A trophic cascade regulates salt marsh primary production

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Nutrient supply is widely thought to regulate primary production of many ecosystems including salt marshes. However, experimental manipulation of the dominant marsh grazer (the periwinkle, Littoraria irrorata) and its consumers (e.g., blue crabs, Callinectes sapidus, terrapins, Malaclemys terrapin) demonstrates plant biomass and production in largely controlled by grazers and their predators. Periwinkle grazing can convert one of the most productive grasslands in the world into a barren mudflat within 8 months. Marine predators regulate the abundance of this plant-grazing snail. Thus, top-down control of grazer density is a key regulatory determinant of marsh grass growth. The discovery of this simple trophic cascade implies that over-harvesting of snail grazers (e.g., blue crabs) may be an important factor contributing to the massive die-off (tens of km²) of salt marshes across the southeastern United States. In addition, our results contribute to a growing body of evidence indicating widespread, predator regulation of marine macrophyte production via trophic cascades (kelps, seagrasses, intertidal algae).

A primary goal of ecology is to understand the relative importance of resource availability (bottom-up forces) and consumers (top-down forces) in controlling plant growth. Strong consumer control of plant structure has been demonstrated in a variety of aquatic (1, 2) and marine (3–6) habitats. In these systems, a trophic cascade controls plant biomass. When predators do not suppress densities of potent herbivores, runaway consumption by grazers reduces plant biomass and, ultimately, denudes the substrate. Palatable algae and simple food webs characterize most of these communities (1–6). Thus, it has been suggested (7) that bottom-up control via trophic cascades may be an idiosyncratic attribute of simple, aquatic systems that are not buffered from run-away consumer effects by multiple predators and/or omnivory and are characterized by weedy, poorly defended primary producers. Recent evidence from temperate (8) and tropical (9) seagrass systems, however, suggests that communities dominated by higher, more heavily defended plants, are also susceptible to cascading consumer effects.

Western Atlantic salt marshes dominated by vascular plants are among the most productive systems in the world (10). Most research in marshes has focused on physico-chemical factors that influence the success of the dominant macrophyte in the community, Spartina alterniflora (salt marsh cordgrass; ref. 10). The prevailing paradigm in marsh ecology for nearly five decades has been that bottom-up forces are the primary determinants of plant production (10, 11).

Early studies in North American salt marshes concluded that plant–herbivore interactions were of little consequence to community dynamics (12–14). None of these investigations, however, experimentally excluded grazers to test explicitly the hypothesis that Spartina growth is unregulated by consumers. All of these studies assumed that dying and senescing marsh plants (detritus) attracted invertebrate grazers and did not test the alternative hypothesis that invertebrate grazers generated these patterns. For nearly half a century, research based on this untested grazer-detrital hypothesis has dominated scientific work within the field and greatly influenced the development of detrital/bottom-up paradigms in other marine systems (seagrasses and mangroves; refs. 15 and 16).

Recent research in Virginia (USA) marshes which did employ grazer exclusions has challenged current marsh theory and suggests that powerful trophic interactions influence the high primary production observed in these communities. By manipulating both snail and nitrogen (N) levels, a season-long caging experiment (17) demonstrated that the most abundant and widespread grazer in East Coast marshes, the marsh periwinkle (Littoraria irrorata),1 exerts strong top-down control over cordgrass growth, and that this effect increases with N fertilization. At moderate densities [144 individuals (ind) per m²], Littoraria, long thought to be a detritivore specialist (17), switched from feeding on dead organic material to live Spartina. Although periwinkles did not consume large quantities of live plant tissue (instead they “farmed” fungi on grazer-induced wounds on green leaves; ref. 17), snail radular activity on the grass surface led to drastic reductions in aboveground production in both unfertilized (62%) and fertilized areas (91%) and near-destruction of the marsh canopy. Because Littoraria is distributed widely and consumed by almost all predators that use marsh habitat (19), Silliman hypothesized (18) that by controlling snail densities, marine predators ultimately regulate the productivity of southeast salt marshes.

Over the past two years, we experimentally investigated the trophic cascade prediction by examining the generality of the Virginia results (17) at Sapelo Island, Georgia (USA), where the hypothesis that marsh grass production is controlled by bottom-up forces was originally developed (10–14). Specifically, we used experimental manipulations of top-down forces (i.e., snail and predator densities) along an intertidal gradient in plant resource availability [i.e., from the short-form Spartina zone in the high marsh (low N availability; ref. 10) to the tall-form Spartina zone along the creek bank (high N availability; ref. 10)] to examine two hypotheses: (i) Littoraria is capable of controlling cordgrass production anywhere on the marsh surface where it reaches sufficiently high densities, and (ii) the high production of cordgrass in southeastern marshes is a consequence of a trophic cascade, where marine predators limit the densities of plant-grazing snails.

To test these hypotheses, we conducted three experiments in both the short- and tall-form Spartina zones2 in two different marshes. (i) We assessed the potential effects of density-dependent snail grazing on cordgrass growth by maintaining constant snail densities in replicated 1-m² cages over a 2-yr period [three density levels: no snails; average snail density in the two experimental marshes (~600 ind per m²); and naturally occurring high densities (~1,200 ind per m²)].3 (ii) We quantified

Abbreviation: ind, individual.

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2In almost all southeast marshes, adult Littoraria densities in the tall Spartina zone along the creek bank are low (0–15 ind per m²), and in the short-form zone, natural densities are near medium (100–700 ind per m²) and occasionally as great as high (1,000–3,000 ind per m²; refs. 10, 17, 19). Correlational data of snail grazing intensity and plant cover from marshes on Sapelo Island, Georgia, suggest that at high densities, periwinkles actively mow down marsh grass and convert large vegetated areas to mudflats (B.R.S., unpublished data).
3Cordgrass typically occurs in two height forms in East coast marshes: the tall form (200–300 cm in height) nearest the water’s edge in well drained soils and short form (40–80 cm in height) in higher, poorly drained soils.
control areas exposed to natural conditions (i.e., with ambient snail densities ~600 ind per m²). Cages and cage controls were roofless and constructed of wooden stakes and 75-cm high wire screening (7-mm mesh, hardware cloth; see ref. 17). Plots in each zone were established at approximately the same elevations (±10 cm), and below-ground plant connections were severed along cage perimeters at the beginning of each growing season. Each treatment was replicated eight times at each site and marsh zone, and snail densities were monitored monthly. Aboveground Spartina growth was measured in November of both years (17). The patterns of periwinkle grazing in each replicate were recorded on August 15 (17).

Habitat-specific growth rates were assessed by caging juvenile snails (shell height = 3 mm; n = 10 marked snails per cage) in the short- and tall-form Spartina zones and comparing changes in shell lengths over a 6-month period. Treatments consisted of replicated (n = 8 per zone) 25-cm² cages constructed of 30 inch-high screening (1.5-mm mesh).

To assess the role of consumers in determining the distribution of Littoraria, we used both predator exclusion and tethering techniques. In both zones in both marshes, we established eight 1-m² predator exclusion cages constructed of 75-cm high screening (3-mm mesh, hardware cloth). Cage and uncaged controls were deployed as described above. The experiment ran for 1 yr, and in March 2001, 4 months after peak snail recruitment, snail-recruit densities in predator exclusions, cage controls, and uncaged controls were enumerated by haphazardly placing a 25 × 25 cm quadrat in each cage and counting all juvenile snails (shell height <4 mm) within that quadrat. We also established relative predation rates across the intertidal zone. To do this, 50 adult snails (shell height >10 mm) were tethered in the short- and tall-form Spartina zone of both marshes, and the loss of snails was monitored daily. Experimental snails were glued to fine nylon line with cyanoacrylic adhesive, given a 10-cm tether and placed in the field by tying the line to a 5-mm thick, poly(vinyl chloride) stake secured in the marsh surface. Tethered animals were placed in each habitat and spaced by at least 2 m. This tethering technique allowed snails to forage on the marsh surface in a 10-cm radius without tangling tethers, permitting natural behavior except for migrating up and down cordgrass stems with the tide to avoid water-born predators. We also caged equal numbers of tethered snails in all experimental areas. Over the entire length of the experiment, no caged, tethered snails detached or died.

We used a combined experimental approach (experiments i, ii, and iii above) to test for a trophic cascade instead of one experiment with just predator exclusion cages because time to adult size for Littoraria (~3–4 yr, when snails can effectively graze on live Spartina) far exceeds the lifetime (~1 yr) of small-mesh (3 mm), galvanized metal cages in the salt marsh.

**Statistical Analysis.** Data from tethering were analyzed by using a χ² test (marsh × zone). All other data were analyzed by using either a two-way (marsh × zone) or three-way ANOVA (marsh × zone × grazer density). For each treatment, n = 8. In analyses, data either exhibited homogeneity of variance and were normally distributed or were transformed by using log transformations for assumption conformity. Only linear contrasts were compared by using Tukey’s post hoc test. Because we found no significant effect of marsh (P > 0.23, all cases) on any response variable, data were pooled from both sites.

**Initial Conditions, Snail Densities, and Cage Effects.** Initial conditions of Spartina mean stem biomass did not significantly differ among treatments (P > 0.46, two-way ANOVA, all cases). The mean weekly deviation in snail density in all treatments never exceeded the assigned level. Mean shell length of snails greater than 5 mm in length was not statistically different between medium and high

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**Materials and Methods**

This study took place on Sapelo Island, Georgia, which is a part of the Georgia Coastal Ecosystems—Long Term Ecological Research site, University of Georgia Marine Institute, Sapelo Island National Estuarine Research Reserve. The experiments were conducted in both the Teal and Dean Creek marshes. Initially, we established snail recruitment and density patterns by using direct-count surveys and snail transplants. (iii) We examined the role ofpredation in regulating snail abundance by using 1-m² predator exclusion cages and tethering techniques. Respectively, these experiments were designed to determine three things: (i) in which Spartina zone top-down control by snails can occur; (ii) the natural distribution of snails, and in which Spartina-zones snails recruit and grow better; and (iii) the degree to which predators control Littoraria densities across the marsh surface. Combined, these experiments elucidate how top-down control of snail abundance by marine predators cascades downward to indirectly regulate Spartina production.

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**Fig. 1.** Effects of grazer density (G) and marsh zone (Z) on (A) grazing intensity on live cordgrass and (B) aboveground Spartina biomass after 8 months. n = 8 per treatment, and probability values given for two-way ANOVAs testing for main and interactive effects. (Bars = ± 1 SE.) All pairwise comparisons are significant (P < 0.02, Tukey test, all cases).
density caged, partially caged, or uncaged control treatments ($P > 0.41$, ANOVA, mean for all treatments $= 12.3 \pm 1.2$ mm). No detectable difference occurred in either Spartina biomass and/or snail density in all experiments between uncaged and partially caged (predator exclusion experiment) and between medium density caged, partially caged, and uncaged control treatments (grazing experiment; $P > 0.41$, ANOVA, all cases).

### Results and Discussion

Manipulation of periwinkle densities across marsh zones supported our hypothesis that Littoraria exerts strong, top-down control of Spartina growth at either naturally occurring moderate or high densities (Fig. 1). A mid-season survey of cordgrass leaves in experimental treatments revealed that snail feeding...
activities resulted in substantial scarring (i.e., radulations) of live plant tissue, and that the intensity of snail grazing increased significantly with increased bottom-up influence, i.e., from low N availability in the short-form Spartina zone to high N availability in the tall-form Spartina zone (Fig. 1A). In both snail density treatments, the total length of radulations per cordgrass stem was nearly fivefold higher in the tall-form Spartina zone. Coincident with the occurrence of grazer-induced wounds on live Spartina was a dramatic decrease in aboveground biomass (Fig. 1). The magnitude of this top-down effect, like snail grazing intensity, depended on marsh zone (a proxy for N availability), as Littoraria exhibited relatively more control of cordgrass growth in the tall-form Spartina zone (Fig. 1B). In the short-form Spartina zone, grazing at naturally occurring high densities reduced end-of-season standing crop by 88%, whereas in the tall-form zone, grazing by snails at the same density transformed one of the most productive grassland systems in the world (up to 3,700 g dry wt C per year; ref. 10) into a barren mudflat within 8 months (Fig. 1B). At medium snail densities, snail-grazing effects were still strong, reducing cordgrass growth in the short-form zone by 64% and in the tall-form zone by 89% (Fig. 1B). By the end of the second growing season, snail grazing at moderate densities also resulted in the conversion of the tall-form Spartina zone into an unvegetated mudflat (Figs. 2 and 3). In Virginia, increased top-down control of fertilized plants was linked to intensified snail grazing on N-rich stems (17), a scenario which likely applies here because of similarly strong interactions between snail grazing intensity and the availability of plant N (Fig. 1).

We did not detect any significant caging artifacts in our snail grazing experiments (see Materials and Methods). Therefore, these manipulations show that (i) Littoraria strongly suppresses cordgrass production anywhere on the marsh surface (both short-form and tall-form Spartina zones) where it reaches sufficiently high densities (i.e., at commonly occurring high and moderate densities); (ii) snail-grazing impacts are strongest in the N-rich, tall-form Spartina zone; and (iii) periwinkle grazing at naturally occurring densities leads to run-away consumer effects and, ultimately, denuding of the marsh substrate where plant resource availability is greatest (tall-form zone).

Snail density surveys and transplant experiments show that although snails are most abundant in the high marsh, they grow and recruit better in the low marsh. In both marshes, snail densities in the short-form Spartina zone were two orders of magnitude higher than in the tall-form zone (Fig. 2), a pattern consistent with the findings of many other studies (10, 17, 19). However, the opposite distribution pattern was found for juvenile snails. At both study sites, juvenile snail densities were nearly 300% higher in the tall-form zone (P < 0.01, two-way ANOVA, for main effect of zone, P < 0.001, Tukey test, x density in tall-form zone = 752 ± 34.5 ind per m²; in short-form zone = 208 ± 12.4 ind per m²). This finding suggests that snail recruitment is much greater in the high marsh, probably because of high larval fluxes on the edges of tidal creeks (20). Moreover, snail transplant experiments showed that Littoraria also grows best (≈200% greater) in the lowest reaches of the marsh (P < 0.02, two-way ANOVA, for main effect of zone, P < 0.001, Tukey test, x change in shell length for tall-form zone = 6.3 ± 0.31 mm; for short-form zone = 2.2 ± 0.12 mm), which is most likely the result of decreased desiccation stress and/or increased food quality (i.e., plants with higher N content; refs. 10, 17, and this study). These findings indicate the following: (i) annual snail recruitment into both zones is relatively high (>200 ind per m² per yr), but higher in the tall-form zone; (ii) Littoraria prefers to live in the N-rich, tall-form Spartina zone; and (iii) if snail recruitment is not strongly suppressed by some mechanism, survival of just 1-yr’s recruitment class to adulthood (≈3 yr) can lead to heavy consumption of Spartina and eventual denuding of the substrate (Fig. 2 and results above).

Results from predator exclusion and tethering experiments support our hypothesis that marine consumers control the distribution and abundance of Littoraria recruits and adults. At both study sites, predator exclusion cages showed that juvenile snail densities are strongly suppressed by consumers, and that the magnitude of this effect increases significantly at lower elevations. In the short-form zone, exclusion of predators increased juvenile snail density by nearly 30%, whereas in the tall-form zone, the same treatment led to even greater effects, as predator exclusion increased recruit density by 2 orders of magnitude (P < 0.02, three-way ANOVA, for main effect of exclusion and zone, and exclusion × zone interaction; P < 0.05, Tukey test, all contrasts; x density in: uncaged short-form zone = 72.1 ± 4.4 ind per m²; caged short-form zone = 93.1 ± 5.2 ind per m²; uncaged tall-form zone = 8.3 ± 2.1 ind per m²; caged tall-form zone = 305 ± 22.4 ind per m²). Tethering experiments in both zones and both marsh sites gave similar results (Fig. 2). Strikingly, 98% of snails tethered in the tall-form zone were eaten (86% crushed, primarily by blue crabs) after two tidal cycles (~24 h), whereas only half the snails tethered in the short-form zone were consumed after more than 2 months (Fig. 2). Although predation rates in the short-form zone were relatively low, they are still highly significant, as caging data suggest that up to 1/3 of the snail population in this zone may be lost annually to predation.

We did not detect any significant caging artifacts in predator exclusion experiments. Our tethering technique quantified relative predation losses without potential differences in behavioral refuges among zones, i.e., tethered snails could not avoid predators via their usual tidal migration up grass stems.

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1Decreased desiccation stress on foraging snails in low marsh habitat could also explain increased top-down control in the tall-form Spartina zone. This scenario, however, seems unlikely given that (i) snails in both zones foraged only at night or on overcast days (B.R.S., personal observations) and (ii) both snail grazing patterns and effects on N-rich plants in this study (tall-form Spartina N content = 3.2 ± 12%, short form = 2.1 ± 0.9%) were nearly identical to that in the Virginia study (17), where N availability was manipulated while holding immersion time constant.

4After 24 h, 86% of uncaged tethers in the tall-form zone were found with crushed shell fragments still attached. Crabs are the only predators of Littoraria that crush shells (10, 18). Turtles and drum fish swallow snails whole (10, 19). Only three crabs in the lower marsh can crush Littoraria shells: the blue crab, C. sapidus, and two species of mud crabs, Panopeus herbstii and Eurytium limosum. However, the primary extraction technique for mud crabs when consuming adult snails is lip peeling and plucking. Therefore, the majority of crushed shells on tethers were likely caused by predation by the blue crab.
grazing experiments (Figs. 1 Bform strongly suppress their densities in the more stressful, short-

**Mean snail density per m² in the two surveyed marsh die-off areas in Louisiana**

10504/H20841 of the U.S. has lead to depleted densities of high-order conservation of salt marshes. Intense fishing off the East Coast southeast marshes.

simple trophic cascade regulates the structure and function of our findings have important implications for the long-term conservation of salt marshes. Intense fishing off the East Coast of the U.S. has lead to depleted densities of high-order predators in estuarine communities (23). For example, densities [i.e., catch per unit of effort (CPUE) per survey trawl] of the commercially and ecologically** important blue crab, *Callinectes sapidus*, a primary predator of *Littoraria* (this study; refs. 19, 24, 24), have dropped precipitously (40–80%) in southeast and gulf coast estuaries over the past 10 yrs (26–28). Understanding how marshes respond to such perturbations is key to the survival of these ecologically and economically important habitats (e.g., marshes temper coastal flooding, filter terrestrial run-off, act as nurseries for commercially important species, and reduce erosion; ref. 29). Our experiments show that predator depletion could result in the conversion of salt marshes to mudflats by plant-grazing snails. Large expanses of salt marsh (in square km) in both Louisiana and Florida are currently experiencing massive die-back (27, 28). Physico-chemical factors and/or pathogens are hypothesized to be the primary causal mechanisms, yet no definitive conclusions have developed (30). We have surveyed two of these die-off areas and found *Littoraria* densities to exceed 500 per m², and snail grazing intensities intermediate to those in southeastern marshes. Here, we experimentally manipulated consumer densities to show that marsh plant communities that dominate shorelines of the southeastern coast of the U.S. are under strong top-down consumer control. Our findings indicate that the high plant production on southeastern marshes is ultimately realized through a trophic cascade, where marine predators limit the densities of plant-grazing snails that are capable of denuding marsh substrate. These results have important conservation implications and suggest that the overexploitation of a major predator may indirectly alter the structure and function of intertidal marsh habitats. In addition, our findings, combined with mounting evidence showing grazer control of plant growth in Argentine (31) and Canadian (32) marshes, suggest that the current paradigm in salt marsh ecology, and the application of this paradigm to other systems, needs to be reevaluated.


**Given that snails can denude the substrate at densities similar to that found in Louisiana marshes, it is possible that intense grazing by snails is a contributing factor to marsh die-off or, at least, it prevents recovery after die-back events occur. Snails could interact with harsh physical conditions such as high salinity to overstress plants and/or facilitate the introduction of pathogens by means of radular grazing. Further investigations of these possibilities as well as examining potential mechanisms of the persistence of high marsh habitat in areas where snail densities are consistently >600 ind per m² are needed. Possible mechanisms of high marsh persistence include increased plant resistance (e.g. palatability, resource allocation) to snail grazing under conditions of low nutrient availability, decreased productivity of growth suppressing fungi on radulated stems with low N content, or both.**

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††The blue crab, *C. sapidus*, is typically abundant in low marsh habitat in almost all salt marshes on the East and Gulf coasts of the U.S. The blue crab is widely considered to be the keystone predator of epifauna in these marshes, regulating both distribution and abundance of myriad organisms (19, 23, 24).

**Mean snail density per m² in the two surveyed marsh die-off areas in Louisiana = 507.3 ± 76.2; mean cm of radulations per stem 142.6 ± 22.1. In each area, 10–50 × 50 cm quadrats were haphazardly placed, and the total number of snails and total length of radulations on 10 randomly chosen stems were enumerated.**