Title: Role of ecological interactions in saltmarsh geomorphic processes

Running title: Ecological interactions and saltmarsh geomorphic processes

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ABSTRACT
Accelerated sea-level rise poses a significant threat to coastal habitats, such as salt marshes, which provide critical ecosystem services. Persistence of salt marshes with rising sea levels relies, in part, on vertical accretion. Ecogeomorphic models emphasize the role of plant production in vertical accretion via sediment trapping and belowground organic matter contribution. Thus, changes in plant production can influence saltmarsh persistence with sea-level rise. However, models of marsh accretion do not consider animal-mediated changes in plant production. We tested how two marsh crabs, *Minuca pugnax* and *Sesarma reticulatum,* which have contrasting effects (facilitation vs. herbivory) on *Spartina alterniflora* production, may indirectly influence sediment deposition and belowground production, through observational surveys and field manipulation. *Minuca* facilitated *Spartina* biomass in some marshes, but not sediment deposition, and had no effect on belowground organic matter contribution, suggesting that in isolation, *Minuca* has little indirect impact on saltmarsh geomorphic processes. *Sesarma* reduced *Spartina* biomass; however, sediment deposition increased, contrary to ecogeomorphic models, likely due to sediment resuspension by *Minuca*. When *Minuca* and *Sesarma* co-occur, the effect on *Spartina* production and sediment deposition depended on the amount of grazing. When *Sesarma* grazing is low, *Minuca* facilitates *Spartina* growth and mitigates the effect of grazing. However, when *Sesarma* grazing is high and vegetation is removed, *Minuca* can resuspend sediment through bioturbation, suggesting the net effect of these species may depend on their relative abundance. This study demonstrates the effects of plant-animal interactions on marsh resilience against sea level rises, are context dependent.

Key words: salt marsh, sea-level rise, ecogeomorphology, fiddler crab, purple marsh crab, vertical accretion, sediment deposition, *Uca pugnax*

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1. INTRODUCTION

Salt marshes are among the most productive ecosystems in the world (Mendelssohn & Morris 2002) and provide important ecosystem services such as storm protection, carbon storage, food production, and tourism (Barbier et al. 2011, Lefcheck et al. 2019). 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 (Morris et al. 2002, Kirwan et al. 2016). Landward migration however, is often inhibited by anthropogenic structures such as roads, sea walls, and houses, causing coastal squeeze (Pontee 2013). Since 14% of the United States shoreline has been hardened (Gittman et al. 2015), understanding the factors that influence accretion is critical to predicting the vulnerability of salt marshes to accelerated sea-level rise.

For vertical accretion, current ecogeomorphic models 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 slow the flow velocity of water, allowing sediment particles to settle out of the water column onto the marsh surface (Friedrichs & Perry 2001). As marsh grass stem density and biomass increase, sediment deposition is enhanced (Friedrichs & Perry 2001, Morris et al. 2002, Fagherazzi et al. 2013a). Therefore, changes in primary production can influence accretion rates. Ecogeomorphic models focus on plant-environment interactions that affect autochthonous and allochthonous deposition, but plant-animal interactions may also be important (Vu et al.

2017). Animals can influence saltmarsh plant production, for example mussels (*Geukensia demissa*) facilitate the growth of *Spartina* (Hughes et al. 2014), while in contrast periwinkles (*Littoraria irrorata*) graze directly on *Spartina* stems (Bertness 1985, Silliman et al. 2005, Coverdale et al. 2012, Failon et al. 2020). Therefore, these ecological interactions merit consideration in studies of marsh accretion. For instance, facilitation of aboveground plant biomass could enhance marsh accretion via increased sediment trapping. Alternatively, herbivory can significantly reduce the abundance and biomass of marsh plants (Silliman & Zieman 2001, Holdredge et al. 2009, Coverdale et al. 2012), and may inhibit vertical accretion. To date, very little research has tested how plant-animal interactions affect physical processes that influence marsh accretion, such as sediment trapping (Elschot et al. 2013, Pages et al. 2018).

In salt marshes along the Atlantic coast of the United States, the Atlantic mud fiddler crab, *Minuca pugnax* (hereafter referred to as *Minuca*) and the purple marsh crab, *Sesarma reticulatum* (hereafter referred to as *Sesarma*) co-occur in the same tidal zone (Seiple 1979, Grimes et al. 1989, Johnson 2014, Wasson et al. 2019). Their direct effects on saltmarsh physical structure have been well studied (e.g., their burrowing activities; Seiple & Salmon 1982, Bertness 1985, McCraith et al. 2003, Hughes et al. 2009, Vu et al. 2017). *Minuca* can increase aboveground biomass of the cordgrass, *Spartina alterniflora* (hereafter referred to as *Spartina*), via nutrient regeneration, biodeposition, and oxygenation of marsh soils (Bertness 1985, Gittman & Keller 2013, Hughes et al. 2014). As a result, *Minuca* may indirectly facilitate sediment trapping by increasing *Spartina* biomass through burrowing activities, and hence increase the aboveground component of marsh accretion. However, burrowing activity by *Minuca* also reduces belowground production and increases decomposition rates at higher densities (Thomas & Blum

2010, Gittman & Keller 2013). *Minuca* activity may therefore have contrasting effects on the above- and belowground components of vertical marsh accretion.

In contrast to the potentially facilitative effects of *Minuca* on aboveground biomass of *Spartina*, *Sesarma* reduces *Spartina* biomass through herbivory on both above- and belowground plant biomass (Seiple & Salmon 1982, Coverdale et al. 2012). While *Sesarma* is also a burrowing species that could facilitate *Spartina* growth similar to *Minuca*, *Sesarma* 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 aboveground sedimentation rates, in addition to preventing contribution of belowground organic matter accumulation, 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 *Minuca* (Gittman & Keller 2013). For instance, in some U.S. Atlantic marshes, overgrazing by *Sesarma* can denude the marsh edge and may lead to marsh loss (Holdredge et al. 2009, Altieri et al 2012, Vu et al. 2017). Given the large geographic distribution of *Sesarma* (Seiple 1979), this crab-driven loss should be widespread in Atlantic salt marshes, but it is not (Wasson et al. 2019). Factors such as *Sesarma* density (Angelini et al. 2018, Wasson et al. 2019) and facilitation of *Spartina* by other species (Gittman & Keller 2013) may prevent *Spartina* die-offs via *Sesarma* herbivory along much of the Atlantic coast.

The overarching goal of this study was to determine how plant-animal interactions may indirectly influence saltmarsh vertical accretion, using sediment deposition and organic matter contribution as proxies for this process. Specifically, we hypothesize that 1) *Minuca* will positively influence vertical accretion by facilitating aboveground *Spartina* biomass and sedimentation, 2) in contrast, *Sesarma* will impede vertical accretion by grazing above- and belowground biomass of *Spartina*, and 3) *Minuca* will ameliorate the negative effects of *Sesarma on Spartina* biomass and ultimately vertical accretion.

2. METHODS

To study the effects of *Minuca* and *Sesarma* on *Spartina* production, aboveground sediment deposition, and belowground organic matter contribution, we conducted two studies: 1) a field survey and 2) a manipulative experiment. The field survey allowed for measurement of responses across a wide range of marshes, with varying hydroperiods and sediment availabilities, to determine if relationships between crab activity, *Spartina* biomass, and sedimentation are consistent across marshes. A caging experiment was used to control confounding factors and to measure process rates (e.g. production, decomposition).

2.1 Effect of *Minuca* on *Spartina* production and sediment deposition

We conducted a field survey of five salt marshes, spanning from Virginia, USA to Massachusetts USA: 1) Goodwin Island (Seaford, Virginia), 2) Boxtree Marsh (Machipongo, Virginia), 3) Phillips Creek (Nassawadox, Virginia), 4) Nag Marsh (Prudence Island, Rhode Island; hereafter referred to as Prudence Island) and 5) Gut Marsh (Wellfleet, Massachusetts; hereafter referred to as Wellfleet) from July-August 2016 (Figure 1). These marshes are dominated by *Spartina*

alterniflora along low elevations, with a band of *S. patens* at slightly higher elevations. The *S. alterniflora* zones are flooded twice daily with the high tides. Differences between sites, such as suspended sediment concentrations and hydroperiod, can be found in the supplementary material (Tables S1, S2, & S3). Along a 100-m span of each marsh, eight 0.0625 m^2 plots were set up in areas with and without *Minuca* burrows each. Because sediment concentration in water decreases with increasing distance from the marsh edge (Friedrichs & Perry 2001, Coleman et al. 2020) each plot was sampled at similar distances from the marsh edge along the channel or creek (Table S2). In each plot, sedimentation, *S. alterniflora* biomass, and soil strength were measured. *Minuca* burrows were also counted.

Sedimentation was measured by deploying two sediment plates, constructed of a pre-weighed 90 mm fiberglass filter secured to a Plexiglas plate staked flush with the marsh surface, in each plot for one week (LeMay 2007). Upon collection, fiberglass filters were dried at 60 °C to a constant mass, weighed, then combusted at 550 °C for two hours and weighed. Plant production was measured, using standing stock biomass as a proxy, by collecting all plants within the plot above the marsh surface. Live and dead stems were washed, separated, counted, then dried at 60 °C to a constant mass and weighed. Soil strength was measured in each plot using a shear vane.

2.2 Effect of *Sesarma* on sediment deposition

To study the effect of *Sesarma* on sedimentation through their grazing of *Spartina*, another set of 0.0625 m^2 plots were set up at the same five sites (Figure 1, Table S1), in three areas, representing a range of grazing intensities: denuded of vegetation (completely grazed; Figure 2), significant grazing (few stems, with shredded and clipped edges, Crichton 1960), and no grazing

(n=8 per area) (Table S3 & S4). Because the negative impacts of increased *Sesarma* densities, and therefore grazing intensity, on *Spartina* are well established (Holdredge et al. 2009, Altieri et al. 2012, Coverdale et al. 2012), we targeted these areas experiencing different levels of grazing intensity, rather than across specific *Sesarma* densities. However, *Sesarma* densities across these plots can be found in Table S4. In each plot, sedimentation, *Spartina* biomass, and soil strength were measured following the same methods described above. *Minuca* burrows were also counted.

2.3 Effects of *Minuca* and *Sesarma* on above and belowground components of vertical accretion

To determine the effect of *Minuca and Sesarma* on above and belowground components of vertical accretion, a caging experiment was conducted at Cushman's Landing, Cape Charles, Virginia USA (Figure 1). This experiment employed a fully factorial design with four treatments: *Minuca* only, *Sesarma* only, *Minuca* and *Sesarma*, and no crabs, with five replicates per treatment. Uncaged reference plots were also created to test the effect of the cage structure on various responses. 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 & Zieman 2001, Holdredge et al. 2010, Gittman & 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 *Minuca* only treatment, 15 adult male and 5 adult female

Minuca were added to the cages. For the *Sesarma* only treatment we simulated a moderate density, with 2 adult *Sesarma* added to the cages, which corresponds to a density of 8 crabs m^{-2} (Holdredge et al. 2009; Table S4). A moderate *Sesarma* density was selected because it represented densities observed at our survey sites (Table S4) and at a high density, crabs could graze all the vegetation in the plot before the end of the experiment and be unable to forage for more beyond the cage. For the *Minuca* and *Sesarma* treatment, 14 adult male *Minuca*, 5 adult female *Minuca*, 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 & Blum 2010). Crabs were caged for 3 months (03 May 2017 – 29 July 2017).

In each cage, aboveground *Spartina* biomass, sedimentation, and soil strength were measured following the same methods as the *Minuca* and *Sesarma* surveys. Sedimentation plates (2 plates per cage) were deployed for nine days, after cage structures were removed. Additional measurements in this experiment included: aboveground production, decomposition, belowground biomass, and sediment characteristics. 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 using an allometric equation of shoot height vs. biomass.

Decomposition was measured by deploying a 5 μm nitex mesh bag filled with 2.5 g of dried *Spartina* roots and rhizomes 5 cm beneath the marsh surface, in each cage at the beginning of the experiment. At the end of the experiment, bags were pulled from the ground and remaining

contents were rinsed through a 500 μm sieve, 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 section 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.

The following soil characteristics were measured, 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, dried at 60 °C to a constant mass and weighed, then combusted in a muffle furnace at 550 °C for 16 hours.

2.4 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 of linear models were transformed to meet assumptions. For the *Minuca* field survey, multiple linear regressions were conducted to determine the effect of *Minuca* burrow density, site, and their interaction on *Spartina* biomass (natural log transformed), sedimentation rates (natural log transformed), and soil strength (natural log transformed). For the *Sesarma* field survey, fixed effects analysis of variance tests (ANOVAs) were used to determine the effect of *Sesarma*

grazing intensity, site, and their interaction on sedimentation (natural log transformed), soil strength (natural log transformed), and *Minuca* burrow density. The 'lsmeans' function in the 'lsmeans' package (Lenth 2016), and a Tukey correction for p-values was used as a post-hoc test to determine where differences occurred among treatments and among sites. For the cage experiment, 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 live aboveground biomass, aboveground production, sedimentation (natural log transformed), decomposition, and soil strength (natural log transformed). The 'multcomp' package (Hothorn et al. 2008), was used for post-hoc analysis. Responses that were measured across depth (belowground biomass, soil characteristics) 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.

3. RESULTS

3.1 Effect of *Minuca* on *Spartina* production and sediment deposition

Minuca density and site interacted to affect *Spartina* biomass ($P = 0.006$, Figure 3A), indicating that there is a site-specific response to *Minuca* burrows. At Goodwin Island and Phillips Creek, plant biomass (natural log transformed) increased linearly with *Minuca* burrows (Goodwin Island: slope = 0.0082, $P = 0.01$; Phillips Creek: slope = 0.0049, $P = 0.025$; Figure 3A). At Boxtree and Wellfleet, there was no relationship between plant biomass and *Minuca* burrow density (Boxtree: slope = 0.0014, $P = 0.56$; Wellfleet: slope = 0.0011, $P = 0.54$; Figure 3A).

Finally, at Prudence Island, *Spartina* biomass decreased linearly with *Minuca* burrow density (slope = -0.0056, P = 0.024, Figure 3A).

There was no relationship between *Minuca* density and sedimentation rates (P = 0.98, Figure 3B), even at sites where plant biomass increased with *Minuca* density (Goodwin Island and Phillips Creek). Site significantly affected sedimentation rates (P << 0.001; Figure 3B). There was no relationship between *Minuca* density and soil strength (P = 0.32, Figure 3B), but a significant effect of site (P << 0.001, Figure 3C).

3.2 Effect of *Sesarma* on sediment deposition

We found a significant interaction between grazing intensity and site on 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 Phillips Creek and Wellfleet were higher in completely grazed areas than areas with no grazing (Figure 4A). 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 4A).

Sesarma grazing intensity also interacted with site to influence belowground soil strength (P = 0.0018; Figure 4B). At Phillips Creek and Prudence Island, mean soil strength was lower in areas completely grazed than in areas with no grazing (Figure 4B). A similar, non-significant, trend exits at Wellfleet (Figure 4B). However, at Boxtree Marsh, grazing intensity had no effect on

mean soil strength (Figure 4B). Due to logistical constraints, soil strength measurements were not collected at Goodwin Island.

Mean *Minuca* burrow density was significantly affected by *Sesarma* grazing intensity ($P = 0.044$; Figure 4C) and site ($P << 0.001$; Figure 4D), 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 4C).

3.3 Effects of *Minuca* 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* production ($P = 0.003$, Figure 5A). Using a Tukey's Honest Significant Difference Test, live aboveground *Spartina* production was lower in the *Sesarma* only treatment, than all other treatments (Figure 5A). Additionally, aboveground *Spartina* biomass was reduced in the *Sesarma* only treatment, compared to other treatments ($P = 0.002$, data not shown).

Nine sediment plates were removed from analysis due to missing >50% of the original filter area through tidal action. Although aboveground biomass and production was affected by treatment, there was no effect on sedimentation rates ($P > 0.05$, Figure 5B). Additionally, treatment had no effect on soil strength ($P > 0.05$, Figure 5C) or decomposition ($P > 0.05$, data not shown).

There was 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 *Spartina* belowground biomass than the *Minuca* only and reference treatments (Figure 6). However, crab treatment did not affect soil characteristics: water content ($P > 0.05$), bulk density ($P > 0.05$), or percent organic content ($P > 0.05$).

4. DISCUSSION

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

4.1 Effects of *Minuca*

Minuca alone did not significantly impact the above- and belowground components of salt marsh vertical accretion, based on results of both the field survey and caging study. *Minuca* can facilitate (Bertness 1985, Thomas & Blum 2010, Gittman & Keller 2013), hinder (Derksen-Hooiberg et al. 2018) or not impact aboveground *Spartina* biomass. Similarly, we found a site-specific response of *Spartina* to *Minuca* burrows, as significant changes in plant production were detected in two of the five sites in the field survey. This indicates that site characteristics may mediate the response of plants to *Minuca* burrowing. For example, the presence of mussels (*Geukensia demissa*), which also facilitate *Spartina* production (Hughes et al. 2014) in zero or low count *Minuca* plots could have prevented a detectable difference in *Spartina* production. At field survey sites where *Minuca* 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 accretion by 156%. In our experiment, *Spartina* biomass was 230% and 173% higher with *Minuca* burrows at two sites, but there was no change in sediment deposition. This lack of influence on sediment deposition rates could be due to measuring sedimentation for a short period of time, which can be highly variable in the short-term. 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. Alternatively, the relationship between plant biomass and sediment deposition or trapping may be site specific (Moskalski & Sommerfield 2012, Reef et al. 2018). For instance, Moskalski & Sommerfield (2012) found that sediment deposition and trapping was not related to plant stem density in a Delaware salt marsh; distance from the creek was more

important and therefore, changes in plant biomass, even within similar distances from the creek, may not have a significant effect on sedimentation.

In addition to having no significant impacts on the aboveground component of vertical accretion (i.e. sediment deposition), *Minuca* had no effect on belowground components of vertical accretion, based on our caging study. Belowground organic matter is critical to maintaining elevation. *Minuca* burrowing can accelerate decomposition of belowground organic matter as burrows can oxygenate the marsh soil (Thomas & Blum 2010). In the current study, *Minuca* 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 & Zieman 2013). Additionally, although other researchers have found a negative relationship between *Minuca* and belowground biomass through increased nutrient access and shifting plant allocation of resources aboveground (Bertness 1985, Holdredge et al 2010, Thomas & Blum 2010), belowground root biomass was not influenced by *Minuca* in this experiment. Because *Minuca* had no significant impacts on above- or belowground components of vertical accretion, this study indicates that they alone may not have a significant impact on vertical accretion, at least in the short term.

4.2 Effect of *Sesarma*

Sesarma grazing drastically reduced aboveground plant biomass in the caging study (Figure 5A), as observed by previous researchers (Holdredge et al. 2009; Angelini et al. 2018). Although we expected a decrease in sediment deposition, we found the opposite. In areas completely grazed by *Sesarma* in the field survey, sedimentation rates were higher than anywhere else measured

(Figure 4A). This is counter to the predictions of ecogeomorphic models of saltmarsh accretion, which demonstrate a positive relationship between plant biomass and sedimentation (Friedrichs & 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. In areas denuded of vegetation, soil strength was much weaker than vegetated areas (Figure 4B), 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, Reef et al. 2018, Mariotti 2018).

Another potential explanation for these counter-intuitive results is bioturbation by *Minuca.* *Sesarma* grazing, which can result in large areas denuded of vegetation (Figure 2), facilitates high densities of *Minuca* within unvegetated areas (Smith 2015, Figure 4C). Without vegetation, the soil is weaker, making it easier for *Minuca* to burrow (Bertness & Miller 1984) and creating preferable habitat for *Minuca* (Smith 2015). Across the field survey sites, *Minuca* burrow densities were higher in the areas denuded of vegetation (Figure 4C), which is similar to the results of other studies (Seliskar & Gallagher 2014, Raposa et al. 2018). When *Minuca* digs or maintains its burrows, it places loose, unconsolidated sediment on the surface, which can be resuspended during tides (Smith & Green 2015, Farron et al. 2020). We hypothesize that the high rates of sedimentation that we measured in unvegetated plots was due to resuspended sediments in the plots and not sediments delivered from the tidal creeks by the tide. Therefore, in areas of high *Sesarma* grazing and complete vegetation loss, *Minuca* may have an erosional effect on sediments.

Based on the field survey, *Sesarma* also reduced soil strength, which poses a threat to marsh stability. Edge erosion is a major source of marsh loss and contraction (Mariotti & 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 (Figure 2). With low soil strength in these areas via *Sesarma* grazing belowground, surface sediments are more susceptible to lateral erosion (van Eerdt 1985, Fagherazzi et al. 2013b, Vu et al. 2017). Erodibility is further enhanced with high densities of *Minuca* burrows, which further weaken marsh soils through bioturbation and resuspension (Farron et al. 2020), and can ultimately lead to elevation loss (Escapa et al. 2008, Smith & 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 (Vu et al. 2017).

4.3 Combined effects of *Minuca* and *Sesarma*

The combined effects of *Sesarma* and *Minuca* depend on the relative level of activity of each species (e.g. high vs. low grazing by *Sesarma*, high vs. low bioturbation by *Minuca*). Based on the field survey, when *Sesarma* grazing intensity is high and vegetation is absent, the positive effects of *Minuca* on plant production is lost. In these large denuded areas, *Minuca* burrow densities were the highest suggesting that fiddler crabs are moving into these habitats. High densities of *Minuca* can prevent *Spartina* seedling establishment, and ultimately hinder plant recolonization of denuded areas (Smith & Tyrell 2012). Thus, high levels of *Sesarma* grazing that lead to complete loss of vegetation combined with *Minuca* burrowing, may have prolonged negative effects on salt marsh persistence with sea-level rise, by removing vegetation and

indirectly preventing its recolonization. Therefore, positive effects of *Minuca* on aboveground *Spartina* biomass are masked when a cascade of events via intense *Sesarma* grazing occurs, shifting the functional role of *Minuca* from facilitative to erosional.

However, when *Minuca* occurs where *Sesarma* grazing intensity is low and vegetation is present, as in our caging study, *Minuca* can ameliorate the negative impacts of *Sesarma* grazing by facilitating aboveground *Spartina* growth. In the caging experiment, aboveground plant biomass was higher when *Minuca* and *Sesarma* were caged together than when *Sesarma* was by itself (Figure 5A), suggesting that the facilitative effects of *Minuca* may mitigate the negative impacts of *Sesarma* grazing aboveground. *Minuca* ameliorates the stress of other *Spartina* grazers (Gittman & Keller 2013), and the results of this study suggest they may do the same with *Sesarma*. Therefore, marshes with low *Sesarma* grazing intensity and fiddler crabs, may be better equipped to respond positively to sea-level rise than marshes with high *Sesarma* grazing intensity.

4.4 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 & 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 (Friedrichs & Perry 2001, Morris et al. 2002, Fagherazzi et al. 2013a, Fagherazzi et al. 2013b), we show that animals may indirectly influence geomorphic processes, through their interactions with marsh plants. While facilitation of plant production by *Minuca* may not be enough to cause

geomorphic change, based on the results of this study, herbivory by *Sesarma* can increase erosion susceptibility. However, *Minuca* may counter the negative impacts of *Sesarma*, when *Sesarma* grazing is low. When *Sesarma* grazing is high and plants are absent, *Minuca* abundances increase and their burrowing may accelerate *Sesarma*-driven elevation loss (Smith & Green 2015) and erosion (Escapa et al. 2008, Fagherazzi et al. 2013b).

The influence of animals on the resilience of coastal wetlands in the face of global change has largely been ignored until recently (He & Silliman 2016, Angelini et al. 2018). Our work highlights that animal-plant and animal-animal interactions may be important to the resilience of coastal wetlands. In instances where overgrazing or other factors leads to plant loss and bare substrate, bioturbators like *Minuca* may increase erosion directly by reworking the sediment and indirectly by preventing recolonization of plants (Smith & Tyrell 2012). For instance, in the Netherlands, the lugworm (*Arenicola marina*) prevents *Spartina anglica* from establishing in bare mudflats (van Wesenbeeck et al. 2007).

Inclusion of animal effects in ecosystem function and resilience also means consideration not only of their presence or absence, but of their abundances. *Sesarma* densities along the U.S. Atlantic coast these can vary from 0 to 170 burrows m^{-2} (Holdredge et al. 2009, Coverdale et al. 2012). *Sesarma* has been observed to convert marsh to mudflat at only the highest burrow (100 burrow m^{-2}; Coverdale et al. 2012) or stocked crab densities (32 crabs m^{-2}; Angelini et al. 2018). These high *Sesarma* densities are not widespread (Wasson et al. 2019, Table S4 this study). In our caging experiment, we used *Sesarma* densities within the range of those observed in our field survey (4-8 crabs m^{-2}; Table S4). At this representative density for *Sesarma*, the presence of *Minuca* prevented *Sesarma* from converting marsh to mudflat. In this way, *Minuca* may prevent erosion and maintain sediment trapping and belowground-biomass contributions by plants that

would be otherwise lost due to *Sesarma* overgrazing. As the relationships between *Minuca* and *Sesarma* depend heavily on the density of each species, knowledge of their densities may be useful for policy makers when considering saltmarsh resilience. While the direct effects of animals may shape an ecosystem (Naiman et al. 1988, Jones et al. 1994, Butler 1995, Vu et al. 2017), we demonstrate that their indirect effects may also be important.

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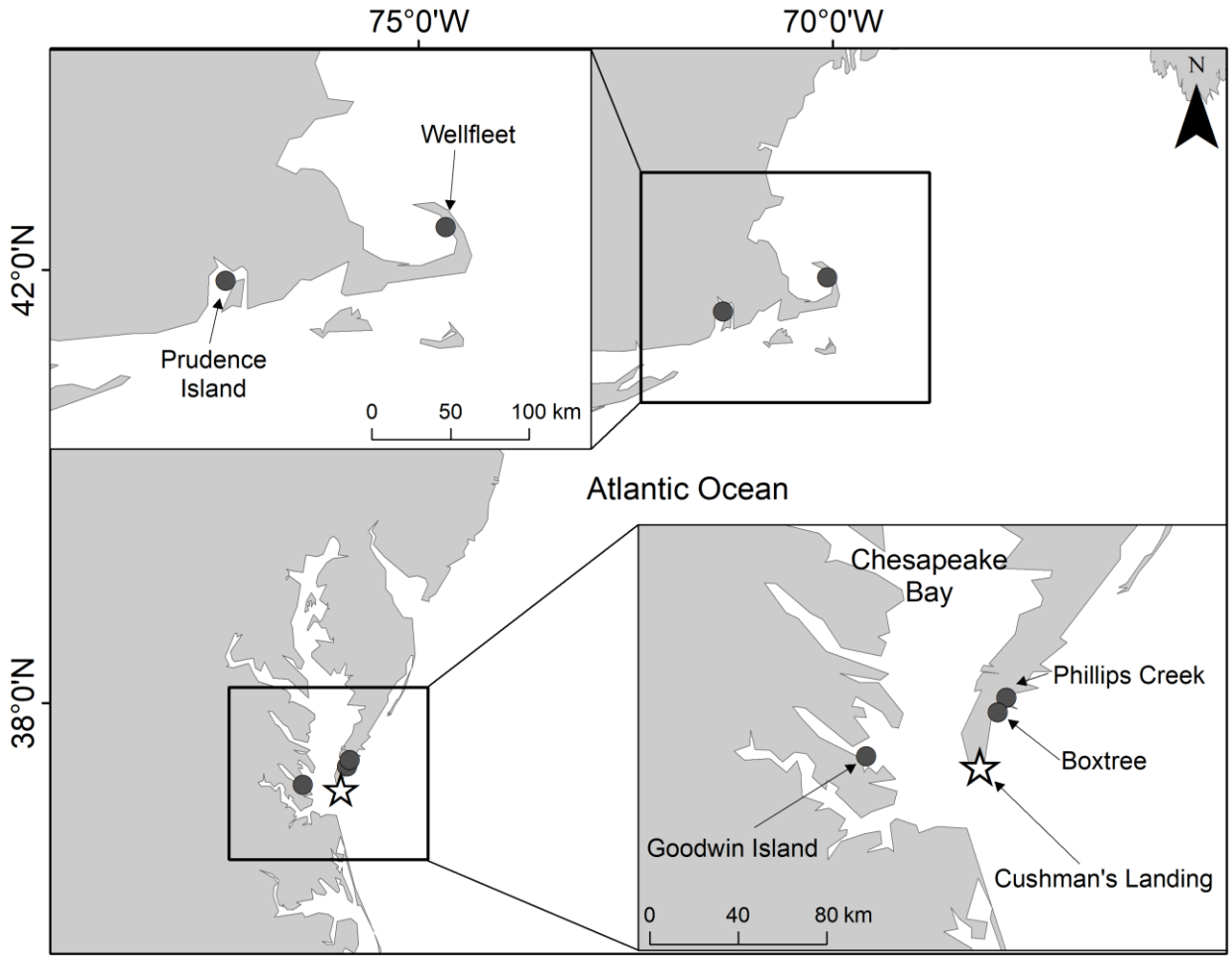

Figure 1: Map of survey and caging experiment sites. Caging experiment site denoted by a star.

Figure 2: A) Zone of marsh denuded of vegetation via *Sesarma* grazing, B) male *Minuca pugnax*, and C) *Sesarma reticulatum*.

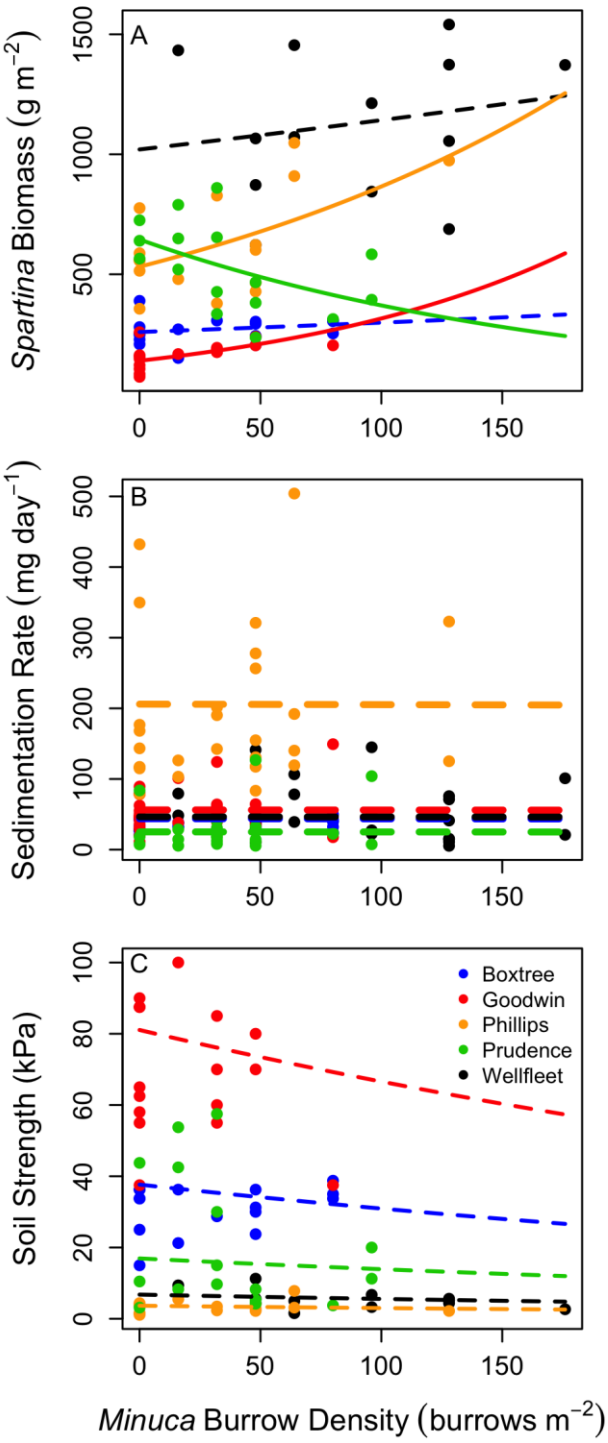

Figure 3: Relationship between *Minuca* burrow density and **A)** *Spartina* biomass, **B)** sedimentation, and **C)** soil strength, across sites. Solid lines indicate significant linear relationship ($P < 0.05$); dashed lines indicate non-significant relationships ($P > 0.05$) based on multiple linear regression on log-transformed data. Trend lines have been back-calculated into normal space for ease of interpretation.

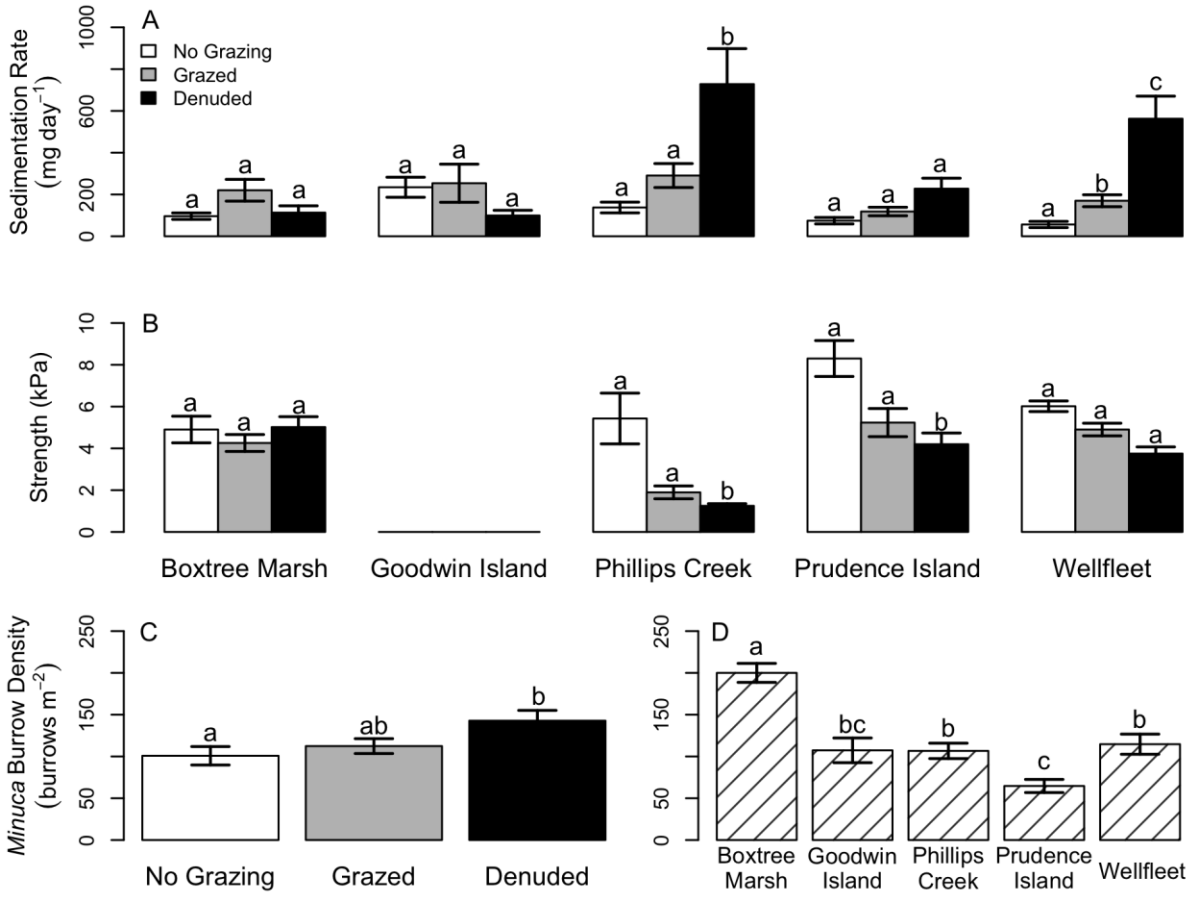

Figure 4: Mean **A)** sedimentation rates, **B)** soil strength, and *Minuca* burrow density across **C)** *Sesarma* grazing intensity and **D)** sites. In A and B, bars that share a letter within a site, indicate no statistical difference. In C and D, bars that share a letter indicate no statistical difference. Hashed bars indicate values are averaged across treatments. Error bars represent standard error. Due to logistical constraints, soil strength was not measured at Goodwin Island.

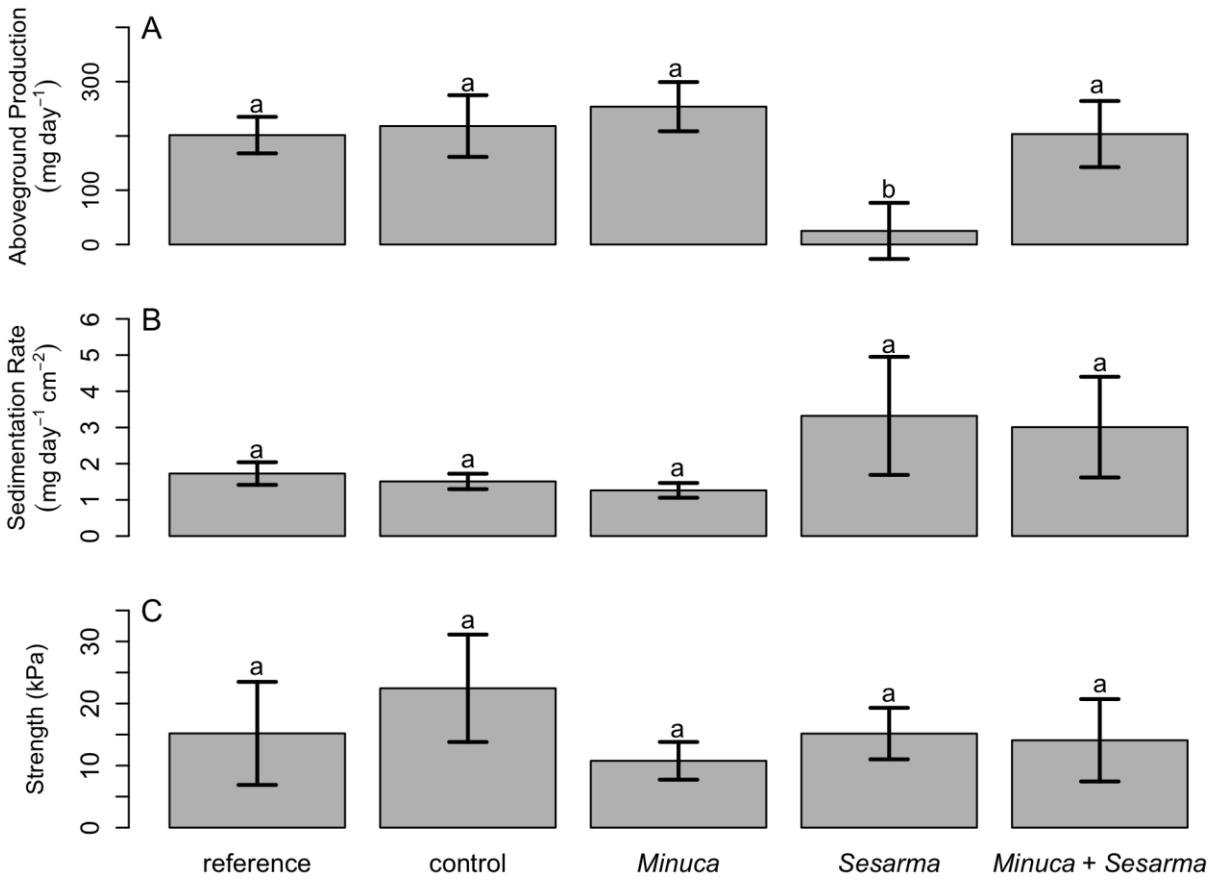

Figure 5. Mean **A)** *Spartina* aboveground production, **B)** sedimentation rates, and **C)** soil strength across cage treatments. Error bars represent standard error. Bars that share letter indicate no statistical difference based on linear mixed effects models.

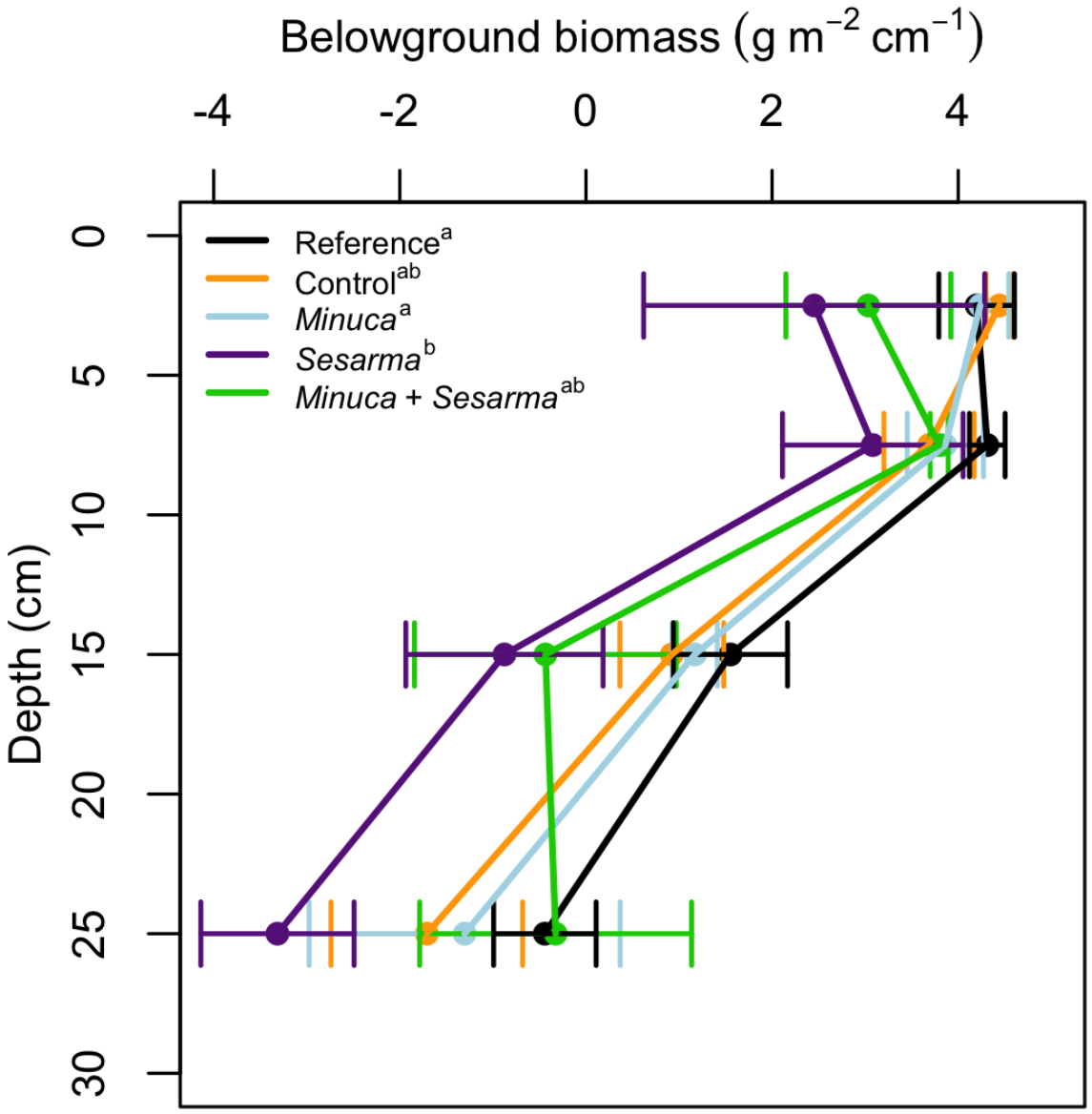

Figure 6: Mean live belowground biomass (natural log + 0.01 transformed). Treatments that share letter in the legend indicate no statistical difference based on linear mixed effects model. Error bars represent standard error

SUPPLEMENTAL MATERIAL

Table S1: Sites selected for surveys and field manipulation. * indicates site used for cage 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	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

Table S2: Site-level characteristics. Mean± standard error (*n* in parentheses) salinity, fixed suspended solids concentrations, and relative tidal heights (as a proxy for hydroperiod) across sites in survey and field manipulation. Relative tidal heights were measured as the difference from the marsh surface to the high water line. * indicates site used for cage manipulation.

Site	Salinity (ppt)	Suspended Solids Concentration (mg L^{-1})	Relative tidal heights (cm)	*Minuca* plots distance from marsh edge (m)	*Sesarma* plots distance from marsh edge
Wellfleet	33.8±11.3 (9)	4.48±0.4 (9)	49.7±2.0 (37)	16.4±0.6 (13)	15.3±0.6 (24)
Prudence Island	33.9±7.4 (21)	3.50±0.4 (21)	40.0±1.0 (39)	3.7±0.2 (16)	2.2±0.1 (24)
Phillips Creek	35.4±8.4 (18)	15.19±1.1 (18)	19.8±1.1 (15)	8.8±0.1 (16)	3.0±0.1 (24)
Boxtree	37.3±10.8 (12)	36.34±1.2 (12)	38.1±0.7 (40)	38.8±0.1 (16)	8.4±0.0 (24)
Goodwin Island	20.9±7.0 (9)	15.95±2.0 (9)	13.5±0.8 (40)	9.0±0.2 (16)	0.83±0.4 (24)
Cushman's Landing*	---	102.4±32.2 (15)	---	---	---

Table S3: Mean± standard error (*n* in parentheses) *Spartina* biomass (g m^{-2}) across *Sesarma* grazing intensity.

Site	Denuded	Grazed	No Grazing
Boxtree	0±0 (8)	190.5±29.7 (7)	737.8±59.0 (8)
Goodwin Island	0±0 (8)	274.1±38.8 (8)	714.3±76.8 (8)
Phillips Creek	0±0 (8)	332.2±35.4 (8)	620.0±44.1 (8)
Prudence Island	0±0 (8)	140.6±15.3 (8)	405.7±29.2 (8)
Wellfleet	0±0 (8)	274.5±43.0 (8)	921.3±129.1 (8)

Table S4: Mean± standard error (*n* in parentheses) *Sesarma* burrow density (burrows m^{-2}) across *Sesarma* grazing intensity and sites. Site densities were calculated from haphazard burrow counts.

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)
Phillips Creek	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)