Harvesting

Most of the farmed salmonids reared in sea water reach the preferred harvest size (3–5 kg) 10 months or more after transfer to sea water. Poor harvesting and handling methods can have a devastating effect on flesh quality, causing gaping in muscle blocks and blood spotting. After a period of starvation to ensure that guts are emptied of feed residues the fish are generally killed by one of two methods. One of these involves immersion in a tank of sea water saturated with carbon dioxide, the other an accurate sharp blow to the cranium. Both methods are followed by excision of the gill arches; the loss of blood is thought to improve flesh quality. It is important that water contaminated with blood is treated to kill any pathogens which might infect live fish.

Ocean Ranching

The anadromous behavior of salmonids and their ability to home to the point of release has been exploited in ocean ranching programs which have been operated successfully with Pacific salmon. Some of these programs are aimed at enhancing wild stocks and others are operated commercially. The low cost of rearing Pacific salmon juveniles, which are released into estuaries within weeks of hatching, makes possible the release of large numbers. In Japan over two billion juveniles are released annually; overall return rates have increased to 2%, 90% of which are chum (*Oncorhynchus keta*) and 8% pink (*Oncorhynchus gorbuscha*) salmon. The success of the operation depends on cooperation between those operating and financing the hatcheries and those harvesting the adult fish. The relatively high cost of producing Atlantic salmon smolts and the lack of control over harvest has restricted ranching operations.

See also

Mariculture Diseases and Health. Ocean Ranching. Open Ocean Convection. Salmon Fisheries: Atlantic; Pacific.

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SALT MARSH VEGETATION

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doi:10.1006/rwos.2001.0088

Introduction

Coastal salt marshes are intertidal features that occur as narrow fringes bordering the upland or as extensive meadows, often several kilometers wide. They occur throughout the world's middle and high latitudes, and in tropical/subtropical areas they are mostly, but not entirely, replaced by mangrove ecosystems. Salt marshes develop along the shallow, protected shores of estuaries, lagoons, and behind barrier spits. Here, low energy intertidal mud and sand flats are colonized by halophytes, plants that are tolerant of saline conditions. The initial colonizers serve to enhance sediment accumulation and over time the marsh expands vertically and spreads horizontally, encroaching the upland or growing seaward. As salt marshes mature they become geomorphically and floristically more complex with establishment of creeks, pools, and distinct patterns or zones of vegetation.

Several interacting factors influence salt marsh vegetation patterns, including frequency and duration of tidal flooding, salinity, substrate, surface elevation, oxygen and nutrient availability, disturbance by wrack deposition, and competition among plant species. Moreover, the ability of individual flowering plant species to adapt to an environment with saline and waterlogged soils plays an important role in defining salt marsh vegetation patterns. Morphological and physiological adaptations that halophytes may possess to manage salt stress include a succulent growth form, salt-excreting glands, mechanisms to reduce water loss, such as few stomates and low surface area, and a C4 photosynthetic pathway to promote high water use efficiency. To deal with anaerobic soil conditions, many salt marsh plants have well-developed aerenchymal tissue that delivers oxygen to below-ground roots.

Salt Marsh Vegetation Patterns

Vegetation patterns often reflect the stage of maturation of a salt marsh. Early in the development, halophytes, such as *Spartina alterniflora* along the east coast of the United States, colonize intertidal flats. These initial colonizers are tolerant of frequent flooding. Once established, the plants spread vegetatively by rhizome growth, the plants trap sediments, and the marsh begins to grow vertically. As noted from A. C. Redfield's classic study of salt marsh development along a coast with a rising sea level, salt marshes often extend seaward over tidal flats, while also accreting vertically and encroaching the upland or freshwater tidal wetlands. With this vertical growth and maturity of the marsh, discrete patterns of vegetation develop: frequently flooded low marsh vegetation borders the seaward portion of the marsh and along creekbanks, while high marsh areas support less flood-tolerant species, such as *Spartina patens*. There is some concern that vertical growth or accretion of salt marshes may not be able to keep pace with accelerated rates of sea level rise, resulting in submergence or drowning of marshes. This has been observed in some areas of the world.

Plant species and patterns of vegetation that dominate the salt marsh vary from region to region of the world and it is beyond the scope of this article to detail this variability; however, the general pattern of low marsh and high marsh remains throughout. There is often variation in vegetation patterns from marshes within a region and even between marshes within a single estuary, but in general, the low marsh is dominated by a limited number of species, often just one. On the Atlantic coast of North America, *Spartina alterniflora* is the early colonizer and almost exclusively dominates the low marsh. In European marshes, *Puccinellia maritima* often dominates the intertidal low marsh. *Spartina anglica*, a hybrid of *Spartina alterniflora* and *Spartina maritima*, has invaded many of the muddier low marsh sites of European marshes over the past century. With increasing elevation of the high marsh, species richness tends to increase. *Spartina patens*, *Distichlis spicata*, *Juncus gerardi*, *Juncus roemerianus*, and short-form *Spartina alterniflora* occupy the US east coast high marsh, with each species dominating in patches or zones to form a mosaic vegetation pattern. In European marshes, the low marsh may give way to a diverse high marsh of *Halimione portulacoides*, *Limonium* sp., *Suaeda maritima*, and *Festuca* sp., among others.

Factors Controlling Vegetation Patterns

The frequency and duration of tidal flooding are mostly responsible for the low and high marsh delineation, but many other factors contribute to the wide variation found in salt marsh vegetation patterns (**Figure 1**). Soil salinity is relatively constant within the low marsh because of frequent tidal flooding, but extremes in soil salinity can occur on the less-flooded high marsh contributing to the vegetation mosaic. Concentrations in excess of 100 parts per thousand can occur, resulting in hypersaline pannes that remain unvegetated or are colonized by only the most salt-tolerant halophytes (e.g., *Salicornia*). Salt marshes of southern temperate and subtropical/tropical latitudes tend to have higher soil salinity because of more intense solar radiation and higher evaporation rates. At the other extreme, soil salinity of the high marsh can be dramatically depressed by rainfall or by discharge of groundwater near the marsh upland border. On salt marshes of the New England coast (USA), *Juncus gerardi* and the shrub, *Iva fructescens*, are less tolerant of salt, and thus, grow at higher elevations where tidal flooding is only occasional or near upland freshwater sources.

For successful growth in environments of high soil salinity, halophytes must be able to maintain a flow of water from the soil into the roots. Osmotic pressure in the roots must be higher than the surrounding soil for water uptake. To maintain this osmotic difference, halophytes have high concentrations of solutes in their tissues (i.e., high osmotic pressure), concentrations greater than the surrounding environment. This osmotic adjustment can be achieved by an accumulation of sodium and chloride ions or organic solutes. To effectively tolerate high internal salt concentrations, many halophytes have a succulent growth form (e.g., *Salicornia*, *Suaeda*). This high tissue water content serves to dilute potentially toxic salt concentrations. Other halophytes, such as *Spartina alterniflora*, have salt glands to actively excrete salt from leaves.

Waterlogged or anaerobic soil conditions also strongly influence the pattern of salt marsh vegetation. Plants growing in waterlogged soils must deal with a lack of oxygen at the rhizosphere and the accumulation of toxins resulting from biogeochemical soil processes (i.e., sulfate reduction). High concentrations of hydrogen sulfide are toxic to root metabolism, inhibiting nitrogen uptake and resulting in decreased plant growth. Many salt marsh plants are able to survive these soil conditions because they have well-developed aerenchyma tissue, or a

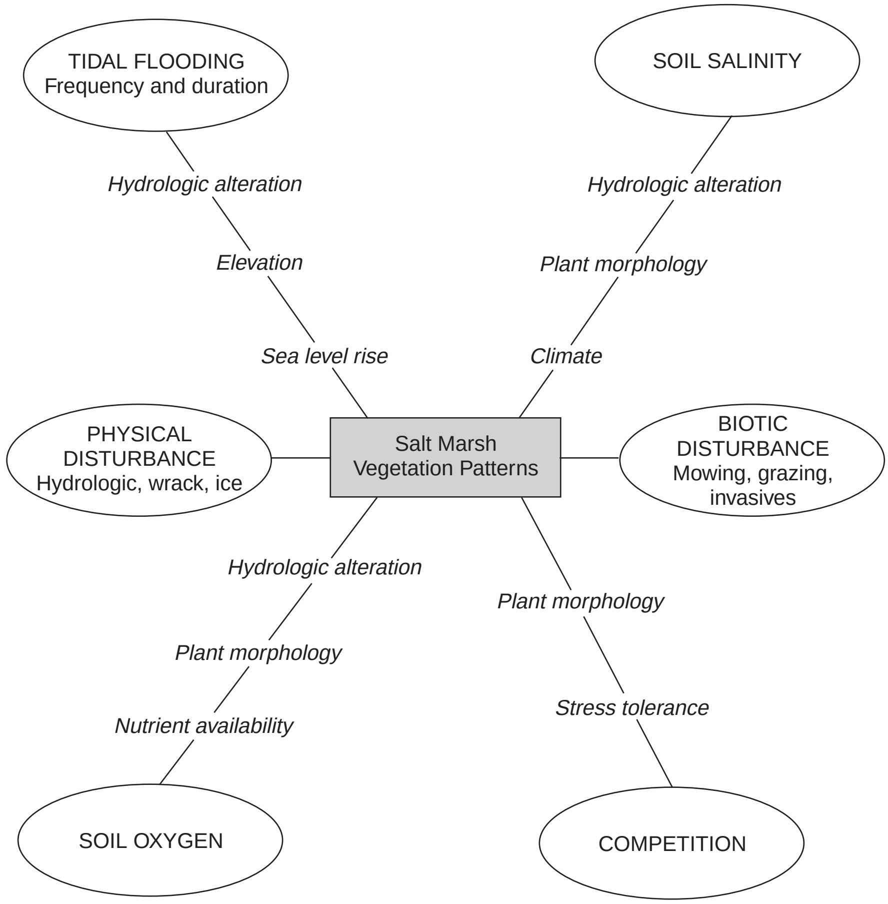

Figure 1 Conceptual model of factors controlling vegetation patterns in salt marshes. Ovals denote major factors and the key interacting parameters are shown in italics. For example, soil salinity responds to hydrologic alterations, climate (e.g., temperature/evaporation and precipitation) influences soil salinity, and a species response to soil salinity is dependent on morphological considerations (e.g., succulence, salt glands, etc.).

network of intercellular spaces that serve to deliver oxygen from above-ground plant parts to below-ground roots. Extensive research has been conducted on the relationships between sediment oxygen levels and growth of *Spartina alterniflora*. Aerenchyma transports oxygen to roots to support aerobic respiration, facilitating nitrogen uptake, and the aerated rhizosphere serves to oxidize reduced soil compounds, such as sulfide, thereby promoting growth. Under severely reducing soil conditions, the aerenchyma may not supply sufficient oxygen for aerobic respiration. *Spartina alterniflora* then has the ability to respire anaerobically, but growth is reduced. It is clear that the degree of soil aeration can dramatically influence salt marsh vegetation patterns. Plants that have the ability to form 1aerenchyma (e.g., *Spartina alterniflora*, *Juncus roemerianus*, *Puccinellia maritima*) or develop anaerobic respiration will be able to tolerate moderately reduced or waterlogged soils, whereas other species will be limited to better-drained areas of the marsh.

Coupled with the physical factors of salinity stress and waterlogging, competition is another process that controls salt marsh vegetation patterns. It has been suggested that competition is an important factor governing the patterning of vegetation near the upland boundaries of the high marsh. Plants that dominate the low marsh, like *Spartina alterniflora*, or forbs in salt pannes (e.g., *Salicornia*), can tolerate harsh environmental conditions and exist with few competitors. However, plant assemblages of the high marsh, and especially near the upland, may occur there because of their exceptional competitive abilities. For example, the high marsh plant, *Spartina patens*, has a dense growth form and is able to out-compete species such as *Distichlis spicata* and *Spartina alterniflora*, each with a diffuse or clumped morphology.

Natural and human-induced disturbances also influence salt marsh vegetation patterns. Vegetation can be killed and bare spots created following deposition of wrack on the marsh surface. The resulting bare areas may then become vegetated by early 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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doi:10.1006/rwos.2001.0087

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