

Substrate mediates consumer control of salt marsh cordgrass on Cape Cod, New England

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Abstract. Cordgrass die-offs in Cape Cod, Massachusetts, USA, salt marshes have challenged the view that the primary production of New England salt marshes is controlled by physical factors. These die-offs have increased dramatically over the last decade and are caused by the common herbivorous marsh crab *Sesarma reticulatum*, but other factors that control crab impacts remain unclear. We examined the influence of plant nutrient supply and disturbances on *Sesarma* herbivory by fertilizing plots and creating experimental disturbances, since previous studies have revealed that they mediate the intensity of herbivory in other Western Atlantic marshes. Neither nutrient enrichment nor experimental disturbances affected crab grazing intensity despite their strong effects in other marsh systems. Within and among Cape Cod salt marshes, however, *Sesarma* burrows are concentrated on peat substrate. Surveys of 10 Cape Cod marshes revealed that burrow density, depth, and complexity are all much higher on peat than on sand or mud substrate, and paralleling these patterns, crab abundance, herbivore pressure, and the expansion of die-off areas are markedly higher on peat than on other substrates. Complementing work hypothesizing that predator release is triggering increased crab herbivory in Cape Cod marshes, these results suggest that cordgrass die-offs are constrained to the peat substrate commonly found on the leading edge of marshes and that the vulnerability of New England salt marshes to crab herbivory and future die-offs may be predictable.

Key words: Cape Cod, New England, USA; consumer pressure; crab herbivory; marsh die-off; peat substrate; salt marsh productivity; *Sesarma reticulatum*; *Spartina alterniflora*; top-down control.

INTRODUCTION

Historically, salt marsh primary production has been considered to be regulated by bottom-up forces (sensu Power 1992, Strong 1992). Physical factors like temperature, salinity, and nutrients are thought to regulate the primary production of salt marsh plants (Teal 1962, Odum 1971, Mendelsohn and Morris 2000). A corollary to this paradigm is that consumers play little role in controlling salt marsh primary production (Smalley 1960, Teal 1962).

Recent research, however, has suggested that human disturbances are triggering consumer control of salt marsh primary production across the western Atlantic (Bertness and Silliman 2008). Rising snow geese populations, fueled by North American nitrogen fertilizer subsidies, have denuded Canadian sub-Arctic marshes, leading to their catastrophic collapse (Jefferies 1997). In New England, localized eutrophication, driven by shoreline development, is increasing insect herbivory and suppressing salt marsh primary production (Bertness et al. 2008). On the Southeastern and Gulf coasts of North America, runaway consumption by native snails,

overfishing, and climate change have precipitated extensive cordgrass die-offs (Silliman and Bertness 2002, Silliman et al. 2005). On the Atlantic coast of South America, high densities of the herbivorous crab, *Chasmagnathus granulata*, likely a consequence of overfishing, maintain large, unvegetated areas in salt marshes (Costa et al. 2003, Alberti et al. 2007). These examples suggest that human disturbances are triggering consumer control in salt marsh systems that have historically been under strong bottom-up control (Bertness and Silliman 2008).

Most recently, salt marsh die-off, characterized by the extensive loss of *Spartina alterniflora* (cordgrass) in the low marsh and along creek banks (Fig. 1) has been reported on Cape Cod in New England (Massachusetts, USA). These events were initially attributed to drought, fungal disease and direct human disturbances (see Smith [2006] for an overview), but simple field experiments have revealed that grazing by a native, burrowing crab, *Sesarma reticulatum* (hereafter referred to as *Sesarma*), is responsible (Holdredge et al. 2009). *Sesarma* is one of the most common macroinvertebrates in western Atlantic salt marshes, from Cape Cod to the Gulf Coast (Gosner 1979, Subrahmanyam and Coultas 1980). They are known herbivores, but our understanding of their impact on marsh systems is entirely anecdotal. The most widely cited paper on *Sesarma* ecology is an observational study noting that *Sesarma* burrows are often

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surrounded by bare, unvegetated substrate that may be maintained by crab grazing (Crichton 1960). They can live communally in large burrow complexes (Seiple 1979, Seiple and Salmon 1982), but their general ecology is largely unstudied.

We recently reported the results of field experiments and surveys demonstrating that *Sesarma* herbivory is responsible for the low-marsh cordgrass die-offs that are epidemic in Cape Cod salt marshes (Holdredge et al. 2009). Nearly 70% of outer and middle Cape Cod marshes are currently experiencing cordgrass die-offs, and *Sesarma* have denuded 10–90% of creek bank habitats within these marshes. Historic photographs reveal that the rate of die-off expansion has more than doubled over the past decade and currently die-off areas are expanding by >8% per year. In contrast, *Sesarma* is common in nearby Narragansett Bay, but its densities are limited there by predators (e.g., blue crabs and tautog) and die-offs are not occurring. On Cape Cod, predation pressure on *Sesarma* is weak, suggesting that the elevated *Sesarma* densities and herbivory are a consequence of predator release (Holdredge et al. 2009).

While elevated herbivore densities appear to be the leading cause of these Cape Cod cordgrass die-offs, factors influencing *Sesarma* distribution and grazing patterns within and among marshes have yet to be investigated. In other marsh systems, natural disturbance, nitrogen enrichment, and substrate preferences have all been shown to mediate the herbivore intensity and may be modulating the occurrence and expansion rate of die-offs on Cape Cod as well.

Natural disturbances often escalate herbivore pressure in ecosystems. Disturbances can kill dominant space holders and generate free space for weedy species that are poorly defended from grazers (Connell and Slayter 1977). This can lead to increased grazer densities and impacts in disturbed habitats (Sousa 1984). In salt marshes, insect (Rand 1999) and small-mammal (Bromberg Gedan et al. 2009) herbivory are higher in disturbance-generated bare space than in undisturbed vegetation. Cape Cod cordgrass die-offs are most frequent on the terrestrial border of the low marsh, a habitat dominated by cordgrass (*Spartina alterniflora*) monocultures in undisturbed marshes, but also where floating plant debris or wrack commonly accumulates, smothering underlying vegetation and generating bare space (Bertness and Ellison 1987). Disturbance-generated bare space in New England salt marshes is usually colonized vegetatively by cordgrass, and since marsh herbivores often prefer young over older shoots (Bortolus and Iribarne 1999), crab grazing could maintain and possibly expand bare patches created by wrack disturbance. The role of disturbance in Cape Cod die-offs, however, has not been explored.

Nutrient enrichment can also stimulate consumer control of plants in natural systems (Auerbach and Strong 1981, Menge 1992). Eutrophication is pervasive in coastal systems (Howarth et al. 2002, Lotze et al.



FIG. 1. Burrow-riddled creek bank at the Cape Cod National Seashore, Wellfleet, Massachusetts, USA in June 2007, illustrating *Sesarma* burrowing activity. Photo credit: M. D. Bertness.

2006), and by releasing plants from nutrient limitation and increasing plant palatability (Pennings et al. 1998), can trigger herbivore pressure and consumer control of plant productivity. Studies in marsh systems have strongly supported the idea that nutrient enrichment can trigger increased consumer control of primary productivity (Stiling et al. 1991, Gough and Grace 1998, Silliman and Zieman 2001, Bertness et al. 2008). Whether nutrient supplies influence crab grazing in New England salt marsh systems or contribute to marsh die-off, however, has not been addressed.

Substrate characteristics can also influence consumer patterns by affecting the distribution and abundance of benthic consumers (Raffaelli and Hawkins 1996, Bertness 2006). In soft-sediment habitats, substrate composition can affect the burrowing and feeding efficiency of benthic invertebrates (Peterson 1982, Lipcius and Hines 1986). In salt marshes, *Uca pugilator* (sand fiddler crab) and *Uca pugnax* (mud fiddler crab), which deposit feed by sieving surface substrate particles with their mouthparts (Crane 1975), have substrate-specific field distributions (Teal 1958). Marsh substrate types also affect the distribution and morphological traits of crab burrows. In soft, muddy substrate, crabs readily form burrows, but due to poor structural support, longer-term burrow-maintenance costs are high (Bertness and

Miller 1984). Marsh peat, the dense accumulation of live and dead marsh plant roots and rhizomes, is more difficult to burrow into, but burrows in peat are not as prone to collapse and have low maintenance costs (Bertness and Miller 1984).

In New England salt marshes, *Sesarma* burrows appear to be most abundant in peat substrate (M. D. Bertness, *personal observation*). The association of *Sesarma* burrows with peaty organic mud rather than sandy inorganic substrates, has been previously noted (Seiple 1979). Since *Sesarma* build extensive, interconnected burrows with multiple openings, their burrows could be dependent on peat for structural support and may be limited in mud or sand substrates due to high burrow maintenance costs and the likelihood of burrow collapse. This pattern, however, has never been examined in peat-based marshes and the consequences for the distribution of *Sesarma* burrowing and herbivory impacts have not been explored.

This paper builds on recent findings that *Sesarma* herbivory is generating cordgrass die-offs in Cape Cod marshes by examining factors that may influence crab herbivory patterns. We examine three hypotheses: (1) disturbances that generate bare space can intensify *Sesarma* herbivory, potentially stimulating the development of die-offs, (2) elevated plant nutrient status triggers *Sesarma* herbivory and cordgrass die-off, and (3) the distribution and impact of *Sesarma* in salt marshes is dictated by peat substrate availability. Our results thus develop a predictive understanding of how *Sesarma* herbivory may impact the future of New England salt marshes.

METHODS

We conducted experiments at the Cape Cod National Seashore (CCNS) (41°55'37.86" N, 70°4'16.48" W) and Indian Neck (41°54'37.61" N, 70°0'55.95" W) marshes in Wellfleet, Massachusetts, USA. Both sites are extensive salt marshes characterized by large low marsh areas that are largely devoid of vascular plants and riddled with crab burrows. Previous research has shown that these sites are experiencing cordgrass die-offs generated by crab herbivory and are representative of Cape Cod salt marshes (Holdredge et al. 2009). All our work was done on the terrestrial border of the low marsh, the highest area of the marsh that is flooded daily by tides, and the tidal height where cordgrass die-off is most commonly occurring on Cape Cod. We also conducted our experiments entirely within this zone to isolate the factors of interest (i.e., disturbance, nutrients, substrate) from the effects of variation in substrate elevation and related factors that potentially vary with submergence time.

Do natural disturbances trigger herbivore-driven die-off of salt marshes?

To examine the hypothesis that natural disturbances can trigger increased *Sesarma* herbivory on cordgrass, we conducted a fully factorial experiment crossing the

presence of crabs with experimental wrack disturbance at the CCNS marsh. In August 2006, we established eight, 3 × 3 m plots in the cordgrass zone, separated by at least 10 m and haphazardly placed along a 300-m stretch of shoreline. The area used for this experiment was 50 m from a large (>150 m²) active die-off area where crab herbivory was maintaining the die-off (Holdredge et al. 2009). The experimental area had a heavy peat base, similar to the nearby die-off area, and high *Sesarma* burrow densities. To create experimental bare areas, vegetation was removed at ground level with a line trimmer and then covered with a black, plastic shade cloth secured to the substrate with stakes to suppress regrowth (see Bertness and Shumway 1994). In April 2007, after the plots had been covered for nine months, the cloth covers were removed. This creates bare areas that closely mimic bare patches generated by wrack coverage (Bertness and Ellison 1987).

To quantify herbivore pressure in the disturbance plots and unmanipulated controls, we transplanted consumer assay cores containing cordgrass culms into the plots. Each experimental bare area and vegetated unmanipulated control area received three transplanted culms (5–8 stems/culm) of *Spartina alterniflora* and the culms were randomly assigned to one of the following treatments: (1) crab exclusion cage, (2) uncaged control (unmanipulated grass), or (3) procedural cage control. Culms (20 cm long) were collected at the CCNS marsh with a 7.5-cm-diameter corer. Caged treatments were made by surrounding the culms with a 1-m-tall galvanized hardware cloth sleeve (7-mm mesh size) and inserting the caged culm into a core hole flush with the marsh surface in a given plot. Cages extended 20 cm below the marsh surface to prevent crab burrowing into cages and were 80 cm tall to prevent crabs from climbing into the cages. Cage controls were identical, but with a 10 × 10 cm door removed from the side to allow crab access. These cages have been successfully used to quantify crab herbivory in our previous work (Holdredge et al. 2009).

We scored the transplants for grazer damage (percentage leaves grazed) every two weeks for two months. Only leaf damage characterized by distinct *Sesarma* shredding was included. Laboratory feeding trials revealed that *Sesarma* grazing on cordgrass was characterized by uneven leaf shredding and rasping, which made leaf scars that were readily distinguishable in the field (Crichton 1960). *Sesarma* damage on cordgrass was easy to distinguish from insect herbivory, the only other common herbivory at the site (see Bertness et al. [2008] for discussion of insect herbivory on cordgrass). We converted the final grazer damage into a rate (percentage of leaves grazed per day), and analyzed whether disturbance triggers increased crab herbivory with a split-plot ANOVA, with experimental disturbance as the plot-level factor and caging treatment as the within-plot factor. Data for this and other analyses were transformed as necessary to meet ANOVA assumptions.

To assess whether *Sesarma* grazing in experimental disturbance patches was similar to grazing in existing die-off areas, we transplanted caged, uncaged, and cage-control cordgrass assay cores into existing die-off areas in June 2007. Ten replicate exclusion cages, controls, and cage controls (as described above) were transplanted into die-off areas 100–200 m from the experimental patches at the same elevation, spaced at 2–3 m intervals. Because crab grazing on transplants in die-off areas was so intense, we scored these transplants for *Sesarma* grazer damage every two days and terminated this experiment after one week because transplants exposed to crab herbivory were almost entirely consumed. The rate of *Sesarma* herbivory in existing die-off areas (percentage of leaves grazed per day) was analyzed using a one-way crab-exclusion ANOVA.

*Can elevated plant nutrient status
trigger Sesarma herbivory?*

To examine whether plant nutrient status can influence the intensity of *Sesarma* grazing on Cape Cod salt marshes, we manipulated nutrient supply and crab access to cordgrass in a fully factorial experiment at the CCNS marsh. We haphazardly located 36, 1×1 m plots spread across a 200 m stretch of shoreline and randomly assigned each to one level of nutrient treatment (nutrient addition or unmanipulated nutrient control) and one level of crab-access treatment (crab exclusion cage, uncaged control, or procedural cage control). Crab exclusion cages ($1 \times 1 \times 1$ m) were constructed of galvanized steel mesh (7-mm mesh) and inserted 10 cm into the substrate. Cage controls had a similar structure, but had 10-cm-tall gaps at the substrate surface to allow crab access. Nutrient-addition treatments were by topical application of Scotts Turfbuilder (Scotts, Maryville, Ohio, USA) fertilizer (30% N, 3% P, 3% K by weight), applied 60 g/m^2 per month, June–August. This level of fertilization has been widely used to experimentally release cordgrass from nutrient limitation (Valiela and Teal 1974, Levine et al. 1998).

We quantified the intensity of *Sesarma* herbivory in August 2007 by scoring 10 random stems/plot for grazing damage (0 = no evidence of grazing, 10 = fully shredded cordgrass nub). To estimate the impact of *Sesarma* herbivory on plant biomass, we harvested end-of-season aboveground biomass in a 0.25×0.25 m quadrat in each plot. These samples were oven dried at 60°C for 72 hours then weighed. Grazing intensity and aboveground biomass were analyzed with a fully factorial, two-way crab-exclusion \times nutrient treatment ANOVA.

*Does substrate dictate the distribution
and impacts of Sesarma?*

We examined the relationship between substrate and *Sesarma* distribution and grazing intensity patterns by: (1) quantifying the density and morphological traits of

Sesarma burrows in the most common substrates in New England salt marshes, mud, sand, and peat; (2) sampling *Sesarma* abundance across these substrate types; (3) measuring grazing intensity and die-off expansion/regrowth rates in these substrate types; and (4) using substrate hardness as a proxy for peat availability, quantified the relationship between peat availability and *Sesarma* distribution patterns within and among marshes experiencing cordgrass die-offs.

Before surveying burrows and crab abundances in mud, sand, and peat, we verified compositional differences in these substrate types (see Appendix for methods and analysis). “Peat substrates” are dense, organic substrates composed of dead belowground plant material bound together with dead and living plant roots. “Mud substrates” are composed of fine particulate sediments that retain water during low-tide exposures; “sand substrates” are composed of larger, primarily inorganic particles, and drain during low-tide exposures.

To quantify substrate effects on burrow density and traits, we randomly placed $10, 0.5 \times 0.5$ m plots in each substrate type at CCNS and Indian Neck marshes and counted all *Sesarma* burrows, determined the number of openings to each discrete burrow, and measured the total length and depth of the largest burrow. Burrow length and depth were measured by excavating haphazardly chosen burrows until we could access their end. Burrow counts and measurements included only burrows that were conclusively determined to be *Sesarma* burrows. *Sesarma* can be distinguished from the other burrows in marshes created by fiddler crabs (*Uca* spp.) by several criteria. Fiddler crab burrows are typically smaller (0.5–2 cm) and have single surface openings. *Sesarma* burrows are larger (2.5–4 cm) and often have multiple openings. Larger fiddler crab burrows often have “hoods” or “chimneys” that distinguish them from *Sesarma* burrows, and fiddler crabs often leave 1–2 mm feeding castings around their burrows (Crane 1975). Since site did not significantly affect any of our burrow measurements, burrow measurements were pooled across sites and analyzed with a one-way substrate-type ANOVA.

We sampled relative crab abundance across substrate types with pit fall traps—plastic cylinders (7 cm diameter \times 21 cm height) sunk flush with substrate surface (Bertness and Miller 1984). We randomly deployed 20 traps in each substrate at CCNS on each of four sampling dates in August 2007. Since *Sesarma* are nocturnal, traps were set at dusk and retrieved at dawn. Crabs caught in the traps were identified to species and counted. *Sesarma* densities (number of crabs per trap) were analyzed with a one-way substrate-type repeated-measures ANOVA.

To test the hypothesis that substrate influences *Sesarma* herbivory pressure, we measured the grazing intensity (as described above) in $10, 0.25 \times 0.25$ m quadrats randomly placed on die-off/cordgrass canopy borders in each substrate type. To verify that differences

in herbivory were independent of potential substrate-specific effects on plant quality, we quantified grazing rates (percentage of leaves grazed per day) on eight caged and eight uncaged cordgrass culms, transplanted from a common source area into each substrate type in July 2007, and terminated the experiment after seven days when peat culms were reduced to shredded nubs (as described above in the disturbance experiment). We did not include cage controls in this experiment since the incorporation of procedural cage control treatments in two previous transplant experiments verified a lack of caging artifacts. To examine whether substrate-specific variation in crab grazing influenced the expansion of die-off areas, we flagged 34 randomly placed 0.5×0.5 m plots in May 2007 on the edge of existing die-off areas at CCNS. Of these quadrats, 12 quadrats were on peat, 12 quadrats on sand, and 10 quadrats on mud. These plots were separated by >4 m, scattered over 0.5 km of shoreline, and were placed with 50% of the plot in unvegetated die-off and 50% in cordgrass canopy. The distance between the initial border flags and the end-of-season die-off/cordgrass canopy border was measured in September 2007 to quantify relative die-off expansion/regrowth. Grazing intensity and frequency, and die-off border movement, were each analyzed with a one-way substrate-type ANOVA.

To assess the impact of substrate on *Sesarma* distribution and herbivory across various substrate types in the low-marsh zone where die-offs occur, we quantified the presence of mud, sand, and peat substrates using substrate hardness as a proxy for substrate type in surveys of *Sesarma* within and among marshes. Peat substrates are a network of compacted roots and rhizomes, and are much harder than mud or sand substrates, making substrate hardness a good measure of relative peat availability. We measured substrate hardness using a penetrometer (see Bertness and Miller 1984), a 50-pound (22.7-kg) top-loading spring scale with a 10-cm-long aluminum rod (1.9 cm diameter) mounted vertically on the weighing pan. Substrate hardness readings were obtained by slowly pushing the rod vertically into the substrate and recording the mass (in kg) required to penetrate to a depth of 5 cm. We recorded 20 penetrometer readings per substrate at CCNS and analyzed substrate hardness using a one-way substrate ANOVA.

To quantify the relationship between substrate hardness and *Sesarma* burrow density, we sampled 50 random 0.25×0.25 m quadrats in die-off areas along 100 m of the shoreline at CCNS marsh in July 2007. In each plot we counted *Sesarma* burrow openings and quantified substrate hardness using a penetrometer. We evaluated the relationship between substrate hardness and burrow density with linear regression.

To examine the relationship between peat availability (substrate hardness) and creek bank die-off areas among marshes, we took penetrometer readings on creek banks with and without die-offs at 10 marshes in middle and

lower Cape Cod (see Holdredge et al. [2009] for site descriptions). There is considerable variation in substrate within and among New England salt marshes reflecting differences in sediment supply, erosion, and the peat depositional history of a marsh (Chapman 1960). At each site, we randomly located three die-off creek banks and adjacent vegetated creek banks. "Die-off areas" were operationally defined as areas with burrow densities >15 burrows/m² and evident grazing. "Vegetated creek banks" were defined as adjacent areas with full cordgrass canopies. At each site, we took 10 random penetrometer readings and examined inter-marsh variation in substrate hardness with a one-way creek-bank-type ANOVA nested within site. We also calculated the proportion of the creek bank at each site characterized by die-off areas (see Holdredge et al. [2009] for methods). The relationship between inter-marsh variation in substrate hardness and the extent of die-off was analyzed with linear regression.

RESULTS

The impact of natural disturbance on Sesarma density and grazing

The creation of experimental disturbances did not increase *Sesarma* grazing rates on cordgrass culms relative to unmanipulated control areas ($F_{1,27} = 0.5414$, $P = 0.4682$). In contrast to the experimental disturbances, crab grazing in existing die-off areas was intense ($F_{2,27} = 29.0401$, $P < 0.0001$). Herbivory rates on cordgrass without crab-exclusion cages in existing die-off areas averaged $10.4\% \pm 1.4\%$ (mean \pm SE) leaves grazed/d, which eclipsed the rate in experimental disturbance areas of only $0.17\% \pm 0.08\%$ leaves grazed/d by nearly two orders of magnitude (Fig. 2). As a consequence, crabs grazed more than twice the number of cordgrass leaves in existing die-off areas within one week than in experimental disturbance areas over two months.

Plant nutrient status and Sesarma herbivory

The intensity of *Sesarma* grazing was detectably greater in nutrient addition plots than in unmanipulated control plots ($F_{1,30} = 5.0872$, $P = 0.0316$; Fig. 3A), but remained low regardless of nutrient treatment with $<10\%$ of cordgrass stems damaged in all treatments. Consequently, the cumulative effects of this minimal crab herbivory were not sufficient to affect end-of-season cordgrass biomass ($F_{2,30} = 0.2639$, $P = 0.7698$; Fig. 3B). Although the addition of nutrients had a minimal effect on grazing rates, it nearly doubled cordgrass biomass ($F_{1,30} = 60.4532$, $P < 0.0001$) indicating that plants were nutrient limited.

Does substrate dictate the distribution and affects of Sesarma?

Substrate strongly influenced *Sesarma* burrow traits (Fig. 4). The density of burrow openings ($F_{2,84} = 291.667$, $P < 0.0001$, Fig. 4A), number of openings per burrow ($F_{2,84} = 31.276$, $P < 0.0001$; Fig. 4B),

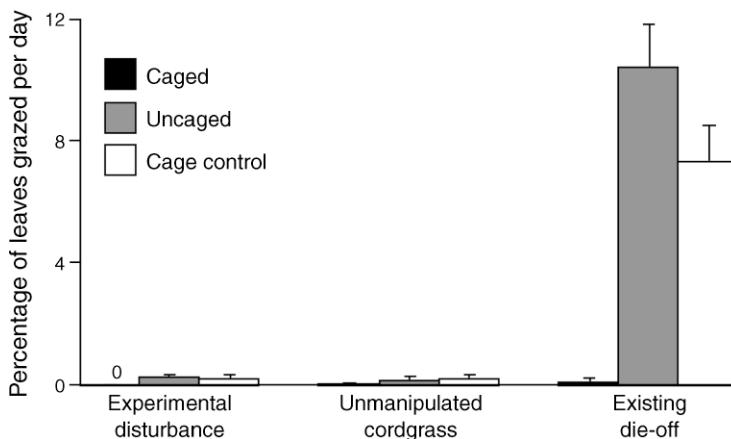


FIG. 2. Percentage of cordgrass leaves grazed per day (mean + SE) for three different caging treatments in experimental disturbance, unmanipulated cordgrass canopy, and existing *Sesarma* die-off areas.

maximum burrow length ($F_{2,84} = 30.925$, $P < 0.0001$; Fig. 4C), and burrow depth ($F_{2,84} = 50.514$, $P < 0.0001$; Fig. 4D) were all >2 times higher in peat than in either mud or sand. The abundance of *Sesarma* varied with substrate type at all four sampling dates ($F_{2,57} \geq 10.2334$, $P < 0.0001$) and reflected the patterns in burrow characteristics: crab densities were $>35\%$ higher in peat (3.18 ± 0.23 [mean \pm SE] crabs/trap) than in mud (2.35 ± 0.26 crabs/trap), and nearly 4 times higher than in sand (0.68 ± 0.10 crabs/trap).

As predicted by their abundance patterns, *Sesarma* herbivory was higher on peat than on mud or sand die-off borders. Grazing intensity on peat borders was nearly 40% higher than on sand and 3.5 times higher than on mud borders ($F_{2,27} = 38.8446$, $P < 0.0001$; Fig. 5A). Similarly, grazing rates on uncaged cordgrass transplants were >3 times higher in peat than in either mud or sand, and undetectable in transplants protected by exclusion cages in all three substrate types ($F_{2,54} = 10.3649$, $P = 0.0002$; Fig. 5B). The intensity of crab grazing also affected movement of die-off borders. On peat substrate, borders expanded nearly 50 cm in one growing season, whereas cordgrass reinvaded die-off areas bordered by mud and sand ($F_{2,31} = 32.4975$, $P < 0.0001$; Fig. 5B).

Substrate hardness varied by substrate type ($F_{2,80} = 173.75$, $P < 0.0001$). Peat (52.1 ± 2.8 kg/cm²) was twice as hard as sand (26.0 ± 1.0 kg/cm²) and nearly 9 times harder than mud (6.2 ± 0.7 kg/cm²). Substrate hardness explained 77% of the variation in *Sesarma* burrow density at CCNS ($P < 0.0001$), with burrow density increasing with hardness (Fig. 6).

The importance of substrate type on herbivory impacts of *Sesarma* detected at our experimental site scaled up to explain large-scale patterns of marsh die-off in our survey of 10 Cape Cod marshes (Fig. 7). Creek banks experiencing die-offs were >3 times harder than vegetated creek banks ($F_{10,24} = 27.7543$, $P < 0.0001$). Among marshes, substrate hardness in die-off creek banks explained over 40% of inter-marsh variation in

the extent of die-off ($R^2 = 0.4149$, $P = 0.0444$), with the extent of die-off increasing with substrate hardness.

DISCUSSION

Disturbance-generated bare space and elevated plant-nutrient status are not major drivers of crab herbivory-

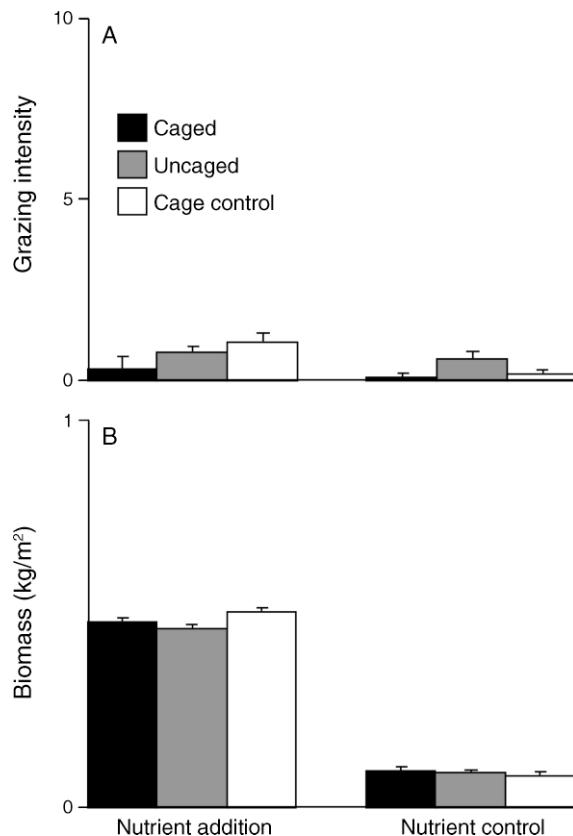


FIG. 3. The effect of nutrient addition on (A) grazing intensity and (B) aboveground biomass. Data are means + SE. In (A) the grazing intensity data are scored on a scale from 0 (no grazing damage) to 10 (shredded cordgrass nub).

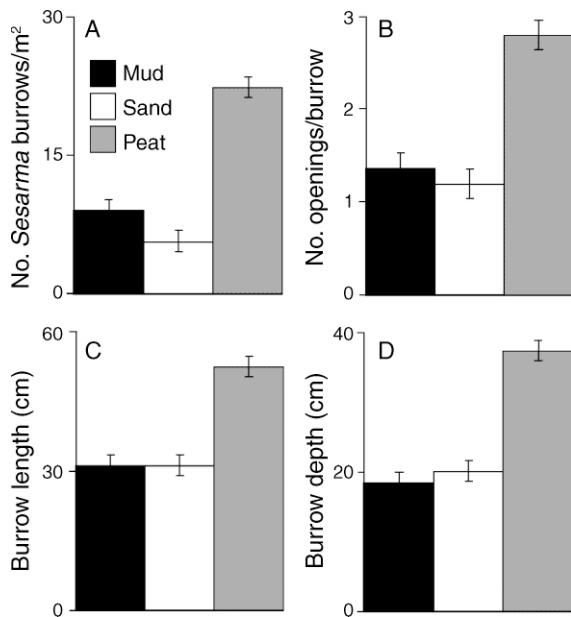


FIG. 4. Differences among mud, peat, and sand substrates in (A) *Sesarma* burrow density, (B) number of surface openings/burrow, (C) burrow length, and (D) burrow depth. Data are means \pm SE.

generated die-off of Cape Cod (Massachusetts, USA) salt marshes. Instead, our results reveal that peat substrate availability strongly affects the distribution and grazing impact of the herbivorous crab, *Sesarma reticulatum*, on Cape Cod marshes, and have important implications for predicting which marsh areas are vulnerable to crab-generated die-offs.

Does disturbance-generated bare space trigger crab herbivory by Sesarma?

We hypothesized that disturbance-generated bare space could trigger *Sesarma* herbivory and the maintenance of bare space on Cape Cod salt marshes based on the spatial distribution of die-off areas and the

preference of salt marsh herbivores for the emergent stems generated during the recovery of marsh plant communities. Our artificial-disturbance experiment, however, detected no evidence that recovering bare areas experience greater herbivory than undisturbed areas (Fig. 2). Thus, the correlation between the high frequency of disturbance on the terrestrial border of the low marsh (Bertness and Ellison 1987), the dominance of new growth often preferred by marsh herbivores (Bortolus and Irbarne 1999), and the die-offs on Cape Cod salt marshes (Holdredge et al. 2009) does not appear to be causal. Wrack disturbance, bare patch generation and subsequent recovery are natural processes in New England salt marshes that should not be confused with the recent marsh die-off phenomena in New England. Exponentially higher grazing rates in die-off areas compared to undisturbed cordgrass canopy and experimental bare patches (Fig. 2) argue that other factors must be influencing the dramatic spatial patterns in crab herbivory across these habitats.

Does increased plant nutrient status increase herbivory by Sesarma?

We also hypothesized that nutrient enrichment could influence crab grazing by increasing the palatability of cordgrass to *Sesarma* and lead to herbivore-generated die-off. This hypothesis was based on a number of examples in the literature (e.g., Vince et al. 1981, Stiling et al. 1991, Gough and Grace 1998) all showing that nutrient additions increase herbivore pressure and impacts on salt marsh plants. Our nutrient-enrichment experiments, however, did not detect a strong nutrient effect on crab herbivory or trigger increased top-down control of marsh grass production as in other marsh systems, suggesting that *Sesarma* herbivory is controlled by factors other than nutrients in this system.

Does peat substrate control the distribution and impact of Sesarma?

Whereas disturbances and nutrients do not appear to markedly stimulate *Sesarma* herbivory, the availability

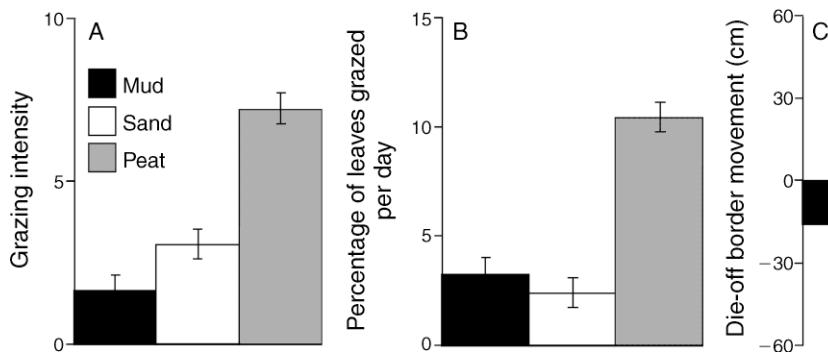


FIG. 5. Differences among mud, peat, and sand substrates in (A) grazing intensity on die-off/cordgrass canopy borders; (B) percentage leaves grazed per day on uncaged culms transplanted from a common source into die-off areas; and (C) border movement, with positive movement indicating expansion of unvegetated die-off areas and negative movement indicating regrowth of cordgrass into die-off areas. Data are means \pm SE.

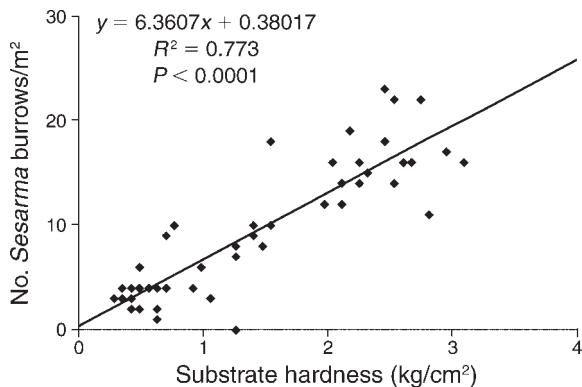


FIG. 6. Results of least-squares linear regression of *Sesarma* burrow density on substrate hardness.

of peat strongly influences the distribution, abundance, and herbivory impact of *Sesarma* in Cape Cod salt marshes. Our results show that *Sesarma* herbivory (Fig. 5A, B), effects on vegetation (Fig. 5C), and burrow densities (Fig. 6) are all positively correlated with substrate hardness (peat). The density, number of surface openings, and depth and length of *Sesarma* burrows were all greater in peat than in either mud or sand (Fig. 4). Burrow densities were 2–4 times greater and the total length and depth of *Sesarma* burrows were nearly 2 times greater in peat than in mud or sand substrates. Since *Sesarma* live in large, communal burrows (Gosner 1978, Seiple and Salmon 1982), the structural support of peat may be necessary to support *Sesarma* burrows and large populations.

Higher burrow and crab densities in peat led to increased herbivory on adjacent cordgrass, and the expansion and growth of die-off areas. The movement of bare-patch borders on peat, mud, and sand substrates differed dramatically. On peat, unvegetated die-off areas

expanded by 47 cm over the growing season, while on sand and mud cordgrass recolonized die-off areas and borders receded by 30 cm and 16 cm, respectively (Fig. 5B). These data suggest that *Sesarma* grazing around peat-dependent *Sesarma* burrow complexes is responsible for the expansion of die-off patches.

Crab herbivory and the future of New England salt marshes

Our results have important implications for predicting the impact of crab herbivory on New England salt marshes. By affecting cordgrass success and vulnerability to peat loss, *Sesarma* could have disproportionately large impacts on New England salt marshes. Since *Spartina alterniflora* is responsible for sediment binding, peat deposition, and the development of New England marshes (Redfield 1965), cordgrass die-off has the potential to compromise the ability of salt marshes to keep pace with sea-level rise. Cordgrass die-off may also increase the vulnerability of salt marshes to disturbance since, as a clonal, stress-tolerant species, it has historically underpinned the resilience of marshes to disturbance by vegetatively recolonizing disturbed habitats (Shumway 1995). Cordgrass loss may also increase physical stress on the high marsh since *Spartina* ameliorates anoxia, hyper-salinity, and wave-exposure stresses (Bertness and Leonard 1997).

The concentration of *Sesarma* burrows in peat may also directly trigger the erosion and collapse of the peat foundation of marshes. On Cape Cod, marsh creek banks are often so riddled with *Sesarma* burrows that they slump and collapse, exposing fresh peat to further burrowing and erosion (C. Holdredge and M. D. Bertness, *personal observations*). Feedbacks between crab herbivory and cordgrass die-off may thus lead to the retreat of marsh edges.

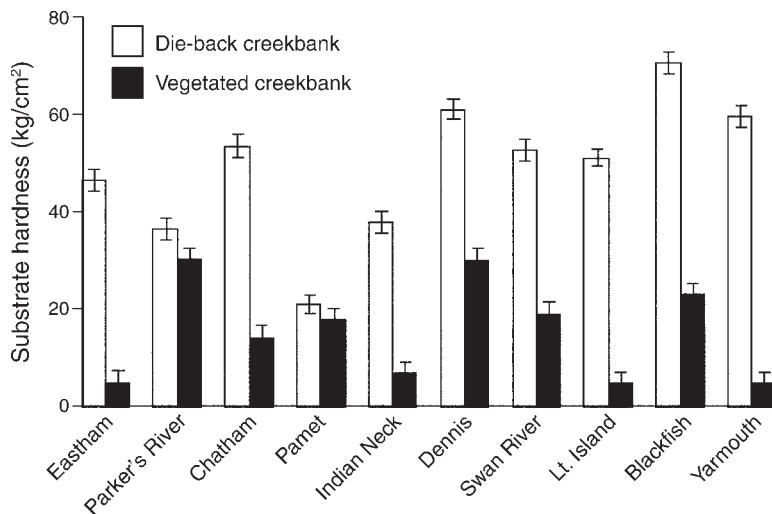


FIG. 7. Substrate hardness of die-off and adjacent vegetated creek banks at 10 Cape Cod (USA) marshes. Data are means ± SE.

Marsh loss from *Sesarma* herbivory is a growing conservation concern in New England, since elevated *Sesarma* densities may be driven by overfishing of marine consumers and climate change-driven shifts in species ranges (Holdredge et al. 2009). Because *Sesarma* herbivory and burrowing target the biogenic foundation of these ecologically valuable systems, conservation measures need to focus on the habitats most susceptible to *Sesarma* herbivory, and consider the perturbations that pushed *Sesarma* populations and their grazing impacts out of equilibrium.

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APPENDIX

Sediment composition analysis (*Ecological Archives* E090-147-A1).