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Increasing grazer density leads to linear decreases in *Spartina alterniflora* biomass and exponential increases in grazing pressure across a barrier island

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ABSTRACT: Researchers now recognize that top-down as well as bottom-up forces regulate salt marsh primary production. However, how top-down forces vary with grazer density is still poorly resolved. To begin to address this void, we (1) surveyed grazing intensity in short-form *Spartina alterniflora* across Sapelo Island, Georgia (USA), and (2) removed varying densities of grazers from 13 sites over 2 yr. Our survey revealed a non-linear relationship between snail abundance and grazing intensity, with grazing scars per stem increasing exponentially with snail density. Further, there appeared to be a threshold at ~80 snails m^{-2}, below which increasing snail density did not significantly increase grazing scars — potentially because snails target dead grass rather than live grass when competition with other snails is low. Increasing snail densities also exponentially reduced stem density within a plot, but only over 80 snails m^{-2}. Our removal experiment showed that snails linearly decreased *S. alterniflora* biomass across a naturally representative range of snails (0–586 snails m^{-2}) and that top-down control of short-form *S. alterniflora* was important at multiple sites across an island, with snail removal on average increasing primary production by 164%. Our results reveal that top-down control of short-form *S. alterniflora* is a common process across this intensively studied island, and that grazing scars increase non-linearly with snail density, while consumer effects on biomass increase linearly. Future models based on marsh plant growth (e.g. geomorphic evolution, primary production) should incorporate both the importance and functional form of grazer control to create more accurate carbon budgets and to better understand marsh network dynamics.

KEY WORDS: Salt marsh · Top-down control · Grazing · *Littoraria* · Cordgrass · Consumers · Sapelo Island

1. INTRODUCTION

For decades, salt marsh theory held that bottom-up factors (e.g. nutrient availability, hydrologic regime) were the primary determinants of ecosystem structure. This paradigm has since been expanded by a number of studies showing that grazers and their predators, in addition to bottom-up processes, shape marsh dynamics (Silliman & Zieman 2001, Jefferies et al. 2006, Altieri et al. 2012, Fariña et al. 2016, Mueller et al. 2017). Meta-analysis has recently confirmed that primary consumers, such as snails, cattle, crabs, and insects, can strongly control the biomass and diversity of foundational marsh plant species, and that this occurs in marshes throughout the world (He & Silliman 2016).

These top-down trophic interactions can have ecosystem-wide ramifications. For instance, in New England, overfishing predators such as blue crabs *Callinectes sapidus* can cause an increase in *C.*

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sapidus prey, grazing *Sesarma* crabs, which in turn overgraze marsh grasses, degrading marsh habitat (Altieri et al. 2012). Similarly, a meta-analysis of livestock grazing on salt marshes found that cattle and sheep decrease cordgrass biomass as well as alter plant and invertebrate community composition (Davidson et al. 2017). Grazers can also influence carbon storage (Elschot et al. 2015), alter microbial community function (Mueller et al. 2017), slow decomposition rates (Mueller et al. 2017), and interact with extreme droughts to cause widespread marsh die-off (Silliman et al. 2005, He et al. 2017).

Although it is now well-established that consumers can impact salt marsh communities, we still do not have a clear idea of how these relationships are influenced by variations in consumer abundance, which is critical for gaining a more accurate understanding of marsh ecosystem dynamics. The shape of the relationship between consumer density and the strength of top-down control in other coastal systems has been shown to be non-linear, which can result in abrupt state changes with small changes in consumer abundance. For instance, in kelp forests, small increases in urchin densities can lead to disproportionately large losses of kelp when urchin abundance is high. In these cases, once urchins reach a density high enough to significantly reduce kelp cover, they form feeding fronts concentrated on the few remaining kelps, dramatically increasing grazing intensity and rapidly transitioning the ecosystem to a rocky barren dominated by coralline algae (Ling et al. 2015). Further, these relationships can exhibit thresholds, below which top-down control is not evident. For instance, researchers have found that a minimum biomass of urchins is needed to advance a feeding front and that below this threshold, the front does not move forward (Scheibling et al. 1999), resulting in a more stable system.

In kelp forests and other ecosystems with non-linear dynamics, the transition from a pristine to a degraded state can be abrupt and, in some cases, the new ecosystem can exhibit hysteresis. In these cases, the system resists transitioning back to its original state, posing a serious problem for restoration efforts. To revert from a barren back to a healthy kelp bed, for instance, urchin densities must be far below the density required to transition to a barren initially. Not only does this reverse transition require a disproportionately low density of urchins to return to a kelp bed, but some also estimate that the time to recovery is 3 times longer than the time to degradation (Ling et al. 2015). Similarly, on coral reefs, changes in the densities of herbivores can trigger a phase shift from a coral-dominated ecosystem to an algal-dominated ecosystem that resists transitioning back to coral domination, particularly when this occurs in tandem with other anthropogenic stressors (Hughes et al. 2010). In these cases, understanding how changes in consumer abundance influence foundation species is critical for both ecology and management.

Although salt marshes are less studied than coral reefs and kelp forests, the relationship between consumer density and consumer impact may be equally important in marshes, particularly if it is non-linear. Much like how kelp forests can transition to a barren alternative state when urchin populations increase, salt marshes can transition to a mudflat alternative state when marsh consumer populations increase (He et al. 2017). If grazing pressure in marshes is disproportionately high at high consumer densities, there may be a critical point above which managers need to implement consumer removal efforts to prevent rapid marsh loss.

In southern US salt marshes, where grazing by fungus-farming snails can be locally important, one study suggested that grazing intensity increases linearly with snail density (Silliman & Zieman 2001), while a more recent study suggested a logarithmic relationship between grazer density and severity of cordgrass damage (Atkins et al. 2015). Still other observational research has suggested that snails do not negatively impact growth of the cordgrass *Spartina alterniflora*. For instance, one correlational study in a South Carolina marsh found that, across a range of low to medium snail densities (8–196 snails m^{-2}), there was a positive relationship between snail density and plant productivity in the winter and no relationship between snail density and productivity in the summer (Kiehn & Morris 2009). This amount of variation is expected given the varying snail densities assessed, natural variation in plant biomass, and snail movement behavior (e.g. snails move towards taller plants on mudflats or die-off areas; Silliman et al. 2005). Observational and experimental work that samples across the much greater span of observed snail densities (0–1500 snails m^{-2}) is needed to begin to provide a clearer and more predictive understanding of how these salt marsh consumers influence primary producers and how generalizable the importance of top-down control is in this ecosystem.

Sapelo Island, Georgia, was the site of foundational research on the processes that govern marsh primary production (Teal 1962, Odum 1980, King et al. 1982) and is one of the best-studied marsh systems in the world. In these salt marshes, the marsh periwinkle snail *Littoraria irrorata* can be an important grazer

(Silliman & Newell 2003) and a common disturbance agent in the mid-marsh zone, which is dominated by short- and intermediate-form *S. alterniflora* (Li & Pennings 2016). Although *L. irrorata* recruit well to the low marsh zone, they are suppressed by predators and are less abundant in the low marsh compared to the mid-marsh zone (Silliman & Bertness 2002). *L. irrorata* prefer to eat fungi that live on standing dead *S. alterniflora* leaves and in snail-induced wounds on live *S. alterniflora*. When grazing on live grasses, *L. irrorata* cut, or radulate, *S. alterniflora* blades and farm fungus in their radulations, which can lead to stem death (Silliman & Newell 2003). In excess, these snails will graze rampantly, forming consumer fronts that can devastate cordgrass marshes (Silliman et al. 2013), but the relationship between *L. irrorata* density and grazing impact on cordgrass remains equivocal.

In this study, we employed observational and experimental work to address the following questions: (1) How does grazing intensity vary with increasing grazer density? (2) Are top-down effects significant when a range of snail densities and sites across the island are included or are they only present at a few marshes? (3) If top-down effects are present across the island, is grazer density a good predictor of the strength of top-down control? To answer these questions, we surveyed 8 marsh sites across Sapelo Island and conducted a 2 yr manipulative snail-removal experiment at 13 sites within 6 randomly chosen salt marshes across the island.

2. MATERIALS AND METHODS

2.1. Study area

All research took place from 2001–2002 on Sapelo Island, Georgia, which is a Georgia Coastal Ecosystems Long Term Ecological Research (GCE LTER) site and a National Estuarine Research Reserve (Fig. 1A). Sapelo Island experiences a semidiurnal tide with a 2–3 m range and average annual precipitation of ~127 cm. Our research focused on the mid-marsh zone, where snail grazing is prevalent, and *Spartina alterniflora* occurs in the short growth form.

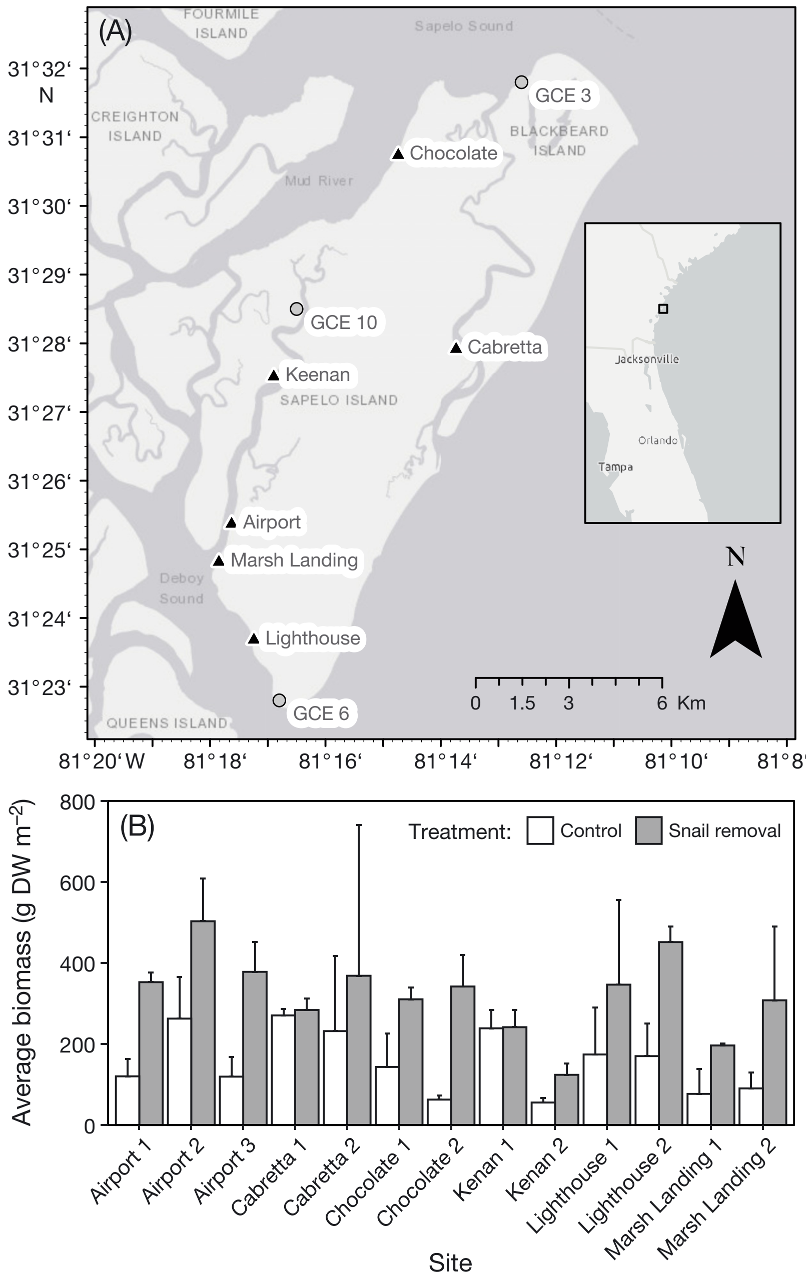

Fig. 1. (A) Haphazardly selected marshes across Sapelo Island (Georgia, USA) used in the grazer-removal experiment (black triangles) and the Georgia Coastal Ecosystems Long Term Ecological Research sites (gray circles). The 6 main marshes from the grazer-removal experiment are shown; there were 2–3 sites (>0.5 km apart) in each marsh. (B) Average cordgrass biomass of control and removal plots at each site across the 2 study years. Units are in grams dry weight (DW) m^{-2} calculated from 25 cm × 25 cm quadrats. Error bars represent 1 SD

2.2. Grazing pressure survey and snail abundance over time

To evaluate the relationship between *Littoraria irrorata* density and grazing intensity in salt marshes on Sapelo Island, we surveyed 8 sites across the island, spaced at least 1 km apart. Each site was chosen from a map and represented a site we had not visited before, so we did not have prior knowledge about whether grazers were present. At each site, we entered the marsh and walked straight towards open water until we encountered short-form *S. alterniflora*. We then randomly selected 6 plots of 1 m^2, at least 10 m apart, within the short *S. alterniflora* zone. In each plot, we counted snail density, live stem density, and radulation length to estimate snail grazing pressure as a function of grazer density.

To place our experiment in the context of general snail abundance through time on Sapelo, we also used data from the 3 GCE LTER sites on the island (Bishop 2000–2008, Alber 2009–2012, Pennings 2013–2017). The 3 GCE sites are spread out geographically: Site 3 is on the northern portion of the island, Site 6 is on the southern tip of the island, and Site 10 is in the middle of the island on the west side (Fig. 1A). Mollusks were surveyed each year in October according to established LTER protocols (Bishop 2000–2008, Alber 2009–2012, Pennings 2013–2017). According to these protocols, 4 quadrats were placed near permanent plots at each site in the mid-marsh zone, and all living gastropods from the groups *Littoraria*, *Melampus*, *Detracia*, *Ilyanassa*, Hydrobiidae, Succineidae, and *Assiminea* in each quadrat were collected and counted. We only used data from LTER mid-marsh *L. irrorata* surveys that were conducted in short *S. alterniflora* from 2000 to 2016 and plotted snail densities over time to examine whether the conditions during our study were common for the island. Although other gastropods were surveyed, they were absent in most quadrats, and far less abundant than *L. irrorata,* and so were not included in our analyses.

2.3. Snail removal manipulation

We tested the influence of the marsh grazer *L. irrorata* by deploying 1 m^2 exclusion cages around Sapelo from 2001 to 2002. There were 2–3 paired (control/exclusion) sites within 6 different salt marshes (Airport, Cabretta, Chocolate, Keenan, Lighthouse, Marsh Landing; Fig. 1A) around the island for a total of 13 replicates across 2 yr. Each site was at least 0.5 km away from the next closest site, and the marshes spanned the island (Fig. 1A). At each randomly selected site in the short *S. alterniflora* zone, we paired caged plots with uncaged plots. In the first year (2001), we also deployed cage controls to test for caging effects, although caging effects using these cages and these snails were not detected in previous studies on Sapelo Island (Silliman & Zieman 2001, Silliman & Bertness 2002, Silliman & Newell 2003, Atkins et al. 2015). Open-top cages were constructed and deployed in early March using an established method (Silliman & Zieman 2001). Uncaged replicates were marked, and snail abundance was measured as an estimate of grazer intensity. All rhizomes were severed around the cage, and all snails were removed from cages. Each cage was visited monthly to maintain snail removals and remove any debris that may have been caught in the cage. In September at the end of each growing season, we collected a 25 × 25 cm quadrat of *S. alterniflora* within the plot and calculated dry biomass.

2.4. Statistics

To examine the relationship between grazing pressure on *S. alterniflora* and snail density, we created models of radulation length/stem versus snail density using the data collected from the grazing pressure survey plots. We fit models using generalized least squares with the R package 'nlme' (Pinheiro et al. 2020) and plotted standard deviations using the package 'twNlme' (Wutzler 2013). When plotted, the survey data looked like they could be linearly or exponentially related. To test which fit better described the relationship between grazing pressure and snail density, we modeled the results with both a linear (Radulations per stem = $a + b \times$ Snail density) and exponential (Radulations per stem = exp[$a + b \times$ Snail density]) model. Since log-transformed data cannot take on a zero value, we removed 6 observations from the dataset that had no radulations, reducing the sample size to 42. For models where residual assumptions were violated and there appeared to be increasing variance with snail density, we also fit a model with a constant plus power variance structure to meet model assumptions. We then compared models using Akaike's information criterion (AIC) and selected the model with the lowest AIC value, given that the ΔAIC was at least 2.

During model creation and assumption testing, we found that models did a poor job of describing the full range of snail densities and that plots with <80 snails m^{-2} appeared to behave differently than those with

>80 snails m^{-2}. We subsequently divided the data into 2 datasets: plots with >80 snails m^{-2} (n = 20) and plots with <80 snails m^{-2} (n = 22). To further explore why this threshold might occur, we examined the relationship between snail density and stem density in a plot. We used the same method described above to create generalized linear models describing stem density as a function of snail density above and below 80 snails m^{-2}.

For the removal experiment, we performed 4 paired, 2-sample, double-sided *t*-tests to test for cage effects, biomass differences between years within treatments, and treatment effects on biomass. To test for snail density differences between years, we used a chi-squared test given that snail counts were integers. Given that we made 5 comparisons, we used the Bonferroni adjusted cutoff of p = 0.01 to determine significance. Data were normally distributed, with the exception of control biomass in the second year and total treatment effects, which we log transformed to meet normality and homogeneity of variance assumptions.

To examine whether the number of snails at a site (i.e. resident snail density, estimated by the number of snails present on the control plot) influences the biomass of snail removal plots, we created models of percent change in cordgrass biomass as a function of resident snail density. We used the same methods described for modeling the radulation data, fitting a linear (Percent change in biomass = $a + b \times$ Snail density) and an exponential (Percent change in biomass = exp[$a + b \times$ Snail density]) model using generalized least squares, with the option of a variance term to meet model assumptions. Because there was no difference between any of our metrics (snail density, removal biomass, control biomass) between years, because there was no significant effect of year when tested with an ANOVA, and because we were interested in the general effect of snails on *S. alterniflora*, we did not include year as a factor. We once again compared model fits using AIC and selected the model with the lowest AIC value. We calculated percent change in cordgrass biomass, or the effect of snail consumers, as the biomass of the snail removal plot (i.e. local growth without consumer pressure) minus the control plot (i.e. local growth given snail presence) divided by the biomass of the control plot multiplied by 100. That meant that larger values corresponded to higher levels of consumer control (i.e. larger biomass increases associated with snail removal). All analyses were conducted in R version 3.6.1 (R Core Team 2019).

3. RESULTS

3.1. Grazing pressure survey and snail abundance over time

Snail densities in grazing pressure survey plots ranged from 0 to 1475 snails m^{-2}, live stem density ranged from 3 to 320 stems m^{-2}, and radulation lengths ranged from 0 to 765 cm m^{-2}, with a normalized radulation length range of 0–38.4 cm stem^{-1}. Cordgrass in survey plots with more snails had longer radulation lengths per stem and the relationship appeared exponential (Fig. 2A).

Between 0 and 80 snails m^{-2}, there was no difference between the linear and exponential model (ΔAIC = 0.54) and no relationship between snail density and grazing pressure (linear: $t = 1.81$, df = 20, p = 0.085, exponential: $t = 1.52$, df = 20, p = 0.143). Above 80 snails m^{-2}, however, there was a significant positive relationship with snail density. Within this range, the exponential model with a constant plus power variance function fit best (ΔAIC = 23.68), suggesting the relationship between grazing pressure and snail abundance was nonlinear. Above 80 snails m^{-2}, an increase of 1 snail was related to a 1.003 times increase in radulation length ($t = 18.28$, df = 18, p < 0.001; Fig. 2A).

Above 80 snails m^{-2}, the relationship between snail density and stem density was also best described by an exponential model with a constant plus power variance function (ΔAIC = 25.07). An increase of 1 snail was related to a 0.004 times decrease in stem density (Fig. 2B). As was the case with radulation length and snail density, below 80 snails m^{-2} there was no significant relationship between snail and stem density (Fig. 2B).

Based on the LTER data, the size of the snail population on Sapelo from 2001 to 2002 does not appear anomalous when compared to snail abundances from 2000 to 2016 (Fig. 3A). Sites 3 and 6 may have been at local maximum in snail density during our study window, and Site 10 may have been at a local minimum, but in general, the years do not appear abnormal for the area, suggesting these results were not a function of abnormal snail densities during our study window.

3.2. Snail removal manipulation

There was no effect of caging on plant biomass (t = 0.84, df = 13, p = 0.41), there was no difference in the average number of snails on control plots between

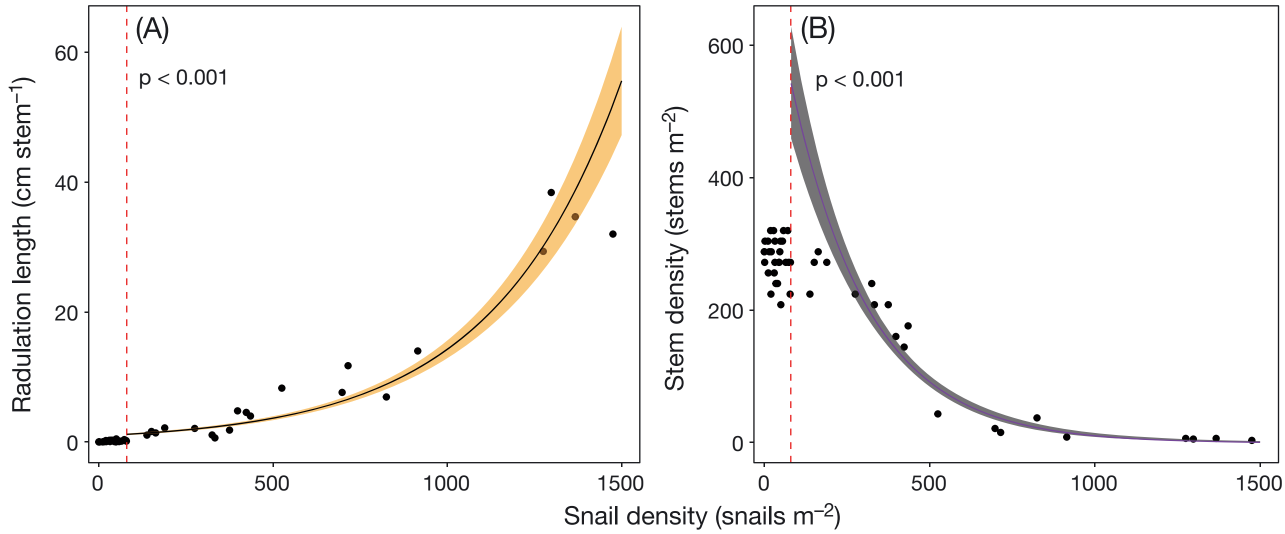

Fig. 2. (A) Exponential model of radulation length per stem as a function of snail density within randomly chosen 1 m^2 plots across Sapelo Island that had snail densities >80 snails m^{-2}. Shading indicates 1 SD from the predicted line, and the dashed line marks the threshold of 80 snails m^{-2}. Only points to the right of the threshold were used in model creation. (B) Exponential model of live stem density as a function of snail density within the same randomly chosen plots. Shading indicates 1 SD from the predicted line, and the dashed line marks the threshold of 80 snails m^{-2}

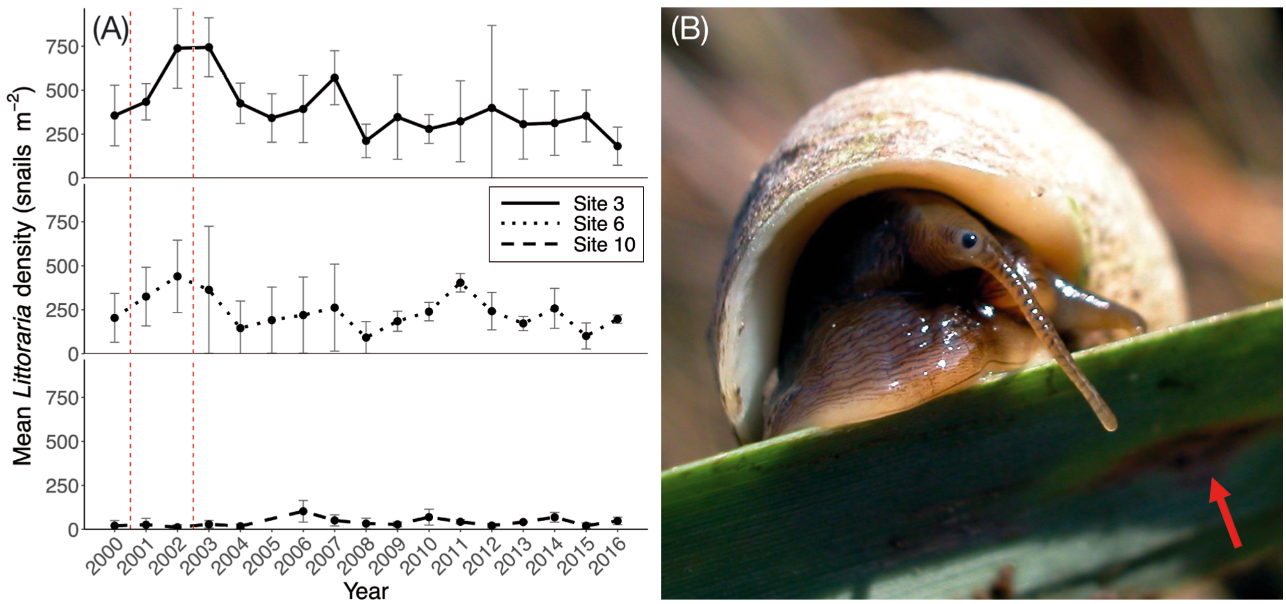

Fig. 3. (A) Snail densities from 2000 to 2016 at the 3 Sapelo Island LTER sites (gray circles in Fig. 1). Dashed vertical lines highlight the observations between 2001 and 2002. Error bars represent 1 SD in either direction, truncated at 0. (B) *Littoraria irrorata* on *Spartina alterniflora*. Arrow indicates a grazing scar. Photo by B. R. Silliman

years (χ^2 = 156, df = 144, p = 0.23), and there was no difference in biomass between years in control plots (t = 1.95, df = 12, p = 0.07) or in snail-removal plots (t = 1.22, df = 12, p = 0.25).

Snail removal significantly enhanced cordgrass biomass; control plots had less biomass than snail removal plots (t = −7.51, df = 25, p < 0.001; Fig. 4A). On average, removing snails increased plant biomass by 164%. The effect of snail density on biomass was best described linearly with a constant plus power variance function (ΔAIC = 12.37). Removing 1 snail was correlated with a 0.76% increase in biomass (t = 8.62, df = 24, p < 0.001; Fig. 4B).

Although these results varied geographically (e.g. top-down control initially appeared less important at the Keenan 1 plot), biomass was generally higher on

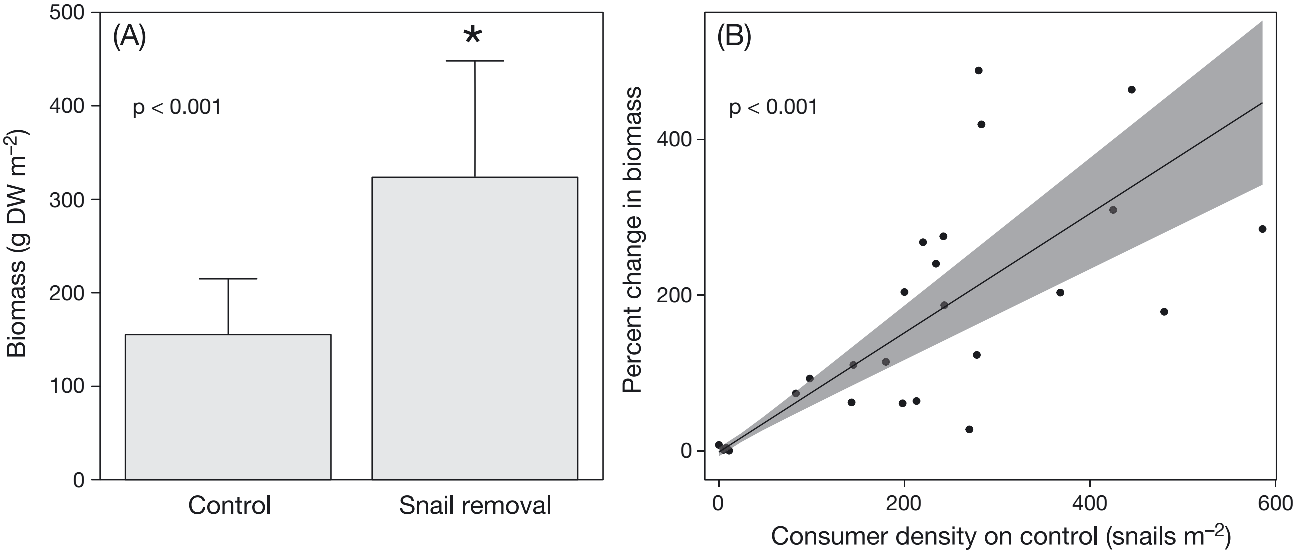

Fig. 4. (A) Average biomass in control (n = 26) and snail-removal (n = 26) treatments for all plots in both years. Measurements are in grams dry weight (DW) m^{-2} calculated from 25 × 25 cm quadrats. Error bars represent 95% confidence intervals and asterisk indicates statistical significance ($p < 0.05$). (B) Linear model of the percent change in *Spartina alterniflora* biomass (i.e. consumer effect) with increasingly dense snail removals. Relative change in biomass was calculated per site per year by dividing the difference between control plot biomass and removal plot biomass by control plot biomass ([removal biomass − control biomass] / control × 100). Shading indicates 1 SD from the predicted values

removal plots across the island, and results did not appear to be driven by one particular site (Fig. 1B). Snail density explains much of the variation across sites, as enhanced plant growth with snail removal increased with increasing resident snail density. The plots with the smallest change in biomass (i.e. Cabretta 1, Keenan 1, and Cabretta 2) also had by far the lowest snail densities (average of 2.5, 10.5, and 45.5 snails, respectively). All other sites had average snail densities >100, and removing snails increased biomass on average by 104–441%, although the maximum increase in a single year was 488%.

4. DISCUSSION

Understanding not only the presence of grazer–plant interactions, but also the shape of their relationship is critical to modeling ecosystem dynamics and predicting ecosystem thresholds (Collie et al. 2004). *Littoraria irrorata* abundance has been shown to have logarithmic (Atkins et al. 2015) and linear (Silliman & Zieman 2001) relationships with grazing intensity, but our results indicate that this relationship can also be exponential. This variation across studies likely represents natural variation in functional relationships that can occur due to varying ranges of snail densities examined, as well as other underlying factors that vary across sites, such as nutrient regime, soil salinity, and fiddler crab density, which can affect grazing intensity (Silliman & Zieman 2001, Silliman et al. 2005, Gittman & Keller 2013). Although we do not fully understand why snail abundance is so variable across marshes, it likely has to do with the interplay between recruitment and predation, which is what drives differences in densities of *L. irrorata* between the tall- and short-form *S. alterniflora* zones, has been observed for other snail species, and is currently being explored for *L. irrorata*.

Our surveys across the island in the short *S. alterniflora* zone showed that *L. irrorata* grazing is common and that there is a non-linear relationship between grazer density and grazing intensity above a threshold of ~80 snails m^{-2}. Above this density, grazing scars on *S. alterniflora* increased exponentially with each additional snail, suggesting that at high snail densities, small increases in snail abundance could have disproportionately large impacts on grazing intensity. The negative relationship we observed between snail density and live stem density may partially explain why this grazer–cordgrass relationship appears different above and below ~80 snails m^{-2}. Above 80 snails m^{-2}, increasing snail abundance was related to exponential decreases in stem density, but below 80 snails m^{-2}, there was no relationship between snail and stem density. It is likely that at these higher *L. irrorata* densities, snails begin killing stems, which drives grazing pressure up as snails congregate on the remaining stems in an area. This relationship may be less pronounced at low snail densities because *L. irrorata* preferentially target dead *S. alterniflora,* which hosts higher concentrations of fungi. When dead grass is available, snails put minimal pressure on live *S. alterniflora*, but once snail density increases and there is more competition for dead grass, snails begin to feed on live stems (B. R. Silliman unpubl. data). This diet switch at higher consumer densities could explain why the effect of increasing consumer density is particularly important above 80 snails m^{-2} and why we found plots above 80 snails m^{-2} to have a different relationship with increasing consumer density.

Although we did observe longer radulations in plots with high snail densities, we did not document how much of the increase in grazing scar lengths was due to an increase in the rate of small scars versus individual snails creating longer radulations versus primarily being driven by a decrease in stem density. However, this should be evaluated in future studies, as longer, deeper radulations may increase the severity of fungal infections (Chalifour et al. 2019), and understanding which form of radulations is occurring could help predict ecosystem impacts.

At high densities, snails can mow down drought-stressed grasses locally and then form fronts on healthy marsh edges (Silliman et al. 2005). These fronts, once formed, can move through marshes and transform vegetated areas into mudflats, which can resist transitioning back into a salt marsh (Silliman et al. 2013). To understand the mechanics of these powerful dynamics, we need to identify key thresholds and understand the shape of the relationship between grazers and their prey. Our work suggests that this relationship can be exponential, meaning that at high densities of snails, the grazing damage caused by each additional snail is much larger than at low grazer densities and that there is a threshold around 80 snails m^{-2} below which snail grazing impact is disproportionally low.

Our experimental results confirm the importance of top-down control in salt marshes on Sapelo Island and show that the grazer *L. irrorata* linearly decreases the biomass of short-form *S. alterniflora* across the island. On average, removing 1 snail m^{-2} increased *S. alterniflora* biomass by 0.76%. At low snail densities (0–11 snails m^{-2}), there was only a small effect of removing snails (<10% increase in *S. alterniflora* biomass), while at higher densities (200+ snails m^{-2}), removing snails increased biomass by upwards of 488%. These experimental results agree with our observational survey, and show that snails have strong density-dependent, top-down effects on *S. alterniflora*. There may also be a consumer density threshold for the effect of snail density on *S. alterniflora* biomass at ~80 snails m^{-2}, but we did not have enough plots in the 0–80 range to examine whether there was a similar threshold for biomass. Future research should expand upon these preliminary results to see whether we can observe similar threshold-like behavior across a suite of *S. alterniflora* response variables.

The strong top-down pressure we show in this study occurred under relatively benign environmental conditions, but top-down pressure can also be exacerbated by anthropogenic disturbances (e.g. climate change-related droughts, eutrophication, overfishing) and affect the resilience of salt marsh ecosystems to global change. Other marsh grazers have been shown to suppress drought resistance, particularly when in combination with salinity stress, and to hamper *S. alterniflora* regrowth after drought (Angelini et al. 2018). Similarly, although some marshes are able to survive grazing or drought, when combined, these factors dramatically increase cordgrass mortality and can turn salt marshes into salt barrens — likely because grazers can remain in an area after plants die and kill any new seedlings that establish (He et al. 2017). In addition to potential increases in grazing intensity, plants may be more susceptible to herbivore-induced damage during droughts, and as sections of marsh die off under stress, grazers may move to remaining live grasses, increasing local grazing pressure above normal levels (Silliman et al. 2005). In these cases, understanding how the density of consumers affects grazer impact can be critically important. At intermediate *L. irrorata* densities, for instance, drought can actually relieve grazing pressure by driving snails to take refuge, which results in less grazing damage (Chalifour et al. 2019). However, at higher snail densities, spatial competition for refuge may be intense, causing snails to remain on the drought-stressed canopy and in turn cause greater than average damage. As climate change and anthropogenic stressors intensify, the context-dependency of these plant–consumer dynamics will become increasingly important to understand, particularly given that the top-down effects of *L. irrorata* appear consistently present across a wide variety of marshes in at least 1 island system.

Given the importance of top-down control in this system, marsh managers may want to implement measures (e.g. protecting predators of snails) to keep snail densities low to reduce the potential for rapid consumption and increase marsh resistance to extreme drought. Ameliorating this local stressor is particularly important in the face of increasing global stress that can act synergistically to drive ecosystem deterioration. That said, these results are representative of 1 island system, and these experiments should be replicated across a broader geographic range to verify the generality of our conclusions, especially since the body size of snails can vary drastically across latitudes (compare Silliman & Zieman 2001 and Silliman & Bertness 2002).

Quantifying the relationship between grazers and cordgrass is critical to modeling salt marsh dynamics, and our results help define this relationship for 2 metrics (i.e. grazing intensity and biomass change). We show that grazer–cordgrass dynamics are nuanced and not always linear, which we hope will help inform management decisions, further our understanding of marsh species interactions, and improve our ability to predict ecosystem transitions in salt marshes.

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