

BIOPHYSICAL FEEDBACKS MEDIATE TIDAL CREEK FORMATION IN SALT MARSHES

A Dissertation Presented to
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In Partial Fulfilment
of the Requirements for the Degree
Doctor of Philosophy

By
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BIOPHYSICAL FEEDBACKS MEDIATE TIDAL CREEK FORMATION IN SALT MARSHES

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Abstract

How organisms and ecological systems respond to global change is of great interest to ecologists. These responses may or may not be beneficial because there might be positive or negative feedbacks that would make the impacts larger or smaller than expected. I conducted laboratory and field experiments to explore the mechanisms driving tidal creek formation in southeastern US salt marshes, focusing on three topics. 1) The effect of crabs on creek growth via four potential mechanisms: sediment excavation, plant removal, subterranean erosion, and decomposition. I found that *Sesarma reticulatum* (henceforth *Sesarma*) is the primary crab species mediating creek growth. *Sesarma* is concentrated at creek heads where plants are dying and creeks eroding. *Sesarma* excavated larger amounts of sediment through burrowing than other crabs, and is unique in creating burrow networks that likely increase belowground erosion and decomposition. *Sesarma* also is the only crab species that directly kills vegetation. Thus, *Sesarma* negatively impacts the marsh plant *Spartina alterniflora* and alters marsh geomorphology by engineering creek growth. 2) The factors mediating crab feeding preferences. I discovered that *Sesarma* did less damage to its food plant *S. alterniflora* in the presence of predators. *Sesarma* prefers and grows better consuming rhizomes than leaves; however, the cost of accessing rhizomes leads to higher mortality if rhizomes are the only diet option. A choice in feeding location allows *Sesarma* flexibility to balance the risks of predation, the nutritional benefit of feeding below-ground, and the survival costs of below-ground feeding. 3) The factors driving the aggregation and movement of *Sesarma* at creek heads. Creek heads are cooler, have higher dissolved oxygen levels, and lower hydrogen sulfide concentrations than elsewhere on the marsh. These superior

conditions drive *Sesarma* aggregation. Additionally, I found that hydrology drives *Sesarma* aggregations when creek conditions were mimicked on the marsh platform. The results of this dissertation suggest that there is a biophysical feedback loop in marsh creek formation: creek growth is driven by a positive feedback between *Sesarma* crabs, which accelerate erosion, and creeks, which create abiotic conditions favorable for *Sesarma* crabs.

TABLE OF CONTENTS

Abstract.....	v
List of Figures.....	ix
Chapter 1: General Introduction	1
1.1 Overview.....	2
1.2 Global changes affecting salt marshes.....	2
1.3 Ecosystem engineers.....	4
1.4 Focus of this dissertation	5
Chapter 2: Interactions between ecosystem engineers drive creek formation in sinking salt marshes.....	9
2.1 Abstract.....	10
2.2 Introduction.....	11
2.3 Materials and Methods.....	13
2.3.1 Study sites and Species.....	13
2.3.2 Relationship between creeks, plants, and crabs in the field.....	15
2.3.3 Percolation rates.....	17
2.3.4 Decomposition of below-ground biomass.....	17
2.3.5 Sediment excavation and herbivory.....	18
2.3.6 Does loss of vegetation increase creek growth?.....	19
2.4 Results.....	20
2.4.1 Relationship between creeks, plants, and crabs in the field.....	20
2.4.2 Percolation rates.....	23
2.4.3 Decomposition of below-ground biomass.....	24

2.4.4	Sediment excavation and herbivory.....	25
2.4.5	Does loss of vegetation increase creek growth?.....	29
2.5	Discussion.....	29
2.5.1	<i>Sesarma</i> are associated with eroding creek heads.....	30
2.5.2	<i>Sesarma</i> crabs excavate large amounts of sediment at creek heads.....	31
2.5.3	<i>Sesarma</i> crabs kill vegetation and enhance creek growth.....	33
2.5.4	Other possible mechanisms by which crabs may mediate creek growth....	34
2.5.5	Conclusion.....	35
Chapter 3: Predators mediate above- versus below-ground herbivory in a salt marsh crab		38
3.1	Abstract.....	39
3.2	Introduction.....	40
3.3	Material and Methods	42
3.3.1	Study cite and Species.....	42
3.3.2	Effects of predators on <i>Sesarma</i> mortality rate.....	42
3.3.3	Do predators affect <i>Sesarma</i> feeding preferences?.....	43
3.3.4	Do <i>Sesarma</i> prefer to eat above- or below-ground biomass?.....	44
3.3.5	How does diet affect growth of <i>Sesarma</i> ?.....	44
3.3.6	Effect of <i>Sesarma</i> feeding on <i>Spartina</i> biomass.....	44
3.4	Results.....	46
3.4.1	Effects of predators on <i>Sesarma</i> mortality rate.....	46
3.4.2	Do predators affect <i>Sesarma</i> feeding preferences?.....	46
3.4.3	<i>Sesarma</i> feeding preference and growth.....	48

3.4.4	Effect of <i>Sesarma</i> feeding on <i>Spartina</i> biomass.....	49
3.5	Discussion	51
3.5.1	Predator-induced behavior changes in <i>Sesarma</i>	51
3.5.2	<i>Sesarma</i> prefer and do better feeding on rhizomes.....	52
3.5.3	Effects of feeding location on <i>Sesarma</i> and <i>Spartina</i>	53
3.5.4	Conclusion.....	53
 Chapter 4: Abiotic conditions explain asymmetric movement of consumer fronts		
	associated with creek heads in salt marshes.....	55
4.1	Abstract.....	56
4.2	Introduction.....	57
4.3	Materials and Methods.....	59
4.3.1	Study site and Species.....	59
4.3.2	Do abiotic conditions differ among different micro-habitats?.....	60
4.3.3	Do conditions created by creek heads attract crabs?.....	62
4.4	Results.....	63
4.5	Discussion	68
4.5.1	Abiotic condition drives asymmetrical growth of <i>Sesarma</i> front.....	68
4.5.2	Hydrology drives <i>Sesarma</i> aggregation.....	69
4.5.3	Movement of <i>Sesarma</i> front limited by creek structure.....	70
4.5.4	Geographical variation in <i>Sesarma</i> front patterns.....	70
4.5.5	Conclusion.....	71
Chapter 5: General discussion		72

References.....	77
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LIST OF FIGURES

Figure 2.1 Distinctive zonation at creek heads.....	15
Figure 2.2 Field measurements of the four creek head zones in South Carolina.....	21
Figure 2.3 Structural Equation Model of crab effects on <i>Spartina</i> production and sediment characteristics in South Carolina.....	22
Figure 2.4 Densities of crabs in four creek head zones.....	23
Figure 2.5 Percolation rates in four marsh zones.....	24
Figure 2.6 Decomposition rates of <i>Spartina</i> roots and rhizomes.....	25
Figure 2.7 Excavation rates of crabs in mesocosms.....	26
Figure 2.8 Potential yearly excavation rates of marsh crabs.....	27
Figure 2.9 Effect of <i>Sesarma</i> density on <i>Spartina</i> productivity.....	28
Figure 2.10 Effects of vegetation removal on creek growth.....	29
Figure 3.1 Mortality rate of <i>Sesarma</i> in the presence of large predatory crabs.....	46
Figure 3.2 Non-consumptive effects of <i>P. herbstii</i> on how <i>Sesarma</i> affects <i>Spartina</i>	47
Figure 3.3 Non-consumptive effects of <i>E. limosum</i> on how <i>Sesarma</i> affects <i>Spartina</i> ...	48
Figure 3.4 <i>Sesarma</i> feeding preferences for above- and below-ground <i>Spartina</i> plant tissue.....	49

Figure 3.5 Effects of <i>Sesarma</i> feeding location on <i>Spartina</i> biomass and <i>Sesarma</i> mortality rate.....	50
Figure 4.1 Distinctive zonation at creek heads and schematic for artificial creek manipulation experiment.....	60
Figure 4.2 Surface and subsurface temperature at six marsh zones.....	63
Figure 4.3 Hydrogen sulfide concentrations in burrow water at six marsh zones.....	64
Figure 4.4 Dissolved oxygen concentrations in burrow water at six marsh zones.....	65
Figure 4.5 Burrow density in July 2012, July 2015, and change in the number of burrows at the control, unmanipulated control, and pipe treatments.....	66
Figure 4.6 Number of <i>S. reticulatum</i> counted in the control, unmanipulated control, and pipe treatments in July 2015.....	67
Figure 4.7 Change in marsh elevation at the control, unmanipulated control, and pipe treatments after three years.....	67
Figure 5.1 Conceptual diagram illustrating the abiotic and biotic drivers of tidal creek formation in Southeastern US Atlantic salt marshes.....	74

Chapter 1

General Introduction

1.1 Overview

How organisms and ecological systems respond to global change is of great interest to ecologists (Peñuelas and Filella 2001, Root et al. 2003, Schmitz et al. 2003, Gonzalez et al. 2010). These responses may or may not be beneficial because there might be positive feedback that would make global change worse than expected or negative feedback that would minimize the effects. Therefore, it is crucial to understand the organismal and ecosystem responses to global changes for the conservation and restoration of habitats

Coastal tidal marshes provide a variety of critical ecosystem services, including erosion buffers, nursery grounds, carbon sequestration, and biochemical filtering (Valiela and Teal 1979, Knutson et al. 1982, Boesch and Turner 1984, Chmura et al. 2003, Cullinan et al. 2004). However, anthropogenic and global changes are threatening these important ecosystems (Silliman et al. 2009, Nicholls and Cazenave 2010). It is important to understand how global changes are mediating changes in tidal marshes, in order to better understand and manage these valuable ecosystems.

1.2 Global change affecting salt marshes

The close proximity of coastal wetlands to the sea make them extremely vulnerable to global changes. Forecasted acceleration in the rate of sea-level rise (SLR), which is already occurring in several regions, threatens ~140 million hectares of salt marshes worldwide (Nydyck et al. 1995, Mitsch and Gosselink 2000, Church and White 2006, Church and White 2011). A common paradigm is that salt marshes respond to SLR by establishing a new equilibrium elevation of the marsh platform through vertical accretion resulting from increased plant productivity and higher rates of inorganic

deposition (Morris et al. 2002). Under this model, if sea-level rise exceeds the rate of marsh accretion, the result will be the submergence and disintegration of the marsh platform (Redfield 1965, Mudd et al. 2010, Mudd et al. 2013). While the submergence paradigm could be observed along the Louisiana coast (Morton et al. 2005), it does not fully explain other possible marsh responses such as increasing tidal creek networks observed in other regions (Shi et al. 1995, Hughes et al. 2009).

Marsh platforms along the Atlantic Coast of the United States remain relatively preserved through the formation of new tidal channels. These new channels enhance the drainage efficiency of the marsh platform and allows it to accommodate the greater tidal prism (the amount of water flowing on and off the marsh on each tide) (Shi et al. 1995, Hughes et al. 2009, D'Alpaos et al. 2010). The mechanisms mediating the formation and expansion of these tidal creeks, however, are not fully understood. Past studies of creek growth, identified physical factors such as topology, accumulation of organic matter, changes in hydrology, and storm events as key drivers of creek change (Cahoon and Reed 1995, Perillo et al. 1996, Kuhn et al. 1999). Biological factors, however, may also play an important role in creek development (Perillo and Iribarne 2003, Paramor and Hughes 2004, Hughes et al. 2009, Wilson et al. 2012). For example, burrowing organisms may increase erosion and water flow, and thereby mediate creek formation (Perillo et al. 1996, Perillo and Iribarne 2003, Hughes et al. 2009, Wilson et al. 2012), and herbivory on plants has been implicated in the widening of existing creeks (Holdredge et al. 2008, Bertness et al. 2009). Therefore, a comprehensive examination of both abiotic and biotic factors is necessary to fully understand the rapid creek growth along the southeastern Atlantic Coast.

1.3 Ecosystem engineers

Ecosystem engineers, organisms that alter the environment by creating, maintaining, modifying, or destroying habitats (Jones et al. 1994, Jones et al. 1997, Wright et al. 2002, Byers et al. 2006), are important in many habitats. Plants are often foundational ecosystem engineers, in that they create new habitats through trapping sediments and preventing soil erosion (Wood and Armitage 1997, Pennings et al. 2001, D'Alpaos et al. 2007, Marani et al. 2013). In tidal marshes, plants enhance sedimentation by directly intercepting sediment and by baffling tidal flow, which increases deposition of suspended sediments (Redfield 1965, 1972, Morris et al. 2002). Plants may also improve conditions for other organisms by ameliorating high temperatures and wave stress (Caspers 1964, Hacker and Bertness 1999).

Animals often act as secondary ecosystem engineers. For example, burrowing organisms increase primary production in wetlands by oxygenating the soil (Montague 1982, Bertness 1985, Lohrer et al. 2004, Holdredge et al. 2010), and marsh bivalves fertilize plants and increase sedimentation by depositing feces and pseudofeces (Jordan and Valiela 1982, Bertness and Grosholz 1985). If the presence of secondary engineers depends on the presence of primary engineers such as plants, this would represent a “facilitation cascade” (Altieri et al. 2007).

In other cases, however, animals may harm plants. In salt marshes, herbivorous geese (Kotanen and Jefferies 1997), snails (Silliman and Bertness 2002, Silliman et al. 2005), and crabs (Holdredge et al. 2008, Bertness et al. 2009, Holdredge et al. 2010, Bertness et al. 2014) can suppress marsh vegetation. Moreover, burrowing crabs that are not herbivorous might incidentally damage plant roots and rhizomes while burrowing. In

either case, by harming the foundational ecosystem engineer, herbivores, and burrowing engineers may alter the services provided by the foundational engineer, and affect marsh responses to global change.

1.4 The focus of this dissertation

The work described in this dissertation was conducted in tidal salt marshes at the Santee Delta, South Carolina and at Sapelo Island, Georgia, USA. Marshes in this region are typical of southeastern U.S. Atlantic Coast (Pomeroy and Wiegert 1981), with lower and intermediate marsh elevations dominated by the grass *Spartina alterniflora*. In addition, the marshes in this region are responding to sea-level rise through the expansion of tidal creek networks (Hughes et al. 2009). Studies by Hughes (2009) and Wilson (2012) suggested that biology may play an important role in the formation and growth of tidal creeks along the southern Atlantic Bight. In particular, the authors found that crab herbivory and crab burrowing activities increased the erodibility of sediment at the leading edge of creeks, allowing the creeks to grow headward into the marsh. These results support past speculations from South American studies that crab bioturbation can greatly influence ecosystem processes on salt marshes (Perillo and Iribarne 2003, Minkoff et al. 2006, Escapa et al. 2007). Nevertheless, we need a mechanistic understanding of the processes involved in the formation of tidal creeks in order to predict how these important ecosystems will change in the coming years.

Therefore, I explored the underlying mechanisms that drive tidal creek growth in Southeastern Atlantic US marshes. In particular, I addressed three topics. In Chapter 2, I evaluated the relative importance of common marsh crabs on creek growth, as well as, the potential mechanisms which crabs mediate creek growth. In Chapter 3, I then

examined the factors that affect the feeding preferences of a common herbivorous crab, *Sesarma reticulatum*, found at creek heads. In Chapter 4, I evaluated the factors driving the aggregation and movement of this herbivorous crab.

Chapter 2: Interactions between ecosystem engineers drive creek formation in sinking salt marshes. Crabs are ecosystem engineers that can alter ecosystem processes on the marsh platform and they may play an important role in the widening and growth of tidal creeks (Perillo et al. 1996, Perillo and Iribarne 2003, Bertness et al. 2009, Hughes et al. 2009, Wilson et al. 2012). However, there are a number crab species in salt marshes—do all have these effects on creek development? Answering this question requires a better understanding of the mechanisms by which crabs mediate creek growth. To address this, I compared four crab species common at the heads of rapidly-growing marsh creeks in the southeastern United States to evaluate the relative importance of each on creek growth via four potential mechanisms: 1) direct excavation of sediments, 2) removal of plant stems that baffle water flow and plant roots that bind sediments, 3) subterranean erosion through burrow networks, and 4) decomposition of subsurface soils due to oxygen penetration through burrow networks.

In this chapter, which is in press in *Ecology*, Dr. Kazik Wieski provided 2009 field measurements of creek heads in South Carolina as well as the structural equation model. I did all of the other field work and statistical analyses and was the lead author on the manuscript.

Chapter 3: Predators mediate above- versus below-ground herbivory in a salt marsh crab. The presence of predators often leads to changes in prey feeding behavior

(Frank 2008, Ripple et al. 2014, Rizzari et al. 2014). The trade-off between foraging behavior and predation risk may result in a trophic cascade that can have important effects on ecosystem processes (Schmitz et al. 2008). The burrowing crab *Sesarma reticulatum* (henceforth *Sesarma*) is a common herbivore (Grosner 1979), feeding on leaves and below-ground rhizomes of the dominant grass *Spartina alterniflora* (henceforth *Spartina*) (Crichton 1960, Bertness et al. 2009, Coverdale et al. 2012). *Sesarma* constructs large burrow networks (Crichton 1960) that may impact marsh biogeochemistry and geomorphology independent of crab effects on plants (Fei et al. 2014). Thus, changes in *Sesarma* burrowing activities could have important ramifications for marsh function. However, we do not know whether *Sesarma* shifts between feeding above- and below-ground in response to predation threats. Therefore, I conducted mesocosm and laboratory experiments to examine the effects of predators on *Sesarma* feeding preferences and whether predator-induced changes in feeding affect burrowing rates and *Spartina* productivity. This chapter is currently in review as a manuscript in Ecology.

Chapter 4: Abiotic conditions explain asymmetric movement of consumer fronts associated with creek heads in salt marshes. High densities of consumers can quickly deplete local resources, forcing consumers to aggregate and form a front along edges of the remaining food resources (Silliman et al. 2005, Silliman et al. 2013). At high densities, *Sesarma* fronts can totally denude an area of *Spartina*, effecting biodiversity and ecosystem processes (Altieri et al. 2012, Vu et al. 2016). The consumer fronts created by *Sesarma* in Southeastern Atlantic US salt marshes are unique. First, the *Sesarma* front is tightly associated with a physical structure (the creek head), which it directly manipulates (Vu et al. 2016). Second, rather than expanding as do many other consumer

fronts (Silliman et al. 2013), the *Sesarma* front remains compact, moving forward with the creek head as it erodes through the marsh. Third, the front moves only in one direction—crabs do not colonize the back of the creek head even though their food plant *Spartina* vigorously recolonizes these areas behind the crab consumer front. Why *Sesarma* fronts are so tightly constrained to the eroding front edge of creek heads is unclear. It is likely that rapidly-flowing water at creek head creates cooler areas with higher dissolved oxygen concentrations and lower concentrations of toxic sulfides. Therefore, I measured abiotic conditions in natural creek heads to test the hypothesis that abiotic conditions were favorable for crabs at the leading edge of the creek head but not the trailing edge, explaining the asymmetrical movement of the front. I also created artificial creek heads in areas that lacked them to experimentally test the hypothesis that the high water flows adjacent to creek heads (as opposed to some other factor) create conditions that provide superior habitat for *Sesarma*.

By studying the interactions between crabs and plant ecosystem engineers (Chapter 2), and physical factors mediating preference, aggregation and movement of an herbivorous crab common to creek heads (Chapters 3 and 4), this work provides new insights into complex interactions between abiotic and biotic factors on salt marshes. Understanding the feedback loops between crabs, plants, and marsh geomorphology is crucial in determining and predicting the resilience of these important ecosystems in the face of sea-level rise.

Chapter 2

Interactions between ecosystem engineers drive creek formation in sinking salt marshes

2.1 Abstract

Ecosystem engineers affect different organisms and processes in multiple ways at different spatial scales. Moreover, similar species may differ in their engineering effects for reasons that are not always clear. We examined the role of four species of burrowing crabs (*Sesarma reticulatum*, *Eurytium limosum*, *Panopeus herbstii*, *Uca pugnax*) in engineering tidal creek networks in salt marshes experiencing sea level rise. In the field, crab burrows were associated with heads of eroding creeks and the loss of plant (*Spartina alterniflora*) stems. *S. reticulatum* was closely associated with creek heads, but densities of the other crab species did not vary across marsh zones. In mesocosm experiments, *S. reticulatum* excavated the most soil and strongly reduced *S. alterniflora* biomass. The other three species excavated less and did not affect *S. alterniflora*. Creek heads with vegetation removed to simulate crab herbivory grew significantly faster than controls. Percolation rates of water into marsh sediments were 10 times faster at creek heads than on the marsh platform. Biomass decomposed two times faster at creek heads than on the marsh platform. Our results indicate that *S. reticulatum* increases creek growth by excavating sediments and by consuming plants, thereby increasing water flow and erosion at creek heads. Moreover, it is possible that *S. reticulatum* burrows also increase creek growth by increasing surface and subsurface erosion, and by increasing decomposition of organic matter at creek heads. Our results show that the interaction between crab and plant ecosystem engineers can have both positive and negative effects. At a small scale, in contrast to other marsh crabs, *S. reticulatum* harms rather than benefits plants, and increases erosion rather than marsh growth. At a large scale,

however, *S. reticulatum* facilitates the drainage efficiency of the marsh through the expansion of tidal creek networks, and promotes marsh health.

Keywords: crab burrowing, crab herbivory, creek growth, marsh geomorphology, marsh hydrology, *Sesarma*, soil erosion.

2.2 Introduction

Ecosystem engineers, organisms that alter the environment by creating, maintaining, modifying, or destroying habitats (Jones et al. 1994, Jones et al. 1997, Wright et al. 2002, Byers et al. 2006), are important in many habitats. Plants are often foundational ecosystem engineers, in that they create new habitats through trapping sediments and preventing soil erosion (Wood and Armitage 1997, Pennings et al. 2001, D'Alpaos et al. 2007, Marani et al. 2013). In tidal marshes, plants enhance sedimentation by directly intercepting sediment and by baffling tidal flow, which increases deposition of suspended sediments (Redfield 1965, 1972, Morris et al. 2002). Plants may also improve conditions for other organisms by ameliorating high temperatures and wave stress (Caspers 1964, Hacker and Bertness 1999).

Animals often act as secondary ecosystem engineers. For example, burrowing organisms increase primary production in wetlands by oxygenating the soil (Montague 1982, Bertness 1985, Lohrer et al. 2004, Holdredge et al. 2010), and marsh bivalves fertilize plants and increase sedimentation by depositing feces and pseudofeces (Jordan and Valiela 1982, Bertness and Grosholz 1985). If the presence of secondary engineers depends on the presence of primary engineers such as plants, this would represent a “facilitation cascade” (Altieri et al. 2007).

In other cases, however, animals may harm plants. In salt marshes, herbivorous geese (Kotanen and Jefferies 1997), snails (Silliman and Bertness 2002, Silliman et al. 2005), and crabs (Holdredge et al. 2008, Bertness et al. 2009, Holdredge et al. 2010, Bertness et al. 2014) can suppress marsh vegetation. Moreover, burrowing crabs that are not herbivorous might incidentally damage plant roots and rhizomes while burrowing. In either case, by harming the foundational ecosystem engineer, herbivores and burrowing engineers may alter the services provided by the foundational engineer, and affect marsh responses to global change.

The most important global change affecting marshes is sea-level rise (Mitsch and Gosselink 2000, Church and White 2006, Meehl 2007), which can drown marshes by increasing the duration and depth of tidal water inundating the marsh at high tide (Morris et al. 2002, Mudd et al. 2010). One way that salt marshes respond to sea-level rise is by expanding creek networks to accommodate the greater tidal prism (the amount of water flowing on and off the marsh on each tide) (Hughes et al. 2009, D'Alpaos et al. 2010). The mechanisms mediating the formation and expansion of new tidal creeks, however, are not fully understood. Past studies of creek growth identified physical factors such as topology, accumulation of organic matter, changes in hydrology, and storm events as key drivers of creek change (Cahoon and Reed 1995, Perillo et al. 1996, Kuhn et al. 1999). Biological factors, however, may also play an important role in creek development (Perillo and Iribarne 2003, Paramor and Hughes 2004, Hughes et al. 2009, Wilson et al. 2012). For example, crab burrowing may increase erosion and water flow, and thereby mediate creek formation (Perillo et al. 1996, Perillo and Iribarne 2003, Hughes et al. 2009, Wilson et al. 2012), and crab herbivory on plants has been implicated in the

widening of existing creeks (Holdredge et al. 2008, Bertness et al. 2009). However, there are a number crab species in salt marshes—do all have these effects on creek development? Answering this question requires a better understanding of the mechanisms by which crabs mediate creek growth.

We compared four crab species common at the heads of rapidly-growing marsh creeks in the southeastern United States to evaluate the relative importance of each on creek growth via four potential mechanisms: 1) direct excavation of sediments, 2) removal of plant stems that baffle water flow and plant roots that bind sediments, 3) subterranean erosion through burrow networks, and 4) decomposition of subsurface soils due to oxygen penetration through burrow networks. Our results show that the crab *Sesarma reticulatum* is a more powerful ecosystem engineer than the other species because it is locally abundant, potentially affects creek growth through all four mechanisms, and is more proficient at each mechanism than the other species.

2.3 Materials and Methods

2.3.1 Study Sites and Species. We worked in South Carolina and Georgia, USA. Marshes in both regions are typical of the southeastern U.S. Atlantic Coast (Pomeroy and Wiegert 1981), with lower and intermediate marsh elevations dominated by the grass *Spartina alterniflora* (henceforth *Spartina*). Common crabs in both areas include the herbivore *Sesarma reticulatum* (henceforth *Sesarma*), predators *Eurytium limosum* (henceforth *Eurytium*) and *Panopeus herbstii* (henceforth *Panopeus*), and detritivore *Uca pugnax* (henceforth *Uca*) (Teal 1958). Both study sites contain headward-eroding tidal creeks (Fig. 2.1) in locations where the marsh platform was previously characterized by low creek density. Average headward erosion rates (~1.9 m/y) were similar at both

locations (Hughes et al. 2009, Wilson et al. 2012). The heads of these growing creeks consist of a fan-shaped depression up to 50 cm deep that can be divided into zones characterized by distinct sediment and vegetative characteristics (Fig. 2.1). The center of the creek head (the “mud zone”) has soft sediments, multiple small crab burrows, and no vegetation. The mud zone is migrating inland into the “dead zone”, a 1-2 m wide band of firm sediment perforated by abundant crab burrows, and numerous dead *Spartina* stems. The dead zone is migrating inland into the “live zone”, a halo around the creek head that extends 15-20 m to each side and 20-40 m inland. It has firm sediments, a high density of crab burrows, and abundant live *Spartina* plants. The surrounding marsh platform, which makes up the majority of the area, has firm sediments, a low density of crab burrows, and abundant live *Spartina* plants. As the creek erodes headward into the marsh platform, sediment is deposited along the terminal borders of the mud zone and robust stands of *Spartina* recolonize the area. This area (the “revegetated zone”) is characterized by soft sediment, a low density of crab burrows, and a high density of live *Spartina*. Based on these patterns, previous workers concluded that marsh crabs facilitate creek growth by killing plants and increasing erosion at the leading edge of the creek head (Hughes et al. 2009, Wilson et al. 2012); however, direct evidence of these putative mechanisms was lacking.

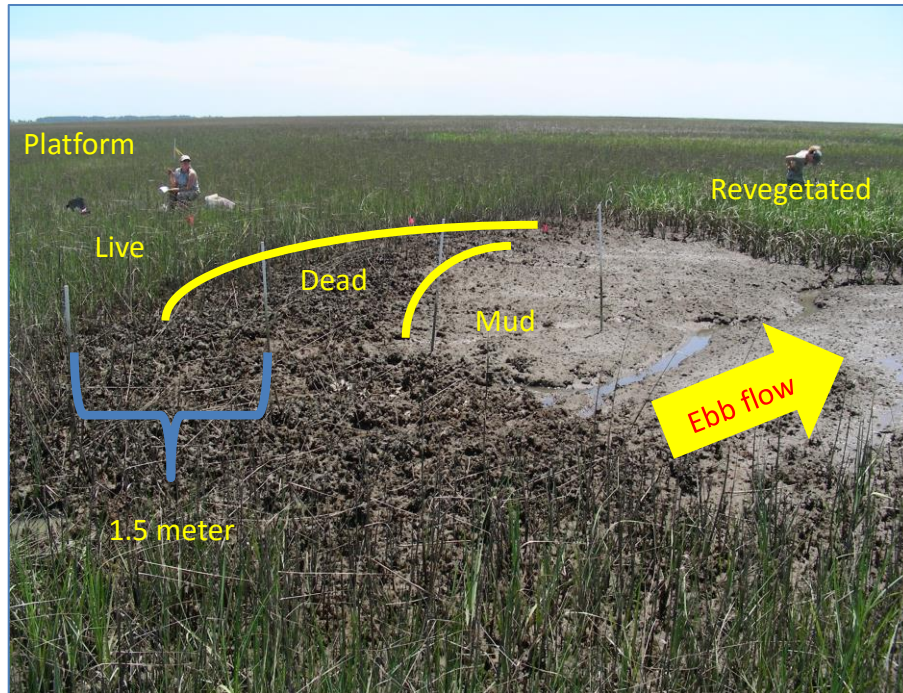


Figure 2.1 Distinctive zonation at creek heads. Zones were characterized by sediment characteristics, burrow densities, and *Spartina* shoot densities. The mud zone at the center of the creek head has soft sediments, multiple small crab burrows, and no vegetation. The dead zone is a 1-2 m wide band of firm sediments perforated by abundant large burrows, supporting numerous standing-dead *Spartina* stems. The live zone is characterized by firm sediments, a high density of crab burrows, and live *Spartina* stems. The surrounding marsh platform is characterized by firm sediments, a low density of crab burrows, and a high density of live *Spartina* stems. Creek heads grow forward into the marsh platform but sediment is deposited at the back and *Spartina* recolonizes. We refer to this area as the revegetated zone which is characterized by soft sediment, low density of crab burrow, and high density of live *Spartina* stems.

2.3.2 Relationships between creeks, plants, and crabs in the field. We conducted field surveys of creeks in Cape Romain, South Carolina (31.4775° N, 81.2417° W). To measure creek growth, we placed 2 PVC stakes at the heads of eight creeks, in line with the axis of the major creek draining the head (and so in the predicted direction of creek growth) and monitored the distance from each stake to the border of the dead/mud zones. Stakes were initially placed in July 2007, with additional measurements taken in May, June or July of 2008-2011. Each year, additional stakes were placed further back on the marsh platform to accommodate continued creek growth.

We measured burrow and stem densities in July 2007, June 2008, and July 2009 in four marsh microhabitats: the marsh platform in between creek heads, and the live, dead, and mud zones of creek heads. In 2008, because the creek head had moved inland, we sampled the new location of the live zone, a new location on the marsh platform, and also re-sampled the 2007 live, dead, and mud zones. In 2009, because the creek head continued to move, we again sampled the new location of the live zone, and a new location on the marsh platform, and also re-sampled the 2007 and 2008 live zones, and the 2007 dead and mud zones. At each zone of each creek, we sampled three 0.25 x 0.25 m quadrats, counting crab burrows, live stems and dead stems; the three quadrats were averaged to give a single data point for each zone at each creek head.

We collected cores for below-ground biomass and bulk density in 2007 only. We collected two cores (7.6 cm diameter, 15 cm deep) from each zone at each creek head. One was washed through a sieve to collect live and dead roots and rhizomes, which were dried at 60° C and weighed. The other core was dried at 50° C, weighed, and bulk density calculated as g/cm³. We compared data among marsh zones using one-way ANOVAs and performed post-hoc means comparisons using Tukey HSD. In addition, we analyzed relationships between crabs, *Spartina* live and dead stems, and soil traits using structural equation modeling (SEM). SEM is a multivariate method to analyze direct and indirect effects in an a-priori identified system of relationships (Grace 2008).

We compared crab species composition and density at four locations (dead zone, border between dead and live zones, live zone, and marsh platform) at nine creek heads in July 2010, with a 25 cm diameter PVC tube that was quickly placed on the marsh and pushed ~30 cm into the sediment (below the depth that burrows extended at this site).

The soil inside of the PVC tube was processed by hand to recover and identify the crabs. We compared crab species composition and densities among marsh zones using one-way ANOVAs with Tukey HSD post-hoc means comparisons.

2.3.3 Percolation rates. Crab burrowing may increase the rate at which water flows through marsh sediments, potentially increasing subsurface erosion. To measure the rate at which water infiltrated into sediments (percolation rates), we inserted bottomless, 2.5 cm diameter, graduated cylinders 2-4 cm into the mud at the Cape Romain study site in July 2009, either over a burrow opening or at a location without burrow openings, and filled them with water. We recorded the water height again when it dropped by ≥ 30 ml, or after 45 minutes, and calculated percolation rates as ml/min. If the cylinder emptied faster than we could fill it, the elapsed time was set at 0.1 minute. We compared percolation rates among marsh zones and treatments (with or without burrows) using ANOVA.

2.3.4 Decomposition of below-ground biomass. Crab burrowing may increase the decomposition rate of below-ground biomass by increasing oxygen concentrations in the soil (Bertness and Miller 1984, Otani et al. 2010, Thomas and Blum 2010). To compare decomposition rates among creek head zones and the marsh platform, we deployed litter bags (1 mm mesh) filled with ~25 g of dried *Spartina* roots and rhizomes at a depth of 10 cm below the marsh surface at six zones (platform, live, live/dead, dead, mud, and revegetated) of a single creek head on Sapelo Island, GA (31.4775° N, 81.2417° W) in November, 2012 (n=10 bags / zone). Bags were collected after 247 days in July 2013, and remaining litter rinsed clean of sediments, dried, and weighed. We compared

decomposition rates among marsh zones using one-way ANOVA with Tukey HSD post-hoc means comparisons.

2.3.5 Sediment excavation and herbivory. To compare the impact of four common crab species on sediment excavation and *Spartina* above-ground and below-ground biomass, we conducted a mesocosm experiment on Sapelo Island, GA. We filled sixty 20-liter buckets with marsh soil in early May 2009. Small holes on the sides of the buckets at the soil level (8 cm below the top of the bucket) and 15 cm below the soil surface (13.7 cm from the bottom of the bucket) allowed water to slowly drain from the upper soils. Five *Spartina* plants, each consisting of a single shoot with roots and rhizomes, were planted in each bucket. Buckets were placed in outdoor water tables filled with 15 cm deep of running seawater that moderated temperature fluctuations. Plants were watered with fresh water for two weeks to allow them to recover from the transplanting process. Thereafter, buckets were filled and drained with seawater twice daily to simulate tides. Plants were allowed to acclimate for an additional three weeks prior to the start of the experiment.

To initiate the experiment, we stocked the buckets with crabs in June 2009. *Sesarma* and *Uca*, which naturally occur at high densities, were stocked at 0, 1, 2, 4 or 8 crabs per bucket (n=4 buckets/species/density). *Eurytium* and *Panopeus*, which do not naturally occur at high densities, were stocked at 0 or 2 crabs per bucket (n=5 buckets/species/density). The experiment ran for 63 days. During this time, predatory crabs were fed dead *Uca* (1 *Uca* per bucket every 2 days); whereas crabs in the *Uca* and *Sesarma* treatments were allowed to feed normally on sediments and plants present within the buckets. Dead fiddler crabs were also placed into controls (0 crab treatment) for the

predatory crab treatment to account for any effect the added nitrogen might have on *Spartina* growth (we observed no measurable effect). Dead experimental crabs were replaced when discovered. We collected all sediment that crabs excavated to the surface daily, dried it for four days at 60° C, and weighed it. We measured the height and number of green leaves of each *Spartina* shoot at the beginning and end of the experiment. At the end of the experiment, we harvested, dried and weighed *Spartina* shoots, rhizomes and roots. We evaluated the effect of crab density on excavation rates using regression. We compared excavation rates among crab species using ANOVA with Tukey HSD post-hoc mean comparisons.

2.3.6 Does loss of vegetation increase creek growth? To test the hypothesis that the loss of *Spartina*, such as we observed at creek heads, would affect creek growth, we conducted a field experiment at the Cape Romain study site. We selected six creeks that branched into two main tributary channels with distinct creek heads. The two heads of each creek were randomly assigned to control or herbicide treatments by flipping a coin. We applied herbicide (glyphosate) to a 4x5 m plot that extended from the border between the live and dead zones 4 m into the live zone, in the center of each removal creek head. This plot represented only a fraction (~ 25 %) of the live zone at the creek head, but was centrally located along the primary axis of the creek. Herbicide was applied once a year for three years, and was effective at removing >80% of the live *Spartina* shoots within each plot. The herbicide plot was moved 1-2 m into the marsh platform each year to accommodate growth of the creek head. To assess creek growth, we measured the distance from the border between the dead and mud zones to a fixed point (a PVC stake)

on the marsh platform at the head of each creek. We compared changes in creek growth rate between the two treatments using a paired t-test.

2.4 Results

2.4.1 Relationships between creeks, plants, and crabs in the field. From July 2007 to July 2011, the eight measured creeks in SC headward eroded an average distance of 7.47 ± 2.10 (SD) m at an average rate of 1.87 ± 0.53 (SD) m y⁻¹. Crab burrows were > 5 times more abundant in the creek head zones than in the marsh platform in 2007 ($F_{3,42}=43.36$, $p<0.0001$) (Fig. 2.2A). Live *S. alterniflora* stems were most abundant on the marsh platform in 2007, decreasing by 30 % in the live zone and by 80 % in the dead zone, and were absent in the bare zone ($F_{3,41}=42.27$, $p<0.0001$) (Fig. 2.2B). As creek heads eroded landward, the dead zone encroached on first the 2007 and then the 2008 live-zone plots, and live-stem densities dropped (Fig. 2.2C). Dead stems did not differ in abundance among the platform, live, and dead zones, but were absent in the mud zone (data not shown).

Below-ground biomass of live and dead roots and rhizomes was greatest in the marsh platform, declined by 30-40 % in the live and dead zones and by >80 % in the bare zone ($F_{3,41}=9.45$, $p<0.0001$) (Fig. 2.2D). Sediment bulk density was similar in platform and live zones, but declined 20 % in the dead zone, then partially recovered in the mud zone ($F_{3,42}=2.49$, $p=0.07$) (Fig. 2.2E). This pattern was only marginally significant in ANOVA ($p=0.07$) and so should be interpreted cautiously, but the means comparisons suggested that the dead zone was significantly different from the platform.

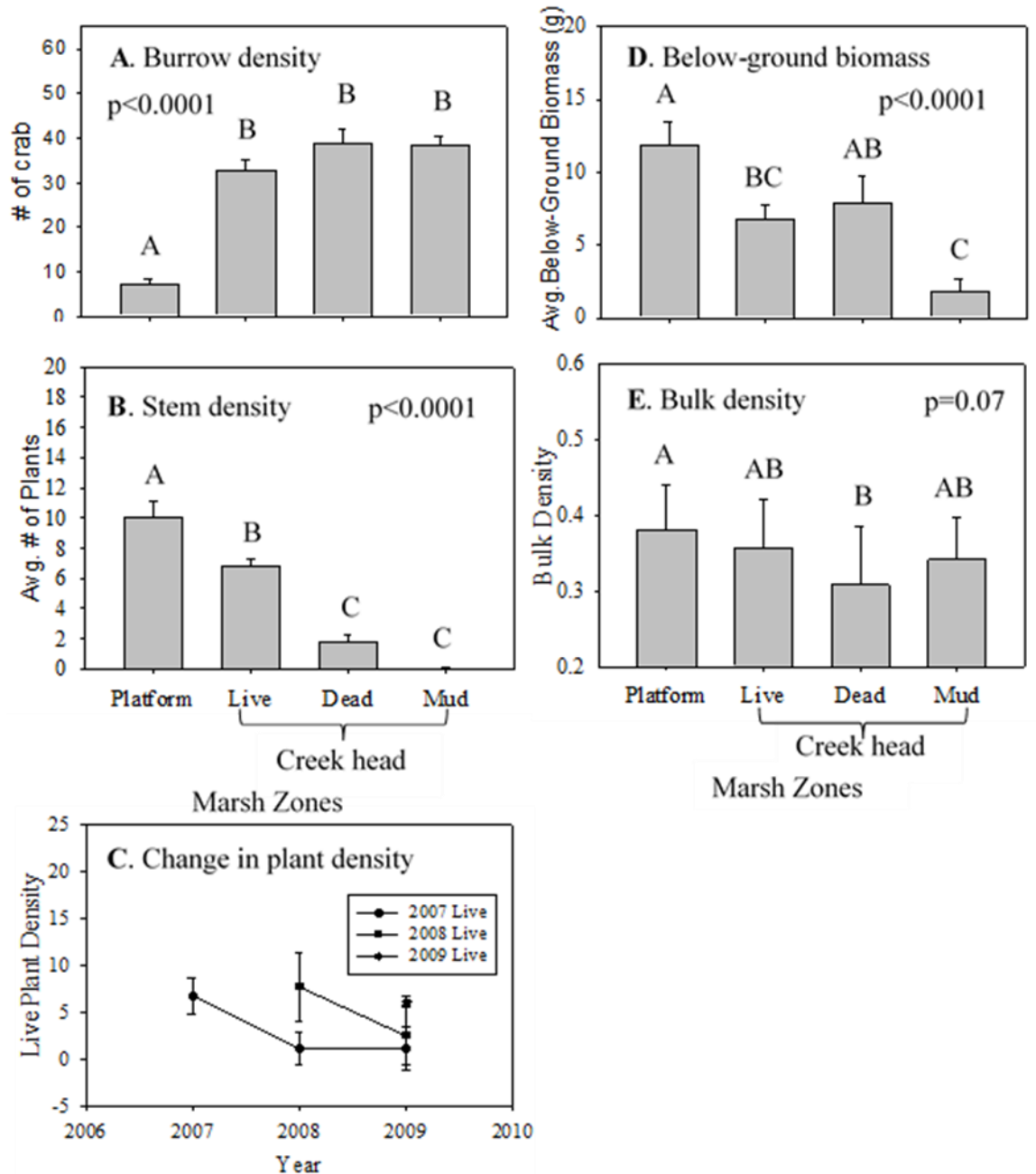


Figure 2.2 Field measurements of the four creek head zones in SC. A, crab densities in 2007 ($F_{3,42}=43.36$, $p<0.0001$); B, plant density ($F_{3,41}=42.27$, $p<0.0001$); C, change in plant density from 2007-2009; D, below-ground biomass in 2007 ($F_{3,41}=9.45$, $p<0.0001$); E, Bulk density in 2007 ($F_{3,42}=2.49$, $p=0.07$). Bars indicate means $\pm$ 1 SE. Letters above bars indicate means that are significantly different (Tukey HSD).

Analysis of these data using SEM indicated that high densities of crab burrows were associated with low densities of live *Spartina* stems, low below-ground biomass of *Spartina*, and low-soil bulk density (Chi square/df=0.72, $p=0.58$, a non-significant p -value indicates that the model is consistent with the data) (Fig. 2.3). Density of dead *Spartina* shoots was positively related to density of live shoots. Both live and dead shoot densities positively co-varied with below-ground *Spartina* biomass.

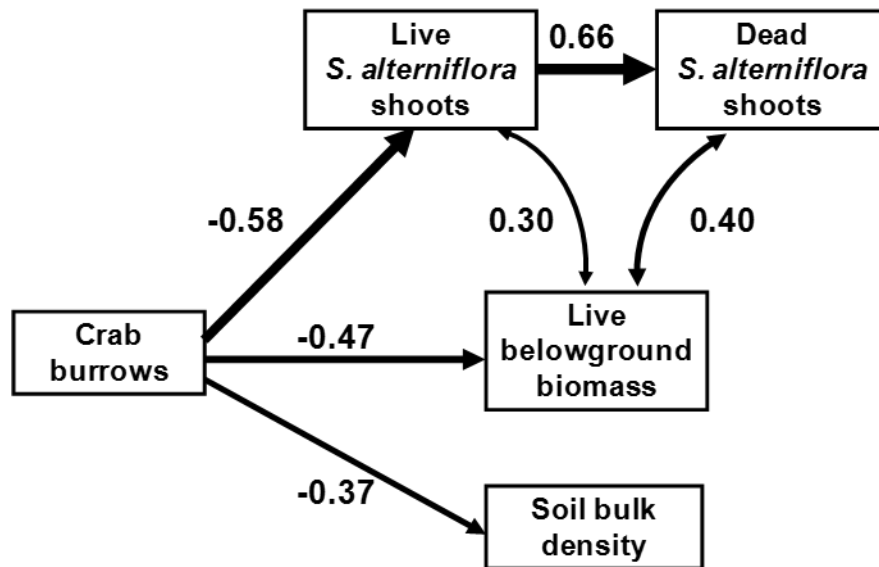


Figure 2.3 SEM model of crab effects on *S. alterniflora* production and sediment characteristics in South Carolina. The model is consistent with the data ($p = 0.58$, Chi square/df = 0.72). Path coefficients describe standardized values showing relative effects of variables upon each other. Arrow width is proportional to the strength of the path coefficient; one headed arrows represent causal relationships; two headed arrows represent correlations; all paths are significant ($p < 0.05$).

The densities of *Uca*, ($F_{3,32}=0.51$, $p=0.67$), *Eurytium*, and *Panopeus*, ($F_{3,32}=1.83$, $p=0.16$), did not differ between the marsh platform and the creek head zones (Fig. 2.4 A and B). *Uca* was common throughout the marsh whereas *Eurytium* and *Panopeus* were rare throughout. *Sesarma* had low populations on the marsh platform but was abundant in

the creek head zones ($F_{3,32}=13.09$, $p<0.0001$) (Fig. 2.4 C), with densities at the border between the live and dead zones 35 times greater than on the marsh platform.

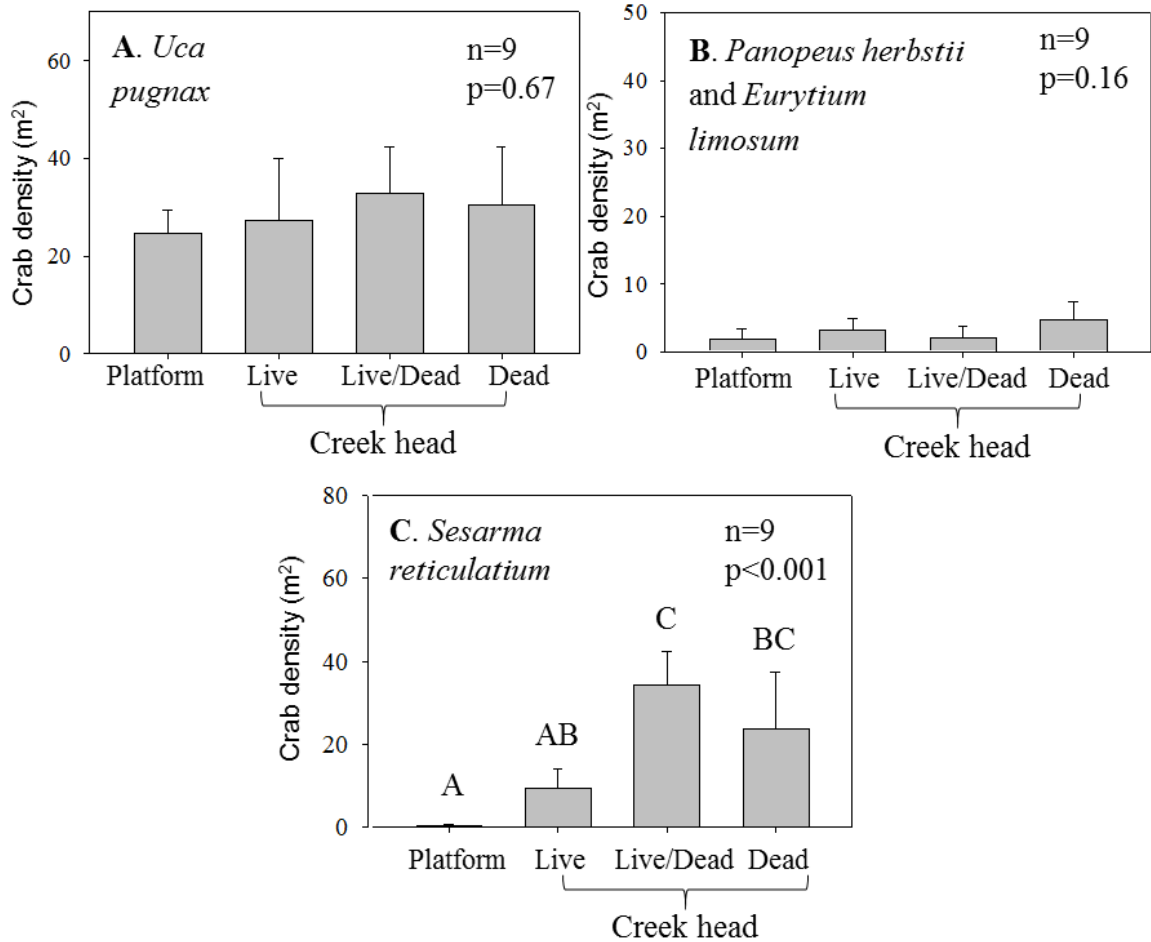


Figure 2.4 Densities of crabs in four creek head zones in SC. A, *Uca pugnax* (ANOVA, $F_{3,32}=0.51$, $p=0.67$); B, *Panopeus herbstii* and *Eurytium limosum* (combined because both were rare) ($F_{3,32}=1.83$, $p=0.16$); C, *Sesarma reticulatum* (ANOVA, $F_{3,32}=13.09$, $p<0.0001$). Live/Dead zones are the border between the live and dead zones. Bars indicate means $\pm$ 1 SE. Letters above bars indicate means that are significantly different (Tukey HSD).

2.4.2 Percolation rates. Percolation rates were generally low (~ 0.32 ml/minute) away from burrows, but more rapid over burrow openings (Marsh zone, $F_{3,32}=80.9$ $p<0.0001$; Burrows, $F_{1,72}=962.1$ $p<0.0001$; Interaction, $F_{3,72}=81.1$ $p<0.0001$) (Fig. 2.5).

Measurements over burrow openings (mostly *Uca* burrows) on the marsh platform were moderate (~100 ml/min), and percolation rates over burrow openings (mostly *Sesarma* burrows) at the creek head zones were extremely rapid (~1000 ml/min), with water in every replicate draining through the cylinders as fast as it was added, and emerging from other burrow mouths further down the creek head slope.

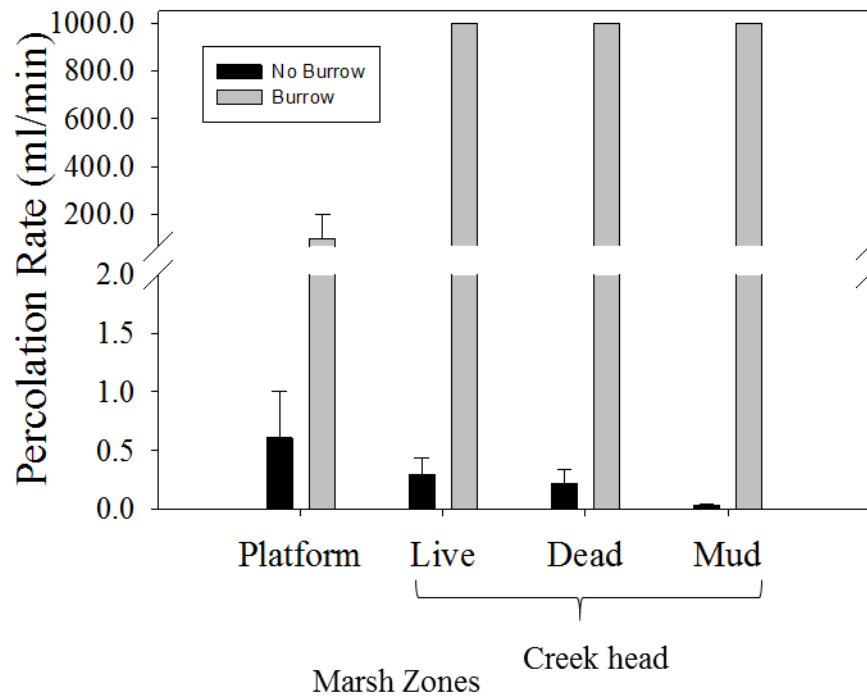


Figure 2.5 Percolation rates in four marsh zones, with rates measured over burrow mouths or away from burrows. * Indicates all readings were the maximum possible. Marsh zone, $F_{3,72}=80.9$, $p<0.0001$; Burrows, $F_{1,72}=962.1$, $p<0.0001$; Interaction, $F_{3,72}=81.1$, $p<0.0001$.

2.4.3 Decomposition of below-ground biomass. Decomposition of buried *Spartina* litter was slowest (~10 % biomass loss) on the marsh platform ($F_{5,54}=10.9$, $p<0.0001$) (Fig. 2.6). Decomposition increased to maximum rates in the heavily-burrowed zones at the leading edge of the creek head (~23 % biomass loss), and

decreased toward the trailing edge of the creek head and the revegetated area behind the creek head.

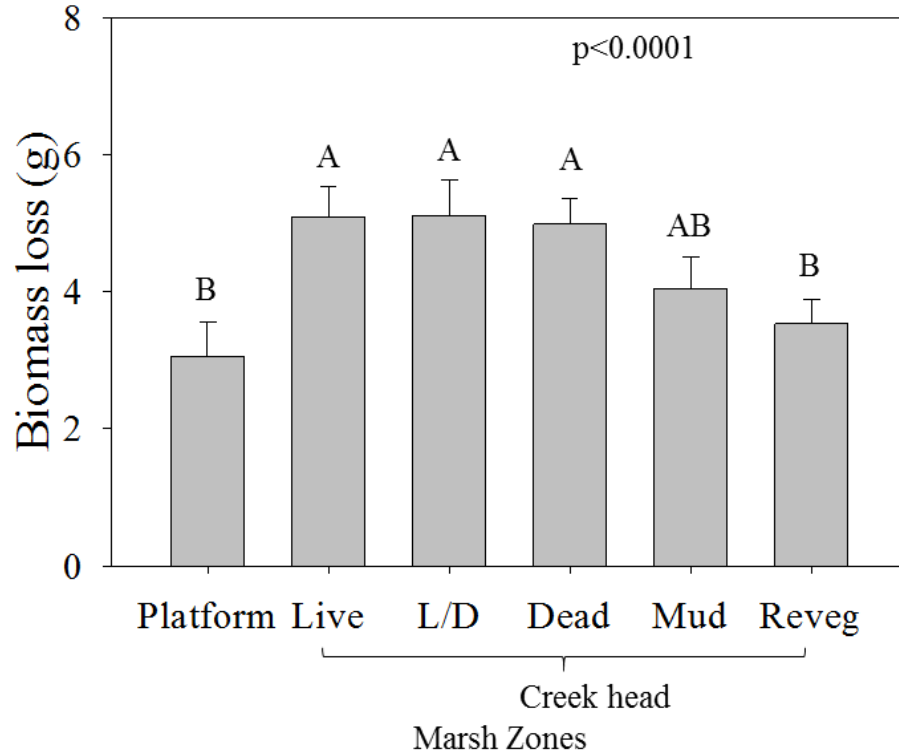


Figure 2.6 Decomposition rates of *Spartina* roots and rhizomes buried in six marsh zones for 247 days (ANOVA, $F_{5,54}=10.9$, $p<0.0001$). Live/Dead zones are the border between the live and dead zones. Bars indicate means ± 1 SE. Letters above bars indicate means that are significantly different (Tukey HSD).

2.4.4 Sediment excavation and herbivory. All four crab species burrowed in the mesocosms. For *Uca* and *Sesarma*, excavation rates initially increased with crab density; however, excavation peaked at four crabs per mesocosm for *Uca* ($F_{2,25}=14.44$, $p<0.0001$, $R^2=0.54$) (Fig. 2.7A) and continued to increase for *Sesarma* to eight crabs per mesocosm ($F_{1,18}=43.20$, $p<0.0001$, $R^2=0.71$) (Fig. 2.7B). At a common density of two crabs per mesocosm, *Sesarma* excavated about 59 % more soil per week than *Uca*, 68 % more than *Eurytium*, and 700 % more than *Panopeus* ($F_{3,122}=14.47$, $p<0.0001$) (Fig. 2.7C).

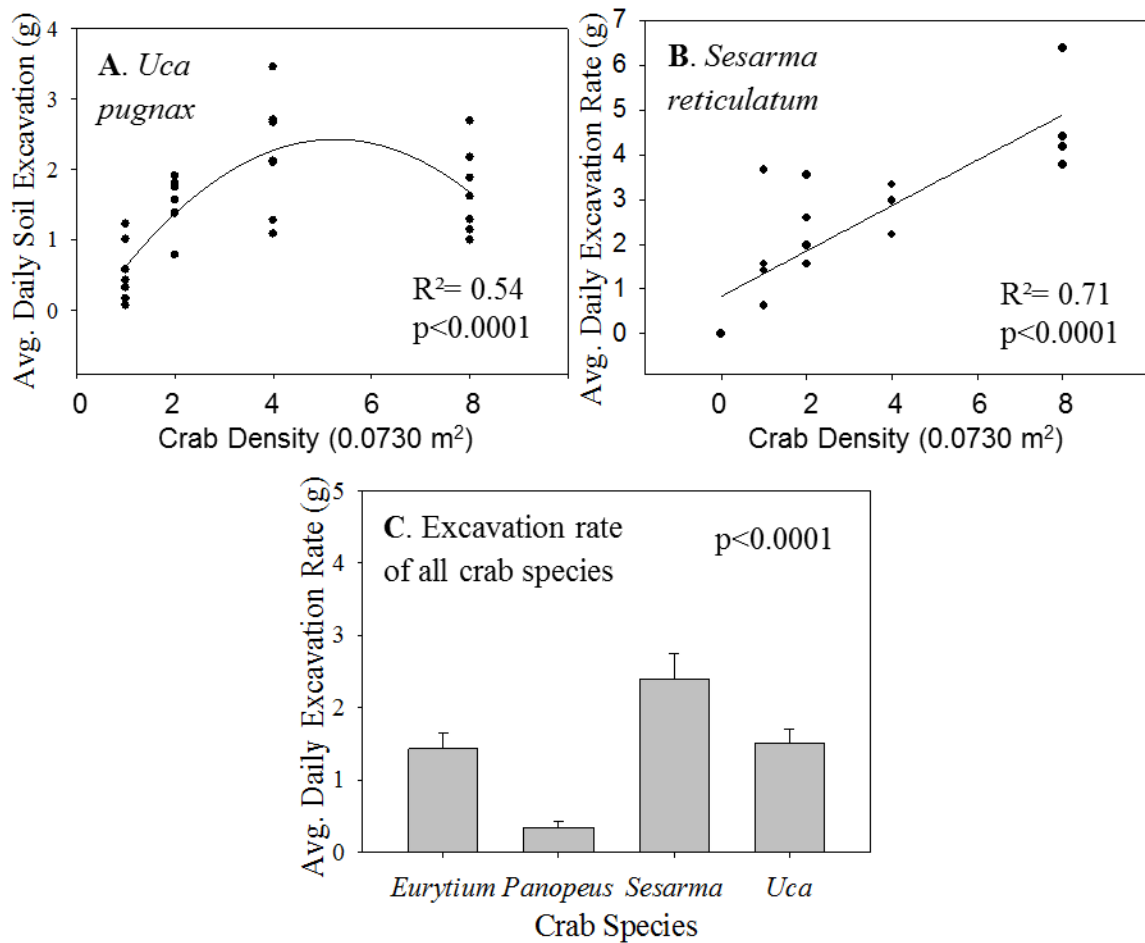


Figure 2.7. Excavation rates of crabs in mesocosms. A, *Uca pugnax* (Regression, $F_{2,25}=14.44$, $p<0.0001$, $R^2=0.54$); B, *Sesarma reticulatum* (Regression, $F_{1,18}=43.20$, $p<0.0001$, $R^2=0.71$); C, Comparison of soil excavation rate of each crab species at similar density (ANOVA, $F_{3,122}=14.47$, $p<0.0001$). Bars indicate means $\pm$ 1 SE. Letters above bars indicate means that are significantly different (Tukey HSD).

We combined the mesocosm excavation rates with field densities to estimate excavation rates in the field in different creek zones. We assumed that excavation rates in the field were the same as in the mesocosms (estimated from the two crabs per mesocosm treatment), crabs were active for eight months out of the year, and burrowing was confined to the upper 25 cm of the marsh sediments. These calculations indicated that the two predatory crabs had modest excavation rates due to their low densities ($F_{3,32}=1.83$,

$p=0.16$) (Fig. 2.8A), fiddler crabs fully excavated the upper marsh sediments about three times a year, regardless of creek zone ($F_{3,32}=0.52$, $p=0.67$) (Fig. 2.8B), and *Sesarma* had minimal effects on the marsh platform, but fully excavated the upper marsh sediments at the creek heads up to six times per year ($F_{3,32}=13.09$, $p<0.0001$) (Fig. 2.8C). As a community, the four crab species had the greatest effect at creek heads, where they fully excavated the upper marsh sediments up to ten times per year ($F_{3,32}=9.95$, $p<0.0001$) (Fig. 2.8D).

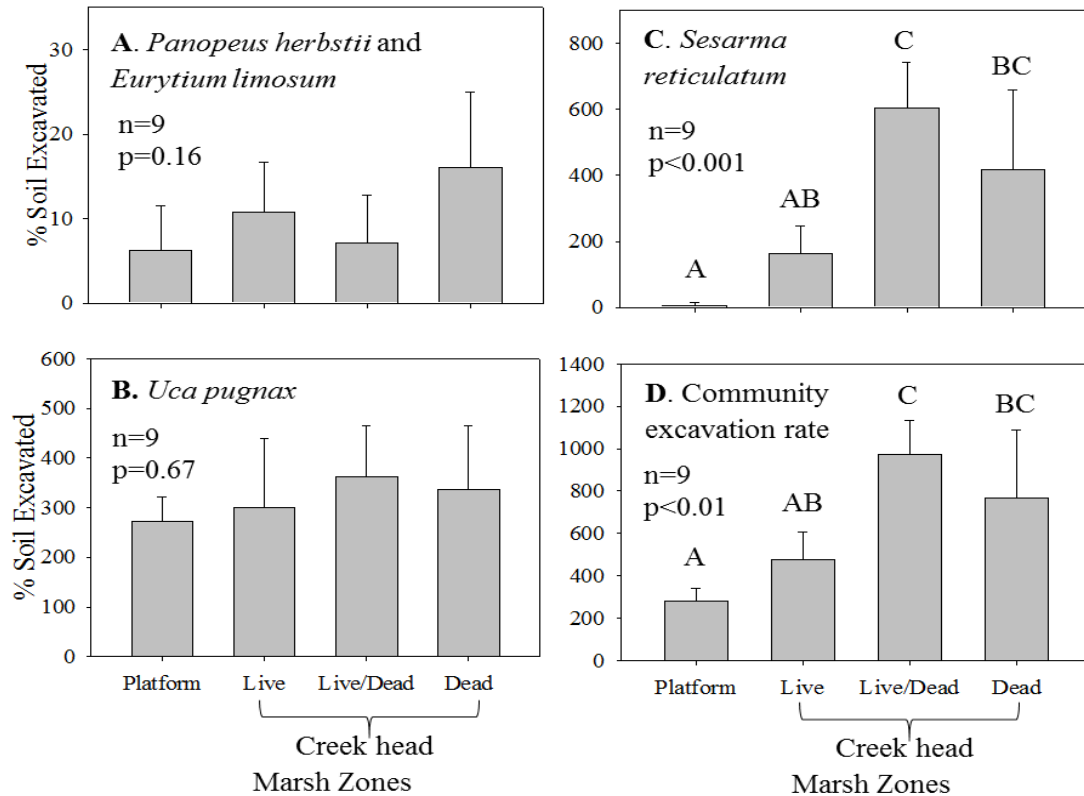


Figure 2.8. Potential excavation rates in the field based on field densities and mesocosm excavation rates. A, *Panopeus herbstii* and *Eurytium limosum* (combined because both were uncommon and therefore, net excavation rate is low) (ANOVA, $F_{3,32}=1.83$, $p=0.16$); B, *Uca pugnax* (ANOVA, $F_{3,32}=0.52$, $p=0.67$); C, *Sesarma reticulatum* (ANOVA, $F_{3,32}=13.09$, $p<0.0001$). D, the entire crab community (all species combined) (ANOVA, $F_{3,32}=9.95$, $p<0.0001$). Live/Dead zones are the border between the live and dead zones. Bars indicate means $\pm$ 1 SE. Letters above bars indicate means that are significantly different (Tukey HSD).

In the mesocosms, *Uca*, *Eurytium*, and *Panopeus* had no significant effect on *Spartina* height, number of leaves, above-ground biomass, or below-ground biomass (data not shown). In contrast, *Sesarma* increasingly suppressed all measures of *Spartina* productivity as crab densities increased (Height, $F_{1,18}=34.29$, $p<0.0001$, $R^2=0.66$; Number of green leaves, $F_{1,18}=41.93$, $p<0.0001$, $R^2=0.70$; Above-ground biomass, $F_{1,18}=16.52$, $p=0.0007$, $R^2=0.48$; and Below-ground biomass, $F_{1,18}=13.52$, $p<0.002$, $R^2=0.43$ (Fig. 2.9A-D).

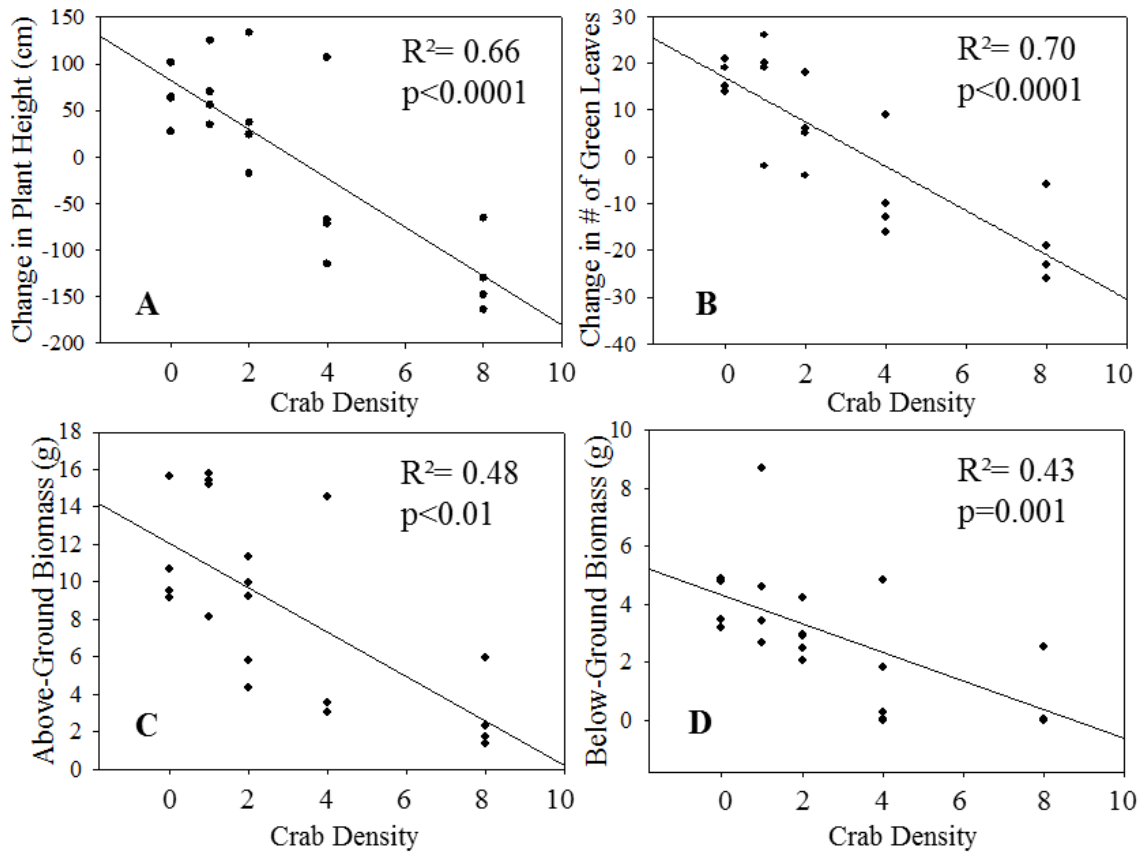


Figure 2.9 Effect of *Sesarma* density on *Spartina* height (Regression, $F_{1,18}=34.29$, $p<0.0001$, $R^2=0.66$) (A), number of green leaves (Regression, $F_{1,18}=41.93$, $p<0.0001$, $R^2=0.70$) (B), above-ground biomass (Regression, $F_{1,18}=16.52$, $p=0.0007$, $R^2=0.48$) (C), and below-ground biomass (Regression, $F_{1,18}=13.52$, $p<0.002$, $R^2=0.43$) (D) in the mesocosm experiment.

2.4.5 Does loss of vegetation increase creek growth? Control creek heads grew ~3 m in two years. Removal of ~25% of the live zone vegetation increased the rate of creek growth in the herbicide treatment by ~38% ($t(10)=2.31$, $p=0.04$) (Fig. 2.10).

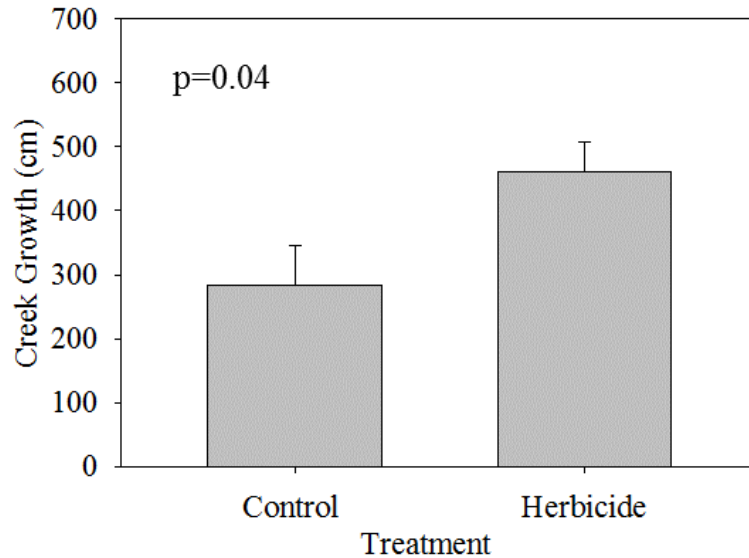


Figure 2.10. Effects of vegetation removal on creek growth (t-Test, $t_{10}=2.31$, $p=0.04$). Bars indicate means $\pm$ 1 SE.

2.5 Discussion

Previous work has suggested a link between crab activity and rapid headward erosion of creeks in south Atlantic tidal marshes (Hughes et al. 2009, Wilson et al. 2012) and in other parts of the world (Perillo and Iribarne 2003, Perillo et al. 2005, Minkoff et al. 2006, Escapa et al. 2007). Our field and mesocosm results provide important insights into the mechanisms by which crabs mediate tidal creek formation in south Atlantic tidal marshes. Our results indicate that *Sesarma* is the primary crab species mediating creek growth. Unlike other crab species, *Sesarma* is concentrated at creek heads where marsh

plants are dying and creeks eroding. *Sesarma* excavates larger amounts of sediment through its burrowing activities than do other crabs, and it alone creates burrow networks that likely increase below-ground erosion and decomposition. *Sesarma* is also the only crab species that directly kills vegetation. Thus, differences in behavior, distribution and feeding between the four crab species explain why *Sesarma* alone negatively impacts *Spartina* and alters marsh geomorphology by engineering creek growth.

2.5.1 *Sesarma* are associated with eroding creek heads. Many tidal marshes along the Southeastern Atlantic Coast of the United States contain numerous creeks that are eroding headward into the marsh platform at rates of ~ 2 m per year, with abundant crab burrows at the creek heads (Hughes et al. 2009, Wilson et al. 2012). Our data from South Carolina and Georgia show that the herbivorous crab, *Sesarma*, is the species primarily responsible for facilitating creek extension. As previously reported by Teal (1958), we found that the fiddler crab, *Uca*, was common throughout all *Spartina*-dominated habitats of the salt marsh. *Uca* feeds on organic matter that is deposited onto the marsh surface by the tides. This feeding strategy requires *Uca* to repeatedly migrate from high-intertidal to low-intertidal areas in search of food, which may explain their similar densities throughout the marsh (O'Connor 1993). Predatory crabs *Eurytium* and *Panopeus* also did not differ in abundance among the habitats that we sampled, and in any case were relatively rare everywhere in the marsh. Our estimates of the density of predatory crabs on the marsh platform were similar to previous estimates from Virginia (Silliman et al. 2004) but lower than previous estimates from Georgia (Kneib and Weeks 1990).

In contrast, densities of *Sesarma* peaked at the creek heads. Our estimates of *Sesarma* density on the marsh platform were similar to those of Teal (1958), who did not sample in creek heads. *Sesarma* is an herbivore (Crichton 1960, Holdredge et al. 2008, Bertness et al. 2009, Bertness et al. 2014) and high densities of *Sesarma* have been linked to loss of *Spartina* in New England marshes (Holdredge et al. 2008, Bertness et al. 2009, Bertness et al. 2014). Similarly, in South Carolina, we found that high densities of *Sesarma* at the creek heads correlated with the loss of *Spartina* stems, a relationship that is readily explained by *Sesarma* herbivory.

High densities of *Sesarma* in the creek head habitats were associated with high densities of burrows (Hughes et al. 2009) and high-percolation rates. As discussed below, higher percolation rates may indicate increased sub-surface flow of water, which might lead to greater erosion at creek heads. High-percolation rates likely also increase oxygen penetration into the marsh, thereby increasing decomposition. Thus, our data indicate that *Sesarma* may increase growth of creek heads by 1) excavating sediments, 2) eating *Spartina* and thereby promoting higher water velocities at the creek heads, 3) increasing surface and subsurface erosion, and 4) increasing decomposition. Below, we discuss these mechanisms in turn.

2.5.2 *Sesarma* crabs excavate large amounts of sediment at creek heads. Crab burrows serve a variety of purposes, such as protection against predators, shelter from unfavorable temperatures, shelter during molting, and as a location for courtship and mating activities (Montague 1980). Crabs are known annually to excavate large proportions of marsh sediment. For example, burrow excavation by *Uca* sp. at the creek bank in Massachusetts and South Carolina excavates 18-48% of the top 15cm of the

surface sediment per year (Katz 1980, McCraith et al. 2003). Because excavated materials are unconsolidated and easily washed away by ebbing tides (Wilson et al. 2012), burrow excavation at creek heads or along creek banks can facilitate rapid erosion of soils (Escapa et al. 2007).

We used field densities and the soil excavation data from the mesocosm experiment to calculate the potential yearly excavation rate for each crab species and the crab community as a whole in each marsh zone. These data almost certainly over-estimate actual field rates, because mesocosms initially lacked burrows, and sediments were relatively soft, making it easy to burrow. Nevertheless, the data are useful for comparative purposes and to give a rough estimate of potential excavation rates. Our results indicated that *Sesarma* is the most vigorous excavator of sediments at creek heads. *Sesarma* excavate large amounts of sediment at creek heads both because it is the most common crab in these habitats and because it excavates sediment at a higher rate than other crab species in order to build extensive, interconnected burrow networks (Seiple and Salmon 1982, Seiple and Salmon 1987). In contrast, fiddler crabs construct simple, isolated burrows (Allen and Curran 1974, Bertness and Miller 1984), and predatory crabs construct simple, isolated lairs (Silliman et al. 2004).

These calculations also indicate that the community of marsh crabs excavated the most soil at creek heads. Moreover, because the creek heads focus the ebb drainage of water from a large area of the marsh platform, creek heads experience the strongest flow velocities within the marsh. Thus, burrowing on the marsh platform away from creeks may not lead to erosion of the marsh surface due to low current velocities. However, concentrated ebb flow at creek heads suggest that these currents are capable of removing

crab excavation pellets leading to erosion at the leading edge of the creek head. Although some of the eroded sediment may be exported by the ebb-dominant tidal creeks (Hughes et al, 2009), sedimentation and revegetation of former mud zones at the back of the creek heads suggests that some of this sediment is redeposited at the trailing edge of the creek heads.

2.5.3 *Sesarma* crabs kill vegetation and enhance creek growth. Burrowing by marsh crabs can enhance *Spartina* productivity (Montague 1980, Bertness 1985, Kostka et al. 2002). *Sesarma*, however, is an herbivore that also eats *Spartina* (Crichton 1960). Studies in New England have linked elevated densities of *Sesarma* with die-back of *Spartina* (Holdredge et al. 2008, Bertness et al. 2009, Bertness et al. 2014). Our mesocosm results support previous findings that *Sesarma* strongly suppresses *Spartina*. In the mesocosms, moderate densities of *Sesarma* matching densities that we found at creekheads (four per mesocosm, or 55 per m²), reduced *Spartina* height, leaf number and biomass by 41-62 %, and high densities of *Sesarma* (eight per mesocosm, or 110 per m²) reduced *Spartina* height, leaf number and biomass by 77-92 %, compared to crab-free controls. These effects were measured after only ten weeks, whereas crabs are present in the field year-round. Thus, the mesocosm results, in combination with other reports in the literature, indicate that *Sesarma* herbivory is responsible for the absence of live *Spartina* at eroding creek heads in the field.

The loss of *Spartina* can have a significant effect on soil erosion (Day et al. 1999). *Spartina* stems exert significant friction and reduce tidal current velocity (Leonard et al. 1998, Yang and Lei 1998, Christiansen et al. 2000, Mudd et al. 2010). *Spartina* roots and rhizomes bind sediments and increase soil shear strength (Pestrong 1969, Rosen

1980, Allen 1989, Howes et al. 2010). Because *Sesarma* herbivory ultimately reduces both above and below-ground *Spartina* biomass, thereby lessening friction and increasing surface flows, as well as reducing sediment shear strength, all these factors may combine to increase erosion at creek heads.

We simulated high *Sesarma* herbivory at creek heads by removing plants from 4 x 5 m plots at creek heads using a systemic herbicide that kills both above and below-ground biomass, and we observed relatively few re-sprouting shoots each year when we re-sprayed the plots. Although these plots simulated *Sesarma* herbivory over only about 1/4 of the creek head, they nevertheless increased creek growth rates by 38 %. Thus, even without considering other mechanisms, crab herbivory alone strongly facilitates growth of headward-eroding creeks.

2.5.4 Other possible mechanisms by which crabs may mediate creek growth.

Our data suggests two other mechanisms by which *Sesarma* may facilitate creek growth by engineering the environment. First, *Sesarma* may increase erosion by increasing surface and subsurface erosion. The presence of crab burrows increases surface roughness, leading to greater turbulence during ebb flows, and increased erosion of the marsh surface (Farron, personal communication). Additionally, *Sesarma* constructs elaborate burrow networks (Seiple and Salmon 1982) that are conducive to lateral water flow that may increase subsurface erosion. Percolation rates over crab burrows were more than 10 times greater at creek heads, where connecting networks of crab burrows were able to drain water, than on the marsh platform, where burrows typically are not connected. We consistently observed turbulent lateral water flow through burrow networks on falling tides at headward eroding creeks in both SC and GA. We currently

do not have data on the velocity of the subsurface flow or the amount of soil lost due to this process, but it is a plausible mechanism by which crab engineering might mediate creek expansion, and deserves further study. Either surface or subsurface erosion would remove sediment from the leading edge of the creek head, facilitating headward growth.

Second, *Sesarma* may increase organic matter decomposition at creek heads, leading to collapse of the sediments. Burrows can increase the marsh soil surface area for oxygen exchange from both tidal water and the atmosphere by up to 290 % (Teal and Kanwisher 1961, Katz 1980, Iribarne et al. 1997, Thomas and Blum 2010). The increase in gas exchange between the atmosphere and the marsh soil increases the decomposition rate of below ground organic matter (Bertness 1985). We observed more than 100 % higher decomposition rates of plant litter at creek heads versus the marsh platform. A number of abiotic factors that might affect decomposition would differ between creek heads and the marsh platform even in the absence of *Sesarma* (e.g., porewater salinity, oxygen and sulfide levels); however, we believe that *Sesarma* likely contributed to this pattern by increasing oxygenation of the creek zone sediments compared to sediments in other zones through their high burrow densities and resulting rapid drainage of water through the interconnected burrow networks. A high decomposition rate at creek heads could lead to subsidence and formation of incipient channels at creek heads (Wilson et al. 2012), focusing ebb flows and increasing creek-head growth. While we do not have data on the amount of marsh subsidence caused by increased decomposition, this is another plausible mechanism by which *Sesarma* engineering could increase erosion at creek heads.

2.5.5 Conclusions

In salt marshes on the southeast Atlantic Coast of the United States, *Sesarma* crabs are closely associated with rapidly headward-eroding creeks. We hypothesize that crabs are not just attracted to such creeks, but also promote their growth. We have documented four possible mechanisms by which crabs might enhance creek growth: 1) direct excavation of sediments, 2) removal of plant stems and roots, 3) increased surface and subsurface erosion, and 4) decomposition of subsurface soils. It is likely that all of these mechanisms contribute to creek growth simultaneously, and we currently lack information on their relative importance. Our results are consistent with field studies examining the effects of herbivorous crabs in salt marshes in other geographic locations. In South American marshes, populations of the grapsid crab *Neohelice granulata* can reduce above ground *Spartina* densities by 87.5 % and excavate up to 2.4 kg/m² per day of sediment (Iribarne et al. 1997). Herbivory and bioturbation by *Neohelice granulata* enhanced creek growth in salt marshes dominated by *Sarcocornia perennis* (Perillo and Iribarne 2003, Escapa et al. 2007). In New England, USA, *Sesarma* crabs affect shorelines rather than creek heads, but again cause plant loss and sediment erosion (Holdredge et al. 2008, Bertness et al. 2009). Why *Sesarma* prefers to colonize channel banks in New England and creek heads in the South Atlantic coast has not been studied, but could be due to differences in the soils between the two regions (Bertness et al. 2009). Although the details of all these studies and ours differ, they agree that marsh crabs can be potent ecosystem engineers, affecting both vegetation structure and soil characteristics.

Previous work has emphasized the positive engineering effects of marsh plants and animals that build salt marsh habitats through facilitation cascades (Bertness and Grosholz 1985, Morris et al. 2002, Thomas and Blum 2010). Our work, together with the previous studies of herbivorous crabs in salt marshes, indicates that abundant herbivorous crabs like *Sesarma* can engineer the geomorphology and biogeochemistry of salt marshes in ways that essentially counteract the positive processes described above, creating a “facilitation meltdown”. At high densities, *Sesarma* reverses the positive effects of other marsh biota on sediment accumulation by increasing erosion. *Sesarma* harms *Spartina* rather than facilitating it as do fiddler crabs and bivalves. The increase in organic matter decomposition associated with *Sesarma* burrowing has negative effects on sediment elevation and stability, rather than the positive effects on nutrient cycling attributed to burrowing by fiddler crabs. The effects of *Sesarma* are negative rather than positive because *Sesarma* is so abundant, its distribution is concentrated in areas that are already prone to erosion, and because *Sesarma* is also an herbivore in addition to an engineer.

Although we have characterized the effects of *Sesarma* at the creek heads as negative, because they kill plants and increase erosion, the overall effects of *Sesarma* on marsh geomorphology are likely positive. As sea level rises, the amount of water moving on and off the marsh platform with each tide (the tidal prism) increases. In the absence of a creek network with the capacity to handle this tidal prism, the likely result would be increased ponding of water on the marsh platform at ebb tide, which would be deleterious to marsh plants. Thus, by promoting creek growth, *Sesarma* may be increasing marsh resilience to sea level rise.

Chapter 3

Predators mediate above- versus below-ground herbivory in a salt marsh crab

3.1 Abstract

Predators can significantly affect prey by removing prey individuals and by changing prey behavior. The trade-off between foraging behavior and predation risk may result in a trophic cascade that can have important effects on ecosystem processes. For herbivores that can feed both above- and below-ground, it is likely that predation risk affects the location of feeding. We tested whether predatory marsh crabs affected feeding behavior of the herbivorous crab, *Sesarma reticulatum*. We found that predatory crabs could kill or injure *Sesarma*, that *Sesarma* did less damage to its food plant *Spartina alterniflora* in the presence of the more dangerous predator. *Sesarma* prefer to feed on and grow better on below-ground rhizomes than above-ground leaves; however, the costs of digging burrows to access rhizomes leads to higher mortality if it is the only diet option. The location of feeding did not affect total biomass of *S. alterniflora*. For *Sesarma*, a choice in feeding location allows the crabs the behavioral flexibility to balance the risks of predation, the nutritional benefit of feeding below-ground and the survival costs of below-ground feeding. Similar tradeoffs are likely to increase the success of other herbivores that can feed both above- and below-ground.

Keywords: above-ground herbivory, below-ground herbivory, crab herbivory, *Eurytium*, non-consumptive effects, predator-prey interactions, *Panopeus*, *Sesarma*, *Spartina*.

3.2 Introduction

Predators can affect prey directly by killing them or indirectly by altering prey behavior. Direct consumption of prey can strongly affect prey densities in marine (Estes et al. 1998) estuarine (Altieri et al. 2012) and terrestrial (Ripple et al. 2014) environments. However, there is growing evidence that indirect effects of predators can have equally effects on the structure and function of ecosystems (Preisser et al. 2005, Heithaus et al. 2007, Davidson et al. 2014).

Indirect effects of predators are important because prey are under considerable pressure to detect and avoid predators. The fear of predators can alter the prey's behavior and feeding patterns, with consequent effects on the prey's resources (Ripple et al. 2001, Rizzari et al. 2014). In the case of herbivores, predation risks can alter foraging behavior, thereby affecting plant diversity, productivity, nutrient exchange, and trophic energy transfer (Schmitz et al. 2008). For example, increased predation pressure from large predators in Yellowstone National Park altered the locations where elk grazed, leading to changes in aspen sapling survival rate (Fortin et al. 2005, Beschta and Ripple 2010).

Herbivores that feed both above and belowground might alter where they feed in response to predators. For example, pocket gophers can feed on leaves or roots, but are exposed to predators when feeding aboveground (Douglas 1969, Feldhamer et al. 2003). Seasonal variation in predation risk may help explain seasonal variation in the relative proportion of leaves versus roots in the diet (Douglas 1969, Feldhamer et al. 2003), but this hypothesis has not been experimentally tested. There are other species of herbivores that feed both above and belowground, but whether predation risk causes a switch in

feeding location is unknown. If predation risk does cause herbivores to be more active belowground; however, this might have widespread effects on ecosystem function, because burrowing affects plant communities and soil moisture, temperature, compaction, nutrient distribution, and decomposition (Huntly and Reichman 1994, Sherrod and Seastedt 2001).

In salt marshes on the Atlantic Coast of the United States, the burrowing crab *Sesarma reticulatum* (henceforth *Sesarma*) is a common herbivore (Grosner 1979), feeding on the dominant grass *Spartina alterniflora* (henceforth *Spartina*) (Crichton 1960, Bertness et al. 2009). *Sesarma* feeds both on leaves and below-ground rhizomes of *Spartina* (Coverdale et al. 2012), and prefers rhizomes over leaves in laboratory feeding assays (Vu et al., unpublished data), but past field studies have only measured feeding on leaves. Focusing only on leaves provides an incomplete view of the damage caused by *Sesarma* because it overlooks below-ground herbivory, which is known to be very important in other ecosystems (Brown and Gange 1989, Gibson et al. 1990, Borowicz 2010).

Sesarma constructs large burrow networks (Crichton 1960) that likely have impacts on marsh biogeochemistry and geomorphology independent of crab effects on plants (Fei et al. 2014). For example, burrowing by *Sesarma* and other marsh crabs may play an important role in the formation of new creeks on marsh platforms that are subject to rising sea levels (Hughes et al. 2009, Wilson et al. 2012). Thus, changes in *Sesarma* burrowing activities could have important ramifications for marsh function.

Sesarma densities are mediated by predation from birds and nekton (Altieri et al. 2012, Coverdale et al. 2012) and from resident marsh crabs (Vu, personal observation), but we do not know if *Sesarma* shifts between feeding above and belowground in response to the threat of predation. We conducted mesocosm and laboratory experiments to examine the effects of predators on above- and below-ground feeding by *Sesarma*, and to test whether predator-induced changes in feeding affect burrowing rates and *Spartina* productivity.

3.3 Materials and methods

3.3.1 Study site and Species. We worked on Sapelo Island, Georgia, USA (31.4775° N, 81.2417° W). Marshes in this region are typical of southeastern U.S. Atlantic Coast (Pomeroy and Wiegert 1981), with lower and intermediate marsh elevations dominated by the grass *Spartina alterniflora*. Common crabs include the herbivore *Sesarma reticulatum* and the predators *Eurytium limosum* (henceforth *Eurytium*) and *Panopeus herbstii* (henceforth *Panopeus*) (Teal 1958).

3.3.2 Effects of predators on *Sesarma* mortality rate. We conducted feeding assays to examine the vulnerability of *Sesarma* to two common predatory crabs. We filled 80, 6.1-liter tubs with 3 cm of wet marsh soil in May 2011. Eighty *Sesarma* (20-25 cm carapace width) were placed into each tub. Forty of the tubs containing *Sesarma* also contained one predatory crab: a small or large (15-20 or 25-30 mm carapace width, respectively) *Eurytium* or *Panopeus* (n=10 of each combination). After 24 h we scored *Sesarma* survival and noted any injuries to surviving *Sesarma*. We compared *Sesarma* mortality rate between treatments using Barnard's exact test.

3.3.3 Do predators affect *Sesarma* feeding preferences? We conducted mesocosm experiments to examine the effects of two common predatory crabs on *Sesarma* feeding, sediment excavation and *Spartina* above- and below-ground biomass. We filled 60, 20-liter buckets with marsh soil in May 2011. Holes on the sides of the buckets at the soil level (8 cm below the top of the bucket) and 15 cm below the soil surface (13.7 cm from the bottom of the bucket) allowed water to slowly drain from the upper soils. Five *Spartina* plants, each consisting of a single shoot with roots and rhizomes, were planted in each bucket. Buckets were placed outdoors under partial shade and watered with fresh water for two weeks to allow plants to recover from transplanting. After this, the buckets were filled and drained with seawater twice daily to simulate tides. Plants were allowed to acclimate for an additional four weeks prior to the start of the experiment.

We stocked the buckets with crabs on June 21, 2011. *Sesarma* were stocked at zero (n=10) or four crabs (n=50) per bucket. Forty of the buckets containing *Sesarma* also included one predatory crab: a small or large (15-20 and 25-30 mm carapace width, respectively) *Eurytium* or *Panopeus* (n=10 of each combination). We removed the propus of both chela of the predators to prevent predation but still allow burrowing. A thin fabric cage capping the bucket prevented crabs from escaping. The experiment ran for 50 days. Dead crabs were replaced when discovered. We collected all sediment that *Sesarma* excavated to the surface daily, dried it for four days at 60° C, and weighed it. We measured the height and number of green leaves on each *Spartina* shoot at the beginning and end of the experiment. At the end of the experiment, we also harvested, dried, and weighed *Spartina* shoots, rhizomes and roots. We compared the

changes in feeding preferences of *Sesarma* using ANOVA with Tukey HSD post-hoc mean comparisons.

3.3.4 Do *Sesarma* prefer to eat above- or below-ground biomass? To document the feeding preferences of *Sesarma*, we conducted a two-choice feeding assay in the laboratory. Individual *Sesarma* were housed in plastic containers (n=10) with a shallow (3 cm) layer of mud, and offered a choice between *Spartina* live leaves and live rhizomes. The two foods were offered at equal initial wet masses. Each replicate was accompanied by a paired no-crab control to account for changes in wet weight of the diets during the experiment (Peterson and Renaud 1989). Each assay ran for 24 h. Food items were weighed before and after the assay, and data analyzed with a paired t-test following Peterson and Renaud (1989).

3.3.5 How does diet affect growth of *Sesarma*? To document the effects of feeding on leaves versus rhizomes on *Sesarma*, we fed crabs live leaves, rhizomes or both (n=10/treatment) for two weeks. Crabs were housed in plastic tubs as above, and weighed at the beginning and at the end of the experiment. We compared the changes in *Sesarma* weight among the different diet using ANOVA with Tukey HSD post-hoc comparisons.

3.3.6 Effect of *Sesarma* feeding on *Spartina* biomass. To determine the effect of above- and below-ground feeding by *Sesarma* on *Spartina*, we conducted a mesocosm experiment in which crabs had access to above-ground only, below-ground only, or both above- and below-ground parts of *Spartina*. Mesocosms consisted of 18-gallon plastic tubs that were divided into a planted half and an unplanted half. Crabs were precluded from accessing different parts of the plants by enclosing either above- or below-ground

plant parts in a plastic hardware cloth cage (1 cm mesh) in the planted half of the mesocosm. Crabs were able to burrow freely in the other half. To control for any direct effects of the hardware cloth, similar amounts of hardware cloth were buried along the sides of the tub in the treatment allowing complete access, and in the no-crab (control) treatment. All tubs were capped with a cage made of the same plastic mesh to prevent *Sesarma* from escaping. Each of the four treatments (1) above-ground herbivory, 2) below-ground herbivory, 3) above- and below-ground herbivory, 4) no herbivory) was replicated 10 times.

Five *Spartina* plants, each consisting of a single shoot with roots and rhizomes, were planted in each tub. Tubs were placed in full sun in outdoor water tables filled with 15 cm of running seawater that moderated temperature fluctuations. Plants were watered with fresh water for four weeks to allow them to recover from transplanting. After this, the tubs were filled and drained with seawater twice daily to simulate tides. Plants were allowed to acclimate for an additional four weeks prior to the start of the experiment.

We stocked the buckets with four *Sesarma* crabs in May 2011. The experiment ran for 80 days. Dead crabs were replaced when discovered. We collected all sediment that crabs excavated to the surface daily, dried it for four days at 60° C, and weighed it. We measured the height and number of green leaves on each *Spartina* shoot at the beginning and end of the experiment. At the end of the experiment, we also harvested, dried, and weighed *Spartina* shoots, rhizomes, and roots. We compared the changes in *Spartina* above- and below-ground biomass among the different treatments using ANOVA with Tukey HSD post-hoc comparisons.

3.4 Results:

3.4.1 Effects of predators on *Sesarma* mortality rate. Larger predatory crabs, *Eurytium* and *Panopeus*, killed 60-100 % of *Sesarma* in laboratory feeding trials (Fig.3.1). No *Sesarma* mortality was observed in trials using small predatory crabs (data not shown); however, all of the surviving *Sesarma* were missing limbs and were found on the opposite side of the mesocosm from the predatory crabs. *Sesarma* housed without predators suffered no mortality and no missing limbs.

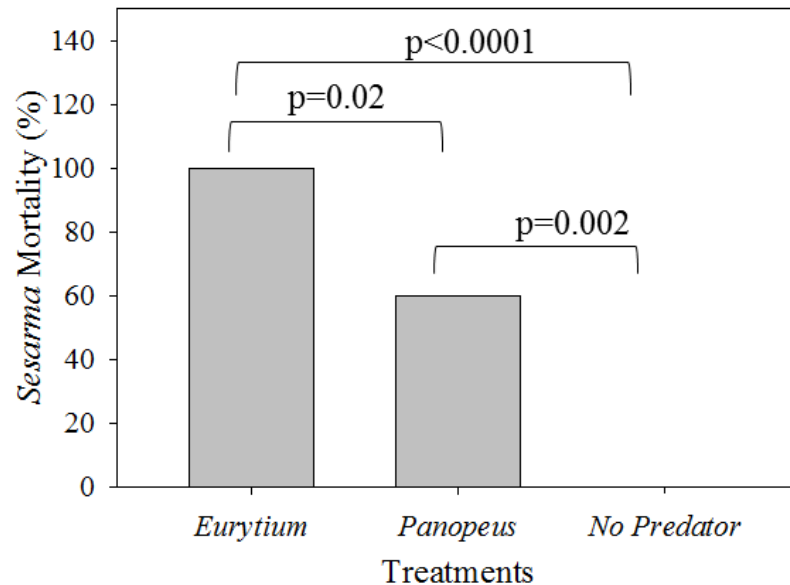


Figure 3.1: Mortality rate of *Sesarma* in the presence or absence of large predatory crabs. P-values indicate that the treatments differed from each other (Barnard's exact test).

3.4.2 Do predators affect *Sesarma* feeding preferences? *Sesarma* by itself reduced *Spartina* above-ground biomass by ~50-65 % ($F_{3,28}=10.42$, $p<0.0001$) (Fig. 3.2A). The two predatory crabs had different non-consumptive effects on *Sesarma*

feeding. *Panopeus* did not significantly alter the feeding behavior of *Sesarma*, although there was a trend towards increased above-ground and reduced below-ground biomass of *Spartina* in the presence of predators, possibly suggesting a small shift in *Sesarma* feeding from above to belowground. In contrast, *Eurytium* strongly altered feeding behavior of *Sesarma*, with a resulting three-fold increase in *Spartina* above-ground biomass, a two-fold increase in below-ground biomass, and an increase in shoot:root ratio ($F_{3,27}=4.24$, $p=0.014$) (Fig.3.3C). The amount of soil excavated by *Sesarma* burrowing did not differ among treatments in either set of trials (data not shown).

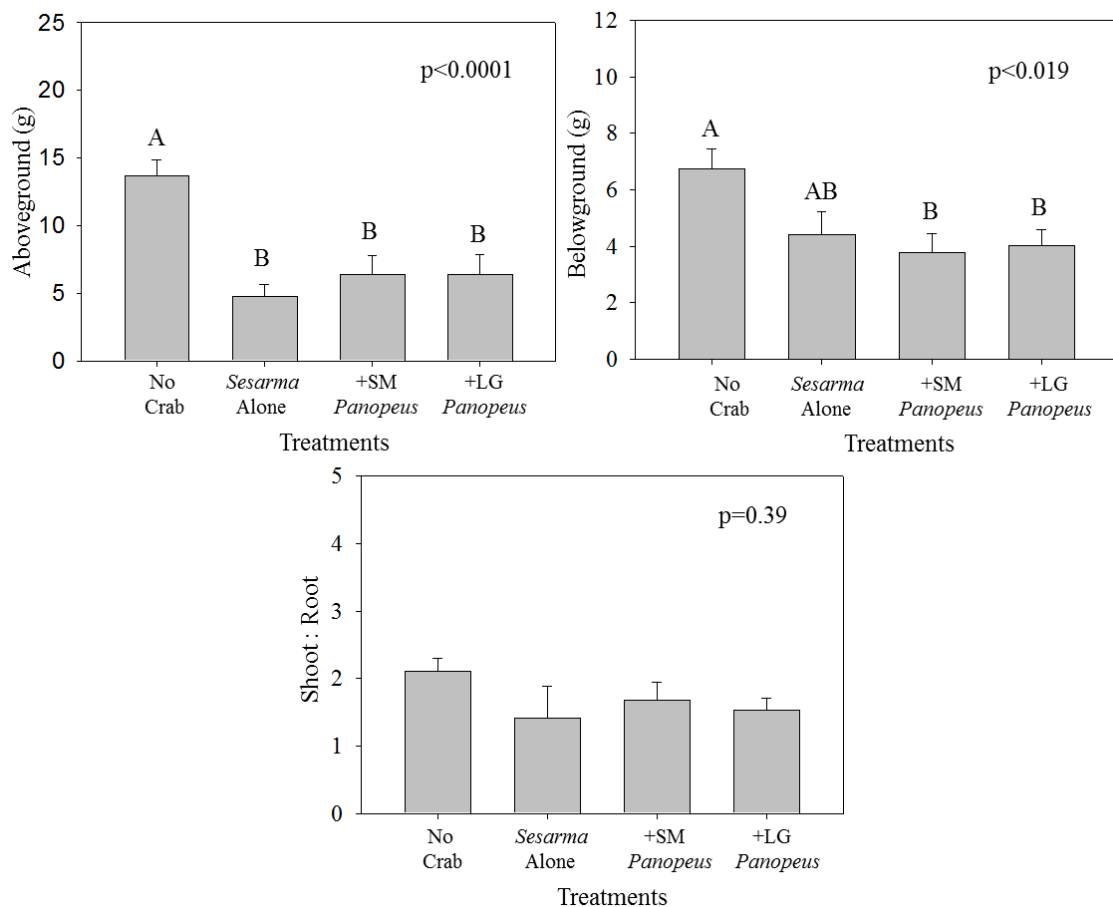


Figure 3.2: Non-consumptive effects of *Panopeus* on how *Sesarma* affects *Spartina* (A) above- (ANOVA, $F_{3,28}=10.42$, $p<0.0001$) and (B) below-ground biomass (ANOVA, $F_{3,28}=3.93$, $p=0.02$), and (C) shoot to root ratio (ANOVA, $F_{3,28}=1.05$, $p=0.39$). Bars indicate means $\pm$ 1 SE. Letters above bars indicate means that are

significantly different (ANOVA with Tukey HSD). Treatments were no crabs, *Sesarma* alone, *Sesarma* with small *Panopeus* predators, and *Sesarma* with large *Panopeus* predators.

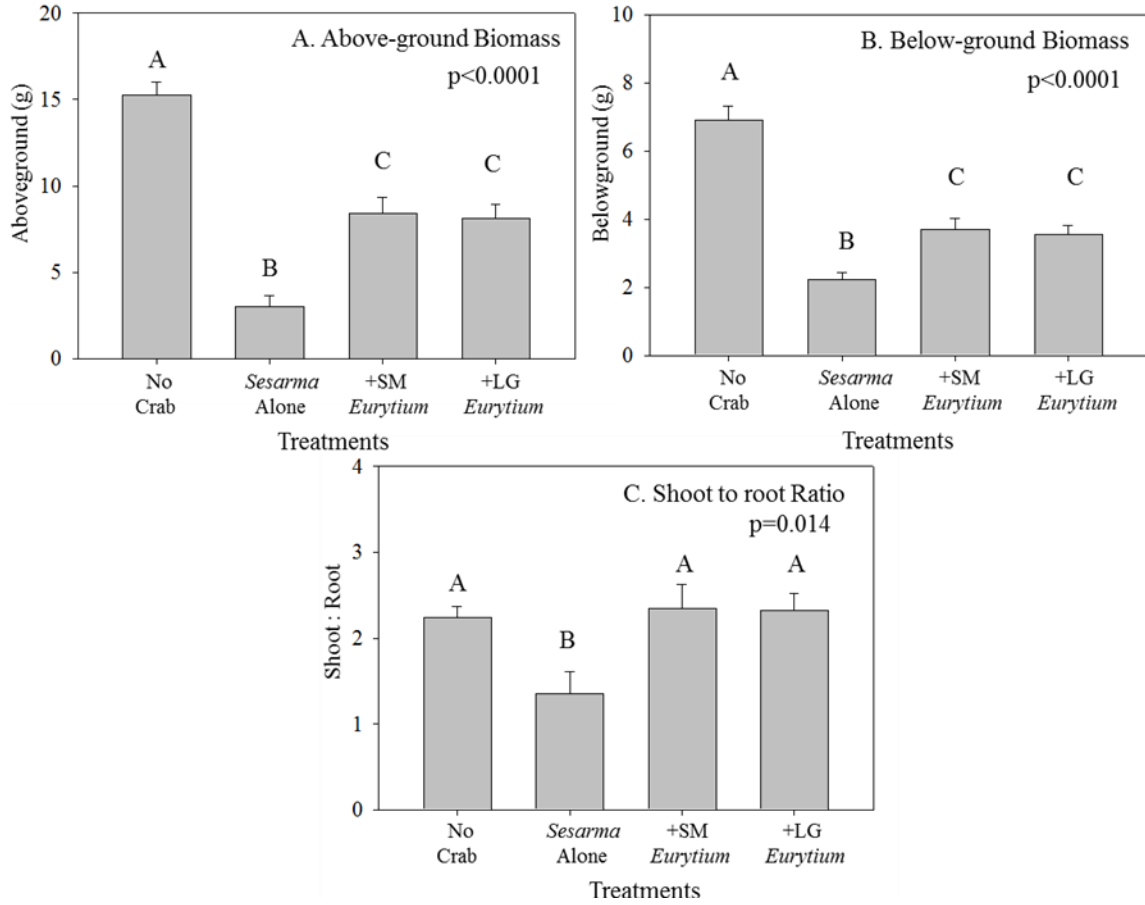


Figure 3.3: Non-consumptive effects of *Eurytium* on how *Sesarma* affects *Spartina* (A) above- (ANOVA, $F_{3,27}=40.44$, $p < 0.0001$) and (B) below-ground biomass (ANOVA, $F_{3,27}=39.91$, $p < 0.0001$), and (C) shoot to root ratio (ANOVA, $F_{3,27}=4.24$, $p = 0.014$). Bars indicate means ± 1 SE. Letters above bars indicate means that are significantly different (ANOVA with Tukey HSD). Treatments were no crabs, *Sesarma* alone, *Sesarma* with small *Eurytium* predators, and *Sesarma* with large *Eurytium* predators.

3.4.3 *Sesarma* feeding preference and growth. *Sesarma* consumed seven times more below-ground (rhizomes) than above-ground (leaves) *Spartina* plant tissue (t -Test, $t=2.27$, $p=0.036$) (Fig. 3.4A). *Sesarma* gained mass on a diet of rhizomes and lost mass

on a diet of leaves ($F_{3,27}=5.79$, $p<0.01$) (Fig. 3.4B). A mixed diet produced intermediate growth.

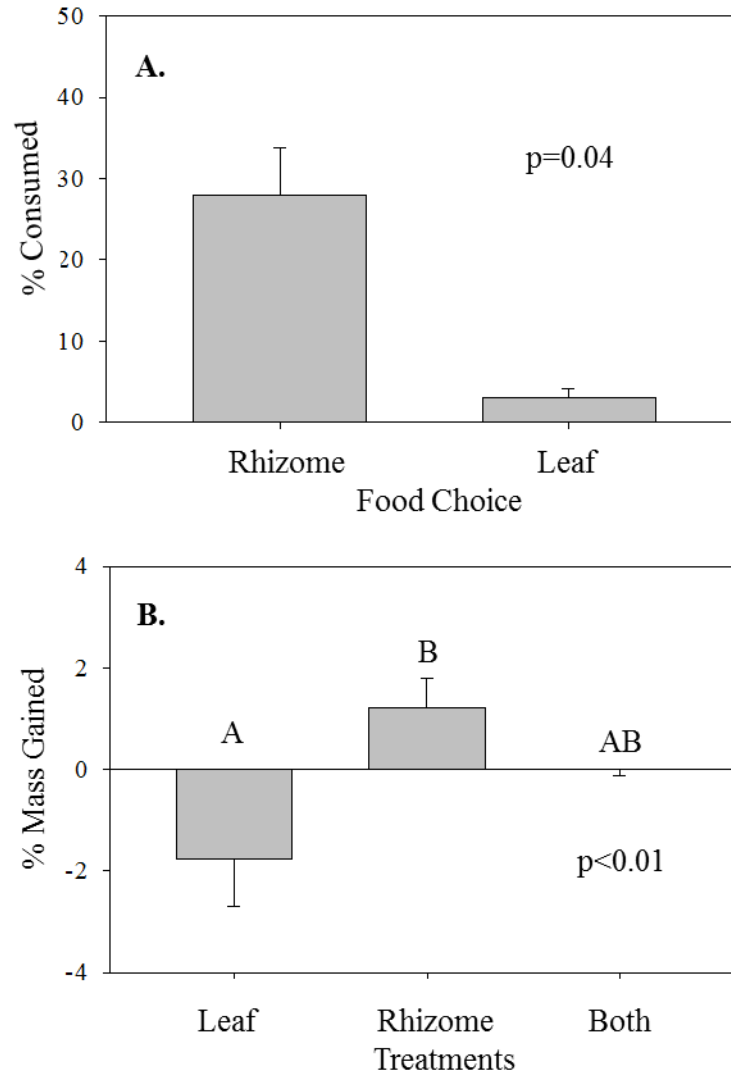


Figure 3.4: (A) *Sesarma* feeding preferences for above- and below-ground plant tissue (t -Test, $t_{18}=2.27$, $p=0.04$). (B) Effects of diet on *Sesarma* growth (ANOVA, $F_{2,27}=5.79$, $p<0.01$). Bars indicate means ± 1 SE. Letters above bars indicate means that are significantly different (ANOVA with Tukey HSD).

3.4.4 Effect of *Sesarma* feeding on *Spartina* biomass. Regardless of where *Sesarma* were allowed to feed (above only, below only, or both), crab herbivory had a

negative impact on *Spartina* productivity (Fig. 3.5). *Sesarma* reduced above-ground biomass by up to 72 % ($F_{3,36}=101.17$, $p<0.0001$) and below-ground biomass by ~66 % ($F_{3,35}=16.17$, $p<0.0001$). *Sesarma* mortality rates were ~ two-fold higher when they were forced to feed below ground versus above-ground or in both locations ($F_{3,27}=8.36$, $p<0.002$). The amount of soil excavated by *Sesarma* burrowing did not differ among treatments (data not shown).

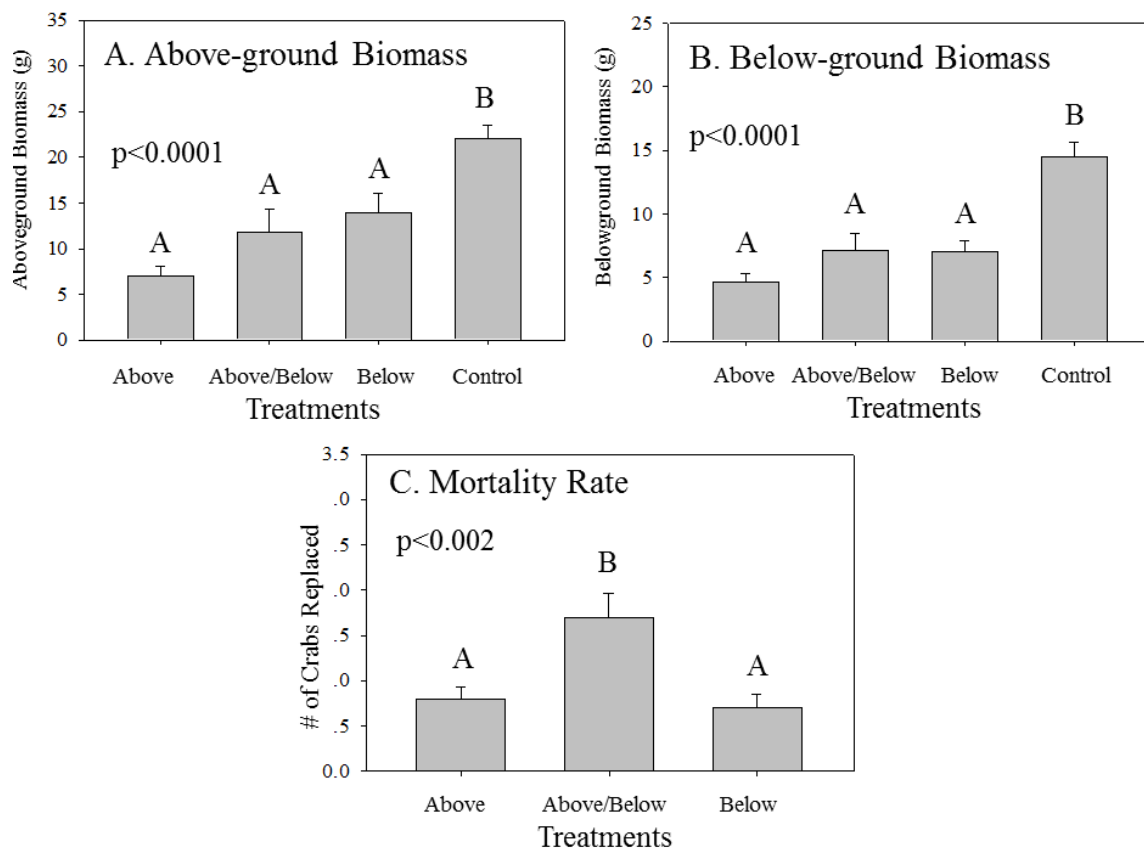


Figure 3.5: Effects of *Sesarma* feeding locations on *Spartina* (A) above- (ANOVA, $F_{3,36}=11.17$, $p<0.0001$) and (B) below-ground biomass (ANOVA, $F_{3,35}=16.17$, $p<0.0001$), and (C) *Sesarma* mortality rate (ANOVA, $F_{3,27}=8.36$, $p<0.002$). Bars indicate means ± 1 SE. Letters above bars indicate means that are significantly different (ANOVA with Tukey HSD).

3.5 Discussion

The presence of predators often leads to changes in prey foraging behavior (Frank 2008, Ripple et al. 2014, Rizzari et al. 2014). We found that predators changed foraging behavior of *Sesarma*, and that these changes affected both *Sesarma* fitness and *Spartina* productivity. In particular, we found that predatory crabs could kill or injure *Sesarma*, and that *Sesarma* did less damage to its food plant *Spartina* in the presence of the more dangerous predator species. *Sesarma* prefer to consume and grow better on below-ground rhizomes than above-ground leaves; however, the costs of digging burrows to access rhizomes lead to higher mortality when rhizomes are the only diet option. The location of feeding did not affect total biomass of *Spartina*. For *Sesarma*, a choice in feeding location allows the crabs the behavioral flexibility to balance the risks of predation, the nutritional benefit of feeding below-ground, and the survival costs of below-ground feeding. Similar tradeoffs are likely to increase the success of other herbivores that can feed both above and belowground.

3.5.1 Predator-induced behavior changes in *Sesarma*. *Sesarma* eats *Spartina* (Crichton 1960), and elevated densities of *Sesarma* can cause die-back of *Spartina* in the field (Holdredge et al. 2008, Bertness et al. 2009, Bertness et al. 2014). Our mesocosm results support previous findings that *Sesarma* strongly suppresses *Spartina*. In the absence of predatory crabs, *Sesarma* reduced *Spartina* above-ground biomass by ~66-81 % and below-ground biomass by ~35-67 %. In the presence of predatory crabs, the effect of *Sesarma* on *Spartina* changed, but this result depended on predator identity. *Eurytium* was the more dangerous of the two predatory crabs, consuming 40 % more *Sesarma* than *Panopeus* in predation trials. In the presence of *Eurytium*, the negative effect of *Sesarma*

on *Spartina* was reduced, leading to three-fold greater above-ground biomass than in the absence of the predator. Moreover, the shoot to root ratio was ~40 % higher in the presence of predators, suggesting that *Sesarma* was altering its behavior by reducing its foraging effects above-ground (Morrison 1999, Werner and Peacor 2003, Hughes et al. 2014). In the predation trials, small *Eurytium* were not able to kill *Sesarma*, but the effect of small *Eurytium* in the mesocosms was identical to that of large *Eurytium*. This suggests that *Sesarma* crabs were either excessively cautious or were unable to accurately assess the size of the *Eurytium* in the mesocosm. *Panopeus* was the less dangerous predatory crab, and *Sesarma* did not significantly respond to its presence in the mesocosms. This suggests that *Sesarma* are able to tell the difference between the two predators, and respond appropriately to the amount of risk that each presents. If *Sesarma* are assessing predation risk based on chemical cues, it should be easier to distinguish among predator species than to gauge predator size.

3.5.2 *Sesarma* prefer and do better feeding on rhizomes. Optimal foraging theory assumes that animal foraging behavior is optimized to maximize the rate of net energy gain (Stephens and Krebs 1986, Parker and Smith 1990). We found that *Sesarma* strongly preferred to feed on rhizomes rather than on leaves of *Spartina*. Rhizomes have higher concentrations of digestible carbohydrates (Gallagher et al. 1984) and are lower in silica (Hou et al. 2010), which is an important defense against herbivory (Vicari and Bazely 1993, Massey and Hartley 2006). Thus, rhizomes may be both more nutritious and easier to eat than leaves, which may explain why *Sesarma* gained mass on a diet of rhizomes but lost mass on a diet of leaves.

3.5.3 Effects of feeding location on *Sesarma* and *Spartina*. Although predation risk affected the location of *Sesarma* feeding, this may not have important consequences for *Spartina*. Feeding by *Sesarma* reduced above- and below-ground *Spartina* biomass, however, the effect of *Sesarma* on *Spartina* did not differ when *Sesarma* were forced to feed exclusively above or below-ground. Although in general below-ground herbivory might be expected to be more damaging to plants than above-ground herbivory (Stein et al. 2010, Coverdale et al. 2012), this is less true for grasses which have a distributed root network rather than a primary taproot where most of the nutrients are concentrated (Reichman and Smith 1985). In addition, herbivores may do less damage below-ground than above-ground because of the costs of burrowing. Vleck (1979) found that gophers expend 360-3,400 times more energy foraging below-ground versus above-ground. The high energetic cost of burrowing for roots and rhizomes may also explain why *Sesarma* had the highest mortality when limited to feeding on only below-ground biomass in the mesocosm experiment, despite growing better on rhizomes versus leaves in laboratory experiments when burrowing was not required to access food.

3.5.4 Conclusions

Predators can have significant effects on prey populations both by removing prey individuals and by inducing changes in prey behavior (Ripple et al. 2001, Beschta and Ripple 2010). The trade-off between foraging behavior and predation risk may result in a trophic cascade that can have important effects on ecosystem processes (Preisser et al. 2005, Heithaus et al. 2007, Davidson et al. 2014). For herbivores that can feed both above and belowground, it is likely that predation risk affects the location of feeding.

We found that predatory crabs could kill or injure *Sesarma*, and that *Sesarma* did less damage to its food plant *Spartina* in the presence of the more dangerous predator. *Sesarma* prefer to feed on and grows better on below-ground rhizomes than above-ground leaves; however, the costs of digging burrows to access rhizomes leads to higher mortality if rhizomes are the only diet option. The location of feeding did not affect total biomass of *Spartina*. For *Sesarma*, a choice in feeding location allows the crabs the behavioral flexibility to balance the risks of predation, the nutritional benefit of feeding belowground and the survival costs of below-ground feeding. Similar tradeoffs are likely to increase the success of other herbivores that can feed both above and belowground.

Chapter 4

**Abiotic conditions explain asymmetric movement of consumer fronts associated
with creek heads in salt marshes**

4.1 Abstract

High densities of consumers can quickly deplete local resources, forcing consumers to aggregate and form a front along edges of the remaining food resources. The formation of these consumer fronts are triggered by common abiotic mechanisms. We examined the abiotic factors that drive *Sesarma reticulatum* aggregation at the leading edge of the creek head but not the trailing edge to explain the asymmetrical movement of the front. In addition, we created artificial creek heads in areas that lacked them to experimentally test the hypothesis that the high water flows adjacent to creek heads (as opposed to some other factor) create conditions that provide superior habitat for *Sesarma*. We found that both surface and subsurface marsh temperatures were ~11-12 % cooler at the creek head zones than at the marsh platform. Hydrogen sulfide concentrations were lower at the Live and Dead zones of the creek head than on the marsh platform (0.0 mg/L versus ~0.58 mg/L). Water flowing through interconnecting burrows during ebb tide resulted in a ~two-fold higher concentration of dissolved oxygen at the Live and Dead zones compared to the marsh platform. We found that hydrological condition drives *Sesarma* aggregation as opposed to other factors. Burrow and *Sesarma* densities were significantly higher when creek head conditions were mimicked compared to the two control treatments. Erosion rate was 3-7 fold higher when creek head conditions were mimicked than in the unmanipulated control treatments. Superior abiotic conditions for crabs at the leading edge of the creek head but not the trailing edge, explaining the asymmetrical movement of the front. Similar physical constraints could provide explanations to asymmetrical consumer front in other ecosystem.

Keywords: Asymmetrical movement, consumer front, tidal creek, hydrology, *Sesarma*.

4.2 Introduction

In many ecosystems, high densities of consumers can quickly deplete local resources, forcing consumers to aggregate, and form a front along edges of the remaining food resources (Silliman et al. 2005). Once formed, the front moves outward to surrounding areas that are rich in resources (Lauzon-Guay et al. 2008). The formation of these consumer fronts is triggered by common abiotic (i.e. seasonality, drought) and biotic (i.e. recruitment events, predatory release) mechanisms (Gueron and Liron 1989, Silliman et al. 2005, Altieri et al. 2012, Kayal et al. 2012).

In salt marshes on the Atlantic Coast of the United States, the burrowing crab *Sesarma reticulatum* (henceforth *Sesarma*) is a common herbivore (Grosner 1979), feeding on the dominant grass *Spartina alterniflora* (henceforth *Spartina*) (Crichton 1960, Bertness et al. 2009, Vu et al. 2016). *Sesarma* are social crabs that excavate and live in communal interconnecting burrows (Holdredge et al. 2010, Altieri et al. 2012). At high densities, *Sesarma* fronts can leave behind marsh that is totally denuded of *Spartina*, with strong effects on associated biodiversity and ecosystem processes (Altieri et al. 2012, Vu et al. 2016). It is believed that human-induced depletion of predatory fish is contributing to the formation of *Sesarma* fronts in New England marshes, resulting in decimation of dozens of marshes (Altieri et al. 2012).

In Southeastern marshes of the US Atlantic Coast, *Sesarma* is common at the leading edges of creek heads and rare elsewhere on the marsh (~ 26 crabs/m² vs. < 1 crab/m² on the marsh platform) (Vu et al. 2016). Although *Sesarma* consumes plants at the creek heads, the overall effect of the crabs may be beneficial to the marsh.

Circumstantial evidence indicates that increased herbivory and burrowing lead to higher erosion rates at creek heads and allow for rapid (~ 1.9 m/yr) growth of these creeks into the marsh platform (Hughes et al. 2009, Wilson et al. 2012). As these creeks grow inward, they increase the drainage efficiency of the marsh, thereby improving the ability of the marsh to cope with rising sea-level by efficiently draining water off the marsh at low tide.

The consumer fronts created by *Sesarma* in Southeastern Atlantic US salt marshes are unique in several ways. First, the *Sesarma* front is tightly associated with a physical structure (the creek head), which it directly manipulates (Vu et al. 2016). Second, rather than expanding as do many other consumer fronts (Silliman et al. 2013), the *Sesarma* front remains compact, moving forward with the creek head as it erodes through the marsh. Third, the front moves only in one direction—crabs do not colonize the back of the creek head even though their food plant *Spartina* vigorously recolonizes these areas behind the crab consumer front. Why *Sesarma* fronts are so tightly constrained to the eroding front edge of creek heads is unclear.

Creek heads are localized depressions on the marsh surface, therefore, water funnels to the area during the outgoing tide (Hughes et al. 2009). It is likely that this rapidly-flowing water creates cooler areas with higher dissolved oxygen concentrations and lower concentrations of toxic sulfides. We therefore measured abiotic conditions in natural creek heads to test the hypothesis that abiotic conditions were favorable for crabs at the leading edge of the creek head but not the trailing edge, explaining the asymmetrical movement of the front. We also created artificial creek heads in areas that lacked them to experimentally test the hypothesis that the high water flows adjacent to

creek heads (as opposed to some other factor) create conditions that provide superior habitat for *Sesarma*.

4.3 Material and Methods

4.3.1 Study site and Species. We worked on Sapelo Island, Georgia, USA (31.4775° N, 81.2417° W). Marshes in this region are typical of southeastern U.S. Atlantic Coast (Pomeroy and Wiegert 1981), with lower and intermediate marsh elevations dominated by the grass *Spartina alterniflora*. The herbivorous crab *Sesarma reticulatum* is common at creek heads (Teal 1958; Vu et al. 2016). The study sites contain headward-eroding tidal creeks that are moving ~1.9 m per year inland in locations where the marsh platform was previously characterized by low creek density (Hughes et al. 2009). The heads of these growing creeks consist of a fan-shaped depression up to 0.50 m deep that can be divided into distinctive zones (Fig. 4.1A) characterized by sediment and vegetative characteristics (Vu et al. 2016). At the center of the creek head, the “mud zone”, has soft sediments, multiple small crab burrows, and no vegetation. The mud zone is migrating inland into the “dead zone”, a 1-2 m wide band of firm sediment perforated by abundant crab burrows, and numerous dead *Spartina* stems. The dead zone is migrating inland into the “live zone”, a halo around the creek head that extends 15-20 m to each side and 20-40 m inland. It has firm sediments, a high density of crab burrows, and abundant live *Spartina* plants. The surrounding marsh platform, which makes up the majority of the area, has firm sediments, a low density of crab burrows, and abundant live *Spartina* plants. As the creek erodes headward into the marsh platform, sediment is deposited along the terminal borders of the mud zone and robust stands of

Spartina recolonize the area. This area (the “revegetated zone”) is characterized by soft sediment, a low density of crab burrows, and a high density of live *Spartina*.

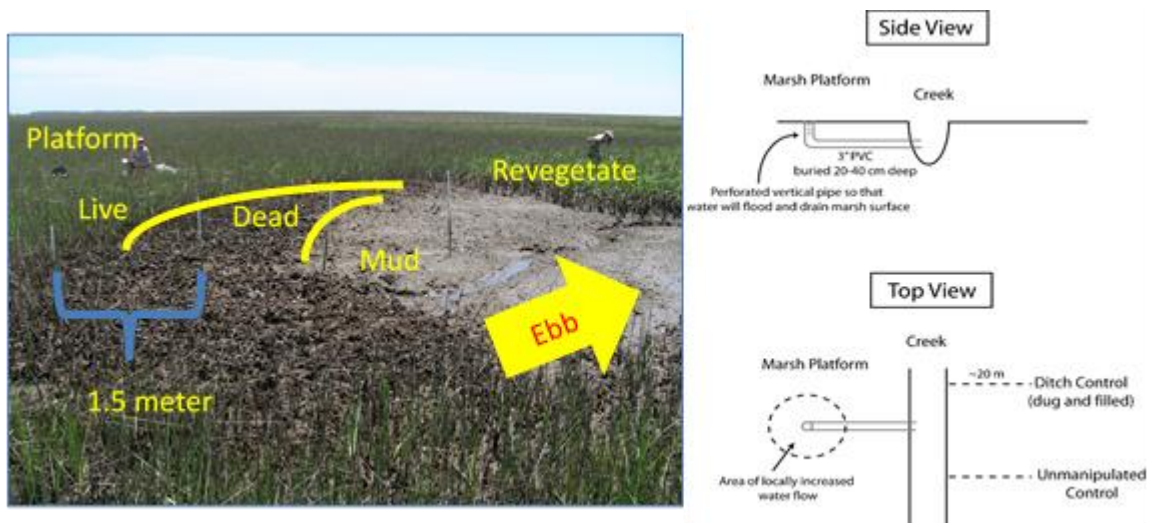


Figure 4.1. A) Distinctive zonation at creek heads (reprinted from Vu et al, in review). Zones were characterized by sediment characteristics, burrow densities, and *Spartina* shoot densities. The mud zone at the center of the creek head has soft sediments, multiple small crab burrows, and no vegetation. The dead zone is a 1-2 m wide band of firm sediments perforated by abundant large burrows, supporting numerous standing-dead *Spartina* stems. The live zone is characterized by firm sediments, a high density of crab burrows, and live *Spartina* stems. The surrounding marsh platform is characterized by firm sediments, a low density of crab burrows, and a high density of live *Spartina* stems. Creek heads grow forward into the marsh platform but sediment is deposited at the back and *Spartina* recolonizes. We refer to this area as the revegetated zone which is characterized by soft sediment, low density of crab burrow, and high density of live *Spartina* stems. B) Schematic for artificial creek manipulation experiment.

4.3.2 Do abiotic conditions differ among different micro-habitats? To identify abiotic factors that might attract crabs to creek heads, we measured temperature, dissolved oxygen levels, and hydrogen sulfide levels at the marsh platform and in the different creek head zones.

Temperature. We measured surface and sub-surface (10 cm below marsh surface) temperature using an infra-red handheld thermometer at six micro-habitats (platform,

live, live/dead, dead, mud, and revegetated) of three creek heads (n=4/micro-habitat/creek) on June 2014 during low tide. We compared the temperature among the different microhabitat using one-way ANOVAs with Tukey HSD post-hoc means comparisons.

Hydrogen sulfide concentrations. We measured hydrogen sulfide concentrations in the water from crab burrows at five micro-habitats (platform, live, dead, mud, and revegetated) at each of 10 creek heads on June 2013. We collected 60 ml water samples from crab burrows using a syringe with 10 cm of plastic tubing. Tubing was rinsed with distilled water before reuse. Samples were placed on ice and taken back to the lab for analysis. Hydrogen sulfide concentrations were determined using the Hatch hydrogen sulfide test kit (Model HS-C). We compared the differences in sulfide concentration among the different zones using a one-way ANOVA with Tukey HSD post-hoc means comparisons.

Dissolved oxygen concentrations. We measured dissolved oxygen levels in the water from crab burrows at five micro-habitats (platform, live, dead, mud, and revegetated) at each of six creek heads on June 2013. We collected 60 ml water samples from crab burrows using a syringe with 10 cm of plastic tubing. Tubing was rinsed with distilled water before reuse. Samples were placed on ice and taken back to the lab for analysis. Dissolved oxygen concentrations were determined using the Hatch dissolved oxygen test kit (Model OX-2P). We compared the differences in dissolved oxygen concentration among the different zones using a one-way ANOVA with Tukey HSD post-hoc means comparisons.

4.3.3 Do conditions created by creek heads attract crabs? To test the hypothesis that the abiotic conditions creek heads attract crabs, we experimentally created artificial creek heads by running 7.62 cm diameter PVC pipe perpendicularly from creek channels to the marsh platform in March 2012 (Fig. 4.1B). The pipes were buried at a depth of 30-40 cm and extended ~20 m from the creek bank into the marsh platform. A vertical 7.62 cm diameter PVC standpipe was attached to the platform end of the pipe. 1.25 cm holes were drilled into the vertical standpipe at 10 cm below and above the marsh surface to allow for water drainage during low tide and for the delivery of water during high tide. Water flow through the pipes on ebb tides was high enough to prevent clogging; however, pipes were checked monthly and cleaned manually as needed.

To account for the disturbance caused by installing the PVC pipes, we dug identical ditches, backfilled them and assigned these as disturbance controls. In addition, unmanipulated control areas were marked but not disturbed. A dummy PVC “standpipe” was installed at each of the control treatments. Each of these three treatments was replicated 6 times, for a total of 18 units, and the three treatments were fully interspersed.

We counted crab burrows in a permanent plot (0.5 m x 0.5 m) centered on each of the standpipes on July 2015. We counted all visible *Sesarma* (typically these were just inside burrow mouths) within two 0.5 x 0.5 m plots immediately adjacent to each standpipe on July 2015. We measured changes in marsh surface elevation relative to the standpipe on July 2015. Differences in burrow densities and elevation change among the three treatments were analyzed using one-way ANOVAs with Tukey HSD post-hoc means comparisons.

4.4 Results:

Both surface and subsurface marsh temperatures were ~11-12 % cooler at the creek head zones than at the marsh platform (Surface, $F_{5,66}=7.18$, $p<0.0001$; Subsurface, $F_{5,66}=3.68$, $p<0.005$) (Fig. 4.2A & B).

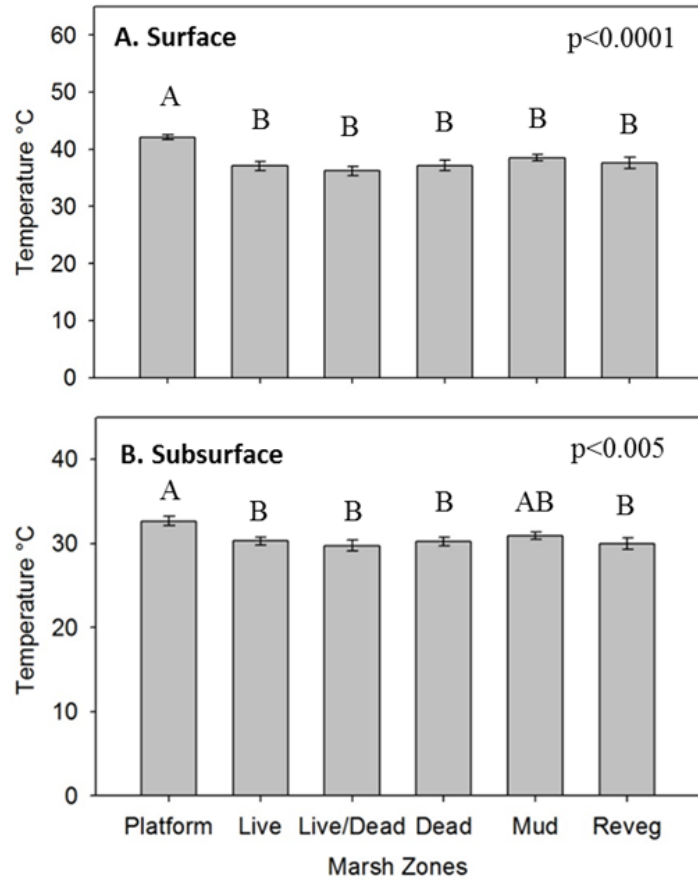


Figure 4.2 Surface (A) (ANOVA, $F_{5,66}=7.18$, $p<0.0001$) and subsurface (B) (ANOVA, $F_{5,66}=3.68$, $p<0.005$) temperature measurements at 6 marsh zones. Bars indicate means ± 1 SE. Letters above bars indicate means that are significantly different (Tukey HSD).

Hydrogen sulfide concentrations were lower (undetectable) at the Live and Dead zones of the creek head than on the marsh platform (0.0 mg/L versus ~0.58 mg/L).

Hydrogen sulfide concentrations increased again in the Mud and Revegetated zones of

the creek heads ($F_{4,45}=11.88$, $p<0.0001$) (Fig. 4.3). Water flowing through interconnecting burrows during ebb tide resulted in a ~two-fold higher concentration of dissolved oxygen at the Live and Dead zones compared to the marsh platform, but dissolved oxygen concentrations dropped again in the Mud and Revegetated zones ($F_{4,25}=31.31$, $p<0.0001$) (Fig. 4.4).

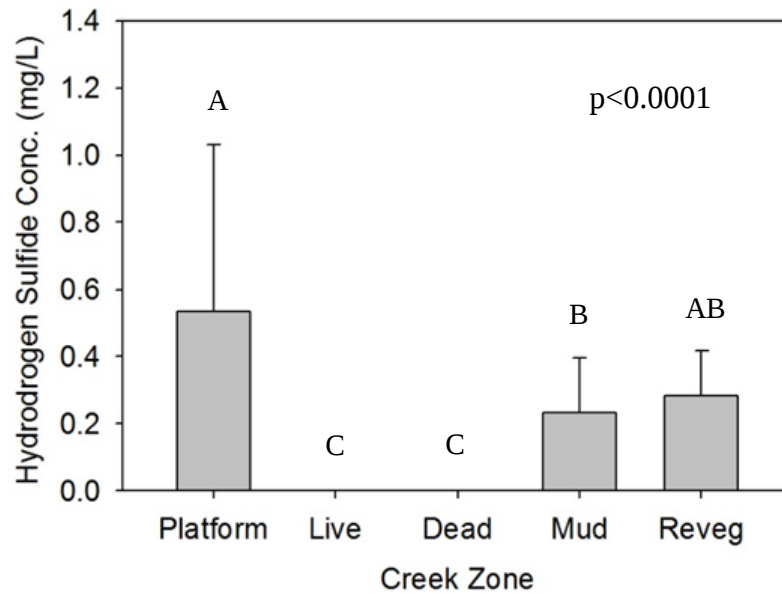


Figure 4.3 Hydrogen sulfide concentrations in burrow water at 6 marsh zones (ANOVA, $F_{4,45}=11.88$, $p<0.0001$). Bars indicate means $\pm$ 1 SE. Letters above bars indicate means that are significantly different (Tukey HSD).

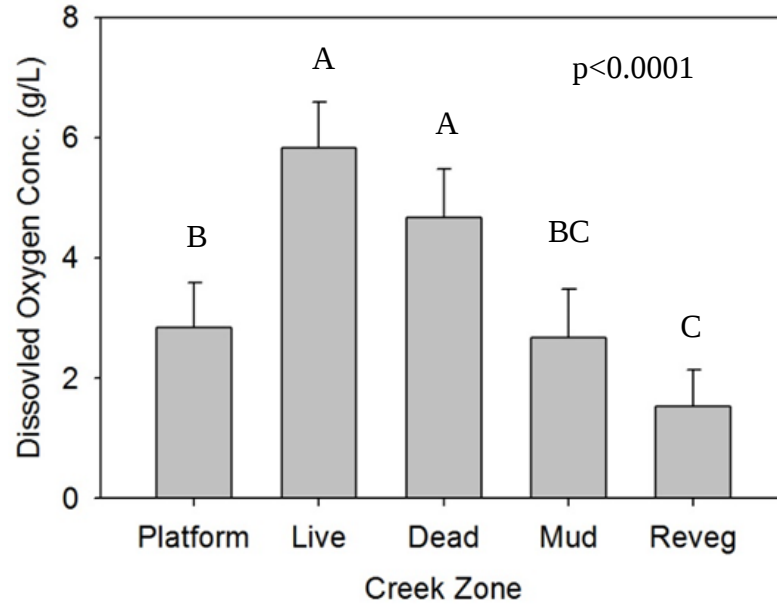


Figure 4.4 Dissolved oxygen concentrations in burrow water 6 marsh zones (ANOVA, $F_{4,25}=31.31$, $p<0.0001$). Bars indicate means $\pm$ 1 SE. Letters above bars indicate means that are significantly different (Tukey HSD).

Burrow densities initially did not differ among treatments in the artificial creek experiment, but increased over time in the pipe treatment compared to the two control treatments (2012, $F_{2,33}=0.08$, $p=0.92$; 2015, $F_{2,33}=15.04$, $p<0.0001$) (Fig. 4.5). *Sesarma* were common in the pipe treatment but not observed in the two control treatments ($F_{2,15}=8.93$, $p=0.003$) (Fig. 4.6). All of the treatments experienced some erosion around the standpipe ($F_{2,15}=8.19$, $p=0.004$) (Fig. 4.7); however, erosion was 3-7 fold higher in the pipe treatment than in the control treatments.

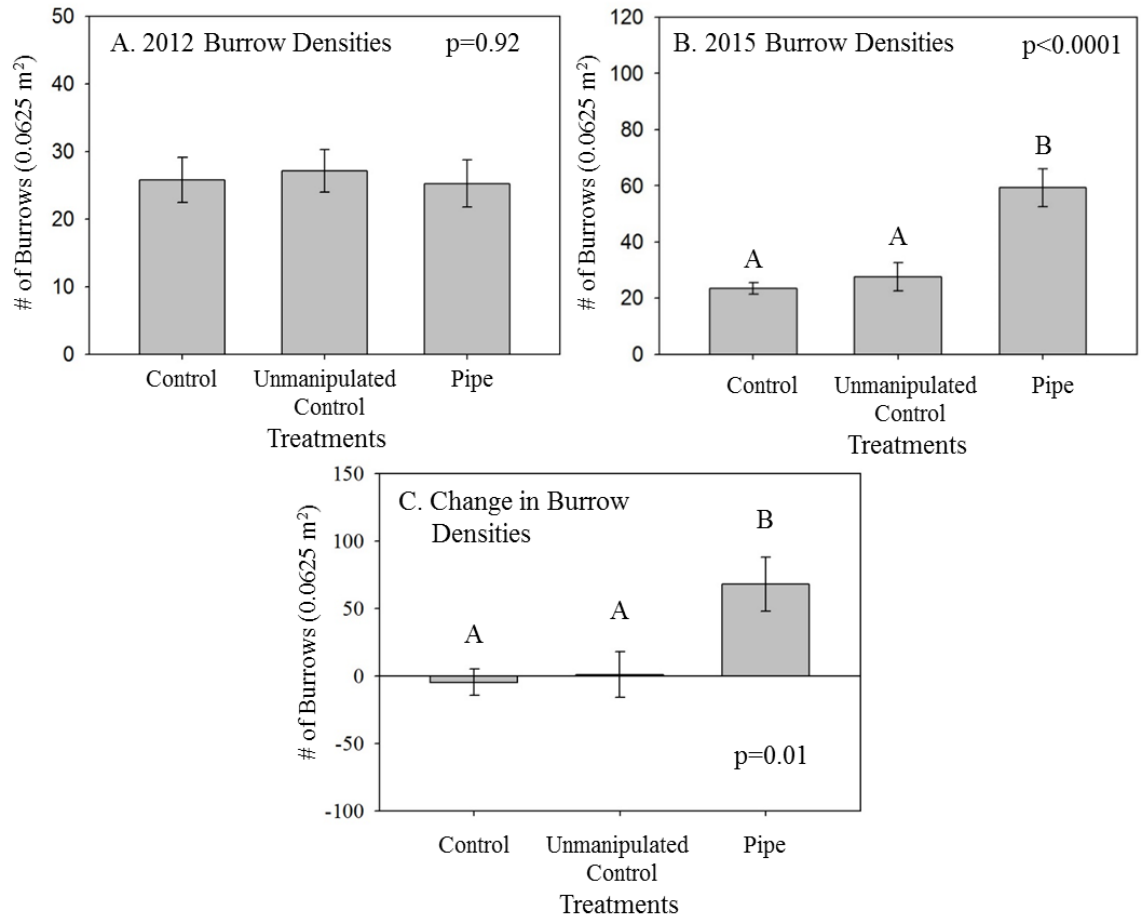


Figure 4.5 Burrow density in A) July 2012 (ANOVA, $F_{2,33}=0.08$, $p=0.92$); B) July 2015 (ANOVA, $F_{2,33}=15.04$, $p<0.0001$); and C) change in the number of burrows at the control, unmanipulated control, and pipe treatments after 3 years (ANOVA, $F_{2,15}=6.29$, $p=0.01$). Bars indicate means $\pm$ 1 SE. Letters above bars indicate means that are significantly different (Tukey HSD).

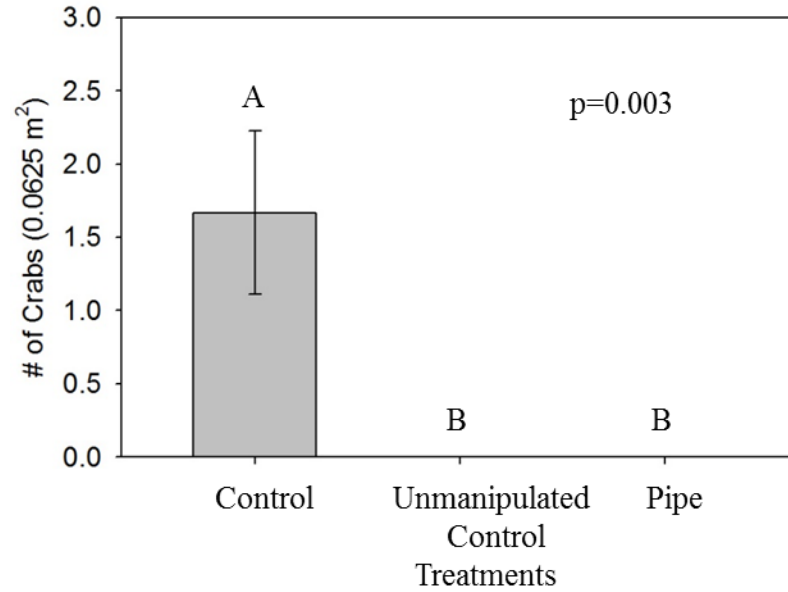


Figure 4.6 Number of *Sesarma* counted in the control, unmanipulated control, and pipe treatments in July 2015. Bars indicate means $\pm$ 1 SE. Letters above bars indicate means that are significantly different (Tukey HSD).

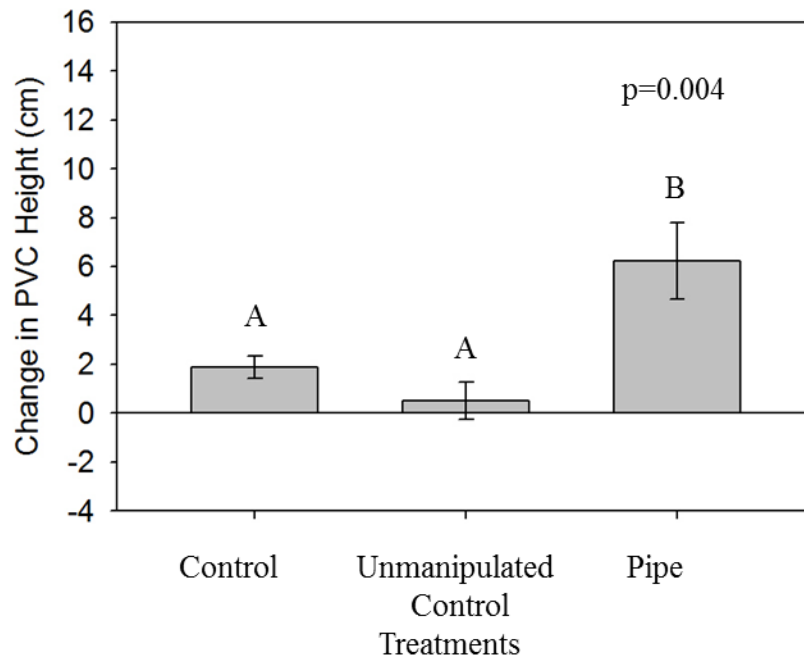


Figure 4.7 Change in marsh elevations at the control, unmanipulated control, and pipe treatments after 3 years. An increase in height indicates erosion or subsidence of the sediment around the base of the PVC pipe (ANOVA, $F_{2,15}=8.19$, $p=0.004$). Bars indicate means $\pm$ 1 SE. Letters above bars indicate means that are significantly different (Tukey HSD).

4.5 Discussion

High densities of consumers can quickly deplete local resources, forcing individuals to aggregate and form a front along the fringes of remaining resources (Silliman et al. 2005, Silliman et al. 2013). We found that the *Sesarma* fronts are tightly constrained to the eroding front edge of creek heads due to abiotic conditions. The leading edge of creek heads provided superior habitats for *Sesarma* than trailing edge or the marsh platform. In particular, we found that the leading edge of creeks were cooler, had higher dissolved oxygen and lower sulfide concentrations than any other locations on the marsh. *Sesarma* preferred areas that mimic creek head conditions. Burrow activities increased due to *Sesarma* aggregation resulting in higher rates of erosion and subsidence of the marsh platform. For *Sesarma*, abiotic constraints limit *Sesarma* front to the leading edge of creek heads, thus, driving the asymmetrical growth of creek heads as front moves further into the marsh. Similar physical constraints could provide explanations to asymmetrical consumer front in other ecosystem.

4.5.1 Abiotic condition drives asymmetrical growth of *Sesarma* front. In salt marshes, burrowing crabs are exposed to high level of naturally occurring toxic compounds in burrow water at low tide (Johns et al. 1997, Vopel and Hancock 2005). However, creek heads are localized depression on the marsh surface, therefore, water funnels to the area during the outgoing tide (Hughes et al. 2009). High water flow at creek heads create superior habitat for *Sesarma*. Temperature, dissolved oxygen and hydrogen sulfide concentrations were best in the leading edge of creek heads. While we did not directly measure toxicity, both low oxygen and high hydrogen sulfide concentrations are widely known to be harmful to macrofauna (Nicholls 1975, Diaz and

Rosenberg 1995, Johns et al. 1997, Brill et al. 2015). This likely explains why *Sesarma* is associated with leading edge of creek heads. The trailing edge of creek heads is characterized soupy, unconsolidated sediment which are unable to support crab burrows (Bertness et al. 2009). The lack of burrows limits gas exchange and tidal flushing of toxic compound resulting in lower dissolved oxygen and higher hydrogen sulfide concentrations, than the leading edge of creek heads, where burrows were more common. Thus, creek growth is driven by a positive feedback between *Sesarma* crabs, which accelerate erosion, and creeks, which create conditions favorable for *Sesarma* crabs. The absence of *Sesarma* from the trailing edges of creek heads is critical because it allows the trailing edges to revegetate, creating the observed asymmetric movement of the *Sesarma* front.

4.5.2 Hydrology drives *Sesarma* aggregation. Physical factors (i.e. water flow) can determine the aggregation rate of many benthic invertebrate species (Eckman 1996, Evin and Talley 2000). We found that burrow densities increased when the hydrological conditions were manipulated on the marsh platform. In addition, higher densities of *Sesarma* were observed at the pipe treatment than the controls. The artificial plumbing of the marsh by the pipe treatment increased water flow; making the area superior habitat relative to the controls. This showed that hydrological changes are sufficient to attract *Sesarma* and that underlying physical factors that determine creek locations (soil shear strength, sedimentation, etc.) were not important.

Once established, *Sesarma* fronts can denude an area of *Spartina*, effecting ecosystem processes (Holdredge et al. 2008, Hughes et al. 2009, Wilson et al. 2012, Vu et al. 2016). *Sesarma* front consumes plants and excavates soil and thereby increases

water flow and erosion of marsh sediment (Hughes et al. 2009, Vu et al. 2016). In addition, interconnecting *Sesarma* burrows increase percolation rates and oxygen penetration into the marsh, thereby increasing decomposition of organic matter. The loss of this organic matter layer reduces the integrity of the marsh soil and ultimately increases the erosion potential of the sediment by 80% (Wilson et al. 2012).

4.5.3 Movement of *Sesarma* front limited by creek structure. The rate of consumer front movement is usually tied to consumer mobility (Duncan 1984, Elkinton and Liebhold 1990, Scheibling et al. 1999). In this case, front movement is slow despite *Sesarma* being mobile. Movement of *Sesarma* front is closely associated with the rate of creek growth (Hughes et al. 2009, Wilson et al. 2012, Vu et al. 2016). Marsh soil are peaty in nature, consisting of a dense layer of live and dead plant matter. The roots and rhizomes of marsh plants bind soil and create a stronger more cohesive substrate that hinder erosion necessary for creek growth. While *Sesarma* herbivory and burrowing activities can increase the erodibility of the marsh soil (Wilson et al. 2012, Vu et al. 2016); these processes are slow. Therefore, the physical structure of the creek constrains the movement of the *Sesarma* front.

4.5.4 Geographic variation in *Sesarma* front patterns. Patterns of *Sesarma* front formation and movement are different in northeastern than southeastern Atlantic US marshes. Anthropogenic induced changes can significant impact on the formation and movement of *Sesarma* front. The removal of predators that would otherwise consume *Sesarma* is a key force in driving the local *Sesarma* population increase (Altieri et al. 2012). In the absence of top-down control by predators, *Sesarma* crabs aggregate and freely propagate throughout the marsh. In New England marsh, *Sesarma* prefers to

aggregate along creek banks, perhaps due to the superior abiotic condition provided by the tidal flushing from the adjacent creek. Unlike the *Sesarma* front in the southeastern Atlantic Coast that are restricted to the creek heads, the front in New England quickly moves higher into the marsh toward the remaining vegetation and away from the creek banks, decimating dozens of marshes in the northeastern US (Altieri et al. 2012, Bertness and Coverdale 2013). A potential explanation for the rapid propagation of the front could be that extensive historical ditching has altered the hydrological conditions of these marshes and increased suitable habitat for *Sesarma* (Silliman et al. 2009, Vincent et al. 2013).

4.5.5 Conclusion

High densities of consumers can quickly deplete local resources, forcing individuals to aggregate and form a front along the fringes of remaining resources (Silliman et al. 2005, Silliman et al. 2013). We found that the *Sesarma* fronts are tightly constrained to the eroding front edge of creek heads due to abiotic conditions. The leading edge of creek heads provided superior habitats for *Sesarma* than trailing edge or the marsh platform. In particular, we found that the leading edge of creeks were cooler, had higher dissolved oxygen and lower sulfide concentrations than any other locations on the marsh. *Sesarma* preferred areas that mimic creek head conditions. Burrow activities increased due to *Sesarma* aggregation resulting in higher rates of erosion and subsidence of the marsh platform. For *Sesarma*, abiotic constraints limit *Sesarma* front to the leading edge of creek heads, thus, driving the asymmetrical growth of creek heads as front moves further into the marsh. Similar physical constraints could provide explanations to asymmetrical consumer front in other ecosystem.

Chapter 5

General discussion

Understanding how organisms and ecological systems respond to global change is of great interest to ecologists. Global sea-level rises are threatening salt marshes worldwide (Mitsch and Gosselink 2000). Therefore, it is crucial to understand how global changes affect salt marsh organisms and ecosystem processes will help conserve and manage these ecosystems. In this dissertation, I provided an explanation to why tidal creeks are growing rapidly along the South Atlantic Bight. In particular, I linked crabs to the unique headward eroding creeks observed in this region and identified potential mechanisms that drive creek growth.

I proposed that there are biophysical feedbacks in tidal creek formation (Fig. 5.1). The presence of *Sesarma* induces changes to many ecosystem processes (removal of sediment, decomposition of organic matter, etc.) that enables the creeks to rapidly erode headward into the marsh platform. As the creeks grow into the marsh platform, they improve hydrological conditions, thus enhancing abiotic factors, making the area conducive to *Sesarma* aggregation. The growth tidal creeks into the marsh platform allows for water to flood and drain off the marsh more efficiently and, thus, increases the resiliency of the marsh to sea-level rise.

My work supports the notion of a link between crab activity and rapid headward erosion of creeks (Escapa et al. 2007, Hughes et al. 2009, Wilson et al. 2012). My results agree with this concept. However, my data provide important insights into the mechanisms by which crabs mediate tidal creek formation in southern Atlantic tidal marshes of the US. I found that the herbivorous crab, *Sesarma*, is the primary crab species mediating creek growth through multiple mechanisms (direct excavation of sediments, removal of plants, increased erosion, and decomposition of subsurface soil).

Positive feedbacks from *Sesarma* herbivory and bioturbation at the leading edge of creek heads enable creeks to rapidly grow into the marsh.

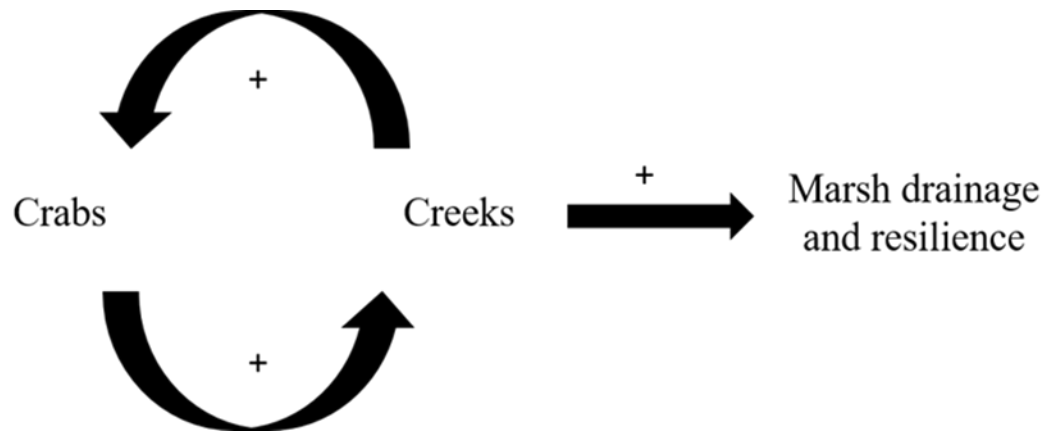


Figure 5.1: Conceptual diagram illustrating the abiotic and biotic drivers of tidal creek formation in southeastern US Atlantic salt marshes. Crab herbivory and bioturbation increases the erodibility of the marsh, leading to the rapid growth of creeks into the marsh platform. As the creeks headward erode, enhancing abiotic conditions of the marsh platform through increased water flow and drive crab aggregation to the area. The asymmetrical growth of tidal creeks increases the drainage efficiency of the marsh and allowing the marsh to cope with sea-level rise.

Sesarma can quickly denude the marsh of *Spartina* (Holdredge et al. 2008).

However, this phenomenon is absent in southeastern US Atlantic marshes. A potential explanation for this geographical disparity is predation pressure (Frank 2008, Ripple et al. 2014, Rizzari et al. 2014). In New England marshes, high densities of *Sesarma* could be attributed to human-induced removal of predators (fish and birds), that would otherwise consume *Sesarma* (Altieri et al. 2012). This allows *Sesarma* population to increase and move unhindered throughout the marsh. On the other hand, in southeastern marshes, the white tipped mud crab, *Eurytium limosum*, readily consumed *Sesarma* in laboratory feeding trials. Furthermore, in the presence of *Eurytium*, *Sesarma* did less damage to its

food plant *Spartina*. *Sesarma* prefer to feed on and grow better on below-ground rhizomes than above-ground leaves; however, the costs of digging burrows to access rhizomes leads to higher mortality if rhizomes are the only diet option. This suggests that predators changed the feeding behavior of *Sesarma*, and that these changes affected both *Sesarma* fitness and *Spartina* productivity. The top-down control of intermediate predators such as *Eurytium* may explain why *Sesarma* induced die-offs are not as common in southern marshes as they are in northern marshes, where heavy fishing pressure has removed many predators of *Sesarma* (Altieri et al. 2012).

Sesarma is very common at the leading edge of creek heads and rare elsewhere on the marsh platform (Vu et al. 2016). At the leading edge of creek heads, increased water flow during ebb tide creates micro-habitats that are cooler, have higher dissolved oxygen and lower hydrogen sulfide concentrations, making them better habitats for *Sesarma* to aggregate than the trailing edge or the marsh platform. In addition, when hydrological conditions were experimentally altered in ‘unfavorable’ locations (areas of the marsh platform that historically lacked tidal creeks), the number of crab burrows and *Sesarma* densities increased at these artificial creek sites. This suggests that hydrology alone is responsible for driving *Sesarma* aggregation and the tight association of *Sesarma* with creek heads.

In addition to driving aggregation, abiotic factors are responsible for mediating the movement of *Sesarma* fronts through the marsh. In New England marshes, increased tidal flushing along the creek banks drives *Sesarma* aggregation to the area and as *Sesarma* densities increase, food resources quickly diminish (Holdredge et al. 2008, Altieri et al. 2012). The lack of food forces the fronts to move away from the creek bank

and onto the marsh platform. Extensive historical ditching of New England marshes for mosquito control significantly altered the hydrology of these marshes and greatly increased the suitable habitat for *Sesarma*, allowing the *Sesarma* fronts to move unhindered. However, *Sesarma* fronts in southeastern Atlantic US salt marshes are driven by abiotic factors and they are unique in several ways. They are tightly associated with physical structures (creek heads). Rather than expanding, the *Sesarma* front remains compact, moving forward with the creek head as it erodes and enhances abiotic conditions through the marsh. The front moves asymmetrically (only in one direction) and the crabs do not colonize the back of the creek due to low dissolved oxygen and high hydrogen sulfide concentrations. This suggests that as the creeks grow, they provide positive feedbacks (improved abiotic conditions), that attract *Sesarma* to the area.

In summary, my dissertation work provides important insights into how global changes are affecting salt marshes. In particular, abiotic and biotic interactions can mitigate the negative effects of global sea-level rise. I have shown that creek growth is driven by a positive feedback between *Sesarma* crabs, which accelerate erosion, and creeks, which create conditions favorable for *Sesarma* crabs. While *Sesarma* could be characterized as having negative impacts at creek heads by removing plants and increasing erosion, the overall effect of *Sesarma* on marsh geomorphology is likely positive. As sea-level rises, the amount of water moving on and off the marsh platform with each tide (the tidal prism) will increase. In the absence of a creek network with the capacity to handle this tidal prism, the likely result would be increased ponding of water on the marsh platform at ebb tide, which would be deleterious to marsh plants. Thus, by promoting creek growth, *Sesarma* may be increasing marsh resilience to sea level rise.

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