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Salt marsh die-off and recovery reveal disparity between the recovery of ecosystem structure and service provision

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ABSTRACT

Coastal ecosystems, such as sand dunes, salt marshes, and mangroves, stabilize shorelines and protect coastal populations. In New England, salt marshes have experienced widespread cordgrass (*Spartina alterniflora*) die-off and habitat loss, and it is unknown how this has affected their ability to provide coastal protection. We quantified wave attenuation and shoreline stability on healthy, die-off and recovered marsh creek banks. We found that coastal protection has been severely compromised by salt marsh die-off, and that to date, *S. alterniflora* recovery, while superficially impressive, has not returned this ecosystem service to the levels of intact marshes. Climate driven sea-level rise and predicted increases in the frequency and severity of storms over the next century will likely further increase the vulnerability of coastal populations. Therefore, recovery of coastal protection is essential for maintaining the ecological and economic wellbeing of coastal communities. Our results suggest that quantification of the recovery of ecosystem services should be employed in order to successfully measure recovery in degraded ecosystems.

1. Introduction

Coastal ecosystems, such as salt marshes, sand dunes and mangroves, have been recognized for their capacity to stabilize shorelines and protect coastal populations (Gedan et al., 2011). In the United States, coastal wetlands are estimated to provide $23.2 B annually in storm protection services, with the loss of 1 ha of coastal wetlands resulting in an average of $33,000 USD in storm damage (Costanza et al., 2008). It is estimated that globally, >65% of wetland habitat has already been lost (Lotze et al., 2006). Furthermore, coastal wetland loss from climate-driven sea-level rise is predicted to cause an additional 20–45% loss of salt marsh habitat globally within this century (Craft et al., 2009).

Such losses will have global implications for human health and well-being. Worldwide, more than 10% of people live within 10 m of sea level (McGranahan et al., 2007) and more than 30% of people live in seashore areas, which make up only 4% of the earth's land surface (UNEP, 2006). Increasing frequency and severity of storms and climate change associated sea-level rise are predicted to increase the vulnerability of low-lying coastal populations (IPCC, 2007; McGranahan et al., 2007; FitzGerald et al., 2008), which may be exacerbated by accelerating losses in storm buffering capacity. Therefore, understanding the ability of coastal ecosystems to protect and stabilize coastlines is essential to supporting coastal communities, determining the full cost of coastal ecosystem degradation, and valuing restoration (Barbier, 2007).

Salt marshes have been shown to decrease coastal storm damage by attenuating waves and decreasing storm surge (Barbier et al., 2013; Shepard et al., 2011; Yang et al., 2012). Marsh vegetation stabilizes coastlines (Gedan et al., 2011; Shepard et al., 2011) and positive feedbacks have been predicted to facilitate vertical marsh accretion reducing the predicted effects of sea-level rise (Morris et al., 2002; Kirwan et al., 2010). Empirical data on the effects of salt marshes on wave attenuation and sedimentation are rare relative to the often-cited importance of salt marshes in shoreline stabilization (Shepard et al., 2011). However, examples of salt marsh degradation worldwide have illustrated that the loss of vegetation reduces marsh resiliency to storm surge (Temmerman et al., 2012), erosion (Silliman et al., 2012), and sea-level rise (Baustian et al., 2012).

One of the most widespread drivers of salt marsh vegetation loss is consumer-driven salt marsh die-off (Bertness and Silliman, 2008). In New England, predator depletion, driven primarily by recreational fishing pressure, has released the native, herbivorous purple marsh crab (*Sesarma reticulatum*) from predator control,

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causing runaway herbivory in the low marsh. Runaway herbivory has led to large-scale die-offs of the smooth cordgrass, *Spartina alterniflora*, the foundation species that builds and maintains these marshes (Altieri et al., 2012). New England salt marsh die-off was first identified in the late 1970s and proliferated in the 2000s (Coverdale et al., 2013). By 2009, over 90% of Cape Cod creek banks were experiencing *S. reticulatum*-driven die-off (Holdredge et al., 2009). However, by Spring 2010, some of these salt marshes began to undergo rapid recovery mediated by positive plant-sediment feedbacks (Altieri et al., 2013) and the opportunistic invasion of an exotic species (Bertness and Coverdale, 2013). In many of these marshes, *S. alterniflora* has fully recolonized the low marsh, with only a narrow band of active die-off remaining along the grazing border (Bertness and Coverdale, 2013). While the mechanisms of die-off and recovery in New England salt marshes have been thoroughly investigated (Holdredge et al., 2009; Altieri et al., 2012, 2013; Bertness and Coverdale, 2013), the effects of this widespread habitat degradation and subsequent recovery on coastal protection, an essential ecosystem service, remain unknown.

In this paper we examine the general hypothesis that recent salt marsh recovery has restored the provisioning of coastal protection to salt marshes affected by *S. reticulatum*-driven die-off. Specifically, we hypothesize that: (1) wave attenuation is reduced on creek banks experiencing die-off compared to healthy and recovered creek banks; and (2) shoreline stabilization is diminished along creek banks experiencing die-off compared to healthy and recovered creek banks.

2. Methods

All fieldwork was carried out on Cape Cod, Massachusetts (41.68°N, 70.20°W) salt marshes (for site details please see Supporting Information), where we have done historical reconstructions using archived aerial photographs to establish the die-off history from the late 1930s to the present (Coverdale et al., 2013).

To initially examine the potential of New England salt marshes to provide coastal protection, we quantified vegetation density and biomass production, which are both positively correlated with wave attenuation and shoreline stabilization (Shepard et al., 2011). Vegetation density and biomass production measurements were taken at three healthy and three die-off salt marshes on Cape Cod, MA (Supporting Information, Appendix S1). Healthy salt marshes are operationally defined as marshes of dense *S. alterniflora* monocultures that have not experienced *S. reticulatum*-driven die-off (Altieri et al., 2012). Die-off marshes are operationally defined as those that previously experienced high levels of die-off and now show recovery (Altieri et al., 2013; Bertness and Coverdale, 2013). Some creek banks recover earlier than others, which allows the study of both die-off and recovered creek banks within the same marsh along the same elevation. Within die-off marshes, recovered creek banks of low marsh *S. alterniflora* and areas of active die-off that have not shown recovery were identified by annual surveys and archived aerial photographs (Coverdale et al., 2013; Bertness and Coverdale, 2013). Recovered habitats were analyzed as independent from die-off habitats as they represent completely different ecological landscapes.

We quantified *S. alterniflora* stem densities in randomly placed 25 cm × 25 cm quadrats in the low marsh zone along the same elevation in healthy marshes and in die-off marshes in areas of both unambiguous *S. reticulatum*-driven die-off (Holdredge et al., 2009) and in areas that have recovered from die-off ($n = 16$ measurements per habitat type site^{-1}) (Altieri et al., 2013). Creek banks of each habitat type were chosen at random. Within habitat type, site stem densities of *S. alterniflora* were similar so data were

pooled across sites for analysis. *S. alterniflora* densities from healthy, die-off and recovered areas were square root transformed to meet the assumptions of ANOVA and a one-factor ANOVA (die-off vs. recovered vs. healthy) was used to determine if *S. alterniflora* densities differed across habitat types. Tukey HSD test was used to perform post-hoc analysis.

To examine biomass patterns we extracted *S. alterniflora* cores (7 cm width) from randomly chosen locations in the same areas of healthy marshes and recovered and die-off areas of die-off marshes to quantify differences in above- and below-ground *S. alterniflora* biomass. Cordgrass culms were extracted with a corer ($n = 16$ culms per habitat type site^{-1}) and above- and below-ground biomasses were separated. Aboveground plant matter (leaves and stems) was dried to a constant weight. Belowground biomass was sieved with deionized water and live plant matter was isolated and dried to a constant weight. *S. alterniflora* above- and below-ground biomasses (g) were log-transformed to meet the assumptions of ANOVA. Within habitat type, site biomasses of *S. alterniflora* were similar so data were pooled across sites for analysis. A one-factor ANOVA (die-off vs. recovered vs. healthy) was used to determine if *S. alterniflora* biomass differed among habitat types. Tukey HSD test was used to perform post-hoc analysis.

2.1. Wave attenuation

To test the hypothesis that wave attenuation is diminished in die-off and has been restored in recovered zones, we quantified wave attenuation over time and maximum flow rate at Wing's Neck marsh (41.68°N 70.62°W) in Bourne, Massachusetts. Wing's Neck marsh has large areas of exposed marsh, which have a patchwork of healthy creek banks that have never experienced die-off, as well as areas of active die-off and recovered low marsh. The geography of Wing's Neck marsh allowed the quantification of wave attenuation among habitat-types with similar seaward flow rates, tidal elevation, and wave exposure.

To examine wave exposure integrated over time (mass flux) we deployed magnesium calcite chalk blocks (Yund et al., 1991) at the same elevation along an exposed creek bank in areas of die-off, recovered, and healthy marsh ($n = 9$ blocks per habitat type). Blocks were cylindrical (5 cm in diameter × 2 cm in height), sealed on the side with polyurethane, pre-weighed and glued to hardware cloth bases with a polyphenol adhesive. They were pinned to the substrate with wire staples and left in the field for five weeks (July–August 2013) and then dried and reweighed. Polyurethane coated chalk blocks dissolve in a uniform matter and differences in dissolution reflect variances in experienced water flow, therefore percent chalk block dissolution was used as a time integrated measure of wave exposure. Chalk block loss was analyzed with a one-factor ANOVA (die-off vs. recovered vs. healthy) to determine if wave attenuation is diminished in die-off and restored in recovered creek banks.

We also measured maximum water velocities with spring dynamometers (Bell and Denny, 1994), placed along the exposed edge of the marsh in areas of die-off, recovered, and healthy marsh ($n = 10$ dynamometers per habitat type). Dynamometers were installed in the field and maximum wave force data was measured after one month. Maximum force was log-transformed to meet the assumptions of ANOVA and analyzed with a one-factor ANOVA (die-off vs. recovered vs. healthy) to determine if maximum wave exposure is diminished in die-off and restored in recovered creek banks.

2.2. Shoreline stabilization

To test the hypothesis that shoreline stabilization is lower in die-off than healthy sites and has been restored in recovered areas,

we quantified sediment surface elevation over time with modified sediment-erosion tables (SETs). SET posts allow the measurement of small changes in sediment elevation over time compared to an initial reference point (Cahoon et al., 1995).

SET posts were installed in Spring 2009 at 14 salt marshes across Cape Cod (Supporting Information, Appendix S2) and distance to the sediment surface (n = 4 constant points at varying distance from center per SET post) was measured twice annually from Spring 2009 to Fall 2013 with the exception of 2012. We installed posts in both habitat types (die-off and healthy) along the same elevation at sites with a mosaic of die-off and healthy areas and one set in marshes characterized by either unbroken die-off or healthy creek banks (n = 10 SET posts per habitat type). Recovery initiated the following year among many of our die-off SET posts. Spring 2009 data was used as the initial time point, with later times measured based on change from the initial point. Each post was classified annually as being in healthy cordgrass, recovered cordgrass, or die-off. Recovered habitat SET posts were analyzed as independent from die-off posts as they represent completely different ecological landscapes. We pooled all posts from each final habitat type (die-off vs. recovered vs. healthy) for analysis. Height data was analyzed with repeated measures ANOVA with vegetation type and time as factors. Height data was transformed by adding a constant and Box–Cox transforming to meet the assumptions of repeated measures ANOVA. Assumptions of sphericity were not met, so Greenhouse–Gessier corrected values were used.

3. Results

S. alterniflora stem densities significantly varied across creek bank habitat types ($F_{2,6}$ = 89.87, $P < 0.0001$). Healthy areas had the highest stem densities (637 ± 45 stems m^{-2}), recovered creek banks intermediate (448 ± 55 stems m^{-2}), and die-off banks the lowest (156 ± 6 stems m^{-2}).

Aboveground *S. alterniflora* biomass significantly varied among habitat types ($F_{2,6}$ = 29.36, $P < 0.001$; Fig 1a). Healthy creek banks had the highest biomass, 140% higher than recovered creek banks, which had 583% higher biomass than die-off areas. Belowground *S. alterniflora* biomass also significantly varied among habitat types ($F_{2,6}$ = 36.57, $P < 0.001$; Fig 1b). Healthy areas had the highest belowground biomass at 109% higher than recovered areas, which were intermediate and 160% higher than die-off areas.

3.1. Coastal protection

Wave exposure, measured by the percent of chalk block dissolved over a month, significantly varied among habitat types ($F_{2,24}$ = 55.45, $P < 0.0001$). Die-off creek bank blocks exhibited the highest erosion and recovered areas were intermediate, experiencing 48.4% higher erosion than healthy creek banks (Fig 2a). Maximum water velocity (N) also significantly varied among habitat types ($F_{2,27}$ = 131.10, $P < 0.0001$). Die-off creek banks experienced the highest maximum water velocity, and recovered areas were intermediate, experiencing 86.6% more force than healthy creek banks (Fig. 2b).

3.2. Shoreline stabilization

Differences in shoreline stabilization over time were observed across the three creek bank habitat types ($F_{6.11, 498}$ = 25.61, $P < 0.0001$; Fig. 3). Shoreline stabilization was lowest in die-off areas, which experienced a sizable net loss of sediment over time. Stabilization was intermediate in recovered areas, with a small net loss of sediment. Healthy areas exhibited the highest shoreline stabilization and experienced small accretions over time.
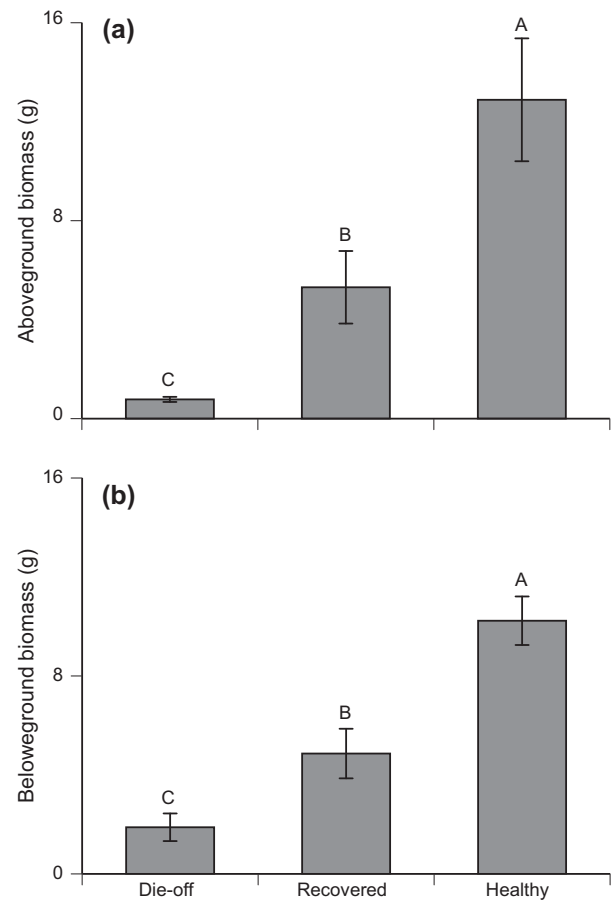

Fig. 1. Vegetation characteristics of low marsh habitat types. (a) Aboveground *S. alterniflora* biomass (g) and (b) Belowground *S. alterniflora* biomass (g) along die-off, recovered, and healthy marsh creek banks (Letters, Tukey HSD).

4. Discussion

4.1. Coastal protection

Storm intensity and frequency are predicted to increase with accelerating sea-level rise, increasing the vulnerability of coastal ecosystems to anthropogenic threats (IPCC, 2007; McGranahan et al., 2007). Although the ability of wetlands to protect shorelines has been recently called into question (Feagin et al., 2009; Pinsky et al., 2013), the majority of current evidence suggests that coastal habitats effectively decrease moderate storm surges (Wamsley et al., 2010) and minimize property damage and human death tolls (Gedan et al., 2011). Even with recent vegetative recovery, the large-scale die-off of low marsh vegetation in New England may decrease the ability of these coastlines to buffer against moderate storm flooding. On Cape Cod, both above- and below-ground *S. alterniflora* biomass (Fig. 1) and stem densities remain significantly lower in recovered and die-off areas and consequently, both wave exposure and maximum wave force are higher in die-off and recovered areas than healthy creek banks (Fig. 2). Full recovery of *S. alterniflora* densities and biomass may be further hindered by the loss of ribbed mussel beds (*Geukensia demissa*), which typically experience mass mortality without the habitat amelioration provided by *S. alterniflora* beds (Bertness, unpublished work). *G. demissa* beds are important facilitators of *S. alterniflora* production (Bertness, 1984) and are slow to recover, potentially limiting the resilience of recovered *S. alterniflora* stands.

The *S. reticulatum*-driven die-off of New England salt marshes only occurs in the intertidal zone, which makes up the first few
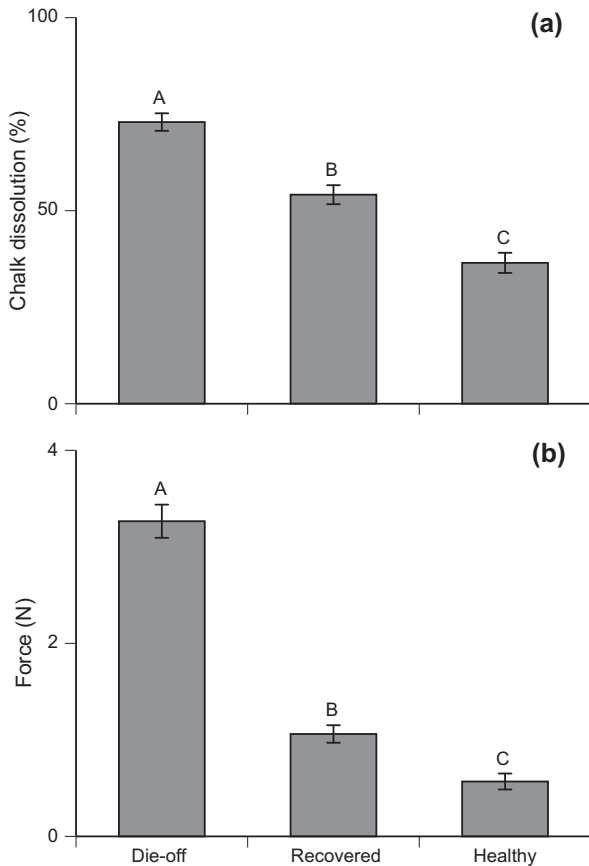
Fig. 2. Coastal protection across different marsh habitat types. (a) The time integrated wave exposure measured by chalk dissolution (%) and (b) The maximum wave force (N) experienced by die-off, recovered, and healthy marsh creek banks (Letters, Tukey HSD).
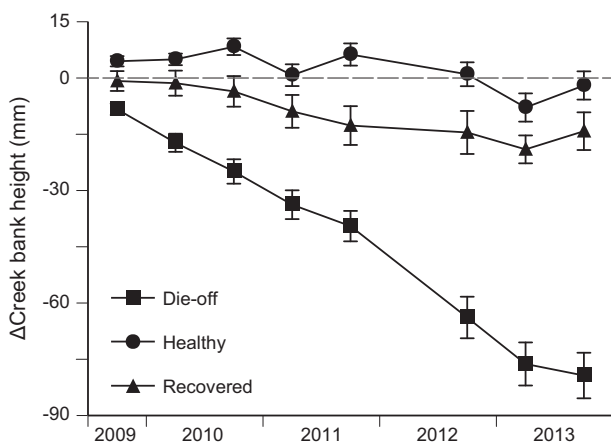

Fig. 3. Heights (cm) of die-off, recovered, and healthy marsh creek banks over time measured by modified sediment erosion tables.

meters of the salt marsh edge, an area shown to be the most critical in wave attenuation and coastal protection (Koch et al., 2009; Gedan et al., 2011). High attenuation rates across short distances have illustrated that even small, narrow wetlands can provide substantial wave protection (Barbier et al., 2008; Morgan et al., 2009). Spatial patterns of vegetation loss have also been shown to strongly affect flood attenuation (Temmerman et al., 2012), such that vegetative die-off along tidal channels and creeks, as seen in our study, has a much stronger effect on landward flood

propagation than inner marsh die-off. Therefore, the diminished ability of New England salt marshes to provide coastal protection in degraded and recovered areas is likely to be non-linear.

4.2. Shore stabilization

Sea-level rise may exceed 9 mm yr^{-1} this century (IPCC, 2007), increasing flooding and erosion risk in low elevation coastal communities (McGranahan et al., 2007). For salt marshes, whether they survive accelerating sea-level rise is largely dependent on how human impacts influence their ability to accrete and migrate landward. Recent research has suggested that feedbacks in vegetation may allow salt marshes to maintain their relative elevation and seaward extent (Kirwan and Megonigal, 2013).

Accretion rates have previously been shown to recover in Louisiana salt marshes experiencing die-off and recovery one year after the BP Deepwater Horizon oil spill (Silliman et al., 2012), illustrating recovery potential in these ecosystems. Our study, however, reveals that natural recovery may not restore coastal protection services as rapidly in New England. Die-off creek banks exhibited high levels of erosion, with ~80 mm lost over four years (Fig. 3). Vegetative recovery initiated in Spring 2010, but recovered creek banks have continued to erode, albeit at a slower rate, for the past four years. In contrast, healthy creek banks experienced small net accretion over the same period (Fig. 3).

4.3. Implications for recovery and restoration

Recovery has been observed in 10–50% of degraded ecosystems, but rarely to historically "healthy" levels (Lotze et al., 2011). Only a third of recovery studies have documented full ecosystem recovery (Jones and Schmitz, 2009). Accordingly, restoration of degraded ecosystems has become increasingly widespread. Unfortunately, ecosystem restoration often appears to promote complete recovery but actually fails to achieve historically healthy levels of ecosystem functioning (Moreno-Mateos et al., 2012). One of the earliest demonstrations of this phenomenon was restoration of the cordgrass *Spartina foliosa* in southern California salt marshes (Zedler, 1993). In restored marshes, *S. foliosa* stem heights were shorter than in naturally occurring marshes and the endangered Light-footed Clapper Rail (*Rallus longirostris levipes*), their conservation target, would not nest.

Our results suggest that the success of recovery and restoration must be measured by the return of ecosystem service provision rather than the appearance of ecosystem structure. Restoration of coastal wetlands is essential to protect low-lying coastal communities and property from flooding associated with sea-level rise and storm fronts. Our study highlights the need to integrate measurements of ecosystem services within healthy, degraded, and recovered ecosystems into restoration ecology and environmental management.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2014.08.013.

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