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ARTICLE

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Mesopredator release moderates trophic control of plant biomass in a Georgia salt marsh

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Abstract

Predators regulate communities through top-down control in many ecosystems. Because most studies of top-down control last less than a year and focus on only a subset of the community, they may miss predator effects that manifest at longer timescales or across whole food webs. In southeastern US salt marshes, short-term and small-scale experiments indicate that nektonic predators (e.g., blue crab, fish, terrapins) facilitate the foundational grass, *Spartina alterniflora*, by consuming herbivorous snails and crabs. To test both how nekton affect marsh processes when the entire animal community is present, and how prior results scale over time, we conducted a 3-year nekton exclusion experiment in a Georgia salt marsh using replicated 19.6 m^2 plots. Our nekton exclusions increased densities of plant-grazing snails and juvenile deposit-feeding fiddler crab and, in Year 2, reduced predation on tethered juvenile snails, indicating that nektonic predators control these key macroinvertebrates. However, in Year 3, densities of mesopredatory benthic mud crabs increased threefold in nekton exclusions, erasing the tethered snails' predation refuge. Nekton exclusion had no effect on *Spartina* biomass, likely because the observed mesopredator release suppressed grazing snail densities and elevated densities of fiddler crabs, whose burrowing alleviates soil stresses. Structural equation modeling supported the hypotheses that nektonic predators and mesopredators control invertebrate communities, with nektonic predators having stronger total effects on *Spartina* than mud crabs by controlling densities of species that both suppress (grazers) and facilitate (fiddler crabs) plant growth. These findings highlight that salt marshes can be resilient to multiyear reductions in nektonic predators if mesopredators are present and that multiple pathways of trophic control manifest in different ways over time to

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mediate community dynamics. These results highlight that larger scale and longer-term experiments can illuminate community dynamics not previously understood, even in well-studied ecosystems such as salt marshes.

KEYWORDS
ecosystem resilience, facilitation, food web, mesopredator release, predation, salt marsh, top-down control

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INTRODUCTION

Predators often play a key role in structuring communities, regulating the behavior and abundance of herbivores that in turn affect plants and microbes (Atwood et al., 2015; Beschta & Ripple, 2012). Such trophic cascades can control the primary productivity of entire ecosystems (Carpenter et al., 1985; Estes & Palmisano, 1974; Hughes et al., 2024; Rosenblatt et al., 2013), as well demonstrated by the collapse of Alaskan kelp forests after sea otter overharvest and cascading increases in herbivorous urchin density (Estes & Duggins, 1995). However, the removal of top predators does not necessarily result in the collapse of primary producers. In some cases when top predators are removed, mesopredator densities increase and can partially or completely replace top-down pressure on herbivores (Prugh et al., 2009), thereby maintaining the structure of primary producers. For example, the extirpation of wolves from the American West in the early 20th century resulted in increased populations of mesopredator coyotes (Miller et al., 2012), and experimental dingo removal in Australia increased densities of mesopredatory red foxes (Castle et al., 2021). Additionally, variation in predator abundance may alter the densities or activities of ecosystem engineers, such as beavers, that alter the abiotic environment in ways that can be more favorable for some community members than others (e.g., Gable et al., 2020). Thus, for studies of predator effects to be most informative, they should consider the responses of entire communities, including changes in mesopredators, herbivores, and ecosystem engineers.

Holistically evaluating predator effects on ecological communities often requires that field experiments be performed at larger-than-typical spatiotemporal scales (Shea et al., 2000). Species that are patchily distributed may be ecologically important, but not included in small-scale experiments. Similarly, the effects of predators on species composition, demography, and ecosystem function may be missed in short-term experiments (Chase, 1996; Schmitz et al., 2000). Thus, larger scale and longer term experiments are more informative, but they remain rare because they are more difficult to conduct and more costly to maintain and monitor over time.

Salt marshes on the Atlantic coast of the United States are one of the most productive ecosystems in the world (Mitsch & Gosselink, 2020) and are subject to strong bottom-up and top-down controls. Variation in abiotic stress influences the productivity of *Spartina alterniflora* (also named as *Sporobolus alterniflorus*, hereafter *Spartina*; Bortolus et al., 2019) along both elevational and estuarine salinity gradients (Odum, 1988; Valiela & Teal, 1979). At the same time, herbivorous periwinkle snails (*Littoraria irrorata*) and purple marsh crabs (*Sesarma reticulatum*) can suppress *Spartina* biomass when their own predators—swimming crabs, fish, and terrapins that enter the marsh on high tides—are uncommon or rare (Altieri et al., 2012; Peterson et al., 2014; Silliman et al., 2004; Silliman & Bertness, 2002). Prior predator exclusion experiments have demonstrated indirect predator control of *Spartina* productivity in Atlantic coast salt marshes (Altieri et al., 2012; Griffin et al., 2011; Silliman & Bertness, 2002). Because these studies employed relatively small 0.5–2 m^2 exclusions and were typically short in duration (<1 year), they could not evaluate longer term dynamics of indirect, cascading predator effects nor could they describe how the range of top-down control varies across a functionally diverse salt marsh invertebrate prey community. In healthy *Spartina* marshes, this invertebrate prey community includes mesopredators (e.g., mud crabs *Eurytium limosum* and *Panopeus herbstii*) that prey on grazing snails and purple marsh crabs as well as abundant ecosystem engineers that facilitate *Spartina* productivity, like filter-feeding ribbed mussels (*Geukensia demissa*) and bioturbating, deposit-feeding fiddler crabs (*Leptuca* and *Minuca* spp.) (Bertness, 1984; Derksen-Hooijberg et al., 2018; Gittman & Keller, 2013; Silliman et al., 2004). To detect the range of direct and indirect predator effects on salt marsh invertebrate community structure and function, longer term and larger scale experiments that evaluate the response of the entire community to predator exclusion will achieve a more robust understanding of the role that predators play in salt marsh systems.

To quantify multiyear nektonic predator control of the mesopredators, detritivores, herbivores, deposit-feeders, and filter feeders that make up a salt marsh invertebrate community, we performed a 3-year, larger scale nektonic predator exclusion experiment in Georgia and monitored changes to *Spartina* and seven resident invertebrate species. These included both juveniles and adults of two abundant species commonly included in past experiments, *L. irrorata*, and the fiddler crab *Minuca pugnax*, as well as more patchily distributed species typically omitted in past work, the herbivorous purple marsh crab *Se. reticulatum*, the mesopredatory mud crabs *E. limosum* and *P. herbstii*, the filter-feeding ribbed mussel *G. demissa*, and the barnacle *Chthamalus fragilis*. Hereafter, all species will be referred to by their common names and the two mud crabs, which are both benthic burrowing crabs that prey on each other, as well as consume all other benthic invertebrates in the community, will be collectively called mud crabs. To gain further insight into the role predation might play in driving changes to marsh community structure and ecosystem functioning (e.g., by mesopredators that were not excluded by our treatments), we also quantified predation on tethered snails, fiddler crabs, and mud crabs and measured soil microbial decomposition rate within the plots.

Based on the results of previous experiments in southern Atlantic salt marshes, we tested two competing hypotheses about how predatory nekton might affect the marsh community. First, we hypothesized that the exclusion of predatory nekton would lead to a strong trophic cascade in which herbivorous snail and purple marsh crab densities would increase and plant biomass would decrease (Silliman & Bertness, 2002). Second, we alternatively hypothesized that this trophic cascade would be moderated, either by increases in mud crab mesopredators (Griffin et al., 2011; Griffin & Silliman, 2011; Silliman et al., 2004) or by increases in ribbed mussels and fiddler crabs that both benefit plants by enhancing nutrient availability and ameliorating soil nutrient, sulfide, and low oxygen stress (Angelini et al., 2015; Derksen-Hooijberg et al., 2019; Gittman & Keller, 2013).

METHODS

Experimental setup

We established the experiment within a salt marsh adjacent to Dean Creek, a tidal creek within the Georgia Coastal Ecosystems—Long-Term Ecological Research (GCE-LTER) domain on Sapelo Island, Georgia, USA (31.387792° N, −81.280049° S). Vegetation at this site is dominated by *Sp. alterniflora* (Bortolus et al., 2019), and the marsh platform is inundated twice daily by tides. High tides deliver a similar density and identity of nektonic predators across the whole site at each inundation, and we did not expect any differences in invertebrate recruitment across the relatively small stretch of creek. The experiment started in summer 2016 (Year 0) with premanipulation observations taken immediately prior to installing treatments and ended after 3 years in fall 2019.

To determine the long-term effects of nektonic predators on marsh structure and function, we established 24 circular plots (diameter = 5 m; area 19.63 m^2) along Dean Creek in July 2016 (Appendix S1: Figure S1). We established plots 15–30 m from the creek bank and 2 m apart along a 0.6-km stretch of the creek. We assigned plots to caged nekton exclusions, uncaged control treatments, and a cage control treatment ($n = 8$ each). The nekton exclusion treatment was built with 1.22-m-tall plastic 2.54-cm vexar mesh, which was tall enough so that the highest spring tides did not flood the top of the cage, with mesh affixed to eight polyvinyl chloride (PVC) posts around the plot perimeter. This mesh size excludes the assemblage of larger bodied nektonic predators present in this system but allows for a free exchange of tidal water and access by small fish like mummichogs (*Fundulus* sp). We buried the vexar mesh 10 cm deep into the marsh sediment to impede crab burrowing and movement. To reduce the shading of vegetation within plot interiors and allow access by birds and terrestrial mammals, we left the tops of exclusion plots open. The control treatment was constructed with eight posts equally spaced around plot perimeters with no mesh attached, allowing access by all predators. To test for experimental artifacts due to shading or added physical structure, we constructed a cage control treatment identical to the exclusion cage but with the outer mesh removed from every other interval between posts such that there were four 2-m gaps that allowed mobile predators to access plot interiors. Within the interior of each plot, 0.5 m from the perimeter, we established four 0.5-m^2 subplots: two devoted to annual invertebrate and biomass sampling and two devoted to destructive sampling or other response variables.

Effects of nekton predator exclusion on benthic invertebrate density over time

Immediately prior to the application of experimental treatments in 2016, and annually thereafter in July or August, we measured the densities of marsh invertebrates in two of the 0.5-m^2 subplots in each plot. We counted all adult snails visible on vegetation or on the marsh substrate. Juvenile snails (<6 mm shell length), found in the microhabitats of furled, senescent, or dead leaves and within leaf sheaths (Angelini et al., 2015; Zengel et al., 2016), were counted within a 15-cm^2 quadrat placed at the center of each subplot. Following the methods of Silliman et al. (2004) and Angelini et al. (2015), we identified and counted the burrows of fiddler crabs, mud crabs (both species pooled, Appendix S1), and purple marsh crabs, using burrow counts as proxies for crab abundance (Macia et al., 2001; Martínez-Soto & Johnson, 2020). We counted all barnacles adhering to the four PVC posts at the corners of each subplot. We separately enumerated both juvenile and adult snails and fiddler crabs because there are important functional disparities between life stages of these organisms (Angelini et al., 2015). For instance, juvenile snails do not actively graze on live *Spartina* like adults (Atkins et al., 2015; Silliman & Newell, 2003; Silliman & Zieman, 2001). Likewise, juvenile fiddler crabs excavate considerably smaller burrows relative to adults, potentially limiting their ability to alleviate redox stress; however, they strongly influence decomposition rate through bioturbation and the promotion of microbial activity (Angelini et al., 2015; Bertness, 1984). We also anticipated that there might be differential predation on different life stages of these two organisms, potentially yielding different effects on *Spartina*.

We used our initial data collection in 2016 as a baseline for each plot and calculated the change from initial conditions for each response variable for each year (e.g., mud crab burrow density change in 2017 = Mud crab burrow density Year$_1$ − Mud crab burrow density Year$_0$).

Effects of nekton predator exclusion on Spartina biomass over time

Concurrent with invertebrate monitoring, we measured vegetation characteristics and snail grazing intensity within the same two subplots. We counted all *Spartina* stems and measured the heights of 10 haphazardly selected stems, converting data to aboveground biomass using an allometric equation (Appendix S1). As with invertebrate response variables, we calculated the change from initial biomass conditions per plot for every year (e.g., Biomass change in 2017 = Biomass Year$_1$ − Biomass Year$_0$).

Quantifying variation in snail and fiddler crab predation pressure

To evaluate predation pressure in each treatment, we conducted tethering trials with adult and juvenile snails and fiddler crabs. In July 2018 and 2019, 10 adult snails (12–14 mm shell height) and 10 juvenile snails (shell height <12 mm) were each glued with cyanoacrylate adhesive to a 30-cm-long monofilament line tied to a PVC stake, which was then inserted into the marsh sediment. This technique allowed snails to freely forage and migrate up and down cordgrass stems (Silliman & Bertness, 2002). For this and subsequent tethering assays, we enumerated remaining organisms each day at low tide until we observed mortalities in plots ≥80% (1 week in this case).

In July 2019, we tethered eight adult (carapace width >1 cm) and eight juvenile (carapace width <0.5 cm) fiddler crabs using similar techniques. Although tethers limited crab horizontal movement, crabs were observed freely burrowing and foraging. We counted the remaining live crabs after 3 days. In response to our observation of increasing densities of mud crabs within exclusion cages in 2019, we tethered adult mud crabs (carapace width >2.5 cm) using similar methods in July 2020 when the plots were still intact but after the formal experiment concluded, to test whether these mesopredators experienced less predation pressure in exclusion cages.

Effects of nekton predator exclusion on snail grazing over time

In order to determine the magnitude of damage to *Spartina* induced by grazing snails, we measured the total length of snail grazing scars on five haphazardly selected plants per subplot at the same time we took vegetation metrics (Silliman & Newell, 2003).

Effects of nekton predator exclusion on tea bag decomposition rates

To explore whether nekton removal affected decomposition—a process that can affect nutrient availability and thus *Spartina* growth and has been formally shown to be affected by burrowing crabs (Hensel & Silliman, 2013), we deployed tea bags via the Tea Bag Index method (Keuskamp et al., 2013) in exclusion and control plots in 2019. This technique utilizes green and rooibos (red) tea as standardized test kits to observe decomposition rates of plant litter and has been used to compare decomposition in freshwater and estuarine wetlands (MacDonald et al., 2018). Because of miniscule variation in initial mass and a consistent homogeneity in composition and particle size within teas, the Tea Bag Index method helps identify differences among treatments in experimental settings rather than absolute, in situ, rates of natural litter.

In April 2019, we buried 15 mesh bags (mesh size of 0.25 mm), within each plot 10 cm below the soil surface. Each bag contained one preweighed green and one preweighed rooibos teabag. We collected five bags per date from each plot for analysis after 82, 114, and 148 days to evaluate changes in decomposition over time ($n = 5$ per plot per timepoint). Collected teabags were dried at 70°C for 48 h before each was cut open, and the remaining contents removed and weighed to the nearest 0.001 g. We measured mass loss from each time point (% dry mass remaining) and calculated decomposition rates as the % loss and grams lost per month for each plot. By running a linear regression with the natural log of % dry mass remaining across all time points and extracting the absolute value of the regression line slope, we also calculated the decay constant k (per day) for each plot. We found no treatment differences in the decomposition rate of rooibos tea (Appendix S1: Figure S1); however, fast-decomposing green tea is more relevant to our study as it more closely mimics marsh grass than the slow-rotting woody material in rooibos tea.

Describing nektonic and terrestrial predator communities

Due to dense vegetation, turbid water and the high mobility of nekton in the study system, we were unable to directly observe nekton use of the experimental plots. We therefore characterized nektonic predators present within the inundated edge of the marsh at Dean Creek using a 30.5 m trammel net as a means to assess the nekton community. The net was deployed parallel to the marsh edge during an outgoing tide with a 10-min soak time. All fish, including elasmobranchs, and other swimming predators like blue crabs, were identified to species, counted, and released. We sampled nekton F22 times between July 2016 and July 2017. To gain insight into the diets of some of these species, we synthesized data from gut content analyses performed by the Georgia Department of Natural Resources (DNR) (Appendix S1).

To determine whether terrestrial predators such as birds and raccoons were visiting the plots, we deployed 12 infrared, motion-activated wildlife cameras (Bushnell Trophy Cam) at the experimental site on June 7, 2019. Camera SD cards were collected 8.5 months later, and all pictures were reviewed to identify animals (Appendix S1).

Statistical analysis

All analyses were conducted in the R statistical software version 4.1.0 (R Core Team, 2022). All data are publicly available through the Georgia Coastal Ecosystems LTER data portal (Georgia Coastal Ecosystems LTER Project and Hensel, 2023). Prior to analysis, we averaged values from the two subplots within each plot to generate a plot-level mean for each variable in every year. We analyzed the effect of our experimental treatments over time on the Δ density (i.e., density–initial density) of each invertebrate species, vegetation biomass, and snail grazing rate per plot using a linear model, allowing treatment, length of experiment (year), and their interaction to predict change in response variables in a factorial ANOVA framework. We chose this model structure because our research questions identified the effect of time (i.e., "year") on our response variables as an important relationship to quantify. We used Tukey's tests for post hoc comparisons with the emmeans package (Length, 2019). We evaluated assumptions of normality of residuals using QQ plots and Shapiro–Wilks tests for normality with the performance package (Lüdecke et al., 2021) and found no violations. We did not detect any statistical differences between the partial cage treatment and the control treatment for any response variables, and for clarity, we have excluded the cage control responses from analyses and figures. We also examined any spatial pseudoreplication effects by quantifying the potential role of "location along creek" (i.e., plot number; Appendix S1: Figure S1) on any of our response variables. We did not expect any ecological reason for plot location to affect any of our response variable, and we found no evidence that adjacent or nearby plots were more correlated with each other. Thus, we excluded plot location from further analyses.

To evaluate the direct and indirect effects of nektonic predators and mud crab mesopredators on the invertebrate community and *Spartina* biomass, we fit a structural equation model. We first identified plausible causal links between nektonic predators, mud crab predators, marsh invertebrates, and *Spartina* biomass based on existing knowledge of the system, incorporating the potential for both negative and positive interactions (Appendix S1: Figure S2). We then modeled the change in *Spartina* biomass in the piecewise SEM package (Lefcheck, 2016). To reduce model complexity due to the limited plot replications in the experiment, we pooled both adult and juvenile fiddler crab densities into one number per plot per year. We fit linear mixed effects models using exclusion treatment and invertebrate densities as fixed effects and year as a random effect to help isolate the role of treatments and different invertebrate densities between years. Detailed statistical methods are provided in Appendix S1.

To analyze the effect of our experimental treatments on predation pressure in tethering trials, we used linear models with treatment and (for snails and fiddler crabs) life stage (juvenile versus adult) as interactive effects. In the case of snails, separate analyses were run for 2018 and 2019 trials (Appendix S1). To quantify differences in teabag decomposition, we compared treatment differences with a Welch two-sample *t*-test and conducted a Pearson's product–moment correlation test to describe the relationship between fiddler crab density and tea bag decay constant. To describe correlations between snail density and snail grazing, and between mesopredatory mud crab burrow density and snail grazing, we fit regressions between these pairs of variables (across all years and treatments) and conducted Pearson's correlation tests.

RESULTS

Effects of nekton predator exclusion on benthic invertebrate density over time

Nekton exclusion and the duration of treatment (i.e., time, in years) had both additive and interactive effects on marsh invertebrate density (Figure 1; Appendix S1: Table S1). Nekton exclusion and time interacted to affect mud crab burrow density (Treatment × Year: $p = 0.03$, Figure 1A). Mud crab burrows were rarely found in any treatments initially or in the first 2 years; however, in Year 3 (2019), mud crab burrow density increased nearly threefold in nektonic predator exclusions, signaling mesopredator release. Predator exclusion tended to increase purple marsh crab burrow density, with crab burrow density in exclusions nearly twice that in controls for every year of the experiment; however, this effect was not statistically significant (Treatment: $p = 0.06$, Figure 1B). The density of ribbed mussels increased in 2017 within exclusions (but not significantly so) and then decreased thereafter (Treatment: $p = 0.12$, Figure 1C). Nekton exclusion had no effect on the density of adult fiddler crab burrows (Treatment: $p = 0.32$, Figure 1D), increased the density of juvenile fiddler crab burrows by 97 burrows/m^2 (Treatment: $p = 0.03$, Figure 1E), and had no effect on barnacles (Treatment: $p = 0.83$, Figure 1F). Nekton exclusion increased adult snail density by 22% (Treatment: $p < 0.01$), a metric that also increased by 10.6% per year regardless of exclusion, mostly due to an increase in control plot snail density in 2019 after mesopredator release (Time: $p < 0.01$, Figure 1G). Nekton exclusion had no effect on the density of juvenile snails (Treatment: $p = 0.47$, Figure 1H). Adult fiddler crab burrows in both treatments increased by ~21 burrows/m^2 over the first 2 years and then decreased back to initial densities in Year 3 (Year: $p = 0.03$, Figure 1D).

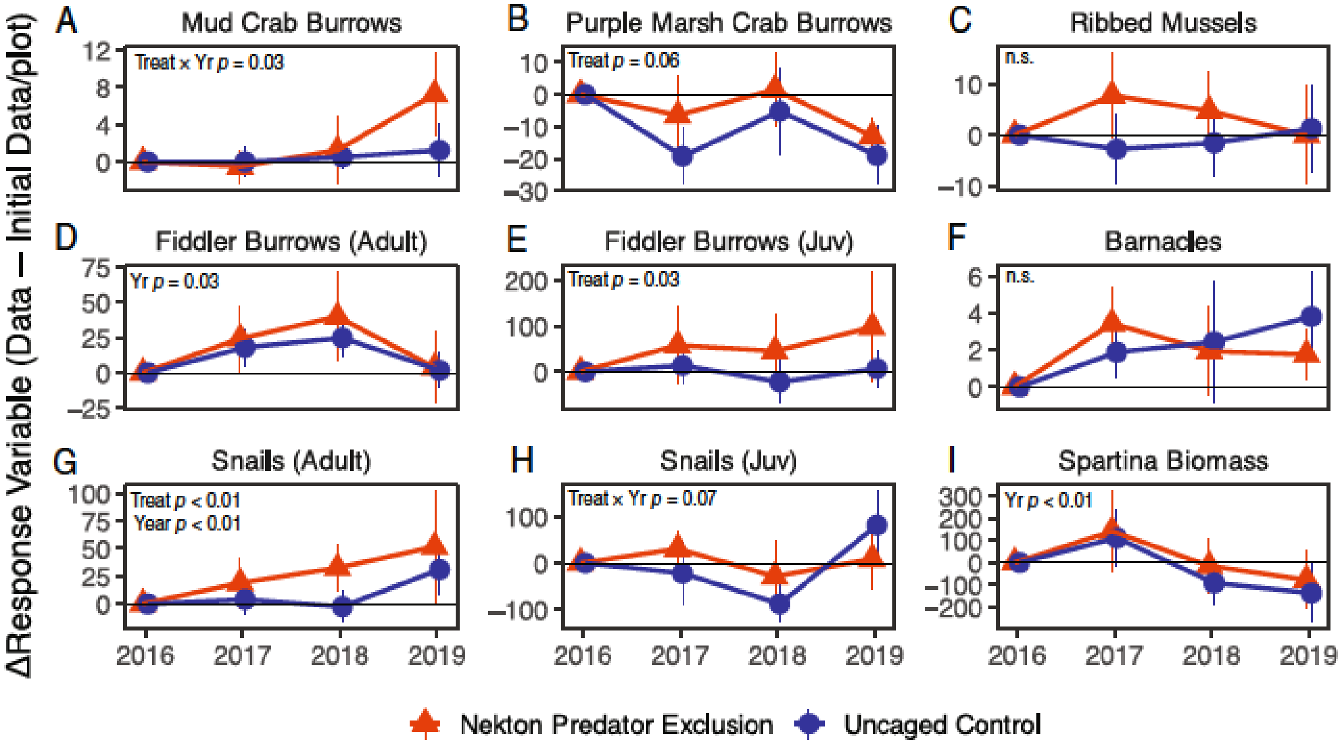

FIGURE 1 Effects of nektonic predator exclusion on marsh invertebrate community and *Spartina* biomass over time. All response variables are standardized as the mean and 95% CI of Δ density or biomass per plot from initial conditions in 2016 (e.g., Year$_1$ density − Year$_0$ density). $n = 8$ per treatment per year. Statistics on plot represent the results of year × treatment ANOVA.

Effects of nekton predator exclusion on Spartina biomass over time

Nekton exclusion had no effect on *Spartina* biomass (Treatment: $p = 0.44$, Figure 1I) in our first analysis. *Spartina* biomass initially increased after Year 1 in both treatments, but then decreased for 2 years with a mean loss of -112 g/m^2 in both treatments at the end of the experiment (Year: $p < 0.01$). The fit structural equation model (Figure 2) described the combined, cascading effects of both nektonic predators and mud crabs on variation in *Spartina* biomass across our experiment. The model explains the data well, as two goodness of fit tests indicate (Fisher's $C = 21.9$, p-value $= 0.24$, $\text{df} = 18$; $\chi^2 = 8.9$, p-value $= 0.45$, $\text{df} = 9$). This model detected that both mud crab burrow density and nektonic predator presence strongly and negatively affected snail densities (snails: $R^2_{\text{Conditional}} = 0.43$), while nektonic predator presence also suppressed purple marsh crab densities (purple marsh crabs: $R^2_{\text{Conditional}} = 0.31$). *Spartina* biomass was positively affected by fiddler crab burrow densities and was reduced by snail and purple marsh crab burrow densities (biomass: $R^2_{\text{Conditional}} = 0.59$). By multiplying the path coefficients to quantify cascading linkages (Appendix S1: Table S2), we found that the indirect effect of nektonic predator presence on *Spartina* biomass was 2.4 times stronger than the indirect effect of mud crab burrows on *Spartina* biomass, mostly due to nektonic predators controlling two marsh grazers that both influence variation in *Spartina* biomass. The SEM did not identify a significant link from predators to fiddler crab density, likely because we combined adult and juvenile fiddler crabs in the analysis to reduce model complexity.

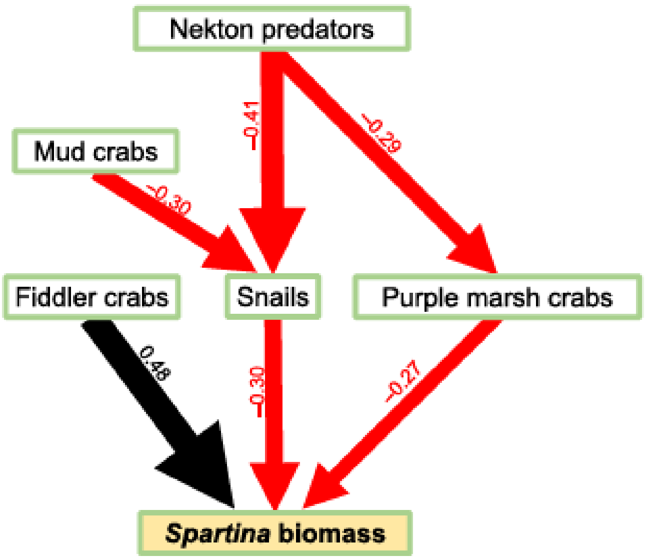

FIGURE 2 Nektonic predator exclusion experiment structural equation model depicting the effect of nektonic predators and mud crab mesopredator burrow density on the salt marsh invertebrate community and *Spartina* biomass. "Mud crabs," "fiddler crabs," and "purple marsh crabs" refer to burrow density response variables (mean burrows per square meter). Arrow width is proportional to the standardized effect size given next to the black (positive effect) and red (negative effect) arrows. Nonsignificant relationships ($p > 0.05$) are omitted for clarity.

Quantifying variation in snail and fiddler crab predation pressure

Predation pressure on tethered fiddler crabs was 1.4 times higher in uncaged control plots than in exclusion cages (Figure 3A; Exclusion Treatment: $F_{1,29} = 19.3$, $p < 0.01$), and adults experienced 14 ± 6% higher predation than juveniles (Life Stage: $F_{1,29} = 6.4$, $p = 0.02$). Predation on tethered snails differed both between juveniles and adults and among years. In 2018, juvenile snail predation pressure was reduced by 29 ± 6% inside of exclusion cages while adult snail predation was low and nearly identical between treatments (Figure 3C; Treatment × Life Stage: $F_{1,58} = 9.8$, $p < 0.01$). However, the effect of nekton exclusion disappeared in our 2019 trials when mud crab density increased in exclosures (Treatment: $F_{1,58} = 0.60$, $p = 0.44$), as only life stage predicted differences in predation pressure (Life Stage: $F_{1,58} = 18.5$, $p < 0.01$). Predation of adult mud crabs tethered in 2020 was also higher in uncaged controls: 81 ± 13% were consumed after 3 days in uncaged control plots, and double the predation rate observed in the nekton exclusion cages (Figure 3B, Exclusion Treatment: $F_{1,14} = 6.6$, $p = 0.02$).

Effects of nekton predator exclusion on snail grazing over time

Mean snail grazing intensity was higher inside of nektonic predator exclusion cages than that of open control plots in 2018 and 2019 (Figure 4A, Treatment × Year: $F_{1,2} = 5.5$, $p < 0.01$). When data from all treatments and years were combined, we found that total grazing on *Spartina* was correlated with increasing densities of both snails (Figure 4B) and mud crabs (Figure 4C).

Effects of nekton predator exclusion on tea bag decomposition rates

Although the green teabags tended to lose more mass in the exclusion versus control treatment, these differences

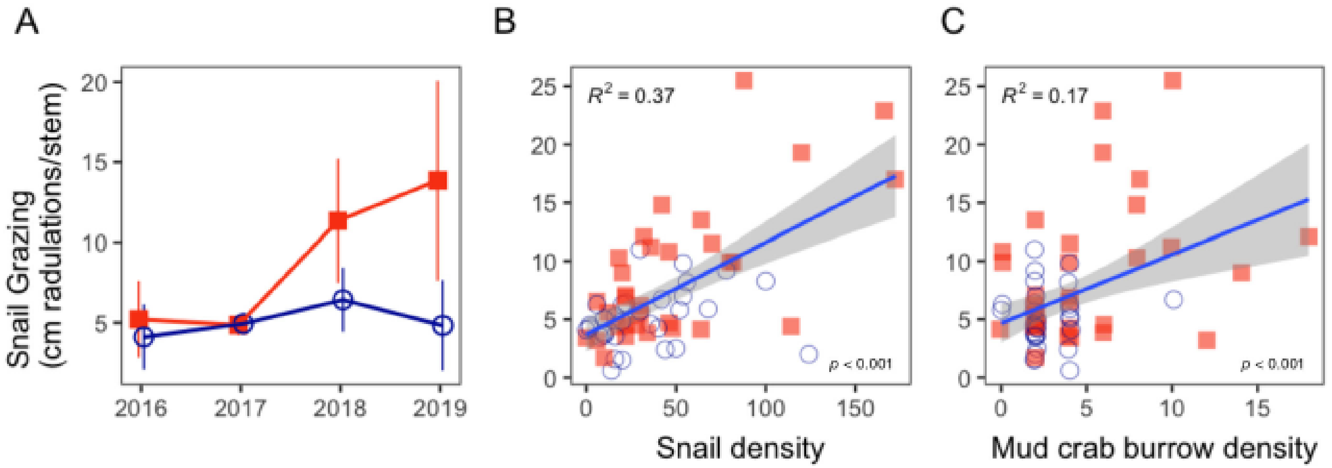

FIGURE 3 (A) Snail grazing amount (mean length of radulations/stem) across all years of the experiment. Snail grazing was significantly higher and more variable in nektonic predator exclusions than in control plots in 2018 and 2019. (B) Snail grazing was positively correlated with increasing snail density (snails per square meter) and positively correlated with (C) mud crab burrow density (burrows per square meter).

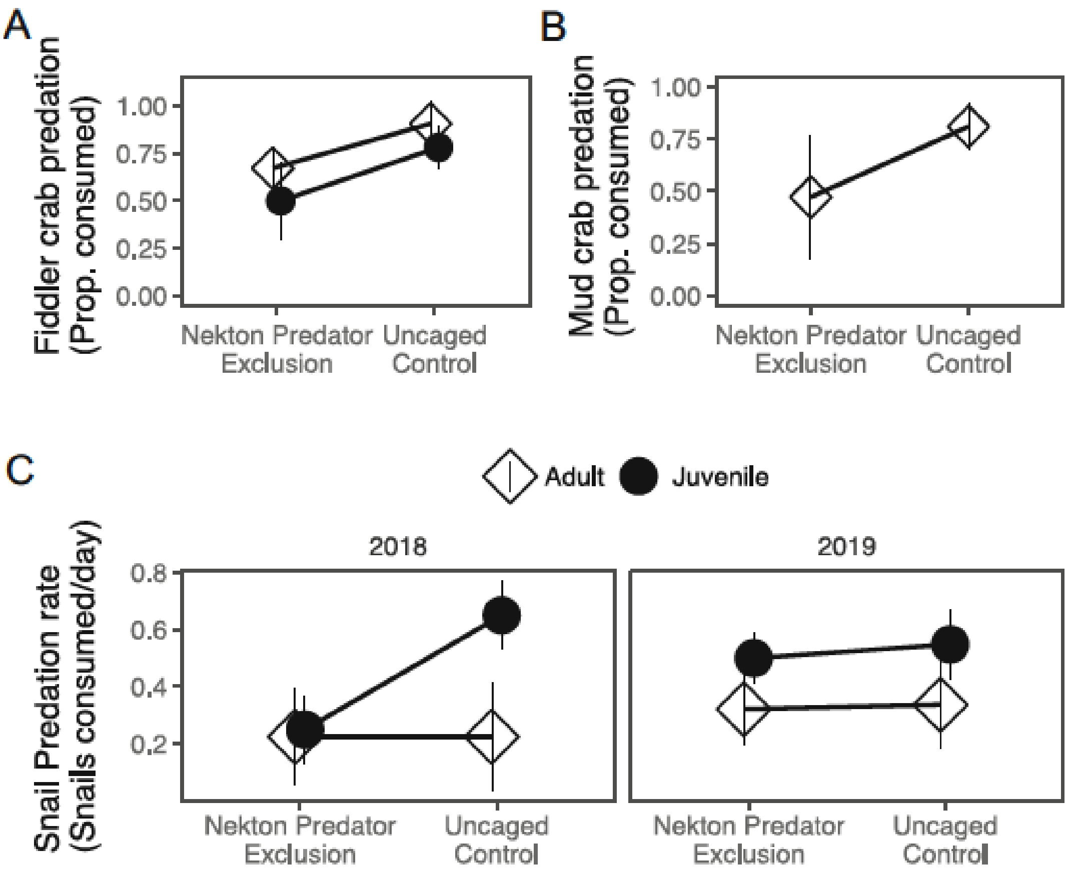

FIGURE 4 Results of tethering trials with (A) adult (diamonds) and juvenile (circles) fiddler crabs, (B) mud crabs, (C) juvenile snails in 2018 (left) and 2019 (right). Data are the mean and 95% CI of the proportion of individuals consumed at the end of the trials.

were not significant (Figure 5A; *t*-test: $t = 1.12$, df = 233.4, $p = 0.26$). Increasing adult fiddler crab burrow density was positively correlated with larger green tea decay constants (Figure 5B; Pearson's cor = 0.52, $t = 2.31$, df = 14, $p = 0.04$).

Describing nektonic and terrestrial predator communities

We collected 17 species of nektonic predators from trammel net samples at Dean Creek, with blue crabs and red

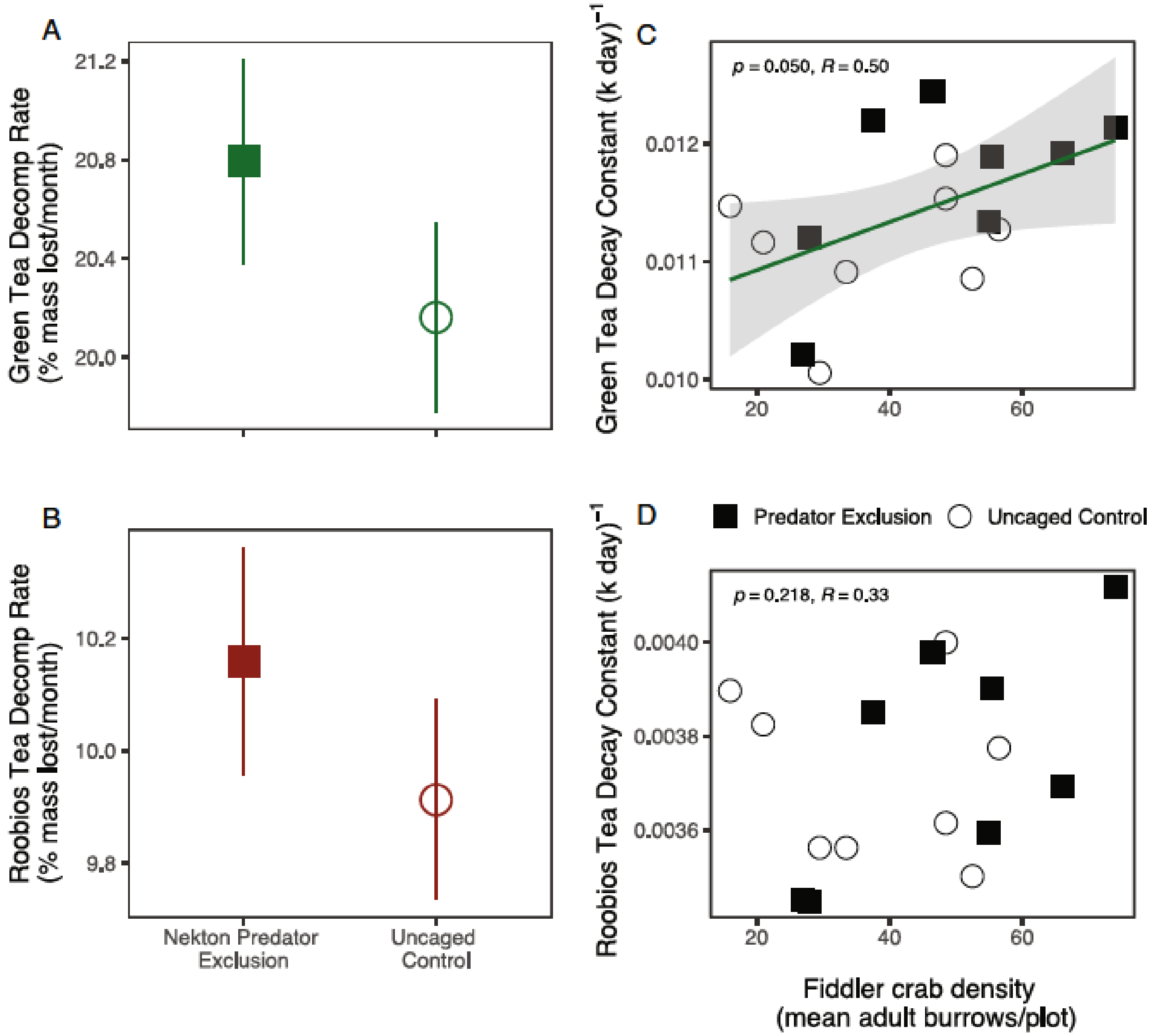

FIGURE 5 Nektonic predator exclusion effects on monthly percent mass loss of (A) green tea bags and (B) rooibos tea bags in 2019. Correlations between the total number of adult and juvenile fiddler crab burrows and decomposition rate (mass lost/month) of (C) green tea bags and (D) rooibos tea bags. Data are mean and 95% CIs across the whole experiment (A) and in each plot (B).

drum the most common (Appendix S1: Figure S3). Marsh invertebrates (marsh crabs, mud crabs, fiddler crabs, mussels, periwinkles) were all present in the diets of at least one of the five predatory fish studied in detail. Terrestrial predators were rarely observed by game cameras (Appendix S1: Table S3), and most were observed adjacent to plots rather than inside.

DISCUSSION

This 3-year experimental exclusion of nektonic predators from a Georgia salt marsh demonstrates that predators exert top-down control over the density of key components of the marsh invertebrate community, including mesopredators, grazers, and ecosystem engineers. Exclusion of nektonic predators such as blue crabs, red drum, and sheepshead increased densities of both grazers and burrowing crabs, groups that have opposing negative and positive effects on plants. We found strong evidence for a delayed mesopredator release, where mud crab burrow densities became elevated only after nektonic predators had been excluded for two full years. Mesopredator release changed the effect of nekton exclusion on predation pressure. Initially, nektonic predator exclusion had a positive effect on the survival of tethered juvenile snails, but this effect disappeared once mud crab burrow densities rose. Increased grazer densities in predator exclusion plots likely did not suppress plant biomass both because of this mesopredator release (as in Griffin & Silliman, 2011; Silliman et al., 2004) and because of compensatory facilitation by ecosystem engineering fiddler crabs (as in: Gittman & Keller, 2013) that benefited from nekton exclusion (Figure 1E). Overall, our findings reveal that: (1) top-down control of salt marsh ecosystems is regulated by an assemblage of both nektonic and benthic predators, rather than a single keystone predator, and (2) nektonic predators and benthic mesopredators provide complementary, layered control over macroinvertebrates, foundational marsh plants, and key ecosystem functions. If mesopredators are present, these results indicate that *Spartina* will likely be resilient to multiyear reductions in swimming predators. More generally, this study underscores the importance of longer-term and larger-scale experiments that incorporate a more complete community to clarify community dynamics and their cascading impacts on ecosystems.

Our first hypothesis, that predator exclusion would result in a trophic cascade in which grazers would increase and *Spartina* biomass would decrease, was only partially supported: grazers (i.e., purple marsh crabs and adult snails) increased in exclusions but did not cascade to suppress the primary producer. Like previous, smaller-scale studies that manipulated nektonic predator presence, snail densities increased in plots where predators were excluded (Figure 1G, Silliman & Bertness, 2002). Initial densities of adult snails at the experimental site were low (~25 snails per m^2) but doubled in exclusions over the course of the experiment. Similarly, juvenile fiddler crab densities increased in exclusions and remained unchanged in control plots (Figure 1E), consistent with previous studies in these marshes showing top-down control of this group (Griffin & Silliman, 2011). The conclusion that densities of snails and fiddler crabs are controlled in part by predation from nektonic predators is further supported by our tethering results which showed increased survivorship of juvenile snails and fiddler crabs inside exclusion cages early in the experiment. Although we do not report gut content analysis of blue crabs here, blue crabs are known predators of snails and smaller crabs and invertebrates in estuaries (Johnson, 2022; Silliman & Bertness, 2002). Blue crabs likely have the most important top-down effects on snails, whereas fish (which rarely eat snails, Appendix S1: Figure S3) likely play more of an important role in controlling fiddler crab and purple marsh crab abundances. As the duration of nekton exclusion approached 3 years, the effects of excluding nekton on the densities of snails disappeared, weakened on fiddler crabs, and actually reversed for juvenile snails. This temporal dynamism is likely explained by our second hypothesis.

Our second hypothesis, that mesopredatory mud crab densities would increase, compensating for the loss of nektonic predators by preying on snails and crabs (Griffin et al., 2011; Griffin & Silliman, 2011; Silliman & Bertness, 2002), was supported but only in the third year of our experiment. This temporally lagged mesopredator release appears to have obstructed a trophic cascade on plant biomass through compensatory trophic processes. Short-term past studies have found that high densities of mud crabs can suppress snail densities (Griffin et al., 2011; Griffin & Silliman, 2011; Silliman et al., 2004), and our comparison of multiyear snail tethering assays further supports the mesopredator-release hypothesis. In 2018, when mud crab densities were negligible inside of all plots, snail survivorship was higher inside exclusion cages; in 2019 when mesopredators densities had tripled inside predator exclusions, that positive effect of predator exclusion on snails disappeared and there was no difference in snail survivorship among treatments. Subsequent tethering assays in 2020 revealed that predation on mud crabs was significantly lower in the absence of nektonic predators (Figure 3B).

During the first 2 years of the experiment, we also observed nonsignificant trends toward positive effects of nekton exclusion on the densities of ribbed mussels and purple marsh crab burrows, both of which can affect marsh plant biomass (Angelini et al., 2018; Coverdale et al., 2012). Herbivorous purple marsh crabs were variable but tended to be more abundant in exclusions every year (Figure 1B) and were linked to lower *Spartina* biomass in our structural equation model (Figure 2). Mussel densities were also quite variable but tended to be higher in exclusion plots early in the experiment. Increased mesopredator predation (Lin, 1990) may have erased the effect of nekton exclusion on mussels by the third year of the experiment.

Consistent with our understanding of salt marsh ecosystem processes, high snail densities led to higher grazing rates (Figure 4B), and high fiddler crab densities were correlated with elevated (although not significantly higher) decomposition rates (Figure 5B) (Thomas & Blum, 2010). Snail grazing rates averaged across all years were about two times higher in the exclusion treatment than the control, as expected, but marsh plants were not significantly suppressed. While past studies have found density-dependent scarring rates on live plants by snails (Renzi & Silliman, 2021; Silliman et al., 2005; Silliman & Bertness, 2002), the highest average density of periwinkle grazers found in our plots (~70 ind. per m^2, Appendix S1: Figure S4) never exceeded the threshold (>80 ind. per m^2) associated with strong top-down control of marsh plants (Renzi & Silliman, 2021). Below this density threshold, periwinkles do not intensively graze live cordgrass and can enhance marsh decomposition by feeding mostly instead on organic detritus, benthic algae, and fungus on dead plant leaves (Hensel & Silliman, 2013). Facilitation by fiddler crab burrowing also may have mitigated the effects of periwinkle grazing (Gittman & Keller, 2013), as indicated by the strong positive effect of fiddler crab burrows on plant biomass in the structural equation model (Figure 2). Fiddler crab burrowing enhances sediment oxygenation, drainage, and remineralization of organic matter (Bertness, 1984; Derksen-Hooijberg et al., 2019; Gittman & Keller, 2013), all of which increase marsh plant production.

Snail grazing averaged over all years of the experiment was correlated with higher mud crab densities (Figure 4C) and was significantly higher in exclusions in 2018 and 2019 (Figure 4A). This seemingly incongruous positive relationship between mesopredator density and snail grazing can be explained by the results of short-term studies that revealed complex nonconsumptive effects of mud crabs on snail vertical migration. Snails climb higher on *Spartina* blades when mud crabs are present to avoid predation risk and switch away from benthic resources to grazing on cordgrass (Davidson et al., 2015). Only after mesopredator release in 2019 did snail grazing begin to increase in our exclusion plots compared to control plots, consistent with the results of these previous studies (Figure 4A).

We conclude that the ability of nektonic predators to indirectly control marsh plant biomass is mediated by mesopredator release, the counteracting effects of facilitation, and whether keystone consumers exceed threshold densities. The mesopredator release, in particular, merits further study as this did not manifest until the third year of the experiment. Thus, even in a well-studied, low-diversity ecosystem like a salt marsh, predicting and rigorously documenting controls on the full food web is not a simple task because of the multitude of possible and often opposing ecological links.

We suggest that similar outcomes might occur in many other ecosystems. For logistical reasons, ecologists have largely focused experimental work on pairwise interactions, and as studies expanded to consider interaction chains of three or even four species, the primary outcome was that a wide variety of indirect effects could occur, making net effects generally unpredictable (Werner & Peacor, 2003). However, understanding the effects of top predators on entire communities is an important problem for ecologists to address because top predators are primary targets of human consumption in many ecosystems (Lennox et al., 2022), and are the species most threatened by habitat loss (Häussler et al., 2020). We demonstrate one route forward here: to manipulate predators at spatial scales large enough to detect their community-wide effects in replicated, long-term experiments that are analyzed with a technique that specifically identifies cascading direct and indirect effects. Although challenging, time-intensive, and costly to implement, these experiments can include indirect and long-term effects, reveal the net effect of important predators on entire communities, and the results can suggest hypotheses such as mesopredator release that may take time to manifest and that merit further study.

AUTHOR CONTRIBUTIONS

Brian R. Silliman and Steven C. Pennings designed the study. Joseph P. Morton, David S. DeLaMater, Rebecca L. Atkins, Kimberly D. Prince, Sydney L. Williams, Anjali D. Boyd, Jennifer Parsons, Emlyn J. Resetarits, Carter S. Smith, Stephanie Valdez, Evan Monnet, Roxanne Farhan, Courtney Mobilian, Julianna Renzi, Dontrece Smith, and Christopher Craft collected data. Marc J. S. Hensel analyzed the data. All authors contributed to writing the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Georgia Coastal Ecosystems LTER Project and Hensel, 2023) are available in the Environmental Data Initiative's EDI Data Portal at https://doi.org/10.6073/pasta/a2c9c9b9541c511c3e4bfab5e8e4d639.

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SUPPORTING INFORMATION

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

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