

SPATIAL PATTERNS IN VULNERABILITY OF ESTUARINE FISHERIES TO CLIMATE
CHANGE IN GEORGIA (USA)

by

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(Under the Direction of Nathan P. Nibbelink)

ABSTRACT

Governing sustainable wild-catch fisheries comes with numerous social and ecological challenges. Coastal ecosystems support many socially important fisheries by providing critical habitat for early life stages of species. These habitats are predicted to be influenced by climate change. This dissertation takes an integrative approach to analyze the problem of climate change concerning a coastal socio-ecological system. Borrowing from the epistemologies of fish, spatial, and political ecologies, I dissect the issue of fishery governance in the face of climate change in the context of a highly productive coastal ecosystem: the estuaries of Georgia (USA). The overall objective is to evaluate the vulnerability of estuarine-based fisheries to climate change. Through a case study, I analyze the governance of a fishery and how it changes a fishing community's vulnerability through inhibiting or helping the building of adaptive capacity to stressors like climate change. From the ecological perspective, I first analyze the drivers of seasonal and inter-annual variability of select nekton species and overall fish diversity. Then, I determine through Random Forest models the landscape structural parameters that are important to creating spatially-explicit critical fish habitat models. Finally, I project the parameterized models into future scenarios of sea level rise. I determined that a coastal fishery with a low

adaptive capacity to long-term press stressors experiences higher vulnerability to short-term pulse stressors. I found evidence that seasonal variability is influenced by abiotic environmental gradients, however inter-annual variability could not always be directly connected to climate trends. Elements of the biotic landscape structure, particularly the proportion of regularly flooded marshes available, were important predictors of habitat availability. Future scenarios of sea level rise may negatively affect the distribution of available habitat for some species, but for other species may lead to an increase in available habitat. These trends are not linear, and governance should consider tipping points or thresholds. Overall, I address how the governance of the fisheries facing climate change, and socio-ecological systems in general, have issues of temporal and spatial scale incongruency.

INDEX WORDS: Spatial ecology, fisheries, socio-ecological systems, vulnerability, climate change, sea level rise, estuary, salt marsh

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DEDICATION

This dissertation is dedicated to my late father, Douglas I. Guy (May 17, 1942 – January 17, 2018). He stoked my interest in fish, the great outdoors, and natural conservation. I am forever grateful for all the knowledge and love he shared, and for teaching me that it is ok to go fishing and not catch anything at all. This is also dedicated to my late ornery cat, Lotte, who was forced on all my adventures with me, cross country and into the field. Finally, I have much gratitude for my family and friends who have been a source of strength and support for me throughout my education.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

INTRODUCTION

Globally, marine fisheries are in decline. According to the UN Food and Agriculture Organization (2016), 31% of the global fisheries are overfished. In the Western Central Atlantic, 44% of the fish stocks are overfished. Overfishing occurs, in part, because challenges of managing the oceans' fisheries for sustainable harvest are numerous even under stable environmental conditions. Conducting accurate stock assessments to avoid overfishing situations of many species remains problematic. Exploited nekton species are difficult to observe at any life stage, particularly their earliest, smallest stages. The vast areas of potential distribution make searching for larval and juvenile nekton time and cost prohibitive. The tendency of many species to aggregate in resource-rich locations can also create problems and result in hazardous overestimations of total population sizes (Rose & Kulka 1999). Secondly, our understanding of the ecosystem as a whole is limited when the focus of fishery assessments is primarily on exploited species (Murawski 2000). Species that are not exploited often receive less attention than exploited species, even if they fulfill an important ecological function. Currently, the effects of change and sea-level rise are altering the dynamics of the oceans (Fairbanks 1989, Harley et al. 2006, Hoegh-Guldberg et al. 2007, Hoegh-Guldberg & Bruno 2010) and global fisheries (Perry et al. 2005, Harley et al. 2006, Cheung et al. 2010), thus increasing challenges for management and governance of this critical resource.

The importance of ocean fisheries to the livelihoods and well-being of people around the world cannot be overstated. According to the Food and Agriculture Organization of the United Nations (FAO 2016), 48% of the world's seafood production comes from marine wild-caught species, which equaled 81.1 million tons in 2014. The FAO estimates that globally 56.6 million people are engaged in fisheries as a means of supporting their livelihoods (FAO 2016). The number of overfished fisheries has been increasing even as the global fleet has declined. Meanwhile, global consumption of seafood has increased steadily from the 1960s by more than 146 million tons in 2014 (FAO 2016).

Coastal ecosystems support many of the world's important fisheries by providing habitat for critical early life stages for certain species (Worm et al. 2006, Barbier et al. 2011). The estimates of the USA population living near a coast (including the Great Lakes) ranges from 37% to 58% (Culliton 1998, Crossett et al. 2004, Crowell et al. 2007). Though these estimates are often mentioned in the context of human vulnerability to the effects of climate change (e.g., an increased frequency of catastrophic storms and flooding), other problems arise from the inevitable degradation to coastal habitats caused by increasing human densities (Eriander et al. 2017, Staehr et al. 2018). Moreover, climate change can further exacerbate the anthropogenic stressors placed on these essential systems. Thus, there is a paradox that the very reason coastal systems are so attractive may be the cause for their environmental declines. A common problem in social-ecological systems may be that a natural resource forms the foundation for the presence of a social-system (Liu et al. 2007).

My dissertation takes an integrative approach to analyze the effects of climate change on a coastal socio-ecological system. Borrowing from the epistemologies of fish ecology and management, spatial sciences, and political ecologies, I dissect the problem of fishery

governance in the face of climate change in the context of a highly productive coastal ecosystem: the estuaries of Georgia, USA. By considering both the ecological and social dynamics of this system side-by-side, I explore the emergent properties of each and how they relate to one another. Rather than seeking win-win solutions to the ecological or social issues of this system, I present the complexity of the system to better understand the challenges and trade-offs in the governance of the system. This approach will hopefully better inform the management of fisheries, landscapes, and the people connected to them by identifying what strategies have been beneficial to the system and what might be needed to ensure a sustainable future.

The overall objective of this dissertation is to evaluate the vulnerability of estuarine-based fisheries to climate change. It is organized into four research chapters and two bookend chapters: an introduction and a final synthesis and conclusion chapter. In Chapter 2, I determine the elements of governance that have conferred or inhibited adaptive capacity to the people that depend on the estuarine fishery. In Chapter 3, I explore the biophysical drivers and the potential shifting temporal distributions of estuarine nekton. In Chapter 4, I define spatially explicit models of estuarine nekton habitat distribution through quantifying the inductive relationships of landscape structure and biophysical variables to the distribution of estuarine nekton. In Chapter 5, I use the models developed in Chapter 4 to determine estuarine nekton habitat vulnerability to sea level rise by evaluating how species richness and abundance respond to three alternate future scenarios. In the final synthesis chapter, I discuss my findings and recommendations. I also consider the successes of this integrative approach and where it may have fallen short of my ambitions. I hope this dissertation will result in novel pathways of understanding fisheries and their governance that simultaneously makes room for both the ecological and social perspective of a complex socio-ecological system.

LITERATURE REVIEW

Socio-Ecological Systems, Vulnerability, and Climate Change

The concept of socio-ecological systems dictates that divisions between nature and social interest in nature are artificial and constructed. Human interaction and influence on natural systems cannot be decoupled from the influence of natural systems on social structures and human action (Berkes et al. 2000, Ostrom 2009, Cioffi-Revilla 2016). Analytical frameworks for measuring vulnerability in social-ecological systems have been suggested to increase the likelihood of governing for sustainability systems (Turner et al. 2003). In general, vulnerability describes the degree to which a social-ecological system is deleteriously changed when exposed to stress.

Vulnerability is comprised of three key components: exposure to stress, sensitivity to the exposure, and the system's (or organism's) adaptive capacity (Ford et al. 2004, Adger 2006). The Intergovernmental Panel on Climate Change (IPCC) adopted a similar framework on Climate Change (Field et al. 2014) in the analysis of the critical vulnerabilities of human communities to climate change. Exposure to stress is predicated on the social-ecological system's physical, biological, spatial, and social structures that might increase the chance of the system intersecting with the stressing event. For instance, an agrarian-based community may be more exposed to the effects of drought than a tourism-based community. I define community as a group of individuals linked to one another either spatially or by common interests. Within an agrarian-based community, a farmer who relies only on water-intensive crops would likely have greater sensitivity to drought than a farmer that has drought-resistant crops. Finally, a farmer who has water-intensive crops but can rotate his fields in times of drought to low-water intensive crops

would have greater adaptive capacity than those who cannot rotate crops during droughts. The balance of these three components speaks to a social-ecological system community's overall vulnerability.

Vulnerability is related to the concept of socio-ecological resilience. Resilience borrows from both the ecological and anthropological definitions where a socio-ecological system can cope or absorb a stressor without fundamentally changing its major processes or characteristics (Walker et al. 2004, Adger et al. 2005b). The erosion of mechanisms that increase resilience can lead to greater vulnerability (Adger 2006, Gallopín 2006). Conversely, the ability to adapt, and those characteristics of a system that increase adaptive capacity, can increase resilience and decrease vulnerability (Smit & Wandel 2006). For instance, in Kenyan fishing communities, greater age conferred more social capital, which gave fishers the ability to network and adapt to changes in the fishery (Cinner et al. 2015). Conversely, those who were younger and did not participate in decision-making not only had a lower adaptive capacity but were sometimes more exposed to risk because their interests and livelihoods were not taken into consideration when resource governance decisions were made (Cinner et al. 2015).

Adequately measuring the components of the vulnerability of socio-ecological systems remains a challenge. Communities experience vulnerability to climate change as a multi-scalar temporal and spatial event (Adger et al. 2005a, Janssen et al. 2007, Cutter & Finch 2008). National assessments that employ standardized metrics (e.g., national wealth) have been used to create a repeatable quantitative assessment of a country's vulnerability to hazards like climate change (Allison et al. 2009). However, not all social processes, like the perception of risk or perceived vulnerability, can be represented by a quantitative metric.

Overlooking the qualitative characteristics that might increase the vulnerability of a community might lead to governing decisions that not only fail to reduce the vulnerability of social-ecological systems but might only benefit those already positioned with low vulnerability and high adaptive capacity (Adger 2006, Gupta et al. 2010). Overlooking the marginalized segments of a community in governing natural resource can lead to responses that decrease the community's overall resilience to future stressors like climate change (Cinner 2015).

Understanding the intangible assets and characteristics (e.g., kinship networks, political influence, and perception of vulnerability) that confer adaptive capacity to a social-ecological system can better help guide governance of the system to increase its overall resilience and decrease its vulnerability.

Fisheries Governance

Declines in fishery stocks have been observed throughout the world's oceans (Pauly et al. 2005, Zeller & Pauly 2005, Worm & Branch 2012). In general, declines have been measured by a decrease in the overall number of individuals harvested and a reduction in the size of the individuals harvested (Shin et al. 2005, Pontecorvo & Schrank 2012). China's commercial fleet has reported increasing harvest rates in recent decades, but this apparent increase is probably caused by over-reporting encouraged by government subsidies offered for increasing fishing productivity (Watson & Pauly 2001). The reality is that many of the major world fisheries are in decline, which jeopardizes economic stability and food sovereignty for many people (FAO

2016). Coastal waters of the eastern U.S. have not been immune to these declines, illustrated for instance by declines in red snapper (*Lutjanus campechanus*) (Goodyear & Phares 1990).

Overexploitation of a fish stock not only directly affects the population of the harvested species but also can cause the decline of other species, even entire ecosystems, linked through by-catch and trophic mechanisms of the target species. This effect can occur either through ‘bottom-up’ or ‘top-down’ trophic cascades (Bearzi et al. 2006, Daskalov et al. 2007). Bottom-up trophic cascades occur when a prey species or producer is removed from a system, causing a decline in consumers. High fishing pressure has been suggested to have caused a bottom-up trophic cascade in the Mediterranean through the decline of European anchovies (*Engraulis encrasicolus*) and sardines (*Sardina* sp.) which caused a subsequent reduction in encounters with tuna (*Thunnus* sp.) and swordfish (*Xiphias gladius*) (Bearzi et al. 2006). The magnitude of effect from removing prey species on top predators is highly dependent on the diet flexibility of the predator and the availability of alternative prey species. More commonly studied and observed are the top-down trophic cascades, where a top predator is removed from a system. This phenomenon was observed in the Black Sea, where an apex predator targeted by fisheries declined due to heavy fishing, which relaxed the ‘top-down’ control on planktivorous fish (Daskalov et al. 2007). Increased planktivory led to decreased zooplankton populations, which allowed phytoplankton abundance to flourish, in turn, depressing dissolved oxygen, making uninhabitable hypoxic environments. While reducing fishing pressure on top predators may allow ecosystems to recover, there is the potential for a critical threshold to be passed at which there is a state or regime shift that may not be easily reversed (Scheffer et al. 2005, Daskalov et al. 2007).

Understanding the history of marine fisheries management and how governance and prevailing theory contributed to the over-harvesting phenomenon is necessary for the future of sustainable fisheries management. Economic theory has been used to understand and inform fisheries management (Gordon 1954). However, fisheries are a common resource, a characteristic that does not allow for the application of a traditional microeconomic theory that describes the mechanisms of supply and demand. Classical microeconomic theory relies on a free market and is used to anticipate the behavior of humans in response to changes in the market environment. That is, markets drive the quantity of commodities available and the resources used to provide these commodities and distribute them between producers or firms (Barney 2001). However, market forces do not control the availability of fish, which acts as both a commodity and a resource. The common law of the waters provides no market mechanism for the commodity or resource to be distributed between fishers based on their investment. Additionally, the trade are privately owned, while the nature of fish as common property also confounds traditional economic theory (Scott 2011). Incorrect application of microeconomic theory to fisheries led early economic theorists to believe that the fisheries of the world were inexhaustible (Gordon 1954).

However, Gordon (1954) revolutionized the field of fishery economics. He identified that some costs of fishing (vessels, supplies for fishing) are not affected by fishing effort. Meanwhile, an increase in fishing effort will eventually see diminishing returns of fish in relation to the cost of that effort. Also, a single fisher or firm cannot take ownership of a section of sea, highlighting the diminishing value of rent as more fishers enter the market. Rent, in economic terms, is the difference between the total cost of production and the price of the commodity. If the sea could be owned like sections of the land, rent would be calculable as the difference between the

expense of fishing a particularly productive part of the sea and the price earned for the catch. Thus, without restriction to where they can fish within a state or national boundary, and with costs remaining the same in spite of the effort made and the number of fishers present, this number is not calculable through common microeconomic methods. Additionally, the competition among fishers tends to focus mostly on fishing areas with the highest productivity to maximize their catch rates without the realization of rent and increasing the chances of overfishing (Gordon 1954). Current fishery economics now play a role in informing management in setting regulations on fishing limits and establishing individual-rights quotas (Scott 2011). Although some traditional economic evaluation methods, such as recognizing opportunity costs and anticipating behavior in relationship to these individual quotas, still can be used, it now is done in combination with the features of common-property management.

With taxa like fish that are not easily visible, can occur in clumped distributions, and are highly mobile, directly observing population parameters is difficult. Instead of a direct measure of biomass, fisheries management often uses indices, like catch-per-unit-effort (CPUE) for assessing stock status. However, using CPUE as an index of abundance is problematic for fishery management because it assumes a consistent effort, which does not consider the ‘arms race’ between fishers to maximize their catch efficiency through increased effort or more efficient gear (Ludwig 2001). Catchability also changes with conditions and locations (Arreguín-Sánchez 1996). Use of CPUE for stock assessment also assumes that there is equal probability of encountering a species throughout the fishing area, and thus a high CPUE could be correlated to high total population abundance or a localized aggregation (e.g., shoaling) of a population with lower abundance in a discrete area with favorable resources (Rose & Kulka 1999). For the same reasons the instantaneous growth rate for the population, as estimated through sequential catches,

might be under or overestimated. Resources themselves may change due to external environmental shifts, such as a change in local salinity or dissolved oxygen in a productive habitat, therefore changing the maximum biomass that a system can support. Given the drivers of fisheries decline, knowing the ecological parameters of the fishery, as well as social dynamics of the fishery is critical to forecast and prevent future fishery declines.

Nekton Habitat Selection: Temporal and Spatial Ecology

Nekton are habitat-limited primarily by abiotic factors and secondarily by biotic factors (Bacheler et al. 2009). Abiotic factors, such as temperature, salinity, and dissolved oxygen vary both temporally and spatially in estuaries. For most species, there is a range of values for these factors at which an individual can maintain physiological equilibrium. At either end of the range are critical minimum and maximum limits beyond which an individual will no longer thrive. Individual mortality may result when thresholds are exceeded due to physiological stress. Within the range of survival, there are optimal values that maximize growth or survival, allowing for a homeostatic condition or physiological optima. The amount of physiological stress experienced has implications not only for individual survival but also for individual fecundity. For instance, red drum (*Sciaenops ocellatus*) larvae have better growth rates at moderate salinities (15 – 25 practical salinity units; psu), although the pelagic eggs will sink at salinities under 25 psu, indicating a critical threshold for the survival of eggs (Buckley 1984, Lanier and Scharf 2007). Stream substrates (muddy bottom vs. rocky bottom) may also contribute to survival or reproductive success (Nemeth 1998, Barnes et al. 2007). Similarly stream morphology, depth, current, and turbidity are important abiotic habitat traits (Hampel et al. 2003), depending on the

system and the species in consideration. In potentially suitable habitat, if the abiotic thresholds do not exceed the critical limits, then biotic traits of the habitat become the limiting features.

Like abiotic traits, optimal biotic environmental structural characteristics promote growth, survival, and fecundity. These characteristics include meeting nutritional requirements for growth or maximized reproductive output, conferring protection from predators, allowing for competitive advantages, and meeting requirements for the survival or growth of offspring. Dietary requirements shift between different life history stages of a species. Juvenile fish with small gapes will feed on prey much smaller in size, often of different taxa, than their adult counterparts (Schmitt & Holbrook 1984, Mayer & Wahl 1997). Biotic variables, like the presence of submerged aquatic vegetation or oyster reefs, also provide structures that allow for nekton to avoid detection by predators, while providing necessary foraging opportunities as well (Beck et al. 2001, Scheinin et al. 2012). The presence or absence of competing species also affects the suitability of a habitat for survival or reproduction (Rosenzweig 1981, Leibold 1991).

Nekton settlement may occur passively or actively. Passive settlement in aquatic organisms most often occurs in the earliest less- or non-motile stages of life. Currents carry pelagic eggs to their settlement sites (Norcross & Shaw 1984). In some species, if a specific habitat is needed as a nursery habitat, spawning will occur in currents that will more likely carry eggs to these habitats (Buckley 1984, Able & Fahay 2010). When an individual is motile after hatching, they may actively move into preferred habitat that meets their abiotic and biotic requirements, engaging in active habitat selection. For example, Pacific salmon migrate up coastal rivers to selected spawning sites (natal homing) within their natal streams (Quinn & Dittman 1990). Once hatched the juveniles return to the ocean until sexually mature and continue the cycle again. These examples also illustrate the temporal nature of habitat use.

Habitat requirements often change with life stage (Able & Fahay 2010). Offspring (usually subadults or older juveniles) and adults of the same species may compete for the same food resources. Habitat segregation reduces competitive pressures and predation on juveniles by adults (Paterson & Whitfield 2000). However, the temporal scale of shifting habitat selection may not be relegated to the length of a species' lifespan, but also between seasons and diurnal cycles. Seasonally, water temperatures fluctuate, as do productivity of vegetation and algae that regulate dissolved oxygen. In coastal areas, freshwater discharge changes with regional precipitation regimes (Cain & Dean 1976, Able & Fahay 2010, Azevedo et al. 2014), which may change productivity. In temperate regions warmer waters and increased photosynthetic activity often lead to an overall increase in productivity within aquatic communities during the spring and summer months (Able & Fahay 2010). Diurnal cycles of tide, light, temperature, and dissolved oxygen may cause distributional shifts in habitat, as well. Species move to areas of greater protection when they are more visible, move into areas of warmer water during daytime feeding to increase metabolic rates, or move into depths where dissolved oxygen is greater (Tyler & Targett 2007). Diurnal movements may be small and localized, whereas seasonal migrations more often cover greater distances, highlighting the importance of spatial scale in habitat distribution.

The spatial scale of habitat distribution at both the micro- and macro-levels can be described using the components of grain and extent. Grain is the smallest resolvable unit in measure, while extent is the size of the area considered. Microhabitat selection generally occurs at a fine grain and small extent (Bissonette et al. 1997, Turner et al. 2001). For instance, the scale of a microhabitat selection study may include patches of salt marsh grass quantified in 1-m² plots (grain) found in a reach of a river (extent). Migration between these patches, selection for

specific habitat characteristics (e.g., stem density, bank slope), and tidal fluctuations of water depths occur over relatively short distances and times. Macrohabitat selection, also known as landscape-level habitat selection, generally occurs at coarse grains and large extents (Turner et al. 2001). An example of a landscape-level study of habitat characteristics may include proportion cover of salt marsh in a river (grain) over all rivers in a sound (extent). As expected, landscape-level migrations to rivers or sounds of aquatic species generally happen over larger distances and longer time periods than microhabitat movements.

Abiotic and biotic characteristics restrict both microhabitat and landscape-level habitat selection (Jackson et al. 2001, Martin 2001). Usually, habitat selection initially occurs at the landscape-level driven by physical components (Jackson et al. 2001, Martin 2001) such as salinity and temperature. Once the abiotic physiological conditions are satisfied, habitat selection is based on the availability of biological components (Jackson et al. 2001), such as community composition and vegetation coverage. After a habitat has been selected at the landscape-level, individuals may make smaller movements between preferred microhabitats (Poizat and Pont 1996, Bissonette et al. 1997) in a spatially hierarchical process of habitat selection. Temporal and spatial characteristics of habitat selection inform the structures of aquatic communities and trophic positions of species within these communities.

Estuarine and Fish Ecology

Estuaries are coastal zones where freshwater, marine saltwater, and land interact with one another. This ecotone between terrestrial and marine ecosystems creates an area characterized by salinity gradients and water depths that fluctuates spatially as well as temporally due to tidal

cycles, hydrological flow, sediment deposition, precipitation regimes, and morphological characteristics.

The highly dynamic estuarine system can be categorized into five major types determined by their geological formation: coastal plain, deltaic, bar-built, tectonic, and fjords. The following descriptions of estuary types were taken from Perillo (1995). Coastal plain estuaries, like the Chesapeake Bay, are drowned river valleys that filled with water after the last glacial period. Deltaic estuaries (e.g., Mississippi River) are formed at the mouths of large rivers, where sediment carried from the river creates most of the land within the estuaries. Estuaries categorized as bar-built are formed through offshore sand transport, wave energy, and sea level fluctuations that create barrier beaches and islands. Behind the protective beaches and barrier islands, lower wave energy allows for sediment to fill in the areas between the islands and the mainland, creating intertidal and supratidal lands. In the Southeastern US, North Carolina, South Carolina, and Georgia have examples of bar-built estuaries. Tectonic estuaries, formations found in California, are created by rifts between tectonic plates. Finally, fjord estuaries (e.g., Puget Sound in Washington State, US) are geological formations created by glaciers and characterized by steep, narrow valleys.

Resident vegetation and faunal communities in estuaries must have high physiological tolerances to the temporal and spatial fluctuations of biochemical conditions (Elliott & Whitfield 2011). Nevertheless, estuaries provide essential fish habitat for numerous species as juveniles (nursery habitat) or as adults (residential habitat) (Odum 1988, Kneib 1997, Beck et al. 2001, Able & Fahay 2010). The reason estuaries are critical to fish habitat is thought to be a result of the high primary productivity of the salt marsh transferring nutrients into the surrounding aquatic habitat through herbivory, detritivory on macrophytes, and consumption of benthic microalgae,

resulting in a trophic relay (Weisberg and Lotrich 1982, Odum 1988, Zimmerman et al. 2000, Baker et al. 2013). As expected, periodicity or length of duration of saltmarsh flooding determines the extent to which the marsh surface is available for nekton utilization (Kneib & Wagner 1994, Rozas 1995).

Spatial and structural characteristics of the marshes also are posited to contribute to biological and biophysical processes that support nekton. Studies have found a positive correlation with marsh edge and the presence of infaunal species, many of which are primary prey for juvenile nekton (Whaley & Minello 2002). Detritus and microalgae that grow on the marsh surface are essential to other primary consumers (Sullivan & Moncreiff 1990, Currin et al. 1995). When salt marsh is thinned, reducing the shading to the marsh surface, it induces changes in microalgae growth and is correlated with a loss of primary consumer species richness (Pomeroy 1959, Whitcraft & Levin 2007). Salt marshes may also provide small nekton with a critical refuge from predation and lower physiological stress. Rountree and Able (2007) suggested that the salt marsh provides nekton with a refuge from other harsh environmental conditions, such as low temperatures in late winter or low dissolved oxygen in the summer.

Some of the biological mechanisms associated with nekton use of the saltmarsh are still uncertain, but studies have shown that there is a correlation between nekton, particularly juveniles, and the vegetated marsh edge and non-vegetated marsh edge (Baltz et al. 1993, Minello et al. 2003, La Peyre and Birdsong 2008). This relationship appears to be highly variable in areas where other habitats may be available, such as submerged aquatic vegetation or oyster reefs. For instance, in areas with red drum but without seagrass beds, early juvenile red drum densities were highest along the marsh-edge interface (Stunz et al. 2002). Conversely, submerged aquatic vegetation may be the preferred habitat when available (Peterson & Turner

1994). Transient estuary-dependent species preferentially use the marsh edge rather than the marsh interior (Peterson & Turner 1994, Connolly 1999 Rozas & Zimmerman 2000, Stunz et al. 2002, Minello et al. 2003). Other influential characteristics of the marsh edge include slope of the bank (gentle slope vs. steep cut), where total species richness was higher in areas with a steep cut bank, and total species abundance was higher on gentler slopes (La Peyre & Birdsong 2008).

Recently, concerns have been raised over rising sea levels threatening the persistence of salt marshes (Craft et al. 2009, Voss et al. 2013). Global sea levels rose over the last 100 years. Historical tidal-gauge data indicates a rate for sea level rise of 1.7 ± 0.2 mm/year which equates to a global sea level rise of approximately 210 mm over the period from 1880 to 2009 (Church & White 2011). Satellite data from 1993-2009 measures a linear trend in global sea level rise of 3.2 ± 0.4 mm/year (Church & White 2011). Current models predict an acceleration in the rate of sea level rise in the 21st century, with projections of sea level rise of 0.5 – 2.4 m over the next 100 years (Brown et al. 2013). The rate of sea level rise will also vary depending on regional differences in geology such as natural tectonic activity and isostatic uplift (Brown et al. 2013). Salt marshes maintain themselves through accretion, where sediment is layered vertically to keep an elevation at which the macrophytes may survive (Redfield 1965). The accelerated rate of sea level rise may not allow for the salt marsh accretion rates to increase the elevation in time to prevent deleterious inundation that would result in a conversion of the salt marsh to unvegetated habitat (Voss et al. 2013). Although salt marshes may transgress horizontally inland, these areas may be untenable to salt marsh migration because human settlements have created barriers to migration. A loss of salt marsh may accelerate future losses of salt marsh by reducing the below-ground root mass, and thereby increasing the rates of erosion (Voss et al. 2013).

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CHAPTER 2
CLIMATE CHANGE AND THE ROLE OF GOVERNANCE, VULNERABILITY, AND
ADAPTIVE CAPACITY IN A COASTAL FISHERY IN GEORGIA, USA¹

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ABSTRACT

Coastal fishing communities are considered highly socially vulnerable to the effects of climate change. Appropriate governance of fisheries can reduce vulnerability to hazards in fishing communities. In this paper I analyze the components of governance and their influence on vulnerability and adaptive capacity building in a coastal fishing community of medium to high vulnerability in Georgia, USA. I identify that distribution of power, agency, and scale of both stress and governance intervention is critical to understanding a complex socio-ecological system of low resilience. Fisheries experiencing a long-term press stressor may experience higher vulnerability to short-term pulse stressors. Focusing on building adaptive capacity to stressors that occur incrementally over time is critical to planning for sustainable futures of resource-based communities. Co-adaptive management practices will likely restore power and agency to fishing communities, decreasing the overall vulnerability by increasing the adaptive capacity of the community to both pulse and press stressors.

INTRODUCTION

Governance of natural resources can influence the vulnerability of natural resource-based communities to external stressors through affecting the community's ability to adapt. Through policy creation, the process of governance can increase the ability of a community to adapt to hazards by raising their social, political, or economic capital (Pahl-Wostl 2009). However, governance can also strip agency to adapt to stressors from communities through practices that shift the power of decision-making away from the community. Lack of decision-making agency can lead to maladaptive practices in the community that can deplete the resources which reduces the ability of the resource to support livelihoods (Hauck 2011, Cinner 2015). These resources are

critical in communities where there are few alternative opportunities for individual livelihoods. The reduction of livelihood opportunities may result in state-changes in a community that is not socially beneficial. Small-scale coastal fisheries provide livelihood opportunities in socially vulnerable exurban communities. Climate change looms as a major stressor to these fisheries (Roessig, et al. 2004), the effects of which have not yet been realized by some fishing communities. An analysis of the influence governance has on the ability of communities to adapt to stressors is necessary to forecast the potential for positive adaptation to future stressors to the fishery, like climate change.

For this research, I explore elements that conferred or inhibited adaptive capacity for a fishing community in a place-based case study, considering a contextual conceptualization of vulnerability (O'Brien et al. 2007). The purpose of this study is to determine how governance affects a fishing community's vulnerability to long-term stressors. Pursuant to this goal, the focal objectives are to 1) identify the primary stressors that caused past declines, 2) describe the elements of governance that helped or hindered positive adaptation responses, and 3) use this information to extrapolate the fishing community's future vulnerability to a long-term stressor like climate change.

The Intergovernmental Panel on Climate Change (IPCC) identifies communities based on natural-resource extraction as more vulnerable to the effects of climate change than other economic systems (IPCC 2014). Coastal fishing communities are likely to experience the effects of anthropogenic climate change (Allison et al. 2009, Badjeck et al. 2010, Cinner et al. 2012, Islam et al. 2014). Climate patterns may directly change the availability or accessibility of a target species. For example, increasing water temperatures can alter the productivity of the waters adjacent to a fishing community or move a target species range outside of the

jurisdictional governance of a community (Perry et al. 2005, Harley et al. 2006, Hoegh-Guldberg et al. 2007, Cheung et al. 2010). Indirectly, the habitat of target species might decline because of the effects of sea level rise (Chesney et al. 2000, Sarwar 2005). Furthermore, the fishing community itself might be sensitive to sea level rise or rising temperatures (Kelly & Adger 2000, Dolan & Walker 2006).

Analysis of vulnerability to climate change can be operationalized in multiple frameworks (Turner et al. 2003a, Turner et al. 2003b, Adger 2006, Maru et al. 2014). For this research, I apply O'Brien et al.'s (2007) concept of contextual vulnerability, which recognizes traits inherent to a community that inhibit or create adaptive capacity, and are a function of social, economic and ecological feedbacks. These traits can be observed in the community responses and their outcomes to stressors applied to the system on which they rely (O'Brien et al. 2007).

Different community adaptive responses may be enacted for a brief acute stressor when compared to a long-term chronic stressor, like climate change. Therefore, classifying the type of stressor experienced is necessary to determine a community's ability to adapt to climate change through an analysis of historical responses to stressors. These stressor types are classified as a press or a pulse event by considering the duration and the magnitude of stressor's effects (Bender et al. 1984). A pulse stressor (e.g. major storm, fire) occurs over a short duration (within a year) with high local effects. A press stressor occurs over a long duration and has cumulative effects over this period (e.g. sea level rise). Making this distinction gives insights into the types of responses that a community may enact awareness allows for predictions to be made community may respond to climate change.

Whereas the concept of vulnerability was initially established within fields of social science, the conceptualization of resilience has its origins in ecological science. Resilience theory posits that multiple states within a system are possible (Holling 1973, Holling 2001), and is defined as the ability of a system to absorb disturbance and changes to system variables while maintaining important processes and relationships within the system at a particular state (Walker et al. 2004). A system of lower resilience would not be able to tolerate changes to its variables, causing changes to function, processes, structure, and ultimately shifting to a new system state. System-states can be resilient and be maladaptive (Carpenter et al. 2001, Nelson 2011). Vulnerability is related to resilience, though one is not necessarily the symmetrical opposite of the other (Gallopín 2006).

Adaptive capacity serves as a ‘boundary object’ between frameworks of social vulnerability and social resilience. Adaptive capacity is the ability of a community to respond to a stressor while maintaining the component parts of their livelihoods or well-being. Boundary objects link different conceptual ideas through a common lens (Star & Griesemer 1989). Greater adaptive capacity of socio-ecological systems to absorb disturbance from stressors can decrease vulnerability and increase the resilience of communities to external changes (Smit & Wandel 2006, Engle 2011). Adaptive capacity is often realized or measured through observed adaptation responses the individual community exhibits (Smit & Pilifosova 2003, Brooks et al. 2005, Smit & Wandel 2006).

Adaptive capacity can be considered in nested scales of individuals, communities, and institutions (Adger et al. 2005, Vincent 2007, Pelling et al. 2008). An individual’s adaptive capacity is created from the resources they have available, which can be monetary, social capital, education or literacy, and the ability to diversify, or have high mobility within their community.

Adaptive capacity in a community can be built through increasing education about stressors and maintaining flexibility to exploit new opportunities for economic growth. In studies of fishers' adaptive capacity in Brazil, individual capacities were realized through the ability to diversify methods of enriching livelihoods, having a high degree of social cohesion (social capital), and the ability to innovate to overcome stressors (Kalikoski 2010). An individual's adaptive capacity depends on their position and context within a community, and the community's collective ability to learn and modify behavior to change. Importantly, Governance enacted at different scales can help or hinder the building of adaptive capacity of natural resource-based communities (Pahl-Wostl 2009).

Whereas adaptive capacities can only be observed through adaptation responses, choosing a community that has experienced stressor events of press and pulse types is vital to understanding future abilities to adapt. The fishing community selected for this study in McIntosh County, Georgia is one that may be exposed to the adverse effects of climate change and has been in a recorded decadal decline of fishery participation. The commercial fishing community in McIntosh County and its activities play a major role in shaping the broader community identity. The commercial shrimp industry and its symbols permeate much of the county. The Darien River borders Darien, GA, the largest city within the county, and the shrimp boats at the docks are often used as representative symbols of the city, appearing in postcards and other publications. Shrimp and shrimp-boat icons are displayed in restaurants and other items for sale to the public. McIntosh County currently supplies most of the wild-caught Georgia shrimp for the state, and the city holds an annual community festival to bless the fleet before the start of the season. Restaurants that display a 'Wild Caught Georgia Shrimp' icon can charge a higher price for the shrimp sold than for imported shrimp. An observer could reasonably assume

that the commercial shrimp industry is still an economically important industry within the county given the prevalence and value conferred upon it by the local community.

However, current data from the Department of Labor and Statistics show only 1.5% of the McIntosh County population generates their income from natural resource extraction (US Census Bureau 2015). In the latter part of the 20th century and the early decades of the 21st century, the community underwent an economic state-shift away from the reliance on commercial fisheries that was not reflected in its cultural values.

The importance of McIntosh County's coastal commercial fishing community as a major economic activity and livelihood has declined. Analyzing the decline of the fishing community through the attrition of the fleet and number of participating fishers in McIntosh County and how governance played a part in the downturn may provide information about the future vulnerability of McIntosh County community's potentially ecotourism-based economy. I consider the role governance played in affecting individual and community adaptive capacity through characterizing the role the components of governance suggested by Pahl-Wostl (2009) played in the decline of fishery participation.

For this case study, decoupling the concept of governance from government is necessary. Governance includes both formal and informal state and non-state institutions and actor networks that are involved in resource management (Pahl-Wostl 2009). Government is a formal state institution that is a component of governance. The United Nations Development Programme (UNDP; Wilde & Nahem 2008) offers the following definition of governance:

“Governance is about the processes by which public policy decisions are made and implemented. It is the result of interactions, relationships and networks between the different

sectors (government, public sector, private sector and civil society) and involves decisions, negotiation, and different power relations between stakeholders to determine who gets what, when and how.”

Resource governance can be distinguished from resource management, wherein the former describes the informal and formal processes that are undertaken by state and non-state actors to negotiate policy towards the resource, and the latter is a set of formalized policy and activities undertaken to allow for sustainability of the resource (Pahl-Wostl 2009). In short, resource management is the result of resource governance.

The four dimensions of governance that will be considered are institutions (formal and informal, regulative, normative, and cultural-cognitive), actor networks, multi-level interactions, and governance modes (Pahl-Wostl 2009). Institutions, both formal and informal, must be considered regarding their effectiveness and relative strength. Informal normative institutions are those that define shared values and accepted norms of behavior for actors. Informal cultural-cognitive institutions are the paradigms that are collectively constructed by actors of the understood boundaries and limitations of a system (e.g., what builds their sense of place and what solutions are possible to problems). An ineffective formal institution with incongruent goals to the informal institution may result in unsustainable resource governance. For instance, if fishing regulations are inadequately enforced, and the fishers value short-term personal profit over shared long-term community well-being, then fishers may be prone to overfish the fishery.

Actor networks describe both local and regional groups and state (e.g., government) and non-state (e.g., non-governmental organizations) groups (Pahl-Wostl 2009). The operational definition of an actor network for this research is a collective of individuals or groups of

individuals with shared objectives. Identifying actor groups and their networks of interaction is critical to determine where resource governance is centered. A diversity of actor participating in policy-making decisions can reinforce the perceived legitimacy of formal policy. Conversely, an incomplete representation of actor networks or an imbalance of power between actor groups can cause failure in later formal policy implementation (Hauck 2011).

The dimension of multi-level interactions describes the way the different centers of authority in resource governance interact with each other (Pahl-Wostl 2009). Formal institutions can influence informal institutions, and actor networks can integrate within state networks or non-state networks, or cross between state and non-state actor networks. These interactions can be vertical, through hierarchical levels of authority and influence, or horizontal at more equitable levels of authority and influence. This polycentric method of governance, if authority and influence are balanced at different levels of integration, provides multiple sources of knowledge generation and can create redundancies in functions of an institution or group's role in resource governance. These redundancies can create a more adaptable system to change (Pahl-Wostl 2009).

Finally, mode of governance is characterized by the relative influence of state and non-state actors and formal and informal institutions (Pahl-Wostl 2009). A mode of governance dominated by formal institutions and state actors generally is based in hierarchies and conducts top-down resource governance. A market-based mode of governance mixes the balanced influence of formal and informal institutions but is dominated by non-state actors. Finally, a mode of governance comprised of informal institutions and non-state actors is largely based on actor networks. Pahl-Wostl (2009) suggests the most effective resource governance occurs when there all three modes are present with strong informal networks.

Through archival analysis and informant interviews, I identify past stressors experienced by the community and develop a timeline of stresses, governance interventions, and adaptation responses. I contextualize the four dimensions of governance for the system in the case study. I then describe the coping mechanisms used by individuals or communities through governance processes including any adaptations employed. Lastly, I describe points of strength and weakness where adaptive capacity was affected by governance. This research suggests that communities whose livelihoods are based in natural resources are vulnerable to novel press and pulse stressors in context of other press stressors, like climate change, and the process of governance reinforces a rigidity in response to stressors.

McIntosh County

McIntosh County is in the center of coastal Georgia. The city of Darien is the county seat. The county's total area is approximately 1098 km², of which only 5% is developed dry-land (Fig. 2.1). Census data records a population estimate of 14,333 in 2010, of which 21.5% were under the age of 18, and 17.3% were over the age of 65 (US Census Bureau 2010). The total estimated number of people over the age of 65 in 2016 had increased to 23%. The racial demographics are predominantly white alone (61.8%), and secondarily black alone (34.1%), and the remaining identified as American Indian/Alaska Native, Asian, Native Hawaiian/Pacific Islander, and Hispanic and Latino descent. Approximately 50.9% of the residents 16 and older are employed in the civilian labor force. Mean household income from 2011-2015 is \$42,988 (\$23,887 per capita), while 24% of the population lives beneath the poverty level. Of the population, 81.4% of adults over the age of 18 have at least a high school education and 13.1% have received a bachelor's degree or higher. Notably, the average income and percent having earned advanced

degrees are below the national average (\$81,400, and 33%, respectively), and the poverty rate is above the 2015 national average (13.5%).

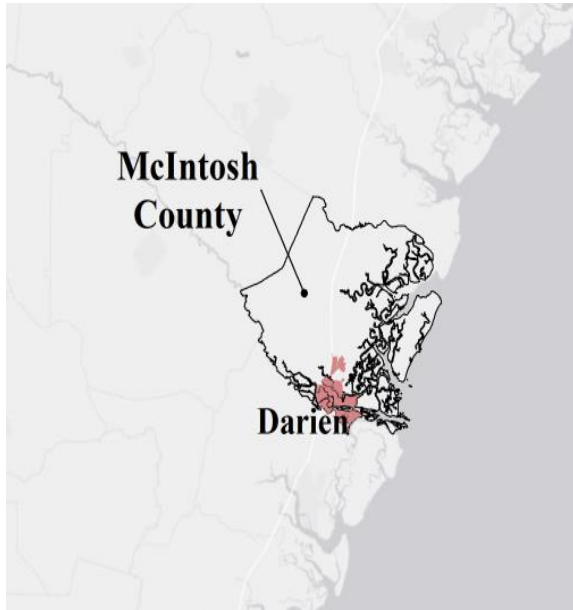


Figure 2.1: McIntosh County, Georgia, USA and its county seat the City of Darien

The labor and statistics data available concurrent with my study (2015) do not have adequate resolution to give a precise estimate of the contributions of the commercial fishing industry to the local economy. Beyond the direct employment on a boat to fish, there are the auxiliary supportive industries (e.g., wholesalers, retailers, processors, packing and shipping, and food services) that profit from the fishery. However, some general patterns can be discussed. Wholesale and retail trade totaled to 13.6% of the employee pool. Of the population, 10.5% percent work in “arts, entertainments, and recreation, and food services,” and 7.8% are in “transportation and warehousing, and utilities.” From these data, a maximum approximation of a

third of the McIntosh County workforce might be directly or indirectly employed through the commercial fishing industry (US Census Bureau 2010).

McIntosh County has a long history of an economic reliance on natural resources. According to local historians, settlers relied on small subsistence farms, eventually expanding to cultivate rice, cotton, sugarcane, and indigo on plantations (Sullivan 1990). Harvesting seafood to support livelihoods has also occurred at multiple scales, from subsistence to commercial, in McIntosh County. Commercial shrimping began in the early 1900s though records of the number of boats that fished and offloaded in Georgia waters was not recorded until the 1970s. The peak number of boat licenses occurred in 1979 before steadily declining to present day numbers (Fig. 2.2; National Oceanic and Atmospheric Association). Between the years of 1959 - 2015, adjusted for 2015 dollars, the value per metric ton of shrimp caught also peaked in 1979. However, the value share per boat license peaked in 1995 (\$79,566/license), before rapidly declining to the 2015 value (\$32,749/license), with the lowest valuation point occurring in 2013 (\$23,779.89). In 2006, 40% of all coastal Georgia's shrimp landings came from McIntosh County (Blount 2006).

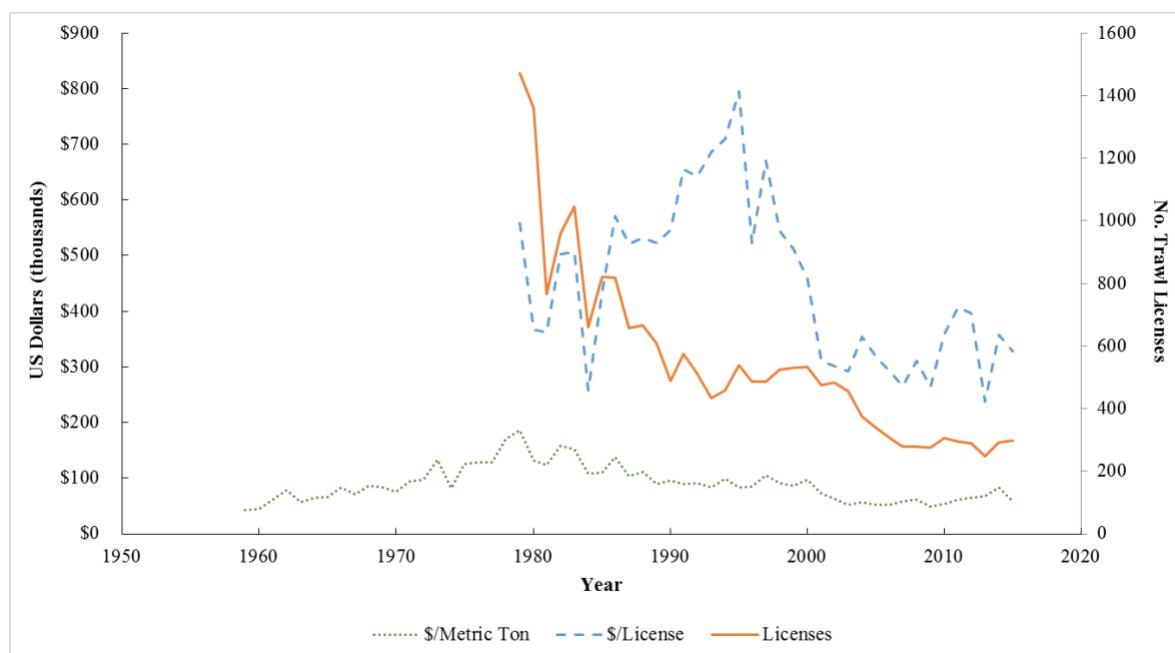


Figure 2.2: Comparison of the annual value in U.S. Dollars (adjusted for inflation for the year 2015) per metric ton of shrimp caught (1960 – 2015), per number of shrimp trawlers licensed (1960 – 2015), and the total number of shrimp trawler's licensed (1978 – 2015) for the state of Georgia, USA (Georgia Department of Natural Resources)

Shrimp fishers support their livelihoods through the sale of white (*Litopenaeus setiferus*) and brown (*Farfantepenaeus aztecus*) shrimp. A trawling operation can consist of a shrimp trawling boat, whose captain may or may not be the owner, and 1 – 3 crew members. Trawlers may stay offshore for multiple days, depending if they are fishing in the state waters or in the federal waters. Catches are kept on ice, and brought back to the docks, where they are sold to a licensed seafood dealer, which is often the dock owner. Dock owners often set the price for the shrimp, as well as sell fuel and ice to boat captains. The profits are split between boat owners, captains, and crew members.

METHODS

To observe adaptive capacity through stress response and adaptation, I used a combination of archival analysis and semi-structured interviews to identify points of historical stress and reaction to the stresses. I also analyzed the community's perception of future stressors to determine the level of community awareness, and hence preparedness, to climate change in the context of the fishery. To contextualize the present status of the fishing community, I used the local media periodical, *The Darien News*, to give insight on the evolution of the real and socially constructed history of the fishery and resulting community attitudes towards the local fisheries. The newspaper is printed once a week and only reports on local news or how national news affected the local community. It is the only McIntosh County-specific periodical. Papers from 1958 - 2015 were included in the dataset, and photographs were taken of every article that directly or indirectly addressed the fishing community. Each article was read, summarized, and coded for themes that included stressor, adaptation response, or governance intervention. Additional ad hoc codes were created as patterns emerged within the news articles. Coded articles were organized chronologically and used to construct a timeline of the major catalyst stressors and the subsequent reactions to these stressors. Chronological patterns and the prevalence of specific stressors were also summarized.

In 2015, I conducted semi-structured interviews (IRB ID#: STUDY00001946) with local commercial shrimp fishers in McIntosh County. Most interviewees were originally identified through the list of current commercial license holders provided by the Georgia Department of Natural Resources (GADNR). Other fishers were identified through a snowball method. Participants from the license list were called and asked if they would be willing to meet for an interview. If no one answered, then the number was called one more time, and then their name

was removed from the list. All license holders in McIntosh County were called. I met each participant at the place of their choice in public, and interviews took 15-60 minutes to complete. Questions were left open-ended to allow for further comment. Interview questions were asked about education and current employment, longevity and familial connections the fishermen had to the McIntosh County fishery, experiences of past stressors, methods for adapting to seasons when shrimp were not profitable, past experiences and participation with governance, identification of future stressors, and general attitude towards the future of the resource and its governance. Interview participants remained anonymous through numeric coding, and their answers were recorded on paper at the time of the interview and transposed the same day to an electronic spreadsheet.

Finally, I lived for several months each year close to the community from 2013 through 2015 and began living full-time near the community in January of 2016. Therefore, I employed an embedded approach to better understand the perceived value of the fishing community from the perspective of the local community of McIntosh County. I made numerous notes on the community values and attitudes towards the fishers and the institution of the fisheries.

Using the three analytical approaches, I triangulated the information from the fishers, the newspaper, and the local community to produce a socially constructed accounting of the fishery decline. I cross-referenced answers from the fishers concerning major past stressors and the governance responses to them with news articles contemporary with the point in time indicated by the interview subject. Then, I created the community-constructed perception of their history concerning the fisheries decline and the reasons for it happening. Using this narrative, I identified the roles the different components of governance regimes played in the fishery during the decline.

In the following sections, I present a summary of the data and my analysis of the system through the lens of the four dimensions and their sub-dimensions of governance as described by Pahl-Wostl (2009) (Table 2.1). These dimensions provide a systematic basis by which the pivotal characteristics of governance of a natural resource can be discussed. After contextualizing the system by these four dimensions of governance, I suggest how governance hindered or helped adaptive capacities in the past, and the implications this has for the future.

Table 2.1: Four dimensions of governance and their sub-dimensions, adapted from Pahl-Wostl (2009)

Dimension	Sub-dimension	Description
Institutions		Rules that influence the actions of individuals
	Formal (Regulative)	Regulatory Frameworks
	Informal (Normative)	Social norms and culturally accepted behavior
	Informal (Cultural-cognitive)	Defining space, understanding of system, understanding problems and solutions.
Actor Networks		State and non-state individuals and groups, and the interactions within groups and between individuals and groups
Multi-level Interactions		Multiple centers of governance; the integration and influence between levels
Governance Modes		
	Bureaucratic Hierarchies	Formal institutions, state actors
	Markets	Formal and informal institutions, non-state actors
	Networks	Informal institutions, non-state and state actors.

RESULTS

From all issues of *The Darien News* considered, 851/2912 (29%) contained content directly or indirectly discussing matters of the fisheries. Beyond stressor, adaptation, and

governance, ad hoc codes for place-building, knowledge-building, shrimp, commercial fishery, or sports fishery, were also identified from the articles. Of the articles analyzed, 764 were front page articles, with most (82%) dealing indirectly or directly with the commercial shrimp industry. Governance and stressors were each mentioned in 33% of the articles, and adaptations were mentioned in 19% of the articles. Sportfishing and commercial fisheries in general were mentioned in less than 10% of all articles. Nearly half of all articles engaged in place-building (e.g., articles about the long history of the fishery and its importance to the community), and 15% of the articles were coded as knowledge-building (e.g., articles about the technology or science of the fishery).

Of the 64 McIntosh County residents with commercial shrimp licenses ($n = 64$), 15 shrimpers consented to a semi-structured interview. Three of the commercial shrimpers were exclusively cast netters, while the rest worked on or owned trawlers. All participants were white males living inside of McIntosh County and were married. All shrimp fishers were 51 years of age or older. Most (12 of 15) of the participants interviewed identified a senior family member as the mechanism by which they became involved in the fishery in the 1970s.

As determined from the interviews, licensed shrimp fisher operations were self-organized into three primary working arrangements: owner-captains of trawlers that worked independently with a crew hired inside or outside the community, owner-captains who worked in family groups whose crew principally were family members and secondarily crew hired from inside or outside the community, and finally boat owners who hired a captain and local or migrant employees. Of these groups of licensed shrimp fishers, only the seafood dealers, who were boat owners but not

captains, expressed the most optimism about their future of remaining in the fishery, indicating movement away from the generational practice of shrimp fishing.

From the articles and interviews, timelines of major events for the entire period 1959 - 2015 were constructed for the commercial shrimp and crab industry in McIntosh County, GA (Fig. 2.3).

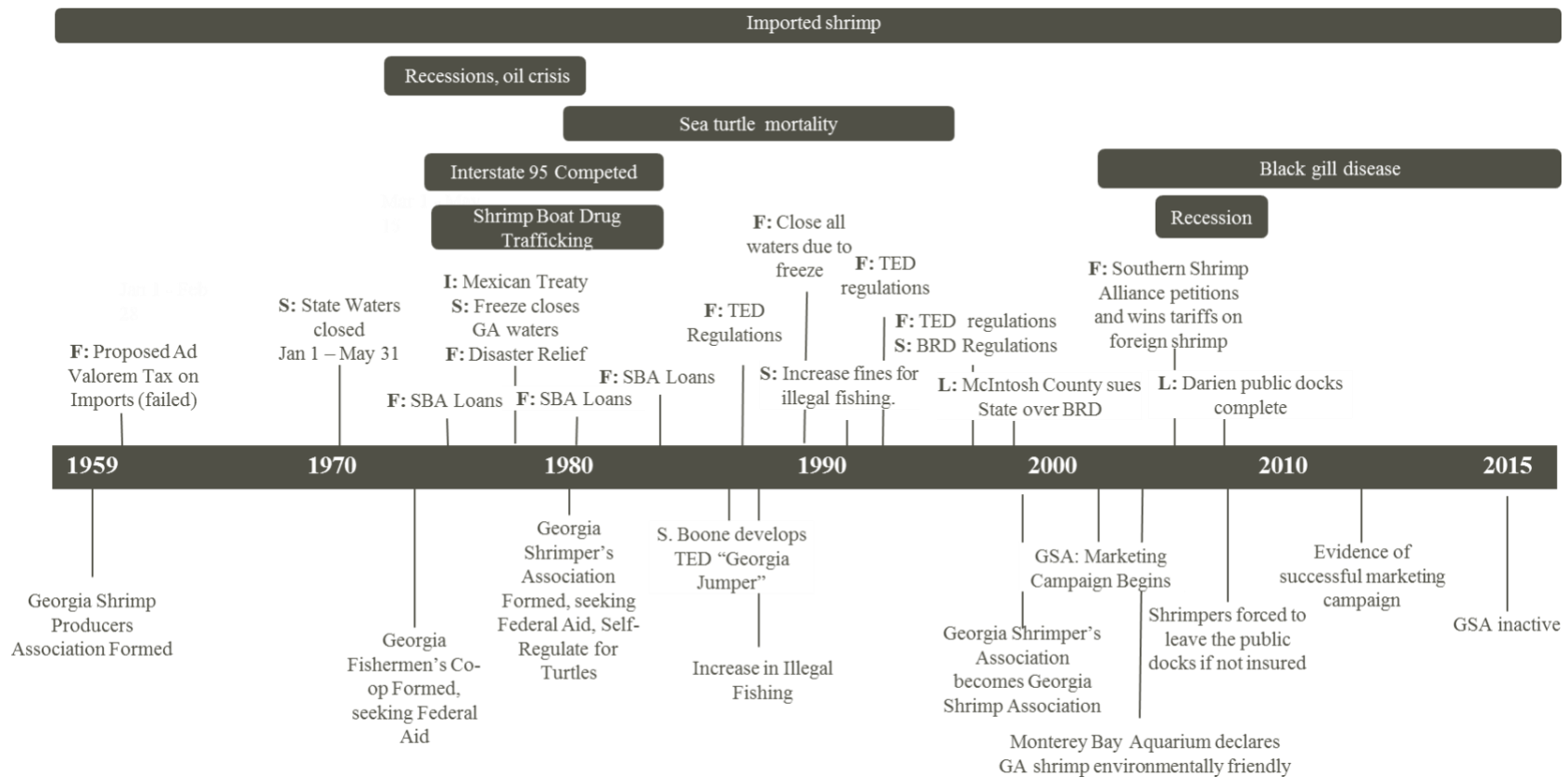


Figure 2.3: Timeline of significant events (stressors, governance interventions, and responses) for commercial shrimp fishers in McIntosh County, GA (USA) constructed from articles in the *The Darien News* periodical from 1958 - 2015. Events in dark bars at the top of the chart are long term events (press), while those bulleted on the timeline are short-term events (pulse). A bold letter in front of a pulse event indicates the scale of governance intervention: I – International, F – Federal, S – State, L – Local

Stressors

Shrimp fishers in both interviews and articles in *The Darien News* identified several primary stressors. Notably, none of the articles and only one shrimper anticipated climate change being an active and future stressor to the fishery. Lack of availability of shrimp to catch was a recurring problem. In articles, low catches, or undersized shrimp were reported several times. These occurrences usually followed major weather events (freezes, heavy rains or droughts) (12/18/1969, 2/3/1977, 6/28/1979, 9/24/1981, 10/11/1984, 6/6/1985, 6/4/1985, 2/6/1986, 4/12/1990, 3/22/2001, 6/14/2007, 6/23/2011, 1/16/2014). Until recently, these events seemed to occur for a season, before the shrimp stock returned to fisher-acceptable levels. However, the growing prevalence of ‘black gill disease’ was perceived to correspond with increased mortality in shrimp (12/26/2002, 12/27/2012, 10/3/2013, 3/9/2015), a perception supported by scientific inquiry (Frischer et al. 2018). Black gill disease becomes most prevalent in the late summer and early fall, affecting the fall harvest which is usually the most productive (Frischer et al. 2018). Rather than being confined to a season, several consecutive years have seen reduced fall harvests, as cited by 10 of the shrimp fishers interviewed.

Another stressor experienced by shrimpers was reduced catchability. Catchability refers both to the return for a given effort and access to the available shrimp stock (9/24/1981, 2/23/1982). Potential reduced efficiency of effort (e.g., the addition of turtle exclusion devices or bycatch reduction devices - 5/30/1996, 8/15/1996) occurred with modification to nets that reduced their capacity to catch target species. In addition, most shrimpers interviewed expressed problems with sharks increasingly attacking their nets for the shrimp and tearing multiple large holes in their gear. Access to the geographical areas where shrimp were available was perceived to be limited in at least three ways. For example, the closing of the sounds was disadvantageous

when shrimp remained in the creeks and rivers during droughts (9/24/1981). Cast netters in smaller vessels had accessibility to the shrimp, but commercial shrimp trawler fishers did not (11/6/1987). Alternatively, when heavy rains or cold weather flushed the shrimp out of the rivers and sounds to the offshore waters, cast netters were at a disadvantage, and commercial shrimp trawlers fishers benefitted (1/3/2008).

A major perceived multi-decadal stressor was the poor market for Georgia-caught shrimp through decreased demand or increased supply. Either increased supply or decreased demand can depress the value for the shrimp, and thus reduce monetary returns to shrimpers. Specifically, recessions affected the affordability and hence decreased the market demand for shrimp (8/8/1974, 1/9/1975, 9/25/1980, 9/10/2009). Oil shortages of 1973 and 1979 also increased operating costs for fishing (8/8/1974, 9/25/1980). Furthermore, undersized shrimp that are caught were valued less than larger shrimp even though the cost and effort put into catching small shrimp were the same as larger shrimp. Supply also created a poor market for Georgia-caught seafood and was a perennial problem. A large supply of shrimp (while demand remains unchanged) will reduce the value of the shrimp. Cited early in *The Darien News* articles, and mentioned by nine shrimp fishers interviewed, the import of inexpensive foreign shrimp into the US markets contributed to a reduction in value of locally-caught shrimp (9/7/1959, 3/17/1960, 8/8/1974, 1/9/1975, 9/25/1980, 4/10/1986, 1/10/1991, 10/16/2003, 6/14/2004, 4/19/2007, 9/10/2009).

Changing public opinion, reflected by conflicting values placed on the practice of commercial shrimp trawling versus other ecosystem services provided by the environment, challenged the fishers. Conflicts in values of ecosystem services occurred most notably when public pressure rose to protect non-commercial species, like endangered sea turtles (9/16/1980,

9/25/1980, 4/23/1987, 7/13/1995). Communities outside of McIntosh County, both inside and outside Georgia, condemned the practice of commercial shrimping as detrimental to turtles (9/25/1980, 5/31/1990). However, several editorials in *The Darien News* demonstrated local support for the shrimp fishers (9/25/1980, 8/6/1992, 5/30/1996). Interests in promoting tourism, particularly sports and recreational fishing tourism also created conflict for the shrimp fishers. In the early 1970s, the construction of Interstate 95 bypassed US Highway 17, which ran through the center of Darien and McIntosh County. US Highway 17 was the major trucking and tourist route on the east coast between Miami, Florida and Washington, District of Columbia. Traffic through town decreased immediately and dramatically according to the newspaper the day the Interstate 95 opened to traffic (1/10/1973). The decision was made to use billboards to promote Darien and McIntosh County for tourism as a “Fisherman’s Paradise” (4/14/1966, 5/14/1970, 2/1/1993). The growth in popularity of sportfishing put commercial shrimp fishers who trawl at odds with alternative uses of the estuary. Protecting favorite sport fish like red drum (*Sciaenops ocellatus*) and whiting (*Menticirrhus americanus*) were often cited as justification for installing BRDs. One shrimp fisher said the Coastal Conservation Association, a regional sportfishing association, has actively campaigned to reduce the shrimp fleet and threatened to physically block trawlers with their boats if sounds were open to them.

Institutions

Marine and estuarine fisheries in Georgia are formally managed through regulations and enforcement at the state and federal level. At the state level, the GADNR’s Board of Natural Resources and legislative House and Senate are responsible for management of the resources. The state sets policy for fishers out to the 3-mile demarcation line. Distributing licenses, permits,

law enforcement, and monitoring of fish stocks are under the jurisdiction of the GADNR. The Board of Natural Resources is comprised of 19 members appointed by the Governor and are tasked with setting rules and regulations and providing budget recommendations to the legislative branches of the state government. The Georgia legislature determines the annual budget for GADNR and can initiate major rule changes to the regulations and management of the resources at the recommendation of the DNR Board of Natural Resources.

At the national level, the major formal governing bodies are the National Oceanic and Atmospheric Administration National Marine Fisheries Service (NMFS) and the legislative and executive branches of government. Management of fisheries by the national government occurs from the 3-demarcation line of state waters out to the 200 nautical-mile delineation of the Economic Exclusive Zone (EEZ). Through fishery stock monitoring and the development of regional councils, NMFS develops regional management plans based on stock assessments. The management plans prescribe catch limits, reporting regulations, and the timing and length of seasons. NMFS also regulates commercial fishing and the distribution of licenses within national waters. The legislature and the executive branches of the US government have the authority to set budgets for fishery management and dictate the scope of NMFS authority and mission through the passage of laws. The federal government can also enter treaties or trade agreements with foreign countries to approve access of fishers into territorial waters.

Another formalized mechanism of resource management is the Georgia Marine Fisheries Advisory Council (MFAC) and its subcommittees. MFAC allowed private and public stakeholders in the fisheries to provide their opinions and knowledge to the GADNR concerning management of the fisheries. This council was created in 2006. MFAC has designated subcommittees: Finfish Advisory Panel, and the Shrimp Advisory Panel. The council and its

subcommittees are comprised of community representatives from commercial enterprises, recreational interests, processing/packaging, and other non-consumptive interests. Members are selected through application or invitation and are geographically evenly distributed throughout the Georgia coast.

The GADNR sets regulations for the 2015 shrimp industry in state waters and the National Marine Fisheries Service in federal waters. Any individual intending on catching seafood with the intent to sell must purchase a commercial fishing license, and trawl fishers are required to pay an additional licensing fee. All commercial fishermen are required to report their landings information to the GADNR.

Commercial food shrimp regulations cover two primary methods: trawl fishing and cast netting. Seining is also an approved method, but it is not as commonly practiced. For trawl fishing, the state waters are permanently closed from March 1 to May 14. The season opens by a declaration by the GADNR Commissioner, which is based on fishery-independent surveys, biological, and physical data. Trawling occurs in the sounds only at the discretion of DNR Commissioner. Federal waters remain open year-round at the discretion of NMFS. All nets, except for some try nets (nets to sample an area for shrimp without deploying a full trawl), are required to have NMFS-approved Turtle Excluder Devices (TEDs), and all nets (including try nets) must have a Bycatch Reduction Device (BRD) installed. Licensed trawl fishers submit a forfeiture bond of \$5,000 with the expectation that they will not violate any laws or regulations.

Cast netting for food shrimp requires an additional license beyond the commercial fishing license, which is limited through a controlled access system. The GADNR only issues 200 annual cast netting licenses. The cast netting season generally overlaps with the commercial trawling season; however, all saltwater areas are open to cast netting, including areas inside the

sounds and tidal creeks. Unlike trawling shrimpers, there is a catch limit allocated per boat for cast netters.

Perceptions by fishers of the formal regulatory framework were widely mixed. Some fishers found regulations too restrictive while others thought they did not go far enough to protect the stock from overfishing or illegal fishing. This disagreement was most widely observed through discourse surrounding the opening or closing of the sounds to shrimp trawling. Closing the sounds decreased access to available shrimp, particularly for vessels too small to pilot in offshore waters, the so-called ‘mosquito fleet’ (5/6/1993). However, some shrimp fishers also recognized the sounds and estuaries as nursery grounds for growing shrimp and believed fishing in the sounds caused the growing shrimp to be caught at small sizes, which reduces the opportunity to catch them later when they would be larger and more valuable. In 1959 and 1961, a special ballot measure attempted and failed to close sounds for the duration of the year. However, in 1963, legislative action successfully closed most sounds in McIntosh County (4/9/1959, 8/24/1961, 3/21/1963). In 1980, the sounds were closed to present-day regulatory limits, a move supported by most shrimp fishers who met with GADNR (9/11/1980). However, a year later, the shrimp fishers were requesting the sounds be reopened, some responding to this change by illegally fishing the sounds (9/24/1981, 8/10/81). GADNR responded by increasing law enforcement. More recently, shrimp fishers have expressed support for re-opening the sounds (4/6/2000). Some shrimpers interviewed believed that the disturbance created by trawling may alleviate the problem of black gill disease and perceive “no biological reason not to have

them open.” At the time of this research, there was no scientific literature or data to support this claim.

Informal normative institutions are those agreements among fishers about appropriate behavior and practices but are not enforced by regulatory frameworks. Among shrimp fishers, there was a strong disdain for fishing undersized shrimp. Also, although shrimpers do not have set territories, dropping trawl nets within perceived proximity to another trawler preparing to fish is considered a form of theft. Boat owners and captains are expected to keep their boats in good working order beyond what is required by GADNR and have received criticism from other fishers for a ‘shabby boat.’ The criticism may be the result of frequent boat fires and trawlers sinking over the years, some at the docks, which caused damage to the boats next to them.

Putting into context the informal normative institutions within the community of McIntosh County and how they also influence the shrimp fishers is necessary. It is generally accepted that buying seafood from local fishers is the preferred practice. However, not until the mid-2000s Georgia shrimp were successfully marketed as superior and ought to be preferred by locals and local restaurants over imported foreign shrimp. Restaurants who sell Georgia shrimp could buy into the “Wild Georgia Shrimp” seal to display on their menus or in their restaurants, allowing them to offer a higher price for their shrimp than if they were selling shrimp from other sources. However, there was little enforcement of the use of the seal. Painted on the side of a popular restaurant on Highway 17 is the statement: “Friends don’t let friends eat foreign shrimp.”

Like many livelihoods that rely on natural resources, shrimp fishers cultural-cognitive institutions are based on generationally acquired local environmental knowledge. As related by several shrimp fishers in interviews, a northeasterly wind direction reliably predicts poor catches.

Most notable from the interviews and *The Darien News* articles, was the prevalent idea that those who were shrimp fishers do so because doing so is ‘in their blood’ and would not be happy with anything else. Many shrimp fishers also expressed deep religious convictions. In both news articles and interviews, fishers made statements regarding their religious faith contributing to their confidence that if one season was bad the next would be better. One fisher is quoted in the newspaper, “We are completely trusting in the Lord to provide for us,” while expressing distrust for the GADNR, particularly their reports of landings (4/6/2000). Another fisher described persistence in fishing as “eternal optimism,” and had a perception that stresses fishers experience were temporary, usually only limited to a season or a year. Trust of the GADNR seemed dependent on the individual’s experience of participation with the regulatory body. Most shrimp fishers shared an attitude that the GADNR does what it can to help but are ultimately helpless because of their lack of control over ‘nature.’ A few shrimpers recalled officials of the GADNR expressing desires to see shrimp fishers completely banned from Georgia waters. Outside of family groups, there appeared to be a general distrust between shrimp fishers, particularly for strikers and captains who were transient to the community. A few shrimp fishers believed the national regulatory institutions are not favorable to their livelihood.

The narrative of fishers’ cultural-cognitive institutions of the McIntosh County community largely was an evolving story of identity and sense of place. In the early articles and into the 1980’s the commercial food-shrimp industry is identified as an important economic activity to McIntosh County (4/9/1959, 3/17/1960, 2/9/1965, 8/25/1969, 2/25/82, 4/8/1984). Multiple residents of McIntosh County expressed that they identified shrimp trawlers as icons of the Darien. Iconography and place-building around the shrimp industry are most prominent during the annual Blessing of the Fleet event held at the Darien waterfront. The Blessing of the

fleet event began in Darien in 1968 and is a large tourist draw to the city. During this event, boats are blessed at the Darien Bridge (US Highway 17) in hopes of conferring safety and prosperity on the fishers. City officials involved in the planning of the Blessing of the Fleet insist it is not intended to be a shrimp festival. However, most boats in the boat parades have been shrimp trawlers, and most of the parade Grand Marshals have been prominent shrimp fishers in the community.

Governance - Actor Networks & Multi-Level Interactions

Over the course of this study, non-state actor networks emerged and reorganized in response to particular stressors. Consistently, there were multilevel interactions and vertical integration of non-state actor networks and state actor networks. The prominent state and non-state actor networks and the gradient of their center of influence (local to global) are illustrated in Table 2.2. The most prominent instances of activating actor networks and state and non-state network integration occurred when addressing the stressors of imports, natural disasters, and competing or oppositional values challenging the practice of shrimp trawling (e.g., sea turtle exclusion devices and bycatch exclusion devices).

Table 2.2: State and non-state actor groups and networks influencing the McIntosh County, Georgia, USA fisher community and the gradient of their regional center of influence.

Actor Groups and Networks		
	State	Non-State
Local ↑ Center of Influence ↓ Global	McIntosh County Chamber of Commerce	McIntosh County Fishers
	Board of McIntosh County Commissioners of Road and Revenues	McIntosh County Fisher Family
	Darien City Council	Georgia Shrimp Association
	Shrimp Advisory Panels	McIntosh County Fisher Community
	Crab Advisory Panels	Residents of McIntosh County
	Coastal Advisory Council	Coastal Conservation Association
	Georgia Department of Natural Resources	Georgia Coastal Fisher Community
	Georgia Assembly	Residents of Coastal Georgia
	South Atlantic Fishery Advisory Council	University of Georgia
	National Marine Fisheries Service	Residents of the State of Georgia
	US. Congress	Southern Shrimp Alliance
	US. International Trade Commission	South Atlantic Coastal Fisher Community
		Residents of South Atlantic States
		Sierra Club (other national NGOs)
Global	Foreign Governments	International NGOs

From the beginning of the study period in 1959 through 2015, both fishers and articles cited imported shrimp as a major problem and a multi-decadal press stressor. In response to this stressor, McIntosh County shrimp fishers formed the Georgia Shrimp Producers Association

(GSPA) in 1959 for the “promotion of the shrimp industry, particularly as it regards prices, and will seek better relations with sports fishermen” (07/09/59). In 1960, the GSPA petitioned Congress for legislation to put a quota or Ad Valorem Tax on shrimp imports. The petition had the support of other local state actors, the Board of McIntosh County Commissioners of Road and Revenues, who voted in a resolution to urge congressional representatives to pass the legislation (3/17/1960). The resolution was not successful. In 1974, shrimp prices were depressed, and GSPA, which had since become defunct, re-emerged as the Georgia Fishermen Cooperative (GFC). At the GFC formation, the importation of shrimp was again identified as problematic for the shrimp fishers (8/8/1974). Though the GFC seemed to be open to all fishers and those interested in the Georgia seafood industry, the language used in the article (“150 shrimpers and other fishermen”), appeared to express the organizations bias towards the commercial food shrimp community. The GFC traveled to Washington to petition members of Congress to help with shrimp imports and declining shrimp prices. However, in 1974 the federal congressional members and political appointees (e.g., a national state actor networks) informed the GFC representatives that they valued free trade over restricting imports and were disinclined to assist the GFC in this way (8/24/1974). Members of Congress were willing to discuss other long-term solutions but could not help with the short-term problems of shrimp fishers “presently experiencing extreme financial difficulties (8/24/1974).” The GFC did successfully obtain Small Business Association (SBA) loans with the US government and negotiated lower insurance rates for their members (5/09/1974). Later the burden of repaying the SBA loans and with increased fuel prices and reduced shrimp prices eventually caused some fishers to declare bankruptcy. The president of the GFC and mayor of Darien, Gene Sumner, traveled to Washington D.C. in support of the American Fisheries Promotion Act (9/25/1980). The actions of Sumner did not

result in the reduction of imports or implementation of import tariffs. In the community, this promoted another actor network, the friends and wives of shrimp fishers, who created the Save our Seafood movement to raise awareness of the problem of foreign shrimp (11/06/1980). After the “worst harvest year on record” in 1984, the US government through the US International Trade Commission suggested they might lead an investigation into the effects of imported shrimp on US shrimpers and approached Georgia fishers with a questionnaire (1/24/1985). However, no follow-up to this questionnaire was published in *The Darien News* and later articles do not clarify if the questionnaire ever was distributed to shrimpers in McIntosh County. In 2002, US Senator Ron Paul proposed the Shrimp Importation Fairness Act, an attempt to change the regulatory framework to combat imported shrimp (10/10/2002). Congress failed to pass the act.

Non-state actor networks had some successes with curbing the effect of imported shrimp through both multi-level integration of state and non-state actor networks and actively seeking partnerships at the local level between non-state networks in McIntosh County. The Georgia Shrimp Association (re-formed from the GFC) partnered with the Southern Shrimp Alliance, an 8-state cooperative of non-state actors, to petition the US Government again for tariffs on imports (06/14/04). Though no tariffs were immediately imposed, the US Government granted the industry \$35 million in relief from the market saturation of foreign shrimp, \$3.3 million that was meant to go to Georgia shrimpers to alleviate the effects dumping of imported shrimp by China (06/14/04). One shrimp fisher interviewed recalled this money never reaching the Georgia shrimpers, and expressed his suspicions that it was not distributed to Georgia as intended. Later, the US International Trade Commission recommended tariffs be imposed on fresh and frozen warm-water foreign shrimp from certain countries in Asia, as well as Ecuador and Brazil

(4/7/2005, US International Trade Commission 2005). The tariff requirement was relaxed for Thailand and Indonesia farm-raised fresh shrimp after the 2005 tsunami.

The second activation of actor network integration occurred from the GSA new Executive Director, George Marra, who was the first non-shrimp fisher to be elected to the position. Under Marra, GSA received a \$50,000 OneGeorgia SEED grant, designed to boost sagging Georgia economies. With this money, he began a marketing campaign for “Sweet Georgia Shrimp,” which eventually became the “Wild Georgia Shrimp” label found in present-day restaurants and seafood retailers. Among community members in McIntosh County, this label allows for Georgia-caught shrimp to be priced higher than imported shrimp. Without oversight in who could use this label though, the authenticity of shrimp labeled as “Wild Georgia Shrimp” was called into question.

Similar actor networks were activated during natural disasters. Mentioned previously, hard winter freezes (1977, 1984, 1986, 1990, 2001) would trigger closing of the seasons in part or total by state or federal agencies for their respective jurisdictional waters. The GFC successfully received state and federal government for aid (05/26/77, 06/09/77), and again received assistance from the Georgia Governor to receive SBA loans (10/25/1984). In 2001, the GSA was unsuccessful in obtaining further SBA loans. Another non-state actor, however, became relevant with the emergence of black gill disease. First mentioned in the Darien News in 2002 (12/26/2002), it was reported to the Coastal Advisory Council and the Shrimp Advisory Panel as a topic of concern. Since then, there have been several studies to learn more about black gill disease and its likely causes. Most of this work has been led by researchers at the Skidaway Institute of Oceanography with grant money from the Georgia Sea Grant program.

The eventual implementation of TEDs involved the shrimp fisher non-state actor network federal and state regulatory actor networks, as well as the environmental advocate non-state actors and sportfishing actor networks. Concern over the deaths of sea turtles was first documented in the news articles in 1980, the GFC meeting to discuss their options to find solutions to prevent more regulations (09/16/1980). The GFC self-imposed informal regulations to minimize drag times and help turtles overboard, but NMFS imposed the use of TEDs in nets. Sinkey Boone, a local shrimper of the prominent Boone fishing family, designed and patented his own TED called the “Georgia Jumper.” His design caused less catch-reduction than the other NMFS approved TEDs and was as efficient at excluding turtles as the NMFS approved devices. It also had the added benefit of excluding debris and trash from the nets (01/22/87). Many shrimp fishers installed these on their boats before the federal TED regulations were put in place (04/28/1988). McIntosh County shrimp fishers repeatedly expressed the sentiment that they felt unfairly targeted in articles (05/31/1990, 08/06/1992) after editorials by students at the Savannah Country Day School advocated for protecting sea turtles. As one shrimp fisher is quoted saying “All I want to do is make an honest living, catching shrimp. Please don’t allow the destruction of my way of life (07/13/1995).” Decisions to install experimental TEDs at the height of the season were blamed on the “federal and state bureaucrats,” which led to shrimp fishers feeling victimized (08/29/95). Georgia shrimp fishers did join with environmental groups, though, to sue the US Government for allowing the importing of wild-caught shrimp from countries not enforcing the use of TEDs (06/13/1996). Further regulations, such as ending trawling at night, were also imposed to protect turtles (05/21/1998). The Sierra Club, an environmental activist group, promoted a complete closure of all nearshore waters (state jurisdictional waters), to shrimp trawlers, but was ultimately unsuccessful (10/28/2000).

Participation of actor networks that integrate state and non-state actors is uneven and perceived with mixed negative and positive outlooks by those fishers interviewed. Nine of the fishers interviewed perceived the current governance with some positive perspective. One of the nine, however, openly admitted to noncompliance with regulations. Three fishers felt that that governance would not make a difference, alluding to “mother nature” as the determining factor in the success or failure of the fisheries. Most views were negative, and some felt the GADNR thought the fishers themselves were the biggest threat to the fishery. Participation in the Advisory Panels or meetings correlated to a favorable view of the fishery for one fisher. The rest felt as if they were not heard or were condescended to when they attended the meetings. Most cited this as a reason they no longer participated in formal state and non-state actor networks. Some did share positive experiences with individuals in the GADNR even if their overall position on the agency was negative. Most fishers cited never being invited to or knowing about the panels. Some expressed a sentiment of exclusion.

Governance - Modes of Governance

The configuration of modes of governance contemporary with the study shared characteristics of all three modes of governance, but informal networks were weak. Governance relied some on the interaction of state and non-state actor networks to inform decision making for the best practices for the management of the fisheries. State and Federal agencies gathered data from the fishers, and fishers voluntarily participated in programs that inform the agencies on the state of the fishery (e.g., tag recovery programs with shrimp). There were also clear top-down mechanics of a hierarchical bureaucracy mode evident in the manifestation of laws and regulations imposed on the fisheries (State Board of Natural Resources, GADNR, GA

legislature, and Federal Entities), with successful vertical integration occurring only during the petitioning for tariffs through a broader regional effort of the Southern Shrimp Alliance.

However, the dominant mode of governance was market driven. Market mode of governance was evident in the long-standing effect of imported shrimp on the fishery and the reluctance of state actors to intervene in the market processes. A clear solution to the stressor of imports was achieved through a market-based solution by increasing the demand for local Georgia shrimp over foreign shrimp.

Past modes of governance were also dominated by the market, with clear hierarchical bureaucratic modes increasing as more regulations and licensing restrictions were imposed. Network modes of governance were not well realized outside of non-state actors until later in the considered period. Distrust among fishers outside of family members may have contributed to their multiple dissolutions over the years.

Adaptation

To analyze adaptations, I consider the individual fisher adaptation and the community's adaptation. Individual fisher adaptations to stressors were categorized into positive and negative adaptation. Positive adaptations were those that allow the fisher to continue making a successful livelihood through lawful means. Of the shrimp fishers, 11 relied on other sources of income or job skills (owned seafood processing/retail warehouses, skills as welders) to carry them through lean years. Four were reliant on the fishery alone. One had converted shrimp trawlers to diversify fishing for other species (cannonball jellyfish), which was valued in Asian markets. An analysis in 1986 by Georgia Institute of Technology Economic Development Laboratory found limited a potential for livelihood diversification within the fisheries of Georgia (07/24/1986). Smaller

vessels of cast netters allowed for greater mobility, mainly by removing them from the water and putting them on a trailer to go to more productive waters or saving money on docking fees.

Trawlers cannot easily be moved, requiring a large amount of fuel and deep-water mooring areas, for which boat owners must pay docking fees.

Individual access to monetary capital also was a strong determinant of positive adaptation to stressors. Access to monetary capital came mostly in the forms of loans provided by banks, the federal government, and state and federal aid programs that assisted in times of disasters. However, the SBA loans were later cited as a source of stress for individuals who received them when the value of their catches was not adequate for paying back the loans (09/25/1980).

Other positive adaptations to stressors were evident in individual innovation that affected the community's resilience at large. Sinkey Boone's "Georgia Jumper," though it did not prevent the final TED regulations, did increase the catchability of shrimp when compared to the original NMFS approved design, and was later adopted by NMFS as one of the approved TED devices. The innovation of the "Wild Georgia Shrimp" marketing campaign successfully addressed the valuation stress of local shrimp, as evidenced by the higher price commanded for Georgia shrimp when compared to imports. Networks of fishers also assisted one another in years when catches were low, and fuel prices were high, through actor-network cooperation. The fishers would send one boat out to 'scout the fishing grounds' for shrimp and report back to other fishers within their network.

Negative adaptations, or activities to support livelihoods that were not lawful and eroded social capital, were also prevalent. Prominent among these activities was the use of shrimp trawlers for transporting illegal drugs into McIntosh County. In the late 1970s through the mid 1980s, the paper reported on several large federal busts of McIntosh County shrimp trawlers

smuggling tons of marijuana (3/30/1978, 6/15/1978, 6/28/1979, 11/20/1980, 1/28/1981, 9/12/1982, 6/10/1982, 4/10/1984). The large bust of the boat *Gigi* shed light on the operations. A trawler would meet with a Colombian “mothership” in international waters beyond the EEZ to load marijuana bales into its hull. The Federal agents involved in the sting operation of the *Gigi* indicated their belief that local law enforcement was involved in the smuggling runs, allegations denied by the Sheriff (9/12/1982). Earlier, a McIntosh County police dispatcher was convicted of supporting the drug smuggling operation on the boat *Murray's Pride* (7/12/1979). The erosion of social capital was made worse when a shrimp fisher murdered an undercover Georgia Bureau of Investigation agent when he was being arrested (1/20/1983, 6/22/1983). This period coincided with the “Just Say No” to drugs program in the US spearheaded by First Lady Nancy Reagan. An editorial article claims “The hope of fantastic profits from even one quick drug haul has blinded previously hard-working honest fishermen. We continue to be proud of our shrimp fishermen who work their trade year after year in a legitimate business for our economic stability.” (1/20/1983). The loss of social capital was apparent when the Georgia Shrimper Association changed its name to the Georgia Shrimp Association, citing the negative views of shrimp fishers (4/29/1999).

The recession and depressed shrimp prices did not solely contribute as the causal element that gave rise to this drug smuggling. The permissiveness or potential participation of local law enforcement and other geopolitical factors might have contributed to increasing drug smuggling activity by some McIntosh County shrimp fishers. Regardless, some members in the McIntosh County community still regarded the running of illicit drugs by shrimp trawlers and fishers as an ongoing activity.

Other individual adaptations included activities that were in direct response to regulations perceived to threaten livelihoods or levied unfairly. Illegal shrimping rose in incidence in response to stricter laws concerning sound closings and night fishing (9/2/1965, 6/19/2014, 10/30/1969, 9/11/1980, 8/10/1981, 11/19/1987, 2/14/1991, 1/8/1998). GADNR and state legislatures responded by increasing fines, making arrests, and seizing boats (2/11/1988, 10/15/1988). Fishers interviewed for this study and in news articles indicated that the problem of illegal fishing is still an issue and law enforcement is not numerous enough to be effective (1/3/1991). Furthermore, some fishers in interviews related that those fishers conducting illegal activity would rely on their familial network to act as lookouts for GADNR law enforcement. This activity stoked distrust among fishers and family actor networks. Members of the community also said that incidents of noncompliance were higher than reported. Specifically, it was suspected that some fishers were engaging in unlicensed and therefore unreported selling of shrimp or sewing closed the BRDs when fishing. Illegal sales were corroborated by the newspaper (10/22/2009). Of course, the harvest from illegal shrimping is not reported to GADNR or NMFS, leading to the fishers' belief that GADNR underestimates total catch.

The most prominent adaptation among shrimp fishers has been attrition from the fishery. Aging fleets, and aging fisher population approaching retirement, and lack of generational replacement signals the shrinking of the industry. Shrimp trawlers were dominantly owned by seafood retailers or wholesalers, who then hired a crew. If shrimping was not profitable, they could rely on other seafood (fish and bivalves) and sell the trawlers which were not required for fish and bivalve production. Only one owner-captain reported that his son of 12 was learning the shrimp fishing trade.

The community residing in McIntosh County, particularly in Darien, has also exhibited a level of adaptation to the shifting economic landscape in the county. Since the construction of Interstate 95, the city and state actors sought to promote a tourism economy in Darien and McIntosh County. As the shrimp industry declined, a shift in focus on inviting tourism into the county increased. For example, the city converted the docks west of Highway 17 from private commercial fishery docks to public docks, after which a seafood restaurant was established in place of a seafood dealer. Requirements for docking boats on the new public docks included proof of insurance for each boat, which forced many shrimp trawlers to leave the county or move to the docks east of Highway 17. In 2017, the Downtown Development Authority approved the sale of the jellyfish processing plant and some other acreage on the east side of Highway 17 to an owner intent on building a boutique hotel with restaurant and retail space. With this announcement, the public concern heightened for the fate of the iconic shrimp trawlers and the shrimp industry's future.

DISCUSSION

The cause of the decline of the McIntosh County shrimp fishery was multifaceted. A steady decline in the participation in the shrimp fishery from 1979 rather than a long-term decline in the available shrimp points to socio-economic stressors rather than ecological stressors as the root cause for the decline. Principal among these stressors was the 'press event' of the ongoing problem of devaluation of local shrimp caused by the excess supply of foreign shrimp. The aging of the trawler fleet and economic recessions also compounded the effects of the imported shrimp. A loss of social capital caused by violations of the formal and informal normative institutions through drug smuggling also contributed to an increased vulnerability of

shrimp fishers. A lack of generational replacement points to a restructuring of commercial shrimping from a family network enterprise with knowledge passed through generations to a hierarchical enterprise where a single entity (seafood processors or dealers) owns the vessels and hires crew from inside or outside of the community. Only in the last decade has availability of shrimp, potentially due to the rise of black gill disease emerged as a new press stressor to livelihoods based in commercial shrimping.

Governance in the fishery did not always aid in the building of adaptive capacities within the community. Actor networks displayed rigidity in their cultural-cognitive beliefs, with a short-term hazard-response cycle but no long-term planned interventions, a so-called rigidity trap (Carpenter & Brock 2008). Rather than directed adaptation through built adaptive capacities and transformation, the fishing community shifted into an increasingly vulnerable state. Formal institutions also reacted to short-term pulse events more effectively than longer-term press events. The formal interventions were exemplified by the distribution of SBA loans in response to freezes or other economic disasters. The loans provided adaptive capacity in the short term, but made reduced adaptive capacity in the long-term, as continued stressors resulted in an inability to repay loans, and thus further attrition from the fishery for those with fewer resources. As press stressors continued, adaptive capacity was lowered, increasing the fishing community's ability to pulse stressors.

More recent efforts of adaptive co-management systems have attempted to give fishers an avenue to participate through vertical and horizontal integration of networks in the management of their fisheries. However, the contemporary sentiment among most fishers was to see the formal regulatory institutions as adversarial rather than helpful, especially since the early decades (pre-1979) the formal regulatory institutions and state actor networks generally operated

in a top-down hierarchical fashion. Despite a shift to co-management adaptive practices through the development of councils and sub-committees that integrated state and non-state actors, the participatory framework does not seem to have achieved its goals of flexible social learning and building adaptive capacities for long-term stressors (Fabricus & Currie 2015). The outcome of the co-management adaptive practices may be caused by the lack of diversity of stakeholders within the meetings to represent the shrimp fishing community. According to the fishers, the timing of the meetings only allowed those who are not obligated to fish continuously for their livelihoods to attend. Those with greater wealth and diversified income have greater agency within the fishery, and their interests were represented to the state actors.

Informal networks conferred greater adaptive capacity to the fisheries than the formal institutions. Family and shrimp fishers amicable with one another were able to self-organize in the system to gain access to greater capital and gain ecological knowledge of the system to realize better efficiency and innovation. Unified non-state actor networks integrated both horizontally (geographically), and vertically (social hierarchies), to achieve some shared goals (e.g., subsidies and tariffs). The ability to act collectively has been cited as an important determinant in adapting to hazards (Adger 2010).

The erosion of trust, however, between state actors and non-state actors, and between non-state actors and non-state actors weakened informal networks. Weak informal networks contributed to the increased vulnerability and decline in fishery participation (Davenport et al. 2007). The inability of state actors to assist with the threat of imported shrimp and the increasingly restrictive regulatory framework in favor of other non-state actor networks (e.g., sea turtle and sports fishing conservation networks over the shrimp fishing networks) perhaps fostered the adversarial sentiment between state actors and the fishers. The rise in illegal fishing

and the perception of corruption within the self-organized fisher networks increased individual vulnerability for those who did not benefit from the activities.

CONCLUSIONS

In the governance of a common resource, the loci of power, agency, and scale are important to understanding individual and community vulnerability to change. It is impossible to say how inclusive the informal networks were in the past, across social and racial backgrounds in McIntosh County. The predominance of the ethnic majority in those who agreed for interviews may indicate the racial minorities and their position within the fishing community are not well-represented in this study. Therefore, the knowledge attained by this study about adaptation responses to stressors does not represent of the community as a whole. The addition of other racial demographics might highlight other cultural practices not shared universally in the fishing community.

Temporal and geographic scale of stressors and the scale of actor networks are also determinants of ability to adapt to changes. In this study, pulse events, like winter freezes, were overcome through a combination of formal top-down governance (e.g., season closures for stock conservation) and the ability to rely on social capital to gain wealth (e.g., loans). Erosion of social capital depleted the ability of some individuals to maintain their livelihood within the fishery. Press events (e.g., importation of shrimp), proved more difficult and took longer to restructure networks to address the threat. The market solution exemplified social learning by shifting from relying on a top-down mode of governance to the market mode of governance to mitigate the influence of imported shrimp, changing the method by which resolution to problems can be achieved. Additionally, the reconfiguration of cognitive-cultural norms, allowing an

individual outside of the shrimp fishery to propose novel solutions proved beneficial. However, the decades required to address the problem demonstrated an overall rigidity in the system that did not allow for creativity and flexibility to emerge until the most vulnerable individuals either left the fishery or resorted to negative adaptive measures.

The relative rigidity of the community and governance and low resilience of most individual fishers to long duration press events (e.g., black gill disease, imported shrimp) may cause poor adaptive capacity of the system to similar press events, like climate change. Those individuals with the highest resilience were those who have the capital (wealth and social), diversified livelihoods, high mobility, and are integrated with resource management. Those fishers integrated with resource management were also predominantly those people with greater capital, diversified livelihoods and high mobility, which indicate an imbalance of power within the system. Historically, unfavorable adaptations by highly vulnerable fishers to changes in governance have resulted in attrition from the fishery, potentially increasing local poverty, or reliance on illegal means to maintain well-being.

The community at large in McIntosh County, while recognizing the reduced economic role of fisheries and moving towards tourism, still maintains a cultural identity with the fishers and the natural resources of the salt marshes. Misalignment between community planning and community values and identities could cause conflict between local stakeholders when balancing this identity against management plans. This outcome is even more probable as climate change threatens the resources that will draw in tourism or the infrastructure needed for support. Further, the lack of clear adaptive mid- and long-term goals may make recognizing future threats and directed adaptation difficult.

Failure of resource governance can lead to maladaptive responses, such as non-compliant fishing, which can lead to inaccuracies in fishery data reported. An underreported catch may lead to mismanagement of the resource. Importantly, fishery resource governance in this case study appears mostly reactionary to stressors rather than proactive with long-term goals and planning in mind. The future of fisheries and fishing communities depends on resource governance that is mindful of power inequalities and builds adaptive capacity to all resource users. Reducing vulnerability requires resource governance to have inclusive co-management practices that are proactive and directed in planning for different resource availability and use under different scenarios of climate change. A fuller awareness of the needs and values of all stakeholders within the system will allow for directed adaptation to new and positive resilient states of the community under the influence of long duration change of the natural resources.

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CHAPTER 3
TEMPORAL PREDICTORS OF VARIABILITY OF ESTUARINE DEPENDENT FISHES
AND PENAEID SHRIMP ²

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ABSTRACT

Climate change may affect temporal patterns of presence and abundance in common estuarine-dependent fishes and crustaceans. Over the last century, climate change has influenced abiotic variables within estuaries. Therefore, the current variability in the patterns of seasonal and annual abundance of nekton may have changed from the historical records for estuaries. We modeled the influence of temperature and salinity as predictors of abundance and diversity from trawl data in estuaries of Georgia, USA. We compared the contribution of anomalous annual and seasonal precipitation to modeled predictions and variation in annual abundance and diversity. Our results did not detect a shift in contemporary patterns of seasonal abundance or diversity compared to the historical record. There were linear trends of declining abundance detected in some common species and of overall diversity. These trends were unrelated to annual precipitation anomalies. Seasonal precipitation anomalies did explain variance in annual diversity for some species. For example, precipitation anomalies were strongly positively correlated with annual abundance ($r^2 = 0.70$) and annual variability ($r^2 = 0.80$) of spot (*Leiostomus xanthurus*). Our findings highlight the need to consider changes to population variance during altered climatic regimes when making estimations of abundance for management purposes. This study also suggests the necessity of long-term datasets at a fine grain to capture patterns in variability, particularly those that might be influenced by long-term processes like climate change.

INTRODUCTION

Understanding temporal variability in species abundance and their climatic drivers within ecological systems is critical for forecasting how species abundance may respond to future

climate conditions. Shifting patterns of precipitation or temperature may affect fish communities of both ecological function and economic importance. Our research seeks to characterize seasonal and inter-annual patterns of juvenile fishes and crustacean variability within the estuaries of Georgia, USA. Life history studies of species have previously recorded the seasonality of recruiting events and settlement patterns for some estuarine species (Muncy 1984, Hales & Van den Avyle 1989, Morton 1989). For many species, this research occurred in only select regions of the species' range, which left life history data from the unstudied areas to estimation and extrapolation. Additionally, life histories were compiled for some species a half-century or more ago. As the climate changes, seasonal dynamics observed when life histories were written may no longer apply. Thus, we compare inter-annual variability with seasonal and inter-annual patterns in abiotic factors to better describe the potential influence of climate change on species occurrence and abundance.

Estuaries provide essential nursery habitat for fishes and crustaceans, including commercially harvested species such as white shrimp *Litopenaeus setiferus*, one of the most profitable commercial fisheries in the U.S. (Beck et al. 2001; Zimmerman et al. 2002; Able & Fahay 2010; NMFS 2016). Other abundant estuarine fishes such as bay anchovy (*Anchoa mitchilli*) have little commercial value but serve as critical prey for commercially and recreationally important predators (Morton 1989; Wang & Houde, 1995). Settlement patterns and species occurrence are primarily driven by broad-scale abiotic factors such as water temperature, salinity, and photoperiod (Able & Fahay 2010). Additionally, high primary productivity in estuaries and refugia provided by wetland vegetation are beneficial to the growth and survival of young fishes and crustaceans (Able & Fahay 2010).

Climate change and anomalous extreme weather events force abiotic and biotic changes to estuaries. Current climate models predict an accelerated sea level rise, rising water temperatures, shifting precipitation patterns, and changing frequency and intensity of storms (Scavia et al. 2002, Polade et al. 2014, Walsh et al. 2016). Resulting biophysical changes include decreasing land elevation relative to sea levels, boundary or edge redistribution of estuarine wetlands, altering wetland to water ratios, and changes to the composition of soil or sediments (Day et al. 2008). Changing patterns in precipitation may also alter salinity regimes, residence time of water within estuaries, and sediment and nutrient delivery to wetlands (Osland et al. 2016). Ecological and physical stressors caused by climate change in estuaries are compounded by centuries of human-driven alteration of estuaries and depletion of resources within them. Anthropogenic coastal development affects the resiliency of estuarine ecosystems (Scavia et al. 2002, Lotze et al. 2006).

Forecasting potential effects of climate change on the persistence of suitable nursery habitat necessitates understanding the influence of broad-scale abiotic variables on the distribution of juvenile crustacean and fishes. Short-term variability of abiotic variables (e.g., water temperatures, salinity) occurs during regular seasonal intervals (Dalhberg & Odum 1970, Bruno et al. 2013). Understanding the timing and influencing factors of seasonal species occurrence or abundance is important to fisheries management for discerning the difference between expected variability and anomalous variability. The absence of a species in any given sample may be caused by the timing of sampling effort rather than suitable habitat availability, potentially leading to spurious conclusions about habitat suitability. For instance, if a species only uses salt marshes in their juvenile stage in the summer, sampling salt marshes in the winter may lead to the conclusion that the habitat is unsuitable year-round. While the literature on the

expected timing of occurrence and abundance for some species, like white shrimp, is extensive throughout their range (Lindner & Anderson 1956, Muncy 1984 Williams 1984), knowledge of the timing and determining factors of juvenile settlement patterns many species is incomplete. Additionally, the high degree of spatial variation in physical processes between estuaries, even those geographically close to one another, suggests the need to test assumptions concerning the seasonal abundance and richness.

Inter-annual variability in abiotic factors may also influence annual estuarine species mean relative abundance and richness. Both drought and increased rainfall have been known to have a relationship with fluctuating populations and community dynamics within estuaries (Meynecke et al. 2006). Whether the effects of precipitation are contemporaneous with patterns of abundance or occurrence or are the results of a lag effect, is less clear. Therefore, understanding inter-annual variance and how it relates to annual environmental changes will better inform temporal trends and produce more robust spatial models of the probable distribution of critical habitat. Anticipating spatially-explicit localities of critical habitat will inform future habitat conservation and management decisions, particularly considering climate change.

Regional Fish Richness and Species Periodicity

In this analysis, we analyzed the temporal patterns of fish species diversity and fish and crustacean species that fulfill an important ecological function or have economic value within the estuaries: bay anchovy, spot (*Leiostomus xanthurus*), and Atlantic croaker (*Micropogonias undulatus*), white shrimp, and brown shrimp (*Farfantepenaeus aztecus*). Although there are life history profiles developed by the U.S. Fish and Wildlife Service for these species for the

Southeastern U.S., it is critical to test the assumptions of these profiles (e.g., Muncy 1984, Hales & Van den Avyle 1989, Morton 1989). It is possible that because surface water temperatures have warmed since these profiles were written that there may be seasonal shifts in occurrence and abundance of species in the estuary (NOAA 2017). Also, the seasonal patterns of diversity or abundance are not described for the estuaries included in this study.

Regional fish species richness and assemblage composition within estuaries are presumably determined in part by biogeochemistry and primary productivity such as the longitudinal salinity gradient (Yanez-Araciba et al. 1988). Seasonal fluctuations in fish species richness are driven by emigration and immigration of marine estuarine-dependent species (Potter et al. 1986, Able & Fahay 2010). These patterns also reflect the strong influence of competition and predator/prey dynamics among species (Livingston et al. 1997). Seasonally, fish species richness coincides with high primary production (Yanez-Araciba et al. 1988). In the Southeastern US, macrophytes and microalgae productivity is highest in spring and summer in North Carolina (Hettler et al. 1989,) and Georgia (Dame et al. 2000). Similar patterns have been observed in estuaries in Australia as well as (Neira et al. 1992).

Atlantic croaker settlement patterns have been extensively studied throughout its range, though not specifically in Georgia estuaries. Larvae are presumed to settle in mesohaline areas of estuaries. Juveniles migrate down-estuary to polyhaline areas as they mature, leaving the estuary to overwinter in deeper waters (Milgarese et al. 1982). In the Chesapeake Bay and North Carolina, spawning occurs in protracted time periods from July to December with a peak in September and October (Barbieri et al. 1994). Croaker spawning and larval ingress occur primarily in fall, winter and spring (Warlen 1982), and larval ingress is highest from November to May in North Carolina (Hare & Able 2006).

Like Atlantic croaker, spot is a demersal sciaenid species and spawns in the deeper offshore waters after which eggs and larvae are transported into the estuaries. Spawning is thought to occur in the South Atlantic Bight from October to March, peaking in winter (Hales & Van den Avyle 1989). Spawning seems to be a temperature-driven phenomenon, where spawning occurs in water temperatures from 17.5 to 25.0°C (Hales & Van den Avyle 1989). Larvae grow into postlarval juveniles in an average of 59 days (Hales & Van den Avyle 1989). Larval and juvenile spot have been detected in estuary nursery habitat in April in Virginia and in January in South Carolina (Shenker and Dean 1979, McCambridge & Alden 1984). As juveniles grow, they move from shallow-water tidal creeks to the deeper waters of the estuaries (Hales & Van Den Avyle 1989).

Bay anchovy annual spawning and juvenile migrations are likely seasonally correlated with peak primary production and when planktonic prey is most abundant. Importantly, the timing of spawning with high primary productivity buffers mortality of starvation-prone bay anchovy larvae (Houde 1978). This relationship was found in Tampa Bay, Florida where the peak postflexion larval densities occur from July to September and exhibit a strong positive correlation with water temperature (Peebles et al. 1996). Similarly, in the Chesapeake Bay, abundance peaks in August through October, when water temperatures average from 26.1 to 16.6°C (Wang & Houde 1995, National Ocean and Atmospheric Administration, www.nodc.noaa.gov/dsdt/cwtg/catl.html accessed December 5, 2017). Georgia estuaries, therefore, are expected to show similar patterns of bay anchovy abundance in a more protracted timeframe across June to November if historical trends remain (National Ocean and Atmospheric Administration, www.nodc.noaa.gov/dsdt/cwtg/catl.html accessed December 5, 2017).

Temperature dominates white shrimp seasonal and inter-annual variability. Spawning of white shrimp begins offshore in spring, specifically from May to September in the Carolinas, and from April to September in Georgia and North Florida (Lindner & Anderson 1956, Williams 1984). Rising water temperatures rather than photoperiod or specific temperature likely trigger spawning. Postlarvae migrate into their estuarine nursery grounds beginning in June in North Carolina with peak migrations occurring during flood tide events during new moons (Williams 1984). Most spawning likely occurs in spring in Georgia as small shrimp appear in catches in July primarily in the estuaries (Lindner & Anderson 1956). Smaller juveniles are found in mesohaline areas of estuaries and then move into polyhaline areas as they mature (Lindner & Anderson 1956). Inter-annual abundance variability is correlated to winter water temperature (Muncy 1984). Mortality of overwintering subadults and juveniles increases when temperatures drop below 8°C and total mortality occurs at temperatures below 3°C (Muncy 1984). Temperature acclimated postlarval and juvenile white shrimp exhibited 50% mortality in 24-hours between 38.3 and 38.9°C (Wiesepape 1975). Though white shrimp may tolerate a wide range of salinities, mortality increases with decreasing temperatures and low salinity (Wiesepape 1975).

Brown shrimp also spawn offshore, and postlarval estuarine migration parallels that of white shrimp. Spawning events are more protracted than white shrimp, and rising water temperature triggers postlarval movement (Williams 1984). Peak recruitment of postlarvae into the estuaries occurs from March to April in North Carolina and from February to March in South Carolina (Williams 1984). Juveniles settle into their nursery habitats between March and July in Georgia (Larson & Van Den Avyle 1989). Inter-annual variability may be attributed to annual water temperature and salinity fluctuations within the nursery grounds. Compared to white

shrimp, brown shrimp have a lower resistance to high temperatures (50% mortality at when held at temperatures from 36 to 38°C for 24 hours; Wiesepepe 1975), and there is a strong negative interaction effect between low salinity and decreased thermal tolerance to low temperatures (Wiesepepe 1975, Larson & Van Den Avyle 1989).

In this paper, we pursue several questions to gain a better understanding of current inter-annual and seasonal variations and trends in diversity and abundance of estuarine species. Our goal for this work was to determine: 1) if current or annual variation of presence or abundance differs from historical record, 2) explore if annual or seasonal trends in the temperature and salinity predictor data explain temporal patterns of diversity or abundance of selected species, and 3) determine whether changes in climatic patterns influence the annual variability in abundance or diversity. Our specific objectives were to: i) conduct a temporal analysis to describe seasonal and annual trends and variability of fish species richness, Atlantic croaker, spot, bay anchovy, white shrimp, and brown shrimp , ii) use a regression analysis to assess the influence of salinity and temperature variables to fish species richness and abundance of species mentioned in the first objective , iii) use regression analysis to determine the influence of precipitation anomalies annual fish species richness and abundance of species mentioned in the first objective.

We hypothesized that climate change altered the abiotic environment since the life history profiles were written. Seasonally, we expected a shift in diversity and abundance shift to earlier time periods than historically predicted for fish species richness and species' abundances. We also anticipated potential trends in the annual richness and abundance that reflect changes in the abiotic environment. We anticipated that salinity would be an influential environmental factor for species diversity, and the abundance of Atlantic croaker, white shrimp and brown

shrimp. Water temperature is expected to influence diversity, and abundance of Atlantic croaker, spot, bay anchovy, white shrimp and brown shrimp. We also hypothesized that inter-annual variability with species diversity and species abundance would be related with annual and seasonal precipitation anomalies, particularly for species whose abundance is affected by salinity.

STUDY AREA

The study area comprises four major estuaries on the Georgia Coast: Wassaw, Ossabaw, Altamaha, and St. Andrew sounds (Fig. 3.1). The major rivers of the sounds are Savannah, Ogeechee, Altamaha, and Satilla rivers. Smooth cordgrass (*Spartina alterniflora*) salt marsh is the dominant terrestrial habitat type in areas of frequent tidal flooding. Brackish marshes transition to black needle rush (*Juncus roemerianus*) and big cordgrass (*Spartina cynosuroides*).

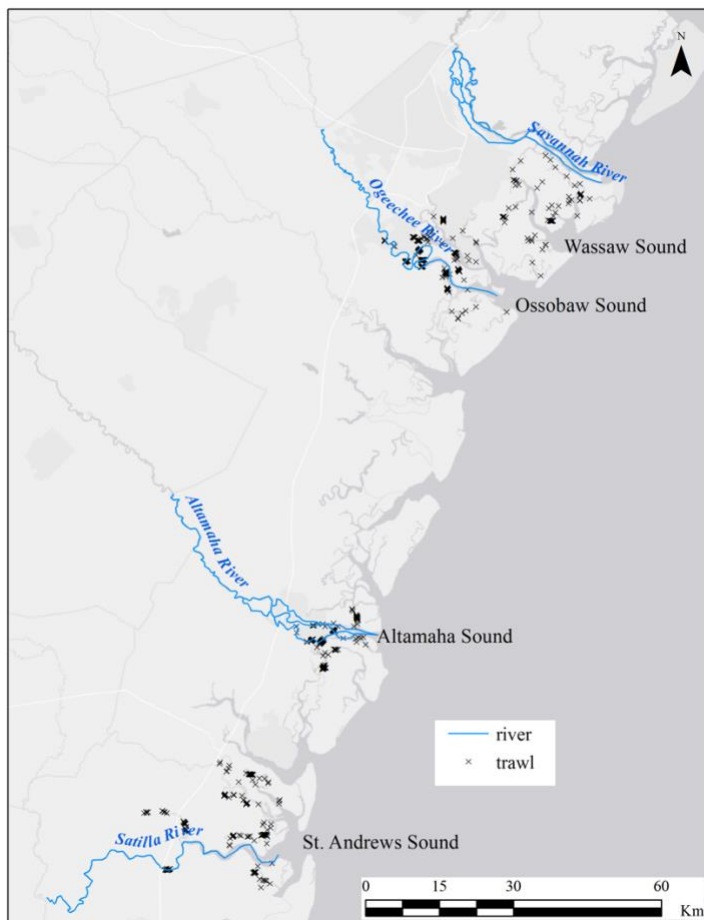


Figure 3.1: Study area on the coast of Georgia, USA showing four major sounds and rivers sampled from 2007-2014 in a Georgia Department of Natural Resources juvenile fishes and crustacean trawling surveys.

Salinity within the estuaries varies (0 – 35 psu) by proximity to riverine systems, season, and tidal cycle. Estuarine areas farthest away from the mouths of rivers sheltered by waves and oceanic currents by landform or bathymetry (e.g., barrier islands and salt marshes), have a longer hydrologic residence time. Long residence time allows for a slower rate of change in salinity in response to pulse events (e.g., local precipitation, spring tides; Wang et al. 2016).

Seasonally, precipitation is highest in summer and early fall, averaging 18.9-cm in August and 7.1-cm in December. From 2006 – 2014, the U.S. Southeast River Forecast region experienced several periods of severe to exceptional drought conditions, notably in 2007, 2008, 2011, and 2012 (NDMC 2016). Annual mean precipitation within GA coastal watersheds was below the 30-year average (1981-2010) for all years but 2009 and 2013 (Fig. 3.2; PRISM 2016).

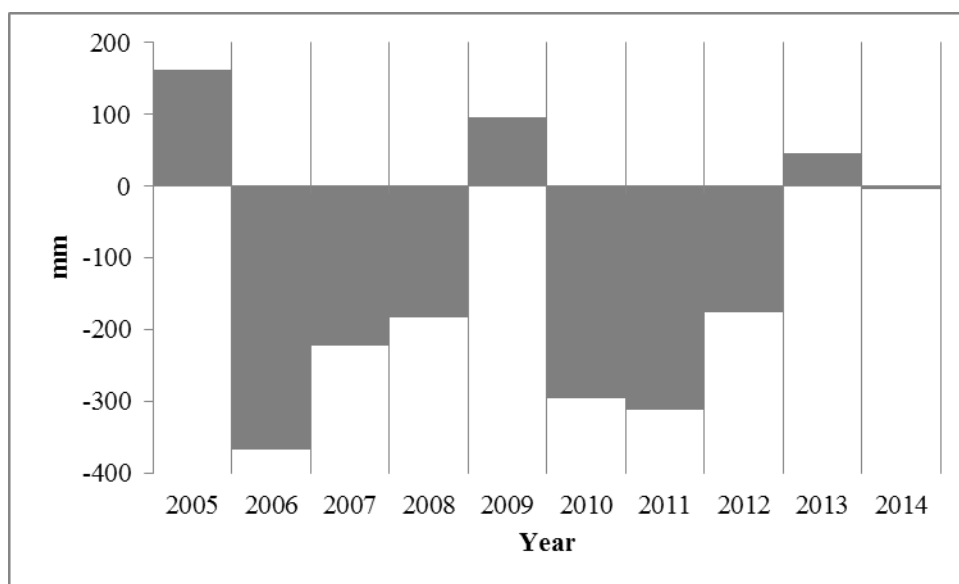


Figure 3.2: Deviation from 30 – year precipitation normal (1981 – 2010) of mean annual precipitation for the years 2005 – 2014 for coastal watersheds, Georgia, USA.

METHODS

Survey data for juvenile fishes and crustaceans were provided by the Georgia Department of Natural Resources – Coastal Resources Division. Surveys were conducted from 2006 to 2014 with a 6.1 m balloon modified otter trawl with 9.5 mm mesh. Trawls took place at low tide at an average speed of 2 kt for approximately five minutes during daylight hours centered at low tide. Sampling in 2006 only covered the latter part of the year and therefore was excluded from the temporal analysis. Sampling events from 2007 – 2010 covered the months of March to November. In 2011, the effort was expanded to include the whole year. For consistency, our analysis was restricted to the months of March through November. Trawling sites were initially randomly distributed throughout the four sound systems, but shoaling and net obstructions required adaptive sampling techniques. We removed stations that were only visited once throughout the trawling effort, so they would not bias the data. Over the course of the sampling period, 30 individual stations were sampled for a total of 915 times, with stations visited at least once per season; most were visited monthly.

Seasonal variability in fish species richness and abundance of Atlantic croaker, spot, bay anchovy, white shrimp, and brown shrimp was analyzed using the Marine Geospatial Ecology Tools (MGET; Roberts et al. 2010). Catch-per-unit-effort (CPUE) was used as an index of abundance. MGET uses the Lombe-Scargle method, similar to a Fourier analysis, to create a spectral periodogram of patterns of richness or abundance over time. A spectral periodogram shows the peaks in abundance or richness by days. A relatively tall peak at 365 days indicates a single annual recruitment event, while a peak at 29 days suggests the influence of lunar cycles on abundance or richness. If the peaks are more diffuse or shorter compared to other peaks, then

recruitment may be protracted over the year with several recruitment events occurring. Results of this analysis were compared to literature estimates of peak abundance or richness.

Several quantitative approaches were used to explore inter-annual variation in richness and abundance. A time-lag regression analysis was used to describe the patterns of variability in annual abundance and determine if species richness or abundance exhibited a directional trend (Collins et al. 2000). This analysis provides a summary of the patterns of the data variability but does not directly model the linear changes to abundance or richness of the data. By accounting for temporal autocorrelation, the results indicate if the patterns in richness or abundances are showing a) change in directional trend, b) stochastic modulation around a constant mean, or c) convergence on a cyclical trend. The analysis is accomplished by calculating the Euclidian distances between the mean annual abundance and fish species richness for each time lag over the period of sampling. Square root transformations of the data were used to mitigate the effects of bias at single-value time-lags, as recommended by Collins et al. (2000). The Euclidian distance for species richness was calculated as:

$$E = \sqrt{(x_i - x_j)^2}$$

Where x_i is the richness in year i , and x_j is the richness in year j . This value is calculated for each time lag. Therefore, over an eight-year dataset there will be a Euclidian distance for seven one-year time lags, six two-year time lags, five three-year time lags, and so on, to one eight-year time lag. In total, we calculated 28 Euclidian distances. Linear regression was then used to evaluate the relationship between the transformed Euclidean distance values to the square root of the time-lags. Significance tests of the regression ($p < 0.05$) with a positive slope indicate a directional pattern and with a negative slope indicate a cyclical dynamic to the pattern (Collins et al 2001). A non-significant slope indicates that variability is stochastic. The magnitude of the

slope indicates the strength of the signal while the r^2 value indicates the amount of variance around the signal (Collins et al. 2001). These results were used in comparison to a linear regression of the model of richness or abundance over time to determine if richness or abundances were increasing, decreasing, or staying the same.

The potential influence of an annual climatic event on abundance to biophysical predictor variables was analyzed using generalized linear mixed effects models (GLMM; Gelman & Hill 2006, Bolker et al. 2009). Mixed model regressions were beneficial for this study because of the ability of the models to partition variance based on temporal grouping, which allows for the relationship of the response variable and the fixed predictor variable to change under different time periods designated as random effects. It also allows for quantification of variance at a factor level, rather than testing specifically for responses at the different factor levels. Importantly, many long-term climatic events probably do not have a direct effect on abundance, but rather abundance responds to climatic events at a time lag, or cumulatively over some period. Once the response is partitioned into its conditional mode (mean predicted value) for each factor of the random effect (e.g., each time step), a regression analysis can be used to determine the relationship between the conditional modes (inter-annual variation) and environmental factors averaged over that time step (Shielzeth & Nakagawa 2013). GLMM's are particularly preferential when response data are not normally distributed, or sampling is imbalanced (Cnaan et al. 1997, Bolker et al. 2009). The characteristics of GLMM were important to our dataset because the sampling design was imbalanced over time even after correcting for a missing season. Additionally, because the fishes and crustacean abundance data were zero-inflated and overdispersed, we used negative binomial regression.

The model for the random intercept mixed model was represented by the following formula:

$$Y_{ij} = (\beta_0 + b_j) + (\beta_1)TEM_i + (\beta_2)SAL_i + (\beta_3)SAL_{ij} \times TEM_{ij}$$

where Y_{ij} is the observed response (abundance or richness) for the i = sample and j = year. The coefficient for intercept was given by the fixed effect β_0 , and the coefficients for the fixed effects of temperature (TEM), salinity (SAL), and their interaction were given by β_1 , β_2 , and β_3 . The random effect term grouped by year j (b_j). Fixed effects were tested for significance using the Wald Z test, and likelihood ratio tests were conducted with each model to test its performance against two null models: an intercept-only model and a fixed effect-only model.

We used simple linear regression to evaluate the relationship between annual and seasonal precipitation anomalies with annual average abundance, coefficients of variation of abundance (CV CPUE), and with conditional modes from the results of the GLMM models. Precipitation anomalies were calculated by using PRISM dataset of a 30-year average (1981 - 2010), and average annual and average monthly precipitation for each year of the sampling period. Annual seasonal precipitation anomalies were estimated by averaging over three-month time periods using the meteorological definition of seasons (winter: December, January, February; spring: March, April, May; summer: June, July, August; fall: September, October, November). Regional values were extracted using the HUC 8 watersheds for the Ogeechee, Altamaha, and Satilla rivers. Annual and seasonal anomalies were calculated by subtracting the annual and seasonal precipitation 30-year average from the average annual and seasonal values over the sampling period.

Lastly, the annual coefficients of variation of richness or abundance were regressed with contemporary annual precipitation anomalies, the previous year precipitation anomalies (Year-

1), the annual seasonal precipitation anomalies contemporary with seasonal peak abundance, and the annual season precipitation anomalies of the season before seasonal peak abundance and richness. The mean predicted intercepts (i.e., conditional modes) from the GLMM analysis were regressed with the annual precipitation anomalies, seasonal precipitation anomalies, and annual precipitation from the previous year. Positive or negative relationships with precipitation anomalies and the conditional modes would indicate that precipitation anomalies influenced the variability in abundance or richness.

RESULTS

Over the 8-year period, 106 fish species and 18 crustacean species were detected, ranging from euryhaline fishes (e.g., Atlantic menhaden, *Brevoortia tyrannus*; spot) to freshwater and marine stenohaline species (e.g., bluegill, *Lepomis macrochirus*; cobia, *Rachycentron canadum*). The species with the highest rate of detection (d_i) were bay anchovy (65%), Atlantic croaker (66%), and white shrimp (61%) (Table 3.1). White shrimp and brown shrimp were the most abundant crustacean species.

Table 3.1: Detection rate (d_i : percent of samples containing the species) and percent of total catch per unit effort (% CPUE) of commonly caught fish and crustacean species with commercial importance, 2007-2014 in Georgia, USA estuaries.

Common Name	Scientific Name	d_i (%)	% CPUE
Atlantic Croaker	<i>Micropogonias undulatus</i>	66	24.31
Bay Anchovy	<i>Anchoa mitchilli</i>	65	25.71
White Shrimp	<i>Litopenaeus setiferus</i>	61	13.07
Spot	<i>Leiostomus xanthurus</i>	43	6.82
Brown Shrimp	<i>Farfantepenaeus aztecus</i>	17	0.94

Seasonal Periodicity

Spectral analysis of abundance from trawl data showed a fair amount of variability in peak heights and cycles within and among measured variables (abundance and richness, Fig. 3.3). Juvenile fish richness, Atlantic croaker, spot, white shrimp, and brown shrimp all had clear peaks at 365 days, indicating a single annual recruitment. However, both spot and brown shrimp had other peaks at equal or greater height, showing variability in the data. Bay anchovy did not exhibit a strong seasonal period pattern. When analyzing monthly lunar patterns, we observed peaks at 29 days for fish richness, bay anchovy, and brown shrimp, potentially indicating that tidal cycles influenced occupancy and CPUE.

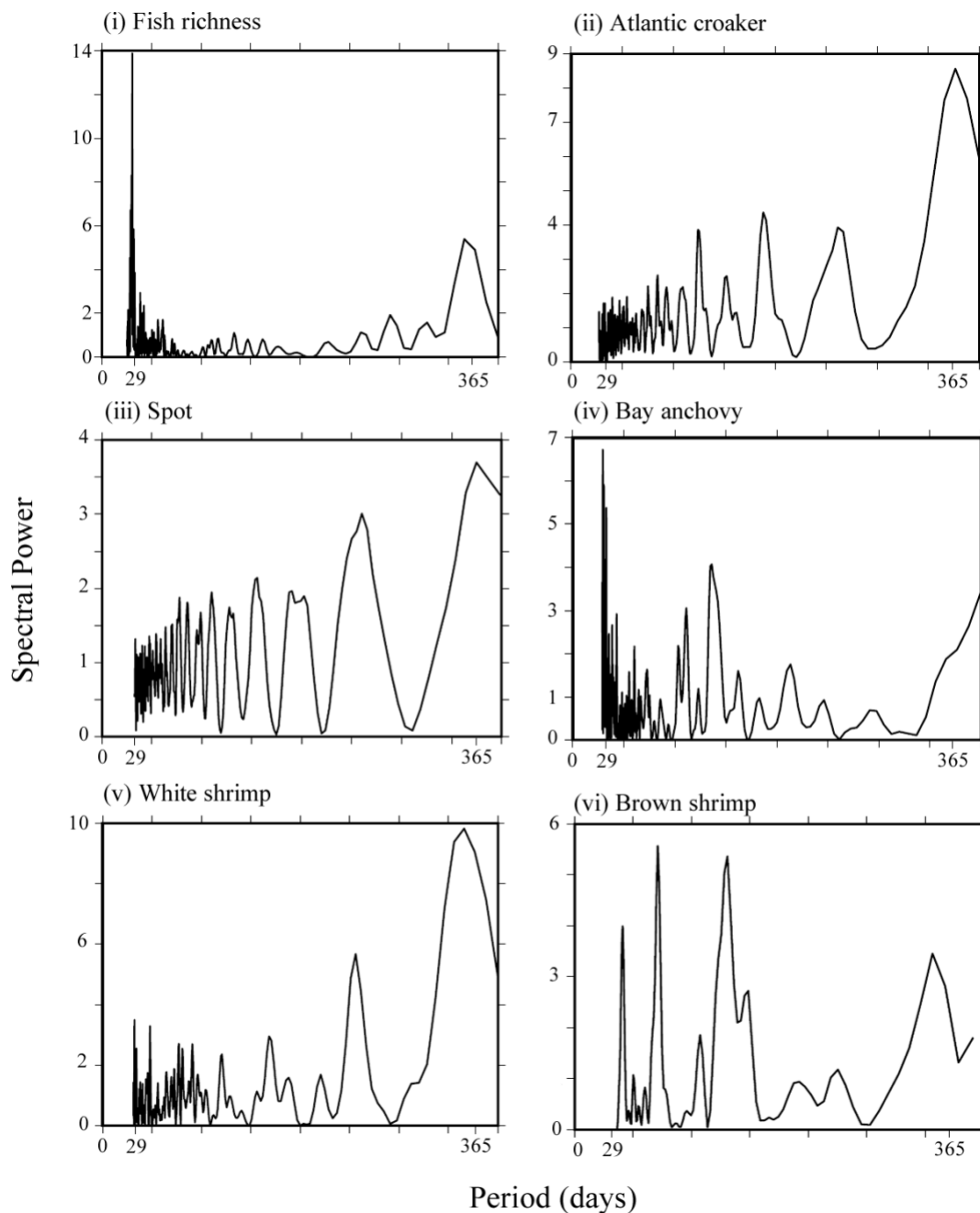


Figure 3.3: Temporal periodicity of mean abundance for juvenile trawl data from 2007-2014 in Georgia, USA estuaries (i) juvenile fish richness, (ii) Atlantic croaker; *Micropogonius undulates*, (iii) spot; *Leiostomus xanthurus*, (iv) bay anchovy; *Anchoa mitchilli*, (v) white shrimp; *Litopenaeus setiferus*, and (vi) brown shrimp; *Farfantepenaeus aztecus*.

Patterns of monthly abundance and species richness complement the results of the spectral analysis (Fig. 3.4). Fish species richness was relatively constant throughout the year but

increased through the spring to a slight peak in the summer months and decreased slightly again in fall and winter. Atlantic croaker and spot had a distinct peak in abundance between April and May, and brown shrimp abundance peaked in June. Notably, the discrete brown shrimp peak contradicted the spectral analysis, where the seasonal spectral power at 365 days was less than other times within the period. The discrepancy between the figures may be due to the relatively low detection rate of brown shrimp compared to the other species analyzed, creating greater variability in the periodogram. On the other hand, white shrimp abundance distinctly increased in July to peak in late summer and declined into fall, with a secondary peak late in the fall.

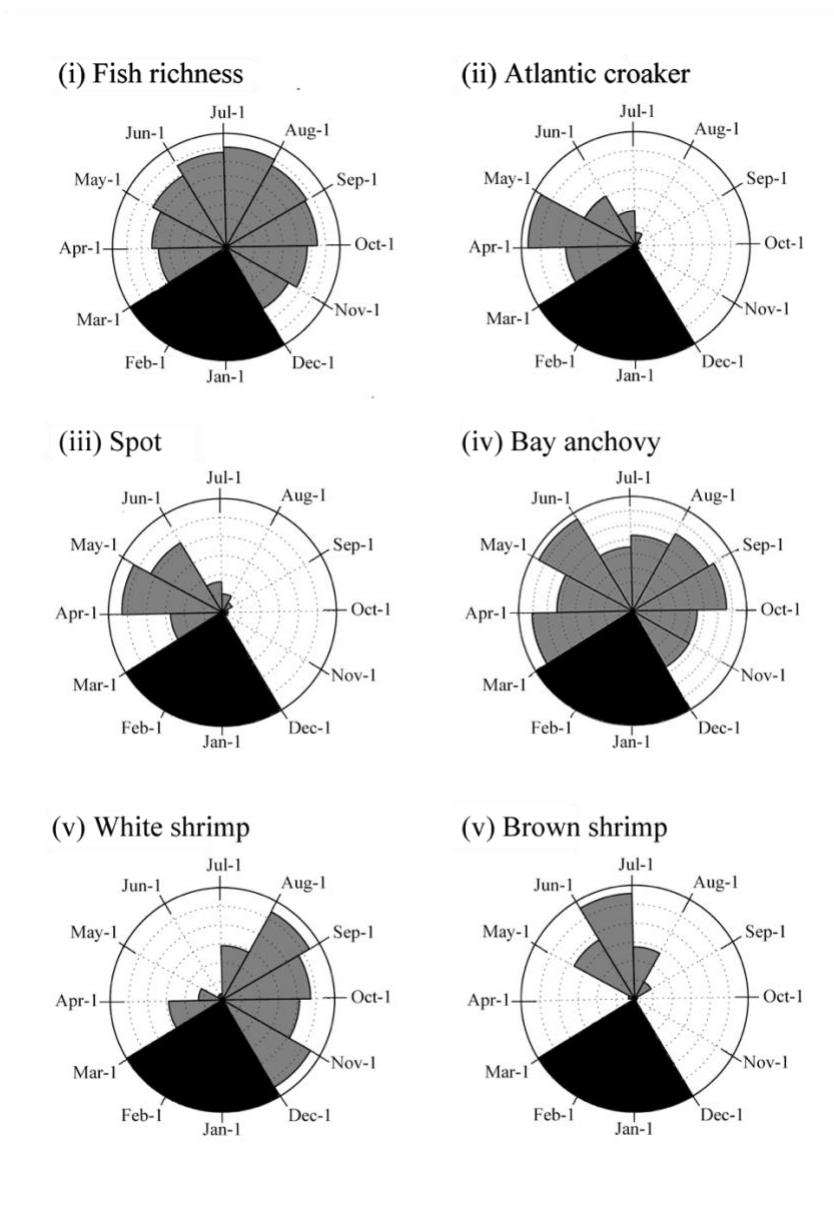


Figure 3.4: Monthly mean (gray) abundance 2007-2014 in Georgia, USA estuaries for (i) juvenile fish richness, (ii) Atlantic croaker; *Micropogonias undulatus*, (iii) Spot; *Leiostomus xanthurus*, (iv) Bay anchovy; *Anchoa mitchilli*, (v) white shrimp; *Litopenaeus setiferus*, and (vi) brown shrimp; *Farfantepenaeus aztecus*. Scale per monthly section is relative to annual richness or species abundance. Months shown in black were not included in the analysis due to limited surveys.

Interannual Trend Analysis

Results of time lag analysis showed only directional trends. Significant directional trends (m) were detected in fish species richness ($m = 0.11, p < 0.01, r^2 = 0.35$) bay anchovy ($m = 0.82, p = 0.02, r^2 = 0.19$), white shrimp ($m = 0.76, p < 0.01, r^2 = 0.44$), and brown shrimp ($m = 0.22, p < 0.01, r^2 = 0.40$). The strength of this relationship is strongest in white shrimp and weakest in bay anchovy. Atlantic croaker ($m = -0.41, p = 0.40$) and spot ($m = -0.25, p = 0.38$) indicated no linear or cyclical pattern in CPUE over the sampling period.

Regression analysis of abundance of spot ($\beta_1 = 0.42, p = 0.93, r^2 = 0.001$) and Atlantic croaker ($\beta_1 = -6.96, p = 0.48, r^2 = 0.09$) showed no trend across years (Fig. 3.5). The abundance of fish richness ($\beta_1 = -0.35, p < 0.01, r^2 = 0.75$), bay anchovy ($\beta_1 = -23.44, p < 0.01, r^2 = 0.51$), white shrimp ($\beta_1 = -10.66, p < 0.01, r^2 = 0.76$), and brown shrimp ($\beta_1 = -0.92, p < 0.01, r^2 = 0.79$) showed significant declines over the period 2007-2014. Therefore, the results of inter-annual averages and time lag analysis implied a moderately to moderately strong evidence of a decline in fish species richness, white shrimp, bay anchovy, and brown shrimp over the 8-year period of record. However, the numeric decline may not be biologically relevant.

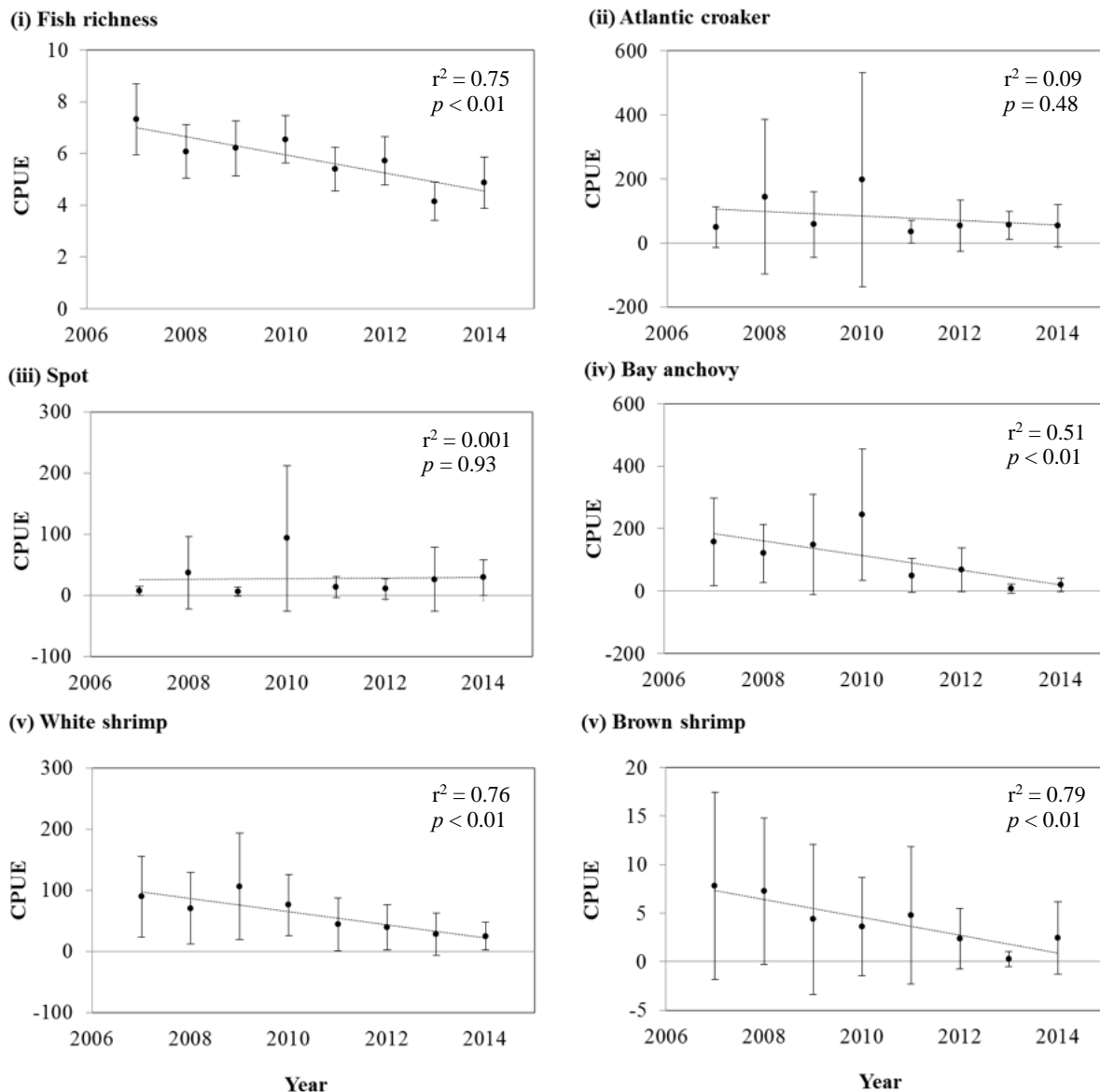


Figure 3.5: Annual average fish species richness and CPUE for individual species from Georgia USA Juvenile Trawl Survey (2007 – 2014) with standard error bars. The line represents a linear regression of CPUE and year.

GLMM Results

The generalized linear mixed models for each response variable regressed against salinity and temperature revealed significant results for some species with the random intercept models partitioned by year (Table 3.2). All models performed significantly better than the null models

with all p-values smaller than 0.001. Intercept terms for all models were significant. Only temperature was a significant fixed effect for fish species richness and spot, with a slight positive relationship. The Atlantic croaker model had a significant positive relationship with temperature and a negative relationship with salinity. A positive relationship with salinity was detected in the bay anchovy model. The white shrimp model had a positive relationship with salinity but a negative interaction coefficient between temperature and salinity. Similarly, the brown shrimp model contained a positive effect of temperature and negative interaction between temperature and salinity. For both shrimp species, this interaction would indicate that low temperature and high salinity are predicted to result in lower observed abundance than with high temperature or high salinity alone.

Table 3.2: Results of negative binomial generalized linear regression model from juvenile trawl surveys (2007-2014) in the Georgia, USA estuaries. Response variables were juvenile fish species richness, Atlantic croaker (*M. undulatus*), spot (*L. xanthurus*), bay anchovy (*A. mitchilli*), white shrimp (*L. setiferus*), and brown shrimp (*F. aztecus*). Fixed effects (β_x) were salinity (SAL) and temperature (TEM) as well as their interactions. Variation of random effects for intercept (b_j) were years (n=8) Reported for each is the Wald Z statistic (Z) and the associated p-value on 913 df. Constants and coefficients that were significant ($\alpha = 0.05$), have been highlighted

	β_x	Z	p	b_j
<i>Fish Richness</i>				
Intercept	1.36	12.70	< 0.01	0.01
TEM	0.01	2.99	< 0.01	
SAL	-1.63E-03	-0.26	0.80	
TEM*SAL	3.13E-04	1.23	0.22	
<i>Atlantic Croaker</i>				
Intercept	4.23	17.2	< 0.01	0.05
TEM	0.02	2.53	0.01	
SAL	-0.04	2.53	0.01	
TEM*SAL	3.70E-04	0.55	0.58	
<i>Spot</i>				
Intercept	2.04	5.69	< 0.01	0.08
TEM	0.06	4.39	< 0.01	
SAL	0.02	1.02	0.31	
TEM*SAL	-1.27E-03	-1.49	0.14	
<i>Bay Anchovy</i>				
Intercept	3.96	13.10	< 0.01	0.13
TEM	3.93E-05	0.00	0.99	
SAL	0.05	3.33	< 0.01	
TEM*SAL	-7.92E-04	-1.23	0.22	
<i>White Shrimp</i>				
Intercept	2.89	8.07	< 0.01	0.08
TEM	0.02	1.67	0.10	
SAL	0.11	5.95	< 0.01	
TEM*SAL	-2.69E-03	-3.67	< 0.01	
<i>Brown Shrimp</i>				
Intercept	-4.96	-4.24	< 0.01	0.13
TEM	0.23	5.44	< 0.01	
SAL	0.02	-0.32	0.75	
TEM*SAL	-2.69E-03	-3.67	< 0.01	

The results of the simple linear regression revealed significant relationships with precipitation anomalies for fish species richness and spot. All other relationships were insignificant ($p > 0.05$). The coefficient of variation for annual fish richness was positively correlated with precipitation anomalies in the fall (Fig. 3.6).

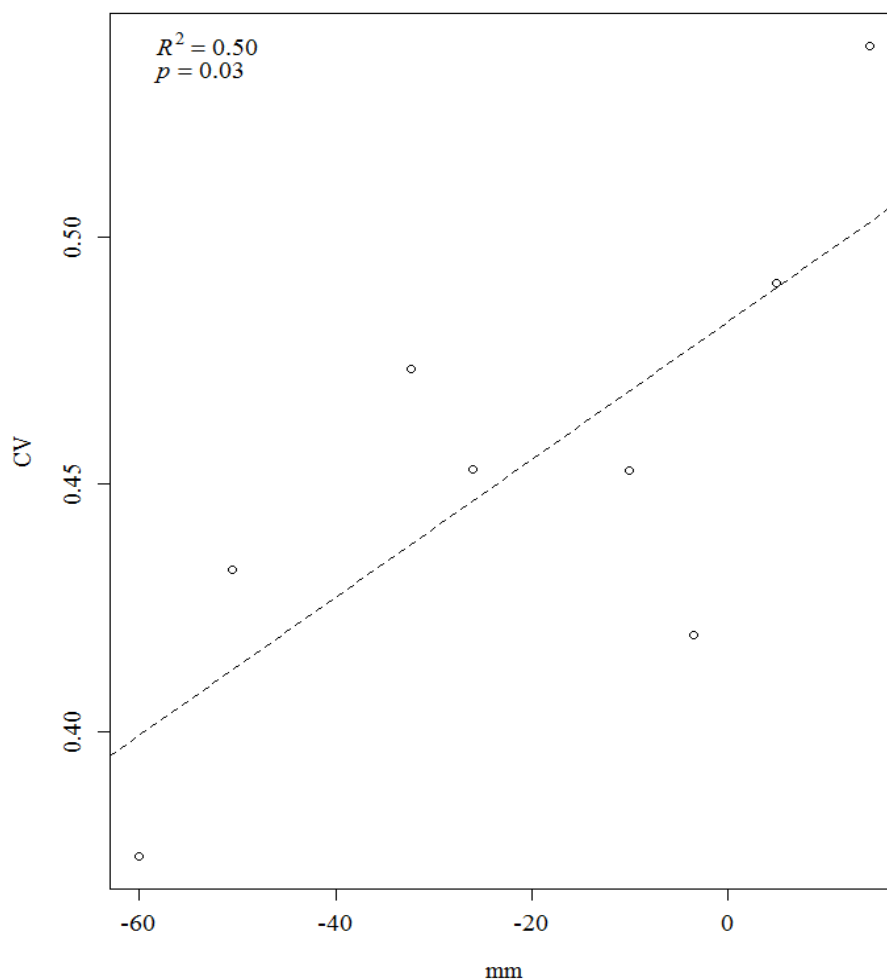


Figure 3.6: Linear regression of annual coefficient of variation (CV) for fish richness (y axis) and the difference of fall precipitation (x-axis, mm) from the 30-year normal for fall precipitation on the coast of Georgia, USA

Models for spot for previous year and winter and summer precipitation had significant positive relationships with abundance, conditional modes, or coefficient of variation (Fig 3.7).

Average annual abundance ($r^2 = 0.70$) and the conditional modes ($r^2 = 0.80$) had a moderately

strong positive relationship with from winter precipitation anomalies. The relationship of abundance and the conditional modes for the previous year's average precipitation anomalies had a weaker positive relationship ($r^2 = 0.45 - 0.50$). The annual coefficient of variation of abundance had a weak positive relationship ($r^2 = 0.52$) with summer precipitation anomalies. Like richness, there was a higher variation in abundance when summer precipitation was above normal than below normal.

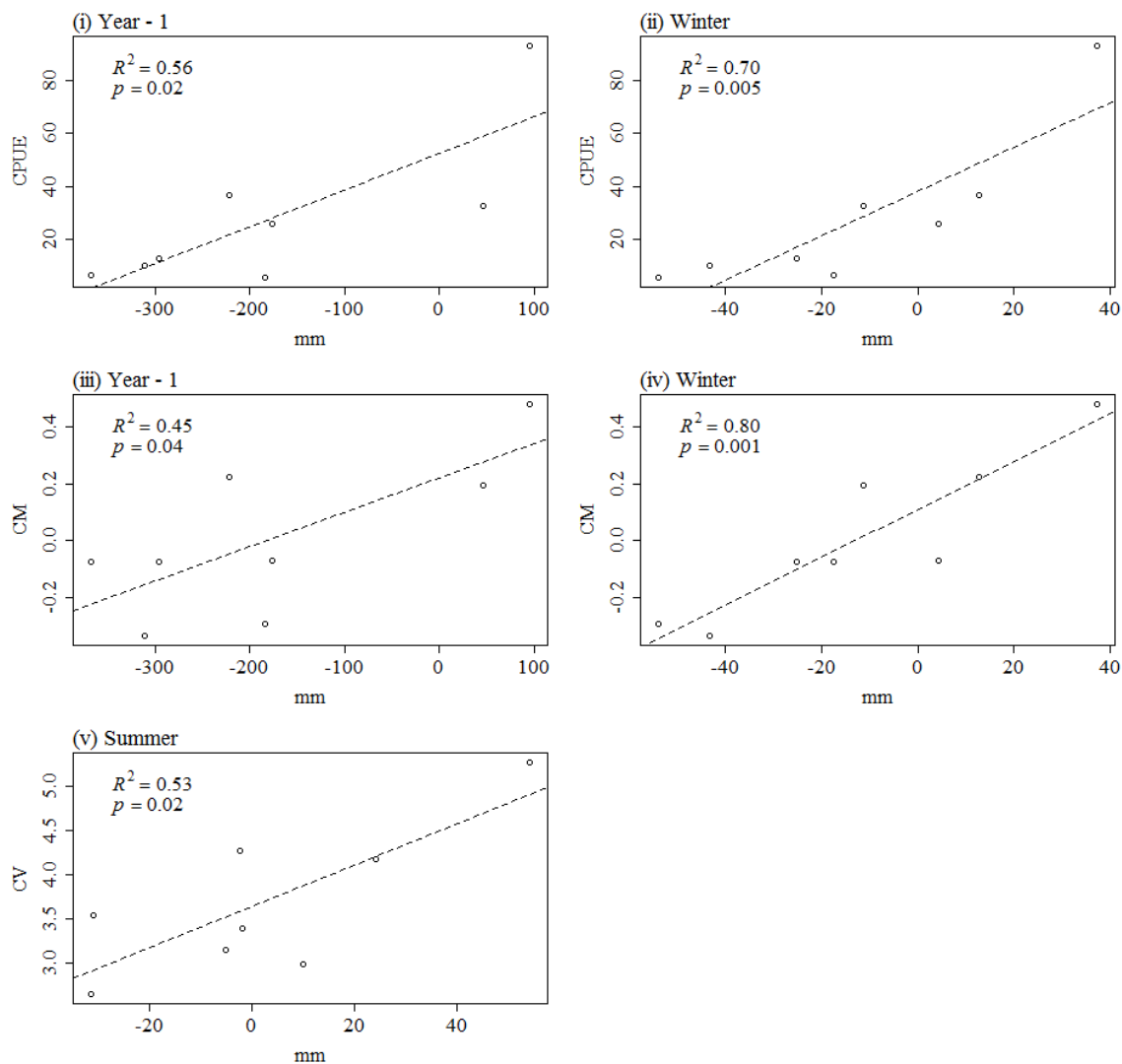


Figure 3.7: Simple linear regression analysis of (i) - (ii) CPUE, (iii)-(iv) conditional modes (CM) from a random-intercept GLMM analysis, and (v) coefficient of variation (CV) of Spot (*Leiostomus xanthurus*) against the difference in annual (2007 – 2014, $n = 8$ years) precipitation from 30-yr normal. The predictor variables of precipitation anomalies were the previous average annual differences (Year -1; (i), (iii)), average annual winter anomalies (Winter; (ii), (iv)), and average annual summer anomalies (Summer; (v))

DISCUSSION

The objectives of this research were to characterize inter-annual and seasonal variability in the context of climate change of estuarine species diversity and abundance and determine the abiotic and climatic drivers that influence variability. We accomplished this through analyses of

the variability of diversity and abundance across years and seasons, identifying annual trends and seasonal patterns, establishing relationships with abiotic variables, and comparing metrics of variability to anomalous precipitation patterns.

Our analysis showed that patterns of seasonal occurrence and abundance of species have not changed from the life history profiles written in the 20th century. Peak species richness and peak abundances of the species coincided with the predictions from past studies. Species richness was highest when productivity is highest in the summer, which was also found in North Carolina estuaries (Hettler 1989). Atlantic croaker and spot abundance in the spring predicted by the literature coincided with the pattern of abundance observed in our models (Shenker and Dean 1979; Warlen 1982; McCambridge & Alden 1984). Analyses of bay anchovy data were expected to show a protracted increasing abundance in summer through fall (NOAA, www.nodc.noaa.gov/dsdt/cwtg/catl.html accessed December 5, 2017). We observed a lack of seasonality or weak seasonality in bay anchovy abundance. The lack of seasonality might indicate that recruitment events are protracted over a long period of time with multiple pulses, biophysical changes (e.g., freezes, drought) within the system caused a shift in the annual recruitment events, naturally high variability in recruitment, or the recruitment is continuous and constant. There was an unexpected peak in the spring, which might correlate with adult ingress into the estuary for spawning. White shrimp abundance was predicted to peak in late summer into fall (Lindner & Anderson 1956) which was observed in the model of our data (Lindner & Anderson 1956). The increased catch in the fall is likely due to the seasonal migration from nursery habitat into the sounds and deeper waters. Juvenile recruitment of brown shrimp was anticipated to be highest in the early summer months, which was observed for Georgia over the study period (Larson & Van Den Avyle 1989).

The results of seasonal patterns of richness or abundance do not imply that seasonal abundance patterns are invariable with climate change, but the temporal resolution of the data may be too coarse to detect fine-scale changes. Moreover, the life history accounts rarely specified temporal patterns at scales less than a season or by month. A seasonal shift in periodicity probably would be on the order of weeks, rather than months over the course of the century, as has been observed in other climate influenced migration timing shifts (Jenni & Kéry 2003).

We did detect declining trends in species richness and abundance of bay anchovy, white shrimp, and brown shrimp over the sampling period. Although these trends were statistically significant, the strengths of the relationships raise the question of whether these are biologically significant trends. Our analyses do not suggest that abiotic factors are responsible for these observed trends. The observed patterns are possibly part of a larger cycle of peaks and troughs of abundance occurring over a longer timeframe. However, if the observed declines in common species like bay anchovy are real, further investigation into these patterns and likely causes is warranted. Trends in Atlantic croaker and spot abundance did not show directional or cyclical trends, and their abundance fluctuated widely throughout the study period. Establishing a trend over time (or lack thereof) for these species may require a longer-term dataset.

Relationships between the abundance of fishes and crustaceans and abiotic environmental variables did not always coincide with our expectations. We expected water temperature to be an essential variable for each response measured; however, salinity was the only significant variable that explained bay anchovy abundance which is in contradiction with the literature (Muncy et al. 1984). This relationship was not anticipated to be prominent for bay anchovy given their reported tolerance of a wide range of salinities. Our expectation that salinity would be important

to the diversity of fish species also was not demonstrated in the models. These findings should be considered with the knowledge that the data was not collected with this type of analysis in mind, and the limitations of the sampling technique may have produced anomalous results. The misalignment of expectations, however, may also be a limitation of the linear model. For instance, species' relationship with salinity or temperature may be non-linear. Regions of an estuary of stable (low or high) salinity regimes might have more diversity than areas with intermediate salinity with high mixing. Estuarine specialists can tolerate wide shifts in salinity of a short period, but there are fewer estuarine specialist species than marine transient species (Able & Fahay 2010). Marine transient species would find the fluctuations in salinity physiological stressful (Able & Fahay 2010). Therefore, transient estuarine species are expected to remain in areas of higher salinity, accounting for higher species richness in these areas.

The negative interactions between salinity and temperature were evident in the models for white and brown shrimp. Although this interaction is primarily noted in the literature during winter freezes, the model indicated that the relationship might exist at other extremes of salinity and temperature. High water temperatures and drought that increases salinity may also contribute to mortality.

Inter-annual variation in species richness and spot abundance could be explained by the seasonal precipitation anomalies. The increase in annual variance in species abundance in years with above normal fall precipitation may reflect the influence of rainfall events on recorded fall migrations of common species in the estuaries (Zein-Eldin & Renauld 1986). Although spot abundance did not show any linear trend within the 8-year dataset, annual CPUE, variation and modeled linear annual average were related to precipitation anomalies. Spot abundance would appear to decline following a year of below-average precipitation. The relationship with below-

average winter rainfall was strongest, indicating that the timing of rain (or lack thereof) during the year may affect spring recruitment. The change in variance in association with precipitation when projecting the trends of abundance is important. The seasonal variation may not be constant between years when comparing years of drought to years of excess or normal precipitation. A greater variance may require more sampling effort to detect trends in population data.

Understanding the temporal variation of our long-term fishery independent datasets better informs the interpretation of models trained using those datasets. Our results indicate climatic conditions, both contemporary and historical, should be considered when estimating seasonal and annual abundance or species richness. Abiotic factors do influence temporal variation, but apparently do not fully explain all the variability within models. Conservation and management practitioners use long-term datasets to model spatial habitat suitability, but seasonal and inter-annual patterns in abundance and species richness indicates a probable change to habitat suitability over time in a landscape. This research highlights the complexity of these issues and illustrates the value of multi-year, multi-season datasets to describe patterns and detect changes in response to stressors like climate change.

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CHAPTER 4
RESOLVING THE RELATIONSHIP OF MARSH LANDSCAPE STRUCTURE WITH
ESTUARINE NEKTON HABITAT IN GEORGIA, USA ³

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ABSTRACT

Estuarine ecosystems provide critical habitat for nekton species of ecological and commercial importance. These ecosystems are undergoing geographical modifications caused by climate change and other anthropogenic stressors. Managing estuarine resources requires understanding the seasonal relationships of environmental gradients, both landscape structural and biophysical, to critical nekton habitat. To address this question, we used estuarine juvenile trawl survey data to develop non-parametric models with the random forests algorithm to identify the seasonal suite of environmental gradients, both biophysical and landscape structural, that predict the distribution of fish species richness, and abundance of five nekton species of ecological or commercial importance. Model results suggest that the relationships of environmental gradients to species richness and abundance varied by species and season. Importantly, management for nekton habitat requires considering the changing seasonal habitat requirements regarding environmental gradients. Research is still needed to understand better the variability of habitat use caused the effects of surface winds, freshwater discharge, and hydrologic circulation.

INTRODUCTION

Defining essential fish habitat (EFH) for exploited species is identified as an important fisheries management tool since its inclusion in the amended Magnuson-Stevens Fisheries Conservation and Management Act (NOAA 2007). Essential fish habitat describes the habitat requirements and conditions broadly needed by a species, including geographic range and substrate necessary for reproduction and growth. From these descriptions, spatial models of EFH have been created for species of interest to aid in management efforts. However, many of these

models are prone to over- or under-predicting areas of suitable habitat, and lack the quantifiable, spatially-explicit parameters needed to forecast the future of these habitats (Rondinini et al. 2006).

Estuarine marshes provide critical nursery habitat for nekton (Rozas & Hackney 1984, Hettler et al. 1989, Halpin 2000, Webb & Kneib 2002, Able & Fahay 2010). These habitats are currently undergoing climate-induced sea level rise and drought, which reduces the total marsh spatial extent and fragments existing habitat (Craft et al. 2009). Knowledge of biophysical characteristics that limit nekton occupancy is well established, but the spatial relationships of nekton with landscape structure are less understood. The purpose of this research is to quantify how nekton occupancy relates to landscape gradients within estuarine marshes. Greater knowledge of the current relationships of estuarine nekton with landscape gradients, which are predicted to change under sea level rise (SLR), will help forecast changes to nekton occupancy.

Spatial modeling of fishes and aquatic habitat has unique challenges compared to terrestrial habitat modeling efforts. In aquatic systems with high turbidity, identifying a species' presence often requires physical capture through netting or trapping, because detection of the animal in their habitat via visual inspection (e.g., scuba diving transects or video capture) is not possible. Additionally, schooling behavior can cause overdispersion in the sampled abundance data and make estimating local population abundance difficult (Hayes et al. 2012). Catchability of a fish may change with species and the gear used to detect it (Thayer et al. 1983, Ruth & Bergen 1989). For these reasons, resolving potentially high variance in nekton data in inductive models is difficult without sample sizes that are representative of the population.

Though some *ex situ* experiments have been conducted to determine biophysical limits (Birtwell & Krunzynski 1989) in large open systems like estuaries, habitat relationships are often

based on observational data (e.g., fisheries dependent or independent collected data) because of the difficulties recreating similar habitat dynamics in a laboratory setting (Able 1999). The observational nature of habitat relationships has led to complaints of ‘data mining’ when building empirical modeling for marine or coastal systems (Anderson et al. 2001, Valavanis et al. 2008). This criticism comes from studies that attempt to use exhaustive model-fitting procedures to explore the statistical relationships between large numbers of environmental variables with species observations, often without *a priori* hypotheses based on a mechanistic understanding of species-environment relationships. This procedure can lead to overfitting of the data and create models that are ill-suited for prediction outside of the extremely localized areas where the training data were collected (Anderson et al. 2001, Rondinini et al. 2006, Valavanis et al. 2008).

Habitat suitability modeling efforts, like EFH mapping, have used deductive modeling approaches to avoid the data-intensive needs of inductive modeling, building models on literature and expert opinion rather than directly relating a spatially georeferenced species observations with local habitat (Rickers et al. 1995, Niklitschek & Secor 2005). Deductive habitat modeling is often best suited for situations where collecting adequate sample sizes of a species is not possible, either due to the extensive geographic range or the rarity of the species. Weaknesses of the deductive approach include overpredicting suitable habitat, introducing model bias through the inherent subjectivity of expert opinion, and potentially missing relationships with environmental variables not yet described in the literature (Boitani & Fuller 2000; Rondinini et al. 2005, Rondinini et al. 2006). A reasonable modeling effort would best be conducted using the best of both inductive and deductive methods. If observational data are available, modeling essential fish habitat should limit the variables to those that have an

ecological case for inclusion. This case can be made from the literature on the life history of the species.

Tidal marshes are important nursery habitat for fishes and crustaceans (Rozas & Hackney 1984, Hettler et al. 1989, Kneib 1997a, Rozas & Minello 1998, Halpin 2000, Kneib 2002, Webb & Kneib 2002, Minello et al. 2003). Structural heterogeneity, such as that found in larger tidal marsh patches, may allow for a variety of species, or similar functional groups, to occupy niches within the same patch (Atairi & Lucio 2001, Dauber et al. 2003). Studies within estuaries indicate that nekton using tidal marshes depend on structural heterogeneity, and particularly the availability of tidal creeks within marsh patches that increase available edge habitat (McIvors & Odum 1988, Webb & Kneib 2002). Whereas the mechanism behind the positive correlation with edge density and species richness is unclear, increased edge caused by exterior marsh variegations and interior marsh creek channels may provide greater access to the marsh platform during high tide events. However, there is also likely an upper limit to the variegation of exterior marsh edge and interior patch edge density, notably if the overall salt marsh cover is reduced by increased edge density.

Studies of nekton relationship with landscape structure have often focused on a local geographic scale (Peterson & Turner 1994, Kneib 1997b, Rozas & Zimmerman 2000). Large-scale studies have been focused on single species distribution or abiotic characteristics (e.g., salinity or temperature) rather than biotic structural elements of the landscape (Stoner et al. 2001, Sunblad et al. 2014). Though physical abiotic environmental variables are certainly limiting factors to species' distribution, this method excludes the potential of structural biotic interactions between species and their habitat. Moreover, these relationships, whether or at the large or small scales, have seasonal components. Some juvenile nekton use estuaries as nursery habitat only

during specific life history stages (Loneragen et al. 1989, Martinho et al. 2007, Able & Fahay 2010).

Nekton species richness provides one metric of diversity by which the influence of landscape structure on habitat selection can be measured. Richness has been used to estimate the effects of fragmentation of forested habitat (Gascon et al. 1999). However, species richness does not provide information about the ecological effects caused by a change in the number of species. The loss of a rare species may not lead to a state change. Solan et al. (2004) suggests that the loss of an abundant species would more critically affect overall ecosystem function. Therefore, abundant lower-level consumers (e.g., critical prey species) should be considered in unison with models of species richness.

The objective of this study was to quantify the spatially explicit relationships of nekton occupancy with landscape gradients, and how these relationships vary by season. This study is the first to evaluate nekton richness and abundance with coastal landscape structure at a broad scale, thus allowing the development of hypotheses about how estuarine nekton communities might respond to changes in landscape structure due to sea level rise.

Pursuant to this objective, we used fishery-independent data to fit models with random forests procedures. The model responses of interest include juvenile fish species richness, and the catch-per-unit-effort (CPUE) of Atlantic croaker (*Micropogonius undulatus*), spot (*Leiostomus xanthurus*), bay anchovy (*Anchoa mitchilli*), white shrimp (*Litopenaeus setiferus*), and brown shrimp (*Farfantepenaeus aztecus*). These individual species were selected to represent changes in assemblages because of their high abundance in the estuaries, thus having high ecological or economic importance. A suite of 10 environmental gradients (eight landscape

gradients and two physical abiotic gradients) were used as predictor variables. As essential habitat changes with seasons, we modeled seasons separately.

STUDY AREA

Coastal Georgia's estuaries contain approximately a half million acres of tidal marsh, roughly a quarter of the salt marsh for the eastern seaboard of the United States. Georgia's mixed semi-diurnal tide range (1.8-2.4 m) is generally higher than other areas in the South Atlantic Bight. Sediments are mostly comprised of clay, silt, and sand, which create highly turbid waters.

The primary riverine systems within the extent of the study area included the Savannah, Ogeechee, Altamaha, and Satilla rivers, which comprise the Wassaw, Ossabaw, Altamaha, and St. Andrews sounds, respectively (Fig. 4.1). Wassaw Sound had the least direct riverine influence, with only tributaries of the Savannah River to the north running into the sound (Turner et al. 2009). Salinity is highly variable throughout the estuary, dependent on tides, river discharge, and rain events. Salinity at the mouth of the Altamaha River can range from 35 psu to near fresh within a period of a few weeks. Water temperatures rarely drop below freezing (0°C) and are often $> 26^{\circ}\text{C}$ in the summer and early fall months. Although subtidal zones are generally well mixed, dissolved oxygen may drop in pooled waters on the marsh surface (intertidal zone) during flood tide.

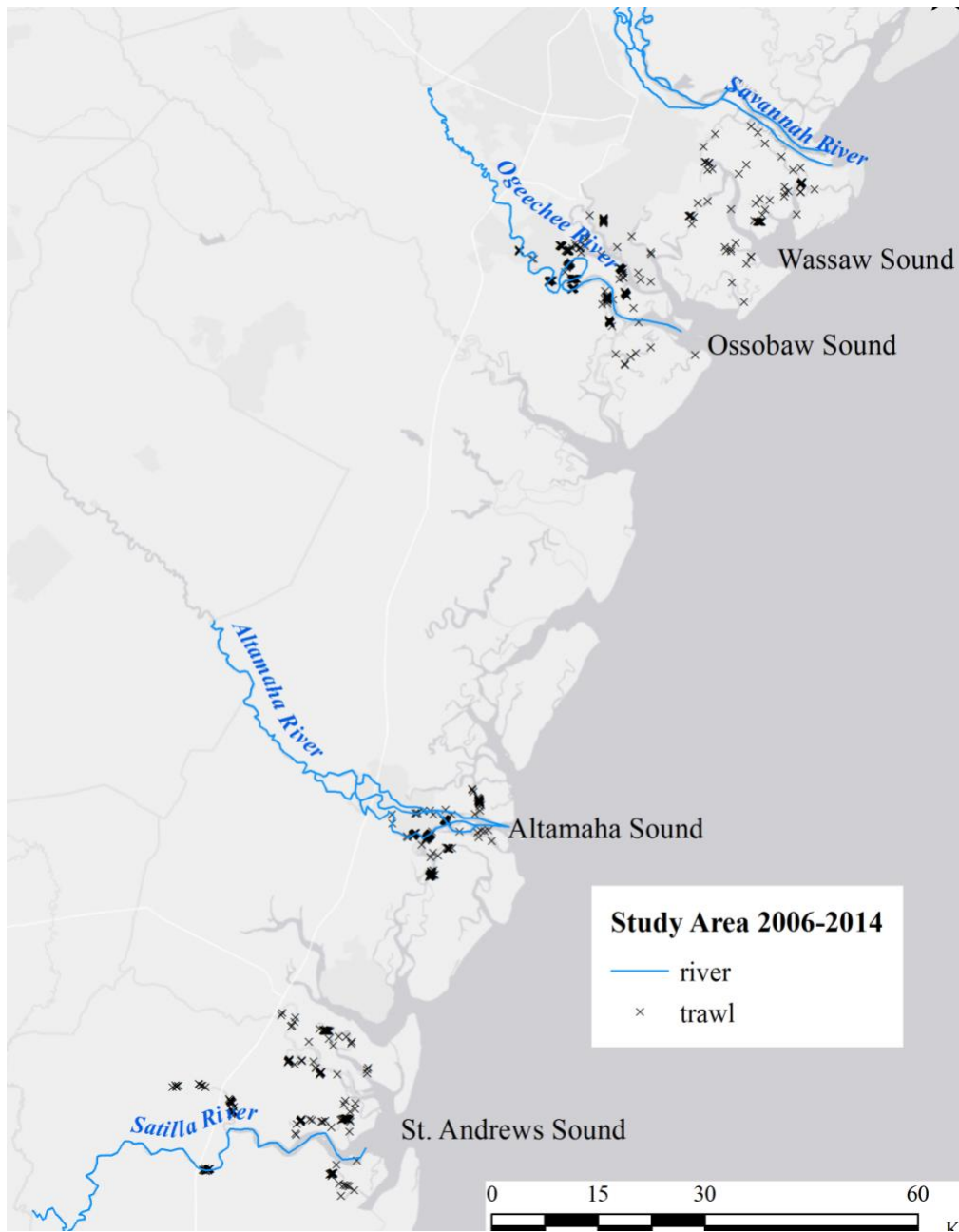


Figure 4.1: Study area in coastal Georgia, USA estuaries, highlighting major riverine systems their associated sounds. Georgia Department of Natural Resources (2006-2014). Sites surveyed by trawls for juvenile fishes and crustaceans are denoted by 'x'.

Vegetation zones are dictated by elevation, salinity regimes, and periodicity of flooding.

Smooth cordgrass (*Spartina alterniflora*) dominates regularly flooded marsh vegetation where

salinities are higher (15 – 31 psu). In higher elevation marshes (irregularly flooded, sometimes brackish conditions), black needle-rush (*Juncus roemerianus*) and sea oxeye daisy (*B. frutescens*) form dense monotypic stands. At fresh to brackish salinities, *S. cynosuroides* replaces *S. alterniflora*. Tidal marsh patches are channelized by small intertidal creeks that drain near completely at mean low tide.

METHODS

Sampling for fishes and crustaceans

We obtained data on the occurrence and abundance of juvenile fishes and crustaceans from trawl surveys conducted by personnel from Georgia Department of Natural Resources – Coastal Resources Division (GADNR) throughout the estuaries and sounds of coastal Georgia (Fig. 1). Sites were randomly selected from a grid of marsh coverage gradients in the Wassaw, Ossabaw, Altamaha, and St. Andrew estuaries. From 2006-2010, sites were sampled once a month from March – November, and in 2011 – 2014 sampling was conducted monthly. Trawls were conducted using a balloon-modified otter trawl that was 6.1 m in length with 9.5 mm mesh. Trawls were conducted at low tide for on average for 5 minutes at an average speed of 2 kt for a length of approximately 500 m. Fish and crustaceans were sorted to the lowest taxonomic level possible. Beginning and end GPS coordinates, bottom salinity, water temperature, and dissolved oxygen values for each trawl were provided with the data.

For the sake of consistency, we consider samples taken only spring (March - May), summer (June - August), and fall (September - November). Temporal variability of abundance was determined using the Marine Geospatial Ecology Tools (Roberts et al. 2010, Chapter 3). Only seasons when species abundance was observed to be increasing or have peak abundance

values were modeled for an individual species (Chapter 3). Catch-per-unit-effort (CPUE) was used as an index of abundance. As some trawl sites overlapped among years, the centroid point of each trawl was buffered by 500 m (the average length of the area sampled) to increase the independence of samples. All overlapping buffers were dissolved into a single polygon, and each point that overlapped with the dissolved buffer was spatially joined. We treated the points within the dissolved polygon as spatially dependent, and the spatial join associated a mean value to the polygon for all sample points. Mean values of CPUE and species richness were calculated from the combined samples within seasons.

Environmental Gradients

We identified a set of environmental gradients (explanatory variables) shown through a literature review to be potentially important for explaining patterns of occupancy and abundance for estuarine nekton (Table 4.1). Eight explanatory variables described landscape structure, and two explained local abiotic physical variables. Dissolved oxygen was not included given the abundance of missing values and questionable records of 0 mg/l. The major sounds were included as a categorical variable to identify the latitudinal geographic position as well as the potential hydrologic and biotic influences of the associated riverine systems.

Table 4.1: Environmental gradient data used as explanatory variables, their associated source, and literature justification for expected relationship to estuarine juvenile nekton in Georgia, USA

Variable	Abbreviation	Unit/500 m	Original Source	Literature
Regularly Flooded Marsh	Reg	Proportion	2007 National Wetlands Inventory	Hettler, W.F. 1989
Irregularly Flooded Marsh	Irreg	Proportion	2007 National Wetlands Inventory	Webb & Kneib 2002; Rozas & Hackney 1984
Subtidal - Marsh Edge Density	ExtE	Proportion	2007 National Wetlands Inventory	Peterson & Turner 1994
Intertidal - Marsh Edge Density	IntE	Proportion	2010 LiDAR Imagery	McIvors & Odum 1988; Webb & Kneib 2002
Distance to Mouth of Estuary	Dist	m	2007 National Wetlands Inventory	Able & Fahay 2010
Mean Marsh Patch Area	Ptch	ha	2007 National Wetlands Inventory	Rozas & Minello 1998
Sound	Snd	Categorical	NOAA Nautical Charts	Loneragan 1999
Landscape Diversity	Div	Shannon-Wiener Index	2007 National Wetlands Inventory	Atauri & Lucio 2001; Daubner et al. 2003
Salinity	Sal	psu	GADNR Juvenile Trawl Survey	Rozas & Hackney 1984; Martino & Able 2003
Water Temperature	Temp	°C	GADNR Juvenile Trawl Survey	Williams 1984;

Derivatives of initial conditions spatial vegetation datasets were generated from the Sea Level Affecting Marshes Model (SLAMM) raster dataset of contemporary land cover conditions (Craft et al. 2009, Clough et al. 2012). Initial conditions were created using the 2007 National Wetlands Inventory (NWI) dataset (Clough et al. 2012).

Irregular and regularly flooded marsh were each extracted from the NWI dataset and converted to binary raster data layers. Distance to the mouth of each estuary was calculated by using NWI shapefiles to determine the boundary between estuary and ocean. A boundary line was extracted where NWI delineated the estuarine waters and open ocean and converted to raster data. A cost surface raster data layer was created for all estuarine bodies of water, assigning a value of one to each pixel classified as estuarine water. Then, a least-cost distance analysis was performed in ArcGIS 10.2 to assign a distance in meters for each pixel of estuarine water from the NWI delineated boundary between the ocean waters and estuarine waters.

The subtidal-marsh edge density was calculated by measuring the density of marsh edge against subtidal estuarine waters. First, irregular and regularly flooded marsh-to-water binary layer was created. An edge layer was defined where any pixel of water (pixel value = 0) and of marsh (pixel value = 1) shared a border using EdgeTools (Prebyl 2014). The resulting assigned a one to pixels that were found at the marsh-water edge interface and a zero to all other pixels.

The 28 m resolution of the initial conditions land-cover data was adequate for describing edge density on the exterior of marsh patches of subtidal waters. However, because of their fine-scale patterns, small intertidal creeks were not represented in the coarser landcover datasets. The 2010 Coastal Light Detection and Ranging (LiDAR) elevation data with corrections (Hladik & Alber 2012) were used to create raster data layer of intertidal creeks within marsh patches. Through previous field observations of high-resolution aerial imagery of Georgia salt marsh (4 cm), we identified > 1.5 m as the threshold width for defining tidal creek. EdgeTools were used to calculate intertidal-marsh edge in the same manner as the subtidal-marsh edge.

Landscape diversity and mean marsh patch area were calculated in FRAGSTATS 4 (McGarigal et al. 2012) with the 2007 National Wetland Inventory dataset. A Shannon-Wiener

Index value was calculated for each map 28 m pixel with a 500 m radius moving window analysis, thus describing landscape structure in the area likely covered by each 500 m trawl. Mean marsh patch area was similarly measured with a 500 m radius moving window, amalgamating both irregularly and regularly flooded marsh types in the measurement.

All other environmental variables were processed in ArcGIS 10.2 with a 500 m moving window analysis (focal statistics) to create a mean value for each pixel summarizing proportion of regularly flooded marsh, irregularly flooded marsh, subtidal-marsh edge density, intertidal-marsh edge density, and mean distance to the mouth of the estuary.

Analyses and Model Fitting

Models were fit using random forests (RF), a machine learning algorithm based on classification and regression trees (CART). CART functions by separating observations at a node based on splitting rules that are determined by the explanatory variables or features at that node. Trees are grown from parent nodes in branches to terminal leaves at which predictions can be made. Hypothetically, groups of observations could be split until there was only a single observation at each leaf. Therefore, CART is prone to overfitting data, resulting and results in models with poor predictive power (Cutler et al. 2007).

The RF algorithm resolves the problem of overfitting by creating an arbitrary number of simple trees (referred to as an ensemble) and randomly bootstrapping explanatory variables rather than response variables to grow each tree for the same observations (Breiman 2001, Cutler et al. 2007). Regression tree ensembles are averaged over all trees to determine the final relationships. The RF algorithm has superior accuracy in ecological modeling applications, particularly where complex nonlinear relationships are expected. The model results are robust even when outliers are present and can tolerate collinearity between explanatory variables

(Cutler et al. 2007). Outputs from RF include measures of variable importance and the ability to explore the contributions of each environmental variable by evaluating partial dependence plots.

Random forests modeling was chosen over other ecological modeling methods (e.g., linear regression) because of the complex nonlinear relationships expected between explanatory and response variables, and the natural collinearity between environmental explanatory variables. Response variables included species richness and the CPUE of individual species. Individual species CPUE data were square root transformed to account for overdispersion. Models were fit using all environmental explanatory variables against the response variables and were run for 100 iterations (5000 trees, one variable tried at each node) in R 3.3.2 running the randomForest package (Liaw & Wiener 2002). Resulting trees contained only the variables that received the most votes. Variable selection was performed by calculating the variables that were included in at least 75% of the averaged trees over the 100 iterations. These variables were included in the final model. To generate a final model, RF was run for 500 iterations, withholding a random 2% of response variable samples for cross-validation. Mean square error (MSE) and the coefficient of determination (r^2) were used to assess model fit. In RF regression, mean square error is calculated by assessing the out-of-bag data error rate. Variable importance was measured by the percent increase in MSE when removed from the model, and partial dependence plots were generated in the R package ForestFloor.

Partial dependence plots represent how changing the value of the predictor variable changes the model predictions or the marginal effect of that predictor variable alone with all other predictors at each point held at an average value. Therefore, interpretation of partial dependence plots is similar to that of linear and logistic regression prediction – response variable plots. The y-axis is on a logit scale and is the measure of contribution to the model's predictions

with changes to the gradient of the predictor variable (x-axis). Therefore, the y-axis should not be interpreted as the direct predicted response. Instead, the shape of the relationship of the predictor variable gradient and its contribution to response is considered in the analysis.

RESULTS

In total, 1,348 trawls were conducted through the sampling period. Fitted models for each response variable differed across seasons and species (Table 4.2). The variables of proportion of regularly flooded marshes and salinity were most often selected as an explanatory variable. Notably, landscape diversity was only included once among important variable among any of the final fitted models.

Table 4.2: Results from random forests models by season (spring: Spr, summer: Sum and Fall) for juvenile fish species richness (Richness), and abundance of Atlantic croaker (*Micropogonius undulatus*), spot (*Leiostomus xanthurus*), bay anchovy (*Anchoa mitchilli*), white shrimp (*Litopenaeus setiferus*), and brown shrimp (*Farfantepenaeus aztecus*) collected in Georgia, USA estuaries from 2006 - 2014.

Response	Predictors	MSE ^a	r ² ^b	n ^c	n-500 ^d
Richness-Spr	Sal ¹ , Reg ² , Dist ³ , IntE ⁴ , Div ⁵ , Snd ⁶ , Ptch ⁷	4.12	0.17	349	53
Richness-Sum	Sal, Reg, Irreg ⁸ , Dist, IntE, ExtE ⁹ , Snd	4.90	0.45	406	65
Richness-Fall	Sal, Temp ¹⁰ , Reg, Dist, ExtE, Snd	3.90	0.23	403	67
Atl. croaker-Spr	Sal, Temp, Irreg, Dist, IntE, Snd, Ptch	21.42	0.31	349	53
Spot-Spr	Sal, Temp, Reg, Irreg, Dist, ExtE, Snd	10.23	0.10	349	53
Bay anchovy-Spr	Sal, Reg, IntE	41.57	0.35	349	53
Bay anchovy-Sum	Sal, Temp, Reg, Irreg, ExtE, Snd, PTch	54.77	0.16	406	65
White shrimp-Sum	Temp, Reg, Dist	14.41	0.31	406	65
White shrimp-Fall	Sal, Reg, Irreg, Dist, IntE, ExtE, Snd	16.52	0.27	403	67
Brown shrimp-Spr	Sal, Temp, Irreg, Dist, IntE, ExtE, Snd	0.25	0.06	349	53
Brown shrimp-Sum	Reg, Irreg, Dist, IntE, Snd, Ptch	2.44	0.06	406	65

Notes. a: mean square error calculated by randomForest; b: coefficient of determination calculated by randomForest; c: total sample size; d: consolidated sample size after samples were averaged into 500 meter buffers 1: salinity; 2: proportion regularly flooded marsh; 3: distance to mouth of estuary; 4: proportion intertidal-marsh edge density; 5: Shannon-Wiener landscape diversity 6: sound; 7: average marsh patch are; 8: proportion irregularly flooded marsh; 9: proportion subtidal-marsh edge density; 10: water temperature

Fish Species Richness

The model fit for fish species richness was best during the summer season ($r^2 = 0.45$), which had the highest values of species richness (0 – 22 fish species; Table 4.2). The variables of salinity, proportion regularly flooded marsh, distance to the mouth of the estuary, and sound were included in models for all seasons indicating that these landscape gradients are consistently important predictors of species richness relative to other environmental variables. The relative importance of these variables measured by the percent increase in mean squared error (IncMSE) if left out of the model differed between seasons (Fig. 4.2). For instance, the models identified regularly flooded marsh as an important variable in all three seasons, but it ranked highest only in spring (IncMSE = 15%; Fig. 4.2). Distance to the mouth of the estuary was of high importance in spring (IncMSE = 10%) and summer (IncMSE = 14%), but most important in the fall (IncMSE = 20%). Proportion intertidal-marsh edge density was included in the spring (IncMSE = 8%) and summer models (IncMSE = 4%), and proportion subtidal-marsh edge density was included in summer (IncMSE = 14%) and fall (IncMSE = 8%). Water temperature was only important in the fall (IncMSE = 10%), and average patch area in spring. (IncMSE = 20%).

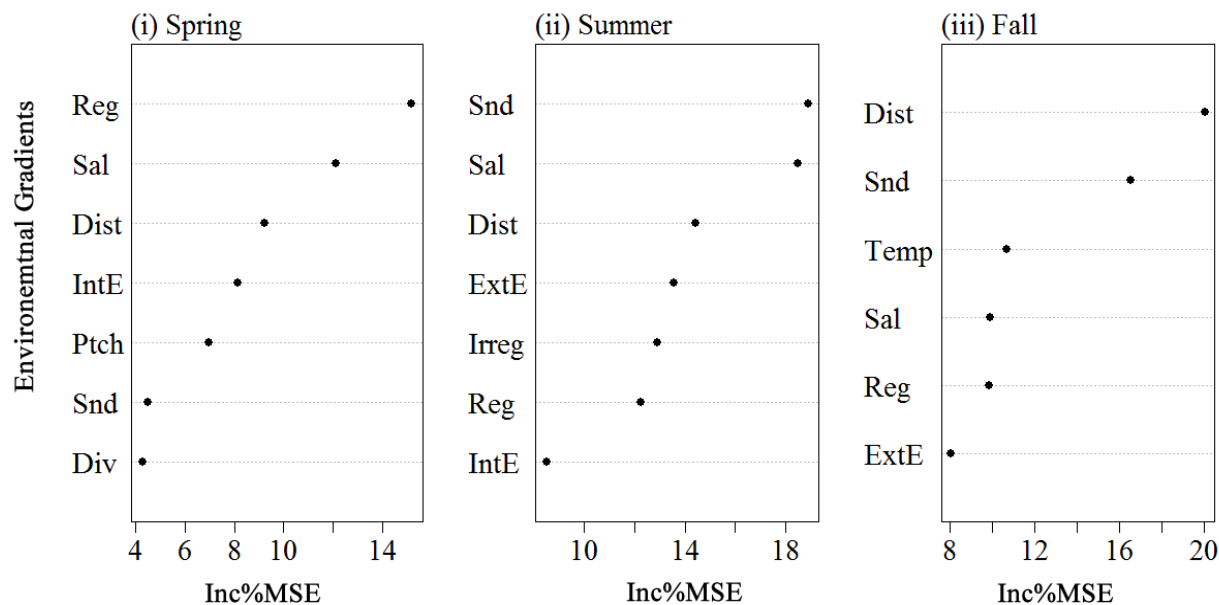


Figure 4.2: Variable importance plots for models of fish species richness (percent increase in mean square error when variables are excluded) generated from data collected in the Georgia, USA estuaries (2006 – 2014) using random forests for three seasons (spring: March-May, summer: June-August, and fall: September-November). Variables are Sal: salinity, Temp: water temperature, Reg: proportion regularly flooded marsh, Irreg: proportion irregularly flooded marsh, Dist: distance to mouth of estuary, IntE: proportion intertidal-marsh edge density, ExtE: proportion subtidal-marsh edge density, Div: landscape habitat diversity, Snd: sounds, and Ptch: mean marsh patch area.

Partial dependence plots for the model developed for fish species richness showed that regularly flooded marsh was consistently correlated in a positive near-linear fashion with predictions of species richness throughout seasons (Figs. 4.3 – 4.5). However, the threshold at which contribution to species richness predictions goes from negative to positive changed among seasons. During the summer months, species richness is predicted to increase where the proportion of regular salt marsh is greater than 0.03, a threshold that is lower than either spring or fall.

Models showed that the distance to the mouth of the estuary gradient predicted species richness decreases in areas farthest upstream and areas closest to the mouth of the estuary in the

spring and summer. In the fall, though, predictive species richness is highest at the mouth of the estuary.

Salinity also was generally positively associated with species richness, though the thresholds of negative to positive contributions also changed between seasons. Contribution to species richness goes from negative to positive from 10 – 15 psu in the spring, and 25 – 30 psu in the summer, and at salinities greater than 30 psu in the fall (Fig. 4.3 – 4.5) Interestingly, Wassaw Sound was consistently a positive contributing factor, and Ossabaw Sound was consistently a negative contributing factor. The summer models also showed a positive contribution to predicted species richness with increasing values of intertidal-marsh edge density ($\hat{p} > 0.2$) and subtidal-marsh edge gradients ($\hat{p} > 0.07$) in the summer.

Some variables only contributed to the model prediction in a single season. Landscape diversity was positive only at the lowest levels of diversity (0.0 – 0.20 H) before falling into a slightly negative at all higher values. Water temperature in the fall has a negative correlation with temperatures below 24°C and a positive correlation above this value, indicating the falling temperatures of the season are related to a reduction of species richness. The relationships to predictions of species richness were relatively weak for the irregularly flooded marsh and the mean marsh patch area gradients.

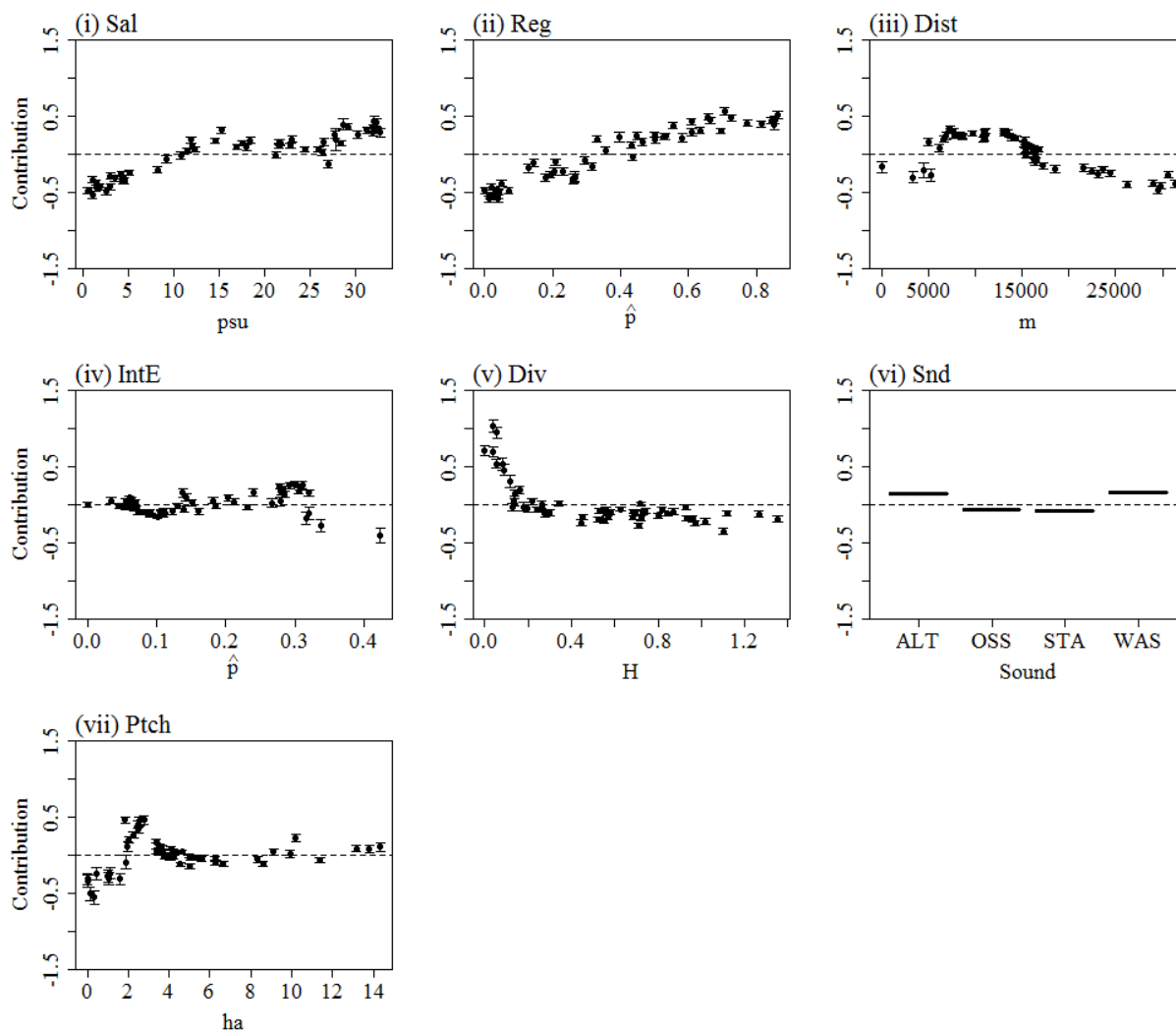


Figure 4.3: Spring (March-May) fish richness partial dependence plots generated through a random forest algorithm from juvenile trawl data for Georgia, USA (2006-2014). Variables are (i) Sal: salinity, (ii) Reg: proportion regularly flooded marsh, (iii) Dist: distance to mouth of estuary, (iv) IntE: proportion intertidal-marsh edge density, (v) Div: landscape habitat diversity (Shannon's H), (vi) Snd: sounds (ALT=Altamaha, Oss=Ossabaw, STA=St. Andrew, WAS=Wassaw), and (vii) Ptch: mean marsh patch area.

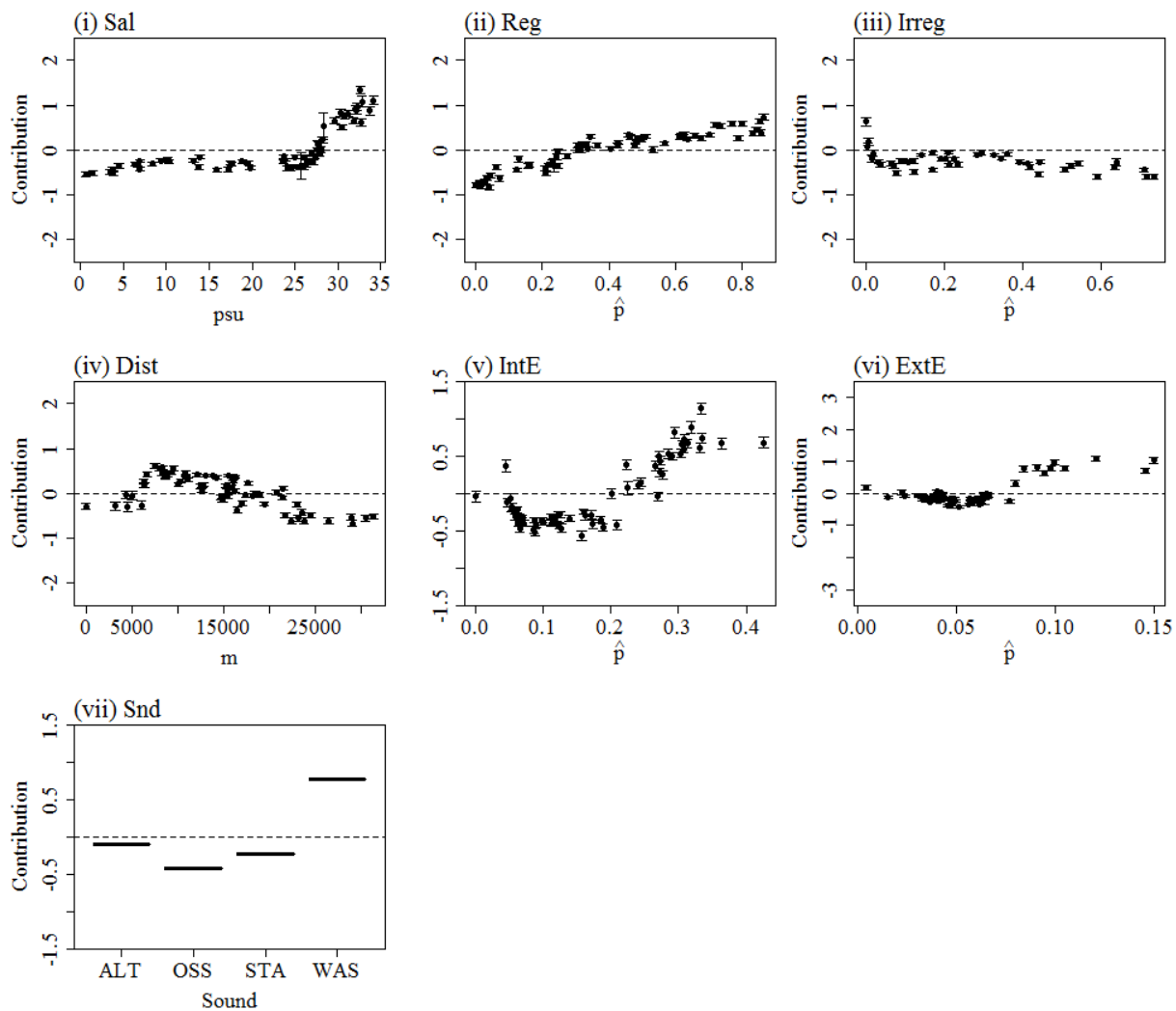


Figure 4.4: Summer (June – August) fish richness partial dependence plots generated through a random forest algorithm from juvenile trawl data for Georgia, USA (2006-2014). Variables are (i) Sal: salinity, (ii) Reg: proportion regularly flooded marsh, (iii) Irreg: proportion irregularly flooded marsh, (iv) Dist: distance to mouth of estuary, (v) IntE: proportion intertidal-marsh edge density, (vi) ExtE: proportion subtidal-marsh edge density, (vii) Snd: sounds (Alt=Altamaha, Oss=Ossabaw, STA=St. Andrew, WAS=Wassaw).

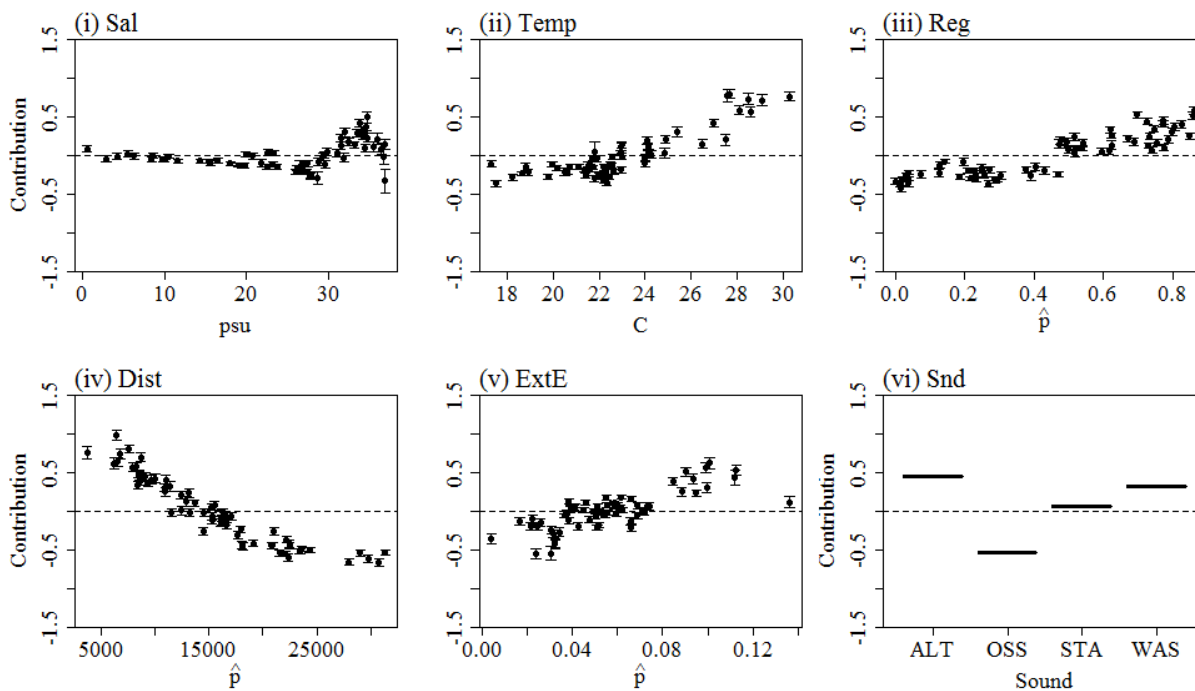


Figure 4.5: Fall (September – November) fish richness partial dependence plots generated through a random forest algorithm from juvenile trawl data for Georgia, USA (2006-2014). Variables are (i) Sal: salinity, (ii) Temp: water temperature, (iii) Reg: proportion regularly flooded marsh, (iv) Dist: distance to mouth of estuary, (v) ExtE: proportion subtidal-marsh edge density, and (vi) Snd: sounds (Alt=Altamaha, Oss=Ossabaw, STA=St. Andrew, WAS=Wassaw).

Atlantic croaker

The spring model ($r^2 = 0.31$; Table 4.2) for Atlantic croaker ($n = 68,607$ fish) identified seven predictor variables, and salinity had the greatest importance to the predictive model (IncMSE = 19%; Fig. 4.6). The contribution of model biophysical variables for the Atlantic croaker trended to higher abundance at cooler water temperatures in oligohaline to mesohaline areas (Fig. 4.7). Salinity values between 0 – 20 psu contributed positively to the abundance of Atlantic croaker. Values over 20 psu were negatively related to abundance. A narrow range of

water temperatures from 19 - 21°C contributed positively to abundance while higher temperatures measured in the spring (22 – 26°C) were weakly negative in their contributions.

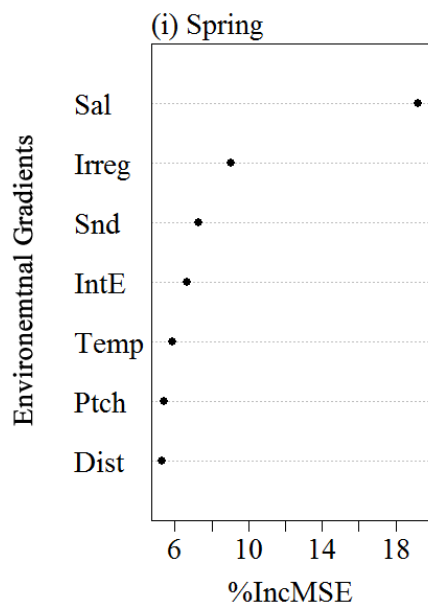


Figure 4.6: Atlantic croaker (*Micropogonius undulatus*) variable importance plots (percent increase in mean square error when variables are excluded) generated from a random forest algorithm taken from catch data from juvenile trawl surveys in Georgia, USA (2006-2014) for spring: (March-May). Variables are Sal: salinity, Temp: water temperature, Irreg: proportion irregularly flooded marsh, Dist: distance to mouth of estuary, IntE: proportion intertidal-marsh edge density, Snd: sounds, and Ptch: mean marsh patch area.

The predicted relationship of Atlantic croaker abundance with landscape structural gradients was strongly positive with increased proportion irregular flooded marsh ($\hat{p} > 0.1$) and increased mean patch area (> 2 ha; Fig 4.7). Additionally, there was a strong positive relationship with Atlantic croaker abundance as distances to the mouth of the area increased ($> 15,000$ m). The two sounds with the largest riverine systems, Altamaha and Ossabaw, related to increasing abundance values.

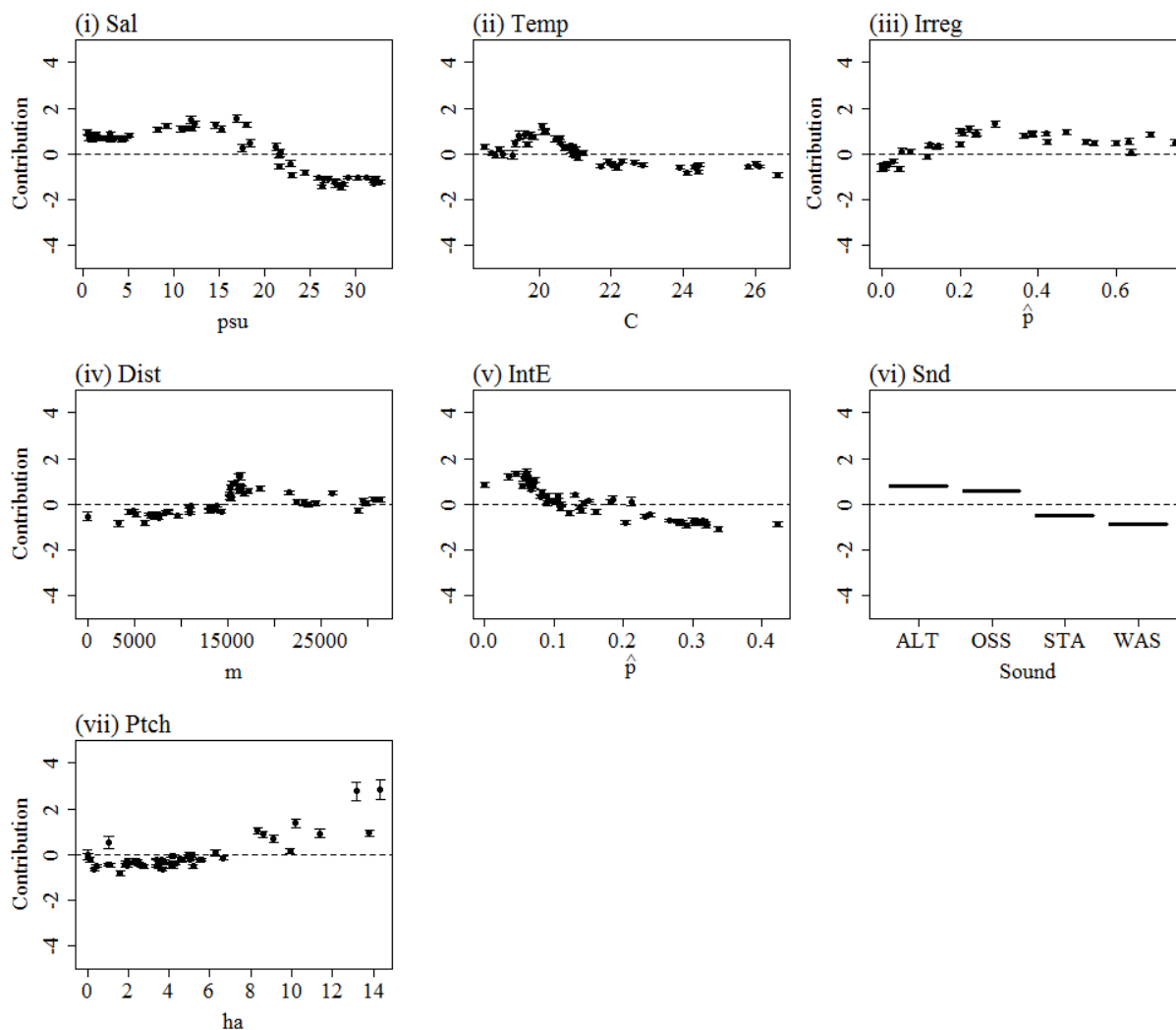


Figure 4.7: Spring (March-May) Atlantic croaker (*Micropogonius undulatus*) partial dependence plots generated through a random forest algorithm from juvenile trawl data for Georgia, USA (2006-2014). Variables are (i) Sal: salinity, (ii) Temp: water temperature, (iii) Irreg: proportion irregularly flooded marsh, (iv) Dist: distance to mouth of estuary, (v) IntE: proportion intertidal-marsh edge density, (vi) Snd: sounds (ALT=Altamaha, Oss=Ossabaw, STA=St. Andrew, WAS=Wassaw), and (x) Ptch: mean marsh patch area.

Spot

The developed model for spring spot abundance (n=21,613 fish) identified seven landscape gradient variables of importance, two physical and five landscape structure variables (Fig. 4.8). Of the fish species, the spot's fitted model described the least amount of variability

(10%) in observed abundance (Table 4.2). Sound was the variable identified as the most important (IncMSE =11%), and proportion subtidal-marsh edge density was least important (IncMSE < 2%)

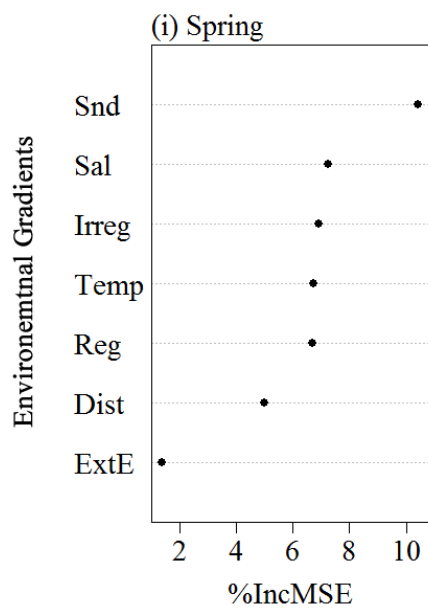


Figure 4.8: Spot (*Leiostomus xanthurus*) variable importance plot (percent increase in mean square error when variables are excluded) generated from a random forest algorithm taken from catch data from juvenile trawl surveys in Georgia, USA (2006-2014) for spring: (March-May). Variables are Sal: salinity, Temp: water temperature, Reg: proportion regularly flooded marsh, Irreg: proportion irregularly flooded marsh, Dist: distance to mouth of estuary, ExtE: proportion subtidal-marsh edge density, and Snd: sounds.

Like Atlantic croaker, spot predicted abundance was higher in areas of lower salinity and temperatures greater than 20°C (Fig 4.9). Salinities from 0 - 15 psu positively contributed to spot abundance, while salinities greater than 15 psu were weakly negative. Temperatures below 20°C were negative, before increasing rapidly in their contribution. At values greater than 22°C the contribution of water temperature is near zero to weakly positive (< 1) contribution (Fig 4.9).

Landscape structural variables indicated a positive relationship with a matrix of marshes with some outer edge complexity ($\hat{p} > 0.04$) in the middle portions of estuaries (10,000 – 20,000

m) that are associated with large or central riverine systems (Altamaha and Ossabaw sound). The patterns of contribution with the predictor of sound were the same as with Atlantic croaker.

However, most of the relationships with the landscape structural gradients were weak.

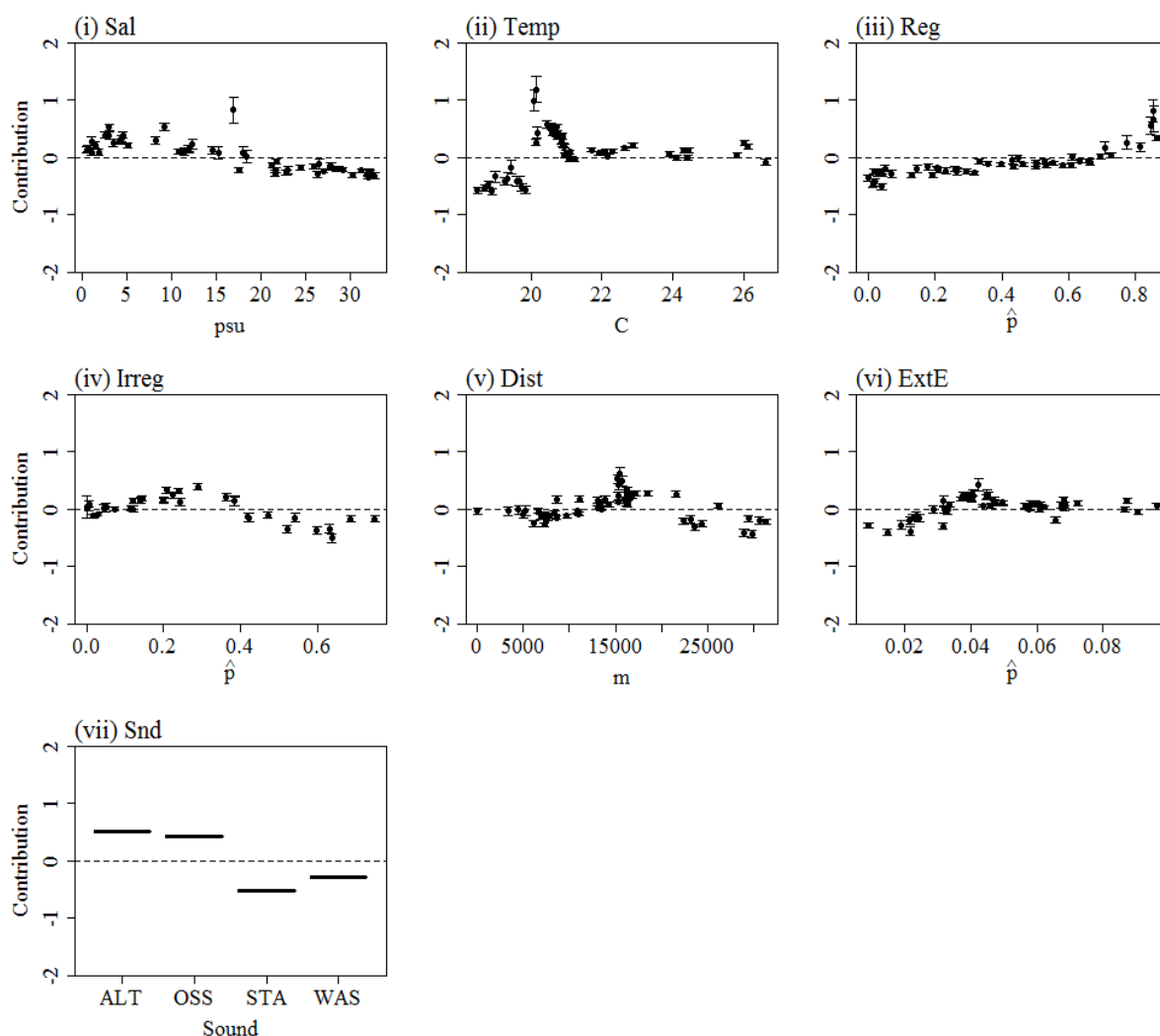


Figure 4.9: Spring spot (*Leiostomus xanthurus*) partial dependence plots generated through a random forest algorithm from juvenile trawl data for Georgia, USA (2006-2014). Variables are (i) Sal: salinity, (ii) Temp: water temperature, (iii) Reg: proportion regularly flooded marsh, (iv) Irreg: proportion irregularly flooded marsh, (v) Dist: distance to mouth of estuary, (vi) ExtE: proportion subtidal-marsh edge density, and (vii) Snd: sounds (Alt=Altamaha, Oss=Ossabaw, STA=St. Andrew, WAS=Wassaw)

Bay anchovy

Only spring ($n = 47,455$ fish) and summer ($n = 50,437$ fish) were modeled for bay anchovy abundance (Fig. 4.10). Spring, when annual recruitment is highest, also produced the model that described the most variability in the data ($r^2 = 35\%$; Table 4.2) with only three contributing variables. The summer model described 16% of the variability with seven contributing variables. Proportion regularly flooded marsh was the most important in the spring (IncMSE = 22%) and remained relatively high importance in the summer. Water temperature was by far the most important variable in the summer model (IncMSE = 12%).

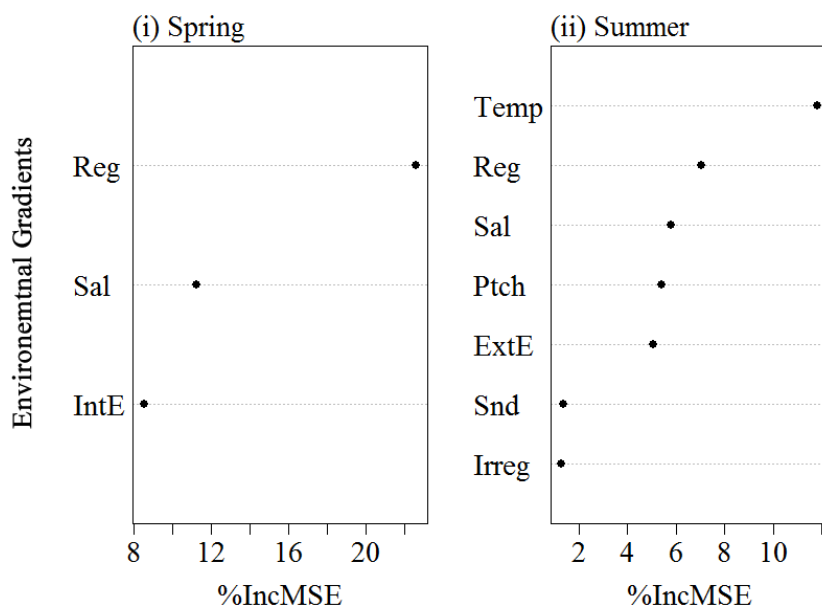


Figure 4.10: Bay anchovy (*Anchoa mitchilli*) variable importance plots (percent increase in mean square error when variables are excluded) generated from a random forest algorithm taken from catch data from juvenile trawl surveys in Georgia, USA (2006-2014) for spring: (March-May) and summer (June-August). Variables are Sal: salinity, Temp: water temperature, Reg: proportion regularly flooded marsh, Irreg: proportion irregularly flooded marsh, IntE: proportion intertidal-marsh edge density, ExtE: proportion subtidal-marsh edge density, Snd: sounds, and Ptch: mean marsh patch area.

The spring model partial dependence plots showed clear relationships with all three variables with bay anchovy abundance (Fig. 4.11). A non-linear trend in the contribution of salinity was detected, but, in general, the model predicted abundance increases with increased salinity values greater than ten psu. Proportion regularly flooded marsh exhibited a clearer positive relationship with abundance as the gradient values increased above 0.4 \hat{p} (Fig 4.11). Proportion intertidal-marsh edge density showed a strong threshold division at values 0.2 with values greater positively contributing to abundance (Fig 4.11).

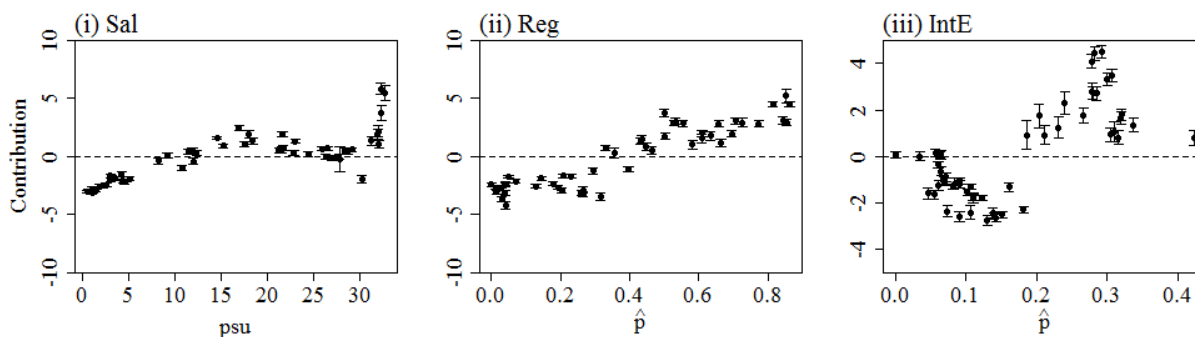


Figure 4.11: Spring (March-May) bay anchovy (*Anchoa mitchilli*) partial dependence plots generated through a random forest algorithm from juvenile trawl data for Georgia, USA (2006-2014). Variables in order are (i) Sal: salinity, (ii) Reg: proportion regularly flooded marsh, and (iii) IntE: proportion intertidal-marsh edge density.

The modeled relationships of bay anchovy abundance with landscape gradients in the summer season showed high importance of biophysical variables, but more landscape structural variables contributed to the model fit (Fig. 4.10). The model predictions of abundance are non-linear with water temperature, becoming strongly positive at temperatures greater than 30°C (Fig. 4.12). The relationship of abundance with salinity was linear, with positive contributions beginning at values greater than 25 psu (Fig. 4.12). Proportion regularly flooded saltmarsh had a more muted positive relationship with abundance than the spring model, though the threshold of change ($\hat{p} > 0.04$) from positive to negative remained approximately the same (Fig 4.12).

Conversely, proportion irregularly flooded marsh had a negative linear trend in contribution to abundance. Larger mean patch area (> 10 ha) and the increased complexity of the edge ($\hat{p} > 0.05$) were important to predicting higher summer bay anchovy abundance (Fig. 4.12).

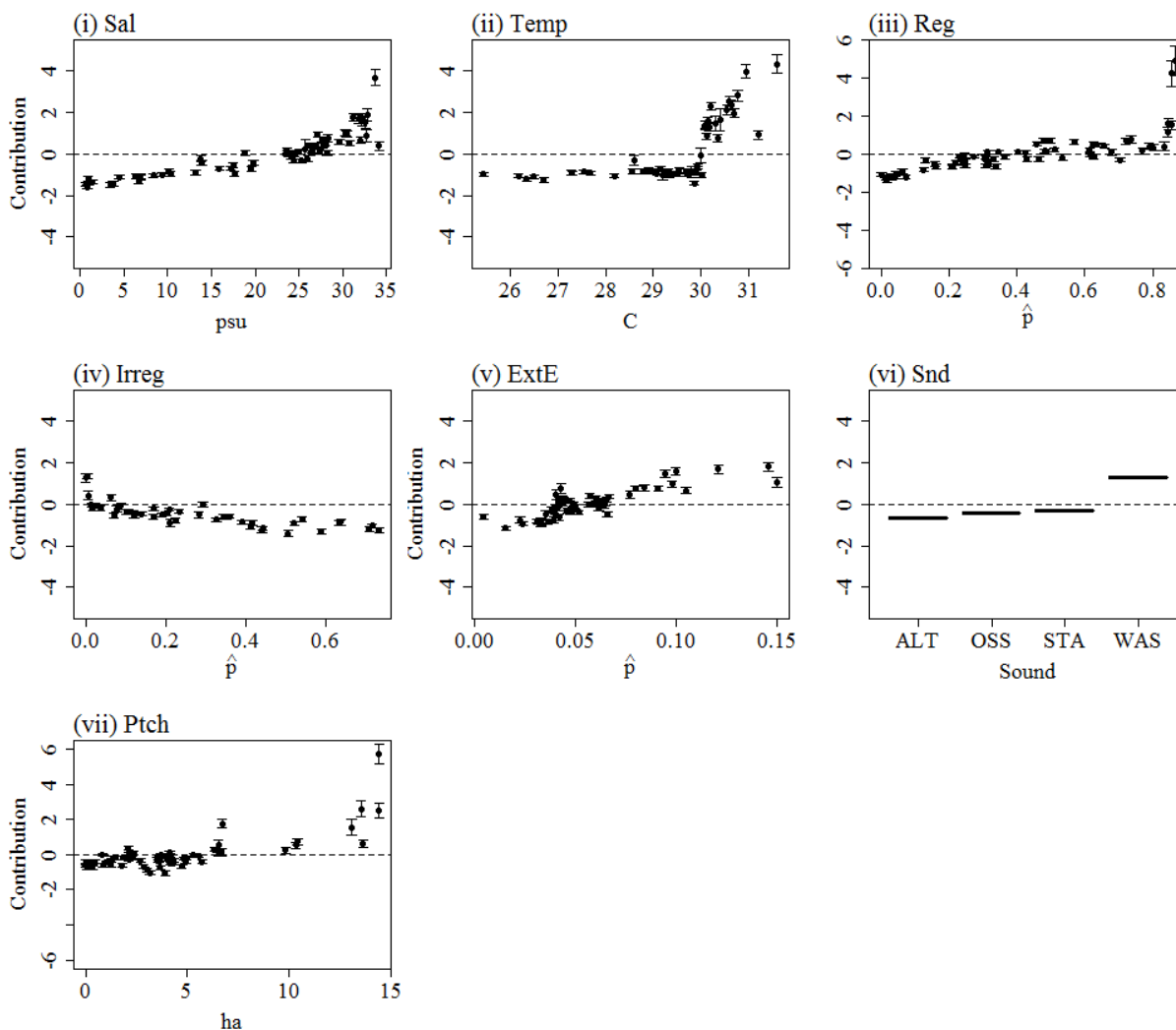


Figure 4.12: Summer (June-August) bay anchovy (*Anchoa mitchilli*) partial dependence plots generated through a random forest algorithm from juvenile trawl data for Georgia, USA (2006-2014). Variables are (i) Sal: salinity, (ii) Temp: water temperature, (iii) Reg: proportion regularly flooded marsh, (iv) Irreg: proportion irregularly flooded marsh, (v) ExtE: proportion subtidal-marsh edge density, (vi) Snd: sounds (Alt=Altamaha, Oss=Ossabaw, STA=St. Andrew, WAS=Wassaw), and (vii) Ptch: mean marsh patch area.

White shrimp

Models for summer ($r^2 = 0.31$, $n = 27,450$ shrimp) and fall ($r^2 = 0.27$, $n = 43,519$) white shrimp were roughly similar in the ability of their predictor variables to capture variability in the data (Table 4.2), though the summer model identified three important variables while fall had seven important variables (Fig. 4.13). Water temperature was most important in the summer (IncMSE = 25%) but was not selected at all in the fall model. The availability of edge habitat in subtidal (IncMSE = 22%) and intertidal areas (IncMSE = 16%) was ranked the highest importance in fall (Fig. 4.13).

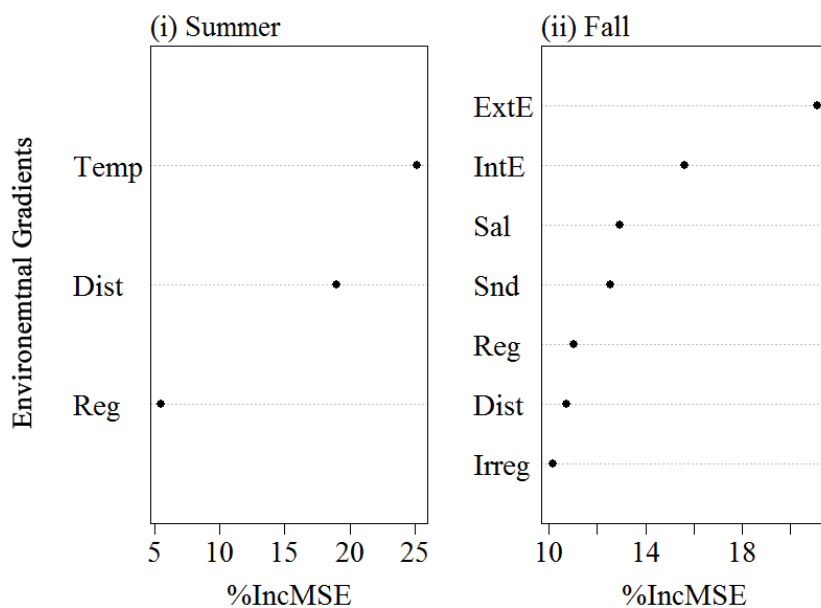


Figure 4.13: White shrimp (*Litopenaeus setiferus*) variable importance plots (percent increase in mean square error when variables are excluded) generated from a random forest algorithm taken from catch data from juvenile trawl surveys in Georgia, USA (2006-2014) for summer (June-August) and fall (September-November). Variables are Sal: salinity; Temp: water temperature; Reg: proportion regularly flooded marsh; Irreg: proportion irregularly flooded marsh; Dist: distance to mouth of estuary; IntE: proportion intertidal-marsh edge density; ExtE: proportion subtidal-marsh edge density; and Snd: sound.

Considering contributions of the selected variables in the summer, most showed a non-linear relationship with the contribution to white shrimp abundance (Fig. 3-14). The relationships indicate a positive relationship with white shrimp abundance when water temperatures are above 30°C, a weaker positive contribution of increasing proportion of regularly flooded marshes, and a positive change to abundance as distances from the mouth of the estuary increase above 10,000 m (Fig 4.14).

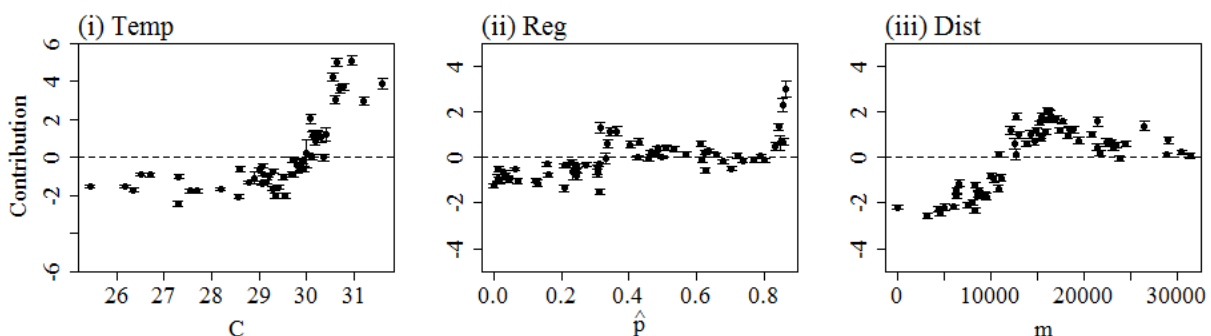


Figure 4.14: Summer (June-August) white shrimp (*Litopenaeus setiferus*) partial dependence plots generated through a random forest algorithm from juvenile trawl data for Georgia, USA (2006-2014). (i) Temp: water temperature, (ii) Reg: proportion regularly flooded marsh, and (iii) Dist: distance to the mouth of the estuary.

Most of the fall variable contributions were non-linear in relation to the environmental gradients measured (Fig. 4.15). The model predicted that fresh to brackish areas (< 10 psu) and areas near seawater salinity (> 30 psu) were associated with lower white shrimp abundance, which situates white shrimp habitat preferences within the brackish estuarine waters away from freshwater input and the open ocean (Fig. 4.15). This pattern is also reflected in the distance to the mouth of the estuary (10,000 – 25,000 m), though within our dataset these variables are not strongly correlated with one another. Proportion regularly flooded marsh displayed a more linear relationship with abundance than the summer model, with positive contributions occurring at $\hat{p} > 0.6$. The relationship with proportion intertidal-marsh edge density indicates a greater sinuosity

of intertidal marsh-edge within the marsh platform ($\hat{p} > 0.3$) increases the abundance of white shrimp (Fig. 4.15). The edge density of marshes bordering subtidal waters partial dependence plot shows a clear threshold where white shrimp abundance benefits from some edge density, but high density ($\hat{p} > 0.06$) of the edge was unfavorable to white shrimp.

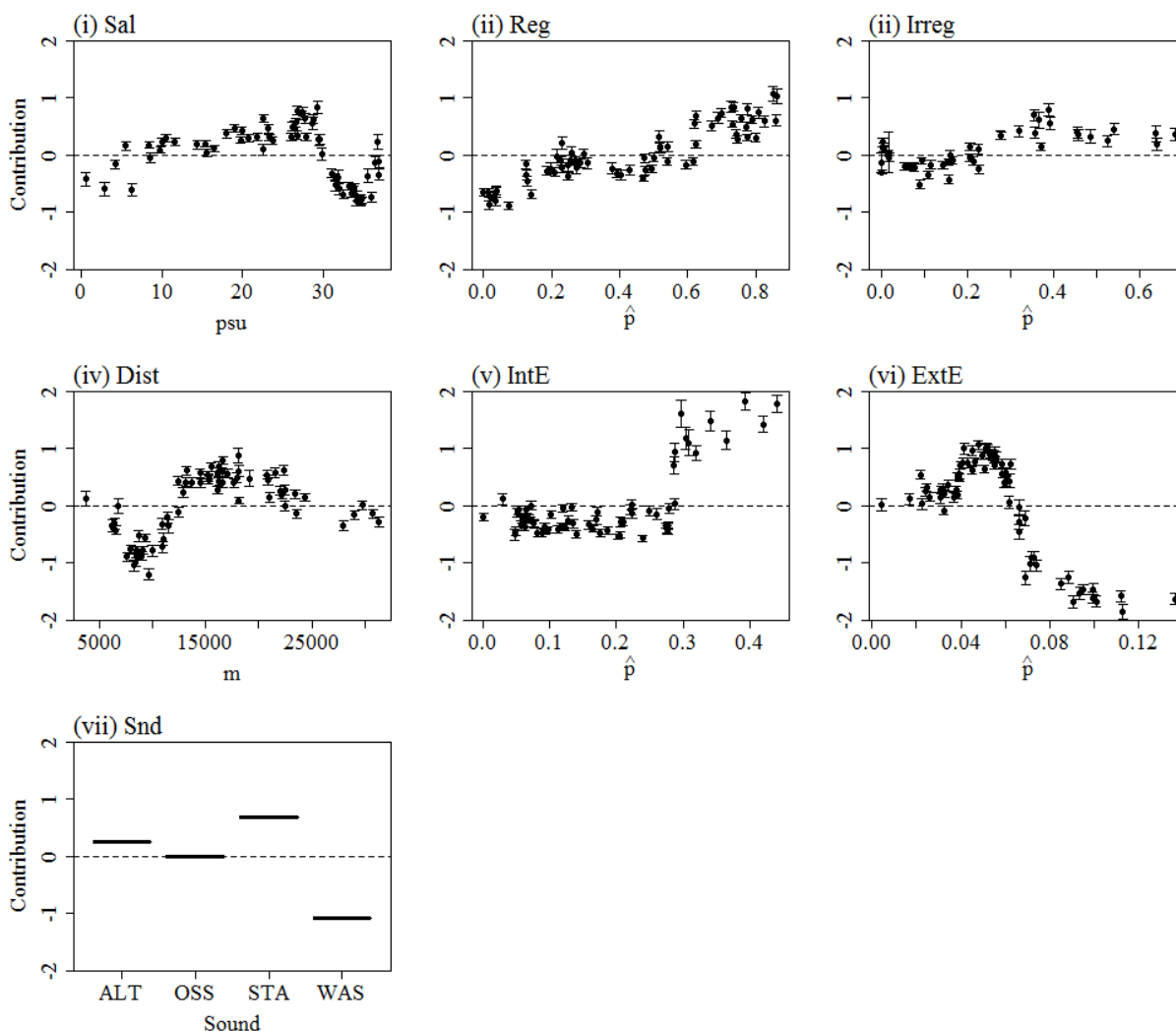


Figure 4.15: Fall (September – November) white shrimp (*Litopenaeus setiferus*) partial dependence plots generated through a random forest algorithm from juvenile trawl data for Georgia, USA (2006-2014). Variables are (i) Sal: salinity, (ii) Reg: proportion regularly flooded marsh, (iii) Irreg: proportion irregularly flooded marsh, (iv) Dist: distance to mouth of estuary, (v) IntE: proportion intertidal-marsh edge density, (vi) ExtE: proportion subtidal-marsh edge density, and (vii) Snd: sounds (Snd; Alt=Altamaha, Oss=Ossabaw, STA=St. Andrew, WAS=Wassaw).

Brown shrimp

Both spring (n = 706 shrimp) and summer (n = 3,441 shrimp) models for brown shrimp were weak in explaining the variance in the abundance data, each only explaining 9% and 6% of the variability, respectively (Table 4.2). The spring models discriminated five variables, and the summer model identified six variables of importance (Fig. 4.16). Biophysical variables only appeared in the spring model. Sound was voted for as highest importance (spring: IncMSE = 12%, summer: IncMSE = 11%) to both models.

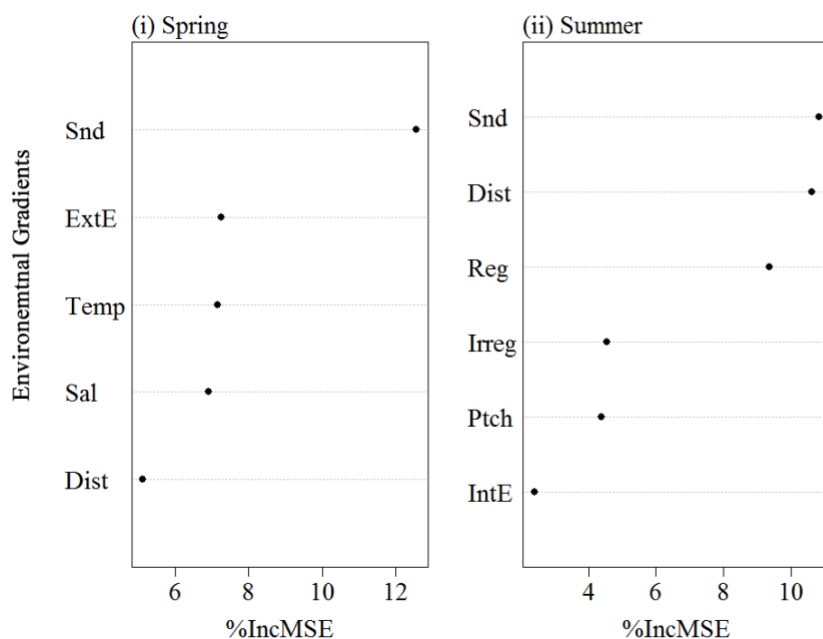


Figure 4.16: Brown shrimp (*Farfantepenaeus aztecus*) variable importance plots (percent increase in mean square error when variables are excluded generated from a random forest algorithm taken from catch data from juvenile trawl surveys in Georgia, USA (2006-2014) for spring (April-May) and summer (June-August). Variables are Sal: salinity, Temp: water temperature, Reg: proportion regularly flooded marsh, Irreg: proportion irregularly flooded marsh, Dist: distance to mouth of estuary, IntE: proportion intertidal-marsh edge density, ExtE: proportion subtidal-marsh edge density, Snd: sound, and Ptch: mean marsh patch area.

Contributions of environmental variables modeled for spring were comparably small, but some trends were evident (Fig. 4.17). Brown shrimp abundance declined as salinity increased and increased with increasing water temperatures ($> 21^{\circ}\text{C}$; Fig. 4.17). Abundance also appears highest in areas farthest away from the mouth of the estuary ($> 25,000\text{ K}$) and areas with higher values (> 0.05) of proportion subtidal-marsh edge density (Fig. 4.17). Catch of brown shrimp was also highest in Ossabaw Sound and lowest in St. Andrew Sound (Fig 4.17).

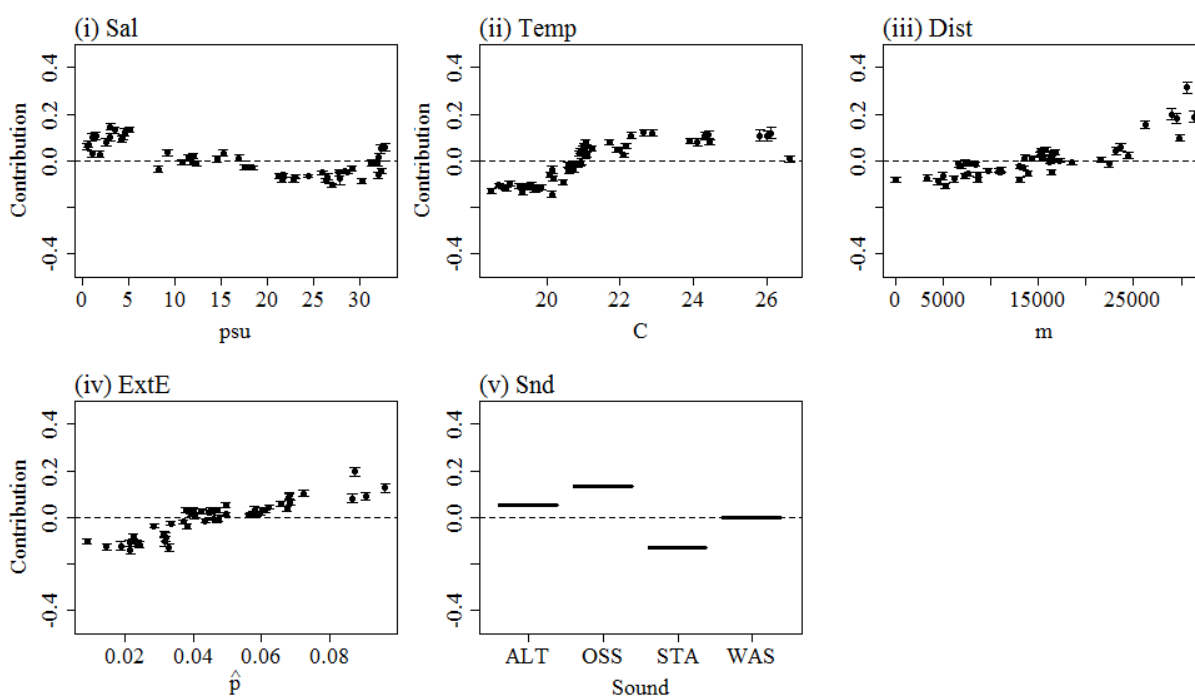


Figure 4.17: Spring (March-May) brown shrimp (*Farfantepenaeus aztecus*) partial dependence plots generated through a random forest algorithm from juvenile trawl data for Georgia, USA (2006-2014). Variables are (i) Sal: salinity, (ii) Temp: water temperature, (iii) Dist: distance to mouth of estuary, (iv) ExtE: proportion subtidal-marsh edge density, and (v) Snd: sounds (Snd; Alt=Altamaha, Oss=Ossabaw, STA=St. Andrew, WAS=Wassaw).

Like spring, RF modeled weak relationships for the summer brown shrimp abundance and the environmental variables (Fig. 4.18). Only proportion regularly flooded marsh showed a clear positive linear relationship with abundance (Fig. 4.18). The Altamaha and St. Andrew

sounds contributed positively to abundance, and Wassaw Sound contributed negatively to abundance (Fig. 4.18). The other variables fluctuated too close to zero to discern a pattern of contribution with their values.

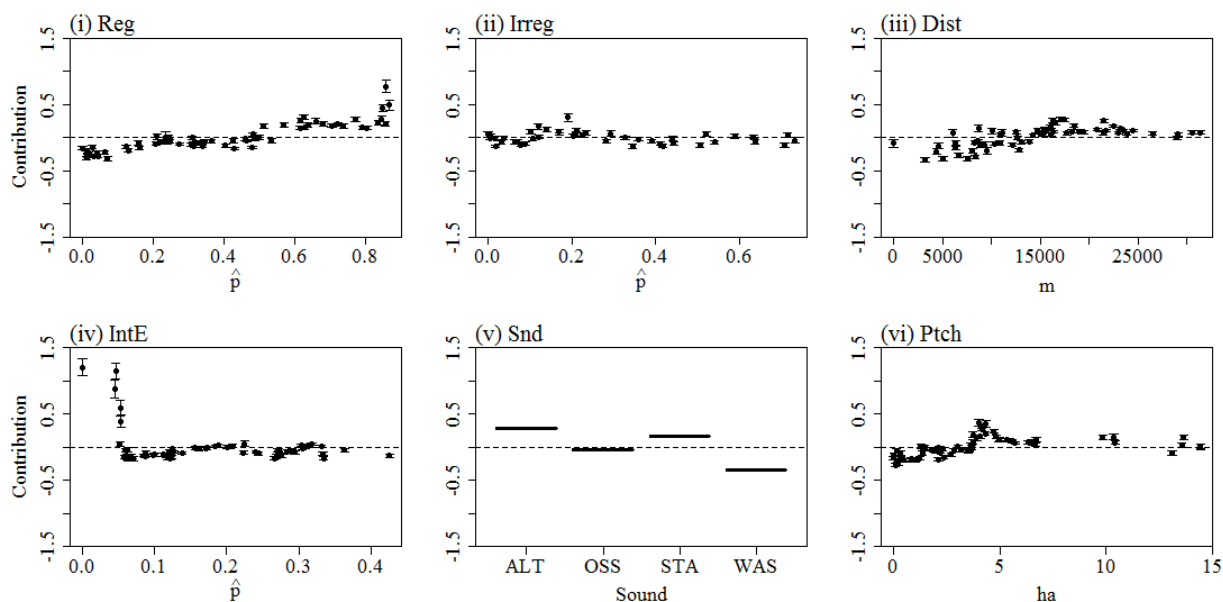


Figure 4.18: Summer (June–August) brown shrimp (*Farfantepenaeus aztecus*) explanatory variable contribution plots generated through a random forest algorithm from juvenile trawl data for Georgia, USA (2006–2014). Variables are (i) Reg: proportion regularly flooded marsh, (ii) Irreg: proportion irregularly flooded marsh, (iii) Dist: distance to mouth of estuary, (iv) IntE: patch interior channelization density, (v) Snd: sounds (Snd; Alt=Altamaha, Oss=Ossabaw, STA=St. Andrew, WAS=Wassaw), and (vi) Ptch: average marsh patch area.

DISCUSSION

Models relating environmental gradients to nekton confirmed that both abiotic variables and landscape structural variables are important to understanding the distribution and abundance of nekton in estuaries. Relationships with salinity differed among response variables, with juvenile fish richness and bay anchovy predicted to have higher values of occupancy or abundance in areas of high salinity and spot, Atlantic croaker, white and brown shrimp were

found less abundantly in areas greater than 30 psu. The salinity threshold change in the species richness model may indicate a shift in the species present in these seasons and their relative salinity tolerances. For instance, spot spawn in the spring and have a greater tolerance to lower salinities (0 – 15 psu) than other estuarine transient species. Water temperature, when included in a model, most often patterned higher values as contributing positively to abundance. The exception for this was the model for spring Atlantic croaker, where contribution to abundance dropped at the higher temperatures. The temptation may be to claim higher temperatures will increase fall species richness, summer white shrimp, and summer bay anchovy catches, but these models only can discriminate among the range of temperatures measured and not those projected higher temperatures that might occur with climate change. Further extrapolation under warm water conditions would require a greater understanding of the upper thermal tolerances of these species within their environment.

All models included at least one landscape structure variable, though some of these relationships were stronger than others. Though of varying importance, proportion regularly flooded marsh was pervasively positive, indicating a strong relationship of species richness and abundance with tidally influenced emergent wetland habitat. Distance to the mouth of the estuary among some models indicated lower abundance in areas closest to the open ocean where the risk of encountering pelagic predators might be highest. The models also showed lower abundance in areas of the estuary upstream in the riverine systems, at maximum distances from the mouth of the estuary. These regions may coincide with tidal fresh waters or regions of high temporal variability of salinity (Wang et al. 2017), which can cause osmoregulatory stress for nekton (Griffiths 2001). Juvenile Atlantic croaker are known to prefer low salinity waters also were more likely to be found in regions farthest from the mouth of the estuary (Miglaresse et al. 1982).

Sounds and structural complexity (intertidal and subtidal edge sinuosity) were frequently selected as important variables for predicting the abundance of a species.

It would be reasonable to conclude there should be a correlation between the distance from the mouth of estuary and salinity. However, salinity regimes in estuaries are predicated on residence time and geography of the estuary in relationship to a riverine system (Wang et al. 2017). Wassaw Sound supported greater species richness and bay anchovy abundance in the summer compared to the spring and fall models but negatively contributed to fall white shrimp abundance. Conversely, the Altamaha Sound had a strong negative relationship with species richness and summer bay anchovy and positively contributing to fall white shrimp catch. Wassaw Sound, of all the estuaries included in this study, experiences the least freshwater input from its nearest associated riverine system (Gross & Werner 1997). Large regions of low elevation marshes that coincide with a more stable salinity regime likely provide optimal habitat for estuarine resident and estuarine transient species (Serafy et al. 1997, Griffiths 2001). The timescale of variability (residence time of water) in these locations in the upper estuaries is likely as important as specific salinity level to many transient or non-resident estuarine species.

When measuring across multiple seasons, the strongest relationship with environmental variables occurred during periods when richness or abundance was highest. We expect this robust relationship with environmental variables during periods when recruitment of juveniles into their nursery habitats are highest, because estuaries and the associated marshes are critical to juvenile survival. Logically, reproduction might be timed for when resources are highest for a given species. Hence, we expect synchronicity of strong relationships with landscape structural variables and peak recruitment. Among seasons, relationships with the landscape and the physical environment change. As might be expected water temperature may be more limiting in

spring or fall. Still, some relationships change in magnitude but remain intact throughout the seasons. A consistent positive relationship with proportion regularly flooded marsh was seen in all seasons measured for species richness, white shrimp and bay anchovy. Other shifts in relationships with landscape variables may indicate a seasonally limited distribution of resources within the estuary, and spatial relationships with the landscape relax when limitations are at their lowest.

Though the models were able to discriminate some feature relationships with response variables each had greater than half of the variability that was not described by the models. Some models, like spot and brown shrimp, did not discriminate variables well at all. In the case of brown shrimp, low catch and high catch variability may also have contributed to the overall poor model fit. For other sources of unexplained variability, there may have been important environmental covariates that were not available for inclusion. The water depth and the benthic characteristics, including the substrate, of estuarine rivers and sounds were unknown. Estuarine bathymetry can change over a relatively short time, especially in response to strong climatic events such as hurricanes and tropical storms. This phenomenon was observed in a back-barrier estuary after Hurricane Sandy struck in 2012 (Miselis et al. 2016). Sediment delivery from the riverine systems flowing into the estuaries might also change seasonally and annually depending on climatic events and anthropogenic activity upstream (Wang et al. 2007). In addition, there are many unknowns concerning the effects of wind over surface waters and how it influences the behavior or detectability of nekton (Rozas 1995). Some variation might also be the result of unknown or unseen habitat characteristics such as submerged hard structures (e.g., dead tree). Characteristics (e.g., size, behavior) of nekton may have affected their catchability and thus affected modeled relationships. For example, some larvae and juveniles may be too small to be

detected by the trawls and therefore would potentially be recorded as a false absence. Finally, distance to the mouth of the estuary offered a rudimentary look at the distance at which nekton travel within the estuary, but a more robust circulation model might parse some of the variability caused by the passive transport mechanisms of the tidal currents.

Despite the unexplained variability, the models indicated some strong relationships with the structural biotic and abiotic landscape characteristics of the estuaries. The models were overall successful in our objective of describing the relationships of nekton occupancy and abundance with landscape gradients, creating spatially-explicit models of nekton distribution over a large landscape. Although there is unexplained variability, these models still can be useful for predicting future habitat change. They also highlight the importance of emergent wetlands within estuaries as critical habitat. However, the amount of uncertainty in these models are undescribed, and conclusions should be made with caution.

Few time-series fishery-independent datasets that capture inter-annual variability are available for estuarine fishes. To our knowledge, our use of such data sets is among the first to successfully relate estuarine nekton to landscape structure at a broad scale. Coastal ecosystems are important habitat for nekton during a variety of life stages, but some current essential fish habitat models lack the spatial explicitness needed to identify regions of critical habitat. Importantly, as estuaries change from anthropogenic development and climate change, our results will contribute to an understanding how the thresholds and structural characteristics of preferred habitat are distributed over large areas and will better inform management and conservation decisions.

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CHAPTER 5
SENSITIVITY OF ESTUARINE NEKTON HABITAT TO SEA LEVEL RISE IN GEORGIA,
USA⁴

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ABSTRACT

Global sea level rise will likely change estuarine salt marsh ecosystems in the coming century. Estuaries and the associated marshes provide important habitat to a variety of nekton of ecological and commercial value. Conservation and management planners may benefit from predictions of potential spatially-explicit changes to habitat within the estuaries caused by sea level rise. Accordingly, the objective for this study was to determine the sensitivity of nekton habitat distribution to three scenarios of sea level rise measured over the next century. Using the Sea Level Affecting Marshes Model and habitat models developed for species richness and three nekton species in estuaries of Georgia (USA), we project the future habitat distribution under three sea level rise scenarios. Results indicate longitudinal transgression of habitat into riverine systems and an overall decline in areas that support high species richness and abundance for most models. Understanding potential changes in the landscape structure of coastal marsh systems due to sea level rise, and how these changes may affect fish habitat is necessary to support future management decisions that will facilitate resilience to anticipated changes.

INTRODUCTION

Sea level rise will likely change coastal ecosystems. Estuaries in Georgia currently contain some of the most expansive emergent tidal grasslands in the USA. These marshes are vulnerable to erosion and inundation caused by sea level rise (SLR), which may lead to a conversion of vegetated habitat to submerged non-vegetated habitat and increase fragmentation of intact grasslands (Adams 2002, Craft et al. 2009). As the estuaries and associated marshes provide important habitat to a variety of nekton of ecological and commercial value (Peterson & Turner 1994, Rozas & Zimmerman 2000), conservation planners and resource managers would

benefit from knowing how SLR-induced changes to marsh/estuarine landscapes may affect diversity and abundance of species. With this information, proactive conservation planners could identify areas critical to protect or restore, but also to help stakeholders prepare to adapt or respond to anticipated changes to species distribution and abundance. In this study, we evaluate potential changes to current estuarine habitat under several SLR scenarios for juvenile fish species richness and three nekton species that fill important ecological niches in Georgia's coastal estuaries or have direct economic value.

Global mean sea level (GMSL) is anticipated to rise during the 21st century at increasing rates. Since the early 20th-century, GMSL has risen 0.19 m according to the Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment (Church & White 2011, Church et al. 2013). The rate of GMSL rise has not been constant. Early estimations of 20th century rates for 1901 - 1990 ranged from 1.2 to 1.7 mm, and 1.7 to 2.3 mm for 1971 - 2010 as measured by tidal gages (Church & White 2011, Church et al. 2013). As satellite altimeters improved the accuracy of sea level estimates from 1993 to 2010 measured SLR from 2.3 to 3.6 mm (Church et al. 2013, Hay et al. 2015). Dangendorf et al. (2017) suggested that previous SLR rates were overestimated, and therefore the increasing rate observed between 1993 - 2010 were faster than initially measured. As oceans continue to warm and land-ice melts, increasing the volume of oceanic water, GMSL rise is likely to continue to accelerate (IPCC 2013).

Not surprisingly, projections of future GMSL vary by general circulation models and weighting of influencing factors (oceanic thermal expansion, land-ice melt, oceanic mass gravitational changes, land subsidence). The IPCC Fifth Assessment predicted a GMSL rise interval of 0.42 – 0.98 m by 2100 (Church et al. 2013). Other research concluded a range from 0.75 – 1.90 m by 2100 (Vermeer & Rahmstorf 2009). Parris et al. (2012) provided scenarios that

ranged from 0.2 m – 2.0 m by 2100. This model uncertainty is compounded when considering the potential departure in regional relative SLR (NOAA 2017). Choosing the appropriate level of GMSL rise to consider when projecting into alternate futures is subjectively dependent on the level of risk that a conservation or resource management question needs to address.

The Sea Level Affecting Marshes Model (SLAMM) predicts the total area of emergent tidal wetlands in estuaries will be reduced and increasingly fragmented by the effects of GMSL rise (Craft et al. 2009). The effect of SLR on shoreline erosion has been modeled since the mid-20th century (Bruun 1962). Coastal wetlands, such as salt marshes, are vulnerable to SLR (Adams 2002). Salt marshes are maintained or migrate through vertical accretion and horizontal migration (Redfield 1965). If accretion rates are unable to keep pace with erosion, then salt marshes are anticipated to decline in total area (Adams 2002, Craft et al. 2009, Crosby et al. 2016). Anthropogenic barriers may also block horizontal migration, and anthropogenic land use can further degrade salt marsh (Bertness 2001, Enwright et al. 2016). There is some concern that current models used to project the effect of SLR on salt marsh do not take into account some biophysical feedbacks, including increased sedimentation (accretion) rates that accompany GMSLR (Kirwan et al. 2016). However, this resilience presumes sediment loads available for re-nourishment are constant, which can be reduced in some areas caused by anthropogenic changes to fluvial processes that deliver sediment into estuaries (Hudson & Mossa 1997, D'alpaos et al. 2011, Ganju 2017).

Fragmentation and loss of habitat can cause declines in species and overall biodiversity (Fahrig 1997, Bender 1998, Hanski 1999). Fragmentation and depletion of salt marshes are of concern to conservation and natural resource management because coastal wetlands provide important habitat for nekton at different life history stages (Peterson & Turner 1994, Rozas &

Zimmerman 2000). Some species that are estuarine and salt marsh-dependent are of ecological or commercial importance. Species included in this study were chosen for their ecological or anthropological value.

Biodiversity is an important metric for understanding ecosystem resilience to perturbations (Worm et al. 2006, Gamfeldt et al. 2008). Richness may be a better metric for biodiversity in fishes than Simpson or Shannon-Wiener indices of biodiversity because it is less influenced by variable species' detection rates due to species behavior (e.g., schooling, gear avoidance; Barrantes, & Sandoval 2009, Iknayan et al. 2014).

Atlantic croaker (*Micropogonias undulatus*) is a highly abundant sciaenid that utilizes shallow tidal creeks in the estuaries in its larval and early juvenile stages during the spring (Able & Fahay 2010). Juveniles of Atlantic croaker are often found in lower fresh to brackish waters (Sink 2011). The species serves as both prey for piscivorous predators and as a consumer of zoobenthos and zooplankton as larvae and juveniles (Hansen 1969, Soto et al. 1998). Atlantic croaker are also pursued by recreational fishermen and are commercially sold in local markets southeastern Atlantic (Mercer 1989, Diamond et al. 1999).

Bay anchovy (*Anchoa mitchilli*) have little to no commercial or recreational value but are of high ecological importance. As an extremely abundant fish in the Atlantic estuaries, it is an important predator of zooplankton and other small invertebrates (Sheridan 1978), and a critical prey species for piscivorous fishes and birds (Scharf et al. 1978, Nzinski & Munroe 2002). In the spring, bay anchovy spawn in the estuaries in small tidal creeks (Able & Fahay 2010). They can tolerate a wide range of salinities, though the larvae and juveniles seem to prefer brackish (< 10 psu) salinities as their nursery habitats (Morton 1989, Rozas & Hackney 1984). Though they are

not found in the vegetated marsh surfaces, their association near marshes may be attributed to the higher densities of their meiofaunal prey (Allen et al. 1995, Castellanos & Rozas 2001).

White shrimp (*Litopenaeus setiferus*) are a widely abundant crustacean whose larvae and juveniles exclusively utilize the estuaries and vegetated areas as nursery habitat in the summer months (Lindner & Anderson 1956, Webb & Kneib 2002, Zimmerman et al. 2002). As the water temperatures decrease, and as they mature during the fall, they move into polyhaline areas in the sound and offshore (Lindner & Anderson 1956, Williams 1984). They are also the focus of a commercial industry that supports local economies and is imbued with cultural significance and identity in the Southeastern US (Blount 2006, Chapter 2).

The vulnerability of Atlantic croaker, bay anchovy, white shrimp, and fish species richness to fragmentation and alteration of habitat at large landscape scale caused by SLR and other elements of climate change in the estuaries is currently unknown. Studies for terrestrial species in salt marshes have predicted varying degrees of sensitivity (Hunter et al. 2015). Of course, other climate change-related stressors exist that may affect suitable habitat distribution aside from SLR. Long-term drought reduces the overall biomass of estuarine vegetation and increases the average salinity within the estuaries (Silliman et al. 2005, Kinney et al. 2014, O'Donnell & Schalles 2016). The loss of habitat is compounded by physiological stress nekton may experience caused by changing salinity regimes within the estuary (Lankford & Targett 1994, Bennet et al. 1995, Palmer & Montagna 2015).

The vulnerability of a system or species to external stressors is partitioned into three primary components: exposure, sensitivity, and adaptive capacity or adaptation (Turner et al. 2003, Adger 2006). Our research considered two components of vulnerability, exposure and sensitivity, to determine how changes to the marsh landscape structure and biophysical

characteristics may affect the distribution, biodiversity and abundance of salt marsh nekton. While SLR scenarios provide the measure of exposure, we evaluated sensitivity using spatially-explicit models of species-environment relationships, quantifying how richness and abundance may respond to landscape change associated with SLR. We focused only on exposure and sensitivity here, as adaptive capacity is dependent on behavior, life history traits (e.g., plastic diets, high fecundity), and the distribution of meta-populations, all of which are beyond the scope of this research. Therefore, we measured the sensitivity of nekton habitat, or the amount of change to suitable habitat, when exposed to a range of potential SLR scenarios through the year 2075.

METHODS

Study Area

The study area includes four major estuaries on the Georgia Coast: Wassaw, Ossabaw, Altamaha, and St. Andrew sounds (Fig. 5.1). Wassaw and Ossabaw sounds have major urbanization within the estuaries with the cities of Savannah and Richmond Hill flanking the estuaries to the north and south. Three sounds have central fluvial influence into their estuaries: Ossabaw (Ogeechee River), Altamaha (Altamaha River), and St. Andrew Sound (Satilla River). The Savannah River runs north of Wassaw Sound, but the sound has no central fluvial system. The average semi-diurnal tidal amplitude is 1.8 m.

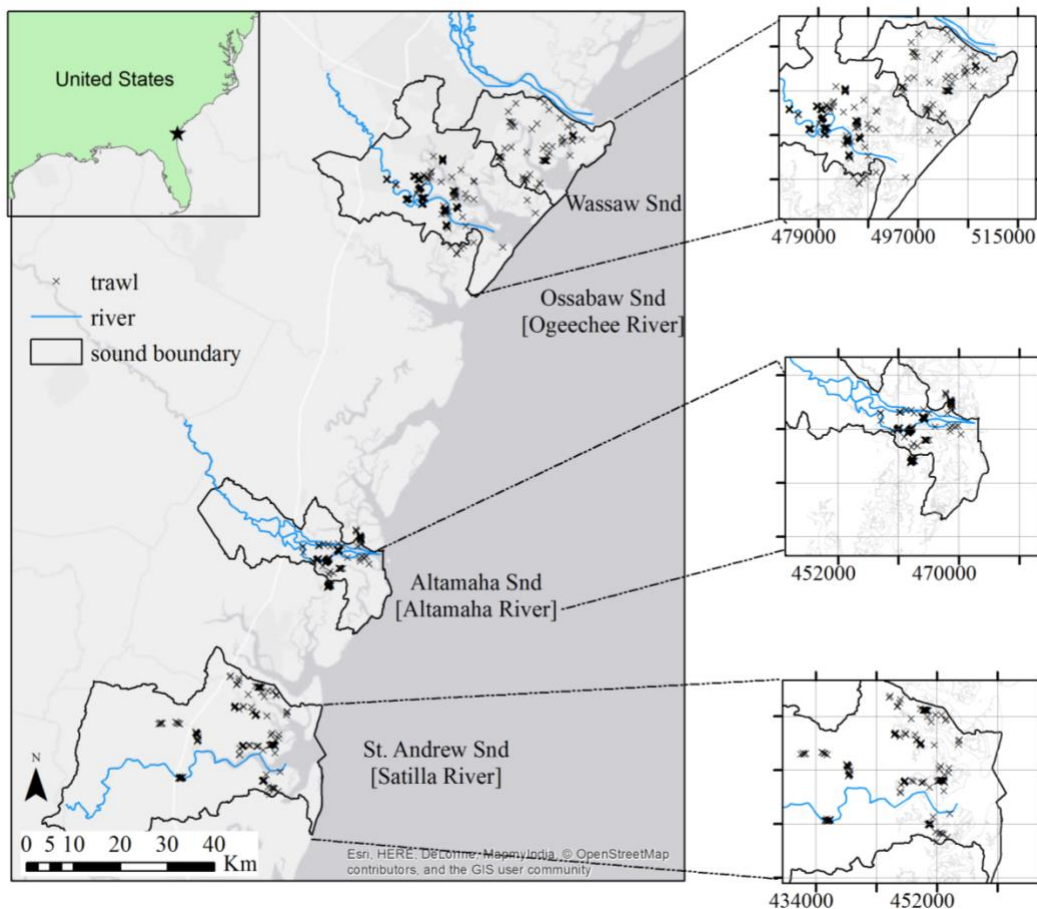


Figure 5.1: Study area on the Georgia (USA) coast in the southeastern Atlantic with associated sample points (trawl locations) from 2006-2014. Sounds included in the study include from north to south Wassaw, Ossabaw, Altamaha, and St Andrew Sounds. Sound boundaries were determined by dissolving 12-digit HUCs.

Salinity within the estuaries is highly variable depending on location within the estuary, season, and tidal cycle (Alber & Sheldon 1999, Wang et al. 2017). Some locations in Georgia's estuaries have a longer hydrologic residence time allowing lower standard deviation in salinity (0 – 1 psu) in comparison with the standard deviation of salinity (6 – 7 psu) in estuaries with direct freshwater input (Wang et al. 2017). Observed salinities (Georgia DNR Juvenile Trawl Dataset) in Ossabaw, Altamaha, and St. Andrew sounds ranged from 0 to 38 psu, and Wassaw Sound fluctuated from 23 to 37 psu from 2006 to 2015.

Emergent wetlands dominate the estuaries of Georgia. Smooth cordgrass (*Spartina alterniflora*) salt marsh is the dominant terrestrial habitat type in areas of frequent tidal flooding. Brackish marshes transition to black needle rush (*Juncus roemerianus*) and big cordgrass (*Spartina cynosuroides*).

Sea Level Rise Scenarios

Three SLR scenarios were considered: 0.7 m, 1.0 m, and 1.5 m SLR by the year 2100. The alternative future scenarios are based on current and future projections of atmospheric CO₂ concentrations (IPCC 2013). These scenarios represent intermediate-low, intermediate, and intermediate-high SLR by the year 2100 (Vermeer & Rahmstorf 2009, Parris et al. 2012, Church et al. 2013).

The three SLR scenarios above were used in parameterizing the Sea Level Affecting Marshes Model (SLAMM v. 6.3, Clough et al. 2012). SLAMM is a modeling algorithm that takes into account abiotic and biotic variables and processes of estuarine wetlands, including sediment accretion rates, sediment erosion, elevation, soil saturation, and salinity, to project the future transitions and changes of landcover types (Clough et al. 2012). Although SLAMM has been criticized for overly simple algorithms that did not take into account stochasticity or marsh accretion rates (Kirwan et al. 2016), more recent versions now allow for local accretion rates to be included in the model. Furthermore, analysis of model uncertainty suggests that the dominant source of variation is likely the variability in SLR futures, rather than model parameter uncertainty or spatial error (Clough et al. 2016).

The 2007 US Fish and Wildlife National Wetland Inventory was used to create the initial landcover condition (USFWS 2007), reclassified into 23 land cover classes, and converted to a

raster dataset with a resolution of 28 m. Using complex decision trees, SLAMM evaluates each pixel under future conditions of SLR and produces a landcover value according to underlying processes and biotic and abiotic values. These were calculated for 25-year increments (2025, 2050, 2075), producing a landcover raster for each time increment under each scenario. These estimates were not extended to 2100 as the estimates at the distal end of the prediction range have the greatest uncertainty.

Nekton Model Scenarios

Season-specific models relating nekton richness and abundance to both biotic and abiotic landscape gradients were developed with the random forest (RF) algorithm from a nine-year (2006 – 2014) juvenile nekton trawl survey dataset provided by the Georgia Department of Natural Resources (Fig. 5.1, Chapter 4). Models were produced for fish species richness and abundance of Atlantic croaker (*Micropogonias undulatus*), spot (*Leiostomus xanthurus*), bay anchovy (*Anchoa mitchilli*), white shrimp (*Litopenaeus setiferus*), and brown shrimp (*Farfantepenaeus aztecus*). However, models for spot and brown shrimp explained ten percent or less of the variability in abundance and thus were not included in our analysis of future projections. Catch-per-unit-effort (CPUE) was used as an index for abundance.

We chose to select models for SLR scenario projections based on seasons in which richness or abundance were best described by the environmental variables: summer fish species richness, spring Atlantic croaker, spring bay anchovy, summer and fall white shrimp models (Table 5.1). These seasons also had the highest species richness and abundance (Chapter 3). Salinity (Sal) and water temperature (Temp) were included as a biophysical predictor variable. The landscape predictor variables included proportion regularly flooded marsh (Reg), proportion

irregularly flooded marsh (Irreg), distance from the mouth of the estuary (Dist), intertidal-marsh edge density (IntE), subtidal-marsh edge density (ExtE), mean marsh patch area (Ptch), and sound (Snd). Each of these environmental gradients was calculated for each 28 m pixel with a 500 m moving window analysis to characterize the area covered by the 500 m trawl surveys.

Table 5.1: Model results for all years of trawling survey in Georgia, USA from random forests models per season (spring:Spr, summer:Sum and Fall), for three response variables, juvenile fish species richness (Richness), bay anchovy (BAAN: *Anchoa mitchilli*), and white shrimp (WHSH: *Litopenaeus setiferus*), and model results from random forest analyses of drought years for bay anchovy and white shrimp.

Response	Predictors	MSE	R ²	n ^a	n-500 ^b
Richness-Sum	Sal ¹ , Reg ² , Irreg ³ , Dist ⁴ , IntE ⁵ , ExtE ⁶ , Snd ⁷	4.90	0.45	406	65
Atl. croaker-Spr	Sal, Temp ⁸ , Irreg, Dist, IntE, Snd, Ptch ⁹	21.42	0.31	349	53
Bay anchovy-Spr	Sal, Reg, IntE	41.57	0.35	349	53
White shrimp-Sum	Temp, Reg, Dist	14.41	0.31	406	65
White shrimp-Fall	Sal, Reg, Irreg, Dist, IntE, ExtE, Snd	16.52	0.27	403	67

Notes. a: total sample size; b: consolidated sample size after samples were averaged into 500 meter buffers 1: salinity; 2: proportion regularly flooded marsh; 3: proportion irregularly flooded marsh; 4: distance to mouth of estuary; 5: proportion patch interior channelization; 6: proportion patch exterior edge 7:sound; 8: water temperature 9: average marsh patch area

The underlying relationships of abundance or diversity with environmental gradients were used to project the models over a spatial surface of these values for initial conditions, and future scenario conditions. All environmental gradient layers, except for IntE and Sal, were derived from the landcover raster datasets produced by SLAMM for each incremental scenario. Processing steps are found in Chapter 4. IntE was derived using 2010 Light Detection and Ranging (LiDAR) elevation data. Using the projected relationship of sea level over time for each scenario we estimated sea level values for incremental time steps: 2025, 2050 and 2075. The predicted mean sea level was subtracted from the LiDAR raster layer to create a dataset

reflective of sea levels for 2025, 2050, and 2075. The remainder of the processing of the IntE raster layers follows the methods in Chapter 4. Sound was defined using National Hydrography Dataset HUC (hydrologic unit code) 12 polygons and extended to include the associated river basins.

The Sal raster was derived using the point salinity values taken during trawls. Point salinity values were averaged over seasons for the 8-year sampling period. Universal kriging was executed for the Sal raster using the Geospatial Analyst interpolation tool in ArcGIS 10.2. A maximum neighborhood of five points and a minimum neighborhood of two points were selected for interpolation with 12 lags. Mean prediction errors for spring (0.07), summer (-0.03), and fall (0.11), were acceptable for gradients of salinity change within an estuary for the models' scales. Minimum and maximum salinity were restricted to 0 psu and 38 psu.

Scenario models were projected using the Marine Geospatial Ecology Tools (Roberts et al. 2010) 'predict random forests' tool for the base year and then each incremental year of the three GMSL rise scenarios. Temperature, when applicable, was applied as a constant predictor by averaging over all sample points in the appropriate season over all years (spring, 21°C). All predictive models were restricted to the observed range for each predictor variable, and results were masked to include only estuaries in which samples were taken using the 12-digit USGS hydrologic unit boundaries.

Sensitivity

Projections consisted of continuous raster data showing forecasts of fish species richness or species-specific abundance (Atlantic croaker, bay anchovy, white shrimp) at the 28 m pixel scale (representing a 500 m radius neighborhood). Results do not confer any information

regarding the instantaneous health of the habitat, which may vary at a temporal or spatial scale not captured by our models. Raster maps for 2007 initial conditions were subtracted from the predicted 2075 raster maps for each SLR scenario to allow for change analysis. Positive values indicate anticipated landscape changes resulting in an increase in species richness or abundance, values at or close to zero are areas where landscape structure remains constant, and negative values indicate areas where anticipated changes in landscape structure result in a decline in species richness or abundance.

The total area of habitat predicted was calculated and compared across years and scenarios. For each scenario and period, a total change in average species richness and supported average species abundance were calculated for the area of predicted habitat.

RESULTS

Forecasts of the influence of SLR on fish species richness and abundance of bay anchovy, Atlantic croaker, and white shrimp were varied. Averaged over the area of the sounds, Wassaw (9.1 species) and St. Andrew (8.1 species) sounds supported higher species richness compared to Ossabaw (7.4 species) and Altamaha (7.1 species) sounds. Models of initial conditions predicted species richness were highest in the lower reaches of St. Andrew and in Wassaw sounds (Fig. 5.2), while areas with strong freshwater discharge around the Ogeechee, Altamaha and upper reaches of the Satilla rivers supported less species richness. The total area of habitat also increased, with increasing species richness supported upriver of the Altamaha and Ogeechee rivers (Fig. 5.2) in 2075. A longitudinal (landward) shift of areas supporting greater species richness is most pronounced in the 1.5 m scenario at the year 2075 in the Ossabaw Sound, where 0.7 m and 1.0 m scenarios show no distinct spatial shifts in habitat. Models of the

Altamaha Sound showed increases in species richness in the upper reach of the estuaries.

Wassaw Sound gained some areas of increasing species richness in the models for the 0.7 m and 1.0 m scenarios at the margins of initial conditions, indicating a conversion of uplands to salt marsh with greater outer edge complexity and patch interior channelization. However, the 1.5 m scenario shows more loss of species richness, particularly in those areas that supported greater species richness.

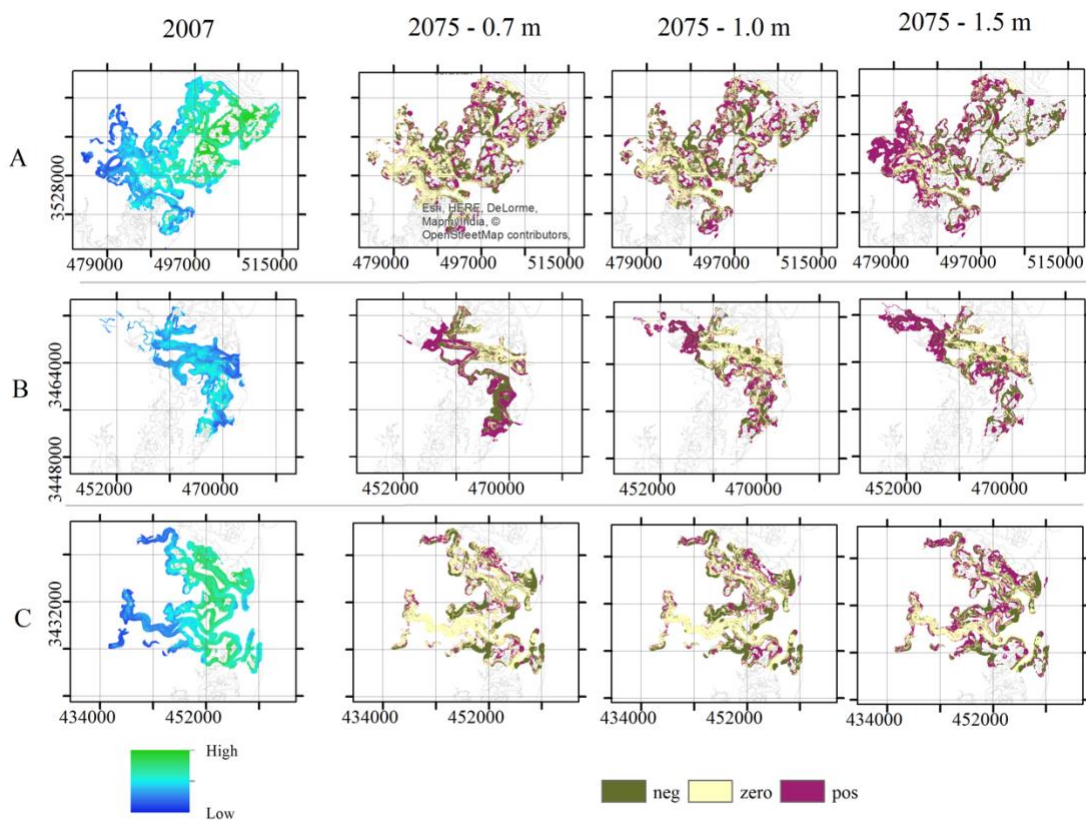


Figure 5.2: Fish richness spatial projections of areas that support high to low species richness, with distributions based on 2007 (first column) biotic and abiotic variables, and the 2075 predicted decrease (neg) or increase (pos) in species richness based on three scenarios of sea level rise (0.7 m: second column, 1.0 m: third column, and 1.5 m: fourth column). These were projected for Wassaw and Ossabaw sounds (row A), Altamaha Sound (row B), and St. Andrew Sound (row C) in Georgia, USA.

Total area supporting fish species richness increases from initial conditions to the year 2075 (Fig. 5.3) peaked in 2025. The increases constituted a 7% gain in predicted habitat area for all scenarios before declining in 2050 and 2075. For each scenario, average species richness supported by the estuaries decreased, of which the highest decline was observed in the 2075 1.5 scenario (-4 %). When considered by sound, the 0.7 m scenario predicted a decline in species richness by 1% in all sounds by 2075. The models for the 1.0 m scenario predicted Wassaw and St. Andrew sounds would have a 1% decline in species richness, and Ossabaw and Altamaha sounds would have a 2% decline in species richness. Wassaw sound was predicted to have the highest decline in species richness (6%) under the 1.5 m scenario by 2075. Models projected the Ossabaw and Altamaha sounds to lose 3% species richness in the 1.5 m scenario by 2075, whereas St. Andrew sound would decline only by 2% by 2075.

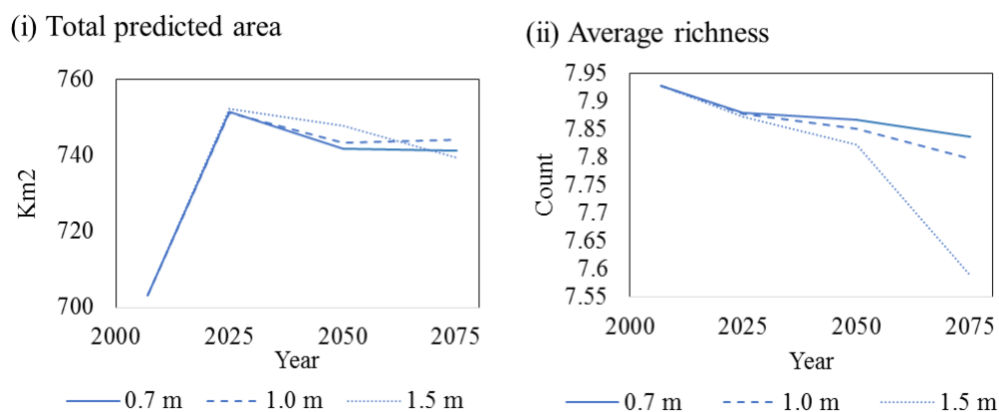


Figure 5.3: Fish richness total predicted habitat area (i) and average fish species richness (ii) from conditions in 2007, 2025, 2050 and 2075 under three scenarios (0.7 m, 1.0 m, and 1.5 m) of sea level rise for estuaries in Georgia, USA.

Initial conditions modeled for Atlantic croaker in the spring, when juveniles recruit into the estuaries, predicted higher abundance in brackish areas with avoidance of higher salinity

areas (Fig. 5.4). The area supporting highest abundance occurred in the mid- to upper reaches of the Ossabaw, Altamaha, and St. Andrew sounds. Areas with lower abundances of Atlantic croaker were distributed in Wassaw Sound and the lower reach of the St. Andrew Sound. Wassaw sound had an increase in abundance by 2075 for each modeled scenario. In Ossabaw Sound, areas either remained unchanged or decreased in predicted abundance in the 0.7 m and 1.0 m scenarios. The 1.5 m scenario predicted increasing abundance longitudinally to the west, indicating habitat moved upstream of the Ogeechee River. The Altamaha Sound had a longitudinal increase of abundance, moving upstream into marshes of the Altamaha River. Lower portions of the estuary remain mostly unchanged, while the areas behind the barrier islands in the southern portion of Altamaha Sound decreased in abundance centrally while increasing at the margins in all scenarios. The St. Andrew Sound model had the greatest decrease in abundance of the three sounds in the 1.0 m scenario (-1%), but much of the areas supporting high abundance remained unchanged. Increases were at the margins of the predicted area of habitat in all scenarios, and the 1.5 m scenario had the greatest increase in total area.

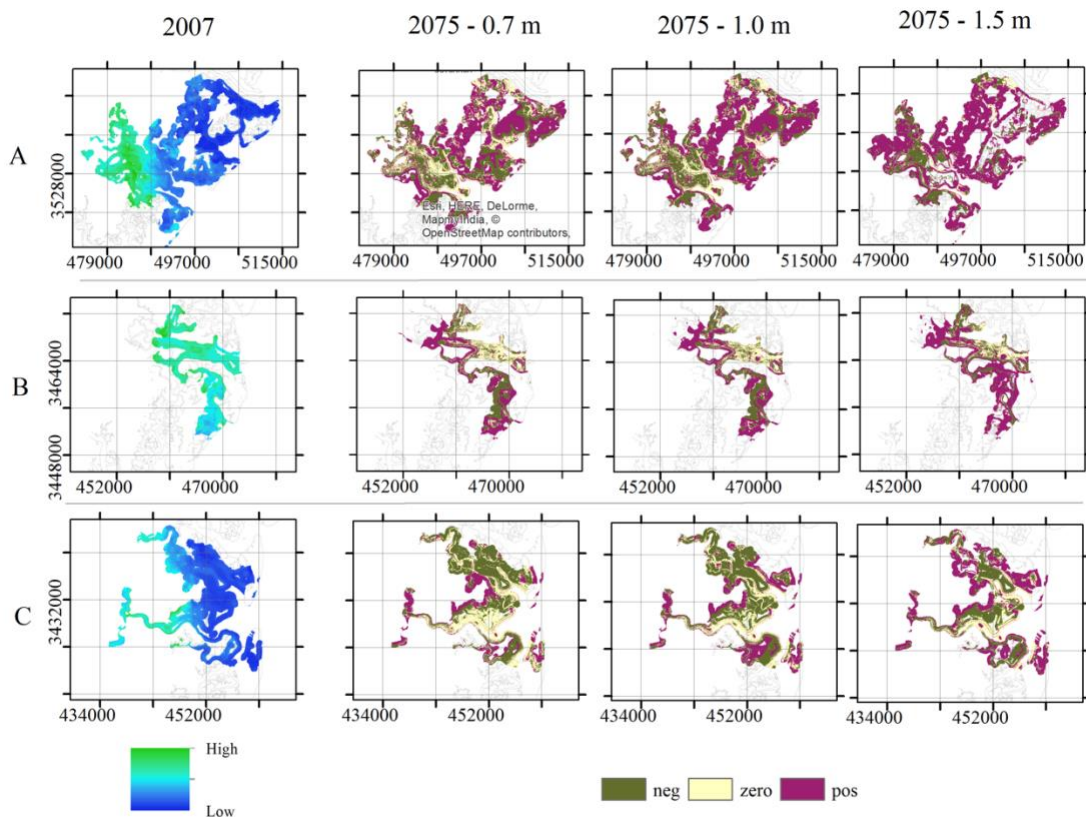


Figure 5.4: Atlantic croaker spatial projections of areas that support high to low species abundance, with distributions based on 2007 (first column) biotic and abiotic variables, and the 2075 predicted decrease (neg) or increase (pos) in abundance based on three scenarios of sea level rise (0.70 m: second column, 1.0 m: third column, and 1.5 m: fourth column). These were projected for Wassaw and Ossabaw sounds (row A), Altamaha Sound (row B), and St. Andrew Sound (row C) in Georgia, USA.

The total area of potential habitat predicted for Atlantic croaker increased at a decreasing rate from 2025 to 2075 for all scenarios (Fig. 5.5). The 0.7 m and 1.5 m scenario models predicted a peak increase for total habitat area of 10 % by 2075. The gain in total habitat area is 9% for the 1.5 m scenario by 2075. Average population abundance of Atlantic croaker in the estuaries was predicted to experience small decreases in the 0.7 m and 1 m scenario (-2 %) and increasing by 2075 in the 1.5 m scenario (+ 12%).

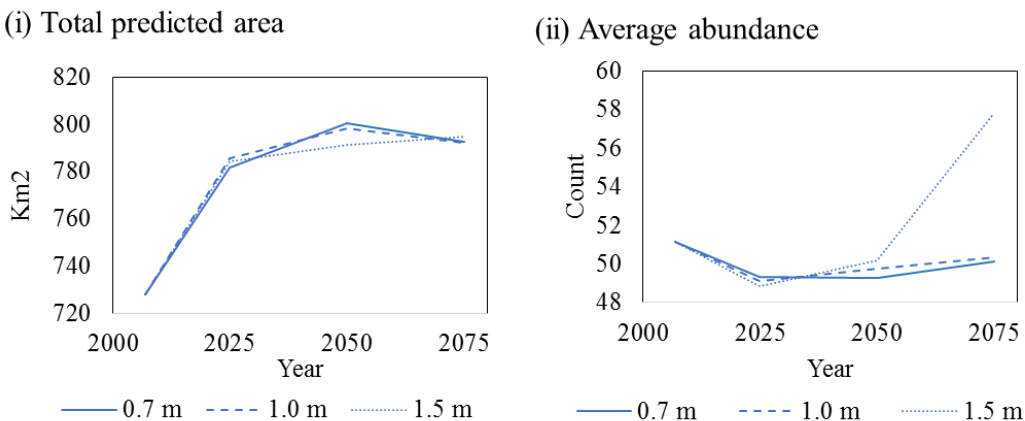


Figure 5.5: Atlantic croaker total predicted habitat area (i) and average abundance (ii) from conditions in 2007, 2025, 2050 and 2075 under three scenarios (0.7 m, 1.0 m, and 1.5 m) of sea level rise for estuaries in Georgia, USA.

The initial condition data modeled areas that support high bay anchovy abundance primarily within the mid to lower areas of the estuaries (Fig. 5.6). In general, the initial conditions far upstream of rivers were predicted to have the lowest bay anchovy abundance. In Ossabaw, Altamaha, and St Andrew sounds, there was a longitudinal shift of abundance increasing upstream while decreasing downstream that grew more pronounced under each scenario of increasing SLR. Of the four sounds in the study area, Wassaw Sound has the greatest apparent loss of predicted abundance in the 1.0 (-19%) and 1.5 m (-43%) scenarios. Areas within Ossabaw Sound had an increase in abundance upstream of the Ogeechee River which was the most expansive in 2075 of all the sounds.

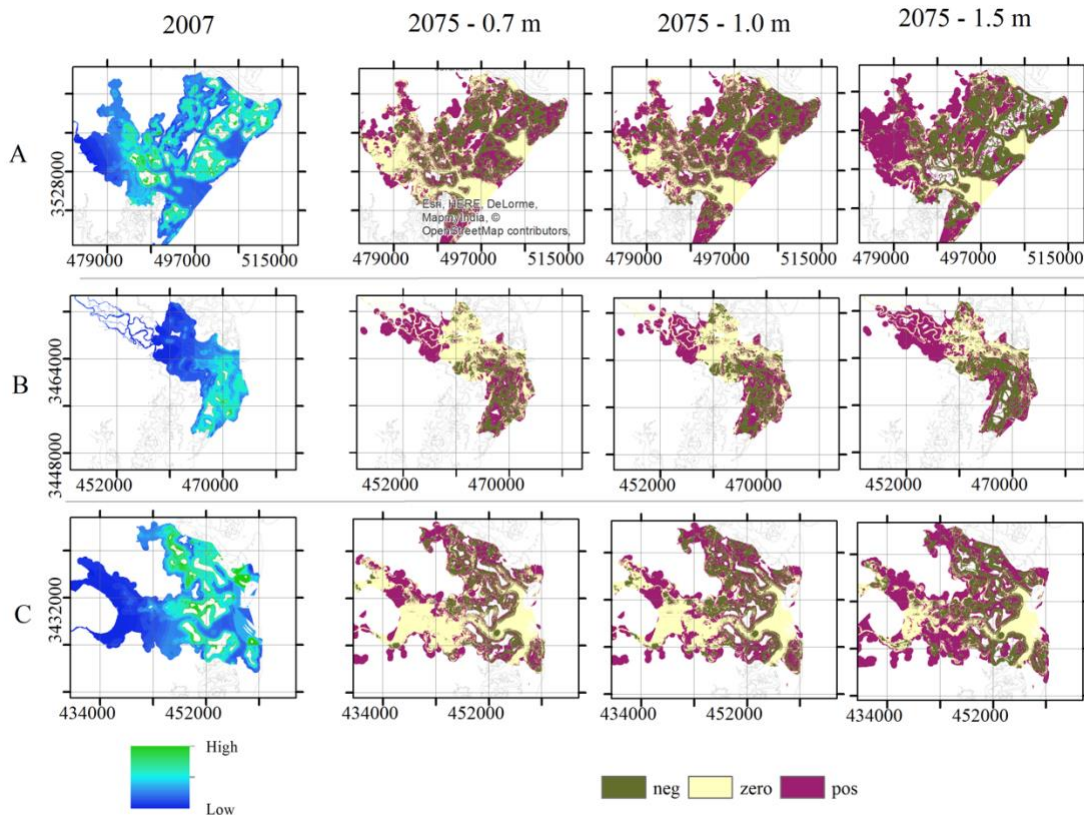


Figure 5.6: Bay anchovy spatial projections of high to low species abundance, with distributions based on 2007 (first column) biotic and abiotic variables, and the 2075 predicted decrease (neg) or increase(pos) in abundance based on three scenarios of sea level rise (0.7 m: second column, 1.0 m: third column, and 1.5 m: fourth column). These were projected for Wassaw and Ossabaw Sounds (row A), Altamaha Sound (row B), and St. Andrew Sound (row C) in Georgia, USA.

Total predicted habitat area for bay anchovy increased from 17 – 20% in all scenarios by 2075 (Fig. 5.7). Average predicted abundance of bay anchovy declined at the same rate for all scenarios between initial conditions and 2025 before the rate leveled and remained stable for the 0.7 m scenario. The 0.7 m scenario showed the smallest decline in average abundance (-10%) and the 1.5 m scenario modeled the largest decline in abundance (-36%).

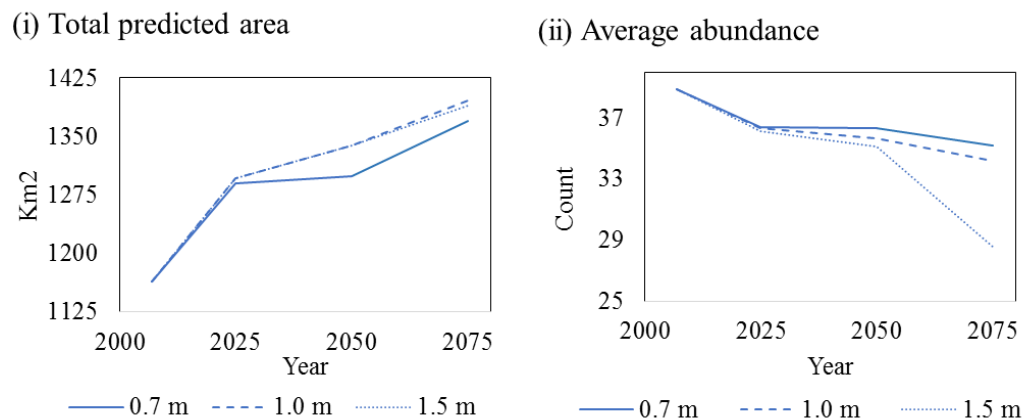


Figure 5.7: Bay anchovy total predicted habitat area (i) and average abundance (ii) from conditions in 2007, 2025, 2050 and 2075 under three scenarios (0.7 m, 1.0 m, and 1.5 m) of sea level rise for estuaries in Georgia, USA.

Initial conditions of summer white shrimp habitat spatial distribution were primarily highest longitudinally towards the western and upstream portions of the study area (Fig. 5.8). In the fall, habitat areas supporting high white shrimp abundance shifts downstream towards the middle and lower areas of the estuary (Fig. 5.8). The summer models for Wassaw, Ossabaw, and Altamaha sounds displayed a decline in areas supporting high abundance in each scenario in the upper reaches of the estuaries but a net increase of abundance in the lower estuary. The greatest negative change occurred in the 1.5 m scenario for summer white shrimp model in the Wassaw (-11%), Ossabaw (-6%), Altamaha (-7%), and St Andrew (-5%) sounds.

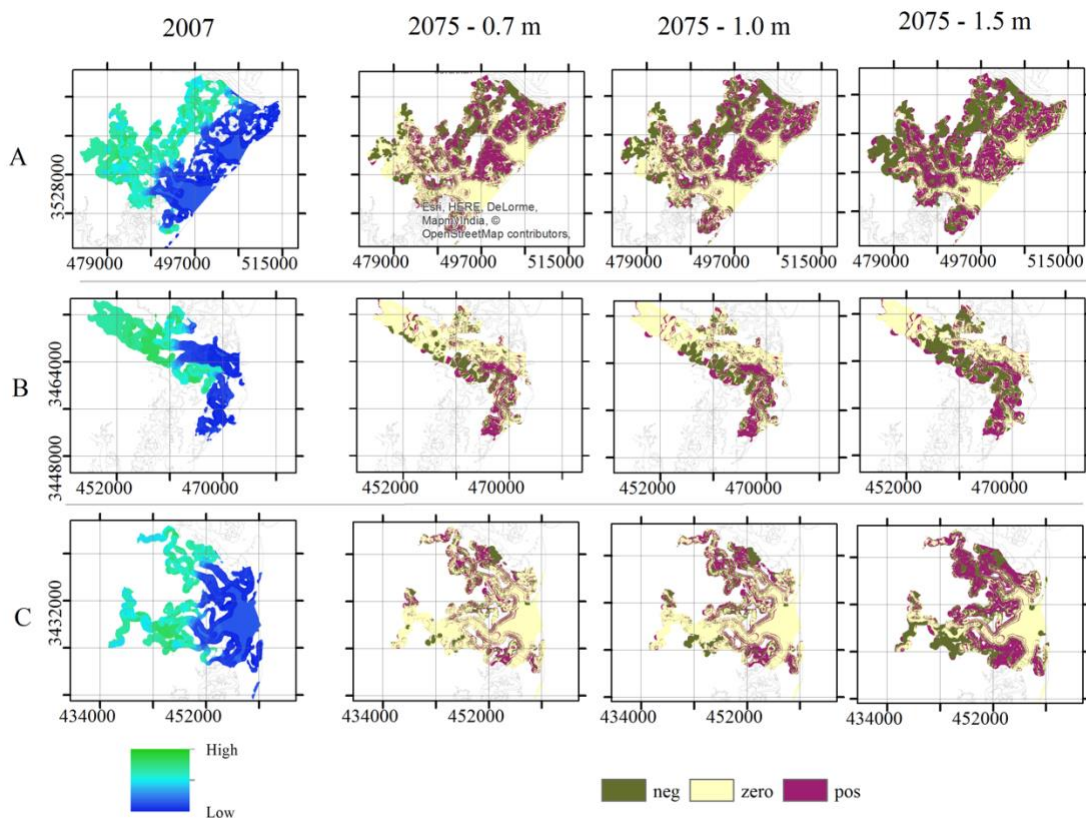


Figure 5.8: Summer white shrimp spatial projections of habitat areas supporting high to low species abundance, with distributions based on 2007 (first column) biotic and abiotic variables, and the 2075 predicted decrease (neg) or increase(pos) in abundance based on three scenarios of sea level rise (0.7 m: second column, 1 m: third column, and 1.5 m: fourth column). These were projected for Wassaw and Ossabaw Sounds (row A), Altamaha Sound (row B), and St. Andrew Sound (row C) in Georgia, USA.

The fall white shrimp model had less consistent longitudinal changes than the summer models (Fig. 5.9). The model predicted areas of supported abundance in the Wassaw Sound among the least favorable sounds and showed predominantly negative changes in abundance in the scenarios of 0.7 m (-7%) and 1.0 m (-7%). The 1.5 m scenario, however, predicted a net positive change in the areas of the lower estuaries, and net negative changes in the upper estuary of Wassaw sound, for a net change of 0% in average abundance. Ossabaw Sound mostly remained unchanged with an even distribution of positive and negative change to abundance in

the 0.7 m and 1.0 m scenarios but averaged a -3 % change in abundance for both scenarios. As observed in Wassaw Sound, the 1.5 m scenario modeled a positive change in abundance in the lower reaches and negative change in abundance in the upper reaches. The Altamaha Sound had a consistent longitudinal positive change upstream of the Altamaha River and a negative change to abundance in the lower areas of the estuary. These patterns increased in magnitude with increasing levels of SLR scenario, for a net change in average abundance of -2% (0.7 m and 1.0 m) and -4% (1.5 m). Changes to supported abundance in the St. Andrew Sound were more diffuse with an even distribution of positive and negative habitat quality changes at the margins of the initial condition habitat in 0.7 m and 1 m scenarios. The model distributes a more negative change in abundance than a positive change in abundance in the 1.5 m scenario, for an average decline in abundance of 6%.

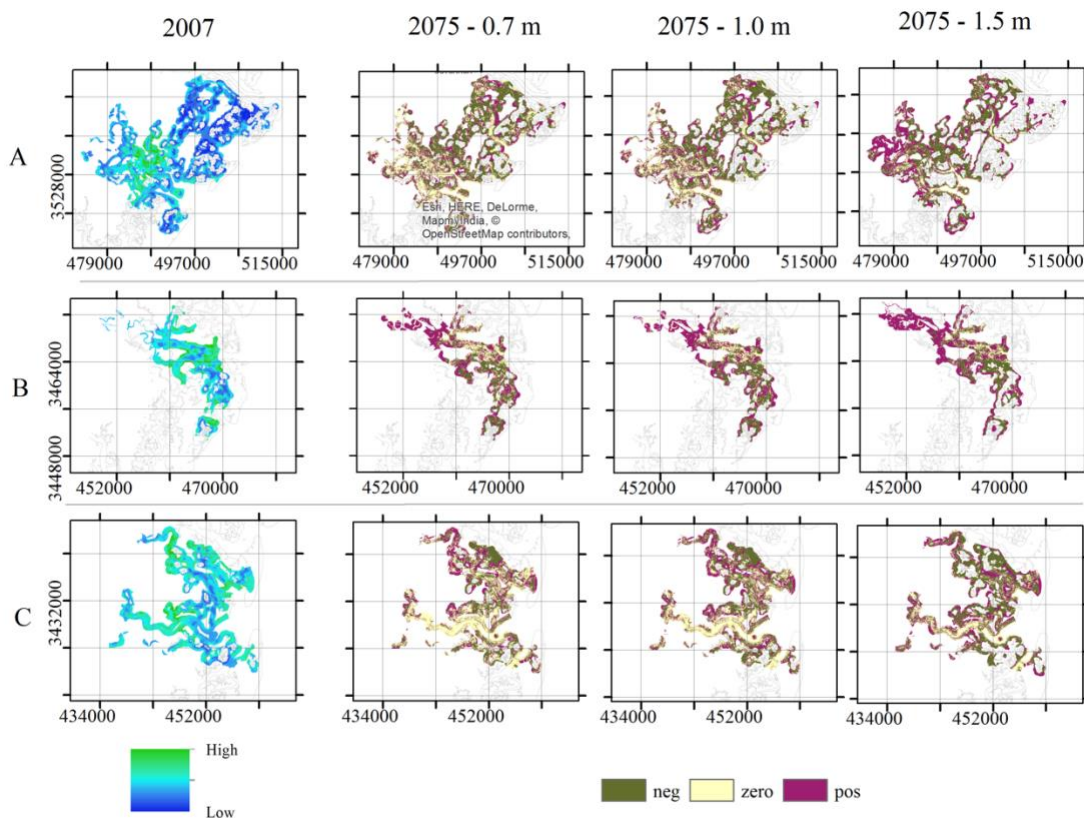


Figure 5.9: Fall white shrimp spatial projections of abundance (high to low species abundance), with distributions based on 2007 (first column) biotic and abiotic variables, and the 2075 predicted decrease (neg) or increase (pos) in abundance on three scenarios of sea level rise (0.7 m: second column, 1 m: third column, and 1.5 m: fourth column). These were projected for Wassaw and Ossabaw Sounds (row A), Altamaha Sound (row B), and St. Andrew Sound (row C) in Georgia, USA.

The total predicted area of habitat increased from 2007 to 2075 in all SLR scenarios modeled for the summer white shrimp distribution (Fig 5.10). This increase is smallest in 0.7 m scenario (5%) and greatest in the 1.5 m scenario (18%). All scenarios had a decline in white shrimp abundance from 2007 to 2025, but this decline stabilized in proceeding years for the 0.7 m (-4%) and 1 m (-5%) scenarios and continued to decline in the 1.5 m scenario (-8%).

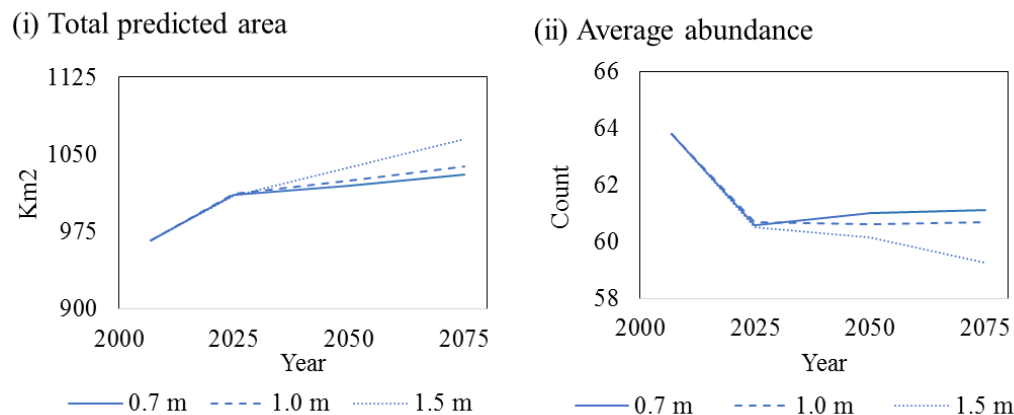


Figure 5.10: Summer white shrimp total predicted habitat area (i) and average abundance (ii) from conditions in 2007, 2025, 2050 and 2075 under three scenarios (0.7 m, 1.0 m, and 1.5 m) of sea level rise for estuaries in Georgia, USA.

Total habitat area modeled for fall white shrimp in each scenario showed a net increase by 2075 (0.7 m: 3%, 1.0 m: 1%, and 1.5 m: 1%) the peak habitat area modeled occurred in 2025 (5%, all scenarios) before declining in the following time-steps (Fig.5.11). Though the change in white shrimp fall abundance in the estuaries was predicted to decline in 2025, it was a relatively small decline (-1 to -2 %).

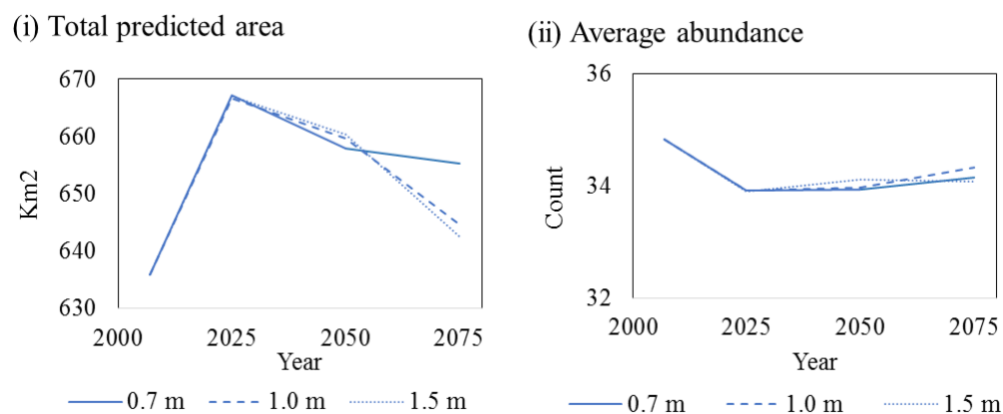


Figure 5.11: Fall white shrimp total predicted habitat area (i) and average abundance (ii) from conditions in 2007, 2025, 2050 and 2075 under three scenarios (0.7 m, 1.0 m, and 1.5 m) of sea level rise for estuaries in Georgia, USA.

DISCUSSION

Our research indicated species might have different sensitivities to SLR, including some likely to benefit from (at least short-term) projected changes, while others may experience declines. The discrepancies between species seem largely dependent on the habitat requirements at points in their life history. Patterns of sensitivity changed with the magnitude of exposure to SLR but did not change in a spatially uniform pattern or linearly over time. Sensitivity to changes to landscape structure also changed between seasons. Overall, at the most extreme scenario (1.5 m) our models predicted landscape structural changes leading to a decline in richness and abundance for bay anchovy and white shrimp, but an increase in Atlantic croaker abundance. However, for juvenile Atlantic croaker, this may be highly dependent on the availability of salinity conditions where habitat is optimal (Moser 1989). Past droughts have seen average estuarine salinities in Georgia increase by ten psu (Silliman et al. 2005).

Distribution of habitat supporting high species richness and abundance showed an apparent lack of uniformity in change within and between estuary systems. Some sounds showed longitudinal shifts of habitat, increasing inland/upstream, as presumably habitat is converted into suitable conditions as sea levels rise. Longitudinal shifts were most evident in sounds with direct river output, which have tidal fresh marsh habitat upstream that would be available for conversion. A sound without direct river output generally would be expected to decrease in total available habitat. Habitat decrease associated with river input was evident in forecasted declines of fish species richness in Wassaw Sound which currently supports the highest species richness.

In our study, the spatial distribution of habitat and its persistence was largely predicated on the hydrology of the local estuary. If there are no future human developments or barriers like infrastructure or building development, habitat can transgress horizontally up fluvial pathways,

converting brackish and freshwater tidal marshes to salt marsh. However, these areas would not likely support high fish biodiversity (Martino & Able 2003). Stability in water chemistry parameters confers greater finfish biodiversity (Griffiths 2001). Areas like Wassaw Sound that were predicted to support high finfish diversity may not experience the pulses of salinity and water temperature changes that accompany river discharge and tidal forcing. These characteristics, though, also increase the sensitivity of the habitat, allowing for little horizontal transgression. Additionally, both Ossabaw and Wassaw sound have a high degree of human development at its peripheries that would prevent habitat conversion. Therefore, we may expect an overall decline in finfish biodiversity in the estuaries as the highly variable salinity regimes will favor estuarine residents (e.g., Cyprinodontidae, *Fundulus spp.*) more tolerant of short-term changes to water chemistry.

For all magnitudes of exposure, the increase in sea level created more available habitat by area for each species and metric we measured from the initial conditions modeled in 2007 to the year 2075. This finding was in line with assumptions often made by the public. Interviews with both commercial and recreational fishers indicated a prevailing belief that SLR will create more habitat and hence increase fishing success (Chapter 2). The effect, however, did not necessarily translate to greater fish species richness or abundance. The cumulative loss of areas that support the most abundance may offset any of the total habitat gains.

Notably, though these models make predictions for individual species, the losses modeled for juveniles of these species in estuarine habitat do not necessarily translate to the overall local abundance of the species. Later life stages might be more ubiquitous in their range (Martino & Able 2003; Peebles et al. 2007). For instance, white shrimp in the fall showed less sensitivity to habitat changes than the same species in the summer. High annual fecundity of these species may

offset relatively small declines of Age 0-year class recruits due to loss of habitat. In addition, the base habitat distribution models used to parameterize the scenarios had unexplained variability. The variability may largely be due to the lack of local dynamics such as predator-prey, competition dynamics, and local hydrodynamics included in these models.

Additionally, as with any modeled projection of future conditions, uncertainties inherent in the model require caution when interpreting results. Uncertainty increases the further in time models are projected as the complex interactions as well as system stochasticity affect the confidence of future projections. For example, human management or intervention in estuarine hydrology may alter the suspended sediments in the water column and may change the resiliency of the salt marshes to SLR (Thrush et al. 2004). Increase in anthropogenic development may create conditions where marsh transgression is unlikely. Prolonged drought or changes to river discharge may also result in earlier declines in salt marsh loss independent of or in combination with SLR (Kinney et al. 2014, O'Donnell & Schalles 2016).

Conservation management is often reactive to declines in populations, especially of exploited stocks. Season openings and closures, slot, and bag limits are management tools often used once stocks are declining or increasing in abundance. Sometimes proactive measures are taken when environmental conditions are likely to be deleterious for recruitment. The National Oceanic and Atmospheric Association will close federal waters to shrimp fishing when water temperatures drop below a threshold for an extended period (NOAA 2018). However, these management actions rarely consider species of low commercial value and often are measures of adult fish rather than the juveniles in their habitat. Preserving breeding stock populations is important to fisheries management, but if the habitat is unavailable for growth and survival of their young, these efforts may be fruitless in slowing population declines.

Identifying current and future essential fish habitat is an necessary step in proactive management. This identification includes not only spatially locating current areas of habitat but also anticipating where that habitat might transgress in the future. This spatial awareness of future landscape structure will assist in designating essential migration corridors for conservation that might persist under a future of SLR. In the case of some species, this might include protecting upstream areas from physical barriers that would prevent future marsh transgression. Multiple scenarios of potential futures better inform land managers of the potential and varying levels of resource vulnerability and may help managers make strategic conservation decisions with knowledge of an acceptable level of risk.

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CHAPTER 6

CONCLUSIONS

In this dissertation, I use an integrative approach to determine if events, like climate change-induced sea level rise, pose risks to a socio-ecological system. My research was aimed at gaining an understanding of the system from multiple perspectives. Ideally, such an understanding would lead to identifying trade-offs and hidden pitfalls in the future of resource governance. Recognizing that my major discipline is in natural sciences, I realize my attempt to make space for a social science approach in my work was limited. The results of my research raised concerns about the deleterious effects climate change may have on fisheries but did not indicate a specific cause-effect relationship between coupled social and ecological processes and climate change. Instead, issues of scale of both space and time emerged among ecological and social analyses when analyzing vulnerability. These common themes highlight future concerns for natural resource management in coastal Georgia, while also suggesting a few more broadly applicable lessons.

The results of the overall vulnerability assessment to the natural resource itself indicated that we might expect declines in some populations of fishes and crustaceans with the effects of climate change. Temporal and spatial analyses revealed a dependence on abiotic and biotic environmental conditions that might be expected to change with sea level rise, changing precipitation patterns, and warming water temperatures. As might be expected, these results were variable among species analyzed. Some abundant fishes or crustaceans will likely have greater

resilience to changing patterns in temporal abiotic and spatial biotic variation than others. Some species may even benefit.

However, several critical issues came to light at the intersection of the temporal and spatial landscape and the nekton species modeled. Temporal and spatial variability of abiotic characteristics are quite high. Abiotic characteristics vary on diel tidal, monthly tidal and annual seasonal cycles; however, the variability within these cycles and the variability of these cycles among years create uncertainty in the instantaneous spatial arrangement of abiotic values. A large climatic event might change the arrangement of abiotic values in the landscape over the short-term, influencing nekton spatial distribution. If such large events are influential and unaccounted for, then error will be introduced into the modeled species distribution. A complete understanding of how these abiotic values change across a landscape over different timescales is limited to specific well-monitored areas, such as the major sounds.

The issue of temporal and spatial variability of an abiotic variable can be illustrated by salinity. On an extensive broad scale, we can estimate where water will likely be fresh, brackish, or saline. However, these broad categories are insufficient for classifying most species whose tolerances may straddle these categories. Also, salinity in estuaries with direct riverine input can change in hours. A rapid salinity change occurred the storm surge of Hurricane Irma in October 2017, as measured on the Altamaha River by the Georgia Coastal Ecosystem Long-term Ecological Research site (GCELTERR). However, little is known about how these events alter the salinity in areas outside of the GCELTERR. Spatial variability in salinity regimes may occur on a variety of temporal scales in nearby estuaries that are not reflective of the Altamaha River estuary. Quantifying spatial and temporal variability in these abiotic variables at a finer

resolution (than currently available) is missing, but it is a crucial piece in understanding the distribution of species' habitat.

Inter-annual variability of fishes and crustacean abundance is also high. At the onset of my dissertation, I conducted a 2-year intensive sampling method using a 1-meter beam trawl deployed from a small watercraft. However, though I sampled at a greater frequency over a shorter period than the GADNR juvenile trawl monitoring program, the variability of detection rates and abundance among two years of my sampling was too high for any models to detect spatial patterns. It is likely the issues of changes in abiotic variables were a source of variation, but this remains unresolved in the data.

The long-term GADNR dataset allowed me to detect trends in nekton spatial distribution and annual abundance. My analysis found unexpected declines that could not be directly related to the contemporary climatic phenomenon. In particular, the decline in bay anchovy and white shrimp is concerning because of the ecological and social implications for the sustainability of the fishery. The white shrimp declines may be attributed to the black gill disease phenomenon noted in Chapter 2, but at this point, there is no known cause for the observed bay anchovy decline. Though, like other Engraulid species, these patterns of abundance could be cyclical over inter-decadal periods (Fréon et al. 2008). Given the moderate coefficient of determination value, the detected trend, though statistically significant may not be biologically relevant.

These findings indicate that the datasets of appropriate spatial and temporal scale are critical for a better understanding of the ecological setting of a socio-ecological system. However, capital for managing natural resources is limited and maintaining sampling frequency over a long can be costly. Therefore, some resource governing institutions have turned to fishery-dependent data to help determine trends in abundance. There are obvious pitfalls with relying on

fishery-dependent data alone (e.g., changing effort, gear, and bias towards commercial species, noncompliant fishing), but there are other hidden issues brought about by the scale of resource governance and vulnerability itself illuminated by this research.

The temporal and spatial scales of experienced stressors influenced a fishing community's experienced vulnerability. Stressors that happened over a short period or were highly localized (e.g., temporary closures of local fishing grounds for a winter freeze) were adapted to, and longer-term stressors at a scale in space beyond the fishing community itself exposed lower adaptive capacities. This lack of resilience to a long-term stressor is likely indicative of how other small-scale fisheries might react to climate change. Climate change is presumed to act like a long-term stressor which effects may include acute changes (e.g., increased major storm events) at higher frequencies or gradual, chronic changes over a longer period (e.g., warming water temperatures).

The likely source of this vulnerability is the scale at which fishers perceive their resource and their natural environment. As supported by the ecological data, over a short period the distribution of resources and the environment itself is variable. In interviews, fishers spoke of adapting to short-term variability while the long-term changes were viewed with optimism for returning to an acceptable 'mean' where the cost of fishing is equal to or less than the benefit received. With a focus on short-term variability, perception to small changes to the overall mean might go unnoticed until a threshold of adaptive capacity is reached. Without strategic planning to address community resilience, changes in the community could be maladaptive and unsustainable in the long-term.

Maladaptive strategies to increased vulnerability can both be the result of changes to the resource as well as the way in which governance is executed. In the USA there has been a shift to

a participatory governance management strategy that incorporates user (fishers) input into management decisions using local advisory councils. However, these councils are restricted by invitation, reinforcing who is a part of the discussion and whose viewpoints are not considered. Fishers who may feel disenfranchised by the system are more likely to be vulnerable to changes in the system. Increased vulnerability, whether realized or perceived, has been known to lead to non-compliance to fishery regulations. Non-compliant fishing is often not reported, skewing the data concerning catch and effort that is used to make sustainable resource management decisions.

LIMITATIONS AND FUTURE DIRECTIONS

What became clear in my studies was the necessity to address the paucity of ecological and social data at the appropriate resolution and extent to detect changes. Unsurprisingly, the lack of data at the appropriate scale is a perennial problem in both ecological and social science studies. Collecting data has monetary and effort costs associated that are often insurmountable for some researchers, resulting in necessary trade-offs to the application of their study.

Current resolution and length of ecological data are inadequate to determine if baselines are shifting. In my ecological studies, I was reliant on species life history accounts that are nearly half-century old. The life history accounts may still be presently applicable as they were then. However, as environmental conditions have changed with climate change, some of the original ranges and the timing of spawning events or recruitment may have shifted. The data I collected with a higher frequency of sampling might have eventually illuminated more precisely the current average of temporal richness and abundance patterns, but the relatively short-term dataset had too high inter-annual variability to detect changes. Determining a methodology that balances

between the two approaches would allow for the detection of long-term trends of not only overall abundance but also seasonal shifts as well.

Collecting high-resolution social data at long time-scales is also a challenge. Ethical concerns of privacy and the cost of repeated efforts must be considered. Therefore, vulnerability assessments are often done at a national scale, where quantitative metrics are readily collected and available. Though these metrics can be determined often at a sub-national scale through census data, the period between samples can make determining the cause for change within a community difficult to pinpoint from data alone. Moreover, the quantitative metrics, while easier to measure miss qualitative indicators that might illuminate perceptions and predict future reactions to stressors.

Innovations in data collection methods that need Big Data (BD) for the study of trends and their causes in socio-ecological systems are needed. In the private sector, BD gleaned from website traffic has already been used in market analyses to bolster commercial campaigns and increase sales. As computing power and analytical methods have advanced it is easier to process large amounts of data for analysis. Collection of BD in natural sciences has increased with networks of surveillance sensors, such as the Global Lake Observatory Network (GLEON), the US National Ecological Observatory Network (NEON), and the NOAA funded National Estuarine Research Reserve System-Wide Monitoring Program (SWMP). Older collections of large amounts of data include species observation databases, like VertNet (formerly MaNIS, HerpNet, FishNET, and ORNIS). The networks have the advantage of advanced technological sensors and conformity to data collection standards that ensure integrity of the data. The sensor networks main disadvantage is that they are still expensive. NEON's implementation cost approached nearly \$500 million to establish its ambitious network across 47 US states. Online

species databases are relatively more cost-effective, relying on voluntary submissions from researchers and citizen-based science efforts. However, the online species databases can lack data standardization of collection methodology which may introduce large errors in analysis.

There is a need for data over long temporal and large landscape scales that are at a finer grain than what is currently available. Finding the social and ecological data in a quantity that is suitably congruent for analysis at scales beyond a large and coarse temporal and spatial scale is difficult. To better address feedbacks and tradeoffs within socio-ecological systems, I suggest an integrative socio-ecological observatory network that considers a collection of ecological and social data at parallel and congruent scales of space and time. However, there are critical problems to address before a network as described can be realized: data quality, data validity, and cost.

The need for an integrative data network has already been recognized as critical to managing for vulnerability. The National Estuarine Research Reserve System (NERRS) recently discussed collecting a suite of social indicator metrics to complement the System-Wide Monitoring Program, a program already collecting environmental data through a water quality sensor network spread across 29 reserves in the US. However, the ability to add a social indicator metrics system that is of the same frequency and quality as a well-established sensor network has proved challenging. Developing an observatory network from the initial conception that makes space for both the social and natural sciences may prove more fruitful in the long run by avoiding the need to ‘shoehorn’ new metrics into an existing system.

Of course, establishing an integrative socio-ecological observatory network is easier to imagine than accomplish. It would not replace the need for hypothesis-driven place-based scientific research. However, I believe the results of my studies indicate that we can expect

socio-ecological systems like fisheries to be altered with climate change. Data collected with the intention to determine the integrative mechanisms of change in the system would allow for potential feedbacks between the social and ecological systems to be understood and therefore predicted. With greater attention to the mechanisms linking the changes in the ecological system to the changes in the social system (and *vice versa*), resource governance can be more proactive. Proactive governance that considers the social-ecological system would confer greater resilience and sustainability to the system.

STRATEGIC COMMUNICATIONS

If the future of monitoring socio-ecological systems will depend on the public and citizen scientists, then the necessity, process, and results of scientific study need to be translated to the public. Translation must be done in terms that are understood at most education levels.

Accordingly, I engaged in several acts of public strategic communication.

After receiving a small scholarship from the Garden Club of America, I was invited as the scholarship representative in 2014 to The Garden Club of America's annual meeting. I delivered a 15-minute presentation about the necessity and process of my research to an audience of 300 Garden Club members, most of whom were a non-technical audience. After the success of this talk, I was invited in 2015 to give longer talks (30 -45 minutes) in Jacksonville, FL, and Augusta, GA to local clubs. Finally, in October of 2015, I spoke at a regional Garden Club meeting in Virginia Beach, VA. A lesson I learned is to be more mindful of the scientific language I take for granted as universally understood. The first longer talk I gave was overly technical for the audience, and I subsequently modified the talk. I also struggled with the inherent politics of climate change and how to communicate my findings to an audience that did

not necessarily believe climate change is a real phenomenon. Connecting the audience through individual stories of people affected by climate change was beneficial in overcoming this barrier.

In 2015 I kept a blog during my research season called “Guy in the Saltmarsh” (guyinthesaltmarsh.org). I cataloged my field experiences and highlighted estuarine species in terms readily understood by the public. Though I have not updated the blog since the end of my field season, the gallery is still regularly visited by people looking to identify fish species.

In 2018, I was invited as a panel expert to speak about climate change and its effect on the fisheries, based on the results of my research, after a public movie screening in Brunswick, GA.

Not directly related to my research, but communicating the effects of large storm events, I created a four-minute video in 2017. It highlights the effects of the storm surge on a barrier island on the Georgia coast using time-lapse photography. It was posted to www.youtube.com at https://www.youtube.com/watch?v=1f_9s_9IWgc. As of this writing, it has over 3,700 views.

CHAPTER 7

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