



Ambient nutrient availability drives the outcome of an interaction between a sponge (*Halichondria melanadocia*) and seagrass (*Thalassia testudinum*)

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ABSTRACT

Nutrient loading is a common human impact in coastal habitats which is driving significant losses of seagrass habitat worldwide. This is concerning, as seagrass beds provide numerous ecosystem services. Although nutrient loading can result in eutrophication and mass mortality of seagrasses, it more often results in subtle alterations of abiotic conditions which, by themselves, are insufficient to drive widespread seagrass mortality. Here we used a month-long field-based experiment to test the influence of anthropogenic nutrient loading on the outcome of an interaction between an epizootic sponge (*Halichondria melanadocia*) and a seagrass (*Thalassia testudinum*). Using a factorial design we manipulated ambient nutrient concentrations by adding fertilizer to plots with and without a sponge in a relatively pristine seagrass bed on Abaco Island, The Bahamas. We measured seagrass growth, below- and above-ground biomass, and the change in shoot density. We found that low levels of nutrient loading (i.e., insufficient to cause increased algal growth and decreased oxygen levels associated with eutrophication) resulted in a non-significant increase in seagrass growth, biomass, and shoot density when a sponge was absent. When a sponge was present, the same level of fertilization resulted in a significant reduction in the response variables. Our results show that anthropogenic nutrient loading can shift the sponge-seagrass interaction away from commensalism toward an interaction that has negative consequences for the seagrass. Additionally, a shift in the outcome of this context-dependent interaction can alter the impact of nutrient loading on seagrass productivity. Our study provides an example of how simple classifications of interspecific interactions (e.g., commensalism) often mask underlying variability. Characterizing the mechanisms driving the variability will allow us to understand when and how the outcome of an interaction will change. Ultimately, this will allow us to better predict how human activities will indirectly impact various ecosystem functions.

1. Introduction

Seagrass beds are an important, globally distributed, coastal ecosystem (Duffy et al., 2014; Lamb et al., 2017) that are disappearing rapidly as a result of myriad anthropogenic threats (Orth et al., 2006; Waycott et al., 2009). The majority of identified threats, including dredging, damage from boats, and eutrophication, result in direct mortality of seagrass. Much seagrass loss attributed to eutrophication is the result of increases in epiphytic algae and water column productivity, significantly decreasing light availability for seagrasses (Burkholder et al., 2007). Low-level anthropogenic nutrient loading (i.e., insufficient to cause increased algal growth and decreased oxygen levels associated with eutrophication) is a common occurrence in coastal systems. However, we know little about how low-level anthropogenic nutrient loading may impact the function of seagrass ecosystems.

Interspecific species interactions play a central role in maintaining

both the structure and function of ecosystems. Understanding the impact of interspecific interactions on ecosystem function is complicated by the fact that outcomes of interactions are often context-dependent; they are influenced by the biotic and/or abiotic conditions in which they occur (Bronstein, 1994; Chamberlain et al., 2014). There is evidence that interactions involving nutrient transfer are particularly sensitive to changes in ambient nutrient availability (Kiers et al., 2010), suggesting that anthropogenic nutrient loading has the potential to disrupt interspecific interactions thereby altering ecosystem function. For example mycorrhizal symbioses, where the plant provides carbohydrates in exchange for nutrients, strongly influence the structure of plant communities (Grime et al., 1987; Hartnett and Wilson, 2002; van der Heijden et al., 1998). These symbioses are context dependent, such that benefits to plants are highest when nutrient availability is low in the soil (Johnson et al., 1997; Neuhauser and Fargione, 2004). Long-term soil fertilization can alter these symbioses and their outcome, influencing plant productivity and the competitive balance between plant

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species (Johnson, 1993; Johnson et al., 2003; Treseder, 2004). As anthropogenic activities increasingly alter abiotic conditions, human influence on the outcome of species interactions is predicted to increase (Kiers et al., 2010).

Despite their potential importance, we know little about context-dependent interactions in marine systems and even less about how shifts in their outcome may influence ecosystem function. Here, we focus on how a small increase in anthropogenic nutrient loading impacts the commensal interaction between the sponge, *Halichondria melanadocia* (de Laudenfels, 1936) and seagrass, *Thalassia testudinum* (Banks & Sol. ex König, 1805), and in turn influences seagrass productivity. The sponge is an epizootic sponge that utilizes the base of seagrass shoots to grow, ultimately shading the blades. Additionally, the sponge is a source of nitrogen and phosphorus; nutrients presumably available to the seagrasses (Archer et al., 2015). In the oligotrophic waters of The Bahamas, where the interaction was first described, the net outcome of the interaction between the sponge and seagrass is commensal, where the sponge likely benefits from the provision of an attachment point on an otherwise soft-bottom system and the seagrass exhibits no measurable effect of hosting the sponge (Archer et al., 2015). We hypothesized that ambient nutrient concentrations influence the outcome of the sponge-seagrass interaction. If the effect of the sponge on the seagrass is a balance of the cost incurred as a result of shading by the sponge and the benefit of the availability of nutrients released by the sponge, increased ambient nutrient availability should change the balance of the interaction so that sponge presence negatively influences the seagrass. In this manuscript, we present the results of a field experiment where we tested whether anthropogenic nutrient loading alters the outcome of the interaction between the sponge and seagrass and, if so, what the impact is for seagrass productivity.

2. Materials and methods

2.1. Study system

This study was conducted on Great Abaco Island, The Bahamas, from 2 June – 3 July 2014. The location of our experiment was a dense seagrass meadow of *Thalassia testudinum* at Jungle Creek (26° 21' 53" N, 77° 01' 25" W). Jungle Creek is a relatively unimpacted, sheltered, tidal system that is bounded by red mangroves (*Rhizophora mangle*) and contains a mosaic of sand flats, hard bottom, and seagrass communities. *Halichondria melanadocia* is abundant in this area (Archer et al., 2015). This site corresponds to the North Bight of Old Robinson described by Stoner et al. (2011) who found low ambient availability of nitrogen (0.51 μM NH_4^+) and phosphorus (0.11 μM soluble reactive phosphorus).

2.2. Experimental design and setup

We conducted a fully crossed 2×2 factorial design with two levels of sponge presence (present or absent) and nutrient enrichment (ambient or fertilized) with 10 plots per treatment combination ($n = 40$). Experimental 20×20 cm plots were arranged in five rows of eight. All plots were separated by at least 1 m. The first plot was haphazardly placed within the seagrass bed. From this plot we searched for the presence of a sponge within 1–3 m. If a sponge was found, the next experimental plot was established with the sponge in the center. If no sponge was found, the plot was established 1 m from the previous plot. Ten plots for each level of sponge presence were randomly assigned to receive fertilizer; a total of twenty plots were fertilized. All plots were delineated using PVC stakes placed at the corners of the plot. Although the sponge treatment could not truly be randomly assigned, we were able to ensure that the sponge plots were spread throughout the seagrass bed. When adding fertilizer we followed protocol outlined by Ferdie and Fourqurean (2004) and Stoner et al. (2014). This involved massaging 40 mg (± 0.05 mg) of Plantacote slow-release fertilizer (N:P

molar ratio = 19:6, Scotts, Columbus, Ohio, USA) into the first 5 cm of the sediment, once at the beginning of the experiment. The amount of fertilizer was chosen based on the findings of Stoner et al. (2014), to increase nutrient availability without resulting in increased algal growth and decreased oxygen levels associated with eutrophication. Fertilization was considered successful if the % nitrogen (%N) of *T. testudinum* blades was significantly higher in fertilized plots; in oligotrophic systems water column nutrients are an unreliable indicator of nutrient dynamics (Allgeier et al., 2011; Allgeier et al., 2013; Ferdie and Fourqurean, 2004) while seagrass tissue is widely used to assess nutrient availability in similar systems (Atkinson and Smith, 1983; Fourqurean and Zieman, 2002).

2.3. Seagrass sampling

As the plots were delineated the initial density of *T. testudinum* shoots was counted. To assess seagrass growth five shoots in each plot were randomly chosen and marked at the base of the shoot with a surgical needle following a standard blade-hole punching technique to measure seagrass growth (Zieman, 1974); the seagrass shoots were marked with two weeks remaining in the month-long experiment. In plots with sponges the seagrass shoot that the sponge was growing around was intentionally marked to directly test the effect of the sponge on its host seagrass shoot. This was done following the methods described in Archer et al. (2015). At the end of the experiment, we recorded final seagrass density within each plot. We then collected marked seagrass shoots for growth measurements. Then, above and below ground seagrass biomass was collected using a 20 cm diameter core pressed 15–20 cm into the substrate. Each core was sieved in the field to remove excess sediment prior to transport. All samples were frozen then transported to North Carolina State University for processing.

In the laboratory, the cores were thawed and sorted into four components: seagrass blades, sheaths, rhizomes, and roots. All components were rinsed in deionized water to remove sand and other foreign particles. Then seagrass blades were gently scraped to remove epiphytes. When sponges were present, they were separated from seagrass tissue and kept. The shoots collected for growth were also scraped to remove epiphytes, the growth was measured, and then the shoots were added to the biomass collected in the core. All seagrass components and sponges were dried at 65 °C for 48–72 h until a stable weight was reached. The dry weight (g) was recorded and a subset of samples ($n = 21$, 5 per treatment combination with the exception of fertilized non-sponge plots for which $n = 6$) were ground to a fine powder for percent carbon (%C) and nitrogen (%N) determination. For %C and %N determination, 3–6 mg of ground material was weighed into tin capsules and sent to the Analytical Chemistry Lab at the University of Georgia for analysis. In addition, epiphytes were ashed at 500 °C for 3 h and ash-free dry weight was recorded after samples cooled.

2.4. Statistical analyses

The difference in sponge dry weight was compared between fertilized and ambient plots using Welch's two sample *t*-test for unequal variance. If nutrient addition influenced sponge growth we would expect to see a difference in sponge dry weight as a congener of this sponge (*Halichondria panacea*) can grow at a rate of 2% per day (Thomassen and Riisgård, 1995). Seagrass growth ($\text{mm}^2 \text{day}^{-1}$), the change in *T. testudinum* shoot density (initial – final shoot density), epiphyte ash-free dry weight (standardized by blade biomass; $\text{g}_{\text{epiphytes}}/\text{g}_{\text{blade}}$), and %C and %N of seagrass blades were each analyzed using a 2-way analysis of variance with nutrient addition (ambient vs fertilized) and sponge presence (sponge vs no sponge) as fixed factors. Although the growth of five seagrass shoots per plot was measured, the average seagrass growth per plot was used as the response variable in our analysis. Type II sums of squares was used for the analysis of %C

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