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RESEARCH ARTICLE

The Mechanisms Underpinning Zoogeochemistry

Mobile consumers influence the shoreward edge of intertidal seagrass ecosystems

Stephanie R. Valdez[1,2] | Carter S. Smith[1,2] | Catherine L. Brenner[2] | Avery B. Paxton[1,3] | Brian R. Silliman[1]

[1]Division of Marine Science and Conservation, Nicholas School of the Environment, Duke University, Beaufort, North Carolina, USA

[2]School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington, USA

[3]National Centers for Coastal Ocean Science, National Ocean Service, National Oceanic and Atmospheric Administration, Beaufort, North Carolina, USA

Correspondence
Stephanie R. Valdez
Email: srv1992@uw.edu

Present address
Avery B. Paxton, Southeast Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Beaufort, North Carolina, USA

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Abstract

1. Habitat edges are often considered environmentally stressful areas, and as such, research has largely focused on the impacts of physical factors in shaping these edges. However, less is known about the relative importance of biotic disturbance agents and bottom-up drivers in shaping habitat edges.
2. Here, we used intertidal seagrass beds as a model system to test how the independent and combined effects of stingrays—a disturbance-generating forager in seagrass beds—and nutrient addition affect the upper elevation edge of seagrasses.
3. A two-season long manipulative experiment with stingray exclusion × nutrient addition revealed that shoreward seagrass edges experienced heightened loss in percent cover when exposed to stingrays ($p = 0.037$) but were not impacted by nutrient additions to marine sediments ($p = 0.13$). Additionally, transplant experiments designed to test whether stingrays could limit intertidal seagrass establishment in higher elevation found that transplanted seagrass had a higher chance of survival when stingrays were excluded ($p < 0.01$), suggesting that seagrass could live higher in the intertidal and that stingrays may limit shoreward expansion. Finally, a multi-site observational survey demonstrated that stingray pit abundance was a strong predictor of the distance between seagrass edge and shoreward habitats.
4. Combined, these results challenge current understanding in plant ecology that seagrass edges are controlled mainly by physical factors and instead suggest that the structure of the seagrass shoreward edge is controlled by both physical and biotic drivers. Our results also indicate that the relative effects of consumer disturbance and physical factors in controlling edge limits are likely predicated on consumer density: in areas with higher densities of large consumers, biotic forcing is likely to be more important.
5. Furthermore, these results could have implications for restoration in areas with high densities of disturbance-generating foragers and align with calls for greater inclusion of animal impacts into restoration schemes. Biotic drivers along environmentally stressful edges are likely not limited to seagrasses and the generality

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of biotic control of habitat edges deserves further exploration across diverse ecosystems.

KEYWORDS
biotic control, disturbance-generating foraging, habitat edge, intertidal, nutrients, seagrass, species interactions, stingray

1 | INTRODUCTION

Habitat edges are highly dynamic areas that differ from interior habitats, and work has described how edge effects influence community structure. For example, species diversity tends to be higher at the habitat edge compared to the interior in temperate forests, whereas it tends to be lower at the habitat edge in tropical forests, although patterns are variable (Willmer et al., 2022). Additionally, unique species can be found at the habitat edge that are not found in the habitat interior (Soria et al., 2022). Habitat edges can also have different physical regimes, such as sediment nutrient content and sediment retention, compared to interior habitats. For example, forest edges are found to have higher nutrient concentrations than the interior of forests (Weathers et al., 2001; Yang et al., 2022), while in mussel beds, there is higher sediment retention within the habitat interior than at the habitat edge (Soria et al., 2022). In the greater context of anthropogenic habitat fragmentation and biological conservation, research has focused on how edge effects impact ecological structure and functioning, including changes to species behaviour and food web dynamics (Cronin, 2009; Ewers & Didham, 2006; Willmer et al., 2022; Wimp et al., 2019). Within habitat interiors, there has been extensive exploration of the relative roles of biotic and abiotic factors in habitat structuring (Borer & Gruner, 2009; Gerwing et al., 2016; Liu et al., 2021; Power, 1992). However, less is known about the relative importance of biotic and abiotic factors in shaping existing habitat edges.

At the habitat edge, research has aimed to apply predictable patterns of the importance of biotic and abiotic factors across a physical stress gradient. For example, species zonation describes the patterning of species presence across an environmental gradient while the species interaction-abiotic stress hypothesis (SIASH) states that environmentally stressful edges are thought to be controlled primarily by physical factors, whereas biotic interactions are more pertinent under amenable environmental conditions (Connell, 1961; Louthan et al., 2015; Menge et al., 1999; Pennings & Callaway, 1992). However, recent research suggests that observed patterns are not as simple as predicted and underlying physical gradients may only partially describe the patterns observed. Shepard et al. (2021) found that the caddisfly's environmentally stressful edge extent was not solely influenced by physical factors but also by competition. Inversely, in environmentally amenable areas thought to be dominated by biotic interactions, such as in grazing halos, research now suggests that physical factors such as nutrients also influence those halos (Bilodeau et al., 2021). Moreover, it is likely that nutrients and consumers have an interactive effect on ecosystems, via consumer-derived nutrients to changes in nutrient cycling from compensatory growth (Bilodeau et al., 2021; Cromsigt & Olff, 2008; Holzer & McGlathery, 2016). Nevertheless, few studies have explored the impacts of both biotic and abiotic factors in shaping complex and environmentally stressful habitat edges. In this study, we therefore investigate the relative effects of biotic interaction (consumer foraging effects) and nutrient addition on the shoreward edge of a seagrass ecosystem.

Seagrass meadows are unique in that they occur in a variety of sizes, shapes and configurations with the possibility of multiple edges. It has long been predicted that the shoreward edge of seagrass is controlled by physical factors such as desiccation, and therefore, there has been significant research on desiccation tolerance and photoacclimation of various species (Björk et al., 1999; Park et al., 2021; Tanaka & Nakaoka, 2004). There are differing accounts of the impacts of desiccation stress on seagrass patterns of zonation in the intertidal and it is likely highly influenced by species identity (Björk et al., 1999; Tanaka & Nakaoka, 2004). In fact, some work suggests that there is likely a complex suite of factors that influence the vertical distribution of intertidal seagrass, including species-specific stress tolerance and growth responses to stress (Shafer et al., 2007). Furthermore, previous work suggests that light or nutrient loads may also be important in determining intertidal distribution for seagrass (Björk et al., 1999; Park et al., 2021). However, there has been limited work exploring factors other than desiccation on intertidal seagrass shoreward edges, such as nutrients or biotic interactions.

Seagrasses are a highly productive plant foundational group that are threatened by many global change factors such as nutrient loading, pollution and coastal development (Duarte & Chiscano, 1999; Dunic et al., 2021; Nordlund et al., 2016; Orth et al., 2006). In North Carolina (NC), USA, seagrass loss has been attributed to increased nutrient levels and poor water quality that is exacerbated 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 support a variety of organisms, including mobile species like salmon and waterfowl that utilize meadows at discrete time periods (Chalifour et al., 2019; Kollars et al., 2017; Nordlund et al., 2016; Turschwell et al., 2021; Unsworth et al., 2019). Stingrays, for example, use seagrass meadows and the area around seagrass as foraging grounds (Ambo-Rappe et al., 2021; Townsend & Fonseca, 1998). In NC, stingrays migrate to seagrass beds in the summer (April–September; Schwartz & Dahlberg, 1978).

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This migration overlaps with the height of seagrass production (Wheeler et al., 2024). Stingrays are disturbance-generating 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 (Figure 1a,b; Howard et al., 1977; Takeuchi & Tamaki, 2014; Townsend & Fonseca, 1998). Stingray foraging can disrupt up to 879 cm^3/m^2/day of sediment (Takeuchi & Tamaki, 2014). Furthermore, foraging is concentrated at the seagrass edge and at depths that can disrupt seagrass root mats (Townsend & Fonseca, 1998). The stingray–seagrass interaction likely occurs across the multiple edges in a meadow, although little is known about the influence stingrays have on shaping these edges.

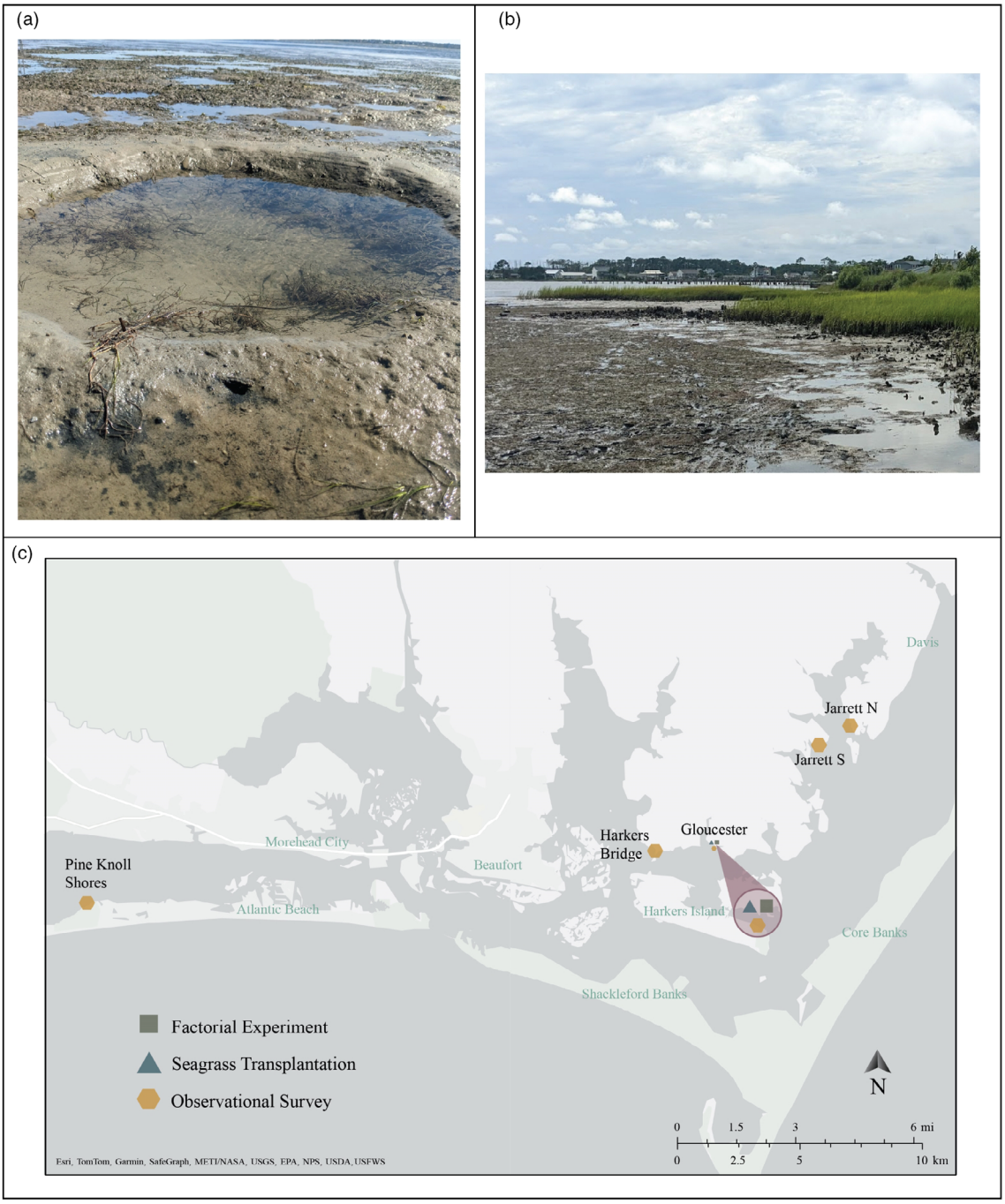

FIGURE 1 Photos and map illustrating (a) a stingray feeding pit with uprooted seagrass, (b) seagrass exposed at low tide with a band of bare space between the seagrass and shoreward marsh and oyster habitat and (c) a map of where different aspects of the project occurred. Methodologies on the map are coded by shape and colour and represent the factorial experiment, the transplantation experiment and the sites for the observational surveys. The base map was generated in Harvard WorldMap in ArcGIS online powered by Esri. Photographs and illustrations created by S. Valdez.

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Here, we utilize manipulative field experiments and observational surveys to explore the separate and interactive impacts of stingray foraging and nutrient addition on the shoreward edge of seagrass. We focused on the shoreward edge due to the observed abundance of feeding pits and because this is a potential location for bed expansion shoreward with sea level rise (Davis et al., 2016). We first asked whether stingray foraging and nutrient addition at the shoreward edge impacted the percent cover of seagrass. Seagrass cover is often lower at the meadow edge (Yarnall et al., 2022), and we predicted that stingray foraging behaviour could be disruptive at the edge of seagrass meadows by creating foraging pits that uproot seagrass and negatively influence the percent cover of seagrass. While nutrient enrichment has a varied response on seagrass productivity, the continued increase in nutrient loading and research on seagrass nutrient enrichment suggest decreased resilience to nutrients and lower seagrass biomass (Cardoso et al., 2004; Gladstone-Gallagher et al., 2018; Turschwell et al., 2021). Therefore, we predicted nutrient enrichment would reduce cover at the shoreward edge. Combined, we predicted that stingrays and nutrient addition could act additively to further limit the shoreward seagrass edge. Second, in addition to understanding impacts on the current meadow extent, we also wanted to explore the potential for stingrays to truncate meadow expansion. To do so, we asked whether stingrays could influence seagrass survival higher in the intertidal than the current meadow extent. We predicted that without stingray interference as a disturbing agent, seagrass would be able to survive higher in the intertidal, demonstrating a biotic control in truncating the seagrass meadow. Finally, we asked whether stingray foraging correlated with the distance between seagrass and shore habitats. Using observational surveys, we predicted that higher coverage of feeding pits, as a proxy for stingray feeding pressure and associated disturbance, would correlate with a longer distance between the shore and the seagrass meadow. If our hypotheses are supported, it would suggest a biotic interaction at the shoreward edge of seagrass. While we do not discount the impacts of physical forces on the intertidal seagrass extent, as there is a finite limit to the physical stressors that seagrass can endure in the high intertidal, the idea that biological factors can also significantly contribute to the shoreward extent of a foundation species at the stressful edge is counter to the current dogma and would have broad implications for ecology and conservation.

2 | MATERIALS AND METHODS

2.1 | Site description

To test our hypotheses, we conducted a suite of field experiments and observations. First, to understand the interaction of stingrays and nutrient enrichment on the shoreward edge of seagrass, we conducted a fully factorial field experiment. Next, we used two seagrass transplantation experiments to explore how stingrays may influence the shoreward extent of seagrass. Finally, to test our hypothesis that there is a correlation between the distance from seagrass to shore habitats and stingrays, we conducted a multi-site observational survey. All experimental tests were conducted in the Straits in Gloucester, NC, USA (34.7244°N, 76.5496°W; Figure 1c). The Straits are part of a larger estuarine ecosystem protected by inner sound islands and barrier islands. This environment has saline waters and is protected against high wave action. The experimental site was selected for: (1) a relatively continuous seagrass meadow that naturally spanned the intertidal to subtidal zone and (2) an observed presence of stingray feeding pits (Figure 1a,b). The observational surveys occurred across three sounds in the same estuarine ecosystem (Figure 1c). Survey sites were selected for continuous seagrass meadows backed by non-eroding shoreline habitats that maintained a bare, unvegetated space between the two habitats. All experimental and survey work was conducted with Institutional Animal Care and Use Committee approval (permit number A059-21-03) and in accordance with NC Department of Environmental Quality (Scientific and Educational Activity Permit numbers 2055740 and 707075).

There are several species of stingrays that utilize NC intertidal areas including the Atlantic stingray (*Hypanus sabinus*), the southern stingray (*Hypanus americanus*), the bluntnose stingray (*Hypanus say*) and the cownose stingray (*Rhinoptera bonasus*). The dominant meadow-forming seagrass species throughout the area is the tropical *Halodule wrightii*. The meadow is intermixed with sparse *Ruppia maritima*, a halophyte commonly found in seagrass meadows in NC, and more temperate *Zostera marina* during the cooler months (November–May). From here on, the seagrass community matrix will simply be referred to as seagrass.

2.2 | Factorial experiment

To assess the independent and combined effects of stingrays and nutrient additions on the edge of a mature seagrass bed, we conducted a fully factorial field experiment from May 2021 until September 2022. We manipulated stingray access to the shoreward edge of the seagrass bed using cages and enriched sediment nutrients resulting in the following four treatments ($n = 7$ for a total of 28, 1 m^2 plots): (1) caged with fertilization, (2) caged without fertilization, (3) no cage with fertilization and (4) no cage without fertilization (Figure 2a). Plots were initially placed on the edge of the seagrass meadow with an average of 42.7% ± 1.9 SE seagrass cover across all plots (Figure S3; Table S2). Plots were randomly assigned treatments. Cages were constructed of 90 cm high bamboo poles that were evenly spaced (20 cm distance, which is smaller than maturation size of the widely sighted Atlantic stingray; Snelson et al., 1988) to limit the entrance of stingrays from the sides and tops of the plots (Nauta et al., 2024). Bamboo posts were monitored every month during the warmer periods (April–October in year 1 and April–September in year 2) and once during the winter. Bamboo posts were replaced as they degraded to maintain the exclosure treatment. There was no evidence of stingrays breaking

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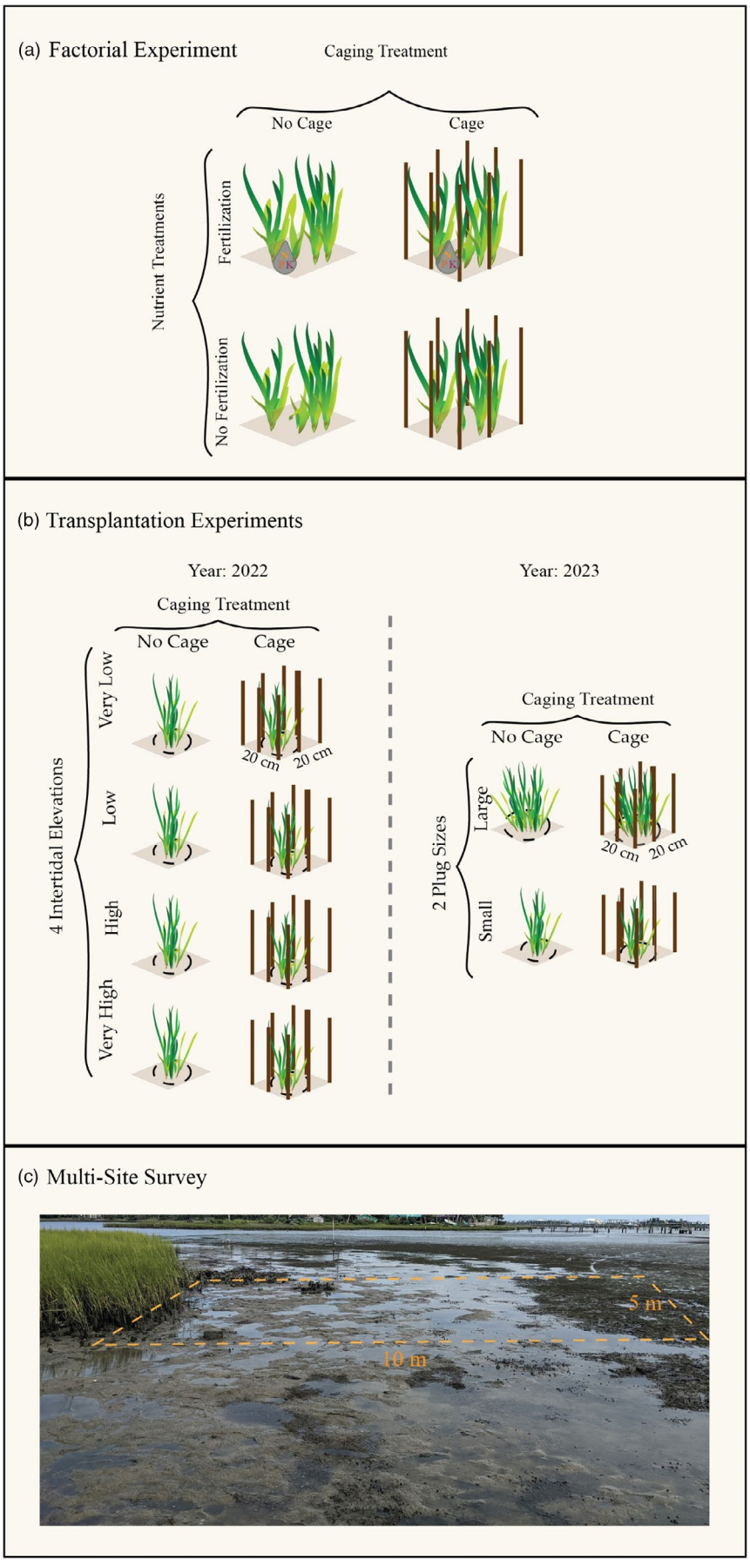

FIGURE 2 Graphical and pictorial depiction of experimental and observational survey set up for (a) the fully factorial, two season stingray exclusion by nutrient addition, (b) the seagrass transplantation experiments in 2022 and 2023 and (c) the multi-site observational survey. Survey plot is drawn approximately to scale. Photographs and illustrations created by S. Valdez.

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or removing posts and no evidence of stingray pits within caged plots throughout the experiment. Control uncaged plots 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, non-caged plots underwent the same mechanical disturbance with bamboo being inserted but removed so as to not deter stingrays. 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, we 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 as seagrass began to senesce.

Plots were fertilized using Jobe's® Tree and Shrub Spikes. Four spikes per plot were placed in a 30 cm × 30 cm square centred in the middle of the plot and completely submerged in the sediment. Premeasured fertilizer spikes (113.3 g/spike) were chosen for their ease of complete burial into the sediment and to limit nutrient enrichment in the surrounding water column. Fertilizer spikes consisted of 16% N, 4% P and 4% K slow-release fertilizer. Spikes were added every 3 months totalling 289.6 g N/m^2/year, 72 g P/m^2/year and 72 g K/m^2/year, more than the estimated annual N budget for *Z. marina* (50 g N/m^2/year; Hemminga et al., 1991). Plots without nutrients received procedural control by inserting a similar sized object into the sediment that mimicked the disturbance of adding the nutrient stakes. In addition, the relative elevation of each plot was quantified using a laser level and levelling rod to ensure each plot experienced similar tidal impacts. After experimental set-up, each plot was assessed periodically over 2 years for percent seagrass cover. Percent seagrass cover was always estimated by the same observer and was estimated at low tide when seagrass was exposed to limit bias among estimates. At the end of the experiment in September 2022, 100 mL of sediment was collected from the centre of each plot. Sediments were analysed for bulk density and total nitrogen. To measure bulk density, 25 mL of the 100 mL sample was dried in a known weight tin at 60°C until a constant weight. Bulk density was calculated from the final weight minus the tin divided by the sample volume (g/cm^3). To evaluate total N, the remaining 75 mL of the sample was sent to the University of Georgia's Agriculture and Environmental Services Laboratory to be analysed. Finally, to assess seagrass edge movement over a summer with and without stingrays, a second caging experiment ran from May to August 2023 with plots centred on the seagrass edge (Supporting Information S1).

2.3 | Seagrass transplantation

To evaluate the shoreward boundary of seagrass with and without stingrays, we conducted a seagrass transplant experiment. In June 2022, we transplanted 40 plugs (6 cm diameter) of seagrass at four elevations. Plugs were only *H. wrightii* and no *Z. marina* or *R. maritima* were observed. Half were randomly assigned to 20 cm × 20 cm caged plots that limited stingray access and half without caging ($n = 5$ at each elevation; Figure 2b). Since the intertidal space was finite, we used smaller cages to limit the amount of space occupied and not impede stingray movement through the experimental area. Cages were constructed of 10 cm separated bamboo stakes (61 cm tall). These cages had shorter spacing than the cages mentioned previously due to the smaller size of the plots (i.e. 20 cm spacing would constitute only corner posts for these plots). We were not concerned that stingrays would enter the cage plots at the 20 cm spacing in the larger cages and therefore were confident that the seagrass was protected from foraging. However, given the excavation power of stingrays and the smaller size of the plots, we were 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, we 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 10 cm from the seagrass plug. Uncaged plots also had bamboo inserted and removed at 10 cm intervals in a 20 × 20 cm^2 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. Each elevation level was marked on a falling tide to ensure differential tidal impact. The lowest elevation was placed in bare space near the existing 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 and no observed seagrass. The remaining two elevations were evenly spaced between the highest and lowest with approximately five horizontal meters between each elevation. We used a laser level to assess the relative elevation of each plot. The four elevations are referred to as very low, low, high and very high from here on with very low near the seagrass edge and very high nearest to the shore. There was a 10 cm vertical difference in elevation (Supporting Information S2; Figure S1; Table S1) and a 15 m horizontal distance from very low to very high. Once seagrass was transplanted, we evaluated survivorship as the presence of any live seagrass in the original plug for each plot every 2 weeks until September 2022.

Since seagrass survival after transplantation is notoriously low and likely reliant on density-dependent intraspecific interactions (Zhang et al., 2021), we conducted an additional transplant experiment with a larger plug size in the subsequent year (Figure 2b). With the second transplants, in addition to stingray foraging pressure, we also evaluated the density-dependent effects of plug size as a potential mechanism for low survival in the first year. In June 2023, we transplanted an additional 40 seagrass plugs: 20 small plug size (6 cm diameter, same as 2022) and 20 large plug size (12 cm diameter). Half were in cages with the same dimensions as above and half were uncaged ($n = 10$). All plots were placed at

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relatively the same elevation between the two intermediate elevations from the previous year's transplantation where we observed seagrass survival (i.e. 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 2 weeks until August 2023 and again in October 2023.

2.4 | Multi-site observational survey

To better generalize the impact of stingray pit abundance in multiple seagrass beds, we conducted a survey across five sites from Core Sound south to Bogue Sound between July and early September 2022 (Figure 1c). The five sites were Gloucester (near the original experiment but avoiding any plots; 34.7241° N, 76.5496° W), Harkers Bridge (34.7254° N, 76.5807° W), Pine Knoll Shores (34.7022° N, 76.8294° W), Jarrett Bay North (34.7758° N, 76.4917° W) and Jarrett Bay South (34.7724° N, 76.5018° W). We 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 neighbouring biogenic habitats. We selected sites that had relatively continuous seagrass beds and neighbouring non-scarped saltmarsh and oyster ecosystems. At each site, we evaluated seven 5 m × 10 m quadrats (Figure 2c). The 5 m long edge of the quadrat was placed along the edge of the saltmarsh and oyster ecosystems and extended 10 m perpendicular toward the seagrass meadows. Within each quadrat, we measured the number of pits, two perpendicular widths (cm) of five random pits and the percent cover of each foundational organism (i.e. saltmarsh grass, oyster and seagrass) within the plot. The five pits were randomly selected by tossing a pen into the quadrat without looking and the pit closest to the pen was measured. Measured pits were marked to ensure they were not re-measured, and the process was repeated five times. We 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. We also measured the distance (m) between the saltmarsh/oyster shore habitat and seagrass, even when it fell outside the quadrat. In addition, wind and water movement can act on seagrass to affect edge dynamics (Momberg et al., 2021; Silinski et al., 2018). Therefore, we also measured wind fetch (m) as a proxy for wind and wave energy 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.

2.5 | Statistical analysis

To assess seagrass percent cover in the factorial experiment, a generalized linear mixed effects model (GLMM) was fitted in the 'glmmTMB' package (Brooks et al., 2017). The model included stingray exclusion (categorical, two levels), nutrient addition (categorical, two levels) and date (categorical, eight levels) as main effects and plot as a random effect to account for the repeated measures for all percent cover collected after initial set up. The model was fit with a beta distribution (Damgaard & Irvine, 2019). Interactions among responses were not included in the final model as the fully additive model had the lowest AIC. Model residuals were visually inspected to meet assumptions and model predictions were comparable to observed (Figure S2). Likelihood ratio tests (LRT) were used to assess the relationship of caging, fertilization and date on seagrass cover.

Additionally, as seagrass coverage peaked in May of both years and began senescence through the summer, we separately calculated the absolute change in seagrass cover as the difference between cover estimates in May 2021 and May 2022. Two-way ANOVAs were used to evaluate the change in percent cover by stingray exclosures, nutrient addition and their interaction. Additionally, to explore impacts of sediment fertilization, two-way ANOVAs were used to assess total N and sediment bulk density by stingray exclosure, nutrient addition and their interaction. Non-significant interactions were removed from all final models.

To assess seagrass transplant survival through time in both 2022 and 2023, we used Cox proportional hazard models (Landes et al., 2020) using the 'survival' package (Kassambara et al., 2021; Therneau & Grambsch, 2000; Therneau, Lumley, et al., 2023). All assumptions for proportional hazard through time were met.

To assess predictors that influence the distance (m) between shore habitat and seagrass meadow edge in the multi-site observational survey, a classification and regression tree (CART) model was constructed using the 'rpart' package (Therneau, Atkinson, & Ripley, 2023). CART models are useful tools to help elucidate the influence of multiple predictors on a single response variable (De'ath & Fabricius, 2000). Predictors included site, average wind fetch per quadrat, longest fetch direction, shore habitat (oysters, marsh or combination of the two), percent cover of 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 was numeric, and the minimum split level was set to 10.

All analyses were conducted in R (version 4.2.2; R Core Team, 2022). For all linear models, data were tested for homogeneity of variance using Levene Tests (Levene, 1960) and for normality of residuals in Q-Q plots. All data for linear models, unless mentioned, met these assumptions.

3 | RESULTS

3.1 | Site description

On average, there were 1.01 pits/$m^2 \pm 0.13$ standard error (SE) in unvegetated space, 1.00 pits/$m^2 \pm 0.24$ SE at the edge of seagrass and 0.20 pits/$m^2 \pm 0.05$ SE in the seagrass meadow (Supporting

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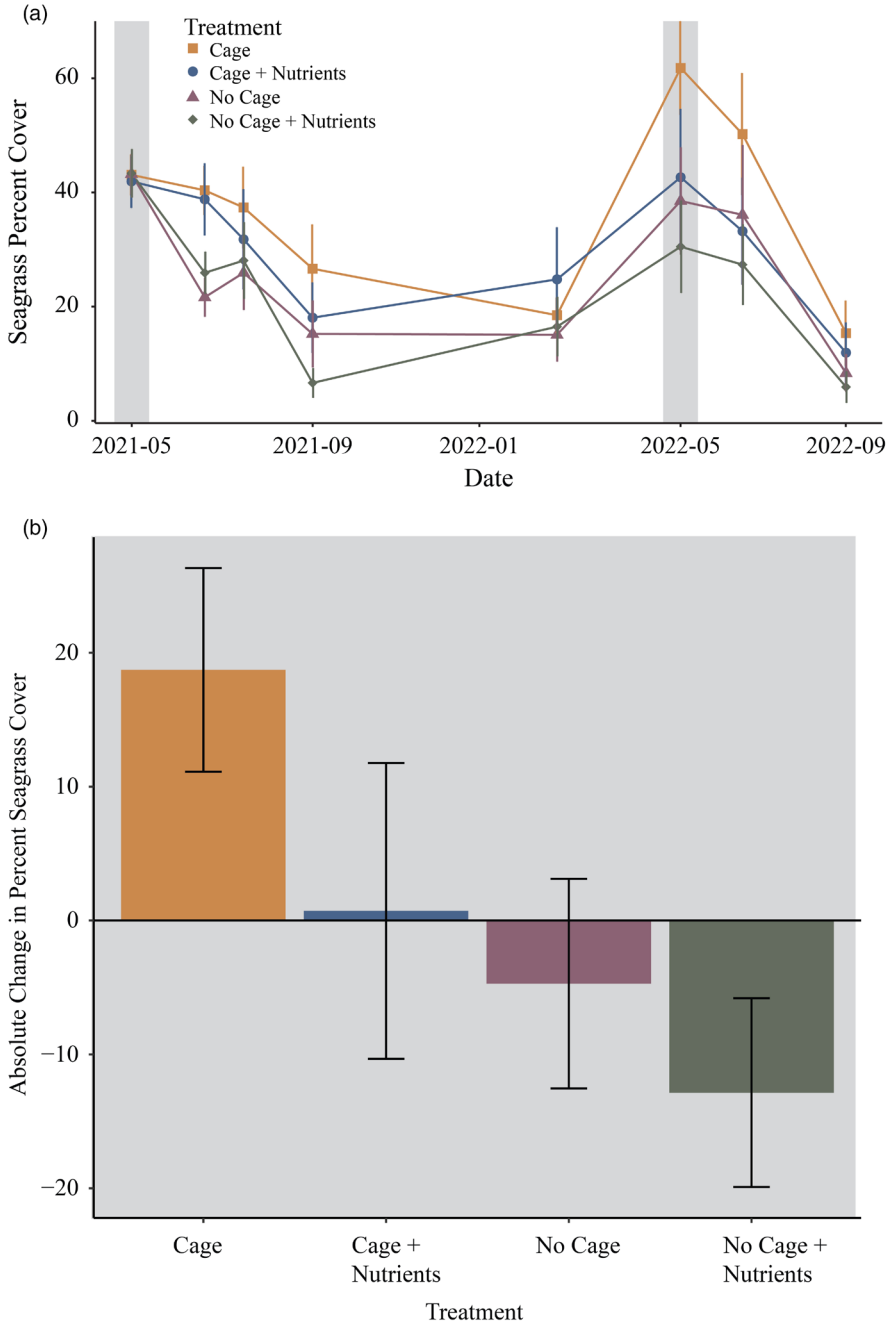

FIGURE 3 Graphs from the factorial stingray exclusion by nutrient addition experiment. (a) The seasonal flux in seagrass percent cover across all treatments over time where shape and colour denote treatment with shapes representing the mean and error bars representing standard error (SE) ($n = 7$). Seasonal peaks in May 2021 and May 2022 highlighted with grey boxes that correspond with (b) change in seagrass percent cover between May 2021 until May 2022 ($n = 7$).

Information S3; Figure S3). In addition, a stingray prey abundance survey found no difference among habitats (Supporting Information S4; Figure S3).

3.2 | Factorial experiment

There was no difference in initial conditions among treatments for percent seagrass cover or relative elevation (Supporting Information S5; Figure S4; Table S2) and we found no impact of caging on water flow (Supporting Information S6; Figure S5; Table S3). Seagrass percent cover peaked each year in May and all plots experienced decline through the rest of the summer (Figure 3a). Date had a significant effect on seagrass percent cover (GLMM, LRT, $\chi^2 = 98.79$, $p < 0.0001$). Seagrass coverage fluctuated seasonally with the peak in May 2022 (average cover of 43.14% ± 5.02 SE across all treatments) and the lowest observed percent cover in September 2022 (average cover of 10.18% ± 2.21 SE across all treatments). Seagrass cover trended higher in caged plots through time compared to uncaged plots, but this effect was not significant (LRT, $\chi^2 = 3.34$, $p = 0.068$) and there was no effect of fertilization on seagrass cover (LRT, $\chi^2 = 1.04$, $p = 0.31$). The change in percent cover between annual seasonal peaks from May 2021 until May 2022 (Figure 3b) was significantly different for caging treatments ($F_{1,25} = 4.84$, $p = 0.037$) and not significant for fertilization ($F_{1,25} = 2.41$, $p = 0.133$, Figure 3b). Caged plots, on average,

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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. For sediment, neither total N nor bulk density were significant (Table S1). For the secondary caging experiment done to evaluate seagrass edge movement in 2023, there was no significant difference between caged and uncaged plots (Figure S6; Table S3).

3.3 | Seagrass transplants

In 2022, seagrass transplants had a 2.7 times greater chance of being absent when uncaged rather than caged ($Z = 2.64$, $p = 0.008$; Figure 4a), while there was no significant effect of elevation. However, the overall model was not significant (LRT = 8.57 on 4 df, $p = 0.073$). At the end of the season, only plugs in low and high elevations remained, all of which were caged, accounting for 10% of the total plugs. In 2023, the pattern repeated with uncaged seagrass transplants having a 2.8 times greater chance of being absent than caged plugs ($Z = 2.78$, $p = 0.005$; Figure 4b). Plug size was not significant ($Z = 0.20$, $p = 0.84$). The overall model was significant in 2023 (LRT = 7.84 on 2 df, $p = 0.019$). At the end of the season, 17.5% of the plugs remained, all but one of which were caged.

3.4 | Multi-site 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 (Figure 5). The average distance from shore to seagrass was 39.2 m ± 5.5 SE for the seven plots at the Pine Knoll Shore site and 7.7 m ± 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 14 m between seagrass and shore, whereas those with less than 31% coverage averaged 7 m.

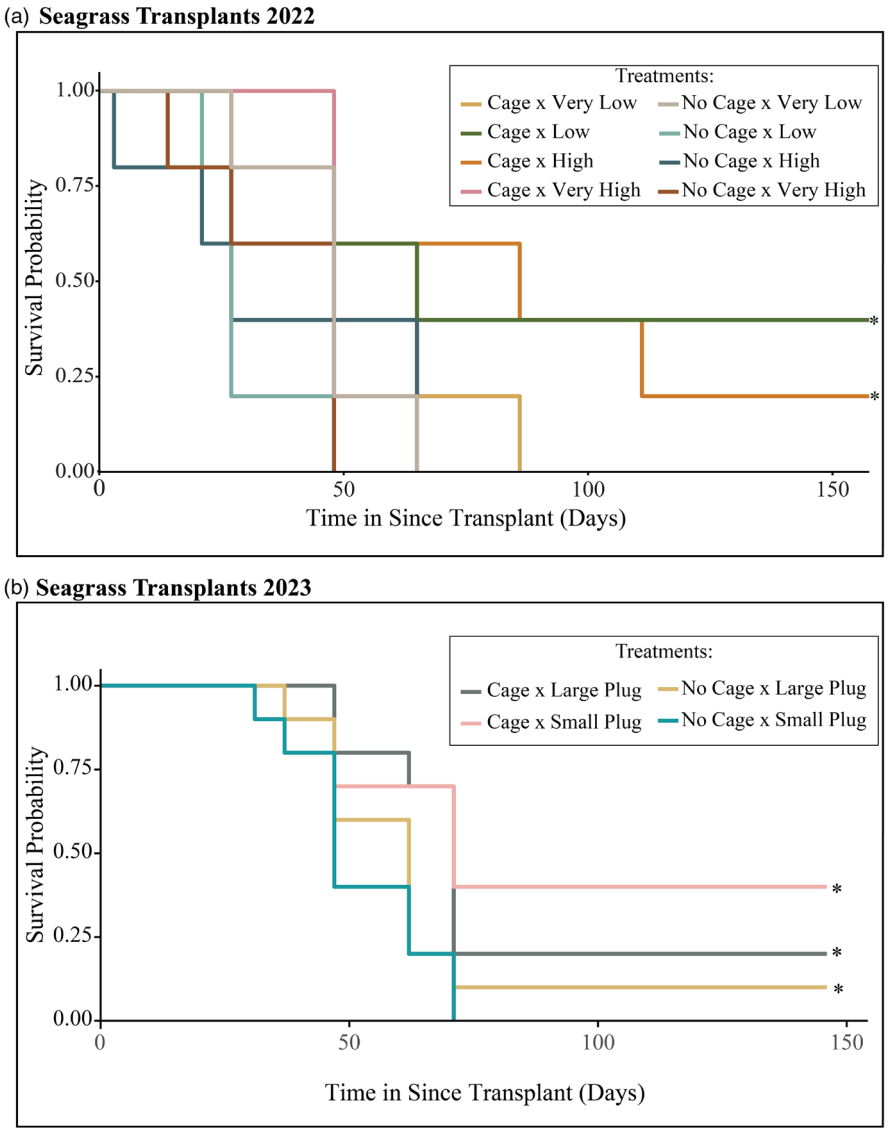

FIGURE 4 Results from seagrass transplantation experiments. (a) Time to event curve for transplanted seagrass with and without caging as protection from stingray feeding at four elevations in 2022. Event curves that truncate with * indicated survival past observed interval. (b) Time to event curve for transplanted seagrass with and without caging as protection from stingray feeding in 2023. Event curves that truncate with * indicated survival past observed interval.

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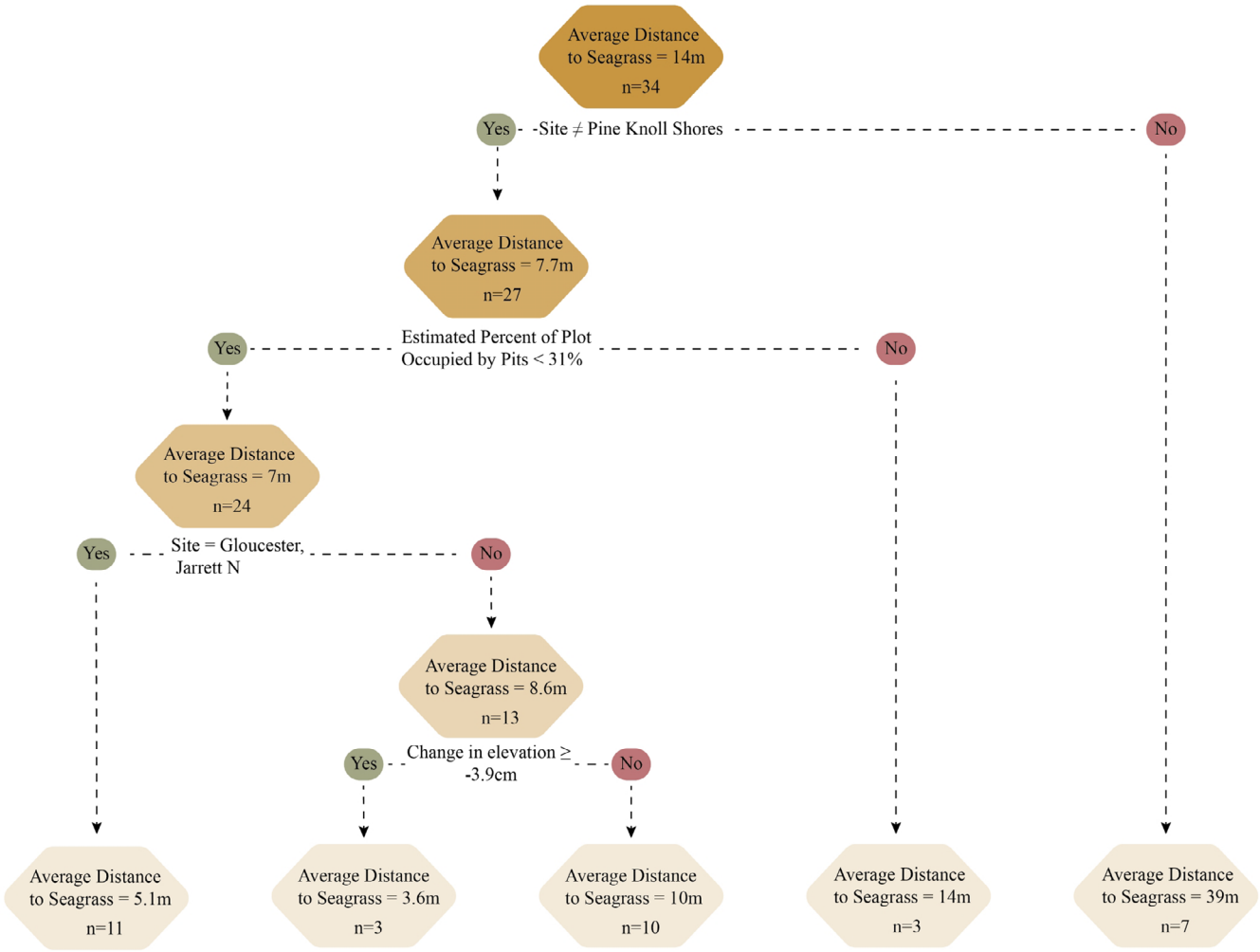

FIGURE 5 Regression tree analysis from the multi-site observational surveys showing the strongest predictors of the distance between seagrass and shoreward biogenic habitats.

4 | DISCUSSION

Through experimental manipulations and observational surveys, we show that stingray foraging can influence the shoreward edge of seagrass. While we do not discount the impact of physical factors, we demonstrate that they are likely not solely responsible for the observed edge structure and vertical positioning. We provide evidence suggesting the coverage of seagrass at the meadow edge is lower when there is stingray foraging and greater distance between seagrass meadows and shore habitats correlated with a greater coverage of stingray pits. Finally, we demonstrated that seagrass can indeed survive higher in the intertidal than the observed meadow when protected from stingrays. These results, along with studies from other ecosystems (Alberti et al., 2007; Louthan et al., 2015; Shepard et al., 2021), call for an expansion of current paradigms (e.g. SIASH) to include experimental testing of the relative role of biological interactions at an environmentally stressful edge.

In the factorial experiment, stingray exclosures minimized the loss of seagrass cover, suggesting that stingrays exert biological control at the stressful edge of this ecosystem. 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 what we would expect if physical factors were solely responsible for setting the shoreward edge as suggested by patterns of species zonation across a physical gradient (Connell, 1961; Menge et al., 1999; Pennings & Callaway, 1992) or SIASH (Louthan et al., 2015) and suggests that the observed meadow may be truncated by stingray foraging. However, these results are supported by work that explores disturbance generating foragers that lower vegetation abundance. For example, in saltmarshes, disturbance from crabs, ragworms and hogs, including burrowing, bioturbation and increased erosion, can diminish saltmarsh abundance (Hensel et al., 2021; Hughes & Paramor, 2004; Szura et al., 2017). Further, study of this ecosystem is complicated by the seasonality and the ephemeral nature of the edge of habitat conditions that makes assessing the impacts of stingrays challenging. We observed the seagrass within our experimental plots reached peak cover in May and senesced through the remainder of the summer. We suggest that the combination of environmental stressors and biological disturbance becomes too much

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for seagrass in NC to overcome and that regardless of the treatment, all seagrass is being lost by the end of each summer. However, we also observed the seagrass rebounded the following spring and in plots that maintained stingray exclosures, rebounded to a greater extent than the uncaged plots. As is the case with most experimental field studies, our study is limited by the scale and duration of the experiments. To fully understand whether stingrays play a prolonged role in truncating seagrass beds in NC needs further exploration via long-term, large-scale exclosures. When exclusions are completed for longer periods of time, a greater understanding of the effect size and mechanisms of biotic control emerge (Hughes et al., 2024; Morton et al., 2024).

Additionally, there was no impact of fertilization on percent cover or higher nutrient content in the soil 3 months after nutrient addition. We hypothesize that this could be due to the high turnover rate for the dominant seagrass, *H. wrightii*, which can grow over 8 mm per day or completely replace above-ground biomass within 21 days (Kowalski et al., 2001; 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 our sampling methods. While not studied here, nutrient additions to the water column can impact seagrass macro-algal overgrowth and diminish light availability (Cabaço et al., 2013; Wang et al., 2022) and may interact with stingrays differently than sediment nutrient addition. Future work should further evaluate the impacts of nutrients in tangent with stingray impacts by testing variations in nutrient delivery methods (water column vs sediment) and nutrient concentrations in large-scale, long-term manipulations.

The idea that stingrays can influence the shoreward edge of seagrass is further supported by our transplantation experiments that tested for the relative effects of biotic disturbance and physical factors in outplant survival beyond the current extent. In both years that transplants were placed higher into the intertidal, the probability of survival increased when plugs were caged. While we cannot distinguish between plugs of seagrass that were lost due to stingray foraging or by some other factors, including substrate type or wave action which may influence both the presence of stingrays and seagrass, the abundance of stingray pits in and around the experimental area suggested that stingray played a contributing role in the seagrass loss. Additionally, the abiotic conditions at the edge of the meadow and higher into the intertidal were likely less stressful than predicted given the survival at these higher intertidal transplants, potentially supporting the idea that these shoreward edges are more complex than theory suggests and additional research is needed to fully understand what factors limit seagrass distribution. However, further research is needed to better evaluate the mechanism behind seagrass plug loss, stingray influence and an abundance of physical factors. 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, it has been challenging to effectively restore. Traditional restoration efforts have focused on minimizing abiotic factors such as poor water quality (Valdez et al., 2020); however, based on our results, restoration efforts need to consider the biological community present in the area. Stingrays act as a disturbing agent in the ecosystem that can uproot planted seagrass. This is not unique to the NC seagrass ecosystem as stingrays are common throughout the world's oceans and overlap with many seagrass ecosystems (Last, 2016; Short et al., 2007). To date, marine restoration has been limited in the incorporation of animal contributors to restoration projects, despite evidence that biotic controls are critically important for restoration success (Xu et al., 2023). Yet, there are active calls for the inclusion of animals in restoration efforts (Sievers et al., 2022). Incorporating animals into restoration design may include changes to site selection criteria, timing of restoration activities or by adding defence mechanisms against biotic disturbance.

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 39 m away from the shore. In this instance, physical factors may have played a dominant role in determining the shoreward extent of seagrass. For example, several additional physical factors such as water velocity, waves and turbulence, along with geochemical properties such as sulfide toxicity, could impact the seagrass edge (Koch, 2001; Uhrin & Turner, 2018). Those physical factors, however, were not captured in our survey. 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. However, the influence of site suggests a context-dependent trade-off between physical and biological interactions influencing the distance from the seagrass edge to the shore. The context dependency of biological versus physical factors altering the edge extent demonstrated by this multi-site survey aids in the notion that ecological theories, such as SIASH, while helpful in hypothesizing patterns, are not all encompassing. Combined, our results show that the shoreward edge of a marine plant ecosystem is controlled by a suite of ecological factors, including physical and biological interactions with stingrays. This aligns with recent calls to expand ecological paradigms including SIASH (Louthan et al., 2015; Shepard et al., 2021) and grazing halos (Bilodeau et al., 2021). However, further research is needed to know the full extent of where and when stingrays and additional physical factors influence the shoreward edge and expansion of seagrass. Biological interactions that alter edge margins of plant ecosystems on what is thought to be a stressful edge may not be constrained to seagrass ecosystems but could be prevalent in many ecosystems. Several examples have emerged to support the influence of biotic interactions at a species edge. For example, in saltmarshes, 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). Terrestrially, caddisfly upslope extent is influenced by competition rather than elevation (Shepard et al., 2021), and

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elephants have been shown to disproportionately impact vegetation on waterward edges, correlating with lower vegetation cover and density (Mukomberanwa et al., 2024). This is not to say, however, that physical factors do not contribute significantly to shaping edges, especially under changing climate conditions. Research has shown a redistribution of organisms following thermal shifts (Hastings et al., 2020; Lenoir et al., 2020). As drivers of global change continue to alter ecosystems, the influence of biological interactions and physical factors on setting species extents may be modified and should be considered in tandem. Therefore, it is imperative that both biological and physical factors are explored to better understand edge habitats and the impacts they can have on foundational ecosystems. Biologically driven changes to habitat edges also have the ability to change the way practitioners and managers approach restoration and conservation of these foundation species. Hence, we call for future research to explore the complex suite of physical and biological factors that set a habitat edge and to use the ecological theories in place as a steppingstone to further ecological knowledge.

AUTHOR CONTRIBUTIONS

Stephanie R. Valdez and Brian R. Silliman conceived research questions and study design. Stephanie R. Valdez, Carter S. Smith and Catherine Brenner conducted data collection. Stephanie R. Valdez, Carter S. Smith and Avery B. Paxton analysed data. Stephanie R. Valdez wrote the manuscript. All authors contributed to editing the manuscript and approved the final submission.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and R script are available in the Zenodo data repository: https://doi.org/10.5281/zenodo.17584820 (Valdez, 2025).

ORCID

Stephanie R. Valdez https://orcid.org/0000-0002-3497-751X
Carter S. Smith https://orcid.org/0000-0002-6652-3010
Avery B. Paxton https://orcid.org/0000-0002-4871-9167
Brian R. Silliman https://orcid.org/0000-0001-6360-650X

REFERENCES

Alberti, J., Escapa, M., Daleo, P., Iribarne, O., Silliman, B. R., & Bertness, M. (2007). Local and geographic variation in grazing intensity by herbivorous crabs in SW Atlantic salt marshes. *Marine Ecology Progress Series*, *349*, 235–243. https://doi.org/10.3354/meps07089

Ambo-Rappe, R., Nafie, Y. A. L., Marimba, A. A., Rismayani, A., & Unsworth, R. K. F. (2021). Bycatch from seagrass fisheries: Implication for conservation. *IOP Conference Series: Earth and Environmental Science*, *860*(1), 012107. https://doi.org/10.1088/1755-1315/860/1/012107

Bilodeau, S. M., Layman, C. A., & Silman, M. R. (2021). Benthic pattern formation in shallow tropical reefscapes: Does grazing explain grazing halos? *Landscape Ecology*, *36*(6), 1605–1620. https://doi.org/10.1007/s10980-021-01239-1

Björk, M., Uku, J., Weil, A., & Beer, S. (1999). Photosynthetic tolerances to desiccation of tropical intertidal seagrasses. *Marine Ecology Progress Series*, *191*, 121–126. https://doi.org/10.3354/meps191121

Borer, E. T., & Gruner, D. S. (2009). III.6 top-down and bottom-up regulation of communities. In *III.6 top-down and bottom-up regulation of communities* (pp. 296–304). Princeton University Press. https://doi.org/10.1515/9781400833023.296

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, *9*(2), 378. https://doi.org/10.32614/RJ-2017-066

Cabaço, S., Apostolaki, E. T., García-Marín, P., Gruber, R., Hernández, I., Martínez-Crego, B., Mascaró, O., Pérez, M., Prathep, A., Robinson, C., Romero, J., Schmidt, A. L., Short, F. T., van Tussenbroek, B. I., & Santos, R. (2013). Effects of nutrient enrichment on seagrass population dynamics: Evidence and synthesis from the biomass-density relationships. *Journal of Ecology*, *101*(6), 1552–1562.

Cardoso, P. G., Pardal, M. A., Lillebø, A. I., Ferreira, S. M., Raffaelli, D., & Marques, J. C. (2004). Dynamic changes in seagrass assemblages under eutrophication and implications for recovery. *Journal of Experimental Marine Biology and Ecology*, *302*(2), 233–248. https://doi.org/10.1016/j.jembe.2003.10.014

Chalifour, L., Scott, D. C., MacDuffee, M., Iacarella, J. C., Martin, T. G., & Baum, J. K. (2019). Habitat use by juvenile salmon, other migratory fish, and resident fish species underscores the importance of estuarine habitat mosaics. *Marine Ecology Progress Series*, *625*, 145–162. https://doi.org/10.3354/meps13064

Connell, J. H. (1961). The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology*, *42*(4), 710–723. https://doi.org/10.2307/1933500

Cromsigt, J. P. G. M., & Olff, H. (2008). Dynamics of grazing lawn formation: An experimental test of the role of scale-dependent processes. *Oikos*, *117*(10), 1444–1452. https://doi.org/10.1111/j.0030-1299.2008.16651.x

Cronin, J. T. (2009). Habitat edges, within-patch dispersion of hosts, and parasitoid oviposition behavior. *Ecology*, *90*(1), 196–207. https://doi.org/10.1890/08-0208.1

Cross, R. E., & Curran, M. C. (2004). Recovery of meiofauna in intertidal feeding pits created by rays. *Southeastern Naturalist*, *3*(2), 219–230. https://doi.org/10.1656/1528-7092(2004)003[0219:ROMIIF]2.0.CO;2

Damgaard, C. F., & Irvine, K. M. (2019). Using the beta distribution to analyse plant cover data. *Journal of Ecology*, *107*(6), 2747–2759. https://doi.org/10.1111/1365-2745.13200

Davis, T. R., Harasti, D., Smith, S. D. A., & Kelaher, B. P. (2016). Using modelling to predict impacts of sea level rise and increased turbidity on seagrass distributions in estuarine embayments. *Estuarine, Coastal and Shelf Science*, *181*, 294–301. https://doi.org/10.1016/j.ecss.2016.09.005

De'ath, G., & Fabricius, K. E. (2000). Classification and regression trees: A powerful yet simple technique for ecological data analysis. *Ecology*,

13652656, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.70218 by Duke University Libraries, Wiley Online Library on [10/02/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

81(11), 3178–3192. https://doi.org/10.1890/0012-9658(2000)081[3178:CARTAP]2.0.CO;2

Duarte, C. M., & Chiscano, C. L. (1999). Seagrass biomass and production: A reassessment. *Aquatic Botany*, *65*(1–4), 159–174. https://doi.org/10.1016/S0304-3770(99)00038-8

Dunic, J. C., Brown, C. J., Connolly, R. M., Turschwell, M. P., & Côté, I. M. (2021). Long-term declines and recovery of meadow area across the world's seagrass bioregions. *Global Change Biology*, *27*(17), 4096–4109. https://doi.org/10.1111/gcb.15684

Ewers, R. M., & Didham, R. K. (2006). Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews*, *81*(1), 117–142. https://doi.org/10.1017/S1464793105006949

Gerwing, T. G., Drolet, D., Hamilton, D. J., & Barbeau, M. A. (2016). Relative importance of biotic and abiotic forces on the composition and dynamics of a soft-sediment intertidal community. *PLoS One*, *11*(1), e0147098. https://doi.org/10.1371/journal.pone.0147098

Gladstone-Gallagher, R. V., Hughes, R. W., Douglas, E. J., & Pilditch, C. A. (2018). Biomass-dependent seagrass resilience to sediment eutrophication. *Journal of Experimental Marine Biology and Ecology*, *501*, 54–64. https://doi.org/10.1016/j.jembe.2018.01.002

Hastings, Z., Ticktin, T., Botelho, M., Reppun, N., Kukea-Shultz, K., Wong, M., Melone, A., & Bremer, L. (2020). Integrating co-production and functional trait approaches for inclusive and scalable restoration solutions. *Conservation Science and Practice*, *2*(9), e250. https://doi.org/10.1111/csp2.250

He, Q., Altieri, A. H., & Cui, B. (2015). Herbivory drives zonation of stress-tolerant marsh plants. *Ecology*, *96*(5), 1318–1328. https://doi.org/10.1890/14-0937.1

Hemminga, M., Harrison, P. G., & van Lent, F. (1991). The balance of nutrient losses and gains in seagrass Meadows. *Marine Ecology Progress Series*, *71*, 81–96.

Hensel, M. J. S., Silliman, B. R., van de Koppel, J., Hensel, E., Sharp, S. J., Crotty, S. M., & Byrnes, J. E. K. (2021). A large invasive consumer reduces coastal ecosystem resilience by disabling positive species interactions. Nature. *Communications*, *12*(1), 6290. https://doi.org/10.1038/s41467-021-26504-4

Holzer, K. K., & McGlathery, K. J. (2016). Cultivation grazing response in seagrass may depend on phosphorus availability. *Marine Biology*, *163*(4), 88. https://doi.org/10.1007/s00227-016-2855-5

Howard, J. D., Mayou, T. V., & Heard, R. W. (1977). Biogenic sedimentary structures formed by rays. *Journal of Sedimentary Research*, *47*(1), 339–346. https://doi.org/10.1306/212F7167-2B24-11D7-8648000102C1865D

Hughes, B. B., Beheshti, K. M., Tinker, M. T., Angelini, C., Endris, C., Murai, L., Anderson, S. C., Espinosa, S., Staedler, M., Tomoleoni, J. A., Sanchez, M., & Silliman, B. R. (2024). Top-predator recovery abates geomorphic decline of a coastal ecosystem. *Nature*, *626*(7997), 111–118. https://doi.org/10.1038/s41586-023-06959-9

Hughes, R. G., & Paramor, O. A. L. (2004). On the loss of saltmarshes in south-east England and methods for their restoration. *Journal of Applied Ecology*, *41*(3), 440–448. https://doi.org/10.1111/j.0021-8901.2004.00915.x

Kassambara, A., Kosinski, M., Biecek, P., & Fabian, S. (2021). *survminer: Drawing survival curves using 'ggplot2'* (version 0.4.9) [computer software]. https://cran.r-project.org/web/packages/survminer/index.html

Koch, E. W. (2001). Beyond light: Physical, geological, and geochemical parameters as possible submersed aquatic vegetation habitat requirements. *Estuaries*, *24*(1), 1–17. https://doi.org/10.2307/1352808

Kollars, N. M., Henry, A. K., Whalen, M. A., Boyer, K. E., Cusson, M., Eklöf, J. S., Hereu, C. M., Jorgensen, P., Kiriakopolos, S. L., Reynolds, P. L., Tomas, F., Turner, M. S., & Ruesink, J. L. (2017). Meta-analysis of reciprocal linkages between temperate seagrasses and waterfowl with implications for conservation. *Frontiers in Plant Science*, *8*, 2119. https://doi.org/10.3389/fpls.2017.02119

Kowalski, J. L., DeYoe, H. R., Allison, T. C., & Kaldy, J. E. (2001). Productivity estimation in *Halodule wrightii* Aschers: Comparison of leaf-clipping and leaf-marking techniques and the importance of clip height. *Marine Ecology Progress Series*, *220*, 131–136. https://doi.org/10.3354/meps220131

Landes, J., Engelhardt, S. C., & Pelletier, F. (2020). An introduction to event history analyses for ecologists. *Ecosphere*, *11*(10), e03238. https://doi.org/10.1002/ecs2.3238

Last, P. R. (Ed.). (2016). *Rays of the world*. Comstock Publishing Associates, a division of Cornell University Press; CSIRO Publishing.

Lenoir, J., Bertrand, R., Comte, L., Bourgeaud, L., Hattab, T., Murienne, J., & Grenouillet, G. (2020). Species better track climate warming in the oceans than on land. *Nature Ecology & Evolution*, *4*(8), 1044–1059. https://doi.org/10.1038/s41559-020-1198-2

Levene, H. (1960). Robust tests for equality of variances. In I. Olkin (Ed.), *Contributions to probability and statistics* (pp. 278–292). Stanford University Press.

Liu, J.-J., Xu, Y., Shan, Y.-X., Burgess, K. S., & Ge, X.-J. (2021). Biotic and abiotic factors determine species diversity–productivity relationships in mountain meadows. *Journal of Plant Ecology*, *14*(6), 1175–1188. https://doi.org/10.1093/jpe/rtab064

Louthan, A. M., Doak, D. F., & Angert, A. L. (2015). Where and when do species interactions set range limits? *Trends in Ecology & Evolution*, *30*(12), 780–792. https://doi.org/10.1016/j.tree.2015.09.011

Menge, B. A., Daley, B. A., Lubchenco, J., Sanford, E., Dahlhoff, E., Halpin, P. M., Hudson, G., & Burnaford, J. L. (1999). Top-down and bottom-up regulation of New Zealand rocky intertidal communities. *Ecological Monographs*, *69*(3), 297–330. https://doi.org/10.1890/0012-9615(1999)069[0297:TDABUR]2.0.CO;2

Momberg, M., Hedding, D. W., Luoto, M., & Le Roux, P. C. (2021). Exposing wind stress as a driver of fine-scale variation in plant communities. *Journal of Ecology*, *109*(5), 2121–2136. https://doi.org/10.1111/1365-2745.13625

Morton, J. P., Hensel, M. J. S., DeLaMater, D. S., Angelini, C., Atkins, R. L., Prince, K. D., Williams, S. L., Boyd, A. D., Parsons, J., Resetarits, E. J., Smith, C. S., Valdez, S., Monnet, E., Farhan, R., Mobilian, C., Renzi, J., Smith, D., Craft, C., Byers, J. E., … Silliman, B. R. (2024). Mesopredator release moderates trophic control of plant biomass in a Georgia salt marsh. *Ecology*, *105*(12), e4452. https://doi.org/10.1002/ecy.4452

Mukomberanwa, N. T., Taru, P., Utete, B., & Ngorima, P. (2024). Modelled vegetation structure and abundance confirms African Savannah elephant-induced damage across space in a dry protected area with diverse vegetation. *African Journal of Ecology*, *62*(3), e13322. https://doi.org/10.1111/aje.13322

Nauta, J., Leurs, G., Nieuwenhuis, B. O., Mathijssen, D. R. A. H., Olff, H., Bouma, T. J., van der Wal, D., Hijner, N., Regalla, A., Pontes, S. L., & Govers, L. L. (2024). Bioturbation by benthic stingrays alters the biogeomorphology of tidal flats. *Ecosystems*, *27*(4), 493–507. https://doi.org/10.1007/s10021-024-00901-4

Nordlund, L. M., Koch, E. W., Barbier, E. B., & Creed, J. C. (2016). Seagrass ecosystem services and their variability across genera and geographical regions. *PLoS One*, *11*(10), e0163091. https://doi.org/10.1371/journal.pone.0163091

North Carolina Department of Environmental Quality (NCDEQ). (2021). *Coastal habitat protection plan 2021 amendment*. https://www.deq.nc.gov/marine-fisheries/coastal-habitat-protection-plan/north-carolina-coastal-habitat-protection-plan-2021-amendment/open

Orth, R. J., Carruthers, T. J. B., Dennison, W. C., Duarte, C. M., Fourqurean, J. W., Heck, K. L., Hughes, A. R., Kendrick, G. A., Kenworthy, W. J., Olyarnik, S., Short, F. T., Waycott, M., & Williams, S. L. (2006). A global crisis for seagrass ecosystems. *BioScience*, *56*(12), 987–996. https://doi.org/10.1641/0006-3568(2006)56[987:AGCFSE]2.0.CO;2

13652656, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.70218 by Duke University Libraries, Wiley Online Library on [10/02/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

O'Shea, O. R., Meadows, M. H., Wrigglesworth, E. E., Newton, J., & Hawkes, L. A. (2020). Novel insights into the diet of southern stingrays and Caribbean whiptail rays. *Marine Ecology Progress Series*, *655*, 157–170. https://doi.org/10.3354/meps13529

Paerl, H. W., Crosswell, J. R., Van Dam, B., Hall, N. S., Rossignol, K. L., Osburn, C. L., Hounshell, A. G., Sloup, R. S., & Harding, L. W. (2018). Two decades of tropical cyclone impacts on North Carolina's estuarine carbon, nutrient and phytoplankton dynamics: Implications for biogeochemical cycling and water quality in a stormier world. *Biogeochemistry*, *141*(3), 307–332. https://doi.org/10.1007/s10533-018-0438-x

Park, S. R., Moon, K., Kim, S. H., & Lee, K.-S. (2021). Growth and photoacclimation strategies of three zostera species along a vertical gradient: Implications for seagrass zonation patterns. *Frontiers in Marine Science*, *8*, 594779. https://doi.org/10.3389/fmars.2021.594779

Pennings, S. C., & Callaway, R. M. (1992). Salt marsh plant zonation: The relative importance of competition and physical factors. *Ecology*, *73*(2), 681–690. https://doi.org/10.2307/1940774

Power, M. E. (1992). Top-down and bottom-up forces in food webs: Do plants have primacy. *Ecology*, *73*(3), 733–746. https://doi.org/10.2307/1940153

R Core Team. (2022). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Schwartz, F., & Dahlberg, M. (1978). Biology and ecology of the Atlantic stingray, *Dasyatis sabina* (Pisces: Dasyatidae) in North Carolina and Georgia. *Gulf of Mexico Science*, *2*(1), 1–23. https://doi.org/10.18785/negs.0201.01

Shafer, D. J., Sherman, T. D., & Wyllie-Echeverria, S. (2007). Do desiccation tolerances control the vertical distribution of intertidal seagrasses? *Aquatic Botany*, *87*(2), 161–166. https://doi.org/10.1016/j.aquabot.2007.04.003

Shepard, I. D., Wissinger, S. A., & Greig, H. S. (2021). Elevation alters outcome of competition between resident and range-shifting species. *Global Change Biology*, *27*(2), 270–281. https://doi.org/10.1111/gcb.15401

Short, F., Carruthers, T., Dennison, W., & Waycott, M. (2007). Global seagrass distribution and diversity: A bioregional model. *Journal of Experimental Marine Biology and Ecology*, *350*(1–2), 3–20. https://doi.org/10.1016/j.jembe.2007.06.012

Sievers, M., Brown, C. J., Buelow, C. A., Hale, R., Ostrowski, A., Saunders, M. I., Silliman, B. R., Swearer, S. E., Turschwell, M. P., Valdez, S. R., & Connolly, R. M. (2022). Greater consideration of animals will enhance coastal restoration outcomes. *BioScience*, *72*, 1088–1098. https://doi.org/10.1093/biosci/biac088

Silinski, A., Schoutens, K., Puijalon, S., Schoelynck, J., Luyckx, D., Troch, P., Meire, P., & Temmerman, S. (2018). Coping with waves: Plasticity in tidal marsh plants as self-adapting coastal ecosystem engineers. *Limnology and Oceanography*, *63*(2), 799–815. https://doi.org/10.1002/lno.10671

Snelson, F. F., Williams-Hooper, S. E., & Schmid, T. H. (1988). Reproduction and ecology of the Atlantic stingray, *Dasyatis sabina*, in Florida coastal lagoons. *Copeia*, *1988*(3), 729–739. https://doi.org/10.2307/1445395

Soria, S. A., Gutiérrez, J. L., Gonzalez, J. A., Callá, S. L., & Palomo, M. G. (2022). Habitat properties and invertebrate composition in mussel-dominated rocky shores: A test of edge effects. *Estuarine, Coastal and Shelf Science*, *277*, 108035. https://doi.org/10.1016/j.ecss.2022.108035

Szura, K., McKinney, R., Wigand, C., Oczkowski, A., Hanson, A., Gurak, J., & Gárate, M. (2017). Burrowing and foraging activity of marsh crabs under different inundation regimes. *Journal of Experimental Marine Biology and Ecology*, *486*, 282–289. https://doi.org/10.1016/j.jembe.2016.10.029

Takeuchi, S., & Tamaki, A. (2014). Assessment of benthic disturbance associated with stingray foraging for ghost shrimp by aerial survey over an intertidal sandflat. *Continental Shelf Research*, *84*, 139–157. https://doi.org/10.1016/j.csr.2014.05.007

Tanaka, Y., & Nakaoka, M. (2004). Emergence stress and morphological constraints affect the species distribution and growth of subtropical intertidal seagrasses. *Marine Ecology Progress Series*, *284*, 117–131. https://doi.org/10.3354/meps284117

Therneau, T., Atkinson, B., & Ripley, B. (2023). *rpart: Recursive partitioning and regression trees* (version 4.1.23) [computer software]. https://cran.r-project.org/web/packages/rpart/index.html

Therneau, T. M., & Grambsch, P. M. (2000). *Modeling survival data: Extending the cox model*. Springer.

Therneau, T. M., Lumley, T., Elizabeth, A., & Cynthia, C. (2023). *Survival: Survival analysis* (version 3.5-7) [computer software]. https://cran.r-project.org/web/packages/survival/index.html

Townsend, E. C., & Fonseca, M. S. (1998). Bioturbation as a potential mechanism influencing spatial heterogeneity of North Carolina seagrass beds. *Marine Ecology Progress Series*, *169*, 123–132. https://doi.org/10.3354/meps169123

Turschwell, M. P., Connolly, R. M., Dunic, J. C., Sievers, M., Buelow, C. A., Pearson, R. M., Tulloch, V. J. D., Côté, I. M., Unsworth, R. K. F., Collier, C. J., & Brown, C. J. (2021). Anthropogenic pressures and life history predict trajectories of seagrass meadow extent at a global scale. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(45), e2110802118. https://doi.org/10.1073/pnas.2110802118

Uhrin, A. V., & Turner, M. G. (2018). Physical drivers of seagrass spatial configuration: The role of thresholds. *Landscape Ecology*, *33*(12), 2253–2272. https://doi.org/10.1007/s10980-018-0739-4

Unsworth, R. K. F., Nordlund, L. M., & Cullen-Unsworth, L. C. (2019). Seagrass meadows support global fisheries production. *Conservation Letters*, *12*(1), e12566. https://doi.org/10.1111/conl.12566

Valdez, S. (2025). Data/code from: Mobile consumers influence the shoreward edge of intertidal seagrass ecosystems [Data set]. *Zenodo*. https://doi.org/10.5281/zenodo.17584820

Valdez, S. R., Zhang, Y. S., van der Heide, T., Vanderklift, M. A., Tarquinio, F., Orth, R. J., & Silliman, B. R. (2020). Positive ecological interactions and the success of seagrass restoration. *Frontiers in Marine Science*, *7*, 91. https://doi.org/10.3389/fmars.2020.00091

Virnstein, R. W. (1982). Leaf growth rate of the seagrass *Halodule wrightii* photographically measured in situ. *Aquatic Botany*, *12*, 209–218. https://doi.org/10.1016/0304-3770(82)90017-1

Wang, X., Bai, J., Yan, J., Cui, B., & Shao, D. (2022). How turbidity mediates the combined effects of nutrient enrichment and herbivory on seagrass ecosystems. *Frontiers in Marine Science*, *9*(February), 787041. https://doi.org/10.3389/fmars.2022.787041

Weathers, K. C., Cadenasso, M. L., & Pickett, S. T. A. (2001). Forest edges as nutrient and pollutant concentrators: Potential synergisms between fragmentation, Forest canopies, and the atmosphere. *Conservation Biology*, *15*(6), 1506–1514. https://doi.org/10.1046/j.1523-1739.2001.01090.x

Wheeler, M., Jarvis, J., & Freshwater, W. D. (2024). Seagrass and epiphyte seasonality in a biogeographic transition zone [preprint]. In Review. https://doi.org/10.21203/rs.3.rs-3864692/v1

Willmer, J. N. G., Püttker, T., & Prevedello, J. A. (2022). Global impacts of edge effects on species richness. *Biological Conservation*, *272*, 109654. https://doi.org/10.1016/j.biocon.2022.109654

Wimp, G. M., Ries, L., Lewis, D., & Murphy, S. M. (2019). Habitat edge responses of generalist predators are predicted by prey and structural resources. *Ecology*, *100*(6), e02662. https://doi.org/10.1002/ecy.2662

Xu, C., Silliman, B. R., Chen, J., Li, X., Thomsen, M. S., Zhang, Q., Lee, J., Lefcheck, J. S., Daleo, P., Hughes, B. B., Jones, H. P., Wang, R., Wang, S., Smith, C. S., Xi, X., Altieri, A. H., van de Koppel, J., Palmer, T. M., Liu, L., … He, Q. (2023). Herbivory limits success of vegetation restoration globally. *Science*, *382*(6670), 589–594. https://doi.org/10.1126/science.add2814

13652656, 0, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.70218 by Duke University Libraries, Wiley Online Library on [10/02/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Yang, J., Blondeel, H., Meeussen, C., Govaert, S., Vangansbeke, P., Boeckx, P., Lenoir, J., Orczewska, A., Ponette, Q., Hedwall, P.-O., Iacopetti, G., Brunet, J., De Frenne, P., & Verheyen, K. (2022). Forest density and edge effects on soil microbial communities in deciduous forests across Europe. *Applied Soil Ecology*, *179*, 104586. https://doi.org/10.1016/j.apsoil.2022.104586

Yarnall, A. H., Byers, J. E., Yeager, L. A., & Fodrie, F. J. (2022). Comparing edge and fragmentation effects within seagrass communities: A meta-analysis. *Ecology*, *103*(3), e3603. https://doi.org/10.1002/ecy.3603

Zhang, Y. S., Gittman, R. K., Donaher, S. E., Trackenberg, S. N., van der Heide, T., & Silliman, B. R. (2021). Inclusion of intra- and interspecific facilitation expands the theoretical framework for seagrass restoration. *Frontiers in Marine Science*, *8*, 296. https://doi.org/10.3389/fmars.2021.645673

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: Graph of relative elevation of seagrass transplants with error bars representing standard error (cm).

Figure S2: Proportion of seagrass cover over time from observed data and GLMM model predictions.

Figure S3: Graphs from survey counts of (A) the number of pits/ m^2 in different habitat types in July 2021 where points over the boxes represent the pit count per transect ($n = 7$) and (B) prey abundance in different habitat types per 12,000 cm^3 core ($n = 3$).

Figure S4: Graphs demonstrating similar conditions across treatments in the factorial caging experiment. (A) Initial percent seagrass cover per treatment and (B) Relative elevation (cm). Error bars represent standard error.

Figure S5: Water flow movement (cm/s) of fishing float among 50 cm × 50 cm plots with varying post numbers.

Figure S6: Seagrass edge movement with and without caging in 2023. Error bars represent standard error.

Table S1: (A) Mean relative elevation for seagrass transplantation experiments. (B) Tukey post hoc test for pairwise differences between mean relative elevation.

Table S2: ANOVA results for initial seagrass cover, relative plot elevation, total sediment N and sediment bulk density.

Table S3: Statistical results for water flow (ANOVA) and seagrass edge movement with and without caging (*t*-test).

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