



Elevation influences salt marsh crab abundance, diversity, and burrowing

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ABSTRACT: Identifying drivers of the spatial distribution of organisms is a key aim of ecology. Salt marsh ecosystems can exhibit extreme gradients in abiotic conditions, including orders of magnitude differences in physical conditions across the marsh platform, which may contribute to the spatial distributions of organisms found in marshes. Small-bodied consumers, such as crabs, have been identified as key residents of salt marshes, with strong impacts on salt marsh persistence and stability at local scales. However, due to a lack of consensus regarding crab impacts across larger biogeographic scales, continued investigation into the factors driving crab community spatiotemporal dynamics is needed. We used an observational approach to investigate the small-scale spatial patterns and environmental correlates of marsh crab abundance, burrowing activity, and community composition in a representative southeastern US salt marsh. We documented contrasting trends in crab abundance and burrowing activity across the marsh platform elevation gradient, with abundance increasing and burrow density decreasing from the creek bank to forest edge. Crab diversity generally increased with distance from tidal creeks, though the effect of marsh zone on crab diversity was site-specific. Finally, we demonstrated elevation as the key environmental predictor of marsh crab abundance, burrowing activity, and community diversity and identified specific elevations that serve as breakpoints in those metrics. Our results contribute to reconciling differences between small-scale manipulative experiments and large-scale biogeographic sampling of these ecosystem engineering salt marsh residents.

KEY WORDS: *Uca* · Sesamid · Panopeid · *Spartina* · Tidal inundation · Marsh elevation gradient · Pitfall

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1. INTRODUCTION

Understanding the factors that contribute to the spatial distribution of organisms has a lengthy history in ecology (Elton 1927, Connell 1961, Brown 1984). Species interactions (e.g. predation, competition, facilitation) and environmental tolerances jointly determine the distribution and abundance of plants and animals, and the relative importance of these factors can differ at varying spatial scales (Levin 1992, Sanford & Bertness 2009). For example, even when sampling across biogeographic regions on the order of 1000s of km, much of the variation in

species abundance can occur at the plot or transect level, on the scale of meters, suggesting that hyper-local physical and biological processes are key determinants of species abundance and community diversity (Fraschetti et al. 2005, Jenkinson et al. 2020).

The importance of small-scale processes is particularly evident in salt marshes. This common ecosystem across temperate coastlines can exhibit extreme gradients in abiotic conditions over small spatial scales (cm to m), mainly as a function of their location within the intertidal zone (Pennings & Bertness 2001, Alberti et al. 2010). These can include orders of magnitude differences in physical conditions across the

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marsh platform, including time spent inundated by the tide, porewater salinity, and nutrient and oxygen concentrations (Howes et al. 1981, Pennings & Callaway 1992, Krask et al. 2022). Despite these potentially stressful environmental conditions, salt marshes provide habitat for a diverse suite of organisms, including brachyuran crustaceans such as fiddler crabs (family: Ocypodidae), shore crabs (family: Sesarmidae) and mud crabs (family: Panopeidae), among others. Crabs can be highly abundant and perform numerous ecosystem functions within salt marshes, including bioturbating sediments (Wilson et al. 2012, Xie et al. 2022), consuming emergent vegetation and benthic microalgae (Holdredge et al. 2009, Johnson et al. 2020), altering creek geomorphology (Hughes et al. 2009, Vu et al. 2017), and serving as a link within food webs between primary producers and upper-level consumers (Bildstein 1983) or across adjacent habitat types (Ziegler et al. 2019).

Targeted manipulative experiments have demonstrated that these small-bodied consumers can negatively impact the persistence of foundational salt marsh vegetation in the face of sea level rise and anthropogenic stressors. Specifically, recreational fishing of top predators can lead to a trophic cascade involving herbivorous crabs and the loss of marsh vegetation (Altieri et al. 2012); high density burrowing zones created by marsh crabs (and facilitated by sea level rise) are leading to landscape-scale biophysical changes within tidal creeks and across the marsh platform (Crotty et al. 2020); and, crab burrowing and grazing can alter emergent vegetation (reduced root biomass) and sediment (reduced bulk density) within salt marshes (Beheshti et al. 2021). However, adverse effects of crabs on salt marshes are not ubiquitous (Wasson et al. 2019) and crab effects on salt marsh vegetation can be strongly influenced by environmental conditions (Walker et al. 2021). In turn, there is contrasting evidence regarding the relative importance of environmental conditions on marsh crab abundance and spatial distributions. In salt marshes along the southeastern coast of the USA, both abiotic environmental conditions (e.g. sediment composition) and biotic interactions (e.g. predation and competition) contribute to crab spatial distributions and activity levels at local scales (Teal 1958, Kneib & Weeks 1990, Nomann & Pennings 1998). In other regions, abiotic drivers (e.g. soil properties, water depth) alone appear to determine the level of marsh crab burrowing activity (Li et al. 2018). Most likely, biotic and abiotic factors interact to determine intertidal crab distribution and activity patterns. For example, vegetation may facilitate favorable abiotic

conditions for crab survival and burrowing activity, thereby expanding the vertical distribution of crabs in coastal habitats (Nobbs 2003, He & Cui 2015). Similarly, inter-specific interactions among burrowing crabs can be dependent on sediment composition (Neylan et al. 2019). Given the potential importance of small-bodied consumers to salt marsh persistence and stability at local scales (Silliman & Bertness 2002, Crotty et al. 2020, Beheshti et al. 2021) but a lack of general crab impacts at larger biogeographic scales (Wasson et al. 2019), continued investigation into the factors driving crab community spatiotemporal dynamics is needed.

Here, we use an observational approach to investigate the small-scale spatial patterns and environmental correlates of marsh crab abundance, burrowing activity, and community composition in a representative southeastern US salt marsh. We conducted passive sampling for crabs paired with non-invasive quadrat surveys and measurements of environmental conditions (elevation, marsh vegetation, sediment characteristics, porewater chemistry) collected as part of a salt marsh monitoring effort within the North Inlet-Winyah Bay National Estuarine Research Reserve, with the goal of elucidating the relationships between different environmental conditions and marsh crab abundance, diversity, and activity.

2. MATERIALS AND METHODS

2.1. Study site

The North Inlet-Winyah Bay National Estuarine Research Reserve (NI-WB NERR) is located on the north coast of South Carolina (USA) and includes the namesake North Inlet estuary, a bar-built, ocean-dominated, semi-diurnal system which includes ca. 33 km² of salt marsh dominated by *Spartina alterniflora*, intersected by numerous tidal creeks, and surrounded by a forested watershed (Allen et al. 2014). Freshwater input into the North Inlet system is limited to run-off from the surrounding watershed and periodic pulses from adjacent Winyah Bay during periods of high river flow (Traynum & Styles 2008). Our focal marsh sites are adjacent to Crabhaul Creek, an intertidal creek located along the western edge of North Inlet estuary, with relatively stable water column salinities which are on average above 30.

The NI-WB NERR maintains 50 permanent vegetation monitoring plots established following stan-

standard marsh monitoring protocols (Roman et al. 2001). Each plot is 1 m², and plots are distributed across 6 transects located in 2 distinct segments of the Crabhaul Creek marsh platform, denoted Segment A (33.3459°N, 79.1954°W) and Segment B (33.3406°N, 79.2024°W) (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m704p055_supp.pdf). Each segment contains 3 parallel transects (7–9 permanent plots per transect) which span the marsh elevation gradient, running from the creek bank to the forest edge. Segment A is 1 km downstream from Segment B and represents a geologically older marsh (Gardner & Porter 2001). As a result, the width of the marsh platform at Segment A is approximately 3 times greater than at Segment B. This coincides with a more diverse vegetation community at Segment A due to the presence of a species-rich mid marsh zone, which includes *Salicornia* species, *Borrchia frutescens*, *Spartina patens* and *Distichlis spicata*. The mid marsh at Segment A is bordered on the creek-ward side by monospecific stands of *S. alterniflora* (i.e. the low marsh zone), which transitions from a short to a tall growth form as elevation decreases. On the forest-ward side of the mid marsh, the high marsh is dominated by *Juncus roemerianus*, hereafter *Juncus*. In contrast, the chronologically younger Segment B has a narrower marsh platform where the *S. alterniflora* monoculture low marsh covers the majority of the marsh platform, with a <5 m strip of high marsh composed primarily of *Juncus* and *S. patens*. Despite these differences, both Segment A and Segment B are representative of salt marsh habitats within estuaries of the southeastern USA.

2.2. Marsh crab community and burrow sampling

Crabs were sampled using pitfall traps to quantify abundance (catch per unit effort, CPUE) and community diversity. Pitfall traps made from plastic tubes (7 cm diameter, 20 cm deep) were buried in the sediment so that the top was flush with the ground surface, and were deployed <1 m from each of the 50 long-term monitoring plots (Fig. S1). Traps were not baited and were allowed to catch crabs for 24 h during a given sampling event. Crabs caught were identified to the lowest taxonomic level (generally species), carapace width measured, and sex determined. Crab sampling occurred once per month over the course of 15 mo from July 2020–September 2021. When pitfall traps were not in use, they were capped to prevent ghost fishing.

Monthly pitfall sampling was accompanied by crab burrow counts which occurred during a 14 d window centered on either side of the pitfall trapping date. We enumerated all burrows >2 mm in diameter inside a 0.25 m² quadrat haphazardly thrown within 1 m of the pitfall trap. Only burrows larger than 2 mm were counted because smaller holes may be excavated by other organisms. Burrow counts were multiplied by 4 to generate total burrow density (m⁻²).

2.3. Abiotic and biotic conditions

To characterize the abiotic and biotic conditions potentially related to the spatial distribution and activity of the marsh crab community, we utilized data on 8 environmental variables collected as part of the long-term salt marsh monitoring program described above (Table 1). First, we measured the orthometric height of each permanent plot using a Trimble R8s real-time kinematic global positioning system (RTK-GPS) referenced to NAVD88. Elevation measurements are based on the mean of triplicate RTK-GPS points taken at each plot between November 2020 and January 2021. Plot-level elevation is a highly correlated proxy for the percent of time a plot spends inundated by the tide during a given year (Krask et al. 2022); broadly, creekside plots were inundated for ~67% of the year with a mean water depth of ~0.5 m, while plots adjacent to the forest were rarely inundated (<4% of the year) by a shallow lens of tidal water, 0.1 m deep. Second, we measured salinity of the sediment porewater at each plot during the growing season (May–August) of 2021 using porewater diffusion equilibrators embedded in the marsh sediment at 3 corners of each permanent plot. We collected triplicate porewater samples each month at each plot, with equilibrator wells (porous PVC pipes) sampling at a depth of 0.25 m. Equilibrator wells contained 25 ml glass scintillation vials filled with deionized water and covered with nitex mesh membranes. Vials were allowed to equilibrate for approximately 1 mo at which point we measured the salinity of each porewater sample using a conductivity probe. Triplicate samples were averaged to generate monthly plot-level porewater salinities; we then calculated the overall growing season mean porewater salinity at each plot by taking the mean of these monthly salinity values. Third, sediment characteristics across the marsh platform were generated from cores collected from the top 10 cm of the marsh surface at each permanent plot during 2020. Full details can be found in Kish (2021); for this analysis, we utilized data on

Table 1. Environmental variables measured at each long-term monitoring plot in association with marsh crab pitfall and burrow sampling. For complete description of sediment characteristics methodology, see Kish (2021). *Juncus*: *J. roemerianus*; *Salicornia*: *S. depressa*; *Spartina*: *S. alterniflora*

Variable	Date (mo/yr)	Method	Details
Elevation	11/2020–01/2021	Real-time kinematic global positioning system	Mean based on triplicate elevation measurements at each plot
Porewater salinity	05/2021–08/2021	Triplicate porewater equilibrators	Equilibrators deployed at 25 cm depth for 1 mo duration, plot-level mean based on average over 4 mo
Sediment bulk density	06/2020–08/2020	Triplicate sediment cores	Top 10 cm of either 2 cm or 4.3 cm inner diameter core, depending on sediment conditions
Sediment % clay	06/2020–08/2020	Single sediment core	Top 10 cm of either 2 cm or 4.3 cm inner diameter core, depending on sediment conditions
% cover <i>Juncus</i>	09/2020	1 m ² quadrat survey	Visual estimate by single observer
% cover <i>Salicornia</i>	09/2020	1 m ² quadrat survey	Visual estimate by single observer
% cover <i>Spartina</i>	09/2020	1 m ² quadrat survey	Visual estimate by single observer
% unvegetated	09/2020	1 m ² quadrat survey	Visual estimate by single observer

sediment bulk density (g cm⁻³) and percent clay. Particle grain size (i.e. percent clay) was determined using a Beckman Coulter LS 13 320 Particle Size Analyzer. Finally, we surveyed salt marsh vegetation during the period of annual peak biomass in September 2020. Within each 1 m² permanent plot, we visually estimated percent cover of each of the 3 dominant vegetation species (*Juncus*, *Salicornia depressa*, and *Spartina alterniflora* [hereafter *Salicornia* and *Spartina*, respectively]) as well as percent unvegetated cover. All percent cover estimates were made by a single observer. Undeniably, above- and below-ground vegetation biomass could be important to marsh crabs; however, the nature of our long-term monitoring effort precludes destructive sampling. Thus, we selected these 4 parameters (percent cover of *Juncus*, *Salicornia*, *Spartina*, and bare ground) to provide general information describing the vegetation community at each plot. The 8 focal environmental variables exhibited limited correlations among one another (Table S1 in the Supplement).

2.4. Data analyses

We grouped monitoring plots into low, mid, and high marsh zones based on elevation and the dominant vegetation type(s) in each plot (Wiegert & Freeman 1990, Pennings et al. 2005). We calculated plot-level means for all environmental parameters (biotic and abiotic). Crab CPUE, our estimate of abundance, is simply the number of crabs caught in a pitfall trap during a 24 h sampling period. We calculated mean CPUE and mean burrow density for a given sampling

event (pooling across all plots) and at the plot-level (across sampling events), as appropriate. To estimate crab community biodiversity, we calculated the exponential Shannon diversity index, e^H (Jost 2006) as:

$$e^H = e^{-\sum_{i=1}^S p_i \ln p_i}$$

where p_i is the proportion of the crab community at a given plot which belongs to species i and S is the total species pool at that plot. Only data for warm season months (April–September), and only organisms for which a species identification could be positively made, were included in this calculation. We compared mean crab CPUE, mean burrow density, and mean exponential Shannon diversity of the crab community at each plot using separate linear mixed models for the 2 marsh segments, for 6 models in total. In each case, Marsh Zone was used as a fixed factor and Transect as a random effect to account for the fact that transects are considered replicates within each marsh segment. We visually inspected residuals to assess normality and tested for homoscedasticity using Levene's test. Of these 6 data sets, only burrow density within Segment A was heteroscedastic; we performed a ln-transformation and these data then met modeling assumptions. All statistical analyses were conducted in the R computing environment (v.4.0.5); mixed models were fit using the nlme package v3.1-152 (Pinheiro 2016).

To assess differences in crab community composition across marsh zones, we conducted permutational multivariate analysis of variance (PERMANOVA) with factors of Segment and Marsh Zone followed by a post-hoc pairwise test to confirm differ-

ences across zones. We then generated a non-metric multi-dimensional scaling (nMDS) plot to visualize crab community data. Both multivariate analyses are based on a Bray-Curtis dissimilarity matrix and were conducted using the *vegan* v.2.5-7 and *pairwise-Adonis* v.0.4 packages (Oksanen et al. 2020, Martinez Arbizu 2021).

To investigate hyper-local (i.e. meter scale) environmental correlates of crab abundance, burrow density, and community diversity, we used generalized additive models (GAMs) and classification and regression trees (CART). GAMs allow for non-linear relationships in the predictor variables through smoothed functions which are informed by the underlying data (Simpson 2018). This GAM analysis proceeded in 2 steps. First, we fit separate models describing crab CPUE, burrow density, and diversity that included smooth functions for each of our 8 environmental predictor variables ('full' models). We then generated the most parsimonious model by eliminating predictor variables from these full models using backwards selection based on 3 criteria: the change in Akaike's Information Criterion (AIC), the change in deviance explained (% DE), and estimates of concurvity (the GAM analogue of collinearity between predictors). All models were fit via restricted maximum likelihood, and the basis complexity parameter (k) was set to 5 for all environmental predictors. All models fully converged and basis complexity was always sufficient based on model diagnostics. Second, the relative importance of each environmental predictor retained in the reduced model for a given response was evaluated using both AIC and the % DE (Hamilton et al. 2022). The relationship between each retained predictor variable and a given response was illustrated with partial effect plots. GAM analyses were conducted using the R package *mgcv* v.1.8-35 (Wood 2021). Finally, we generated classification and regression trees to provide a graphical understanding of how all 8 environmental conditions interact to affect each of the 3 response variables. This is valuable because the importance of a parameter may depend on its interaction with other parameters (Liaw & Weiner 2002). CART produces trees that can be used to visualize the specific breakpoints driving outcomes for a response variable as well as the interactions among important predictors. We created pruned regression trees using the customary 1SE rule which optimizes tree size and maximizes fit to the data while limiting cross-validation error (Breiman et al. 1984, Harper et al. 2011). The CART analysis was conducted using the *rpart* v.4.1-15 package (Therneau et al. 2015).

3. RESULTS

During 15 mo of pitfall trap sampling, we caught nearly 700 crabs across 9 taxonomic groups (species or genus), with fiddler crabs (*Minuca minax*, *Leptuca pugilator*, *Minuca pugnax* *Uca* spp.), shore crabs (*Armases cinereum*, *Sesarma reticulatum*) and mud crabs (*Eurytium limosum*, *Panopeus obesus*, *Eurypanopeus depressus*) caught most frequently (Fig. S2, Table S2). Crabs ranged in size from recently settled juveniles ~2 mm carapace width (CW) to juvenile blue crabs (*Callinectes sapidus*) >60 mm CW. Generally, larger crabs were collected at lower elevations closer to tidal creeks; mean crab size decreased moving up to the mid and high marsh zones, where the crab community was dominated by fiddler crabs and shore crabs (Table S3). Both marsh crab CPUE and crab burrowing activity were higher in Segment A than Segment B (Table S4), and both metrics peaked during warm months from spring through early fall (Fig. S2). Because of this near absence of crabs from pitfall traps during the winter, all results presented below are based on data collected during the months of April through September across 2 yr ($n = 9$ months) and pooled to conduct plot-level statistical analyses.

Mean crab CPUE was significantly lower in the low marsh zone of each segment than in the Segment A mid or high marsh ($F_{2,19} = 16.31$, $p < 0.0001$) or Segment B high marsh ($F_{1,22} = 25.47$, $p < 0.0001$; Fig. 1). Crab CPUE in the mid and high marsh zones of Segment A were not significantly different from one another based on a post-hoc Tukey test (Fig. 1). Despite a clear pattern of higher burrow density in the low marsh zone within Segment A (Fig. 1), mean burrow density within this segment was not significantly different across the 3 marsh zones ($F_{2,19} = 0.519$, $p = 0.6$ based on ln-transformed data). This is likely due to the high variability in burrow density within the low marsh zone. Within Segment B, the low and high marsh zones also did not differ in crab burrow density ($F_{1,22} = 0.006$, $p = 0.94$; Fig. 1). Exponential Shannon diversity did not differ across marsh zones within Segment A ($F_{2,18} = 0.53$, $p = 0.6$), but the crab community was significantly more diverse in the high marsh compared to the low marsh within Segment B ($F_{1,21} = 5.314$, $p = 0.03$; Fig. 2).

We observed differences in marsh crab community composition across both marsh zones (Pseudo- $F_{2,44} = 7.94$, $p < 0.001$) and marsh segments (Pseudo- $F_{1,44} = 3.14$, $p = 0.007$), with each of the 3 marsh zones different from one another based on pair-wise post-hoc tests (all $p < 0.015$). The nMDS ordination illustrates these differences across marsh zones, with plots in

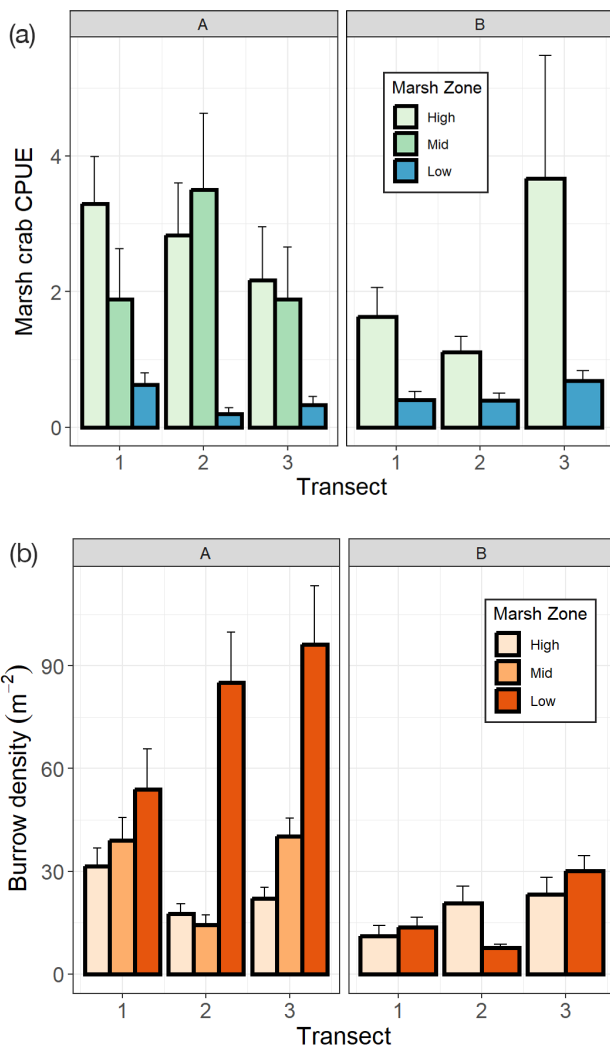


Fig. 1. Salt marsh crab (a) catch per unit effort (CPUE) and (b) burrow density, pooled across warm season months (April–September, $n = 9$) and grouped by marsh zone (high, mid, and low). Data are from July–September 2020 and April–September 2021 for Segment A (left panels, representing a geologically older marsh) and Segment B (right panels). Zone means are calculated from plot-level means across the 9 sampling events. Error bars are +1 SE

the low marsh clustering separately from the mid and high marsh zones. These differences can be attributed to the species that were strongly associated with each of the marsh zones: low marsh plots tended to contain more mud crabs and juvenile blue crabs while mid and high marsh plots were dominated by fiddler and shore crabs (Fig. 3).

GAMs describing the relationship between our 8 environmental predictor variables and crab abundance, burrowing activity, and diversity illustrated the complex relationships between the environmental gradients observed within salt marshes and a key

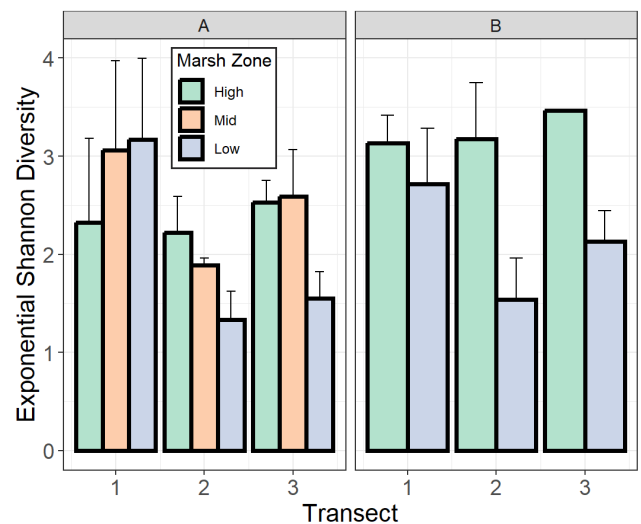


Fig. 2. Salt marsh crab community biodiversity, calculated as the exponential Shannon diversity index using marsh crab catch data pooled across warm season months (April–September) and grouped by marsh zone (high, mid, and low). Data are from July–September 2020 and April–September 2021 for Segment A (left panel) and Segment B (right panel). Zone means are calculated from plot-level means across the 9 sampling events. Error bars are +1 SE

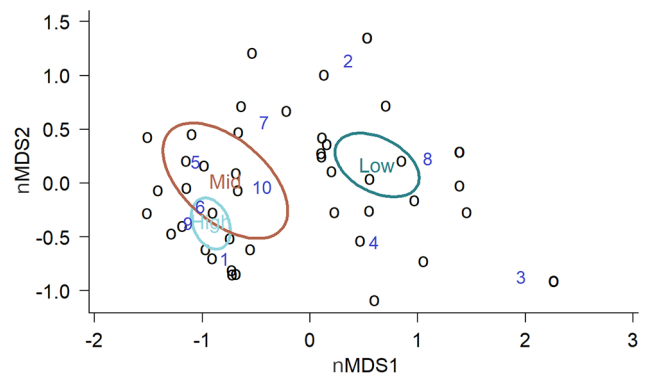


Fig. 3. Non-metric multidimensional scaling (nMDS) ordination ($k = 2$, stress = 0.11) based on Bray-Curtis dissimilarity of marsh crab communities sampled from 50 plots across warm season months (April–September). Points represent pooled community composition at individual plots; ovals indicate 95% confidence ellipses for each marsh zone (Low, Mid, High); blue numbers denote species strongly associated with plots in that ordination space. Species codes: (1) *Armases cinereum*, (2) *Callinectes sapidus*, (3) *Eurypanopeus depressus*, (4) *Eurytium limosum*, (5) *Leptuca pugilator*, (6) *Minuca minax*, (7) *Minuca pugnax*, (8) *Panopeus obesus*, (9) *Sesarma reticulatum*, (10) *Uca* spp.

set of marsh inhabitants. Final models including a subset of smoothed environmental predictor variables provided reasonable fits to the data, with deviance explained ranging from 40 to 69%, though at most, only 3 of our 8 predictors were included in

Table 2. Output from generalized additive models investigating relationships between 8 environmental variables and 3 marsh crab response variables: crab catch per unit effort (CPUE), burrow density, and exponential Shannon diversity. Akaike's information criterion (AIC) and deviance explained (DE) are provided for each of the 3 final, reduced models (one per response). The relative importance of each environmental predictor variable for a given response can be evaluated based on the change in AIC or DE (δ AIC or δ DE). For δ AIC, increasingly negative values suggest a worse fit to the data without that parameter in the model while accounting for the overall number of parameters included. δ DE values represent the proportion of deviance explained; higher values indicate important environmental variables for a given response. Blank cells indicate when that predictor was not retained in the final model, and predictors for which there was a statistically significant effect ($p < 0.05$) are in **bold**

	Crab CPUE		Burrow density (m ⁻²)		Exponential Shannon diversity	
	AIC/ δ AIC	% DE/ δ DE	AIC/ δ AIC	% DE/ δ DE	AIC/ δ AIC	% DE/ δ DE
Reduced model	115.57	68.9	499.83	45.1	133.16	40.1
Elevation	-24.29	22.1	-0.93	10.5	-7.6	16.1
% cover <i>Juncus</i>						
% cover <i>Salicornia</i>						
% cover <i>Spartina</i>	-5.23	5.2	-6.66	18.5	0.524	3.0
% unvegetated						
Porewater salinity	-11.30	10.8			-6.01	17.4
Sediment bulk density						
Sediment % clay			2.33	1.8		

the final models; similarly, up to 3 predictors exhibited statistically significant relationships with any particular response variable (Table 2). Both elevation and porewater salinity exhibited positive relationships with crab CPUE, while CPUE was negatively related to % cover of *Spartina* (Fig. 4). Burrow density was (non-linearly) negatively related to % cover

of *Spartina*, driven mainly by the high burrow densities found in the high marsh zone where *Spartina* is absent (Fig. 4). Burrow density exhibited a hump-shaped relationship with elevation, peaking at ~ 0.0 m NAVD88 and had a weak positive relationship with % clay in the sediment (Fig. 4, Table 2). Finally, elevation was also positively and linearly

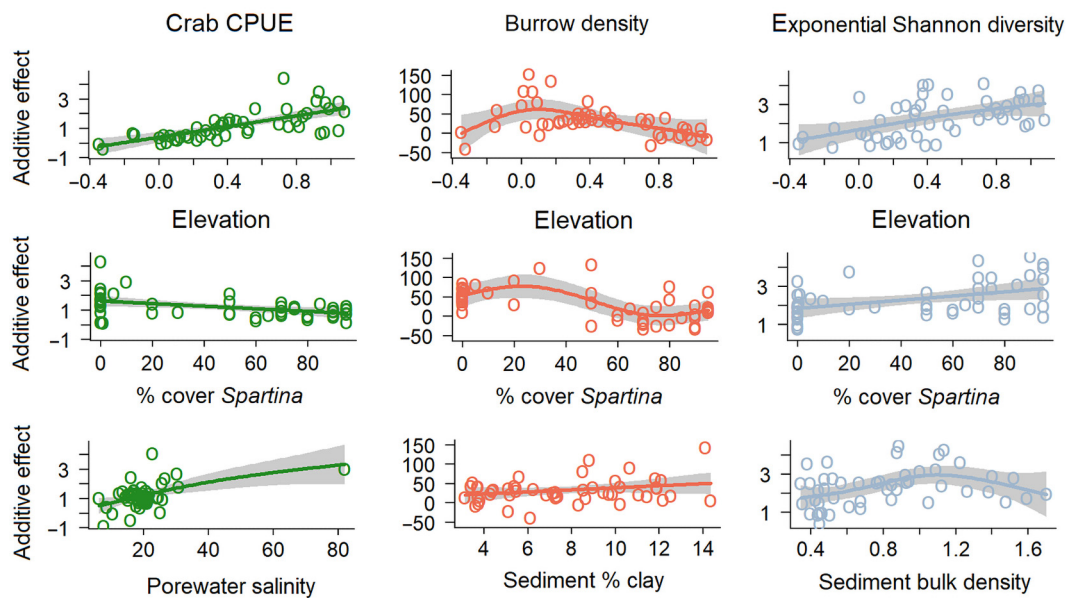


Fig. 4. Generalized additive model response plots illustrating relationships between crab catch per unit effort (CPUE), burrow density (m⁻²), exponential Shannon diversity and environmental predictor variables retained in the final model for each response. All models retained both Elevation and % cover *Spartina*, but the final variable retained was different for each model (see x-axes on lower 3 panels). Points are plot-level values (N = 50 for CPUE and crab burrows, N = 48 for Shannon diversity). Grey shaded area is SE of the estimated smooth fit

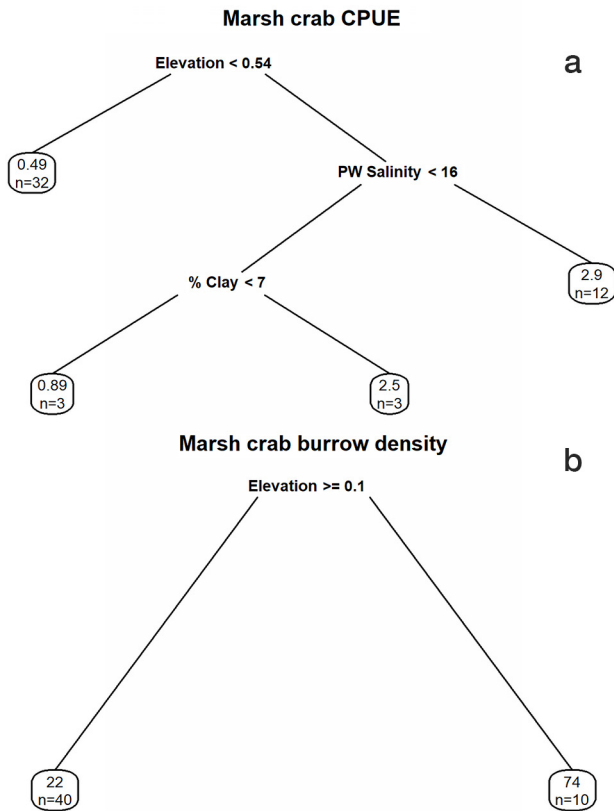


Fig. 5. Pruned classification and regression trees for (a) crab catch per unit effort (CPUE) and (b) burrow density. Each 'circle' represents a leaf node; the top value in the leaf is the mean of all observations in that node, and the bottom value is the number of observations. PW: porewater. The trees were pruned based on cross-validation using cost-complexity penalization. 'Yes' is the left branch coming from a particular breakpoint, 'No' is the right branch

related to exponential Shannon diversity, with high diversity observed at higher elevation plots, substantial variability in diversity observed at medium elevations ranging from 0 to 0.5 m NAVD88, and low diversity at low elevation, creekside plots (Fig. 4). Diversity was also positively related to % cover of *Spartina* and exhibited a hump-shaped relationship with bulk density of the sediment, peaking at $\sim 0.9\text{--}1.1\text{ g cm}^{-3}$.

Elevation was the root node in each of our CART analyses, though the specific height identified as a breakpoint varied across the 3 response variables. For crab CPUE, 0.54 m (NAVD88) was identified as a key elevation at which crab abundance diverged. Pitfall traps at plots located higher than 0.54 m caught, on average, approximately 5 times more crabs than plots lower than this elevation, and at these higher elevation plots, porewater salinity and % clay in the sediment were both related to crab

CPUE (Fig. 5a). For crab burrow density, plots at elevations >0.1 m (NAVD88) exhibited low-to-intermediate burrow densities (22 m^{-2} on average) while higher burrow densities were observed at plots located at elevations <0.1 m (74 m^{-2} on average; Fig. 5b). For marsh crab diversity, an elevation of 0.26 m was identified as the root breakpoint, although bulk density and porewater salinity drove the subsequent groupings among our sampling locations (Fig. S3).

4. DISCUSSION

Crabs are a ubiquitous component of salt marsh communities throughout the distribution of this coastal habitat (Mazumder 2009, Alberti et al. 2015, Li et al. 2018, Wasson et al. 2019), and like many species that have evolved to inhabit the intertidal zone, marsh crabs are able to withstand extreme gradients in environmental conditions. Based on observational data collected over 2 consecutive years, we confirm previous results that marsh crabs are most abundant at mid to high elevations across the marsh platform, while ecosystem engineering effects of crabs (excavation of burrows) are most prevalent adjacent to creek banks. We likely observed this pattern for 2 reasons. First, the tremendous abundance of 2 species of fiddler crabs (red-jointed and sand fiddlers; Fig. S2), which are most commonly observed in mid- and high-marsh zones, largely drove the positive relationship between crab CPUE and elevation. Second, burrowing can be restricted to certain marsh zones by competition among crabs or by the physical characteristics of the sediment (Teal 1958) while foraging activities can occur across much of the marsh platform. This would subject crabs to pitfall trap sampling beyond the zones where they excavate burrows. In addition, our marsh crab community exhibited higher species richness than previous landscape-scale marsh crab monitoring efforts in other locations (e.g. Raposa et al. 2018) and included approximately half as many species as were caught in a previous continent-scale sampling effort (Wasson et al. 2019). Crab exponential Shannon diversity generally increased with distance from tidal creeks, though the effect of marsh zone on diversity was site-specific. We encourage future investigations of the relationships between crab community diversity, marsh ecosystem functioning and community stability across spatial and temporal scales. Finally, we demonstrate the primacy of elevation as the key environmental predictor of marsh crab abundance,

burrowing activity, and community diversity and identify specific elevations that are important to each of those responses. Identification of high-resolution patterns in the current spatial distribution and ecosystem engineering effects of crabs across the marsh platform, as well as the estimation of elevation levels which are key to crab communities, will allow for predictions of crab impacts as marshes migrate due to sea level rise.

A previous effort to understand crab distribution and activity at sites distributed across a continental scale found that burrow density and crab abundance were inversely related to one another; burrows were more abundant near creeks while crab CPUE was highest farther from creek banks (Wasson et al. 2019). Similarly, marshes distributed across tens of kilometers within a single large estuary exhibited site-specific differences in crab CPUE and burrowing but demonstrated the same trends within marsh sites: relative crab abundance was highest on the marsh platform while burrow density increased at creekbanks (Raposa et al. 2018). The findings presented here from 2 sites along a single tidal creek demonstrate the same pattern, with highest burrow densities in a narrow elevation zone occurring in the low marsh, and crab abundance increasing with distance from the tidal creek (Fig. 2). In addition to distance from the creek bank, inundation time and porewater salinity can be important determinants of marsh crab burrowing (Li et al. 2018), and both are highly dependent on elevation relative to the tidal frame. Similarly, vegetation can differentially affect the distribution of even congeneric crabs due to differences in behavior (e.g. sexually selected waving by some fiddler crab species but not others; Nobbs 2003). Here, both porewater salinity and 2 sediment characteristics were identified in our classification tree analysis (Figs. 5 & S3). However, across all 3 response variables, elevation was the dominant environmental variable determining classification of our sampling plots (Figs. 5 & S3). The specific orthometric heights identified as important breakpoints (CPUE: 0.54 m; burrows: 0.1 m; diversity: 0.26 m; all relative to NAVD88) reflect key physical and biological locations on the marsh platform. In our system, mean sea level occurs at ~ 0.0 m NAVD88, suggesting that inundation time is a contributing factor to crab burrowing activity. Similarly, mean higher high water is located at ~ 0.7 m NAVD88, just above the height identified as key to crab CPUE. The transition between short- and tall-form *Spartina* occurs at ~ 0.3 m NAVD88 (within marsh Segment A), suggesting that the ecotone between these 2 vegetation

growth forms could be important to crab diversity. Because of the spatial resolution of our long-term plots, which are spread over hundreds of meters, these heights should be considered estimates in terms of their applicability as drivers of crab community dynamics.

In addition to the abiotic factors described above, top-down control by predators is also a potential driver of marsh crab community dynamics. Marsh crabs serve as a prey resource for a diverse suite of predators, including raccoons (Nomann & Pennings 1998, authors' pers. obs.), blue crabs (Johnson 2022), fishes (Ziegler et al. 2019), birds (Bildstein 1983, Nomann & Pennings 1998), and other resident marsh crabs including *Eurytium limosum* (Kneib & Weeks 1990). The ability and effectiveness of these predators to forage for crabs on the marsh platform is highly dependent on a combination of elevation and tide stage, and as a result, the relative strength of top-down control on marsh crabs is also likely spatially variable at relatively small scales. Changes in top-down pressure on marsh crabs have been linked to higher trophic levels, including recreational harvest of predatory fishes (Altieri et al. 2012); however, increasing populations of predatory birds that consume crab-eating fishes (e.g. osprey *Pandion haliaetus*) have also been hypothesized to affect marsh crab abundance and ecosystem function via a trophic cascade (Raposa et al. 2018). Undoubtedly, both top-down control by predators and bottom-up processes such as sea level rise will interact to determine the impacts of crabs in salt marshes under future environmental conditions (Raposa et al. 2018).

Many investigations of marsh crab abundance and spatial distribution focus on a single species (e.g. Kneib & Weeks 1990), or a few related species of marsh crabs, such as fiddlers (e.g. Teal 1958, Behum et al. 2005, Zengel et al. 2016). This approach can elucidate the impacts of certain species within a community which may be particularly important due to their keystone nature (Crotty et al. 2020), abundance (Raposa et al. 2020), or range expansion (Zajac et al. 2022). A community-based framework can provide additional insights into the role of small-bodied crabs in salt marshes because their impacts are often context-dependent. For example, the strength of ecosystem functions performed by salt marsh crabs can vary across marsh sites and as a function of the densities of co-occurring species (Williams & Johnson 2021). This can lead to variability in the influence of the crab community on ecogeomorphic processes (Williams & Johnson 2021). Similarly, different fid-

Other crab species demonstrate complementarity (as opposed to redundancy) in their burrowing activity, even while exhibiting habitat preferences and antagonistic behavior, such that interspecific interactions can determine the relative importance of each species as a bioturbating agent (Neylan et al. 2019). Thus, a restricted taxonomic focus can lead to an incomplete understanding of the roles and functions performed by marsh crabs due to a lack of community and environmental context. Similar to a narrow taxonomic focus, limiting the spatial scope of marsh crab investigations to zones of the marsh which are susceptible to the effects of grazers or bioturbators can overestimate the negative effect of crabs on marshes at larger scales. While small-scale, targeted studies suggest strong impacts of marsh crabs on, for example, above- and below-ground vegetation biomass (Beheshti et al. 2021), marsh plant resilience to drought (Angelini et al. 2018), and greenhouse gas flux (Xiao et al. 2021), a landscape-level view leads to a vastly different interpretation of the relative importance of crabs (Wasson et al. 2019). Across 15 marsh sites distributed throughout North America and the Caribbean, Wasson et al. (2019) did not observe strong negative impacts of crabs on salt marsh vegetation despite clear relationships between crab burrowing activity and marsh elevation, distance to creek, and soil characteristics. Our sampling scheme incorporates the variability in conditions (biotic and abiotic) that are exhibited across the entire marsh platform, from forest edge to creek bank. In doing so, we provide additional evidence of the spatial gradients in potential crab impacts on salt marshes. Substantial crab burrowing is strongly related to % cover of *Spartina* and elevation within the tidal frame (Figs. 4 & 5). However, bioturbation is only one mechanism by which crabs can impact marshes; herbivory can be a key structuring force within these plant communities (Alberti et al. 2007, He et al. 2015), and how crab grazing interacts with environmental conditions (at high spatial resolution) to impact marshes remains a key question.

Salt marsh vegetation can have a major effect on marsh platform stability and sediment accretion (Morris et al. 2002, Fagherazzi et al. 2012, Kirwan & Megonigal 2013), but in addition to vegetation, a diverse suite of animals have also been identified as potential drivers of ecosystem functioning both above- and below-ground in salt marshes (Gittman & Keller 2013, Rinehart et al. 2017, Beheshti et al. 2021, Walker et al. 2021). Crabs in particular may be a key predictor of salt marsh persistence in the face of changing coastal conditions (Hughes et al.

2009, Vu et al. 2017, Angelini et al. 2018, Crotty et al. 2020). To date, targeted experiments have often focused on a few key species within the salt marsh animal community. These are typically grazers that can directly consume marsh vegetation, including *Littoraria irrorata* (periwinkle snails) and *Sesarma reticulatum* within US Atlantic coast marshes, and *Pachygrapsus crassipes* (lined shore crabs) in marshes along the US Pacific coast. However, ecological interactions, both positive and negative, have the potential to mitigate the impacts of these herbivores (Gittman & Keller 2013, Williams & Johnson 2021). This may explain the lack of a general negative effect of crabs on salt marsh vegetation over the marsh landscape and across diverse types of marshes (Wasson et al. 2019).

Crabs are ecosystem engineers and thus are not passive inhabitants of salt marshes (Vu et al. 2017, Angelini et al. 2018, Crotty et al. 2020, Beheshti et al. 2021, Xie et al. 2022). Consequently, crab abundance and burrow density (and possibly even diversity) are each potentially both driving and responding to the environmental conditions observed in marshes, particularly sediment bulk density and porewater salinity. This has been demonstrated previously: high densities of shore crabs can reduce bulk density of marsh sediments (Beheshti et al. 2021). Our observational approach cannot isolate specific mechanisms driving marsh crab abundance, diversity, or burrowing activity, nor can we identify causes versus responses between crabs and environmental variables. Nonetheless, we have identified clear spatial patterns in crab abundance and burrowing activity, and to a lesser extent, diversity across environmental gradients within a representative southeastern US salt marsh. We have also documented key biotic and abiotic conditions most closely associated with each metric of this crab community under current environmental conditions. Increased recognition of the roles played by the diverse animals that inhabit salt marshes, and improved understanding of the environmental conditions contributing to organismal abundance and distribution should enhance our ability to manage salt marshes under future climate and sea level scenarios.

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