

Thresholds of ecosystem response to nutrient enrichment from fish aggregations

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Abstract. Biogeochemical hotspots can be driven by aggregations of animals, via excretion, that provide a concentrated source of limiting nutrients for primary producers. In a subtropical seagrass ecosystem, we characterized thresholds of ecological change associated with such hotspots surrounding artificial reef habitats. We deployed reefs of three sizes to aggregate fishes at different densities (and thus different levels of nutrient supply via excretion) and examined seagrass characteristics that reflect ecosystem processes. Responses varied as a function of reef size, with higher fish densities (on larger reefs) associated with more distinct ecological thresholds. For example, adjacent to larger reefs, the percentage of P content (%P) of seagrass (*Thalassia testudinum*) blades was significantly higher than background concentrations; fish densities on smaller reefs were insufficient to support sharp transitions in %P. Blade height was the only variable characterized by thresholds adjacent to smaller reefs, but lower fish densities (and hence, nutrient input) on smaller reefs were not sufficient for luxury nutrient storage by seagrass. Identifying such complexities in ecological thresholds is crucial for characterizing the extent to which biogeochemical hotspots may influence ecosystem function at a landscape scale.

Key words: artificial reefs; bottom-up control; consumer-mediated nutrient supply; facilitation; fish aggregations; long-term nutrient enrichment; seagrass ecosystems; *Thalassia testudinum*.

INTRODUCTION

A biogeochemical hot spot is a specific form of spatial heterogeneity represented by a patch of intensified biogeochemical reaction rates (McClain et al. 2003). One potential driver of such hotspots is aggregations of animals that provide limiting nutrients for primary producers (McNaughton et al. 1988, McIntyre et al. 2008). For example, ungulates in the Serengeti maintain areas of substantially higher grass productivity through excretion and egestion (McNaughton et al. 1988). Boundaries of such hotspots are easily defined when biological, hydrological, and geological gradients coincide (Post et al. 2007). For instance, riffles and runs in rivers support different fish assemblages, and these geomorphic features can be used to predict hotspots of ecosystem function (McIntyre et al. 2008). When boundaries are less well defined, and gradients of

ecosystem function are continuous, more nuanced approaches are necessary to delineate thresholds of change that define the spatial extent of hotspots (McClain et al. 2003).

Hotspots driven by aggregations of animals are especially likely in oligotrophic ecosystems where other sources of nutrient input are low relative to animal excretion (McIntyre et al. 2008). Subtropical and tropical seagrass beds are representative of such oligotrophic systems, where relatively small increases in nutrient input can alter primary producer community structure, nutrient limitation regimes, and rates of production (Lapointe et al. 1994, Fourqurean et al. 2001, Layman et al. 2011, Allgeier et al. 2013). For example, localized hotspots of seagrass productivity around bird perches in Florida Bay are driven by concentrated nutrient input from guano (Powell et al. 1991).

In the present study, we characterized thresholds of ecosystem change associated with biogeochemical hotspots that result from dense fish aggregations. We take advantage of a long-term experiment (~2.5 years) with

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artificial reef habitats constructed in a shallow seagrass ecosystem. In a spatially explicit fashion, we identified the presence of thresholds, i.e., points at which there is an abrupt change in an ecological property such that small changes in an environmental driver produce large changes in ecosystem response (Groffman et al. 2006). In this case, small increases in distance away from artificial reef habitats (which serve to aggregate fishes) may be related to markedly different ecosystem responses because of sharp gradients in nutrients supplied by the fishes (the underlying ecological driver). In doing so, we provide an example of how basic natural history of particular species and ecosystems can be used to characterize thresholds of ecological change.

METHODS

Artificial reefs are increasingly used to enhance fisheries production as part of coastal conservation and management strategies, particularly in structure-limited environments (Bohnsack and Sutherland 1985, do Carmo et al. 2011). An artificial reef is defined as any structure (e.g., reef ball, tree stump, and so on) that is added to the benthic environment, often serving to aggregate fishes at high densities (Bohnsack 1989, Carr and Hixon 1997). Artificial patch reefs have proved to be particularly important experimental tools because they mimic the habitat provided by natural patch reefs, yet provide units easier to create and manipulate (Hixon and Beets 1989, Connell 1997). Fish communities on artificial patch reefs have been observed to be similar to those on natural patch reefs in the Bahamas (Alevizon 2002) and thus can be used to mimic natural population-, community-, and ecosystem-level dynamics. In this study, reef sites were created at least 100 m apart to minimize among-reef movements of more transient fish species (Hixon and Carr 1997). Our study site was a large bay on Abaco Island, Bahamas, with the dominant vegetation being turtle grass, *Thalassia testudinum* (Yeager et al. 2011).

Two a priori-designated comparisons comprise the base study design. First, we were interested in effects of fish density on characteristics of seagrass beds with relatively sparse initial seagrass cover (mean seagrass cover < 20% surrounding the selected experimental sites; see Yeager et al. 2011). Fifteen sites were chosen, and treatments (reef size) were randomly assigned to each. Since more fishes are found on larger artificial reef habitats, and fish density is positively correlated with nutrient supply (Allgeier et al. 2013), we constructed reefs of three sizes: 40-block reefs (termed “40 Low”, $n = 5$, $\sim 1.2 \text{ m}^2$ at base and $\sim 1.2 \text{ m}$ tall; see Fig. 1), 10-block reefs ($n = 5$, $\sim 0.75 \text{ m}^2$ at base and $\sim 0.40 \text{ m}$ tall) and 0-block sites for controls ($n = 5$). All of these experimental treatments, including controls, are referred to as “reefs” herein. Second, we wanted to examine whether initial seagrass characteristics (e.g., seagrass cover) affected the

nature of the observed responses. To this end, we constructed five reefs (termed “40 High” herein) in areas with a higher percentage of *T. testudinum* cover (mean cover > 25% surrounding the selected sites). Depth of sites ranged from 1.3 to 2.5 m at low tide ($1.8 \pm 0.3 \text{ m}$ [mean \pm SD]).

We measured four variables: three characteristics of *T. testudinum*, as well as fish density. For assessing responses in seagrass, we measured: blade tissue percentage phosphorus (%P), blade tissue percentage nitrogen (%N), and mean blade height (August 2011, ~ 29 months following reef construction). Seagrass response variables were measured in a spatially explicit fashion on three transects radiating from each reef; transects were oriented $\sim 120^\circ$ apart. Measurements were taken within 1-m^2 quadrats placed at seven distances, 0–1, 1–2, 2–3, 4–5, 6–7, 8–9, and 10–11 m. Mean blade height was estimated by randomly selecting a point within each quadrat and measuring height (relative to shoot sheath) of the five closest blades. This was repeated three times for each quadrat ($n = 15$ blades/quadrat). Blade height was averaged for each distance on each reef, and then averaged across reefs for each distance within each reef category (0, 10, 40 Low, 40 High). *T. testudinum* was collected (~ 25 blades) across one of the three transects, at each transect distance ($n = 7$ collections per reef). Seagrass blades were frozen and transported to the Florida International University (Miami, Florida, USA) for processing.

Nutrient content of seagrass blades has been widely used to assess nutrient availability in coastal ecosystems (Atkinson and Smith 1983, Duarte 1992, Fourqurean and Zieman 2002). Seagrass nutrient content is believed to reflect ambient nutrient conditions over a relatively long time frame (i.e., months) as compared with ambient water nutrients. All *T. testudinum* short shoots and photosynthetic living tissue were rinsed with deionized water, and then blades were scraped to remove epiphytes. Blades were dried at 65°C for 72 h and ground to a powder with a mortar and pestle. Ground samples were analyzed for carbon and nitrogen content with a CHN Carlo-Erba elemental analyzer (FISONS NA1500; Thermo Scientific, Delft, The Netherlands) and for phosphorus using dry oxidation-acid hydrolysis extraction followed by a colorimetric analysis (Fourqurean et al. 1992). Elemental content was calculated based on proportion of sample dry mass.

A multivariate analysis of covariance (MANCOVA) was used to assess the relative importance of treatment (40 Low, 10, and 0) with respect to distance from reef (covariate), as well as their interaction, on the three seagrass response variables. A separate MANCOVA was used to assess the difference between the 40 High and 40 Low treatments with respect to distance from the reef (covariate), as well as their interaction. Data were

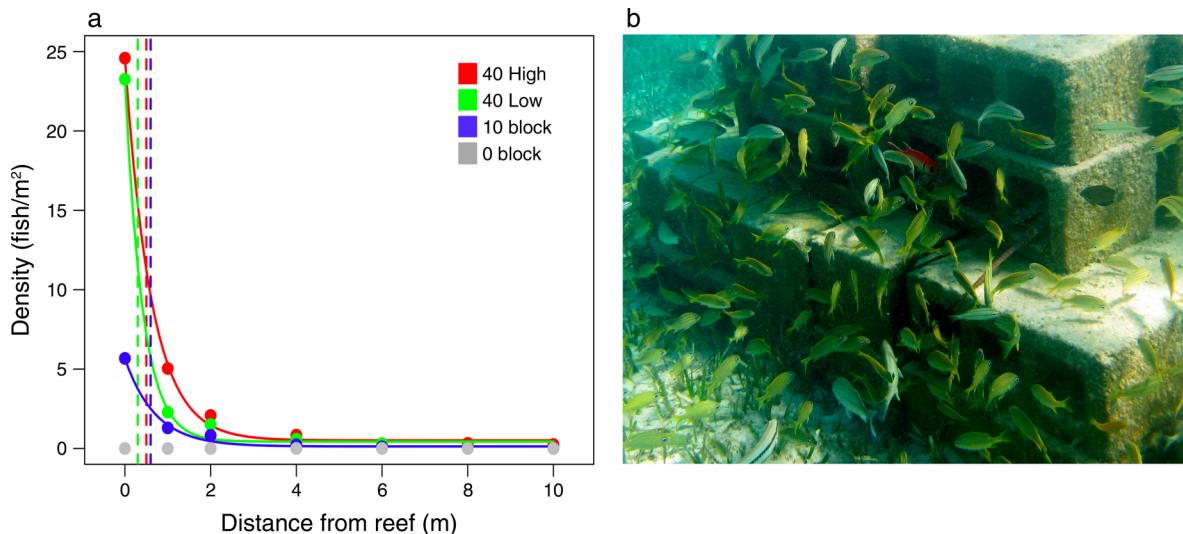


FIG. 1. (a) Fish density estimates, as a function of distance from reef, based on underwater visual census for the four treatment categories in artificial reefs in The Bahamas: 40-block reefs in areas with high seagrass cover (40 High), 40-block reefs in areas of low seagrass cover (40 Low), 10-block reefs, and controls (0 blocks). Three of the relationships were best fit by nonlinear models, and the threshold values for these are designated by dashed lines. (b) A photo of one reef ~29 months after deployment.

transformed to meet assumptions of normality and homoscedasticity.

Because there was a significant effect of distance in the models, regression analysis was used to assess the relative importance of distance for each of these variables. We used either a three parameter exponential decay nonlinear model or a simple linear regression model to characterize the relationship between the three response variables and distance away from reef. The best models were determined by lowest Akaike's Information Criteria (AIC) score (Burnham and Anderson 2002; which always coincided with the highest R^2 value in this case). A nonlinear model inherently suggests that a changepoint or threshold exists, i.e., a point at which the statistical properties (herein slope) change significantly (Chen and Gupta 2012). We note that the linear models in this study would be nonlinear given more data points at further distances from reefs (i.e., the values would ultimately converge with control values). Yet, for clarity, we describe the models within confines of the data presented. For those data that were best described by a nonlinear model, we identified the threshold in the functional relationship between distance and the response variable using the function "cpt.reg" of the R package "changept" (Killick and Eckley 2011). This analysis was performed on predicted values drawn from the nonlinear model analysis. MANCOVA and change-point analyses were conducted using R software (R Development Core Team 2008).

Estimates of fish density were collected in December 2011 in a similar spatially explicit sampling design as the seagrass data. Fish densities were estimated by under-

water visual census with mask and snorkel (Brock 1954, Layman et al. 2004). Prior to surveys, 1-m² areas were designated at the distances identified above on four transects for each reef (oriented roughly 90° from one another). The corners of the quadrat were marked with small stones, allowing for assessment of densities without disturbing fishes by placing a quadrat on the substrate. On each survey transect, one author (C. A. Layman) slowly approached the designated survey area, waited between 20 and 60 s, and then took a snapshot count of the fishes within the 1-m² area. On a given day, each of the four transects on a reef were surveyed, and then reefs were surveyed on multiple days over a two-week period. A total of 145 transects were surveyed (1015 individual 1-m² surveys). Estimated densities at each distance were averaged across survey dates for a reef to yield a mean density of fishes at each survey distance. Then, these mean abundances were averaged across reefs, yielding a mean density of fishes at each distance for each reef category (40 High, 40 Low, 10, and 0). Such averaging across sampling dates and reefs provides a more reliable proxy for fish density, and is less biased by variation that can be induced with snapshot fish surveys. To further examine if UVC density estimates were biased by the presence of the observer, we also estimated densities using underwater video cameras (see Appendix A).

Similar to seagrass analysis, an ANCOVA was used to assess the relative importance of treatment (40 Low, 10, and 0) with respect to distance from reef (covariate), as well as their interaction, on fish density. ANCOVA also was used to assess the difference between the 40 High

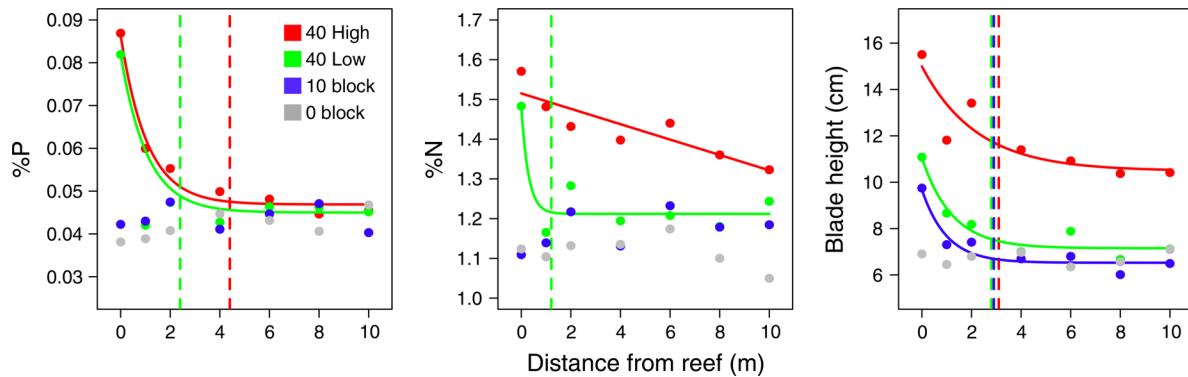


FIG. 2. Mean seagrass (*Thalassia testudinum*) response variables (percentage P [%P], percentage N [%N], and blade height) by reef type (four treatment categories; see Fig. 1), as a function of distance from each reef. When relationships were best described by nonlinear models, threshold values are identified by dashed lines. Note that patterns with distance, across the treatment categories, are different for each of the three response variables. See Fig. 1 for a description of the treatments.

and 40 Low treatments with respect to distance from the reef (covariate), and their interaction. Relationships between fish abundance (number of fish/m²) and distance from the reef for each reef type was analyzed in the same way as the seagrass variables.

RESULTS

There was a significant effect of treatment (for reef size, 40 Low, 10, and 0 reefs, $F_{2,85} = 4.8$, $P < 0.001$) and distance ($F_{1,85} = 5.9$, $P = 0.001$) and their interaction ($F_{2,85} = 3.3$, $P = 0.004$) on seagrass response variables in the global MANCOVA model (Fig. 2; Appendix B). The interaction between treatment and distance was significant for blade height ($F_{2,85} = 4.7$, $P = 0.01$), and %P ($F_{2,85} = 4.0$, $P = 0.021$), but not for %N ($F_{2,85} = 2.5$, $P = 0.09$), suggesting that the relationship for the first two response variables with distance was different among reef sizes.

Comparing the 40 High and 40 Low reefs, there was a significant effect of treatment and distance in the global model ($F_{1,56} = 4.7$, $P < 0.001$ and $F_{1,56} = 4.2$, $P < 0.001$, respectively), but not their interaction (Appendix B). A significant treatment effect for blade height ($F_{1,56} = 47$, $P < 0.001$) and %N ($F_{1,56} = 11.5$, $P < 0.001$) were found. A significant effect of distance was identified for blade height ($F_{1,56} = 19.2$, $P < 0.001$), %P ($F_{1,56} = 15.0$, $P < 0.001$), and %N ($F_{1,56} = 4.5$, $P = 0.037$). No interaction was significant, suggesting the relationship between each response and distance was similar between 40 High and 40 Low reefs.

Nonlinear relationships with respect to %P and distance from the reef were found for 40 High and 40 Low, %N for 40 Low reefs, and for blade height for 40 High, 40 Low, and 10 reefs (Fig. 2). Nonlinear models for %N and %P on the 40 Low reefs did not have significant slopes, but remained a better model fit than the linear model (Appendix B). A significant linear

regression was found with respect %N for 40 High reefs. Here the AIC (-21.41, -21.07) and R^2 (0.74, 0.77) for the nonlinear model and the linear model, respectively, were similar. In this case, the linear (i.e., the most parsimonious) was retained. No regressions for the zero block (control) treatments were significant. Thresholds were identified for %P on the 40 High and 40 Low reefs at 4.4 m and 2.3 m, respectively, for %N on the 40 Low reefs at 1.2 m, and for blade height for the 40 High, 40 Low, and 10 reefs at 3.1, 2.8, and 2.9 m, respectively.

For fish densities, there was a significant effect of treatment, distance, and their interaction among 40 Low, 10, and 0 reefs (all $F > 21$, $P < 0.001$), but no treatment effect between 40 High and 40 Low ($F_{1,56} = 0.24$, $P = 0.62$). Thresholds were found at 0.5, 0.3, and 0.6 m for 40 High, 40 Low, and 10 reefs, respectively (Fig. 1). Fish density did not vary with distance for 0 reefs.

DISCUSSION

A complimentary study, using theoretically derived excretion rates to estimate nutrient supply by fishes, has demonstrated a strong link between fish abundance and local-scale nutrient supply (Allgeier et al. 2013). In coral-seagrass coupled ecosystems, fishes often forage widely at night in seagrass, yet aggregate around more structurally complex reefs during the day (Ogden and Ehrlich 1977, Meyer et al. 1983, Meyer and Schultz 1985, Yeager et al. 2011). This dynamic serves to concentrate nutrients in a relatively small area within the seascape (Allgeier et al. 2013). Our data suggest biogeochemical hotspots are created by these fish aggregations, with associated ecological thresholds that vary as function of reef size and the particular ecosystem variable used to delineate the hotspots.

High fish densities on 40 High and 40 Low reefs resulted in distinct thresholds in %P values adjacent to



PLATE 1. Consumers, especially fishes forming large aggregations, can supply limiting nutrients to primary producers in oligotrophic coral and seagrass ecosystems. Photo credit: Zachary Jud.

reefs. That is, %P was significantly elevated adjacent to the 40 High and 40 Low reefs, and converged with control values (i.e., areas without fish aggregations) with increasing distance (>4 m for 40 High and >2 m for 40 Low) from reefs. Phosphorus is typically the most limiting nutrient for *T. testudinum* in biogenic carbonate sediments (Lapointe and Clark 1992) and is expected to be rapidly taken up by primary producers (as well as adsorbed to sediments). This is consistent with the distinct thresholds found for both 40 High and 40 Low treatments. The linear relationship of %N and distance for 40 High reefs was driven in part the fact that %N remains significantly higher in seagrass tissues at distances further from the reefs than we sampled. Since P is more limiting, it is rapidly taken up adjacent to reefs. But with high quantities of N (relative to P) supplied by fish aggregations (Layman et al. 2011, Allgeier et al. 2013), elevated %N in blade tissues was observed over a wider area.

Of the three responses, blade height was the only one that was characterized by a threshold response for 10 block reefs. Immediately adjacent to these reefs, *T.*

testudinum likely has increased growth rates because of elevated nutrient supply from relatively small fish aggregations. Yet this level of nutrient supply is apparently not sufficient for luxury nutrient storage (Larkum et al. 2006). Increased nutrient availability seems to be allocated first to increased seagrass growth, but only at higher levels of nutrient supply will tissue nutrient content increase (Allgeier et al. 2013). These data highlight the ecological significance that subtle differences in nutrient supply, either as a function of distance from reefs or size of fish aggregations, can lead to very different spatial patterns of ecosystem responses.

Ecological thresholds may be manifest at much larger spatial scales than those identified herein, and more research is needed to characterize the extent of biogeochemical hotspots surrounding structurally complex habitats in marine ecosystems. A next step is to explore the spatial scale of ecological thresholds surrounding habitats that support higher animal abundance and/or animals of much larger body size. For example, nutrient limitation regimes in seagrasses may be affected >100 m from bird rookeries (Fourqurean et

al. 1992). Likewise, consumer-mediated nutrient supply may influence ecosystem properties over much larger spatial scales surrounding coral reefs, systems where fishes may forage over much greater distances (hundreds of meters) in adjacent seagrass habitat (Ogden and Ehrlich 1977; see Plate 1).

Equally important to contextualize these results is the temporal scale over which biogeochemical hotspots have developed. Seagrass characteristics were measured 29 months after reef habitats were created, at which time thresholds were relatively close to the reefs (the furthest identified was at 4.4 m: %P for 40 High reefs). We hypothesize that thresholds will be found progressively further from reefs as nutrients continue to be supplied by fishes. Because of their tendency to retain phosphorus, carbonate sediments adjacent to reefs may become saturated (Herbert and Fourqurean 2008), and thus, phosphorus supply may extend further from reefs over time. This hypothesis underscores the importance of considering both spatial and temporal dimensions of biogeochemical hotspots (McClain et al. 2003).

“Halos”, i.e., a bare sand ring surrounded by dense seagrass cover, are a commonly observed feature associated with structurally complex habitats in marine systems that may be caused by herbivory (Sweatman and Robertson 1994). Sand halos were not observed in this study, which also may be a function of both spatial and temporal aspects of the study design. First, herbivores are a relatively small proportion of the fish aggregations (Yeager et al. 2011), and thus may not be grazing at a rate sufficient to create sand halos. Herbivore feeding behavior may also be restricted by presence of predatory fishes (Madin et al. 2011). From a temporal perspective, it may simply take longer for sand halos to develop, be it through direct grazing, bioturbation, or other means.

Ecological thresholds can be complex to identify and interpret because of the multiple interacting causes and effects (Groffman et al. 2006), yet are critical to identify as they directly link ecological drivers (e.g., consumer nutrient supply) and the relevant ecosystem response (e.g., primary productivity and nutrient limitation regimes). Although patch reef habitats have long been a focal study unit for population- and community-level dynamics (Sale and Douglas 1984, Hixon and Beets 1989, Forrester 1990, Carr and Hixon 1997), their role as hotspots of ecosystem function remains underappreciated. Our study is one of the first to characterize these hotspots, and suggests that even relatively small reefs may be critical nodes of ecosystem function in a larger seascape context. We further show how the natural history of species and ecosystems can be used to characterize thresholds of ecological change. Given the on-going threats to coastal ecosystems, seagrass beds in particular, increased understanding of such nonlinear responses will be increasingly crucial (Koch et al. 2009).

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SUPPLEMENTAL MATERIAL

Appendix A

Underwater video methodology for estimating fish densities ([Ecological Archives E094-044-A1](#)).

Appendix B

Results of MANCOVA models and regression analysis ([Ecological Archives E094-044-A2](#)).