Quick guide

Salt marshes

Brian R. Silliman

Figure 1. Salt marsh.
Extensive salt marsh on Sapelo Island, Georgia, USA. Three distinct plant zones are visible: brown needlerush in the foreground, tall cordrass along the creeks and in circles in the mid-marsh, and zones of short pickleweed in between. Photo: Johan van de Koppel.

What is a salt marsh? Salt marshes are lush, intertidal grasslands renowned for their productivity. The yearly accumulation of plant and animal tissue in salt marshes rivals and often exceeds that observed in other highly productive ecosystems, including coral reefs and tropical rain forests. Although the local diversity of plants and animals found in salt marshes is comparatively low, the abundance of organisms that do occur in marshes is often breathtaking. The abundance per square meter of one species of fiddler crab or snail routinely reaches 100–400 individuals, at times over 1000, and over larger spatial scales the density of one species of non-insect invertebrate (mussels, crabs and snails) can often reach 50,000,000 per square kilometer. Globally, plant species richness in salt marshes is surprisingly high, with over 500 salt marsh plant species known.

Where are salt marshes found? Found in the temperate zone on protected shorelines throughout the world, salt marshes are limited in polar expansion by the destructive forces of ice and in significant occurrence in tropical regions by competitively dominant mangroves that are far superior in gathering nutrients and light. Within the temperate zone, plant competition again constrains the range of salt marshes, as freshwater plants like cattails and sedges are better competitors for nutrients and prevent salt marsh plants from migrating up rivers. Although salt marsh plants can grow on sandy shorelines, the intense wave action of open coasts prevents their establishment on exposed beaches. To develop as an ecosystem, marshes must be protected from wave action by some kind of landmass, be it barrier islands, peninsulas, or the outer coast. As an ecosystem, salt marshes are thus limited in occurrence to the salty, shallow, and sheltered waters of bays, estuaries and lagoons in the temperate regions of the world (Figure 1).

The size of specific salt marshes varies wildly, from small football-field sized marshes commonly found in New England and Europe to the massive salt marshes that stretch 10s of kilometers in width and length along the coast of Louisiana. Salt marsh size is driven overwhelmingly by geology and geomorphology. Gently sloping continental shelves as well as abundant sediment supply are critical to the expansive growth of salt marshes, as is the case in the deltaic plain of the Mississippi and the salt marshes along the southeastern coasts of China and the US. Smaller marshes are most often found on coastlines characterized by a steep continental shelf and/or lack of sediment input from rivers. Here, marsh plant and ecosystem expansion are greatly limited by the lack of extensive, shallow water areas.

How can plants and animals live in such a stressful environment? Plants and animals living in salt marshes must have adaptations to deal with the harsh physical stressors found in this intertidal habitat, including high salt concentrations, intense heat, and low oxygen in waterlogged soils. Many salt marsh plants deal with low soil oxygen levels by shunting oxygen down to their roots through straw-like vascular tissue called aerenchyma. Plant adaptations to high salt stress are more varied and include salt exclusion in the roots, salt excretion in leaves and increasing the salt concentration (amino acids) in their own cells to become more isosmotic. Comparatively, marine animals living in the marsh have little issue with salt concentrations or low oxygen availability in the soils, but instead must deal with intense heat stress. Animal adaptations to avoid intense thermal stress, which can reach 136 degrees F at the marsh surface, include climbing above the substrate (snails), retreating to burrows (crabs), or cooling through evaporation (mussels). Over evolutionary time, few plants and animals have overcome these intense physical obstacles, but for those individuals that have, there seems to have been a huge reward — access to abundant resources, protection from predators and huge potential for growth for both them and their offspring.

How are salt marshes organized? Open space in salt marshes is usually hard to come by, and one of the most distinct characteristics of salt marshes is the zonation of the plant community into tight, linear bands of mono-specific dominance. These distinct species bands most often run perpendicular to the elevation gradient. The lower boundary of these plant zones is typically set by plant tolerance to physical stress (usually low oxygen) while the upper boundary is set by competition with other plant species that are superior competitors for nutrients. This nearly universal pattern has an underlying evolutionary mechanism: there is a clear and measureable trade-off between the competitive ability of plants to take up nutrients and the ability of plants to get oxygen to their roots. Thus, plants that are stress tolerators occupy the lower reaches of the marshes while competitive dominants occupy the upper elevations that are less stressful.

Room on the marsh surface for establishment and growth of new seedlings in these tightly-packed, plant zones is at a premium. Weedy plants that are neither competitive dominants nor the best stress tolerators must rely on outside disturbance to open bare space for colonization. Lucky for them, this happens often in salt marshes and die-off of dominant plants can occur from ice scouring, lack of drainage, temporary water pooling, intense grazing, and/or smothering by large, floating rafts of dead grass called wrack.

Plant community structure and growth are also strongly affected by a diverse suite of positive species interactions. Marsh plant mutualisms with burrowing crabs, sediment-depositing mussels, and mycorrhizal fungi can double plant growth by increasing oxygen and nutrient supply in the soil. In contrast, facultative mutualisms between fungal-farming invertebrate grazers and the fungi they facilitate in plant tissues can lead to drastic reductions in growth of plants that act as a farming substrate. Plant–plant facilitations are also key drivers of marsh plant ecology. For example, large bushes or initial plant colonizers of bare areas can shade the substrate and reduce salt accumulation in the soils and thereby facilitate colonization by many other plant species. Indeed, experimental studies have shown that without facilitative interactions among plants, recovery from disturbance events in salt marshes would be uncommon to rare.

Salt marsh plant communities and production are also highly influenced from both the bottom-up and top-down. Complex, but predictable, biogeochemical cycles in marsh soils lead to nitrogen limitation of plant growth despite the fact that inorganic nitrogen is in high concentrations in soils. This paradox occurs because marsh soils also have high concentrations of both sulfide and sodium ions — both of which interfere with nitrogen uptake by plants.

Figure 2. A food chain in southern US salt marshes.
(A) American alligator feeding on a blue crab in a marine salt marsh creek. Photo: James Nifong. (B) Swimming blue crab reaching above the flood tide in a marsh to feed on fungal-farming snails. Blue crabs facilitate and protect salt marsh grasses from overgrazing by consuming large amounts of these powerful little molluscs. Photo: Emily Legout. (C) Marsh periwinkle snail that farms fungus on grazer-induced wounds on live salt marsh plants. Photo: Brian Silliman.

Although for decades salt marsh plants were thought to be immune to consumer pressure because of high levels of chemical defenses, recent work has convincingly overturned this paradigm. Manipulative field studies from Argentina, Brazil, Canada, China, Europe and the entire East and Gulf Coast of the US have revealed that this top-down force is primarily generated by herbivorous crabs, fungal-farming snails, and/or large vertebrates (Figure 2). In many instances, populations of these grazers are regulated by predators whose decline can lead to grazer outbreaks that demolish marsh plant landscapes and generate an alternative mudflat state, as is the case in Southeastern Canada, New England, and in the Southeastern US. These grazer outbreaks often manifest themselves as consumer fronts, or long, linear bands of high densities of grazers. Fronts of geese, crabs and snails have been observed destroying marshes in Canada, New England, and along the Mid-Atlantic, Southeastern and Gulf Coast shorelines in the US. These consumer fronts can last for one season or multiple years and are powerful forces that leave gigantic mudflats in their wake. Recovery of salt marshes after these large-scale die-offs is highly dependent on breakup of the consumer fronts, either through compensatory predation or spatial processes, and vegetative regrowth facilitated by positive interactions among plants and between plants and mussels. Given this overwhelming amount of experimental evidence of strong top-down control across marsh plant communities worldwide, salt marsh ecosystems are no longer held up in ecology as the quintessential ecosystem controlled only from the bottom-up. Ironically, they are now championed as systems that are under dynamic control by powerful and complex trophic feedbacks and cascades.

How do salt marshes benefit people? Beyond their luxuriant production, distinct zonation, intense physical gradients, and strong impacts of species interactions, salt marshes are also famous for their provisioning of valuable services to humans. For example, shorelines and bulkheads with salt marshes in front of them are better defended and experience less erosion from wave-induced stress as grasses baffle incoming waves. Salt marshes also enhance human well-being by acting as critical nursery habitats for important fisheries, large sinks for carbon sequestration, and nutrient filtration systems that increase water quality in nearby estuaries by dampening the harmful affects of agricultural run off.

What threatens salt marshes and the valuable services they provide? Despite the valuable services salt marshes provide coastal populations, they are under siege from human disturbance on a global scale. Not long ago, coastal scientists and managers championed salt marshes as one of the most resilient and resistant ecological communities and even promoted these systems as natural buffers that could protect other shoreline ecosystems (*e.g.* seagrasses) from intensifying human impacts (*e.g.* absorption of nutrients in waste water and terrestrial run-off). Research over the past decade, however, has revealed that this notion of unrivaled resilience in salt marshes is a myth.

Reclamation activities, once thought to be under control and now banned in most European and North American countries, are still common throughout the rest of the world. Those marshes that do remain are now threatened from many co-occurring stressors, including species invasions, small- and large-scale eutrophication, trophic cascades, runaway consumer fronts, pollutants including oil spills, altered hydrologic regimes, and climate-change-induced effects including sea-level rise, increasing air and sea surface temperatures, increasing CO_2 concentrations and increased frequency of intense drought. In many cases, these stressors can act additively or synergistically to hasten salt marsh decline. For instance, intense drought stress intensifies grazing pressure and stimulates formation of consumer fronts because it severely weakens plant defenses to herbivory. Given the multitude of threats facing salt marshes, it is very likely that if new and expanded conservation measures are not taken by conservation managers and policy makers, the long-term persistence of salt marshes and the services they provide will be severely threatened.

What can we do to protect the salt marshes that remain? To save salt marshes, conservation practitioners must think outside the box and use measures and models that deal with multiple, co-occurring and potentially synergistic threats. This new approach to marsh conservation must also be regional in scale. Historically, there has been a scaling mismatch between local, or ‘one marsh at-a-time’, conservation measures and the reality of regional-scale, multi-marsh distribution of human-induced impacts. To save the marshes we have left, this old framework of marsh conservation and the outdated dogma of salt marsh ecology must be changed to reflect new trends in general conservation strategies and the new science that challenges our old way of thinking about these systems, for example, incorporating top-down control and food-web interactions. State and federal agencies can no longer act independently and at local scales. Conservation of existing habitat and restoration of degraded habitat must take into consideration the distribution of nearby marshes for sources of propagules, links for migratory species and endangered species, management of invasive species, etc.

One of the most important and effective acts that conservation practitioners can begin to make to ensure the long-term protection and persistence of salt marsh habitats is to champion the use of marine protected areas in marsh management. These protected areas must: (1) include associated marine habitats, such as seagrass beds and oyster reefs; (2) incorporate extensive areas of undisturbed terrestrial border to buffer marshes from excessive eutrophication via run-off and allow for their landward migration as sea-level rises; (3) account for the inclusion of positive interactions at all levels of biological association (*e.g.* trophic cascades, cross ecosystem–nursery benefits); and (4) be large, numerous and appropriately spaced. Around the world, coral and rocky reef conservation practitioners and scientists lead the field of marine conservation in this effort. Salt marsh conservationists and ecologists are far behind this work and, thus, should look to these fields for lessons learned and guidance when establishing marine protected areas for temperate coastal areas whose intertidal zone is dominated by salt marshes. Because of the notoriety associated with the designation of a site as a marine protected area, using this method as a means to preserve marshes will also raise public awareness as to the critical role marshes play in the ecology and economy of local human communities.

Where can I find out more?

Bertness, M.D. (1984). Fiddler crab regulation of Spartina alterniflora production on a New England salt marsh. Ecology *66*, 1042–1055.
Bertness, M.D., and Shumway, S.W. (1993). Competition and facilitation in marsh plants. Am. Nat. *142*, 718–724.
Bradley, P.M., and Morris, J.T. (1990). Influence of oxygen and sulfide concentration on nitrogen uptake kinetics in Spartina alterniflora. Ecology *71*, 282–287.
Daleo, P., Alberti, J., Canepuccia, A., Escapa, M., Fanjul, E., Casariego, A.M., Silliman, B.R., Bertness, M.D., and Iribarne, O. (2008). Mycorrhizal fungi determine salt-marsh plant zonation depending on nutrient supply. J. Ecol. *96*, 431–437.
Jefferies, R.L. (1997). Long-term damage to sub- arctic coastal ecosystems by geese: ecological indicators and measures of ecosystem dysfunction. In *Disturbance and Recovery in Arctic Lands: an Ecological Perspective*, ed. R.M.M., Crawford, pp.151–166. Boston: Kluwer Academic.
Kirwin, M., and Megonigal, P. (2013). Tidal wetland stability in the face of human impacts and sea-level rise. Nature *504*, 53–60.
Mullan, C., Silliman, B.R., Bertness, S., and Bertness, M.D. (2004). Physical and biotic drivers of plant distribution across estuarine salinity gradients. Ecology *85*, 2539–2549.
Silliman, B.R., and Bertness, M.D. (2002). A trophic cascade regulates salt marsh primary production. Proc. Natl. Acad. Sci. USA *99*, 10500–10505.
Silliman, B.R., Grosholtz, T., and Bertness, M.D., editors. (2009). Human Impacts on Salt Marshes: A Global Perspective. University of California Press.
Silliman, B.R., van de Koppel, J., Bertness, M.D., Stanton, L., and Mendelsohn, I. (2005). Drought, snails, and large-scale die-off of southern U.S. salt marshes. Science *310*, 1803–1806.

Division of Marine Sciences and Conservation, Nicholas School of the Environment, Duke University, Beaufort, North Carolina, USA.
E-mail: brian.silliman@duke.edu