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Role of Crab Herbivory in Die-Off of New England Salt Marshes

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Abstract: *Die-offs of cordgrass are pervasive throughout western Atlantic salt marshes, yet understanding of the mechanisms precipitating these events is limited. We tested whether herbivory by the native crab,* Sesarma reticulatum, *is generating die-offs of cordgrass that are currently occurring on Cape Cod, Massachusetts (U.S.A.), by manipulating crab access to cordgrass transplanted into die-off areas and healthy vegetation. We surveyed 12 Cape Cod marshes to investigate whether the extent of cordgrass die-off on creek banks, where die-offs are concentrated, was related to local* Sesarma *grazing intensity and crab density. We then used archived aerial images to examine whether creek bank die-off areas have expanded over the past 2 decades and tested the hypothesis that release from predation, leading to elevated* Sesarma *densities, is triggering cordgrass die-offs by tethering crabs where die-offs are pervasive and where die-offs have not yet been reported. Intensity of crab grazing on transplanted cordgrass was an order of magnitude higher in die-off areas than in adjacent vegetation. Surveys revealed that* Sesarma *herbivory has denuded nearly half the creek banks in Cape Cod marshes, and differences in crab-grazing intensity among marshes explained >80% of variation in the extent of the die-offs. Moreover, the rate of die-off expansion and area of marsh affected have more than doubled since 2000. Crab-tethering experiments suggest that release from predation has triggered elevated crab densities that are driving these die-offs, indicating that disruption of predator–prey interactions may be generating the collapse of marsh ecosystems previously thought to be exclusively under bottom-up control.*

Keywords: cordgrass, ecosystem collapse, herbivory, marsh die-off, salt marsh, *Sesarma reticulatum*, *Spartina alterniflora*, top-down control

Papel de la Herbivoría de Cangrejos en la Declinación de Marismas de Nueva Inglaterra

Resumen: *La declinación de marismas es extensiva en el Atlántico occidental, sin embargo el entendimiento de los mecanismos que la causan es limitado. Probamos sí la herbivoría de un cangrejo nativo,* Sesarma reticulatum, *está causando la declinación del pasto* Spartina alterniflora *en Cape Cod, Massachusetts (E.U.A.), mediante la manipulación del acceso de cangrejos a pasto trasplantado en áreas en declinación y con vegetación saludable. Muestreamos 12 marismas de Cape Cod para investigar si la extensión de la declinación de pasto en las riberas de arroyos, donde se concentran las declinaciones, se relacionaba con la intensidad de forrajeo de* Sesarma *y con la densidad de cangrejos. Posteriormente utilizamos imágenes aéreas de archivo para examinar sí las áreas de declinación se han expandido en las dos ultimas décadas y probamos la hipótesis de que la liberación de la depredación, que lleva a densidades elevadas de* Sesarma, *está disparando las declinaciones de pasto al concentrar a los cangrejos donde las declinaciones son extensivas y donde las declinaciones aun no han sido reportadas. La intensidad del forrajeo de pasto por cangrejos fue un orden de magnitud mayor en las áreas de declinación que en la vegetación adyacente. Los muestreos revelaron que la herbivoría de* Sesarma *ha denudado casi la mitad de las riberas de arroyos en marismas de Cape Cod, y las diferencias en la intensidad del forrajeo de cangrejos explicó >80% de la variación en la extensión de las declinaciones. Más aun, la tasa de expansión de la declinación y el área de marismas afectadas han aumentado más del doble desde el año 2000. Los experimentos de encierro de cangrejos sugieren que la liberación de la depredación ha disparado el incremento de las densidades de cangrejos que están produciendo*

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estas declinaciones, lo que indica que la disrupción de las interacciones depredador-presa pueden estar generando el colapso de los ecosistemas de marisma que previamente se pensaba que estaban exclusivamente bajo control de abajo hacia arriba.

Palabras Clave: colapso del ecosistema, control arriba-abajo, declinación de marismas, herbivoría, marisma, *Sesarma reticulatum*, *Spartina alterniflora*

Introduction

The ecological collapse of shallow-water systems driven by human disturbances is one of the most critical environmental problems of our times (Jackson et al. 2001; Lotze et al. 2006). In recent decades coral reefs, seagrass meadows, and salt marshes have been deteriorating as a consequence of overfishing, disease, climate change, persistent eutrophication, and shoreline development (Jackson et al. 2001; Bertness et al. 2002; Myers & Worm 2003; Harvell et al. 2004; Pandolfi et al. 2005; Lotze et al. 2006). Loss of these systems threatens the ecological services they provide, challenges current conservation practices, and brings into question our conceptual understanding of coastal ecosystems (Hughes et al. 2005).

Salt marshes are critical coastal habitats because of the role they play as nursery grounds, biochemical filters, and buffers against shoreline erosion (Valiela & Teal 1979; Boesch & Turner 1984; Bertness 2006). The primary production of salt marshes has long been thought to be regulated by bottom-up forces (Strong 1992), such that the growth and species composition of vascular plants in marsh ecosystems are controlled by physical factors, like temperature, salinity, and nutrient availability (e.g., Teal 1962; Odum 1969; Mendelssohn & Morris 2000). A strong corollary to the physical-control paradigm of salt marsh primary production is that consumers play a negligible role in regulating salt marsh community structure or primary production (Smalley 1960; Teal 1962). The bottom-up control paradigm of salt marshes has not only dominated ecological thought but has exclusively shaped salt marsh ecosystem management and conservation strategies.

Recent research, however, has revealed that top-down consumer control of salt marsh primary production is being triggered by human disturbances throughout the western Atlantic (Bertness & Silliman 2008), threatening the services they provide to nearshore ecosystems. In the Canadian subarctic, grazing by snow geese (*Anser caerulescens caerulescens* L.), fueled by nitrogen subsidies to farmlands in North America, has decimated hundreds of thousands of hectares of salt marsh (Jefferies 1997). On the southeastern and Gulf coasts of North America disease-mediated consumer control by the periwinkle *Littoraria irrorata*, likely released from top-down control by commercially harvested marine predators, has also precipitated large-scale cordgrass (*Spartina alterniflora*) die-offs (Silliman & Bertness 2002; Silliman et al. 2005). Even in exhaustively studied New England salt marshes, where herbivores have been considered unimportant to salt marsh dynamics, local eutrophication is triggering consumer control by herbivorous insects, which can suppress primary production by over 50% (Bertness et al. 2008).

The recent reports of marsh die-offs on Cape Cod have been an alarming addition to the patchwork of marsh vegetation die-off events recorded throughout the western Atlantic coast over the past decade (Bertness & Silliman 2008). These die-offs, identified as swaths of denuded and eroding substrate in the low marsh (Fig. 1), were first noticed in 2004 National Park Service surveys of Cape Cod Bay salt marshes (Smith 2006) and since have attracted considerable media attention (e.g., Lewis 2007). Die-off areas are characterized by extensive loss of cordgrass, which is the primary foundation species in New England salt marshes because of its ability to build marsh peat through biogenic binding of sediment and to ameliorate physical and abiotic stresses that would otherwise limit other marsh species (Chapman 1960; Redfield 1965; Hacker & Bertness 1999). Most proposed explanations for cordgrass die-off on Cape Cod have focused on pathogenic diseases, soil toxicity, and climate change, but no consensus has emerged owing to lack of experimental evidence (Smith 2006). Prior to this study, herbivores were not investigated as a potential cause because previous research indicated that consumer control was not important in these systems (Smalley 1960; Teal 1962; Nixon 1982) and the grazers generating die-offs in other marsh systems (Jefferies 1997; Silliman & Bertness 2002; Bertness & Silliman 2008) are not present in Cape Cod marshes.

We hypothesized that the recently reported marsh die-offs are caused primarily by increases in grazing pressure by the native, nocturnal burrowing crab *Sesarma reticulatum* (hereafter, *Sesarma*). We based this hypothesis on the presence of characteristic crab herbivory damage (e.g., shredded and clipped cordgrass on the edges of die-off areas [Crichton 1960]) to the grass bordering die-off areas and our initial observations of a strong positive association between locations of die-off areas and high densities of *Sesarma* burrows. Relative to geographically proximate and climatically similar Narragansett Bay marshes (Rhode Island), where the size of *Sesarma* bare patches along creek banks have not increased in nearly 25

(a)

(b)

Figure 1. Healthy and die-off creek banks in New England salt marshes: (a) Coggeshall marsh (Prudence Island, Rhode Island) in the Narragansett Bay region, where Sesarma *density and herbivory impacts are low, and (b) Parker River marsh (West Dennis, Massachusetts) in the Cape Cod region, where 90% of creek banks are denuded of cordgrass and crab burrowing is extensive.*

years of observation (M. Bertness, personal observation), *Sesarma* densities and herbivory effects appeared to be locally elevated on Cape Cod. Present in salt marshes from Texas to Cape Cod (Gosner 1979; Seiple & Salmon 1982; Williams 1984), *Sesarma* is one of the most widespread benthic macroinvertebrates on the Atlantic coast of the United States. Nevertheless, their ecology is largely unstudied (Seiple 1979), and little is known about the density of *Sesarma* throughout its range or the natural predators and environmental factors that may be limiting its abundance. They are herbivores, although the most commonly cited paper on their feeding ecology is a 50-year-old anecdotal study that simply says high concentrations of *Sesarma* burrows often are found within patches of bare substrate that may be maintained by their grazing (Crichton 1960).

We examined the relationship between *Sesarma* grazing and cordgrass die-off by surveying crab density, grazing intensity, and the extent of die-off at marshes throughout Cape Cod. We then experimentally tested the impact of crab herbivory on cordgrass in marshes in Cape Cod, where there is extensive die-off, and in Narragansett Bay, Rhode Island, where *Sesarma* is less abundant and denuded areas are small (<9 m^2) and uncommon. We also conducted tethering experiments to investigate the hypothesis that release from predation is triggering elevated *Sesarma* densities and impacts on Cape Cod. Finally, using archived aerial images of salt marshes, we examined whether the effects of *Sesarma* have increased over the past 25 years. Using this combination of experimental and large-scale correlative perspectives, we present compelling evidence that herbivory by *Sesarma*, triggered by release from predation, is generating and expanding salt marsh die-offs on Cape Cod.

Methods

Marsh Die-Off Surveys

At 12 marshes located in central and outer Cape Cod (a list of surveyed sites is available on request from C.H.), we surveyed the entire marsh area for the presence of the most common type of marsh die-off (S. Smith, personal communication)—denuded, burrow-riddled creek banks. These areas are easily identified in the field and in aerial photographs and sharply contrasted with cordgrass-covered creek banks common in New England marshes (Fig. 1).

We walked the total length of tidal creeks in each marsh at low tide and quantified the extent of cordgrass die-off as the proportion of the length of the creek bank characterized by denuded, burrow-riddled substrate with evidence of crab herbivory on bordering cordgrass. To measure the intensity of *Sesarma* grazing on cordgrass, we quantified the proportion of 50 random cordgrass blades grazed by *Sesarma* in each of 10 0.5 × 0.5 m quadrats randomly placed along die-off borders at each marsh. In the field we were able to distinguish *Sesarma* grazing damage from other types of leaf scarring due to distinct signatures of rasping and shredding on cordgrass leaves, as described in the literature (Crichton 1960) and verified in lab feeding trials in June 2007.

At the 9 survey marshes where trapping was permitted, we sampled crab density on die-off creek banks by randomly setting 20–30 pitfall traps, which we constructed out of open-top plastic cylinders (7.5 cm diameter × 21 cm tall) with small (2 mm) drainage holes in the bottom. We installed the traps vertically with their top flush with the substrate (Bertness & Miller 1984). Because *Sesarma* are nocturnal, traps were set at dusk and sampled the following dawn after one tidal cycle. Although 4 Narragansett Bay marshes were also surveyed, we did not include data from these sites in the analysis because there was no evidence that die-offs were occurring. Small, bare *Sesarma* patches characterized <5% of creek-bank area and had not expanded in size in more than 2 decades of observation. We analyzed the relationships among *Sesarma* grazing intensity, the extent of die-off, and *Sesarma* density with linear regression.

Exclusion Experiment

To test the hypothesis that *Sesarma* herbivory drives patterns of cordgrass mortality and die-off, we experimentally manipulated crab access to transplanted cordgrass in creek-bank areas in Cape Cod marshes (Great Island and Lieutenant's Island in Wellfleet, Massachusetts), where die-off areas are ongoing, and in Narragansett Bay marshes (Rumstick Point, Barrington, Rhode Island, and Coggeshall, Prudence Island, Rhode Island), which have moderate *Sesarma* burrow densities (5–10 burrows/m^2) associated with small bare areas. In June 2007 we used a 7.5-cm diameter corer to extract 48 cordgrass culms (5–8 undamaged stems each) at all 4 experimental sites and assigned each culm to 1 of 6 treatments in a fully factorial design that crossed crab exclusion treatment (caged, caged control, uncaged control) with creek-bank type (denuded and vegetated banks).

Crab-exclusion cages were constructed by securing a cylinder of galvanized hardware cloth (7-mm mesh size) around cordgrass culms and inserting caged transplants into core holes in experimental creek banks. Crab exclusion cages extended from 80 cm above the marsh surface to 20 cm below the marsh surface to prevent crabs from crawling and burrowing into cages. To account for caging artifacts, we constructed caged controls that were similar to the crab exclusion cages, but had a 10 × 10 cm opening at the marsh surface to allow crab access. The crab exclusion cages appeared to effectively exclude crabs because grazing damage characteristically inflicted by *Sesarma* was common on cordgrass that was uncaged or in caged controls, but was not observed on cordgrass in cages.

Transplanted culms were scored biweekly for *Sesarma* damage by quantifying the percentage of cordgrass blades grazed in each treatment. The experiment was terminated after 2 months when crab-accessible culms (uncaged and caged controls) in Cape Cod die-off areas were entirely consumed. Because initial analyses revealed that sites within a region (Cape Cod and Narragansett Bay) did not differ, we pooled the data by region and analyzed the effect of caging treatment and type of creek bank on *Sesarma*-grazing damage (transformed to meet assumptions of analysis of variance [ANOVA]) with a 2-factor ANOVA nested within region.

Tethering Experiment

To experimentally measure differences in predation pressure on *Sesarma* populations in Cape Cod and Narragansett Bay marshes, we conducted a fully factorial tethering experiment at 2 sites in each region (locations described earlier) in August 2007. We tethered crabs in creek banks that were either denuded or vegetated and placed each individual either in the open (predator access) or within a 60 × 35 cm (height × diameter) predator-exclusion cage (35 cm diameter × 60 cm tall) constructed of galvanized-steel hardware cloth (7-mm mesh size). Thirty crabs (separated by >2 m) were placed in each creek bank by caging treatment combination for a total of 120 individually tethered crabs at each site. All experimental crabs had a carapace width of 22–26 mm and were collected with pit fall traps at Blackfish Creek marsh in Wellfleet, Massachusetts.

Tethers were tied around the carapace of crabs between the second and third pair of walking legs and secured to the carapace with cyanoacrylic glue. Each 15-cm tether was constructed of braided fishing line (Stren 50 pound Super Braid, Spirit Lake, Iowa) and secured to a 10-cm stake sunk flush with the marsh substrate. Crabs walked freely within the radius of their lines and had access to existing crab burrows. Crabs were kept moist and cool during handling and transporting between sites to minimize stress and desiccation. *Sesarma* were deployed at dusk, and survivorship data were collected at dawn after one tidal cycle. Crabs that died owing to desiccation or stress (e.g., crab body intact, no signs of predation) were rare (<1% of crabs tethered) and distinguishable from those that were eaten (crab body dismembered, often only broken carapace and legs remained). We used chi-square analyses to test differences in proportional survivorship. We pooled data from sites within regions because they did not differ ($\chi^2 < 3.53, p > 0.05$).

To quantify whether crab densities in Cape Cod and Narragansett Bay marshes reflected regional differences in observed predation pressure on *Sesarma*, we deployed 10 pitfall traps in denuded creek-bank areas at our 4 experimental sites in August 2007. The number of *Sesarma* caught per a trap was log-transformed to meet normality assumptions, and differences between sites were analyzed with a one-way ANOVA nested within region and followed by a Tukey's honest significant difference test post hoc.

Recent History and Development of Cape Cod Marsh Die-Off Areas

We used color infrared aerial marsh images (Cape Cod National Seashore National Park Service) from September

1984 (pixel resolution: 1.0 m) and October 2000 (pixel resolution: 0.5 m) to track historic creek-bank die-off expansion and development. Our analysis of die-off development was limited to the 5 survey sites for which archived, high-resolution images were available. Scanned images were georectified with ARCGIS (version 9.1) software (ESRI, Redlands, California) and 2001 aerial photo mosaics (available from MassGIS) and then projected in UTM (NAD83) coordinates (zone 19N). All images were taken at low tide, providing clear resolution of the seaward edge of the cordgrass zone and creek banks. Die-off areas were recognizable as discrete brown disruptions in the otherwise red cordgrass zone along creek banks, and their spatial extent was estimated with the polygon function in ARCGIS. In November 2007 we used a Trimble GeoXT GPS with Trimble Pathfinder Office (version 3.0) software (Trimble, Sunnyvale, California) to demarcate the perimeter of 28 randomly chosen die-off areas in the same 5 survey marshes. We then imported the current die-off data into ARCGIS to calculate the area of each die-off in 2007 and project these areas onto historic images to measure the development of individual die-off areas over time. The average expansion rate of individual die-off areas within a given marsh for the intervals 1984–2000 and 2000–2007 was calculated as the percent increase in die-off area per year.

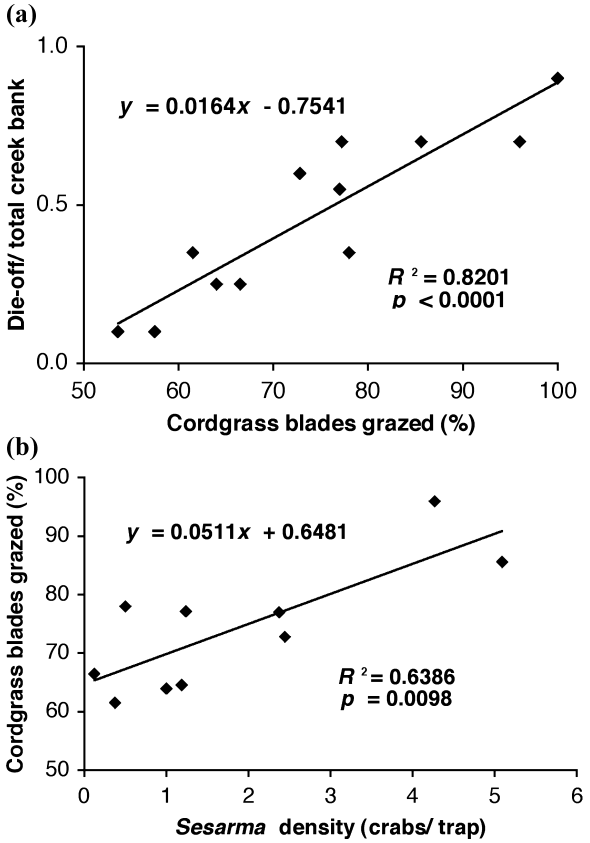

Figure 2. Relationship between (a) mean Sesarma *grazing intensity (scored as the percentage of cordgrass blades grazed along die-off borders) and the extent of die-off (the proportion of total creek bank length characterized by die-off) at 12 marshes across Cape Cod and (b) mean* Sesarma *density and* Sesarma *grazing intensity at 9 marshes.*

Results

We observed denuded creek banks at all 12 Cape Cod salt marshes that we surveyed. Cordgrass die-off affected 10–90% of creek-bank area at each site (Fig. 2; mean 46.0% [SE 7.6]). All die-off areas had 10–25 burrows/m^2 and cordgrass along die-off borders was generally grazed down to stubble and had characteristic shredding along blade margins (Crichton 1960). Grazing intensity along die-off borders ranged from 54 to 100% of cordgrass blades grazed by crabs across all sites and correlated strongly with the extent of die-off (Fig. 2a; $R^2 = 0.8201$, $p < 0.0001$). Among the 9 marshes where we sampled crab density, *Sesarma* abundance explained nearly 65% of variation in intensity of crab herbivory on cordgrass (Fig. 2b; $R^2 = 0.6386$, $p < 0.01$).

After only 2 weeks *Sesarma* herbivory had dramatic effects on the mortality of cordgrass transplants (Fig. 3). Within denuded areas *Sesarma* grazing was 10 times higher on crab accessible (uncaged and cage control) transplant cordgrass on Cape Cod than in Narragansett Bay (mean [SE] 65.0% [8.2] and 6.6% [2.1] grazed, respectively; $F_{1,64} = 76.8367$, $p < 0.0001$). In crab exclusion cages transplants grew vigorously and were undamaged in denuded areas in both regions (10.9% [3.3] and 6.3% [1.7] grazed, respectively; $F_{1,31} = 1.9174$, $p < 0.1760$). In vegetated creek-bank habitats *Sesarma* grazing on uncaged cordgrass transplants was also greater in

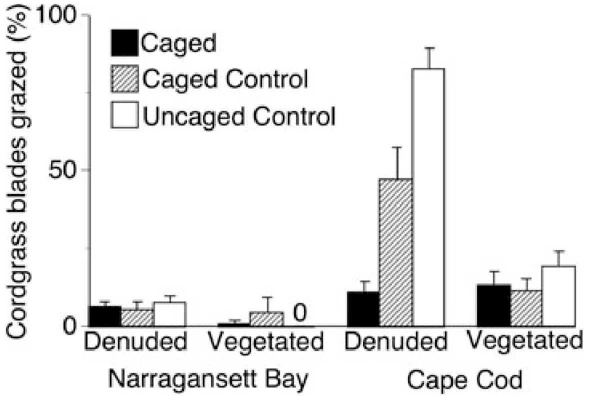

Figure 3. Effect of Sesarma *herbivory on cordgrass transplant mortality in vegetated and denuded creek banks in Narragansett Bay and Cape Cod. Mean percentage (SE) of cordgrass blades grazed after 2 weeks in crab-exclusion cage, caged control, and uncaged control treatments.*

Cape Cod than in Narragansett Bay (15.6% [2.9] and 0.2% [0.2] grazed, respectively, $F_{1,48} = 14.21$, $p < 0.0001$). After 2 months, the experimental treatments and regions had diverged further ($F_{4,154} = 6.5619, p < 0.0001$), and *Sesarma* grazing in Cape Cod die-off areas had reduced cordgrass transplants without crab exclusions to stubble (90% [5.7] grazed).

Predation pressure on *Sesarma* was dramatically lower in Cape Cod marshes ($\chi_{27,449} = 309.37, p < 0.0001$) than in Narragansett Bay. On Cape Cod virtually all crabs survived, whereas nearly 90% of tethered crabs were eaten in denuded creek-bank areas of Narragansett Bay (Fig. 4a). As predicted by our tethering results, *Sesarma* densities on Cape Cod were nearly 10 times higher than in Narragansett Bay (Fig. 4b; $F_{1,56} = 71.02, p < 0.0001$).

Creek-bank die-offs were present in 1984 at all 5 marshes we investigated, but have expanded significantly in size and developed in new locations within each marsh over the past 23 years. The rate of die-off expansion has accelerated from 3.3% (0.7) per year (1984–2000) to 7.9% (0.7) per year (2000–2007). Consequently, die-off areas have nearly quadrupled in size since 1984, and more than doubled in the past 7 years alone (Table 1).

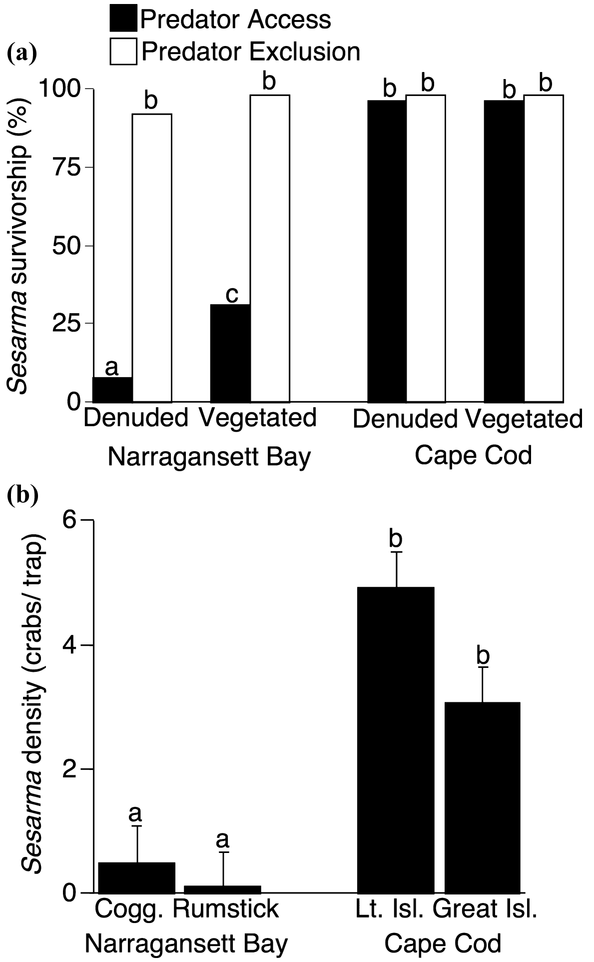

Figure 4. (a) Proportion of Sesarma *tethered in vegetated and denuded creek bank areas in Narragansett Bay, Rhode Island, and Cape Cod, Massachusetts, surviving after one tidal cycle in the presence and absence of predators. (b) Mean (SE)* Sesarma *density (crabs caught per trap) at our 4 experimental sites: Coggeshall (Cogg.) and Rumstick Point (Rumstick) marshes in Narragansett Bay, Rhode Island, and Lieutenant's Island (Lt. Isl.) and Great Island (Great Isl.) marshes in Cape Cod, Massachusetts. Different letters above bars indicate treatments that differed significantly.*

Discussion

Our results provide compelling evidence that grazing pressure by a common, native crab, *Sesarma reticulatum* is leading to the loss of cordgrass and the current die-off of salt marshes on Cape Cod, Massachusetts. These results contribute to growing evidence that human disturbances are triggering increased consumer control in salt marshes and driving these ecosystems to collapse throughout the western Atlantic. Although bottom-up, physical factors have long been thought to control salt marsh productivity (e.g., Teal 1962; Odum 1969; Nixon 1982), results from our study and studies of a diversity of other marsh ecosystems from the Canadian sub-Arctic (Jefferies 1997) to the southeastern coast of the United States (Silliman et al. 2005) and Argentina (Alberti et al. 2008) suggest that human activities, such as overfishing and eutrophication, are stimulating consumer densities and their impacts. This shift toward strong top-down, consumer control is precipitating large-scale vegetation die-offs (Bertness & Silliman 2008). Because salt marshes provide invaluable coastal ecosystem services (i.e., storm buffering, chemical filtering, nursery grounds) and are currently managed exclusively as systems controlled by bottom-up forces, this new evidence of marsh vulnerability to top-down forces has critical implications.

Our study provides several lines of evidence that marsh die-offs are common in Cape Cod salt marshes and are driven by crab densities and herbivore pressure. All 12 of the marshes surveyed had cordgrass die-offs, characterized by high densities of burrows and denuded substrate, that affected nearly half (46.0% [SE 7.6]) of the creek banks at each site. Differences in *Sesarma* grazing pressure and associated crab density explained >80% of intermarsh variation in the extent of die-off of Cape Cod salt marshes, and crab exclusions demonstrated experimentally that the extensive cordgrass die-offs in Cape Cod salt marshes are driven by crab herbivory. Cordgrass transplanted into denuded creek banks on Cape Cod was rapidly eaten unless protected in cages from herbivorous crabs. Furthermore, our results confirm that salt marsh die-offs are a growing problem on Cape Cod. Although

Table 1. Development of Cape Cod, Massachusetts (MA) marsh die-off areas (1984–2007).

Survey marsh, town (MA)	*No. of die-offs tracked*	*Area (m^2) 1984*[a]	*Area (m^2) 2000*[a]	*Area (m^2) 2007*[a]	*1984-2000 expansion rate*[b]	*Mean 2000-2007 expansion rate*[b]
Bridge Road, Eastham	3	4.2	14.9	93.4	5.7 (5.7)	12.1 (2.2)
Lt. Island, Wellfleet	8	116.5	305.9	790.9	3.91 (1.1)	8.12 (0.9)
Chatham Harbor, Chatham	7	248.4	345.48	563.7	1.52 (0.7)	5.09 (1.1)
Sacquatucket Harbor, Harwich	5	288.3	383.03	753.3	2.1 (1.3)	6.2 (1.5)
Round Hill, Wellfleet	5	40.6	87.24	430	4.4 (1.2)	10.5 (1.1)
Cumulative	28	698.0	1136.6	2631.4	3.3 (0.7)	7.9 (0.7)

[a] *Area of die-offs pooled across each surveyed marsh (georectified image resolution [SE 1]).*
[b] *Mean (SE) percent change in die-off area per year.*

denuded areas in creek banks were detected in 1984 aerial images, the rate of expansion of cordgrass die-off has doubled over the past decade. Our data demonstrate that *Sesarma* herbivory causes die-offs of creek-bank cordgrass, die-offs are affecting most low marsh habitats in Cape Cod salt marshes, and the expansion of die-offs has increased dramatically over the past 2 decades. This implies that *Sesarma* populations on Cape Cod have been released from previous limitations.

Results from our tethering experiment and trapping surveys support the hypothesis that release from top-down consumer control is leading to the elevated abundance and herbivory impacts of *Sesarma* observed in Cape Cod salt marshes. In Narragansett Bay, where denuded *Sesarma* burrow areas are relatively small (<9 m^2), uncommon, and have not increased in size recently, predation rates on *Sesarma* were an order of magnitude higher and crab densities an order of magnitude lower than on Cape Cod. This suggests that predation pressure is currently controlling *Sesarma* densities and impacts in Narragansett Bay and that reduced predation pressure in Cape Cod marshes is driving the rapid expansion of die-off areas and higher *Sesarma* densities (Fig. 4; Table 1).

This geographic variation in top-down control and die-off of marshes could be explained by the decline on Cape Cod of many large predators that forage in shallow coastal water and, historically, could have exerted consumer control on *Sesarma*. The tautog (*Tautoga onitus*), a fish that primarily feeds on intertidal invertebrates (Auster 1989), was extremely abundant throughout Cape Cod until the mid-1980s, when a substantial commercial fishery developed for this species. Since a documented population crash in 1994, tautog abundances have failed to recover in Massachusetts (King et al. 2007), and this severe reduction in tautog coincides with the accelerating impacts of *Sesarma* detected in our aerial image analysis. Similar to tautog, Black-crowned Night Herons (*Nycticorax nycticorax*) have also been historically abundant intertidal foragers on Cape Cod, but a recent census indicates their populations have declined over 50% in the past few decades (R. Prescott and M. Brady, personal communication). In Narragansett Bay all of the predation on tethered *Sesarma* we observed directly was by blue crabs (*Callinectes sapidus*), which are commercially and recreationally harvested throughout the Atlantic Coast of the United States. The current northern range limit of blue crabs is associated with the thermal boundary at Cape Cod (Williams 1984), which suggests that their control of *Sesarma* could expand to the die-off marshes in eastern Cape Cod if their distribution moves to higher latitudes with climate change, as has been the case with other shallow water marine species (Sagarin et al. 1999; Rosenzweig et al. 2007). On the other hand, further population declines of blue crabs associated with increased harvesting or habitat degradation could expand the geographic extent of marshes susceptible to die-off due to uncontrolled *Sesarma* populations, as observed where the snail *L. irrorata* has denuded lower-latitude salt marshes in areas of low predator abundance (Silliman et al. 2005).

The consequences of the loss of secondary consumers from coastal ecosystems are just beginning to be understood (Jackson et al. 2001; Worm et al. 2006), and creek-bank die-offs of cordgrass on Cape Cod may be an unanticipated result of the degradation of coastal food webs. Overfishing of large consumers (sensu Myers & Worm 2003), the general degradation of coastal ecosystems (Lotze et al. 2006), and shifting range limits associated with climatic variation (Sagarin et al. 1999) could all be contributing to the release of *Sesarma* from consumer control on Cape Cod marshes, but separating the interactive effects of these forces on *Sesarma* populations and their impact remains to be explored.

Our work contributes to mounting evidence that human activities are triggering consumer-driven die-offs that are pushing salt marsh ecosystems toward collapse by affecting the plant species that build and maintain them (Bertness & Silliman 2008). This emerging pattern of salt marsh die-off across the western Atlantic is particularly disturbing because rising sea levels and permanent impacts of human modification, such as ditching and filling, threaten the resilience of these systems (Donnelly & Bertness 2001; Bromberg & Bertness 2005). Although the long-term effects of marsh die-offs are unknown, future efforts to conserve and manage coastal marshes need to incorporate the emerging role of consumer control.

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Literature Cited

Alberti, J., M. Escapa, O. Iribarne, B. R. Silliman, and M. D. Bertness. 2008. Crab herbivory regulates plant facilitative and competitive processes in Argentinean marshes. Ecology **89:**155–164.

Auster, P. J. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (North Atlantic and Mid-Atlantic)—Tautog and Cunner. Biological report 82 (11.105). U.S. Fish and Wildlife Service. Washington, D.C.

Bertness, M. D. 2006. Atlantic shorelines: natural history and ecology. Princeton University Press, Princeton, New Jersey.

Bertness, M. D., C. Crain, C. Holdredge, and N. Sala. 2008. Eutrophication and consumer control of New England salt marsh primary productivity. Conservation Biology **22:**131–139.

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

Bertness, M. D., and T. Miller. 1984. The distribution and dynamics of *Uca pugnax* (Smith) burrows in a New England salt marsh. Journal of Experimental Marine Biology and Ecology **83:**211–237.

Bertness, M. D., and B. R. Silliman. 2008. Consumer control of salt marshes driven by human disturbance. Conservation Biology **22:**618–623.

Boesch, D. F., and R. E. Turner. 1984. Dependence of fishery species on salt marshes- the role of food and refuge. Estuaries **7:**460–468.

Bromberg, K. D., and M. D. Bertness. 2005. Reconstructing New England salt marsh losses using historical maps. Estuaries and Coasts **28:**823–832.

Chapman, V. J. 1960. Salt marshes and salt deserts of the world. Interscience Publishers, New York.

Crichton, O. W. 1960. Marsh crab: intertidal tunnel-maker and grass-eater. Estuarine Bulletin **5:**3–10.

Donnelly, J. P., and M. D. Bertness. 2001. Rapid shoreward encroachment of salt marsh cordgrass in response to accelerated sea-level rise. Proceedings of the National Academy of Sciences of the United States of America **98:**14218–14223.

Gosner, K. L. 1979. A field guide to the Atlantic seashore. Houghton Mifflin, New York.

Hacker, S. D., and M. D. Bertness. 1999. Experimental evidence for factors maintaining plant species diversity in a New England salt marsh. Ecology **80:**2064–2073.

Harvell, D., et al. 2004. The rising tide of ocean diseases: unsolved problems and research priorities. Frontiers in Ecology and the Environment **2:**375–382.

Hughes, T. P., D. R. Bellwood, C. Folke, R. S. Steneck, and J. Wilson. 2005. New paradigms for supporting the resilience of marine ecosystems. Trends in Ecology & Evolution **20:**380–386.

Jackson, J. B. C., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science **293:**629–638.

Jefferies, R. L. 1997. Long-term damage to sub-arctic coastal ecosystems by geese: ecological indicators and measures of ecosystem dysfunction. Page 644 in R. M. Crawford, editor. Disturbance and recovery in Arctic lands: an ecological perspective. Kluwer Academic, Boston.

King, J., M. Camisa, V. Manfredi, and S. Correia. 2007. Massachusetts fishery resource assessment: F-56-R-15. Massachusetts Division of Marine Fisheries, Gloucester, Massachusetts.

Lewis, R. C. 2007. Cape salt marsh decline linked to native crab. The Boston Globe 19 November: D1.

Lotze, H. K., H. S. Lenihan, B. J. Bourque, R. H. Bradbury, R. G. Cooke, M. C. Kay, S. M. Kidwell, M. X. Kirby, C. H. Peterson, and J. B. C. Jackson. 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science **312:**1806–1809.

Mendelssohn, I. A., and J. T. Morris. 2000. Ecophysiological constraints on the primary productivity of Spartina alterniflora. Pages 59–80 in N. P. Weinstein and D. A. Kreeger, editors. *Concepts and Controversies in Tidal Marsh Ecology.* Kluwer Academic, Boston.

Myers, R. A., and B. Worm. 2003. Rapid worldwide depletion of predatory fish communities. Nature **423:**280–283.

Nixon, S. W. 1982. The ecology of New England high salt marshes: a community profile. Report FWS/OBS-81/55. U.S. Fish and Wildlife Service, Washington, D.C.

Odum, E. P. 1969. Fundamentals of Ecology. Saunders, Philadelphia, Pennsylvania.

Pandolfi, J. M., et al. 2005. Ecology—are U.S. coral reefs on the slippery slope to slime? Science **307:**1725–1726.

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

Rosenzweig, C., G. Casassa, D. J. Karoly, A. Imeson, C. Liu, A. Menzel, S. Rawlins, T. L. Root, B. Seguin, and P. Tryjanowski. 2007. Assessment of observed changes and responses in natural and managed systems. Pages 79–131 in M. L. Parry, O. F. Canziani, J. P. Palutikof, P. J. van der Linden, and C. E. Hanson, editors. Climate change 2007: impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom.

Sagarin, R. D., J. P. Barry, S. E. Gilman, and C. H. Baxter. 1999. Climate-related change in an intertidal community over short and long-time scales. Ecological Monographs **69:**465–490.

Seiple, W. H. 1979. Distribution, habitat preferences and breeding periods in the crustaceans *Sesarma cinereum* and *S. reticulatum* (Brachyura: Decapoda: Grapsidae). Marine Biology **52:**77–86.

Seiple, W. H., and M. Salmon. 1982. Comparative social behavior of two grapsid crabs, *Sesarma reticulatum* (Say) and *S. cinereum* (Bosc). Journal of Experimental Marine Biology and Ecology **62:**1–24.

Silliman, B., and M. Bertness. 2002. A trophic cascade regulates salt marsh primary production. Proceedings of the National Academy of Sciences of the United States of America **99:**10500–10506.

Silliman, B. R., J. van de Koppel, M. D. Bertness, L. E. Stanton, and I. A. Mendelssohn. 2005. Drought, snails, and large-scale die-off of southern U.S. salt marshes. Science **310:**5755–5758.

Smalley, A. E. 1960. Energy flow of a salt marsh grasshopper population. Ecology **41:**672–677.

Smith, S. M. 2006. Report on salt marsh dieback on Cape Cod (2006). National Park Service, North Truro, Massachusetts.

Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. Ecology **73:**747–754.

Teal, J. M. 1962. Energy flow in the salt marsh ecosystem of Georgia. Ecology **43:**614–625.

Valiela, I., and J. M. Teal. 1979. Nitrogen budget of a salt-marsh ecosystem. Nature **280:**652–656.

Williams, A. J. 1984. Shrimps, lobsters and crabs of the Atlantic coast of the Eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, D.C.

Worm, B., et al. 2006. Impacts of biodiversity loss on ocean ecosystem services. Science **314:**787–790.