Shorescape-level factors drive distribution and condition of a salt marsh facilitator (Geukensia Demissa)

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Recommended Citation

Shorescape-level factors drive distribution and condition of a salt marsh facilitator (*Geukensia Demissa*)

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Abstract. Ribbed mussels (*Geukensia demissa*) are a highly abundant bivalve filter feeder throughout the salt marshes of the U.S. Atlantic Coast. These mussels form a mutualistic relationship with smooth cordgrass *Spartina alterniflora* wherein the grass provides habitat and shade to the mussels, and the mussels stabilize the sediment and fertilize the grass. Salt marshes are, however, rapidly changing and eroding as humans modify the coast, and the rate of sea level rise is accelerating. In order to understand how ribbed mussels may respond to their changing habitat, we collected mussel density and distribution data from 30 marshes covering the range of geomorphic settings found in lower Chesapeake Bay. We used a combination of in situ and GIS-derived spatial variables to develop spatially applied models of ribbed mussel density and physical condition. Of the estimated 1.06 billion ribbed mussels in Virginia, we found that mussels were most abundant along the front edge of marshes in wide creeks, rivers, or bays with dense *Spartina* and minimal proximal forest, set in agriculturally dominated areas. In contrast, mussel condition was highest in fringing marshes located in narrow tidal creeks. Ribbed mussels responded to factors at a variety of scales, ranging from extremely local (0.5 m) to larger shorescapes (≥300 m). The methods that we used to create models linking both aquatic and terrestrial variables to explain the variation in ribbed mussel populations along the shoreline provide a valuable tool for identifying baselines and assessing potential for change across estuary-level spatial scales not only for ribbed mussels in the Chesapeake Bay, but also for other sessile, intertidal species in other systems.

Key words: coastal ecology; distribution; ecosystem services, ribbed mussels; exposure; fringing marshes; land use; seascape; *Spartina*.

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INTRODUCTION

Salt marshes are one of the major vegetated interfaces between land and water throughout the world's temperate zones and are among the most productive ecosystems on the planet (Lieth 1972), providing a wealth of ecosystem functions and services including wave energy reduction and erosion control (Cooper 2005), nitrogen removal (Valiela and Teal 1979, Nelson and Zavaleta 2012), and habitat provisioning (Díaz-Ferguson et al. 2010, Angelini et al. 2015, Valiela 2015). Unfortunately,

marshes have been shrinking due to a number of natural and anthropogenic causes such as sea level rise (Craft et al. 2008, Bilkovic et al. 2009), coastal development such as housing and roads (Kittinger and Ayers 2010, Bilkovic et al. 2016), and natural and boat wake-induced erosion (Schwimmer 2001, Silinski et al. 2015). On the East Coast of the United States, smooth cordgrass (*Spartina alterniflora* Loisel.; simply *Spartina* hereafter) dominates the lower marsh (more frequently inundated), while salt meadow hay (*Spartina patens* (Ait.) Muhl.) dominates the upper marsh.

Integrated into the surface of the salt marsh are ribbed mussels (*Geukensia demissa* Dillwyn, 1817). Ranging from Cape Cod, Massachusetts, to southern Florida, ribbed mussels form a mutualistic relationship with *Spartina* in the low marsh (Bertness 1984). The ribbed mussel lives in the brackish intertidal zone in salinities from 8‰ to 30‰ (Lent 1969). Ribbed mussels typically burrow down into the sediment where they bind their byssal threads to the roots, rhizomes, and stems of *Spartina* (Lin 1990), while leaving their posterior end exposed above the surface. By attaching themselves to these plant structures, they also bind the sediment, thereby increasing the stability of the marsh by reducing erosion (Moody 2012). Ribbed mussels are also noted for being extremely efficient filter feeders (Galimany et al. 2015). Their ability to improve water quality rivals that of oysters, and even exceeds oysters at the smallest particle sizes (Kreeger and Newell 2001). While filter feeding, ribbed mussels excrete ammonia, which effectively serves to fertilize the smooth cordgrass (Jordan and Valiela 1982). The fertilized *Spartina* increases its aboveground biomass, which then facilitates increased sedimentation (Bertness 1984). This partnership between ribbed mussels and *Spartina* results in a more resilient marsh (Smith and Frey 1985).

Ribbed mussels are bivalves in the family Mytilidae (Ruppert et al. 2003) that exhibit external fertilization with planktonic veliger larvae. The larvae remain in the water column for 12–43 d (Loosanoff and Davis 1963), where they grow to ~200 μm. During the pediveliger stage (~200+ μm), they maintain a position in the upper water column, likely to maximize their chances of moving onto the marsh with an incoming tide (Baker and Mann 2003). Larvae are most likely to initially settle on structure, such as *Spartina* stems, and then metamorphose (Porri et al. 2007). After metamorphosis, juveniles may further disperse either short or long distances to select for better habitat (Baker and Mann 1997, Franz 2001). Post-settlement movement is thought to cease once the mussels reach sexual maturity, around 25 mm (Franz 2001).

Ribbed mussels are not distributed homogeneously across the surface of the marsh. In general, ribbed mussel densities are typically highest at the front (seaward) edge of the marsh and decline with increasing distance into the marsh (Bertness and Grosholz 1985, Bilkovic et al. 2017).

Throughout their range, ribbed mussels self-organize into dense aggregations, ranging from 0 to 7000 individuals/m² (Bertness and Grosholz 1985, Stiven and Gardner 1992). The causes of the variation in mussel densities are unclear at large scales, given that very few studies have examined ribbed mussel distribution across multiple marshes (see Angelini et al. 2016 and Bilkovic et al. 2017 for exceptions), and to our knowledge, no studies have attempted to identify the spatial scales at which land- and seascape factors are important. At small scales, researchers have identified a clear, positive relationship between ribbed mussel densities and smooth cordgrass stem densities (Bertness 1984, Angelini et al. 2015) as well as a possible preference for adult conspecifics. This is unsurprising given the mutualistic relationship between the two species, though the causality (ribbed mussels increasing stem densities, or increased stem densities attracting more ribbed mussels) is still debated (Hughes et al. 2014).

The role of ribbed mussels as a salt marsh facilitator has been explored for the past couple of decades in a variety of regions along the U.S. Atlantic Coast (Bertness and Leonard 1997, Angelini et al. 2015, 2016). Ribbed mussels improve the marsh not only for the *Spartina*, but for the other organisms found there as well. The tendency of ribbed mussels to aggregate into large groups results in increased moisture retention and the creation of microclimates. Moisture retention by aggregates of adult ribbed mussels provides a more stable environment for the juvenile ribbed mussels as well as other benthic invertebrates. The stabilized marsh resulting from the *Spartina*/ribbed mussel mutualism also supports increased species richness and functional diversity (Angelini et al. 2015). Increased ribbed mussel abundances further attracts predators such as blue crabs (*Callinectes sapidus* Rathbun, 1896), Atlantic mud crabs (*Panopeus herbstii* H. Milne Edwards, 1834), black ducks (*Anas rubripes* Brewster, 1902), and raccoons (*Procyon lotor* Linnaeus, 1758), which all feed extensively on ribbed mussels (Seed 1980, Brousseau 1984, Bertness and Grosholz 1985, Lin 1990, Eichholz et al. 2009). In addition to facilitating diversity and resilience, ribbed mussels are also important for their role in nitrogen removal. Recent studies (Bilkovic et al. 2017) have suggested that the mutualism between *Spartina* and ribbed mussels

may increase the rate of denitrification in marshes (Bilkovic et al. 2017), thereby providing a valuable ecosystem service that contributes to water quality management goals throughout their range. Taken all together, the ecosystem functions provided by ribbed mussels make them a vital member of the marsh community along the U.S. Atlantic Coast.

Relatively little is known about how ribbed mussels are likely to respond to the previously noted rapidly changing environmental conditions, and even less is known about their responses in estuaries with lower salinities. It is important to document broad distributions of ribbed mussels and evaluate factors that may limit the capacity of ribbed mussels to facilitate diversity, stabilize marshes, and enhance water quality at both a regional scale (shorescape, defined here as the zone along tidal shorelines encompassing riparian, intertidal, and nearshore littoral areas; Hershner et al. 2016) and a local scale (within the marsh). This study was performed with the following objectives: (1) to determine the primary local and shorescape factors influencing the current distribution and condition of ribbed mussels within a marsh and throughout an estuary and (2) to use empirically derived relationships to model ribbed mussel distribution throughout the lower Chesapeake Bay, Virginia, USA.

Methods

Study area

Our study area encompassed the lower Chesapeake Bay (Fig. 1), Virginia, USA. Salinities in our study area ranged from 8‰ to 22‰, while
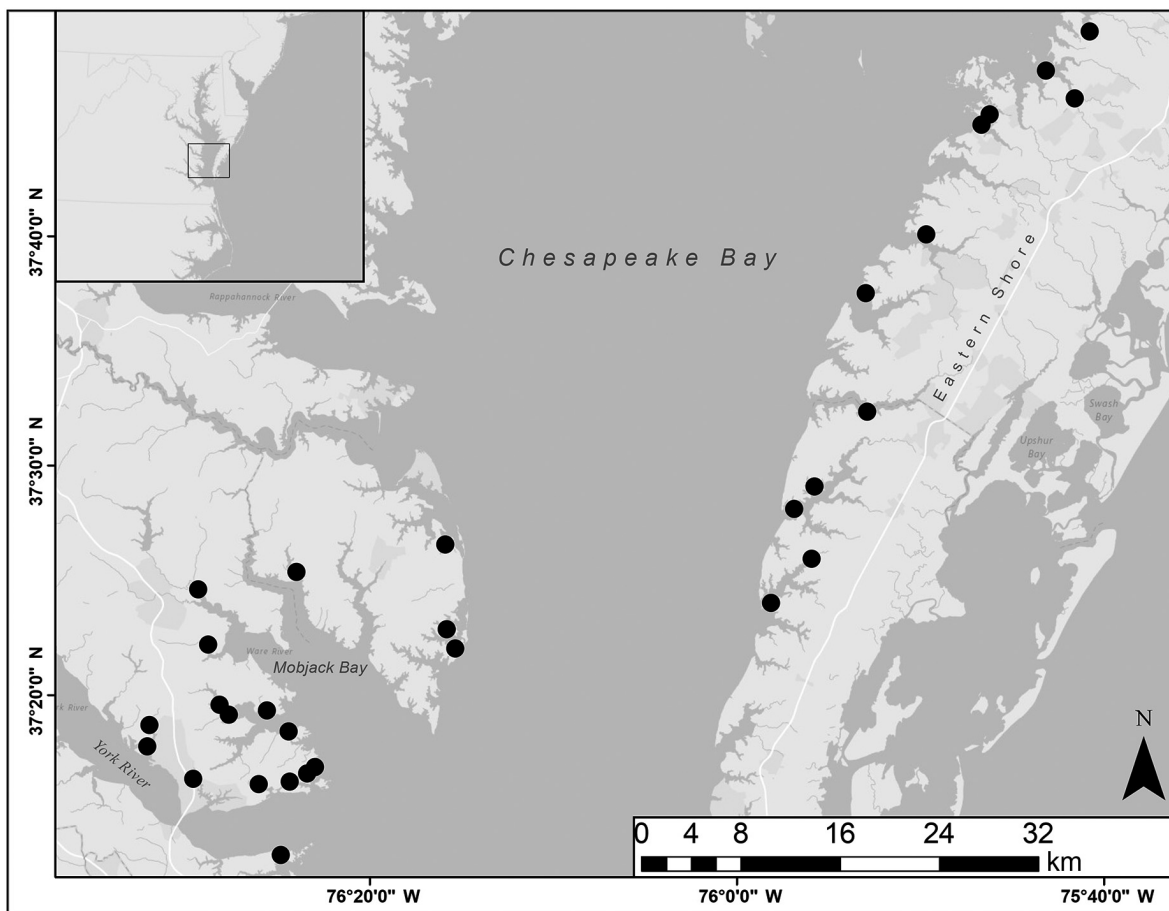

Fig. 1. The study area in Virginia's Chesapeake Bay. Study sites (black dots) were located along the western and eastern shores of the Chesapeake Bay.

water temperatures vary annually from ~3° to 32°C. Marshes selected for the study were exclusively *Spartina alterniflora* dominated in the low marsh, while the high marsh was typically *Spartina patens* dominated, with occasionally high densities of *Distichlis spicata* (L.) Greene. *Juncus romerianus* (Scheele) was often found in the transition zone from low to high marsh.

Site selection

Study sites were selected from the Eastern Shore of Virginia, the York River, and Mobjack Bay using a stratified random sampling approach to target marshes in a variety of settings within 5 km of water or terrestrial access locations. Access locations included public and private boat launches, roads, and homes. In total, 30 sites (Fig. 1) were randomly selected using ArcGIS 10.0 (ESRI 2017) and Geospatial Modeling Environment (Beyer 2014) along an exposure (i.e., open water area within a 500-m radius) gradient. Sites were accessed by kayak, canoe, or motor boat.

Field sampling

We sampled each site once during the summer months (June–August) of 2015 (N = 13) and 2016 (N = 17). At each site, we sampled four transects, spaced at least 5 m apart, inward from the water toward the upland. Transects were sampled using a 0.25 m^2 quadrat, placed to span the first 50 cm of each meter, every meter for the first 5 m of marsh. We counted the number of juvenile (<20 mm shell length) and adult ribbed mussels in each quadrat for each transect. In addition to the ribbed mussels, we recorded plant species, height, and shoot density for each quadrat. We also recorded the distance from water to the last ribbed mussel along the transect if the distance is >10 m. Up to 20 adult and juvenile ribbed mussels representative of the size distribution on site were collected at each distance from the edge to be processed in the laboratory for condition indices (see *Condition index*). Ribbed mussels were not collected if absent or in extremely low abundance for a given distance within a marsh. Each collected ribbed mussel was measured (height, length, width), weighed for total wet weight (shell and tissue combined; g), then shucked into pre-weighed aluminum weigh boats (shell and tissue separately), dried at 65°C for 48 h, and reweighed.

In addition to counts of flora and fauna, we recorded physical characteristics of each site. Marshes were categorized as platform or non-platform marshes based on the morphology of the front edge of the marsh. If the front edge of the marsh was actively eroding with a steep, often vertical face from the *S. alterniflora* to the subtidal, the marsh was classified as a platform marsh. All other marshes were classified as non-platform marshes. We also recorded the salinity (ppt) at each site using a salinity refractometer, as well as water temperature (°C) using a digital thermometer.

Condition index

Condition indices have been used to describe an individual bivalve based on the amount of mass it has allotted to its shell vs. soft tissue, adjusted for its volume (Crosby and Gale 1990). Ribbed mussels with a high condition index would have a higher soft tissue weight to shell ratio than mussels with a low condition index. If the relative amount of soft tissue weight is low, then environmental conditions are likely unfavorable. A condition index for each mussel was calculated using Eq. 1 (Crosby and Gale 1990):

$$CI = \left(\frac{\text{dry soft tissue wt (g)} \times 1000}{\text{internal shell cavity capacity (g)}} \right) \quad (1)$$

where internal shell cavity capacity is calculated as the total wet weight of the individual − the dry shell weight. Although the term internal shell cavity capacity gives the impression of volume, it actually represents the ratio of dry tissue to wet tissue (including residual water in the shell). A shell-to-tissue ratio (STR) was also calculated using Eq. 2.

$$STR = \left(\frac{\text{dry shell wt (g)}}{\text{dry tissue wt (g)}} \right) \quad (2)$$

Geospatial variables

Shorescape variables were obtained using ArcGIS v.10.4.1 (ESRI 2017). Given known impacts of surrounding land use on a variety of marine and aquatic organisms (Seitz et al. 2006, Bilkovic and Roggero 2008, Isdell et al. 2015), we identified the proportion of agriculture, forest, marsh, and impervious surface within increasing concentric circles (neighborhoods) of the site. Land use data were derived from the VA CCAP land

cover dataset (1-m pixel resolution; resampled to 5-m pixel resolution using a majority assignment). We selected radii from 20 to 500 m (20, 40, 60, 80, 100, 150, 200, 300, 400, and 500 m) to span the range of local to shorescape-level impacts. We also included the percentage of water within the same radii of a site to serve as a proxy for exposure (defined here as the amount of physical energy from waves and tidal flow to which a location is subjected). Sites along a straight shoreline with a wide channel (e.g., a river) would have ~50% water at greater distances, while sites in narrow tidal creeks would have a much lower % water. We included this descriptor given that a previous study in the area (Bilkovic et al. 2017) found increased densities of ribbed mussels along large waterbodies and other highly exposed shorelines when compared with marshes in less exposed settings.

Statistical analyses and spatial application

All statistical analyses were conducted using R (R Development Core Team 2011). To model ribbed mussel density, we used the site-averaged quadrat density (adults and juveniles; Σ(mussel abundance in quadrats of first two meters of all transects at a site/number of quadrats), with a $\log(X + 1)$ transformation to meet assumptions of normality. Using the site average eliminates any potential for pseudoreplication. Average ribbed mussel condition index (calculated the same as mussel density) for the first two meters of a site was the response variable for condition index models. We used a generalized linear model (function glm() in base R) with a Gaussian distribution for all analyses given the lack of fixed effects. We used a two-tiered approach to variable selection and model selection. We selected stem density, % water, % marsh, % forest, % agriculture, and % impervious surface as predictor variables and evaluated all spatial variables at the 10 radii from 20 to 500 m. All variables were first run in univariate models to identify those with a lower Akaike's information criterion, corrected for sample sizes (AICc) value than the null model ($y_i = \beta_0$). For each spatial variable, if multiple scales were better than the null model, the scale with the lowest AICc value was selected. Only variables with AICc values lower than the null model were selected for generalized linear regression (Table 1). All selected

Table 1. AICc table of the variables and scales that performed better than the null model for mussel density.

Variable	Scale	K	AICc	Δ AICc
Stems	local	3	110.48	0.00
Water	300 m	3	116.00	5.53
Forest	60 m	3	120.57	10.10
Ag	300 m	3	122.65	12.18
Null	N/A	2	122.76	12.28

Note: AICc, Akaike's information criterion, corrected for sample sizes.

variables were checked for autocorrelation using the Pearson correlation coefficient (PCC; function cov() in base R) prior to their inclusion in any model. If autocorrelation was found (PCC ≥ 0.7; Leu et al. 2011), only one of the autocorrelated variables was included. All possible combinations of the variables were then allowed to compete (Doherty et al. 2012), unless there were fewer than three variables that were better than the null, in which case a single model was run with the best performing variables. The top models with a cumulative ≥95% of the AICc weight were then model averaged (Burnham and Anderson 2002), resulting in a final model. The final model predictions were compared to the original data to obtain an R^2 value. The model was then spatially applied to the study area using the raster calculator tool in ArcGIS 10.4.1 to obtain ribbed mussel density estimates along the marsh edges by holding any on-site, non-spatially derived variables at their mean value. The total estimated number of ribbed mussels in Virginia was obtained by extracting only the raster cells along the front edge of the marshes. We converted that to a total number of mussels per cell by multiplying the value times 10 (length of cell [5 m] × first two meters) because each cell represented the number of ribbed mussels per m². The resulting values were summed to get the total. We also ran two additional scenarios in which we examined a low estimate (1st quartile value of the variable) and a high estimate (3rd quartile value of the variable) because the local variables had to be held constant. Total mussel estimates for the two additional scenarios were calculated the same way as described above.

We used an independently collected dataset (Bilkovic et al. 2017) of ribbed mussel density at the front edge of the marsh (N = 20) for model verification. Spatial variables for each site were

extracted to each point using ArcGIS v. 10.4.1. The model-averaged formula was then applied to each site to obtain predicted values. Predicted values were compared to observed values to obtain an R^2 value to assess goodness of fit.

RESULTS

Mussel distribution

Throughout the study area, ribbed mussel densities ranged from 0 to 3808 mussels/m². Overall, ribbed mussel densities declined from the edge to the interior of the marsh (Fig. 2), with the vast majority of the ribbed mussels (84.2%) being located within the first two meters of the marsh. Both adult and juvenile ribbed mussel densities displayed nearly identical patterns of decreasing density with increasing distance into the marsh. Exposure at the marshes ranged from 6.7% water to 78.4% water within a 500-m radius. Exactly half of the observed marshes (N = 15) were classified as platform marshes on site. Mean exposure at the front edge of the marsh (± standard error) was 50.8 ± 5.1% for platform marshes and 30.0 ± 4.8% for non-platform marshes. Ribbed mussel density was considerably higher on platform marshes (374.0 ± 94.8) than on non-platform marshes (58.5 ± 17.0; Fig. 3). Water temperatures at the study sites ranged from 22.2° to 35.6°C in the water immediately adjacent to the marsh at the time of sampling.

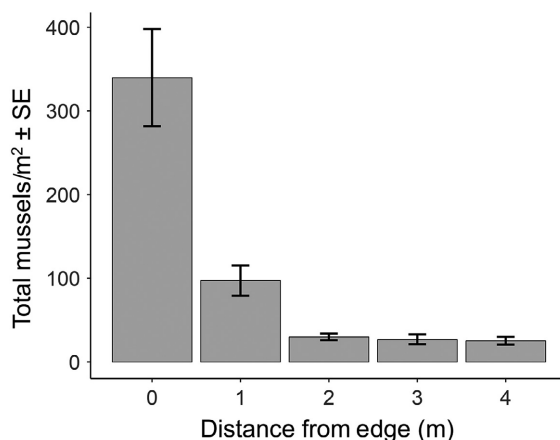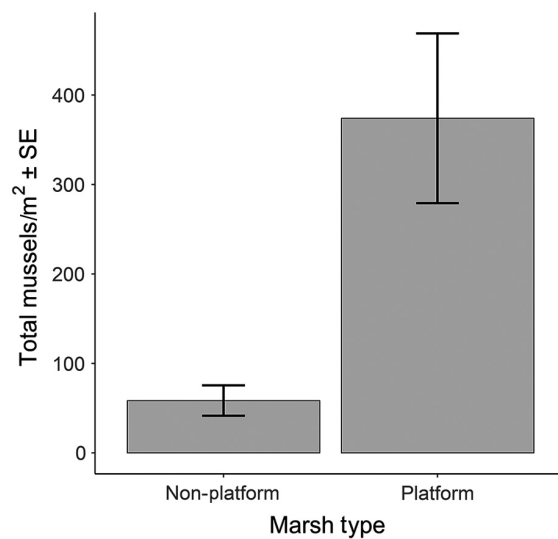Ribbed mussel density was nearly homogeneous in marshes beyond the first two meters,

Fig. 3. Average mussel density (± standard error) in platform and non-platform marshes.

making statistical inferences about among site variations difficult. As such, we focused our statistical efforts on the front edge (first two meters: 0 and 1 m combined) of the marsh, where the majority of the population and greatest variation among sites was observed. The univariate modeling indicated that *Spartina* stem density (on-site count), % water (300-m radius), % forest (60-m radius), and % agriculture (300-m radius) all performed better than the null model based on AICc values (Table 1; Fig. 4; Appendix S1). Note that the distance for % water identified as the best explanation of ribbed mussel density via AICc (300 m) differs from the scale we originally selected for our exposure gradient (500 m). The PCC matrix indicated that there was not significant autocorrelation (all R^2 values <0.25) and could be included together in subsequent models. All possible combinations of the variables were then run (16 models; Appendix S2), and the top 7 (cumulative AICc weight = 0.95) were selected for model averaging (Table 2). The final, averaged model was

$$\log(\text{mussels}) = 0.5337 + 0.0363 \times \text{Stems} \\ + 0.0125 \times \% \text{ Water} - 0.0133 \\ \times \% \text{ Forest} + 0.0009 \\ \times \% \text{ Agriculture}$$

and had an adjusted R^2 value of 0.48.

Fig. 2. Average mussel density (± standard error) at each meter into the marsh for all sites.
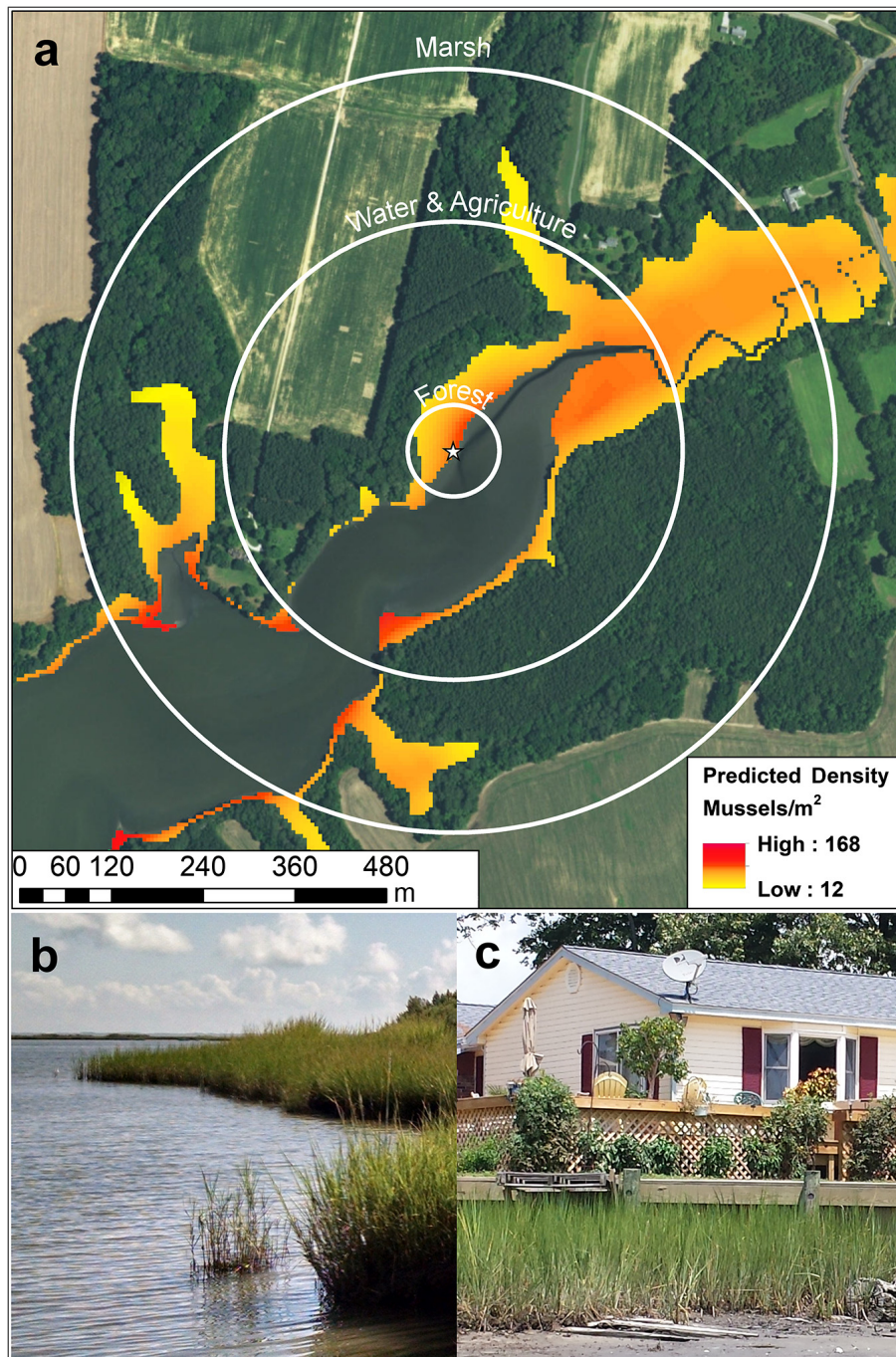
Fig. 4. (a) Scales of most importance for significant variables in the mussel density or condition index models. Each circle is scaled to the distance at which the variable name above it was most important (lowest AICc value). Predicted mussel density is also overlaid for reference. Note that the densities, while displayed across the entirety of the marsh, are only applicable to the very edge of the marsh and are only shown across the surface to improve visibility. (b) and (c) Representative marsh types where high (b) and low (c) densities would be expected.

Table 2. AICc and coefficient table for the models included in final, averaged model (bottom row indicates the weighted average values for each parameter) for mussel density.

Model	Intercept	SE	Stems	SE	Forest	SE	Water	SE	Ag	SE	AICc	ΔAICc	wt	Adj wt
7	1.055	0.586	0.039	0.009	−0.026	0.012					108.5	0.0	0.280	0.292
6	−0.023	0.643	0.033	0.010			0.027				108.7	0.2	0.250	0.260
12	0.479	0.742	0.034	0.010	−0.018	0.014	0.018	0.015			109.7	1.2	0.160	0.167
2	0.650	0.588	0.041	0.010							110.5	2.0	0.100	0.104
14	0.997	0.646	0.039	0.010	−0.027	0.014			0.006	0.024	111.3	2.8	0.070	0.073
13	−0.032	0.789	0.033	0.011			0.027	0.014	0.001	0.023	111.6	3.1	0.060	0.063
16	0.334	0.821	0.035	0.010	−0.020	0.015	0.019	0.015	0.011	0.024	112.6	4.1	0.040	0.042
avg	0.534	0.654	0.036	0.010	−0.013	0.007	0.012	0.004	0.001	0.004				

Notes: AICc: Akaike's information criterion, corrected for sample sizes; Adj wt: AICc weight adjusted for the top models; Ag: agriculture; SE: standard error; wt: AICc weight.
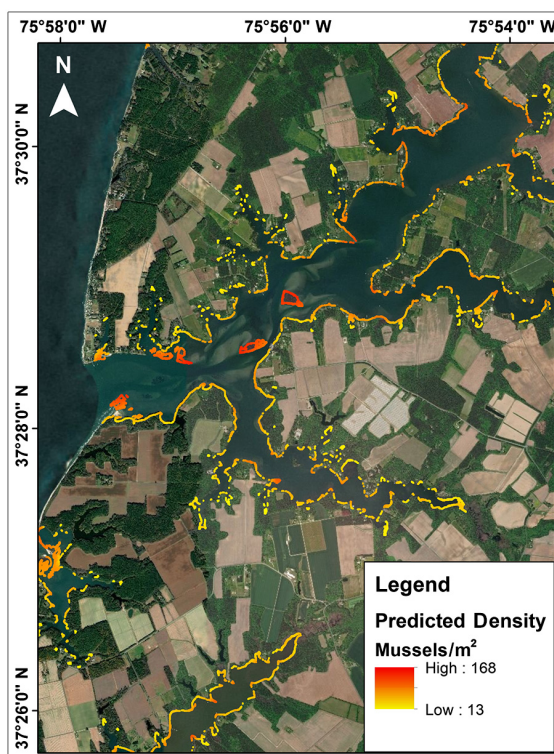

Fig. 5. Predicted mussel density along the front edge (first two meters) of the marsh. Red areas indicate high predicted densities, while yellow areas indicate low predicted densities.

Using the independent dataset for model verification, the predicted vs. observed had a significant, positive slope ($P < 0.001$) and an R^2 value of 0.62. After spatial application of the model (Fig. 5), we estimate that there are 1.06 billion ribbed mussels along the front edges of Virginia's Chesapeake Bay marshes. Varying the stem density from the 1st quartile (120.24 stems/m^2) to the 3rd quartile (254.76 stems/m^2) provided estimates of 0.43–1.47 billion ribbed mussels.

Condition index

Overall, condition index significantly ($P = 0.002$) declined with increasing distance into the marsh (Fig. 6). Again focusing on the front edge (0–2 m into the marsh) site-averaged data (N = 24), only ribbed mussel density and % marsh within a 500-m radius (Fig. 4) were found to have lower AICc values than the null model. Using scaled and centered variables to better estimate the effect size of each variable, the resulting model was

$$\text{Condition Index} = 88.51 - 10.17 \times \log(\text{mussels}) - 6.15 \times \% \text{ marsh}$$

and had an adjusted R^2 value of 0.46. Thus, effect sizes were similar for both mussel density and %
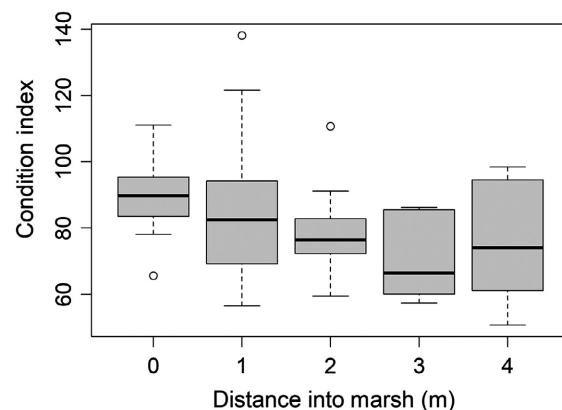

Fig. 6. Condition index of mussels at each meter into the marsh.

marsh, with mussel density having a slightly larger effect.

When considering the complete dataset (N = 1381), condition index significantly ($P < 0.001$) decreased with increasing shell length when accounting for variations due to site and distance into marsh. While the overall trend may have been negative, trends within a given site were much more variable with no clear pattern. Within a given marsh, ribbed mussel condition index may increase, decrease, or remain static with increasing shell length (see Fig. 7 for typical responses). Shell-tissue ratios for the ribbed mussels showed no clear pattern with increasing distance into the marsh (Fig. 8). However, the log-transformed STR showed a clear and significant ($P < 0.001$) increase with increasing % water within 500 m (Fig. 9). The STR showed no association with ribbed mussel length ($P = 0.825$).

DISCUSSION

Distribution and condition index

We found that ribbed mussels were most abundant along the front edge of marshes in wide creeks, rivers, or bays with dense *Spartina alterniflora* and minimal proximal forest, set in agriculturally dominated areas. In contrast, ribbed mussel condition is likely to be highest in fringing marshes located in narrow tidal creeks. This is the first known instance in which the impacts of shorescape-level factors on ribbed mussels have been synthesized into a framework that allows for broad spatial application.

The decrease in ribbed mussel density with increasing distance into the marsh provides additional support for the long-standing, recognized ecological importance of the front edge of the marsh (Bertness 1984, Peterson and Turner 1994).
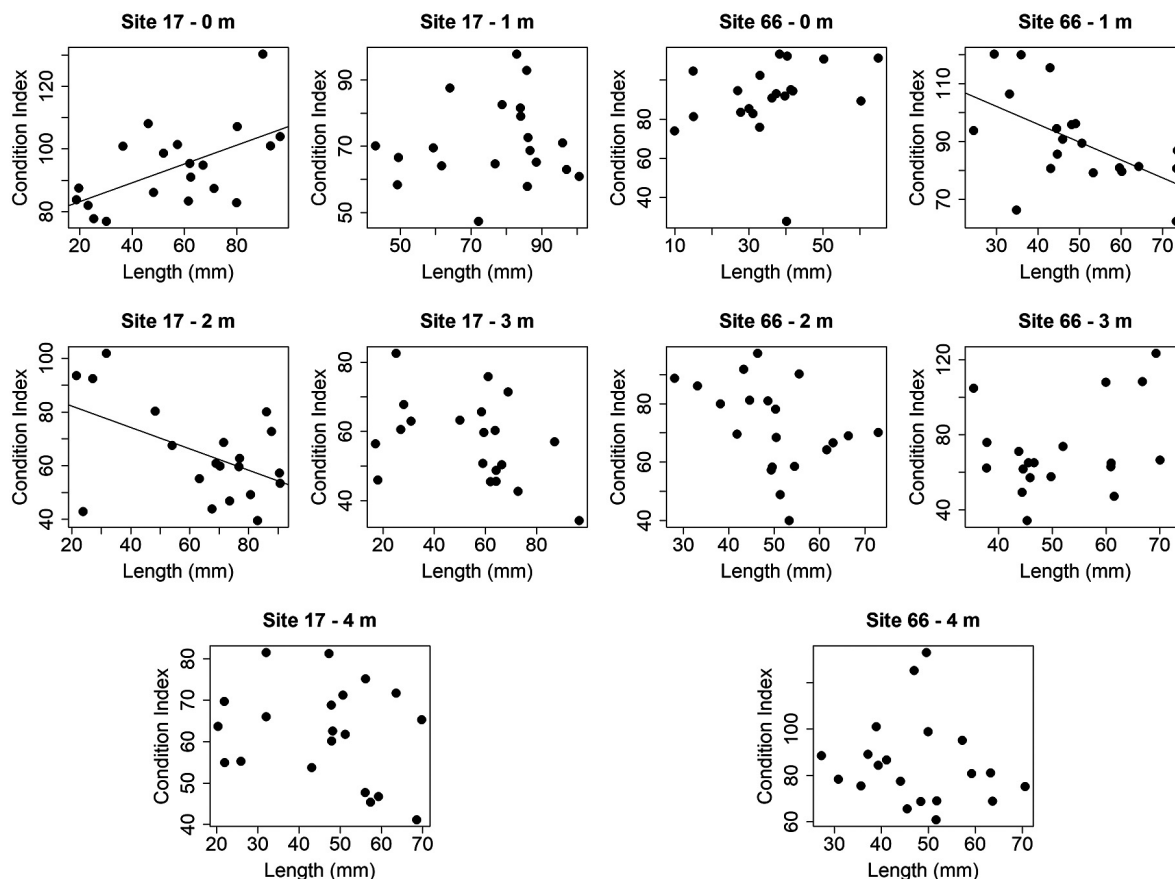

Fig. 7. Condition index as a function of shell length at each distance into two representative marshes. Lines of best fit are provided for significant ($P < 0.05$) slopes.
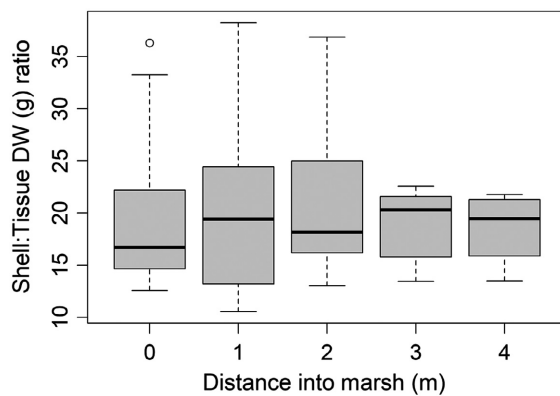
Fig. 8. Shell-to-tissue ratios of ribbed mussels for each meter into the marsh.
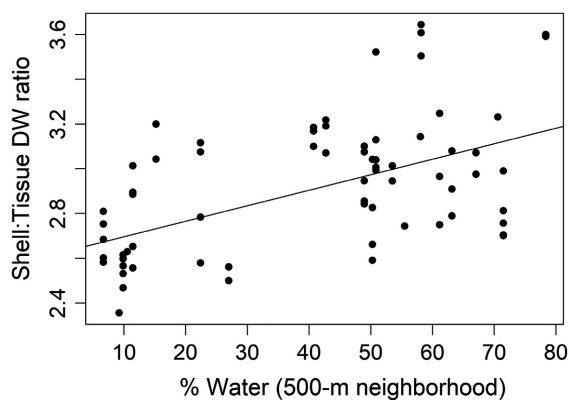

Fig. 9. Shell-to-tissue ratios as a function of % water within a 500-m neighborhood.

Numerous species, ranging from decapods and molluscs to fish and reptiles, use and rely on the front edges of marshes as critical habitat where they obtain food and shelter (Peterson and Turner 1994, Silliman and Bertness 2002, Whitelaw and Zajac 2002). Angelini et al. (2015) suggested that ribbed mussels are important or even responsible for increased diversity within the marsh. The decreasing ribbed mussel density with increasing distance into the marsh is likely a result of a combination of factors including particle settling dynamics, conspecific attraction, and inundation duration. Competent-to-settle pediveliger ribbed mussels are still small enough (Baker and Mann 2003) to be influenced by the high viscosity dynamics which apply to organisms and particles with low Reynold's numbers

(Vogel 1994). At low Reynold's numbers, drag on particles is sufficiently great that particle movement is almost entirely controlled by the surrounding fluid. As such, ribbed mussel larvae are likely to settle out of suspension when they encounter the *S. alterniflora* at the front edge of a marsh which baffles the water and reduces flow, with fewer and fewer larvae remaining in suspension with increasing distance into the marsh (Leonard and Luther 1995, Christiansen et al. 2000, Leonard and Croft 2006). Ribbed mussel larvae are attracted to adult conspecifics, potentially resulting in a positive feedback loop at the front edge of the marsh (Nielsen and Franz 1995). The front edge of the marsh is inundated for longer than any other part of the marsh over a tidal cycle, resulting in increased feeding opportunity and decreased thermal and desiccation stress (Chapman and Underwood 1996, Charles and Newell 1997), which are essential for the highly vulnerable, recently metamorphosed juveniles. Our observations of ribbed mussel distribution patterns in brackish systems are consistent with previous observations from euhaline systems (Bertness and Grosholz 1985, Stiven and Gardner 1992). The above explanations for why ribbed mussels are most abundant at the edge are similarly applicable as reasons for why *Spartina* stem density was the most important predictor in the mussel density model. The effects of *Spartina* on settling and survival likely increase with increasing stem density along the edges of marshes. Marshes with lower *Spartina* stem density are less likely to baffle the water and promote settlement, and after settlement, will provide less shading and predator protection. All else being equal, the increased stresses of a low *Spartina* stem density marsh edge should result in decreased ribbed mussel density relative to higher *Spartina* stem density marsh edges.

Ribbed mussels may be more abundant in wider, more exposed waterbodies for a variety of reasons. The percentage of water within a 300-m radius of a site is likely a proxy for exposure, rather than a direct driver. Three-hundred meters may also be the scale at which scarping begins to occur, thereby resulting in the platform marshes which supported much higher densities of ribbed mussels. Alternatively, delivery of particulate matter (Temmerman et al. 2005a, b), such as food and larvae, and tidal flushing of sediments

(Wilson and Gardner 2006) may all be greater in more expansive waters. The preceding possibilities are further supported by the STR results. The increased STR at higher % water values (Fig. 9) indicates that ribbed mussels in more exposed sites are putting either more resources into shell growth or less into soft tissue. It is possible that increased shell thickness in more exposed sites may be a result of increased wave exposure or predation pressure in those areas. Alternatively, density-dependent competition may be occurring in the higher exposure sites where mussels are more concentrated, resulting in fewer resources for soft tissue (Franz 1993). One additional possibility is that ribbed mussels in the higher exposure sites simply put more effort into reproduction (i.e., a greater proportion of soft tissue is dedicated to gamete production than somatic growth). Franz (1993, 1997) has shown that ribbed mussels provided with an abundance of food will increase gametic output compared to those provided with fewer resources. Furthermore, Borrero (1987) has noted that even within a site, variable access to resources driven by reduced feeding times as a function of increasing distance into the marsh can result in delayed gamete production. This delay in reproduction may span several months, making within-site reproductive timing potentially more variable than latitudinal, temperature-driven reproduction. All of these possibilities may contribute to the highly variable length-condition index relationships shown in Fig. 7.

Coincident with increased exposure is increased erosion. The marshes where ribbed mussels are most abundant are also where erosion rates are likely to be highest. While ribbed mussels may be able to respond to a limited amount of erosion by colonizing the marsh immediately behind the edge, there is likely a limit to this capability. Researchers in Delaware Bay, USA, have noted that while ribbed mussel presence is correlated with reduced erosion, it is only in the less exposed reaches of their habitat (Moody 2012). In order for there to be high densities of ribbed mussels that include adults (>25 mm, ~1–2 yr old) along the front edge of the marsh, erosion rates should not exceed 1 m/yr to allow for the growth rate of ribbed mussels and their recruitment patterns to keep up with erosion. Greater erosion rates would require high densities of ribbed mussels beyond

the front edge of the marsh to already be established before erosion reached the previously interior location in the marsh, which is unlikely given the precipitous decline in ribbed mussel density with increasing distance into the marsh observed in this study.

Agriculture was an important predictor of ribbed mussel density at a scale of 300 m. Mussels are likely responding to localized effects of agriculture, rather than whole watershed (Fig. 4). Other examples of agricultural impact on the nearshore environment are numerous and have ranged from runoff carrying nutrients, sediment, and chemicals (Jordan et al. 2003, Vymazal and Březinová 2015) to increasing movement of synanthropic predators across the landscape (Beasley and Rhodes 2010). All of these may have an impact on ribbed mussels. Elevated nutrients help to fuel phytoplankton and benthic microalgae, important food sources for ribbed mussels at both juvenile and adult stages (Kreeger and Newell 2001, Jacobs et al. 2015). Increased nutrients also enhance aboveground growth of *S. alterniflora* (Darby and Turner 2008, Deegan et al. 2012), thereby increasing both stem density and shading potential. Increased sediment input may also help the marsh to maintain its height profile as the sea level rises (Morris et al. 2002). Thus, marshes in close proximity to agriculture may be more stable, allowing for better long-term establishment of mussel populations. Other studies have found that sediment input from agriculture has contributed to marsh areal growth (Baldwin et al. 2012). Contrary to the possible mechanisms for agriculture benefiting mussels, agriculture may also negatively impact mussels through the use of chemicals such as insecticides. Some insecticides have been observed to inhibit byssal thread formation (Ayad et al. 2011), while others inhibit the activity of acetylcholinesterase, an enzyme responsible for muscle relaxation (Fulton and Key 2001). Besides chemicals, agriculture is also known to attract a variety of synanthropic predators (Leu et al. 2008), such as raccoons, which are known to feed on ribbed mussels (Stiven and Gardner 1992). The small effect of agriculture compared to the rest of the variables in the model may be a result of all of these effects offsetting each other. Despite the scale being 5× larger than forested land use, it is still relatively localized—only encompassing the nearest field

or two. A scale of 300 m, therefore, may indicate that variation in the farming practices of individual farmers, such as riparian buffer width and fertilizer use, could be more important than how much farming is occurring within the watershed.

The negative relationship between ribbed mussels and nearby forest is more than likely an indirect effect or association than a direct impact. The relatively small scale of forest's influence at 60 m could be indicative of the effects of shading on *Spartina* growth and density (Chen et al. 2005). In very narrow fringing marshes, riparian overhang may be sufficient to detrimentally shade the *Spartina* underneath, thereby resulting in reduced growth and stem density. Alternatively, the negative relationship between ribbed mussels and nearby forest could also be an indicator of marshes suffering from coastal squeeze (Pontee 2013). If erosion rates outpace landward migration of the marsh, the marsh will eventually disappear. Coastal squeeze has been noted in a number other systems (Doody and Williams 2004, Torio and Chmura 2013) and represents one of the major ecological concerns for intertidal habitats with accelerating sea level rise. In one of the major sub-estuaries of the Chesapeake Bay, the York River, researchers identified that fringing and extensive marshes were the most at-risk marsh types, while embayed marshes are doing well (Mitchell et al. 2017). The areas of greatest loss were developed watersheds with greater exposure dominated by fringing marshes—areas where we would expect high densities of ribbed mussels. Embayed marshes are typically at the heads of small, tidal creeks in very low exposure settings. Not only do we expect those areas to have fewer ribbed mussels, but lower condition ribbed mussels as well. Should this trend continue, we may see considerable decline in the services that ribbed mussels provide to those areas.

Ribbed mussels are responding to factors beyond the marsh, though it is unclear whether the response is a result of pre- or post-settlement processes. Consideration of the spatial scales at which an organism interacts with and responds to its environment has been the subject of a great deal of research in the terrestrial and even marine settings (Collinge 2009, Hitt et al. 2011, Wedding et al. 2011), but few have attempted to apply the concepts of landscape ecology to the terrestrial-aquatic ecotone (Boström et al. 2011, Isdell et al. 2015). Identification of the most important factors and scales provides valuable insight into what explains observed patterns in ribbed mussel distribution and density. For ribbed mussels, the technique we have developed in this work has allowed us to create spatially explicit estimates of density across a large area that could be used for future analyses, such as projecting the impacts of land use change and marsh loss on mussel populations. Identification of any potential trends in ribbed mussel population changes within an area will provide the opportunity to take proactive steps to facilitate expansion or mitigate loss.

Conclusions

Throughout the Chesapeake Bay, ribbed mussels are predominately found within the first two meters of a marsh. Ribbed mussels are also more likely to occur in areas where there is increased exposure. In the coming half-century, we expect to see a net loss of this high-exposure marsh edge habitat due to erosion and barriers to inland migration (Bilkovic et al. 2017). Throughout Virginia, approximately 30% of all marshes fall into the exposure regime typical of the high-mussel density platform marshes of this study. These high-mussel density marshes primarily occur along rivers and bays where Bilkovic et al. (2017) estimated rates of marsh loss of 20% by 2050, which is considerably higher than the marshes in less exposed areas (~10% estimated loss to erosion) with the lowest densities of ribbed mussels. As the rate of sea level rise and the frequency of severe weather are expected to increase for the foreseeable future (IPCC 2014, Boon and Mitchell 2015), erosion rates will also likely increase (Mariotti and Fagherazzi 2010) as marshes attempt to keep apace of sea level rise. In other estuaries where erosion rates are artificially high due to boat wakes, ribbed mussels are no longer most abundant in high-exposure areas, but rather in the narrow tidal creeks with lower exposure (Moody 2012). The spatial shift in higher ribbed mussel density indicates that there may be a point at which mussel recruitment and survival can no longer keep up with erosion. This study has identified trends in ribbed mussel density

both within and among marshes throughout the Chesapeake Bay. Our results provide a baseline for monitoring and identifying changes to ribbed mussel populations through time and space. As an important component of salt marsh ecosystems throughout the Atlantic Coast, ribbed mussels contribute to marsh persistence and valued ecosystem services. Understanding the potential impacts of natural and anthropogenic stressors on ribbed mussel populations is vital to sustaining the health of our coastal ecosystems.

Beyond the Chesapeake Bay, our findings may be useful and applicable to other coastal regions throughout the ribbed mussel's range. Whether it is Barnegat Bay in New Jersey or the Albemarle Sound in North Carolina, much of the U.S. Atlantic Coast has been modified by human actions that have had and will continue to have an impact on marshes and their inhabitants. By determining the spatial distribution of ribbed mussels in the Chesapeake Bay through linking landscape factors to mussel density, we have effectively established a method by which researchers and managers may assess the implications of system changes or management actions on mussel distribution and ecosystem service provision (e.g., water filtration). This method allows for the examination of ribbed mussel, or other intertidal sessile species, distribution patterns in a larger shorescape context to consider the role of factors beyond the marsh—factors that are driven by or are the result of human actions. This process thereby provides tools and insight to researchers and managers interested in setting baselines and assessing potential for change across broad spatial scales.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2449/full