THE IMPACT OF SEA LEVEL RISE ON FIDDLER CRAB (UCA PUGNAX) POPULATIONS IN SOUTHERN DELAWARE SALT MARSHES

by

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A thesis submitted to the Faculty of the University of Delaware in partial fulfillment of the requirements for the degree of Master of Science in Marine Studies

Summer 2014

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ACKNOWLEDGMENTS

“Learn from yesterday, live for today, hope for tomorrow. The important thing is not to stop questioning” - Albert Einstein

My greatest appreciation goes to my advisor, Dr. Douglas C. Miller, for guiding me through this whole process with wisdom, experience, and encouragement, while giving me the freedom to learn and develop confidence in my own skills. I would also like to thank my other committee members, Dr. Jonathan H. Cohen and Dr. Charles E. Epifanio, for their diligent support, positive attitude, and direction with this project. I want to extend further gratitude to Dr. Cohen for the additional mentorship he provided during the beginning of my graduate career on a separate larval behavior research project and in multiple classes. I also wish to recognize Dr. Robert Scarborough of DNREC for his assistance with SLAMM modeling, and acting as my tech support in desperate and frustrating times of need. Furthermore, I would like to acknowledge the funding from Delaware Sea Grant and the University of Delaware that made this work all possible.

Additional thanks goes to my labmates and interns that taught me, helped me, kept me sane, and made work fun: Emily Maung-Douglass, Emily Olson, Meghan Owings, Ian Combs, Samantha Goodwin, Geoff Udoﬀ, Joanna Marrufo, and Seaver Wang. I also truly appreciate all the assistance and support I received from Janis Lopez, Peggy Conlon, Joe Scudlark, Marcia Pettay, and the rest of the SMSP staff along the way. I am grateful to Solid Ground Community Church and all of the lovely
people there who kept me grounded in my faith, provided me with reassurance, a support system, and a home away from home during my time in Delaware. Finally, a big thank you to all of my family and friends near and far who put up with stressed-out “grad school Cynthia” for the past couple years, and provided the encouragement and support I needed whether you understood my research or not; especially Troy Ferrio who faithfully endured a long distance relationship the entire time without ever ceasing to believe in me. I could not have done it without you. Thank you all for helping make this possible.
DEDICATION

I dedicate this thesis to my mother, Joleen R. Hanson, who is my continual inspiration to never stop learning. She has always encouraged me to followed my passions and use my talents to the best of my ability, while providing support every step of the way. Leading by example she has reminded me that knowledge and curiosity are gifts, and nothing is impossible with enough determination and prayer. Love and thanks Mom.
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ABSTRACT

While the fiddler crab, *Uca pugnax*, is a dominant macrofaunal species in coastal salt marshes along the Atlantic coast of the United States, little research has been done to characterize their population distributions in the Mid-Atlantic. With this region facing increased rates of sea level rise (SLR) due to geological land subsidence and other hydrological factors, understanding local crab populations and how they will be affected by SLR is important to further understanding the ability of marshes in the region to survive and recover. In this thesis, I use data from field surveys to characterize *Uca pugnax* distribution for two representative southern Delaware salt marshes (Broadkill and Canary Creek) and generate models of fiddler crab presence and abundance. I compare these models with SLR model predictions for the same study marshes to predict how crab distribution may change with SLR, and determine what this means for marsh habitats in the future. The *Uca pugnax* surveys revealed that local populations are present throughout the entirety of the marshes, except for areas of vegetation dieback and pond formation where the substrates are flooded and inhospitable for burrows. Abundances of *Uca pugnax* are consistently highest in areas conducive to burrowing and near water banks, including the edges of some of the dead ponds. Sea level affecting marshes model (SLAMM) simulations showed no loss—and even growth in Canary Creek—in *Uca pugnax* habitat until sea levels surpassed a threshold of 0.5 m of rise; after which both marshes saw sharp declines of 60-100% of suitable habitat and predicted losses of millions of crabs. To examine the effects of population crowding caused by the loss of habitat on *Uca pugnax*, I conducted an
enclosure field experiment in Canary Creek marsh. However, due to a breach in the enclosures all that could be confirmed was that when crowded, fiddler crabs will distribute themselves to a preferred density of ~50 crabs/m$^2$ with a male-biased sex ratio of 1.4:1. Overall, this indicates that *Uca pugnax* may spread landward with marsh migration, and adapt to different habitat types in an attempt to distribute themselves as preferred habitats disappear. My research suggests that high levels of SLR in the future will eliminate the majority of marshland and suitable *Uca pugnax* habitat in southern Delaware. Unless steps are taken toward wetland conservation and climate management, this will have a strong negative effect on crab population size and distribution.
Chapter 1

INTRODUCTION AND LITERATURE REVIEW

1.1 Introduction

The Atlantic marsh fiddler crab, *Uca pugnax*, is the dominant macrofauna in salt marsh habitats along the east coast of the United States, and is important to maintaining natural ecosystem functioning (Wolf et al. 1975; Katz 1980; Montague 1980; Hoffman et al. 1984; Bertness 1985; Grimes et al. 1989; Gribsholt et al. 2003; Holdredge et al. 2010). The spatial distribution of *Uca pugnax* populations has been well documented in salt marshes along the Atlantic coast of the United States to the north in New England (Katz 1980; Bertness and Miller 1984; Bertness 1985; Holdredge et al. 2010; Luk and Zajac 2013), and to the south in Georgia and the Carolinas (Teal 1958; Wolf et al. 1975; Aspey 1978; Cammen et al. 1984; Colby and Fonseca 1984; Behum et al. 2005). However, there are few data available on fiddler crab distributions in Mid-Atlantic salt marshes where rates of sea level rise (SLR) are rising more quickly than the global average (Davis 1987; Phillips 1986; Ericson et al. 2006; Kreeger et al. 2010; Sallenger et al. 2012).

High rates of SLR put those marsh habitats that avoid complete inundation at risk of drastic structural and environmental changes (Brinson et al. 1995; Christian et al. 2000; Gedan et al. 2009; Smith 2009; Kreeger et al. 2010; Luk and Zajac 2013; Wetz and Yoskowitz 2013), limiting the space and resources available to resident species such as *Uca pugnax*. Because of their regulatory role in the marsh, fiddler
crabs may be integral to the restoration and recovery of new marshlands (Levine et al. 1998; Luk and Zajac 2013); so predicting how the environment and *Uca pugnax* populations will be affected by SLR could aid in planning conservation efforts and the preservation of marsh ecosystems in the future. The main purpose of this thesis is to assess the *Uca pugnax* populations in southern Delaware marshes in order to characterize Mid-Atlantic fiddler crab distributions, as well as determine the scale of the potential impact that SLR will have on the local saltmarsh habitat and crab populations. This chapter aims to introduce my research project and discuss the large body of literature on *Uca pugnax*, SLR, and marsh morphology; summarizing the sections that are relevant to this study of Delaware and the Mid-Atlantic.

1.2 The Atlantic Marsh Fiddler Crab (*Uca pugnax*)

1.2.1 Biological Description

The Atlantic marsh fiddler crab, *Uca pugnax*, is one of the most abundant and bio-energetically significant organisms found in the salt marsh ecosystem on the east coast of the United States, ranging from Cape Cod in Massachusetts to Florida and the Gulf of Mexico (Wolf et al. 1975; Barnwell and Thurman 1984; Grimes et al. 1989; Bergey and Weis 2008; Nabout et al. 2010; Thurman et al. 2010). The carapace of an adult male is typically around 23 mm wide with the female measuring only 18 mm and is mostly brown in color with a bright blue patch on the anterior margin near the eyestalks. Fiddler crabs are also sexually dimorphic in that males have one enlarged chela and females have two small chelae (Grimes et al. 1989; Bergey and Weis 2008).

*Uca pugnax* are very resilient and adaptable organisms, and to survive in the variable conditions of the marsh ecosystem they have developed a tolerance to a range
of temperatures, oxygen levels, and salinities (Teal 1958; Grimes et al. 1989; Shock et al. 2009; Nabout et al. 2010; Thurman et al. 2010). These crabs can even adjust to geographic displacement/ altered tidal cycles (Lopez-Duarte et al. 2011), and varying levels of pollution ranging from oil spills to sewage and organic contaminants (Berger and Weis 2008).

While they provide a food source for various predatory species of fish, shorebirds, mammals, and even larger crabs (Grimes et al. 1989; Bergey and Weis 2008), *Uca pugnax* are primarily detritivores. They forage during low tide and sift organic matter, microbes, and meiofauna from the substrate with their minor chelae and mouthparts, while discarding indigestible material as fecal pellets (Montague 1980; Robertson et al. 1980; Grimes et al. 1989).

1.2.2 Behavior

Adult *Uca pugnax* are semi-terrestrial and dig burrows in the marsh sediments for short term uses such as protection and access to water, as well as longer term uses like molting and reproduction (Bertness and Miller 1984; Genoni 1991). Fiddler crabs typically leave burrows on a daily basis to feed, and exhibit some burrow fidelity. However, if an old burrow is stolen due to intraspecific burrow competition, a crab will often dig a new burrow rather than fight to reclaim it (Bertness and Miller 1984). In a study by Genoni in 1991 it was also found that under certain conditions (such as low food) fiddler crabs may actively dig additional burrows even if there are unoccupied ones available. *Uca pugnax* exhibit relatively aggressive and agonistic behavior toward other species in the area when competing for burrows. While this competition has no effect on the *Uca pugnax* population, they can have a negative effect on the other species such as *Uca pugilator* (Aspey 1978).
Fiddler crabs are most active on the marsh in the spring and summer during mating season and when temperatures are typically warmer. When temperatures drop in fall and winter, they tend to stay dormant belowground in their burrows (Katz 1980). Research conducted by Colby and Fonseca (1984) found that while populations of *Uca pugnax* are typically widely dispersed during active parts of the year, the crabs become progressively more aggregated during inactive winter periods in burrows. This could be due to reduced competition or physical limitations of the substrate to support burrows only in certain areas. Similar to the crabs themselves, populations of *Uca pugnax* also show resilience long term, and have been shown to recover from losses of 65-70% in only a couple of years (Cammen et al. 1984).

**1.2.3 Reproduction and Development**

The spawning season for *Uca pugnax* is typically from mid-June through September, with females often able to produce multiple clutches of eggs in a season and larvae reaching peak abundance in August (Greenspan 1982; Lambert and Epifanio 1982). The males begin the mating process with a visual and auditory display—waving their enlarged chelae and stamping their feet—until they attract a female. A male-biased sex ratio is reported among many *Uca spp.*, and the heavy competition for females during mating season can often result in fights between males in the form of clasping their large chelae against the others’ (Johnson 2002).

When she has selected a male, the female will follow him into his burrow to mate (Grimes et al. 1989; Bergey and Weis 2008). Mating behavior is synchronized to the local tidal cycle around spring tides, with females carrying the fertilized eggs under their abdomens until they are ready to be released on the following spring tide (Greenspan 1982). Females release larvae into secondary estuaries and tidal creeks on
nocturnal spring tides, and the larvae migrate out to primary estuaries or nearby continental shelves using endogenous tidal swimming behavior (Brookins and Epifanio 1985; Epifanio et al. 1988; Lopez-Duarte et al. 2011).

Larvae develop as meroplankton through five zoeal stages and one megalopal stage, and return to the marsh as megalopae for settlement and metamorphosis on nocturnal flood tides using endogenous rhythms (Epifanio et al. 1988; DeVries et al. 1994; Tankersley and Forward 1994; Tankersley et al. 1995; Petrone et al. 2005). Settlement typically occurs in areas populated by adult conspecifics, and juveniles do not travel far after metamorphosis, so settlement patterns are good predictors of future adult population distributions (Epifanio et al. 1988; O’Connor 1993).

1.2.4 Larval Recruitment and Habitat Preferences

Juvenile fiddler crabs and newly settled megalopae have been shown to prefer similar habitats to adult conspecifics and are found in highest abundances in areas with fine muddy sediments and moderate vegetation (Behum et al. 2005). This is reflected in findings showing most returning larvae preferentially settle in areas already populated by adult crabs (O’Connor 1993). There have been several studies that suggest larvae have some control over where settlement occurs by accepting or rejecting locations based on both positive and negative environmental cues (Woodin 1991; O’Connor 1993). These cues include factors like salinity (O’Connor and Epifanio 1985; Epifanio et al. 1988), sediment type (Christy 1989; O’Connor and Judge 1997), and adult conspecific chemical cues (O’Connor and Gregg 1998; O’Connor and Judge 1999; O’Connor 2005; O’Connor and Van 2006).

Megalopae experience a drop in salinity as they leave the coastal shelf or primary estuary and enter the secondary estuary and marsh, and this thought to be the
first indicator of adult habitat to induce settlement (O’Connor and Epifanio 1985). Salinity level has been shown to act as a possible “gross filter” to separate the larval settlement and thus the population distributions of *Uca pugnax* with a relatively high salinity tolerance and a related species *Uca minax* which typically live further upstream at lower salinities (Epifanio et al. 1988). When settling, megalopae also can preferentially accept or reject areas based on sediment or habitat that they encounter. As mentioned previously, *Uca pugnax* larvae have been found to preferentially settle in similar habitats to adults with fine, muddy sediments and plenty of vegetation such as *Spartina alterniflora* for cover from predators (Christy 1989; O’Connor and Judge 1997).

O’Connor has conducted several studies that suggest chemical cues from adult fiddler crabs in both marsh water and sediments have the strongest effect on megalopal settlement and metamorphosis, causing molting 1-3 days sooner than when chemical cues were absent (O’Connor and Gregg 1998; O’Connor and Judge 1999; O’Connor 2005; O’Connor and Van 2006). This may be an adaptive strategy to help larvae find suitable habitats; rather than needing to detect and process an assemblage of other environmental cues to determine if an area is suitable for settlement and habitation, megalopae can focus on detecting a main cue that other fiddler crabs are living and surviving nearby in the area that is suitable.

1.2.5 Adult Habitat Preference

One common name of *Uca pugnax*, the “mud” fiddler crab, hints at the preferred sediment of this marsh dweller. These crabs have been known to favor fine-grained muddy substrates that are conducive to burrowing (Aspey 1978; Grimes et al. 1989), and be attracted to areas with a moderate amount of vegetation (commonly, the
cordgrass *Spartina alterniflora*) for both added structural support for burrows (Ringold 1979; Brodie et al. 2005), and protective shielding from predators (Nomann and Pennings 1998). While they are good osmoregulators and have a relatively wide salinity tolerance (Thurman et al. 2010), *Uca pugnax* prefer areas of moderate to high salinities (>15 ppt) in the marsh. This places the higher densities in the mid to lower tidal areas, and distinguishes them from neighboring *Uca minax* which favor lower salinity and a higher tidal range (Miller and Maurer 1973; Brodie et al. 2005; Shock et al. 2009). Other variable factors such as food availability, tidal exposure, and presence of other fauna may also affect *Uca pugnax* distribution within its habitat short term (Wolf et al. 1975).

Although there is little research examining population distributions and habitat preferences of fiddler crabs around the Delaware and Chesapeake Bays, there have been several studies in New England, the Carolinas, and Georgia. Two studies—one by Bertness and Miller in Rhode Island, and the other by Teal in Georgia—nicely describe the typical habitat preferences seen by *Uca pugnax* in different areas of its range.

Bertness and Miller (1984) broke down the study site marsh into three main zones characterized by vegetation and tidal elevation (Figure 1). They found that these fiddler crabs were present throughout most areas of the marsh, but that the population density of any given area was limited by the substratum composition and the ability of crabs to burrow in it. Highest abundances were found in the marsh flat tall-form *Spartina* zone, where there was moderate to high salinity and the sediments were muddy and soft with enough root mat to provide support for burrow structures. The marsh bank and short-form *Spartina* zones had lower abundances of crabs, being
either too soft without enough root support, or too thick and difficult to dig through, respectively (Bertness and Miller 1984). Root mat density is thought to be another factor in distinguishing species ranges of *Uca*, with *Uca minax* able to tolerate thicker root mass in the higher marsh areas, *Uca pugnax* dominating moderate root mat regions, and *Uca pugilator* the most prevalent species in low root mat regions (Ringold 1979). The vegetation zones defined in this study match those seen in my Delaware marshes, suggesting crabs might be distributed in a similar way in response to root mat. However, the presented changes in elevation in the Rhode Island marsh were much steeper than in the Mid-Atlantic and could also alter crab distribution (Bertness and Miller 1984; Chapter 2).

Teal (1958) went into even more detail and dissected the Georgia marshes in his study into 8 different types based on elevation, soil type, and organisms present (Figure 2). He also found *Uca pugnax* present in almost all areas of the marsh, but it was the differences in density distribution that indicated species habitat preference and the limiting range factors. Like Bertness and Miller, Teal saw the highest abundances of *Uca pugnax* in the intermediate/mid-range tidal levels where the sediments were muddy and had a moderate growth of tall *Spartina alterniflora*. He determined the primary factors that limited population range to be poor substratum composition for burrowing, salinity (lower salinities caused a decline in population), and dryness or lack of access to the streambed/estuary (Teal 1958).

A more recent study in Connecticut by Luk and Zajac (2013) had similar findings to the previously mentioned case studies, with one major difference: they suggest *Uca pugnax* are beginning to show a migratory response to SLR. As in the others, fiddler crabs were found through the entire marsh, with highest abundances in
the low marsh with tall form *Spartina alterniflora* and near the creek banks, and lowest abundances in the thick root mat of short form *Spartina alterniflora*. But this study found increased crab numbers and activity in high marsh areas with different vegetation like *Spartina patens* and *Distichlis spicata*, which the authors suggest could be the beginning of a range adaptation to changing marsh morphology initiated by increased SLR (Luk and Zajac 2013).

The marshes in southern Delaware and fringing Delaware Bay have proven to be a very suitable and preferred habitat for *Uca pugnax* as they are the dominant faunal species, and are one of the most abundant species of crab larvae in the bay and adjacent coastal shelf (Epifanio et al. 1988; Epifanio et al. 2013). However, little research has been done on population distributions of *Uca pugnax* within the marshes of the Mid-Atlantic of the United States. With SLR potentially changing the conditions of these marshes, it is important to understand the current state of populations and how they may or may not react to these changes.

### 1.2.6 Importance in the Marsh

The burrowing activity of *Uca pugnax* has been widely studied for the role it plays in the maintenance of the marsh ecosystem, making these fiddler crabs an important resident to this habitat (Figure 3). The crabs’ active burrowing creates bioturbation by digging up sediment from below the surface and mixing surface sediments downward into the burrow. This promotes drainage and nutrient mixing while increasing the surface area of the marsh, allowing increased oxygenation and aerobic decomposition to penetrate deeper into the substrate and change the sediment chemistry (Katz 1980; Grimes et al. 1989; Gribsholt et al. 2003). A typical fiddler crab burrow is U or Y shaped, sometimes connecting to other burrows, and can extend 15-
30 cm under the surface (Aspey 1978). One study found that in a year, a population of 42 crabs per m² could turnover 18% of the upper 15 cm of the entire marsh and increase the surface area by 59% (Katz 1980).

*Uca pugnax* are primarily detritivores and feed on decomposing organic matter, microorganisms, and meiofauna that they find in marsh sediments. The crabs sift through the substrate with their small chelae and mouthparts for food, creating addition bioturbation as they go. While feeding, any indigestible material is discarded as fecal pellets that are incorporated back into marsh sediments, and ultimately aid in accretion (Grimes et al. 1989). Fiddler crab grazing has been shown to be an important regulatory force of meiofauna populations and may secondarily mediate additional sediment decomposition that the meiofauna control (Montague 1980; Hoffman et al. 1984). *Uca pugnax* also play a major role in the general flow of energy and food web dynamics of the marsh; eating microbes and base organic matter while providing food for the majority of all other marsh macroorganisms, if not directly as prey, then indirectly by aiding in plant growth (Wolf et al. 1975; Luk and Zajac 2013).

The nutrient enrichment of sediments produced by burrowing along with clearing of accumulating organic material through increased decomposition and detritivorous behavior promotes production from marsh vegetation such as the cordgrass, *Spartina alterniflora* (Montague 1980; Holdredge et al. 2010; Gittman and Keller 2013). *Spartina alterniflora* is an important marsh plant which not only serves as a food source to many different organisms, but possesses roots that provide stability to the substrate and prevent erosion. Increasing cordgrass growth also aids in vertical marsh accretion, a complex process in which the marsh gains elevation through inorganic mineral sedimentation and belowground incorporation of organic matter.
(Figure 4) (Stumpf 1983; FitzGerald et al. 2008; Cahoon 2010). Plants like *Spartina alterniflora* both produce belowground growth and trap particles aboveground, doubly assisting in accretion (Turner et al. 2000; Delgado et al. 2013).

Several studies have shown that crab burrowing has a significant effect on *Spartina* growth and may actually be crucial to the maintenance of healthy, robust cordgrass populations (Bertness 1985; Holdredge et al. 2010; Thomas and Blum 2010; Gittman and Keller 2013). Fiddler crabs are able to manipulate *Spartina alterniflora* growth so well through burrowing activity that they have even used this skill to become “farmers.” *Uca pugnax* have been found to increase burrowing activity when food supply is low to promote aboveground *Spartina alterniflora* growth, allowing them to then feed on the detritus that is produced and caught by the plants (Genoni 1991). There is even the potential for fiddler crabs to increase the range of different marsh plants by “breaking ground” and increasing nutrient availability in new areas (Levine et al. 1998), exemplifying their influence over their environment.

Bertness suggested a mutualistic relationship between fiddler crabs and cordgrass in his study looking at their interaction in the marsh. He found that burrowing increased both aboveground production and belowground decomposition; while crab removal decreased aboveground production in *Spartina alterniflora* by 47%, and increased belowground root mat by 35% due to a nutrient-deficiency stress response in the plant (Bertness 1985). Through these observations, Bertness noticed that when crabs were removed the cordgrass began to resemble the “short form” of its species at higher tidal elevation where crabs typically were not found; a form that typically did not manage as well in the lower areas of the marsh. The increased root mat would also make it more difficult for new crabs to be recruited to the area to
provide the bioturbation necessary to restore the cordgrass to its original “tall form” state. He proposed that the crabs maintain the plants through burrowing activity, and in return the plants provide the support structures that the crabs depend on for their burrows (Bertness 1985). With everything between these two foundational species in balance, a functional marsh ecosystem is maintained.

There have been several studies looking at what happens when this balance is disrupted or faced with conditions outside its tolerance range. Smith and Tyrrell found that in areas where *Spartina alterniflora* is absent or has been cleared, the presence of too many fiddler crabs can prevent new growth and colonization of seedlings. The bioturbation from burrowing was shown to displace seeds and uproot new seedlings (Smith and Tyrrell 2012), which may inhibit marsh recovery. Also, while under normal circumstances the burrowing activity of *Uca pugnax* maintains a stable marsh state with *Spartina alterniflora*, it has been documented that too much bioturbation from crabs—increased perhaps by lack of vegetation (Genoni 1991) or a disproportionately large number of crabs—can actually slow the process of marsh accretion (Thomas 2004). This is due to a shift in the balance of belowground production and decomposition; disproportionately increasing decomposition while limiting production and causing most of the organic matter in the soil to decompose faster than it can be produced. Because belowground production is the largest addition of organic matter to the soil and a large part of marsh accretion is made up of compact organic matter, accretion rates slow with excessive burrowing (Thomas and Blum 2010). So if the *Uca-Spartina* balance is upset by too many burrowing crabs it puts the marsh at risk of submergence, especially when facing rapidly rising sea levels.
The role of *Uca pugnax* in maintaining the balance of the marsh ecosystem may make it a good indicator species to use as a monitor of a stable marsh. Because of their large numbers and prominence they would make an easy species to track, and the mutualistic relationship with marsh production directly ties populations to the condition of the ecosystem. Ghost crabs (*Ocypode quadrata*) are a close relative of fiddler crabs and play a similar bioenergetic role in the coastal beach ecosystems they inhabit. Several studies have already shown ghost crabs to be good bioindicators of anthropogenic and environmental impacts on their natural habitat (Turra et al. 2005; Barros 2006; Neves and Bemvenuti 2006); perhaps *Uca pugnax* could play a similar role for tidal salt marshes. Some recent research has begun to take advantage of this and uses fiddler crabs as indicators of pollutant levels in marsh habitats (Bergey and Weis 2008; Giblock and Crain 2013), but the potential exists to monitor more aspects of environmental stability in the marsh.

1.3 **Sea Level Rise**

1.3.1 **Current Rates and Predictions**

One prominent effect of the rapid warming of our planet has been that is causing the level of our oceans to rise at an increasingly rapid rate over the past couple decades (Figure 5). Sea level rise (SLR) is essentially caused by the melting of large bodies of ice such as glaciers and ice sheets as well as thermal expansion of the ocean itself (FitzGerald et al. 2008; Akumu et al. 2011). In fact, multiple studies have directly tied the increase in global SLR to the increase in global temperatures, suggesting that these mechanisms are heat-driven (Rahmstorf 2007; Vermeer and Rahmstorf 2009). As sea levels rise, the relative elevation of coastal land is lowered,
increasing flooding and inundation. This poses a threat to civilizations and natural environments near coastlines and at low altitudes, putting large amounts of land at risk of submergence. Many studies are already predicting the damage and planning prevention methods (FitzGerald et al. 2006; Glick et al. 2008; Industrial Economics Incorporated 2010; Kreeger et al. 2010; Akumu et al. 2011).

There has been a great deal of research on recent trends and predictions of rates and levels for the future. However when studying long term patterns like SLR or accretion rates it is important to consider the scale and time frame over which the data are collected and/or considered, because it can skew or alter the results drastically (Day et al. 1999; Allen 2000; Collilieux and Wöppelmann 2011; Swaney et al. 2012; Delgado et al. 2013). For example, because of its relevance, many people study global SLR rates; but because they focus on data grouped into different timeframes—groupings or numbers of years—a range of current rates have been reported with a spectrum of urgency related to the threat they pose. Most research is either focused on the current or recent historical trends, or future trends culminating around the year 2100. Global SLR began increasing in rate from a steady 1 mm/yr at the end of the 19th century (Figure 5) (Akumu et al. 2011). Predictions of current global rates range between 1.6 and 1.8 mm/yr (Church and White 2006; Domingues et al. 2008; FitzGerald et al. 2008; Akumu et al. 2011); but the predictions for 2100 vary widely from smaller ranges like 2.8-3.4 mm/yr (Church and White 2006) or 1.1-4.4 mm/yr (FitzGerald et al. 2008; Akumu et al. 2011), to larger ones like 5-14 mm/yr (Rahmstorf 2007) or even 7.5-19 mm/yr (Vermeer and Rahmstorf 2009). The greater variation in predictions is due to the uncertainty of the outcome of all the variables that contribute to SLR and climate change in general. The Intergovernmental Panel on
Climate Change (IPCC) has created a suite of scenarios to look at possible predictions with varying human influence (Table 1), but there are many non-anthropogenic factors at play as well that make SLR hard to predict with certainty (FitzGerald et al. 2008).

SLR can also vary on a smaller scale by location and conditions of an area. In New England, a study showed rates from the 20th century to be 2.4 mm/yr and predicted them to increase to at least 6 mm/yr throughout the 21st century (Gedan et al. 2011); while in Delaware rates of SLR are currently reported between 2.75-3.5 mm/yr (Thomas 2004) and predicted to have reached 8-17 mm/yr by 2100 (Kreeger et al. 2010). Regardless of the variations, the overall message seen in the literature is that SLR across the board is increasing, and most coastal wetlands are predicted to disappear by 2100 (Day et al. 1999). However, each ecosystem may respond slightly differently as a unique situation, and should be addressed as such in terms of conservation (Orson et al. 1985; Allen 2000).

1.3.2 Environmental Effects

Marshes have a natural compensatory mechanism against SLR called vertical accretion that allows them to maintain elevation and grow vertically at a comparable rate (Morris et al. 2002). Vertical accretion is a complex process that is primarily composed of inputs from aboveground inorganic mineral sedimentation and belowground incorporation of organic matter into the substrate (Figure 4) (Reed 1995; FitzGerald et al. 2008; Cahoon 2010; Kirwan and Mudd 2012). Because of its complexity, many factors affect and influence accretion rates and ability of a given marsh, including: elevation, geomorphic features, substrate density, sediment availability/supply, vegetation, plant stress, organic matter inventory, human modification/interference, tidal range, runoff, and creek/river flows (Orson et al. 1985;
Oertel et al. 1989; Orson et al. 1990; Childers et al. 1993; Chmura and Hung 2004; FitzGerald et al. 2006; French 2006; Delgado et al. 2013; Kirwan and Megenigal 2013). Numerous studies have agreed that organic accumulation contributes more to vertical accretion than mineral sedimentation (in some cases up to 5x more effective in raising elevation), and that vegetation health can be the determining factor in whether a marsh is able to keep pace with SLR (Stumpf 1983; Turner et al. 2000; Morris et al. 2002; Chmura and Hung 2004; Morris 2007).

SLR itself and the different conditions associated with it can often act as indicators in a feedback system to maintain healthy marsh accretion to keep pace with the local sea level (Reed 1995; Morris et al. 2002; Nyman et al. 2006; Cahoon 2010; Kirwan and Mudd 2012). Some research suggests that natural state marshes may have been able to adapt and change accretion rates to match the rapidly increasing rates of SLR; but because of human interference and modifications such as dikes, impoundments, and coastal development, natural accretion abilities have been inhibited and coastal marshes are no longer able to keep up with sea levels (Morris 2007; Delgado et al. 2013). There are other common geological factors in marshes that work against accretion to lower that total elevation such as decomposition, substrate compaction, and land subsidence; leaving habitats more vulnerable to the rising water (Cahoon et al. 1995; Donnelly and Bertness 2001). For this reason, most studies predict that the majority of marshes along the Atlantic coast of the US will be lost to SLR within the next century (Orson et al. 1985; Donnelly and Bertness 2001; Gedan et al. 2009; FitzGerald et al. 2008; Kreeger et al. 2010).

In addition to loss of land due to flooding and submergence, climate change and SLR are associated with other negative factors that can dramatically alter those
coastal wetlands and marshes that stay above sea level in many ways that can still make the habitats unsuitable for the organisms that they once supported. Tidal regimes are altered, changing hydrological, nutrient, and sediment flows as well as the chemical properties of the water; which often increases the overall salinity and causes saltwater incursions of freshwater habitats further inland or upstream (Brinson et al. 1995; Christian et al. 2000; Akumu et al. 2011; Wetz and Yoskowitz 2013). Increased wave action creates intensified erosion of shorelines and creek banks while overwashing foreign sediments into the environment (Brinson et al. 1995; Schwimmer 2001; Gedan et al. 2009; Hughes et al. 2009; Smith 2009). Higher sea levels also raise the water table; which decreases drainage, causes excessive ponding, and makes marshes more vulnerable to flooding and destruction from storm events which are also increased by climate change (Brinson et al. 1995; Gedan et al. 2009; Wetz and Yoskowitz 2013). The frequent flooding increases substrate saturation, salinity, and sulfide content, while drastically decreasing the redox potential (Warren and Niering 1993). As a result the marsh becomes stressed, and vegetation patterns change and migrate away from the damaged habitats, leaving the remains of the ecosystem dramatically altered in structure and function by SLR (Brinson et al. 1995; Christian et al. 2000; Gedan et al. 2009; Smith 2009; Kreeger et al. 2010; Luk and Zajac 2013; Wetz and Yoskowitz 2013).

1.3.3 Delaware and the Mid-Atlantic

While there is a global average rate, SLR is not uniform worldwide. Sea levels are actually decreasing locally in some areas, while most regions report different rates of SLR. These varying rates are based on factors like local climate, hydrology and geomorphology. Globally sea levels are rising at increasing rates as discussed above,
and unfortunately the Mid-Atlantic region of the United States is considered an SLR “hotspot,” rising even more rapidly than the global average (Kreeger et al. 2010; Sallenger et al. 2012). This is due to several dynamic processes that include both climate-induced changes to flows and hydrology of the nearby Gulf Stream, and subsidence of the Atlantic Coastal Plain (Davis 1987; Sallenger et al. 2012).

The region of Delaware Bay and surrounding wetlands are not immune to this problem, and are experiencing what is called a “destructional delta system,” where what was once the delta formed by the Delaware River has been altered by sea level rise and is deteriorating (Phillips 1986; Ericson et al. 2006). The Delmarva Peninsula is also facing rapid land subsidence (sinking) at rates around 1-2 mm/yr; a common problem of many river delta areas which is made more serious by SLR (Cahoon et al. 1995; Thomas 2004; Kreeger et al. 2010). Deltas are also less able to deal with increased SLR because they typically have slower rates of accretion, lots of loose sediments that are easily eroded, and are at greater risk of storm surge and inundation due to land subsidence (Phillips 1986; Schwimmer 2001; Ericson et al. 2006; Sallenger et al. 2012).

In Delaware, accretion rates are predicted to initially increase with SLR with current rates already reaching 3 mm/yr (Nikitina et al. 2000), but quickly plateau and fall behind due to all of the factors working to submerge the marshes (Reed et al. 2008). Unless drastic steps are taken to restore and protect local marshes to prepare them naturally for SLR by promoting accretion with flood-resistant vegetation and encouraging strong sedimentation flows, there is a high possibility many coastal wetlands around Delaware Bay will be lost (Morris 2007).
1.3.4 Effects on *Uca pugnax*

As suitable habitat disappears to SLR, resources and space will become limited. *Uca pugnax* will be forced into smaller areas and likely have a difficult time sustaining robust numbers under such stressful conditions. Not only is there the threat to adult populations of suitable habitat submersion and alteration, but larval settlement and colonization of new populations may also be at risk. As previously mentioned, megalopae use adult cues, sediment/habitat type, and changes in salinity to aid in settlement selection (O’Connor and Epifanio 1985; Epifanio et al. 1988; Christy 1989; O’Connor and Judge 1997; O’Connor and Gregg 1998; O’Connor and Judge 1999; O’Connor 2005; O’Connor and Van 2006). SLR could displace adult populations (eliminating chemical cues), alter hydrology/flow patterns of the estuaries, change the habitat type or even submerge once suitable habitat, and increase salinity further inland, all of which would interfere with natural settlement patterns (Borgianini et al. 2012). Megalopae can delay metamorphosis for several days to continue searching if suitable habitat has not been found, but studies have shown that mortality rates increase the longer they wait to molt (Christy 1989; O’Connor and Van 2006). So if SLR requires larvae to travel greater distances to settle and metamorphose, the populations may suffer lower recruitment due to larval mortality. While *Uca pugnax* has proven to be a fairly hearty and adaptable salt marsh species, it does exhibit preferences and requirements from its habitat as exemplified in the above sections. SLR and the related effects have the potential to drastically impact populations of fiddler crabs throughout the east coast.
1.4 Marsh Pooling

Marsh pooling or ponding is a phenomenon that typically occurs in marshes with poor drainage and/or areas of vegetative dieback, and there is some indication that it is increasing in coastal marshes as a result of SLR raising the water table (Allen 2000; Gedan et al. 2009). Pooling is a natural process in which multiple ponds appear and remain on the marsh surface with no direct flow to estuarine rivers or creeks; only being flushed when the tide reaches them.

There are several speculations as to how these pools are formed. A commonly suggested cause begins with the dieback of vegetation that was either smothered from wrack, overgrazed in an area, or killed off by a pathogen or drought. The dead zone then becomes depressed from lack of structure and begins to retain water (Holdredge et al. 2008; Smith 2009; Gedan et al. 2011; Wilson et al. 2012). Ponds could also simply begin as areas of low elevation (especially if below the vegetation growth elevation range) in the marsh with poor drainage that accumulate and retain water over time until pools form. These pools develop anoxic states which cause subsequent vegetation die-off, and enlarge as bordering elevation dips from lack of root support (Ewanchuk and Bertness 2004a; Hinkle and Mitsch 2005; Cahoon 2010). This type of pooling behavior has been documented to recover and vary naturally throughout marshes; but it is a slow process that can take between 2-4 years and only fully recovers in the right conditions (Ewanchuk and Bertness 2004a; Smith 2009).

Some blame for pooling has been put on human influence, claiming that more ponds are forming in marshes that have been diked or impounded due to the lack of drainage (Stocks and Grassle 2003; Hinkle and Mitsch 2005; Holdredge et al. 2008; Gedan et al. 2009). Initially and under the right conditions, these pools can have a positive effect on the marsh environment; creating a “pristine” marsh state by:
increasing plant diversity (the appearance of halophytic forbs like *Agalinis maritime, Atriplex patula, Glaux maritime, Triglochin maritimum, Limonium nashii,* and *Suaeda linearis*), providing habitat for new fish, and supplying food for a greater diversity of birds. However, pools can also hinder a marsh’s ability to deal with SLR long term, and lead to dead zones in the ecosystem (Ewanchuk and Bertness 2004a; Ewanchuk and Bertness 2004b).

Regardless of exact cause, this pattern of ponding has been seen more frequently along the Atlantic coast of the US in recent years (Ewanchuk and Bertness 2004b; Smith 2009; Gedan et al. 2011). Marsh pooling and vegetation dieback may be the early warning signs of SLR damage from within, and healthy marsh transitioning to tidal flat habitat; evidence of how ill-prepared our coastal wetlands are to deal with climate change (Luk and Zajac 2013).

### 1.5 Open Marsh Water Management

Historically there has been a great deal of human involvement and manipulation of marshes that have changed the hydrology and morphology of many areas, including building impoundments for salt hay farming as well as parallel grid ditching to increase drainage and prevent mosquito breeding (Ewanchuk and Bertness 2004a; Gedan et al. 2009). Much of this anthropogenic interference is believed to be responsible for many of the marsh problems today; including low biodiversity, drainage issues, and poor accretion for impending SLR (Niering and Warren 1980). In more recent years, there has been a large movement called “Open Marsh Water Management” (OMWM) that attempts to fix some of the damage done by these past projects and restore marshes to a more natural state through controlled manipulation.
OMWM began in the 1970s in Massachusetts but was soon adopted by Mid-Atlantic states, and was originally intended to provide better natural mosquito control than pesticides and to be healthier for the marshes than the 1930s grid ditching program (Wolfe 1996; Wolfe 2005; Lesser 2011). It eventually evolved to double as a marsh restoration project that—while following strict guidelines and protocols—uses selective manipulation of the marsh to reestablish pre-ditched marsh environments. The strategies used are tailored to each specific marsh because each situation has its own complex set of needs for the environment (Wolfe 1996; James-Pirri et al. 2009; James-Pirri et al. 2012), but they can include procedures like restoring or plugging old parallel grid ditches, and installing new closed ponds, radial ditches, and/or sill ditches (Wolfe 2005; Leisnham and Sandoval-Mohapatra 2011; James-Pirri et al. 2012) (Figure 6). Ditch-plugging alone has often been shown to act as an impoundment and severely inhibit marsh drainage. While this will create potentially desired pools, if the plugging is not supplemented with newer, better designed radial or sill ditches for drainage, the marsh could easily become waterlogged (Adamowicz and Roman 2002; Stocks and Grassle 2003; Hinkle and Mitsch 2005; Vincent et al. 2013). Some projects understand the importance of drainage with increasing SLR and are working to open manmade dikes and create channels in poorly drained areas (Teal and Weishar 2005).

The overall goals for environmental improvement from OMWM are to improve water quality through proper flow, and increase biodiversity of plants, fish, and birds at natural pond areas. The idea being that this is an improvement over the current state of most marshes that have been heavily ditched in the past, and in times of stress only a few hardy species have flourished. This work is especially focused on re-cultivating plant diversity around marsh pools in higher elevation areas that will in
turn provide food for larger fauna. Unfortunately, many of these forb plants contribute markedly less to marsh accretion rates than the hardier grasses like *Spartina alterniflora* that are currently dominant in the marsh, and may weaken the accretion response to growing SLR (Adamowicz and Roman 2002; Ewanchuk and Bertness 2004b; Gedan et al. 2011; Lesser 2011).

OMWM has been implemented in Delaware since 1979. Historic grid ditching greatly reduced pooling in the past and because of the conditions of local marshes the current plan has been to keep the flow open with no addition impoundments or ditch-plugging to create additional standing water. Instead, work focused on restoring the existing ditches, and installing closed ponds with radial and semi-open sill ditches (Figure 6). So far the project has been successful with a drop in the water table, but as with most OMWM projects it will require routine maintenance and monitoring to ensure success long term (Meredith et al. 1985; Wolfe 1996; Meredith and Lesser 2007).

1.6 Study Site Description

The Delaware Bay is a large, shallow coastal plain estuary that is primarily fed by the Delaware River to the north. The majority of its borders are made up of salt marshes and the smaller rivers and creeks that also empty into it behind a thin layer of sand beach. The bay and these adjacent wetlands at one time formed a delta for the Delaware River, but as sea level has risen the estuary has migrated further upstream and altered the system, making it a more saline and destructive environment rather than constructive one (Phillips 1986).

The wetland marshes that line Delaware Bay have varied salinities that can fluctuate between 0 and 30 ppt over the course of several years through hydrological
or storm events, but typically range between 10-20 ppt and 15-25 ppt depending on their proximity to the mouth of the bay. Tidal ranges of these marshes also vary somewhat but are approximately 1.5 m (Stocks and Grassle 2003). Marsh vegetation is dominated by *Spartina alterniflora* with patches of *Spartina patens* and *Distichlis spicata* present in higher areas and *Juncus roemerianus (gerardi)* along the landward edge (Bertness and Ellison 1987; Schwimmer 2001; Stocks and Grassle 2003). Marshes that are further inland—either further from the mouth of the bay up the Delaware River or away from the bay shore along other input flows—tend to have lower salinity and tidal ranges of around 5-18 ppt and 0.8-1.0 m respectively. However, inland salt marshes that have not fully converted into freshwater marshes will still retain a similar distribution of vegetation as those near the coast (Hinkle and Mitsch 2005).

The Broadkill River is a major freshwater flow into Delaware Bay in southern Delaware. It is representative of the many other fresh-fed inputs on the western side of the bay (such as Mispillion, Murderkill, Mill, Primehook, etc.), and similar to Delaware Bay, 85% of Broadkill River is bordered by marshland. The lower regions of the Broadkill Estuary have conditions similar to those in the bay; while the upper Broadkill Estuary fluctuates more, with slowed tidal cycles and characteristics of both a well-mixed and partially mixed estuary (Dewitt and Daiber 1973).

The state of Delaware has tidal wetlands covering approximately 8% of the state’s surface area; the highest of any state (Meredith and Lesser 2007). It also has the lowest mean elevation of any state in the United States and is relatively flat throughout; with the marshes covering its eastern coast no exception. Most local salt marshes are low in elevation and regularly flooded with the tidal cycles in the estuary.
They are also typically very flat, having less than a meter of variation in elevation range across the topography (Phillips 1986). Many Delaware marshes also have an elaborate network of ditches dug perpendicular to the main river/creek to increase drainage as part of 20th century mosquito control efforts (Meredith et al. 1985).

The two study sites that I selected for this thesis (designated “Canary Creek” and “Broadkill”) are both located within the region known as “The Great Marsh” (Figure 7). The Canary Creek site is adjacent to Roosevelt Inlet and closer to the mouth of Delaware Bay, while the Broadkill site sits further inland beside the Broadkill River. Both are ditched and regularly flooded salt marshes, and are representative of much of the salt marshland present in both the Broadkill River estuary and along the Delaware Bay coastline described above.

1.7 Hypotheses and Objectives

With this thesis I examine the species distribution of *Uca pugnax* in southern Delaware marshes with extensive field work, and predict the effects of sea level rise (SLR) on the local populations through modeling and field experiments. I propose the hypothesis that increased SLR due will negatively impact available habitat for *Uca pugnax*, limiting overall abundance and distribution of the population. To address this hypothesis, my thesis is divided into three main sections with respective chapters to examine my three primary objectives over the course of this research:

1. Characterize *Uca pugnax* distribution in Mid-Atlantic salt marshes.

2. Predict local SLR outcomes and their potential impact on marsh habitat and *Uca pugnax* populations.

3. Determine *Uca pugnax* response to crowding as an effect of habitat loss.
1.8 **Summary of Field and Laboratory Work**

In this thesis I present a description of the field research and mathematical modeling comprising my project separated into chapters. In this chapter (Chapter 1), I have provided a general overview of *Uca pugnax* as a species, the issue of SLR, other factors influencing marsh health, and a rationale for my research. I also introduce my primary hypothesis and research objectives in this chapter.

Chapter 2 focuses on the distribution of *Uca pugnax* in Southern Delaware marshes, addressing the first research objective. In this section I worked under the secondary hypotheses that *Uca pugnax* are present throughout the majority of the study marsh area, and that they are more abundant in areas of low elevation, high salinity, and moderate vegetation. The chapter covers the different field surveys that were conducted and suggests the best predictor variables for both fiddler crab presence and abundance. It presents models for presence and abundance across both study marshes, and discusses habitat preferences of the crabs, as well as what implications these current distributions and preferences may have for the population should the environment change.

Chapter 3 deals with the second research objective; examining predictions of SLR for the study region, and the potential influence it will have on the established *Uca pugnax* populations and their suitable marsh habitat. Here, I proposed the secondary hypothesis that *Uca pugnax* will lose at least 50% of suitable habitat in southern DE due to SLR by 2100. The section contains multiple SLR scenarios run in the Sea Level Affecting Marshes Model (SLAMM) and offers an analysis of potential losses considering the results of Chapter 2. A discussion of habitat change and crab survival response in the face of loss is also included.
Chapter 4 addresses the last research objective by looking at the effects of crowding on *Uca pugnax* mortality and burrowing behavior in an attempt to predict the small scale impact that loss of habitat would cause to a population as it is forced into a smaller area. It includes an enclosure field experiment to simulate different levels of crowding, in which I secondarily hypothesize that crowding increases mortality and decreases the burrowing activity of *Uca pugnax*. This section also discusses the application of these conditions to SLR-derived habitat loss and the possible responses of crab population to this loss.

Chapter 5 offers a final summary of this thesis project. It addresses the primary and secondary hypotheses with the conclusions drawn in the research, and reiterates the main points made in each chapter. Suggestions for regional applications of the findings and further study on the subject both at the local and regional scale are discussed.
Figure 1. Marsh zones characterized by tidal elevation and vegetation in a Rhode Island marsh (Bertness and Miller 1984).

Figure 2. Marsh zones characterized by tidal elevation, soil type, and organisms present in a Georgia marsh (Teal 1958).
Figure 3. A conceptual model of the integral positive influence of fiddler crabs on salt marsh ecology across their range (Grimes et al. 1989).
Figure 4. A conceptual model of the common major factors affecting salt marsh elevation, primarily the complex processes involved with vertical accretion (FitzGerald et al. 2008).
Figure 5. Global sea level rise over the past century. Current rates are estimated between 1.6 and 1.8 mm/yr and are increasing sharply (FitzGerald et al. 2008).
Figure 6. Various marsh excavations and alterations used in OMWM technique in Delaware. Intended to increase drainage and restore natural marsh hydrology. The darkened spots represent former mosquito-breeding depressions (Meredith et al. 1985).
Figure 7. Maps of study sites. *Top*: Delaware Bay and study marshes in the bay coast of southern Delaware. *Middle left*: The Great Marsh in Sussex County, DE highlighted in red. *Middle right*: Canary Creek marsh study site. *Bottom*: Broadkill marsh study site.
Table 1. Projected trends of SLR based on different IPCC warming scenarios (FitzGerald et al. 2008).

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Chapter 2

*UCA PUGNAX DISTRIBUTION IN SOUTHERN DELAWARE SALT MARSHES*

2.1 Introduction

*Uca pugnax* is the dominant and most abundant macroinvertebrate in salt marshes on the Atlantic coastline of the United States, and can usually be observed everywhere from the water’s edge to the landward border of the marsh (Bertness and Miller 1984; Bertness 1985; Epifanio et al. 2013; Luk and Zajac 2013). Its abundance is regulated by several environmental characteristics, though these determining factors can vary geographically (Teal 1958; Bertness and Miller 1984; Luk and Zajac 2013). In New England, densities of fiddler crabs typically range from 30-45 crabs/m² (McCaffrey 1977; Katz 1980; Bertness 1985; Luk and Zajac 2013). In southern states like Georgia and the Carolinas abundances are commonly much higher—between 130 and 280 crabs/m² (Wolf et al. 1975; Behum et al. 2005)—but can also be as low as 18-61 crabs/m² depending on the local environment and sampling method (Teal 1958; Wolf et al. 1975).

Generally, *Uca pugnax* are most abundant in areas conducive to burrowing, with intermediate levels of root mat and substrate hardness to provide enough support without becoming impenetrable (Ringold 1979; Bertness and Miller 1984; Bertness 1985; Jaramillo and Lunecke 1988; Grimes et al. 1989; Nomann and Pennings 1998; Luk and Zajac 2013). Crabs will also associate with softer substrates as long as hard structural elements such as vegetation stalks or ribbed mussels are available to support
their burrows (Bertness and Miller 1984; Bertness 1985; Grimes et al. 1989; Luk and Zajac 2013). Several studies show *Uca pugnax* to have an affinity for mid-high salinities and low marsh elevations (Grimes et al. 1989; Luk and Zajac 2013). The highest abundances of fiddler crabs are found in the lower, tall-form *Spartina alterniflora* marsh zones and near creek and ditch banks (Katz 1980; Bertness 1985; Grimes et al. 1989; Wilson et al. 2012; Luk and Zajac 2013). Crab abundance is lowest in short-form *Spartina alterniflora* marsh zones; typically due to the thicker root mat and harder substrates that make burrowing more difficult (Bertness and Miller 1984; Bertness 1985; Grimes et al. 1989; Luk and Zajac 2013). These higher regions also tend to flood less regularly and have poor drainage, which can lead to low oxygen/high sulfide pools with soft substrates and no structural vegetation that crabs will also avoid (Bertness and Miller 1984; Bertness 1985; Luk and Zajac 2013). Recent studies have shown that anthropogenic pollution levels can also affect crab distributions (Bergey and Weis 2008), and that fiddler crabs may be changing and/or broadening habitat preferences due to climate change (Luk and Zajac 2013).

Abundance sampling of *Uca pugnax* can be difficult due to their speed and burrowing behavior. Researchers have suggested an observational count method that involves scanning the selected area from a specific distance for a determined period of time and conducting visual surface counts (Colby and Fonseca 1984; Nobbs and McGuinness 1999). Surface scanning can yield highly erroneous results if done inconsistently, but has been shown to be efficient and effective in presence/absence surveys when exact numbers are less important (Nobbs and McGuinness 1999). Some researchers propose variations of high tide and pitfall traps to survey populations. These are installed in the marsh for a set period of time to capture crabs passing
through the region (Ringold 1979; Bertness and Miller 1984; Cammen et al. 1984; Nomann and Pennings 1998; Johnson 2002; Holdredge et al. 2008; Holdredge et al. 2010). However, this method measures abundances in areas over a long time period (tidal cycle, day, week, etc.) rather than a momentary snapshot of the current population of an area. Due to the key role burrowing plays in fiddler crab life and behavior, several studies have also suggested that burrow counts can be an accurate relative estimate of the crab density (Katz 1980; Colby and Fonseca 1984; Jaramillo and Lunecke 1988; Bergey and Weis 2008; Luk and Zajac 2013).

Overall, classic collection and excavation of sites (to remove all burrowed and hiding crabs) is recognized as the most accurate “true count” of crabs in an area; as burrow counts tend to overestimate, and visual scans typically underestimate crab densities (Bertness and Miller 1984; Cammen et al. 1984; Colby and Fonseca 1984; Bergey and Weis 2008). As long as the methods used in any given study are scientifically supported and consistent with each sampling, they should yield viable data (Wolf et al. 1975). Studies agree that sampling should be conducted during summer months when the crabs are most active and their range and biomass are highest (Katz 1980; Wolf et al. 1975; Luk and Zajac 2013). After sampling, crab and environmental data can be analyzed and applied to a larger area of land through a variety of predictive regression modeling techniques (Fiske and Chandler 2011; Hijmans and Elith 2013; Schmiing et al. 2013).

While researchers have thoroughly investigated *Uca pugnax* distribution to the north and south, habitat preference remains largely undefined in the Mid-Atlantic region of the United States. Because preference can vary with geographic location, and because there has been evidence of a potential shifts in habitat preference in
relation to sea level rise (SLR) response, it is important to assess *Uca pugnax* distribution in the Mid-Atlantic to see how it compares to the rest of the coastline. Fiddler crabs are not only one of the most dominant and abundant native species in saltmarsh habitats, but they play an important role in maintaining balance of cordgrass growth and marsh health (Chapter 1). Understanding the distribution of these crabs in southern Delaware will provide insight into the current health of these marshes and the weight of their role in the ecosystem as it becomes threatened by SLR.

The primary objective of this chapter was to characterize the local *Uca pugnax* populations within southern Delaware salt marshes through surveys in two representative sites. I hypothesized fiddler crabs would be present throughout the majority of the marsh, with highest abundances in areas of low elevation, high salinity, and moderate vegetation. To test these hypotheses I conducted a series of field surveys in Canary Creek and Broadkill marshes looking at both occurrence across the marshes and abundance in different marsh types. I also compiled the survey data to create abundance and distribution models for both study marshes to define larger patterns.

### 2.2 Methods

#### 2.2.1 Site Selection

I selected two marshes that are typical representations of much of the marshland in the area to serve as the foci of my study; designated “Canary Creek” and “Broadkill” for two main rivers/tributaries running through each (Canary Creek and Broadkill River, respectively). Approximately 4 km apart, both study marshes are technically part of “The Great Marsh” which is representative of the salt marsh conditions throughout Sussex County, Delaware (Figure 7). The Broadkill site is also
just across the river from (but not included in) the largest protected marshland in southern DE, the Prime Hook National Wildlife Refuge.

Canary Creek marsh is located at 38.786°N, -75.166°W, next to Roosevelt Inlet in Lewes, DE. It is riddled with mosquito ditches dug in the early 20th century that drain the marsh into Canary Creek, a tributary of the Broadkill River that meanders through the center of the marsh and eventually empties into the inlet. Canary Creek marsh is relatively flat with little surface variation (Chapter 3), and its proximity to the mouth of Delaware Bay results in relatively high salinities (20-30 ppt) in the waterways as well as the marsh itself (Aurand and Daiber 1973; Dicker and Smith 1981; Weisberg et al. 1981). The vegetation in Canary Creek marsh is largely dominated by *Spartina alterniflora*, with varied patches of *Distichlis spicata* and rarely *Spartina patens* throughout the middle and landward edges.

Broadkill marsh is located further inland at 38.801°N, -75.203°W, adjacent to the Broadkill River, at the end of Oyster Rocks Road in Milton, DE. Selected to better represent marshes in the region further upriver where salinity may be lower and post-larvae would have further to travel to reach habitat in which to settle, Broadkill has a much smaller area than Canary Creek, but is also ditched with a generally level elevation (Chapter 3). The vegetation at the Broadkill site is more varied, and while still dominated by *Spartina alterniflora*, *Distichlis spicata* is much more prevalent than in Canary Creek. There are also much larger areas of *Spartina patens* near the landward edge at Broadkill. Drainage is poorer in this marsh, and there are several large pools of standing water throughout. The region of the marsh bordering the Broadkill River is an area commonly used for recreational fishing and boat launching.
by the local community. This activity has created a worn path along the river’s edge that disrupts the natural habitat (Personal Observation).

2.2.2 Presence/Absence Survey

To determine the range and distribution of *Uca pugnax* populations, I conducted presence/absence surveys across each study marsh. I sampled at points every 20 m along transect lines set in a grid across both marshes (and every 40 m along the NNE-SSW lines in Canary Creek marsh) to cover as much area as possible (Figure 8). Sampling began at a flag marking the end of a transect line, and entailed scanning an area of ~1 m radius for any live fiddler crabs on the surface. Within this sample area, I recorded a suite of environmental variables to determine possible predictors of *Uca pugnax* presence, including: elevation, *Uca pugnax* burrows, % vegetation cover, presence/absence of specific flora (*Spartina alterniflora, Spartina patens, Juncus roemerianus, Salicornia virginica, Distichlis spicata*), presence/absence of specific other fauna (*Sesarma reticulatum, Geukensia demissa, Littorina irrorata*), soil shear, soil compression, and substrate saturation. Vegetation cover and species presence were determined from visual inspection, while soil characteristics were measured with a handheld AMS pocket penetrometer and Field Scout shear testing device. The penetrometer and shear vane measured the compressive and shear strengths of the soil in kg/cm$^2$, with higher values indicating harder, stronger substrates. I marked burrows and substrate saturation on graded scales: number of burrows were either recorded as None (0), Few (<25), or Many (>25); and substrate saturation was recorded as the result of a visual “step” test as Dry (visibly dry, crumbles underfoot), Damp (visibly damp, feels wet and smears underfoot with no excess water), Saturated (visibly wet, water seeps out underfoot,
fully saturated), or Inundated (flooded or visibly under water). I also recorded the latitude and longitude of each sample point, but elevation had to be calculated afterwards in GIS using GPS locations and 2005 Sussex County LiDAR satellite data (Delaware Geological Survey and USGS 2005) because the handheld GPS device was not accurate enough in vertical measurements. I repeated this process at successive points along the entire length of each transect line.

I repeated this survey monthly for all transect lines across both Canary Creek and Broadkill marshes, with four full assessments of each marsh from June-September 2013—as well as an incomplete preliminary assessment from May 2013—to identify any temporal variation throughout the summer season. I conducted all surveys during the daylight low tide period, and prior to sampling I recorded the temperature and salinity of the main waterway (Canary Creek or Broadkill River) for reference as the current local marsh conditions for the sampling period (Tables 2 and 3).

### 2.2.3 Abundance Survey

In addition to the presence/absence surveys, I also conducted abundance surveys in each study marsh to determine abundance distribution of the *Uca pugnax* populations. Abundance surveys took place within three defined 5 x 5 m sample sites within each marsh, designated “Up,” “Mid,” and “Bank” sites, meant to represent the range of environment types within the marsh habitat (Figure 8). Site classifications were based on distance from the creek/river (Bank = on the bank, Mid = Middle of the marsh, Up = Landward marsh edge) and vegetation type (Bank = Tall-form *Spartina alterniflora*, Mid = Short-form *Spartina alterniflora*, Up = *Distichlis spicata*, Short-form *Spartina alterniflora*, and *Spartina patens*). Initially, elevation was going to guide site determination with Bank sites being lowest and Up sites being highest, but
preliminary measurements revealed less than 0.5 m vertical variation across the entire marsh which was not enough to use elevation as a factor (Figures 29 and 30). I divided each sample site into a 10 x 10 grid of 0.25-m² quadrats labeled A1-J10 for random sampling (Figure 9). To prevent loss in counts during abundance sampling because of the speed of fleeing *Uca pugnax*, I constructed a “walled” quadrat consisting of four polycarbonate roofing panels—cut 0.5 m long and 0.15 m high—screwed together through metal corner brackets. This created a 0.25-m² sampling area with 0.15 m high walls that could be pushed into the mud to prevent scatter and escape of crabs during collection (Figure 10).

During each survey period, I randomly selected 5 quadrats for sampling from each site with a random number generator. Sampling consisted of placing the walled quadrat onto the selected grid area and collecting all fiddler crabs from the surface into a bucket (Figure 10). With the quadrat still in place, I recorded the environmental variables, including: number of *Uca pugnax* burrows, burrow water temperature and salinity, % vegetation cover, presence/absence of specific flora (*Spartina alterniflora, Spartina patens, Juncus roemerianus, Salicornia virginica, Distichlis spicata*), presence/absence of specific other fauna (*Sesarma reticulatum, Geukensia demissa, Littorina irrorata*), soil shear, and soil compression. As with the presence/absence surveys, I determined vegetation cover and species presence from visual inspection, and measured soil characteristics with a handheld penetrometer and shear vane. However, in abundance sampling I reported the actual number of fiddler crab burrows within the quadrat rather than a graded scale. I obtained burrow water temperature and salinity using a ground water syringe, 50 mL test tubes, and a YSI salinity probe; but data were dependent on water levels within the site, and I only got readings on 20% of
the samples. As with presence/absence surveys, I also recorded latitude and longitude of each sampled quadrat and calculated elevations back at the lab using GPS locations and satellite data.

After variables were recorded, I excavated the quadrat area to a depth of 20 cm with shovels and collected any remaining fiddler crabs from the substrate into the bucket. I then counted, sexed, measured carapace width with Vernier calipers, and returned the crabs to the marsh, before replacing the disturbed substrate to its quadrat area. Any crabs smaller than 5-mm carapace width were excluded from the survey because of the difficulty of accurately sampling them. Finally, I collected a small handful (~30 g) of marsh sediment in a plastic bag from the quadrat area to process substrate saturation and grain size as potential variables as well. Back at the lab, I weighed sediment samples wet, then dried them in an oven at 60 °C for 72 hours before reweighing them and calculating the % water content (% water = ((wet – dry) / wet) * 100). I also compared samples to a sand grain size chart (from silt to very coarse sand) after drying when the particles were easier to distinguish.

I repeated this process monthly for all three sites in both Canary Creek and Broadkill marshes, alternating weeks with the presence/absence surveys. I collected four full assessments of each marsh from June-September—along with an incomplete preliminary assessment from May—to identify any temporal variation throughout the summer season. As in the presence/absence surveys, I conducted abundance sampling during the daylight low tide period, and prior to sampling I measured and recorded the temperature and salinity of the main waterway (Canary Creek or Broadkill River) for reference as the current local marsh conditions for the sampling period (Tables 2 and 3).
2.2.4 Data Analysis

To determine habitat preference of *Uca pugnax*, I used statistical regression techniques in R—using the “leaps,” “fields,” “BMA,” “glmnet,” “bestglm,” and “ROCR” packages—to define the most significant environmental predictor variables for both presence and abundance. Model generation for presence prediction drew from the set of possible predictor variables gathered during presence/absence surveys and included: % vegetation cover, *S. alterniflora*, *S. patens*, *J. roemerianus*, *S. virginica*, *D. spicata*, *G. demissa*, *L. irrorata*, *S. reticulatum*, soil shear, soil compression, and substrate saturation. While data collected on burrows was valuable for other analyses, it was not included in model selection as a possible predictor variable because burrows are created by the crabs themselves, and not truly an environmental factor of the habitat. Other variables that could determine an area’s suitability for burrowing, such as soil properties and vegetation, were included instead to account for any burrow-dependent distribution effects. For crab presence range, I used logistic regression to generate a set of possible models to predict the occurrence of *Uca pugnax* from the recorded possible predictor variable data (Table 5). From the top generated models, I selected the best-fit model of environmental predictor variables (habitat features with the most influence on presence of crabs) based on the lowest Akaike information criterion (AIC) and Bayesian information criterion (BIC) values, and highest area under receiver operating characteristic curve (AUC) values (Table 5). To determine the best-fit model, the AIC, BIC, and AUC model weights were calculated for the top five models (Burnham and Anderson 2004; Wagenmakers and Farrell 2004), and the weights of all three criteria were averaged into an “overall model weight” (Table 5).

To predict abundance, I analyzed the same set of possible predictor variables from the abundance survey data—the only differences being that abundance data had
the additional variable of soil grain size and used substrate % water content instead of substrate saturation—using multiple linear regression analysis techniques to generate a set of possible predictive models for the abundance of *Uca pugnax*. Through this analysis I chose the best-fit model of abundance predictor variables for each marsh based on the lowest $R^2$ and BIC values, and highest adjusted $R^2$ values (Table 6). To determine the best-fit model, the $R^2$, BIC, and adjusted $R^2$ model weights were calculated for the top five models (Dawes and Corrigan 1974; Burnham and Anderson 2004; Wagenmakers and Farrell 2004), and the weights of all three criteria were averaged into an “overall model weight” (Table 6).

I ran further analysis on the abundance survey data to look for patterns in size, sex, and overall abundance distribution between the general marsh types, and analyzed Broadkill and Canary Creek separately to reveal any notable differences between the marshes. I compared the abundances of total fiddler crabs, male crabs, and female crabs between the different sample sites (Bank, Mid, and Up) with one-way analysis of variance (ANOVA) testing. To examine size distributions between marsh types, I also ran an ANOVA test on mean carapace widths between sites (Table 4). If a significant difference ($p < 0.05$) was found between sites, I performed a Tukey’s Honest Significant Difference (HSD) post-hoc test to isolate the differences. I also ran linear regression tests to look at the relationship between the number of burrows and the abundance of *Uca pugnax*, and determine whether burrow counting is an accurate method of determining the crab density of an area (Figure 11).

### 2.2.5 Graphical Distribution and Abundance Models

To better visualize the *Uca pugnax* populations in my study marshes, I developed graphical fiddler crab distribution and abundance models from the
previously analyzed survey data using GIS and R software. I interpolated the point values of the significant predictor variables—determined in the best-fit logistic (distribution) and multiple (abundance) regression models (Tables 7-10)—from the survey data across the entire area of each marsh using both nearest neighbor and kriging techniques in the GIS “3D Analyst Toolbox,” resulting in individual data raster layers for each variable. Upon further review, the nearest neighbor rasters more accurately matched the survey data than those generated from kriging, and were chosen for use in the final graphical models.

To visualize occurrence predictions based on model interpolations, I loaded the presence predictor variable rasters into R, and stacked them separately for each marsh using the “raster” and “lattice” packages. I then generated a predictive model raster of *Uca pugnax* occurrence for each entire marsh area using the best-fit logistic regression models (Tables 7 and 8) and the stacked predictor variables with the “rgdal,” “dismo,” and “SDMTools” packages. To visualize the abundance distributions based on model interpolations, I repeated the process with the abundance predictor variable rasters for both marshes, and generated predictive model rasters of *Uca pugnax* abundance for each entire marsh area from the best-fit multiple regression models (Tables 9 and 10).

2.3 Results

2.3.1 Spatial Distribution Modeling

Presence/Absence data from Canary Creek marsh revealed only 17 absences out of 580 observations (Figure 12), and did not have enough variation to construct an accurate list of predictors for the *Uca pugnax* distribution model. For this reason, I applied the best-fit logistic regression model generated from Broadkill
presence/absence data to Canary Creek as well, to construct distribution predictions for both marshes. Comparison of AIC, BIC, and AUC values of different generated logistic regression models for Broadkill marsh resulted in a best-fit model with five significant predictor variables of *Uca pugnax* presence: % vegetation cover, presence of *Spartina alterniflora*, soil shear, soil compression, and substrate saturation (Tables 5 and 7). This model also fit Canary Creek marsh data when applied, showing similar patterns of prediction, though not as strongly due to the extreme lack of absence data (Table 8). The generated predictive distribution model for Canary Creek portrays high *Uca pugnax* presence throughout the entirety of the marsh, which coincides with the high presence found throughout during sampling (Figures 12, 17 and 21c). The predictive distribution model for Broadkill also shows high *Uca pugnax* presence throughout the majority of the marsh, with the exception of areas of flooding/pooling with low vegetation cover of *Spartina alterniflora*, and soft sediments (Figures 13, 18 and 21a).

### 2.3.2 Comparisons of Marsh Types

The data showed that abundances of different sexes, different sizes, and overall crabs did vary with abundance sample site (marsh type) in both study marshes (Figures 14-16, Table 4). In Canary Creek marsh, *Uca pugnax* were significantly most abundant at the Bank site, with male and female abundances mirroring the same pattern (Figure 14). Size distribution also showed the Bank site to stand out with significantly larger crabs found there than the other two Canary Creek sample sites. However, the Mid and Up sites differed in size distribution; with the Mid site having the statistically smallest-sized crabs and the Up site having the “intermediate” range of sizes (Figure 15).
In Broadkill Marsh, there was a similar pattern, however all three sites were significantly different from each other and there were generally lower numbers than Canary Creek overall (Figure 16, Table 4). As in Canary Creek, *Uca pugnax* were most abundant at the Bank site, but other two sites varied from each other with the Up site having a moderate number of crabs and the Mid site having the fewest (Figure 16). The abundances of male crabs at Broadkill had the same pattern as the abundances in Canary Creek with significantly higher numbers at the Bank site, and lower, similar counts at the Mid and Up sites (Figure 16). Broadkill female abundances create the shift in total abundance distribution showing equal numbers in both the Bank and Up sites with significantly fewer females in the Mid site (Figure 16). Size distribution in Broadkill was much less defined, with only the crabs at the Bank site being significantly larger than those at the Up site (Figure 15).

### 2.3.3 Abundance Modeling

When examining abundance data for Canary Creek marsh, comparisons of $R^2$, adjusted $R^2$, and BIC values of the top generated multiple regression models resulted in a best-fit model with five significant predictor variables of *Uca pugnax* abundance: presence of *Spartina alterniflora*, presence of *Distichlis spicata*, presence of *Sesarma reticulatum*, soil compression, and substrate % water content (Tables 6 and 9). This best-fit abundance model for Canary Creek portrays higher *Uca pugnax* abundance near the creek as well as certain “hotspots” throughout the marsh (Figure 19). This generally coincides with the survey abundance data that found highest abundance by the creek and ditch banks (Figure 14).

Broadkill abundance data generated a best-fit model of only two significant predictor variables: presence of *Distichlis spicata* and substrate % water content
(Tables 6 and 10). Both of these variables are also present in the Canary Creek abundance model as significant predictors. Broadkill’s best-fit abundance model shows areas of high *Uca pugnax* abundance near the riverbank, along the edges of Oyster Rocks Road that serves as “higher” marsh area, and in smaller “hotspots” that appear to be along the edges of the flooded/pooling areas (Figures 20 and 21).

Overall, models show that *Uca pugnax* are present throughout the majority of marsh habitat available with the exception of areas with soft, water-saturated substrates lacking vegetation such as dead pools found in the mid and upper marsh. These crabs appear to be most abundant near creek/water banks and show lowest abundance in the mid marsh where substrates and root mat are harder. The data shows no significant temporal differences in these patterns in either marsh when observed independently by month of collection, suggesting that they are consistent throughout the active summer season.

### 2.4 Discussion

#### 2.4.1 Spatial Distribution Patterns

Presence/absence surveys revealed that *Uca pugnax* were present throughout the marsh habitat in both Broadkill and Canary Creek (Figures 12 and 13). The only areas where fiddler crabs were absent were within large areas of vegetative dieback and pooling (Figure 13). Because *Uca pugnax* were present nearly everywhere in Canary Creek marsh, it was difficult to determine which environmental variables had the greatest effect on presence there. This reflected how prevalent the species is in the marsh environment, but inhibited the generation of an accurate logistic regression. In Broadkill marsh, *Uca pugnax* were also very common throughout most of the habitat,
but the relationship between occurrence and marsh pooling was reflected in the significant predictor variables generated by the logistic regression analysis. The best model of environmental variables to predict *Uca pugnax* presence in Broadkill indicated % vegetation cover, presence of *Spartina alterniflora*, and soil compression were positively related to crab presence while soil shear, and substrate saturation were negatively related (Table 7).

The high likelihood of finding fiddler crabs with higher levels of vegetation (specifically *Spartina alterniflora*) is likely due to the food supply, shelter from predators, and structural burrow support that the plants provide (Bertness and Miller 1984; Genoni 1991; Nomann and Pennings 1998). Soil compression strength examines the relative “hardness” of the substrate as a whole; while soil shear strength determined the substrate’s “workability” or resistance to shear stresses (Wilson et al. 2012). Overall, the substrate was relatively soft in the Broadkill marsh (<1.5 kg/cm²), so it is likely that the affinity for higher soil compressions is linked to the need to provide enough structural support to maintain burrows. However, the substrate could not be so compact that it was unworkable; thus if the soil shear strength was too high, the probability of finding crabs decreased. *Uca pugnax* prefer substrates hard enough to support burrow structure without collapsing, but are able to be dug into with the least amount of energy expenditure. Fiddler crabs avoid saturated and/or flooded areas because waterlogged soils make burrowing more difficult, and as semi-terrestrial crabs they cannot handle extended periods of submersion without drowning (Teal 1958; Shock et al. 2009).

The variables found to predict *Uca pugnax* presence also illustrate the crabs’ aversion to the pooled areas of marsh dieback. Pools are flooded (fully saturated) areas
with soft and silty soils and little to no structural vegetation. This makes them inhospitable areas in which to burrow, leaving crabs waterlogged and exposed to predators when on the surface. Thus it is natural that fiddler crabs would preferentially avoid these areas in the marsh. When this logistic regression model was run for Canary Creek marsh, the variables all showed similar effects though to a lesser degree because of the lack of absence data points (Table 8). Canary Creek marsh did not have the same degree of pooling effects as Broadkill so fewer areas of absence appeared in the surveys. However, this does suggest that the model selected important factors in the determination of *Uca pugnax* presence and preferred habitat overall.

The graphical distribution models generated from the logistic regression model for each study marsh offer a helpful visualization of population patterns throughout the marshes. As expected, fiddler crabs are highly likely to be present throughout all of Canary Creek marsh (Figures 17 and 21c). The distribution model of Broadkill shows fairly clear outlines of the pooling areas in the mid-upper marsh region through a low likelihood of crab presence, as well as a higher probability of crabs near the low creek/river banks, and a lower probability in the mid-marsh where burrowing is difficult (Figures 18 and 21a).

### 2.4.2 Comparison of Marsh Types

Overall abundance of *Uca pugnax* was found to be highest—and carapace widths were the largest—at the Bank sample sites of both survey marshes (Figures 14-16). Fiddler crabs clearly favor this marsh type as a suitable habitat over other regions. Areas along the banks of waterways such as creeks, ditches, and rivers are characteristically lower in elevation, and the first to be flooded at high tide. This means slightly higher salinity, and a greater influx/replenishment of food matter,
which can be attractive to crabs and cause them to grow larger more quickly (Montague 1980; Hoffman et al. 1984). Close proximity to the water also means easy access to tidal currents for larval release during reproduction in the summer months that these surveys were conducted, so many of the larger, sexually mature crabs may position themselves closer to water for reproduction (Katz 1980; Greenspan 1982; Lambert and Epifanio 1982; Colby and Fonseca 1984). The substrate is also often softer near water banks (though supported by tall-form *Spartina alterniflora*), making burrowing easier, especially for larger crabs and males with weaker burrowing ability (Bertness and Miller 1984; Bertness 1985).

In Broadkill marsh, where the Mid site had the lowest abundance (Figure 16), the data emphasize the importance of burrowing conditions and habitat drainage to *Uca pugnax*. The higher abundance but smaller sizes found in the Up site regions (Figures 15 and 16) could be explained by smaller crabs with better burrowing ability (Ringold 1979) seeking out the increased vegetation cover as protection from predators (Nomann and Pennings 1998); but it also calls attention to the idea that has been raised by Luk and Zajac (2013) that crabs may be shifting preference to new environments on the marsh edge to prepare for landward habitat migration in the face of climate change.

Male crab abundance distribution in both marshes—mirroring the pattern of total abundance in Canary Creek, with high abundance at the Bank sites and much lower abundances at the Mid and Up sites (Figures 14 and 16)—is most likely caused by many of the same reasons as the size distributions, as males are typically larger and can have more difficulty burrowing and feeding due to their enlarged claws. The larger populations of males near the banks may also be an explanation for why the
The overall population is so high at bank sites; skewing the numbers due to the male-biased sex ratio among *Uca pugnax* (Johnson 2002).

The patterns of female *Uca pugnax* abundance were the same as the others in Canary Creek marsh (Figure 14), but differed in Broadkill with equal abundances in the Bank and Up sites (Figure 16). The affinity for the Bank sites in both marshes is most likely due to waterway access for reproduction, as the vast majority of gravid females collected during these surveys were found at the Bank sites. The increased abundance in the Up sites is likely due to the male-biased sex ratio of the species; females are a rarity, and therefore must be protected and sheltered. Studies have shown that females spend more time belowground in burrows and less time exposed/feeding on the surface than males, especially during mating season (Wolf et al. 1975; Bergey and Weis 2008). The Up marsh area has denser vegetation for better protection from predators (Nomann and Pennings 1998), and has better burrowing conditions than the Mid sites. Because females are smaller, better burrowers, and more efficient feeders, they can better survive with the harder substrates with less food away from the banks (Johnson 2002).

### 2.4.3 Abundance Distribution Patterns

The best multiple regression model of environmental variables to predict *Uca pugnax* abundance in Canary Creek showed that presence of *D. spicata* was positively related to abundance, and presence of *Spartina alterniflora*, presence of *S. reticulatum*, soil compression, and substrate % water content had a negative relationship with abundance (Table 9). With these significant variables it is interesting to note that *Spartina alterniflora* and soil compression had the opposite effect on abundance as they did on fiddler crab presence (Tables 8 and 9). This suggests that these variables...
are very important in determining habitat preference, and that *Uca pugnax* prefer them in moderate amounts. They need enough soil compression strength to support burrow structures (positive slope with crab presence), but the substrates cannot be so hard as to prevent the possibility of burrowing (negative slope with crab abundance). Some *Spartina alterniflora* is important for shelter, structure, and food (positive presence slope), but too much root mass makes burrowing more difficult and drives the local population down (negative abundance slope). This alternating slope between models trend could also be highlighting the pattern of interaction between *Uca pugnax* and the marsh pools. The interior of the pools is inhospitable to the crabs, while the edges of the pools create substitute bank regions that can support large densities of crabs, so data gathered near the edges of pools may show a large range in abundance and presence based on the slight changes in vegetation and substrate compression moving from the interior of the pool to the edge.

The multiple regression model expresses the *Uca pugnax* aversion to flooding and saturated soils with high water content in the substrates predicting lower abundances. The negative relationship with the purple marsh crab (*Sesarma reticulatum*) can easily be explained by interspecific competition for territory, food, and burrows in similar habitats. *Sesarma reticulatum* is much larger than *Uca pugnax* and would create an agonistic environment (Aspey 1978). *Sesarma* has also been linked to overgrazing and increased erosion rates along creek banks in marshes, creating a less suitable environment for *Uca pugnax* (Holdredge et al. 2008).

The one positive relationship with abundance was *Distichlis spicata*, which suggests that vegetation is still important to the density of fiddler crab populations. *Distichlis spicata* is more common in the higher marsh but has a less dense root mat
than *Spartina alterniflora*, so it may serve to break up the tougher soils without making them too tangled for burrows. This affinity could also explain the higher abundance found in the Up marsh sites of the abundance surveys.

The “best-fit” multiple regression model to predict fiddler crab abundance in Broadkill only found two of the five variables used in the Canary Creek model significant: presence of *Distichlis spicata* and substrate % water content. However, both variables showed the same relationships with abundance in each marsh: *Distichlis spicata* had a positive influence on abundance and % water content had a negative influence. Again, the aversion to flooding is made clear, and the support gained from *Distichlis spicata* may be helpful enough to aid burrowing in the softer substrates of Broadkill without the root mass becoming too thick like the short-form *Spartina alterniflora*. The affinity for *Distichlis spicata* may also indicate the beginnings of *Uca pugnax* adaptation and migration to higher marsh habitats as the bank areas become more unstable with the changing climate (Luk and Zajac 2013). These overlaps in significant variables between both marshes may suggest that vegetation and substrate saturation are two of the most prominent determining factors of *Uca pugnax* abundance overall.

As with the distribution models, the graphical abundance models generated from the multiple regression over the entire area of each study marsh offer a more detailed visualization of population patterns throughout the marshes. In Canary Creek, the abundance model shows higher predicted numbers along the creek bank, tree-line marsh edge, and at several “hotspots” in the mid-marsh; and lower predicted counts throughout the middle “short-form *Spartina*” range of the marsh (Figures 19 and 21d). This illustrates the affinity of *Uca pugnax* for the creek bank habitat and better shelter
of the underbrush in the high marsh. The “hotspots” that are seen in the southern region are actually areas around two marsh pools that have formed. Unlike Broadkill where extensive marsh pooling is taking place (Figures 12 and 18), Canary Creek marsh has only a smattering of small pools; most of which were not large enough to register in the surveys and/or graphical models. However, the two abundance “hotspots” are located around the edges of two of the largest pools in Canary Creek, and demonstrate that though crabs may avoid entering the pools themselves, they tend to congregate around the edges as if it were a miniature creek bank habitat (Figure 21).

The abundance model of Broadkill displays a similar pattern with very high predicted numbers along the riverbank and around the edges of the pooling areas (Figures 20 and 21b). This abundance model also had relatively moderate-high abundance along the edges of Oyster Rocks Road that serves as “higher” marsh area, and generally predicted low numbers in the mid-marsh regions that were not bordering pools (Figure 20). The *Uca pugnax* preference for bank areas—likely due to food, burrowing and reproduction—is clearly displayed with this model, as is the inclination towards the higher “Up” marsh areas seen in the abundance surveys for better burrow conditions than the mid-marsh and increased shelter from predators. As with Canary Creek, the “hotspots” of abundance in the Broadkill mid-marsh border the large pooling areas, with the most prominent in the mid-western section of the marsh (Figure 21). The edges of these pools are similar to bank areas in that they are not flooded, but have softened substrates and enough vegetation provide shelter and burrow support. There is also some suggestion that bacterial and microorganismal growth may be increased around these pools, increasing the food supply for crabs (Montague 1980).
2.4.4 Comparisons of Distribution and Abundance Patterns

The southern Delaware study sites used in this research are similar in morphology, vegetative composition, and tidal regime to others in Delaware, New Jersey, Maryland, and the greater Mid-Atlantic area (Childers et al. 1993; Stocks and Grassle 2003; Hinkle and Mitsch 2005; Teal and Weishar 2005; Bergey and Weis 2008). Because *Uca pugnax* distribution and abundance appear to be controlled primarily by these factors, it logical to predict that fiddler crab populations across the Mid-Atlantic are similar to those presented here.

This research corroborates fairly well with other studies of *Uca pugnax* distribution and abundance in different regions of the United States Atlantic coast, with the main themes being that *Uca pugnax* are present nearly everywhere in marsh habitats (Bertness and Miller 1984; Bertness 1985; Epifanio et al. 2013; Luk and Zajac 2013), and the suitability of an area for burrowing largely determines its crab abundance (Ringold 1979; Bertness and Miller 1984; Bertness 1985; Jaramillo and Lunecke 1988; Grimes et al. 1989; Nomann and Pennings 1998; Luk and Zajac 2013).

My data most closely resembles the findings of New England studies, with abundance estimates of ~50 crabs/m² close but slightly higher than reported numbers in New England of 30-45 crabs/m² (McCaffrey 1977; Katz 1980; Bertness 1985; Luk and Zajac 2013). Like a study by Bertness and Miller (1984), I found that *Uca pugnax* are primarily limited by substrate quality for burrowing, preferring moderate vegetation and substrate hardness. The recent research of Luk and Zajac (2013) describes a shift in *Uca pugnax* abundance to higher marsh zones with vegetation like *Distichlis spicata* and *Spartina patens* rather than *Spartina alterniflora*, and suggests that this could be evidence of fiddler crabs shifting to new habitat preferences in response to climate-induced marsh migration. This is similar to the abundance pattern
that I observed in Broadkill. While the highest abundances were found on the riverbank, the higher marsh sites with *Distichlis spicata* showed larger abundances than the mid-marsh short-form *Spartina alterniflora* zones. The extensive pooling and poor drainage of Broadkill could already be mimicking climate effects and altering the habitat preferences of *Uca pugnax* in Delaware.

My research suggests that *Uca pugnax* populations in the Mid-Atlantic are less similar to those found in the southern coastal states. While they have comparable preferences—muddy sediments with moderate vegetation, and limited by burrow suitability of the substrate—the general marsh structure differs and changes crab distribution and abundance throughout the available habitat. Teal (1958) found that *Uca pugnax* in Georgia was most abundant at the medium tidal range and less numerous near the banks, which is the opposite of my findings in the Mid-Atlantic. Reported densities of fiddler crabs in southern states are much larger with numbers averaging between 130 and 280 crabs/m² (Wolf et al. 1975; Behum et al. 2005). Southern marshes are typically much larger and more spread out, and substrate densities can vary from northern marshes (Teal 1958). These differences in geomorphology of the habitat are the likely explanation for the difference seen in the populations.

The collected burrow count data for both survey marshes did show that burrow abundance can be used as a relative representation of crab density for a given area with a general ratio of 7 crabs to 10 burrows (Figure 11), supporting the findings of several other studies (Katz 1980; Colby and Fonseca 1984; Jaramillo and Lunecke 1988; Bergey and Weis 2008; Luk and Zajac 2013). This also serves to corroborate the
other findings of this research that *Uca pugnax* distribution is influenced by the variables affecting an area’s suitability for burrowing.

### 2.4.5 *Uca pugnax* Habitat Preferences and Sea Level Rise

This study showed that the most significant variables influencing *Uca pugnax* populations are the quality of the substrate (shear, compression, water saturation), and the amount and type of vegetation present (Tables 5 and 6). This suggests that the suitability of the habitat depends largely on the crabs’ ability to burrow and find shelter, which are important for the survival of a prey species such as *Uca pugnax* (Bertness and Miller 1984; Bertness 1985; Grimes et al. 1989; Nomann and Pennings 1998; Luk and Zajac 2013). All of the top models for both occurrence and abundance had substrate saturation (or water content) as a significant factor (Tables 5 and 6) which indicates that changes in marsh hydrology by influences such as SLR could significantly impact populations.

Although they were generally similar, the main difference displayed between the two study marshes was the extensive formation of marsh pools in Broadkill compared to Canary Creek, which influenced the distribution and habitat preferences of the *Uca pugnax* populations they contained. Marsh ponding can be a side effect of SLR and is expected to increase as the water table rises (Ewanchuk and Bertness 2004b; Smith 2009; Gedan et al. 2011; Luk and Zajac 2013); so the variation in *Uca pugnax* presence around these pools may be a preview of SLR’s impact on fiddler crab populations. Broadkill marsh has much smaller area than Canary Creek and overall poorer drainage which has led to formation of larger standing pools that take up a greater percentage of the marsh surface area. Canary Creek had some pooling formation but they were much smaller in size, more likely to be temporary/mutable,
and were negligible within the larger marsh area as a whole. As a result, presence of *Uca pugnax* in Broadkill marsh varied around these pools and appeared to be the limiting population factor; whereas *Uca pugnax* were present throughout the entirety of Canary Creek marsh and the population was more limited by abundance factors.

Overall, Canary Creek appears to be a more suitable marsh habitat than Broadkill for *Uca pugnax*. With its flooding and poor drainage, Broadkill could be an example of the changes that marshes will undergo as they are altered by SLR, and how that change is beginning to be reflected in the *Uca pugnax* as well. The higher abundances of crabs in the landward edge of the marsh have been seen in other recent studies and differ from past analyses of fiddler crab distributions (Teal 1958; Bertness and Miller 1984; Luk and Zajac 2013). This could be evidence of fiddler crab species moving into different habitat types as landward migration of the marsh takes place (Brinson et al. 1995; Luk and Zajac 2013).

All the models created through this study are representative of the *Uca pugnax* populations of the region during peak activity of the survey year: at low tide hours in summer months (Katz 1980; Bertness and Miller 1984). However, these surveys and models do not account for daily or tidal temporal patterns in population distribution which would require challenging extra sampling during different points in the tidal cycle. Cammen et al. (1984) also suggest that fiddler crab populations can undergo a great deal of yearly fluctuation in both abundance and distribution, and that long term monitoring is required to form a more complete picture of the nature of the local populations. Still, the models created from this research designate areas of habitat preference and provide a rough baseline for the characterization of *Uca pugnax*.
populations in southern Delaware salt marshes which will help predict the impact of SLR in the region will have on the species.

2.5 Conclusion

The *Uca pugnax* distribution and abundance models for two southern Delaware salt marshes (Broadkill and Canary Creek) supported my first hypothesis; showing that *Uca pugnax* are present throughout the majority of marsh habitats, and only appear to be absent from regions of extreme flooding/pooling accompanied by a dieback of vegetation. My second hypothesis was not directly supported or rejected, but more accurately was modified to give a more comprehensive picture of *Uca pugnax* abundance. Models show that fiddler crabs are most abundant along marsh banks and where the substrate is most conducive to burrowing. This means areas with soft to moderate substrate density (either from soil, root, or hard structure properties) are preferred, along with access to waterways for food and reproduction. High water content in the substrate as a result of poor drainage and lack of flooding relief had a negative effect on both presence and abundance of crabs, suggesting that marsh habitats altered by sea level rise will have a strong negative impact on populations.
Figure 8. Survey plans for Broadkill (Top) and Canary Creek (Bottom) marshes. White lines denote presence/absence survey tracks and yellow polygons denote abundance survey sites.
Figure 9. Visualization of abundance survey site grid. The total site is 5 x 5 m (25 m²), with each grid quadrat measuring 0.5 x 0.5 m (0.25 m²).
Figure 10. Collecting surface crabs with the use of the “walled” quadrat during the first phase of abundance sampling.
Figure 11. Linear regression comparisons of burrow counts to *Uca pugnax* abundance in Canary Creek (Top) and Broadkill (Bottom) marshes with 95% confidence intervals.
Figure 12. Presence/absence survey data from Canary Creek marsh. Blue dots denote presence and red circles denote absence.
Figure 13. Presence/absence survey data from Broadkill marsh. Blue dots denote presence and red circles denote absence.
Figure 14. Mean abundances per quadrat (0.25 m²) of total crabs, males, and females at each sample site in Canary Creek marsh. Error bars denote 1 standard error. Within each abundance type, different letters denote significant differences between sites (P < 0.05).
Figure 15. Mean crab carapace width within 0.25 m$^2$ for both study marshes at each sample site. Error bars denote 1 standard error. Within each marsh, different letters denote significant differences between sites ($P < 0.05$).
Figure 16. Mean abundances per quadrat (0.25 m$^2$) of total crabs, males, and females at each sample site in Broadkill marsh. Error bars denote 1 standard error. Within each abundance type, different letters denote significant differences between sites (P < 0.05).
Figure 17. *Uca pugnax* occurrence probability distribution for Canary Creek marsh interpolated from the best-fit logistic regression model (Model 2 in Table 5).
Figure 18. *Uca pugnax* occurrence probability distribution for Broadkill marsh interpolated from the best-fit logistic regression model (Model 2 in Table 5).
Figure 19. *Uca pugnax* abundance predictions for Canary Creek marsh (crabs/0.25 m²) interpolated from the best-fit multiple regression model (Canary Creek Model 3 in Table 6).
Figure 20. *Uca pugnax* abundance predictions for Broadkill marsh (crabs/0.25 m$^2$) interpolated from the best-fit multiple regression model (Broadkill Model 2 in Table 6).
Figure 21. *Uca pugnax* occurrence probability distribution and abundance prediction (crabs/0.25 m$^2$) models for both study marshes. Scale is not consistent, though Broadkill maps use the same scale (Figures 18 and 20) and Canary Creek maps use the same scale (Figures 17 and 19). a) Broadkill distribution showing presence throughout most of the marsh except two large areas of low predicted presence where vegetation dieback and marsh pooling have occurred. b) Broadkill abundance showing high abundances near the riverbank, pool edges, and marsh edge areas, and lower abundances in the mid-marsh. c) Canary Creek distribution showing high *Uca pugnax* presence throughout the entirety of the marsh. d) Canary Creek abundance showing higher abundances near the creek bank and “hotspot” areas, and lower abundances in the mid-marsh.
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<td>47</td>
<td>25.3</td>
<td>21.4</td>
<td>Clear</td>
</tr>
<tr>
<td>9/5/2013</td>
<td>15:06 P/A</td>
<td>Abundance</td>
<td>84</td>
<td>25.7</td>
<td>19.9</td>
<td>Cloudy</td>
</tr>
<tr>
<td>9/17/2013</td>
<td>13:20 Abundance</td>
<td>5</td>
<td>19.9</td>
<td>24.1</td>
<td>Clear</td>
<td></td>
</tr>
<tr>
<td>9/18/2013</td>
<td>14:14 Abundance</td>
<td>8</td>
<td>21.2</td>
<td>24.7</td>
<td>Cloudy</td>
<td></td>
</tr>
<tr>
<td>9/19/2013</td>
<td>15:04 Abundance</td>
<td>2</td>
<td>19.6</td>
<td>24.4</td>
<td>Clear</td>
<td></td>
</tr>
</tbody>
</table>
Table 4. ANOVA table comparing the mean abundances and carapace widths per quadrat between survey sites (Bank, Mid, and Up) at Canary Creek and Broadkill marshes.

<table>
<thead>
<tr>
<th>Location</th>
<th>Variable</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canary Creek</td>
<td>Total Crab Abundance</td>
<td>25.081</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Canary Creek</td>
<td>Male Abundance</td>
<td>22.012</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Canary Creek</td>
<td>Female Abundance</td>
<td>10.775</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Canary Creek</td>
<td>Carapace Width</td>
<td>39.246</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Broadkill</td>
<td>Total Crab Abundance</td>
<td>35.508</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Broadkill</td>
<td>Male Abundance</td>
<td>24.166</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Broadkill</td>
<td>Female Abundance</td>
<td>22.558</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Broadkill</td>
<td>Carapace Width</td>
<td>6.607</td>
<td>0.003</td>
</tr>
</tbody>
</table>
Table 5. Statistical comparisons of predictive logistic regression models of *Uca pugnax* presence for Broadkill marsh. These best selected models describe presence \( (P) \) as a function of elevation \( (E) \), percent vegetation \( (P_v) \), *Spartina alterniflora* \( (S_a) \), *Geukensia demissa* \( (G_d) \), *Sesarma reticulatum* \( (S_r) \), soil shear \( (S_s) \), soil compression \( (S_c) \), and substrate saturation \( (S_b) \). Model weight is calculated as the likelihood of the model relative to the other candidate models based on all three statistical values. The “best-fit” model based on weight is shown in bold.

<table>
<thead>
<tr>
<th>Model</th>
<th>Model Structure</th>
<th>Number of Variables</th>
<th>AIC</th>
<th>BIC</th>
<th>AUC</th>
<th>Model Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>( P = P_v + S_a + S_c + S_b )</td>
<td>4</td>
<td>377.58</td>
<td>-3174</td>
<td>0.886</td>
<td>0.702</td>
</tr>
<tr>
<td>2</td>
<td>( P = P_v + S_a + S_s + S_c + S_b )</td>
<td>5</td>
<td>371.95</td>
<td>-3175</td>
<td>0.891</td>
<td>0.962</td>
</tr>
<tr>
<td>3</td>
<td>( P = E + P_v + S_a + S_s + S_c + S_b )</td>
<td>6</td>
<td>371.36</td>
<td>-3171</td>
<td>0.894</td>
<td>0.816</td>
</tr>
<tr>
<td>4</td>
<td>( P = P_v + S_a + S_r + S_s + S_c + S_b )</td>
<td>6</td>
<td>371.35</td>
<td>-3171</td>
<td>0.892</td>
<td>0.816</td>
</tr>
<tr>
<td>5</td>
<td>( P = P_v + S_a + G_d + S_s + S_c + S_b )</td>
<td>6</td>
<td>373.11</td>
<td>-3171</td>
<td>0.892</td>
<td>0.717</td>
</tr>
</tbody>
</table>
Table 6. Statistical comparisons of predictive multiple linear regression models of *Uca pugnax* abundance for both marshes. These best selected models describe abundance (A) as a function of salinity (S), percent vegetation (Pv), *Spartina alterniflora* (Sa), *Spartina patens* (Sp), *Distichlis spicata* (Ds), *Littorina irrorata* (Li), *Sesarma reticulatum* (Sr), soil compression (Sc), and substrate percent water content (Pw). Model weight is calculated as the likelihood of the model relative to the other candidate models based on all three statistical values. The “best-fit” model for each marsh based on weight is shown in bold.

<table>
<thead>
<tr>
<th>Marsh</th>
<th>Model</th>
<th>Model Structure</th>
<th>Number of Variables</th>
<th>R²</th>
<th>Adjusted R²</th>
<th>BIC</th>
<th>Model Weight</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>A = Pw</td>
<td>1</td>
<td>0.408</td>
<td>0.398</td>
<td>-23.768</td>
<td>0.699</td>
</tr>
<tr>
<td>Broadkill</td>
<td>2</td>
<td>A = Ds + Pw</td>
<td>2</td>
<td><strong>0.534</strong></td>
<td><strong>0.518</strong></td>
<td>-34.262</td>
<td><strong>0.991</strong></td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>A = Sp + Ds + Pw</td>
<td>3</td>
<td>0.553</td>
<td>0.529</td>
<td>-32.672</td>
<td>0.900</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>A = Sp + Ds + Sc + Pw</td>
<td>4</td>
<td>0.560</td>
<td>0.528</td>
<td>-29.506</td>
<td>0.785</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>A = Pv + Sp + Ds + Sc + Pw</td>
<td>5</td>
<td>0.567</td>
<td>0.528</td>
<td>-26.438</td>
<td>0.726</td>
</tr>
<tr>
<td>Canary Creek</td>
<td>1</td>
<td>A = Sa + Ds + Pw</td>
<td>3</td>
<td>0.559</td>
<td>0.535</td>
<td>-31.252</td>
<td>0.947</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>A = Sa + Li + Sc + Pw</td>
<td>4</td>
<td>0.594</td>
<td>0.563</td>
<td>-31.985</td>
<td>0.992</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>A = Sa + Ds + Sr + Sc + Pw</td>
<td>5</td>
<td><strong>0.622</strong></td>
<td><strong>0.585</strong></td>
<td>-32.018</td>
<td><strong>0.994</strong></td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>A = Sa + Ds + Li + Sc + Pw</td>
<td>6</td>
<td>0.644</td>
<td>0.602</td>
<td>-31.519</td>
<td>0.962</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>A = S + Sa + Ds + Li + Sr + Sc + Pw</td>
<td>7</td>
<td>0.661</td>
<td>0.613</td>
<td>-30.242</td>
<td>0.894</td>
</tr>
</tbody>
</table>
Table 7.  Parameter estimate results of best-fit logistic regression model for Broadkill marsh (Model 2 from Table 5). The null deviance was 629.88 on 563 df, the residual deviance was 359.95 on 558 df.

| Variable               | Estimate | Standard Error | z value | Pr > |z| |
|------------------------|----------|----------------|---------|-------|
| (Intercept)            | -1.1894  | 0.9483         | -1.997  | 0.046 |
| % Vegetation Cover     | 0.0450   | 0.0051         | 8.820   | <0.001|
| *S. alterniflora*      | 3.0103   | 0.6894         | 4.367   | <0.001|
| Soil Shear             | -0.8059  | 0.2999         | -2.687  | 0.007 |
| Soil Compression       | 0.8914   | 0.2185         | 4.081   | <0.001|
| Substrate Saturation   | -0.9942  | 0.1834         | -5.422  | <0.001|

Table 8.  Parameter estimate results of best-fit logistic regression model for Canary Creek marsh (Model 2 from Table 5). The null deviance was 153.33 on 576 df, the residual deviance was 145.38 on 571 df.

| Variable               | Estimate | Standard Error | z value | Pr > |z| |
|------------------------|----------|----------------|---------|-------|
| (Intercept)            | 1.7963   | 1.3160         | 1.365   | 0.172 |
| % Vegetation Cover     | 0.0139   | 0.0106         | 1.233   | 0.218 |
| *S. alterniflora*      | 1.6342   | 0.8142         | 2.007   | 0.045 |
| Soil Shear             | -0.7037  | 0.3979         | -1.796  | 0.073 |
| Soil Compression       | 0.5163   | 0.3572         | 1.446   | 0.136 |
| Substrate Saturation   | -0.2046  | 0.3407         | -0.601  | 0.548 |
Table 9. Parameter estimate results of best-fit multiple linear regression model for Canary Creek marsh (Canary Creek Model 3 from Table 6). F-statistic = 15.68 on 5 and 57 df, and p-value < 0.001.

| Variable            | Estimate    | Standard Error | t value | Pr > |t| |
|---------------------|-------------|----------------|---------|------|----|
| (Intercept)         | 84.6008     | 11.6499        | 7.262   | <0.001 |
| S. alterniflora     | -16.4987    | 3.9876         | -4.137  | <0.001 |
| D. spicata          | 18.9523     | 6.2475         | 3.034   | 0.004 |
| S. reticulatum      | -1.5286     | 0.7017         | -2.178  | 0.034 |
| Soil Compression    | -3.1618     | 1.4601         | -2.165  | 0.035 |
| % Water Content     | -0.7028     | 0.1957         | -3.592  | <0.001 |

Table 10. Parameter estimate results of best-fit multiple linear regression model for Broadkill marsh (Broadkill Model 2 from Table 6). F-statistic = 33.47 on 2 and 60 df, and p-value <0.001.

| Variable            | Estimate    | Standard Error | t value | Pr > |t| |
|---------------------|-------------|----------------|---------|------|----|
| (Intercept)         | 64.6670     | 6.4398         | 10.042  | <0.001 |
| D. spicata          | 5.5795      | 1.5061         | 3.705   | <0.001 |
| % Water Content     | -0.7728     | 0.0946         | -8.166  | <0.001 |
Chapter 3

PREDICTED SEA LEVEL RISE IMPACT ON *UCA PUGNAX* HABITAT

3.1 Introduction

The rapid warming of the planet as a result of climate change is causing large scale ice melts and thermal expansion of Earth’s oceans; growing ocean volumes and increasing the rate of global sea level rise (Rahmstorf 2007; FitzGerald et al. 2008; Vermeer and Rahmstorf 2009; Akumu et al. 2011). Current global sea levels are reported to be rising between approximately 1.6 and 1.8 mm/yr and rates are predicted to be anywhere from 3 to 19 mm/yr by 2100, depending on many anthropogenic and environmental factors (Church and White 2006; Rahmstorf 2007; Domingues et al. 2008; FitzGerald et al. 2008; Vermeer and Rahmstorf 2009; Akumu et al. 2011).

Relative sea level rise (SLR) rates can vary geographically as a result of local climate, geology, and hydrology. Around Delaware Bay, sea levels are rising faster than the average global rate primarily due to land subsidence of the Mid Atlantic coastline of the United States (Phillips 1986; Cahoon et al. 1995; Schwimmer 2001; Adam 2002; Morris 2007; Sallenger et al. 2012). The current rate of SLR in Delaware is approximately 3 mm/yr, with 1-2 mm/yr lost to land subsidence of the Delmarva Peninsula. By 2100 rates for the region are expected to reach between 8 and 17 mm/yr (Nikitina et al. 2000; Thomas 2004; Kreeger et al. 2010).

The primary concerns associated with SLR are flooding and submergence of land as climbing water levels overtake the low elevations of coastal regions, threatening many unique ecosystems as well as a large percentage of Earth’s human
population that live in coastal communities (Kreeger et al. 2010). Marsh habitats naturally compensate for SLR through the processes of vertical accretion and landward migration (Donnelly and Bertness 2001; FitzGerald et al. 2008). However, these are complex processes, and with human interference in marsh habitat and the sharp increase in SLR rates, most marshes will not keep pace, ultimately becoming submerged (Donnelly and Bertness 2001; Morris 2007; Reed et al. 2008; Delgado et al. 2013).

Habitats that manage to remain above water can still be drastically altered by the other negative effects associated with SLR and climate change, including: altered tidal regimes, increased erosion, overwash of foreign sediments, saltwater incursion on freshwater ecosystems, raising of the water table, and higher frequency of storm events (Oertel et al. 1989; Warren and Niering 1993; Brinson et al. 1995; Schwimmer 2001; Hughes et al. 2009; Smith 2009; Akumu et al. 2011; Wetz and Yoskowitz 2013). All of these factors can transform the structure and function of coastal environments, leaving behind damaged ecosystems that may no longer be able to function.

As the habitats are damaged, many organisms suffer as well. For example, several studies on shorebird habitats both in the United States and Australia have found that if rates of SLR continue in the current pattern, important shorebird habitats will lose hundreds of square meters of land. In these scenarios some birds are predicted to lose up to 70% of their nesting and feeding grounds which will undoubtedly cripple their populations (Galbraith et al. 2002; Akumu et al. 2011). Faster SLR in the Mid-Atlantic means more intense effects on coastal habitats and harsher environmental change forced upon the organisms that live there. Species must
be more resilient and adapt more quickly to survive. This makes Delaware a prime research location for examining fiddler crab populations impacted by SLR, because it may exhibit extreme changes more quickly than other areas of the Atlantic coast.

Several methods have been used to model and predict SLR with varying degrees of resolution and cost. These range from simple inundation models that track and predict areas that will become flooded or submerged with various scenarios of SLR on local, regional, and global scales; to more intricate ecological landscape and spatial simulation models that focus on SLR-driven changes to a complex system or process such as hydrodynamic flow, sediment transport, or habitat function. Some models are designed for large-scale projects and only have the resolution for global or national predictions, while others are able to address changes on local and regional scales (Mcleod et al. 2010).

The Sea Level Affecting Marshes Model (SLAMM) is a GIS-based, open source model developed in 1986 by Richard A. Park with EPA funding (Clough et al. 2010). It tracks and simulates changes in marsh area and habitat type by using a complex decision tree that incorporates the geometric and qualitative characteristics of each data cell through time. Changes are based around the five dominant processes involved in wetland conversions and shoreline modifications during long-term sea level rise: inundation, erosion, overwash, saturation, and accretion (Glick et al. 2008; Clough et al. 2010; Industrial Economics Incorporated. 2010; Kreeger et al. 2010; Mcleod et al. 2010; Akumu et al. 2011). The model works from a set of base maps of the target area (elevation, slope, NWI wetland categories) provided by the user, and divides the area into equal cells; each with its own elevation, slope, and land cover class. Within each time step of the simulation, relative SLR is computed based on the
site parameters provided by the user, and each cell is individually analyzed and transformed accordingly (Clough et al. 2010; Mcleod et al. 2010; Akumu et al. 2011). Most accurate when operating on the local or regional scale, the default cell resolution of SLAMM is 30 m x 30 m, but this can be altered larger or smaller depending on the resolution of the base maps that are used (Clough et al. 2010; Mcleod et al. 2010). SLAMM currently recognizes 22 different wetland categories/types in its models, defined by the elevation, salinity, vegetation and tidal rage of each cell (Figure 22). Outputs can be specified to certain map areas and can include a GIS map, tabular data, and image pasted to Microsoft Word for all time stamps (Glick et al. 2008; Clough et al. 2010; Mcleod et al. 2010; Akumu et al. 2011).

Since its conception, SLAMM has undergone several changes and upgrades and is currently in version 6.0 which was released in December 2009 and distributed under Warren Pinnacle Consulting, Inc. This latest version is the first iteration to be open source—though GIS and Microsoft Excel are required to run it properly—and it adds many new features that provide simulations with more detail and accuracy, including an accretion feedback component and salinity model (Clough et al. 2010; Kreeger et al. 2010).

SLAMM has previously been used in various SLR studies looking at species and habitat conservation (Galbraith et al. 2002; Akumu et al. 2011), as well as the impact on human coastal communities and the economy (Industrial Economics Incorporated. 2010; Kreeger et al. 2010). SLAMM was recently used extensively to predictively map SLR in the Delaware and Chesapeake Bays for marsh conservation (Glick et al. 2008; Industrial Economics Incorporated. 2010; Kreeger et al. 2010). However, each individual marsh system is unique, and while the large scale SLAMM
data is available for southern Delaware, it is still wise to re-model my target marshes on my own smaller scale—with my own specified parameters and scenarios—to get the clearest projections of SLR impact in my survey area (Orson et al. 1985; Oertel et al. 1989; Adam 2002; Kreeger et al. 2010). SLAMM is a practical model choice for this thesis project because of its focus on wetland changes in addition to simple inundation that will allow me to better determine the impact of SLR on *Uca pugnax* habitats. It is also low cost, and has a high resolution for local, small-scale research sites such as my two study marshes.

The primary objectives of this chapter were to develop a predictive SLR model for my two representative study marshes (Canary Creek and Broadkill), and use it to propose potential impacts on *Uca pugnax* habitats and populations for the region (introduced in Chapter 2). Based on local predictions of SLR rates and the distribution of fiddler crab populations characterized in Chapter 2, I hypothesized that *Uca pugnax* will lose at least 50% of suitable habitat in southern Delaware due to SLR by 2100. To test this hypothesis, I ran a series of SLR scenarios on my study location using SLAMM. I then compared the output results of wetland conversion to *Uca pugnax* habitat preference and population distribution/abundance from Chapter 2 to determine the potential effects on local fiddler crabs.

### 3.2 Methods

**3.2.1 Model Selection**

To adequately model predictions of SLR in southern Delaware marshes in a way that addressed the needs of my project, I chose to use Warren Pinnacle Consulting, Inc.’s Sea Level Affecting Marshes Model (SLAMM). SLAMM is open-
source, free to use, and allowed me to focus on both land submergence and changes to habitat type on the local level on my target marshes. I considered other models that can also track habitat changes such as the Barataria-Terrebonne Ecosystem Landscape Spatial Simulation (BTELSS), Dynamic Interactive Vulnerability Assessment (DIVA), and SimCLIM; but they proved to either be too costly or better suited to a larger scale with poor resolution at my level of study.

### 3.2.2 Data Processing

SLAMM requires three main data layers from which to run a simulation: A digital elevation map (DEM) file, a slope map file, and a SLAMM categories (National Wetlands Inventory [NWI] wetland categories) map file. I also included two optional layers to contribute more detail to the model: a dike map and a “percent impervious” map, which refer to land development and resistance to flooding. Before running a model simulation, preprocessing of these base data layers in GIS is required to ensure consistent format and alignment for SLAMM.

I used high resolution LiDAR elevation data from the 2005 Delaware Coastal Program Lidar: Sussex County dataset (Delaware Geological Survey and USGS 2005) for the DEM layer of this project. I selected a region of coastal southern Delaware that contained both Broadkill and Canary Creek marshes and loaded the raster layer into ArcGIS 10.1. Using the spatial analyst toolbox, I used the DEM layer to create a layer of slope in degrees with the same dimensions and cell resolution. I also acquired “percent impervious” data from the National Land Cover Database 2006 (Fry et al. 2011) for the same general area of southern Delaware that included both study marshes, and loaded the layer into ArcGIS for processing.
To construct the wetland categories layer, I clipped a region similar to the one selected for my DEM that encompassed both target marshes from the NWI Wetlands Mapper (U. S. Fish and Wildlife Service. 2010). When loaded into ArcGIS, this NWI layer is presented as a series of polygons representing the different wetland types rather than one cohesive raster, and dry/developed land is left blank. I created dry land polygons to fill the blank space and combined them with the wetland polygons using the Merge tool to create one complete layer. I then added two new fields to the attribute table of this new layer: SLAMM codes (to translate the NWI category designation of the polygon to the correct number code to be recognized by the SLAMM model), and dikes (whether the area is diked/developed and less permeable to SLR or not based on NWI codes). I used the resulting final layer to create “SLAMM categories” and dike rasters for the study area; selecting “SLAMM codes” and “dikes” as the value fields for conversion respectively.

With all five raster layers (DEM, Slope, SLAMM categories, % impervious, and Dikes) collected in ArcGIS, I used the data management toolbox to verify that they were aligned to the same coordinate system (WGS_1984), vertical datum (NADV88), had the same cell resolution (5 m x 5 m), and were clipped to the exact same size and alignment to be read by SLAMM (1122 col, 779 rows, corners aligned). I then converted each raster layer to a text file; the required format for the SLAMM interface.

3.2.3 Model Execution and Analysis

Before execution of my model simulation, the SLAMM interface required pre-processing. I loaded the five base files post-GIS processing and rechecked their format and alignment in SLAMM. I then visually reviewed the integration of these layers into
my complete SLAMM map representing the region at mean tide level, and defined Broadkill and Canary Creek marshes as my output sites in the Set Map Attributes menu (Figure 23). I also updated my input map with the correct data specifications in the Site Parameters menu (Table 11), so the model had the correct initial conditions. To run the model, I set my time step for 25 years and selected a suite of SLR rate scenarios to simulate a range of possible effects. Because SLR in Delaware is predicted to be between 0.8 m and 1.7 m by 2100 (Kreeger et al. 2010), I ran scenarios of 0.5 m, 1.0 m, and 1.5 m of rise by 2100, as well as the IPCC’s A1B Max scenario. I simulated each of these scenarios with the connectivity algorithm to create more realistic/accurate inundation transitions in each time step (Clough et al. 2010), and chose the option to “protect developed dry land” to limit wetland migration into developed areas because human influence is very present in southern Delaware, and is unlikely to disappear in the future.

3.2.4 Fiddler Crab Habitat Associations

To apply the SLAMM outputs to *Uca pugnax* populations, I used findings on fiddler crab population distribution and habitat preference from Chapter 2 to determine the potential impact for each SLR scenario that was modeled. Of the 22 wetland categories there were three that best defined suitable *Uca pugnax* habitat established in Chapter 2 based on elevation, salinity, vegetation, and tidal pattern: transitional salt marsh, irregularly flooded marsh, and regularly flooded marsh. Transitional salt marsh zones represent the edge of fiddler crab preference with thicker vegetation, lower salinity and higher elevation; regularly flooded marsh zones are the most preferred with conditions indicative of creek banks (frequent flooding, high salinity, low elevation); and irregularly flooded marsh zones are the intermediate between the other
two (Clough et al. 2010). On the initial SLAMM map, these three categories encompassed the entire marsh range in which fiddler crab populations were observed in Chapter 2 surveys (Figures 12, 13, and 21). The model results from these three categories were combined for each scenario and analyzed as a new category labeled “Uca pugnax Habitat” (Tables 12-14).

In addition to the amount of suitable land lost to SLR, I calculated the approximate change in the crab population as a result of the habitat loss (assuming no migration or range adaptation). To do this, I converted the average abundances for each region of the marsh found in Chapter 2 from numbers per 0.25 m² to numbers per hectare (10,000 m²), the unit area given in SLAMM outputs. I used these values to calculate the change in crab numbers based on the change in area of land determined by the model results of each scenario (Table 15). The abundances used were averages of the local populations and offer possible mid-range predictions of crab losses relative to habitat destruction in similar-structure Mid-Atlantic marshes.

Transitional salt marsh regions are typically drier, high elevation, and on the edge of Uca pugnax tolerance levels, so I multiplied these areas by half of the “Up” marsh abundance. Irregularly flooded marsh areas represent the higher marsh edge and were multiplied by the full “Up” marsh abundance. Regularly flooded marsh regions made up the majority of current Uca pugnax habitat and had to be divided spatially into “Bank,” “Mid,” and “Up,” marsh regions (Figures 24 and 25). The wetland change for regularly flooded marsh in each scenario was divided between these spatial regions, and multiplied by the corresponding crab abundance (Table 15). I combined the total changes in crab numbers from all relevant habitat types for Broadkill and
Canary Creek to determine the total crab loss due to SLR-induced habitat change (Table 14).

### 3.3 Results

Broadkill marsh was initially dominated by suitable *Uca pugnax* habitat—primarily regularly flooded salt marsh—which covered ~82% of the area (Figure 26a). All SLR scenarios in Broadkill predict a consistent decline in fiddler crab habitat, but to different degrees of severity (Figure 28). In the 0.5 m SLR by 2100 scenario, Broadkill wetlands remained relatively stable and only lost a minor amount of fiddler crab habitat (Figure 26b, Table 14). The A1B Max scenario (which resulted in SLR of ~0.63 m by 2100) effectively cut available *Uca pugnax* habitat in half (Figure 26c, Table 14), while scenarios 1.0 m and 1.5 m eliminated nearly all suitable habitat from Broadkill completely (Figures 26d and 26e, Table 14). All scenarios maintained stable habitat area for the first time step of 25 years before larger declines became apparent (Figure 28).

As in Broadkill, in its initial state, Canary Creek was primarily covered in suitable *Uca pugnax* habitat (71%); and of this habitat, most was regularly flooded salt marsh (Figure 27a). While the end result of all SLR scenarios was some degree of decline in fiddler crab habitat; interestingly, all scenarios in Canary Creek show a slight increase in *Uca pugnax* habitat from 2007 to 2025 (Figure 28) as salt marsh wetlands migrate landward and overtake undeveloped dry land areas but before sea levels are high enough to drastically erode or inundate major tracts of habitat. Even though wetland transitions were taking place, there was very little overall *Uca pugnax* habitat loss in the 0.5 m SLR by 2100 scenario for Canary Creek (Figure 27b, Table 14). However, this changed beginning with the A1B Max scenario which—as in
Broadkill—predicted a drop of just over 50% in Uca pugnax habitat (Figure 27c, Table 14). Scenarios 1.0 m and 1.5 m were not as extreme in Canary Creek as Broadkill, and did not completely remove suitable fiddler crab habitat; but they did cause a loss of the vast majority of preferred habitat (Figures 27d and 25e, Table 14).

The pattern consistently seen in both marshes was a sharp decline in suitable Uca pugnax habitat after sea level reached over 0.5 m of rise. This pattern cannot truly be seen in the 0.5 m scenarios because sea level does not reach sufficient height by the end of the simulation, but both marshes experience it in the other three scenarios just after the year 2050 (Figure 28). At this threshold point, available habitat shifts from relatively stable levels to dropping by ~50% across all scenarios. Much of the initial loss seen is a result of widening waterways and the destruction of bank habitats where crab abundance is high (Figures 26 and 27). This sharp decline in habitat is maintained as sea levels rise further, with only a small decline in rate after ~1.0 m of rise or until habitats have vanished completely (Figure 28, Table 14). Both marshes also lost defined river boundaries in the 1.5 m SLR scenarios as the majority of land became fully inundated by 2100 (Figures 26e and 25e).

The initial total crab population calculated for Broadkill was 2.0x10⁷, and 7.2x10⁷ for Canary Creek. Predicted population losses were relatively minor in both marshes in the 0.5 m SLR scenario; but as available habitat rapidly declined from A1B Max to 1.5 m scenarios, crab numbers fell proportionally (Table 14). Mirroring habitat, populations decrease just over 50% in both marshes in the A1B Max scenario (Table 14). In response to the near total habitat loss in Broadkill marsh in the 1.0 m and 1.5 m scenarios, the crab population falls to only 3.3x10⁵ and 5.5x10⁴ respectively; 1% and <1% of the initial populations (Table 14). Uca pugnax
populations in Canary Creek also suffer high losses with the higher SLR scenarios, maintaining only $6.6 \times 10^6$ (10% of the initial population) after 1.5 m of SLR (Table 14).

3.4 Discussion

Under initial conditions, the majority of land in both Broadkill and Canary Creek marshes is covered by wetlands considered suitable *Uca pugnax* habitat (Figures 26a and 27a), which agrees with the relatively high abundance of 50-70 crabs/m$^2$ and occurrence of the species found in Chapter 2. Even though the marshes differed in that Broadkill was smaller, had poorer drainage, and was further inland; the same general pattern was seen in both with regard to SLR and wetland conversions for all scenarios (Figures 26-28). This suggests that these findings are indicative of southern Delaware salt marshes and a similar pattern will be observed in marshes throughout the Delaware Bay and Mid-Atlantic regions. Across all scenarios, there was little change in available *Uca pugnax* habitat until sea levels reached 0.5 m. After this point there was loss of 60-100% in *Uca pugnax* habitat, and potentially millions of crabs.

The stability of and even increase in suitable habitat for *Uca pugnax* in Broadkill and Canary Creek respectively in the first time step of all SLR scenarios from 2007 to 2025 (Figure 28) illustrates the marshes’ natural response and resistance to SLR in the form of increased accretion and landward migration (Brinson et al. 1995; Donnelly and Bertness 2001). The early images of Canary Creek in the 2025 time step mark this migration, showing that undeveloped dry land bordering the marsh converted to irregularly and regularly flooded wetlands types; and this expansion is still visible in the final outputs of the scenarios of lower rise (Figure 27). However,
after this period—usually around 2050 in the simulations or after a sea level of 0.5 m has been reached—in most scenarios the rate of SLR becomes too great and these natural defenses can no longer keep pace, resulting in extensive losses in wetlands; specifically those suitable for fiddler crab habitats (Figures 26-28, Table 14). The reason that the habitat loss threshold appears to be just over 0.5 m may be explained by the fact that average elevations in Broadkill and Canary Creek determined from the LiDAR maps are around 0.35 m and 0.3 m respectively, with few maximum elevation points reaching just above 0.5 m (Figures 29 and 30). The threshold is a bit higher than the current mean elevation to account for accretion and natural marsh responses in the early stages of the simulation, before SLR overtakes these processes completely (Morris 2007; Delgado et al. 2013). Both marshes are relatively flat with <1 m variation in elevation (Figures 29 and 30), so once that SLR threshold is passed, wetland degradation is rapid (Figures 26-28) until in the 1.5 m scenarios, the majority of both marshes are completely submerged (Figures 26e and 27e).

Even though there was little overall *Uca pugnax* habitat loss in the 0.5 m scenarios, it does not mean that the wetland types within each marsh did not change; there was a shift in the composition of the three wetlands that comprise suitable *Uca pugnax* habitat. Initially, both Canary Creek and Broadkill had all three suitable wetland types: transitional salt marsh, irregularly flooded marsh, and regularly flooded marsh. The natural shift under SLR conditions is that transitional salt marsh will change to irregularly flooded marsh, which will turn to regularly flooded marsh. By the end of the 0.5 m scenario, all of the transitional salt marsh, and most of the irregularly flooded marsh had disappeared, with the remaining stable area of *Uca pugnax* habitat being made up almost entirely of regularly flooded marsh (Figures 26b
and 27b). Regularly flooded marsh appears to be the most preferred of the three wetland types for fiddler crabs (Chapter 2) and would not likely negatively affect populations, but the changes in wetland diversity and availability are important. Regularly flooded marshland is more susceptible to internal pooling/ponding (Chapter 2), and more easily converted to tidal flats or other less suitable habitats. This puts the regions at greater risk of further SLR which can be seen clearly in subsequent scenarios of higher rise (Figures 26 and 27).

When comparing the final SLAMM output models with the population models developed in Chapter 2, a specific problem becomes apparent. As marsh habitats degrade from rising sea levels, the first areas to disappear are those with direct access to waterways, such as bank regions. In fact, one of the first signs of change in the SLAMM simulation maps is the widening of rivers and creeks, and the alteration of bordering marshland to tidal flats (Figures 26 and 27). By the end of the 1.0 m scenarios, Canary Creek had more than doubled in width and the main stream on the western boundary of Broadkill marsh had more than tripled (Figures 26d and 27d). Currently, the highest abundances of fiddler crabs are found in these bank areas of the marsh (Figures 14, 16, and 21), so loss of habitat in these key areas will have a greater impact on the populations than in others. This may result in earlier population crashes of *Uca pugnax*; which would in turn limit natural marsh defenses such as accretion, amplifying the negative impacts of SLR (Grimes et al. 1989). There is the possibility for expansion of bank habitat as widening rivers form new banks further inland and the small creeks and ditches become more pronounced. However, the erosion that drives this process and the fast rate at which it takes place prevents much vegetation and other stabilizing organisms from colonizing these new banks before they are worn.
away further (Hughes et al. 2009). This makes the new banks transient, too soft for burrows, and less hospitable for fiddler crabs. Changes in the hydrology of the marshes’ creeks and rivers also affect the distance *Uca pugnax* larvae need to travel during development and to settle back into the habitat (Tankersley and Forward 1994; Lopez-Duarte et al. 2011; Borgianini et al. 2012). If the system hydrodynamics are altered too much, populations may suffer simply from poor recruitment.

It is also interesting to note that the first major area of marsh to be converted to tidal flat away from the banks in Broadkill marsh is the region of pooling seen in Chapter 2 (Figures 18 and 26c), confirming that poor drainage in these areas makes them more susceptible to habitat alteration and destruction from SLR and rising water tables (Allen 2000; Gedan et al. 2009). As the water rises, more ponds will likely form in the middle of the marsh, and while *Uca pugnax* were shown to cluster around the edges of these ponds, none were found inside them (Chapter 2). The small temporary population benefit will be negated as the pools expand in size and meet the encroaching tidal level, submerging the bank-like pond edges as well.

The calculated crab losses within the local populations were based on typical crab abundances found in the different marsh regions, and are only a rough estimate of the negative impact of habitat loss. These calculations did not take into account the impressive mobility and adaptability of *Uca pugnax* as a species (Robertson et al. 1980; Cammen et al. 1984; Luk and Zajac 2013; Chapter 4), and it is prudent to assume these numbers might overestimate the actual loss. Cammen et al. (1984) also found in a long-term study that fiddler crab populations are able to recover from losses of over 50% in less than 5 years; so if enough stable land remains to support them after the crash, the *Uca pugnax* in Delaware could recover. There is also no evidence
to suggest that fiddler crabs would not adjust to living at higher densities in the limited habitat available, as they have been seen at abundances over 196 crabs/m² in Georgia (Wolf et al. 1975). There is early evidence that some populations of fiddler crabs have already begun to alter habitat preferences to higher marsh conditions rather than remain in low bank areas at greater risk of SLR; which is thought to be the species shifting with climate change to follow the patterns of landward marsh migration (Luk and Zajac 2013). This would also change the predicted losses as the abundance concentrations between the different areas of the marsh shift.

However, while crab numbers in these marshes may not decrease as sharply as projected here, significant habitat loss is still imminent and populations will likely decline (Figure 28, Table 14). Human development has created hard boundaries that limit landward marsh migration and will eventually allow rising sea levels to overtake much of the remaining habitat (Gedan et al. 2009; Figures 26 and 27). And as crab populations decrease, the lack of bioturbation and marsh maintenance that *Uca pugnax* provide will suffer as well; slowing marsh accretion rates and quickening the effects of SLR. This level of variation in accretion rates is not accounted for in the SLAMM model (Clough et al. 2010), suggesting that once the sharp decline in *Uca pugnax* habitat and populations begins, overall marsh loss may become more severe than predicted by these SLAMM simulations (Figures 26-28).

Most marshes and coastal wetlands (especially those in the Mid Atlantic where SLR is accelerated) are at high risk and predicted to be largely eliminated by 2100 under current SLR trends (Orson et al. 1985; Donnelly and Bertness 2001; Gedan et al. 2009; FitzGerald et al. 2008; Kreeger et al. 2010). Even though this research shows that SLR will eventually have a strong negative impact on *Uca pugnax* in the marshes
of southern Delaware, there is no guarantee that the majority of their habitat and thus their population will be lost. The SLAMM model does not account for biological factors like vegetation growth and stabilizing *Geukensia demissa* that affect accretion levels and mitigate erosion. And as the simulations show, only minor losses may be seen if the rate of increase in SLR is slowed and sea levels are constrained to under 0.5 m by 2100 (Figure 28, Table 14). Marshes will also be more likely to survive if the development of nearby dry land is restricted to allow for additional landward marsh migration (Gedan et al. 2009). The more suitable habitat that survives, the less stress will be put on *Uca pugnax* populations which will increase chances of their continued stability.

### 3.5 Conclusion

Initially, SLAMM predictive model simulations of four different SLR scenarios (A1B Max, 0.5 m, 1.0 m, 1.5 m) for both Broadkill and Canary Creek showed little change in *Uca pugnax* habitat with only gradual loss and landward migration of wetland types. However, once water levels rose ~0.5 m above current levels there was a rapid decline in suitable marsh habitat and thus predicted crab numbers. This pattern was consistent in both marshes and across all scenarios. As a result, the 0.5 m of SLR by 2100 simulation did not show much significant damage to *Uca pugnax* with only 11% and 8% habitat loss in Broadkill and Canary Creek marshes, respectively. But beginning with A1B Max (which amounted to ~0.63 m by 2100), the subsequent simulations predicted habitat loss of 61-100% in Broadkill and 56-93% in Canary Creek, resulting in an equally striking predicted loss of millions of fiddler crabs. These findings support my hypothesis that *Uca pugnax* will lose more than 50% of suitable habitat by 2100 for SLR scenarios that are above 0.5 m.
While SLAMM has a high level of confidence, it does not track the effect of biological factors (changes in bioturbation, primary production, erosion stabilization) on wetland status. Also, population predictions were based solely on current densities and did not account for effects of marsh pooling, altered larval recruitment, adaption to new habitats or increased population accommodation. This research provides a strong, rational analysis of the future of *Uca pugnax* populations in Mid-Atlantic salt marshes, though these uncertainties may lead to deviations from the predictions presented.
Figure 22. Color legend for all 22 SLAMM categories/wetland types used in SLAMM simulations and modeling. Of these, Trans. Salt Marsh (Olive), Regularly Flooded Marsh (Teal), and Irreg. Flooded Marsh (Peach) were classified as suitable *Uca pugnax* habitat.
Figure 23. SLAMM model input area base map integrated from the five base raster layers. Output sites for Broadkill marsh (left) and Canary Creek marsh (right) are defined by white boxes. Color represents habitat type (Figure 22).
Figure 24. Spatial divisions of Regularly Flooded Marsh (teal) in Broadkill used with Table 15 for calculations of changes in crab density from SLAMM outputs.
Figure 25. Spatial divisions of Regularly Flooded Marsh (teal) in Canary Creek used with Table 15 for calculations of changes in crab density from SLAMM outputs.
Figure 26. SLAMM initial and output images at year 2100 for Broadkill marsh SLR scenarios. a. Initial marsh conditions. b. Condition after 0.5 m of SLR. c. Condition under A1B Max scenario of SLR (resulting in ~0.63 m of rise). d. Condition after 1.0 m of SLR. e. Condition after 1.5 m of SLR. Color represents habitat type (Figure 22).
Figure 27. SLAMM initial and output images at year 2100 for Canary Creek marsh SLR scenarios. a. Initial marsh conditions. b. Condition after 0.5 m of SLR. c. Condition under A1B Max scenario of SLR (resulting in ~0.63 m of rise). d. Condition after 1.0 m of SLR. e. Condition after 1.5 m of SLR. Color represents habitat type (Figure 22).
Figure 28. Percent of total land area made up of suitable *Uca pugnax* habitat over time for each SLR scenario in both Broadkill marsh (Top) and Canary Creek marsh (Bottom). Significant declines in habitat can be seen in most scenarios after the year 2050 when sea levels begin to reach heights past 0.5 m.
Figure 29. Elevation profile of Broadkill Marsh. Shading indicates marsh region: blue=Bank, green=Mid, yellow=Up.

Figure 30. Elevation profile of Canary Creek Marsh. Shading indicates marsh region: blue=Bank, green=Mid, yellow=Up.
Table 11. Site parameters used for southern Delaware SLAMM simulations.

<table>
<thead>
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<th>Parameter</th>
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</tr>
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<td>DEM Date</td>
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</tr>
<tr>
<td>Direction Offshore</td>
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<td>Historic Trend (mm/yr)</td>
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<td>GT Great Diurnal Tide Range (m)</td>
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<td>Salt Elev. (m above MTL)</td>
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<td>Reg. Flood Marsh Accr (mm/yr)</td>
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<td>Irreg. Flood Marsh Accr (mm/yr)</td>
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<td>Tidal Fresh Marsh Accr (mm/yr)</td>
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Table 12. Summary of changes in wetland categories for each SLR scenario in Broadkill marsh. Categories in bold combined to create “Uca Habitat” category.

<table>
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<tr>
<th>Category</th>
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<th>1.5 m</th>
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<tr>
<td></td>
<td>Δ Land Cover (ha)</td>
<td>Δ Land Cover (%)</td>
<td>Δ Land Cover (ha)</td>
<td>Δ Land Cover (%)</td>
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<td>0</td>
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<td>Tidal Flat</td>
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<tr>
<td>Uca Habitat</td>
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Table 13. Summary of changes in wetland categories for each SLR scenario in Canary Creek marsh. Categories in bold combined to create “Uca Habitat” category.

<table>
<thead>
<tr>
<th>Category</th>
<th>A1B Max</th>
<th>0.5 m</th>
<th>1 m</th>
<th>1.5 m</th>
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<td>Δ Land Cover (ha)</td>
<td>Δ Land Cover (%)</td>
<td>Δ Land Cover (ha)</td>
<td>Δ Land Cover (%)</td>
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Table 14. Summary of predicted impact of SLR scenarios on *Uca pugnax* suitable habitat and general population numbers for both study marshes.

<table>
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<th>Scenario</th>
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<th>Canary Creek</th>
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<td>Habitat Lost (ha)</td>
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<td>0.5 m</td>
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<td>1.0 m</td>
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<td>1.5 m</td>
<td>40.2</td>
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Table 15. Average densities (in millions) of *Uca pugnax* per hectare of each wetland type in each marsh used for population change calculations.

<table>
<thead>
<tr>
<th></th>
<th>Transitional Salt Marsh</th>
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<tr>
<td></td>
<td></td>
<td></td>
<td>Up</td>
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<tr>
<td>Broadkill</td>
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Chapter 4

UCA PUGNAX RESPONSE TO CROWDING

4.1 Introduction

*Uca pugnax* is a resilient species whose adaptability has allowed it to become the dominant macrofauna in the harsh and variable saltmarsh environment. Over the course of a tidal cycle, the marsh can change from a wet, cool, low salinity environment to a hot, drier, saltier one, and back again (Bertness and Ellison 1987; Nomann and Pennings 1998). Numerous studies have shown these crabs’ ability to osmoregulate, survive without food, and withstand extreme temperatures, allow them to endure in salt marshes where other species suffer (Teal 1958; Robertson et al. 1980; Colby and Fonseca 1984; Genoni 1991; Shock et al. 2009; Nabout et al. 2010; Thurman et al. 2010). Because of their dominance, *Uca pugnax* exhibit aggressive competitive behavior with other fiddler crabs that encourages their dispersal throughout the habitat (Aspey 1978). Robertson et al. (1980) determined that fiddler crabs can clear a region of food quickly and are accustomed to foraging large distances from their burrows if necessary. They are also efficient eaters, and it can take up to 5 days for the benthic algae to recover in an area after foraging crabs have grazed there (Robertson et al. 1980).

Fiddler crabs display agonistic behavior when in competition for food and burrows, and populations may decline when stressed. However, of the regional *Uca spp.* studied (*Uca pugilator, Uca pugnax, Uca minax*), *Uca pugnax* have been shown
to be the most aggressive and exhibit the highest tolerance for crowding (Aspey 1978). While aggressive and adaptable, fiddler crabs have environmental limits and will travel to new, more viable areas if the habitat becomes unsuitable either from lack of food (Aspey 1978) or harsh conditions (Luk and Zajac 2013).

With rates of sea level rise (SLR) increasing in recent years, the threat of habitat loss for *Uca pugnax* has intensified (Chapter 3). Marshes that remain above sea level are at risk of drastic transformation due to other related negative effects such as: increased erosion, overwash of foreign sediments, raising of the water table, hydrology changes, and higher frequency of storm events (Oertel et al. 1989; Warren and Niering 1993; Brinson et al. 1995; Schwimmer 2001; Hughes et al. 2009; Smith 2009; Akumu et al. 2011; Wetz and Yoskowitz 2013). These changes can make habitat unsuitable for marsh organisms like *Uca pugnax*, and limit resources available to sustain populations. While some habitat area may be preserved through the natural compensation mechanisms of marshes such as vertical accretion and landward wetland migration, these processes are slow and predicted to be overtaken by rapid SLR rates in the near future (Oertel et al. 1989; Donnelly and Bertness 2001; Smith 2009).

Human development has also impeded marsh compensation by creating a barrier to landward marsh migration, and limiting the rates of accretion in coastal wetlands (Ewanchuk and Bertness 2004b; Gedan et al. 2009); increasing the chances of larger habitat loss.

Earlier in this thesis I established that *Uca pugnax* are prevalent throughout the majority of the local study marshes and appear to dominate the fauna of similar salt marsh environments (Chapter 2). With the rate of SLR increasing with climate change, *Uca pugnax* are predicted to lose a substantial amount of suitable
habitat over the next century (Chapter 3). While *Uca pugnax* are a very mobile and adaptable species (Robertson et al. 1980; Luk and Zajac 2013), and it is unlikely that the entire population will disappear, the lack of favorable territory will force the remaining crabs into a smaller area. Even with the inland migration of marsh habitats, the rapid disappearance of the lower, seaward environment will prevent survival of the same area of salt marsh as before (Oertel et al. 1989; Donnelly and Bertness 2001; Gedan et al. 2009). As the habitat shrinks, these once spread-out, fiddler crab populations of tens of millions of crabs (Chapter 3) will be confined long-term to the remaining marsh to compete for space and resources.

The primary objective of this study was to determine the effect of crowding due to loss of habitat on *Uca pugnax* mortality and burrowing activity within a population. I hypothesized that the lack of space and resources available to the crabs, paired with their agonistic and competitive nature, would limit burrowing activity and cause an increase in mortality among the crabs at high densities. To test these hypotheses I conducted a field experiment in Canary Creek marsh, using abundance-manipulated enclosures to examine *Uca pugnax* responses to different levels of crowding conditions in the marsh habitat.

4.2 Methods

4.2.1 Site Selection

I conducted this field experiment entirely within Canary Creek marsh at 38.78717°N, -75.16302°W, in an area of high marsh near the tree line (Figure 31). The site also falls into the category that was characterized as “Up” marsh in my abundance surveys (Chapter 2). I chose this area because it best emulates the conditions of a
natural crowding scenario. With its slightly higher elevation and thicker vegetation as well as its proximity to the edge of the marsh, the high marsh is the most likely habitat type to remain available to the fiddler crabs after inundation and loss of land due to SLR (Chapter 3). So logically if the *Uca pugnax* populations are forced into a crowding situation, it would be into an area of this marsh type.

### 4.2.2 Enclosure Construction

To examine the *Uca pugnax* response to crowding conditions, I constructed 0.5 x 0.5 m enclosures in August, 2013, for the monitoring of different crab abundance treatments in the same controlled area of the marsh. The small size was easy to maintain and monitor, while large enough to avoid disruption of the habitat within. This is also the same area as the abundance survey quadrats in Chapter 2, which facilitated initial population calculations. I built the enclosure pens with guidance from previous fiddler crab field studies in the literature (Greenspan 1982, Bertness 1985, Genoni 1991, Holdrege et al 2010, Thomas and Blum 2010). Each pen was 30 cm tall and consisted of four vertical wooden 1x2” stakes in the corners, connected from top to bottom with window screening. I bent a 10-cm strip of aluminum flashing over each of the top edges to create 5 cm of smooth, reflective surface on either side around the entirety of the pen to prevent crabs from climbing over the top (Figure 32). In the field, I inserted the enclosures 15 cm into the substrate to deter burrowing from underneath (Figure 33).

### 4.2.3 Field Experiment

In preparation for this field experiment, I calculated a mean of 12 fiddler crabs per enclosure area (0.25 m$^2$) for the “Up” marsh habitat type from my abundance
survey data (Chapter 2), and used this value as the baseline or “non-crowded” population count. I then installed 15 enclosures, consisting of three replicates of five different density manipulation treatments. The five abundance treatments included: a control, containing whatever crabs were naturally within the enclosure after installation; treatment x1, containing the calculated average number of crabs for the area (12); treatment x0.5, containing half the calculated average number of crabs for the area (6); treatment x2, containing twice the calculated average number of crabs for the area (24); and treatment x3, containing three times the calculated average number of crabs for the area (36). I also took into account the sex ratio of the crabs into my experiment. Based on my abundance survey data from Chapter 2, I determined the sex ratio of males to females in this habitat type to be approximately 7:5 (or 1.4:1), so I selected the sex of the crabs placed into each enclosure accordingly to match this ratio. The exception to this was in abundance treatment x0.5 as there were only six crabs, and I had to use a ratio of 2:1 with four males and two females instead. I installed the enclosures in a 3x5 grid spaced 3 m apart, and randomly assigned abundance treatments within the grid to minimize any spatial effects within the study site (Figure 34).

To ensure the regulation of enclosure population numbers, a week before the experiment began I performed daily surface removal of any crabs remaining within the enclosures after installation, with the exception of the control enclosures which remained untouched. On the first day of the experiment I added the randomly assigned number of crabs to each enclosure, and monitored them weekly for four weeks. Each monitoring consisted of counting burrows, surface crabs, and surface mortality within each enclosure. At the end of four weeks I counted all burrows, crabs, and deaths
including a plot excavation to assess everything within the substrate. The full experiment ran from August 5 to September 3, 2013.

4.2.4 Data Analysis

To analyze the effects of crowding on mortality and burrowing activity, I compiled the data for all abundance treatments from all enclosures, and made several statistical comparisons using one-way analysis of variance (ANOVA) testing. To determine any effects on burrowing behavior I compared the mean number of burrows between abundance treatments, as well as the ratio of number of burrows to number of crabs (burrows:crabs) between treatments. I tested for differences in mortality by comparing the mean number of total deaths over the course of the experiment between abundance treatments, and I examined how the total number of crabs between the treatments changed over the course of the experiment by comparing the mean total number of crabs between treatments. To be thorough and check for any temporal patterns in the data, I also ran ANOVA tests on number of deaths between weeks of the experiment, as well as number of burrows between weeks. In each of these cases if a significant difference (p<0.05) was found between abundance treatments, I performed a Tukey’s Honest Significant Difference (HSD) post-hoc test to isolate the differences.

4.3 Results

The data showed that the number of burrows in each enclosure did not vary between abundance treatments except that Treatment x3 had significantly more burrows than Treatment x1 (Figure 35, Table 16). The ANOVA testing revealed no significant difference (p=0.64) in burrowing ability (ratio of burrows:crabs) between
any of the abundance treatments (Table 17), supporting the null hypothesis that
crowding had no effect on burrowing.

Total mortality showed low values in all abundance treatments, but Treatment
x3 did have significantly more deaths than Treatment x0.5 and the Control (Figure 36,
Table 18). However, mortality alone was not high enough to explain the change in the
number of crabs per enclosure by the end of the experiment, which had equalized out
across all treatments to an average of approximately 13 crabs per 0.25 m²-enclosure
(Figure 37, Table 19), and is equivalent to 52 crabs/m².

At the end of the experiment, the mean ratios of males to females within each
abundance treatment had not changed from the initial male-biased 1.4:1 (7M:5F) ratio
that was introduced at the beginning of the experiment (Table 21), and they were not
significantly different from each other between treatments (Table 20). Even the
control enclosures—in which the sex ratio was not manipulated at the beginning of the
experiment—exhibited this ratio in the final counts, and was not significantly different
from the manipulated treatments.

There was no significant difference in the number of burrows between weeks
(Table 22), but week 4 (the final sampling of the experiment) had more recorded
deaths than any other week (Figure 38, Table 23). However, this was most likely due
to the method of sampling that allowed for the discovery of more dead crabs in the
week 4 excavations.
4.4 Discussion

4.4.1 Burrowing Behavior

Crowding was not shown to have an effect on the burrowing behavior of *Uca pugnax*. There was no significant difference in the ratio of burrows to crabs over the course of the experiment (Table 17), supporting the null hypothesis that the crabs present were not changing their digging behavior in crowded situations. However, true burrowing activity may have been masked by sampling methods. For instance, burrows were counted within treatment enclosures each week but there was no way to determine if the burrows were newly dug or recounted from the previous week. This is brought further into question by the discovery that while the number of crabs in each enclosure changed for all treatments over the course of the experiment (Figure 37), there was little variation between the number of burrows in each enclosure between abundance treatments (Figure 35, Table 16). These findings appear contradictory, and suggest that burrowing activity could have been monitored more effectively to account for actual number of crabs, and the differentiation between old and new burrows.

4.4.2 Mortality

This experiment did show an increase in *Uca pugnax* mortality when faced with increased crowding, with the x3 abundance treatment averaging 4 more deaths per 0.25-m² enclosure than the control and x0.5 abundance treatment (Figure 36). The most likely reasons that higher crab densities could cause mortality would be the depletion of available food in the area (Robertson et al. 1980), or burrow competition resulting in the lack of adequate shelter (Aspey 1978). The highest numbers of recorded deaths in a given week averaged ~2 deaths/0.25 m² and were in the final
week of the study (Figure 38). This low number suggests that the crabs could endure for several weeks in unsuitable conditions before beginning to die, which agrees with research that found *Uca pugnax* to have a high crowding tolerance (Aspey 1978). However, these results could alternatively be due to the sampling method of the experiment. In an effort leave the environment inside the enclosures undisturbed, I could only conduct mortality counts of surface deaths until the last week of the experiment when I was able to fully excavate the enclosures to find all dead crabs in the quadrat. I was also unable to account for any deaths of crabs lost to predation, which was a possibility due to the open-top enclosure setup.

### 4.4.3 Other Effects

Recorded total mortality was low (<25%) across all treatments and could not possibly account for the changes that were seen in crab numbers, which rose in some cases and dropped by almost 20 crabs in others (Figure 37). By the end of the experiment, none of the treatments were significantly different from each other with regard to crab numbers at 13.13 ± 1.12 (mean ± SE) fiddler crabs per 0.25-m² enclosure (Table 19). This means that abundance treatments x2 and x3 lost an average of over 10 crabs per enclosure, while the other manipulated treatments and the control actually gained crabs (Figure 37); something which should not have been possible. The only way that crab numbers could be increasing is if the enclosures were insecure and breached, with the fiddler crabs able to come and go without restriction.

The fact that the enclosures did not maintain true crowding scenarios for the duration of the experiment contradicts any prior potential results regarding crowding effects on burrowing behavior of mortality. If repeated, increased monitoring and altering of enclosure construction is necessary to maintain the integrity of the
experiment. Enclosures should be dug deeper into the sediment and extend higher above the vegetation to prevent future breaching. I would give consideration to adding a removable screen cover to limit predation and ensure no crabs would crawl in or out of enclosures. However, predation is a natural occurrence that I may want to consider in the experiment, and other studies have cautioned against other internal environmental problems caused by having a cover on enclosures (Bertness 1985, Holdrege et al 2010, Thomas and Blum 2010). Similar crowding experiments could be conducted in a lab setting to maintain more control, but the natural setting of a field experiment would be lost.

It is important to note that once the crabs were able to move freely, the number in each 0.25 m$^2$ enclosure equalized to approximately 13—close to the calculated average of 12 at the beginning of the study—sugge[235]sting that it was a fairly accurate estimate of natural abundance in this habitat. The field densities for the “Up” marsh region of Canary Creek in Chapter 2 from which this number was calculated indicate an average abundance of 12.4 ± 1.4 crabs/0.25 m$^2$, which is consistent with the final abundances of 13.13 ± 1.12 found in this experiment. Moving up to the larger scale of 1 m$^2$ of habitat, the differences in relative abundance becomes even smaller between ~50 crabs/m$^2$ from Chapter 2, and ~52 crabs/m$^2$ from this experiment. These numbers are slightly higher than reported *Uca pugnax* densities in the high marsh regions of New England which average between 30-45 crabs/m$^2$ (McCaffrey 1977; Katz 1980; Bertness 1985; Luk and Zajac 2013), but this small difference could be caused by the morphological differences between marshes such as the larger slope and range in elevation in New England compared to the Mid-Atlantic. Reported abundances of *Uca pugnax* populations on the southern Atlantic coast vary greatly from 25 crabs/m$^2$
(Gittman and Keller 2013) to $176 \pm 16$ crabs/m$^2$ (Wolf et al. 1975) so they are difficult to compare; but while the marsh geomorphologies and vegetation vary some, my determined average abundance does fall within the documented range. It is logical to predict that on regional scales of km$^2$ and larger, these abundances will be consistent as long as the environment remains consistent, as patchiness and aggregations within $Uca$ $pugnax$ populations usually occur based on changes in the habitat (Katz 1980; Robertson et al. 1980; Bertness 1985; Luk and Zajac 2013).

The sex ratio of 1.4:1 in favor of males determined in the beginning of the experiment was also maintained across all abundance treatments including the control, which also supports literature findings that the natural sex ratio is male-biased (Wolf et al. 1975; Johnson 2002; Bergey and Weis 2008). This ratio is very close to the male-biased 1.3:1 sex ratio reported by Wolf et al. (1975) in Georgia marshes; though both of these findings show the disparity to be much lower than Bergey and Weis (2008) in New Jersey, where the number of males was reported to be almost double that of females.

The findings of this study show that $Uca$ $pugnax$ do have an aversion to crowding scenarios, and if able, will work to overcome physical obstacles and obstructions to spread themselves to a more “comfortable” distribution (which in the Mid-Atlantic seems to be about 50 crabs/m$^2$). Other research has shown $Uca$ $pugnax$ to be a very mobile species—with the ability to forage up to 20 m from their burrows each day (Montague 1980; Grimes et al. 1989)—and willing to migrate to new territory if current conditions are unsuitable (Robertson et al. 1980). Even if the new territory is not ideal, as long as it is preferable to the current situation they may colonize it and adjust along the way; which may be the case if SLR removes most of
the current *Uca pugnax* habitat (Luk and Zajac 2013). The large population once spread across a wider range will be forced into a smaller available habitat as it is washed away. This population stress could cause a migration to less preferable landward habitats to maintain established crab densities.

### 4.5 Conclusions

The enclosures constructed for this field experiment were ineffective at maintaining the assigned treatments of crab numbers necessary for the determination of crowding effects on *Uca pugnax* mortality and burrowing behavior. The study rejected my first hypothesis, showing no significant difference in the burrowing activity between treatments. Results also showed increased mortality with crowding (supporting my second hypothesis), but no treatments had high enough mortality to account for the changes in total crab numbers by the end of the experiment. This may have been due to a breach of the enclosures and questions the reliability of the rest of the findings.

The numbers of crabs per enclosure across all treatments equalized to an average of 13 by the end of the experiment, which is very close to the calculated average of 12 (Chapter 2) used at the beginning of the study, and only slightly higher than proposed abundances from other studies ranging from 8-11 crabs/0.25 m$^2$ (Katz 1980; Bertness 1985; Luk and Zajac 2013). This suggests that *Uca pugnax* are averse to crowding and may be agonistic towards each other in larger numbers. When faced with a crowding situation, these fiddler crabs will work to spread themselves into new available areas to maintain a comfortable, natural distribution; even if it means overcoming physical obstacles or challenging terrain. In the context of habitat loss and SLR, this could mean the migration and possible range adaptation of crabs to less a
suitable habitat while they attempt to distances themselves from each other. What happens when crabs are forced into a smaller area by SLR and an immobile barrier such as developed land has yet to be determined and cannot be concluded from this study.

Figure 31. Map of experimental field site in Canary Creek marsh. Enclosures were installed in the higher elevation of the marsh further from the river and near to the tree/shrub line (Left). They were spaced evenly in a grid pattern within this marsh type (Right).
Figure 32. Overhead view of an enclosure after installation in the marsh.
Figure 33. Side-view diagram of an enclosure in the marsh with measurements. Not drawn to scale.
Figure 34. Diagram of enclosure grid and assigned abundance treatments. C represents “control” treatments, and other numbers represent the multiple of the calculated average number of crabs (12) in the designated enclosure. Each enclosure is 0.25 m$^2$. Not drawn to scale.
Figure 35. Mean weekly number of burrows per enclosure by abundance treatment. Error bars denote 1 standard error. Different letters denote significant differences between treatments ($P < 0.05$) determined from post-hoc testing.
Figure 36. Mean total mortality over the course of the experiment by abundance treatment. Error bars denote 1 standard error. Different letters denote significant differences between treatments (P < 0.05) determined from post-hoc testing.
Figure 37. Mean number of crabs per enclosure by abundance treatment. Error bars denote 1 standard error. Different letters denote significant differences between treatments (P < 0.05) determined from post-hoc testing. Initial values were counts at the beginning of the 4-week experiment, and final values were counts at the end of the 4 weeks.
Figure 38. Mean mortality per enclosure by week of the experiment. Error bars denote 1 standard error. Week 0 represents the initial conditions of the experiment. Different letters denote significant differences between weeks (P < 0.05) determined from post-hoc testing.

Table 16. One-way ANOVA comparing the weekly mean numbers of burrows/0.25 m² between abundance treatments.

<table>
<thead>
<tr>
<th>Source</th>
<th>Sum of Squares</th>
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<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>38.213</td>
<td>4</td>
<td>3.225</td>
<td>0.017</td>
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<tr>
<td>Residuals</td>
<td>207.333</td>
<td>70</td>
<td></td>
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</tr>
</tbody>
</table>
Table 17. One-way ANOVA comparing the mean ratios of burrows to crabs between abundance treatments.

<table>
<thead>
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<tbody>
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<td>Treatment</td>
<td>0.041</td>
<td>4</td>
<td>0.653</td>
<td>0.638</td>
</tr>
<tr>
<td>Residuals</td>
<td>0.159</td>
<td>10</td>
<td></td>
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</table>

Table 18. One-way ANOVA comparing the mean numbers of total deaths between abundance treatments.

<table>
<thead>
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</tr>
</thead>
<tbody>
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<td>Treatment</td>
<td>39.333</td>
<td>4</td>
<td>4.470</td>
<td>0.025</td>
</tr>
<tr>
<td>Residuals</td>
<td>22.000</td>
<td>10</td>
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</table>

Table 19. One-way ANOVA comparing the mean numbers of crabs/0.25 m$^2$ between abundance treatments at the end of the experiment.

<table>
<thead>
<tr>
<th>Source</th>
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<tr>
<td>Treatment</td>
<td>75.333</td>
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<td>1.811</td>
<td>0.203</td>
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<tr>
<td>Residuals</td>
<td>104.000</td>
<td>10</td>
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</tr>
</tbody>
</table>

Table 20. One-way ANOVA comparing the mean ratios of males to females between abundance treatments at the end of the experiment.

<table>
<thead>
<tr>
<th>Source</th>
<th>Sum of Squares</th>
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<th>P</th>
</tr>
</thead>
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<tr>
<td>Treatment</td>
<td>0.6272</td>
<td>4</td>
<td>0.2069</td>
<td>0.9288</td>
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<tr>
<td>Residuals</td>
<td>7.5802</td>
<td>10</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 21. One-way ANOVA comparing the mean differences in the ratio of males to females from the beginning to the end of the experiment between abundance treatments.

<table>
<thead>
<tr>
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<tbody>
<tr>
<td>Treatment</td>
<td>1.5832</td>
<td>3</td>
<td>0.601</td>
<td>0.6323</td>
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<tr>
<td>Residuals</td>
<td>7.0250</td>
<td>8</td>
<td></td>
<td></td>
</tr>
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Table 22. One-way ANOVA comparing the mean numbers of burrows/0.25 m$^2$ between weeks of the experiment.

<table>
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<th>P</th>
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</thead>
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<tr>
<td>Week</td>
<td>15.680</td>
<td>4</td>
<td>1.194</td>
<td>0.321</td>
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<tr>
<td>Residuals</td>
<td>229.870</td>
<td>70</td>
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</table>

Table 23. One-way ANOVA comparing the mean numbers of deaths/0.25 m$^2$ between weeks of the experiment.

<table>
<thead>
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</thead>
<tbody>
<tr>
<td>Week</td>
<td>28.677</td>
<td>4</td>
<td>11.944</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Residuals</td>
<td>42.000</td>
<td>70</td>
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Chapter 5
SUMMARY AND FURTHER APPLICATION

5.1 Summary of Hypothesis

This thesis examined the hypothesis that increased sea level rise (SLR) due to climate change will negatively impact the available habitat for *Uca pugnax*, limiting overall abundance and distribution of the population. To better evaluate this hypothesis I completed three main research objectives described in Chapters 2-4:

1. Characterize *Uca pugnax* distribution in Mid-Atlantic salt marshes
2. Predict local SLR outcomes and their potential impact on marsh habitat and *Uca pugnax* populations
3. Determine *Uca pugnax* response to crowding as an effect of habitat loss

The findings of this thesis support the hypothesis stated above that increased SLR will negatively impact *Uca pugnax* habitat, therefore likely limiting population abundance and distribution. However, while these fiddler crabs have definite habitat preferences and needs for survival, they have also exhibited strong adaptive qualities. The loss of habitat to SLR may have drastic negative consequences initially for *Uca pugnax* populations, but it is possible that the species will adapt to new environments and rebound over time.
5.2 Overall Conclusions

Chapter 2 characterized *Uca pugnax* populations in Broadkill and Canary Creek marshes through distribution and abundance models, addressing the first objective. I expected that *Uca pugnax* would be present throughout the majority of the study marsh area, and that they would be more abundant in areas of low elevation, high salinity, and moderate vegetation. I found that my predictions were mostly correct. *Uca pugnax* are a dominant macrofaunal species and are likely to be found in all regions of the marsh except for where vegetative dieback and internal pond formation has occurred. Broadkill had much more excessive marsh pooling than Canary Creek—most likely due to poor drainage—and this was reflected in the population as large areas devoid of fiddler crab presence. Fiddler crab abundances are consistently highest near water banks, including the edges of some of these internal ponds, and in areas conducive to burrowing. Both presence and abundance were negatively affected by high substrate saturations and flooding, suggesting that higher water levels will restrict and constrain crab populations.

In Chapter 3, I developed predictive SLR models for the entire study region using SLAMM, to address the second research objective. In this study, I expected to see losses of at least 50% of suitable *Uca pugnax* habitat to SLR by 2100. My model outputs showed minimal loss—and even small growth in Canary Creek—of wetlands deemed suitable *Uca pugnax* habitat (SLAMM wetland categories: Transitional salt marsh, irregularly flooded marsh, and regularly flooded marsh) until sea levels rose over 0.5 m above the current state. After this threshold point, sharp declines in available habitat can be seen across all scenarios, which translate to major losses in crab numbers and negative consequences for *Uca pugnax* populations in southern Delaware marshes. Depending on the extent of SLR run in the simulation, habitat...
losses ranged from only ~10% at 0.5 m of rise by 2100, to around 60% with the A1B Max scenario from the Intergovernmental Panel on Climate Change (IPCC), and nearly complete loss of 90-100% with the elevated 1.0 m and 1.5 m by 2100. This means that my secondary hypothesis was supported if SLR exceeds 0.5 m by 2100.

Chapter 4 addressed the final objective and examined the effects of crowding on *Uca pugnax* through a field experiment in Canary Creek marsh. While the initial intent was to monitor mortality and burrowing activity under crowd stress—with the secondary hypothesis being that both would be negatively affected—the enclosures for the experiment were not secure, and ineffective at maintaining the assigned numbers of crabs necessary to draw these conclusions. So even though the data showed “crowded” enclosures to have higher mortality and no effect on burrowing behavior, these claims cannot be concluded from this study because true crowded conditions were not maintained. However, the experiment did reveal that *Uca pugnax* are averse to crowding, and when placed in such conditions, they will spread across obstacles (including ineffective experimental enclosures) to an ideal free distribution of ~50 crabs/m²; which is only slightly higher than other reported densities of this marsh type in New England of 30-45 crabs/m² (McCaffrey 1977; Katz 1980; Bertness 1985; Luk and Zajac 2013). This spreading behavior, matched with their adaptability, could explain the trend of fiddler crab populations shifting landward to less suitable habitats as they begin to lose marshland to SLR.

5.3 Final Discussion

In summary, while surveys and models show that *Uca pugnax* populations are currently thriving in the salt marshes of southern Delaware, under current climate trends they stand to lose the majority of their suitable marsh habitat to SLR by 2100.
This will certainly result in heavy crab losses, which will only magnify the damage to the ecosystem. With current modeled predictions, local marshes appear to be able to naturally sustain themselves through accretion and landward migration (Allen 2000)—both processes aided by *Uca pugnax*—for another few decades or until sea levels reach 0.5 m above current heights; but after this point the decline is steep and disastrous.

The results of this research are only educated predictions based on the current state of local marshes and climate conditions, and are not a guaranteed outcome. My research suggests that the large-scale loss of habitat is expected to severely limit space and resources for *Uca pugnax* and decimate populations. Other environmental changes involved with these wetland transformations not addressed in this study, such as shifts in river flows and tidal regimes during this major transgression period, will likely impact populations as well. Tidally-dependent larval transport processes may be interrupted or altered in such a way that megalopae are unable to find and/or return to suitable adult habitats, causing inadequate settlement and repopulation of marshes to occur (Tankersley and Forward 1994; Lopez-Duarte et al. 2011; Borgianini et al. 2012). The settling megalopae that do make it back to the marsh may delay metamorphosis in their search for missing adult chemical cues, increasing the chance of mortality, and decreasing the recruitment (Christy 1989; O’Connor and Van 2006).

However, *Uca pugnax* are also an incredibly robust and adaptive species, having shown evidence of a habitat preference shift to the high marsh (Luk and Zajac 2013), and landward migration that parallels that of the vegetation, marsh zones, and the very habitat itself (Levine et al. 1998; Luk and Zajac 2013; Wasson et al. 2013). In a long-term population study in North Carolina, Cammen et al. (1984) found that *Uca*
*pugnax* populations recovered from major losses of over 65% in less than five years. So like individuals, fiddler crab populations can be resilient, and it is reasonable to expect that while numbers may suffer initially, populations may rebound quickly to fill their new environment. The survival of *Uca pugnax* populations is even more probable if SLR can be limited and suitable habitat loss is minimized, minimizing the initial damage to crab numbers as well as the need for accelerated adaptation.

Predictions of marsh survival and recovery in southern Delaware are low if current conditions and patterns continue; with the IPCC’s predicted trend in SLR rate still resulting in *Uca pugnax* habitat losses of over 50%, and potential accelerated scenarios eliminated those habitats completely. The most effective way to prevent the total loss of future saltmarsh ecosystems is to develop a conservation plan that limits anthropogenic influences over the environment while encouraging the natural processes of SLR compensation and adaptation that marshes exhibit on their own (Allen 2000; Adam 2002; Neckles et al. 2002; Stocks and Grassle 2003; Morris 2007; Day et al. 2008; Gedan et al. 2009; Gedan et al. 2011; Vincent et al. 2013).

Dikes, levees, and impoundments are major human influences on marshes that inhibit drainage and disrupt natural sediment flows, leaving marshes more vulnerable to the effects of SLR (Adam 2002; Stocks and Grassle 2003; Gedan et al. 2009; Delgado et al. 2013). There have been several documented cases of successful marsh restoration efforts that have opened up blocked impoundments and let marshes reestablish natural tidal hydraulics; ultimately increasing the longevity of these marshes when facing SLR (Teal and Weishar 2005; Weishar et al. 2005). Many marshes along the Atlantic coast are covered in man-made mosquito/drainage ditches, and over the years the environment has adapted and used this space to create thriving
habitat space for fish and invertebrates like *Uca pugnax*. Plugging ditches has been shown to lead to pond formation in several marshes, and some have argued that it should be used as a positive restoration technique for wetland shorebirds (Adamowicz and Roman 2002; Wolfe 2005; James-Pirri et al. 2012). However, when ponds form, this only means that drainage has decreased in the marsh. While this may provide a short term improvement for the birds, it weakens the marsh’s SLR response long term, and eventually the bird habitat will disappear under the water too (Gedan et al. 2009; Gedan et al. 2011; Vincent et al. 2013). Rather than plugging these ditches—which would act as impoundments and cripple the marshes’ defense against SLR—in an attempt to undo the massive human influence of the past, wetland managers should turn their attention to working with the natural marsh adaptations around these ditches and streams, and maintain them as vital micro-ecosystems (Morris 2007; Day et al. 2008; Gedan et al. 2009; Gedan et al. 2011; Vincent et al. 2013).

Coastal development needs to be limited near salt marshes to leave room for landward migration and recovery as sea levels rise; and as development is kept further away, levels of pollution and contamination that also threaten species sustaining the marsh will likely drop as well (Adam 2002; Day et al. 2008; Gedan et al. 2009). It is also important to limit contributions to climate change and globally rising temperatures (a main driver behind SLR) to keep rates of SLR to a minimum. As shown by the simulations in this thesis, if SLR can be held below 0.5 m by 2100, coastal salt marshes and *Uca pugnax* populations may have a chance to survive and recover.
5.4 Applications

5.4.1 Future Study in Delaware Marshes

Long term, multi-year patterns are incredibly important to consider when studying population dynamics and climate-related processes like SLR (Cammen et al. 1984; Allen 2000; Neckles et al. 2002; Day et al. 2008; Gedan et al. 2011; Delgado et al. 2013). And while the data provided by this thesis research is a valuable piece to the big picture of the response of *Uca pugnax* to SLR and climate change, it should be seen as a starting point for repeated monitoring surveys to determine the larger patterns at work. Because changes are happening so quickly, I suggest yearly or biannual surveys to establish a more inclusive *Uca pugnax* population model, with continued monitoring to observe the changes as sea levels rise and habitats are altered. There are also many different ways to model *Uca pugnax* populations in addition to logistic and multiple regression analyses, from MaxEnt (Maximum Entropy Modeling) to GARP (Genetic Algorithm for Rule-set Production). It would be beneficial to take the additional data gained in the continued surveys and model populations in multiple ways to look for variation and similarities, and to tease out the strongest patterns and any remaining error. It would also be simpler to view presence and abundance predictions in one combined population distribution model.

The population modeling from this research did reveal the importance of marsh pooling on limiting *Uca pugnax* range in the marsh; while some of the highest regions of abundance were found at the edges of the ponds, similar to creek banks. Because some research suggests a connection between the formation of these ponds and SLR (Allen 2000; Gedan et al. 2009), more work could be done to examine the interactions between fiddler crabs and marsh pools. And as with the *Uca pugnax* populations, it is
also important to continue to monitor SLR conditions and rates into the future. The results presented in this thesis are only the best predictions at this time, but the variables and inputs are not static, and staying current with frequent monitoring is the best way to prepare for the future.

The enclosure experiment in Chapter 4 ended up providing insight into *Uca pugnax* behavior in that they tend to distribute themselves when faced with crowded conditions. And while this may suggest how crabs might react as habitat is lost, it did not achieve the intended goal of the experiment. The enclosure design can be improved and reworked to be implemented securely in the marsh, and this experiment can be run again to acquire the desired results addressing mortality and burrowing behavior under crowded conditions. I would also change the monitoring procedure slightly as well to check the enclosures daily rather than weekly to catch any problems early and gain a more detailed description of the changes taking place.

Overall, the data presented in this thesis is a valuable starting point for *Uca pugnax* and marsh conservation studies in the face of SLR, but there is much more work to be done.

### 5.4.2 Regional Applications of Research

The findings presented here have significance in the realm of science but also for those involved in conservation, coastal policy, and the general public. Marshes are important coastal ecosystems for wildlife and people. They protect coastlines, filter water, and support many organisms; and *Uca pugnax* play a vital role in their health and regulation. This thesis describes the general population distribution of *Uca pugnax* in typical salt marshes of the Delaware Bay and Mid-Atlantic regions of the United States that have previously been undocumented. The study sites used in this research
are similar in morphology, vegetative composition, and tidal regime to others in Delaware, New Jersey, Maryland, and the greater Mid-Atlantic area (Childers et al. 1993; Stocks and Grassle 2003; Hinkle and Mitsch 2005; Teal and Weishar 2005; Bergey and Weis 2008). Thus, this data found here can be applied to similar wetlands in the region to aid in conservation and marsh monitoring programs. Due to their species’ dominance and integral part in marsh functioning, *Uca pugnax* populations can be used as bioindicators of a marsh’s stability and perhaps even stage of response to SLR. This research provides a baseline from which to build monitoring and survey programs elsewhere in the Mid-Atlantic while rates of SLR continue to increase.

The SLR predictions presented here show the possibility of nearly all the coastal salt marshes in Delaware disappearing, which emphasizes the need to minimize human interference with natural marsh processes and response to changing sea levels; specifically the importance of decreasing anthropogenic factors contributing to increased SLR rates. This work can be used to promote positive marsh interaction such as the removal and prevention of dikes and impoundments, reasonable management of existing pools and ditches, limitation of marsh pollution, and avoidance of coastal development too close to marsh wetlands that prevents landward migration. The data presented in this thesis suggests an SLR limit of 0.5 m or below by 2100 for the best chance of natural marsh survival and recovery in the region. With the Mid-Atlantic already at higher risk of SLR damage due to land subsidence and hydrology factors (Davis 1987; Phillips 1986; Ericson et al. 2006; Kreeger et al. 2010; Sallenger et al. 2012), every action taken towards conserving essential organisms like *Uca pugnax*, and reducing contributions to climate change and the impact of SLR, is crucial to the survival of salt marshes and a healthy coastline.
REFERENCES


Behum ME, Brodie RJ, Staton JL. 2005. Distribution of juvenile *Uca pugnax* and *U. pugilator* across habitats in a South Carolina estuary, assessed by molecular techniques. Marine Ecology Progress Series. 288: 211–220.


Jaramillo E, Lunecke K. 1988. The role of sediments in the distribution of Uca pugilator (Bosc) and Uca pugnax (Smith) (Crustacea, Brachyura) in a salt marsh of Cape Cod. Meeresforschung 32: 46–52.


Smith SM, Tyrrell MC. 2012. Effects of mud fiddler crabs (Uca pugnax) on the recruitment of halophyte seedlings in salt marsh dieback areas of Cape Cod (Massachusetts, USA). Ecological Research. 27: 233–237.


Appendix

TABLE AND FIGURE JUSTIFICATION

All available tables and figures displayed in this thesis were created by the author.