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Habitat fragmentation has some impacts on aspects of ecosystem functioning in a sub-tropical seagrass bed

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ABSTRACT

Habitat fragmentation impacts ecosystem functioning in many ways, including reducing the availability of suitable habitat for animals and altering resource dynamics. Fragmentation in seagrass ecosystems caused by propeller scarring is a major source of habitat loss, but little is known about how scars impact ecosystem functioning. Propeller scars were simulated in seagrass beds of Abaco, Bahamas, to explore potential impacts. To determine if plant-herbivore interactions were altered by fragmentation, amphipod grazers were excluded from half the experimental plots, and epiphyte biomass and community composition were compared between grazer control and exclusion plots. We found a shift from light limitation to phosphorus limitation at seagrass patch edges. Fragmentation did not impact top-down control on epiphyte biomass or community composition, despite reduced amphipod density in fragmented habitats. Seagrass and amphipod responses to propeller scarring suggest that severely scarred seagrass beds could be subject to changes in internal nutrient stores and amphipod distribution.

1. Introduction

Habitat fragmentation is a process through which a continuous landscape is broken into smaller fragments or patches (Laurance et al., 2002; Feeley and Terborgh, 2008), often resulting in reduced areal coverage, higher proportion of edge habitat, and increased predation risk (Turner et al., 2001). In coastal marine ecosystems, habitat fragmentation can be a natural process driven by waves or currents (Fonseca et al., 1998), as well as by anthropogenic activities such as boat traffic, dredging, and eutrophication (Short et al., 2011). The rate of seagrass loss has accelerated in recent decades with global seagrass coverage reduced by one-third since 1879 (Waycott et al., 2009). These losses can be associated with substantial loss of ecosystem services (Waycott et al., 2009).

Edges caused by fragmentation are dynamic regions characterized by variable microclimates with temperatures, water/airflow, and habitat complexity different from habitat interiors (Turner et al., 2001; Bologna and Heck, 2002; Ries and Sisk, 2004). This increased variability in edge habitats can affect the ecological relationships among organisms. For example, decreases in faunal abundances at the edge of seagrass patches are often attributed to increased predation (Irlandi, 1994; Bell et al., 2001; Peterson et al., 2001; Uhrin and Holmquist, 2003). Uhrin and Holmquist (2003) found crab and mollusk densities were lower up to 5 m away from recently-made scars in seagrass meadows (Uhrin and Holmquist, 2003). Conversely, some invertebrate prey species, including gammaridean amphipods, are found at higher densities at edges (Bologna and Heck, 1999; Eggleston et al., 1999; Arponen and Boström, 2012). Amphipods are hypothesized to settle in these edge habitats because current flow is reduced by the aboveground structure of seagrass (Fonseca et al., 1982), providing a more amenable environment (Tanner, 2003).

Gammaridean amphipods are important grazers in seagrass systems, consuming macro- and micro-algae growing on the substrate or on seagrass leaves. Gammaridean amphipods have strong impacts on regulating epiphyte growth on seagrasses, and can reduce the impacts of epiphyte-induced shading of seagrasses even under eutrophic conditions (Orth and van Montfrans, 1984; Neckles et al., 1993; Hughes et al., 2004; Jaschinski and Sommer, 2008;

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Spivak et al., 2009; Cook et al., 2011; Whalen et al., 2013; McSkimming et al., 2015). Species identity, richness, and diversity of amphipods mediates the top-down effect on seagrasses. A diverse amphipod community may efficiently reduce epiphytes belonging to different phototrophic groups because different amphipod species have different feeding preferences and abilities (Duffy and Harvilicz, 2001). As such, grazer diversity facilitates more complete use of epiphyte resources and (Duffy et al., 2001), depending on the composition of grazer species, can even increase seagrass biomass indirectly via epiphyte removal (Duffy et al., 2003). This also has implications for higher trophic levels, as amphipods are a major food source for many predatory fish and decapod species (Brook, 1977; Young and Young, 1978).

Few studies have investigated effects of fragmentation on amphipod communities in continuous seagrass beds. Most studies examining amphipod responses to fragmentation have instead been conducted using small, artificial, seagrass patches in unvegetated habitats adjacent to continuous seagrass beds (Healey and Hovel, 2004; Arponen and Boström, 2012; Pierri-Daunt and Tanaka, 2014). Understanding of amphipod responses to changes in patch size and level of isolation from the main seagrass patch was enhanced, but the studies did not focus on actual habitat fragmentation in natural systems (see Fahrig, 2003). The objective of our study was to examine if fragmentation caused by propeller scarring impacts the structure and function of seagrass ecosystems, as mediated by changes in resource availability and amphipod grazer communities (Fig. 1; Table 1). To test this, we simulated propeller scars in a seagrass bed on Abaco, The Bahamas. Additionally, we measured effects of grazers on epiphyte communities by removing grazers from half our experimental plots. We evaluated seagrass primary production (hypothesis 1 – see Table 1), nutrient and isotope values (hypotheses 2–3), epiphyte biomass and community structure (hypotheses 4–5), grazer abundance and community structure (hypotheses 6–7), and plant-grazer interactions (hypothesis 8).

2. Materials and methods

2.1. Site description and experimental design

The study was conducted at two sites in Abaco, The Bahamas (26 °25′N, 77 °10′W) from August to October 2014. The coastal areas of Abaco are primarily phosphorus-limited (Allgeier et al., 2010). Allochthonous nutrient input is localized in areas of high human populations around Abaco (Stoner et al., 2011), and can influence seagrass productivity and epiphyte community composition. One site, Cherokee Sound, was located closer to human influences than the other site, Jungle Creek. Both sites were characterized by depths of ~1.5 m at high tide with >50% *Thalassia testudinum* cover (Fig. 2). Forty experimental plots were established across a continuous seagrass landscape, and replicates of each treatment combination (n = 10) were randomly assigned (Fig. 3). Amphipod abundance and fragmentation treatments were manipulated over the course of 5 weeks at the two sites (site was one factor in the design). The factor of "grazing" consisted of two levels (amphipod exclusion and control). The factor of "fragmentation" also consisted of two levels (fragmented and continuous control). Edge and interior sampling plots were collected from the fragmented treatments only to test for edge effects (Table 2). Seagrass, amphipod, and epiphyte samples were collected within 15 cm of carbaryl blocks or control plot markers at continuous, interior, and edge locations at the end of the experiment.

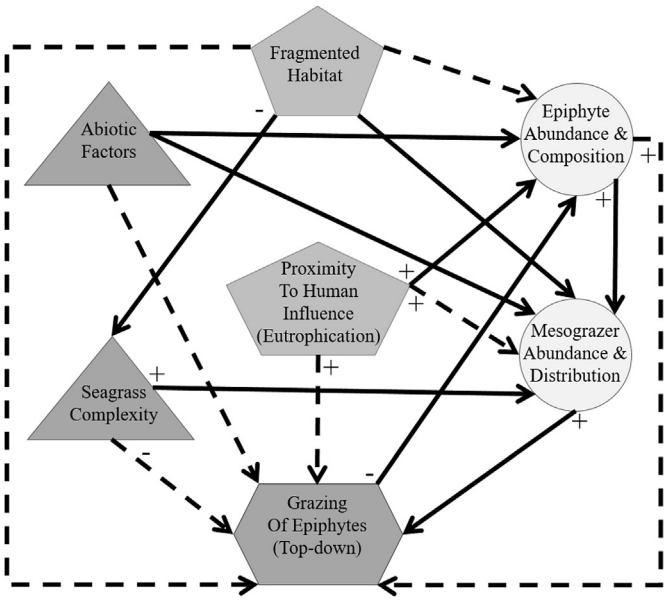

Fig. 1. Conceptual diagram of hypothesized direct (solid lines) and indirect (dashed lines) interactions among abiotic factors, seagrass complexity, epiphyte abundance & composition, mesograzer abundance & composition, fragmented habitat, nutrient enrichment, and epiphyte grazing (top-down control). Interactions are designated as positive (+) or negative (–). No symbol indicates a change that is not determined to be either positive or negative. Pentagons are anthropogenic stressors (independent variables), the hexagon is a natural stressor (independent variable), circles are dependent variables, and triangles are independent variables.

2.2. Fragmentation treatment

Plots were chosen based on homogeneous cover of benthic vegetation (seagrasses and macroalgae) across a circular area 6.5 m in diameter, then were randomly assigned as a control or fragmented treatment. A simulated propeller scar was created around the circumference of the fragmented plots to a width of 25 cm (approximate width of propeller scars in the area) using hedge clippers. Circular plots were chosen so samples collected from plot interiors were equidistant from the scar in all directions. This scar design, while rare in shallow seagrass ecosystems, also allowed for us to test the effects of scarring and fragmentation, as would be seen in moderate-to severely-scarred seagrass beds, while controlling for the age of the scar, distance to patch edge, patch shape, and patch size. This configuration was chosen to simulate a moderately scarred seagrass bed, such as that found by the entrance or exit of a channel. Scars crisscross in these areas creating a patchy environment. Simulated scars in our study were used to simulate this patchy environment, but they also had to be sufficiently large to identify an edge effect, if any. To create the scars, seagrasses and macroalgae were removed at the sediment surface, and regrowth was trimmed weekly. Rhizomes were severed at the scar edge to prevent transfer of nutrients from adjacent short shoots. Actual propeller scars caused by motor boats often remove sediment and destroy the rhizosphere of seagrasses thereby increasing the time to full recovery of a scarred seagrass bed. As such, results from this experiment are conservative. All experimental plots had a diameter of 6.5 m (6 m internal diameter and 0.25 m propeller scar around the perimeter of fragmented plots, 6.5 m diameter for continuous plots) with an area of 33.2 m^2. Plot centers were 10 m apart to ensure no cross-contamination by treatments with carbaryl (Fig. 3).

To test for fragmentation effects, samples were collected from the center of both fragmented and continuous plots. Samples were also collected from the edges and interior locations of a fragmented

Table 1
Predicted and observed responses to habitat fragmentation in seagrass ecosystems from Abaco, The Bahamas. E = Edge and I= Interior. Predictions were derived from previous studies on the effects of propeller scarring in seagrass ecosystems, and habitat fragmentation or patch dynamics of gammaridean amphipods.

Metric	Prediction	Supported (Y) or not (N)
1. Seagrass primary production	Increase at E	N
2. Seagrass nutrient content	Decrease at E	Y
3. Seagrass isotopic content	Increase at E	Y
4. Epiphyte biomass	Decrease in grazer control	N
5. Epiphyte community composition	Change with grazer removal	N
6. Amphipod density	Decrease at I and E plots	Y,N
7. Amphipod community composition	Change with fragmentation	N
8. Amphipod grazing	Reduced at E	N

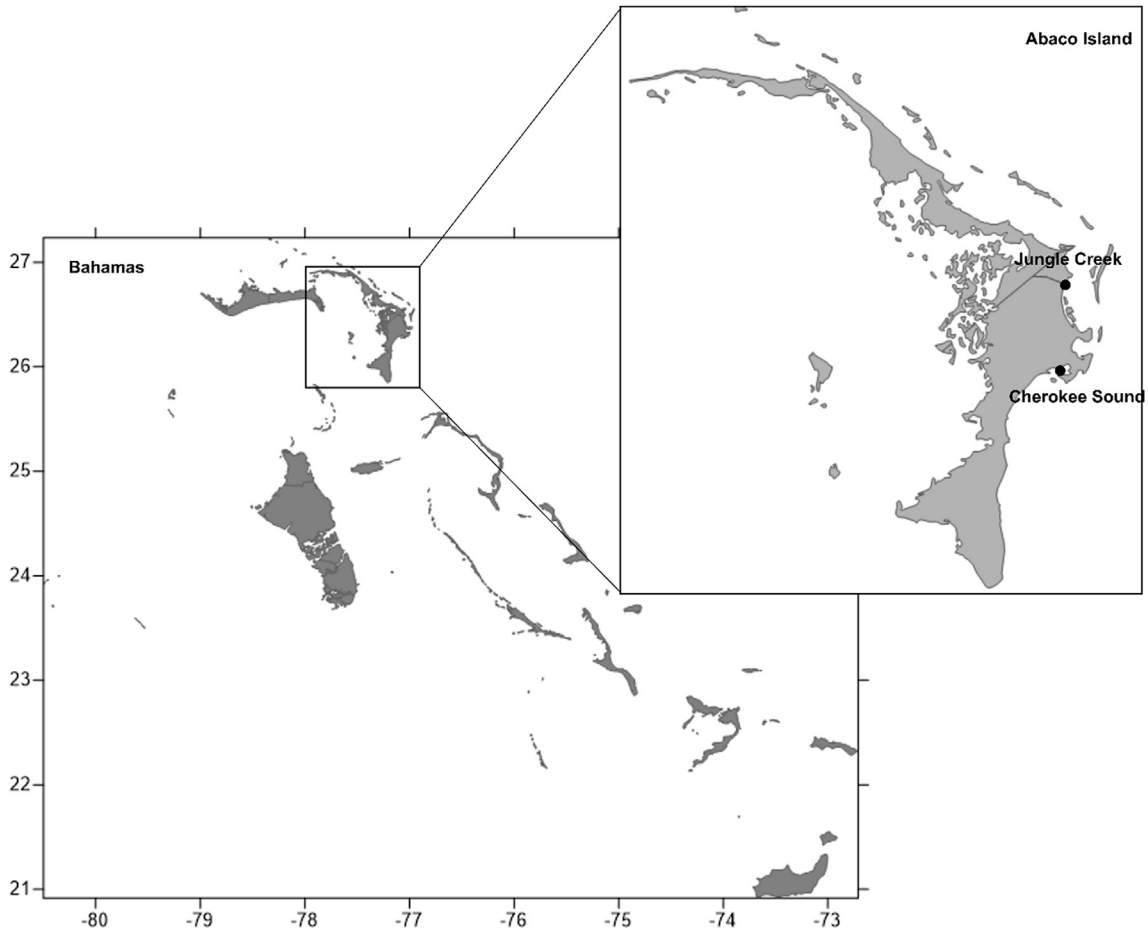

Fig. 2. Map of study area. Black points indicate experimental sites.

patch to test for edge effects (Table 2; Fig. 3). Edge plots were randomly assigned a cardinal direction to control for the potential effects of current.

2.3. Grazer treatment

Amphipods were excluded from half of the experimental plots using carbaryl-infused plaster blocks as a test of hypothesis 8: amphipod grazing will be reduced at edge habitats (Table 1). Carbaryl is a water-soluble arthropod deterrent used to remove insects in agriculture (Tomlin, 2000). Current marine applications include removal of arthropod pests in oyster farms (Dumbauld et al., 2001) and parasitic sea lice in fish farms (Høy and Horsberg, 1991). Carbaryl has a half-life of 5 h in seawater and degrades rapidly in the presence of light (undetectable after 96 h; Armbrust and Crosby, 1991). Carbaryl effectively removes invertebrates, such as, amphipods, some gastropods, and burrowing shrimp (Duffy and Hay, 2000; Dumbauld et al., 2001; Douglass et al., 2008; Poore et al., 2009; Cook et al., 2011; Whalen et al., 2013; Duffy et al., 2015), with no effects on fish, molluscs, polychaetes, seagrasses or algae (Carpenter, 1986; Roth et al., 1993; Dumbauld et al., 2001; Poore et al., 2009).

Slow-release blocks were infused with a low concentration of carbaryl pesticide using 18.5 g carbaryl to 222 mL water and 555 g plaster of paris (3.3% carbaryl by dry weight plaster; Whalen et al., 2013) and secured to the sediment surface using wire hooks. Carbaryl blocks were replaced weekly to maintain grazer exclusion. Control plots were unmanipulated (i.e., no block). Block controls (plaster blocks without carbaryl) were not used because data from a pilot experiment found no significant difference in amphipod

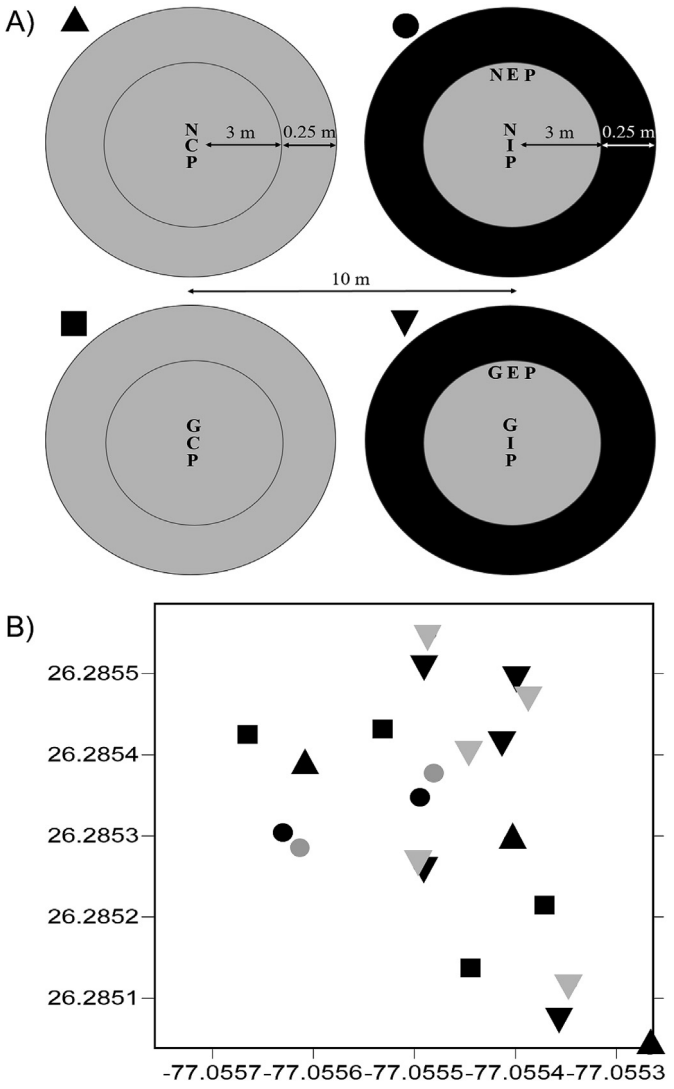

Fig. 3. Schematic of experimental plots. A) Black shading indicated simulated propeller scar where seagrasses were removed, and grey coloring indicates where seagrasses are intact. Arrows indicate distance between plots (0.25 m is the width of the scar; 3 m is the distance from the scar to the patch center) or patch centers (10 m). Letters indicate where samples were collected: N = Grazer exclusion; G = Grazer control; C= Continuous sample location; I= Interior sample location; E = Edge sample location; P= Productivity samples. Figure not drawn to scale. B) Map of selected sampling plots from Cherokee Sound for illustration of plot locations. Each of the four treatments above are plotted below using symbols (upright triangle, circle, square, upside down triangle), which are identified above.

Table 2
Table detailing plots and initial models used to test for fragmentation or edge effects. CS= Cherokee Sound, and JC = Jungle Creek.

	Fragmentation Effects	Edge Effects
Plots	Continuous and Interior	Interior and Edge
Model(s)	Y ~ Site × Habitat × Grazer[a]	Y_{CS} ~ Habitat × Grazer Y_{JC} ~ Habitat × Grazer

[a] The factor 'grazer' was removed from the model after the initial run indicated a significant site × grazer interaction to test for fragmentation effects in unmanipulated plots.

abundances between the control block and ambient control plots ($p = 0.910$ reported in Appendix A, also see Whalen et al., 2013), and carbaryl successfully excluded amphipods from sample plots up to a distance of 30 cm from the treatment block ($p < 0.05$ reported in Appendix A; also see Whalen et al., 2013).

2.4. Seagrass responses

Abundance of all benthic flora was estimated as percent cover of each species present in a 0.25 m^2 quadrat placed at each sample location. Shoot density was calculated by counting shoots in a 0.02 m^2 quadrat. *Thalassia testudinum* productivity rates were estimated using the modified hole-punch technique (Fourqurean et al., 2001). Shoots were marked adjacent to the sample location (Fig. 3), and three to seven marked shoots were harvested a week later to measure morphometrics (leaf length and width) and determine areal productivity (g m^{-2} d^{-1}). All destructive sampling was conducted at the end of the experiment after amphipod samples had been collected. In the lab, shoots marked for productivity were gently scraped free of epiphyte material, processed for growth metrics, and dried in an oven at 80 °C (Fourqurean et al., 2005). Epiphytes were stored in foil-wrapped scintillation vials in the freezer until further processing. Dried seagrass shoots were weighed and homogenized for nutrient and isotope analyses. Total phosphorus content of *T. testudinum* leaves was determined using a dry-oxidation, acid hydrolysis extraction with colorimetric analysis (Fourqurean et al., 1992). Carbon and nitrogen content were analyzed using a CHN analyzer (Fisions NA1500).

Seagrass blade tissue from Cherokee Sound were analyzed for stable isotope ratios ($\delta^{13}C$, $\delta^{15}N$). Samples used for isotope analyses were fumed for 7 days with concentrated HCl to remove any carbonates, and re-dried in an oven at 80 °C to a constant weight (Fourqurean et al., 2005). Stable isotope content was determined using elemental analyzer isotope ratio mass spectrometer (EA-IRMS) procedures. Organic matter was combusted in the elemental analyzer and gases were reduced to N_2 and CO_2, which were measured on a Finnigan MAT Delta C IRMS in continuous flow mode. Results are presented in standard delta notation (δ) using the international standards of atmospheric nitrogen (N_2) and Vienna Pee Dee belemnite (V-PDB) for carbon. Based on sample replicates, reproducibility of reported δ values was better than ±0.08‰ for carbon and ±0.20‰ for nitrogen.

2.5. Epiphyte responses

High performance liquid chromatography (HPLC) was used to determine phytopigment abundance per sample, which measures relative concentrations of the accessory pigments fucoxanthin (found in diatoms), peridinin (found in dinoflagellates), zeaxanthin and echinenone (found in cyanobacteria), and chlorophyll *b* (found in chlorophytes). Pigment abundance was estimated as μg pigment per cm^2 seagrass leaf, and were presented as a percentage of the sum of the masses of all measured pigments. Abundances of these different pigments were used as indicators of the relative biomass, as taxon-specific chlorophyll *a*, for the various photosynthetic epiphyte groups. Scraped epiphyte material was lyophilized to obtain a dry weight. Epiphyte pigments were extracted using methanol/acetone/N,N-dimethylformamide/water (Hagerthey et al., 2006) and analyzed using HPLC analysis according to the methods described in Louda et al. (1998). Total epiphyte load was estimated as leaf-specific chlorophyll *a* (μg Chl *a* leaf $area^{-1}$). Epiphyte autotrophic index (μg Chl *a* g^{-1} epiphyte dry mass) was also calculated.

2.6. Amphipod identification

Amphipod samples were collected at all grazer exclusion or grazer control treatment plots using a modified Virnstein Grabber (Virnstein and Howard, 1987). The Virnstein Grabber collects seagrass above-ground biomass and associated epifauna from an area of 400 cm^2 without collecting large amounts of sediment or infauna (Douglass et al., 2008). Samples were rinsed through 400 μm filter bags, transported on ice and then frozen. In the lab, samples were

thawed and seagrass and macroalgae removed. The remaining sample was filtered through a 500 μm sieve to remove smaller particulates and organisms from the sample. Fauna collected in the sieve were then preserved in 5% formalin before being rinsed, identified, and stored in 70% ethanol. Seagrass and algae were first dried to a constant weight at 80 °C (dry weight = DW) (Fourqurean et al., 2005). The samples were then combusted at 500 °C for four hours and weighed to the nearest 0.0001 g. Ash-free dry weight (AFDW) was calculated by subtracting the weight of the ashes from the DW. Amphipods were identified to the species level (following LeCroy, 2002) under a dissecting microscope. Amphipod density per g macrophyte biomass was calculated for each species as amphipod abundance divided by AFDW (number of amphipods g^{-1} macrophyte AFDW per 400 cm^2 sample) (Whalen et al., 2013).

2.7. Statistical analyses

Univariate statistical analyses were conducted using R Studio (R Core Team, 2015) and the following packages: 'car' (Fox and Weisberg, 2011), 'nlme' (Pinheiro et al., 2015), 'multcomp' (Hothorn et al., 2008), and 'MASS' (Venables and Ripley, 2002). Because interior and edge locations do not meet the assumption of independence for ANOVA when analyzing for fragmentation effects, we created two separate datasets. The first dataset includes data collected from fragmented-interior and continuous plots only, and is used to test for fragmentation effects between sites, habitats, grazer treatments, and all interaction terms in a 3-way analysis of variance (ANOVA). The second dataset includes data collected from fragmented-edge and interior plots, and was used to test for an effect of the edge. All analyses testing for edge effects were done using 2-way ANOVA within each site (two separate analyses), thereby removing site as a factor in the model (Table 2). Dependent variables were epiphyte biomass and autotrophic index, and seagrass abundance, productivity, and nutrient content (N and P).

Stable isotopes values ($\delta^{13}C$ and $\delta^{15}N$) of seagrass leaves in fragmentation and grazing treatments (Cherokee Sound only) were analyzed using 2-way ANOVA. Edge effects, or within-patch differences, in isotopic content between fragmentation and grazer treatments were also analyzed using 2-way ANOVA.

Community analyses were conducted using Primer 6 software (version 6.1.15; Primer-E 2012). Epiphyte communities, as described by the accessory pigment relative abundances, were analyzed using a 3-factor permutational analysis of variance (PERMANOVA) where site, fragmentation, and grazer treatment were the three main factors. Differences in amphipod community structure between sites and fragmentation treatments were determined using Bray-Curtis dissimilarity index calculated on a matrix of amphipod densities of each species. Differences in community structures were visually examined using nonmetric multidimensional scaling (nMDS) ordination (Fig. 7 generated using the vegan package in R; Oksanen et al. (2015)), and significance was determined using PERMANOVA. The most influential taxa contributing to observed differences were determined using similarity percentage (SIMPER) analyses for both epiphyte and amphipod communities.

3. Results

3.1. Overview

Thalassia testudinum percent cover was significantly higher at Cherokee Sound ($P < 0.001$, $\bar{x}$=80%) than Jungle Creek ($\bar{x}$=62%) (Table 3). The habitat was more complex at Cherokee Sound, with significantly longer leaves, greater leaf area per short shoot, more leaves per short shoot, higher short shoot density, and larger standing crop biomass (all $P < 0.001$). Productivity (areal productivity g m^{-2} day^{-1}, and leaf area productivity cm^{-2} m^{-2} day^{-1}) of *T. testudinum* was significantly higher at Cherokee Sound as well ($P < 0.001$ for both) (Table 3).

3.2. Seagrass responses to fragmentation

Thalassia testudinum cover ranged from 40% to 100% cover at Cherokee Sound and 28%–100% at Jungle Creek at the end of the experiment. *Thalassia testudinum* cover was significantly higher in continuous habitats ($\bar{x}$=76%) than interior ($P = 0.025$; $\bar{x}$=66% cover) and edge ($P = 0.021$; $\bar{x}$=65% cover) habitats. Within fragmented plots, *T. testudinum* cover was not significantly different between edge and interior locations, or grazer treatment plots.

Seagrass nutrient content (C, N, P) was significantly different between sites. Carbon and nitrogen were significantly higher at Jungle Creek ($\bar{x}$=38.47% for carbon; $\bar{x}$=2.12% for nitrogen) than at Cherokee Sound ($p < 0.0001$; $\bar{x}$=35.02% for carbon; $\bar{x}$=1.91% for nitrogen), but were not different across within-patch locations or grazer treatments at either site (Fig. 4).

Phosphorus (%P) was significantly higher at Cherokee Sound ($\bar{x}$=0.066%; $P < 0.001$) than Jungle Creek ($\bar{x}$=0.059%). Phosphorus was not affected by fragmentation (fragmented-interior vs. continuous plots) or grazer treatments. At Jungle Creek, there was no effect of edge on % P in seagrass tissues (Fig. 5a), but % P was significantly higher in plots where grazers were present ($P = 0.014$; Fig. 5b). Conversely, % P was higher at continuous plots ($\bar{x}$=0.069; $P = 0.001$) than edges ($\bar{x}$=0.058%; Fig. 5c) in Cherokee Sound, but was unaffected by grazer treatment (Fig. 5d).

Stable isotope content ($\delta^{13}C$ and $\delta^{15}N$) was analyzed in seagrass tissues at Cherokee Sound because of the observed depletion of P at edges. $\delta^{13}C$ was significantly enriched ($P = 0.004$) at edges ($\bar{x}$=-9.53) than continuous ($\bar{x}$=-10.37) habitats. No significant differences between habitats were detected for $\delta^{15}N$. Both $\delta^{13}C$ and $\delta^{15}N$ appeared unaffected by fragmentation and grazer treatments. A weak but significant, negative relationship ($P = 0.01$, $R^2 = 0.09$) was detected between $\delta^{13}C$ and phosphorus content.

3.3. Epiphyte responses to fragmentation and grazing

Leaf-specific epiphyte biomass was 0.68 ± 0.06 μg Chl *a* leaf $area^{-1}$ at Cherokee Sound and 0.72 ± 0.12 μg Chl *a* leaf $area^{-1}$ at Jungle Creek. Leaf-specific epiphyte biomass was 0.71 ± 0.09 μg Chl *a* leaf $area^{-1}$ in fragmented habitats, and 0.67 ± 0.07 μg Chl *a* leaf $area^{-1}$ at continuous habitats. Epiphyte biomass in grazer control treatments was 0.68 ± 0.07 μg Chl *a* leaf $area^{-1}$, while epiphyte biomass in grazer exclusion plots was 0.72 ± 0.11 μg Chl *a* leaf $area^{-1}$. Edge habitats were 0.78 ± 0.14 μg Chl *a* leaf $area^{-1}$ at Cherokee Sound and 0.81 ± 0.32 μg Chl *a* leaf $area^{-1}$ Jungle Creek. Leaf-specific epiphyte biomass was not significantly different for site, fragmentation, or grazer treatments, nor were there significant edge effects (Table 4).

The epiphyte autotrophic index was 348.9 ± 25.9 μg Chl *a* g^{-1} epiphyte dry mass at Cherokee Sound and 235.7 ± 12.8 μg Chl *a* g^{-1} epiphyte dry mass at Jungle Creek. The autotrophic index was 290.9 ± 20.1 μg Chl *a* g^{-1} epiphyte dry mass in fragmented habitats and 293.7 ± 22.3 μg Chl *a* g^{-1} epiphyte dry mass at continuous habitats. Grazer control treatments had 286.8 ± 25.8 μg Chl *a* g^{-1} epiphyte dry mass, while grazer exclusion plots had 296.7 ± 16.7 μg Chl *a* g^{-1} epiphyte dry mass. Edge habitats had 353.7 ± 73.0 μg Chl *a* g^{-1} epiphyte dry mass at Cherokee Sound; whereas, the epiphyte autotrophic index at Jungle Creek was 239.3 ± 26.1 μg Chl *a* g^{-1} epiphyte dry mass. Epiphyte autotrophic indices were significantly higher ($P < 0.005$) at Cherokee Sound than at Jungle Creek. The higher autotrophic index at Cherokee Sound suggests the presence of epiphytes with more chlorophyll *a* relative to their total mass.

Table 3
Average values ± standard error for seagrass percent cover and productivity across treatments at each site. Differences between sites are significantly different for each seagrass metric. Tt = *Thalassia testudinum*; LAI = Leaf Area Index.

	Units	Cherokee Sound	Jungle Creek	P-value
Tt Abundance	%	79.7 ± 2.8	61.7 ± 3.5	<0.0001
Short Shoot Density	ss m^{-2}	789.5 ± 30.2	519.4 ± 20.1	<0.0001
Standing Crop	g m^{-2}	123.7 ± 8.8	56.5 ± 4.3	<0.0001
Leaf Mass per Short Shoot	mg	156 ± 10.1	108.8 ± 7.1	0.0003
Leaf Length	mm	161.2 ± 7.3	129.5 ± 4.3	0.0004
Leaf Area	cm^2 ss^{-1}	38.6 ± 2.5	26.2 ± 1.6	0.0001
LAI	m^2 m^{-2}	3.1 ± 0.2	1.4 ± 0.1	<0.0001
Areal Productivity	g m^{-2} d^{-1}	2.2 ± 0.2	1.3 ± 0.2	<0.0001
Leaf Area Productivity	Cm^2 m^{-2} d^{-1}	487.8 ± 33.4	274.9 ± 15.6	<0.0001
Specific Productivity	mg g^{-1} d^{-1}	19.3 ± 1.4	22.7 ± 1.1	0.0055

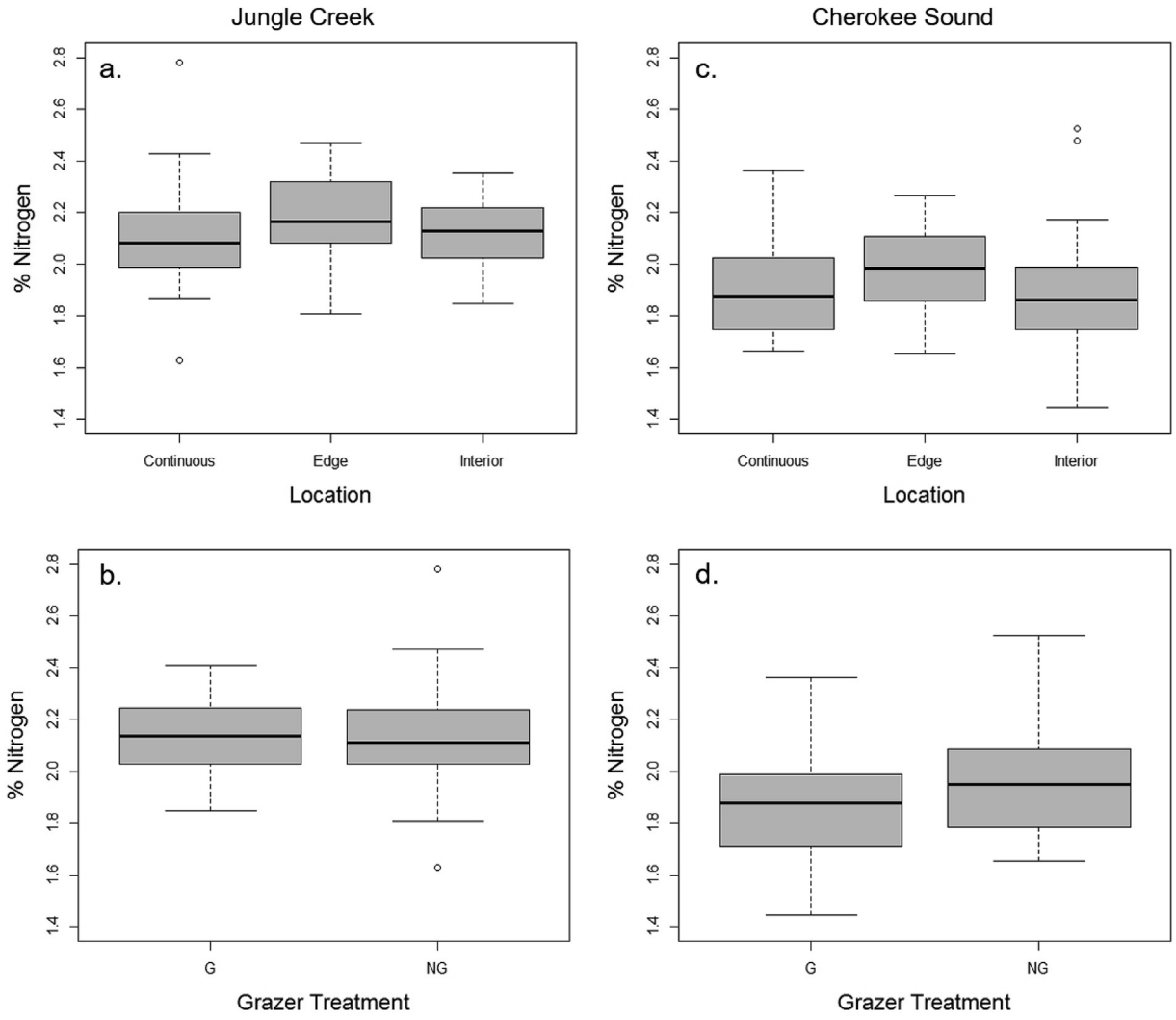

Fig. 4. Nitrogen content in seagrass photosynthetic tissues within sites. Differences in nitrogen content by sampling location (panels a and c), and grazer treatments (panels b and d). G = Grazer control; NG = Grazer exclusion. Significant differences indicated by letters above error bars.

Within-patch analyses of the epiphyte autotrophic indices were not significantly different among plots for either site (Table 4).

The most abundant epiphyte phototrophic groups identified in this study were diatoms (average relative abundance across sites: 56.7%) and chlorophytes (average relative abundance across sites: 32.1%). Dinoflagellates (average relative abundance across sites: 8.2%) and cyanobacteria (average relative abundance across sites: 3.0%) were identified as well, but in lower abundances. Epiphyte community composition was significantly different between sites ($P = 0.001$; Fig. 6), but was unaffected by fragmentation and grazer treatments. Diatoms were the most abundant epiphyte group at Cherokee Sound (74.4% average relative abundance), and chlorophytes were the most abundant epiphyte group at Jungle Creek (52.6% average relative abundance). Within sites, epiphyte community composition was not significantly different across fragmentation or grazer treatments.

3.4. Amphipod responses

A total of 314 individual amphipods were collected from 7

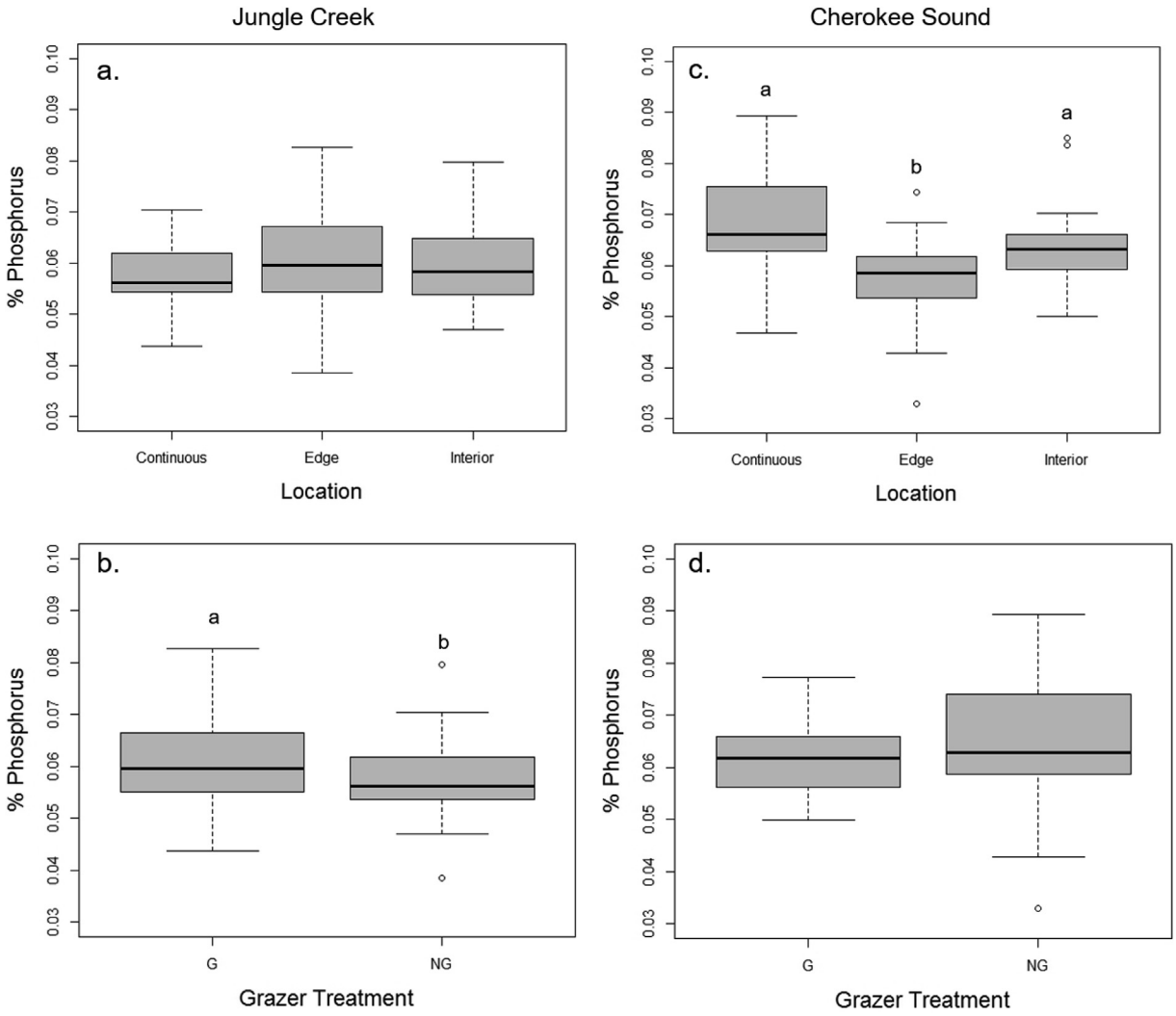

Fig. 5. Phosphorus content in seagrass photosynthetic tissues within sites. Differences in phosphorus content by sampling location (panels a and c), and grazer treatments (panels b and d). G = Grazer control; NG = Grazer exclusion. Significant differences indicated by letters above error bars.

Table 4
Minimum, mean and maximum epiphyte biomass by main effect (site, habitat type, and grazer treatment) as described by the epiphyte autotrophic index (μg Chl *a* g^{-1} epiphyte dry mass) and leaf specific epiphyte biomass (μg Chl *a* leaf $area^{-1}$).

Main Effect		Leaf Specific Epiphyte Biomass			Epiphyte Autotrophic Index		
		Min	Mean	Max	Min	Mean	Max
Site	Cherokee Sound	0.02	0.68	2.38	79.79	348.89	1439.12
	Jungle Creek	0.02	0.73	6.91	23.27	235.71	559.50
Habitat	Continuous	0.15	0.67	2.38	60.68	293.68	703.88
	Fragmented	0.18	0.63	1.85	143.59	288.38	483.45
Treatment	Grazer control	0.02	0.66	2.38	23.27	282.60	1439.12
	Grazer exclusion	0.09	0.74	6.91	27.99	302.20	663.85

families representing 14 unique taxa. At Cherokee Sound, 188 individuals were collected from 3 families representing 7 different species. Jungle Creek was more diverse with 126 individuals collected from 6 families representing 10 species. Of the collected amphipods, 2 families representing 3 species were collected at both sites (Family Aoridae: *Grandidierella bonnieroides*; Family Ampithoidae: *Cymadusa compta* and *C. filosa*). Amphipod density was 0.74 ± 0.09 amphipods g^{-1} seagrass AFDW per plot at Cherokee Sound and 0.79 ± 0.14 amphipods g^{-1} seagrass AFDW per plot at Jungle Creek. Amphipod density was 1.10 ± 0.12 amphipods g^{-1} seagrass AFDW per plot grazer control plots, and 0.43 ± 0.10 amphipods g^{-1} seagrass AFDW per plot grazer exclusion plots. In continuous plots 0.98 ± 0.18 amphipods g^{-1} seagrass AFDW per plot. In fragmented plots, amphipod density was 0.74 ± 0.13 amphipods g^{-1} seagrass AFDW per plot in interior plots and 0.57 ± 0.10 amphipods g^{-1} seagrass AFDW per plot in edge plots.

Amphipod density was not significantly different between sites or fragmented treatments, but was lower in grazer exclusion plots ($p < 0.001$) than grazer control plots. The interaction between site and grazer treatments was significant ($P = 0.02$). Amphipod density was higher in grazer control plots ($\bar{x}$= 1.22 ± 0.10 amphipods g^{-1} seagrass AFDW) than exclusion plots ($\bar{x}$= 0.27 ± 0.06 amphipods g^{-1} seagrass AFDW) at Cherokee Sound (Tukey HSD post hoc analysis; $P < 0.001$). No significant differences between grazer control and exclusion plots were observed at Jungle Creek indicating carbaryl was ineffective at this site. Carbaryl use to understand the ecological interactions between amphipods and primary producers is widespread in temperate seagrass ecosystems (see Duffy et al., 2015). The efficacy of carbaryl in tropical study systems, however, has been inconclusive to date (J. Campbell, personal

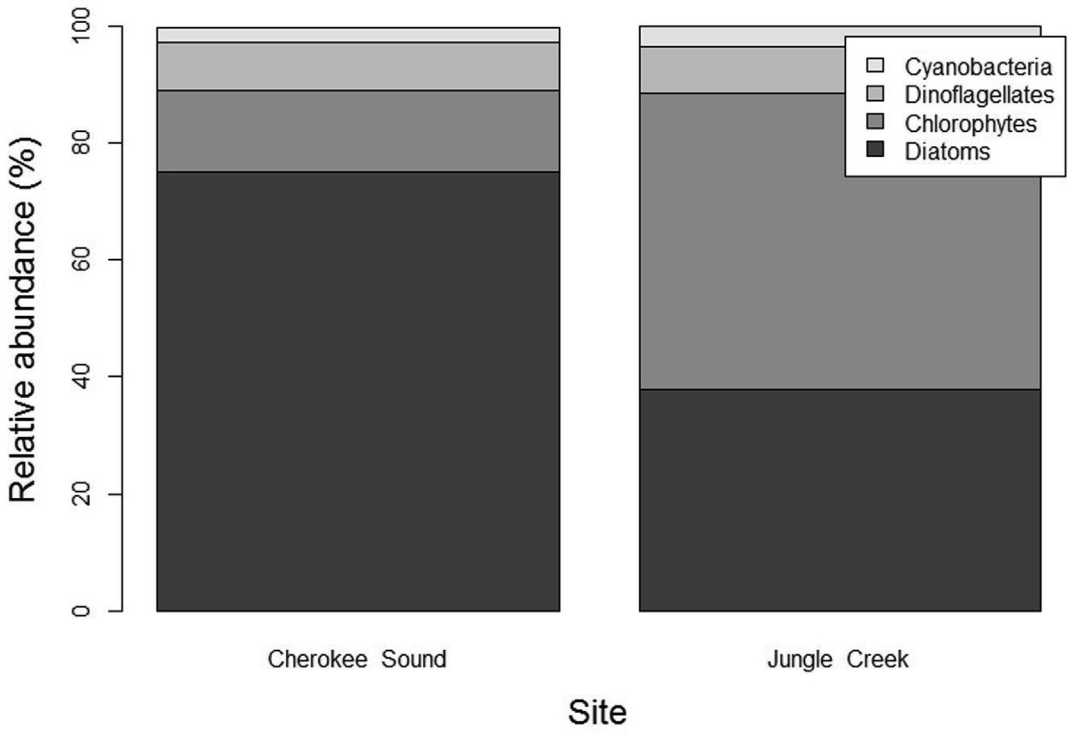

Fig. 6. Relative abundance of epiphytes by major taxonomic group at each site. CS= Cherokee Sound, JC = Jungle Creek.

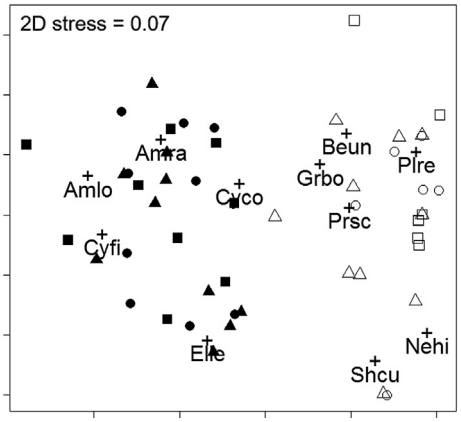

Fig. 7. Non-metric multidimensional scaling plot illustrating community structure differences between sites, but not across locations within sites. Jungle Creek plots are indicated by open shapes and Cherokee Sound plots are in solid shapes. Circles are interior plots, squares are edge plots, and triangles are continuous plots. Codes for amphipod taxa consist of four letters and '+', where Amlo is *Ampithoe longimana*, Amra is *Ampithoe ramondi*, Cyco is *Cymadusa compta*, Cyfi is *Cymadusa filosa*, Elle is *Elasmopus levis*, Beun is *Bemlos unicornis*, Grbo is *Grandidierella bonnieroides*, Plre is *Plesiolembos rectangulatus*, Prsc is *Protohadzia schoenerae*, Nehi is *Neomegamphopus hiatus*, and Shcu is *Shoemakerella cubensis*.

communication). We caution against assuming carbaryl is universally effective in eliminating amphipod grazers from seagrass beds, even when study sites are in relative close proximity as in our study, and recommend pilot studies at the experimental sites prior to establishing larger-scale studies to test the efficacy of carbaryl at the study site.

Because of the significant site*grazer treatment interaction, and the ineffectiveness of carbaryl at Jungle Creek, we removed the grazer exclusion plots from the analyses for fragmentation and edge effects on amphipod density. Amphipod density was significantly reduced in fragmented plots ($P = 0.004$), but not significantly impacted by edges (i.e., no difference between interior or edge locations) at Cherokee Sound or Jungle Creek.

Amphipod community composition differed between sites ($P < 0.001$), but were unaffected by fragmentation. The most common species identified at Cherokee Sound included *Ampithoe ramondi* (relative abundance = 34%), *Elasmopus levis* (relative abundance = 24%), and *Cymadusa filosa* (relative abundance = 23%). At Jungle Creek, *Plesiolembos rectangulatus* (relative abundance = 47%), *Grandidierella bonnieroides* (relative abundance = 13%), *Bemlos unicornis* (relative abundance = 13%), and *Shoemakerella cubensis* (relative abundance = 8%) were the most abundant species. Within sites, amphipod community composition was not significantly different between edge and interior treatments (Fig. 7).

4. Discussion

Habitat fragmentation in Bahamian seagrass meadows caused some changes in the functioning of seagrass ecosystems. The most noticeable pattern occurred in edge habitats where concurrent nutrient depletion and heavier $\delta^{13}C$ were detected, both of which are indicative of increased light availability in seagrass ecosystems (Abal et al., 1994; Campbell and Fourqurean, 2009). Amphipod density was reduced in fragmented patches and exclusion plots, but there was no edge effect on amphipod density. We found no evidence of changes in top-down control with fragmentation, because reduced amphipod density did not reduce epiphyte biomass or change epiphyte community composition in study patches. In this experiment, higher levels of allochthonous nutrient inputs at Cherokee Sound than at Jungle Creek were possible because of the close proximity to a larger human population (Stoner et al., 2011). Allochthonous nutrient inputs at Cherokee Sound could account for higher seagrass productivity, higher phosphorus content, and different epiphyte community composition than at Jungle Creek.

Propeller scarring in Cherokee Sound caused a shift in nutrient and isotopic content of seagrass photosynthetic tissues in edge habitats. Phosphorus content became depleted in edge plots, while $\delta^{13}C$ increased, indicating a change in seagrass physiological processes initiated by altering the physical environment (Durako and Hall, 1992; Abal et al., 1994; Campbell and Fourqurean, 2009). When seagrasses are shaded they have lighter $\delta^{13}C$ values in photosynthetic tissues (Durako and Hall, 1992; Abal et al., 1994; Campbell and Fourqurean, 2009). Propeller scars remove aboveground tissues, which relieves adjacent seagrasses from self-shading by allowing increased light penetration, exposing more photosynthetic tissue to light. Light is not a limiting factor at either site in this study because of the clear, shallow, water column. However, short-shoot density was higher at Cherokee Sound than Jungle Creek. Higher short-shoot density in conjunction with changes in seagrass nutrient content and isotope values in edge habitats at Cherokee Sound suggests seagrasses here may be self-shading.

Fragmentation created by simulated propeller scars reduced amphipod density overall. This is in contrast with other fragmentation studies; for example, no fragmentation effects were detected on epifauna and nekton communities in eelgrass fragments created in the lower Chesapeake Bay (Lefcheck et al., 2016). Reduced abundance of gammaridean amphipods has also been attributed to the loss of habitat associated with fragmentation. After fragmentation of artificial seagrass patches in Brazil, amphipod abundances were reduced in smaller experimental fragments (Pierri-Daunt and Tanaka, 2014). The study conducted by Reed and Hovel (2006) was most similar to our study in that they fragmented natural seagrass beds and sampled habitats after 4 and 8 weeks. Abundance of epifauna, including amphipods, was reduced in live seagrass beds in San Diego, California, but only after habitat area was reduced by 90% (Reed and Hovel, 2006). Amphipod densities were reduced after fragmentation in our study as well, but the amount of habitat loss was much less than 90% and fragments were embedded within a continuous seagrass bed.

We found no impact of edge effects on amphipod density (amphipod densities in edge and interior plots were not significantly different), despite the presence of predators, such as *Geres cinereus* (yellowfin mojarra) and *Lutjanus apodus* (schoolmaster snapper; Rooker, 1995) at both sites. While predators may be preying on amphipods in our study, they are not preferentially hunting in edge habitats as was evidenced by no reduction in amphipod density in edge plots. In southwest Finland, amphipod densities in fragmented treatments were higher than in continuous treatments (Arponen and Boström, 2012), which the authors attributed to an edge effect. In other cases, edges, like those created by propeller scars in seagrass beds, can increase predation on some invertebrate species, causing reduced abundance (scallops: Bologna and Heck, 1999; decapods: Tanner, 2005).

Epiphyte biomass (measured as chlorophyll *a*) on seagrasses was not significantly different between Jungle Creek and Cherokee Sound despite differences in amphipod densities and community composition. Epiphyte community composition, on the other hand, differed significantly between Cherokee Sound and Jungle Creek. Diatoms and chlorophytes were the most abundant phototrophic groups within the seagrass epiphyte communities at both sites, but the relative abundance of each phototrophic group was different. Diatoms were the most abundant phototrophic group at Cherokee Sound, whereas chlorophytes were the most abundant phototrophic group at Jungle Creek. In Florida Bay, the relative abundance of diatoms decreased and the relative abundance of chlorophytes (chl *b*) increased with experimental phosphorus enrichment (Armitage et al., 2006; Frankovich et al., 2009). In our study, diatom abundance was higher at phosphorus-enriched Cherokee Sound. Nutrient enrichment has occurred over a longer time period (decades) and is indicative of ambient nutrient availability (i.e., not experimental fertilization). As such, differences between studies could be attributed to the type (experimental, short-term enrichment as opposed to persistent enrichment from runoff) and duration of nutrients present.

Gammaridean amphipods exhibit species-specific feeding preferences on epiphytic algae (Duffy and Hay, 1994; 2000; Duffy and Harvilicz, 2001), possibly contributing to differences in epiphyte community composition between the study sites. The most abundant amphipod species at Jungle Creek include *Plesiolembos rectangulatus*, which accounted for 47% of the individual amphipods collected at this site, and *Bemlos unicornis*, which accounted for 13%. The abundance of these species (60% combined) suggests they would have a large impact on the composition of the epiphyte community at Jungle Creek. However, little to no information is available on the feeding ecology of these species. *Grandidierella bonnieroides* also consisted of 13% of sampled amphipods at Jungle Creek. *G. bonnieroides* is a specialized grazer on epiphytic diatoms and particulates of detritus attached to seagrass leaves (Zimmerman et al., 1979). At Cherokee Sound, the most abundant amphipod species was *Ampithoe ramondi*, which accounted for 34% of amphipods collected. *A. ramondi* feeds primarily on diatoms and filamentous green algae (Brawley and Adey, 1981). *Elasmopus levis* and *Cymadusa filosa* consisted of 24% and 23% of the sampled amphipod community, respectively, and both species graze on chlorophytes (Buza-Jacobucci and Pereira-Leite, 2014; Ceh et al., 2005; Bruno & O'Connor, 2005; Duffy and Hay, 2000). Diatoms and chlorophytes, the most abundant epiphytes at Cherokee Sound, are also important food sources for less abundant species in this site, such as *G. bonnieroides* (Zimmerman et al., 1979) and *A. longimana* (Bousfield, 1973). More information on the feeding ecology of both *P. rectangulatus* and *B. unicornis* is needed, however, to draw conclusions about the top-down control of amphipods on epiphyte community composition between sites in this study.

At Cherokee Sound, where carbaryl was effective at excluding amphipods from half the experimental plots, epiphyte biomass was similar in amphipod control and exclusion plots and in fragmented and continuous plots. No evidence for top-down control of epiphyte biomass was detected, despite the reduction of amphipod densities in fragmented plots. Furthermore, epiphyte phototrophic groups did not differ between amphipod control and exclusion plots, suggesting that amphipods are not exerting top-down control on particular phototrophic groups within Cherokee Sound. Previous studies indicate that amphipods fail to reduce overall epiphyte biomass, but can alter the community composition of epiphytes on seagrasses (Duffy and Hay, 2000). However, such top-down responses differ because of site-specific factors. In a meta-analysis of 15 sites in the *Zostera* Experimental Network (ZEN), top-down control of epiphytes was moderate but grazer and algal biomass were better predicted by site-specific variability in *Zostera* sp. and grazer diversity (Duffy et al., 2015).

Mechanical damage caused by increased boat traffic is likely to increase as coastal development continues (Short et al., 2011; Hallac et al., 2012). As such, studies are needed to address the gaps in our understanding of how propeller scarring will alter the ecological functioning of seagrass ecosystems. This study demonstrates that light mechanical damage can alter the stoichiometry of seagrass ecosystems, even over the short duration (5 weeks) of this study. Severely scarred seagrass beds may suffer from depletion of internal nutrient stores and redistribution of amphipods if more habitat is lost. Furthermore, actual scars excavate sediment and destroy the seagrass rhizosphere complicating restoration and recovery of scars. As such, the results reported in this study are a conservative estimation of the impacts of propeller scarring on

seagrass ecosystem functioning. Experimental duration was a factor not considered in this experiment that could play a role in amphipod community composition and abundance. Experiments of longer timeframes are needed to assess the persistence of the influences of propeller scarring on seagrass ecosystem functioning. The impacts of the scars on amphipod densities could become more apparent over time as seagrass shoot density decreases and habitat loss increases (see Walker et al., 1989; Kenworthy et al., 2002; Whitfield et al., 2002; Di Carlo and Kenworthy, 2008). This study brings to light the need for future studies investigating the impacts of propeller scarring on seagrass-amphipod interactions.

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Appendix A. Methods & results from pilot experiment

Methods

The purpose of this pilot study was to test the effectiveness of carbaryl in a dense, tropical seagrass bed (methods closely follow Whalen et al., 2013). This study was conducted from 6 to 15 May 2013 in Florida Bay at 25 ° 5′ 13.784″ N and 80 ° 27' 8.985" W. Plots were created using 5 cm × 5 cm squares (8 per plot) cut from a natural fiber air conditioner filter secured to mesh strips in two parallel rows at 10 cm, 30 cm, 60 cm, and 100 cm from a plaster block secured to the sediment surface (Fig. A1). To eliminate potential effects of current on the distribution of carbaryl into the water-column and cross contamination from neighboring plots, plots were established at a minimum distance of 2 m apart and each plot was randomly assigned one of the eight 45 ° angles from north (Poore et al., 2009; Whalen et al., 2013).

To test the effectiveness of carbaryl on eliminating crustacean grazers, two concentrations of carbaryl were dissolved into plaster of paris blocks. Low concentration blocks (3.3% carbaryl by dry weight plaster) were created using 18.5 g carbaryl to 222 mL water and 555 g plaster of paris. High concentration (10% carbaryl by dry weight plaster) blocks were created by mixing 55.5 g carbaryl into 222 mL water and 555 g plaster (Whalen et al., 2013). I included two control treatments. Control blocks used the same amount of water and plaster with no carbaryl, and ambient plots contained no plaster block. I included 5 replicates of each treatment for a total of 20 plots.

I removed one row of filter squares from each of the 20 plots 4 days after set-up. Each filter square was placed in a 100 mL specimen cup and the lid was immediately replaced. The second row of filter squares was collected 9 days after set-up. After each filter square was removed and placed securely in a cup, I collected data on habitat complexity (species present, percent cover, and shoot counts) within 400 cm^2 quadrats placed immediately adjacent to each filter square. Samples were transported on ice to the lab where they were processed. Grazers (amphipods, isopods, and shrimp) were removed from filter squares and placed on preweighed Nitex mesh (500 μm) squares. Biomass (mg) of grazers was determined as the wet weight.

I tested for effects of habitat complexity on amphipod biomass with regression analysis. Shoot counts of *Thalassia testudinum* were used as a proxy for habitat complexity because of discrepancies in data collected by different divers for both percent cover and species present. Furthermore, *Thalassia* was the most dominant macrophyte present at my study site.

I tested for the effects of treatment (no-block control, carbaryl-free block control, low concentration carbaryl block, and high concentration carbaryl block), distance (10 cm, 30 cm, 60 cm and 100 cm), and time (4 or 9 days) on crustacean biomass using a split-plot design where pesticide treatment was the whole plot ($n = 5$ per treatment). Time was treated as a two-level within-plot (subplot) factor because I only sampled at days 4 and 9 after experimental setup. Epifaunal biomass was log transformed to meet assumptions of homoscedasticity. Distance was treated as a covariate.

Results

Thalassia shoot density did not influence the biomass of grazers in any of the treatment plots (Table A1; Fig. A2). Carbaryl effectively prevented colonization of filter squares by crustacean grazers at close range (Fig. A3). Grazer biomass was significantly higher in control plots than plots containing carbaryl (Table A2; $p < 0.0001$), and biomass increased with distance from source (Table A2; $p < 0.0001$). Grazer biomass was higher in the 9-day duration (Time) plots. This was possibly due to the large variation in the 9-day control treatments. Carbaryl treatments significantly reduced grazer biomass when compared to controls (Table A2; $p < 0.0001$). However, no reduction in grazer biomass occurred between low and high carbaryl concentration treatments or between the ambient control and the control block.

Table A1
Relationship between grazer wet biomass (mg) and *Thalassia* shoot density.

Treatment	P-value	R^2 value
Ambient Control	0.69	0.0040
Control Block	0.90	0.0005
Low Concentration	0.17	0.0480
High Concentration	0.94	0.0002

Table A2
ANOVA results for linear model of grazer biomass (mg) by Treatment, Distance, and Time. Significant differences are denoted by bold text and $p < 0.05$.

Between factors			
	DF	F value	P value
Treatment	3	23.09	**<0.0001**
Controls vs Deterrent	1	67.47	**<0.0001**
Low vs High	1	1.800	0.198
Ambient vs Block Control	1	0.013	0.910
Residuals	16		
Within Factors			
	DF	F value	P value
Distance	1	24.91	**<0.0001**
Time	1	19.13	**<0.0001**
Trt*Dist	3	7.07	**0.0002**
Trt*Time	3	1.64	0.1825
Dist*Time	1	0.41	0.5249
Trt*Dist*Time	3	1.79	0.1524
Residuals	128		

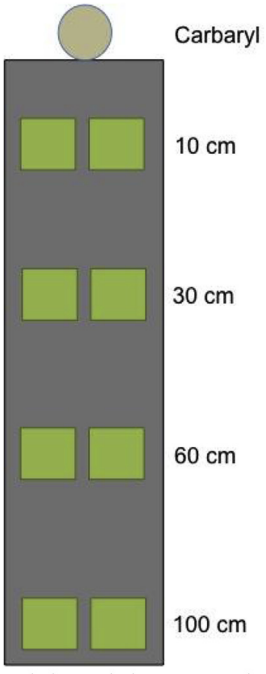

Fig. A1. Schematic: Experimental plots. Circles represent slow-release blocks, green squares represent filter squares, and grey rectangle represents mesh screen to which filter squares are attached.

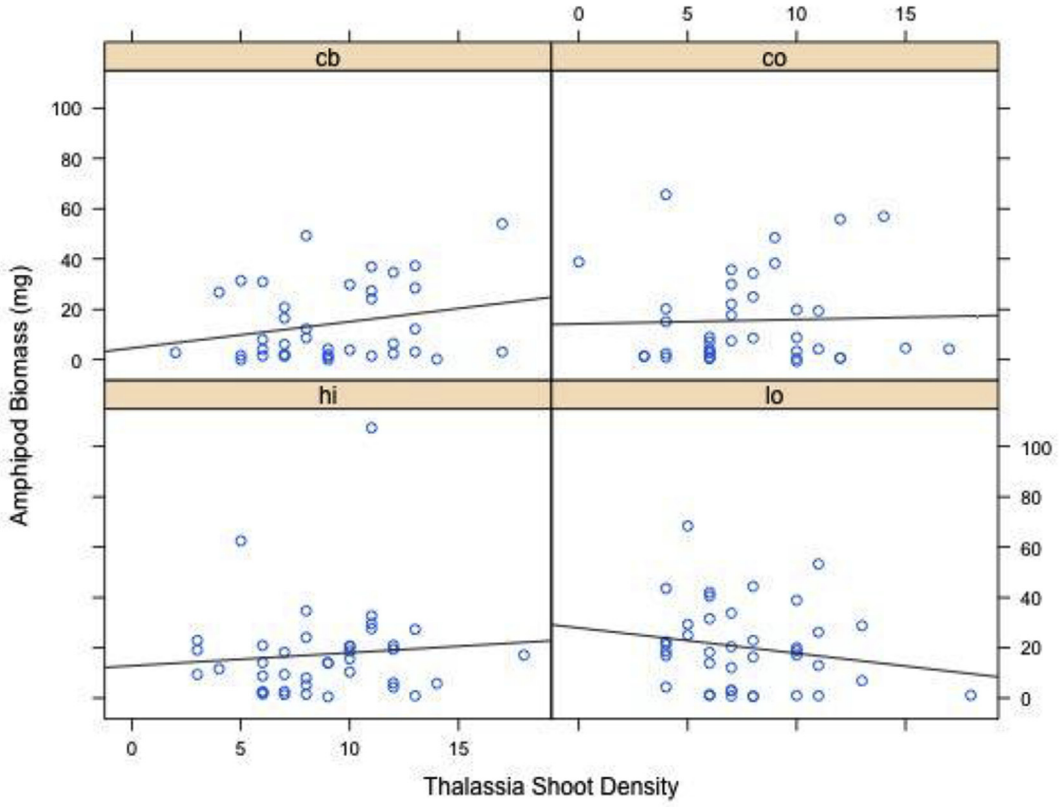

Fig. A2. Relationship between Grazer biomass (mg) and *Thalassia testudinum* shoot density by treatment. Treatments are labeled as follows: cb (control block), co (ambient control), hi (high concentration), and lo (low concentration).

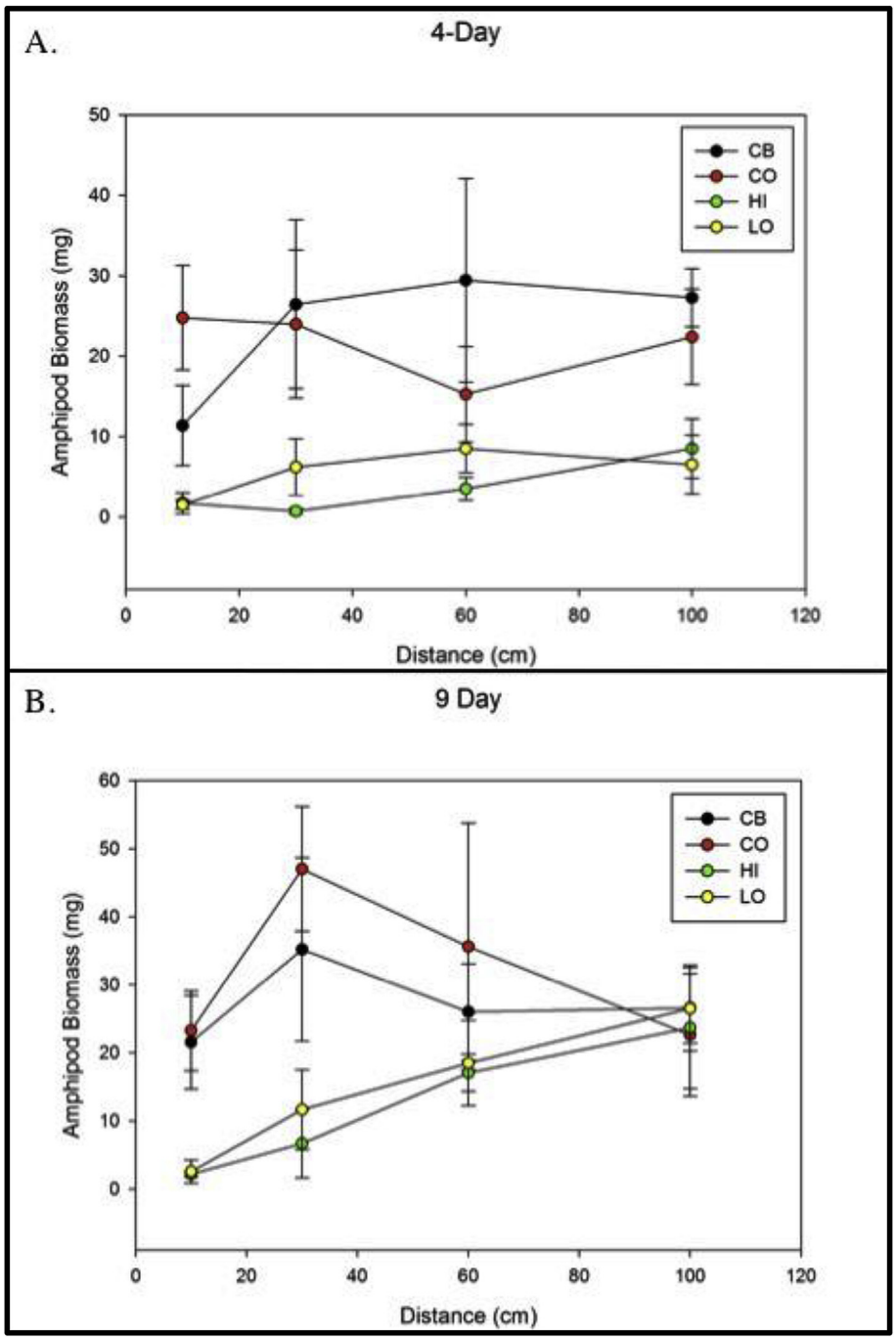

Fig. A3. Grazer biomass (mg) after A) 4 days and B) 9 days. Colors represent different treatments: black (cb-control block), red (co-ambient control), green (hi-high concentration), and yellow (lo-low concentration). Error bars represent ± standard error.

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