Mechanistic evidence of enhanced production on artificial reefs: A case study in a Bahamian seagrass ecosystem

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ABSTRACT

The attraction-production question, i.e., do artificial reefs support new fish biomass or instead primarily attract fishes from other areas, is one of the most nuanced in coastal marine conservation. Here we provide a novel perspective on this issue, specifically regarding the nutrient dynamics of biogeochemical hotspots that develop following artificial reef construction. Fishes can translocate nutrients (i.e., nitrogen and phosphorus) from the surrounding seascape and concentrate them around artificial reefs, often increasing localized primary production. We discuss an example of this in a seagrass ecosystem, using a case study demonstrating the specific mechanism by which aboveground primary production is enhanced. Namely, when nutrient supply exceeds an ecological threshold, non-linear shifts in nutrient allocation occurs to aboveground tissues, serving to increase localized primary production. Identifying such ecological thresholds in resource allocation provides a powerful predictive tool in the context of fishery management. We suggest that such an ecosystem-level perspective should become more prominent in discussions regarding the attraction-production question of artificial reefs.

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1. Introduction

Ecological thresholds occur when small changes in an environmental driver produce large changes in ecosystem response, often in non-linear fashion (Groffman et al., 2006). Thresholds are related to specific tipping points at which an environmental driver(s) cause dramatic shifts in community- or ecosystem states (Suding and Hobbs, 2009; Kelly et al., 2015). For example, in the Florida Everglades, human activities substantially increase phosphorus loading, the nutrient which is commonly most limiting in this oligotrophic system. When phosphorus levels are above a threshold value, interacting positive feedbacks drive the system away from natural sawgrass (*Cladium*) prairies to cattail (*Typha*) dominated marshes. Identifying this nutrient threshold is critical for understanding ecological dynamics, and can serve as a primary target for managing phosphorous loading to the system (Hagerthey et al., 2008). Likewise, there is much potential to use the threshold concept in proactive efforts to reverse environmental deterioration, for example, in restoration efforts (Suding et al., 2004; Suding and Hobbs, 2009) or attempts to replenish depleted fishery stocks (McClanahan et al., 2011).

Artificial reefs can be broadly defined as any submerged structures placed on substratum to mimic some characteristics of a natural reef, often to augment fishery yields. Other structures are not designed for this purpose, yet effectively function as artificial reefs, e.g., jetties. Ranging in size from small concrete reef balls to massive offshore oil rigs, these artificial structures can support extremely high densities of fish (Seaman, 2000). For example, it was recently suggested that oil and gas platforms off the coast of California have the highest fish production per unit area of any marine habitat worldwide, as much as an order of magnitude higher than other marine ecosystems (Claisse et al., 2014). But a critical question remains regarding the nature of such fish aggregations—to what degree do these fishes represent new biomass/production for these systems or, instead, are fish just attracted from other areas (Pickering and Whitmarsh, 1997; Seaman, 2000; Powers et al., 2003)? If artificial structures do provide for additional fish biomass, this practice could become a core component of fisheries management strategies. But if they primarily serve as fish attractors, artificial reefs may facilitate over-exploitation by making extraction easier for fishers. This "attraction vs. production" question regarding artificial reefs is challenging to resolve for many reasons, one of which is that fundamental ecosystem shifts generated by reef construction are often not well understood (Pickering and Whitmarsh, 1997; Seaman, 2000; Powers et al., 2003).

Efforts to reconcile this question revolve almost exclusively on the fishery species of interest, e.g., estimating secondary production per unit area on an artificial reef and comparing this to natural habitats (e.g., Claisse et al., 2014). But alternative ecological viewpoints may reveal valuable insights, especially embedding the study of artificial reefs in a more general ecosystem ecology context. For example, deployment of artificial reefs in seagrass beds can result in formation of distinct biogeochemical hotspots in otherwise homogeneous seascapes (Dewsbury and Fourqurean, 2010; Allgeier et al., 2013; Layman et al., 2013; Peterson et al., 2013). The main mechanism is translocation and then concentration of nutrients (nitrogen and phosphorus) in a localized area via excretion from aggregated fishes, resulting in a strong bottom-up effect on local ecosystem processes.

Yet this rather general observation leaves much unexplained about specific mechanistic links between fish nutrient supply and seagrass traits. For instance, reef construction seems to initiate a series of positive feedbacks loops, whereby greater seagrass productivity and structural complexity supports higher invertebrate densities, which in turn may feedback to enhance secondary production of fishes (Yeager et al., 2012). Higher fish and invertebrate densities supply more nutrients to seagrasses, further increasing seagrass productivity over time. The specific underlying ecological mechanisms by which aboveground primary production is enhanced adjacent to reefs ultimately mediates all of the feedback dynamics. Elucidating these mechanisms would reveal critical aspects of the function of artificial reefs in a broader ecosystem context and provide critical information for their design.

We provide a case study that highlights the need for a broader discussion of artificial reefs in an ecosystem context. Specifically we explored the mechanism by which seagrass production is enhanced around an artificial reef. Theory holds that the relative allocation of resources between above- and belowground seagrass tissues should vary predictably at different levels of nutrient supply (Tilman, 1988). We test this assumption by taking advantage of a spatial gradient in nutrient supply, where the highest nutrient cycling rates are immediately adjacent to reefs due to fish aggregating closely to the reef structure (Layman et al., 2013). Two questions framed the research: (1) Are there thresholds at which seagrasses shift resource allocation among tissue structures (blades, roots, rhizomes) across spatial gradients around reefs?; (2) Are aboveground seagrass traits predictable based on biomass and/or nutrient content of belowground structures? We then use these data to discuss how shifts in ecosystem function provide a novel context to evaluate the attraction vs. production question and, more generally, evaluate the efficacy of artificial reefs in enhancing fish production.

2. Materials and methods

This case study was based in the Bight of Old Robinson, Abaco, The Bahamas, a semi-enclosed bay that has a complex benthic mosaic comprised predominantly of sand, seagrass (primarily turtle grass *Thalassia testudinum*), and hard bottom/patch reef habitat. We sampled an artificial reef (N 26° 20.549′, W77° 00.874′) that had similar spatial patterns in aboveground seagrass traits as other patch reefs (both natural and artificial) in seagrass beds of this area (Allgeier et al., 2013; Layman et al., 2013). This reef (dimensions ~1.2 m² at base and ~1.2 m tall) was constructed in March 2009 using 40 cinder blocks arranged in pyramid fashion (Yeager et al., 2011). Samples (December 2013) were taken in spatially-explicit fashion on 3 transects radiating from each reef; transects were oriented ~120° apart in random directions. Cores were taken with a 12.7 cm diameter pvc pipe at set distances (m) from the reef on each transect: 1, 2, 3, 4, 6, 10, 15, 100. The core was driven ~16 cm into the sediment and manually excavated, placing one

hand under the bottom of the core as it was pulled out. Visual inspection demonstrated cores successfully remove all seagrass tissues from the sampled area. Water was drained from the cores and sand was rinsed off with seawater and then they were placed in individual plastic bags and immediately frozen.

In the laboratory, cores of seagrass biomass were thawed and separated into aboveground biomass (all attached green leaves of shoots) and belowground biomass (rhizomes and roots). Shoots were enumerated and morphology of blades (length and width) was measured. As a proxy for grazing intensity, we measured the total number of grazing scars on all blades in the core (Valentine and Duffy, 2006). Blades were gently scraped with a razor blade to remove epiphytes; belowground material was rinsed with deionized water. Tissues were dried for 72 h at a constant temperature of 65 °C and dry weight (to the nearest 0.01 g) was recorded. Dried samples were ground into a fine powder using a PRECELLYS$_{24}$ grinder and subsamples of each were analyzed for percent of carbon (C), nitrogen (N), and phosphorous (P). Percent C and N content were determined using a CHN Carlo-Erba elemental analyzer (Fison NA1500). Percent P was determined by dry oxidation acid hydrolysis extraction followed by colorimetric analysis (Fourqurean and Zieman, 1992).

To explore potential thresholds in allocation of resources between different tissue structures, we first partitioned total plant nutrients into the various tissues from which these measurements were obtained (n = 48 for each tissue type, n = 144 total). Partitions included: % blade nutrients to total (whole-plant) nutrients, % total belowground (root + rhizome) to total, % root to total, % rhizome to total, % roots to total belowground, and % rhizome to total belowground. Generalized additive models (gam) were then used to describe the relationship of these data with respect to distance from the reef. If the relationship was non-linear, a changepoint analysis, using the package "changepoint" in R, was used to determine the distance from the reef at which the threshold was reached. Relationships between belowground and aboveground traits were tested using least squares regression. Data were log transformed and satisfied model assumptions.

3. Results

Blade length, blade biomass and shoot density were highest adjacent to the reef (Fig. 1), consistent with previous aboveground seagrass data from 14 other artificial reefs in this system (Layman et al., 2013). Total root biomass had a similar pattern, but no apparent negative decline was found for rhizome biomass (Fig. 1). C, N, and P content decreased for each tissue farther from the reef (Appendix A of Supplementary data). Nutrient allocation shifted among different seagrass tissue structures at specific spatial thresholds. Of the 18 nutrient allocation relationships represented in Fig. 2, 13 were non-linear. Thresholds were found for N in all cases, and for C and P in 4 and 3 of the scenarios, respectively. Relative nutrient allocation shifted away from blades and roots, and into rhizomes, with increased distance from the reef. Most importantly, allocation shifted toward aboveground (relative to total belowground structure) closer to the reef, with this relationship being non-linear for N. In all cases where a threshold was identified, the threshold distance was 7–9 m from the reef structure. This suggests that this biogeochemical hotspot, i.e., the area over which ecosystem processes were significantly altered by the fish-derived nutrient supply, covered as much as 250 m² (initiated from a reef with a footprint of only ~1.2 m²).

Aboveground seagrass traits were well generally predicted by belowground seagrass traits (total biomass and total percent nutrient content) in 14 of 24 potential models (four of which were only significant at the level of α < 0.1; Table 1). Surprisingly,