colonizers (e.g., *Salicornia*). In northern regions, ice scouring can dramatically alter the creek or bayfront of marshes. Also, large blocks of ice, laden with sediment, are often deposited on the high marsh creating a new microrelief habitat, or these blocks may transport plant rhizomes to mud or sand flats and initiate the process of salt marsh development.

Regarding human-induced disturbances, hydrologic alterations have dramatic effects on salt marsh vegetation patterns throughout the world. Some salt marshes have been diked and drained for agriculture. In others, extensive ditching has drained salt marshes for mosquito-control purposes. In yet another hydrologic alteration, water has been retained or impounded within salt marshes to alter wildlife habitat functions or to control mosquitoes. Impoundments generally restrict tidal inflow and retain fresh water, resulting in conversion from salt-tolerant vegetation to brackish or freshwater vegetation. Practices that drain the marsh, such as ditching, tend to lower the water-table level and aerate the soil, and the resulting vegetation may shift toward that typical of a high marsh. Another type of hydrologic alteration is the restriction of tidal flow by bridges, culverts, roads, and causeways. This is particularly common along urbanized shorelines, where soil salinity can be reduced and water-table levels altered resulting in vegetation changes, such as the conversion from *Spartina*-dominated salt marsh to *Phragmites australis*, as is most evident throughout the north-eastern US. The role of hydrologic alterations in controlling vegetation patterns is clearly identified in **Figure 1** as a key physical disturbance, and also as a variable that influences tidal flooding, soil salinity, and soil oxygen levels.

Grazing by domestic animals, mostly sheep and cattle, and mowing for hay are two practices that have been ongoing for many centuries on salt marshes worldwide, although they seem to be declining in some regions. Studies in Europe have demonstrated that certain plant species are favored by intensive grazing (e.g., *Puccinellia*, *Festuca rubra*, *Agrostis stolonifera*), whereas others become dominant on ungrazed salt marshes (e.g., *Halimione portulacoides*, *Limonium*, *Suaeda*).

Conclusions

Vegetation zones of salt marshes have been described as belts of plant communities from creekbank or bayfront margins to the upland border, or most appropriately, as a mosaic of communities along this elevation gradient. All salt marsh sites display some zonation but because of the complex of interacting factors that influence marsh vegetation patterns, there is extraordinary variability in zonation among individual marshes. Moreover, salt marsh vegetation patterns are constantly changing on seasonal to decadal timescales. Experimental research and long-term monitoring efforts are needed to further evaluate vegetation pattern responses to the myriad of interacting environmental factors that influence salt marsh vegetation. An ultimate goal is to model and predict the response of marsh vegetation as a result of natural or human-induced disturbance, accelerated rates of sea level rise, or marsh-restoration strategies.

See also

Coastal Circulation Models. Intertidal Fishes. Mangroves. Salt Marshes and Mud Flats. Sea Level Change.

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SALT MARSHES AND MUD FLATS

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Structure

Salt marshes are vegetated mud flats. They are above mean sea level in the intertidal area where higher plants (angiosperms) grow. Sea grasses are an exception to the generalization about higher plants because they live below low tide levels. Mud flats are vegetated by algae.

Geomorphology

Salt marshes and mud flats are made of soft sediments deposited along the coast in areas protected from ocean surf or strong currents. These are long-term depositional areas intermittently subject to erosion and export of particles. Salt marsh sediments are held in place by plant roots and rhizomes (underground stems). Consequently, marshes are resistant to erosion by all but the strongest storms. Algal mats and animal burrows bind mud flat sediments, although, even when protected along tidal creeks within a salt marsh, mud flats are more easily eroded than the adjacent salt marsh plain.

Salinity in a marsh or mud flat, reported in parts per thousand (ppt), can range from about 40 ppt down to 5 ppt. The interaction of the tides and weather, the salinity of the coastal ocean, and the elevation of the marsh plain control salinity on a marsh or mud flat. Parts of the marsh with strong, regular tides (1 m or more) are flooded twice a day, and salinity is close to that of the coastal ocean. Heavy rain at low tide can temporarily make the surface of the sediment almost fresh. Salinity may vary seasonally if a marsh is located in an estuary where the river volume changes over the year. Salinity varies within a marsh with subtle changes in surface elevation. Higher marshes at sites with regular tides have variation between spring and neap tides that result in some areas being flooded every day while other, higher, areas are flooded less frequently. At higher elevations flooding may occur on only a few days each spring tide, while at the highest elevations flooding may occur only a few times a year.

Some marshes, on coasts with little elevation change, have their highest parts flooded only seasonally by the equinoctial tides. Other marshes occur in areas with small lunar tides where flooding is predominantly wind-driven, such as the marshes in the lagoons along the Texas coast of the United States. They are flooded irregularly and, between flooding, the salinity is greatly raised by evaporation in the hot, dry climate. The salinity in some of the higher areas becomes so high that no rooted plants survive. These are salt flats, high enough in the tidal regime for higher plants to grow, but so salty that only salt-resistant algae can grow there. The weather further affects salinity within marshes and mud flats. Weather that changes the temperature of coastal waters or varying atmospheric pressure can change sea level by 10 cm over periods of weeks to months, and therefore affect the areas of the marsh that are subjected to tidal inundation.

Sea level changes gradually. It has been rising since the retreat of the continental glaciers. The rate of rise may be increasing with global warming. For the last 10 000 years or so, marshes have been able to keep up with sea level rise by accumulating sediment, both through deposition of mud and sand and through accumulation of peat. The peat comes from the underground parts of marsh plants that decay slowly in the anoxic marsh sediments. The result of these processes is illustrated in **Figure 1**, in which the basement sediment is overlain by the accumulated marsh sediment. Keeping up with sea level rise creates a marsh plain that is relatively flat; the elevation determined by water level rather than by the geological processes that determined the original, basement sediment surface on which the marsh developed. Tidal creeks, which carry the tidal waters on and off the marsh, dissect the flat marsh plain.

Organisms

The duration of flooding and the salinities of the sediments and tidal waters control the mix of higher

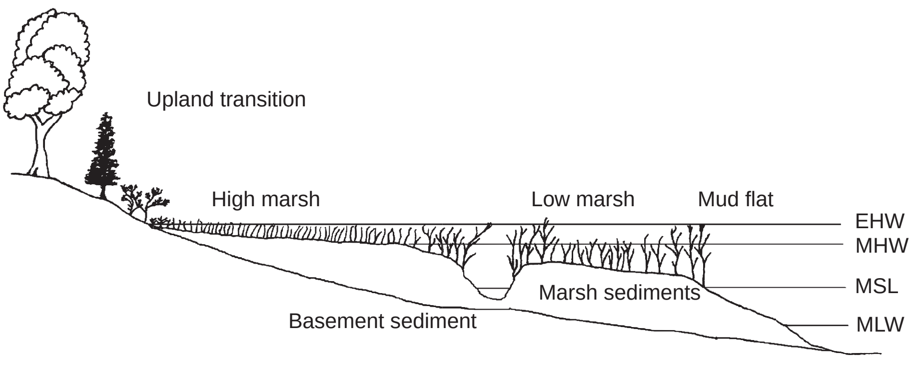

Figure 1 Cartoon of a typical salt marsh of eastern North America. The plants shown are mostly grasses and may differ in other parts of the world. MLW, mean low water; MSL, mean sea level; MHW, mean high water; EHW, extreme high water. The mud flat is shown as a part of the marsh but mud flats also exist independently of marshes.

vegetation. Competitive interactions between plants and interactions between plants and animals further determine plant distributions. Duration of flooding duration controls how saturated the sediments will be, which in turn controls how oxygenated or reduced the sediments are. The roots of higher plants must have oxygen to survive, although many can survive short periods of anoxia. Air penetrates into the creekbank sediments as they drain at low tide. Evapotranspiration from plants at low tide also removes water from the sediments and facilitates entry of air. Most salt marsh higher plants have aerenchyma (internal air passages) through which oxygen reaches the roots and rhizomes by diffusion or active transport from the above-ground parts. However, they also benefit from availability of oxygen outside the roots.

The species of higher plants that dominate salt marshes vary with latitude, salinity, region of the world, and tidal amplitude. They are composed of relatively few species of plants that have invested in the ability to supply oxygen to roots and rhizomes in reduced sediments and to deal with various levels of salt. Grasses are important, with *Spartina alterniflora* the dominant species from mid-tide to high-tide levels in temperate Eastern North America. *Puccinellia* is a dominant grass in boreal and arctic marshes. The less regularly flooded marshes of East Anglia (UK) support a more diverse vegetation community in which grasses are not dominant. The salty marshes of the Texas coast are covered by salt-tolerant *Salicornia* species. Adjacent to the upper, landward edge of the marsh lie areas flooded only at times when storms drive ocean waters to unusual heights. Some land plants can survive occasional salt baths, but most cannot. An extreme high-water even usually results in the death of plants at the marsh border.

Algae on the marsh and mud flat are less specialized. Depending upon the turbulence of the tidal water, macroalgae (seaweeds) may be present, but a diverse microalgal community is common. Algae live on or near the surface of the sediments and obtain oxygen directly from the air or water and from the oxygen produced by photosynthesis. Their presence on surface sediment is controlled by light. In highly turbid waters they are almost entirely limited to the intertidal flats. In clearer waters, they can grow below low-tide levels. Algae growing on the vegetated marsh plain and on the stems of marsh plants get less light as the plants mature. Production of these algae is greatest in early spring, before the developing vegetation intercepts the light.

Photosynthetic bacteria also contribute to marsh and mud flat production. Blue-green bacteria can be abundant enough to forms mats. Photosynthetic sulfur bacteria occupy a thin stratum in the sediment where they get light from above and sulfide from deeper reduced levels for their hydrogen source but are below the level of oxygen penetration that would kill them. These strange organisms are relicts from the primitive earth before the atmosphere contained oxygen.

Salt marsh animals are from terrestrial and marine sources; mud flat inhabitants are limited to marine sources. Insects, spiders, and mites live in marsh sediments and on marsh plants. Crabs, amphipods, isopods and shrimps, polychaete and oligochaete annelids, snails, and bivalves live in and on the sediments. Most of these marine animals have planktonic larval stages that facilitate movement between marshes and mud flats. Although burrowing animals, such as crabs that live at the water edge of the marsh, may be fairly large (2–15 cm), in general burrowers in marshes are smaller than those in mud flats, presumably because the root mats of the higher plants interfere with burrowing.

Fish are important faunal elements in regularly flooded salt marshes and mud flats. They can be characterized as permanent marsh residents; seasonal residents (species that come into the marsh at the beginning of summer as new post-larvae and live in the marsh until cold weather sets in); species that are primarily residents of coastal waters but enter the marshes at high tide; and predatory fish that come into marshes on the ebb tide to feed on the smaller fishes forced off the marsh plain and out of the smaller creeks by falling water levels.

A few mammals live in the marshes, including those that flee only the highest tides by retreating to land, such as voles, or those that make temporary refuges in tall marsh plants, such as raccoons. The North American muskrat builds permanent houses on the marsh from the marsh plants, although muskrats are typically found only in the less-saline marshes. Grazing mammals feed on marsh plants at low tide. In Brittany, lambs raised on salt marshes are specially valued for the flavor of their meat.

Many species of birds use salt marshes and mud flats. Shore bird species live in the marshes and/or use associated mud flats for feeding during migration. Northern harriers nest on higher portions of salt marshes and feed on their resident voles. Several species of rails dwell in marshes as do bitterns, ducks, and some wrens and sparrows. The nesting species must keep their eggs and young from drowning, which they achieve by building their nests in high vegetation, by building floating nests, and by nesting and raising their young between periods of highest tides.

Functions

Marshes, and to some extent mud flats, produce animals and plants, provide nursery areas for marine fishes, modify nutrient cycles, degrade organic chemicals, immobilize elements within their sediments, and modify wave action on adjacent uplands.

Production and Nursery

Plant production from salt marshes is as high as or higher than that of most other systems because of the ability of muddy sediments to serve as nutrient reservoirs, because of their exposure to full sun, and because of nutrients supplied by sea water. Although the plant production is food for insects, mites and voles, large mammalian herbivores that venture onto the marsh, a few crustacea, and other marine animals, most of the higher plant production is not eaten directly but enters the food web as detritus. As the plants die, they are attacked by fungi and bacteria that reduce them to small particles on the surface of the marsh. Since the labile organic matter in the plants is quickly used as food by the bacteria and fungi, most of the nutrient value of the detritus reaches the next link in the food chain through these microorganisms. These are digested from the plant particles by detritivores, but the cellulose and lignin from the original plants passes through them and is deposited as feces that are recolonized by bacteria and fungi. Besides serving as a food source in the marsh itself, a portion of the detritus–algae mixture is exported by tides to serve as a food source in the marsh creeks and associated estuary.

The primary plant production supports production of animals. Fish production in marshes is high. Resident fishes such as North American *Fundulus heteroclitus* live on the marsh plain during their first summer, survive low tide in tiny pools or in wet mud, feed on the tiny animals living on the detritus–algae–microorganism mix, and grow to migrate into small marsh creeks. At high tide they continue to feed on the marsh plain, where they are joined by the young-of-the-year of those species that use the marsh principally as a nursery area. The warm, shallow waters promote rapid growth and are refuge areas where they are protected from predatory fishes, but not from fish-eating herons and egrets.

The fishes are the most valuable export from the marshes to estuaries and coastal oceans. Some of the fishes are exported in the bodies of predatory fishes that enter the marsh on the ebb tide to feed. Many young fishes, raised in marshes, migrate offshore in the autumn after having spent the summer growing in the marsh.

Nutrient and Element Cycling

Nitrogen is the critical nutrient controlling plant productivity in marshes. Phosphorus is readily available in muddy salt marsh sediments and potassium is sufficiently abundant in sea water. Micro-nutrients, such as silica or iron, that may be limiting for primary production in deeper waters are abundant in marsh sediments. Thus nitrogen is the nutrient of interest for marsh production and nutrient cycling.

In marshes where nitrogen is in short supply, blue-green bacteria serve as nitrogen fixers, building nitrogen gas from the air into their organic matter. Nitrogen-fixing bacteria associated with the roots of higher plants serve the same function. Nitrogen fixation is an energy-demanding process that is absent where the supply is sufficient to support plant growth.

Two other stages of the nitrogen cycle occur in marshes. Organic nitrogen released by decomposition is in the form of ammonium ion. This can be oxidized to nitrate by certain bacteria that derive energy from the process if oxygen is present. Both nitrate and ammonium can satisfy the nitrogen needs of plants, but nitrate can also serve in place of oxygen for the respiration of another group of bacteria that release nitrogen gas as a by-product in the process called denitrification. Denitrification in salt marshes and mud flats is significant in reducing eutrophication in estuarine and coastal waters.

Phosphorus, present as phosphate, is the other plant nutrient that can be limiting in marshes, especially in regions where nitrogen is in abundant supply. It can also contribute to eutrophication of coastal waters, but phosphate is readily bound to sediments and so tends to be retained in marshes and mud flats rather than released to the estuary.

Sulfur cycling in salt marshes, while of minor importance as a nutrient, contributes to completing the production cycle. Sulfate is the second most abundant anion in sea water. In anoxic sediments, a specialized group of decomposing organisms living on the dead, underground portions of marsh plants can use sulfate as an electron acceptor – an oxygen substitute – in their respiration. The by-product is hydrogen sulfide rather than water. Sulfate reduction yields much less energy than respiration with oxygen or nitrate reduction, so these latter processes occur within the sediment surface, leaving sulfate reduction as the remaining process in deeper parts of the sediments. The sulfide carries much of the free energy not captured by the bacteria in sulfate reduction. As it diffuses to surface layers, most of the sulfide is oxidized by bacteria that grow using it as an energy source. A small amount is used by the photosynthetic sulfur bacteria mentioned above.

Pollution

Marshes, like the estuaries with which they tend to be associated, are depositional areas. They tend to accumulate whatever pollutants are dumped into coastal waters, especially those bound to particles. Much of the pollution load enters the coast transported by rivers and may originate far from the affected marshes. For example, much of the nitrogen and pesticide loading of marshes and coastal waters of the Mississippi Delta region of the United States comes from farming regions hundreds or thousands of kilometers upstream.

Many pollutants, both organic and inorganic, bind to sediments and are retained by salt marshes and mud flats. Organic compounds are often degraded in these biologically active systems, especially since many of them are only metabolized when the microorganisms responsible are actively growing on other, more easily degraded compounds. There are, unfortunately, some organics, the structures of which are protected by constituents such as chlorine, that are highly resistant to microbial attack. Some polychlorinated biphenyls (PCBs) have such structures, with the result that a PCB mixture will gradually lose the degradable compounds while the resistant components will become relatively more concentrated.

Metals are also bound to sediments and so may be removed and retained by marshes and mud flats. Mercury is sequestered in the sediment, while cadmium forms soluble complexes with chloride in sea water and is, at most, temporarily retained.

Since marshes and mud flats tend, in the long term, to be depositional systems, they remove pollutants and bury them as long as the sediments are not remobilized by erosion. Since mud flats are more easily eroded than marsh sediments held in place by plant roots and rhizomes, they are less secure long-term storage sites.

Storm Damage Prevention

While marshes and mud flats exist only in relatively protected situations, they are still subject to storm damage as are the uplands behind them. During storms, the shallow waters and the vegetation on the marshes offer resistance to water flow, making them places where wave forces are dissipated, reducing the water and wave damage to the adjoining upland.

Human Modifications

Direct Effects

Many marshes and mud flats in urban areas have been highly altered or destroyed by filling or by dredging for harbor, channel or marina development. Less intrusive actions can have large impacts. Since salt marshes and mud flats typically lie in indentations along the coast, the openings where tides enter and leave them are often sites of human modification for roads and railroads. Both culverts and bridges restrict flow if they are not large enough. Flow is especially restricted at high water unless the bridge spans the entire marsh opening, a rare situation because it is expensive. The result of restriction is a reduction in the amount of water that floods the marsh. The plants are submerged for a shorter period and to a lesser depth, and the floodwaters do not extend as far onto the marsh surface. The ebb flow is also restricted and the marsh may not drain as efficiently as in the unimpeded case. Poor drainage could freshen the marsh after a heavy rain and runoff. Less commonly, it could increase salinity after an exceptionally prolonged storm-driven high tide.

The result of the disturbance will be a change in the oxygen and salinity relations between roots and sediments. Plants may become oxygen-stressed and drown. Tidal restrictions in moist temperate regions usually result in a freshening of the sediment salinity. This favors species that have not invested in salt control mechanisms of the typical salt marsh plants. A widespread result in North America has been the spread of the common reed, *Phragmites australis,* a brackish-water and freshwater species. Common reed is a tall (3 m) and vigorous plant that can spread horizontally by rhizomes at 10 meters per year. Its robust stem decomposes more slowly than that of the salt marsh cord grass, *Spartina alterniflora* and as a result, it takes over a marsh freshened by tidal restrictions. Since its stems accumulate above ground and rhizomes below ground, it tends to raise the marsh level, fill in the small drainage channels, and reduce the value of the marsh for fish and wildlife. Although *Phragmites australis* is a valuable plant for many purposes (it is the preferred plant for thatching roofs in Europe), its takeover of salt marshes is considered undesirable.

The ultimate modification of tidal flow is restriction by diking. Some temperate marshes have been diked to allow the harvest of salt hay, valued as mulch because it lacks weed seeds. Since some diked marshes are periodically flooded in an attempt to maintain the desired vegetation, they are not completely changed and can be restored. Other marshes, such as those in Holland, have been diked and removed from tidal flow so that the land may be used for upland agriculture. Many marshes and mud flats have been modified to create salt pans for production of sea salt and for aquaculture. The latter is a greater problem in the tropics, where the impact is on mangroves rather than on the salt marshes of more temperate regions.

Indirect Effects

Upland diking The upper borders of coastal marshes were often diked to prevent upland flooding. People built close to the marshes to take advantage of the view. With experience they found that storms could raise the sea level enough to flood upland. The natural response was to construct a barrier to prevent flooding. Roads and railroads along the landward edges of marshes are also barriers that restrict upland flooding. They are built high enough to protect the roadbed from most flooding and usually have only enough drainage to allow rain runoff to pass to the sea. In both cases, the result is a barrier to landward migration of the marsh. As the relative sea level rises, sandy barriers that protect coastal marshes are flooded and, during storms, the sand is washed onto the marsh. As long as the marsh can also move back by occupying the adjacent upland it may be able to persist without loss in area, but if a barrier prevents landward transgression the marsh will be squeezed between the barrier and the rising sea and will eventually disappear. During this process, the drainage structures under the barrier gradually become flow restrictors. The sea will flood the land behind the barrier through the culverts, but these are inevitably too small to permit unrestricted marsh development. When flooding begins, the culverts are typically fitted with tide gates to prevent whatever flooding and marsh development could be accommodated by the capacity of the culverts.

Changes in sediment loading Increases in sediment supplies can allow the marshes to spread as the shallow waters bordering them are filled in. The plant stems further impede water movement and enhance spread of the marsh. This assumes that storms do not carry the additional sediment onto the marsh plain and raise it above normal tidal level, which would damage or destroy rather than extend the marsh.

Reduced sediment supply can destroy a marsh. In a river delta where sediments gradually de-water and consolidate, sinking continually, a continuous supply of new sediment combined with vegetation remains, accumulating as peat, and maintains the marsh level. When sediment supplies are cut off, the peat accumulation may be insufficient to maintain the marsh at sea level. Dams, such as the Aswan Dam on the Nile, can trap sediments. Sediments can be channeled by levées so that they flow into deep water at the mouth of the river rather than spreading over the delta marshes, as is happening in the Mississippi River delta. In the latter case, the coastline of Louisiana is retreating by kilometers a year as a result of the loss of delta marshlands.

Introduction of foreign species Dramatic changes in the marshes and flats of England and Europe occurred after *Spartina alterniflora* was introduced from the east coast of North America and probably hybridized with the native *S. maritima* to produce *S. anglica*. The new species was more tolerant of submergence than the native forms and turned many mud flats into salt marshes. This change reduced populations of mud flat animals, many with commercial value, and reduced the foraging area for shore birds that feed on mud flats. A similar situation has developed in the last decades on the north-west coast of the United States, where introduced *Spartina alterniflora* is invading mud flats and reducing the available area for shellfish.

Marsh restoration Salt marshes and mud flats may be the most readily restored of all wetlands. The source and level of water is known. The vascular plants that will thrive are known and can be planted if a local seed source is not available. Many of the marsh animals have planktonic larvae that can invade the restored marsh on their own. Although many of the properties of a mature salt marsh take time to develop, such as the nutrient-retaining capacity of the sediments, these will develop if the marsh is allowed to survive.

See also

Fish Feeding and Foraging. Fish Larvae. Mangroves. Nitrogen Cycle. Primary Production Processes. Salt Marsh Vegetation. Tides.

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