



# Variability in herbivory in subtropical seagrass ecosystems and implications for seagrass transplanting

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## ABSTRACT

Herbivory structures ecosystems in multiple and complex ways and is capable of affecting the success of ecological restoration projects that involve reestablishing plant communities. Direct herbivory on experimental planting units assembled from leaves of the seagrasses *Thalassia testudinum*, *Syringodium filiforme*, and *Halodule wrightii* was assayed in 2009–2010 in south Florida, USA. Seagrass biomass loss to herbivory was compared with elemental composition of donor and ambient seagrass leaves as well as with fish communities at the assay sites. Seagrass herbivores were capable of removing substantial biomass from our experimental planting units, and this varied across seagrass species, location, and time. Seagrass biomass loss to herbivory ranged from 0% to 82%. More biomass was lost during the spring assays than in fall and winter assays. Biomass loss was greatest in *S. filiforme* and *H. wrightii*, and negligible in *T. testudinum*. The assay site closest to tidal cuts leading to the coral reef tract experienced the highest average levels of herbivory. C:N ratios and salinity were predictors of seagrass biomass loss, but not C:P ratios, temperature, or herbivorous fish abundance. Leaf loss to seagrass herbivores appears to be a spatially variable but critically important determinant of seagrass transplanting success. We recommend that local knowledge of herbivory pressure be considered during restoration planning. In our system, a conservative approach to seagrass transplanting, limiting projects to winter months, and refraining from seagrass transplanting all together in areas proximal to coral reefs, are likely to maximize the potential for success.

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## 1. Introduction

Because of the ecological importance of seagrasses and rapid rates of seagrass loss along the world's coastlines (Waycott et al., 2009), resource managers aim to both stop the loss of seagrasses and restore degraded or destroyed seagrass habitat. Disturbances to seagrass ecosystems may result in loss of or a reduction in their ability to provide key ecosystem functions. As a result, there has been increasing interest in seagrass restoration since the mid 1970's (Fonseca, 2011).

Ecological restoration often attempts to reestablish plant communities that have been destroyed or degraded. For restoration to be successful, ecological attributes of the system such as structure and function must be reestablished (Higgs, 1997; Hobbs and Norton, 1996). Herbivores are capable of altering ecosystem structure and function (Milchunas et al., 1988; Parker et al., 2006) through interacting effects of stress from grazing and release from competitive exclusion (Connell, 1978; Grime, 1973; Paine, 1971). In terrestrial grasslands, the success of restoration and recovery trajectories in restoration projects that target rehabilitation of plant communities may be influenced

by selective herbivory (Fraser and Madson, 2008; Howe and Lane, 2004; Young et al., 2005).

In seagrass meadows, herbivory structures ecosystems in multiple and complex ways such as directly removing biomass, facilitating energy flow through food webs, controlling epiphytic growth, stimulating primary and secondary production, and altering species composition (Heck and Valentine, 2006). Epiphytic microalgae on seagrass plants and benthic microalgae are critical food sources for micrograzers (Bologna and Heck, 1999; Moncreiff and Sullivan, 2001). The seagrasses themselves are also directly consumed by certain herbivores. Mega-herbivores such as green turtles and sirenians are capable of consuming a substantial amount of biomass, and can influence spatial distribution and standing biomass of seagrass meadows (Fourqurean et al., 2010; Lal et al., 2010). Direct herbivory on seagrasses by fish and urchins is also an important process (Alcoverro and Mariani, 2004; Cebrián and Duarte, 1994, 1998; Kirsch et al., 2002; Rose et al., 1999). Seagrasses support high levels of secondary production as a result (Mateo et al., 2006). Fish grazing can regulate local seagrass species composition and density (Armitage and Fourqurean, 2006; Randall, 1965; Tribble, 1981; Valentine and Heck, 1999).

Like grazers in terrestrial environments (Mattson, 1980), seagrass grazers may preferentially consume plants with higher nutrient content (Goeker et al., 2005; Heck and Valentine, 2006; McGlathery, 1995; Prado and Heck, 2011; Williams, 1988) or faster growing plants

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(Cebrián and Duarte, 1998). Nutrient content in seagrass leaves varies among species, and also spatially within species (Duarte, 1990). In south Florida and the Caribbean, the dominant seagrass species include *Thalassia testudinum*, *Syringodium filiforme*, and *Halodule wrightii*, which occur in both monospecific and mixed beds (McMillan and Phillips, 1979; Thorhaug, 1981). Nutrient content varies among and within these species over relatively small spatial scales in response to terrestrial, oceanic, groundwater, or point source inputs (Caccia and Boyer, 2005; Campbell and Fourqurean, 2009; Fourqurean et al., 1992; Peterson et al., 2012). Thus local seagrass landscapes can exhibit substantial variation in community composition and stoichiometry, to which herbivores may respond.

Seagrass transplanting is a common restoration method, used to more quickly replace lost plant structure and associated functions than would otherwise occur through a relatively slower natural recovery process (Fonseca et al., 1998; Lewis, 1987). Seagrass restoration projects involving transplanting are often designed to mimic observed patterns of succession by incorporating the principle of “modified compressed succession” (sensu Durako and Moffler, 1985). In these projects, an early successional, faster-growing seagrass species (e.g., *H. wrightii* and/or *S. filiforme* in the subtropical western Atlantic region) is transplanted under the assumption that they will colonize more quickly than slower-growing climax species (e.g., *T. testudinum*), which in time, will reestablish dominance in the restoration area. Experimental evidence exists that transplanted, early-successional seagrasses may be preferentially consumed through selective herbivory (Armitage and Fourqurean, 2006; Fraser and Madson, 2008; Howe and Lane, 2004; Prado et al., 2010). However, despite the literature record as well as cautionary notes of the potential impact of herbivory to planting unit survival (Fonseca et al., 1998), the impacts of herbivores on transplanting success in seagrass meadows remain largely unstudied.

This study aimed to evaluate herbivory pressure on transplanted seagrasses. Herbivory is suspected as the cause of poor performance of some seagrass transplanting efforts that have been conducted to repair injuries from vessel groundings in Biscayne National Park, adjacent to the Miami metropolitan area in south Florida, USA. Qualitative observations of these transplanting efforts, which took place during the period 2007–2008, led us to several hypotheses as to the loss of the planted seagrasses. During these efforts, planting unit biomass was lost overnight or within days of planting at some locations, and we hypothesized that loss was due to herbivory rather than transplanting shock to the transplanted clones. In the previous restoration projects, planting unit success differed among restoration sites, so for the current study, we hypothesized that biomass loss to herbivory varied across space. Apparent interspecific differences in rates of loss between seagrass species led us to hypothesize that biomass loss to herbivory varied with seagrass species, possibly suggesting consumer feeding preferences. Since herbivores may choose high-nutrient plants, we hypothesized that rates of herbivory would be related to plant nutrient content. In a landscape with patchy distribution of seagrass species with variable stoichiometry, transplantation of these species for restoration may result in the presentation of a more preferred food source in some areas. Further, since we suspected that the herbivores responsible for the observed loss of seagrass transplants were fish, we expected rates of herbivory to be related to the size and species composition of the fish community. Given that fish community abundance is correlated with water temperature (Serafy et al., 2003; Tremain and Adams, 1995) we also expected herbivory to vary throughout the year.

## 2. Methods

### 2.1. Study system

Southern Biscayne Bay is a shallow (<3 m) subtropical estuary located at the southeastern tip of the Florida peninsula (Fig. 1). The

extensive seagrass communities in southern Biscayne Bay are dominated by dense *T. testudinum*. *S. filiforme* and *H. wrightii* are also found throughout this area in lower abundance and with patchy distributions. This study was conducted at four shoals: Biscayne Channel, No Name Shoal, East Featherbed Bank, and Cutter Bank (Fig. 1), which are characterized by thriving seagrass communities, but have been impacted by multiple vessel grounding injuries over the past two decades. Vessel groundings remove seagrass and excavate sediment in discrete patches on shallow seagrass shoals. Existing vessel grounding injuries selected at each shoal as study sites were unvegetated patches surrounded by a dense seagrass community, and ranged from 40 to 60 m<sup>2</sup>.

### 2.2. Experimental design

Seagrass and fish community surveys, herbivory assays, and elemental analysis of seagrass leaf tissue were conducted during the Spring of 2009 through the Winter of 2010.

### 2.3. Seagrass community surveys

Seagrass community composition was documented in undisturbed seagrass habitat in the vicinity (within 100 m) of each herbivory assay site. Seagrass and macroalgae abundance was estimated within randomly placed 0.25-m<sup>2</sup> PVC quadrats according to a modified Braun–Blanquet cover-abundance scale (Fourqurean et al., 2001). The number of quadrats varied per site (18–268), as did the timing and frequency of monitoring efforts. For each site, quadrat data from all available monitoring events were pooled for analysis. At No Name Shoal, data from a single monitoring event conducted in March 2011 were available (111 quadrats). At Biscayne Channel, East Featherbed Bank, and Cutter Bank, four monitoring events were conducted at each site during the 20-month period from December 2009 through July 2011, providing 71, 400, and 1070 total quadrats for analysis, respectively.

### 2.4. Fish community surveys

Two fish surveys were conducted at each assay site in October 2009 (Fall09) and in February–March 2010 (Win10), respectively (4 sites × 2 events × 2 surveys per site per event = 16 fish surveys) using a modification to the roving diver technique (Schmitt and Sullivan, 1996). For each survey, a snorkeler slowly surveyed one half of a 50-diameter circle (total survey area approximately 980 m<sup>2</sup>), as delimited with a 25-m transect tape attached to a central stake, for 30 min. The snorkeler counted fish observed within the survey area and identified them to species (when possible) or genus. Water temperature and salinity were measured for each survey using a YSI Model 30 instrument. Fish taxa expected to directly consume seagrass were categorized as seagrass herbivores (Ferreira and Floeter, 2004; Floeter, 2004; Valentine and Duffy, 2006). Note that while sea urchins are known to be important consumers of seagrass biomass, few sea urchins were observed at the study sites. As such, the role of sea urchins in removing seagrass biomass was not evaluated in this study, and was suspected to be minimal.

### 2.5. Herbivory assays

Herbivory pressure was examined through herbivore exclusion in a year-long study conducted in 2009–2010. A full factorial design was employed, with the following factors and levels: location (Biscayne Channel, E. Featherbed, Cutter Bank, No Name Shoal); seagrass species (*T. testudinum*, *H. wrightii*, *S. filiforme*); time (spring, summer, fall, winter), and herbivore exclusion (no cage, partial cage, full cage).

Planting units (PUs) designed to mimic the growth form and appearance of natural seagrass (sensu Hay, 1981; Kirsch et al., 2002) were used as experimental units in the herbivory assays. PUs

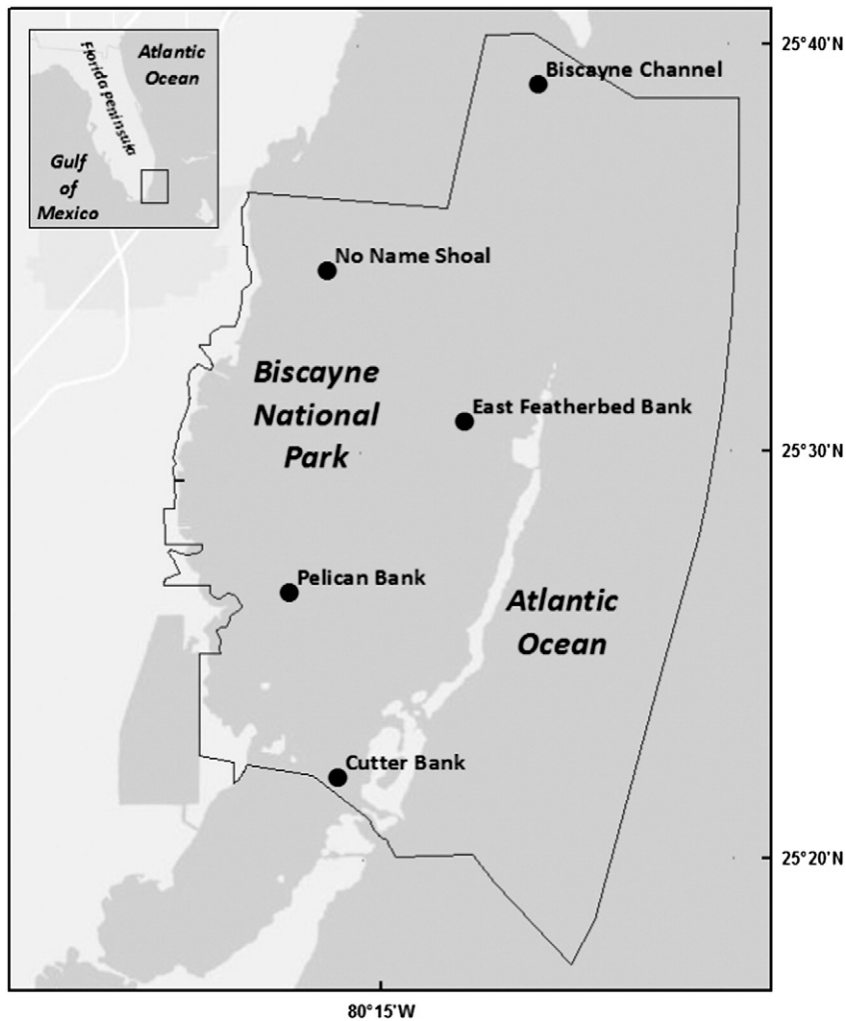


Fig. 1. Location of study sites in southern Biscayne Bay, Biscayne National Park, Florida, USA.

consisted of freshly-harvested seagrass leaf material inserted into simulated short shoots (binder clips) affixed to a simulated rhizome (labeled semi-rigid 30-cm plastic strip cut from cable tie). For deployment, the “rhizome” of the PU was gently pressed into bottom sediments and held in place with a U-shaped sod staple. This approach was beneficial for three reasons. It enabled the standardization of plant leaf tissue biomass used in each PU across species. It also eliminated consideration of non-photosynthetic and belowground tissue biomass that may mask leaf tissue biomass loss. Lastly, impacts to donor beds were minimized by removing only leaf material but leaving belowground tissues intact.

Seagrass shoots for use in constructing PUs were collected from a single donor site: Pelican Shoal (Fig. 1). Collecting donor material from a single location ensured that a sufficient supply of all three seagrass species was available for all assays over the year-long study. Shoots were collected on the morning of each assay deployment. Intact green leaves were selected from the collection for PUs; age of leaf tissue was not considered. Leaf tissue for each PU was spun in a salad spinner to remove excess water, gently wiped clean of epiphytes, and patted dry. Leaf tissue biomass was standardized across the three seagrass species, and approximately 1.5 g of fresh seagrass leaf material was used for each PU. After weighing, the leaf tissue for each PU was carefully clipped into the set of binder clips attached to each plastic rhizome. PUs were then placed into individual zip lock bags flooded with fresh seawater, for transport to the study site in seawater-filled coolers.

Herbivore exclusion cages were constructed of 0.635-cm black plastic aquaculture mesh. This mesh size was chosen as appropriate for excluding juvenile and adult fish of species known to directly consume seagrasses in the subtropical western Atlantic such as pinfishes and parrotfishes (Valentine and Heck, 1999). Full cages were formed of cylinders approximately 40 cm in height with a flat top approximately 30 cm in diameter. To control for possible influences of the cage structures on the PUs not related to herbivory, we also deployed partial cages as “cage controls”. Partial cages had two sides and a top, and were open on two sides. The partial cages were approximately 30 cm × 30 cm × 30 cm in size. Full and partial cages had lengths of lead-core line cable-tied to the bottom edges that rested on the sediment to help keep them upright. U-shaped sod staples were inserted through mesh into the sediments to further stabilize the cages. A cage contained a single PU.

Ten replicate PUs per seagrass species were randomly assigned to each of the three herbivore exclusion treatments, for a total of 90 PUs (per assay deployment, per site). Each PU with its respective caging treatment was randomly placed at 0.5 m intervals in rows in existing grounding injury features at each location. Placing PUs in the unvegetated injuries was intended to mimic a transplanting scenario. The configuration (number and length of rows) of the array varied according to the injury shape.

In each assay, PUs were deployed for a period of 72 h. Upon retrieval, the PUs were disassembled in the lab. Plant material was again spun and gently patted dry, then reweighed. Change in biomass was

expressed as the percent biomass loss per planting unit, determined by calculating the proportional loss in wet weight of each planting unit following the assay.

Herbivory assays were conducted at each site four times over a one-year period in 2009–2010: in May–June 2009 (Spr09), August 2009 (Sum09), November 2009 (Fall09), and February–March 2010 (Win10). These time periods were selected in order to coincide with warm (summer), cold (winter), and intermediate (spring, fall) water temperatures in this subtropical system. During each event, water temperature and salinity were measured at each site using a YSI Model 30 instrument.

## 2.6. Seagrass elemental composition

Seagrass leaf tissue was collected from each study site and the donor site for elemental content (total carbon = C, total nitrogen = N, total phosphorus = P) analyses. Leaf tissue was collected in triplicate (one replicate = six *T. testudinum* leaves, thirty *S. filiforme* leaves, or thirty *H. wrightii* leaves) during each of the four seasonal assays, from all seagrass species present at the study site at that time (*S. filiforme* and *H. wrightii* were not observed at every assay). Seagrass leaves were gently scraped to remove epiphytes, dried at 80 °C, and ground to a fine powder in a ball mill grinder. Total phosphorus content was determined through a dry-oxidation, acid hydrolysis extraction followed by colorimetric analysis of phosphate concentration in the extract (Fourqurean et al., 1992). Total carbon and total nitrogen were determined using a CHN analyser. Elemental content was calculated on a dry weight basis (mass of element/dry weight of sample) × 100%. Elemental ratios were calculated as molar ratios.

## 2.7. Data analyses

Due to difficulty distinguishing sea bream (*Archosargus rhomboidalis*) and pinfish (*Lagodon rhomboides*) in the field, survey data for these two species were grouped for analysis. Variation in square-root-transformed herbivore abundance was evaluated using a two-way analysis of variance (ANOVA) on square root transformed herbivore abundance data, with site and sampling time as fixed factors. Post-hoc tests on the species factor were conducted using Sidak's pairwise comparisons.

Data from herbivory assays (% biomass loss per PU) were not normally distributed (Shapiro–Wilk test,  $p < 0.05$ ), and were rank-transformed prior to analysis. The potential for a caging artifact was analysed using a one-way ANOVA with herbivore exclusion treatment as a fixed factor, followed by Sidak's post hoc comparisons. Differences in biomass loss between the uncaged and partial cage treatment was used as the indicator of caging artifact.

Variation in herbivory pressure was analysed using a three-way ANOVA on rank-transformed biomass loss data, with seagrass species, site, and time as fixed factors. Sidak's post hoc pairwise comparisons were used for significant main effects, and on the site × time × species interaction, to evaluate herbivory pressure across seagrass species at different times of the year at each site.

Variation in C:N and C:P ratios of seagrasses from Pelican Shoal (the donor site) was evaluated using two-way ANOVA (with species and time as factors) and Sidak's post-hoc comparisons on rank-transformed C:N ratios and on untransformed C:P ratios, with species and sampling time as fixed factors.

Donor seagrasses from Pelican Shoal and ambient seagrasses from each assay sites were compared for potential differences in elemental composition. Pairwise comparisons were conducted on seagrass C:N and C:P ratios between the donor site and assay site for each site/species/time combination. For elemental variables with normal distributions (C:P – all species; C:N – *T. testudinum* and *H. wrightii*), independent sample *t*-tests were used. Mann–Whitney *U*-tests were used for data with non-normal distributions (C:N – *S. filiforme*).

C:N and C:P ratios, temperature, salinity, and herbivorous fish abundance were used in stepwise multiple regression analyses to predict seagrass biomass loss. In each of the two regression analyses conducted, herbivory assay data from the three uncaged and partial cage treatments were pooled, and data from each seagrass species at each site were treated as replicates ( $n = 12$  replicates per sampling event). The first analysis included C:N and C:P ratios, temperature, and salinity for all four sampling events ( $n = 48$ ). The second analysis included herbivorous fish abundance in addition to C:N ratios, C:P ratios, temperature, and salinity. However, because fish surveys were conducted on only two of the four sampling events, the second analysis only included data from the Fall and Winter sampling events ( $n = 24$ ).

## 3. Results

### 3.1. Seagrass community composition

Dense seagrass communities dominated by *T. testudinum* surrounded the assay sites (Table S1). The median Braun–Blanquet score for this species was 5.0 (75–100% cover) at each site except at No Name Shoal, with a median score of 3.0 (25–50% cover). *S. filiforme* was not present in the seagrass monitoring quadrats at Biscayne Channel or Cutter Bank, though it was sampled at Biscayne Channel during the Summer 2009 herbivory assay. Sparse *S. filiforme* was detected at East Featherbed Bank, though it wasn't located there during any of the herbivory assays. *H. wrightii* was not present in the seagrass monitoring quadrats at Biscayne Channel or East Featherbed Bank, though it was sampled at Biscayne Channel during the Summer 2009 and Winter 2010 herbivory assays. Sparse *H. wrightii* was detected at Cutter Bank in seagrass monitoring quadrats, though it wasn't located there during any of the herbivory assays. Both *S. filiforme* and *H. wrightii* were found at No Name Shoal during all four herbivory assays and in the seagrass monitoring quadrats.

### 3.2. Fish community composition

A total of 1439 individuals of 25 taxa were observed during the sixteen fish surveys (Table S2). Of these, 594 individuals were classified as herbivorous (parrotfish) or omnivorous (bream/pinfish) across seven taxa. Total fish abundance ranged from 88 to 766 individuals during the Fall 2009 surveys, but dropped to less than 10% of those values during the Winter 2010 surveys. At the Cutter Bank winter survey, no fish were observed. Water temperatures recorded during the Fall 2009 surveys ranged from 29.5 °C to 31.3 °C, and dropped to between 17.6 °C and 19.5 °C during the Winter 2010 surveys (Table S2).

The three most abundant taxa observed over all surveys were sea bream/pinfish (*A. rhomboidalis*/*L. rhomboides*), grey snapper (*L. griseus*), and juvenile grunt species (*Haemulon* spp.), respectively (Table S2). Of the 597 herbivorous fish observed during all surveys, 77% were sea bream/pinfish. Pinfish undergo an ontogenetic shift from a carnivorous to herbivorous diet at approximately 100 mm in length (Luczkovich and Stellwa, 1993; Stoner and Livingston, 1984). The majority of the pinfish we observed were at least 100 mm in length. Herbivores represented 21%–46% of the fish abundance during the Fall 2009 surveys. During the Winter 2010 surveys, 85% of the fish observed at No Name Shoal and the single fish observed at Biscayne Channel and Cutter Bank, respectively, were pinfish/sea bream. Herbivore abundance was higher in the fall (242 fish) than in the winter surveys (68 fish) (ANOVA:  $F_{1, 16} = 26.7$ ,  $p = 0.001$ ; Table S2). Herbivore abundance varied by site (ANOVA:  $F_{3, 16} = 8.4$ ,  $p = 0.007$ ; Table S2), and was highest and No Name Shoal and East Featherbed Bank. The site × event interaction was not significant ( $p = 0.359$ ).



**Table 1**

Results from three-way ANOVA and Sidak's tests of Site, Time, and Species on rank-transformed herbivory assay data (i.e., biomass loss in experimental planting units). Data from partial and uncaged treatments are pooled. Bold p values indicate significance at  $\alpha = 0.05$ . Superscript letters in Sidak's test results indicate significant groupings of factor levels at  $\alpha = 0.05$ . Site codes: BC = Biscayne Channel, NN = No Name Shoal, EF = East Featherbed Bank, CB = Cutter Bank Species codes: HW = *Halodule wrightii*, SF = *Syringodium filiforme*, TT = *Thalassia testudinum*.

Source	df	MS	F	P
Donor site C:N ratios				
Site	3	4,203,922.2	110.7	<b>&lt;0.001</b>
Time	3	1,208,611.3	31.8	<b>&lt;0.001</b>
Species	2	6,287,059.1	165.5	<b>&lt;0.001</b>
Site * Time	9	1,360,768.8	35.8	<b>&lt;0.001</b>
Site * Species	6	18,260.0	0.5	0.823
Time * Species	6	432,034.1	11.4	<b>&lt;0.001</b>
Site * Time * Species	18	183,689.9	4.8	<b>&lt;0.001</b>
Error	953	37,989.9		
Sidak's tests				
Site: BC <sup>a</sup> , NN <sup>ac</sup> , EF <sup>b</sup> , CB <sup>c</sup>				
Time: Spr09 <sup>a</sup> , Sum09 <sup>ab</sup> , Fall09 <sup>b</sup> , Win10 <sup>c</sup>				
Species: HW <sup>a</sup> , SF <sup>b</sup> , TT <sup>c</sup>				

**Table 2**

Results from two-way ANOVA and Sidak's tests of Time and Species on carbon:nitrogen (C:N, rank-transformed) and carbon:phosphorus (C:P, untransformed) molar ratios in seagrasses from Pelican Shoal, the donor site for herbivory assays. Bold p values indicate significance at  $\alpha = 0.05$ . Superscript letters in Sidak's test results indicate significant groupings of factor levels at  $\alpha = 0.05$ . Species codes: HW = *Halodule wrightii*, SF = *Syringodium filiforme*, TT = *Thalassia testudinum*.

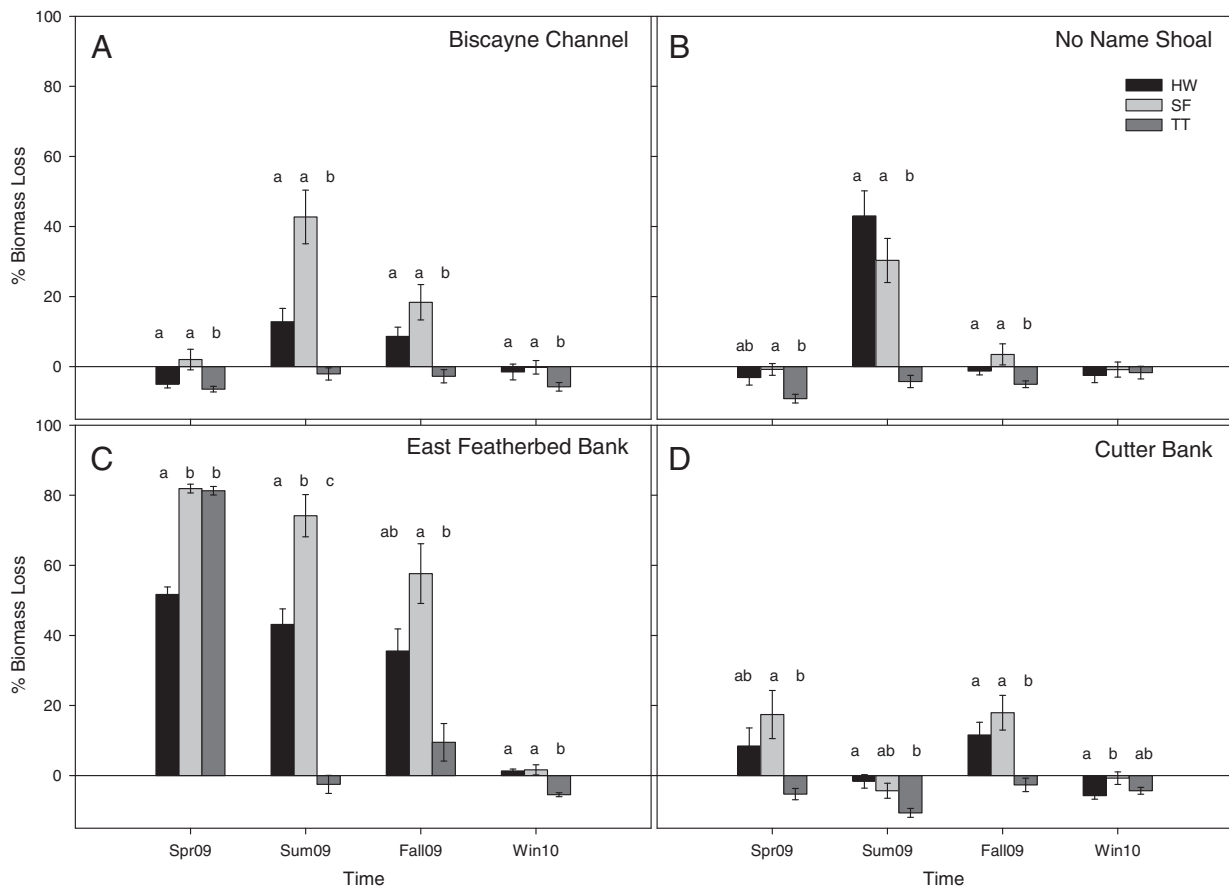
Source	df	MS	F	P
Donor site C:N ratios				
Time	3	383.3	43.1	<b>&lt;0.001</b>
Species	2	913.6	102.8	<b>&lt;0.001</b>
Time * Species	6	115.8	13.0	<b>&lt;0.001</b>
Error	24	8.9		
Sidak's tests				
Time: Spr09 <sup>a</sup> , Sum09 <sup>ab</sup> , Fall09 <sup>b</sup> , Win10 <sup>c</sup>				
Species: HW <sup>a</sup> , SF <sup>b</sup> , TT <sup>c</sup>				
Donor site C:P ratios				
Time	3	171,995.0	36.6	<b>&lt;0.001</b>
Species	2	15,775.5	3.4	0.052
Time * Species	6	60,136.6	12.8	<b>&lt;0.001</b>
Error	24	4704.2		
Sidak's tests				
Time: Spr09 <sup>a</sup> , Sum09 <sup>a</sup> , Fall09 <sup>b</sup> , Win10 <sup>a</sup>				

3.3. Herbivory assays

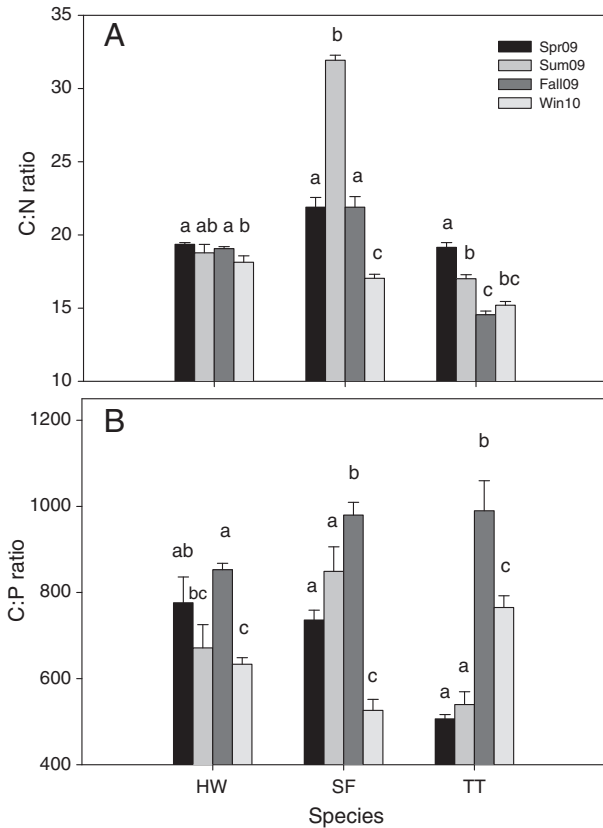
Seagrass biomass removal varied with caging treatment in our study (ANOVA:  $F_{2, 1452} = 40.8, p < 0.001$ ), but no caging artifact was observed. Among the exclusion treatments, mean biomass loss did not differ between the partial cage and open cage treatments ( $9.8 \pm 1.2\%$  and  $14.8 \pm 1.4\%$ , respectively; Sidak's test:  $p = 0.729$ ). Mean biomass loss was lower in the fully caged treatment ( $3.1 \pm 0.3\%$ ) than in the partial

cage and uncaged treatments (Sidak's test:  $p < 0.001$ ). Because no caging artifact was observed, herbivory assay data from partial and open cage treatments were pooled and full cage data excluded for subsequent analyses.

Patterns of herbivory pressure varied across site, time, and species (ANOVA:  $p < 0.001$ ; Table 1, Fig. 2). Note that negative biomass loss



**Fig. 2.** Mean ( $\pm$  se) percent seagrass biomass loss through time by species within each assay site. Seagrass biomass data from the uncaged and partial herbivore exclusion treatments are pooled. Lowercase letters indicate statistical significance among species within each site:time pair at  $\alpha = 0.05$ . Species codes: TT = *Thalassia testudinum*, SF = *Syringodium filiforme*, HW = *Halodule wrightii*.



**Fig. 3.** Mean ( $\pm$ se) carbon:nitrogen (C:N) and carbon:phosphorus (C:P) molar ratios in seagrass leaves from the donor site, Pelican Shoal, by species and time. Lowercase letters indicate statistical significance among times within each species at  $\alpha = 0.05$ . Species codes: HW = *Halodule wrightii*, SF = *Syringodium filiforme*, TT = *Thalassia testudinum*.

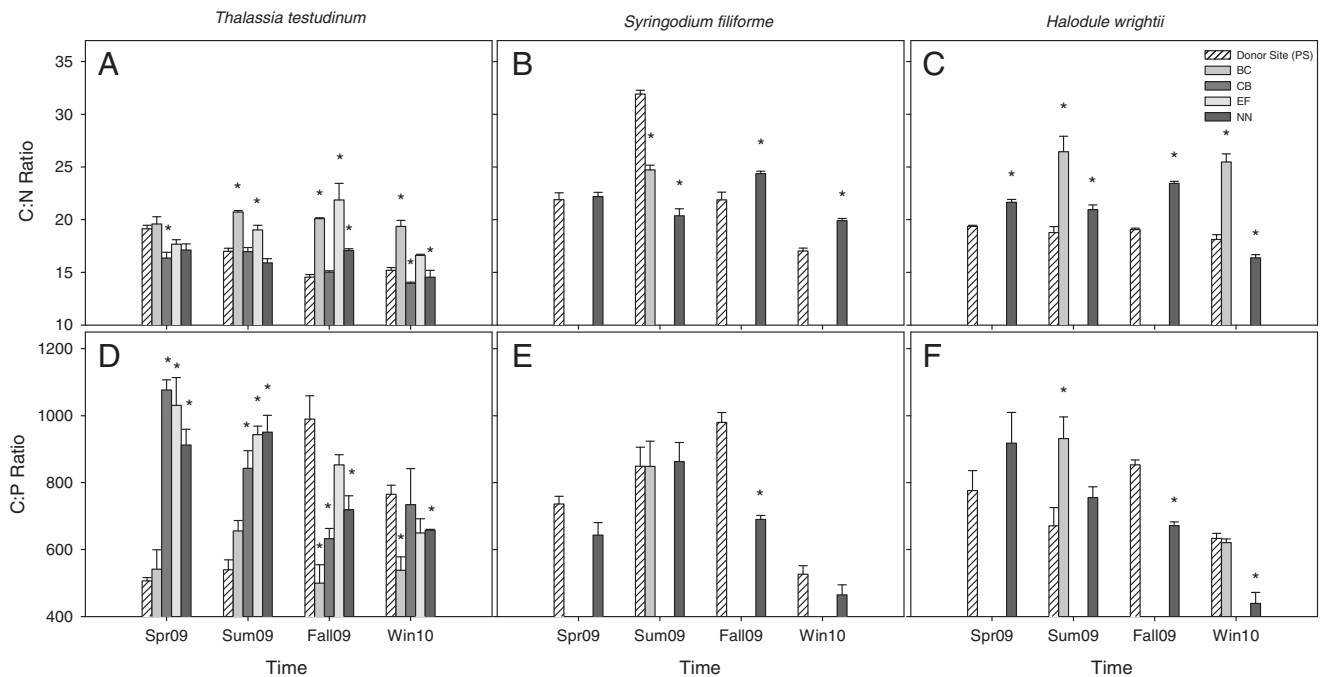
values, or biomass gain, were attributed to seagrass growth. At East Featherbed Bank, an average of  $25.5 \pm 1.9\%$  of planting unit biomass was lost. At Biscayne Channel and No Name Shoal mean biomass loss

was  $2.4 \pm 0.9\%$  and  $1.6 \pm 0.9\%$ , respectively. At Cutter Bank, mean biomass increased by  $0.1 \pm 0.8\%$ . More seagrass biomass was lost during the Spring 2009 ( $12.7 \pm 1.7\%$ ) and Summer 2009 ( $11.6 \pm 1.6\%$ ), than in Fall 2009 ( $8.2 \pm 1.3\%$ ) and Winter 2010 ( $-2.2 \pm 0.4\%$ ). Mean biomass loss was greatest in *S. filiforme* ( $22.3 \pm 1.9\%$ ), and was  $12.7 \pm 1.4\%$  and  $2.3 \pm 1.3\%$  for *H. wrightii* and *T. testudinum*, respectively.

Herbivory pressure varied with seagrass species at different times of the year at each site, as indicated by a significant site  $\times$  time  $\times$  species interaction in the three-way ANOVA ( $p < 0.001$ ; Table 1; Fig. 2). At East Featherbed Bank, biomass loss was high in both *H. wrightii* and *S. filiforme*, ranging from  $35.6 \pm 6.3\%$  (*H. wrightii*, Summer 2009) to  $81.9 \pm 1.3\%$  (*S. filiforme*, Spring 2009). Biomass loss also was high at this site for *T. testudinum* during Spring 2009 ( $81.3 \pm 1.2\%$ ), but remained low during the Summer 2009, Fall 2009, and Winter 2010 assays ( $-2.5 \pm 2.6\%$ ,  $9.5 \pm 5.3\%$ , and  $-5.5 \pm 0.6\%$  respectively). In the Spring and Fall 2009 assays at Cutter Bank, loss ranged from  $8.5 \pm 5.2\%$  to  $11.6 \pm 3.6\%$  for *H. wrightii* and from  $17.4 \pm 6.9\%$  to  $17.9 \pm 5.0\%$  for *S. filiforme*. Biomass increase was documented for all four *T. testudinum* assays, and for *H. wrightii* and *S. filiforme* in the Summer 2009 and Winter 2010 assays at Cutter Bank. At Biscayne Channel only four of the twelve assays resulted in biomass loss, specifically in the Summer and Fall 2009 assays with *H. wrightii* ( $12.8 \pm 3.8\%$  and  $8.6 \pm 2.6\%$ , respectively) and *S. filiforme* ( $42.7 \pm 7.7$  and  $18.4 \pm 5.2$ , respectively). The other eight assays, including all *T. testudinum* assays, resulted in biomass increase. At No Name Shoal, the only two assays resulting in biomass loss were for *H. wrightii* ( $43.0 \pm 7.1\%$ ) and *S. filiforme* ( $30.3 \pm 6.3\%$ ) in Summer 2009; all other assays at this site showed biomass increase.

**3.4. Seagrass elemental content**

C:N and C:P ratios from Pelican Shoal donor seagrasses varied with time, and C:N ratios also varied with seagrass species (ANOVA:  $p < 0.001$ ; Table 2; Fig. 3). C:N ratios differed in the Spring 2009, Summer 2009, Fall 2009, and Winter 2010, respectively (Sidak's test:  $p < 0.001$ , Table 2), and were lowest in Winter 2010 ( $16.8 \pm 0.46$ )



**Fig. 4.** Mean ( $\pm$ se) carbon:nitrogen (C:N, top row) and carbon:phosphorus (C:P, bottom row) molar ratios in seagrass leaves through time by site within species. Absence of a bar in a species/time group indicates that a species was not present for collection. Asterisks indicate differences from donor site values at  $\alpha = 0.05$ . Site codes: PS = Pelican Shoal, BC = Biscayne Channel, NN = No Name Shoal, EF = East Featherbed Bank, CB = Cutter Bank.

and highest in Summer 2009 ( $22.5 \pm 2.4$ ). *T. testudinum* had the lowest average C:N ratio ( $16.5 \pm 0.6$ ), followed by *H. wrightii* ( $18.8 \pm 0.2$ ) and *S. filiforme* ( $23.2 \pm 1.7$ ), respectively (Sidak's test:  $p < 0.001$ , Table 2). C:P ratios in Fall 2009 ( $940.9 \pm 31.3$ ) were higher (Sidak's test:  $p < 0.001$ , Table 2) than in Spring 2009 ( $672.8 \pm 46.0$ ), Summer 2009 ( $686.5 \pm 51.0$ ), or Winter 2010 ( $641.6 \pm 36.4$ ), respectively. The lowest C:N ratios in each species occurred in Winter 2010: *T. testudinum* ( $14.0 \pm 0.1$ ), *H. wrightii* ( $16.4 \pm 0.3$ ) and *S. filiforme* ( $17.0 \pm 0.3$ , Fig. 3).

The difference between the C:N and C:P ratios from Pelican Shoal donor seagrasses and the ambient seagrasses at each assay varied as a function of species, time, and site (Table S3, Fig. 4). In *T. testudinum*, donor C:N ratios were lower than ambient ratios in 44% of assays, not different in 44% of assays, and higher in 12% of assays than ambient ratios (Table S3, Fig. 4). *S. filiforme* was present in the surrounding seagrass community at five of the sixteen assays; donor C:N ratios were lower than ambient ratios in 40% of those assays, not different in 20% of assays, and higher in 40% of assays. *H. wrightii* was present in the surrounding seagrass community at six of the sixteen assays; donor C:N ratios were lower than ambient ratios in 83% of and higher in 17% of assays.

### 3.5. Predictors of seagrass biomass loss

Several variables used to predict seagrass biomass loss were collinear. Herbivore abundance was correlated with C:P ratio and

**Table 3**

Pearson correlations between predictor variables seagrass carbon:nitrogen (C:N) ratios, seagrass carbon:phosphorus (C:P) ratios, temperature, and salinity (all  $n = 48$ ), and herbivorous fish abundance (square root transformed,  $n = 24$ ). Single (\*) or double (\*\*) asterisks indicate significant correlations at the 0.05 and 0.01 levels, respectively.

	Herbivore abundance	C:N ratio	C:P ratio	Temperature
C:N ratio	0.237			
C:P ratio	0.597**	0.221		
Temperature	0.555**	0.457**	-0.049	
Salinity	-0.022	0.195	0.094	0.329*

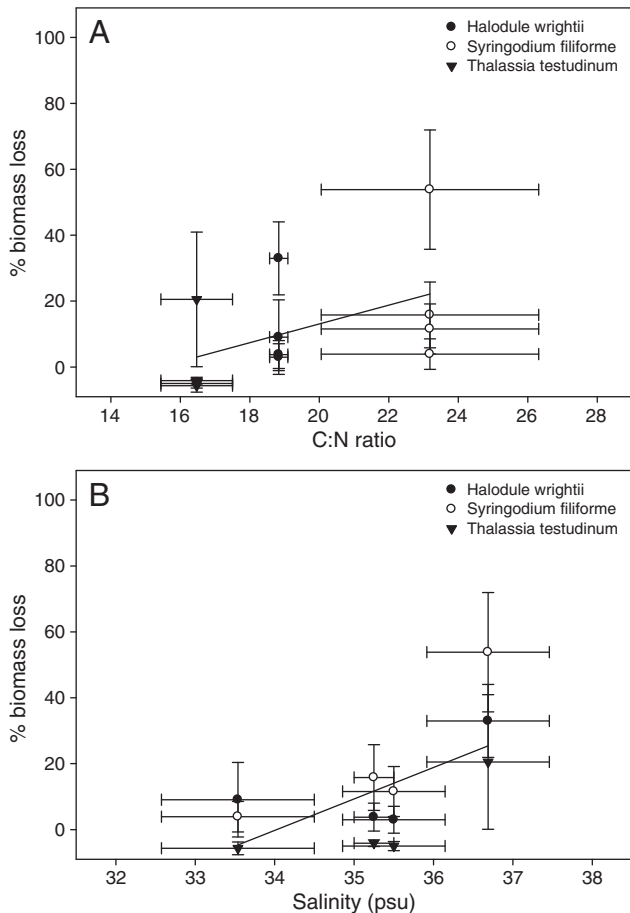
temperature ( $p < 0.001$ , Table 3). In addition, C:N ratio and temperature were correlated ( $p < 0.001$ , Table 3), as were temperature and salinity ( $p < 0.05$ , Table 3). In the first stepwise regression analysis, containing C:N ratio, C:P ratio, temperature, and salinity as variables, C:N and salinity were independent predictors variables of seagrass biomass loss:  $y = -98.95 + 0.36(\text{C:N ratio}) + 0.34(\text{salinity})$  ( $F_{2, 45} = 9.6$ ,  $p < 0.001$ ,  $r^2 = 0.30$ , Fig. 5). In the second stepwise regression analysis, with herbivorous fish abundance included as a fifth variable, C:N ratio was the sole predictor of seagrass biomass loss:  $y = -34.09 + 0.70(\text{C:N ratio})$  ( $F_{1, 22} = 20.9$ ,  $p < 0.001$ ,  $r^2 = 0.49$ ). Herbivorous fish formed a substantial component of the fish community during most fish surveys, and biomass loss was observed only when herbivorous fish were present, despite the absence of a linear relationship between biomass loss and herbivore abundance (Fig. 6).

## 4. Discussion

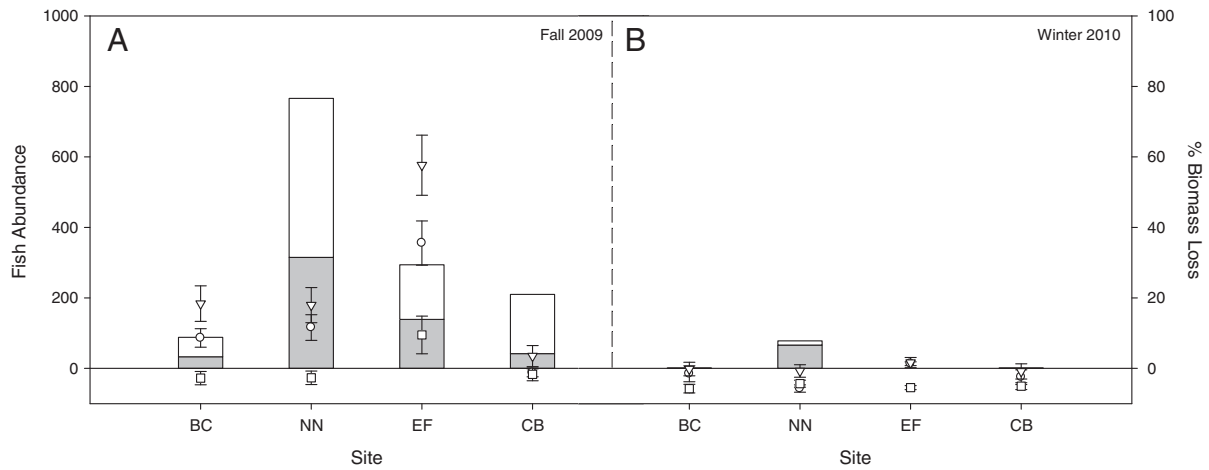
We established that fish herbivores are capable of removing substantial quantities of seagrass biomass in our study system, and this pressure varied across sites, seagrass species, and times of the year, though with lack of consistent patterns. Herbivore exclusion cages were effective in protecting our planting units from herbivory. Caging restoration sites has been suggested as a means to enhance planting unit success in restoration projects (Fonseca et al., 1998). However, we suggest that caging on the scale of a seagrass restoration site is not a practical solution given tidal currents, maintenance requirements, and a desire to minimize the use of artificial structures in the marine environment.

We were unable to link seagrass biomass removal to abundance patterns of herbivorous fish. More robust and repeated fish surveys may provide the data necessary to establish this link. However, fish are transient across the landscape at the small scale of our assay sites, and it is possible for roving, grazing schools to pass through a restoration area, resulting in episodic grazing events. Our herbivory assays were deployed for only 72 h. If the time of deployment determines the likelihood that an episodic grazing event would occur, then our results may underestimate herbivory pressure.

Herbivores preferentially graze on nutrient-enriched seagrasses (Heck and Valentine, 2006; McGlathery, 1995; Williams, 1988) or on faster growing, more palatable plants (Cebrián and Duarte, 1998). Goecker et al. (2005) observed selective feeding based on seagrass nitrogen content by the bucktooth parrotfish (*Sparisoma radians*). In contrast, other studies have shown that leaf nutrient concentration may not be a reliable indicator of nutritional quality (Cebrián and Duarte, 1998; Kirsch et al., 2002; White et al., 2011). We observed a positive relationship between seagrass biomass removal and C:N ratio. Overall, *S. filiforme* and *H. wrightii* had higher C:N ratios, but were grazed more heavily than *T. testudinum* (Table 3). While this study was not explicitly designed to test herbivore feeding preferences, our results suggest that factors other than nutrient content play a role in seagrass herbivory. Fish herbivores may be using other cues to select plant resources, or responding to other selective pressures (e.g., predation risk). Our study intentionally placed PUs in clearings in order to simulate the conditions of an actual restoration project.



**Fig. 5.** Mean ( $\pm$  se) percent seagrass biomass loss vs. mean ( $\pm$  se) carbon:nitrogen (C:N) molar ratios in donor site seagrass leaves and mean ( $\pm$  se) salinity, displayed by seagrass species. Error bars are displayed to show variance in the observations, but regression analyses assumed that mean values for each point were the independent units of observation. Regressions were significant ( $p < 0.001$ ). Seagrass biomass data from the uncaged and partial herbivore exclusion treatments are pooled.



**Fig. 6.** Fish abundance (left axes) and biomass loss (mean  $\pm$  se, right axes) at the assay sites in Fall 2009 (left panel) and Winter 2010 (right panel). The stacked bars divide abundance into two feeding guilds: herbivorous fish (grey bars) vs. other fish (white bars). Percent biomass loss data from the uncaged and partial cage treatments are pooled, and presented by seagrass species (*Thalassia testudinum*, squares; *Syringodium filiforme*, triangles; *Halodule wrightii*, circles). Site codes: BC = Biscayne Channel, NN = No Name Shoal, EF = East Featherbed Bank, CB = Cutter Bank.

Open space could be viewed as a higher risk microhabitat to small herbivorous fish (Orth et al., 1984), but the attraction of new accessible and palatable food source, potentially of higher nutrient value, may positively influence foraging behavior in these areas.

Another consideration is that C:N and C:P ratios are generally lower during winter months and peak in the summer and fall (Fourqurean et al., 2001). The same seasonal patterns can be found for fish densities (which may be a good reason to limit studies of relationships between of nutrient content and herbivory to warmer months). Localized herbivory pressure may be driven more by fish grazer abundance than by plant nutrient content.

Despite the near absence of herbivory on *T. testudinum* that we observed, herbivory on this species is well documented (e.g. Goecker et al., 2005; Kirsch et al., 2002), and we did observe one of the most important *T. testudinum* herbivores, juvenile parrotfish, in our fish surveys. Overall, herbivory pressure on *T. testudinum* was absent or very low in our study with the exception of the Spring 2009 assay at East Featherbed Bank, when  $81.3 \pm 1.2\%$  of seagrass biomass was removed from PU. The highest overall levels of herbivory were at East Featherbed Bank, which is close to major tidal cuts that provide access for fish using coral reef habitat to the east. The oceanic input at this site is also evident from the coarse sediment and abundance of small stony and soft corals. The lack of a strong herbivory signal for *T. testudinum* in the other three study sites may be due to the location of the sites within southern Biscayne Bay – several kilometers west from the coral reefs which are the likely source of herbivores, and parrotfishes in particular. Herbivory pressure seemed consistently low at Cutter Bank, which was close to a mangrove shoreline.

Winter 2010 fish surveys revealed dramatic differences in fish abundance from the Fall 2009 surveys, and herbivorous fish abundance was positively correlated with water temperature. It is important to note that the Winter 2010 assay followed a rare extreme cold event in south Florida during January 2010. The average water temperature in January and February at this location ranges between 20° and 21 °C (Biscayne National Park, unpublished data). During the cold snap, water temperatures remained below 15 °C for the 12-day period between 4 and 16 January 2010, and reached a low of 9.2 °C on 11 January 2010. Fish abundance may have been abnormally low due to this cold event which was accompanied by fish kills in the area (personal observation, Adams et al., 2012). However, even during more typical winter conditions, fish abundance is expected to be lower, since abundance of some species is positively correlated with water temperature (Serafy et al., 2003; Tremain and Adams, 1995). Because our study was not replicated seasonally, we cannot predict if the

herbivory patterns we saw are representative through longer time frames, and our results should be interpreted accordingly. However, our results strongly suggest that transplanting activities in southern Biscayne Bay may be at lower risk from herbivory if conducted during winter months.

In some of our herbivory assays, a large proportion of the seagrass biomass in the planting units was removed (up to  $81.9 \pm 1.2\%$ ). Entire leaves were removed more often than bite marks in the leaves. But, herbivory impact on the scale of a seagrass landscape may be less extreme than on the scale of a restoration planting unit. Because of the rhizophytic morphology and clonal life history strategy of seagrasses, seagrass clones are able to tolerate herbivory, at least to a degree, and acute removal of leaves or shoots is not likely to cause a well-established clone to perish. Of the three species used in our study, *S. filiforme* and *H. wrightii* have rapid rhizome elongation rates (Marba and Duarte, 1998), and resources can be translocated among ramets along rhizomes (Marba et al., 2006). The availability of stored carbon and nutrient reserves can influence a plant's ability to replace leaves lost to herbivores (Christianen et al., 2012; Vergés and Pérez, 2008); and it may be the exhaustion of these reserves that lead to plant mortality following chronic, repeated grazing leaf loss (Fourqurean et al., 2010).

In restoration projects, seagrasses are usually transplanted as plugs or sods that are obtained with a coring device or shovel, or as bundles of bare rhizomes that contain a few shoots per rhizome (Fonseca et al., 1998). Some degree of transplant shock is expected, so newly transplanted seagrasses may be in a compromised condition. Subsequent removal of leaves or shoots in a planting unit through grazing may have far more serious implications to a clone that may already be stressed and may have few photosynthetic shoots and low nutrient and carbohydrate reserves to grow and colonize the restoration area.

## 5. Conclusions

Leaf loss to herbivores may be a spatially variable but critically important determinant of seagrass restoration success. Given the highly variable nature of herbivory across sites, time, and species, we recommend that future restoration projects be designed with a *priori* knowledge of site-specific herbivory pressure. This knowledge can be used to evaluate the potential risk of herbivory to seagrass transplants and inform decisions on donor species selection, planting unit type and density, project success criteria, and the potential need for future corrective actions. In our work, herbivory pressure on Featherbed Banks was high enough to suggest that transplanting seagrasses at that site is likely to



fail. And, given that *T. testudinum* is grazed at a lower rate than *H. wrightii* or *S. filiforme*, it should be a candidate for transplanting in areas with high herbivory pressure. Further, transplant efforts could be limited to winter months when herbivore pressure is low, as long as other conditions in the winter are amenable to planting survival. In areas subject to high and constant herbivory pressure, such as coral reef environments with abundant parrotfish which are known to feed on seagrasses (Armitage and Fourqurean, 2006; Kirsch et al., 2002; Maciá and Robinson, 2005), the wisest course of action may be to not attempt seagrass transplantation as part of a seagrass restoration project.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.jembe.2013.03.014>.

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