New England Salt Marsh Die-Off: Causes and Consequences

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Over half of Americans live within 50 miles of the coast, placing a disproportionate amount of stress on coastal ecosystems. Additionally, coastal ecosystems bear the brunt of both land- and ocean-based human impacts. Over the past 40 years, coral reefs, seagrass beds, and salt marshes have faced record levels of deterioration due to a combination of overfishing, climate change, eutrophication and human development. This is a pressing conservation issue because coastal ecosystems and the species that inhabit them provide important ecosystem services to humans. Coastal wetlands limit erosion, stabilize shorelines and provide $23.2 billion per year in storm protection. Loss of just one hectare of coastal wetlands results in a cost increase of $33,000 in storm damage.

The first line of defense in coastal wetland protection is salt marshes. They sequester nitrogen and carbon, filter runoff water, and reduce nitrogen input to estuaries. Salt marshes also provide essential refuge habitat for young fish and crustaceans, provisioning coastal fisheries that account for 90 percent of the world's fish catch. Arguably the most important ecosystem service salt marshes provide is to act as natural sea barriers because grasses bind soils, prevent shoreline erosion, attenuate waves and reduce coastal flooding.

Creek bank experiencing salt marsh die-off and creek bank erosion.

Today, one of the arguments for protecting salt marshes is to increase the quality and quantity of these services. However, human impacts threaten to limit the natural ability of salt marshes to continue provisioning ecosystem services.

Human Impacts: Salt Marsh Die-off

At Brown University, Professor Mark Bertness has been studying salt marsh creek bank die-off along the US eastern seaboard since the early 2000s. Salt marsh die-off, identified as denuded, muddy swaths of substrate in the low marsh, was first noticed in the 2004 National Park Service surveys of Cape Cod Bay salt marshes. Die-off occurs when a portion of the salt marsh loses its cordgrass, the plants whose underground roots hold sediment together and provide a foundation for the marsh to build upon as it slowly accretes. Cordgrass species (genus *Spartina*) also ameliorate the harsh physical conditions of the marsh, allowing other plants to grow and providing a more ideal environment for crabs, mussels, and invertebrates in the marsh. When salt marsh die-off occurs, cordgrass no longer binds the sediment and erosion of creek banks ensues. Sometimes this results in chunks of marsh calving, where they eventually dissolve into suspended sediment in a process similar to a melting glacier.

In 2008, Christine Angelini led the Bertness lab's initial investigations into the mystery of salt marsh die-off on the western Atlantic. By this point, scientists had proposed many different explanations for cordgrass morbidity, including eutrophication, hypersaline soils, disease, climate change, anoxic sediments and pollution. Angelini and colleagues found compelling evidence for a different explanation: a trophic cascade resulting in runaway herbivory of cordgrass (*Spartina alterniflora*) by elevated populations of the native purple marsh crab (*Sesarma reticulatum*).

In 2012, Andrew Altieri and colleagues performed a series of experiments designed to elucidate the mechanisms driving marsh die-off more specifically. Purple marsh crabs are normally preyed upon by blue crabs (*Callinectes sapidus*) and fish like striped bass (*Morone saxatilis*) and smooth dogfish (*Mustelus canis*). Although the cascading effects of overfishing have been demonstrated across various ecosystems, research on predator depletion has focused almost exclusively on the impact of large-scale commercial overfishing. However, Altieri and colleagues demonstrated that predators of purple marsh crabs are overexploited by recreational anglers.

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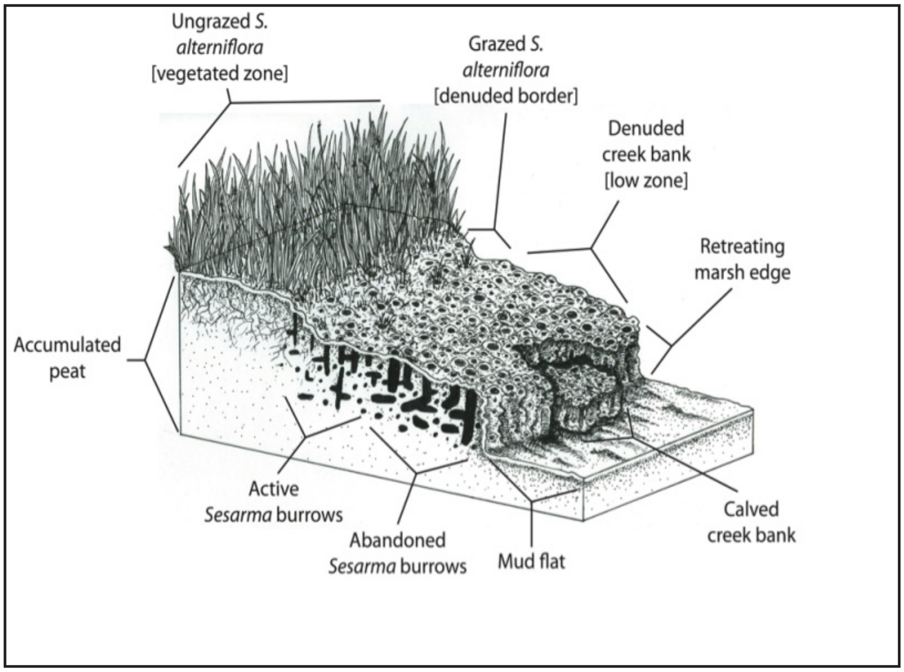
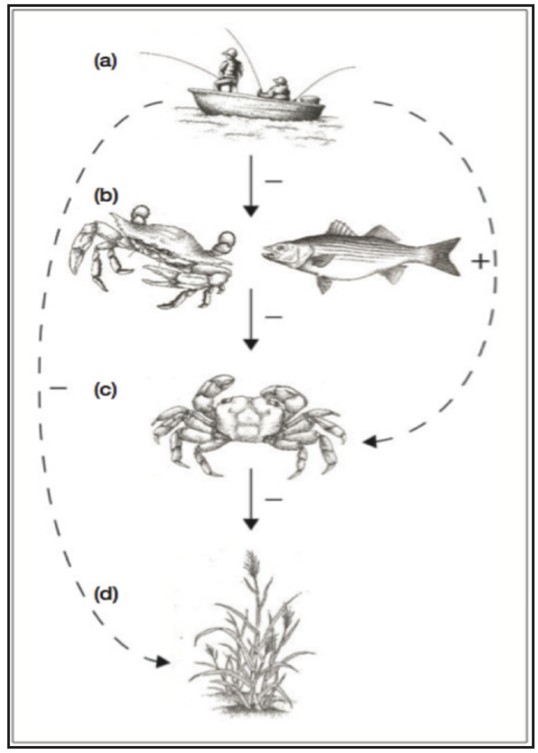


Diagram depicting salt marsh die-off. Drawn by Elena Suglia.



A trophic cascade that drives salt marsh die-off in the western Atlantic

Die-off and healthy marshes differ dramatically in recreational fishing pressure, as anglers were observed only at die-off sites. Die-off marshes had half the biomass of top-level predators found at healthy sites. Additionally, the predation rate on purple marsh crabs at healthy sites was triple that of die-off sites and crabs consumed four times more cordgrass at die-off sites than at healthy sites. Historical reconstructions showed that little net marsh loss from 1939-2005 occurred at currently healthy sites. In contrast, die-off marshes exhibited the onset of die-off in the mid-70s, with consistently increasing vegetation loss through 2005, at which time more than a fifth of the total marsh area was lost to die-off and greater than 80 percent of the cordgrass zone was unvegetated.

The purple marsh crab, *Sesarma reticulatum*

This divergence between die-off and vegetated marshes in vegetation loss coincides with a period of rapid increase in the number of docks and boat slips before the mid-70s that resulted in the establishment of more than 70 percent of the fishing infrastructure currently present at die-off marshes. These results provide strong evidence that releasing the purple marsh crab from predation pressure due to recreational overfishing by anglers is driving a trophic cascade that is responsible for extensive marsh die-off throughout southern New England.

Altieri and colleagues further hypothesized that historic, large-scale, industrialized overexploitation of fish in the northwest Atlantic increased marsh vulnerability to the effects of localized recreational fishing to the point that large-scale die off ensued, and that resultant localized die-offs could coalesce into complete, region-wide marsh die-off if overexploitation of top consumers continues.

Geographic Extent of Salt Marsh Die-off

Mark Bertness and his team have collected a body of evidence for this hypothesis and put together more pieces of the puzzle even as salt marsh die-off has progressed southward down the coast and increased in intensity on Cape Cod. The rate of die-off expansion and area of marsh affected have more than doubled since 2000. Now, die-off is currently expanding by greater than eight percent per year, and more than 150,000 square meters of marsh area has been lost to die-off across 14 sites on Narragansett Bay, Rhode Island.

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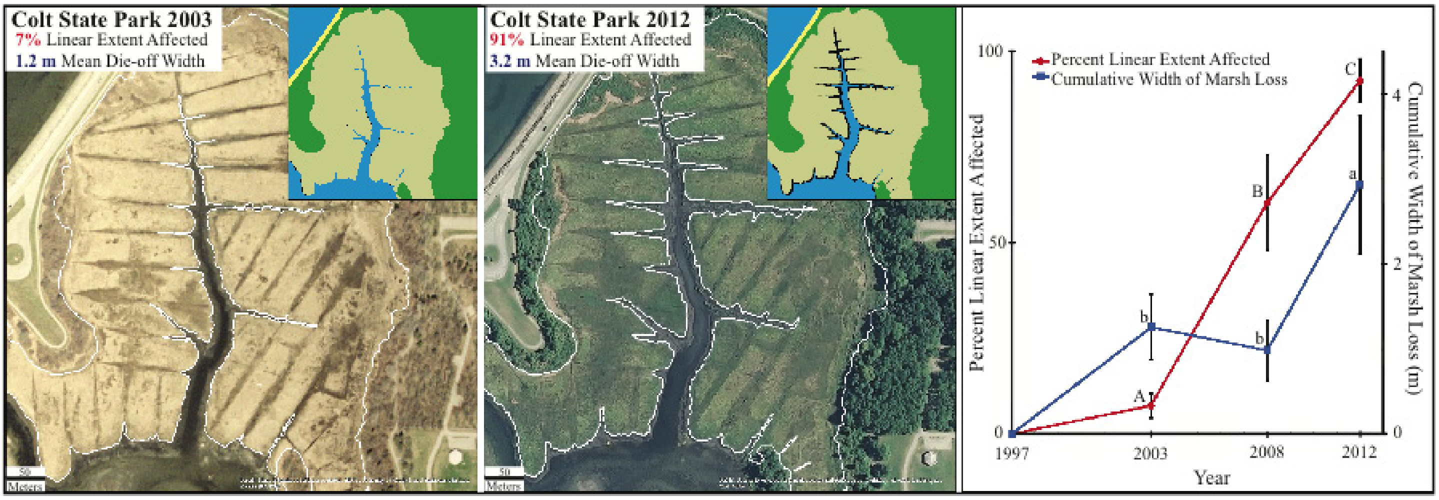

Historical reconstruction of study sites in Narragansett Bay. Images and analysis of study site aerial photographs illustrate the progression from a healthy state in 2003 (Left) to a declining state with high levels of die-off in 2012 (Center). Please note that the color differences between the pictures are due to differences in picture quality between 2003 and 2012. Take note of the white line tracing die-off in the main pictures and the highlighted black area denoting die-off in the pictures in the upper right hand corners. Percent linear extent and cumulative width of marsh lost to die-off rapidly accelerated at Narragansett Bay salt marshes over the past decade (Right). Letters indicate significant differences in variables among time intervals (ANOVA, Tukey HSD). Figure from Bertness et al 2014.

Most recently, Bertness and colleagues used the spread of die-off into Narragansett Bay to test the relative importance of all proposed hypotheses. Across 14 sites with broad ranges of conditions, Bertness quantified the amount of die-off, nitrogen availability, pollution and disease with common source transplants, wave exposure, herbivory, substrate hardness, and predation. Differences in herbivory were able to explain over 70 percent of site differences in die-off, while other factors were unable to explain any residual differences.

Predator Exclusion

Until this point, however, most of the work was strongly correlational and could not provide causation for the trophic cascade hypothesis. To finally test this unequivocally, Bertness' next step was to perform a fully factorial predator exclusion experiment that directly manipulated the presence of the purple marsh crab's predators in the marsh and experimentally induced die-off on small patches of a healthy salt marsh in Cape Cod. The scientists chose a site in the North Bay, Osterville, Massachusetts that borders a marina frequented by recreational fishermen. The lab has extensive long-term data for this site, which has a history of die-off in the early 2000s. In recent years, the site has experienced recovery of cordgrass in the low marsh as a result of compensatory predation by the invasive European green crab (*Carcinus maenas*).

Bertness used 1 square meter (m^2) plots located on the marsh grazing border where crab burrowing and herbivory are concentrated. Exclusion cages with closed tops were inserted 5 centimeters (cm) into the ground to prevent access by predators but allow underground access to *Sesarma* via extensive underground burrow networks. Procedural cage controls lacked tops and were elevated 15 cm above the substrate to allow access by predators; controls were un-manipulated natural plots. By denying predators access to *Sesarma* with exclusion cages, the crab populations increased within the confines of the cages, where runaway herbivory and the characteristic pockmarked, heavily denuded marsh substrate of die-off areas developed in the marsh. By the end of the growing season, Bertness and his colleagues had triggered localized die-off; predator exclusion plots saw a 100 percent increase in herbivory and a 150 percent increase in un-vegetated bare space relative to control plots. Nutrient availability and wave action did not differ significantly among treatments and did not explain plot differences in cordgrass death. Combined with the past decade of research on salt marsh die-off across over 70 sites in New England, Bertness' predator exclusion experiment provides compelling, causal evidence in support of the trophic cascade hypothesis, whereby depletion of the top predators releases the purple marsh crab from consumer control, leading to overgrazing of cordgrass, collapse of creek banks and loss of marsh area.

Since cordgrass is responsible for sediment binding and peat deposition, cordgrass die-off may compromise the ability of salt marshes to keep pace with sea-level rise. The detrimental effects trophic cascades have had on marshes not only reduce the biodiversity, health, and aesthetic appeal of these ecosystems, but also compromise the ability of marshes to provide key ecosystem services to human populations. Understanding the potentially synergistic interaction between current threats, such as salt marsh die-off, and future impacts, such as sea-level rise and ocean acidification, is an important goal for marsh conservation and management and is the future direction for work in the Bertness lab.

Marsh Management

Despite a significant body of evidence for the trophic cascade hypothesis, there remains controversy in the scientific community over what drives salt marsh die-off. Salt marshes have long been believed to be controlled primarily by bottom-up forces, a paradigm that has become entrenched in the conceptual understanding of salt marsh ecosystems.

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Die-off (Continued from Page 8)

Additionally, trophic cascades were originally thought to be rare. However, it has become clear that top-down forces play a critical role in the structure and function of salt marsh ecosystems. Conservation of ecosystems affected by trophic cascades has not adequately incorporated top-down control into their management and restoration plans and efforts, but emerging research emphasizes that this is necessary to protect the services provided by these ecosystems.

Recreational fishing is responsible for marsh die-off throughout southern New England by directly and efficiently targeting top predators. If recreational fishing continues at its current pace, marsh die-off will become a regional threat to coastal communities. Over the next century, coastal ecosystems will be impacted by sea-level rise, ocean acidification and overexploitation, making preserving coastal ecosystems an immediate goal. Predicted increased frequency and severity of storms with climate change and sea-level rise will increase the vulnerability of low-lying coastal populations, making coastal populations more susceptible to the negative effects of climate change. Elucidating the mechanisms of current threats and the interactions between impacts is an important step towards understanding marsh resilience, developing targeted conservation and management strategies, and protecting coastal communities in the future.

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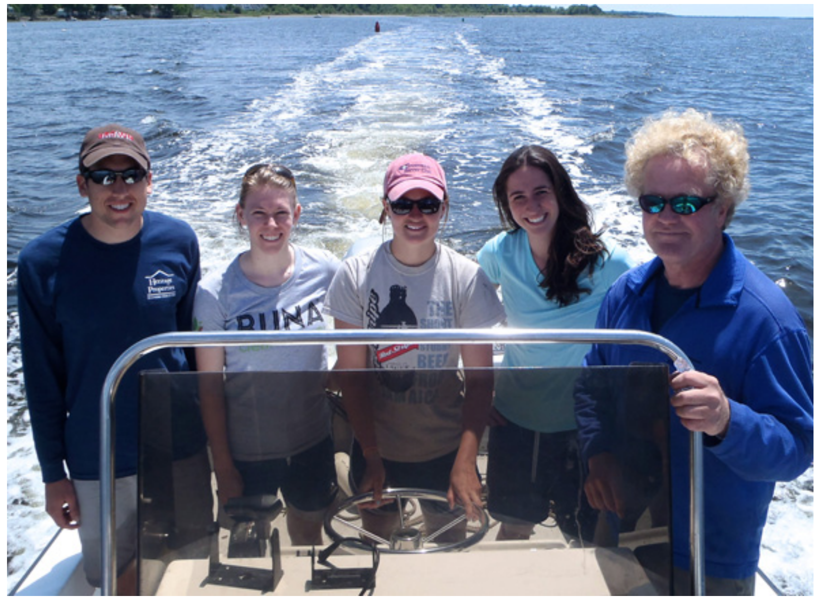

Bertness lab members, L-R: Matthew Bevil, Elena Suglia, Caitlin Brisson, Sinead Crotty, Mark Bertness. Bertness Lab, Summer 2013

Bertness Lab, Summer 2014

Predator exclusion cage with increased burrowing and loss of cordgrass