January 2008

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HABITAT CONDITION AND ASSOCIATED MACROFAUNA REFLECT DIFFERENCES BETWEEN PROTECTED AND EXPOSED SEAGRASS LANDSCAPES

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ABSTRACT: Seagrass landscape configurations associated with different physical settings can affect habitat-structure and plant-animal relationships. We compared shoal grass *(Halodule wrightii)* habitat and macrofaunal variables between two fragmented seagrass landscapes at barrier-island locations subject to different disturbance regimes. Five seagrass habitat variables including above ground biomass (AGB), shoot number, per shoot biomass, epiphyte biomass and below ground biomass (BGB), differed significantly between the island landscapes. Per shoot biomass and epiphyte biomass also varied significantly over the seagrass growing season; and epiphyte biomass showed a strong landscape-time interaction. Abundances of microgastropods normalized to AGB differed significantly between landscapes. An inverse relationship between the abundance of microgastropods and epiphyte loading suggests a possible functional link. However, additional temporal mismatch between epiphyte loading and microgastropod abundance indicates that controls on epiphyte loading were complex. Seagrass habitat was more fragmented within the Cat Island (CI) landscape. Wind direction and strength imply that the CI landscape experienced more physical disturbance than the Horn Island (HI) landscape. This study highlights some potential links involving landscape configuration, habitat structure, and macrofaunal associations which can be further addressed using hypothesis-driven research.

INTRODUCTION

Seagrass ecosystems exist as hierarchically organized habitats in various states of fragmentation, mediated by landscape-scale forces (Pittman et al. 2004). Hierarchical spatial patterns arise from the interaction of broad-scale external effects on habitat configuration and local internal effects on habitat structure (Boström et al. 2006). For example, physical disturbance induces variability in the spatial configuration of patches of varying sizes and interpatch distances within the seagrass landscape (Fonseca and Bell 1998). Furthermore, processes occurring at broad spatial scales may constrain those occurring at local spatial scales (Allen and Starr 1988). Consequently, landscape-scale features, such as areal cover, patch size, and interpatch distance, may covary with habitat-structure (Boström et al. 2006), as expressed by shoot density, above ground biomass (AGB), below ground biomass (BGB), epiphyte loading (Moore and Fairweather 2006) or associated macrofauna (Hovel et al. 2002).

Although macrofaunal associations change with the spatial arrangement of seagrass habitat (Turner et al. 1999, Frost et. al 1999), responses by individual taxa can vary relative to landscape configuration (e.g., patch size and distance) (Bell et al. 2001). The apparent inconsistency reflects the fact that macrofaunal taxa relate individualistically to different environmental scales (Boström et al. 2006), thus accounting for different response thresholds to habitat fragmentation.

Seagrass ecosystems also form complex trophic networks defined by internal feedbacks on habitat function, including those exerted by macrofauna (Connolly and Hindell 2006). For example, some bivalves enhance seagrass condition by locally increasing both light accessibility and sediment nutrients (Peterson and Heck 2001). Such links also may be decoupled by broad-scale physical disturbance or habitat fragmentation. Again, critical thresholds in functional links with decreasing habitat connectivity depend on the species' biology and the physical setting (With and Crist 1995, Fonseca and Bell 1998, Monkonnen and Reunanen 1999).

The first step towards understanding habitat function relative to landscape-scale factors is to identify potential habitat-scaling relationships. So we compared shoal grass *(Halodule wrightii)* habitat and macrofaunal metrics during the seagrass growth phase between two barrier- island landscapes exposed to different levels of disturbance. Habitat metrics included: above ground biomass (AGB); epiphyte biomass; shoot number; per shoot biomass; and below ground biomass (BGB); macrofaunal metrics included abundances of microgastropods, peracarid grazers, capitellid polychaetes, *Neanthes* polychaetes, and macrofaunal diversity. Our working hypothesis was that seagrass landscape, habitat and faunal metrics should differ concertedly between more disturbed Cat Island (CI) and less disturbed Horn Island (HI) landscapes.

STUDY AREA

Two seagrass landscapes separated by 45 km extended along the north-central HI shoreline and around the western tip of CI (Figure 1). Horn Island is part of the Gulf Islands National Seashore under the jurisdiction of the US National Park Service. Waters surrounding CI were managed only by state and federal dredge and fill regulations prior to and during the time frame of this study (CI was acquired by US NPS in 2003). The HI landscape: (1) is apparently less exposed to physical disturbance than CI; and (2) has been protected from trawling within 1.6 km of shore since May 1995 by the U.S. National Park Service.

MATERIALS AND METHODS

Disturbance and habitat fragmentation

Physical disturbance within the CI and HI landscapes over four months prior to and during the study period from 15 May until 9 August 1998 was estimated from hourly measurements of wind direction, wind speed, and wave height taken at NOAA Data Buoy 42007 located off the north point of the Chandeleur Islands (30°05'24" N; 88°46'12" W), 19 km south of HI and 40 km southeast of CI. Monthly mean (± 1 se) wind directions were calculated using circular statistics (Oriana Ver 1.0; Kovach 1994). Salinity was compared between the eastern and western portions of Mississippi Sound using data obtained from the MS Department of Marine Resources for roughly 40 stations during the May – June (80 vs. 90 observations) and July – August (171 vs. 29 observations) periods.

Seagrass fragmentation was quantified from 4m resolution digital aerial photographs of seagrass cover taken in March 1998. ArcGIS 8.2 was used to digitize seagrass patches occurring within 13 hectares both off the west tip of CI and along the northwest central side of HI. The digitized areas coincided with the landscape areas used for this study (Figure 1). Four, one hectare quadrats were randomly placed within each of the two island landscapes with the restrictions that they could not overlap with each other or fall outside of the seagrass-depth contour within designated areas.

Field sampling

Three sites separated by ~ 0.3 km were located within each of the two island landscapes (Figure 1). Three monthly sampling events during the seagrass growth phase ensued on 3 June, 22 June, and 5 August, 1998. At each site, three cores of seagrass and associated macrofauna (i.e., subsamples) were randomly taken within a ~ 0.01 km² area using a 16.0 cm diameter plexiglass corer to extract 0.02 m²

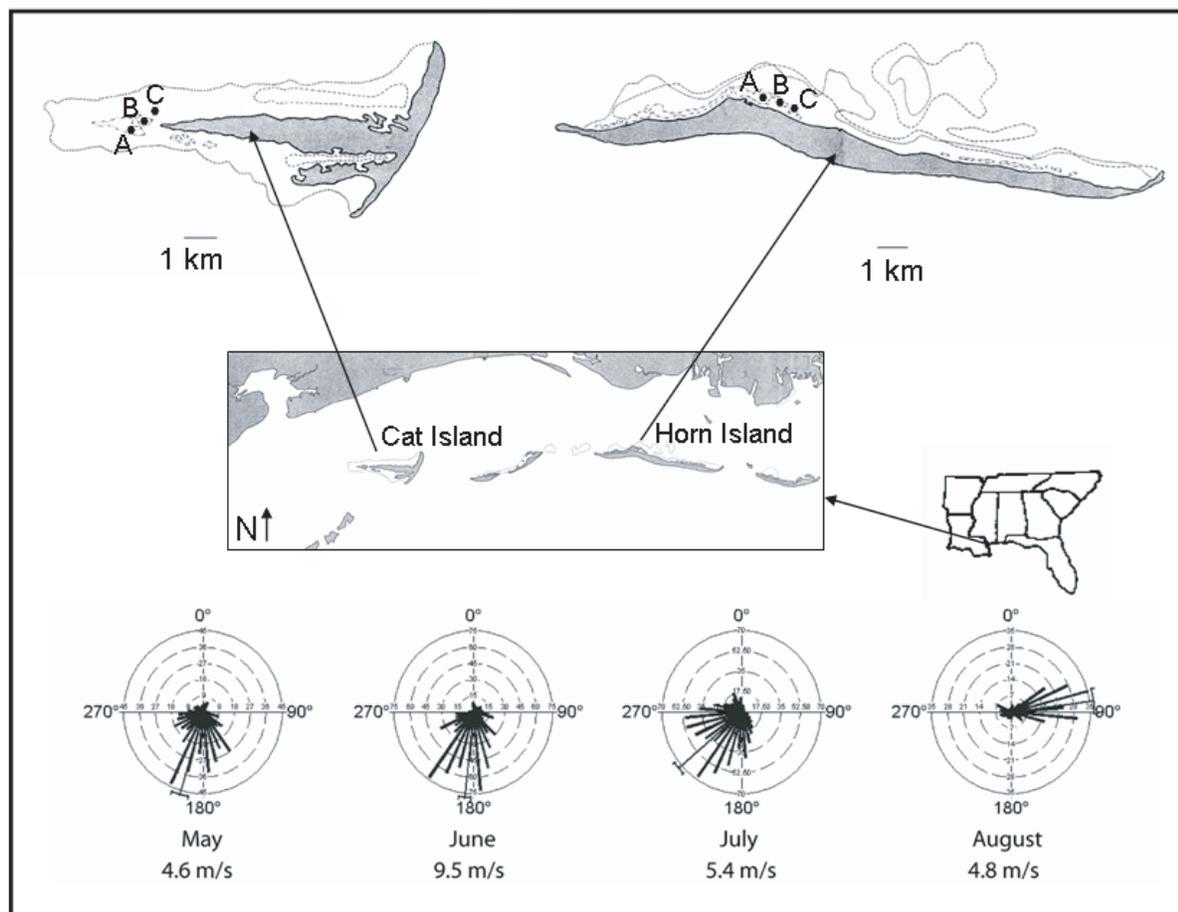**Figure 1.**
Map of the study region showing the two barrier-island landscapes and the six sites. Circular graphs depict monthly wind direction vectors, along with mean (± 95% CI) wind velocities measured at NOAA Data Buoy 24007 during the study.

TABLE 1. *Variation in wind and wave strength over the study period between 15 May and 9 August 1998 measured at NOAA Data Buoy 42007 (30°05′24″ N; 88°46′12″ W). Values represent monthly means (± 1 se) obtained by aggregating hourly data for each day and daily values for each month. Monthly means (± 1 se) of wind directions were calculated using circular statistics, Oriana Ver 1.0 (Kovach 1994). Significant wave height (meters) was calculated as the mean of the highest one third of all of the wave heights during the 20 minute sampling period.*

Month	Wind speed (m sec⁻¹)	Wind direction (°)	Significant wave height (m)	Mean wave period (sec)
May 15 - 31	4.56 ± 0.281	196.2 ± 3.11	0.35 ± 0.057	3.00 ± 0.036
June 1 - 30	5.24 ± 0.325	186.0 ± 2.21	0.48 ± 0.033	3.84 ± 0.103
July 1 - 31	4.41 ± 0.249	229.3 ± 2.36	0.27 ± 0.025	2.98 ± 0.237
August 1 - 9	4.79 ± 0.503	82.6 ± 4.31	0.57 ± 0.079	3.71 ± 0.193

sediment plugs to a depth of 15 cm. A total of 54 cores were taken (i.e., 2 landscape areas x 3 sites x 3 cores x 3 periods). A 0.5 mm mesh polypropylene sieve was used to remove fines, while still retaining all plant material and associated macrofauna. Water column salinity (psu), turbidity (NTU), water temperature (°C), water depth (m), substrate type, and photosynthetically active radiation (PAR) (μmol photons m⁻² sec⁻¹) were recorded for each sampling event.

Laboratory processing

Plant material was carefully separated by gentle rinsing in tapwater and frozen for later processing. Associated coarse sediment and macrofauna were rewashed in a 0.5 mm mesh sieve and preserved in 10% formalin. Ten randomly selected shoots were used to quantify the epiphyte load by scraping shoots and leaves with a dull razor blade. Shoot and epiphyte fractions were dried at 105 °C for 24 h or until a constant weight was obtained, and then weighed to the nearest 0.001 g using an O'Haus microbalance. In addition, remaining AGB and separated BGB fractions were dried and weighed (mg) as described above. Preserved macrofaunal organisms were sorted, identified to the lowest practical taxonomic level, and enumerated.

Data analysis

Metrics for comparing seagrass fragmentation included number of patches, total patch area, patch area percent cover, mean patch size, and standard deviation in patch size. Patch metrics were compared between HI and CI using Students independent-sample t-tests (p < 0.05). Two-tailed t-tests were based on assumptions of equal or unequal variance, depending on the outcome of Levene's tests of homogeneity of variance in SPSS 13.0 (SPSS 2004).

Habitat and macrofaunal variables examined included the number of short shoots (shoot number), above-ground biomass without epiphytes (AGB), epiphyte biomass (= arcsine square-root (epiphyte biomass/(epiphyte biomass + AGB))), below ground biomass (BGB), per shoot biomass, microgastropod abundance (normalized to AGB), peracarid grazer abundance (normalized to AGB), capitellid

abundance, *Neanthes* abundance, and macrofaunal diversity (Shanon-Wiener H′; base 2). Macrofaunal abundances were log transformed (i..e, $\log_{10}$ (N+1)) prior to analysis.

To accommodate spatial and repeated time effects, the Linear Mixed Models (LMM) procedure was employed in SPSS 13 (SPSS 2004). LMM is very flexible in that it can model covariance and heterogeneous variability in the context of concurrent fixed and random effects (Verbeke and Molenberghs 2000). The Unstructured Covariance Model was fit as it provides the least restricted covariance structure and is equivalent to the multivariate form of Repeated Measures ANOVA. Site was treated as a subject variable and time as a repeated effect. Landscape and time were considered fixed main effects, and the landscape-time interaction term was also included. Tests of fixed effects utilized Type III sums of squares. Cases for LMM comprised means of the three cores per site-time event.

For selected seagrass and macrofaunal variables, means (± 1 se) were plotted for each of the three sites from each island landscape across the three sampling dates. An inverse hyperbolic curve of the form $Y = a\,X^{-b}$ between the abundance of microgastropods (i.e., *Bittiolum varium* and *Astyris lunata*) and epiphyte mass (as the proportion of total AGB) was fit for the 54 cores.

RESULTS

Disturbance and habitat fragmentation

Wind direction and strength measured at NOAA Data Buoy 42007 implied that the CI landscape was more exposed to physical disturbance than the HI landscape just prior to and during the study period. Winds typically originated from the south-southwest for the three month period between 15 May and 9 August (Figure 1; Table 1). However, CI sites were relatively protected near the end of the study period in early August, when winds primarily originated from the east. Wave action in concert with wind strength was relatively high in June, when the mean wave height was 0.48 ± 0.033 m (mean ± 1 se) while the mean wind velocity was 5.24 ± 0.325 m sec⁻¹. Although HI sites are lo-

cated farther than CI sites from several major freshwater discharge sources, including the Bonnet Carré Spillway, and the Jourdan and Pearl Rivers (90 km vs. 46 km, 67 km vs. 25 km, and 80 km vs. 35 km, respectively), salinity was similar between the two island landscapes during the study period. Salinity averaged 14.8 ± 4.5 ($\bar{x}$ ± 1 sd) vs. 17.0 ± 4.3 between western and eastern portions of Mississippi Sound during May – June 1998; and 22.7 ± 4.5 psu vs. 22.5 ± 4.4 psu during July – August 1998. Other conditions including water temperature, depth, turbidity, sediment composition (i.e., sand) and light were also similar between areas.

Seagrass habitat was notably more fragmented within the CI landscape than in the HI landscape (Table 2). The number of patches, total patch area, and mean patch size, were significantly different between island landscapes (t-tests; all $p \leq 0.002$). The mean number of 20.75 patches per hectare at CI was more than three-fold higher than at HI; whereas, the mean total patch area of 4520.89 m^2 per hectare (i.e., 45.21% seagrass cover) at HI was nearly four-fold higher than at CI (i.e., 12.35% seagrass cover). The grand mean patch size of 645.84 m^2 at HI was ten-fold larger than at CI.

Seagrass habitat variables

All five seagrass habitat variables including AGB, shoot number, per shoot biomass, epiphyte biomass, and BGB differed significantly between island landscapes (Table 3). Per shoot biomass and epiphyte biomass, also varied significantly in time. The landscape-time interaction was significant for epiphyte biomass, and marginally significant for BGB.

AGB was usually higher within the HI landscape, espe-cially in August (Figure 2A). Over the study period, mean AGB ranged from 0.59 to 0.96 g dw per 0.02 m^2 at HI; whereas it ranged from 0.45 to 0.62 g dw per 0.02 m^2 at CI. Conversely, shoot number was slightly higher at CI (Figure 3A). However, per shoot biomass was clearly higher at HI than at CI, and also increased during the study period (Figure 3B). Between June and August, per shoot biomass increased from 0.0061 to 0.0113 g dw at HI, whereas it increased from 0.0040 to 0.0067 g dw at CI. Epiphyte biomass was markedly higher at the CI landscape (Figure 4A); however, this metric also declined markedly in time at CI, while remaining nearly the same at HI. Monthly epiphyte biomass ranged from 3.7 to 9.4 percent of total AGB at HI; whereas it ranged much higher, from 11.3 to 41.3 percent of total AGB at CI. BGB values were also consistently higher at HI over the three sample periods (Figure 2B); although BGB increased over time at CI (Table 3). Mean BGB ranged from 3.0 to 3.9 g dw per 0.02 m^2 at HI; whereas BGB ranged from 0.9 to 1.6 g dw per 0.02 m^2 at CI.

Macrofaunal variables

Macrofaunal species richness (S) was similar between the two barrier island landscapes: 86 taxa were collected from both of the landscapes, each of which yielded 32 unique taxa. Thus, a total of 118 taxa were enumerated over the study period. Diversity (i.e., macrofaunal H'; base 2) was the only macrofaunal metric for which the landscape-time interaction was even marginally significant. Otherwise, Diversity was similar between landscapes and sample periods; mean diversity ranged from

TABLE 2. *Seagrass landscape metrics reflecting differences in habitat fragmentation from digital aerial images of the Cat Island and Horn Island landscapes taken in March 1998. Values represent means (± 1 sd) of metrics for four randomly selected 1-hectare (ha) quadrats within each designated 13.2-ha bounding plot area.*

CAT ISLAND

Plot	Total Plot Area (m²)	Number of Patches	Total Patch Area (m²)	% Seagrass Cover	$\bar{x}$ Patch Size (m²)	Patch Size sd (m²)
1	10000	17	1316.14	13.16	77.42	103.67
2	10000	23	617.59	6.18	26.85	78.91
3	10000	21	2439.89	24.40	116.19	115.24
4	10000	22	567.42	5.67	25.80	24.66
Aggregate	**40000**	**83**	**4941.04**	**12.35**	**59.53**	**84.59**

HORN ISLAND

Plot	Total Plot Area (m²)	Number of Patches	Total Patch Area (m²)	% Seagrass Cover	$\bar{x}$ Patch Size (m²)	Patch Size sd (m²)
1	10000	5	4558.46	45.58	759.74	1559.66
2	10000	7	5439.96	54.40	777.14	912.15
3	10000	8	3300.78	33.01	412.60	876.66
4	10000	7	4784.37	47.84	683.48	905.43
Aggregate	**40000**	**27**	**18083.55**	**45.21**	**645.84**	**1020.11**

TABLE 3. *Linear Mixed Models (LMM) results for nine seagrass habitat and macrofaunal variables. Landscape and time are considered fixed effects. Time is also considered to be a repeated factor and sites are regarded as subjects. Unstructured (= completely general covariance matrix) LMM model used, as explained in the text; No. model parameters = 12. AGB = Above Ground Biomass; BGB = Below Ground Biomass; GRZ PERACARIDS = Grazing Peracarids. Faunal abundances tested on $\log_{10}(N+1)$ scale. Epiphyte biomass tested as arcsine square-root proportion of total AGB. Bold = significant, Bold underline = marginally significant.*

Dependent Variable	-2RLL	LNDSCP F	p	TIME F	p	LND x TIME F	p
AGB	-14.546	8.666	**0.042**	0.973	0.453	2.027	0.247
SHOOT NUMBER	102.216	12.597	**0.024**	0.345	0.727	0.430	0.677
PER SHOOT BIOMASS	-72.863	118.749	**<0.001**	15.783	**0.013**	2.577	0.191
EPIPHYTE BIOMASS	-39.295	123.619	**<0.001**	47.888	**0.002**	31.608	**0.004**
BGB	25.592	17.508	**0.014**	0.257	0.786	4.464	**<u>0.096</u>**
MICROGASTROPODS	-14.664	155.083	**<0.001**	27.161	**0.005**	0.413	0.687
GRZ PERACARIDS	3.574	0.602	0.481	2.053	0.243	1.140	0.406
CAPITELLIDS	-1.550	6.557	**<u>0.063</u>**	2.971	0.162	3.658	0.125
NEANTHES	-8.639	0.421	0.552	1.961	0.255	1.992	0.251
DIVERSITY	7.336	0.906	0.395	1.640	0.302	5.488	**<u>0.071</u>**

2.32 to 2.82 per 0.06 m² (i.e., for 3 cores combined). The overall macrofaunal density was notably four-fold higher at HI (mean (± 1 se) = 247.1 (± 35.7) per 0.02 m²) than at CI (mean (± 1 se) = 61.0 (± 5.0) per 0.02 m²). Typical seagrass-associated macrofauna included the amphipods, *Ampelisca holmesi* and *Cymadusa compta*; the isopods, *Edotea triloba* and *Erichsonella attenuata*; the gastropods, *Astyris lunata* and *Diastoma varium*, the caridean shrimp, *Hippolyte zostericola*, *Latreutes parvulus*, and *Palaemonetes pugio*; the brachyuran crab, *Callinectes sapidus*; and anomuran crabs, *Pagurus* spp. The macrofauna primarily comprised microgastropods (52.0% HI vs. 10.4% CI), peracarid crustaceans (18.1% HI vs. 9.6% CI), and infaunal polychaetes (13.6% HI vs. 23.4% CI).

Microgastropod abundances differed significantly between landscapes; abundances were higher by an order of magnitude at HI (Figure 4B). They also varied significantly in time. Microgastropods comprised 84% *Bittiolum varium* and 16% *Astyris lunata*. Changes in log abundances were parallel across the sample period between landscapes, first decreasing, and then increasing to the highest levels. Mean microgastropod abundances ranged from 33.0 to 296.4 per g dw AGB at HI; and from 5.3 to 22.7 per g dw AGB at CI. A significant inverse hyperbolic relationship was apparent between the abundance of microgastropods and the epiphyte load (Figure 5). Although low epiphyte values corresponded with a fairly wide range in microgastropod abundance, high epiphyte values (i.e., ≥ 20 percent of total AGB) never occurred in association with high snail abundances.

When scaled to AGB, abundances of peracarid grazers did not differ significantly between island landscapes; mean abundances ranged from 8.4 to 35.7 per g dw AGB. Major peracarid grazers included the ampithoid amphipods

(*Ampithoe* and *Cymadusa*) and the isopod, *Erichsonella*. Infaunal polychaetes mostly consisted of the nereid, Neanthes (65% of total) and capitellids (18% of total; mainly *Capitella* and *Mediomastus*). Mean abundances of *Neanthes* ranged widely from 4.3 to 34.9 per 0.02 m². Mean abundances of
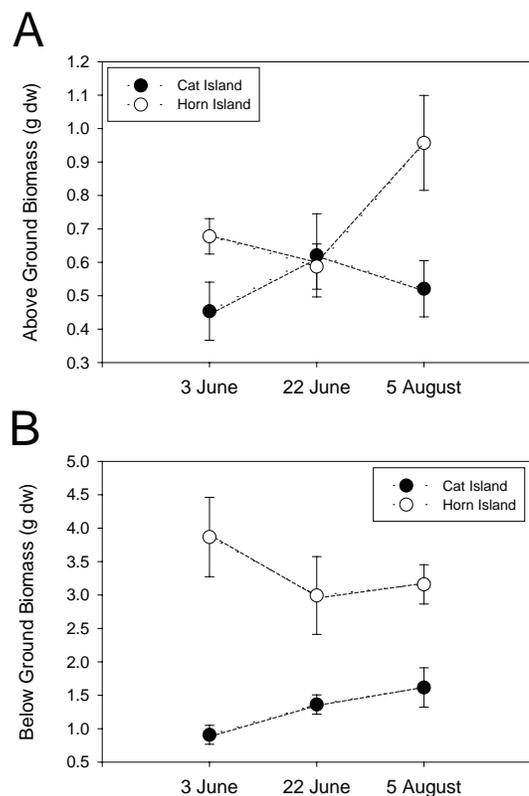

Figure 2.
A. Variation in mean (± 1 se) AGB during the study period.
B. Variation in mean (± 1 se) BGB during the study period.
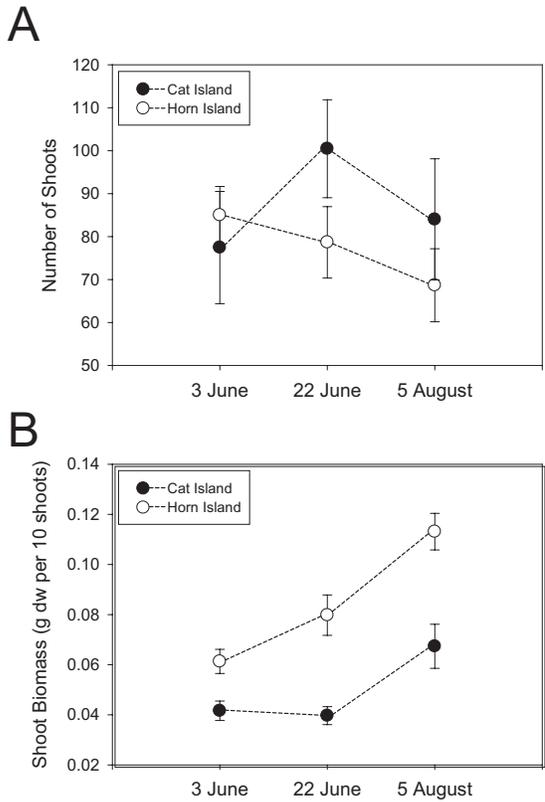
15

A

B

Figure 3.
A. Variation in the mean (± 1 se) number of shoots during the study period.
B. Variation in mean per shoot biomass (± 1 se) (per 10 shoots) during the study period.

A

B

Figure 4.
A. Variation in the mean (± 1 se) epiphyte biomass as a proportion of total ABG during the study period.
B. Variation in the mean (± 1 se) abundance of microgastropod snails scaled to AGB.

capitellids ranged from 1.7 to 11.3 per 0.02 m² at HI; whereas at CI they ranged noticeably lower, from 0.8 to 1.4 per 0.02 m²; and the difference in capitellid abundances between island landscapes was marginally significant (Table 3).

DISCUSSION

Fonseca and Bell (1998) established that physical setting is the main determinant of seagrass landscape configurations, ranging from continuous to widely-dispersed patches with increasing disturbance. Other former studies also document patchy landscapes in high energy environments (Boström et al. 2006). The CI landscape was more exposed to physical disturbance in the form of winds and wave action than HI. Although both seagrass landscapes were fragmented, the seagrass landscape was correspondingly more fragmented at CI (i.e., 12% cover at CI vs. 45% cover at HI). Fonseca and Bell (1998) proposed the critical threshold of ~ 50% coverage, below which the loss of structural habitat integrity accelerates with increasing fragmentation.

Low seagrass coverage at CI corresponded with relatively low per shoot biomass, high epiphyte loading, and low BGB. A feasible link between effects of external and internal processes on habitat function might involve epiphyte loading. High epiphyte loading is known to suppress photosynthetic
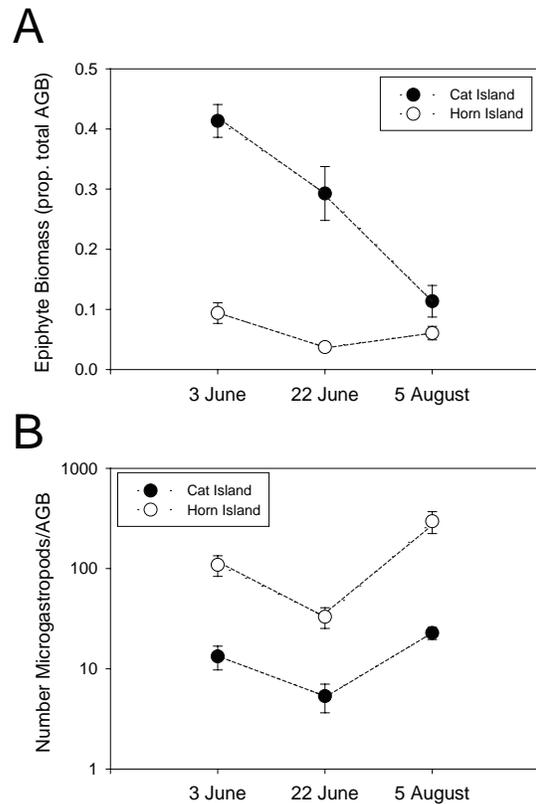
efficiency by preempting light, water column nutrients, carbon, and oxygen (Sand-Jensen 1977, Sand-Jensen et al. 1985). Epiphyte loading may also exacerbate physical disturbance by increasing hydrodynamic impacts (Jernakoff et al. 1996).

A recent paradigm shift in seagrass ecology recognizes the relative importance of top-down rather than bottom-up controls on epiphyte loading (Jernakoff et al. 1996); and calls for full consideration of the role of plant-animal interactions in studies of eutrophication effects in seagrass ecosystems (Hughes et al. 2004). However, attempts to link landscape-scale metrics and faunal responses in seagrass ecosystems have been equivocal (Bell et al. 2001). Macrofauna potentially exert internal feedbacks on habitat function in a variety of ways (Connolly and Hindell 2006), and these feedbacks might also be susceptible to disruption from physical disturbance and resulting habitat fragmentation.

Any important plant-animal relationship requires two conditions. First, the animal should exhibit either direct or indirect functional links to plant habitat via actions affecting plant condition. Examples include predation on grazers, epiphyte grazing, or nutrient retention or delivery. Second, the strength of the functional link should vary with specific density of the animal (sensu Murphey and Fonseca 1995), or with abundance normalized to some habitat met-

ric (e.g., AGB). The latter condition also implies potential sensitivity to landscape-scale changes in seagrass habitat. Accordingly, we examined abundances of microgastropods and peracarid grazers in relation to ABG. In this study, the clearest indication of a functional plant-animal link was an inverse relationship between the abundance of microgastropods and epiphyte loading. The dominant microgastropod, *Bittiolum varium*, is an important grazing component in seagrass ecosystems (van Montfrans et al. 1982, Edgar 1990, Neckles et al. 1993). Thus, microgastropods potentially enhance seagrass condition by removing epiphytes and redirecting nutrients to the sediments. Recently, Fong et al. (2000) showed that gastropod grazers, *Clithon* spp., directly improved the condition of *Zostera japonica* by removing epiphytic algae. But gastropod densities were positively correlated with seasonally high epiphytic loading in their system.

Extremes in spatial configurations of seagrass habitat must bracket habitat fragmentation thresholds for individual taxa, above which dispersal and recolonization becomes ineffective (Monkkonen and Reunanen 1999, Boström et al. 2006). For example, some threshold level of habitat fragmentation might impair the seagrass-epiphyte-microgastropod relationship by disrupting dispersal (Bell et al. 2001) or by increasing the chance of local extinction (Fahrig 2002). Recruitment of *Bittiolum varium* involves the production of seasonal cohorts via a planktonic larval stage that persists for about three weeks in the water column (Qurban 2000). Planktonic dispersal of larval gastropods implicates landscape fragmentation within the context of source-sink dynamics; it would behoove larvae to settle before they are swept away from suitable habitat. Spatial isolation of seagrass beds from sources of planktonic larvae might occur. Extinction rates of macrofaunal populations might also be increased within fragmented seagrass habitat due to edge-effects (i.e. perimeter:area) that foster increased predation or emigration within smaller beds (Bologna and Heck 1999, Hovel and Lipcius 2001).

Additional temporal mismatch between epiphyte biomass and microgastropod abundance suggests that controls on epiphyte loading were complex. This incongruence could have arisen from changes in the rate of seagrass senescence across the summer period (Nelson 1997, Fong et al. 2000). Higher rates of senescence and resultant lower epiphyte loading may occur as rates of seagrass production increase seasonally with water temperature (Peterson and Heck 2001). Another possible cause of seasonal decline in epiphyte loading at CI could involve exacerbated loss of seagrass shoots with high epiphyte loads due to consequent hydrological disturbance (Jernakoff et al. 1996). Seasonal differences in nutrient availability could also limit the development of epiphytes.

Temporal mismatch between epiphyte biomass and microgastropod abundance could also reflect algal successional patterns, possibly involving interactions with microgastropods. Microgastropod grazers consume mostly diatoms (van

Montfrans et al. 1982); however, there were clearly large quantities of filamentous epiphytic algae at the CI site (pers. obsv.). An alternate algal successional pattern might be fostered by lower grazing pressure on the biofilms of surfaces of seagrass shoots. As has been shown for various peracarids (Duffy et al. 2001), selective grazing by microgastropods could favor slower growing early successional epiphytes, perhaps by conditioning seagrass surfaces. Alteration of the algal canopy by grazing might also facilitate colonization by early successional epiphytes (Sommer 1999). For whatever reasons, other studies show that the epiphyte community of disturbed seagrass habitat shifts towards filamentous algae and away from diatoms (Pinckney and Micheli 1998).

Although the importance of the seagrass canopy to secondary production is known, the role of the seagrass rootrhizome mat is not well understood. In this study, capitellids appeared to be more abundant at the HI landscape, where BGB was also consistently higher. This suggests a facultative association for this infaunal deposit feeder in seagrass habitats. Indeed, it is thought that below-ground seagrass production may also foster infaunal secondary production (Orth et al. 1984, Williams and Heck 2001).

Despite limitations, this study highlights some potential links involving landscape configuration, habitat structure, and macrofaunal associations which can be further addressed using hypothesis-driven research. Of course, the generality of this study is limited by the lack of interspersion of seagrass landscape types. Furthermore, potential complexity of relationships involving multiple spatiotemporal scales ob-
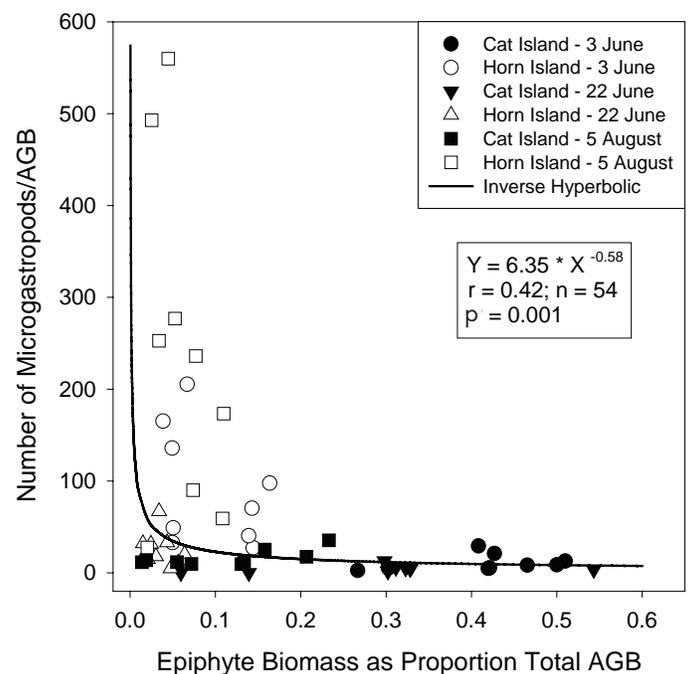

Figure 5.
Inverse hyperbolic relationship between the abundance of microgastropod snails normalized to AGB versus epiphyte biomass expressed as the proportion of total AGB.

scures progress toward a coherent seagrass landscape-habitat function paradigm. Such a paradigm is especially important for successful seagrass restoration, which is predicated on knowing the right abiotic and biotic conditions for the re-establishment of the entire plant and faunal community

(Fonseca et al. 1998, Pranovi et al. 2000). Such formidable challenges can only be met with experimental studies of specific mechanisms and effects that are relevant on the landscape scale.

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