

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 are 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 predators (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 top-down 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*),[†] 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* zones[‡] 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 ($\approx 1,200$ ind per m²)].[†] (ii) We quantified

Abbreviation: ind, individual.

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[†]In 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).

[‡]Cordgrass 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.

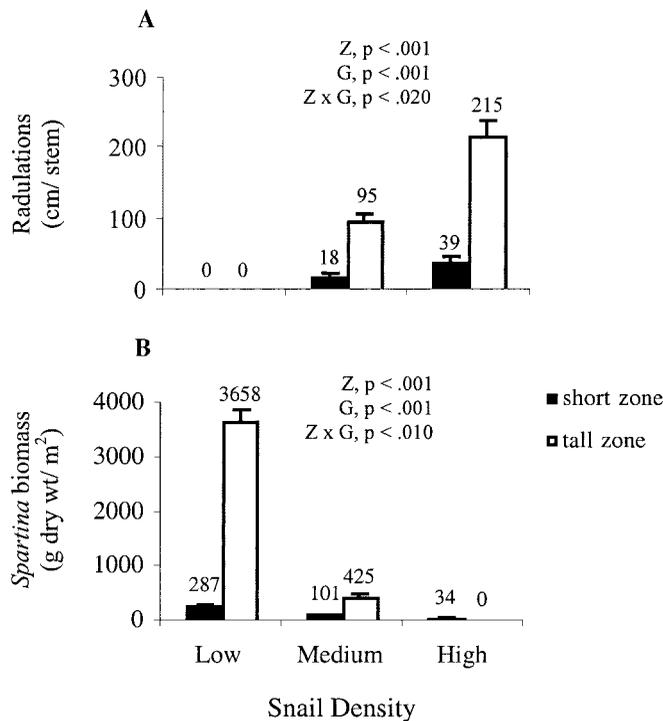


Fig. 1. Effects of grazer density (G) and marsh zone (Z) on (A) grazing intensity on live cordgrass and (B) aboveground *Spartina* biomass after 8 months. $n = 8$ per treatment, and probability values given for two-way ANOVAs testing for main and interactive effects. (Bars = ± 1 SE.) All pair-wise comparisons are significant ($P < 0.02$, Tukey test, all cases).

snail abundance, larval recruitment rates, and zone-specific growth rates by using direct-count surveys and snail transplants. (iii) We examined the role of predation 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.

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 across the marsh surface in February 2000. In both zones at both marshes, we quantified adult snail (shell height >10 mm) abundance by haphazardly throwing 50–25 × 25 cm quadrats in each zone. Juvenile snail (shell height <4 mm) densities were quantified in late November, just after peak *Littoraria* recruitment (10, 19).

In each zone, we established 1-m² experimental plots assigned to the following treatments: (i) caged with 1,200 snails = “high”; (ii) caged with the average snail density in the two experimental marshes (≈ 600 ind per m²; see Fig. 2) = “medium”; (iii) caged with all snails removed = “low”; (iv) caged manipulation controls (i.e., three sides instead of four); and (v) uncaged

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-borne 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 χ^2 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

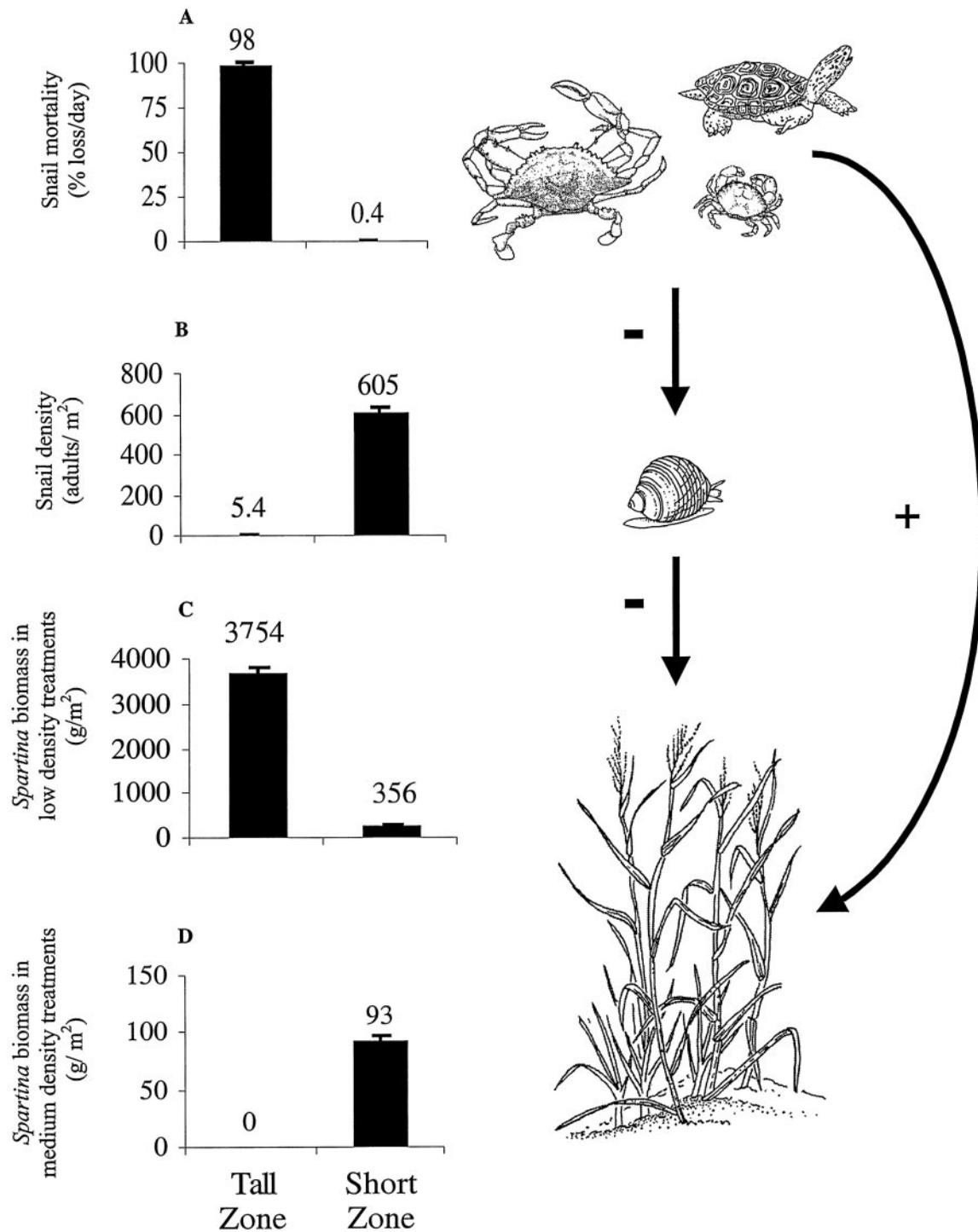


Fig. 2. A comparison between short-form and tall-form *Spartina* zones. (A) Predation rates on tethered snails (>10 mm). (B) Natural density of adult *Littoraria*. (C) *Spartina* biomass in low density treatments after 22 months. (D) *Spartina* biomass in medium density treatments (≈ 600 snails per m^2) after 22 months. All pair-wise comparisons in B, C, and D were significant at $P < 0.01$ for the effect of zone in the two-way ANOVA. (Bars = ± 1 SE.) For the effect of zone on tethering, see A: $\chi^2_1 = 121.34$, $P < 0.01$. The proposed mechanism of the marsh trophic cascade is portrayed in the marginal cartoon. Snail predators pictured include (from left to right) a blue crab, terrapin, and mud crab. (Illustrations by Jane K. Neron.)

density caged, partially caged, or uncaged control treatments ($P > 0.41$, ANOVA, mean for all treatments = 12.3 ± 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

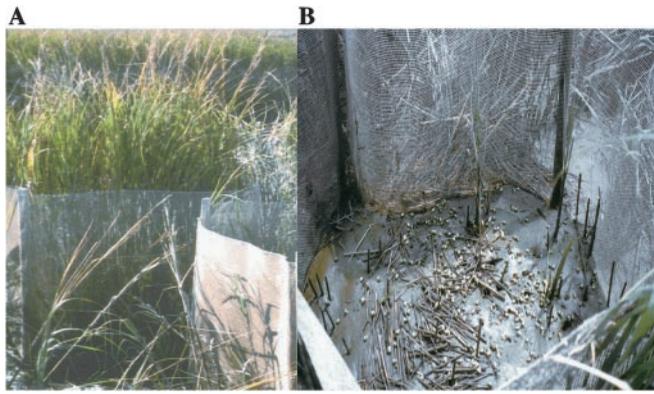


Fig. 3. Effects of periwinkle grazing on *Spartina* standing crop and canopy structure in the tall zone after 8 months. (A) Low-density plot. (B) High-density plot. After 20 months, cordgrass in all medium-density plots was reduced wholesale, and the marsh substrate was completely denuded (B).

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 m^2 ; in short-form zone = 205 ± 12.4 ind per m^2). This finding suggests that snail recruitment is much greater in the low marsh, probably because of high larval fluxes on the edges of tidal creeks (20). Moreover, snail transplant experiments showed that *Littoraria* also grows best ($\approx 200\%$ 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 = $6.3 \pm .31$ mm; for short-form zone = $2.2 \pm .12$ 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 m^2 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 \times zone interaction; $P < 0.05$, Tukey test, all contrasts; x density in: uncaged short-form zone = 72.1 ± 4.4 ind per m^2 ; caged short-form zone = 93.1 ± 5.2 ind per m^2 ; uncaged tall-form zone = 8.3 ± 2.1 ind per m^2 ; caged tall-form zone = 305 ± 22.4 ind per m^2). 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

[§]Decreased 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 = $3.2 \pm .12\%$, short form = $2.1 \pm .09\%$) were nearly identical to that in the Virginia study (17), where N availability was manipulated while holding immersion time constant.

[¶]After 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.

(see *Materials and Methods*). Additionally, because these snails rarely move more than 50 cm over a tidal cycle (21) and behaved relatively normally when tethered, tethering them did not result in artifacts often associated with tethering more mobile prey (22). Therefore, predator exclusion experiments, as well as tethering experiments, indicate that marine predators exclude plant-grazing snails from optimal growth and recruitment areas in the tall-form *Spartina* zone, and that they strongly suppress their densities in the more stressful, short-form *Spartina* zone. Combined with the results from the snail grazing experiments (Figs. 1B, 2C and D, and 3), these findings show that predators, by controlling snail densities, indirectly facilitate the high levels of primary production observed in salt marsh communities. In effect, these results suggest that a simple trophic cascade regulates the structure and function of southeast marshes.

Our findings have important implications for the long-term conservation of salt marshes. Intense fishing off the East Coast of the U.S. has led 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 our medium and high snail density treatments.** Given that blue crab densities have recently declined precipitously (≈50% drop in CPUE per trawl; ref. 27) along the gulf coast and in these states (27, 28), it is possible that the cascading consumer

effects shown in our experiment may already be at work in southern marshes.^{††}

Salt marsh communities dominated by vascular plants have long been viewed as a classic example of a bottom-up-regulated system dominated by relatively unpalatable plants controlled by physical conditions and nutrient supplies. This entrenched theory has had a profound and long-lasting influence on the field of ecology and has provided an intellectual framework for the ecosystem/bottom-up perspective in other marine macrophyte communities. 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.

were haphazardly placed, and the total number of snails and total length of radulations on 10 randomly chosen stems were enumerated.

^{††}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

- Carpenter, S. R. & Kitchell, J. F. (1993) *Trophic Cascades in Lakes* (Cambridge Univ. Press, Cambridge, U.K.).
- Power, M. E. (1992) *Ecology* **73**, 733–746.
- Bertness, M. D. (1984) *Ecology* **65**, 370–381.
- Paine, R. T. & Vadas, R. L. (1969) *Limnol. Oceanogr.* **14**, 710–719.
- Paine, R. T. (2002) *Science* **296**, 736–739.
- Estes, J. A. & Palmisano, J. (1974) *Science* **185**, 1058–1060.
- Strong, D. R. (1992) *Ecology* **73**, 747–754.
- Duffy, J. E., Macdonald, K. S., Rhode, J. M. & Parker, J. D. (2001) *Ecology* **82**, 2417–2434.
- Jackson, J. B. (1997) *Proc. 8th Int. Coral Reef Symp.* **1**, 23–32.
- Mitsch, W. J. & Gosselink, J. G. (2001) *Wetlands* (Van Nostrand Reinhold, New York).
- Odum, E. P. & del la Cruz, A. (1967) in *Estuaries*, ed. Lauff, G. H. (Am. Assoc. Adv. Sci. Publ. 83), pp. 383–385.
- Odum, E. P. & Smalley, A. E. (1959) *Proc. Natl. Acad. Sci. USA* **45**, 617–622.
- Teal, J. M. (1962) *Ecology* **43**, 614–624.
- Marples, T. G. (1966) *Ecology* **47**, 270–277.
- Odum, W. E., McIvor, C. C. & Smith, T. J., III (1982) *The Ecology of the Mangroves of South Florida: A Community Profile* (U.S. Fish and Wildlife Service, Washington, DC), FWS/OBS-87/17.
- Zieman, J. C. (1981) *The Foodwebs Within Seagrass Beds and Their Relationships to Adjacent Habitats* (U.S. Fish and Wildlife Service, Washington, DC), Special Report FWS/OBS-80/59.
- Silliman, B. R. & Zieman, J. C. (2001) *Ecology* **82**, 2830–2845.
- Silliman, B. R. (1999) Master's thesis (Univ. of Virginia).
- Daiber, F. C. (1982) *Animals of the Tidal Marsh* (Van Nostrand Reinold, New York).
- Leonard, G. H., Levine, J. M., Schmidt, P. R. & Bertness, M. D. (1998) *Ecology* **79**, 1395–1411.
- Hamilton, P. V. (1978) *Mar. Biol. (Berlin)* **46**, 49–58.
- Peterson, C. H. & Black, R. (1994) *Mar. Ecol. Prog. Ser.* **111**, 289–297.
- Jackson, J. B., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W., Bourque, B. J., Bradbury, R. H., Cooke, R., Erlandson, J., Estes, J. A., et al. (2001) *Science* **293**, 629–631.

24. West, D. L. & Williams, A. H. (1985) *J. Exp. Mar. Biol. Ecol.* **100**, 75–95.
25. Schindler, D. E., Johnson, B. M., MacKay, N. A., Bouwes, N. & Kitchell, J. F. (1994) *Oecologia* **97**, 49–61.
26. Lipcius, R. N. & Stockhausen, W. T. (2002) *Mar. Ecol. Prog. Ser.* **226**, 45–61.
27. Jordan, S. (1998) *J. Shellfish Res.* **17**, 367–587.
28. Guillory, V. & Perret, W. S. (1998) *J. Shellfish Res.* **17**, 435–442.
29. Boesch, D. F. & Turner, R. E. (1994) *Estuaries* **7**, 460–472.
30. McKee, K. L., Mendelssohn, I. A., Materne, M. D., Carlson, P. L., Jr., & Yarbo, L. A. (2001) *Abstracts for Coastal Marsh Dieback in the Northern Gulf of Mexico: Extent, Causes, Consequences, and Remedies*.
31. Bortolus, A. & Iribarne, O. (1999) *Mar. Ecol. Prog. Ser.* **178**, 78–88.
32. Jefferies, R. L. (1997) in *Disturbance and Recovery in Arctic Lands*, ed. Crawford, R. M. (Kluwer, Dordrecht, The Netherlands), pp. 151–165.