



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.

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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 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,

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