DREXEL UNIVERSITY
Graduate
College

DISSERTATION/THESIS APPROVAL FORM

This form is for use by all doctoral and master's students with a dissertation/thesis requirement. Please print clearly as the library will bind a copy of this form with each copy of the dissertation/thesis. All doctoral dissertations must conform to university format requirements, which is the responsibility of the student and supervising professor. Students should obtain a copy of the Thesis Manual located on the Graduate College or library website.

Dissertation/Thesis Title: Geospatial variation of ribbed mussel (Geukensia demissa) ecosystem services across the salt marsh landscape

Author: Joshua Andrew Moody

This dissertation/thesis is hereby accepted and approved.

Signatures:

Examining Committee

Chair Susan S Kilham

Members

Elizabeth Watson

Academic Advisor Danielle Kreeger

Department Head

Graduate College 3141 Chestnut Street Main 301 Philadelphia, PA 19104
Tel: 215.895.0366 Fax: 215.895.0495 Email: graduatecollege@drexel.edu Web: www.drexel.edu/graduatecollege

(Last Updated 3/1/2016)

Geospatial Variation of Ribbed Mussel (*Geukensia demissa*) Ecosystem Services across the Salt Marsh Landscape

A Thesis

Submitted to the Faculty

of

Drexel University

by

Joshua Andrew Moody

in partial fulfillment of the

requirements for the degree

of

Doctor of Philosophy

December 2017

Acknowledgements

I would like to dedicate this work to my beautiful and wonderful partner Kat Buchanan and our two amazing children, Cooper Kathleen and Liam James. Kat, without your love and support I never could have completed this work. Your endless patience, understanding, and sacrifice are deeply appreciated and unwaveringly acknowledged. I love you as big as the sky and deep as the ocean; you are my everything.

I would like to thank my parents for their ability to see “the long game”, and for their support and love as I searched for my path.

I would like to thank my committee: Dr. Susan Kilham; Dr. Danielle Kreeger, Dr. David Bushek; Dr. Tracy Quirk; Dr. Elizabeth Watson; and Dr. Robert Chant. Thank you for all of the time you have invested in my training, the comments you have provided on this work, and the encouragement to see this endeavor through.

I would especially like to thank Dr. Danielle Kreeger and Dr. David Bushek, my greatest professional champions, for taking a chance on me so many years ago. Thank you for seeing something in me that gave you both the confidence to invest so many resources in my development. You have deeply changed my life, and I am lucky to be able to work with you both. Words cannot convey the breadth of my gratitude.

I would also like to thank my colleagues Angela Padeletti, Kurt Cheng, and LeeAnn Haaf, who have helped me in so many ways since the beginning of this effort. Whether it was field support, intellectual motivation, questions that birthed new ideas, or simply being there when I needed you, thank you. I am lucky to know and work with you all, hopefully for many years to come.

Additionally, thank you to the entire staff of the Partnership for the Delaware Estuary (past and present) who have provided support, especially: Sarah Bouboulis; Spencer Roberts; Sandra Demberger; Ryan Flannary; Emily Baumbach; Pricilla Cole; Laura Whalen; and many others.

Finally I would like to thank the Environmental Protection Agency Region II (Irene Purdy and Kathleen Drake) as well as the EPA Office of Research and Development Atlantic Ecology Division (Marty Chintala and Suzanne Ayvazian) for their support of this work via Regionally Applied Research Effort (RARE) Grant Number 83523301.

Table of Contents

List of Tables

List of Figures

Abstract

Geospatial Variation of Ribbed Mussel (*Geukensia demissa*)
Ecosystem Services across the Salt Marsh Landscape
Joshua Andrew Moody

Salt marshes are a hallmark feature of the Atlantic coastline, where they provide a variety of ecosystem services such as: protection from flooding; nutrient and pollutant sequestration; economic uplift from recreational and commercial ventures; and habitat for a variety of finfish, birds, invertebrates, and mammals. Ribbed mussels (*Geukensia demissa*) are the functionally dominant animals of Gulf and Atlantic salt marshes, living in facultative mutualism with salt marsh cordgrass (*Spartina alterniflora)*. The cordgrass provides habitat and attachment sites for mussels. In turn, the mussels, through the filtration of seston, provide nutrients for plant production through biodeposition. The magnitude of this pelagic-benthic coupling depends on ribbed mussel population density and the quantity and quality of seston. Since mussels are not evenly dispersed across the salt marsh landscape, their ecosystem services are geospatially variable which may have implications for resource managers interested in sustaining or enhancing mussel-mediated benefits.

This dissertation's objective was to quantify the annual variability in particle and nutrient filtration across three habitats of the salt marsh landscape: low marsh habitats along primary tidal channels; intra-marsh creek networks; and vast expanse of high marsh platform. Four representative salt marshes were selected for this study: Dividing Creek, Dennis Creek, and Maurice River in New Jersey along the Delaware Bay; and Coggeshall Cove in Rhode Island in the Narragansett Bay. The relevance of seston filtration data for understanding ecosystem services was demonstrated by estimating the spatial distribution and magnitude of net particulate nitrogen removal and the contribution of biodeposits to vertical marsh accretion.

Clearance rates of water by ribbed mussels exhibited little spatial variation, but were dependent on seasonal temperatures. Filtration rates of seston varied with both space and time, since seston quantity and quality was variable at the same scales. Therefore, annual water processing rates can be extrapolated across regions that share similar temperature profiles, but local knowledge regarding seston variability is required to calculate particle filtration services. Annual gross filtration of total suspended solids (TSS) ranged between 4,500 & 11,000 kg ha^{-1} yr^{-1} at three locations in New Jersey and 3,800 kg ha^{-1} yr^{-1} at one location in Rhode Island. Filtration of particulate nitrogen (PN) ranged between 38 & 92 kg ha^{-1} yr^{-1} in New Jersey, assuming 60% of filtered nitrogen was either incorporated into somatic tissue or biodeposited, and 31 kg ha^{-1} yr^{-1} in Rhode Island, assuming 43% of filtered nitrogen was either incorporated into somatic tissue or biodeposited. This translated into contributions to vertical accretion between 39 & 93 mm in New Jersey and 26 mm in Rhode Island, if distributed evenly across the salt marsh landscape at the four study sites.

The majority of mussel-associated ecosystem services were located in small, mussel-rich, creek networks of both New Jersey (74%) and Rhode Island (69%). However, large discrepancies in mussel density along the primary tidal channels between New Jersey and Rhode Island marshes, resulted in low service provisioning in New Jersey (3%) relative to Rhode Island (28%) in this “shoreline” habitat. The ability to understand the geospatial variation in mussel-mediated services provides natural resource managers with the ability to prioritize areas of high service value for conservation. Additionally, areas where services are underrepresented relative to regional potentials, presumably because of erosion or degradation, can be targeted for restoration or enhancement to maximize ribbed mussel biomass and service potential.

Chapter 1: Introduction

1.1 Mid-Atlantic Salt Marshes

Salt marsh ecosystems are a hallmark feature of our coastal environments (Mitsch and Gosselink 1993), particularly in the Delaware Estuary which is naturally sediment-rich and fringed with a near contiguous band of tidal wetlands (TREB 2017). At the interface between the terrestrial and aquatic environments they act as: natural filtration systems, removing watershed sourced nitrogen pollution (Nelson and Zavaleta 2012); buffer zones against storm hazards (Costanza et al. 2008; Temmerman et al. 2012); breeding and juvenile refuges for many commercial and recreational fish species (Weinstein et al. 1984; Weinstein and O'Neil 1986); and habitat for a myriad of local and transitory species (Werme 1981; Kneib 1994). Salt marshes also export dissolved and organic particulate matter to deeper water (Odum 1968), contributing to the sub-tidal food web (Dame et al. 1986; Valiela et al. 2012)

Mid-Atlantic salt marshes are typically characterized by the native smooth cordgrass *Spartina alterniflora* which is valuable for maintaining shoreline habitat (Warren et al. 2007). Tall form *Spartina alterniflora* is found along the mid-intertidal zone and levee at the marsh edge, and along intra-marsh creek networks. In the high marsh, the vegetative community transitions to species more tolerant of dryer, saline conditions including short form *Spartina alterniflora*, *Spartina patens*, *Salicornia virginica,* and *Disticlis spicata* (Kuenzler 1961; Bertness 1984). Salt marshes serve as habitat for many important resident invertebrates, such as bivalves (*Geukensia demissa*), crustaceans (*Uca tangeri*), gastropods (*Melampus bidentatus)*, various nematodes and annelids, as well as vertebrates such as fish (*Fundulus heteroclitus*), turtles (*Malaclemys terrapin*), mammals (*Ondatra zibethicus*) and a large variety of birds (*Ammodramus caudacutus, Agelaius phoeniceus*). The organic matter of salt marsh producers serves as the basis for salt marsh and subtidal food webs, and although emergent vascular plants are the most conspicuous producers in a salt marsh, benthic algal production can also be high (Peterson et al. 1986; Currin et al. 1995; Deegan and Garritt 1997). Within salt marshes, decomposing vascular plant material in the form of detritus supports a rich heterotrophic community of bacteria, protists, and fungi which can also be important sources of nutrition for benthic predators and scavengers.

1.2 Ecosystem Services of Salt Marshes

Ecosystem services have been defined as "the benefits human populations derive, directly or indirectly, from ecosystem functions" (Costanza et al. 1997). These services include regulation of large scale processes including climate regulation, water cycling, and food production, as well as localized services such as erosion control, nutrient cycling and soil and peat formation. The monetary value of ecosystem services has been estimated to be within the range of $16-54 trillion per year for the biosphere (Costanza et al. 1997; Daily et al 1997; de Groot et al. 2002). The Millennium Wetland Assessment has cited wetlands as providing an array of ecosystem services including storm protection nutrient cycling, water quality, and carbon storage. The New Jersey Department of Environmental Protection has estimated the average value of ecosystem services located along the Delaware Bay, many of them from wetlands, to be between $1,000-$12,000 per acre (Liu et al. 2010), greater than other natural habitats in the State.

At the interface of the land and the water, salt marsh ecosystems provide a buffer to maritime storms and flooding. In a meta-analysis of studies examining the role of salt marshes in protecting terrestrial environments from maritime sourced damage, Shepard et al. (2011) found that vegetation density, biomass production, and marsh size were all positively correlated with wave attenuation and shoreline stabilization. Coastal vegetative communities have also been shown to decrease the likelihood and magnitude of property loss and injury due to coastal hazards in vulnerable communities (Arkema et al. 2013).

Besides flood protection, nutrient cycling is another primary function of coastal wetlands. Salt marsh halophytes act as nutrient sinks for nitrogen (Sousa et al. 2008) and phosphorous (Lillebo et al. 2004), leading to their removal from the ecosystem (Ibanez et al. 2009). Land-based agriculture, and other anthropogenic activities (Nixon et al. 1986), and groundwater-borne nutrients (Valiela et al. 1990) are primary sources of nutrients in coastal waters. Salt marshes are able to serve as buffers, intercepting nutrients before they reach aquatic environments, and the retention of these nutrients within the salt marsh has been shown to reduce coastal eutrophication and enhance water quality (Sousa et al. 2010).

The productivity from nitrogen uptake allows wetland plants to fix and sequester greater amounts of atmospheric carbon in the soil (Armentano and Meges 1986). Salt marsh peat soils have the largest carbon content of all soils (Bridgham et al. 2006) due to high net primary production in wetlands relative to other terrestrial ecosystems (Amthor and Huston 1998; Keddy 2000), combined with low decomposition rates due to anaerobic conditions present during inundation (Stevenson and Cole 1999; White and Reddy 2000). As primary production increases and salt marsh biomass grows, dead organic matter is deposited on the salt marsh platform. Over time, the burial of this organic matter leads to below ground carbon storage. Although wetland soils make up a relative small percentage of terrestrial soils, they are estimated to contain approximately 20-25% of terrestrial soil carbon (Amthor and Huston 1998).

Although salt marsh plants can help to sequester a portion of available nitrogen, excess nitrogen may compromise salt marsh stability and health. For example, Deegan et al. (2012) showed that nutrient levels elevated to those considered being eutrophic increased above ground production at the expense of below ground production, and enhanced microbial decomposition. These results imply that salt marshes currently not under nitrogen limitation may provide smaller belowground contributions to vertical accretion, which is imperative to keep pace with sea level rise. In addition, the nitrogen uptake allocated to above ground material was not completely sequestered in the marsh platform, but partially exported from the marsh as detritus. The increased microbial decomposition further reduced the organic peat layer, lowering the elevation of the marsh platform. The combination of returning nitrogen to the system, lowering the elevation of the marsh, and decreasing the amount of below ground biomass could result in accelerated marsh deterioration as sea level rises and other physiological stressors increase.

1.3 Impacts of Sea Level Rise on Mid-Atlantic Salt Marshes

Currently, global sea level is rising at the rate of approximately 3mm yr^{-1} (IPCC 2007), which is expected to accelerate (Church and White 2006). In the Delaware Estuary, relative sea level rise rates are slightly higher (TREB 2017). Redfield and Rubin (1962) suggested that without ample sediment availability, most marshes will not be able to keep pace with projected increases in sea level rise (Friedrichs and Perry 2001). Marshes build elevation by either capturing suspended sediments or accumulating organic matter produced *in situ*. Recently, it has been suggested that many marshes have already lost the ability to maintain themselves under current sea level rise estimates due to insufficient sediment for sustainable vertical accretion (Delaune et al. 1983; Stevenson et al. 1985; Kearney et al. 1988, 1994; Hartig et al. 2002; McKee et al. 2004; Turner et al. 2004).

In The Delaware Bay, comparisons of aerial photography and historic maps have shown extensive salt marsh loss since the 1840s (Philipp 2005). Along the New Jersey coast, accretion rates of 1.7 mm yr^{-1} have been measured (Erwin et al 2006), which fall below current rates of sea level rise. Accretion and subsidence rates can be highly variable spatially, but insufficient net accretion may be one factor explaining why Delaware Bay marshes are losing acreage in most areas (TREB 2017). Furthermore, subsidence due to ground water extraction and post-glacial rebound can be as high as 2mm yr^{-1} (Sun et al. 1999; TREB 2017). Although marshes are able to migrate landward to some extent, seaward losses have outpaced landward gains, and this trend is expected to accelerate (Kreeger et al. 2010). The Delaware Estuary has experienced wetland loss of 6,500 acres between 1996 and 2006, and currently, 37% of existing wetlands are categorized as severely stressed, 37% moderately stressed, and 27% minimally stressed (Kreeger and Padeletti 2013). Marsh edge retreat greater than 1m yr^{-1} has been measured along coastlines of the Delaware Bay (Moody et al. 2011), and if this rate continues, we may experience a 25-75% wetland loss by 2100 (Partnership for the Delaware Estuary 2010).

As plant community structure is influenced by elevation within a tidal prism (Mudd et al. 2009; Baustian et al. 2012), salt marsh vegetative communities shift positions in response to rising sea levels. Woody up-land plants are being replaced by high marsh vegetation, which in turn are being replaced by low marsh vegetation. This transitory marsh migration, referred to as marsh transgression, is impeded by anthropogenic infrastructure barriers in many locations (Thorne et al. 2012). In areas where landward transgression is impeded, habitats such as coastal wetlands are ultimately converted to mudflat ecosystems once sea level rise surpasses the ability of plant communities to keep vertical pace.

The vertical growth of salt marshes is dependent on contributions from peat accumulation and decomposition and the capture of inorganic sedimentations. The relative contributions of these factors vary considerably among locations and studies. For example, the accumulation of the peat layer in salt marsh habitats has been cited as the primary driver in vertical marsh growth (DeLaune et al. 1978; Neubauer 2008). Halophytes have exhibited steep declines in belowground production with increased inundation (Voss et al. 2013) indicating that as sea levels rise, new additions to the peat layer can decrease. Since decomposition is a reductive process, it had been thought that tidal inundation of wetlands may slow below ground decomposition rates, offsetting reductions in new peat, allowing marshes to grow vertically. However, recent studies suggest that inundation by tidal waters does not slow belowground decomposition (Kirwan et al. 2013), and additional material (i.e. sediment capture) will be needed for vertical accumulation to keep pace with projected increases in the rate of sea level rise.

Another factor contributing to vertical accretion is the accumulation of sediment deposited from coastal waters on the flood tide. As sediment rich water moves across the marsh platform, salt marsh plant communities slow the movement of the water resulting in sediment deposition leading to vertical marsh growth (Bricker-Urso et al. 1989, Leonard and Luther 1995). *Spartina alterniflora*, the dominant lower marsh vegetation in Delaware Bay, production has been shown to be impacted when its optimum depth below mean high water is exceeded (Morris et al. 2002; Morris 2007). Therefore, as sea levels rise, we can expect low growing *Spartina alterniflora* densities to decrease, minimizing its ability to baffle water and accrete vertically. Additionally, rapid landward migration may reduce belowground production along the waterward edge, minimizing root mass which helps to stabilize sediments, increasing erosive potential (Bertness 1984). The relative importance of plant production, peat accumulation, external sediment supplies, canopy density, and hydroperiod to vertical accretion is the subject of much debate and local covariates may be dependent on site-specific conditions. Nutrient loadings (see below) can also affect these complex interrelationships. Regardless of which biophysical factor is locally limiting, clearly the ability to keep pace with sea level rise becomes more limited as the rate of local rise increases, especially in nutrient-stressed or sediment-deficient areas.

1.4 The Life History of the Ribbed Mussel (*Geukensia demissa*)

The class Bivalvia within the phylum Mollusca includes such organisms as clams, oysters, scallops, and mussels. The physical structure of bivalves is distinguished by two, laterally compressed, calcium carbonate shells, joined at a hinge which are opened and closed through the use of one or more adductor muscles. Originally described by Lewis Weston Dillwyn in 1817, the ribbed mussel is a member of the Family *Mytilidae*, the only family in the Order *Mytiloida*. It is placed in the genus of western Atlantic mussels *Geukensia* and is of the species *demissa*, or ribbed mussels. Adult ribbed mussel shells are generally 4-10cm in length, toothless at the hinge, and oblong with a slight curvature. Ribbed mussels are characterized by an asymmetrical shell and a thick periostracum. The periostracum is dark in coloration, and its longitutinal grooves, or ribs, extend from the umbo to the posterior edge. The animal uses a muscular foot for movement in the sediment, and it secretes protein complexes called byssal threads used for attachment and movement on stable substrate.

The life history of the ribbed mussel initiates with the fertilization of eggs by sperm in the water column during a broadcast spawning event. Ribbed mussels are iteroparous with reproductive output varying with age. Young mussels tend to invest more resources into growth, while older individuals allocate more effort to reproduction (Bayne 1976). Kuenzler (1961) measured as high as 17% reproductive effort, as a proportion of total production, contributed by adult ribbed mussels, which is a low percentage compared to other bivalve species possibly due to the energetic constraints of survival in the mid to upper intertidal zone.

Body weight is the primary determinant of sexual maturation in ribbed mussels, which is influenced by the position of the animal in terms of proximity to the marsh edge (Borrero 1987). At the marsh edge, ribbed mussels commonly become sexually mature during their second growing season, but maturation of mussels in high marsh habitat may be delayed an additional year due to a reduction in submersion, and therefore feeding time. The minimum size for gametogenesis is approximately 12 and 17mm at the edge and at a distance of 3m from the edge, respectively (Borrero 1987). Spawning is triggered by an increase in water temperature in the early summer, although a secondary spawning event of a lesser magnitude can take place in the late summer or early fall.

1.5 Ecology of the Ribbed Mussel (*Geukensia demissa*)

Ribbed mussels attach to the rhizome complex of *S. alterniflora* using their secreted byssal threads. Ribbed mussels can grow and detach from these strands, allowing them to change their position among both the root systems of the cord grass and the local mussel population (Franz 2001). Ribbed mussels supply *S. alterniflora* with nutrients through the deposition of pseudofeces and (often nutrient rich) feces, enhancing ecological productivity (Bertness 1984). The enhanced productivity provides new attachment sites for ribbed mussels, which in turn, provides the cord grass with additional nutrients. This mutualistic relationship facilitates the development of natural levees along marsh edges, which facilitates passive precipitation of suspended sediments from the water column, enhancing the vertical growth of the marsh (Bertness 1984). Bertness (1984) found that the removal of ribbed mussels from experimental field plots resulted in the landward movement of the marsh edge, while conversely; untouched plots containing high densities of ribbed mussels saw water-ward movement.

Ribbed mussels are suspension feeders that actively pump water through gills for respiration and to capture suspended particulate material in order to derive nutrition. Three types of cilia, frontal cilia, laterofrontal cirri, and lateral cilia, are beat to maximize water movement (Aiello and Sleigh 1972) through the gills where particles can be trapped on mucus coated surfaces. Particles are then transported in free suspension or mucus movement by the frontal cilia towards the labial palps where they are sorted to either be transported to the mouth or rejected as pseudofeces (Newell and Langdon 2004).

Although the initial capture of particulate matter is indiscriminate, sorting results in selected matter being passed into the mouth and rejected material is passed to the marsh platform. The primary foods of ribbed mussels have been shown to be nano, micro, and bacterioplankton (Wright et al. 1982; Kemp et al. 1990; Langdon and Newell 1990), but ribbed mussels are considered omnivorous and can derive nutrition also from heterotrophic flagellates, large-celled benthic micro-algae, as well as cellulosic detritus (Kreeger et al. 1988; Kreeger and Newell 2000, 2001). Major growth events in ribbed mussels occur in conjunction with blooms of the most nutritious particles, typically in the spring and summer months. Ribbed mussels appear to be more nutritionally-limited by nitrogen than carbon or energy when living in a naturally nitrogen-limited salt marsh environment (Kreeger and Newell, 2000). This is one reason researchers believe that ribbed mussels have become adapted to feeding on bacteria, which are more nitrogen-rich than phytoplankton (Kreeger and Newell 2000). The main predators of ribbed mussels along the marsh edge are the blue crab (*Callinectes sapidus*), mud (*Panoperous herbstii*) crabs (Lin 1989 and 1990), and shorebirds including clapper rails (*Rallus longirostris*) (Cohen 2005).

1.6 Spatial Variation of the Ribbed Mussel (*Geukensia demissa*) in Salt Marshes

Ribbed mussels populations are not evenly distributed across the salt marsh landscape. After their planktonic life stage, larvae settle from the water column, with the majority of settlement occurring along the edge of the marsh (Bertness and Grosholz 1985; Nielsen and Franz 1994; Franz 2001) in close proximity to previously established mussel populations (Nielsen and Franz 1994). The interstitial space of the shell assemblages, along with the stability provided by the larger mussel and *Spartina* complexes, provide refuge from predation and ice dislodgement, enhancing chances of survival (Bertness and Grosholz 1985).

Recruits to the marsh edge show a higher growth rate (Bertness and Grosholz 1985) and mature at a smaller size class (Franz 1996), but also display a lower survivorship (Franz 2001) than those in the high marsh. Mussel populations in the high marsh include larger and older size classes than populations along the marsh edge. With the exception of the first two years of growth, high marsh mussels show a higher survivorship per year class (Franz 2001). Although high marsh mussels mature at a slower rate than their counterparts along the marsh edge, their lifetime reproductive outputs are similar; although high marsh mussels require ~15 years to generate an output equivalent to the 5 year output of edge populations (Franz 2001).

1.7 The Ribbed Mussel (*Geukensia demissa*) and the Nitrogen Cycle

Nitrogen is essential for all organisms to construct amino and nucleic acids, and is considered the primary limiting nutrient for production in coastal ecosystems (Sprent 1987). The major nitrogen inputs to salt marshes are dissolved organic, inorganic, and particulate nitrogen delivered by tidal waters, as well atmospheric nitrogen fixation by bacterial communities; lesser contributions are provided by precipitation and ground water fluxes (Valiela and Teal 1979). In the salt marsh environment, energy rich ammonia is oxidized to nitrate which can subsequently be removed from the ecosystem through either the anoxic process of microbial denitrification or by transport in tidal waters. Nitrogen export has been measured to be equivalent to total input in typical reference marshes, indicating that the within-marsh cycle of nitrogen fixation (N_2-NH_3), nitrification (NH_3-NO_3), and denitrification (NO_3-N_2) are important for salt marsh communities to meet their internal nitrogen demands through recycling of limited nitrogenous compounds (Valiela and Teal 1979).

In salt marsh ecosystems, changes in nitrogen imports and exports can have ecological effects. For example, increased nitrogen input can enhance plant productivity, assuming carbon availability (Valiela and Teal 1979). As global atmospheric CO_2 levels are expected to increase (IPCC 2001), productivity-generated carbon sequestration may be important and limiting levels of available nitrogen has been shown to reduce this function (Reich et al. 2006). In some areas, the export of nitrogen from salt marshes can in turn increase primary production of algae in coastal waters which has been linked to decreased biological diversity (Valiela et al. 1990). Ribbed mussels can deliver nitrogen filtered from the water column directly to plants, providing simultaneous water column nutrient removal (Jordan and Valiela 1982) and plant production services (Bertness 1984).

Ribbed mussels, which outweigh all other metazoans in the marsh, are considered to be the functional dominant animals in salt marsh ecosystems (Kuenzler, 1961 Fell et al., 1982; Jordan and Valiela, 1982; Bertness 1984), helping to govern mass biogeochemical relationships such as nitrogen retention and export. For example, ribbed mussels have been shown to be able to filter 1.8 times the particulate nitrogen exported from the marsh through tidal flushing (Jordan and Valiela 1982). Hence, where mussels are dense, they can significantly alter the nitrogen budget of a salt marsh, shifting the equilibrium to net nitrogen retention, enhancing productivity. Conversely, when ribbed mussels are not abundant, marshes may be net nitrogen exporters.

Ribbed mussels only retain approximately 10% of their ingested nitrogen for growth, and approximately 50% is deposited into the marsh in the forms of feces and pseudofeces (Jordan and Valiela 1982). *Spartina alterniflora* stands associated with aggregates of ribbed mussels exhibit higher soil nitrogen levels than stands without marsh mussels, indicating that feces and pseudofeces were nitrogen rich and made available for plant production in the marsh environment (Bertness 1984). This result is significant in that the nitrogen not selected for by the ribbed mussels was not necessarily removed from the salt marsh ecosystem and exported to coastal waters, but was retained and incorporated, or buried, within the marsh (Jordan and Valiela 1982).

Approximately 27% of filtered nitrogen is excreted as ammonia, hence ribbed mussels also remineralize more ammonia into the marsh ecosystem than all other groups of organisms at the population level (Jordan and Valiela 1982). This release provides electron donors to microbial communities and thusly a secondary input of nitrogen at the ecosystem level. These metrics create a nitrogen budget for ribbed mussels within which ~77% of the available filtered nitrogen is returned to the salt marsh as either bio-deposits or dissolved compounds in the water or sediment. The combination of nitrogen input in the forms of feces, pseudofeces and ammonia therefore greatly increase nitrogen transformation and net retention in the salt marsh ecosystem, enhancing the availability of this limiting nutrient to vascular plants, benthic algae, and microbes. Of the remaining ~23% of nitrogen retained, 2% was invested in byssal thread production (which are ultimately lost to environment), 11% was retained internally for growth and 10% was released as gametes (Jordan and Valiela 1982). Nitrogen cycling stimulated by ribbed mussel feeding therefore plays an important role in delivering nitrogen to an otherwise nitrogen-limited salt marsh community, and could be substantial enough to help govern overall nutrient removal and transformation services rendered by salt marshes.

1.8 Research Questions and Dissertation Structure

The key goal of this dissertation was to determine the geospatial distribution of ribbed mussel ecosystem services across the salt marsh landscape, as exemplified by the filtration of total suspended solids (TSS) and particulate nitrogen (PN) and the contribution of mussel biodeposits to marsh accretion. Additionally, this research aimed to utilize regional differences in the distribution of these services to try and identify current areas of underrepresented services and to estimate the magnitude of service increase through the augmentation of ribbed mussel populations. The three focal research questions in this dissertation were as follows:

1. Does the water processing rates of ribbed mussels vary across space and time?
2. How does the magnitude of mussel mediated-ecosystem services vary across the salt marsh landscape?
3. Are the current levels of services as measured within New Jersey salt marshes representative of their maximized regional potential?

These questions were investigated in Chapters 2, 3, and 4 respectively. The objective of chapter 2 was to determine spatial and temporal variability of water processing rates of ribbed mussels by measuring seasonal physiological processing of natural seston by ribbed mussels collected from three habitats across the salt marsh landscape (high marsh, low marsh along primary channels (river), and low marsh along intra-marsh creek networks (creeks)), and from two regions (Delaware Bay, NJ and Narragansett Bay, RI. Ribbed mussel population density and feeding time availability across the three habitats and two regions were then quantified in chapter 3, permitting the spatial magnitude of ribbed mussel filtration services to be assessed within and among the study marshes. Chapter 4 evaluated these data regionally to: 1) identify spatial discrepancies in mussel-mediated services among regional habitats; and 2) estimate how ribbed mussel losses and gains could influence the extent of these services. Chapter 5 discusses the findings from chapters 2-4 in the context of natural resource management and restoration ecology. As new technologies are employed to mitigate current and future coastal vulnerabilities, it will be important to opportunistically target areas of high potential return for mitigation/restoration activities. The ability to identify areas that are appropriate ribbed mussel habitat, but are currently supporting low populations, may allow for intervention activities that enhance ribbed mussel biomass in tandem with other site-specific goals, such as shoreline stabilization, to maximize the ecosystem service outcomes of management and restoration activities.

Chapter 2: Temporal and Spatial Variation of the Gross Removal of Total Suspended Solids and Particulate Nutrients by Ribbed Mussels (*Geukensia demissa*) in Salt Marshes of the Mid-Atlantic Region, USA

2.1 Abstract

Ribbed mussels (*Geukensia demissa*) are a ubiquitous intertidal animal of eastern North American salt marshes, often living in close association with salt marsh cordgrass *Spartina alterniflora*. They are typically concentrated at the lower extent of the vegetated zone along tidal channels, but are also found across the marsh platform at higher intertidal elevations, albeit at lower densities. As filter-feeding bivalves, ribbed mussels remove suspended micro-particulate matter and associated nutrients from the water column, potentially resulting in benefits to water quality. However, the magnitude of such ecosystem services may depend on temporal and spatial variation in the mussel's water clearance and particle filtration rates.

Seasonal (spring, summer, and fall) water clearance and particle filtration rates were quantified for ribbed mussels collected from three habitats: low marsh along the main tidal channels; low marsh along intra-marsh creek networks; and high marsh. To examine broader spatial variation, the experiments were replicated in four representative marshes, three in New Jersey (NJ), and one in Rhode Island (RI), USA. Ecosystem services were represented by the gross filtration rate of total suspended solids (TSS) and particulate nitrogen (PN), normalized for mussel dry tissue biomass. Clearance rates varied with seasonal temperatures, but exhibited low spatial variability among habitats and marshes. In contrast, filtration rates of TSS and PN were highly variable, driven largely by spatial variation in seston availability. Seston services can therefore be predicted from body size, seasonal temperature, and site-specific seston composition.

2.2 Introduction

As filter-feeding bivalves, ribbed mussels play a key role in the pelagic-benthic coupling of intertidal salt marsh ecosystems. The transfer of nutrient rich particulate matter from the water column to either the animal through physiological assimilation or the subsurface of the salt marsh platform represents a nutrient sink with potential benefits to water quality. Similar to many global coastal habitats, mid-Atlantic estuaries experience considerable eutrophic degradation, fueled by excess nutrient runoff (Nixon et al. 1986; Valiela 1992; Rabalais et al. 2009). Since much of these excess nutrients are taken up by phytoplankton (Valiela et al. 1990; Sfriso et al. 1992; D'Avanzo and Kremer 1994), there has been strong interest in restoring native bivalve populations, such as oysters, to exert grazing pressure on algal blooms and to potentially facilitate nutrient burial and microbial denitrification via bivalve bio-deposits (Landry 2002; Higgins et al. 2011; Stadmark and Conley 2011; Gallardi 2014; Petersen et al. 2014).

Despite their large population sizes (Bertness 1984; Bertness and Grosholz 1985; Franz 2001; Evgenidou and Valiela 2002), interest in ribbed mussels for nutrient mitigation has remained low relative to oysters, even though they have comparable water processing rates (Riisgard 1988). Clearance rates of ribbed mussels, defined as the volume of water swept clear of particles per unit time, have been shown to be temperature dependent, with mussels clearing water at a lower rates in colder water than in warmer water (Jordan and Valiela 1982, Kreeger et al. 1988; Kreeger and Newell 2000). In temperate climates, this translates to seasonal variability in physiological processing with summer months being the most active, and lower rates observed in the fall and spring months. In general, bivalves clear water at constant rates across a wide spectrum of food (seston) concentrations and qualities (Bayne et al. 1987, 1988), with the exception that they reduce feeding activity at very low or very high concentrations that become inefficient for optimal foraging (Willows 1992).

Filtration rates, defined as the weight of material filtered from the water column per unit time, reflect the interplay between clearance rates and the food available for filtering. As clearance rates can be similar across a food availability gradient (Bayne et al. 1987, 1988), filtration rates of animals clearing water at similar capacities can differ spatially due to differences in food availability. Additionally, even though ribbed mussel populations are concentrated at lower intertidal elevations along main tidal channels and intra-marsh creeks, they are found across the marsh platform at higher intertidal elevations, albeit at lower densities (Bertness 1984; Bertness and Grosholtz 1985; Franz 1993). This distributional variability across an elevation gradient results in spatial differences regarding feeding time availability per day. Therefore, bivalve water clearance and particle filtration services, and subsequently water quality benefits, can vary widely over space and time.

Less well understood is whether the physiological capacity of mussels to filter seston varies across the diverse marsh landscape or among marshes having different seston character. To assess the potential water quality benefits of ribbed mussels, it is vital that the seasonal interplay between water processing rates and *in situ* food composition be understood across the salt marsh landscape. In this study, the temporal and spatial variation in ribbed mussel water clearance and particle filtration rates were assessed within and among representative salt marshes. To be broadly representative and provide the basis for geospatial extrapolation, key physiological processing rates were determined seasonally for ribbed mussels fed natural diets collected from three representative marsh sub-habitats (low marsh along main tidal channels, intra-marsh creek networks, and high marsh) and compared among four different marsh systems in two estuaries (three in Delaware Bay, NJ, and one in Narragansett Bay, RI). Physiological experiments were repeated seasonally in spring, summer and fall in NJ, and only once during summer in RI.

2.3 Methods

Physiological experiments were conducted using natural seston diets to ensure that mussel physiology did not react to a change in diet quantity or quality. The onset of feeding was also timed to synchronize with site-specific immersion schedules. Since physiological metrics also vary with body size, a range of mussel sizes were tested to be representative of the local population from each study marsh. Seasonal experiments were conducted at ambient water temperatures.

2.3.1 Study Sites and Habitat Delineation

Mussels for physiological rate studies were collected from three representative study salt marshes in New Jersey and one in Rhode Island (Fig. 2.1). New Jersey salt marshes were chosen in Dennis Creek (DN), Dividing Creek (DC) and the Maurice River (MR), which are tributary watersheds along the Delaware Bay. In Rhode Island, the study marsh was Cogshall Cove (RI), located on Prudence Island in Narragansett Bay.

These marshes were selected due to their proximity to long-term wetland monitoring stations, including surface elevation tables. At each site, three subhabitats were selected from which mussels were collected: low marsh along the main tidal channel, referred to as low marsh river (LMR); high marsh (HM); and low marsh along a representative intra-marsh creek referred to as low marsh creek (LMC). Low marsh river habitat was delineated as being along the marsh's primary tidal channel that does not drain completely at low tide, and was characterized by a 1-2 meter band of tall-form *Spartina alterniflora* between the marsh edge and the high marsh platform. High marsh habitat was delineated by vegetation community composition comprised of either a mono culture or mix of: short-form *Spartina alterniflora*; *Spartina patens; Distichlis spicata*; *Juncus* spp. and/or *Salicornia* spp. Low marsh creek (LMC) habitat was characterized by a 2-4 meter band of tall-form *Spartina alterniflora* bisected by an inter-marsh drainage creek that drained fully at low tide.

2.3.2 Ribbed Mussel and Seston Collection

Fifteen ribbed mussels, of which 7-8 animals were selected for experimental use, representing the observational size range of the local population were collected from each habitat in each study marsh on the falling tide of the date of each seasonal experiment (Table 2.1). During transport to the nearby (outdoor) experiment site, mussels were placed in small containers and wrapped in wet paper towels to keep them moist and at constant temperature. Mussels were gently rinsed using water collected on site, byssal threads were trimmed to the shell margin, and animals were laid on a damp towel until the commencement of each experiment. Mussels were collected from the same location for each seasonal experiment (Table 2.1).

Additionally, 20L of water was collected from the primary tidal channel for use in physiology experiments and for natural seston analysis. Seston collection carboys were submerged 5-10cm below the water surface, being careful not to re-suspend soft material from the benthos or collect surface material. Water was mixed and then passed through a 100 μm sieve to remove large debris and particles too large for mussels to effectively filter.

Temperatures were monitored prior to and during experiments to ensure that they never deviated more than 3°C from *in situ* water temperatures.

2.3.3 Experimental Approach

Experiments were initiated approximately six hours after mussel collection to mimic incoming tide to preserve natural feeding patterns. Clearance rates were assessed in static aquaria consisting of individual ribbed mussels held in 1 liter beakers. The experimental design consisted of 24 beakers of mussels (n= 8 habitat^{-1}) and 6 non-feeding controls for Dennis Creek (NJ) and Cogeshall Cove (RI), and 21 beakers for mussels (n= 7 habitat^{-1}) and 4 non-feeding controls for Dividing Creek (NJ) and Maurice River (NJ). All beakers were filled with 800mls 100μm-sieved natural water from each site, and were vertically mixed prior to sampling by plunging gently with a 100ml graduated cylinder.

Ten milliliter water samples were collected from each beaker just prior to the addition of bivalves at the start of the feeding experiment. After mussels were added, water samples were taken at four 30min intervals once feeding had initiated, determined by the opening of valves, protrusion of siphons and the presence of feces. Delayed feeding of approximately 60 minutes occurred during the (colder) fall experiments. Water samples were taken from the just beneath the water surface in the middle of each beaker, approximately 1 min following gentle mixing which was observed to be sufficient to allow any resuspended biodeposits such as feces to settle. Each 10ml water sample was added to a 20 ml Coulter vial, fixed with 4 drops of acid Lugol's solution, and stored at room temperature for later analysis.

2.3.4 Mussel Body Metrics

At the conclusion of each feeding experiment, ribbed mussel shell height was measured to ±0.01 mm and weighed to ±0.01 g. Animals were sacrificed, shells were dried and weighed, and tissues (and associated liquor) were frozen in pre-weighted 20ml Coulter vials at -20°C, and subsequently freeze-dried and weighed to ±0.00001 g for determination of dry tissue weight (DTW) for subsequent allometric standardization of physiological rate functions to body weight.

2.3.5 Clearance Rate Calculation

Water samples were analyzed for the concentration of particles having diameters between 2-63 μm using a Coulter Multi-Sizer II (Beckman Coulter, La Brea, USA). Intrinsic variability among water samples was normalized using a fitted regression curve of the decline in particle concentration for the total feeding interval for each animal. This equation was used to determine the initial and final particle concentration. If particle concentration of a sample was measured at <50% of the initial concentration, it was deleted from the regression to avoid potential negative responses in feeding activity due to declining food quantity.

Clearance rates per animal were then calculated using the equation of Coughlan (1969):

$$\textit{Clearance Rate } (Lh^{-1}) = [\log Ci - \log Cf] * [V\,T^{-1}]$$

where Ci = initial particle concentration, Cf = final particle concentration, V = water volume, and T = incubation time. Clearance rates were subsequently corrected for values measured in control beakers, thus accounting for any changes in suspended particle concentrations that may have resulted from processes other than mussel grazing activity, such as microbial activity or particle settlement. Clearance rate was allometrically normalized for each animal for a final clearance rate in the units: l $h^{-1}gDTW^{-1}$.

2.3.6 Seston Composition

The quantity and quality of microparticulate matter that mussels were fed on was determined by assessing the TSS, POM, %OM, C:N molar ratio, and PN of seston in each water type (i.e. marsh per season). Replicate samples (n=6 $marsh^{-1}$ $season^{-1}$) of seston were collected from each water type on pre-combusted glass fiber filters (Whatman GF/F, retention 0.7 μm) using vacuum filtration. Volumes of water filtered were equal to 90% of the pre-determined clogging volume per watertype. Post-filtration, the filter and funnel were rinsed with 5 ml of 0.5 M ammonium formate to remove inorganic salts. Filters were frozen until analysis.

Each filter was cut in half using a cutting template to insure exact, replicable cutting of each filter. One half of each filter was used for determination of total suspended solids (TSS), particulate organic matter (POM), and percent organic content (%OM) using the loss-on-ignition method (Davies 1974). Weights of TSS and POM were multiplied by 2 (to account for the other half of the filter) and divided by the filtered volumes to calculate concentrations (mg/L). The second half of each filter was analyzed for the molar concentrations of carbon and nitrogen to calculate C:N and total particulate nitrogen (which was divided by the filtered volume) of TSS using a Flash EA112 elemental analyzer. Filters were subsampled using a hole punch. Standard quality assurance methods were followed, including the running of check standards, and every fifth sample was run in duplicate.

2.3.7 Filtration Rate Calculation

Clearance rates (l hr^{-1}) were converted to filtration rates (grams seston hour $^{-1}$) by multiplying measured clearance rates by the measured mean ambient seston concentration appropriate for each treatment group (*n*=6).

2.3.8 Allometric Scaling of Physiological Rates

Filtration rates increase with increasing bivalve size (Winter 1978), which can also vary widely among species. To facilitate comparisons among studies and to enable ecosystem service calculations for natural bivalve populations, clearance and filtration rates were adjusted for body dry tissue weight (DTW). Weight-adjusted rates were determined by least squares linear regression analyses on log-log data of mussel DTW and physiological rates, following the approach of Kreeger et al. (2001). A separate regression equation was determined seasonally per habitat per marsh (i.e. each treatment group, total of 36 regressions). Where slopes of resulting equations were similar (e.g. among different habitats and among different marshes for the same season), a subsequent regression equation was generated on pooled data to minimize error. Weight standardization allowed for the best comparability of rate functions among species, environmental conditions, and studies.

2.3.9 Statistical Analyses

All data were tested for normality using a Shapiro-Wilk test prior to ANOVA analysis, the results of which were presented as mean ± standard error (se). If a 2-way ANOVA interaction term was identified as significant, main effects were not reported as to not violate the principle of marginality, and a simple main effects test was subsequently performed. If interactive effects were not significant, a secondary two-way ANOVA was run isolating individual factor effects with no interaction term. As mussels were collected from the same locations for each seasonal experiment; size and weight statistics were pooled across seasons and evaluated per habitat per marsh. ANOVA analyses were conducted using a linear model approach, employing a type III sum of squares for unbalanced designs. Where significant treatment effects were identified, Tukey HSD post-hoc analyses were performed.

Correlations among average seasonal water processing clearance rates and seston characteristics among marshes were performed using the percentage bend correlation method available in the WRS2 package. All analyses were conducting using R statistical software version 3.0.3 (R Core Team 2014)

2.4 Results

2.4.1 Mussel Body Metrics

Generally, mussels had longer shell lengths and greater dry tissue weights in the channelside habitats (i.e. LMR and LMC) than in the high marsh, but this difference was not always statistically significant (Table 2.2). This trend was consistent across all marshes with the exception of the Maurice River where shell length and dry tissue weight were closer in value across all habitats (Table 2.2). The Dividing Creek and Rhode Island marshes generally exhibited a wider range of dry tissue weights per habitat than both Dennis Creek and Maurice River which contained the smallest mussels per habitat. On average across habitats, mussels in Rhode Island were significantly larger than in New Jersey ($p<0.006$; NJ $\bar{x}=0.55\pm0.04$ gDTW; RI $\bar{x}=0.87\pm0.14$ gDTW). Pooling data by habitat per region, New Jersey and Rhode Island mussels did not differ in weight in the LMC and HM habitats ($p>0.99$ and $p>0.96$ respectively), but mussels in the LMR habitat in Rhode Island were significantly heavier than their counterparts in New Jersey ($p<0.001$).

2.4.2 Seston Composition

There were significant interactions between marsh and season for all seston metrics ($p<0.001$ for all metrics) with the exception of C:N which displayed no significant differences among factor levels (marsh: $p> 0.45$; season: $p> 0.20$; marsh*season: $p> 0.06$). Partitioning data by season, simple main effects tests for all other seston metrics showed significant differences in metric values among marshes per season, with no consistent pattern among seasons (Table 2.3). Total suspended solids, POM, and PN followed similar seasonal patterns among marshes, with Dennis exhibiting significantly greater values than Dividing Creek and Maurice River in the summer and fall, while Maurice was highest in the spring (Table 2.3). Percent organics were greatest in Rhode Island (27.73±2.52, Table 2.3), and although some statistically significant differences were measured among all New Jersey marshes seasonally, the ranges were similar and values were at least 35% lower than in Rhode Island (Table 2.3).

TSS was significantly correlated with POM within New Jersey marshes (Dividing Creek: $t=23.91$, $p<0.001$, $r^2=0.99$; Dennis Creek: $t=15.77$, $p<0.001$, $r^2=0.97$; and Maurice River: $t=12.62$, $p<0.001$, $r^2=0.95$), but was just above the statistical threshold of $\alpha=0.05$ in Rhode Island ($t=2.34$, $p<0.08$, $r^2=0.76$). TSS correlated inversely with %OM in Dividing Creek ($t=-7.08$, $p<0.001$, $r^2=0.87$) and Maurice River ($t=-2.27$, $p<0.04$, $r^2=0.49$), but not in Dennis Creek ($t=0.08$, $p>0.93$, $r^2=0.02$) or Rhode Island ($t=-0.97$, $p>0.38$, $r^2=0.43$). Percent organic were higher among the NJ sites near the Delaware Bay mouth and decreased moving up Bay. Percent organic matter was almost twice as high in Rhode Island than at the New Jersey sites in the summer (Table 2.3). Of note is that fall samples were collected 11 days after hurricane Sandy, which may have contributed to higher than normal seasonal fall values for some seston components.

2.4.3 Clearance Rates

Generally, clearance rates increased seasonally with temperature from fall, to spring, and summer in all marshes (Table 2.4). There was a significant interactive effect between marsh and season, and a simple main effects test showed no significant variability among marshes in the fall ($p>0.07$) or summer ($p>0.15$), but Maurice River differed significantly from Dividing and Dennis Creeks in the spring ($p<0.001$ for both marshes).

Partitioning data by season, there was minimal variability among habitat types within marshes. Two-way ANOVA analysis showed no significant habitat or marsh effects on clearance rate in the fall (marsh: $p>0.06$; habitat: $p>0.10$; marsh-habitat interaction: $p>0.14$; $\bar{x}=0.044\pm0.007$ l hr^{-1} $gDTW^{-1}$) or summer (marsh: $p>0.15$; habitat: $p>0.27$; marsh:habitat: $p>0.38$; $\bar{x}=0.614\pm0.039$ l hr^{-1} $gDTW^{-1}$), but a significant interactive effect was present in the spring ($p< 0.005$). Simple main effect tests showed that the spring Dividing Creek clearance rate in the LMC habitat (0.51±0.06 l hr^{-1} $gDTW^{-1}$) was significantly greater than those in the LMR ($p<0.001$, 0.17±0.03 l hr^{-1} $gDTW^{-1}$) and HM ($p<0.005$, 0.27±0.04 l hr^{-1} $gDTW^{-1}$) habitats which did not differ from each other ($p>0.31$). No significant differences in spring clearance rates among habitats were detected in Dennis Creek ($p>0.41$) or Maurice River ($p>0.42$). Seasonal mean clearance rates per marsh are reported in Table 2.4 and habitat specific clearance rates per season per marsh are reported in Appendix A. There were no significant correlations between clearance rates and any seston metrics (Appendix B).

2.4.4 Filtration Rates

There was a significant interactive effect between marsh and season for both TSS ($p<0.01$) and PN ($p<0.01$) filtration rates. Average TSS filtration per marsh significantly differed among all seasons ($p<0.05$ for all marshes), except in Dennis Creek in which TSS filtration rates did not significantly differ between the fall and spring ($p>0.97$, Table 2.5). Seasonally, average PN filtration per marsh displayed greater seasonal homogeneity with spring and fall rates similar in Dennis Creek ($p>0.99$), and summer and spring rates similar ($p> 0.97$) in Maurice River (Table 2.5).

Among marshes, seasonal TSS and PN filtration did not follow any consistent pattern. Maurice River had the highest rates in the spring and Dennis Creek had the highest in the summer and fall (Table 2.5). Pooling data regionally, seasonal averages of TSS filtration (mg l^{-1} $gDTW^{-1}$) increased with temperature in New Jersey (fall: 5.65±0.77; spring: 28.69±3.85; summer: 43.27±2.69), and summer filtration was significantly higher ($p<0.01$) than in Rhode Island (7.23±1.22). Similar trends were measures for PN filtration in New Jersey (fall: 0.04±0.01; spring: 0.21±0.03; summer: 0.48±0.03) and were significantly higher than Rhode Island (0.06±0.01 mg l^{-1}, $p<0.01$) in the summer.

2.5 Discussion

Ribbed mussels are increasingly being studied for their role in pelagic-benthic coupling and biogeochemical relationships in Atlantic salt marshes (Galimany et al. 2013, Bilkovic et al. 2017). To evaluate how ribbed mussel populations affect water quality and cycling of particulate matter, it is vital to understand the factors that govern key physiological rates associated with their suspension-feeding behavior. Although this study confirms previous work that has shown a generally positive relationship between water temperature and bivalve water processing rates (Widdows and Bayne 1971; Bayne et al. 1988; Wilbur and Hibish 1989; Kreeger and Newell 2001), the temporal and spatial variability of these processes within and among salt marshes are less understood.

Seasonal water processing rates were similar within and among marshes, with some significant variability identified during the spring, when mussels were emerging from winter inactivity. Spring differences among marshes and among habitats in Dividing Creek could be attributed to varying stages of physiological adaptation to quickly changing temperatures. Kreeger and Newell (2001) did not find consistent significant differences in ribbed mussel clearance rates (per diet type) between the winter (5°C) and spring (21°C) and between the summer (26°C) and autumn (16°C), even though each seasonal pair had a wide temperature differential. These results indicate a lag response in emerging and regressing from minimum (winter) and maximum (summer) water processing rates, respectively. In this study, even though mean spring temperature (15.4°C) was similar to Kreeger and Newell's autumn temperatures (16°C), the measured clearance rate was similar to Kreeger and Newell's spring rate (5.6°C temperature difference). The similarity between clearance rates at 21°C (Kreeger and Newell 2001) and 15.4°C (this study) may be due to the amount of time the mussels had been exposed to each temperature, with mussels in recently warmed water exhibiting a clearance rate that still reflects their previous environmental conditions that had been consistent for a longer duration. Alternatively, feeding rate differences per temperature might have been influenced by other factors such as food quality and nutritional status.

In this experiment the mussels from the Maurice River had significantly higher clearance rates in the spring than those in Dennis and Dividing Creeks (Table 2.4), which may indicate that water in the Maurice River had been increasing in temperature for a longer duration than in Dennis and Dividing Creeks. Delayed response in clearance rate to changes in temperature is supported by Wilbur and Hilbish (1989), who reported an increase in clearance rates from 0.53 (l hr^{-1}) to 0.77 (l hr^{-1}) when temperatures were raised from 15°C to 25°C, and that further increases to 1.17(l hr^{-1}) were observed after 21 days.

Conversely, animals kept at 15°C displayed no physiological changes over the course of the experiment.

The clearance rate reported by Wilbur and Hilbish at 15°C was within the range of values reported by Kreeger and Newell (2001) at 21°C and in this study at 15.4°C. This may reflect local variability in response to rising spring water temperatures and further studies should be conducted to identify key temperature thresholds and exposure times that regulate physiological response. Mohlenberg and Riisgard (1979) showed that water processing rates among bivalves acclimated to different temperature regimes, were not significantly different. These results indicate that long term water processing rates for ribbed mussels may be similar across regions, but should be calculated from multiple experiments spanning the inter-annual variability of local water temperatures with animals acclimated to experimental target values.

Spatially within marshes, there was little significant variability among habitats. These results are supported by Bayne et al. (1988) and Jordan and Valiela (1982) that found no significant reductions in water processing rates of suspension feeding bivalves due to increased aerial exposure (elevation differences among habitats and/or marshes) or reduced feeding times. These results suggest that ribbed mussels clear water at the maximum capacity that temperature allows independent of emersion time. Tidal influence on feeding rates has been explored in other bivalve species. Widdows and Shick (1985) compared clearance rates between inter- and subtidal populations of *Mytilus edulis* and *Cardium edule* and found no evidence that intertidal individuals compensated for reduced feeding time by increasing clearance rates relative to subtidal individuals.

The clearance rates reported in this paper were generally lower than some reported values for *Geukensia demissa* feeding on natural diets (≥1 l hr^{-1} $gDTW^{-1}$, Jordan and Valiela

1982, Riisgard 1988, Galimany 2013), but were within the ranges reported by others (Kreeger and Newell 2001, Lonsdale et al. 2009). A potential source of this discrepancy was the extremely high concentrations of TSS in the New Jersey feeding experiments relative to studies reporting comparatively higher rates. For example, Galimany et al. (2013) reported June-October average clearance rates between 0.84±0.09 and 3.12±0.26 l hr^{-1} for ribbed mussels processing water that has seston concentrations between ~4-18 mg l^{-1}. The range of average clearance rates found in this study (Table 2.4) were within the range found in Kreeger and Newell (2001, 0.03±0.01 l hr^{-1} – 1.24±0.05 l hr^{-1}), which were conducted using natural seston diets between 14 and 30 mg l^{-1}. Galimany et al. 2013 found that clearance rates of ribbed mussels decreased significantly with particle load, and the decline in average clearance rates from Galimany et al. (2013) to Kreeger and Newell (2001) to this study (Table 2.3) fits that pattern.

Although the low New Jersey clearance rates in this study fit that pattern of decline with increasing TSS, the summer Rhode Island clearance rates conducted with a natural diet of 13.24±2.34 mg l^{-1} does not. This may be due to regional differences in food quality (Table 2.3). Minor differences in clearance rates can occur when food quality is low, and Delaware Bay contains high concentrations of refractory detritus which may affect water processing. Another potential source of clearance rate variability may be the lack of post-handling acclimation time in these experiments. Jordan and Valiela (1982), Kreeger and Newell (2001), and Galimany (2013) allowed time for mussels to acclimate to their experimental surrounding post handling (2+ weeks, 18hrs, and 2hrs respectively). Mussels in these experiments were collected at low tide, cleaned of sediment and any attached byssal threads, and placed almost immediately into experimental beakers with no submerged acclimation time. This may have contributed to increased stress and the lower physiological rates measured here. Whether or not clearance rates were suppressed due to either high levels of TSS or from a stress response due to recent handing, the clearance rates presented here are within the range of previously reported values, and represent a conservative measure for of seasonal clearance rates fed on natural seston diets.

In contrast to clearance rates, filtration rates varied widely across space and time (Table 2.5). Seston availability and composition was highly variable (Table 2.3), and hence filtration rate followed these patterns closely. Summer TSS and PN filtration rate variability generally reflected the natural spatial variability of seston across marshes (Tables 2.3 & 2.5). Subtle variability in filtration rates among different mussel groups could also have been influenced by changes in food quality and seasonal nutritional demands, or salinity differences which were not accounted for in this study. For example, higher summer filtration rates of New Jersey mussels compared to Rhode Island mussels (Table 2.5) might have resulted from the comparatively lower food quantity and higher food quality of Rhode Island seston, even with the larger-on-average Rhode Island mussel biomass and slightly lower temperature (Table 2.3). Unlike clearance rates, filtration rates are rarely reported in the literature, which may be due to their dependence on site-specific TSS qualities. Therefore, we were unable to compare these values to rates from others studies under similar TSS and seasonal conditions.

Despite minor differences, water processing rates were generally consistent across marshes and habitats for a given temperature. As temperature changed seasonally, water processing rates responded in a positive fashion. These data highlight the importance of understanding the inter-annual variability in physiological rates when calculating annual estimates. For example, employing water processing rates calculated at summer temperatures as a measure of average annual function, will greatly overestimate water processing capabilities. Conversely, as these data showed little variation across space, it would be reasonable to extrapolate previously measured water processing rate estimates (e.g. seasonal, annual, etc…) across estuaries and bays that share similar temperature and seston characteristics.

As filtration rates reflect *in situ* seston concentrations, which were highly variable across both time and space, spatial variation in ribbed mussel ecosystem services may be driven by site-specific food differentials. Thusly, site-specific data for seston quality and quantity are required to assess particle (and associated nutrient) filtration, and filtration rates may be spatially constrained to greater degree than clearance rates. As both of these rates are per unit dry tissue weight of ribbed mussels, calculation of the spatial and temporal distribution of ribbed mussel ecosystem services requires the integration of regional seasonal clearance rates, site-specific seston quality and quantity, as well as spatial estimates of ribbed mussel biomass, and feeding time availability.

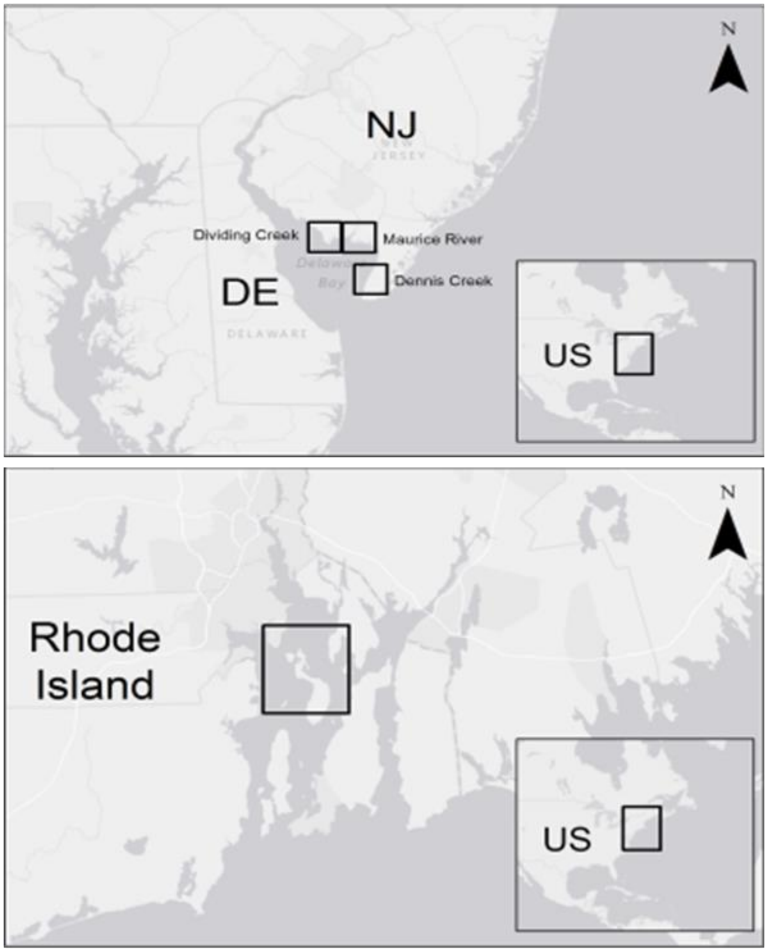


Figure 2.1 Marshes where ribbed mussels were collected for seasonal physiological experiments

Table 2.1 Location of ribbed mussel collection sites, collection dates, and range of water temperatures throughout experiments. DC=Dividing Creek; DN=Dennis Creek; MR=Maurice River; RI=Coggeshall. DC, DN, and MR are all located in New Jersey.HM=High Marsh; LMR= Low Marsh River; LMC= Low Marsh Creek.

Marsh	State	Estuary	Experimental Dates & Sample Size	Water Temp (°C)	HM Coordinates	LMR Coordinates	LMC Coordinates
DC	NJ	Delaware Bay	Fall: 11/13/2012; 7 Spring: 04/29/2013; 7 Summer: 08/28/2013; 7	Fall: 7.5-8.2 Spring: 14.6-15.3 Summer: 24.4-25.1	39.219N -75.107E	39.219N -75.108E	39.220N -75.107E
DN	NJ	Delaware Bay	Fall: 11/08/2012; 8 Spring: 04/25/2013; 8 Summer: 08/27/2013; 8	Fall: 7.5-8.2 Spring: 15.0-16.2 Summer: 23.9-25.3	39.180N -74.852E	39.179N -74.851E	39.180N -74.852E
MR	NJ	Delaware Bay	Fall: 11/13/2012; 7 Spring: 04/29/2013; 7 Summer: 08/28/2013; 7	Fall: 7.2-7.8 Spring: 14.6-15.2 Summer: 24.4-25.6	39.229N -75.032E	39.230N -75.032E	39.229N -75.031E
RI	RI	Narragansett Bay	Summer: 09/18/2013; 8	Summer: 20.5-21.7	41.653N -71.343E	41.652N -71.343E	41.653N -71.342E

Table 2.2 Mean ± se for shell length (mm) and dry tissue weight (g) of ribbed mussels by habitat per marsh, pooled over seasons (n). Letters denote significant differences between habitats within marshes calculated using a post-hoc Tukey's test of honestly significant differences; habitats within marshes that share a letter were not significantly different. DC=Dividing Creek; DN=Dennis Creek; MR=Maurice River; and RI=Coggeshall. HM=High Marsh; LMR= Low Marsh River; LMC= Low Marsh Creek.

Marsh	Habitat	n	Shell Length (mm)	DTW (g)
DC	HM	18	59.65 ± 3.04 (a)	0.41 ± 0.06 (a)
	LMC	19	78.91 ± 3.61 (b)	1.06 ± 0.14 (b)
	LMR	21	70.46 ± 4.38 (ab)	1.06 ± 0.18 (b)
DN	HM	22	46.61 ± 2.23 (a)	0.20 ± 0.03 (a)
	LMC	24	55.29 ± 2.47 (ab)	0.45 ± 0.05 (ab)
	LMR	23	56.99±3.95 (b)	0.58 ± 0.11 (b)
MR	HM	18	55.38 ± 2.22 (a)	0.32 ± 0.03 (a)
	LMC	21	57.10 ± 2.98 (a)	0.39 ± 0.07 (a)
	LMR	19	59.67 ± 2.91 (a)	0.46 ± 0.05 (a)
RI	HM	8	51.01 ± 3.52 (a)	0.37 ± 0.07 (a)
	LMC	8	62.96 ± 5.21 (ab)	0.77 ± 0.16 (a)
	LMR	8	76.57 ± 7.65 (b)	1.48 ± 0.29 (b)

Table 2.3 Mean ± se for five qualities regarding seston composition collected at each marsh per season: TSS = total suspended solids; POM = particulate organic matter; %Org = percent organics; C:N = carbon to nitrogen molar ratio; and PN = particulate nitrogen. Water temperature (maximum) and salinity are also included per season per marsh. Letters denote significant differences between marshes per season calculated using a post-hoc Tukey's test of honestly significant differences; marshes within seasons that share a letter were not significantly different. DC=Dividing Creek; DN=Dennis Creek; MR=Maurice River; and RI=Coggeshall.

Season	Marsh	Water Temp (°C)	Salinity (o/oo)	TSS (mg/L)	POM (mg/L)	%Org	C:N	PN (mg/L)
Spring	DC	15.3	20	53.85 ± 7.87 (a)	7.69 ± 1.01 (a)	14.44 ± 0.63 (a)	9.11 ± 0.73	0.35 ± 0.01 (a)
	DN	15.7	23	38.51 ± 0.40 (a)	6.87 ± 0.35 (a)	17.82 ± 0.81 (b)	10.43 ± 0.98	0.31 ± 0.04 (a)
	MR	15.2	13	118.21 ± 3.37 (b)	16.77 ± 0.19 (b)	14.24 ± 0.39 (a)	8.90 ± 0.57	0.87 ± 0.05 (b)
Summer	DC	24.8	19	39.88 ± 0.77 (a)	6.70 ± 0.12 (a)	16.83 ± 0.36 (a)	7.89 ± 0.96	0.77 ± 0.02 (a)
	DN	25.2	24	112.24 ± 15.76 (b)	16.77 ± 2.04 (b)	15.07 ± 0.22 (b)	9.10 ± 0.34	0.90 ± 0.05 (b)
	MR	24.8	14	61.09 ± 1.21 (a)	9.27 ± 0.16 (a)	15.18 ± 0.23 (b)	8.71 ± 0.55	0.70 ± 0.08 (a)
	RI	20.9	35	13.12 ± 2.34	3.51 ± 0.51	27.73 ± 2.52	8.36 ± 0.67	0.11 ± 0.01
Fall	DC	8.2	20	120.05 ± 0.79 (a)	13.84 ± 0.25 (a)	11.52 ± 0.14 (a)	10.06 ± 0.58	0.66 ± 0.03 (a)
	DN	7.2	26	170.63 ± 15.57 (b)	30.26 ± 4.38 (b)	17.34 ± 0.92 (b)	8.26 ± 0.22	1.45 ± 0.15 (b)
	MR	8.2	18	95.03 ± 0.99 (a)	12.17 ± 0.14 (a)	12.80 ± 0.07 (a)	8.25 ± 0.17	0.74 ± 0.07 (a)

Table 2.4 Seasonal mean± se clearance rate for data pooled among habitats by marsh (per season DC/MR: n=7; DN/RI: n=8). Marshes that displayed significant seasonal differences from other marshes are denoted with a "+", and marshes that contained significant seasonal differences among habitats are denoted with an "*". DC=Dividing Creek; DN=Dennis Creek; MR=Maurice River; RI=Rhode Island. DC, DN, and MR are all located in New Jersey.

Marsh	Spring Clearance Rates (l hr^{-1} $gDTW^{-1}$)	Summer Clearance Rates (l hr^{-1} $gDTW^{-1}$)	Fall Clearance Rates (l hr^{-1} $gDTW^{-1}$)
DC	0.315 ± 0.041*	0.691 ± 0.088	0.022 ± 0.004
DN	0.212 ± 0.027	0.506 ± 0.030	0.046 ± 0.006
MR	0.555 ± 0.060+	0.714 ± 0.081	0.064 ± 0.021
RI	X	0.551 ± 0.093	X

Table 2.5 Seasonal mean± se filtration rates of total suspended solids (TSS) and particulate nitrogen (PN) for data pooled among habitats by marsh (per season DC/MR: n=7; DN/RI: n=8). Letters denote seasonal significant differences among marshes from a Tukey post-hoc test of honestly significant differences. DC=Dividing Creek; DN=Dennis Creek; MR=Maurice River; RI=Rhode Island. DC, DN, and MR are all located in New Jersey.

Marsh	Spring		Summer		Fall	
	TSS FR (g hr^{-1} $gDTW^{-1}$)	PN FR (g hr^{-1} $gDTW^{-1}$)	TSS FR (g hr^{-1} $gDTW^{-1}$)	PN FR (g hr^{-1} $gDTW^{-1}$)	TSS FR (g hr^{-1} $gDTW^{-1}$)	PN FR (g hr^{-1} $gDTW^{-1}$)
DC	16.94 ± 2.22 (a)	0.11 ± 0.02 (a)	27.55 ± 3.49 (a)	0.39 ± 0.05 (a)	2.63 ± 0.46 (a)	0.01 ±0.002 (a)
DN	8.16 ± 1.03 (a)	0.06 ± 0.01 (a)	56.75 ± 3.35 (b)	0.53 ± 0.03 (a)	7.94 ± 0.87 (b)	0.07 ± 0.006 (b)
MR	65.66 ± 7.02 (b)	0.49 ± 0.05 (b)	43.60 ± 4.94 (c)	0.50 ± 0.06 (a)	6.09 ± 1.95 (ab)	0.05 ± 0.01 (ab)
RI	x	x	7.23 ± 1.22 (d)	0.06 ± 0.01 (b)	x	x

Chapter 3: Ecosystem Services of the Ribbed Mussel (*Geukensia demissa*) Across the Salt Marsh Landscape

3.1 Abstract

Ribbed mussels are ubiquitous in Mid-Atlantic salt marshes where, through filter-feeding activity, they remove suspended particles, contribute to nutrient cycling, and potentially help marshes keep pace with sea level rise. Ribbed mussels live in multiple habitats across the salt marsh landscape - along edges of the primary marsh shoreline, within marsh drainage creeks, as well as high marsh areas. Although abundant, the spatial distribution of ribbed mussels, and their habitats, are not consistent within or among marshes. This variation in spatial population demographics and relative habitat size affects the distribution of mussel mediated ecosystem services.

The spatial distribution of the three marsh habitats described above were delineated within each of four representative marshes across two regions (3 NJ, 1 RI). Mussel population densities and demographics were quantified in each habitat of each marsh through field surveys and GIS extrapolation. Particle removal services, represented by the gross filtration rate of TSS and particulate nitrogen (PN) normalized for mussel dry tissue biomass, were assessed for each marsh habitat and adjusted for differences in feeding times across the landscape. The average gross filtration of TSS and PN by ribbed mussels measured between $3.83*10^3$ -$1.11*10^4$ kg ha $^{-1}$ yr^{-1} and 30.9-92.5 kg ha^{-1} yr^{-1}, respectively. Particulate nitrogen biodeposition was estimated between 22.8±8.36 and 55.5±23.1 kg ha^{-1} yr^{-1} in New Jersey and 13.3±4.52 kg ha^{-1} yr^{-1} in Rhode Island, contributing between 0.39±0.14 and 0.93±0.38 mm yr^{-1} in NJ marshes and 0.28±0.09 mm yr^{-1} in RI to vertical marsh enhancements. Most ecosystem services were concentrated in creeks for all marshes (>65%). However, New Jersey marshes had much lower services (<10%) along marsh

shorelines compared to Rhode Island (>25%), potentially because of higher erosion along New Jersey marshes.

3.2 Introduction

Ribbed mussels are suspension feeders that actively pump water to capture suspended particulate material in order to derive nutrition. Water movement is driven through the gills where particles are indiscriminately retained through efficient use of three types of cilia (frontal cilia, laterofrontal cirri, and lateral cilia). Trapped particles are then transported, in free suspension or mucous movement, by the frontal cilia towards the labial palps where they are sorted to either be selected for ingestion or rejected as pseudofeces (Newell and Langdon 1996). Ingested matter passes into the gut where it can either be absorbed or rejected (Fig 3.1a). Particulate matter that is not digested is passed through the gut and defecated (rejected; Fig. 3.1a). Through these complex pre-ingestion sorting and post-ingestion processes, mussels can enrich their diet and digest matter that best suits their current physiological demands.

Nitrogen is essential for all organisms to construct amino and nucleic acids, and is considered the primary limiting nutrient for production in coastal ecosystems (Sprent 1987), especially salt marshes (Odum 1968). The major natural nitrogen inputs to salt marshes are dissolved organic, inorganic, and particulate nitrogen delivered by tidal waters, as well atmospheric nitrogen fixation by bacterial communities; lesser contributions are provided by precipitation and ground water fluxes (Valiela and Teal 1979). In the salt marsh environment, nitrogen export has been measured to be equivalent to total input, indicating that the within-marsh cycle of nitrogen fixation (N_2-NH_3), nitrification (NH_3-NO_3), and denitrification (NO_3-N_2) are important for salt marsh communities to meet their internal nitrogen demands through recycling of limited nitrogenous compounds (Valiela and Teal 1979). Additionally, changes in nitrogen imports and exports can have ecological effects. Increased nitrogen input enhances plant productivity and belowground decomposition rates (Valiela and Teal 1979, Turner et al. 2002; Deegan et al. 2012; Kirwan and Mudd 2012; Watson et al. 2014). In some areas, the export of nitrogen from salt marshes can in turn increase primary production of algae in coastal waters which has been linked to decreased biological diversity (Valiela et al. 1990).

Ribbed mussels, the functional dominant animals in salt marsh ecosystems (Kuenzler 1961; Fell et al. 1982; Jordan and Valiela, 1982; Bertness 1984), help to govern mass biogeochemical relationships such as nitrogen retention and export. They have been reported to filter 1.8 times the particulate nitrogen exported from the marsh by tidal flushing (Jordan and Valiela 1982), and hence, where mussels are dense, their presence can significantly alter the nitrogen budget of the salt marsh. Jordan and Valiela (1982) modeled a nitrogen budget for ribbed mussels in Great Sippewissett Marsh, MA (Figure 3.1bi). Measurements showed that mussels absorbed 50% of ingested nitrogen, with the other 50% being passed through the animal in the form of feces and pseudofeces (biodeposition). Of the 50% absorbed, mussels only retained approximately 10% of their ingested nitrogen for growth while ~12% was allocated for the production of gametes and byssal threads, and 27% was immediately returned to the environment as excreted ammonia. Hence, most nitrogen that filtered by ribbed mussels was either assimilated or deposited to the benthos (~60%) and not quickly returned to coastal waters (Jordan and Valiela 1982).

Subsequent studies have confirmed these cycling values as being a good annual estimator, with summer experimental clearance values being slightly higher and winter and spring values slightly lower (Bayne et al. 1988; Wilbur and Hilbish 1989; Kreeger and

Newell 1996 and 2001). Galimany et al. (2013) reported higher absorption efficiencies of 71% in a study conducted between Milford, CT and Bronx, NY. These sites had lower particulate matter with higher POM concentrations in the natural seston. Kreeger and Newell (2000, 2001) showed that absorption efficiencies vary widely across food types, being higher for diets with more nutritious particles such as bacteria and benthic diatoms. Under Galimany et al. absorption rates, and assuming equal fate partitioning percentages for the absorbed materials, only 44% of the absorbed materials are removed from the short-term nitrogen cycle due to enhanced ammonia and byssal production (Fig 3.1bii).

The combination of nitrogen in feces, pseudofeces and ammonia represents a sizeable nitrogen transformation, thus contributing to *in situ* biogeochemical cycling wherever mussels are abundant. Additionally, by moving suspended matter to sediment via feces and pseudofeces (a.k.a benthic-pelagic coupling), dense mussel beds could hypothetically facilitate marsh accretion both directly by enhancing sedimentation and indirectly by fertilizing plants (Leonard and Luther 1995; Nepf 1999) making plants near mussels more productive (Bertness, 1984).

Although ribbed mussels are abundant in salt marshes along the eastern coast of the US, their spatial distribution is not consistent within or among marshes (Bertness and Grosholz 1985; Franz 2001) and thusly, neither are their effects on particle and nitrogen cycling. Salt marsh ecosystems are composed of a variety of micro-habitats delineated by hydroperiod and ecological relationships (Bertness 1991). Mussel densities are typically greatest along tidal channels in low marsh areas (Bertness and Grosholz 1985; Franz 2001), likely due to advantages of this positioning (e.g. increased feeding times and tidal flushing) outweighing the drawbacks (e.g. increased physical stress and predation). The majority of settlement occurs among conspecifics along the edge of the marsh in close proximity to previously established mussel populations, resulting in a positive feedback loop between mussel density and recruitment (Bertness and Grosholz 1985; Nielsen and Franz 1994; Franz 2001). Low marsh areas provide longer inundation/feeding time than high marsh habitats, and mussels in the low marsh exhibit higher growth rates (Jordan and Valiela 1982; Stiven and Gardner 1992; Franz 1993) and mature at a smaller size class (Franz 1996) than those in the high marsh. In contrast, mussels in the high marsh are longer-lived and have higher survivorship (Franz 2001), but the smaller size and density of high marsh mussels means that the biomass of the high marsh population (per unit area) is lower than in low marsh areas (Bertness and Grosholz 1985). These differences in vertical positioning of ribbed mussels across the landscape will also have an effect on the time available for filtration- mussels at higher elevations have less time to feed than those at lower vertical positions.

Previous studies investigating ribbed mussel filtration services have focused on quantifying water (Widdows and Bayne 1971; Bayne et al. 1988; Wilbur and Hibbish 1989; Kreeger and Newell 2001; and Galimany et al. 2013) or nutrient (Jordan and Valiela 1982; Bilkovic et al. 2017) processing without accounting for landscape level spatial variability. This study aimed to characterize the current mussel-mediated ecosystem service contributions across the entire salt marsh landscape, including the edges of main tidal channels and intra-marsh creek networks, as well as in the vast high marsh areas. To investigate services at the landscape level, each of the three habitats described above were delineated in three representative marshes in NJ and one in RI, which were subsequently assessed for mussel population densities and demographics. Results were integrated with habitat-specific and marsh-wide filtration rates of ribbed mussels fed on natural seston from the previous studies and normalized by the each habitat's elevation-based feeding time availability (i.e. time of submersion), to quantify the spatial distribution of representative ecosystem services. These data were subsequently used to investigate marsh-wide implications of seston filtration and biodeposition: a) contribution to vertical marsh building through the deposition of inorganic material biodeposited as feces and pseudofeces; and b) the term removal of particulate nitrogen from coastal waters.

3.3 Methods

3.3.1 Site Selection

Study locations were selected in three representative study salt marshes in New Jersey, and one in Rhode Island. New Jersey salt marshes were chosen in Dennis Creek, Dividing Creek and the Maurice River, which are tributaries along the Delaware Bayshore (Fig. 3.2A). In Rhode Island, the study marsh was Cogshall Cove, located on Prudence Island in Narragansett Bay (Fig. 3.2B). These locations were deemed to be representative of typical eastern U.S.A. salt marshes based on biological and physical traits for a broader array of coastal wetlands being monitored for the Mid-Atlantic Coastal Wetland Assessment in New Jersey (Partnership for the Delaware Estuary 2014) and as related by the Environmental Protection Agency Office of Research and Development Atlantic Ecology Division in Rhode Island. Within each of the four representative salt marsh systems, three replicate study sites were chosen. The lower position (1) was selected near the river/channel mouth, the upper position (3) was selected at the furthest extent upriver where observationally representative mussel populations were present, and the middle position (2) was located between the other two, at a location with similar observational mussel populations (Fig. 3.2C-F). All study sites contained a mussel population and the three habitats of interest

3.3.2 Habitat Delineation

The three habitats that were surveyed at each site per marsh were: low marsh along the main marsh shoreline, referred to as low marsh river (LMR); high marsh (HM); and low marsh along a representative small creek that drained fully at low tide referred to as low marsh creek (LMC). Widths of LMR and LMC habitats generally correspond to tall-form *S. alterniflora* zonation, and for standardization these were based on average widths from literature and as measured from long-term Delaware Bay data sets (Deegan, 2012; PDE Partnership for the Delaware Estuary 2014). Low Marsh River habitat, for example, was delineated as being along the main river/channel of the marsh that does not drain at low tide, and characterized by, at least, a 1-2m band low marsh vegetation (*Spartina alterniflora* tall-form) from the water's edge to the high marsh platform. High Marsh habitat was delineated by vegetation community composition, including: *Spartina alterniflora* short-form; *Spartina patens; Distichlis spicata*; *Juncus* spp. and *Salicornia* spp. Low Marsh Creek habitat was characterized by a minimum of a 2-4 meter band of tall-form *Spartina alterniflora* bisected by an intra-marsh drainage creek. The boundaries of these habitat types were mapped at each site using a high resolution RTK-GPS, and were extrapolated in subsequent analysis by digitization of high resolution aerial images (IKONOS 2013, 1:300 scale).

3.3.3 Transect and Sampling Plot Layout

Within each study site, three parallel transects were spaced 10m apart, oriented perpendicular to the main tributary channel axis, and spanning the three habitats types of interest (Fig. 3.2G). In general, the origin of each transect was fixed at the seaward extent og contiguous vegetation in LMR habitat, crossed landward through HM habitat, and ended in LMC habitat. The length of each transect varied from 45m - 100m in length.

One study plot was centered on each transect within each of the three habitat types (n=3 plots/transect; n=3 plots/habitat/site). Each plot had an associated paired set of 1 m^2 sampling quadrats. One was designated for destructive sampling, and one for non-destructive sampling. These paired quadrats were centered 0.5m to the left and right of each transect. Looking landward into the marsh from the transect origin, the destructive and non-destructive paired data collection plots were located to the left and right of each transect, respectively (Fig 3.2G). The position of the paired data collection plots allowed for movement along each transect without disturbing the study areas, while retaining a proximity that allowed for data to be representative of the study plot. Additionally, as some data collection techniques can be invasive to the marsh, by grouping destructive and non-destructive methods in separate plots, less marsh area needed to be disturbed and one plot always retained its structural integrity (could be useful for potential future data collection). Each site contained 3 paired destructive/non-destructive sampling quadrats per habitat, totaling n=18 sampling quadrats/habitat/marsh.

3.3.4 Physiological Rates, Total Suspended Solids (TSS) and Particulate Nitrogen (PN) Concentrations

To estimate annual seston filtration rates per marsh, each seasonal weight specific clearance rate (WSCR; spring, summer, and fall) from previous studies (Chapter 2) were assumed representative of the average WSCR of 25% of the year for each marsh. Mussels were assumed to filter negligibly during winter (Kreeger and Newell 2001), so each marsh received a number of winter clearance rates of 0 lhr^{-1} $gDTW^{-1}$ equal to their seasonal sample size. Total Suspended Solid (TSS) and PN values were calculated from 18 measurements/marsh (n=6/season) in New Jersey and six observations in Rhode Island collected during the summer.

Since seasonality was not assessed for Rhode Island marshes, spring and fall weight specific clearance rates were estimated from summer rates by assuming a similar seasonal physiological scaling to the New Jersey marshes. The ratio of summer New Jersey WSCR: Rhode Island WSCR was calculated and used as a correction factor to predict fall and spring

New Jersey WSCR for Rhode Island mussels (Table 3.1). Twenty-four observations of each seasonal value (8 habitat^{-1}) were added to the WSCR data set, with an addition 24 values of "0" representing winter WSCRs, to balance the influence of the 24 experimental summer values. These values (n=96; 24 observed in summer and 24 each estimated in fall, spring and winter) were used to calculate the annual Rhode Island WSCR. Due to the use of a single WSCR replicated eight times to independently calculate both fall and spring physiological processing, there was no variability among Rhode Island values for those seasons.

3.3.5 Ribbed Mussel Density and Size Demographics

Ribbed mussel densities were assessed using both rapid and intensive measures. As a rapid measure of mussel density, the visible presence of live mussels was counted within sampling quadrats by counting the shell bills, or "lips". Ribbed mussel lip counts were collected in each paired destructive and non-destructive plot during early spring 2011, before the vegetation came out of senescence. By conducting the survey at this time of year, the surface of the marsh was more visible than it would have been during the growing season. A 1m^2 quadrat was placed on the marsh surface at each destructive and non-destructive data collection plot. The quadrat was divided into four equal sections by placing two meter sticks perpendicular to each other at the 0.5m mark of each side of the quadrat. Beginning in the lower right hand corner facing into the marsh on the side of the quadrat nearest to a body of water and moving landward, the lips of visible mussels were counted. This was repeated in all four sections of the quadrat, yielding a total mussel lip count per 1 m^2 quadrat.

To account for unobserved mussels due to either sampling error or mussel burial, a 0.25m^2 subsection of each destructive quadrat was excavated for a more accurate mussel count. Excavated marsh samples were located on the edge adjacent to river and creek in LMR and LMC plots respectively, and in the center of each HM plot. Quadrats were excavated to a depth of approximately 25cm to ensure that all mussels would be removed. The excavated marsh mud, peat and plant material was added to buckets filled partially with water so that mud could be rinsed from plants and rhizomes, thereby making all attached mussels visible. Mussels were separated and transferred to a clean bucket. All mussels >10 mm in shell height were then counted. A randomly selected subgroup of twenty five mussels from each sample (when available) were then measured using calipers (Absolute Digimatic) to ±0.01 mm shell height. Mussel densities in each 0.25m^2 destructive quadrat were multiplied by four to estimate densities of the entire 1m^2 quadrat. A correction factor was then derived to estimate actual densities by comparing mean densities in excavated destructive plots to lip counts in the destructive plots. The mussel density in each non-destructive quadrat was then calculated by multiplying this correction factor by the non-destructive quadrat lip counts. A summary of calculations is given in Table 3.2.

3.3.6 Ribbed Mussel Biomass

Ribbed mussel Dry Tissue Weight (DTW) to Shell Height (SH) allometric relationships were derived from measured and sacrificed mussels used in physiology experiments conducted seasonally in 2012-2013. These allometric relationships were derived separately for each habitat of each marsh (n=21 or 24 mussels/marsh/habitat) and a power regression curve of the form DTW=b*SH^m (b= intercept; m=slope) was fitted for each group of mussels by marsh and habitat. (Table 3.3). These marsh and habitat specific allometric relationships were then used to predict the dry tissue weight of each of the 25 ribbed mussels measured within each of the excavated destructive quadrats. The average DTW of mussels per destructive quadrat was then calculated and was multiplied by the predicted mussel density of the destructive quadrat to estimate the total mussel biomass in each $1m^2$ destructive plot. To estimate the mussel DTW in each non-destructive plot, the average DTW per mussel in the associated paired destructive quadrat (DQ) was multiplied by the non-destructive quadrat (NDQ) predicted mussel density.

3.3.7 Inundation time per Habitat

Nine HOBO U20-001-01-Ti water level data loggers (referred to as "sensors") were used to measure inundation time per day across the HM, LMC, and LMR habitats. An additional sensor was placed above the marsh platform as a control to measure ambient atmospheric pressure. Measurements were collected only at site 2 (middle site) in Dennis Creek (3 Aug – 4 Sep 2015), Dividing Creek (5 Sep – 27 Oct 2015) and the Maurice River (27 Oct – 9 Dec 2015). Deployment was of a length of time sufficient to capture water levels during two neap and spring tides at each location. Data sets were cropped so that each contained the same number of days relative to tidal events to standardize temporal inundation patterns across sites.

Due to limitations of sensor availability, sensors were not deployed during the same time frames among marshes, and inundation times assessed at each site 2 were assumed representative for sites 1 and 3 per marsh. Among marshes, there were no significant large scale water level anomalies during the times of deployment that would have skewed data abnormally. Within marshes, sensors were deployed in the center of each plot along the monitoring transects (n=3 $habitat^{-1}$ $marsh^{-1}$). Sensors were secured in 6" PVC housing drilled with ¼" holes spaced 3cm apart along the bottom to allow water access while preventing debris from coming in contact with the sensor. The housing was attached to two 2.5' ¼" PVC stakes used to secure the sensor at the marsh surface. The location of each sensor was surveyed using a Trimble R6 RTK-GPS unit.

Each sensor measured changes in pressure relative to the atmospheric control which were correlated to inundation greater than 0 cm, 1 cm and 2.5 cm above the sensor using the HOBOware software provided with the data loggers. The 2.5 cm inundation depth was selected as a conservative indicator of complete submergence relevant to ribbed mussel filtration. This avoided potentially false readings due to localized sedimentation and flooding at the HOBO sensor that could possibly occur using the 0cm and 1cm calculations. A percent time of inundation (PTI) was calculated by the software as the percent of time during the deployment that the sensors measured more than 2.5cm inundation. This value was used to calculate the daily inundation time (hrs day^{-1}).

Arcsine square root transformed PTI was regressed against the RTK-GPS elevation (NAVD88 m) measurements at each plot at site 2 for each New Jersey marsh (Table 3.4). The slope and intercept of each New Jersey marsh-specific regression were used to calculate the arcsine square root PTI for each plot at sites 1&3 in the their respective marshes (n=3 habitat^{-1} site^{-1}), which was back transformed to an elevation-based PTI estimate for each plot (n=3 habitat^{-1} site $^{-1}$ marsh^{-1}). As HOBO sensors were not able to be deployed at the Rhode Island marshes, relative percent inundation time per plot within at the Rhode Island sites was calculated as a function of the measured plot percent distance from mean water (MW) and arcsine square root PTI at each site 2 in New Jersey.

For all site 2 New Jersey plots at which water level sensors were deployed (n=27; 3 habitat^{-1} marsh^{-1}), percent distance from mean tide line (MTL) was calculated (using -0.038m NAVD88; NOAA Fortescue, NJ datum 8536931) as the plot distance above MTL (no plots were located below MTL) divided by the total distance (m) between MTL and mean higher high water (r^2=0.67, F-stat=24.79 on 1 and 25, p>0.001). The slope (-0.90921) and intercept (2.01281) were used to back-calculate the daily percent inundation time of the

Rhode Island plots using Rhode Island percent distance from MTL calculations. Rhode Island percent distance from MTL per plot (N=27; n=3 habitat^{-1} site^{-1}) was calculated using the distance of RTK-GPS elevation data collected in each Rhode Island plot from the elevation of the MTL (-0.051m NAVD88; NOAA Newport, RI datum 8452660).

3.3.8 Habitat Delineation and Percent Habitat Area

The area of each habitat type (LMR, HM, and LMC) was assessed in the vicinity surrounding each study site. The assessment area for the habitat mapping was bounded by a 300m buffer applied to the midpoint of the center transect (transect 2) and without crossing the main channel/river, referred to as the habitat assessment area (HAA). The total HAA was calculated using the Calculate Geometry tool in ArcGIS 10.2. IKONOS 2014 digital imagery (0.82m black and white, 3.28m multispectral resolution) was used to digitize creek and river edges at 1:300 scale within the 300m buffer site. A 2m buffer was applied to the digitized main channel and creek edges from the edge moving into the marsh and was classified as LMR and LMC habitat, respectively. The area between digitized paired inter-marsh creek edges was considered open water and was excised from the total area of the site using the Erase tool. By subtraction, the remaining area not classified as LMR or LMC was classified as HM habitat. The relative percentage of space occupied by each habitat within the HAA was considered the percent habitat area. The percentage of the total area comprised of the three habitat types was then used to estimate marsh-wide mussel DTW and associated ecosystem services.

3.3.9 Calculation of Filtration Rate of Total Suspended Solids and Particulate Nitrogen

Site specific filtration rates of TSS and PN (SSFR-TSS and SSFR-PN, respectively) per marsh per habitat were calculated using the following equation:

$$SSFR\left(\frac{kg}{yr\ ha}\right) = FR\ \left(\frac{mg}{hr\ gDTW}\right) * ImT\left(\frac{hr}{day}\right) * HabBio\left(\frac{gDTW}{m^2}\right) * PerHab(\%) * ConF(\frac{kg\ m^2 day}{mg\ ha\ yr})$$

FR = the annual mean filtration rate by marsh calculated by multiplying the mean annual weight-specific clearance rate by the mean annual TSS or PN values; ImT = immersion time calculated using the water level data loggers; HabBio = mussel biomass estimates; PerHab = percent area of each habitat; and ConF = conversion factor used to correct the units to the appropriate final values. Site-specific filtration rates per marsh per habitat were used to calculate the marsh-wide and habitat-specific per marsh filtration rates of TSS and PN.

3.3.10 Contribution to Vertical Accretion

Potential vertical enhancement describes the potential contribution to elevation building by the portion of the filtered material that is deposited onto the marsh through pre-ingestion rejection as psedofeces or post-ingestion fecal deposits by ribbed mussels. Pseudofeces and feces contain both rejected organics and inorganics. As a conservative estimate however, only the inorganic portion was considered for vertical accretion. The annual mean percent inorganic material (PIM) of TSS filtered by ribbed mussels for each marsh was calculated as:

$$Annual\ Mean\ TSS\ Percent\ Inorganic = 1 - Annual\ Mean\ TSS\ Percent\ Organics$$

The habitat-specific FR-TSS for each site per marsh was multiplied by the annual mean PIM to calculate the amount of inorganic material (kg ha^{-1} yr^{-1}) filtered annually (n=3 per habitat per marsh). The volume:weight conversion ratio of 1g:1cm^3 of water was used as a conservative estimate to convert the mass of filtered material to a volume as follows:

$$\begin{aligned} &Mass\ Filtered\ (kg\ ha^{-1}\ yr^{-1}) \rightarrow Mass\ Filtered\ (mg\ mm^{-2}yr^{-1}) \rightarrow use\ 1mg = 1mm^{3} \\ &= Mass\ Filtered\ (mm^{3}mm^{-2}yr^{-1}) \\ &= Potential\ Vertical\ Enhancement\ (mm\ yr^{-1}) \end{aligned}$$

This estimate was considered conservative as biodeposits can contain rejected organics, and so biodeposit masses will be greater than assessed using just the inorganic portion.

3.3.11 Net Removal of Particulate Nitrogen (PN)

Net particulate nitrogen removal refers to the quantity of particulate nitrogen removed from the water column through either bio-deposition or growth (i.e. shell or tissue growth not including byssal thread or gamete production). Bio-deposition and growth were calculated by multiplying the habitat-specific FR-PN for each site per marsh by the estimated deposition and growth percentages (Figure 3.1B). In New Jersey, the fate of filtered nitrogen was estimated based on the nitrogen budget of the ribbed mussel reported in Jordan and Valiela, 1982 (Fig. 3.1bi) where 50% of filtered nitrogen was absorbed and 50% was biodeposited. Of the absorbed nitrogen, 10% was estimated to be assimilated as somatic and shell growth. Therefore biodeposition and somatic growth were calculated as habitat-specific FR-PN multiplied by 0.5 and 0.1 respectively. For Rhode Island, a higher absorption efficiency of 71% as reported in Galimany et al. (2013; Fig. 3.1bii) was employed. The TSS and POM values reported by Galimany et al. (2013) were representative of the values measured at the Rhode Island sites, and thusly this higher absorption efficiency was used to calculate net particulate nitrogen removal in Rhode Island. As 71% was estimated to be retained, 29% was considered available for biodeposition. In New Jersey, 20% of the absorbed nitrogen (10% of total filtered nitrogen) was assumed to be assimilated for growth. Assuming the same proportion of filtered nitrogen was allocated for growth in Rhode Island, habitat-specific FR-PN was multiplied by 20% of the absorbed nitrogen: habitat-specific FR-PN*0.14=Rhode Island Growth. All percentages used as fate coefficients are listed in Table 3.5.

3.3.12 Statistical Analyses

Prior to analysis, all data were tested for normality using a Shapiro-Wilk test, and for homogeneity of variance using either a Bartlett or Levene test for normal and non-normal data respectively. Where there was evidence that data were non-normally distributed, but variances were equal across factor levels, a Kruskal-Wallis test was used to calculate differences in medians of dependent variables among factor levels. When there was evidence that data were non-normally distributed and the variances were not equal across factor levels, results of a Kruskal-Wallis test were interpreted as differences in mean ranks of the dependent variables among factor levels. Non-parametric post-hoc analysis following a rejection of a Kruskal-Wallis were conducted using a Dunn's test of multiple comparisons using rank sums (Dunn 1964) with a Bonferroni correction to minimize type-I error (dunn.test package, Dinno and Dinno 2017). Both Kruskal-Wallis and Dunn's test are appropriate for non-normal and unbalanced data sets, as well as data with tied ranks.

When no evidence was provided that data were not from a normal distribution and the variability among factor levels displayed homogeneity, differences in metrics among habitats, marshes, and regions were calculated using a nested linear mixed model in the nlme package (Pinheiro et al. 2017) and ANOVA testing. Habitat was considered a fixed factor, and site nested in marshes were treated as random factors. When a significant difference among factor levels was detected using ANOVA analysis, post-hoc analysis of differences among factor levels was conducted using a Tukey test of honestly significant differences in the glht function in the multcomp package (Hothorn et al 2017). All statistical calculations were conducted using R 3.0.3 open source statistical software.

3.4 Results

3.4.1 Physiological Rates, Total Suspended Solids (TSS) and Particulate Nitrogen (PN) Concentrations

Annual weight specific clearance rates were significantly different among marshes ($p<0.02$). Dennis Creek annual WSCR were significantly lower than Maurice River ($p<0.02$), but not Rhode Island ($p<0.92$) or Dividing Creek ($p>0.42$) marshes. Dividing Creek, Maurice River, and Rhode Island marshes did not differ from each other (Table 3.6, Appendix D). Annual total suspended solids (TSS) and particulate nitrogen (PN) concentrations in Rhode Island were significant lower than concentrations in all New Jersey marshes, which did not differ from each other (Table 3.6, Appendix D). Regionally, New Jersey TSS and PN averaged 89.9±6.29 and 0.75±0.05 mg l^{-1} respectively and Rhode Island averages were approximately 15% of these (Table 3.6).

Annual marsh-wide weight specific filtration rates of TSS and PN did not follow the same ordinal pattern as WSCR (Table 3.6). Dennis Creek had the lowest WSCR, but the second highest WSFR, likely due to having the largest concentration of TSS/PN. Conversely, Dividing Creek ranked second in WSCR, but due to the lower concentration of TSS/PN relative to the other New Jersey marshes, ranked third in overall WSFR. These data could suggest that WSFR is largely driven by the concentrations of material present to be removed, but Maurice River, which ranked second for TSS/PN loads, was ranked first for both WSCR and WSFR TSS/PN. This ranking is likely due to the magnitude of the WSCR relative to the other marshes. The Rhode Island ranking dropped from third for WSCR to fourth for WSFR, and as noted above this marsh also ranked last for TSS/PN concentrations.

3.4.2 Ribbed Mussel Biomass

Mussel biomass densities were not normally distributed (Shapiro-Wilks $p<0.05$ per marsh per habitat) and data distributions differed among (Levene test: $p<0.001$) and within marshes in the LMR (Levene test: $p<0.001$) and LMC (Levene test: $p<0.02$) habitats, but were similar in the HM (Levene test: $p>0.85$). Kruskal –Wallis tests indicated no significant mussel biomass differences among medians of marshes in HM areas ($p>0.09$; Fig 3.3a) but indicated significant differences among marshes in the LMC and LMR habitats ($p< 0.001$ for both; Figs 3.3b & 3.3c respectively). As the data distributions in these habitats were significantly different, these result indicate significant differences in the magnitude of the marsh-specific distributions of mussel density.

Dunn post-hoc analysis indicated that LMC habitat in the Maurice River had a significantly different distribution than all other marshes ($p<0.001$, Fig. 3.3b), while there was no evidence to support differences among the other marshes ($p<0.90$ for all other pair-wise comparisons, Fig. 3.3b). Along rivers, post-hoc analysis showed Rhode Island had a significantly greater distribution than all New Jersey marshes ($p<0.001$, Fig 3.3c), which when analyzed independently, showed no evidence of distributional differences ($p<0.49$ for all pair-wise comparisons; Fig.3.3d).

There were no significant differences in the magnitude of ribbed mussel biomass among New Jersey marshes, but all New Jersey marshes displayed smaller ranges of values than Rhode Island (Table 3.7 marsh-wide values; test results in Appendix D). Pooling data across New Jersey marshes, the distribution of ribbed mussel biomass along the LMC (83.8 gDTW m^{-2}) was significantly greater than along the LMR (0.07 gDTW m^{-2}) and in the HM (2.27 gDTW m^{-2}; $p<0.001$ for both tests), which did not differ from each other ($p>0.13$). Among New Jersey marshes, Dividing and Dennis Creeks LMC mussel biomass distributions were significantly greater than both the LMR and HM habitats ($p<0.01$ for all tests) which did not rank differently from each other in either marsh ($p>0.99$ both tests; Table 3.7). Pair-wise ranking in the Maurice River did not identify any significant distributional differences in ribbed mussel biomass among habitats (LMC-HM $p>0.82$; LMR-HM $p>0.85$; LMC-LMR $p>0.36$; Table 3.7). Rhode Island HM habitat had a significantly lower density than both the LMC and LMR habitats ($p<0.01$ for both tests), which did not significantly differ from each other ($p>0.29$; Table 3.7).

Although the Rhode Island LMR and LMC habitats did not statistically differ the LMR had an average ribbed mussel biomass 102% greater than in the LMC habitat, and had 1,812%, 34,251%, and 736% percent greater average mussel biomass than along LMR habitats in Dividing Creek, Dennis Creek, and Maurice River respectively (Table 3.7). Although not as striking a discrepancy, the Rhode Island LMC habitat had average ribbed mussel biomass 58%, 12%, and 554% greater than the LMC habitats in Dividing Creek, Dennis Creek, and Maurice River, respectively (Table 3.7). There were less percentage differences between the HM habitats in Rhode Island and New Jersey marshes, with Rhode Island only having ~2% more mussel biomass than in Dennis Creek and Maurice River, but 43% more than in Dividing Creek. Even though this percentage seems large, the average biomass was so low in the Rhode Island HM (9.60 gDTW m^{-2}), its value was nearly negligible (Table 3.7).

Although all statistical comparisons were conducted using medians, means±se were used in calculating the scaling of ecosystem services by biomass. All patterns regarding means of ribbed mussel biomass at the marsh and habitat levels followed the patterns exhibited by the medians. All marsh and habitat specific means are located in Table 3.7 and all site and habitat specific values are listed in Appendix E.

3.4.3 Inundation time and Elevation per Habitat

In New Jersey marshes, a general pattern of increasing inundation time from HM, to LMC, to LMR habitats was present, whereas in Rhode Island, LMC received the longest inundation time followed by LMR and then HM. There was no significant interaction between marsh and habitat (p>0.62) regarding inundation and elevation time in NJ marshes, but both marsh and habitat were independently significant (p<0.001 for both). These results indicate that although inundation time and elevation varies within and among marshes, their pattern is similar across NJ marshes (Fig. 3.4a). Daily inundation and elevation differed among all habitats in Dennis Creek (p<0.0001 for all), and nearly in Dividing Creek (p<0.001 for elevation) with only river and creek habitats not significantly differing by daily inundation time (p>0.063). Dividing Creek mean inundation and elevation were 10.51 hr d^{-1} and 0.60m, 8.81 hr d^{-1} and 0.77m, and 12.07 hr d^{-1} and 0.39m for the creek, high marsh and river habitats respectively (Fig. 3.4a). Dennis Creek mean inundation and elevation were 11.39 hr d^{-1} and 0.67m, 9.74 hr d^{-1} and 0.84m, and 14.61 hr d^{-1} and 0.37m respectively (Fig. 3.4a). In the Maurice River, the inundation of the river habitat (10.83 hr d^{-1}) differed from the creek (7.58 hr d^{-1}; p=0.04) and the high marsh (6.83 hr d^{-1}; p=0.01), and elevation differed between the river (0.52m) and the high marsh (0.78m; p<0.03), but not between either of the previous habitats and the creek (0.74m; Fig. 3.4a).

In RI, inundation time significantly differed among all habitats (p<0.0001) as did elevation (p<0.001). Inundation time and elevation displayed converse patterns with creek receiving the most inundation and sitting at the lowest elevation (13.35 hr/d and 0.14m; Fig. 3.4a) and the high marsh receiving the least inundation and at the greatest elevation (5.31 hr/d and 0.65m; Fig. 3.4a) , with the river habitat in the middle (9.17 hr/d and 0.38m; Fig 3.2B). All site and habitat specific values are listed in Appendix E.

3.4.4 Percent Habitat Area

Results of a Kruskal-Wallis rank sum test show significant differences in percent area among habitats within marshes (DC: $p<0.03$; DN $p<0.01$; MR: $p<0.03$; and RI $p<0.03$). In all marshes, the HM comprised the largest percent area of all marshes (DC= 0.79; DN=0.69; MR=0.68; RI=0.68; Fig. 3.4b) and the LMR habitat comprised the least (DC= 0.05; DN=0.03; MR=0.03; RI=0.08; Fig. 3.4b). Although creek habitat size was greater than the river habitat size in all marshes, it was closer to river values than to the high marsh values (DC= 0.16; DN=0.28; MR=0.29; RI=0.24; Fig. 3.3C). All site and habitat specific values are listed in Appendix E.

3.4.5 Filtration Rate of Total Suspended Solids and Particulate Nitrogen

Marsh-wide annual mean gross filtration services of TSS and PN measured between $1.15*10^4 \pm 2.64*10^3$ and $3.34*10^4 \pm 5.64*10^3$ kg ha^{-1} yr^{-1} and 92.8±21.3 and 277±47 kg ha^{-1} yr^{-1} respectively (Table 3.7). There was a significant interaction between marsh and habitat for filtration rates of TSS and PN ($p<0.001$ for both tests). Simple main effects tests showed that Dennis Creek had significantly higher filtration rates for both TSS and PN ($p<0.01$ for all pair-wise tests) than all other marshes, which did not significantly differ from each other (Appendix D). Partitioning by habitat, mean filtration rates of TSS and PN were significantly higher in LMC habitat than in the LMR and HM habitats, which did not differ from each other, in Dennis and Dividing Creeks and in Rhode Island (Table 3.8). Maurice River filtration rates of TSS and PN did not significantly differ among habitats (Table 3.8). Generally, mean filtration rates in New Jersey marshes were higher in the LMC and HM habitats than in the LMR habitat. In Rhode Island, the largest average was along the LMC habitat, but the LMR habitat showed larger average filtration rates than in the HM habitat (Table 3.7).

3.4.6 Contribution to Vertical Accretion

The marsh-wide contribution of mussel inorganic biodeposits to vertical marsh accretion ranged between 1.16±0.60 and 2.78±0.47 mm yr^{-1} in New Jersey and was calculated to be 0.83±0.19 mm yr^{-1} in Rhode Island. In all New Jersey marshes, inorganic biodeposition generally increased from LMR to HM to LMC across the landscape. Rhode Island habitats did not follow this pattern. As with New Jersey, mussel deposits in the LMC habitat had the greatest contribution to vertical marsh building, but was followed by the LMR habitat, with HM supplying the lowest calculated contribution (Table 3.7).

3.4.7 Net Removal of Particulate Nitrogen (PN)

In New Jersey marshes, between 68.5±35.2 and 166±23 kg PN ha^{-1} yr^{-1} were net removed from the water column (Table 3.7). Approximately 83% of the net removed material was deposited into the substrate and 17% was retained for growth. The marsh-wide averages were most similar to the HM contributions, which like the other filtration services, were generally second in terms of habitat contributions to a marsh-wide total, after the LMC habitat (Table 3.7). Rhode Island estimated net filtration services of PN were lower than in New Jersey at 39.9±9.2 kg ha^{-1} yr^{-1}, with the highest services located in the LMC, followed by the LMR habitat, and lastly the HM. Since absorption was estimated to be higher in Rhode Island (71%, Table 3.5), the retention of PN for growth in Rhode Island was generally similar to Dividing Creek and Maurice River in New Jersey (Table 3.7). Average retention for growth was higher in Rhode Island than in NJ regarding LMR habitat for all marshes, and higher than Maurice River regarding LMC habitat (Table 3.7).

3.5 Discussion

Ecosystem services furnished by ribbed mussels scale with population biomass which can vary widely among different marshes, and across the marsh landscape. Filtration services also scale with the abundance and composition of seston, which can also vary widely across space and time. Based on previous population studies (Bertness and Grosholz 1985; Stiven and Gardner 1992; Evgenidou and Valiela 2001; Franz 2001; Bilkovic 2017), we expected to find high densities of ribbed mussels along the edge of the main tidal channel (LMR), and a decline with increasing elevation extending to high marsh (HM) habitat. Densities of mussels along the small marsh creeks (LMC) were expected to be moderate. This pattern was evident in the studied Rhode Island marsh, but not at three different locations in New Jersey (Table 3.7). But among habitats, greater mussel biomass did not necessarily result in greater habitat-specific services, as services also scaled with percent area of each habitat. In Rhode Island, 66% of the mussel biomass was concentrated in the LMR habitat, but the bulk of the filtration services were actually concentrated in the LMC habitat which contained only 32% of the mussel biomass, but represented a greater portion of the total area (Table 3.7; Fig. 3.4b). Additionally, mussel biomass in Rhode Island LMR and LMC habitats was 1.8 and 17.7 times greater on average than in their New Jersey counterparts, and although seston concentrations in Rhode Island were lower than in Delaware Bay, the resulting gross filtration by mussels was not significantly different between Rhode Island and Dividing Creek and Maurice River (Table 3.7; Appendix D).

This indicates that the percentage of services provided by mussels are not solely driven by mussel biomass, they are also dependent on food availability. Dennis Creek, provided significantly higher filtration services despite the low biomass relative to Rhode Island, primarily due to the high TSS availability (Table 3.7). Among New Jersey marshes, Dividing and Dennis Creeks had similar overall average mussel biomass (47.4±10.1 and 58.5±13.8 g DTW m^{-2} respectively; Table 3.7), but Dividing Creek only provided 53% of the filtration services of Dennis Creek because TSS and PN concentrations in Dividing Creek were only 66% of those in Dennis Creek. These data show the interactive nature between ribbed mussel biomass, food availability, and spatial population distributions in determining the total amount of seston captured by ribbed mussels across the marsh platform. If filtration services were solely driven by mussel biomass, Rhode Island would have provided the highest quantity of services, and conversely, if food availability was the primary driver, gross filtration rate ranking among New Jersey marshes would have followed the TSS/PN patterns (Table 3.7) for gross TSS and PN removal.

Seston filtration rates therefore represent the integration of the mussel's physiological activity (i.e. clearance rates) and food availability. Delaware Bay is a naturally turbid estuary having measured TSS concentrations in excess of those in other large American estuaries (Uncles and Smith 2005). In this study, TSS ranged from 71.3±8.8 to 107±14 mg l^{-1} in New Jersey marshes along Delaware Bay, compared with 13.1±2.3 mg l^{-1} in Rhode Island. Hence, when clearing particles at similar rates, greater filtration rates were measured in New Jersey relative to Rhode Island. Higher filtration rates do not necessarily equate with greater nutritional benefits to New Jersey mussels, however, due to the higher concentration of inorganic material (Table 3.7; Kreeger 2013) and high proportion of refractory organics in Delaware Bay (Kreeger 2013). The inorganic content of suspended particles (seston) was between 83.3±0.5% and 85.9±0.3% in the New Jersey marshes, compared to 72.3±2.5% in marshes of Rhode Island. The higher organic content of Rhode Island seston could have also been more nutritionally available if comprised mainly of phytoplankton or benthic diatoms, compared with Delaware Bay marshes. As discussed by Kreeger and Newell (2000), the low quality of seston in Delaware Bay marshes forces ribbed mussels to derive a portion of their carbon and nitrogen demands from the less nutritious detritus complex.

Similar to other suspension-feeding bivalves, ribbed mussels represent a pelagic-benthic coupling mechanism because they transfer material from the water column to the marsh surface. Smith and Frey (1985) found that ribbed mussels can account for a large portion of annual sedimentation budget in Georgia salt marshes. In New Jersey, if displaced uniformly across the platform per marsh, biodeposition of just the inorganic fraction of the filtered seston can contribute between 1.16±0.60 and 2.78±0.47 mm yr^{-1} to vertical salt marsh accretion, assuming no resuspension and export of the biodeposits (Table 3.7). This is not an inconsequential value considering that sea level rise (SLR) projections of ~4 mm yr^{-1} along the northeastern USA (Sallenger et al. 2012; Boon 2012) and the ability of salt marshes to keep pace is a major concern. This range of potential vertical enhancement values represents a vertical contribution of between 29% and 70% of the rate of SLR.

In Rhode Island, dense assemblages of ribbed mussels along both the LMR and LMC habitats were estimated to produce enough inorganic biodeposits to contribute 0.24±0.11 and 0.57±0.13 mm yr^{-1} respectively (Table 3.7). These values represent a contribution of between 6% and 14% of an ~4mm yr^{-1} SLR rate, and a 17% to 40% contribution to the measured net mean elevation gain of 1.40mm yr^{-1} calculated from a network of RI surface elevation tables (Raposa et al. 2016). In NJ, the majority of biodeposition was calculated to occur in the LMC habitat where mussel density was greatest. For example, in Dividing Creek, the LMC mussels were estimated to contribute 1.12±0.26 mm yr^{-1} and 2.34±0.42 mm yr^{-1} in the Dennis Creek LMC habitat. These values show the potential contributions of dense assemblages of ribbed mussels to vertical marsh enhancement along low marsh habitats in New Jersey.

To calculate potential contributions to vertical marsh accretion, we assumed that 100% of the inorganic TSS was biodeposited in feces and pseudofeces. Resuspension and export of biodeposited materials was not considered here, and therefore may make the biodepositional estimates liberal in magnitude.   However, the exclusion of the organic components of feces and pseudofeces likely skewed the estimate to be conservative. Any re-suspended biodeposits could also be re-filtered and re-deposited by mussels. Additional study of the fate of biodeposits is needed to clarify these factors.

New Jersey PN concentrations (0.59±0.08 - 0.89±0.12 mg L^{-1}, Table 3.7) were between 13 and 20 times greater than in Rhode Island (0.12±0.01 mg L^{-1} in summer, Table 3.7), and were consistent with other values reported for New Jersey (Partnership for the Delaware Estuary 2014) and Rhode Island (Cary et al. 2017). Although the total PN loads were higher in New Jersey, the percent organics were higher in Rhode Island indicating a richer food source (Table 3.7 =100-PIM). Discussion of the fate of filtered nitrogen must take into account temporal differences regarding the rates of return, as the ultimate fates of the filtered materials may differ over different time scales. The time frame of interest for these data is the annual time frame as filtration services are scaled to annual rates.

Bilkovic et al. (2017) show that in a salt marsh environment with ribbed mussels present, denitrification efficiency is large enough to produce net nitrogen removal (65.12% efficiency). Coupled with the strong relationship between ribbed mussel density and *Spartina alterniflora* production (Bertness 1984) and annual primary production and nutrient addition (Darby and Turner 2008), biodeposition of particulate nitrogen is likely to facilitate permanent nitrogen losses via denitrification, burial in peat, or otherwise bound in the food web. Unlike ammonia excretion and gamete and byssal thread production which are quickly returned to the water column, the recycling of nitrogen used for somatic growth, of either shell or soft tissue production, is slower by comparison. Any nitrogen bound in buried peat or mussel shells can also be returned, but the time frame in which that occurs will be longer and spatially dependent on marsh-specific, or event-based, processes such as erosion and/or decomposition rates.

Typically, the organic fraction of TSS decreases with increasing particulate matter, and as a result, net selection efficiency increases with organic content (Hawkins et al. 1996; Galimany 2013). The differences in TSS and POM concentrations between New Jersey and Rhode Island marshes likely indicate a higher percentage absorption of PN in Rhode Island than in New Jersey marshes (71% and 50%, respectively; Table 3.2), but a potential overall lower net nitrogen retention. In Rhode Island, 55% of filtered nitrogen was estimated to be returned to the water column through gamete and byssal thread production and NH_3 excretion, compared to 39% in New Jersey (Table 3.5). Only 20% of the total PN filtered was assumed to be allocated for growth, and as a result the greater the portion absorbed, the greater the portion returned. This indicates that that in areas of high food quantity and low food quality, ribbed mussels may be less efficient at using the ingested material, thereby leading to greater transfers from water column to benthos via rejected biodeposits. Indeed, since this study assumed that post-ingestion nitrogen partitioning in ribbed mussels in New Jersey marshes was similar to mussels in Great Sippewissett marsh (Jordan and Valiela 1982), it is plausible that even lower percent nitrogen filtered was absorbed (<50%) due to generally lower seston quality in Delaware Bay than in other estuaries. Additionally, as mussel absorption efficiencies vary widely depending on seston composition (Kreeger and Newell 1996, 2001), the fate may also vary with seston character. Further study of post-ingestion nitrogen processing along TSS and nutrient enrichment gradients is warranted to investigate these relationships further.

The total mussel-mediated biodeposition varied between 57.1±29.3 and 138±23 kg ha^{-1} yr^{-1} in New Jersey and 26.9±6.2 kg ha^{-1} yr^{-1} in Rhode Island (Table 3.7) when averaged over the entire marsh platform (higher loadings likely where mussels are most abundant). Previous studies have reported deterioration associated with shifts in belowground to above ground biomass ratios, impacting the vertical growth and stability of the marsh edge and platform in salt marshes experiencing high nitrogen loads (Valiela et al. 1976; Deegan et al. 2012; Wigand et al. 2014). These results have raised concerns regarding the enhancement of ribbed mussel populations (e.g. living shoreline projects) as vectors to transport nitrogen from the water column to the marsh, relationships between nutrients loading, vertical marsh building, and ribbed mussel density need more study. Recent studies were unable to detect any impacts of fertilization on salt marsh elevation capital in Long Island Sound (Anisfeld and Hill 2012) or links between nitrogen availability and vegetation die-back (Bertness et al. 2014) or belowground biomass and accretion rates (Cary et al. 2017) in Narragansett Bay. These results indicate that the link between nitrogen availability and elevation deficiencies in salt marshes may co-vary with a variety of other factors, and that the importance of ribbed mussel biodeposition in nutrient rich estuaries may have various positive and negative impacts to salt marsh resiliency.

Comparison of the LMC habitats in New Jersey and Rhode Island show that these areas are capable of supporting similar levels of mussel biomass. The largest discrepancy between regional populations was along the LMR habitat. Marsh edge retreat rates greater than 1 meter per year and as high as 8 meters per year have been measured recently in Delaware Bay (Moody et al. 2011; Kreeger 2015), and more than 81% of random shoreline assessment points (Haaf et al. 2017) have recently been assessed as net eroding. These high rates of edge erosion along the Delaware Bay marsh shorelines may in fact explain the lower mussel densities in New Jersey LMR sites since mussels may not have sufficient time to recruit and grow along edges that are receding so quickly. For example, we reported that ribbed mussel biomass was 8.36, 19.12, and 343.70 times greater along the LMR habitat in Rhode Island than in Maurice River, Dividing Creek, and Dennis Creek respectively, and that biomass was one of the main drivers of filtration services. The observation that Delaware Bay marsh edges are rapidly eroding, combined with this study's dearth of mussel biomass along LMR habitats in the New Jersey marshes, suggests that mussel-delivered ecosystem services are in decline in marshes bordering Delaware Bay. Scaling vertical enhancement and net PN removal services along the river in New Jersey marshes to their potential under similar ribbed mussel biomass as Rhode Island, the current average vertical enhancement potential along rivers would increase from 0.06 to 1.05mm yr$^{-1,}$ and net PN removal would increase from 3.54 to 62.3 kg ha^{-1} yr^{-1}. Summed across marshes, New Jersey would net an increase of 176.11 kg ha^{-1} yr^{-1} PN removal at mussel densities equal to those measured along the rivers in Rhode Island.

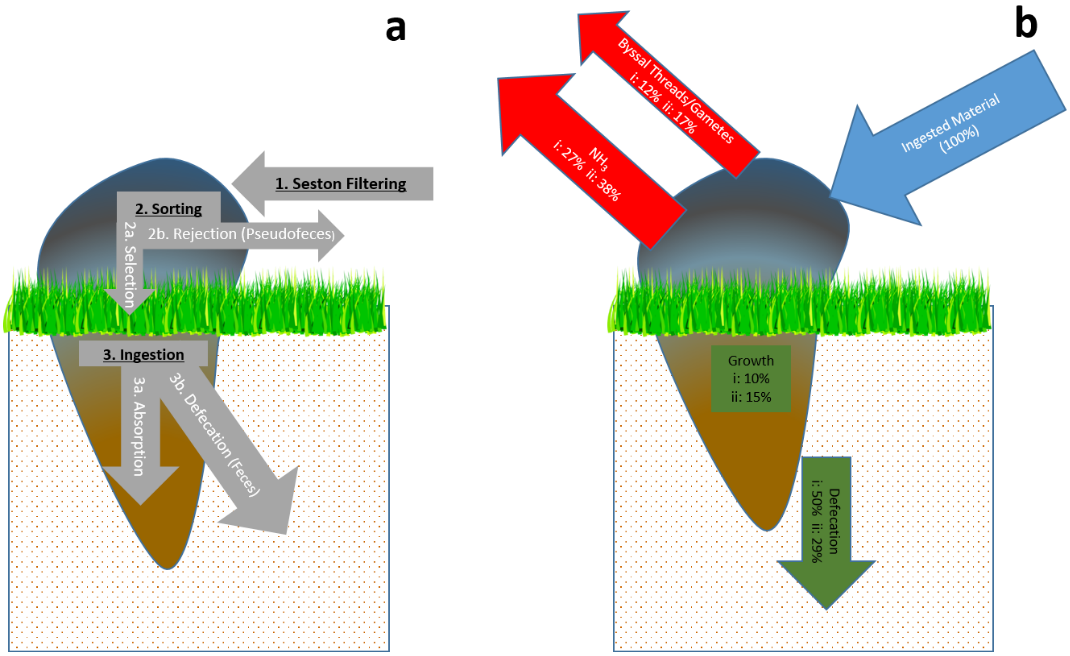


Figure 3.1 Feeding models of the ribbed mussel (*Geukensia demissa*). a) Generalized model highlighting the three fundamental stages of particle filtration: 1. Seston filtration where particles are siphoned and trapped by the animal; 2. Sorting at the gills and labial palps where particles are either selected for ingestion or rejected as pseudofeces; and 3. Ingestion of selected particles into the gut to either be digested and absorbed or biodeposited as feces. b) The fate of ingested nitrogen as modeled by i) Jordan and Valiela, (1982) under 50% absorption efficiency, and ii) as modeled by using Galimany et al. (2013) under 71% absorption efficiency assuming equal fate partitioning percentages as Jordan and Valiela (1982) for the absorbed nitrogen. In B, green box and arrow indicate a long-term removal from the water column, and the red arrows indicate a short-term return.

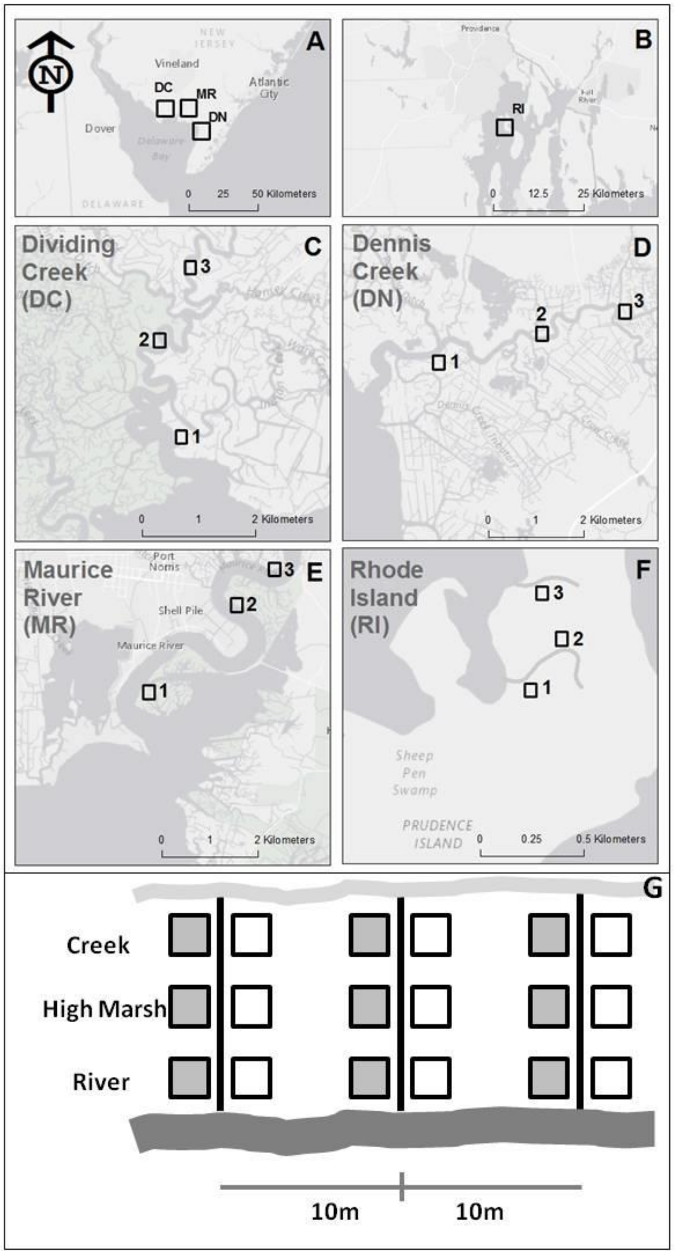


Figure 3.2 Marsh and site locations of the four study marshes. A: Location of study marshes in the NJ; B: Location of study marsh in RI; C-F: location of replicate study sites in each representative study marsh; G: schematic of transect and sample plot layout within each study site per marsh. Numbers in maps C-F denote the sites within marshes. In schematic F, grey boxes represent destructive plots where ribbed mussel lip counts and dig out occurred. White boxes indicate non-destructive plots where only ribbed mussel lip counts occurred.

Table 3.1 Seasonal weight-specific clearance rates (WSCR) for pooled NJ and RI marshes. Estimated values are denoted by "<>" markings. Rhode Island estimated values were calculated by multiplying NJ seasonal values by the ratio of RI:NJ measured summer values. All winter WSCR values are estimated to be zero.

Season	NJ Mean WSCR (L hr^{-1} $gDTW^{-1}$)	RI WSCR (L hr^{-1} $gDTW^{-1}$)
Spring	0.35	<0.31>
Summer	0.63	0.55
Fall	0.04	<0.04>
Winter	<0.00>	<0.00>

Table 3.2 Mussel density calculations for each destructive (DQ) and non-destructive (NDQ) sampling quadrat.

		Area	**Equation**	**Result**
D1	DQ Mussel Lip Count	1m^2		Number of mussels visible in DQ
D2	DQ Mussel Excavation	0.25m^2		Actual number of mussels in subset of DQ
D3	DQ Predicted Mussel Density	1m^2	D2*4	Estimation of actual number of mussels in entire DQ
D4	DQ Mussel Density Correlation Factor	1m^2	D3/D1	Ratio of Estimated Mussel Density to Observed Mussels in DQ
ND1	NDQ Mussel Lip Count	1m^2		Number of mussels visible in NDQ
ND2	NDQ Predicted Mussel Density	1m^2	ND1*D4	Estimation of actual number of mussels in NDQ; accounts for non-visible individuals

Table 3.3 Power regression statistics for shell height (SH) to dry tissue weight (DTW) relationships. Number of mussels used to calculate each regression was between 21-24 mussels per habitat collected at the same locations in the fall 2012 and the spring and summer 2013.

Marsh	Habitat	Slope (m)	Intercept (b)	R^2	p
Dividing Creek	High Marsh	2.56	1.00E-05	0.82	<0.001
Dividing Creek	Low Marsh Creek	2.80	4.00E-06	0.83	<0.001
Dividing Creek	Low Marsh River	2.24	6.00E-05	0.83	<0.001
Dennis Creek	High Marsh	2.29	3.00E-05	0.86	<0.001
Dennis Creek	Low Marsh Creek	2.75	5.00E-06	0.93	<0.001
Dennis Creek	Low Marsh River	2.37	3.00E-05	0.89	<0.001
Maurice River	High Marsh	2.36	2.00E-05	0.87	<0.001
Maurice River	Low Marsh Creek	2.65	8.00E-06	0.85	<0.001
Maurice River	Low Marsh River	2.60	1.00E-05	0.94	<0.001
Rhode Island	High Marsh	2.44	2.00E-05	0.83	<0.001
Rhode Island	Low Marsh Creek	2.86	5.00E-06	0.98	<0.001
Rhode Island	Low Marsh River	2.29	6.00E-05	0.87	<0.001

Table 3.4 Regression statistics for Percent Time Inundation (PTI) and Elevation of waterlevel loggers placed in all plots at site 2 within each marsh. Nine sensors were deployed in each marsh, three per habitat.

Marsh	Slope	Intercept	R^2	p
DC	-0.70	1.85	0.76	>0.01
DN	-0.88	2.11	0.91	>0.001
MR	-0.99	1.93	0.59	0.016

Table 3.5 Coefficients for fate of filtered nitrogen in NJ and RI. Filtered nitrogen was considered either biodepositied (feces and pseudofeces production) or absorbed. The absorbed portion was either retained (somatic growth) or returned to the water column (gamete and byssal thread production; NH_3 excretion). Dark grey and light grey cells indicate the proportions of filtered nitrogen removed or returned respectively from the water column for a time period greater than 1 year. Asterisks refer to values directly sourced from the primary citation. Non-asterisk RI values were calculated assuming similar proportional fates as NJ.

	Biodeposited	**Absorbed**				
Region	**Total**	**Total**	**Somatic Growth**	**Gamete/Byssal**	**Excretion NH_3**	**Primary Citation**
NJ	0.50*	0.50*	0.10*	0.12*	0.27*	Jordan and Valiela 1982
RI	0.29*	0.71*	0.14	0.17	0.38	Galimany et al. 2013

Table 3.6 Annual, marsh-specific mean±se weight specific clearance rates (WSCR), total suspended solids (TSS), and particulate nitrogen (PN) concentrations. Superscript letter represent significant differences among marshes per metric (column) as a result of Tukey post-hoc analysis. DC=Dividing Creek; DN=Dennis Creek; MR=Maurice River; RI= Rhode Island.

Marsh	**n**	**WSCR (L hr^{-1} gDTW^{-1})**	**TSS (mg L^{-1})**	**PN (mg L^{-1})**	**WSFR TSS (mg hr^{-1} gDTW^{-1})**	**WSFR PN (mg hr^{-1} gDTW^{-1})**
DC	79	0.27±0.04^{ab}	71.3±8.8^{a}	0.59±0.08^{a}	19.4	0.16
DN	93	0.20±0.02^{a}	107±14^{a}	0.89±0.12^{a}	20.9	0.17
MR	79	0.34±0.04^{b}	91.4±5.8^{a}	0.77±0.04^{a}	31.5	0.27
RI	96	0.23±0.03^{ab}	13.1±2.3^{b}	0.11±0.01^{b}	2.9^{b}	0.02^{b}

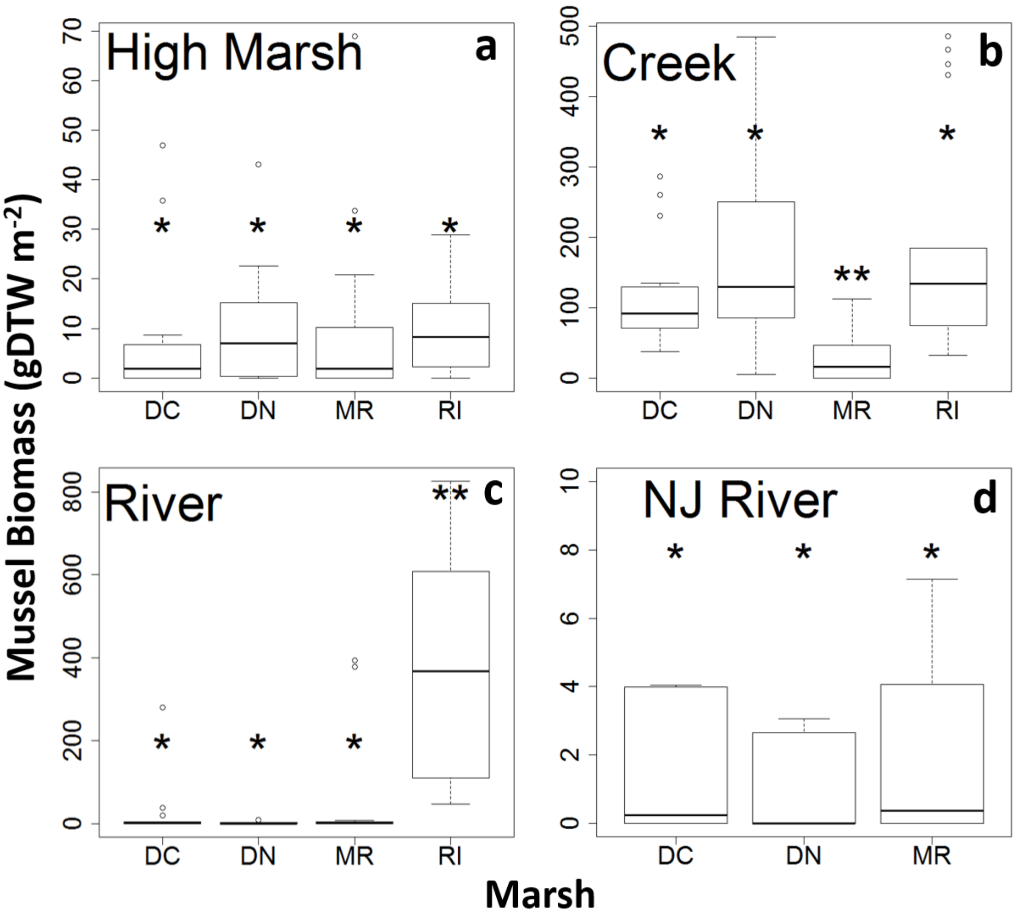


Figure 3.3 Boxplots of the difference in ribbed mussel biomass (gDTW m^{-2}) between marshes per habitat type: a) high marsh (HM); b) low marsh creek (LMC); c) low marsh river (LMR); and d) low marsh river in New Jersey Marshes only (NJ LMR). Lower and upper extents of each box represent the 25th and 75th percentiles respectively. The dark line within each box represents the 50th percentile. Whiskers display the range of data and outliers are represented as open circles. Asterisks denote significant differences among marshes per habitat type as per results of a Dunn post-hoc analysis. DC=Dividing Creek; DN=Dennis Creek; MR=Maurice River; RI= Rhode Island.

Table 3.7 Annual mean±se values per habitat per marsh for metrics of interest. TSS=total suspended solids; PN= particulate nitrogen; FR= filtration rate. DC=Dividing Creek; DN=Dennis Creek; MR=Maurice River; RI= Rhode Island.

Marsh	Habitat	TSS (mg l^{-1})	PN (mg l-1)	Percent Inorganic (%)	Mussel Biomass (g DTW m^{-2})	FR-TSS (kg ha^{-1} yr^{-1})	FR-PN (kg ha^{-1} yr^{-1})	Estimated Vertical Accretion (mm yr^{-1})	Estimated Net PN Removal (kg ha^{-1} yr^{-1})		
		(n=18 NJ; n=6 RI)			(n=18 plots $habitat^{-1}$)	(n=7-8 mussels $habitat^{-1}$ $season^{-1}$)			Total	Biodeposit	Growth
DC	Creek	71.3 ± 8.8	0.59±0.08	85.8 ± 0.6	116 ± 16	$1.30*10^4 \pm 3.03*10^3$	108 ± 25	1.12 ± 0.26	65.3 ± 15.2	54.4 ± 12.7	10.9 ± 2.5
	High Marsh				6.71 ± 3.08	$4.15*10^3 \pm 3.23*10^3$	34.7 ± 27.0	0.36 ± 0.28	20.8 ± 16.2	17.3 ± 13.5	3.5 ± 2.7
	River				19.4 ± 15.5	$6.33*10^2 \pm 5.26*10^2$	5.3 ± 4.4	0.05 ± 0.04	3.2 ± 2.6	2.6 ± 2.2	0.5 ± 0.4
	Marsh-wide				**47.4 ± 10.1**	**$1.78*10^4 \pm 2.25*10^3$**	**149 ± 56**	**1.53 ± 0.57**	**89.2 ± 33.5**	**74.4 ± 27.9**	**14.9 ± 5.6**
DN	Creek	107.1 ± 14.8	0.89±0.12	83.3 ± 0.5	164 ± 27	$2.81*10^4 \pm 5.01*10^3$	233 ± 41	2.34 ± 0.42	140 ± 25	116 ± 20	23.4 ± 4.2
	High Marsh				9.54 ± 2.63	$5.20*10^3 \pm 2.81*10^3$	43.2 ± 23.7	0.43 ± 0.23	25.9 ± 14.0	21.6 ± 11.7	4.3 ± 2.3
	River				1.08 ± 0.50	38 ± 23	0.3 ± 0.2	0.01 ± 0.01	0.19 ± 0.11	0.2 ± 0.1	0.1 ± 0.1
	Marsh-wide				**58.5 ± 13.8**	**$3.34*10^4 \pm 5.64*10^3$**	**277 ± 47**	**2.78 ± 0.47**	**166 ± 23**	**138 ± 23**	**27.7 ± 4.7**
MR	Creek	91.4 ± 5.8	0.77±0.04	85.9 ± 0.3	28.0 ± 7.9	$6.97*10^3 \pm 3.86*10^3$	58.8 ± 32.6	0.60 ± 0.33	35.3 ± 19.5	29.4 ± 16.3	5.9 ± 3.3
	High Marsh				9.42 ± 4.15	$5.12*10^3 \pm 2.81*10^3$	43.2 ± 23.7	0.44 ± 0.24	25.9 ± 14.2	21.6 ± 11.9	4.3 ± 2.4
	River				44.4 ± 29.3	$1.45*10^3 \pm 1.43*10^3$	12.2 ± 12.1	0.12 ± 0.11	7.3 ± 7.2	6.1 ± 6.0	1.2 ± 1.2
	Marsh-wide				**27.3 ± 10.2**	**$1.35*10^4 \pm 6.95*10^3$**	**114 ± 59**	**1.16 ± 0.60**	**68.5 ± 35.2**	**57.1 ± 29.3**	**11.4 ± 5.9**
RI	Creek	13.1 ± 2.3	0.12±0.01	72.3 ± 2.5	183 ± 37	$7.90*10^3 \pm 1.84*10^3$	63.7 ± 14.9	0.57 ± 0.13	27.4 ± 6.4	18.5 ± 4.3	8.9 ± 2.1
	High Marsh				9.60 ± 1.94	339 ± 73	2.7 ± 0.6	0.02 ± 0.01	1.2 ± 0.3	0.8 ± 0.2	0.4 ± 0.1
	River				371 ± 66	$3.26*10^3 \pm 1.57*10^3$	26.3 ± 12.7	0.24 ± 0.11	11.3 ± 5.4	7.6 ± 3.7	3.7 ± 1.8
	Marsh-wide				**188 ± 32**	**$1.15*10^4 \pm 2.64*10^3$**	**92.8 ± 21.3**	**0.83 ± 0.19**	**39.9 ± 9.2**	**26.9 ± 6.2**	**13.0 ± 3.0**

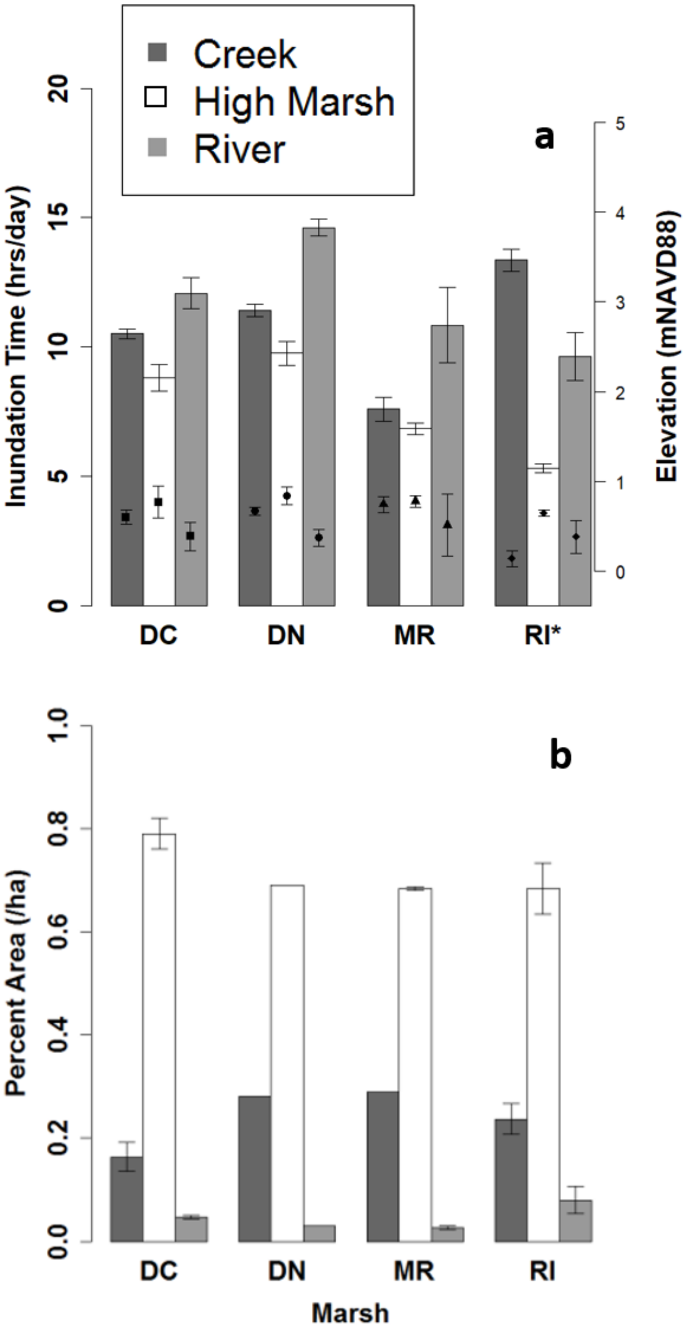


Figure 3.4 Means± standard error Inundation Time and Elevation (a), and Percent Area (b) by habitat within marshes. DC=Dividing Creek; DN=Dennis Creek; MR=Maurice River; RI=Rhode Island. RI* indicates that the inundation time was not directly measured with water level loggers, but calculated using NJ elevations and inundation times.

Table 3.8 Pair-wise comparisons of filtration rates of TSS and PN between habitats per marsh using a post-hoc Tukey Test for Honestly Significant Differences.

Marsh	Pair-wise Comparison	Estimate	Std. Error	z value	Pr(>|z|)
DC	HM – LMC	-8875	2234	-3.972	<0.001
	LMR – LMC	-12394	2234	-5.548	<0.001
	LMR - HM	-3520	2234	-1.575	0.256
DN	HM – LMC	-22929	4687	-4.892	<0.001
	LMR – LMC	-28087	4687	-5.993	<0.001
	LMR - HM	-5158	4687	-1.101	0.514
MR	HM – LMC	-1848	2961	-0.624	0.807
	LMR – LMC	-5523	2961	-1.865	0.149
	LMR - HM	-3675	2961	-1.241	0.429
RI	HM – LMC	-7562	1882	-4.017	<0.001
	LMR – LMC	-4637	1882	-2.464	0.037
	LMR - HM	2925	1882	1.554	0.266

Chapter 4: Implications of Habitat Loss and Declining Ribbed Mussel (*Geukensia demissa*) Ecosystem Services

4.1 Abstract

Bivalve shellfish provide a variety of ecosystem services which scale with population densities and distributions. In Atlantic US salt marshes, ribbed mussels are the functionally dominant animal, facilitating nutrient cycling, vertical accretion, and salt marsh structural integrity. Ribbed mussel populations are denser in low marsh habitat along intertidal channels and creeks. In areas where these populations are underrepresented compared to reference conditions, mussel-mediated ecosystem services are suboptimal. To evaluate whether ribbed mussel ecosystem services along the low marsh fringe in New Jersey were representative of their service potential, regional population and physiological data were compared among three marshes in New Jersey and one in Rhode Island.

Although creek habitats in New Jersey and Rhode Island marshes were able to support similar populations of ribbed mussels, mussel population densities were largely suppressed along the marsh shoreline in New Jersey relative to Rhode Island. Marsh shorelines in New Jersey have been eroding approximately an order of magnitude faster than in Rhode Island, likely preventing mussel recruitment and population establishment in New Jersey marshes. Ribbed mussel population enhancements, such as might be achieved using living shoreline tactics, are estimated to boost particulate nitrogen removal between 376% and 1,616% if ribbed mussel biomass density can be increased to levels currently measured either in New Jersey creeks or along the marsh shoreline in Rhode Island, respectively. Additionally, since the benefits of mussel filtration for water quality (e.g. particulate nitrogen filtration) also scale with spatial seston composition, the location of ribbed mussel enhancement projects

can also be an important factor regarding the magnitude of the resulting ecosystem services.

4.2 Introduction

Bivalve shellfish provide a number of valuable ecosystem services including: food provisioning; nutrient cycling (Jordan and Valiela 1982; Newell et al. 2002); shoreline protection (Bertness 1984; Scyphers et al. 2011); and recreation and tourism (Beaumont et al. 2007). As spatially aggregated animals, the magnitude of their provisional goods and services is spatially dependent on population density. Efforts aimed at augmenting populations of important species therefore typically target the most suitable habitats where animal densities are greatest. Historically in the Delaware Estuary, the eastern oyster (*Crassostrea virginica*) has been the primary focus of shellfish restoration efforts. Oyster reefs provide habitat for a variety of finfish and invertebrates (Coen et al. 2009), while also contributing greatly to local economies (Murry and Hudson 2013). Research since the mid-1970s has shown that ribbed mussels can provide many of the same ecosystem services as oysters without being constrained by regulatory restrictions imposed upon species available for commercial harvest (Jordan and Valiela 1982; Newell et al. 2002; Galimany et al. 2013; Bilkovic et al. 2017). For certain ecosystem services, such as bacteria filtration, ribbed mussels are reported to be superior to oysters (Langdon and Newell 1990; Kreeger and Newell 1996).

As the functional dominant animal of eastern US salt marshes (Kuenzler 1961; Lent 1969; Jordan and Valiela 1982), ribbed mussels remove suspended particulate matter from the water column, facilitating marsh accretion and nutrient sequestration (Chapter 3), helping to maintain water quality. Additionally, dense aggregations of ribbed mussels provide structural integrity to the edge of salt marsh habitats by binding sediments through attachment to vegetation roots and rhizomes with their byssal thread complexes (Bertness 1984). Ribbed mussels are principally found along the low marsh fringe of salt marsh environments, along the waterward edge of the primary and intra-marsh drainage networks, and although ribbed mussels are found across the high marsh platform, these populations are significantly lower than their low marsh counterparts (Kuenzler 1961, Bertness 1984, Franz 2001). As these edge environments are typically considered ribbed mussel "hot spots", they also represent areas of concentrated mussel-mediated ecosystem services. Given the substantial ecosystem services contributed by ribbed mussels, protection and restoration strategies aimed at optimizing mussel population biomass should be given consideration by natural resource managers and restoration practitioners who are focused on protecting water quality and coastal wetlands. It is important to note that ribbed mussel enhancement should not be considered a direct replacement for oyster restoration, as they occupy different, but sometimes overlapping, niches.

In the Delaware Estuary, current rates of coastal wetland loss have been measured to be approximately an acre per day (Kreeger et al. 2010; TREB 2012, 2017), and a variety of new tactics are emerging for stemming this retreat, such as various living shoreline methods, thin layer sediment enhancement, and hydrological repairs. As many of these tactics intersect with ribbed mussel habitat, there is opportunity to pair coastal restoration strategies with ribbed mussel population enhancement efforts to maximize shellfish mediated ecosystem services in areas receiving restoration efforts. Since ribbed mussel populations are not distributed evenly across the salt marsh landscape (Bertness and Grosholz 1985, Nielsen and Franz 1994, Franz 2001), comparing the spatial distributions of ribbed mussel populations in stable (e.g. non-eroding) reference marshes to those in marshes that are currently experiencing degradation and/or erosion can pinpoint places where mussel-delivered services might be improved, such as by increasing habitat suitability and hence mussel population biomass. In this study we compared ribbed mussel populations across two regions, Delaware Bay, New Jersey and Narragansett Bay, Rhode Island, to characterize the spatial distributions of marsh-specific services and to evaluate whether those services were representative of other locations.

4.3 Methods

4.3.1 Site Selection and Habitat Delineation

To investigate the implications of ribbed mussel habitat loss on mussel-mediated ecosystem services, four representative salt marshes having different rates of edge erosion were selected for study. In New Jersey, Dividing Creek (DC), Dennis Creek (DN), and Maurice River (MR), and in Rhode Island, Coggeshall Cove (RI) located on Prudence Island in Narragansett Bay have been the location of multiple research efforts (Fig. 4.1 a-f). All marshes were considered representative of their respective regions based on long-term monitoring data from Mid-Atlantic Coastal Wetland Assessment (MACWA) in New Jersey (Partnership for the Delaware Estuary 2014) and the Environmental Protection Agency Office of Research and Development Atlantic Ecology Division in Rhode Island (Martina Chintala, personal communication, 2012). Three study sites containing locally representative ribbed mussel populations along the marsh shoreline were selected per marsh. Due to the shorter length of the primary channels in the RI marsh, the three sites were located along two primary channels sharing a similar observable ribbed mussel densities. Within each site, three habitats of interest were delineated by vegetation cover and proximity to the nearest drainage channel: low marsh river; low marsh creek; and high marsh.

Low marsh river (LMR) habitat was located along the primary tidal channel of each marsh that drained into either Delaware Bay (NJ) or Narragansett Bay (RI), characterized by a 1-2m band of tall form *Spartina alterniflora* along the contiguous vegetated marsh edge. Low marsh creek (LMC) habitat was located along smaller, intra-marsh channels that drained fully at low tide and flowed into the primary marsh channel along which the LMR habitat was located. This habitat was also comprised of a monoculture of tall form *Spartina alterniflora* in a 2-4m band that was bisected by the intra-marsh creek. High marsh (HM) habitat was located on the marsh platform between the LMR and LMC habitats and was comprised of populations of a variety of vegetation types that can exist in areas of lesser tidal inundation such as: *S. alterniflora* short-form; *Spartina patens; Distichlis spicata,* and/or *Salicornia* spp. At each site, three transects oriented perpendicular to the primary channel were placed so that they interested each of the three habitats, within which sampling plots were fixed (Fig. 4.1g).

4.3.2 Percent Habitat Area

For each site, the area of each habitat type was calculated as the percent area of each habitat within a 300m buffer of the center transect, without crossing the primary channel as delineated using ArcGIS 10.2. IKONOS 2014 digital imagery (0.82m black and white, 3.28m multispectral resolution). Low Marsh River and LMC habitats were delinated a 2m band along the primary and secondary channel edges based on average widths reported for tall form *S. alterniflora* low marsh fringe (Deegan et al. 2012; Partnership for the Delaware Estuary 2014). The area between digitized paired inter-marsh creek edges was considered open water and was excised from the total area of the site. By subtraction, the remaining area not classified as LMR or LMC was classified as HM habitat. The relative percentage of space occupied by each habitat was considered the percent habitat area.

4.3.4 Ribbed Mussel Biomass

In each sampling plot per habitat per site, per marsh, all ribbed mussels were counted, and a subset (up to n=25) were measured. Shell length to dry tissue weight relationships were used to estimate the dry tissue weight of the sub-sample of measured mussels, the average of which was multiplied by the total population count for each plot. For full details regarding biomass estimations, see chapter 3.

4.3.5 Filtration of Total Suspended Solids and Particulate Nitrogen

Clearance (water processing) rates (l hr^{-1} $gDTW^{-1}$) from seasonal physiological experiments conducted Fall 2012, Spring 2013, and Summer 2013 per marsh per habitat using natural seston diets were multiplied by seston total suspended solid (TSS) and particulate nitrogen (PN) concentrations (mg l^{-1}) to calculate seasonal gross TSS and PN filtration rates (mg hr^{-1} $gDTW^{-1}$), as reported in chapter 2. Annual habitat-specific filtration rates were calculated for each habitat (n=3) per site (n=3 per marsh) by averaging the seasonal clearance rates (with the addition of an equal number of "filtration rate=0" observations to account for winter inactivity) and multiplying by the average annual TSS and PN concentrations (n=6 $season^{-1}$ $marsh^{-1}$). Rhode Island data included measured summer filtration rates and spring and fall estimations based a seasonal scaling values in New Jersey (see chapter 3 for details). These site and habitat-specific filtration rates were multiplied by the average measured ribbed mussel biomass, the percent area of each habitat, and the average hours per day inundation (collected through the deployment of water level loggers, see chapter 3) to calculate the marsh-wide gross TSS and PN filtration for each habitat per marsh (n=3 habitat values per marsh) which were subsequently evaluated by region. Full details of the above methods are available in chapter 3.

4.3.6 Lateral Marsh Movement

Lateral marsh movement (i.e. erosion and accretion) was calculated from data collected by the Partnership for the Delaware Estuary for New Jersey marshes (Haaf et al. 2017) and by the Rhode Island Coastal Restoration Council for Rhode Island marshes (http://www.crmc.ri.gov/maps/maps_shorechange.html) from the years 1970-2014 and 1939-2003, respectively. Both data sets were generated using the USGS Digital Shoreline Analysis Software (DSAS) through an ArcGIS interface, by calculating the lateral change in shoreline position between the start and end years reported as an end-point rate (EPR) ± standard error in the DSAS output. Negative values indicate landward movement (i.e. erosion) and positive values waterward movement (i.e. accretion).

4.3.7 Statistical Analyses

Marsh-level data were checked for normality and homogeneity of the variance. Metrics that followed a normal distributions were analyzed using a linear mixed effects model able to handle unbalanced designs (nlme package, Pinheiro et al. 2017). Marsh and site were treated as random effects and habitat was considered a fixed effect. Metrics that followed non-normal distributions were evaluated using a Kruskal-Wallis test to evaluate differences among marshes. Tests between factors with similar distributions were interpreted as testing for a difference among medians, while tests between factors of varying distributions were interpreted as testing for dominance between distributions. Non-parametric post-hoc analysis following a rejection of a Kruskal-Wallis were conducted using a Dunn's test of multiple comparisons using rank sums (Dunn 1964) with a Bonferroni correction to minimize type-I error (dunn.test package, Dinno and Dinno 2017). Both Kruskal-Wallis and Dunn's test are appropriate for non-normal and unbalanced data sets (e.g. unbalanced comparisons among regions). All statistical calculations were conducted using R 3.0.3 open source statistical software.

4.4 Results

4.4.1 Percent Habitat Area

The relative proportion of marsh occupied by the three habitats (i.e. percent habitat area) did not significantly differ among the four study marshes (HM $p>0.3$; LMC $p>0.3$; LMR $p>0.1$). High marsh habitat dominated percent area similarly among the four marshes ($p>0.09$, mean 71±>1%), however percent area of LMR and LMC habitats differed among some marshes ($p< 0.03$ for both). Rhode Island had a greater percent area of LMR habitat than Maurice River (Dunn test, $p<0.04$, 3.00±0.00% and 8.00±0.03% respectively), but Maurice River contained a greater percent area of LMC habitat relative to Dividing Creek ($p<0.01$, 29±0>1% and 16±>1%). All other pair-wise comparisons showed no significant differences. Regionally, HM and LMC percent area were not significantly different between New Jersey and Rhode Island ($p>0.22$ and $p>0.44$ respectively), but Rhode Island had significantly more LMR habitat than New Jersey ($p<0.03$, Table 4.1).

4.4.2 Ribbed Mussel Biomass

Across regions, ribbed mussel biomass averages were similar in the high marsh and creek habitats, but differed by an order of magnitude along rivers (Table 4.1). Data distributions differed by marsh in the LMR (Levene test: $p<0.001$) and LMC (Levene test: $p<0.02$) habitats, but were similar in the HM (Levene test: $p>0.85$). Kruskal –Wallis tests indicated no significant differences among marshes in high marsh areas ($p>0.09$), but indicated significant differences among marshes in the LMC and LMR habitats ($p< 0.001$ for both tests). Dunn post-hoc analysis indicated that the LMC habitat in the Maurice River had a significantly different distribution than all other marshes ($p<0.001$, median=15 gDTW m^{-}

^{2}), while there was no evidence to support differences among the other marshes ($p<0.9$ for all other pair-wise comparisons; medians: Dividing Creek=91 gDTW m^{-2}, Dennis Creek=129 gDTW m^{-2}, and Rhode Island=134 gDTW m^{-2}). Post-hoc analysis showed that the Rhode Island marsh had a significantly greater density of LMR habitat than all New Jersey marshes ($p<0.001$, median=367 gDTW m^{-2}), which when analyzed independently, showed no evidence of distributional differences ($p<0.49$ for all pair-wise comparisons; New Jersey LMR median= 0.07 gDTW m^{-2}).

4.4.3 Filtration of Total Suspended Solids and Particulate Nitrogen

TSS filtration averaged 22.4±1.9 mg hr^{-1} gDTW^{-1} in New Jersey and 0.2±0.0 mg hr^{-1} gDTW^{-1} in Rhode Island. Filtration of PN averaged 7.23±1.22 mg hr^{-1} gDTW^{-1} in New Jersey and 0.06±0.01 mg hr^{-1} gDTW^{-1} in Rhode Island. Means ± se of gross TSS and PN services from seasonal physiological experiments per region per habitat are reported in Table 4.1. As gross particle filtration is largely dependent on seston quantity and quality, which was significantly lower in the Rhode Island marsh relative to New Jersey marshes (Chapter 3), no statistical comparisons of gross particle filtration were made among regions. Instead, comparison of the geospatial distribution of the percent of services across the salt marsh landscape was employed. In Rhode Island and New Jersey, percent of gross filtration services was highest along creeks (Table 1; 69% and 74% respectively), but differed in regards to the order of percent services provided services provided by the LMR and HM habitats. In Rhode Island, the LMR habitat provided a greater percentage of services (28%) than the HM habitat (3%), while in NJ the HM habitat provided a greater percentage of services (22%) than the LMR habitat (3%) habitat (Table 4.1).

4.4.4 Lateral Marsh Movement

New Jersey marshes had erosion rates between 4-7 times greater than Rhode Island (Fig. 4.2 & Table 4.2). Distributions of lateral marsh movement were similar in Dividing and Dennis Creeks (p>0.4), but Maurice River (p<0.004) and Rhode Island (p<0.001) differed from all other marshes (Fig. 4.3). Maurice River had the largest median erosion rates, while Rhode Island had the smallest (Table 4.2).

4.5 Discussion

Low marsh habitats along primary tidal channels and marsh creeks typically have higher mussel densities and longer submersion times relative to the high marsh (Bertness 1984, Bertnees and Grosholtz 1985; Franz 1999). Therefore, these represent areas of higher concentrations of mussel-mediated services, relative to the high marsh platform that comprises the greatest area (Table 4.1). When mussel biomass density is compromised along the LMR and LMC habitats, the resulting loss of services can therefore have a major impact on the marsh-wide provisioning of mussel-delivered benefits.

The Rhode Island marsh had dense ribbed mussel aggregations along both the LMR and LMC habitats (Table 4.1), providing an example of the potential for ribbed mussel biomass in multiple low marsh habitats. Dividing Creek, Dennis Creek, and Rhode Island marshes had similar ribbed mussel biomass in the LMC habitat, indicating that New Jersey marsh creeks and high marsh are capable of supporting ribbed mussel biomass at a similar levels as the Rhode Island marsh (Fig. 4.3). The significant difference in mussel biomass along the LMR habitat between New Jersey and Rhode Island marshes (Table 4.1) suggests that mussel densities along marsh shorelines in New Jersey are comparatively lowernthan in Rhode Island, which serves as a reference.

New Jersey marshes had shoreline erosion rates 4-7 times greater than Rhode Island, and vastly lower mussel density along the marsh shoreline (Table 4.1). These data do not account for potential increases in erosion rates along the Rhode Island marsh between 2004 and 2014 or positional differences, and were calculated using a much smaller data set (Table 4.2) relative to the New Jersey marshes. Nevertheless, the Rhode Island marsh can still serve as an example of the mussel biomass potential along the LMR habitat. The mussel-dense LMR habitat in Rhode Island provided 28% of the marsh-wide filtration services despite comprising only 7% of the total marsh area. In contrast, mussel services along the shoreline in New Jersey marshes were only 3% in 3% of the marsh area (Table 4.1).

The spatial patterns of mussel population density in the more stable Rhode Island marsh provide a reference against which to evaluate the effects of marsh erosion on mussel-delivered services in New Jersey. In New Jersey, LMR habitat contained the lowest ribbed mussel biomass, and combined with the small percent area, resulted in a very low relative percentage of filtration services (3%; Table 4.1) compared to LMR habitat in Rhode Island (28%; Table 4.1). As a result of the lower percent of services along the shorelines in NJ, the relative percent of marsh-wide services in creeks and HM were greater (Table 4.1). This shift of services to a low mussel biomass areas indicates an overall reduction in services across the landscape.

Comparing the ratio of ribbed filtration capacity among low marsh habitats (i.e. LMR:LMC), we find that the Rhode Island LMR habitat was able to provide ~41% of the services found in the LMC habitat, while only ~4% of the services provided in New Jersey LMC habitat were provided along the LMR. It is important to note that magnitude of gross filtration services is dependent on the food availability at each marsh (i.e. TSS concentrations), and that the New Jersey marshes had much higher concentrations relative to the Rhode Island marsh (Chapter 3), and therefore the magnitude of a single percent differs greatly among regions. For example, 1% of the gross TSS filtration services was almost double in New Jersey (215 kg ha^{-1} yr^{-1}) relative to Rhode Island (115 kg ha^{-1} yr^{-1}; Table 4.1) marshes. Bilkovic et al. (2017) showed the potential loss of ribbed mussel ecosystem services along the main channels of the York River in the Chesapeake Bay, MD, based on projected erosion rates, and estimated a 15% reduction in current filtration potential. In the New Jersey marshes, filtration services along the LMR may have already been lost. This suggests that strategies might be used to enhance populations and their services.

As ribbed mussel services along marsh shorelines in Delaware Bay have likely been reduced from historic levels due to shoreline erosion, tactics that stabilize erosion and enhance shoreline habitats (e.g., living shorelines) represent opportunities to integrate mussel-mediated services with restoration strategies. In Delaware Bay, natural and nature-based techniques are increasingly being used to achieve shoreline stabilization and water quality improvement, via enhanced shellfish populations and associated pollutant filtration. In this study, the mean mussel biomass along the LMR habitat in New Jersey was measured to be 21 gDTW m^{-2} (Table 4.3) and the annual filtration rates were measured at 22.4 and 0.2mg hr^{-1} $gDTW^{-1}$ for TSS and PN, respectively (Table 4.3). At these values, the long-term "net" removal of PN (i.e. deposition and incorporation somatic tissue) was estimated to be 60% of gross filtered nitrogen in New Jersey marshes (Chapter 3). Under current conditions, a 100m length of untreated shoreline (1m wide) along New Jersey marshes is therefore estimated to provide a net removal of PN of 1.10 kg ha^{-1} yr^{-1} (Table 4.3). If ribbed mussel biomass along this shoreline was enhanced to be similar to that in typical New Jersey tidal creeks, net PN removal is estimated to be increased by 385% to 5.36 kg ha^{-1} yr^{-1}.

Further, if ribbed mussel density along the untreated New Jersey shoreline was enhanced to be similar to marsh shorelines (LMR habitats) in the Rhode Island "reference" marsh, net PN is estimated to be 19.5 kg ha^{-1} yr^{-1}, an increase of 1,666% (Table 4.3).

Although shoreline enhancement tactics have the potential to boost or restore mussel populations along New Jersey marsh shorelines, resulting in greater ecosystem services, widespread implementation is currently limited. The current lack of commercially available ribbed mussel seed requires that either natural recruitment and/or translocation of existing mussel populations are employed for populating a living shorelines.

Data presented here show that New Jersey marshes have the potential to support mussel populations similar to marshes in Rhode Island in the HM and LMC habitats. In New Jersey, high rates of erosion may be responsible for the low mussel biomass along the LMR habitat relative to LMC habitat, and this discrepancy in biomass has resulted in a shift of the concentration of mussel-mediated ecosystem services from potentially high mussel density edge habitats, to the low mussel density high marsh platform (Table 4.1). Although net PN removal is estimated to be higher in New Jersey than in Rhode Island marshes (Table 4.4), this is likely due to the greater PN availability in New Jersey compensating for the low PN and larger mussel populations along the marsh shoreline in Rhode Island (Tables 4.1 & 4.4). But, Rhode Island mussels were able to remove between 25% and 58% of the PN of New Jersey marshes while having only between 13% and 20% of the PN concentration (mg l^{-1}) available to filter (Table 4.4), likely due to the enhanced mussel populations along the shorelines.

By identifying where ribbed mussel ecosystem services are currently located and where they may be lacking, natural resource managers can employ a two-fold management approach of conservation and enhancement to maximize local services. Identification of current resource hot-spots (i.e. along small marsh creeks in New Jersey) will allow for the targeted conservation of services through either the stabilization of compromised habitat and/or the protection of existing stable habitat. Further, the location of suitable habitat areas where services are currently underrepresented (i.e. marsh shorelines in New Jersey), can guide geospatial selection of high priority areas for habitat enhancement.

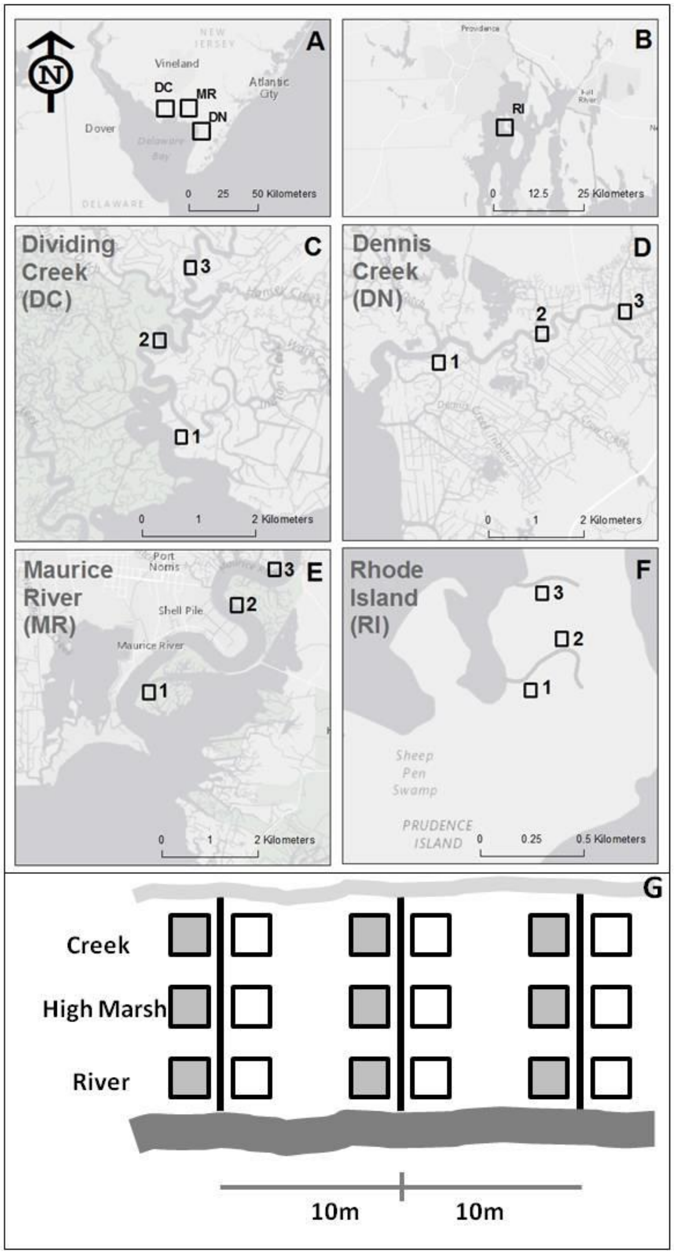


Figure 4.1 Marsh and site locations of the four study marshes. A: Location of study marshes in the NJ; B: Location of study marsh in RI; C-F: location of replicate study sites in each representative study marsh; G: schematic of transect and sample plot layout within each study site per marsh. Numbers in maps C-F denote the sites within marshes. In schematic G, grey boxes represent destructive plots where ribbed mussel lip counts and dig out occurred. White boxes indicate non-destructive plots where only ribbed mussel lip counts occurred.

Table 4.1 Median percent area (n=9 NJ and n=3 RI) and ribbed mussel biomass (n=54 habitat^{-1} NJ and n=18 habitat^{-1} RI), mean±se annual gross total suspended solid (TSS) and particulate nitrogen (PN) filtration rates (n=27 habitat^{-1} NJ and n= 9 habitat^{-1} RI), and annual percent regional habitat services per habitat per region. HM=high marsh; LMC=low marsh creek; LMR= low marsh river; NJ=New Jersey; RI=Rhode Island.

Habitat	**Region**	**Percent Area (ha^{-1})**	**Mussel Biomass (g DTW m^{-2})**	**Gross TSS Filtration (Kg ha^{-1} yr^{-1})**	**Gross PN Filtration (Kg ha^{-1} yr^{-1})**	**Percent of Services (Regional Habitat^{-1})**
HM	NJ	69	2	$4.82*10^3 \pm 1.49*10^3$	40.4 ± 12.5	22%
	RI	65	8	$3.39*10^2 \pm 0.73*10^2$	2.7 ± 0.6	3%
LMC	NJ	28	83	$1.60*10^4 \pm 3.74*10^3$	133 ± 31.1	74%
	RI	25	134	$7.90*10^3 \pm 1.84*10^3$	63.7 ± 14.9	69%
LMR	NJ	3	0.07	$7.05*10^2 \pm 4.85*10^2$	5.9 ± 4.1	3%
	RI	7	367	$3.26*10^3 \pm 1.57*10^3$	26.3 ± 12.7	28%

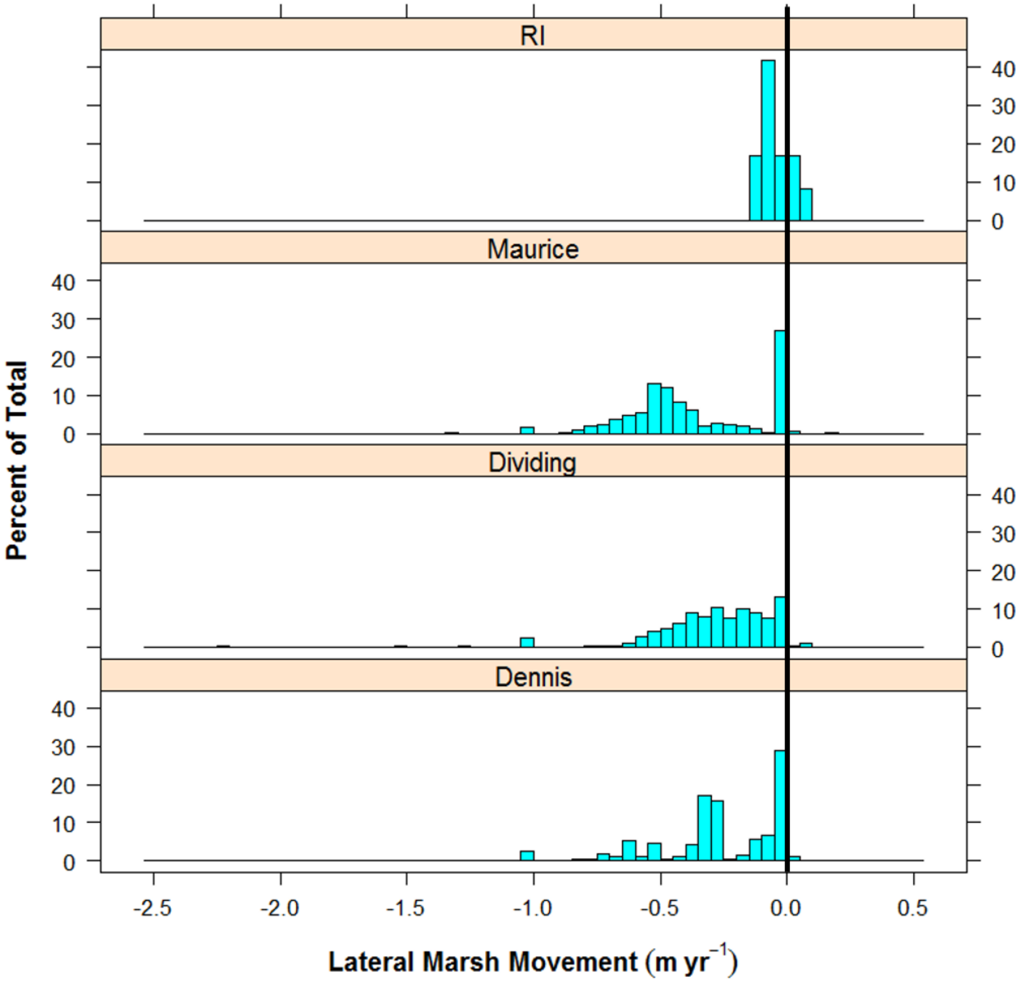


Figure 4.2 Histogram of lateral mash movement rates per marsh. Black vertical line indicates no net movement. Histogram bars to the left of the line (negative values) indicate landward movement of the marsh edge, and bars to the right of the line (positive values) indicate waterward movement of the marsh edge. The marsh for which each histogram displays values is noted above the bars.

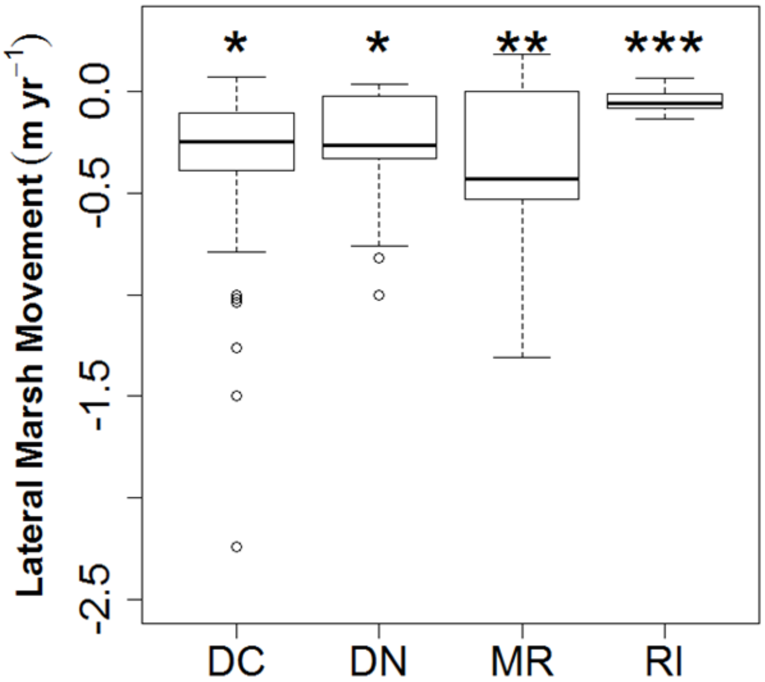


Figure 4.3 Boxplots of lateral marsh movement (m yr^{-1}) per marsh. Lower and upper extents of each box represent the 25th and 75th percentiles respectively. The dark line within each box represents the 50th percentile. Whiskers display the range of data and outliers are represented as open circles. Asterisks denote significant differences among marshes per habitat type as per results of a Dunn post-hoc analysis. DC=Dividing Creek; DN=Dennis Creek; MR=Maurice River; RI= Rhode Island.

Table 4.2 Statistics for lateral marsh movement (m yr^{-1}) per marsh.

Marsh	Median	Min	Q1	Q3	Max	n
DC	-0.25	-2.24	-0.39	-0.11	0.07	264
DN	-0.27	-1.00	-0.33	-0.03	0.03	212
MR	-0.43	-1.31	-0.53	0.00	0.18	302
RI	-0.06	-0.14	-0.08	-0.02	0.06	12

Table 4.3 Estimation of gross annual filtration rates of Total suspended solids (TSS) and particulate nitrogen (PN) and net PN filtration along a 100m length * 1m wide length of shoreline under various mussel density (gDTW m^{-2}) scenarios. Row 1 calculates gross and net filtration under current average measured mussel densities along the low marsh river (LMR) habitat pooled across the three New Jersey (NJ) marshes (Dividing Creek, Dennis Creek, and Maurice River). Rows 2 and 3 calculate the same metrics under current average measured mussel densities along the low marsh creek (LMC) habitat pooled across the three New Jersey marshes, and under current average measured mussel densities along the low marsh river (LMR) habitat at the Rhode Island (RI) marsh respectively.

Density	Mean Mussel Biomass (g DTW m^{-2})	Living Shoreline Length (m)	Annual Filtration Rate (mg hr^{-1} $gDTW^{-1}$)	Gross Annual FR-TSS (kg yr^{-1})	Gross Annual FR-PN (kg yr^{-1})	Net FR-PN (kg yr^{-1})	Increase
NJ LMR	**21**	**100**	**22.4 (TSS)** **0.2 (PN)**	**206**	**1.83**	**1.10**	
NJ LMC	**102**			**1,000**	**8.93**	**5.36**	**385%**
RI LMR	**371**			**3,639**	**32.5**	**19.5**	**1,666%**

Table 4.4 Estimation of gross annual particulate nitrogen (PN) and net PN filtration per marsh. DC=Dividing Creek; DN=Dennis Creek; MR=Maurice River; RI= Rhode Island.

Marsh	PN ($mg\ l^{-1}$)	Estimated Net PN Removal ($kg\ ha^{-1}\ yr^{-1}$)
DC	0.59±0.08	89.2±33.5
DN	0.89±0.12	166±23
MR	0.77±0.04	68.5±35.2
RI	0.12±0.01	39.9±9.2±

Chapter 5: Conclusion

Natural infrastructure is increasingly being valued for the ecosystem services that it provides to society. For example, shellfish reefs and coastal wetlands help to filter pollutants, sequester carbon, and buffer coastlines from storms, as well as supporting habitat for fish, shellfish and wildlife species needed for fisheries and ecotourism. Elements of natural infrastructure that remove or transform sizeable quantities of total suspended solids and associated nutrients promote pelagic-benthic coupling and therefore need to be understood to model and manage water quality. For these reasons, the restoration of bivalve shellfish is increasingly motivated by the benefits to water quality. However, these restoration tactics have rarely been applied to non-commercial native species such as the ribbed mussel, *Geukensia demissa*, and have historically focused on commercial species (e.g. oysters, clams).

Due to their typically robust population size, ribbed mussels have the potential to enhance coastal water quality through the filtration of TSS and associated particulate nitrogen in Atlantic coastal estuaries that have significant salt marsh acreage, which is the preferred habitat for *G. demissa*. Estimation of pollutant filtration by ribbed mussels requires knowledge of seasonal and spatial variation in key physiological rates associated with suspension feeding processes, as well as data on their population size and biomass, and seston composition. Results from this study show however that basic particle clearance rates were generally consistent among ribbed mussels living in different salt marsh settings ranging from small tidal creeks (LMC), to large river edges (LMR), and onto the high marsh platform. Clearance rates (l hr^{-1} $gDTW^{-1}$) were typically maximized, constrained mainly by seasonal temperature, displaying little variation across space. The temporal variability highlights the need for seasonal measurements of water processing rates when calculating annual water processing and seston filtration.

In addition, filtration of particles is governed by both clearance rates and the actual availability and composition of seston (mg l^{-1}), which can vary widely across space and time. Therefore, to estimate local filtration capacity per animal (mg hr^{-1} $gDTW^{-1}$), clearance rates measured under similar annual temperature regimes may be sufficient, but data regarding the spatial and temporal variability of seston is required. For spatial modeling of gross seston capture by populations of mussels, models must also consider the variability of mussel population demographics and available feeding time within and among marshes. In this study, for example, annual clearance rates were measured to be between 0.20 and 0.34 (l hr^{-1} $gDTW^{-1}$) with the lowest measured values (winter was estimated to be negligible) in fall (7-8°C; 0.02 to 0.06 l hr^{-1} $gDTW^{-1}$) and highest values in the summer (20-25°C; 0.51 to 0.71 l hr^{-1} $gDTW^{-1}$). Seston values ranged between 38.51 and 170.63 mg l^{-1} across marshes and seasons in New Jersey and averaged 13.1 mg l^{-1} in the summer in Rhode Island.

At a landscape level, ribbed mussels were shown to provide a gross removal of TSS between 3,834 and 11,119 kg ha^{-1} yr^{-1} and between 30.93 and 92.48 kg ha^{-1} yr^{-1} of PN. Applying peer-reviewed models regarding the fate of the filtered materials, ribbed mussel populations in New Jersey and Rhode Island marshes were found to make contributions to vertical marsh enhancement and water quality improvement based on their collective filtration, deposition, and net removal of PN. If uniformly distributed across the marsh surface, inorganic biodeposits from ribbed mussels were calculated to contribute between 0.39 and 0.93 mm yr^{-1} in New Jersey and 0.28 mm yr^{-1} in Rhode Island to vertical salt marsh accretion, representing a contribution of between 9.8% and 23.3% and 7.0% of a 4mm yr^{-1} rate of sea level rise, respectively.

Net nitrogen removal through biodeposition and somatic growth was estimated to remove between 68.5 and 166 kg ha^{-1} yr^{-1} in New Jersey and 39.9 kg ha^{-1} yr^{-1} in Rhode Island. On a hectare-to-hectare basis, aquaculture oyster models from Chesapeake Bay have estimated net nitrogen removal per farm to be ~331 kg ha^{-1} per unit time as a result of commercial oyster harvest (1-2 years; Higgens et al. 2011). This estimate assumes 226 oysters m^{-2}, a density much greater than the New Jersey mussel populations evaluated in this study. But, the marsh-wide net PN removal estimated for Dennis Creek, which had the highest mussel density of all New Jersey marshes, averaged 166 kg ha^{-1} yr^{-1}, which was similar assuming that the time to harvest for the oysters was 2 years. Additionally, high density mussel farming has also been shown to remove large quantities of nitrogen (544 kg ha^{-1} yr^{-1}, Petersen et al. 2014), but the mussel density requirements for extraction of this magnitude are typically higher than observed in natural marshes. Galimany et al. (2017) estimated that raft-based bioextration efforts using ribbed mussels in the Hudson River, NY could remove ~62.6 kg of nitrogen per season (March-November), a value similar to the per hectare values estimated in this study, which contain a similar amount of mussel biomass as the bioextratction estimate. Although bioextraction will likely be a valuable tool for mitigating water quality where shellfish are available and able to be "harvested", techniques to develop high density mussel culture systems for extraction are not fully developed. It is important to remember that salt marsh mussel populations are not harvested but still provide similar services year after year, whereas bioextraction efforts depend on harvesting and replenishing mussels, and must be maintained over time.

The approach taken in this study paired physiologically-based measurements under simulated field conditions with field assessments of mussel densities and seston loads. The actual contributions of mussel feeding processes to vertical accretion and PN sequestration *in situ* will depend on many other factors that were not studied here. For example, portions of the water that are filtered might be (re)filtered by the same or adjacent mussels, biodeposits could be resuspended and exported, and/or the fate of filtered matter such as nitrogen may vary with mussel nutritional status and seston quality. Conversely, the hydrodynamics of salt marshes are complex, and some of the TSS flushing the marsh might not be accessible to mussel filtration. More study will be needed to deduce actual cause-effect relationships between mussels and "levee-building" services, as well as the other purported ecosystem services associated with water quality enhancement.

As filtration services by ribbed mussels scale with biomass and food availability, hotspots of services in Rhode Island were located along creeks and rivers where mussel densities were highest and feeding times were maximized. Although ribbed mussel populations were similar in New Jersey and Rhode Island HM and LMC habitats, they significantly differed along LMR habitats. As a result, gross filtration rates in New Jersey along LMR habitats were only 11% of their Rhode Island counterparts. The evaluation of lateral marsh movement along the LMR habitats per marsh showed median erosion rates of 32 and 6cm yr^{-1} in New Jersey and Rhode Island, respectively. These data indicate that rapid marsh edge loss in New Jersey may be compromising LMR habitat to a greater extent than in the Rhode Island marsh. The unstable nature of this low marsh region in New Jersey could be a contributing factor to the low population densities in this habitat. As a result, mussel mediated ecosystem services along both main river edge habitats (i.e. LMR and LMC) in New Jersey comprised only 77% of the filtration services and has shifted the relative percentages of spatial services in NJ into areas of low mussel density. Whereas in Rhode Island, the low marsh areas provided 97% of the services, with only 3% of the services from the vast expanses on low mussel density HM areas. As exemplified by Rhode

Island marshes, areas of high mussel density were capable of supporting high levels of filtration services. In New Jersey, low marsh habitats were shown to support similar populations of ribbed mussels and their associated ecosystem services as Rhode Island in the marsh interior (HM and LMC); however, in highly eroding areas along the primary tidal channels, the populations were significantly lower.

A two-fold strategy is suggested to maximize ribbed mussel-mediated ecosystem services in salt marsh habitats: 1) conserve areas of currently high ecosystem service value (e.g. small tidal creeks in New Jersey, marsh shorelines in Rhode Island); and 2) enhance areas where the habitat suitability has become compromised resulting in reduced ecosystem services (e.g. marsh shorelines in New Jersey). If habitat instability is undermining the long-term potential for mussel-mediated ecosystem services along New Jersey LMR habitat, natural and nature-based infrastructure practices that sustain or enhance ribbed mussels may promote both shoreline stabilization and ater quality improvements. Ribbed mussels are capable of filtering large quantities of TSS and PN, and since 44%-60% is removed as a result of biodeposition and somatic growth, mussels can clearly promote water clarity and quality. The methods provided in this dissertation can guide managers in identifying and calculating marsh-specific distributions of ribbed mussels and their ecosystem service contributions, which will provide direction regarding the spatial selection of areas appropriate for conservation and enhancement. Implementing measures to sustain current ribbed mussel populations where they exist, and to restore/enhance areas where they appear to have been lost, will promote service maximization by this functional dominant marsh consumer.

List of References

Adam, P., 1993. *Saltmarsh ecology*. Cambridge University Press.

Aiello, E. and Sleigh, M.A. 1972. The metachronal wave of lateral cilia of Mytilus edulis. *The Journal of cell biology*, *54*(3): 493-506.

Amthor, J.S. and Huston, M.A. 1998. Terrestrial ecosystem responses to global change: a research strategy. *ORNL Technical Memorandum*, *27*, p.37.

Anisfeld, S.C. and Hill, T.D., 2012. Fertilization effects on elevation change and belowground carbon balance in a Long Island Sound tidal marsh. *Estuaries and Coasts*, *35*(1), pp.201-211.

Arkema, K.K., Guannel, G., Verutes, G., Wood, S.A., Guerry, A., Ruckelshaus, M., Kareiva, P., Lacayo, M. and Silver, J.M. 2013. Coastal habitats shield people and property from sea-level rise and storms. *Nature Climate Change*, *3*(10), pp.913-918.

Armentano, T.V. and E.S. Menges. 1986. Patterns of change in the carbon balance of organic soil wetlands of the temperate zone. *Journal of Ecology* 74: 755-774.

Bayne, B. L. 1976. The biology of mussel larvae, p. 81-120. Zn B. L. Bayne [ed.], Marine mussels.

Beaumont, N.J., M.C. Austen, J.P. Atkins, D. Burdon, S. Degraer, T.P. Dentinho, S. Derous, P. Holm, T. Horton, E. van Ierland, A.H. Marboe, D.J. Starkey, M. Townsend, T. Zarzycki. 2007. Identification, definition, and quantification of goods and services provided by marine biodiversity: Implications for the ecosystem approach. *Marine Pollution Bulletin* 54: 253-265.

Bayne, B.L., Hawkins, A.J.S. and Navarro, E., 1987. Feeding and digestion by the mussel Mytilus edulis L.(Bivalvia: Mollusca) in mixtures of silt and algal cells at low concentrations. *Journal of Experimental Marine Biology and Ecology*, *111*(1), pp.1-22.

Bayne, B.L., Hawkins, A.J.S. and Navarro, E., 1988. Feeding and digestion in suspension-feeding bivalve molluscs: the relevance of physiological compensations. *American zoologist*, pp.147-159.

Bertness, M. D. 1984. Ribbed Mussels and *Spartina alterniflora* production in a New England salt marsh. *Ecology* 65(6):1794-1807.

Bertness, M. D. and E. Grosholz. 1985. Population dynamics of the ribbed mussel, *Geukensia demissa*: The costs and benefits of an aggregated distribution. *Oceologia* 67: 192-204.

Bertness, M.D., 1991. Zonation of *Spartina patens* and *Spartina alterniflora* in New England salt marsh. *Ecology*, *72*(1), pp.138-148.

Bertness, M.D. and Callaway, R., 1994. Positive interactions in communities. *Trends in Ecology & Evolution*, *9*(5), pp.191-193.

Bertness, M.D., Brisson, C.P., Bevil, M.C. and Crotty, S.M., 2014. Herbivory drives the spread of salt marsh die-off. *PloS one*, *9*(3), p.e92916.

Bilkovic, D.M., Mitchell, M.M., Isdell, R.E., Schliep, M. and Smyth, A.R., 2017. Mutualism between ribbed mussels and cordgrass enhances salt marsh nitrogen removal. *Ecosphere*, *8*(4).

Boon, J.D., 2012. Evidence of sea level acceleration at US and Canadian tide stations, Atlantic Coast, North America. *Journal of Coastal Research*, *28*(6), pp.1437-1445.

Borrero, Francisco J. 1987. Tidal height and gametogenesis: reproductive variation among populations of Geukensia demissa. *The Biological Bulletin* 173.1: 160-168.

Bricker-Urso, S., Nixon, S. W., Cochran, J. K., Hirschberg, D. J., & Hunt, C. 1989. Accretion rates and sediment accumulation in Rhode Island salt marshes. *Estuaries*, *12*(4), 300-317.

Bridgham,S.D., J.P. Megonigal, J.K. Keller, N.B. Bliss, C. Trettin. 2006. The carbon balance of North American wetlands *Wetlands*, 26: 889–916

Baustian, J.J., I.A. Mendelssohn, M.W. Hester. 2012. Vegetation's importance in regulating surface elevation in a coastal salt marsh facing elevated rates of sea level rise. *Global Change Biology*: 18: 3377-3382.

Cambridge. -7 C. J. BAYNE,

Carey, J.C., S.B. Moran, R.P. Kelly, A.S. Kolker, and R.W. Fulweiler. 2017. The declining role of organic matter in New England salt marshes. *Estuaries and Coasts*, 40:626-639.

Church, John A., and Neil J. White. 2006. A 20th century acceleration in global sea-level rise. *Geophysical research letters* 33.1: L01602.

Cohen, M. C. L., H. Behling, and R. J. Lara. 2005. Amazonian mangrove dynamics during the last millennium: the relative sea-level and the Little Ice Age." *Review of Palaeobotany and Palynology* 136.1: 93-108.

Costanza, R. and Daly, H.E. 1992. Natural capital and sustainable development. *Conservation biology*, *6*(1), pp.37-46.

Costanza, R., R. d'Arge, R. de Groot, S. Farber, M. Grasso, B. Hannon, K. Limberg, S. Naeem, R. V. O'Neill, J. Paruelo, R. G. Raskin, P. Sutton and M. van den Belt. 1997. The value of the world's ecosystem services and natural capital. *Nature* 387: 253-260.

Costanza, Robert, Octavio Perez-Maqueo, M. Luisa Martinez, Paul Sutton, Sharolyn J. Anderson and Kenneth Mulder. 2008. The value of coastal wetlands for hurricane protection. *AMBIO: A Journal of the Human Environment*. 37(4): 241-248.

Coen, L.D., Knott, D.M., Wenner, E.L., Hadley, N.H., Ringwood, A.H. and Bobo, M.Y., 1999. Intertidal oyster reef studies in South Carolina: design, sampling and experimental focus for evaluating habitat value and function. *Oyster reef habitat restoration: a synopsis and synthesis of approaches. Virginia Institute of Marine Science Press. Gloucester Point, Virginia*, pp.133-158.

Coughlan, J., 1969. The estimation of filtering rate from the clearance of suspensions. *Marine Biology*, *2*(4): 356-358.

Currin, C.A., S.Y. Newell and H.W. Paerl. 1995. The role of standing dead *Spartina alterniflora* and benthic microalgae in salt marsh food webs: Considerations based on multiple stable isotope analysis. *Marine Ecology Progress Series* 212: 99-116.

D'Avanzo, C. and J. N. Kremer, 1994. Diel oxygen dynamics and anoxic events in an eutrophic estuary of Waquoit Bay, Massachusetts. *Estuaries and Coasts*, *17*(1), pp.131-139.

Davies, B.E., 1974. Loss-on-ignition as an estimate of soil organic matter. *Soil Science Society of America Journal*, *38*(1): 150-151.

Daily GC, S. Alexander, and P.R. Ehrlich . 1997. Ecosystem services: benefits supplied to human societies by natural ecosystems. Issues Ecol 2:1–16.

Dame, R.F. 1986. Book Review: *The oyster: the life and lore of the celebrated bivalve,* by R.A. Hedeen. *Estuaries* 9: 382-383.

Dame, R.F. 2012. *Ecology of Marine Bivalves: An Ecosystem Approach*, 2nd edn. Taylor & Francis, London.

Darby, F.A. and Turner, R.E., 2008. Effects of eutrophication on salt marsh root and rhizome biomass accumulation. *Marine Ecology Progress Series*, *363*, pp.63-70.

de Groot RS, Wilson MA, and Boumans RJM. 2002. A typology for the classification, description and valuation of ecosystem functions, goods and services. Ecol Econ41:393–408.

Deegan L.A. and R. H. Garritt. 1997. Evidence for spatial variability in estuarine food webs. *Marine Ecology Progress Series* 147: 31-47.

Deegan, L.A., D.S. Johnson, R.S. Warren, B.J. Peterson, J.W. Fleeger, S. Fagherazzi, and W.M. Wollheim. 2012. Coastal eutrophication as a driver for salt marsh loss. *Nature* 490: 388-392.

DeLaune, R. D., W. H. Patrick, Jr., andR. J. Buresh. 1978. Sedimentation rates determined by^{137}Cs dating in a rapidly accreting salt marsh.*Nature* 275:532–533

DeLaune, R. D., C. J. Smith, and W.H. Patrick. 1983. "Relationship of marsh elevation, redox potential, and sulfide to Spartina alterniflora productivity." *Soil Science Society of America Journal* 47.5: 930-935.

Dinno, A. and Dinno, M.A., 2017. Package ‘dunn. test’.

E.K. Hartig, V. Gornitz, A. Kolker, F. Muschacke, D. Fallon. 2002. Anthropogenic and climate-change impacts on salt marshes of Jamaica Bay, New York City *Wetlands*, 22: 71–89

Emery, N.C., Ewanchuk, P.J. and Bertness, M.D., 2001. Competition and salt-marsh plant zonation: stress tolerators may be dominant competitors. *Ecology*, *82*(9), pp.2471-2485.

Evgenidou, A. and I. Valiela. 2002. Response of growth and density of a population of *Geukensia demissa* to land-derived nitrogen loading, in Waquoit Bay, Massachusetts. *Estuarine, Coastal and Shelf Science* 55: 125-138

Fell, P.E., N.C. Olmstead, E. Carlson, W, Jocob, D. Hitchcock, and G. Silber. 1982. Distribution and abundance of macroinvertebrates on certain Connecticut tidal marshes, with emphasis on dominant molluscs. *Estuaries* 5: 234-239.

Franz, D.R., 1993. Allometry of shell and body weight in relation to shore level in the intertidal bivalve Geukensia demissa (Bivalvia: Mytilidae). *Journal of Experimental Marine Biology and Ecology*, *174*(2), pp.193-207.

Franz, D. R. 1996. Size and age at first reproduction of the ribbed mussel, *Geukensia demissa*, in relation to shore level in a New York salt marsh. *Journal of Experimental Marine Biology and Ecology* 205 (1996) 1-13.

Franz, D. R. 1997. Resource allocation in the intertidal salt marsh mussel *Geukensia demissa* in relation to shore level. *Estuaries* 20:134-148.

Franz, D. R. 2001. Recruitment, survivorship, and age structure of a New York ribbed mussel population (*Geukensia demissa*) in relation to shore level – a nine-year study. *Estuaries* 24:319-327.

Friedrichs, Carl T., and James E. Perry. 2001. Tidal salt marsh morphodynamics: a synthesis. *Journal of Coastal Research*: 7-37.

Galimany, E., Rose, J.M., Dixon, M.S. and Wikfors, G.H., 2013. Quantifying feeding behavior of ribbed mussels (Geukensia demissa) in two urban sites (Long Island Sound, USA) with different seston characteristics. *Estuaries and Coasts*, *36*(6), p.1265.

Gallardi, D., 2014. Effects of bivalve aquaculture on the environment and their possible mitigation: a review. *Fisheries and Aquaculture Journal*, *5*(3), p.1.

Gleason, M.L. and Zieman, J.C., 1981. Influence of tidal inundation on internal oxygen supply of *Spartina alterniflora* and *Spartina patens*. *Estuarine, Coastal and Shelf Science*, *13*(1), pp.47-57.

Haaf, L., S. Demberger, A. Padeletti, and D. Kreeger. 2017. Mid Atlantic Tidal Rapid Assessment: Development of the shoreline attribute using historical change analysis. Partnership for the Delaware Estuary. PDE Report No. 17-##.

Hawkins, A.J.S., Smith, R.F.M., Bayne, B.L. and Heral, M., 1996. Novel observations underlying the fast growth of suspension-feeding shellfish in turbid environments: Mytilus edulis. *Marine Ecology Progress Series*, pp.179-190.

Higgins, C.B., Stephenson, K. and Brown, B.L., 2011. Nutrient bioassimilation capacity of aquacultured oysters: quantification of an ecosystem service. *Journal of environmental quality*, *40*(1), p.271.

Hothorn, T., Bretz, F., Westfall, P., Heiberger, R.M., Schuetzenmeister, A., Scheibe, S. and Hothorn, M.T., 2017. Package ‘multcomp’.

Howes, B.L., Dacey, J.W.H. and Goehringer, D.D., 1986. Factors controlling the growth form of *Spartina alterniflora*: feedbacks between above-ground production, sediment oxidation, nitrogen and salinity. *The Journal of Ecology*, pp.881-898.

Huang, S.C. 2000. A comparison of temporal and spatial variation in nutritional resources and the nutritional demands of the marsh musse, *Geukensia demissa*. Dissertation, University of Maryland, College Park, Md, USA.

Ibanez, C., P.J. Sharpe, J. W. Day, J.N. Day, and N. Prat. 2009. Vertical accretion and relative sea level rise in the Ebro Delta Wetlands (Catalonia, Spain). *Wetlands* 30: 979-988.

Intergovernmental Panel on Climate Change. 2001. Climate Change 2001: The Scientific Basis. Cambridge Univ. Press, New York, 2001.

Intergovernmental Panel on Climate Change. Climate Change 2001: The Scientific Basis (Cambridge Univ. Press, New York, 2001).

Jordan, T. E. and I. Valiela. 1982. The nitrogen budget of the ribbed mussel, *Geukensia demissa*, and its significance in nitrogen flow in a New England salt marsh. *Limnology and Oceanography* 27: 75-90.

Jordan, T. E. and I. Valiela. 1982. The nitrogen budget of the ribbed mussel, *Geukensia demissa*, and its significance in nitrogen flow in a New England salt marsh. *Limnology and Oceanography*. 27: 75-90.

Kearney, M.S.; Grace, R.E., and Stevenson, J.C., 1988. Marsh loss in Nanticoke Estuary, Chesapeake Bay. Geographical Review, 78, 205-220.

Kearney, Michael S., J. Court Stevenson, and Larry G. Ward. 1994. Spatial and temporal changes in marsh vertical accretion rates at Monie Bay: Implications for sea-level rise. *Journal of Coastal Research*: 1010-1020.

Keddy, P.A. 2000 *Wetland Ecology: Principles and Conservation. Cambridge University Press, Cambridge, UK*

Kemp, P.F., S.Y. Newell and C. Krambeck. 1990. Effects of filter-feeding by the ribbed mussel *Geukensia demissa* on the water-column microbiota of *Spartina alterniflora* saltmarsh. *Marine Ecology Progress Series* 59: 1149-131.

Kirwan, Matthew L., and A. Brad Murray. 2007. A coupled geomorphic and ecological model of tidal marsh evolution. *Proceedings of the National Academy of Sciences* 104(15): 6118-6122.

Kirwan, M.L. and Mudd, S.M., 2012. Response of salt-marsh carbon accumulation to climate change. *Nature*, *489*(7417): 550-553.

Kirwan, M.L. and Megonigal, J.P. 2013. Tidal wetland stability in the face of human impacts and sea-level rise. *Nature*, *504*(7478): 53-60.

Kneib, R.T. 1994. Spatial pattern, spatial scale and feeding in fishes. Pages 171-185 *in* D.J. Stouder and R.J. Feller, editors. Theory and application in fish feeding ecology. University of South Carolina Press, Columbia, South Carolina, USA.

Kreeger, D. A., C. J. Langdon, and R. I. E. Newell. 1988. Utilization of refractory cellulosic carbon derived from *Spartina alterniflora* by the ribbed mussel *Geukensia demissa*. *Marine Ecology - Progress Series* 42: 171-179.

Kreeger, D. A., Newell, R. I., & Langdon, C. J. 1990. Effect of tidal exposure on utilization of dietary lignocellulose by the ribbed mussel Geukensia demissa (Dillwyn)(Mollusca: Bivalvia). *Journal of experimental marine biology and ecology*, *144*(2), 85-100.

Kreeger, D. A., & Langdon, C. J. 1994. Digestion and assimilation of protein by Mytilus trossulus (Bivalvia: Mollusca) fed mixed carbohydrate/protein microcapsules. *Marine Biology*, *118*(3), 479-488.

Kreeger, D. A. and R. I. E. Newell. 1996. Ingestion and assimilation of carbon from cellulolytic bacteria and heterotrophic flagellates by the mussels *Geukensia demissa*and *Mytilus edulis* (Bivalva, Mollusca). *Aquatic Microbial Ecology* 11: 205-214.

Kreeger, D.A. and R. I. E. Newell. 2000. Trophic complexity between producers and invertebrate consumers in salt marshes. In Concepts and Controversies in Tidal Marsh Ecology, M. P. Weinstein and D. A. Kreeger (eds). Dordrecht: Kluwer Academic Publishers, pp. 187- 213

Kreeger, D. A. and R. I. E. Newell. 2001. Seasonal utilization of different seston carbon sources by the ribbed mussel, *Geukensia demissa* (Dillwyn) in a mid-Atlantic salt marsh. *Journal of Experimental Marine Biology and Ecology* 260: 71-91.

Kreeger, D. A., J. Adkins, P. Cole, R. Najjar, D. Velinsky, P. Conolly, and J. Kraeuter. 2010. Climate change and The Delaware Estuary: Three case studies in vulnerability assessment and adaptation planning. delawareestuary.org/science_projects_climate_ready_products.asp

Kreeger, D. A. and A. T. Padeletti. 2013. Monitoring and assessment of representative tidal wetlands of the Delaware Estuary. Partnership for the Delaware Estuary final report to the United States Environmental Protection Agency. PDE Report No. 13-03. 114p.

Kreeger, D.A. 2013. Analysis of particulate nutrients and seston weights from 2009 to 2011 at Delaware Bay oyster stations. Academy of Natural Sciences of Drexel University. Final Report to Rutgers University as part of the U.S. Army Corps of Engineers Delaware River and Bay Monitoring Study. August 28, 2013. 40 p.

Kreeger, D., J. Moody, M. Katkowski, M. Boatwright, and D. Rosencrance. 2015. Marsh Futures: Use of scientific survey tools to assess local salt marsh vulnerability and chart best management practices and interventions. Partnership for the Delaware Estuary, Wilmington, DE. PDE Report No. 15-03.

Kuenzler, E. J. 1961. Structure and energy flow of a mussel population in a Georgia salt marsh. *Limnology and Oceanography*. 6: 191-204.

Landry, T., 2002. The potential role of bivalve shellfish in mitigating negative impacts of land use on estuaries. *Can. Tech. Rep. Fish. Aquat. Sci./Rapp. Tech. Can. Sci. Halieut. Aquat.*, (2408), pp.155-157.

Langdon, C.J. and R.I.E. Newell. 1990. Utilization of detritus and bacteria as food sources by two bivalve suspension-feeders, the oyster *Cassostria virginica* and the mussel *Geukensia demissa*. *Marine Ecology-Progress Series* 58: 299-310.

Lent, C. M. 1969. Adaptation of the ribbed mussel, Modiolus demissus (Dillwyn), to the intertidal habitat. *American Zoologist* 9: 283-292.

Leonard, L.A. and M.E. Luther. 1995. Flow hydrodynamics in tidal marsh canopies. *Limnology and Oceanography* 40(8): 1474-1484.

Levine, J.M., Hacker, S.D., Harley, C.D. and Bertness, M.D., 1998. Nitrogen effects on an interaction chain in a salt marsh community. *Oecologia*, *117*(1-2), pp.266-272.

Lillebo, A.I., J.M Neto, M.R. Flindt, J.C. Marques, and M.A. Pardal. 2004. Phosphorous dynamics in a temperate intertidal estuary. *Estuarine, Coastal, and Shelf Science* 61(1): 101-109.

Lin, Junda. 1989. Influence of location in a salt marsh on survivorship of ribbed mussels. *Marine ecology progress series. Oldendorf* 56.1: 105-110.

Lin, Qianxin, and Irving A. Mendelssohn. 1996. A comparative investigation of the effects of south Louisiana crude oil on the vegetation of fresh, brackish and salt marshes." *Marine Pollution Bulletin* 32.2: 202-209.

Liu, S., Costanza, R., Troy, A., D'Aagostino, J. and Mates, W., 2010. Valuing New Jersey's ecosystem services and natural capital: a spatially explicit benefit transfer approach. *Environmental management*, *45*(6), pp.1271-1285.

Lonsdale, D.J., R.M. Cerrato, R. Holland. 2009. Influence of suspension-feeding bivalves on the pelagic food webs of shallow, coastal embayments. *Aquatic Biology 6*: 263-279.

McCaffrey, Richard J., and John Thomson. 1980. A record of the accumulation of sediment and trace metals in a Connecticut salt marsh." *Advances in geophysics* 22: 165-236.

McKee, Karen L., Irving A. Mendelssohn, and Michael D Materne. 2004. Acute salt marsh dieback in the Mississippi River deltaic plain: a drought-induced phenomenon *Global Ecology and Biogeography* 13(1): 65-73.

Mendelssohn, I.A., 1979. The influence of nitrogen level, form, and application method on the growth response of *Spartina alterniflora* in North Carolina. *Estuaries*, *2*(2), pp.106-112.

Mendelssohn, I.A., McKee, K.L. and Patrick, W.H., 1981. Oxygen deficiency in *Spartina alterniflora* roots: metabolic adaptation to anoxia. *Science*, *214*(4519), pp.439-441.

Mitsch, W.J. and J.G. Gosselink. 1993. Editor: C. J. Barrow. Wetlands (2nd Edition). Reinhold, New York.

Mohlenberg, F. and H. U. Riisgard. 1979. Filtration rate, using a new indirect technique, in thirteen species of suspension-feeding bivalves. *Marine Biology 54*: 143-148.

Moody, Joshua A. (2011) *The Relationship between the ribbed mussel (Guekensia demissa) and salt marsh shoreline erosion* (Master's Thesis). Rutgers, the State University of New Jersey, New Brunswick, New Jersey.

Morris, James T.,P.V. Sundarehwar, C.T. Nietch, B. Kjerfve, and D.R. Cahoon. 2002. Responses of coastal wetlands to rising sea level. *Ecology* 83.10: 2869-2877.

Morris, J.T. 2007. Ecological engineering in intertidial saltmarshes. *Hydrobiologia*, *577*(1): 161-168.

Mudd, Simon M., Susan M. Howell, and James T. Morris. 2009. Impact of dynamic feedbacks between sedimentation, sea-level rise, and biomass production on near-surface marsh stratigraphy and carbon accumulation. *Estuarine, Coastal and Shelf Science* 82(3): 377-389.

Murray, T.J. and Hudson, K.L., 2013. *Economic activity associated with shellfish aquaculture in Virginia, 2012*. Virginia Institute of Marine Science.

Nelson, J.L. and Zavaleta, E.S. 2012. Salt marsh as a coastal filter for the oceans: changes in function with experimental increases in nitrogen loading and sea-level rise. *PloS one*, *7*(8), p.e38558.

Nepf, H. M. 1999. Drag, turbulence, and diffusion in flow through emergent vegetation. *Water resources research* 35.2: 479-489.

Neubauer, Scott C. 2008. Contributions of mineral and organic components to tidal freshwater marsh accretion. *Estuarine, Coastal and Shelf Science* 78(1): 78-88.

Newell, R. C., & Field, J. G. 1983. The contribution of bacteria and detritus to carbon and nitrogen flow in a benthic community. *Mar. Biol. Lett.*, *4*(1), 23-36.

Newell, R.I., 2004. Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: a review. *Journal of Shellfish Research*, *23*(1): 51-62.

Newell,R.I.E. and C.J Langdon, 2004. Mechanisms and physiology of larval and adult feeding. In V.S Kennedy, R.I.E Newell, A. Eble (Eds.), The Eastern Oyster, *Crassostrea virginica*. Maryland Sea Grant Publication, College Park, MD, pp. 185–230.

Nicholls, R. J., F.M.J. Hoozemans, and M. Marchand. 1999. Increasing flood risk and wetland losses due to global sea-level rise: regional and global analyses. *Global Environmental Change* 9: 69-87.

Nicholls, Robert J. and Lowe, Jason A. 2004 Benefits of mitigation of climate change for coastal areas. Global Environmental Change A: Human and Policy Dimensions, 14, (3), 229-244.

Nielsen, K.J. and Franz, D.R., 1995. The influence of adult conspecifics and shore level on recruitment of the ribbed mussel *Geukensia demissa* (Dillwyn). *Journal of Experimental Marine Biology and Ecology*, *188*(1), pp.89-98.

Nilsson, H.C., and R, Rosenberg. 1994. Hypoxic response of two benthic marine benthic communities. *Marine Ecology Progress Series* 115: 209-217.

Nixon, S.W., C.D. Hunt and B.L. Nowicki. 1986. The Retention of Nutrients (C, N, P), Heavy Metals (Mn, Cd,Pb,Cu, and Petroleum Hydrocarbons in Narragansett Bay. *Elsevier Oceanography Series*, Volume 43: Pages 99-122

Odum, E.P. 1968. A research challenge: evaluating the productivity of coastal and estuarine water. Proceedings of the second Sea Grant conference, University of Rhode Island, Kingston, Rhode Island, USA.

Partnership for the Delaware Estuary. 2010. *State of the Estuary 2010 Climate Report.* http://delawareestuary.org/pdf/Climate/Climate%20Change%20and%20the%20Delaware%20Estuary_PDE-10-01.pdf

Partnership for the Delaware Estuary. 2014. Site Specific Intensive Monitoring of Coastal Wetlands in Dividing Creek New Jersey Watershed, 2012-2013. PDE Report No. 14-04. 29pp.

Pennings, S.C. and Bertness, M.D., 2001. Salt marsh communities. *Marine community ecology*, pp.289-316.

Petersen, J.K., Hasler, B., Timmermann, K., Nielsen, P., Tørring, D.B., Larsen, M.M. and Holmer, M., 2014. Mussels as a tool for mitigation of nutrients in the marine environment. *Marine pollution bulletin*, *82*(1), pp.137-143.

Peterson, B.J., R.W. Howarth and R.H. Garritt. 1986 Sulfur and carbon isotopes as tracer of salt marsh organic matter flow. *Ecology* 67: 865-874.

Philipp, K.R., 2005. History of Delaware and New Jersey salt marsh restoration sites. Ecol. Eng. 25, 214–230.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B. and Maintainer, R., 2017. Package 'nlme'. *Linear and Nonlinear Mixed Effects Models, version 3.1-131*, pp.3-1.

Rabalais, N.N., Turner, R.E., Díaz, R.J. and Justić, D. 2009. Global change and eutrophication of coastal waters. *ICES Journal of Marine Science: Journal du Conseil*, *66*(7), pp.1528-1537.

Raposa, K.B., M.L. Cole Ekberg, D.M. Burdick, N.T. Ernst, and S.C. Adanowicz. 2016. Elevation change and the vulnerability of Rhode Island (USA) salt marshes to sea level rise. *Regional Environmental Change*. Doi:10.1007/s10113-016-1020-5.

Redfield, Alfred C., and Meyer Rubin. "The age of salt marsh peat and its relation to recent changes in sea level at Barnstable, Massachusetts." *Proceedings of the National Academy of Sciences of the United States of America* 48.10 (1962): 1728.

Reich, P. B., et al. 2006. Nitrogen limitation constrains sustainability of ecosystem response to CO2. *Nature* 440.7086: 922-925.

Reich, Peter B., et al. 2006. Nitrogen limitation constrains sustainability of ecosystem response to CO2. *Nature* 440.7086: 922-925.

Riisgård, H.U., 1988. Efficiency of particle retention and filtration rate in 6 species of Northeast American bivalves. *Marine Ecology Progress Series*, pp.217-223.

Sallenger Jr, A.H., Doran, K.S. and Howd, P.A., 2012. Hotspot of accelerated sea-level rise on the Atlantic coast of North America. *Nature Climate Change*, *2*(12), pp.884-888.

Scyphers, S.B., Powers, S.P., Heck Jr, K.L. and Byron, D., 2011. Oyster reefs as natural breakwaters mitigate shoreline loss and facilitate fisheries. *PloS one*, *6*(8), p.e22396.

Sfriso, A., Pavoni, B., Marcomini, A. and Orio, A.A., 1992. Macroalgae, nutrient cycles, and pollutants in the Lagoon of Venice. *Estuaries and Coasts*, *15*(4), pp.517-528.

Shepard C.C., C.M. Crain, and M.W. Beck. 2011 The Protective Role of Coastal Marshes: A Systematic Review and Meta-analysis. PLoS ONE 6(11): e27374. doi:10.1371/journal.pone.0027374

Smith, J.M. and Frey, R.W., 1985. Biodeposition by the ribbed mussel Geukensia demissa in a salt marsh, Sapelo Island, Georgia. *Journal of Sedimentary Research*, *55*(6).

Sousa, A.I., A.I. Lillebo, I. Cacador, and M.A. Paradel. 2008. Contribution of *Spartina maritime* to the reduction of eutrophication in estuarine systems. *Environmental Pollution* 156: 628-635.

Sousa, A.I., Lillebø, A.I., Pardal, M.A. and Caçador, I. 2010. Productivity and nutrient cycling in salt marshes: contribution to ecosystem health. *Estuarine, Coastal and Shelf Science*, *87*(4), pp.640-646.

Sprent, Janet I. *The ecology of the nitrogen cycle*. Cambridge University Press, 1987.

Stadmark, J. and Conley, D.J., 2011. Mussel farming as a nutrient reduction measure in the Baltic Sea: consideration of nutrient biogeochemical cycles. *Marine pollution bulletin*, *62*(7), pp.1385-1388.

Stevenson, J. C. M. S., Michael S. Kearney, and Edward C. Pendleton. 1985. Sedimentation and erosion in a Chesapeake Bay brackish marsh system. *Marine Geology* 67.3: 213-235.

Stevenson, F. J., and M. A. Cole. 1999. The carbon cycle. *Cycles of Soil. Eds. Stevenson and Cole* : 1-45.

Stiven, A.E. and Gardner, S.A., 1992. Population processes in the ribbed mussel *Geukensia demissa* (Dillwyn) in a North Carolina salt marsh tidal gradient: spatial pattern, predation, growth and mortality. *Journal of Experimental Marine Biology and Ecology*, *160*(1), pp.81-102.

Sun G.L.*, O.* Diaz*, B.* Salomon*, R.* Von Bothmer. 1999 Genetic diversity in *Elymus caninus* as revealed by isozyme, RAPD, and microsatellite markers*. Genome,* 42*,* 420–431

Temmerman, Stijin, Mindert B. De Vries and Tjeerd J. Bouma. 2012. Coastal marsh die-off and reduced attenuation of coastal floods: A model analysis. *Global and Planetary Change*. 92-93: 267-274.

Thorne, Karen M.; Takekawa, John Y.; Elliott-Fisk, Deborah L. 2012. Ecological Effects of Climate Change on Salt Marsh Wildlife: A Case Study from a Highly Urbanized Estuary. *Journal of Coastal Research* 28(6): 1477-1487.

TREB: Technical Report for The Delaware Estuary and Basin. 2017. Partnership for the Delaware Estuary. Report Number 12-01. 255 pages.

Turner R.K. and Pearce, D. in *Economics and Ecology: New Frontiers and Sustainable Development* (ed. Barbier, E.D.) 177-194 (Chapman and Hall, London, 1993).

Turner, R.E., Swenson, E.M. and Milan, C.S., 2002. Organic and inorganic contributions to vertical accretion in salt marsh sediments. *Concepts and controversies in tidal marsh ecology*, pp.583-595.

Turner, R.E., Swenson, E.M., Milan, C.S., Lee, J.M. and Oswald, T.A. 2004. Below-ground biomass in healthy and impaired salt marshes. *Ecological Research*, *19*(1), pp.29-35.

Uncles, R.J. and Smith, R.E., 2005. A note on the comparative turbidity of some estuaries of the Americas. *Journal of Coastal Research*, pp.845-852.

Valiela, I. and Teal, J.M., 1974. Nutrient limitation in salt marsh vegetation. *Ecol Halophytes*.

Valiela, I., Teal, J.M. and N.Y. Persson. 1976. Production and dynamics of experimentally enriched salt marsh vegetation: belowground biomass. *Limnology and Oceanography*, *21*(2), pp.245-252.

Valiela, I. and J. M. Teal. 1979. The nitrogen budget of a salt marsh ecosystem. *Nature* 280: 652-656.

Valiela, I., J. Costa, K. Foreman, J.M. Teal, B. Howes and D. Aubrey. 1990. Transport of groundwater-borne nutrients from watersheds and their effects on coastal waters. *Biogeochemisrty* 10: 177-197.

Valiela, I., 1992. Coupling of watersheds and coastal waters: an introduction to the dedicated issue. *Estuaries and Coasts*, *15*(4), pp.429-430.

Valiela, I., J. McClelland, J. Hauxwell, P. J. Behr, D. Hersh and K. Foreman. 1997. Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences*. Limnology and Oceanography,* 42(5 pt 2): 1105-1118.

Voss, C.M., Christian, R.R. and Morris, J.T., 2013. Marsh macrophyte responses to inundation anticipate impacts of sea-level rise and indicate ongoing drowning of North Carolina marshes. *Marine Biology*, *160*(1), pp.181-194.

Warren, C.R. 2007: Perspectives on the 'alien' versus 'native' species debate: a critique of concepts, language and practice*. Progress in Human Geography* 31, 427–46.

Watson, E.B., Oczkowski, A.J., Wigand, C., Hanson, A.R., Davey, E.W., Crosby, S.C., Johnson, R.L. and Andrews, H.M., 2014. Nutrient enrichment and precipitation changes do not enhance resiliency of salt marshes to sea level rise in the Northeastern US. *Climatic Change*, *125*(3-4), p.501.

Weinstein, M.P., L. Scott, S.P O'Neil, R.C.I. Sigfried, and S.T. Szedlmayer. 1984. Population dynamics of spot, *Leiostomus xanthurus*, in polyhaline tidal creeks of the York River Estuary, Virginia. *Estuaries* 7: 444-450*.*

Weinstein, M.P. and S.P O'Neil. 1986. Exchange of marked juvenile spots between adjacent tidal creeks in the York River Estuary, Virginia. *Transactions American Fisheries Society* 115: 93-97.

Werme CE. 1981. Resource partitioning in a salt marsh fish community. PhD thesis, Boston University

White J.R. and K.R. Reddy. 2000. Nitrification and denitrification rates of everglades wetland solis along a phosphorous impacted gradient. *Journal of Environmental Quality* 32(6): 2436-

2443.

Widdows, J. and Bayne, B.L., 1971. Temperature acclimation of Mytilus edulis with reference to its energy budget. *Journal of the Marine Biological Association of the United Kingdom*, *51*(04), pp.827-843.

Widdows, J., 1976. Physiological adaptation ofMytilus edulis to cyclic temperatures. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology*, *105*(2), pp.115-128.

Widdows, J., J. M. Shick. 1985. Physiological responses of *Mytilus edulis* and *Cardium edule* to aerial exposure. *Marine Biology 85(3)*, pp 217-232.

Wigand, C., Roman, C.T., Davey, E., Stolt, M., Johnson, R., Hanson, A., Watson, E.B., Moran, S.B., Cahoon, D.R., Lynch, J.C. and Rafferty, P., 2014. Below the disappearing marshes of an urban estuary: historic nitrogen trends and soil structure. *Ecological Applications*, *24*(4), pp.633-649.

Wilbur, A.E. and Hilbish, T.J., 1989. Physiological energetics of the ribbed mussel Geukensia demissa (Dillwyn) in response to increased temperature. *Journal of Experimental Marine Biology and Ecology*, *131*(2), pp.161-170.

Willows, R.I., 1992. Optimal digestive investment: A model for filter feeders experiencing variable diets. *Limnology and Oceanography*, *37*(4), pp.829-847.

Wright, R.T., Coffin, R.B., Ersing, C.P. and Pearson, D., 1982. Field and laboratory measurements of bivalve filtration of natural marine bacterioplankton. *Limnology and oceanography*, *27*(1), pp.91-98.

Appendix A: Seasonal Clearance Rates per Habitat per Marsh

Seasonal mean ± se of clearance rates per habitat per marsh (l hr^{-1} gram dry tissue $weight^{-1}$). DC=Dividing Creek; DN=Dennis Creek; MR=Maurice River; RI=Rhode Island. DC, DN, and MR are all located in New Jersey. CR-LMR=clearance rate in low marsh river habitat; CR-HM=clearance rate in high marsh habitat; and CR-LMC= clearance rate in low marsh creek habitat. The number in parenthesis after each clearance rate value indicates the number of mussels from which it was calculated.

Season	Marsh	CR-LMR (n)	CR-HM (n)	CR-LMC (n)
Spring	DC	0.16 ± 0.03 (7)	0.27 ± 0.04 (7)	0.51 ± 0.06 (7)
	DN	0.26 ± 0.06 (8)	0.18 ± 0.04 (8)	0.19 ± 0.03 (8)
	MR	0.56 ± 0.07 (7)	0.66 ± 0.14 (6)	0.46 ± 0.09 (7)
Summer	DC	0.65 ± 0.12 (7)	0.73 ± 0.22 (7)	0.69 ± 0.11 (7)
	DN	0.48 ± 0.04 (8)	0.43 ± 0.03 (8)	0.60 ± 0.07 (8)
	MR	0.59 ± 0.09 (7)	0.90 ± 0.13 (7)	0.65 ± 0.17 (7)
	RI	0.56 ± 0.19 (8)	0.75 ± 0.18 (8)	0.35 ± 0.06 (8)
Fall	DC	0.02 ± 0.01 (7)	0.03 ± 0.01 (4)	0.03 ± 0.01 (5)
	DN	0.05 ± 0.01 (7)	0.03 ± 0.02 (6)	0.06 ± 0.02 (8)
	MR	0.11 ± 0.05 (5)	0.01 ± 0.02 (5)	0.07 ± 0.04 (7)

Appendix B: Correlations between Clearance Rates and Seston Metrics

Correlations between seasonal mean clearance rate (l hr $^{-1}$ gram dry tissue weight^{-1}) and mean values of seston metrics among marshes (n=3 fall and spring; n=4 in summer). CR= clearance rate; TSS = total suspended solids; POM = Particulate Organic Matter; %Org = Percent Organics; C:N = carbon nitrogen ratio; PN = particulate nitrogen.

Season	Correlation	t	df	p-value
Spring	CR ~ TSS	10.104	1	0.0628
	CR ~ POM	4.7773	1	0.1314
	CR ~ %ORG	-1.1484	1	0.4561
	CR ~ C:N	-1.3453	1	0.4069
	CR ~ PN	4.5363	1	0.1381
Summer	CR ~ TSS	-0.4514	2	0.6943
	CR ~ POM	-0.542	2	0.6421
	CR ~ %ORG	-0.5706	2	0.6258
	CR ~ C:N	-0.8541	2	0.483
	CR ~ PN	0.3123	2	0.7844
Fall	CR ~ TSS	-0.0498	1	0.9683
	CR ~ POM	0.2	1	0.8743
	CR ~ %ORG	0.5358	1	0.6869
	CR ~ C:N	-4.1263	1	0.1514
	CR ~ PN	0.3915	1	0.7624

Appendix C: Correlations between Filtration Rates and Seston Metrics

Correlations between seasonal mean filtration rate (l hr^{-1} gram dry tissue $weight^{-1}$) and mean values of seston metrics among marshes (n=3 fall and spring; n=4 in summer. FR= filtration rate; POM = Particulate Organic Matter; %Org = Percent Organics; C:N = carbon nitrogen ratio; PN = particulate nitrogen.

Season	Correlation	t	df	p-value
Spring	FR ~ POM	14.7898	1	0.04298
	FR ~ %ORG	-0.8692	1	0.5445
	FR ~ C:N	-1.0148	1	0.2261
	FR ~ PN	12.7714	1	0.04975
Summer	FR ~ POM	3.9819	2	0.05767
	FR ~ %ORG	-2.7558	2	0.1103
	FR ~ C:N	1.4198	2	0.2915
	FR ~ PN	2.6783	2	0.1157
Fall	FR ~ POM	1.0098	1	0.4969
	FR ~ %ORG	1.8926	1	0.3094
	CR ~ C:N	-2.6969	1	0.2261
	FR ~ PN	1.4468	1	0.385

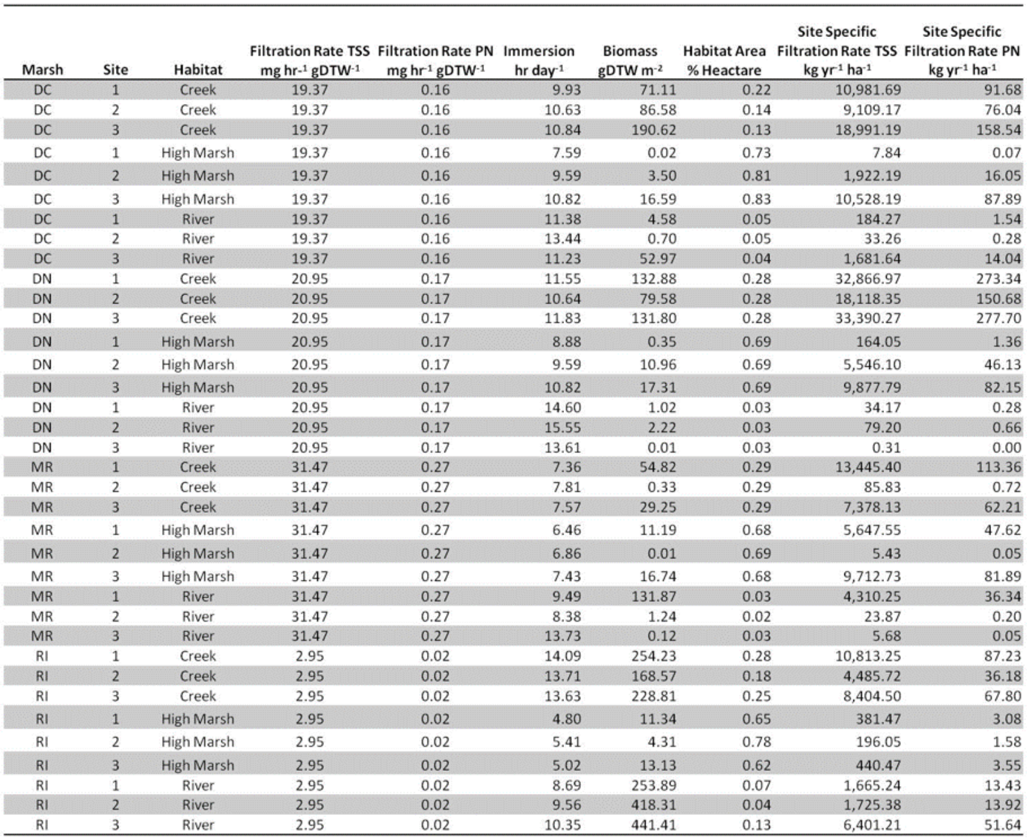
Appendix D: P-values for Paired Marsh Metrics

P-values for paired marshes regarding: annual weight-specific clearance rate (WSCR, l hr^{-1} gDTW^{-1}); total suspended solid concentration (TSS, mg l^{-1}); particulate nitrogen concentration (mg l^{-1}); marsh-wide mussel biomass; annual filtration rate of TSS (FR-TSS, mg hr^{-1} gDTW^{-1}); and annual filtration rate of PN (FR-PN, mg hr^{-1} gDTW^{-1}). DC=Dividing Creek; DN=Dennis Creek; MR=Maurice River; RI=Rhode Island.

Marsh-pairs	Annual WSCR	TSS	PN	Mussel Biomass	Annual FR-TSS	Annual FR-PN
DC-DN	0.42	0.07	0.07	>0.99	<0.01	<0.01
MR-DN	0.50	0.69	0.74	0.16	<0.01	<0.01
MR-DC	0.02	0.49	0.45	0.19	0.21	0.22
RI-DN	0.78	<0.01	<0.01	<0.01	<0.01	<0.01
RI-DC	0.92	0.03	0.02	<0.00	0.35	0.31
RI-MR	0.07	<0.01	<0.01	<0.01	0.99	0.99

Appendix E: Annual Site and Habitat-Specific Filtration Services

Annual site and habitat-specific total suspended solid (TSS) and particulate nitrogen (PN) filtration services per habitat per site per marsh. Included are all values used for calculations: annual TSS and PN filtration rate, ribbed mussel immersion time, ribbed mussel biomass, and percent area of each habitat type. DC=Dividing Creek; DN=Dennis Creek; MR=Maurice River; RI=Rhode Island. Sites refer to the sub-areas studied per marsh: 1 was close to mouth; 2 was near first meander; and 3 was at the upper extent of representative mussel presence.



Marsh	Site	Habitat	Filtration Rate TSS mg hr^{-1} gDTW^{-1}	Filtration Rate PN mg hr^{-1} gDTW^{-1}	Immersion hr day^{-1}	Biomass gDTW m^{-2}	Habitat Area % Heactare	Site Specific Filtration Rate TSS kg yr^{-1} ha^{-1}	Site Specific Filtration Rate PN kg yr^{-1} ha^{-1}
DC	1	Creek	19.37	0.16	9.93	71.11	0.22	10,981.69	91.68
DC	2	Creek	19.37	0.16	10.63	86.58	0.14	9,109.17	76.04
DC	3	Creek	19.37	0.16	10.84	190.62	0.13	18,991.19	158.54
DC	1	High Marsh	19.37	0.16	7.59	0.02	0.73	7.84	0.07
DC	2	High Marsh	19.37	0.16	9.59	3.50	0.81	1,922.19	16.05
DC	3	High Marsh	19.37	0.16	10.82	16.59	0.83	10,528.19	87.89
DC	1	River	19.37	0.16	11.38	4.58	0.05	184.27	1.54
DC	2	River	19.37	0.16	13.44	0.70	0.05	33.26	0.28
DC	3	River	19.37	0.16	11.23	52.97	0.04	1,681.64	14.04
DN	1	Creek	20.95	0.17	11.55	132.88	0.28	32,866.97	273.34
DN	2	Creek	20.95	0.17	10.64	79.58	0.28	18,118.35	150.68
DN	3	Creek	20.95	0.17	11.83	131.80	0.28	33,390.27	277.70
DN	1	High Marsh	20.95	0.17	8.88	0.35	0.69	164.05	1.36
DN	2	High Marsh	20.95	0.17	9.59	10.96	0.69	5,546.10	46.13
DN	3	High Marsh	20.95	0.17	10.82	17.31	0.69	9,877.79	82.15
DN	1	River	20.95	0.17	14.60	1.02	0.03	34.17	0.28
DN	2	River	20.95	0.17	15.55	2.22	0.03	79.20	0.66
DN	3	River	20.95	0.17	13.61	0.01	0.03	0.31	0.00
MR	1	Creek	31.47	0.27	7.36	54.82	0.29	13,445.40	113.36
MR	2	Creek	31.47	0.27	7.81	0.33	0.29	85.83	0.72
MR	3	Creek	31.47	0.27	7.57	29.25	0.29	7,378.13	62.21
MR	1	High Marsh	31.47	0.27	6.46	11.19	0.68	5,647.55	47.62
MR	2	High Marsh	31.47	0.27	6.86	0.01	0.69	5.43	0.05
MR	3	High Marsh	31.47	0.27	7.43	16.74	0.68	9,712.73	81.89
MR	1	River	31.47	0.27	9.49	131.87	0.03	4,310.25	36.34
MR	2	River	31.47	0.27	8.38	1.24	0.02	23.87	0.20
MR	3	River	31.47	0.27	13.73	0.12	0.03	5.68	0.05
RI	1	Creek	2.95	0.02	14.09	254.23	0.28	10,813.25	87.23
RI	2	Creek	2.95	0.02	13.71	168.57	0.18	4,485.72	36.18
RI	3	Creek	2.95	0.02	13.63	228.81	0.25	8,404.50	67.80
RI	1	High Marsh	2.95	0.02	4.80	11.34	0.65	381.47	3.08
RI	2	High Marsh	2.95	0.02	5.41	4.31	0.78	196.05	1.58
RI	3	High Marsh	2.95	0.02	5.02	13.13	0.62	440.47	3.55
RI	1	River	2.95	0.02	8.69	253.89	0.07	1,665.24	13.43
RI	2	River	2.95	0.02	9.56	418.31	0.04	1,725.38	13.92
RI	3	River	2.95	0.02	10.35	441.41	0.13	6,401.21	51.64

Vita

Joshua Andrew Moody
Senior Restoration Coordinator, Partnership for the Delaware Estuary
110 S. Poplar St Ste 202 | Wilmington, DE 19801| 267-242-2505 |
jmoody@delawareestuary.org

EDUCATION

Ph.D., Environmental Science Drexel University, Philadelphia, PA
M.S., Ecology, Rutgers University, New Brunswick, NJ
Graduate Certification in Geospatial Information Science. Rutgers University Center for Remote Sensing and Spatial Analysis, New Brunswick NJ.
B.S., Biology, Temple University, Philadelphia, Pa

Selected Publications

Moody, J., D. Kreeger, S. Bouboulis, S. Roberts, and A. Padeletti. 2016. Design, implementation, and evaluation of three living shoreline treatments at the DuPont Nature Center, Mispillion River, Milford, DE. Partnership for the Delaware Estuary, Wilmington, DE. PDE Report No. 16-12. 79 p.

Yepsen, M., **Moody, J.,** Schuster, E., 2016. A Framework for developing monitoring plans for coastal wetland restoration and living shoreline projects in New Jersey. A report prepared by the New Jersey Measures and Monitoring Workgroup of the NJ Resilient Coastlines Initiative, with support from the NOAA National Oceanic and Atmospheric Administration (NOAA) Coastal Resilience (CRest) Grant program (NA14NOS4830006).

Kreeger, D., **J. Moody**, M. Chintala and E. Watson. 2015. Geospatial and seasonal variation in the capture, flux and fate of seston and associated nitrogen by ribbed mussels (*Geukensia demissa*) in representative mid-Atlantic salt marshes. Partnership for the Delaware Estuary, Wilmington, DE. PDE Report No. 15-04. 135 p.

Honors and Awards:

2014 Best Student Talk Award at the National Shellfisheries Association Annual Conference. April 2, 2014 Jacksonville, Florida.
2014 Best Student Talk Award at the Atlantic Estuarine Research Society annual conference. Marsh 29, 2014 Ocean City, MD.
2012 Best Student Talk Award at the Restore America's Estuaries 6th National Conference on Coastal Ecosystems. October 23, 2012 Tampa, Florida.
2011 Best Student Talk Award at the Delaware Estuary Science and Environmental Summit, Sponsored by the Partnership for the Delaware Estuary, Cape May, NJ.
2010-2011 Delaware National Estuarine Research Reserve Graduate Research Fellowship: $20,000
2010 National Shellfisheries Association Carriker Student Research Grant: $1,250
2010 Society of Wetland Scientists Student Research Grant: $1,000
2010 Atlantic Estuarine Research Society Spring Conference Travel Award. $125