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**Predation Effects on Mid-marsh Ribbed Mussel Mortality, Cluster Size, and
Facilitation of Cordgrass Growth**

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Abstract

Reciprocal facilitation between *Geukensia demissa*, ribbed mussels, and *Sporobolus alterniflorus*, cordgrass, has a positive effect on salt marsh ecosystems. Mussel clusters enhance cordgrass growth and drought resistance and cordgrass provides attachment and shade for mussel aggregations. Along with benefits for both mussels and cordgrass, the mutualism facilitates increased biodiversity and shoreline stabilization and enhances marsh ecosystem functions. Aspects of mussel patch configuration including cluster size, perimeter and connectivity modulate the reciprocal facilitation effects of cordgrass and mussels on marsh ecosystems. In a northern South Carolina marsh system, mussel patch configuration positively influenced cordgrass biomass. Predation affected mussel patch configuration (e.g., cluster size), and patch configuration affected predation (e.g., mussel mortality). The effects of predation on mussel patch configuration and potential cascading effects on cordgrass biomass facilitation were examined in a field experiment varying predation (caged = no predation, uncaged = predation) and cluster size (0 to 240 m²). Results from the 2 mo. experiment conducted in a mid-marsh elevation indicated no interaction between mussel mortality from predation and facilitation of cordgrass biomass. However, initial mussel cluster size positively affected cordgrass biomass. Predation effects on mussel patch configuration and potential cascading effects on cordgrass biomass within mid-marsh elevations apparently are not short-term, occurring over a few months, but may be more pronounced over longer periods (years) and/or in marsh elevations (low-marsh) more exposed to predators.

Introduction

In estuarine marsh ecosystems, foundation species including grasses and mussels increase biodiversity, both through physical and chemical processes (Angelini et al. 2015). Biodiversity effects occur directly through physical manipulation of the environment and indirectly through facilitation and inter-trophic interactions (Angelini et al. 2015). Recent decreases in estuarine marsh biodiversity has accelerated efforts to conserve and restore marsh environments and focused attention on the roles of foundation species in the process (Halpern et al. 2007).

Evidence suggests positive interactions between species typically are essential to the functioning and stability of estuarine environments, increasing physical stability, resource availability, or both (Stachowitz 2001; Donadi et al. 2013). A well-known positive interaction in salt marshes occurs between *Guekensia demissa*, the ribbed mussel, and *Sporobolus alterniflorus*, marsh cordgrass. In the mussel-cordgrass mutualistic relationship, grasses shade, reducing dehydration, and provide attachment for mussels, potentially reducing predation, and mussels increase nutrient availability, soil stability, and oxygen levels facilitating grass growth (Bertness 1984).

Mussel patch configuration, including cluster size and spatial distribution, determine the extent of the cordgrass-mussel facilitation (Crotty 2018). Cluster size and distribution is affected by mussel loss (e.g., disease, senescence, predation) resulting in a cascade effect on cordgrasses and marsh biodiversity (Crotty & Bertness 2015). Ribbed mussel predators include both aquatic (e.g., *Callinectes sapidus*, the blue crab,) and terrestrial species (e.g., *Procyon lotor*, the North American raccoon, wading birds) (Lin 1989). While cluster size has been shown to be important, the effects of predation on the facilitation between cordgrass and ribbed mussels has not been researched thoroughly.

In this paper, I examine the effects of predation on *G. demissa* on the facilitation of *S. alterniflorus* biomass within a South Carolina salt marsh. Initially, mussel densities and cluster size effects on predator mortality and cordgrass biomass were examined for various marsh elevations. An experiment in which predator exposure and cluster size were manipulated in a mid-marsh elevation was conducted to examine interactive effects on mussel facilitation of cordgrass biomass. Predation is hypothesized to affect mussel patch configuration resulting in a negative indirect effect on the facilitation of cordgrass biomass.

Methods

Study Area

All samples were collected and all experiments were conducted within intertidal salt marshes located on the backside of a barrier island; Waties Island, South Carolina, USA (33.8488° N, 78.5747° W). Low-marsh was characterized by tall (>0.5 m) cordgrass tillers, mid-marsh was predominated by relatively short, <0.5 m, cordgrass, and high-marsh typically contained mixed plant communities and very short, <0.25 m, cordgrass tillers.

Mussel Density

Mussel densities were determined along an ~200 m long transect from low- to high-marsh elevations. All individuals were collected from 0.25 m² quadrats (n = 4) randomly placed within each elevation: low, mid, high, and high-high.

Predation on Mussel Clusters

Predation effects on mussels were examined in an experiment similar to Lin (1989) in which the size of mussel clusters was varied. Locally collected mussels were returned to the lab and glued together at the umbo end using Super Glue into clusters of different size (1, 2, 4, 6, or

8 mussels per cluster). Clusters were maintained in aerated seawater overnight, returned to the field after <24 h, and haphazardly placed within mid-marsh excavations. Although buried in the sediment, all mussels protruded just above the sediment surface. Mussel survival was assessed after ~2 mo.

Mussel Facilitation of Cordgrass Biomass

Effects of existing mussel clusters on cordgrass biomass were determined from 0.0625 m² quadrats collected from low- and mid-marsh elevations. All tillers within quadrats haphazardly selected from sites with or without mussels were cut at the sediment surface, bagged, and returned to the lab for processing. Mussels also were collected from quadrats where present. In the lab all cordgrass was dried at 60 °C for a week and weighed to 0.001 G.

Mussel Predation Effects on Cordgrass Biomass

The predation-facilitation experiment was conducted between June and October 2019. Mussels used in the experiment were collected haphazardly from a nearby rock abutment located at the base of a causeway over Dunn Sound. Only individuals between 30 to 60 mm in shell length, a size still susceptible to predation (Seed 1982), were selected to create mussel clusters. To limit predation on mussel clusters, cages (20 cm dia., 50 cm ht.) were created out of 4.5 mm Nitex mesh. Caged and uncaged mussel clusters were distributed haphazardly within the mid-marsh location at sites with visible cordgrass tillers but no mussels. At each site, sediments were excavated to ~25 cm depth limiting damage to extant cordgrass, and 0, 3, 9, or 15 mussel clusters created in either caged or uncaged treatments (n = 10 replicates of each cluster size and cage treatment). Excavated sediments were processed to break up rhizomes and provide loose sediments in each caged or uncaged treatment. Individual mussels were placed umbo end down

in the sediments within caged or uncaged excavations. GPS coordinates were recorded for each flagged treatment site.

Caged and uncaged treatments were resampled ~4 mos. later before the typical seasonal cessation of cordgrass growth (Shi & Bao 2007). To quantify cordgrass biomass, a .0625 m² quadrat was centered over each caged or uncaged mussel cluster and all above-ground cordgrass collected. In the lab, each cordgrass sample was dried for >4 d at 60°C and dry mass recorded to 0.001 G.

Statistical Analysis

Data were analyzed with general linear (Quinn & Keough 2002) or loglinear models (Agresti 2013). Model assumptions were tested and any violations addressed before reporting results. A one-way ANOVA was used to analyze mussel density differences among elevations (low, mid, high, high-high). Cluster size (1, 2, 4, 6, or 8 mussels per cluster) effects on survival was evaluated in an RxC analysis. A t-test was used to analyze mussel presence or absence effects on cordgrass biomass within low- and mid-marsh elevations. Predator effects on mussel facilitation of cordgrass were evaluated in a two-way ANOVA with cluster size (0, 3, 9, 15 mussels) and cage (caged, uncaged) treatments. Treatment effect sizes or odds ratios were calculated for each test. Analyses were run using SPSS[®] (IBM Corporation, 2016) and various online applications (e.g., Ellis 2009).

Results

Mussel Density

Mussel densities varied from a low of 0 m⁻² to a high of 17 m⁻² along the selected transect (Fig. 1). Densities were not different among elevations ($F_{3,12} = 1.503$, $p = 0.27$), but elevation did have a medium effect on density ($\omega^2 = 0.086$).

Predation on Mussel Clusters

Mid-marsh mortality was dependent on cluster size ($\chi^2_4 = 12.721$, $p = 0.013$), with clusters of only 1 mussel suffering 42% mortality, greater than any other cluster size (Fig. 2). Single mussels were half as likely (Odds Ratio = 0.52) to survive as 8 mussel clusters.

Mussel Facilitation of Cordgrass Biomass

Mussel effects on cordgrass biomass varied between low- and mid-marsh elevations (Fig. 3). The presence of mussels in the low-marsh did not appear to increase cordgrass biomass ($t_7 = 1.761$, $p = 0.122$) although the effect was rather large (Cohen's $d = 1.126$). In the mid-marsh, the presence of mussels did increase cordgrass biomass ($t_{18} = 2.182$, $p = 0.042$), again with a large effect (Cohen's $d = 0.975$). Mussel presence increased cordgrass biomass in the low-marsh by 85.3% and in the mid-marsh by 48.2%. Lack of a meaningful low-marsh mussel effect likely is a result of the small sample size; low-marsh $n = 8$, mid-marsh $n = 20$.

Mussel Predation Effects on Cordgrass Biomass

The size of mussel clusters was the only effect identified ($F_{3, 69} = 3.33$, $p = 0.024$, $\omega^2 = 0.083$). No cage by cluster size interaction ($F_{3, 69} = 1.03$, $p = 0.384$, $\omega^2 = 0.001$) or cage effects were identified ($F_{1, 69} = 0.56$, $p = 0.455$, $\omega^2 = -0.005$). Cluster size has a medium effect on cordgrass growth (Cohen 1988). The cluster size effect primarily is between the 0 and 15 mussel treatments (Figure 4, Tukey's HSD, $p = 0.05$). Percent difference between 0 and 15 mussel treatments was 48.14% on average.

Discussion

Results presented in this paper show that the ribbed mussel does in fact play a role in increasing the growth potential of the above ground portions of cordgrass. The largest difference between the 0 and 15 mussel treatments give insight into this potential, in which the 15 mussel treatments, on average, had nearly 50% more mass than those at the 0 mussel treatments. These results reinforce our first hypothesis, as well as the results of other experiments, in which ribbed mussels play a major role in dictating cordgrass growth and ultimately salt marsh stability (Bertness 1984, Crotty 2018). Our findings also demonstrate that while predation effects cluster size, it does not significantly affect the ability of *S. alterniflorus* and *G. demissa* to engage in facultative mutualism. Due to there not being a significant difference in the growth of *S. alterniflorus* between caged and uncaged treatments, we can reject our second hypothesis.

The role of predation and other population reducing factors on the mutualistic relationship between mussels and cordgrass in salt marshes is largely unexplored. While predation does not seem to be an important factor in this location, other reduction factors may play an important role in areas similar to the one studied in this experiment. Most organisms that live in and interact with the salt marsh potentially have influence on the growth of cordgrass, and ultimately the growth of the marsh. With estuary and marsh restoration becoming a growing topic of concern, more experiments regarding the manipulation of organisms that share relationships must be done, in order to gain a greater understanding of these habitat-modifying processes.

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Figure Legends

Figure 1. Mussel density ($\bar{x} \pm se$) among low-, mid-, high-, and high-high-marsh elevations at Waties Island, SC.

Figure 2. Percent mussel mortality among 1, 2, 4, 6, 8 mussel clusters established within the mid-marsh at Waties Island, SC.

Figure 3. Cordgrass biomass ($\bar{x} \pm se$) for 0.0625 m² quadrats collected in low- and mid-marsh elevations at sites with and without mussels.

Figure 4. Cordgrass biomass ($\bar{x} \pm se$) for 0.0625 m² quadrats collected in a mid-marsh elevation at sites with different mussel cluster (0, 3, 9, 15 mussels) and predator exclusion treatments (caged, uncaged).

Fig. 1

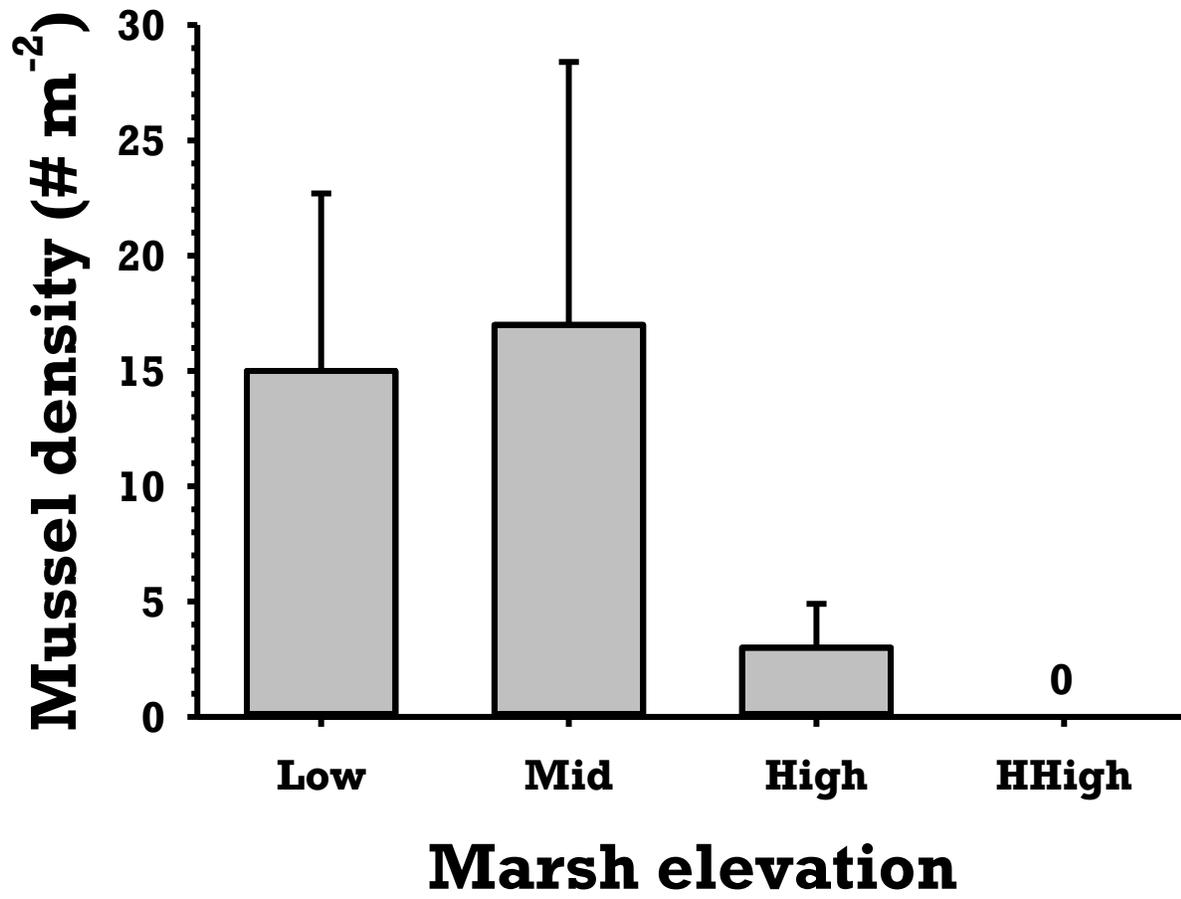


Fig. 2



Fig. 3

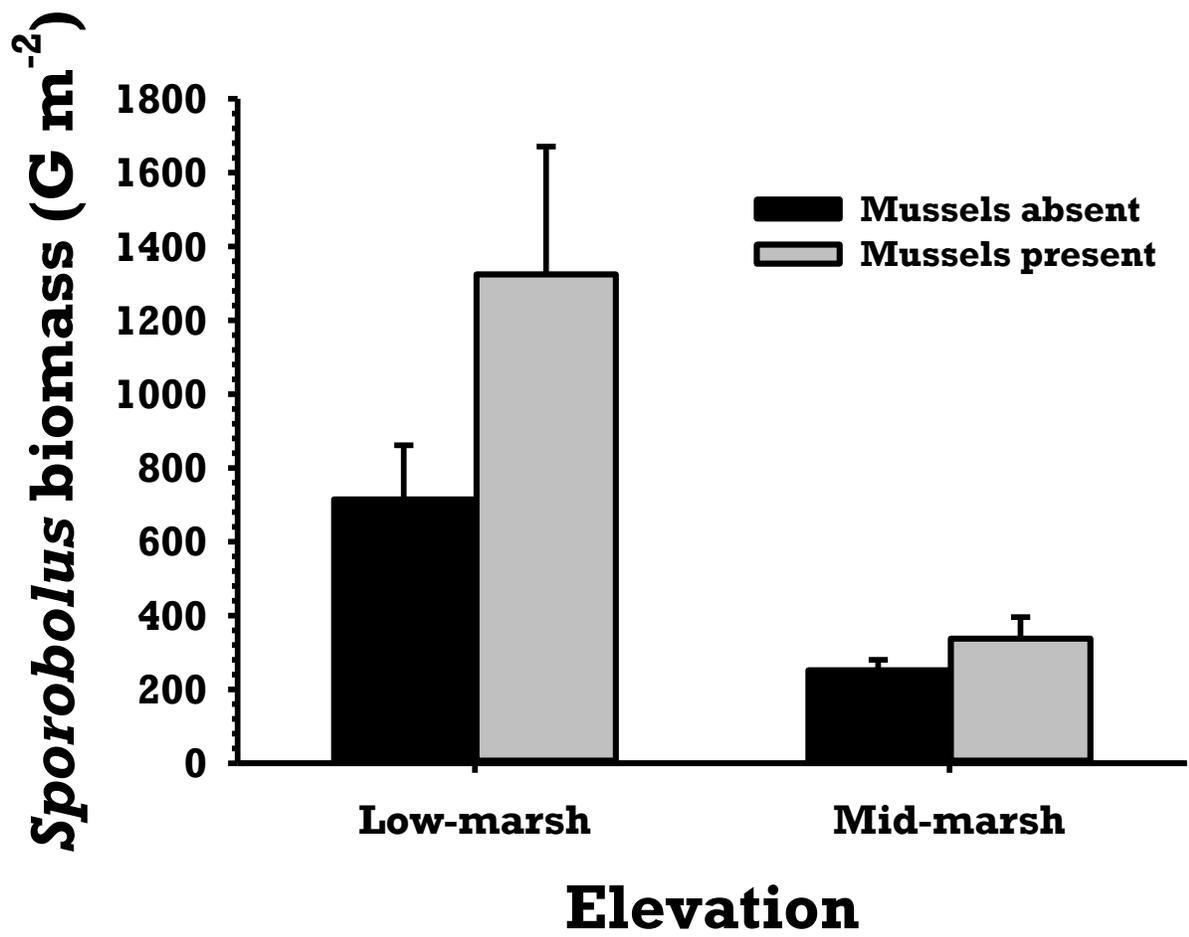


Fig. 4

