Geographic Variation in the Structure of Salt Marsh Arthropod Communities

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A Thesis

Presented to

the Faculty of the Department of Biology and Biochemistry

University of Houston

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In Partial Fulfillment

of the Requirements for the Degree

Master of Science

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By

Brittany DeLoach McCall

May 2011

GEOGRAPHIC VARIATION IN THE STRUCTURE OF SALT MARSH ARTHROPOD COMMUNITIES

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**ABSTRACT**

The natural environment shows variation at multiple scales, and determining how large-scale patterns relate to the local community's structure and function is a fundamental goal of ecology. Salt marshes along the Atlantic and Gulf coasts are similar in many ways, and are inhabited by the same plant and insect species. However, the Atlantic and Gulf coast areas have different tidal regimes, which may result in the two areas not functioning exactly the same. In addition, abiotic factors that vary with latitude or longitude may lead to differences between northern and southern or eastern and western sites.

I hypothesized that structure and function of the coastal salt marsh varies geographically. To test this, I characterized abiotic conditions and the plant and arthropod communities at 11 sites along each coast in the late summers of 2009 and 2010. I also manipulated wrack (dead plant stems) and nutrient availability in 2 x 3 m plots at each site to evaluate geographic differences in community response. The experiment was established in 2009 and allowed to run to 2010.

My sampling documented that some abiotic factors varied geographically, as did plant height, nitrogen content, and thatch cover. Although the total number of arthropods collected did not differ geographically, the trophic composition of samples showed marked variation among regions. Large-scale differences in latitude and mean tidal range are likely driving much of this variation. Arthropod community structure was little affected by wrack addition, but responded strongly to fertilization; and, the effect of fertilization varied geographically for some trophic levels. Although salt marshes are superficially similar from Maine to Texas, they may be structured differently throughout this geographic range. Therefore, extrapolating results from one geographic region to another should be done with caution.

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**Introduction**

The natural environment is composed of a mosaic of different ecosystems, and within each natural ecosystem there exists a mosaic of abiotic and biotic conditions. This inherent variation within and among natural systems leads to communities that can be highly specific in their local processes and structure compared to neighboring communities. A localized, detailed picture is not completely representative of an ecosystem, however, because patterns found at the local scale are influenced by the surrounding environment and vice-versa (Levin 1992, Travis 1996). Determining how local processes are altered by environmental conditions to produce large-scale patterns of community structure and dynamics is important for full comprehension and a fundamental goal of ecology.

Understanding large-scale patterns is important for two reasons. First, ecologists spend a considerable amount of time and resources conducting experiments or taking measurements at single sites. In order to develop general principles about community structure, we need to know how far the results of studies at a single site can be generalized across broad spatial scales (Bertness and Pennings 2000). Second, some processes such as climate and tidal range vary only at large scales and so must be studied at large scales in order to understand their impacts (Gripenberg and Roslin 2007).

The field of "macroecology" represents one attempt to understand large-scale patterns using a largely descriptive approach (Blackburn 2004). Although significant logistical obstacles constrain our ability to conduct large-scale manipulative experiments, the experimental approach offers significant advantages over a purely descriptive approach (Blackburn 2004, Gripenberg and Roslin 2007), and it has been used successfully to explore large-scale variation in

some processes such as plant-herbivore interactions and plant community richness (Menge et al. 2002, Kikvidze et al. 2005, Pennings and Silliman 2005).

Here, I consider geographic variation in coastal salt marsh community structure and function.  In the United States, marshes are the dominant intertidal habitat along the Atlantic and Gulf Coasts (Mitsch and Gosselink 1993) and are important links in both aquatic and terrestrial food webs.  The salt marsh has proven to be a useful model system for understanding ecological processes because it has structural simplicity and there are clear community patterns across strong gradients of physical stress (Pennings and Bertness 2001).  Tidal marshes are also of interest because they provide a suite of ecosystem services to humanity, including shoreline erosion protection, gas and nutrient regulation, provision of plant and animal diversity, support of primary and secondary production  and ecotourism industries for local communities (Odum 1988, Pennings and Bertness 2001).  Some of these services have quantifiable values associated with them.  In 1994, global intertidal systems were estimated to produce $1.64 trillion per year in ecosystem services, which equates to $2.43 trillion in 2010 dollars (Costanza et al. 1997).  Because of the wide range of functions and uses, there is a definite and practical benefit to increasing our understanding of marsh dynamics in order to protect the system.

Salt marshes along the Atlantic and Gulf coasts are physically similar in many ways, including the same plant and insect species pools; however, there is a major contrast between the Atlantic and Gulf coast in that the two areas are characterized by different tidal regimes. The Gulf experiences a small, diurnal tidal range of about 1 m which is often overwhelmed by local weather events, resulting in unpredictable rounds of flooding and exposure of the marsh surface.  While weather in the Atlantic is just as strong as in the Gulf, it is moderated by a strong

lunar cycle producing a semidiurnal tide of about 3 m for the Atlantic that is relatively regular.

Tides inundate the marsh platform which submerges plants; allows for water, gas, and nutrient

exchange between the water and soil; and, removes or adds debris.  Therefore, this geographic

difference in tidal regime may impact the amount of debris carried out by ebb tides and

deposited with high tides, as well as how much area receives water and nutrient exchange

during high tide, which can have profound ecological consequences (McKee and Patrick 1988).

Tides may also impact the biotic aspects of the salt marsh.  Dead plant material (wrack

and thatch) in the marsh can enhance spatial variation in the habitat, which can be critical

because the habitat structure that wrack provides attracts predators (mostly spiders) and

increases the strength of top-down predator effects on herbivores (Dobel et al. 1990,

Langellotto and Denno 2004, Denno et al. 2005).  High tides can submerge plants completely,

which either drives arthropods inland or exposes them to aquatic predators such as small fish

and shrimp.  Tides also allow for exchange of nutrients and water between the salt marsh and

accompanying estuary, which affects abiotic soil conditions of the local community, as well as

the plant community structure (McKee and Patrick 1988, Mitsch and Gosselink 1993).  These

consequences of differing tidal regimes are important because it likely alters ecological

processes between the two coasts, hence complicating the application of concepts from one

coast to another and making it more difficult to generalize experimental results from one area.

There is already some evidence of varying patterns of plant diversity between the coasts (Kunza

and Pennings 2008), as well as differences in dispersal capability between the coasts for the

dominant herbivore, *Prokelisia* (Denno et al. 1996).  Moreover, experiments from South

American marshes reveal that tidal regimes can have significant impacts on community

structure (Costa et al. 2003, Farina et al. 2009).

Within these two coastlines, there is also evidence of geographic variation. Although the northern Gulf of Mexico is considered one geographic province, the Mississippi River splits the north Gulf into western and eastern sub-regions. The Mississippi River delta represents a break in the continental shelf separating these sub-regions, and its discharge mainly flows westward over the Texas-Louisiana shelf (Rouse Jr. et al. 2005). Over half of the freshwater and nutrient input into the Gulf of Mexico is contributed by the Mississippi River (Moody 1967), which stimulates a massive area of hypoxia that the Louisiana Coastal Current takes westward (Rabalais et al. 2002). I do not know of any studies that have looked at variation in salt marsh characteristics along this coast, but there are instances of differences in marine organisms between the western and eastern Gulf (Herke and Foltz 2002, Keeney et al. 2005, Williams et al. 2008). Along the salt marshes of the Atlantic Coast, there is an established latitudinal gradient in a variety of biotic traits (Turner 1976). As latitude increases, plant height and herbivory intensity decrease. This is paralleled by an increase in leaf nitrogen and plant palatability (Pennings et al. 2003, Pennings et al. 2009). Intracoastal variability is likely to play a role in the function of the intertidal salt marsh because differences in some community characteristics have the potential to impact other aspects of the salt marsh.

Geographic variation within and between coasts may affect how individual marshes function. The strong salinity and flooding gradients found within individual marshes are known to affect bottom-up and top-down effects, two forces that affect how communities function (Moon and Stiling 2002a, Goranson et al. 2004, Denno et al. 2005). Both top-down and bottom-up effects can change the abundance, biomass or diversity of different trophic levels in a community. Top-down effects may cascade down from the predators through the food web until they affect primary producers (Silliman and Bertness 2002). Bottom-up effects are caused

by changes in the productivity, nutrient content, physiology, and/or physical structure of primary producers which can then flow up through the food web to finally affect top predators (Wimp et al. 2010). These two forces work together to impact herbivorous insect populations (Stiling and Rossi 1997, Forkner and Hunter 2000, Denno et al. 2005), and interactions between top-down and bottom-up factors can be key to mediating the structure of biological communities. Two factors that can regulate top-down and bottom-up effects are predator abundance and nutrient availability (Moon and Stiling 2002b, Denno et al. 2005). Within an Atlantic Coast marsh, areas with strong tidal action have little dead plant material (thatch and wrack) but higher nutrient loads, causing bottom-up effects to predominate (Denno et al. 2005). Areas with weaker tidal action have lower nutrient loads but more thatch and wrack, which attracts predators (mostly spiders), causing top-down effects to be stronger (Finke and Denno 2002, Langellotto and Denno 2004). These results suggest that geographic differences in climate and tidal forcing may create geographic variation in processes that structure arthropod communities.

No studies have examined how geographic variation in marsh processes, such as bottom-up and top-down effects, impact the arthropod communities in coastal salt marshes. The biogeographic, manipulative field experiment reported in this thesis was designed to determine how the arthropod communities along the Atlantic and Gulf coasts were structured and if they responded differently to manipulation. I hypothesized that Gulf Coast sites would have more dead plant material than the Atlantic Coast sites because they experience a much smaller tidal range. I further predicted that, as a result of increased three-dimensional habitat structure provided by wrack, Gulf Coast food webs would have more predators, causing strong top-down pressure (Dobel et al. 1990, Finke and Denno 2002, Langellotto and Denno 2006). If

so, experimental wrack additions would increase predator density in both regions, but less so in the Gulf where dead plant material and predators would already be abundant.  I also hypothesized that nitrogen addition would increase plant biomass and quality, and also (as a result of high productivity) thatch abundance.  When combined, I hypothesized that the addition of both wrack and nitrogen would lead to herbivore outbreaks in the Atlantic where predators are relatively rare (Bertness et al. 2008), but not in the Gulf, where predators are relatively abundant and would suppress herbivores.

Because much more work has been done in Atlantic than in Gulf marshes, and because few studies have directly compared processes on the Atlantic and Gulf Coasts, this study greatly enhances our understanding of geographic variation in salt marsh community structure.  My work complements the many studies that have been done at individual sites by putting them into the context of a broader spatial scale, and it sheds new light into the generality of ecological processes across geographic scales.  The work also helps predict how marshes may respond to current threats from climate changes, such as sea level rise and eutrophication.  In order to properly manage both coastlines, we must understand how the marsh functions as a unique ecosystem and not assume that models based on one coastal region will automatically apply to another (Farina et al. 2009).

Figure 1. Map of field site locations.  Circles indicate western Gulf sites; diamonds indicate eastern Gulf sites; squares indicate southern Atlantic sites; and, triangles indicate northern Atlantic sites.

**Materials and Methods:**

*Study Sites and System.*   Field work was conducted at eleven sites on the Gulf Coast and

eleven sites on the Atlantic Coast of the United States spanning a distance of over 2100 mi.

(Figure 1, Appendix Table 1).  Sites were the unit of replication for this study, and all data were

averaged within a site to yield a single number for each variable for each site.  Data for tidal

range at each site was obtained from NOAA's Tides and Currents website (NOAA 2011).  Sites

were visited four times (early and late summers of 2009 and 2010), in each case on a single trip

that began in South Texas and ended in Maine after five weeks; sites were visited in roughly the

same sequence on each trip.  All sites were characterized by salt marsh vegetation, and were

exposed to regular flooding by seawater.  The vegetation at each site consisted of a zone of

*Spartina alterniflora* at the lowest marsh elevations, which transitioned into high marsh

vegetation dominated by pure stands or mixtures of *Juncus roemerianus*, *Spartina patens*,

*Distichlis spicata*, *Sarcocornia* spp., *Batis maritima*, *Borrichia frutescens*, *Avicennia germinans*, or

*Scirpus* spp., depending on the site.  At each site, I conducted transect sampling and a

manipulative experiment at the upper edge of the *Spartina alterniflora* zone.

The arthropod community found in extensive stands of *Spartina alterniflora* was focused

on because this is the most abundant plant in salt marshes along both the Atlantic and Gulf

Coasts and its arthropod community has been well studied (Kneib 1984, Denno et al. 2000,

Denno et al. 2002, Denno et al. 2003, Denno et al. 2005, McFarlin et al. 2008).  Arthropod

samples were sorted in the laboratory to 25 taxa (Appendix Table 2).  I grouped appropriate taxa

into five major trophic groups (sucking herbivores, stem-boring herbivores, predators,

parasitoids, and detritivores).

The *Spartina* arthropod food web is dominated by phloem-feeding planthoppers, mainly

*Prokelisia marginata* and *P. dolus* (Hemiptera: *Delphacidae*).  Two other delphacid planthoppers,

*Delphacodes penedetecta* and *Megamealus lobatus*, are common but far less abundant.

Additional sap-feeders found in *Spartina* are the phloem-feeding leafhopper *Sanctanus*

*aestuarium* (Hemiptera: Cicadellidae) and the mesophyll-feeding bug *Trigonotylus uhleri*

(Hemiptera: Miridae).  All six sap-feeders are monophagous and feed exclusively on *Spartina*

*alterniflora*; chewing herbivores are present but not as common in this system.  Flies with stem-

boring larvae are also found in *Spartina alterniflora*.  The most common families found in the

samples were consistent with information in the literature (Pfeiffer and Wiegert 1981, Stiling

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and Strong 1983, Grevstad et al. 2004, Gratton and Denno 2005, Wimp et al. 2010).  Because

stems were not sampled for larvae, adults collected were counted.

Generalist spiders are the most common natural enemies of planthoppers and also prey

upon small flies in the system.  They include the lycosid spider, *Pardosa littoralis*, and the

linyphiid, *Grammonota trivitatta*. The chief natural enemy of *Prokelisia* eggs is the mirid bug

*Tytthus vagus*.  A diversity of other spider species (such as *Marpissa* spp., Clubionidae spp., and

*Tetragnatha* spp.), along with predators in other orders are also found in *Spartina* but not as

abundantly (Pfeiffer and Wiegert 1981).  Salt marsh spiders are broad generalists and are known

to feed on a variety of prey items associated with *Spartina* habitats, including the mirid

*Trigonotylus uhleri* and small flies such as chloropids, dolichopodids, and ephydrids (Marples

1966, Gratton and Denno 2003b).  Dead plant material in the marsh consists of fallen and

standing-dead leaves (thatch) and fallen stems (wrack) and its accumulation can enhance the

habitat's spatial variation.  Complex-structured habitats enhance top-down effects by promoting

accumulation of these predators, enhancing their numerical response, and dampening intraguild

predation (Dobel et al. 1990, Denno et al. 2002, Finke and Denno 2002, Langellotto and Denno

2004).

Parasitoids and detritivores are also commonly found in the *Spartina alterniflora* zone

(Pfeiffer and Wiegert 1981, Gratton and Denno 2005, Wimp et al. 2010).  The vast majority of

Hymenoptera collected were parasitoid wasps; thus, all wasps collected were grouped into the

parasitoid trophic level.  Collembola was the most common detritivorous taxa collected.  Even

though more than one order was present, all collembolans collected were grouped together

because this subclass is primarily detritivorous.

*Transect Sampling.* Transect sampling was conducted to characterize the soils,

vegetation and arthropod community at each site. A 100 m transect was located 1-2 m into the

*Spartina alterniflora* zone, running parallel to the boundary between the high marsh vegetation

and the *Spartina alterniflora* zone. Transects were sampled in the late summers of 2009 and

2010 (the location of the 2009 transect was not marked, so the 2010 transect was taken in a

similar but not identical position to the 2009 transect at each site). Transect sampling was also

done in the early summer of 2009, but these data are not presented here because the late

summer samples are more comparable with the experimental samples. Soil samples (about 10

cm deep) were collected at four locations along each transect and pooled. Soil samples were

weighed on a portable balance to determine wet weight, and then air dried until returned to the

laboratory. In the lab, I dried soils at 60°C for 4 days, measured soil water content

gravimetrically, and ground and mixed dry soils with a mortar and pestle. Dried soils were

rehydrated with a known volume of distilled water, the salinity measured after 24h, and back-

calculated to the original water content to estimate pore water salinity; soil organic content was

measured as loss on ignition in a muffle furnace at 440°C for 24hr.

The vegetation was characterized at four locations along each transect. I measured the

percent cover of live *Spartina* plants, and of wrack and thatch combined, with a 0.5 x 0.5 m

quadrat divided into 100 cells by monofilament line. I recorded the height of the tallest *Spartina*

*alterniflora* plant in each quadrat, and I collected the third leaf from the top of two plants

adjacent to each quadrat. A *Spartina* biomass index for each quadrat was calculated by

multiplying percent cover by the height. The leaves were air-dried with heat provided by a 60-

watt bulb until they were returned to the laboratory, where they were lyophilized for 72hr,

ground with a Spex 8000M Mixer/Mill, and analyzed for carbon and nitrogen content at the UGA

Chemical Analysis Lab.  In addition, in 2010 only, I estimated the quantity of light transmitted through the vegetation by collecting four pairs of integrated measurements of light availability above the canopy and at the soil surface using a SunScan Canopy Analysis System with a 1 m wand.

The arthropod community was sampled with a DVAC suction sampler (Gratton and Denno 2003b, Brook et al. 2008), with eight ten-second DVAC suction samples (0.0706 $m^2$ suction head) spaced evenly along the transect to total an area of 0.56 $m^2$.  Arthropod samples were then stored in ethanol and sorted in the laboratory (Appendix Table 2).

Transect data from 2009 and 2010 were averaged (correlations between dates are provided in Appendix Tables 3a and b) to provide a single estimate of the abiotic and biotic characteristics of each site.  Data were transformed as appropriate to improve normality and analyzed with ANOVA, with sites assigned to one of four major geographic areas (West Gulf, East Gulf, South Atlantic, North Atlantic).  The Gulf coast was split by the Mississippi River into western and eastern areas; the Atlantic coast was split by latitude 35° into southern and northern areas.  Because of the small sample size (n = 5 or 6), adjustment for multiple comparisons was not made to limit Type II errors.

 Structural equation modeling (SEM) was performed on the averaged data  which allows one to examine the strength of direct and indirect effects between causally related variables (Grace and Kelley 2006, Grace et al. 2010).  Building an SEM model consists of several consecutive steps.  It starts with a priori identification of the causal relationships between the variables and is followed by estimation of the path parameters, performed by screening the matrix of covariances over the hypothetical model.  Finally, model fit is determined by comparing the predicted matrix of covariances with that from the original data.  I used software

package AMOS 18; the parameters of the model were estimated with the maximum likelihood method, and the model fit was tested by the likelihood chi-square value.

*Field Experiment*.   During spring 2009 (April 27 - May 31), I set up a manipulative experiment at each site, with 4 treatments:  1) ambient control, 2) wrack addition, 3) nitrogen addition, and 4) wrack plus nitrogen addition.  Plots measured 3x2 m, were separated by at least 3m, and were placed at the boundary between the high marsh and the upper *Spartina* zone. The plots extended 3m from the boundary into the *Spartina* zone to allow predators to move from the high marsh into the *Spartina* zone (Lewis and Denno 2009).  Plots were delineated by PVC stakes and surrounded by plastic netting (~0.5 m high) to keep added wrack within the appropriate plots and to keep ambient wrack out of the other plots.  Slow-release Agriform© fertilizer tablets (20-10-5 NPK) were placed 10 cm deep into the soil (eight 21 g tablets/$m^2$) to give an application rate of 32g N $m^{-2}$ (McFarlin et al. 2008).  I punched holes in the soil of the plots that were not fertilized to control for any effects of the physical act of fertilizing.  Wrack was collected from nearby areas and placed in a monolayer at the base of the stems in the appropriate plots to approximately double the ambient cover of dead plant material in the plot (Gratton and Denno 2003b, Hines et al. 2006).  Plots that did not receive wrack additions were disturbed to control for any effect of the physical placement of wrack.

In the late summer of 2009, the lower 2 $m^2$ of the plots was sampled with the D-vac to assess the effects of the treatments on the arthropod community (five adjacent eight-second suction samples, avoiding the edges of the plots).  Samples were stored in ethanol and sorted in the laboratory as described above.  Plant community characteristics were not measured . Treatments (fertilizer and wrack) were reapplied to plots in late summer 2009 and early summer

2010, and plots were sampled again in the late summer of 2010. Along with the arthropod community, the vegetation in the lower 2 m$^2$ of each plot was characterized in 2010. The percent cover of live *Spartina* plants, the percent cover of wrack and thatch combined, the height of the tallest plant, and the percent light intercepted through the vegetation was measured as described above with one quadrat per plot. Data were transformed as appropriate to improve normality and homogenize variances.

Data from 2009 and 2010 were analyzed separately with ANOVA, because two Gulf Coast sites were lost to storm activity (Port St. Joe during the 2009 season, and Eleven Mile during the 2010 season - Appendix Table 1). The ANOVA models tested for effects of geographic area (with site nested within area to control for any site effects), wrack addition treatment, fertilizer addition treatment, and the interactions between the treatments as well as between geographic area and the two treatments. Plant community data were log and arcsine(square root) transformed as appropriate to best fit the model's assumptions. For arthropod community data, counts were log transformed but proportions were left unchanged since the arcsine(square root) transformation did not improve the data's fit. Because of the small sample size (n = 3, 5 or 6), adjustment for multiple comparisons was not made to limit Type II errors.

**Results**:

*Transect Sampling*. Mean tidal range at the Atlantic Coast sites was over four times greater than at the Gulf Coast sites (p=0.0001). A variety of other abiotic and plant variables, as well as some insect variables, differed between the Gulf and Atlantic Coasts (Appendix Table 4a). These variables rarely differed between the eastern and western portions of the Gulf Coast (Appendix Table 4b); however, many variables differed between the north and south portions of

the Atlantic Coast (Appendix Table 4c).  Because variables differed both within and between

coasts, I used ANOVA to analyze my results, with sites grouped into four geographic regions:

west and east Gulf, and north and south Atlantic.
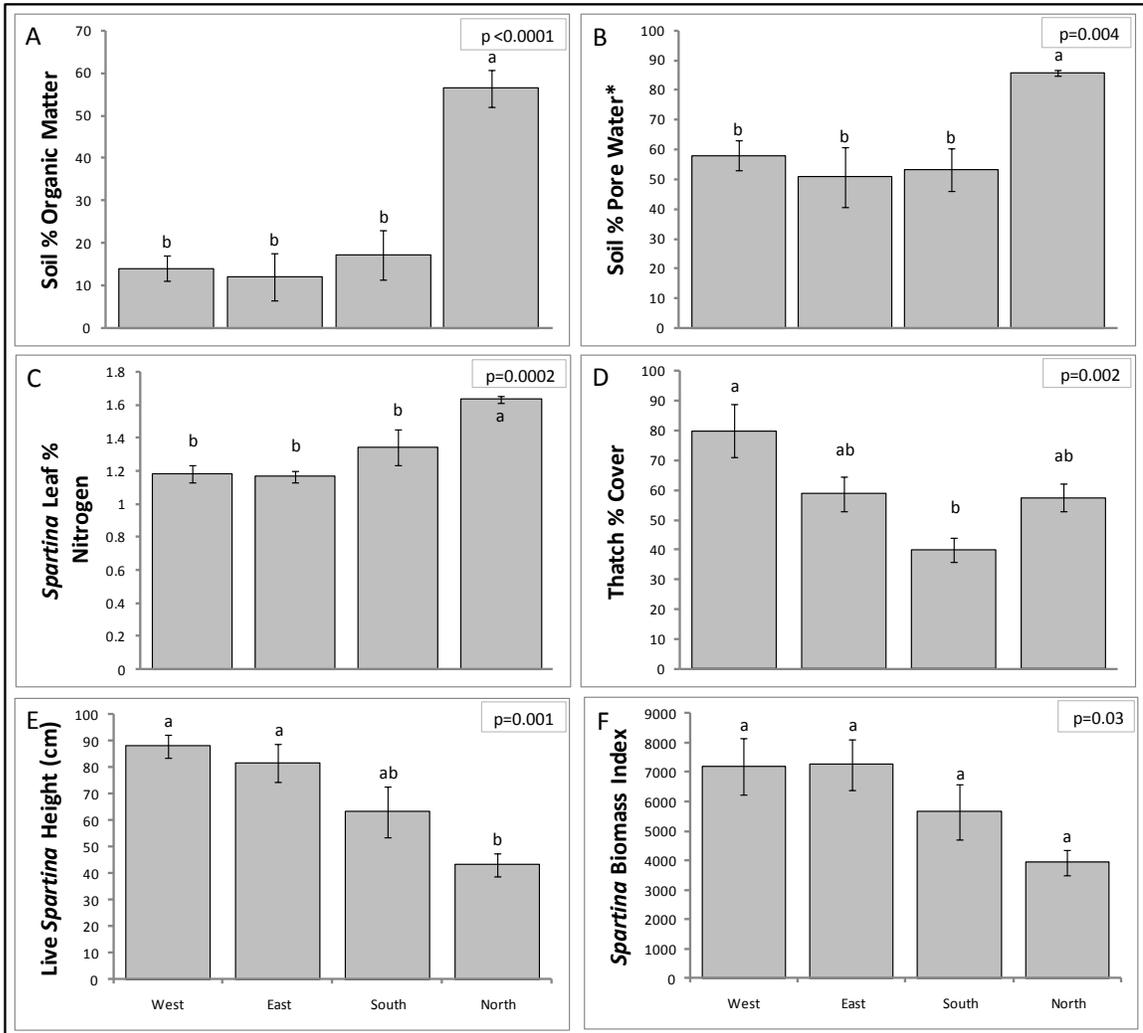


Figure 2. Variation in abiotic and plant community variables among geographic regions.  Tests
done with transformed data indicated with an asterisk; data were
arcsine(squareroot(proportion)) transformed before analysis.

The abiotic environment differed among geographic regions (Figure 2; Appendix Table 5). Tidal range was approximately four times greater in the Atlantic regions than in the Gulf regions. Soil organic content and water content were higher in the north Atlantic than in the other three regions (Figure 2A & 2B). Soil salinity did not differ between the four regions.

Plant community variables differed among regions (Figure 2; Appendix Table 5). *Spartina* leaf nitrogen content was higher in the north Atlantic than in the other regions (Figure 2C). Thatch percent cover was highest in the western Gulf and lowest in the south Atlantic (Figure 2D). The ratio of live *Spartina* to thatch followed the same pattern, with the highest ratio in the western Gulf. *Spartina* plants were tallest in the two Gulf regions and shortest in the north Atlantic (Figure 2E). The *Spartina* biomass index followed this pattern (Figure 2F); however, *Spartina* percent cover did not differ among regions.

The arthropod community also varied geographically (Figure 3; Appendix Table 5). Total counts of arthropods captured in the samples did not differ among regions (Figure 3A), but the composition of the community changed considerably. The proportion of predators in a sample was highest in the western Gulf and lowest in the south Atlantic (Figure 3B). When broken down into the two major feeding guilds, the herbivores showed different patterns. The proportion of sucking herbivores showed a trend (p=0.074) towards being higher in the Atlantic than in the Gulf (Figure 3C); the proportion of stem-boring herbivores was highest in the eastern Gulf and southern Atlantic regions and lowest in the north Atlantic (Figure 3D). Finally, the proportion of parasitoids was higher in the Gulf regions than in the Atlantic, with the western Gulf having larger proportions than the eastern region; and, the proportion of detritivores in a sample was highest in the western Gulf (Figures 3E & 3F).
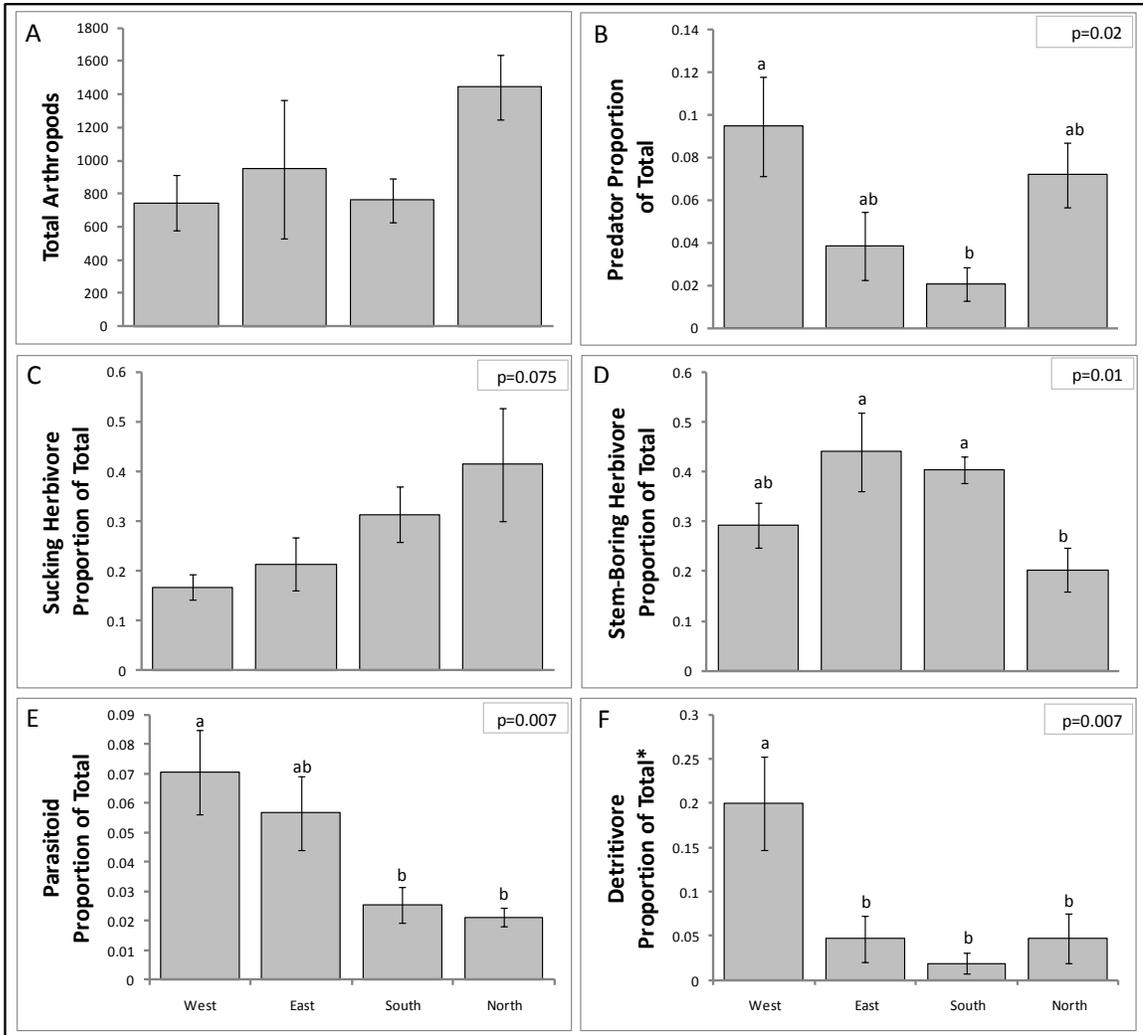
Figure 3. Variation in arthropod community structure among geographic regions. Data were left untransformed for analysis.

Structural equation modeling was performed on the transformed transect data, pooled across all geographic regions, to visualize broad reaching relationships (Figure 4). The final model is a good fit with a posterior predictive p-value of 0.04 and chi-square value of 53.65. Bayesian estimation achieved convergence with a posterior predictive p-value of 0.22. Latitude is the major determinant of soil organic matter content, leaf nitrogen content, and *Spartina* height; it also weakly affects thatch percent cover. Mean tidal range is the major determinant

of thatch percent cover; it also weakly affects leaf nitrogen content. *Spartina* height affects

proportion of parasitoids. Thatch percent cover affects the proportions of predators,

herbivores, and detritivores.
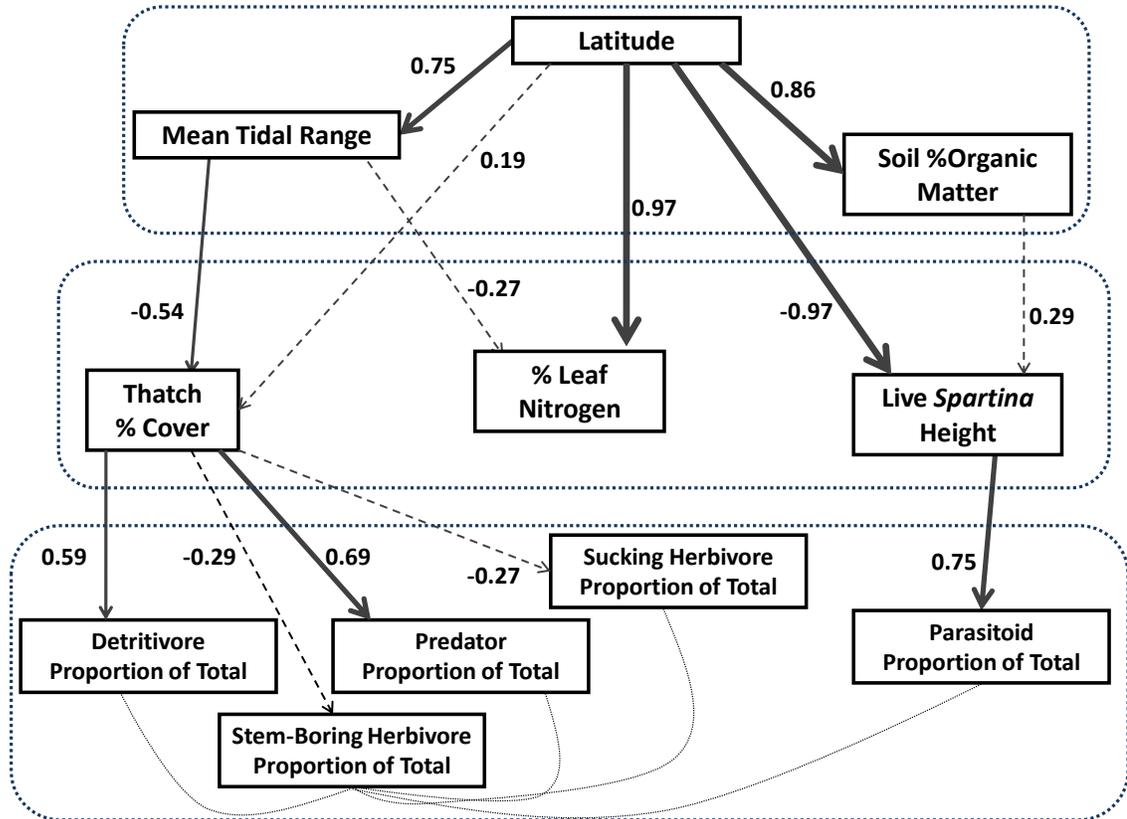


Figure 4. Structural equation model of transect data pooled across all regions. Large rectangular boxes group abiotic, plant community, and arthropod community variables. Solid arrows represent significant relationships at an alpha of 0.05; dotted arrows represent non-significant relationships. The strength of a relationship is indicated by the width of the arrows. Coefficients included next to arrows specify direction and strength of a relationship. Proportions are connected because of covariance.

*Field Experiment.*   Data from 2009 showed an effect of geography on all categories, with

the majority of variables showing patterns consistent with the geographic variation found in the

transect sampling (Appendix Table 6a).  Some arthropod categories responded to both fertilizer

and wrack additions, as well as to their interaction.  Wrack addition decreased numbers of total

arthropods and sucking herbivores; fertilizer addition increased numbers and the proportion of

parasitoids.  Data from 2010 revealed a striking swing towards dominance of fertilizer on all of

the categories (Appendix Table 6b).  Because it is likely that the fertilizer additions did not fully

affect plants until 2010, sixteen months after the initiation of fertilization, I focused on analyzing

the 2010 data.  For almost all variables in both 2009 and 2010, data from control plots were

correlated across sites with data from the transect sampling (Appendix Table 7).

Plant community variables inside plots show geographic variation consistent with results

from the transect sampling (Figure 5).  Thatch percent cover was highest in the western Gulf and

lowest in the north Atlantic, and the ratio of live *Spartina* to thatch followed this pattern

(Figures 5B & 5C).  *Spartina* plants were shortest in the north Atlantic, and the *Spartina* biomass

index followed this pattern with the most biomass in the Gulf regions and the least in the north

Atlantic (Figures 5D & 5E).  *Spartina* percent cover and percent light intercepted did not differ

among regions (Figures 5A & 5F).  These variables also reveal that fertilizer addition impacted

growth by increasing *Spartina* height, biomass index, and percent light intercepted by the

canopy.  Wrack addition did not increase thatch percent cover or any other plant variable

measured.

Figure 5. Variation in plant community variables and their response to manipulation among geographic regions in 2010. Significant ANOVA p-values are shown (full ANOVA results are in Appendix Table 6b). Tests done with transformed data indicated with an asterisk. When transformations were done, proportional data were arcsine(squareroot(proportion)) transformed, and numerical data were natural log transformed.

Arthropod community variables responded strongly to the fertilization treatment (Figure 6). Fertilization increased total arthropods collected (Figures 6A). Fertilized plots had more predators, sucking herbivores, and parasitoids (Figures 6B, 6C, & 6E). There was an interaction between area and fertilization for the proportions of stem-boring herbivores and detritivores. For stem-boring herbivores, fertilization increased proportions in the western Gulf

while decreasing proportions in the eastern Gulf and southern Atlantic; the northern Atlantic region showed no change (Figures 6D). Fertilization only increased detritivore proportions in the eastern Gulf with no change in the other regions (Figures 6F). Although wrack addition affected the arthropod community in 2009, sometimes in interactions with fertilizer or area, no affects of wrack or its interactions were seen in 2010.
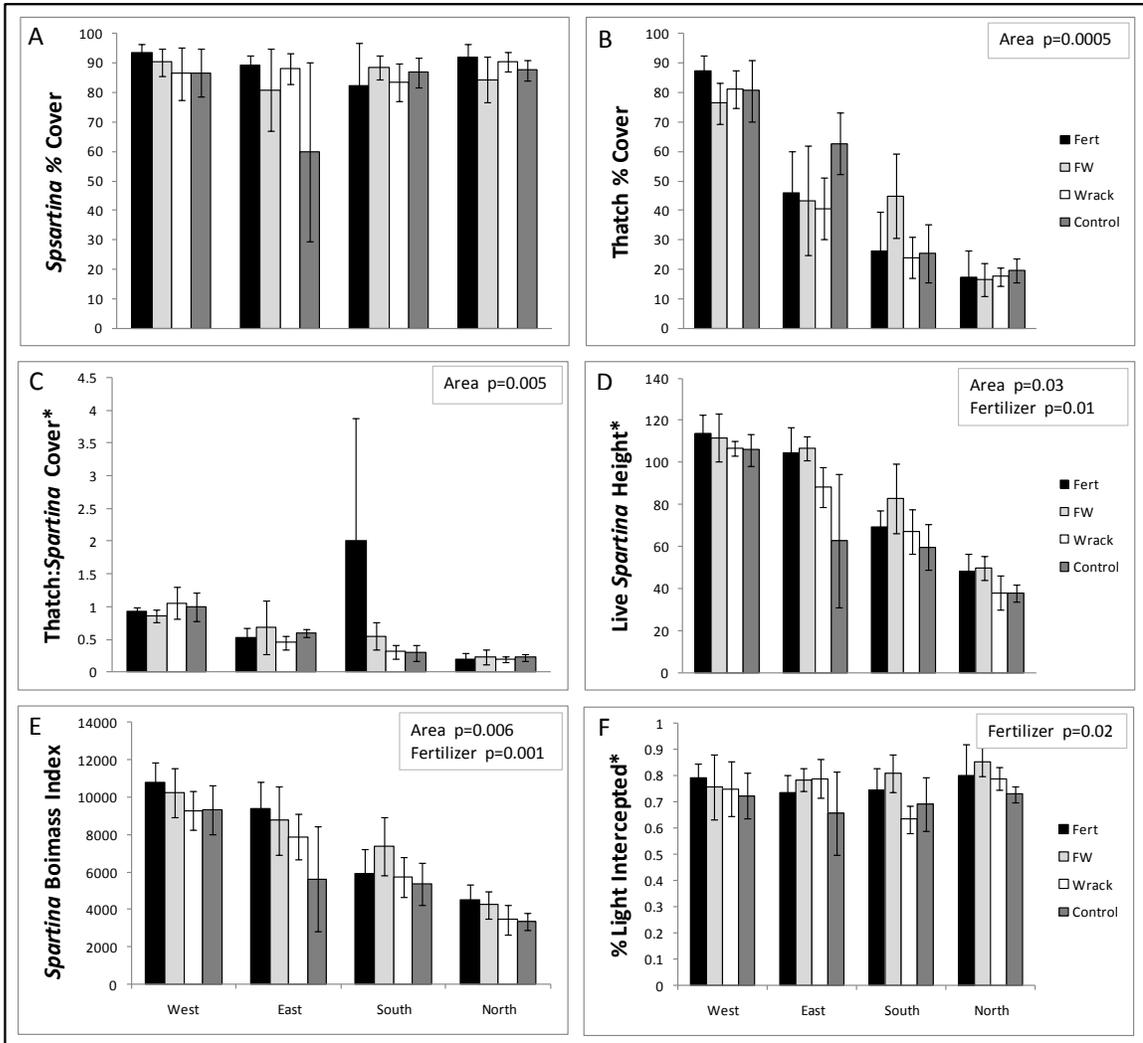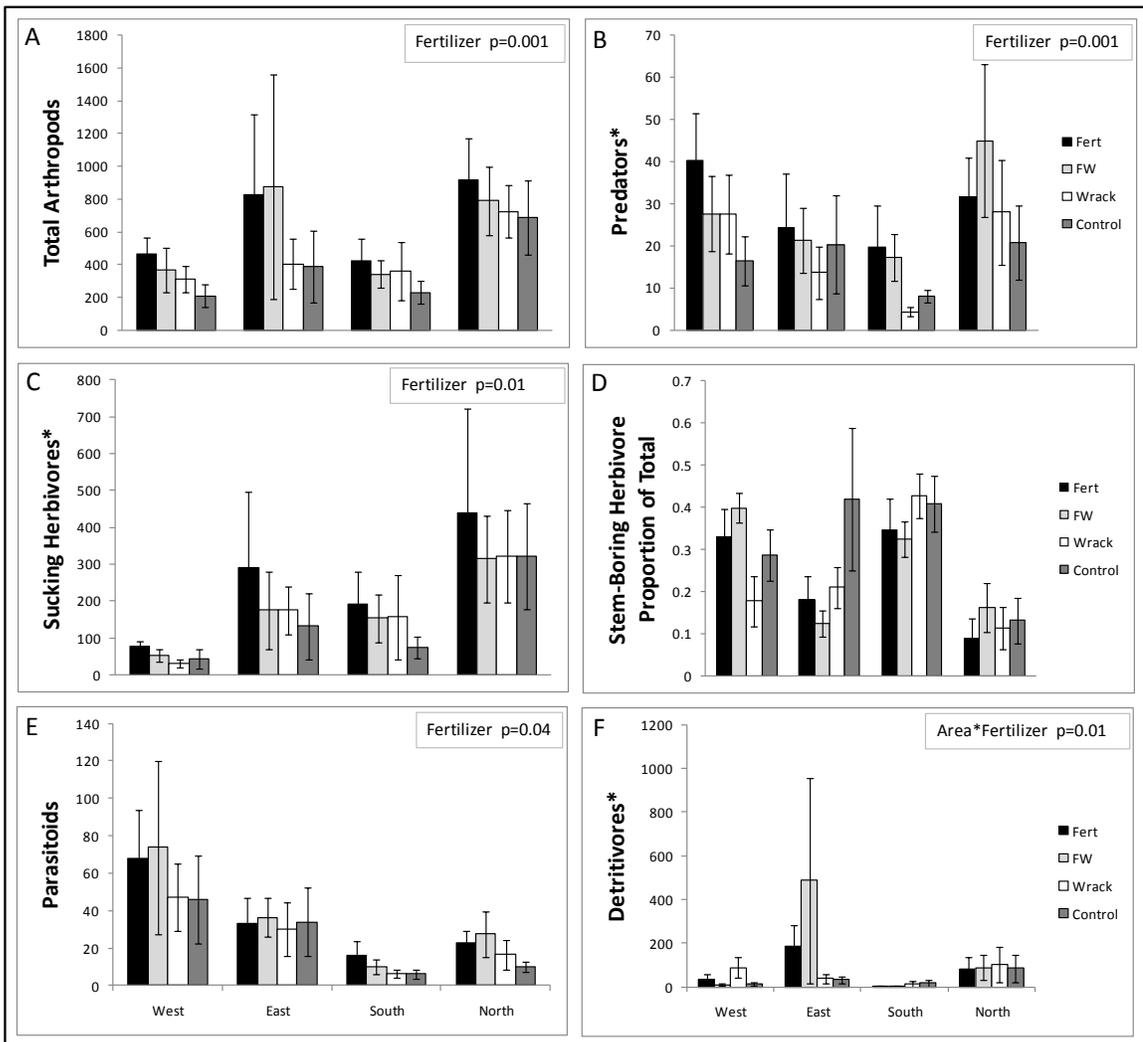


Figure 6. Variation in arthropod community variables and their response to manipulation among geographic regions in 2010. Significant ANOVA p-values are shown (full ANOVA results are in Appendix Table 6b). Tests done with transformed data indicated with an asterisk. When transformations were done, data were natural log transformed before analysis.

**Discussion**

Numerous studies have investigated the relative importance of top-down and bottom-up controls on the arthropod community (Hunter and Price 1992, Stiling and Rossi 1997, Moon and Stiling 2002c, Denno et al. 2005), but this is the first study to put these factors into the context of large-scale geography. This approach is important because past results from single sites may not be general, and in order to have a broad understanding of the system we need to determine how factors vary across multiple sites and larger spatial scales (Levin 1992, Gripenberg and Roslin 2007). Because intertidal salt marshes are under threat from increasing global changes such as rising sea levels, nutrient levels, and $CO_2$ levels, it is important to understand their community dynamics. Realizing what is motivating a response and any geographic variation in that response is essential for assessing what steps should be taken to ameliorate pressure on the habitat. Results from the general sampling reveal that, despite similarities in plant and arthropod species, salt marshes differ markedly among geographic regions. Experimental data, however, shows that fertilization has such a strong impact on the arthropod community that background variation can be overshadowed.

Geographic variation in salt marsh community structure

Transect sampling data indicates that although the *Spartina alterniflora* community's species pool is shared along both the Atlantic and Gulf coasts, there are differences in community structure along these coastlines. The two most obvious explanations for geographic variation in the community are factors that vary with latitude, such as temperature, and different tidal regimes. If variation is due to latitude, the northern Atlantic latitudes should be

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on one extreme followed by southern Atlantic latitudes and then by the Gulf coast.  The Gulf

coast is slightly lower in latitude than the southern Atlantic, so the two Gulf regions may differ

from the southern Atlantic.  If variation is due to differences in tidal regime, the Gulf coast

regions should be different from the entire Atlantic coast.  Furthermore, the driver of variation

may be more complex with both forces interacting to shape the distribution.

Soil organic content, water content, and *Spartina* leaf nitrogen appear to follow a strict

latitudinal gradient with higher contents at higher latitudes.  The decreased temperatures at

higher latitudes decrease decomposition rates and allow the dead material to be incorporated

into the sediment (Aerts 2006, Zhang et al. 2008).  Soil water content mimicked this pattern

because soils high in organic content retain more water (Huntington 2006).  The lower solar

energy inputs at high latitudes also lower evaporation rates, which may decrease soil salinities

(Bertness and Pennings 2000).  My samples, however, did not show any differences in soil

salinity between regions.  This may be because of the limited sampling I was able to do at such a

broad spatial scale.  Soil salinities will fluctuate with precipitation, distance to riverine input, and

even how recently the tide was high, so a few salinity measurements per geographic area may

not be enough to document subtle spatial trends.  Alternatively, it may be that geographic

variation in soil salinity was not detected because high spatial variability at a local scale (due to

distance from a freshwater source) made it hard to detect any pattern.  *Spartina* leaf nitrogen

content also showed a latitudinal pattern with higher amounts at higher latitudes, which is

consistent with previous studies (Siska et al. 2002, Salgado and Pennings 2005, Pennings et al.

2009).  Nitrogen content is an important nutritional quality of leaves, and many studies report

herbivores selectively eating plants with higher nitrogen content (Bowdish and Stiling 1998,

Gratton and Denno 2003a).  This latitudinal gradient is found in leaves of plants worldwide, and

is likely a response to geographic variation in growing season length and soil nutrient availability (Reich and Oleksyn 2004).

Thatch percent cover, the ratio of live *Spartina* to thatch, live *Spartina* height, and the *Spartina* biomass index all display a more complicated pattern that may represent a joint effect of latitude and mean tidal range. The micro-tidal range in the Gulf has higher thatch cover than its latitudinal equivalent in the meso-tidal south Atlantic. This is expected since smaller tidal ranges have a lesser volume of water flowing over the marsh platform at a lower speed, allowing dead plant material to remain in the marsh instead of carrying it out into the estuary. It is also consistent with patterns found within individual salt marshes where higher elevations have less intense flooding and greater amounts of thatch (Denno et al. 2005). The north Atlantic also had high thatch cover, which is most likely due to the harsher winters in high latitudes that kill off many plants and the slower decomposition rates that allow thatch to accumulate. The ratio of live *Spartina* to thatch followed the same pattern as thatch cover, with the highest ratio in the western Gulf, and seemed to be driven by the differences in thatch because *Spartina* percent cover did not differ among regions. *Spartina* plants were tallest in the two Gulf Coast regions and shortest in the north Atlantic. Gulf Coast plants may be taller because they occur at slightly lower latitudes than those on the Atlantic coast, and there is a noted latitudinal gradient in height consistent with previous studies (Anderson and Treshow 1980, Travis and Grace 2010). Alternatively, *Spartina* may be taller in the Gulf because of the irregular flooding and micro-tidal range. The smaller tides reduce the growth range for *Spartina* and possibly the subsequent gradients within marshes that delineate tall and short-form along the Atlantic (Anderson and Treshow 1980, McKee and Patrick 1988, Costa et al. 2003). Along the meso-tidal Atlantic, I found a difference in height consistent with previous studies (Anderson and Treshow 1980,

Travis and Grace 2010), with shorter plants in the north due to latitudinal differences in growing

season, energy inputs, and winter weather conditions.  The *Spartina* biomass index also

followed this pattern and was most likely driven by the height differences because *Spartina*

percent cover did not differ among regions.  This biomass pattern is consistent with previously

reported latitudinal gradients in *Spartina* productivity (Turner 1976, Kirwan et al. 2009).

The arthropod community did not differ among regions in number but did show

differences in compositional make-up.  The proportion of predators in a sample was highest in

the western Gulf and lowest in the southern Atlantic.  This distribution is similar to that of

thatch cover; and, when considered across all regions, the proportion of predators was

positively correlated with thatch percent cover.  This is likely due to increased habitat structure,

which has been shown to increase predator numbers by decreasing intraguild predation (Dobel

et al. 1990, Finke and Denno 2002, Denno et al. 2004, Langellotto and Denno 2004, 2006).  The

two major feeding guilds of herbivores showed different patterns across geographic regions.

The proportion of sucking herbivores did not significantly change across regions, but the

proportion of stem-boring herbivores did.  Stem-boring flies had highest proportions in the

eastern gulf and lowest in the north Atlantic.  Although not much is known about stem-borer

distributions, recent work in the Atlantic has found higher frequencies in the high biomass tall

morph *Spartina* when compared to the short morph (Gaeta and Kornis 2010).  Parasitoids

represented a higher proportion of the arthropod samples in the Gulf regions, suggesting tidal

range as an indirect driver.  In fact, the proportion of parasitoids was highly correlated with

*Spartina* height and biomass index which are both in turn related to tidal range.  The increased

habitat structure provided by the taller, thicker vegetation may affect this group's searching

movement, keeping it on the vegetation longer (Randlkofer et al. 2010).  Detritivore proportions

were highest in the western Gulf.  This mimics the distribution of thatch, which is to be expected

since thatch forms a large part of the base for the detrital food web (Hines et al. 2006), and the

proportion correlated positively with thatch percent cover.

Structural equation modeling shows that both latitude and mean tidal range directly

drive differences in the abiotic and plant characteristics.  These two large-scale forces act on the

arthropod community indirectly via changes in the plant community.  In the model, latitude

impacts mean tidal range.  Because the Gulf is lower in latitude than the Atlantic coast, this is

simply the difference in mean tidal range between the two coastlines.  Latitude is a strong force

shaping soil organic matter content, leaf nitrogen content, and *Spartina* height.  This is

consistent with previous studies that have shown latitudinal gradients in all three variables

(Siska et al. 2002, Travis and Grace 2010).  The model shows that *Spartina* height, in turn, drives

the relative abundance of parasitoids.  Mean tidal range is the principal driver of thatch cover

which is consistent with the hypothesis that lower tidal ranges lead to increased dead plant

material left on the marsh platform.  In turn, the amount of thatch shapes the relative

abundances of detritivores, predators, sucking herbivores, and stem-boring herbivores.  The

positive impact of thatch on detritivores is not surprising given the fact that thatch forms a main

part of the detrital food web in the salt marsh (Hines et al. 2006).  The positive relation of

predators to thatch is consistent with previous work showing aggregation of this guild in highly

complex habitats (Langellotto and Denno 2004); and, the herbivores' negative relation to higher

amounts of thatch is consistent with predators being more capable of suppressing prey in

habitats that have more thatch (Finke and Denno 2002, 2006).  The model demonstrates that

broad scale factors, such as latitude and mean tidal range, are important forces impacting the

local salt marsh community and should be taken into account when drawing conclusions from experimental studies.

Geographic variation in response to manipulations

Control plots were highly correlated with the background environment documented through the transect sample. When manipulated, the plant community inside the experimental plots retained the geographic variation found in the transect sampling. Thatch cover, the ratio of live *Spartina* to thatch cover, live *Spartina* height, and the *Spartina* biomass index all followed the same distributions. Conversely for the arthropod community, when plots were manipulated the geographic patterns observed in the transects were much less important than the response to experimental manipulations.

Sixteen months of fertilization produced taller *Spartina alterniflora* with increased biomass and a canopy that intercepted more light. Salt marsh plant communities are nitrogen limited (Valiela and Teal 1979), so fertilization with nitrogen releases an important constraint on growth (Anderson and Treshow 1980, Gratton and Denno 2003a). Because nitrogen is a limiting element in this stressful habitat, stimulated plant growth is expected and consistent with results from all geographic regions studied (Levine et al. 1998, Pennings et al. 2002, Sala et al. 2008). My experimental data suggests that moderate inputs of fertilizer into this nitrogen-limited community impact the primary producers, as well as the arthropod community.

Although many arthropod categories were correlated between the transect sampling and the control plots, the geographic variation found in the adjacent background environment was not as important in the experiment. Fertilization of *Spartina* affected multiple categories of

arthropods, and the significance of the manipulation overshadowed any geographic pattern.

The total number of arthropods increased in fertilized plots.  Fertilized plots also had more

predators, sucking herbivores, and parasitoids than plots that received no fertilizer.  This

increase in multiple trophic categories is consistent with earlier studies.  Gratton & Denno

(2003) reported increased abundances of predators, selective colonization by *Prokelisia*

herbivores, and increased numbers of potential prey items in fertilized plots.  It appears that

manipulating nitrogen not only affects the herbivores in the system, it can cascade to impact

predators and parasitoids (Bowdish and Stiling 1998, Siemann 1998, Moon and Moon 2010,

Wimp et al. 2010); and, these results develop in spite of striking ambient variation between

geographic regions.  Although this local response is consistent across large distances, it is

unclear whether these results reflect actual population changes or selective migration into

healthier stands of plants.  If populations were adjusting to the increased nitrogen, this would

signify a functional response which could potentially be scaled up to inform on eutrophication of

an entire salt marsh.  If arthropods are selectively occupying nitrogen enriched plots, the

response may or may not scale up.  These would be productive avenues for future research that

would inform on our understanding of the salt marsh ecosystem's functional response to

eutrophication.

My experiment detected that the fertilization impacts varied among geographic regions

for the proportions of stem-boring herbivores and detritivores.  Fertilization increased

proportions of stem-boring herbivores in the western Gulf while decreasing proportions in the

eastern Gulf; the Atlantic regions showed no change.  Fertilization only increased the proportion

of detritivores in the eastern Gulf with no change in the other regions.  The geographic

difference in response of these arthropod groups could have implications for management goals

in each region since they both occur in large numbers and are important components of the

*Spartina alterniflora* system.  Salt marshes are at risk from habitat changes that can potentially

affect the processes that control functions in the ecosystem.  These results add to the growing

body of experimental evidence that shows eutrophication of the intertidal salt marsh impacts

several trophic levels and can alter the community structure (Bertness et al. 2002, Gratton and

Denno 2003a, Valiela et al. 2004, Deegan et al. 2007, Wimp et al. 2010).  In broad terms this

holds true, however my results also indicate some variation in this general response due to

geography.  For stem-boring flies and detritivores, the full impact of fertilization, and thus the

details of how the arthropod community structure is changing, depends upon what region it is

located in.

Wrack addition had no effect on any variable measured, plant or arthropod.  In past

studies, wrack addition to salt marsh plots in New Jersey increased predator densities and

reduced interference among predators, which resulted in decreased herbivore densities (Dobel

et al. 1990, Denno et al. 2002, Finke and Denno 2006, Langellotto and Denno 2006).  My results

from 2009 were consistent with decreased herbivore densities, but by 2010 I observed no effect

of wrack on any variable.  Wrack addition did not noticeably impact percent cover of thatch in

the experimental plots, which may explain my observation of no effect on the arthropod

community.  The failure to see a response to wrack manipulation may be due to decomposition

of the added material; usage of wrack instead of strictly thatch; simply adding to the natural

environment and not having any zero treatment to compare to; or, removal from plots by

weather and/or tides despite our best efforts to maintain increased levels.  Alternatively, it is

possible that the influence of wrack addition on predators at the local scale only occurs in some

places and so was undetectable across this spatial scale.  Although we cannot distinguish

between these possibilities, it is clear that manipulating wrack (and thus presumably

manipulating predators) had far less of an effect than manipulating plant nutrition through

fertilizing.


**Conclusion**

Unraveling the relationship between habitat composition and the arthropod assemblage

is important for understanding how marsh communities function, which is critical for properly

protecting a habitat that provides so many ecosystem services.  Insight into community

structure and function is especially needed with current increasing global changes such as rising

sea levels, nutrient levels, and $CO_2$ levels potentially threatening marshes.  In addition to

understanding local influences, it is important to understand how coastal marshes vary

geographically in order to determine what models are appropriate for use in the system.  I show

that geography indeed affects abiotic conditions and plant characteristics through latitudinal

gradients, differences in mean tidal range, and the combination of these two large-scale forces.

The arthropod community also varies geographically and this tracks the plant community's

variation in a predictable manner.  Accordingly, the intertidal salt marsh community is different

in different places.  Because of these results, I caution against widespread extrapolation over

broad spatial scales without considering the large-scale  geographic patterns .  Even in a

seemingly homogenized habitat such as the salt marsh, which has very little difference in either

plant or arthropod species pool across broad geographic regions, there is striking variation in the

composition of the community as well as evidence of some variation in its response to

manipulation.  Nonetheless, the experiment reveals that even moderate amounts of

eutrophication, a common anthropogenic impact on marshes, can overshadow this natural

variation and enhance insect numbers regardless of location.  Similarly, eutrophication favors

the same marsh plants across broad geographic ranges (Pennings et al. 2002, Pennings et al.

2005).  The combined results from this project demonstrate that salt marshes are structured

differently across large spatial scales, but the functional response to eutrophication is not as

variable.

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**APPENDIX**

Table 1. Study sites and sampling dates.  Name, location, and sampling dates for all sites on Atlantic and Gulf Coasts.  Site/date combinations that involved only transect sampling are indicated with an asterisk.  Transect samples collected in the early summer of 2009 were not included as part of the data analysis because I focused instead on the two late-summer samples that were collected at the same time as samples from the field experiment.

| Site Name | Latitude | Longitude | Sampling Dates | | |
|---|---|---|---|---|---|
| | degree, minute | degree, minute | day | month | year |
| **West Gulf** | | | | | |
| Aransas_NWR* | N28 13.213 | W96 59.161 | 29 | 4 | 2009 |
| Aransas_NWR | N28 13.213 | W96 59.161 | 22 | 7 | 2009 |
| Aransas_NWR | N28 13.213 | W96 59.161 | 15 | 8 | 2010 |
| Brazoria_NWR* | N29 03.598 | W95 14.365 | 28 | 4 | 2009 |
| Brazoria_NWR | N29 03.598 | W95 14.365 | 22 | 7 | 2009 |
| Brazoria_NWR | N29 03.598 | W95 14.365 | 14 | 8 | 2010 |
| Anahuac_NWR* | N29 34.510 | W94 33.137 | 5 | 5 | 2009 |
| Anahuac_NWR | N29 34.510 | W94 33.137 | 28 | 7 | 2009 |
| Anahuac_NWR | N29 34.510 | W94 33.137 | 16 | 8 | 2010 |
| Sabine_NWR* | N29 53.340 | W93 24.056 | 1 | 5 | 2009 |
| Sabine_NWR | N29 53.340 | W93 24.056 | 29 | 7 | 2009 |
| Sabine_NWR | N29 53.340 | W93 24.056 | 17 | 8 | 2010 |
| Cocodrie_LA* | N29 16.123 | W90 39.047 | 4 | 5 | 2009 |
| Cocodrie_LA | N29 16.123 | W90 39.047 | 30 | 7 | 2009 |
| Cocodrie_LA | N29 16.123 | W90 39.047 | 18 | 8 | 2010 |
| Grand_Isle_St_Park* | N29 15.727 | W89 57.158 | 3 | 5 | 2009 |
| Grand_Isle_St_Park | N29 15.727 | W89 57.158 | 30 | 7 | 2009 |
| Grand_Isle_St_Park | N29 15.727 | W89 57.158 | 20 | 8 | 2010 |

| Site Name | Latitude | Longitude | Sampling Dates | | |
|---|---|---|---|---|---|
| | degree, minute | degree, minute | day | month | year |
| **East Gulf** | | | | | |
| Bay_St._Louis_MS* | N30 20.298 | W89 20.014 | 6 | 5 | 2009 |
| Bay_St._Louis_MS | N30 20.298 | W89 20.014 | 1 | 8 | 2009 |
| Bay_St._Louis_MS | N30 20.298 | W89 20.014 | 23 | 8 | 2010 |
| Bon_Secour_NWR* | N30 14.731 | W87 56.419 | 7 | 5 | 2009 |
| Bon_Secour_NWR | N30 14.731 | W87 56.419 | 3 | 8 | 2009 |
| Bon_Secour_NWR | N30 14.731 | W87 56.419 | 24 | 8 | 2010 |
| St_Joe_Bay_Buffer_Preserve* | N29 47.357 | W85 18.114 | 11 | 5 | 2009 |
| St_Joe_Bay_Buffer_Preserve | N29 47.357 | W85 18.114 | 4 | 8 | 2009 |
| St_Joe_Bay_Buffer_Preserve | N29 47.357 | W85 18.114 | 25 | 8 | 2010 |
| Eleven_Mi_Rd_FL* | N29 42.489 | W85 09.182 | 11 | 5 | 2009 |
| Eleven_Mi_Rd_FL | N29 42.489 | W85 09.182 | 5 | 8 | 2009 |
| Eleven_Mi_Rd_FL* | N29 42.489 | W85 09.182 | 26 | 8 | 2010 |
| Boatramp_FL* | N29 55.434 | W84 24.901 | 12 | 5 | 2009 |
| Boatramp_FL* | N29 55.434 | W84 24.901 | 5 | 8 | 2010 |
| Boatramp_FL* | N29 55.434 | W84 24.901 | 26 | 8 | 2009 |
| **South Atlantic** | | | | | |
| Baitshop_FL* | N30 23.942 | W81 28.549 | 13 | 5 | 2009 |
| Baitshop_FL | N30 23.942 | W81 28.549 | 7 | 8 | 2010 |
| Baitshop_FL | N30 23.942 | W81 28.549 | 27 | 8 | 2009 |
| Sapelo_Visitor_Center* | N31 27.200 | W81 21.924 | 14 | 5 | 2009 |
| Sapelo_Visitor_Center | N31 27.200 | W81 21.924 | 10 | 8 | 2010 |
| Sapelo_Visitor_Center | N31 27.200 | W81 21.924 | 30 | 8 | 2009 |
| ACE_Basin_SC* | N32 33.472 | W80 26.372 | 15 | 5 | 2009 |
| ACE_Basin_SC | N32 33.472 | W80 26.372 | 24 | 8 | 2009 |
| ACE_Basin_SC | N32 33.472 | W80 26.372 | 31 | 8 | 2010 |

| Site Name | Latitude | Longitude | Sampling Dates | | |
|---|---|---|---|---|---|
| | degree, minute | degree, minute | day | month | year |
| USC_Baruch* | N33 19.672 | W79 12.314 | 16 | 5 | 2009 |
| USC_Baruch | N33 19.672 | W79 12.314 | 13 | 8 | 2009 |
| USC_Baruch | N33 19.672 | W79 12.314 | 1 | 9 | 2010 |
| Zeke's_Island_NC* | N33 57.561 | W77 56.539 | 19 | 5 | 2009 |
| Zeke's_Island_NC | N33 57.561 | W77 56.539 | 14 | 8 | 2009 |
| Zeke's_Island_NC | N33 57.561 | W77 56.539 | 2 | 9 | 2010 |
| Ft_Macon_St_Park* | N34 41.901 | W76 41.977 | 18 | 5 | 2009 |
| Ft_Macon_St_Park | N34 41.901 | W76 41.977 | 15 | 8 | 2009 |
| Ft_Macon_St_Park | N34 41.901 | W76 41.977 | 5 | 9 | 2010 |
| **North Atlantic** | | | | | |
| VCR* | N37 27.702 | W75 50.274 | 31 | 5 | 2009 |
| VCR | N37 27.702 | W75 50.274 | 22 | 8 | 2009 |
| VCR | N37 27.702 | W75 50.274 | 6 | 9 | 2010 |
| Jacques_Cousteau_NERR* | N39 31.819 | W74 19.129 | 26 | 5 | 2009 |
| Jacques_Cousteau_NERR | N39 31.819 | W74 19.129 | 21 | 8 | 2009 |
| Jacques_Cousteau_NERR | N39 31.819 | W74 19.129 | 7 | 9 | 2010 |
| Waquoit_Bay_NERR* | N41 33.201 | W70 30.381 | 27 | 5 | 2009 |
| Waquoit_Bay_NERR | N41 33.201 | W70 30.381 | 17 | 8 | 2009 |
| Waquoit_Bay_NERR | N41 33.201 | W70 30.381 | 8 | 9 | 2010 |
| Plum_Island_LTER* | N42 44.740 | W70 50.583 | 28 | 5 | 2009 |
| Plum_Island_LTER | N42 44.740 | W70 50.583 | 18 | 8 | 2009 |
| Plum_Island_LTER | N42 44.740 | W70 50.583 | 10 | 9 | 2010 |
| Wells_Bay_ME* | N43 19.276 | W70 34.440 | 29 | 5 | 2009 |
| Wells_Bay_ME | N43 19.276 | W70 34.440 | 19 | 8 | 2009 |
| Wells_Bay_ME | N43 19.276 | W70 34.440 | 11 | 9 | 2010 |

Table 2. Taxonomic categories for DVAC arthropod sampling.  Common species that were important parts of the food web were sorted to species or genus; other taxa were sorted to family or order.

| | Order | Family | Proportion of Sample | |
|---|---|---|---|---|
| **Herbivores (sap-sucking)** | | | **0.278** | **Proportion of Category** |
| *Trigonotylus* | Hemipteran | *Miridae* | | 0.0271 |
| Leafhoppers | Hemipteran | *Cicadellidae* | | 0.0146 |
| *Prokelisia* planthoppers (2 spp) | Hemipteran | *Delphacidae* | | 0.2632 |
| *Delphacodes* planthoppers | Hemipteran | *Delphacidae* | | 0.0270 |
| *Megamealus* planthoppers | Hemipteran | *Delphacidae* | | 0.0325 |
| Immature planthoppers | Hemipteran | *Delphacidae* | | 0.6232 |
| Other Planthoppers | Hemipteran | Misc. | | 0.0073 |
| *Ischnodemus* | Hemipteran | *Blissidae* | | 0.0049 |
| **Herbivores (stem-boring)** | | | **0.378** | **Proportion of Category** |
| *Chaetopsis* Fly | Diptera | *Ulidiidae* | | 0.0157 |
| Chloropidae | Diptera | *Chloropidae* | | 0.9463 |
| Cecidomyiidae | Diptera | *Cecidomyiidae* | | 0.0237 |
| Dolichopodidiae | Diptera | *Dolichopodidae* | | 0.0153 |
| **Predators** | | | **0.058** | **Proportion of Category** |
| *Tytthus vagus* | Hemiptera | *Miridae* | | 0.0697 |
| *Naemia* | Coleoptera | *Coccinellidae* | | 0.0036 |
| *Hogna* spiders | Araneae | *Lycosidae* | | 0.0081 |
| *Pardosa* spiders | Araneae | *Lycosidae* | | 0.1487 |
| *Marpissa* spiders | Araneae | *Salticidae* | | 0.0241 |
| other Salticid spiders | Araneae | *Salticidae* | | 0.0727 |
| Clubionid spiders | Araneae | *Clubionidae* | | 0.0562 |
| Tetragnatha spiders | Araneae | *Tetragnathidae* | | 0.0761 |
| *Grammonota* spiders | Araneae | *Linyphiidae* | | 0.1915 |
| Other Spiders | Araneae | Misc. | | 0.3091 |
| Other Predators (Pseudoscorpions, Reduviidae, Mantids) | Misc. | | | 0.0407 |
| **Parasites** | | | **0.043** | **Proportion of Category** |
| Wasps | Hymenoptera | Misc. | | 1 |
| **Detritivores** | | | **0.081** | **Proportion of Category** |
| Collembola | Collembola | Misc. | | 1 |

Table 3a. Correlations between sampling dates for all variables measured in transects at Atlantic Coast field sites.  Significant relationships are indicated in bold font.

| Atlantic Coast | 09May v. 09Aug | | 09May v. 10Aug | | 09Aug v. 10Aug | |
|---|---|---|---|---|---|---|
| Variable | $r^2$ | p | $r^2$ | p | $r^2$ | p |
| Soil % Organic | 0.99 | **<0.0001** | 0.90 | **0.0003** | 0.94 | **0.0001** |
| Soil % Water | 0.98 | **<0.0001** | 0.91 | **0.0002** | 0.94 | **0.0002** |
| Soil Salinity | 0.88 | **0.0007** | 0.54 | 0.10 | 0.49 | 0.14 |
| Leaf Nitrogen | -0.03 | 0.91 | 0.52 | 0.12 | 0.33 | 0.34 |
| % *Spartina* Cover | 0.69 | **0.025** | 0.04 | 0.90 | 0.11 | 0.77 |
| % Thatch Cover | 0.27 | 0.44 | 0.28 | 0.42 | -0.06 | 0.87 |
| Live *Spartina* Height | 0.95 | **<0.0001** | 0.89 | **0.0005** | 0.93 | **0.0002** |
| Thatch:*Spartina* Cover | -0.27 | 0.44 | 0.28 | 0.42 | -0.13 | 0.72 |
| *Spartina* Biomass | 0.94 | **<0.0001** | 0.81 | **0.004** | 0.84 | **0.004** |
| Arthropod Total | 0.48 | 0.15 | 0.08 | 0.81 | 0.20 | 0.57 |
| Predator | -0.27 | 0.45 | 0.27 | 0.44 | 0.31 | 0.38 |
| Predator Proportion | -0.12 | 0.73 | 0.39 | 0.26 | 0.42 | 0.22 |
| Sucking Herbivore | -0.26 | 0.45 | 0.02 | 0.95 | 0.34 | 0.33 |
| Sucking Herbivore Proportion | -0.44 | 0.19 | 0.11 | 0.74 | 0.22 | 0.53 |
| Stem-Boring Herbivore | 0.52 | 0.12 | 0.26 | 0.46 | -0.11 | 0.74 |
| Stem-Boring Herbivore Proportion | 0.41 | 0.23 | -0.16 | 0.65 | 0.23 | 0.52 |
| Parasitoid | -0.55 | 0.09 | 0.08 | 0.81 | 0.18 | 0.60 |
| Parasitoid Proportion | -0.22 | 0.53 | 0.88 | **0.0007** | 0.11 | 0.75 |
| Detritivore | 0.73 | **0.01** | 0.66 | **0.03** | 0.96 | **<0.0001** |
| Detritivore Proportion | 0.38 | 0.27 | 0.35 | 0.31 | 0.81 | **0.004** |

Table 3b. Correlations between sampling dates for all variables measured in transects at Gulf Coast field sites.  Significant relationships are indicated in bold font.

| Gulf Coast | 09May v. 09Aug | | 09May v. 10Aug | | 09Aug v. 10Aug | |
|---|---|---|---|---|---|---|
| Variable | $r^2$ | p | $r^2$ | p | $r^2$ | p |
| Soil % Organic | 0.91 | **0.0001** | 0.86 | **0.0006** | 0.95 | **<0.0001** |
| Soil % Water | 0.91 | **0.0001** | 0.85 | **0.0009** | 0.85 | **0.0009** |
| Soil Salinity | 0.81 | **0.002** | 0.30 | 0.36 | 0.47 | 0.14 |
| Leaf Nitrogen | 0.74 | **0.008** | 0.47 | 0.14 | 0.46 | 0.15 |
| % *Spartina* Cover | 0.82 | **0.002** | 0.80 | **0.002** | 0.62 | **0.04** |
| % Thatch Cover | 0.45 | 0.15 | 0.64 | **0.03** | 0.16 | 0.63 |
| Live *Spartina* Height | 0.81 | **0.002** | 0.69 | **0.01** | 0.71 | **0.01** |
| Thatch:*Spartina* Cover | 0.79 | **0.003** | 0.72 | **0.01** | 0.70 | **0.01** |
| *Spartina* Biomass | 0.88 | **0.0003** | 0.77 | **0.005** | 0.72 | **0.01** |
| Arthropod Total | 0.42 | 0.25 | 0.32 | 0.38 | 0.85 | **0.003** |
| Predator | 0.62 | 0.07 | 0.89 | **0.001** | 0.84 | **0.004** |
| Predator Proportion | 0.42 | 0.25 | 0.75 | **0.01** | 0.59 | 0.09 |
| Sucking  Herbivore | 0.79 | **0.01** | 0.28 | 0.46 | 0.55 | 0.12 |
| Sucking Herbivore Proportion | 0.58 | 0.09 | 0.53 | 0.090 | 0.35 | 0.34 |
| Stem-Boring Herbivore | 0.42 | 0.25 | 0.37 | 0.32 | 0.64 | **0.05** |
| Stem-Boring Herbivore Proportion | 0.72 | **0.02** | 0.59 | 0.08 | 0.79 | **0.01** |
| Parasitoid | 0.65 | **0.05** | 0.37 | 0.31 | 0.76 | **0.01** |
| Parasitoid Proportion | 0.04 | 0.90 | -0.06 | 0.86 | 0.44 | 0.23 |
| Detritivore | -0.32 | 0.38 | -0.33 | 0.37 | 0.61 | 0.08 |
| Detritivore Proportion | -0.23 | 0.54 | -0.23 | 0.54 | 0.72 | **0.02** |

Table 4a. Mean, standard error, and Student's T-test results for all variables measured in transects compared between Atlantic and Gulf Coast field sites. Significant relationships are indicated in bold font. Tests done with transformed data indicated with an asterisk. When transformations were done, proportional data were arcsine(squareroot(proportion)) transformed, and numerical data were natural log transformed.

| Variable | Continent | | | | |
| | Atlantic | SE | Gulf | SE | p-Value |
|---|---|---|---|---|---|
| Mean Tidal Range (m) | 1.55 | 0.186 | 0.346 | 0.037 | **0.0001** |
| Soil % Organic | 35.01 | 7.14 | 13.21 | 2.83 | **0.01** |
| Soil % Water * | 68.03 | 6.37 | 54.74 | 5.17 | 0.10 |
| Soil Salinity * | 34.24 | 4.65 | 29.15 | 3.46 | 0.36 |
| Leaf Nitrogen | 1.36 | 0.081 | 1.17 | 0.030 | **0.04** |
| % *Spartina* Cover* | 89.17 | 2.32 | 84.11 | 4.99 | 0.34 |
| % Thatch Cover | 47.90 | 3.96 | 70.35 | 6.24 | **0.006** |
| Thatch: *Spartina* Cover* | 0.539 | 0.047 | 1.02 | 0.238 | **0.01** |
| Live *Spartina* Height | 54.23 | 6.18 | 85.18 | 3.95 | **0.0004** |
| *Spartina* Biomass* | 4868.3 | 589.74 | 7227.1 | 617.64 | **0.01** |
| Arthropod Total | 1072.3 | 152.11 | 837.68 | 201.09 | 0.36 |
| Predator * | 48.27 | 16.59 | 44.63 | 10.59 | 0.71 |
| Predator Proportion | 0.044 | 0.011 | 0.069 | 0.016 | 0.22 |
| Sucking Herbivore* | 425.64 | 102.58 | 177.00 | 52.40 | **0.03** |
| Sucking Herbivore Proportion | 0.360 | 0.059 | 0.189 | 0.027 | **0.01** |
| Stem-Boring Herbivore* | 321.11 | 60.29 | 280.89 | 80.39 | 0.35 |
| Stem-Boring Herbivore Proportion | 0.312 | 0.039 | 0.359 | 0.047 | 0.45 |
| Parasitoid | 20.81 | 2.74 | 56.86 | 15.44 | **0.04** |
| Parasitoid Proportion | 0.023 | 3.47E-03 | 0.064 | 9.44E-03 | **0.001** |
| Detritivore* | 35.63 | 18.79 | 148.68 | 53.29 | 0.20 |
| Detritivore Proportion* | 0.03 | 0.01 | 0.130 | 0.038 | **0.02** |

Table 4b. Mean, standard error, and Student's T-test results for all variables measured in transects at Gulf Coast field sites - splitting the West Gulf from the East Gulf (west and east of the Mississippi River respectively). Significant relationships are indicated in bold font. Tests done with transformed data indicated with an asterisk. When transformations were done, proportional data were arcsine(squareroot(proportion)) transformed, and numerical data were natural log transformed.

| Variable | Gulf | | | | |
| | East | SE | West | SE | p-Value |
| --- | --- | --- | --- | --- | --- |
| Mean Tidal Range (m) | 0.423 | 0.047 | 0.281 | 0.040 | **0.04** |
| Soil % Organic | 12.13 | 5.47 | 14.11 | 3.03 | 0.74 |
| Soil % Water | 50.78 | 10.09 | 58.03 | 5.02 | 0.51 |
| Soil Salinity | 23.47 | 3.96 | 33.89 | 4.85 | 0.14 |
| Leaf Nitrogen | 1.16 | 0.035 | 1.18 | 0.050 | 0.81 |
| % *Spartina* Cover* | 87.57 | 3.71 | 81.22 | 8.86 | 0.46 |
| % Thatch Cover | 58.77 | 5.85 | 80.00 | 8.89 | 0.089 |
| Thatch: *Spartina* Cover* | 0.679 | 0.056 | 1.30 | 0.41 | 0.15 |
| Live *Spartina* Height | 81.77 | 7.135 | 88.02 | 4.44 | 0.46 |
| *Spartina* Biomass | 7256.7 | 847.96 | 7202.4 | 958.71 | 0.96 |
| Arthropod Total | 948.30 | 418.36 | 745.50 | 166.86 | 0.67 |
| Predator | 40.90 | 18.42 | 47.75 | 13.45 | 0.76 |
| Predator Proportion | 0.038 | 0.016 | 0.094 | 0.023 | 0.088 |
| Sucking Herbivore* | 234.60 | 106.59 | 129.00 | 38.49 | 0.97 |
| Sucking Herbivore Proportion | 0.214 | 0.053 | 0.167 | 0.025 | 0.42 |
| Stem-Boring Herbivore* | 395.95 | 167.41 | 185.01 | 31.10 | 0.37 |
| Stem-Boring Herbivore Proportion | 0.441 | 0.078 | 0.292 | 0.045 | 0.12 |
| Parasitoid | 60.10 | 25.19 | 54.16 | 21.17 | 0.85 |
| Parasitoid Proportion | 0.056 | 0.012 | 0.070 | 0.014 | 0.49 |
| Detritivore* | 79.60 | 67.64 | 208.75 | 75.88 | 0.14 |
| Detritivore Proportion* | 0.046 | 0.026 | 0.199 | 0.052 | **0.03** |

Table 4c. Mean, standard error, and Student's T-test results for all variables measured in transects at Atlantic Coast field sites - splitting the North Atlantic (Virginia to Maine) from the South Atlantic (Florida to North Carolina).  Significant relationships are indicated in bold font. Tests done with transformed data indicated with an asterisk. When transformations were done, proportional data were arcsine(squareroot(proportion)) transformed, and numerical data were natural log transformed.

| Variable | Atlantic | | | | |
| | North | SE | South | SE | p-Value |
| --- | --- | --- | --- | --- | --- |
| Mean Tidal Range (m) | 1.69 | 0.364 | 1.43 | 0.179 | 0.51 |
| Soil % Organic | 56.40 | 4.34 | 17.19 | 5.91 | **0.0006** |
| Soil % Water * | 85.75 | 0.798 | 53.26 | 7.27 | **0.004** |
| Soil Salinity * | 26.53 | 1.28 | 40.67 | 7.75 | 0.11 |
| Leaf Nitrogen | 1.56 | 0.058 | 1.16 | 0.075 | **0.003** |
| % *Spartina* Cover* | 90.87 | 3.47 | 87.75 | 3.30 | 0.54 |
| % Thatch Cover | 57.45 | 4.65 | 39.95 | 3.92 | **0.01** |
| Thatch: *Spartina* Cover | 0.614 | 0.057 | 0.477 | 0.066 | 0.16 |
| Live *Spartina* Height | 43.35 | 4.38 | 63.31 | 9.55 | 0.11 |
| *Spartina* Biomass* | 3931.8 | 424.96 | 5648.7 | 941.73 | 0.14 |
| Arthropod Total | 1443.7 | 194.54 | 762.83 | 132.17 | **0.01** |
| Predator * | 91.90 | 25.06 | 11.91 | 3.06 | **0.0009** |
| Predator Proportion | 0.071 | 0.015 | 0.020 | 7.83E-03 | **0.01** |
| Sucking Herbivore | 616.20 | 180.69 | 266.83 | 75.65 | 0.089 |
| Sucking Herbivore Proportion | 0.414 | 0.114 | 0.314 | 0.056 | 0.42 |
| Stem-Boring Herbivore | 352.11 | 118.56 | 295.28 | 60.52 | 0.66 |
| Stem-Boring Herbivore Proportion | 0.203 | 0.044 | 0.404 | 0.027 | **0.003** |
| Parasitoid | 27.80 | 2.30 | 15.00 | 3.03 | **0.01** |
| Parasitoid Proportion | 0.021 | 3.21E-03 | 0.025 | 5.97E-03 | 0.57 |
| Detritivore* | 60.80 | 38.95 | 14.66 | 9.51 | 0.68 |
| Detritivore Proportion* | 0.047 | 0.028 | 0.018 | 0.011 | 0.47 |

Table 5. One Way ANOVA values for all variables measured in transects at Atlantic and Gulf Coast field sites. Atlantic sites are split into North (Virginia to Maine) and South (Florida to North Carolina). Gulf sites are split into West and East (west and east of the Mississippi River, respectively). Significant relationships are indicated in bold font. Tests done with transformed data indicated with an asterisk. When transformations were done, proportional data were arcsine(squareroot(proportion)) transformed, and numerical data were natural log transformed. Letters adjacent to means indicate geographic regions that were significantly different (Tukey HSD with alph 0.05).

| Variable | One Way Anova | West Gulf n=6 | | East Gulf n=5 | | South Atlantic n=6 | | North Atlantic n=5 | |
|---|---|---|---|---|---|---|---|---|---|
| | p-value | Mean | SE | Mean | SE | Mean | SE | Mean | SE |
| Mean Tidal Range (m) | **0.0001** | 0.281 b | 0.185 | 0.423 b | 0.203 | 1.43 a | 0.185 | 1.69 a | 0.203 |
| Soil % Organic | **<0.0001** | 14.11 b | 4.61 | 12.13 b | 5.05 | 17.19 b | 4.61 | 56.40 a | 5.05 |
| Soil % Water* | **0.004** | 58.03 b | 5.02 | 50.78 b | 10.09 | 53.26 b | 7.27 | 85.75 a | 0.798 |
| Soil Salinity (PSU)* | 0.12 | 33.89 | 4.85 | 23.47 | 3.96 | 40.67 | 7.75 | 26.53 | 1.28 |
| Leaf Nitrogen (%) | **0.0002** | 1.18 b | 0.050 | 1.16 b | 0.035 | 1.16 b | 0.075 | 1.56 a | 0.058 |
| % *Spartina* Cover* | 0.59 | 81.22 | 8.86 | 87.57 | 3.71 | 87.75 | 3.30 | 90.87 | 3.47 |
| % Thatch Cover | **0.002** | 80.00 a | 6.05 | 58.77 ab | 6.62 | 39.95 b | 6.05 | 57.45 ab | 6.62 |
| Live *Spartina* Height (cm) | **0.001** | 88.02 a | 6.62 | 81.77 a | 7.25 | 63.31 ab | 6.62 | 43.35 b | 7.25 |
| Thatch:*Spartina* Cover* | **0.01** | 1.30 a | 0.413 | 0.679 ab | 0.056 | 0.477 b | 0.066 | 0.614 ab | 0.057 |
| *Spartina* Biomass Index (g/m2)* | **0.03** | 7202.4 | 958.71 | 7256.7 | 847.96 | 5648.7 | 941.73 | 3931.8 | 424.96 |
| Arthropod Total | 0.18 | 745.5 | 228.05 | 948.3 | 249.82 | 762.8 | 228.05 | 1443.7 | 249.82 |
| Predator* | 0.19 | 47.75 | 13.45 | 40.90 | 18.42 | 11.91 | 3.07 | 91.90 | 25.06 |
| Predator Proportion | **0.02** | 0.094 a | 0.016 | 0.038 ab | 0.017 | 0.020 b | 0.016 | 0.071 ab | 0.017 |
| Sucking Herbivore* | 0.15 | 129.00 | 38.49 | 234.60 | 106.59 | 266.83 | 75.65 | 616.20 | 180.69 |
| Sucking Herbivore Proportion | 0.075 | 0.167 | 0.063 | 0.214 | 0.069 | 0.313 | 0.063 | 0.414 | 0.069 |
| Stem-Boring Herbivore* | 0.60 | 185.01 | 31.10 | 395.95 | 167.41 | 295.28 | 60.52 | 352.11 | 118.56 |

| Variable | One Way Anova | West Gulf n=6 | | East Gulf n=5 | | South Atlantic n=6 | | North Atlantic n=5 | |
|---|---|---|---|---|---|---|---|---|---|
| | p-value | Mean | SE | Mean | SE | Mean | SE | Mean | SE |
| Stem-Boring Herbivore Proportion | **0.01** | 0.292 ab | 0.048 | 0.441 a | 0.052 | 0.404 a | 0.048 | 0.203 b | 0.052 |
| Parasitoid | 0.19 | 54.16 | 15.67 | 60.10 | 17.16 | 15.00 | 15.67 | 27.80 | 17.16 |
| Parasitoid Proportion | **0.007** | 0.070 a | 0.009 | 0.056 ab | 0.010 | 0.025 b | 0.009 | 0.021 b | 0.010 |
| Detritivore* | 0.28 | 208.75 | 75.88 | 76.60 | 67.65 | 14.66 | 9.51 | 60.80 | 38.95 |
| Detritivore Proportion* | **0.007** | 0.199 a | 0.052 | 0.046 b | 0.026 | 0.018 b | 0.011 | 0.047 b | 0.028 |

Table 6a. ANOVA values for all variables measured in plots at Atlantic and Gulf Coast field sites during August 2009. Atlantic sites are split into North (Virginia to Maine) and South (Florida to North Carolina) areas. Gulf sites are split into West and East areas (west and east of the Mississippi River, respectively). Significant relationships are indicated in bold font. Tests done with transformed data indicated with an asterisk. When transformations were done, proportional data were arcsine(squareroot(proportion)) transformed, and numerical data were natural log transformed.

| Variable | Area | Fert | Wrack | F*W | Area*Fert | Area*Wrack |
|---|---|---|---|---|---|---|
| Arthropod Total* | **0.03** | 0.98 | **0.02** | **0.01** | 0.88 | 0.90 |
| Predator* | **0.01** | 0.47 | 0.16 | 0.16 | 0.89 | 0.83 |
| Predator Proportion | **0.04** | 0.62 | 0.57 | 0.37 | **0.04** | 0.82 |
| Sucking Herbivore | **0.01** | 0.55 | **0.01** | 0.28 | 0.099 | 0.20 |
| Sucking Herbivore Proportion* | 0.24 | 0.80 | 0.18 | 0.96 | 0.21 | 0.78 |
| Stem-Boring Herbivore* | 0.65 | 0.56 | 0.41 | 0.51 | 0.43 | 0.53 |
| Stem-Boring Herbivore Proportion* | 0.095 | 0.42 | 0.31 | 0.19 | 0.27 | 0.48 |
| Parasitoid | 0.64 | **0.006** | 0.76 | 0.83 | 0.20 | 0.70 |
| Parasitoid Proportion* | **0.007** | **0.005** | 0.89 | **0.02** | 0.54 | 0.26 |
| Detritivore | **0.04** | 0.75 | 0.91 | **0.003** | 0.73 | 0.44 |
| Detritivore Proportion | 0.068 | 0.94 | 0.76 | **0.004** | 0.19 | 0.32 |

Table 6b. ANOVA values for all variables measured in plots at Atlantic and Gulf Coast field sites during August 2010. Atlantic sites are split into North (Virginia to Maine) and South (Florida to North Carolina) areas. Gulf sites are split into West and East areas (west and east of the Mississippi River, respectively). Significant relationships are indicated in bold font. Tests done with transformed data indicated with an asterisk. When transformations were done, proportional data were arcsine(squareroot(proportion)) transformed, and numerical data were natural log transformed.

| Variable | Area | Fert | Wrack | F*W | Area*Fert | Area*Wrack |
|---|---|---|---|---|---|---|
| *Spartina* %Cover | 0.81 | 0.36 | 0.70 | 0.47 | 0.79 | 0.75 |
| Thatch %Cover | **0.0005** | 0.79 | 0.49 | 0.43 | 0.33 | 0.23 |
| *Spartina*:Thatch * | **0.005** | 0.91 | 0.71 | 0.54 | 0.37 | 0.91 |
| Live *Spartina* Height* | **0.03** | **0.01** | 0.070 | 0.33 | 0.10 | 0.59 |
| *Spartina* Biomass Index | **0.006** | **0.001** | 0.45 | 0.72 | 0.74 | 0.59 |
| %PAR Intercepted* | 0.46 | **0.02** | 0.22 | 0.87 | 0.72 | 0.80 |
| Arthropod Total | 0.35 | **0.001** | 0.96 | 0.19 | 0.29 | 0.97 |
| Predator* | 0.68 | **0.001** | 0.45 | 0.27 | 0.85 | 0.50 |
| Predator Proportion* | 0.056 | 0.34 | 0.53 | 0.70 | 0.32 | 0.51 |
| Sucking Herbivore* | 0.38 | **0.01** | 0.18 | 0.17 | 0.59 | 0.49 |
| Sucking Herbivore Proportion* | 0.21 | 0.41 | 0.24 | 0.89 | 0.58 | 0.23 |
| Stem-Boring Herbivore | 0.86 | 0.20 | 0.59 | 0.72 | 0.15 | 0.72 |
| Stem-Boring Herbivore Proportion | 0.19 | 0.32 | 0.24 | 0.10 | **0.004** | 0.30 |
| Parasitoid | 0.18 | **0.04** | 0.69 | 0.83 | 0.44 | 0.90 |
| Parasitoid Proportion | 0.13 | 0.17 | 0.85 | 0.46 | 0.20 | 0.54 |
| Detritivore | 0.80 | 0.066 | 0.23 | 0.81 | **0.01** | 0.46 |
| Detritivore Proportion | 0.28 | 0.52 | 0.30 | 0.41 | **0.02** | 0.70 |

Table 7. Correlations between transect and control variables measured at both Atlantic and Gulf Coast field sites during August 2009 and August 2010. Significant relationships are indicated in bold font.

| | Control v. Transect | |
|---|---|---|
| 2009 Variable | $r^2$ | p-value |
| Arthropod Total | 0.49 | **0.02** |
| Sucking Herbivore | 0.54 | **0.01** |
| Sucking Herbivore Proportion | 0.83 | **<0.0001** |
| Stem-Boring Herbivore | 0.53 | **0.01** |
| Stem-Boring Herbivore Proportion | 0.56 | **0.007** |
| Predator | 0.60 | **0.003** |
| Predator Proportion | 0.69 | **0.0005** |
| Parasitoid | 0.70 | **0.0003** |
| Parasitoid Proportion | 0.46 | **0.03** |
| Detritivore | 0.50 | **0.01** |
| Detritivore Proportion | 0.42 | 0.054 |
| | | |
| 2010 Variable | $r^2$ | p-value |
| Spartina %Cover | 0.63 | **0.004** |
| Thatch %Cover | 0.88 | **<0.0001** |
| Spartina:Thatch | 0.83 | **<0.0001** |
| Live Spartina Height | 0.90 | **<0.0001** |
| Spartina Biomass Index | 0.81 | **<0.0001** |
| %PAR Intercepted | 0.70 | **0.001** |
| Arthropod Total | 0.80 | **<0.0001** |
| Sucking Herbivore | 0.89 | **<0.0001** |
| Sucking Herbivore Proportion | 0.77 | **0.0001** |
| Stem-Boring Herbivore | 0.49 | **0.03** |
| Stem-Boring Herbivore Proportion | 0.43 | 0.062 |
| Predator | 0.70 | **0.0008** |
| Predator Proportion | 0.56 | **0.01** |
| Parasitoid | 0.48 | **0.03** |
| Parasitoid Proportion | 0.85 | **<0.0001** |
| Detritivore | 0.18 | 0.44 |
| Detritivore Proportion | 0.16 | 0.49 |