Can Co-Occurring Secondary Foundation Species Increase Restoration Success?

by

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Executive Summary:

Our global environment is ever-changing, and the science of conservation and restoration must maintain pace to stay abreast of the most recent and emerging issues. To reverse the negative trends of biodiversity and ecosystem loss, we must address both the symptoms of loss and their root causes. While large-scale change addressing these root causes is perhaps best conducted through well informed policy implementation, local and regional change, in the form of physical restoration projects, can be maximized by capitalizing on the most current science and restoration techniques. For salt marsh ecosystem restoration, this means to increase restoration efficiency and therefore the chances of success, we need to understand the context of, and harness, facilitative species interactions.

Salt marshes, some of the most productive environments in the world, are consistently threatened by environmental change spurred on by anthropogenic perturbations. Coastal eutrophication and development, erosion and pollution, sea level rise and invasive species, are just some of the degradative factors which threaten these ecosystems and require continuing restoration efforts to maintain pace with consistently evolving problems. Our continual adaptation to these problems is likely to be more successful if we modify restoration practices to fit the context of a project and utilize facilitative species relationships as a productivity driver. When multiple facilitative relationships exist, they may generate a cascade of positive benefits, and when restored together, they may provide a synergistic effect that increases the overall success of a restoration project.

In the search for these facilitation cascades, we examined the effects of co-occurring secondary foundation species, (*Crassostrea virginica* and *Geukensia demissa*) on marsh plant restoration (*Spartina alterniflora*), seeking to test whether *C. virginica* provided associational predator defense to *G. demissa* thereby increasing survivorship and enhancing the overall beneficial effect on *S. alterniflora*. A separate but related experiment tested the effects of the marsh periwinkle snail (*Littoraria irrorata*) on recently transplanted *S. alterniflora.* We hypothesized that oysters, positioned above benthic mussels, would provide associational defenses and, through decreased mussel mortality, would provide synergistic effects to *S. alterniflora* productivity while the presence of *L. irrorata* was predicted to have a negative effect on *S. alterniflora* transplants.

To test these hypotheses, we designed a 2x2 factorial transplant experiment, utilizing oysters and mussels as factors assessed at two levels, with and without. The four treatments were spartina control, mussel addition, oyster addition, and oyster and mussel addition. *S. alterniflora* stem density, stem heigh, flowering stems, and mortality within mussel addition treatments were measured to evaluate significant differences among the treatments. To test the effects of *L. irrorata*, exclusion cages were constructed around separate *S. alterniflora* transplants as well as an elevated cage to act as a cage control, and finally a simple *c* transplant control. This exclusion experiment used *L. irrorata* as a single factor, assessed at two levels (with and without) and *S. alterniflora* and *L. irrorata* densities were measured over time.

Our experimental transplants show that an oyster shell canopy fails to produce any synergistic effect or reduce predation on the benthic *G. demissa*. We also present evidence of *L. irrorata* preferentially grazing *S. alterniflora* associated with *G. demissa* addition treatments while avoiding treatments with *C. virginica*. While not statistically significant, we observed the increased productivity of *S. alterniflora* in the mussel addition treatments despite playing host to a numerically larger snail burden. Additionally, our exclusion experiment showed this marsh was under significant top-down control while *L. irrorata* also displayed a significant preference for the cage control treatment.

The findings from this study show the importance of evaluating the context of restoration projects, particularly marsh elevation and predator density, while providing suggestive evidence for the previously uninvestigated relationship between the *L. irrorata* and *C. virginica* as well as their preference for *S. alterniflora* associated with *G. demissa*. The former relationship could act as the basis for a novel restoration method meant to manipulate snail densities in a restoration area to decrease top-down control on *S. alterniflora*. Advancing our ecological understanding in an ever-changing world requires us to understand species interactions and the influence of context dependent environmental and anthropogenic variables under numerous spatiotemporal circumstances. This study illustrates the complexity of species interactions while highlighting the importance of holistic conservation and the potential for novel restoration techniques.

Abstract:

Salt marshes, some of the most productive environments in the world, are consistently threatened by anthropogenic disturbance. To conserve and restore salt marsh ecosystems more efficiently, we need to understand the context of, and harness, facilitative species interactions to increase their chance of success. We examined the effects of co-occurring secondary foundation species, (*Crassostrea virginica* and *Geukensia demissa*) on marsh plant restoration (*Spartina alterniflora*), seeking to test whether *C. virginica* provided associational predator defense to *G. demissa* thereby increasing survivorship and enhancing the overall beneficial effect on *S. alterniflora*. In our experimental transplantation, we show that an oyster shell canopy fails to produce this synergistic effect or meaningfully reduce predation on the benthic *G demissa*. We also present evidence of *Littoraria irrorata* preferentially grazing *S. alterniflora* associated with *G. demissa* while avoiding *C. virginica* associated treatments.

Introduction:

As the Earth's human population continues to grow, so too does our influence and impact on the natural world. As anthropogenic effects manifest themselves in a myriad of ways, many ecosystems are at risk from air, water, chemical and plastic pollution, climate change, and eutrophication to name just a few. As these issues become more apparent and persistent, so too have the motivations to act. The United Nations has declared our current decade, the decade of restoration and implores members to help in, "preventing, halting and reversing the loss of nature" (UN Decade on Restoration, n.d.). As the United Nations rallies support for impacted ecosystems around the world, those areas of decreasing abundance or that are functionally threatened are the focus of restoration efforts. One such ecosystem is the world's highly productive and fragile salt marshes. As the challenges we all face become clearer and resources are spread thinner, it has become apparent that finding the most effective and efficient methods of marsh restoration will require a well-informed interdisciplinary approach.

While there might be debate on the best or most effective policies for protecting marsh ecosystems, their ecological importance in terms of nutrient sequestration, nursery habitat, and wave attenuation has been long understood as has the need to conserve these ecosystems (Broome et al., 1988). As one of the most productive ecosystems in the world, their very existence is somewhat imperiled, particularly in the Southeastern United States where the frequency of hurricanes, coastal development, and eutrophication have all led to marsh declines (Campbell et al., 2022; Carneiro et al., 2024). To help restore the functionality of these areas, many scientists have called for new or more effective approaches to be considered that align with the most recent scientific research and understanding of these dynamic ecosystems (Angelini et al., 2011; Gagnon et al., 2020; Thomsen et al., 2018).

Restoration and management practices that have historically largely focused on single species have begun to shift to, and recognize the importance and incorporation of, foundation species (Angelini et al., 2011; Broome et al., 1988). Recent science, seeking to optimize restoration efforts have been shifting their focus to positive relationships among marsh species and suggest that their incorporation to restoration practices may facilitate greater success (Hammann et al., 2021; Renzi et al., 2019; Silliman et al., 2015). Long-distance facilitations, such as that of *Spartina alterniflora* (smooth cordgrass) and fringing reefs of *Crassostrea virginica* (Eastern oyster), help to attenuate wave energy and prevent erosion in salt marshes, while adding to habitat heterogeneity and suitable settlement structure which serves to increase biodiversity, is one well known relationship (Fivash et al., 2021; Renzi et al., 2019). The relationship between *Geukensia demissa* (ribbed mussel) and *S. alterniflora* is another. Mussels settle on and attach themselves with byssal threads to the roots and rhizomes of cordgrass where they filter nutrients from the water column and deposit them, in the form of pseudofeces, into the sediments immediately adjacent to these roots, thereby providing a direct natural fertilizer and increasing the productivity of cordgrass (Bertness, 1984; Bilkovic et al., 2017). As science continues to elucidate marsh paradigms, discoveries help to inform new practices by our restoration practitioners. In an era where change is the only certainty, the continual accumulation of knowledge is absolutely necessary.

One such discovery that flipped a commonly held paradigm was the discovery of top-down control in salt marshes, which complicated the bottom-up theory, as well as the ecosystem's susceptibility to disturbance (Bertness & Silliman, 2008). At the turn of the last century, it was recognized that the *Littoraria irrorata* (marsh periwinkle), a small snail, actively fed on algae growing from radulation wounds on otherwise healthy cordgrass which then precipitated a top-down trophic cascade within the marsh (Silliman & Zieman, 2001). These wounds would eventually kill the cordgrass, while the snails moved on, leaving behind barren mud flats. In many marshes, after the expansive monoculture of cordgrass is devoured, the mutualistic ribbed mussels, are left behind and struggle to survive, faced with an increased risk of predation and thermal stress (Abbas et al., 2023). These barren areas are prime locations for restoration by transplantation of *S. alterniflora* and by incorporating mutualistic mussels*,* overall success may improve (Angelini et al., 2015; Bertness, 1984; Bilkovic et al., 2017). However, newly replanted areas which are generally spaced at appropriate distances to limit competition between plants may leave mussels susceptible to predation (Silliman et al., 2015).

To harness these relationships and adapt them to restoration practices, we can look to an invasive species in the Wadden Sea for ideas stemming from the natural world. *Magallana gigas* (Pacific oyster), while an invasive species has demonstrated the ability to facilitate the survival of the native mussels, *Mytilus edulis*, by the creation of a vertical oyster canopy under which mussels settle and live, protected from predation by the larger, thicker shelled oysters (Reise et al., 2017). While the invasive oyster initially displaced the native mussels and disrupted the natural distribution and functioning of the marsh, the added habitat heterogeneity paradoxically provided increased suitable settlement substrate, protected from predators, for the mussels to reestablish themselves and thrive alongside their invasive neighbor (Fischman et al., 2024; Reise et al., 2017).

Drawing on our knowledge of current marsh paradigms and the suggestion that co-occurring secondary foundation species can enhance individual effects and biodiversity, we designed a study that sought to experimentally test if the presence of both *C. virginica* and *G. demissa* would generate a synergistic effect for cordgrass productivity (Thomsen et al., 2018). By linking the defensive properties of oysters to an increased survival rate of mussels which, in turn, provide increased nutrient facilitation to cordgrass, we provide the artificial assemblage of a three-tiered facilitation cascade. Through experimental manipulations like this, we hope to reveal previously unrecognized facilitative relationships which may be scaled and incorporated into new restoration techniques.

By abandoning the models of single species management and instead utilizing a multispecies approach that focuses on naturally occurring beneficial relationships and the incorporation of co-occurring foundation species, we may see higher success and increased habitat heterogeneity and overall biodiversity (Thomsen et al., 2018). As an ecosystem with a high capability to sequester carbon and nutrients, while buffering storm effects and providing nursery habitat, the successful restoration of marshes is critical. This experiment is an attempt to push forward this field to maintain pace with the increasing risks associated with accelerated sea level rise and other anthropogenic stressors (Rolando et al., 2023).

Methods:

Study Sites

The field experimental sites were located at two different coastal salt marshes in Carteret County North Carolina. Favorable sites existed on Atlantic Beach near Hoop Pole Creek, off the Newport River on the Salt Tract of North Carolina State Game Lands (SGL), and along Highway 101 near Russell Creek. Die-off areas of a suitable size were located in each of the first two marshes while the latter was rejected due to the severe instability of the marsh soils. The primary experimental sites, one in each marsh, were approximately 5.5m x 2.5m while the secondary site on the SGL was 3.5m x 2.5m with fewer replicates due to the smaller area available. In each location, we utilized for transplantation the form of *S. alterniflora* that was immediately adjacent to the experimental site. For the Hoop Pole Creek site (HPC), we utilized intermediate form cordgrass (75-125cm) while the primary SGL site (SGL A) utilized short form (<50cm) and secondary site (SGL B) used tall form (>1.5m) (Silliman & Zieman, 2001). The form of *S. alterniflora* was associated with marsh elevation where the tall form occupied the lowest elevation with the greatest tidal inundation while the short form was located at the highest elevation and lowest tidal exposure. The exclusion experiment site was immediately adjacent to the HPC site at an intermediate marsh elevation.

Transplant Experiment Design and Setup

The 2 x 2 factorial design tested four different treatments as we looked at the relationships and combined effects of *G. demissa* and *C. virginica* on their own survival rates and the regrowth of *S. alterniflora* at the experimental restoration sites. The four treatments were: (1) control, (2) mussel addition, (3) oyster addition, (4) mussel and oyster addition (hereafter referred to as ‘Both’). All three experimental sites were arranged in a rectangular grid pattern with 50cm spacing between replicates. In the primary sites (HPC and SGL-A) each treatment was replicated (n=10) and arranged into four parallel rows of randomized treatments with ten replicates per row. SGL-B had fewer replicates per treatment (n=6) due to area size constraints and was arranged in four rows of six.

At each site, *S. alterniflora* plugs were transplanted from adjacent or nearby healthy marsh areas, into the mud flat left after the die-off. To the greatest extent possible, initial conditions were maintained with each transplant plug containing three stems with root structure and rhizomes extending approximately 10cm below the ground level. Any horizontally branching roots or rhizomes were severed to better monitor and assess any new growth of above ground stems. Plugs were pressed into spade cut holes at 50cm intervals to prevent nutrient resource sharing among the transplants while in situ mussels, if present, were removed. Transplants were monitored and replanted if dislodged by tidal action.

The mussels and oysters for the treatments were gleaned from the surrounding marsh and fringing reefs. HPC received more mussels (n=8) for its mussel addition and both treatments while SGL-A and SGL-B received fewer (n=6). All mussels were embedded vertically in the soil around the perimeter of the transplant plug however, no measurements of biomass, biovolume, or individual length were assessed for mussels or oysters. Instead, mussel length at HPC was approximated at 10cm while those at both SGL sites were smaller at 8cm. Oyster clusters were fragmented and arranged in such a way as to overlay the mussels and surround the transplanted *S. alterniflora* plug.

Exclusion Experimental Design and Setup

The exclusion experiment was designed to assess the effects of *L. irrorata* on transplanted *S. alterniflora* at two levels, with and without. To do this, I utilized three treatments: (1) control, (2) cage control, and (3) exclusion. Each treatment was replicated (n=10) and arranged in three, treatment specific, parallel rows. All treatments utilized the methods of *S. alterniflora* transplantation from above but without bivalve additions. The exclosures for the cage control and exclusion treatment utilized 3' wide galvanized hardware mesh with grid openings of .25". These were arranged in a cylindrical shape and attached vertically to a single wooden landscape stake and then anchored approximately 50cm into the marsh substrate. The bottom edge of each exclosure in the exclusion treatment were driven into the substrate approximately 2.5cm-3cm to prevent *L. irrorata* from entering the exclosure in the event of soil or exclosure movement. The cage control setup was similar except the hardware mesh cylinder was raised above the marsh surface approximately 10cm to allow free movement.

Assessing Snail and Stem Densities

Each experimental location was established in June, except the exclusion experiment, which was established in early July. This timeline sought to maximize the summer growing season for *S. alterniflora.* At all sites, snail and stem counts were conducted at approximately two-week intervals for the duration of the four-month study. Counted snails were not removed from replicates. In addition to the assessment of these metrics, we monitored mussel mortality and repositioned oyster clusters apparently moved by wind, predators, or tide. At the study's conclusion, in addition to snail and stem counts, we assessed the number of flowering *S. alterniflora* stems per replicate and measured the height of each viable stem.

Statistical Analysis

Stem and snail counts taken at the weekly site visits resulted in a data time series for which we utilized the date as the repeated measure for Analysis of Variance (ANOVA) tests. Stem heights, flowering stems, and mussel mortality were measured at the conclusion of the study and totalized among treatments for assessment.

For statistical significance evaluation of snail counts, we initially assessed the data with a two-way Analysis of Variance (ANOVA) but the residuals violated normalcy. From this point, we used a Kruskal-Wallis test and Dunn's post-hoc to identify significance among treatments. This data was reevaluated with a Repeated Measures ANOVA with Mauchly's Test for Sphericity and both Greenhouse-Geisser and Huynh-Feldt corrections followed by a Pairwise Wilcoxon post-hoc test. Lastly a negative binomial Generalized Linear Mixed Model (GLMM) was applied with Tukey's post-hoc test to corroborate results.

Stem density was evaluated with a Linear Mixed Model and pairwise post-hoc with Bonferroni correction while a Welch's ANOVA with Games-Howell post-hoc were utilized to assess significance in the exclusion cage experiment. To evaluate stem height at HPC and SGL-A, both a Welch's ANOVA and Kruskal-Wallis tests were conducted with no post-hoc tests as the results were not significant. Mussel mortality was evaluated with a Chi-Square and Fisher's Exact test. Shapiro-Wilks and QQ Plots were utilized to evaluate normalcy where appropriate while Levene's, Bartlett's, and Flinger-Killeen Tests were applied to evaluate homogeneity of variance.

Results:

Significance of Time and Treatments Effects

While not measured or statistically evaluated, initial conditions were approximated at all experimental sites to maintain equality within each. For all treatments, time had a significant effect ($p<.0001$, all cases) with increases in both snail counts and stem densities.

The comparison of mussel mortality between the mussel addition and both treatments at HPC and SGL-A (Fig 1) yielded no significant differences ($p=0.7$, $p=0.9$). Stem heights and densities at HPC and SGL-A (Fig 2) yielded no significant effects between treatments ($p=0.5$, $p=.29$ and $p=1.0$ all cases, respectively).

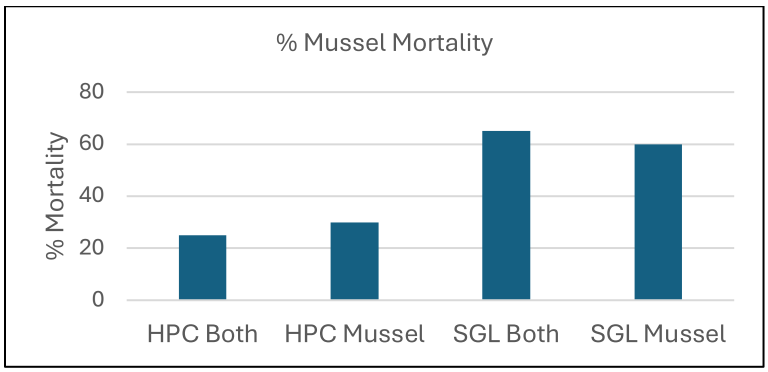

Figure 1. Chi-Square and Fisher's Exact test yielded no significant differences between mussel addition and both treatment (p=>.05, all cases) at each primary site (HPC and SGL A). The table depicts mortality as a percentage of total treatment.

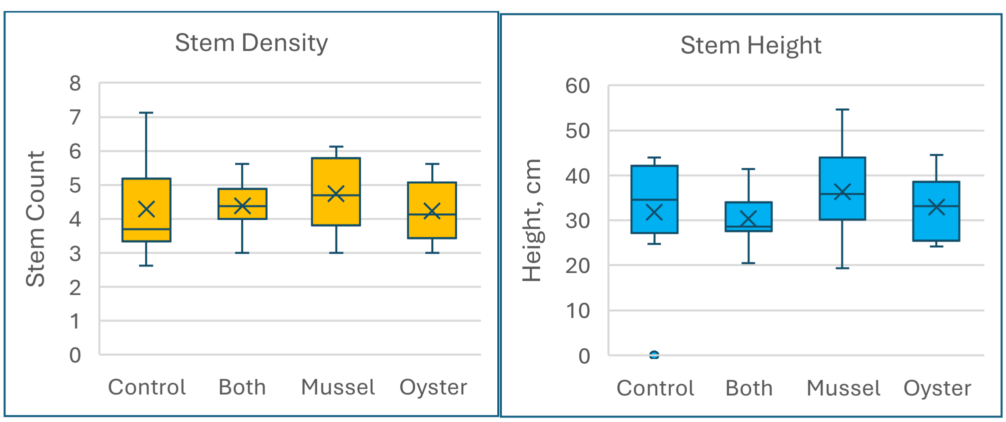

Figure 2. Stem Density and Heights were evaluated with a Linear Mixed Model (LMM), Welch's ANOVA, and Kruskal-Wallis tests with no significance differences between treatments at HPC. These plots show little variation among treatments.

Utilizing the number of flowering stems to compare the productivity of cordgrass we notice that both primary sites (HPC and SGL-A) saw an overall increase in the number of stems (HPC, n=120 to n=172; SGL-A, n=124 to n=161) while having relatively few flowers (32% and .018% of total for all treatments at HPC and SGL-A respectively). However, SGL-B while suffering a significant decline in stem count (n=111 to n=38) had 100% of remaining stems flower. No significant treatment effects on flowering success at any of the three sites was discovered.

The snail densities at the exclusion site yielded a result where the cage control harbored significantly more snails than did the control ($p=1x10^{-5}$). Adjacent to the exclusion experiment, the snail densities at the HPC site yielded no significant differences when compared to the control, however, there were significant differences when comparing treatments: mussel-both (p=.0008), mussel-oyster (p=.0191).

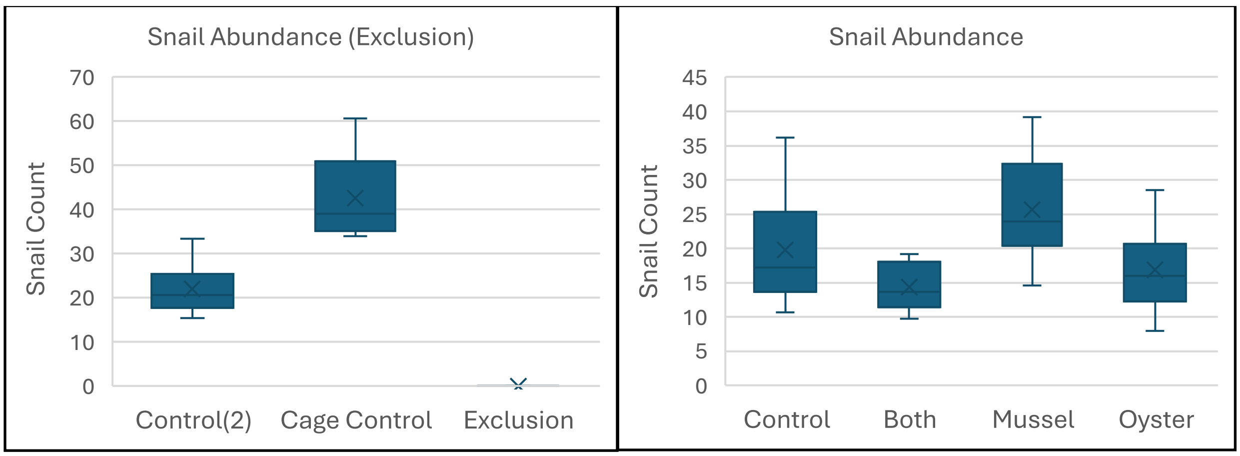

Figure 3. Snail Abundance graphs for the Exclusion experiment and transplant experiment in HPC. Note the different y-axis scales. Significant difference between Control(2) and Cage Control, Mussel and Both, Mussel and Oyster.

Confounding Factors

Precisely measuring and controlling initial conditions as well as a statistical analysis of those measurements would have been beneficial to eliminate potential confounding variables. While some of these unmeasured or unobserved metrics may be true confounders, it would have been equally beneficial to eliminate them as such. At any rate, initial *S. alterniflora* biomass, height, pore water redox potential, soil nutrient content, predator density estimates etc. while not necessarily impactful, all would have been beneficial to inform the conclusions and observed trends within the study. Instead, all transplants were taken from the same area in an attempt to maintain similar initial nutrient condition.

For the primary transplant experiments, the near total mortality of oysters, apart from SGL-B in the low marsh, deprived the study of any synergistic effects which living oysters may have provided. However, with the shell structure serving to ameliorate some thermal stressors via shading, we deemed it unnecessary to replace the deceased oysters, surmising that the shells would be sufficient to adequately test our associational defense hypothesis. I made no estimate of initial predator densities in any area which could have served to correlate the differing magnitudes in mussel mortality at the experimental sites.

Additionally, the lack of anchor stakes to maintain the placement of oyster shell clusters over a treatment's mussels may have limited the ability of the oysters to provide any type of meaningful defense to the mussels. The varied shape of oyster shell clusters and their propensity to gape after death provided numerous areas for periwinkles to seek shelter from thermal stress as well as predators. This behavior is likely to have obscured some count data despite the researcher's best efforts to account for it. Any future study should precisely measure initial *S. alterniflora* metrics, assess vertebrate and invertebrate predator densities, anchor oyster shell clusters to limit movement, and establish an estimate for the initial soil nutrient content.

Discussion:

Effects of co-occurring secondary foundation species

In this experimental context there does not appear to exist any discernable benefit to co-occurring secondary foundation species, as it pertains to *S. alterniflora* productivity or the prevention of mussel mortality. Mussel mortality between treatments displayed no significant differences despite the presence of oyster shells which ostensibly would protect the mussels from predation. The similarity between mortality rates were maintained between the two primary experimental sites, HPC and SGL-A, even though they differed in magnitude. This suggests the relationship is locally generalizable between these marshes and maintained under different predator densities. The differences in magnitude most probably stems from SGL-A's position in the high marsh, where thermal stress and remote location led to increased mortality as terrestrial predators were likely less inhibited by human presence.

When comparing the stem densities, the only significant factor was that of time. As measurements were repeated throughout the study, *S. alterniflora* continued to replicate and new stems emerged, as was expected throughout the growing season. However, there were no significant differences between treatments suggesting that oysters and mussel additions in all variations did not provide any synergistic effects to our experimental sites. Additionally, the evaluation of flowering stems and stem heights, measured at the conclusion of the study, gave no indication of synergistic effects or significant differences among the treatments. While no results were statistically significant, we observed that the mussel treatments appeared healthier and produced higher stem density, height, and flowers.

The short study duration, movement of oyster treatments, and mussel densities were all likely contributing factors to these nonsignificant findings. A multi-season or multi-year study, one with a higher mussel addition density, and anchored oysters would likely yield significant results as the mussel's fertilization effects would have a longer time to act on *S. alterniflora* and for differences among treatments to compound in magnitude (Carneiro et al., 2024).

Snail densities

The bulk of this study's significant findings relate to the habits of the marsh periwinkle snails, *L. irrorata*. While the snail counts centered around two experimental sites (HPC and Exclusion) in one marsh and therefore lacked generality, they nonetheless delivered significant differences when compared between treatments. The exclusion experiment yielded differences in snail densities between every treatment (control, cage control, and exclusion). Assessing survivorship of *S. alterniflora*, the cage control had a total loss of above ground *S. alterniflora* biomass while the control presented the same results a couple weeks later. While monitoring the cage control, which maintained the highest snail density of any treatment, the observed rate of decline outpaced *S. alterniflora's* ability to store nutrients in its underground rhizomes and as a result this treatment does not appear capable of reestablishing itself during the next growing season. Interestingly, the control, which also suffered a total above ground biomass loss, seems to have viable rhizomes that may reemerge. The exclusion treatment maintained the highest average stem density across all treatments and experimental sites (Avg=5.5 stems/replicate) which shows this ecosystem is under top-down control, as areas where snails are removed or reduced by predators or cages, *S. alterniflora* thrives even without the added benefit of mutualist bivalves. In the relationship between *S. alterniflora* and *G. demissa*, there are a great many benefits to each organism, however, when ecosystem imbalances exist that tip the scales, we witness the ensuing trophic cascade precipitated by *L. irrorata* (Angelini et al., 2016; Chalifour et al., 2019; Fischman et al., 2024).

While the exclusion experiment's cage control yielded extreme snail densities, the HPC primary site yielded some peculiar snail distributions. While no treatment was significant when compared to the control, the mussel addition averaged higher snail densities throughout the duration of the experiment at a nearly significant level. The two treatments with oyster shells (oyster addition, and both) had significantly fewer snails, when compared to the mussel addition. It appears the presence of oyster shells in a treatment, despite an assumed thermoregulatory benefit to the snails (the cage control's effect) or associational predator defenses, resulted in fewer snails (Iacarella & Helmuth, 2011; Muñoz et al., 2005). The mechanism of suppression for snail density in these treatments is likely the instability of the oyster shells or predator avoidance behavior since the heterogeneity of oyster shell could easily hide the predators of *L. irrorata.*

As snails inundated the HPC site, we observed *S. alterniflora* from the mussel addition treatments appeared more resilient than all other treatments. Snail count data, stem height, and stem density data all later revealed this to be true, displaying the highest averages in all categories, despite never passing the alpha level ($p < .05$). Given our observations and what is known of their grazing behavior and proclivity for algae and senescent *S. alterniflora,* it appears that periwinkles select for what are likely to be the most resilient plants, those associated with mussels (Klinges et al., 2024). Studies on related species recognize similar behaviors, which may have significant implications for marsh ecosystems under the increasingly stressful climatic regimes of the future (Chalifour et al., 2019; Muñoz et al., 2005).

Indeed, beginning with the first exposure and maintaining the highest density throughout the study's duration, the marsh periwinkles seemed to demonstrate a preference for the mussel addition treatment. This is noteworthy because the experiment was assembled in a random grid configuration on a mud flat 3m from the nearest *S. alterniflora* and within two weeks, the site was swarmed by periwinkles, a species that is known to generally travel 5m or less in a year (Silliman et al., 2005). From this initial occupation, the counts increased and decreased but maintained remarkably similar ratios between treatments. This suggests any successive wave of snail immigration to the site continually selected the mussel addition treatment. Considering what is known of their eye structure and visual acuity, movement behavior, and their ability to detect both airborne and waterborne predator cues, this finding is interesting but not altogether surprising but seems to be an underrepresented area of study (Carroll et al., 2018; Hamilton, 1977; Hamilton et al., 1983; Rahman et al., 2000; Warren, 1985). Our findings show *L. irrorata* can identify this combination and appears to benefit from this relationship as *G. demissa* helps to sustain *S. alterniflora* for a longer period as they feed on algae and senescent cells.

Conclusion:

It is clear from the results that the ecological circumstances surrounding a restoration project should be carefully considered to maximize the potential for success. In this restoration context, vertebrate and invertebrate predator densities should be assessed to estimate their effects on both *S. alterniflora* transplants and *G. demissa*, while more broadly projects should consider effects on both target species and facilitative species. The focus of future research should seek to understand the mechanisms which drive periwinkle selection to different *S. alterniflora* transplant arrangements. While this study suggests a preference toward *S. alterniflora* associated with mussels, the number and type of alternative arrangements possible in a restoration project, to include fertilized treatments, novel substrate, and bivalve mimics, should be considered and monitored. Additionally, the periwinkle's apparent preference for shade may be overshadowed by avoidance behavior pertaining to heterogenous assemblages of oyster shells acting as predator habitat or simply unstable substrate.

These experiments showed excessive top-down control of *L. irrorata* on *S. alterniflora* but also the maximum productivity of the plants when released from these pressures which, notably, occurred without their mutualist mussels at a snail density of zero. In a restoration context, it is not feasible to exclude all snails, so maximizing *S. alterniflora* productivity with mussel additions and adapting what is known of their apparent dislike or fear of oyster shells may be a promising novel method of restoration. Despite being a well-studied ecosystem, the dynamic changes to our coastal ecosystems change the variables rapidly, necessitating our continued study and adaptation of restoration methods.

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