Variable Responses to Consumer and Nutrient Availability in Coastal Wetland Plants

by

Stephanie Rene Valdez

Marine Science and Conservation
Duke University

Defense Date: April 23rd, 2024

Approved:

Brian Reed Silliman, Chair

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David Johnston

Fredrick Joel Fodrie

Dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Marine Science and Conservation in The Graduate School of
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ABSTRACT

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Abstract

Top-down and bottom-up factors, such as grazing and nutrient availability, are powerful forces that control patterns in plant communities across diverse ecosystems. In most ecosystems, however, testing the effects of top-down and bottom-up forces on plant communities has been focused on a subset of plant traits or a small portion of the species in a plant community. Thus, the general effect of top-down and bottom-up controls may often be unknown. In this dissertation, to help address this intellectual void, I explore how grazers, a top-down force, and nutrient additions, a bottom-up force, influence multiple plant traits, plant diversity, and range limits in two coastal wetlands. In my first chapter, I analyzed data from a fully factorial field experiment in a salt marsh in Virginia, U.S. I explored how grazing intensity and nutrient availability separately and interactively affect a suite of traits of the foundational salt marsh plant, *Spartina alterniflora*. This represents an analysis of unpublished data from experimental work first presented by Silliman and Zieman 2001. Three trait categories were measured for a total of nine responses for belowground characteristics, litter production, and reproduction. Fertilization led to greater cordgrass belowground biomass ($p= 0.039$). In comparison, the highest grazing intensity negatively impacted belowground biomass ($p= 0.049$). These grazing results contrast past studies suggesting grazer impacts are relegated to aboveground plant growth in this system. In addition, grazers and fertilization interacted to alter standing dead mass ($p<0.0001$), leaf litter ($p=0.0001$), and flowering ($p=0.011$). These results revealed both predicted and unexpected effects of grazing and nutrient

availability on understudied traits in a foundational plant. These findings were not entirely predictable based on understanding the impacts on aboveground biomass alone. Next, I explored how nutrient addition and grazer presence impacted plant diversity and species-specific trait responses at the low-high marsh transition zone. The transition from one plant community to an adjacent plant community can be a zone of unique species diversity and interactions. These zones could be important indicators of environmental change due to climate change. From a multi-year factorial experiment, results show that species richness is negatively affected by grazer presence ($p=0.0003$) and nutrient additions ($p=0.016$). At the same time, nutrient additions alone negatively impacted Shannon's diversity index ($p=0.004$). Additionally, my results show that grazers suppress while nutrients increase total aboveground biomass (gazers; $p=0.001$, nutrients; $p=0.001$). I also found that the top-down vs bottom-up effects varied by species. In plots with nutrient additions, the competitive inferior, *S. alterniflora*, increased in aboveground biomass, shoot length, and cover. This supports previous research in New England salt marshes. They found that nutrient additions invert the competitive hierarchy of marsh transition zones, favoring the stress-tolerant species. I predicted that grazers would act antagonistically to nutrient additions. The dominant grazers in U.S. southern salt marshes are thought to feed overwhelmingly on *S. alterniflora*. Therefore, I predicted grazers would help maintain diversity as *S. alterniflora* becomes the competitive dominant with nutrient enrichment. My results, however, do not support this hypothesis and suggest that grazers suppress diversity. This unexpected effect of grazers likely occurred because the marshes grazers in this study (insects and snails) acted as generalists, not specialist grazers in the high marsh. My results also contrast with the theory that states grazers generally help maintain plant species diversity in highly productive ecosystems. For the third chapter, I transitioned to seagrass habitats at their shoreward range limit. Here, physical forces, such as heat stress and desiccation, are thought to control the shoreward range limit. There has been limited consideration of testing the relative effects of biotic interactions in setting range margins under stressful conditions. Still, recent consumer-stress studies suggest these interactions could play a significant role. Using manipulative field experiments and observational surveys, I tested the effects of stingrays, a destructive forager in seagrass beds, and nutrient addition on the shoreward range limit of seagrasses. The stingray exclusion x nutrient addition experiment found that those exposed to stingrays had a greater loss in cover ($p=0.037$). In comparison, nutrient addition had no significant impact on seagrass cover at its upper range limit. In a follow-up experiment, I found that survivorship of seagrasses transplanted at higher intertidal elevations than observed increased when stingrays were excluded in 2022 ($p<0.01$) and again in 2023 ($p<0.01$). Finally, a multi-site survey found that stingray pit abundance strongly predicted the spatial extent of the intertidal range limit of seagrass. These findings suggest that consumers may be a more common contributing factor in setting range limits of plant communities on physically stressful boundaries than is currently thought. Throughout these experiments, I discovered that ecological theory, often used to inform and make decisions, does not always hold. In each chapter, I discuss how ecological theories should be more broadly tested across species ranges and traits, especially when used to make management decisions.

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Acknowledgements

I want to acknowledge the funding sources that have made the numerous field adventures possible and supported me through the years. These include the NSF Graduate Research Fellowship, Nicholas School Dean's Discretionary Award, Women Divers Hall of Fame—Susan L. Williams Memorial Fellowship, the Luce Foundation and Kenan Institute Anthropocene Fellowship, the Stern Fellowship, the American Dissertation Fellowship through AAUW, and the Duke Wetland Center.

I would also like to thank everyone who made this dissertation possible. To my current and past advisors, committee, and colleagues, thank you for fostering my ideas and helping to make them a reality. To my peers and friends, thank you for supporting me. Whether you joined me during long field days with questionable weather or insisted on a break from work to go to the beach, your contributions were invaluable. To my family, my sister and husband, you have been my most incredible supporters and champions. Thank you for joining me on this journey and always being a beacon of hope and encouragement. Finally, to my mother who instilled in me a strong work ethic, drive and determination, and a kindness to help whenever possible. She also was the first to ignite my curiosity and give me the freedom to explore. She gave me everything so I could follow my dreams.

Thank you everyone, this dissertation would not have been possible without all of you.

1. Introduction

A complex suite of biotic and abiotic factors structure ecosystems. After much debate, there is a consensus that both top-down factors, such as consumers, and bottom-up factors, such as environmental conditions, structure vegetative ecosystems (Borer et al., 2014; Burkepile & Hay, 2006; Gruner et al., 2008; Hillebrand et al., 2007). These factors can influence many aspects of an ecosystem, including many plant traits (Aerts et al., 1991; Ericsson, 1995; Karban & Baldwin, 2007), species composition, and coexistence (Borer et al., 2014; Denyer et al., 2010; Souza et al., 2016; Wilkinson & Sherratt, 2016). These factors can even determine the range in which species exist (Louthan et al., 2015). Top-down and bottom-up factors have been examined as an influential part of ecological study (Borer & Gruner, 2009; Hairston et al., 1960; Hanley & Pierre, 2015; Power, 1992). While several studies have explored many patterns in plant communities associated with top-down and bottom-up controls, there is still a need for more knowledge that could be valuable for assessing future responses to environmental change.

As top-down factors, consumers can mediate lower trophic levels consumptively and non-consumptively. In plant ecosystems, consumptive controls can take the form of direct grazing of plant tissues or indirect trophic cascades. For example, direct grazing of large herbivores in savannah ecosystems consistently limits shrub and tree abundance (Staver et al., 2021). Direct grazing can also lead to compensatory responses in vegetation and increase production (Gulick et al., 2021). The evaluation of indirect consumptive control can be more challenging to assess as several trophic levels are involved. However, researchers have found that these trophic cascades shape ecosystems. For example, a typical example of a trophic cascade is sea otter facilitation of kelp through the consumption of urchins (Estes et al., 2004). Non-consumptive consumer controls can alter the ecosystem through an animal's behavior. Ecosystem engineers, for example, alter ecosystems by changing environmental conditions (A. Hastings et al., 2007; C. G. Jones et al., 1997). Common examples include elephant trampling in forests that create space for understory vegetation (Maicher et al., 2020; Poulsen et al., 2018) and beavers that alter hydrology and geomorphology in riparian zones (Brazier et al., 2021; Wright et al., 2002).

Bottom-up controls of plant communities include resources (e.g., nutrients) and resource-regulating physical factors (e.g. temperature). Throughout this dissertation, I focus on nutrient availability as the bottom-up control. With the rise of industrial fertilization and its widespread impacts (Beman et al., 2005; Matson et al., 1997), understanding the effects of nutrient additions is valuable to the future mitigation of nutrient runoff. Research has found that nutrients, whether excessive or as a limiting factor, can impact plant biomass and species diversity (Bedford et al., 1999; Bracken et al., 2015; Harpole et al., 2016; Pekin et al., 2012; Stevens et al., 2004). In recent decades, research has explored how top-down and bottom-up factors can work additively, synergistically, or antagonistically to shape ecosystems. For example, research in seagrass suggests that a trophic cascade mediates the effects of eutrophication (Hughes et al., 2013), while grazers and nutrients interact to influence salt marsh biomass (Silliman & Zieman, 2001).

These controls have been explored primarily on a subset of individual traits as proxies for overall health and function. Generally, these traits tend to be associated with aboveground properties such as biomass or primary production (Gruner et al., 2008). However, there may be essential deviations from patterns derived from this subset of traits that could be imperative to ecosystem health and require further examination across traits. For example, research in salt marshes has demonstrated that nutrient additions diminish belowground biomass, structures that are important to marsh stability (Deegan et al., 2012). With the loss of belowground biomass, marshes are more susceptible to erosion and loss, patterns not observed by predictions from response to aboveground biomass alone (Deegan et al., 2012). A varied trait response to top-down and bottom-up factors would suggest that a subset of traits may not be the best proxies for ecosystem health. A broader understanding of trends and patterns that persist across categories of traits could become indispensable to understanding the impacts of global change on ecosystems.

Ecological patterns are also generally observed within a species or ecosystem's core zone. However, patterns at the transition between two communities or at a species range margin may diverge from predicted. The transition between plant communities is often marked by increased biodiversity and unique species interactions (Kark, 2013; Kark et al., 2007; Traut, 2005). These transition zones may also be occupied by species not found elsewhere or at their range margins (Ferro & Morrone, 2014; Kark & Van Rensburg, 2006; Van Rensburg et al., 2009). Additionally, transition zones mark areas of environmental change (Smith & Goetz, 2021). Given the unique structure of biotic communities and abiotic factors, ecological theory may not persist in these regions. Furthermore, paradigms that predict species range limits may only partially account for altered top-down and bottom-up factors. Range limit theory and the Species Interactions–Abiotic Stress Hypothesis (SIASH) state that bottom-up factors set a species' range limit at the environmentally stressful edge (Louthan et al., 2015). However, these patterns may not fully explain species ranges, and researchers have called for additional testing of this paradigm across various ecosystems (Louthan et al., 2015). With this call in place, researchers are finding biotic influencers at environmentally stressful edges previously thought to be controlled by physical factors alone (Shepard et al., 2021). This divergence from the predicted patterns at transition zones and species range margins are likely valuable information for predicting the future impacts of global change. These areas may be some of the first indications of environmental alteration in an ecosystem due to climate change, requiring further ecological understanding. Many transition zones and range limits are studied specifically for movement as an indication of climate change (Brownstein et al., 2015; Kupfer & Cairns, 1996; Smith & Goetz, 2021; Wasson et al., 2013), but still lack a basic ecological understanding of the patterns observed.

Coastal wetlands are vulnerable yet valuable ecosystems to explore unique responses to top-down and bottom-up impacts. Coastal wetlands provide coastal protection, carbon sequestration, and harbor immense culturally and commercially valuable wildlife (Barbier et al., 2011). Salt marshes are estimated to sequester millions of tons of carbon a year (Mitsch & Gosselink, 2007), while seagrass provides a nursery habitat for a fifth of the top global fisheries (Unsworth et al., 2019). However, they also face significant threats like coastal development and rising sea levels (Newton et al., 2020; Schuerch et al., 2018). I focus on low-elevation monospecific salt marshes, multi-species high salt marshes, and seagrass meadows.

Within this dissertation, I explore top-down and bottom-up forces across a variety of plant traits (Ch. 1) and understudied areas in ecosystems, including a transition zone (Ch. 2) and a species range limit (Ch.3). I conducted this research within the low, monospecific salt marsh, multi-species high marsh meadows, and intertidal seagrass meadows. In the first chapter, I ask how various traits of the dominant, low marsh species, *Spartina alterniflora*, respond to top-down snail grazers and bottom-up nutrient additions. I predicted varied responses among traits with belowground biomass, reproduction, and litter production, all negatively impacted by nutrient additions. Meanwhile, I predicted grazers would increase belowground biomass but limit reproduction and litter production. In the second chapter, I explore how grazers (snails and insects) and nutrient additions impact species diversity and species-specific trait responses at the low-high marsh transition zone. I predicted nutrient additions would be limited while grazers would promote species diversity by consuming the most abundant plant species. I also predicted responses to treatment would be species-specific, with some species responding favorably to nutrients and grazers while others exhibited negative responses. Finally, in the third chapter, I explore variations in ecological patterns at the shoreward range limit of seagrass. Given the high density of destructive stingray foragers in the area, I predicted that biotic factors at the environmentally stressful edge would impact seagrass range limits. These projects aimed to elucidate when and where ecological theories are maintained or diverge among understudied vegetation traits and zones. Under global change factors, a better understanding of a holistic response to top-down and bottom-up factors could be increasingly valuable to conservation and management decisions.

2. Variable Responses to Top-Down and Bottom-Up Control on Multiple Traits in the Foundational Plant, *Spartina alterniflora*

This chapter was published as "Variable responses to top-down and bottom-up control on multiple traits in the foundational plant, *Spartina alterniflora*" in PLoS ONE in 2023. It is reprinted under a Creative Commons Attribution License from Valdez SR, Daleo P, DeLaMater DS III, Silliman BR. (2023). Variable responses to top-down and bottom-up control on multiple traits in the foundational plant, *Spartina alterniflora*. PLoS ONE 18(5): e0286327. https://doi.org/10.1371/journal.pone.0286327. Copyright 2023 Valdez et al. The accompanying supporting information is included in Appendix A

2.1 Introduction

Despite a general acknowledgment that both top-down (i.e, consumers) and bottom-up (i.e., resources) drivers can simultaneously regulate plant communities, it is unclear how the relative importance of these factors varies across different plant traits (Burkepile & Hay, 2006; Gruner et al., 2008). Most work exploring the effects of bottom-up and top-down forces in simultaneously regulating plant traits has focused primarily on changes in standing aboveground plant biomass (Gruner et al., 2008), largely ignoring changes in other traits (Alward & Joern, 1993; Deegan et al., 2012). However, both herbivory (Karban & Baldwin, 2007)and resource availability (Aerts et al., 1991; Ericsson, 1995) have been shown to induce dramatic variation in traits other than aboveground biomass. The variance in these traits is often unrelated to variance in aboveground biomass, such that measuring aboveground biomass alone does not sufficiently characterize plant response to top-down or bottom-up forcing or indicate plant health (Turner et al., 2004). Furthermore, these changes in trait values, while unrelated to aboveground biomass, have still been found to have profound effects on ecosystem function (Bardgett et al., 1998; De Deyn et al., 2008; Holland et al., 1996; Mcleod et al., 2011). Thus, by limiting observations to changes in aboveground biomass, we constrain our ability to predict possible responses to climate change and other anthropogenic stressors.

Ecological studies in salt marshes formed the basis of the bottom-up paradigm of coastal wetland ecology (Duarte et al., 2013; Gedan et al., 2011; Odum & Smalley, 1959; Smalley, 1960; Teal, 1962). However, it has since become clear that top-down forces also play a significant role in governing marsh plant biomass and are common in marshes around the world (Alberti et al., 2010; Beheshti et al., 2021; He & Silliman, 2016; Silliman & Zieman, 2001). Despite the important role salt marshes play in coastal ecosystems, the mechanisms governing their structure and function remain largely ambiguous in relation to top-down vs. bottom-up effects. This is especially true regarding plant traits, other than aboveground biomass.

The provisioning of salt marsh ecosystem services, such as shoreline protection from erosion (Gedan et al., 2011; Silliman et al., 2019) and carbon sequestration (Mcleod et al., 2011), depend not only on the high productivity of aboveground biomass, but also on other inherent properties that are increasingly threatened by pervasive anthropogenic stressors such as nutrient enrichment and altered trophic structures (Silliman et al., 2009). Decreases in root-to-shoot biomass allocation ratio, caused by eutrophication or heavy oiling, for example, drive decreases in geomorphic stability, which increases rates of coastal erosion (Deegan et al., 2012; Silliman et al., 2012). Salt marshes are also recognized as extremely valuable carbon sinks (Mcleod et al., 2011), which depends, in large part, on living roots and soil litter inputs (De Deyn et al., 2008). Furthermore, seed production, through flowering, can have important consequences not only for granivorous species of birds and rodents (Canepuccia et al., 2008; Dierschke & Bairlein, 2004) but also for bare patch dynamics (Daleo et al., 2014), and thus, system resilience against disturbance. Additionally, changes in the production of new stems can affect stand stem density, thereby affecting water flow, sediment stability and retention, evaporation, and soil salinity, as well as refugia availability (Brusati & Grosholz, 2006; Cardoni et al., 2011). Despite the evident importance of other traits beyond aboveground biomass, only a small proportion of marsh studies focus on top-down and bottom-up effects on other plant traits. For example, a comprehensive meta-analysis that synthesized trends in nutrient effects on plant-herbivore interactions in salt marshes and mangroves showed that 68 out of 80 studies focused on standing aboveground biomass while only 9 focused on belowground biomass (Table S1).

Here, we focus on the relative impacts of top-down and bottom-up drivers on other aspects of plant life history, including belowground characteristics, reproduction, and litter production, using the dominant salt marsh plant - smooth cordgrass (*Spartina alterniflora*) as a model species. Employing a manipulative field experiment, we hypothesized an array of interactions among top-down (i.e. snail grazers) and bottom-up (i.e. nutrient availability) factors and their impact on some often-overlooked plant traits in salt marsh ecology. We predicted that with increased nutrient availability there would be increased cordgrass reproduction and litter production due to increased aboveground biomass (Silliman & Zieman, 2001), while belowground biomass would decrease with increased nutrient availability (Darby & Turner, 2008; Deegan et al., 2012b; Turner et al., 2009). Comparatively, we predicted that grazer pressure would decrease cordgrass reproductive outputs and litter production while increasing belowground biomass by potentially shifting growth allocation from leaf tissues to root structures (Blue et al., 2011). If there were a change to resource allocation with grazing, there would potentially be an interaction in which grazers mitigate the negative impacts of increased nutrient availability on cordgrass. Given the context of human direct and indirect alteration to nutrient cycles and food webs in estuarine systems, improving our knowledge about the separate and interactive effect of these controls on often overlooked plant traits may simultaneously advance knowledge and allow us to more accurately predict human impacts on natural systems and their functions linked to specific plant traits.

2.2 Methods

2.2.1 Study Site

A field experiment was carried out on Hog Island, Virginia USA (Fig.1) in the growing season (May through September) of 1997. This island, a barrier island in central Virginia, USA, is part of the Virginia Coast Reserve Long Term Ecological Research (VCR LTER) project. We were granted permission by the Nature Conservancy in collaboration with the VCR to conduct the study within the LTER. While no official permits were required for this study, we followed standard practices and observed the stated laws. Hog Island is a barrier island bordering the Atlantic Ocean on the east and

Hog Island Bay on the west. Sediments are characterized as a mix of mud and sand – with sand originating from frequent overwash events on this narrow barrier island. Work was done on the southern portion of the island in the intermediate *S. alterniflora* zone, where salt marsh periwinkle snails (*Littorina irrorata*) are abundant. Original methods for the experimental setup are described in Silliman & Zieman (2001). Here we present original, unpublished data from that 1997 experiment.

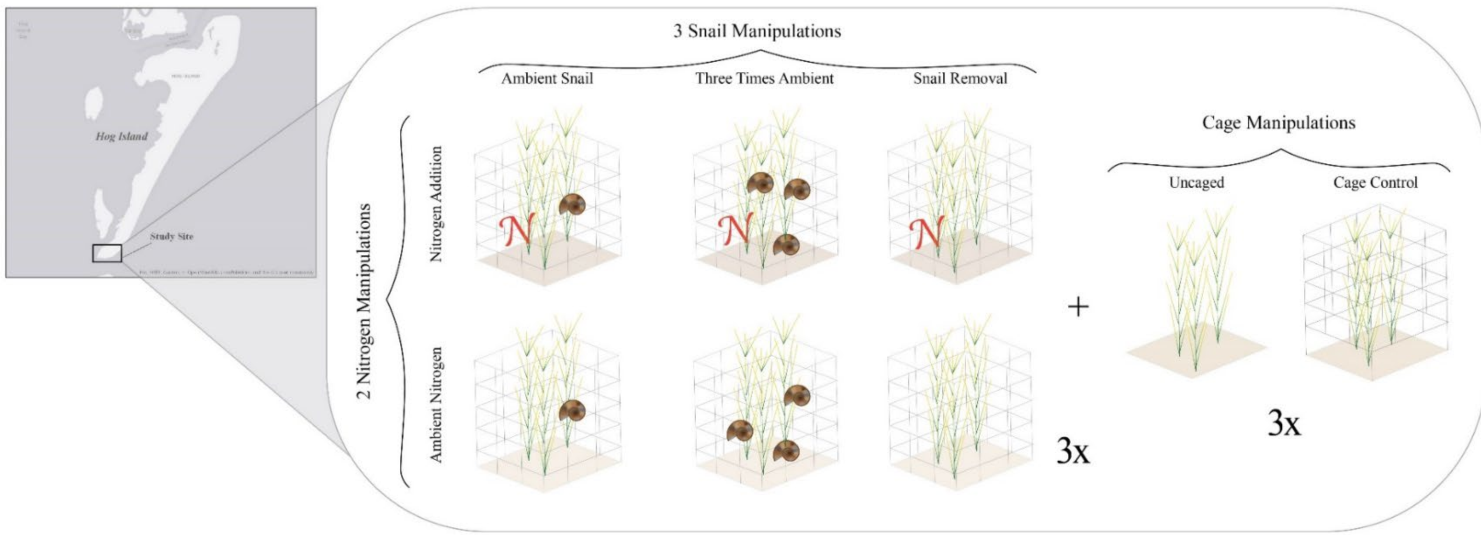

Figure 1: Map and conceptual illustration of experimental design. Map of study site on Hog Island, Virginia, USA and conceptual illustration of experimental design with the following treatments: 1) Nitrogen addition with ambient snails, 2) nitrogen addition with three times ambient snails, 3) nitrogen addition without snails, 4) ambient nitrogen with ambient snails, 5) ambient nitrogen with three times ambient snails, and 6) ambient nitrogen without snails. The figure also depicts cage controls and uncaged plots used to assess caging effects on marsh plants. The map in the figure was created in R using ggmap (Kahle & Wickham, 2013) from ©OpenStreetMap under a ODb license, with permission from OpenStreetMapFoundation, original copyright 2018. https://www.openstreetmap.org/copyright.

2.2.2 Experimental Design

To evaluate the separate and interactive effects of bottom-up (i.e. nutrient availability) and top-down (i.e. grazing pressure) forces, we implemented a 2x3 factorial experiment manipulating the availability of the main limiting nutrient (i.e. nitrogen; Mendelssohn, 1979) to marsh plant growth and the abundance of an important grazer (i.e. the marsh periwinkle; (Silliman & Zieman, 2001)) in the system (Fig. 1). The experiment was initiated on 5 May 1997 and monitored until the first week of September 1997. Two levels of nitrogen availability (ambient and fertilized) and three levels of grazer manipulation were applied (ambient snail abundance, three times ambient snail abundance, and snail removal). The resulting six treatments are referred to as: 1) snail removal, 2) snail control, 3) snail addition, 4) snail removal + nitrogen, 5) snail control + nitrogen, and 6) snail addition + nitrogen (Fig. 1, n=3). We measured the response of these treatments on nine traits and/or characteristics that we categorized as follows: 1) belowground characteristics include belowground biomass (g/m^2), the ratio of belowground to aboveground biomass (g/m^2), and organic soil content (% organic matter), 2) litter production includes standing dead mass (dry mass g/m^2) and leaf litter (dry mass g/m^2), and 3) reproduction includes the number of flowering shoots/ m^2, proportion of total shoots that are flowering, number of new shoots/ m^2, and mean length of new shoots from sediment (cm). All plots were enclosed within 1 m^2 roofless cages constructed of 12.7 mm galvanized hardware mesh 76.2 cm high. Two additional cages were constructed for each treatment for destructive sampling. Cages were extended 5 cm into the sediment to prevent snail movement, and plant root systems were cut up to 40 cm depth to prevent resource sharing outside of the plots. All plots were placed at the same elevation to control for water inundation. A wooden boardwalk was created to walk between plots without sediment disruption.

Caging effects, if any, were assessed from uncaged plots and control cages (n=3). Cage control plots were implemented using cages of the same dimensions as experimental plots, but were not manipulated for snails and nitrogen fertilization, and cages were lifted off the sediment, leaving a small gap to allow snail movement between the plot and the surrounding area. Uncaged plots were plots of the same area without any caging material. The same sampling procedure for treatment plots occurred in the three uncaged plots and three caged controls for belowground biomass, number of flowering shoots, number of new shoots, and length of new shoots.

2.2.3 Nitrogen Enrichment

Nitrogen, as ammonium chloride (NH_4Cl), was added to the sediment via 16 evenly spaced 15mL centrifuge tubes filled with 3.4g of NH_4Cl wrapped in nylon mesh to promote slow release (S. L. Williams & Ruckelshaus, 1993). Enough NH_4Cl was added to nitrogen fertilized plots to theoretically double the production of *S. alterniflora* (projected from Mendelssohn, 1979; 1996 *S. alterniflora* aboveground production at this site = 425 g dry mass m^{-2} yr^{-1}). No fertilizer was added to ambient nitrogen plots. Empty tubes were inserted into non-fertilized plots as disturbance controls for the added structure. At the conclusion of the experiment, organic soil content was measured by extracting a 1mL round core from the surface using a 5 ml syringe that was rinsed with seawater between samples. Organic content was determined by weight from loss of ignition at 450℃.

2.2.4 Grazer Densities

Naturally occurring snail densities were determined at the start and conclusion of the experiment by counting snails in 75 randomly placed 1 m^2 quadrats in stands of intermediate height form *S. alterniflora*. At the beginning of the experiment, snails were removed from all enclosures. Snails were reintroduced by pre-determined grazer levels in snail control and snail addition treatments. Control snail treatments had naturally occurring densities (48 snails/ m^2) while snail addition treatments had three times the amount of snail control treatments (144 snails/ m^2), a naturally occurring high snail density for mid-Atlantic marshes (Morton & Silliman, 2020; Renzi & Silliman, 2021).

Snail densities were monitored weekly, and snails were added or removed if they strayed from intended levels. Average snail shell height of 45 randomly selected snails was calculated every two weeks to account for variation in snail size. Furthermore, due to the enhanced growth of smooth cordgrass in the presence of the Atlantic marsh fiddler crabs (*Uca pugnax*) and the ribbed mussels (*Geukensia demissa),* density of these organisms was also assessed every two weeks (Bertness, 1984, 1985). The purple marsh crab (*Sesarma reticulatum*), another grazer of *S. alterniflora*, was excluded by cage treatments and no burrows were observed within plots. No differences in mussel or fiddler crab densities were observed between treatments (Silliman & Zieman, 2001).

2.2.5 Plant Measurements

At the conclusion of the experiment, sediment cores (15 cm diameter and 30 cm deep) were taken from each plot to measure plant biomass. The cores were taken to 30 cm depth as that is the approximate extent to which *S. alterniflora* extends its roots and root growth takes place in the intermediate marsh zone (Gallagher et al., 1984). The above- and belowground portions of the plants were separated, dried to a constant weight, and reported as dry mass (g)/ m^2. Aboveground biomass data (reported in Silliman & Zieman, 2001) was used to calculate the ratio of belowground to aboveground biomass. Leaf litter was collected from the marsh surface of 0.25m^2 corner of the 1m^2 plots. Standing dead mass was removed from the entirety of the plots. Both leaf litter and standing dead mass were dried, weighed, and reported as mass (g/m^2). The effectiveness of snail manipulation treatments on the abundance and length of grazing scars known as radulations on live *S. alterniflora*, was measured previously (Silliman & Zieman, 2001). In short, there were no radulations within total grazer exclosure treatments and nearly double the radulations marks in addition treatments, showing that grazer exclusion and additions were effective in manipulating grazer pressure (Silliman & Zieman, 2001).

Flowering *S. alterniflora* shoots per m^2 were counted in September 1997 (i.e. 4 months after treatments began). The proportion of flowering shoots was calculated from the total shoot density, also taken in September. The abundance of new shoots was counted from a 0.25 m^2 quadrat within plots in the first week of August 1997, and again in the first week of September 1997 based on height differential from adult plants. The length (cm) of each new shoot was measured from the sediment to the tip of the longest blade and the mean was derived for each treatment.

2.2.1 Statistical Analysis

All analyses were conducted in R version 4.1.1 (R Core Team, 2022). Potential effects of caging were assessed for belowground biomass, proportion of flowering shoots, and number of new shoots, using t-tests between uncaged and caged control plots.

We assessed the effects of treatments on belowground biomass (g/m^2), ratio of belowground to aboveground biomass (g/m^2), leaf litter (g/m^2), standing dead mass (g/m^2), organic soil content (% organic content), number flowering, and proportion of flowering shoots using two-way Analysis of Variance (ANOVA) followed by Tukey's post-hoc test for each dependent variable separately. In all cases, the degrees of freedom for the main effects of nitrogen level, grazer level, and nitrogen by grazer interaction were 1, 2, and 2, respectively. ANOVA model assumptions were evaluated and met in all cases.

Additionally, for the number of new shoots and mean length of new shoots, two-way, repeated measures ANOVAs were used with the "ez" package in R (Lawrence, 2016). Neither repeated measure ANOVA resulted in significant snail, nitrogen, and time interactions. Therefore, we conducted two-way ANOVAs evaluating the treatment effects of nitrogen and snail manipulation for each month (August and September) separately.

2.3 Results

We did not detect differences between cage controls and uncaged plots in the six variables examined (Table S2, Figs. S1 and S2). Independent effects of both nitrogen availability and grazer density were detected for belowground biomass where belowground biomass increased by 26% with fertilization ($F_{1,12}$= 5.4, P= 0.039) and decreased by 26.3% between snail removal and snail addition ($F_{2,12}$= 3.9, P= 0.049; Fig. 2A, Table1, see also S3 Table). However, the ratio between belowground and aboveground biomass decreased with fertilization by 66.8% ($F_{1,12}$= 122.9, P< 0.0001) and increased with snail density by 51.6% from snail removal to snail addition ($F_{1,12}$= 50.8, P< 0.0001; Fig. 2B, Table 1, see also Table S3). Organic soil content was not influenced by either fertilization or snail density (Fig. 2C, Table 1). Traits related to litter production demonstrated interactive effects of fertilization and snail density (leaf litter: $F_{2,12}$= 20.3, P= 0.0001; standing dead mass: $F_{2,12}$= 31.42, P< 0.0001; Fig. 3, Table 1, see also Table S3). Here, leaf litter increased by 274.2% between fertilized plots without grazers versus those with grazer additions but decreased under ambient nutrient conditions by 78.9% from no grazer to grazer additions. Standing dead mass peaked by 3-fold in fertilized plots with ambient grazer density compared to fertilization without grazers.

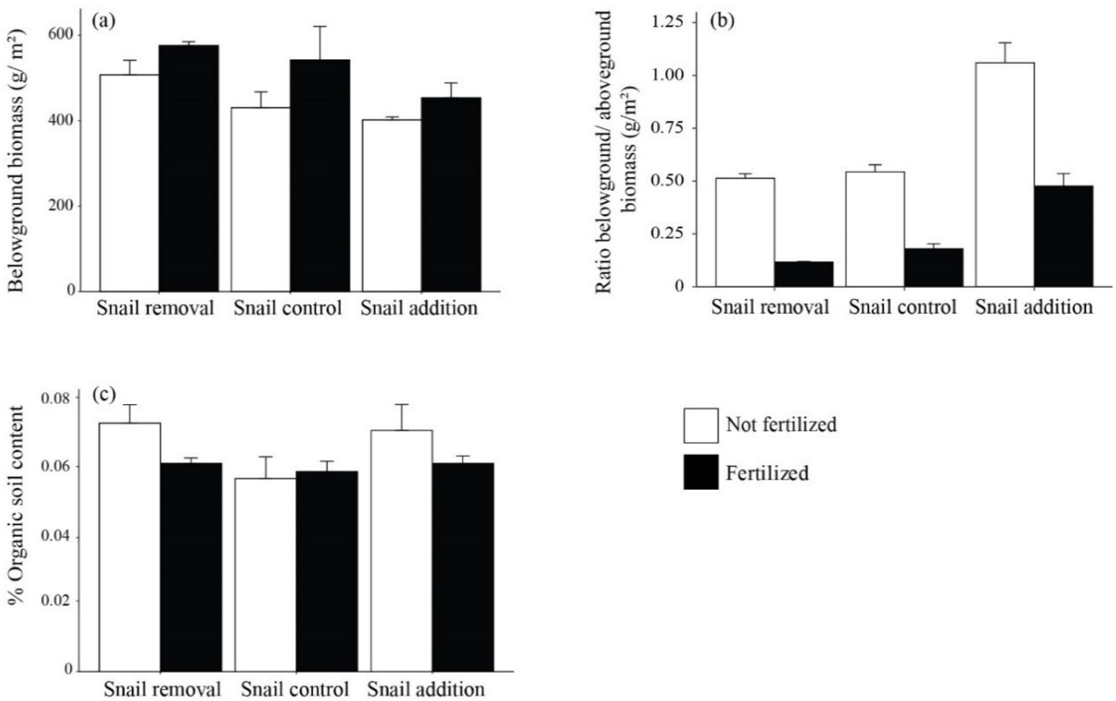

Figure 2: Effects of fertilization and snail (Littorina irrorata) density manipulation on belowground characteristics.(A) *Spartina alterniflora* belowground biomass (g/m^2), (B) Ratio of belowground to aboveground biomass of *S. alterniflora* (g/m^2) and (C) % organic soil content. Results of two-way ANOVAs given, testing the main and interactive effects of grazers (G) and fertilization (N). Error bars represent standard error (n=3).

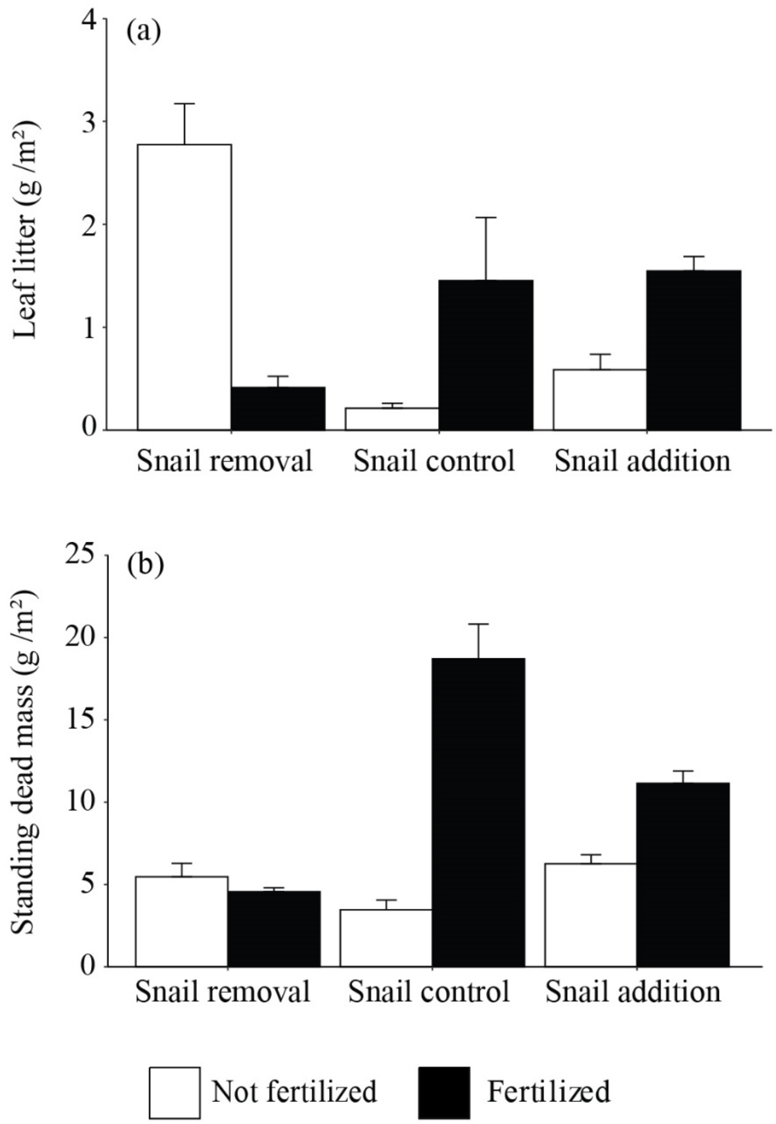

Figure 3: Effects of fertilization and snail (*Littorina irrorata*) density manipulation on litter production.(A) aboveground standing dead mass (dry weight (g)/m^2) and (B) leaf litter (dry weight (g)/m^2). Error bars represent standard error (n=3).

Table 1: Reported mean values and corresponding ANOVA significance.

A) Means

Measured Traits

Nitrogen *Grazer Level*	Belowground Biomass (g/m2) ± SE	Ratio Below: Aboveground Biomass (g/m2) ± SE	Radulations (cm/ Stem) ± SE	Organic Soil Content± SE	Standing Dead (dry mass g/ m2) ± SE	Leaf Litter (dry mass g/ m2) ± SE
Ambient						
Removal	507.3 ± 34.0	0.513 ± 0.02	0.003 ± 0.002	0.070 ± 0.005	5.47 ± 0.82	2.78 ± 0.40
Control	430.3 ± 36.6	0.543 ± 0.03	0.40 ± 0.14	0.055 ± 0.006	3.47 ± 0.58	0.21 ± 0.05
Addition	401.6 ± 6.86	1.06 ± 0.10	0.80 ± 0.34	0.068 ± 0.007	6.26 ± 0.54	0.59 ± 0.15
Fertilized						
Removal	575.7 ± 8.85	0.117 ± 0.003	0.008 ±0.003	0.059 ± 0.002	4.56 ± 0.25	0.41 ± 0.11
Control	542.2 ± 78.4	0.180 ± 0.02	0.93 ±0.39	0.057 ± 0.003	18.71 ± 2.12	1.45 ± 0.62
Addition	453.3 ± 35.0	0.477 ± 0.06	1.42 ±0.61	0.059 ± 0.002	11.14 ± 0.75	1.55 ± 0.24

Nitrogen *Grazer Level*	Number Flowering/ m2 ± SE	Proportion Flowering /m2 ± SE	August New Shoots/ m2 ± SE	September New Shoots/ m2 ± SE	August Mean Length of New Shoots (cm) ± SE	September Mean Length of New Shoots (cm) ± SE
Ambient						
Removal	25.33 ± 1.76	10.56 ± 0.23	218.67 ± 14.11	458.67± 103.83	5.98± 0.33	8.14± 0.60
Control	10.0 ± 1.53	4.92 ± 0.67	144.0 ± 9.23	277.33± 61.51	4.37± 0.73	7.45± 1.45
Addition	2.67 ± 0.88	1.68 ± 0.41	74.67 ± 14.11	197.33± 37.33	4.90± 0.33	6.73± 0.14
Fertilized						
Removal	56.0 ± 6.93	17.4 ± 2.88	384.0 ± 64.66	506.67± 52.53	8.66± 0.23	9.11± 0.76
Control	20.67 ± 5.21	7.91± 2.88	181.33 ± 29.69	373.33± 74.09	8.36± 1.54	12.31± 0.33
Addition	6.33 ± 2.73	3.69 ± 2.62	292.33 ± 61.51	325.33± 65.54	7.32± 0.18	10.99± 1.28

B) ANOVA

Source	Below ground Biomass	Ratio Below: Aboveground Biomass	Radulations	Organic Soil Content	Standing Dead	Leaf Litter
Nitrogen (N)	*	***	NS	NS	***	NS
Grazer Level (G)	*	***	*	NS	**	NS
N + G	NS	NS	NS	NS	***	**

Source	Number Flowering	Proportion Flowering	August New Shoots	September New Shoots	August Mean Length of New Shoots	September Mean Length of New Shoots
Nitrogen (N)	***	**	**	NS	***	**
Grazer Level (G)	***	***	*	*	NS	NS
N + G	*	NS	NS	NS	NS	NS

Sexual reproduction traits had varying impacts of fertilization and grazer density. The number of flowering shoots demonstrated interactive effects of fertilization and grazer density ($F_{2,12}$=6.64, P= 0.011) in which flower density increased with fertilization and decreased with greater grazer density (Fig. 4A, Table 1, see also Table S3). There was an 88.6% decrease in flowering between fertilized plots with no grazers and fertilized plots with grazer addition. The proportion of flowering shoots had similar trends with fertilization (60.2% increase in flowering in fertilized versus unfertilized treatments) and grazer density (83.9% decrease in flowering in no grazer versus grazer addition treatments) but no interaction (fertilization; $F_{1,14}$= 16.71, P= 0.0015, snail density; $F_{2,14}$= 47.3, P< 0.0001) (Fig. 4B, Table 1, see also Table S3). Finally, asexual reproductive traits revealed impacts of fertilization and grazer density, although not consistent through time. The number of new shoots in August increased by 25.9% with fertilization ($F_{1,14}$= 19.03, P= 0.0009) and decreased by 65.9% with snail density ($F_{2,14}$= 7.17, P=0.009) (Fig 5A, C, Table1, see also Table S3). The length of new shoots in August only increased with fertilization by 91.1% between unfertilized and fertilized treatments without grazers ($F_{1,14}$=25.6, P=0.0003). In September, the number of new shoots decreased with grazer density by 56.9% between no grazer and grazer additions in unfertilized treatments ($F_{2,14}$= 5.46, P= 0.02) and no effect of fertilization while the length of new shoots increased by 65.2% with fertilization ($F_{1,14}$=21.2, P= 0.0006) and no effect of grazer density (Fig.5B, D, Table 1, see also Table S3).

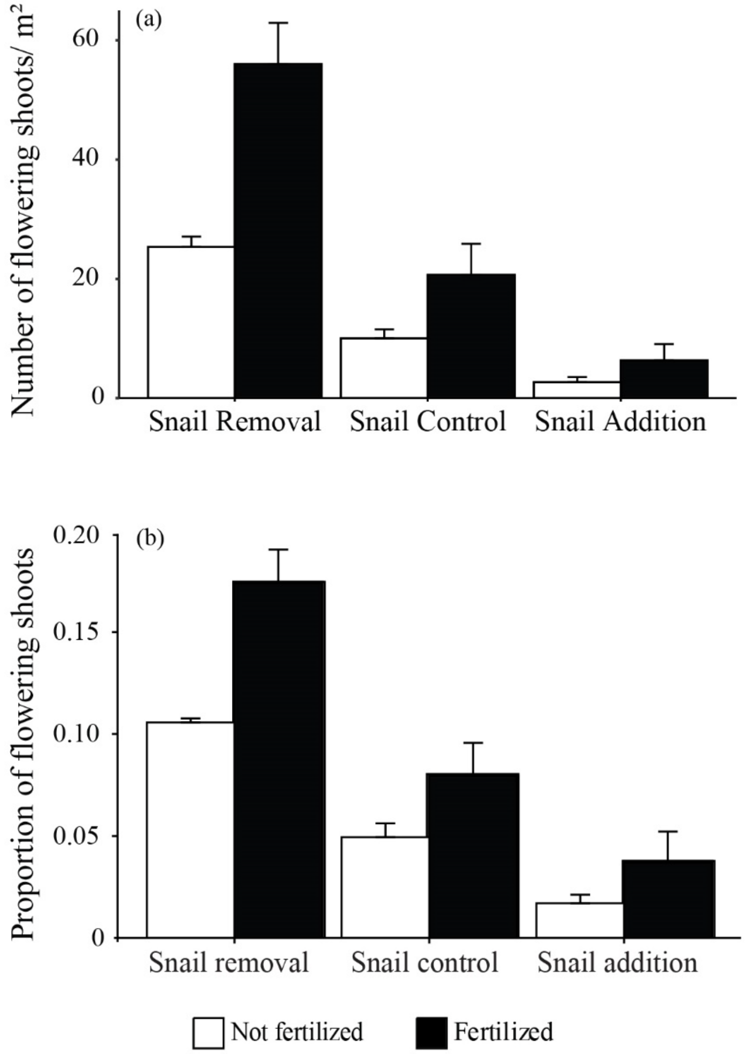

Figure 4: Effects of fertilization and snail (*Littorina irrorata*) density manipulation on sexual reproduction.(A) number flower/ m^2 and (B) proportion of flowering shoots. Error bars represent standard error (n=3).

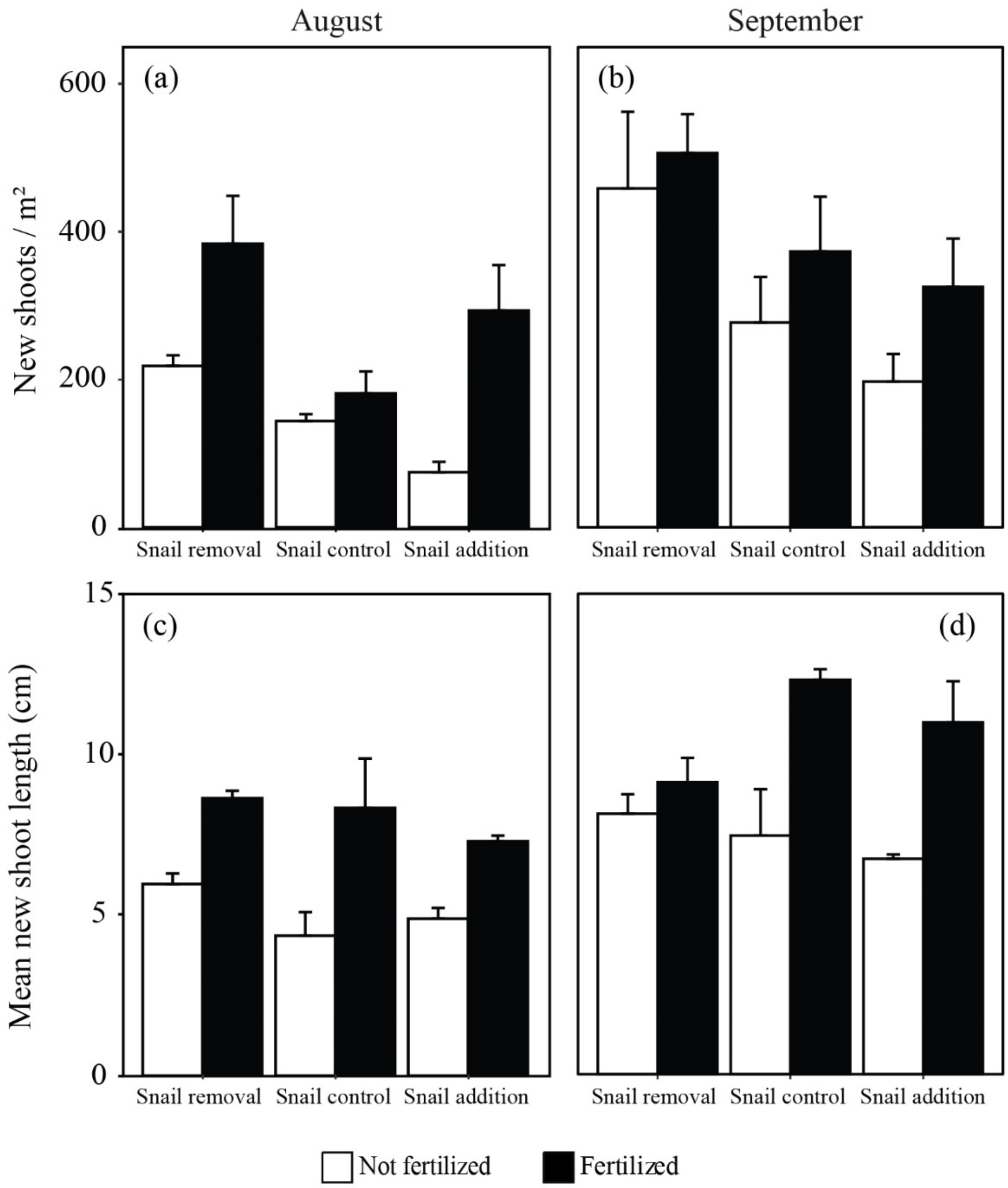

Figure 5: Effects of fertilization and snail (*Littorina irrorata*) density manipulation on asexual reproduction. The number of new shoots in August (A) and September (B), and length (cm) of new shoots in August (C) and September (D) under nitrogen and snail (*Littorina irrorata*) density manipulations. Error bars represent standard error (n=3).

2.4 Discussion

Our results show that both top-down and bottom-up forces impact a suite of traits beyond the commonly measured aboveground responses. All three classes of traits measured (belowground characteristics, litter production, and reproduction) demonstrated effects of increased nutrient availability and grazer density. However, the occurrence, direction, and size of these effects were not consistent across traits, including aboveground biomass. Three of the nine traits measured demonstrated an interaction between fertilization and grazing: leaf litter, standing dead mass, and number of flowering shoots. Of the six remaining traits measured, one showed no impact of either grazing or fertilization: organic soil content. The other five responses measured were affected by fertilization, grazing, or both as main effects.

Belowground characteristics, such as the root structure and biomass, are critical in determining the stability of marshes in the face of rising seas (F. Darby & Turner, 2008) and in carbon storage (Kulawardhana et al., 2015). Here, as nitrogen availability increased, so did belowground biomass (Fig. 2). This is in contrast with our predictions and with other experimental findings that have found decreases in belowground biomass with fertilization (Darby & Turner, 2008; Deegan et al., 2012b; Turner et al., 2009). This discrepancy may be due to the disparate locations in the marsh (high vs. low marsh) in which the studies took place. An increase in belowground structure could lead to more stable substrate, thereby improving erosion protection and increased carbon storage through sediment accretion and burial of belowground plant material (Lo et al., 2017; Lovelock et al., 2014; Sousa et al., 2010; Turner et al., 2004). However, and potentially more ecologically significant, the ratio between belowground to aboveground biomass decreased with nitrogen additions due to a larger increase in aboveground biomass (Silliman & Zieman, 2001), which supports what is commonly found across wetland plant species (Fig.3; Darby & Turner, 2008; Holechek, 1982). Although both above and belowground biomass increase, the shift to relatively dominant aboveground structure could have consequences for marsh functioning, stability, and may negate some of the positive impacts mentioned above generated by increased belowground structures. As the ratio between above and belowground biomass becomes more disparate, the resisting forces to erosion and sediment loss provided by belowground biomass may be exceeded by eroding forces such as hydrodynamic action on aboveground biomass (Silliman et al., 2019). This could create a net negative impact on cordgrass, even though both above and belowground biomass increase with nutrient availability. For example, eutrophication via agricultural run-off has generally resulted in diminished biomass accumulation over the long-term, leading to potential changes in ecosystem services (Darby & Turner, 2008; Turner et al., 2009) and resilience in salt marshes to edge erosion and collapse (Deegan et al., 2012). Future research is needed to resolve when and where belowground biomass in marsh plants either positively or negatively responds to nitrogen enrichment and this work should be conducted across marsh plant zones.

Grazing also had effects on both belowground biomass and the ratio between below- and aboveground biomass. As grazing pressure increased, belowground biomass decreased while the ratio between below and aboveground biomass increased. Our results combined with those previously presented (Silliman & Zieman, 2001) show a dramatic decrease in aboveground biomass, demonstrate a holistic change to plant structure in a single growing season. This likely occurred because of the strong top-down effect of snails on aboveground structures which then likely lead to increased demand for resources from belowground storage structures. Studies in grasslands suggest that the loss of aboveground tissue to grazing results in a change in resource allocation from belowground root structures to aboveground leaf tissue to compensate for the loss (Blue et al., 2011). Further studies are needed to better understand the relationship and potential compensation between below and aboveground biomass with grazing in salt marshes.

Fertilization and grazing interactively affected litter production (i.e. standing dead mass and leaf litter, Fig. 3), where dead material generally increased with fertilization, especially with grazers present, which is a similar pattern seen in standing live aboveground biomass (Silliman & Zieman, 2001). This pattern suggests a shift in grazing pressure so that snail impact on live grass increases with increasing nitrogen availability. This possibility is supported by published results of this experiment (Silliman & Zieman, 2001) that show increased per capita snail grazing on fertilized plants. Periwinkle snails have been considered part of the brown food web, largely consuming detrital material. However, research has found that periwinkle snails engage in fungal farming behavior by grazing live leaf tissue and facilitating fungal growth by depositing spore-laden feces into the grazing wounds (Silliman & Newell, 2003). The increase in aboveground, nutrient-rich biomass with fertilization could shift snail feeding preference from standing dead detrital material to fungal farming on live grass (He & Silliman, 2015), allowing an accumulation of leaf litter and increasing plant susceptibility to disease, stress, and die off, resulting in more standing dead mass (Silliman et al., 2005; Silliman & Newell, 2003). The likely fate of this increased production of dead plant material will either become part of the detrital food web (*in situ* consumption of dead material by marsh invertebrates), be washed out of the system, or become buried carbon that contributes to a long-term carbon pool (Bouchard & Lefeuvre, 2000; Bulmer et al., 2020; Mcleod et al., 2011). Detrital material plays an important role in marsh ecosystem functioning and nutrient recycling, including supporting higher trophic levels (Schrama et al., 2012). Additionally, an expanded brown food web caused by increased detrital production can extend to other ecosystems post-consumption through the transportation of organisms, thereby supporting adjacent food webs such as deeper water fish communities (Deegan et al., 2002; Valiela et al., 2002). Therefore, the impacts of increased detrital production may be far-reaching and diverse in ecosystem response. Comparatively, increased dead plant material contribution to a carbon pool may establish long-term changes to carbon storage with increased nutrient loads that may be coupled with changes to belowground biomass (Bulseco et al., 2019; Deegan et al., 2012). The interacting impacts of grazers and nutrients on detrital material are likely far reaching and complicated but are valuable to ecosystem functioning and require more investigation.

Grazing and fertilization had mixed effects on cordgrass reproduction, both sexual and asexual. The number of flowering shoots was the other trait (besides litter production traits) that exhibited an interaction between grazing and nutrient enrichment (Fig. 4). In general, fertilization increased the number of flowering shoots. However, at high levels of snail grazers, the number of flowering shoots was diminished with and without fertilization. This could suggest a shift in plant growth allocation away from reproduction to self-maintenance under grazer pressure, regardless of fertilization (Hawkes & Sullivan, 2001). Fertilization increased both the proportion of flowering shoots, the number of new shoots, and the mean length of new shoots (Figs. 4 and 5). The increase in aboveground adult plant biomass with fertilization, previously described (Silliman & Zieman, 2001), combined with our findings of the greater number of new shoots, increased length of new shoots, and increased proportion of flowering shoots with fertilization, suggests a cumulative increase in areal coverage of cordgrass and an increased investment in sexual reproduction following increased nitrogen availability. The combined effects of more aboveground biomass and flowering are consistent with previous results that suggest cordgrass is more likely to flower with greater biomass and height (Liu & Pennings, 2019). The increase in both the proportion of flowering and new shoots could lead to a strengthening of existing ecosystem services salt marshes provide, as well as contribute to and expand local salt marsh systems. For example, the increase in new shoots indicates increased primary productivity and is tied to trophic transfer through the food web, carbon sequestration rates, and sedimentation that may provide resilience to sea level rise(Choi & Wang, 2004; Leuven et al., 2019; Pauly & Christensen, 1995). Alternatively, increased grazing pressure either reduced or had no effect on cordgrass asexual reproduction (abundance and length of new shoots) while it decreased sexual reproduction (flowering). For example, grazing pressure did not influence the length of new shoots. This suggests that grazers may either focus efforts on older individuals, not impacting new shoot lengths, or new shoots that do experience grazing may not frequently survive which is supported by the decrease abundance of new shoots with increased grazing pressure. Additionally, these results could have been observed because increased grazing decreases belowground biomass creating a deficit in energy available to support new shoots through the initial growth stages. Young plants are dependent on carbon storage and are not yet a carbon source for the greater genet. Additionally, the proportion of flowering shoots decreased with increased grazers. Cordgrass mostly depends on vegetative reproduction, given the low seed viability (only lasting a year) and the lack of reliable seed banks on salt marshes (Jones et al., 2019). The reliance on vegetative reproduction may be detrimental to long-term survival as marshes face many anthropogenic stressors. A decrease in overall reproductive output could diminish ecosystem function and services provided by the marsh as well as an increase in marsh susceptibility to global change stressors.

Periwinkles, the grazing snail used in this study, have been shown to dramatically reduce the biomass of cordgrass, creating large die-off areas, lowering the plant's ability to withstand environmental stress, and diminishing associated ecosystem services (Bertness & Silliman, 2008; Bouchard & Lefeuvre, 2000; Brisson et al., 2014; He & Silliman, 2015; Silliman et al., 2005). Researchers found that this diminution is not a linear function of area loss, as up to half of salt marsh sediment storage ability is lost when a quarter of the marsh dies off (Donatelli et al., 2018). The continuum of positive and negative impacts of grazing and fertilization across traits demonstrates the converging, and often conflicting, forces of top-down and bottom-up effects on the structure and function of primary foundation species. Furthermore, nutrient enrichment greatly increased herbivory in salt marshes. In this way, these opposing top-down and bottom-up forces could create a negative feedback loop, which would dampen and stabilize any effects presented on their own (Silliman et al., 2005). However, other combinations of top-down and bottom-up effects might be more detrimental in certain environmental contexts. For example, drought decreases cordgrass growth and its ability to resist herbivores, which results in mass die-offs of cordgrass and a collapse of these systems (Bouchard & Lefeuvre, 2000) which may be exacerbated under high nutrient loads. For now, the interactive effects of top-down and bottom-up forces are largely suggestive. Therefore, more spatially diverse and highly replicated research is needed to fully understand these interacting forces on many traits.

While the knowledge of herbivory and fertilization as oppositional top-down and bottom-up forces on a suite of cordgrass traits is useful to elevate our understanding of how these forces contribute to the structure and function of natural systems, it also provides knowledge which might be used to better manage salt marsh systems. By understanding the effects that elevated herbivory or fertilization might have on more than one cordgrass trait, we could also better predict impacts of local and global changes on marshes. These predictions and management strategies can be better informed using a compilation of interacting traits, rather than the limited response to aboveground biomass, which, as we have demonstrated, does not depict the full impacts of changing nutrient availability and grazer pressure. While this is useful knowledge to anticipate effects on marsh habitat, the full picture of what forces regulate salt marsh habitats is undoubtedly far more complicated than the two oppositional forces of herbivory and fertilization.

3. Herbivory and nutrient additions control vegetation diversity and biomass in a salt marsh transition zone.

The accompanying supporting information is included in Appendix B

3.1 Introduction

Understanding how top-down and bottom-up drivers interact to shape plant communities has long been a primary goal in ecology (Borer & Gruner, 2009; Hairston et al., 1960; Hanley & Pierre, 2015; Power, 1992). Direct and indirect top-down drivers of plant biomass and diversity exist across various ecosystems. For example, plant biomass and species coexistence can be regulated directly by grazers and indirectly by predators controlling grazer densities. Grazer control occurs in kelp forests (Estes et al., 2004), grasslands (Jia et al., 2018), low salt marshes in the United States (Silliman & Zieman, 2001; Valdez et al., 2023), high salt marshes in Europe (Bakker et al., 2020), and eastern Pacific rocky shores (Menge & Sutherland, 1976; Paine, 1966). Bottom-up forces, like nutrient availability, also control plant growth and diversity. Nutrients can be a limiting factor, for example, in heterogeneous open-water phytoplankton communities (Moore et al., 2013; Tilman et al., 1982). Nutrients can also be an overly abundant factor under eutrophication, leading to toxic algal blooms in similar open-water environments (Heisler et al., 2008). Both nutrient conditions lead to changes in plant biomass and species diversity (Bedford et al., 1999; Bracken et al., 2015; Geng et al., 2022; Harpole et al., 2017; Pekin et al., 2012; Stevens et al., 2004).

Synthesis of top-down versus bottom-up forces across ecosystems shows that the interaction between consumers and nutrients is often complex and system-dependent

(Hillebrand et al., 2007; Meserve et al., 2003; Whalen et al., 2013). However, an extensive meta-analysis suggests that the relative effects of grazers and nutrients, on average, vary predictably across a primary productivity gradient (Hillebrand et al., 2007). This synthesis found that grazers generally increased plant species richness in highly productive ecosystems but decreased richness in lower productivity ecosystems. Alternatively, fertilization generally lowered richness in highly productive environments while increasing richness in low-productivity environments (Hillebrand et al., 2007). There is still a need to better understand the relative effects of top-down and bottom-up forces, especially at the transitions between plant communities, where species from both communities overlap.

The transition zone between neighboring plant communities can create a unique assemblage of species and associated interactions. In ecology, multiple terms describe transition zones, including ecotone and ecocline. Ecotones, for example, are categorized as the sharp or relatively rapid transition between two homogenous ecological communities or ecosystems (Attrill et al., 2000; Hufkens et al., 2009; Kark, 2013; Kent et al., 1997; van der Maarel, 1990). Typical examples of ecotones include the transitions between forest and tundra (Hofgaard & Wilmann, 2002), forests and prairies (DeSantis et al., 2011; J. W. Williams et al., 2009), and estuarine salt to fresh water ecosystems (Attrill et al., 2000). In comparison, ecoclines are more gradual fluxes in environmental conditions that result in a gradation in community transition (van der Maarel, 1990). For example, the elevation gradient in montane habitats influences plant species community composition from hardwood trees to herbaceous shrubs with increased elevation (Attrill et al., 2000; Magee & Antos, 1992; van der Maarel, 1990). Additionally, the habitat mosaic concept encompasses ecological transitions that result in varying habitats across an ecosystem, termed patches or mosaics (Gain et al., 2016; Sheaves, 2009; Stanford et al., 2005; van der Maarel, 1990; Wimberly, 2006). These mosaics are often related to disturbance and environmental fluxes, resulting in dynamic and sometimes ephemeral mosaics across an ecosystem (Gain et al., 2016; Sheaves, 2009; Wimberly, 2006). Transition zones between ecological communities are thus unique zones where species, often outside of their observed core zones interact. This zone can – but not always – represent a biodiversity peak in the area (Kark, 2013; Kark et al., 2007; Kent et al., 1997; Smith & Goetz, 2021). As a potential hotspot of biodiversity, transition zones have been marked for conservation consideration (Araújo & Williams, 2001; Gaston et al., 2001; Smith et al., 2001; Wasson et al., 2013). Changes in community structure in transition zones are also considered as a potential indicator of future pathways to environmental alteration due to climate change (Brownstein et al., 2015; Kupfer & Cairns, 1996; Smith & Goetz, 2021; Wasson et al., 2013). It is unclear, however, whether ecological theory developed from studying distinct ecological communities applies to these important transitional areas. For example, it is unknown if the predictability of the effect of global change factors, such as nutrient enrichment and changing grazing intensity, will manifest in these areas. Some research already suggests that theories do not function well across environmental stress gradients (Fariña et al., 2009).

In southeastern U.S. salt marshes, there are several plant community transition zones. First, on the seaward edge, there is the transition from marine, near-shore habitats characterized by oyster reefs and mud flats to low elevation, monospecific salt marsh grasses. Second, on the landward edge, the transition from high marsh community to maritime forest. Third, hummocked or raised elevation areas within the low marsh zone create small patches of high marsh with sharp transitions from the low marsh communities. In some cases, these transitions can happen rapidly, within a few meters (Bertness et al., 2002). In the southeastern U.S., the low salt marsh community tends to be dominated by monospecific meadows of the stress-tolerant salt marsh cordgrass, *Spartina alterniflora*. At higher elevations, high marsh meadows exist, occupied by shrubs like marsh elder (*Iva frutescens*) and, in some cases, more terrestrial plants like wax myrtle (*Myrica cerifera*). Graminoids and forbs like salt marsh hay (*Spartina patens*), saltgrass (*Distichlis spicata*), and sea oxeye (*Borrichia frutescens*) occupy the transition zone between low and high marsh meadow. Furthermore, the transition between low and high marsh can be zoned into monospecific bands when higher nutrient soils promote competitive dominance (Bertness, 1991; Levine et al., 1998; Pennings et al., 2002). Alternatively, high marsh meadows can also exist as a mix of species maintained by lower-nutrient soils (Penk et al., 2020; Theodose & Roths, 1999). Much of the marsh work exploring bottom-up factors focuses on what maintains the bands of monospecific marsh, such as salinity, tidal inundation, fertilization, and competition (Bertness, 1991; Bockelmann et al., 2002; Crain et al., 2004; Eleuterius & Eleuterius, 1979; Ewanchuk & Bertness, 2004; Levine et al., 1998; Pennings & Callaway, 1992). In addition, work explores how this transition zone shifts with global change factors, specifically sea level rise (Jobe IV & Gedan, 2021; Wasson et al., 2013).

Research on grazing often focuses on the effects of large ungulate herbivores in the high marsh (Bakker et al., 2020; Howison et al., 2015; Jobe IV & Gedan, 2021) or invertebrate grazers in the low marsh (Beheshti et al., 2021; Crotty et al., 2020; Renzi & Silliman, 2021; Silliman & Zieman, 2001). No studies, however, have examined the relative effects of top-down and bottom-up forcing on species diversity at the low-high marsh transition zone.

Here, I ask how species diversity responds to fertilization and total grazer exclusion at the transition between low marsh and mixed species high marsh meadow in a southeastern U.S. salt marsh. Grazers, in this system, refer to insect grazers and the salt marsh periwinkle snail (*Littoraria irrorata*). I predicted that ecological theory that predicts the effects of grazers across a productivity gradient would hold for this productive environment. Specifically, I hypothesized that 1) fertilization would negatively impact species diversity (Borer et al., 2014; Hillebrand et al., 2007) and 2) that grazers would help maintain diversity as salt marshes are relatively highly productive ecosystems (Barbier et al., 2011; Hillebrand et al., 2007; Mitsch & Gosselink, 2007; White et al., 1978). I also predicted that grazers would be specialists and graze primarily on the most abundant species – *S. alterniflora*, and thereby enhance species diversity (Borer et al., 2014; Emery et al., 2001; Wilkinson & Sherratt, 2016). I also explored how fertilization and grazer presence impacted species-specific responses in multiple traits, including aboveground biomass, vegetation height, and percent cover. I hypothesized that response to aboveground biomass, height, and cover would vary by species (Pennings et al., 2005). I also predicted species-specific responses would be partly due to a shift in competitive hierarchy (Emery et al., 2001). When fertilized, the inferior competitor for nutrients, *S. alterniflora*, would become the competitive dominant for light (Emery et al., 2001; Levine et al., 1998). In this case, I predicted *S. alterniflora* would have greater biomass, shoot length, and cover with nutrient additions but display lowered measurements in these traits with grazer presence (Gustafson et al., 2006; Renzi & Silliman, 2021; Silliman & Zieman, 2001). I expected other species, such as *S. patens* and *D. spicata,* would have lower biomass, height, and cover with nutrient additions but higher with grazers. To my knowledge, this is the first total grazer exclusion by nutrient addition experiment conducted at the low-high marsh transition zone. This zone has the potential to experience early environmental change due to global change factors such as sea level rise and could act as an indicator zone (Wasson et al., 2013). Therefore, a better ecological understanding that informs theory is needed to infer ecosystem health and the impacts of impending environmental changes.

3.2 Methods

3.2.1 Site Description

The experiment occurred in a salt marsh in Fulcher Creek along the North River in Beaufort, North Carolina (NC), U.S. (34.761043, -76.621524). This site is an extensive salt marsh dominated by *S. alterniflora* at lower elevations. Along the creek boundary, hummocks of higher elevations create a steep gradient from low marsh vegetation dominated by a single species to high marsh meadow vegetation occupied by several species. The rapid change in vegetation provides the ideal environment to explore how top-down and bottom-up factors influence species diversity and species-specific trait responses in a transition zone. There were seven species of vegetation observed in this zone, including *S. alterniflora* (smooth cordgrass)*, S. patens* (marsh hay)*, D. spicata* (saltgrass)*, B. frutescens* (sea oxeye)*, Limonium carolinianum* (Carolina sea lavender)*, Symphyotrichum spp.* (marsh aster)*,* and *Salicornia spp.* (pickleweed). I could not distinguish between the species of pickleweed and aster present in NC and, therefore, combined *Salicornia* and *Symphyotrichum* at the genus level *Limonium carolinianum, Symphyotrichum,* and *Salicornia* were considerably rarer than the other four species and only appeared ephemerally in a handful of plots.

3.2.2 Experiment

A fully factorial grazer manipulation by nutrient addition experiment started in May 2021 with four treatments (n=6, 0.25m^2 plots): 1) grazers with nutrient addition, 2) grazers with ambient nutrients, 3) no grazers with nutrient addition, and 4) no grazers with ambient nutrients. Plots had approximately 50% *S. alterniflora* cover at the onset of the experiment and a similar number of species. Hardware mesh, roofless cages (0.25 cm mesh by 76.5 cm tall) encircled all plots. Cages were held in place by 5.1 x 2.5 cm wooden garden stakes, and hardware mesh was dug 10 cm into the sediment to prevent snail escape under the mesh frame (Fig. 6A). To avoid resource sharing with plants outside of the plots, roots were severed at the perimeter of plots to 30 cm depth (Silliman & Zieman, 2001). At this site, the dominant grazers were the marsh periwinkle (*L. irrorata*, here on referred to as snails) and insect grazers, mainly in the order Orthoptera (e.g., tettigoniid grasshoppers and katydids) and Hemiptera (e.g., sap-sucking leafhoppers). I did not target specific insect grazers. Instead, I used a relied-upon method of spraying non-grazer plots with a garden insecticide for 20 seconds (~48ml) once a month throughout the experiment. I used BioAdvance® Complete Insect Killer (imidacloprid 0.72%, beta-cyfluthrin 0.36%). This is a systematic insecticide with a similar chemical makeup to insecticides used in previous marsh experiments (Bertness et al., 2008; Sala et al., 2008). Insecticide was applied to vegetation on a falling tide to prevent it from being washed out by tides. For snail grazing, I initially removed all snails from the plots, enumerated them, and added back the average number of snails per plot (30 snails). To achieve nutrient treatments, I inserted one slow-release fertilizer spike (Jobe's® Tree and Shrub Spike) per plot once a year at the beginning of the growing season in May. Nutrient additions resulted in an added 16.9g N, 3.4g P, and 3.4g K per year. As a procedural control, ambient nutrient plots received a similar soil disturbance as inserting the fertilizer spike into nutrient addition plots. The experiment ran for three growing seasons and concluded in August 2023.

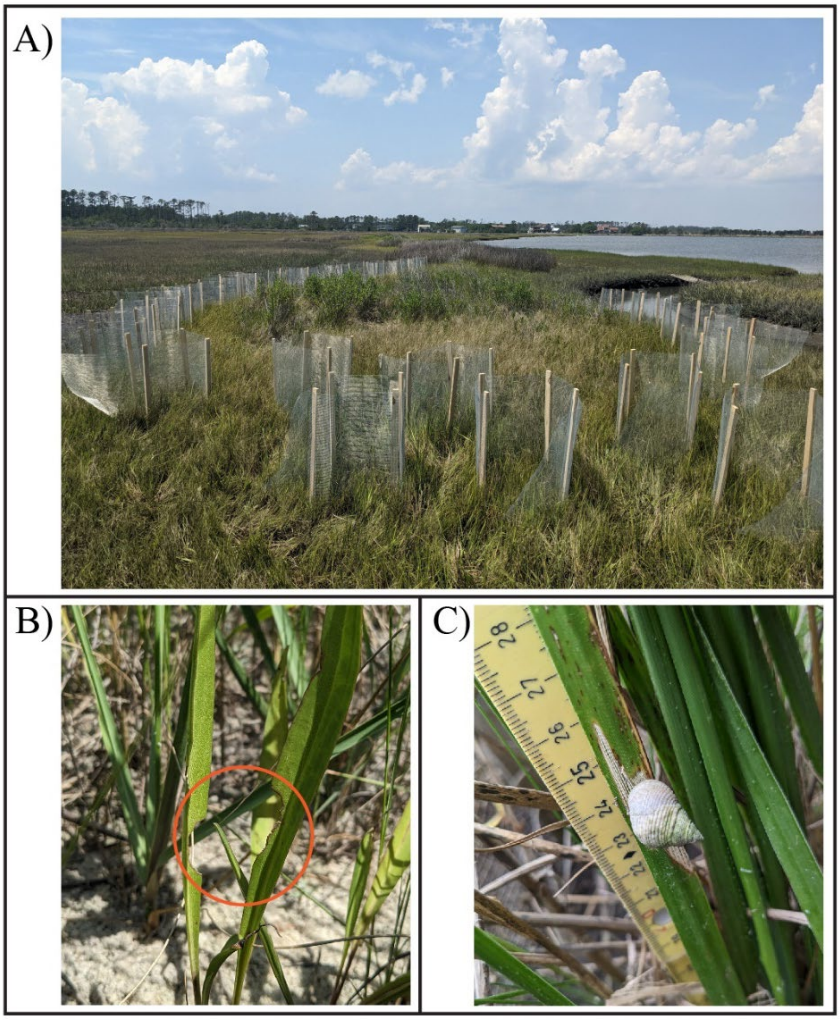

Figure 6: Experimental and grazing photos. A) Photo of experimental area during cage construction. B) Photos of insect grazing scar, circled in orange, on *L. carolinianum*. C) Snail grazing scar with snail on *S. alterniflora*.

At the beginning of the experiment, I measured shoot counts for *S. alterniflora*, as well as percent cover and shoot lengths for each species. I measured the percent cover and shoot lengths again at the end of the experiment in August 2023. I estimated the percent cover throughout the experiment for continuity. Shoot length was measured from sediment to the tip of the tallest blade or stalk for five random shoots of each species. In

August 2023, I also measured the length of grazing scars on *S. alterniflora* from the same five random shoots used to measure shoot length. Insect and snail grazing scars were delineated on the shoots based on appearance (Fig. 6B & C). I did not measure sap-sucking insect scars. Insect grazers like grasshoppers leave clean edges and complete removal of biomass-type scars, while snails use the radula to scrape the exterior of plant tissue, leaving scratch-like scars. Scar length was standardized by dividing the scar length by the shoot length.

At the conclusion of the experiment in August 2023, I collected destructive measures of biomass (above and belowground) from a 20cm x 20cm representative square in each plot. Belowground biomass was taken from the same sampling square to 30cm depth. The aboveground samples were separated into living and dead tissues and dried to a constant weight. Dead tissue was determined if the stem or leaf was greater than 75% browned and lumped across all species, while living tissue was separated by species. Belowground biomass was thoroughly washed to remove sediment and large chunks of dead or unrelated debris. Samples were dried to a constant weight.

Experimental cages are commonly used in marsh experiments (Hughes et al., 2024; Valdez et al., 2023). However, I still wanted to account for any caging effects. Therefore, I set up an additional six control plots in May 2021. Three had complete, lifted cages that organisms could pass under freely (cage controls), and three were fully open and marked with two diagonal posts (controls, n = 3). In August 2023, I sampled aboveground biomass from these plots in the same manner as described above.

3.2.3 Statistical Analysis

All analyses were done in R version 4.2.2 (R Core Team, 2022). I tested caging artifacts among my control and cage-control plots using Welch's two-sample t-tests for the aboveground biomass of the four most common species (*S. alterniflora, S. patens, D. spicata,* and *B. frutescens*), dead aboveground mass, and species richness. To assess initial conditions and ensure that plots started with similar species richness and abundance of *S. alterniflora*, I used a two-way Analysis of Variance (ANOVA) with grazing, nutrient addition, and the interaction between the two as factors.

Two-way ANOVAs with grazers, nutrients, and the interaction between the two as factors were used to assess differences in species richness, biomass, shoot length, percent cover, and grazing scars. All data were tested for homoscedasticity using Levene's test (Levene, 1960). The normality of residuals was assessed from visual observations of q-q plots and Shapiro-Wilks tests (Shapiro & Wilk, 1965). Data that did not meet the assumptions for linear models were transformed using logarithmic, square root, or reciprocal transformations based on the structure of the data (Table S1). In one case, the percent cover of *S. patens* data could not be transformed to meet the normality assumption, so I used the non-parametric Kruskal-Wallis tests (Kruskal & Wallis, 1952).

Total plot aboveground biomass was assessed by summing aboveground biomass across species. It was also assessed separately by species. Because rare species (*L. carolinianum, Symphyotrichum,* and *Salicornia*) only had a handful of observations, they were summed per plot for aboveground biomass and percent cover. Additionally, these rare species data did not meet the assumptions for normality. Therefore, Kruskal-Wallis tests were used to test differences between means in grazer/ no grazer and nutrient/ ambient nutrient treatments.

Species richness and Shannon's diversity index (H'; Shannon, 1948) were calculated in the 'vegan' package (Oksanen et al., 2022). Shannon H' was calculated from the percent cover estimated for each species (Lönnqvist et al., 2021; Onaindia et al., 2004; Rodríguez-Loinaz et al., 2008). Shannon H' did not meet the assumption of normality. Therefore, to test differences between means in grazer/ no grazer and nutrient/ ambient nutrient treatments I used Kruskal-Wallis tests. Due to their patchy presence, rarer species were dropped from analysis for shoot length. There were plots without *S. patens* at the end. Therefore, the sample size is uneven when assessing the shoot length of *S. patens.*

3.3 Results

There were no significant caging effects on the live biomass of the common species, dead mass, or species richness (Fig. S1, Table S2). Also, there was no significant difference between initial shoot counts of *S. alterniflora* and species richness across treatments (Fig. S2, Table S3). Plots started with an average of 31.6 shoots ± 2.04 (mean ± SE) of *S. alterniflora* and 4.46 species ± 0.18.

Species richness was negatively affected by both grazers ($F_{1,20}$= 18.97, p=0.0003) and nutrient additions ($F_{1,20}$= 6.89, p=0.016; Fig. 2). Plots exposed to grazing had 4.0 species ± 0.2 SE while plots without grazing had 5.3 ± 0.3 species. Additionally, nutrient addition had a negative impact on species richness, with plots exposed to nutrient additions having 4.3 species ± 0.3 and plots with ambient nutrients having 5.0 species ±

0.3. Additionally, Shannon diversity only exhibited effects of nutrients (χ^2= 8.33, p=0.004; Fig. 7). Similar to richness, plots with nutrient additions had lower Shannon H' (0.85 ± 0.09) compared to plots with ambient nutrients (1.17 ± 0.03; Fig. 7).

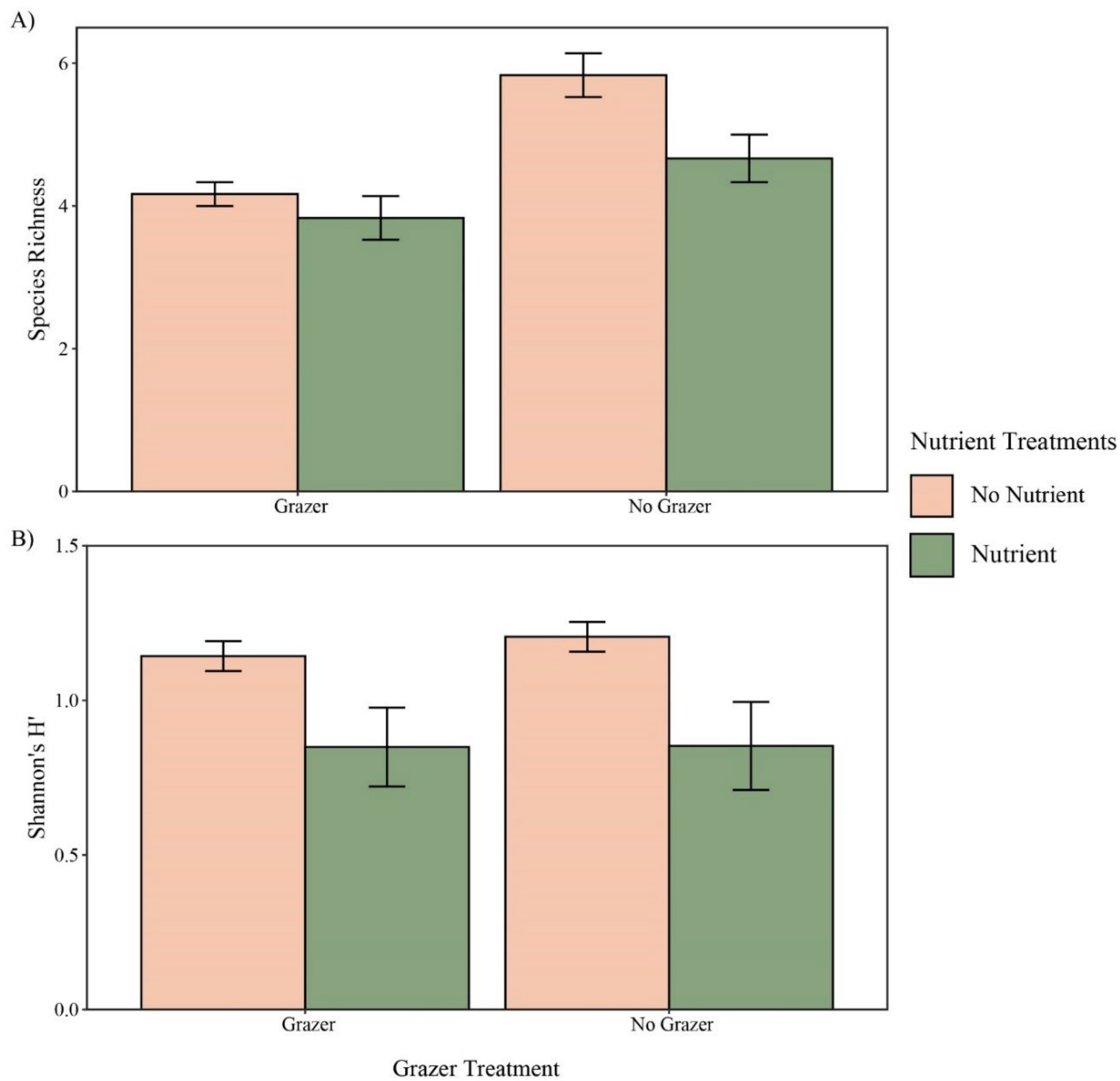

Figure 7: Response of plant diversity metrics to grazing and nutrient additions. A) species richness and B) Shannon's index (H'). Error bars represent standard error.

Total summed aboveground biomass was higher in non-grazer plots ($F_{1,20}$= 14.59, p=0.001) and nutrient addition plots ($F_{1,20}$= 14.36, p=0.001; Fig 8A, Table 2) than in grazer and ambient nutrient plots respectively. Plots with grazers had a total aboveground biomass of 639.5 g/m^2 ± 98.6 while non-grazer plots had 1131.4 g/m^2 ± 129.0. Nutrient addition plots had a total aboveground biomass of 1129.4 g/m^2 ± 144.0 compared to 641.5 g/m^2 ± 76.0 in plots without nutrients. *Spartina alterniflora* aboveground biomass was the only species to have effects of nutrient additions ($F_{1,20}$= 20.2, p=0.0002; Fig. 3, Table 3 & 4). There was no impact of grazers on *S. alterniflora* aboveground biomass. There was 634.5 g/m^2 ± 106.3 of *S. alterniflora* aboveground biomass with fertilization compared to 134.4 g/m^2 ± 38.7 without. *Distichlis spicata* demonstrated grazer influence on aboveground biomass ($F_{1,20}$= 9.54, p=0.007; Fig. 8, Table 3 & 4). There was 40.9 g/m^2 ± 20.7 of *D. spicata* aboveground biomass with grazers compared to 187.4 g/m^2 ± 49.1 without grazers. Grazing and nutrient additions did not influence the aboveground biomass for the two remaining common species (*S. patens* and *B. frutescens*: Fig. 8, Table 3 & 4). For the rarer species, grazers had a negative effect on aboveground biomass (χ^2= 9.32, p=0.002) and marginally positive influence by nutrient additions (χ^2= 2.98, p=0.084). Plots without grazers had 104.8g/ m^2 ± 52.69 of aboveground biomass of rare species compared to 0.3 g/ m^2 ± 0.3 of aboveground biomass in grazer plots (Fig. 8, Table 3 & 4). Additionally, plots with nutrient additions had 58.9 g/ m^2 ± 52.8 of aboveground biomass of rare species compared to 46.2 g/ m^2 ± 22.0 in ambient nutrient plots (Fig. 8, Table 3 & 4). Belowground biomass and the belowground: aboveground biomass ratio showed no differences between treatments (Fig. 9A & B, Table 2). Dead mass was 2.2 times greater in plots with nutrient addition than ambient nutrients ($F_{1,20}$= 7.77, p=0.01), but grazers had no effect (Fig. 9C, Table 2).

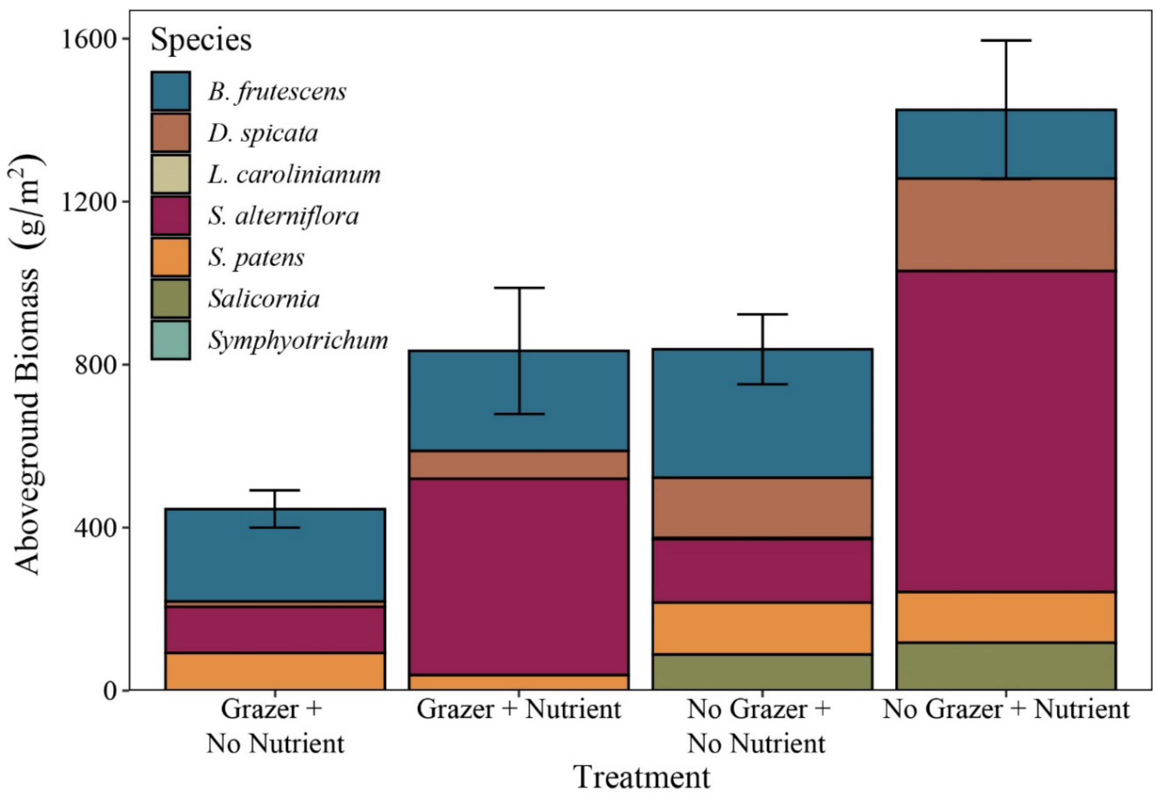

Figure 8: Aboveground biomass. Total aboveground biomass (g/m2), with stacked bars representing individual species' aboveground biomass. Colored bands represent the mean biomass per species displayed within the pooled aboveground biomass. Error bars represent standard errors for pooled aboveground biomass.

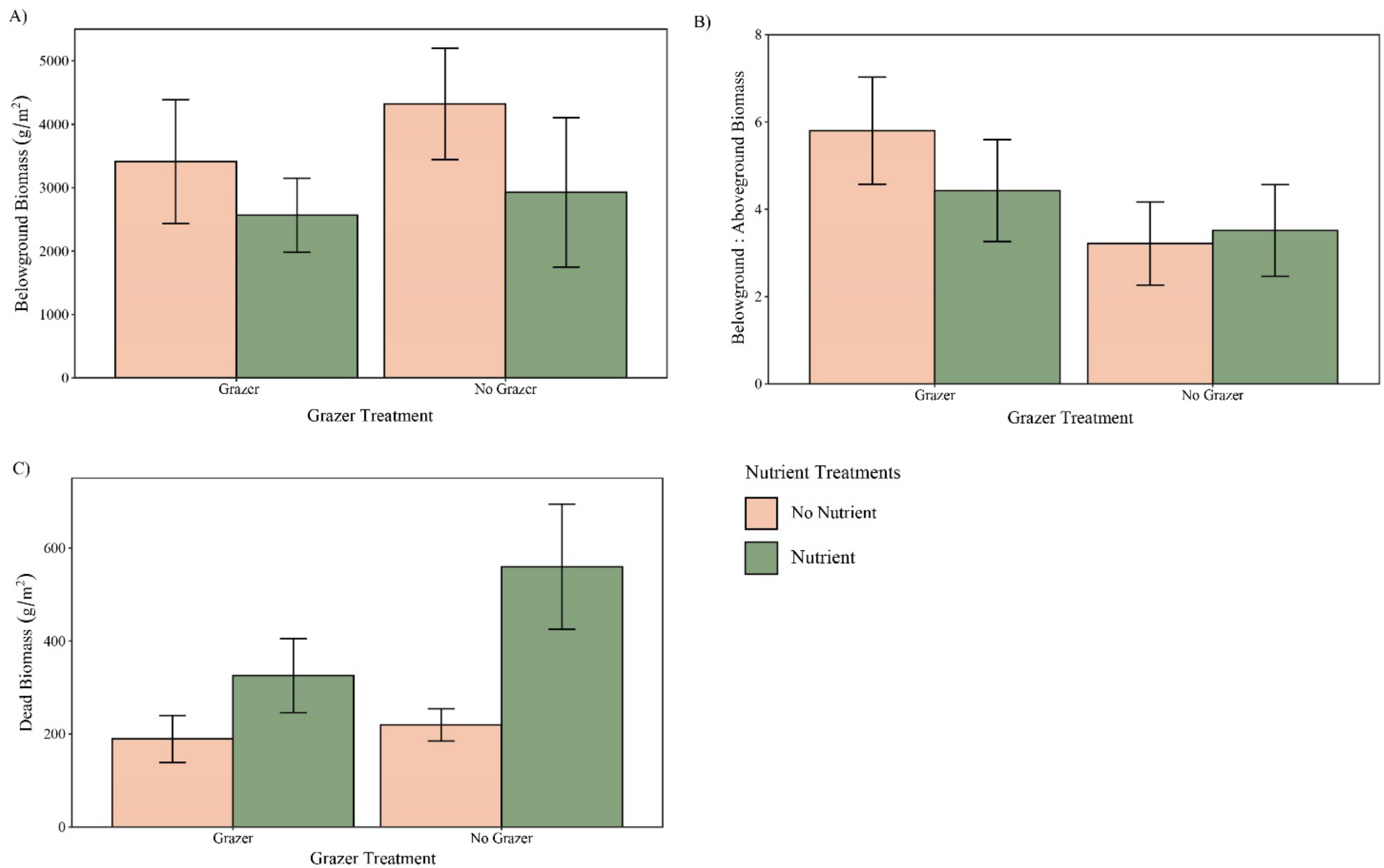

Figure 9: Response of additional biomass and dead plant mass measures to grazing and fertilization. A) belowground biomass (g/m^2), B) the ratio of belowground to aboveground biomass, and C) dead aboveground biomass (g/m^2). Error bars represent standard error.

Table 2: Means, standard errors, and ANOVA results for biomass response to grazing and fertilization. A) Means for biomass measurements, including total aboveground biomass, belowground biomass, and dead mass. B) Two-way ANOVA results.

A) Means				
	Measurement			
Grazer Level ***Nutrients***	**Total Aboveground Biomass (dry mass g/ m2) ± SE**	**Belowground Biomass (dry mass g/ m2) ± SE**	**Ratio Below: Above ground Biomass ± SE**	**Dead Mass (dry mass g/ m2) ± SE**
Removal				
Fertilized	1425.2 ± 175.6	4321.5 ± 877.4	3.5 ± 1.1	559.7 ± 134.8
Ambient	837.6 ± 88.5	2927.4 ± 1778	3.2 ± 1.0	219.5 ± 85.1
Addition				
Fertilized	833.7 ± 159.5	3410.3 ± 977.1	4.4 ± 1.2	325.7 ± 79.6
Ambient	445.3 ± 47.1	2565.3 ± 583	5.8 ± 1.2	189.3 ± 123.7

B) ANOVA				
Source	**Total Aboveground Biomass**	**Belowground Biomass**	**Ratio Below: Above ground Biomass**	**Dead Mass**
Nutrients (N)	***	NS	NS	**
Grazers (G)	***	NS	NS	NS
G + N	NS	NS	NS	NS

Notes: *P < 0.05; **P < 0.01; ***P < 0.001; NS, not significant (P > 0.05)

Table 3: Means and standard error results for species-specific response to grazing and fertilization.

	Measurement		
Grazer Level ***Nutrients***	**Aboveground Biomass (dry mass g/ m2) ± SE**	**Shoot Length (cm) ± SE**	**Percent Cover ± SE**
Species: ***S. alterniflora***			
Removal			
Fertilized	787.6 ± 117.7	87.5 ± 5.8	53.3 ± 7.1
Ambient	155.6 ± 76.3	55.0 ± 2.3	18.7 ± 7.3
Addition			
Fertilized	481.4 ± 162.7	64.1 ± 5.6	28.3 ± 9.0
Ambient	113.2 ± 24.1	44.9 ± 2.2	7.8 ± 1.9
Species: ***S. patens***			
Removal			
Fertilized	124.3 ± 75.3	54.6 ± 4.9	3.7 ± 2.0
Ambient	127.2 ± 35.9	36.4 ± 2.2	6.9 ± 3.3
Addition			
Fertilized	38.1 ± 23.4	45.7 ± 3.5	3.8 ± 2.4
Ambient	91.7 ± 35.4	31.2 ± 5.3	7.9 ± 3.9

Species: *D. spicata*			
Removal			
Fertilized	226.8 ± 89.2	40.3 ± 7.0	14.2 ± 3.3
Ambient	148.0 ± 44.8	37.1 ± 4.9	23.5 ± 6.6
Addition			
Fertilized	68.7± 39.0	32.0 ± 5.7	14.5 ± 4.3
Ambient	13.0 ± 7.1	25.2 ± 3.7	7.3 ± 4.6
Species: *B. frutescence*			
Removal			
Fertilized	168.6 ± 81.4	40.9 ± 7.7	4.7 ± 1.3
Ambient	315.0 ± 53.1	37.8 ± 2.0	13.3 ± 1.7
Addition			
Fertilized	245.5 ± 97.0	34.8 ± 7.6	3.8 ± 1.5
Ambient	226.8 ± 33.6	31.1 ± 3.9	12.5 ± 2.8
Species: *Rare Species*			
Removal			
Fertilized	117.8 ± 104.2	-	1.0 ± 0.8
Ambient	91.9 ± 36.0	-	4.4 ± 1.5
Addition			
Fertilized	0 ± 0	-	0 ± 0
Ambient	0.5 ± 0.5	-	2.5 ± 2.5

Table 4: Statistical results from two-way ANOVAs for species-specific response to grazing and fertilization.

Source	Aboveground Biomass (dry mass g/ m2)	Shoot Length (cm)	Percent Cover
Species: *S. alterniflora*			
Nutrients (N)	***	***	***
Grazers (G)	NS	***	*
N + G	NS	NS	NS
Species: *S. patens*			
Nutrients (N)	NS	***	NS
Grazers (G)	NS	NS	NS
N + G	NS	NS	NS
Species: *D. spicata*			
Nutrients (N)	NS	NS	NS
Grazers (G)	**	~	NS
N + G	NS	NS	NS
Species: *B. frutescence*			
Nutrients (N)	NS	NS	***
Grazers (G)	NS	NS	NS
N + G	NS	NS	NS
Species: *Rare Species*			
Nutrients (N)	NS	-	NS

Grazers (G)	**	-	**
Notes: ~ P<0.08; *P < 0.05; **P < 0.01; ***P < 0.001; NS, not significant (P > 0.05); - No test			

Species-specific shoot length exhibited variable responses to treatments. *Spartina alterniflora* was the only species to show impacts of both grazers ($F_{1,20}$= 15.9, p=0.0007) and nutrients ($F_{1,20}$= 37.1, p<0.0001; Fig. 10A, Table 3 & 4). *Spartina alterniflora* shoots exposed to nutrients were 75.8 cm ± 5.2 compared to 50.0 cm ± 2.2 with ambient nutrients. *Spartina alterniflora* shoot lengths were 54.5 cm ± 4.1 when exposed to grazing compared to 71.3 cm ± 5.7 without grazing. Nutrients alone positively affected *S. patens* shoot length ($F_{1,16}$= 16.3, p= 0.001; Fig. 10B, Table 3 & 4). *Spartina patens* shoots exposed to nutrients were 50.2 cm ± 3.3 and 34.0 cm ± 2.7 with ambient nutrients. *Distichlis spicata* was marginally affected by grazers alone ($F_{1,20}$= 3.43, p=0.079; Fig. 10C, Table 3 & 4). *Distichlis spicata* shoot lengths were 28.60 cm ± 3.4 when exposed to grazing compared to 38.7 cm ± 4.1 without grazing. Neither grazers nor nutrient additions impacted *B. frutescens* shoot length (Fig. 10D, Table 3 & 4).

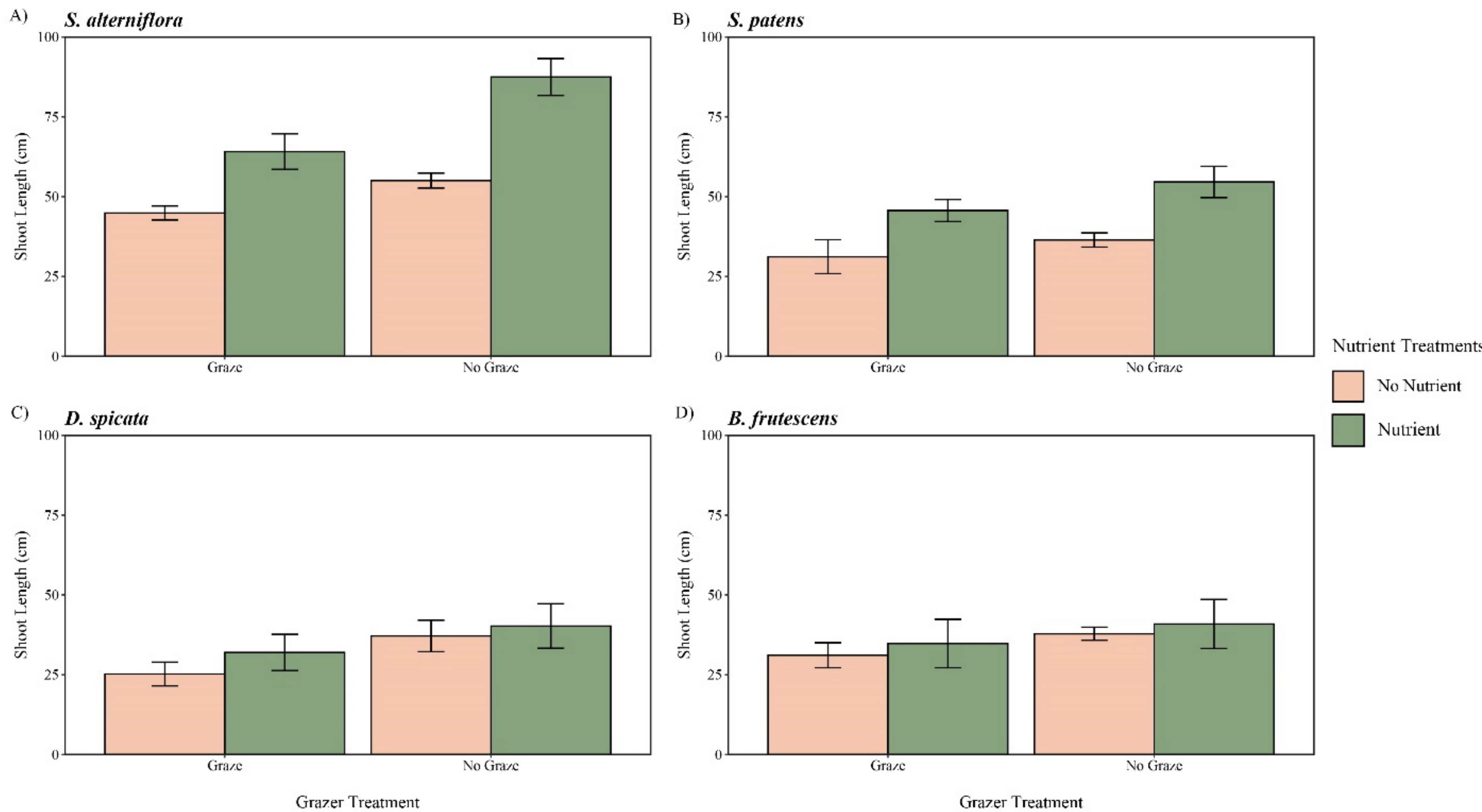

Figure 10: Shoot length (cm) response by species for the four common species to grazing and fertilization. A) *Spartina alterniflora*, B) *Spartina patens*, C) *Distichlis spicata*, and D) *Borrichia frutescens.* Error bars represent standard error.

Percent cover response also varied by species with treatment. *Spartina alterniflora* was negatively influenced by both grazers ($F_{1,20}$= 6.77, p=0.017) and ambient nutrients ($F_{1,20}$= 16, p=0.0007; Fig. 11A, Table 3 & 4). Percent cover in plots with grazers was 18.1 % ± 5.4 SE, while plots without grazers were 36.0 % ± 7.2. Furthermore, plots without nutrients had 13.3 % ± 4.0 cover, while plots with added nutrients had 40.8 % ± 6.7. Nutrient additions had the opposite effect for *B. frutescens* -- nutrient additions were associated with lower percent cover ($F_{1,20}$= 20.7, p=0.0002; Fig. 11D, Table 3 & 4). Plots with nutrient additions had 4.5 % ± 1.0 cover, while plots without had 12.9 % ± 1.6 cover. The remaining two common species (*S. patens* and *D. spicata*) showed no significant impact on nutrient conditions or grazer presence (Fig. 11, Table 3 & 4). For the combined percent cover of the rarer species, there was a negative influence of grazers on percent cover (χ^2=6.9, p=0.009) and a marginally negative impact of nutrient addition on percent cover (χ^2=3.2, p=0.073; Fig. 11E, Table 3 & 4). Plots with grazers had 1.4 % ± 1.3 cover, whereas plots without grazers had 2.7 % ± 1.0 cover. Plots with nutrient additions had 0.52% ± 0.4 cover, while plots with ambient nutrients had 3.4 % ± 1.4.

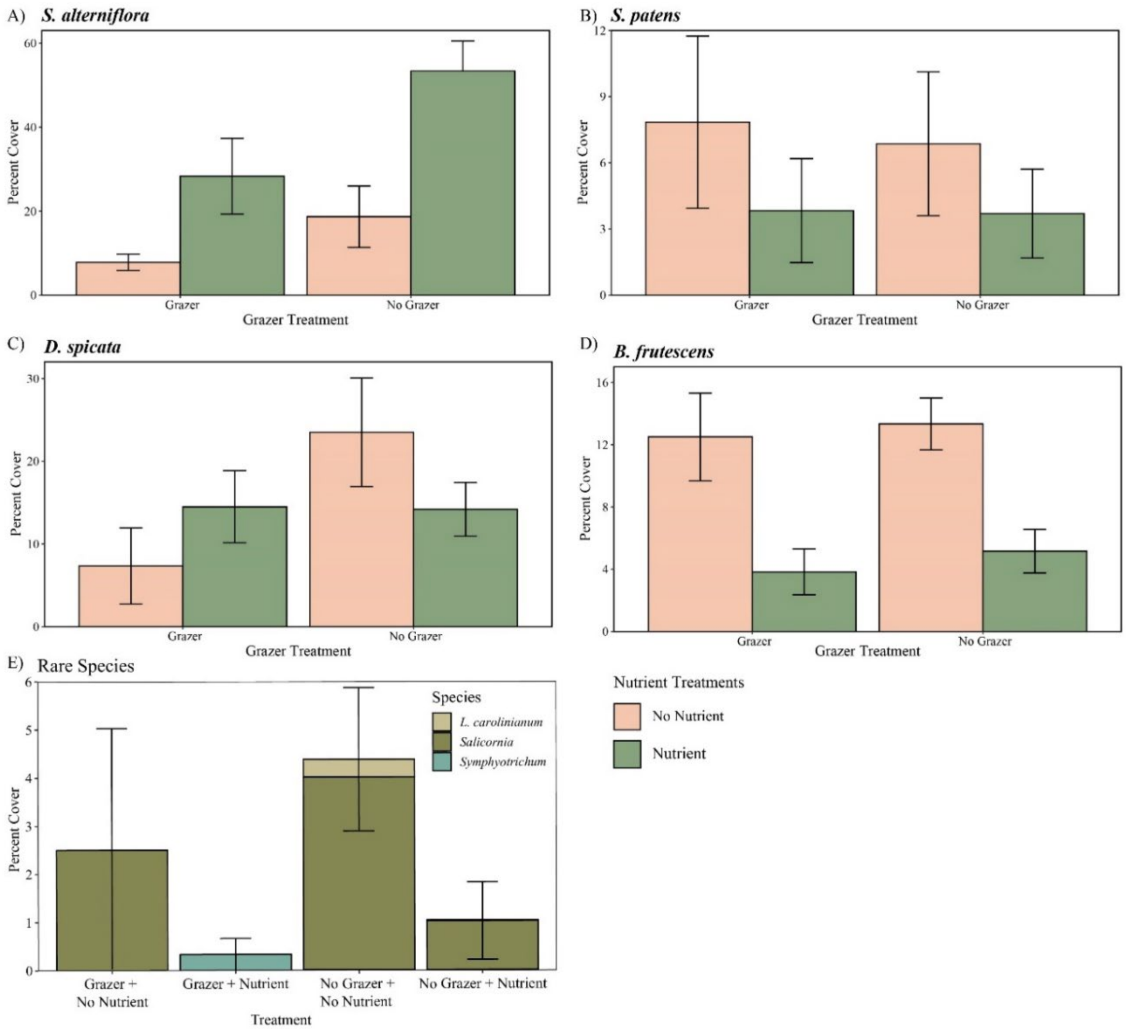

Figure 11: Response of percent cover by species to grazing and nutrient additions. A) *Spartina alterniflora*, B) *Spartina patens*, C) *Distichlis spicata*, D) *Borrichia frutescens*, and E) combined rare species color-coded by species in stacked bars. Error bars represent standard error. Error bars for rare species represent the pooled standard error of the mean percent cover of rare species.

Finally, grazing scar length standardized by shoot length was greater in grazer treatments than in non-grazer treatments (insect; $F_{1,20}$= 43.7, p<0.0001, snail; $F_{1,20}$= 57.5, p<0.0001; Fig 12). Nutrient addition had a marginally positive impact on insect grazing scar length ($F_{1,20}$= 3.7, p=0.068). The pattern did not persist for the snail grazing scar length. Insect grazing scars were 0.15 cm/ cm of shoot ± 0.06 in grazing treatments compared to 0.04 cm/ cm of shoot ± 0.03 in non-grazing treatments. Additionally, insect grazing scars were 0.11 cm/ cm of shoot ± 0.02 in nutrient addition treatments compared to 0.08 cm/ cm of shoot ± 0.02 in ambient nutrient treatments. Snail grazing scars were 0.08 cm/ cm of shoot ± 0.03 in grazing treatments compared to 0.008 cm/ cm of shoot ± 0.009 in non-grazing treatments.

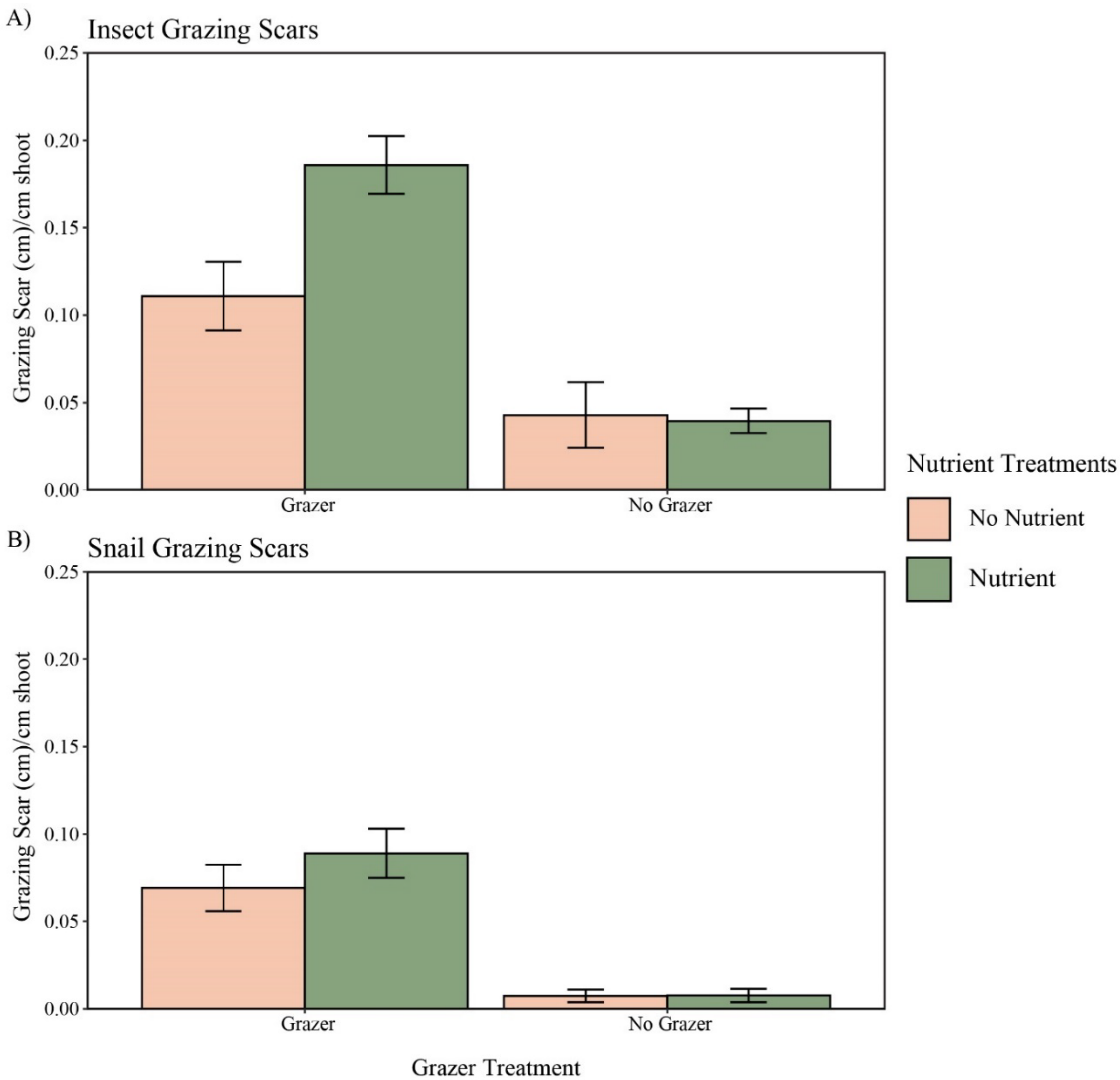

Figure 12: Response of grazing scar length delineated by insect and snail grazers standardized by shoot length of *S. alterniflora* for grazers and fertilization treatments. A) Insect scar length (cm/cm of shoot) and B) snail scar length (cm/ cm of shoot). Error bars represent standard error.

3.4 Discussion

This multi-year experiment demonstrates that top-down (grazers) and bottom-up (nutrient additions) forces impact plant diversity, biomass, height, and percent cover at the low-high marsh transition zone. As predicted, an increase in nutrients to the sediment lowered plant species diversity. However, the paradigm for grazer maintenance of diversity in productive ecosystems was not supported (Borer et al., 2014; Hillebrand et al., 2007; Wilkinson & Sherratt, 2016). Diversity, specifically species richness, was lower under grazer pressure. The mechanisms by which grazers support plant diversity is suggested as the consumption of more common plants that allows rarer plants to exist (Hillebrand et al., 2007). However, this mechanism is not universal (Hillebrand et al., 2007) and in this system the species specific responses may elucidate a mechanistic change that help explain the deviation from prediction. Plant species responded variably to grazer presence and nutrient conditions. As predicted*, S. alterniflora* consistently had higher aboveground biomass, shoot length, and cover in nutrient addition treatments, while grazing negatively impacted shoot length and cover. *Spartina patens* and *B. frutescence* showed no impact of grazer presence and limited impact of nutrient addition. *Spartina patens* only positively responded to shoot length with nutrient addition, while *B. frutescens* demonstrated a negative response to percent cover with nutrient additions. Nutrient additions did not impact *D. spicata,* while grazers negatively affected aboveground biomass and shoot length. Additionally, rare species' aboveground biomass and cover were both suppressed by grazers, but there was no impact of nutrient additions. Generally, the pattern observed in one metric for a species was maintained or not observed in the remaining metrics. Finally, dead plant mass was greater with nutrient additions. Neither grazers nor nutrient additions impacted belowground biomass or the ratio between below and aboveground biomass.

Nutrient additions negatively impacted plant species diversity at the transition zone between low and high marsh plant communities. Specifically, the increase in nutrient availability in fertilized plots likely impacted the competitive structure between plant species by eliminating nutrient deficiencies. It has been well documented that *S. alterniflora* can thrive in the high marsh but is competitively inferior for nutrients (Bertness, 1991; Pennings et al., 2005). When nutrients no longer become a limiting factor, plants switch from competing for nutrients to competing for light, and *S. alterniflora,* the tallest native marsh plant, outcompetes neighboring species (Emery et al., 2001; Levine et al., 1998). My results indicate that *S. alterniflora* is nutrient-limited at the low-high marsh transition zone. Without nutrient limitation, *S. alterniflora* can move higher in the marsh and dominate the area (Emery et al., 2001; Levine et al., 1998). Increased nutrient availability in the high marsh could have a multi-phase impact. The initial response could be species displacement by *S. alterniflora,* which then lowers species diversity. This could be followed by a loss of *S. alterniflora,* similar to the low marsh response to eutrophication (Deegan et al., 2012), leading to low vegetation density and potential erosion. A similar process has occurred with nutrient-fueled *Phragmites* invasion in diverse high marsh communities (Bertness et al., 2002; Silliman & Bertness, 2004).

Grazing also suppressed species diversity, further complicating the respective role of top-down and bottom-up processes in maintaining plant diversity. I predicted plant species diversity would benefit from grazer presence via focused grazing on *S. alterniflora,* which occupied the most space at the onset of the experiment. Previous research has shown that invertebrate grazer presence limits the same plant traits nutrient addition enhances in *S. alterniflora* (Gustafson et al., 2006; Renzi & Silliman, 2021; Sala et al., 2008; Silliman & Zieman, 2001). Therefore, I expected nutrient enrichment and grazers to act antagonistically on *S. alterniflora* to maintain diversity. I did observe negative impacts of grazing on shoot length and cover but not aboveground biomass. Work by Sala and colleagues (2008) found that insect grazers only diminished *S. alterniflora* aboveground biomass with fertilization. While I did find longer grazing scars from insects in fertilized plots, grazing did not translate to lower aboveground biomass for *S. alterniflora* in either nutrient condition. This, combined with the negative grazer impacts on *D. spicata* and the rare species, suggests an unexpected, varied diet of the grazer community. While not tested, I observed grazing scars on other plant species in the high marsh, specifically *L. carolinianum* (Fig. 6B). Work on marsh grazer impacts on plant species other than *S. alterniflora* has been sparse in Eastern U.S. salt marshes. In New England salt marshes, at least two types of insects graze on *L. carolinianum* (Eiseman & Jensen, 2015). Others have reported high abundances of herbivorous insects in monotypic stands of either *S. patens* or *D. spicata* (Pfeiffer & Wiegert, 1981), but we still lack insight into how grazers influence these species. Additional research is needed to elucidate invertebrate grazer feeding preferences and how such grazer preferences may correspond to species diversity in the transition zones.

Potential mechanisms for lowered species richness with nutrient addition and grazer presence could lie in the species-specific responses to treatment. While not tested here, species could have directly or indirectly responded to treatment. For example, the only negative impact observed from nutrient additions was the percent cover of *B. frutescens*. This negative impact could be a direct response and indicate a low tolerance to nutrient shifts, low efficiency in nutrient acquisition by *B. frutescens,* or that is it easily outcompeted for nutrients. *Borrichia frutescens* is often found in low-nutrient environments such as sandy soils (Lonard et al., 2015) and could suggest a limited tolerance for high nutrient conditions or increasing presence of competitors for nutrients. In regards to interspecific competition, the change in *S. alterniflora* dominance with fertilization has been show to alter alters the competitive structure in New England salt marshes (Emery et al., 2001; Levine et al., 1998). Likewise, Pennings and colleagues (2002) added nutrients to the borders between monotypic stands of *S. alterniflora* and *B. frutescens*. They found an increase in *S. alterniflora* biomass with a marginal decrease in *B. frutescens* biomass. This could suggest an alteration in competitive dominance for nutrients. Finally, the lower percent cover of *B. frutescens* could be linked indirectly to other species' responses that change additional abiotic factors. In this case, *S. alterniflora* and *S. patens* had greater shoot lengths with nutrient additions. Increased vegetation height could have created low light conditions that negatively influenced the cover of *B. frutescens*. Research in grasslands has attributed lower species diversity to nutrient additions that cause shoot extension that alters canopy light conditions (Borer et al., 2014; Hautier et al., 2009). The species-specific responses seen here are likely a combination of all three. Further research is needed to clarify the mechanisms driving species-specific responses and how these responses may translate to differences in species diversity.

Dead plant mass was higher with nutrient additions, but neither the belowground biomass nor the below-to-aboveground biomass ratio demonstrated impacts from nutrient or grazer conditions. This further suggests that patterns observed in low-marsh ecosystems are not maintained and are further complicated in the transition between low and high-marsh communities. Previous research in a low marsh, *S. alterniflora* dominant ecosystem found an interactive effect of fertilization and grazing on dead mass (Valdez et al., 2023). However, I only observed a positive effect of fertilization on dead mass here. Increasing foliar nutrient concentrations should increase grazing on live leaf tissues and for snails, which also act as detritivores, away from grazing on dead material (Currin et al., 1995; He & Silliman, 2015; Kemp et al., 1990; Silliman & Zieman, 2001; Valdez et al., 2023). While I did observe greater scar lengths for insect grazers in nutrient-enriched plots, this did not hold for snail grazing scars. These results support previous research exploring snails (Silliman & Zieman, 2001) and insect grazing individually (Sala et al., 2008). This indicates that grazing response to nutrients and the cascading effects of grazing on plant traits is not uniform across all grazers. Finally, I manipulated grazer presence to ambient and removal levels in this system. Accumulation of snail grazers in high densities at the border of salt marsh die-off has been shown to effectively create a front of grazing that further exacerbates marsh die-off (Silliman et al., 2005). The abundance of snails in these studies, which showed strong top-down impacts, far exceeds that observed for the marsh in this experiment. Potent effects of grazers may not be observed until a certain threshold above ambient levels is reached. Renzi & Silliman (2021) found strong snail grazing effects in the low, *S. alterniflora* dominated marsh when there were over 80 snails/ m^2. The abundance of snails within my experiment (120 snails/ m^2) would suggest similar biomass reduction. However, this could again point to a difference in grazing preference at the low-high marsh transition zone.

The lack of impacts for belowground biomass and the ratio between below and aboveground biomass is also intriguing. Previous research suggests that belowground biomass either diminishes or, if it does increase, the ratio of below: aboveground biomass ratio effectively limits any belowground gains in *S. alterniflora* (Darby & Turner, 2008; Deegan et al., 2012; Turner et al., 2009; Valdez et al., 2023). Belowground structures are imperative to maintaining ecosystems for resource acquisition and erosion protection (Lo et al., 2017). However, physiological differences among species could affect the lack of results observed in belowground biomass. A single pooled sample of belowground biomass could miss species-specific patterns. For instance, while one species' root mass may have diminished throughout the experiment, another could have expanded, effectively creating a net zero impact on belowground biomass. This pattern could also explain the null result for the ratio between below and aboveground biomass, given the observed species-specific responses to aboveground biomass alone. Limited work has explored each species' belowground response to aboveground grazers and nutrient conditions in mixed species communities. However, grazing and nutrient addition likely change root structural integrity and abundance. Research on *S. patens* under nutrient additions found that nutrient enrichment decreased root strength (Hollis & Turner, 2021). Additionally, work in an *S. patens* mixed meadow found that grazing by nutria (*Myocastor coypus*) lowered belowground production (Ford & Grace, 1998). In addition, research in multi-species grasslands and crop fields suggests that nutrient resources may not be the primary driver of root biomass. These studies suggest root biomass is significantly influenced by a complicated suite of interspecific interactions between vegetation species and soil biota (de Kroon et al., 2012). The impact on belowground structures is likely significantly more complicated than biomass differences.

The transition between low and mixed species high marsh meadows is potentially a valuable “canary in the marsh” for global change factors (Wasson et al., 2013). The lack of ecological understanding, however, limits the ability to make reliable predictions about how transition zones will respond at best and, at worst, applies a mismatched ecological paradigm. While I elucidated novel patterns at this high-low marsh transition, further research is still needed, especially along environmental gradients. Environmental context-dependency can influence patterns and predictions observed. Research in marshes suggests that additional environmental conditions may influence herbivores and fertilization impacts (Alberti et al., 2010; Fariña et al., 2009). Transition zones often represent a species range margin and an overlap with a unique set of species that may not occur in other places (Bridle & Vines, 2007). Understanding ecological patterns in transition zones is valuable to future conservation measures (Araújo & Williams, 2001; Fariña et al., 2009; Gaston et al., 2001; Kark, 2013; Smith et al., 2001; Wasson et al., 2013), but this zone requires different considerations from the dominant zones of ecosystems (Bridle & Vines, 2007; Hill et al., 2011; Svenning et al., 2014).

4. Mobile consumers can control range limit in an intertidal seagrass ecosystem

The accompanying supporting information is included in Appendix C

4.1 Introduction

Range limit margins of species are set by a combination of biological and physical factors. In amenable environmental conditions, the range limit is assumed to be set by biological interactions, such as competition and consumption (Brown, 1996; Louthan et al., 2015; MacArthur, 1984). In less-than-ideal environmental conditions where physical stressors are prevalent, these physical stressors are assumed to set range limits (Brown, 1996; MacArthur, 1984; Wilson et al., 2005). This paradigm in range limit theory is referred to as the Species Interactions–Abiotic Stress Hypothesis (SIASH) (Louthan et al., 2015). A well-known example occurs in mountain habitats. At high elevations or high latitudinal areas, an obvious tree line occurs where physical factors, such as temperature, dictate the limit of tree coverage rather than species interactions (Ettinger et al., 2011; Körner, 2021). In contrast, when physical stress is decreased at lower elevations and lower latitudes in the same mountain environments, species interactions, namely competition, set the range limits (Ettinger et al., 2011). Another example of these principles, although using different vernacular, can be found in the rocky intertidal where the patterns of horizontal, nearly monospecific bands of organisms (e.g. mollusks, barnacles, algae) growing on rocks perpendicular to the sea are referred to as zonation. Nevertheless, the ideas of where and when biotic and abiotic forces dictate a species range remain similar. Ecologists have found a general pattern of the physically benign edge of the species' range limit being set by species interactions such as competition and predation while the physically stressful limits are set by abiotic factors such as exposure (Bertness, 1991; Lubchenco, 1980; Pennings & Callaway, 1992). However, these studies do not incorporate animal movement into their assessments of controls on range limit. Many consumers are highly mobile, only exerting a top-down influence during finite periods of time that may also be shifting with climate change (Bauer & Hoye, 2014; Kubelka et al., 2022; Peller et al., 2023; Shaw, 2016). Consequently, SIASH may not fit every situation (Shepard et al., 2021), especially in ecosystems with highly mobile consumers and when consumers can readily reach all range limit sides of an organisms distribution. Therefore, knowing how mobile consumers interact with other global change factors, such as nutrient enrichment, that have been more widely studied will increase my ability to understand the relative effects of biotic and physical factors in controlling species range limits.

The exploration of top-down and bottom-up factors that shape ecosystems has been at the center of ecological study for well over 50 years (Borer & Gruner, 2009; Hairston et al., 1960; Hanley & Pierre, 2015; Power, 1992). However, there are still gaps in knowledge regarding how top-down and bottom-up factors interact to alter ecosystems, especially when the actors involved do not fit the assumed hypotheses. For example, many animals that exert top-down control are highly mobile and can exhibit seasonally driven migrations. This temporal and spatial variety makes their impacts on plant foundation species more difficult to assess; however, it is likely that these temporal and spatial fluxes are key to shaping the foundation species through their cascading impacts

(Holdo et al., 2007, 2011). For example, the migration of waterfowl across Europe increases plant dispersal (Brochet et al., 2009). Mobile consumers can also act on foundation species outside of food web dynamics, exerting non-consumptive forcing, such as disturbance, and acting as ecosystem engineers (Hastings et al., 2007; Jones et al., 1997). By simply occupying certain spaces, animals and other organisms can create physical conditions that plants must manage or sometimes rely on for healthy ecosystem functioning. For example, forest elephants maintain forest ecosystems by knocking down trees that allow light gaps for new growth and trampling the understory to encourage plant turnover (Maicher et al., 2020). Of course, plant foundation species are not solely at the whim of animal populations and can also be influenced by variations in other abiotic factors, such as nutrient availability (Cleland & Harpole, 2010), temperature tolerance (Lancaster & Humphreys, 2020), wind stress (Momberg et al., 2021), or wave stress in marine ecosystems (Silinski et al., 2018).

In recent history, physical factors driven by global change have altered ecosystems. In particular, understanding the impacts of increased nutrient availability have been of ecological interest due to the introduction of industrialized agriculture and increased use of fertilizer (Lu & Tian, 2017; Ngatia et al., 2019). The input of nutrients can vastly shift plant community composition, and there have been numerous studies across plant ecosystems exploring the impacts of nutrient increase, especially nitrogen, phosphorus, and potassium. For example, research in grasslands globally has shown that plant diversity and productivity consistently decrease with increased fertilization (Borer et al., 2014; Hautier et al., 2015; Isbell et al., 2013). As global change factors continue to alter ecosystems, a better understanding of which factors impact ecosystems is needed for predicting their future states. Furthermore, understanding how these factors shape areas of high variability, such as at species range limit margins, could have implications for future conservation and restoration strategies. Therefore, I chose to investigate the relative effects of a biotic interaction (consumer foraging effects) and nutrient increase on the marginal range limit of seagrass ecosystems.

Seagrasses are a highly productive plant foundational group that supports many ecosystem functions and services in the marine environment (Duarte & Chiscano, 1999; Nordlund et al., 2016). However, seagrasses are in decline due to many global change factors and in North Carolina, seagrass loss has been attributed to nutrient levels and poor water quality that is exacerbated by pulse influx brought on by storms and heavy runoff (North Carolina Department of Environmental Quality (NCDEQ), 2021; Orth et al., 2006; Paerl et al., 2018; Turschwell et al., 2021). Seagrasses harbor a variety of organisms, including top predators like sharks, and provide fish nursery habitat that supports fisheries production (Gallagher et al., 2022; Nordlund et al., 2016; Orth et al., 2020; Unsworth et al., 2019). Seagrass habitats can also host migratory species, such as salmon and waterfowl, that utilize meadows at discrete time periods (Chalifour et al., 2019; Kollars et al., 2017; Leblanc et al., 2023). Stingrays, for example, are a large organism that use seagrass as foraging grounds stochastically (Ambo-Rappe et al., 2021; Townsend & Fonseca, 1998). In North Carolina (NC), USA, stingrays migrate to seagrass beds in warmer months (April- September; Schwartz & Dahlberg, 1978). This overlaps with the height of seagrass production (Wheeler et al., 2024). Stingrays are destructive, bottom foragers that use electro-receptors to hunt for buried prey such as bivalves, crustaceans, and annelids (Cross & Curran, 2004; O'Shea et al., 2020). To dislodge prey, they use their wide bodies and modified pectoral fins to make large feeding indentations in the sediment, which are referred to as pits (Fig. 13A & B; Howard et al., 1977; Townsend & Fonseca, 1998). Stingray foraging has been shown to be concentrated on the intertidal edge of seagrass beds and at depths that can disrupt seagrass root mats (Townsend & Fonseca, 1998). Seagrass meadows have two local range limits, the intertidal, shoreward edge and the subtidal, waterward edge. However, data on stingrays and their utilization of seagrass meadows is limited and few studies have explored the impacts of stingray foraging on either seagrass range limits.

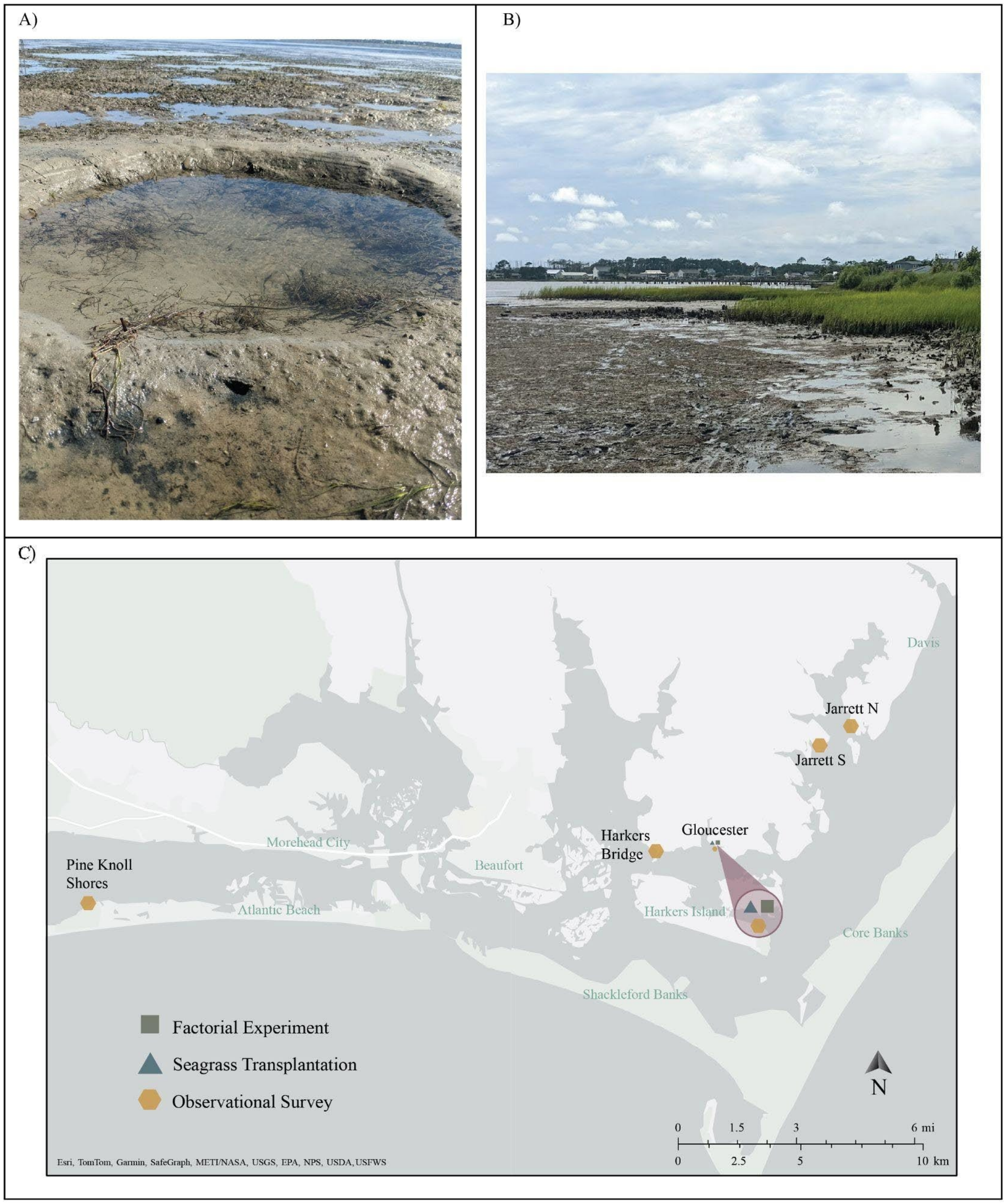

Figure 13: Stingray pit and seagrass edge photos with map for project locals. A) a stingray feeding pit and uprooted seagrass, B) seagrass exposed at low tide with a band of bare space between the seagrass and the shore marsh and oyster habitat, and C) a map of where different aspects of the project occurred. Methodologies on the map are coded by shape and color and represent the factorial experiment, the transplantation experiment and the sites for the observational surveys, all three of which occurred around the Gloucester site denoted by the call out. The base map was generated in Harvard WorldMap in ArcGIS online powered by Esri.

Here, I utilize manipulative field experiments and observational surveys to explore the separate and interactive impacts of stingray foraging and nutrient addition on the intertidal range limit of seagrass. I first asked whether stingray foraging and nutrient additions at the seagrass shoreward edge impacted the percent cover of seagrass. I predicted that the destructive foraging behavior at the edge of seagrass meadows would negatively influence the percent cover of seagrass and that loss would be exacerbated by nutrient additions. While nutrient enrichment has a varied response on seagrass productivity, the continued increase in eutrophication and research on seagrass nutrient enrichment suggest decreased resilience to nutrient loading with lower seagrass biomass (Cardoso et al., 2004; Gladstone-Gallagher et al., 2018; Turschwell et al., 2021). Lower seagrass biomass is often observed at the meadow edge and therefore, I predict nutrient enrichment would contribute to lesser shoreward range extent. Second, I asked whether seagrass could survive higher in the intertidal than observed naturally when protected from stingray foraging. I predicted that without stingray interference, seagrass would be able to survive higher in the intertidal, demonstrating biotic control even on the more physically stressed edge. Finally, I asked whether stingrays could have a generalized effect on seagrass distance from shore in NC seagrass meadows. Using observational surveys, I predicted that higher coverage of feeding pits, as a proxy for stingray feeding pressure and associated disturbance, would correlate to a longer distance between the shore and seagrass meadow. Again, if found this pattern were observed it would suggest biotic control of shoreward range limit in seagrasses. While I do not discount the impacts of physical forces on the marginal range limit of seagrass, the idea that biological factors can significantly contribute to the range limit of a foundation species at the stressful edge is counter to the current range limit theory paradigm and would have broad implications for ecology and conservation measures.

4.2 Methods

4.2.1 Site Description

The experimental tests were conducted in the Straits in Gloucester, NC (34.724409, -76.549580; Fig. 13C). The Straits are part of a larger estuarine system protected by inner sound islands and barrier islands. The environment has saline waters but is protected against high wave action, a key attribute for successful deployment of cages in seagrass systems. The site was selected for 1) a relatively continuous seagrass meadow that naturally spanned the intertidal to subtidal zone and 2) an observed abundance of stingray feeding pits (Fig. 13A & B). The dominant meadow forming seagrass species is *Halodule wrightii* at this site. The meadow is intermixed with sparse *Ruppia maritima*, a halophyte commonly found in seagrass meadows in NC, and during the cooler months (November- May), sparse *Zostera marina* can also be found. From here on, the seagrass community matrix will simply be referred to as seagrass. Stingrays are prevalent in the area (personal observation and enumeration of indentations left from feeding, here on referred to as pits). The several species of stingrays that utilize NC seagrass beds include mainly the Atlantic stingray (*Hypanus sabinus*), the southern stingray (*Hypanus americanus*), the bluntnose stingray (*Hypanus say*), and the cownose stingray (*Rhinoptera bonasus*).

4.2.2 Stingray Exclusion by Nutrient Addition Experiment

To assess the impacts that stingrays and nutrient additions have on the edge of a mature seagrass bed, I conducted a fully factorial field experiment from May 2021 until September 2022. I manipulated stingray access to the edge of the seagrass bed using cages and enriched sediment nutrients resulting in the following four treatments (n=7 for a total of 28, $1m^2$ plots): 1) caged with fertilization, 2) caged without fertilization, 3) no cage with fertilization, and 4) no cage without fertilization (Fig. 14A). Cages were constructed of evenly spaced (20cm distance, roughly the maturation age of the Atlantic stingray, Snelson et al., 1988) bamboo poles, 90cm high to limit the entrance of stingrays from the sides and tops of the plots. Control plots were partial cages that had bamboo posts at the diagonal corners to mark the plots. This design allowed for access of stingrays while also unifying any effects of bamboo addition across treatments. As an additional procedural control to account for the disturbance of adding bamboo posts in caged plots, partially caged plots underwent the same mechanical disturbance with bamboo being inserted but removed as to not deter stingrays. Furthermore, the open spacing of the bamboo posts was additionally intended to reduce impacts on water movement. Finally, the presence of bamboo stakes could have acted as a catchment for debris. Therefore, I removed any accumulated material from caged plots every couple of weeks throughout the summer seasons. In general, debris was only observed in the late summer season in relatively small amounts as seagrass began to senesce.

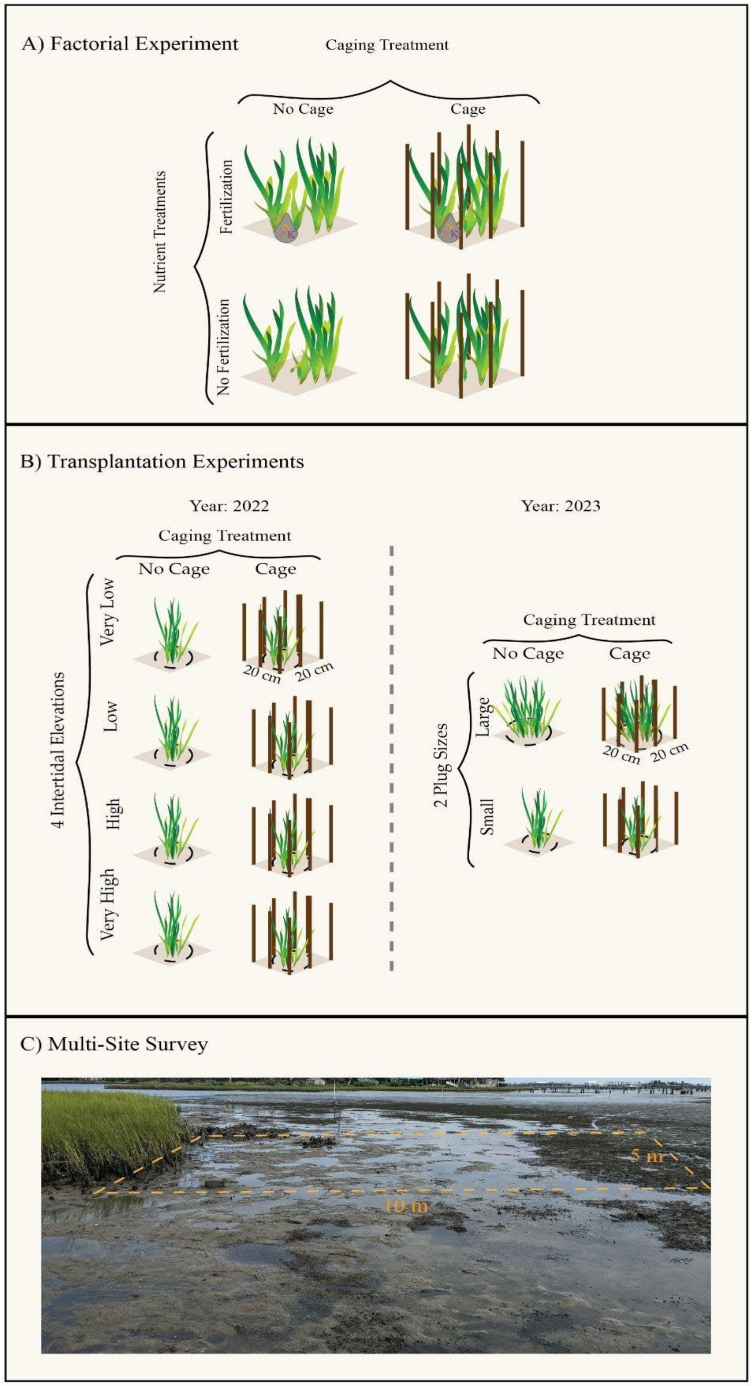

Figure 14: Graphical and pictorial depiction of experimental and observational survey set up. A) the fully factorial, two season stingray exclusion by nutrient addition, B) the seagrass transplantation experiments in 2022 and 2023, and C) the multi-site observational survey. Survey plot is drawn approximately to scale.

Plots were fertilized using Jobe's ® Tree and Shrub Spikes. Four spikes per plot were added to the sediment in a 30cm x 30cm square centered in the middle of the plot. Spikes were added every three months, which was more than enough to account for seagrass nutrient requirements (289.6g N/ m^2/ year, 72g P/ m^2/ year, 72g K/ m^2/ year; Hemminga et al., 1991). Nutrients were added directly to the sediment to evaluate the effects on the seagrass rather than a potential interaction with algae and irradiance that occurs when nutrients are added to the water column (Leoni et al., 2008). Plots without nutrients received procedural control by inserting a similar sized object into the sediment that mimicked the disturbance of adding the nutrient stakes. Plots were initially placed on the edge of the seagrass meadow with approximately 42.7% ± 1.9 standard error (SE) seagrass cover. In addition, relative elevation of each plot was quantified using a laser level and leveling rod to ensure each plot experienced similar tidal impacts. After experimental setup, each plot was assessed periodically over 2 years for percent cover. Percent cover was estimated both visually and using photographs. The visual estimates were taken in the field by the same person to ensure consistency among estimates.

4.2.3 Stingray Pit Surveys

At the experimental site, all pits were enumerated and measured (i.e., for two perpendicular widths and depth) along 2m x 50m belt transects in July 2021 (n=7 transects). The seagrass edge was oriented at 10m along the transect tape so that the first 10m evaluated pit abundance and size in unvegetated space, while avoiding neighboring shore habitats. Each pit along the transect was denoted by habitat types as either bare (0-8.9 m along the transect), edge (9-10.9m along the transect), or seagrass (11+ m along the transect). The transect tape marked the center of the belt transects and all pits within 1m of the tape were measured (i.e. a pit could extend beyond 1m from the tape but would be counted as long as the edge was within 1m). Transects were spaced at least 10 m apart. While I are confident that the majority of these pits were created by stingrays, due to their size as well as personal observation of numerous stingrays in the area, I cannot rule out that some were made by other pit forming organisms such as flounder and drum in the case of smaller pits. Regardless, the formation of pits from stingrays and other pit-forming organisms likely results in similar impacts on sediment and vegetation.

4.2.4 Stingray Prey Survey

To assess where stingray infaunal prey items were found, a simple survey was conducted inside and outside of the seagrass bed at the experimental site in May 2023. Sediment from 20cm x 20cm plots was removed to approximately 30cm deep (12,000 cm^3) and sieved through a 500μm mesh bag. Plots were placed 5m shoreward from the edge of seagrass (bare), at the seagrass edge (edge), and 5m into the seagrass (seagrass; n=3). The infaunal contents of the sieved material were roughly categorized into class (i.e. gastropoda, polychaeta, etc.) and enumerated.

4.2.5 Seagrass Edge Caging

Since the seagrass edge was not centered in the plot or measured for in the original experiment, an additional set of cages were constructed in May 2023. An additional 10, $1m^2$ (n=5 for each caged and uncaged) plots were measured for edge movement over the growing season. The same cage construction was used as above to exclude stingrays from caged plots while partially caged plots were marked with a single bamboo stake but underwent the same procedural control. Three smaller bamboo posts, spaced 25 cm apart, were added at the edge of the seagrass and used to evaluate edge movement as the distance (cm) from those posts to the seagrass edge at the end of the growing season in August 2023.

4.2.6 Seagrass Transplants

To evaluate if seagrass could survive higher in the intertidal than observed from the existing meadow when stingrays were excluded, I conducted a seagrass transplant experiment with and without stingray access. In June 2022, I transplanted 40 plugs (28.27 cm^2) of seagrass at four elevations. Half were randomly assigned to 20cm x 20cm caged plots that limited stingray access and half without caging (n=5 at each elevation; Fig. 14B). Cages were constructed of 10cm separated bamboo stakes (61cm tall). These cages had shorter spacing than the cages mentioned previously due to the smaller size of the cages. I was not concerned that stingrays would enter the cage plots at the 20cm spacing in the larger cages and therefore were fairly confident that the seagrass was protected from foraging. However, given the excavation power of stingrays and the smaller size of the plots, I was concerned that if foraging took place near a smaller plot, it may impact the seagrass plug within the cage. For example, at 20 cm spacing, if one post was dislodged, half of the plot would be exposed to foraging at this smaller size. Therefore, I added an additional bamboo post to each side of the plot to create additional deterrents and safeguards around seagrass plugs. Uncaged plots had a single bamboo corner post 10cm from the seagrass plug. Uncaged plots also had bamboo inserted and removed at 10 cm intervals in a 20 x 20cm square as a procedural control to ensure the same sediment disturbance from inserting bamboo. Elevations were chosen based on the current edge of the seagrass meadow, the length of the bare space to shore, and the tidal range. The lowest elevation was placed in bare space near the edge of the seagrass meadow where patchy seagrass existed. The highest elevation was placed at the transition from bare space to oyster and shore habitats. The remaining two elevations were evenly spaced between the highest and lowest with approximately 5 horizontal m between each elevation. I used a laser level to assess the relative elevation of each plot. The four elevations are referred to as very low (relative elevation = 172.08 cm ± 0.98 SE), low (170.56 cm ± 0.41 SE), high (167.20 cm ± 0.48 SE), and very high (161.86 cm ± 0.3 SE) from here on with very low near the seagrass edge and very high nearest to the shore. Once seagrass was transplanted, I evaluated survivorship as the presence of any live seagrass in the original plug for each plot every two weeks until September 2022.

Since seagrass survival after transplantation is notoriously low and likely reliant on density-dependent intraspecific interactions (Zhang et al. 2021), and because of the high rate of loss in 2022, I repeated the transplant experiment with a larger plug size in the subsequent year (Fig. 14B). In June 2023, I transplanted an additional 40 seagrass plugs: 20 small plug size (28.27 cm^2, same as 2022) and 20 large plug size (113.1 cm^2). Half were in cages with the same dimensions as above and half were uncaged (n=10). All plots were placed at relatively the same elevation between the two intermediate elevations from the previous year's transplantation where seagrass survived best (high and low elevations). New transplants did not overlap with the previous space to avoid any residual impacts from the previous experiment. Seagrass survival was evaluated as the presence of any live seagrass every two weeks until August 2023 and again in October 2023.

4.2.7 Multi-Site Stingray Pit Survey

To better generalize the impact of stingray pit abundance in multiple seagrass beds, I conducted a survey across five sites from Core Sound south to Bogue Sound between July and early September 2022 (Fig. 13C). The five sites were Gloucester (near the original experiment but avoiding any plots; 34.724110, -76.549552), Harkers Bridge (34.725389, -76.580687), Pine Knoll Shores (34.702177, -76.829387), Jarrett Bay North (34.775833, -76.491667), and Jarrett Bay South (34.772381, -76.501837). I wanted to evaluate how the percentage of space occupied by pits – a proxy for feeding pressure and sediment disturbance – impacted the cover of seagrass and the distance between neighboring biogenic habitats. I selected sites that had relatively continuous seagrass beds and neighboring non-eroding salt marsh and oyster ecosystems. At each site I evaluated seven, 5m x 10m quadrats (Fig. 14C). The 5m long edge of the quadrat was placed along the edge of the salt marsh and oyster ecosystems and extended 10m perpendicular toward the seagrass meadows. Within each quadrat, I measured the number of pits, two perpendicular widths (cm) of five random pits, and the percent cover of each foundational organism (i.e., salt marsh grass, oyster, and seagrass) within the plot. I used the average pit size of the five pits and the number of total pits to calculate the estimated percent cover of pits per plot. I also measured the distance (m) between the salt marsh/oyster shore habitat and seagrass even when it fell outside the quadrat. I also measured wind fetch (m) for each quadrat, by manually estimating the distance over open water for the four cardinal directions using Google Earth (version 10.48.0.2). At each plot, fetch was averaged for a single value.

4.2.8 Statistical Analysis

All analyses were conducted in R (version 4.2.2, R Core Team, 2022).To evaluate initial percent cover and relative elevation, a two-way Analysis of Variance was used (ANOVA). For all linear models, data was tested for homogeneity of variance using Levene Tests (Levene, 1960) and for normality of residuals using q-q plots and Shapiro-Wilk's tests (Shapiro & Wilk, 1965). All data for linear models, unless mentioned, met these assumptions.

For seagrass percent cover in the factorial experiment, a linear mixed effects model was employed with stingray exclusion, nutrient addition, date, and their interactions as main effects and plot as a random effect for all percent cover data in the 'lme4' package (Bates et al., 2015). Date was treated as a category in the model. Data were cube root transformed to meet the assumption of equal variance. Additionally, change in seagrass cover was calculated between May 2021 to May 2022. Seagrass coverage peaked in May for both years and began to senesce through the summer. Therefore, to reduce seasonal variation and to begin to assess the impacts of nutrients and stingrays at this highly dynamic edge, I evaluated the change in seagrass coverage from the seasonal peaks in May 2021 until a year later in May 2022. Two-way ANOVAs were used to evaluate the change in percent cover by stingray exclosure, nutrient addition and their interaction. Non-significant interactions were removed from final models.

A generalized linear model with a negative binomial distribution to account for overdispersion using the ‘MASS’ package (Venables & Ripley, 2002) was used to assess pit count at the three habitat types (bare, edge, and seagrass) for July 2021. An offset was employed to account for different area measurements per habitat type. One-way ANOVAs were used to assess differences in pit depth and prey abundance across the three habitat types (seagrass, seagrass edge, and bare space).

A Welch’s Two Sample t-test was used to assess edge movement of caged and uncaged plots. Cox proportional hazard models (Landes et al., 2020) were used to assess seagrass transplant survival through time in both 2022 and 2023 using the ‘survival’ package (Therneau et al., 2023; Therneau & Grambsch, 2000). All assumptions for proportional hazard through time were met.

A Classification and Regression Tree (CART) was constructed to assess the importance of different predictors on distance (m) between shore habitat and seagrass meadow edge for the multi-site observational survey using the ‘rpart’ package (Therneau et al., 2023). Predictors included site, average wind fetch per quadrat, longest fetch direction, shore habitat (oysters, marsh, or combination of the two), percent covers oyster, marsh, and algae, relative change in elevation between shore habitat and seagrass meadow edge, and the estimated percent of the plot occupied by pits. The method was set to ANOVA since the dependent variable is numeric, the minimum split level was set to 10.

4.3 Results

4.3.1 Initial Conditions and Caging

There was no difference among treatments for initial percent seagrass cover and relative elevation (Fig. S1, Table S1). Plots had an initial percent cover of and relative elevation of 172.13 cm ± 0.27 SE.

4.3.2 Stingray Exclusion by Nutrient Addition Experiment

Seagrass percent cover peaked each year in May and all plots experienced decline through the rest of the season (Fig. 15A). The mixed model exhibited marginally significant caging (df= 25, t= -1.92, P=0.066) and date effects. Dates that were significant were representative of the non-growing season (September 2021; df= 162, t= -6.40, P<0.0001, February 2022; df= 162, t= -4.24, P<0.0001, and September 2022; df= 162, t= -8.69, P<0.0001). Across all dates, plots that experienced caging had 32.03% ± 2.38 SE seagrass cover while plots with partial cages had 21.34% ± 1.90 SE. There was no impact of nutrient condition. Additionally, as mentioned previously, seagrass coverage fluctuates seasonally with the peak in May 2022 (average 43.14% ± 5.02 SE across all treatments) and the lowest observed percent cover in September 2022 (average 10.18 ± 2.21 SE across all treatments). The change in percent cover between annual seasonal peaks from May 2021 until May 2022 (Fig. 15A) was significantly different for caging ($F_{1, 25}$=4.84, P=0.037) and not significant for fertilization (Fig 15B). Caged plots, on average, increased percent cover by 9.7% ± 6.91 SE in a year versus uncaged plots that lost 8.8% ± 5.18 SE cover over the same period. Still, no effect of nutrient condition was observed.

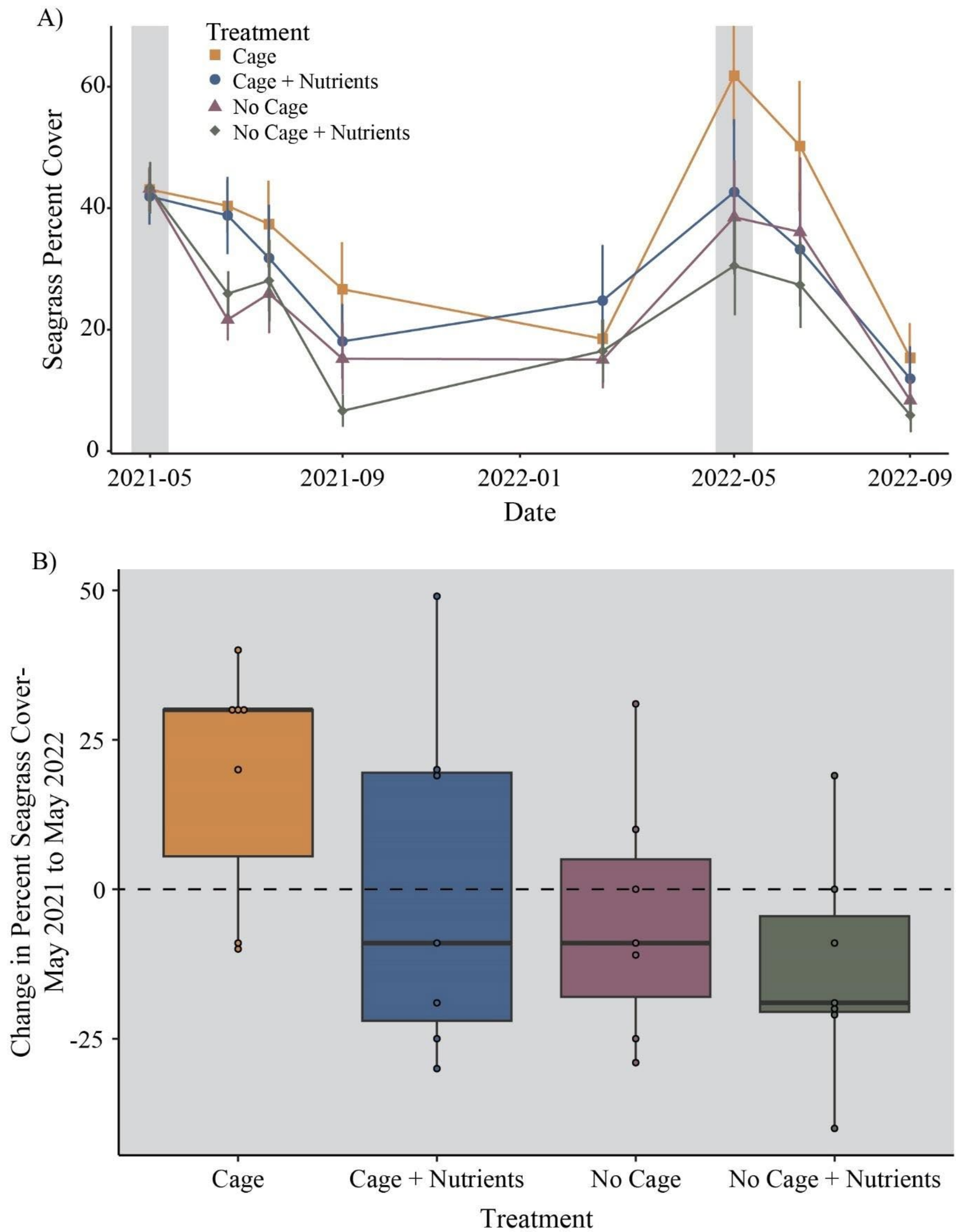

Figure 15: Graphic seagrass percent cover flux and change in percent cover. A) Seasonal flux in seagrass percent cover across all treatments. Seasonal peaks in May 2021 and May 2022 highlighted with gray boxes that correspond with B) change in seagrass percent cover between seasonal peaks from initial experimental set up in May 2021 until May 2022 (n=7 per treatment).

4.3.3 Stingray Pit Surveys

While there was no difference in prey abundance, habitat type demonstrated a difference in pit abundance in July 2021 (*Z*= -6.77, P < 0.001; Fig. 16A). There were 5.05 and 5.01 times more pits observed in bare and edge habitat, respectively, than in seagrass habitat. Depth (cm) of stingray pits did not vary among habitats ($F_{2, 18}$=1.88, *P*=0.18). Mean pit depth was 5.72cm ± 0.0.34 SE for seagrass habitat, 3.97cm ± 1.07 SE for edge habitat, and 4.19cm ± 0.44 SE for bare habitat.

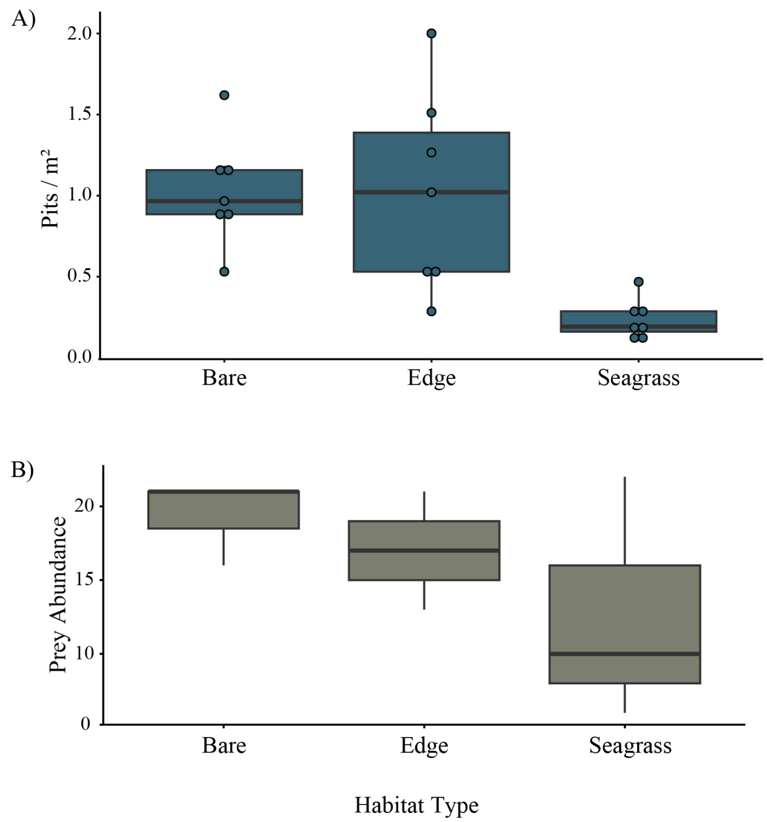

Figure 16: Pit and prey survey graphs.A) The number of pits/ m^2 in different habitat types for July 2021. Dots over boxes represent the pit count at each habitat type for each transect (n=7). B) prey abundance in different habitat types per 12,000 cm^3 core (n=3).

4.3.4 Stingray Prey Survey

There was no difference among prey abundance per habitat type ($F_{2,6}$=1.10, *P*= 0.39; Fig.16B).

4.3.5 Seagrass Edge Caging

There was no difference in edge movement in caged and uncaged plots (Fig. S2, Table S2). On average, all plots moved shoreward (6.53cm ± 6.41 SE for uncaged and 10.97cm ± 2.7 SE for caged plots) during the 2023 season.

4.3.6 Seagrass Transplants

In 2022, seagrass transplants had a 2.7-times greater chance of being absent when uncaged rather than caged (Z= 2.64, *P*= 0.008; Fig 17 A & B) while there was no significant effect of elevation. However, the overall model was only marginally significant (LRT= 8.57 on 4 df, *P*=0.073), which justified repeating the experiment in 2023. Observationally, three caged transplants survived until May 2023 at high and low elevations. In 2023, the pattern repeated with uncaged seagrass transplants having a 2.8-time greater chance of being absent than caged plugs (Z= 2.78, *P*=0.005; Fig 17 C & D). Plug size was not significant (Z=0.20, *P*= 0.84). The model was significant in 2023 (LRT= 7.84 on 2 df, *P*= 0.019)

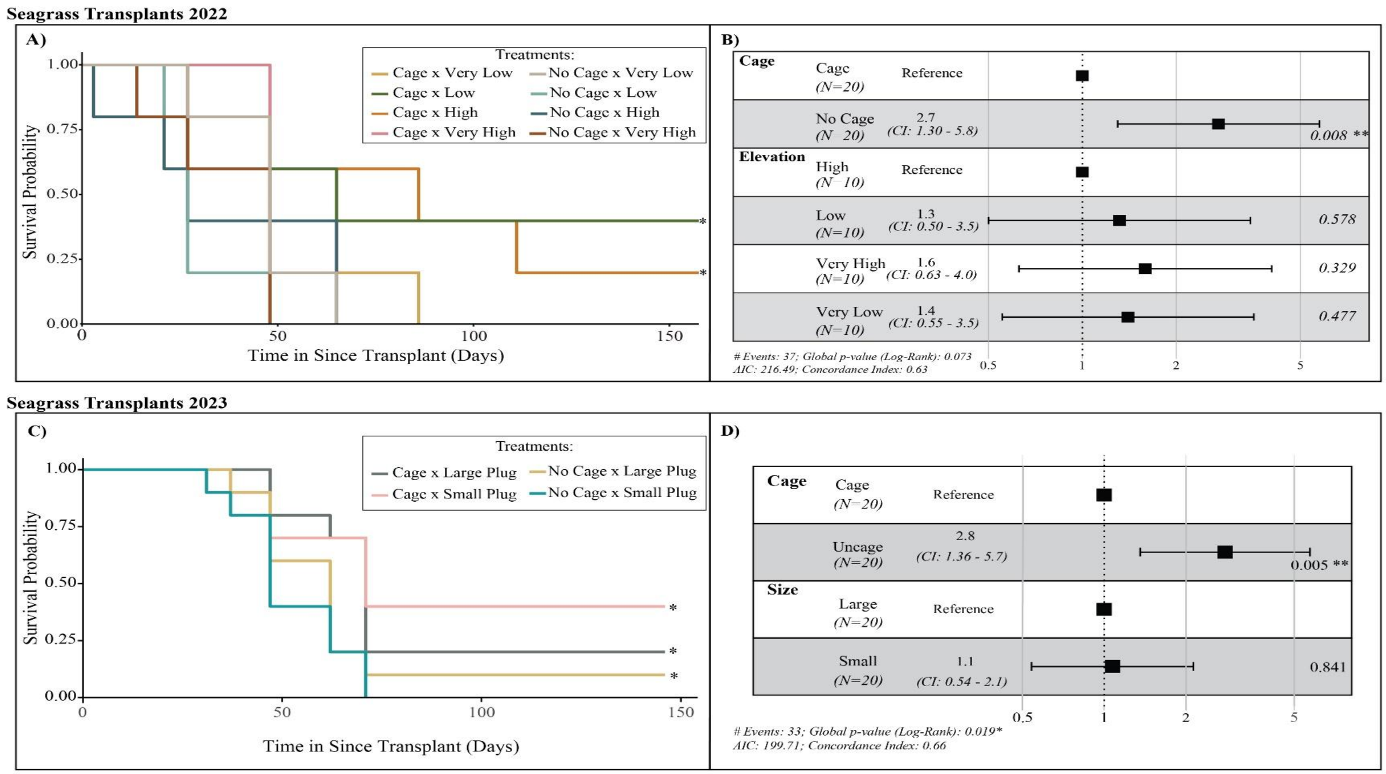

Figure 17: Seagrass transplant survival curves and graphical model results. A) Time to event curve for transplanted seagrass with and without caging as protection from stingray feeding at four elevations in 2022. Event curves that truncate with * indicated survival past observed interval. B) Graphical results from cox proportional hazard model output for 2022 with hazard ratios, confidence intervals, and p-values. Significant treatments denoted with ** and do not have confidence intervals that cross 1. Model significance is determined from global p-value less than 0.05. C) Time to event curve for transplanted seagrass with and without caging as protection from stingray feeding in 2023. Event curves that truncate with * indicated survival past observed interval. D) Graphical results from cox proportional hazard model output for 2023 with hazard ratios, confidence intervals, and p-values. Significant treatments denoted with ** and do not have confidence intervals that cross 1. Model significance is determined from global p-value less than 0.05. Graphs created using ‘survminer’ package (Kassambara et al., 2021).

4.3.7 Multi-Site Stingray Pit Survey

The final regression tree had a complexity parameter of 0.01 and four splits. From the regression tree analysis, site was indicated as the most important predictor with all but one site (Pine Knoll Shore) being lumped together (Fig. 18). The average distance from shore to seagrass was 39.2m ± 5.5 SE for the seven plots at the Pine Knoll Shore site and 7.7m ± 1.56 SE for the plots across the rest of the sites combined. For all sites except for Pine Knoll Shore, the best predictor of the distance from shore to seagrass was the estimated percent of the plot occupied by pits. Plots that had greater than 31% pit coverage averaged 14m between seagrass and shore, whereas those with less than 31% coverage averaged 7m.

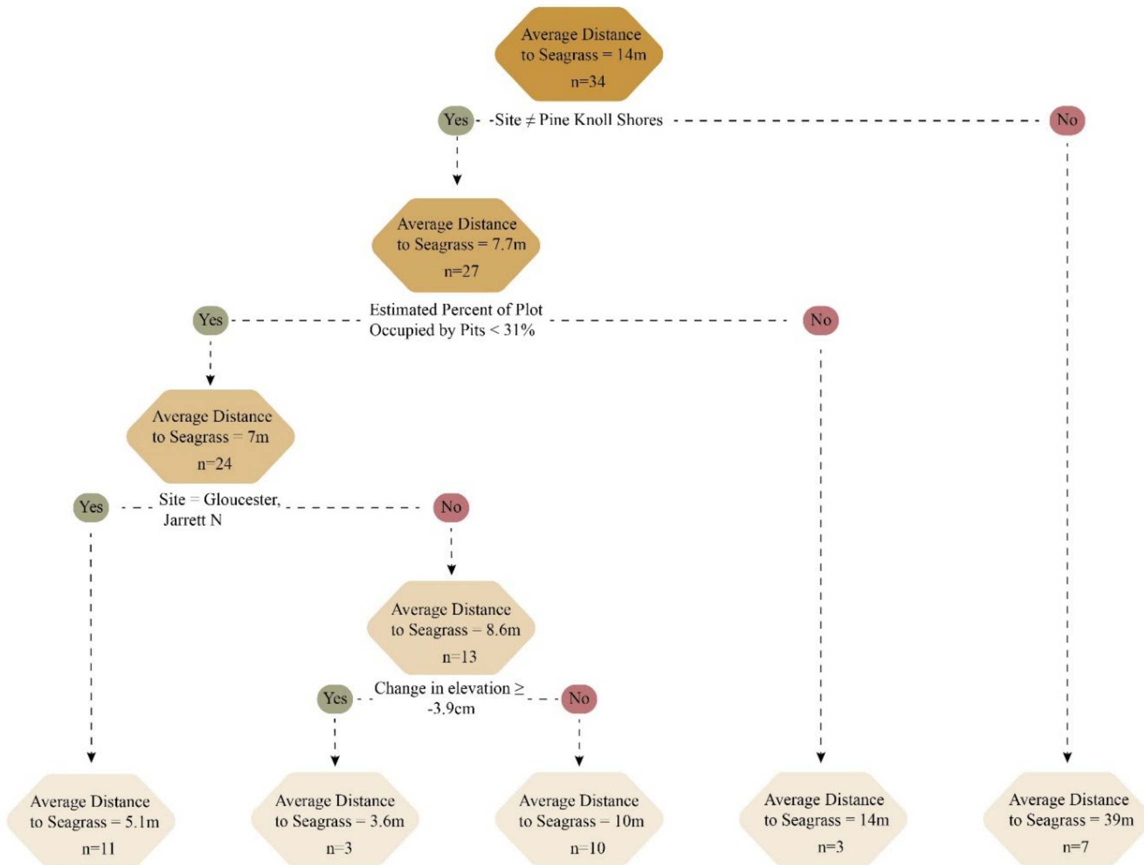

Figure 18: Multi-site observational survey regression tree.

4.4 Discussion

Through experimental manipulations and observational surveys, I show that stingray foraging can influence the shoreward (read stressful edge) range limit of seagrass. This is in contrast to the current SIASH paradigm that suggests the stressful edge of a species range limit is set by physical factors (Louthan et al., 2015). I provide evidence that suggests that the coverage of seagrass at the meadow edge is truncated when inundated with stingray foraging and that the distance between seagrass meadows and shore habitats lengthens with a greater coverage of pits as a proxy for the intensity of stingray feeding. Finally, I demonstrate that seagrass can indeed survive higher in the intertidal than observed when protected from stingrays. Combined these results, along with studies from other systems (Alberti et al., 2007; Shepard et al., 2021) call for an expansion of the current range limit theory to include biological interactions at the environmentally stressful edge.

The increased prevalence of foraging pits in shoreward bare space and near the edge of seagrass meadow, with no perceivable difference in prey abundance suggests that feeding pressure is concentrated in these areas, rather than the adjacent mature seagrass bed. On average, pits scoured depths enough to disturb the seagrass root layer and could visibly uproot seagrass in excavated pits (Fig. 13A, Pangallo & Bell, 1988; Townsend & Fonseca, 1998). These findings support a previous study in NC that found that stingray pit abundance was concentrated in bare and seagrass edge habitats at depths that can disrupt seagrass (Townsend & Fonseca, 1998). The abundance of pits in the bare and edge habitat could be due to increased effort needed to forage through an ever-present root mat within the seagrass meadow. Optimal foraging theory describes consumer behavior as a set of trade-offs that minimize the cost of finding food (Pyke & Starr, 2021). In this instance, stingrays may prefer to forage in open spaces as they do not have to dig through a heavy root mass that obscures their prey. This is observed in other ecosystems where consumers have a choice between vegetative and bare space to forage. For example, several species of birds are known to preferentially forage in recently mowed and bare habitats over highly vegetative areas (Korniluk et al., 2021; Tagmann-Ioset et al., 2012).

In the factorial experiment, the impacts of stingray exclosure minimized the loss of seagrass cover, alluding to a biological control at the stressful edge of this system. Both the percent cover over the course of the experiment and the change in percent cover between annual peaks demonstrated higher coverage of seagrass when protected from stingray foraging. This is counter to the current paradigm (Louthan et al., 2015) and suggests that the observed meadow may be truncated by stingray foraging. As previously mentioned, this ecosystem is further complicated by the seasonality and the ephemeral nature of the edge of habitat conditions that makes assessing impacts of stingrays challenging. I observed the seagrass within my plots at the edge of the meadow peak in May and senesce through the remainder of the summers. I suggest that the combination of environmental stressors and biological disturbance becomes too much for seagrass in NC to overcome and that regardless of the treatment, all seagrass is being lost to an effective net zero at the end of each summer. However, I observed the seagrass rebound each spring and in plots that maintained stingray exclosures, rebound to a greater extent than the previous year. Whether the stingrays play a prolonged role in truncating seagrass beds in NC needs further exploration where a long term, large scale exclosure is maintained and additional measures such as above and belowground samples are collected throughout the season. There was no impact of fertilization on percent cover. These are similar results to those found in previous transplant experiments done with *H. wrightii* in NC where fertilization did not influence growth or survival of transplants

(Judson Kenworthy & Fonseca, 1992). I predict this could be due to the high turnover rate for this seagrass or an inadequate amount of fertilizer being added to the system. *H. wrightii* can completely replace aboveground biomass within 21 days or a turnover rate of once every nine days (Virnstein, 1982). The amount of fertilizer added could have been incorporated quickly and lost with seasonal shedding of leaves that were not accounted for in my sampling methods.

The idea that stingrays can influence the shoreward range limit is further supported by my transplantation experiments. In both years that transplants were placed higher into the intertidal, the probability of survival increased when plugs were caged. While I cannot distinguish between plugs of seagrass that were lost due to stingray foraging or by some other matter, the abundance of stingray pits in and around the experimental area suggest they had a contributing role in the seagrass loss. Further research is needed to better evaluate the mechanism behind seagrass plug loss and stingray influence. The transplant experiments were conducted similarly to how seagrass is transplanted for restoration and therefore, combined with the results demonstrating high feeding activity in bare and edge habitats, have implications for seagrass restoration. Seagrass is a threatened foundational plant group but, to this point, has been challenging to effectively restore and traditional restoration efforts have focused on minimizing the negative physical factors such as water quality (Valdez et al., 2020). However, based on my results, restoration efforts also need to consider the biological community present in the area as well. Stingrays act as a disturbing agent in the ecosystem that can uproot freshly planted seagrass. This is not unique to this seagrass ecosystem as stingrays are common throughout the world's oceans and overlap with many seagrass ecosystems (Last, 2016; Short et al., 2007). Marine restoration has been limited in the incorporation of animal contributors to restoration projects and there are active calls for the inclusion of animals in restoration efforts (Sievers et al., 2022).

Across the multi-site survey, site was the dominant predictor of the distance from shore habitat to the edge of the seagrass meadow. However, this was primarily due to a single site, the Pine Knoll Shores site, where seagrass was on average 39m away from the shore. In this instance, physical factors may have played a dominant role in determining the shoreward extent of seagrass. Although wind fetch did not appear as a significant predictor in my regression tree analysis, the average wind fetch measured at the Pine Knoll Shores site was far greater than the other four sites. From a greater fetch, it can be assumed that the wind and wave action acting on the seagrass meadow was greater than other locations. Wave and wind stress can exceed certain thresholds and have been shown to diminish seagrass cover and patch size (Uhrin & Turner, 2018) and may be a contributing factor to shaping the seagrass meadow at the Pine Knoll Shores site. For all other sites, the best predictor of distance between the seagrass and the shore was the percentage of the plot occupied by pits. This suggests that at most sites surveyed, pit prevalence and thereby stingray foraging influenced the distance between seagrass and shoreward habitat. The context dependency of a biological versus potential physical factors altering the range limit demonstrated by this multi-site survey aids in the notion that ecological theories, such as range limit theory, while helpful in hypothesizing patterns, are not all encompassing.

Combined, my results show that the shoreward range limit of this marine plant ecosystem is controlled by a suite of ecological factors, including physical and biological interactions with stingrays. Further research is needed to know the full extent of where and when stingrays influence the shoreward range limit of seagrass. Biological interactions that change the range limits of plant ecosystems on their stressful edges may not be constrained to seagrass systems but could be prevalent in many ecosystems. A review by Louthan et al. (2015) suggests a more thorough testing of range limit theory and of how species interactions change across stress gradients. Even in mountainous habitats, where elevation is considered a dominant factor in setting species range limits, there are examples where biotic interactions play a substantial role. Shepard et al. (2021) found that the caddisfly upward slope range was heavily influenced by competition rather than elevation. Furthermore, in salt marshes, research has found that disruption by crabs is more pronounced at the vegetation's environmentally stressful edge and potentially truncates marsh extension (Alberti et al., 2007; He et al., 2015). This is not to say, however, that physical factors do not contribute significantly to range limits, especially under climate change. Research has shown a redistribution of organisms following thermal shifts (Hastings et al., 2020; Lenoir et al., 2020). However, as global change factors continue to alter ecosystems, the influence of biological interactions and physical factors on setting species range limits may be modified and should be considered in tangent. Therefore, it is imperative that both biological and physical factors are explored to better understand species range limits and the cascading impacts they can have on plant foundational ecosystems. Biologically driven changes to range limit also have the ability to change the way practitioners and managers approach restoration and conservation of these foundation species. Hence, I call for future research to explore the complex suite of physical and biological factors that set a species marginal range limit and to use the ecological theories in place as a steppingstone to further ecological knowledge.

5. Conclusion

Ecological theories are valuable for evaluating and predicting ecosystem function and health, especially with climate change. My dissertation aimed to elucidate instances when typical ecological patterns falter to assess different aspects of ecosystems. I provide evidence for novel insights into how top-down and bottom-up factors influence various vegetation traits, a plant community transition zone, and a species range limit in coastal wetlands. Evidence within this dissertation suggests that the theory of how top-down and bottom-up forces interact and generally affect plant communities still needs further investigation and refinement. The response to top-down and bottom-up factors is not always predictable based on theory across traits or regions of an ecosystem. These findings generate a better understanding of the ecology of valuable coastal wetlands and call for both expansion and refinement of the ecological paradigms used to evaluate them.

Appendix A

Supplementary material for section 2 (chapter 1).

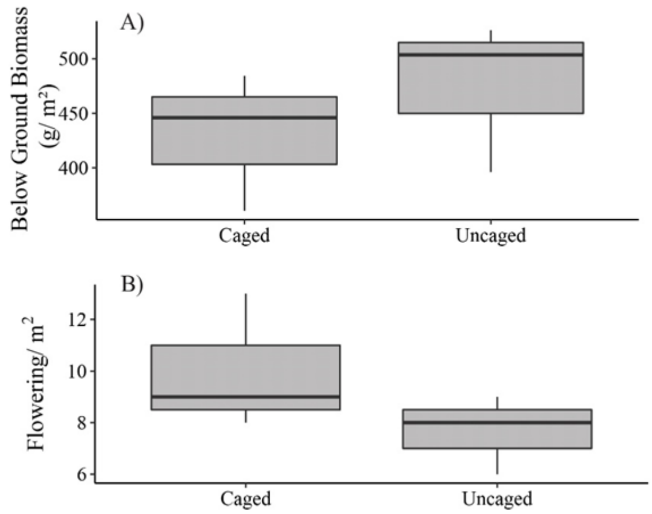

Figure S1: Graphical comparison of caged and uncaged plots. A) belowground biomass (g/m^2) and B) number of flowering shoots/ m^2.

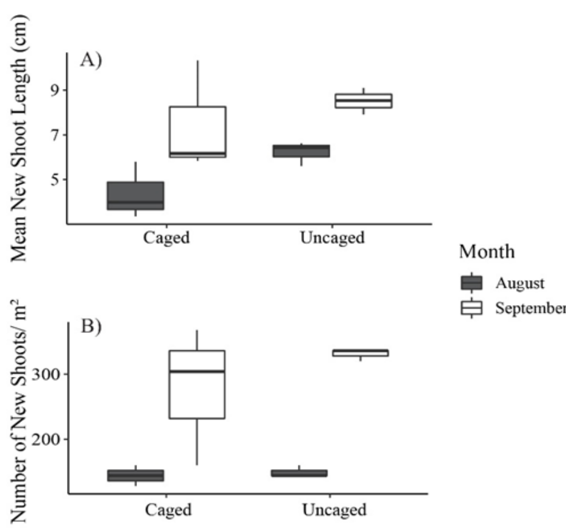

Figure S2: Graphical comparison of cages and uncaged plots. A) mean length of new shoots (cm) and B) number of new shoots/ m^2 in August and September

Table S1: Literature review of studies that explored traits beyond aboveground biomass.

Code	Aboveground biomass	Belowground biomass	Others
A001	yes		
A002	yes	yes	
A003	yes		
A004	yes		
A005			Plant nutrient parameters
A006	yes		
A007	yes		
A008	yes		
A009	yes		
A010	yes		
A011	yes	yes	
A012	yes		
A013			Plant nutrient parameters
A014	yes		
A015	yes		
A016	yes		
A017			Plant nutrient parameters
A018	yes		
A019	yes		

Code	Aboveground biomass	Belowground biomass	Others
A001	yes		
A020			Plant nutrient parameters
A021	yes		
A022	yes	yes	
A023	yes		
A024	yes		
A025	yes		
A026			Plant nutrient parameters
A027			
A028	yes		
A029			Insect survival, abundance or biomass
A030	yes		
A031	yes		
A032	yes		
A033	yes		
A034			Insect survival, abundance or biomass
A035	yes		
A036	yes		
A037	yes		
A038	yes		

Code	Aboveground biomass	Belowground biomass	Others
A001	yes		
A039			Insect survival, abundance or biomass
A040	yes		
A041	yes	yes	
A042	yes		
A043	yes		
A044	yes		
A045			Gall density, plant nutrient parameters
A046			Gall density, plant nutrient parameters
A047	yes		
A048			Gall density, plant nutrient parameters
A049	yes	yes	
A050	yes		
A051			Hydraulic connectivity
A052	yes		
A053	yes		
A054			Leaf damage by herbivores
A055	yes		
A056	yes		

Code	Aboveground biomass	Belowground biomass	Others
A001	yes		
A057	yes	yes	
A058	yes		
A059	yes		
A060	yes		
A061	yes		
A062	yes		
A063	yes		
A064	yes	yes	
A065	yes		
A066	yes		
A067	yes		
A068	yes		
A069	yes		
A070	yes		
A071	yes		
A072	yes		
A073	yes		
A074	yes	yes	
A075	yes		
A076	yes		
A077			NA
A078			Leaf damage by herbivores

Code	Aboveground biomass	Belowground biomass	Others
A001	yes		
A079	yes		
A080	yes	yes	

Estimation of the number of studies focused on cordgrass (*Spartina alterniflora*) standing aboveground biomass, on belowground biomass or on other response variables. Used publications are those included in He and Silliman (2015), see below for the full citations associated with the codes.

A001. Jefferies, R.L. & Perkins, N. (1977). The effects on the vegetation of the additions of inorganic nutrients to salt marsh soils at Stiffkey, Norfolk. *J. Ecol.*, 65, 867-882.

A002. Haines, E.B. (1979). Growth dynamics of cordgrass, *Spartina alterniflora* Loisel., on control and sewage sludge fertilized plots in a Georgia salt marsh. *Estuaries*, 2, 50-53.

A003. Mendelssohn, I.A. (1979). The influence of nitrogen level, form, and application method on the growth response of *Spartina alterniflora* in North Carolina. *Estuaries*, 2, 106-112.

A004. Covin, J. & Zedler, J. (1988). Nitrogen effects on *Spartina foliosa* and *Salicornia virginica* in the salt marsh at Tijuana Estuary, California. *Wetlands*, 8, 51-65.

A005. Stiling, P., Brodbeck, B.V. & Strong, D.R. (1991). Population increases of planthoppers on fertilized salt-marsh cord grass may be prevented by grasshopper feeding. *Fla. Entomol.*, 74, 88-97.

A006. Clarke, P.J. & Allaway, W.G. (1993). The regeneration niche of the grey mangrove (*Avicennia marina*): effects of salinity, light and sediment factors on establishment, growth and survival in the field. *Oecologia*, 93, 548-556.

A007. Osgood, D.T. & Zieman, J.C. (1993). Factors controlling aboveground *Spartina alterniflora* (smooth cordgrass) tissue element composition and production in different-age barrier island marshes. *Estuaries*, 16, 815-826.

A008. Feller, I.C. (1995). Effects of nutrient enrichment on growth and herbivory of dwarf red mangrove (*Rhizophora mangle*). *Ecol. Monogr.*, 65, 477-505.

A009. Boyer, K.E. & Zedler, J.B. (1996). Damage to cordgrass by scale insects in a constructed salt marsh: Effects of nitrogen additions. *Estuaries*, 19, 1-12.

A010. Dai, T. & Wiegert, R.G. (1996). Ramet population dynamics and net aerial primary productivity of *Spartina alterniflora*. *Ecology*, 77, 276-288.

A011. Koch, M.S. & Snedaker, S.C. (1997). Factors influencing *Rhizophora mangle* L. seedling development in Everglades carbonate soils. *Aquat. Bot.*, 59, 87-98.

A012. Ruess, R.W., Uliassi, D.D., Mulder, C.P.H. & Person, B.T. (1997). Growth responses of *Carex ramenskii* to defoliation, salinity, and nitrogen availability: Implications for geese-ecosystem dynamics in western Alaska. *Ecoscience*, 4, 170-178.

A013. Stiling, P. & Rossi, A.M. (1997). Experimental manipulations of top-down and bottom-up factors in a tri-trophic system. *Ecology*, 78, 1602-1606.

A014. Boyer, K.E. & Zedler, J.B. (1998). Effects of nitrogen additions on the vertical structure of a constructed cordgrass marsh. *Ecol. Appl.*, 8, 692-705.

A015. Levine, J.M., Brewer, J.S. & Bertness, M.D. (1998). Nutrients, competition and plant zonation in a New England salt marsh. *J. Ecol.*, 86, 285-292.

A016. Gough, L. & Grace, J.B. (1998). Effects of environmental change on plant species density: Comparing predictions with experiments. *Ecology*, 80, 882-890.

A017. Rossi, A.M. & Stiling, P. (1998). The interactions of plant clone and abiotic factors on a gall-making midge. *Oecologia*, 116, 170-176.

A018. Boyer, K.E. & Zedler, J.B. (1999). Nitrogen addition could shift plant community composition in a restored California salt marsh. *Restor. Ecol.*, 7, 74-85.

A019. van Wijnen, H.J. & Bakker, J.P. (1999). Nitrogen and phosphorus limitation in a coastal barrier salt marsh: the implications for vegetation succession. *J. Ecol.*, 87, 265-272.

A020. Moon, D.C., Rossi, A.M. & Stiling, P. (2000). The effects of abiotically induced changes in host plant quality (and morphology) on a salt marsh planthopper and its parasitoid. *Ecol. Entomol.*, 25, 325-331.

A021. Moon, D.C. & Stiling, P. (2000). Relative importance of abiotically induced direct and indirect effects on a salt-marsh herbivore. *Ecology*, 81, 470-481.

A022. Boyer, K.E., Fong, P., Vance, R.R. & Ambrose, R.F. (2001). *Salicornia virginica* in a Southern California salt marsh: Seasonal patterns and a nutrient-enrichment experiment. *Wetlands*, 21, 315-326.

A023. Emery, N.C., Ewanchuk, P.J. & Bertness, M.D. (2001). Competition and salt-marsh plant zonation: Stress tolerators may be dominant competitors. *Ecology*, 82, 2471-2485.

A024. Silliman, B.R. & Zieman, J.C. (2001). Top-down control of *Spartina alterniflora* production by periwinkle grazing in a Virginia salt marsh. *Ecology*, 82, 2830-2845.

A025. Denno, R.F., Gratton, C., Peterson, M.A., Langellotto, G.A., Finke, D.L. & Huberty, A.F. (2002). Bottom-up forces mediate natural-enemy impact in a phytophagous insect community. *Ecology*, 83, 1443-1458.

A026. Moon, D.C. & Stiling, P. (2002). The effects of salinity and nutrients, on a tritrophic salt-marsh system. *Ecology*, 83, 2465-2476.

A027. Moon, D.C. & Stiling, P. (2002). The influence of species identity and herbivore feeding mode on top-down and bottom-up effects in a salt marsh system. *Oecologia*, 133, 243-253.

A028. Pennings, S.C., Stanton, L.E. & Brewer, J.S. (2002). Nutrient effects on the composition of salt marsh plant communities along the southern Atlantic and Gulf coasts of the United States. *Estuaries*, 25, 1164-1173.

A029. Denno, R.F., Gratton, C., Dobel, H. & Finke, D.L. (2003). Predation risk affects relative strength of top-down and bottom-up impacts on insect herbivores. *Ecology*, 84, 1032-1044.

A030. Feller, I.C., Whigham, D.F., McKee, K.L. & Lovelock, C.E. (2003). Nitrogen limitation of growth and nutrient dynamics in a disturbed mangrove forest, Indian River Lagoon, Florida. *Oecologia*, 134, 405-414.

A031. Feller, I.C., McKee, K.L., Whigham, D.F. & O'Neill, J.P. (2003). Nitrogen vs. phosphorus limitation across an ecotonal gradient in a mangrove forest. *Biogeochemistry*, 62, 145-175.

A032. Gratton, C. & Denno, R.F. (2003). Inter-year carryover effects of a nutrient pulse on *Spartina* plants, herbivores, and natural enemies. *Ecology*, 84, 2692-2707.

A033. Gratton, C. & Denno, R.F. (2003). Seasonal shift from bottom-up to top-down impact in phytophagous insect populations. *Oecologia*, 134, 487-495.

A034. Moon, D.C. & Stiling, P. (2003). The influence of legacy effects and recovery from perturbations in a tritrophic salt marsh complex. *Ecol. Entomol.*, 28, 457-466.

A035. Tessier, M., Vivier, J.P., Ouin, A., Gloaguen, J.C. & Lefeuvre, J.C. (2003). Vegetation dynamics and plant species interactions under grazed and ungrazed conditions in a western European salt marsh. *Acta Oecol.*, 24, 103-111.

A036. Tyler, A.C., Mastronicola, T.A. & McGlathery, K.J. (2003). Nitrogen fixation and nitrogen limitation of primary production along a natural marsh chronosequence. *Oecologia*, 136, 431-438.

A037. Lovelock, C.E., Feller, I.C., McKee, K.L., Engelbrecht, B.M.J. & Ball, M.C. (2004). The effect of nutrient enrichment on growth, photosynthesis and hydraulic conductance of dwarf mangroves in Panama. *Funct. Ecol.*, 18, 25-33.

A038. McFalls, T.B. (2004). Effects of disturbance and fertility upon the vegetation of a Louisiana coastal marsh. Southeastern Louisiana University

A039. Moon, D.C. & Stiling, P. (2004). The influence of a salinity and nutrient gradient on coastal vs. upland tritrophic complexes. *Ecology*, 85, 2709-2716.

A040. Ngai, J.T. & Jefferies, R.L. (2004). Nutrient limitation of plant growth and forage quality in Arctic coastal marshes. *J. Ecol.*, 92, 1001-1010.

A041. Wigand, C., Thursby, G.B., McKinney, R.A. & Santos, A.F. (2004). Response of *Spartina patens* to dissolved inorganic nutrient additions in the field. *J. Coast. Res.*, 134-149.

A042. Bos, D., Drent, R.H., Rubinigg, M. & Stahl, J. (2005). The relative importance of food biomass and quality for patch and habitat choice in Brent Geese Branta bernicla. *Ardea*, 93, 5-16.

A043. Huang, X.Q. & Morris, J.T. (2005). Distribution of phosphatase activity in marsh sediments along an estuarine salinity gradient. *Mar. Ecol. Progr. Ser.*, 292, 75-83.

A044. Hines, J., Lynch, M.E. & Denno, R.F. (2005). Sap-feeding insect communities as indicators of habitat fragmentation and nutrient subsidies. *J. Insect Conserv.*, 9, 261-280.

A045. Stiling, P. & Moon, D.C. (2005). Quality or quantity: the direct and indirect effects of host plants on herbivores and their natural enemies. *Oecologia*, 142, 413-420.

A046. Stiling, P. & Moon, D. (2005). Are trophodynamic models worth their salt? Top-down and bottom-up effects along a salinity gradient. *Ecology*, 86, 1730-1736.

A047. Traut, B.H. (2005). Effects of nitrogen addition and salt grass (*Distichlis spicata*) upon high salt marsh vegetation in northern California, USA. *Estuaries*, 28, 286-295.

A048. Albarracin, M.T. & Stiling, P. (2006). Bottom-up and top-down effects on insect herbivores do not vary among sites of different salinity. *Ecology*, 87, 2673-2679.

A049. Hines, J., Megonigal, J.P. & Denno, R.F. (2006). Nutrient subsidies to belowground microbes impact aboveground food web interactions. *Ecology*, 87, 1542-1555.

A050. Huberty, A.F. & Denno, R.F. (2006). Consequences of nitrogen and phosphorus limitation for the performance of two planthoppers with divergent life-history strategies. *Oecologia*, 149, 444-455.

A051. Lovelock, C.E., Ball, M.C., Feller, I.C., Engelbrecht, B.M.J. & Ewe, M.L. (2006). Variation in hydraulic conductivity of mangroves: influence of species, salinity, and nitrogen and phosphorus availability. *Physiol. Plantarum*, 127, 457-464.

A052. van der Graaf, A.J., Stahl, J., Veen, G.F., Havinga, R.M. & Drent, R.H. (2007). Patch choice of avian herbivores along a migration trajectory-from temperate to arctic. *Basic Appl. Ecol.*, 8, 354-363.

A053. Crain, C.M. (2007). Shifting nutrient limitation and eutrophication effects in marsh vegetation across estuarine salinity gradients. *Estuar. Coast.*, 30, 26-34.

A054. Feller, I.C. & Chamberlain, A. (2007). Herbivore responses to nutrient enrichment and landscape heterogeneity in a mangrove ecosystem. *Oecologia*, 153, 607-616.

A055. Feller, I.C., Lovelock, C.E. & McKee, K.L. (2007). Nutrient addition differentially affects ecological processes of *Avicennia germinans* in nitrogen versus phosphorus limited mangrove ecosystems. *Ecosystems*, 10, 347-359.

A056. Lovelock, C.E., Feller, I.C., Ellis, J., Schwarz, A.M., Hancock, N., Nichols, P. et al. (2007). Mangrove growth in New Zealand estuaries: the role of nutrient enrichment at sites with contrasting rates of sedimentation. *Oecologia*, 153, 633-641.

A057. Tyler, A.C., Lambrinos, J.G. & Grosholz, E.D. (2007). Nitrogen inputs promote the spread of an invasive marsh grass. *Ecol. Appl.*, 17, 1886-1898.

A058. Bertness, M.D., Crain, C., Holdredge, C. & Sala, N. (2008). Eutrophication and consumer control of New England salt marsh primary productivity. *Conserv. Biol.*, 22, 131-139.

A059. Sala, N.M., Bertness, M.D. & Silliman, B.R. (2008). The dynamics of bottom-up and top-down control in a New England salt marsh. *Oikos*, 117, 1050-1056.

A060. McFarlin, C.R., Brewer, J.S., Buck, T.L. & Pennings, S.C. (2008). Impact of fertilization on a salt marsh food web in Georgia. *Estuar. Coast.*, 31, 313-325.

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Table S2: T-test results between cage and cage control plots for six variables

Variable	df	T	P
Belowground Biomass (g/m2)	3.9	-0.83	0.45

Number Flowering/ m2	3.2	1.3	0.27
August New Shoots/ m2	3.2	0.5	0.65
September New Shoots/ m2	2.0	-0.86	0.47
August Mean Length of New	2.7	-2.3	0.11
September Mean Length of New	2.2	-0.72	0.54

Table S3: Tukey post-hoc test determining the significant difference between means (n=3) of dependent variables.

Variable	Sources	Compared Treatments	Difference in Means	*P*
Belowground Biomass (g/m^2)	**Grazer level**			
		Removal-Addition	114.1	0.027
	Nitrogen			
		Fertilized-Ambient	77.4	0.028
Ratio Below: Aboveground Biomass (g/m^2)	**Grazer Level**			
		Addition- Removal	0.453	<0.001
		Addition- Control	0.406	<0.001
	Nitrogen			
		Fertilized: Ambient	0.448	<0.001
Radulations (cm/stem)	**Grazer Level**			
		Addition-Removal	1.10	0.010
Standing Dead Mass (g/m^2)	**Interaction**			
		Addition: Fertilized - Control: Ambient	7.67	0.0021
		Control: Fertilized - Control: Ambient	15.24	<0.001
		Addition: Fertilized - Removal: Fertilized	6.58	0.0072
		Control: Fertilized - Removal: Fertilized	14.15	<0.001
		Addition: Fertilized - Removal: Ambient	5.67	0.021
		Control: Fertilized - Removal: Ambient	13.24	<0.001
		Addition: Fertilized - Addition: Ambient	4.88	0.051
		Control: Fertilized - Addition: Ambient	12.45	<0.001
		Control: Fertilized - Addition: Fertilized	7.57	0.002
	Grazer Level			
		Addition- Removal	3.69	0.010
		Control- Removal	6.07	<0.001
	Nitrogen			
		Fertilized: Ambient	6.4	<0.001
Leaf Litter (g/m^2)	**Interaction**			
		Addition: Fertilized - Control: Ambient	0.33	0.090
		Removal: Ambient - Control: Ambient	0.64	0.001
		Removal: Ambient - Removal: Fertilized	0.59	0.002
		Removal: Ambient - Addition: Ambient	0.55	0.003
		Removal: Ambient - Control: Fertilized	0.33	0.090

	Grazer Level			
		Removal- Control	0.19	0.077
Number Flowering/ m^2	**Interaction**			
		Control: Nitrogen - Addition: Ambient	18	0.054
		Removal: Ambient - Addition: Ambient	22.67	0.013
		Removal: Nitrogen - Addition: Ambient	53.33	<0.001
		Removal: Ambient - Addition: Nitrogen	19	0.040
		Removal: Nitrogen - Addition: Nitrogen	49.67	<0.001
		Removal: Nitrogen - Control: Ambient	46	<0.001
		Removal: Nitrogen - Removal: Ambient	30.67	0.001
	Grazer Level			
		Control-Addition	10.83	0.039
		Removal-Addition	36.17	<0.001
		Removal-Control	25.33	<0.001
	Nitrogen			
		Nitrogen-Ambient	15	<0.001
Proportion Flowering/ m^2				
	Grazer Level			
		Control-Addition	0.037	0.03
		Removal-Addition	0.11	<0.001
		Removal-Control	0.08	<0.001
	Nitrogen			
		Fertilized-Ambient	0.04	0.002
August New Shoots/ m^2				
	Grazer Level			
		Removal-Addition	117.33	0.050
		Removal-Control	138.67	0.020
	Nitrogen			
		Fertilized-Ambient	140.44	0.002
September New Shoots/ m^2				
	Grazer Level			
		Removal-Addition	221.33	0.010
		Removal-Control	157.33	0.070
August Mean Length of New Shoots (cm)	**Nitrogen**			
		Fertilized-Ambient	3.03	<0.001
September Mean Length of New Shoots (cm)	**Nitrogen**			
		Fertilized-Ambient	3.36	0.001

Only the significant differences reported in table 1 are reported here.

Appendix B

Supplementary information for section 3 (chapter 2).

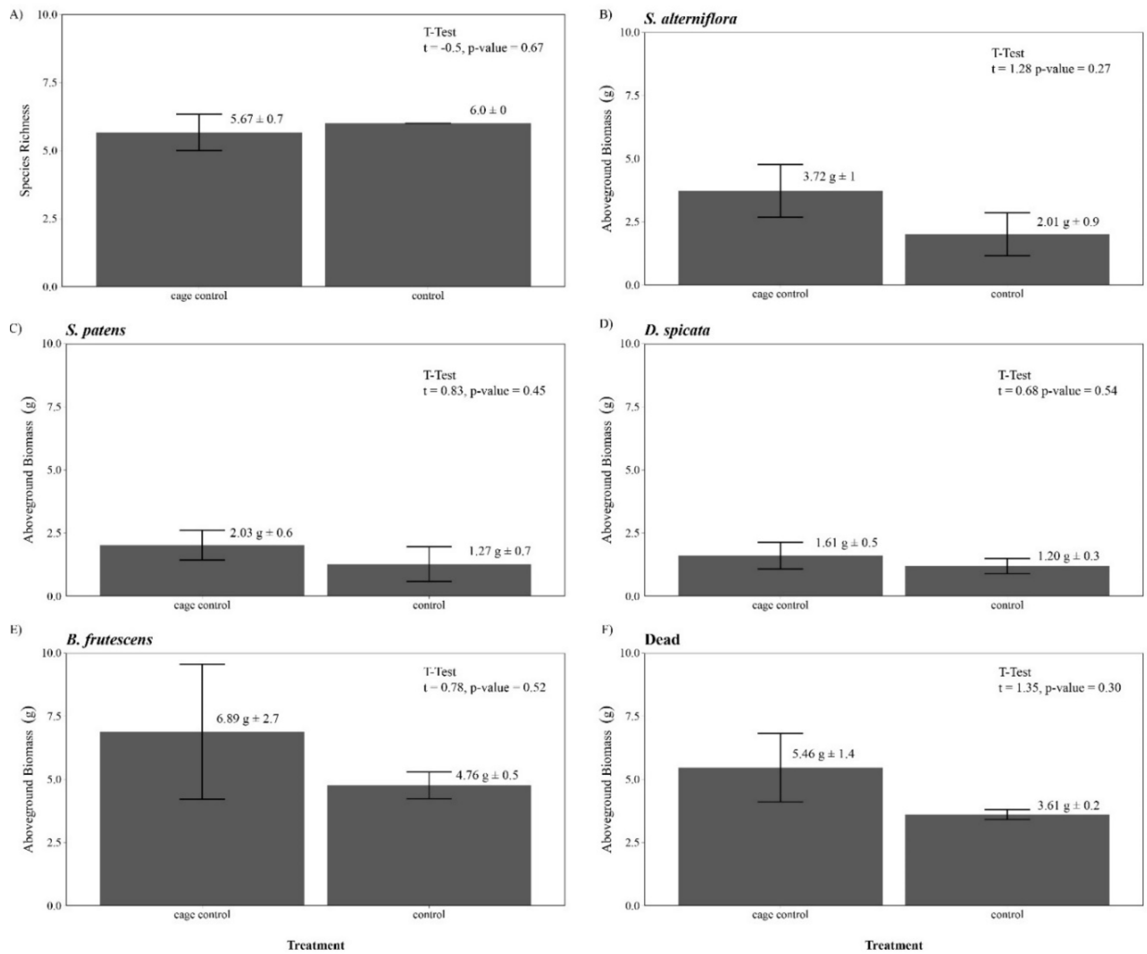

Figure S1: Biomass response to cage controls and open control plots. A) species richness, B) *S. alterniflora*, C) *S. patens*, D) *D. spicata*, E) *B. frutescens*, and F) dead mass. Error bars represent standard error. T-test results are reported with mean ± standard error above each bar.

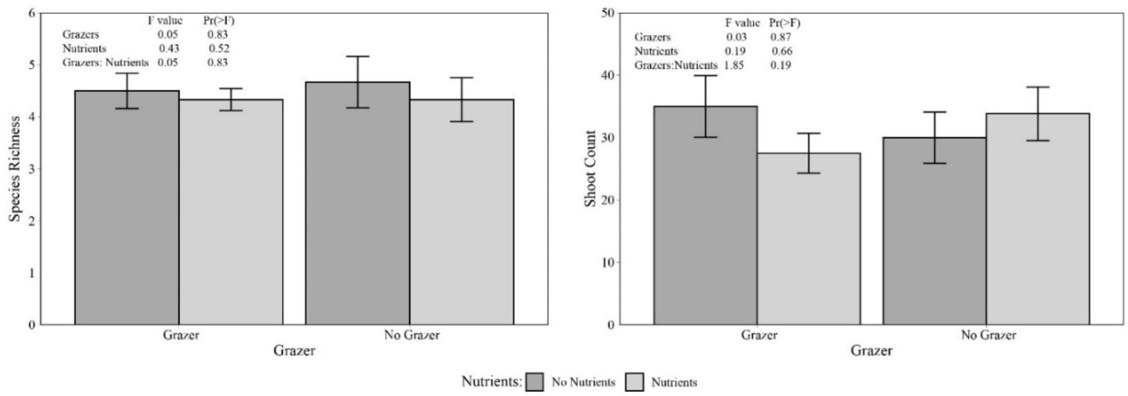

Figure S2: Initial conditions across treatments.
A) species richness and B) shoot count of *S. alterniflora*. Two-way ANOVA results are reported on the graph layout. Error bars represent standard errors.

Table S1: List of statistical tests and transformations used on the various metrics.

Measurement	Test	Transformation
Species Richness	Two-Way ANOVA	None
Shannon H'	Kruskal-Wallis	None
Total Aboveground Biomass	Two-Way ANOVA	None
Belowground Biomass	Two-Way ANOVA	Square Root
Ratio Below: Aboveground Biomass	Two-Way ANOVA	None
Dead Mass	Two-Way ANOVA	Square Root
Aboveground- *S. alterniflora*	Two-Way ANOVA	Square Root
Aboveground- *S. patens*	Two-Way ANOVA	Square Root

Aboveground- *D. spicata*	Two-Way ANOVA	Square Root
Aboveground- *B. frutescence*	Two-Way ANOVA	None
Aboveground- Rare Species	Kruskal-Wallis	None
Shoot Length- *S. alterniflora*	Two-Way ANOVA	Logarithmic
Shoot Length- *S. patens*	Two-Way ANOVA	None
Shoot Length- *D. spicata*	Two-Way ANOVA	None
Shoot Length- *B. frutescence*	Two-Way ANOVA	Logarithmic
Percent Cover- *S. alterniflora*	Two-Way ANOVA	None
Percent Cover- *S. patens*	Kruskal-Wallis	None
Percent Cover- *D. spicata*	Two-Way ANOVA	None
Percent Cover- *B. frutescence*	Two-Way ANOVA	None
Percent Cover- Rare Species	Kruskal-Wallis	None
Grazing Scar Length- Insect	Two-Way ANOVA	Square Root
Grazing Scar Length- Snail	Two-Way ANOVA	Square Root

Table S2: T-test results for cage controls where cage controls are lifted full cages and controls are open plots.

Variable	df	T	p
***S. alterniflora* Aboveground Biomass**	3.85	1.28	0.23
***S. patens* Aboveground Biomass**	3.91	0.83	0.45
***D. spicata* Aboveground Biomass**	3.17	0.68	0.54
***B. frutescence* Aboveground Biomass**	2.16	0.78	0.51
Dead Aboveground Biomass	2.08	1.35	0.30
Species Richness	2.00	-0.5	0.67

Appendix C

Supplementary information for section 4 (chapter 3).

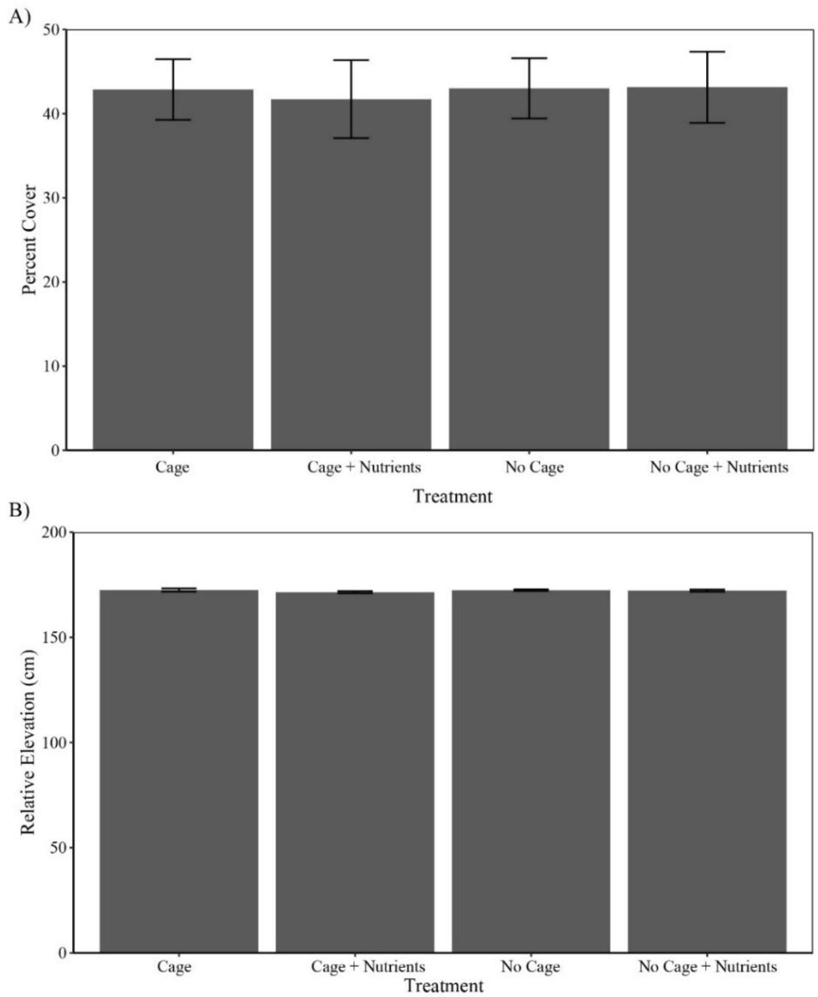

Figure S1: Graphs demonstrating similar conditions across treatments. A) Initial percent seagrass cover per treatment and B) Relative elevation (cm), with and without caging. Error bars represent standard error.

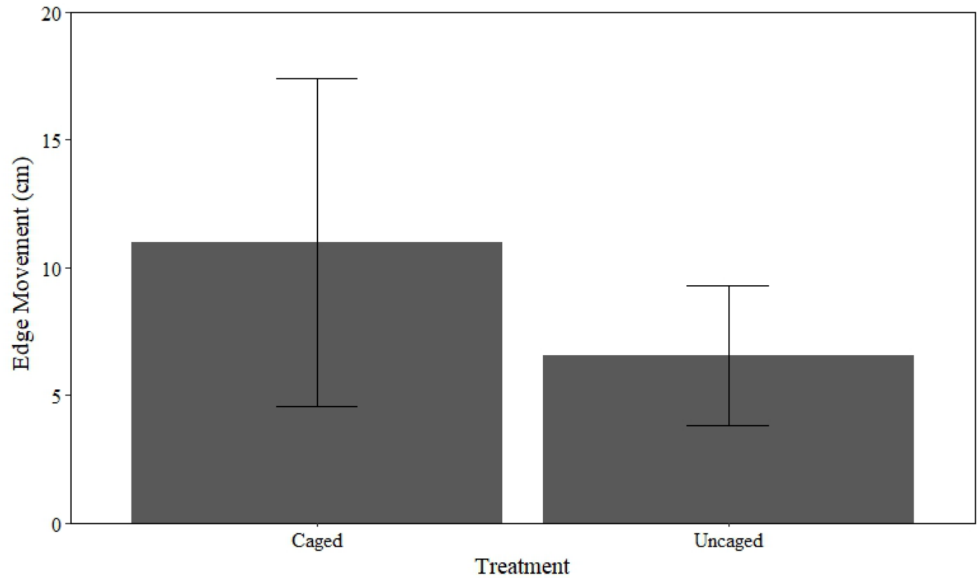

Figure S2: Seagrass edge movement with and without caging in 2023. Error bars represent standard error.

Table S1: ANOVA results for initial seagrass cover and relative plot elevation

Source	**Initial Seagrass % Cover**	**Relative Elevation**
Nutrients (N)	$F_{1,24}$= 0.04, p=0.85	$F_{1,24}$= 0.35, p=0.56
Cage (C)	$F_{1,24}$= 0.02, p=0.90	$F_{1,24}$= 1.3, p=0.26
C + N	$F_{1,24}$= 0.03, p=0.87	$F_{1,24}$= 0.56, p=0.46

Table S2: T-test results for water flow and seagrass edge movement with and without caging.

Variable	**df**	**T**	**p**
Seagrass Edge Movement	5.41	0.64	0.55

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