

Unity through nonlinearity: a unimodal coral–nutrient interaction

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Abstract. The magnitude and direction of biological effects of environmental disturbances can vary considerably, especially among studies that use presence/absence manipulations. Because nonlinearities (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., two-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.

Key words: coral reef; environmental stressor; eutrophication; heterogeneous response; hump-shaped relationship; nutrient enrichment; *Porites*.

INTRODUCTION

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 (Fig. 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 overarching 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

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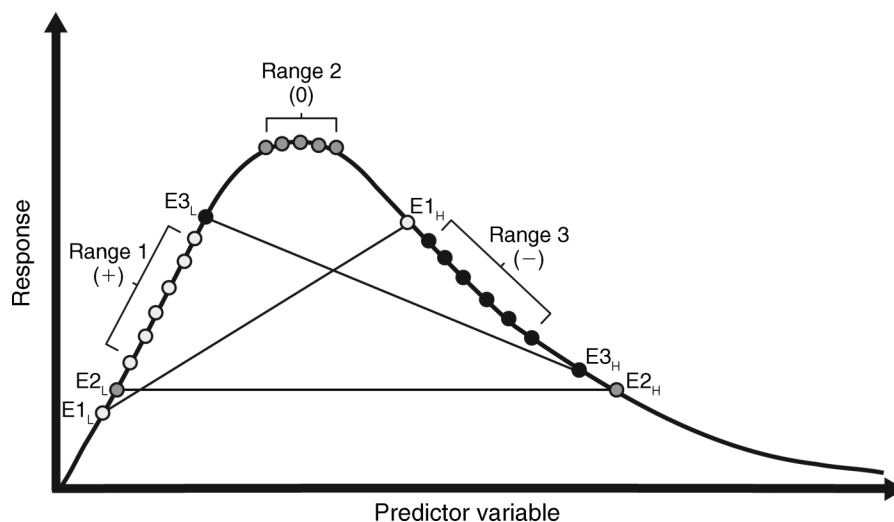


FIG. 1. Conceptual diagram illustrating disparities that can arise when a nonlinear (in this case unimodal) underlying relationship exists, and investigators examine either few levels or a limited range of the predictor variable of interest. Each point on the curve can be thought of as a hypothetical 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 exceeds two, the use of a narrow range of a predictor variable can yield positive (+), neutral (0), or negative (–) effects (labeled as Range 1, 2, and 3, respectively).

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 (Fig. 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 (Fig. 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 (Appendix). Previous studies examining the effect of nutrient enrichment on corals have tested few (most often two) 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). 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 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.

MATERIALS AND METHODS

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 *Porites* (a complex comprised of *Porites lutea* and *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 seven nutrient-enrichment treatments, and each coral was secured to the head of a nylon bolt using Reef Glue gel (Boston Aqua, Boston, Massachusetts, 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 eight 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 south-southeast 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 (see Plate 1). 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 two to three 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, Marysville, Ohio, 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 (P. Fong, *personal communication*). Fertilizer was added on day 1 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 (P. Fong, *personal communication*), 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 NO_x) concentrations at the University of Florida/IFAS Analytical Services Laboratories (Gainesville, Florida, USA). 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 et al. 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:

$$C = \phi(F + b)e^{-\sigma(F+b)} \quad (1)$$

where C is coral growth rate (mg·cm⁻²·d⁻¹), ϕ 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 σ 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 Eq. 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 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 1). Dissolved inorganic nitrogen, NH₃ + NO_x, in the 125-g fertilizer treatment (5.8 ± 1.1 μmol/L [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 μmol/L at a site just inshore from the study reef (data *available online*).² The concentration of nitrates and nitrites (NO_x) from the 0-g fertilizer treatment (0.66 ± 0.025 μmol/L) was similar

² <http://metacat.lternet.edu/knb/metacat/knb-lter-mcr.1034.5/lter>

TABLE 1. Summary of the effectiveness of fertilizer treatments.

Measurement and addition	Day	<i>N</i>	Treatments (g)	Slope	L. ratio	<i>P</i>
Fertilizer loss (g)						
1	1–14	14	all	0.22	47.83	<0.0001
2	15–28	55	all	0.22	267.50	<0.0001
NH ₃ (μM)						
1	5	55	all	0.026	38.96	<0.0001
2	19	15	25, 125	0.023	1.28	0.26
2	24	15	25, 125	0.022	4.35	0.037
NO _x (μM)						
1	5	55	all	0.0067	38.01	<0.0001
2	19	15	25, 125	0.0051	0.091	0.76
2	24	15	25, 125	0.0056	4.55	0.033

Notes: 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; NH₃ and NO_x concentrations are based on water samples collected from all or a subset of treatments.

to the ambient levels measured annually from nearby sites (NO_x = 0.57 ± 0.085 μmol/L; see footnote 2), 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 (Fig. 2). The Ricker model (Eq. 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 (ϕ = 0.070 ± 0.016) and scaling exponent (σ = 0.014 ± 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 (Fig. 2).

DISCUSSION

Regression-based approaches can allow us to better understand the nature of ecological processes that yield nonlinear 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

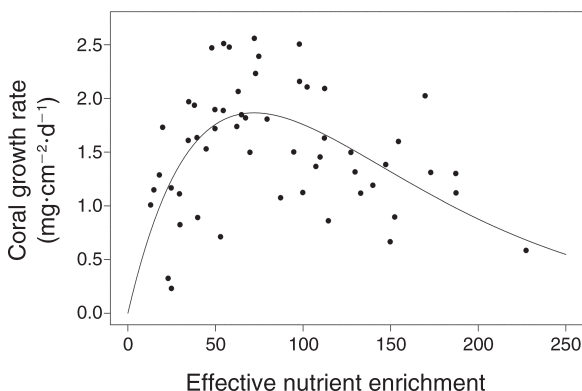


FIG. 2. Coral growth rate across effective nutrient enrichment (fertilizer treatment (in grams) adjusted by the blocking term; $F + b$ in Eq. 1) over the full 28-day experiment (each point represents an individual juvenile *Porites* coral colony, *N* = 55 colonies). The unimodal model (black line) was 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).



PLATE 1. The experimental unit in the field, consisting of a juvenile *Porites* coral glued to a nylon bolt and fixed to a plastic grate above the nutrient-diffusing cup (not pictured). The unit was protected from coral predators using a 2.5-cm-mesh galvanized steel cage. Photo credit: M. A. Gil.

the growth rate of an organism is optimized at an intermediate nutrient intake (Fig. 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.

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SUPPLEMENTAL MATERIAL

Appendix

Collection of coral growth–nutrient studies showing heterogeneous interactions using a variety of methods ([Ecological Archives E094-169-A1](#)).

Supplement

R code used to run mixed-effects model comparisons ([Ecological Archives E094-169-S1](#)).