COMMUNITY STRUCTURE AND FOOD-WEB DYNAMICS IN NORTHEASTERN U.S. TIDAL MARSHES

By

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An Abstract of the Thesis Presented
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Tidal marshes represent one of the most productive natural systems on the globe, but because they are so physiologically stressful, they have low species richness. Consequently, tidal marsh communities are relatively homogenous across large spatial scales. Within saltmarshes, scale-dependent processes and patterns can be identified with the reduction of variation in community dynamics due to low species turnover. I conducted two studies in tidal marshes along the northeastern U.S. coast to explore the abiotic and biotic factors that influence food-web dynamics and community structure. I explored the effect of temporal and spatial variables on community composition of tidal-marsh invertebrates. I found evidence that invertebrate communities are structured primarily by local- and marsh-level variables whereas regional effects were weak. In addition, my results indicated that invertebrate communities may shift in response to accelerated sea-level rise (SLR), potentially affecting biotic feedbacks that normally allow marshes to keep pace with SLR. Secondly, I tested whether saltmarsh birds exert top-down control on local food-webs. I further explored whether the strength or direction of top-down forces changed across spatial or temporal scales. I conducted avian exclosure experiments in eight tidal marshes along a latitudinal gradient and used a multi-trophic level approach to

explore lower-trophic responses to avian exclusion. My results suggest that total invertebrate abundance was most affected by local bird abundance, whereas examining Order-specific responses showed little evidence of spatial variation. Invertebrate response to avian exclusion did not vary across the growing season, but varied year to year. Importantly, plant response was the most consistent across space and time, providing evidence that plant-level measurements may be the best method to reveal the strength and direction of top-down control at large spatial scale. Together, the two studies provide valuable insight into the processes influencing tidal-marsh communities and the scale at which these processes are the most important.

DEDICATION

To my husband

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CHAPTER 1: INTRODUCTION

1.1. Tidal Marsh Ecosystem

Tidal marshes form a natural transition zone between marine and terrestrial communities (Reinold 1977; Mitsch and Gosselink 1993) and comprise only 45,000 km^2 of the earth's surface (Greenberg et al. 2006). Despite their limited extent, tidal marshes act as a buffer against ocean storms and erosion, and provide critical nursery habitat for both marine species and tidal marsh specialists (Daiber 1986, Boesch and Turner 1984, Brown et al. 2002, Greenberg et al. 2006).

As ecotonal systems, tidal marshes are harsh environments for both terrestrial organisms (due to high salinity levels and tidal inundation) (Adam 1990) and marine organisms (due to periodic drying). These physiological challenges, along with resource subsidies from both terrestrial watersheds and marine tidal basins, lead to an ecosystem with low organismal diversity, but high productivity (Kirwan et al. 2009; Wimp et al. 2010). Gradations in these physiological challenges create clear zonation of plant species in low- and high-marsh communities. The low marsh floods during each daily high tide, whereas the high marsh is slightly higher in elevation and floods only during a few tides each lunar cycle. Species that occupy high- and low-marsh zones differ in their ability to tolerate salinity and flooding frequency as well as their ability to compete for space (Bertness 1991; Pennings and Callaway 1992; Pennings et al. 2005). Within tidal marshes in the northeastern U.S., the low marsh is dominated by tall-form *Spartina alterniflora*, whereas the high marsh is characterized by short-form *S. alterniflora*, *S. patens*, *Juncus gerardii*, and *Distichlis spicat*a.

Much like the plant species, tidal marsh animals are characterized by low diversity and high abundance. Among northeastern U.S. marshes, the invertebrate communities include snails, amphipods, and crabs that are important detritivores, whereas insects are the most abundant herbivores (Denno 1977; Denno and Roderick 1990). Herbivorous insects are generally divided into two groups: chewers and sap-feeders, among the common Orders Orthoptera, Thysanoptera, Lepidoptera (larvae), and Hemiptera (Vince et al. 1981). Predators include web-building and hunting spiders along with endemic tidal-marsh birds; including Saltmarsh Sparrow (*Ammodramus caudacutus*) and Seaside Sparrow (*A. maritimus*).

Tidal marshes are predicted to be affected by accelerated sea-level rise (SLR), especially the high-marsh zone that is occupied by species with lower tolerance to flooding and salinity. Indeed, *S. patens* biomass declines when exposed to longer durations of flooding and researchers predict it will experience a linear decline with increased sea-level rise (Smith et al. 2012; Langley et al. 2013; Watson et al. 2016). Interestingly, northeastern tidal marshes have kept pace with sea-level rise for approximately 3,000 years through a combination of elevation gain via peat and sediment accretion (Redfield 1965). Peat accretion is the process of undecomposed plant matter (mostly roots) building up over years (Warren and Niering 1993; Nyman et al. 2006). This plant matter is also important for sediment accretion because it traps sediment and other particulates brought in by the tide (Harrison and Bloom 1977) and over time, the fine particles build up, increasing surface elevation.

Tidal marshes are dynamic systems and their ability to keep pace with accelerated SLR is not independent of the animal communities that occupy the marshes. In southeastern U.S. marshes, herbivores contribute to plant diebacks, resulting in the conversion of marsh to mudflats (Silliman and Zieman 2001; Silliman and Bertness 2002) and reducing the potential of peat and sediment accretion. Tidal-marsh detritivores are not known to greatly reduce peat accretion, but high-marsh zones with greater resilience to erosion are characterized by having higher levels of organic matter in the soil and lower abundance of detritivores (Wigand et al. 2010). Before predictions can be made about tidal marsh resilience to SLR, researchers need a clear understanding of its food-web dynamics to foresee biotic interactions that may negatively affect plant species.

1.2. Food-web Dynamics in Tidal Marshes

Ecologists strive to understand what influences community structure and stability. Consumer-resource interactions control the abundance of organisms at different trophic levels through both direct and indirect effects (Hairston et al. 1960). Systems can be structured by top-down forces, where consumers control the abundances of lower trophic levels, and bottom-up, where primary productivity or detritus availability drives the abundance at all higher trophic levels. Most systems are controlled by the duality of these two forces (Price et al. 1980; Denno and McClure 1983; Hunter and Price 1992; Stiling and Rossi 1997; Denno et al. 2002), but different stressors can reduce or enhance relative importance of top-down and bottom-up forces (Power 1992; Polis and Strong 1996). Understanding the abiotic and biotic gradients that drive spatial and temporal variation in top-down and bottom-up forces is essential to predict shifts in food-web dynamics, especially in a changing environment.

Tidal marshes are often used as a study system to explore food-web concepts because they have low species diversity (Greenberg et al. 2006). Within the high-marsh zone of tidal wetlands in the northeastern U.S., the food chain is a four-tiered system with weak and strong interactions: tertiary consumers (avian predators, spiders), secondary consumers (spiders, omnivorous invertebrates), primary consumers (invertebrate herbivores, detritivores, and omnivores), and primary producers (grasses and rushes).

Biotic interactions (i.e. predator-prey interaction, herbivory pressure) in tidal marshes vary across different spatial and temporal scales. On a regional scale, plant palatability decreases in lower latitudes while herbivory pressure increases (Pennings et al. 2001; Pennings et al. 2009; Schemske et al. 2009). At the marsh scale, top-down forces are stronger in the high marsh whereas low marsh is more affected by bottom-up forces (Denno et al. 2005). Insect phenology and changes in climate variables can affect invertebrate abundances, resulting in potential shifts in predator-prey ratios throughout a growing season and/or between years. For my thesis, I explored the abiotic and biotic factors that influence trophic dynamics of high-marsh communities. First, I explored the spatial and temporal variables driving invertebrate community structure. Second, I tested the top-down control of avian predators on lower trophic levels and identified sources of variation in prey response. For each objective, I related major results to tidal marsh resilience in the face of sea-level rise. For both studies, I conducted surveys and experiments during two growing seasons in tidal marshes along the northeastern U.S. coast to explore the impact of temporal and spatial scales.

CHAPTER 2: EXPLORING THE SPATIAL VARIABLES THAT DRIVE COMMUNITY COMPOSITION OF INVERTEBRATES IN NORTHEASTERN U.S. TIDAL MARSHES

2.1. Abstract

Ecological processes affect community structure at different temporal and spatial scales. Tidal marshes represent a well-studied system where scale-dependent variables drive plant zonation. Conversely, the invertebrate communities that occupy marsh plants are less well-studied and little is known about the patch- and regional-level variables that influence their community composition. I identified temporal and spatial-scale variables that drive community composition of invertebrates occupying *Spartina patens*, a high marsh plant species. During the 2014 and 2015 growing season, I collected invertebrates in seven tidal marshes across the northeastern U.S. coast and used redundancy analysis to reveal the temporal and spatial scales at which tidal-marsh invertebrate communities were structured. The best predictors of the dominant Orders of invertebrates (hemipterans and snails) occurred at the patch (thatch height and channel distance) scale, but not at the regional scale. The relative abundance of snails also was predicted by Julian date. Interestingly at the community level, invertebrate community composition within *S. patens* of the Northeast U.S. appear structured by ecological processes operating at the patch and regional scales. I discuss the implications for these finding on community composition changes as a result of sea-level rise.

2.2. Introduction

Community structure can be driven by mechanisms operating at different spatial scales (Kraft et al. 2011). Latitudinal and elevational trends are documented across the globe

(Jablonski et al. 2006; Moser at el. 2007; Weir and Schluter 2007; McCain and Grytnes 2010; Schemske et al. 2009), and a multitude of smaller scale processes can result in communities that deviate from these known patterns (Okuda et al. 2004; Nogués-Bravo et al. 2008). Because ecological processes affect communities at different scales, the ability to make predictions about the effects of disturbances on communities is difficult without an understanding of the scale at which communities respond to spatial and temporal variables (Okuda et al. 2004).

Tidal marshes are well-suited study systems for testing underlying ecological mechanisms of community diversity and assembly (Pennings et al. 2003). Species composition is relatively homogeneous across a wide range in latitude, and overall diversity is low compared to many other mid-latitude ecosystems (Pennings et al. 2001). Latitudinal trends within tidal marshes exist in plant palatability (Pennings and Silliman 2005), trophic cascade direction (Schemske et al. 2009), and the importance of facilitation (Pennings et al. 2003). Meso-scale differences in climate also can affect marsh communities. Plant species are more productive in marshes with higher temperatures and longer growing seasons (Kirwan et al. 2009), although these increases in productivity run counter to the dominant latitudinal trend in plant species richness for eastern North American saltmarshes, where diversity is highest in the north (Bertness 2007). Evidence of latitudinal trends highlight that tidal marsh communities are influenced by abiotic factors that change over large spatial scales.

Tidal marshes are also structured by local processes. The few plant species that occupy tidal marshes are separated into relatively homogenous zones, driven by well-defined within-marsh patch gradients (Adam 1990; Bertness 2007). Within a given marsh, the number and size of channels can drive plant distribution and species assemblages (Sanderson et al. 2000, 2001). At the patch level, elevation relative to the mean high tide drives plant zonation (Chapman

1960). On the eastern U.S. coast, the low marsh is inundated with water during daily high tides, while the high marsh generally floods for only a few days each month during lunar high tides (Bertness 1992). Plant species are distributed by their ability to tolerate salinity and flooding and by their competitive ability (Gleason and Zieman 1981; Adam 1990; Bertness 1992; Pennings and Callaway 1992; Pennings et al. 2005).

While the ecological mechanisms that drive plant zonation in tidal marshes are well understood at different spatial scales, it is unclear if higher trophic levels exhibit similar patterns, either because of plant zonation or independently due to the same underlying abiotic processes. Evidence for micro-elevational (high versus low marsh) and latitudinal trends exist for some functional and taxonomic invertebrate groups, but not for all (Pennings et al. 2009). Differences in invertebrate communities within marshes are at least partially predicted by species' ability to tolerate salinity, flooding, and plant assemblage (Döbel et al. 1990; Finch et al. 2007; David et al. 2016). At larger scales, chewing herbivores cause greater plant damage in lower latitudes (Pennings and Silliman 2005), but sap-feeders, the most abundant herbivore in tidal-marshes, show no evidence for latitudinal trends in herbivory intensity (Pennings et al. 2009) or changes in density or richness (Andrew and Hughes 2005b).

Similar to the plant community, tidal marsh invertebrates are characterized by low diversity and high abundance. Among northeastern U.S. marshes, snails (Class Gastropoda) and amphipods (Order Amphipoda) are the primary detritivores (Zimmer et al. 2004), whereas insects are the most abundant herbivores (Bertness 2007). Predators include web-building and hunting spiders (Order Araneae) as well as predator specialists, such as egg-predators of sap-feeders (Order Hemiptera). Because tidal marshes are characterized as having relatively simple food webs, many studies have focused on the food-web dynamics of this system (Silliman and

Zieman 2001; Denno et al. 2002; Finke and Denno 2002, 2006; Silliman and Bertness 2002; Langellotto and Denno 2004; Pennings and Silliman 2005; Wimp et al. 2010; Wimp et al. 2011), but few have explored the environmental factors that structure the community as a whole (Levin and Talley 2000; Pétillon et al. 2008). In addition, most tidal-marsh studies occur in *Spartina alterniflora*, the dominant plant of the low marsh along the Atlantic Coastline (Adam 1990; Denno et al. 1996). Along the coast of the northeastern U.S., *Spartina patens*, a foundation species (Gedan and Bertness 2010; Watson et al. 2016), occupies the high marsh by outcompeting *S. alterniflora* for higher elevation and reduced tidal action (Bertness 1991). Information about ecological process in *S. alterniflora* dominated systems may not, however, apply to *S. patens*. For example, runaway herbivory can cause *S. alterniflora* dieback (Silliman and Zieman 2001; Silliman and Bertness 2002), while experimental and field studies find little evidence for similar trophic cascades in *S. patens* (Pennings and Silliman 2005).

Spartina patens modifies the abiotic environment by reducing salinity and increasing moisture levels through shading (Gedan and Bertness 2010; Watson et al. 2016). In addition, this grass is a main contributor to peat accumulation and encourages sediment deposition, processes that allow tidal marshes to keep pace with sea-level rise through vertical accretion (Redfield 1965). Unfortunately, *S. patens* is predicted to decline with accelerated sea-level rise, due to prolonged flooding in the high marsh (Gleason and Zieman 1981; Warren and Niering 1993; Watson et al. 2016). In addition, higher sea-levels have allowed marine herbivores to migrate and colonize *S. patens* dominated areas and led to lower S. *patens* stem density (Smith et al. 2012). Together these changes could alter a marsh's ability to accrete in the face of sea-level rise. Understanding the scale at which environmental features drive invertebrate community structure is necessary to predict invertebrate community dynamics in a changing coastal landscape and will help us understand how community structure operates more broadly. Here, I compare the ability of marsh patch- and regional-scale variables to predict invertebrate community composition across a 1200 km transect in *S. patens*-dominated high marshes.

2.3. Methods

In 2014 and 2015, I collected invertebrates at seven tidal marshes along the northeastern U.S. coast, from Maine to New Jersey (Table 2.1). These sites describe a 1200 km long transect (600 km in a straight line from the two most distant sites) along the coast, oriented approximately north to south. This study is an extension of an experiment conducted at each selected marsh (Chapter 3) and study sites were selected in proximity to that experiment's location. At each site, I selected a *S. patens*-dominated area and sampled a 4 x 4 m plot in 2014. In 2015, I selected new study plots in unsampled areas within 25 m of the 2014 plots. At the Sachuest Point National Wildlife Refuge (NWR) study site, the second plot was located approximately 325 m away due to the scarcity of *S. patens* dominated area in the marsh.

2.3.1. Invertebrate sampling

In my study, I use community composition as a metric to understand the factors that drive community structure. To explore temporal variation in community composition, I sampled invertebrates approximately once every month at each study plot from May to September for a total of four sampling periods per site per year. I divided the 4 x 4 m sampling area into a grid with 16, 1 x 1 m blocks. For each sampling event, I sampled three randomly selected blocks, and no block was sampled twice in a season.

Table 2.1: Location of study plots and associated spatial parameters for exploring scale-dependent predictors of invertebrate community composition in seven tidal marshes along the northeastern U.S. coast, 2014 - 2015.

Study Plot	Town	State	Latitude (decimal degrees)	Average Thatch Height (cm)	Channel Distance (m)	Average Summer Precipitation (in)[a]
Scarborough Marsh[b]	Scarborough	ME	43.572142	5.60	101	17.63
Nonesuch Marsh[b]	Scarborough	ME	43.554047	5.31	346	17.63
Wells Marsh[c]	Wells	ME	43.290931	9.13	537	12.45
Chapman's Landing[d]	Stratham	NH	43.039319	7.83	153	13.38
Sachuest Marsh[e]	Middletown	RI	41.487681	7.33	300	11.37
Hammonasset Marsh[f]	Madison	CT	41.258208	6.75	23	8.31
Forsythe Marsh[g]	Smithville	NJ	39.501256	7.83	508	17.93

[a] Average summer precipitation was calculated from total rainfall from May to September and averaged between years.

[b] Maine Department of Inland Fisheries and Wildlife

[c] Rachel Carson National Wildlife Refuge (NWR)

[d] New Hampshire Fish and Game Dept. Great Bay Reserve

[e] Sachuest Point NWR

[f] Connecticut Department of Energy and Environmental Protection

[g] Edwin B. Forsythe NWR

For invertebrate collection, I used a leaf blower in reverse with a paint thinner bag attached to the end of the hose to catch vacuumed invertebrates. Within a cylindrical sampling frame (height = 50.8 cm, diameter = 66 cm), the leaf blower sampled invertebrates for two minutes while the operator simultaneously disturbed the plant substrate to dislodge individuals. Collected invertebrates were immediately placed in plastic bags and then sprayed with a broad-spectrum insecticide. I stored invertebrates in a freezer until processing. Once in the laboratory, I used 1 mm sieves to separate invertebrates from vegetation. After separation, I identified individuals to Order (Arthropoda) or Class (Mollusca). For each sampling period, I averaged across the three samples for each site for a total of 56 samples (2014 and 2015 combined).

2.3.2. Temporal and spatial variables

To understand how tidal-marsh invertebrate communities are structured across the landscape, I identified environmental and habitat variables as potential predictors of community composition and categorized them as regional or patch scale. Patch-level variables change within a marsh and are similar to site features while the regional scale represent variables that change across Northeast U.S. area. I estimated and assigned all candidate predictive variables at the site-scale, despite my hypotheses that their influence on the invertebrate community operated at different scales. My reasons for this were two-fold. First, I did not want the values to be nested in their ability to describe variation, such that the scale of their assignment would alter their ability to correlate with community variation. For instance, if the value of some variables varied by patches, sites, and broad regions, while others varied only by sites or by regions (but all patches received the same value), one might predict *a priori* that even randomly generated covariates varying at all three scales would be more likely to predict changes in community composition varying at all three scales. Second, I gathered some covariates (e.g., thatch depth) separately for each year, while others (e.g., latitude) did not vary between years. In a similar way to the scale of spatial variation, one might expect covariates with finer temporal resolution to be more likely to predict invertebrate communities that possessed interannual variation. By calculating site-specific values for all candidate predictors and averaging them across years, I was able to compare the ability for different scales to predict community assembly (because each variable had a hypothesized scale of ecological process underlying it), without biasing the results toward predictors that more closely matched the sampling regime.

For my regional-scale level, I tested for the influence of latitude and summer precipitation. Latitude is a proxy for many abiotic factors with broad regional gradients that influence invertebrate community composition, including temperature and seasonality (Musolin 2007; Deutsch et al. 2008). I tested for both linear and quadratic trends of latitude after initial data exploration indicated that total raw invertebrate abundance peaked mid-latitude of the study area. For an estimate of total rainfall during the growing season for each site, I combined total rainfall in the months of May through September (records retrieved from the nearest weather station, http://www.weather.com) for each of the two sampling years and averaged between years. This approach only includes precipitation that would most likely influence community structure when invertebrates are active. *S. patens* is occupied by terrestrial invertebrates that require freshwater to survive (Foster 2002), and variability in rainfall could structure invertebrate communities.

At the marsh-patch scale, I estimated distance from each sampled patch to the nearest tidal channel (hereafter, channel distance). Sites situated nearer to a channel may be inundated for a longer period during lunar high tides compared to those farther from the channel that begin to drain soon after the tide ebbs (Sanderson et al. 2000, 2001). Conversely, floods provide valuable nutrient input from the marine system that increases plant quality and provides a benefit to the marsh due to bottom-up forces (Odum et al. 1995). To calculate a single channel distance for each site (i.e., patch), I used ArcMap 10.0 and the measure tool to calculate the distance from an area in between 2014 and 2015 study plots to the nearest channel edge. For the 2015 Sachuest Marsh plot (i.e., the only site where patches were more than 25 m distant from each other), I erected the plot in a patch approximately the same distance from the channel as the 2014 plot. This similar channel distance was assigned to both 2014 and 2015 plots at this marsh.

Thatch, the dead plant material from last year's growth, is an important predictor of habitat complexity, and it varies widely across a given marsh (Denno et al. 1996). *S. patens* thatch lies mostly horizontally and provides architectural complexity for invertebrate habitat (Finke and Denno 2002, 2006). With increased habitat complexity, predators and prey increase in abundance due to increased niche space and ability to avoid detection (Finke and Denno 2002, 2006; Langellotto & Denno 2006; Kovalenko et al. 2012). For this patch-level variable, I measured maximum thatch depth within each 1 m^2 sample block at each visit and averaged the measurements across sampling periods and years to assign a site-level value.

Invertebrate phenology can influence community composition when different taxa peak in abundance at different times. Insect abundance generally peaks in mid to late-summer months and can be a major driver of community differences (Bertness et al. 1987; Denno and Roderick 1990; Wimp et al. 2010). To control for this variability, I included Julian date (calendar day) of sampling. All spatial and temporal variables were scaled to allow for comparison of coefficient estimates and to compare their relative strength in predicting community structure. In addition, I tested for correlation among potential predictor variables by running Spearman's rank-order correlation tests between each potential predictor and found all variables were at most weakly correlated (all $r_s < 0.50$).

2.3.3. Statistical analysis

Constrained ordination techniques can explore the relationship between potential predictor variables and community structure (Legendre and Legendre 2012). To test for the ability of variables representing ecological processes at different scales to predict community composition, I first used a redundancy analysis (RDA). I then used three multiple linear regressions (once for each of the dominate Orders, as identified by high percentage of total abundance of all samples, Table 2.2) to estimate relative effect sizes of the correlated spatial and temporal variables revealed by the RDA. Finally, because all potential predictors were only unique to site, I determined whether highly ranked predictors were just those that could differentiate among the most unique sites. All analyses were conducted in Program R (R Core Team 2016, version 3.3.1).

The RDA constrains ordination axes in community data by their relationships with independent variables to maximize correlation (Manly 2005,) in a method similar to multivariate regression. Essentially, RDA is a tool to identify the most influential abiotic and/or environmental variables on community composition. For analysis, I used a Hellinger transformation on community abundance data to redefine sample counts as relative abundance and reduce the potential influence of large abundances and zeros (Legendre and Gallagher 2001). I conducted an RDA in Program R using the vegan package (Oksanen et al. 2015) and tested for single-term significance using Monte Carlo tests (999 permutations). In addition, I investigated the correlation of temporal and spatial variables to the relative abundance of Orders using the canonical coefficients and the vector length and angle projected on the biplot (Manly 2005).

For Orders showing strong correlations with predictor variables in the RDA, I ran multiple linear regressions *post hoc* to estimate the variance explained by and the effect size of the correlated temporal and spatial variables on the Orders' relative abundance. I ran separate multiple linear regressions, ("lm" function in base R), with their relative abundance (calculated for each sample) as the dependent variable. If an Order's relative abundance was not normally distributed, I logarithm (plus 0.001) transformed or square-root transformed the relative abundance, depending on which transformation best satisfied the normality assumption. In addition, I ran a series of simple and multiple linear regressions to investigate the ability of single variables to predict relative abundance independently and to test the potential influence of particular sites on model estimates for their respective Order. First, I compared the predictive ability of the best set of independent variables by running simple regressions with each Order's correlated variables. Second, I ran each of the full multiple regression models with the best set of independent variables, removing one site during each run to assess the direction, size, and significance of coefficients when certain sites are remove.

An assumption of linear regression is that errors are independent, but this study's dataset has nested samples (sampling periods and patches nested within marshes). In an ordinary least squares (OLS) framework, the coefficient sizes are unbiased (Draper 1998), but the standard errors are frequently underestimated (Millar and Anderson 2004). I recalculated standard errors by "clustering" the errors by site. This post-regression estimate accounts for errors being correlated among sites (i.e., marshes) and assumes independence between sites (Liang and Zeger 1986, Cameron and Miller 2015). The cluster-robust standard errors are more conservative, but control for Type I errors with nested data. They also account for lack of independence, justifying the avoidance of a linear mixed-model framework in which the random effect, site, would consume much of the variation and potentially mask the site-specific variables' prediction power (Oksanen 2001). The cluster-robust standard errors were calculated for every regression that follows. *P*-value adjustments were not used throughout the analysis because cluster-robust standard errors have been shown to have a rejection rate of 0.11 in simulations with six cluster levels (Bertrand et al. 2004), and *P*-value adjustments would most likely increase the chance of false negatives (Feise 2002).

2.4. Results

In total, I collected 31,165 invertebrates from 11 different taxonomic groups (Table 2.2). Snails were the only Gastropods sampled, and for simplicity, will be referred to simply as "snails" hereafter. Order Hemiptera had the greatest number of individuals and comprised 65% of the total abundance of all invertebrates, followed by Araneae (10.9%), Amphipoda (7.5%), Snails (5.4%), and Diptera (5.2%). The other five Orders made up less than 5% of the total abundance. Order Hemiptera was the dominant Order (relative abundance > 0.50) in 27 of the 56 samples and although I did not identify lower than Order, sap-feeders were by far the most abundant hemipterans. Orders Amphipoda and Diptera each were only dominant in one sample while Snails were dominant in two samples.

The RDA revealed that community composition was significantly related to channel distance, average summer precipitation, average thatch height, and Julian date. Further, the Monte Carlo permutation test revealed that community composition was correlated with a quadratic (each with $P<0.01$; Table 2.3), but not linear ($P>0.05$) term for latitude (adjusted $R^2 = 0.26$). The first RDA axis explained 62% of the variance, and the first two axes explained 82%. The biplot reveals that thatch and latitude^2 were positively correlated with Order Hemiptera (Figure 2.1). Channel distance, Julian date, and precipitation are negatively correlated with snails. Orders Amphipoda, Araneae, and Diptera were correlated with each other and weakly,

Table 2.2: Invertebrate relative abundance at study plots in seven tidal marshes along the northeastern U.S. coast, 2014 - 2015.

Study Plot[a]	Hemiptera	Snail	Amphipoda	Araneae	Diptera	Coleoptera	Isopoda	Orthoptera	Hymenoptera	Thysanoptera	Pseudoscorpionida
2014											
Scarborough	0.510	0.021	0.040	0.180	0.150	0.005	0.076	0.011	0.006	0.000	0.000
Nonesuch	0.476	0.002	0.177	0.168	0.074	0.023	0.057	0.017	0.006	0.000	0.000
Wells	0.788	0.013	0.030	0.083	0.027	0.011	0.028	0.003	0.016	0.000	0.000
Chapman’s	0.512	0.016	0.028	0.173	0.212	0.007	0.011	0.028	0.013	0.000	0.000
Sachuest	0.120	0.005	0.449	0.267	0.110	0.029	0.001	0.002	0.016	0.001	0.001
Hammonasset	0.545	0.130	0.115	0.127	0.029	0.015	0.032	0.001	0.006	0.000	0.000
Forsythe	0.758	0.011	0.037	0.097	0.027	0.022	0.030	0.009	0.007	0.002	0.001
2015											
Scarborough	0.607	0.026	0.019	0.220	0.070	0.011	0.020	0.024	0.002	0.000	0.000
Nonesuch	0.393	0.006	0.313	0.197	0.057	0.018	0.011	0.000	0.004	0.002	0.000
Wells	0.881	0.001	0.020	0.040	0.017	0.006	0.023	0.009	0.001	0.003	0.000
Chapman’s	0.765	0.019	0.066	0.094	0.008	0.004	0.008	0.033	0.002	0.000	0.000
Sachuest	0.236	0.004	0.197	0.330	0.189	0.021	0.000	0.000	0.005	0.000	0.018
Hammonasset	0.318	0.396	0.039	0.066	0.043	0.005	0.055	0.065	0.008	0.004	0.000
Forsythe	0.661	0.002	0.018	0.085	0.082	0.015	0.044	0.088	0.004	0.000	0.001

[a] Study plots arranged in order from high to low latitude.

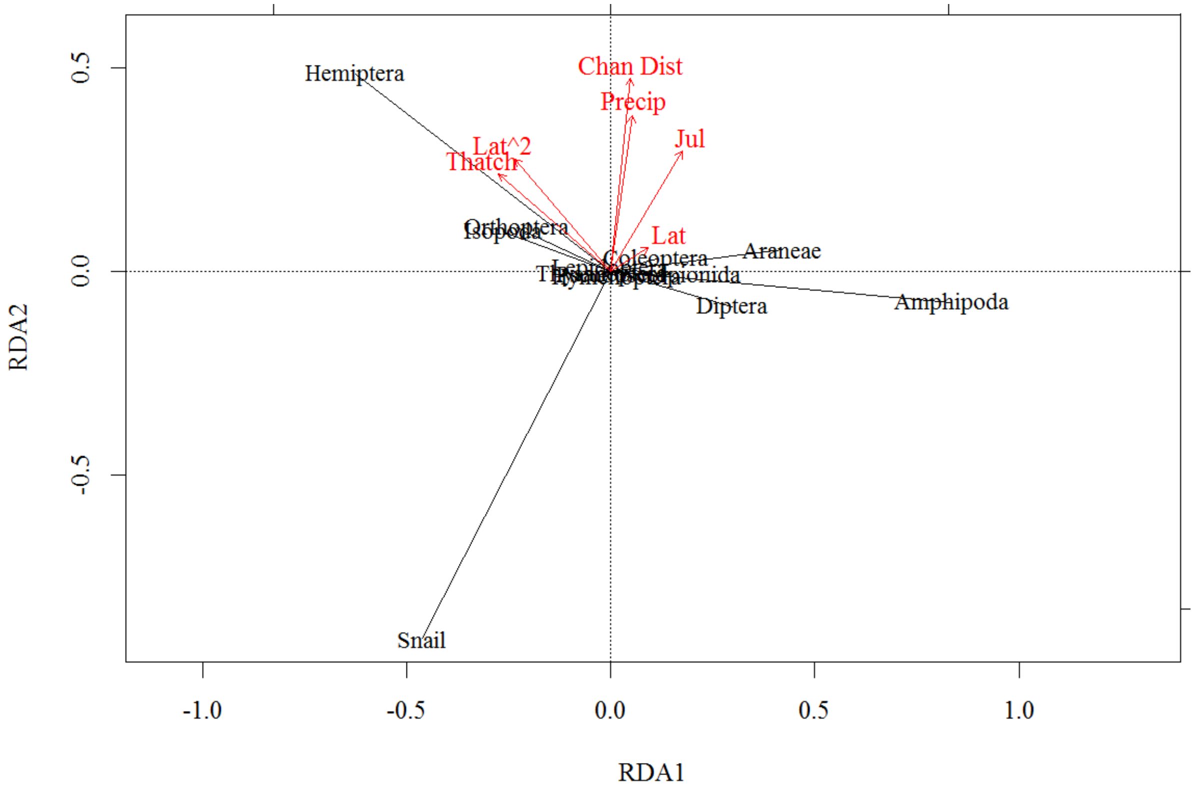

Figure 2.1: Redundancy analysis (RDA) biplot of invertebrate community composition in seven tidal marshes along the northeastern U.S. coast, 2014 - 2015. Red lines represent biplot values for temporal and spatial variables and black lines are for Orders/Class.

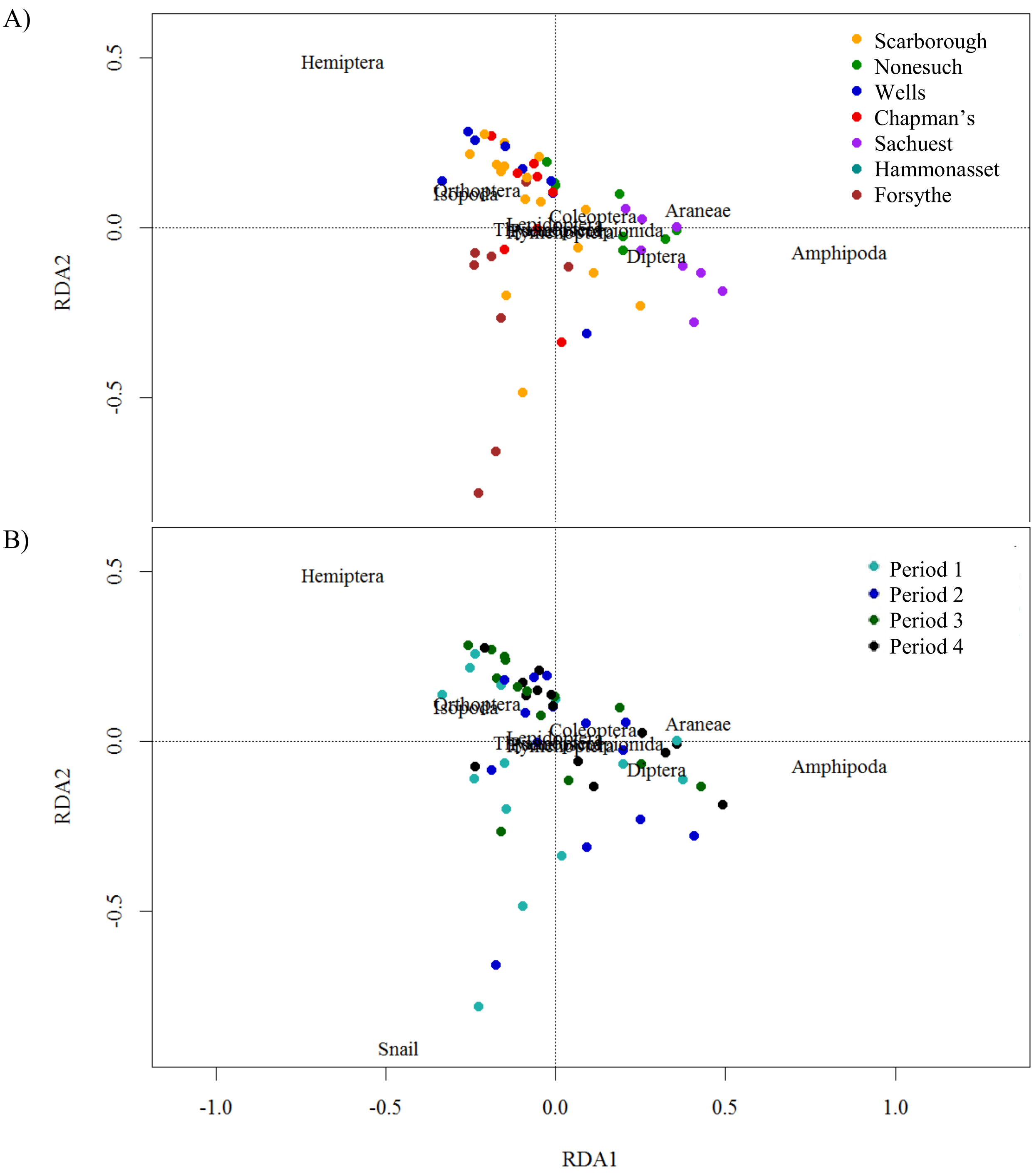

Figure 2.2: Redundancy analysis (RDA) biplots depicting each site (A) and sampling period (B) and Order/Class relationship of invertebrate community composition in seven tidal marshes along the northeastern U.S. coast, 2014 - 2015. A). Study plots are ordered from high to low latitude. B). The first sampling period occurred in May or early June and the last sampling period occurred in late August, early September.

negatively correlated with latitude^2 and thatch. Because hemipterans, amphipods, and snails were the three most dominant Orders and occupied different areas in ordination space (Figure 2.1), I ran individual multiple linear regressions with their respective relative abundance as the dependent variables and their correlated spatial and temporal variables (identified by the RDA biplots) as independent variables.

In univariate regressions, thatch consistently predicted the relative abundance of Order Hemiptera, while latitude (quadratic and linear terms) did not (Table 2.4). In the multiple regression, Order Hemiptera was more dominant at taller thatch heights ($\beta = 0.12$, $P<0.001$) and had a positive, but not significant quadratic and linear relationships with latitude ($\beta = 0.12$, $P=0.06$; $\beta = 0.12$, $P=0.12$, respectively; adjusted $R^2 = 0.21$; Table 2.4). In the simple regression, thatch was still positively related to Order Hemiptera ($\beta = 0.10$, $P<0.001$), but explained a smaller amount of variance without latitude (adjusted $R^2 = 0.11$; Table 2.5). In addition, simple regressions again showed that latitude (quadratic and linear terms) was not a significant predictor of hemipteran relative abundance ($\beta = 0.06$, $P=0.06$; $\beta = 0.10$, $P=0.12$, respectively; Table 2.5).

Relative abundance of snails was logarithm transformed to meet assumption of normality. In the multiple regression, snail relative abundance decreased with increasing channel distance ($\beta = -0.30$, $P=0.008$) and Julian date ($\beta = -0.26$, $P=0.02$), but did not have a significant relationship with precipitation ($\beta = -0.23$, $P=0.12$; adjusted $R^2 = 0.29$; Table 2.4). In the simple regressions, channel distance and Julian date were significant predictors, but precipitation was not (Channel Distance, $\beta = -0.38$, $P=0.04$; Julian, $\beta = -0.26$, $P=0.02$; Precipitation $\beta = -0.32$, $P=0.14$; Table 2.5). Channel distance alone explained the most variance (adjusted $R^2 = 0.17$), followed by precipitation and Julian date (adjusted $R^2 = 0.12$; adjusted $R^2 = 0.07$, respectively; Table 2.5).

Table 2.3: Parameter significance from Monte Carlo permutation tests for exploring the correlation of tidal-marsh invertebrate community composition with spatial and temporal variables along the northeastern U.S. coast, 2014 - 2015.

Parameter	F	*P*
Latitude (linear)	0.79	0.52
Latitude (quadratic)	10.63	<0.01
Thatch	3.22	<0.01
Precipitation	4.03	<0.01
Julian Date	2.95	<0.01
Channel Distance	4.14	<0.01

Table 2.4: Parameter estimates from multiple linear regressions for temporal and spatial scale predictors describing relative abundance from seven tidal marshes along the northeastern U.S. coast, 2014 – 2015.

Parameter	Estimate	SE	*P*
Hemiptera[a]			
Intercept	0.32	0.10	<0.001
Thatch	0.12	0.02	<0.001
Latitude (linear)	0.12	0.07	0.12
Latitude (quadratic)	0.12	0.06	0.06
Snail[b]			
Intercept	-2.05	0.14	<0.001
Channel Distance	-0.30	0.11	<0.01
Julian	-0.26	0.11	0.02
Precipitation	-0.23	0.14	0.12
Amphipoda[c]			
Intercept	0.36	0.11	0.003
Thatch	-0.07	0.04	0.07
Latitude (linear)	-0.08	0.09	0.38
Latitude (quadratic)	-0.08	0.07	0.32

[a] Hemipteran model explained 21% of the variance (adjusted $R^2 = 0.21$)

[b] Snail model explained 29% of the variance (adjusted $R^2 = 0.29$)

[c] Amphipod model explained 13% of the variance (adjusted $R^2 = 0.13$)

Table 2.5: Simple linear regressions for temporal and spatial scale predictors for hemipteran, snail, and amphipod relative abundance from seven tidal marshes along the northeastern U.S. coast, 2014 – 2015.

Model	Parameter Estimate (±SE)[a]	Adjusted R^2
Hemiptera ~ Thatch	**0.10 (±0.02)**	0.11
Hemiptera ~ Latitude (linear)	-0.01 (±0.06)	<0.01
Hemiptera ~ Latitude (quadratic)	0.06 (±0.03)	0.04
Snail ~ Channel Distance	**-0.38 (±0.18)**	0.17
Snail ~ Julian	**-0.26 (±0.10)**	0.07
Snail ~ Precipitation	-0.32 (±0.21)	0.12
Amphipoda ~ Thatch	-0.06 (±0.04)	0.06
Amphipoda ~ Latitude (linear)	0.00 (±0.05)	<0.01
Amphipoda ~ Latitude (quadratic)	-0.03 (±0.03)	0.01

[a] Significant parameters are bolded (*P*<0.05).

Table 2.6: Parameter estimates from multiple linear regressions to explore site influence on temporal and spatial scale predictors for hemipteran and snail relative abundance from seven tidal marshes along the northeastern U.S. coast, 2014 – 2015.

	Hemiptera[a]			Snail[a]		
Study Plot Removed[b,c]	Thatch	Latitude (linear)	Latitude (quadratic)	Channel Distance	Julian Date	Precipitation
Scarborough	**0.10**	0.09	0.12	**-0.28**	-0.19	-0.24
Nonesuch	**0.10**	0.08	0.12	**-0.32**	**-0.27**	-0.17
Wells	0.10	0.09	0.13	-0.29	**-0.28**	-0.22
Chapman’s	**0.12**	0.09	0.14	**-0.34**	-0.22	-0.24
Sachuest	**0.13**	0.04	0.04	**-0.27**	**-0.33**	**-0.33**
Hammonasset	**0.16**	**0.27**	**0.21**	-0.12	**-0.26**	-0.01
Forsythe	**0.15**	0.18	0.13	**-0.39**	**-0.32**	**-0.31**

[a] Significant fixed effects in relative abundance models are in bold (*P*<0.05).

[b] Study plots were removed one at a time and parameter estimate for fixed effects are listed.

[c] Study plots arranged in order from high to low latitude.

Relative abundance of amphipods was square-root transformed to satisfy the normality assumption for linear regressions. In the multiple regression model for amphipods, latitude (linear and quadratic terms) and thatch height were not significant predictors of relative abundance (β = -0.08, *P*=0.38; β = -0.07, *P*=0.32; β = -0.07, *P*=0.07, respectively; Table 2.4). In addition, the three variables lacked the ability to predict amphipod relative abundance in each of their respective simple regression (Thatch, β = -0.06, *P*=0.15; Latitude, β = -0.002, *P*=0.95; Latitude^2, β = -0.03, *P*=0.24; Table 2.6).

When certain sites were removed from regression models of relative-abundance for specific Orders, the direction of parameter estimates was consistent for all predictors, but significance of the predictors changed depending on the site removed (Table 2.6). Site had a small effect on the predictors of relative abundance of hemipterans, whereas it had a larger influence on the predictors of snail relative abundance. Thatch was consistent in significantly predicting Hemiptera relative abundance, while latitude (linear and quadratic terms) were not. Channel distance and Julian date were significant predictors in 5 out the 7 tests while precipitation was only significant in 2 out the 7.

2.5. Discussion

The tidal-marsh invertebrate communities that occupy *S. patens* are structured by regional- and patch-level ecological processes. Patch-level (thatch height and channel distance) gradients were the best predictors of the relative abundance of dominant Orders, while latitude (regional-level) was only important when predicting the invertebrate community as a whole. Hemipterans, the most abundant Order and herbivorous group, increased with taller thatch heights whereas relative abundance of snails correlated with patch-level features and were also the only taxonomic group to be correlated with the temporal gradient. Orders Amphipoda, Diptera, and Araneae were similar in that their relative abundance was correlated only weakly with temporal and spatial scales, indicating that the candidate variables were poor predictors for their relative abundance and/or that underlying biotic influences are stronger than the spatial and temporal variables included.

The RDA and regression analyses revealed that thatch height was consistently important for hemipterans, more than the quadratic relationship with latitude (a proxy for temperature and many other abiotic factors). Increased habitat complexity reduces predator-prey interactions and promotes food web stability (Kovalenko et al. 2012). Indeed, richness and diversity of sap-feeders (herbivorous hemipterans) increase with increased habitat complexity (Denno and Roderick 1990). Conversely, thatch complexity can strengthen top-down control on hemipterans in *S. alterniflora* food webs by decreasing intraguild predation (e.g. adult spiders consuming juvenile spiders: Finke and Denno 2002, 2006; Langellotto & Denno 2006) and increasing predation pressure on sap-feeders (Finke and Denno 2006). If this pattern was true at the study sites, one would expect the relative abundance of spiders, the top predators of sap-feeders (Döbel et al. 1990; Döbel and Denno 1994; Wimp et al. 2011), to be positively correlated with thatch height and for Order Hemiptera to be either negatively correlated or have no correlation with thatch height. However, the RDA showed no evidence of this. The importance of thatch height may be an artifact of correlations with last year's plant biomass, but this is unlikely because hemipterans had a weak relationship with latitude, which is correlated with productivity (Kirwan et al. 2009). In addition, fertilizer experiments, resulting in greater plant biomass, result in greater increases in spider populations than herbivores (Wimp et al. 2010). The importance of thatch height is more likely due to habitat complexity and decreases in predation than changes in food availability.

Abundance and richness of tidal-marsh spiders are affected by elevation (Döbel et al. 1990; Denno and Peterson 2000), vegetation composition and structure, (Döbel et al. 1990; Finch et al. 2007), and salinity (Desender and Maelfait 1999; Pétillon et al. 2008). Unlike the other Orders (including Hemiptera), spiders occupied every site during each sampling period, indicating that regional and temporal scales did not drive their occupancy in this study. The abundance of hunting spiders in *S. patens* varies within time as individuals migrate from upland habitats into the high and low marsh (increasing May through September) and recolonization after high tides (Denno et al. 2003). Identifying spiders to lower taxonomic levels and separating by size class and functional type are likely necessary to elucidate the abiotic covariates of Araneae abundance in *S. patens* across a latitudinal gradient.

Similar to spiders, results from Order Amphipoda were not correlated with either temporal or spatial scales. The two sites with the highest relative abundance of amphipods were the Sachuest Point NWR (Rhode Island) and Nonesuch Marsh (Maine) (Figure 2.2), suggesting that amphipod relative abundance is not governed by simple regional factors. Amphipods are common detritivores in tidal marsh systems and associated with thatch-producing marsh plant species (Desender and Maelfait 1999). In high densities, adult amphipods will outcompete juveniles, resulting in age-class structure skewed to an abundance of older individuals (van Dolah 1978). The lack of correlation with thatch (their preferred food source, Rietsma et al. 1982) may result from amphipod relative abundance remaining constant, but the population being made up of larger body-sized individuals.

Snails, which are mainly detritivores in *S. patens* (Rietsma et al. 1982; Kneib 1984; Zimmer et al. 2004), were strongly correlated with temporal and marsh-level scales. Snail relative abundance was negatively correlated with Julian date (Figure 2.1), indicating that communities were more snail dominant earlier in the season than later (Figure 2.2). This may be due more to insect phenology than any absolute decrease in snails through time. Indeed, in May through mid-June, many hemipteran species are still in the nymph stage (Raupp and Denno 1979; Denno and Roderick 1990) and may have been too small to capture. In addition, snail relative abundance was negatively correlated with channel distance, indicating that snails are more successful in areas that are flooded longer. For example, *Melampus bidentatu*, the coffee bean snail, is an abundant detritivore found primarily in *S. patens* (Rietsma et al. 1982; Zimmer et al. 2004), and has a large range of tolerances to salinity, time submerged, and temperature (Kneib 1984). Their response to channel distance may reflect their greater ability to tolerate flooding compared to the other invertebrates inhabiting *S. patens*.

At the regional scale, latitude had at most a weak relationship with a single Order, only after controlling for thatch height (Hemiptera: Table 2.3, 4). Latitude is a proxy for many abiotic variables that increase or decrease along the northeastern U.S. coast, including temperature, season length, tide height, marsh size, and productivity (Kirwan et al. 2009; McCall and Pennings 2012). The lack of a latitudinal gradient in community composition was surprising, given other studies have found latitudinal trends in biotic interactions in tidal marshes (Pennings et al. 2001; Pennings et al. 2009; Schemske et al. 2009). In addition, raw abundance revealed a quadratic relationship with latitude, but all Orders increased relatively the same amount, with community composition changing only slightly. Other tidal marsh and coastal studies found similar results where latitude was not important in predicting invertebrate community structure after controlling for plant species (Andrew and Hughes 2005a, b) or including different scale-dependent variables (David et al. 2016). Precipitation, another regional-scale variable, only had a weak relationship with snails and lacked the ability to predict their relative abundance. The consistency of thatch height, channel distance, and Julian date in predicting the relative abundance of their respective Order/Class (Figure 2.2) provide evidence that tidal marsh invertebrates are structured more strongly by patch-level than regional scales after controlling for plant species.

2.5.1. Implications for sea-level rise

S. patens is a foundation species that provides habitat for many of the terrestrial invertebrates that have less tolerance for salinity and tidal action than invertebrates occupying mid to low marsh. Unfortunately, plant surveys in tidal marshes revealed that *S. patens* is declining and being replaced by short form *S. alterniflora* (Warren and Niering 1993) and predicted to continue to do so with accelerating sea-level rise (Watson et al. 2016). My results indicate that this herbivore (hemipterans) dominated community will decline with the decline in *S. patens*, in response to the reduction of thatch. Possibly, this community will be replaced with a more detritivore-dominated community.

Snails are tolerant of flooding and salinity, allowing them to occupy areas closer to channels. In addition, amphipods were not correlated with channel distance and different species occupy high and low marsh, implying that amphipod density will not fluctuate greatly with sea-level rise and a conversion to lower marsh. Importantly, both detritivores will be present in areas of stressed *S. patens* (submerged longer) and available to break down detritus. There is no evidence that tidal-marsh invertebrates greatly reduce the thatch layer, but the increased relative abundance of detritivores in areas of stressed *S. patens* may negatively affect peat and sediment accretion in a way not seen before. Given the lack of regional controls on the invertebrate community reported here, the community shift and potential impacts on marsh elevation should be similar across the northeastern U.S. Coast. The greater patch-level influence on invertebrate-specific relative abundances, however, suggests that local management actions may have the potential to achieve desired changes to tidal-marsh food webs.

CHAPTER 3: SPATIAL AND TEMPORAL VARIATION IN THE RESPONSE OF LOWER TROPHIC LEVELS TO AVIAN EXCLUSION

3.1. Abstract

Avian exclosure experiments are useful for measuring the impact of avian predators on lower trophic levels. Despite mounting evidence that excluding insectivorous birds increases arthropod abundance and decreases plant damage, individual experiments still show large variation in arthropod and plant response, making generalized conclusions about ecosystem processes difficult. I conducted a large-scale, multi-year avian exclosure experiment in tidal marshes across the northeastern U.S. coast to identify how avian influences on invertebrates varies in space and time. My study overlapped with the range and breeding habitat of Saltmarsh Sparrows (*Ammodramus caudacutus*), an invertivore with rapidly declining populations. Local bird abundance was the main driver of variation in the response of total invertebrate abundance to avian exclusion. Plant biomass, however, increased consistently with avian exclusion across space and time. The increase in plant biomass is contrary to most exclosure studies and suggests the indirect actions of intermediate trophic levels. The effect of exclosures on individual invertebrate Orders varied temporally (Amphipoda), but not spatially. Time of year and latitude were strong predictors of abundance for multiple invertebrate Orders, but were unrelated to the effect of avian exclosures. The results reemphasize the need for spatially and temporally replicated models, and provide the first evidence that the functional loss of tidal marsh birds will influence food-web dynamics and primary marsh productivity in northeastern U.S. marshes.

3.2. Introduction

Within the past few decades, avian exclosure experiments have shown the importance of avian invertivores in controlling arthropod abundances (Holmes et al. 1979; Greenberg et al. 2000; Perfecto et al. 2004; Philpott et al. 2004; Van Bael and Brawn 2005; Van Bael et al. 2008) and reducing vegetation damage (Atlegrim 1989; Greenberg et al. 2000; Sanz 2001; Hooks et al. 2003; Van Bael et al. 2003, 2008; Mäntylä et al. 2011). Indeed, a meta-analysis by Mäntylä et al. (2011) found that bird presence is positively associated with plant biomass and negatively associated with leaf damage and plant mortality. The majority of studies included in this meta-analysis were exclosure experiments conducted across many natural and agricultural ecosystems from diverse regions around the world (e.g. Finland, Panama). The indirect effects of avian absence to primary producers appear consistent across large spatial scales.

At smaller spatial scales, however, individual exclosure studies exhibit high variability in invertebrate response across space and time (Joern 1992; Branson 2005; Van Bael and Brawn 2005; Barber and Marquis 2009). Branson (2005) conducted an avian exclosure experiment at two different mixed grassland sites (~200 km distance between sites). Over three years, the exclusion of avian insectivores affected grasshopper communities differently in both the direction and strength of the effect depending on the year and site. Even in a study with greater spatial replication that controlled for site variation, the strength of arthropod response varied over time and among sites, with no consistent effect on herbivores overall (Barber and Marquis 2009). Despite this variability in both strength and direction on herbivores, avian exclusion significantly decreased leaf damage across all sites (Barber and Marquis 2009). Importantly, the temporal and spatial scales of an exclosure study may be a source of variability in invertebrate response, but the effect of avian exclusion may trickle down to primary producers even if higher trophic-levels do not show a measurable response.

With finite resources, many experimental studies are limited by their spatial extent and duration, predisposing them both to high variability in their estimates of exclosure effect and preventing researchers from quantifying the drivers of this variation. In this study, I used a spatially replicated avian exclosure experiment along a 1200 km transect over two years to explore the spatial and temporal sources of variability in invertebrate and plant response to avian absence. In addition, I utilized a multiple-trophic-level approach to test if invertebrate community-level response is driven by particular taxonomic Orders. Using identical methods in similar communities, I tested for the ability of spatial and temporal factors to explain variation in the strength of top-down forces from an avian predator on its invertebrate prey and lower trophic levels.

Tidal marshes provide an ideal location to test predator control on a system across a large spatial scale. Marshes have low species diversity, but high abundance and plant productivity (Bertness 2007). Strong (1992) hypothesized that systems with low diversity are more vulnerable to trophic cascades, and Terborgh et al. (2010) found that highly productive systems exhibited stronger trophic cascades. Additionally, tidal-marsh specialist birds are declining (Correll et al. 2016), and conservation actions would be assisted by a better understanding of the role of avian predators in food-web dynamics and how their loss may trickle down to lower trophic levels. Finally, tidal marshes are characterized by two features that allow for simplification in the number of factors that change over large spatial scales. First, tidal marshes are characterized by distinct ecological zones that possess similar plant taxa over large scales, due to the small species pool that can tolerate relatively high salinity levels and flooding regimes

(Bertness 2007). By focusing on a single ecological zone, not only can one limit the potential confounding effects of a changing species pool across space, but site variation is also reduced by incidentally controlling for elevation, tidal regime, and salinity. Second, while the strength of herbivory generally increases at lower latitudes (Schemske et al. 2009), tidal-marsh plants decrease in palatability with decreasing latitude (Pennings et al. 2001), therefore reducing variation in lower trophic level response to avian exclusion across a latitudinal gradient.

The predator community in these systems is also simple. I conducted the study in sites across most of the breeding range of the fastest declining avian tidal-marsh specialist, the Saltmarsh Sparrow (*Ammodramus caudacutus*) (Correll et al. 2016). This species is an exclusive invertivore (consumes only invertebrates) during the breeding season (Greenlaw and Rising 1994), breeds along the eastern coast of the United States from Maine to Virginia, and uses similar nesting habitat across their range (Greenlaw and Rising 1994; Hodgman et al. 2002; Post and Greenlaw 2006; Shriver et al. 2010). The Saltmarsh Sparrow provides an opportunity to conduct an exclosure experiment across a species' range with limited site variation. In addition, while predator diversity often can dampen trophic cascades (Finke and Denno 2004, 2005), Saltmarsh Sparrows coexist with few other avian tidal marsh specialists that are invertivores, mainly the closely related Nelson's Sparrow (*Ammodramus nelson*) in the northern portion of their range (Greenlaw and Rising 1994; Hodgman et al. 2002) and Seaside Sparrow (*Ammodramus maritimus*) in their mid and southern range (Greenlaw and Rising 1994, Post and Greenlaw 2006). These two species are closely related to the Saltmarsh Sparrow and have similar prey preferences, foraging habitat, and body size (Greenlaw 1993; Greenlaw and Rising 1994; Post and Greenlaw 2006; Shriver et al. 2011). In addition, Saltmarsh and Nelson's

Sparrows hybridize (referred to as Sharp-tailed Sparrow) and their hybrids coexist with parent species in similar preferred habitats (Hodgman et al. 2002).

Top-down forces are strongest in the high-marsh zone (Denno et al. 2005), the preferred nesting habitat for Saltmarsh Sparrows (Gjerdrum et al. 2005). Previous work on food-web dynamics in this system has focused exclusively on the importance of spiders in suppressing phloem-feeding hemipterans (sap-feeders), the most abundant herbivores in tidal marshes (Denno 1977). To my knowledge, no study has examined the role of avian invertivores in controlling the abundance of invertebrate predators (i.e., spiders), herbivores, or detritivores in the tidal high-marsh zone.

The goal of this study was to test for a multiple-trophic-level response to avian exclusion and to understand if the response varies more across space or time. I did not seek to explain the mechanisms behind the variation, but to describe the pattern driving variation in lower trophic-level response to avian exclusion. By identifying the source of variation at different trophic levels, this study provides insight into the underlying food-web dynamics that may drive variation in a community-level response.

3.3. Methods

I conducted exclosure experiments in eight tidal marshes along the northeastern U.S. coast, from Maine to New Jersey (Table 3.1). These sites describe a 1200 km long transect (600 km linear distance between the furthest sites) along the eastern US coast, oriented approximately north to south, that covers two thirds of the roughly 1800 km long Saltmarsh Sparrow breeding range (Greenlaw and Rising 1994; Hodgman et al 2002; Shriver et al. 2010; Correll et al. 2016).

Table 3.1: Location of study plots, bird abundance, and timing of sampling for evaluating invertebrate and plant response to avian exclusion in tidal marshes along the northeastern U.S. coast.

Study Plot	Town	State	Latitude (decimal degrees)	Average Bird Abundance[a]	Years Included
Scarborough Marsh[b]	Scarborough	ME	43.572142	6.75	2014
Nonesuch Marsh[b]	Scarborough	ME	43.554047	5.5	2014 and 2015
Wells Marsh[c]	Wells	ME	43.290931	4	2014 and 2015
Chapman's Landing[d]	Stratham	NH	43.039319	4.25	2014 and 2015
Sachuest Marsh[e]	Middletown	RI	41.487681	7.75	2014 and 2015
Barn Island Marsh[f]	Stonington	CT	41.339025	4	2015
Hammonasset Marsh[f]	Madison	CT	41.258208	6.5	2014 and 2015
Forsythe Marsh[g]	Smithville	NJ	39.501256	14.75	2014 and 2015

[a] Average resident avian invertivore within 50 m of study plot across all years.

[b] Maine Department of Inland Fisheries and Wildlife

[c] Rachel Carson National Wildlife Refuge (NWR)

[d] New Hampshire Fish and Game Dept. Great Bay Reserve

[e] Sachuest Point NWR

[f] Connecticut Department of Energy and Environmental Protection

[g] Edwin B. Forsythe NWR

3.3.1. Experimental design

I selected *Spartina patens* dominated areas to match the preferred habitat of Saltmarsh Sparrows (Gjerdrum et al. 2005) at seven study sites in 2014. I constructed one exclosure and one control plot ("A" plots), which prevented or allowed (respectively) birds' access to 25 m^2 of marsh from May or early June to late August or early September (i.e., the breeding season). In 2015, I again erected one exclosure and control plot on the same locations of the 2014 plots ("A" plots) to measure multiple-year responses to avian exclusion.

In 2015, I also constructed one new exclosure and control plot during the breeding season within 50 m of the "A" plots to investigate year to year differences at seven sites (hereafter, "B" plots). At the Sachuest Point National Wildlife Refuge study site, the "B" plots were approximately 300 m away from the "A" plots due to the scarcity of *S. patens*-dominated area in the marsh. To increase sample size, I added a new site in 2015 at Barn Island Wildlife Management Area in Connecticut (see details in Table 3.1). Plots were maintained for the same period for 2015 "A" and "B" plots (May or early June to late August or early September).

Each exclosure and control plot was a 5 x 5 m square, stationed less than 20 m from each other. Four flags marked the corners of the control. Birds were excluded from the treatment plots with a 5 x 5 x 1 m PVC-pipe frame covered with 2.5-cm-mesh bird netting. I did not sample within a 0.5 m wide buffer around the edge of each plot to reduce the chance of edge effects, resulting in 4 x 4 m sampling area.

Within the plots, I collected invertebrate samples to measure prey response to avian predator removal. In addition, I collected above-ground plant biomass to measure indirect trophic effects of avian exclusion. To understand the role spatial and temporal factors play on the strength of top-down forces, I collected site-specific measurements to include as covariates.

To validate the assumption that the tidal-marsh invertebrates sampled are in fact prey items for avian predators, I collected fecal samples from Saltmarsh Sparrows caught near each exclosure site for diet analysis.

3.3.2. Invertebrate and plant biomass sampling

For invertebrate sampling within control and exclosure plots, I divided the 4 x 4 m sampling area into a grid with 16, 1 m^2 blocks. For each sampling effort, I sampled three, randomly selected blocks, and no block was sampled twice in a season. The same blocks were sampled in the control and exclosure plots at all sites for a given sampling period. The first sampling period occurred approximately two months after exclosures were installed, ensuring prey response was due to avian exclusion and not disturbance during exclosure set-up. To measure within-season variation in prey response, I conducted another sampling effort approximately one month after the first sampling period. I followed the invertebrate sampling scheme for 2014 “A” plots and 2015 “B” plots. Due to time constraints, I did not sample invertebrates in 2015 “A” plots (multiyear experiment).

For invertebrate collection, I used a leaf blower in reverse with a paint thinner filter bag attached to the end of the hose to catch vacuumed invertebrates. Within a cylindrical sampling frame (height = 50.8 cm, diameter = 66 cm), the leaf blower sampled invertebrates for two minutes while the operator simultaneously disturbed the plant substrate to dislodge individuals. Collected invertebrates were immediately placed in plastic bags and then sprayed with a broad-spectrum insecticide. I stored invertebrates in a freezer until processing. Once in the laboratory, I used 1 mm sieves to separate invertebrates from vegetation. After separation, I identified individuals to taxonomic Order (all Arthropods) or Class (Gastropods) and then stored in 70%

ethanol. Finally, I dried the samples in a 60 º C drying oven and measured biomass for each Order or Class in each sample.

For the analysis, I focused on three Orders that each represented a different feeding guild and had the highest three abundances of all sampled arthropods. The three Orders were Hemiptera (herbivores), Amphipoda (detritivore), and Araneae (predators). In tidal marshes, the majority of individuals in Order Hemiptera are sap-feeding herbivores (Denno 1977; Denno et al. 2002; pers. obs.), although the Order does represent other feeding guilds. These three groups are known to be prey items for Saltmarsh Sparrows (Greenlaw and Rising 1994; Post and Greenlaw 2006).

I collected above-ground plant biomass samples during the last sampling period for each plot in 2014 and 2015, including the multiple-year plots (2015 "B" plots). Using a 10 x 10 cm quadrat, I clipped five areas within each of the exclosure and control plots in blocks that had not been sampled for invertebrates. I sorted dead vegetation from live growth. Then, I placed collected vegetation in a drying room for two weeks to obtain dried mass. Ash-free dry mass (AFDM) was obtained after burning dried samples in a 500º C oven.

3.3.3. Spatial and temporal variables

To test if spatial and temporal variables affect the strength of top-down forces, I identified variables that would potentially interact with treatment effect. For temporal variables, I identified Julian date (quadratic and linear terms) and year. Invertebrate abundances peak at different times of the summer in different regions due to abiotic cues, such as temperature (Birch 1953; Davis and Gray 1966; Price et al. 2011). I included a quadratic term for Julian date because invertebrate abundances generally peak in July and decline later in the summer months.

Further, the additive variable allowed us to control for phenological differences among the three taxa that I modeled.

For spatial variables, I identified latitude (quadratic and linear terms) and average bird abundance at each site. For latitude, preliminary data exploration revealed that overall invertebrate abundance showed a strong quadratic relationship with latitude. In addition, tidal-marsh bird abundances generally increase with decreasing latitude over the range of the exclosure plots (Wiest et al. 2016). I predicted that sites with more abundant avian invertivores would exhibit stronger differences between exclosure and control plots. To calculate bird abundance, I surveyed tidal-marsh birds that are known to forage on terrestrial invertebrates in *S. patens*, including Saltmarsh Sparrow, Nelson's Sparrow (*A. nelsoni*), Seaside Sparrow (*A. maritimus*), Savannah Sparrow (*Passerculus sandwichensis*), Song Sparrow (*Melospiza melodia*), Marsh Wren (*Cistothorus palustris*), and Willet (*Tringa semipalmata*). I did not include species in migration, or those whose core breeding home ranges do not overlap *S. patens* in the high marsh. In addition, I excluded aerial avian insectivores (e.g., swallows and swifts), because they do not forage in plant substrate. At each site, I collected bird census data within a 50-m radius of the exclosure with point counts following a standardized procedure (www.tidalmarshbirds.org; Wiest et al. 2016). Each site had two surveys conducted during the breeding season (between mid-June and late July) in each of the two study years. I averaged the counts for the four surveys for each site and average bird count was assigned to each paired control and exclosure plot.

3.3.4. Tidal-marsh sparrow diet analysis

I used high throughput sequencing techniques to quantify tidal-marsh sparrow diet. I collected fecal samples from Saltmarsh Sparrows, Nelson's Sparrows, and Sharp-tailed Sparrow (hybrid between Saltmarsh and Nelson's Sparrow) during captures performed by demographic survey crews from the Saltmarsh Avian and Habitat Research Program (SHARP) at sites within a few kilometers of the exclosure sites. Adult birds were captured with mist nets during either systematic or targeted netting efforts (standardized protocols available on www.tidalmarshbirds.org; Ruskin et al. 2016) and chicks were hand captured from nests during nest monitoring and banding. In 2014, crews collected fecal samples from adults and chicks opportunistically. In 2015, captured birds were placed in brown paper bags with foil attached to the bottom of each bag. The crew removed the bird from the bag within five minutes, with or without sample. For both years, the fecal samples were collected with an alcohol swab and wrapped in aluminum foil and frozen until processed.

I extracted prey DNA using the Mo Bio Power Fecal (Mo Bio Laboratories, Carlsbad, CA) extraction kits, following manufacturer protocols. I included one negative control per 12 samples for quality control. High-throughput DNA sequencing was conducted using an Illumina HiSeq2500 Sequencer. I followed protocols for library development and amplicon sequencing outlined in Vo and Jedlicka (2014) and used an arthropod primer. The library development included the attachment of unique indexing barcodes, which enable tracking sequences from each individual sample.

3.3.5. Statistical analysis

I constructed five statistical models to test for the influence of temporal and spatial variables on the effect of bird removal. I used abundance of each of three taxonomic Orders (Araneae, Hemiptera, and Amphipoda) or biomass (plants) as dependent variables to explore the response of multiple trophic levels to avian exclusion. For the fifth model, I used summed invertebrate abundance across all Orders to assess the overall invertebrate community response to the treatment.

I used Program R (3.3.1 R Development Core Team 2016) for all statistical analysis. For abundance response variables, I ran generalized linear mixed effects models (package ‘lme4’) using a negative binomial distribution with a log-link function to account for overdispersion. For plant biomass models, I square-root transformed biomass to meet model assumptions and used linear mixed effects models (package ‘lme4’). For invertebrate and plant biomass models, site was modeled as a random effect to account for multiple sampling of each plot. All continuous variables were scaled.

I conducted a two-step model selection for each invertebrate response variable. The first step identified the best set of additive temporal variables to explain invertebrate abundance. I selected the best performing model from among six potential models (all combinations of the temporal variables: Table 3.4). All candidate models (including the nulls) contained the random effect of site identity. For the second step, the resulting set of temporal variables was incorporated into all candidate models to control for either phenological patterns in abundance or overall abundance differences between the two years.

The second model selection step then identified treatment and covariate interactions that influenced the strength of top-down controls. I predicted that the strength and direction of top-down forces could vary with spatial and temporal variables. To test this, I ran a series of candidate models that each included a single interaction of treatment type (exclosure or control) with each spatial and temporal covariate and compared the performance of these models to a null model. For the invertebrate abundance models, the interactions with treatment type included those with latitude (linear and quadratic terms), average bird abundance, Julian date (linear and quadratic terms), and year. The invertebrate null models contained treatment type and the set of important temporal variables identified in the first model-selection step as fixed effects and site identity as a random effect.

Mäntylä et al. (2011) provided evidence that across the globe the presence of birds positively affect plant quality and reduce plant damage. To test if plant response shows less variability than invertebrate response, I ran a series of plant biomass models that mirrored the second step of invertebrate abundance models and compared them to a single treatment-effect model and a null model, both containing site as a random effect. All models contained data from all plots (both "A" and "B" for both years) and to test for an effect of year, I included three year categories to represent 2014 "A" plots, 2015 "A" plots, and 2015 "B" plots.

I compared model performance during both model selection steps using Akaike Information Criterion corrected for small sample size (AICc) and Akaike weights (w_i). Models with ΔAICc less than 2.0 were considered equivalent models (Burnham and Anderson 2002). If multiple models had ΔAICc less than 2.0 during the first step of model selection, I included the variable/s that were significant in all top-ranking models in the second step of model selection. When models possessed significant interaction terms, I report parameter estimates and confidence intervals using the "Wald" method and the conditional r-squared to assess model fit.

3.3.6. Outliers

I removed a few outliers that either biased or misrepresented the data. I removed first sampling period in 2015 at the USFWS Rachel Carson National Wildlife Refuge site (Wells Marsh, Table 3.1). At this location on the first sampling period (July 21, 2015), hemipterans showed a 387% increase peak in abundance from the second, which greatly influenced the slope of regression line and reduced model fit (Table A.1). Also, I removed 2015 "B" plot plant

Table 3.2: Invertebrate abundance and plant biomass (mean, SD) in control and avian exclosure plots at eight tidal marshes along the northeastern U.S. coast, 2014-2015.

	Control[a]					Exclosure[a]				
Study Plot	Total	Hemiptera	Spiders	Amphipoda	Plant Biomass[c,d]	Total	Hemiptera	Spiders	Amphipoda	Plant Biomass[c,d]
2014										
Scarborough	96.3	51.0	16.7	2.8	4.2	120.7	77.8	17.2	5.5	6.2
	± 38.0	± 52.5	± 12.8	± 3.2	± 0.6	± 45.5	± 53.2	± 7.3	± 3.6	± 1.9
Nonesuch	68.8	31.0	12.7	12.5	3.9	46.7	15.8	12.8	10.5	4.0
	± 46.7	± 35.1	± 9.7	± 11.1	± 1.2	± 21.9	± 18.9	± 6.5	± 5.5	± 1.8
Wells Marsh	256.8	192.2	24.3	12.5	6.4	592.8	498.5	21.0	9.3	7.4
	± 171.2	± 132.0	± 18.5	± 12.4	± 3.2	± 189.6	± 159.4	± 16.4	± 9.9	± 2.2
Chapman’s	205.8	111.3	31.7	6.0	5.7	132.3	84.3	20.8	5.8	6.1
	± 97.9	± 59.4	± 20.6	± 4.6	± 1.5	± 71.0	± 34.8	± 17.3	± 5.5	± 3.9
Sachuest	122.5	7.2	31.2	54.7	3.8	110.7	12.5	26.0	35.3	6.0
	± 62.2	± 6.0	± 9.7	± 26.2	± 0.9	± 48.3	± 7.7	± 8.6	± 31.6	± 1.3
Barn Island	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Hammonasset	190.3	87.5	35.0	34.3	5.2	213.3	135.8	42.8	2.3	4.9
	± 118.2	± 76.6	± 16.2	± 68.2	± 1.3	± 136.4	± 118.4	± 14.7	± 2.7	± 0.7
Forsythe	94.7	41.0	24.3	8.8	5.4	56.2	24.3	17.8	4.5	4.7
	± 36.6	± 26.2	± 6.6	± 7.7	± 1.5	± 22.5	± 13.6	± 8.1	± 2.7	± 1.1
2015										
Scarborough	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Nonesuch	59.3	25.3	12.7	10.5	3.4	85.5	35.5	11.7	28.5	2.4
	± 61.4	± 29.0	± 11.3	± 5.5	± 2.0	± 92.8	± 39.8	± 11.2	± 30.3	± 0.3
Wells	98.7	55.3	16.7	13.3	6.8	227.7	111.3	56.7	26.7	7.9
	± 61.5	± 28.1	± 4.0	± 15.5	± 1.8	± 216.4	± 11.6.6	± 52.8	± 19.0	± 2.9
Chapman’s	77.1	340.8	31.0	17.2	4.7	308.0	205.7	49.3	31.2	4.7
	± 10.8	± 328.4	± 7.4	± 6.4	± 1.6	± 128.2	± 106.0	± 24.7	± 25.8	± 1.1
Sachuest	88.3	37.0	52.8	33.2	6.0	131.2	45.2	35.2	27.0	6.9
	± 13.2	± 22.4	± 26.6	± 5.8	± 1.0	± 34.5	± 27.0	± 9.0	± 14.1	± 1.5
Barn Island	378.3	75.8	35.3	200.5	2.7	357.8	43.2	42.5	223.0	2.2
	± 260.6	± 50.0	± 25.9	± 151.9	± 0.8	± 154.0	± 25.2	± 28.6	± 111.7	± 1.1
Hammonasset	156.0	72.8	17.5	8.3	6.5	228.5	89.0	22.3	18.2	5.9
	± 40.8	± 15.6	± 9.6	± 5.8	± 4.0	± 51.7	± 54.0	± 8.8	± 13.3	± 1.6
Forsythe	144.5	87.7	18.5	1.7	9.1	110.7	50.5	14.2	5.0	9.7
	± 85.0	± 79.9	± 12.0	± 1.6	± 1.6	± 51.3	± 17.9	± 5.1	± 3.6	± 2.6

[a] The mean and standard deviation are calculated from samples across three sampling periods (approx. late June to early September).

Table 3.2: continued

[b] Study plots arranged in order from high to low latitude.

[c] Above-ground plant biomass in ash-free dry mass.

[d] Does not include “A” plot’s 2015 plant biomass averages (multiple year effect).

and invertebrate samples at Scarborough Marsh because the exclosure netting was not secured upon setup and birds were found inside the exclosure.

3.4. Results

Over both years, I collected 29,813 invertebrates (2014 = 13,848, 2015 = 15,965; excluding outliers) among twelve taxonomic Orders. These included Hemiptera (15,373 individuals), Amphipoda (5,011), Spiders (4,284), Diptera (1,583), Gastropoda (1,090), Isopoda (924), Orthoptera (693), Coleoptera (497), Hymenoptera (267), Thysanoptera (42), Pseudoscorpioninda (30), Lepidoptera (2), and unknown (17). See Table 3.2 for site averages by taxonomic group and treatment type. Figure 3.1 and 3.2 depict effect sizes (estimated by calculating the natural log of the quotient of mean abundance in the experimental plots divided by the mean in the control plots) for each site for each year. 2014 and 2014 effect sizes varied from site to site and year to year. In 2015, effect sizes were relatively positive (meaning higher values in exclosure plots than control), but this was not consistent at each site.

In the control plots, average plant biomass slightly increased in 2015 (A plot mass ± SD = 5.58 ± 2.59; B plot = 5.24 ± 2.72) from 2014 (A plot = 4.97 ± 1.78). In the exclosure plots, I had a similar trend with 2015 samples having higher biomass than 2014 (2015 A plot = 7.35 ± 3.64; B plot = 5.65 ± 3.08; 2014 A plot = 5.62 ± 2.19). Figure 3.3 depicts effect sizes for each site and year, calculated similarly to the invertebrate abundance effect sizes. In total, effect sizes were positive in total for both single-year experiments and multiple-year experiment.

During 2014 and 2015 point counts, I counted a total of 214 individuals of the seven resident invertivorous bird species listed in methods. Each site’s average bird abundance is listed on Table 3.1. Average bird abundance was negatively correlated with latitude (Pearson's correlation = -0.73).

3.4.1. Tidal-marsh sparrow diet analysis

In 2014 and 2015, 563 samples were collected and sequenced to quantify tidal-marsh sparrow diet. The success rate of the sequencing was 29% (fecal DNA is naturally degraded and difficult to obtain quality results) and the successful, higher-quality sequenced samples included 61 from Saltmarsh Sparrows, 12 from Nelson's Sparrows, and 92 from Sharp-tailed Sparrows (165 samples in total). I assigned nestling and juvenile samples as Sharp-tailed Sparrows because species cannot be determined by the plumage at this age. For age groups, I collected 90 adults, 30 juveniles, and 45 nestling samples. In total, the samples contained 12 different Orders, including Araneae (spiders), Coleoptera (beetles), Diptera (flies), Hemiptera (bugs), Hymenoptera (e.g., ants, wasps, bees), Lepidoptera (butterflies and moths), Sarcoptiformes (mites and ticks), Trichoptera (thrips), Ephemeroptera (mayflies), Orthoptera (e.g., grasshoppers, crickets, katydids), Mantodea (mantises), and Trombidiformes (mites). For all bird species and age groups, Diptera, Lepidoptera, and Araneae were the most common operational taxonomic units (OTU) (Table 3.3).

3.4.2. Additive phenological and year effects for invertebrate models

All the best-performing invertebrate abundance models during the first model selection step included additive temporal variables except the model for Araneae (Table 3.4). Total abundance and hemipterans peaked mid-season and had higher abundances in 2015 while amphipods linearly increased throughout the summer season, similarly for both years, and spider abundance did not change much among and between years. For the Araneae model, the null

Table 3.3: Relative percentages of each unique operational taxonomic unit (OTU), at the Order level, within the diet of each tidal-marsh sparrow species along the northeastern U.S. coast, 2014 - 2015.

	Sample Size	Araneae	Coleoptera	Diptera	Hemiptera	Hymenoptera	Lepidoptera	Other[a]
Bird Species[b]								
NESP	12	20.29	0.00	46.38	4.35	2.90	26.09	0.00
SALS	61	19.95	5.44	42.23	9.84	2.59	19.43	0.52
STSP	92	21.90	3.96	40.63	9.23	2.37	20.58	1.32
Age Group								
Adult	90	21.12	3.92	41.40	8.35	2.90	21.64	0.13
Juvenile	30	21.71	4.57	38.86	14.29	2.86	16.00	0.86
Nestling	45	21.31	3.28	39.34	10.38	0.55	23.50	0.82

[a] Other Orders include Sarcoptiformes (mites and ticks), Trichoptera (thrips), Ephemeroptera (mayflies), Orthoptera (grasshoppers, crickets, katydids, etc…), Mantodea (mantises), and Trombidiformes (mites).

[b] Nelson’s Sparrow (NESP), Saltmarsh Sparrow (SALS), and Sharp-tailed Sparrows (STSP)

Table 3.4: Candidate models[1] for additive temporal variables that predict invertebrate abundance at eight tidal marshes along the northeastern U.S. coast, 2014 - 2015.

Candidate Models[a]	AICc	ΔAICc	w_i
Total ~ Julian* + Julian^2* + Year*	**1909.6**	**0**	**0.744**
Total ~ Julian* + Year	1913.2	3.56	0.125
Total ~ Julian*	1913.8	4.16	0.093
Total ~ Julian* + Julian^2	1915.6	6.01	0.037
Total ~ Year	1944.1	34.51	0
Total ~ Null	1945.0	35.41	0
Spider ~ Null	**1340.3**	**0**	**0.424**
Spider ~ Year	**1341.8**	**1.52**	**0.199**
Spider ~ Julian	1342.4	2.10	0.148
Spider ~ Julian + Julian^2 +Year	1343.2	2.94	0.098
Spider ~ Julian + Year	1343.9	3.64	0.069
Spider ~ Julian + Julian^2	1344.1	3.82	0.063
Hemiptera ~ Julian* + Julian^2* + Year*	**1704.6**	**0**	**0.799**
Hemiptera ~ Julian* + Year*	1707.5	2.92	0.185
Hemiptera ~ Julian*	1713.0	8.45	0.012
Hemiptera ~ Julian* + Julian^2	1714.9	10.36	0.005
Hemiptera ~ Year*	1726.2	21.57	0
Hemiptera ~ Null	1729.5	24.87	0
Amphipoda ~ Julian*	**1273.0**	**0**	**0.427**
Amphipoda ~ Julian* + Year	**1273.9**	**0.87**	**0.227**
Amphipoda ~ Julian* + Julian^2	**1274.5**	**1.52**	**0.200**
Amphipoda ~ Julian* + Julian^2 + Year	1276.0	3.02	0.094
Amphipoda ~ Null	1284.4	11.37	0.001
Amphipoda ~ Year	1284.8	11.75	0.001

[a] Top ranking model/s (within 2 ΔAIC_c from top model) are in bold.

* indicates when fixed effects are significant.

model ranked the highest (model weight = 0.42) followed by the model with ‘year’ (ΔAICc < 2.0; model weight = 0.20), but the 95% confidence intervals for ‘year’ included zero, so I did not include this variable when testing for interactions with treatment type in the second step of model selection. For Amphipoda, three additive temporal models outperformed the null and ranked within ΔAICc of two from each other. Julian date (linear term) was the only significant variable in any of the top models; therefore, I only included that term for the second step. For the remaining two models (overall invertebrate abundance and hemipterans), the best performing additive temporal model included the effect of year and both the linear and quadratic effects of Julian date (Table 3.4).

3.4.3. Interactions between the treatment and spatial and temporal correlates

The top-ranking model for predicting total invertebrate abundance for the second model selection step was the model with an interaction between treatment type (exclosure or control) and average bird abundance (model weight = 0.49, Table 3.5). This model had reasonable fit (conditional $R^2 = 0.34$) and the interaction term was significant (Table 3.6). Without the interaction, the additive terms for treatment type and average bird abundance were not significant predictors of total invertebrate abundance (β= 0.02*,* SE± 0.09, *P*=0.83; β= -0.21, SE± 0.19, *P*=0.28, respectively). No other interaction outperformed the null model with ΔAICc > 2.0. The abundance of Araneae was best predicted by latitude (linear and quadratic terms) while treatment interactions were not good predictors. For the Araneae model, the quadratic latitude term interaction model ranked the highest (model weight = 0.74, Table 3.5), but the interaction was not significant (β= -0.11*,* SE± 0.10, *P*=0.30, Table 3.5) as well as the treatment effect (β= 0.12*,* SE± 0.14, *P*=0.38), but linear and quadratic terms for latitude were significant (β= -0.25*,* SE± 0.09, *P*<0.01; β= -0.30*,* SE± 0.10, *P*<0.01, respectively). The null model ranked the highest for

Table 3.5: Treatment-interaction candidate models[a,b] for predicting invertebrate abundance and above-ground plant biomass[3] at eight tidal marshes along the northeastern U.S. coast, 2014 - 2015.

Candidate Models	AICc	ΔAICc	w_i
Total Abundance ~ Treatment x Bird Abundance*	**1909.2**	**0**	**0.486**
Total Abundance ~ Treatment x Latitude^2	1911.6	2.42	0.145
Total Abundance ~ Null	1911.8	2.57	0.134
Total Abundance ~ Treatment x Latitude	1912.4	3.17	0.100
Total Abundance ~ Treatment x Julian^2	1913.9	4.68	0.047
Total Abundance ~ Treatment x Year	1914.0	4.78	0.045
Total Abundance ~ Treatment x Julian	1914.0	4.78	0.044
Spider Abundance ~ Treatment x Latitude^2	**1338.2**	**0**	**0.737**
Spider Abundance ~ Null	1342.3	4.10	0.095
Spider Abundance ~ Treatment x Bird Abundance	1342.8	4.58	0.075
Spider Abundance ~ Treatment x Latitude	1344.6	6.41	0.030
Spider Abundance ~ Treatment x Year	1344.8	6.53	0.028
Spider Abundance ~ Treatment x Julian^2	1345.1	6.91	0.023
Spider Abundance ~ Treatment x Julian	1346.5	8.23	0.012
Hemiptera Abundance ~ Null	**1706.7**	**0**	**0.248**
Hemiptera Abundance ~ Treatment x Year	**1707.6**	**0.94**	**0.155**
Hemiptera Abundance ~ Treatment x Latitude^2	**1077.7**	**1.00**	**0.150**
Hemiptera Abundance ~ Treatment x Bird Abundance	**1708.0**	**1.32**	**0.128**
Hemiptera Abundance ~ Treatment x Latitude	**1708.2**	**1.48**	**0.118**
Hemiptera Abundance ~ Treatment x Julian^2	**1708.4**	**1.72**	**0.105**
Hemiptera Abundance ~ Treatment x Julian	**1708.6**	**1.91**	**0.095**
Amphipoda Abundance ~ Treatment x Year*	**1268.5**	**0**	**0.712**
Amphipoda Abundance ~ Treatment x Julian^2*	1271.0	2.50	0.214
Amphipoda Abundance ~ Null	1275.1	6.63	0.026
Amphipoda Abundance ~ Treatment x Latitude^2	1275.5	6.99	0.022
Amphipoda Abundance ~ Treatment x Bird Abundance	1276.4	7.86	0.014
Amphipoda Abundance ~ Treatment x Latitude	1276.4	7.93	0.013
Amphipoda Abundance ~ Treatment x Julian	1277.2	8.68	0.009
Plant Biomass ~ Treatment*	**311.0**	**0**	**0.603**
Plant Biomass ~ Null	**312.0**	**1.00**	**0.365**
Plant Biomass ~ Treatment x Bird Abundance	318.8	7.79	0.012
Plant Biomass ~ Treatment x Latitude	319.6	8.67	0.008
Plant Biomass ~ Treatment x Latitude^2	320.0	9.04	0.007
Plant Biomass ~ Treatment x Year	320.4	9.46	0.005

[a] Additive temporal-control variables not listed; see Table 3.4.

[b] Top ranking model/s (within 2 ΔAIC$_c$ from top model) are in bold.

[c] Ash-free dry mass

* indicates significant interactions in invertebrate models and significant fixed effects in plant biomass model.

Table 3.6: Parameter estimates for top models, predicting invertebrate abundance and plant biomass from tidal marshes along the northeastern U.S. coast, 2014 - 2015.

Model	Parameter[a]	Estimate	95% CI[b]
Total Abundance	**Intercept**	**5.09**	**(4.76, 5.42)**
	Treatment	0.02	(-0.13, 0.17)
	Average Bird Abundance	-0.21	(-0.53, 0.11)
	Julian (linear)	**-0.35**	**(-0.44, -0.27)**
	Julian (quadratic)	**-0.30**	**(-0.46, -0.10)**
	Year	**0.42**	**(0.19, 0.65)**
	Treatment x Average Bird Abundance	**-0.20**	**(-0.35, -0.05)**
Amphipoda Abundance	**Intercept**	**2.98**	**(2.32, 3.65)**
	Treatment	**-0.56**	**(-0.93, -0.19)**
	Year	-0.28	(-0.66, 0.10)
	Julian (linear)	**-0.30**	**(-0.44, -0.17)**
	Treatment x Year	**0.99**	**(0.47, 1.50)**
Plant Biomass	**Intercept**	**2.18**	**(1.94, 2.42)**
	Treatment	**0.17**	**(0.06, 0.27)**

[a] Significant fixed effects are bolded.

[b] Confidence intervals were calculated using "Wald" method.

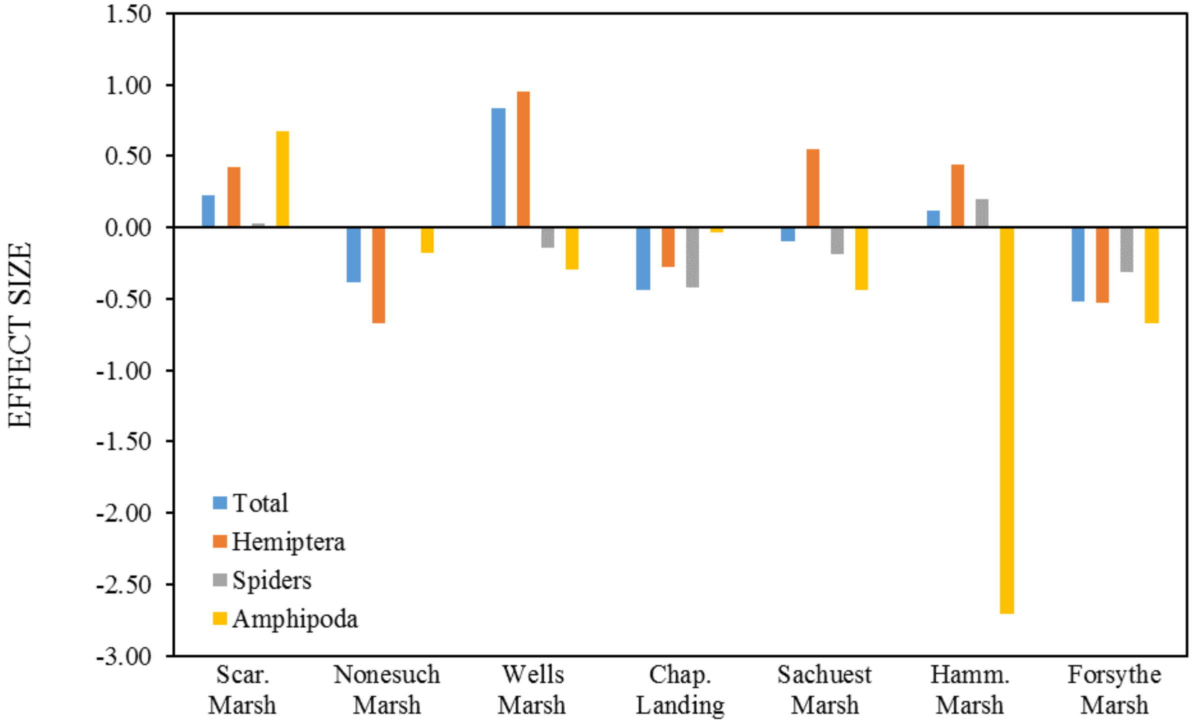

Figure 3.1: 2014 invertebrate abundance effect sizes (LN(experiment average/control average)) for eight tidal marshes along the northeastern U.S. coast. Sites are ordered by latitude, with the most Northern site on the left and the most Southern on the right. Positive values indicate that exclosure value is larger than the control.

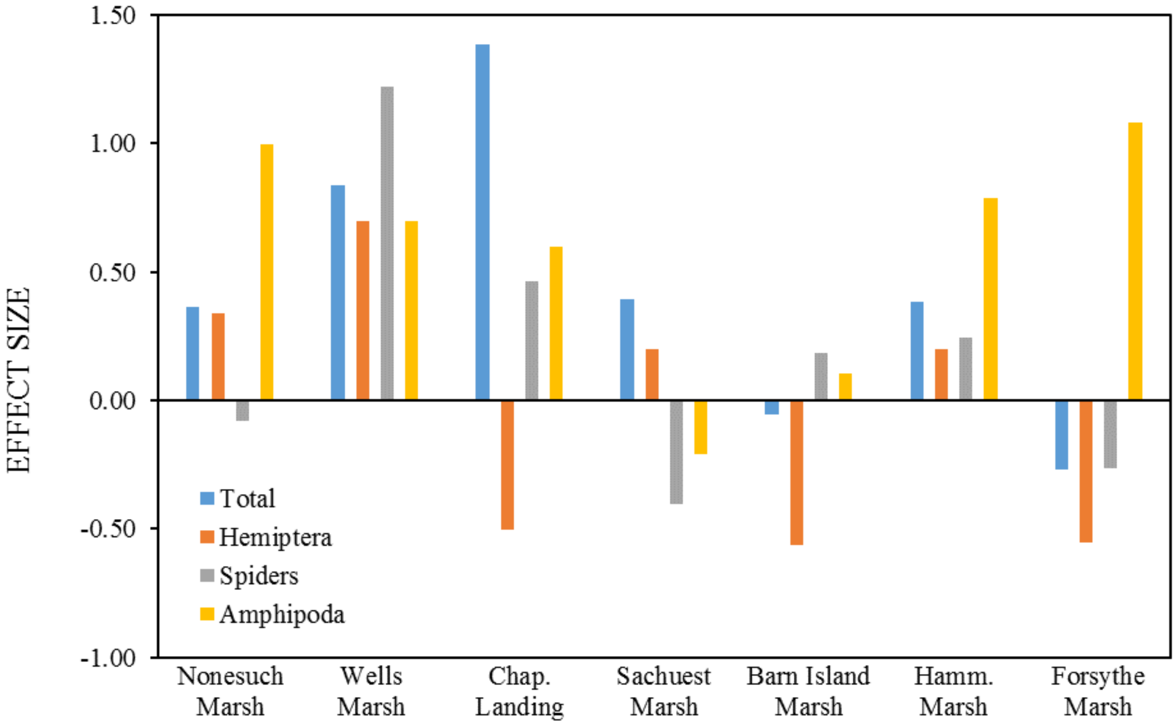

Figure 3.2: 2015 invertebrate abundance effect sizes (LN(experiment average/control average)) for eight tidal marshes along the northeastern U.S. coast. Sites are ordered by latitude, with the most Northern site on the left and the most Southern on the right. Positive values indicate that exclosure value is larger than the control.

Figure 3.3: Above-ground plant biomass effect sizes (LN(experiment AFDM average/control AFDM average)) for eight tidal marshes along the northeastern U.S. coast, 2014 - 2015. Sites are ordered by latitude, with the most Northern site on the left and the most Southern on the right. Positive values indicate that exclosure value is larger than the control. 2014 “A” and 2015 “B” plots represent single-season plots and 2015 “A” plots represent multi-year plots.

Order Hemiptera; all models were within two ΔAICc from each other; and no interaction term was significant in any of the models (Table 3.5). Hemiptera and Araneae abundance also did not differ by treatment type (β= 0.04*,* SE± 0.14, *P*=0.79; β= 0.12*,* SE± 0.14, *P*=0.38, respectively). For Amphipoda, the model with the interaction between treatment and year ranked the highest (model weight = 0.71, Table 3.5) with a significant interaction (Table 3.6) and the conditional R^2 was 0.56.

The simple treatment type model ranked the highest among the candidate models for above-ground plant biomass (model weight = 0.60, Table 3.5). The null model differed by its AICc with less than 2.0, but the treatment effect was significant (Table 3.6), and the model conditional R^2 was 0.43. In total, plant biomass was higher in the exclosure than in control for both years (Figure 3.3).

3.5. Discussion

My results provide better understanding of the source of variation for invertebrate and plant response to avian exclusion. The variation in invertebrate abundances within site (large standard deviations) was driven by Julian date (Table 3.2, .4). After controlling for temporal variation in invertebrate abundances where it existed, I found wide variation in the effect of avian removal. Among sites, overall invertebrate abundance was variously larger or smaller in the exclosure versus control plots, and the magnitude of difference depended on the local bird abundance at the site, as would be expected for prey that are controlled by predation pressure. This pattern, however, was not reflected by the abundances in the most common invertebrate Orders (representing multiple levels in the food web). Hemiptera and Araneae abundance did not change in response to avian exclusion. For amphipods, the strength and direction of top-down forces varied among, but not within, years. Importantly, even though spatial and temporal variation impacted invertebrate response to avian exclusion, plant response was consistent across space and time on average in this study.

In 2014 and 2015, the total average above-ground plant biomass was higher in the exclosure plots than the controls. The treatment effect on plant biomass was small and compared to invertebrate response, varied only slightly from site to site and among years (Figure 3.1,.2,.3). Despite the variation, treatment type alone was the best predictor of plant biomass and models containing treatment interactions with spatial and temporal variables ranked lower than the null. The multiple-year experiment showed the greatest difference between the exclosures and controls, however, indicating that in the system that I studied, the effect of exclosure may increase with time. The difference between years, however, was not great enough to cause a treatment by year interaction. I did not collect invertebrates from the combined-year plots so I cannot elucidate the mechanisms driving these results. This experiment provides further evidence that plant response to avian exclusion may be the most consistent measurement across space and time. My results, and those of Mäntylä et al. (2011), highlight that temporally and spatially replicated exclosure studies may not be needed if the goal of an experiment is to measure plant response to avian presence (i.e. agricultural studies). A different measurement of plant response may have shown larger effect sizes. Indeed, trophic cascades in terrestrial systems are more easily measured using plant damage instead of plant biomass (Schmitz et al. 2000; Halaj and Wise 2007), and the magnitude of the effect of exclosure is greater in plant damage (Mäntylä et al. 2011).

The plant biomass results were unique in that plant biomass increased with avian exclusion. Most avian exclosure studies found that predator removal negatively affects primary producers (Atlegrim 1989; Greenberg et al. 2000; Sanz 2001; Hooks et al. 2003; Van Bael et al. 2003, 2008; Mäntylä et al. 2011). The positive response in plant biomass suggests that intermediate predators played a role in suppressing herbivores, although I did not measure a significant spider response (intermediate predator) to avian exclusion. Top-down control from spiders has been documented in these marshes, however (Denno et al. 2005), and this study's diet analysis showed that tidal-marsh sparrows prey on spiders. One alternative would be if the plant biomass changes were a function of the exclosure design. The most likely impact of the exclosure on plant growth directly would be shading (which was minimal to absent, as the netting was a very fine thread with a mesh gauge of 2.54 cm), which should decrease, not increase, *Spartina* growth. Further, past exclosure studies did not find differences in microclimates, including temperature and rainfall, between exclosures and controls (Joern 1986; Fowler et al. 1991; Bock et al. 1992).

Saltmarsh Sparrows and other avian tidal-marsh specialists occupying the study sites are generalist invertivores (Judd 1901; Hill 1968; Greenlaw and Rising 1994; Arcese et al. 2002; Post and Greenlaw 2006; Shriver et al. 2011), and thus their cumulative foraging impacts might be better measured at the invertebrate community level than at individual Orders. It might, therefore, be unsurprising that individual Orders were variable in their response to avian predator exclusion across sites and through time, but the community, as a whole, was more consistent. Further, the variability for invertebrate Orders also may result from different mechanisms at even finer taxonomic levels within Orders (e.g., avian prey preferences, within guild predation and competition) for which I have no information. Regardless, bird abundance was the best predictor for the response of total invertebrate abundance. In fact, the effect of exclosure was variable enough that the ‘treatment’ variable was not significant without controlling for the interaction with local bird abundance.

While there was temporal variation in invertebrate abundance both within years (Amphipoda, Hemiptera, Total Invertebrates) and between years (Hemiptera and Total Invertebrates), I only detected temporal variation in the exclosure effect between years for one Order (Amphipoda). Climatic changes have explained this sort of variation in invertebrate response to predator removal in other systems (Fowler et al. 1991; Bock et al. 1992; Turchin et al. 1999; Noemi Mazia et al. 2004). Surprisingly, I did not find significant between-year variation in amphipod abundance without the interaction despite the addition of a new study site in 2015 (Barn Island Marsh). Regardless, with year-to-year variation reported here and elsewhere, researchers need to be cautious when interpreting results from single-year exclosure experiments.

Given the temporal (Amphipoda) and spatial (total abundance) variation in the effect of exclosures, treatment alone was not a significant predictor for any invertebrate Order or for the community as a whole. If tidal-marsh avian invertivores strongly control their prey abundance, they do so heterogeneously across space and through time. Although Saltmarsh Sparrows and other avian invertivores in the study system are unlikely to be keystone predators, my study highlights that the invertebrate response to avian predators can be more evident at the community level; varies spatially and temporally and by the taxonomic Order of the invertebrates involved; and that changes in bird abundance can affect invertebrate response, but not plant response. In addition, tidal-marsh birds indirectly affect primary producers, and bird exclusion resulted in a consistent plant response. Despite time of year and latitude being strong predictors of invertebrate abundance, spatial and temporal interactions with exclosure effect were absent at most lower trophic levels. The loss of avian invertivores from the tidal marsh, either in their entirety, which appears likely, or functionally in an era of accelerated climate change, which has already occurred in many marshes (Correll et al. 2016) appears sufficient to alter food-web dynamics and primary production. More research is needed to elucidate the mechanisms behind these patterns.

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APPENDIX: CHAPTER 3 OUTLIERS

Table A.1: Candidate models for predicting hemipteran abundance with outliers included, at eight tidal marshes along the northeastern U.S. coast, 2014 - 2015.

Candidate Models*	AICc	ΔAICc	w_i
Hemiptera Abundance ~ Null	**1811.2**	**0**	**0.225**
Hemiptera Abundance ~ Treatment x Julian^2	**1811.4**	**0.27**	**0.196**
Hemiptera Abundance ~ Treatment x Year	**1811.4**	**0.27**	**0.196**
Hemiptera Abundance ~ Treatment x Julian	**1811.9**	**0.77**	**0.153**
Hemiptera Abundance ~ Treatment x Latitude^2	**1812.4**	**1.22**	**0.122**
Hemiptera Abundance ~ Treatment x Bird	1813.9	2.71	0.058
Hemiptera Abundance ~ Treatment x Latitude	1814.2	3.03	0.049

*Bolding signifies top ranking models

BIOGRAPHY OF THE AUTHOR

Laura Garey was a Nebraskan native with high aspirations. She graduated from High Plains Community High School with the goal of becoming a scientist of something. This led her to the great hills of Missouri to attend a liberal arts school, Truman State University. As a biology undergraduate, her interest in research lead her to videotape snail mating behavior and to study the morphology of their reproductive organs. Naturally, her interest transitioned to include lizard distribution of clonal lines in Southeast Colorado. After graduating with a Bachelor of Science in May 2010, Laura’s undergraduate research experience somehow provided the skills to qualify for a shorebird monitoring position in San Francisco Bay. After falling in love with the marsh and its pungent smells, she continued working in coastal areas, with an avian-conservation research focus. Laura is a candidate for the Master of Science degree in Ecology and Environmental Sciences from the University of Maine in May 2017.