



Within-marsh and Landscape Features Structure Ribbed Mussel Distribution in Georgia, USA, Marshes

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Abstract

Ribbed mussels, *Geukensia demissa*, are marsh fauna that are used in coastal management and restoration due to the ecosystem services they provide. Ribbed mussel restoration efforts may be improved with a greater understanding of the environmental drivers of ribbed mussel distribution at multiple spatial scales to predict areas where restoration could be successful. This study sought to estimate the effects of within-marsh (4 m) and landscape (500 m) factors on ribbed mussel distribution. Ribbed mussel densities were surveyed at 11 sites along the coast of Georgia, USA, and overlaid with spatial data for within-marsh factors (elevation, distance to marsh features, slope) as well as landscape factors (percent cover by subtidal creek, forest, and development within a 500-m radius). The distribution model was then validated using three previously unsurveyed marshes and explained 55% of the variance in ribbed mussel abundance. Ribbed mussel abundances and occupancy were most sensitive to changes in within-marsh factors (elevation and distance to subtidal creeks, bodies of water inundated during the full tidal cycle) but were also sensitive to landscape features (percent landcover of forests and development). The highest ribbed mussel densities were found in mid-elevation areas (~0.7 m NAVD88), far from subtidal creeks, and in marshes surrounded with forest and development. These results contrast with distributions in the northeastern USA, where ribbed mussels are distributed along subtidal creek banks. This work suggests that restoration may be most effective when focused on appropriate elevations and at locations away from the marsh-creek ecotone.

Keywords Species distribution model · Spatial scale · Intertidal · Salt marsh

Introduction

Species distribution modeling is an ecological tool that combines abundance or occupancy data with explanatory environmental variables to 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. 2012), and finding suitable habitat for protected areas (Fong et al. 2015; Kaky and Gilbert 2016) and restoration (Zellmer et al. 2019). Species distribution models can be helpful when managing species and habitats; however, models that incorporate data at appropriate spatial scales, e.g., extent (area covered by the study) and grain size (size of the observable unit in which data have a singular value such as a pixel) may be more informative (Wiens 1989). Ecological processes that drive species distribution occur across multiple scales, and the magnitude and direction of these processes (e.g., recruitment, predation) can vary depending on the grain size and total area of the processes observed and/or modeled (Wiens 1989). Species distribution models typically explain more variation when they incorporate data across different spatial scales (e.g., 0.5–10 km scale for distribution of biting midges in

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Germany; Lühken et al. 2016; 165–1215 m scale for bird distribution in Oregon; Hallman and Robinson 2020).

Understanding how ecological processes might change with scale is critical for species and/or ecosystem management, particularly as these processes drive species' distributions. Perception of the critical factors and processes that affect species distribution may change across multiple scales, and this could ultimately affect management strategies. For example, at broad spatial scales (~kms), salinity is thought to be the major driver of alligator (*Alligator mississippiensis*) distribution in urban areas, whereas the presence of human structures is considered most important at fine scales (~m; Beal and Rosenblatt 2020). Generally, models that include variables at multiple scales offer the best predictions for species distribution. Models of reef fish abundance including factors on both fine scales (depth and coral cover; < 25 m) and broad scales (distance to shore; > 150 m) explained more variation than single-scale models (Goodell et al. 2018). Likewise, model averaging reveals that microhabitat (1 m) and landscape (500 m) scale factors are both important in structuring the distribution of ants in the genus *Tetramorium* (Cordonnier et al. 2019). In some cases, interactions occur between processes at different scales, such as interactions between fine-scale (~1 m) seagrass stem density and patch-scale (~3 m) edge effects for blue crab (*Callinectes sapidus*) survivorship (Mahoney et al. 2018). Species' characteristics can affect which processes at which scales influence species distribution; pollution-sensitive fish species may be more affected by large scale (~km) factors, such as upstream landcover types, while more robust species can be structured primarily by finer-scale factors such as local catchment temperatures (m; Markovic et al. 2019). Therefore, it is critical to incorporate multiple factors across multiple spatial scales into species distribution models.

In intertidal ecosystems, drivers of species' distributions can differ based on the scale at which a study is conducted. On large, biogeographic scales (100 s km), the distribution and abundance of intertidal mollusks are primarily related to the propagule supply of intertidal organisms (Hughes 1990). At seascape scales (10 s m to km), the types, diversity of, and proximity to different habitats can have strong influences on species distribution patterns and demography of mollusks (Carroll et al. 2015, 2019; Ziegler et al. 2018). At finer scales (~m), species' distributions of intertidal mollusks are often controlled by elevation, which determines submergence times (Jensen 1992). Increased submergence time may benefit organisms by increasing foraging and growth rates (Seed 1969; Peterson and Black 1988; Jensen 1992; Stiven and Gardner 1992), although increased submergence could also increase the risk of predation (Fodrie et al. 2014; Johnson and Smee 2014). Trade-offs between growth and survival drive species' distributions into specific ranges

of intertidal elevation. Therefore, it is often necessary to explore the distribution of intertidal organisms at both fine and broad spatial scales.

Salt marshes are globally distributed, complex intertidal ecosystems characterized by salt-tolerant vegetation, which provide 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 (Breux et al. 1995; Morgan et al. 2009). As in other intertidal ecosystems, elevation structures small-scale (1 m) species distribution across the salt marsh where distributions of both flora and fauna are restricted to specific zones within the marsh (e.g., Kuenzer 1961; Schalles et al. 2013; Hunter et al. 2017; Li et al. 2018; Viswanathan et al. 2020). Distinct faunal communities can be linked to plant communities that are strongly influenced by elevation (e.g., Teal 1958; Schalles et al. 2013; Schwarzer et al. 2020). Beyond elevation, however, distance to different marsh features, such as upland habitats and creeks (Hunter et al. 2017; Crotty and Angelini 2020; Schwarzer et al. 2020) and marsh patch size (Puzin and Pétilon 2019) can influence species' distributions within salt marshes.

Ribbed mussels (*Geukensia demissa*) are ecologically important bivalves found in salt marshes along the Atlantic coast of the USA. Ribbed mussels are found attached to each other by byssal threads in large aggregations around the marsh grass root system. Ribbed mussels are considered a secondary foundation species in salt marshes because they provide multiple ecological services and facilitate healthy marshes (Kuenzler 1961; Bertness 1984; Smith and Frey 1985; Kreeger and Newell 2001; Altieri et al. 2007). Living embedded in the marsh sediment and marsh grass root system, ribbed 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 ribbed mussels can facilitate saltmarsh cordgrass (*Spartina alterniflora*) recovery in dieback areas (Derksen-Hooijberg et al. 2018) and help maintain grass growth in periods of drought stress (Angelini et al. 2016). Ribbed mussels also contribute to other functions, including water filtration (Kreeger and Newell 2001), nutrient cycling (Kuenzler 1961), and habitat complexity (Newell 2004). Although historically omitted from marsh management strategies, there is increasing interest in the role that ribbed mussels can play as part of living shorelines, where they may facilitate the growth of marsh vegetation (Moody et al. 2013). Given the multiple services provided by ribbed mussels and interest in their use for restoration projects, it is critical to understand the factors that might influence ribbed mussel distribution in marshes.

Along the northeastern US coast, ribbed mussels are found in thick bands immediately along the marsh edge (Bertness 1984; Bertness and Grosholz 1985; Franz and Tanacredi 1993; Franz 2001; Moody and Kreeger 2021), except for some marshes in the state of New Jersey where mussel densities are low along marsh edges likely due to chronic erosion (Moody and Kreeger 2021). In southeastern US estuaries, ribbed mussels are commonly found in clumps throughout the marsh platform (Lin 1989; Angelini et al. 2015). More specifically, ribbed mussels in the southeastern USA are typically found around creek heads, delta-like areas in the marsh where many drainage channels merge into a single creek that floods and drains the platform (Keunzler 1961; French and Stoddart 1992; Crotty and Angelini 2020). The differences in the local distribution across their range may be a result of variability in tidal heights, which can range from as low as 0.12 m in Maryland to as high as 3 m in the state of Georgia (Stiven and Gardner 1992), and the associated elevation gradients in these marshes. While previous studies have focused on factors that may influence ribbed mussel distribution throughout their range, typically focusing on factors at fine scales, such as vegetation type/density (Keunzler 1961; Watts et al. 2011; Schalles et al. 2013; Honig et al. 2015) and distance to marsh edge (Lin 1989; Stiven and Gardner 1992; Nielson and Franz 1995), more recent studies have considered both fine- and broad-spatial scale factors (Isdell et al. 2018; Julien et al. 2019; Crotty and Angelini 2020), although these recent studies usually only examined two or three factors (but see Crotty and Angelini 2020).

A species distribution model for ribbed mussels could be useful to managers. One application could be to estimate ecosystem services provided to different regions of the marsh, such as filtration rates (Moody and Kreeger 2020) and cordgrass growth and recovery (Crotty and Angelini 2020), and how those services might change with ribbed mussel abundance due to harvest (Julien et al. 2020) or climate change (Isdell et al. 2020). In the Chesapeake Bay in the mid-Atlantic USA, a species distribution model estimated that 50% of ribbed mussel populations could be lost by 2050 due to sea-level rise (Isdell et al. 2020). These models could also be used to create targets for elevation enhancement projects to maximize ribbed mussel habitat.

Due to increased interest in incorporating ribbed mussels into salt marsh management strategies (Moody et al. 2013; Derksen-Hooijberg et al. 2018; Kreeger et al. 2018; Moody et al. 2020; Bilkovic et al. 2021), it is critical to examine how multiple local, marsh-scale factors, and broader, landscape-scale factors may affect mussel distribution. Therefore, the main objective of this study was to create a model of predicted ribbed mussel densities across

the coast of Georgia, USA, by combining within-marsh (~4-m grain size, i.e., elevation, slope, distance to within-marsh features) and landscape (500-m radius, i.e., percent cover of forested and developed areas, subtidal creeks, distance to ocean) variables. Ribbed mussel densities, obtained using transect surveys at 11 different marshes (Fig. 1), were modeled as functions of geomorphological features such as elevation, slope, distance to subtidal creek, and distance to intertidal creek heads, as well as landscape features such as percent landcover by forest, development, and water. Based on initial observations, we expected ribbed mussel densities to be higher far away from subtidal creek banks and on the marsh platform. The distribution model was then validated by surveying three additional marshes.

Methods

Study Sites

Ribbed mussel (*Geukensia demissa*) surveys were conducted in 2019–2021 at 14 (11 test and 3 validation) *Spartina alterniflora*-dominated marsh sites spanning coastal Georgia (Fig. 1). These sites were clustered in three regions due to the logistics of site access (the city of Savannah, the state-managed barrier island Sapelo Island, and the city of Brunswick) with sites on Sapelo Island having less development and more forest than the Savannah and Brunswick sites. Georgia marshes are heterogeneous landscapes defined by changes in elevation, soil composition, and vegetation (Schalles et al. 2013) with an extreme (~3-m spring tide) tidal range (O’Connell et al. 2017). Each marsh can be classified into three zones based on elevation: creek levee, marsh platform, and upland (Fig. 2). Creek levees are raised elevation areas along subtidal and intertidal creek banks, dominated by tall form *S. alterniflora* along the lower levees. The marsh platform is the mid-elevation area of the marsh, dominated by medium to short-form *S. alterniflora* and is frequently flooded. The upland area is infrequently flooded and is populated by high marsh vegetation such as black needlerush (*Juncus roemerianus*) and pickleweed (*Salicornia virginica*) (Kuenzler 1961).

Estimating Ribbed Mussel Densities

At each site, 3–5 transects were established from the edge of a subtidal creek to the salt marsh/forest ecotone. Every 5 m, a 0.25-m² quadrat was haphazardly dropped and ribbed mussels were non-destructively counted. These counts are considered conservative as buried individuals

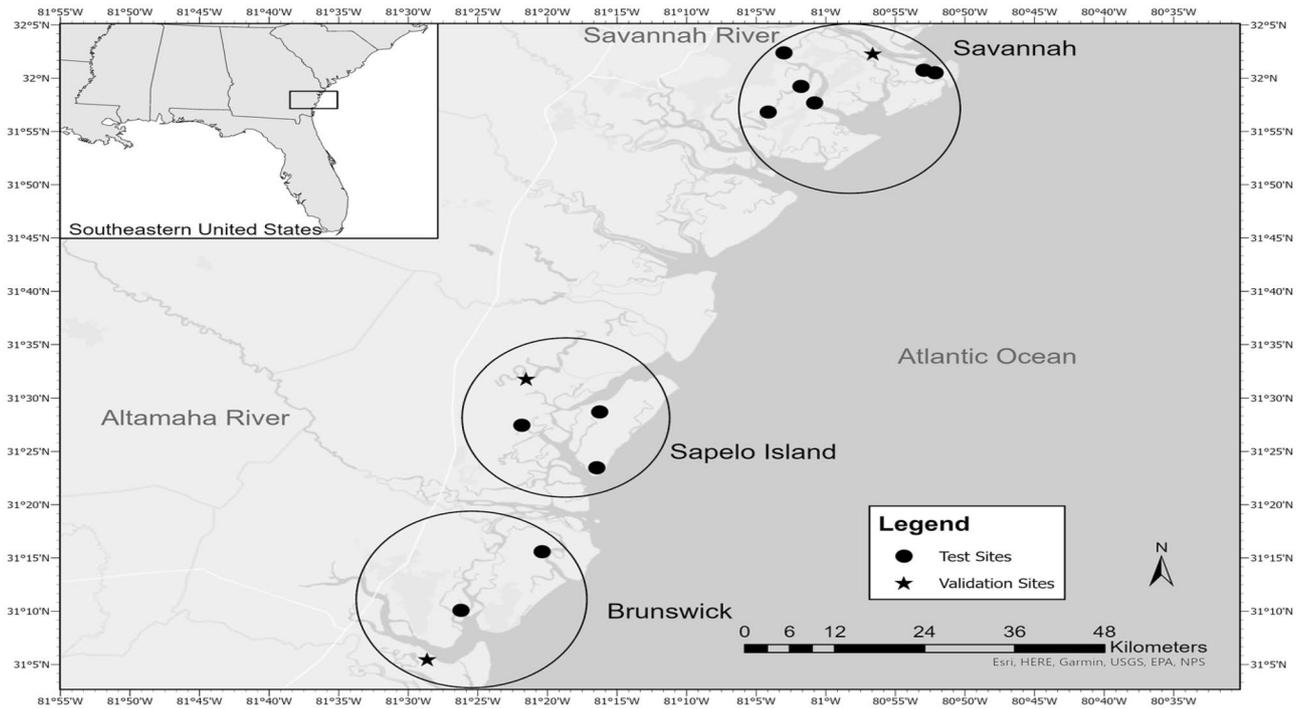


Fig. 1 *Geukensia demissa* (ribbed mussel) survey and validation sites across the coast of Georgia, USA. Circles indicate geographic clusters from the city of Savannah, state-managed barrier island Sapelo Island, and the city of Brunswick

may be missed (Nielson and Franz 1995). We did not consider spatial autocorrelation to be an issue with this sampling design as ribbed mussels have a limited movement

once established and the sizes of ribbed mussel clumps in Georgia are typically ~ 1 m in diameter (Kuenzler 1961). GPS coordinates were recorded using a Garmin GPSMAP

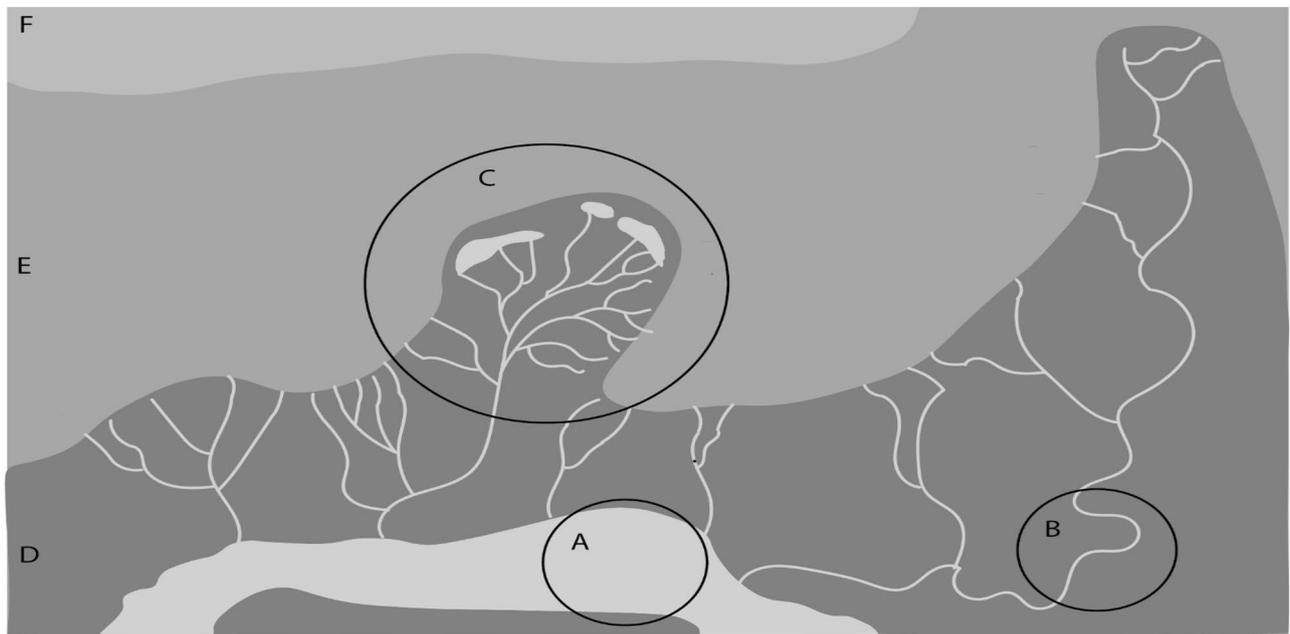


Fig. 2 Marsh features defined by Kuenzler (1961) used to predict *Geukensia demissa* (ribbed mussel) densities. A–C refer to different marsh features (circled): A subtidal creek, B intertidal creek, and

C creek head. D–F refer to different marsh regions (shaded regions): D creek levee, E marsh platform, and F upland habitat

Table 1 Description of explanatory variables used in hurdle model of ribbed mussel (*Geukensia demissa*) densities

Parameter	Scale	Description
Elevation	Within-marsh	Elevation relative to NAVD88 datum
Elevation2	Within-marsh	Quadratic term for elevation
Slope	Within-marsh	Slope in degrees
Subtidal	Within-marsh	Distance to subtidal creeks. Subtidal creeks refer to bodies of water inundated during full tidal cycle
Intertidal	Within-marsh	Distance to intertidal creeks. Intertidal creeks refer to bodies of water only inundated during part of tide cycle
Head	Within-marsh	Distance to intertidal creek heads. Creek heads refer to where intertidal creeks first spill onto the marsh platform
Upland	Within-marsh	Distance to upland. Upland refers to forested or developed land surrounding a marsh
Ocean	Landscape	Distance a marsh site is upriver from ocean
Subtidal500	Landscape	Percent land cover of subtidal creeks within a 500-m radius
Forest500	Landscape	Percent land cover of forests within a 500-m radius
Development500	Landscape	Percent land cover of development within a 500-m radius

78sc handheld GPS Unit¹ (horizontal accuracy: 3.6576 m). Notes were then taken of any elevation change and the presence of creeks and creek heads to be used for verifying raster data. Transects were spaced ~35 m apart, and 3–5 transects were sampled until 800–1000 m of the marsh had been surveyed (Supplementary Figs. S1–S11).

Spatial Data

Within-marsh variables included elevation, slope, distance to subtidal creek, distance to intertidal creek, distance to creek head, and distance to upland (Table 1). Elevation and slope rasters were created using data collected by the National Oceanic and Atmospheric Administration (NOAA) 2010 LiDAR surveys of the Georgia coast. The elevation data (4-m grain size) were collected in feet relative to the NAVD88 datum (North American Vertical Datum of 1988), corrected for vegetation height (mean error for elevation: -0.003 ± 0.10 (SD) m; Hladik et al. 2013). The correction factors for each vegetation class are as follows: 0.25 m for tall *Spartina alterniflora*, 0.11 m for medium *S. alterniflora*, 0.05 m for short *S. alterniflora*, 0.04 m for intertidal mud, 0.04 m for *Salicornia virginica*, 0.04 m for *Batis maritima*, 0.03 m for salt pan, 0.17 m for *Juncus roemerianus*, and 0.12 m for *Borrchia frutescens* (Hladik et al. 2013). These corrected elevation data were used to calculate marsh slope. Subtidal creeks (Fig. 2a) were defined as bodies of water inundated during the full tidal cycle and were acquired from the National Wetlands Inventory (NWI; U. S. Fish and Wildlife Service 2014). All other features

were delineated using aerial imagery taken in 2018 by NOAA, including intertidal creeks (the bodies of water that were not always submerged), creek heads (the points where intertidal creeks spill onto the marsh platform), and upland areas (forested or developed areas surrounding the marsh site) (Fig. 2). Separate Euclidean distance rasters were created using the subtidal, intertidal, creek head, and upland features as input layers.

Landscape variables included distance from the ocean and percent land cover by forest, development, and creek within a 500-m radius (Table 1). Euclidean distance rasters for ocean distance were generated using ocean shapefiles from the NWI as input layers and creek outline shapefiles as barrier layers, such that distance to ocean was calculated along waterways. The percent land cover rasters using resampled data collected from the National Land Cover Data Base (30-m grain size resampled to 4-m grain size; NLCD; Dewitz 2019) and NWI. Data for percent subtidal creek were acquired from the NWI data. The landcover rasters were imported into FRAGSTATS V4 (McGarigal et al. 2012), a spatial statistics software. Moving window analyses were conducted using 500-m radius circles to calculate the percent cover of each landcover type. A radius of 500 m resulted in the greatest variability of percent cover values for the ribbed mussel sampling points – smaller radii resulted in most points having percent cover values of zero, and larger radii resulted in very similar percent cover values for all points.

All rasters were resampled to a 4-m grain size. This grain size both adequately represented the accuracy of the handheld GPS unit (3–4 m) 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.

¹ Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

Statistical Analysis

To determine which marsh factors affected ribbed mussel distribution, data were analyzed using a hurdle model in which an occurrence process was modeled separately from a zero truncated abundance process. Occurrence and abundance were modeled separately because of the large separation between zero data and count data – where ribbed mussels were present, they tended to be highly abundant (i.e., very few counts were of 1–2 ribbed mussels). Explanatory variables (Table 1) were first examined for collinearity using a Pearson correlation coefficient cut-off of $|r| < 0.5$ (Supplementary Table S1). The final model included elevation, slope, distance to subtidal creek, distance to creek head, distance to upland, percent landcover by subtidal creeks, percent landcover of forest, and percent landcover of development. 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) – All other variables were modeled to have linear effects. An interaction between distance to creek head and distance to subtidal creek was included as creek heads associated with longer creeks have higher ribbed mussel densities (Crotty and Angelini 2020). All variables were scaled from 0 to 1 to ensure model convergence. The model used to estimate the probability of occupancy (ψ) was

$$\omega_i \sim \text{Bernoulli}(\psi_i) \tag{1}$$

$$\text{Logit}(\psi_i) = a_0 + a_1 * \text{Elevation}_i + a_2 * \text{Elevation}^2_i + a_3 * \text{Slope}_i + a_4 * \text{Subtidal}_i + a_5 * \text{Head}_i + a_6 * \text{Upland}_i + a_7 * \text{Subtidal500}_i + a_8 * \text{Dev500}_i + a_9 * \text{Forest500}_i + a_{10} * \text{Subtidal}_i * \text{Head}_i \tag{2}$$

where ω_i are the presence/absence data in which 1 refers to mussel presence and 0 refers to mussel absence for the i th quadrat, ψ_i is the probability of occupancy for the i th quadrat, Elevation_i is the elevation for the i th quadrat, Elevation^2_i is the quadratic term of elevation for the i th quadrat, Slope_i is the slope for the i th quadrat, Subtidal_i is the distance to subtidal creek for the i th quadrat, Head_i is the distance to the creek head for the i th quadrat, Upland_i is the distance to upland habitat for the i th quadrat, Subtidal500_i is the percent landcover by subtidal creeks within a 500-m radius for the i th quadrat, Dev500_i is the percent landcover by development within a 500-m radius for the i th quadrat, and Forest500_i is the percent landcover by forest within 500-m radius for the i th quadrat. The model used to estimate abundance (λ) was

$$C_i \sim \text{Negative Binomial}(\lambda_i, \alpha) \tag{3}$$

$$\text{Log}(\lambda_i) = b_0 + b_1 * \text{Elevation}_i + b_2 * \text{Elevation}^2_i + b_3 * \text{Slope}_i + b_4 * \text{Subtidal}_i + b_5 * \text{Head}_i + b_6 * \text{Upland}_i + b_7 * \text{Subtidal500}_i + b_8 * \text{Dev500}_i + b_9 * \text{Forest500}_i + b_{10} * \text{Subtidal}_i * \text{Head}_i \tag{4}$$

where C_i are the zero truncated mussel count data for the i th quadrat, λ_i is the abundance for the i th quadrat, and α is the dispersion parameter. To calculate the overall mussel density in a quadrat, the probability of occupancy and abundance were multiplied together such that

$$D_i = \psi_i * \lambda_i \tag{5}$$

where D_i is the mussel density for the i th quadrat.

Data analysis was conducted using JAGS through R (R Core Team 2020) using the package runjags (Denwood 2016). The model was run with 500,000 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 discrepancies between actual data and data simulated from the model, forty-eight thousand new mussel density data sets were generated using estimate parameters and the root mean squared errors of these data sets were compared. Well-fitting models have values close to 0.5 and distant from 0 or 1.

Sensitivity Analysis

To determine which factors had the greatest effects on occupancy and abundance, we performed a sensitivity analysis by increasing and decreasing each mean estimated coefficient for an environmental predictor by 5% and examining the percent change in predicted high-density areas (in m^2) for the ribbed mussel species distribution model. To predict ribbed mussel densities, occupancy and abundance rasters were created by multiplying mean model coefficients by raster layers and these two rasters were multiplied to yield a density raster (following Eq. (5)). We then classified pixels as high density if their values were within the top quartile range of all predicted values.

Model Validation

Model predictions were validated by collecting field data at three additional sites (Fig. 1) that had characteristics that mostly fell within the range of conditions surveyed at the initial sites. Only 12% of points had one characteristic (e.g., elevation, distance to upland) that was outside of the range of values sampled at the initial sites. Ribbed mussel density rasters were created for the three validation sites and were stratified into low (<2 ribbed mussels quadrat⁻¹), medium (2–4 ribbed mussels quadrat⁻¹), and high (>4

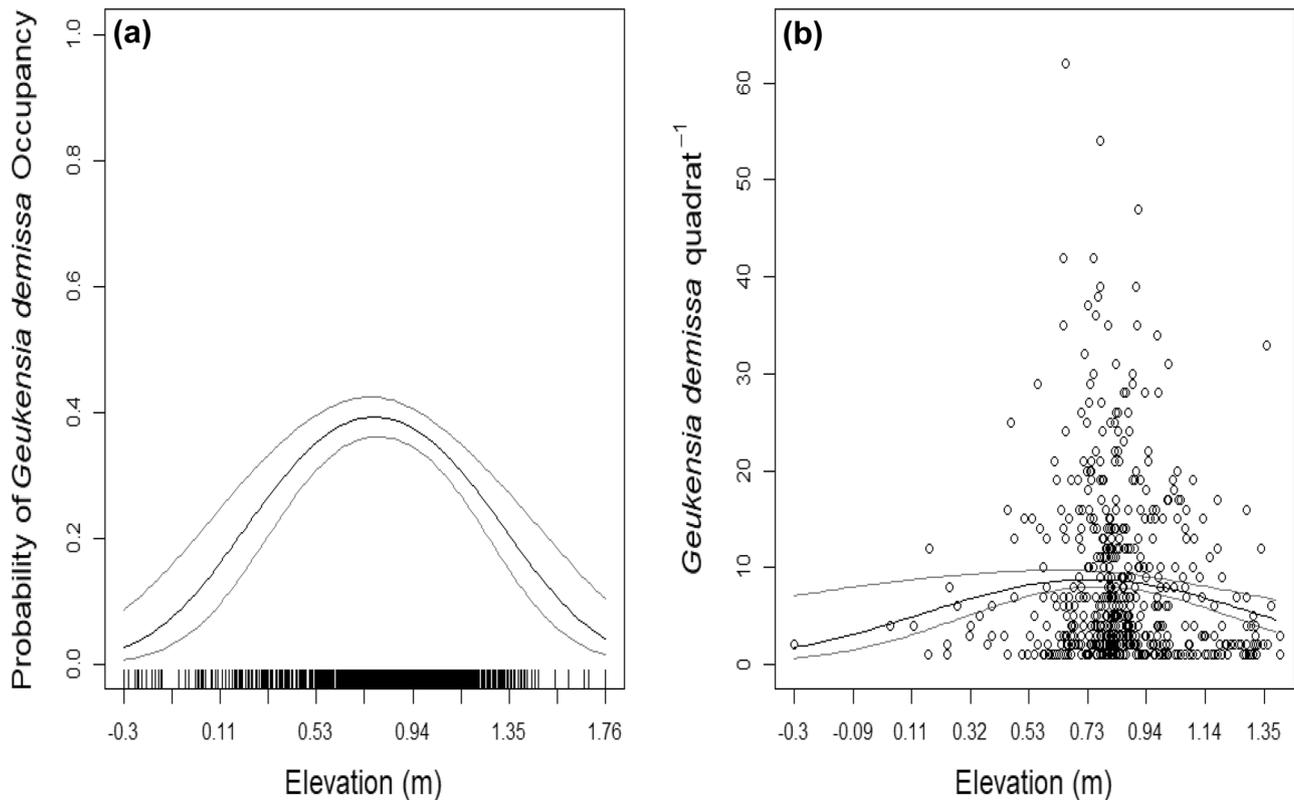


Fig. 3 Probability of *Geukensia demissa* **a** occupancy and **b** abundance (individuals 0.25 m^{-2}) as a function of elevation (m). Gray lines represent a 95% credible interval. **a** marks represent data points

where *Geukensia demissa* are present ($n=1541$ observations) at 11 sites and **b** dots represents zero truncated *G. demissa* counts 0.25 m^{-2} ($n=569$ observations) at 11 sites

ribbed mussels quadrat⁻¹) mussel density areas (Supplementary Figs. S12–S14). Stratified random sampling was used to generate 20 random points in each stratum and at each site using the sampleStratified function in the “raster” R package (Hijams 2020). Ribbed mussel densities at each of these points were measured using a 0.25-m^2 quadrat. The predicted and actual ribbed mussel densities were used to calculate an R^2 value for the abundance model and predicted and actual occurrence data were used to calculate an area under the receiver-operator-characteristic curve (AUC) value for the occurrence model. The predicted occurrence was calculated by thresholding the predicted density output at 0.5 (values <0.5 were predicted non-occurrence, and values >0.5 were predicted to have ribbed mussels occur).

Results

Observed ribbed mussel (*Geukensia demissa*) densities ranged from 0 to 62 ribbed mussels quadrat⁻¹. Observed ribbed mussel densities were higher than predicted values, but models still explained patterns in average ribbed mussel distribution (Supplementary Fig. S15). The occupancy

model yielded a Bayesian p -value of 0.46, and the abundance model yielded a Bayesian p -value of 0.35. Any predictor variables for which the 95% credible intervals did not overlap zero were considered to affect ribbed mussel distribution. Both ribbed mussel occupancy and ribbed mussel abundance were driven by elevation, which had a quadratic effect. Occupancy and abundance were maximized at an elevation of ~ 0.7 m NAVD88 (Fig. 3). Ribbed mussel occupancy also decreased with increasing slope, decreased with distance away from creek heads (i.e., greater occupancy near creek heads), and was greater in areas with both higher forested and developed land cover (Table 2; Fig. 4). Ribbed mussel abundance increased with distance away from subtidal creeks and was lower in areas with higher percent landcover of both forested and developed areas (Table 2; Fig. 4). Combining occupancy and abundance model outputs led to predicted ribbed mussel density and distribution being highest in mid-elevation marsh platforms, close to creek heads, and away from subtidal creeks (Fig. 5).

Results of the sensitivity analysis indicate that for both the abundance and occupancy model, elevation had the largest effect on high ribbed mussel density areas (Fig. 6). For the abundance model, distance to subtidal creek had the

Table 2 Posterior means with 95% credible intervals for hurdle model of ribbed mussel (*Geukensia demissa*) distributions across the state of Georgia using density data collected in 2019–2020

Occupancy		
Parameters	Post Mean	Credible Interval (95%)
Intercept	-4.252	-5.661, -2.868
Elevation	12.326	7.582, 17.165
Elevation²	-11.823	-16.254, -7.493
Slope	-1.643	-3.105, -0.284
Subtidal	0.245	-0.576, 1.081
Head	-1.389	-2.630, -0.194
Upland	-0.094	-0.547, 0.360
Subtidal 500	-0.203	-0.625, 0.208
Forest 500	1.381	0.893, 1.859
Development 500	1.605	1.140, 2.068
Subtidal*Head	1.403	-0.910, 3.745
Abundance		
Parameters	Post Mean	Credible Interval (95%)
Intercept	0.698	-0.503, 2.111
Elevation	6.311	1.405, 9.981
Elevation²	-6.287	-9.575, -2.020
Slope	-0.338	-1.669, 1.020
Subtidal	0.932	0.312, 1.567
Head	0.098	-0.927, 1.148
Upland	0.053	-0.512, 0.612
Subtidal 500	-0.116	-0.475, 0.253
Forest 500	-0.423	-0.818, -0.023
Development 500	-0.411	-0.726, -0.084
Subtidal*Head	-1.153	-3.010, 0.705

Bold indicates credible intervals do not overlap with zero. Asterisk (*) represents an interaction effect. Parameter definitions are found in Table 1. All parameters had priors with a normal distribution, a mean of 0, and an SD of 0.01

second largest effect on high ribbed mussel density area, followed by percent landcover by forest and percent landcover by development (Fig. 6). For the occupancy model, percent landcover by forest had the second largest effect on high ribbed mussel density area, followed by percent landcover by development and distance to creek heads (Fig. 6).

When the ribbed mussel model was applied back to the predictors, the top quartile threshold value (the cutoff used to determine areas of high abundance) was 4.12 ribbed mussels quadrat⁻¹. The amount of high abundance area was most sensitive to changes in elevation but was also sensitive to changes in distance from subtidal creek and the amount of forest landcover (Fig. 6). When we validated the model with an independent data set, the model had poor performance in predicting the probability of mussel occurrence within a randomly placed quadrat (AUC=0.53); however, when ribbed mussels were present, the model explained a high proportion ($R^2 = 0.55$) of the observed variance in mussel abundance.

Discussion

Our predictions of ribbed mussel (*Geukensia demissa*) distribution in coastal Georgia followed those in previous studies in southeastern US estuaries, with the highest ribbed mussel densities at mid-elevations on marsh platforms further from subtidal creeks (Kuenzer 1961; Lin 1989; Crotty and Angelini 2020). Other factors, however, also contributed to the species' distribution at both within-marsh (4-m grain size) and landscape (500-m grain size) scales. Although the landscape features of percent cover by forest and development had effects on both occupancy and abundance, different within-marsh factors influenced occupancy (distance to creek head) and abundance (distance to subtidal creek). When validated using independent data from three previously unsurveyed marshes, the model successfully explained 55% of the variance in ribbed mussel abundance. The model was most sensitive to small changes in elevation, but other factors had relatively minimal effects, highlighting the

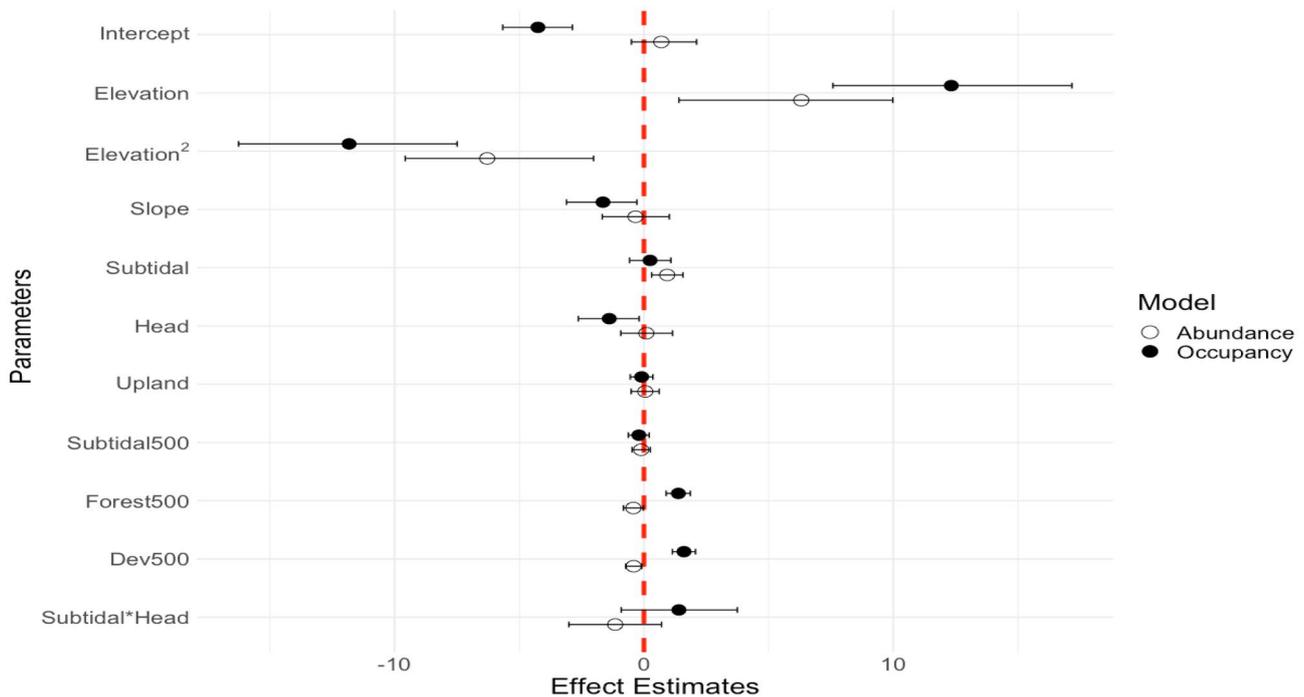


Fig. 4 Estimated effects of explanatory variables on occupancy (solid circles) and abundance (open circles) of *Geukensia demissa* in Georgia salt marshes from 2019 to 2020. Model beta parameters with 95% credible interval shown. Red dotted line represents an effect estimate

of zero. Note that estimated effects cannot be compared to effect size as variables were not standardized in the same way. Refer to Fig. 6 for effect sizes

overall importance of elevation for the distribution of ribbed mussels in southeastern US marshes.

The elevation is commonly the critical factor influencing the distribution of intertidal mollusks such as *Mytilus edulis* (Seed 1969), *Cerastoderma edule* (Jensen 1992), and *Crassostrea virginica* (Fodrie et al. 2014) and was by far the most important predictor of ribbed mussel distribution in this study. The sensitivity analysis suggested that even small (5%) changes in elevation in either direction could result in large changes (compared to the effects of other factors) in ribbed mussel densities. This distribution pattern likely reflects trade-offs between biotic and abiotic stressors linked to exposure and submergence. Although intertidal organisms experience increased foraging times (Seed 1969; Jensen 1992), reduced desiccation risk (Connell 1972; Widdows et al. 1979; Lamb et al. 2014), and faster growth (Kuenzler 1961; Striven and Gardner 1992) at lower elevations because they are submerged longer, prolonged submergence increases predation risk (Fodrie et al. 2014; Johnson and Smee 2014). Therefore, these biotic interactions can drive some intertidal organisms which cannot adapt to the increased predation risk into higher elevations and set the lower distributional limits (Connell 1972; Fodrie et al. 2014; Johnson and Smee 2014). Abiotic stressors related to temperature (Jost and Helmuth 2007) and desiccation stress (Angelini et al. 2016), however, can lead to mortality

if ribbed mussels are at tidal elevations that are too high, setting the upper distributional limit. This study suggests that ribbed mussels in the southeastern USA are distributed within a narrow band of elevation (0.5 m and 0.9 m relative to NAVD 88), likely in response to these trade-offs. This matches the finding of previous ribbed mussel studies (Julien et al. 2019) and other studies on intertidal organisms such as *C. virginica* (Fodrie et al. 2014), *M. edulis* (Seed 1969), and algae (Sibaja-Cordero and Vargas-Zamora 2006). Similar patterns exist for tree species around freshwater wetlands, where elevation affects inundation times from flooding (Hough-Snee 2020). In addition, the upper and lower elevation limits mirror the vertical zonation of vascular epiphytes (Sanger and Kirkpatrick 2015), mosses (Acebey et al. 2003; Sporn et al. 2010), and insects (Neves et al. 2014) on trees.

Location within the marsh platform relative to other marsh features also influenced both ribbed mussel abundance and occupancy. After elevation, the next greatest effect on ribbed mussel abundance was a distance away from subtidal creeks. Ribbed mussels were more common away from the marsh-creek ecotone. This pattern likely reflects negative edge effects common in many ecosystems, which are typically driven by increased predation pressure at ecotones in forests (Kolbe and Janzen 2002; Batary and Baldi 2004; Vetter et al. 2013), grasslands (Ardizzone and Norment 1999; Renfrew et al. 2005; Kuli-Revesz 2021),

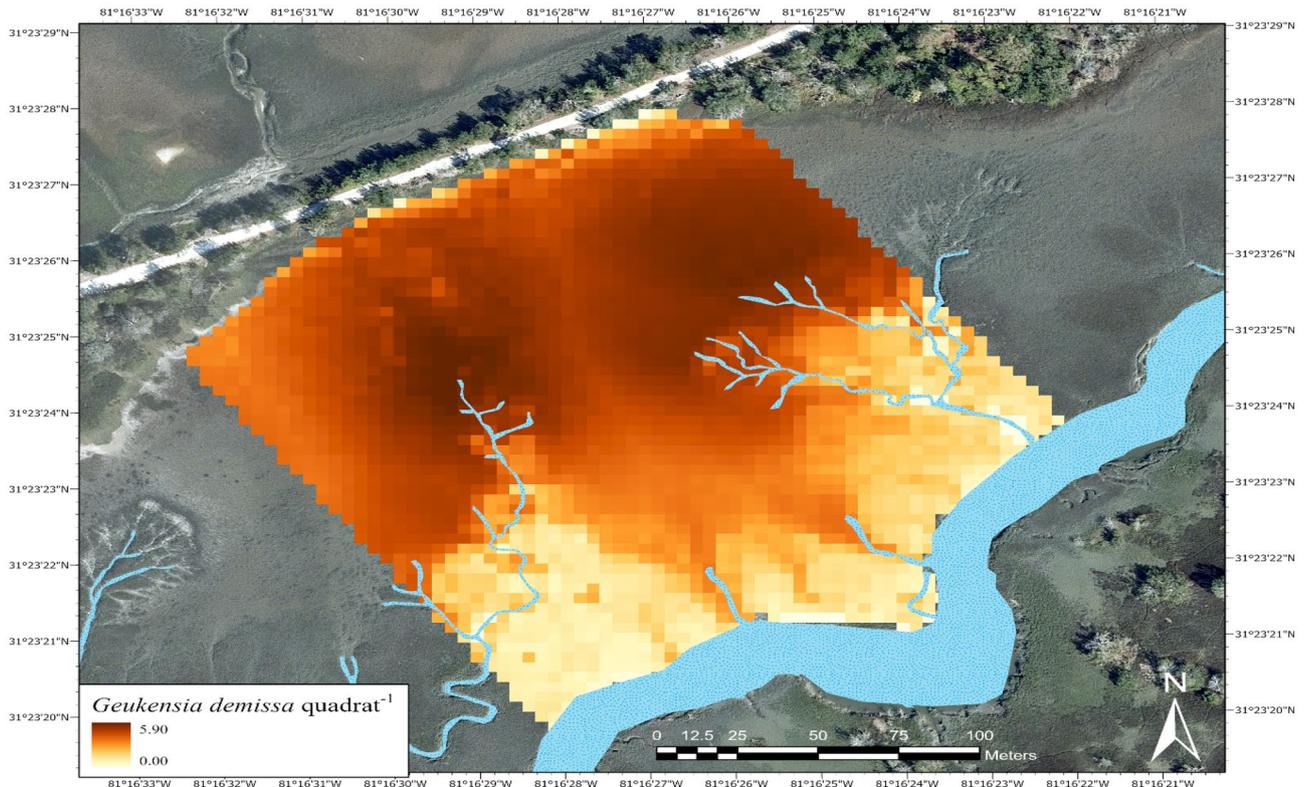


Fig. 5 Predicted *Geukensia demissa* densities (individuals 0.25 m^{-2}) along Dean Creek on Sapelo Island, Georgia, a product of outputs of occupancy and abundance models. Darker shades represent higher

predicted *G. demissa* densities. Base map acquired from 2018 aerial imagery by National Oceanic and Atmospheric Administration

and seagrass beds (Peterson et al. 2001; Smith et al. 2011; Mahoney et al. 2018), among others. In Georgia's marshes, ribbed mussels may be limited near subtidal creeks due to intense predation that occurs close to the marsh edge/subtidal creek ecotone (Lin 1989), most likely by blue crabs (*Callinectes sapidus*; Fitz and Wiegert 1991; Honig et al. 2015), which were also observed in the study's marsh sites (Annis 2021; Carroll et al. 2021). Additionally, the lack of ribbed mussels along subtidal creeks may be due to erosion, which has been suggested for some sites in Delaware Bay in the mid-Atlantic USA (Moody and Kreeger 2021). Alternatively, levees of slightly higher elevation are common along subtidal creeks in Georgia marshes (Keunzler 1961). Slightly higher elevations could potentially expose ribbed mussels to desiccation stress (Widdow et al. 1979; Lamb et al. 2014; Angelini et al. 2016), while funneling food and larvae onto the marsh at creek heads, which are further away from subtidal creek edges (Crotty and Angelini 2020). Occupancy was also highest around creek heads, which flood and drain the marsh platform, likely due to food availability and propagule supply (Crotty and Angelini 2020), indicating a positive edge effect of these features. These areas might also be locations for predator foraging (Crotty et al. 2020), however, potentially confounding the positive

effects. When occupancy and abundance were combined, the distribution model predicted mussel density may be highest on the marsh platform, away from subtidal creeks, and near creek heads. The validation study supports this distribution pattern ($R^2=0.55$), and high densities on the marsh platform have also been observed in other studies within the region (Keunzler 1961; Lin 1989; Julien et al. 2019; Crotty and Angelini 2020). Overall, actual ribbed mussel densities in our study were higher than predicted values (Supplementary Fig. S15), but the model still explained the overall patterns in ribbed mussel densities. This discrepancy between predicted and actual ribbed mussel densities likely resulted from the clumped distribution of ribbed mussels in the study region (Keunzler 1961; Crotty and Angelini 2020), and therefore, the predicted values account for spaces between ribbed mussel clumps, lowering the mean predicted value.

Landscape factors also had effects on ribbed mussel distribution in our study. Percent landcover by forest in a 500-m radius had the second largest effect on ribbed mussel occupancy. At sites with larger percent landcover by forest and sites with larger percent cover of development, the probability of ribbed mussel occurrence was higher, but abundance was lower. Highly forested or developed areas can also act as corridors for predators (Carlton and Hodder 2003; Hunter et al.

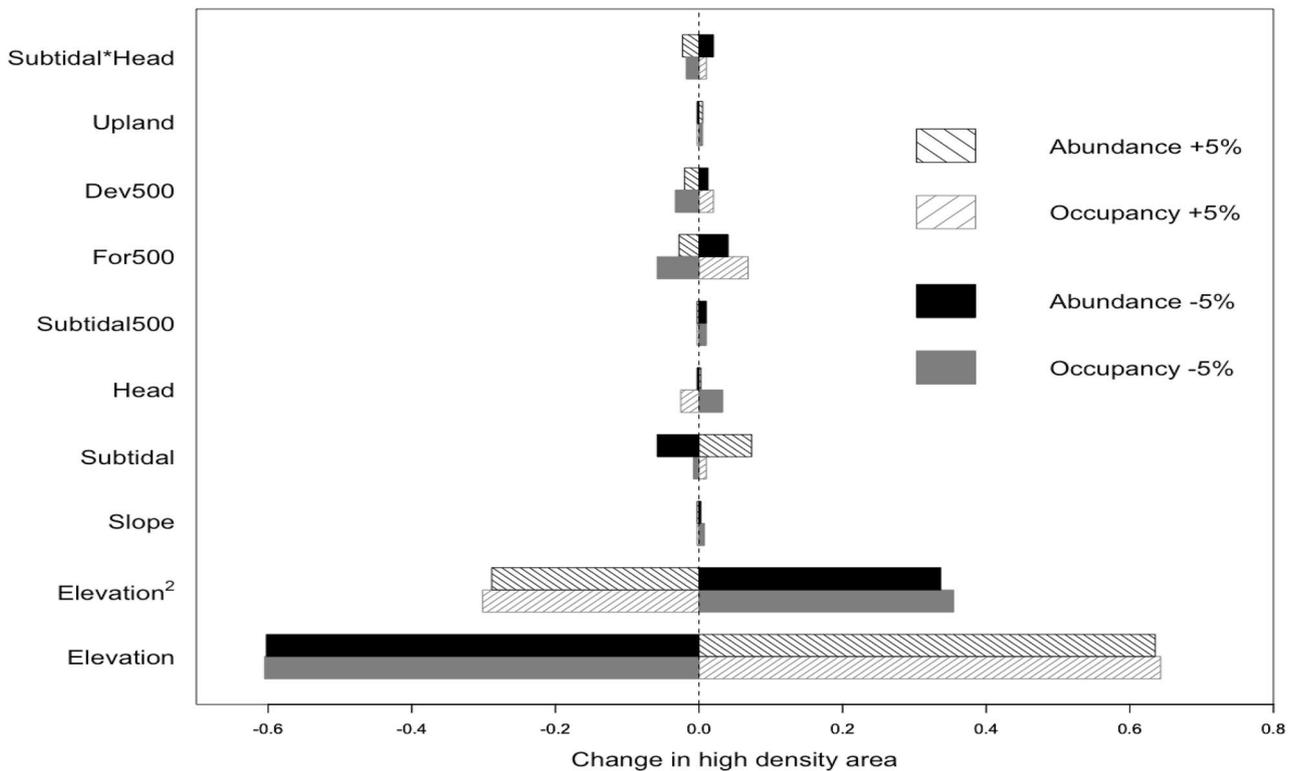


Fig. 6 Sensitivity of *Geukensia demissa* densities to small changes ($\pm 5\%$) in 10 explanatory variables. Sensitivity is a proportional change in the high *G. demissa* density area when the mean estimated coefficient of the parameter is changed by $\pm 5\%$. Black bars represent

abundance parameters, and gray bars represent occupancy patterns. Dashed bars represent a 5% increase, and solid bars represent a 5% decrease

2017), which could explain the negative effect of forest land-cover on ribbed mussel abundance. The reason for the discrepancy between occupancy and abundance was not clear, but the occupancy effect was stronger than the abundance effect, resulting in an overall positive effect of forests and development on predicted ribbed mussel densities. Because the percent landcover by forest and percent landcover by development affected mussel densities in the same direction, it seems these factors may be describing marsh width, thus acting as a cap for the positive effect of distance from subtidal creek.

The model was successful at predicting high abundance/density areas, explaining over half of the variance in ribbed mussel abundances when ribbed mussels were found. For management applications, the model accurately identified areas of high ribbed mussel abundance and elevation as the key factor influencing this distribution. Abundance models can provide useful information to managers (Bried and Pellet 2012), particularly by providing insights into which factors are necessary to support large populations (Stratmann et al. 2020) and could be used to predict population declines (Pollock 2006). The model performed poorly at predicting ribbed mussel occupancy during validation. This poor performance, however, is likely attributable to the sample design of the

validation process rather than limitations to the model itself. Ribbed mussels are distributed in clumped aggregations in southeastern US marshes (Kuenzer 1961; Crotty and Angelini 2020). Randomly placing quadrats likely missed ribbed mussel clumps in “high occupancy” areas. An alternative way to validate this model, given the clumped distribution of ribbed mussels, could be to aggregate ribbed mussel densities on a larger scale and ignore the occupancy process. Another explanation for the poor performance of the occupancy model is that there could have been spatial autocorrelation in the sampling design which could have led to poor model performance; however, we felt this was unlikely due to the distance between sampling events and size of ribbed mussel clumps. In addition, all the explanatory variables are likely spatially autocorrelated as well. Despite the occupancy model’s poor performance, we felt it was important to validate our model at unsurveyed marshes to demonstrate the model’s ability to accurately predict ribbed mussel abundance at sites across the coast of Georgia and give users of this model confidence in its predictions of ribbed mussel densities, and because other studies addressing ribbed mussel distribution have not validated their models with independent samples (Julien et al. 2019; Crotty and Angelini 2020). One final caution to the use

of this model is that the site selection process was subject to sample bias due to only selecting marshes around areas with public road access. As such, the model results may not be applicable to marshes that are not attached to upland habitat, such as marsh islands.

In conclusion, species distribution models of ecologically important organisms are important tools for management. This study supports the findings of previous research (Keunzler 1961; Lin 1989; Crotty and Angelini 2020) that the distribution of ribbed mussels in the southeastern USA 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 the marsh-creek ecotone (Bertness 1984). High species' densities, however, may not always indicate high-quality habitat (Vanhorne 1983), and areas with low density may not necessarily be low-quality habitats but rather reflect other processes (i.e., recruitment limitation; Hughes 1990). Thus, without future research, this model cannot determine if areas like subtidal creekbanks with low densities are unsuitable habitats or the result of other processes (recruitment). Although creek banks are often the site of marsh restoration projects that might incorporate ribbed mussels in other parts of their range (Moody et al. 2013), this study highlights the importance of using local data when creating species distribution models and making management decisions regarding vital coastal species. Further research on ribbed mussel demographic rates is warranted to determine why ribbed mussels exhibit the distribution pattern on the marsh platform near creek heads.

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