Effects of Epibenthic Jellyfish, *Cassiopea* spp., on Faunal Community Composition of Bahamian Seagrass Beds

Elizabeth W. Stoner*,1, Lauren A. Yeager 1,2, and Craig A. Layman1,3

**Abstract** - Pelagic jellyfish blooms have been observed frequently in many parts of the world, which can affect various aspects of marine ecosystems. While specific effects of jellyfish blooms on pelagic marine communities are well described, there is little information on the effects of epibenthic jellyfish on benthic marine fauna. *Cassiopea* spp. (upside-down jellyfish) are relatively sessile, epibenthic jellyfish that live in seagrass habitats, and may be found in high densities in shallow coastal water bodies. In this study, we surveyed seagrass beds on Abaco, The Bahamas, that had similar seagrass cover but naturally varying densities of *Cassiopea*. We found that benthic taxa richness was lower in plots with high jellyfish densities; however, overall benthic animal densities and biomass did not differ between plots. Benthic community composition differed between plots with high versus low jellyfish densities. Our findings suggest that *Cassiopea* jellyfish may have subtle effects on benthic fauna communities, perhaps mediated through several mechanistic pathways.

**Introduction**

Gelatinous zooplankton, (e.g., jellyfish), are conspicuous and ecologically important organisms in marine environments. Although there is a paucity of long-term jellyfish-density data, there is compelling evidence to suggest that some jellyfish populations are increasing in certain parts of the world, likely due to anthropogenic disturbances (Condon et al. 2012, Purcell 2012, Richardson et al. 2009). These jellyfish “blooms” can have substantial effects on pelagic community composition and ecosystem function (Arai 2001, Lynam et al. 2006, Purcell and Arai 2001, West et al. 2009a).

Jellyfish blooms may affect pelagic ecosystems through several mechanistic pathways. For example, predation by jellyfish can affect the abundance of targeted prey (zooplankton) directly (Carr and Pitt 2008, Purcell and Arai 2001, Uye 2011). Jellyfish blooms may also lead to intensified interspecific competition with zooplanktivores for shared food resources (Brodeur et al. 2008). Jellyfish blooms may contribute increased inorganic nutrients via excretion that can stimulate planktonic primary production, and dead jellyfish may act as food for benthic fauna (i.e., jellyfish “falls”) (Pitt et al. 2009; West et al. 2009a, b; Yamamoto et al. 2008).

While our understanding of effects of jellyfish blooms on pelagic communities has improved in recent years, there has been little research regarding potential impacts of epibenthic jellyfish on benthic faunal communities. Jellyfish belonging to

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1Biological Sciences Department, Florida International University, North Miami, FL 33181.  
2Current address - Institute of Marine Sciences, University of North Carolina at Chapel Hill, Morehead City, NC 28557.  
3Current address - Department of Applied Ecology, North Carolina State University, Raleigh, NC 27695.  
*Corresponding author - eston002@fiu.edu.  
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the genus Cassiopea (upside-down jellyfish, hereafter referred to as Cassiopea) are relatively-sessile, epibenthic jellyfish, and contain photosynthetic dinoflagellates (zooxanthellae) that provide energy to the jellyfish, supplementing heterotrophically derived sources of nutrition (Verde and McCloskey 1998). Cassiopea are globally distributed in tropical environments and are ubiquitous in seagrass beds, reefs, lagoons, and mangrove habitats (Fleck and Fitt 1999, Holland et al. 2004, Niggl and Wild 2010).

Cassiopea may play an important ecological role by exerting top-down and bottom-up controls on nearshore food webs. For instance, Cassiopea may reduce macrophyte cover primarily via shading, diminishing food and habitat availability for benthic fauna. Cassiopea may also compete for space with other benthic flora and fauna, and some fauna (e.g., fishes) may avoid areas with high jellyfish densities as a result of nematocysts that are released regularly by Cassiopea (Stoner et al. 2011). Further, Cassiopea contribute organic nutrients (C and N) through mucoid exudate, and they may facilitate the release of inorganic nutrients (N and P) from the sediment–water interface via chronic bell pulsation. Finally, Cassiopea may consume zooplankton and particulate organic matter (POM), affecting food availability to benthic fauna (Jantzen et al. 2010, Larson 1997, Niggl et al. 2010). Cassiopea may also be an important food resource for some marine consumers, though to date, only one nudibranch species in Puerto Rico has been definitively reported to consume Cassiopea oral arms (Brandon and Cutress 1985).

In The Bahamas, Cassiopea are abundant in seagrass beds, systems which are critical habitats for numerous other benthic organisms (Antón et al. 2011, Heck et al. 2008, Nagelkerken et al. 2000). Recently, Stoner et al. (2011) demonstrated that Cassiopea are over 95% more abundant as well as larger in human-impacted coastal areas in The Bahamas, potentially affecting benthic fauna in nearshore systems including seagrass beds. Our objective was to evaluate whether seagrass beds with naturally varying densities of Cassiopea were associated with different assemblages of benthic animals. We hypothesized that there would be lower taxa richness, animal density, and biomass, as well as different community composition, in areas with high jellyfish densities.

**Field-site Description**

We conducted benthic surveys in two nearshore seagrass beds (sites referred to as Snake Cay [SC; 26°27′22″N, 77°03′27″W] and Jungle Creek [JC; 26°21′53″N, 77°01′25″W]) on Abaco Island, The Bahamas, in May and June 2011 (Fig. 1). Both study sites were directly adjacent to mangrove habitat, and each was dominated by >50% Thalassia testudinum Banks ex König (Turtle Grass) cover, <2 m in depth at low tide, and characterized by silty-sandy sediment (≈0.05 mm particle size), which suggests lower water velocities. Sediment was classified by collecting sediment samples (n = 3/site) from each site, visually estimating percent sediment contributions in each sample, and classifying sediment type using the USDA soil classification triangle (Schoeneberger et al. 2002). Both Snake Cay and Jungle Creek are coastal areas that were identified by Stoner et al. (2011) as relatively unimpacted by human activities. Few buildings were located in areas adjacent to these sites, which we used
as a proxy for human population density (buildings within a 3-km radius from the mid-point of each site: SC = 0.3 buildings/km², JC = 0.24 buildings/km²).

Methods

Prior to conducting surveys, we identified areas with high and low densities of jellyfish within each of the sites. High-density plots (HD; \( n = 7 \) for both sites) were defined as areas with \( >3 \) jellyfish/m², which was based on the approximate mean number of jellyfish in human-impacted sites in Stoner et al. (2011). In the present study, the mean number (± SD) of jellyfish found within HD plots was \( 4.5 \pm 1.4 \) jellyfish/m². Low-density plots (LD; \( n = 6 \) in Snake Cay, \( n = 7 \) in Jungle Creek), contained an average of \( 0.3 \pm 0.31 \) jellyfish/m². HD and LD plots at each site were interspersed, and each plot was 16 m² in size and at least 5 m apart. Cassiopea are relatively sessile and move infrequently, typically only when disturbed. Research by Jantzen et al. (2010) on Cassiopea mobility suggested Cassiopea will remain within a 1-m² area for an average of \( \approx3 \) days. As such, we expected that the study areas had fairly stable jellyfish-density levels over a timespan of days to weeks, a period of time long enough to influence local floral and faunal traits.

Figure 1. Map of Abaco Island, Bahamas (A) indicating the two survey sites represented by squares, in nearshore seagrass beds in Snake Cay (B) and Jungle Creek (C). Both sites are directly adjacent to shallow Rhizophora mangle L. (Red Mangrove) habitat.
One potential pathway in which *Cassiopea* may affect benthic seagrass community composition is through altered seagrass density. Seagrass characteristics (e.g., shoot biomass, shoot density, and leaf morphology) have been previously shown to be important factors affecting composition of benthic animal communities (Ansari et al. 1991, Heck and Wetstone 1977, Orth et al. 1984). In an attempt to isolate the direct effects of *Cassiopea* on benthic fauna independent of seagrass density, we selected sites a priori with apparently similar seagrass cover. We estimated % seagrass cover with 1-m² quadrats (*n* = 5/plot). In order to assess seagrass characteristics in more detail, a seagrass core (plastic bucket without bottom, diameter = 23 cm, depth = 22.5 cm) was used to collect and quantify above- and belowground seagrass biomass (*n* = 4/plot).

To sample benthic fauna, we haphazardly placed a cylindrical, plastic, throw trap (area ≈0.75 m²) in each plot. 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 in Hammerschlag-Peyer et al. 2013). Animal specimens collected were >0.5 mm as that was the size of mesh for the smallest dip net used. Although some benthic infauna were collected (i.e., clams), most of the taxa collected were motile benthic epifauna. Animals were then placed on ice in the field and frozen for later processing. *Cassiopea* found within each plot were enumerated.

We sorted and identified animal samples in the laboratory to the lowest taxonomic level practical, then dried them at 60 °C to ascertain dry biomass. For mollusks, as well as *Phascolion* spp. (sipunculan worms found in cerith snail shells), shells were removed and only soft tissue was dried and weighed. Seagrass samples were cleared of mud and debris by gently rinsing them under deionized water, then separated into aboveground biomass (all attached green leaves of short shoots), dead seagrass, and belowground biomass (rhizomes and roots). We removed any adhered epiphytes from intact short shoots by carefully scraping blades with a razor. Seagrass above- and belowground biomass was dried at 60 °C for 48–72 hours and weighed in order to obtain dry weight (g).

**Statistical analyses**

Seagrass percent cover and aboveground and belowground seagrass biomass from cores were averaged by plot. Three plots (LD plots from Jungle Creek) were discarded from analysis as they did not adhere to our initial seagrass criteria (>50% seagrass cover). We used a two-way ANOVA in order to determine whether seagrass percent cover and biomass differed between HD and LD plots and/or between sites (IBM SPSS v. 20.0).

Animal communities were evaluated based on taxa richness, density (i.e., the number of animals found per m²), biomass (dry weight of animals found per m²), diversity, and community composition. We calculated species diversity using the Shannon-Weiner diversity index (H’). A two-way ANOVA was used to determine whether univariate response variables (taxa richness, density, biomass, and diversity) varied between HD and LD plots and between sites (Snake Cay or Jungle Creek). In the event of a significant interaction between jellyfish density category and site, we used a Tukey post-hoc test to evaluate which groups differed from one other (SAS® software v.9.2).
Benthic animal densities were square-root transformed to down-weight the influence of dominant taxa (Clarke 1993), and a Bray-Curtis similarity matrix was calculated for all species contributing at least 1% to the total animal density. We used a two-way analysis of similarity (ANOSIM) to determine if there were differences in community composition between sites and/or treatments (PRIMER® v6) (Clarke 1993). Post-hoc one-way ANOSIMs were used to test for a difference in community composition between HD and LD plots for each site, and a SIMPER analysis was used to evaluate which taxa may be driving differences. We used non-metric multidimensional scaling (nMDS) plots to visualize similarities/dissimilarities in benthic animal communities between HD and LD plots.

Results

Initial estimates of percent seagrass cover did not vary between HD and LD plots (mean HD ± SD = 67.2 ± 15.2%, LD = 70.9 ± 7%; \( F_{1,20} = 1.0, P = 0.32 \)), but did differ between the two sites (mean JC ± SD = 63.2 ± 11.4%, SC = 75.4 ± 10.3%; \( F_{1,20} = 7.0, P = 0.01 \)). Aboveground seagrass biomass from core samples indicate that there was no difference in seagrass biomass between HD and LD plots (\( F_{1,20} = 3.6, P = 0.07 \)) nor between sites (\( F_{1,20} = 0.30, P = 0.58 \)). Likewise, belowground seagrass biomass did not vary between plot type (\( F_{1,20} = 0.51, P = 0.60 \)) nor between sites (\( F_{1,20} = 0.39, P = 0.53 \)).

A total of 51 animal taxa were collected, representing 45 families and seven phyla. The most abundant and frequently observed animals were molluscs, crustaceans, and polychaetes (Table 1). Mean taxa richness was lower in HD plots (mean ± SD: HD = 10.2 ± 2.6, LD = 14.3 ± 3.5; \( F_{1,20} = 8.5, P = 0.009 \)) and in Jungle Creek

<table>
<thead>
<tr>
<th>Scientific name</th>
<th>Common name</th>
<th>Low Cassiopea density</th>
<th>High Cassiopea density</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bulla umbilicata Roding</td>
<td>Common West Indian Bubble (snail)</td>
<td>1.4 ± 1.4</td>
<td>4.2 ± 4.5</td>
</tr>
<tr>
<td>Hermodice carunculata (Pallas)</td>
<td>Bearded Fireworm</td>
<td>1.3 ± 1.4</td>
<td>0.4 ± 0.9</td>
</tr>
<tr>
<td>Holothuria mexicana Ludwig</td>
<td>Donkey Dung Sea Cucumber</td>
<td>3.8 ± 2.9</td>
<td>0.6 ± 1.4</td>
</tr>
<tr>
<td>Ophionereis reticulata (Say)</td>
<td>Reticulated Brittle Star</td>
<td>1.9 ± 2.6</td>
<td>1.3 ± 1.0</td>
</tr>
<tr>
<td>Phascolion spp. (in cerith shells)</td>
<td>Sipunculan worms</td>
<td>8.6 ± 4.5</td>
<td>6.3 ± 4.7</td>
</tr>
<tr>
<td>Pitho mirabilis (J.F.W. Herbst)</td>
<td>Pitho Crab</td>
<td>1.9 ± 1.7</td>
<td>1.3 ± 2.3</td>
</tr>
<tr>
<td>Tellina listeri Roding</td>
<td>Speckled Tellin (clam)</td>
<td>6.1 ± 3.0</td>
<td>2.5 ± 2.1</td>
</tr>
</tbody>
</table>

Jungle Creek

<table>
<thead>
<tr>
<th>Scientific name</th>
<th>Common name</th>
<th>Low Cassiopea density</th>
<th>High Cassiopea density</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bulla umbilicata</td>
<td>Common West Indian Bubble</td>
<td>16.3 ± 9.1</td>
<td>18.1 ± 13.3</td>
</tr>
<tr>
<td>Cerithium spp.</td>
<td>Cerith snails</td>
<td>12.9 ± 6.7</td>
<td>3.3 ± 3.3</td>
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<td>Bearded Fireworm</td>
<td>2.3 ± 3.3</td>
<td>1.3 ± 3.0</td>
</tr>
<tr>
<td>Parvilucina spp. Dall</td>
<td>Lucinid clam</td>
<td>8.3 ± 9.5</td>
<td>3.6 ± 7.0</td>
</tr>
<tr>
<td>Phascolion spp. (in cerith shells)</td>
<td>Sipunculan Worms</td>
<td>1.3 ± 2.0</td>
<td>3.6 ± 4.6</td>
</tr>
<tr>
<td>Pitho mirabilis</td>
<td>Pitho Crab</td>
<td>1.5 ± 2.2</td>
<td>0.2 ± 0.3</td>
</tr>
<tr>
<td>Prunum apicinium (Menke)</td>
<td>Common Atlantic Marginella</td>
<td>2.3 ± 1.0</td>
<td>0.9 ± 1.6</td>
</tr>
</tbody>
</table>
Figure 2. Mean (± SD) taxa richness (A), total animal density (B), and total animal biomass (C) between plots with high and low densities of *Cassiopea* jellyfish in Snake Cay (SC) and Jungle Creek (JC). * denotes a significant effect of jellyfish density (low density [LD] vs. high density [HD]). Different letters above bars denote a significant site effect at α = 0.05.
(mean ± SD: JC = 10.2 ± 3.5, SC = 13.4 ± 3.3; F$_{1,20}$ = 4.9, P = 0.04) (Fig. 2A). Taxa diversity (H’) did not differ between plot type (mean ± SD: HD = 1.9 ± 0.40, LD = 2.2 ± 0.45; F$_{1,21}$ = 1.5, P = 0.22), but was lower in Jungle Creek (mean ± SD: JC = 1.7 ± 0.46, SC = 2.3 ± 0.23; F$_{1,21}$ = 12.1, P = 0.002). Animal density and biomass did not significantly differ between HD and LD plots (P > 0.05; Figs. 2B, 2C). Total benthic animal density differed between sites (F$_{1,20}$ = 4.4, P = 0.04), being higher at Jungle Creek (mean ± SD: JC = 57.4 ± 29.3 ind./m$^2$, SC = 39.5 ± 11.8 ind./m$^2$; Fig. 2B). Animal biomass was lower in Jungle Creek (mean ± SD: JC = 0.20 ± 0.05 g/m$^2$, SC = 0.35 ± 0.07 g/m$^2$; F$_{1,20}$ = 25.3, P < 0.001; Fig. 2C).

Community composition differed marginally between HD and LD plots (global R = 0.17, P = 0.053) and differed between sites (global R = 0.33, P = 0.001). In Snake Cay, benthic animal community composition differed between HD and LD plots (global R = 0.28, P = 0.006; Fig. 3A). The observed difference in community composition between HD and LD plots were likely driven by a few taxa. In LD plots, clams (Tellina listeri [Speckled Tellin] and Parvilucina spp.) and Cerithium spp. (i.e., several species of cerith, hereafter collectively referred to as “cerith snails”) were some of the most abundant taxa, while in HD plots, the snail Bulla umbilicata Roding (Common West Indian Bubble), were more abundant (Table 1). No difference in community composition was found between plot types in Jungle Creek (global R = 0.02, P = 0.3; Fig. 3B).

**Discussion**

Our findings demonstrate that epibenthic jellyfish have subtle effects on benthic fauna. As we hypothesized, we found lower taxa richness in HD plots than LD plots, and a difference in faunal community composition between HD and LD plots at one of the two study sites. We did not detect a significant difference in animal density or biomass, though many individual taxa were less abundant in HD plots than LD plots, likely attributable to a higher abundance of some opportunistic taxa that may benefit in some way from high jellyfish densities. We discuss several possible mechanisms that may have driven these findings below.

![Figure 3](image_url)
Lower fauna richness and differences in faunal community composition may be attributed to direct and indirect effects that *Cassiopea* have on seagrass faunal communities. First, some taxa may actively avoid areas with high *Cassiopea* densities, perhaps due to *Cassiopea* mucus, filled with nematocysts, which is regularly released by the jellyfish (Niggl and Wild 2010). Observations from seagrass beds with high jellyfish densities suggest that there are fewer mesograzers and small, scarrid parrotfish grazing scars on seagrass leaves compared to areas with no jellyfish present, suggesting avoidance of *Cassiopea* (E. Stoner, unpubl. data). Second, high densities of *Cassiopea* may also limit available habitat for several animals, including sessile invertebrates (e.g., clams) and slow-moving animals that require space to successfully forage (e.g., sea cucumbers). Third, consumption by *Cassiopea* of POM may limit food availability to dominant benthic suspension feeders (e.g., molluscs). In addition to filtering POM, *Cassiopea* ingest zooplankton (e.g., copepods, ostracods, tanaids, nematodes, fish eggs, and mollusk veligers; Larson 1997), driving declines in food resources available to other benthic fauna found in this study. Another set of indirect effects on fauna may be mediated through seagrass cover, although that was not explored here because we attempted to limit our study to plots with similar levels of seagrass cover.

Although taxa richness and overall community composition differed between HD and LD plots, we did not observe any difference in total animal density or biomass. This finding is largely due to an increased abundance of opportunistic taxa that might be responding to jellyfish presence. For instance, the Common West Indian Bubble Snail is a nocturnal, herbivorous, gastropod which feeds in seagrass beds (Malaquias and Reid 2008). We have frequently observed bubble snails adjacent to *Cassiopea*, perhaps because they utilize *Cassiopea* as refugia to minimize predation risk, but there are no data or studies to either support or refute this or any alternative hypothesis. This example underscores how little is known about interactions of *Cassiopea* with other species, information that is clearly needed to elucidate their role in the structure and function of seagrass ecosystems.

It is important to note that jellyfish densities found in HD plots are lower than what has been observed in many human-impacted seagrass beds. For instance, in one bay on Abaco, *Cassiopea* densities were found to be >13/m², 3 times the density in HD plots from these surveys (Stoner et al. 2011). It is possible that more substantial effects would be apparent at much higher *Cassiopea* densities. Experimental manipulation of jellyfish densities is a logical next step to further describe the role of *Cassiopea* blooms in structuring seagrass communities. This understanding will be critical, as the frequency and magnitude of jellyfish blooms may be increasing in anthropogenically disturbed marine systems.

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**Literature Cited**


