Physical factors mediate effects of grazing by a non-indigenous snail species on saltmarsh cordgrass (*Spartina alterniflora*) in New England marshes

Megan C. Tyrrell, Michele Dionne, and Jessica A. Edgerly

Tyrrell, M. C., Dionne, M., and Edgerly, J. A. 2008. Physical factors mediate effects of grazing by a non-indigenous snail species on saltmarsh cordgrass (*Spartina alterniflora*) in New England marshes. – ICES Journal of Marine Science, 65: 746–752.

In the southeastern US, grazing by a common indigenous littorinid snail has caused large declines in the biomass of saltmarsh cordgrass (*Spartina alterniflora*). In northeastern marshes, a closely related but non-indigenous snail may also negatively affect production of this key marsh-building plant. We manipulated densities of the gastropod *Littorina littorea* at two sites to investigate the effect of its grazing on plant production and sediment accumulation. The effects of the manipulation differed between sites. The site with longer inundation periods, lower elevation, and poorer drainage attributable to smaller sediment grain size had more stressful conditions for *S. alterniflora*. At that site, protection from snail grazing resulted in higher end-of-season plant biomass than all the other treatments and controls. Rates of sediment accumulation were also lower at that site, and the difference between sites increased as the season progressed. At the site where physical conditions were benign, snail manipulation had no effect on *S. alterniflora* biomass. The nature of the physical conditions at a site may influence the susceptibility of *S. alterniflora* to grazing pressure by this ubiquitous snail species. Accelerating anthropogenic impacts, such as sea-level rise, could further stress saltmarsh plants, leaving them increasingly susceptible to herbivory.

Keywords: cordgrass, grazing, introduced species, inundation, *Littorina littorea*, periwinkle, saltmarsh, sediment accumulation, sediment grain size, *Spartina alterniflora*.

Received 14 June 2007; accepted 31 December 2007; advance access publication 27 February 2008.

M. C. Tyrrell, M. Dionne and J. A. Edgerly: Wells National Estuarine Research Reserve, 342 Laudholm Farm Road, Wells, ME 04090, USA. Correspondence to M. C. Tyrrell: tel: +1 207 8418129; fax: +1 207 6462930; e-mail: mtyrrell@alumni.macalester.edu.

Introduction

Smooth cordgrass (*Spartina alterniflora*) is the primary species responsible for saltmarsh expansion and sediment accretion in New England (Redfield, 1965). *Spartina alterniflora* facilitates seaward expansion of saltmarsh hay (*S. patens*), which is less tolerant of tidal inundation than *S. alterniflora* (Bertness and Ellison, 1987). *Spartina patens* is the major peat-forming plant in saltmarshes, so the two species together contribute to the capacity of meadow marshes to keep pace with sea-level rise. Factors that affect the abundance of *Spartina* sp. are particularly important to document and understand given the cumulative impacts such as marsh fragmentation and ditching, disease, species introductions, and physical shifts associated with climate change, such as accelerating sea-level rise and storm intensity.

Recent experiments in southeastern US saltmarshes have revealed dramatic declines in biomass of *S. alterniflora*, attributable to grazing by an indigenous snail, *Littoraria irrorata* (Silliman and Zieman, 2001; Silliman and Bertness, 2002). High densities of a similar herbivorous littorinid in New England saltmarshes may similarly affect the distribution and abundance of *S. alterniflora*. In the Gulf of Maine, the numerically dominant saltmarsh snail, *Littorina littorea*, is a non-indigenous species. Although the invasion status of *L. littorea* was questioned based on genetic analyses (Wares *et al.*, 2002), a review of archaeological and genetic evidence, including a re-examination of the Wares *et al.* (2002) genetic data, indicates that the presence of *L. littorea* in North America is the result of an anthropogenically mediated introduction in the mid-19th century (Blakeslee, 2007; Chapman *et al.*, 2007). Documentation of all ecological impacts of this non-indigenous snail in marshes is important to developing appropriate marsh protection and management actions, regardless of the length of time that it has been present in the region.

Littorina littorea was previously implicated in exerting strong control over *S. alterniflora* abundance and therefore in the persistence of a fringing marsh in New England (Bertness, 1984), but its influence in meadow marshes may be mitigated by reduced wave exposure and the lack of hard substrata underlying meadow marshes. Surprisingly, no further research has been conducted to document the generality of the results of Bertness (1984) to other sites with different physical conditions.

Given that the viability of New England's meadow marshes is threatened by a multitude of factors, including accelerating sea-level rise (Donnelly, 2006), it is important to understand whether *L. littorea* reduces *S. alterniflora* biomass in northern meadow marshes to the same extent as *L. irrorata* in southeastern meadow marshes. *Spartina alterniflora* production affects marsh sediment accumulation (Morris *et al.*, 2002), so intense grazing

by this non-indigenous snail species could affect the ability of New England's marshes to maintain their elevations while simultaneously facing increased inundation periods. We hypothesized that *L. littorea's* grazing would negatively affect *S. alterniflora* and, because its above-ground production is less in northern latitudes (Mendelssohn and Morris, 2000), the deleterious effect of snail grazing would be more pronounced than in southeastern marshes. To investigate this issue, we documented the effects of grazing by *L. littorea* on *S. alterniflora* production and sediment accumulation in two saltmarshes in southern Maine. We manipulated snail densities in plots located at the seaward edge of the tall-form *S. alterniflora* zone, the zone where Bertness *et al.* (2004) reported that *L. irrorata* grazing had the greatest impact on *S. alterniflora* in Georgia's saltmarshes. Our main objective was to determine whether grazing by this highly abundant, non-indigenous snail affects the marsh-building and maintenance capacity of *S. alterniflora* by reducing its growth or sediment-accumulation function. Physical factors, such as inundation time and drainage, which affect *S. alterniflora's* growth, were monitored at both study sites to assess their contribution to the results. The grazing rates of *L. littorea* on *S. alterniflora* were also investigated to assess its potential to affect *S. alterniflora* biomass under laboratory conditions.

Methods

Study sites

The study was carried out in two saltmarshes located in two adjacent southern Maine estuaries within the Wells National Estuarine Research Reserve (Figure 1). The Little River and Webhannet River study sites were chosen to have the same orientation and similar elevations in a depositional low meadow marsh at the transition from *S. alterniflora* to mudflats. The only prominent herbivore in this zone of these marshes is the common periwinkle, *L. littorea*. The average density of *L. littorea* in the zone is ~160 per m^2 ($\pm$ 12 s.e.), with densities ranging from 16 to 550 per m^2 (MCT and JAE, unpublished).

Snail-density manipulations

Our experiment consisted of five treatments: snail exclusion (E), medium density (40 *L. littorea* per 0.25 m^2, D), twice density (80 *L. littorea* per 0.25 m^2, T), cage controls (C) with only three sides, and unmanipulated plots (N) with no cage structure. Each plot was 0.25 m^2, and each treatment was replicated nine times for a total of 45 plots in each estuary. Cages were constructed of 6 mm mesh galvanized hardware cloth, with sides 61 cm high. Bamboo stakes were placed at the corners outside of the hardware cloth for stability. Rhizomes were severed around each plot to a depth of 12 cm to isolate experimental from non-experimental plants. Plots were arranged in sets of five, with the treatment randomly assigned to each plot. In all cases, the set of five plots encompassed a homogenous, gently sloping section of the marsh at the transition from *S. alterniflora* to bare substratum. Small sections of each study area did not fit these criteria (e.g. the transition between *S. alterniflora* and bare substratum was a bank rather than a low angle); these patches were omitted, and the next set of plots was located in the closest suitable section of marsh.

After construction of the cages, initial counts of both live and standing-dead stems were made. The initial biomass of each plot was estimated by measuring the height of the first 30 live plants that were closest to two diagonal rods placed from corner to

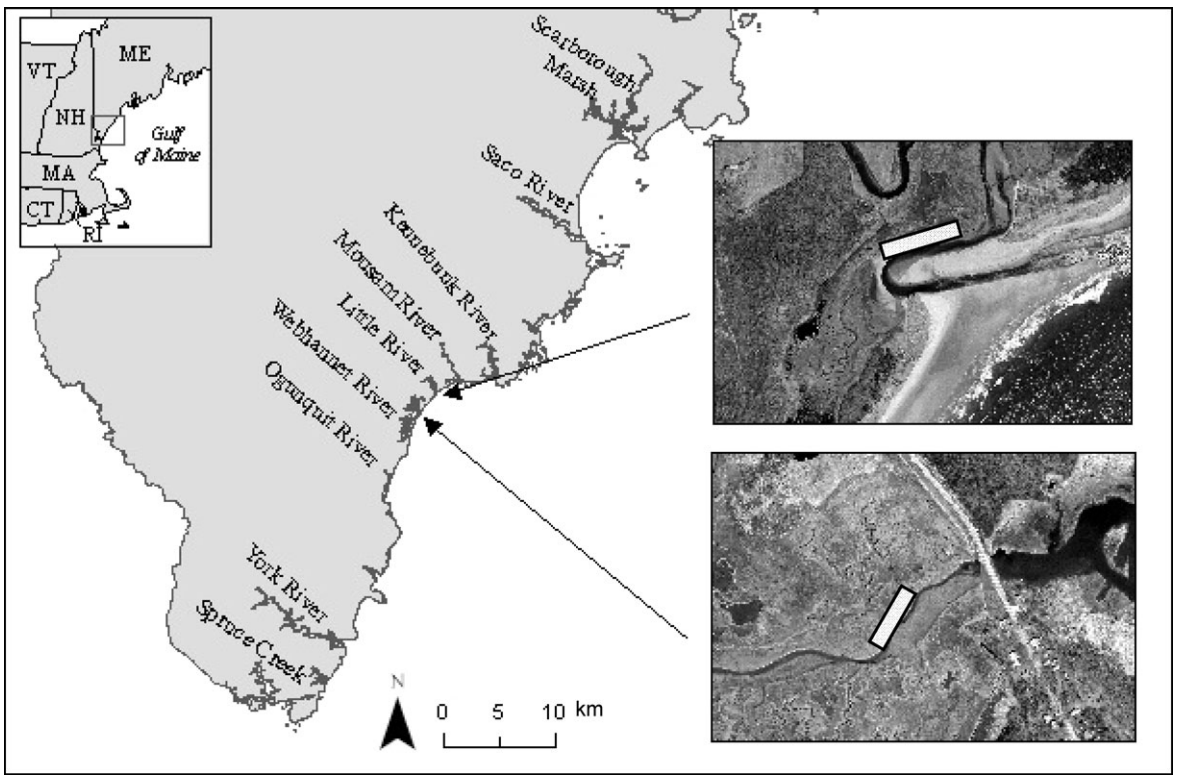

Figure 1. Map showing the Little River and Webhannet River study areas in southern Maine, New England, USA. White boxes indicate the low angle transition of *S. alterniflora* to bare substratum, where the snail-density manipulations were conducted.

corner within each plot. A regression of stem height against dry stem biomass ($r^2 = 0.92$) was used to calculate initial biomass values for each plot.

Physical parameters

Physical factors that affect *S. alterniflora's* production, such as elevation, inundation time, sediment characteristics, and deposition rates, were assessed at each site. Elevations of the central plot in each set of five plots were obtained using a Leica TCRA 1205 total survey station. Inundation times were evaluated with three data-loggers (Onset Hobo U20 temperature/pressure loggers) that recorded temperature and pressure every 15 min over a 2-week interval. On 30 August 2005, the loggers were placed at each of the end plots and the central plot at the Little River. After those 2 weeks, the data were downloaded, and the loggers were placed at the Webhannet River study site on 15 September 2005, for a 2-week inundation monitoring period.

At the conclusion of the experiment, a sediment sample of 50 g from the central plot in each five-plot set was collected for grain-size and organic-content analyses. For grain-size analysis, a 25 g portion was rinsed through a set of 2 mm (coarse sand), 500 μm (medium sand), 250 μm (fine sand), 125 μm (very fine sand), and 63 μm (silt) sieves. Each fraction, including the fraction that passed through the 63 μm sieve, was individually retained and dried at 60°C for 24 h before measuring its dry weight. Separate sediment samples were used to determine weight loss on ignition, a proxy for organic content (Craft *et al.*, 1991). The dried sediment samples were heated in a 450°C muffle furnace for 4 h and weighed after cooling in a desiccator.

Sediment accumulation was monitored in July, August, and September using Mylar sediment traps, following Morgan and Short (2002). We used small sediment traps (18.32 mm^2) to allow them to be placed within the *S. alterniflora* plots with minimal disturbance to snails or plants. Initial weights were recorded before the traps were deployed for three 14 d periods at each study site. The traps were dried at 60°C for >48 h, then weighed again. Deployment dates in 2005 in the Little River were 30 June, 12 August, and 21 September; in the Webhannet River, they were 1 July, 15 August, and 22 September.

The experiment was initiated by stocking or removing snails from the snail manipulation treatments on 7 and 9 June 2005 in the Little River and on 17 June 2005 in the Webhannet River. To avoid disturbing natural snail densities in the cage control and unmanipulated plots, all snails added to the D and T plots were collected >30 m from each study site.

The number of snails in each plot was monitored at least once per week, and adjustments were made to snail densities as necessary. Drift algae that accumulated in the cages was also removed during the weekly checks.

The experiment was terminated on 11–13 October 2005 and 18–21 October 2005 in the Little and Webhannet rivers, respectively. At the same time, all above-ground biomass was harvested. Dry biomass measurements were made after the *S. alterniflora* had been rinsed and dried at 80°C for 24 h.

Laboratory grazing rates

Grazing rates of *L. littorea* on *S. alterniflora* as the sole food source were assessed in a laboratory experiment. Our methods closely followed Silliman and Zieman (2001), except that we used 2 l jars with ventilation provided by 5 mm holes in the cap. Live *S. alterniflora* stems were collected from the Little River, rinsed, and a 200 mg piece was placed in each jar. Half the 24 replicates were randomly assigned as controls, and no snails were added to the jars. The other half of the jars had four starved (>23 h) snails added to them. All containers were misted with saltwater twice per day to simulate the local tidal cycle. After 48 h, the blotted plant tissue was reweighed. These methods were repeated using the same amount of dead *S. alterniflora*, to determine whether snail-grazing rates were greater on dead plant tissue than on live plants. We conducted an additional grazing rate trial using six starved *L. littorea* with 200 mg of live *S. alterniflora* over a 3 d period, because we observed that snail encounter rates with the plant tissue were relatively low in the 2 l container.

Statistical analysis

Analysis of variance was used (SYSTAT 8.0) to examine differences in response variables measured during or at the conclusion of the experiments. We used a two-way ANOVA examining the effects of site, treatment, and their interaction on total (live + standing dead) end-of-experiment biomass. The two-way ANOVA indicated that the study site had a significant influence on the results, so for subsequent statistical analyses we used one-way ANOVA for each site separately. One-way ANOVA was also used to examine the rates of sediment accumulation for each month at each site.

Data that were not normally distributed or did not have homogeneity of variance were square-root transformed before statistical analysis. *Post hoc* comparisons were made with Bonferroni tests. Physical differences between the two sites, such as sediment grain size and organic content were evaluated with *t*-tests. One-tail *t*-tests were used to evaluate the difference between control (no snails) and experimental treatments for each grazing rate trial.

Results

Initial conditions

At the start of the experiment, the density of live stems and the estimated biomass were not significantly different between the two sites (all $p > 0.232$), nor were they different between the treatment types at either of the study sites (all $p > 0.322$). The estimated biomass at the Little River was 6.82 ± 0.31 g 0.25 m^{-2}, and at the Webhannet River it was 6.55 ± 0.25 g 0.25 m^{-2}. The mean number ($\pm$ s.e.) of standing-dead stems at the Webhannet River site (18.04 ± 1.45) was more than twice that at the Little River site (7.44 ± 0.70), and this difference was statistically significant (*t*-test, $t = 6.57$, d.f. = 98, $p < 0.001$), but the mean number of live stems was similar between sites (Little River, 144.18 ± 7.20; Webhannet River, 130.02 ± 9.31).

Although the two study sites were selected because of their initial similarity, subtle differences in their physical characteristics accrued throughout the course of the experiment and led to noticeably disparate growth rates of *S. alterniflora*, rates of sediment accumulation, and snail densities and rates of movement. A two-way ANOVA examining the effects of site, treatment, and their interaction on total (live+standing-dead) end-of-experiment biomass of *S. alterniflora* demonstrated a significant effect of study site on the results ($F = 222.85$, d.f. = 80, $p < 0.001$). Dissimilar trajectories in plant production attributable to differences in physical characteristics between the sites could overwhelm any treatment effects related to the snail manipulations, so subsequent statistical analyses were conducted for each site individually.

One-way ANOVA was used to examine the effect of treatment on final total biomass, final biomass of all live plant material, and final biomass of all standing-dead plant material at each site. Additionally, the treatment effect on the rates of sediment accumulation was examined using one-way ANOVA for July, August, and September data separately.

Physical parameters

The Webhannet River study site was at a slightly lower elevation (using NAVD 88) than the Little River site, resulting in increased submersion times and higher physiological stress for *S. alterniflora*. The Webhannet River plots were, on average, 0.4 m lower than the Little River plots. The pressure-logger data indicated that they were submerged for ~10.25 h longer in a 14-d period, which translates to ~70 h more submersion time over the course of the study. Additionally, a significantly larger portion of the sediment grain size was concentrated in the 63 μm (silt) and <63 μm fractions at the Webhannet study site than at the Little River site (*t*-test, $t = -2.457$, d.f. = 17, $p = 0.025$; Table 1). Despite the differences in sediment grain size, sediment organic content was similar between the two sites (*t*-test, $t = 1.022$, d.f. = 17, $p = 0.321$; Table 1).

The rates of sediment accumulation at the Little River site far exceeded those at the Webhannet River site, and the difference between the sites increased as the season progressed (Figure 2). In August and September 2005, Little River accumulation rates were an order of magnitude higher than Webhannet River rates (Table 2). The rank order of sediment accumulation patterns reveals that treatment type did not have a consistent effect over time in either estuary (Table 2). There was no significant treatment effect (by one-way ANOVA) on sediment accumulation rates for July, August, or September 2005 at the Little River or the Webhannet River site (all $p > 0.136$).

Initial plant biomass and snail-migration rates

Although initial biomass was similar between sites, by the end of the experiment, the average total biomass of all live and standing-dead *S. alterniflora* in the unmanipulated, cage control, and snail-exclusion treatments was more than three times lower in the Webhannet River than in the Little River (Figure 3a and b). The between-site difference was even greater for the two levels of snail-density manipulation. The rates of snail migration also differed between sites. At the Little River site, the average weekly deviation from target densities never exceeded 20%, whereas at the Webhannet River, there were five instances where the weekly average deviation from target density attributable to emigration was >20%. The highest rates of migration were from the 2× density treatment at the Webhannet River site.

Table 1. Comparison of Little River and Webhannet River study sites in terms of average percentage of sediment in each of five standard sediment grain-size classes, and the percentage of organic content.

Grain size class	Little River	Webhannet River
2 mm	0.44 (0.14)	1.87 (0.43)
500 μm	6.72 (1.04)	3.34 (0.60)
250 μm	17.89 (0.79)	7.82 (0.33)
125 μm	44.52 (2.12)	50.18 (1.49)
63 μm	10.39 (0.78)	14.47 (0.62)
<63 μm	20.07 (1.50)	22.33 (1.09)
Percentage organic content	5.11 (0.45)	4.38 (1.77)

Standard error in parentheses.

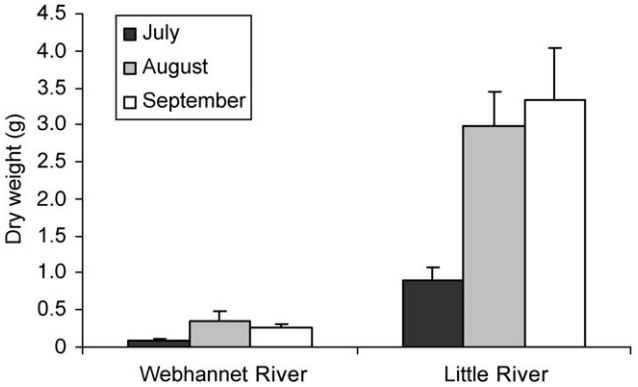

Figure 2. Average sediment deposition over a 2-week period at the Webhannet and Little rivers in July, August, and September. Error bars represent +1 s.e.

Snail manipulation experiment

After being subjected to the experimental manipulations for 4 months, treatment had a significant effect on the biomass of live *S. alterniflora* at the Webhannet River (one-way ANOVA, $F = 5.790$, d.f. = 40, $p = 0.001$; Figure 3a). The biomass of *S. alterniflora* in the snail-exclusion treatment was significantly higher than in plots exposed to snail grazing ($p < 0.04$ by Bonferroni *post hoc* tests; Figure 3a). Total biomass (live and standing-dead plant material) was also significantly different between treatments (one-way ANOVA, $F = 4.659$, d.f. = 40, $p = 0.004$); total biomass in the snail-exclusion treatment was significantly greater than in the medium-density ($p = 0.028$) and 2× density treatments ($p = 0.002$, by Bonferroni *post hoc* tests; Figure 3a). The total biomass of *S. alterniflora* in the unmanipulated and cage-control treatment was similar to that of the medium-density treatment, indicating that the cage structure did not have a major effect on the plants' productivity (Figure 3a). *Littorina littorea* in the medium-density treatment reduced total biomass by 32% compared with exclusions, and when snails were maintained at twice their normal density, the biomass was 42% lower than the snail-exclusion treatment. There was also a significant treatment effect on standing-dead biomass of *S. alterniflora* at the end of the experiment (one-way ANOVA, $F = 4.172$, d.f. = 39, $p = 0.007$). The unmanipulated treatment had significantly more standing-dead biomass than the snail-exclusion, medium-density, and 2× density treatments ($p < 0.03$), but not more than the cage-control experiment ($p > 0.05$).

In contrast to the results from the Webhannet River, at the Little River there was no effect of snail herbivory on the live biomass of *S. alterniflora* (one-way ANOVA, $F = 0.713$, $p = 0.588$; Figure 3b), standing-dead biomass (one-way ANOVA, $F = 1.691$, $p = 0.172$), or total biomass (one-way ANOVA, $F = 0.621$, $p = 0.650$; Figure 3b). The biomass of *S. alterniflora* in the unmanipulated and cage-control treatment was similar to that of the medium-density treatment, indicating that the cages did not have a great influence on the plants' pattern of biomass accumulation (Figure 3b).

Table 2. Mean rates of sediment deposition (± s.e.) and rank by factor on 18.32 mm^2 traps over a 2-week period in June, July, and August at the Little River and Webhannet River study sites.

Treatment	July	July rank	August	August rank	September	September rank
Little River						
N	0.85 (0.37)	2	1.90 (0.93)	4	1.60 (0.34)	5
C	0.81 (0.28)	3	3.18 (1.04)	3	4.02 (2.02)	2
E	0.55 (0.13)	5	1.76 (0.23)	5	2.19 (0.75)	4
D	0.63 (0.22)	4	3.89 (1.33)	2	3.96 (1.66)	3
T	1.63 (0.79)	1	4.22 (1.18)	1	4.89 (2.25)	1
Webhannet River						
N	0.10 (0.02)	2	0.31 (0.21)	3	0.47 (0.16)	1
C	0.09 (0.02)	3	0.69 (0.28)	1	0.30 (0.10)	2
E	0.12 (0.05)	1	0.66 (0.62)	2	0.13 (0.05)	5
D	0.08 (0.02)	4	0.04 (0.02)	4	0.21 (0.14)	3
T	0.06 (0.01)	5	0.04 (0.01)	5	0.18 (0.11)	4

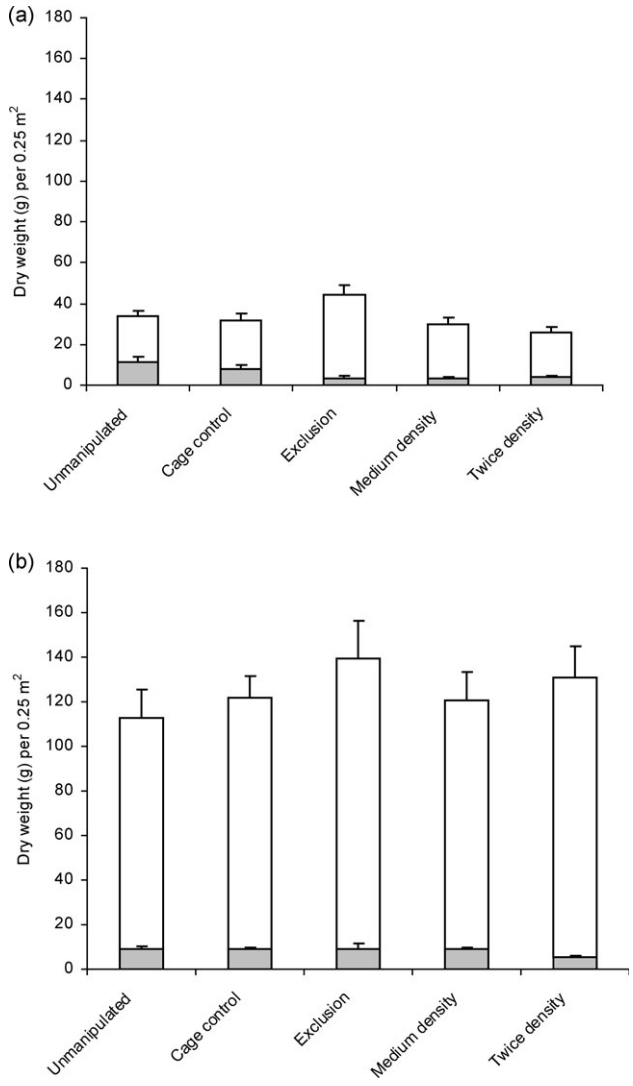

Figure 3. Mean (+s.e.) biomass of *S. alterniflora* after 4 months of *L. littorea* density manipulations at (a) the Webhannet River and (b) the Little River. Empty bars are live biomass; shaded bars are standing-dead biomass.

Laboratory grazing rates

For the 48 h experiment, there was no difference in the weight of *S. alterniflora* exposed to snail grazing vs. the controls; this was true for both live and dead plant tissue (*t*-test, $p > 0.13$ in both cases; data not shown). For the 3 d grazing trial with six snails, *L. littorea* grazing led to a significantly greater loss of *S. alterniflora* weight (*t*-test, $t = 1.791$, $p < 0.044$) relative to controls. This 3 d, six-snail laboratory grazing rate translates to 0.58 mg loss of *S. alterniflora* tissue per *L. littorea* per day. Over the course of the study, the laboratory-based grazing rate, which represents a maximum value, would account for the loss of ~56 mg of *S. alterniflora* biomass per *L. littorea*, which translates to ~2.24 g m^{-2}.

Discussion

Our experiments were not designed to test explicitly how stressful abiotic conditions may affect snail grazing on *S. alterniflora*, but the results are consistent with physical conditions having a substantial influence on this interaction. At the beginning of the study, both sites had similar densities of live plants and biomass of *S. alterniflora*. As the experiment progressed, the discrepancy in growth rates of *S. alterniflora* between the sites became apparent, likely the consequence of a combination of grazing pressure and the less-benign physical conditions at the Webhannet River site. Tidal inundation is stressful for saltmarsh plants and is the reason that the competitively superior *S. patens* occupies a position higher than *S. alterniflora* in northeastern US marshes (Bertness and Ellison, 1987). Soil drainage also affects the growth of *S. alterniflora* (Mendelssohn and Seneca, 1980). The small grain size resulted in waterlogged sediments and a shallow depth to the anoxic layer at the Webhannet River site (MCT and JAE, pers. obs.), typical of the low marsh environment. At the Little River, the plots were located close to the inlet, which is characterized by coarse, dynamic sediments. Together, the greater immersion time and poor drainage at the Webhannet River site resulted in physically stressful conditions for *S. alterniflora*, as evidenced by the lower end of experiment biomass in the snail-exclusion plots at Webhannet River compared with Little River. The reduced total plant biomass at the Webhannet River site led to a measurable snail-grazing effect.

The small sediment grain size at the Webhannet River site also resulted in *L. littorea* spending more time on *S. alterniflora* (MCT

and JAE, pers. obs.). Compared with other marsh snails, the ability of *Littorina littorea* to move in silty sediments is limited (Chandrasekara and Frid, 1998), and rather than moving over the sediment surface, they frequently climbed plant stems at the Webhannet River site (MCT, pers. obs.). This greater amount of contact time likely increased the impact of the *L. littorea* grazing. In contrast to southeastern marshes, the activity levels of littorind snails at our sites were similar when they were exposed to air or submersed by the tide (MCT, pers. obs.); the longer inundation time at the Webhannet River site was not likely to be the primary cause of the greater impact of snail grazing there.

Snail grazing damages live *S. alterniflora* tissue, leading to fungal infection and senescence (Silliman and Newell, 2003). Standing-dead *S. alterniflora* is an important food source for *L. irrorata* and other marsh consumers (Currin *et al*., 1995). It seems likely that the manner in which the grazing of *L. irrorata* leads to fungal infection and senescence of *S. alterniflora* in southeastern marshes (Silliman and Zieman, 2001) is similar to the situation with *L. littorea* in New England. In a latitudinal survey of five Atlantic coast marshes, the Wells Reserve had the greatest fungal biomass on *S. alterniflora* (Newell and Porter, 2000). Our Webhannet River results—that both the snail exclusion and the medium-density and 2× density treatments had significantly lower biomass of standing-dead *S. alterniflora* than the unmanipulated treatment—may initially appear counter-intuitive. In the grazer-exclusion treatment, *S. alterniflora* was left to senesce at natural rates (e.g. not influenced by a non-indigenous grazer). In contrast, the low standing-dead biomass in the medium-density and 2× density treatments could be explained by *L. littorea* grazing leading to fungal infection and the snails consuming the dead *S. alterniflora* tissue. The percentage reductions in total *S. alterniflora* biomass that we obtained were similar to the values reported by Silliman and Zieman (2001) for *L. irrorata* in southeastern marshes.

Sediment accretion is critical for marshes to avoid drowning as sea-level rises (Croft *et al*., 2006), and sediment accumulation rates are positively correlated with the amount of *S. alterniflora* (Gleason *et al*., 1979; Morris *et al*., 2002). The increasing discrepancy in sediment accumulation rates between the two study sites with time can be explained partially by the lower level of plant biomass accumulation at the Webhannet River site. The lack of a consistent treatment effect on the rates of sediment accumulation could be attributed to snail faecal pellets, which would increase the weight of sediment on the Mylar, or snail movement, which could transport a thin layer of sediment off the Mylar. In addition, the scale at which sediment-deposition dynamics operate is likely larger than the size of the plots used in this study. Nevertheless, the reduction in *S. alterniflora* biomass because of grazing is likely the primary negative influence of this non-indigenous snail species on marsh sediment accretion.

Further investigation in additional meadow marshes that encompass a range of physical conditions and plentiful *L. littorea* is warranted to determine the generality of these results. Manipulation of several of the abiotic factors that affect *S. alterniflora* growth (e.g. inundation time, sediment grain size) could be performed to narrow the list of the physical conditions that most influence the *L. littorea*–*S. alterniflora* interaction.

Our results demonstrate that grazing by a non-indigenous snail can significantly depress the biomass of a pioneer marsh plant, but that this effect is mediated by site-specific physical conditions. Species introductions, in addition to other accelerating anthropogenic impacts such as eutrophication (Bertness *et al*., 2002) and sea-level rise (Phillips, 1986; Donnelly, 2006), are affecting the extent and integrity of saltmarshes. The seaward edge of *S. alterniflora* is a critical zone for marsh building and maintenance (Redfield, 1965). In addition to the longer inundation times, salinity stress, and anoxic soils, pioneering *S. alterniflora* in New England that encroach upon mudflats are subject to grazing by an abundant, non-indigenous snail species. In locations where stressful physical conditions, such as small sediment grain size, impede soil drainage, the production of *S. alterniflora* can be significantly diminished by snail grazing. The finding that *L. littorea* can reduce the production of *S. alterniflora* appears more likely to apply at sites where the plants are otherwise compromised by stressful conditions, such as those observed in the Webhannet River study site. Evidence of accelerating anthropogenically induced stressors for saltmarsh plants is accumulating (Bertness *et al*., 2002), so the likelihood of synergistic interactions, such as increased susceptibility to grazing under stressful physical conditions, is increasing for *S. alterniflora*. The cumulative impact of these threats on New England marshes could lead to a substantial loss in acreage of this highly productive coastal habitat.

Acknowledgements

We acknowledge the following for their assistance: Katherine Walker, Martin Junco, June Yeung, Sarah Eberhardt, Jeremy Miller, Michael Haas, Martin Smith, Ray Konisky, Andrea Leonard, and Matthew McBride. Funding for JAE was provided by Bates College and the Laudholm Trust, and for MCT by the Ford Postdoctoral fellowship. The manuscript benefited greatly from comments on the submitted draft by A. M. H. Blakeslee, J. Pederson, and three anonymous reviewers.

References

Bertness, M. D. 1984. Habitat and community modification by an introduced herbivorous snail. Ecology, 65: 370–381.

Bertness, M. D., and Ellison, A. M. 1987. Determinants of patterns in a New England salt marsh plant community. Ecological Monographs, 57: 129–147.

Bertness, M. D., Ewanchuk, P. J., and Silliman, B. R. 2002. Anthropogenic modification of New England salt marsh landscapes. Proceedings of the National Academy of Science, 99: 1395–1398.

Bertness, M., Silliman, B. R., and Jefferies, R. 2004. Salt marshes under siege. American Scientist, 92: 54–61.

Blakeslee, A. M. H. 2007. Resolving the 150 year debate over the ecological history of the common periwinkle snail, *Littorina littorea*, in northeast North America. PhD dissertation, University of New Hampshire, Durham, NH, 136 pp.

Chandrasekara, W. U., and Frid, C. L. J. 1998. A laboratory assessment of the survival and vertical movement of two epibenthic gastropod species, *Hydrobia ulvae* (Pennant) and *Littorina littorea* (Linnaeus), after burial in sediment. Journal of Experimental Marine Biology and Ecology, 221: 191–207.

Chapman, J. W., Carlton, J. T., Bellinger, M. R., and Blakeslee, A. M. H. 2007. Premature refutation of a human-mediated marine species introduction: the case history of the marine snail *Littorina littorea* in the northwestern Atlantic. Biological Invasions, 9: 737–750.

Craft, C. B., Seneca, E. D., and Broome, S. W. 1991. Loss on ignition and Kjeldahl digestion for estimating organic carbon and total nitrogen in estuarine marsh soils: calibration with dry combustion. Estuaries, 14: 175–179.

Croft, A. L., Leonard, L. A., Alphin, T. D., Cahoon, L. B., and Posey, M. H. 2006. The effects of thin layer sand renourishment on

tidal marsh processes: Masonboro Island, North Carolina. Estuaries and Coasts, 29: 737–750.

Currin, C. A., Newell, S. Y., and Paerl, H. W. 1995. The role of standing dead *Spartina alterniflora* and benthic microalgae in salt marsh food webs: considerations based on multiple stable isotope analysis. Marine Ecology Progress Series, 121: 99–116.

Donnelly, J. P. 2006. A revised late Holocene sea-level record for northern Massachusetts, USA. Journal of Coastal Research, 22: 1051–1061.

Gleason, M. L., Elmer, D. A., Pien, N. C., and Fisher, J. S. 1979. Effects of stem density upon sediment retention by salt marsh cord grass, *Spartina alterniflora* Loisel. Estuaries, 2: 271–273.

Mendelssohn, I. A., and Morris, J. T. 2000. Eco-physiological controls on the productivity of *Spartina alterniflora* Loisel. *In* Concepts and Controversies in Tidal Marsh Ecology, pp. 59–80. Ed. by M. P. Weinstein, and D. A. Kreeger. Kluwer, Boston. 875 pp.

Mendelssohn, I. A., and Seneca, E. D. 1980. The influence of soil drainage on the growth of salt marsh cordgrass, *Spartina alterniflora* in North Carolina. Estuarine and Coastal Marine Science, 11: 27–40.

Morgan, P. A., and Short, F. T. 2002. Using functional trajectories to track constructed salt marsh development in the Great Bay Estuary, Maine/New Hampshire, USA. Restoration Ecology, 10: 461–473.

Morris, J. T., Sundareshwar, P. V., Nietch, C. T., Kjerfve, B., and Cahoon, D. R. 2002. Response of coastal wetlands to rising sea level. Ecology, 83: 2869–2877.

Newell, S. Y., and Porter, D. 2000. Microbial secondary production from saltmarsh-grass shoots, and its known and potential fates. *In* Concepts and Controversies in Tidal Marsh Ecology, pp. 159–185. Ed. by M. P. Weinstein, and D. A. Kreeger. Kluwer, Amsterdam. 875 pp.

Phillips, J. D. 1986. Coastal submergence and marsh fringe erosion. Journal of Coastal Research, 2: 427–436.

Redfield, A. C. 1965. Ontogeny of a salt marsh estuary. Science, 147: 50–55.

Silliman, B. R., and Bertness, M. D. 2002. A trophic cascade regulates salt marsh primary production. Proceedings of the National Academy of Science, 99: 10500–10505.

Silliman, B. R., and Newell, S. Y. 2003. Fungal farming in a snail. Proceedings of the National Academy of Science, 100: 15643–15648.

Silliman, B. R., and Zieman, J. C. 2001. Top-down control of *Spartina alterniflora* production by periwinkle grazing in a Virginia salt marsh. Ecology, 82: 2830–2845.

Wares, J. P., Goldwater, D. S., Kong, B. Y., and Cunningham, C. W. 2002. Refuting a controversial case of a human-mediated marine species introduction. Ecology Letters, 5: 577–584.

doi:10.1093/icesjms/fsn009