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Approaches to Restoration: Assessing the Roles of Structure and Function in Saltmarsh Restoration in Light of Climate Change

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Approaches to restoration: Assessing the roles of structure and function in saltmarsh

restoration in light of climate change

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ABSTRACT

The aim of this thesis is to review the current goals and methods for salt marsh restoration, to question how those goals and methods may change in light of global change, and to present a case study that offers a look at the kinds of information that can be gleaned by studying both structure and functionality in restoration. Salt marsh restoration has traditionally relied on restoring the structural components of the marsh, with a focus on hydrology and plant species composition and distribution. Because climate change is predicted to have broad-ranging effects on the structure of New England salt marshes, the ways in which practitioners approach restoration may need to be reassessed so as to include measures of functionality when traditional measures of structure are impractical. The case study was conducted in a restoring marsh and a nearby reference marsh in Newcastle, Maine. The study described the terrestrial arthropod community in relation to recently established plant communities. Stable isotope analysis was used to explore the functional relationships between the plant and arthropod communities. The plant community in the restoring marsh supports a wide variety of arthropods, from herbivores to top predators. Arthropod carbon isotope values indicate that the recently established *Spartina alterniflora* serves as a main food source for arthropods living in the low marsh. Stable isotope analysis revealed that when arthropod community structure differed between sites, functionality (i.e., transfers of carbon and nutrients to higher trophic levels) persisted. The case study suggests that stable isotope analysis of plant and arthropod communities provides an opportunity to assess restoration in terms of functionality in conjunction with structure, rather than relying on structure as a proxy for functionality. As such, the restoring system could be considered a success, based on measures of functionality. In the context of global change, changes to the community structure of both restoring and reference systems may be inevitable; however, an emphasis on monitoring functionality allows researchers to assess restoration in terms of resiliency despite structural changes.

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INTRODUCTION

New England salt marshes have experienced remarkable changes over the past century as a result of direct and indirect human influences (Bertness et al. 2002, Smith 2009). Historically, threats to salt marshes were often direct and purposeful (e.g., ditching, draining, and grazing), but current threats tend to be indirect and unintentional (e.g., warming temperatures, exposure to invasive species, and eutrophication) and often relate to climate change (Gedan et al. 2009). Because of the indirect nature of these impacts, it can be difficult for restorationists to assess impacts and to define restoration goals. Some restorationists are approaching this problem by focusing on restoring resilience and other measures of functionality to impacted marshes, rather than only focusing on structural components (Gedan et al. 2011). In this case, resilience can be defined as "the capacity to absorb disturbance" while maintaining structure and function (Walker et al. 2004).

A hurtle in assessing ecosystem functionality is in defining what "functionality" means. Broadly, salt marsh functionality can be defined by many measures, including: biomass production, nutrient content, nutrient cycling, carbon cycling, resilience, and provision of services such as storm buffering and water filtration (Palmer et al. 1997, Giller and O'Donovan 2002, Blondel 2003, Cortina et al. 2006). Alternatively, structure is often defined in terms of hydrology, salinity, water quality, and species composition and complexity (Committee staff on restoration of aquatic ecosystems 1992, Maestre et al. 2006, Cortina et al. 2006, Cui et al. 2011). Measures of *structure* describe, for instance, what plant species are present, as well as the diversity and distribution of those species. Measures of *functionality* describe how primary productivity is transferred

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through complex trophic interactions. While functionality refers to what is happening in an ecosystem, structure describes what organisms are performing the tasks. In restoration, the problem of defining success arises when a system has a diversity of organisms performing limited ecosystem functions (complex structure, low functionality) rather than a diversity of organisms performing a wide range of ecosystem services (complex structure, high functional diversity). Restoration would be considered a success in both cases if assessed only using the structure metric.

Traditionally, salt marsh restoration projects focus on restoring the structure of a disturbed system, often in order to reflect an ideal of a past, "pristine" state (Konisky et al. 2006 Vander Zanden et al. 2006). The assumption is that restored functionality results from restored structure (Bradshaw 1984). In a salt marsh, restructuring may involve removing tidal restrictions, stabilizing banks, filling in mosquito ditches, and planting native vegetation (Konisky et al. 2006) in hopes that energy and nutrients will transfer through the food web. While restoring the physical structure of a marsh is essential for developing a base on which the marsh can thrive, the practice does not guarantee that the marsh will develop into a fully-functioning system. The degree to which functionality follows structure is debated.

This study combines a literature review of current practices in salt marsh restoration and a case study that examines food web interactions as a measure of functionality in salt marsh restoration. In this thesis, I:

1. Argue that salt marsh restoration efforts typically focus on restoring structure. By monitoring functionality, and particularly by tracking food web interactions using stable isotope analysis, practitioners gain a better

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understanding of the higher-level impacts (and, perhaps, success) of restoration efforts. It is these higher-level functions for which salt marshes are often valued. I argue that viewing restorations through the lens of functionality may spark a reassessment of how restoration practitioners define goals and endpoints, particularly in light of uncertainties around the impacts of rising sea levels and the need to build resilient and/or adaptive systems.

2. Present a case study that argues for using stable isotope analyses of terrestrial arthropod communities to describe food web structure (species composition) and functionality (carbon flow) in order to assess salt marsh restoration success.

CHAPTER 1: Current practices in salt marsh restoration and the future of evaluating restoration success in light of climate change

Current trends and results in assessing salt marsh restoration

In New England, many salt marshes have been ditched, dammed, or drained at some point during the past 200 years. Tidal flow may be restricted or cut-off, stream banks may be unstable or channeled, and the marsh peats may be compacted (Gedan et al. 2009). These changes to the hydrology of a salt marsh can lead to dramatic, successive changes in species composition and ecosystem functioning (e.g., Roman et al. 2002, Cox et al. 2003, Wozniak et al. 2006, Gedan et al. 2009). Because the interplay between inundation and salinity can cause the greatest, furthest-reaching impacts to the marsh, restoring hydrology is often the focus of salt marsh restoration projects (covered in-depth by Roman and Burdick 2012).

In less impacted systems, such as those with intact peats, seed bank, and nearby propagule sources, hydrologic restoration is often enough to bring back vegetation; in more impacted systems (e.g., ditched marshes) active plant restoration may be used as a secondary restoration method (Green et al. 2009). Because plant species distributions are tightly coupled to hydrology in salt marshes, restored hydrology generally brings with it the typical salt marsh plant community. Restoration projects focus on restoring plant communities with the hope that higher trophic levels will, as a result, fill in (Reid et al. 2009, Moreno-Mateos and Comin 2010).

A review by Konisky et al. (2006) found that while 89% of restoration studies in New England monitored vegetation, fewer than half of these monitored higher trophic

levels, including nekton and bird communities, and even fewer monitored nutrient cycling or other ecosystem functions. Some restoration projects went more in-depth with their assessments by monitoring and manipulating invasive species. Yet, even in studies that catalogue the community composition of higher taxa and work to remove invasive species, the focus of restoration success is evaluated using the structural components of the marsh. The transfers of energy, carbon, and nutrients between species are the presumed result of restoring basic structures.

There are several reasons why restoration practitioners focus on structure. The first is because many measures of structure are relatively simple and inexpensive to collect. The second is because classic studies of restoration define restoration as human intervention that leads to succession-like changes in structure and function (Bradshaw 1984, Cortina et al. 2006) in an attempt to "reset the ecological clock" (Hobbs and Cramer 2008). In other words, a successful restoration is one that creates a foundation for the system to recover to a state that is ultimately nearly indistinguishable from an undisturbed system. By defining restoration as succession-like changes, researchers assume that there is a clear, predictive sequence of changes that should occur during restoration, leading to a clear endpoint.

Indeed, there is evidence from other systems that supporting community structure can lead to enhanced functionality through a series of successional changes. For example, long-term (45 years) protective fencing around semi-arid dune communities in northeastern China allowed successional changes in plant communities, which in turn led to increased soil fertility, increased organic matter accumulation, soil sheltering, protection from wind erosion, and other measures of functionality (Zhang et al. 2005).

Naeem (2006) presents what he calls a "biodiversity-ecosystem functioning perspective," by which "any change in a community has its consequences for ecosystem functioning, and vice versa". Naeem's perspective lays a foundation for the assumption that biodiversity serves as a driver of successive changes leading to increased functionality. While biodiversity may drive trophic complexity and resilience, the way in which that process occurs has been debated. Giller and O'Donovan (2002) present two opposing models that suggest different roles of biodiversity as a predictor of functionality. In one scenario, the majority of species have little impact on system functionality and instead keystone species are drivers of ecosystem function. Alternatively, the redundant species hypothesis suggests that species loss has a negligible effect to ecosystem function until a threshold is met whereby enough species are lost that redundancies in a system are removed and function is lost.

Because salt marshes generally have low plant richness, neither model by Giller and O'Donovan may suit salt marsh systems. In a Texas salt marsh, as few as four species represented 73.4 – 85.9 % of the relative cover in brackish and salt marshes, respectively (Judd and Lonard 2002). Plant species richness in those marshes varied from 18 to 32 species. Interpreting these results in regards to the importance of maintaining biodiversity for restoration can be tricky. On the surface, it may appear that the salt marshes can function with very few species. At the same time, it may be that small patches of high plant diversity, such as in forb pannes (Griffin et al. 2011), support key ecosystem functions.

It is unclear if plant diversity is a strong driver of consumer diversity in salt marsh systems. Many salt marsh arthropods are resource-specific (tettigonids: Wason and

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Pennings 2008; cicadellids: Rossi and Strong 1990; aphids: Hacker and Bertness 1995), so one might expect that a variety of plant species yields a variety of arthropod species. Zedler et al. (2001) noted that studies have found associations between salt marsh biodiversity and a variety of ecological functions, including productivity, resiliency, and resistance to invasive species. Yet, there are many circumstances in other systems (particularly in grasslands) where this contention is not supported.

Research in grasslands has yielded mixed results with regard to the ability of plant biodiversity to drive functionality, as measured by trophic complexity. For example, plant species richness has been shown to be correlated with arthropod species richness, though the relationship between plant diversity and arthropod diversity may depend on the trophic position of those arthropods (Perner et al. 2003, Haddad et al. 2009). Although plant diversity was significantly correlated with arthropod diversity in a brome (*Bromus*) field in Minnesota, arthropod diversity was more strongly correlated with the diversity of predators and parasites (Siemann et al. 1998). Chain modeling by Siemann et al. (1998) suggested that grassland arthropod diversity may have been more strongly driven by relationships among the arthropods themselves (competition within functional groups, and predation among functional groups), than by the diversity of producers.

These studies on biodiversity may call into question the reliance on using plant diversity as an indicator of function. Furthermore, the restoration techniques that would be used for the goal of increasing biodiversity are not always the same techniques that might be used to mimic a reference system. Restoration practitioners in Northern Europe often encounter salt marshes that have been grazed for centuries; the invertebrate community composition (different species, trophic structure, overall invertebrate

abundance) is impacted indirectly by the grazing, which raises soil temperature and reduces vegetation height (Ford et al. 2012). Grazed land in these marshes supported a lower diversity of terrestrial arthropods overall, but a greater abundance of saltmarsh specialist species (defined as "those species that are only found in inter-tidal or estuarine habitats", Ford et al. 2012) than ungrazed marshes. If restoration efforts are aimed at supporting the greatest diversity of arthropods (a structural goal), grazing should continue as a mechanism for maintaining arthropod diversity. However, arthropod diversity itself does not guarantee specific functional trophic interactions. Higher-level predators (birds, fish, and mammals) may be better sustained by the large invertebrates (higher quality prey) that favored the ungrazed marsh (Ford et al. 2012).

In some cases, restoration practitioners may encounter projects where measures of structure do not match restoration goals, even though the site appears to function appropriately. Hilderbrand et al. (2005) warn against common myths of "carbon copy" and "fast forward" restoration that place emphasis on restoration as accelerated succession, when in fact, there is evidence that disturbed systems will not, and should not, be expected to perfectly mirror an undisturbed reference system. An inherent complication in monitoring structure through vegetation is that unusual conditions like temporarily suppressed tidal cycles or salinity changes due to unusual weather patterns, or other assembly influences (Keddy 1999) at the beginning of a restoration might select for atypical vegetation. The plants that prefer those initial conditions might dominate the more typical salt marsh species in the future simply because they established first. This "alternate state" could lead to the conclusion that the restoration was not successful, because the plant taxa composition is atypical. However, it may be that the marsh is a

highly productive system that supports a broad array of trophic interactions. In this way, the marsh is structurally different than a typical marsh in that region, but may function to support a strong network of consumers.

The specific taxa and the functions achieved by those taxa are often essential in defining successful restoration. One way to approach restoration of plant systems may be to focus on a few key species, rather than attempting a copy-paste of an entire ecosystem (Zedler et al. 2001). In New England salt marsh systems, the bulk of productivity is driven by *Spartina alterniflora*. Yet, the majority of this productivity is exported to downstream estuaries in the form of wrack (Wilson 2002, McLusky and Elliott 2009). While many restoration efforts focus on managing *Spartina* populations, some stable isotope analyses indicate that managers should focus salt marsh restoration efforts on physical creek structure and monitoring algal populations rather than high-marsh vascular plant assemblages. Studies by Currin et al. (1995) and Kwak and Zedler (1997) used carbon, nitrogen, and sulfur isotope mixing models to determine that, surprisingly, high marsh vegetation had very little influence on the majority of the consumer food web. Instead, low marsh *Spartina*, macroalgae, and microalgae served as the primary carbon sources for nekton (Currin et al. 1995, Kwak and Zedler 1997), benthic invertebrates (Currin et al. 1995, Kwak and Zedler 1997), and the top consumer (Light-Footed Clapper Rail) (Kwak and Zedler 1997). These trophic interactions and carbon/nutrient transfers would not have been apparent without studying the functionality of the marsh. It is clear that managers need to consider the utility of focusing monitoring efforts on channel morphology versus high-marsh plant community restoration, and that there is much to be learned from measures of functionality.

Further evidence from natural abundance (Brusati and Grosholz 2008) and enrichment (Galván et al. 2011) studies using stable isotopes suggest that salt marsh invertebrate food webs are supported by algae rather than macrophytes. While invasives (i.e., *Phragmites australis*) can have dramatic impacts on salt marsh food web structure (Gratton and Denno 2005, Bedford and Powell 2005) and functionality (Gratton and Denno 2006), Brusati and Grosholz (2008) found that invasive, hybrid *Spartina* (introduced *S. alterniflora* X native *S. foliosa*), caused structural changes to the salt marsh without altering functionality. While epifauna did not shift their diets in response to *Spartina* hybrid invasion (Brusati and Grosholz), some infaunal communities in the same marsh did show changes in carbon isotopes (Levin et al. 2006). These data suggest that not only do guilds respond dissimilarly to changes in macrophyte communities, but that infaunal and epifaunal populations may not share carbon sources. Furthermore, if vegetation monitoring is focused on monitoring only macrophyte communities, food web interactions based on algae carbon sources will be overlooked.

Given the uncertainties around the ability of structural measures to serve as appropriate proxies for functionality, how do restorationists incorporate functional measures into monitoring restoration regimes? After all, tracking changes in plant cover and pore water salinity, for example, are generally less expensive and easier to conduct than describing trophic interactions and nutrient transfers. One way to step beyond relying entirely on structural endpoints is to define the goals of restoration in terms of maximized functionality, rather than prescribed structure. In this way, a restored site may not need to mimic an undisturbed site, so long as the "restored" site performs functionally. Another way to think of this effort is to look beyond the term *restoration*,

and allow for *rehabilitation* (mending a damaged system), or *reallocation* (creating an alternative system) as suggested by Hobbs and Cramer (2008).

<u>Viewing restorations through the lens of functionality, in light of climate change</u>

As coastal systems that are highly influenced by hydrology and salinity regimes, salt marshes could be particularly vulnerable to climate change. Yet, the extent to which those pressures will impact salt marsh systems is debated and has evolved over time. Those plant species that have thrived in salt marshes for the past century may struggle as a result of changing tide cycles, salinity fluctuations, increased temperatures, or altered precipitation patterns. When preparing sites for restoration, restoration ecologists may not be able to use the past as a guide. Instead, they may ask, "How can we best prepare new, fragile sites for possible dramatic changes?" Should the focus be on restoring to mirror the past, or *restructuring* to prepare for maintaining function in the future?

In order to explore other ways in which to define restoration "endpoints," we must first reassess the goals of restoration. We can break down the goal of restoring a "fully functioning" marsh, for example, as a resilient system that supports multi-trophic species diversity, ecosystem complexity, and nutrient cycling; these goals describe the function of a restored system without defining the intended structure. I believe that the best approach for defining restoration endpoints is to define endpoints in terms of a combination of structural goals (e.g., plant community composition) and functional goals (e.g., nutrient cycling).

Changes resulting from climate change
Using structural goals to define restoration is problematic when the baseline for appropriate structure shifts as a result of climate change. Sea level rise is one of the

biggest concerns for estuarine systems because sediment accretion rates may not keep pace with sea level rise (Warren and Niering 1993, Andersen et al. 2011), particularly in newly-restored marshes (Callaway et al. 2007). Some sea-level modeling suggested that sea level changes are unlikely to have strong impacts on salt marsh systems, except in marshes with mesotidal ranges (Simas et al. 2001). However, there is evidence for decreased accretion rates paired with increased tidal inundations rates (Andersen et al. 2011), and relatively small tidal ranges many not impart immunity on salt marshes. For example, recent research predicts broad impacts to estuarine habitats in the Chesapeake Bay as a result of more frequent and prolonged tidal inundation and increased variability in salinity (Najjar et al. 2010). Thus, sea level rise could be a driver of salt marsh change in the future.

Accretion varies between marshes based on the origin of the materials (organogenic or mineralogenic) and, for mineralogenic marshes in particular, on tidal regimes. In organogenic marshes, accretion is generally a result of accumulating roots and rhizomes, whereas in mineralogenic marshes, accretion is a result of allochthonous materials from creeks/estuaries – outside of the marsh (Kolker et al. 2009). Whereas mineralogenic mesotidal marsh accretion is mainly driven by storms, macrotidal mineralogenic marshes, such as those in New England (Goodman et al. 2007), are influenced more by the magnitude of tidal inundation (Stumpf 1983). In New England, a relatively large portion of the inorganic material deposited on the high marsh (generally around 5%, but as high as 20%) can be deposited by ice rafting (Wood et al. 1989).

Accretion has a reciprocal relationship with the plant community; small changes in accretion rates affect flooding on the high marsh, and, as a result, influence the plant

community, which is very sensitive to changes in salinity and flooding (Pennings et al. 2005). The plant community itself can, in turn, influence accretion, though the mechanisms that control deposition of organic material are debated (Nyman et al. 2006). *Spartina alterniflora* indirectly contributes to low marsh accretion by trapping sediments along the edges of tidal creeks (Morris et al. 2002), but can also contribute to accretion through vegetative growth when sedimentation is consistent (Nyman et al. 2006). Conversely, much of the biomass from *Spartina alterniflora* is exported downstream in New England marshes (McLusky and Elliott 2009) and does not directly contribute to high marsh accretion, whereas much of the detritus from the high-marsh species *Spartina patens* is deposited on the high marsh surface, which decomposes slowly in the anoxic soil conditions, thus leading to accretion (Foote and Reynolds 1997). If rising sea levels force *Spartina alterniflora* to invade the high marsh, as observed by Donnelly and Bertness (2001), it is unclear if accretion rates will keep up (Charles and Dukes 2009). Because of the different ways that *S. alterniflora* and *S. patens* contribute to accretion in New England salt marshes, the types of sediments that contribute to accretion (organic or inorganic) will change.

Other changes in plant community composition are likely to result from rising sea levels. Warren and Niering (1993) found that high marsh areas experiencing increased tidal inundation caused by decreased accretion rates had fewer pure stands of *Spartina patens* and *Juncus gerardii* and increased abundance of other salt marsh species. These changes took place in New England salt marshes between the late 1940s and 1980s and were consistent across marshes in the area. In mineralogenic marshes, the high marsh

plant species composition (a structure) may not have a similar effect on accretion (a function), since the marsh is not dependent on detrital deposition.

Salt marsh salinity regime shifts resulting from climate change are difficult to predict because of many confounding influences. Studies suggest that New England salt marshes will experience dramatic salinity fluctuations seasonally (Callaway et al. 2007, Najjar et al. 2010) as climate change proceeds. Research conducted by scientists at the EPA predicts increased precipitation in the Northeastern US that is likely to occur as a result of increased frequency of heavy precipitation events (IPCC 2007). Increased precipitation is predicted to occur mainly in the winter, with as much as a 15.9% increase, mainly in the form of rain (Jacobson et al. 2009). These heavy precipitation events could lead to strong runoff events that have short-term, though dramatic, influences on salinities. It is possible that earlier springtime melts (Hodgkins et al. 2003) could, along with increased temperature, increase spring and summer salinities due to longer periods of evaporation that concentrate the salts in the stream and soil pore water. At the same time, increased inundation in New England marshes resulting from rising sea levels and decreased accretion could further increase salinities (Callaway et al. 2007).

Any influences on salinity are likely to have far-reaching effects on the plant community. Salinity is the strongest driver for plant community zonation, followed by tidal amplitude (Snedden and Steyer 2013). High salinity (Snedden and Steyer 2013) and increased temperature (Gedan and Bertness 2009) correlate with reduced high marsh plant diversity, particularly on the high marsh. Compounding pressures from increased CO_2 exposure could lead to further changes in the salt marsh plant community composition, but these impacts will likely be species-specific. For example, experiments

in which salt marsh plants in the Chesapeake Bay were exposed to increased CO_2 concentrations suggest that C_3 *Schoenoplectus americanus* (formally *Scirpus olneyi*) experienced increased growth, whereas C_4 *Spartina patens* growth was not altered by increased CO_2 (Erickson et al. 2007).

A shift from C_4 plants like *S. patens* to C_3 plants like *Schoenoplectus americanus* or *Juncus gerardii* could have important consequences for herbivore communities. Many herbivorous insects are host-specific; delphacid planthoppers are notoriously monophagous or oligophagous feeders (Thompson and Althoff 1999). If high marsh C_4 plants like *S. patens* are displaced by C_3 plants, specialist herbivorous like *Delphacodes detecta* will also be disrupted (Denno 1980). In fact, *D. detecta* is only one of several monophagous planthoppers (Delphacidae) and leafhoppers (Cicadellidae) found on *Spartina patens* (Price et al. 2011). Because the nutrition of C_3 plants and C_4 plants differ, and because the ability to assimilate that nutrition into tissue varies between herbivores (Barbehenn et al. 1999), changes in the plant community could have wide-ranging effects on transfers of carbon and nutrients through the food web (Haddad et al. 2009).

Changes in community structure at higher trophic levels in salt marsh and coastal species have been reported as a result of rising sea levels. In the tropics, mesocosm experiments on the dengue-transmitting mosquito *Aedes aegypti* have indicated that rising temperatures concurrent with IPCC 2007 predictions lead to significant decreases in pupation, smaller adults, and a greater proportion of female adults (Mohammed and Chadee 2011). Even relatively conservative models for climate change based on predicted temperature and precipitation changes suggest a northward expansion of ranges for the common house mosquito, *Culex pipiens,* on a decadal timescale (Hongoh et al.

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2012). Changes in insect communities could lead to dramatic changes in predator communities (fish, birds), particularly for migrating birds that rely on consistent food sources in the spring and fall.

Rising sea levels and coastal erosion has led to a 21 % loss of in island land area in Tangier Sound (Chesapeake Bay) over 13 yeaers, along with remarkable declines in shorebird nesting pairs. For example, a 60 % decline has occurred in common terns and 43% decline has occured black skimmers; both species have historically nested on those islands (Erwin et al. 2004). In New England, the saltmarsh sparrow (*Ammodramus caudacutus*) is already recognized as a vulnerable species and could be particularly susceptible to changes in sea level rise. Its breeding success is strongly influenced by centimeter-scale changes in tidal inundation (Bayard and Elphick 2011) and it is dependent exclusively on high marsh habitats for nesting (BirdLife International 2012).

While some of the structural impacts of climate change on salt marshes are becoming apparent, the associated functional changes have been less clear. For example, it is unclear if changes in plant phenology will match those in herbivore abundance, or if anadromous fish migrations will coincide with migrations of the birds that consume those fish. Although there is evidence that saltmarsh sparrows experience nesting failures resulting from increased flooding, incomplete baseline data confound these findings (Bayard and Elphick 2011). The changes in trophic interactions resulting from structural changes are largely undocumented.

How these changes affect restoration goals
There are many uncertainties concerning how climate change pressures will affect salt marsh structure. As a result, there are even more uncertainties surrounding how those structural changes may affect the functioning of salt marsh systems – especially those

undergoing restoration. A short-term concern is that even the most "successful" restoration projects do not directly address functionality, so that in conducting restoration projects, we may be crafting systems that are ill-prepared for even small perturbations. Many questions also surround how the future *structure* of the marsh might ultimately alter *functionality* as a result of pressures from climate change. Will the marsh continue to support a wide array of breeding waterfowl? Will the marsh continue to provide flood control from storms?

Current restoration practices may, in the long run, be more disruptive than the original disturbance. If a disturbed system is not allowed to exist as a functional, yet atypical system, but rather pushed to conform to a familiar salt marsh form, we may inadvertently be nurturing ecosystems that are incapable of responding to rapid changes from climate change. It is possible that highly functional systems that have alternate structure when compared to reference systems are as resilient, or even more resilient, than typical reference systems. For example, salt marshes that have naturally recovered from a recent perturbation may be recolonized with species adapted for current conditions (temperature, salinity, weather patterns, and inundation), and so would already be a step ahead of those systems that have been in place and relatively stable for hundreds of years. Harris et al. (2006) point out that the pressures of a changing climate could lead to restored systems that are not only different than historical systems, but also unable to mimic past systems' functionality. In such situations, it is not only difficult, but often impossible to restore the system to its previous structure.

Hobbs et al. (2006) refer to these alternate states as "novel ecosystems" – those systems that are shaped by humans (directly or indirectly) such that they contain new

combinations of species (or perhaps altogether new species) that form a fairly stable ecosystems, which are often maintained by positive feedback loops. Others argue that a call to reassess restoration efforts in a way that leaves room for novel ecosystems might not be defined as restoration, but instead as *remediation* or *regeneration* (Higgs 2003). However, the important question is not so much in the definition, but in the outcomes of the effort. Harris et al. (2006) state that *process*, rather than *structure*, will prevail in such systems; I in turn define that process as *functionality*.

Ultimately, is it more important to support a highly functional ecosystem, or to preserve a system that mimics the past? If restoration practitioners strive to create a historical model for restoration, what point in history should serve as the guide? In North America, the goal of restoration is to recreate systems (usually defined by plant community and hydrological structure) that mimic pre-European settlement. In Northern Europe, where grazing has impacted salt marshes for centuries, defining a reference system is more tricky. Higgs (2003) recounts a debate at an early Society for Ecological Restoration meeting over whether grasslands that have been grazed by livestock for nearly 1000 years should continue to be managed in order to protect the system from forest succession. Both the structure and functionality of the grazed grassland was very different than it was before large-scale farming. Yet, presumably, the grazed grassland had developed a complex, intricate landscape that functioned to support a wide-range of grassland species. For instance, rare species in the United Kingdom such as the native short-haired bumblebee (*Bombus subterraneus*) are likely in decline in the grasslands because of shifts in farming practices from species-rich hay-meadows to silage production (Goulson et al. 2005).

A more extreme example is the controversial *Oostvaardersplassen*, a Dutch nature reserve designed by Dr. Frans Vera to mimic hypothetical Pleistocene-era landscapes. In an effort to introduce large grazers to the area, Vera imported Konik horses and Heck cattle as substitutes for extinct megafaunal species (Marris 2009). The nature reserve was designed to perform ecological functions rather than to preserve species. On one hand, the project may support proxy species that, ideally, perform the same functions as extinct species would have in historically "pristine" conditions. On the other hand, the project may compromise support for other native organisms that currently inhabit the system, only to preserve conditions that are no longer natural. This project is an example of a "Jurassic Park" model with limited ecological value (Harris et al. 2006). If nothing else the *Oostvaardersplassen* serves as a jumping board for discussions over how to define an endpoint for restoration – should an endpoint be a reflection of the past, or of the future?

It is clear that defining an endpoint for restoration projects can be a complicated, if not controversial, endeavor. In salt marsh restoration, restorationists must find a balance between structural goals and functional goals. In extreme circumstances, researchers may choose to forgo traditional structures (e.g., species composition), in favor of specific functional goals (e.g., large-scale grazing). In salt marsh restorations, a less radical example may be allowing for a few atypical plant or consumer species, in favor of supporting strong trophic interactions that self-established during the restoration process. In this way, the restorationist may be nurturing a self-sustaining system that is capable of withstanding pressures from climate change, without the intensive intervention methods centered around cultivating a "pure," traditional community of species.

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CHAPTER 2: A case study assessing salt marsh restoration success by using stable isotope analysis to describe food web structure and functionality

Introduction

  There have been numerous calls to measure functionality directly to better understand restoration as a means to rehabilitate a complete ecological system (Committee on Restoration of Aquatic Ecosystems: Science, Technology et al. 1992, Palmer et al. 1997, Naeem 2006, Vander Zanden et al. 2006). In heeding the call, researchers have used a diversity of methods to characterize functionality in restoring ecosystems, including the use of stable isotopes to describe arthropod food-webs (Gratton and Denno 2006), evaluating resilience by focusing on cause-effect mechanisms (Zedler and Callaway 2000), reassessing linear structure-function models in favor of state-and-transition models (Cortina et al. 2006), and using multimetric indices to describe restoration endpoints (Langman et al. 2012). Despite these efforts, routine assessment of functionality is rarely conducted, and practitioners instead continue to rely on measures of structure (e.g., plant community composition, pore water salinity) to serve as proxies for measures of functionality. In fact, most monitoring guides recommend measurements of structure, and rarely of function (e.g., Steyer and Stewart 1992, Neckles et al. 2002).

  A combination of top-down analysis of food web functionality, along with typical measures of structure, may provide a clearer assessment of restoration. Understanding functionality, for example, means understanding how primary productivity is passed through a system, regardless of what species are present. A restored system may not support target plant species. However, through measures of functionality, especially those that assess the source of carbon, it may be apparent that the community's primary

productivity does support a diverse and productive suite of consumers, predators, and decomposers.

In 2002/2004, New England researchers developed the Global Programme of Action Coalition (GPAC) protocol as a standardized method for monitoring salt marsh restoration (Neckles et al. 2002, updated in 2004) to allow for comparisons of restoration efficacy (Taylor 2008). This protocol emphasized monitoring pore-water salinity, creek water quality, and vegetative composition. In an attempt to describe functionality, the authors also recommended a regime for monitoring nekton, avian, and mosquito species in order to address utilization of the marsh by consumers. Nekton and bird community composition can indicate that a system is supporting a range of consumers. However, both groups of organisms may have large home ranges and therefore may not exclusively feed or breed in the restored marsh. While the presence of certain fish and bird species indicates the potential for food web complexity, they do not consistently demonstrate clear pathways of nutrient and carbon transfers from the restoring plant community to the integrated system of consumers, predators, and decomposers.

When researchers have monitored nutrient and carbon transfers from producers to consumers, they have often assessed aquatic food webs by examining diets of fish and other vertebrates (for an in-depth discussion, see Pasquaud et al. 2007). This method has inherent limitations: diets of small organisms (e.g., zooplankton) are difficult to quantify, soft-bodied prey may be under-represented because they are more easily digested, and the data only provide a one-time snapshot of feeding. Thus adequate quantitative descriptions of prey distributions require numerous diet samples distributed over many time periods (Baker et al. 2013), which is labor intensive. Importantly for assessing functionality, diet

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analysis rarely can be used to identify the primary producers that are supporting the system without additional chemical analysis.

A reliable, cost effective solution is to use stable isotope analysis to describe the source of carbon and the number of trophic transfers (as tracked using nitrogen) in food webs. The most common isotopes for carbon and nitrogen are ^{12}C and ^{14}N, although the stable isotopes (e.g., ^{13}C and ^{15}N) exist naturally in all environments at very low abundances. The process of photosynthesis preferentially selects for lighter carbon isotopes. The ratios in which $^{12}C/^{13}C$ are incorporated into tissues differ between C_3, C_4, and CAM photosynthetic pathways; these differences in incorporation rates can be detected by stable isotope analysis. The ratio of $^{13}C/^{12}C$ (as compared to a standard and denoted as $\delta^{13}C$, in ‰) in primary producer tissues persists in the tissues of consumers. Thus, $\delta^{13}C$ can also be used to reveal the source of primary productivity throughout the consumer-based food web, although an isotopic shift of +0.05 ‰ is typical between trophic transfers because of metabolic processes (McCutchan et al. 2003, Wozniak et al. 2006). New England salt marshes are typically dominated by C_4 *Spartina* species with lower abundances of C_3 plants like *Juncus gerardii* and *Schoenoplectus maritimus*. Just as *Spartina* abundance can be used as an indicator of successful plant community restoration, the C_4 signature that persists in the tissues of herbivores and other consumers that rely on *Spartina* as a carbon source can indicate transfers of primary productivity through the food web.

The lighter isotope ^{14}N is preferentially excreted by consumers, which causes ^{15}N to accumulate by an average value of 3-4 ‰ between trophic levels (Peterson and Fry 1987, Post 2002, Vander Zanden and Rasmussen 2001). This accumulation can be used

to describe trophic complexity by quantifying the number of trophic transfers. For instance, the predatory ladybeetle Coccinellidae is enriched in ^{15}N relative to the herbivorous aphids it consumes. Furthermore, a spider that consumes a diversity of prey, based on a diversity of carbon sources, will have an intermediate carbon value compared to a ladybeetle that only eats aphids that are, in turn, supported by one species of plant.

A powerful approach to assessing marsh functionality using invertebrates combines community surveys of terrestrial arthropods with stable isotope analysis. In their 2005 study, Gratton and Denno recorded changes in arthropod assemblages in a salt marsh undergoing removal of invasive *Phragmites australis*. These results indicated that changes in plant communities altered arthropod communities. In a later iteration of the study, stable isotope analysis revealed that the restored *Spartina* marsh was functioning to support typical salt marsh arthropods (herbivores through top consumers) within one year of final *P. australis* removal (Gratton and Denno 2006). The arthropod survey in the 2005 study revealed the community structure of the restoring marsh, whereas the 2006 stable isotope work provided the functional framework for describing the changing trophic interactions between those species before, during, and after removal of invasive species.

The ability to detect the functional impact of non-native plants such as *Phragmites australis* in restoring ecosystems is particularly important because large scale disturbances may release a pulse of nutrients (Portnoy 1999, Theodose unpublished). This pulse may allow invasives such as *P. australis* to outcompete other brackish species (Rickey and Anderson 2004).

While Gratton and Denno (2005 and 2006) approached salt marsh restoration from the prospective of invasive species removal in an otherwise intact system, my study examined salt marsh restoration of a system that underwent dramatic changes to the entire ecosystem. In 1934, the state built a road and berm that blocked tidal exchange between Sherman Marsh, Newcastle, Maine, and the Marsh River, a shallow 90-ha freshwater lake. In October 2005, a portion of the berm washed away in a storm, draining the lake and naturally restoring partial tidal flow to the Marsh River (Figure 1). The tidal creek and high marsh surfaces were essentially intact. In the spring of 2006, Dr. Karen Wilson and her graduate student Laura Jones began monitoring pore water salinity, creek water salinity, and tidal signals. They also installed permanent vegetation monitoring transects across Sherman Marsh and a reference site immediately upstream of the old dam site. These data indicate that *Juncus gerardii* was one of the first plants to establish throughout Sherman Marsh, along with limited *Spartina alterniflora* populations along the low marsh of the inlet area of Sherman Marsh (Jones 2007).

Since it was first detected in Sherman Marsh in 2007, invasive *P. australis* was very patchy and maintained a relatively diverse assemblage of lower-growing plant species between stems. The invasive patch of *P. australis* in the upstream portion of the nearby reference marsh, however, had clearly-defined borders and tall, dense stems, and was located within 200 m of a large patch of native haplotype *P. australis*. These differences allowed for comparisons of structure and functionality of both native and invasive haplotypes of *P. australis* (Saltonstall et al. 2004).

Because of the groundwork conducted by Wilson and Jones, Sherman Marsh served as an ideal model system for this study; the structure of the marsh had been

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monitored since the first growing season following the dam breech. My study builds upon the existing monitoring efforts by incorporating structural measures with functional measures. I assessed structure by monitoring plant and terrestrial arthropod communities on Sherman Marsh and the nearby reference marsh. I used stable isotope analysis to track food web interactions between arthropod and plant; these results were used to integrate measures of functionality (i.e., carbon and nitrogen transfers within the food web).

I hypothesized that areas with similar plant community structure in Sherman Marsh and the reference marsh would support similar food web interactions, as evidenced by similar ^{13}C and ^{15}N values within arthropod functional groups. In addition, I expected that carbon stable isotopes would be more similar for sessile herbivores and their target plants as compared to mobile herbivores, and that spiders, as top predators, would be relatively enriched in ^{15}N compared to other consumers. I also compared structural and functional measures between native and invasive *Phragmites australis* patches in Sherman Marsh and reference systems; I hypothesized that native *P. australis* would be better integrated into the food web than would invasive *P. australis* as measured by similarities in carbon stable isotope values of herbivores and consumers found in the *Pragmites* patches.

I determined the extent to which functionality mirrored structure in this restoring marsh by:

(1) assessing *structural measures* in Sherman Marsh and nearby reference marshes through plant and arthropod community structure.

(2) assessing *functionality*, as described by C and N transfers, within patches of similar plant species in Sherman Marsh and nearby reference marshes.
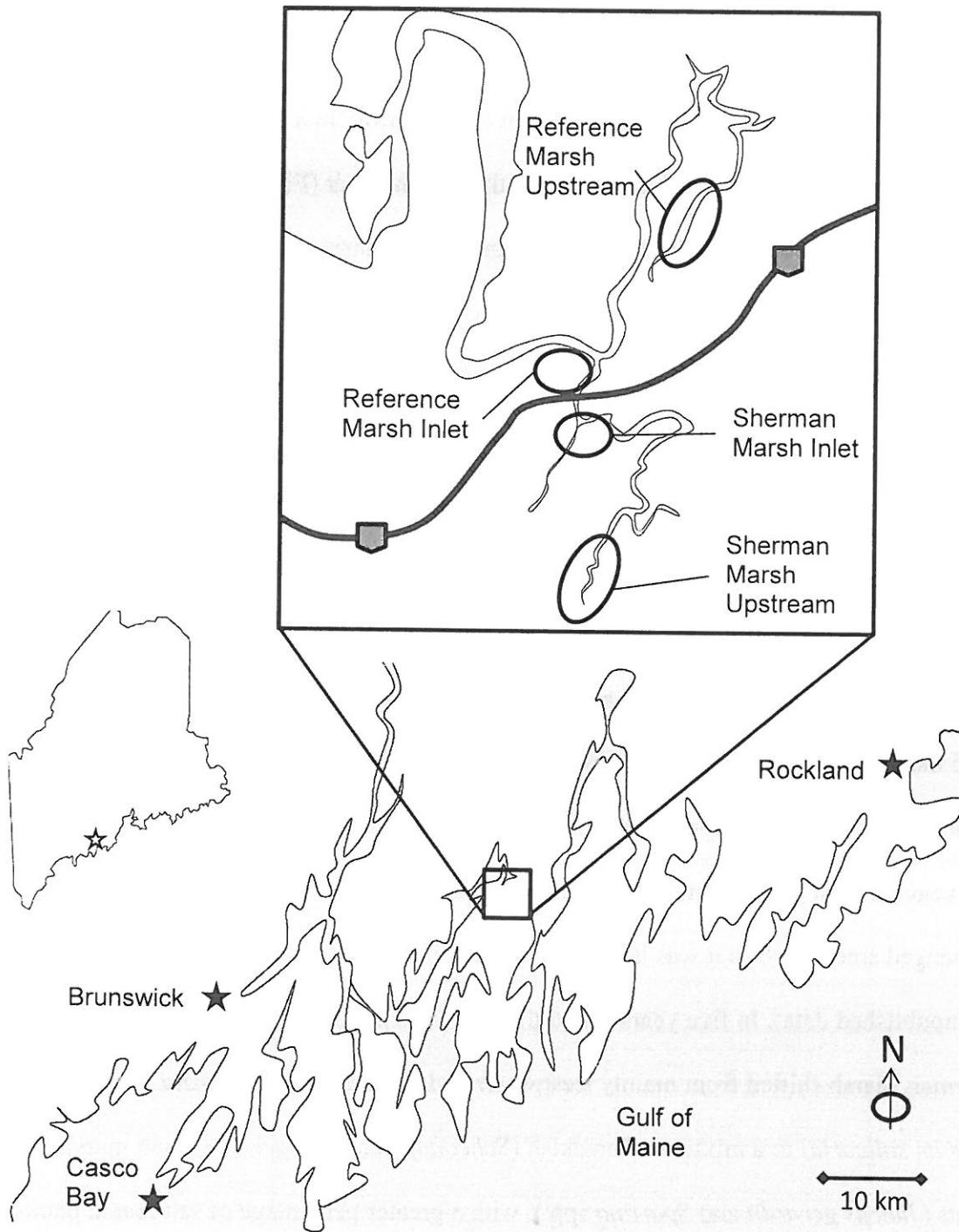
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Figure 1. Map of study sites. Sherman Marsh is located in Newcastle, Maine. The marsh north of Route 1 served as the reference sites and the marsh south of Route 1 (Sherman Marsh) is undergoing restoration.

Methods

Site Description

In October 2005, a portion of the berm washed away in a storm, draining the lake and naturally restoring partial tidal flow with the Marsh River (Figure 1). A restoration project was implemented by the Maine Department of Transportation and other partners, in conjunction with Dr. Karen Wilson at the University of Southern Maine. The reference marsh is located adjacent to, and north of, the restored inlet, and represents an interior salt marsh plant community typical of the area (Jones 2007).

Vegetative regrowth, soil salinities, and creek water quality have been monitored in Sherman Marsh and in the Reference Marsh since the first growing season following the berm wash-out (Jones 2007, Wilson et al. unpublished data). Pore-water salinities have increased since summer 2006 as a result of increased tidal inundation, particularly since the inlet into Sherman Marsh continued to expand as a result of successive storm events in May 2006 and April 2007, and after the inlet reconstruction in October 2008. The vegetation in the inlet area of the reference marsh (RMI) has remained relatively unchanged since 2006 as it was largely unaffected by the 2005 washout event (Wilson et al. unpublished data). In five years (2006 through 2011), the dominant vegetation in Sherman Marsh shifted from mainly freshwater and upland plants (*Zizanzia sp.* and *Lithrum salicaria)* to a mixture of brackish (*Scheonoplectus pungens*) and salt marsh plants (*Juncus gerardii* and *Spartina* spp.), with a greater percentage of salt marsh plants towards the inlet.

The upstream portion of the reference marsh (RMU) was added to the vegetation and salinity monitoring regimes in 2009. The RMU was dominated by freshwater inputs,

with a flora typical of brackish marshes and was used as a reference for the upstream portions of Sherman Marsh (SMU). It was dominated by *Spartina patens, Spartina pectinata,* and *Carex* spp. and was relatively undisturbed by human activity (although in the past it was ditched and hayed).

Small (mean 185 m^2), sparse (6.1 stems/m^2) patches of invasive *Phragmites australis* were widespread throughout Sherman Marsh in 2009 when this study was conducted and in one large (approximately 60 m by 25 m) dense patch was well established in the reference marsh upstream (unpublished data). Additionally, a native haplotype of *P. australis* was present in the RMU, but not in Sherman Marsh nor in the RMI.

<u>Experimental Design</u>

Selection of Target Plant Patches

Arthropods were collected from patches of three target plants: (1) *Juncus gerardii,* (2) *Spartina alterniflora* and (3) *Phragmites australis. J. gerardii* established in 2006 on Sherman Marsh and has remained the most abundant species, along with *Typha spp.* and *Schoenoplectus maritimus.* All three of these abundant species are C$_3$ plants. Arthropods that use these plants for food or shelter therefore had 3-4 years to establish on the marsh. *Spartina alterniflora* established along the banks of the Sherman Marsh inlet (SMI) in 2006 and dominated the creek-edge of the reference marsh. As a C$_4$ plant, its carbon stable isotope values are shifted approximately -10-15 ppt from those of C$_3$ plants. *Spartina alterniflora* was not well established in the SMU by the summer of 2009. Beginning in 2007, *Phragmites australis* (non-native haplotype) expanded rapidly (> 1 m patch diameter per year, personal observation) throughout Sherman Marsh and was established in the RMU. Large areas of native *P. australis* were present in the RMU and

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therefore provided a rare opportunity to compare arthropod communities between native and invasive haplotypes.

Target vegetation patches were chosen randomly from mapped swaths of vegetation in each marsh area: SMI, SMU, RMI, RMU (Figure 1). Rectangular swaths were drawn perpendicular to the creek edge starting at mean sea level, and parallel but offset by 3 m to the north from to existing permanent transects used for vegetation monitoring. Swaths were large enough to include at least ten patches of target plant species, and thus ranged from 10 to 20 m wide, and 30 to 70 m long. I mapped dominant vegetation patches in these swaths using a 2003 Trimble GEOXT, collecting eleven data points at each vertex for accuracy.

From each mapped swath, I randomly selected three replicate 1 m^2 plots of each target plant species by overlaying 1 m^2 grids on the mapped target vegetation patches using ArcMap9.3 (2008) and an Excel random number generator. However, not all target plant species were equally abundant in each marsh-area (Table 1).

Plots were characterized by plant species composition and percent cover on July 7, 9, and 10, 2009 using the point-intercept method, modified from Caratti (2006) so as to slide dowels into place, rather than mat the vegetation with a pre-formed grid. Because plant cover may overlap at any given point, the total percent cover for a plot may reach a sum of >100 % cover. Plants were identified according to Tiner (1987), Uva et al. (1997), and Crow and Hellquist (2000) to the lowest possible taxonomic level, usually species and/or genus, but sometimes family. Taxonomic names were standardized using the online USDA PLANTS Database and the New England Wildflower Society website.

Table 1. Mean (± SE) percent cover representing the most abundant plant taxa from each site. The "other" category represents an average cover of all other species in each marsh-area. Plant species that were present in the plot but did not "hit" any of the 50 points are assigned 1% cover. [Plant abbreviations: JunGer = *Juncus gerardii*, PhrAuN = native *Phragmites australis*, PhrAus = invasive *Phragmites australis*, SpaAlt = *Spartina alterniflora*, SpaPat = *Spartina patens*. Site abbreviations: SMU = Sherman Marsh Upstream, RMU = Reference Marsh Upstream, SMI = Sherman Marsh Inlet, RMI = Reference Marsh Inlet.]

Target Plant	Site	JunGer C3	PhrAuN C3	PhrAus C3	SpaAlt C4	SpaPat C4	Other C3
JunGer	SMU	100.0 ± 0.0					36.3 ± 22.1
JunGer	RMU	41.3 ± 0.7				100.0 ± 0.0	0.7 ± 0.7
JunGer	SMI	90.7 ± 9.3				46.3 ± 24.7	23.3 ± 15.7
JunGer	RMI	100.0 ± 0.0					9.0 ± 4.5
PhrAuN	RMU		35.3 ± 8.7				136.0 ± 12.4
PhrAus	SMU	22.0 ± 11.4		50.0 ± 8.1			34.3 ± 16.5
PhrAus	RMU			84.7 ± 10.5		7.3 ± 7.3	15.7 ± 7.4
SpaAlt	SMI				100.0 ± 0.0	0.3 ± 0.3	24.3 ± 24.3
SpaAlt	RMI				92.7 ± 7.3	98.7 ± 1.3	1.3 ± 1.3

Arthropod Community Sampling

    I collected arthropods in the plant plots on July 12, 14, and 17, 2009 after plant sampling, plus an additional sampling on August 6, 7, 13, and 18, 2009 to allow the arthropods to resettle after the disturbance. I only collected on days with partial to full sun in order to avoid differences in temperature-driven changes in metabolic rates (Frazer et al. 1997) and because small flying insects are less active on cool and/or windy days (Peng et al. 1992). Researchers in a previous study (Wu et al. 2008) collected terrestrial saltmarsh arthropods on sunny days between 10 am and 3 pm in June and August. Consequently, appropriate days for arthropod sampling were limited in 2009, which at that time was the rainiest summer on record in Maine, with over 55 cm of rain over three months; the average rainfall for the previous 30 year period was just over 24 cm (NOAA National Weather Service 2009).

    In July, arthropods were collected using a combination of timed hand-collection, sweep-netting, and pitfall traps. Hand-collections were made by myself and an assistant using an aspirator and forceps for 2 minutes. Sweep samples were consistently performed by myself by sweeping three fast, consistent sweeps across the vegetation in the plot using a 38 cm diameter canvas sweep net. Unbaited clear plastic pitfall traps (11.4 cm dia. x 7.6 cm deep) were placed for 2 hours at the center of each plant plot so that the top lip of the trap was even with the surface of the marsh. Some traps (especially in *S. alterniflora* patches) were flooded by the tide and discarded from analysis. For the August collections, arthropods were collected using a Black and Decker CHV1568 DustBuster (15.6 V) handheld vacuum. Vegetation in the plot was vacuumed for 45 seconds, and the contents of the vacuum were transferred to zipper-sealed bags.

Arthropods were stored in a small cooler with freezer packs and then frozen upon returning from the field.

Arthropods were identified to the lowest taxonomic level possible and were generally identified to family level; however, Collembola and Thysanoptera were identified to order (Borror et al. 1976, Merritt and Cummins 1995, Ubick et al. 2009).

Food Web Analysis

Base of food web (Primary producers, litter and soil)

To provide food web context for the arthropods, I collected samples of live vegetation, leaf litter, and soil from each replicate arthropod plot. Vegetation samples consisted of leaves and stems from five or more individual target plants within the arthropod plots. Soil samples were collected with a trowel from the top 10 cm of soil. Litter was comprised of a representative sample of all dead plant matter in the plot. Samples were kept cool in the field and frozen in the lab within eight hours of collection.

Plant and litter samples were processed by rinsing vigorously in tap water, followed by thorough rinsing with deionized water. Soil samples were not rinsed. All samples were thawed, then dried at 65°C for at least 48 hours, ground using a mortar and pestle, and passed through a 500 μm sieve. Samples were packaged in tin capsules and sent to the University of California Stable Isotope Facility (Davis, California, USA) and were analyzed for ^{15}N and ^{13}C natural abundance. Because of budgetary constraints and because biomass was limited in some plots, all replicate samples within a target vegetation area (e.g., the three replicate plots of *J. gerardii* in the RMU) were pooled for each study area before analysis.

Arthropods

Arthropods from each plot were sorted according to trophic level (detritivore, herbivore, and predator). Herbivores were further divided into sessile and motile types based on differences in dispersal capabilities. Sessile types (e.g., aphids), tending to remain *in situ*, would be expected to have carbon signatures closely reflecting those of their host plants. By contrast, motile types (e.g., plant hoppers), by hopping or flying from plant-to-plant, would be expected to show less host fidelity in their carbon signatures. Furthermore, motile herbivores could be passing through the site without consuming the target vegetation, unlike sessile herbivores. Because spiders function as top predators within arthropod food webs, they were separated from other predators, as in Gratton and Denno (2006).

Taxa that could not be separated into distinct functional feeding groups were not used for stable isotope analyses (Borror et al. 1976, Merritt and Cummins 1995). For example, chironomids were not included in stable isotope analyses because, within this broad family, some larvae filter feed, while others are leaf-miners, and still others are predaceous, and most chironomids do not feed as adults (Merritt and Cummins 1995). These feeding groups cannot be defined without identifying the midges to genus or species, which is particularly difficult.

Because many of the specimens were very small, arthropod samples were only rinsed with deionized water when mud or debris was clearly stuck to the sample. Whole organisms were dried at 65 °C for ≥ 24 hours and ground using a mortar and pestle. Several individuals or taxa within one functional feeding group were usually pooled in order to provide enough biomass for stable isotope analysis. Because spiders can be large and often have bulky, bulbous abdomens, there is some discussion over whether to

exclude the guts (Oelbermann and Scheu 2002), whether to use just the cephalothorax or the legs (Collier et al. 2002), or whether to use the whole organism (Gratton and Denno 2006) for stable isotope analysis. Most of the spiders I collected were very small, so I used whole organisms. Additionally, there is evidence that removing the guts of marine invertebrates has virtually no effect on ^{15}N and ^{13}C values (Mateo et al. 2008). Arthropod samples were sent to the same lab as the soil and plant samples.

Results

Target Plant Patch Community Composition

Overall, the plant community structure was comparable between the RMI and the SMI (Table 1). *Spartina alterniflora* and associates were the dominant species in low marsh target plant patches (90.7 ± 9.3 % and 100.0 ± 0.0 %, mean ± SE cover) in the SMI and the RMI, respectively. Although some less abundant saltmarsh species found in the reference marsh (i.e., *Triglochin maritima*, *Distichlis spicata*) had colonized the SMI by 2009, they were either absent or in low abundance (≤ 10 % cover) in SMI plots.

Juncus gerardii was the dominant plant species throughout much of the SMU, with 100% cover in target plant patches. In contrast, *J. gerardii* (41.3 ± 0.7 % cover) was always mixed in with *S. patens* (100.0 ± 0.0 % cover) in the RMU. On the other hand, *S. patens* was not well established in the SMU and did not appear in any of our 2009 plots.

The plant community structure differed remarkably between native and invasive *Phragmites* stands (Table 1). While invasive *P. australis* was patchy, relatively sparse (average of 50.0 ± 8.1 % cover), and supported an average of 34.3 ± 16.5 % cover of other plant species in the SMU, the invasive patch in the RMU was dense (average of 84.7 ± 10.5 % cover) and did not support a variety of other plant species (average of 15.7

± 7.4 % cover). Native *P. australis* stems were generally thinner in diameter and shorter (personal observation) than the invasive form, therefore reducing average cover (35.3 ± 8.7 %). Plant species richness was greatest in native stands, with a cumulative average cover of 136.0 ± 12.4 % for other plant species.

Base of Food Web

Carbon values from target C^3 plants (*J. gerardii*, native *P. australis*, and invasive *P. australis*, together ranging from -25.9 to -27.7 ‰) did not differ greatly among species or marshes, which is typical for these plants (Table 2). Carbon values for the target C_4 plant (*S. alterniflora)* were also comparable between the RMI and the SMI (-13.0 ‰ and -13.3 ‰, respectively), falling within the range of published values (Currin et al. 1995, Peterson 1999, Wozniak et al. 2006). Nitrogen values were more variable, ranging from a low of -0.6 ‰ to a maximum of 4.7 ‰ and occasionally fell outside the ranges documented in published literature (Table 2). These differences between nitrogen values did not appear to follow a pattern among marshes or target plants although nitrogen values increased as expect up trophic levels in all areas.

Soil and litter samples tended to have more intermediate (mixed C_3/C_4 origin) carbon values than target plants (Table 2). Carbon values of litter gathered in *J. gerardii* plots (-16.5 ‰) in the RMU were enriched in ^{13}C compared to the *J. gerardii* plant sample from the same plot (-27.0 ‰), and instead reflected the C_4 plant carbon values (Table 2). In the same way, litter values in invasive *P. australis* in both the SMU and the RMU were enriched in ^{13}C (-21.5 ‰ and -19.2 ‰, respectively) compared to the target plants (-27.2 ‰ and -27.7 ‰). Native *Phragmites* in the RMU was more abundant along the upland edges of the marsh, rather than near the creek; the carbon signatures of litter (-28.2 ‰) and soil (-26.6 ‰) in native *Phragmites* patches were more typical of C_3 plants.

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Nitrogen values again varied for both litter (-0.1 ‰ to 4.6 ‰) and soil (0.3 ‰ to 5.0 ‰) samples throughout the two marshes.

Arthropod Community

Some sites lacked one or more of the trophic levels used for stable isotope analysis (i.e., no detritivores in SMI *S. alterniflora*, SMU *J. gerardii*, or RMU *J. gerardii*; no non-spider predators in native *Phragmites*) (Table 3). Although there were trophic levels unaccounted for in some sample sites, it is likely that some trophic levels were missing because many taxa were difficult to identify in the detail necessary for trophic group designation (e.g., Acari, Heteroceridae, Collembola), or because collection methods and/or seasonal sampling (especially during an unusually rainy summer) may have led to lower sampling success of certain taxa. For instance, a lack of sessile herbivores during July and August sampling occurred despite observing larval Lepidoptera throughout the marsh at other points during the summer, including abundant case-bearer moths (Coleophoridae) on *J. gerardii*.

Among target plant plots, the community composition of arthropods was generally similar between the reference and restoring sites, with one interesting exception. While SMI and RMI *S. alterniflora* sites both supported communities of Chloropidae, Ephydridae, and Thysanoptera, the most abundant motile herbivore in the SMI was Delphacidae (34 of 57 motile herbivores) and in the RMI was Cicadellidae (41 of 50 motile herbivores) (Figure 2). Cicadellids were not found in the SMI samples and delphacids were not found in the RMI samples. Cicadellids were also abundant in *J. gerardii* plots in RMU, but not in other *J. gerardii* patches.

Table 2. Carbon and nitrogen isotope values for plant, litter, and soil samples. Because replicates were not possible with these data, literature values are included for comparison. Plant and site abbreviations provided in Table 1.

Type of sample	Target Plant	δC^{13} this study				δ^{13}C lit	δN^{15} this study				δ^{15}N lit	Literature Source
		SMI	SMU	RMI	RMU		SMI	SMU	RMI	RMU		
Plant	JunGer (C3)	-26.2	-27.1	-25.9	-27.0	-27.4 to -23.4	-0.6	1.7	2.5	0.8	2.0 to 3.5	Wozniak et al. 2006
	SpaAlt (C4)	-13.3		-13.0		-13.3 to -12.9	2.2		4.7		5.3 to 7.7	Currin et al. 1995, Peterson 1999; Wozniak et al. 2006
	PhrAus (C3)		-27.2		-27.7	-26.7 to -23.4		2.2		4.1	3.1 to 6.5	Wozniak et al. 2006
	PhrAuN (C3)				-26.7					1.3		
Litter	JunGer	-26.0	-26.4	-24.0	-16.5		1.2	3.0	2.7	1.0		
	SpaAlt	-14.7		-14.7		-12.9	4.2		4.6		9.8	Gratton and Denno 2006
	PhrAus		-21.5		-19.2	-26.2		2.6		2.7	8.7	Gratton and Denno 2006
	PhrAuN				-28.2					-0.1		
Soil	JunGer	-24.0	-25.7	-25.9	-18.3		1.7	2.9	3.0	1.6		
	SpaAlt	-20.8		-18.7		-20	2.4		5.0		7.3	Gratton and Denno 2006
	PhrAus				-22.6	-23				2.2	6.8	Gratton and Denno 2006
	PhrAuN				-26.6					1.3		

Table 3. Dominant arthropod taxa by trophic level. Not all trophic levels are represented at each study site. Plant and site abbreviations provided in Table 1.

|			Dominant Arthropod Taxa			
Target Plant	Site	Sessile Herbivore	Motile Herbivore	Predator	Spider	Detritivore
JunGer	SMU		Chloropidae	Saldidae/Carabidae	Linyphiidae	Amphipoda
JunGer	RMU		Cicadellidae	Saldidae	Lycosidae	Amphipoda
JunGer	SMI		Delphacidae/Ephydridae	Saldidae	Lycosidae/Araneidae/Unkn	Amphipoda
JunGer	RMI		Cicadellidae	Saldidae	Lycosidae/Unkn.	Amphipoda
PhrAuN	RMU	Aphid	Chloropidae/Cicadellidae		Lycosidae/Salticidae	Amphipoda
PhrAuS	SMU	Aphid	Cicadellidae	Saldidae	Lycosidae/Araneidae/Unkn	Amphipoda
PhrAuS	RMU	Aphid	Delphacidae/Cicadellidae/Gryllidae	Saldidae	Lycosidae	Amphipoda
SpaAlt	SMI		Chloropidae/Delphacidae/Ephydridae	Dolichopodidae, Reduviidae, Saldidae	Lycosidae/Linyphiidae/Unkn	
SpaAlt	RMI		Cicadellidae	Coccinellidae	Lycosidae	Amphipoda

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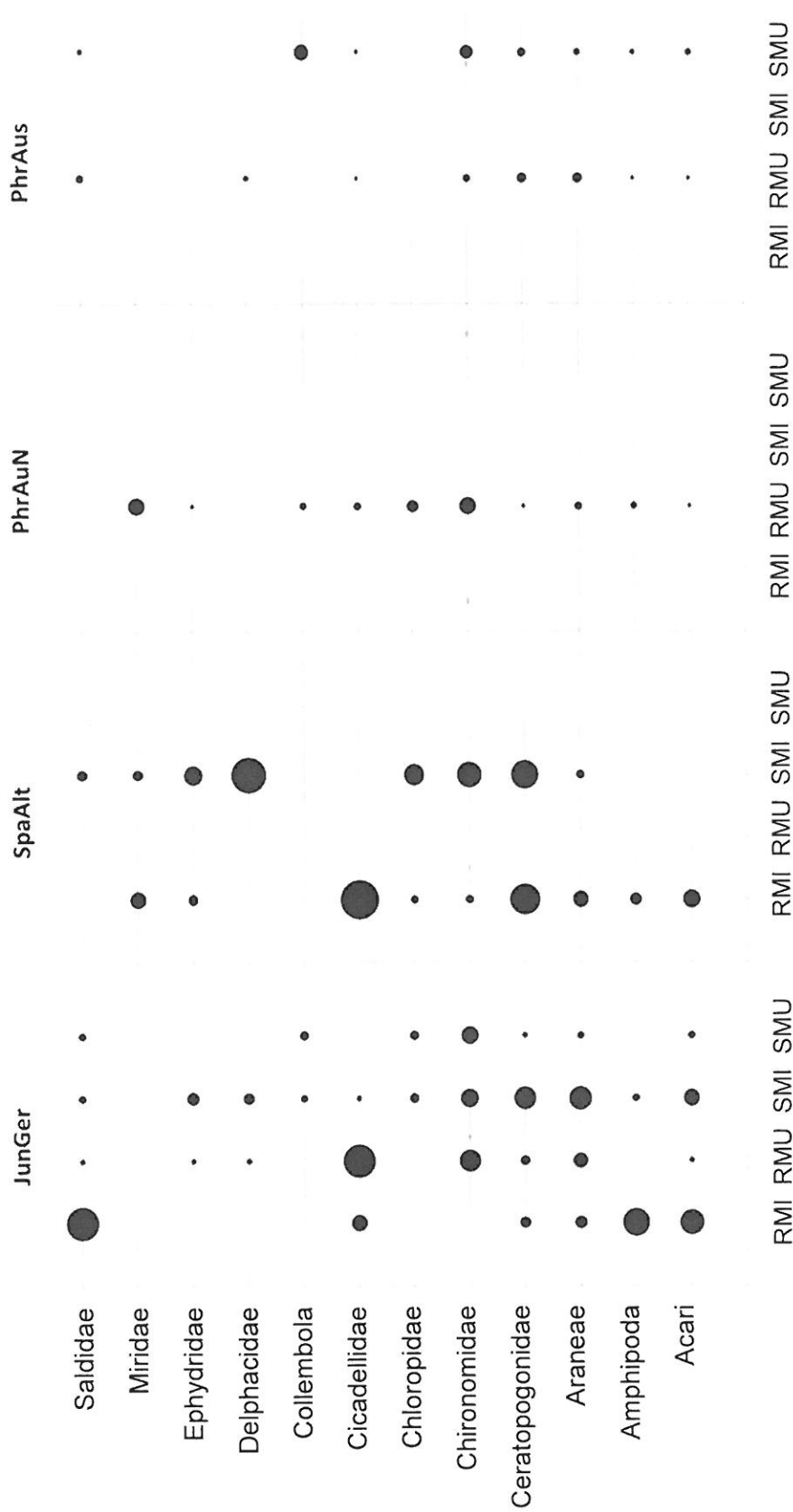
Figure 2. Relative abundance of the twelve most abundant taxa (those with at least twenty individuals) at each of the four marsh-areas. Aphids are not included in this figure because their relative abundance is remarkably high. The dots are scaled by area for abundance. Plant and site abbreviations provided in Table 1.

Arthropod Food Web

Generally, the arthropod community structures were similar and had comparable carbon and nitrogen isotope values when collected from comparable plant communities (Figures 3 and 4). With the exception of motile herbivores collected on *S. alterniflora* in the RMU, both sessile and motile herbivore carbon isotope values reflected either the target plant from which they were collected (Figure 3). Detritivores, however, had carbon values more similar to those of C_3 species (-24.1 ‰ to -19.3 ‰), regardless of where they were collected. In all marshes, spiders exhibited slightly more mixed carbon values (22.5 ‰ in C_3 plots and 15.4 ‰ in C_4 plots) than those of other predators (23.6 ‰ in C_3 plots and 13.5 ‰ in C_4 plots). Spiders were generally more enriched than other predators and the rest of the food web in ^{15}N values within each plot.

When target plant densities differed, the arthropod consumers reflected those differences. Motile herbivores collected on *J. gerardii* in RMU, where *S. patens* was remarkably abundant, were enriched in ^{13}C compared to samples in other *J. gerardii* plots (Figure 3). When target plant communities were comparable between marshes, but the arthropod community composition differed, arthropod taxa within the same functional feeding group exhibited similar carbon and nitrogen values, despite differences in taxonomy (Figures 3 and 4). This trend was particularly apparent with motile herbivores (mainly Cicadellidae, but also Ephydridae, Tettigoniidae, and Delphacidae), which had clear C_4 carbon signatures (-12.24 ‰). Though the taxa differed between the two sites, motile herbivores on *S. alterniflora* in the SMI and RMI marshes had remarkably similar carbon and nitrogen values (-13.94 $\delta^{13}C$, 6.83 $\delta^{15}N$ and -14.04 $\delta^{13}C$, 7.01 $\delta^{15}N$, respectively).

Although there were clear differences in the plant structure between the three *P. australis* sites, the consumers at all three *P. australis* sites were dominated by aphids (116-460 total aphids per site) which wholly comprised the sessile herbivore community on *P. australis*, with the exception of one *Simyra insularis* larva. In all *P. australis* sites, sessile herbivore carbon values were similar to plant carbon values (within 0.8 ‰ δ^{13}C), whereas motile herbivore values varied up to 3.8 ‰ δ^{13}C from the plant values. Predators, spiders, and motile herbivores on invasive *P. australis* tended to have more intermediate ^{13}C values (-23.3 ‰ to -21.1 ‰) than those found in native *P. australis* plots(-21.9 ‰ to -24.9 ‰), when compared to the plant values. All samples, including soil, litter, plant, and arthropod samples, in the native *P. australis* were depleted in ^{15}N by an average of 1.83 ‰, when compared to either invasive site.
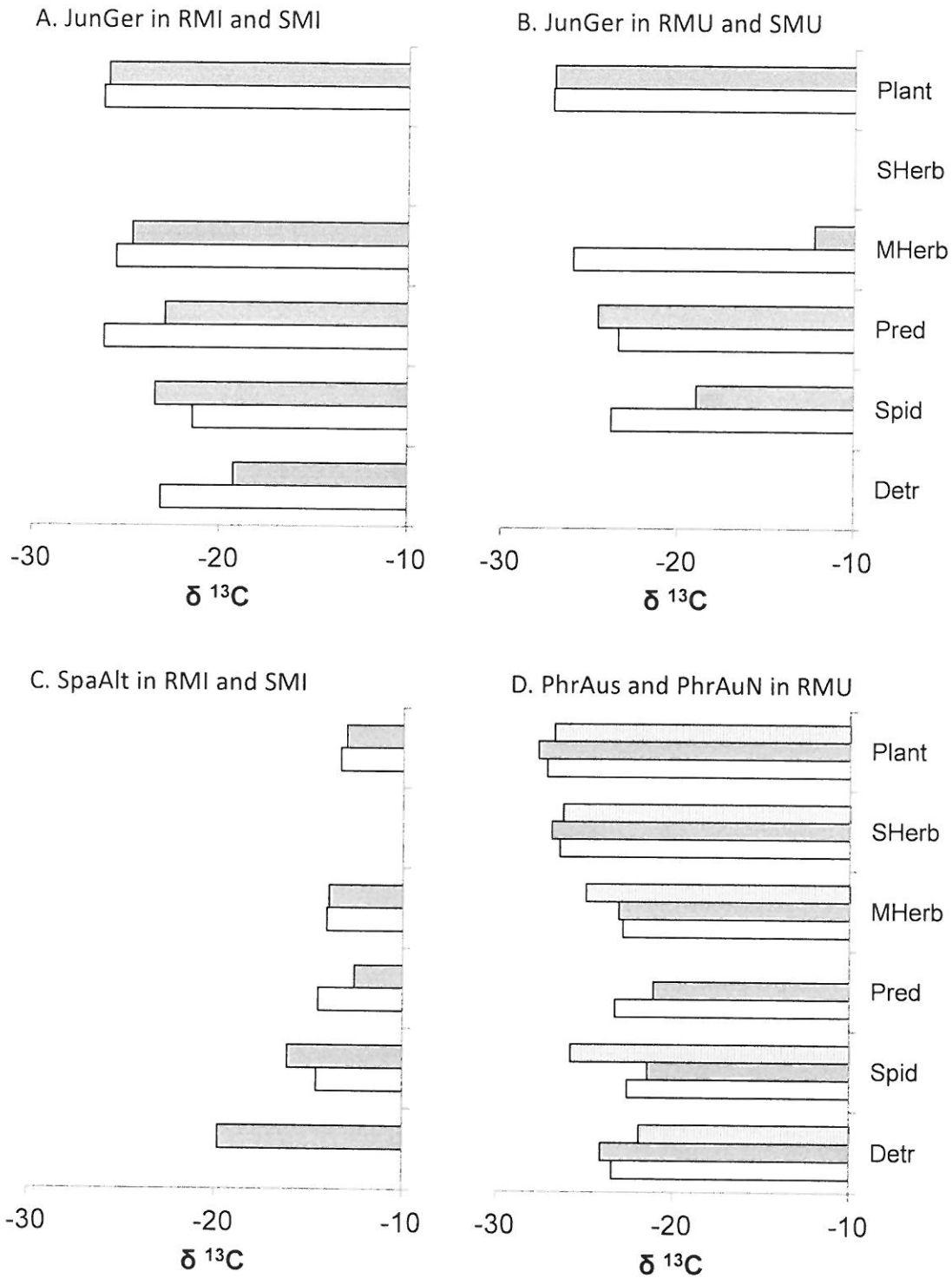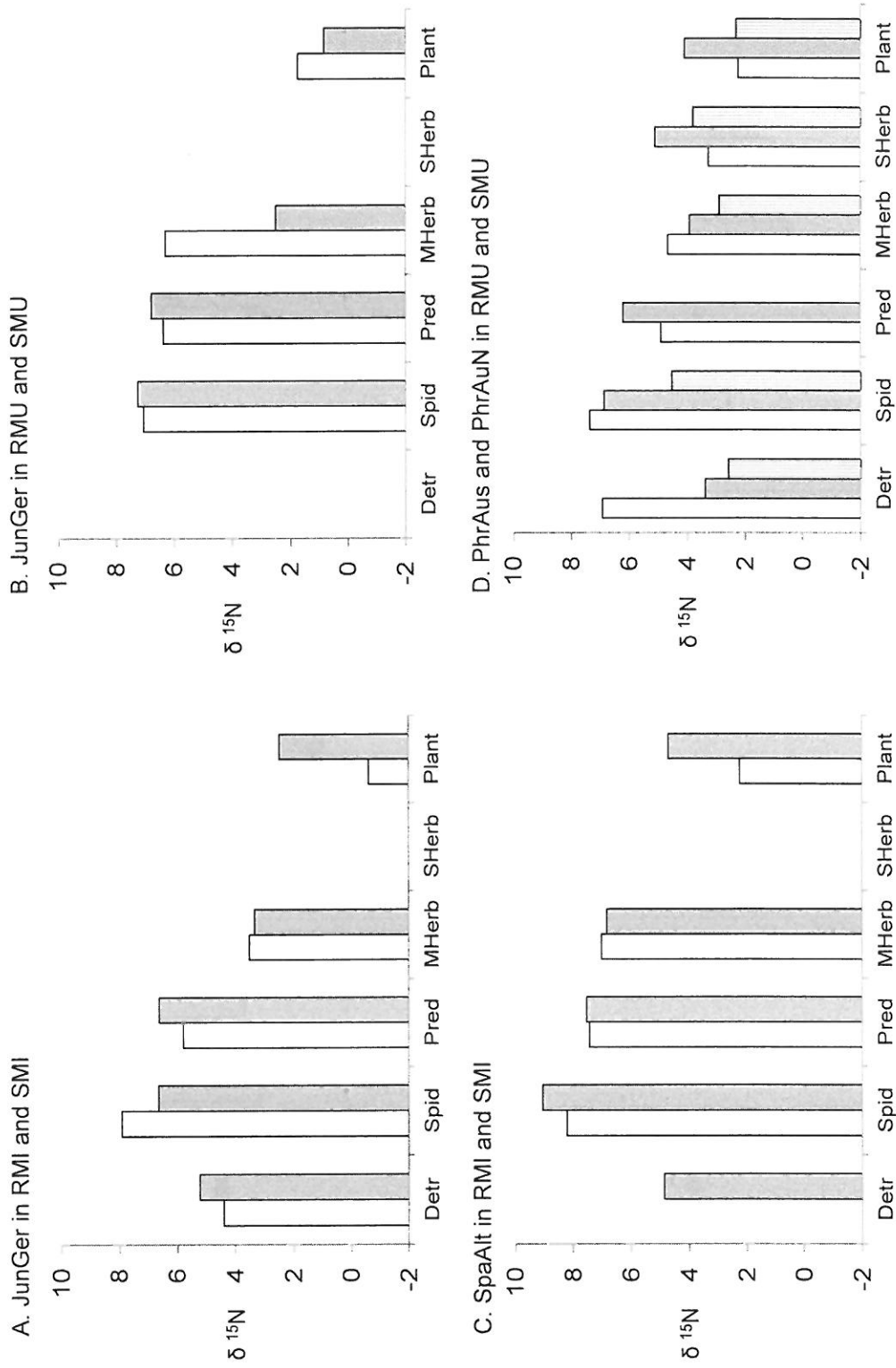
Figure 3. Carbon isotope values of arthropods collected on target plants, grouped by trophic level (Plant = target plant sample, SHerb = sessile herbivore, MHerb = motile herbivore, Pred = predator, Spid = spider, Detri = detritivore). Reference sites are indicated by solid grey bars and restoring sites are indicated by white bars. Striped grey bars represent native *Phragmites australis* in the RMU. Plant and site abbreviations provided in Table 1.

Figure 4. Nitrogen isotope values of arthropods collected on target plants, grouped by trophic level. Reference sites are indicated by solid grey bars and restoring sites are indicated by white bars. Striped grey bars represent native *Phragmites australis* in the RMU. (Plant = target plant sample, SHerb = sessile herbivore, MHerb = motile herbivore, Pred = predator, Spid = spider, Detri = detritivore). Plant and site abbreviations provided in Table 1.

A. JunGer in RMI and SMI

B. JunGer in RMU and SMU

C. SpaAlt in RMI and SMI

D. PhrAus and PhrAuN in RMU and SMU

Conclusions

Arthropod Integration into the Plant Community

Trophic structure and carbon transfers were remarkably similar between the restoring marsh and the reference marsh, despite some differences in plant community structure. These results suggest that although plant structure might differ, energy and carbon captured by restoring marsh primary producers is still functionally transferring through the food web. In most cases, sessile and motile herbivores exhibited only small differences in carbon values between the restoring and reference communities while there were slightly larger differences between spiders and predators collected in the different marshes. Though the actual ^{15}N values differed between sites, the values indicated that trophic differentiation was consistent between sites.

Although most of the target plant patches were comparable between marshes in terms of their plant community composition, there were some interesting exceptions that were reflected in the carbon values of arthropods captured in those patches. *Juncus gerardii* did not grow in dense, 100% cover patches in the RMU, as it did throughout Sherman Marsh and in the RMI. As such, motile herbivores and spiders collected in *J. gerardii* patches in the RMU had carbon values that were reflective of the abundant *S. patens* in those patches.

The differences in aphid abundance between sites likely resulted from the colonial nature of aphids that was not accounted for by our sample methods, and do not likely reflect noteworthy difference in density per plant. While it is clear that the sessile herbivores living on native and invasive *P. australis* relied on the plant as the primary

carbon source, other consumers on invasive *P. australis* consumed a broader range of carbon sources, including C_4 sources (Figure 3).

Motile herbivores on *P. australis* at all sites were enriched in ^{13}C relative to the plant values. This pattern was especially pronounced with invasive *P. australis*, despite abundant *S. patens* in the RMU native *Phragmites* stands and a scarcity of C_4 plants in *P. australis* patches in the Upstream portion of Sherman Marsh. Litter samples (-19.2 ‰ C^{13}) in invasive *Phragmites* plots in the RMU suggested that most of the detritus in invasive *Phragmites*, which grows along the main tidal creek, was from *Spartina spp.* These results suggest that consumers on *P. australis* rely on a variety of carbon sources, including, perhaps, rafted C_4 litter; similar findings have been reported in another study (Gratton and Denno 2006). The difference between the native and invasive sites suggests that invasive *P. australis* is not functioning as an integral part of the ecosystem.

The carbon values of the arthropods revealed part of the story of trophic interactions and functional energy and carbon movement in the restored marsh, but the nitrogen values are more problematic in that fractionation between trophic levels was less than the generally observed average fractionation of +3.4 ‰ with each trophic level. However, McCutchan et al. (2003) found evidence that $\delta^{15}N$ enrichment between trophic levels is lower for consumers with plant-based diets than for those with protein-rich diets, and that enrichment between trophic levels was lower for invertebrates than for vertebrates, although neither trend was significant. Furthermore, within invertebrates, $\delta^{15}N$ can change seasonally (Mestre et al. 2013), and trophic position, with those of herbivores being the most variable (Vander Zanden and Rasmussen 2001). Despite the smaller differences in fractionation between trophic levels observed in this study, trophic

structure was apparent in all marshes in this study. Spiders and other predators were generally more enriched in ^{15}N compared to herbivores and plants. ^{15}N values between trophic groupings often overlapped in my study, particularly between motile herbivores and predators.

When designing this study, I expected to collect sessile herbivores from each target plant patch. I observed many slow-moving herbivores throughout both marshes, including abundant Coleophoridae on *J. gerardii* and the salt marsh moth *Estigmene acrea* on *Typha* and *P. australis*. However, I did not find any sessile herbivores outside *P. australis* plots. Because of the scarcity of sessile herbivores, I could only compare isotope values of sessile herbivores between native and invasive *P. australis*. In all three cases, sessile herbivores had carbon isotope values more similar to the plant values than did motile herbivores. The nitrogen isotopes did not exhibit any clear patterns between the herbivores and plant samples.

Evaluating the Restoration Success of Sherman Marsh
In a broad sense, Sherman Marsh can be considered restored based on both structural and functional measures. The successive serendipitous and planned restoration of tidal inundation has helped *Spartina spp.* establish throughout the marsh, although the process has been much slower in the upstream portion of Sherman Marsh than near the inlet. Based on the plant community composition and tidal regimes, the Inlet area of Sherman Marsh meets the criteria defined in some restoration guides (Steyer and Stewart 1992, Neckles et al. 2002) for a successful restoration. In fact, it has been cited as a successful restoration in the book Tidal Marsh Restoration (Roman and Burdick 2012). However, in the SMU, *Spartina spp.* have been slow to establish and invasive *Phragmites* persists at low densities despite herbicide treatments (Wilson unpublished data). Still,

both *S. patens* and *S. alterniflora* have increased in abundance since the time of my study (Wilson unpublished data). When examining individual components of the system in the context of evaluating restoration, the determination of "success" becomes more complicated.

My study reveals that, functionally, the SMI is maintaining an arthropod food web that supports a wide variety of taxa and trophic interactions. Although *J. gerardii* became abundant on the marsh in the first growing season (2006) while *S. alterniflora* lagged behind, both *J. gerardii* and *S. alterniflora* are supporting a complex web of consumers. *Juncus gerardii* plays a larger role as a carbon source in Sherman Marsh than in the Reference Marsh. Yet, stable isotope analysis confirmed that both the unusually abundant *J. gerardii* and the newly-established *Spartina spp.* were used by consumers on the restoring marsh much the same as in the reference marsh. However, the structure of the herbivore arthropod community was not identical to the reference marsh, despite relatively similar plant communities. Although delphacids and cicadellids are morphologically similar, taxonomically, the two families are only related at the order level (Hemiptera) (Bourgoin 2014, Takiya and Dmitriev 2014). Despite taxonomic differences, the cicadellids and delphacids are functioning similarly as sap-suckers in both marshes. Although our results cannot define the precise path through which these herbivores are consumed, it is clear that there is a community of predators and top consumers supplemented by *Spartina*-based carbon sources.

It is not clear why there are different herbivore communities on *S. alterniflora* in the restoration and reference areas. While researchers have an understanding of some of the influences controlling established arthropod populations, the mechanisms that drive

recruitment are unclear, and few studies describe terrestrial arthropod communities on salt marshes in general. It is possible that wrack and tidal transport contribute to arthropod recruitment, as well as rafted and ice-transported peat; these phenomena are not clearly documented. Saltmarsh delphacid *Prokelisia marginata* populations can be influenced by seasonal habitat suitability (Denno and Grissell 1979), food quality (Gratton and Denno 2003b), and by cyclical patterns of parasitism by *Anagrus delicates* (Reeve et al. 1994). *Prokelisia* abundance can be stimulated for up to 3 years by nutrient pulses (Gratton and Denno 2003a), as might have occurred as freshwater plants decomposed following the draining of Sherman Marsh (Portnoy 1999, Theodose unpublished). In some circumstances, distance from an existing arthropod community may be the limiting factor that drives recolonization. For instance, as little as 400 m between restoring and "feeder" reference sites can be enough to disrupt reestablishment of herbivore-plant interactions in wetland restoration (Watts and Didham 2006). Though *P. marginata* migrate between summer and overwintering habitat (Denno and Grissell 1979), it is unclear how far is too far for these migrations, or if movement is season-dependent.

Even when a restoration site is in close proximity to undisturbed "feeder" sites, incursion by invasive species can inhibit food web rehabilitation. A "successful restoration" of functionality on Sherman Marsh is complicated by the persistence of invasive *P. australis*. In both the restoring marsh inlet and upstream areas, carbon originating from invasive *P. australis* is not as well incorporated into the arthropod food web as carbon from C_4 plant sources, despite the relative lack of C_4 plant tissue (living or detrital) in the upstream portion of Sherman Marsh. This reliance on detrital and algal

carbon sources appears typical in salt marshes with invasive *P. australis* (Gratton and Denno 2006), and though many animal species of wide-ranging taxa use *P. australis* as a food, shelter, or resting resource, few exclusively rely on *Phragmites* as a carbon source (Kiviat 2013).

In many cases of restoration where native plant communities are reestablished, arthropod communities have been shown to rebound quickly. In a salt marsh in New Jersey, terrestrial arthropod communities reestablished within five years following the removal of invasive *P. australis* (Gratton and Denno 2005). Likewise, terrestrial arthropods sampled in a grassland that had been transplanted with donor grassland turf exhibited relatively stable arthropod communities following a brief disturbance period, suggesting a fairly elastic arthropod community that recolonizes disturbed sites quickly (Cullen and Wheater 1993). The rapid return of plant communities to Sherman Marsh following a 70-year freshwater inundation was certainly advantageous for arthropod recruitment.

Implications for Defining Restoration Practices
When evaluating the restoration success, is alternate structure acceptable if functional goals are achieved? How much can the structure of a restoring marsh deviate from a reference condition and still be considered restored? Ultimately, as structure has traditionally stood as a proxy for functionality, one could argue that restoration is complete, at least in the SMI. Furthermore, despite some differences in the structure between the restoring and reference marshes, functionality is largely maintained. Though the plant community structure in *S. alterniflora* plots was similar between the SMI and the RMI, the motile herbivore community structure differed, yet maintained similar carbon and nitrogen transfers (i.e., functionality). As a relatively stable system in terms of

hydrology, salinity regimes, and species composition (climate change not withstanding), the SMI is functionally restored, with the upstream portion trailing behind as *Spartina* communities become established.

Of course, even a successfully restored system can experience change over time. Sherman Marsh is still a dynamic system that is still experiences structural and functional changes. Since this study was conducted, *S. alterniflora* and *S. patens* have become more abundant in the upstream portion of Sherman Marsh (Wilson Unpublished Data). As of 2011, *S. alterniflora* had covered the upstream creek-edge where *Eleocharis parvula* and algae mats once dominated. Additionally, invasive *P. australis* patches have been treated annually since this study. The extent to which *P. australis* will persist in the system is still unclear. As such, it is likely that the upstream portion, in particular, will experience further changes to the trophic interactions as a result of these structural changes.

Through a better understanding of the food web interactions in a restoring marsh, restorationists can better monitor and define restoration success. Because there is little research conducted on arthropod recruitment following tidal restoration, relying on structural measures like vegetation community composition to serve as indicators of functional restoration may not be adequate. However, nearby sources for plant and arthropod (and other fauna, for that matter) recruitment will likely facilitate functional restoration.

Without using the stable isotope analysis, we would not have known if alternate arthropod community structure (i.e., herbivores on restoring *S. alterniflora*) is passing carbon through the food web in the same way as in the reference marsh. Similarly, we would not know that the arthropods, with the exception of aphids, in invasive *P. australis*

patches had diets based on C_4 plants rather than on the *P. australis* itself. These findings can help practitioners make better-informed decisions about defining restoration endpoints.

Some structural changes are sure to result from global change. How these changes will affect the functioning of existing marshes is unclear, though climate change may not bode well for native *P. australis* and *S. alterniflora*. Evidence suggests that Eurasian *P. australis* will outcompete North American *P. australis* in response to increased CO_2 and N availability (Mozdzer and Megonigal 2012) and that increased atmospheric CO_2 favors C_3 *Schoenoplectus americanus* (formally *Scirpus olneyi*) when paired with C_4 *Spartina patens* (Erickson et al. 2007). Furthermore, the ways in which global change will impact the recruitment and trophic interactions of arthropod species in restoring marshes is an even greater unknown. By incorporating monitoring of functionality with standard monitoring practices, practitioners may be able to nurture resiliency in a changing system.
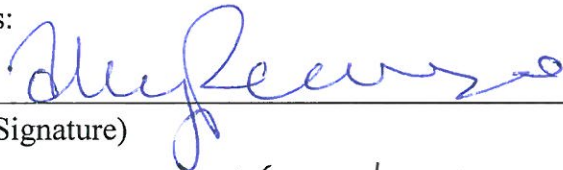
Appendix A

USM BIOLOGY MASTERS PROGRAM

Graduate Student Advisory Committee
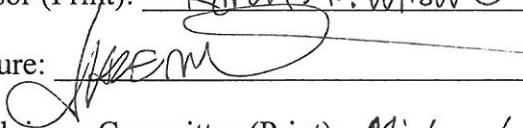
Graduate Student: _Abby Pearson_ Thesis/Non Thesis: _Thesis_

Date of Enrollment in Biology Graduate Program: _Fall 2008_

Anticipated date of graduation: _December 2014_
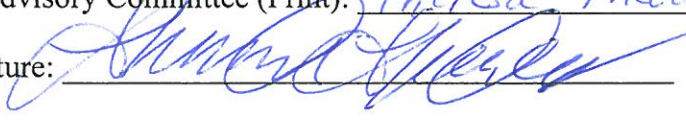
Signatures:

Student: _(signature)_ Date: _10/8/14_

    (Signature)

Primary Advisor (Print): _Karen A. Wilson_
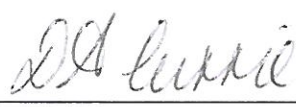
    Signature: _(signature)_ Date: _9/25/2014_

Member of Advisory Committee (Print): _Michael Mazurkiewicz_

    Signature: _Michael Mazurkiewicz_ Date: _9/25/2014_

Member of Advisory Committee (Print): _Theresa Theodose_

    Signature: _(signature)_ Date: _9/25/2014_

Graduate Coordinator (Signature): _(signature)_ Date: _9/25/2014_

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