



Size and density of upside-down jellyfish, *Cassiopea* sp., and their impact on benthic fluxes in a Caribbean lagoon

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ABSTRACT

Anthropogenic disturbances may be increasing jellyfish populations globally. Epibenthic jellyfish are ideal organisms for studying this phenomenon due to their sessile lifestyle, broad geographic distribution, and prevalence in near-shore coastal environments. There are few studies, however, that have documented epibenthic jellyfish abundance and measured their impact on ecological processes in tropical ecosystems. In this study, the density and size of the upside-down jellyfish (*Cassiopea* spp.) were measured in Codrington Lagoon, Barbuda. A sediment core incubation study, with and without *Cassiopea*, also was performed to determine their impact on benthic oxygen and nutrient fluxes. Densities of *Cassiopea* were 24–168 m⁻², among the highest reported values in the literature. Under illuminated conditions, *Cassiopea* increased oxygen production >300% compared to sediment alone, and they changed sediments from net heterotrophy to net autotrophy. *Cassiopea* increased benthic ammonium uptake, but reduced nitrate uptake, suggesting they can significantly alter nitrogen cycling. Future studies should quantify the abundance of *Cassiopea* and measure their impacts on ecosystem processes, in order to further determine how anthropogenic-related changes may be altering the function of tropical coastal ecosystems.

1. Introduction

Globally, there have been increasing reports of massive jellyfish blooms (Purcell et al., 2007). These blooms have been attributed to several factors, including overfishing, climate change, eutrophication, translocation, and marine construction and development (Purcell et al., 2007; Dong et al., 2010; Duarte et al., 2013). Long-term data on jellyfish abundance is lacking, thus making it difficult to identify trends and relate it to changes in the environment (Condon et al., 2013). However, analyses of anecdotal data suggest that jellyfish populations have been increasing since the 1950s (Brotz et al., 2012). Regardless of the causes, changes in the relative proportion of jellyfish within marine communities may have important consequences for ecosystem function, yet these consequences have rarely been documented.

The upside-down jellyfish *Cassiopea* spp. (Scyphozoa, Rhizostomidae) are epibenthic organisms that harbor photosynthetic endosymbionts. They are commonly found in ecologically- and economically important habitats, such as around coral reefs, and within seagrass

beds and mangrove-dominated lagoons (Ohdera et al., 2018). *Cassiopea* geographic ranges have increased, they may be increasing in abundance in coastal ecosystems due to anthropogenic disturbances (Stoner et al., 2011), and may act as bio-invasers (Keable and Ah Yong, 2016; Morandini et al., 2017). Yet, few studies have quantified the abundance of *Cassiopea* and their ecological impacts. Densities up to 7 m⁻² have been described in the Bahamas (Stoner et al., 2011) and densities as high as 31 m⁻² and 42 m⁻² were found in the Red Sea (Niggli and Wild, 2010) and Mexico's Nichupte Lagoon System (Colado Vides et al., 1998), respectively. Stoner et al. (2011) suggested that *Cassiopea* density and size may be related to nutrient availability, as *Cassiopea* and their algal symbionts are generally nutrient limited. Anthropogenic disturbances that promote nutrient loading may thereby enhance *Cassiopea* populations (Arai, 2001; Stoner et al., 2011). High nutrient availability can increase symbiont density (Stoner et al., 2016), although it is not clear if this is due to increased water column nutrients or through increased secondary production (*i.e.*, increased jellyfish prey). *Cassiopea* tissues also can assimilate nitrogen directly

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from the water column to support nitrogen demands (Freeman et al., 2016).

High densities of *Cassiopea* alter benthic invertebrate community composition in seagrass beds (Stoner et al., 2014a) and reduce relative coverage and shoot density of seagrass (Stoner et al., 2014b). The pumping motion of the bell on the sediment promotes exchange between porewater and the water column (Jantzen et al., 2010); in addition, direct assimilation of dissolved inorganic nitrogen by *Cassiopea* couples benthic and pelagic environments (Jantzen et al., 2010; Welsh et al., 2009). Blooms and subsequent decay of jellyfish populations can lead to major changes in biogeochemical cycles in coastal ecosystems, as jellyfish can mediate pathways for assimilation and recycling of carbon, nitrogen, and phosphorous (West et al., 2009; Chelsky et al., 2016).

The aims of this study were to quantify the density and size distribution of *Cassiopea* populations within a portion of Codrington Lagoon (Barbuda, West Indies) that is affected by anthropogenic nutrients, as well as to determine impacts of *Cassiopea* on benthic fluxes. Although local citizens reported increases in the prevalence of *Cassiopea* in recent years (Ruttenberg et al., 2018), no previous studies have collected quantitative measurements to document abundance or other changes through time. We expected oxygen demand and nitrogen effluxes would increase in the presence of *Cassiopea* under dark conditions. In contrast, light conditions would promote oxygen production and nitrogen assimilation. The insights from this study were then used to suggest potential management practices.

2. Materials and methods

2.1. Study site

The study was performed on the island of Barbuda, which is part of the nation of Antigua and Barbuda, located in the Lesser Antilles area of the Caribbean (Fig. 1). Barbuda (161 km²) is a sparsely populated, low-lying, coral island with only one town (Codrington); the rest of the island remains largely undeveloped (Fig. 1). Codrington had a population of ~1800 prior to Hurricane Irma in 2017, but was devastated by the hurricane and has had much fewer residents since then (Boger et al., 2016). Codrington Lagoon (~18 km²; Fig. 1) is located on

the west side of the island and it supports commercial and subsistence fishing, as well as tourism (Ruttenberg et al., 2018). Soils on Barbuda are highly permeable and shallow with groundwater less than 1.5 m from the soil surface. Barbuda has no centralized sewage treatment system and most residences have only septic systems or pit latrines (US Army Corps of Engineers, 2004). Therefore, wastewater likely enters groundwater and may impact drinking water supplies; for example, coliform bacteria have been found in groundwater wells throughout Barbuda (Boger et al., 2014).

2.2. *Cassiopea* survey

Cassiopea populations were sampled during February 2014 in a section of Codrington Lagoon locally known as Pearl Harbor. It is adjacent to the northwest portion of the town of Codrington. Three sites within Pearl Harbor were sampled, including one site at the mouth of a creek where commercial fishermen keep moorings for their boats (Site 1), and two sites adjacent to mangrove islands that were further from the creek (Sites 2 and 3; Fig. 1). The sites were located >20 m apart, water depth was < 1 m, and the tide was ebbing during sample collection. Discussions with local fishermen and naturalists suggested that Site 1 would be most disturbed due to its proximity to the commercial activity in the creek. At each site, we randomly tossed a 0.25 m² quadrat six times and counted the number of individuals within each quadrat. After completing the density measurements, 25–30 *Cassiopea* were randomly selected at each site, and the bell diameter (cm) was measured. The mean densities and bell diameters were used to estimate benthic coverage (%) for each site as this was not directly measured in the field (Niggli and Wild, 2010). Mean bell diameter (cm) was converted to m² and then multiplied by the mean density (No. m⁻²). Salinity in Pearl Harbor was measured with a refractometer, and a Hach® HQ30d luminescent dissolved oxygen probe (Loveland, CO) was used to measure temperature and oxygen. Leaf fragments (n = 10) were collected from seagrass (*Thalassia testudinum*) beds adjacent to the three study sites in Pearl Harbor. The fragments were dried at 60 °C, ground into a powder, and measured on a PerkinElmer 2400 Series II CHN analyzer (PerkinElmer Life and Analytical Sciences, Shelton, CT; Zarnoch et al., 2017). The % carbon and nitrogen were used as a proxy for nu-

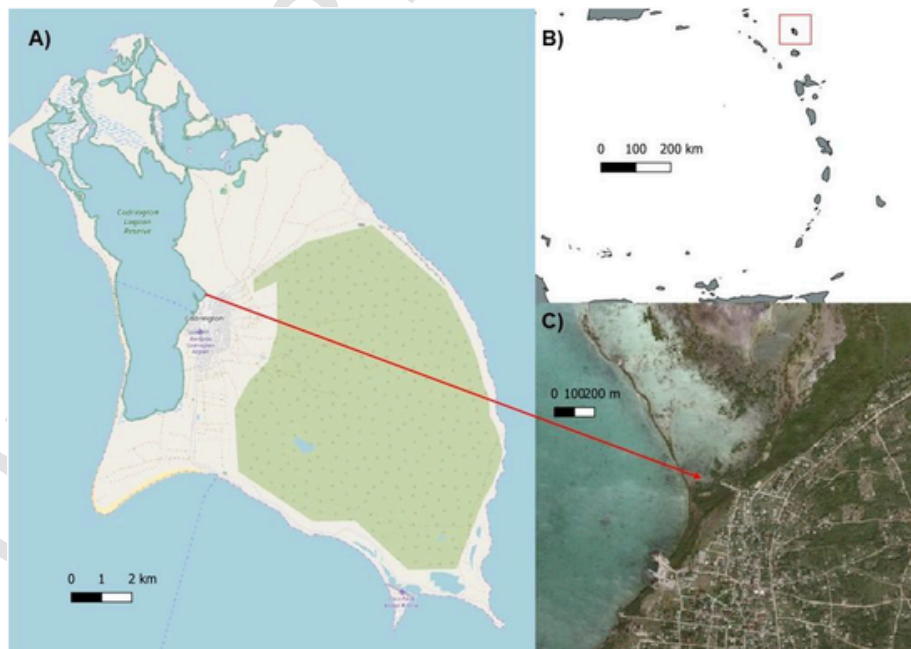


Fig. 1. A map of the study site in Codrington Lagoon in Barbuda (A), a part of Antigua and Barbuda in the Caribbean's Lesser Antilles (B; Barbuda is in the box). The *Cassiopea* were surveyed near the mangrove islands in an area of the lagoon called Pearl Harbor (C). Barbuda has only one town (Codrington) and the remainder of the island is largely undeveloped.

trient loading assuming an enriched site would have high % nitrogen (Stoner et al., 2011; Duarte 1990).

2.3. Benthic fluxes

Sediment cores (acrylic, 25 cm length x 7.6 cm width) were collected at Site 3 in Pearl Harbor using a coring device with a one-way valve designed to reduce disturbance of the sediment-water interface (Gardner et al., 2006). The cores were inserted into the sediment to a depth of ~12 cm and had a volume of ~620 mL of overlying site water. Three of the sediment cores collected included a single *Cassiopea* (~6 cm bell diameter) and three of the cores included sediment only. All core samples were taken within 3–5 m of each other. One additional core was collected with only site water to serve as a water column blank (total of 7 cores). Three 20 L carboys of site water were collected from Pearl Harbor for use in static core incubations and for determining ambient ammonium (NH_4^+), nitrate (NO_3^-), and soluble reactive phosphorous (SRP). The sediment cores and site water were placed in dark coolers and brought back (<1 h travel time) to the Barbuda Research Complex to perform benthic flux incubations. Approximately 90% of the overlying water within each core was carefully removed with a 60 mL plastic syringe and replaced with new site water. Each core was submerged in site water within a 19 L container and carefully fitted with a gas-tight lid with no head space or gas bubbles in the cores. Each core had a 2.5 cm magnetic stirrer that was rotated by an external magnet. Cores were stirred slowly to prevent O_2 stratification, sediment resuspension, and disturbance to *Cassiopea*. Light and dark incubations were performed under *in situ* temperature conditions for ~2.8 h. Light incubations were performed under ambient light at mid-day and then dark incubations were performed, with the same cores, in an enclosed black container. The overlying water (~90%) in each core was carefully removed and replaced with new site water in between the light and dark incubation. Net flux rates were calculated as the average of the light and dark flux rates (Eyre and Ferguson, 2005).

Samples were collected at the beginning and end of each incubation period for measuring gas and nutrient concentrations. Nutrient samples were withdrawn from the cores with a plastic syringe and filtered (0.2 μm nylon syringe filters, Thermo Scientific, Rockwood, TN, USA) into three 20 mL scintillation vials and frozen at -20°C until measurement of NH_4^+ , NO_3^- , and SRP. Water samples from the cores were also transferred into triplicate 12 mL exetainer vials (Labco Ltd., Lampeter, United Kingdom). Each vial was filled slowly from the bottom and allowed to overflow for several volumes before adding 200 μL of 50% zinc chloride (McCarthy et al., 2007). The vials were capped ensuring no air in the headspace and stored underwater at 4°C until measurement of dissolved gases. Dissolved inorganic nutrients were measured on an Autoanalyzer III (Seal Analytical, Inc., Mequon, WI) using the phenol hypochlorite technique for NH_4^+ (Solorzano, 1969), the antimonyl tartrate method for SRP (Murphy and Riley, 1962), and the cadmium reduction method for NO_3^- (APHA, 1998). Dissolved inorganic nitrogen (DIN) fluxes were calculated as the sum of the NH_4^+ and NO_3^- fluxes. Concentrations of dissolved O_2 was determined with membrane inlet mass spectrometry (MIMS; Bay Instruments, Easton, MD, USA; Kana et al., 1994). Standards consisted of artificial seawater maintained at constant temperature (28°C ; Circulating Bath, VWR International, Radnor, PA, USA), equilibrated to atmospheric gases by stirring at low speed (Lab Egg RW11 Basic, IKA Works, Inc., Wilmington, NC, USA). Samples were corrected for instrument drift with standard water throughout the run. Nutrient and O_2 fluxes were calculated as the concentration at the start of the incubation minus the concentration at the end of the incubation and were adjusted for surface area of the core, incubation time, and core water volume (flux units = $\mu\text{mol element m}^{-2} \text{ h}^{-1}$; Eyre et al., 2013). Each flux was also cor-

rected with the flux determined from the blank (water column) core. A negative value for nutrient fluxes indicated uptake by sediment or sediment and jellyfish, and a positive value indicated a flux to the water column. The detection limit of the fluxes (i.e., flux near zero) were assumed to be a flux where the standard error did not overlap with zero (Hoellein et al., 2015). Gross benthic primary production was determined from each core as the difference between light O_2 fluxes (net production) and dark O_2 fluxes (total respiration; Eyre et al., 2013). The overall effect of *Cassiopea* on benthic fluxes in Pearl Harbor was estimated using the mean fluxes with *Cassiopea* and mean benthic coverage (16.8%) and compared to the sediment only fluxes. For example, the flux with *Cassiopea* was multiplied by 0.168 (i.e. the proportion of the benthos covered by *Cassiopea* per m^2) and added to the flux of the sediment alone multiplied by 0.832 (i.e. the proportion of the benthos without *Cassiopea* per m^2). These calculations were performed for nutrient and O_2 fluxes under light and dark conditions. A daily flux was estimated using the total hours of light (13 h) and dark (11 h) in Barbuda at the time of sampling.

2.4. Sediment characteristics

Upon completing the core incubations, the *Cassiopea* were removed, and seawater was drained from each core. Triplicate 25 cm^3 sediment samples were removed from the surface (0–3 cm) of each core and frozen at -20°C until processed in the laboratory. Sediment samples were defrosted and homogenized to determine organic matter content and sediment chlorophyll-*a*. Sediment organic matter (%) was determined by drying triplicate subsamples at 60°C for > 48 h to determine the dry weight and then ashing the samples at 500°C (Benfield, 2006). Sediment porosity was calculated following Berner (1971) after having determined the mass of water in the sample, density of the sediment, and density of the seawater. Triplicate 5 cm^3 subsamples were treated with acetone and extracted overnight under dark conditions at 4°C . Chlorophyll-*a* was determined spectrophotometrically following Parsons et al. (1984). The extracted sediment was then dried at 60°C for > 48 h to determine the dry weight, and chlorophyll-*a* was calculated as $\mu\text{g g}^{-1}$ dry sediment.

2.5. Statistics

Differences in density and bell diameter of *Cassiopea* were examined among sites with a one-way ANOVA. A Tukey *post hoc* test was used to determine differences among sites. The sediment characteristics of the sediment alone, and sediment + *Cassiopea* treatments, from the core incubations were compared with *t*-tests. Differences among sites and between treatments should be interpreted cautiously given the low sample size and limited spatial scope of the study. All statistical analyses were performed in SigmaPlot 11 (Systat Inc., Chicago IL). The data are presented as mean \pm standard error (SE).

3. Results

3.1. *Cassiopea* survey and water quality characteristics

Cassiopea densities ranged from 24 to 168 individuals m^{-2} at our three study sites. The *Cassiopea* located near the mangrove islands (sites 2 and 3) had a mean density of $\sim 100 \text{ m}^{-2}$ (± 7.4) which was more than double the density at site 1 ($45 \text{ m}^{-2} \pm 8.8$; ANOVA; $F = 10.1$; $p = 0.002$; Fig. 2A). Although site 1 had a lower mean density, the *Cassiopea* had a 37% larger bell diameter ($7.2 \text{ cm} \pm 0.6$) compared to the other two sites ($4.5 \text{ cm} \pm 0.2$; ANOVA; $F = 13.13$; $p < 0.001$; Fig. 2B). The calculated benthic coverage was similar across all sites with values of 18.4%, 17.8%, and 14.3% for sites 1, 2, and 3 respectively.

The water column nutrient concentrations in Pearl Harbor were $8.18 \mu\text{mol L}^{-1}$ (± 0.46) for NH_4^+ , $0.37 \mu\text{mol L}^{-1}$ (± 0.06) for NO_3^-

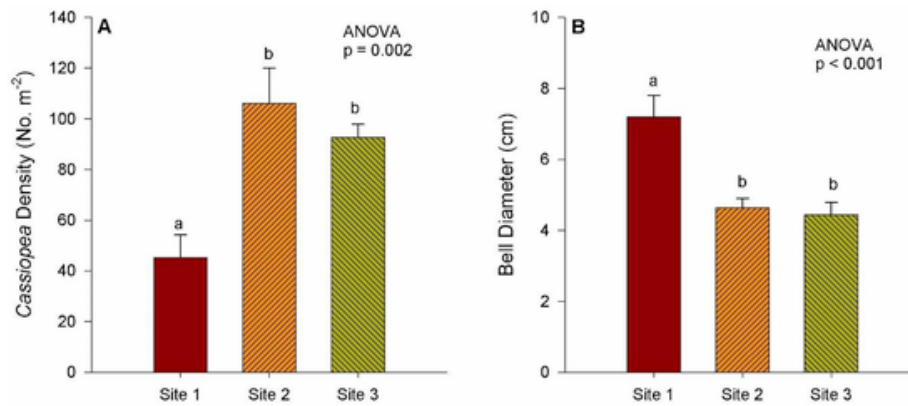


Fig. 2. Density (A; No. m⁻²; n = 6 site⁻¹) and bell diameter (B; cm; n = 25–30 site⁻¹) of *Cassiopea* at three sites in Codrington Lagoon, Barbuda.

, and SRP was 0.07 $\mu\text{mol L}^{-1}$ (± 0.03). Water column chlorophyll-*a* was low (0.58 $\mu\text{g L}^{-1}$ ± 0.03). The temperature was 28 °C, and salinity was 38. The mean nutrient content of *Thalassia testudinum* in Pearl Harbor was 31.7 (± 1.1) for % carbon and 1.5 (± 0.1) for % nitrogen.

3.2. Benthic fluxes

Net oxygen fluxes showed a similar temporal pattern for both sediment and sediment + *Cassiopea* treatments, with O₂ production occurring under light conditions and net uptake occurring under dark conditions (Fig. 3A). The magnitude of the fluxes, however, were different between the treatments. In cores containing *Cassiopea*, net O₂ production was over 300% higher under light conditions, and net uptake was 92% higher under dark conditions, relative to cores containing only sediment. The magnitude of difference between the light and dark fluxes resulted in the sediment + *Cassiopea* treatment having net production, and the sediment alone had net uptake (Fig. 3A). Gross benthic primary production was 3.8 fold higher in the sediment + *Cassiopea* treatment (Fig. 3B).

There were no significant fluxes of DIN in the sediment treatment, but uptake of DIN was evident in the sediment + *Cassiopea* (Fig. 4A). Patterns of NH₄⁺ (Fig. 4B) and NO₃⁻ (Fig. 4C) fluxes differed between treatments. Ammonium fluxes in cores containing only sediment were not significantly different from zero in both the light and dark treatments. In contrast, we observed net uptake of NH₄⁺ in the sediment + *Cassiopea* cores under both light and dark conditions, with dark uptake over 230% greater than light uptake. Nitrate fluxes were near zero in both treatments under light conditions. Under dark conditions, both treatments had an uptake of NO₃⁻, with uptake

>500% greater in the sediment-alone treatment. The magnitude of flux was much higher for NH₄⁺ than of NO₃⁻. The cores containing both sediment and *Cassiopea* acted as a net sink for NH₄⁺, while cores with only sediment provided a comparatively smaller net sink for NO₃⁻. There were no net fluxes of SRP under light conditions, but net uptake under dark conditions, resulting in both treatments providing a small net sink for SRP (Fig. 4D).

The overall effect of *Cassiopea* on benthic fluxes given their benthic coverage (Table 1) was largely consistent with the pattern observed for net fluxes. The DIN fluxes showed less release of DIN to the water column under light conditions in the *Cassiopea* treatment while dark conditions resulted in greater than 2-fold uptake of DIN. This pattern was largely due to the NH₄⁺ fluxes which indicated that the sediment alone was a source of NH₄⁺ while the *Cassiopea* treatment was a sink for NH₄⁺. The NO₃⁻ and SRP fluxes were similar for both the sediment and the sediment with *Cassiopea* treatments. There was greater O₂ production under light conditions and greater O₂ uptake under dark conditions in the *Cassiopea* treatment as compared to sediment alone. The daily O₂ flux indicated that the sediment alone was heterotrophic while the *Cassiopea* treatment was autotrophic.

3.3. Sediment core characteristics

Sediment chlorophyll-*a* in the sediment + *Cassiopea* treatments (12.6 $\mu\text{g g}^{-1}$ ± 2.0) was twice as high as the sediment treatment (5.8 $\mu\text{g g}^{-1}$ ± 2.3), ($t = -2.2$; $df = 4$; $p = 0.09$). There were no statistically significant differences in sediment organic matter ($t = -3.1$; $df = 4$; $p = 0.37$) or porosity ($t = -1.4$; $df = 4$; $p = 0.24$) between the sediment and sediment + *Cassiopea* treatments from the core incu-

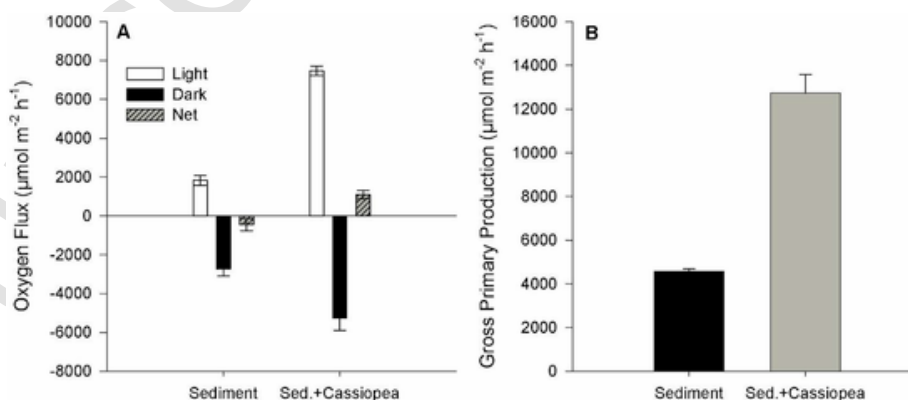


Fig. 3. The oxygen flux (A) and gross benthic primary production (B) from sediment core incubations with treatments of sediment or sediment (Sed.) and *Cassiopea*. Incubations were performed under light and dark conditions.

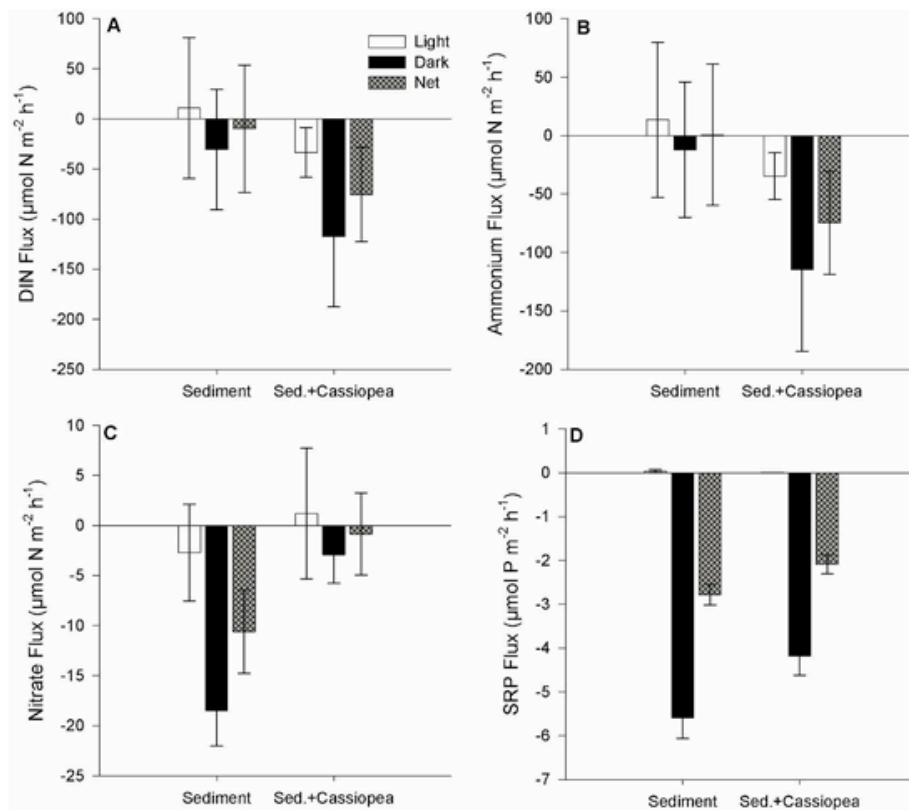


Fig. 4. Benthic fluxes of dissolved inorganic nitrogen (DIN; A), ammonium (B), nitrate (C), and soluble reactive phosphorous (SRP; D) from sediment core incubations with treatments of sediment or sediment (Sed.) and *Cassiopea*. Incubations were performed under light and dark conditions. Net flux was calculated as the average of light and dark fluxes.

Table 1

The calculated benthic fluxes of the sediment alone and fluxes with mean benthic coverage of *Cassiopea* (16.8%). The units for the light and dark fluxes are $\mu\text{mol m}^{-2} \text{h}^{-1}$ and units for daily fluxes are $\mu\text{mol m}^{-2} \text{day}^{-1}$.

Flux	Sediment	Sediment + <i>Cassiopea</i>
<i>Dissolved Inorganic Nitrogen</i>		
Light	10.7	3.3
Dark	-30.6	-45.2
Daily	-197.2	-454.6
<i>Ammonium</i>		
Light	13.4	5.3
Dark	-12.1	-29.3
Daily	41.7	-253.1
<i>Nitrate</i>		
Light	-2.7	-2.1
Dark	-18.5	-15.9
Daily	-238.8	-201.5
<i>SRP</i>		
Light	0.03	0.03
Dark	-5.6	-5.4
Daily	-61.1	-58.6
<i>Oxygen</i>		
Light	1828.7	2776.3
Dark	-2739.2	-3164.3
Daily	-6358.4	1284.3

bations. The organic content was $8.2\% (\pm 1.9)$ and $11.3\% (\pm 2.4)$, while the porosity was $0.71 (\pm 0.12)$ and $0.83 (\pm 0.02)$ in the sediment and sediment + *Cassiopea* treatments, respectively.

4. Discussion

Densities of *Cassiopea* observed in Codrington Lagoon, Barbuda, are the highest reported values in the literature. In contrast, the mean bell diameters are among the smallest reported (Table 2). A negative relationship between *Cassiopea* density and bell diameter, as observed in the current study, would seem logical as prey and nutrient availability can become limited. Benthic space could become limited at higher *Cassiopea* densities but was probably not limited in the current study (benthic coverage $\sim 14\text{--}18\%$). Stoner et al. (2011) suggested that *Cassiopea* were both more dense and larger in size in an anthropogenically impacted ecosystem, and the authors argued that this was due to higher nutrient loading. An increase in production could have supported higher prey densities which led to the difference in *Cassiopea* between the impacted and unimpacted ecosystems. Based on the significant variation in density and size of *Cassiopea* reported in the literature (Table 2), it would be useful for future studies to report both variables so that benthic coverage can be calculated. Benthic coverage provides a more meaningful variable for making inferences on the ecological impacts of *Cassiopea* (e.g. Table 1). It also would be informative to have repeated measurements of these variables to document how populations may change over time.

There are likely many other locations with similar or higher densities and/or benthic coverage. Studies documenting new records of *Cassiopea* invasions do not provide quantitative data, but have included photographs that show extremely high benthic coverage in coastal lakes of New South Wales (Australia; Keable and Ahyong, 2016) and the Itajuru Channel (Cabo Frio, Rio de Janeiro State, Brazil; Morandini et al., 2017). More studies that quantify geographic distribution, density, size, and benthic coverage of *Cassiopea* are critical to understanding how they may be influenced by climate change, eutrophication, and other anthropogenic stressors.

Table 2

Mean densities and bell diameter of *Cassiopea* spp. reported in the literature. A range in reported density or bell diameter is given when means were not reported. N/A = data not available.

Location	Density (No. m ⁻²)	Bell Diameter (cm)	Calculated Benthic Coverage (%)	Study
Codrington, Barbuda				<i>This Study</i>
Site 1	45.3	7.2	18.4	
Site 2	106.0	4.6	17.8	
Site 3	92.7	4.4	14.3	
Abaco Island, Bahamas (multiple sites)	0–6.9	N/A	N/A	Stoner et al. (2011)
	6.9	12.4	8.3	
Abaco Island, Bahamas				Stoner et al., (2014a),b
Naturally Occurring				
Experimental manipulation	<2	N/A		
	10	7–10	3.8–7.9	
Aqaba, Jordan				Niggel & Wild 2010
Reef	1.6	10.3	1.3	
Transition Zone	7.9	13.1	10.6	
Seagrass Meadow	0.4	8.3	0.2	
Sand Flat	1.3	13.5	1.9	
Nichupte Lagoon System, Mexico	42	N/A	N/A	Collado Vides et al. (1998)

Empirical (Stoner et al., 2011) and anecdotal (Arai et al., 2001) evidence suggest that *Cassiopea* abundance is positively related to nutrient loading; however, documenting such a relationship across ecosystems is difficult. Ammonium levels in Pearl Harbor were higher than values previously reported in the coastal waters of Bonaire (Slijkerman et al., 2014), mangrove systems with and without aquaculture impact in New Caledonia (Molnar et al., 2013), and at anthropogenically-impacted sites in the Abaco Islands (Bahamas; Allgeier et al., 2010; Stoner et al. 2011). Nitrogen loading into Codrington Lagoon may originate from groundwater discharge enriched from wastewater. Given high densities of *Cassiopea* and DIN concentrations at Pearl Harbor relative to published values, the data suggest a relationship between water column DIN and *Cassiopea* abundance is possible. Stoner et al. (2011) found no relationship between NH_4^+ and *Cassiopea* density. Instead, the authors noted a positive relationship between density and total phosphorous which suggests that phosphorous was more limited in this system. It is also possible that specific ratios of nutrients (i.e., system stoichiometry), dissolved inorganic nutrients, and nutrient fluxes may all contribute to patterns of *Cassiopea* density across ecosystems. Labeled nutrient sediment core incubations (e.g., isotopic ammonium; Hoellein et al., 2015) and measurement of nitrogen-isotopic signatures in tissues may be particularly useful to examine the relationship between *Cassiopea* and nutrient dynamics.

The analysis revealed a clear pattern in which *Cassiopea* and their algal symbionts changed benthic metabolism from net heterotrophic to net autotrophic. Sediment O_2 demand was greater than O_2 production in the Pearl Harbor sediment cores, but the presence of *Cassiopea* increased O_2 production >300% under light conditions. The survey of *Cassiopea* found that they cover 14–18% of the benthic environment in Pearl Harbor. The calculations (Table 1) with mean benthic cover-

age of *Cassiopea* suggest that benthic environment is net autotrophic ($1284 \mu\text{mol O}_2 \text{ m}^{-2} \text{ h}^{-1}$) while the sediment without *Cassiopea* would be net heterotrophic ($-6358 \mu\text{mol O}_2 \text{ m}^{-2} \text{ h}^{-1}$). A similar study of *Cassiopea* in a mangrove lagoon in Queensland, Australia also found much higher rates of O_2 production than consumption, which shifted benthic metabolism to autotrophy, with sediment alone net heterotrophic (Welsh et al., 2009). These authors found that light intensity alters the magnitude of the O_2 fluxes, where O_2 production increases with light intensity until saturation at $\sim 400 \mu\text{E m}^{-2} \text{ s}^{-1}$ (Welsh et al., 2009). The measurements in Barbuda were performed at mid-day likely under light saturating conditions, thus, future studies should consider patterns of light intensity over a diel cycle when measuring the impact of *Cassiopea* on benthic metabolism.

Presence of *Cassiopea* altered benthic nitrogen cycling, with differing effects on NH_4^+ and NO_3^- . Pearl Harbor sediment had no net flux of NH_4^+ under both light and dark conditions, but sediment + *Cassiopea* greatly enhanced NH_4^+ uptake. This response was likely due to 1) direct assimilation by *Cassiopea* and their algal symbionts or 2) effects of *Cassiopea* on sediment microbial processes. Cnidarians and associated *Symbiodinium* have the enzymes needed to assimilate NH_4^+ and NO_3^- directly from the water column, with the majority of uptake by *Symbiodinium* (Pernice et al., 2012; Radacker et al., 2015). It is also possible that O_2 production helped establish oxic conditions needed to enhance nitrification (i.e., bacterial oxidation of NH_4^+ to NO_3^-), which removes NH_4^+ from the environment. Welsh et al. (2009) suggested that *Cassiopea*-mediated photosynthetic O_2 production stimulated sediment nitrification, which led to greater NO_3^- production in an Australian mangrove lagoon. It is also important to note, that *Cassiopea* may harbor nitrifying bacteria within their tissues or on the surface of their tissues (Welsh et al., 2009; Freeman et al., 2016), as has been found in bivalves (Welsh et al., 2015; Arfken et al., 2017) and other marine invertebrates (Welsh and Castadelli, 2004). Nitrate produced via nitrification may be immediately assimilated or denitrified in this system since there were low water column NO_3^- concentrations and fluxes. The potential for *Cassiopea* to affect nitrification requires more careful study to uncover the underlying pathways and mechanisms. Future studies on *Cassiopea* impacts on benthic nitrogen cycling could use phylogenetic (e.g., 16S rRNA) and metagenomic techniques to describe microbial community composition and use tracers to follow NH_4^+ from the water column into potential sites of uptake and transformation (Arfken et al., 2017).

The effects of *Cassiopea* on NO_3^- flux may be linked to the redox conditions that control nitrification and denitrification. Denitrification (i.e., reduction of nitrate to dinitrogen gas) is an important nitrogen-removal process, particularly in eutrophic ecosystems (Radacker et al., 2015; Zarnoch et al., 2017), and requires organic carbon, anoxia, and NO_3^- . In our study, NO_3^- flux was near zero in light conditions, regardless of the presence of *Cassiopea*; however, in the dark, NO_3^- flux was greater without *Cassiopea*. We suggest that intense O_2 production by *Cassiopea* during light conditions promotes sediment nitrification and enhances diffusion of O_2 to greater depths in the sediment. This would mean that anaerobic sediments that support denitrifying microbes in *Cassiopea*-adjacent sediment would be active deeper in the sediment, and may receive less water column NO_3^- due to greater distance of the diffusion gradient. Conversely, the uptake of O_2 by *Cassiopea* in dark conditions could decrease this diffusion gradient. Understanding this combination of temporal variation in redox conditions, nitrification, denitrification, and sediment profiles driven by *Cassiopea*'s pulsing motion will be essential to predict impacts on sediment nitrogen dynamics. Future studies should also perform incubations with *Cassiopea* alone (i.e. no sediment) to understand how their metabolic activities and interactions with the sediment alter nutrient and gas fluxes.

Environmental context (e.g., sediment characteristics) is critical to document when conducting comparative studies of benthic fluxes

in coastal ecosystems (Smyth et al., 2015). For example, Welsh et al. (2009) found *Cassiopea* to be a source of nitrogen under dark conditions, while our study found *Cassiopea* to create a greater sink for nitrogen in sediments. Collectively, these data suggest that *Cassiopea* may promote nitrogen recycling and assimilation, but limit nitrogen removal via denitrification, which could significantly alter nutrient dynamics in subtropical and tropical coastal ecosystems. Thus, effects of *Cassiopea* could be positive or negative depending on the environmental conditions of the ecosystem. It is important for future studies to clarify the relationship between *Cassiopea* (and other jellyfish) abundance and nutrient loading to provide a context for interpreting benthic nitrogen fluxes.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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