



## Modification of a seagrass community by benthic jellyfish blooms and nutrient enrichment



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### ARTICLE INFO

#### Article history:

Received 29 March 2014

Received in revised form 28 July 2014

Accepted 9 August 2014

Available online 27 August 2014

#### Keywords:

*Cassiopea* spp.

Eutrophication

Global change

Habitat complexity

Jellyfish blooms

*Thalassia testudinum*

### ABSTRACT

Anthropogenic activities are increasing the number and intensity of disturbances, often acting in concert, in ecosystems across the globe. One result of human activities in many marine ecosystems is an increased abundance of jellyfish (jellyfish blooms), which have garnered recent attention for their detrimental ecological and economic impacts. We conducted a field experiment to determine effects of proliferations of benthic jellyfish, *Cassiopea* spp., and another common disturbance, anthropogenic nutrient enrichment (via fertilizer additions), on a shallow seagrass community in Abaco, Bahamas. Results suggested a reduction in seagrass abundance and habitat complexity in both jellyfish and nutrient enrichment treatments. Jellyfish additions were associated with reduced faunal densities; nutrient enrichment drove shifts in faunal community composition. Grazing frequency was substantially higher in nutrient-enriched plots, and lower in plots with jellyfish alone or jellyfish combined with nutrients, suggesting that jellyfish may act as a deterrent to grazers. These findings highlight the inherent complexities in predicting ecological changes within shallow seagrass ecosystems.

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### 1. Introduction

As anthropogenic activities intensify globally, a fundamental concern for resource managers is predicting how multiple disturbances will interact (Crain et al., 2008; Darling and Côte, 2008; O'Gorman et al., 2012; Williams et al., 2013). Anthropogenic disturbances can have independent and cumulative effects on a wide range of abiotic and biotic components, including biodiversity (Fitch and Crowe, 2012; Williams et al., 2013), and ecosystem function (Aber et al., 2001). Anthropogenic disturbance can also facilitate proliferations of certain taxa, often exotic species, which may interact with other human-induced stressors to affect community and ecosystem dynamics (Crain et al., 2008; Didham et al., 2007; Martone and Wasson, 2008; Silliman et al., 2005; Stachowicz et al., 2002). Marine ecosystems may be particularly susceptible to multiple human-driven disturbances acting in concert, as a result of intense human activities (e.g., overfishing) (Halpern et al., 2008).

In several human-impacted marine and estuarine environments, gelatinous zooplankton (hereafter referred to as jellyfish) exhibit rapid

and extreme increases in population densities (i.e., jellyfish blooms). Although there is a paucity of historic jellyfish population density data, the abundance of many jellyfish has increased since the 1970s (Condon et al., 2013), linked to various disturbances including climate change (Brodeur et al., 2008), overfishing (Lynam et al., 2006; Purcell and Arai, 2001), nutrient loading (Arai, 2001; Stoner et al., 2011), introduction of invasive jellyfish species (Mills, 2001), and habitat modification (Duarte et al., 2012; Hoover and Purcell, 2009; Lo et al., 2008). In anthropogenically-disturbed systems in which jellyfish are abundant, jellyfish may exert strong top-down controls on community structure and ecosystem function. For instance, increased predation by jellyfish can dramatically reduce the abundance of zooplankton such as fish larvae (Purcell and Arai, 2001). One study conducted on jellyfish predation in the early 1980s found a decline of over 50% of the larval herring population during weeks when the volume of young *Aurelia aurita* medusae (6–50 mm bell diameter) exceeded 75 ml per 100 m<sup>3</sup> in the Kiel Fjord, Western Baltic Sea (Möller, 1984). Jellyfish blooms may also affect ecosystems through bottom-up pathways. Following a bloom of *Crambionella orsini* off of the coast of Oman in 2002, dead jellyfish carcasses covered >90% of the seabed in some areas. The carbon input associated with these carcasses exceeded the annual organic carbon inputs into this region by an order of magnitude, and created localized “hot spots” of nutrient availability (Billett et al., 2006).

These examples pertain to pelagic jellyfish, but much less is known about how benthic jellyfish affect benthic communities and ecosystem dynamics. Benthic jellyfish, which refers to the genus *Cassiopea* spp. (also called upside-down jellyfish due to their relatively-sessile nature and bell orientation; hereafter *Cassiopea*), are globally-distributed in

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sub-tropical and tropical environments, and are found in several habitat types including mangrove forests, seagrass beds, and coral reefs (Holland et al., 2004; Niggli and Wild, 2010; Stoner et al., 2011). These animals host populations of endosymbiotic dinoflagellates (i.e., zooxanthellae) which provide carbon to the jellyfish, though they do still require heterotrophically-derived sources of nutrition (i.e., zooplankton) through predation (Verde and McCloskey, 1998; Mortillaro et al., 2009). *Cassiopea* have been previously shown to be more abundant and larger in human-impacted systems in The Bahamas, likely due to elevated nutrient availability which stimulates zooxanthellae productivity (Stoner et al., 2011). However, little is known about how an increased abundance of these animals impact benthic nearshore community and ecosystem dynamics.

Nutrient loading and jellyfish may act in concert to affect seagrass and fauna through several direct and indirect mechanistic pathways. For instance, high levels of nutrient enrichment may drive reductions in seagrass as a result of several mechanisms, including increased epiphytic loads, algal shading, ammonium ( $\text{NH}_4^+$ ) toxicity, and sulfide intrusion (Burkholder et al., 2007). However, low-moderate nutrient concentrations have been shown to benefit seagrass, usually in oligotrophic systems, by enhancing productivity and growth (Allgeier et al., 2013). High jellyfish densities may drive declines in seagrass primarily by shading photosynthetic tissue (i.e., resting on seagrass and inhibiting photosynthesis), physically disturbing seagrass shoots, and by preventing clonal development of seagrass via space reduction. Nutrient and jellyfish-driven declines in seagrass may also have cascading effects on fauna, as seagrass abundance and associated structural complexity (i.e., shoot density and leaf morphology) have been shown to positively influence benthic faunal densities (Orth, 1984). Alternatively, jellyfish may directly lead to declines in benthic fauna, as fauna may avoid areas with high jellyfish densities. It is also possible that nutrients may have positive effects on some benthic fauna, namely grazers that benefit from nutrient-enriched seagrass (Heck and Valentine, 2006; Holzer et al., 2013; McGlathery, 1995; Valentine and Heck, 1999). Grazing can serve to reduce seagrass biomass directly, or benefit seagrass by suppressing epiphyte growth, depending on the grazer species and other environmental conditions (Valentine and Heck, 1999).

Our goal was to examine the effects of jellyfish blooms and elevated nutrients in a shallow, subtropical, seagrass ecosystem. We manipulated jellyfish density and sediment nutrient availability to simulate conditions that are found across gradients of human impact in Bahamian coastal systems. We examined how these two disturbances may affect a number of seagrass characteristics, as well as benthic fauna that utilize the seagrass bed as habitat. These data are the first from an experimental manipulation of benthic jellyfish density and nutrient availability, providing an important step toward a more thorough understanding of how human activities may affect the structure and function of seagrass ecosystems.

## 2. Materials and methods

### 2.1. Site description and experimental design

We conducted a  $2 \times 2$  factorial field experiment in a relatively unimpacted nearshore seagrass bed (known as Jungle Creek,  $26^\circ 21' 53'' \text{ N}$ ,  $77^\circ 01' 25'' \text{ W}$ ) on Abaco Island, Bahamas. *Cassiopea* are naturally present in this seagrass bed, but at a relatively low density ( $<2$  jellyfish medusa/ $\text{m}^2$ ). The benthos was dominated by  $>50\%$  *Thalassia testudinum* (turtle grass) cover,  $<2$  m in depth at low tide, and was characterized by silty-sandy sediment ( $\sim 0.05$  mm particle size, as classified by the USDA soil classification triangle (Schoeneberger et al., 2002)).

The experiment was conducted over a 53 day period from May–July in 2012, the period when seagrass productivity is at an annual high in this system. There were four experimental plot types ( $1 \text{ m}^2$  plots): controls (C), nutrient enrichment (N), jellyfish addition (J), and jellyfish and nutrient additions (J + N), with 10 replicates for each ( $n = 40$ ),

randomly assigned among plots. We used an open (i.e., no cage) experimental setup to better simulate natural conditions. Plots were separated by  $\sim 5$  m. The average low tide depth within plots was  $0.68 \pm 0.02$  m (range =  $0.38 \text{ m}$ – $1.35 \text{ m}$ ); there was no difference in mean depth across plot type (one-way ANOVA,  $F_{3, 36} = 0.52$ ,  $P = 0.67$ , SPSS IBM v. 20.0).

Prior to the start of the experiment, we visually estimated seagrass (*T. testudinum*) % cover using a single,  $1 \text{ m}^2$  quadrat in each plot. We detected no difference in seagrass cover across treatments (one-way ANOVA:  $F_{3, 36} = 0.90$ ,  $P = 0.44$ ). Ambient nutrients in the water column in this system are extremely low, with nutrients taken up rapidly by plants, algae and microbial communities. Therefore, water column nutrients may not be the best measure of nutrient availability (Allgeier et al., 2011). Alternatively, nutrient content from macrophytes (e.g., seagrass) reflects ambient nutrient concentrations over a longer time frame (i.e., months), and provides a more reliable estimate of nutrient availability in nearshore ecosystems (Layman et al., 2013). As such, we harvested seagrass shoots immediately adjacent to each plot (to avoid disturbing the seagrass within each plot), to assess initial seagrass nutrient concentrations (%N and %P).

### 2.2. Experimental manipulation of jellyfish and nutrients

For jellyfish addition plots (J, J + N), we added 10, medium-sized (7–10 cm diameter), jellyfish medusae, a density representing the  $\sim 75$ th percentile of all jellyfish densities from human-impacted sites on the island (Stoner et al., 2011). Each week, jellyfish were enumerated, and then added or removed as necessary to maintain 10 jellyfish per plot. To simulate eutrophication, we added Plantacote slow-release fertilizer (N:P molar ratio = 19:6, Scotts, Columbus, Ohio, USA), a compound frequently used in marine enrichment studies (Heck et al., 2000, 2006). We elevated nutrients by massaging the fertilizer ( $1000 \text{ g}/\text{m}^2$ ) into the top 5 cm of sediment, which allows for chronic nutrient release over the duration of the experiment following protocol outlined in Ferdie and Fourqurean (2004). This method is an effective way to diffuse nutrients through sediment porewater and into the water column, which can be utilized by both seagrass, as well as *Cassiopea* (via uptake of porewater nutrients from bell pulsations) (Jantzen et al., 2010). We selected the sediment diffusion method over directly adding nutrients to the water column (e.g., via PVC pipe fertilizer diffusers in each plot) to ensure that nutrients remained within the immediate plot area. In control plots, we simulated the disturbance of massaging nutrients in nutrient-enriched plots by replicating the same sediment massaging action. Nutrient loading rates were estimated to be  $0.81 \text{ g N m}^{-2} \text{ d}^{-1}$  and  $0.25 \text{ g P m}^{-2} \text{ d}^{-1}$  over the duration of the experiment. We determined rates of N and P loading by filling two fine mesh laundry bags with 1000 g of fertilizer, securing the bags with wooden stakes in  $1 \text{ m}^2$  plots  $\sim 100$  m from the experimental site, and calculating total loss of N and P over the course of the experiment. These loading rates were comparable to those reported by Ferdie and Fourqurean (2004), a similar carbonate system in the Florida Keys.

### 2.3. Seagrass and fauna sampling

Several seagrass and fauna characteristics were sampled to assess impacts of jellyfish and nutrient enrichment. We analyzed seagrass % cover, biomass, shoot densities and leaf morphometrics (leaf length and width). Seagrass cover, shoot densities and nutrients in seagrass tissue were measured at the start and end of the experiment, as they required no destructive sampling; the other variables were sampled only at the end of the experiment. Shoot densities were enumerated using 4,  $900 \text{ cm}^2$ , quadrats, haphazardly placed within each plot. Samples for biomass and morphometrics were taken using a seagrass corer (diameter = 23 cm,  $n = 3$  per plot). To assess grazing intensity, we extracted 7 additional seagrass shoots from each plot and froze them for later processing in the laboratory.

Benthic fauna (infauna within the top ~5 cm of sediment and all epifauna) were sampled using a cylindrical, plastic, throw trap (Area = 0.75 m<sup>2</sup>). The enclosed area was sampled using two mesh dip nets (10 mm and 0.5 mm mesh size) until three consecutive sweeps yielded no additional animals (following protocol outlined in Hammerschlag-Peyer et al., 2013). Although some benthic infauna were collected, most of the taxa collected were motile epifauna. Animals were then placed on ice in the field and frozen for later processing. *Cassiopea* found within each plot were enumerated.

#### 2.4. Sample processing

To analyze %N and %P concentrations, *T. testudinum* leaves were gently scraped to remove epiphytes, dried at 80 °C, and ground into a fine powder. %N in leaf tissue was evaluated from duplicate samples using a Carlo Erba CN analyzer. %P in seagrass leaf tissue was analyzed using dry-oxidation acid hydrolysis extraction in addition to colorimetric analysis with a CHN autoanalyzer (Fisons NA1500) (Fourqurean et al., 1992). The analytical detection limit for %P was 0.02 µm.

Seagrass leaves were measured for total length and width (mm). Cores of seagrass biomass were separated into aboveground biomass (all attached green leaves of short shoots), dead seagrass, and belowground biomass (rhizomes and roots). All seagrass tissues were then dried at 60 °C for 48–72 h and weighed. To analyze grazing intensity, we measured the total number of grazing scars made by small, scarid, parrotfishes from the additional seagrass shoots collected (Alcoverro et al., 1997; Peterson et al., 2013). Grazing by parrotfishes was characterized as small crescent shaped bite marks. Epiphytes were quantified on these same blades by removing any adhered epiphytes (including inorganic carbonates) by scraping blades with a razor blade, drying epiphytes at 70 °C, and obtaining their weight.

Faunal samples were sorted and identified to the lowest taxonomic level possible, then dried at 60 °C to ascertain dry biomass. For mollusks, as well as sipunculan worms found in cerith snail shells, shells were removed and only soft tissue dried and weighed.

#### 2.5. Statistical analyses

We calculated proportional change for %P (seagrass), %N (seagrass), % seagrass cover, and shoot densities from the start to the end of the experiment. Proportional change in %P and %N were arcsine-transformed to meet assumptions of normality and homoscedasticity. Seagrass biomass (above- and belowground), epiphyte dry weight (values + 1), and total grazing intensity (values + 1) were natural log-transformed to meet assumptions of normality and homoscedasticity. All aforementioned nutrient and seagrass metrics, in addition to leaf length and width, were analyzed independently using fixed-factor 2-way ANOVA's to compare main effects of nutrient enrichment and jellyfish additions (SPSS IBM v.20.0).

Differences in jellyfish densities (enumerated at the end of the experiment in each plot) among treatments were analyzed using a 2-way ANOVA (SPSS IBM v.20.0). Benthic animal density, richness, and biomass (g dry weight/m<sup>2</sup>) (square-root transformed to better meet assumptions of normality and homoscedasticity) were also analyzed using 2-way ANOVAs (SPSS IBM v.20.0). One driver of faunal change may have been mediated through differences in seagrass densities (see text in Introduction). To this end, we employed separate linear regressions with seagrass shoot density as the predictor, and animal density, richness, and biomass as response variables (SPSS IBM v.20.0).

In order to evaluate benthic animal community composition, a Bray–Curtis similarity matrix was calculated for all species contributing at least 1% to the total animal density. *Cassiopea* were not included in any of the faunal community analyses. Data were 4th root transformed to down-weight the influence of dominant taxa prior to calculation of similarity metrics (Clarke, 1993). A permutational multivariate analysis of variance (PERMANOVA) was used to determine if there were

differences in community composition among treatments (PRIMER© v6) (Anderson, 2001).

### 3. Results

At the end of the experiment, *Cassiopea* collected within each plot were enumerated and were found to be significantly higher in jellyfish addition plots (J, J + N;  $F_{1, 36} = 42.6, P < 0.0001, 4.9 \pm 0.4$  jellyfish/m<sup>2</sup>) than densities in non-jellyfish addition plots (N, C,  $0.9 \pm 0.3$  jellyfish/m<sup>2</sup>) (Fig. 1). %P in seagrass tissue was affected by nutrient enrichment, but not jellyfish additions (Table 1). There was no significant effect of either factor on %N in seagrass tissue (Table 1).

Mean seagrass % cover and shoot densities were significantly lower at the end of the experiment as a result of both nutrient enrichment and jellyfish additions (Table 1, Fig. 2a, b). At the plot level, seagrass cover was 121% lower in J + N plots than in C plots, and shoot densities were reduced by 335% compared to C plots (Fig. 3a, b). Nutrient enrichment reduced mean seagrass aboveground biomass and leaf length, but jellyfish had no significant effect on either of these variables (Table 1, Fig. 2c, e). Seagrass aboveground biomass from J + N plots was 50% lower than biomass in C plots, and leaf length from J + N plots was 16% lower than in C plots (Fig. 3c, e). Nutrient enrichment and jellyfish additions did not have a significant effect on belowground seagrass, leaf width, or epiphyte dry weight (Table 1, Fig. 2d, f, g). At the plot level, belowground seagrass biomass and leaf width were lowest in J + N plots (Fig. 3d, f). Epiphyte dry weight varied minimally between experimental plots (Fig. 3g).

Grazing intensity (i.e., frequency of total bites by parrotfishes on seagrass shoots) was strongly influenced by both jellyfish and nutrient additions (Table 1, Fig. 2h). We found a significant jellyfish × nutrient interaction in which grazing intensity was substantially lower on seagrass shoots from J plots and significantly higher on seagrass from N plots (Table 1). Specifically, grazing scars were 94% less abundant on shoots from J plots than in N plots, and 60% less abundant on shoots in J + N plots than in N plots (Fig. 3h).

A total of 83 different benthic animal taxa were collected, representing 8 phyla; some of the most common taxa included mollusks, crustaceans, and marine worms (Table 2). Jellyfish, but not nutrient enrichment, reduced mean animal density (Table 1, Fig. 4a). At the plot level, mean animal density was 33% lower in J + F plots than in C plots (Fig. 5a). Mean animal richness and biomass were not affected by jellyfish and nutrient additions (Table 1, Fig. 4b, c), and varied minimally across plots (Fig. 5b, c). Seagrass density was positively related to animal richness ( $R^2 = 0.10, F_{1, 37} = 4.1, P = 0.04$ ) and density ( $R^2 = 0.10, F_{1, 37} = 4.3, P = 0.04$ ), but not biomass ( $R^2 = 0.03, F_{1, 38} = 1.4, P = 0.24$ ). Changes in animal community composition were associated with nutrient enrichment (pseudo- $F_{1, 33} = 2.7, P = 0.01$ ), but not jellyfish (pseudo- $F_{1, 33} = 1.4, P = 0.21$ ). Several species of cerith snails, collectively referred to as *Cerithium* spp., as well as sipunculan worms living in empty cerith snail shells, were most abundant from C plots. *Bulla occidentalis* (Common



Fig. 1. *Cassiopea* medusae resting in a jellyfish addition only (J) plot. The seagrass, *Thalassia testudinum*, surrounds the jellyfish.

**Table 1**  
Summary of two-way ANOVA of nutrient enrichment and jellyfish on nutrient, seagrass, and faunal response variables. Nutrient concentrations, as well as seagrass % cover and shoot densities, represent change in values from the start to the end of the experiment. All reported nutrient and seagrass values reflect data averaged across treatments, and seagrass and faunal data were transformed if necessary. Significant values (at  $\alpha = 0.05$ ) are highlighted in bold.

Variable	df	F	P	Variable	df	F	P
<i>Nutrient concentrations</i>				<i>Nitrogen in seagrass (% dry weight)</i>			
<i>Phosphorus in seagrass (% dry weight)</i>				<i>Nitrogen in seagrass (% dry weight)</i>			
Nutrient enrichment	1	6.4	<b>0.01</b>	Nutrient enrichment	1	0.07	0.93
Jellyfish	1	0.56	0.45	Jellyfish	1	0.37	0.54
J × N	1	0.14	0.71	J × N	1	0.47	0.49
Error	31			Error	28		
<i>Seagrass</i>				<i>Shoot density (# shoots/cm<sup>2</sup>)</i>			
<i>% cover</i>				<i>Shoot density (# shoots/cm<sup>2</sup>)</i>			
Nutrient enrichment	1	7.2	<b>0.01</b>	Nutrient enrichment	1	26.0	<b>&lt;0.0001</b>
Jellyfish	1	4.5	<b>0.04</b>	Jellyfish	1	31.7	<b>&lt;0.0001</b>
J × N	1	0.16	0.68	J × N	1	0.15	0.69
Error	36			Error	36		
<i>Aboveground biomass (g dw/m<sup>2</sup>)</i>				<i>Belowground biomass (g dw/m<sup>2</sup>)</i>			
Nutrient enrichment	1	6.3	<b>0.01</b>	Nutrient enrichment	1	1.5	0.21
Jellyfish	1	2.9	0.09	Jellyfish	1	0.60	0.44
J × N	1	2.2	0.14	J × N	1	0.32	0.86
Error	36			Error	36		
<i>Leaf length (mm)</i>				<i>Leaf width (mm)</i>			
Nutrient enrichment	1	4.5	<b>0.04</b>	Nutrient enrichment	1	0.59	0.44
Jellyfish	1	0.54	0.46	Jellyfish	1	1.4	0.24
J × N	1	0.42	0.52	J × N	1	0.16	0.69
Error	29			Error	28		
<i>Epiphyte dry weight (g dw/shoot)</i>				<i>Herbivore grazing intensity (# bites/shoot)</i>			
Nutrient enrichment	1	1.8	0.17	Nutrient enrichment	1	32.3	<b>&lt;0.0001</b>
Jellyfish	1	1.6	0.20	Jellyfish	1	109.7	<b>&lt;0.0001</b>
J × N	1	0.00	0.92	J × N	1	13.7	<b>&lt;0.0001</b>
Error	36			Error	265		
<i>Benthic fauna</i>				<i>Richness (# taxa/m<sup>2</sup>)</i>			
<i>Density (# animals/m<sup>2</sup>)</i>				<i>Richness (# taxa/m<sup>2</sup>)</i>			
Nutrient enrichment	1	3.3	0.07	Nutrient enrichment	1	2.1	0.15
Jellyfish	1	4.8	<b>0.03</b>	Jellyfish	1	1.1	0.28
J × N	1	1.3	0.24	J × N	1	0.72	0.40
Error	36			Error	36		
<i>Biomass (g dw/m<sup>2</sup>)</i>							
Nutrient enrichment	1	0.58	0.44				
Jellyfish	1	0.16	0.68				
J × N	1	0.03	0.85				
Error	36						

West Indian bubble shell snail) were more abundant from nutrient enrichment plots (N and J + N plots) (Table 2).

#### 4. Discussion

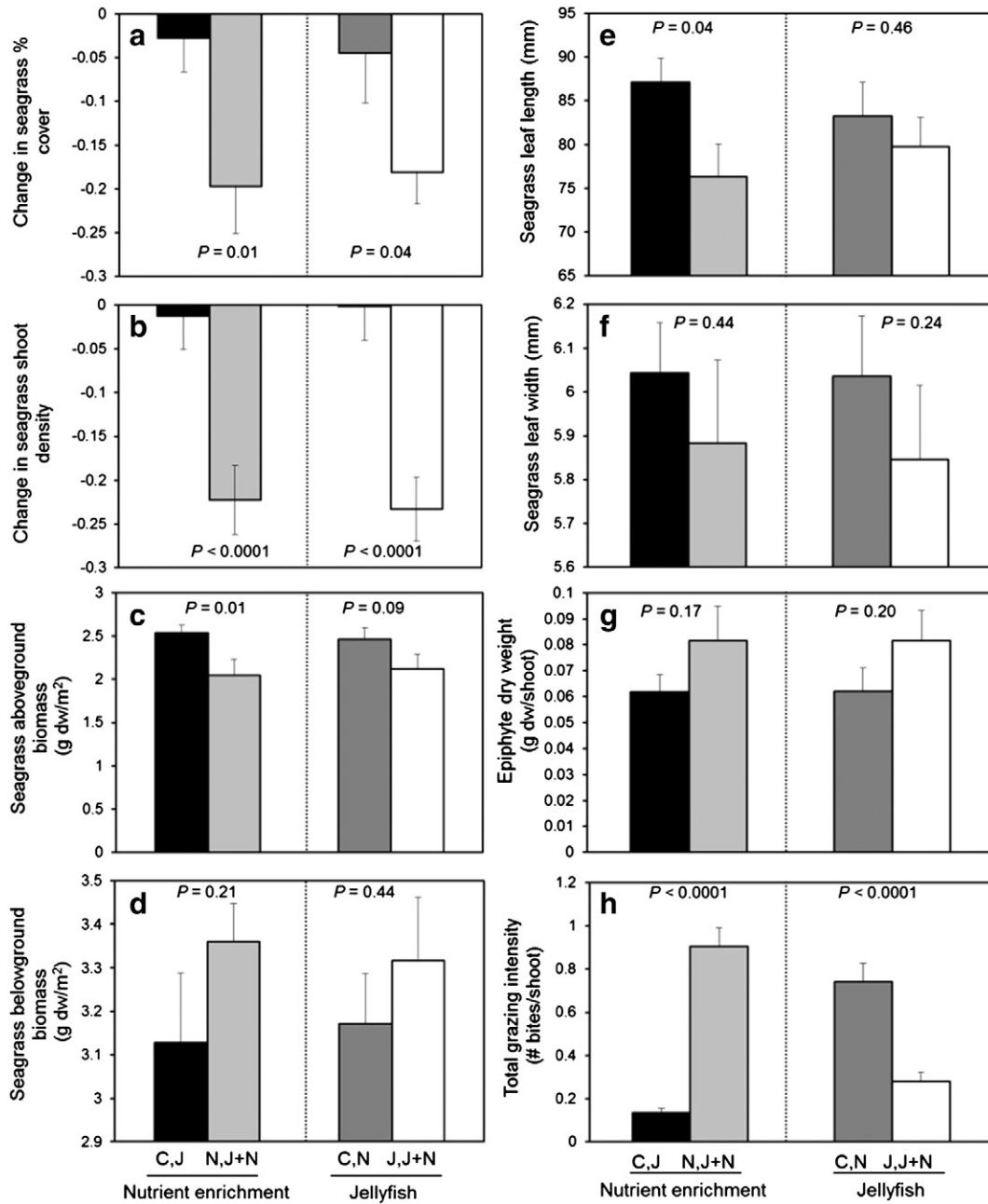
The results of this study demonstrate that elevated nutrient loads and proliferations in benthic jellyfish influence seagrass communities, most notably by modifying seagrass structure and biomass. Herein, we describe how nutrients and jellyfish impact seagrass communities through differing mechanistic pathways.

Nutrient additions had a strong influence on seagrass characteristics, and mean *T. testudinum* cover, shoot density, leaf length, and aboveground biomass all declined as a result of enrichment. One frequently cited cause of seagrass mortality in nutrient-enriched environments is reduced light availability, driven by excessive epiphytic growth on seagrass (Burkholder et al., 2007). However, in this experiment, we did not observe any difference in epiphytic loads on seagrass from fertilized plots, suggesting seagrass loss was not related to this mechanism. These findings mirror results from a recent nutrient enrichment experiment conducted in Mobile Bay, Alabama in which reductions in *Halodule wrightii* abundance and structural complexity occurred, with no evidence of increased epiphyte loads on seagrass leaves in fertilized plots (Antón et al., 2011). Instead, it is possible that the observed reduction in seagrass abundance and complexity could be attributed to a shift in abiotic conditions (e.g., lowered dissolved oxygen concentrations) at

the sediment–water interface as a result of nutrient enrichment (Burkholder et al., 2007).

Jellyfish were also shown to have negative effects on seagrass (seagrass cover and shoot densities). In seagrass beds on Abaco Island, *Cassiopea* are commonly found resting on top of seagrass leaves, and have been suggested to reduce seagrass cover in areas where *Cassiopea* are abundant (Stoner et al., 2014). One reason may be that high densities of relatively sessile *Cassiopea* prevent sunlight from reaching seagrass blades, as well as inhibiting gas exchange across the seagrass leaf surface. High densities of *Cassiopea* may also limit space for seagrass, indirectly affecting seagrass by preventing clonal seagrass development in areas in which seagrass would otherwise grow. In addition, respiration by *Cassiopea* at night depletes dissolved oxygen concentrations at the sediment–water interface (Verde and McCloskey, 1998). Finally, chronic bell pulsation by *Cassiopea* visibly disturbs seagrass shoots, likely reducing the stability of shoots in the sediment (E. Stoner, personal observation).

Grazing intensity by herbivores (i.e., parrotfishes) on seagrass leaves was affected by both nutrient and jellyfish additions, and may have contributed to the modification in seagrass structure and biomass. Specifically, grazing scar frequency was highest on leaves from N plots. While there was no increase in foliar %N from seagrass in N plots, a characteristic that is often linked to increased grazing pressure (Goecker et al., 2005; Heck and Valentine, 2006; McGlathery, 1995), foliar %P was elevated in N plots, potentially resulting in heightened grazing intensity. These findings mirror results from a 2012 study conducted on herbivory of nutrient-enriched *T. testudinum* in Jamaica, in which scarid



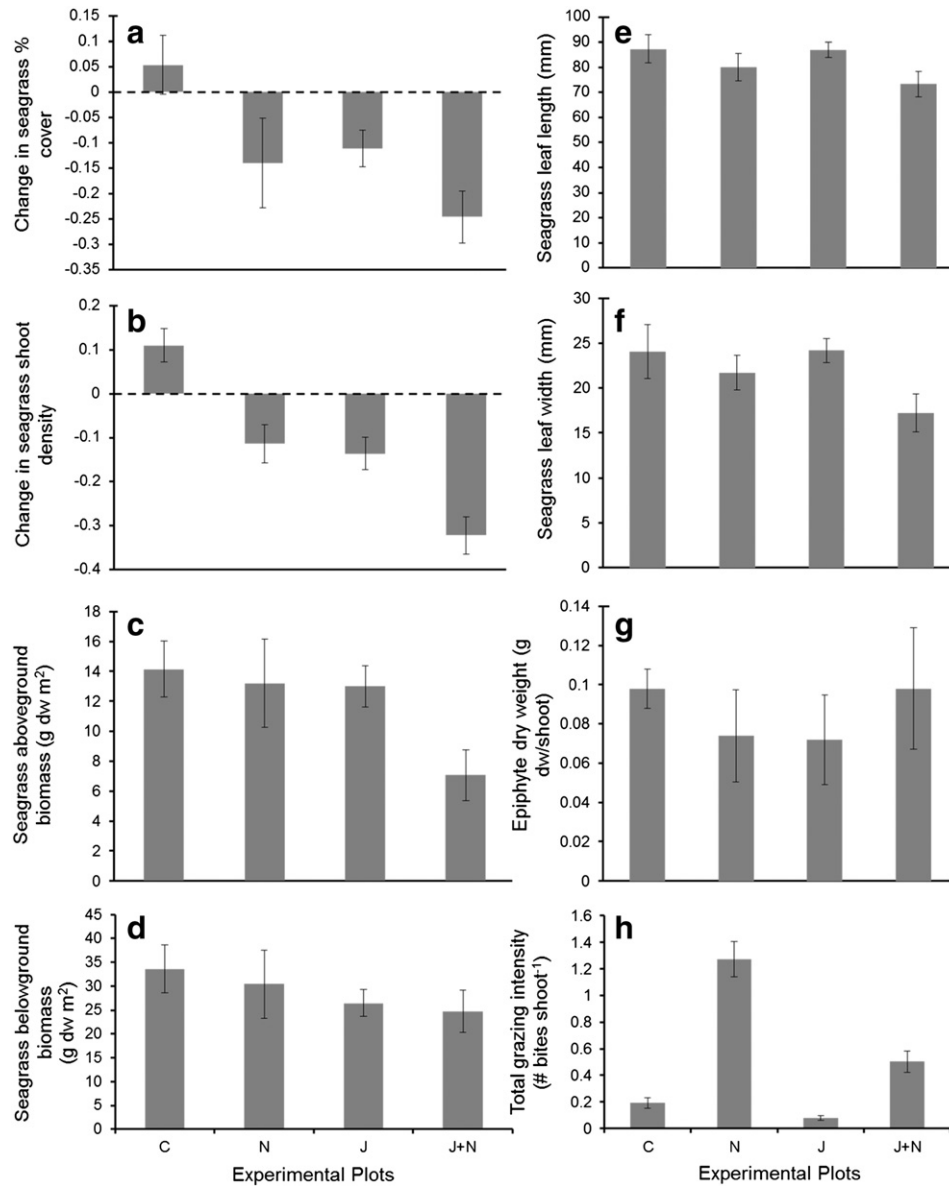
**Fig. 2.** Main treatment effects (nutrient and jellyfish additions) on (a) change in seagrass % cover, (b) change in seagrass shoot density, (c) seagrass aboveground biomass, (d) seagrass belowground biomass, (e) seagrass leaf length, (f) seagrass leaf width, (g) epiphyte dry weight, and (h) total grazing intensity. Values are mean  $\pm$  SE. Experimental plots are C, control; N, nutrient enrichment; J, jellyfish addition; J + N, jellyfish + nutrients. *P* values indicate comparisons of 2-way ANOVA main treatment effects in each panel.

parrotfishes preferentially selected seagrass with elevated P content (Peterson et al., 2012). The authors suggest that herbivores in tropical marine environments may consume seagrass with increased foliar P in order to meet nutritional demands, as phosphorus is the limiting nutrient as a function of carbonate sediments.

One common outcome of increased grazing on seagrass is a shift in seagrass habitat complexity (e.g., lower seagrass density) (Fourqurean et al., 2010; Holzer et al., 2013; McGlathery, 1995). For example, Heck et al. (2006) observed that *H. wrightii* aboveground biomass was substantially lower following experimental nutrient enrichment, which they suggested was a result of increased grazing by large pinfish and crustaceans on nutrient-enriched leaves. Herbivory by fishes has often been found to modify seagrass communities, for instance, in one seagrass bed within the Indo-Pacific, grazing by herbivorous fishes alone has been estimated to drive a loss of up to ten times the daily

seagrass growth (Unsworth et al., 2007). In the wider Caribbean region, parrotfish grazing has been suggested to be a strong, yet underestimated control on seagrass production (Kirsch et al., 2002). Though further research is necessary to establish the magnitude by which seagrass loss in N plots in this experiment is attributable to increased parrotfish grazing pressure, it is possible that grazing played a role in altering seagrass habitat complexity in N plots.

Responses of benthic fauna to jellyfish and fertilizer additions were also complex. Specifically, we found that jellyfish additions drove a reduction in faunal densities, but we observed no effects of jellyfish on taxa richness or biomass. Several of the taxa sampled in our experiment were mobile epifauna that may avoid jellyfish. Consistent with this hypothesis, grazing intensity was lowest in J and J + N plots, perhaps because fishes (e.g., parrotfishes) avoid areas with high jellyfish densities. This is likely a result of mucus regularly released by *Cassiopea*,



**Fig. 3.** Descriptive differences in seagrass characteristics across experimental plots on (a) change in seagrass % cover, (b) change in seagrass shoot density, (c) seagrass aboveground biomass, (d) seagrass belowground biomass, (e) seagrass leaf length, (f) seagrass leaf width, (g) epiphyte dry weight, and (h) total grazing intensity. Values are mean  $\pm$  SE. Experimental plots are C, control; N, nutrient enrichment; J, jellyfish addition; J + N, jellyfish + nutrients.

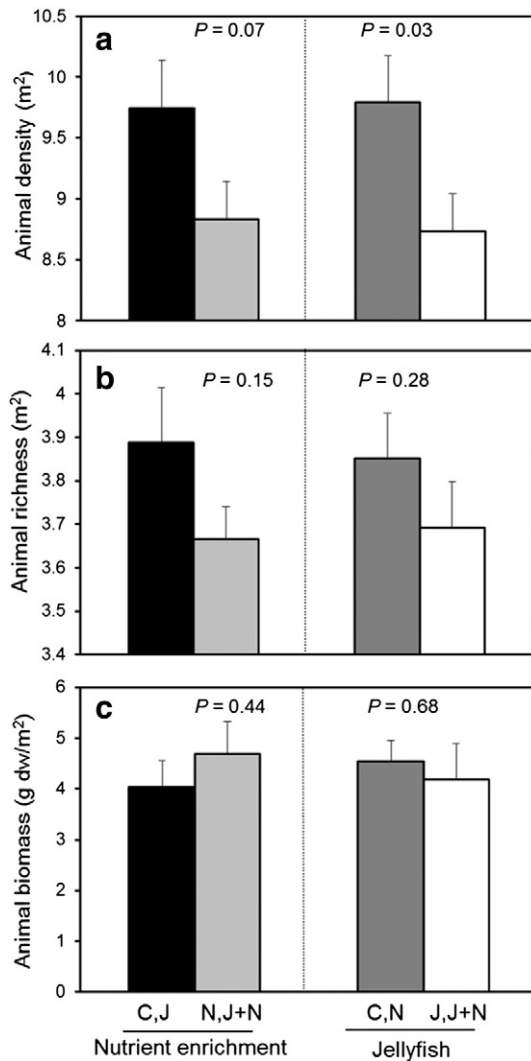
which contains nematocysts. For example, we have observed yellowfin mojarra (*Gerres cinereus*) die after swimming through mucus released from *Cassiopea* (E. Stoner, personal observation). Chronic bell pulsations by *Cassiopea* may also prevent epifauna from adequately utilizing seagrass as a food or habitat resource (e.g., via physical movement of seagrass leaves). Finally, and perhaps most importantly, jellyfish may limit available seagrass habitat for epifauna. In fact, we found that

seagrass density was positively related to both fauna density and richness, suggesting that a reduction in seagrass mediated through jellyfish (and nutrient) additions could affect faunal densities.

We observed no significant effects of nutrient enrichment on faunal univariate response variables. This result is surprising, largely because less available seagrass habitat would have led to fewer fauna (as described above). For example, a nutrient enrichment study found

**Table 2**  
Mean densities  $\pm$  standard error for the most abundant benthic fauna/m<sup>2</sup> for each experimental plot (C, control; N, nutrient enrichment; J, jellyfish addition; J + N, jellyfish + nutrients). The highest density for each taxon is in bold.

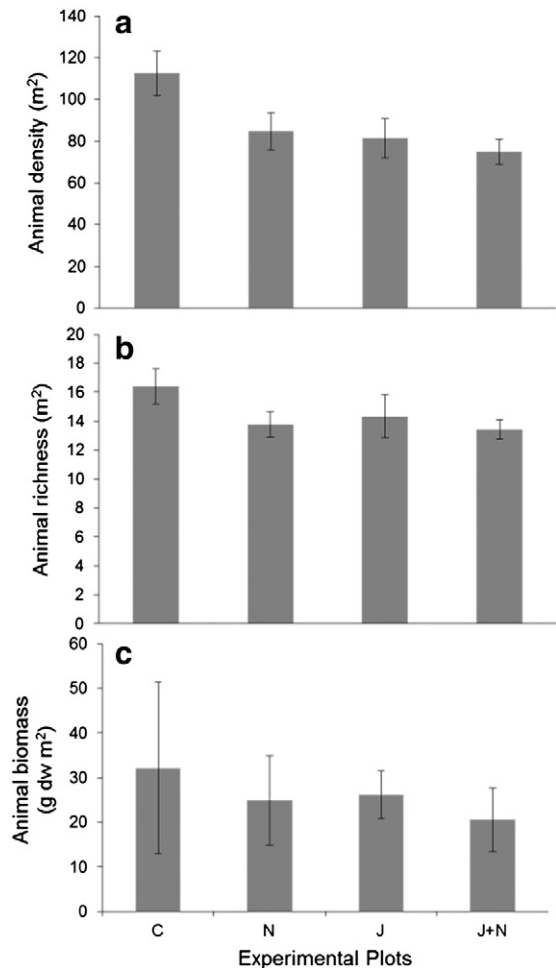
Scientific name	Common name	C	N	J	J + N
<i>Alpheus heterochaelis</i>	Big claw snapping shrimp	<b>5.2 <math>\pm</math> 0.2</b>	4.4 $\pm$ 0.4	4.9 $\pm$ 0.2	4.3 $\pm$ 0.2
<i>Tellina</i> spp.	Tellin clams (multiple species)	<b>3.5 <math>\pm</math> 0.2</b>	2.5 $\pm$ 0.5	2.7 $\pm$ 0.4	3.4 $\pm$ 0.3
<i>Phascolion</i> spp.	Sipunculan worms in cerith shells	<b>3.1 <math>\pm</math> 0.4</b>	1.8 $\pm$ 0.4	1.5 $\pm$ 0.3	2.5 $\pm$ 0.3
<i>Cerithium</i> spp.	Cerith snails (multiple species)	<b>2.9 <math>\pm</math> 0.2</b>	2.1 $\pm$ 0.5	2.6 $\pm$ 0.3	1.4 $\pm$ 0.2
<i>Bulla occidentalis</i>	Common West Indian bubble	1.9 $\pm$ 0.3	<b>2.8 <math>\pm</math> 0.5</b>	1.0 $\pm$ 0.3	2.6 $\pm$ 0.3
<i>Panopeus</i> spp.	Mud crabs (multiple species)	<b>1.7 <math>\pm</math> 0.2</b>	1.0 $\pm$ 0.3	1.2 $\pm$ 0.2	1.3 $\pm$ 0.2



**Fig. 4.** Main treatment effects (nutrient and jellyfish additions) on (a) animal density, (b) animal richness, and (c) animal biomass. Values are mean  $\pm$  SE. Experimental plots are C, control; N, nutrient enrichment; J, jellyfish addition; J + N, jellyfish + nutrients. P values indicate comparisons of 2-way ANOVA main treatment effects in each panel.

that a reduction in seagrass (*H. wrightii*) structural complexity resulted in lower benthic faunal abundance (Antón et al., 2011). Additionally, elevated nutrients may have indirect, negative, effects on benthic fauna abundance in seagrass beds, mediated through shifts in oxygen dynamics (Deegan et al., 2002). However, moderate increases in nutrient concentrations can also lead to higher epifaunal densities, usually grazers, which will consume nutrient-enriched seagrass (Gil et al., 2006). It is possible that we did not observe lower faunal densities and richness as a result of nutrient enrichment because some opportunistic taxa proliferated from elevated nutrients, offsetting declines in more sensitive taxa. For example, the common West Indian bubble snail *B. occidentalis*, one of the most abundant taxa in across all treatments, was most prevalent in N and J + N plots. Little is known about the ecology of this herbivorous gastropod, but one hypothesis for their heightened abundance in nutrient-enriched plots is that increased microphytobenthos on the sediment following nutrient additions (and concomitant declines in seagrass) provided enhanced algal food resources.

It is important to recognize that our findings may vary based on the number of stressors, system location and type, and number of abiotic and biotic factors present. For instance, it is possible that in seagrass beds with higher ambient nutrient concentrations, anthropogenic



**Fig. 5.** Descriptive differences in animal characteristics across experimental plots (a) animal densities, (b) animal richness, and (c) animal biomass. Values are mean  $\pm$  SE. Experimental plots are C, control; N, nutrient enrichment; J, jellyfish addition; J + N, jellyfish + nutrients.

nutrient loading and jellyfish blooms could exacerbate seagrass loss. For example, when nutrients were added to a eutrophic Bermudian seagrass (*T. testudinum*) system, filamentous mat macroalgae increased by an estimated 60–100%, driving declines in seagrass abundance (McGlathery, 1995). In addition, the plots in our experiment were small ( $\sim 1$  m<sup>2</sup>), perhaps not representing the scale at which jellyfish bloom events and nutrient loading occur. Finally, our experiment did not simulate the chronic (i.e., years) nutrient loading that actually occurs in many coastal ecosystems. Prolonging our experiment may have revealed other patterns that were not manifest here.

The results from our study provide another example of the inherent complexity in evaluating ecological responses to multiple stressors (Crain et al., 2008). The role that jellyfish have in structuring ecological systems through top-down and bottom-up processes will increase, as anthropogenic disturbances result in a greater frequency of jellyfish bloom events. Understanding the ecological responses to these blooms, and how they interact with additional stressors, will be important to predict ecological consequences.

#### Acknowledgments

We would like to thank S. Archer, J. Peters and K. Weisenborn for their assistance with field work. We thank Friends of the Environment for their logistical support and the Department of Marine Resources of The Bahamas for research permits. This project was funded by an EPA Star fellowship to EWS, an NSF Graduate Research Fellowship and

a FIU Dissertation Year Fellowship to LAY, and NSF OCE #0746164 to CAL. Comments made by S. Archer, S. Giery, R. Rossi, and two anonymous reviewers enhanced the quality of this manuscript. [SS]

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