# **State of the Knowledge Report**

Assessing the South Carolina Blue Crab Fishery in the Face of Climate Variability and Change

Kelsey McClellan<sup>1</sup>, Julie Davis<sup>2</sup>, Michael Childress<sup>3</sup>, Amy Fowler<sup>4</sup>

<sup>1</sup> College of Charleston
 <sup>2</sup> South Carolina SeaGrant
 <sup>3</sup> Clemson University
 <sup>4</sup> South Carolina Department of Natural Resources

# **Contents**

Executive Summary	3
Glossary	6
Introduction:	9
Defining Climate Change	9
Why Callinectes sapidus?	12
Chapter 1:	17
Changes in the Blue Crab's Saltmarsh Habitat	17
Sea Level Rise	17
Increased Estuarine Salinity	19
Predator-Prey Dynamics of Callinectes sapidus on Saltmarsh Degradation	21
Chapter 2:	22
Physiological and Behavioral Adaptations to Changing Abiotic Conditions	22
Blue Crab Physiology	22
Respiration	24
Osmoregulation	25
Increased Water Temperatures	25
Rising Salinities in Coastal Estuaries	29
Ocean Acidification	31
Disease	32
Chapter 3:	35
Larval Settlement and Juvenile Dispersal	35
Life cycle of the Blue Crab	35
Influence of Abiotic Factors on Larval Settlement and Juvenile Dispersal	39
Chapter 4:	41
South Carolina Blue Crab Market Characterization	41
Historical Context	41
Current Trends in Blue Crab Landings and Value	44
Current Trends in Dealers, Harvesters, and Vessels Engaged in the Blue Crab	
Fishery	47
Market Characterization	
Literature Gaps and Research Needs	52
References	56

# **Executive Summary**

### State of the Resource

At a recent workshop entitled "Research Needs for the Sustainable Management of Crustacean Resources in the South Atlantic Bight", a team of scientists and managers explored ecological challenges that blue crabs face in the Southeastern United States (Brunson et al. 2015). One of the key knowledge gaps identified during this workshop was the lack of a state-of-the-knowledge report concerning the impacts of climate and habitat change on blue crab populations. Blue crabs support substantial commercial and recreational fisheries along the US Southeast and Gulf coasts and play an integral role in marine and estuarine ecosystems as both predator and prey. However, current research suggests that a combination of fishing pressure and climatic conditions, such as drought, are interacting to decrease blue crab abundances throughout the entire Southeastern United States. In South Carolina, since the long-term drought of 1998-2002, blue crab catch-per-unit-effort has declined in the commercial fishery and two fisheries-independent surveys (SCDNR OFM, Fowler and DeLancey 2014). Therefore, the focus of this report is to perform a condensed literature review of current knowledge on how climate change may impact the ecology of and fishery for South Carolina blue crabs.

In the introduction, an overview of climate change, global warming, and the impacts of each on the blue crab is presented. Climate change is best described as long-term changes in global and regional climate patterns caused by increased levels of carbon dioxide in the atmosphere, largely due to emissions from-man made sources. Climate change can have several environmental impacts, including extreme heat, rainfall extremes, sea level rise, hurricane intensity, and ocean acidification.

In the first chapter, the impact of climate change on the habitat utilized by blue crabs is discussed. Coastal areas of the Southeastern United States are subject to sea level rise and increased estuarine salinity, especially in tidal marshes that are prime blue crab habitat. Due to both of these stressors, acute marsh dieback has occurred throughout the Southeastern United States, including in South Carolina. Salt marsh loss has direct negative impacts on marine fish, invertebrates, and birds as the roots of marsh plants help to accumulate and retain sediments and provide habitat. The blue crab also plays an integral role in maintaining the integrity of the saltmarsh, as they prey upon snails that would otherwise remove salt marsh vegetation through grazing. Since both sea level and salinity intrusion are expected to increase in the future, understanding the complex ecosystem impacts of these two stressors is integral to effectively preserve this valuable habitat.

In the second chapter, specific impacts of climate change on blue crabs in South Carolina, focusing on water temperature increases, inland salinity intrusion, and ocean acidification, is discussed. Blue crabs have experienced climate extremes in the past and have several physiological and behavioral adaptations to tolerate a broad range of environmental conditions (i.e., temperature, salinity, pH, oxygen). The physiological processes employed by the blue crab to handle these dynamic environmental factors are respiration rates and osmoregulation, while they also use behavioral mechanisms to cope with shifting abiotic gradients. However, the physiological stress placed upon individual blue crabs while coping with environmental stressors may make them more susceptible to disease. Understanding the mechanisms and processes of how blue crabs adapt or acclimate to changing climatic conditions may indicate the potential of this species to continue to survive under more stressful conditions in the future.

The third chapter explains the life cycle of the blue crab followed by an examination into how abiotic factors, such as oceanic currents, alteration of the hydrological cycle, shifts in temperature and salinity, can influence juvenile blue crab settlement and dispersal. Blue crabs have a multi-stage life cycle that takes place in several different estuarine and marine ecosystems (i.e., open ocean, estuaries, tidal creeks, oyster reefs, and seagrass beds). These changing abiotic factors have the potential to influence blue crab development and disrupt biotic processes. For example, the South Carolina blue crab fishery is dependent on successful recruitment of blue crabs into the system each year. Conditions that disrupt or impair that process would be detrimental to the fishery. Therefore,

understanding how climate change impacts the successful recruitment of blue crabs into coastal waters is paramount to explaining shifts in blue crab abundance over time.

The fourth chapter explores recent trends in blue crab value and compares the results of market characterization interviews conducted with South Carolina crab dealers in 2015. As environmental conditions dictate where crabs will be within the estuarine system, those same conditions also influence where crab pots will be set. Whether or not those crabs become part of the fishery record depends upon someone pulling those pots and landing the product, which is a factor dictated by the market demand for crabs. Any description of the fishery should take into account the activity of the market for blue crabs. During 2015, market characterization interviews were conducted with wholesale crab dealers and retailers in South Carolina to better understand recent market trends, infrastructure needs, and what is vital to remaining competitive in the market. Results of these interviews and recent trends (2004-2015) in landings and value are presented to aid in understanding the fishery from a fisherman's perspective.

Finally, future research objectives for examining the South Carolina blue crab population in relationship to climate change and global warming are outlined in the "Literature Gaps and Research Needs" section. Climate change can encompass a multitude of environmental factors, but as these environmental factors continue to change, a call for further research is necessary to elucidate the complex issue of how climate change, through processes such as ocean acidification, salinity intrusion, and global warming, is influencing both juvenile and adult blue crab populations in South Carolina. In addition to these research directions, a reliable stock assessment is imperative for blue crabs in South Carolina to understand the status of the fishery. Even though blue crabs are currently managed at the state level, additional connectivity studies sampling blue crabs throughout the entire South Atlantic Bight are needed to determine whether blue crabs should be considered a state or regional stock.

# **Glossary**

**Acute** – adjective – present or experienced to a severe or intense degree for a short period of time

**Ambient** – noun – of or relating to the immediate surroundings of something

**Benthic** – adjective – of, relating to, or occurring at the bottom of a body of water

**Branchial chamber** - noun – area between the body and exoskeleton where the gills can be found; found in fish, shrimp, and other organisms that have gills

**Brood** - noun – a number of young produced or hatched at one time

**Chronic** – adjective – persisting for a long time or constantly recurring

**Copulation** – noun – sexual intercourse

**Detritus** – noun – gravel, sand, silt, or other material produced by erosion; organic matter produced by the decomposition of organisms

**Estuarine** – adjective – growing in, inhabiting, or found in an aquatic ecosystem characterized by fluctuating salinity

**Estuary** – noun – partly enclosed coastal body of salt water with one or more rivers or streams flowing into it and with a free connection to the open sea; transition between freshwater and saltwater environments

**Euryhaline** – adjective – (of an aquatic organism) able to tolerate a wide range of salinities

**Exoskeleton** - noun – a rigid external covering for some invertebrates providing support and protection

**Fisheries dependent data** – noun – data collected from commercial sources (vessel or dealer reports) and recreational sources (individual anglers, party or charter boats)

**Fisheries independent data** – noun – data collected by scientists or citizen scientists, usually as part of a long-term resource monitoring program, that are designed to follow consistent methods using the same gear over the entire survey period to develop unbiased and independent indices of abundance

**Generation longevity**- noun – the length of time it takes for all of the individuals

born and living at the same time to die

**Gill lamellae** - noun – thin pieces of tissue that contain capillary beds across which respiration and excretion take place; found in fish, shrimp, and other organisms that have gills

**Habitat** – noun – the natural home or environment of an animal, plant, or other organism

**Ingress** – noun – the act of entering

**Megalopae** – noun – the final larval stage of shrimp, crabs, and lobsters

**Molt** – verb – (of an animal) shed old feathers, skin, hair, or an old shell, to make way for new growth

**Ocean acidification** – verb – reduction in the pH of the ocean over an extended period of time, caused primarily by the uptake of carbon dioxide from the atmosphere. It occurs when carbon dioxide gas is absorbed by the ocean and reacts with seawater to produce acid.

**Organism** – noun – an individual animal, plant, or single-celled life form

**Osmoregulation** – noun – the maintenance of constant osmotic pressure in the fluids of an organism by the control of water and salt concentrations

ovigerous - noun - bearing eggs

**pH** – noun – a figure expressing the acidity or alkalinity of a solution on a logarithmic scale; 7 is neutral, lower values are more acidic, and higher values are more alkaline

**Physiological** – adjective – relating to the biological study of the functions and processes of living organisms, including all physical and chemical aspects

**Recruitment dynamics** - noun – the processes and patterns of the increase in a natural population as juveniles grow and immigrants arrive

**Respiration** – noun – a process in living organisms involving the production of energy, typically with the intake of oxygen and release of carbon dioxide from the oxidation of complex organic substances

Salinity – noun – dissolved salt content of a body of water

**Salt marsh mediators** – noun – a plant or animal that plays an influential role in ecosystem dynamics through predator-prey interactions or other ecological interactions

**Sessile** – adjective – (of an organism) fixed in one place; immobile

**Solute** – noun – the minor component in a solution, dissolved in the solvent

 $\mbox{\bf Spermathecae}$  - noun - in a female invertebrate, a receptacle in which sperm is stored after mating

**Zoea** – noun – planktonic larvae of shrimp, crabs, and lobsters

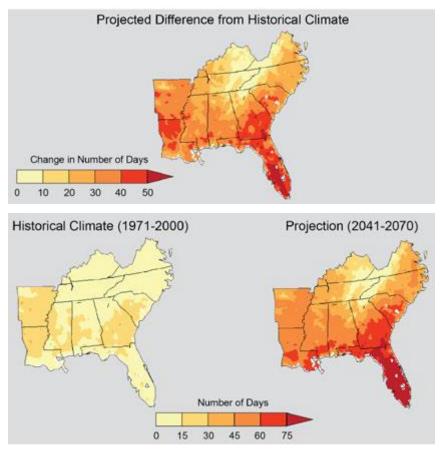
# **Introduction:**

Climate change and global warming are occurring at an unprecedented rate in coastal ecosystems. While there is a plethora of economic and environmental impacts of climate change in South Carolina, the focus of this report will be on the economic, ecological, and cultural importance of blue crabs.

# **Defining Climate Change**

Climate change is best described as long-term changes in global and regional climate patterns caused by increased levels of carbon dioxide in the atmosphere, largely due to emissions from-man made sources. Climate change can have several environmental impacts, including extreme heat, rainfall extremes, sea level rise, hurricane intensity, and ocean acidification (Carter et al. 2014). Another commonly used term, global warming, refers to only the increase in the average surface temperature of Earth.

The environmental impacts of climate change have rapidly increased over the past 100 years due to human activities that have accelerated greenhouse gas emissions and land and water consumption (Harvell et al. 2002, Doney et al. 2012). The increased production of greenhouse gases has also led to an overall  $\sim 0.2^{\circ}$ C increase in global air temperatures over the last three decades (Hoegh-Guldberg and Bruno 2010, Doney et al. 2012). In the Southeastern United States, air temperature increases have been observed (Figure 1), and other environmental impacts of climate change could significantly influence economics and public health. For example, sea level rise poses threats to the economy and environment through the destruction of property and the loss of saltmarsh ecosystems, extreme heat could negatively affect public health and crop production, and decreased water availability could result in economic loses and put further stress on the environment (IPCC 2001, CCTWG 2013, USGCRP 2014).



**Figure 1:** Historical and projected average number of days per year with maximum temperatures above 95°F from 1971-2000 compared to 2041 to 2070. Figure source: NOAA NCDC/CICS-NC. Figure adapted from Carter et al. (2014).

Climate change influences both terrestrial and marine systems by altering relationships between animals, plants, and the ecosystems they inhabit (Harvell et al. 2002). Observed changes in marine ecosystems due to climate change include shifts in the water cycle, increased disease susceptibility of harvested fish, accelerated loss of marine plants, and changes to the non-living components of saltmarsh and estuarine habitats (i.e. sediment loss, erosion, and changes in water temperature and salinity) (Lee and Frischer 2004, Knapp et al. 2008, Heck et al. 2001, de Groot et al. 2002, Więski et al. 2010, Hughes et al. 2012, Costanza et al. 2014, Altieri et al. 2012). These non-living components are often referred to as abiotic factors, where the 'a' indicates without, from Latin roots, and biotic means living. Through reshaping abiotic (non-living) conditions within an ecosystem, climate change can influence biotic (living) factors dependent on abiotic conditions

(Harvell et al. 2002, Parmesan 2006, Altizer et al. 2013). The timing of phenological events such as migration, pollination, and reproduction are examples of biotic functions disrupted through changing or altered abiotic conditions (Parmesan 2006). In addition, the ranges of plant and animal species are shifting, depending on habitat requirements (Harvell et al. 2002, Parmesan 2006, Altizer et al. 2013). While mobile species can expand their range to find new habitats, sessile, or immobile, species like plants and trees must acclimate to changes to the environment.

Climate change models are predicting an increase in both the number and strength of hurricanes (USGCRP 2009). Hurricanes and severe tropical storms are not the only threat to our coastal ecosystems; observable sea level rise (SLR) has been recorded along the coastline of the Southeast and increased storm frequency, excessive heat events, and drought are all threatening the regional coastal ecosystems (USGCRP 2009). Increasing sea levels are due to a combination of thermal expansion of water, melting of land-based ice sheets and glaciers, and vertical land movement (Pritchard et al. 2009, Carter et al. 2014). Sea level rise threatens coastal development and economy, and 8 million people in the Southeastern United States are currently at risk of coastal flooding (Kunkel et al. 2013). In addition, the loss of present and future development due to erosion, sea level rise, and increased storm frequency is a very real danger.

This report will focus not on compromised infrastructure (i.e., personal homes, businesses, property, etc.), but rather how Southeastern estuarine and marine ecosystems will fare in response to a changing climate. Our dependence on the ocean's resources through commercial, subsistence, and recreational fishing is growing as the global population continues to increase. This pertinent issue requires a direct examination of anthropological practices on a personal, local, regional, and global scale. While many species, both aquatic and terrestrial, have been and will be impacted by climate change, we have chosen to examine how the various facets of climate change will affect one of the most iconic of all marine species on the Atlantic coast of North America: the blue crab, *Callinectes sapidus*.

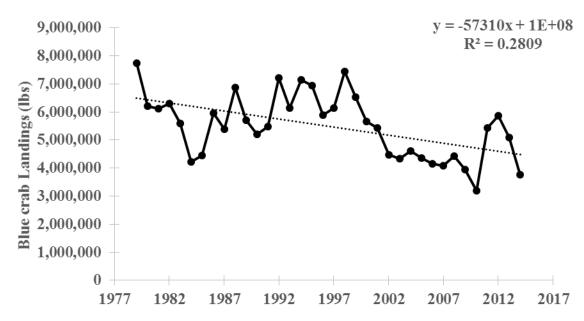
# Why Callinectes sapidus?

The blue crab, *Callinectes sapidus*, has an expansive range along the east coast of North and South America, specifically from Nova Scotia to Argentina (Figure 2; Milliken and Williams 1984). Blue crabs support substantial commercial and recreational fisheries along this range and play an integral role in marine and estuarine ecosystems as both predator and prey (Milliken and Williams 1984). The blue crab is one of the most economically important marine species in South Carolina, where it accounts for 25% of the total value of all commercial fisheries landings (SCDNR, Office of Fisheries Management). The harvest was



**Figure 2:** The common habitat range of *Callinectes sapidus*, depicted in orange. Figured created by Kelsey McClellan using ESRI ArcGIS 10.3.

valued at \$5.8 million in 2014 and was the third most valuable fishery behind shrimp and offshore finfish (SCDNR, OFM). In the past, the blue crab fishery was considered the most stable fishery in the state of South Carolina, with average annual landings of 6 million pounds (Blue Crab Update 2007). In recent years, South Carolina blue crab landings have declined to under 5 million pounds in 10 of the last 13 years (Figure 3). This decline could be partly attributed to lower fishing effort (Blue Crab Update 2007), but could also be due to long-term changes in estuarine salinity (Childress 2010, Alber et al. 2008, Gilbert et al. 2012).

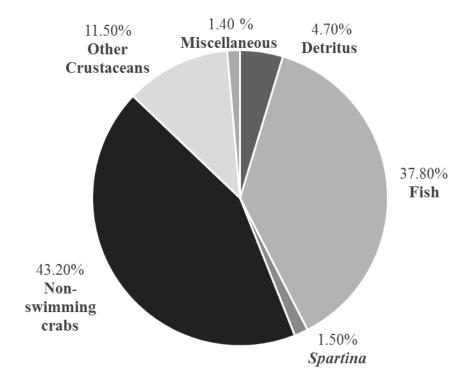


**Figure 3:** Reported annual blue crab commercial landings from 1966-2014 in South Carolina. The reported landings of the 2014 blue crab harvest were the second lowest (4 million pounds), behind 2010 landings (3 million pounds). Data and graph provided by SCDNR, OFM (2015).

Recreationally, the blue crab represents a culture of artisanal fishing tradition passed down through generations (Burrell et al. 2009). The recreational fishery is economically valuable, as it incorporates licensing fees, local landing access fees, and gear purchased from local bait shops. While recreational anglers can use up to two pots per person, they may also employ drop nets or bait (chicken necks) attached to a string. In addition, the recreational fishery can be substantial. A study completed in 1997 showed that the recreational blue crab fishery constituted 28% of all blue crabs fished, both commercially and recreationally, in South Carolina (Low 1998).

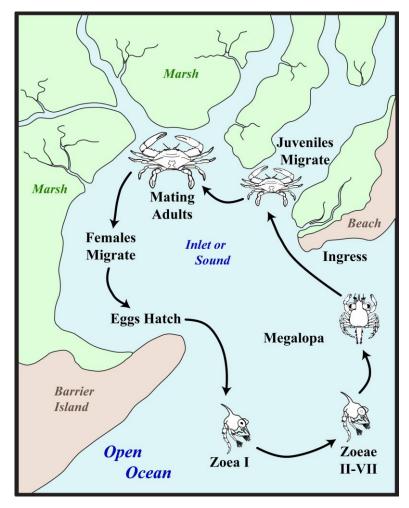
The blue crab plays an integral role in the tidal salt marsh ecosystem as a keystone predator and maintains several different ecosystem functions through various predator-prey interactions (Hines et al. 1990, Posey and Hines 1991). Because of the highly migratory nature of the blue crab, both daily and seasonally, they are predators of multiple saltmarsh organisms such as crabs, small fish, marsh plants (e.g., *Spartina* sp.), detritus (dead, decomposing organic material), mollusks (clams, mussels), and other crustaceans (Figure 4, Fitz & Weigert 1991). The blue crab is a detritivore, scavenger, and cannibal (Darnell 1959), but is also a predator

that plays an important role in defining predator-prey dynamics. Blue crabs can have indirect effects on potential prey items even without direct predation. For example, as mud crabs are a prey item of blue crabs, chemical cues released from blue crabs can reduce mud crab predation on oysters by nearly 25%, thus releasing oysters from predation pressure (Hill and Weissburg 2013). Additionally, the blue crab is a known predator of the periwinkle snail *Littoria irrorata*, notably one of the most abundant marsh grass grazers. Blue crab predation on this snail can have a positive impact on marsh grass abundance (Silliman et al. 2005). If predatory regulation of the periwinkle snail population by the blue crab decreases, via a reduced population of the blue crab from the ecosystem, the periwinkle snail will overgraze— potentially resulting in salt marsh grass die off (Silliman et al. 2005).



**Figure 4:** Diet composition of the blue crab. In a gut-content analysis conducted by Fitz and Weigert (1991), they found the primary prey items of the blue crab to be non-swimming crabs, fish, organic debris, and *Spartina alterniflora*. Figure adapted from Fitz and Weigert (1991).

Blue crabs are known to inhabit a variety of ecosystems along the United States Atlantic and Gulf coasts, including seagrass beds, oyster reefs, mangrove forests, and tidal flats (Lipcius et al. 2005). The majority of research concerning blue crabs has been conducted in the Chesapeake Bay and North Carolina, where substantial fisheries for this species exist. Large open bays (Chesapeake Bay), sounds (Pamlico Sound, North Carolina), and an abundance of submerged aquatic vegetation (SAV) (both Chesapeake Bay and Pamlico Sound) generally characterize these intensively studied regions. Many researchers have demonstrated the importance of structured habitats, like SAV, as nursery refuges for crabs in those areas (Hines 2003, Ralph and Lipcius 2014); however, those systems are fundamentally different from South Carolina's estuaries and tidal rivers. The saltmarshes of South Carolina, characterized by relatively high tidal ranges and an absence of SAV, have expansive intertidal areas with little available subtidal structured habitat. Similar estuarine conditions are found in Georgia and southern North Carolina. Tidal marsh vegetation, dominated by Spartina alterniflora, and the unstructured shallow-water habitats surrounding tidal marshes are essential resources for all life stages of the blue crab in South Carolina (Figure 5, Zimmerman et al. 2000, Heck et al. 2001, Lipcius et al. 2005, Minello et al. 2008). Tidal saltmarsh is important habitat for blue crabs as it provides primary productivity, which forms the food base for saltmarsh animals, and structured habitat for protection against predators during high tide.



**Figure 5:** Simplified habitat utilization of the blue crab throughout various life stages. (Graphic provided by SCDNR, Marine Resources Division).

The remainder of this document is divided into four chapters, focusing on different climate change factors that affect the ecology of and fishery for the South Carolina blue crab, including blue crab habitat, physiology, ecology, and market trends. We recognize that the published literature on blue crabs is extensive, however, to remain focused on locally relevant data, we have purposely restricted the scope of our review to studies with a clear connection to blue crabs in South Carolina.

# Chapter 1:

# Changes in the Blue Crab's Saltmarsh Habitat

Coastal areas of the Southeastern United States are subject to sea level rise and increased estuarine salinity, especially in tidal marshes that are prime blue crab habitat. Due to both of these stressors, acute marsh dieback has occurred throughout the Southeastern United States, including in South Carolina. Salt marsh loss has direct negative impacts on marine fish, invertebrates, and birds as the roots of marsh plants help to accumulate and retain sediments and provide habitat. The blue crab also plays an integral role in maintaining the integrity of the saltmarsh, as they prey upon snails that would otherwise remove salt marsh vegetation through grazing. Since both sea level and salinity intrusion are expected to increase in the future, understanding the complex ecosystem impacts of these two stressors is integral to effectively preserve this valuable habitat.

# Sea Level Rise (SLR)

The increase in global temperatures is a complex process that can lead to alterations in other processes, such as sea level rise (SRL) (CCTWG 2013). In addition to the thermal expansion of water due to increasing temperatures, increasing sea levels are due to a combination of the melting of land-based ice sheets and glaciers and vertical land movement (Pritchard et al. 2009, Carter et al. 2014). Over the past 100 years, global sea levels have risen about eight inches on average (Carter et al. 2014). An increase in sea level poses a problem not only for human interaction with the coast due to flooding, but also for coastal ecosystems, which will face the same flooding challenges but may not be equipped to adapt at a pace sufficient to withstand and outlast the challenge.

The Southeastern United States is an area vulnerable to SRL, which threatens coastal infrastructure and natural ecosystems alike (Figures 6 and 7). Coastal infrastructure costs millions to alter in the face of SLR, while natural ecosystems (such as saltmarshes) have already begun to retreat landward (Carter et al. 2014).

Marshes are formed by sediments being trapped in the root systems of several different species of marsh plants, and this is referred to as marsh accumulation. In order to preserve the physical integrity and structure of the saltmarsh, marsh elevation must rise at an equal or faster rate than the rate of SLR (Daniels et al. 1993, Kirwan and Patrick 2013). If the rate of SLR outpaces the rate of sediment accumulation in the salt marsh, flooding will occur. Flooding caused by SLR has been observed on vast marsh flats in the Gulf of Mexico and in tributaries along the Chesapeake Bay, quickly transforming these areas into open water (Reed 1995, Kearney et al. 2002, Carniello et al. 2009, Kirwan and Patrick 2013). An adaptation strategy for the saltmarsh could be increasing vertical growth or expanding shoreward into areas not previously inhabited (Donnelly and Bertness 2001). The economic costs of such vast habitat destruction and alteration are difficult to predict; but, if the valuations of salt marsh systems provided by Costanza et al. (2014) were accurate, there would be significant negative economic impacts. Coastal communities derive direct economic benefits from the ecosystem services provided by salt marshes, including but not limited to, commercial and recreational fisheries and storm protection. Indirect economic benefits provided include tourism and tax revenues collected from waterfront property, both of which are reliant on the aesthetic and other less tangible aspects of being near or on the water.

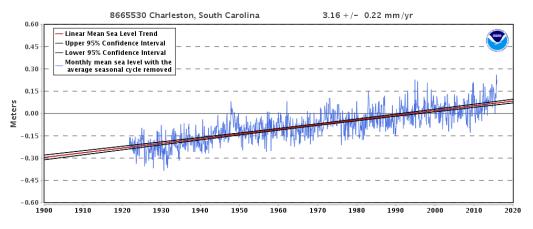
# Vulnerability to Sea Level Rise Virginia Beach Charleston New Orleans

Very High

**Figure 6:** Vulnerability to sea-level rise. Map of the Southeastern region of the United States showing a relative measure of the system's natural vulnerability to the effects of sea level rise. Figure from Carter et al. (2014).

High

Moderate



**Figure 7:** Tidal gauge data from Charleston, SC depicts an increase in mean sea level of  $\sim$ 1.03 feet in 100 years and 3.16 ± 0.22mm per year. Figure from the National Oceanic and Atmospheric Administration.

### *Increased Estuarine Salinity*

Tidal salt marshes in the Southeastern United States are, on average, increasing in salinity as a direct result of multiple, concurrent changes in the water cycle (i.e. uncommon droughts or floods). This is somewhat surprising since regional climate forecasts predict average to higher than average precipitation for the southeastern US. Recent hydrological modeling for the Edisto River watershed

suggests that observed declines in freshwater flow run counter to model predictions from observed levels of precipitation. This suggests that water withdraw for human use has exceeded climate driven increases in precipitation (Dan Tufford personal communication). In combination with coastal development, nutrient runoff, additional freshwater runoff, and changes in the intensity and duration of droughts and flood events, salinity shifts are modifying sensitive marine ecosystems such as saltmarshes (Knapp et. al 2008). For example, salinity intrusion in saltmarsh ecosystems influences plant establishment by negatively affecting both reproduction and propagation and can shift the distribution and abundance of vegetation to match the salinity gradient of an estuary (Short and Neckles 1999, White and Alber 2009).

Shifting salinities can transform blue crab saltmarsh habitat (Short and Neckles 1999, Orth et al. 2006, White and Alber 2009) and can have a negative impacts on the vegetation in salt marsh ecosystems. For example, reduced freshwater inflow, a product of a drought event, can cause acute marsh dieback (AMD), which is an extensive die-off of vegetation in a tidal salt marsh ecosystem (Alber et al. 2008). AMD was observed throughout the Southeastern United States in the early 2000s and was specifically observed in South Carolina in 2001-2002 (Alber et al. 2008, Hughes et al. 2012). Bearing in mind that 2001 and 2002 were drought years for South Carolina, the freshwater inflow to the local estuarine system was reduced. A study conducted on a marsh island in the North Inlet/Winyah Bay area found that hypersaline porewater, which is the groundwater held in soils and released into the environment during drought events, triggered AMD at that particular location (Hughes et al. 2012). While some marsh plants can survive saline conditions, hyper-salinity (i.e., extremely high saline conditions) can cause mortality of many species. Hypersaline conditions were observed during moderate droughts, supporting the hypothesis that drought is a stressor for marsh plants (Hughes et al. 2012).

### *Predator-Prey Dynamics of Callinectes sapidus on Saltmarsh Degradation*

SLR and increases in salinity are not the only causes for saltmarsh habitat loss. Blue crabs can play a role as well by manipulating the densities of snails that graze on salt marshes. In an experimental manipulation of periwinkle snail (*Littoraria irrorata*) grazing activity, Silliman et al. (2002) altered the densities of the periwinkle snail and found that blue crab predation on that particular species of snail was a determining factor of marsh grass growth (Silliman et al. 2002). Another study conducted by Silliman et al. (2005), looking at the interaction of experimentally manipulated drought conditions and periwinkle snail grazing pressure on salt marsh plants, found that drought stressors (decreased soil moisture, elevated salinities in marsh soils and estuarine waters) were mainly responsible for marsh loss and initial dieback in sites in Louisiana, Georgia, and South Carolina. In addition, the highest densities of grazing snails were found at the edge of the salt marsh dieoff area, indicating that snail grazing exacerbated marsh die-off (Silliman et al. 2005). The presence of the periwinkle snail on the die-off edge allows the snails to move through healthy marsh, causing vegetation loss (Silliman et al. 2005). This study illuminates the broader-scale issues at hand, which is that climate change stressors, such as drought and SLR, can affect not only the habitat but also the organisms within the marsh ecosystem.

# **Chapter 2:**

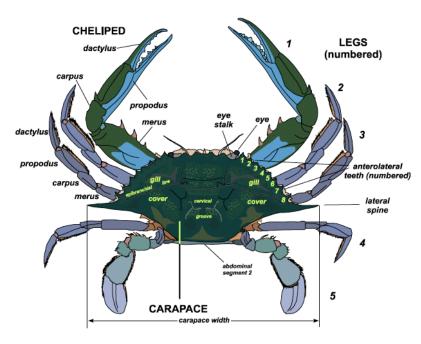
# Physiological and Behavioral Adaptations to Changing Abiotic Conditions

In the previous chapter, the impact of climate change on the habitat utilized by blue crabs was discussed. In this chapter, we discuss specific impacts of climate change on blue crabs in South Carolina, focusing on water temperature increases, inland salinity intrusion, and ocean acidification. Blue crabs have experienced climate extremes in the past and have several physiological and behavioral adaptations to tolerate a broad range of environmental conditions (i.e., temperature, salinity, pH, oxygen). The physiological processes employed by the blue crab to handle these dynamic environmental factors are respiration rates and osmoregulation, while they also use behavioral mechanisms to cope with shifting abiotic gradients. However, the physiological stress placed upon individual blue crabs while coping with environmental stressors may make them more susceptible to disease. Understanding the mechanisms and processes of how blue crabs adapt or acclimate to changing climatic conditions may indicate the potential of this species to continue to survive under more stressful conditions in the future.

### Blue Crab Physiology

Before delving further into specific physiological responses of the blue crab, defining the term *physiology* is critical to understanding this chapter. Animal physiology is an integrative science, which examines the functions and activities of organisms and the physical and chemical processes involved (Hill et al. 2012). Physiological responses of an organism, at the cellular and systems levels, are best understood by examining the chemical, physical and evolutionary processes involved (Hill et al. 2012). The anatomical structures of the blue crab provide the substrate for physiological processes (Figures 8 and 9). The particular physiological mechanism that enables blue crabs to acclimate to abiotic conditions will differ

depending on what environmental variable they are exposed to, with both acute (quick) and chronic (long-lasting) physiological responses.



**Figure 8:** The dorsal view of a male blue crab. Figure originally published in Ward (2012).

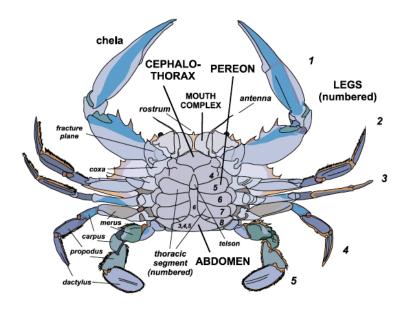
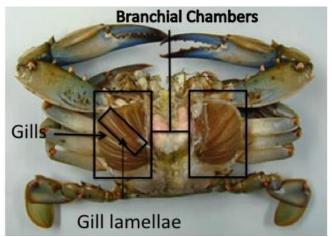


Figure 9: The ventral view of the male blue crab. Figure originally published in Ward (2012).

# Respiration

The blue crab is an estuarine and marine organism that is able to "breathe" underwater by taking in water through openings near the base of each leg and passing the water over the gills (Figures 8 and 9, Ward 2012). Blue crabs have two sets of branchial (gill) chambers with one located on each side of the body. Blue crabs are unusual for marine crabs in that they have eight gills (each composed of two rows of very closely spaced flat gill lamellae) in each branchial chamber, while most marine crabs have nine (Figure 10). The gill lamellae are responsible for gas exchange and transporting oxygen into the blue crab's blood, or hemolymph, while blocking the absorption of carbon dioxide and ammonia, which are toxic when absorbed into the blood (Ward 2012). In addition to gas exchange, the gills closest to the abdomen play an important role in the transfer of salt ions. The oxygen transfer rate (i.e., how quickly an adult crab can "pull" oxygen from the water) of an adult intermolt crab varies with body mass, but the rate doubles with both molting and swimming activities and has a positive correlation with temperature (Towle and Burnett 2007, Ward 2012). Once through the gills, the water passes through the gill rakers, or "scaphognathites", which pump the oxygen-depleted water out of the respiratory system through ports near the mouth.



**Figure 10:** Gill structures in the branchial chambers of the blue crab. The gill lamellae make up each gill. Photo adapted from the Smithsonian Environmental Research Center.

# Osmoregulation

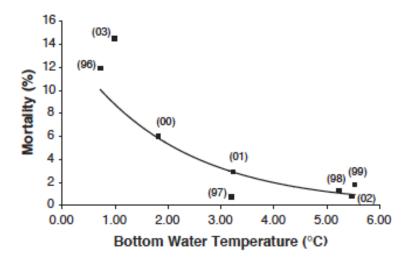
The gills play a large role in osmoregulation (i.e., the ability of an organism to maintain water balance in relation to the surrounding fluid). Osmoregulation is an important physiological process as it controls the water content of the body and protects cells by avoiding too much water entering or leaving them. As blue crabs experience a wide range of salinities throughout their life cycle, they are considered strong osmoregulators because they are able to maintain hemolymph composition at a standard rate regardless of salinity fluctuations (Pequeux 1995, Bauer and Miller 2010). In salinities from 27 to 35 ppt, blue crabs are an "osmoconformer", which means the salt concentrations in the blood are in balance with salt concentration in the surrounding water (Tagatz 1971, Guerin and Stickle 1997, Ward 2012). Once below about 27ppt, blue crabs become hypertonic to their environment, i.e., if the salinity of the environment surrounding the blue crab drops, their blood retains salt to stay at 27ppt. The blue crab is a noted efficient osmoregulator in low salinity waters meaning it can survive in low salinity water conditions indefinitely (Ward 2012). In freshwater, blue crabs remove as much as 20% of their body weight in the form of urine in order to survive (Cameron and Batterton 1978, Ward 2012). With this expulsion of urine, the crab also loses salts important to vital functions, and the intake and the posterior gills moderate replacement of the salts (Ward 2012).

# *Increased Water Temperatures*

Rising ocean temperatures as a product of climate change have both positive and negative outcomes for the South Carolina blue crab. Adult blue crabs from South Carolina tolerate a temperature range of 3.2°C to 35.2°C (McKenzie 1970, Milliken and Williams 1984). In general, increasing water temperatures decrease blue crab overwintering mortality (Rome et al. 2005, Bauer and Miller 2010). Blue crabs overwinter to avoid cold temperatures by burying down as deep as 10cm in the sediment and stopping all feeding, molting, and breeding. Overwintering behavior also delays the settlement and dispersal of juvenile crabs and increases the overall

blue crab generation time, which is the time between two consecutive generations in the lineages of a population (Hines et al. 2010, Ward 2012). These winter temperatures are important to blue crabs, as overwintering mortality impacts recruitment dynamics and regulate blue crab populations in the Chesapeake Bay (Strasser and Pieloth 2001, Bauer and Miller 2010).

Overwintering mortality of blue crabs is a function of the spatial distribution of the population. More overwintering behavior and mortality is observed in naturally cooler waters in northern states (Milliken and Williams 1984, Sharov et al. 2003, Rome et al. 2005, Bauer and Miller 2010, Colton et al. 2014), while warmer winter bottom water temperatures result in less winter mortality in southern waters (Figure 11, Davis 1999). There can also be spatial variability in winter severity even within a particular estuary, as seen in the Chesapeake Bay system. The lower Bay experiences shorter, less severe, and higher salinity winters than the upper Bay (Bauer and Miller 2010). In this system, winter mortality is thought to be higher in the upper Bay as it experiences lower temperatures and lower salinities (Bauer and Miller 2010). Therefore, from the perspective of the blue crab, increased winter temperatures, particularly north of North Carolina, could be a positive outcome of changing environmental conditions.



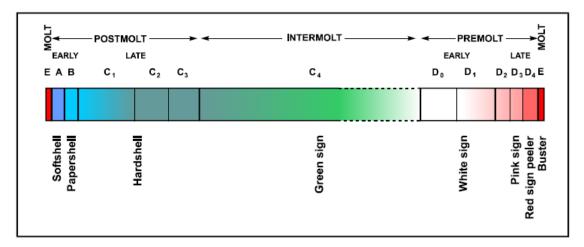
**Figure 11:** Annual overwintering mortality of blue crabs as a function of February bottom water temperature from Maryland Department of Natural Resources fisheries-independent winter dredge surveys (1996-2003). The recorded year is the number in parenthetical notation. Figure originally published in Rome et al. (2005).

In South Carolina, the average winter water temperatures range from 10-14°C (NOAA 2015), and South Carolina winters are not as long nor as severe as those in the Chesapeake Bay. Colton et al. (2014) compared the state landings data of blue crab from Delaware to Georgia. Looking specifically at South Carolina, winter temperature was an important variable for age-0 crabs suggesting that South Carolina blue crabs do not overwinter, and therefore colder temperatures are more likely to lead to higher mortality rates (Bauer and Miller 2010, Hines et al. 2010, Colton et al. 2014). However, the impact of overwintering mortality rates and behavior on South Carolina's population of blue crab is currently unknown, and further studies should address this issue.

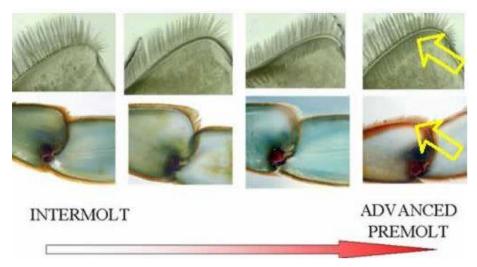
Molting patterns of blue crabs, like overwintering behavior, is dependent on water temperature (Brylawski and Miller 2006, Ward 2012). Blue crabs need to molt in order to grow, and there are 13 different molt stages between a "soft", or newly molted, and "hard", or firm exoskeleton, crab (Figures 12, 13). Molting frequency is determined by food availability and water temperature, with increased growth rates and molting frequency occurring at higher water temperatures with plentiful food (Brylawski and Miller 2006, Ward 2012). The molting process of blue crabs halts when temperatures fall below ~9-11°C (Brylawski and Miller 2006, Hines 2007, Smith and Chang 2007, Bauer and Miller 2010). In winter, the period between molts can be up to three to four times longer than the rest of the year (Ward 2012). Estuarine systems like the Chesapeake Bay often encounter winter water temperatures of 10°C, and thus in the Chesapeake Bay, the longevity of blue crabs was conventionally thought to be 3 years maximum (Rugolo et al. 1998). Lower latitudes, such as South Carolina, reach the minimum temperature of ~9-11°C rarely, and blue crab growth at these latitude is thought to be uninterrupted by overwintering which allows blue crabs to mature in less than a year (Smith and Chang 2007, Bauer and Miller 2010). It is evident the precise age of blue crabs is unclear, and may be dependent on latitude as growth is controlled by abiotic factors that can differ latitudinally and even within estuaries.

Warmer seasons throughout the year may positively affect population growth with rapid molting, development and reproduction (Lonsdale and Levinton

1985, Reaka 1986, Hines 1989, Dugan et al. 1991, Hines et al. 2010). However, it is currently unknown how increasing water temperatures, as a function of a changing climate, would affect the molting frequency of the blue crab. It could be hypothesized that increased water temperature would lead to increased molting frequency. This could lead to several results including faster growth rates and shortened time to maturity of the blue crab (due to increased molting), more broods of eggs per year, potentially lower mortality rates due to a faster molting process, but higher predation rates upon blue crab due to their vulnerability after shedding the exoskeleton. On the other hand, increased molting rates and faster growth rates may enable blue crabs to reach a size refuge against predation much more quickly. Future studies are needed to address these questions.



**Figure 12:** The molt stages of a blue crab defined in a linear manner, with the common name of the molt stages below. The color scale is reflective of the "molt sign" identified on the swimming "fin". Original figure from Ward (2012).



**Figure 13:** Molt stages from the intermolt to advanced premolt stages for the blue crab depicting the red "molt sign" on the swimmeret. Imagery provided courtesy of the Smithsonian Environmental Research Center.

### Rising Salinities in Coastal Estuaries

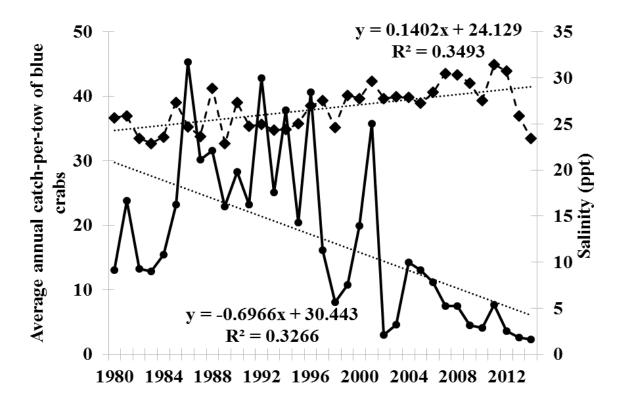
The spatial distribution of blue crabs varies depending on the developmental stage, sex of the individual, and season of the year (Tagatz 1971). Developmentally, each life stage of the blue crab has a specific salinity tolerance. Larval and megalopal blue crabs are found in high, oceanic salinities ranging from 20 to 30 ppt (Sandifer 1975, Milliken and Williams 1984), while juvenile and adult blue crabs are euryhaline and can tolerate a fairly wide range of salinities ranging from 1 to 30 ppt (Milliken and Williams 1984). Life strategy and reproductive behaviors are based on salinity cues (Childress 2010), and the blue crab implements both behavioral and physiological responses to salinity (Parmenter 2012). Larvae develop in the open ocean or close to the mouths of the estuary in high salinity waters, while juveniles and adults are found in estuaries and tidal salt marsh systems where the water transitions from brackish to fresh (Tagatz 1971). The adult males are more commonly found in lower salinity water, while adult females migrate seaward and will be more abundant in intermediate and higher salinities, as spawning typically takes place in high oceanic salinities (Tagatz 1971).

Climate change related drought is considered a stressor of Southeastern United States tidal salt marshes and is predicted to increase in rate of occurrence, intensity, and longevity (Alber et al. 2008, Childress 2010, Gilbert et al. 2012, CCTWG 2013). It

is difficult to establish a frequency prediction of severe weather in South Carolina because there has been no statewide paleoclimate (historical climate) study of the state (CCTWG 2013). The overarching prediction is an increase in intense storm events, which could affect flooding frequency and duration especially when paired with periods of prolonged drought (CCTWG 2013).

During a drought, the lack of freshwater inflow can result in increased salinity in estuarine river systems, which is termed "salinity intrusion" (Childress 2010). In Texas, salinity intrusion further inland due to lack of freshwater run-off created a hypersaline environment for blue crabs in areas that normally had moderate salinities (Ward 2012). In this case, blue crabs respond both behaviorally, by following the salt wedge up the tidal river, and physiologically, by performing osmoregulation in varying salinities (Ward 2012).

Long-term fisheries independent surveys along the South Carolina coast, conducted by the SCDNR have shown an overall increase in salinities from 1980 to 2012 with a concurrent decrease in blue crab catch (Figure 14). This correlation suggests that reduced rainfall and river flow rates may be related to declining crab population abundance. This could potentially be explained by several mechanisms, including decreased optimal nursery habitat, negative physiological responses to higher salinity, increased disease prevalence (*Hematodinium* sp.), and declining numbers of spawners due to differential catch rates of males and females.



**Figure 14:** Crab catch per unit effort (CPUE) from SCDNR trawl data collected from 1980-2014 in the solid black line, and the salinity (ppt) recordings in the dotted black line. Recorded salinities are increasing over time while the crab catch has been decreasing. Data and graph compiled by David Whitaker (SCDNR).

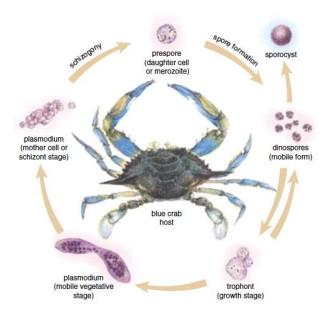
### Ocean Acidification

Since the industrial revolution (around 1750), there has been a significant increase of carbon dioxide released into the atmosphere. The oceans have been absorbing approximately half of this carbon dioxide (CO<sub>2</sub>), and this process of carbon sequestration, or the intake of excess atmospheric carbon dioxide, has altered the ocean carbon chemistry on a global scale (Sabine et al. 2004, Widdicombe and Spicer 2008, Ward 2012). In general terms, the increased carbon sequestration by the ocean has made seawater slightly more acidic over time (termed "ocean acidification"), which can impact the physiology of marine organisms quite substantially. While much of the current research on ocean acidification concerns sessile benthic organisms, such as corals and oysters, this more acidic water may impact the molting process of the blue crab (Whiteley 2011). Specifically, blue crabs need to extract calcium carbonate from seawater in order to

make a hard exoskeleton, but the changes in seawater chemistry due to ocean acidification make the extraction process difficult, resulting in the inability of individuals to make a hard shell. While hardening the exoskeleton has been shown to take twice as long in a more acidic environment (Cameron 1985), juvenile and adult blue crabs exposed to more acidic water had increased growth rates and increased calcification of their exoskeleton and acidification had no impact on the formation of calcium carbonate in the exoskeleton (Ries et al. 2009). The impact of ocean acidification on the development of the blue crab shell remains unclear, as the current literature is contradictory and most of the literature reviews are dependent on comparative studies. There is a need for future research in this field, particularly in the Southeastern United States.

### Disease

Changes in environmental conditions, such as higher temperatures or more acidic water, can lead to a weakened physiological state and make blue crabs more susceptible to disease. For example, in areas of high salinity, such as a drought-plagued salt marsh, there is a greater risk of blue crabs being exposed to the parasitic dinoflagellates of the genus *Hematodinium* sp. (Lee and Frischer 2004). Once the parasite is inside the hemolymph, or "blood", of the host, it multiplies in the tissues and organs and highjacks the host's metabolic products (Figure 15), thereby causing muscle necrosis and metabolic exhaustion, which results in changes in crab behavior and eventual death (Rowley et al. 2015). The prevalence of the parasite in blue crab populations has been as high as 100% in outbreaks along the United States Atlantic coast, and infected crabs can die in as little as 14 days after exposure (Messick 1994, Messick and Shields 2000, Coffey et al. 2012).



**Figure 15:** Life cycle of the parasitic dinoflagellate, *Hematodinium* sp. The majority of the parasite's life cycle is spent inside the blue crab. The dinospores stage of *Hematodinium* sp. is thought to be the infectious stage of the parasite's life cycle and can last in the water for prolonged periods of time. Transmission of the parasite is still not fully understood, however, consumption of infected amphipods or crustaceans by blue crabs may lead to infection. Figure from Lee and Frischer (2004).

Both temperature and salinity are primary factors in limiting the distribution and intensity of *Hematodinium* sp., and it has been found in blue crabs from North Carolina to the Gulf of Mexico since the 1970s (Lee and Frischer 2004). Blue crab samples taken in South Carolina in 1968-69 did not contain *Hematodinium* sp. (Newman and Johnson 1975), but the disease was identified in samples from the 1970's. Interestingly, *Hematodinium* sp. infections in blue crabs have not been observed in salinities below 11ppt or when winter water temperatures were below 10°C (Newman and Johnson 1975, Messick and Shields 2000, Lee and Frischer 2004, Coffey et al. 2012). This suggests either that the transmission of the parasite to new hosts is not possible in low salinities or the parasite cannot develop in crabs living in salinities below 11ppt or temperatures below 10°C (Coffeey et al. 2012). The impact of *Hematodinium* sp. on blue crabs in South Carolina appears to be more profound during the fall months with high water temperatures and salinities greater than 11ppt, both of which are more likely during drought conditions (Overstreet 1978, Parmenter et al. 2013). Furthermore, crabs infected with Hematodinium sp. exhibit differences in carapace shape and have shorter lateral spines. Shorter lateral spines may make small crabs more vulnerable to predators and further increase their risk of predation (Parmenter 2012, Parmenter et al. 2013).

The decline in blue crabs along the United States Atlantic and Gulf of Mexico coasts may be influenced by epizootic outbreaks of *Hematodinium* sp. (Messick and Shields 2000, Lee and Frischer 2004). Lee and Frischer (2004) attributed the majority of the blue crabs population decline in Wassaw Sound, GA to the prevalence of *Hematodinium* sp. However, such assumptions cannot be made for South Carolina's population of blue crab as infection rates rarely exceed 5% of the population total (Parmenter et al. 2013). As climate change has the potential to increase the number and longevity of drought events, it is possible that blue crabs could experience more epizootic outbreaks of *Hematodinium* sp. due to increasing salinities and water temperatures. Further efforts to model the effect of climate change and disease impacts on blue crabs are needed in South Carolina to document these interactions (Childress 2010, Childress and Parmenter 2012, Childress 2014).

# **Chapter 3:**

# **Larval Settlement and Juvenile Dispersal**

Blue crabs have a multi-stage life cycle that takes place in several different estuarine and marine ecosystems (i.e., open ocean, estuaries, tidal creeks, oyster reefs, and seagrass beds). These changing abiotic factors have the potential to influence blue crab development and disrupt biotic processes. For example, the South Carolina blue crab fishery is dependent on successful recruitment of blue crabs into the system each year. Conditions that disrupt or impair that process would be detrimental to the fishery. Therefore, understanding how climate change impacts the successful recruitment of blue crabs into coastal waters is paramount to explaining shifts in blue crab abundance over time. In this chapter, the life cycle of the blue crab will be explained, followed by an examination into how these abiotic factors can influence juvenile blue crab settlement and dispersal.

# Life cycle of the Blue Crab

In the Southeastern United States, the blue crab occupies a wide range of saltmarsh habitat after several larval stages in offshore, oceanic water. The complex life cycle of blue crabs has three main phases: (1) a planktonic larval stage, which occurs in the open ocean; (2) a benthic juvenile stage, occurring in estuaries; and (3) a migratory adult stage, which occurs in both estuaries and the open ocean and is highly dependent on whether the crab is male or female (Mense and Wenner 1989, Parmenter 2012).

Blue crabs must molt in order to grow (Mense and Wenner 1989, Parmenter 2012). After molting, the blue crab will absorb water, expanding in width by 25% or more (Figure 16). It takes larval blue crabs approximately 15 to 20 months to reach a carapace width of five inches, which is the legal size for commercial and recreational harvest within South Carolina (Archambault et al. 1990, Rugolo et al. 1998, Parmenter 2012).



**Figure 16:** A female blue crab undergoing the molting process in chronological order (top right to bottom right). Provided courtesy of the Smithsonian Environmental Research Center and Alicia Young-Williams.

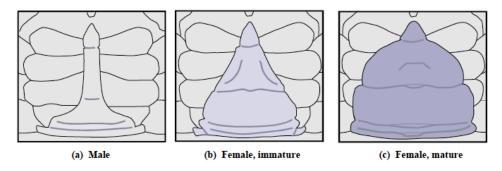
Females must reach a mature state in order to copulate; this mature stage is achieved through a terminal, or last, molt. These terminal-molt females comprise the bulk of the spring soft shell crab fishery. Male crabs physically carry (or "cradle") females who are ready for their terminal molt until they start to molt. At that point, the male releases the female until she sheds her exoskeleton. Once she has molted, the male begins copulation by positioning himself ventrally to the female and utilizes his copulatory stylets to introduce sperm to the spermathecae in the female; copulation may last for several hours. After mating, the male protects the female until her exoskeleton has hardened. While males can mate multiple times, most females mate only once during their lifetime and retain spermatozoa for multiple spawns (Van Engel 1958, Milliken and Williams 1984).

Archambault et al. (1990) found that blue crab mating in the Charleston Harbor occurred throughout the spring and early summer into the fall in lower salinity profile areas of the estuary, based on the molting cycle of pubertal females. The majority of mating pairs were found in July, August, and September, with some mating extending into June and October. While mating usually occurs in fresher water, ovigerous females from Charleston Harbor were not found in salinities of 10ppt or less or water temperatures less than 14°C (Archambault et al.

1990). After mating, females migrate toward higher salinity areas (28-32ppt) near the mouth of the estuary, larger inlets or harbors and prepare to spawn; male crabs remain in the fresher water upriver (0-10 ppt) (Darnell 1959, Archambault et al. 1990). Females will not release any eggs until at least two months after mating (Van Engel 1958, Milliken and Williams 1984). Females extrude and attach their eggs underneath the abdomen to an anatomical structure commonly referred to as the "apron" during summer (Figures 17 and 18) where the eggs develop for 14-15 days before hatching (Churchill 1919, Sandoz and Rogers 1944, Milliken and Williams 1984, Carr et al. 2004). Eggs will hatch at slightly faster rates at higher temperatures (Churchill 1919). Ovigerous females collected from the Chesapeake Bay produce between 700,000 and 6 million eggs per brood (Milliken and Williams 1984, Prager et al. 1990). However, on average, only one out of every million eggs survives to become a mature adult (Van Engel 1958).



**Figure 17:** A female blue crab "in sponge". Image provided by the Smithsonian Environmental Research Center.



**Figure 18:** Differentiation of blue crab sexes based on abdominal structures image originally published by Ward (2012).

In both the Chesapeake Bay and coastal South Carolina, the majority of eggs usually hatch in June and July, with a second peak in August (Darnell 1959, Archambault et al. 1990). In South Carolina, the June/July hatch is likely from females that overwintered as "sooks" (mature adults) and spawned in April. The August hatch is probably eggs from combination of sooks and females that molted and mated in April. After hatching, blue crabs transition through several life stages, including eight to nine planktonic larval stages, nine to ten benthic juvenile stages, and a migratory adult stage, all within one to one and a half years (Darnell 1959, Milliken and Williams 1984, Figure 5).

All of these stages occur throughout a wide salinity profile, varying from low (0-10 ppt) to high salinities (30-32ppt) (Archambault et al. 1990, Blue Crab Update 2004, Childress 2010). Eggs hatch near the mouth of a bay, with salinities over 20 ppt (Darnell 1959), and are swept by currents out into the open ocean where further development occurs over the next month in salinities of 32ppt or more (Darnell 1959, Rugolo et al. 1998). After approximately seven zoea stages, the blue crab develops into the planktonic megalopae stage and begins ingress to the estuarine system using tidal currents (Mense and Wenner 1989, Parmenter 2012). Once within the estuary, the blue crab transitions from the planktonic megalopal stage to a benthic juvenile stage that has the adult blue crab morphology (Mense and Wenner 1989). At this point, in shallow estuarine habitats, megalopae settle onto benthic habitat (e.g., submerged aquatic vegetation, oyster reefs) (Heck and Thoman 1981, Orth and van Montfrans 1987, Etherington and Eggleston 2000). Juveniles remain in these protected benthic habitats until they reach the fifth to seventh instar stage and begin to migrate through the estuarine system (Johnson and Eggelston 2010). In the Chesapeake Bay, it is commonly thought that blue crabs undergo anywhere from 18 to 20 molts before reaching maturity (Van Engel 1958, Milliken and Williams 1984).

## Influence of Abiotic Factors on Larval Settlement and Juvenile Dispersal

The larval life phase of the blue crab is a complex process dependent on wind driven and/or current driven larval transport to coastal and nursery habitats, benthic structure, food availability, salinity, and water temperature (Eggleston et al. 2009, Hines et al. 2010, Ward 2012). While larval dispersal may vary by region due to differences in oceanography (Ward 2012), there are a few general themes. After hatching, the planktonic larvae are transported to the inner continental shelf via currents (Figure 5). The dispersal of zoeae and megalopae is dependent on the nearshore and shelf currents, and they can disperse both latitudinally and longitundally offshore (Ward 2012). As the dispersal is a function of currents and wind, only some megalopae are carried back into the nearshore zone, where they are potentially transported back into the estuaries (Ward 2012, Figure 5). If the larvae survive the journey offshore and back into the mouths of estuaries, the nursery (estuary) habitat is critical for further development. In the ACE Basin National Estuarine Research Reserve, larval crab settlement was highest for marsh locations closest to St. Helena Sound and decreased at locations further inland but did not differ significantly between drought and normal flow years (Parmenter 2012). Abiotic factors such as oceanic currents, alteration of the hydrological cycle, shifts in temperature and salinity may strongly influence larval settlement.

Alterations of wind and/or currents due to climate change, including increased frequency and severity of hurricanes, typhoons, and other storm events (Eggleston et al. 2009), may negatively impact megalopae if those winds and currents move megalopae offshore and inhibit their ability to enter an estuary (Goodrich et al. 1989, Johnson and Eggleston 2010). Few studies have been conducted to investigate the impact of increased storm frequencies on blue crab larval settlement into the estuaries, but Bakun (1990) suggests increased storm frequency may increase coastal upwelling, which may impact the strength and direction of both surface and bottom currents. Additionally, since much of the larval recruitment time period coincides with the hurricane season, the increased frequency and intensity of storm events may affect larval recruitment through the

disturbance of offshore surface current and creation of "dead zones" through nutrient run-off within estuary systems (Najjar et al. 2010, Hines et al. 2010). Colton et al. (2014) further suggests that blue crab production along the United States east coast is linked to larger oceanographic processes like the Gulf Steam Index (GSI) and the North Atlantic Oscillation (NAO), both of which are broadscale climate indices. While the GSI is the position of the north wall of the Gulf Stream (Taylor 1996), the NAO is a measure of the atmospheric pressure difference between the Arctic and Atlantic regions (Hurrell et al. 2003). Both of these climate indices have the potential to be altered due to climate change, especially in relation to global changes in weather patterns such as increased temperatures, drought, and changing ocean winds or currents. This has the potential to disrupt current patterns and processes of blue crab juvenile recruitment and warrants further research, especially in South Carolina.

Water temperature and salinity can also impact larval and juvenile blue crab survival (Hines et al. 2010, Ward 2012). Larvae cannot survive water temperatures above 30°C or below 20°C (Milliken and Williams 1984), and Williams (1984) found in laboratory studies that larval growth ceases in salinities above 31.1ppt and below 20.1ppt. In laboratory studies, blue crab larvae grew into megalopae and, eventually, the first crab stage at similar paces between 20.1ppt and 30.1ppt at 25°C (Milliken and Williams 1984).

Due to climate change, the water temperatures across the Southeastern United States are expected to increase (CCTWG 2013) resulting in warmer, shorter winters (Najjar et al. 2010, Hines et al. 2010). These more temperate winters may reduce larval and juvenile mortalities (Najjar et al. 2010, Hines et al. 2010). Some models also predict winters with higher levels of precipitation, therefore reducing salinity and potentially increasing mortality during the colder months (Hines et al. 2010). However, further research is needed to determine the effects of extreme heat events and increased freshwater runoff in shallow water habitats on blue crab mortality.

# **Chapter 4:**

### South Carolina Blue Crab Market Characterization

As environmental conditions dictate where crabs will be within the estuarine system, those same conditions also influence where crab pots will be set. Whether or not those crabs become part of the fishery record depends upon someone pulling those pots and landing the product, which is a factor dictated by the market demand for crabs. Any description of the fishery should take into account the activity of the market for blue crabs. During 2015, market characterization interviews were conducted with wholesale crab dealers and retailers in South Carolina to better understand recent market trends, infrastructure needs, and what is vital to remaining competitive in the market. Results of these interviews and recent trends (2004-2015) in landings and value are presented to aid in understanding the fishery from a fisherman's perspective.

#### Historical Context

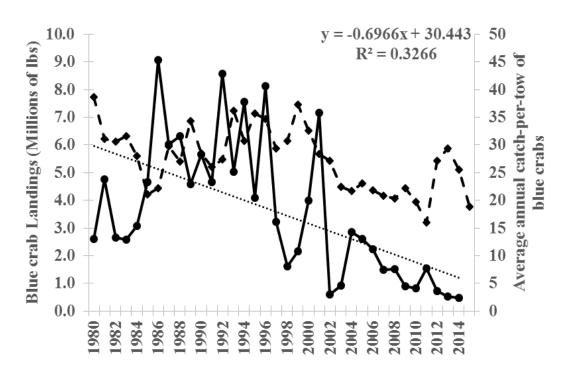
The market for South Carolina blue crabs is, and has historically been, geographically-speaking, a regional market. The end consumer is located in major mid and north Atlantic hubs including Washington, Baltimore, Philadelphia, and New York City. Crabs from the mid and South Atlantic states as well as the Gulf of Mexico serve these markets, and since the late 1990s an increasing amount of imported crab has been needed to meet consumer demand.

Hard blue crabs are the largest sector of the blue crab fishery in South Carolina and continue to be marketed and distributed much the same as they were twenty years ago. Crab buyers from mostly Maryland and Virginia travel south, filling up trucks with bushels of crab that are then delivered to picking houses in Virginia and Maryland. A smaller portion are sold to live markets in major northeast cities. Prior to 1980, many of South Carolina's blue crabs were processed at picking houses within the state, with surplus crabs put on northbound trucks (Burrell et al.

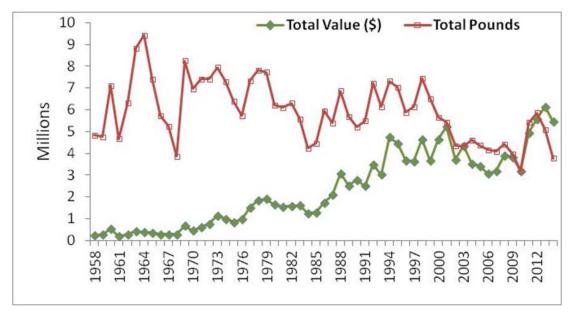
2009). With the closure of picking houses in the late 1980s, with the last one closing in the early 2000s, the volume of crab leaving the state increased.

Peeler crabs, which are the crabs purchased by shedding facilities to produced soft-shell crabs, are secondary in landings to hard blue crabs in South Carolina, becoming a larger part of the fishery in the 1980s when peeler trap technology was introduced to the state. Prior to the 1980s, most peeler crab caught in South Carolina went to large shedding facilities in Virginia. Export of peeler crabs to Virginia peaked in the late 1980s when Virginia shedding facilities began employing temperature controlled closed systems for shedding. This allowed the Virginia shedding facility owners to procure peelers from Southern states when ambient seawater temperatures remained cool in Virginia. This situation was short-lived because shedding facilities became more numerous and/or increased in capacity in South Carolina, reducing the number of peelers available for movement into northern markets. Surplus peelers continue to be shipped northward, but in smaller volumes than in year's past.

Historical landings data clearly demonstrates a decline in crab landings beginning in 1998 and continuing through 2010 (Figures 20, 21). From 1958 through 1997, on average, six million pounds of crab were landed annually in South Carolina; from 1998 through 2015 that average has declined to four million pounds annually. The value of landings indicated in Figure 20 are actual values, in other words they are not corrected for inflation, so naturally, a gradual increase in landings value is to be expected. These values are, however, valuable in demonstrating variation in value over shorter time periods. Later, we will examine changes in the value of landings when value is adjusted for inflation.



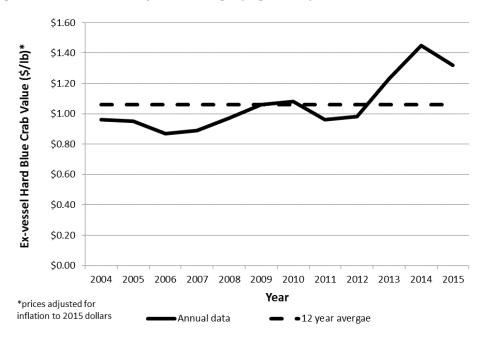
**Figure 20:** A comparison of commercial blue crab landings (dotted line) reported from 1966 to 2013 and average blue crab catch per tow (solid line) during fisheries independent surveys conducted by SCDNR from 1978 to 2013. There is a decrease in the fisheries independent survey catch per tow, but a slight increase in commercial landings from 2010-2011. This increase in commercial landings is followed by a decrease in reported commercial landings in 2013. Figure provided by David Whitaker (SCDNR).



**Figure 21**: Amount (in millions of pounds) and value (in US dollars) of blue crab landed in South Carolina from 1958-2014. (SCDNR, Office of Fisheries Management)

## Current Trends in Blue Crab Landings and Value

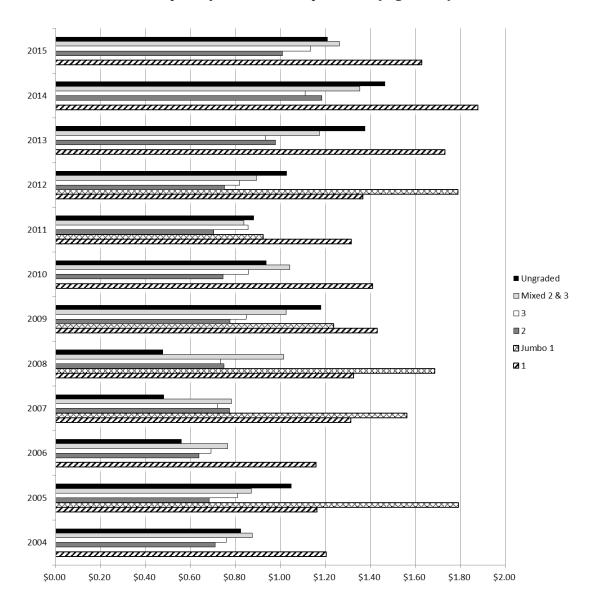
Using data from the SC Department of Natural Resources Statistics Office, an analysis was conducted to demonstrate trends in landings and value of the blue crab fishery over the past twelve years (2004-2015). All values presented have been adjusted for inflation in accordance with federal inflation rates. The market for South Carolina blue crab has recently experienced an increase in value of blue crab, more specifically the value of hard blue crab products the past three years has been 20% higher than the twelve year average (Figure 22).



**Figure 22**. Value of hard blue crab landings in South Carolina over the past twelve years. The dashed line represents the 12-year average.

The total value of all hard crab landings in South Carolina over the past twelve years is \$50,275,897; an average of \$4,189,658 per year. Price paid by wholesalers to crab harvesters was fairly steady from 2004 until 2009, when the price jumped to \$1.06/lb (2015 dollars, \$0.96 in 2009 dollars). Landings in 2009 and 2010 were 3.9 and 3.2 million pounds, respectively. This is similar to landings in 2014 and 2015 (3.7 and 3.0 million pounds, respectively), but in those years crabs were purchased for \$1.45 and \$1.32/pound, respectively. In the previous three years (2011-2013), an average of \$1.06/lb was paid to the harvester.

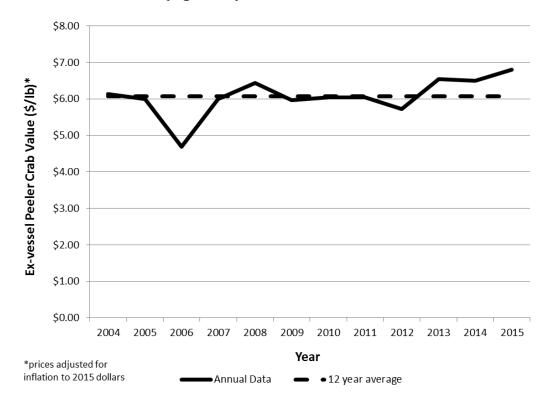
By volume, 52,029,494 pounds of hard blue crabs have been landed in the state over the past twelve years; on average 4,335,791 lbs/year. The most frequently reported products over the past twelve years have been #1s, #3s, and Mixed #2s and #3s. These have also, typically been the highest value products, though in recent years ungraded crab, though low in volume, has been of higher value than the more frequently encountered products (Figure 23).



Ex-vessel Price/lb. (adjusted for inflation to 2015 dollars)

**Figure 23**. Value of various grades of hard crab landed in South Carolina from 2004-2015. Prices adjusted for inflation to 2015 dollars. Years where the 'jumbo' category is absent indicates those landings have been combined with the '#1' category to protect data reporting confidentiality.

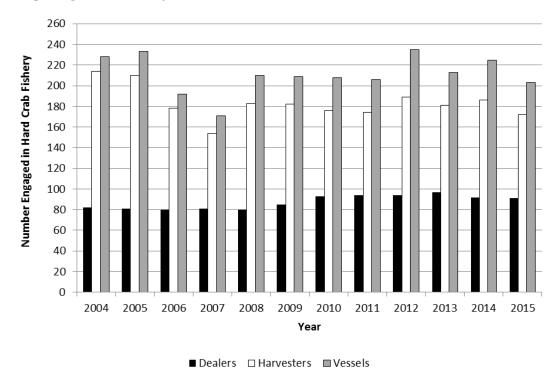
The peeler crab fishery has accounted for less than 10% of the total landings in the South Carolina blue crab fishery from 2004-2015. Peeler crab landings have totaled 590,959 lbs; on average 49,246 lbs/year. On average, when corrected for inflation, harvesters have received \$6.08/lb for peeler crabs, with a total value from 2004-2015 of \$3,219,683 (Figure 24).



**Figure 24**. Value of peeler crab landings (price/lb) in South Carolina from 2004-2015. The dashed line represents the 12-year average. Prices have been adjusted for inflation to 2015 dollars.

Although price paid for peeler crabs has remained fairly steady, we have yet to determine trends in soft-shell crab prices. Soft-shell crab remains a popular, high value, seasonal item thus, one would assume, driving the price for peelers. However, there are many additional aquaculture production costs associated with producing a soft shell crab so the price paid for peeler crab is not an accurate representation of the value of the soft shell crab fishery product. The values presented here represent the peeler fishery and should not be misinterpreted as representing the value of the soft-shell crab industry.

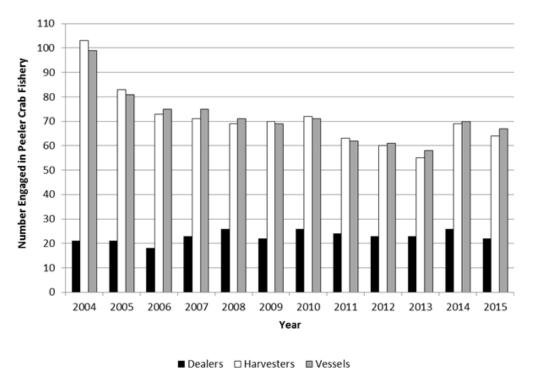
In any characterization of a fishery or market for a fishery product, just as important as considering price, it is vital to include information about the number of people engaged in the activity; often the two are related. In South Carolina, despite recent increases in the value of the crab being landed, we have not experienced an increase in the number of dealers, harvesters, or vessels engaged in the fishery (Figure 25). With respect to the hard crab fishery, over the past twelve years, there have been  $88 \pm 6.5$  dealers,  $183 \pm 16.1$  harvesters, and  $211 \pm 18.1$  vessels participating in the fishery.



**Figure 25**. Participation in the South Carolina hard blue crab fishery from 2004-2015.

In the peeler crab fishery we see a similar cyclical pattern in the number of dealers, harvesters, and vessels participating in the fishery. From 2004-2015 there have been  $23 \pm 2$  dealers,  $71 \pm 12$  harvesters, and  $72 \pm 11$  vessels participating in the peeler crab fishery (Figure 26). Higher participation by harvesters and vessels in 2004 skews the data; with 2004 removed the number of harvesters and vessels varies by only 7.4 and 6.8 over the remaining 11 year period. While the number of

dealers has remained fairly steady over the past twelve years, possibly a reflection of the number of people with shedding facilities, there is a marked decline in the number of harvesters and vessels from 2004-2006 and then again from 2011-2013. During recent interviews, all interviewees remarked that there have been changes in the timing and duration of the peeler crab season in the past 10 years so this cycle may be explained by learning to adapt to this new timing.



**Figure 26**. Participation in the South Carolina peeler blue crab fishery from 2004-2015.

The most important factor not captured by this data, both for hard crabs and peeler crabs, is the number of pots each vessel is fishing. Anecdotally, most fishermen report having to significantly increase the number of pots they fish in recent years to land the same number of crabs as in year's past.

#### Market Characterization

In 2015 a series of interviews were conducted with willing selection of wholesalers and major retailers from across the state to gather basic information to characterize the market for blue crabs landed in South Carolina. In addition, we

discussed and confirmed historic trends in the crab market with persons knowledgeable in crab markets north of South Carolina. Information was gathered on the following topics:

Number of Competitors and Intensity of Competition
Current Market Size
Projected Market Changes
Equipment Required
Barriers to Entry
Seasonal and Cyclical Factors
Strategic Fits with Other Businesses Owned
Capital Requirements
Industry Profitability and Return
Social, Political and Regulatory Factors
Production and Operations Skills Required
Environmental Factors

The majority (67%) of people interviewed had been in the crab business for over 20 years, with the remainder in the business more than 10 years. In addition to being a wholesaler, most reported personally fishing for crab to supplement or support their business. Most wholesale dealers we spoke to rely on 5-10 harvesters to supply them with product on a daily basis. Dealers communicate with their harvesters via cell phone or text message as to whether or not they will be buying crab on any given day.

The wholesalers we spoke to that are primarily wholesalers dealers reported that, on average, 78% of their business profits are a result of their participation in the blue crab fishery. The wholesale dealers we spoke to that have a retail operation as part of their business structure reported that, on average, 38% of their profits are a result of their involvement in the blue crab fishery.

As previously discussed, the market for South Carolina blue crab is a regional one, however, there is a distinct difference between hard crab and soft shell crab markets. All wholesale dealers we spoke with that are primarily wholesale reported that 75-100% of their hard crab product is sold out of state, however, the soft shell crab producers we spoke to are selling 50-100% of their soft shell product within the state of South Carolina. In addition to competition from other South Carolina-based dealers, our interviewees noted that out-of-state truck-based dealers were a

direct source of competition. The intensity of this competition varies seasonally depending on availability within the region. Those we spoke to report October and November being the months when they move the most crabs and January-May being the period during which they move the least crabs. With respect to profitability, March-June are reported as the most profitable months in a crab business which handles soft-shell crab in addition to hard crabs. If speaking solely about hard crabs, December and January are the most profitable months.

All of the dealers we spoke to consider refrigeration, both for crabs destined for sale and bait, and transportation vital to their ability to compete, and be profitable, in the market. The majority (60%) report they have been moving product the same way and with the same fundamental equipment for over 20 years; the remainder have been doing the same for 15-20 years.

Capital improvements to infrastructure have been minimal over the past 10 years, and when they have been made have mainly focused on boat improvements for fuel efficiency or purchasing pots as opposed to improvements in refrigeration, transportation, or marketing. An increased in cost of goods sold was reported by all interviewees. Cost of goods sold, often thought of as the 'production cost', is the amount of money it costs to bring a product to market. Increases in fuel costs have been off-set with more efficient engines, but cost of bait has steadily risen and effort needed to land crabs has increased, thereby increasing all associated costs (i.e. labor, fuel, wear and tear on the boat, capital investment for pots, etc.). Greater availability of crabs, establishment of in-state picking houses, and the ability to move more crabs during the late summer and early fall were all cited as ways to improve profitability.

The skill sets present within each crab business in South Carolina varies depending on the capabilities and willingness of, what are, for the most part, owner/operator businesses clocking 12-14 work days, supported by 3-5 permanent staff members. Additional staff (1-3) are hired during the peeler season to supervise and cull the shedding tanks. South Carolina wholesale dealers consider the staff working for them to be skilled at what they do, though finding skilled labor is hard, but owners are willing to spend 1-12 months training their staff in order to improve

production and increase retention. Most dealers consider being able to relate to the fishermen as a skill vital to their business, those most report wishing they were better at it.

The majority of dealers interviewed feel that over the next five years we can expect the market to become more accepting of the higher prices for blue crab and with this may come a cultural shift in where blue crab is being consumed (i.e. may see more crab in fine dining establishments). Most felt that the market will continue to be regional, with major mid and northeastern Atlantic cities driving the demand. The majority of interviewees felt that the dominant factor that is and could continue to affect the crab population in South Carolina is an increase in the number of fishermen entering the fishery, followed by environmental changes.

# **Literature Gaps and Research Needs**

### South Carolina Call for Research

One of the purposes of this document was to fill a key knowledge gap for South Carolina blue crabs identified from the Crustacean Workshop held at the SC DNR's Marine Resources Research Institute in April of 2014 (Brunson et al. 2015). Among the issues addressed was the lack of a state-of-the-knowledge report concerning the impacts of climate and habitat change on South Carolina blue crabs. Climate change can encompass a multitude of environmental factors, but as these environmental factors continue to change, further research is necessary to elucidate the complex issue of how climate change, through processes such as ocean acidification, salinity intrusion, and global warming, influences both juvenile and adult blue crab populations in South Carolina. In addition to these research directions, a reliable stock assessment is imperative for blue crabs in South Carolina to understand the status of the fishery. Even though blue crabs are currently managed at the state level, additional connectively studies sampling blue crabs throughout the entire South Atlantic Bight are needed to determine whether blue crabs are a regional stock. Additional funding is needed to support a workshop to explore the various factors that would need to be accounted for in a regional stock assessment and to expand and develop models of population structure and connectivity.

#### Future studies

#### Blue Crab Salt Marsh Habitat

As blue crabs can mitigate saltmarsh die off by keeping the abundance of snail grazers from reaching levels that could effectively destroy saltmarsh plants, understanding how sea level rise influences this relationship could shed light on unexplored trophic implications of climate change. Further research demonstrating the importance of predator-prey interactions and the regulatory role blue crabs play

in mitigating healthy marsh grass habitat through top-down predation is needed *in situ*. In addition, modeling the impacts of sea level rise on South Carolina's estuaries, incorporating both GIS and LIDAR surveys, is essential to understand the extent to which sea level rise will inundate current saltmarsh habitat. This modeling exercise should be paired with field experiments that examine altered blue crab habitat usage under simulated sea level rise scenarios.

# Larval Dispersal and Juvenile Settlement in South Carolina

Larval dispersal and juvenile settlement is dependent on several environmental variables including salinity, currents, benthic structure, and water temperature. As discussed throughout this document, climate change is altering these abiotic factors in a variety of ways such as salinity intrusion, increased storm events, habitat die-off, and extreme water temperatures.

Understanding larval development and transport into estuaries, with application to the South Carolina coastal system, is imperative to describe fluctuations in adult abundances. In particular, research is needed to examine how larger oceanographic processes may impact larval dispersal offshore and the ability of larvae to settle in non-vegetated habitats in South Carolina's bays and estuaries. In addition, very little is known regarding juvenile dispersal and habitat preferences, especially in regards to possible impacts of climate change (e.g., higher precipitation during the winter, drought conditions in the summer, extreme water temperature fluctuations). How different abiotic conditions within specific habitats influence juvenile growth and survival rates are also currently unknown in South Carolina. Both of these research gaps could potentially aid in explaining trends observed in the current fishery (i.e., declining catch rates). Moving forward, little is known regarding the exact implications of increasing water temperatures on blue crab growth rates and female brood frequency but could be studied using individual-based population models. It is possible that an extended summer season could allow blue crabs in South Carolina to reach maturity quicker and produce more broods, but this has not been explored.

## The Influence of Climate Change on Blue Crab Physiology

Abiotic stressors are a residual effect of climate change. Changing water temperatures, salinities, and pH levels can affect the physiology, behavior, and vulnerability of blue crabs to predation and disease. However, of particular interest is how ocean acidification could affect the molting process and overall osmoregulation of the blue crab. Recent research has found conflicting results and more detailed studies are needed. In addition, the combined effects of different abiotic factors will need to be explored for blue crabs. In particular, there is a need to determine how the effects of extreme heat events and increased freshwater runoff in shallow water habitats affect blue crab mortality, especially during the juvenile growth phase. Along the same vein, the increased occurrence of extreme weather events, including winter cold snaps, is known to impact other crustacean species in South Carolina, but this has not been explored specifically for blue crabs in the region. For example, the impact of overwintering mortality rates and behavior on South Carolina's population of blue crab is currently unknown, and further studies should address this issue. In addition, of particular interest is the impact of abiotic stressors on the ability of blue crabs to successfully resist diseases such as *Hematodium* sp. Results from laboratory experiments evaluating multiple stressors, both biological and environmental, could be used to model the population structure of this dynamic system.

## Socio-economic Research on the Blue Crab Fishery

To further our understanding of the blue crab fishery in South Carolina and, specifically, how well equipped the fishery is to adapt to changes, including those it may face as a result of climate variability and change, a thorough socio-economic profile of the fishery is needed. This may include such things as the following: 1) a description of the South Carolina blue crab supply chain, from boat to consumer, 2) a demographic description of who participates in the fishery, 3) a description of the soft-shell crab market and better understanding of South Carolina's contribution to

it, 4) a better description of costs associated with producing blue crab in order to inform economic models that may help fishermen fish more efficiently, and 5) basic product research on more efficient refrigeration systems for crab, as most systems used within the state are aging, including available incentives for infrastructure upgrade or replacement.

# References

- Alber, M., Swenson, E. M., Adamowicz, S. C., & Mendelssohn, I. A. (2008). Salt marsh dieback: an overview of recent events in the US. *Estuarine, Coastal and Shelf Science*, 80(1), 1-11.
- Altieri, A. H., Bertness, M. D., Coverdale, T. C., Herrmann, N. C. & Angelini, C. (2012). A trophic cascade triggers collapse of a salt-marsh ecosystem with intensive recreational fishing. *Ecology*, 93(6), 1402-1410.
- Altizer, S., Ostfeld, R. S., Johnson, P. T. J., Kutz, S., & Harvell, C. D. (2013). Climate change and infectious diseases: from evidence to a predictive framework. *Science*, 341, 514–519.
- Archambault, J. A., Wenner, E. L., & Whitaker, J. D. (1990). Life history and abundance of blue crab, *Callinectes sapidus* Rathbun, at Charleston Harbor, South Carolina. *Bulletin of Marine Science*, 46, 145-158.
- Bakun, A. (1990). Global climate change and intensification of coastal ocean upwelling. *Science*, 247(4939), 198-201.
- Bauer, L. J., & Miller, T. J. (2010). Spatial and interannual variability in winter mortality of the blue crab *Callinectes sapidus* in the Chesapeake Bay. *Estuaries and Coasts*, 33(3), 678-687.
- Bell, G. W., Eggleston, D. B., & Noga, E. J. (2009). Environmental and physiological controls of blue crab avoidance behavior during exposure to hypoxia. *The Biological Bulletin*, 217(2), 161-172.
- Bishop, J. M., Olmi III, E. J., Whitaker, J. D., & Yianopoulos, G. M. (1983). Capture of blue crab peelers in South Carolina: An analysis of techniques. *Transactions of the American Fisheries Society*, 112(1), 60-70.
- Blue Crab Update (2004). State of South Carolina's Coastal Resources. South Carolina Department of Natural Resources. http://www.dnr.sc.gov/marine/mrri/pubs/yr2004/statebluecrab. Accessed February 18 2016.
- Blue Crab Update (2007). State of South Carolina's Coastal Resources. South Carolina Department of Natural Resources. http://www.dnr.sc.gov/marine/mrri/pubs/yr2007/crabs07.pdf. Accessed February 18 2016.
- Brunson, J., Kingsley-Smith, P., Leffler, J., Keppler, B., Fowler, A. E., DeLancey, L., & Whitaker, D. (2015). Research needs for the sustainable management of crustacean resources in the South Atlantic Bight. Technical report for South Carolina Sea Grant Consortium from workshop held April 9-10, 2014 at the SCDNR Marine Resources Research Institute in Charleston, SC.
- Burrell, V. G., Whitaker, J. D., Wenner, E. L., & DeLancey, L.B. (2009). History of the South Carolina Blue Crab Fishery. South Carolina Department of Natural Resources, Marine Resources Division, 108pp.

- Brylawski, B. J., & Miller, T. J. (2006). Temperature-dependent growth of the blue crab (*Callinectes sapidus*): a molt process approach. *Canadian Journal of Fisheries and Aquatic Sciences*, 63(6), 1298-1308.
- Cameron, J. N. (1985). Molting in the blue crab. Scientific American, 252, 102-109.
- Cameron, J. N, & Batterton, C. V. (1978). Antennal gland function in the freshwater blue crab, *Callinectes sapidus*: water, electrolyte, acid-base and ammonia excretion. *Journal of Comparative Physiology*, 123, 143-148.
- Carniello, L., Defina, A., & D'Alpaos, L. (2009). Morphological evolution of the Venice lagoon: Evidence from the past and trend for the future. *Journal of Geophysical Research*, 114, F4.
- Carr, S. D., Tankersley, R. A., Hench, J. L., Forward, R. B., & Luettich, R. A. (2004). Movement patterns and trajectories of ovigerous blue crabs *Callinectes sapidus* during the spawning migration. *Estuarine, Coastal and Shelf Science*, 60(4), 567-579.
- Carter, L. M., Jones, J. W., Berry, L., Burkett, V., Murley, J. F., Obeysekera, J., Schramm, P. J. & Wear, D. (2014). Southeast and the Caribbean. In: Melillo, J. M., Richmond, T. C. & Yohe, G. W. (Eds.). Climate Change Impacts in the United States: The Third National Climate Assessment, U.S. Global Change Research Program, pp. 396-417.
- Churchill, E. P. (1919). Life history of the blue crab. *Bulletin of the U.S. Bureau of Fisheries*, 36, 91-128.
- Coffey, A. H., Li, C., & Shields, J. D. (2012). The effect of salinity on experimental infections of a *Hematodinium* sp. in blue crabs, *Callinectes sapidus*. *Journal of Parasitology*, 98(3), 536-542.
- Costanza, R., de Groot, R., Sutton, P., van der Ploeg, S., Anderson, S. J., Kubiszewski, I., Farber, S., & Turner, R. K. (2014). Changes in the global value of ecosystem services. *Global Environmental Change*, 26, 152-158.
- Childress, M. J. (2010). Modeling the impact of drought on South Carolina blue crabs using a spatially-explicit individual-based population model. Abstract from the Proceedings of the 2010 South Carolina Water Resources Conference, Columbia. SC.
- Childress, M.J. (2014). Going with the flow: forecasting the impact of climate change on South Carolina blue crabs. Proceedings of the 2014 South Carolina Water Resources Conference, Columbia, SC.
- Childress, M.J. and K.J. Parmenter. (2012). Dying of thirst: impact of reduced freshwater inflow on South Carolina blue crabs. Proceedings of the 2012 South Carolina Water Resources Conference, Columbia, SC.
- Climate Change Technical Working Group. (2013). Climate Change Impacts to Natural Resources in South Carolina. South Carolina Department of Natural Resources. http://www.dnr.sc.gov/pubs/CCINatResReport.pdf. DOA: September 18, 2015.
- Colton, A. R., Wilberg, M. J., Coles, V. J., & Miller, T. J. (2014). An evaluation of the synchronization in the dynamics of blue crab (*Callinectes sapidus*) populations in the western Atlantic. *Fisheries Oceanography*, 23(2), 132-146.

- Daniels, R. C., White, T. W., & Chapman, K. K. (1993). Sea-level rise: destruction of threatened and endangered species habitat in South Carolina. *Environmental Management*, 17(3), 373-385.
- Darnell, R. M. (1959). Studies of the life history of the blue crab (*Callinectes sapidus* Rathbun) in Louisiana waters. *Transactions of the American Fisheries Society*, 88(4), 294-304.
- Davis, G.R. (1999). The winter dredge survey. Oral presentation. Chesapeake Bay Stock Assessment Committee Meeting, Annapolis, MD. Maryland Department of Natural Resources.
- De Groot, R. S., Wilson, M., & Boumans, R. (2002). A typology for the description, classification and valuation of ecosystem functions, goods and services. *Ecological Economics*, 41(3), 393–408.
- Doney, S. C., Ruckelshaus, M., Emmett Duffy, J., Barry, J. P., Chan, F., English, C. A., Galindo, H.M., & Talley, L. D. (2012). Climate change impacts on marine ecosystems. *Annual Review of Marine Science*, 4(1), 11–37.
- Donnelly, J. P., & Bertness, M. D. (2001). Rapid shoreward encroachment of salt marsh cordgrass in response to accelerated sea-level rise. *Proceedings of the National Academy of Sciences of the United States of America*, 98(25), 14218–14223.
- Dugan, J.E., Wenner, A.M., & Hubbard, D.M. (1991). Geographic variation in the reproductive biology of the sand crab *Emerita analoga* (Stimpson) on the California coast. *Journal of Experimental Marine Biology and Ecology*, 150, 63-81.
- Etherington, L. L., & Eggleston, D. B. (2000). Large-scale blue crab recruitment: linking postlarval transport, post-settlement planktonic dispersal, and multiple nursery habitats. *Marine Ecology Progress Series*, 204, 179-198.
- Fitz, H. C., & Wiegert, R. G. (1991). Utilization of the intertidal zone of a salt marsh by the blue crab *Callinectes sapidus*: Density, return frequency, and feeding habits. *Marine Ecology Progress Series*, 76(3), 249-260.
- Fowler, A.E., & DeLancey, L.B. (2014). State of the resource update: Blue Crabs.

  Marine Resources Division, South Carolina Department of Natural Resources.

  http://www.dnr.sc.gov/marine/species/bluecrab.html. Accessed 28 Oct 2014.
- Gilbert, S., Lackstrom, K., & Tufford, D. (2012). The impact of drought on coastal ecosystems in the Carolinas State of the knowledge report. Research Report CISA-2012-01 Columbia, SC: Carolinas Integrated Sciences and Assessments.
- Goodrich, D. M., van Montfrans, J., & Orth, R. J. (1989). Blue crab megalopal influx to Chesapeake Bay: evidence for a wind-driven mechanism. *Estuarine, Coastal and Shelf Science*, 29(3), 247-260.
- Guerin, J., & Stickle, W. (1970). A comparative study of two sympatric species within the genus *Callinectes*: osmoregulation, long-term acclimation to salinity and the effects of salinity on growth and moulting. *Experimental Marine Biology and Ecology*, 218, 165-186.

- Harvell, C. D., Mitchell, C.E., Ward, J.R., Altizer, S., Dobson, A.P., Ostfeld, R.S., & Samuel, M.D. (2002). Climate warming and disease risks for terrestrial and marine biota. *Science*, 296, 2158-2162.
- Heck, K. L., Jr., Coen, L. D., & Morgan, S. G. (2001). Pre-and post-settlement factors as determinants of juvenile blue crab *Callinectes sapidus* abundance: results from the north-central Gulf of Mexico. *Marine Ecology Progress Series*, 222, 163-176.
- Heck, K. L., Jr., & Thoman, T. A. (1981). The nursey role of seagrass meadows in the upper and lower reaches of the Chesapeake Bay. *Estuaries* 7, 70-92.
- Hill, J., & Weissburg, M. (2013). Predator biomass determines the magnitude of non-consumptive effects (NCEs) in both laboratory and field environments. *Oecologia*, 172(1), 79-91.
- Hill, R. W., Wyse, G. A., & Anderson, M. (2012) *Animal Physiology*, 3rd ed., Sinauer Associates, Inc.
- Hines, A. H. (1989). Geographic variation in size at maturity of brachyuran crabs. *Bulletin of Marine Science*, 45, 356-368.
- Hines, A.H. (2003). Ecology of juvenile and adult blue crabs: summary of discussion of research themes and directions. *Bulletin of Marine Science*, 72(2), 423-433.
- Hines, A. H. (2007). Ecology of juvenile and adult blue crabs. In: Kennedy, V. S. & Cronin, L. E. (Eds.). *Biology of the Blue* Crab, Maryland Sea Grant College Press, College Park, MD. pp. 565–654.
- Hines, A. H., Haddon, A. M., & Wiechert, L. A. (1990). Guild structure and foraging impact of blue crabs and epibenthic fish in a subestuary of Chesapeake Bay. *Marine Ecology Progress Series*, 67, 105–126.
- Hines, A. H., Johnson, E. G., Darnell, M. Z., Rittschof, D., Miller, T. J., Bauer, L. J., Rodgers, P., & Aguilar, R. (2010). Predicting Effects of Climate Change on Blue Crabs in Chesapeake Bay. In: Kruse, G. H., Eckert, G. L., Foy, R. J., Lipcius, R. N., Sainte-Marie, B., Stram, D. L., & Woodby, D. (Eds.). *Biology and Management of Exploited Crab Populations under Climate Change*. Alaska Sea Grant, University of Alaska Fairbanks.
- Hoegh-Guldberg, O., & Bruno, J. F. (2010). The impact of climate change on the world's marine ecosystems. *Science*, 328(5985), 1523-1528.
- Hughes, A. L. H., Wilson, A. M., & Morris, J. T. (2012). Hydrologic variability in a salt marsh: Assessing the links between drought and acute marsh dieback. *Estuarine, Coastal and Shelf Science*, 111, 95–106.
- Hurrell, J. W., Kushnir, Y., Ottersen, G. & Visbeck, M. (2003). An overview of the North Atlantic Oscillation. In: Hurrell, J. W., Kushnir, Y., Ottersen, G. & Visbeck, M. (Eds.) *The North Atlantic Oscillation: Climate significance and environmental impact.* Geophysical Monograph 134. 279 pp.
- Intergovernmental Panel on Climate Change (IPCC). (2001). Climate Change 2001: The Scientific Basis. In: Houghton, J. T., Ding, Y., Griggs, D. J., Noguer, M., van der Linden, P. J., Dai, X., Maskell, K., & Johnson, C. A. (Eds.). *Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 881pp.

- Johnson, E. G., & Eggleston, D. B. (2010). Population density, survival and movement of blue crabs in estuarine salt marsh nurseries. *Marine Ecology Progress Series*, 407, 135-147.
- Kearney, M. S., Rogers, A. S., Townshend, J. R., Rizzo, E., Stutzer, D., Stevenson, J., & Sundborg, K. (2002). Landsat imagery shows decline of coastal marshes in Chesapeake and Delaware Bays. *EOS, Transactions of the American Geophysical Union*, 83(16), 173-178.
- Kirwan, M. L. M., & Patrick, J. (2013). Tidal wetland stability in the face of human impacts and sea-level rise. *Nature*, 504(7478), 53–60.
- Knapp, A. K., Beier, C., Briske, D. D., Classen, A. T., Luo, Y., Reichstein, M., & Weng, E. (2008). Consequences of more extreme precipitation regimes for terrestrial ecosystems. *BioScience*, 58(9), 811–821.
- Kunkel, K. E, Stevens, L. E., Stevens, S. E., Sun, L., Janssen, E., Wuebbles, D., Konrad II, C. E., Fuhrman, C. M., Keim, B. D., Kruk, M. C., Billet, A., Needham, H., Schafer, M. & Dobson J. G. (2013). Regional climate trends and scenarios for the U.S. national climate assessment. Part 2. Climate of the Southeast U.S., NOAA Technical Report NESDIS 142-2, 94 pp.
- Lonsdale, D.J., & Levinton, J.S. (1985). Latitudinal differentiation in copepod growth: An adaptation to temperature. *Ecology*, 66:1397-1407.
- Lee, R. F., & Frischer, M. E. (2004). The decline of the blue crab. *American Scientist*, 92, 548–553.
- Lipcius, R. N., Seitz, R. D., Seebo, M. S., & Colón-Carrión, D. (2005). Density, abundance and survival of the blue crab in seagrass and unstructured salt marsh nurseries of Chesapeake Bay. *Journal of Experimental Marine Biology and Ecology*, 319(1), 69-80.
- Low, R. A. (1998). Survey of recreational blue crabbing by marine recreational fisheries stampholders. Technical Data Report 30. South Carolina Department of Natural Resources, Marine Resources Division, Office of Fisheries Management.
- McKenzie, M. D. (1970). Fluctuations in abundance of the blue crab and factors affecting mortalities. Technical Data Report 1. South Carolina Department of Natural Resources, Marine Resources Division, Office of Fisheries Management.
- Mense, D. J., & Wenner, E. L. (1989). Distribution and abundance of early life history stages of the blue crab, *Callinectus sapidus*, in tidal marsh creeks near Charleston, South Carolina. *Estuaries*, 12, 157-168.
- Messick, G. A. (1994). *Hematodinium perezi* infections in adult and juvenile blue crabs *Callinectes sapidus* from coastal bays of Maryland and Virginia, USA. *Diseases of Aquatic Organisms*, 19, 77–82.
- Messick, G. A., & Shields, J. D. (2000). Epizootiology of the parasitic dinoflagellate *Hematodinium* sp. in the American blue crab *Callinectes sapidus*. *Diseases of Aquatic Organisms*, 43, 139–152.
- Milliken, M. R., & Williams, A. B. 1984. Synopsis of biological data on the blue crab, *Callinectes sapidus* Rathbun. National Oceanic and Atmospheric Administration Technical Report. National Marine Fisheries Service 1, Food and Agriculture Organization of the United Nations Fish Synopsis, 138: 1-39.

- Minello, T. J., Matthews, G. A., Caldwell, P., & Rozas, L. P. (2008). Population and production estimates for decapod crustaceans in wetlands of Galveston Bay, Texas. *Transactions of the American Fisheries Society*, 137, 129–146.
- Najjar, R., Pyke, C. R., Adams, M. B., Breitburg, D., Hershner, C., Kemp, M., Howarth, R., Mulholland, M., Paolisso, M., Secor, D., Sellner, K., Wardrop, D., & Wood, R. (2010). Potential climate-change impacts on the Chesapeake Bay. *Estuarine, Coastal Shelf Science*, 86:1-20.
- National Oceangraphic and Atmospheric Administration (NOAA). (2015). Water Temperature Table of the Southern Atlantic Coast. NCEI. Retrieved from http://www.nodc.noaa.gov/dsdt/cwtg/index.html. DOA: February 12, 2016.
- Newman, M. W., & Johnson, C. A. (1975). A disease of blue crabs (*Callinectes sapidus*) caused by a parasitic dinoflagellate, *Hematodinium* sp. *The Journal of Parasitology*, 61(3), 554–557.
- Orth, R. J., Carruthers, T. J. B., Dennison, W. C., Duarte, C. M., Fourqurean, J. W., Heck, K. L., Hughes, A. R., Kendrick, G. A., Kenworthy, W. J., Olyarnik, S., Short, F. R., Waycott, M., & Williams, S. L. (2006). A global crisis for seagrass ecosystems. *BioScience*, 56(12), 987–996.
- Orth, R. J. & van Montfrans, J. (1987). Utilization of a seagrass meadow and tidal marsh creek by juvenile blue crabs, *Callinectes sapidus*. I. Seasonal and annual variations in abundance with emphasis on post-settlement juveniles. *Marine Ecology Progress Series*, 41, 238-294.
- Overstreet, R. M. (1978). *Marine maladies? Worms, germs, and other symbionts from the northern Gulf of Mexico*. Mississippi-Alabama Sea Grant Consortium (MASGP-78-021), Ocean Springs, Mississippi.
- Parmenter, K. (2012). The Effects of Drought on the Abundance of the Blue Crab, *Callinectes sapidus*, in the ACE Basin NERR in South Carolina. Unpublished PhD dissertation, Clemson University, Clemson, South Carolina.
- Parmenter, K. J., Vigueira, P. A., Morlok, C. K., Micklewright, J. A., Smith, K. M., Paul, K. S., & Childress, M. J. (2013). Seasonal prevalence of *Hematodinium* sp. infections of blue crabs in three South Carolina (USA) rivers. *Estuaries and Coasts*, 36(1), 174-191.
- Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, 37, 637-669.
- Péqueux, A. (1995). Osmotic regulation in crustaceans. *Journal of Crustacean Biology*, 15 (1), 1-60.
- Posey, M. H., & Hines, A. H. (1991). Complex predator-prey interactions within an estuarine benthic community. *Ecology*, 72(6), 2155-2169.
- Prager, M. H., McConaugha, J. R., Jones, C. M., & Geer, P. J. (1990). Fecundity of blue crab, *Callinectes sapidus*, in Chesapeake Bay: Biological, statistical and management considerations. *Bulletin of Marine Science*, 46(1), 170-179.
- Pritchard, H. D., Arthern, R. J., Vaughan, D. G., & Edwards, L. A. (2009). Extensive dynamic thinning on the margins of the Greenland and Antarctic ice sheets. *Nature*, 461, 971-975.

- Ralph, G. M. & Lupcius, R. N. (2014). Critical habitats and stock assessment: agespecific bias in the Chesapeake Bay blue crab population survey. *Transactions of the American Fisheries Society*, 143(4), 889-898.
- Reaka, M. L. (1986). Biogeographic patterns of body size in stomatopod Crustacea: Ecological and evolutionary consequences. In: Gore, R. H. & Heck, Jr., K. L. (Eds.), *Crustacean Biogeography*. Balkema Press, Rotterdam, pp. 209-235.
- Reed, D. J. (1995). The response of coastal marshes to sea-level rise: survival or submergence? *Earth Surface Processes and Landforms*, 20, 39–48.
- Ries, J. B., Cohen, A. L., & McCorkle, D. C. (2009). Marine calcifiers exhibit mixed responses to CO2-induced ocean acidification. *Geology*, 37(12), 1131-1134.
- Rome, M. S., Young-Williams, A. C., Davis, G. R., & Hines, A. H. (2005). Linking temperature and salinity tolerance to winter mortality of Chesapeake Bay blue crabs (*Callinectes sapidus*). *Journal of Experimental Marine Biology and Ecology*, 319(1–2), 129–145.
- Rowley A. F., Smith A. L., & Davies, C. E. (2015). How does the dinoflagellate parasite *Hematodinium* outsmart the immune system of its crustacean hosts? PLoS Pathogens, 11(5), e1004724.
- Rugolo, L. J., Knotts, K. S., Lange, A. M., & Crecco, V. (1998). Stock assessment of Chesapeake Bay blue crab (*Callinectes sapidus* Rathbun). *Journal of Shellfish Research*, 17 (2), 493-517.
- Sabine, C. L., Feely, R. A., Gruber, N., Key, R. M., Lee, K., Bullister, J. L., Wanninkhof, R., Wong, C., Wallace, D. W., Tilbrook, B. & Millero, F. J. (2004). The oceanic sink for anthropogenic CO<sub>2</sub>. *Science*, 305, 367-371.
- Sandifer, P. A. (1975). The role of pelagic larvae in recruitment to populations of adult decapod crustaceans in the York River estuary and adjacent lower Chesapeake Bay, Virginia. *Estuarine and Coastal Marine Science*, 3(3), 269-279.
- Sandoz, M., & Rogers, R. (1944). The effect of environmental factors on hatching, moulting, and survival of zoea larvae of the blue crab *Callinectes sapidus* Rathbun. *Ecology*, 25, 216–228.
- "SERC Education K12: Blue Crab Anatomy." *SERC: Blue Crab Anatomy*. Smithsonian Environmental Research Center, n.d. Web. 05 Oct. 2015.
- Sharov, A. F., Volstad, J. H., Davis, G. R., Davis, B. K., Lipcius, R. N., & Montane, M. M. (2003). Abundance and exploitation rate of the blue crab (*Callinectes sapidus*) in Chesapeake Bay. *Bulletin of Marine Science*, 72, 543–565.
- Short, F. T., & Neckles, H. A. (1999). The effects of global climate change on seagrasses. *Aquatic Botany*, 63(3–4), 169–196.
- Silliman, B. R., & Bertness, M. D. (2002). A trophic cascade regulates salt marsh primary production. *Proceedings of the National Academy of Sciences*, 99(16), 10500-10505.
- Silliman, B. R., Van de Koppel, J., Bertness, M. D., Stanton, L. E., & Mendelssohn, I. A., (2005). Drought, snails, and large-scale die-off of southern US salt marshes. *Science*, 310(5755), 1803-1806.
- Smith, S. G., & Chang, E. S. (2007). Molting and growth. In: Kennedy, V. S., & Cronin, L. E. (Eds.). *The blue crab,* Callinectes sapidus, pp. 197-254.

- South Carolina Department of Natural Resources. (2013). Climate change impacts to natural resources in South Carolina. Retrieved from: http://www.dnr.sc.gov/lwc/climatereport.html.
- Strasser, M. & U. Pieloth. (2001). Recolonization pattern of the polychaete *Lanice* conchilega on an intertidal sand flat following the severe winter of 1995/96. *Helgoland Marine Research*, 55, 176–181.
- Tagatz, M. E. (1968a). Biology of the blue crab, *Callinectes sapidus* Rathbun, in the St. Johns River, Florida. *Fisheries Bulletin*, 67 (1), 17-33.
- Tagatz, M. E. (1968b) Growth of juvenile blue crabs, *Callinectes sapidus* Rathbun, in the St. Johns River, Florida. *Fisheries Bulletin*, 67 (2), 281-288.
- Tagatz, M. E. (1971). Osmoregulatory ability of blue crabs in different temperature-salinity combinations. *Chesapeake Science*, 12 (1), 14-17.
- Taylor, A. H. (1996). North-South shifts of the Gulf Stream: ocean-atmosphere interactions in the North Atlantic. *International Journal of Climatology*, 16, 559–583.
- Towle, D., & Burnett, L. (2007). Osmoregulatory, digestive, and respiratory physiology. In: Kennedy, V. S., & Cronin, L. E. (Eds.). *The blue crab,* Callinectes sapidus, pp. 419- 449.
- US EPA, C. C. D. (2013). Southeast Impacts & Adaptation [Overviews & Factsheets,]. Retrieved January 8, 2015, from http://www.epa.gov/climatechange/impacts-adaptation/southeast.html.
- United States Global Change Research Program (USGCRP). (2009). Global Climate Change Impacts in the United States. In: Karl, T.R., Melillo, J. M., & Peterson, T. C. (Eds.). *United States Global Change Research Program*. Cambridge University Press, New York, NY, USA.
- Van Engel, W. A. (1958). The blue crab and its fishery in Chesapeake Bay. Part I-Reproduction, early development, growth, and migration. *Commercial Fisheries Review*, 20(6): 6-17.
- Ward, G. H. (2012). The Blue Crab: A Survey with Application to San Antonio Bay. Center for Research in Water Resources. 210 pg.
- Whiteley, N. M. (2011). Physiological and ecological responses of crustaceans to ocean acidification. *Marine Ecology Progression Series*, 430, 257-271.
- Widdicombe, S., & Spicer, J. I. (2008). Predicting the impact of ocean acidification on benthic biodiversity: What can animal physiology tell us? *Journal of Experimental Marine Biology and Ecology*, 366(1-2), 187–197.
- Więski, K., Guo, H., Craft, C. B., & Pennings, S. C. (2010). Ecosystem functions of tidal fresh, brackish, and salt marshes on the Georgia coast. *Estuaries and Coasts*, 33(1), 161-169.
- Zimmerman, R. J., Minello, T. J., & Rozas, L. P. (2000). Salt marsh linkages to productivity of penaeid shrimps and blue crabs in the northern Gulf of Mexico. In: Weinstein, M. P. & Kreeger, D. A. (Eds.). *Concepts and controversies in tidal marsh ecology*, Springer, Netherlands. pp. 293-314.