



Note

Effects of anthropogenic disturbance on the abundance and size of epibenthic jellyfish *Cassiopea* spp.

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ABSTRACT

Jellyfish blooms in pelagic systems appear to be increasing on a global scale because of anthropogenic impacts, but much less is known about the link between human activities and epibenthic jellyfish abundance. The aim of this study was to investigate whether the epibenthic jellyfish, *Cassiopea* spp., were found in greater abundance, and attained larger sizes, in coastal habitats adjacent to high human population densities compared to sites adjacent to uninhabited areas on Abaco Island, Bahamas. *Cassiopea* spp. were found to be significantly more dense and larger in areas with high human population densities. Ambient nutrient levels and nutrient content of seagrass were elevated in high human population density sites, and may be one mechanism driving higher abundance and size of *Cassiopea* spp. *Cassiopea* spp. may have important effects on community structure and ecosystem function in critical coastal ecosystems (e.g., seagrass beds), and their impacts warrant further study.

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1. Introduction

Jellyfish blooms appear to be increasing on a global scale, fundamentally affecting ecosystem functioning and services provided by these systems (Arai, 2001; Graham, 2001; Mills, 2001; Purcell and Arai, 2001). For example, the annual catch of one of the largest jellyfish in the world, *Nemopilema nomurai*, increased 250% from 2000 to 2003 in the East China and Yellow Seas (Dong et al., 2010) devastating fisheries in those areas. Similarly, the bloom of jellyfish within the Bering Sea region has been so severe that the Alaskan Peninsula has been dubbed the “Slime Bank” because of the large numbers of jellyfish in fishery hauls. Further, it is now estimated that jellyfish consume an average of 5% of the annual crop of zooplankton in the Bering Sea, leading to a distinct shift in food web structure (Brodeur et al., 2002).

While it is sometimes difficult to ascertain mechanisms driving pelagic jellyfish blooms, it has been suggested that several anthropogenic disturbances are likely involved. These include overfishing (Purcell and Arai, 2001; Lynam et al., 2006), nutrient loading (Arai, 2001; Lo and Chen, 2008), marine construction (Lo et al., 2008; Hoover and Purcell, 2009), introduction of exotic species (Mills, 2001), increased sedimentation (Arai, 2001) and global climate change (Brodeur et al., 2008). Many of these disturbances may

interact synergistically to drive jellyfish population blooms (Purcell et al., 2007; Jackson, 2008).

Little is known, however, about links between anthropogenic disturbances and epibenthic jellyfish populations. *Cassiopea* spp. are an epibenthic jellyfish, endemic to sub-tropical and tropical nearshore ecosystems and are sessile as medusae. *Cassiopea* spp. are nicknamed ‘upside-down jellyfish’ because they lie flat on their bells on soft-bottom substrates using photosynthetic zooxanthellae that live in *Cassiopea* tissues to provide the host with a substantial source of energy (Fitt and Costley, 1998; Jantzen et al., 2010). *Cassiopea* spp. have been linked anecdotally to synergistic human impacts such as eutrophication and marine construction (Arai, 2001), and may invade new habitats through ship and live rock transportation (Holland et al., 2004; Bolton and Graham, 2006). However, while there is some information regarding the distribution and abundance of *Cassiopea* spp. in coastal ecosystems (Collado-Vides et al., 1988; Holland et al., 2004; Niggli and Wild, 2009), there is very little quantitative information regarding specific anthropogenic disturbances that may influence the size of *Cassiopea* spp. populations.

Here we examine the abundance and size of epibenthic *Cassiopea* jellyfish across a gradient of human population densities. We hypothesized that *Cassiopea* spp. densities, as well as the size of individuals, would be greater in coastal areas adjacent to human population centers. As such, we attempted to link human population densities to the distribution and characteristics of an epibenthic jellyfish, an organism that may play an important role in shallow coastal ecosystems of the tropics and sub-tropics.

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2. Materials and methods

2.1 Study site

The study was conducted in nearshore habitats on Abaco Island, Bahamas (26°25'N, 77°10'W) from June to July 2009. Sites were chosen *a priori* and assigned to one of two categories: (1) adjacent to relatively high-density human population centers or (2) adjacent to uninhabited watersheds. Sites adjacent to human population centers were considered to be disturbed by human activities. Likely anthropogenic disturbances include nutrient loading through point (e.g., sewage outfalls) and non-point sources (e.g., waste water run-off), construction of artificial structures (e.g., docks), and sedimentation driven by land-use practices. As a proxy for human population size, we estimated the number of buildings within a 3 km radius of the mid-point of each site (counted in Google Earth® v 5.1) (Google Inc., 2010). Second, large tracts of many Bahamian islands, including those on Abaco, remain undeveloped and uninhabited, allowing sites with relatively little human impact to be included for comparative purposes (Layman et al., 2007; Allgeier et al., 2010).

Ten systems were chosen: five high human population density sites (84–1712 buildings; Cherokee, Hopetown, Little Harbour, Marsh Harbour, Treasure Cay) and five low human population density sites (0–10 buildings; Barracuda Creek, Cross Harbour, North Bight of Old Robinson, Snake Cay, Sucking Fish Creek) (Fig. 1). For each site, 100 points within 100 m of shore were randomly generated using ArcMap GIS v 9.3.1 (ESRI 2008) and The Nature Conservancy (TNC) habitat layers. From these points, six 'sub-sites' were selected within each of the 10 main sites. Sub-sites were visited

sequentially in the randomly-generated order and the first six sites that met two criteria were selected: (1) a low tide water depth of 2 m or shallower, as *Cassiopea* spp. are typically found in shallow water (Arai, 2001), and (2) substrate comprised of silty-sandy sediment (~0.05 mm particle size as determined by the USDA soil classification triangle; Schoeneberger et al., 1998), i.e., a proxy for flow velocity, as *Cassiopea* spp. typically occur in low energy areas (Arai, 2001). As such, all sites were in shallow water in areas without significant current flow.

Study sites were within tidal creeks, embayments, and along low energy coastlines. Tidal creek channels are formed by scouring of the calcium carbonate substrate and are typically lined with red mangrove, *Rhizophora mangle*. Moving landward, the creeks open to broad, shallow flats that often support extensive beds of *Thalassia testudinum* seagrass (Hammerschlag-Peyer and Layman, 2010; Layman et al., 2007; Valentine-Rose et al., 2007). Substrate in tidal creeks varies from hard bottom to biogenic sand; in this study, sites ranging in silt to coarse biogenic sand substrate were selected. Semi-enclosed embayments in this system are typically shallow (<3 m), and are comprised of seagrass (predominately *T. testudinum*) and sandy substrate (Yeager et al., in press). Sites selected within semi-enclosed embayments and low-energy coastlines were typically in close proximity to shorelines because of the depth criterion, and thus were often adjacent to *R. mangle* or sandy beaches.

2.2 Sampling and analytical methods

Surveys and sampling were conducted during diurnal low tides. *Cassiopea* spp. were enumerated in 10 m × 10 m plots at each of the six pre-determined sub-sites. From these plots, the first 30 *Cassiopea* spp. were measured (bell diameter). Five, 1 m × 1 m quadrats were haphazardly placed in each plot, and percent cover of submerged aquatic vegetation (SAV) was estimated. Water samples were taken to determine ambient nutrient concentrations. Water samples were immediately filtered with Whatman 0.45 μm and 0.20 μm nylon membrane filters and frozen for later analysis. Seagrass (*T. testudinum*) was also collected, if present, in each plot for nutrient analysis. Seagrass nutrient content provides insight into nutrient dynamics over a longer time frame than ambient water nutrient concentrations (Duarte, 1990; Allgeier et al., 2010). Near-surface water temperatures and salinity were measured with a portable multi-parameter water quality meter (YSI 85-10), and water depth was recorded. If boats were present, they were enumerated to provide an additional proxy for human impact at each site.

Analysis of nutrient concentrations of water and seagrass were conducted at Florida International University. *T. testudinum* blades were scraped to remove epiphytes and dried at 80 °C ($n = 15$ per site, if present). Dried *T. testudinum* was ground into a fine powder and % nitrogen (N) was evaluated by analyzing duplicate samples of the seagrass using a Carlo Erba CN analyzer. Percent phosphorus (P) of *T. testudinum* blades were analyzed using dry-oxidation acid hydrolysis extraction in addition to the use of a colorimetric analysis, using a CHN analyzer (Fisons NA1500) (Fourqurean et al., 1992). Total phosphorus (TP) of sample water was analyzed using the same methodologies as for %P of *Thalassia* blades. The analytical detection limit for the CHN analyzer for %P of seagrass and TP of water was 0.02 μM. Water samples were processed for ammonium (NH_4^+) and soluble reactive phosphorus (SRP) following the Indophenol blue method, using a CHN analyzer (Fisons NA1500) with a machine analytical detection limit of 0.05 μM.

To compare the number of buildings, our proxy for human population densities between high and low human population density sites, we used a Kruskal–Wallis test, as data did not meet assumptions of normality ($P < 0.05$, SAS v 9.2). Number of boats, salinity,

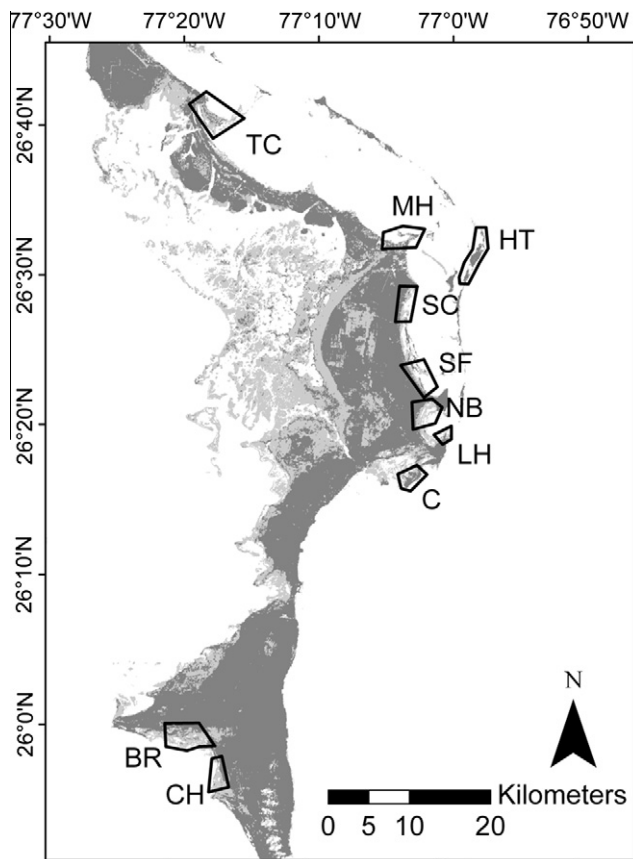


Fig. 1. Study sites on Abaco, Bahamas designated by polygons. Five sites were in high population density areas (C, HT, LH, MH and TC) and five sites were in locations with low human population densities (BR, CH, NB, SC, and SF). See Table 1 for key site codes.

Table 1

Nutrient concentrations and site characteristics for high and low human population density sites. All nutrient concentrations are reported in μM , salinity was measured in ppt. Results of *t*-tests comparing all variables except # of buildings between high and low human population density sites are given. Statistical values for # of buildings are reported in text due to a difference in statistical test used. SRP = soluble reactive phosphorus in water, TP = total phosphorus in water, %P = percent phosphorus in *Thalassia testudinum* tissues, NH_4^+ = ammonium in water, %N = percent nitrogen in *T. testudinum* tissues, %SG cover = percent cover of *T. testudinum*. N/A = samples were not collected for that site. See text for detailed explanation of all variables.

Site Name	Site Code	SRP	TP	%P	NH_4^+	%N	Salinity	%SG cover	# Boats	# Buildings
<i>High human population density</i>										
Cherokee	C	0.13	0.83	N/A	8.56	N/A	32	8	18	165
Hopetown	HT	0.08	0.96	0.10	1.15	1.8	32	6	16	362
Little Harbour	LH	0.08	1.16	0.13	0.41	1.9	35	20	3	84
Marsh Harbour	MH	0.08	0.67	0.13	3.90	2.3	29	8	13	1712
Treasure Cay	TC	0.08	0.74	0.11	7.69	1.9	27	12	0	492
Mean values		0.09	0.09	0.12	4.36	2.0	31	14	10	563
Standard deviation (\pm)		0.03	0.11	0.02	5.60	0.1	3	32	8	662
<i>Low human population density</i>										
Barracuda	BR	0.07	0.52	0.06	4.36	1.9	32	2	0	0
Cross Harbour	CH	0.08	0.53	0.07	1.46	1.7	35	20	0	0
North Bight of Old Robinson	NB	0.11	0.47	0.07	0.51	1.8	33	29	0	7
Snake Cay	SC	0.10	0.51	0.09	1.91	2.5	18	3	0	10
Sucking Fish	SF	0.10	0.50	0.11	0.42	1.7	36	4	0	0
Mean values		0.09	0.51	0.07	1.73	1.9	31	12	0	3.4
Standard deviation (\pm)		0.03	0.11	0.01	2.30	0.15	7	27	0	4.77
Test statistic (<i>t</i>)		0.04	6.58	3.91	2.35	0.19	0.03	0.59	2.74	
Degrees of freedom		58	55	13	57	13	58	58	58	
<i>P</i> -value		0.97	<0.001	0.002	0.022	0.85	0.97	0.55	0.008	

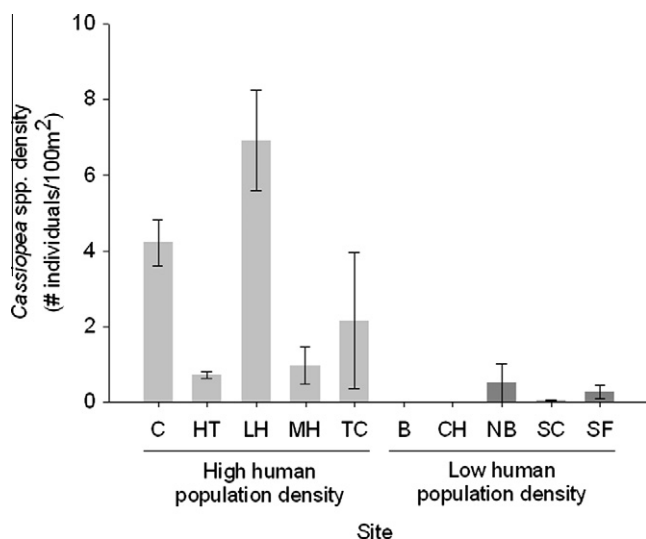


Fig. 2. Mean *Cassiopea* spp. density (# individuals/100 m²) from sites with high and low human population densities. Sites shown without bars indicate that no jellyfish were present within these locations.

% seagrass cover, and nutrient concentrations (SRP, TP in water, NH_4^+ , %P in *T. testudinum*, and %N of *T. testudinum*) were compared between high and low human population density sites using *t*-tests (SPSS v 14.0).

In order to determine the relationship between *Cassiopea* spp. bell diameter and dry weight, *Cassiopea* spp. collected from the sampling sites were dried for 24 h at 70 °C (Lucas 2008). \log_{10} transformed *Cassiopea* spp. dry weight were regressed against \log_{10} transformed bell diameter measurements ($\log_{10}(\text{dry weight}) = 2.09 \times \log_{10}(\text{bell diameter}) - 4.09$, $R^2 = 0.72$; $n = 149$ individuals). This relationship was used to estimate the dry weight (biomass) of the 30 *Cassiopea* spp. individuals from each sub-site for which bell diameter was measured. We compared mean *Cassiopea* spp. density between high and low human population density sites using a *t*-test (SPSS v 14.0). We compared the size (biomass) distribution of *Cassiopea* spp. between high and low human popu-

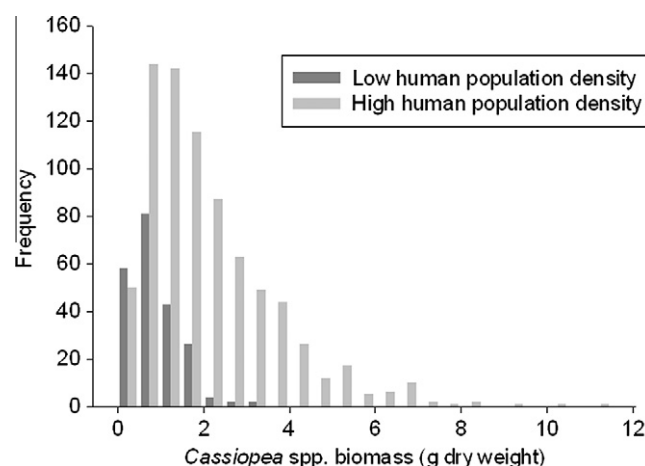


Fig. 3. Size-frequency distribution of *Cassiopea* spp. from sites with high and low human population densities.

lation density sites using a Kolmogorov–Smirnov test (SPSS v 14.0). Median *Cassiopea* spp. size was then compared between high and low human population density sites using a Kruskal–Wallis test, as data did not meet assumptions of normality ($P < 0.001$ in both cases) (SPSS v 14.0).

Nutrients in pelagic systems can be taken up by jellyfish, potentially driving enhanced jellyfish growth (Richardson et al., 2009). Therefore, Pearson correlations (bivariate) were run to test for relationships between nutrients (SRP, %P, %N, TP in water, NH_4^+) and both (1) *Cassiopea* spp. density, and (2) *Cassiopea* spp. size (SPSS 14.0). Correlations between *Cassiopea* spp. density and nutrient concentrations are reported in this paper. Correlations between *Cassiopea* spp. size and nutrients were comparable to those reported for density, and thus are not included here.

3. Results

Consistent with our initial site selections, the 5 sites with high human population densities had a greater number of buildings,

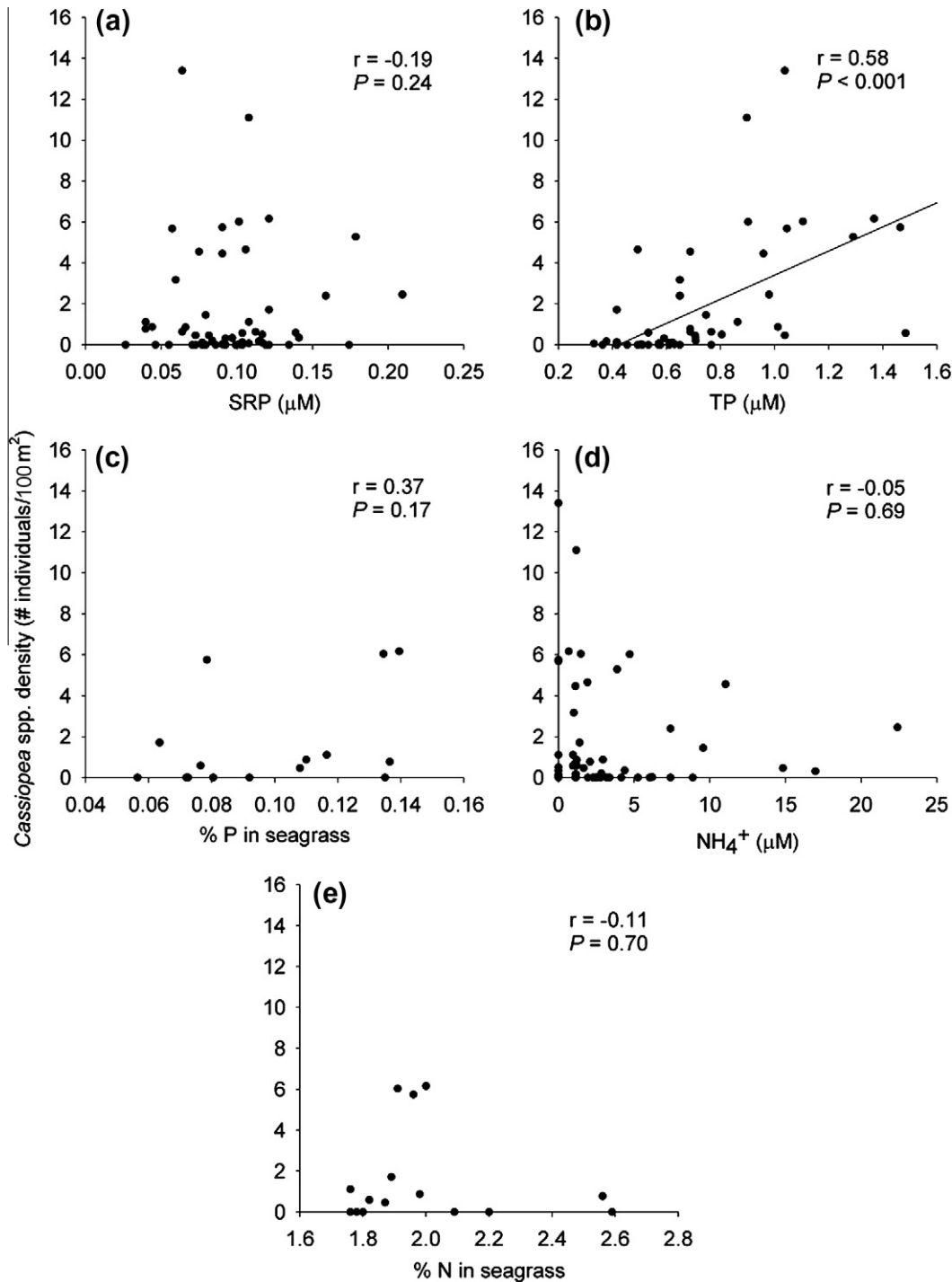


Fig. 4. Correlations between *Cassiopea* spp. densities and (a) soluble reactive phosphorous concentration in water, (b) total phosphorus concentration in water, (c) percent phosphorus in *Thalassia testudinum* tissue, (d) ammonium concentration in water and (e) percent nitrogen in *Thalassia testudinum* tissue. r = Pearson correlation coefficient and P = P -value for Pearson correlation. A trendline was added for correlations where $P < 0.05$.

our proxy for population density within the watershed ($\chi^2 = 6.98$, $df = 1$, $P = 0.008$). The number of boats was also greater in high human population density sites, indicating additional human activity ($t = 2.75$, $df = 58$, $P = 0.008$, Table 1). Salinity and % seagrass cover were not significantly different between high and low human population density sites (Table 1). However, water concentrations of TP, NH_4^+ , and %P in *T. testudinum* were significantly higher at high human population density sites (Table 1). SRP and %N from *T. testudinum* tissue did not differ between high and low human population density sites. Overall, nutrient concentrations were low,

consistent with other nearshore sites in The Bahamas (Koch and Madden, 2001; Allgeier et al., 2010).

Mean *Cassiopea* spp. density was greater in sites with high human population densities ($t = 4.57$, $df = 58$, $P < 0.001$, Fig. 2). The size distribution of *Cassiopea* spp. also differed between high and low human population density sites ($Z = 5.43$, $df = 1$, $P < 0.001$, Fig. 3), with median size being more than two times greater at high human population density sites ($\chi^2 = 161.07$, $df = 1$, $P < 0.001$). Little Harbour had both the highest density of *Cassiopea* spp. (mean = 6.9 jellyfish/m²) and the largest *Cassiopea* spp. mean size

(mean diameter = 12.4 cm, mean dry weight = 3.5 g). Furthermore, Little Harbour had the greatest number of jellyfish in a sub-site with 1340 jellyfish in a 10 m × 10 m plot, as well as the largest individual jellyfish collected in any site (diameter = 22 cm, dry weight = 11 g). Interestingly, Little Harbour had the fewest number of buildings for a high human population density site; however, point sources of pollution were observed at this site indicating direct and acute human impact. Two of the five low human population density sites had no jellyfish present at any sub-site sampled (Sucking Fish Creek and Cross Harbour), and Barracuda had only two jellyfish present within a single sub-site.

Cassiopea spp. density was found to be positively correlated to TP ($r = 0.58$, $P < 0.001$, Fig. 4). No other individual correlations between *Cassiopea* spp. density and nutrients were significant ($P > 0.05$, Fig. 4).

4. Discussion

Our results suggest that *Cassiopea* spp. are more abundant, and are larger, in areas adjacent to relatively high human population densities. These findings are some of the first to demonstrate such a pattern, and suggest that some aspect of anthropogenic disturbance may affect densities and size of this epibenthic organism. Anthropogenic nutrient loading in particular may affect *Cassiopea* spp. Because *Cassiopea* spp. host symbiotic zooxanthellae in their tissue, they may be able to capitalize on increased nutrient availability in nutrient-enriched areas. Zooxanthellae in *Cassiopea* spp. tissues supply much of the carbon requirements to the host, and are critical to the metamorphosis of ephyrae and the survival of the jellyfish (Fleck and Fitt, 1999; Pitt et al., 2009). In zooxanthellate corals, uptake of nutrients from water has been shown to increase the population density of zooxanthellae (Bythell, 1990; McAuley, 1994). In a similar manner, nitrogen (primarily ammonium) and phosphorous in the water column may be taken in by *Cassiopea* spp. Various systems in The Bahamas, including tidal creeks and embayments, have been found to be extremely oligotrophic (Koch and Madden, 2001; Lapointe et al., 2004; Allgeier et al., 2010). Therefore, any input of anthropogenically-introduced nutrients may help support productivity of the zooxanthellae, which would release additional photosynthate to the host, potentially enhancing its growth (Belda and Yellowlees, 1995; Fitt and Costley, 1998; Jantzen et al., 2010). The positive correlation between TP and *Cassiopea* spp. density, and increased concentrations of TP in sites adjacent to high population densities, supports the hypothesis that nutrient loading can lead to blooms of epibenthic jellyfish.

While there was a reasonably clear relationship between *Cassiopea* spp. densities and TP, the relationship with ammonium was more complex. We found that there was greater variation in *Cassiopea* spp. densities in sites with low ammonium concentrations, whereas sites with high ammonium concentrations had consistently low densities of *Cassiopea* spp. While there was not a linear correlation between NH_4^+ and *Cassiopea* spp. density, the relationship does suggest that at high densities, *Cassiopea* spp. may locally depress ammonium in the water (Fig. 4). Ammonium specifically has been suggested to be limiting to tropical zooxanthellae populations (Falkowski et al., 1993; Fitt and Cook, 2001). Therefore, zooxanthellae living within the tissues of *Cassiopea* spp. may preferentially uptake ammonium from seawater. However, it is necessary to mechanistically-test this hypothesis to provide further insight into this potential relationship.

A higher abundance of *Cassiopea* spp. associated with human disturbance may have substantial implications for community structure and functioning of seagrass ecosystems through a variety of mechanistic pathways. First, *Cassiopea* spp. may compete with

benthic flora for light, essentially covering seagrasses and other submerged aquatic vegetation. Second, because *Cassiopea* spp. feed on zooplankton, they may directly compete with other filter-feeding consumers for food. Third, *Cassiopea* spp. have few predators (e.g., nudibranchs and sea turtles, Brandon and Cutress, 1985; Arai, 2005), so energy assimilated by these animals may be locked in a dead-end trophic pathway that may not be transferred to upper levels of the food web. Finally, reduced species richness and diversity in benthic marine habitats resulting from the previous mechanisms may affect the nature of nutrient cycling, and thus ecosystem functioning, within these habitats (Bracken et al., 2008). As such, further studies on the effects of increased epibenthic jellyfish in coastal ecosystems are needed to explore potential ways they may alter community structure and ecosystem function.

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