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REVIEW

Uncertain future of New England salt marshes

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ABSTRACT: Salt marsh plant communities have long been envisioned as dynamic, resilient systems that quickly recover from human impacts and natural disturbances. But are salt marshes sufficiently resilient to withstand the escalating intensity and scale of human impacts in coastal environments? In this study we examined the independent and interactive effects of emerging threats to New England salt marshes (temperature increase, accelerating eutrophication, consumer-driven salt marsh die-off, and sea level rise) to understand the future trajectory of these ecologically valuable ecosystems. While marsh plant communities remain resilient to many disturbances, loss of critical foundation species and changing tidal inundation regimes may short circuit marsh resilience in the future. Accelerating sea level rise and salt marsh die-off in particular may interact to overwhelm the compensatory mechanisms of marshes and increase their vulnerability to drowning. Management of marshes will require difficult decisions to balance ecosystem service tradeoffs and conservation goals, which, in light of the immediate threat of salt marsh loss, should focus on maintaining ecosystem resilience.

KEY WORDS: Climate change · Sea level rise · Salt marsh die-off · Eutrophication · Invasive species · *Phragmites australis* · Management

INTRODUCTION

Salt marshes are perhaps the most important but misunderstood of the world's major ecosystems. These coastal wetlands have long been valued for their benefits to human society including the provision of food, fuel, building materials, livestock fodder and, more recently, for their ability to filter pollutants, buffer against storms, sequester carbon, and provide aesthetic and recreational opportunities (Gedan et al. 2009). Conservation efforts to preserve the provision of these ecosystem services are based largely on promoting the historic resilience of salt marshes. However, recent research in the western Atlantic, and in New England in particular, where salt marsh conservation science was founded, is revealing ecological interactions and shifts in marsh landscapes that question the fundamental assumptions of marsh resilience. The rules thought to govern salt marsh community structure and stability, based largely on nutrients and physical factors, need to be rewritten to include the unprecedented consumer control and sea level rise, which could interact to override marsh resilience.

HISTORICAL RESILIENCE OF SALT MARSH ECOSYSTEMS

Historically, salt marshes have been considered resilient to natural and anthropogenic disturbances for several reasons. First, salt marshes are young features by geologic standards, rapidly built by ecosystem engineering plants that trap and bind sediments (Redfield 1965, Niering 1977), which suggests that salt marshes would quickly reform if destroyed. Second, natural disturbances, such as the deposition of wrack (accumulations of dead plant material) and sand on spring and storm tides, are routine in salt marshes (Chapman 1940, Donnelly et al. 2001), and salt marsh vegetation is resilient to these small-scale physical disturbances (Niering 1977). Finally, due to evolutionary adaptations to cope with stressfully anoxic and saline soils, salt marsh plants are uncommonly resistant to many toxic pollutants, such as heavy metals (Weis & Weis 2004). Historically, these resilient characteristics have allowed salt marsh ecosystems to rebound after extreme impacts from human activities (e.g. Hackensack Meadowlands example in Weis & Butler 2009).

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However, in the decades since Niering et al. (1977) stressed the resilience of New England salt marsh vegetation dynamics to human activities and natural sea-level fluctuations, it has become apparent that other shallow-water coastal communities, including coral reefs and kelp forests, have been devastated by anthropogenic disturbances (Jackson et al. 2001). In light of persistent human pressure on coastal habitats, we ask in this paper: how will New England salt marshes respond to the multiple, large-scale human impacts they will face over the next century? Niering recognized signatures of anthropogenic impacts in New England salt marshes (Niering et al. 1977, Niering & Warren 1980), and pioneered the study of how coastal wetlands respond to human activities. Over the past several decades, however, eutrophication, overfishing, and climate change have emerged as global threats to coastal ecosystems (Jackson et al. 2001, Lotze et al. 2006). Can salt marsh plant communities and their provision of ecosystem services persist in the face of accelerating global change? What conservation steps will be necessary to maintain such marsh resilience?

ECOSYSTEM SERVICES OF SALT MARSHES

Human impacts are concentrated in coastal ecosystems due to a synergism of nearshore human activities, spillover from terrestrial impacts, and the concentration of human settlement along shorelines (UNEP 2006). Although human activities often degrade coastal areas, human populations have long relied heavily on coastal ecosystem services. Estuaries and salt marshes provide more services per unit area than any other ecosystem worldwide (UNEP 2006). Since prehistoric times, marshes have provided edible plants and animals, thatch and fiber for building material, fodder for livestock, and fuel for cooking fires. More recently, marshes have become additionally valued for storm protection (Costanza et al. 2008), biogeochemical filters (Valiela & Cole 2002), carbon sequestration (Chmura et al. 2003), and as nurseries for commercially harvested fin- and shellfish (Boesch & Turner 1984). To preserve these functions and their aesthetic and recreational value, many New England marshes have been designated as conservation areas (Bromberg & Bertness 2005).

HISTORY OF HUMAN IMPACTS ON NEW ENGLAND SALT MARSHES

Ecologists have long studied ecosystem patterns and processes in New England salt marshes. Pioneering studies of plant succession (Clements 1916), community organization (Chapman 1940), and salt marsh development (Redfield 1965), as well as advances in community (Bertness 1991) and ecosystem (Valiela & Teal 1979) ecology were made in New England salt marshes. Thorough understanding of marsh ecosystems developed from dozens of experimental studies and decades of observation should enable us to predict how New England marshes will respond to human impacts more accurately than in regions where scientific information is more limited.

New England salt marshes have sustained centuries of human impacts (Gedan et al. 2009). Some of the first European colonists to New England settled adjacent to salt marshes for their natural treeless pasture and hay products, marine access, and environmental similarity to coastal Europe (Hatvany 2003). Intense clearing of the upland and the resulting eroded sediment promoted rapid marsh expansion, at least in parts of the region (Kirwan et al. 2011). During the American Industrial Revolution, many marshes were tidally restricted by dams, polluted by industrial runoff, intensively ditched for mosquito control, and used for refuse disposal and sewers (Crain et al. 2009). The rarity of salt marsh ponds and waterlogged panne depressions in southern New England is, in part, a historical artifact of intense mosquito ditching (Ewanchuk & Bertness 2004a).

New England salt marshes have the longest history in North America of outright land conversion (Gedan & Silliman 2009). Conversion for agriculture, port development, and urbanization has resulted in a 37% net loss of salt marshes across the region (Bromberg & Bertness 2005). In 1972 the Clean Water Act regulated dredge and fill activities in salt marshes in the United States. While direct conversion is restricted, New England salt marshes are now assaulted by other continuing, and emerging, human impacts. In the following sections we discuss how predicted increases in temperature, eutrophication, consumer-driven die-offs, and sea level rise may be generating a 'perfect storm' for future New England marsh loss.

TEMPERATURE INCREASE

Like other temperate ecosystems, salt marshes are predicted to experience substantial temperature increases over the next century (IPCC 2007). In New England, a 2 to 3°C increase in average summer air temperature is predicted by mid-century (2035–2064) relative to the 1961–1990 average (Hayhoe et al. 2006). How will increasing temperatures affect salt marsh plant communities? For one effect, temperature can define species ranges, and many recent shifts in species distributions have been correlated with shifts in climate (IPCC 2007).

Field manipulations of temperature have shown that the climate warming expected over the next century will increase salt marsh plant productivity, confirming predictions based on latitudinal correlations between temperature and productivity (Turner 1976, Kirwan et al. 2009). Mild warming of <3°C with open top chambers in Rhode Island and Maine increased cordgrass *Spartina alterniflora* productivity by 15 to 45% (Fig. 1) (Gedan 2009) with similar effects on salt marsh hay *S. patens* (Gedan & Bertness 2010). Since *Spartina* grasses dominate New England marshes, these findings predict there will be increases in ecosystem primary productivity associated with warming over the next century and higher levels of productivity shifting poleward into northern New England (Fig. 1B).

Temperature-driven effects on plant and soil water balance are also important in New England salt marshes. Forb pannes are mid-elevation features of northern New England salt marshes that are sensitive to climate. Assemblages of halophytic forbs (Fig. 2) occur in these anoxic, waterlogged habitats that provide competitive refuge from clonal marsh grasses (Ewanchuk & Bertness 2004b). Experimentally increasing temperature in forb pannes increases evapotranspiration and causes forb species to be rapidly outcompeted and displaced by high marsh grasses. These results reveal that temperature increases predicted over the next century will reduce the area of forb panne habitats, driving already rare forb assemblages to local extinction in southern New England and reducing their dominance in northern New England (Fig. 2) (Gedan & Bertness 2009).

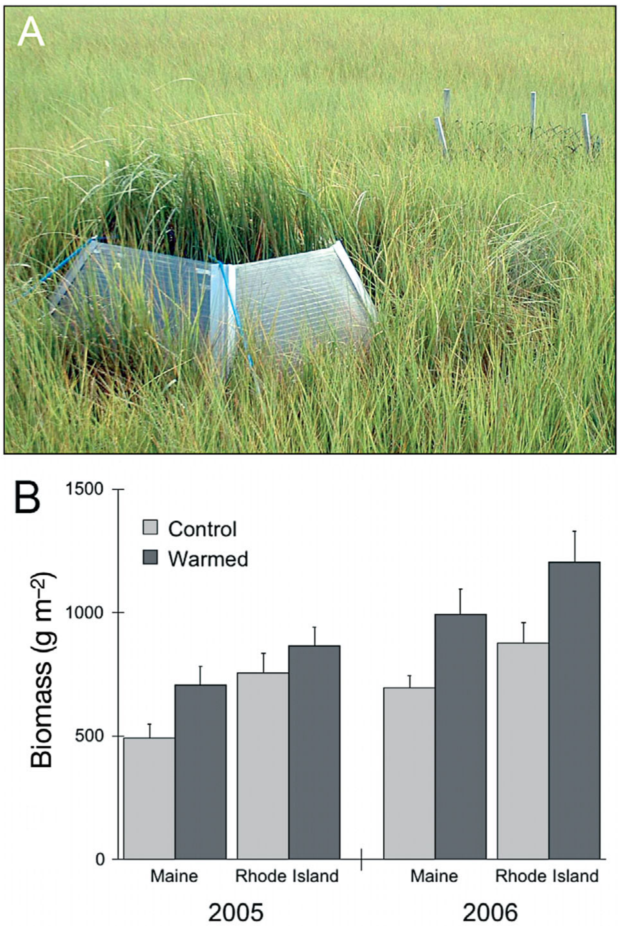

Fig. 1. (A) Warming with passive open top chambers increased *Spartina alterniflora* aboveground biomass (B) relative to control treatments (±1 SE) at 2 New England sites in 2005 and 2006. See Gedan & Bertness (2009) for details

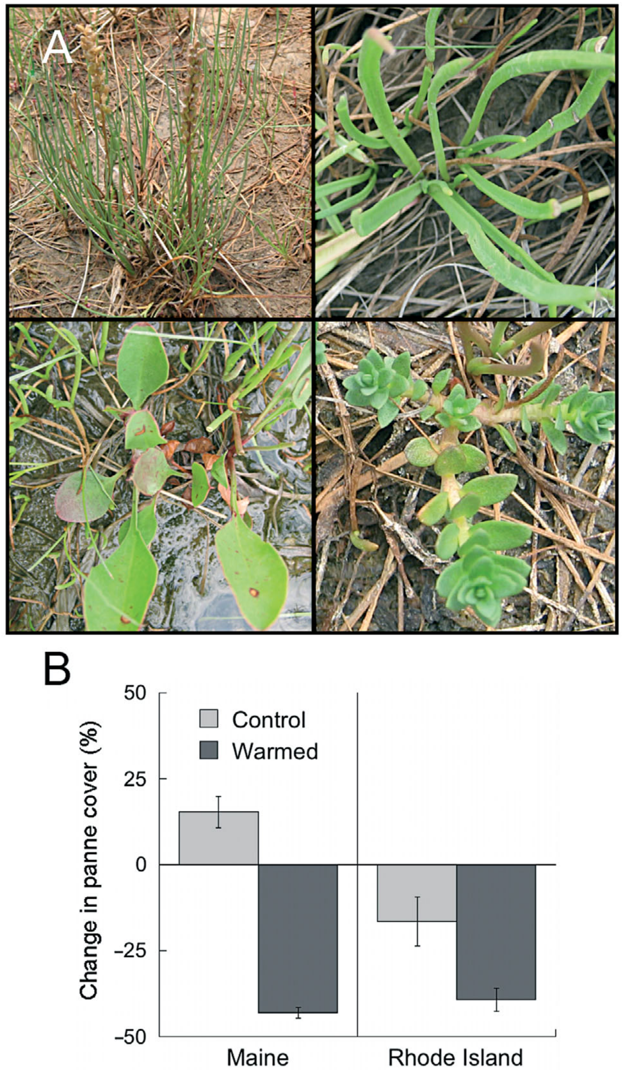

Fig. 2. (A) Salt marsh forb pannes are dominated by a unique assemblage of species, including, clockwise from top left, *Triglochin maritima*, *Plantago maritima*, *Glaux maritima*, and *Limonium nashii*. (B) Warming with open top chambers reduced the cover of forb panne species by 43 and 39% relative to baseline conditions in Maine and Rhode Island, respectively (±1 SE) (see Gedan & Bertness 2009)

Beyond shifts in plant productivity and community composition, there may be additional, as yet unknown, effects of climate warming on New England plant communities. For example, temperature-mediated effects on productivity may cascade to other linked ecosystem processes such as decomposition. Temperature increase could also drive range shifts in species that strongly interact with salt marsh plants, such as fiddler crabs (*Uca* spp.) or the herbivorous crab *Sesarma reticulatum*, both of whose ranges currently end at the biogeographic barrier of Cape Cod. The effects of temperature increase on these higher level interactions is uncertain. Increases in atmospheric carbon dioxide, the causal driver of temperature increase, could cause additional shifts in plant species composition. In carbon dioxide enrichment experiments, C_3 plant species such as the sedge *Schoenoplectus americanus* replace C_4 plant species such as cordgrass and salt marsh hay (Erickson et al. 2007), but it is not clear how concurrent increases in temperature and carbon dioxide will affect species composition.

Due to strong agreement between observed patterns across latitudinal climate gradients and results of experimental warming studies, we are more certain that temperature increase will increase productivity and reduce diversity in New England salt marsh plant communities. Shifts in plant species composition due to increases in warming and carbon dioxide, however, are of less management concern than other impending impacts on marsh plant communities that disable marsh accretion — a process central to the maintenance and persistence of the salt marsh habitat.

EUTROPHICATION

Eutrophication (nutrient loading) has and will continue to contribute to the shifting structure of New England salt marsh communities. Southern New England estuaries are among the most eutrophic in North America, whereas eutrophication symptoms are largely absent in northern New England estuaries (Bricker et al. 2007). Eutrophication is correlated with population density and land clearing in New England and is driven by sewage inputs to groundwater that are evident in salt marsh food webs (Bannon & Roman 2008). Although there are plans to reduce nutrient loading in New England estuaries through wastewater management, the cover of impervious surfaces is escalating and water quality continues to decline in most coastal areas (Bricker et al. 2007).

Denitrification and nitrogen storage in salt marshes reduce estuarine nutrient loading, protecting seagrass ecosystems (Valiela & Cole 2002) and reducing the frequency of hypoxic events and macroalgal blooms (Valiela et al. 1997). This ecosystem service, however, comes at a cost to salt marsh health and function. Anthropogenic nutrient loading can cause dramatic shifts in the community structure of salt marshes, which have historically been nitrogen-limited. Nitrogen enrichment can increase the aboveground productivity of salt marsh plants (Valiela & Teal 1974, Levine et al. 1998). But high levels of eutrophication can trigger consumer control by insects leading to reduced aboveground productivity (Bertness et al. 2008) and can reduce belowground biomass allocation and organic matter accumulation (Turner et al. 2009). Nitrogen enrichment reduces belowground competition for nutrients, favoring large aboveground biomass producers that win competition for light, stimulating the shoreward creep of cordgrass (Levine et al. 1998) and the seaward invasion of the common reed *Phragmites australis* (Bertness et al. 2002).

The invasion and spread of the exotic genotype of *Phragmites australis* (Saltonstall 2002) has caused some of the most conspicuous changes to New England salt marshes in the last century (Fig. 3; Chambers et al. 1999). *P. australis* spreads rapidly, facilitated by freshwater runoff, nutrients, and disturbance (Minchinton 2002, Silliman & Bertness 2004), competitively excluding other salt marsh plants and forming a dense monoculture (Minchinton et al. 2006) that raises the marsh platform by increasing sedimentation and litter deposition, and lowers the water table by wicking away water through transpiration (Rooth & Stevenson 2000). While some salt marsh services such as carbon, nutrient, and pollutant sequestration are maximized in *P. australis* invaded marshes (Weis & Weis 2003, 2004, Hershner & Havens 2008), *P. australis* dominance causes a major shift in salt marsh structure and geomorphology, and drives the loss of plant diversity and the native plant assemblage (Silliman & Bertness 2004, Meyerson et al. 2009). *P. australis* invasion of New England salt marshes is among the most conspicuous consequences of human eutrophication, with a direct causal link to shoreline development (Chambers et al. 1999, Bertness et al. 2002, King et al. 2007). A forested upland buffer that intercepts and processes runoff remains the best way to protect salt marshes from upland eutrophication and *P. australis* takeover (Bertness et al. 2009b).

SALT MARSH DIE-OFF

The unexpected die-off of salt marsh vegetation is an emerging disturbance in New England salt marshes (Fig. 4). Salt marsh die-offs have become epidemic throughout the western Atlantic, and human perturbations of food webs have been identified as the cause of

Fig. 3. *Phragmites australis* in a marsh on the Palmer River in Rehoboth, MA

Fig. 4. Crab herbivory driven die-off on creek banks in West Dennis, MA

these events (Bertness & Silliman 2008). Reports of die-off in New England marshes emerged on Cape Cod in the summer of 2002 (Smith 2006). Field experiments and inter-site correlations between grazing pressure and the occurrence and extent of die-offs have revealed that herbivory by the native, nocturnal crab *Sesarma reticulatum* on cordgrass is responsible for the Cape Cod marsh die-offs that currently affect nearly 50% of Cape Cod marsh shorelines (Holdredge et al. 2009). These die-offs are concentrated in cordgrass areas along low marsh creek banks, and crab herbivore intensity explains nearly 80% of among marsh variation in the extent of die-off (Holdredge et al. 2009). Current evidence suggests that the increase in herbivory by *S. reticulatum* generating these die-offs is being driven by overfishing and the release of *S. reticulatum* populations from predation by recreationally fished species (A. H. Altieri et al. unpubl.). On Cape Cod, Narragansett Bay, and Long Island Sound marshes, these die-offs are closely associated with heavily fished areas around marinas, boat ramps, and population centers, and are facilitated by mosquito and drainage ditches, which provide stable burrowing habitats with low burrow maintenance costs (Bertness et al. 2009a).

These die-offs are particularly troubling because they attack cordgrass on the seaward edge of marshes, the habitat that is most critical to the growth and maintenance of marsh ecosystems. Additionally, through negative feedbacks (e.g. hypersaline, anoxic, and sediment starved peat), the denuding of marsh soils prevents or slows the recovery of vegetation (Bertness & Silliman 2008). Without vegetation, the ecosystem services provided by salt marshes are limited or lost altogether, and the sedimentary foundation of the marsh can erode away. On Cape Cod, die-off areas are expanding at a rate of >10% per yr (Holdredge et al. 2009) and are triggering creek widening and marsh loss (Smith 2009).

SEA LEVEL RISE

Compounding the loss of creekbank cordgrass, sea level rise in New England has accelerated during the last century from 1.0 mm yr^{-1} (1300 to 1850) to 2.4 mm yr^{-1} in the 20th century (Donnelly et al. 2004). New England salt marshes have kept pace with sea level rise over the last century (Roman et al. 1997), but they could fall behind with predicted increases in the rate of sea level rise, particularly with the die-off of cordgrass, the foundation species that builds and binds New England salt marsh peat (Kirwan et al. 2008). The IPCC (2007) predicts that the rate of sea level rise may climb as high as 5.9 mm yr^{-1} this century, more than double today's rate. Other scientists predict even more extreme rates of sea level rise, up to 16.3 mm yr^{-1} (Vermeer & Rahmstorf 2009), which would submerge even intact salt marshes (Kirwan et al. 2010).

Salt marsh accretion is complex, with feedbacks between sedimentary and biological processes (Morris et al. 2002, FitzGerald et al. 2008). Despite variation in these feedbacks across marsh types, many models of marsh accretion predict future marsh drowning and loss if sea level rise increases as predicted (FitzGerald et al. 2008, but see Kirwan et al. 2010). The peat-based marshes of New England are some of the least likely to keep pace with sea level rise due to low accretion and sediment inputs (FitzGerald et al. 2008, Kirwan et al. 2010). However, the shoreward migration of low marsh vegetation into the high marsh (Donnelly & Bertness 2001) may allow the persistence of salt marshes as sea level rises, at least where human-built barriers are not encountered. Unfortunately, available data suggests that built barriers are widespread. For example, in Casco Bay, Maine, an area more sparsely populated than most of New England, 20% percent of the shoreline is armored (Kelley & Dickson 2000).

In contrast to the negative effect of temperature on waterlogged forb panne areas, sea level rise may drive the expansion of forb pannes (Warren & Niering 1993). The initiation and expansion of ponds in the high marsh is an additional mechanism of marsh loss attributed to sea level rise in mid-Atlantic salt marshes (Hartig et al. 2002). Where salt marsh areas are converted to unvegetated mudflat or open water, marsh ecosystem services are lost (Craft et al. 2009). Although there are few quantitative estimates of the expected marsh loss in New England due to sea level rise, it is anticipated to be severe. Using current IPCC sea level rise scenarios and a 'sea level affects marshes model' (SLAMM) of salt marsh accretion, Craft et al. (2009) predicted that 20 to 45% of salt marsh area in a Georgia estuary will be converted to low salinity marsh, tidal flat, or open water by 2100.

Interactions between sea level rise and other stressors will affect the capacity of marshes to keep pace with sea level rise. Marsh accretion models have shown that vegetation loss combined with sea level rise can lead to permanent marsh loss (Kirwan et al. 2008). Recent marsh loss on Cape Cod suggests that sea level rise and salt marsh die-off are already rapidly converting low marsh to open water without compensatory gains of marsh habitat at the terrestrial border (Smith 2009). Where plant canopies remain intact, temperature increase and sea level rise stressors may counteract one another: temperature-driven stimulation of plant productivity can increase accretion and slow or prevent marsh drowning by sea level rise (Kirwan et al. 2009). Climate warming also reduces forb panne areas whereas sea level rise expands pannes, potentially canceling out or creating lags in panne dynamics.

21ST CENTURY CHALLENGES FOR NEW ENGLAND SALT MARSHES

Accelerating human impacts are overwhelming salt marsh development and recovery by altering inundation regimes and the presence, identity, and productivity of salt marsh foundation species. Despite the cessation of land conversion and the implementation of conservation efforts focused on coastal wetlands, larger-scale human impacts continue to degrade New England salt marshes and could override their historic resilience. The likelihood of habitat loss due to accelerated sea level rise and its interactions with other stressors, particularly salt marsh die-off, are the new prism through which all salt marsh conservation measures must be evaluated.

Salt marsh conservation strategies need to focus on preserving resilience. Dynamic feedback processes, such as the submergence-productivity loop (Morris et al. 2002), are a natural way that salt marshes can maintain development despite sea level rise, whereas shorelines hardened by seawalls and restricted tidal regimes limit the capacity of salt marshes to respond. 'Soft' alternatives to hardened shorelines, such as the reestablishment of an intertidal buffer zone between the sea and relocated human communities (Pethick 2002) and 'living shoreline' restorations of ecosystem engineers like salt marsh grasses or oysters to prevent erosion (Swann 2008) facilitate coastal habitat retention using the natural resilience of shoreline habitats to protect property and human communities (Gedan et al. 2011). For example, in Long Island, NY, The Nature Conservancy is to working to conserve the dynamism of the coastline by using digital elevation, sea level rise, and salt marsh accretion models to identify barriers to marsh migration and quantifying the economic consequences of inaction (The Nature Conservancy 2010). Conservation of critical foundation species such as cordgrass can help ensure that salt marshes retain the capacity to respond to global change. Protecting salt marsh foundation species will require acknowledging the linkage between overfishing and salt marsh die-offs, to minimize the predator depletion that can trigger herbivore-driven salt marsh die-off (Bertness & Silliman 2008). Since the predominant paradigm shaping management decisions has been that salt marsh ecosystems are primarily controlled by physical rather than biotic forces, this will be difficult to accomplish. As we have presented, physical and biotic factors interact to shape salt marsh plant communities and they must be given equal attention by managers. The rapid rate at which herbivore driven die-offs have impacted marshes (affecting >50% of Cape Cod marsh shorelines in only 30 yr; Holdredge et al. 2009), however, makes this shift in management philosophy urgent.

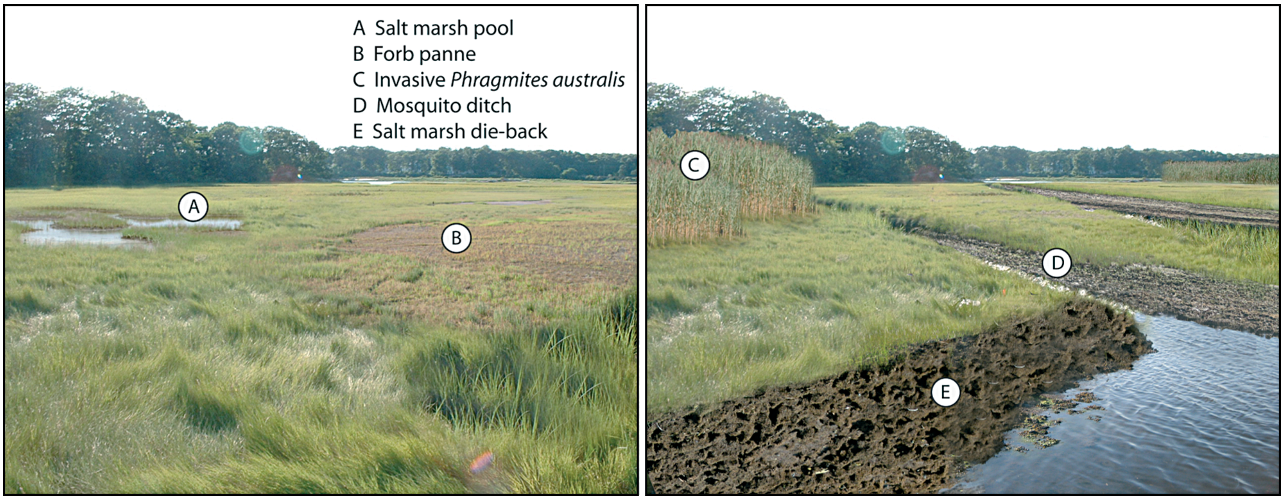

Fig. 5. Representations of a pre-impact New England salt marsh (left), with (A) salt marsh pool and (B) forb panne features, and a heavily impacted New England salt marsh (right) featuring (C) invasive *Phragmites australis*, (D) mosquito ditches, and (E) salt marsh die-back. The 2 landscapes were digitally constructed to emphasize labeled features. Graphic by Francisco Jurado-Emery and Keryn Gedan

Managing for marsh persistence, resilience, and ecosystem services may, in some cases, conflict with other management goals, such as conserving biodiversity. For example, *Phragmites australis* invasion increases accretion rates and reduces marsh drowning. Eutrophication and ditching to increase *P. australis* dominance could be an answer to managing New England salt marshes to keep pace with sea-level rise and to preserve shoreline buffering and nutrient processing services. However, this would reduce native plant diversity and nursery ground function since *P. australis* eliminates the waterlogged areas and high marsh pools that play a large role in the nursery function of marshes, but would maximize many other ecosystem services provided by New England salt marshes (Hershner & Havens 2008). Confronting these difficult decisions and tradeoffs will be unavoidable in the future conservation of New England salt marshes. Current management approaches, such as mosquito control methods that involve plugging drainage ditches and constructing ponds to create fish reservoirs (James-Pirri et al. 2008), may benefit wading birds in the short term, but will likely increase the vulnerability of marshes to sea level rise drowning over the long term.

Since New England salt marshes already look different than they did 300 yr ago (Fig. 5), and their historic resilience has been compromised by emerging anthropogenic threats, they should be actively managed in order for continued provision of ecosystem services in the face of global change. The challenge for marsh conservation is to develop adaptive management strategies to respond to local, regional, and global threats that are based on our mechanistic understanding of salt marsh ecosystem dynamics.

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