities of algae (low [open points] and high [4×low; closed points]). Note that we observed only one forager in the low initial algal density treatment at 30 m from structural refuge habitat.
CHAPTER 6
CONCLUSION

My studies revealed that enrichment effects on primary producers in coral reefs depend on multiple factors, including the magnitude and spatial extent of enrichment, as well as the presence of high sedimentation and overfishing and the spatial habitat context within the system. Furthermore, results from my field experiment testing for interactive effects among nutrient enrichment, sedimentation and overfishing (Ch. 3) suggest that herbivores can control enrichment effects in small plots, over short time scales (6 months). This finding echoes the results from a meta-analysis of field experiments that similarly crossed manipulations of nutrient enrichment with consumer exclusions (Burkepile and Hay 2006). However, my modeling study (Ch. 4) indicates that this control of enrichment by herbivores depends on the spatial scale of enrichment manipulations, partially or fully diminishing as enrichment increases from small experimental spatial scales to larger spatial scales that are more representative of actual enrichment events (i.e., on the order of square kilometers and greater; Smith et al. 1981, Penna et al. 2004, Paerl et al. 2006, Bell et al. 2014). I further found that while herbivory is inhibited by distance from refuge habitat, this effect weakened when we imposed algae at higher densities (to mimic enrichment effects). This finding suggests that even when herbivore movement is partially constrained by perceived risk of predation, herbivores are still able to counteract enrichment effects on primary producers. Thus, my findings point to two distinct conclusions regarding enrichment in coral reefs: my experiments suggest that herbivores can control the effects of natural nutrient enrichment on algae, while my modeling study suggests that herbivores cannot control effects of natural nutrient enrichment on algae. To understand which of these
conclusions is more likely to operate in a natural system, we must consider timescales beyond those of my studies.

My studies spanned scales in space and in biological organization, from sub-m² plots (Ch. 3) to landscapes (Ch. 4 & 5) and from single organisms (Ch. 2) to communities (Ch. 3-5). However, the inference provided by my work is limited by the short temporal scale that characterized each of my studies. Indeed, a general problem in ecology is that we observe patterns in nature at scales that are limited by perceptual, technological and logistical constraints (Steele 1978), and these patterns can be difficult to relate to processes of interest that occur at different scales in space, time or biological organization (Levin 1992). This issue is well articulated by my finding that expanding enrichment to realistic spatial scales (Ch. 4) can qualitatively change effects on primary producers from what is observed in small-scale enrichment studies (e.g., Ch. 3; Burkepile and Hay 2006). Because the temporal scale of my studies failed to capture population dynamics of herbivores (Ch. 3-5), the extent to which these studies provide realistic insights about natural systems in the long term will depend on the potential for demographic responses of the herbivore population to enrichment. Furthermore, to truly understand the ecological threat posed by anthropogenic nutrient enrichment, which continues to increase globally (Vitousek et al. 1997, Nixon 2009), future works must examine consumer numerical responses, both via migration and via population dynamics, in a context that matches data to spatial and temporal scales of interest.

My dissertation research points to several recommendations for ecosystem-based management of coral reefs and other similarly enriched systems that are spatially heterogeneous with large-bodied, roving herbivores (e.g., seagrass meadows, kelp
forests). These systems would likely benefit from: (1) limits on the magnitude and spatial extent of enrichment and sedimentation, e.g., through waste-treatment facilities and restrictions on coastal development and fertilizer use; (2) strict prohibition of the overharvesting of consumers (e.g., herbivorous fishes); and (3) prevention of the loss and fragmentation of reef structural habitat that provides refuge to herbivores. To implement these recommendations requires integrated coastal zone management, an approach that, to date, is seldom implemented; instead, marine management plans often entirely disregard terrestrial activities (Pandolfi et al. 2005). As nearshore marine systems continue to experience increases in (1) the frequency and magnitude of enrichment (Fabricius 2005, Nixon 2009), and (2) loss and fragmentation of biogenic structural habitat, e.g., corals (Bellwood et al. 2004); seagrasses (Orth et al. 2006), kelp, (Steneck et al. 2002), management interventions are increasingly needed to sustain the vital services provided by these systems to entire cultures and regions of people (Moberg and Folke 1999, Barbier et al. 2011).
APPENDIX A
SUMMARY OF CONFLICTING FINDINGS OF PAST NUTRIENT-CORAL GROWTH EXPERIMENTS

Table A-1: Previous coral growth experiments. The following studies measured coral growth in response to nutrient enrichment, with the qualitative effects observed denoted as “+” for positive, “0” for neutral (i.e., no effect), and “-” for negative. These studies observed nearly equal frequencies of positive (12 out of 37), neutral (13 out of 37), and negative (12 out of 37) coral growth responses to nutrient enrichment. This table also highlights the variety of enrichment methods, study types and durations, nutrient contexts, coral species, and response metrics used across these studies.

<table>
<thead>
<tr>
<th>Reference</th>
<th>Effect</th>
<th>Enrichment method</th>
<th>Study type</th>
<th>Duration</th>
<th>Ambient (control) nutrient levels</th>
<th>Coral tested</th>
<th>Response measured</th>
</tr>
</thead>
<tbody>
<tr>
<td>Meyer and Schultz 1985a and b</td>
<td>+</td>
<td>Measured effects of fish whose waste significantly increased N (4.59-9.10 mg yr(^{-1})) and P (0.61-0.75 mg yr(^{-1})) from nearby well</td>
<td>Field exp.</td>
<td>2.5 yr</td>
<td>2.94 - 6.5 mg yr(^{-1}) N, 0.30 - 0.67 mg yr(^{-1}) P</td>
<td><em>Porites furcata</em></td>
<td>Skeleton deposition, volume and density</td>
</tr>
<tr>
<td>Atkinson et al. 1995</td>
<td>+</td>
<td>Constantly pumped in high-nutrient seawater (~0.6 µM PO(_4^{3-}); ~5µM NO(_3^-); ~2 µM NH(_4^+)) from nearby well</td>
<td>Lab study</td>
<td>1 yr</td>
<td>n/a</td>
<td><em>Coral community</em></td>
<td>Branch length every 6 months and wet weight</td>
</tr>
<tr>
<td>Koop et al. 2001</td>
<td>+</td>
<td>Twice daily, during low tide, nutrients were added in 3 pulses, to maintain a concentration of 20 µM NH(_4^+) for 5-6 h</td>
<td>Field exp.</td>
<td>13 mo</td>
<td>6.5 ± 6.9 µM NH(_4^+), 0.2 ± 0.06 µM PO(_4^{3-}) (mean ± sd)</td>
<td><em>Acropora longicyathus</em> (adults)</td>
<td>Buoyant mass</td>
</tr>
<tr>
<td>Koop et al. 2001</td>
<td>+</td>
<td>Twice daily, during low tide, nutrients were added in 3 pulses, to maintain a concentration of 4 µM PO(_4^{3-}) for 5-6 h</td>
<td>Field exp.</td>
<td>13 mo</td>
<td>6.5 ± 6.9 µM NH(_4^+), 0.2 ± 0.06 µM PO(_4^{3-}) (mean ± sd)</td>
<td><em>Acropora palifera</em> (adults), <em>Acropora longicyathus</em> (adults), <em>Pocillopora damicornis</em> (nubbins)</td>
<td>Linear extension (adult <em>A. palifera</em> and <em>A. longicyathus</em>) and buoyant mass (adult <em>A. palifera</em> and <em>A. longicyathus</em>, and <em>P. damicornis</em> nubbins)</td>
</tr>
<tr>
<td>Reference</td>
<td>Effect</td>
<td>Enrichment method</td>
<td>Study type</td>
<td>Duration</td>
<td>Ambient (control) nutrient levels</td>
<td>Coral tested</td>
<td>Response measured</td>
</tr>
<tr>
<td>-----------</td>
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</tr>
<tr>
<td>Koop et al. 2001</td>
<td>+</td>
<td>Twice daily, during low tide, nutrients were added in 3 pulses, to maintain concentrations of 20 µM NH₄⁺ and 4 µM PO₄³⁻ for 5-6 h</td>
<td>Field exp.</td>
<td>13 mo</td>
<td>6.5 ± 6.9 µM NH₄⁺, 0.2 ± 0.06 µM PO₄³⁻ (mean ± sd)</td>
<td>Acropora palifera (adults), Acropora longicyathus (adults and nubbins)</td>
<td>Linear extension (adult A. palifera &amp; A. longicyathus) and buoyant mass (A. longicyathus nubbins)</td>
</tr>
<tr>
<td>Tanaka et al. 2007</td>
<td>+</td>
<td>Corals incubated for 0, 5, or 10 days in continuously enriched waters (2.1 µM NO₃⁻, 0.06 µM NO₂⁻, 0.03 µM NH₄⁺, and 0.09 µM PO₄³⁻, on average)</td>
<td>Lab exp.</td>
<td>10 d</td>
<td>0.2-1.5 µM NO₃⁻, 0.2-1.0 µM NH₄⁺, and 0.02-0.08 µM PO₄³⁻</td>
<td>Acropora pulchra</td>
<td>Calcification rate (using ¹³C-labeled dissolved inorganic C)</td>
</tr>
<tr>
<td>Holbrook et al 2008</td>
<td>+</td>
<td>Measured effects of fish whose biomass had a positive relationship with output of NH₄⁺ (led to average within-colony NH₄⁺ elevation of ~0.04 to 0.45 µM).</td>
<td>Field exp.</td>
<td>1 mo</td>
<td>Not reported</td>
<td>Pocillopora spp.</td>
<td>Buoyant mass</td>
</tr>
<tr>
<td>Sotka and Hay 2009</td>
<td>+</td>
<td>Corals were attached to cinderblocks, and 3 or 6 stakes of tree fertilizer were replaced in sealed cinder block chambers every 15-39 days. Within-chamber average DIN and SRP levels ranged from about 6,400 µM and 500 µM (Day 1) to ~23 µM and 15 µM (Day 32), respectively.</td>
<td>Field exp.</td>
<td>4.5 mo</td>
<td>&lt;1 µM DIN and &lt;0.3 µM SRP</td>
<td>Porites</td>
<td>Linear extension</td>
</tr>
<tr>
<td>Reference</td>
<td>Effect</td>
<td>Enrichment method</td>
<td>Study type</td>
<td>Duration</td>
<td>Ambient (control) nutrient levels</td>
<td>Coral tested</td>
<td>Response measured</td>
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<tr>
<td>Davies 1990</td>
<td>0</td>
<td>Outplanted corals at three sites along a natural nutrient gradient with a range of 0.74-4.92 µg L⁻¹ NO₃⁻/NO₂⁻ and 0.05-0.17 µg L⁻¹ PO₄³⁻</td>
<td>Field study</td>
<td>3 d</td>
<td>Low-enrichment site: 0.74 ± 0.15 µg L⁻¹ NO₃⁻/NO₂⁻, and 0.07 ± 0.08 µg L⁻¹ PO₄³⁻ (mean ± sd)</td>
<td><em>Porites</em> (nubbins)</td>
<td>Buoyant mass</td>
</tr>
<tr>
<td>Stambler et al. 1991</td>
<td>0</td>
<td>Stock solutions of KH₂PO₄ continuously pumped into treatment tanks, reaching 0.5-2µM PO₄³⁻</td>
<td>Lab exp.</td>
<td>28 d</td>
<td>0.1 µM PO₄³⁻ and 2 µM NH₄⁺</td>
<td><em>Pocillopora damicornis</em> (adults)</td>
<td>Linear extension</td>
</tr>
<tr>
<td>Koop et al. 2001</td>
<td>0</td>
<td>Twice daily, during low tide, nutrients were added in 3 pulses, to maintain a concentration of 20 µM NH₄⁺ for 5-6 h</td>
<td>Field exp.</td>
<td>13 mo</td>
<td>6.5 ± 6.9 µM NH₄⁺, 0.2 ± 0.06 µM PO₄³⁻ (mean ± sd)</td>
<td><em>Acropora aspera</em> (adults)</td>
<td>Buoyant mass</td>
</tr>
<tr>
<td>Koop et al. 2001</td>
<td>0</td>
<td>Twice daily, during low tide, nutrients were added in 3 pulses, to maintain a concentration of 4 µM PO₄³⁻ for 5-6 h</td>
<td>Field exp.</td>
<td>13 mo</td>
<td>6.5 ± 6.9 µM NH₄⁺, 0.2 ± 0.06 µM PO₄³⁻ (mean ± sd)</td>
<td><em>Acropora longicyathus</em> (nubbins), <em>Pocillopora damicornis</em> (nubbins)</td>
<td>Buoyant mass</td>
</tr>
<tr>
<td>Koop et al. 2001</td>
<td>0</td>
<td>Twice daily, during low tide, nutrients were added in 3 pulses, to maintain concentrations of 20 µM NH₄⁺ and 4 µM PO₄³⁻ for 5-6 h</td>
<td>Field exp.</td>
<td>13 mo</td>
<td>6.5 ± 6.9 µM NH₄⁺, 0.2 ± 0.06 µM PO₄³⁻ (mean ± sd)</td>
<td><em>Acropora aspera</em> (adults), <em>Acropora palifera</em> (adults), <em>Acropora longicyathus</em> (nubbins), <em>Stylophora pistillata</em> (nubbins)</td>
<td>Buoyant mass</td>
</tr>
<tr>
<td>Koop et al. 2001</td>
<td>0</td>
<td>Twice daily, during low tide, nutrients were added in a single pulse to reach initial concentrations of 10 µM NH₄⁺ and/or 2 µM PO₄³⁻ (N crossed with P addition)</td>
<td>Field exp.</td>
<td>15 mo</td>
<td>NH₄⁺ averaged 6.5 ± 6.9 µM, PO₄³⁻ averaged 0.2 ± 0.06 µM</td>
<td><em>Acropora palifera</em> (adults), <em>Acropora longicyathus</em> (adults and nubbins), <em>Pocillopora damicornis</em> (nubbins)</td>
<td>Linear extension (adult <em>A. palifera</em> &amp; <em>A. longicyathus</em>) and buoyant mass (<em>A. longicyathus</em> and <em>P. damicornis</em> nubbins)</td>
</tr>
<tr>
<td>Reference</td>
<td>Effect</td>
<td>Enrichment method</td>
<td>Study type</td>
<td>Duration</td>
<td>Ambient (control) nutrient levels</td>
<td>Coral tested</td>
<td>Response measured</td>
</tr>
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</tr>
<tr>
<td>Kinsey and Domm 1974 and Kinsey and Davies 1979</td>
<td>-</td>
<td>Pulsed fertilizer at low tide to maintain PO$_4^{3-}$ at 2µM and N (90% urea, 10% NH$_4^+$) at 20 µg atoms L$^{-1}$ for 3 h daily</td>
<td>Field exp.</td>
<td>8 mo</td>
<td>~0.2 µM PO$_4^{3-}$, &lt; 0.5 µM NO$_3^-$</td>
<td>Patch reef coral community</td>
<td>Reef calcification</td>
</tr>
<tr>
<td>Davies 1990</td>
<td>-</td>
<td>Outplanted corals at three sites along a natural nutrient gradient with a range of 0.74-4.92 µg L$^{-1}$ NO$_3^-$/NO$_2^-$, and 0.05-0.17 µg L$^{-1}$ PO$_4^{3-}$</td>
<td>Field study</td>
<td>3 d</td>
<td>Low-enrichment site: 0.74 ± 0.15 µg L$^{-1}$ NO$_3^-$/NO$_2^-$, and 0.07 ± 0.08 µg L$^{-1}$ PO$_4^{3-}$ (mean ± sd)</td>
<td>Montastrea annularis (nubbins)</td>
<td>Buoyant mass</td>
</tr>
<tr>
<td>Stambler et al. 1991</td>
<td>-</td>
<td>Stock solutions of KH$_2$PO$_4$ and/or (NH$_4^+$)$_2$SO$_4$ continuously pumped into treatment tanks, reaching 0.5-2µM PO$_4^{3-}$ and 7 or 15µM NH$_4^+$</td>
<td>Lab exp.</td>
<td>44 d</td>
<td>2 µM NH$_4^+$ and 0.1 µM PO$_4^{3-}$</td>
<td>Pocillopora damicornis (adults)</td>
<td>Linear extension</td>
</tr>
<tr>
<td>Marubini and Davies 1996</td>
<td>-</td>
<td>Corals continuously incubated in 1, 5 and 20 µM NO$_3^-$</td>
<td>Lab exp.</td>
<td>30-40 d</td>
<td>0.05 µM PO$_4^{3-}$, 0.2 µM NO$_3^-$</td>
<td>Porites and Montastrea annularis</td>
<td>Buoyant mass</td>
</tr>
<tr>
<td>Ferrier-Pages et al. 2000</td>
<td>-</td>
<td>NH$_4^+$ (10 µM for 4 weeks then 20 µM for 5 weeks) and/or PO$_4^{3-}$ (2µM for 9 weeks)</td>
<td>Lab exp.</td>
<td>63 d</td>
<td>&lt;0.5 N and &lt;0.1 P</td>
<td>Stylophora pistillata</td>
<td>Buoyant mass</td>
</tr>
</tbody>
</table>
Table A-1. Continued

<table>
<thead>
<tr>
<th>Reference</th>
<th>Effect</th>
<th>Enrichment method</th>
<th>Study type</th>
<th>Duration</th>
<th>Ambient (control) nutrient levels</th>
<th>Coral tested</th>
<th>Response measured</th>
</tr>
</thead>
<tbody>
<tr>
<td>Koop et al. 2001</td>
<td>-</td>
<td>Twice daily, during low tide, nutrients were added in 3 pulses, to maintain a concentration of 20 µM NH₄⁺ for 5-6 h</td>
<td>Field exp.</td>
<td>13 mo</td>
<td>6.5 ± 6.9 µM NH₄⁺, 0.2 ± 0.06 µM PO₄³⁻ (mean ± sd)</td>
<td>Acropora palifera (adults), Acropora longicyathus (adults), Pocillopora damicornis (nubbins)</td>
<td>Linear extension (adult A. palifera &amp; A. longicyathus) and buoyant mass (adult A. palifera and P. damicornis nubbins)</td>
</tr>
<tr>
<td>Koop et al. 2001</td>
<td>-</td>
<td>Twice daily, during low tide, nutrients were added in 3 pulses, to maintain a concentration of 4 µM PO₄³⁻ for 5-6 h</td>
<td>Field exp.</td>
<td>13 mo</td>
<td>6.5 ± 6.9 µM NH₄⁺, 0.2 ± 0.06 µM PO₄³⁻ (mean ± sd)</td>
<td>Acropora aspera (adults)</td>
<td>Buoyant mass</td>
</tr>
<tr>
<td>Koop et al. 2001</td>
<td>-</td>
<td>Twice daily, during low tide, nutrients were added in 3 pulses, to maintain concentrations of 20 µM NH₄⁺ and 4 µM PO₄³⁻ for 5-6 h</td>
<td>Field exp.</td>
<td>13 mo</td>
<td>6.5 ± 6.9 µM NH₄⁺, 0.2 ± 0.06 µM PO₄³⁻ (mean ± sd)</td>
<td>Pocillopora damicornis (nubbins)</td>
<td>Buoyant mass</td>
</tr>
<tr>
<td>Ferrier-Pages et al. 2001</td>
<td>-</td>
<td>Stock solutions of NaNO₃ were diluted to 2 µM N and continuously pumped into treatment tanks</td>
<td>Lab exp.</td>
<td>3 wk</td>
<td>&lt;0.4 µM NH₄⁺, &lt;1 µM NO₃⁻, &lt;0.2 µM PO₄³⁻</td>
<td>Stylophora pistillata</td>
<td>Buoyant mass</td>
</tr>
</tbody>
</table>
SEDIMENT MANIPULATION, NUTRIENT TREATMENT EFFECTIVENESS, AND STATISTICS SUMMARY

**Sediment Manipulation:** Sediment was collected at the mouth of the nearby Opunohu River (17°30'54"S, 149°50'60"W), rinsed thoroughly with fresh water to remove residual organic matter and sterilized in boiling water to kill microorganisms. The grain size composition, determined by sieving dried samples from six different locations within the collection site, was as follows: >500 µm, 0.6 ± 0.4%; 250 - 500 µm, 7.7 ± 5.2%; 125 - 250 µm, 76.8 ± 6.5%; 63 - 125 µm, 14.2 ± 4.8%; and 20 - 63 µm, 0.7 ± 0.5%. Studies show that a large amount of sediment deposited onto coral reefs is of terrestrial origin and falls well within our collected grain size range (Hernandez et al. 2009, Storlazzi et al. 2009, Bannister et al. 2012).

Each week, a pair of SCUBA divers performed 4-6 sediment additions over 2-3 days. During each addition, the divers poured a precise amount of sediment onto the units using a measuring cup and a metal sediment application frame placed over the entire experimental unit (pictured in Figure 3-2) to control for variable flow and to ensure that all sediment settled within the perimeter of the experimental unit (this could easily be verified visually). Additionally, a mosquito net stretching across the opening of the sediment application frame ensured that the sediment trickled slowly and evenly onto each unit. Using this method, we achieve a weekly manipulated sediment deposition rate of 200 mg cm\(^{-2}\) d\(^{-1}\) (this amount plus the local ambient sedimentation rate of 12 mg cm\(^{-2}\) d\(^{-1}\) yielded a total sedimentation rate of 212 mg cm\(^{-2}\) d\(^{-1}\) for sediment treatment units, compared to 12 mg cm\(^{-2}\) d\(^{-1}\) for control units; LTER). We manipulated
sedimentation at this rate, because: 1) it greatly exceeds natural (i.e., ‘pristine’) sedimentation rates (Rogers 1990), 2) it falls well within known sedimentation rates affecting various coral reefs (Table B-1), and 3) similar sedimentation rates have been shown to negatively affect or even kill various coral species (Erftemeijer et al. 2012).

Table B-1: Observed sedimentation rates on coral reefs around the world.

<table>
<thead>
<tr>
<th>Sedimentation rate (mg cm$^{-2}$ d$^{-1}$)</th>
<th>Location</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.5 - 1</td>
<td>Jamaica</td>
<td>Dodge et al. (1974)</td>
</tr>
<tr>
<td>3 - 10</td>
<td>Puerto Rico</td>
<td>Rogers (1983)</td>
</tr>
<tr>
<td>1 - 45</td>
<td>Malaysia</td>
<td>Nakajima et al. (2013)</td>
</tr>
<tr>
<td>30 - 60</td>
<td>Thailand</td>
<td>Yeemin et al. (2013)</td>
</tr>
<tr>
<td>0.9 - 82</td>
<td>Venezuela</td>
<td>Bastidas et al. (1999)</td>
</tr>
<tr>
<td>2 - 89</td>
<td>Barbados</td>
<td>Tomascik and Sander (1985)</td>
</tr>
<tr>
<td>0.7 - 127</td>
<td>China</td>
<td>Li et al. (2013)</td>
</tr>
<tr>
<td></td>
<td>US Virgin</td>
<td></td>
</tr>
<tr>
<td>1 - 169</td>
<td>Islands</td>
<td>Edmunds and Gray (2014)</td>
</tr>
<tr>
<td>30 - 300</td>
<td>Costa Rica</td>
<td>Cortes and Risk (1984)</td>
</tr>
<tr>
<td>3 - 304</td>
<td>Australia</td>
<td>Hopley et al. (1990)</td>
</tr>
<tr>
<td>3 - 357</td>
<td>Australia</td>
<td>Mapstone et al. (1989)</td>
</tr>
<tr>
<td>&lt;10 - &gt;490</td>
<td>Hawaii</td>
<td>DeMartini et al. (2013)</td>
</tr>
<tr>
<td>0.6 - 900</td>
<td>Australia</td>
<td>Marshall and Orr (1931)</td>
</tr>
</tbody>
</table>
Figure B-1: Water-column nutrient (nitrate + nitrite) concentrations in μM (mean ± SE) from three complete experimental blocks. This included twelve unenriched units and twelve nutrient-enriched units, sampled 4 and 23 days following a monthly nutrient pulse (i.e., replacement of fertilizer within experimental unit; see Figure 3-2). Enrichment had a significant positive effect on nutrient concentration ($p = 0.03$), as revealed by a linear mixed effects model, with unit as a random effect (Pinheiro 2012, Team 2013).
Table B-2: Summary of statistical modeling results for main effects and interactions for algal growth and coral growth and survival data. Significance codes for estimated model coefficients: 0 '***' 0.001 *** 0.01 ** 0.05. Blocking was significant only for main effects on *P. rus* growth.

<table>
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<th>Coefficient</th>
<th>P</th>
<th>Signif.</th>
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<td>Coral recruits</td>
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<td>S × N × C</td>
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<td>Caging</td>
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<td>&lt; 0.001</td>
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<td>0.034</td>
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<td></td>
<td>S × N × C</td>
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APPENDIX C
LITERATURE SURVEY AND MATURATION VS. STUDY DURATION FOR BOTTOM-UP VS. TOP-DOWN FIELD EXPERIMENTS

Literature Survey Methods

We surveyed the literature for field experiments that fully crossed herbivore exclusions (using physical barriers; e.g., cages) with nutrient additions. Most of the experiments we surveyed came from the database compiled by and used in Gruner et al. (2008), which covered studies from 1965-2006. We used ISI web of knowledge and search strings including [herbivor* or graz* or consum*] and [resourc* or nutrient* or fertili*]; [top–down and bottom–up and ecolog*] to find additional experiments from 2007-2013. We recorded the experimental plot size used in each experiment, experimental duration, and the focal herbivore being excluded. When the focal herbivore was not reported, we assigned a known dominant herbivore from other studies of the same system. We then searched the literature for empirical estimates of individual movement range and age to sexual maturity for the focal herbivores, or, when this information was not available, that of a close relative (i.e., congener or confamilial). We used the subset of studies (n=38) for which we could find information on both the movement range and age to maturation of the herbivore to create Figure 3-1 & C-1 (references used to create these figures are included below). We report herbivore movement range in surface area (m²). When movement range was reported in linear distance, we calculated the surface area of a circle (m²) with a radius equal to the linear distance, except for studies in freshwater streams, for which we calculated surface area from the measured herbivore movement distance along the stream multiplied by the stream width.
Figure C-1: Turnover time in previous experiments. Here we compare herbivore age to sexual maturity to experimental duration in previous top-down versus bottom-up field experiments (nutrient addition fully crossed with herbivore exclusion) across systems and taxa. The line indicates the 1:1 relationship, and overlapping points were jittered to show all points. In over 70% (27/38) of the studies, herbivore maturation time exceeded experimental duration, and the ratio of experimental duration to herbivore maturation time ranged from 0.010 to 9.9, with a median of 0.14.

**References Used to Create Figure C-1 and 3-1**


Bazterra, M. C., M. F. Alvarez, C. M. Bruschetti, F. J. Hidalgo, M. E. Fanjul, O. Iribarne, and F. Botto. 2013. Factors controlling macroalgae assemblages in a Southwest Atlantic


APPENDIX D
INCORPORATING A TYPE II FUNCTIONAL RESPONSE INTO THE MODEL

In the main text, we evaluated the effects of herbivores on the density of primary producers in the presence of nutrient enrichment. To do so, we assumed herbivores had a Type I functional response. Here, we relax that assumption and show that if herbivores exhibit a Type II functional response, our qualitative results are unaffected: i.e., the equilibrium density of primary producers in enriched plots \( (P^*_{E,+}) \) increases with an increase in the size of the enriched plot \( (S_E) \): i.e., \( \frac{dP^*_{E,+}}{dS_E} > 0 \). This is the same result that we obtained in the main text, but with a Type I functional response (4-8).

Under a Type II functional response, 4-5 and 4-6 change to

\[
\frac{dP_{E,+}}{dt} = r_E P_{E,+} \left(1 - \frac{P_{E,+}}{K_E}\right) - \frac{\alpha}{1 + ahP_{E,+}} H_{E,+} P_{E,+} \quad \text{and} \quad (D-1)
\]

\[
\frac{dP_{E,+,out}}{dt} = r_U P_{E,+,out} \left(1 - \frac{P_{E,+,out}}{K_U}\right) - \frac{\alpha}{1 + ahP_{E,+,out}} H_{E,+ ,out} P_{E,+ ,out}, \quad (D-2)
\]

respectively, where \( h \) is the handling time associated with the consumption of the primary producer (all other parameters remain the same as in the main text). By assuming an ideal free distribution and non-dynamic herbivore populations, we obtain:

\[
r_E S_E \left(1 - \frac{P^*}{K_E}\right) \left(1 + ahP^*\right) + r_U S_U \left(1 - \frac{P^*}{K_U}\right) \left(1 + ahP^*\right) - \alpha N_T = 0, \quad (D-3)
\]

where \( P^* = P^*_{E,+} = \left.P^*_{E,+ ,out}\right| \) and \( S_U = S_T - S_E \). D-3 has the solutions:
\[ P^* = \frac{-ah(r_E S_E + r_U S_U) + \left( \frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U} \right) \pm \sqrt{(ahr_E S_E + ahr_U S_U - r_E S_E - r_U S_U)^2 + 4ah \left( \frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U} \right)(r_E S_E + r_U S_U - \alpha N_T)}}{-2ah \left( \frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U} \right)}. \]

For convenience, we reorganize the square root part to get:

\[ P^* = \frac{-ah(r_E S_E + r_U S_U) + \left( \frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U} \right) \pm \sqrt{(ahr_E S_E + ahr_U S_U - r_E S_E - r_U S_U)^2 + 4ah \left( \frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U} \right)(r_E S_E + r_U S_U - \alpha N_T)}}{-2ah \left( \frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U} \right)}. \]  

(D-4)

For persistence of both the herbivore and primary producer, the growth rate of the primary producer (in the enriched patch and its surrounding habitat) at low density must exceed the consumption by the herbivores: i.e., \( r_E S_E + r_U S_U > \alpha N_T \). As a result, it can be shown that the sum of the terms under the square-root > 0. Thus, the solutions in D-4 are real (and not complex).

Next, we examine how the equilibrium density of primary producers changes with plot size. Thus, we implicitly find the derivative of D-3, and obtain:

\[ \frac{\partial P^*}{\partial S_E} = \frac{(-ahP^* - 1)(\frac{r_U}{K_U} - \frac{r_E}{K_E})P^* + (r_E - r_U)]}{ah(r_E S_E + r_U S_U - \frac{r_E S_E}{K_E} - \frac{r_U S_U}{K_U})(2ahP^* + 1)}. \]

(D-5)

Note that this solution is a function of \( P^* \). By inserting D-4 into D-5, it can be shown that the denominator of D-5 is not equal to 0.
Next, we would like to show that \( \frac{\partial P_+^*}{\partial S_E} > 0 \). However, given the complexity of \( P_+^* \) for a Type II functional response, it is difficult to prove that \( \frac{\partial P_+^*}{\partial S_E} > 0 \). Instead, below we take the opposite approach and prove that all of the conditions required to obtain \( \frac{\partial P_+^*}{\partial S_E} \leq 0 \) cannot occur. Thus, we indirectly prove that \( \frac{\partial P_+^*}{\partial S_E} > 0 \).

To start, recall that \( r_E > r_U, K_E > K_U \), and that \( P^* > 0 \). Note also, that D-5 has the general form \( \frac{\partial P^*}{\partial S_E} = \frac{A}{C} \). Because \( A \) is always <0, we can specify 3 ways to achieve \( \frac{\partial P^*}{\partial S_E} \leq 0 \): 1) \( B = 0 \); 2) \( B > 0 \) and \( C > 0 \), and 3) \( B < 0 \) and \( C < 0 \). We impose these three conditions, solve for \( P^* \) subject to these conditions, and later demonstrate that \( P^* \) cannot take on those values.

1) \( B = 0 \): If \( \left( \frac{r_U}{K_U} - \frac{r_E}{K_E} \right) P^* + (r_E - r_U) = 0 \), then:

\[
P^* = \frac{r_E - r_U}{r_U - r_K} \frac{K_U}{K_E}.
\]

(D-6)

2) \( B > 0 \) and \( C > 0 \): If \( \left( \frac{r_U}{K_U} - \frac{r_E}{K_E} \right) P^* + (r_E - r_U) > 0 \) and \( a h (r_E S_E + r_U S_U) - \left( \frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U} \right) (2 a h P^* + 1) > 0 \), then:

2i) when \( \frac{r_E}{K_E} - \frac{r_U}{K_U} \leq 0 \), B is always >0, so from C>0, we get: \( P^* < \frac{1}{2} \left( \frac{r_E S_E + r_U S_U}{K_E} \right) \left( \frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U} - \frac{1}{a h} \right) \), or

2ii) when \( \frac{r_E}{K_E} - \frac{r_U}{K_U} > 0 \), we get:

\[
P^* < \min \left( \frac{r_E - r_U}{r_U - r_K} \frac{K_U}{K_E}, \frac{1}{2} \left( \frac{r_E S_E + r_U S_U}{K_E} \right) \left( \frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U} - \frac{1}{a h} \right) \right) = \frac{1}{2} \left( \frac{r_E S_E + r_U S_U}{K_E} \right) \left( \frac{r_E S_E}{K_E} + \frac{r_U S_U}{K_U} - \frac{1}{a h} \right).
\]

(D-7)
3) B<0 and C<0: If \((r_E - r_U)P^* + (r_E - r_U) < 0\) and \(\alpha h(r_E S_E + r_U S_U) - (r_E S_E + r_U S_U)2\alpha hP^* + 1 < 0\), then from B<0, we get that:

- 3i) if \(\frac{r_E}{K_E} - \frac{r_U}{K_U} > 0\), then \(P^* > \frac{r_E - r_U}{K_E - K_U}\);
- 3ii) if \(\frac{r_E}{K_E} - \frac{r_U}{K_U} < 0\), then \(P^* < \frac{r_E - r_U}{K_E - K_U} < 0\), which cannot be true; and
- 3iii) if \(\frac{r_E}{K_E} - \frac{r_U}{K_U} = 0\), then B<0 cannot be satisfied; and from C<0, we get \(P^* > \frac{1}{2} \left( \frac{r_E S_E + r_U S_U}{K_E - K_U} \right) - \frac{1}{\alpha h}\).

Because there is only one possible inequality from B<0 (3i-3iii) that can be true (inequality 3i), we combine this inequality with that from C<0 to yield the third possible condition for \(\frac{\partial P^*}{\partial S_E} \leq 0\) as:

\[
P^* > \max \left( \frac{r_E - r_U}{K_E - K_U}, \frac{1}{2} \left( \frac{r_E S_E + r_U S_U}{r_E S_E + r_U S_U} - \frac{1}{\alpha h} \right) \right) = \frac{r_E - r_U}{K_E - K_U} \text{ with } \frac{r_E}{K_E} - \frac{r_U}{K_U} > 0.
\]

Equations D-6, D-7, and D-8 define three possible conditions on \(P^*\), and at least one must be satisfied to obtain \(\frac{\partial P^*}{\partial S_E} \leq 0\). We next ask if these conditions on \(P^*\) are possible, and below, we show that they are not. Therefore, we prove that \(\frac{\partial P^*}{\partial S_E} > 0\). To do this, we use D-4 to define the range of possible values of \(P^*\). There are two solutions to D-4.

Let’s start with one of those solutions:
\[ P_1^* = \frac{-ah(r_{ES} + r_{U}S) + \left(\frac{r_{ES}}{K_E} + \frac{r_{US}}{K_U}\right) + \sqrt{(ahr_{ES} + ahr_{US} + \frac{r_{ES}}{K_E} + \frac{r_{US}}{K_U})^2 - 4ah \frac{r_{ES}}{K_E} aN_T - 4ah \frac{r_{US}}{K_U} aN_T}}{2ah \left(\frac{r_{ES}}{K_E} + \frac{r_{US}}{K_U}\right)}. \]  

Because \(-4ah \frac{r_{ES}}{K_E} aN_T - 4ah \frac{r_{US}}{K_U} aN_T < 0\), we can re-express D-9 as:

\[ P_1^* > \frac{ah(r_{ES} + r_{US}) - \left(\frac{r_{ES}}{K_E} + \frac{r_{US}}{K_U}\right) - \sqrt{(ahr_{ES} + ahr_{US} - \frac{r_{ES}}{K_E} - \frac{r_{US}}{K_U})^2 - 2ah \left(\frac{r_{ES}}{K_E} + \frac{r_{US}}{K_U}\right)}}{2ah \left(\frac{r_{ES}}{K_E} + \frac{r_{US}}{K_U}\right)} = -\frac{1}{ah}. \]  

Alternatively, because \(r_{ES} + r_{US} > aN_T\), we can also re-express D-9 as:

\[ P_1^* < \frac{ah(r_{ES} + r_{US}) - \left(\frac{r_{ES}}{K_E} + \frac{r_{US}}{K_U}\right) - \sqrt{(ahr_{ES} + ahr_{US} - \frac{r_{ES}}{K_E} - \frac{r_{US}}{K_U})^2 - 2ah \left(\frac{r_{ES}}{K_E} + \frac{r_{US}}{K_U}\right)}}{2ah \left(\frac{r_{ES}}{K_E} + \frac{r_{US}}{K_U}\right)}. \]  

If \(ahr_{ES} + ahr_{US} - \frac{r_{ES}}{K_E} - \frac{r_{US}}{K_U} \geq 0\), then:

\[ P_1^* < 0. \]  

On the other hand, if \(ahr_{ES} + ahr_{US} - \frac{r_{ES}}{K_E} - \frac{r_{US}}{K_U} < 0\), then:

\[ P_1^* < \frac{ah(r_{ES} + r_{US}) - \left(\frac{r_{ES}}{K_E} + \frac{r_{US}}{K_U}\right)}{ah \left(\frac{r_{ES}}{K_E} + \frac{r_{US}}{K_U}\right)} < 0. \]  

Equations D-10 through D-13 define the range of \(P_1^*\), and this range is \(-\frac{1}{ah} < P_1^* < 0\). Thus, the solution to \(P_1^*\) is not possible (because \(P^*\) cannot be less than zero).

Next, we turn to the second solution:
\[ P_2^* = \frac{-ah(r_{ES} + r_{US}) + \left( \frac{r_{ES}}{K_E} + \frac{r_{US}}{K_U} \right) - \sqrt{(ahr_{ES} + ahr_{US} + \frac{r_{ES}^2}{K_E} + \frac{r_{US}^2}{K_U})^2 - 4ah \frac{r_{ES}^2}{K_E} aN_T - 4ah \frac{r_{US}^2}{K_U} aN_T}}{-2ah \left( \frac{r_{ES}}{K_E} + \frac{r_{US}}{K_U} \right)}. \] (D-14)

Because \(-4ah \frac{r_{ES}}{K_E} aN_T - 4ah \frac{r_{US}}{K_U} aN_T < 0\), we can re-express D-14 as:

\[ P_2^* < \frac{-ah(r_{ES} + r_{US}) + \left( \frac{r_{ES}}{K_E} + \frac{r_{US}}{K_U} \right) - \sqrt{(ahr_{ES} + ahr_{US} + \frac{r_{ES}^2}{K_E} + \frac{r_{US}^2}{K_U})^2}}{-2ah \left( \frac{r_{ES}}{K_E} + \frac{r_{US}}{K_U} \right)} = \frac{r_{ES} + r_{US}}{\frac{r_{ES}}{K_E} + \frac{r_{US}}{K_U}}. \] (D-15)

Alternatively, because \(r_{ES} + r_{US} > aN_T\) we can re-express D-14 as:

\[ P_2^* > \frac{-ah(r_{ES} + r_{US}) + \left( \frac{r_{ES}}{K_E} + \frac{r_{US}}{K_U} \right) - \sqrt{(ahr_{ES} + ahr_{US} - \frac{r_{ES}^2}{K_E} - \frac{r_{US}^2}{K_U})^2}}{-2ah \left( \frac{r_{ES}}{K_E} + \frac{r_{US}}{K_U} \right)} = \frac{r_{ES} + r_{US}}{\frac{r_{ES}}{K_E} + \frac{r_{US}}{K_U}}. \] (D-16)

If \(ahr_{ES} + ahr_{US} - \frac{r_{ES}^2}{K_E} - \frac{r_{US}^2}{K_U} \geq 0\), D-16 becomes

\[ P_2^* > \frac{r_{ES} + r_{US}}{\frac{r_{ES}}{K_E} + \frac{r_{US}}{K_U}} - \frac{1}{ah}. \] (D-17)

Alternatively, if \(ahr_{ES} + ahr_{US} - \frac{r_{ES}^2}{K_E} - \frac{r_{US}^2}{K_U} < 0\), D-16 becomes

\[ P_2^* > 0. \] (D-18)

By combining condition D-15 and either D-17 or D-18, we get:

\[ \max \left( \frac{r_{ES} + r_{US}}{\frac{r_{ES}}{K_E} + \frac{r_{US}}{K_U}} - \frac{1}{ah}, 0 \right) < P_2^* < \frac{r_{ES} + r_{US}}{\frac{r_{ES}}{K_E} + \frac{r_{US}}{K_U}}. \] (D-19)
Finally, we will look at the three conditions, of which one must be met for \( \frac{\partial P^*}{\partial S_E} \leq 0 \), and we will show that each condition cannot be satisfied, beginning with condition 1). Under D-6:

if \( \frac{r_E}{K_E} - \frac{r_U}{K_U} > 0 \), then from D-19, we get \( P^* < \frac{r_E S_E + r_U S_U}{K_E + \frac{r_E S_E + r_U S_U}{K_U}} < \frac{r_E - r_U}{K_E - K_U} \), which violates condition 1);

if \( \frac{r_E}{K_E} - \frac{r_U}{K_U} < 0 \), then \( P^* < 0 \), which cannot be true; and

if \( \frac{r_E}{K_E} - \frac{r_U}{K_U} = 0 \), then condition 1) becomes \( r_E - r_U = 0 \), which also cannot be true.

Next, we show that condition 2) cannot be satisfied. Under D-7,

if \( \frac{r_E S_E + r_U S_U}{K_E + \frac{r_E S_E + r_U S_U}{K_U}} - \frac{1}{ah} > 0 \), then from D-19, we get \( P^* > \frac{r_E S_E + r_U S_U}{K_E + \frac{r_E S_E + r_U S_U}{K_U}} - \frac{1}{ah} > \frac{1}{2} \left( \frac{r_E S_E + r_U S_U}{K_E + \frac{r_E S_E + r_U S_U}{K_U}} - \frac{1}{ah} \right) \), which violates condition 2);

and

if \( \frac{r_E S_E + r_U S_U}{K_E + \frac{r_E S_E + r_U S_U}{K_U}} - \frac{1}{ah} \leq 0 \), then \( P^* < 0 \), which cannot be true.

Finally, we show that condition 3) cannot be satisfied:

Because \( \frac{r_E}{K_E} - \frac{r_U}{K_U} > 0 \), from D-19, we get \( P^* < \frac{r_E S_E + r_U S_U}{K_E + \frac{r_E S_E + r_U S_U}{K_U}} < \frac{r_E - r_U}{K_E - K_U} \), which violates D-8.

In summary, none of the complete set of three possible conditions required for \( \frac{\partial P^*}{\partial S_E} \) to be less than or equal to zero can be satisfied. We have therefore shown that \( \frac{\partial P^*}{\partial S_E} > 0 \). Thus, herbivores with a Type II functional response should
respond in a qualitatively similar way to a change in experimental scale as herbivores with a Type I functional response, as we discuss in the main text.
APPENDIX E
GROUND-TRUTHING FOR LANDSCAPE SURVEY AND EXPERIMENTAL UNIT

We used ground-truthing to verify the accuracy of the metrics we extracted (using ArcGIS software) from our landscape survey map. At each site in the field, we used transect tape with a fixed 10 m radius to estimate the proportion of benthic surface area within 10 m of each site that was covered in structural refuge habitat (defined as any structure ≥ 0.3 m in height; i.e., short structures like rubble piles were excluded). We compared our field-measured values to our map-extracted values, using a linear regression, which verified that our map values explained most of the variation in structural refuge habitat cover that we observed directly in the field ($r^2 = 0.93; p < 0.0001$; Figure E-1).
Figure E-1. Comparison of field vs. map measurements of relative cover of structural refuge habitat in the area within a 10 m radius of each survey site.
Figure E-2: A foraging event from one of our experimental units, captured in one of our videos (*Zebrasoma scopas* biting a strand of *Acanthophora spicifera*).
APPENDIX F
STOCHASTIC MODEL OF ALGAL LOSS

To model the algal predatory process, we used a death process, which is a well-known continuous time and discrete states Markov Process (Allen 2010). Let \( N(t) \) be the size (in integers) of the algae offered at time \( t \) for a given species of algae at a given site. We denote the initial amount of algae \( N(0) \) as \( m \). Heuristically, the death process can be described as a process wherein starting with an initial algal size, algae is being lost one unit at a time, at a rate \( \mu_n \) and at random time intervals. The death rate, which is our object of inference, is denoted as \( \mu_n \). The \( n \) subscript emphasizes the fact that this rate of algal loss can be specified as any arbitrary function of the total amount of algae present \( n \). We note in passing that here we use the convention that random variables are written with capital letters and realized values as lower case letters. Hence, \( n(t) \) denotes the observed and remaining number of algae units at time \( t \) and thus, one realization of the random variable \( N(t) \).

The death process can be formulated so that it embodies a suite of plausible biological hypotheses regarding the unfolding of the algal herbivory process. Not only can the algae loss rate be specified as a function of the total amount of algae present, but also it can be written in standard regression format as a function of one or more discrete or categorical variables. The categorical variable of interest here was the patch quality (high and low) and the continuous variable of interest was the distance of the experimental cinder block from the reef. Using standard stochastic process results one may arrive at an analytical expression for the probability that at any given time \( t \), the algae is of size \( N(t) = n(t) \) as a function of the death rate, which is in turn modulated by
the categorical and quantitative variables of interest. We denote the \( \Pr(N(t) = n(t)) \) as \( p_n(t) \). The resulting expression for \( p_n(t) \) under each biological hypothesis served as the direct link that connected the observations with the proposed probabilistic model. In what follows, we briefly review the general derivation of this probability and explain how we used it to make statistical inferences regarding the nature of the algal loss rate under each experimental setting.

The general death process formulation applied to our case assumes that there exists an arbitrarily small amount of time \( \Delta t \) during which at most one unit of algae can be lost, that the probability of losing a single algae unit during this time interval is \( \mu_n(\Delta t) \) and that the probability that no loss occurs is \( 1 - \mu_n(\Delta t) \). Finally, it also assumes that the probability of any other event is negligible, i.e., that only “deaths” (algae losses and not gains) can be observed. Accordingly,

\[
\frac{p_n(t + \Delta t)}{p_n(t)} = \left( \frac{\Delta t}{1 - \mu_n(\Delta t)} \right) \mu_n(\Delta t) + \left( 1 - \mu_n(\Delta t) \right) \frac{p_{n+1}(t)}{p_n(t)}. \tag{F-1}
\]

As \( \Delta t \to 0 \) and after a simple manipulation, this equation tends to the following system of Ordinary Differential Equations (ODEs):

\[
\frac{dp_{n-1}(t)}{dt} = \mu_n p_n(t) - \mu_{n-1} p_{n-1}(t),
\]

where \( n = m, m-1, m-2, \ldots, 2, 1, 0 \). If we let for example \( \mu_n = \mu n \) then the stochastic model has as its deterministic counterpart the ODE model for algae size.
\[
\frac{dn}{dt} = -\mu n. \quad \text{Assuming this form of death (loss) rate and taking into account the initial conditions } p_m(0) = 1, p_n(t) = 0 \text{ if } n > m \text{ or } n < 0 \text{ the above system of ODEs can be solved (Allen 2010) to yield}
\]

\[
p_n(t) = \left( \frac{m}{n} \right) (e^{-\mu})^n (1 - e^{-\mu})^{m-n}. \tag{F-2}
\]

In other words, the amount of algae at time \( t \), \( N(t) \) is binomially distributed with probability of success \( e^{-\mu} \). This quantity denotes the probability that no algae loss occurs during time the time period \((0,t)\). According to the properties of the Binomial distribution, the time-dependent average algae size is given by \( \mathbb{E}[N(t)] = me^{-\mu} \) and its variance by \( \mathbb{V}[N(t)] = me^{-\mu} \left( 1 - e^{-\mu} \right) \). Hence, on average, the process behaves like its deterministic counterpart, an exponentially decaying total algae size. Its variability, however, is modulated by both, the death (loss) rate and the amount of elapsed time.

To solve the system of ODEs above, one arrives first at an expression for the (random) total amount of loss since the beginning of the process. This amount of loss, denoted \( X(t) \) from here on, turns out to be Binomially distributed with parameters \( m \) and \( 1 - e^{-\mu} \) from which F-2 follows.

The basic data unit consists of the observed pairs (algae size) and (time):

\[
(n_0, t_0), (n_1, t_1), (n_2, t_2), \ldots, (n_q, t_q),
\]

where \( q + 1 \) is the total number of observed time points. Regarding each observation as the initial condition for the next one, from F-2 it follows that
Now, using the Markov property and letting $\tau_i = t_i - t_{i-1}$ to simplify notation, the joint probability of the observations or likelihood function for the observations

$$\Pr(N(t_i) = n_i \mid N(t_{i-1}) = n_{i-1}) = \left( \frac{n_{i-1}}{n_i} \right) \left( e^{-\mu(t_{i-1})} \right)^{n_i} \left( 1 - e^{-\mu(t_{i-1})} \right)^{n_{i-1} - n_i}$$

$$= f(n_i, t_i - t_{i-1} \mid n_{i-1}).$$

This formulation however assumes that the per-algae unit loss rate $\mu$ is constant.

Hence, to incorporate our different biological hypotheses regarding the factors influencing the death rate we wrote $\mu$ as a log-linear model of the categorical and continuous variables of interest, i.e., $\log(\mu) = \text{linear regression model}$. The different types of linear regression models we used are summarized in Tables G-2. Then, maximizing the likelihood function (F-3) with these regression models in place of $\mu$ yields estimates of the effects of each of the hypothesized factors.

The assumption that $\mu_n = \mu n$ embodies the specific hypothesis that the loss rate is proportional to the existing amount of algae. If it is assumed that $\mu_n = \mu$, a constant independent of the current amount of algae, then solving the above system of equations one finds that the random amount loss during a time period $\tau$, $X(\tau)$ is Poisson distributed with mean $\mu \tau$, in which case the likelihood function equivalent to F-3 is
simply written as the product of Poisson probability mass functions evaluated at the amount of loss during each time interval. Here again, the role of the experimental conditions can be tested using the likelihood function by maximizing it after writing as a log-linear regression model.

Finally, to compare the relative merit of every model we computed Akaike’s Information Criterion (AIC). Using this information theoretic framework, the rule is to deem as the best model the one with the lowest AIC value. Confidence intervals for all the model parameters were obtained using Parametric Bootstrapping, which involved simulation of 100 datasets and estimation under each considered model.
APPENDIX G
STATISTICAL MODEL SUMMARIES FOR ALGAL LOSS AND HERBIVORE TRAITS

Table G-1: Statistical model fitting summary (AIC values reported: lower value = better fit to data) from our field survey of herbivory on *Acanthophora spicifera*. Here “prop.” represents proportion of coverage over the host reef boulder for patch-level predictors, or the proportion of surface area covered by structural refuge habitat (reef) out of the total surface area within either a ring or a circular buffer centered at each site. We denoted whether each modeled algal loss rate was based on a binomial or Poisson probability distribution (see Methods and Supplement for more details on statistical modeling). The best-fit model is in bold.

<table>
<thead>
<tr>
<th>Predictor variable</th>
<th>Scale of predictor</th>
<th>Prob. dist.</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>none (null model)</td>
<td>NA</td>
<td>binomial</td>
<td>28,397.50</td>
</tr>
<tr>
<td>prop. damselfish territory</td>
<td>patch</td>
<td>binomial</td>
<td>25,277.41</td>
</tr>
<tr>
<td>depth</td>
<td>patch</td>
<td>binomial</td>
<td>27,130.96</td>
</tr>
<tr>
<td>number of urchins</td>
<td>patch</td>
<td>binomial</td>
<td>26,370.87</td>
</tr>
<tr>
<td>number of vermetids</td>
<td>patch</td>
<td>binomial</td>
<td>27,088.54</td>
</tr>
<tr>
<td>prop. live massive Porites coral</td>
<td>patch</td>
<td>binomial</td>
<td>26,950.60</td>
</tr>
<tr>
<td>prop. macroalgae</td>
<td>patch</td>
<td>binomial</td>
<td>26,406.03</td>
</tr>
<tr>
<td>prop. live Porites rus coral</td>
<td>patch</td>
<td>binomial</td>
<td>26,781.59</td>
</tr>
<tr>
<td>prop. reef 10-15 m</td>
<td>landscape</td>
<td>binomial</td>
<td>24,230.17</td>
</tr>
<tr>
<td>prop. reef 15-25 m</td>
<td>landscape</td>
<td>binomial</td>
<td>24,101.54</td>
</tr>
<tr>
<td>prop. reef 25-35 m</td>
<td>landscape</td>
<td>binomial</td>
<td>24,592.77</td>
</tr>
<tr>
<td>prop. reef 35-50 m</td>
<td>landscape</td>
<td>binomial</td>
<td>24,101.54</td>
</tr>
<tr>
<td>prop. reef ≤ 10 m</td>
<td>landscape</td>
<td>binomial</td>
<td>24,349.00</td>
</tr>
<tr>
<td>prop. reef ≤ 25 m</td>
<td>landscape</td>
<td>binomial</td>
<td>24,063.48</td>
</tr>
<tr>
<td>prop. reef ≤ 35 m</td>
<td>landscape</td>
<td>binomial</td>
<td>24,216.85</td>
</tr>
<tr>
<td>prop. reef ≤ 50 m</td>
<td>landscape</td>
<td>binomial</td>
<td>24,625.51</td>
</tr>
<tr>
<td>distance from contiguous reef</td>
<td>landscape</td>
<td>binomial</td>
<td><strong>20,452.63</strong></td>
</tr>
<tr>
<td>none (null model)</td>
<td>NA</td>
<td>Poisson</td>
<td>42,974.82</td>
</tr>
<tr>
<td>prop. damselfish territory</td>
<td>patch</td>
<td>Poisson</td>
<td>42,279.65</td>
</tr>
<tr>
<td>depth</td>
<td>patch</td>
<td>Poisson</td>
<td>42,373.93</td>
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Table G-1. Continued

<table>
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<th>Predictor variable</th>
<th>Scale of predictor</th>
<th>Prob. dist.</th>
<th>AIC</th>
</tr>
</thead>
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<tr>
<td>number of urchins</td>
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<td>Poisson</td>
<td>42,373.03</td>
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<td>prop. live massive Porites coral</td>
<td>patch</td>
<td>Poisson</td>
<td>42,363.26</td>
</tr>
<tr>
<td>prop. macroalgae</td>
<td>patch</td>
<td>Poisson</td>
<td>42,361.48</td>
</tr>
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<td>prop. live Porites rus coral</td>
<td>patch</td>
<td>Poisson</td>
<td>42,367.32</td>
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<td>landscape</td>
<td>Poisson</td>
<td>42,840.03</td>
</tr>
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<td>Poisson</td>
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</tr>
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<td>Poisson</td>
<td>42,892.10</td>
</tr>
<tr>
<td>prop. reef 35-50 m</td>
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<td>Poisson</td>
<td>42,841.71</td>
</tr>
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<td>Poisson</td>
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<td>Poisson</td>
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<td>Poisson</td>
<td>42,598.47</td>
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</table>
Table G-2: Statistical model fitting summary from our field experiment for all five types of algae, including four species of macroalgae and algal turf. We denoted whether each model included or excluded a blocking term for experimental trial and whether each modeled algal loss rate was based on a binomial or Poisson probability distribution (see Methods and Supplement for more details on statistical modeling). Best-fit models for each algal type are in bold.

<table>
<thead>
<tr>
<th>Model</th>
<th>Type</th>
<th>Block</th>
<th>Prob. dist.</th>
<th>A. spicifera</th>
<th>A. rhodantha</th>
<th>A. taxiformis</th>
<th>S. pacificum</th>
<th>algal turf</th>
</tr>
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<tbody>
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<td>$y = \beta_0$</td>
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<td>no</td>
<td>binomial</td>
<td>4012.11</td>
<td>2181.04</td>
<td>1760.24</td>
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<td>89.04</td>
<td>339.72</td>
<td>554.35</td>
<td><strong>127.77</strong></td>
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<td>1995.13</td>
<td>1624.99</td>
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<td>3670.79</td>
<td>1064.15</td>
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<td>1926.20</td>
<td>1628.05</td>
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<td>1016.24</td>
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<tr>
<td>Model</td>
<td>Type</td>
<td>Block</td>
<td>Prob. dist.</td>
<td>A. spicifera</td>
<td>A. rhodantha</td>
<td>A. taxiformis</td>
<td>S. pacificum</td>
<td>algal turf</td>
</tr>
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<td>--------------</td>
<td>--------------</td>
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<td>--------------</td>
<td>------------</td>
</tr>
<tr>
<td>$y = \beta_{\text{trial}} + \beta_{\text{dist}} \times \text{dist} + \beta_{\text{qual}} \times \text{qual}$</td>
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<td>130.95</td>
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<td>1129.67</td>
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<td>73.03</td>
<td>279.84</td>
<td>396.41</td>
<td>140.96</td>
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<td>no</td>
<td>binomial</td>
<td>3902.27</td>
<td>1909.91</td>
<td>1616.90</td>
<td>3637.87</td>
<td>1017.77</td>
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<td>yes</td>
<td>binomial</td>
<td>433.61</td>
<td>70.73</td>
<td>278.80</td>
<td>511.14</td>
<td>132.93</td>
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<td>yes</td>
<td>Poisson</td>
<td>4944.23</td>
<td>1670.72</td>
<td>1464.43</td>
<td>3418.00</td>
<td>1131.39</td>
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<td>yes</td>
<td>Poisson</td>
<td>515.50</td>
<td>66.48</td>
<td>281.83</td>
<td>397.97</td>
<td>159.61</td>
<td></td>
</tr>
</tbody>
</table>
Table G-3: Statistical model fitting summary (AIC values reported: lower value = better fit to data) from our field experiment for three observed traits of herbivores. Measured traits for herbivores that visited our experimental sites included individual bite rate, total foraging time (sum of all foraging times per site), and body length. Each model was a mixed effects model, in which study location was treated as a random effect. Best-fit models for each forager response are in bold.

<table>
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<tr>
<th>Response</th>
<th>Statistical models</th>
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</thead>
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<td>$y = \beta_{\text{location}}$</td>
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<tr>
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</tr>
<tr>
<td>Individual bite rate (bites·sec$^{-1}$)</td>
<td>1215.89 1194.77</td>
</tr>
<tr>
<td>Total foraging time (sec)</td>
<td>446.07 424.63 437.39 415.86</td>
</tr>
<tr>
<td>Forager body length (cm)</td>
<td>3048.24 3015.46 3050.5 3018.85</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Response</th>
<th>$y = \beta_{\text{location}} + \beta_{\text{distance}} \cdot \text{distance}$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>y = $\beta_{\text{location}} + \beta_{\text{density}} \cdot \text{density}$</td>
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<tr>
<td></td>
<td>$y = \beta_{\text{location}} + \beta_{\text{distance}} \cdot \text{distance} + \beta_{\text{density}} \cdot \text{density}$</td>
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<tr>
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<td>1215.89 1194.77</td>
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<th>Response</th>
<th>$y = \beta_{\text{location}} + \beta_{\text{distance}} \cdot \text{distance} + \beta_{\text{density}} \cdot \text{density} + \beta_{\text{dist.} \cdot \text{density}} \cdot \text{dist.} \cdot \text{density}$</th>
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<tr>
<td>Individual bite rate (bites·sec$^{-1}$)</td>
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BIOGRAPHICAL SKETCH

Michael grew up in Humble, Texas and attended the University of Texas at Austin, where he was named a Dean’s Honored Graduate when he received his BS in biology in 2008. He received his Ph.D. from the Department of Biology at the University of Florida in the fall of 2015.