



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



Elizabeth W. Stoner^{*}, Lauren A. Yeager¹, Jennifer L. Sweatman², Serina S. Sebilian², Craig A. Layman³

Biological Sciences Department, Florida International University, North Miami, FL 33181, USA

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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 m³ 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

^{*} Corresponding author at: 3000 NE 151st Street, North Miami, FL 33181, USA. Tel.: +1 305 919 4002; fax: +1 305 919 4030.

E-mail address: eston002@fiu.edu (E.W. Stoner).

¹ Current address: Institute of Marine Sciences, University of North Carolina at Chapel Hill, Morehead City, NC 28557, USA.

² Current address: Department of Marine and Ecological Sciences, Florida Gulf Coast University, Ft. Myers, FL 33965, USA.

³ Current address: Department of Applied Ecology, North Carolina State University, Raleigh, NC 27695, USA.

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 (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 2×2 factorial field experiment in a relatively unimpacted nearshore seagrass bed (known as Jungle Creek, $26^\circ 21' 53''$ N, $77^\circ 01' 25''$ W) on Abaco Island, Bahamas. *Cassiopea* are naturally present in this seagrass bed, but at a relatively low density (<2 jellyfish medusa/ 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 (~ 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 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 ~ 5 m. The average low tide depth within plots was 0.68 ± 0.02 m (range = 0.38 m– 1.35 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 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 ~ 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 m^2 plots ~ 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 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.

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