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# Assessing Habitat Suitability of Ribbed Mussels (Geukensia Demissa) in Georgia Salt Marshes by Examining Predicted Mussel Densities and Mussel Population Parameters

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# ASSESSING HABITAT SUITABILITY OF RIBBED MUSSELS (*GEUKENSIA DEMISSA*) IN GEORGIA SALT MARSHES BY EXAMINING PREDICTED MUSSEL DENSITIES AND MUSSEL POPULATION PARAMETERS

by

WILLIAM ANNIS

(Under the Direction of John Carroll)

## ABSTRACT

The salt marshes of coastal Georgia are ecologically and economically important ecosystems that are threatened by erosion as a result of sea level rise. Naturally these marshes are stabilized by the mutualistic relationship between *Spartina alterniflora* (cordgrass) and *Geukensia demissa* (ribbed mussel). Together these two organisms hold sediment in place through the intertwined connections of mussel byssal threads and cordgrass' roots. In addition, the nitrogenous waste of mussel has been found to increase the growth of cordgrass. Due to these interactions, mussels have the potential to contribute to the success of salt marsh restoration. However, little is known about the drivers of the spatial distribution of mussels in Georgia. Understanding the factors that contribute to the distribution of mussels in Georgia can help inform managers on choosing locations to optimize the survivorship of mussels in restoration projects. This study sought to model mussel densities across the coast of Georgia and to compare predicted mussel densities in local marshes with mussel population parameters  as means to gauge habitat suitability. Mussel densities were collected through a series of field surveys across a range of salt marshes along the coast of Georgia. These data were then overlaid with spatial data such as distance to creek heads (the ends of intertidal creeks which flood the marsh platform), elevation, and slope. Highest predicted mussel densities occurred at an elevation of 0.7m relative to NAVD 88, close to creek heads and far from subtidal creeks. Using the predicted mussel densities from the model, low, medium and high density mussel sites were selected at two geographic locations, Cannon's Point Preserve, St. Simons, Georgia and Dean Creak, Sapelo Island, Georgia, to conduct mussel growth, predation, and recruitment experiments. In areas with higher predicted mussel densities, mussel recruitment and growth rates were the highest. Despite being statistically significant, differences in growth rates may not be biologically meaningful. While not statistically significant, predation risk was lowest in areas of high predicted mussel densities and increased with decreasing density. This indicates that in areas of low predicted mussel densities, recruitment and predation risk are likely the limiting factor to mussel densities.

INDEX WORDS: Ribbed mussels, Georgia, Species distribution model, Growth rates, Recruitment, Predation

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Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

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# CHAPTER 1

# ELEVATION AND MARSH FEATURES STRUCTURE RIBBED MUSSEL (*GEUKENSIA DEMISSA*) DISTRIBUTION IN GEORGIA'S SALT MARSHES.

## **Introduction**

Species distribution modeling is an ecological tool that combines abundance or occupancy data with explanatory environmental variables to understand and predict the distribution of species (Elith and Leathwick 2009). These models have many management applications ranging from predicting areas vulnerable to invasive species (Peterson et al. 2003; Stolhgen et al. 2010; Blanco et al. 2021), understanding how a species distribution may vary with climate change (Peterson et al 2001; Bateman et al. 2010), and finding suitable habitat for protected areas (Fong et al. 2015; Kaky and Gilbert 2016). Due to the ability to be used in a large amount of systems, species distribution modelling can helpful when managing species and habitats.

In intertidal ecosystems, the spatial distribution of intertidal mollusks is primarily related to the propagule supply (Hughes 1990), the types, diversity of, and proximity to different habitats (Carroll et al. 2015; Zeigler et al. 2018; Carroll et al. 2019), biotic interactions (Connell 1972; Peterson and Black 1991; Johnson and Smee 2014), and elevation/exposure (Jensen 1992). Elevation within the tidal prism affects submergence times; prolonged submergence may benefit organisms by increasing foraging and growth rates (Seed 1969; Peterson and Black 1988; Jensen 1992; Stiven and Gardner 1992), although it could also increase risk of predatory mortality (Fodrie et al. 2014; Johnson and Smee 2014). The trade-offs between growth and survival drives species distributions into specific ranges of intertidal elevation. Elevation may also interact with other factors that could influence species distribution, including wave energy (Robles et al.

2010), shading (Lamb et al. 2014), and density dependent effects (Robles et al. 2010). Therefore, while elevation is critical for understanding the distribution of intertidal species, it is important to consider other factors that may influence distributions.

Salt marshes are globally-distributed, complex intertidal ecosystems that are characterized by salt tolerant vegetation that provide a suite of ecosystem services for coastal communities such as erosion control (Moller et al. 1999), high primary production (Silliman and Bortolus 2003), carbon sequestration (Chmura et al. 2003), habitat for economically important organisms (Kennedy and Barbier 2016), and water filtration (Breaux 1995; Morgan et al. 2009). Like other intertidal ecosystems, elevation structures the composition of species across the salt marsh where distributions of both flora and fauna are restricted to specific zones within the marsh (Kuenzer 1961; Schalles et al. 2013; Hunter et al. 2016; Li et al. 2018; Viswanathan et al. 2020). In Atlantic salt marshes, tall form *Spartina alterniflora* is found in the lowest elevation zones and marsh succulents such as *Salicornia* sp. found in high elevation areas (Schalles et al. 2013), and distinct faunal communities exist associated with these vegetation zones (Schalles et al. 2013; Schwarzer et al. 2020). For example, the distribution of both fiddler crabs and littorinid snails has been linked to different *Spartina* growth forms (Teal 1958; Schalles et al. 2013). In addition, distance to different marsh features, such as upland habitats and creeks, can an also shape marsh species distributions (Hunter et al. 2016; Crotty and Angelini 2020; Schwarzer et al. 2020).

The ribbed mussel (*Geukensia demissa*) is an ecologically important bivalve species found in salt marshes along the Atlantic coast of the United States. These mussels are found attached to each other in large aggregations around the marsh grass root system using byssal threads. Ribbed mussels are considered a secondary foundation species in salt marshes because they provide a variety of important ecological services and facilitate healthy marshes (Altieri et al. 2007). Living embedded in the marsh matrix, mussels improve marsh plant resilience to stressors by adding nutrients (Bertness 1984), reducing erosion (Altieri et al 2007), and enhancing sediment accretion (Smith and Frey 1985). The presence of mussels can facilitate *Spartina* recovery in dieback areas (Rachel Guy, Sapelo Island National Estuarine Research Reserve, *pers. comm.*) and help maintain grass growth in periods of drought stress (Angelini et al. 2016). Mussels also perform other functions, including water filtration (Kreeger and Newell 2001), nutrient cycling (Kuenzler 1961), and increased habitat complexity (Newell 2004). Although historically omitted from marsh management strategies, there is increasing interest in their role in marsh restoration, particularly for living shorelines where mussels might facilitate rapid grass growth (Moody et al. 2013). Given the multiple services provided by mussels and interest in their use for management, it is critical to understand the factors that might influence mussel distribution in marshes.

Since mussel distributions vary across their geographic range, managers should have knowledge on local mussel distributions before they can be incorporated into restoration and management efforts. The differences in distribution across their range may be a result of variability in tidal heights, which can range from as high as 3 meters in Georgia to as low as 0.12 meters in Maryland (Stiven and Gardner 1992), and the associated elevation gradients at these marshes. Along the northeastern US coast, mussels are found distributed in thick bands immediately along the marsh edge (Bertness 1984), whereas in southeastern estuaries, they are commonly found in clumps dispersed throughout the marsh platform (Lin 1989; Angelini et al. 2015). More specifically, mussels in the southeast US are typically found around creek heads, delta-like areas in the marsh in which many drainage channels merge into a single creek that flood and drain the platform (Keunzler 1961; French and Stoddart 1992; Crotty and Angelini 2020). While previous studies have focused on mussel distributions at different points along their range, most studies only focus on one or two factors such as elevation (Julien et al. 2019), vegetation type/density (Keunzler 1961; Watts et al. 2011; Schalles et al. 2013; Honig et al. 2015), distance to marsh features (Keunzler 1961; Lin 1989; Stiven and Gardner 1992; Nielson and Franz 1995; Crotty and Angelini 2020), water quality (Julien et al. 2019), and surrounding landcover (Isdell et al. 2018). As the distributions of intertidal mollusks can be influenced by multiple factors, it is important to examine distribution patterns across multiple within marsh factors in order to successfully model mussel distributions.

The objective of this study was to identify which within marsh factors influence the distribution of ribbed mussel densities in Georgia with the goal of creating a model of mussel densities across the coast of Georgia. This model could be used to help inform managers on where to utilize mussels in restoration projects in Georgia. Mussel densities, obtained using transect surveys, were related to spatial data of geomorphological features such as elevation, slope, distance to subtidal creek and distance to intertidal creek heads (Figure 1.1). Due to trade-offs between ecological processes, and variation in within marsh factors, I made the following predictions: (1) mussel density would be greatest far away from subtidal creeks at mid tidal elevations; (2) an interaction between creek fetch, distance to creek heads and distance to subtidal creeks would drive mussel density in the survey area as previous studies indicated creek length can positively affect mussel densities near creek heads (Crotty and Angelini 2020).

## **Methods**

### *Study Sites*

Mussel surveys were conducted at 11 *Spartina alterniflora*-dominated marsh sites in coastal Georgia (Figure 1.2). Georgia marshes are heterogeneous landscapes defined by changes in elevation, soil composition, and vegetation (Schalles et al. 2013) with extreme (~3m spring tide) tidal range (O'Connell et al. 2017). Each marsh can be broken into 3 zones based on elevation: creek levee, low marsh platform, and mid marsh platform (Kuenzler 1961). Creek levees are high elevation areas along subtidal creek banks, dominated by tall form *S. alterniflora*. The low marsh platform is the lower elevation area of the marsh, dominated by medium to short form *S. alterniflora* and is frequently flooded. The high marsh platform is infrequently flooded and is populated by high marsh vegetation such as *Juncus roemerianus* and *Salicornia virginica*.

### *Estimating Mussel Densities*

Mussel densities were counted using transect surveys. At each site, a series of transects were established from the edge of a subtidal creek to the salt marsh/forest ecotone (Figure 1.3). Every 5m, a 0.25m$^2$ quadrat was haphazardly dropped and mussels were non-destructively counted, with mussels harvested every 10 mussel counts (i.e. 50 m) in order to measure condition index, a measure of mussel health, and mussel scarring, a proxy for predation (see Appendix 1 for details). This led to a conservative estimate as buried individuals may be missed (Nielson and Franz 1995). The GPS coordinates were recorded using a Garmin GPSMAP 78sc handheld GPS Unit. Notes were then taken of any elevation change and presence of creeks and creek heads to be used for ground-truthing raster data. Transects were spaced 35m apart, and 3-5 transects were conducted until 800-1000m of marsh were surveyed (Figure 1.4).

### *Spatial Data*

Numerous spatial variables, including elevation, slope, distance to subtidal creek, distance to intertidal creek, and distance to creek, were examined for effects on mussel distribution. Elevation and slope rasters were created using data collected by the National Oceanic and Atmospheric Administration (NOAA) 2010 LiDAR surveys. The elevation data were collected in feet relative to NAVD88 datum, corrected for vegetation height (Hladik et al. 2013), and used to calculate marsh slope using ArcMap. A quadratic term was used for elevation as intertidal species tend to have upper and lower elevation limits (Connell 1972, Robles et al. 2010, Fodrie et al. 2014). Subtidal creeks were defined as bodies of water inundated during the full tidal cycle and were acquired from the National Wetlands Inventory (NWI). Intertidal creeks, the bodies of water that were not always submerged, and creek heads, the points where intertidal creeks spill onto the marsh platform, were delineated using aerial imagery taken in 2018 by NOAA. Separate Euclidean distance rasters were created using the subtidal, subtidal/intertidal, and creek head features as input layers.

### *Scale Selection*

All rasters were resampled to a 4m grain size. This grain size both adequately represented the accuracy of the handheld GPS unit (3-4m) and was the finest grain size possible given the elevation data. Ribbed mussels are affected by fine scale changes in marsh elevation which can alter submergence/exposure times. Because of this sensitivity to fine scale elevation changes, the smallest grain size possible was used.

### *Statistical Analysis*

In order to determine which marsh factors affected mussel distribution, data were analyzed using a zero inflated negative binomial model, a type of n-mixture model, with a random effect for site. Explanatory variables were first examined for collinearly using a Pearson correlation coefficient cutoff of $|r|<0.50$. All variables were scaled from 0 to 1 to ensure model convergence. N-mixture models are hierarchical models that allow for estimation of abundance and occupancy in relation to predictor variables **(**Royles 2004**)**. Zero inflated models are n-mixture models that allow estimation of count data when the data are over dispersed with zeros by modelling two processes: probability of occupancy (Bernoulli distribution) and abundance (Poisson or Negative Binomial) (Martin et al. 2005). The model for count data (C) can be written in the following manner:

$$\omega_{ij} \sim \text{Bernoulli}(\psi_{ij}) \ (1)$$

$$\text{Logit}(\psi_{ij}) = a_0 + a_1 * \text{elevation}_{ij} + a_2 * \text{elevation}^2_{ij} + a_2 * \text{slope}_{ij} + a_3 * \text{creek head distance}_{ij} + a_4 * \text{subtidal creek distance}_{ij} + a_5 * \text{creek head distance}_{ij} * \text{subtidal creek distance}_{ij} + a_6 * \text{site}_j \ (2)$$

$$C_{ij} \sim \text{Negative Binomial}(\omega_{ij} * \lambda_{ij}, \alpha) \ (3)$$

$$\text{Log}(\lambda_{ij}) = b_0 + b_1 * \text{elevation}_{ij} + b_2 * \text{elevation}^2_{ij} + b_2 * \text{slope}_{ij} + b_3 * \text{creek head distance}_{ij} + b_4 * \text{subtidal creek distance}_{ij} + b_5 * \text{creek head distance}_{ij} * \text{subtidal creek distance}_{ij} + b_6 * \text{site}_j \ (4)$$

where $\omega_{ij}$ is a binary variable in which 1 refers to mussel occupancy and 0 refers to lack of mussel occupancy for the ith quadrat at the jth site, $\psi_{ij}$ is the probability of occupancy for the ith quadrat in the jth site, $\text{elevation}_{ij}$ is the elevation for the ith quadrat at the jth site, $\text{elevation}^2_{ij}$ is the quadratic term of elevation for the ith quadrat at jth site, $\text{slope}_{ij}$ is the slope for the ith quadrat at the jth site, creek head $\text{distance}_{ij}$ is the distance to the creek head for the ith quadrat at the jth site, subtidal creek $\text{distance}_{ij}$ is the distance to subtidal creek for the ith quadrat at the jth site, and $\text{site}_j$ is a random effect for the jth site, C is mussel density for the ith quadrat at the jth site and $\lambda_{ij}$ is the abundance for the ith quadrat in the jth site.

Data analysis was conducted using JAGS through R (R Core Team 2020) using the package runjags (Denwood 2016). The model was run with 200,000 iterations and convergence was verified by checking trace plots. Model fit was assessed by calculating a Bayesian p value, a posterior predictive check (Gelman et al. 1996). To compare discrepancy between actual data and simulated data, eighteen thousand new mussel density data sets were generated using estimate parameters and likelihood of these data sets were compared. Well-fitting models have values close 0.5, further from 0 or 1. The model yielded a Bayesian p value of 0.769. Shell scaring and condition index were analyzed using a different analysis (Appendix 1).

## Results

Observed mussel densities ranged from 0 to 62 mussels per $0.25\text{m}^2$. Both mussel occupancy and mussel abundance were driven by a quadratic effect of elevation. Both the highest mussel occupancy and abundance were predicted at an elevation of 0.7m (Figure 1.5). These elevation terms had the largest effect on both occupancy and abundance; the probability of mussel occurrence increased by 0.070 for every 10 cm of elevation compared to -0.002 for every 1m away from a creek head and -0.035 for every 1 degree of slope. Mussel abundance increased by 0.750 mussels for every 10 cm of elevation compared to 0.018 mussels for every 1m away from a subtidal creek.

Although, elevation had the largest effect on occupancy and abundance , both were also significantly affected by other marsh factors. Mussel occupancy had negative relationships with both slope (Table 1.1; Figure 1.6) and distance to creek heads (Table 1.1; Figure 1.6), being highest in areas with low slopes and decreasing with distance from creek heads (Table 1.1; Figure 1.6). In addition, there was a significant positive interaction between distance to creek head and distance to subtidal creek on mussel occurrence (Table 1.1; Figure 1.6), indicating higher occupancy at longer creek heads and a reduced effect of creek head on occupancy. Mussel abundance was only influenced by elevation and distance to subtidal creeks, with abundance increasing with  distance into the marsh (Table 1.1; Figure 1.6). Predicted mussel densities and distribution is the combination of occupancy and abundance from the model outputs. Highest mussel density was predicted in mid elevation marsh platforms, close to creek heads (Figure 1.7).

Mussel condition index was not significantly affected by any within-marsh factor, and only shell scarring had an effect on mussel condition (heavily scarred mussels had lower condition; Appendix 2a). Mussels were more heavily scarred further away from creek heads (Appendix 2b).

## **Discussion**

Location within the marsh and associated within-marsh features, had significant impacts on where mussels were found across the 11 surveyed marshes.  Elevation was the most important predictor of occupancy and abundance, with both occurring within a small range of elevations and having the same optimal elevation.  In addition, outside of elevation, both occupancy and abundance were impacted by different marsh features (e.g. occupancy was affected by distance to creek heads and slope; abundance was affected by distance to subtidal creeks). Therefore, in this study, the distribution of ribbed mussels displayed similar patterns to other intertidal organisms such as blue mussels (Seed 1969), cockles (Jensen 1992), and oysters (Fodrie et al. 2014) which likely reflect trade-offs between abiotic and biotic stressors (e.g. competition, predation, feeding time, and temperature; Connell 1972; Widdows et al. 1979; Peterson and Black 1991; Jensen 1992; Fodrie et al. 2014; Lamb et al 2014).

The most important predictor of ribbed mussel distribution was elevation, with both occupancy and abundance occurring within the same optimal elevation range. This distribution pattern is likely linked to trade-offs between exposure and submergence. At lower elevations, organisms are submerged longer, which can benefit intertidal organisms by increasing foraging times (Seed 1969; Jensen 1992) while reducing desiccation risk (Connell 1972; Widdows et al. 1979; Lamb et al. 2014). In prior studies, ribbed mussels grow much faster at lower elevations (Kuenzler 1961; Striven and Gardner 1992). However, longer submergence times can increase predation risk (Fodrie et al. 2014; Johnson and Smee 2014) and competition (Peterson and Black 1991), and these biotic interactions tend to drive intertidal organisms into higher elevations (Peterson and Black 1991; Fodrie et al. 2014; Johnson and Smee 2014). However, abiotic stressors related to temperature (Jost and Helmuth 2007) and prolonged exposure times (Angelini et al. 2016) can lead to mortality if mussels are located at tidal elevations that are too high. Therefore, ribbed mussels in Georgia marshes are distributed, in terms of both occupancy and abundance, within a narrow band of elevation (0.5m and 0.9m relative to NAVD 88) likely in response to these trade-offs.

After elevation, mussel occupancy was also controlled by position relative to creek heads on the marsh platform, where mussels were more likely to occur closer to creek heads on the marsh platform. In Georgia, areas around creek heads typically have a high density of mussels (Kuenzler 1961; Crotty and Angelini 2020). Therefore, the increased probability of occurrence predicted by the model may be due to increased recruitment and food supply (Crotty and Angelini 2020). While occupancy increased close to creek heads, there was no significant effect on mussel abundance, and the current study cannot discern the divergence between occupancy and abundance in the model. However, predicted density, which is the product of occupancy and abundance, was highest around creek heads. There was also an interaction between distance to creek heads and creek length; the probability of occurrence was higher near creek heads on longer intertidal creeks. Longer creeks may have greater tidal prisms which could affect larval supply onto the marsh platform (Crotty and Angelini 2020). Finally, occupancy was also affected by marsh slope, with probability of occurrence being higher in areas with low slope (i.e. the platform).

For mussel abundance, the only other meaningful predictor after elevation was position relative to the subtidal creeks, with abundance increasing with distance away from subtidal creeks. The most likely explanation for this pattern is predation risk. Subtidal creeks are access points of predators onto the marsh. As the marsh is flooded, blue crabs are able to forage for food in the marsh zones (Fitz and Wiegert 1991), and intense predation occurs close to the marsh edge/subtidal creek ecotone (Lin 1989). These negative edge effects, where organisms suffer higher mortality in edge habitats, are common across many ecosystems (Kolbe and Janzen 2002; Batary and Baldi 2004; Vetter et al. 2013; Mahoney et al. 2018). The potential high predation pressure may limit the abundance of mussels close to the subtidal creek banks. In addition, the portion of marsh adjacent to the subtidal creek also tends to form a levee of slightly higher elevation in Georgia marshes (Keunzler 1961), which could also limit mussels due to potential prolonged exposure and desiccation stress (Widdow et al. 1979; Lamb et al. 2014; Angelini et al. 2016).

In intertidal ecosystems, elevation is often the only factor considered when examining the distributions of species (Connell 1972; Johnson and Black 2008; Schalles et al. 2013), and it did have the largest effect on mussel distribution in my study. However, other within marsh factors also significantly impacted the abundance of mussels within their preferred elevation, including distance to different marsh features. This illuminates the importance of considering multiple factors when modelling species distributions, particularly spatial patterning of key habitat features. In order to have stronger predictive power, multiple factors should be incorporated into species distribution models (Elith and Leathwick 2009). Although the models used in this study included multiple marsh factors along with elevation, they have limitations to their explanatory power. For example, incorporating other environmental factors could have improved the model predictions (Elith and Leathwick 2009), and these could include vegetation density (Keunzler 1961; Schalles et al. 2013) and predator abundance (Lin 1989). In addition, landscape scale factors such as landcover types (i.e. forest, development) and creek characteristics could also improve model predictive power (Isdell 2018). Further model limitations could be due to sample bias at a limited subset of marshes across the coast. Logistic access limited sampling to only sites attached to upland habitat that were easily accessible by vehicle, so the model results may not be applicable to marshes that are not attached to upland habitat, such as marsh islands. Therefore, while my model was useful in predicting mussel distribution due to key marsh features, future models should take in account both landscape scale characteristics of sites, as well as environmental qualities within sites.

One application of species distribution models is predicting future populations (Elith and Leathwick 2009). As a result of being confined to tight elevation limits, sea level rise may negatively affect population sizes of mussels in Georgia. In the Chesapeake Bay, a species distribution model was used to estimate the effects of 30 years of sea level rise on mussel populations; the model estimated that 50% of mussel populations could be lost by 2050 due to sea level rise (Isdell et al. 2020), although similar predictions for mussels in Georgia have not been made. Distribution models can also be used to estimate ecosystem services provided to different regions of the marsh, such as filtration rates (Moody and Kreeger 2020) and cordgrass-mussel facilitation (Crotty and Angelini 2020). These models would be useful in determining how mussel loss due to harvesting (Julien et al. 2020) or climate change (Isdell et al. 2020) will affect water quality (Kreeger and Newell 2001), marsh vegetation growth (Angelini et al. 2016), and diversity of other marsh organisms (Newell 2004).

Finally, the model outputs may be useful when considering mussel restoration and transplantation, although further research should be conducted. Importantly, high species densities may not always correlate to high quality habitat (Vanhorne 1983). In this study, areas with low mussel density may not necessarily be low quality habitats, and low density may reflect other processes (i.e., recruitment limitation; Hughes 1990). Creek banks are often the site of marsh restoration projects due to the large amount of erosion these areas can receive (Moody et al. 2013), although the model predicts these areas are devoid of mussels. This model cannot determine if low predicted mussel density areas, such as creek banks, are not suitable for mussel transplantation, or if low density areas are driven by recruitment limitation, for example. In order for this model to be useful to managers, information regarding population parameters of mussels across their distribution is needed.

In conclusion, species distribution models of ecologically important organisms are an important tool for management. This study supports findings of previous research (Lin 1989; Crotty and Angelini 2020) that the distribution of ribbed mussels in the southeast is primarily on the marsh platform near creek heads, in stark contrast to other portions of the ribbed mussel geographic ranges where they are found in dense bands along subtidal creeks (Bertness 1984). Areas near subtidal creeks in Georgia are devoid of mussels, although this study could not determine the suitability of these areas for mussels. Overall, this study highlights the importance of using local data when creating species distribution models and making management decisions regarding vital coastal species. Further research should be conducted on mussel demographic rates to determine why mussels exhibit the distribution pattern on the marsh platform near creek heads.

Table 1.1: Prior distribution and posterior means with 95% credible intervals for zero inflated negative binomial model of ribbed mussel distributions across Georgia using density data collected in 2019-2020. Elevation refers to elevation in meters relative to NAVD88, Elvation2 refers to the quadratic term for elevation in meters relative to NAVD88, slope refers to slope in degrees, subtidal refers to distance to subtidal creek n meters, head refers to distance to creek head in meters, and subtidal*head refers to the interaction between distance to subtidal creek and distance to creek head. Parameters in bold indicate credible intervals do not overlap with zero.

| | Occupancy | | | | | Abundance | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Parameters | Prior | Prior Mean | Pstdev | Post Mean | Credible Interval (95%) | Prior | Prior Mean | Pstdev | Post Mean | Credible Interval (95%) |
| Intercept | normal | 0 | 0.01 | -2.898 | -5.077 - -0.712 | normal | 0 | 0.01 | -0.527 | -2.48 - 1.366 |
| Elevation | **normal** | **0** | **0.01** | **16.253** | **9.95 - 22.838** | **normal** | **0** | **0.01** | **8.343** | **2.292 - 14.691** |
| Elevation2 | **normal** | **0** | **0.01** | **-16.653** | **-23.252 - -10.628** | **normal** | **0** | **0.01** | **-8.136** | **-13.801 - -2.738** |
| Slope | **normal** | **0** | **0.01** | **-3.07** | **-5.693 - -0.714** | normal | 0 | 0.01 | -0.343 | -2.372 - 1.787 |
| Subtidal | normal | 0 | 0.01 | -1.014 | -2.578 - 0.371 | **normal** | **0** | **0.01** | **1.179** | **0.209 - 2.152** |
| Head | **normal** | **0** | **0.01** | **-3.694** | **-5.911 - -1.708** | normal | 0 | 0.01 | 0.419 | -1.016 - 1.896 |
| Subtidal*Head | **normal** | **0** | **0.01** | **7.034** | **3.224 - 11.736** | normal | 0 | 0.01 | -2.484 | -5.188 - 0.241 |

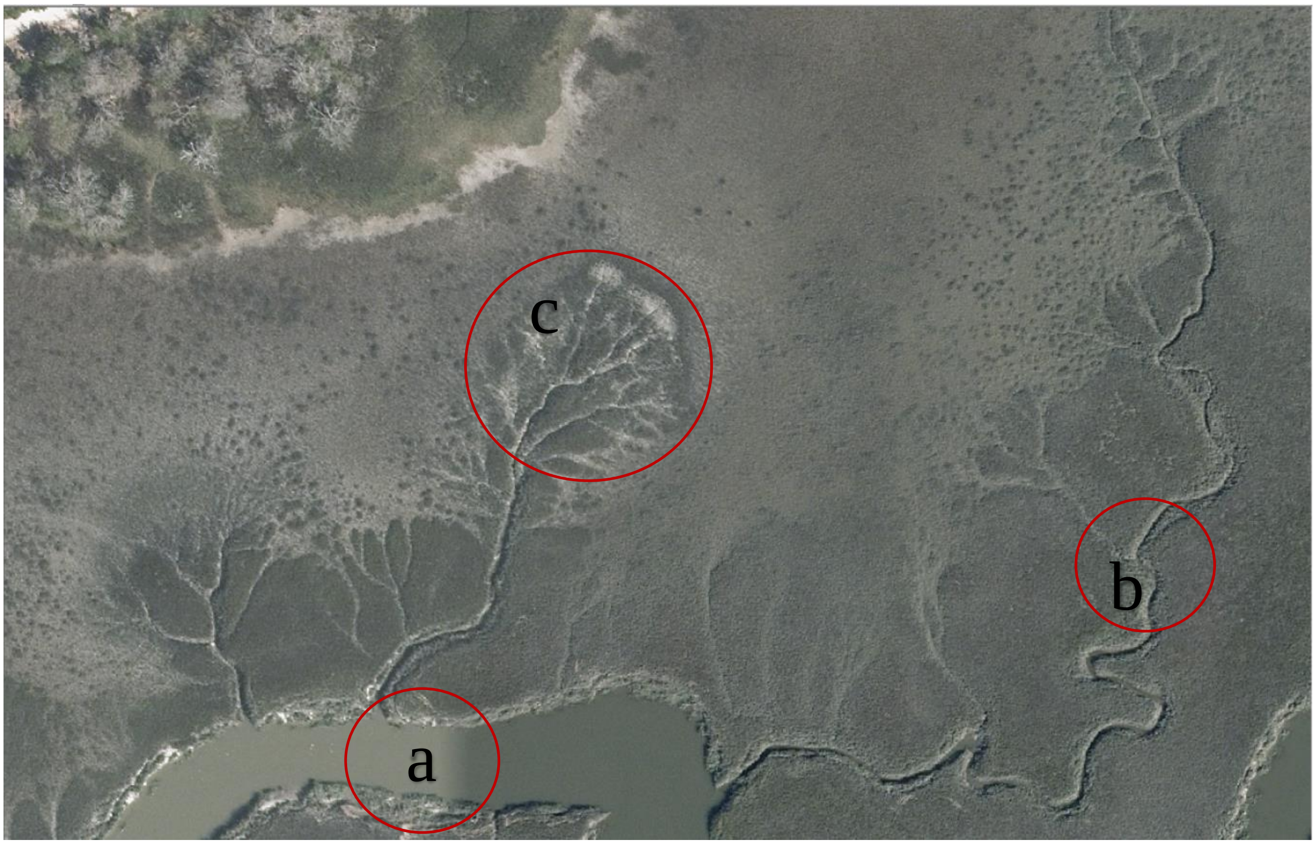


Figure 1.1: Marsh scale features used to predict ribbed mussel densities: subtidal creek (a), intertidal creek (b) and creek head (c).

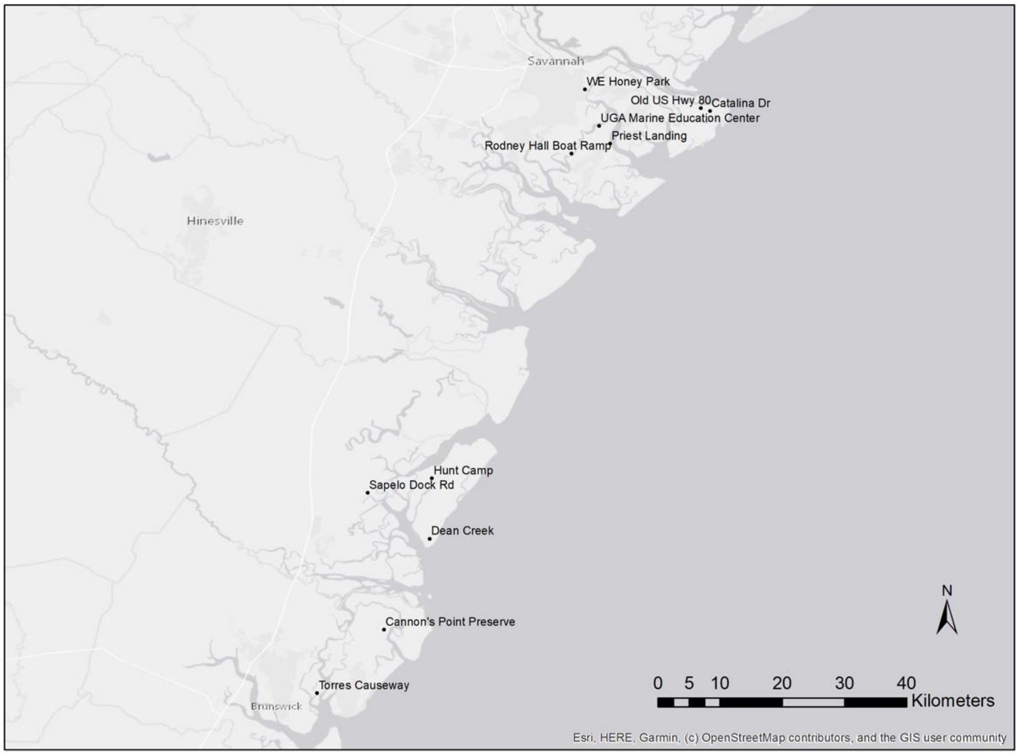


Figure 1.2: Location of ribbed mussel surveys across the coast of Georgia, USA.

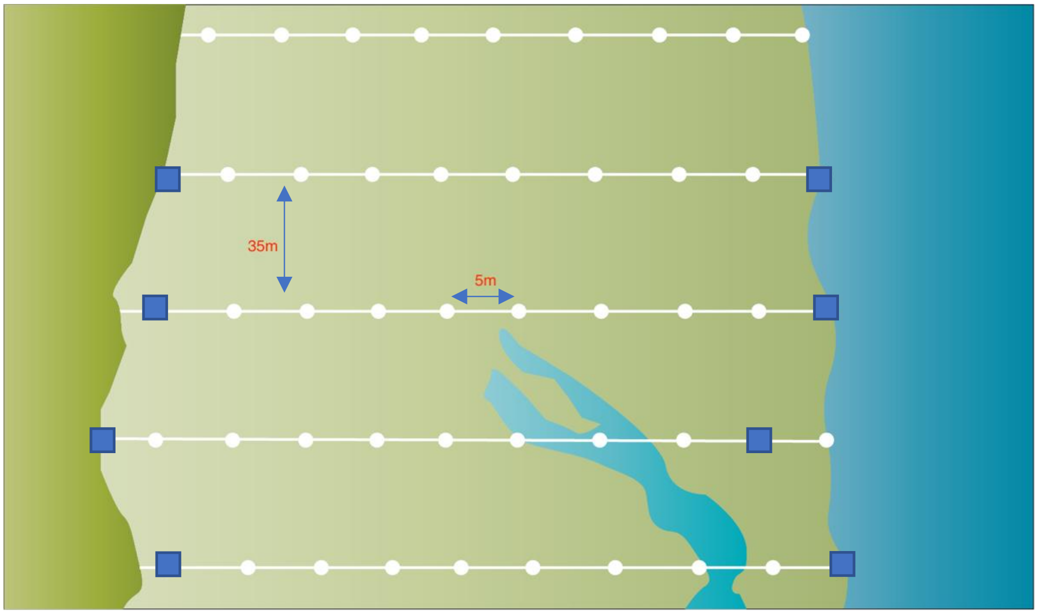


Figure 1.3: Diagram illustrating the transect survey design at each sampled marsh. White lines represent transect lines constructed from upland to creek with each point representing a mussel count within a $0.25m^2$ quadrat. Boxes indicate quadrates in which mussels were harvested.

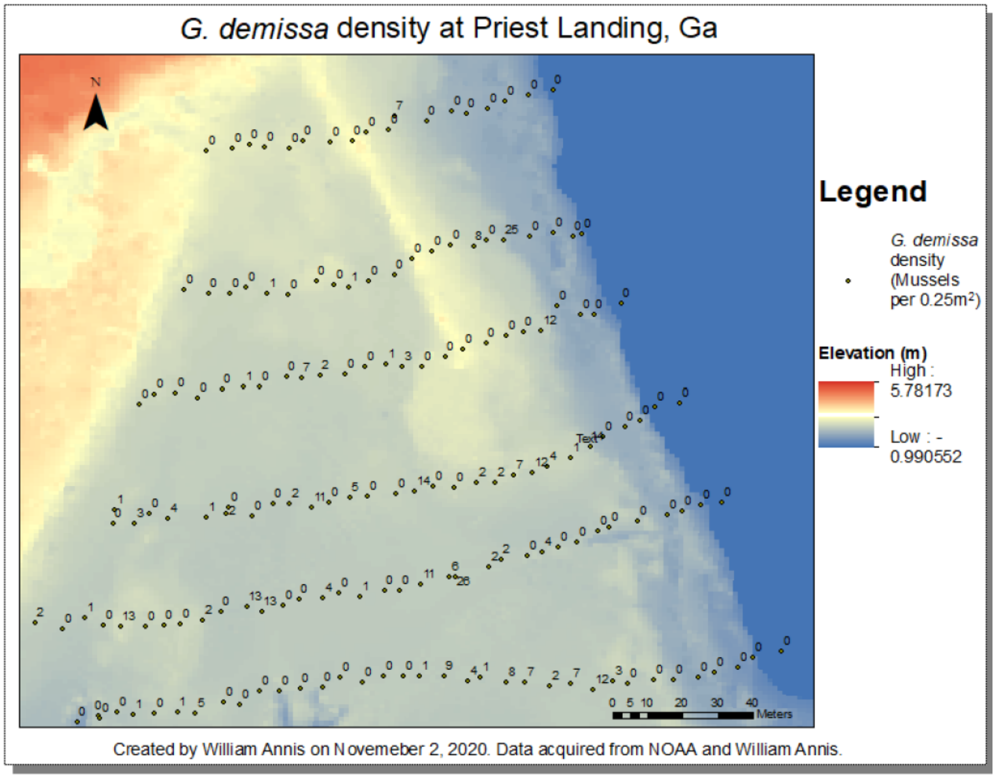


Figure 1.4. Example of mussel survey data from the survey at Priest landing on Skidaway Island, Georgia, overlayed with elevation data (m relative to NAVD88). Each point represents a ribbed mussel count in mussels per $0.25m^2$.

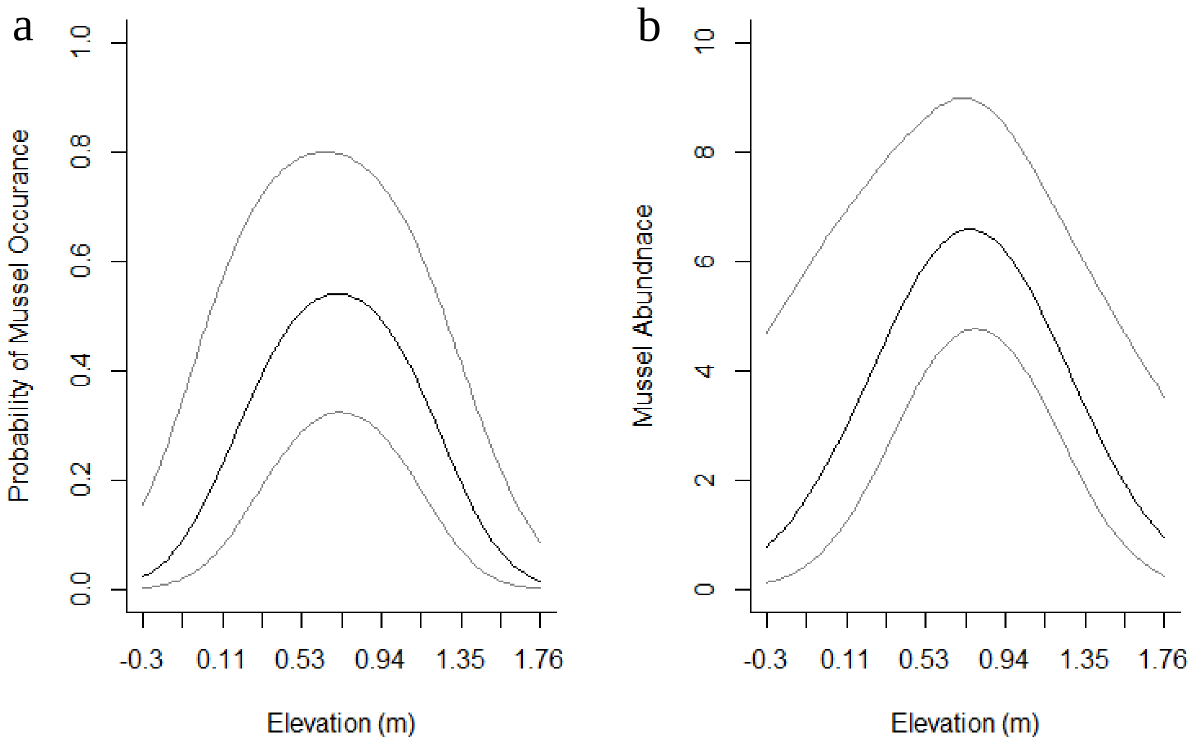


Figure 1.5: Probability of mussel occurrence (a) and abundance (b) as a function of elevation (m). Gray lines represent 95% Credible Interval. n=1541 observations at 11 sites.

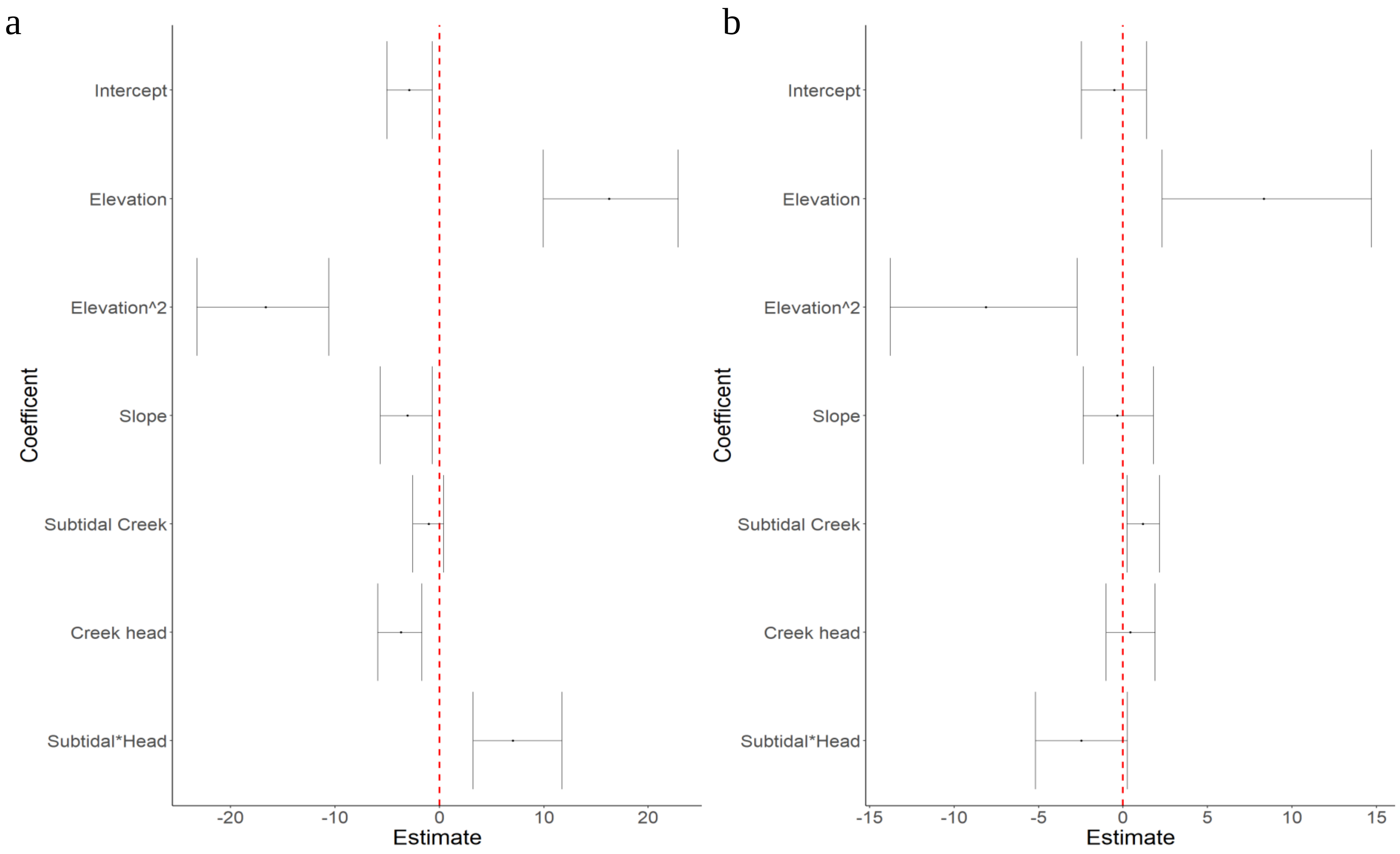
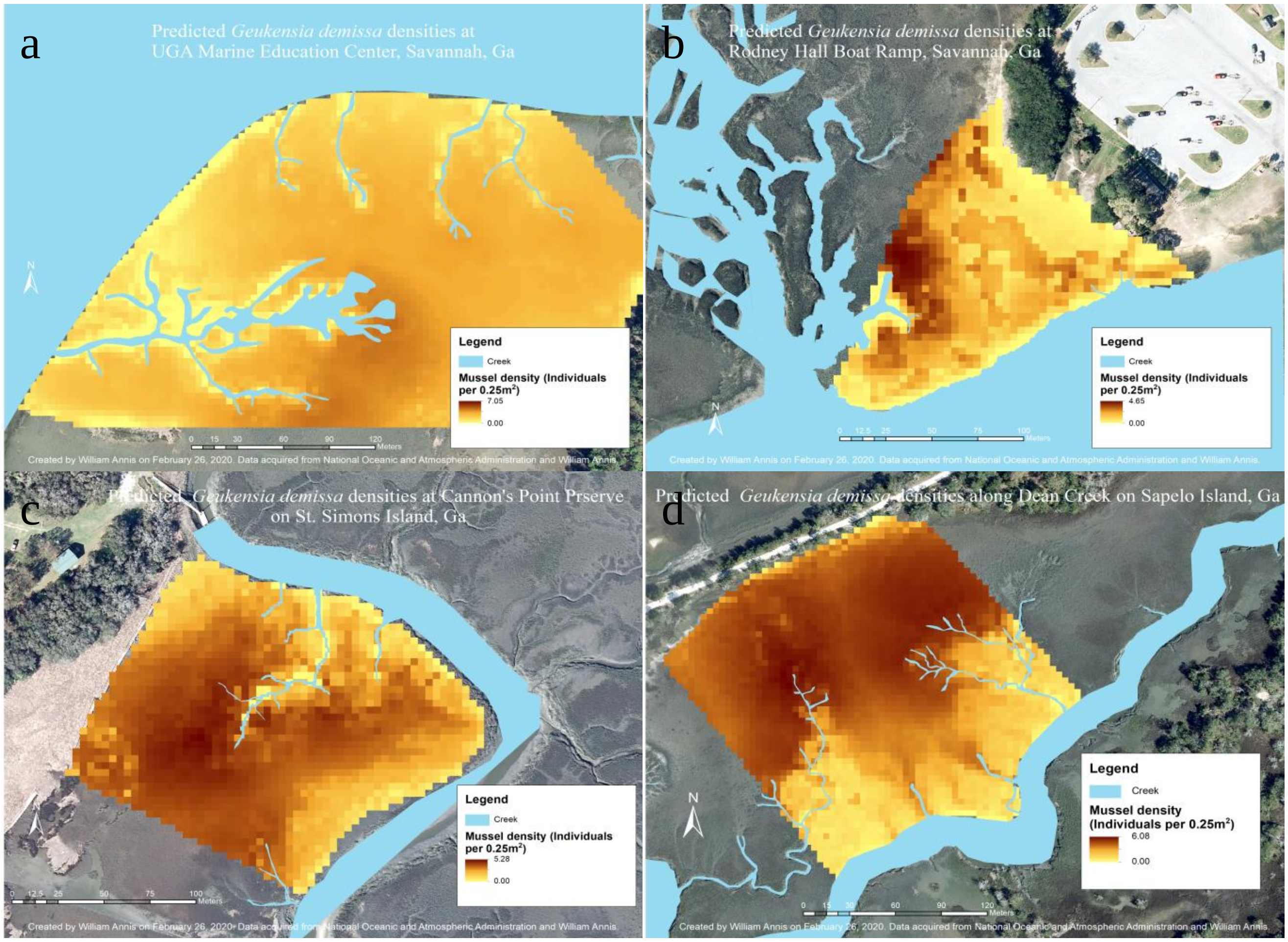


Figure 1.6: Estimates of mussel occupancy (a) and abundance (b) model beta parameters with 95% credible interval. Subtidal creek and creek head refer to distance from each feature. Subtidal*Head refers to the interaction between distance to creek heads and distance to subtidal creeks (i.e. distance from creek heads associated with longer creeks has a lesser effect).



Predicted *Geukensia demissa* densities at UGA Marine Education Center, Savannah, Ga

Created by William Annis on February 26, 2020. Data acquired from National Oceanic and Atmospheric Administration and William Annis.

Predicted *Geukensia demissa* densities at Rodney Hall Boat Ramp, Savannah, Ga

Created by William Annis on February 26, 2020. Data acquired from National Oceanic and Atmospheric Administration and William Annis.

Predicted *Geukensia demissa* densities at Cannon's Point Prserve on St. Simons Island, Ga

Created by William Annis on February 26, 2020. Data acquired from National Oceanic and Atmospheric Administration and William Annis.

Predicted *Geukensia demissa* densities along Dean Creek on Sapelo Island, Ga

Created by William Annis on February 26, 2020. Data acquired from National Oceanic and Atmospheric Administration and William Annis.

Figure 1.7: Example predicted mussel densities (mussels per 0.25m$^2$) at UGA Marine Education Center in Savannah, Georgia (a), Rodney Hall Boat Ramp in Savannah Georgia (b), Cannon's Point Preserve on St. Simon's Island, Georgia (c), and Dean Creek on Sapelo Island, Georgia (d).

# CHAPTER 2

# POPULATION PARAMETER OF RIBBED MUSSELS (*GEUKENSIA DEMISSA*) VARY ACROSS A GRADIENT OF PREDICTED MUSSEL DENSITIES

## Introduction

Population distributions in open systems are often related to population parameters such as propagule supply, subsequent survival, and growth (Connell 1972; Hughes 1990). For intertidal marine populations, these key processes interact with elevation and tidal exposure. In some populations, growth is limited by the supply of new individuals (Connell 1985; Hughes 1990; Armsworth 2002), while in others, post settlement processes structure populations **(**Jernakoff and Fairweather 1985; Doherty and McWilliams 1988**)**. Intertidal ecosystems have been well studied for population dynamics, since they offer a gradient of biotic and abiotic factors, accessibility from land, and are home to many easy-to-study sessile organisms. Intertidal organisms often have distributions within the tidal prism that are structured by both biotic (competition, predation) and abiotic (exposure, submergence) factors along a gradient of elevation (Seed 1969; Connell 1972; Peterson and Black 1988; Schalles et al. 2013).

Numerous studies have explored the distribution of marine fauna in various intertidal habitats, including rocky intertidal (Seed 1969; Connell 1972; Robles et al. 2010; Lamb et al. 2014), mud and sand flats (Peterson and Black 1988,1991; Jensen 1992), oyster reefs (Bishop and Peterson 2006; Fodrie et al. 2014; Johnson and Smee 2014), and salt marshes (Lin 1989; Stiven and Gardner 1992; Nielson and Franz 1995; Franz 2001; Crotty and Angelini 2020). A commonality across these coastal habitats is that the distribution of marine fauna is the result of interactions between biotic and abiotic variables. However, the distribution of organisms throughout intertidal habitats is not uniform. For example, the effect of elevation on the population parameters in salt marsh organisms are complicated through interactions of vegetation and marsh geomorphology (Kuenzer 1961; Eckman 1983; Schalles et al. 2013; Crotty and Angelini 2020). Since marshes are vital coastal habitats, it is important to understand the mechanisms driving species distribution across these intertidal marshes for effective management.

The ribbed mussel (*Geukensia demissa*) is found in salt marshes across the Atlantic coast of the United States and plays a critical role in marsh function. Mussel aggregations are key features that provide numerous functions to salt marshes, where mussels aid in stabilizing the marsh sediments with a matrix of roots and byssal threads (Altieri et al. 2007), fertilize plants through nitrogenous wastes (Bilkovic et al. 2017), and make grass more resilient to other stressors (Angelini et al. 2016). In addition, marsh restoration projects experience increased cordgrass growth and survival when mussels were restored along with cordgrass (Derksen-Hooijberg et al. 2018). Throughout most of their geographic range, ribbed mussels are found in dense bands along the marsh- subtidal creek edge (Bertness 1984), although in portions of the southeast US, including South Carolina and Georgia, mussels are found in clumped distributions on the marsh platform far from the marsh edge (Keunzler 1961; Lin 1989; Crotty and Angelini 2020). This distribution may be attributable to predation (Lin 1989), although the mechanisms behind this distribution are not fully explored. For example, mussels on the marsh platform are found in lower elevations near intertidal channels that flood and drain marshes (Crotty and Angelini 2020), which may also be corridors where predators travel (Crotty et al. 2020). Areas of slightly lower elevation may lead to enhanced larval delivery and prolonged feeding (Jensen 1992; Crotty and Angelini 2020), although these factors may interact with marsh parameters (i.e.

stem density/canopy height; Eckman 1983, Altieri et al. 2007). Given the importance of mussels to coastal ecosystems, it is critical to understand the drivers that influence their distribution.

Since the local distribution of species is driven by recruitment of new individuals, long-term survival, and growth, it is important to consider how marsh features (elevation, marsh plant density, distance from marsh features, etc.) might influence both environmental conditions and the component processes of population demographics. Location within in a marsh plays an important role in species processes; in some marshes, recruitment is the highest along the marsh edge and drops off moving into the marsh interior (Nielson and Franz 1995; Franz 2001), while recruitment is greatest in close proximity to intertidal creek heads in other marshes (Crotty and Angelini 2020). Once they recruit to the population, mussel growth rates have been linked to within-marsh patterns in elevation, where growth is highest at low elevations with prolonged submergence (Stiven and Gardner 1992; Crotty and Angelini 2020). Predatory mortality may be also be highest in the low elevation parts of the marsh (Stiven and Gardner 1992; Honig et al. 2015; Lin 1989), whereas mortality due to exposure stress and elevated temperatures are more common far from creek edges and at higher elevations (Stiven and Gardner 1992; Jost and Helmuth 2007).

In addition to influencing the distribution of mussels, marsh characteristics also influence the density of other organisms, including marsh grasses and predators, all of which may confound mussel recruitment, growth, and survival. Mussel recruitment is enhanced (Nielsen and Franz 1995), while growth ( Stiven and Gardner 1992) and predatory mortality (Crotty and Angelini 2020) are reduced, in areas of higher mussel density. Marsh plant density and morphology influences mussel processes by providing refuge from nekton predators (Crotty et al. 2020), increasing recruitment of mussels via passive deposition (Eckman 1983), and providing a shading effect to the mussels (Altieri et al. 2007). Proximity to other marsh fauna can also influence recruitment, growth and survival. High densities of crab burrows can increase predation risk (Crotty and Angelini 2020), and ultimately reduce recruitment (O'Beirn et al. 2000). Predation risk also influences growth rates, as mussels experiencing predation risk tend to exhibit reduced shell extension (Gosnell et al. 2017). Thus, patterns in the distribution of multiple marsh species can ultimately influence the establishment and persistence of mussel patches in southeastern marshes.

Finally, marsh features and the influence of other species can interact with overall water quality to effect mussel distribution. Although mussel growth rates are increased and desiccation is reduced in high salinity zones, the abundance of predators may be increased in areas of higher salinity (Honig et al. 2015). As a tradeoff, mussel densities are the greatest in areas of mid salinity (Honig et al. 2015, Julien et al. 2019). Since mussels graze on phytoplankton, suspended bacteria, and detritus (Langdon and Newell 1990), the quantity of food supply in the water also affects mussel growth (Peterson and Black 1991), which can vary within mashes, among marshes, and across seasons (Moody and Kreeger 2020), and can be affected by densities of marsh plants (Kreeger et al. 1988) and competitors (Peterson and Black 1991).

In summary, a confluence of interacting variables related to water quality, marsh geomorphology, and species distributions can potentially influence the population parameters of mussels in marshes. Since there is interest in using ribbed in marsh restoration projects (Moody et al. 2013), it is critical to not only understand how the population parameters of these mussels change across their local distribution. This study sought to examine the mechanisms behind the distribution of the ribbed mussel in Georgia. Specifically, this study tested how mussel (1) recruitment, (2) growth rate, and (3) mortality varied across the mussels' local distribution, and linked that variation to biotic and abiotic factors, including cordgrass density and canopy height, density of mussel conspecifics, food availability, and water quality. This study builds off the results from chapter 1 using the density model to generated predicted mussel densities. I predicted that recruitment would be highest in areas with high predicted mussel densities due to proximity to creek heads and greater access to tidal flow (Crotty and Angelini 2020), growth rates would be highest in areas with high predicted mussel densities due to increased feeding times, higher food availability, and lower temperatures (Altieri et al. 2007), and that predatory mortality would be highest at areas with lower predicted mussel densities due to lower vegetation density and greater predator access (Lin 1989; Honig 2015). To address these predictions (Figure 2.1), I conducted a series of *in situ* experiments at two different Georgia salt marshes.

## **Methods**

### *Study Site*

*In situ* experiments were conducted on a marsh bordering Dean Creek (31.391021 -81.274222) within the Sapelo Island National Estuarine Research Reserve (SINERR) and Cannon's Point Preserve (CPP; 31.25989 -81.339917), Georgia, USA. Both sites have expansive marshes dominated by *Spartina alterniflora* with patches of *Salicornia virginica* and *Juncus roemerianus* in higher elevation areas. Dean Creek is bordered by a subtidal creek at the lower end and small forest patches and roads at the upper end and is has 35,555 $m^2$ of marsh area (Figure 2.2a). The marsh at CPP is about 48,937 $m^2$, framed by a bend in a major subtidal creek on two sides with a forest patch on the upland side (Figure 2.2b). At both sites, the major subtidal creek is roughly the same fetch and is bordered by a high elevation levee. Numerous intertidal creeks dissect the levee with heads that spill into the marsh platform. The platform gradually increases in elevation until it reaches the forest ecotone.

### *Mussel Distribution and Experimental Plot Selection*

In order to select plots to conduct *in situ* experiments, predicted mussel densities were generated at both study sites using the density model from Chapter 1. This model was created using mussel densities collected from the two focal marshes and 9 additional sites. The model was then applied to rasters for each site to develop a species distribution model for each site. Predicted mussel densities were divided into three ranges: low (<1.59 mussels per 0.25m$^2$), medium (1.60-4.70), and high (>4.71) density areas. Highest predicted mussel densities were at of mid elevation areas (around 0.7 m**)** on the marsh platform in close proximity to creek heads and further away from subtidal creeks. Lowest predicted mussel densities were found at both high and low elevation regions along subtidal creeks and in upland marsh areas.

Stratified random sampling was used to select 15 plots with unique density values at each site, with 5 plots for each density level, using the sampleStratified function in R package raster (Hijams 2020). An additional two sets of points were generated as back up sites. All points were transferred to a handheld GPS. At CPP and Dean Creek, the area of the plot location was ground-truthed to ensure the point reflected the assigned density treatment before experimental plots were established. Backup locations were used if the initial location was not reflective of the appropriate density treatment, this only occurred in one instance.

### *Mussel Collection and Preparation*

Mussels were harvested from salt marshes near Savannah, Georgia prior to the growth and predation experiments and held in artificial seawater until the experiments. Mussels were subsampled in order to assess preliminary mussel condition. Subsampled mussels were measured, dissected for tissues, dried and weighed. Condition index was calculated by dividing dry tissue weight by dry shell weight (Davenport and Chen 1987).

### *Growth Rate Experiments*

Mussel growth rates were measured across the gradient of predicted mussel densities using three 12-week long field experiments in 2020 (February 3th/5th to May 6th/ 8th; May 13th/14th to August 18th; September 3rd/4th to December 3rd/5th). Mussels were separated into 5 size classes: 20-40mm, 40-50mm, 50-60mm, 60-70mm, 70-80mm. Individuals were given unique labels, measured, and divided into groups of 6 mussels – one of each size class except for two from the 60-70mm class. Mussels were then transported to the field and deployed at the experimental plots. Live mussels were placed into the sediments vertically and buried with a portion of the shell exposed, mimicking natural conditions. Mussels used in growth experiments were protected from predation by cages constructed of PVC and 0.3175cm mesh.

After 12 weeks, the mussel clumps were returned to the laboratory, where they were checked for survival, identified, and measured. Individuals were then dissected, tissues removed, dried and weighed. Condition index was calculated as above.

### *Predatory Mortality*

At each established plot, predatory mortality was monitored using tethering experiments. One mussel from two size classes (35-45mm and 55-65mm) were tethered for 24 hours and checked for predation. Missing individuals, and individuals that showed signs of predation (cracked, crushed shells, missing periostracum; Hillard and Walters 2009), were considered depredated. This was repeated for 3 consecutive days for each experiment (3 deployments). Individual mussels were tethered to a PVC stake, placed 0.5m away from the growth cage, using fishing line to ensure relocation. Tethers were deployed during a spring tide for a period of 4 days (3 deployments) in each of June, July, August, October and December of 2020. Only 2 deployments occurred in July because the spring tide occurred over the holiday which prevented access to the sites. Deployments during the summer were monthly since predation should be highest during that period (Fitz and Wiegert 1991).

Predator densities were examined across the different predicted mussel density zones by deploying crab traps (Ketcham Traps) adjacent to the experimental plots. A total of six traps, baited with crushed mussels, were deployed at each site and were moved each day to ensure each plot received at least one crab trap during the three-day period and ensuring that each mussel density zone was sampled with 2 traps on each 24 hour period. These traps were closely monitored with falling tides to avoid mortality of predators. Predators, when present, were counted. Blue crabs were measured for carapace width and released. Fish were identified and released. The presence of smaller predators (i.e. mud crabs) was quantified by counting borrow density in $0.25m^2$ quadrat within the vicinity of the experimental plots.

### *Recruitment*

Recruitment of new mussels to the different marsh zones was monitored monthly over 1 year (February 2020 -January 2021) using recruitment collectors. Since mussel spawning times can vary annually (Heffernan and Walker 1989; Honig 2015), recruitment was measured over a full year to ensure recruitment was captured. Mussels tend to settle amongst adult conspecifics (Nielsen and Franz 1995), so recruitment collectors consisted of a 5.08cm X 5.08cm X 4.50cm flowerpot filled with ambient sediment (Nielsen and Franz 1995; Honig 2015) and a clump of 4 dead, rearticulated mussel shells. Dead shell was selected as to not artificially influence recruitment to these areas. Valves were initially reattached using silicone aquarium sealant (Aqueon) attached at both posterior and anterior ends of each individual. Due to the high number of shells detached using the initial method, the sealant used on the mussel mimics was changed to 100% silicone sealant (GE) in June of 2019. To ensure each collector has approximately the same shell volume, two rearticulated mussels from each of two size classes (50-80mm and 80-100mm) were placed in each collector. Collectors were embedded in the marsh sediment at each experimental plot 0.5m from the growth cage. At each monthly interval, the collectors were removed and replaced with a new collector.

Each collector was returned to the lab and the contents were screened with a 500µm sieve since mussel recruits tend to settle at sizes of at least 500µm (Nielson and Franz 1995).The contents were examined under a dissecting microscope and the number of recruits were counted. (Nielsen and Franz 1995; Honig 2015).

### *Site Characteristics*

Biotic and abiotic variables were measured at each plot throughout the experimental period. At the start of each growth experiment, *Spartina alterniflora* density was measured by counting the number of shoots within a 0.25m quadrat around the growth cages and recruitment collectors (n=2 for each plot, 10 for each predicted mussel density zone). *Spartina alterniflora* height was calculated by recording the heights of 10 haphazardly selected shoots. The number of mussels inside of each quadrat were counted.  These characteristics were also measured around the predation tether at the start of each predation study.

Each month, water quality parameters were assessed within 30 minutes of the peak high tide of a flood tide. Temperature, pH, salinity, and dissolved oxygen measurements were collected using a handheld YSI (Xylem Inc) Pro-DSS.  The YSI was recalibrated prior to each collection.  In addition, since temperature was considered critical for the survivorship of mussels (Jost and Helmuth 2007), I also continuously monitored water temperature by placing data loggers in mussel growth cages. An iButton 1922L (Maxim) temperature logger, protected with Plasti Dip (Plasti Dip International) was placed in a rearticulated mussel shells (80-85mm shell length) and sealed with waterproof 100% silicone sealant (GE; Jost and Helmuth 2007) during each growth experiment. The loggers were set up to record the temperature every 30 minutes with a resolution of 0.0625°C. Loggers were initially placed in each cage (n=30), however, problems arose with the mussels leaking and damaging certain loggers. During the final growth experiment, a HOBO Pendant temperature logger (Onset) was also added to each cage at the sediment level to collect additional temperature data.

Water samples were collected from each plot to estimate food availability. One sterile 500mL sample bottle was filled at each location, placed on ice and returned to the lab for processing. Because mussels can consume detritus, phytoplankton, and bacteria (Langdon and Newell 1990), I measured chlorophyll *a* (Chl *a*) concentration, particulate organic matter (POM), and bacteria density. Chl *a* and POM samples were first filtered through 25µm nitex mesh to ensure that only particles small enough to be utilized by mussels was quantified (Huang et al. 2003). 60ml of pre-filtered water was filtered onto Whatman GF/F 0.7µm glass fiber filters (GE), and chl *a* concentrations were quantified using standard fluorometric techniques (Arar and Collins 1997). The remaining sample was filtered onto pre-weighed, pre-ashed Whatman GF/F 0.7µm glass fiber filters (GE) for POM analysis. As much water as possible was passed through the filter, and the volume filtered was quantified to standardize POM per mL. POM filters were placed into a drying oven for 48 hours at $70^0$C and reweighed. Filters were then combusted at $450^0$C for 4 hours in a muffle furnace (Fisher Scientific). Filters were removed and weighed and POM was calculated by using the percent loss-on-ignition (Armstrong 1958).

Bacteria samples were fixed using 3% glutaraldehyde (final concentration 0.001) and stored at $-80^0$C until enumeration via flow cytometry following the methods of Marie et al. (1999). Briefly, samples thawed at $37^0$C and were then run through a 2.7 µm glass fiber filter

(GE) to remove large particles that may damage the flow cytometer, since 93-99% of estuarine bacteria are smaller than 3µm (Palumbo et al. 1984). Samples were stained with 1% SYBR1 Green solution (final concentration 0.0001) and run through a BD Accuri C6 Flow Cytometer to enumerate bacteria density (Gatza et al. 2013). Bacteria samples were compared to field blanks to determine bacterial contamination due to the sampling process. Blanks were brought to the field site and went through all processing.

### *Statistical Analysis*

All analyses were performed in R (R Core Team 2020) with the LME4 (Bates et al. 2015), and MASS(Venables and Ripley 2002) packages. In order to see if growth rate, condition index, mortality, and predation changed with mussel density, season, and site, the data were analyzed with generalized linear mixed effect models and generalized linear models with mussel density, initial mussel length, site, and season as fixed effects and cage ID was added as a random effect (for growth rate, condition index, and predation only). Predation was analyzed using a logistic regression, with each mussel either being depredated or not over a 24 hour period. Monthly recruitment data were summed by season and analyzed using a negative binomial regression. Shells remaining in collector and total time deployed were added as fixed effects to the recruitment model to control for sampling "effort" differences among the collectors.

In order to see how site characteristics changed across predicted mussel densities, season, and site, site characteristics were analyzed using generalized linear models with the explanatory variables added as fixed effects. Particulate organic matter, chlorophyll *a* concentration, water quality (T, S), mussel temperature, and canopy height were all analyzed using a normal distribution. Bacteria counts, cordgrass shoot counts, and crab burrows were analyzed using a

Poisson distribution and log link function, while the actual mussel density was analyzed using a negative binomial generalized linear model.

## Results

Growth rates varied across season, predicted mussel densities, site, and mussel size classes explaining 54% of variability in growth rates (Table 2.1). Mussels grew twice as fast in the summer and fall growth experiments than they did in the spring (Figure 2.4a), and growth rates at CP were about 33% slower than Dean Creek (Figure 2.4b). Mussel growth rates were higher at areas with higher predicted mussel densities (Figure 2.4c). Initial size of the mussels impacted growth rates, such that smaller mussels grew faster than larger mussels (Figure 2.4d). Mussel condition index varied seasonally, by mussel size class, and by site. The model explained 29% of variability in mussel condition (Table 2.1). Condition was 20% higher during the summer growth experiment than the spring and fall (Figure 2.5a), higher at Dean Creek than CP (Figure 2.5b) and was lower in larger mussels (Figure 2.5c).

Multiple factors were measured that may contribute to growth rates which varied across predicted mussel densities. Average temperatures (Figure 2.7a) and average daily maximum temperatures (Figure 2.7b) of mussels increased with predicted mussel densities. However, food availability, including bacteria density (Figure 2.6a) and chl *a* concentration (Figure 2.6b), were both negatively related to predicted mussel densities. POM did not vary significantly with predicted mussel densities (POM changed by -0.396 mg/L per an increase in 1 mussel, -1.415 – 0.622 95CI; Table 2.4)

Predator based mortality varied across mussel size and season and this explained 43% of variability in predation risk (Table 2.2). Larger mussels experienced lower predation rates (Figure 2.8a). Predation was lowest during the winter months, where only one instance of predation was recorded, but consistent across other seasons (Figure 2.8b). There was an overall negative relationship between predicted mussel densities and predation risk (i.e., higher predicted mussel densities had lower predation, Figure 2.8c), although this was not statistically significant (Predation risk changed by -0.238 units per an increase of 1 mussel, -0.488-0.012 95CI; Table 2.2). The abundance of predators did vary across season and site, but not across predicted mussel densities, explaining 43% of variability (Table 2.2). No predators were detected in the winter survey, resulting in this survey being removed from the analysis to allow for model convergence. Predator abundance peaked in the fall (Figure 2.9a) and was higher at CP than at Dean Creek (Figure 2.9b). Mussel recruitment increased with predicted mussel densities (Figure 2.10), but not across season or site. The model explained 44% of variability in recruitment (Table 2.3)

Marsh canopy height, *Spartina* density, mussel density, and crab burrow density may affect predation and recruitment and were all related to predicted mussel densities; the density of both *Spartina* (Figure 2.11a) and mussels (Figure 2.11b) increased with mussel predicted mussel densities, while canopy height (Figure 2.11c) and crab burrow densities (Figure 2.11d) decreased with increasing predicted mussel densities.

## Discussion

Growth rates varied across sites and seasons, decreased with initial size, and increased with predicted mussel densities. Areas with high predicted mussel densities were associated with lower food supply and higher maximum temperatures, and yet mussels grew about 50% faster at the areas with the highest predicted mussel densities than areas with the lowest predicted mussel densities. While variation in growth rates was statistically significant across predicted mussel densities, the changes were not likely to be biologically relevant (i.e. 0.03mm per day greater at highest predicted mussel densities versus lowest predicted mussel densities). The observed differences in growth rates may be attributable to increased submergence time (Seed 1969; Peterson and Black 1988; Jensen 1992) associated with lower elevation portions of the marsh platform (Stiven and Gardner 1992; Crotty and Angelini 2020). Using the sampleStratified function in R to select plots resulted in almost all (i.e., 9 out of 10) low mussel density plots across both sites to be established in higher elevation regions of the marsh platform relative to the medium and high density plots. The only low density plot selected was the lowest elevation of all plots, and when protected from predatory mortality, the mussels exhibited the highest measured growth rates. Submergence times are strongly tied to elevation, with small decreases in elevation leading to large increases in submergence times (Jensen 1992), and it is likely that elevation patterns across the plots selected are driving growth rates more than mussel density. The lower food supply in the areas of higher predicted mussel densities was unexpected but may have resulted from increased grazing from higher mussel densities.

Across all predicted mussel densities, growth rates did vary significantly over season, with highest growth rates in the summer and fall; mussels grew twice as fast in both seasons compared to the spring. Elevated growth rates in the summer may be explained by an increase in concentration in food supply (bacteria, chl *a*; Rheault and Rice 1996). Temperature also plays an important role in growth rates of intertidal organism (Lamb et al. 2014), which were highest during the high growth seasons. Mussel temperature unexpectedly increased with predicted mussel density, although maximum temperatures were below those found to be stressful for ribbed mussels (Jost and Helmuth 2007). Salinity has been shown to increase growth rates in the gulf ribbed mussel (*Geukensia granosissima;* Honig et al. 2015), and salinity in this study peaked at the same time growth rates were highest. However, there was not enough variability of salinity within the sites to find any further patterns. Condition index is a metric for mussel health that might respond quicker to environmental changes than shell extension (Knights 2012), and it also peaked in the summer. This is probably reflective of increasing food supply and increased somatic growth, as well as the development of gametes in mature individuals (Keunzler 1961; Rheault and Rice 1996). The decrease in condition from summer to fall could indicate the release of gametes produced during the summer (Keunzler 1961), or a decline in food quantity/quality as the seasons change (Rheault and Rice 1996).

Predation varied seasonally, as expected, however, there was not a statistically significant relationship with predicted mussel densities. Overall, predation was low, which may have impacted the ability to discern statistically significant trends with predicted mussel densities. However, a mussel placed in the lowest predicted mussel density plot was over twice as likely to be eaten than a mussel in the highest predicted mussel density plot, so despite not being statistically significant, this trend is likely to be biologically relevant. These areas of high predicted mussel densities were further away from subtidal creeks and were associated with higher density of conspecifics and more dense vegetation. Proximity to subtidal creeks has been associated with predation by blue crabs (Lin 1989). In addition, high mussel density can reduce individual risk to predation (Crotty and Angelini 2020), and dense vegetation reduces predation rates (Mahoney et al. 2018; Crotty et al. 2020). Abundance of large, mobile predators like blue crabs also did not show any significant trend with predicted mussel densities, however, mud crab burrow density was negatively correlated with predicted mussel densities. Mud crabs can be major predators of ribbed mussels (Hughes and Seed 1981), particularly of smaller mussels which experienced higher predation than larger mussels. As expected, predation was lowest in the winter when large predators were rare and when overall abundance and activity of decapods drops on the marsh (Fitz and Wiegert 1991). When all predation evidence is considered, this study suggests it is an important factor influencing the distribution of mussels.

Recruitment of new individuals varied significantly across predicted mussel density; collectors placed in areas of low predicted mussel densities rarely received any recruits, whereas highest recruitment occurred in areas of high predicted mussel densities. Higher predicted mussel density areas were mid-elevation locations generally within close proximity to creek heads, which flood the marsh platform and may enhance recruitment (Crotty and Angelini 2020). However, the geomorphology characteristics (elevation, proximity to creek heads) may not be the only drivers of mussel recruitment. Mussel recruitment is heavily dependent on mussel conspecifics (Nielson and Franz 1995), and experimental plots in high predicted mussel density areas had greater surrounding mussel densities. Previous studies show that the addition of mussels boost recruitment, even in areas typically devoid of mussels (Nielson and Franz 1995). The pattern observed in this study is similar to other studies, where mussel recruitment was observed on mussel mounds and minimal recruitment in areas devoid of mussels (Crotty and Angelini 2020). The strong density dependent effects on recruitment make it difficult to determine if high recruitment areas are more suitable for recruitment, or if recruitment to areas with high predicted mussel densities is driven by higher mussel densities in the surrounding area. Recruitment did not vary between the two study sites, and both sites have similar creek fetches and surrounding landcover. Large creek fetches may influence recruitment by impacting larval supply (Isdell et al. 2018), although determining patterns in supply was beyond the scope of this study.

Mussel recruits were observed across all seasons and did not vary significantly over time. This contradicts earlier recruitment studies in which mussels spawn in the summer, and peak recruitment is seen in the early fall (Keunzler 1961; Hefferman and Walker 1989; Nielson and Franz 1995; Franz 1996). The lack of an observable recruitment peak may indicate multiple spawning events throughout the year, and the decrease in mussel condition from summer to fall suggests there was a potential spawning event during that period (Keunzler 1961). While a prior recruitment study in Georgia showed a distinct recruitment peak, this study is over thirty years old (Hefferman and Walker 1989), and the current study suggests the potential of a protracted recruitment period for ribbed mussels in Georgia. For example, bay scallops in western Florida transitioned from having a defined recruitment peak, to a year round protracted recruitment period over a decade of monitoring (Gieger et al. 2010), which could be related to changes in water temperature. Sea temperatures have risen over $0.94^0$C since the 20th century average (NOAA 2016) and are expected to continue to rise as a consequence of climate change. Water temperature could affect the time larvae can stay in the water column (Gieger et al. 2010), potentially prolonging the settlement period. In lab studies, ribbed mussel larvae survived longer and grew faster at temperatures above $19^0$C (Virgin et al. 2019). Warmer seas temperatures could allow larvae, which typically can survive around three weeks (Virgin et al. 2019), to survive longer past spawning events.

Species distribution models such as the one used to select study locations here may be helpful in determining the current location of individuals. However, these models may not be the best indicator of where mussels can be restored. While predicted mussel density was significantly related to both growth rates and recruitment, the models only described about half of the variation. Fine scale factors, such as vegetation density or crab burrows, may influence the population parameters of mussels and may not vary consistently across the predicted mussel density model. Vegetation density decreases temperatures (Altieri et al. 2007), provides refuge from predators (Crotty et al. 2020), and increases recruitment by passive deposition (Eckman 1983). Abundance of crab burrows can increase the chance of mussel predation (Crotty and Angelini 2020). The addition of fine scale factors may improve model performance when trying to gauge mussel population parameters in different marsh zones.

Applying the concept of habitat quality to this study, it seems that on the scale of the mussel density model, recruitment is the significant driver of mussel densities. While variation in growth rates was statistically significant across predicted mussel densities, the changes were not likely to be biologically relevant (i.e. 0.03mm per day greater at highest predicted mussel densities versus lowest predicted mussel densities) and all mussels experienced growth. The presence of recruits at both sites indicate that at the scale of coastal Georgia there is likely sufficient recruitment occurring to these populations. Within the marsh, however, the results seem to indicate that the mussel populations are controlled locally at very fine spatial scales by recruitment within sites. The scope of this experiment does not allow us to separate the effects of mussel density on recruitment (Nielson and Franz 1995) with the effects of the site characteristics (i.e. elevation, grass density, distance from marsh features) of high mussel density areas. When managing ribbed mussels and modelling future distributions, it will be important to consider variables that affect mussel larval supply and dispersal.

Examining habitat quality in addition to population density can provide more information to managers on how species can be utilized in different areas. This study indicates that a density-based suitability metric may only be an indicator for the amount of recruitment an area receives, which can inform managers on how to handle the installation of new populations. While there has been a push to implement mussels in restoration projects such as living shorelines (Moody et al. 2013), mussels in Georgia are typically absent from the creek banks (Lin 1989) where these projects take place. The model used in this study predicts low mussel densities at subtidal creek banks (Chapter 1), although the impacts on mussels placed in these locations is mixed. Growth rates may be minimally affected, and may even be enhanced, by placement at low elevations along subtidal creeks, however, predation risk is higher in these locations. Further, current recruitment in these areas of the marsh may be too low to sustain transplanted populations in these areas unless density is more important that marsh features. If living shorelines restoration projects plan to use ribbed mussels in southeastern marshes, it will be important to address predation and recruitment issues. Since predation risk drops with increasing mussel size (Hughes and Seed 1981), larger mussels may survive predation attempts and should be used, and mussels should be transplanted in the winter when predation risk is the lowest. Due to the density dependent nature of mussel recruitment (Nielsen and Franz 1995), placing a large number of mussels may influence recruitment to these regions as well. Further work should also focus on how broad scale factors such as creek fetch and surround landcover can affect mussel populations.

Table 2.1: Mixed effect model results with $R^2$ values for fixed effects with 95% confidence intervals for ribbed mussel growth rates (mm/day) and mussel condition index (unitless). Intercept represents the response variable at the site at Cannon's Point during the spring season. Initial length refers to length from mussel's anterior to posterior end and density refers to predicted mussel densities.

| Growth Rate R2=0.54 | | |
|---|---|---|
| | Est. | 95% CI |
| (Intercept) | 0.093 | 0.079 – 0.108 |
| Initial length | -0.001 | -0.002 – -0.001 |
| Dean Creek | 0.013 | 0.004 – 0.022 |
| Density | 0.004 | 0.000 – 0.007 |
| Summer | 0.029 | 0.024 – 0.034 |
| Fall | 0.029 | 0.024 – 0.034 |
| Condition Index R2=0.29 | | |
| | Est. | 95% CI |
| (Intercept) | 7.79 | 6.988 - 8.593 |
| Density | 0.003 | -0.177 – 0.184 |
| Initial length | -0.014 | -0.022 – -0.006 |
| Dean Creek | 0.698 | 0.233 – 1.164 |
| Summer | 1.624 | 1.356 – 1.892 |
| Fall | 0.0551 | -0.233 – 0.343 |

Table 2.2: Mixed effect model results with $R^2$ values for fixed effects with 95% confidence intervals for probability of predation and blue crab abundance (crabs per trap). Intercept represents the response variable at the site at Cannon's Point during the summer season. Length refers to length from mussel's anterior to posterior end and density refers to predicted mussel densities.

| Predation R2=0.43 | | |
|---|---|---|
| | Est. | 95% CI |
| (Intercept) | 1.186 | -0.051 – 2.43 |
| Density | -0.238 | -0.488 – 0.012 |
| length | -0.035 | -0.053 – -0.016 |
| Dean Creek | 0.415 | -0.239 – 1.069 |
| Fall | -0.25 | -0.687 – 0.186 |
| Winter | -4.07 | -6.044 – -2.095 |
| Predators R2=0.42 | | |
| | Est. | 95% CI |
| (Intercept) | -0.567 | -1.421 – 0.287 |
| Density | -0.084 | -0.311 – 0.143 |
| Dean Creek | -0.747 | -1.327 – -0.168 |
| Fall | 1.707 | 1.254 – 2.160 |

Table 2.3: Mixed effect model results with $R^2$ values for fixed effects with 95% confidence intervals for ribbed mussel recruitment (recruits per season). Intercept represents the response variable at the site at Cannon’s Point during the fall season. Density refers to predicted mussel densities, number of shells refers to the number of rearticulated shells remaining in the collector, and total days refers to the length of time collectors were left in the marsh.

| Recruitment R2=0.44 | | |
|---|---|---|
| | Est. | 95% CI |
| (Intercept) | -3.709 | -9.666 – 2.249 |
| Density | 0.466 | 0.101 – 0.832 |
| Dean Creek | 0.621 | -0.275 – 1.518 |
| Number of Shells | 0.618 | -0.148 – 1.383 |
| Spring | 2.538 | 0.771 – 4.306 |
| Summer | -0.496 | -2.901 – 1.909 |
| Total Days | -0.027 | -0.083 – 0.029 |

Table 2.4: Mixed effect model results with $R^2$ values for fixed effects with 95% confidence intervals for bacteria (bacteria /uL), Particulate organic matter (mg/L), and chlorophyll a (ug/L). Intercept represents the response variable at the site at Cannon's Point during the fall season. Density refers to predicted mussel densities.

| Bacteria R2=0.19 | | |
|---|---|---|
| | Est. | 95% CI |
| (Intercept) | 4.117 | 4.019 – 4.215 |
| Density | -0.141 | -0.165 – 0.118 |
| Dean Creek | 0.297 | 0.235 – 0.359 |
| Spring | 0.126 | 0.039 – 0.214 |
| Summer | 0.462 | 0.393 – 0.530 |
| POM R2=0.31 | | |
| | Est. | 95% CI |
| (Intercept) | 9.544 | 5.490 – 13.597 |
| Density | -0.396 | -1.415 – 0.622 |
| Dean Creek | -2.978 | -5.510 – -0.446 |
| Spring | 7.001 | 3.786 – 10.215 |
| Summer | 6.016 | 3.241 – 8.792 |
| CHLA R2=0.27 | | |
| | Est. | 95% CI |
| (Intercept) | 12.522 | 10.103 – 14.941 |
| Density | -1.285 | -1.893 – -0.678 |
| Dean Creek | -0.507 | -2.046 – 1.033 |
| Spring | -2.477 | -4.438 – -0.515 |
| Summer | 1.304 | -0.377 – 2.985 |

Table 2.5: Mixed effect model results with $R^2$ values for fixed effects with 95% confidence intervals for salinity (ppt), water temperature (${}^0$C), dissolved oxygen (mg/L), and pH. Intercept represents the response variable at the site at Cannon's Point during the fall season. Density refers to predicted mussel densities.

| Salinity R2=0.79 | | |
|---|---|---|
| | Est. | 95% CI |
| (Intercept) | 30.053 | 28.886 – 31.221 |
| Density | -0.554 | -0.845 – -0.264 |
| Dean Creek | -0.2647 | -1.015 – 0.485 |
| Spring | -8.175 | -9.082 – -7.267 |
| Summer | -3.319 | -4.227 – -2.411 |
| Water Temperature R2=0.20 | | |
| | Est. | 95%CI |
| (Intercept) | 17.593 | 12.770 – 22.417 |
| Density | 1.011 | -0.190 – 2.211 |
| Dean Creek | -3.201 | -6.300 – -0.102 |
| Spring | -0.872 | -4.622 – 2.879 |
| Summer | 6.97 | 3.220 – 10.721 |
| Dissolved Oxygen R2=0.62 | | |
| | Est. | 95% CI |
| (Intercept) | 7.258 | 6.919 – 7.597 |
| Density | -0.065 | -0.154 – 0.024 |
| Dean Creek | -0.129 | -0.359 – 0.101 |
| Summer | -1.103 | -1.330 – -0.876 |
| pH R2=0.68 | | |
| | Est. | 95% CI |
| (Intercept) | 7.691 | 7.483 – 7.900 |
| Density | -0.048 | -0.100 – 0.004 |
| Spring | 1.059 | 0.897 – 1.221 |
| Summer | 0.24 | 0.078 – 0.402 |
| Dean Creek | 0 | -0.134 – 0.134 |

Table 2.6: Mixed effect model results with $R^2$ values for fixed effects with 95% confidence intervals for average mussel temperature ($^0$C), seasonal maximum mussel temperature ($^0$C), and average daily maximum mussel temperature ($^0$C). Intercept represents the response variable at the site at Cannon’s Point during the fall season. Density refers to predicted mussel densities

| Average Temperature R2=0.99 | | |
|---|---|---|
| | Est. | 95% CI |
| (Intercept) | 22.51 | 22.264 – 22.756 |
| Density | 0.115 | 0.051 – 0.179 |
| Spring | -4.547 | -4.745 – -4.348 |
| Summer | 5.465 | 5.261 – 5.670 |
| Dean Creek | 0.014 | -0.150 – 0.178 |
| Seasonal Maximum Temperature R2=0.72 | | |
| | Est. | 95% CI |
| (Intercept) | 34.139 | 32.203 – 36.076 |
| Density | 0.269 | -0.239 – 0.776 |
| Spring | -7.446 | -9.008 – -5.883 |
| Summer | 1.492 | -0.122 – 3.107 |
| Dean Creek | 1.29 | -0.002 – 2.582 |
| Daily Maximum Temperature R2=0.95 | | |
| | Est. | 95% CI |
| (Intercept) | 24.224 | 23.411 – 25.038 |
| Density | 0.335 | 0.122 – 0.548 |
| Spring | -3.39 | -4.046 – -2.733 |
| Summer | 7.819 | 7.141 – 8.497 |
| Dean Creek | 0.243 | -0.299 – 0.786 |

Table 2.7: Mixed effect model results with $R^2$ values for fixed effects with 95% confidence intervals for canopy height (mm), cordgrass density (shoots per $0.25m^2$), mussel density (mussels per $0.25m^2$), and crab burrow density (individuals per $0.25m^2$). Intercept represents the response variable at the site at Cannon’s Point during the spring season except for crab burrows whose intercept represents the site at Cannon’s Point during the summer season as burrows were not measured in spring. Density refers to predicted mussel densities.

| Canopy Height R2=0.42 | | |
|---|---|---|
| | Est. | 95% CI |
| (Intercept) | 70.389 | 58.837 – 81.940 |
| Density | -7.903 | -10.643 – -5.163 |
| Dean Creek | -1.859 | -8.933 – 5.215 |
| Summer | 22.662 | 12.776 – 32.548 |
| Fall | 34.678 | 24.792 – 44.563 |
| Winter | 28.044 | 18.158 – 37.929 |
| Vegetation Density R2=0.08 | | |
| | Est. | 95% CI |
| (Intercept) | 3.237 | 3.125 – 3.348 |
| Density | 0.086 | 0.059 – 0.113 |
| Dean Creek | -0.22 | -0.288 – -0.153 |
| Summer | -0.154 | -0.249 – -0.059 |
| Fall | -0.1 | -0.193 – -0.006 |
| Winter | 0.074 | -0.015 – 0.164 |
| Mussel Density R2=0.11 | | |
| | Est. | 95% CI |
| (Intercept) | -4.652 | -6.273 – -3.031 |
| Density | 1.18 | 0.814 – 1.545 |
| Dean Creek | -0.916 | -1.71 – -0.126 |
| Summer | 0.707 | -0.435 – 1.848 |
| Fall | 1.593 | 0.495 – 2.692 |
| Winter | 1.575 | 0.476 – 2.673 |
| Crab Burrow R2=0.08 | | |
| | Est. | 95% CI |
| (Intercept) | 3.6 | 3.468 – 3.731 |
| Density | -0.132 | -0.166 – -0.097 |
| Dean Creek | -0.074 | -0.163 – 0.015 |
| Fall | -0.02 | -0.126 – 0.085 |
| Winter | -0.142 | -0.251 – -0.033 |

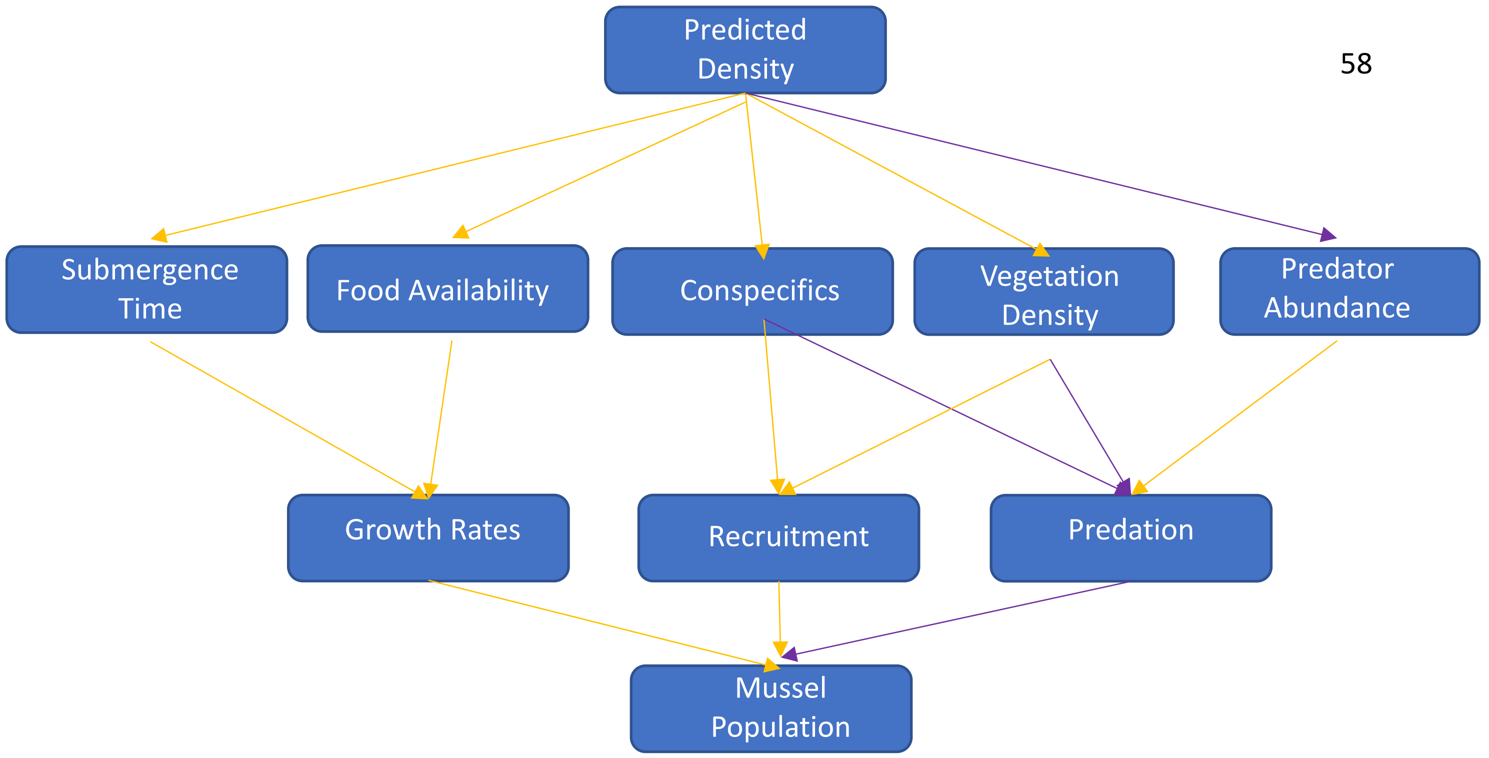


Figure 2.1: Predictions on how environmental parameters vary across predicted ribbed mussel densities and how these parameters affect the population parameters of the ribbed mussel. Yellow lines indicate positive interactions and blue lines indicate negative interactions. Food availability refers to bacteria concentration, particulate organic matter, and chlorophyll a concentration. Conspecifics refers to densities of ribbed mussels surrounding each plot. Predator abundance refers to the amount of blue crabs and the density of burrows around a plot.

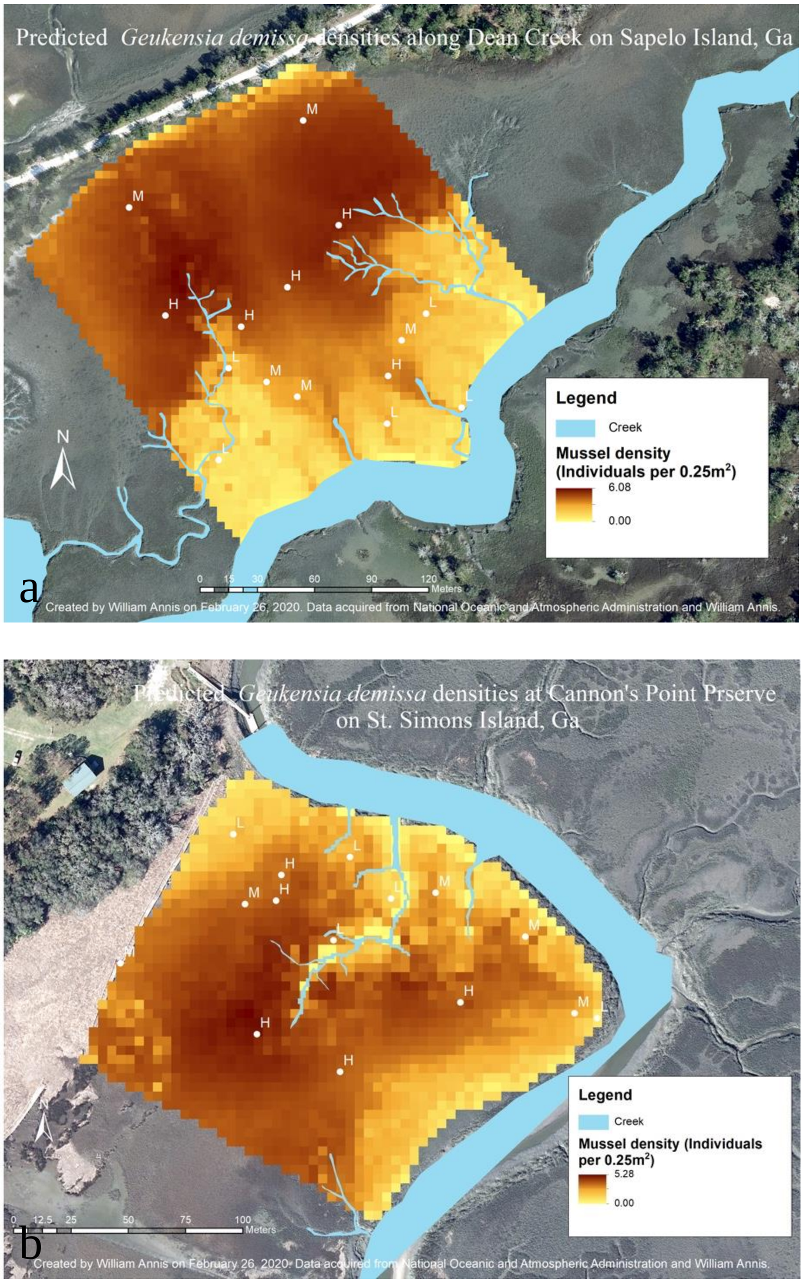


Figure 2.2: Study Site at Dean Creek on Sapelo Island, Georgia (a) and Cannon’s Point Preserve on St. Simon’s Island, Georgia (b). Each point represents an experimental plot (L = low mussel suitability, M = medium mussel suitability, and H = high mussel suitability). At each experimental plot, ribbed mussel growth, recruitment, and predation experiments were conducted.

| | February | March | April | May | June | July | August | September | October | November | December | January |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Place Growth Experiment | ● | | | ● | | | | ● | | | | |
| Collect Growth Experiment | | | | ● | | | ● | | | | ● | |
| Predation Experiment | | | | | ● | ● | ● | | ● | | ● | |
| Measure Recruitment | | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● |
| Water quality and food availability measurements | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | ● | |
| Measure Site characteristics | ● | | | ● | | | | ● | | | ● | |

Figure 2.3: Timeline of ribbed mussel experiments and environmental parameter measurements between February 2020 and January 2021. Growth experiment measured mussel growth rates in mm/day over three months, predation experiments measured probability of predation and blue crab abundance, and recruitment experiment measured number of recruits per month. Water quality referred to temperature, salinity, dissolved oxygen, and pH. Food availability referred to particulate organic matter, bacteria, and chlorophyll a. Site characteristics referred to mussel densities, crab burrow densities, cordgrass densities, and canopy height.

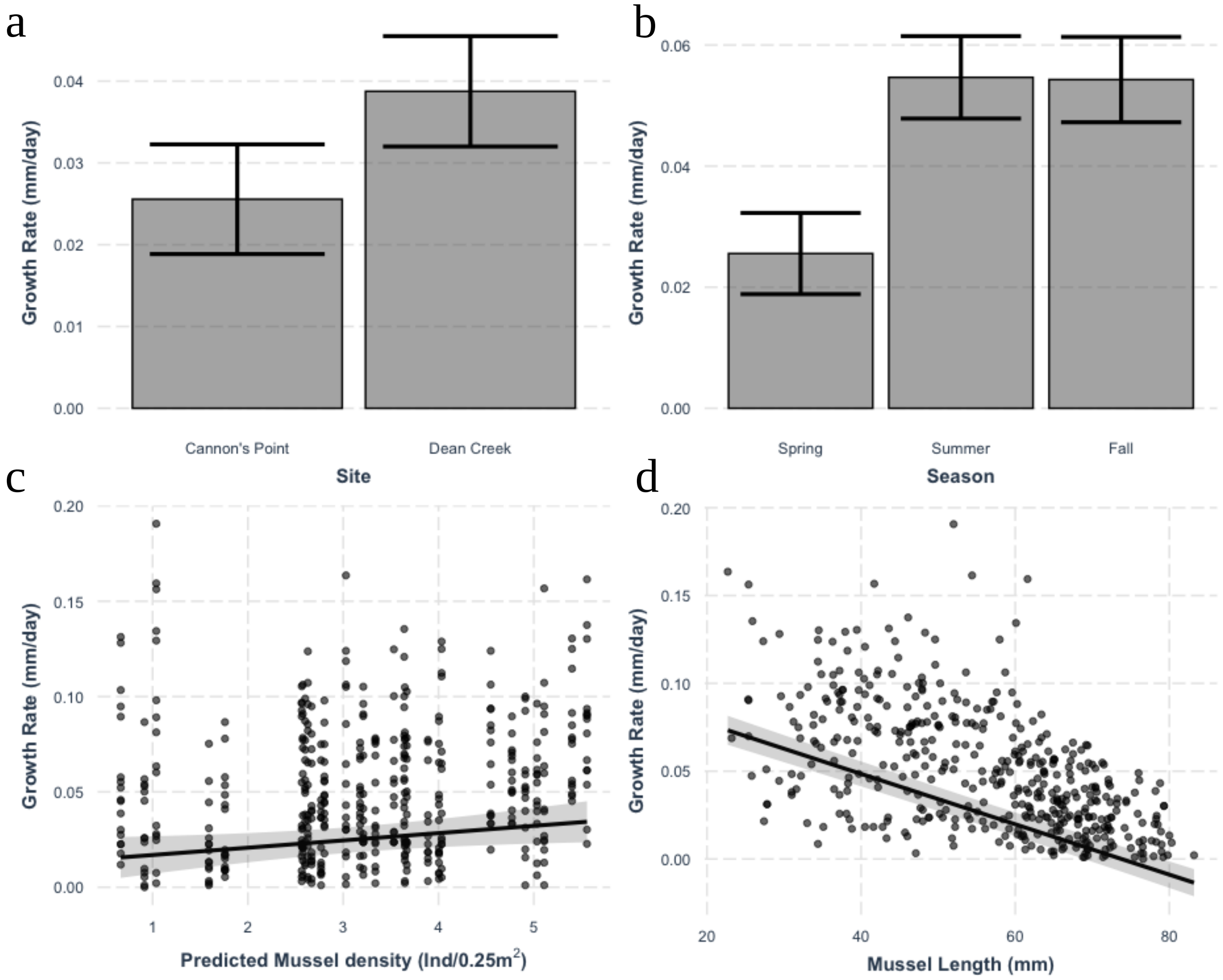


Figure 2.4: Mussel growth rates (mm/day) ± 95% CI for individual effects for site (a), season (b), predicted mussel density (mussels/0.25m$^2$; c), and length (mm; d) with all other factors held constant. n= 452 observations at 30 growth cages over three seasons.

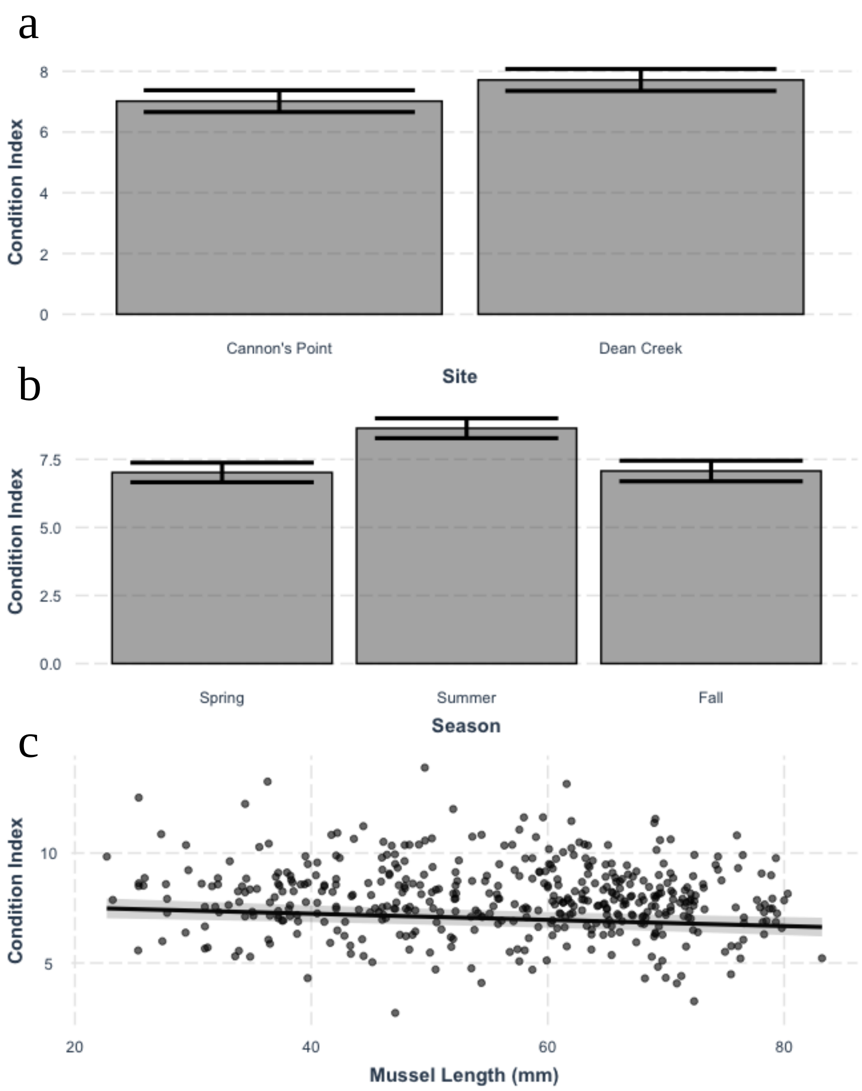


Figure 2.5: Mussel condition index (Unitless)± 95% CI for individual effects for site (a), season (b), and length (mm; c) with all other factors held constant. n= 452 observations at 30 growth cages over three seasons.

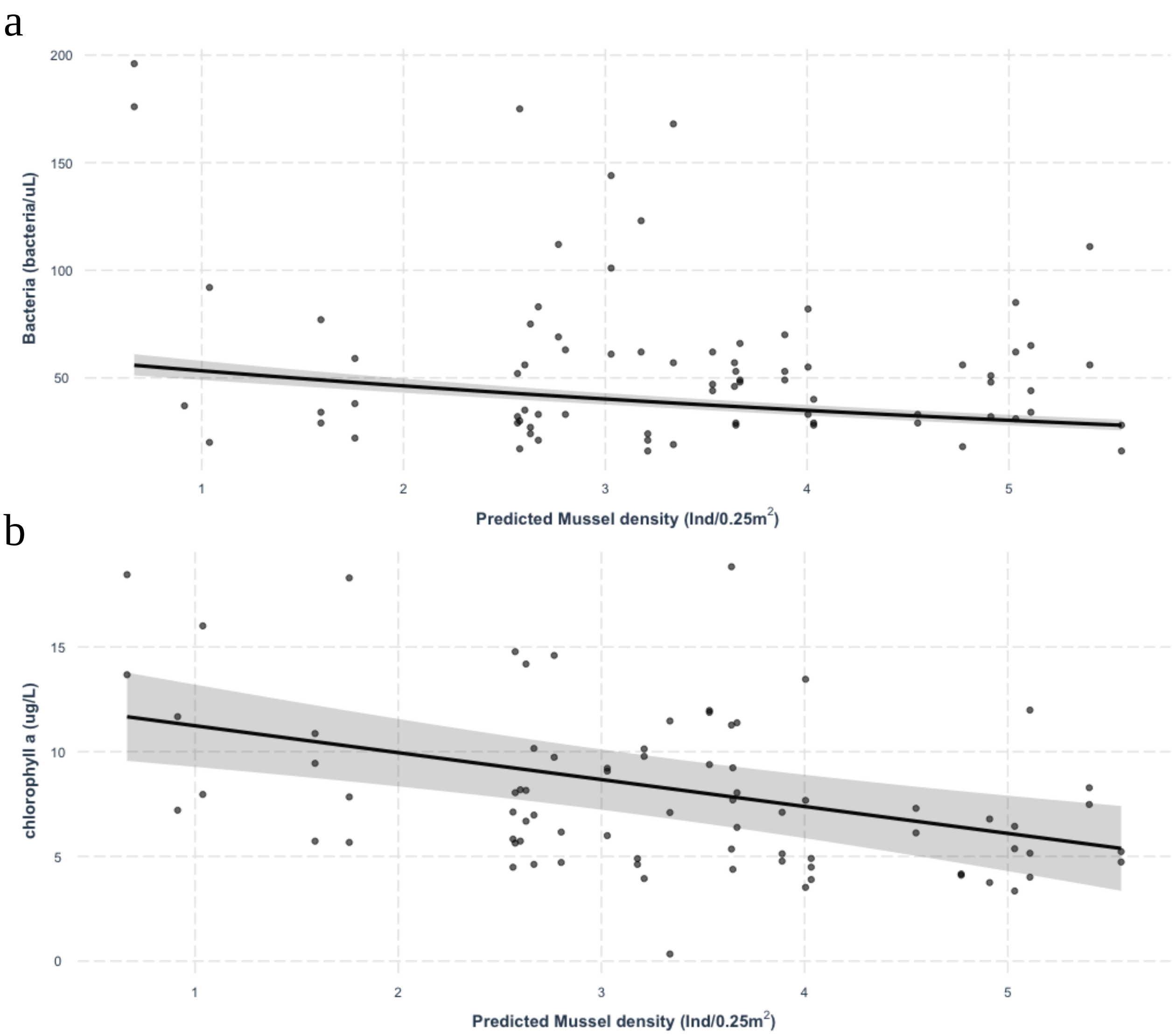


Figure 2.6: Bacteria concentration (individuals/uL; a) and chlorophyll a concentration (ug/L; b) ±95% CI for individual effects for predicted mussel density (mussels/0.25m$^2$) with all other factors held constant. n=90 observations at 30 plots over 3 seasons.

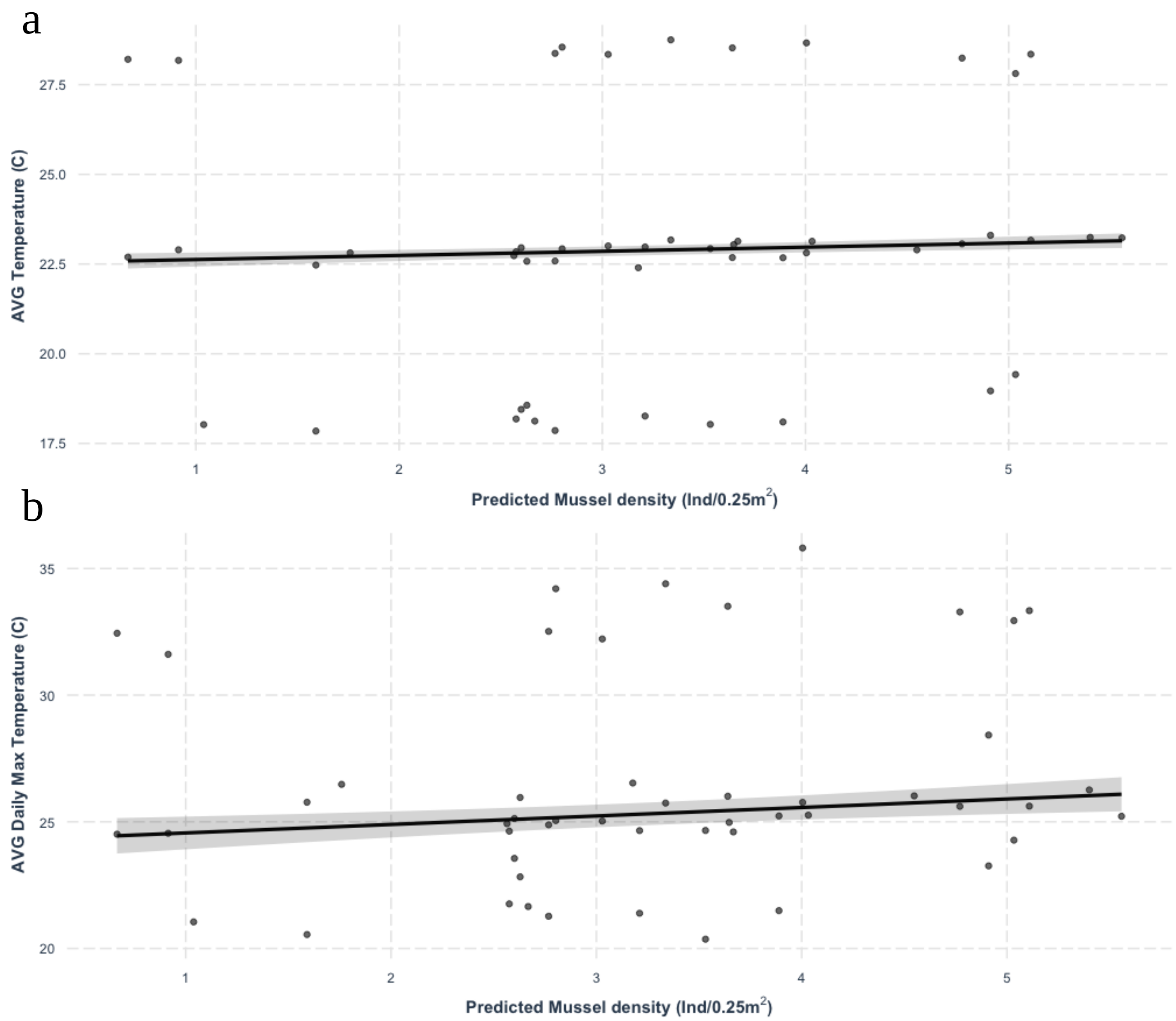


Figure 2.7: Average temperatures ($^0$C; a) and average daily maximum temperature ($^0$C; b) ±95% CI for individual effects for predicted mussel density (mussels/0.25m$^2$) with all other factors held constant. n=50 observations at 30 plots over 3 seasons.

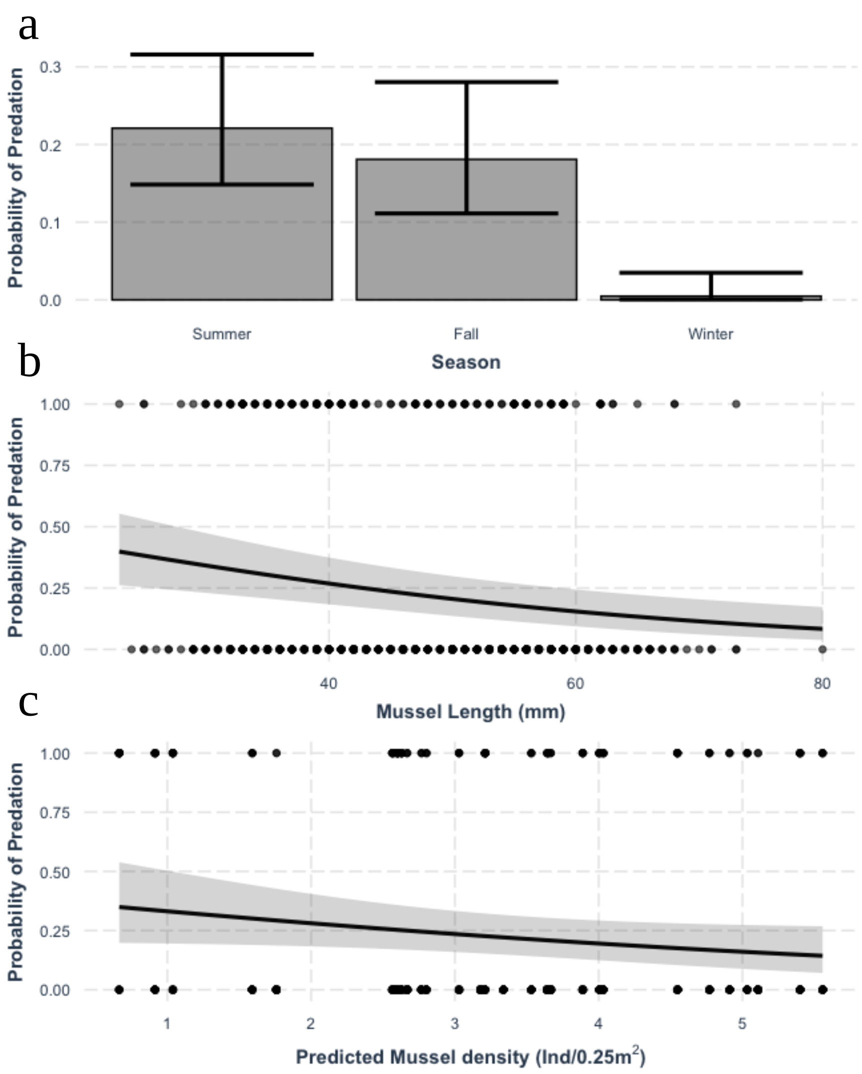


Figure 2.8: Probability of mussel predation (mm/day) ± 95% CI for individual effects for season (a), length (mm; b), and predicted mussel density (mussels/0.25m$^2$; c)with all other factors held constant. n=709 observations from 30 plots over 5 experiments.

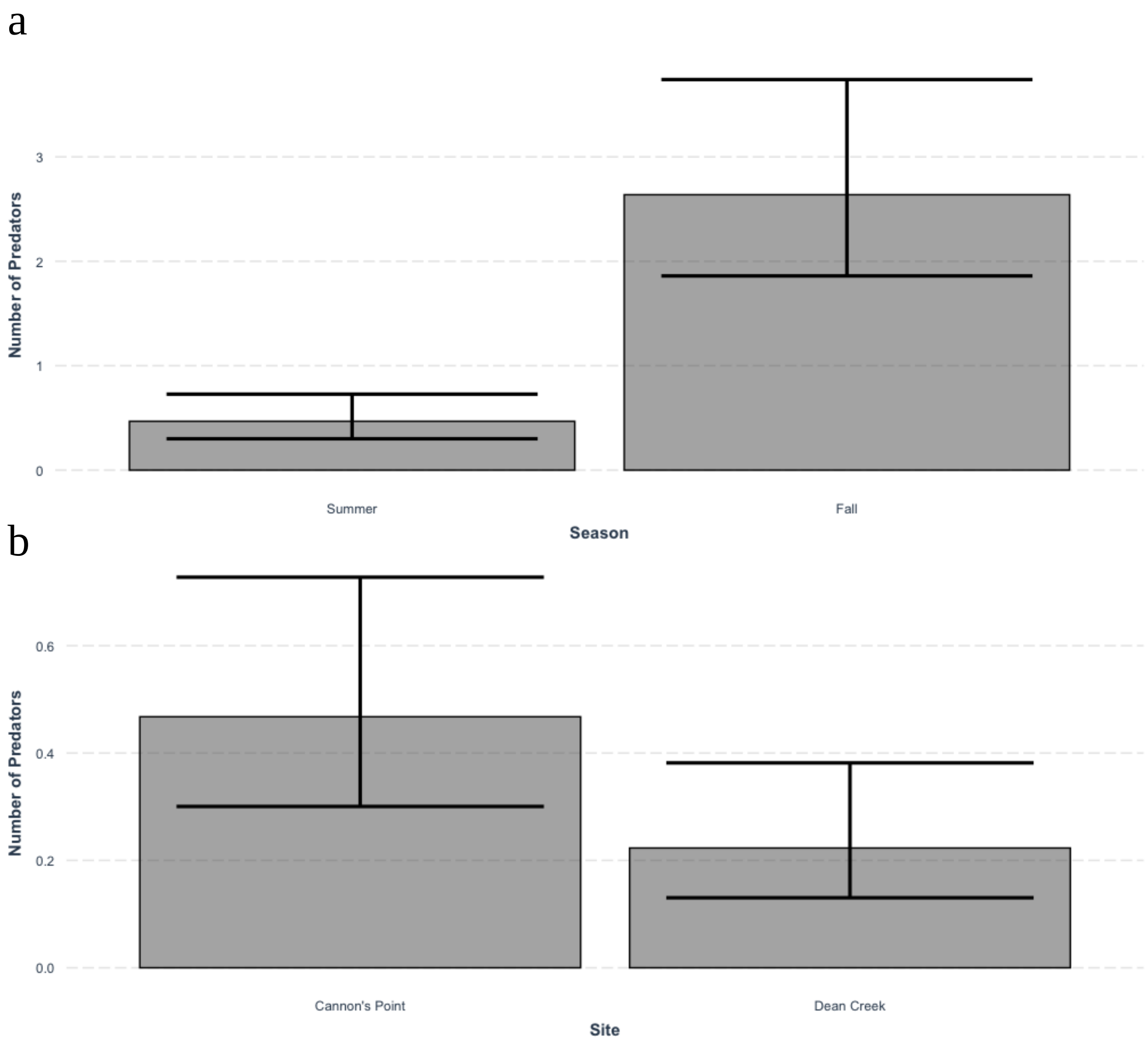


Figure 2.9: Number of blue crabs (individuals per trap) ± 95% CI for individual effects for season (a) and site (mm; b) with all other factors held constant. n=136 observations from 30 plots over 5 experiments.

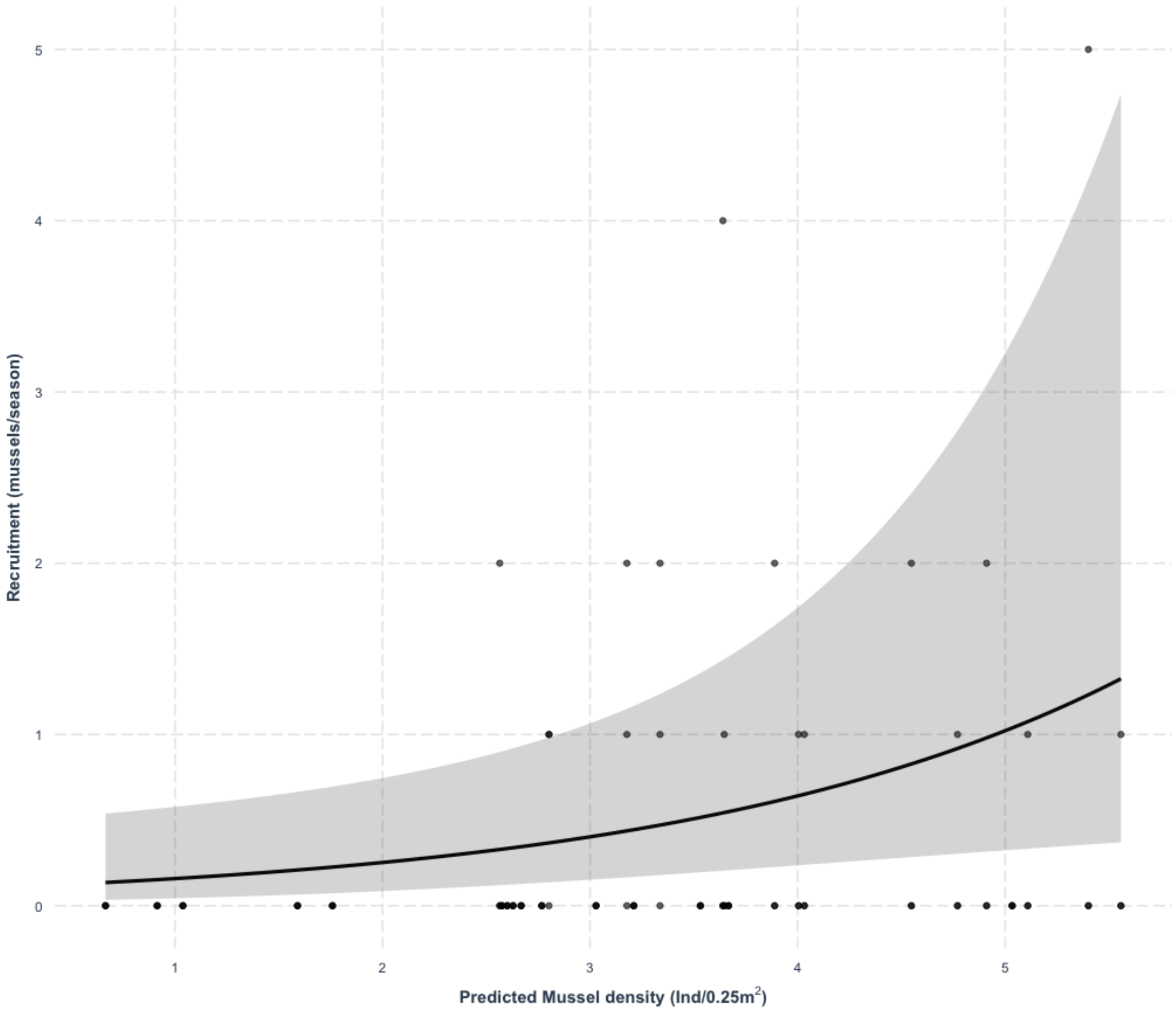


Figure 2.10: Ribbed mussel recruitment (mussels per season) ±95%CI for individual effects for predicted mussel density (mussels/0.25m$^2$) with all other factors held constant. n=90 observations at 30 recruitment collectors over three seasons.

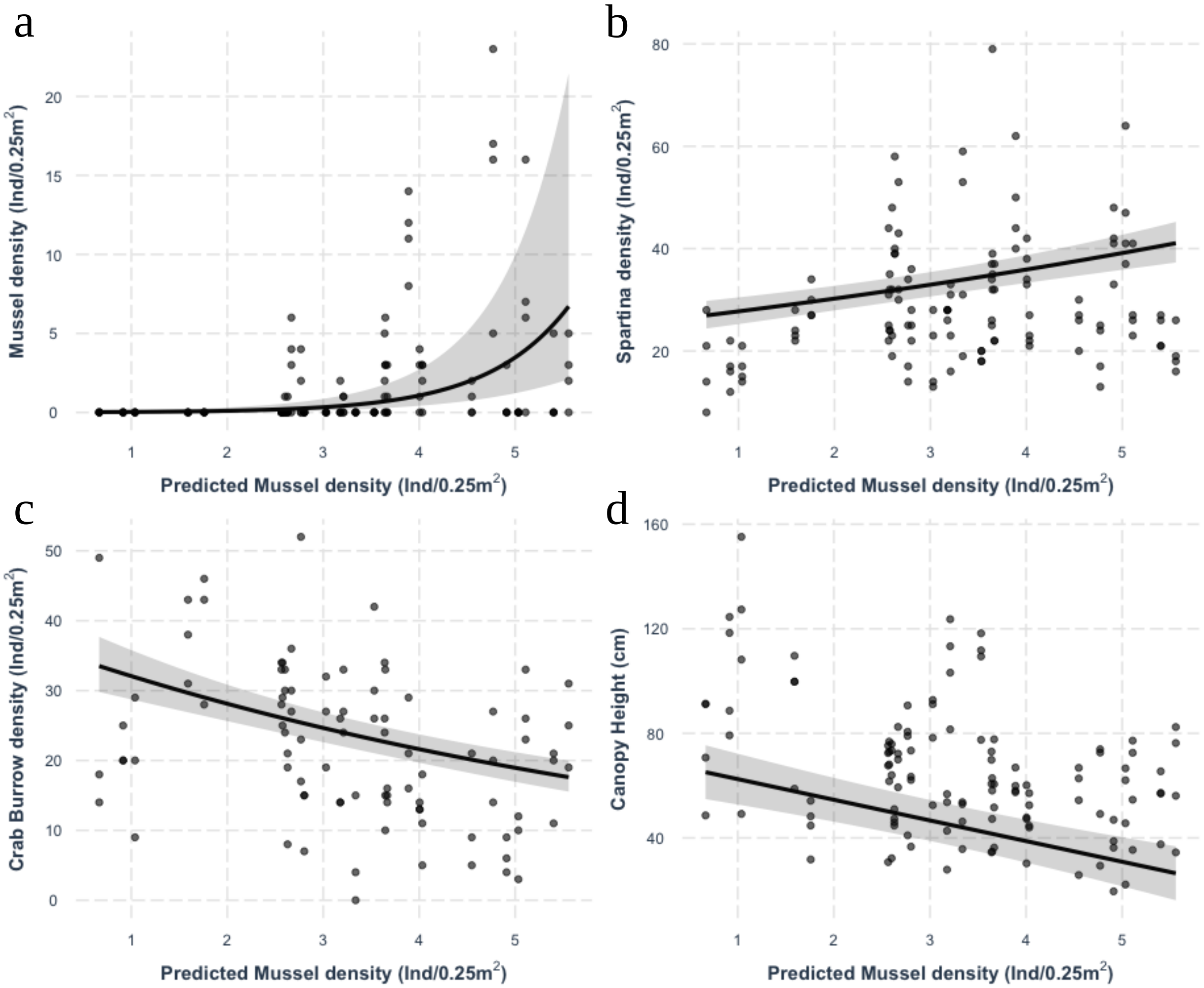


Figure 2.11: Ribbed mussel density (individuals/0.25m$^2$; a), cordgrass density (individuals/0.25m$^2$; b), crab burrow density (individuals/0.25m$^2$; c), and cordgrass canopy height (mm; d) ±95% CI for individual effects for predicted mussel density (mussels/0.25m$^2$) with all other factors held constant. n=120 observations at 30 plots over four seasons.

# REFERENCES

Altieri, A. H., B. R. Silliman, and M. D. Bertness. 2007. Hierarchical organization via a facilitation cascade in intertidal cordgrass bed communities. American Naturalist **169**:195-206.

Angelini, C., J. N. Griffin, J. van de Koppel, L. P. M. Lamers, A. J. P. Smolders, M. Derksen-Hooijberg, T. van der Heide, and B. R. Silliman. 2016. A keystone mutualism underpins resilience of a coastal ecosystem to drought. Nature Communications **7**:8.

Angelini, C., T. van der Heide, J. N. Griffin, J. P. Morton, M. Derksen-Hooijberg, L. P. M. Lamers, A. J. P. Smolders, and B. R. Silliman. 2015. Foundation species' overlap enhances biodiversity and multifunctionality from the patch to landscape scale in southeastern United States salt marshes. Proceedings of the Royal Society B-Biological Sciences **282**:9.

Arar, E. J., and G. B. Collins. 1997. In vitro determination of chlorophyll a and pheophytin a in marine and freshwater algae by fluorescence. Pages 1-22, Washington, DC: United States Environmental Protection Agency, Office of Research and Development, National Exposure Research Laboratory.

Armstrong, F. A. J. 1958. Inorganic suspended matter in seawater. Journal of Marine Research **17**:23-34.

Armsworth, P. R. 2002. Recruitment limitation, population regulation, and larval connectivity in reef fish metapopulations. Ecology **83**:1092-1104.

Batary, P., and A. Baldi. 2004. Evidence of an edge effect on avian nest success. Conservation Biology **18**:389-400.

Bateman, B. L., J. VanDerWal, S. E. Williams, and C. N. Johnson. 2012. Biotic interactions influence the projected distribution of a specialist mammal under climate change. Diversity and Distributions **18**:861-872.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software **67**:1-48.

Bertness, M. D. 1984. Ribbed mussels and spartina-alterniflora production in a new england salt-marsh. Ecology **65**:1794-1807.

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

Bishop, M. J., and C. H. Peterson. 2006. Direct effects of physical stress can be counteracted by indirect benefits: Oyster growth on a tidal elevation gradient. Oecologia **147**:426-433.

Blanco, A., A. R. Larrinaga, J. M. Neto, J. Troncoso, G. Mendez, P. Dominguez-Lapido, A. Ovejero, L. Pereira, T. M. Mouga, R. Gaspar, B. Martinez, M. F. L. Lemos, and C. Olabarria. 2021. Spotting intruders: Species distribution models for managing invasive intertidal macroalgae. Journal of Environmental Management **281**.

Breaux, A., S. Farber, and J. Day. 1995. Using natural coastal wetlands systems for waste-water treatment - an economic benefit analysis. Journal of Environmental Management **44**:285-291.

Carroll, J. M., B. T. Furman, L. J. Jackson, E. A. Hunter, and B. J. Peterson. 2019. Propagule risk in a marine foundation species: Seascape effects on Zostera marina seed predation. Journal of Ecology **107**:1982-1994.

Carroll, J. M., J. P. Marion, and C. M. Finelli. 2015. A field test of the effects of mesopredators and landscape setting on juvenile oyster, Crassostrea virginica, consumption on intertidal reefs. Marine Biology **162**:993-1003.

Chmura, G. L., S. C. Anisfeld, D. R. Cahoon, and J. C. Lynch. 2003. Global carbon sequestration in tidal, saline wetland soils. Global Biogeochemical Cycles **17**.

Connell, J. H. 1972. Community Interactions on Marine Rocky Intertidal Shores. Annual Review of Ecology and Systematics **3 (1972)**:169-192.

Connell, J. H. 1985. he consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. Journal of Experimental Marine Biology and Ecology **93(1-2)**:11-45.

Crotty, S. M., and C. Angelini. 2020. Geomorphology and Species Interactions Control Facilitation Cascades in a Salt Marsh Ecosystem. Current biology : CB.

Crotty, S. M., C. Ortals, T. M. Pettengill, L. M. Shi, M. Olabarrieta, M. A. Joyce, A. H. Altieri, E. Morrison, T. S. Bianchi, C. Craft, M. D. Bertness, and C. Angelini. 2020. Sea-level rise and the emergence of a keystone grazer alter the geomorphic evolution and ecology of southeast US salt marshes. Proceedings of the National Academy of Sciences of the United States of America **117**:17891-17902.

Davenport, J., and X. G. Chen. 1987. A comparison of methods for the assessment of condition in the mussel (mytilus-edulis-l). Journal of Molluscan Studies **53**:293-297.

Denwood, M. 2021. Interface Utilities, Model Templates, Parallel Computing Methods and Additional Distributions for MCMC Models in JAGS.

Derksen-Hooijberg, M., C. Angelini, L. P. M. Lamers, A. Borst, A. Smolders, J. R. H. Hoogveld, H. de Paoli, J. van de Koppel, B. R. Silliman, and T. van der Heide. 2018. Mutualistic interactions amplify saltmarsh restoration success. Journal of Applied Ecology **55**:405-414.

Doherty, P. J., and D. M. Williams. 1988. The replenishment of coral-reef fish populations. Oceanography and Marine Biology **26**:487-551.

Eckman, J. E. 1983. HYDRODYNAMIC PROCESSES AFFECTING BENTHIC recruitment. Limnology and Oceanography **28**:241-257.

Elith, J., and J. R. Leathwick. 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. Annual Review of Ecology Evolution and Systematics **40**:677-697.

Fitz, H. C., and R. G. Wiegert. 1991. Utilization of the intertidal zone of a salt-marsh by the blue-crab callinectes-sapidus - density, return frequency, and feeding-habits. Marine Ecology Progress Series **76**:249-260.

Fodrie, F. J., A. B. Rodriguez, C. J. Baillie, M. C. Brodeur, S. E. Coleman, R. K. Gittman, D. A. Keller, M. D. Kenworthy, A. K. Poray, J. T. Ridge, E. J. Theuerkauf, and N. L. Lindquist. 2014. Classic paradigms in a novel environment: inserting food web and productivity lessons from rocky shores and saltmarshes into biogenic reef restoration. Journal of Applied Ecology **51**:1314-1325.

Fong, A., N. V. Davila, and G. M. Lopez-Iborra. 2015. Amphibian Hotspots and Conservation Priorities in Eastern Cuba Identified by Species Distribution Modeling. Biotropica **47**:119-127.

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

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

French, J. R., and D. R. Stoddart. 1992. Hydrodynamics of salt-marsh creek systems - implications for marsh morphological development and material exchange. Earth Surface Processes and Landforms **17**:235-252.

Gatza, E., F. Hammes, and E. Prest. 2013. Assessing Water Quality with the BD Accuri™ C6 Flow Cytometer[White Paper]. BD Biosciences.

Geiger, S. P., S. P. Stephenson, and W. S. Arnold. 2010. Protracted recruitment in the bay scallop argopecten irradians in a west florida estuary. Journal of Shellfish Research **29**:809-817.

Gelman, A., X. L. Meng, and H. Stern. 1996. Posterior predictive assessment of model fitness via realized discrepancies. Statistica Sinica **6**:733-760.

Gosnell, J. S., K. Spurgin, and E. A. Levine. 2017. Caged oysters still get scared: Predator presence and density influence growth in oysters, but only at very close ranges. Marine Ecology Progress Series **568**:111-122.

Heffernan, P. B., and R. L. Walker. 1989. Gametogenic cycles of three bivalves in Wassaw Sound, Georgia. 3. Geukensia demissa (Dillwyn, 1817). Journal of Shellfish Research **8**:327-334.

Hijams, R. J. 2020. raster: Geographic Data Analysis and Modeling. R package version 3.4-5.

Hillard, R., and K. Walters. 2009. Prevalence, patterns, and effects of shell damage on Geukensia demissa in South Carolina estuarine habitats. Marine Biology **156**:2149-2160.

Hladik, C., J. Schalles, and M. Alber. 2013. Salt marsh elevation and habitat mapping using hyperspectral and LIDAR data. Remote Sensing of Environment **139**:318-330.

Honig, A., J. Supan, and M. La Peyre. 2015. Population ecology of the gulf ribbed mussel across a salinity gradient: recruitment, growth and density. Ecosphere **6**.

Huang, S. C., D. A. Kreeger, and R. I. E. Newell. 2003. Tidal and seasonal variations in the quantity and composition of seston in a North American, mid-Atlantic saltmarsh. Estuarine Coastal and Shelf Science **56**:547-560.

Hughes, R. N., and R. Seed. 1981. Size selection of mussels by the blue-crab callinectes-sapidus - energy maximizer or time minimizer. Marine Ecology Progress Series **6**:83-89.

Hughes, T. P. 1990. Recruitment limitation, mortality, and population regulation in open systems - a case-study. Ecology **71**:12-20.

Hunter, E. A., N. P. Nibbelink, and R. J. Cooper. 2016. Threat predictability influences seaside sparrow nest site selection when facing trade-offs from predation and flooding. Animal Behaviour **120**:135-142.

Isdell, R. E., D. M. Bilkovic, and C. Hershner. 2018. Shorescape-level factors drive distribution and condition of a salt marsh facilitator (Geukensia demissa). Ecosphere **9**:16.

Isdell, R. E., D. M. Bilkovic, and C. Hershner. 2020. Large Projected Population Loss of a Salt Marsh Bivalve (Geukensia demissa) from Sea Level Rise. Wetlands **40**:1729-1738.

Jensen, K. T. 1992. Dynamics and growth of the cockle, cerastoderma-edule, on an intertidal mud-flat in the danish wadden sea - effects of submersion time and density. Netherlands Journal of Sea Research **28**:335-345.

Jernakoff, P., and P. G. Fairweather. 1985. An experimental-analysis of interactions among several intertidal organisms. Journal of Experimental Marine Biology and Ecology **94**:71-88.

Johnson, K. D., and D. L. Smee. 2014. Predators influence the tidal distribution of oysters (Crassostrea virginica). Marine Biology **161**:1557-1564.

Johnson, M. S., and R. Black. 2008. Effects of contrasting tidal habitats on growth, survivorship and dispersal in an intertidal snail. Journal of Experimental Marine Biology and Ecology **363**:96-103.

Jost, J., and B. Helmuth. 2007. Morphological and ecological determinants of body temperature of Geukensia demissa, the Atlantic ribbed mussel, and their effects on mussel mortality. Biological Bulletin **213**:141-151.

Julien, A. R., A. W. Tweel, N. Hadley, and P. R. Kingsley-Smith. 2020. DEMOGRAPHICS OF the ribbed mussel geukensia demissa (dillwyn, 1817) and the effects of its simulated manual harvest on salt marsh health in south carolina, USA. Journal of Shellfish Research **39**:66-75.

Julien, A. R., A. W. Tweel, D. J. McGlinn, G. W. Sundin, N. H. Hadley, and P. R. Kingsley-Smith. 2019. Characterization of ribbed mussel geukensia demissa (dillwyn, 1817) habitat in relation to tidal elevation and salinity in a south carolina estuary. Journal of Shellfish Research **38**:53-61.

Kaky, E., and F. Gilbert. 2016. Using species distribution models to assess the importance of Egypt's protected areas for the conservation of medicinal plants. Journal of Arid Environments **135**:140-146.

Kennedy, C. J., and E. B. Barbier. 2016. The economic value of freshwater inputs to an estuarine fishery. Water Resources and Economics **13**:46-59.

Knights, A. M. 2012. Spatial variation in body size and reproductive condition of subtidal mussels: Considerations for sustainable management. Fisheries Research **113**:45-54.

Kolbe, J. J., and F. J. Janzen. 2002. Spatial and temporal dynamics of turtle nest predation: edge effects. Oikos **99**:538-544.

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

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

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

Lamb, E. A., H. M. Leslie, and J. L. Shinen. 2014. Both like it hot? Influence of temperature on two co-occurring intertidal barnacles in central Chile. Journal of Experimental Marine Biology and Ecology **453**:54-61.

Langdon, C. J., and R. I. E. Newell. 1990. Utilization of detritus and bacteria as food sources by 2 bivalve suspension-feeders, the oyster crassostrea-virginica and the mussel geukensia-demissa. Marine Ecology Progress Series **58**:299-310.

Li, S. Z., B. S. Cui, T. Xie, J. H. Bai, Q. Wang, and W. Shi. 2018. What drives the distribution of crab burrows in different habitats of intertidal salt marshes, Yellow River Delta, China. Ecological Indicators **92**:99-106.

Lin, J. 1989. Influence of location in a salt-marsh on survivorship of ribbed mussels. Marine Ecology Progress Series **56**:105-110.

Mahoney, R. D., M. D. Kenworthy, J. K. Geyer, K. A. Hovel, and F. J. Fodrie. 2018. Distribution and relative predation risk of nekton reveal complex edge effects within temperate seagrass habitat. Journal of Experimental Marine Biology and Ecology **503**:52-59.

Marie, D., F. Partensky, D. Vaulot, and C. Brussaard. 1999. Enumeration of phytoplankton, bacteria, and viruses in marine samples. Current protocols in cytometry **10(1)**:11-11.

Martin, T. G., B. A. Wintle, J. R. Rhodes, P. M. Kuhnert, S. A. Field, S. J. Low-Choy, A. J. Tyre, and H. P. Possingham. 2005. Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. Ecology Letters **8**:1235-1246.

Moller, I., T. Spencer, J. R. French, D. J. Leggett, and M. Dixon. 1999. Wave transformation over salt marshes: A field and numerical modelling study from north Norfolk, England. Estuarine Coastal and Shelf Science **49**:411-426.

Moody, J., and D. Kreeger. 2020. Ribbed mussel (Geukensia demissa) filtration services are driven by seasonal temperature and site-specific seston variability. Journal of Experimental Marine Biology and Ecology **522**.

Moody, J., L. Whalen, D. Kreeger, D. Bushek, and S. Rothrock. 2013. Living Shorelines for All: From Estuary-wide Planning to Pilots on the Ground. Partnership for the Delaware Estuary 2013.

Morgan, P. A., D. M. Burdick, and F. T. Short. 2009. The Functions and Values of Fringing Salt Marshes in Northern New England, USA. Estuaries and Coasts **32**:483-495.

Newell, R. I. E. 2004. Ecosystem influences of natural and cultivated populations of suspension-feeding bivalve molluscs: A review. Journal of Shellfish Research **23**:51-61.

Nielsen, K. J., and D. R. Franz. 1995. The influence of adult conspecifics and shore level on recruitment of the ribbed mussel geukensia-emissa (dillwyn). Journal of Experimental Marine Biology and Ecology **188**:89-98.

NOAA. 2016. Extended reconstructed sea surface temperature (ERSST.v4). National Centers for Environmental Information.

O'Beirn, F. X., M. W. Luckenbach, J. A. Nestlerode, and G. M. Coates. 2000. Toward design criteria in constructed oyster reefs: Oyster recruitment as a function of substrate type and tidal height. Journal of Shellfish Research **19**:387-395.

O'Connell, J. L., D. R. Mishra, D. L. Cotten, L. Wang, and M. Alber. 2017. The Tidal Marsh Inundation Index (TMII): An inundation filter to flag flooded pixels and improve MODIS tidal marsh vegetation time-series analysis. Remote Sensing of Environment **201**:34-46.

Palumbo, A. V., R. L. Ferguson, and P. A. Rublee. 1984. Size of suspended bacterial-cells and association of heterotrophic activity with size fractions on particles in estuarine and coastal waters. Applied and Environmental Microbiology **48**:157-164.

Peterson, A. T., M. Papes, and D. A. Kluza. 2003. Predicting the potential invasive distributions of four alien plant species in North America. Weed Science **51**:863-868.

Peterson, A. T., V. Sanchez-Cordero, J. Soberon, J. Bartley, R. W. Buddemeier, and A. G. Navarro-Siguenza. 2001. Effects of global climate change on geographic distributions of Mexican Cracidae. Ecological Modelling **144**:21-30.

Peterson, C. H., and R. Black. 1988. RESPONSES OF GROWTH TO ELEVATION FAIL TO explain vertical zonation of suspension-feeding bivalves on a tidal flat. Oecologia **76**:423-429.

Peterson, C. H., and R. Black. 1991. Preliminary evidence for progressive sestonic food depletion in incoming tide over a broad tidal sand flat. Estuarine Coastal and Shelf Science **32**:405-413.

Rheault, R. B., and M. A. Rice. 1996. Food-limited growth and condition index in the eastern oyster, Crassostrea virginica (Gmelin 1791), and the bay scallop, Argopecten irradians irradians (Lamarck 1819). Journal of Shellfish Research **15**:271-283.

Robles, C. D., C. Garza, R. A. Desharnais, and M. J. Donahue. 2010. Landscape patterns in boundary intensity: a case study of mussel beds. Landscape Ecology **25**:745-759.

Royle, J. A. 2004. N-mixture models for estimating population size from spatially replicated counts. Biometrics **60**:108-115.

Schalles, J. F., C. M. Hladik, A. A. Lynes, and S. C. Pennings. 2013. Landscape Estimates of Habitat Types, Plant Biomass, and Invertebrate Densities in a Georgia Salt Marsh. Oceanography **26**:88-97.

Schwarzer, A. C., W. A. Cox, and B. Tornwall. 2020. Factors influencing occupancy and density of salt marsh songbirds in northeast Florida. Journal of Field Ornithology **91**:156-169.

Seed, R. 1969. Ecology of mytilus edulis l (lamellibranchiata) on exposed rocky shores .2. Growth and mortality. Oecologia **3**:317-&.

Silliman, B. R., and A. Bortolus. 2003. Underestimation of Spartina productivity in western Atlantic marshes: marsh invertebrates eat more than just detritus. Oikos **101**:549-554.

Smith, J. M., and R. W. Frey. 1985. Biodeposition by the ribbed mussel geukensia-demissa in a salt-marsh, sapelo-island, georgia. Journal of Sedimentary Petrology **55**:817-828.

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

Stohlgren, T. J., P. Ma, S. Kumar, M. Rocca, J. T. Morisette, C. S. Jarnevich, and N. Benson. 2010. Ensemble Habitat Mapping of Invasive Plant Species. Risk Analysis **30**:224-235.

Teal, J. M. 1958. Distribution of fiddler crabs in georgia salt marshes. Ecology **39**:185-193.

Team, R. C. 2020. R: A language and environment for statistical computing. R Foundation for Statistical
Computing, Vienna, Austria.

Vanhorne, B. 1983. DENSITY AS A MISLEADING INDICATOR OF HABITAT QUALITY. Journal of Wildlife Management **47**:893-901.

Venables, W. N., and B. D. Ripley. 2002. Modern Applied Statistics with S. Fourth Edition. Springer, New York.

Vetter, D., G. Rucker, and I. Storch. 2013. A meta-analysis of tropical forest edge effects on bird nest predation risk: Edge effects in avian nest predation. Biological Conservation **159**:382-395.

Virgin, S. D. S., K. A. Sorochan, A. Metaxas, and M. A. Barbeau. 2019. Effect of temperature on the larval biology of ribbed mussels (Geukensia demissa) and insights on their northern range limit. Journal of Experimental Marine Biology and Ecology **512**:31-41.

Viswanathan, C., R. Purvaja, J. J. J. Jeevamani, V. D. Samuel, R. Sankar, K. R. Abhilash, G. A. Geevarghese, R. Muruganandam, M. Gopi, S. Raja, R. R. Das, S. Patro, P. Krishnan, and R. Ramesh. 2020. Salt marsh vegetation in India: Species composition, distribution, zonation pattern and conservation implications. Estuarine Coastal and Shelf Science **242**.

Watt, C., D. J. Garbary, and C. Longtin. 2011. Population structure of the ribbed mussel Geukensia demissa in salt marshes in the southern Gulf of St. Lawrence, Canada. Helgoland Marine Research **65**:275-283.

Widdows, J., B. L. Bayne, D. R. Livingstone, R. I. E. Newell, and P. Donkin. 1979. Physiological and biochemical responses of bivalve mollusks to exposure to air. Comparative Biochemistry and Physiology a-Physiology **62**:301-308.

Ziegler, S. L., J. H. Grabowski, C. J. Baillie, and F. J. Fodrie. 2018. Effects of landscape setting on oyster reef structure and function largely persist more than a decade post-restoration. Restoration Ecology **26**:933-942.

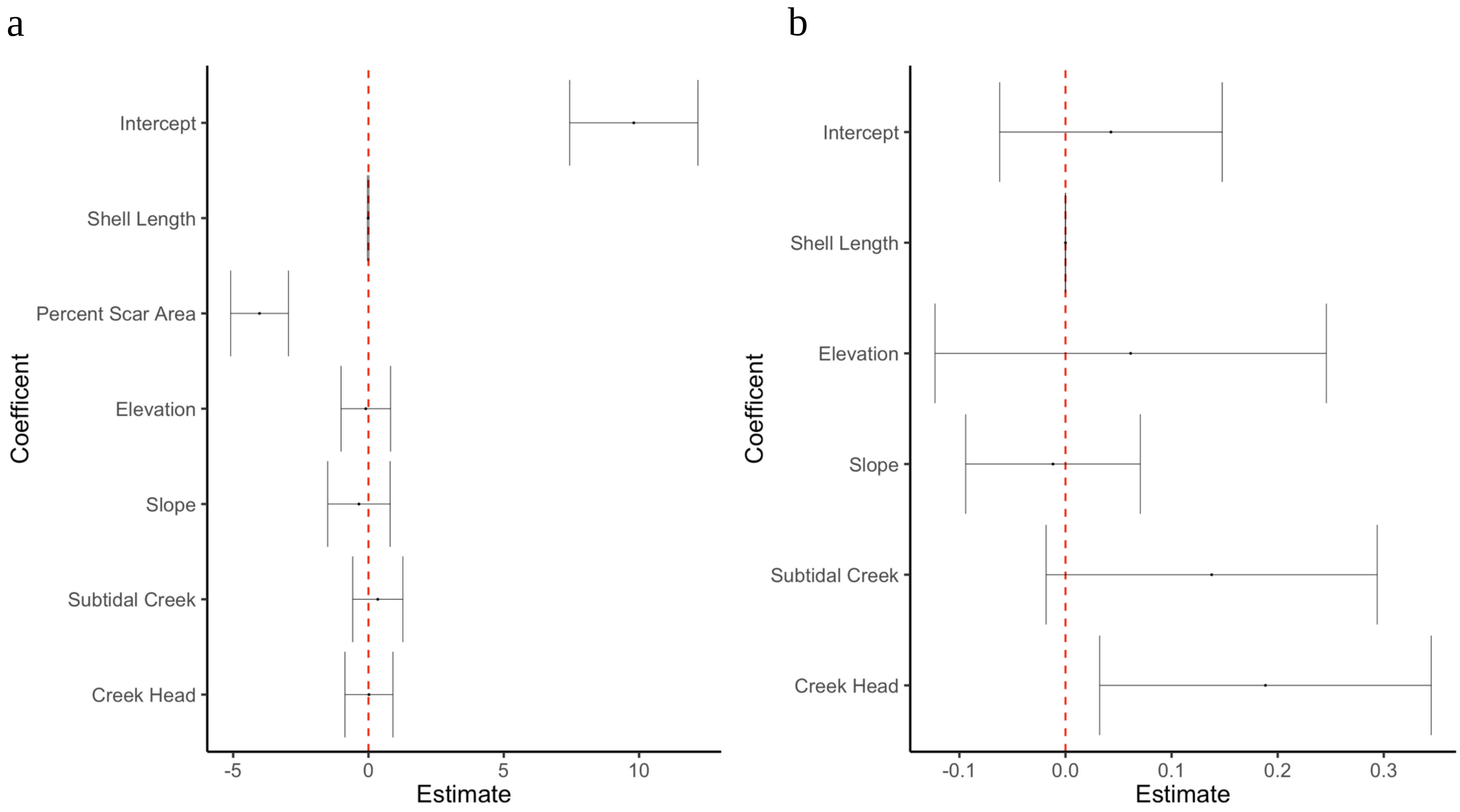
APPENDIX 1:COMPETITIVE MODELS (ΔAIC<2) FOR MUSSEL CONDITION (A) AND SCARRING (B). Condition index was calculated as a ratio of dried tissue to shell weight. Scarring was the percent of a shell's surface area covered in scars. To determine the factors that determine shell scarring and condition index, a linear mixed effect model was chosen with spatial variables as fixed effects and site as a random effect and every possible combination of each model were generated. Creek head and subtidal creek refers to distance to these features. Shell length refers to the distance from posterior to anterior part of mussel shell.

a

| Intercept | Elevation | Creek Head | Subtidal | Scarring | Length | Slope | df | logLik | AICc | delta | weight |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 8.57438415 | NA | NA | 0.79187915 | -3.9500681 | NA | NA | 5 | -193.62338 | 397.734568 | 0 | 0.08694098 |
| 10.8080852 | NA | NA | NA | -4.1657088 | -0.0235631 | -0.7840117 | 6 | -192.63964 | 397.967815 | 0.23324625 | 0.07737056 |
| 10.7034052 | NA | NA | NA | -4.0553923 | -0.0235313 | NA | 5 | -193.89676 | 398.281331 | 0.5467629 | 0.06614491 |
| 10.4527158 | NA | NA | 0.61861899 | -4.2600718 | -0.0223016 | NA | 6 | -192.84298 | 398.374482 | 0.63991357 | 0.06313483 |
| 8.64990787 | NA | NA | 0.69175047 | -3.953648 | NA | -0.4190933 | 6 | -192.95359 | 398.595695 | 0.86112671 | 0.05652404 |
| 11.169656 | -0.4845054 | NA | NA | -4.0866914 | -0.024239 | -0.9960298 | 7 | -191.84095 | 398.607528 | 0.87295927 | 0.05619062 |
| 8.50384863 | NA | 0.40608796 | 0.78764989 | -4.073114 | NA | NA | 6 | -193.02871 | 398.745949 | 1.01138049 | 0.05243316 |
| 10.5889886 | NA | NA | 0.48986836 | -4.2982634 | -0.0226438 | -0.5977264 | 7 | -191.94018 | 398.805974 | 1.07140606 | 0.05088287 |
| 8.86149289 | NA | NA | NA | -3.7713048 | NA | -0.7109269 | 5 | -194.20358 | 398.894972 | 1.16040385 | 0.04866828 |
| 8.6372289 | -0.1167919 | NA | 0.810488 | -3.9302789 | NA | NA | 6 | -193.12107 | 398.930672 | 1.19610354 | 0.04780727 |
| 8.77501594 | NA | NA | NA | -3.7034323 | NA | NA | 4 | -195.31259 | 398.947768 | 1.21319992 | 0.04740034 |
| 11.0203828 | NA | -0.5060712 | NA | -3.939569 | -0.0263215 | NA | 6 | -193.15793 | 399.004383 | 1.26981437 | 0.04607739 |
| 11.0259435 | NA | -0.365976 | NA | -4.0738701 | -0.0255489 | -0.7127269 | 7 | -192.06953 | 399.064678 | 1.33010999 | 0.04470898 |
| 10.996048 | -0.5705878 | NA | 0.52945114 | -4.2147551 | -0.0233593 | -0.8297864 | 8 | -191.04928 | 399.298566 | 1.56399748 | 0.03977469 |
| 10.7219701 | NA | -0.4091686 | 0.58358021 | -4.1581995 | -0.0246034 | NA | 7 | -192.22932 | 399.384265 | 1.64969627 | 0.03810636 |
| 8.58206396 | NA | 0.47382942 | 0.66795505 | -4.0977525 | NA | -0.5006851 | 7 | -192.25713 | 399.439887 | 1.70531887 | 0.03706118 |
| 8.86126841 | -0.3506712 | NA | 0.71751543 | -3.8953817 | NA | -0.5479619 | 7 | -192.26685 | 399.45931 | 1.72474202 | 0.036703 |
| 10.5817663 | -0.2068745 | NA | 0.6512974 | -4.2244092 | -0.022521 | NA | 7 | -192.3197 | 399.565018 | 1.83045003 | 0.03481347 |
| 8.78040727 | NA | 0.51726622 | NA | -3.9399198 | NA | -0.7937671 | 6 | -193.44233 | 399.573177 | 1.83860851 | 0.03467175 |
| 10.7057703 | -0.0032145 | NA | NA | -4.0546263 | -0.0235377 | NA | 6 | -193.44482 | 399.578169 | 1.843601 | 0.03458531 |

b

| Intercept | Elevation | Creek Head | Subtidal | Length | Slope | df | logLik | AICc | delta | weight |
|---|---|---|---|---|---|---|---|---|---|---|
| 0.06036439 | NA | 0.21369502 | 0.18004087 | NA | NA | 5 | 87.1003431 | -163.71288 | 0 | 0.48414649 |
| -0.0092962 | 0.13838454 | 0.1801623 | 0.14888853 | NA | NA | 6 | 87.2683274 | -161.84813 | 1.86475106 | 0.19056855 |



APPENDIX 2: ESTIMATES OF MUSSEL CONDITION INDEX (A) AND SHELL SCARRING (B) MODEL BETA PARAMETERS WITH 95% CONFIDENCE INTERVAL AFTER MODEL AVERAGING. Subtidal creek and creek head refer to distance from each feature.