

## TOP-DOWN CONTROL OF *SPARTINA ALTERNIFLORA* PRODUCTION BY PERIWINKLE GRAZING IN A VIRGINIA SALT MARSH

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**Abstract.** Top-down forces, such as grazing and predation, have long been thought to be unimportant in controlling plant growth in salt marshes. Instead, bottom-up forces, such as porewater ammonium and oxygen availability, are thought to be the primary regulating factors. In the field, we observed the periwinkle, *Littoraria irrorata*, grazing on live salt-marsh cordgrass, *Spartina alterniflora*. To examine the relative importance of periwinkle grazing and nutrient availability in controlling marsh grass growth, we manipulated snail and nitrogen levels in a season-long field experiment in a Virginia salt marsh.

Snails differentially affected plant growth at varying nitrogen levels. In unfertilized plots, snail removal increased *S. alterniflora* aboveground production by 38%, whereas in nitrogen addition plots, snail removal increased cordgrass growth by 78%. Snail addition decreased aboveground production by 51% in unfertilized stands, while in fertilized stands, snail addition led to even greater reductions (66%). By comparison, nitrogen addition increased *S. alterniflora* production by 443% in snail removal treatments, while in controls and snail addition treatments, fertilization effects were dampened significantly, as nitrogen enrichment increased marsh grass growth by 322% and 189%, respectively.

Feeding assays examining the rate at which snails ingested live *S. alterniflora* revealed that snail consumption alone could not be responsible for these large biomass reductions. Experimental results suggest that grazer-induced defoliation and grazer control of plant demand for nitrogen fertilizer were the likely mechanisms involved. A survey of salt marshes from Maryland to Georgia showed that periwinkle grazing on live *S. alterniflora* is widespread.

Our results show that *L. irrorata* can exert strong top-down control of *S. alterniflora* production, and that this effect increases with increasing nitrogen availability. Together, these findings question the widely accepted notion that grazers play a relatively unimportant role in the salt marsh community.

**Key words:** cordgrass; grazing; *Littoraria irrorata*; mesograzers; nitrogen enrichment; periwinkles; plant–herbivore interactions; salt marsh; *Spartina alterniflora*; top-down vs. bottom-up control; trophic cascade.

### INTRODUCTION

Understanding how plant distributions are shaped by resource availability (bottom-up effects) and consumer pressure (top-down effects) is one of the primary goals of community ecology. In marine systems, it has long been established that both resource limitation (e.g., Redfield 1958, Ryther and Dunston 1971, Valiela and Teal 1974) and higher-order interactions (e.g., Odum and Smalley 1959, Bertram and Bertram 1968, Lubchenco 1978) can regulate the distribution of plants independently, but only recently have studies examined their relative importance. This new approach has provided keen insight into how plant assemblages are structured and has prompted many ecologists to re-evaluate the way they think about certain systems (e.g., coral reefs, Jackson 1997; seagrasses, Williams and Ruckelshaus 1993, McGlathery 1995, Heck et al. 2000;

rocky shores, Menge et al. 1997, Leonard et al. 1998). The relative influence of these factors, however, is not well understood in most marine systems.

In salt marshes along the east coast of North America, most research on the control of primary production has focused on physico-chemical factors that influence the success of *Spartina alterniflora* Loisel, the dominant structure-forming plant in the community. *S. alterniflora* growth has been shown to be positively correlated with porewater oxygen concentrations (Howes et al. 1981, Mendelssohn et al. 1981) and nutrient availability in the substrate (Sullivan and Daiber 1974, Osgood and Ziemann 1993), and negatively correlated with both porewater sulfide (King et al. 1982, Bradley and Morris 1990) and salt concentrations (Haines and Dunn 1976, Bradley and Morris 1991). Since each of these controls is either a resource or a resource-regulating factor that influences cordgrass production, most investigations on marsh-grass productivity have demonstrated bottom-up rather than top-down controls (Menge 1992).

Early saltmarsh studies concluded that: (1) saltmarsh

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TABLE 1. Reported densities of *L. irrorata* in salt marshes of the Mid-Atlantic, Southeast, and Gulf Coasts of the United States.

Site	Snail density (ind./m <sup>2</sup> )	Reference
Hog Island, Virginia	48	This study
Raccoon Island, Virginia	158	B. R. Silliman, <i>personal observation</i>
Cobb Island, Virginia	88	B. R. Silliman, <i>personal observation</i>
North Carolina	>100	Stiven and Kuenzler (1979)
South Carolina	43	Tucker et al. (1995)
Georgia	>100	Newell et al. (1989)
Georgia	400–700	Pomeroy and Wiegert (1981)
Florida	300	Warren (1985)
Alabama	145	West and Williams (1986)
Louisiana	24	Alexander (1979)
Texas	>100	Vaughn and Fisher (1988)

plants are resistant to most forms of herbivory, and (2) a relatively small percentage of energy in salt marshes is transferred through the grazing food web (Smalley 1959, 1959a, 1960, Kale 1964, Marples 1966). Recent investigations have challenged the first conclusion and shown that herbivores do graze on *S. alterniflora*, and that their grazing may significantly affect *S. alterniflora* growth and reproduction. For instance, grazing by feral horses (Turner 1987, Furbish and Albano 1994), snow geese (Smith and Odum 1983), nutria (Evans 1970, Taylor and Grace 1995), and sesarmid crabs (Jackewicz 1973, Kraueter and Wolf 1974, Pennings et al. 1998) may dramatically decrease *S. alterniflora* aboveground biomass. Grazing by high densities of insects can elicit similar effects on plant sexual reproduction and, at times, end-of-season standing crop (e.g., Bertness et al. 1987, Bertness and Shumway 1992, Daehler and Strong 1995, 1996).

These examples of herbivory demonstrate the potential for consumer regulation of plant growth. Nonetheless, the relative importance of these grazers as controls of *S. alterniflora* is diminished because, unlike bottom-up controls, their individual effects are limited spatially or temporally. Feral horses, nutria, and snow geese are present at only a small proportion of salt-marsh sites (Smith and Odum 1983, Turner 1987, Taylor and Grace 1995) and, while sesarmid crabs are present in most salt marshes, their densities rarely reach levels that impact *S. alterniflora* growth (Kraueter and Wolf 1974, Pomeroy and Wiegert 1981, Pennings et al. 1998). Moreover, intense herbivory by grasshoppers most often occurs during late summer and early fall when *S. alterniflora* has already completed the majority of its aboveground growth (Pomeroy and Wiegert 1981, Mitsch and Gosselink 1993). For an animal to be an important top-down determinant of *S. alterniflora* growth, it must control cordgrass production on both extensive spatial and temporal scales.

Along the mid-Atlantic, Southeast, and Gulf coasts of the United States, the saltmarsh periwinkle, *Littoraria irrorata* Say (synonym *Littorina irrorata* Say; see Reid 1989), is one of the most abundant and conspicuous invertebrates of salt marshes (Pomeroy and

Wiegert 1981, Daiber 1982). In areas dominated by short- and intermediate-form *S. alterniflora*, periwinkles routinely occur at densities >100 individuals/m<sup>2</sup> (Table 1). Periwinkles are permanent marsh residents and rarely move >5 m/yr (Hamilton 1978, Vaughn and Fisher 1992). During low tide, *L. irrorata* browse on organic matter on the marsh surface (both live and dead material) and, as the tide floods, ascend cordgrass stems and feed on standing-dead *S. alterniflora* and its associated microbial assemblages (Odum and Smalley 1959, Marples 1966, Alexander 1979, Newell and Barlocher 1993). Gut content and stable isotope analyses have shown that *L. irrorata* is a rasping detritivore specialist (Marples 1966, Alexander 1979, Kemp et al. 1990, Currin et al. 1995). However, in Maryland, Virginia, North Carolina, and Georgia salt marshes, we have observed *L. irrorata* grazing directly on live *S. alterniflora* tissue.

To examine the effect of snail grazing on *S. alterniflora* growth and how the magnitude of this effect varies with increased bottom-up influence, we manipulated both snail and nitrogen (N) levels in a four month field experiment (5 May 1997–5 September 1997) in a Virginia salt marsh. Based on our observations, we hypothesized that: (1) *L. irrorata* would exert top-down control on marsh grass growth, (2) N fertilization would enhance the growth of *S. alterniflora*, and (3) N enrichment would be more important than snail grazing in controlling marsh grass growth.

## METHODS

### Study site

Fieldwork was carried out at Hog Island, Virginia, a barrier island off the southeastern coast of the Delmarva Peninsula. This island is part of the Virginia Coast Reserve Long Term Ecological Research project. The primary site for this study is part of a narrow band of relatively old (>150 yr; Walsh 1998) salt marsh (Broadwater marsh) on the southern portion of the island. In the low marsh, the emergent plant community consists only of the cordgrass *S. alterniflora*. Within this monospecific stand, there are three distinct growth

forms: tall, intermediate, and short *S. alterniflora*. Tall-form *S. alterniflora* (typically >1.5 m tall) is confined to narrow areas (1–3 m in width) of high tidal flushing along the bay–marsh interface, and then gives way to extensive stands (10–30 m in width) of intermediate-form (~75–125 cm tall) and then short-form *S. alterniflora* (typically <50 cm tall), with increasing tidal elevation. Equally conspicuous in this marsh is the prosobranch gastropod, *L. irrorata*. Snails are most abundant in intermediate and short *S. alterniflora* stands where densities range from 13 to 102 snails/m<sup>2</sup> (B. R. Silliman, *personal observation*). Our experiment was carried out in the intermediate *S. alterniflora* zone, the area of observed maximum snail abundance (48 snails/m<sup>2</sup>).

#### *Experimental design and setup*

A 2 × 3 factorial design with two levels of nitrogen (ambient and fertilized) and three levels of grazer density (zero, ambient, and 3 × ambient) was used. We referred to the six treatments as: (1) snail removal, (2) control snails, (3) snail addition, (4) snail removal + N, (5) control snails + N, and (6) snail addition + N. Treatments consisted of replicated ( $n = 3$ ) 1-m<sup>2</sup> roofless cages constructed of 30" (76.20 cm) high wire screening (12.7-mm mesh galvanized hardware cloth). Galvanized hardware cloth was used as caging material because it provides both a physical and chemical barrier (i.e., the zinc coating deters contact) to snail migration (Bertness 1984b). Two extra cages for each treatment were constructed for destructive sampling purposes. Three uncaged controls were also monitored to examine potential caging artifacts. All plots were established at identical elevations. Cages extended 5 cm into the substrate to prevent snail migration in and out of the cages and to exclude predators, and belowground connections between plants were severed to a 40 cm depth along the outside perimeter of each cage to prevent resource sharing between experimental and non-experimental plants. A wooden boardwalk made of untreated pine was constructed for access to plots to minimize the impact of sediment compaction.

#### *Animal densities*

Mean snail density in the zone of intermediate-form *S. alterniflora* (~900 m<sup>2</sup> area) was determined at the beginning and end of the experiment by counting all snails in 75 haphazardly thrown, 1-m<sup>2</sup> quadrats. On 5 May, all snails were removed from the enclosures. Snails were reintroduced to the control snails and snail addition treatments according to pre-assigned grazer levels. Density in control treatments was maintained at the naturally occurring density (48 snails/m<sup>2</sup>) and in snail addition treatments at three times that amount (144 snails/m<sup>2</sup>). These densities lie well within the natural range of periwinkle densities found on Hog Island and other Atlantic Coast salt marshes (Table 1).

Snail density in the cages was monitored weekly,

and any variation in snail abundance from assigned level was immediately corrected. To account for variation in snail size between treatments, the mean shell height of 45 randomly chosen snails from control snails and snail addition treatments and uncaged controls was calculated every two weeks.

Because cordgrass growth is enhanced by the mud fiddler, *Uca pugnax*, and the ribbed mussel, *Geukensia demissa* (Bertness 1984a, 1985), crab and mussel densities within each plot were monitored once every two weeks. Cages prevented the purple marsh crab, *Sesarma reticulatum*, a consumer of live *S. alterniflora* (Jackewicz 1973, Kraueter and Wolf 1974), from moving into experimental pens. No *S. reticulatum* burrows were found in caged areas.

#### *Nitrogen enrichment*

Nitrogen is commonly the limiting nutrient for *S. alterniflora* growth (e.g., Sullivan and Daiber 1974, Valiela and Teal 1974, Mendelssohn 1979). Ammonium chloride was used as the N fertilizer and was added to the sediments in 15-mL plastic centrifuge tubes with 16 holes (hole diameter 0.16 cm) drilled in the sides (Williams and Ruckelshaus 1993). Each tube contained 3.4 g of NH<sub>4</sub>Cl wrapped in nylon mesh to promote slow release. On 5 May, 5 June, and 5 July 1997, each N enrichment plot was fertilized by placing 16 tubes in the marsh substrate at evenly spaced intervals. Ammonium-free tubes were placed in unfertilized plots as disturbance controls. In total, enough NH<sub>4</sub>Cl (163.2 g NH<sub>4</sub>Cl = 42.6 g N) was added in each plot to theoretically double ambient cordgrass production (projected from Mendelssohn 1979: Table 1; 1996 *S. alterniflora* aboveground production at this site = 425 g dry mass·m<sup>-2</sup>·yr<sup>-1</sup>).

#### *Plant growth and structure of stems*

Aboveground growth of *S. alterniflora* was measured monthly using the method of Morris and Haskin (1990). The census involved tagging all stems within a centered 25-cm<sup>2</sup> productivity plot with numbered bird bands and measuring the height of tagged stems every ~30 d. Change in biomass over the growing season was calculated from height measurements using regression plots of stem height vs. stem biomass. To account for varying stem allometric relationships among treatments, treatment-specific regression models were constructed once every two months. This was done by generating allometric models with stems collected from within the destructive sampling cages. Aboveground growth of *S. alterniflora* is reported as net production (g dry mass·m<sup>-2</sup>·[4 mo]<sup>-1</sup>), mean daily productivity for each month (g dry mass·m<sup>-2</sup>·d<sup>-1</sup>), and standing crop at the end of the experiment (g dry mass/m<sup>2</sup>). End-of-experiment stem density and height of standing-dead stems were also measured.

To document snail grazing on live cordgrass, the pattern of periwinkle grazing on 45 stems from each

treatment was recorded during the first week in September. Number of dead leaves and total length of snail-induced wounds (hereafter referred to as "radulations") on live tissue were documented for the first 15 stems which came in contact with a 30 cm long, 1.27 cm diameter PVC pipe, haphazardly placed on the marsh surface in each replicate. In addition, 30 randomly chosen radulations of varying sizes (mean length =  $7.6 \pm 2.3$  cm), and 30 uninjured green leaves, were examined microscopically (100 $\times$ ) to quantify fungal infections using a modified method of Jones and Mollison (1948). Wounds and control areas on green leaves were covered with clear tape and then mounted in lacto phenol cotton blue on a microscope slide. The number of hyphae per visual field ( $n = 10$  per radulation) were then enumerated (Jones and Mollison 1948).

To assess treatment effects on plant tissue N levels, aboveground *S. alterniflora* tissue was collected every two months as whole-plant specimens (5 May, 5 July, and 5 September). On each sampling, three stems were harvested from a different corner of each experimental cage and pooled as one sample for that replicate. Because the number of stems harvested was <1% of original stem density, we assumed that removal of these samples was similar among treatments and would not affect the results of the study. Samples were prepared and analyzed for N content using the protocol of Os-good and Zieman (1993). N concentration in above-ground plant material is reported on a per stem (% N) and per m<sup>2</sup> basis (total N in aboveground tissue = stem N concentration-standing crop).

#### *Consumption rates and gut contents*

Field observations indicated that periwinkles do not graze live plant material as a typical herbivore, consuming green tissue directly. Instead, snails seem to concentrate their radular activity on grazer-induced wounds on live *S. alterniflora* leaves and consume primarily associated senescing and dead tissue along with infectious fungi. Based on these observations, we hypothesized that snail consumption of green plant tissue alone would likely not account for observed differences in plant biomass between grazed and ungrazed treatments. In an attempt to test this hypothesis, no-choice grazing experiments were completed in the lab to estimate a potential maximum rate at which periwinkles can consume uninjured, green cordgrass. Grazer treatments consisted of four *L. irrorata* (shell height >15 mm) starved for 48 h, presented with 200 mg of blotted dry, green *S. alterniflora* in two sections of horizontally cut leaf. Control treatments were identical, but without snails. Plant samples were taken from the field <1 h of the beginning of the experiment and rinsed thoroughly with seawater to remove any debris. Treatments were replicated 15 times in 60-mL jars, capped with 2-mm window screening. Each jar was sprayed two times each day with fresh seawater to simulate the twice daily wetting of *S. alterniflora* by diurnal tides in the

field. After 2 d, the grass was blotted dry and weighed. Consumption rates were assessed by subtracting the mean change in the mass of grass strips in grazer treatments from that in control treatments. Microscopic examination (100 $\times$ ) of plant tissue at both the beginning and end of the experiment suggested that leaf sections were free of fungi. Although some fungal infection may have occurred, we assumed the amount was not significant given that: (1) plant samples were fresh and rinsed before the feeding trial and (2) the short duration of the experiment.

To test whether or not snails consumed live cordgrass tissue during the four-month field experiment, a quantitative assessment of the field diet of *L. irrorata* was completed in August by randomly collecting 15 snails from each grazer treatment and examining their gut contents microscopically. Harvested snails were immediately put in 10% buffered formalin solution and microscopically analyzed (100 $\times$ ) for gut contents within 2 h. Both the number of snails with green plant material in their stomachs and the relative abundance (percentage of contents) of material (e.g., live plant material, detritus, diatoms, etc.) present were recorded (Alexander 1979).

#### *Substrate chemistry*

To quantify treatment effects on substrate chemistry, porewater nutrient pools, redox potential, salinity, and temperature were measured each month. Porewater samples were taken 10 d after each fertilization event and again on 15 August and 5 September. Samples were collected from a suction lysimeter using the method of Chambers and Odum (1990). Each lysimeter was installed 12.5 cm outside the productivity plot, in the middle of a juxtaposed square of fertilizer tubes at 10 cm depth. Porewater redox potential, pH, temperature, and salinity were determined using the protocol of Tyler and Zieman (1999). Dissolved ammonium was determined in the lab using the indophenol colorimetric method (Parsons et al. 1984) and sulfide using the method of Cline (1969) as modified by Otte and Morris (1994).

#### *Assessing the prevalence of periwinkle grazing*

Snail grazing data were collected from six sites in Virginia (two on Hog Island, two on Cobb Island, one on Racoon Island, and one on Parramore Island) two sites in Maryland (Assateague Island), two sites in North Carolina (Atlantic City and Tarlanding Marsh), and two sites in Georgia (Sapelo and Tybee Island) in an attempt to generalize the results of this experiment. At each site in either August 1997 or August 1998, ten 1-m<sup>2</sup> quadrats were haphazardly thrown in intermediate-form *S. alterniflora*, and periwinkle density, and the total length radulations on 15 randomly selected plants was recorded. A linear regression plot was then generated, using snail density to predict mean total length of radulations per stem.

### Statistical analysis

In most cases, more than one value for a single response variable was recorded for each cage (e.g., for total length of radulations/stem,  $n = 15$  stems/cage). Therefore, we used the mean of multiple values for each measured variable as a single datum per cage for statistical analyses. Each cage was considered as one replicate, and for all measured variables in the field experiment,  $n = 3$ . Only three replicates were used because an a priori power analysis performed on a similarly designed, three-month pilot study revealed power to be  $>0.9$ . Treatment differences in response variables measured at the end of the experiment were assessed using two-way Analysis of Variance (ANOVA) followed by Tukey's post-hoc test. In all cases, the degrees of freedom for the main effects of Nitrogen level, Grazer level, and for Nitrogen  $\times$  Grazer interaction were 1, 2, and 2 respectively. Data used for two-way ANOVAs either exhibited homogeneity of variance and were normally distributed or were transformed using log transformations for analysis. Data on variables measured monthly or every two months were assessed with repeated-measures ANOVA using dates as repeated measurements. Nitrogen and grazer level were tested against the interaction of nitrogen and grazer level using the Wilks' Lambda test. Because all repeated-measures ANOVAs revealed significant time  $\times$  nitrogen  $\times$  grazer interactions and because we were only interested in treatment effects within and not between dates, differences among treatments for each sampling date were analyzed using two-way ANOVA followed by Tukey's post-hoc test. We did not adjust the experimentwise error rate since we were interested in individual comparisons among treatments (as stated in a priori hypotheses), and not the family of comparisons in the entire experiment (Carmer and Walker 1982, Soto and Hulbert 1991, Williams and Ruckelshaus 1993). Although all Tukey tests were conducted on the means of response variables and refer to the presence or absence of a significant difference, variation in the mean of response variables between treatments are described as percentage differences to convey more clearly trends in the data.

### RESULTS

#### *Initial conditions, confounding factors, and snail densities*

Initial conditions of *S. alterniflora* mean stem biomass, height, density, and percent N were not significantly different among treatments ( $P > 0.46$ , two-way ANOVA, all cases). There were no significant differences in the concentrations of any of the pre-identified, potentially confounding factors (i.e., fiddler crab and ribbed mussel density, porewater redox potential, pH, salinity, temperature, and  $S^{2-}$  concentrations) among treatments ( $P > 0.30$ , two-way ANOVA, all cases). Over the duration of the experiment, no differences

were detected in the mean shell height of *L. irrorata* among treatments with snails ( $P > 0.55$ , two-way ANOVA, all cases; mean shell height for all treatments =  $20.13 \pm 0.45$  mm). Mean *L. irrorata* density in the intermediate-form *S. alterniflora* zone at the beginning ( $47.6 \pm 2.29$  snails/m<sup>2</sup>) and end of the experiment ( $50.2 \pm 3.31$  snails/m<sup>2</sup>) did not differ significantly ( $P > 0.15$ ,  $t$  test). The mean weekly deviation in snail density in control snails and snail addition treatments never exceeded the assigned level by more than 10%. On average, only three snails per week were removed from snail exclusion treatments. There was no statistical difference in mean *S. alterniflora* aboveground net primary production (ANPP) or *L. irrorata* density between uncaged and caged controls ( $P > 0.40$ ,  $t$  test, both cases).

#### *Process of periwinkle grazing on live S. alterniflora*

Periwinkle grazing on live *S. alterniflora* began in early season as evidenced by the appearance of small wounds ( $<1$  cm in length and  $<2$  mm in width) on the outermost green leaves. Snails continued to graze these lesions (see Fig. 1) and, within a few weeks of their appearance, the lesions visually appeared infected, most likely the result of attack by opportunistic fungi whose spores are nearly ubiquitous on the surface of *S. alterniflora* (Newell and Porter 2000). The inner edge of each radulation was a distinctive light brown and noticeably shredded, while the 1–3 mm tissue border had senesced, changing from green to yellow–brown in color. By the end of the season, the mean radulation length was  $\sim 3$  cm, although radulations  $\leq 10$  cm long were not uncommon (see Fig. 1). Microscopic examination of radulations revealed infestation by fungi ( $>40$  stained hyphae per visual field,  $100\times$ ) compared to nonwounded, green leaves ( $<5$  stained hyphae per visual field,  $100\times$ ). Although fungi were not identified, it is likely that a substantial portion of fungi present were the ascomycete *Phaeosphaeria spartanicola*, since microbial colonization of naturally senescing *S. alterniflora* is dominated by this species (Newell et al. 1986, 1989).

Gut content analysis showed that periwinkles ingested live *S. alterniflora*, as 29% of the snails collected from the field had green cordgrass material in their stomachs. However, neither fertilization nor snail density significantly affected the likelihood of snails having green plant material in their gut ( $P > 0.45$ , two-way ANOVA, both cases). Approximately 95% of snail gut contents were dead vascular plant material and clay, while live plant material composed less than 2% of gut contents. These results are consistent with Alexander's (1979) study in a Louisiana marsh which showed that green plant material composed only 3% of the gut contents of  $>250$  snails.

#### *Effects of periwinkle grazing and N enrichment on S. alterniflora growth*

The one-time survey of radulation abundance on live cordgrass leaves revealed that snail feeding activities



FIG. 1. *L. irrorata* grazing a radulation on a green *S. alterniflora* leaf during flood tide. Note that tissue immediately surrounding radulations is yellow-brown in coloration, indicating senescence and probable infection by parasitic microbes.

resulted in substantial scarring of live plant tissue, and that the intensity of snail grazing was significantly greater in fertilized areas (Fig. 2a). In both control snails and snail addition treatments, the total length of radulations per cordgrass stem nearly doubled with the added treatment of N ( $P < 0.01$ , Tukey test, both cases).

Coincident with the occurrence of grazer-induced wounds on live *S. alterniflora* was a dramatic decrease in aboveground growth (Fig. 2b). The magnitude of this top-down effect, like snail grazing intensity, was dependent on N level, as *L. irrorata* exhibited relatively more control of *S. alterniflora* growth in fertilized plots (Fig. 2b). In unfertilized treatments, snail removal increased aboveground net primary production (ANPP) by 38% relative to controls ( $P < 0.04$ , Tukey test), whereas in nitrogen addition plots, snail removal increased production by 78% ( $P < 0.001$ , Tukey test). Likewise, snail additions to unfertilized stands of *S. alterniflora* decreased aboveground growth by 51% relative to controls, while in fertilized stands, snail additions led to even greater reductions (66%;  $P < 0.01$ , Tukey test, both cases).

Experimental enrichment of belowground ammonium concentrations had a striking effect on *S. alterniflora* aboveground growth, which was dependent on grazer level (Fig. 2b). In snail removal treatments, N fertilization increased ANPP by 443%, while in control snails and snail addition treatments, N enrichment increased ANPP by 322% and 189%, respectively ( $P < 0.001$ , Tukey test, all cases).

The effects of grazer density on the daily rate of plant biomass accrual depended on both nitrogen level and time and were most pronounced in midseason (Fig. 3a and Table 2). In August, snail removal in unfertilized plots increased *S. alterniflora* productivity by 17% relative to controls, although the effect was not significant ( $P = 0.13$ , Tukey test). In fertilized treatments, however, the effect was significant, as productivity increased by 39% when snails were removed ( $P < 0.001$  Tukey test). Similarly, snail addition to unfertilized cordgrass stands decreased productivity by 38% relative to controls, while in fertilized stands, the same additions led to even larger reductions (45%;  $P < 0.001$  Tukey test, both cases).

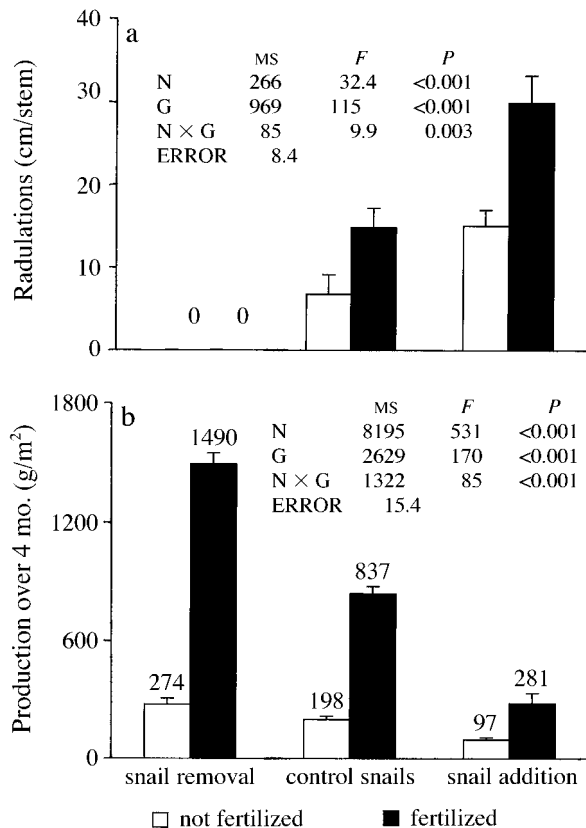


FIG. 2. Interactive and separate effects of periwinkle density and nitrogen fertilization on (a) the total length of grazer-induced wounds per stem and (b) aboveground *S. alterniflora* production. Probability values given for two-way ANOVAs testing for main and interactive effects. N = main effect of nitrogen fertilization, and G = main effect of grazing. Error bars represent +1 SE ( $n = 3$ ).

Within the first month of the study, N enrichment significantly enhanced *S. alterniflora* productivity and continued to do so until the end of the experiment (Fig. 3a and Table 2). By August, the effect of N fertilization on cordgrass growth depended on grazer level (Fig. 3a and Table 2). In snail removal treatments, N fertilization increased productivity by 387%, while in control snails and snail addition treatments, N enrichment increased the daily rate of biomass accrual by 198% and 281%, respectively ( $P < 0.001$ , Tukey test, all cases).

There was a significant effect of grazer level on mean stem density, which did not depend on N level (Fig. 4a). On average, snail removal increased stem density (28%) relative to controls ( $P < 0.05$ , Tukey test), while snail addition resulted in a significant decrease (31%;  $P < 0.001$ , Tukey test). N effects on stem density were also strong and did not depend on grazer level (Fig. 4a). By the end of the experiment in September, mean stem density was, on average, 31% greater in fertilized stands of *S. alterniflora* ( $P < 0.001$ , Tukey test).

Another outcome of *L. irrorata* grazing was to increase the abundance of its preferred food source (Bar-

locher and Newell 1994), standing-dead *S. alterniflora* (Fig. 4b). Snail grazing at ambient densities increased the mean total length of standing-dead stems/m<sup>2</sup> by 94% relative to snail removal treatments, while at enhanced densities, there was an even greater effect, as the total length of standing-dead stems increased by 245% ( $P < 0.002$ , Tukey test, both cases). This pattern coincided with the decline in mean stem density in the same treatments, indicating that *L. irrorata* did not immediately consume all the plant material killed through its grazing activities. There was no effect of N fertilization on the total length of standing-dead stems/m<sup>2</sup> (Fig. 4b).

Both mean stem biomass and height were differentially affected by grazer density in fertilized and unfertilized treatments (Table 3). For example, in unfertilized treatments, snail addition decreased mean stem biomass by 36% relative to controls, whereas in nitrogen addition plots, snail addition led to even greater reductions (48%;  $P < 0.001$ , Tukey test, all cases). The effect of grazer level on mean number of dead leaves was also significant, but did not depend on N level (Table 3). In comparison to snail removal, snail addition, on average, nearly doubled the mean number of dead leaves/stem ( $P < 0.001$ , Tukey test).

N fertilization differentially affected both mean stem biomass and height depending on grazer level (Table 3). For example, in snail removal treatments, N fertilization increased mean stem biomass by 230%, while in control snails and snail addition treatments, N enrichment increased mean stem biomass by 190% and 142%, respectively ( $P < 0.001$ , Tukey test, all cases).

Although N enrichment did not affect the number of dead leaves/stem, it had a strong effect on stem N content (Table 3). By the end of the experiment, stems in fertilized areas were, on average, 50% higher in N concentration ( $P < 0.001$ , Tukey test).

Grazer density differentially affected total N in aboveground plant tissue depending on N level and time (Fig. 3b and Table 2). In unfertilized treatments, there was no effect of grazer density ( $P > 0.49$ , Tukey test, both cases). In fertilized treatments, however, snail grazing at ambient densities reduced total aboveground N/m<sup>2</sup> by 38% in September relative to snail removal treatments ( $P < 0.001$ , Tukey test), while at enhanced densities, this effect was even more dramatic, as periwinkle grazing reduced total aboveground N by 79% (measured as N/m<sup>2</sup>;  $P < 0.001$ , Tukey test). These differences in aboveground N were due overwhelmingly to large disparities in standing crop (Table 3).

The effect of grazer density on porewater ammonium concentrations also depended on N level and time (Fig. 3c and Table 2). In unfertilized treatments, there was no effect of grazer density ( $P > 0.41$ , Tukey test). In fertilized treatments, however, porewater ammonium levels in control snail and snail addition treatments were elevated by an order of magnitude in August and September, in contrast to all other treatments ( $P < 0.05$ ,

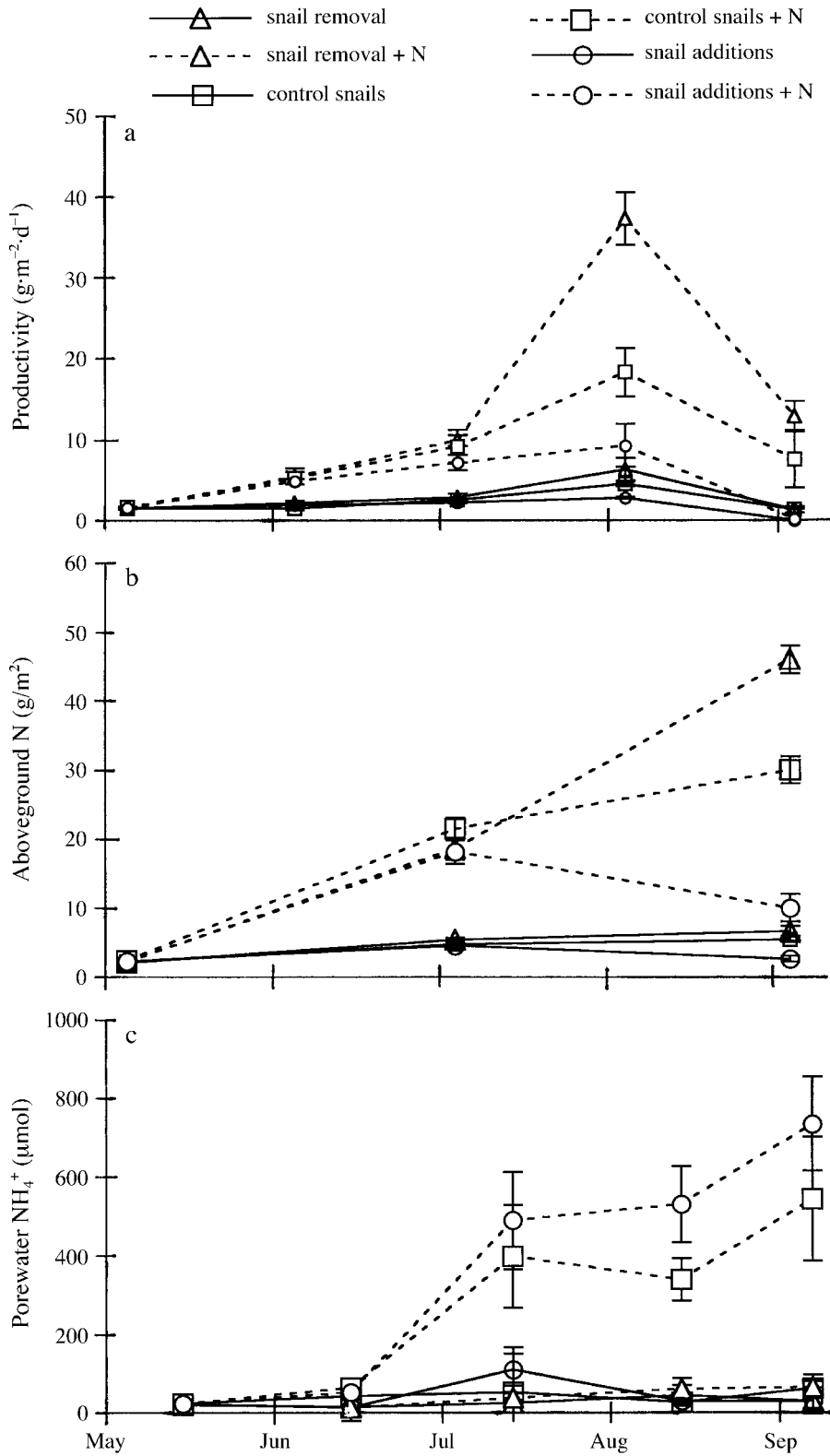


FIG. 3. Interactive and separate effects of periwinkle density and nitrogen fertilization on (a) *S. alterniflora* aboveground productivity, (b) total nitrogen in aboveground *S. alterniflora* tissue, and (c) the concentration of ammonium in the marsh porewater at a depth of 10 cm. Error bars represent  $\pm 1$  SE ( $n = 3$ ).

TABLE 2. Results of repeated-measures ANOVA for cordgrass productivity, total aboveground nitrogen in plant material, and the concentration of ammonium in the marsh porewater.

Variable	Sources	df	MS	F	P
Productivity					
Between subjects	Nitrogen	1	1 019.6	237.2	<0.0001
	Grazer	2	170.8	39.8	<0.0001
	Nitrogen $\times$ Grazer	2	102.5	23.9	<0.0001
	Error		4.3		
Within subjects	Date	4	369.9	78.5	<0.0001
	Date $\times$ Nitrogen	4	206.4	65.9	<0.0001
	Date $\times$ Grazer	8	64.7	8.6	<0.0001
	Date $\times$ Nitrogen $\times$ Grazer	8	38.5	7.1	0.0003
	Error	48	5.5		
Total N					
Between subjects	Nitrogen	1	2 324.3	342.2	<0.0001
	Grazer	2	251.4	37.2	<0.0001
	Nitrogen $\times$ Grazer	2	153.9	22.8	<0.0001
	Error	12	6.8		
Within subjects	Date	2	1 003.7	382.3	<0.0001
	Date $\times$ Nitrogen	2	705.4	274.2	<0.0001
	Date $\times$ Grazer	4	225.5	25.4	<0.0001
	Date $\times$ Nitrogen $\times$ Grazer	4	158.4	20.6	<0.0001
	Error	24	4.3		
Ammonium					
Between subjects	Nitrogen	1	540 000	99.8	<0.0001
	Grazer	2	110 000	20.7	<0.0001
	Nitrogen $\times$ Grazer	2	91 820	16.8	0.0003
	Error	12	5 444.7		
Within subjects	Date	4	190 000	29.8	<0.0001
	Date $\times$ Nitrogen	4	170 000	25.3	<0.0001
	Date $\times$ Grazer	8	2 912.8	3.1	0.0211
	Date $\times$ Nitrogen $\times$ Grazer	8	31 178.5	4.3	0.0048
	Error	48	3 144.3		

Notes: Date represents the effects of different dates on which we sampled, Grazer represents the effects of snail density, and Nitrogen represents the effects of fertilization. The effects are computed either as between subjects or within subjects.

Tukey test, all cases). The timing of this extreme porewater ammonium elevation corresponded to large reductions in plant productivity and total aboveground N (per m<sup>2</sup>) in the same treatments (Fig. 3a and b).

Lab experiments testing snail grazing rates indicated that one snail can consume  $\leq 0.4$  mg of live *S. alterniflora* per day ( $P < 0.04$ ,  $t$  test,  $n = 15$ ). Based on these grazing rates, *L. irrorata* could have consumed 2.3 g/m<sup>2</sup> of green *S. alterniflora* at ambient densities and 6.9 g/m<sup>2</sup> at high densities over the length of the study. These consumption rates account for <3% of the difference in ANPP between treatments with no snails, and treatments with either ambient or high densities.

#### How prevalent is periwinkle grazing?

An examination of the relationship of snail density and mean total length of radulations per stem in 10 East Coast marshes revealed that snail density alone predicted 89% of the observed plant damage ( $P < 0.001$ ,  $r^2 = 0.8966$ ; see Fig. 5). This regression predicts

that for every 50 snails/m<sup>2</sup> the total length of radulations per stem will increase by  $\sim 5$  cm, which indicates that grazing by *L. irrorata* on live *S. alterniflora* is a density-dependent interaction. In addition, these data show that: (1) signs of periwinkle grazing on live cordgrass can be absent at low snail densities (<25 snails/m<sup>2</sup>), (2) periwinkle grazing is widespread in mid-Atlantic and Southeast salt marshes, and (3) grazing intensities comparable to and much higher than those in snail addition treatments occur naturally in many other marshes.

## DISCUSSION

### Top-down control of marsh grass growth

Manipulation of periwinkle densities supports our hypothesis that *L. irrorata* can exert top-down control of *S. alterniflora* growth. In both fertilized and unfertilized treatments, snails drastically reduced *S. alterniflora* aboveground production. By the end of the experiment, the marsh canopy in snail addition treatments

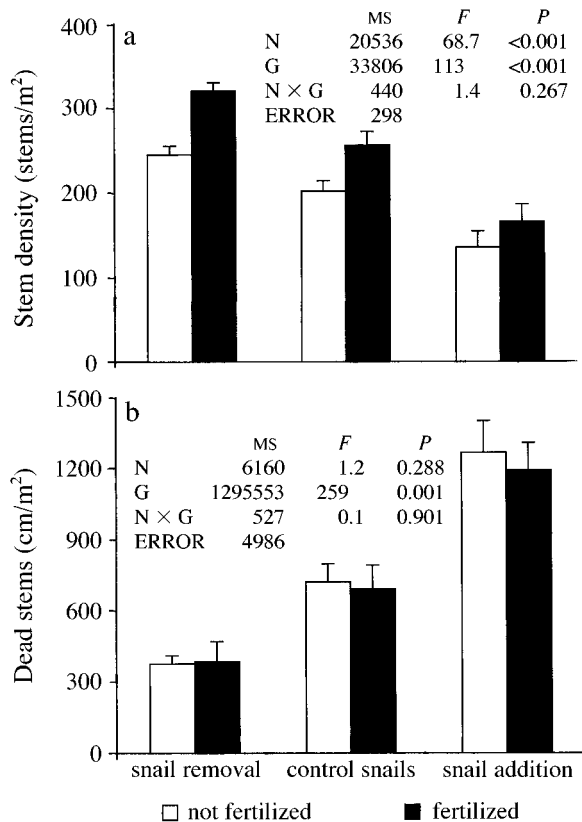


FIG. 4. Interactive and separate effects of periwinkle density and nitrogen fertilization on end-of-experiment *S. alterniflora* (a) stem density and (b) total length of standing dead stems. Probability values are given for two-way ANOVAs testing for main and interactive effects at each sampling date. N = main effect of nitrogen fertilization, and G = main effect of grazing. Error bars represent +1 SE ( $n = 3$ ).

was almost completely destroyed (e.g., see Fig. 6), and, on average, standing crop was reduced by nearly 85% in comparison to ungrazed treatments (Table 3). This dramatic reduction in *S. alterniflora* aboveground growth was due primarily to decreased stem biomass, stem height, and stem density (Table 3).

Taylor and Bardner (1968) investigated the effects of leaf grazing by beetle larvae on the yields of turnips (*Brassica rupa*) and radishes (*Raphanus sativus*), and found that the rasping of leaf veins by beetle larvae resulted in the death of much more leaf tissue than was consumed and, ultimately, drastic reductions in plant growth. Similarly, our findings suggest that the formation and maintenance of wounds on live *S. alterniflora* leaves by the rasping activities of snails results in the death of much more biomass (i.e., stems and leaves) than is consumed and, subsequently, suppression of plant growth. This mechanism of top-down control (i.e., defoliation) indicates that periwinkle grazing expedites the conversion of live plant material to detritus, a phenomenon we have noticed outside the experimental treatments. In two marshes on Hog Island,

where snail densities are routinely  $>200$  snails/m<sup>2</sup>, we have observed large areas of intermediate- and short-form *S. alterniflora* ( $>30$  m<sup>2</sup>) that were almost completely defoliated in mid-August, usually the time of maximum productivity for *S. alterniflora* in Virginia marshes (see Fig. 3a). Stems were riddled with radulations and  $>70\%$  of aboveground cordgrass was in the form of standing-dead material (B. R. Silliman, unpublished data). Comparatively, grasses in the lower portion of the marshes, where snails were absent, were robust, green, healthy, and devoid of radulations. Although we did not examine specifically the fate of defoliated plant tissue at these sites or in this experiment, it is highly probable that *L. irrorata* ingested a substantial portion of killed biomass given that fungal-occupied standing-dead cordgrass is the preferred food of *L. irrorata* (Barlocher and Newell 1994) and that periwinkles can consume  $\leq 37\%$  of ANPP, primarily in the form of standing-dead material (Kemp et al. 1990). Probable mechanisms of cordgrass defoliation include plant resource withdrawal from grazed areas (i.e., leaves and stems with radulations), as has been shown in numerous other studies (Smith 1996 and references therein), and tissue death due to microbial infection, a possibility suggested by our results indicating increased fungal density on grazer-induced wounds.

The effects of snail grazing on *S. alterniflora* growth documented in this study are among the strongest marsh grazer effects in the literature in terms of both standing crop and ANPP reduction; they rival and, in some cases, exceed those of both feral horses (Turner 1987, Furbish and Albano 1994) and snow geese (Smith and Odum 1983: geese consumed rhizomes and live plant material, not fungal-rich tissue). Moreover, our grazer survey suggests that periwinkle grazing on live *S. alterniflora* is widespread along the mid-Atlantic and Southeast coasts, and that grazing intensities comparable to those in our snail addition treatments are found in other salt marshes (Fig. 5). These findings suggest that the strong top-down control of *S. alterniflora* growth exhibited by saltmarsh periwinkles in this study occurs on a regional spatial scale. In addition, given the fact that radulations were present on live cordgrass leaves throughout the growing season, and that snails controlled both standing crop (Table 3) and ANPP (Fig. 2b), periwinkle grazing effects on live *S. alterniflora* likely occur throughout the growing season. Therefore, top-down control of *S. alterniflora* growth by *L. irrorata* has the potential to be extensive on both spatial and temporal scales.

#### Process of periwinkle grazing

Based on our results, there are two important inferences that can be made about *L. irrorata* mode of feeding on live cordgrass: (1) snails may facilitate microbial infection of live plant tissue and (2) snails graze live *S. alterniflora* even when standing-dead material is available for consumption.

TABLE 3. (A) Effects of periwinkle grazing and nitrogen fertilization on end-of-experiment *S. alterniflora* stem structure and standing crop and (B) ANOVA results.

A) Means					
Grazer level	Dependent variable				
	Stem biomass (g)	Stem height (cm)	No. of dead leaves/stem	Stem N concentrations (%)	Standing crop (g/m <sup>2</sup> )
Not fertilized					
Zero	1.3 <sup>a</sup> (0.11)	56.8 <sup>a</sup> (4.26)	2.1 <sup>a</sup> (0.26)	2.31 <sup>a</sup> (0.03)	231 <sup>d</sup> (28.4)
Control	1.1 <sup>b</sup> (0.19)	55.2 <sup>a</sup> (1.89)	2.9 <sup>b</sup> (0.24)	2.31 <sup>a</sup> (0.05)	155 <sup>b</sup> (14.8)
High	0.7 <sup>c</sup> (0.08)	52.2 <sup>a</sup> (3.05)	4.0 <sup>c</sup> (0.31)	2.35 <sup>a</sup> (0.31)	51 <sup>c</sup> (15.8)
Fertilized					
Zero	4.3 <sup>d</sup> (0.31)	96.1 <sup>b</sup> (1.32)	1.9 <sup>a</sup> (0.18)	3.44 <sup>b</sup> (0.18)	1340 <sup>a</sup> (62.4)
Control	3.2 <sup>e</sup> (0.14)	85.1 <sup>c</sup> (1.43)	2.8 <sup>b</sup> (0.23)	3.50 <sup>b</sup> (0.23)	726 <sup>e</sup> (37.7)
High	1.7 <sup>f</sup> (0.14)	75.4 <sup>d</sup> (2.54)	3.7 <sup>c</sup> (0.33)	3.51 <sup>b</sup> (0.33)	147 <sup>f</sup> (36.2)
B) ANOVA					
Source	Stem biomass	Stem height	No. of dead leaves/stem	Stem N concentration	Standing crop
Nitrogen (N)	***	***	NS	***	***
Grazer level (G)	**	**	***	NS	**
N × G	*	*	NS	NS	*

Notes: Data in (A) are means, with 1 SE in parentheses ( $n = 3$ ). Different superscript letters within a column represent significant differences ( $P < 0.05$ ).

\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ; NS, not significant ( $P > 0.05$ ).

Gut content analysis and feeding assays, strongly suggest that snails do not consume large amounts of green tissue when grazing on live *S. alterniflora*. Instead, snails create and maintain wounds on live cordgrass leaves and graze the senescing portion of those wounds. Based on observations that fungal hyphae are more abundant on radulations than on green plant tissue, we hypothesize that *L. irrorata*, through its grazing

activities, promotes microbial growth on live cordgrass, which it then utilizes as a food source. This scenario would reconcile the apparent contradiction between our observations that *L. irrorata* graze extensively on live *S. alterniflora* and other investigations which have shown that the preferred food of *L. irrorata* is fungal-occupied, dead cordgrass (Barlocher and Newell 1994) or that *L. irrorata* is a detritivore (Al-

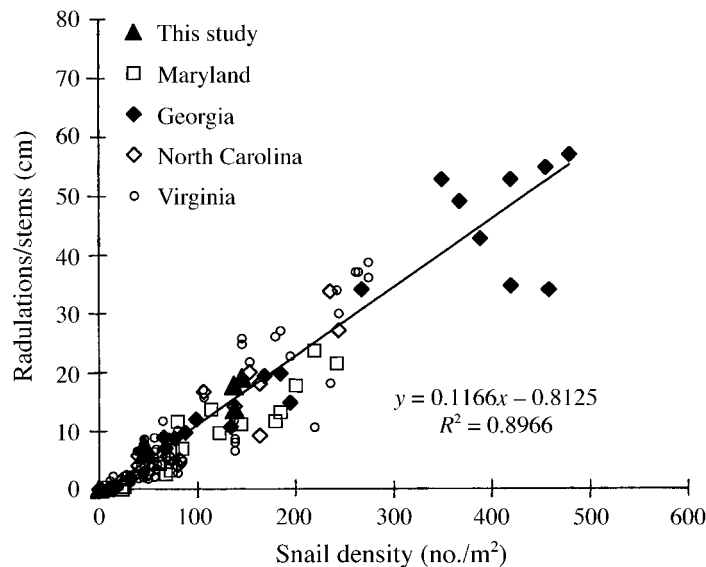


FIG. 5. Least-squares linear relationship of *L. irrorata* density and mean total length of radulations per stem in the zones of intermediate-form and short-form *S. alterniflora* for six marshes within the Virginia Coast Reserve (two in North Carolina, two in Maryland, two in Georgia) and for this experiment (overall  $n = 116$ ).



FIG. 6. The effect of periwinkle grazing on *S. alterniflora* standing crop and canopy structure in unfertilized plots at the end of the experiment: (a) snail removal plot and (b) snail addition plot. Visual inspection of snail addition treatments clearly gives the impression of runaway grazer effects. Standing-dead stems devoid of leaves were commonplace, multiple leaves on surviving stems were shredded to threads, and the marsh substrate was easily visible due to reduced stem density and health of surviving stems.

alexander 1979, Stiven and Kuenzler 1979, Currin et al. 1995). The possibility that *L. irrorata* promotes fungal growth through feeding activities is further suggested by: (1) other gastropods capabilities for microbial gardening (Conner and Quinn 1984), (2) an abundant supply of microbial propagules in low marsh habitats (i.e., fungi spores are nearly ubiquitous on live *S. alterniflora*, Newell and Porter 2000), and (3) a pattern showing that fungi which typically invade *S. alterniflora* tissue do so only after leaves have naturally senesced or when they have been abraded by a physical or biological disturbance (Newell et al. 1989).

Our work also suggests that periwinkles apportion at least some of their foraging time to grazing on live plant tissue, even when dead material is available for consumption. Standing-dead material was available in all treatments throughout the experiment (B. R. Silliman, unpublished data). The fact that *L. irrorata* still grazed on live cordgrass, given that its preferred food

source was also available, suggests that (1) snails prefer wound grazing over grazing on dead grass (possibly because nutritional quality could be higher on these lesions), (2) *L. irrorata* receive nutritional benefit from ingesting live plant tissue (i.e., micro-nutrient acquisition), or (3) there was insufficient standing-dead material to ensure that snails would always have a choice between dead and live tissue. The behavior of periwinkles grazing on live tissue even though standing-dead is present has also been observed in Louisiana (Alexander 1979). In Maryland, North Carolina, and Georgia marshes (this study), radulations on live cordgrass were common, even though standing-dead cordgrass was visibly abundant (B. R. Silliman, personal observation). The effect of variability in standing-dead plant material on the intensity of periwinkle grazing on live *S. alterniflora* remains to be investigated.

#### Effects of N enrichment

The observed effect of N enrichment on *S. alterniflora* ANPP supports our initial hypothesis that N fertilization would greatly increase cordgrass growth. Patterns of *S. alterniflora* yield and tissue response to N fertilization in this study are consistent with those reported in many other studies (e.g., Sullivan and Daiber 1974, Gallagher 1975, Chalmers 1979, Mendelssohn 1979, Dai and Wiegert 1997).

#### Top-down vs. bottom-up control

We did not reject or accept the initial hypothesis that N enrichment would be relatively more important than snail grazing in controlling *S. alterniflora* growth in the Broadwater marsh. Both N availability and snail grazing alone exerted strong control of *S. alterniflora* growth (Fig. 2b). In addition, neither bottom-up nor top-down influences were eliminated in treatments where both factors were present. N fertilization effects on plant growth were marked under all grazer densities indicating that the system is highly regulated by N availability both in the presence and absence of periwinkles, and snail grazing effects were strong under both fertilized and unfertilized conditions indicating that the marsh system is simultaneously under strong top-down control by periwinkle grazing.

Although the effects of fertilization were an order of magnitude higher than grazer effects, we did not conclude that N availability was relatively more important because: (1) the effects of periwinkle grazing were marked under both fertilized and unfertilized conditions, and (2) despite increased availability of inorganic N in the substrate which could have lessened the negative effects of periwinkle grazing, N fertilization actually increased the relative impact of top-down control. In our experiment, increases in cordgrass production due to nitrogen supplements in the absence of *L. irrorata* were completely eliminated in the presence of high snail densities (see Fig. 2b). In other words, the ANPP of the unfertilized marsh without snails (274 g

$\text{C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ; Fig. 2b) was statistically the same as the ANPP of the fertilized system with snails ( $281 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ ; Fig. 2b). Snail grazing at high densities did not eliminate the effects of N enrichment (N fertilization enhanced ANPP within snail addition treatments by  $>190\%$ , see Fig. 2b), but it did eliminate the ANPP gains due to N addition which were seen in ungrazed cordgrass. This result, combined with the finding that snail grazing under unfertilized conditions markedly reduces cordgrass growth (e.g., snail addition in unfertilized areas reduced standing crop by nearly 80% in comparison to snail removal treatments), clearly demonstrates that top-down forces have the potential to dominate the low marsh plant community at densities that are common in nature.

In treatments with snails, the total length of radulations per stem nearly doubled when the marsh was fertilized. This was likely due to increased radular activity on N-rich plants, a scenario that is consistent with other fertilization studies showing enhanced grazing by herbivores on fertilized plants (e.g., McGlathery 1995, fish; Vince et al. 1981, Boyer and Zedler 1996, insects; and Valiela et al. 1985, mammals). There was, however, no coincidental increase in defoliated plant tissue with the observed increase in snail grazing (Figs. 2 and 4, Table 3). This result strongly indicates that other mechanisms besides defoliation were involved in leading to increased top-down control in fertilized areas.

Analyses of substrate and plant tissue nutrient concentrations suggest that one important mechanism was grazer control of plant demand for N fertilizer. In many instances, herbivory has been shown to stimulate nutrient uptake by plants, primarily when grazing is discontinuous, providing a recovery window for compensatory growth (e.g., McNaughton 1983 and references therein, Caldwell et al. 1987, Wallace and Macko 1993). Grazing by periwinkles is relatively continuous throughout the growing season and, therefore does not afford *S. alterniflora* an intervening period of recovery. In fertilized treatments with snails, porewater ammonium concentrations were increased by an order of magnitude in August and September (Fig. 3c). It could be argued that this pattern was due to increased mineralization rates as a consequence of snail-induced defoliation or snail excretion. However, these possibilities are unlikely considering the fact that porewater ammonium concentrations in unfertilized treatments with snails were never elevated. An alternative explanation is that snail grazing inhibited the ability of *S. alterniflora* to take up the N fertilizer. Stem N concentration, however, was not reduced by snail density, which would be expected if N uptake efficiency was negatively affected by grazing activities (Table 3). It is more likely that the reduction in *S. alterniflora* growth, as a product of snail grazing activities, resulted in decreased plant demand for porewater ammonium on a per  $\text{m}^2$  basis. A simple estimation of the daily N demand of fertilized stands of *S. alterniflora* during peak growth

in August (mean daily productivity/ $\text{m}^2$  in August  $\cdot$  mean stem N concentration in August) provides further support for this contention. This calculation shows that N demand (per square meter) was  $\sim 5\times$  higher in fertilized treatments without snails ( $1.41 \pm 0.19 \text{ g dry mass N}\cdot\text{m}^{-2}\cdot\text{d}^{-1} = 38.2 \text{ g dry mass}\cdot\text{m}^{-2}\cdot\text{d}^{-1} \times 3.7\% \text{ N}$ ) compared to those with enhanced snail densities ( $0.28 \pm 0.15 \text{ g dry mass N}\cdot\text{m}^{-2}\cdot\text{d}^{-1} = 7.2 \text{ g dry mass}\cdot\text{m}^{-2}\cdot\text{d}^{-1} \times 3.9\% \text{ N}$ ).

The amount of porewater ammonium made available to *S. alterniflora* through fertilization in this study is comparable to the amount available in the tall-form *S. alterniflora* zone (Osgood and Ziemann 1998). This suggests that the indirect negative effects of snail grazing on the nitrogen-*S. alterniflora* interaction observed in this experiment have the potential to occur in the natural environment. In addition, because the occurrence of high snail densities ( $>100$  snails/ $\text{m}^2$ ) is much more common than elevated concentrations of porewater ammonium in the short- and intermediate-form *S. alterniflora* zones (Pomeroy and Wiegert 1981, Mitsch and Gosselink 1993), strong top-down control of cordgrass growth by *L. irrorata* is more likely to be observed in the natural environment than enhanced plant growth due to increased N availability.

#### Potential for a trophic cascade

Trophic cascades occur when runaway consumption leads to downward dominance in food chains and are especially likely in systems where herbivore densities lead to wholesale reductions in plant cover, and herbivore populations are controlled to a large extent by predation (Strong 1992). *L. irrorata* has been identified as a primary food source for most predators that utilize saltmarsh habitats as foraging areas. Snails are consumed by terrapins (*Malaclemys terrapin*; Tucker et al. 1995), blue crabs (*Callinectes sapidus*; Hamilton 1976, Warren 1985) conchs and whelks (Hamilton 1976, Warren 1985), blacked-clawed mud crabs (*Panopeus herbstii*; B. R. Silliman, C. Layman, K. Geyer, and J. C. Ziemann, unpublished manuscript), clapper rails (*Rallus longirostris*; Heard 1952, Oney 1951), American Oyster Catchers (*Haematopus ostralegus*; Boates and Goss-Custard 1992) and, specifically, in the case of small snails ( $<7$  mm), raccoons (B. R. Silliman, personal observation) and large mummichogs (*Fundulus heteroclitus*; Daiber 1982). Further suggestions of predation include myriad piles of empty shells, broken shells, and shell fragments in salt marshes throughout the Southeast (Hamilton [1976]; Warren [1985], Florida; West and Williams [1985], Alabama; B. R. Silliman, personal observation, Virginia, Maryland, North Carolina, South Carolina, and Georgia). Additionally, the large proportion of live snails ( $\leq 56\%$ ) that bear scars on their shells is indicative of frequent encounters with shell-crushing crabs (Blundon and Vermeij 1983, Warren 1985).

Given the intensity of predation on marsh periwink-

kles and our findings that these snails are capable of regulating cordgrass growth, we hypothesize that Southeastern salt marshes are characterized by powerful, but inconspicuous, trophic cascades. We suggest that by controlling snail densities, large predators may ultimately be responsible for the luxuriant primary production and standing crop observed in these communities.

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