

Belowground herbivory increases vulnerability of New England salt marshes to die-off

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Abstract. Belowground herbivory is commonly overlooked as a mechanism of top-down control in vegetated habitats, particularly in aquatic ecosystems. Recent research has revealed that increased densities of the herbivorous crab *Sesarma reticulatum* have led to runaway herbivory and widespread salt marsh die-off on Cape Cod, Massachusetts, USA. Aboveground herbivory is a major driver of this cordgrass habitat loss, but the role of belowground grazing is poorly understood. *Sesarma* live in communal burrows typically consisting of 1–2 openings and containing 2–3 crabs. However, at die-off sites, burrow complexes can cover >90% of the low marsh zone, with crab densities as high as 50 crabs/m² and burrow opening densities of 170 openings/m². The magnitude of belowground *Sesarma* activity in association with salt marsh die-off provides an excellent opportunity to extend our knowledge of belowground herbivory impacts in coastal wetlands. Since *Sesarma* burrows allow access to cordgrass roots and rhizomes, and *Sesarma* are frequently restricted to burrows by thermal stress and predation, we hypothesized that belowground herbivory would be widespread in die-off areas. We experimentally demonstrate that *Sesarma* readily eat belowground roots and rhizomes in addition to aboveground cordgrass leaves. We then partitioned above- and belowground herbivory with field manipulations and found that belowground grazing is not only common, but can cause total plant mortality. Additional experiments revealed that plants remain vulnerable to belowground herbivory even after reaching a size refuge from aboveground grazing. This suggests that belowground herbivory contributes to salt marsh die-offs and adds to growing evidence that belowground herbivory is a widespread structuring force in plant communities that can limit habitat persistence.

Key words: aboveground herbivory; belowground grazing; burrowing; cordgrass die-off; herbivory; salt marsh; *Sesarma reticulatum*; *Spartina alterniflora*.

INTRODUCTION

The impacts of belowground herbivory are often overlooked in plant communities. Despite its potential to affect individual plant chemistry and fitness (e.g., Maron 1998, Bezemer and van Dam 2005), predator–prey interactions (e.g., Wäckers and Bezemer 2003, Preisser et al. 2006), and overall community structure (e.g., Brown and Gange 1989, Stein et al. 2010), our understanding of belowground processes lags behind more conspicuous aboveground interactions (Strong and Phillips 2001). This aboveground focus stems from an outdated view that belowground herbivory is not sufficiently different from aboveground herbivory to warrant separate study as well as the relative difficulty of studying biological interactions belowground (Anderson 1987, Strong and Phillips 2001). Recent evidence, however, indicates that the effects of belowground herbivory are fundamentally different from aboveground grazing and can be significantly more deleterious

for both the target plant (McGinley and Whitham 1985, Cantor and Whitham 1989) and the plant community as a whole (Brown and Gange 1989, Stein et al. 2010). Furthermore, recent technological advances have allowed enhanced study of belowground herbivory and other biotic interactions occurring in the rooting zone (Strong and Phillips 2001).

While evidence for the importance of belowground herbivory is accumulating from a variety of ecosystems, including coastal grasslands (Strong et al. 1999, Preisser 2003), agricultural systems (Rasmann and Turlings 2007, Erb et al. 2008, Kaplan et al. 2008), and mountain meadows (Cantor and Whitham 1989), little is known about its role in salt marshes (but see Smith and Odum 1981). We hypothesized that belowground herbivory could play an important role in salt marsh dynamics for several reasons. First, following decades in which salt marshes were thought to be structured exclusively by bottom-up forces (Odum 1971), the role of herbivores has recently become appreciated as consumer-driven salt marsh die-offs spread throughout the western Atlantic (Silliman et al. 2005, Jefferies et al. 2006, Alberti et al. 2008, Holdredge et al. 2009). Second, New England (USA) salt marshes are dominated by monospecific

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stands of relatively few plant species that occur in discrete, predictable zones that spread mainly by belowground clonal rhizomes (Benner et al. 1991, Bertness 1991). Third, an overlapping spatial distribution of common herbivorous crabs leads to strong, easily quantified interactions between grazers and plants. Fourth, herbivorous crabs maintain burrows at the same depth as marsh plant roots and rhizomes, making burrow–root interactions common (Seiple 1979). Moreover, burrowing herbivores also play an important role as bioturbators and can impact plant fitness through substrate disturbance in addition to direct consumption of roots (Andersen 1987). Finally, in New England, both above- and belowground herbivory on the cordgrass *Spartina alterniflora* is almost entirely by the native purple marsh crab *Sesarma reticulatum* (see Plate 1), which is the only species capable of causing die-off in Cape Cod (New England) marshes and whose burrows and grazing scars are easily identified (Holdredge et al. 2009). Herbivory by grasshoppers (*Orchelimum* sp.) and planthoppers (*Prokelesia* sp.) is less common, easily distinguished from *Sesarma* herbivory, and does not cause salt marsh die-off (Bertness et al. 2008).

Many plants are grazed simultaneously above- and belowground, and the additive and interactive effects of above- and belowground herbivory remain poorly understood (Bezemer et al. 2003). The recent crab-driven salt marsh die-off on Cape Cod, Massachusetts, USA, provides an opportunity to study the individual and interactive effects of above- and belowground herbivory. First reported in 2002, this die-off has been linked to grazing by the native, nocturnal herbivorous crab *Sesarma reticulatum* (Holdredge et al. 2009, Smith 2009). *Sesarma* create and maintain large, communal burrows and feed almost exclusively within 1–2 m of their burrows on the low marsh cordgrass, *Spartina alterniflora*. At natural densities, *Sesarma* burrows typically house 2–3 crabs with carapace widths between 20 and 35 mm, and have 1–2 surface openings. With decreased predation pressure on crabs, however, *Sesarma* densities can increase fourfold, resulting in significantly higher aboveground grazing that can entirely denude creek bank habitats (Altieri et al. 2012; Fig. 1). These die-off areas can be maintained for decades and spread laterally through the cordgrass zone as *Sesarma* locally deplete their food resource. At high-density sites, *Sesarma* burrows can harbor up to 25 individuals and have burrow densities as high as 170 surface openings/m². Contact between burrows and cordgrass roots and rhizomes is common at high crab densities, as are signs of belowground grazing. Belowground herbivory leaves characteristic clipped roots and grazing scars caused by *Sesarma* and can be associated with partial or complete aboveground mortality (Fig. 1). These patterns suggest that belowground herbivory can potentially drive local patterns of aboveground cordgrass mortality in marshes with high *Sesarma* densities and thus could contribute to wider patterns of salt marsh die-off.

In this study we examine the role of above- and belowground herbivory and *Sesarma* burrowing in limiting plant survivorship, degrading substrate quality, and contributing to patterns of plant distribution and persistence in New England salt marshes. We use field experiments and surveys to evaluate the biotic and abiotic pressures that necessitate *Sesarma* burrowing, investigate the impact of burrowing and herbivory by *Sesarma* at high densities, and elucidate the impacts of above- and belowground grazing on cordgrass. We hypothesized (1) that *Sesarma* are obligate burrow dwellers to avoid predation and thermal stress and that burrows are a major disturbance to the belowground root zone, (2) that burrows provide access to belowground plant material that is readily consumed by *Sesarma*, and (3) that belowground grazing affects above- and belowground plant mortality.

METHODS

Study sites

This study was conducted from August 2010 to September 2011 at 12 salt marsh sites on Cape Cod, Massachusetts, USA, that were previously found to represent the full spectrum of regional die-off severity. Classifications reflecting historical die-off severity (Coverdale 2010) were used to compare herbivory and burrowing effects across sites. Salt marshes on Cape Cod show striking zonation with both the native marsh crab *Sesarma* and tall-form cordgrass restricted to the low marsh zone in areas along creeks and drainage ditches that are tidally inundated twice daily (Bertness et al. 2009). All field experiments and surveys were conducted within this zone, and experiments examining the relative importance of above- and belowground grazing were conducted at sites with active herbivore-driven die-off.

The impact and drivers of Sesarma burrowing behavior

Sesarma excavate extensive, branching burrow complexes that are energetically costly to dig and maintain (Bertness and Miller 1984). To assess the extent of burrowing we quantified burrow volume and densities of burrow openings at each study site. We also performed a field experiment to test whether *Sesarma* are dependent on burrows to reduce predation and/or thermal stress.

The density of surface burrow openings was quantified in randomly placed quadrats (25 × 25 cm; $n = 15$ quadrats/site). Only burrows of >20 mm diameter were included to avoid inclusion of *Uca pugnax* burrows, which typically have diameters <15 mm and are further distinguished by the presence of feeding pellets.

Burrow volume was estimated by measuring the belowground dimensions of 10 randomly selected replicate burrows within the rooting zone (0–10 cm depth) per site. The total length of all burrow branches from a given burrow opening were measured within 10 cm of the opening, and multiplied by the average of three burrow diameter measurements. The proportion of



FIG. 1. (A) Photograph of heavily burrowed and eroding banks with high *Sesarma* burrow density and widespread consumption of cordgrass. The photo was taken in August 2011 by T. C. Coverdale at one of the study sites (Parker River site, West Yarmouth, Massachusetts; 41°38'12.74" N, 70°13'33.46" E). (B) Examples of intact, aboveground grazed, and belowground grazed cordgrass ramets. Note the root blackening in the ramet grazed aboveground (middle) and the complete aboveground mortality of the ramet grazed belowground (right).

peat bank excavated at each site was estimated by multiplying mean burrow volume by the mean burrow opening density in the survey area, and then dividing by the potential volume of peat in the survey area. Data were arcsine square-root transformed to meet assumptions of parametric statistics and analyzed with a single-factor ANOVA to investigate differences between healthy and die-off sites.

To quantify the effect of *Sesarma* herbivory on peat breaking strength, bars of peat ($1 \times 5 \times 10$ cm; $n = 15$ peat bars per zone per site) were collected from heavily grazed banks and adjacent vegetated areas at four sites experiencing conspicuous die-off in November 2010. Only bars without burrows were included in the analysis to isolate the effects of reduced belowground biomass on peat breaking strength. Each bar was anchored on one end and attached to a 5-kg spring scale at the other end

with a large binder clip. The scale was drawn back until the peat bar broke and the maximum pull force was recorded. Data were log-transformed and analyzed using a nested ANOVA with sites treated as independent replicates and individual tearing-strength data nested within their respective zones for each site.

To test the hypothesis that *Sesarma* are dependent on burrows because of predation and temperature stress, we ran a fully factorial experiment crossing predator exclusion and burrow access at two sites in August 2010. Predator treatments consisted of either a cage with roof and walls ($40 \times 40 \times 40$ cm) or an unmanipulated control, and burrow access treatments consisted of either a floor (40×40 cm) that prevented burrow access or an unmanipulated control. Cages and cage floors were constructed of galvanized hardware cloth (12 mm mesh). Replicates were placed > 2 m

apart ($n = 15$ replicates/treatment combination). Crabs were tethered with ~ 15 cm of braided fishing line to the center of each plot to allow access to burrows in treatments without floors, and their survivorship and cause of mortality were scored after 24 h. Previous tethering experiments (Holdredge et al. 2009, Altieri et al. 2012) revealed that *Sesarma* behavior and survivorship are not affected by tethering, and that tethers remain intact, dead crabs and broken carapaces, which signify mortality by thermal stress and predation, respectively. Data were arcsine square root transformed and analyzed using a two-factor ANOVA to investigate the role of predation and temperature stress in driving patterns of mortality.

Sesarma feeding preference and cordgrass size refuge

To assess potential feeding preferences of *Sesarma* for cordgrass roots and leaves, we conducted a laboratory feeding trial in which individual *Sesarma* were presented a choice of either the belowground or aboveground portion of cordgrass ramets. Individual *Spartina alterniflora* ramets (18–20 cm tall) were collected from a single source site and transported to the laboratory where they were rinsed in saltwater, patted dry, and weighed. Pairs of plants were placed in nested 4-L buckets with two 3-mm holes drilled in the floor of the inner bucket ($n = 15$ pairs). One plant was placed in its natural orientation with leaves exposed within the inner bucket and roots protected in the space between buckets, while the other was placed with roots exposed and the leaves protected between buckets. A single *Sesarma* was randomly placed in each bucket with ~ 2 cm of seawater and allowed to feed overnight on a 12:12 h light : dark cycle. *Sesarma* fed naturally at the onset of the dark period and both plant components were available for consumption for the duration of the experiment. Above- and belowground biomasses were quantified after 24 h, log-transformed to meet normality assumptions, and analyzed using a paired t test to determine if *Sesarma* showed a preference for root or leaf material.

To assess the ability of *S. alterniflora* to reach a size refuge from aboveground herbivory, we quantified the intensity of herbivory for two size classes (<15 cm and >50 cm stem height) of cordgrass. Ten replicate plants of each size class were examined for signs of *Sesarma* grazing at each survey site. *Sesarma* grazing produces characteristic rasped and frayed edges on partially consumed plants, making it easy to distinguish from insect herbivory (Holdredge et al. 2009). Data were log-transformed and analyzed using a split-plot ANOVA to test for differences in grazing intensity on large and small plants at sites with high and low herbivore pressure.

Due to the potential for belowground grazing to contribute to patterns of cordgrass die-off, we also quantified the ability of cordgrass to reach a size refuge from either above- or belowground herbivory by transplanting single cordgrass ramets of two size classes (tall plants 113 ± 2 cm [mean \pm SE] and short plants 19

± 1 cm, $n = 15$ ramets/ treatment) from a single source location into a heavily burrowed creek bank (39 ± 6 burrows/m²) near burrow openings to maximize the potential for grazing. All plants were collected after two weeks in the field and scored in two ways. First, the proportion of above- and belowground biomass consumed by *Sesarma* was quantified by comparison with pre-deployment photographs. Second, live and dead aboveground biomass were separated, dried at 60°C to a constant mass, and weighed to determine the percentage of aboveground biomass that remained alive at the conclusion of the experiment. Complete aboveground mortality in the absence of aboveground grazing damage indicated indirect plant death due to belowground grazing. Data were analyzed with ANOVA to determine whether above- and belowground grazing intensity differed between plant size classes and whether the percentage of aboveground biomass remaining alive differed at the end of the experiment.

Relative impact of above- and belowground grazing

To assess the relative impact of above- and belowground grazing by *Sesarma*, we deployed a fully factorial caged-*Spartina* transplant experiment crossing access to above- and belowground plant components in May 2011 in heavily burrowed *Sesarma* habitat (71 ± 10 burrows/m² [mean \pm SE]). Uniformly sized cordgrass culms (12–15 stems <20 cm tall and associated roots and rhizomes) were collected from a single source site with a 7-cm-diameter corer and transplanted into 7-cm-diameter holes after being randomly assigned to one of four treatments that crossed belowground and aboveground grazing: open, caged belowground only, caged aboveground only, and caged above- and belowground ($n = 8$ culms/treatment). Belowground cages consisted of 6-mm mesh hardware cloth wrapped tightly around the sediment core with mesh caps on the top and bottom of the cage to prevent crab access to belowground material. Aboveground cages consisted of hardware-cloth tubes with a hardware-cloth cap at the sediment surface that enclosed the leaves and stems of the cordgrass culm. Above- and belowground caged treatments were wrapped in a single piece of hardware cloth with a cap at the bottom to prevent burrowing into the root zone. After three months all plants were divided into live above- and belowground components, dried at 60°C for two weeks, and weighed. Biomass data were log-transformed to meet normality assumptions for ANOVA. Data were analyzed to determine the separate and interactive impacts of above- and belowground herbivory on aboveground, belowground, and total biomass.

RESULTS

The impact and drivers of Sesarma burrowing behavior

The density and volume of *Sesarma reticulatum* burrows were both significantly higher at *Spartina alterniflora* die-off sites than at healthy sites ($F_{1,10} =$

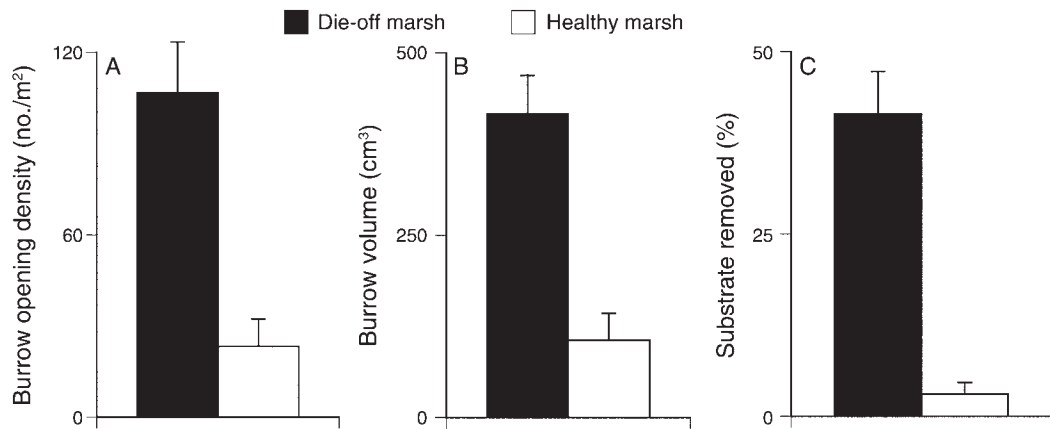


FIG. 2. Results of *Sesarma* burrow surveys at healthy (white) and die-off (black) cordgrass sites on Cape Cod, Massachusetts, USA. The (A) density of burrow openings, (B) individual burrow volume, and (C) percentage of peat substrate removed by burrowing are significantly higher at die-off sites. Data are means and SE.

14.8, $P = 0.0013$ and $F_{1,10} = 50.6$, $P < 0.0001$, respectively; Fig. 2). The number of burrow openings ranged from 0 openings/m² at sites with few *Sesarma* to >170 openings/m² at heavily impacted sites. At die-off sites, *Sesarma* burrows displaced as much as 66% of the total belowground volume in the top 10 cm of peat, whereas sites with low *Sesarma*-driven die-off had correspondingly low peat excavation (Fig. 2). Sites with greater historical die-off also tended to have both wider (23.5 ± 7.5 mm vs. 6.6 ± 1.4 mm [mean \pm SE]) and longer (221.3 ± 18.0 mm vs. 95.7 ± 32.8 mm) burrows than healthy sites.

Sesarma herbivory and the associated removal of above- and belowground plant material had a significant effect on peat breaking strength. Peat from heavily grazed areas was significantly weaker than peat from adjacent vegetated areas ($F_{6,112} = 7.04$, $P < 0.0001$). The average breaking strength of vegetated, unburrowed

peat was >2 times greater than adjacent, burrowed peat (3.73 ± 0.19 kg vs. 1.78 ± 0.18 kg [mean \pm SE]).

Data from each treatment in the *Sesarma* predation and temperature stress experiment did not differ between sites ($\chi^2 \leq 1.42$, $df = 1$, $P \geq 0.23$) and was pooled for analyses. Predation and thermal stress were major drivers of *Sesarma* mortality, but were dramatically alleviated by access to burrows (predation-exclusion effect, $F_{1,4} = 8.25$, $P < 0.05$; burrow-exclusion effect, $F_{1,4} = 190.82$, $P < 0.001$; Fig. 3). Survivorship was lowest in the cage-floor-only treatment, which exposed *Sesarma* to both predation and heat stress; signs of predation (carapace fragments, scattered appendages) were the most commonly encountered indicator of mortality source after 24 h. Survivorship was slightly higher when predators were excluded, and dramatically higher when access to the burrows was allowed. The majority of crabs in predator-exclusion cages with access to burrows survived, with the only source of mortality

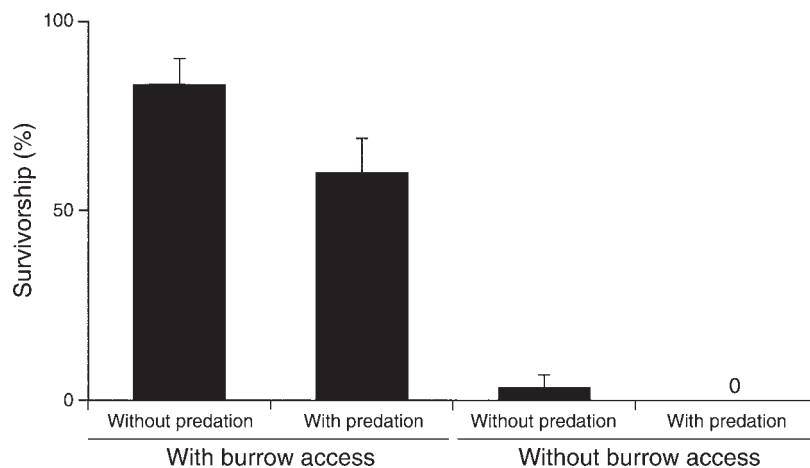


FIG. 3. Results of *Sesarma* tethering experiment with predator-exclusion and burrow-access manipulations. Survival was highest in treatments with burrow access and declined sharply when burrow access was manipulated with cage floors. Predation and thermal stress were major drivers of *Sesarma* mortality. Data are means and SE.

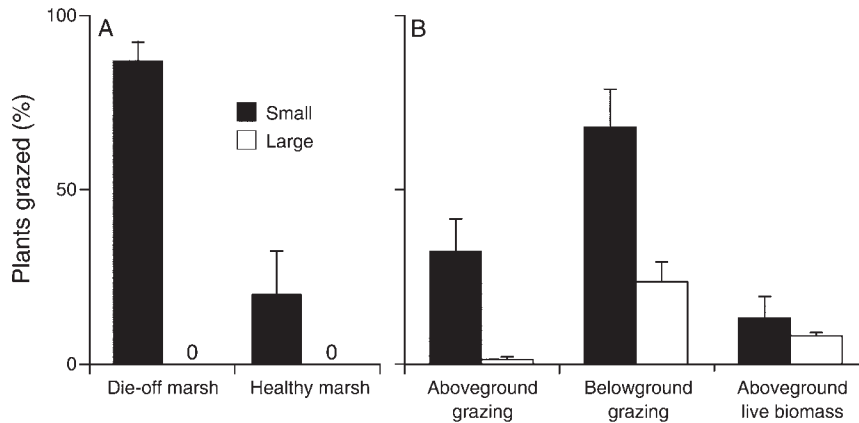


FIG. 4. (A) Results of survey of size refuge at healthy and die-off sites. (B) Results of experimental grazing assay. Small (<20 cm) plants were grazed aboveground significantly more at die-off than healthy sites. Large plants (>50 cm) reached a size refuge from aboveground but not from belowground herbivory and suffered similar aboveground mortality from belowground grazing. Data are means and SE.

being predation by burrow-dwelling predators (e.g., green crabs *Carcinus maenas*), which were likely hidden in burrows within the cage at the onset of the experiment.

Sesarma feeding preference and cordgrass size refuge

There was no difference between initial plant biomass between treatments ($\chi^2 = 25.8$, $df = 1$, $P = 0.58$). All *Sesarma* consumed both above- and belowground material in the 24 h laboratory feeding trial. *Sesarma* consumed $19.5\% \pm 3.2\%$ (mean \pm SE) of exposed roots and $15.6\% \pm 2.0\%$ of exposed leaves. Despite showing a slight preference for belowground material in $\sim 75\%$ of replicates, there was no significant difference in *Sesarma* preference for above- or belowground material ($F_{1,14} = 1.67$, $P = 0.115$).

Aboveground grazing surveys revealed a strong plant size \times site type interaction. Aboveground grazing at die-off sites was significantly higher on plants <15 cm tall than on plants >50 cm tall, and was greater than grazing on any plants at the healthy sites (site type \times plant size effect, $F_{1,10} = 15.11$, $P = 0.003$; Fig. 4A). In fact, no plants >50 cm tall showed any signs of aboveground *Sesarma* herbivory across all sites.

Sesarma grazing in the size-specific grazing transplant experiment was significantly more intense on small plants than on large plants ($F_{1,28} = 13.09$, $P = 0.0012$; Fig. 4B). *Sesarma* consumed approximately one-third of the aboveground biomass of small plants in the size-specific experiment, and aboveground herbivory was recorded on only a single leaf on one large plant. Combined with the field survey and laboratory feeding trial, these results indicate an aboveground size refuge from *Sesarma* herbivory. Belowground grazing, however, was higher than aboveground grazing for both cordgrass size classes: more than half of the belowground root and rhizome material was consumed across the short cordgrass plants (Fig. 4B). *Sesarma* burrows

naturally extended to include experimental plant roots during the course of the experiment and, where this occurred, nearly all of the belowground material was consumed. Similarly, *Sesarma* consumed nearly a quarter of the roots and rhizomes of tall plants.

Both short and tall individual cordgrass ramets showed widespread aboveground stress and mortality due to belowground grazing. Over half of the tall plants suffered complete mortality as a result of only belowground herbivory, which rivaled the mortality rate of 66% for short plants suffering from the combined effects of both above- and belowground grazing. As a consequence, the percentage of total aboveground material alive at the conclusion of the experiment did not differ between treatments ($F_{1,26} = 0.19$, $P = 0.67$; Fig. 4B).

Relative impact of above- and belowground grazing

Aboveground herbivory had a significant effect on aboveground, belowground, and total dry biomass ($F_{1,23} \geq 20.50$, $P < 0.001$ for all cases; Fig. 5), as expected from previous work (Holdredge et al. 2009). Belowground herbivory also had a significant effect on aboveground, belowground, and total biomass ($F_{1,23} \geq 4.84$, $P < 0.05$ for all cases). The most detrimental effects on cordgrass biomass resulted from the treatment that combined both above- and belowground herbivory, which significantly depressed both aboveground and belowground biomass (Fig. 5).

DISCUSSION

While aboveground herbivory by *Sesarma* is the most conspicuous driver of salt marsh die-off on Cape Cod, Massachusetts, USA (Holdredge et al. 2009, Altieri et al. 2012), our results suggest that belowground herbivory by *Sesarma* contributes to patterns of salt marsh die-off in several distinct ways. In addition to directly consuming belowground plant material, belowground

herbivory alone is sufficient to impact aboveground cordgrass biomass and survival, and is the only form of herbivory capable of killing larger plants that have reached a refuge size from aboveground herbivory. Furthermore, belowground herbivory and burrowing weakens peat banks and decreases the potential for recovery in die-off marshes.

Are Sesarma obligate burrow dwellers?

Based on the high energy costs of excavating and maintaining extensive communal burrow complexes, we hypothesized that *Sesarma* are obligate burrow dwellers that utilize burrows to avoid predation and thermal stress. A similar reliance on burrows has been demonstrated for mangrove crabs (Warner 1969, Warren 1990). Our experimental results demonstrate that similar pressures drive burrow use in salt marshes: without burrow access, *Sesarma* were more likely to succumb to predation and thermal stress, and experienced 100% mortality when exposed to both types of stress for only 24 h (Fig. 3).

This obligate reliance on burrows has led to extensive burrowing in areas of high *Sesarma* density (Fig. 2). At sites with long histories of *Sesarma* activity, burrows can displace >66% of the belowground volume in the cordgrass root zone. Sites with higher *Sesarma* densities also had wider and longer burrows, perhaps as a result of the increased volume necessary to accommodate more crabs per burrow or due to increased belowground foraging following aboveground food limitation. The greater burrow width, length, and volume at marsh die-off sites increases the incidence of *Sesarma*-root interactions, allows higher rates of belowground herbivory and reduces the amount of intact peat available for root growth and vegetative expansion.

Just as dense stands of aboveground cordgrass play a vital role in marsh accretion and stabilization (Redfield 1965, Gleason 1979), belowground cordgrass roots and rhizomes play a vital role in marsh health and resiliency. The storage of resources in belowground structures is important for cordgrass survival through New England winters following the senescence of aboveground material and is critical for vegetative expansion into naturally occurring bare spaces (Shumway and Bertness 1994). Belowground cordgrass roots and rhizomes also contribute to peat toughness by physically binding peat (Niering and Warren 1980) and increase resistance to creek-bank calving, a phenomenon that is common in die-off marshes. Similar losses of sediment accretion and binding have been observed after loss of aboveground plant structures (Altieri et al. 2012), suggesting that the combination of above- and belowground herbivory may dramatically increase shoreline erosion and peat calving in areas where both impacts are common.

What are the consequences of Sesarma feeding patterns?

Results from laboratory trials and field experiments and surveys demonstrated a clear distinction between

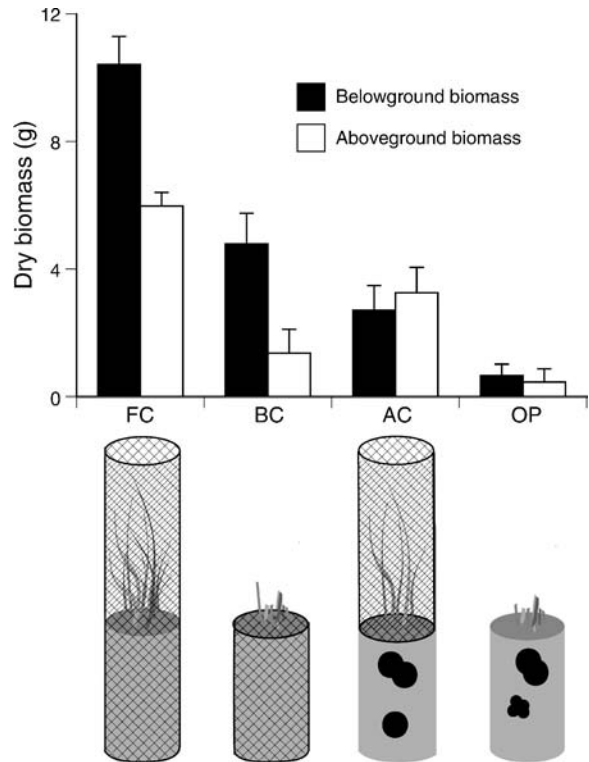


FIG. 5. Results of the partitioned grazing experiment. Fully caged (FC) plants had significantly higher above- and belowground biomass than did plants caged only belowground (BC), only aboveground (AC), or neither (OP, open). Aboveground and belowground grazing had significant effects on aboveground, belowground, and total plant biomass. Data are means + SE.

patterns of aboveground and belowground herbivory in relation to plant size (Fig. 4). Laboratory feeding trials demonstrated that there is no preference for above- or belowground material for short plants, while field surveys indicated that cordgrass reaches a size refuge from aboveground *Sesarma* grazing at ~50 cm. Belowground plant material, however, was vulnerable to *Sesarma* grazing regardless of plant height, and our field experiments confirmed that *Sesarma* can gain access to roots and rhizomes by burrowing and consume the belowground portion of both short and tall plants. This resulted in similar mortality of tall and short plants, even though *Sesarma* failed to attack the aboveground portion of tall plants. The size refuge from aboveground, but not belowground, herbivory suggests that belowground herbivory may play an important role in promoting and maintaining marsh die-off on Cape Cod.

Several morphological differences between size classes could explain the difference in vulnerability to herbivory. *Sesarma* typically consume aboveground plant material by clipping through the base of the stem and feeding the plant into their mouths from base to tip, or bending the outer leaves to the sediment surface and consuming them from tip to base (T. Coverdale,



PLATE 1. A large *Sesarma reticulatum* exits a burrow during a predawn foraging trip in a denuded creek bank at Wings Neck Marsh, Cape Cod, Massachusetts, USA. The only remaining cordgrass nearby shows characteristic signs of shredded and browned aboveground stems resulting from above- and belowground herbivory, respectively. Photo credit: T. C. Coverdale.

personal observation). Taller plants have thicker basal diameters, potentially preventing *Sesarma* from clipping through the stem. They also have a greater basal stem height below the first node, which could limit access to thinner leaf tips via bending. More mature plants may also employ chemical and/or structural defenses. The exact mechanism of cordgrass size refuge deserves further study, but the ability of plants to defend against aboveground herbivory suggests that herbivory on roots and rhizomes may play an important role in maintaining die-offs in areas dominated by tall cordgrass ramets.

Herbivory effects and implications for salt marsh recovery

The results of our partitioned herbivory experiment indicate that both aboveground and belowground herbivory have the potential to affect total plant biomass and survival (Fig. 5). While it is perhaps not surprising that belowground herbivory reduced total and belowground biomass, the associated indirect reduction in aboveground plant biomass has important implications for the trajectory of salt marsh die-off on

Cape Cod. Size-independent belowground herbivory affects the potential for the low marsh to rebound from die-off in two ways. First, consumption of the belowground roots and rhizomes of plants that have attained a size refuge from aboveground herbivory can lead to partial or complete aboveground mortality, negating the effects of an aboveground refuge. Second, by consuming rhizomes as they invade excavated burrows, belowground herbivory can directly reduce the ability of cordgrass to spread vegetatively and recolonize denuded areas, while burrow excavation exposes roots to stressful belowground conditions. Belowground roots and rhizomes growing into burrow openings are vulnerable to belowground herbivory, decreasing the potential for recovery at sites with well-established, widespread burrow complexes.

Aboveground herbivory by *Sesarma* also reduced total, aboveground and belowground biomass. This suggests that, in addition to the demonstrated effects of aboveground herbivory on salt marsh plant communities (Holdredge et al. 2009; Altieri et al. 2012), grazing

on stems and leaves may promote salt marsh die-off via more cryptic pathways. First, by reducing the photosynthetic potential of plants during the growing season, aboveground grazing may indirectly affect the growth and spread of adventitious roots and the recolonization of herbivore-driven bare patches. Research on succession in stress-driven bare patches has shown that vegetative growth is the dominant mode of cordgrass reproduction (Shumway and Bertness 1994). This could act in concert with direct belowground consumption of roots to reduce recovery potential. Second, by causing partial belowground mortality and biomass loss, aboveground grazing likely reduces the ability of plants to seasonally store nutrients in belowground rhizomes, potentially leading to multiyear cycles of reduced storage and increased vulnerability to subsequent aboveground herbivory.

Implications for salt marsh die-off

Salt marshes are one of the most ecologically and economically valuable coastal ecosystems in the world (Barbier et al. 2011) and salt marsh die-off is among the greatest threats to these systems (Bertness and Silliman 2008). Belowground burrowing and herbivory by *Sesarma* contributes to the growing problem of New England salt marsh die-off in two ways. First, by directly causing belowground mortality and indirectly reducing aboveground plant biomass, belowground herbivory exacerbates the plant mortality that has already led to widespread habitat loss. Crab herbivory at heavily impacted sites has been directly tied to a loss of salt marsh habitat that rivals the contribution of decades of human development (Coverdale 2010). Second, by removing up to ~70% of the peat substrate within the cordgrass root zone, *Sesarma* burrowing increases the vulnerability of belowground plant components to additional grazing, increases the magnitude of creek-bank erosion and the likelihood of creek-bank calving, and reduces available nutrients for plant growth and reproduction. *Sesarma* burrowing and belowground herbivory threaten to break the cycle of accretion and marsh expansion that is critical to marsh maintenance and expansion by destroying the creek-bank habitat most critical to marsh growth.

CONCLUSIONS

Our results add to a growing appreciation of belowground herbivory as a major structuring force in plant communities. Recent attention to belowground herbivory has demonstrated that the impacts of above- and belowground grazing can differ dramatically. While many plants, including cordgrass, can recover from nearly complete aboveground consumption (McGinley and Whitham 1985) and others even benefit from moderate to high levels of aboveground herbivory (Paige and Whitham 1987, Hik and Jefferies 1990), intense belowground herbivory is nearly always deleterious (Cantor and Whitham 1989). Here, we find support for

the latter: belowground herbivory by *Sesarma* decreases above- and belowground biomass and reduces plant survivorship in the absence of aboveground herbivory. Because *Sesarma* crabs are large relative to previously studied root-consuming arthropods, and can consume up to 100% of cordgrass belowground biomass, their impact on cordgrass growth and survival represents the upper end of belowground grazing intensity studied to date.

The role of belowground herbivory is often overlooked, particularly in systems with conspicuous aboveground grazers. Nowhere is this more apparent than salt marshes, where the loss of aboveground cordgrass disrupts the very processes that build and maintain the ecosystem. Belowground processes, however, clearly play an important role in driving patterns of aboveground plant distribution by directly and indirectly impacting cordgrass survival and reproduction. Accordingly, the role of belowground herbivory must be incorporated into our conceptual understanding of the dynamics of this and other ecosystems.

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