Feedbacks underlie the resilience of salt marshes and rapid reversal of consumer-driven die-off

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Abstract. Understanding ecosystem resilience to human impacts is critical for conservation and restoration. The large-scale die-off of New England salt marshes was triggered by overfishing and resulted from decades of runaway crab grazing. In 2009, however, cordgrass began to recover, decreasing die-off ~40% by 2010. We used surveys and experiments to test whether plant–substrate feedbacks underlie marsh resilience. Initially, grazer-generated die-off swept through the cordgrass, creating exposed, stressful peat banks that inhibited plant growth. This desertification cycle broke when banks eroded and peat transitioned into mud with fewer herbivores, less grazing, and lower physical stress. Cordgrass reestablished in these areas through a feedback where it engineered a recovery zone by further ameliorating physical stresses and facilitating additional revegetation. Our results reveal that feedbacks can play a critical role in rapid, reversible ecosystem shifts associated with human impacts, and that the interplay of facilitative and consumer interactions should be incorporated into resilience theory.

Key words: alternate community state; cordgrass die-off; facilitation; feedback; group benefits; herbivory; human impact; phase shift; resilience; salt marsh recovery; Sesarma reticulatum; Spartina alterniflora.

Introduction

Understanding the resilience of ecosystems to anthropogenic disturbances is an important practical goal of ecology (Walker 1995, Biggs et al. 2009), particularly as the environmental demands of a burgeoning human population continue to increase (MEA 2005). Human population growth and activities have escalated extinctions (Barnosky et al. 2011), ecosystem phase shifts (Hughes 1994), and habitat loss (Vitousek 1994), threatening the persistence of natural ecosystems (e.g., Schröter et al. 2005). Ecosystem recovery after anthropogenic disturbances has been documented in some terrestrial (Broadbent et al. 2006), freshwater (Schindler 1974), and marine systems (Worm et al. 2006), but full recovery of impacted systems has been observed in only a third of ecological recovery studies (Jones and Schmitz 2009). Thus, elucidating mechanisms of resilience is essential to inform conservation and to test ecological theory (Folke et al. 2004, Carpenter et al. 2009).

Since Holling (1973) introduced the concept of resilience, the ability of systems to recover from or tolerate natural or human disturbances, it has been widely discussed and often invoked, but experimental and observational studies that reveal the mechanisms underlying shifts in ecosystems, necessary to predict resilience, have been lacking to date (Thrush et al. 2009). Human impacts on ecosystems such as habitat loss, species diversity reduction, and top predator depletion have long been thought to reduce ecosystem resilience, making instances of recovery in heavily impacted ecosystems particularly valuable opportunities for discovering natural mechanisms of resilience (Folke et al. 2004). This mechanistic understanding could ultimately allow for managing resilience of anthropogenically disturbed ecosystems to attain sustainable development (e.g., Walker et al. 2004).

Coastal areas are among the most human-impacted ecosystems (Lotze et al. 2006). They continue to be degraded by overfishing (Worm et al. 2006), eutrophication (Vitousek et al. 1997), climate change (Harley et al. 2006), and disease (Harvell et al. 2002). Due to the compromised state of coastal ecosystems, understanding the drivers of their resilience is a pressing objective. Salt marshes are model systems for examining resilience since globally they are among the most valuable ecosystems per unit area (de Groot 1994) and have been heavily exploited, modified, and developed for millennia, resulting in an estimated loss of 67% of coastal wetlands worldwide (Lotze et al. 2006, Bromberg Gedan et al. 2009).

Recently, the die-off of Cape Cod salt marshes led to loss of up to 90% of smooth cordgrass (*Spartina alterniflora* Loisel, hereafter "cordgrass"), the founda-

tion species that builds New England salt marshes (Holdredge et al. 2009). This collapse is the most recent occurrence of salt marsh die-offs which are spreading through the Western Atlantic, ranging from the Canadian subarctic (Jefferies et al. 2006) to the Gulf of Mexico (Silliman and Bertness 2002). Unprecedented consumer control has contributed to these die-offs (Bertness and Silliman 2008). On Cape Cod, humans have triggered marsh die-off through a trophic cascade, where recreational fishing depleted predators, allowing populations of the native, herbivorous purple marsh crab (*Sesarma reticulatum* Say, hereafter *S. reticulatum*) to explode and denude the lower marsh of cordgrass (Altieri et al. 2012). These die-offs have expanded rapidly and steadily for decades, beginning in the 1970s (Coverdale et al. 2013).

In 2010, we found that many of the most heavily impacted marshes on Cape Cod had begun recovering from die-off. We observed that recovery followed a similar trajectory across sites. Cordgrass recolonization began in low marsh elevations on unconsolidated muddy creek banks, produced from the erosion and slumping of die-off peat, and was followed by vegetative spread up the bank to higher elevations and laterally into other unvegetated areas (Fig. 1). This pattern suggests that substrate characteristics and reduced herbivory at low elevations allow cordgrass recoloniza-tion, and that habitat modification by cordgrass facilitates its regrowth. Similar positive interactions are fundamental structuring forces in many ecological communities (Bruno et al. 2003, Angelini et al. 2011), and their importance for conservation and ecological restoration has recently been recognized (Byers et al. 2006, Crain and Bertness 2006, Halpern et al. 2007). However, the interaction between multiple mechanisms, including group benefits and herbivory, that underlie shifts in ecological states and the resilience of impacted ecosystems is largely unstudied (Thrush et al. 2009).

Herbivory triggered by anthropogenic impacts has recently been identified as a general mechanism for converting marshes to harsh, unvegetated landscapes (Bertness and Silliman 2008). Positive interactions driven by habitat amelioration are critical in the secondary succession of salt marshes following natural disturbance (Bertness and Shumway 1993). Therefore, we hypothesized that plant–soil feedbacks play a critical role in driving shifts between vegetated and die-off states in salt marshes and contribute to the recent, rapid recovery of vegetation at die-off sites. In particular, we predicted that substrate characteristics associated with initial die-off conditions inhibit plant growth, that subsequent clonal integration and facilitation through habitat amelioration allow cordgrass to overcome stressful conditions and expand into unvegetated areas, and that the shift between states characterized by these feedbacks was mediated by changes in consumer pressure. We tested these hypotheses by quantifying die-off and recovery areas and experimentally investi-gating herbivory and cordgrass growth in these areas. We found that feedbacks play a major role in the resilience of salt marshes to human-driven collapse.

Methods

Site description

We studied recovery at 15 sites on Cape Cod, Massachusetts, USA, where we have an understanding of how contemporary (Altieri et al. 2012) and historic (Coverdale et al. 2013) human impacts, herbivory (Holdredge et al. 2009), and substrate characteristics (Bertness et al. 2009) have generated die-off of salt marshes (see Appendix A for a list of study sites and locations). Historical reconstruction from archived aerial photographs (Coverdale et al. 2013) revealed that five of the sites had never experienced die-off (hereafter "healthy sites"), and were treated as controls in comparison to the other 10 sites in various stages of die-off and recovery (hereafter "recovering sites"). At recovering sites, we identified three zones based on vegetation, and tidal elevation: (1) The "recovery zone," the lowest marsh elevation that includes regrowing cordgrass and unconsolidated muddy substrate. (2) The "die-off zone," an unvegetated strip of bare peat substrate maintained by active herbivory and riddled with *S. reticulatum* burrows above the recovery zone. (3) The "high zone," where the grazing border exists between vegetated and denuded peat above the die-off zone (Fig. 1).

Extent and trajectory of die-off and recovery

We quantified the extent of die-off and recovery at all 15 sites by: (1) quantifying historical mosquito ditch widening, (2) analyzing long-term (1939–2010) spatial extent of die-off and recovery of marsh vegetation, and (3) tracking recent vegetation border movement associ-ated with recovery and die-off. To assess the extent of erosion and habitat loss caused by die-off over the last ~70 years, we measured changes in ditch widths with archived aerial photographs taken at low tide (sources: MassGIS, U.S. Geological Survey, Cape Cod National Seashore, Towns of Mashpee and Bourne, Massachu-setts, USA) using GIS software (ArcGIS v10.1; ESRI, Redlands, California, USA). During the Great Depres-sion, mosquito ditches were dug to a consistent width across Cape Cod to drain mosquito habitat (Bromberg Gedan et al. 2009), making the extent of erosion and ditch widening a standard measure of die-off intensity and habitat loss. Ditch widening is driven by repeated episodes of *S. reticulatum* grazing, burrowing, and creek bank erosion, followed by slumping and calving of weakened creek banks. At each site, eight points were randomly assigned to mosquito ditches and measured through time using aerial photo series (1939, 1976, 1994, 2005). We directly quantified ditch widening over time, measuring width as the distance between unsubmerged habitat perpendicular to the major axis of the ditch. Width was set to a minimum of 1.5 m due to early

photograph resolution. Site differences were analyzed with repeated measures ANOVA (SAS JMP v5 used for this and other analyses [SAS Institute 2003]).

We used GIS analysis of georeferenced aerial photographs from 1939 to 2010 to quantify changes in the spatial extent of die-off and recovery. For each site and time period, we randomly overlaid six 100-m transects along the seaward edge of marshes where die-off occurs (Altieri et al. 2012). At eight points along each transect, we measured the width of die-off and total width of the cordgrass zone. For each transect, we quantified the percentage of die-off in the cordgrass zone by dividing the total die-off area (calculated by multiplying the average width of die-off by 100 m) by the total area of the cordgrass zone (mean width of cordgrass zone × 100 m). For analysis, six transects per site were averaged to yield a single estimate of die-off for each marsh.

We examined current recovery rates by haphazardly placing 20 polyvinyl chloride stakes at each of the 10 recovering sites in May 2010: 10 along the border between the low recovery zone and the middle die-off zone, and 10 along the border between the die-off zone and the vegetated high zone. We quantified the distance between these benchmarks and the new borders in October 2010. Border movement across sites was analyzed with paired t tests.

Vegetation–sediment interactions

Since cordgrass traps, aerates, and binds sediment, which can have important effects on subsequent plant growth (Howes et al. 1986, Bertness 1988), we hypothesized that recovering areas would have more fine sediment on the marsh surface, more oxygenated soil, and lower erosion than die-off areas. First, we compared sediment between recovering and unvegetated areas by collecting sediment cores (1 cm diameter × 3 cm deep) in June 2010 at a representative recovering site (Blackfish Creek) with extensive areas of each habitat. To determine organic and inorganic mass, five cores were collected from each habitat, dried at 60°C for 14 days, sieved into >0.063-mm and <0.063-mm fractions, and weighed before and after burning at 550°C for six hours. Second, we quantified redox potential in unvegetated and vegetated areas at high and recovery zones in June 2010 at Blackfish Creek. Redox was measured with a redox electrode (Orion 9180BNMD, Thermo Fisher Scientific, Waltham, Massachusetts, USA) in paired vegetated and unvegetated areas at the same elevation in each zone ($n = 10$ per area per zone). All redox measurements were made at root depth within a two-hour period at low tide, alternating area and zone between measurements. Third, we measured erosion/accretion rates at the 10 recovering sites in die-off and vegetated areas at high, die-off, and recovery zones with sediment elevation posts driven vertically into the marsh to refusal ($n = 10$ posts/zone [Cahoon et al. 2002]). In June and October 2010, we measured substrate elevation by taking the mean height of four pins resting on the

Fig. 1. Photographs of the stages of salt marsh recovery from die-off with no cordgrass (*Spartina alterniflora*) remaining below the active grazing front (top), establishment of cordgrass in the low zone where grazing pressure and stress associated with die-off conditions are both lowest (center), and vegetative spread facilitated by group benefits up the bank to near closure of the die-off area (bottom). Recovery of vegetation starts and radiates from the low zone, even in instances where herbivory by the native purple marsh crab *Sesarma reticulatum* continues in the high zone at the top of the bank.

marsh surface that were slid through a T-bar placed on each post. Differences in fine-sediment mass, redox potential, and sediment height were analyzed with paired t tests.

We experimentally tested the hypothesis that recovering vegetation affects sediment quality by eliminating cordgrass from recovery areas. In the recovery zone at Parker River, where a mosaic of unvegetated die-off and vegetated regrowth areas existed, we established three plot types in May 2011: naturally unvegetated, naturally vegetated, and experimentally cleared of vegetation ($n = 10$ per plot type). We applied herbicide and clipped all aboveground vegetation with shears to establish experimentally cleared plots. Each plot was 3 m long and spanned the width of the recovery zone. In each plot, we measured substrate erosion/accretion rates with sediment elevation posts, changes in the relative amount of fine-grain sediment (<0.063 mm), and organic content as described previously. We also sampled each plot for salinity of porewater squeezed from a $3 \times 3 \times 3$ cm plug cut from each plot onto a hand-held refractometer (A366ATC, Atago USA, Bellevue, Washington, USA). Changes in substrate elevation and sediment quality through time were analyzed with paired t tests, and differences in sediment deposition and salinity across experimental treatments were analyzed with ANOVA.

Since regrowth always originated in the recovery zone rather than the die-off zone, and our grazing experiment (see Consumer pressure) revealed that the survivorship of ramets was highest in the recovery zone, even when S. reticulatum were excluded, we hypothesized that the recovery zone is less stressful and more conducive to cordgrass growth than the die-off zone because of differences in substrate. We experimentally tested this hypothesis by conducting a reciprocal substrate transplant between the peaty die-off and muddy recovery zones at Blackfish Creek. In each zone, we removed substrate from forty $30 \times 30 \times 30$ cm holes (>1 m apart), and randomly selected whether the hole in each plot would be filled with ambient substrate as a control or substrate from the other zone ($n = 20$ plots per treatment $\times$ zone combination; $n = 80$ plots total). We transplanted a cordgrass ramet (roots of all transplanted ramets rinsed of substrate) into each plot in May 2010, protected each with a grazer exclusion cage to isolate the effect of physical conditions, and scored survivorship three weeks later in mid-June.

Facilitation through group benefits

To examine the relative importance of vegetative and sexual reproduction to recovery, we destructively sampled individual plants in recovering areas in June 2010. We haphazardly plucked 100 small stems suspected to be seedlings (>25 cm apart) in five regrowth areas at six recovering sites, and identified them as seedlings (stems not attached to rhizomes) or ramets of clones. Once we could identify cordgrass seedlings with certainty we counted seedlings in 10-m transects (12

transects per site $\times$ 9 sites) along recovering creek banks and marked all seedlings found during 1.5 person-hours of searching per site ($n = 44$ total seedlings). We scored these marked seedlings in September 2010 for survivorship.

To test whether group benefits (Bertness and Leonard 1997) drive recovery by ameliorating physical stress, we conducted two experiments. In the first experiment, we transplanted 30 cordgrass ramets into regrowth and unvegetated die-off areas in the recovery zones at two representative recovering sites, Blackfish Creek and Lieutenant Island, in May 2010 ($n = 120$ total), and scored survivorship after three weeks.

In a second group benefit experiment, we created vegetated plots of differing size in the unvegetated recovery zone habitat to isolate the effects of neighbors from previously existing physical variation that may have driven patterns of vegetation in the first experiment. At Blackfish Creek, we established plots (>1 m apart) with treatments of a single ramet, a culm (7.5 ± 1.1 stems; mean $\pm$ SE), or three culms bundled together (26.4 ± 2.0 stems; $n = 10$ plots per treatment). In each replicate, a single transplanted ramet was marked at the start of the experiment in May 2010, and scored for survivorship after five weeks. Differences between treatments in both group benefits experiments were analyzed with a Kaplan-Meier survivorship analysis. We also measured redox potential as a proxy for edaphic stress in each plot to examine whether it varied with stem density.

Consumer pressure

We examined the relationship between herbivory and recovery dynamics by measuring S. reticulatum density, burrow density, substrate hardness, and herbivory pressure in high zones with active die-off borders and in revegetated zones at each of the 10 recovering sites. We quantified relative S. reticulatum densities using overnight deployments of 10 pitfall traps per zone at each site (Altieri et al. 2012). S. reticulatum burrow density was quantified in the three zones using a haphazardly tossed 0.25×0.25 m quadrat ($n = 12$ per zone per site). We measured substrate hardness with a penetrometer ($n = 12$ per zone per site), because substrate toughness can limit the ability of S. reticulatum to maintain burrows (Bertness et al. 2009). To quantify grazing pressure, we measured the proportion of 50 random stems that had characteristic grazing damage (Holdredge et al. 2009) in each of 12 1-m^2 plots (>1 m apart). Differences between zones were analyzed with paired t tests.

We experimentally examined the separate and interactive effects of S. reticulatum grazing and physical stress at three representative recovering sites (Blackfish Creek, Lieutenant Island, and Parker River). At each site, we transplanted 30 cordgrass ramets into each of the three zones (high, die-off, and recovery), and assigned each ramet to one of three caging treatments
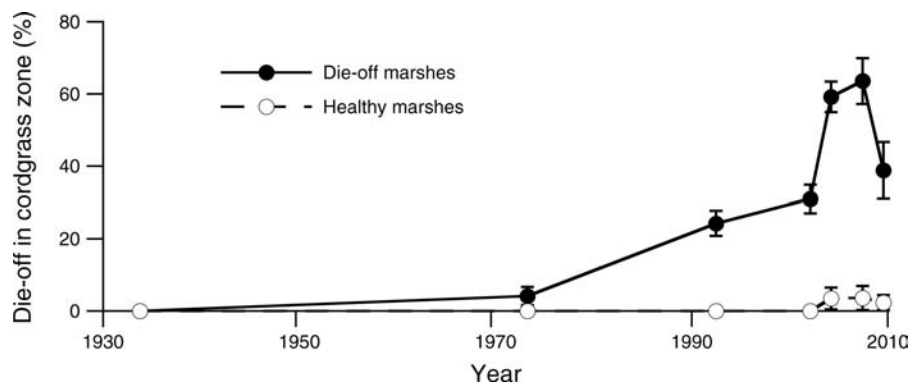
FIG. 2. Our GIS analysis of archived aerial images revealed a steady increase in die-off area for nearly a half-century, starting in the 1970s when sites characterized by marsh die-off diverged from unimpacted healthy marshes due to recreational fishing (Altieri et al. 2012) associated with increase in infrastructure and the latent effects of marsh ditching (Coverdale et al. 2013). Since 2008 there has been reversal in the trajectory of die-off due to the revegetation of marshes, which demonstrates the resilience of salt marshes. Data points are mean ± SE.

(full cage, procedural control, open plot). Cages were constructed of hardware cloth (6-mm mesh), and either extended from the ground to a height of 60 cm for the full cage treatment, or had a 3-cm gap at the bottom to mimic cage structure but allow *S. reticulatum* to enter for procedural cage controls. The experiment was initiated in May 2010, and after three weeks we scored survivorship. We noted whether ramets in open plots (which were vulnerable to biotic and abiotic stress) had died from grazing (ramet shredded) or stress (ramet intact but brown and limp). Since we observed differences in *S. reticulatum* abundance among sites, we analyzed sites separately with chi-square analysis. First, to identify the relative importance of grazing across zones, we examined the interaction between caging treatment and elevation for the proportion of ramets surviving at the end of the experiment. Second, to examine whether the relative importance of stress and grazing varied by zone, we examined the proportion of dead ramets in open plots that had succumbed to stress or grazing.

RESULTS

Extent of die-off and recovery

Mosquito ditch widths at vegetated and die-off sites did not differ in 1939 or 1976. By 1994, however, ditch widths at die-off sites were significantly greater and continued to diverge in 2005 ($F_{3,36} = 10.92$, $P < 0.0001$). Ditches at die-off sites widened by 379% ± 110% from 1939 to 2005, while ditches at vegetated sites increased by only 50% ± 33%.

GIS analysis of aerial images revealed that healthy and recovering sites were similar in 1939, and that from 1976 to 2008 unvegetated area increased dramatically only at die-off sites ($F_{6,72} = 16.33$, $P < 0.0001$, Tukey's HSD post hoc; Fig. 2). There was a significant decrease (Tukey's HSD post hoc) of 39% in die-off area from 2008 to 2010, indicating net recovery. Of the seven die-off sites identified in our 2009 surveys, the extent of die-

off in 2010 had decreased at six sites (i.e., vegetation cover increased), and changed by <1% at the last die-off site. All recovery sites showed peak die-off in 2008, followed by a decrease in 2010, and 64% ± 12% of survey points along transects showed cordgrass regrowth, indicating widespread recovery.

The change in the location of marked borders revealed cordgrass expansion from the recovery zone ($t_{1,8} = 2.70$, $P < 0.05$) and loss of cordgrass at the lower border of the high zone ($t_{1,7} = 3.75$, $P < 0.01$). Gains at the recovery zone border over the five-month growing season were 5.9 ± 2.1 cm, while grazing losses in the high zone were 9.2 ± 2.5 cm. Gains at the recovery zone border were attributable to encroachment of clonal runners from the upper border (Fig. 1); losses at the high-zone margin were caused exclusively by herbivory, evident by clipped stems characteristic of *S. reticulatum* grazing (Holdredge et al. 2009).

Vegetation–sediment interactions

More fine surface sediment (<0.063 mm) was retained in recovery areas ($F_{1,7} = 12.89$, $P < 0.01$) (46.4% ± 1.8% of total) than in nearby unvegetated sediments (33.9% ± 3.1%). Organic matter in sediments was also higher in recovery areas ($F_{1,7} = 31.74$, $P < 0.001$) (24.9% ± 0.2%) than in unvegetated die-off (15.1% ± 1.7%).

Redox stress was higher in the unvegetated (−138 ± 49 mV) than regrowth (−21 ± 30 mV) areas of the low zone (mean pair difference = 116 ± 36 mV, $t_{1,9} = 4.48$, $P < 0.001$). Likewise, redox values near the upper die-off border were lower in the peat of active die-off (18 ± 7 mV) than peat of vegetated (55 ± 12 mV) areas (mean pair difference = 37 ± 8 mV, $t_{1,9} = 3.24$, $P < 0.01$). This difference was greatest at lower elevations ($F_{1,18} = 4.66$, $P < 0.05$).

Substrate elevation, as measured by our sediment elevation posts over four months of the growing season, decreased in high-zone grazing areas (−1.2 ± 0.3 mm, $t_{1,6} = 3.92$, $P < 0.01$) and in established mid-zone die-off
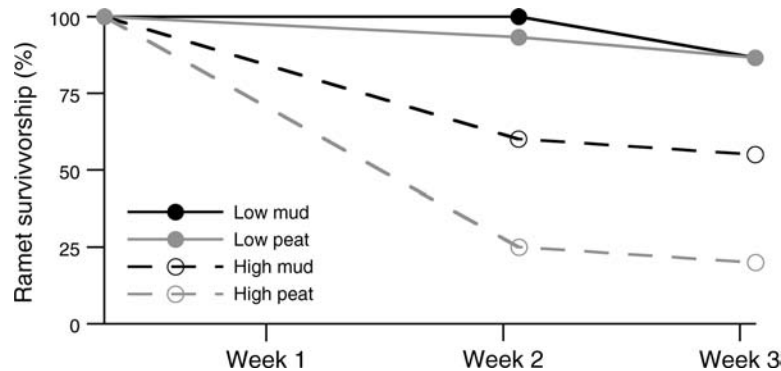
Fig. 3. Survivorship of cordgrass ramets in substrates that were reciprocally transplanted between the peat of die-off areas in the mid-zone and mud from the regrowth areas in the low zone revealed that low survivorship of cordgrass ramets in die-off areas is due to interactive stresses of substrate (die-off peat) and elevation (mid-zone). This explains why cordgrass recovery initiates in the less stressful low zone.

areas (-3.6 ± 1.0 mm, $t_{1,2} = 3.809$, $P < 0.05$). In the vegetated recovery zone, average elevation across sites did not change significantly ($t_{1,4} = 0.35$, $P = 0.74$), but four of five sites showed a trend of positive elevation gains.

Experimental removal of cordgrass in the recovery zone affected sediment quality relevant to plant survivorship and growth, including sediment elevation, accumulation of fine sediment, accumulation of organic sediment, and soil salinity ($F_{2,25/27} \geq 3.6$, $P < 0.05$; Appendix B: Table B1). (F and P values were summarized from multiple analyses; some denominator degrees of freedom were 25, and some were 27.) In all cases, post hoc analysis revealed that areas where cordgrass was experimentally removed were different from regrowth areas and were similar to naturally unvegetated die-off areas.

Substrate manipulations revealed an interactive effect of substrate type and zone on the survival of transplanted cordgrass ramets ($\chi^2 = 24.79$, $P < 0.001$). Post hoc analysis found that survivorship was greatest in the low zone regardless of substrate type, but in the more stressful mid-elevation die-off zone, survivorship was lower due to the compounded effects of both the elevation and substrate type typical of die-off (Fig. 3).

Facilitation through group benefits

Seedlings were rare relative to clonal runners at recovering sites ($0.4\% \pm 0.1\%$ of total stems). We also found only 0.59 ± 0.37 seedlings/10-m transect at nine sites, and seedling density was not correlated with recovery across sites ($R^2 = 0.05$, $P = 0.58$). No marked seedling survived.

Survivorship of ramets transplanted into vegetated recovery areas was higher than transplants in unvegetated banks ($\chi^2 = 34.45$, $P < 0.0001$); this difference was consistent across sites (site effect, $\chi^2 < 0.73$, df $= 1$, 8, $P > 0.52$). The presence of conspecifics more than doubled the proportion of surviving ramets (Fig. 4A).

Ramets individually transplanted into die-off areas experienced the lowest survivorship ($\chi^2 = 31.20$, $P < 0.0001$), while those associated with culms and larger blocks had 100% survivorship (Fig. 4B; see Plate 1). Redox potential showed the same trend; culms (6 ± 36 mV) and blocks (10 ± 20 mV) were similar to one another, and had lower stress ($F_{2,27} = 29.87$, $P < 0.0001$) than individual ramets (-302 ± 39 mV). All mortality in both group benefit experiments was attributed to edaphic stress since dead ramets were whole, wilted, and brown.

Consumer pressure

At recovering sites, the density of *S. reticulatum* was an order of magnitude higher ($t_{1,5} = 1.65$, $P < 0.05$) in the actively grazed high zone (1.6 ± 0.6 individual per trap) than in the recovery zone (0.1 ± 0.1 individual per trap). Burrow densities were also an order of magnitude higher ($t_{1,8} = 6.98$, $P < 0.01$) in the grazed high zone (5.5 ± 0.8 burrows/m^2) than the recovery zone (0.4 ± 0.1 burrows/m^2). The density of burrows was likely limited by substrate hardness, which was nearly an order of magnitude lower in the recovering zone (1.2 ± 0.2 kg) than actively grazed areas (10.9 ± 0.63 kg) ($t_{1,8} = 16.67$, $P < 0.0001$). Herbivore damage was also nearly an order of magnitude greater ($t_{1,5} = 8.6$, $P < 0.01$) in the high zone ($24.9\% \pm 3.7\%$) than in the recovery zone ($0.3\% \pm 0.1\%$) at die-off sites.

Comparison of caged and uncaged transplants at the three experimental sites revealed that grazing was a significant cause of plant mortality ($\chi^2 > 26.61$, df $= 8$, 77/81, $P < 0.001$ all sites). Post hoc analysis revealed that grazing effects were limited to the high and mid-zones and were never significant in the low zone. Additional analysis of the uncaged transplants revealed that survivorship was highest in the low zone, where physical stress was the only source of mortality, and that survivorship decreased with increasing elevation due to the combination of physical stress and grazing ($\chi^2 > 13.45$, df $= 4$, 24, $P < 0.001$ all sites; Fig. 5).
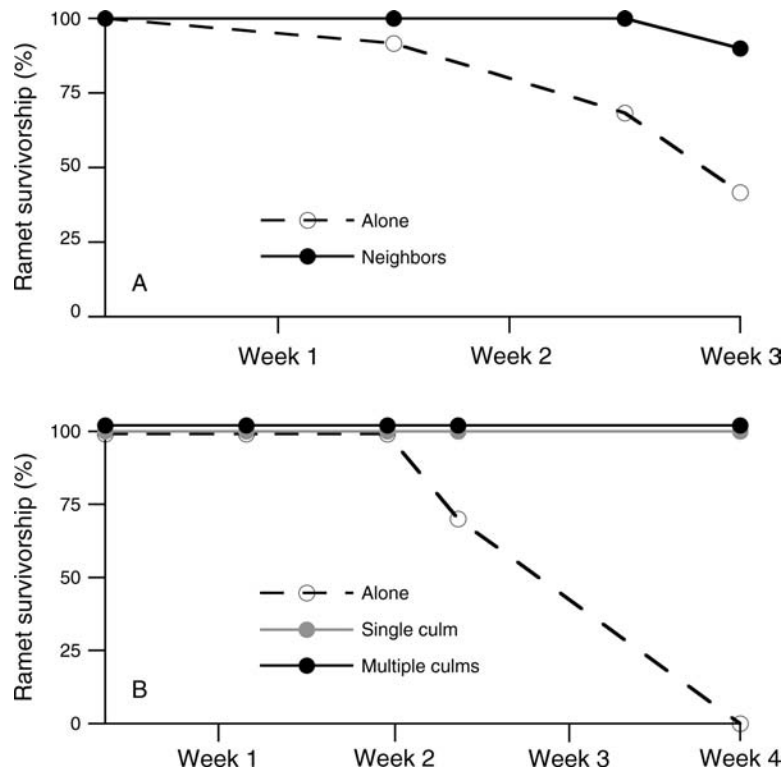
Fig. 4. Results of experiments testing the importance of group benefits for the recovery of cordgrass. (A) In the first experiment, cordgrass ramets were transplanted to the same elevation inside or outside existing patches of recovering vegetation, and survivorship was found to be higher within patches, indicating that physical factors limiting survivorship were ameliorated by neighbors. (B) In the second experiment, we created artificial patches of vegetation to control for potentially different conditions underlying the location of recovering vegetation, and similarly found that survivorship of transplanted cordgrass ramets was higher among neighbors in culms regardless of patch size (see Plate 1). Data from the two experimental sites are pooled in panel (A), and overlapping treatments with 100% survivorship are visually offset for clarity in panel (B).

Discussion

Our results reveal that consumer pressure and associated substrate can tip the balance between feedback loops, leading to rapid, reversible transitions between vegetated and die-off states in a salt marsh ecosystem. Herbivory drives marsh die-off and generates stressful substrate conditions that further limit plant survivorship, but group benefits via habitat modification can overcome these stresses, allowing revegetation of die-off areas and promoting marsh resilience. These mechanisms underlying marsh resilience have generated a widespread reversal of decades of marsh loss.

Spatial patterns and feedbacks associated with creek bank die-off and recovery

We identified discrete shifts between vegetated and die-off states through both time and space. Analysis of archived aerial images revealed a constant expansion of die-off area across Cape Cod marshes until 2008, when the trend reversed with a ~40% reduction in die-off area at our study sites in just two years. Within salt marshes, banks had three distinct zones: a high zone defined by remnant vegetation and active grazing, a mid-zone of die-off characterized by crab-riddled, unvegetated peat,

and a low zone composed of mud and recovering vegetation.

We conclude that the reversal of die-off, evident in 2010, is attributable to recovery and not year-to-year variation, for several reasons. First, the trajectory is consistent through time prior to 2010, as well as in another study with historic data from different years that found individually tracked die-off areas consistently expanded prior to the reversal in 2010 (Holdredge et al. 2009). Second, the reversal observed in 2010 is of significant magnitude and was consistent across multiple sites. Lastly, we identified the mechanisms underlying the observed recovery associated with substrate, facilitation, and consumers interacting through feedbacks.

The rapid recovery of marshes from die-off and the sharp boundary between unvegetated and revegetated areas are characteristic of systems with positive feedbacks (Wilson and Agnew 1992). Positive feedbacks between consumers and vegetation or between vegetation and substrate can accelerate change of an ecosystem from one state to another (Knowlton 2004). In our system, there are two distinct feedbacks that reinforce the unvegetated peat and revegetated cordgrass states (Fig. 6).
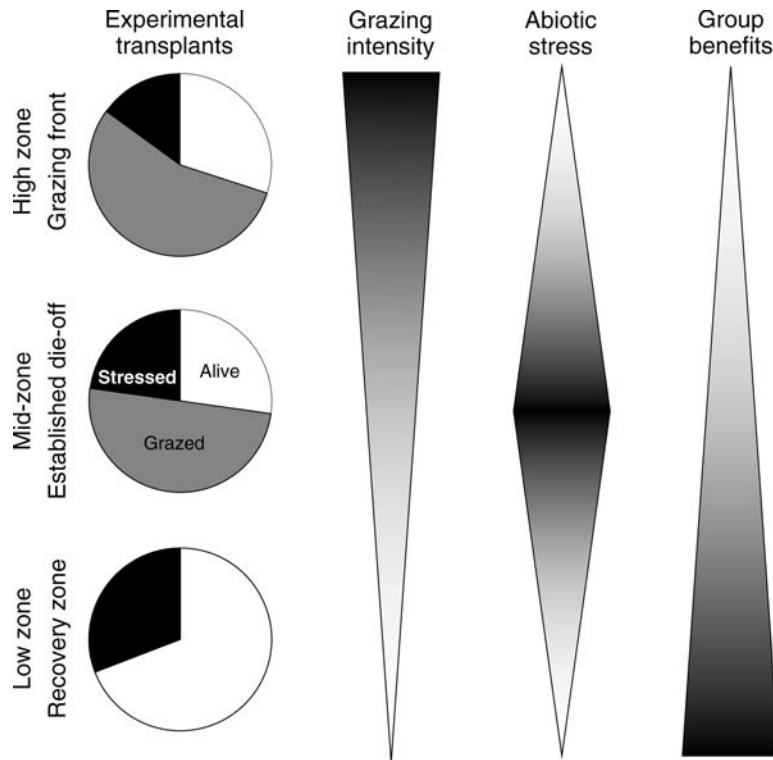
FIG. 5. Pie graphs depict the average final proportions of cordgrass ramets in each zone that were alive (white), dead from grazing (gray), or dead from edaphic stress (black). Grazing mortality was greatest in the high zone, moderate in the mid-zone, and nonexistent in the low zone. Edaphic stress mortality (the proportion of ungrazed ramets found dead but whole, brown, and wilted) was greatest in the mid-zone. Due to the combination of these factors, overall mortality of ramets was highest in the unvegetated mid-zone, which explains why recovery starts in the low zone where stress can be overcome by group benefits. The relative importance of these three factors across zones is illustrated by increasing width and shading of the polygons, with darker shading indicating the stronger effects.

First, lack of vegetation in the die-off zone creates stressful edaphic conditions that inhibit cordgrass regrowth. This is homologous to the positive feedbacks that drive "desertification" of subarctic marshes, where die-off results from overgrazing by Snow Geese (Jefferies et al. 2006). Our surveys and experiments revealed that cordgrass mortality was higher in the unvegetated die-off zone than in the recovery zone due to elevated edaphic stress. Our experimental removal and creation of cordgrass patches also demonstrated how edaphic stress increases in the absence of cordgrass, as observed in other systems (de la Cruz et al. 1989, Bertness 1991, Castellanos et al. 1994).

Second, plant recolonization in the low zone aerates and shades the substrate, reducing edaphic stresses, and facilitating survivorship of new ramets. Although the low recovery zone was less stressful relative to die-off areas, recovery from die-off is still dependent on positive
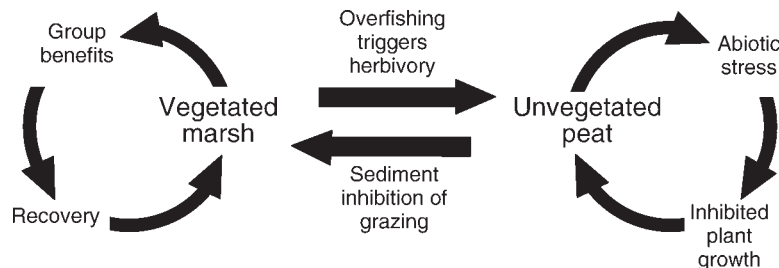

FIG. 6. Conceptual model of consumer-driven state shifts underlying the resilience of marshes from die-off. The shifts from vegetated to unvegetated marsh state is triggered by increased herbivory associated with a recreational-fishing-induced trophic cascade, and the return to a vegetated state is attributed to decreased grazing due to substrate limitation of herbivores. The states are reinforced by feedbacks including facilitation through group benefits in the vegetated state and the desertification of substrate in the unvegetated state.
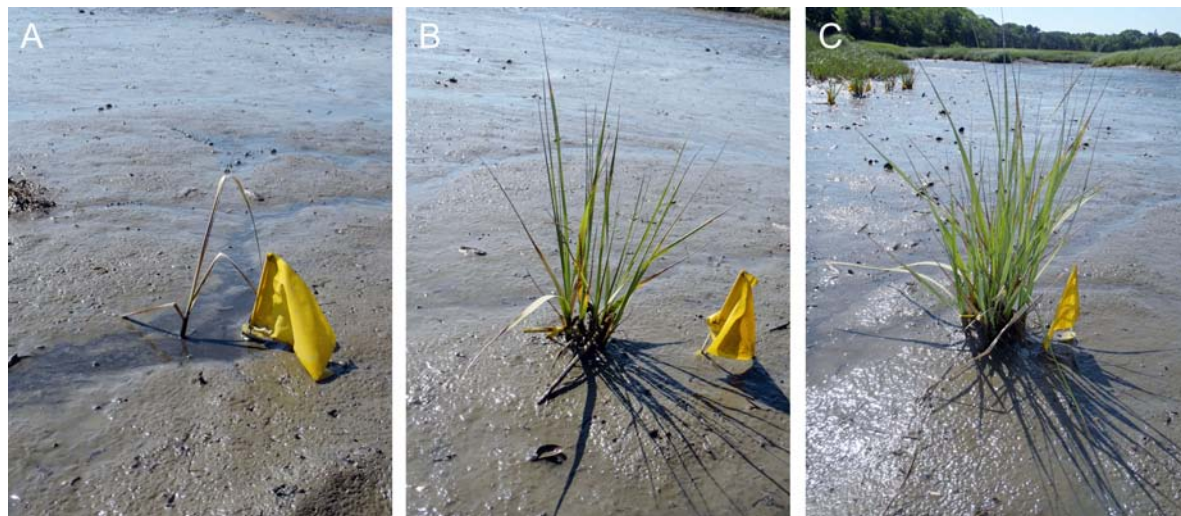
PLATE 1. Cordgrass transplanted into the recovery zone on creek banks. (A) Individual ramets succumbed to abiotic conditions including redox stress, whereas ramets in (B) culms and (C) larger blocks had higher survivorship because of group benefits through stress amelioration. Photo credits: A. H. Altieri.

interactions in the form of group benefits. In our experiments, cordgrass ramets with neighbors thrived, whether they were transplanted into existing or experimentally created regrowth patches, whereas solitary ramets died. Likewise, our surveys and tagging experiment with natural seedlings revealed their trivial contribution to recovery. Closure of natural-disturbance-generated patches in the high marsh is similarly driven by feedbacks related to group benefits (Bertness and Shumway 1993). Similar feedbacks that reinforce large-scale or long-term patterns between vegetated and unvegetated states have been inferred in a variety of systems and species including seagrass beds (van der Heide et al. 2011), coral reefs (Hughes 1994), diatoms (Van de Koppel et al. 2001), and streams (Dudley and D'Antonio 1991).

What triggered the shift between ecosystem states and the recovery of marshes?

What is responsible for the "switch" (sensu Wilson and Agnew 1992) between the two states in our system: vegetated creek banks, and *S. reticulatum*-riddled, eroding creek banks? We have previously demonstrated that predator depletion by recreational fishing tips the system from a vegetated to unvegetated state by releasing *S. reticulatum* from consumer control (Altieri et al. 2012). In the present study, we found that the shift back to a vegetated state and recovery of the marsh was dependent on the creation of unconsolidated sediments associated with creek bank slumping and creek widening following marsh die-off. These muddy substrates are edaphically less stressful for cordgrass and provide a spatial refuge from the active grazing front in the high zone because they do not support *S. reticulatum* burrows. The jump between positive feedback loops that maintained either unvegetated or recovering states

in this system, and other classic examples such as kelp beds (Konar and Estes 2003) and coral reefs (Hughes 1994), was ultimately produced by shifts in grazing pressure, supporting the idea that alternate community states are deterministic and under consumer control (Bertness et al. 2002). We found that consumer-driven die-off degrades the habitat for grazers, leading to reduced grazing pressure and stimulating recovery.

The small-scale co-occurrence of feedbacks and state shifts identified in these marshes emphasizes their importance and makes them a model system for studying the mechanisms underlying resilience (Knowlton 2004). We found zonation of die-off and vegetation on marsh banks to be dynamic, explaining why recovery could take place even as grazing proceeded. The high vegetation border with active *S. reticulatum* grazing and the upper border of recovering vegetation simultaneously advanced away from creek centers. The grazing front of *S. reticulatum* advanced up the creek bank similar to grazing fronts observed in kelp forests (Konar and Estes 2003), mussel beds (Witman et al. 2003), and other marsh systems (Silliman et al. 2005). Trailing this front was a halo of stressful, unvegetated peat in which *S. reticulatum* were restricted due to their need for hard substrate to support burrow complexes and limited foraging range of ~1 m (Bertness et al. 2009), analogous to halos created by other herbivores with limited mobility from shelters (Ogden et al. 1973, Schwindt et al. 2001). This die-off halo was bordered along its eroding lower edge by unconsolidated mud, where cordgrass expanded upward through positive interactions beyond the lower reach of *S. reticulatum* foraging.

Conclusions

We identified feedbacks associated with marsh resilience that led to rapid reversal of a decades-long die-off

trajectory and to revegetation in New England salt marshes. The rapid rate of initial cordgrass recovery is consistent with recovery rates of variables measured across a wide range of human-impacted aquatic and terrestrial systems (Jones and Schmitz 2009). Rapid and synchronous recovery among marsh sites, after decades of die-off, suggests that a system-wide shift in trophic dynamics may have allowed the positive interactions underlying marsh recovery to emerge, despite the ongoing recreational fishing pressure that initiated marsh die-off.

However, the full recovery of New England salt marshes is not assured, nor will it be immediate. Although we observed a net decline in die-off areas, grazing continued in the high zone. Moreover, die-off on Cape Cod led to the loss of 150–250 years' worth of accreted marsh peat in many marshes (T. Coverdale, *unpublished data*). Since recovery areas in some marshes are small relative to the large areas lost to calving, slumping, and creek and ditch widening associated with human-triggered die-off, the full recovery of these marshes to their original extent will likely take centuries. Further study in this and other human-impacted ecosystems will reveal the relationships between mechanisms of resilience, rates of state shifts, and return times of ecosystem structure and function.

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SUPPLEMENTAL MATERIAL

Appendix A

A table of study site locations (*Ecological Archives* E094-148-A1).

Appendix B

Results of experiment comparing the effect of regrowth vegetation on sediment characteristics relative to die-off and experimental areas with regrowth removed (*Ecological Archives* E094-148-A2).