

Habitat size, flora, and fauna: Interactions in a tidal saltwater marsh

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Abstract

Anthropogenic habitat fragmentation is increasingly problematic in both terrestrial and aquatic systems. Fragmentation reduces the size of habitat patches, so examining the effect of patch size on community structure can provide insight into the potential effects of fragmentation. In this study, we examined the effect of habitat size on the density of *Spartina alterniflora* shoots in tidal saltwater marshes, as well as on the two predominant macrofaunal species, the marsh periwinkle *Littoraria irrorata* and fiddler crabs *Uca* spp. We estimated the density of shoots in three different marsh habitats, (1) large island marshes, (2) small island marshes, and (3) large fringing marshes, in Indian Field Creek, York River, Chesapeake Bay. We manipulated shoot density in each of the marsh types to distinguish between the effects of marsh grass density and marsh type on crab and *Littoraria* densities in the system. We found significant differences in grass density among the three marsh types as well as significant species-specific effects of grass density, marsh type, and distance from edge on faunal abundance. Decreasing the shoot density resulted in a decrease in *Littoraria* density in the large marshes. *Littoraria* density increased with distance from edge in the small marshes and in the first 5 m of the fringing marshes, then decreased with distance from edge after 5 m in the fringing marshes. Shoot density had a negative effect on crabs in both the large and small marshes. These results suggest that fragmentation would have a negative effect on the community structure by lowering the densities of both the flora and fauna.

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1. Introduction

1.1. Patterns in a fragmented landscape

It has long been recognized in ecology that a significant interaction exists between habitat size and the dynamics of species interactions in both terrestrial and aquatic systems. These interactions have received

attention because human activities often result in the fragmentation of habitats, breaking large patches into several smaller ones. A major driving force in these interactions is the edge-to-interior ratio of the habitat, as many factors, such as physical stress, consumer pressure, and food availability vary with the distance to edge (Fagan et al., 1999). For example, in terrestrial systems, the edge of a habitat is often associated with a higher level of physical stress; wind stress and dehydration are higher on forest edges, reducing plant growth, increasing mortality. This can change the plant community by allowing species adapted to these stressors to grow (Laurance et al., 1997). Similarly,

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animals can be affected by proximity to the edge, either directly, since predators that forage from the outside of a habitat can cause higher predation pressure on the edge (e.g. Wilcove, 1985), or indirectly, through the reduction in density of the flora that serves as food or shelter.

In marine systems, much of the research in landscape ecology has been done in seagrass beds. There is an interaction between patch size and seagrass density in seagrass beds; however, correlations can be negative (Hovel and Lipcius, 2002) or positive (Irlandi, 1997). This correlation between seagrass density and patch size can confound experiments involving faunal species that focus on either grass density (or structural complexity) or patch size (e.g. Bell et al., 1987; Worthington et al., 1992; Irlandi, 1997; Bell et al., 2001; Hovel and Lipcius, 2002), because both are frequently important (Hovel and Lipcius, 2001). Thus, it is important to design experiments to distinguish between direct effects of habitat size (i.e. edge effects), and indirect effects (i.e. habitat complexity). For example, high seagrass density reduces predator foraging efficiency and thus predation pressure (Eggleston et al., 1999). Patch size can have varying effects on predation; Hovel and Lipcius (2001) found a negative relationship between patch size and juvenile blue crab density, likely because of a positive relationship between patch size and predator abundance. Alternatively, there is a positive relationship between patch size and bay scallop survival, perhaps because the predators of scallops forage from outside of the patches (Irlandi et al., 1995).

1.2. Tidal saltwater marshes

Extensive *Spartina alterniflora* marshes are productive habitats in estuaries along the North Atlantic coastlines that are important in water and nutrient cycles and provide habitat for animals (Mitsch and Gosselink, 1993). Marsh periwinkles, *Littoraria* (formerly *Littorina*) *irrorata*, and fiddler crabs, *Uca minax*, *Uca pugilator*, and *Uca pugnax*, are among the important macroinvertebrate species in marshes because of their strong interactions with *Spartina* (Teal, 1958).

Littoraria grazes on *Spartina*, removing both grass tissue and fungal biomass from the leaves (Haines and Montague, 1979; Graça et al., 2000, Silliman and Newell, 2003). *Littoraria* can exert significant top-down control on *Spartina* production through grazing (Silliman and Zieman, 2001; Silliman and Bertness, 2002). *Littoraria* populations can be food- and habitat-limited (Stiven and Kuenzler, 1979), although predation, primarily by the blue crab, *Callinectes sapidus*, can also be important in structuring them (Hamilton, 1976; Schindler et al., 1994). *Spartina* provides a refuge from blue crab predation;

Littoraria migrates up and down stalks during the tidal cycle to avoid predators (Hovel et al., 2001).

Fiddler crabs have a mutualistic relationship with *Spartina*. Crab burrows help to oxidize the sediment, increase the decay of detritus, and possibly boost nutrient regeneration, all of which enhance *Spartina* production (Bertness, 1985). *Spartina* roots help to stabilize the sediment, preventing burrow collapse (Teal, 1958; Bertness, 1985), while the shoots provide a refuge from predation (Teal, 1958) and stress from heat and desiccation (Bortolus et al., 2002).

Very little work has been published on the effects of habitat size on salt marsh ecosystems. Bruno and Kennedy (2000) found that stabilization of cobble beaches behind *Spartina* marshes and subsequent colonization of the cobble beaches by other plants was dependent on the length of the marsh, but no work has been done looking at the flora and fauna within the marsh. Our study examined the effect of habitat size on *Spartina* density and then manipulated shoot density to distinguish between the effects of edges and habitat complexity (i.e. shoot density) on the populations of *Littoraria* and fiddler crabs.

2. Materials and methods

2.1. Study site

This study was conducted in Indian Field Creek (Fig. 1), an inlet off the York River (Chesapeake Bay, Virginia, USA), during the springs of 2003 and 2004. This shallow mesohaline estuarine system contains several patches of well-established saltwater marsh; there are two large island marshes, three small island marshes, and two fringing marshes that run up onto the beach (Fig. 1). We used GIS to calculate the area, perimeter, and edge-to-area ratio for each of the marshes (Fig. 1). The island marshes are completely inundated during every tidal cycle and consist of habitat classified as tall *Spartina* marsh (Teal, 1958). The fringing marshes experience a gradient of inundation along the elevation gradient. The inundation gradient leads to a vegetation gradient, with *S. alterniflora* in the lower areas of the marsh, followed by *Spartina patens* at higher elevations, and finally by *Juncus* spp. and *Phragmites* spp. in the high marsh. This study was only conducted in the *S. alterniflora* section of the fringing marsh.

2.2. Grass density

In February 2003, 25 plots (35 cm×35 cm) were randomly selected in each of the three marsh types. In

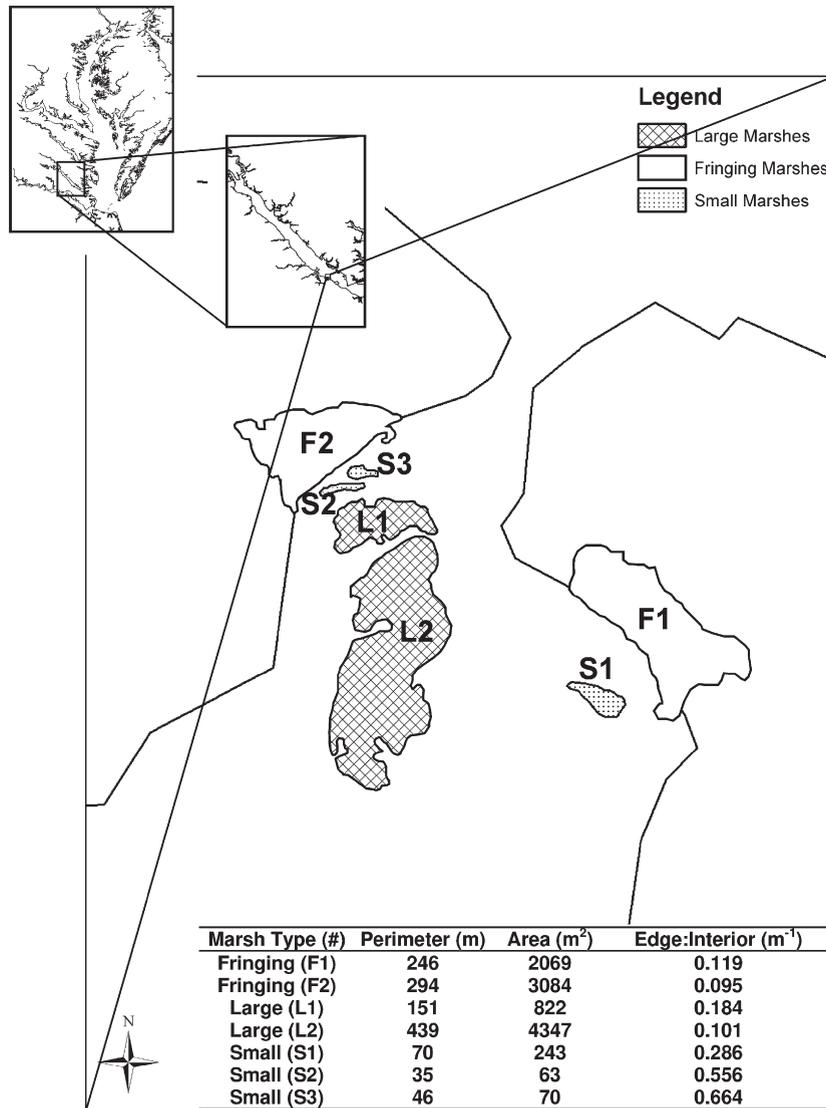


Fig. 1. Map of Chesapeake Bay (left inset), York River (middle inset), and Indian Field Creek (N 37°16'0" W 76°33'40") showing the marshes in which we sampled. Table shows the area, parameter, and edge:area ratio of each marsh.

each plot, the number of grass shoots was counted, the relative elevation was measured using a theodolite, and the distance to water was measured. In April 2004 the same procedure was followed except that only 20 plots were measured and we did not measure elevation. We analyzed the shoot density with an analysis of variance (ANOVA) with marsh type and marsh number (nested within marsh type) as factors. When the data were heteroscedastic (Levene's test), the ANOVA was rejected at an α value lower than that for the test of homogeneity of variance to maintain the type I error rate at 0.05 (Underwood, 1981). Where an effect of a factor

was found, a Tukey's pair-wise multiple comparison test was performed.

2.3. Shoot density manipulation

In April 2003, we performed an experiment in the large and fringing marshes to determine the effect of shoot density on the faunal populations. The large and fringing marshes were chosen because they differed in shoot density naturally but were of approximately equal size, thus controlling for edge effects. Within each marsh type, 10 experimental plots (35 cm × 35 cm) were

Table 1
ANOVA table for shoot density in both years

Source of variation	2003				2004			
	df	MS	F	P	df	MS	F	P
MT	2	14641	5.17	0.008	2	8791.1	13.29	<0.0005
MN(MT)	4	1139	0.40	0.807	4	1247.8	1.89	0.126
Error	68	2834			53	661.3		
Total	74				59			

MT = marsh type and MN = marsh number.

randomly selected. We used scissors to reduce grass densities down to five shoots per plot (low grass density) in five plots, and to 30 shoots per plot (high grass density) in the other five. As a procedural control, 10 more plots were randomly selected in each marsh type and treated similarly to the experimental plots but without cutting any grass. The control plots were selected to fall into a range of low (5–20 shoots per plot, mean=14.0) and high shoot densities (21–45 shoots per plot, mean=37.1). The plots were marked and left for two weeks. Upon return, the number of *Littoraria* and the number of crab burrows were counted in each plot. Crab burrows are an appropriate proxy for crab density because only one crab occupies each burrow, and unoccupied burrows collapse within two weeks (Bertness, 1985). The density of crabs and *Littoraria* was analyzed with fully crossed ANOVAs with plot type (experimental or control), marsh type, and shoot density (high or low) as factors and marsh number (nested within marsh type) as a nested factor. Where a significant interaction effect was detected, an SNK (Student–Newman–Keul’s post-hoc multiple comparison) test was performed (Underwood, 1997).

In April 2004, we expanded on the 2003 study by performing an experiment which examined the effects of both shoot density and distance from edge on fauna

populations in all three marsh types. By varying the shoot density independently of distance from edge, we were able to distinguish between the effects of each. Ten experimental plots were randomly chosen in each marsh type; half had grass densities clipped down to 15 shoots per plot, and half had 30 shoots per plot. Ten control plots were also selected in each marsh type. Distance from edge was recorded. After two weeks, the numbers of *Littoraria* and crab burrows in each plot were counted. Faunal densities were analyzed with fully crossed three-way analysis of covariance (ANCOVA) with plot type (experimental or control) and marsh type as factors, either shoot density or distance from edge as a covariate, and marsh number (nested within marsh type) as a nested factor. Crab densities were square-root transformed prior to analysis to attain homogeneity of variance. Differences between levels of the factors were analyzed with Tukey’s tests. Where a significant interaction effect was detected, a separate regression was performed for each level.

3. Results

3.1. Grass density

The effect of marsh type on shoot density was the same in both 2003 and 2004 (Table 1); the fringing marshes had significantly higher densities than the large and small marshes (Fig. 2). The fringing marshes had significantly higher elevation than the small and the large marshes had an intermediate elevation (Fig. 3; ANOVA; $F_{2,68}=8.73$, $P<0.0005$). There was also a significant effect of marsh number on elevation (ANOVA; $F_{4,68}=61.06$, $P<0.0005$); small marsh number 1 had a lower elevation than the other two small marshes (Tukey’s test). Distance from edge had no effect on shoot density in 2003 in any marsh type.

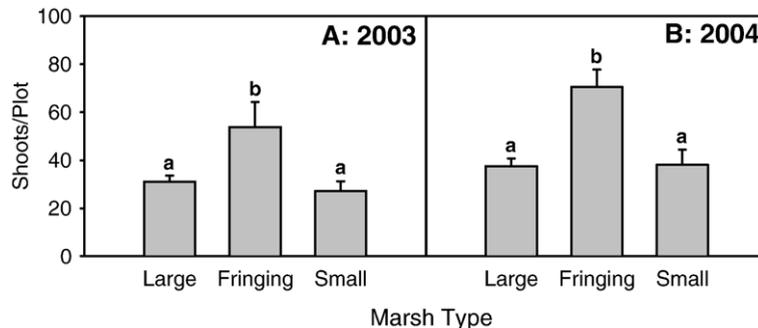


Fig. 2. *Spartina alterniflora* shoot density in the three marsh types in 2003 (A) ($n=25$) and 2004 (B) ($n=20$). Bars show means +1 SE. Bars marked with different letters are significantly different at the 0.05 level (SNK test).

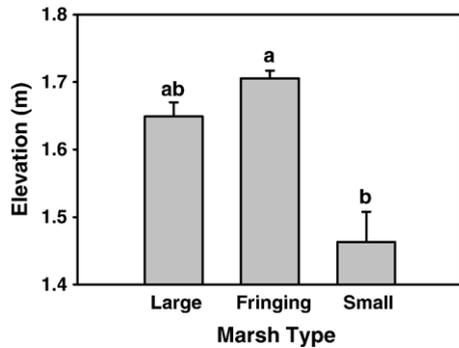


Fig. 3. Elevation of *Spartina alterniflora* in the three marsh types in 2003. Bars show means+1 SE ($n=25$). Bars marked with different letters are significantly different at the 0.05 level (SNK test).

In 2004, however, there was a significant positive relationship between distance from edge and shoot density in both the small and fringing marshes (Fig. 4).

3.2. Faunal density

In 2003, there was a significant interaction effect between shoot density and marsh type, and no effect of plot type on *Littoraria* densities, suggesting that manipulation of the plots did not significantly affect

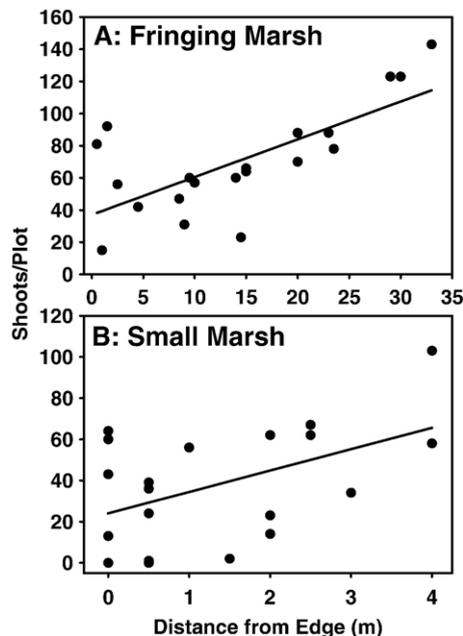


Fig. 4. Regression analysis of distance from marsh edge on *Spartina alterniflora* shoot density, 2004. A) Fringing marsh ($r^2=0.47$, $P=0.0005$). B) Small marsh ($r^2=0.19$, $P=0.0092$). Note change in scale on x-axis.

Table 2
Three-way ANOVA results for 2003 faunal density experiments

Source of variation	<i>Littoraria</i>				Crab burrows ^{-0.5}		
	df	MS	F	P	MS	F	P
Plot type	1	15.62	0.61	0.442	0.23	0.06	0.816
Marsh type	1	1002.83	38.92	<0.0005	23.49	5.76	0.023
Shoot density	1	87.76	3.41	0.075	2.06	0.51	0.482
PT*MT	1	5.62	0.22	0.644	0.23	0.06	0.816
PT*SD	1	21.75	0.84	0.366	0.91	0.22	0.640
MT*SD	1	154.42	5.99	0.020	0.17	0.04	0.838
PT*MT*SD	1	5.95	0.23	0.634	0.70	0.17	0.682
MN(MT)	2	1.92	0.07	0.928	3.65	0.89	0.420
Error	30	25.77			4.08		

PT = plot type, MT = marsh type, SD = shoot density, and MN = marsh number.

the fauna after two weeks (Table 2, Fig. 5). There was no effect of shoot density on the *Littoraria* population in the fringing marshes, but there was a significant positive effect of shoot density on *Littoraria* density in the large marshes, and the fringing marshes had lower densities of *Littoraria* than the large marshes (SNK, Fig. 5).

In 2004, there was no significant effect of shoot density on *Littoraria* density (Table 3; ANCOVA). There was a significant interaction effect between marsh type and distance from edge on *Littoraria* density (Table 4; ANCOVA). Regression analysis was used to examine the effect of distance from edge on *Littoraria* density in each of the three marshes. There was a significant effect in the fringing (Fig. 6A) and small (Fig. 6B) marshes but not in the large marsh ($P=0.29$).

In 2003, there was a significant effect of marsh type on crab abundance but no effect of shoot density; the large marsh had higher densities (Table 2, Fig. 7). In 2004, there was a three-way interaction between marsh

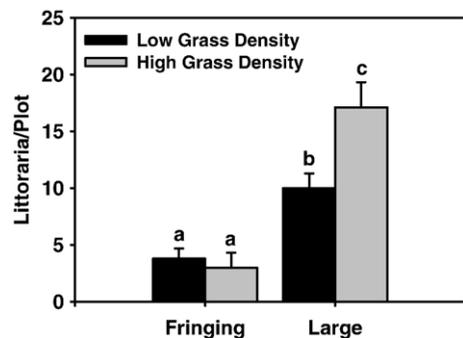


Fig. 5. Effect of *Spartina alterniflora* shoot density and marsh type on *Littoraria irrorata* populations in 2003. Bars show mean+1 SE ($n=10$). Bars marked with different letters are significantly different at the 0.05 level (SNK).

Table 3
Three-way ANCOVA results for 2004 faunal density experiments with shoot density as a covariate

Source of variation	<i>Littoraria</i>				Crab burrows ^{-0.5}		
	df	MS	F	P	MS	F	P
Plot type	1	15.62	0.61	0.442	23.05	1.70	0.199
Marsh type	1	1002.83	38.92	<0.0005	336.67	24.80	<0.0005
Shoot density	1	87.76	3.41	0.075	206.62	15.22	<0.0005
PT*MT	1	5.62	0.22	0.644	17.96	1.32	0.277
PT*SD	1	21.75	0.84	0.366	37.30	2.75	0.105
MT*SD	1	154.42	5.99	0.020	103.35	7.61	0.001
PT*MT*SD	1	5.95	0.23	0.634	27.75	2.04	0.142
MN(MT)	2	1.92	0.07	0.928	26.09	1.92	0.124
Error	30	25.77			13.58		

PT = plot type, MT = marsh type, SD = shoot density, and MN = marsh number.

type, plot type, and distance from edge (Table 4). However, as regression analysis only found a weak negative correlation between distance from edge and crab densities in experimental plots in the large marshes ($P=0.041$, $r^2=0.35$), as this correlation is not observed in the large marshes as whole ($P=0.500$, $r^2=0.00$), and as we do not see this difference between experimental and control plot elsewhere, we believe this is likely a type I error. There was a significant interaction between marsh type and shoot density (Table 3). Crab density was negatively correlated with shoot density in the large (linear regression, Fig. 8A) and small (Fig. 8B) marshes, but not in the fringing marsh ($P=0.90$).

4. Discussion

4.1. Grass density

The distribution of *Spartina* in the fringing marsh is consistent with observations elsewhere (Teal, 1958; Bertness, 1985), with a zone of tall, lower density grass

on the edge of the marsh grading into a zone of shorter and more dense grass as distance from edge and elevation increase. Thus, in our study, the fringing marshes had the highest shoot density and elevation compared to the other marsh types because our sampling area included this high density zone.

The large island marshes had a lower density of *Spartina* than the fringing marshes, which may be explained by the slightly lower (albeit non-significant) elevation and the lack of short, high density *Spartina*. These marshes correspond with Bertness' (1985) description of the "marsh flat" habitat in his fringing

Table 4
Three-way ANCOVA results for 2004 faunal density experiments with distance from edge as a covariate

Source of variation	<i>Littoraria</i>				Crab burrows ^{-0.5}		
	df	MS	F	P	MS	F	P
Plot type	1	39.15	0.94	0.337	4.85	7.31	0.010
Marsh type	2	283.61	6.83	0.003	11.49	17.32	<0.0005
D	1	145.8	3.51	0.068	7.28	10.97	0.002
PT*MT	2	58.17	1.40	0.257	1.49	2.24	0.118
PT*D	1	31.67	0.76	0.387	0.90	1.35	0.251
MT*D	2	139.79	3.36	0.044	3.58	5.39	0.008
PT*MT*D	2	26.68	0.64	0.531	2.41	3.64	0.034
MN(MT)	4	52.53	1.26	0.298	3.27	4.93	0.002
Error	44	41.55			0.66		

PT = plot type, MT = marsh type, D = distance to edge, and MN = marsh number.

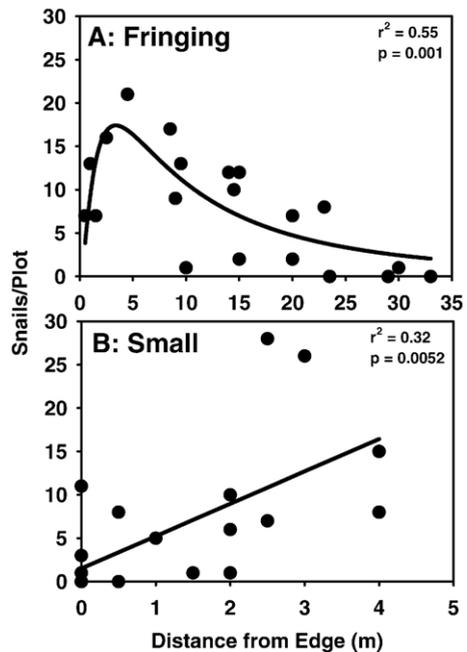


Fig. 6. Regression analysis of distance from edge on *Littoraria irrorata* density in 2004. A) Fringing marsh. B) Small marsh. Note change in scale on x-axis.

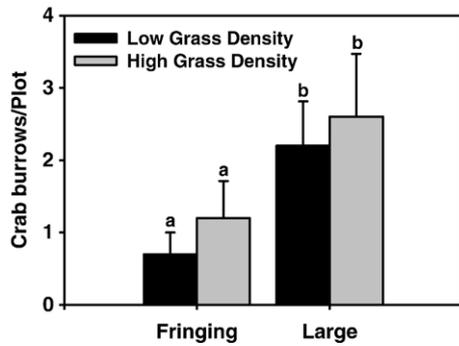


Fig. 7. Effect of *Spartina alterniflora* shoot density and marsh type on fiddler crab (*Uca* sp.) populations in 2003. Bars show mean + 1 SE ($n=5$).

marshes, where he observed no change in shoot density or elevation.

To our knowledge, there is no published data on natural marshes the size of our small island marshes, so our findings on the flora and fauna in these habitats are unique. Our study cannot conclusively distinguish between the effect of marsh size and marsh elevation when comparing the small marshes to the other marsh types, because the small marshes had significantly lower elevation than the other marsh types. The grass density was the same in the small as in the large marshes. The velocity of water in salt marshes is inversely proportional to the distance to the water, relative elevation, and shoot density (Leonard and Luther, 1995; Christiansen et al., 2000), and this gradient of tidal velocity may in part explain the correlation between shoot density and distance from edge.

Marsh shoot density changes with season, and our data was collected in February 2003 and in April 2004. Although the trends in the fringing and small marshes observed in 2004 were not observed in the 2003 data, this is likely due to the differences in sampling time; intra-marsh distributions of *Spartina* may not become obvious until later in the growing season.

4.2. Fauna densities

In both the small marshes and the first 5 m of the fringing marshes, a positive correlation between distance from edge and *Littoraria* densities was observed. *Littoraria* on the edges of the marshes may be vulnerable to pelagic and epibenthic predators, especially blue crabs, foraging at the edges of marshes (Hamilton, 1976; Schindler et al., 1994). Blue crab abundance is highest at the edge of marshes and declines by about 70% within the first 5–6 m (Minello and Rozas, 2002), and both predation on *Littoraria* and blue

crab abundance are higher at marsh edges than in the interior (Lewis and Eby, 2002). This suggests that predation may be the dominant force structuring the population of *Littoraria* in the edges of marshes. Although we did not observe this trend in the large marshes, this was probably due to the low number of samples taken along the edges in this habitat.

In the fringing marsh, a peaked relationship between distance from edge and *Littoraria* densities was observed; after increasing over the first 5 m, the densities decline. Although the three-parameter log-normal relationship was not significantly better than the two-parameter linear relationship (F -test, $P=0.054$), we present the former because it fits better with the trends observed in the small marshes. There are two potential explanations for this pattern. First, the upper limit of the range of intertidal snails is set by their tolerance for heat and desiccation stress (Evans, 1948; McMahan and Russell-Hunter, 1977), both of which increase with distance from edge in the fringing marshes. Thus, the pattern could be caused by physiological limits. Second, although the density of *Spartina* increases with distance from edge, the height decreases (e.g. Teal, 1958) because decreased soil drainage at the intermediate elevations leads to greater soil anoxia, sulfide levels, and salinity. This in turn decreases nitrogen uptake levels, stunts plant growth, and most likely decreases its quality

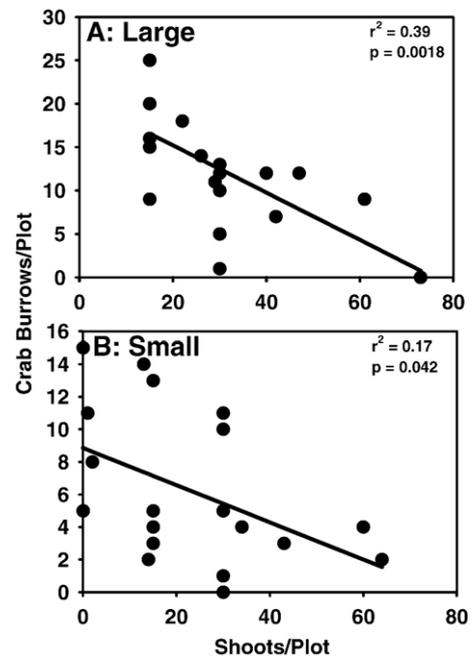


Fig. 8. Regression analysis of *Spartina alterniflora* shoot density on crab (*Uca* sp.) populations in 2004. A) Large marsh. B) Small marsh.

as a food source (Howes et al., 1986), making it less suitable as habitat and food for *Littoraria*. Either of these observations or a combination of the two may explain the pattern of *Littoraria* in the fringing marshes.

In large marshes, *Littoraria* densities increased with higher shoot density but were unrelated to distance from edge, though this too may be due to a low number of observations along the marsh edge. The *Littoraria* populations in these large marshes were relatively high, with more than 200 *Littoraria*/m² (only 2 out of 11 sites ranging from Virginia to Texas summarized in Silliman and Zieman, 2001 had higher densities). The large marshes have a lower edge-to-interior ratio than the small marshes, which could lead to a lower overall effect of predation. We hypothesize that the populations in these marshes are high enough to be influenced by habitat and food availability (i.e., limitation) in the form of *Spartina* shoots. *Spartina* represents both habitat and food to *Littoraria*, who seem to distribute themselves in a constant number of *Littoraria* per shoot (about 1), which would decrease intra-specific competition for resources. Increasing *Littoraria* densities in enclosures on a marsh decreases *Littoraria* growth, indicating that intra-specific competition could be significant in this system (Stiven and Kuenzler, 1979).

Fiddler crab (*Uca* sp.) populations also varied among the marsh types. Overall, highest fiddler crab densities were in the large marsh. We suggest that this pattern is caused by an interaction between predation and habitat complexity. Higher predation along the prominent edges of small marshes, as has been discussed for *Littoraria*, would also explain the higher overall crab abundances in the large marsh (with a smaller edge-to-interior ratio). In both large and small marshes, fiddler crab distribution was negatively correlated with shoot density and uninfluenced by distance from edge. High shoot densities may inhibit fiddler crab movement, leading them to live elsewhere. Our regressions in both the large and the small marshes have remarkably similar x -intercepts, 76 and 77 shoots/plot respectively, suggesting that this is the critical shoot density at which the crabs do not live. The fringing marsh had low densities of fiddler crabs and high shoot densities; the mean shoot density in the fringing marsh (near 70 shoots/plot) is about the same as our calculated critical shoot density, which is probably the reason we observed so few crab burrows there.

5. Conclusions

This study represents one of the first attempts to quantify the effects of marsh size on the flora and fauna in the marsh. Though it is limited in both scope and

scale, it provides a starting point for future investigations. We first demonstrated that *Spartina* densities differ among marsh types, and are correlated with distance from edge. Since the faunal populations could be affected either directly, by edge effects, or indirectly, through the differences in habitat complexity (i.e. shoot density), we manipulated the shoot densities independently of distance from edge, allowing us to distinguish between the two. *Littoraria* densities varied with distance from edge, whereas fiddler crab densities were more influenced by shoot densities. At this point, we can only hypothesize about the mechanisms behind these patterns, but knowing the primary factors will help focus further experiments. This work also suggests that edge effects can lead to a reduced overall density of flora and fauna in small saltwater marshes where the edge:interior ratios are high, so that several small marshes are not functionally equivalent to a single large marsh of equal area (McNeill and Fairweather, 1993).

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