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The Role of Ecological Interactions in Saltmarsh Geomorphic Processes

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The role of ecological interactions in saltmarsh geomorphic processes

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of the Requirements for the Degree of

Master of Science

by

Bethany L. Williams

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This thesis is submitted in partial fulfillment of

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ABSTRACT

Accelerated sea-level rise poses a significant threat to coastal habitats. Salt marshes are critical coastal ecosystems, providing a host of services such as storm protection, food production, and carbon storage. Persistence of salt marshes in the face of rising sea levels relies, in part, on vertical accretion. Current ecogeomorphic models and empirical studies emphasize the importance of the positive relationship between plant production and vertical accretion via sediment trapping by stems aboveground and belowground organic matter production. Thus, changes in plant production influence salt marsh persistence with sea-level rise. However, studies and models of marsh accretion do not consider the effects of animal-mediated changes in plant production. Here, I tested how two co-occurring marsh crustaceans, *Uca pugnax* (marsh fiddler crab) and *Sesarma reticulatum* (purple marsh crab), which have contrasting effects on smooth cordgrass (*Spartina alterniflora*) production, indirectly influence sediment deposition and belowground organic matter contribution, through observational surveys and field manipulation. *S. reticulatum* feeds directly on *S. alterniflora*, while *U. pugnax* facilitates *S. alterniflora* production through burrowing and biodeposits. I found that *U. pugnax* facilitated *S. alterniflora* biomass in some marshes, but not others. However, this facilitation of *S. alterniflora* biomass did not enhance sediment deposition. *U. pugnax* had no effect on belowground components of vertical accretion (i.e. root production and decomposition). These results suggest that in isolation, *U. pugnax* has little impact on saltmarsh geomorphic processes. *S. reticulatum* reduced *S. alterniflora* above- and belowground biomass; however, sediment deposition increased as *S. alterniflora* biomass decreased, contrary to models of ecogeomorphology. This trend was likely due to sediment being resuspended by crab bioturbation, as *U. pugnax* abundances were higher in *S. reticulatum*-grazed areas than in non-grazed areas. When *U. pugnax* occurred in areas of low *S. reticulatum* grazing, *S. alterniflora* biomass and sedimentation was similar to areas with only *U. pugnax*. I suggest that the negative impacts of *S. reticulatum* are exaggerated when intense grazing results in completely unvegetated areas and subsequent increases in *U. pugnax* density, where bioturbation erodes sediments. Thus, while *S. reticulatum* can increase the susceptibility of marsh sediments to physical erosion by removing vegetation, it may also do so by facilitating *U. pugnax* bioturbation. However, when *S. reticulatum* grazing intensity is low, facilitation of *S. alterniflora* growth by *U. pugnax* can mitigate the negative effect of grazing, which suggests that the net effect of these species may depend on their relative abundance. This study demonstrates that ecological interactions, in addition to physical processes, have significant effects on marsh persistence as sea level rises, and merit incorporation into ecogeomorphic models and empirical studies of marsh accretion.

The role of ecological interactions in saltmarsh geomorphic processes

INTRODUCTION

Salt marshes are among the most productive ecosystems in the world (Mendelssohn and Morris 2002) and provide important ecosystem services such as storm protection, carbon storage, food production, and tourism (Barbier et al. 2011). Habitat loss due to accelerated sea-level rise is a major concern for salt marshes, especially in regions where accelerations of sea-level rise rates are higher than the global average, like Atlantic coast of the United States. Here, the rate sea-level rise is increasing 3-4 times faster than the global average (Sallenger et al. 2012). Salt marsh persistence in the face of sea-level rise relies on landward migration and vertical accretion (Kirwan et al. 2016). Landward migration however, is often inhibited by anthropogenic structures such as roads, sea walls, and houses, causing a coastal squeeze (Pontee 2013). Since 14% of the United States shoreline has been hardened (Gittman et al. 2015), understanding the factors that influence accretion will be important to predict the vulnerability of salt marshes to accelerated sea-level rise.

For vertical accretion, current ecogeomorphic models, supported by empirical studies, stress the importance of sediment trapping by marsh grass (i.e. smooth cordgrass *Spartina alterniflora*) and the contribution of organic matter via belowground production (Morris et al. 2002; Fagherazzi et al. 2013a; Morris et al. 2013). Marsh plants are foundation species that slow the flow velocity of water, allowing sediment particles to settle out of the water column onto the marsh surface (Friedrichs and Perry 2001). As marsh grass stem density and biomass increase, sediment deposition is enhanced (Friedrichs and Perry

2001; Morris et al. 2002; Fagherazzi et al. 2013a). Therefore, changes in primary production can influence accretion rates.

Hydrology, in addition to marsh plants, influences salt marsh vertical accretion. With greater inundation and hydroperiod, the marsh is flooded for a longer period of time, allowing for more sediment deposition to occur, and thus contributing to vertical accretion (Friedrichs and Perry 2001; Fagherazzi et al. 2013a). In addition to sediment delivery, hydrology can control plant production. As flooding increases, *Spartina* production is stimulated, but in a parabolic pattern, such that when hydroperiods are extremely high, marsh plants drown (Morris et al. 2002; Morris et al. 2013).

Current ecogeomorphic models of marsh accretion focus on physical processes that affect plant production and sediment deposition, but ecological interactions may also be important. Animals can influence saltmarsh plant production (Bertness 1985; Coverdale et al. 2012; Hughes et al. 2014) and thus merit consideration in ecogeomorphic studies of marsh accretion. For instance, facilitation is a positive interaction that occurs when one organism makes the environment more hospitable for another (Stachowicz 2001). Facilitation of aboveground plant biomass could enhance marsh accretion via increased sediment trapping. In contrast to the positive effects of facilitation on plant biomass, herbivory has negative effects on plant production (Silliman and Zieman 2001; Holdredge et al. 2009; Coverdale et al. 2012). Because herbivory can significantly reduce the abundance and biomass of marsh plants, it could potentially inhibit vertical accretion. However, to my knowledge, no tests of how plant-animal interactions affect physical processes that influence marsh accretion, such as sediment trapping, have been conducted.

In salt marshes, the marsh fiddler crab, *Uca pugnax* (hereafter referred to as *Uca*) and the purple marsh crab, *Sesarma reticulatum* (hereafter referred to as *Sesarma*) co-occur in the same tidal zone in salt marshes along the Atlantic coast of the United States (Seiple 1979; Grimes et al. 1989; Johnson 2014). While their direct effects on saltmarsh physical structure have been well studied (e.g., their burrowing activities; Seiple and Salmon 1982; Bertness 1985; McCraith et al. 2003; Hughes et al. 2009; Vu et al. 2017), their indirect effects have received little attention. In terms of aboveground biomass, *Uca* is a facilitator species that increases the biomass of the cordgrass, *Spartina alterniflora* (hereafter referred to as *Spartina*), via nutrient regeneration, biodeposits, and oxygenation of marsh soils (Bertness 1985; Gittman and Keller 2013; Hughes et al. 2014). However, this process is often mediated by soil characteristics (Holdredge et al. 2010; Michaels and Zieman 2013). Generally, by increasing *Spartina* biomass through burrowing activities, *Uca* may indirectly facilitate sediment trapping, the aboveground component of marsh accretion. However, burrowing activity by *Uca* also reduces belowground production and increases decomposition rates (Thomas and Blum 2010; Gittman and Keller 2013). Therefore, they may have contrasting effects on the above- and belowground components of vertical accretion.

In contrast to the facilitative effects of *Uca* on aboveground biomass of *Spartina*, *Sesarma* reduces *Spartina* biomass through herbivory on both above- and belowground plant biomass (Seiple and Salmon 1982; Coverdale et al. 2012). While *Sesarma* is also a burrowing species, and could facilitate growth similar to *Uca* through this activity, its grazing offsets any positive effects of burrowing, sometimes resulting in major die-backs of *Spartina* (Holdredge et al. 2009; Coverdale et al. 2012). Through the negative effect of *Sesarma* grazing on *Spartina* biomass, this crab could indirectly decrease sedimentation rates aboveground, in addition to preventing contribution of organic matter belowground, thus indirectly and strongly inhibiting vertical accretion.

The negative effects of *Sesarma* on plants may be offset by positive effects of other species such as *Uca* (Gittman and Keller 2013). In New England, *Spartina* die-offs have occurred where *Sesarma* is overabundant because of predator release (i.e. a trophic cascade) (Holdredge et al. 2009; Altieri et al 2012). Given the large geographic distribution of *Sesarma* (Seiple 1979), these die-offs should be widespread in Atlantic salt marshes where removal of predators has increased, but they are not. Facilitation of *Spartina* by *Uca* can ameliorate the negative effects of other grazers (Gittman and Keller 2013), and thus may prevent the prevalence of *Spartina* die-offs via *Sesarma* herbivory along much of the Atlantic coast.

The overarching goal of this research is to determine how ecological interactions between animals and saltmarsh plants may indirectly influence saltmarsh vertical accretion, using sediment deposition and organic matter contribution as proxies for this process. Specifically, *Uca* may positively influence vertical accretion by facilitating aboveground *Spartina* biomass and sedimentation (Figure 1). In contrast, *Sesarma* may impede vertical accretion by grazing above- and belowground biomass of *Spartina* (Figure 1). However, *Uca* may ameliorate the negative effects of *Sesarma*, aboveground, by facilitating *Spartina* shoot growth. To test these hypotheses, I targeted three specific objectives: 1) Determine how natural variation in *Uca* density influences *Spartina* production, and ultimately sediment deposition, 2) determine how natural variations in *Sesarma* grazing intensity influence sediment deposition, and 3) test the individual and combined effects of *Uca* and *Sesarma* on components of vertical accretion via changes in above- and belowground *Spartina* production, decomposition, and sedimentation, using experimental field manipulations. By incorporating the role of animal-mediated controls on primary production into ecogeomorphic models of marsh accretion, we can more clearly understand the capacity of salt marshes to keep pace, as accelerated sea-level rise threatens these critical coastal ecosystems.

MATERIALS AND METHODS

To study the effects of *Uca* and *Sesarma* on *Spartina* production, aboveground sediment deposition, and belowground organic matter contribution, I approached these questions in two ways: 1) field observations and 2) a manipulative experiment. Field observations allowed for measurement of responses across a wide range of marshes, with varying hydroperiods and sediment availabilities, to determine if trends occur across marshes. A manipulative experiment was used to control confounding factors and to measure process rates (e.g., production, decomposition).

Effect of *Uca* on *Spartina alterniflora* production and sediment deposition

Study Sites: I conducted a field survey of five salt marshes (Goodwin Island, Seaford, Virginia; Boxtree Marsh, Machipongo, Virginia; Lower Phillips Creek, Nassawadox, Virginia; Nag Marsh, Prudence Island, Rhode Island; Gut Marsh, Wellfleet, Massachusetts; Figure 2; Table 1) from July-August 2016. These marshes are dominated by *Spartina* at the low elevations, with a band of *S. patens* at slightly higher elevations. The *Spartina* zones are flooded twice daily with the high tides. Sampling at this wide range of sites was done to test the generality of results across marshes with varying hydroperiods and sediment availabilities (Table 2, Table 5).

Plot Setup: Along a 100-m span of each marsh 0.0625 m^2 plots were set up in areas with and without *Uca* burrows (n = 8/area type). *Uca*-present plots were interspersed with *Uca*-absent plots. Because sediment concentration decreases with increasing distance from the marsh edge (Friedrichs and Perry 2001) each plot, within site, was sampled at similar distances from the marsh edge (Table 2).

Measurements: Sedimentation was measured by deploying two sediment plates in each plot for one week. Sediment plates were constructed by rubber banding a pre-weighed 90 mm fiberglass filter to a Plexiglas plate, and staking it to the ground so it is flush with the marsh surface (LeMay 2007). Upon collection, fiberglass filters were carefully removed from the sediment plate and dried at 60 °C to a constant mass, then weighed. To examine only inorganic deposition, filters were combusted at 550 °C for two hours and weighed. Because the sedimentation plates experienced high levels of fiddler crab biodeposition (fecal pellets), a site-specific correction factor was used to adjust the masses of the filters after deployment. This correction factor was calculated by weighing individual fecal pellets from each site (n=50/site) to determine an average fecal pellet weight for each site. Then, fecal pellets on filters were enumerated and multiplied by the average pellet weight for that site. This value was then subtracted from the total mass of the filter and sediment, to provide a more accurate value of sedimentation. Inorganic deposition rate was calculated using the following equation:

$$\text{Sedimentation Rate (mg/day)} = \frac{\text{(Corrected total ash mass (mg)-Filter mass (mg))}}{\text{\# days deployed}} \qquad \textit{Equation 1}$$

Spartina production was measured using standing stock biomass as a proxy. After sedimentation plates were collected, all plants within the 0.0625 m^2 plot were collected by clipping the plants at the marsh surface. Live and dead stems were washed, separated, enumerated, then dried at 60 °C to a constant mass and weighed. *Uca* burrow densities were measured by enumerating the number of burrows (> 1 cm) within each plot. Any other burrowing species and invertebrates (i.e. ribbed mussels, *Geukensia demissa*) were also recorded.

Soil strength was measured in each plot using a shear vane placed in the center of the plot to a depth of 10 cm. Because inundation period can also affect sediment deposition, and elevation determines inundation period, relative elevation was measured in the form of relative tidal heights between plots using the tide stick method (Smith and Warren 2007). This method is performed by deploying tall garden stakes covered in colored craft glue in each plot. After one tidal cycle, the height at which the glue was washed away was measured, providing the relative tidal height within each plot.

Site characteristics, including sediment availability, and *Uca* population estimates were also measured. At each site, water samples were collected at points every 10 m along the 100-m span of plots (n = 3/point), to assess variation in sediment availability along this range. Water samples were filtered onto 47 mm glass fiber filters, dried at 60 °C for forty-eight hours, and weighed to calculate total suspended solids concentration. These filters were muffled in a furnace at 550 °C for two hours and weighed, to calculate fixed suspended solids concentration. Population estimates of *Uca* were measured by enumerating burrows within haphazardly tossed 0.0625 m^2 quadrats (n=10).

Statistical Analyses: All statistical analyses were conducted in R (Version 3.3.2., R Core Team, 2016). Data were examined for normality and homoscedasticity. Data that did not meet assumptions were transformed to meet assumptions. Multiple linear regressions were conducted to determine the effect of *Uca* burrow density, site, and their interaction on *Spartina* biomass (natural log transformed), sedimentation rates (natural log transformed), and soil strength (natural log transformed) at each site. To test for differences in hydroperiod across *Uca*-present and *Uca*-absent plots, I ran a t-test within each site. Within site comparisons were made because hydroperiod depends on tidal height, which changes daily, and measurements across sites were not made on the same day.

Effect of *Sesarma* on sediment deposition

Plot setup: To study the effect of *Sesarma* on sedimentation through their grazing of *Spartina*, another set of 0.0625 m^2 plots were set up in three areas, representing a range of grazing intensities: denuded of vegetation (completely grazed), significant grazing (few stems, with shredded and clipped edges [Crichton 1960]), and no grazing (n=8/area) (Figure 3). This study was performed in the same five sites as the field survey for *Uca* (Figure 2, Table 1).

Measurements: Sedimentation, *Spartina* production, soil strength, and elevation were measured following the same methods described above. I controlled for distance from the marsh edge (Table 2), similar to the *Uca* field survey. Additionally, crab burrows were enumerated within each plot, to measure the suitability of each area type for *Uca*. *Uca* burrows were distinguished from *Sesarma* burrows by their smaller size and the lack of a hood over the top of the burrow (Seiple and Salmon 1982).

Statistical Analyses: All statistical analyses were conducted in R software (Version 3.3.2., R Core Team, 2016). All data were examined for normality and homoscedasticity assumptions. Data that did not meet the criteria was transformed to meet assumptions. I conducted fixed effects analysis of variance tests (ANOVAs) to determine the effect of *Sesarma* grazing intensity, site, and their interaction on the following responses: sedimentation (natural log transformed), soil strength (natural log transformed), and *Uca* burrow density. The lsmeans function in the lsmeans package (Lenth 2016), with a Tukey correction for p-values was used as a post-hoc test to determine where differences occurred among treatments and among sites. To test the difference in hydroperiod across sampled plots, I conducted an ANOVA within each site. Sites were analyzed separately because hydroperiod varies with tidal height, which differs across days, and sites were not measured on the same day.

Effects of *Uca* and *Sesarma* on above- and belowground components of vertical accretion

To determine the effect of *Uca and Sesarma* on above- and belowground components of vertical accretion, a caging experiment was conducted at Cushman's Landing, Cape Charles, Virginia USA (Figure 2, Table 1). For logistical purposes, this site was chosen instead of one of the previous survey sites. Creating cage structures is costly and time-intensive, so to accompany the field surveys, I performed the field experiment at only one site. To create the cage structures, a large area of marsh was needed. Boxtree Marsh and Lower Phillips Creek sites featured many long-term monitoring transects, making it unusable. Additionally, cage structures attract *Sesarma* (Marc Hensel, personal communication), so to prevent *Sesarma* intrusion into cages I used a site with evidence of lower *Sesarma* populations. Thus, Boxtree Marsh, Lower Phillips, and Wellfleet, were not ideal sites because of high *Sesarma* grazing rates, evidenced by large denuded, burrow-riddled areas. Finally, cage maintenance was performed bi-weekly, so the site needed to be in Virginia, rather than one of the New England Sites (Prudence Island or Wellfleet). Goodwin Island can only be accessed by boat, making it less accessible. Therefore, Cushman's Landing was chosen as the ideal experimental site (Figure 2, Table 1).

Treatments: The field manipulation employed a fully factorial design with four treatments: *Uca* only, *Sesarma* only, *Uca* and *Sesarma*, and no crabs, with five replicates per treatment. Uncaged reference plots were also deployed. Cages (0.25 m^2) were constructed of PVC poles and vinyl-coated wire mesh (0.635 cm) in the intermediate *Spartina* zone and dug 15 cm into the sediment. To prevent crab escape or entrance, the top 10 cm of cages were lined with aluminum flashing, which crabs are not able to pass (Silliman and Zieman 2001; Holdredge et al. 2010; Gittman and Keller 2013). Cages were arranged in a blocked design with five blocks, with one cage of each treatment placed at least 1 m apart from each other and at the same distance from the creek edge. Densities and sex ratio of crabs for treatments were determined using population estimates at the site, corresponding to 80 crabs m^{-2}. For the *Uca* only treatment, 15 adult male and 5 adult female *Uca* were added to the cages. For the *Sesarma* only treatment, 2 adult *Sesarma* were added to the cages. For the *Uca* and *Sesarma* treatment, 14 adult male *Uca*, 5 adult female *Uca*, and 1 *Sesarma* were added to the cages. For control cages, a pit trap (7.5 cm diameter, 21 cm deep) was deployed in each to capture any crabs that were not removed upon cage setup (Thomas and Blum 2010). Crabs that were smaller than the wire mesh (< 6 mm carapace width) could move freely in and out of the cages, but because these are juveniles with very small or no burrows, I assume their effects are negligible. Crabs were caged from May 03 2017 – July 29 2017, and checked bi-weekly to ensure crabs were not escaping or intruding. Cages were removed July 29 2017, prior to the taking of measurements, which occurred on August 9-10 2017.

Measurements: In each cage, aboveground *Spartina* biomass, sedimentation, soil strength, and relative tidal heights were measured following the same methods as the *Uca* and *Sesarma* surveys. For this experiment, sediment plates (2 plates per cage) were deployed for nine days, after cage structures were removed. In 45% of the filters, portions were missing after 9 days, likely due to the power of incoming tides. To keep these observations in analyses, digital images were taken of each filter and analyzed in imageJ (Schneider et al. 2012) to estimate the area of the filter missing, and more accurately calculate sedimentation rate. Any filters that were missing over 50% of their area were not included in analyses.

Additional measurements in this experiment included: aboveground production, root production, decomposition, belowground biomass, sediment characteristics, and root-to-shoot ratio. Aboveground production was measured by comparing final live plant biomass to estimated initial live plant biomass within a 0.0625 m^2 sub-section of the caged area. Initial live plant biomass was estimated by measuring the heights of all live shoots within the sub-section and using a site-specific allometric equation of shoot height vs. biomass (Equation 2). Aboveground production was calculated as the difference in live biomass between the beginning and end of the experiment, divided by the time the experiment ran.

$$\text{Estimated shoot biomass} = 0.17 * e^{\text{shoot height}*0.04} \qquad \textit{Equation 2}$$

Root production was measured by deploying a 5.08 cm wide x 25 cm long root ingrowth bag constructed of polypropylene produce bags filled with 75 g of dried peat moss, in each cage at the beginning of the experiment. Root ingrowth bags were removed at the end of the experiment and the contents of bags were rinsed through a 1 mm mesh sieve within twenty days of retrieval. Roots grown into the bag were then dried at 60 °C to a constant mass and weighed.

Decomposition was measured by deploying a bag (n=1/cage) constructed of 5 µm nitex mesh and filled with 2.5 g of dried and homogenized *Spartina* roots and rhizomes 5 cm beneath the marsh surface, at the beginning of the experiment. At the end of the experiment, bags were pulled from the ground. To ensure no dirt entered the bags, remaining contents of bags were rinsed through a 500 µm sieve. After rinsing, remaining root matter was dried at 60 °C to a constant mass and weighed. Decomposition was calculated as the percent of mass lost over the course of the experiment.

Belowground *Spartina* biomass was measured by taking a 7.62 cm diameter core to a depth of 30 cm around a single shoot of the biomass sub-section of each cage. Cores were sectioned into the following increments: 0-5 cm, 5-10 cm, 10-20 cm, 20-30 cm, to create a depth profile. A smaller core (2.5 cm wide, 5 cm long) was taken from each depth increment to measure sediment characteristics. The remainder of the cores were rinsed through stacked sieves (6 mm, 1 mm) to remove any dirt. Roots and rhizomes were separated live, from dead then dried at 60 °C to a constant mass and weighed.

I measured the following soil characteristics, using the smaller cores removed from the belowground biomass core: water content, bulk density, and loss on ignition (LOI). Small cores were removed from the larger core and weighed wet. Small cores were then dried at 60 °C to a constant mass and weighed. Finally, small cores were combusted in a muffle furnace at 550 °C for 16 hours.

Root-to-shoot ratio was measured by summing the live root/rhizome mass from all depths of the belowground biomass cores and comparing it to the shoot biomass, from which the core was taken around. The ratio was calculated by dividing the shoot biomass by the root biomass. Values greater than 1 indicate more shoot than roots, values less than 1 indicate more roots than shoot.

Statistical Analyses: All statistical analyses were conducted in R (Version 3.3.2., R Core Team, 2016). All data were examined for normality and homoscedasticity prior to analysis. Mixed effects ANOVAs, using the nlme package (Pinheiro et al. 2017) were performed to determine the effect of treatment, with block as a random effect, on the following responses: live aboveground biomass, aboveground production, sedimentation (natural log transformed), decomposition (measured as percent loss), soil strength (natural log transformed), and belowground production (natural log transformed). The multcomp package (Hothorn et al. 2008), was used for post-hoc analysis. Responses that were measured across depth were analyzed with mixed effects ANOVAs with treatment and depth as fixed effects, and block as a random effect. The following responses were measured across depth: live belowground biomass (natural log + 0.01 transformed), percent water of soil (arcsine square root transformed) and percent organic of soil (arcsine square root transformed). Two cages were excluded from all analyses, due to lack of cage effectiveness.

RESULTS

Effect of *Uca* on *Spartina alterniflora* production and sediment deposition

Uca density and site interacted to affect *Spartina* biomass (P = 0.006, Figure 4), indicating that there is a site-specific response to *Uca* burrows. At Goodwin Island and Phillips Creek, plant biomass (natural log transformed) increased linearly with *Uca* burrows (Goodwin Island: slope = 0.0082, P = 0.01; Phillips Creek: slope = 0.0049, P = 0.025; Figure 4). At Boxtree and Wellfleet, there was no relationship between plant biomass and *Uca* burrow density (Boxtree: slope = 0.0014, P = 0.56; Wellfleet: slope = 0.0011, P = 0.54; Figure 4). Finally, at Prudence Island, *Spartina* biomass decreased linearly with *Uca* burrow density (slope = -0.0056, P = 0.024, Figure 4).

There was no difference in hydroperiod between plots with and without *Uca* burrows, except at Boxtree Marsh, where hydroperiod was greater in Uca absent plots (Table 3). There was no relationship between *Uca* density and sedimentation rates (P = 0.98, Figure 5), even at sites where plant biomass increased with *Uca* density (Goodwin Island and Phillips Creek). Site significantly affected sedimentation rates (P = << 0.001; Figure 5). There was no relationship between *Uca* density and soil strength (P = 0.32, Figure 5), but a significant effect of site (P << 0.001, Figure 6).

Effect of *Sesarma* on sediment deposition

There was no difference in hydroperiod across grazing intensity plots, except at Prudence Island, where hydroperiod was lower in the no grazing plots than the denuded and grazed plots (Table 5). I found a significant interaction between grazing intensity and site when modeling sedimentation ($P << 0.001$). This interaction indicates that the difference in sedimentation rates between grazing intensities, depends on the site. Based on results of post-hoc analysis, mean sedimentation rates at Lower Phillips and Wellfleet were higher in completely grazed areas than areas with no grazing (Figure 7A), contrary to my hypothesis. Prudence Island showed a similar, but non-significant trend, while Boxtree Marsh and Goodwin Island, showed no difference in mean sedimentation rates within the respective site (Figure 7A).

Sesarma grazing intensity also interacted with site to influence belowground soil strength ($P = 0.0018$; Figure 7B). At Lower Phillips and Prudence Island, mean soil strength was lower in areas completely grazed than in areas with no grazing (Figure 7B). A similar, non-significant, trend exits at Wellfleet (Figure 7B). However, at Boxtree Marsh, grazing intensity had no effect on mean soil strength (Figure 7B).

Mean *Uca* burrow density was significantly affected by *Sesarma* grazing intensity ($P = 0.044$; Figure 8) and site ($P << 0.001$; Table 4), while their interaction had no effect ($P = 0.59$). Mean burrow densities were higher in areas denuded of vegetation than areas with no grazing ($P = 0.034$, Figure 8).

Effects of *Uca* and *Sesarma* on above- and belowground components of vertical accretion

Across all responses, there was no difference between control and reference cages, indicating no significant effect of a cage structure on measured responses. There was a significant effect of crab treatment on live aboveground *Spartina* biomass ($P = 0.002$, Figure 9A). Using a Tukey's Honest Significant Difference Test, I found that live aboveground *Spartina* biomass was lower in the *Sesarma* only treatment, than all other treatments (Figure 9A). Additionally, aboveground *Spartina* production was reduced in the *Sesarma* only treatment, compared to other treatments ($P = 0.003$, Figure 9B).

Nine sediment plates were removed from analysis due to missing >50% of the original filter area through tidal action. Although aboveground biomass was affected by treatment, there was no effect on sedimentation rates ($P > 0.05$, Figure 10).

I found a significant effect of treatment ($P = 0.01$) and depth ($P < 0.0001$) on live belowground biomass such that the *Sesarma* only treatment had lower live belowground biomass than the *Uca* only and reference treatments (Figure 11A). However, crab treatment did not affect soil characteristics: water content ($P > 0.05$, Figure 11B), bulk density ($P > 0.05$, Figure 11C), or percent organic content ($P > 0.05$, Figure 11D). Additionally, treatment had no effect on soil strength ($P > 0.05$, Figure 12B).

Treatment had no effect on *Spartina* root-to-shoot ratio ($P > 0.05$, Figure 12A), indicating there was no difference in allocation of resources, in response to crabs. Finally, treatment had no effect on root production ($P > 0.05$, Figure 13A) or decomposition ($P > 0.05$, Figure 13B).

DISCUSSION

Ecogeomorphic theory emphasizes the importance of plants in promoting marsh persistence as sea level rises through vertical accretion (Friedrichs and Perry 2001; Morris et al. 2002; Fagherazzi et al. 2013a). In this study, I demonstrate that animals can impact components of vertical accretion, and in turn, may influence the ability of salt marshes to keep pace with accelerated sea-level rise through their interactions with plants and each other. At some sites, *Uca* facilitated *Spartina* growth, but not enough to enhance sedimentation rates. *Uca* had no effect on belowground components of vertical accretion (e.g. decomposition, organic matter contribution). *Sesarma* grazing of *Spartina* increased *Uca* burrowing and decreased soil strength and belowground organic matter contribution. *Uca* ameliorated the negative impacts of *Sesarma* on aboveground plant biomass, but only at low rates of *Sesarma* grazing. When *Sesarma* grazing intensity was high, *Uca* bioturbation likely increased marsh erosion. These results suggest that *Sesarma* and *Uca* have a density-dependent impact on components of vertical accretion, and thus their relative population size may influence the ability of salt marshes to keep pace with sea-level rise.

Uca did not significantly impact the above- and belowground components of salt marsh vertical accretion. Facilitation of aboveground *Spartina* by *Uca* has been demonstrated in many marshes (Bertness 1985; Thomas and Blum 2010; Gittman and Keller 2013), and my results provide some support for this process. However, I found a site-specific response of *Spartina* to *Uca* burrows, as significant changes in plant production were detected in two of the five sites. This indicates that site characteristics may mediate the response of plants to *Uca* burrowing. For example, nutrient-limited short-form *Spartina* responds more strongly to fiddler crabs than does the non-limited tall-form (Bertness 1985). A similar pattern is seen in fertilization studies of *Spartina* (Morris et al. 2013, Johnson et al. 2016). Thus, site specificity of the response of *Spartina* production to *Uca* burrowing may be due, in part, to nutrient availability. Additionally, controlling for distance from the marsh edge made it difficult to target specific *Uca* burrow densities, resulting in low replication at many densities. Higher replication may have resulted in significant relationships between *Uca* burrows and plant biomass at more sites. Because the relationship between *Uca* and aboveground plant biomass was density-dependent, the lack of significant increases in *Spartina* biomass in the manipulative experiment may be due to choosing a mean *Uca* density.

At sites where *Uca* facilitated *Spartina* growth, there was no change in sediment deposition. These results appear to contradict the predictions of marsh ecogeomorphic models, as sediment deposition should increase with plant biomass. Morris et al. 2002 found that a 320% increase in *Spartina* biomass enhanced vertical by 156%. In my experiment, *Uca* facilitated *Spartina* by 230% and 173% at two sites, but there was no change in sediment deposition. This lack of influence on sediment deposition rates is likely due to measuring sedimentation for a short period of time. Morris et al. (2002) measured accretion and sediment deposition after 1.5 years with surface elevation tables, but in the present study sedimentation was only measured after one week with sediment plates. Because *Uca* can freely move in and out of the plots during the measurement period, measuring sedimentation for a longer period of time would have resulted in inaccurate estimates of *Uca* density within the plot. Therefore, although *Uca* promoted *Spartina* growth on a similar scale as other studies, this study was not able to capture a similar effect on sediment deposition. However, with time, ecogeomorphic theory suggests that *Uca* should have a positive density-dependent influence on sedimentation.

In addition to having no significant impacts on the aboveground component of vertical accretion (i.e. sediment deposition), *Uca* had no effect on belowground components of vertical accretion. One such component is belowground organic matter contribution by plants. The continued existence of belowground organic matter is critical to maintaining elevation. *Uca* burrowing can accelerate decomposition belowground organic matter as burrows can bring oxygen beneath the marsh surface (Thomas and Blum 2010). In the current study, *Uca* had no effect on decomposition. While burrows may increase oxygen penetration belowground, this change is extremely localized, occurring only within 2 mm of burrows (Michaels and Zieman 2013). Thus, I was unable to capture the effect of *Uca* burrowing on decomposition, because crabs didn't burrow within 2 mm of the decomposition bags. In addition to the continued existence of belowground organic matter, root production is an important component of vertical accretion. Although other researchers have found a negative relationship between *Uca* and root production because of increasing nutrient access and shifting plant allocation of resources aboveground (Bertness 1985; Holdredge et al 2010; Thomas and Blum 2010), I found no such effect. Neither root production nor standing stock belowground root biomass was influenced by *Uca*. Because *Uca* had no impacts on above- or belowground components of vertical accretion, this study indicates that they may not have a significant impact on vertical accretion, in isolation.

While *Uca* may have no effect on vertical accretion in isolation, *Sesarma* can have significant negative impacts on both above- and belowground components of vertical accretion. *Sesarma* grazing drastically reduced aboveground plant biomass (Figures 9A & 9B; Holdredge et al. 2009). Although a subsequent decrease in sediment deposition was expected, the opposite was detected in this study. In areas completely grazed by *Sesarma*, sedimentation rates were higher than anywhere else measured (Figure 7A). This is counter to the predictions of ecogeomorphic models of saltmarsh accretion, which demonstrate a positive relationship between plant biomass and sedimentation (Friedrichs and Perry 2001, Morris et al. 2002, Fagherazzi et al. 2013a). One explanation for this trend may be that a portion of the inorganic sediment deposited in these areas is resuspended from the marsh surface, not delivered by the tides. The relationship between marsh plant biomass and sediment deposition only accounts for sediment coming in with the flooding water, not sediment that is resuspended off the marsh surface. Thus, our measurements of sedimentation in areas grazed by *Sesarma* may be confounded by marsh surface sediments. In areas denuded of vegetation, soil strength was much weaker than vegetated areas (Figure 7B), suggesting greater potential for surface sediments to be resuspended by tidal scour and deposited onto the plates used to measure sedimentation (Fagherazzi et al. 2013b).

Another potential explanation for these counter-intuitive results is bioturbation by *Uca* (Figure 14). *Sesarma* grazing, which results in large areas of grass die-back, facilitates the establishment of high densities of *Uca* in these unvegetated areas (Smith 2015, Figure 8). Without vegetation, the soil is weaker, making it easier for *Uca* to burrow (Bertness and Miller 1984) and creating preferable habitat (Smith 2015). Across the survey sites, *Uca* burrow densities were higher in the areas denuded of vegetation (Figure 8). Furthermore, *Uca* burrowing activities can cause suspension of sediment from the marsh surface (Smith and Green 2015), which supports the idea that sediment measured on the sediment plates was from the marsh surface, not the water column. Additionally, higher *Uca* burrow densities combined with weaker soil strength in areas grazed down by *Sesarma*, may have resulted in crabs excavating their burrows directly onto sediment plates, further confounding our measurements of sedimentation rates. Therefore, while *Uca* may have an indirect accretive effect on marsh geomorphology in isolation, in areas of high *Sesarma* grazing, it may instead have an erosional effect.

Sesarma also negatively influenced belowground components of vertical accretion. *Sesarma* grazing reduced belowground biomass (Figure 11A), similar to other studies (Coverdale et al. 2012). Through continued reduction of belowground biomass, *Sesarma* grazing can decrease contribution of belowground organic matter. However, *Sesarma* had no effect on root production in this study. In the manipulative experiment, root production measured plant allocation of resources towards belowground growth, because crabs could not access roots in the ingrowth bags. Similarly, based on root-to-shoot ratio, there’s further evidence that *Sesarma* grazing doesn’t influence allocation of resources towards above- or belowground growth. When plants are grazed, two defense strategies can be utilized: overproduction of biomass or chemical defense (Herms and Mattson 1992). *Sesarma* negatively impacted aboveground *Spartina* production and had no impact on belowground production, which indicates that plants are instead investing in chemical defenses, rather than producing more biomass. However, *Sesarma* did reduce belowground biomass, based on analysis of cores. Consumption of roots over longer periods, combined with plants investing in chemical defense over biomass production, could lead to an overall decrease in organic matter accumulation through continued reduction in standing stock of belowground biomass.

Sesarma also reduced soil strength, which poses a threat to marsh stability. Edge erosion is a major source of marsh loss and contraction (Mariotti and Fagherazzi 2010; Tonelli et al. 2010; Fagherazzi et al. 2013b). At four of the five survey sites, the areas denuded of vegetation existed at the marsh edge, spanning a distance up to 3 m wide. With low soil strength in these areas via *Sesarma* grazing belowground, surface sediments are more susceptible to erosion (van Eerdt 1985; Fagherazzi et al. 2013b; Vu et al. 2017). Erodibility is further enhanced with high densities of *Uca* burrows, which weaken the sediments even more through bioturbation and resuspension, and can ultimately lead to elevation loss (Escapa et al. 2008; Smith and Green 2015). The results of this study suggest *Sesarma* grazing can negatively impact marsh persistence in the face of sea-level rise by promoting edge erosion, and reducing above- and belowground *Spartina* biomass.

The combined effects of *Sesarma* and *Uca* are dependent on the relative level of activity of each species (e.g. high vs. low grazing by *Sesarma*, high vs. low bioturbation by *Uca*). When *Sesarma* grazing intensity is high, the positive effects of *Uca* on plant production are masked. *Sesarma* grazing led to increased burrow densities (Figure 8; Smith 2015). In these large denuded areas, *Uca* can prevent *Spartina* seedling establishment, and ultimately plant recolonization of denuded areas (Smith and Tyrell 2012). Thus, high levels of *Sesarma* grazing combined with *Uca* burrowing, may have prolonged negative effects on salt marsh persistence with sea-level rise, by removing vegetation and indirectly preventing its recolonization. Additionally, *Uca* burrowing in these unvegetated areas can lead to sediment resuspension and subsequent elevation loss (Smith and Green 2015). Therefore, positive effects of *Uca* on aboveground *Spartina* biomass are masked when a cascade of events via intense *Sesarma* grazing occurs, resulting in *Uca*-induced erosion. Ultimately, *Uca*, which can positively influence salt marshes by facilitating primary production, can also have negative impacts on salt marsh persistence with sea-level rise depending on the intensity of *Sesarma* grazing.

However, when *Uca* exists when *Sesarma* grazing intensity is low, *Uca* may ameliorate the negative impacts of *Sesarma* grazing by facilitating aboveground *Spartina* growth. In the cage experiment, aboveground plant biomass was higher when *Uca* and *Sesarma* were caged together than when *Sesarma* was by itself (Figure 9A), suggesting that the facilitative effects of *Uca* may mitigate the negative impacts of *Sesarma* grazing aboveground. *Uca* ameliorates the stress of other *Spartina* grazers (Gittman and Keller 2013), and the results of this study suggest they may do the same with *Sesarma*.

Therefore, marshes with low *Sesarma* grazing intensity, may be better equipped to respond positively to sea-level rise than marshes with high *Sesarma* grazing intensity.

Conclusions

The continued provision of ecosystem services by salt marshes relies on their ability to keep pace with accelerated sea-level rise through vertical and lateral movements (Barbier et al. 2011; Kirwan and Megonigal 2013; Weston 2014; Kirwan et al. 2016). While the importance of marsh plants, such as *Spartina*, in promoting marsh stability and accretion have long been demonstrated (Morris et al. 2002; Friedrichs and Perry 2001; Fagherazzi et al. 2013a; Fagherazzi et al. 2013b), I show that animals can indirectly influence geomorphic processes, through their interactions with marsh plants. While facilitation of plant production by *Uca* isn't enough to cause geomorphic change, based on the results of this study, herbivory by *Sesarma* can have extremely negative impacts on marsh persistence as sea-level rises, through increased erosion susceptibility and reduced contribution of roots belowground. However, *Uca* may counter the negative impacts of *Sesarma*, when *Sesarma* populations are low. Alternatively, when *Sesarma* populations are high, *Uca* burrowing may accelerate *Sesarma*-driven elevation loss (Smith and Green 2015) and erosion (Escapa et al. 2008; Fagherazzi et al. 2013b). While the direct impacts of animals on the physical shape of an ecosystem have been well-studied (Jones et al. 1994; Butler 1995; Naiman et al. 1988; Vu et al. 2017), this study demonstrates that their indirect impacts can also be important. Thus, the incorporation of animals and their population estimates into ecogeomorphic models may help produce a more holistic understanding of how salt marshes will respond to a rising sea in a changing climate.

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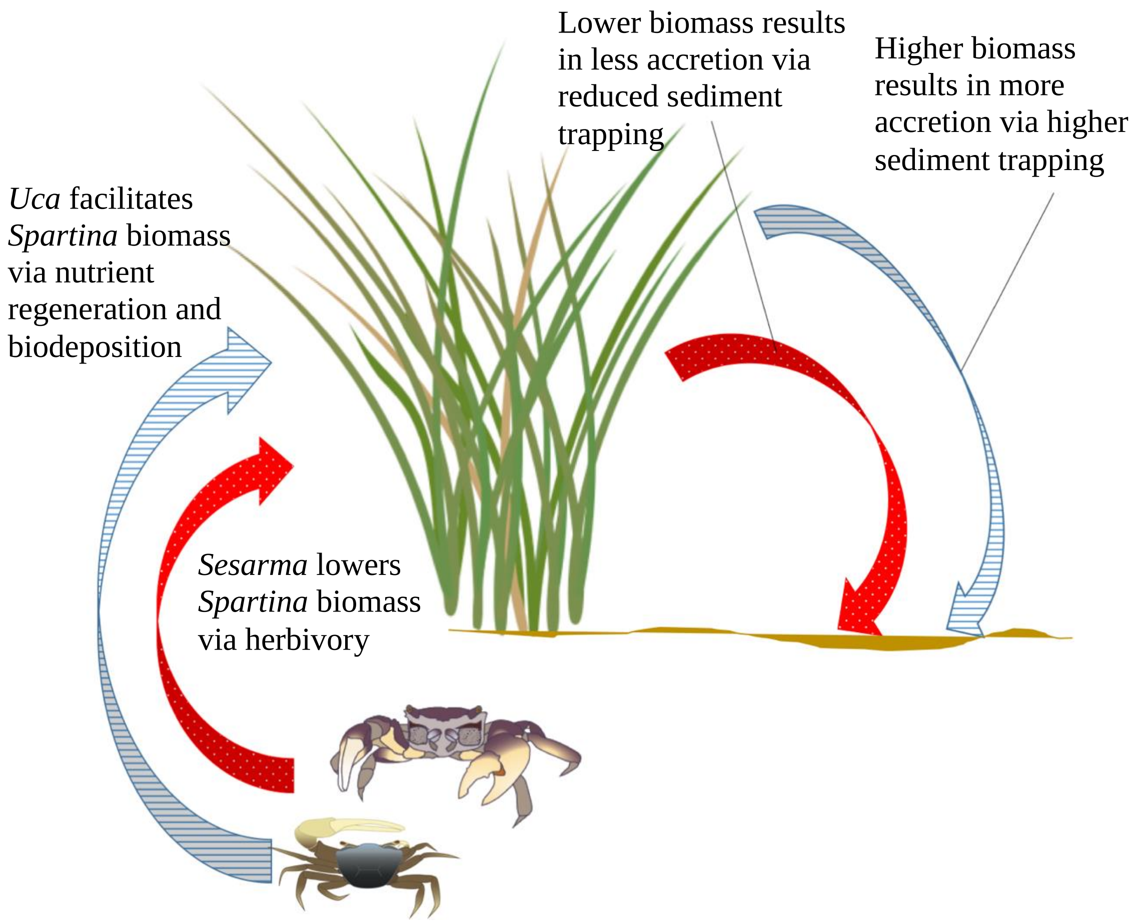


Figure 1: Conceptual diagram for the potential effects of two crustacean species, the marsh fiddler crab (*Uca pugnax*), and the purple marsh crab (*Sesarma reticulatum*) on salt marsh geomorphic processes through their interactions with *Spartina alterniflora*. Images courtesy Tracy Saxby, IAN Image Library and Lauren Huey.

Table 1: Sites selected for surveys and field manipulation. * indicates site used for field manipulation.

City, State	Location	Marsh Name	Latitude, Longitude	Notes
Wellfleet, Massachusetts	Cape Cod National Seashore	Gut Marsh	41.930871 N -70.068266 W	National Park
Prudence Island, Rhode Island	Narragansett Bay	Nag Marsh	41.625476 N -71.326034 W	National Estuarine Research Reserve
Nassawadox, Virginia	Eastern Shore of Virginia	Lower Phillips Creek	37.453680 N -75.835666 W	Long-Term Ecological Research Site
Machipongo, Virginia	Eastern Shore of Virginia	Boxtree Marsh	37.394436 N -75.870237 W	Long-Term Ecological Research Site
Seaford, Virginia	Goodwin Island		37.215953 N -76.404900 W	National Estuarine Research Reserve
Cape Charles, Virginia*	Cushman’s Landing		37.174337 N -75.942386 W	Long-Term Ecological Research Site

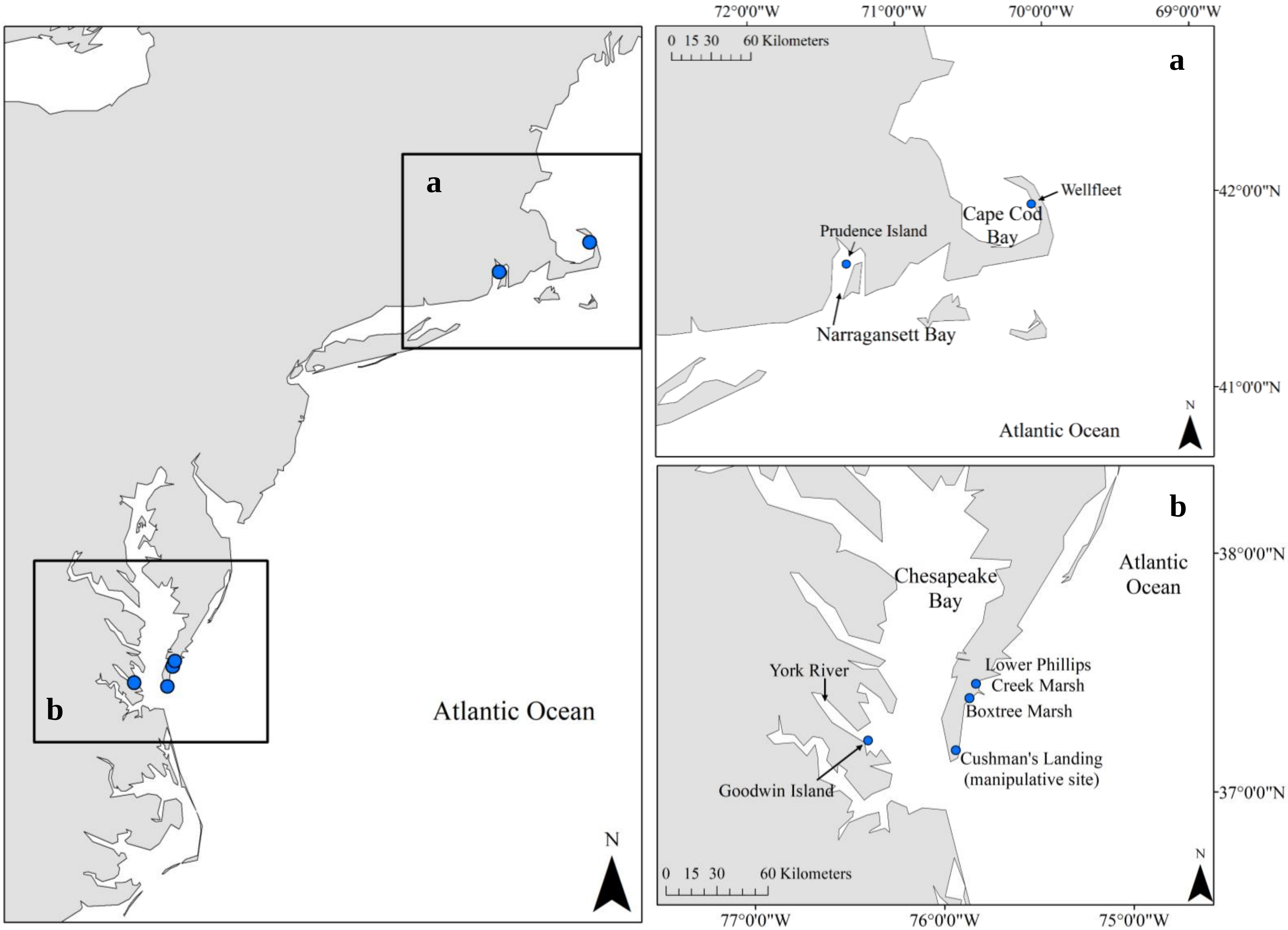


Figure 2: Map of survey and field manipulation sites

Figure 3: *Sesarma* grazing intensity plot types. **A)** denuded **B)** significantly grazed and **C)** no grazing.

Table 2: Site-level characteristics. Mean± standard error (*n* in parentheses) salinity and fixed suspended solids concentrations across sites in survey and field manipulation. * indicates site used for cage manipulation.

Site	Salinity (ppt)	Suspended Solids Concentration (mg L^{-1})	*Uca* plots distance from marsh edge (cm)	*Sesarma* plots distance from marsh edge
Wellfleet	33.8±11.3 (9)	4.48±0.4 (9)	16.4±0.6 (13)	15.3±0.6 (24)
Prudence Island	33.9±7.4 (21)	3.50±0.4 (21)	3.7±0.2 (16)	2.2±0.1 (24)
Lower Phillips	35.4±8.4 (18)	15.19±1.1 (18)	8.8±0.1 (16)	3.0±0.1 (24)
Boxtree	37.3±10.8 (12)	36.34±1.2 (12)	38.8±0.1 (16)	8.4±0.0 (24)
Goodwin Island	20.9±7.0 (9)	15.95±2.0 (9)	9.0±0.2 (16)	0.83±0.4 (24)
Cushman's Landing*	---	102.4±32.2 (15)	---	---

Table 3: Mean± standard error (*n* in parentheses) relative tidal heights (cm) across *Uca* present and absent plots at five survey marshes. Values that share superscripted letters indicate no statistical difference based on ANOVA ($P > 0.05$).

Site	Present	Absent	P-value
Boxtree	39.7±0.4 (8)	42.9±0.5 (8)	**0.01**
Goodwin Island	12.0±1.0 (8)	12.3±0.4 (8)	0.69
Lower Phillips	18.4±1.0 (8)	21.4±1.0 (7)	0.21
Prudence Island	34.5±0.8 (8)	33.8±1.0 (8)	0.59
Wellfleet	34.5±1.9 (8)	36.4±0.5 (5)	0.45

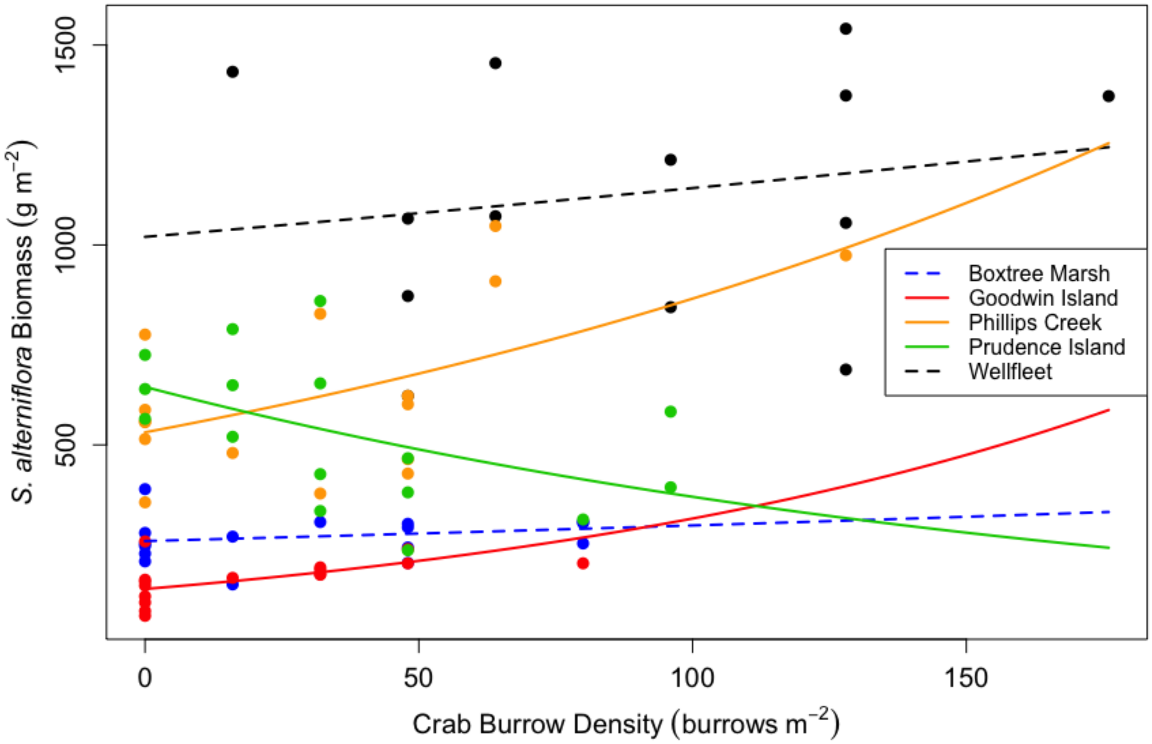


Figure 4: Relationship between *Uca* burrow density and *Spartina* biomass across sites. Data displayed is untransformed, but model was applied to log-transformed data. Trendlines are based on back-calculated estimates from model outputs. Solid lines indicate significant linear relationship ($P < 0.05$); dashed lines non-significant relationships ($P > 0.05$) based on multiple linear regression.

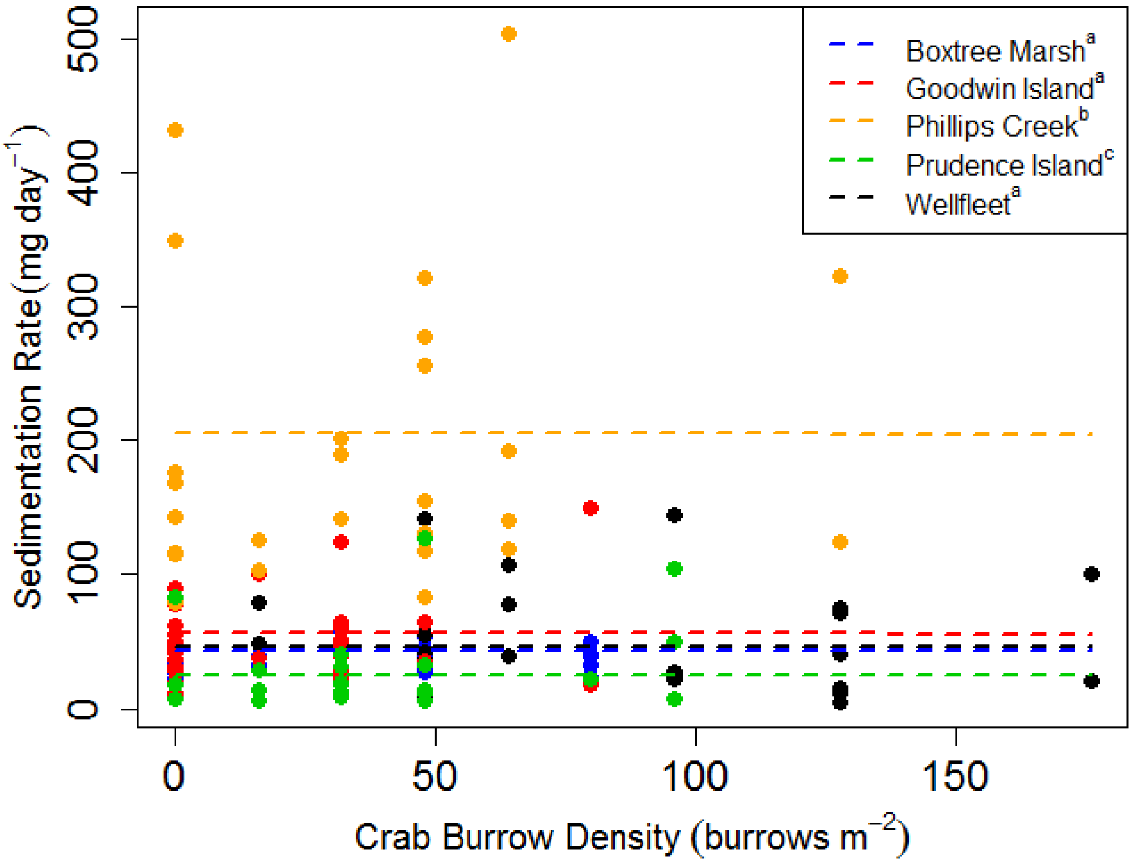


Figure 5. Relationship between *Uca* burrow density and sedimentation rates across sites. Data displayed is untransformed. Models were run on natural log transformed data. Dashed lines indicate non-significant relationships between burrow density and sedimentation rates ($P > 0.05$) based on multiple linear regression Sites that share a superscripted letter have similar sedimentation rates.

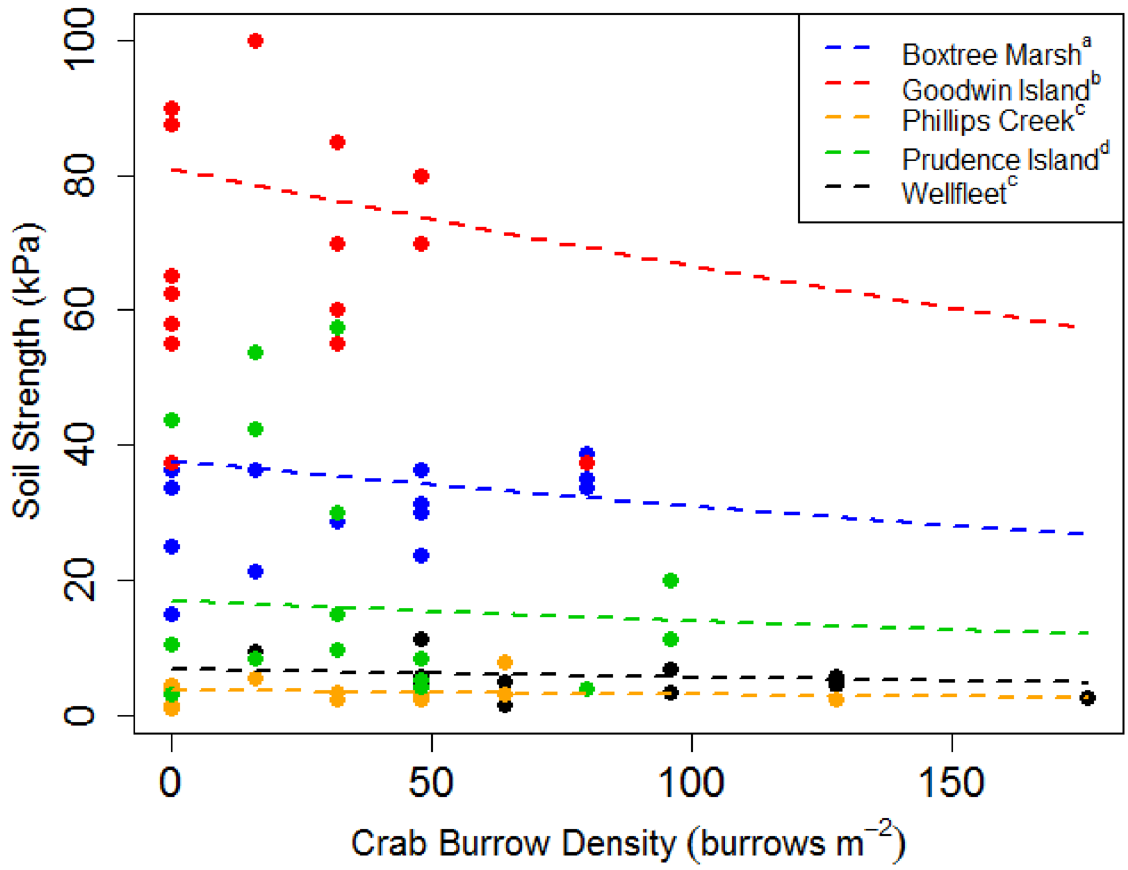


Figure 6. Relationship between soil strength and *Uca* burrow densities across sites. Data depicted is untransformed while models were run on natural log transformed data. Dashed lines indicate non-significant relationships based on multiple linear regression. Sites that share a superscripted letter indicate no statistical difference.

Table 4: Mean± standard error (*n* in parentheses) *Spartina* biomass (g m^{-2}) across *Sesarma* grazing intensity and mean *Uca* burrow density (burrows m^{-2}), averaged across grazing intensity, across sites at field survey marshes. Burrow densities that share a superscripted letter indicate no statistical difference through post-hoc analysis ($P > 0.05$).

Site	Denuded	Grazed	No Grazing	*Uca* burrow density
Boxtree Marsh	0±0 (8)	190.5±29.7 (7)	737.8±59.0 (8)	196±11 (24)^{a}
Goodwin Island	0±0 (8)	274.1±38.8 (8)	714.3±76.8 (8)	99±14 (24)^{b}
Lower Phillips Creek	0±0 (8)	332.2±35.4 (8)	620.0±44.1 (8)	106±9 (24)^{bc}
Prudence Island	0±0 (8)	140.6±15.3 (8)	405.7±29.2 (8)	63±8 (24)^{c}
Wellfleet	0±0 (8)	274.5±43.0 (8)	921.3±129.1 (8)	111±12 (24)^{b}

Table 5: Mean± standard error (*n* in parentheses) relative tidal heights (cm) across *Sesarma* grazing intensity zones at five survey marshes. Lower Phillips site was not sampled for relative tidal heights. Values that share superscripted letters, within site, indicate no statistical difference based on ANOVA.

Site	Denuded	Grazed	No Grazing	P-value
Boxtree	34.9±0.9 (8)^a	38.1±1.7 (7)^a	34.8±1.4 (8)^a	0.17
Goodwin Island	11.4±1.4 (8)^a	16.9±2.9 (8)^a	14.9±1.9 (8)^a	0.22
Lower Phillips	---	---	---	---
Prudence Island	47.3±1.2 (8)^a	45.9±0.9 (8)^a	39.5±1.2(8)^b	**0.0002**
Wellfleet	61.1±2.8 (8)^a	56.7±1.8 (8)^a	54.9±2.5 (8)^a	0.19

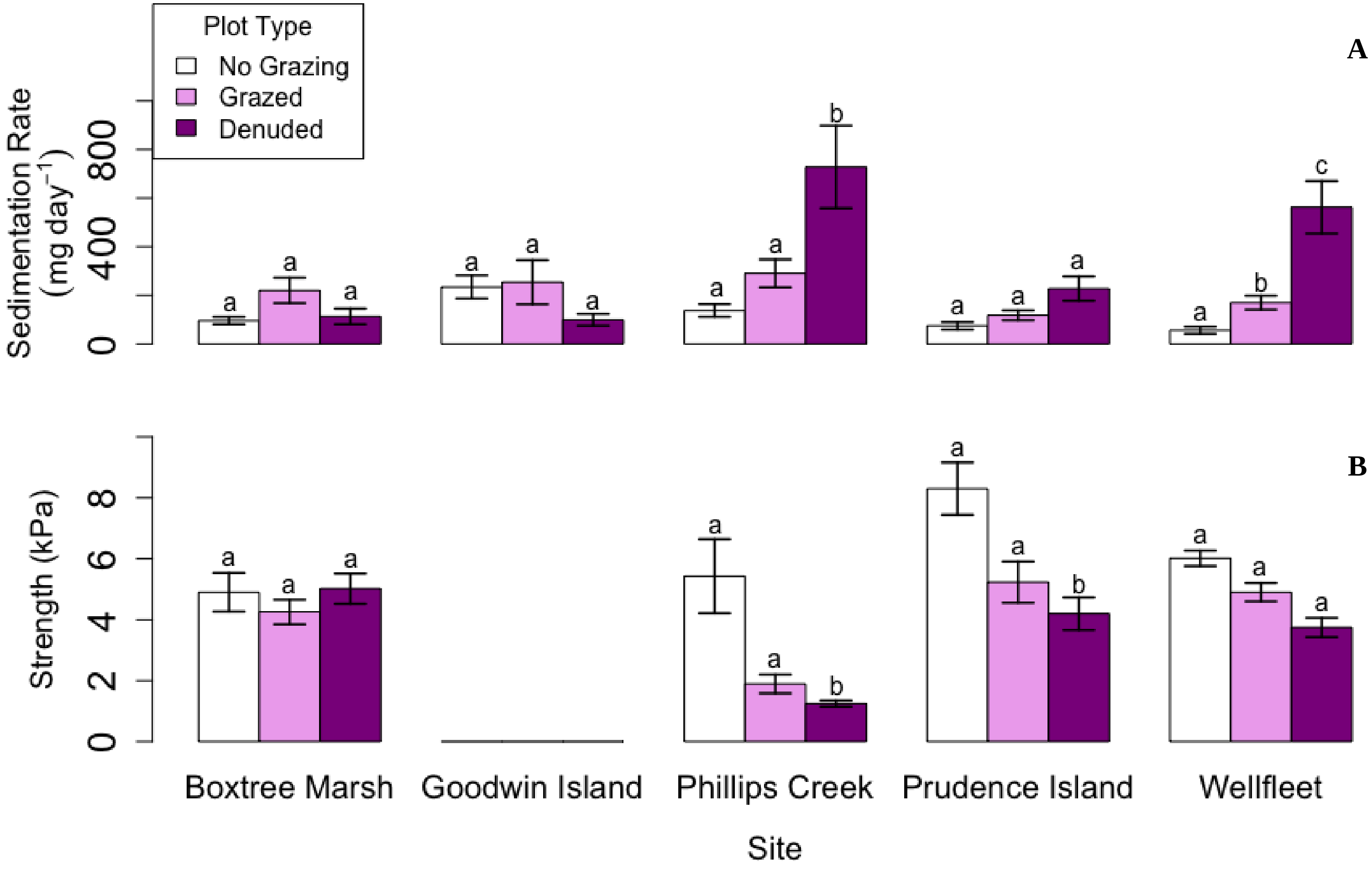


Figure 7: Mean **A)** sedimentation rates and **B)** soil strength across *Sesarma* grazing intensity and sites. Error bars represent standard error. Due to significant interaction between grazing intensity and plot type (P << 0.001), bars that share a letter *within site* indicate no statistical difference. Analyses were performed on long-transformed data. Data above is untransformed.

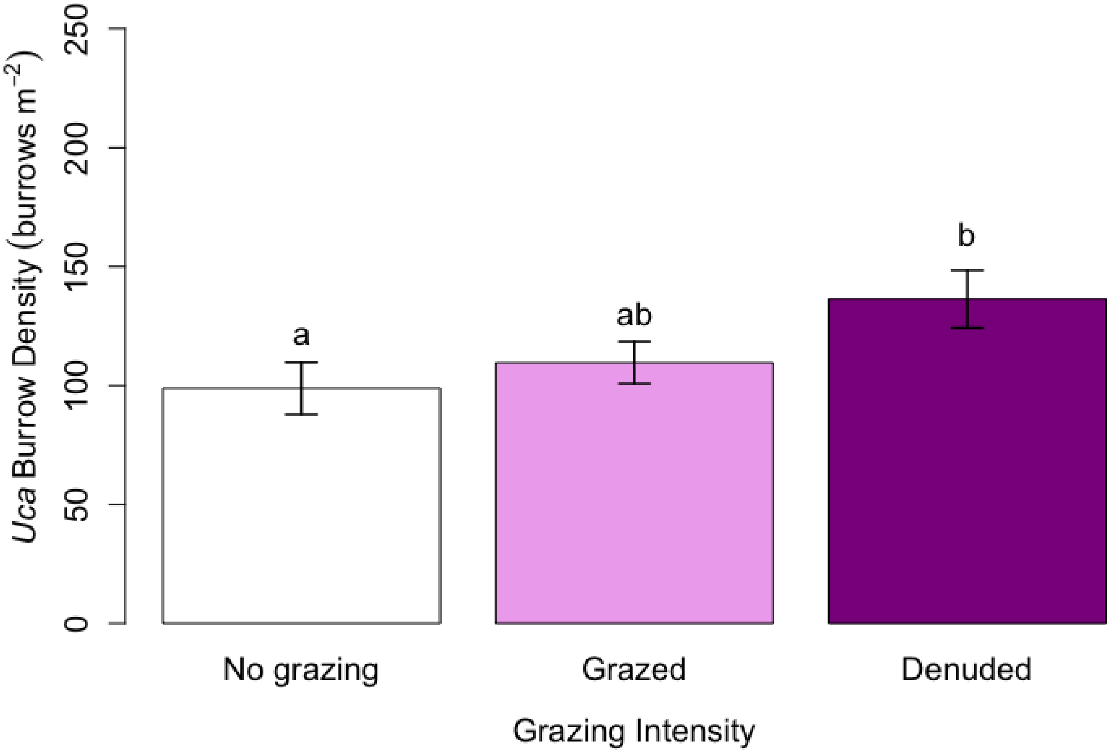


Figure 8: Mean *Uca* burrow density across *Sesarma* grazing intensity (n = 40 per intensity). Bars that share a letter indicate no statistical difference based on post-hoc analysis ($P > 0.05$). Error bars represent standard error.

Table 6: Mean *Sesarma* burrow densities (burrows m^{-2}) across grazing intensity plots and sites. Site densities were calculated from haphazard burrow enumerations.

Site	Denuded	Grazed	No Grazing	Site
Boxtree	12±5(8)	0±0 (8)	0±0 (8)	17.6±5.6 (10)
Goodwin Island	16±4 (8)	2±2 (8)	6±4(8)	4.8±2.4 (10)
Lower Phillips	2±2 (8)	0±0 (8)	0±0 (8)	0±0 (10)
Prudence Island	0±0 (8)	2±2 (8)	4±3(8)	1.6±1.6 (10)
Wellfleet	2±2 (8)	10±3 (8)	0±0 (8)	3.2±2.1 (10)

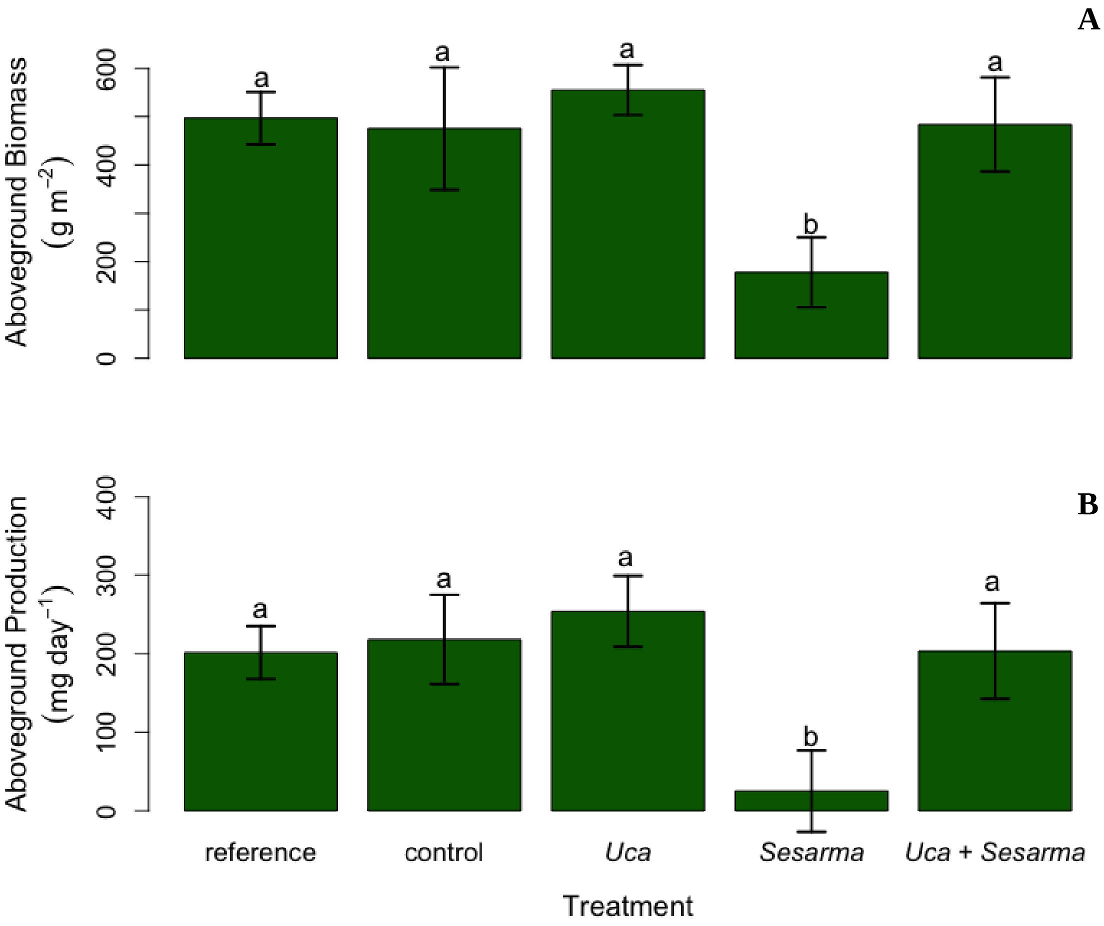


Figure 9. Mean *Spartina alterniflora* aboveground **A)** biomass and **B)** production across cage treatments. Error bars represent standard error. Bars that share letter indicate no statistical difference based on linear mixed effects model.

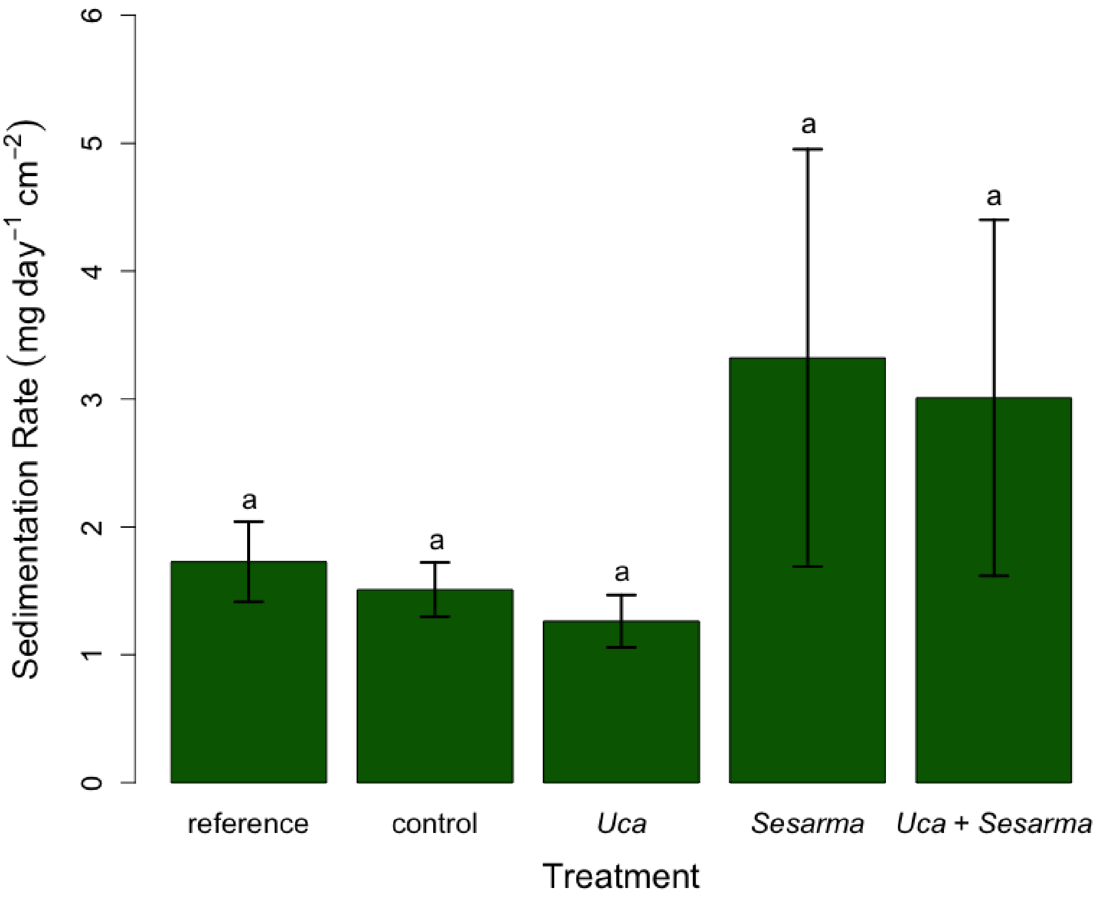


Figure 10: Mean sedimentation rates across cage treatments. Error bars represent standard error. Bars that share a letter indicate no statistical difference, based on analysis of natural log-transformed data in linear mixed effects model.

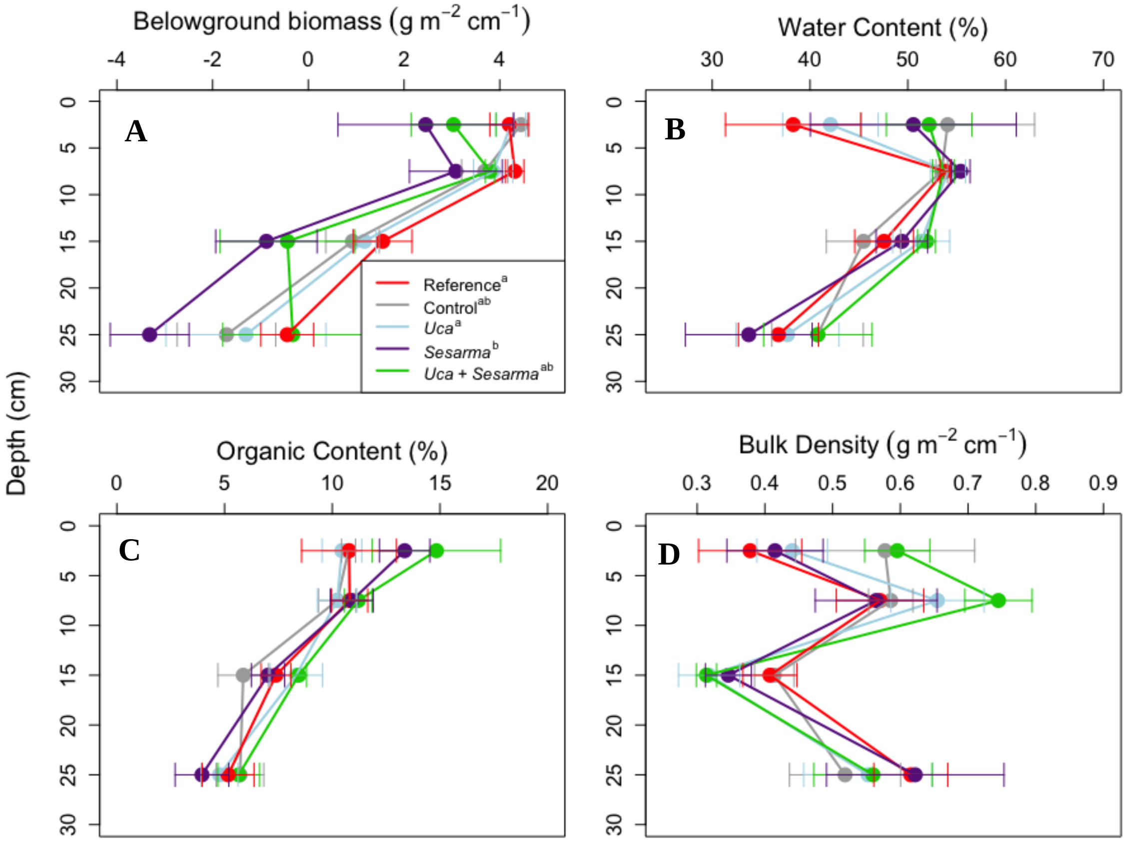


Figure 11: Mean **A)** live belowground biomass (natural log + 0.01 transformed) **B)** water content, **C)** organic content, and **D)** bulk density across cage treatments and depths. Treatments that share letter in the legend indicate no statistical difference based on linear mixed effects model. Responses in plots without a legend have no difference across treatments. Error bars represent standard error.

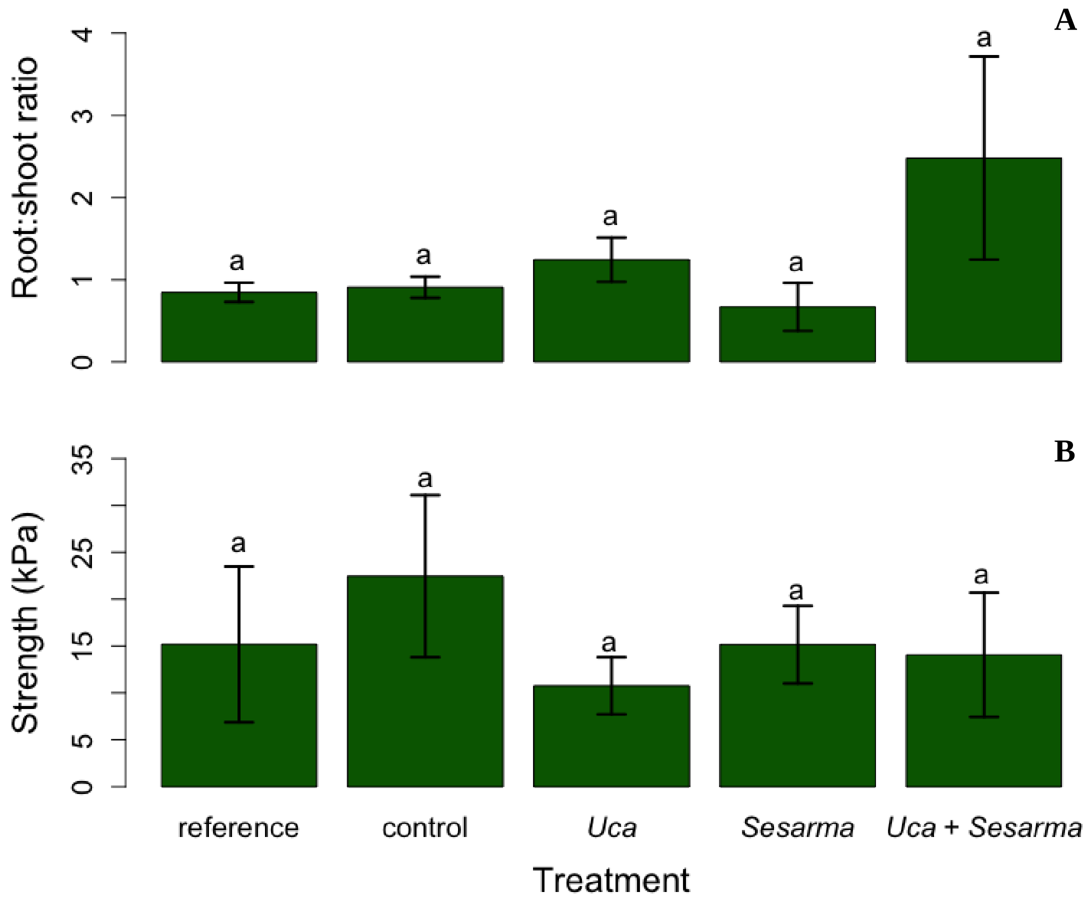
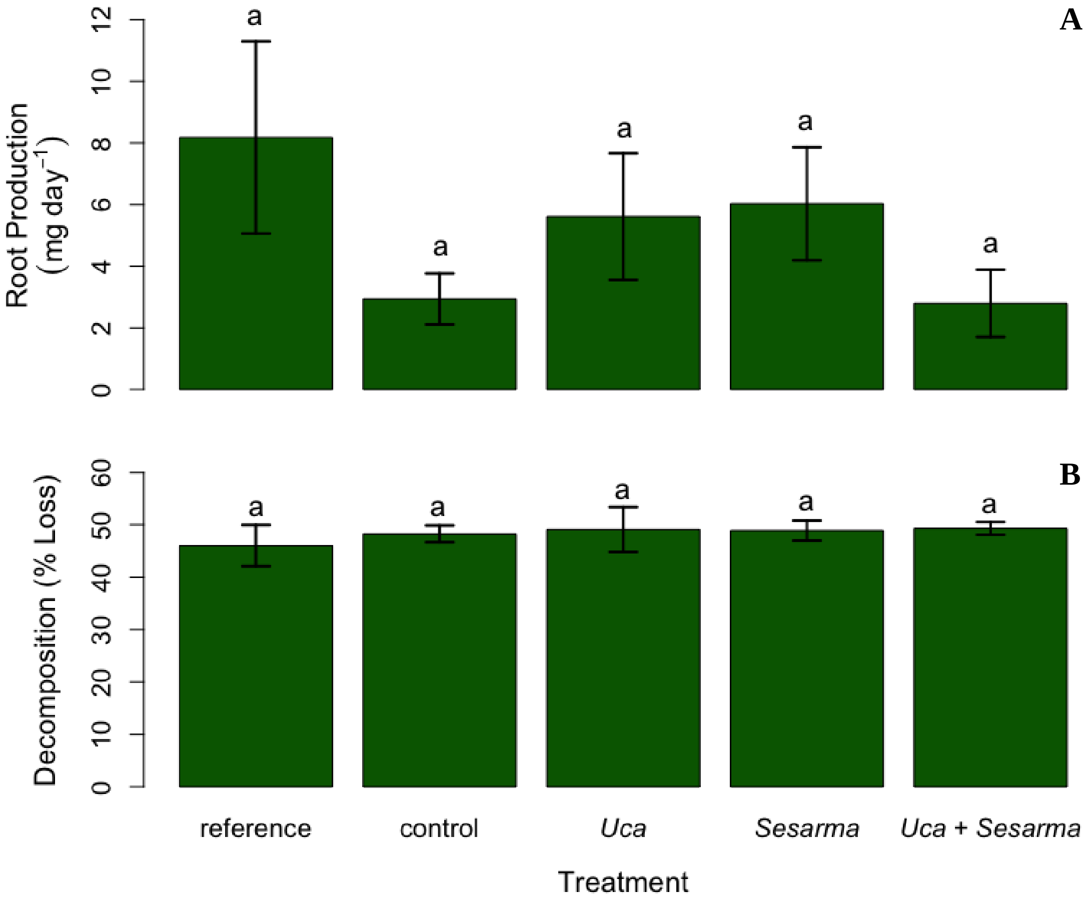


Figure 12: **A)** Mean *Spartina alterniflora* root-to-shoot ratio across cage treatments. Value greater than 1 indicates more roots than shoots, while a value less than 1 indicates more shoots than roots. **B)** Mean soil strength across cage treatments. Error bars represent standard errors. Bars that share a letter indicate no statistical difference based on linear mixed effects model.



Figures 13: Belowground processes across cage treatments. **A)** Mean *Spartina alterniflora* root production and **B)** Mean decomposition of *Spartina* roots and rhizomes. Error bars represent standard error. Bars that share a letter represent no statistical difference based on linear mixed effects model.

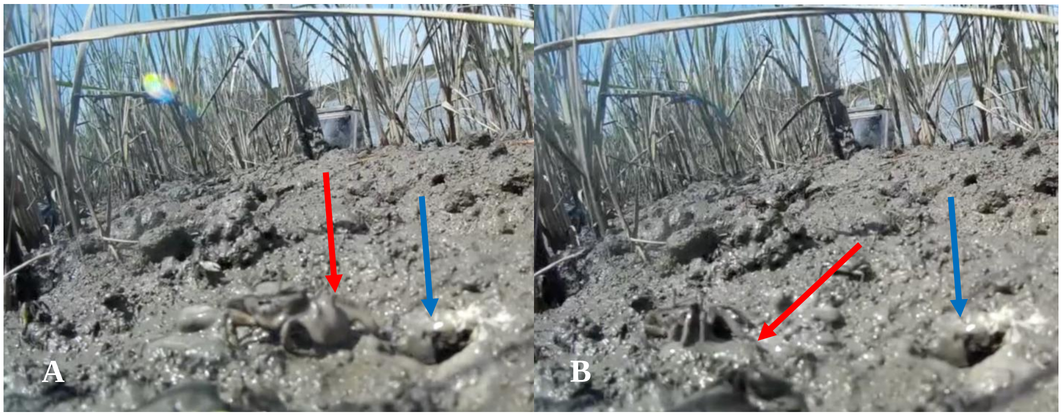


Figure 14: In situ capture of female Uca excavating a burrow. **A)** *Uca* carrying mud from burrow and **B)** mud deposited on marsh surface by *Uca*. Images are 3 seconds apart and captured from a GoPro video. Red arrows point to sediment carried by crab. Blue arrow points to burrow excavated from. Video taken at Lower Phillips Creek marsh, July 2017.