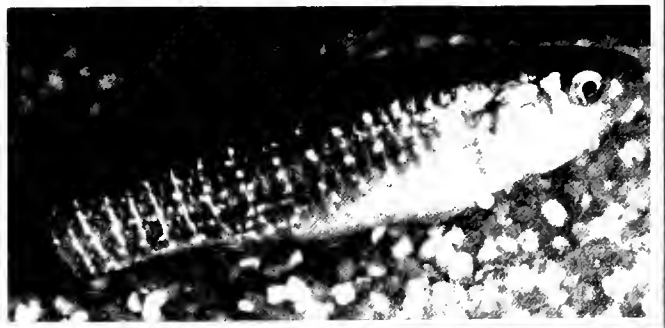


Biological Report 85(7.4)
June 1986



**THE ECOLOGY
OF REGULARLY
FLOODED SALT
MARSHES OF
NEW ENGLAND:**

A COMMUNITY PROFILE



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**THE ECOLOGY OF REGULARLY FLOODED SALT MARSHES
OF NEW ENGLAND: A COMMUNITY PROFILE**

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PREFACE

Salt marshes, especially the muddy, wet, intertidal portions of them that are described in this report, have often been considered wastelands--areas to be filled to make useful land or to be dredged to make useful water. From the scientific point of view, the past few decades of research on salt marshes have provided a much better basis for evaluating marshes than before. From the esthetic point of view, we probably value little that has not been appreciated for the last several hundred years. But esthetics usually do not play a large part in decisions regarding the preservation of salt marshes.

Energy flow in a salt marsh was outlined twenty years ago (Teal 1962) in an effort to put together everything then known about the way the Georgia marsh system functioned. Energy transfer was the descriptive tool. Since everything produced within the marsh was not consumed there, the author concluded that some of it must be exported and, as a result, contribute to the support of consumer organisms in the estuaries. This export, which was called "outwelling," was also proposed by others (see Odum 1980, Nixon 1980, Dow 1982). Teal's data were based on studies of the intertidal parts of the salt marsh and the conclusion did not really extend beyond the tidal creeks within the marsh itself. The notion of salt marsh support of estuarine life was widely accepted and became one of the arguments for salt marsh preservation.

In the past twenty years, a good deal has been learned about the way salt marshes function, but there is still a vigorous controversy about the role of marshes as supporters of production in the waters associated with them. Nixon (1980), in a detailed review of the questions surrounding marsh export in its

various possible forms, pointed out the uncertainty of much of the data and the limit of our understanding of the interactions between marshes and coastal waters. Note his comment on the inadvisability of trading "our credibility for political advantage." It is all too easy for a scientist, believing he has achieved a new way of understanding some natural phenomenon, to promote his idea for some management purpose. This has certainly happened in relation to salt marshes. Both the need for, and the lack of need for, the preservation of marshes have been supported on the basis of incomplete understanding.

There are occasions when it is necessary to act on the basis of less-than-complete information. Scientists should do their best to make the results of their efforts available to those who make decisions. If scientists do not, managers will, as they must, make decisions based on whatever information they have. Unfortunately, those decisions may be based only on politics or outdated knowledge. Scientists should make the best information available. They should remain skeptical about their own conclusions. They should be willing to test their ideas repeatedly when the opportunity arises. They should not go to the most conservative extreme and never be willing to give an opinion about the wisdom of some proposed action. The difficulty lies in distinguishing between the best scientific judgment of what the consequences of an action will be, and one's personal opinion about the consequences of the action based on extrapolation from scientific knowledge.

This report was written to provide a summary of the current state of scientific knowledge about intertidal salt marshes.

It has been restricted principally to New England to concentrate on a specific habitat type. Other intertidal salt marsh regional types are detailed in other reports in this series. This profile draws very heavily on the past 12 years of research at Great Sippewissett Salt Marsh, Falmouth, Massachusetts. Scientists at the Woods Hole Oceanographic Institution, the Boston University Marine Program, and the Marine Biological Laboratory have been studying Great Sippewissett Salt Marsh extensively since 1970; studies of this and other local marshes done prior to 1970 are also included in this Community Profile.

In this profile, the reader is led through a general description of the marsh, into a discussion of the organisms that dwell there and their adaptations to the environment. Special attention is given to the marsh plants, particularly Spartina alterniflora, since much of the way the marsh looks and how it works depend on this plant. The production of both plants and animals is discussed, as well as what controls production rates. Nutrient cycling, decomposition processes,

export from the marsh to coastal waters, and marsh values are all considered.

The author did not try to cover all aspects of the ecology of salt marshes, nor are those considered dealt with in equal detail. There is no exhaustive literature review and no detailed list of marsh species. The interested reader can get a good idea of the birds that make use of the salt marsh by referring to the appendix on birds in the New England tidal flats community profile of this series (Whitlatch 1982). Though one must use appropriate reservations, it is safe to say that most birds that use mudflats also use the marsh open places. Those making more specialized use of marshes, e.g., for nesting, are mentioned in the text.

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CONVERSION TABLE

Metric to U.S. Customary

<u>Multiply</u>	<u>By</u>	<u>To Obtain</u>
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
kilometers (km)	0.6214	miles
square meters (m ²)	10.76	square feet
square kilometers (km ²)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m ³)	35.31	cubic feet
cubic meters	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees	1.8(°C) + 32	Fahrenheit degrees

U.S. Customary to Metric

inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft ²)	0.0929	square meters
acres	0.4047	hectares
square miles (mi ²)	2.590	square kilometers
gallons (gal)	3.785	liters
cubic feet (ft ³)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees	0.5556(°F - 32)	Celsius degrees

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I wish to thank all the collaborators who have worked on salt marshes with me over the 30 years that I have had that pleasure. These include scientists, high school through post-graduate students, marsh landowners, and, occasionally, even developers who were considering filling or dredging but wanted more information about the consequences of their actions before they proceeded. I want to thank my fellow workers from the Sapelo Island Marine Institute of the University of Georgia where I got started with my career in salt marshes: L.R. Pomeroy, E.P. Odum, H.T. Odum, H. Kale, and the late R.J. Reynolds, Jr. More recently, I am in considerable debt to the individuals who have been a part of the Great Sippewissett Salt Marsh project at Woods Hole Oceanographic Institution, Boston University Marine Program, and Marine Biology Laboratory.

My principal partner has been I. Valiela. Too many others have contributed to list them all, but I would like to thank B. Howes, J. Dacey, D. Goehring, A. Giblin, R. Van Etten, C. Cogswell, N. Butler, and C. Werme. I also want to mention Dorothea Gifford, Andrew Diddel, and Salt Pond Sanctuaries, on whose marshlands most of our research on New England salt marshes was done. I am grateful to the reviewers of this effort, especially Ralph Andrews, and to my editor Martha Young for her understanding of my difficulties and long, advice-filled telephone conversations. Rob Brown and Penny Herring at NCET assisted in editing and rewriting the manuscript. Keyboarding of the manuscript was done by Daisy Singleton and Sue Frederickson. Sue Lauritzen designed the layout, and the layout was formatted by Daisy Singleton.



Salt marshes have a beauty all their own, a product of the marsh grasses and the edge of the sea on which they are formed. Above, a marsh in Nova Scotia; below, a portion of Great Sippewissett Salt Marsh, Massachusetts. Photos by J.M. Teal, Woods Hole Oceanographic Institution.

CHAPTER 1. DEFINITION AND DISTRIBUTION

1.1 DEFINITION

The regularly flooded tidal salt marshes of eastern North America are almost exclusively Spartina alterniflora marshes. These marshes are flooded by all tides under normal conditions in areas with semidiurnal tides. They are flooded by seawater or water that is sufficiently salty to inhibit growth of plants such as cattail, Phragmites or reed, or Scirpus species. In New England flooded marshes make up the "low marsh"; in contrast, the "high marsh" comprises infrequently flooded Spartina patens salt hay marshes (Nixon 1982). In Georgia the "high marsh" is covered by a stunted form of S. alterniflora rather than S. patens.

This profile is restricted to the low marshes in New England. I will subsequently refer to these regularly flooded tidal saline marshes dominated by Spartina alterniflora as "salt marshes." Under the Fish and Wildlife Service's Wetland Classification system (Cowardin et al. 1979), these marshes would be classed as in the estuarine system, the intertidal subsystem, and the emergent class.

1.2 GENERAL DESCRIPTION

Regularly flooded tidal salt marshes are readily recognizable all along the east coast even from a distance or from the air. They are flat, grassy areas with meandering tidal creeks running through them (Figure 1). They lie behind some sort of barrier that protects them from the full force of the ocean's waves. Numerous small ponds or pannes occur between the tidal creeks. The occurrence and nature of these ponds have been greatly modified as a result of the numerous, straight ditches dug to control salt marsh mosquitoes. Although many or

most of the ditches lie in the high or infrequently flooded parts of the salt marsh (Nixon 1982), they are also found in the low marsh.

On closer examination, other features of the tidal marsh are readily apparent. The marsh sediments are typically, but not always, muddy and soft, saturated with water, and generally highly reduced (lacking in oxygen or other oxidizing compounds and black in color). They smell of sulfides and other volatile sulfur compounds when disturbed. Although there are undecomposed roots and rhizomes within the mud, low marsh sediments are mostly nonorganic and cannot be classified as peat.

Spartina alterniflora is frequently divided into two forms, tall and short. The tall form occurs along the banks of the tidal creeks and on accreting areas within the marsh. In New England, the tall form generally reaches 1.25 to 2 m in height (Shea et al. 1975). The stems are thick and widely spaced. The short form grows on the remaining marsh. These plants may be as short as 10 cm, have thinner stems, and grow more densely packed. In areas of poorest growth, the plants may be very thin, short, and widely spaced. Although there is a continuous gradation between the tall and short forms, the transition between them is often dramatic in that it takes place within a very short distance. Though this type of salt marsh is almost a natural monoculture of Spartina alterniflora, a few other higher plants such as Salicornia (glassworts) also occur. Algae grow on the sediment surface between the grass stems, often in sufficient abundance to color the surface.

There is an abundance of wildlife common to these marshes. Though

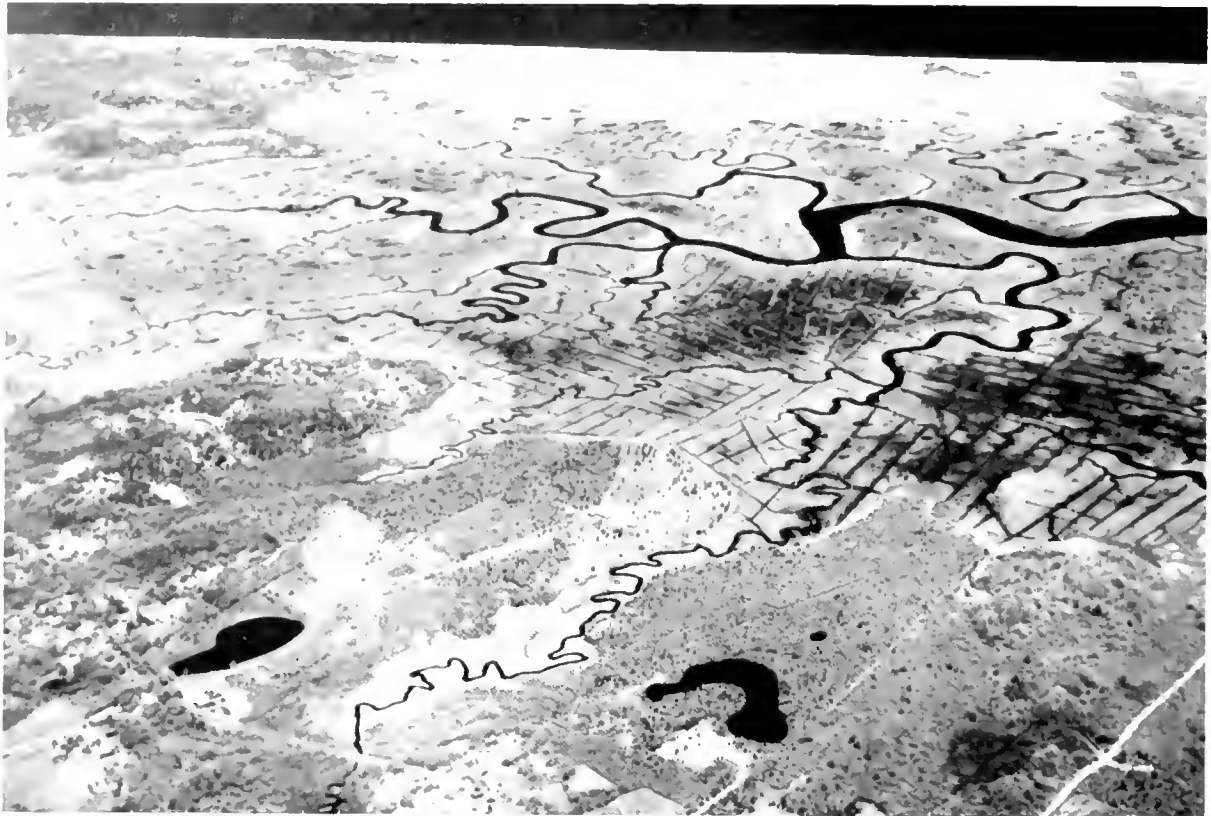


Figure 1. Great Barnstable Marsh, Cape Cod, Massachusetts, with the typical meandering tidal creeks and the barrier beach in the background. Photo by J.M. Teal, Woods Hole Oceanographic Institution.

relatively few kinds of insects occur here, those species present can be very abundant, as illustrated by the annoying mosquitoes and greenhead flies. Snails, crabs, amphipods, mussels, and, at high tide, small fishes are present in large numbers. Wading birds are often conspicuous feeders on the fish and invertebrates; rails, wrens, and other less conspicuous birds are also common. Canada geese may feed on the leaves of *Spartina* and, in winter, snow geese may dig for rhizomes. Small mammals, mink, otters, and raccoons come onto the low marsh to feed on grasses, invertebrates, and small fishes. Raccoons sometimes build nests in the high grass to wait out the high tide.

There are conspicuous seasonal changes in the salt marshes. In the north, winter typically brings a thick ice

cover that is moved by the higher tides. Occasionally, ice frozen firmly to the underlying marsh rips a chunk of marsh up when rising with the tide and leaves it lying on the marsh surface. These ice-rafted chunks interrupt the otherwise dead, frozen, level surface. Though birds may rest on the marsh in winter, in general, there is little activity.

Spring warming comes slowly: the regular inundation by the more slowly warming ocean waters delays the greening of the marsh in relation to the neighboring uplands. The mud surface is first to color as it is warmed by the sun at low tide and algae grow quickly enough to take advantage of the brief warm intervals between tides. When in early summer the marsh turns bright green with grass, the algal color fades, robbed of the necessary light by shading of the

higher plants. The marsh is at its height of activity at this time. The mud surface shows signs of feeding by the swarms of crabs, snails, worms, and insects that make this their home. Swallows feed in the air and harriers sail over the grass looking for meadow mice which eat the succulent bases of the grass.

By late summer the taller Spartina has flowered and set seed. Leaf tips turn yellow first in the short Spartina and gradually the entire marsh turns yellow, then brown. Cooling of the mud is delayed by the water, now warmer than the land. Migrant shorebirds feed on the small invertebrates still active and present in large numbers as bird migration reaches its peak. But cold eventually claims the marsh which enters dormancy again.

To the south, one encounters more and more winter activity. In Georgia, Spartina begins to send up new shoots as soon as the old ones die after flowering, so that although the autumn marsh is golden with dead leaves, a closer look at the bases of the grasses shows the beginning of next year's green. It does not ordinarily get cold enough to kill these shoots, although mild freezes do occur along the Georgia coast.

1.3 GEOGRAPHIC DISTRIBUTION

1.3.1. Worldwide

Spartina alterniflora marshes are found along the east coast of North America from the Gulf of Mexico to the Gulf of St. Lawrence, in Argentina, and in western Europe. Their greatest abundance is along the east coast of the United States. Toward the tropics this type of salt marsh is replaced by mangrove swamps. North of the Gulf of St. Lawrence other species of grasses, principally Puccinellia phryganodes, replace S. alterniflora.

The European S. alterniflora marshes are at Southampton, England and spots along the French and northern Spanish coasts. Most of the Spartina marshes in Europe are occupied by the native S. maritima (southern England to Morocco), or by the new species, S. anglica. Spartina anglica is a fertile polyploid

product of the infertile S. townsendii which, in turn, arose as a natural hybrid of S. maritima and introduced S. alterniflora in the late 19th century near Southampton (Ranwell 1972). Spartina anglica now forms salt marshes from Ireland and Scotland to northwest Spain. This species is still spreading naturally and by human activity, thus creating new marshes both naturally and artificially.

1.3.2. Distribution in Eastern United States

The northernmost salt marshes containing S. alterniflora are found in Newfoundland and along the north shore of the Gulf of St. Lawrence. In these regions, the coastline has had little time since the retreat of the last continental glacier to accumulate sediments in protected areas that could be the basis for the formation of salt marshes. Most of the salt marshes in these areas are little pocket marshes that fill the head of a bay or fringe the edge of a tidal flat. There are, however, a few notable salt marshes east of Yarmouth, and occasionally elsewhere, in Nova Scotia. The marshes in the Bay of Fundy are special exceptions. The several bays at the head of the Bay of Fundy lie in an easily eroded sedimentary basin and have vast salt marshes. Large areas of these were diked and converted into hay fields in the 18th century. Small marshes are the rule for much of the U.S. coast north of Boston, Massachusetts, although the Scarborough marshes in Maine, Hampton marshes in New Hampshire, and Parker River marshes in Massachusetts are extensive.

As one moves south into the regions where the coast is older, salt marshes occupy more and more of the coastline. There are fairly extensive marshes in southern New England and New York although they have suffered considerable destruction over the years. For example, much of the Back Bay region of Boston was originally salt marsh that was filled in the 19th century. Large parts of Kennedy Airport in New York City and Logan Airport in Boston were originally salt marshes that were both dredged and filled to create runways.

Farther south, marshes become more extensive all along the coast and in the large, drowned-valley estuaries (the Delaware and Chesapeake Bays). Many of the marshes along the mid-Atlantic coast are fairly brackish and have Spartina alterniflora only on the creek banks in the saltier regions. The largest of the

South Atlantic coastal marshes are in South Carolina and Georgia, where 68% of the east coast's regularly flooded S. alterniflora marshes occur (Table 1). Spartina alterniflora remains the dominant higher plant until, in Florida, mangrove swamps gradually replace salt marshes.

Table 1. The acreage of Spartina alterniflora marsh in the States of the Atlantic seaboard (Spinner 1969).

State	Marsh area	Percent of total
Maine	1,455	0.16%
New Hampshire	375	0.04%
Massachusetts	7,940	0.86%
Rhode Island	645	0.07%
Connecticut	2,077	0.23%
New York	11,530	1.25%
New Jersey	20,870	2.26%
Delaware	43,756	4.75%
Maryland	15,980	1.73%
Virginia	86,100	9.34%
North Carolina	58,400	6.34%
South Carolina	345,650	37.50%
Georgia	285,650	30.99%
Florida east coast	41,200	4.47%
Totals	921,628	100.00%

CHAPTER 2. PHYSICAL ENVIRONMENT

2.1 PROTECTIVE BARRIERS AND SEDIMENTS

Salt marshes require muddy or sandy sediments in areas which receive tidal flushing, but which are protected from the full force of breaking waves. Although old and compact marsh peat is somewhat resistant to erosion by wave action and is sometimes seen on beaches where old marsh sediments are exposed by sand movements, the formation of a marsh requires a quieter environment for the accumulation of sediment and growth of marsh plants. Small marshes protected by rocky outcrops or headlands can be found in Maine and the Canadian Maritimes. By far, the majority of salt marshes are protected by sand structures, e.g., barrier beaches and islands and spits. Redfield (1972) illustrated vividly how the Great Barnstable Marsh grew through historical time and how sediments and peat accumulated as sea level rose (Figure 2). The barrier beach that protects the marsh grew out from one edge of an indentation in the coast, converting it into a protected bay now filled with marsh. The close connection between barrier formation and marsh existence is further shown by the response of Georgia marshes to changes in their protective barriers over the recent geological past (Pomeroy and Wiegert 1981).

Growth of sandy barriers since the retreat of continental glaciers, coupled with changes in sea level, has created large areas in which marshes have formed over most of the eastern United States. Sea level has been rising between 1 and 3 mm yr⁻¹ over the past few thousand years. (A detailed description of long- and short-term changes in sea level and their causes can be found in Nixon 1982.) The marsh level keeps pace with sea level rise through both the accumulation of sediment and, to a lesser extent, the accumulation

of organic matter. The sediment is transported to the marsh by rivers and coastal circulation which brings marine sediment into estuaries and sheltered embayments. Water movement slows in the protected areas; the flow has less capacity to carry particles which then settle to the bottom. Thus, the basin becomes progressively shallower until it can be colonized by marsh plants. Plant stems further impede flow and concentrate sediment accumulation along the edge of the marsh. This process leads to higher elevations (or levees) along the marsh face and the edges of tidal creeks. Such levees are quite evident in Georgia marshes.

Not only do marshes expand into the estuary or bay as a result of sediment accumulation, but they also extend into the adjacent land as the sea level rises. The central portion of the marsh generally keeps pace with sea-level rise. Thus, the parts of Barnstable Marsh with the deepest peat are some distance from the present landward edge. All of the area between the deepest peats and the present upland represent former land now buried beneath salt marsh. In many cases, a barrier built at the back end of the marsh prevents marsh growth over the upland. A railroad line forms such a barrier in Great Sippewissett Salt Marsh. A similar situation exists for almost every salt marsh in an urban setting. In most of these cases, as sea level rises, the marsh cannot extend over the upland. Since the barrier beach does move inland with the rising water, the marsh, if it has already reached the inland barrier, gets progressively smaller.

In a creek bank in Barnstable Marsh, Redfield found a cavity which held a cache of cobbles. He interpreted this as the remains of a small boat ballasted with small stones that had been abandoned on

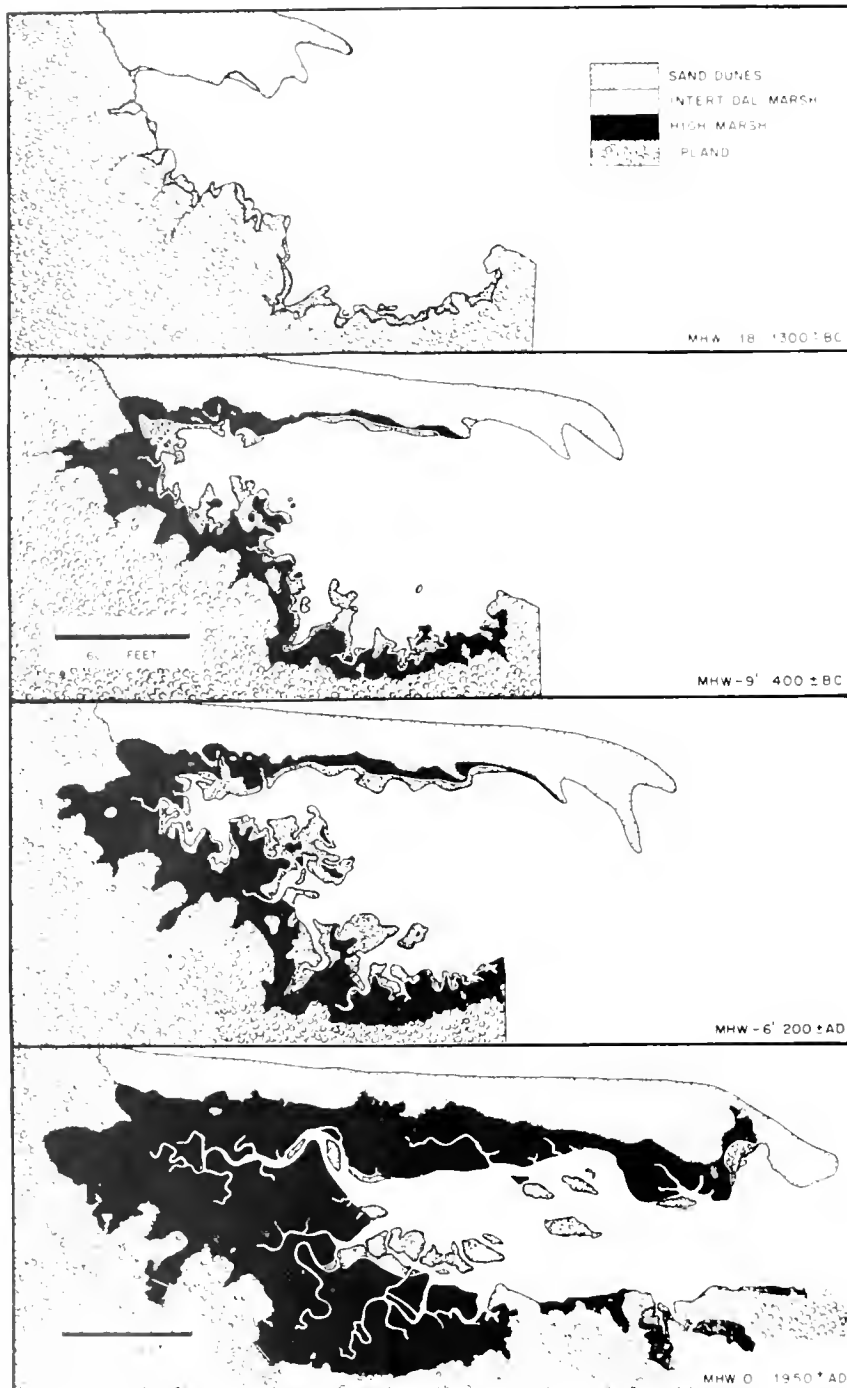


Figure 2. Growth of Great Barnstable Marsh (Redfield 1972). The development of the barrier beach, beginning growth at the edge of the water of intertidal marsh, and eventual succession to high marsh are shown at four time periods since 1300 B.C. MHW indicates mean high water in relation to that in 1950. The marsh has grown both out into the increasingly protected bay, and up to keep pace with the rise in sea level.

the marsh surface in the 17th century. The wood had rotted, the marsh surface had risen about 30 cm keeping up with the change in sea level, but the stones remained in place.

As one would expect from the way marshes grow, coarser sediments are found at the growing edges of the marsh and on the adjacent flats, while finer particles penetrate further into the grasses. This picture varies depending on the particular site and its proximity to the sediment source. In New England, the newly forming parts of the marsh typically have a sand sediment which changes to silty muds further into the marsh. Farther south, where a more abundant sediment supply comes down the rivers, marsh substrates contain less sand and more silts and clays. This general pattern is modified by processes, such as changes in the seaward barrier, that mobilize sand and allow it to be carried into the marsh by flood tides. This results in sandy sediments well within the marsh.

Storms cause masses of sand to be carried over the barrier and onto the marsh, where the sand may be deposited on a large area of marsh surface (called a washover). Wind-blown sand can have a similar result. Niering et al. (1977) found that severe storms of the past few decades could be recognized in Connecticut marsh cores by the sand layers they deposited (Figure 3). The sand layers on the marsh surface were subsequently buried as sea level and the marsh surface rose.

In New England, sand is also carried onto the marsh surface by "ice rafting." Ice rafting occurs when ice forms on a beach or sand flat; a subsequent high tide lifts the ice mass including this layer of sand, and wind and currents carry the mass into the marsh where it becomes stranded. On melting, a layer of sand remains on the marsh surface, raising the local elevation. The mosaic pattern of tiny changes in elevation and vegetation that can form the boundary between high and low marshes is at least partly formed in this manner.

Pieces of low marsh can also be stranded by ice rafting. This can occur when a block of marsh is frozen into the

ice. The tide lifts the ice and marsh block, and carries it up onto some other part of the salt marsh. The result is mounds of *S. alterniflora* sticking above the marsh surface in either high or low marsh. The *Spartina* usually dies and the sediment mound either erodes or becomes a site for the growth of marsh edge plants like *Iva*. It may take several years before the spot returns to its former elevation.

Low spots can also be found in the marsh. These low spots, if they become permanently filled with water, are called pannes. Pannes may result from having marsh growth occur all around a spot on a tidal flat (Redfield 1972). This area is isolated from the sediment supply in the flooding water by the surrounding new marsh. It cannot fill with sediment or drain, so it remains below the local surface level, water-filled all the time. Low spots on the marsh may also be associated with patches of wrack stranded on the marsh. The wrack covers and kills the grass and a low spot may result.

2.2 TIDAL CIRCULATION

Marshes are flooded and drained through characteristic, meandering tidal creeks. In the process of formation, the marshes fill up the basins in which they form and numerous tidal creeks of sufficient size always remain to carry the tidal waters that cover the marshes at the highest tides. This equilibrium condition is modified as the creeks erode the outside back of their bends, while depositing sediments on the inside bank. The positions of the creeks change slightly with time, but the total watercourse area, which is determined by the marsh elevation in relation to sea level, remains approximately the same. Marsh vegetation plays a considerable role in stabilizing the position of the creeks.

Garofalo (1980) found that the bank of a freshwater stream migrated 0.32 m/yr, while a comparable salt marsh stream migrated only two-thirds as much because the peat sediment bound by the fibrous grass roots resisted erosion. Another indication of the erosion protection provided by *Spartina* can be seen in the

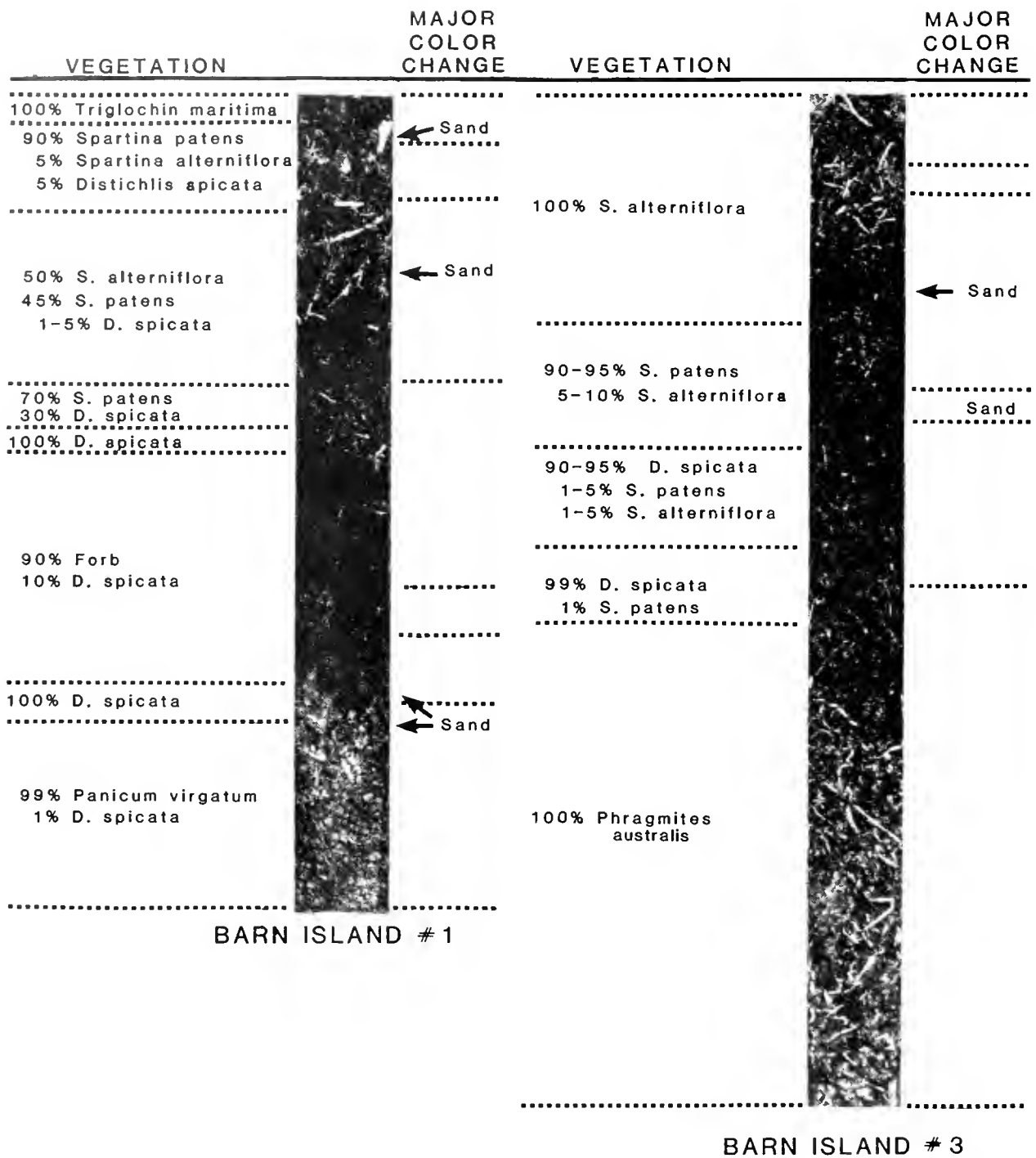


Figure 3. Labelled cores from sediments of Barn Island Marsh, Connecticut (Niering et al. 1977). Core 1 site began with *Panicum* (bottom layer), probably on the edge of the marsh, which was replaced by typical marsh grasses as sea level rose. After the 1938 hurricane, indicated by the uppermost sand layer, the vegetation changed again. The site of core 3 began as a *Phragmites* marsh in brackish water which was replaced by *Spartina* as sea level rose.

experimental oiling of Whittaker Creek salt marsh in Chesapeake Bay (Hershner and Lake 1980). This marsh was closed off by natural spits vegetated with marsh plants. When the *Spartina* was killed on oiled sites, the spits eroded on their exposed sides, although there were no erosional changes in the unoiled sites.

High tide does not necessarily occur at the same time nor reach the same absolute height above sea level in all parts of a given marsh. Water movement into large marshes is slowed by bottom friction so that high water at the extreme inner portions of the marsh may occur hours later than high water at the edge of the marsh and the sea. The tidal range may differ between the mouth and inner parts of a large marsh. A strong wind blowing into a marsh may hold water in, doing away with normal low tide, while the opposite wind can depress the height of high water. The enormous 7-m tides of northern Maine are naturally less modified by wind than the tiny 30-40 cm tides of the south shore of Cape Cod. The latter are often more controlled by wind than gravity. Typically, south of Cape Cod the tidal range is about 1 m while north of the Cape it is about 3 m.

Freshwater may enter a marsh through rivers or streams flowing into the upper portions of the marsh, often through a freshwater marsh. In many marshes, at least in New England, there is also significant freshwater input in the form of groundwater entering from the surrounding uplands. This water enters most readily in sandy parts of the marsh (such as creek bottoms).

2.3 CHEMICAL ENVIRONMENT

The chemical environment of salt marshes is dominated by twice-daily flooding with seawater. The environment is saline, even occasionally hypersaline, so that the higher plants (terrestrial in origin) must have mechanisms for dealing with both the water stress of the high osmotic potential and the abundance of sodium chloride and other major components of seawater. Since percolation of water into salt marsh sediments is slow, the interstitial salinity changes less rapidly

than that of surface water. Therefore, interstitial salinity, the salinity around the plant roots, is often not the same as that of the water flooding the marsh.

Sediment salinity is also changed by evapotranspiration. Water evaporates from leaves and the marsh surface, but the salts stay behind, thereby increasing the soil salinity. Sediment salinity may be reduced by the influence of rain or groundwater.

Tidal waters are the principal source of plant nutrients since seawater contains abundant supplies of calcium, potassium, magnesium, and many other elements essential for plant growth. Nitrogen and phosphorus are exceptions; however, they are the elements which limit plant production in the sea, and we will consider their role in marshes in Section 5.3.

Conditions in the marsh sediments are greatly influenced by the abundance of sulfate in seawater. Under anoxic conditions, there are some bacteria that use sulfate as an electron acceptor, decompose organic matter, and produce sulfide. The resulting sulfide is primarily responsible for the degree of reduction in marsh sediments. Sulfide is highly toxic to most organisms, so those that inhabit marsh sediments must either deal with it or avoid contact with it. Metals, especially iron, are also abundant in marsh sediments, and much of the sulfide produced is bound up as metal sulfides (King 1983; Howarth and Giblin 1983).

Another major factor in the chemical environment of marsh organisms is their exposure to air and sometimes rain during low tide. The higher plants, as far as their leaves are concerned, are terrestrial at low tide. Their leaves are exposed to air and subjected to the same conditions of light, drying, and CO₂ availability as nearby upland grasses. Marsh animals that can breathe air have an abundant oxygen supply. Gases, which diffuse ten thousand times more rapidly in air than in water, are much more available in the very uppermost layer of the sediments at low tide than at high tide. The extent to which water drains from

sediments and is replaced by air at low tide determines how much of the upper layer alternates between aquatic and aerial conditions.

The exposure of the marsh surface to rainfall can rapidly change the salinity both at and below the surface. The freshwater can penetrate furthest in openings such as crab burrows along the edges of the creeks. These changes in oxygen and salinity are some of the principal stresses to which many marsh organisms must adapt.

The hydrology of salt marsh sediments is not well-studied. Hemond and Burke (1981) measured the infiltration of about 1 cm of water into a marsh sediment as the tide flooded, and an exfiltration of about 0.8 cm on the following ebb tide. Hemond (1982) has preliminary measurements of pressure changes in marsh sediments of up to 70 cm H₂O which drive water movement during tidal cycles to an extent determined by peat porosity. Large amounts of water evaporate from plants which are even more important than the tides in controlling water movement through marsh sediments during the growing season (Dacey and Howes 1984). Water movement into marsh sediments controls the supply of dissolved substances (such as plant nutrients and sulfate); water movement out of marsh sediments controls the supply of oxygen to sediment organisms. Both sulfate and oxygen are involved in the decomposition cycle and formation of detritus in salt marshes.

Since marshes in areas of rising sea level are depositional systems, they accumulate both sediments and materials sorbed to sediments. Marshes also serve as collectors for materials that act as sediments in the water. Pieces of plastic and other non-degradable materials discarded into the sea collect in the drift lines or wrack zone on marshes. Pollutants, such as heavy metals and hydrocarbons, that are attached to particles deposited by tidal waters or that fall directly from the air also accumulate on the marsh surface.

Salt marshes, then, are systems subject to both marine and terrestrial conditions in a fairly regular alternating fashion. Marshes are well-watered with seawater; their sediments are anoxic and have an active sulfur cycle.

At Great Sippewissett Salt Marsh in Massachusetts, biologists from Woods Hole have been experimenting with salt marshes since 1970, principally by fertilizing small marsh plots and following the consequences. Figure 4 shows the layout of the experiments and the levels and types of fertilizer used. The rest of this report concentrates heavily upon the extensive Massachusetts data to help elucidate how salt marshes function, though similar or related experiments done at other places are also drawn upon.

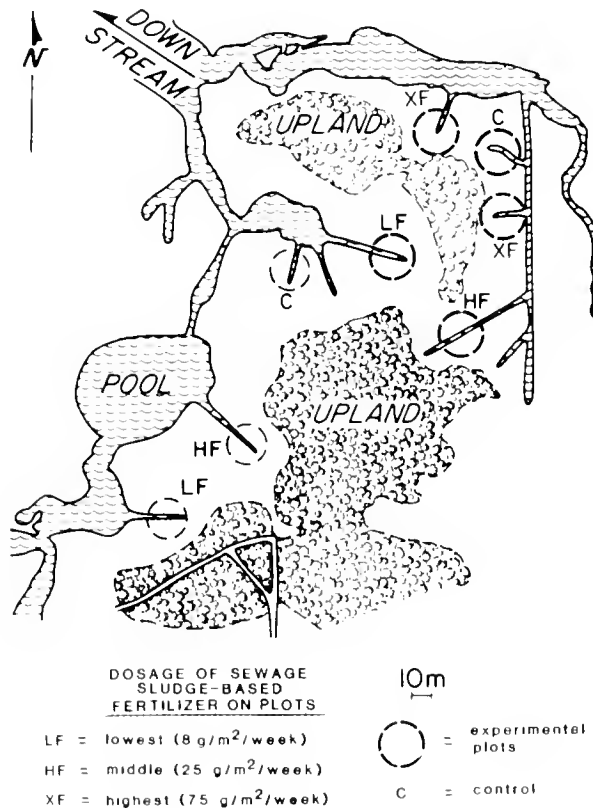


Figure 4. Layout of the experimental plots at Great Sippewissett Salt Marsh (from Valiela et al. 1975).

CHAPTER 3. MARSH FLORAS

3.1 HIGHER PLANTS

The salt marsh we are concerned with here is almost a monoculture of Spartina alterniflora. Since this plant so dominates the appearance and structure of the marsh, we will spend considerable space discussing what is known of its ecology. Any environmental change that affects the abundance and distribution of S. alterniflora will have a corresponding effect on the salt marsh.

The principal features of the plant cover apparent to the observer are the variations in height, density, and color of the sward rather than the presence of other species (Figure 5). A few other species can be found in the low marsh, however. Sea lavender (Limonium nashii) is the most common "other plant" in the New England low marsh. There are occasional glassworts (Salicornia), especially where the marsh has been disturbed. We have also found other plants growing in the regularly flooded intertidal areas: seaside aster (Aster tenuifolius); spike grass (Distichlis spicata); gerardia, a small purple flower called by its generic name (Gerardia (= Agalinis) maritima), that is semiparasitic on marsh grass roots; salt hay (Spartina patens); and sand spurrey (Spergularia marina). But these "non-Spartina alterniflora" plants are much more common on the high marsh than in low marsh. Widgeongrass (Ruppia maritima) occurs in pools and creeks within the low marsh area, but these areas are not really a part of the regularly flooded marsh.

Spartina alterniflora is a rhizomatous, coarse grass that can grow to as much as 3 m in height and has a number of adaptations for life in salt marshes. Like most wetland plants, it has a mechanism for supplying oxygen to its

underground parts. Unlike freshwater wetland plants, it also has a mechanism for dealing with salts and the consequent high osmotic concentration in the solution around its roots. It belongs to a group of tropical grasses characterized by the C-4 photosynthetic pathway. These plants



Figure 5. Spartina alterniflora growing on banks of tidal creeks, Massachusetts. Photo by J.M. Teal, Woods Hole Oceanographic Institution.

have modified the regular photosynthetic pathway (C-3) so that they can be effective at higher temperatures, higher light levels, and lower CO₂ concentrations. Because of these modifications, they are more productive in tropical conditions than the C-3 plants. They also do well in temperate summers. The best known example of a C-4 plant is corn (maize).

3.1.1. Physiological Adaptations

Water/salt balance. Terrestrial and marsh plants must maintain contact with the air, via stomata on their leaves, to obtain CO₂ for photosynthesis. These openings expose moist cell membranes to the air so that plants lose water by evaporation. This water must be replaced from water surrounding the roots. Water loss through the leaves and replacement through the roots is termed "evapotranspiration." In the case of salt marsh plants, the water surrounding the roots is saline, which leads to a problem of maintaining salt, as well as water, balance.

The outermost cells of Spartina plants are waterproof so that water does not enter the plant through leaves but rather is supplied through the root/xylem system. The saline water surrounding the roots has an osmotic pressure of about -25 bars (about -25 atmospheres). Therefore, a pull of about 25 atmospheres is required to pull water through the root membranes against the osmotic pressure of the soil water. This pull is supplied by evaporation at the leaf surface and is transmitted along the columns of water in the xylem system to the roots. Since the water potential in air at even 98% humidity is less than -25 bars, evaporation can easily pull water out of the pore solution, through the plant, and out into the atmosphere.

All the plant cells are in contact with the internal water system and, therefore, must have a lower osmotic potential to maintain plant turgor. Most higher plants simply wilt in seawater: because the osmotic potential is lower in the seawater than in the cells, water moves out of the cells and into the seawater producing a loss of turgor.

Spartina solves this problem by accumulating salts in the cell vacuoles. As a result, the cells can maintain their internal pressure (turgor) against the 25 atmosphere pull generated in the xylem system.

The root membrane preferentially admits water, but small amount of salts also pass into the plant. Although all ions in saltwater are discriminated against, some enter the plant more readily than others. McGovern et al. (1979) found that the ratio of sodium to potassium in the xylem fluid (Na/K = 18.8) is similar to that in seawater (Na/K = 27.7). However, the ratios for sodium to sulfate, calcium, and magnesium are greater in the plant than in seawater (Na/SO₄ = 62 and 4.0; Na/Ca = 410 and 26.5; Na/Mg = 7300 and 8.3 for Spartina and seawater, respectively) (McGovern et al. 1979). The difference between these plant and seawater ratios results from selective uptake of ions by the plant. Similar discrimination among ions has been found in culture studies of Spartina (Smart and Barko 1980). Measurements of the chloride concentration in the xylem sap of Spartina indicate it makes up about 5% of the concentration in the pore water around the roots (Teal, unpubl. data). The fact that chloride is the principal anion in the sap indicates a 20 to 1 discrimination against the sum of the cations in seawater.

Since salts in excess of the plant's need enter the plant, a mechanism must exist to eliminate the surplus. Spartina has salt glands on its leaf surfaces that can secrete a concentrated salt solution. The secretion takes place against a very high gradient. We have found the secreted solution to be about 20 times as concentrated as the solution in the xylem (Teal et al., unpubl. data). In other words, the plant can lose 19 times more water through transpiration than through secretion and still maintain its safe balance. The secretion is 20 times more concentrated than the sap which is 20 times less concentrated than the pore water around the roots. Thus, the secretion is approximately as saline as the pore water. When this concentrated secretion is exposed to the air, it typically dries completely and forms salt crystals that sparkle in the sun (Figure 6).



Figure 6. Salt crystals on a leaf of *Spartina alterniflora* resulting from the drying of solution secreted by the salt glands on the leaves. Photo by J.M. Teal, Woods Hole Oceanographic Institution.

Although *Spartina* can effectively deal with salts at normal seawater concentrations, there is a limit to that tolerance. As salinity increases, the plants exhibit higher respiration rates (Figure 7) and reduced productivity (Figure 8). Above salinities of 40-45 ppt (parts per thousand), the increased respiration and reduced growth become particularly obvious (Woodhouse et al. 1972; Haines and Dunn 1976). Survival at these elevated salinities decreases as length of exposure increases.

Spartina depends on the integrity of its salt barrier to maintain its salt balance. Damage to the salt barrier allows full-strength seawater to enter the plant, disrupting the salt balance and

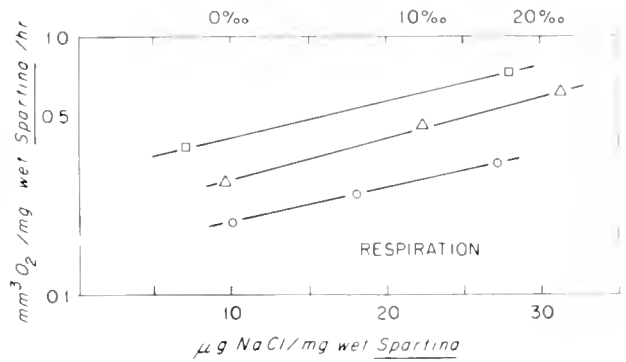


Figure 7. Respiration of *Spartina* leaves grown at different salinities. The data are for leaves of different ages, with the youngest leaves represented by the top line (J.M. Teal, unpubl. data).

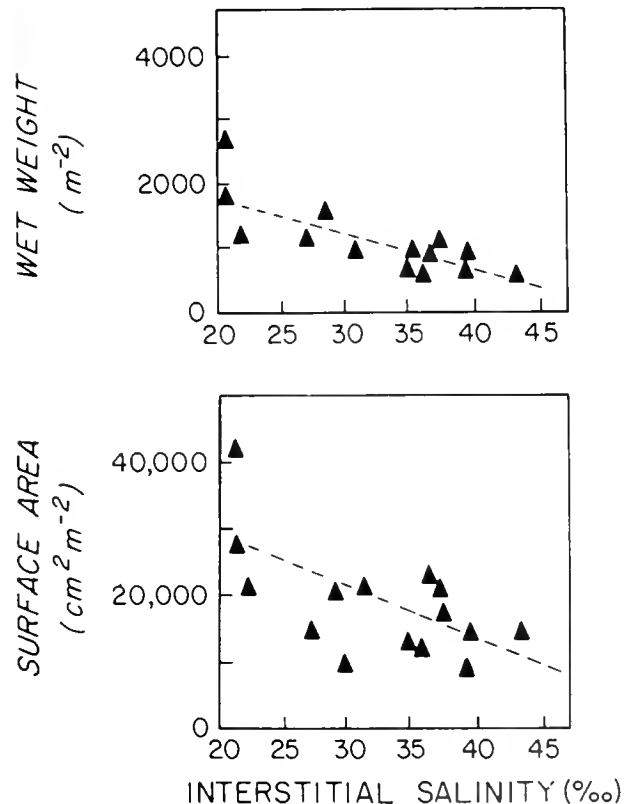


Figure 8. Growth of *Spartina alterniflora* at various salinities as measured by wet weight and by leaf area (Nestler 1977).

killing the cells. Hence, trampling or driving on the marsh, especially when water is present, results in the death of the Spartina stems.

Oxygen supply. Another problem that S. alterniflora has in relation to its habitat is that sediments around its roots are typically anoxic. Its roots, while able to exist without oxygen for short periods, must have oxygen for their respiration for long-term survival. This oxygen passes through air spaces that are continuous with the stomata on the leaves, through aerenchyma (air passages) in leaves and stems, through the hollow central space in the rhizomes, to the central air space in the roots. Air moves by diffusion through these spaces with sufficient ease to supply the demands of the underground parts of the plants. It used to be thought that this flux was sufficient to supply oxygen to the sediment immediately surrounding the roots as well (Teal and Kanwisher 1966). More recent work suggests that while this may be true in drained sediments where the roots are surrounded by gases (e.g., at low tide on creek banks), it is not the case when the roots are surrounded by water in saturated muds. Howes et al. (1981) have suggested that some other oxidant may be coming from the roots. An oxidant of some type is expected because the roots are often surrounded by a layer of oxidized iron, and the soil redox potential around productive Spartina is higher than that around poorly growing Spartina which, in turn, is higher than that in sediments without plant cover.

There is little doubt that the internal gas spaces transmit oxygen to the roots for their own respiration. Gleason and Zieman (1981) showed that the oxygen concentration in the underground plant parts declined during high tide in the dark when oxygen could not be replenished by either diffusion from the air or by photosynthesis. They suggested that this internal oxygen store helps to set the lower limit at which the plants can grow in the intertidal zone. The approximate mid-tide lower limit of S. alterniflora and the inability of S. patens to successfully invade the regularly flooded parts of the salt marsh could be explained in this manner.

In highly reduced, waterlogged soils, the air spaces are not sufficient to maintain oxic metabolism in S. alterniflora roots. This may be a reason for small plant stature in such sites. Mendelssohn et al. (1981) showed that in the more oxidized marsh sediments, Spartina roots function aerobically most of the time. When muds become anoxic, the roots produce malate as the product of their metabolism. Malate is non-toxic and can be accumulated in the roots without damage, but this metabolic pathway produces no net energy for the plant. In highly reduced sediments, the roots develop alcohol dehydrogenase and produce ethanol. Though ethanol is toxic, its production does yield energy for root growth and maintenance but at lower levels than oxygen-supported respiration. The ethanol produced apparently diffuses through the sediments readily enough so that it may not affect the roots. In the most waterlogged conditions where this diffusion is reduced, the ethanol toxicity may contribute to the stunted condition of Spartina.

Oxygen supply to the roots is also intimately connected with the nitrogen and sulfur metabolism of Spartina. It is, therefore, connected with the cycles of these elements in the marsh system and with resistance of Spartina to soil toxins (Mendelssohn et al. 1982). These points will be addressed in Section 5.3.

3.2 SALT MARSH ALGAE

Both macro- and microscopic algae live on the surface of sediments in the salt marsh and are attached to vegetation and other marsh organisms (Figure 9). Ascophyllum nodosum (knotted wrack) and Fucus vesiculosus (rockweed) grow at the lower edge of the S. alterniflora zone and sometimes form fairly dense mats. The macroscopic green algae Enteromorpha (hollow green weeds) and Ulva (sea lettuce) can be abundant, especially early in summer. Codium fragile (green fleece) grows on suitable substrates such as oyster shells. Some of these macroalgae are very abundant at times. In early summer, before much growth of marsh grasses at Great Sippewissett Salt Marsh, Ascophyllum nodosum may appear to have a



Figure 9. Ascophyllum nodosum (knotted wrack) growing at the base of Spartina stems in a creekbank marsh. Photo by J.M. Teal, Woods Hole Oceanographic Institution.

greater biomass than S. alterniflora. No good measure of the production of these species at Great Sippewissett is available. Ascophyllum does disappear rather rapidly in spring, suggesting that, at the very least, it is contributing to the detritus food web on the marsh. There is abundant evidence that the green algae are preferred food items for a number of detrital-algal feeders such as snails (Gieselmann 1981). Ulva and Enteromorpha are also eaten by brant and some ducks.

Microscopic algae--mostly diatoms, and green and blue-green algae (the latter now usually classified as bacteria)--are abundant on the surface of the salt marsh. Algal mats may be the dominant vegetation on recently formed sand flats that will subsequently be invaded by S. alterniflora. These mats are even more abundant at higher elevations than in the

regularly flooded parts of the marsh. According to Blum (1968), the algae found under tall, creekbank Spartina in Massachusetts are mostly diatoms. The shorter grass form supports filamentous types of a variety of algal species: on the mud surface are mostly blue-green bacteria and growing up the lower parts of the grasses are the blue-green Symploca and the chrysophyte Vaucheria. In late winter, early spring (Blum 1968), and early summer, before grass growth shades the mud surface (Van Raalte et al. 1976), there are conspicuous blooms of filamentous greens and blue-greens on the mud surface, even under what will be tall grass. In Georgia, Pomeroy (1959) found mostly pennate diatoms (but also other algae such as green flagellates and dinoflagellates) in low, wet sediments. Blue-greens were found especially in late winter and early spring.

Some of the blue-green bacteria are especially significant to the function of the marsh since the heterocystous, filamentous blue-greens are responsible for nitrogen fixation on the marsh surface. In Massachusetts, where algal mats dominate the marsh surface, Calothrix is the important genus. Under the grass, Stigonema is responsible for most of the nitrogen fixation (Van Raalte et al. 1976).

3.3 BACTERIA AND FUNGI

An abundance of bacteria function in the anoxic muds and play a very important role in the salt marsh. They are responsible for processes varying from photosynthesis to various aspects of decomposition. Fungi are also active in decomposition though their ecology is much less well understood. Because fungi are aerobic organisms, their activities are limited to the surface layers of the marsh.

A number of kinds of bacteria are abundant enough in salt marshes to be visible to the naked eye en masse. For example, the red photosynthetic sulfur bacteria form layers just under the surface where they are protected from oxygen, which poisons them, but where they still get enough light to photosynthesize. Their red pigments are often visible on the surface of sand layers, but they are also present and visible with careful examination in muddy areas. These organisms photosynthesize using H_2S as a source of hydrogen for reducing power. They produce sulfur as a byproduct. (Green plants use H_2O and produce oxygen.) The sulfur oxidizers are often seen as a white layer on the marsh surface. The sulfur granules resulting from the oxidation of H_2S are stored within the cells and enable us to see the microbes.

Beggiatoa is a common genus that derives energy from oxidizing reduced sulfur. Bacteria that reduce sulfate are common in salt marshes and are occasionally noticed because of the smell of the H_2S they produce. These are not visible except for the general black color of the marsh sediments to which they contribute. Bacteria that oxidize sulfide or use it as a hydrogen source depend on

the reducers for their source of raw materials.

Pichia spartinae, a yeast, is reported to be an abundant organism in the microflora of Louisiana salt marshes (Meyers et al. 1975). It is extremely common on the surface of, and in fluid-filled cavities within stems of, Spartina alterniflora. It can survive on Spartina lipids and has an active B-glucosidase system (for hydrolysis of sugars derived from cellulose). It probably makes important contributions to marsh decomposition processes once the cellulose has been initially attacked (a process in which other fungi are active).

Pichia spartinae and another yeast (Kluyveromyces drosophilorum) made up over 70% of salt marsh yeasts found by Meyers et al. (1973) in undisturbed Louisiana marshes. Pichia ohmeri became one of the most abundant yeasts in a Louisiana salt marsh as the result of controlled additions of oil (Meyers et al. 1973).

Species of the yeast Candida are significant contributors to oil degradation in east coast salt marshes. Claviceps purpurea, the ergot fungus, infects Spartina seeds throughout the Atlantic and gulf coasts (Eleuterius and Meyers 1974). Ergot, which is responsible for poisoning of rye flour, is widely distributed in salt marshes, but may be of little ecological significance there. Though marsh fungi are important in the formation of detritus from Spartina (J. Hobbie, Marine Biological Laboratory, unpubl. data), they need more study.

In this report, most of the important microbes in the marsh system are identified by their functions. To a considerable extent this has been done even by microbiologists in the past. It is now known that even some of the apparently compact groups are really microbes of widely differing ancestry. Some of these groups are responsible for denitrification, nitrification, nitrogen fixation, and methane production. The largest functional group, "decomposers," is even less unified for it includes most non-photosynthetic and chemosynthetic microbes.

CHAPTER 4. MARSH FAUNAS

4.1 ORGANISMS OF TERRESTRIAL ORIGIN

4.1.1. Insects and Spiders

Although there are many kinds of insects on salt marshes, they are mostly confined to the higher elevations. Those significant to the ecology of the regularly flooded portions include those that feed on Spartina alterniflora, some that are associated with detritus, and some that are predators. No group is represented by a large number of species.

Vince (1979) divided the insect herbivores in Great Sippewissett Salt Marsh into chewers and sap-suckers. The dominant chewer is the long-horned grasshopper, Conocephalus spartinae, but thrips (Anaphothrips sp.) and crickets are also present. Sucking insects are much more abundant and include plant bugs (Miridae, Trigonotylus sp.), plant hoppers (Delphacidae, Prokelisia marginata, and Cicadellidae, Graminella nigrifrons), aphids, and scale insects. The latter two types of insects are patchily distributed: rare on another leaf of the same plant and absent a few meters away. They may be locally abundant enough to kill blades of grass. Patches of scale insects may occur 30 cm below the level of barnacles growing on Spartina, which indicates they are well adapted to immersion in saltwater (Tippins and Beshear 1971). Prokelisia marginata is the numerically dominant herbivorous insect (by orders of magnitude). It also has 10 times more biomass/m² than any other species.

In fertilized experimental plots in the Cape Cod marshes, the herbivorous insects have become more equitably distributed (smaller differences in numbers of individuals between the different species) than prior to fertilization. There were relatively

greater increases in the initially less abundant species, i.e., mirids, cicadellids, and grasshoppers. The fertilization increased the nitrogen in the grass, making it a more suitable substrate. This, in turn, led to increased fecundity and survival in the insects. Migration into the experimental area was of secondary importance (Vince 1979). Presumably, this equal abundance and distribution occur naturally in productive creekbank stands of S. alterniflora. Vince (1979) believes that the non-creekbank marsh is barely adequate for the maintenance of some of the rarer herbivorous insects. Stiling et al. (1982) have found that leaf-miners in Florida are nitrogen-limited as are the herbivorous insects mentioned above.

Some insects live within, rather than upon, the Spartina stems. These are usually larvae rather than adults. For example, larvae of otitid flies (genus Chaetopsis) live within Spartina stems where they eat and kill the terminal bud, thereby causing the death of the shoot. The ecology of such insects is poorly known in New England. Studies in Florida indicate that the otitid larvae reduce competition in their limited environment by stabbing and killing other larvae they encounter (Stiling and Strong 1983). Though the dead larva represents a valuable source of protein, the body is not eaten; i.e., they are murderers rather than predators.

Other insects found in the low marsh include chloropids, dolichopodids, and ephydriids. These are all flies that feed on a variety of plant secretions, algae, and detritus both as adults and as larvae. Biting midges and horse flies (such as the infamous "green head") live in the mud as larvae; as adults, the females attack

people and large animals to obtain the blood meal they need to mature their eggs.

The marsh mosquito, Aedes sollicitans, lays its eggs on wet mud in the higher marsh rather than in the low marsh. The eggs develop to the hatching point, then wait until they are flooded by an extra high tide or heavy rain before hatching. In warm weather they can become adults in about one week, emerging from the pools in hordes. Were the eggs laid in the low marsh, the eggs (or larvae) would be rapidly eaten by the predators that come in on the high tide. Even though the low marsh is not involved in mosquito reproduction, it has been heavily ditched for "mosquito control." The marsh often suffers heavily from damage during ditching and from careless disposal of the spoils from the ditches. The effects on the mosquitoes are minimal.

Insects are preadapted to survival in the marsh. Their impermeable exoskeleton evolved to prevent drying on land, and also prevents water loss to seawater or entry of salts into the body. Their excretion of waste nitrogen as water-saving uric acid reduces their need for water, so many can survive on plant juices or the body fluids of prey. Some avoid submersion by walking up the grass or flying at high tide, but others can sit it out and survive underwater.

Predators on insects include some parasitic wasps and, more important, a variety of spiders from web spinners to wolf and jumping spiders. In some of the experiments at Great Sippewissett Salt Marsh, the plant hoppers did not increase proportionately to other herbivores because of intense spider predation. Apparently, most of the predation was by the tiny, web-spinning Grammonota inornata and Dictyna roscida, neither of which is more than 2 mm in length (Vince 1979). The former species, which is the most abundant spider in Massachusetts marshes, builds a sheet web close to the ground as a very effective means of trapping plant hoppers.

The larger insect herbivores (such as plant bugs) in New England salt marshes are eaten mainly by the large wolf spider, Pardosa distincta. Pardosa actively hunt

prey both visually and tactilely instead of building a web. Pardosa prey upon marsh amphipods about their own size, which they flip over and bite on their less-protected underside.

Another spider, Clubiona maritima, also hunts, but moves much more slowly and detects its prey by touch. Though spiders sometimes climb Spartina as the tide rises, they can survive underwater. Their greatest need at high tide is a refuge from predators.

4.1.2. Reptiles

Reptiles, such as sea turtles and marine crocodiles, can be fully adapted to seawater. Although the author has seen alligators, rattlesnakes, and water snakes in salt marshes of the southeastern U.S., the only reptile seen in any great numbers in New England salt marshes is the diamond-backed terrapin (Malaclemys terrapin). The terrapin, common in unpolluted waters all along the Atlantic coast south of Cape Cod, is not a "sea turtle" but is more closely related to the terrestrial box turtles. It feeds on a variety of small animals including fish, mollusks, and crustaceans abundant in the marsh creeks. The terrapin does not live on the low marsh but feeds there during low tide. Terrapins used to be much more abundant than at present, but their population was reduced by coastal development and by hunting during the height of their popularity as a food item.

4.1.3. Birds and Mammals

One of the most widely recognized values of salt marshes is their support of both migrant and resident bird populations. Very few bird species actually nest in regularly flooded marshes. Those that do include clapper rails (Rallus longirostris) (Figure 10), willets (Catoptrophorus semipalmatus), long-billed marsh wrens (Cistothorus palustris), boat-tailed grackles (Quiscalus major), red-winged blackbirds (Agelaius phoeniceus), and sharptailed and seaside sparrows (Ammospiza caudacuta and A. maritima).

The number of species that nest in drier areas but feed on the low marsh or



Figure 10. Clapper rail (Rallus longirostris) standing on the high marsh area at Great Sippewissett Salt Marsh, Massachusetts. Clapper rails feed on animals of the intertidal salt marsh and may also nest in its upper edges. Photo by J.M. Teal, Woods Hole Oceanographic Institution.

make seasonal use of it is much larger. Dabbling ducks of various kinds sieve seeds and small animals from the sediments. In winter, black ducks (Anas rubripes) feed extensively on the salt marsh, especially at high tide when they pluck the snail Melampus from the grass. Snow geese (Chen caerulescens) eat roots and rhizomes of the grass (Figure 11); Canada geese (Branta canadensis) graze on Spartina (Figure 12). Many kinds of shorebirds probe for invertebrates (insect larvae, mollusks, crustacea, and worms) in the more open areas. Herons, egrets, bitterns, and ibis stalk fishes and crustaceans along the creeks and in the ponds while ospreys, kingfishers, and

various terns dive from the air above. Though most of the feeding activity is in the creeks adjacent to the grassy parts of the marsh, it is nevertheless connected to the functioning of the marsh.

Exceptionally high tides in autumn occasionally force insects to the tops of the Spartina, and many kinds of birds, from sparrows and warblers to terns and gulls, come to feed on this bonanza of exposed insects. Swallows capture flying insects in the air above the marsh much as they do over upland meadows. Birds are like insects, adapted to marsh living by their water-saving uric acid excretion and by orbital glands which secrete excess salt from their blood.

Mammals constitute a smaller and generally less conspicuous part of the marsh fauna. The most abundant marsh mammal in New England is the meadow mouse or vole, Microtus pennsylvanicus. In the high marsh, where meadow mouse runs are obvious beneath the grass, the mouse is a more conspicuous resident. Although the meadow mouse's feeding is restricted to low tide in the low marsh, the large fraction of plants damaged by the mice indicates that the Microtus is a significant part of the marsh system. The damage to the sward by the meadow mouse is far greater than the actual consumption of Spartina. Microtus cuts off the base of a plant and eats a small portion of the tender basal part; the rest of the stem is left to wither and die. Under natural conditions on Great Sippewissett Salt Marsh, about 7% of the short S. alterniflora plants show signs of insect damage whereas about 2.5% show damage by mice. In the fertilized plots where Spartina productivity is enhanced, the insect damage drops to about 5%, but 20%-30% of the plants are damaged by mice (Vince 1979; Valiela and Teal, unpubl. data). Thus, under these conditions, Microtus can have a significant effect on Spartina production.

White-footed mice (Peromyscus leucopus), which are primarily seed eaters, occasionally come down into the low marsh. In the marshes of the southern United States, the rice rat, Oryzomys palustris, is a permanent resident in tall Spartina areas. Small mammals such as



Figure 11. Snow geese concentrated on a salt marsh. Photo by Rex Schmidt; courtesy U.S. Fish and Wildlife Service.

these attract predatory birds and mammals: harriers (Circus cyaneus), short-eared owls (Asio flammeus), rough-legged hawks (Buteo lagopus), weasels (Mustela sp.), raccoons (Procyon lotor), minks (Mustela vison), otters (Lutra canadensis), and, more rarely, foxes (Vulpes fulva). Some larger mammals occasionally feed in the salt marsh vegetation also: rabbits (Sylvilagus floridanus and S. transitionalis), and white-tailed deer (Odocoileus virginianus) feed on the vegetation. Muskrats (Ondatra zibethica) feed on the low marsh but prefer less salty marshes with small tides. Where they are abundant, mammals can be an important part of the marsh. However, they are not a conspicuous part, since they are generally nocturnal and are seldom noticed.

Mammals of the marsh avoid getting wet for the most part. Some, like mice, are adapted to the high salinity environment of the salt marsh. Because mice can concentrate and expel salt in

their urine, their need for freshwater to wash out salt acquired in their diet is reduced.

4.2 ORGANISMS WITH MARINE ORIGINS

4.2.1. Invertebrates

Most of the low marsh fauna are invertebrates. The larger ones have been fairly well-studied, the smaller much less so.

Meiofauna. Benthic meiofaunal animals are defined operationally by their ability to pass through a 0.5- or 0.3-mm mesh. They include such groups as nematodes, foraminiferans, harpacticoid copepods, soil mites, and oligochaetes. Many of these organisms are abundant in marsh sediments. For example, Teal and Wieser (1966) found nematodes numbering $10^7/m^2$ and weighing 7.6 g in Georgia marsh soils. Similar numbers of nematodes have been found in marsh soils of South



Figure 12. Canada geese (*Branta canadensis*) landing on a marsh. This species eats leaves of *Spartina alterniflora*, especially those in the more productive parts of the marsh. In New England, Canada geese may nest on salt marshes and, therefore, concentrate their feeding on marshes during the nesting season. Photo by Rex Schmidt; courtesy U.S. Fish and Wildlife Service.

Carolina (Sikora et al. 1977) and Great Sippewissett (K. Foreman, Boston University Marine Program, Woods Hole, Mass., pers. comm.). The numbers of soil foraminiferans are comparable to those of nematodes, but the other groups are generally less abundant.

Water flooding the marsh at high tide contains many planktonic forms. Many of these come from the coastal waters and/or estuaries associated with the marshes. In addition, some of the planktonic animals come from the marsh itself. These are primarily eggs and larvae of marsh inhabitants. Adult benthic meiofauna may also be dislodged and suspended in the flooding water. All forms of plankton are food for filter feeders on the marsh or for plankton-feeding fish which advance into the marsh on the flooding tide. Plankton leaving on the ebb tide are a food source for filter feeders in channels, on mudflats, and in the estuary proper.

Macrofauna. The typical marsh invertebrates--the best studied and probably the most important to the functioning of the intertidal marsh--are the macrofauna. Their definition is complementary to that of the meiofauna: they are retained on a 0.5-mm sieve. The epibenthic fauna (those living above the bottom) are the most familiar even though the infauna (those living within the mud) are usually more abundant.

Two species of fiddler crabs, *Uca pugilator* and *U. pugnax* (Figure 13), are abundant south of Cape Cod, where there can be 120 individuals/m² along the creek banks (Krebs and Valiela 1977). Mud crabs (*Panopeus* sp.), marsh crabs (*Sesarma reticulatum*), and green crabs (*Carcinus maenas*) make very conspicuous holes at the edges of marsh creeks. Blue crabs (*Callinectes sapidus*), where abundant, are important predators on other marsh animals. They occur as

far north as Massachusetts Bay though they are usually seen only south of Cape Cod.

Littorina littorea, the common periwinkle, is a common marsh resident in New England, but in Maryland marshes it is replaced by L. irrorata (gulf periwinkle). Littorina obtusata occurs near the lower edge of the marsh among the rockweeds with which it is commonly associated. Melampus bidentatus (salt marsh snail) is a pulmonate snail on the marsh. All these snails feed by scraping off the surface layer of algae and detritus from the surface of the mud and from the lower parts of the grass. The tiny snail Hydrobia totteni, which feeds by digesting organic matter and microbes from ingested sediment (Newell 1965), may be very abundant. Mud snails (Ilyanassa obsoletus) are more typical of intertidal mudflats, but they do occur in the marshes as well, where they feed mostly on benthic algae (Connor 1980).

Ribbed mussels, Geukensia (=Modiolus) demissa, often live in clusters throughout the marsh and serve as hard substrate for other organisms such as barnacles and



Figure 13. Male fiddler crab (Uca pugnax) on salt marsh. This crab has been cornered by the plastic pipe. The male's large claw is used for defending its territory and signaling females. The small claw is used in feeding. Photo by J.M. Teal, Woods Hole Oceanographic Institution.

hydroids. Barnacles may also sometimes be found on the bases of Spartina growing at the lowest elevations. Amphipods and isopods are common on the mud surface between the grass stems and are especially abundant under any accumulations of wrack. Several kinds of small shrimps, including the sand shrimp (Crangon septemspinus) and the grass shrimp (Palaemonetes pugio), are often very abundant. They can be seen drifting up even the smallest marsh creeks as the tide rises.

Although the above organisms are all epifauna, many more organisms are found among the infauna in this same environment. The marsh infauna includes a variety of polychaetes, oligochaetes, insects (especially as larvae), and crustaceans, but little is known about most of these. As one moves south of New England, other species join or replace the marsh fauna. Among these are the marsh clam (Polymesoda caroliniana), the wharf crab (Sesarma cinereum), the brown shrimp (Penaeus aztecus), and the white shrimp (P. setiferus), all of which use the shallow waters of the marshes and estuaries. Other species, such as the blue crab, become more abundant south of New England; the blue crab can support an intense fishery in the marsh creeks along the southern Atlantic coast.

Macrobenthic organisms play a number of important roles in the functioning of the salt marsh. They churn up the surface layers of the sediment in their search for food and in their burrowing. Katz (1980) found that the burrowing of Uca pugnax at a density of 42 animals/m² turned over 18% of the upper 15 cm of sediment per year. Their burrows increased the surface area of the marsh by 59%. Cammen et al. (1980) showed that the epifaunal fiddler crabs and marsh periwinkles in a North Carolina marsh consumed an amount of organic matter equivalent to about one-third of the net production of S. alterniflora and benthic algae.

The infauna may have an even more significant impact on the marsh than do the epifauna. A population of the polychaete worm Nereis succinea "ingested four times as much sediment and detritus" as the fiddler crabs and snails (Cammen 1979). All these animals grind up the

detritus and inoculate it with microbes in the course of feeding (Welsh 1975). Cammen et al. (1980) found that the epifauna assimilated (i.e., used for their own life processes) only about one-tenth of what they consumed. Thus, nine-tenths passed through their bodies as feces, ground and inoculated with microbes in the process. The macrofauna are important consumers of algae, detritus, and meiofauna on the surface of the mud; they, in turn, are fed upon by fish and birds, thereby linking them to the productivity of the salt marsh.

4.2.2. Fishes

Salt marsh fishes are among the most highly valued animals of the marsh because of their commercial and recreational importance. The fishes of the salt marsh can be divided into the relatively permanent residents and those that spend only their early life stages there (Table 2). Werme (1981) provided an excellent description of the marsh fishes of the Great Sippewissett Salt Marsh, and the bulk of the following comes from that work.

The silverside is a small, schooling fish that is resident in inshore waters throughout its life. The species is present in Cape Cod marshes from spring through summer and reaches its maximum abundance in August. Silversides generally live only 1 year. The relatively few that survive the winter by retreating to deeper water return in spring to spawn and produce the next generation. Nevertheless, silversides are the most abundant fish in the marshes by midsummer. Silversides occur mostly in midwater in the marsh creeks, though as much as 30% of the population may be found in the *Spartina* on the creek banks at high tide (Werme 1981) (Figure 14). The omnivorous silversides feed mostly on planktonic animals, but algae and detritus have also been found in their guts after they have been on the marsh surface. Horseshoe crab eggs and small amphipods from the marsh may be their major food items in summer; mysid shrimp and copepods are important foods in autumn.

The mummichog (Figure 15), which can live for several years, is the fish most

Table 2. Fishes inhabiting Great Sippewissett Salt Marsh, Massachusetts (from Werme 1981). They are listed in approximate order of abundance within each group.

Common name/ Scientific name
Fishes that spend most of their lives within the marsh:
Atlantic silverside <u>Menidia menidia</u>
mummichog <u>Fundulus heteroclitus</u>
striped killifish <u>Fundulus majalis</u>
sheepshead minnow <u>Cyprinodon variegatus</u>
four-spined stickleback <u>Apeltes quadracus</u>
three-spined stickleback <u>Gasterosteus aculeatus</u>
common eel <u>Anguilla rostrata</u>
Fishes that use the marsh mostly as a nursery area:
winter flounder <u>Pseudopleuronectes americanus</u>
tautog <u>Tautoga onitis</u>
sea bass <u>Centropristes striata</u>
alewife <u>Alosa pseudoharengus</u>
menhaden <u>Brevoortia tyrannus</u>
bluefish <u>Pomatomus saltatrix</u>
mullet <u>Mugil cephalus</u>
sand lance <u>Ammodytes americanus</u>
striped bass <u>Morone saxatilis</u>

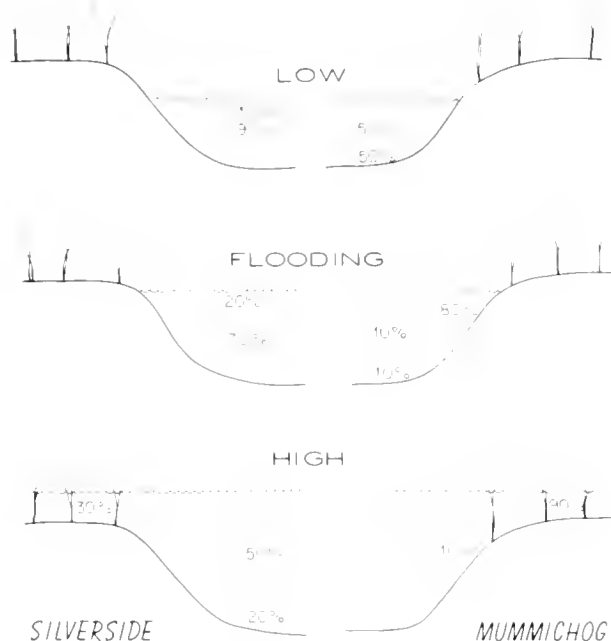


Figure 14. Vertical distribution (near surface, midwater, and near bottom) of two most abundant marsh fishes at different tide stages (from Werme 1981). Silversides (*Menidia menidia*) are mostly plankton eaters and tend to remain in the open water. Mummichogs (*Fundulus heteroclitus*) hug the bottom and go up into the grass to feed at high tide.



Figure 15. Mummichog (*Fundulus heteroclitus*) is the typical marsh minnow in the New England salt marshes. Mummichogs feed among the bases of *Spartina* stems and live in the marsh throughout the year, although they bury themselves in the mud in the coldest weather.

intimately associated with the grassy parts of the regularly flooded marsh. It is probably best known of all the marsh minnows. At low tides, mummichogs lie near the bottoms of creeks, but return toward the grass with flood tides. At high tide, they are found almost entirely within the *Spartina* (Figure 14). Although mummichogs feed on all sorts of plant material (including algae and detritus), they lack the digestive system required to derive much nutrient value from it (Prinslow et al. 1974). Animals compose a large part of the mummichog diet early in the year; algae constitute the major portion later in the year when animal populations have declined. Over 50% of the diet of 1- to 3-cm long mummichogs is meiofauna (Werme 1981); mummichog young form an important link between the meiofauna they consume and the other fish which consume them.

Mummichogs spawn beside grass stems and macroalgal clumps at spring tides. The eggs fall into and are hidden in crevices which prevents their being eaten (often by their parents). The eggs attach to plants or other objects by means of adhesive threads. The fry, as well as the adults, are resistant to stresses such as high temperatures or low oxygen levels. Mummichog fry are the minute fish often seen in pools on the marsh surface at low tides. Mummichogs survive winter at the bottoms of the marsh creeks, often in the uppermost, brackish parts of the marsh system, or they may lie semidormant in the muddy bottoms of marsh pools.

The striped killifish, the other *Fundulus* species of New England marshes, is more likely to spend winter in the deeper waters of marsh creeks and associated bays on more sandy bottoms than the mummichog uses. The striped killifish is omnivorous: it consumes more animals, including horseshoe crab eggs, than does the mummichog. It has a longer snout than the mummichog, which enables it to dig deeper into the mud for prey. As a result, killifish guts contain more *Gemma gemma* and *Hydrobia* than do mummichog guts. Although they go into the grass at high tide, they take a smaller proportion of their food from the grassy parts of the marsh than does the mummichog. The sand in their guts indicates that they obtain

the majority of their food from areas other than the marsh. Perhaps the grass is of greater relative value for the killifish as a refuge from predation rather than as a food resource. Both Fundulus species take less than 10% of their food from the zooplankton.

The sheepshead minnow also occurs in New England salt marshes, though less regularly than the related Fundulus species. Its longer gut is characteristic of feeders on vegetable materials and is typically full of algae and detritus. Thus, the sheepshead minnow is apparently more herbivorous than its relatives (Werme 1981).

Of the marsh sticklebacks, the three-spined (Gasterosteus aculeatus) is present in New England marshes only in early spring during its breeding activities. While there, it feeds principally on zooplankton during daytime high tides. The three-spined stickleback is a typical nest builder. The male builds a barrel-shaped nest out of grass and other bits of vegetation glued together with a secretion from his kidneys. He attracts females to spawn within the nest, fertilizes the eggs, and then fiercely guards the nest area. Just before hatching occurs, he tears the top off the nest to aid the fry's escape and continues to guard them until they can care for themselves. The four-spined stickleback (Apeltes quadracus) is a permanent resident of the salt marsh. It also feeds mostly during daylight. This species feeds on meiofauna in the marsh shallows to which it has access only at high tides. The nine-spined stickleback (Pungitius pungitius) is a more northern species than the other two and is common in salt marshes north of Cape Cod.

Common eels (Anguilla rostrata) live in the marshes only after they arrive as elvers from the sea. Adult eels spawn in the center of the Sargasso Sea at some unknown depth. For about a year after hatching, the young drift with the currents as transparent, leaf-shaped larvae (leptocephali) until they near the shore. They then become cylindrical in shape (elvers) and enter the coastal areas. Eels may merely pass through the salt marshes as they move through the area

into freshwater as elvers or out of freshwater as adults. However, they may also spend their entire lives in salt marshes where they are found mainly in the muddy marsh creeks. Werme (1981) found that the eels in her samples had fed mostly upon benthic invertebrates. Eels eat fish readily as can be seen by putting minnow traps into the marsh creeks overnight: mummichogs enter the traps and serve as bait for the eels that enter at night; by morning, the mummichogs have been eaten and the eels remain in the traps.

The more common fishes that use Great Sippewissett Salt Marsh as a nursery are listed in Table 2. These are the commercially and recreationally significant fishes found in the New England salt marshes. Not as abundant as the residents, they rarely get up into the grassy parts of the marsh but are generally confined within the creeks. Alewives pass through the marsh en route to their freshwater spawning grounds, and their juveniles live in the marsh during late summer. Menhaden, which are much more abundant in the marshes of the southeastern U.S. coast, also live in Great Sippewissett in summer. They eat phytoplankton, whereas the alewives eat zooplankton. The primary value of the marsh for schools of these young fish is probably as a shallow refuge area. Mullet feed on detritus and benefit from marsh productivity as well as from its protective shallows.

The remainder of the fish listed in Table 2 also primarily use the New England marsh in their young stages. Young winter flounder are present throughout the summer; tautog and seabass appear in late summer. These three species are all bottom feeders and seem to prefer the sandier parts of the marsh. Tautog and bass eat amphipods and isopods, although the bass also eat small fish and shrimp. The young winter flounder concentrate their feeding on annelid worms. Werme (1981) has shown that young flounder, tautog, and seabass all have larger mouths than the same size killifish. As a result, they eat food items larger than can be handled by the killifish and so do not compete with them for food. During summer when these non-residents are

present in the marsh, they are about the same size as the residents but feed more (indicated by gut fullness), are more carnivorous, and grow faster (Figure 16), thus making maximal use of the marsh productivity.

Striped bass and bluefish enter salt marsh creeks as moderate- to large-sized

adults. The size of fish that can enter the marsh depends on the depth of the creeks and the height of the tides. These adults prey directly upon the smaller fishes in late summer. The use of the marsh by these larger fish species is perhaps more to be likened to the use by fish-eating birds than by other fishes. Small prey are plentiful for these carnivores.



Figure 16. Comparison of resident and non-resident fishes of Great Sippewissett Salt Marsh, Massachusetts, in summer (from Werme 1981). There are many more residents in the creeks during summer and they average about the same size as non-residents which are present only in warm weather. The non-residents feed more actively, are more carnivorous, and grow faster during the period they live within the salt marsh.

CHAPTER 5. SALT MARSH PROCESSES

5.1 PRODUCTIVITY

5.1.1. Higher Plants

For years the salt marsh has been considered one of the most productive natural systems on earth (Teal 1962; Odum 1971). Production values range from nearly 4,000 g/m² per year in the streamside marshes of Georgia (Odum and Fanning 1973) to only a little more than one-tenth of that in the short Spartina alterniflora marshes of Rhode Island (Nixon and Oviatt 1973) and Massachusetts (Ruber et al. 1981). There is a latitudinal variation in salt marsh productivity, with the highest values occurring in the southern States. Levels decrease by one-half to two-thirds in the north, presumably due to the shorter growing season and lower solar input at the higher latitudes (Turner 1976). In the salt marshes of the eastern United States there appears to be about a threefold variation in production over the latitudes at which Spartina alterniflora marshes grow, and also about a threefold variation in production within any one marsh.

Part of the variation in Spartina productivity within a marsh is related to sediment salinity (Nestler 1977; Smart and Barko 1980). Spartina can, in fact, grow well in almost freshwater sites if normally occurring freshwater plants are removed. If such plants are present, they outcompete (grow better than) Spartina and crowd it out. Spartina does well in more saline locations because it has mechanisms for coping with salt stress (as discussed in Chapter 3). However, an increase in respiration is necessary for the plants to maintain the higher osmotic gradient required at high salinities (Figure 7); this lowers production. Increased respiration uses up some of the plant's

resources and may also reduce oxygen availability to the roots which could, in turn, inhibit nutrient uptake.

Soil density is another factor which can affect Spartina productivity. DeLaune et al. (1979) found that in Louisiana, Spartina is more productive in soils of high density. This high density is the result of great amounts of mineral matter and accompanying high nutrient levels. In addition, the higher density soils in Louisiana are also those without much peat. As a result, they are more permeable to water movements and attendant flushing actions.

A substantial portion of the production of Spartina alterniflora has been measured in the belowground parts of the plants: the roots and rhizomes (Table 3). These data indicate there is typically more production underground than aboveground in the most productive parts of the marsh, and considerably more underground production in the less productive areas. All salt marsh production (i.e., photosynthesis) takes place in the leaves. However, in the less productive parts of the marsh, a great deal of the organic matter produced is translocated underground and used to construct roots and rhizomes. The grasses seem to behave as if they first produce enough underground parts to acquire necessary nutrients and then put any excess into the photosynthetic machinery, i.e., leaves. In the richer parts of the marsh (the creek banks or tall grass marsh), nearly equal amounts of biomass are produced above and below the sediment surface. This distribution of biomass has considerable significance for what eventually happens to salt marsh primary production, a point to which we will return.

Table 3. Comparison of above- and belowground productivity in Spartina alterniflora in g dry weight/m²/yr.

Area	Type of grass	Above-ground	Below-ground	Ratio below/above	Reference
Mississippi		1,960	c.5,000	2.6	de la Cruz 1974
		1,090	c.7,300	6.7	de la Cruz 1977
Georgia	tall	3,700	2,100	0.6	Gallagher et al. 1980
	short	1,300	2,020	1.6	Gallagher and Plumley 1979
North Carolina	tall	1,300	1,360	1.0	Stroud 1976
	short	330	420	1.3	Stroud 1976 ^a
North Carolina	tall	1,300	2,800	2.2	Stroud 1976 ^a
	short	330	2,600	7.9	Stroud 1976 ^a
New Jersey		500	2,300	4.6	Smith et al. 1979
Massachusetts	tall	1,320	3,315	2.5	Valiela et al. 1976
	short	420	3,500	8.3	Valiela et al. 1976
Nova Scotia	"old stands"	514	720	1.4	Livingston and Patriquin 1981

^aRecalculated using method of Valiela et al. (1976).

Odum (1969) suggested that this high productivity was due to a tidal subsidy. In other words, the tides contributed something to the marsh that enhanced plant production. Steever et al. (1976) found they could associate about 90% of the variation in Spartina productivity in Long Island Sound with the tidal range, which varied from 0.7 m to nearly 2.3 m. In one site, a portion of the marsh was behind a tide gate that restricted tidal movement and reduced the plant production by 26% relative to the rest of the marsh. Furthermore, they showed that a strong relation exists between production and tidal range all along the Atlantic coast. Clearly, water movement is associated with salt marsh production; the mechanisms involved include nutrient supply, waste removal, and salinity control, or all of these combined.

Salt marsh productivity is high, especially that of the Spartina alterniflora growing along the creek banks, because of the almost ideal factors for growth found there. There is a lack of competition along creek banks, which gives the plants space and an abundance of sunlight. The water supply is plentiful and Spartina has mechanisms for dealing

with the salts in the water. All of the minor nutrients needed by plants, as well as the major nutrient potassium, are present in seawater. The major nutrients--nitrogen, phosphorus, and potassium (N, P, and K)--are also in good supply in the marsh mud along the creek banks. (Potassium is plentiful throughout the marsh since it is so abundant in seawater.) Carbon dioxide not only enters the plant from the atmosphere through its leaves, but also through its roots from CO₂ reserves in creek bank soils. With these plentiful nutrients, Spartina growing on New England creek banks has a productivity comparable to that of plants growing naturally anywhere. The maximum total annual marsh production in New England is less than that of more southerly marshes only because the growing season is shorter in the north.

Experiments at Great Sippewissett Salt Marsh have shown that the addition of fertilizer increases the productivity of Spartina alterniflora in all parts of the marsh except the already highly productive creek banks (Valiela and Teal 1974). Once the addition of nitrogen to the marsh produces its maximum effect, production can be further increased by adding phosphorus (Figure 17), though phosphorus

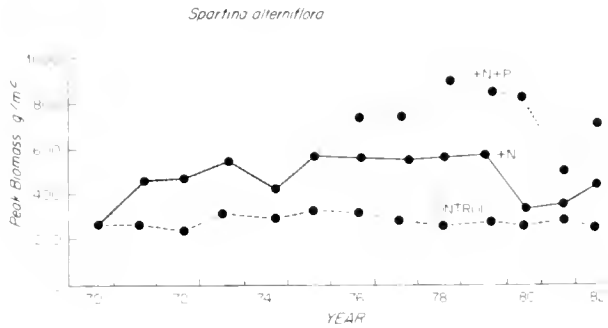


Figure 17. Peak biomass of *Spartina alterniflora* in experimental plots to which nitrogen alone (+N) or nitrogen and phosphorus (+N+P) were added at rates of 2.5 g N/m²/week and 1.5 g P/m²/week. Controls were not fertilized. (Teal and Valiela, unpubl. data, Great Sippewissett Salt Marsh, MA).

added without nitrogen has no effect. Fertilization increases marsh production as a whole two- to threefold and converts the least productive parts of the marsh almost to creek bank production levels. At that point, further growth of *Spartina* may be light-limited rather than nutrient-limited. Similar results have been seen in many other salt marshes (Sullivan and Daiber 1974; Broome et al. 1975; Gallagher 1975; Chalmers 1979).

Measurements of nitrogen reductase (an enzyme involved in nitrogen uptake), comparison of nutrient content of *Spartina* from various parts of marshes from Nova Scotia to Louisiana (Stewart et al. 1973; Stewart and Rhodes 1978; Mann 1978; Mendelsohn 1979), and experimental results from nutrient enrichment studies all lead to the conclusion that salt marsh plants are usually nitrogen-limited in most parts of natural marshes.

Sediment redox. In view of the studies suggesting nutrient limitation, it seems paradoxical to find that the amounts of dissolved ammonium and phosphate in interstitial waters of salt marsh sediments are very high. These levels are more than sufficient to provide all that *Spartina* can take up if the roots are in an oxidized environment (Valiela and Teal 1978; Morris 1980). Nitrate nitrogen concentrations range from 0 to 50 µg-at/l and ammonia nitrogen from 10 to 500

µg-at/l. For phosphate, the range is 5 to 20 µg-at/l (Valiela and Teal 1974). The concentrations of these ions in seawater are usually less than 1 µg-at/l.

Nitrogen uptake rates by *Spartina* in an experimental, oxidized medium are faster than uptake rates in the usually reduced sediments in the field (Morris 1980). In cultivated rice, which also grows in anoxic soils, nutrient uptake rates depend on the oxygen concentration of the soil (Ponnamperuma 1972). *Spartina* shows very reduced uptake of dissolved inorganic nitrogen when the oxygen content of the growing medium is low (Morris and Dacey 1984). These observations suggest that redox conditions at the roots are involved in limiting nutrient uptake (Linthurst 1979; Howes et al. 1981). In experiments in Georgia, Wiegert et al. (1983) drained marsh soils with plastic tile lines that carried water from the soils to the creeks; *Spartina* production was increased presumably because of increased sediment oxidation.

Stands of taller plants grow in relatively more oxidized sediments while short plants are found in more reduced situations (Figure 18). The higher redox

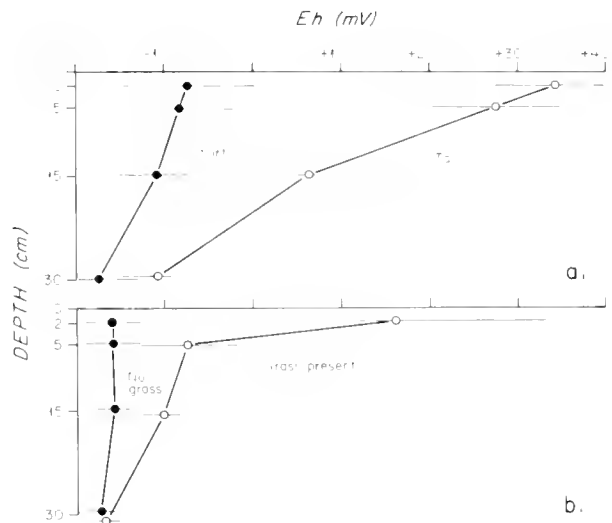


Figure 18. Redox (Eh) profiles in a) sediments with tall and short *Spartina alterniflora*, and b) an area of marsh in which grass was smothered and a nearby area in which the grass was becoming reestablished (Howes et al. 1981).

values are partly due to differences in physical properties of the sediments that lead to increased rates of water percolation. In addition, the taller, more vigorous plants are more efficient in oxidizing the sediments than are the short plants. This results in a complex feedback system in which plants, redox level, and nitrogen availability interact to control marsh production (Howes et al. 1981, 1986). If productivity of a stand of Spartina is stimulated by nutrient additions, there is increased oxidation of the sediments by the plants. The more biomass of the plants increases, the more oxidation occurs, which should (theoretically) lead to more uptake of nitrogen and increased productivity. A substantial part of the observed increase in oxygenation of sediments is caused by water removal from the sediments by transpiration of Spartina. As the water is removed, the sediment does not decrease in volume but the spaces previously occupied by water become filled with air (Dacey and Howes 1984). The sediment still retains the majority of its pore water much like a sponge which has been allowed to drain. Sediment oxidation may also be aided by transport of gases in gas spaces inside the plant (Teal and Kanwisher 1966), or by release of organic oxidants such as glycolate from the roots (Armstrong 1967), or by both.

The opposite tendency (i.e., the sediment becomes more reducing) is the result of microbial decomposition. Because of the limited ability of oxygen to move through sediments by diffusion, oxygen is usually absent below the top few millimeters of marsh muds. The decomposers below this depth depend principally on the reduction of sulfate for their energy. They "respire" using sulfate rather than oxygen and produce sulfide as a product. The redox of salt marsh soils is closely correlated with sulfide concentration. The balance between the very high reducing power resulting from microbial activity and the oxidative action of higher plants determines the redox state of the soil, which in turn affects nutrient uptake. Usually the reducing activities of the micro-organisms prevail and, although the plants may make the soils less reduced, an oxidized state is rare and the majority of

marsh sediments are highly reduced. Spartina roots can respire anoxically, but in conditions of extreme waterlogging and reduction, the plants cannot compensate, so production is severely reduced and dieback may occur (Mendelssohn et al. 1981).

Sulfide, which is responsible for the low redox values of salt marsh soils, is toxic to wetland plants. This has been demonstrated for rice by Joshi et al. (1975) and for Spartina by Mendelssohn et al. (1982). In very reduced marsh sediments, such as those where short plants of Spartina grow, sulfides undoubtedly contribute to the inhibition of further growth by counteracting the oxidizing activities of roots and perhaps by poisoning them.

To explain the conclusive results of fertilization experiments in Great Sippewissett Salt Marsh, one must understand the relationships between sediment redox and Spartina physiology. The Sippewissett marsh experiments suggest that under reducing conditions, much less nitrogen can be picked up by plants than is possible in oxidized soils. Thus, in reduced sediments, only a greatly increased concentration of dissolved nitrogen (such as is provided by fertilizing) allows uptake to occur at rates similar to those found in oxidized soils. This hypothesis is supported by the findings of Linthurst (1980), who showed in greenhouse experiments that while the addition of nitrogen doubled the biomass of Spartina, nitrogen addition plus aeration of the rooting medium increased biomass by a factor of 4.5. He suggested that Spartina production in the marsh is regulated by a combination of nitrogen, salinity, pH, and aeration.

5.1.2. Other Autotrophs

Total production of the salt marsh system is the sum of the production of the higher plants and that of all the other autotrophs, including the algae living on surfaces, phytoplankton in the water, photosynthetic sulfur bacteria, and chemoautotrophic iron (and sulfur) bacteria. The contributions of none of these autotrophs have been accurately measured and are assumed to be small

relative to the other primary producers. The chemosynthetic organisms do not contribute to overall marsh production if they are oxidizing reduced substances produced in the marsh (see Section 5.5.4.).

Measurements of benthic microalgal production along the Atlantic coast (Table 4) indicate that algal production in the grassy parts of the Massachusetts marsh is limited by low light during the darker parts of the year (Van Raalte et al. 1976). There is little indication of inhibition by high light intensity in any studies (see Pomeroy and Wiegert 1981). Competition for available nutrients by grasses during their growing season also limits algal production.

Microscopic algae make a significant contribution to total salt marsh production because they contain low amounts of refractory structural compounds and, thus, are better food than higher plants. The lignins and celluloses of higher plants are all relatively resistant to digestion by animals. We usually speak of them as "resistant to degradation," implying that they are attacked only by microbes and, in the case of lignins, very slowly. Algae, on the other hand, are eaten readily by benthic animals, as has been demonstrated by excluding mud snails from marsh areas and observing the increase in algal biomass (Pace et al. 1979). Pace et al. (1979) found that the snails only reduced algal populations by grazing and caused no related increases in algal productivity in their Georgia marsh. On the other hand, Connor et al. (1982)

found that at moderate population levels, the nutrients (ammonia) excreted by the snails stimulated algal production. An increase in production when grazers are excluded has also been shown in early spring when blooms of Beggiatoa were produced in Great Sippewissett Salt Marsh by fencing Fundulus out of marsh creeks (J.M. Teal, unpubl. data).

Salt marsh phytoplankton productivity may be high, especially at high tide when the water is clear from being filtered by the marsh and nutrient levels are maintained by marsh-to-water exchanges. In Georgia marshes, phytoplankton are estimated to contribute about half as much to the system as do benthic algae (Pomeroy and Wiegert 1981); in Massachusetts, phytoplankton productivity may be about equal to that of benthic algae (Van Raalte et al. 1976). Pomeroy and Wiegert (1981) showed that phytoplankton photosynthesis in Georgia is inhibited by low temperatures in winter; Glibert et al. (1984) have found high levels of phytoplankton photosynthesis in Massachusetts coastal inshore waters during winter. If this difference is real, then phytoplankton may be even more important to New England marsh creeks than we previously thought.

Algal production in surface pools of a salt marsh was measured by Ruber et al. (1981). They estimated an ash-free dry weight value of 514 g/m²/yr, which is a little more than the production of dwarf Spartina in New England and slightly less than half that of tall Spartina. Planktonic diatoms and dinoflagellates

Table 4. Production of benthic algae in salt marshes along the Atlantic coast.

State	Benthic algal production (g C/m ² /yr)	Percent of aboveground grass production (%)	Reference
Georgia	180	25	Pomeroy 1959
Georgia	190	25	Whitney and Darley 1981
Delaware	80	33	Gallagher and Daiber 1974
Massachusetts	42	25	Van Raalte et al. 1976

were responsible for most of this production; floating mats of Cladophora were also important.

5.2 DECOMPOSITION

5.2.1. Aboveground

A part of the marsh grass produced each year is eaten directly by herbivores feeding on the grasses and by animals eating the algae from the marsh surface or filtering it out of the water. Another measurable amount of production is released directly into the water when living leaves are immersed by high tides. This portion amounts to about 60 kg C/ha/yr in Georgia (Gallagher et al. 1976), which is a little less than 1% of the total production for that region. This material is very readily absorbed by microbes and can promptly enter the food web. The loss is probably similar in New England (Valiela et al., unpubl. data).

Almost three-quarters of the aboveground plant biomass produced is not consumed directly. It dies in place on the marsh surface and decomposes to variable extents before being eaten by animals. It may decompose in place or in a location to which it has been carried by the tides. The greatest exception to this is in areas where snow geese congregate during the winter; they may eat over half of the annual production, which at that time may be stored mainly belowground as rhizomes (Smith and Odum 1981). Since geese have very inefficient digestive systems that remove only soluble compounds from their food, most of what they eat is still decomposed on the surface of the marsh by bacteria and fungi. The cellulose in the grass passes through the digestive systems of the geese almost unchanged except that it is broken into small bits and is probably more readily attacked by the micro-organisms as a result.

Late in the growing season, plants enter senescence and the grass decomposition process begins. The leaves become leaky to both organic compounds and to nutrients and lose large amounts of soluble compounds to the water. The dead leaves fall onto the mud surface and are

invaded by fungi and bacteria. In Great Sippewissett Salt Marsh, the aboveground decay process occurs in three stages once the plants have died and become a part of the litter. In the leaching phase, the litter loses about one-third of its weight within 2 weeks as a result of further loss of soluble components. In the second or decomposer phase, the structural parts of the leaf are attacked by micro-organisms. The loss of material from the litter is slower than in the leaching phase but occurs more rapidly the more frequently the litter is submerged. At the end of a year only about 10% of the original litter remains (Figure 19). The refractory phase, which begins about 1 year after the plants die, occurs, as the name implies,

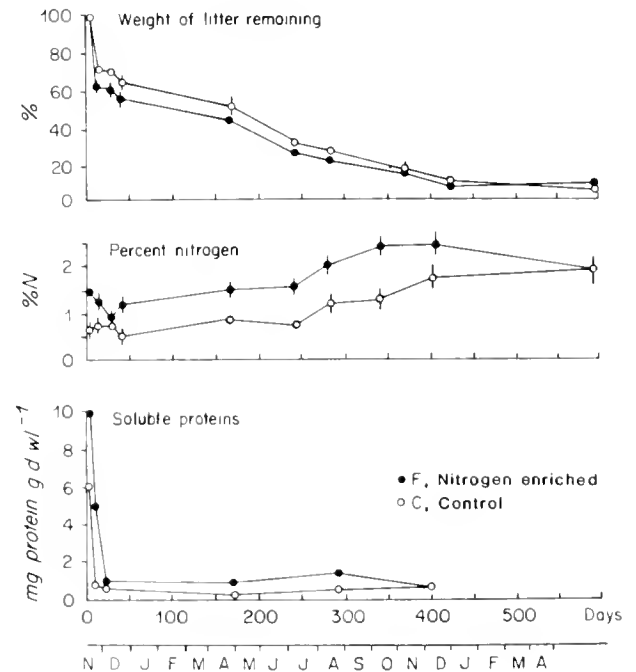


Figure 19. Results of aboveground decomposition experiments at Great Sippewissett Salt Marsh. These litter bags were incubated in creek bank marsh. The leaching phase is shown by the rapid weight loss between the first two points; the decomposer phase is the period of steady decline in weight up to the second winter; the refractory phase follows with very little weight loss. (Teal and Valiela, unpubl. data, Great Sippewissett Salt Marsh, MA).

very slowly. After 2 years, about 5% of the initial litter still remains. These remnants are indistinguishable from the organic matter of the sediments and are presumably what accumulates as marsh peat.

During both the leaching and decomposition phases, the more luxuriant the marsh that produces the litter, the more nitrogen the litter will contain and the more rapid will be its decomposition (Figure 19). In the Great Sippewissett Salt Marsh, the rate of decomposition also increased if the extra nitrogen was added to the marsh soil rather than being within the leaf. The same effect was produced if nitrogen was enriched in the soil water either experimentally or by pollution of the marsh (Valiela et al. 1984) (Figure 20). The fact that nitrogen enhances decomposition whether it is in the plant tissue or the environment of the decomposer organisms implies that there is a nitrogen limitation to decomposition as well as to primary production in the marsh.

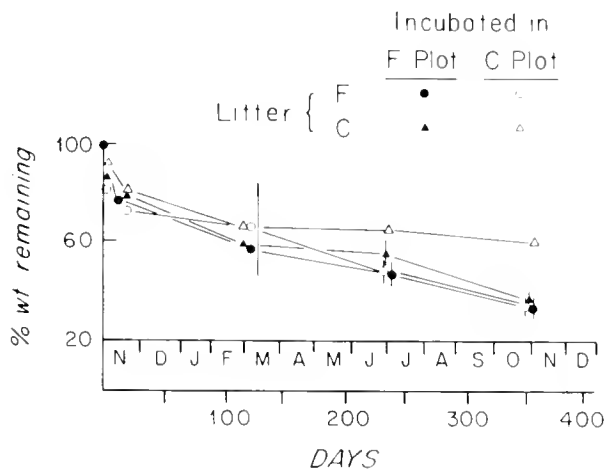


Figure 20. Decay of *Spartina* litter under different conditions of nitrogen presence. Litter from control plots (C Plot) was incubated in the plots in which they grew and in fertilized plots (F Plot) where there was higher nitrogen in the litter's environment. Litter from fertilized plots was similarly treated. Only control litter in unfertilized plots decayed more slowly than the others. (Teal and Valiela, unpubl. data, Great Sippewissett Salt Marsh, MA).

Since the initial losses of nitrogen from litter are soluble, it is not surprising that over time, the remaining nitrogen in the detritus is less and less soluble. After 1 year, amino acids still constitute about 20% of the remaining nitrogen, but they are almost entirely bound to insoluble compounds in the litter and are presumably resistant to decay.

It has been known for some time that as detritus ages, its relative concentration of nitrogen increases (Odum and de la Cruz 1967; Figure 19). Scientists initially believed that this increase represented the nitrogen in microbes on the detritus and that aged detritus was improved as a food source for marsh animals. Later, researchers found that bacteria contribute only a small percent of the total nitrogen in decaying *Spartina* (Ruble et al. 1978). Fungi may contain about one-fifth of the non-protein nitrogen in detritus (Odum et al. 1979a). In any event, there is not sufficient microbial biomass to account for all of the nitrogen in the detritus (Lee et al. 1980). A portion of this unaccounted-for nitrogen is certainly in the form of extracellular compounds produced by microbes; many of these compounds are probably resistant to decomposition. Some nitrogen is also bound as proteins to oxidized phenolic compounds that come from the degradation of lignin (a structural component of plants) or that are present in the plant as so-called "secondary products" (compounds which may protect the plant from being eaten). Aside from the microbial biomass itself, most of the nitrogenous compounds in detritus are not readily available as food for the detritivores. Therefore, relative increases of nitrogen in detritus do not necessarily enhance its food value for animals.

Animals are able to harvest microbes from detritus (Jeffries 1972; Welsh 1975; Wetzel 1975, 1976). Microbes will recolonize the particles and grow at the expense of compounds like cellulose that are not readily digested by animals. Animals can then reprocess detritus and harvest the microbes again. Algae also grow on processed detritus and may significantly enhance its food value. Apparently, pure detritus is not as

nourishing as was once thought. For example, while mummichogs will eat detritus, they cannot gain weight on a detrital diet that is not supplemented with protein (Prinslow et al. 1974). Marsh killifishes, especially mummichogs, feed on detritus though much of it may get into their stomachs by accident when they are really seeking animals in marsh sediments.

Detritivores accelerate the decomposition rate of Spartina litter by grinding the particles (thus creating more surface by digesting the particles to a small extent) and by stimulating the growth of decomposers by cropping them. Such feeding activities stir up the particle accumulations, increase the available nutrients and oxygen, and perhaps remove anti-microbial substances from particle surfaces. Although the relative importance of these various mechanisms is not clearly understood, the exclusion of macrofauna from some decomposition experiments tripled the amount of litter that normally remained after 1 year (Valiela et al. 1984).

5.2.2. Belowground

As described in Section 5.1.1., much of the production in salt marshes goes into the belowground parts of the plants, the roots and rhizomes. The marsh surface accumulates only a small percent of the total plant production because most of it decomposes in place or is washed away by the tides. The belowground parts cannot be washed out and, therefore, they decompose within the marsh sediments. Some of this underground decomposition occurs through the same aerobic processes as aboveground decomposition. But since most of the sediment is anoxic, the major portion of underground decomposition occurs by anoxic means.

Anoxic processes common to marine systems use nitrate (denitrification) and sulfate (sulfate reduction) as electron acceptors in place of oxygen. These anoxic processes yield less energy to the microbes that perform them than oxygen-consuming processes do to aerobic microbes. There is slightly less energy produced in the case of denitrification but substantially less in the case of

sulfate reduction. A vertical cross section of marsh sediments might reveal the oxygen-using organisms at the surface, denitrifiers below them, and finally the sulfate reducers in deeper layers. As long as oxygen is present, organisms that can use oxygen outcompete the others simply because they can obtain energy from organic matter more efficiently and thus grow faster. At the depth where all of the oxygen has been used, the denitrifiers are most efficient, and at the depth where the nitrate is also exhausted, the sulfate reducers come into their own.

Carbon dioxide is another potential electron acceptor. Its use by microbes produces reduced carbon or methane. But, because of the abundance of sulfate in seawater and the small potential energy available from methane production compared with sulfate reduction, this path of decomposition is of minimal importance in salt marshes.

Decomposers that use nitrate and sulfate as electron acceptors can usually use only a limited number of organic molecules (e.g., acetate and simple organic acids) as substrates. These compounds are made by microbial fermentation that breaks apart the more complex organic molecules in Spartina roots and rhizomes.

Anoxic decomposition is slower than aerobic decomposition. The underground leaching phase is similar to that aboveground, but the subsequent phases are slower. After 2.5 years, less than 20% of the original litter remained in belowground field experiments in Great Sippewissett Salt Marsh (Valiela et al., unpubl. data). These researchers also found that belowground litter enriched in nitrogen decayed more rapidly than unenriched litter in control experiments. This indicates that nitrogen limitation plays a role in anoxic decomposition in salt marshes. There are other differences from aboveground decomposition: lignin decomposes poorly in anoxic conditions, and fungi are not active in the absence of oxygen.

The actual amounts of decomposition that proceed via these various paths are not very well known. The greater part of

underground production is probably decomposed through the fermentation and sulfate reduction pathways (Howes et al. 1984). Sulfate reducers are not efficient at converting nutrients into microbial cells and the carbon to nitrogen ratio of anoxic litter is about 45:1 after 1 year compared with 20:1 for aerobically decomposing litter. Thus, in the former case, about half of the nitrogen has been lost to the sediment pore water or mineralized. This lack of nitrogen conversion into microbial biomass may be one of the reasons for the generally high nitrogen levels in marsh sediments and for the eutrophic nature of salt marshes since the water oozing out of the mud is high in nitrogen. Less than 3 g C/m²/yr is accounted for by the denitrifiers in Great Sippewissett Salt Marsh (Kaplan et al. 1979), because there is not a large supply of nitrate available to the denitrifiers. Net methane loss to the atmosphere is less than 4 g C/m²/yr (Howes et al. 1985), which is less than 1% of total decomposition. Methane loss has been increased 2.5 times by poisoning sulfate reducers with molybdate (Howes et al., unpubl. data). This indicates that more methane is produced in the marsh than is lost to the air, but it is consumed by sulfate reducers.

Recent measurements from the Great Sippewissett Salt Marsh indicate that decomposition via respiration with oxygen accounts for approximately half of estimated underground production (Howes et al. 1984). But since a substantial part of the salt marsh production is too far underground to be reached by oxygen, a major fraction of this is decomposed through the sulfate reduction pathway.

5.3 NUTRIENT CYCLING

5.3.1. Nitrogen

The nitrogen cycle is of great importance to the ecology of the marsh. Nitrogen clearly controls a wide variety of marsh processes. The level of available nitrogen and its uptake by the plants determines the productivity of the marsh. The more nitrogen that is available, the greater the percentage of grasses that set seed. The relative

abundance of the grasses on the marsh also seems to be determined by nitrogen availability. Salt marsh algae are more productive when their nitrogen supply is increased in the spring; in summer, increased nitrogen supplies enhance the growth of the marsh grass and algal production is reduced due to shading by the grass canopy.

Marsh herbivores are also nitrogen limited: the more nitrogen in their food, the higher their production. For example, insects are more abundant in parts of the marsh where the grass has a higher nitrogen content. Those parts of the marsh are also much more attractive to geese and voles.

The food quality of salt marsh detritus is also affected by nitrogen availability. Salt marsh detritus is not a very nutritious food for animals. Its carbon to nitrogen ratio (C/N) varies from 20:1 to 60:1 while phytoplankton, protein, and bacteria have values that range from 4.5:1 to 6:1. Since animals require a C/N ratio of about 17:1 for minimal maintenance, nitrogen content is of great importance in the detritus cycle in the marsh. When the amount of nitrogen in detritus was experimentally doubled, there was a four- to fivefold increase in the abundance of detritivores on the marsh surface (J.M. Teal, unpubl. data), but no change in the abundance of animals living in the bottoms of the marsh creeks (Wiltse et al. 1984). There is some evidence that the fish in the marsh grow faster in the fertilized parts of the marsh than they do in control areas, but the response is not as clear as it is with either the plants or marsh surface detritivores (Connor 1980).

Nitrogen enrichment affects the spacing of grass stems. In the more productive parts of the marsh, the stems are thicker but farther apart than elsewhere. Hartman et al. (1982) report that in the highly productive creek banks, about 40% of the surface area lies between the grass stems, while in the less productive low marsh the space between the stems is only half as great. The marsh fishes are much more successful in hunting among these widely spaced stems than they are among the closely spaced stems in the

less productive parts of the marsh (Vince et al. 1976).

Nitrogen also has an effect on the decomposers in the marsh. Decomposition rates were found to be slightly increased in areas with added nitrogen (Valiela et al. 1984). The difference is small and only means that in the less productive parts of the marsh the detritus lasts a little longer since the normal decomposition process eventually does away with almost all of the organic matter that is produced in the marsh.

The following discussion of the marsh nitrogen cycle draws mostly on data from Great Sippewissett Salt Marsh (Valiela and Teal 1979). This is the only salt marsh anywhere for which there is a complete published nitrogen budget at the present time (Table 5). Except when identified as measured in low marsh, the data refer to the nitrogen budget for that entire marsh including the regularly flooded intertidal marsh and also high marsh, pannes, sand flats, and creeks. Great Sippewissett Salt Marsh is enclosed behind a barrier beach and interacts with the bay through a single channel in which many of the measurements of exchange were made. The exchanges between the different parts of the marsh were not measured, so the regularly flooded marsh cannot be discussed in isolation.

Nitrogen is supplied to the marsh by both physical and biological processes (Figure 21). Ground water and flood tides bring nitrogen into the marsh system; ebb tides remove it. If there is significant river or stream flow into a marsh, this can be an important source of nitrogen. Bacteria and blue-green algae fix nitrogen gas from the air and denitrifying bacteria convert the nitrogen in nitrate back to gaseous form. Plants and micro-organisms build nitrogen, mostly from ammonia and nitrate, into organic compounds such as amino acids, proteins, and nucleotides. Some of the export from the marsh is in the form of organic matter (as organic detritus, plankton, and animals) containing these nitrogen compounds.

By far the largest fluxes of nitrogen both into and out of the marsh are those carried in the tidal flows. In Great Sippewissett Salt Marsh, over 70% of the inputs and nearly 90% of the outputs were carried by the tides (Table 5). The tidal creeks carrying this water occupy about 34% of the total marsh area, a situation similar to that in other mature marshes that have completely filled their basins. The largest part of the nitrogen exchange is in the form of dissolved organic nitrogen (DON) which did not change much in concentration between inflow and outflow (Table 6). Because the concentration did not change measurably, it is assumed that most of this organic

Table 5. Nitrogen budget for Great Sippewissett Salt Marsh. Values are in kg N/yr for the entire marsh of 48.3 ha (Valiela and Teal 1979, and unpubl. data).

Source	Inputs	Outputs	Net exchanges
Rain	380	-	380 in
Ground water	6,120	-	6,120 in
Nitrogen fixation			
algae	300	-	
bacteria (rhizosphere)	2,980	-	3,280 in
Tidal exchange	26,200	31,600	5,350 out
Denitrification	-	3,490	3,490 out
Sedimentation	-	1,295	1,295 out
Other (gulls, clams)	9	26	17 out

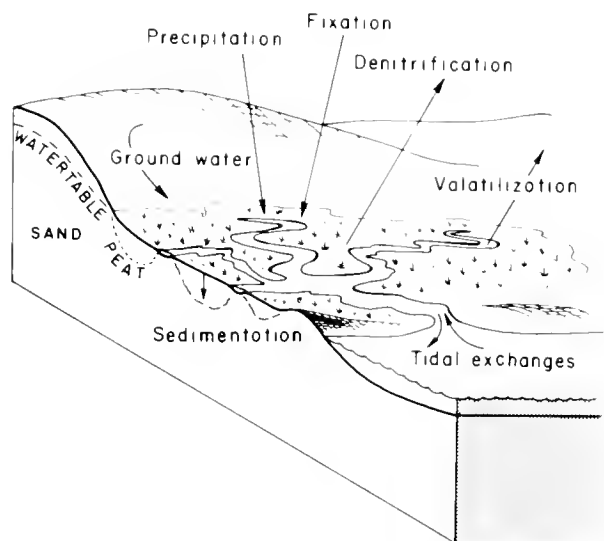


Figure 21. Nitrogen fluxes between a salt marsh and surroundings.

nitrogen is not very active biologically and does not contribute much to the nitrogen cycle of either marsh or estuary.

Dissolved inorganic nitrogen (DIN), on the other hand, exhibits significant changes in concentrations with time and tide--changes which have implications for both marsh and estuary. The major part of the inorganic nitrogen is in the form of ammonium ion (NH_4). For most of the year ammonium concentrations were similar in the incoming and outgoing tides in Great Sippewissett Salt Marsh and there was

little exchange of nitrite (NO_2) or nitrate (NO_3) (Figure 22).

Ground water contributed about $12.5 \text{ g N/m}^2/\text{yr}$ to Great Sippewissett Salt Marsh. Some marshes have significantly less ground water flow than Great Sippewissett Salt Marsh, although in most marshes this has not been measured. Flax Pond Marsh on Long Island has a lower salinity than Long Island Sound, which probably indicates ground water intrusion. There is likely to be a substantial contribution of nitrogen from the ground water. Other salt marshes along the southeastern coast may receive nitrogen from the river flow entering the estuaries. This amount has been estimated to be about $3 \text{ g N/m}^2/\text{yr}$ to southeastern salt marshes (Windom et al. 1975). At Great Sippewissett Salt Marsh, there was about half as much nitrogen in rainwater as in the ground water. Only about 1% of the nitrogen input came from direct rainfall and 16% came from ground water flow (Valiela et al. 1978b). This resulted from the much larger area of the watershed in comparison to that of the marsh itself.

As sea level rises, the surface of a healthy salt marsh maintains its relative tidal level by accumulating sediments from the water and peat from the grasses. Organic nitrogen is buried in these sediments until it is deep enough to be beyond the reach of roots. This loss was a small quantity in the nitrogen budget for the marsh, amounting to about 1% of the nitrogen contained in the upper 15 cm

Table 6. Annual nitrogen exchanges for Great Sippewissett Salt Marsh. All values are in kg/yr (Valiela and Teal 1979, and unpubl. data).

Form	Input	Output	Net change	Net change/input
NO_3	3,420	1,220	2,200	64%
NH_4	3,150	3,550	-400	-13%
DON^a	19,200	18,500	700	4%
Particulate N	6,750	8,200	-1,460	-22%
N_2	3,280	3,490	-210	-6%

^a dissolved organic nitrogen.

of marsh sediment and available to *Spartina* roots. Another minor component of the total nitrogen budget was the loss of ammonia to the air from the marsh surface.

Nitrogen is fixed from the atmosphere by nitrogen-fixing bacteria associated with the roots of the grasses and by algae growing on the surface of the marsh. Rates of nitrogen fixation between different parts of the marsh vary as much as between different marshes (Valiela 1982). About 10% of the nitrogen input may result from nitrogen fixation primarily by the bacteria associated with

roots of *Spartina* (Teal et al. 1979). While this is a relatively small percentage, it is very important to the plant because it occurs just at the site of uptake and, therefore, is most readily available for the plant's use. Denitrification is the microbial process that returns nitrogen to the air as nitrogen gas. There are several smaller biological components of the budget: organic nitrogen is transported out of the marsh by shellfish harvesting by humans or by fish swimming out of the marsh; organic nitrogen is transported into the marsh by feces deposition by birds, such as gulls, that have fed outside the marsh but come there to rest.

Seasonal changes in the nitrogen cycle at Great Sippewissett Salt Marsh gave us insight into the processes which controlled it. At the beginning of the most active growing season for the grasses, there was substantial import of ammonium from the bay to the marsh (Figure 22). At that time the *Spartina* needed nearly 40 kg N/day. The ground water input of inorganic nitrogen amounted to a little less than 10 kg N/day; the tides supplied about 8 kg N/day to the marsh. The resulting deficit of over 20 kg N/day had to be made up by processes within the marsh itself. A little later, in August, when the plants had matured, flowered, and were beginning to become senescent, as much as 12 kg N/day of ammonium were exported from the marsh to the bay via the tides. Not only was most of the ground water nitrogen not being intercepted by the marsh, but the plants were leaching nitrogen into the water.

Denitrification in a New England marsh, like nitrogen fixation performed by bacteria, varies in response to the marked seasonal temperature changes (Figure 23). Denitrification rates were highest (5 mg N/m²/hr) in tidal creek bottoms which carry out most of the total denitrification for the entire marsh. The short *Spartina* parts of the marsh accounted for most of the remaining denitrification. When denitrification for the marsh as a whole is compared with the input of nitrate from ground water and the export of nitrate to the bay, it is apparent that nitrate is exported only during those seasons when denitrification

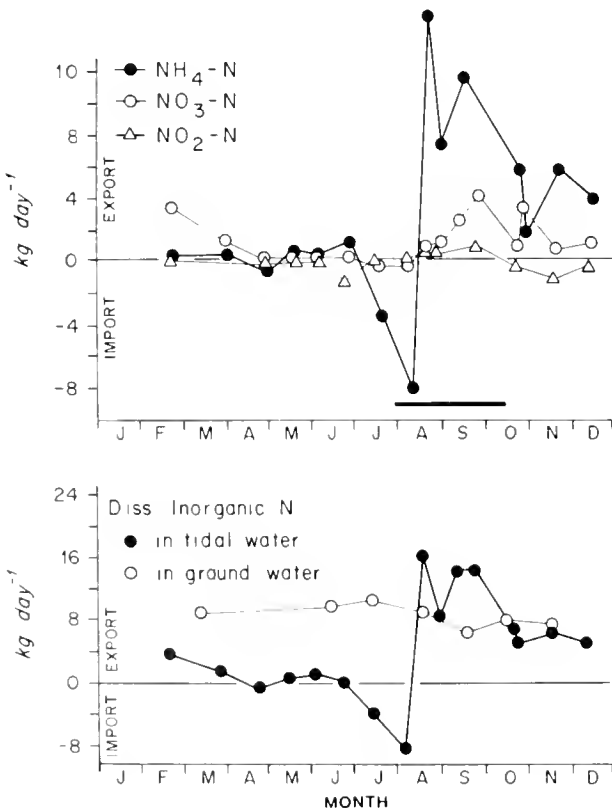


Figure 22. Net exchanges of inorganic nitrogen between Great Sippewissett Salt Marsh and Buzzards Bay (top) and the bay and ground water (bottom). Heavy black bar indicates period of *Spartina* senescence. The bottom graph compares the input of nitrate from ground water to the summed total exchanges of all forms of inorganic nitrogen by tides (Valiela and Teal 1979).

is at a minimum (Figure 23). During the warm weather, most of the nitrate is intercepted and denitrified upon entering the marsh, probably in the anoxic sediments of the creek bottoms.

The overwhelming portion of nitrogen exchange is driven by physical forces, with only 15% being entirely biological in nature (Table 5). The salt marsh is driven by its physical setting: the tides, the salty water, and the anoxic sediments, which determine the character of the living things that can survive there. But the biological components are the ones with which we are primarily concerned. The living organisms determine how the marsh looks and persists and in what ways it is important to us.

Another way of looking at the nitrogen budget is to examine the balances for the various forms of nitrogen (Table 6). Unfortunately, we can only lump all of the dissolved organic nitrogen together as one number in this table. Table 6 emphasizes that although the total amount of DON is very large, there is relatively

little difference between the amounts entering and leaving the marsh. Examination of the values controlled by biological processes show some interesting aspects of biological activity within the marsh system. For example, the values for nitrogen fixation and denitrification are approximately equal. The measured values for denitrification in the muddy creek bottoms are about equal to the net input of nitrate (Howes et al., unpubl. data). There is a much smaller amount of denitrification on *Spartina*-covered areas, the nitrate for which is probably supplied by oxidation of nitrogen compounds at the surface of the mud. If one adds up all the sources of nitrogen available to support marsh grass growth (i.e., net input of ammonia, nitrogen fixation, net input of DON) and subtracts from this the net losses to the sediments, the total is about 1,600 kg N/yr. But the total production of marsh grass requires nearly 9 tons of nitrogen per year. Much of this is supplied by cycling within the very large "pool" within the sediments, which balances the various demands. The cycling is mostly due to the activities of microbes. Animals play a smaller role through feeding and excreting nitrogen within the marsh, thereby stimulating the rates of microbial activities. For example, marsh mussels deposit as pseudofeces much of what they filter out of the water and thus create a substrate on which microbes are active (Jordan and Valiela 1982). Fiddler crabs and snails turn over the surface layers of the sediments and stimulate microbes.

To sum up the role of Great Sippewissett Salt Marsh as an example of New England marshes, one can say that if the marsh were not there: (1) more inorganic nitrogen would reach coastal waters, (2) the nitrogen would be in the more oxidized form (NO_3 rather than NH_4), (3) nitrogen would enter coastal waters more uniformly throughout the year rather than principally as a pulse in autumn, and (4) there would be less nitrogen exported as particulate organic nitrogen (detritus and living cells), the form of nitrogen that can be consumed directly by coastal animals such as filter feeders.

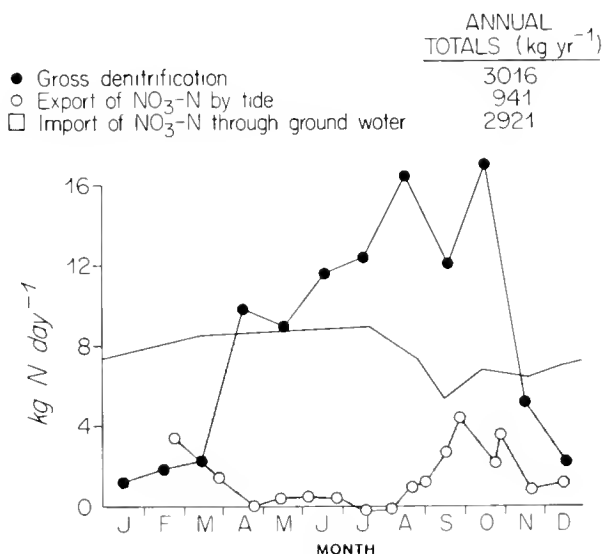


Figure 23. A comparison of nitrate input from ground water, nitrate export by tides, and denitrification within Great Sippewissett Salt Marsh (Valiela and Teal 1979).

5.3.2. Phosphorus

Phosphorus is an essential element for organisms and often limits production on land and in freshwater, though rarely in coastal waters. It enters marshes bound to sediment particles and dissolved in ground and tidal waters. Experimental additions of phosphorus alone had no effect on marsh production, though when added to marsh plots already receiving a high dose of nitrogen, phosphorus did increase plant growth (Teal 1984). Two generalizations can be made about the relationship between phosphorus and salt marshes (see Nixon 1980 for a recent review): (1) marshes seem to act as phosphorus sinks, accumulating phosphorus in their sediments; (2) marsh sediments lose some of their phosphorus both from pumping by Spartina and from diffusion, and may well serve as a source for reactive phosphorus to the surrounding waters (Nixon 1980). Nitrogen is generally the factor thought to limit plant production in coastal oceans areas; however, in situations where phosphorus is limiting to plankton production (such as in an enclosed lagoon where an active iron cycle may remove phosphorus from the water as ferric phosphate), a neighboring marsh could support productivity by supplying phosphorus from marsh sediments.

5.3.3. Sulfur Cycle

Because of the abundant supply of sulfur in seawater, sulfur is never limiting to marsh organisms. This abundance is exemplified by one of the characteristic odors of the salt marsh: dimethylsulfide, a reduced sulfur compound. Hydrogen sulfide, which is obvious as the rotten egg smell occasionally apparent (especially on disturbed marshes), also attests to sulfur's abundance. Hydrogen sulfide is toxic to higher plants, and even those plants that grow in wetlands (e.g. rice, Spartina) are harmed when their tolerance is exceeded (Joshi et al. 1975).

Howarth (1980) measured the annual cycle of sulfate reduction in Great Sippewissett Salt Marsh, and found the same sort of seasonal cycle as was evident in other microbial annual cycles except that the maximum sulfate reduction rate

was displaced towards the fall. There was a time lag between maximum temperature and maximum sulfate reduction activity. The substrate for sulfate reduction is organic matter from decaying or leaking roots and rhizomes. Most of these die in the fall which explains the increased reduction at this time.

Some of the sulfide produced is fairly rapidly bound up as pyrite, a form in which the sulfur is not toxic to the higher plants (Howarth 1980). But the ability of Spartina roots to oxidize sulfide in sediments is the principal mechanism by which it lives in an environment that would otherwise have toxic levels of hydrogen sulfide. Spartina also has the ability to take up dissolved sulfide and apparently oxidize it enzymatically within the roots, another possible mechanism for resisting toxicity (Carlson and Forrest 1982).

The amount of energy available to organisms through sulfate reduction is very much less than is available through oxidation of the same organic compound with oxygen. For example, the oxidation of glucose in the presence of oxygen provides a little over 39 kilojoules per gram (kJ/g) of glucose carbon; oxidation via the sulfate reduction cycle provides only about 8 kJ/g. The 31 kJ/g difference does not, of course, disappear. Since the organic matter is oxidized all the way to carbon dioxide and water, there is no energy left in organic matter. The "missing" energy, as one would suspect, is locked up in the sulfide. This sulfide diffuses to the oxidizing layers in the marsh sediments where it is then reoxidized (either chemically or by sulfide-oxidizing organisms) to produce sulfate. The energy produced by this reaction is over 30 kJ/gC, the difference between what was available to the sulfate reducers and what would have been available had the organic matter been oxidized by an aerobic organism. The oxidation of sulfide may be incomplete and produce thiosulfate or other intermediate products. Correspondingly, less energy is yielded at each step in the process, but the sum of energy from all the steps will remain about the same.

Although this much energy is made available by the oxidation of sulfide, it is not very efficiently captured by the marsh microbes. Only recently has it been shown that Beggiatoa, a common marsh microbe that oxidizes sulfide (Figure 24), can capture any significant part of the available energy (Nelson and Jannasch 1983).

Most of the sulfide oxidizers are bacteria; however, these may live within higher organisms. The bacteria oxidize sulfide as a source of energy and fix carbon, making organic matter from carbon dioxide. The host animals provide the bacteria a place to live and, in return, derive food from them. This symbiotic association has been found in mud-flat

worms in North Carolina (Ott et al. 1983) and clams living in Massachusetts eel grass beds (Cavanaugh 1983), and has recently been discovered to be the basis for life occurring around the deep-sea vents (Cavanaugh et al. 1981). It is reasonable to expect that further investigations will reveal the same symbiosis in some organisms, such as worms and clams, living in marsh sediments.

5.3.4. Carbon

The carbon cycle is discussed primarily in sections 5.1 (Productivity) and 5.2 (Decomposition). Two further points connected with the sulfur cycle shed light on processes involving carbon within the marsh.



Figure 24. Beggiatoa growing at the low edge of the salt marsh. This microbe is visible as tiny white threads on the marsh surface. The color is due to grains of sulfur that result from the microbe's oxidation of sulfide. Photo by J.M. Teal, Woods Hole Oceanographic Institution.

The first is that estimates of total CO₂ production from marsh sediments indicate there is little loss of reduced sulfur from the marsh. All of the final decomposition processes produce carbon dioxide as an end product, so the total CO₂ produced is a measure of total decomposition. Oxygen is consumed when the decomposition is via respiration and also when the decomposition products (e.g., sulfides and methane) are reoxidized. So if the CO₂ produced is balanced by the O₂ consumed, there is little net loss of carbon produced from the system (Figure 25; Howes et al. 1984). The CO₂ production is higher than O₂ consumption early in the season because reduced sulfur compounds are being accumulated; but later the relationship is reversed as the reduced sulfur is reoxidized at the mud surface.

The second point is that carbon isotopes, especially when combined with sulfur isotopes, can tell us something about the marsh food web. Carbon-13 is a natural stable isotope of carbon present in small amounts in all carbon compounds

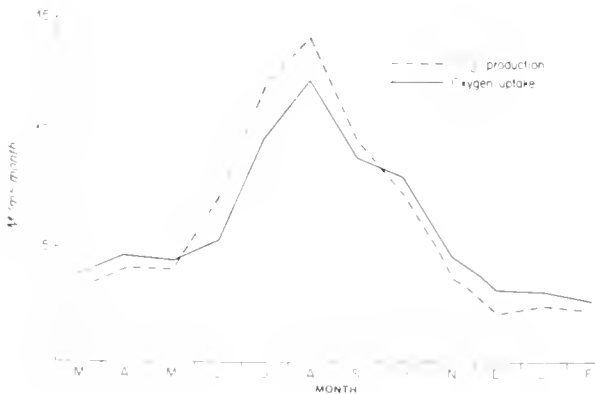


Figure 25. Annual cycle of carbon dioxide production and oxygen consumption in Great Sippewissett Salt Marsh. The total production and consumption are equal. The offset between the curves indicates the accumulation of sulfide when decomposition (as measured by CO₂) exceeds oxidation early in the year, and the reverse later in the season when accumulated sulfides are oxidized (Howes et al. 1981).

on earth. Its abundance in samples of organic matter can be analyzed and compared to a standard called PDB Chicago, which is a fossil cephalopod (a belemnite). The analytical results are expressed as d¹³C, the fraction of carbon-13 compared to carbon-12 in the sample divided by that in the standard minus one times 1000:

$$d^{13}C = \left(\frac{^{13}C/^{12}C \text{ sample}}{^{13}C/^{12}C \text{ standard}} - 1 \right) \times 1,000$$

Negative values come from samples in which there is less ¹³C than there is in the standard. Organisms should have less ¹³C in their tissues than is present in their carbon source because it takes a little more energy to build a compound with carbon weighing 13 atomic units than it takes to build with carbon weighing only 12 units. The bicarbonate in seawater has d¹³C of about 0 ppt; CO₂ in the atmosphere has a value on the order of -7 ppt. Spartina and other plants with the C-4 photosynthetic pathway (see Sect. 3.1) have values from -12 to -14 ppt. Most temperate terrestrial plants, which have the C-3 pathway, have values of -22 to -34 ppt. Phytoplankton range from about -20 to -30 ppt, benthic diatoms in the marsh from about -15 to -18 ppt.

One would expect animals to have a d¹³C value that reflects the food that they eat (subject to some minor constraints); for example, animals that feed principally upon Spartina detritus might be expected to have d¹³C values of -12 to -14 ppt. Haines (1976a,b) and Dow (1982) found this to be true for organisms like the marsh grasshopper, which feeds upon living Spartina. A similar value was found in some of the omnivorous crabs in the Georgia marshes. These crabs are very close to Spartina in the food web and at times feed directly on decaying Spartina leaves. The grass shrimp in the Georgia marshes also have values that are similar to Spartina, which is consistent with a diet of Spartina detritus. Fundulus heteroclitus d¹³C values suggest that their carbon comes from a mixture of Spartina and benthic algae carbon (via the animals that form the main part of their prey) (Kneib et al. 1980).

Other Georgia marsh animals have $d^{13}C$ values that are considerably lower, much closer to the values for phytoplankton, benthic diatoms, and terrestrial C-3 type plants than they are to Spartina. Haines (1978) suggested that these carbon isotope data support the idea that particulate organic detritus in Georgia estuarine waters comes from offshore phytoplankton production rather than from the marsh, and that the marsh is actually accumulating organic matter from offshore phytoplankton production rather than exporting detritus to the estuaries. Dow (1982) reviews the difficulties in using carbon isotopes alone to determine the origin of the food of marsh organisms.

Peterson et al. (1984) have included an analysis of the sulfur isotope, ^{34}S , in their interpretation of food webs in Great Sippewissett Salt Marsh for added resolution in determining food sources because, compared to plankton, Spartina is depleted in ^{34}S . Peterson et al. (1984) found that the mud snails Ilyanassa obsoleta and Fundulus heteroclitus were very close to Spartina in both carbon and sulfur isotopes. Marsh mussels, Geukensia demissa, varied in isotopic composition showing that they fed principally on phytoplankton near the marsh entrance to the bay and about equally on Spartina detritus and phytoplankton in the innermost reaches of the marsh.

CHAPTER 6. SALT MARSH VALUES AND INTERACTIONS

6.1 VALUES

For some decades, salt marshes have been considered or known to be valuable for a number of reasons. They are aesthetically pleasing for their open coastal spaces and attractive expanses of grasses. They are also valuable as habitat for shore birds and waterfowl, and as refuges and nursery areas for many kinds of small and young fishes; these values are associated with the exceptionally high productivity of the regularly flooded intertidal wetlands.

Marshes are valuable to the public as a whole, to those who harvest fish and shellfish, and, of course, to those who own the marshes. To some owners, the principal value of a marsh is as a piece of real estate, which often means they either fill in the marsh for building or dredge it for boating. But, aesthetic values can also be important for the owner directly. For example, in 1965 people in New England were willing to buy salt marshes for from \$100 to \$1,000 an acre (as much or more than they would have had to pay for poor farmland) just to acquire the view, access to the water, or "a place to fly a kite," with the knowledge that the buyers could make no other appreciable use of the "land" (Mass. Reporter 1976). With these facts in mind, we can look at the present situation with regard to those general values of wetlands.

6.2 MARSH EXPORTS

There is still considerable interest in the question of outwelling of detritus. In the 1962 description of energy flow in a Georgia salt marsh, Teal estimated export from the marsh surface of approximately 40% of the marsh productivity. While export estimates were

extrapolated to the estuary, the author's data actually referred only to export from the grassy portions of the marsh to the marsh creeks.

Odum (1980) summarized evidence that the export does go further than the marsh creeks and that there actually is an outwelling to coastal waters. Hopkinson and Wetzel (1982) showed that the nutrient and oxygen fluxes in a Georgia coastal benthic ecosystem supported Odum's conclusion. Direct measurement has shown the same general level of export from Great Sippewissett Salt Marsh as the 1962 estimate from the Georgia marsh. Particulate carbon (detritus) equivalent to 40% of the aboveground production is exported from Great Sippewissett Salt Marsh to Buzzards Bay (Valiela and Teal 1979). Prouse et al. (1983) indicated a sizable export of plant material to estuarine waters from marshes in the Bay of Fundy. Schwinghamer et al. (1983) demonstrated that salt marsh detritus is widely distributed in the upper parts of the Bay of Fundy. Nixon (1980) concluded that available data indicate that the total flux of organic carbon from salt marshes is between 100 and 200 g C/m²/yr.

The structure of a marsh system affects its export-import role. Odum et al. (1979b) have classified marshes into three types according to their flow and tidal exchange characteristics. The first are those in which there is a restricted tidal flow. The flow may be restricted by a long and narrow exchange channel, by natural sills with a depositional basin on the marshward side of them, or by man-made restrictions such as dikes with culverts or bridges with a constricted channel for the passage of tidal flow. The second type includes marshes where the flow is more open and unrestricted. The third has completely free flow. All three types of

marshes are common along the east coast. The exchanges determined by these morphologies would be enhanced by increased tidal amplitude or increased freshwater input. It seems logical that the first type of salt marsh would normally have restricted export of organic matter, while the other two would be characterized by a much greater tidal export.

The age of a marsh may have a significant influence on its behavior as an exporter of organic detritus. A marsh eventually fills its basin to the high tide level and acts as a sediment sink only in relation to the rise in sea level. For example, the Great Sippewissett Salt Marsh exports suspended particulate organic carbon through the marsh creek to Buzzards Bay while the younger Flax Pond Marsh shows net import of suspended particulate organic carbon from Long Island Sound (Table 7). Houghton and Woodwell (1980) indicate that there is a large export of litter in the form of dead *Spartina* stems from Flax Pond, principally at times of storms. As Dow (1982) points out, "Even systems which import organic carbon to marshes, based on sampling of selected tidal cycles, can become

exporters when catastrophic events are considered."

The significance of organic carbon export must be considered in the context of the coastal zone it reaches. Nixon (1980) emphasized this, concluding that the export of organic carbon "may provide a . . . significant fraction of the open water primary production in many areas of the South . . . but it does not appear to result in any greater production of . . . fish than is found in other coastal areas without salt marsh organic supplements." Nixon was writing about production on a regional basis. On a local basis, enhancement of production can be important to the population of a small area. The contribution to the total fish catch in Massachusetts of a small port where all of the fishing is inshore from small boats might be almost insignificant. While the most valuable portion of the State catch comes from the Georges Bank, that local catch may be very important to the citizens of the small port and essential to their economy. An inshore fishery in Massachusetts may be marsh- and estuarine-dependent even though the offshore fishery is totally independent of these coastal features. Recreational fishing is almost

Table 7. Comparison of age and properties of two northeast United States salt marshes (Valiela 1982).

Age and properties	Flax Pond Marsh	Great Sippewissett Marsh
Age of marsh (yr)	180	2,000
Indicators of maturity:		
Average accretion rate (mm/yr)		
Expanding part of marsh	1.5-37	14
Established part of marsh	2-6.3	1
(Accretion/net production) x 100% in terms of carbon	37	5
% of area non-vegetated	47	37
% of area covered by tall <i>Spartina alterniflora</i>	37	18
Average aboveground standing crop of <i>S. alterniflora</i> (g/m ²)	975	350
% of area in high marsh	7	18
Number of higher plant species	13	22

totally inshore so both catch and economics are dependent on coastal features.

There is little doubt that marshes export organic matter in the form of young fish that enter the marshes as larvae, postlarvae, or juveniles in early summer. During the warm part of the year they grow rapidly, becoming better able to survive in coastal waters in the autumn (Werme 1981). Turner (1977) has shown that there is a significant correlation between the areal extent of subtidal and regularly flooded intertidal vegetation in an estuary and the size catch of the inshore shrimp fishery in the Gulf of Mexico. Successful commercial blue crab fisheries are associated with salt marshes as are sport fisheries (Pomeroy and Wiegert 1981).

A timely visit to most salt marshes along the Atlantic coast will convince a visitor that the marsh killifish is an important food source for wading birds and as such provides the basis for an export in the form of heron and egret biomass. In Georgia, the bird biomass similarly exported may be that of the white ibis which seemed, in one Georgia nesting area, to be feeding almost exclusively on grass shrimp from salt marshes (Teal 1965). Black ducks feed extensively on Hydrobia and Melampus from salt marshes. Canada geese are very attracted to and take a significant amount of Spartina production from salt marshes in Cape Cod (Buchsbaum et al. 1982).

6.3 POLLUTANTS AND MARSHES

6.3.1. Heavy Metals

Marsh sediments act as filters and tend to accumulate heavy metals. Most heavy metals form insoluble sulfides, and are sorbed onto clays, organics, and precipitates such as iron hydroxides. The marsh sediments have high sulfide concentrations so that the insoluble metal sulfides tend to be deposited in the sediments and accumulate there. As a result of several decades of research on the behavior of heavy metals in salt marshes, much is now known about what actually takes place when heavy metals

arrive in salt marshes. The interested reader should look at reviews by Giblin et al. (1980), Nixon (1980), Giblin (1982), and Teal et al. (1982).

Sea level has been continuously rising since the retreat of the Pleistocene glaciers. This regular rise makes it possible to assign approximate dates to core depths independent of dating the material in the core itself. Figure 26 is a profile of lead found in cores from New England marshes. The concentrations increased dramatically toward the surface, i.e., in the more recently deposited sediments. This increase began about the time market hunting of shore birds in the marsh was prevalent and was accelerated during industrialization. The present high level is correlated to the burning of leaded gas in automobiles. The high sample value from the Neponset River Marsh was taken near a major highway (Banus et al. 1974). A similar profile has been found in other marshes (Siccama and Porter 1972; McCaffrey 1977). These marsh studies all indicate that as

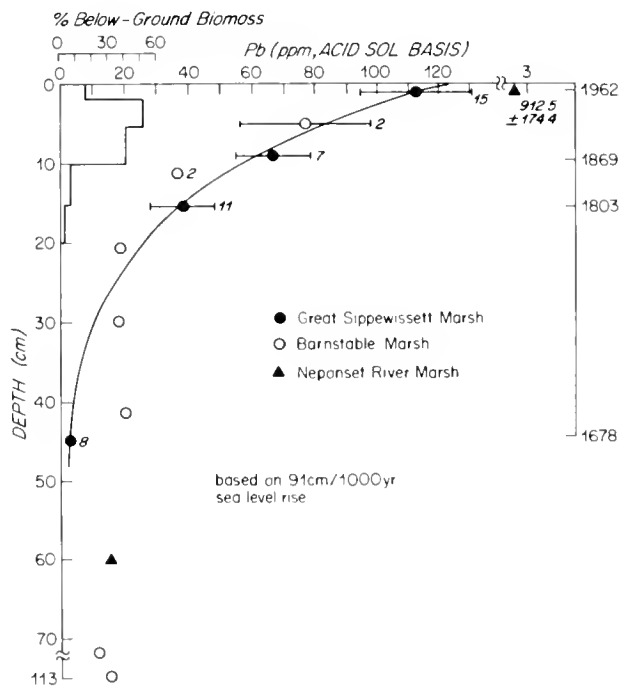


Figure 26. Lead distribution and concentration in cores from New England salt marshes (Banus et al. 1974).

industrial activity has increased and more metals have been discharged into the environment, the levels of the metals in marsh sediments have also increased.

At the other extreme, Giblin et al. (1980) found that cadmium forms soluble complexes as well as sulfides in seawater. If the application or supply of cadmium to the marsh is stopped, it only takes about 2 years for the metal to disappear from the marsh muds. Other metals occupy intermediate positions between lead and cadmium in their transit through the marsh. Metals such as copper and chromium are fairly well retained by marsh sediments; metals such as zinc pass through the system rapidly. Where salt marsh retention of experimentally applied heavy metals has been examined (e.g., the Great Sippewissett Salt Marsh), retention of the added metals is always less complete than that of the "naturally arriving metals in the control plots" (Giblin 1982); perhaps this is because the "naturally arriving" metals are more effectively bound to particles. Giblin (1982) also stated, "Although in a geochemical sense wetlands are sinks for some metals, . . . they may not function as efficient traps for all metals."

The marsh grasses stabilize sediments so that they stay in place, become anoxic, and are thereby able to interact with heavy metals in seawater. In addition, grasses take up metals, to a varying extent, from the sediment. Metals are concentrated in leaves and stems of the grass. When the plant dies and becomes detritus, these contained metals are exported from the marsh to surrounding waters. Giblin (1982) summarizes data showing that there is little contamination of tissues of salt marsh plants by arsenic, manganese, mercury, or lead but considerable contamination by cadmium, zinc, copper, and chromium. In other words, if salt marsh plants and sediments are heavily contaminated with certain metals, they can form a long-term source for contamination of coastal areas.

Plants can also mobilize heavy metals by oxidizing sediments, a process which turns insoluble sulfides into soluble thiosulfates and sulfates. In experimental plots at Sippewissett, where

metals were added along with nutrients in sewage sludge, mobilization of metals from sulfides was accentuated. The nutrient addition stimulated Spartina growth which accentuated the tendency of Spartina roots to oxidize sediments. This process both stimulated mobilization of metals from sulfides and enabled enhanced plant uptake of metals applied to the marsh in the sludge. The stimulation of production and sediment oxidation after applications of this type may be delayed for one or two seasons so that it may initially appear that marsh sediments are more efficient at sequestering or holding heavy metals than may eventually prove to be the case.

There is additional accumulation of heavy metals in dead leaves and fresh detritus formed from marsh plants as they begin to decompose (Breteler et al. 1981a). Detritus may be enriched to potentially toxic levels by uptake of metals in the more oxidized surface layers of marsh sediments or by metals associated with surface organic layers, just as the detritus is about to enter the food chain. If the amounts of metals are small, they will have no effect, but in larger concentrations, the marsh products may reach toxic levels.

There is little data on what levels of heavy metals are damaging to the marsh itself. The heavily polluted Berry Creek portion of Hackensack Meadowlands contains so much mercury that it could be considered a mercury ore. Such extreme cases are rare and considerably lower levels are far more common. In the Great Sippewissett Salt Marsh, there is no indication that the marsh ecosystem has been damaged by 12 years of experimental application of sewage sludge containing heavy metals at levels nine times higher than those normally used in sludge disposal in uplands (Giblin 1982).

6.3.2. Organic Contaminants

Though we have some knowledge of the behavior of heavy metals in a salt marsh, far less is known about the behavior of organic pollutants. The added sewage sludge in the Great Sippewissett Salt Marsh studies contained aldrin during the early years, at which time there was a 50% reduction of fiddler crab populations in

the treated areas (Figure 27; Krebs et al. 1974). Aldrin was apparently closely bound to sediment particles because the effect was absent as little as 1 m downstream from the treated area (Krebs and Valiela 1977). Judging from its lack of movement in the sediments, aldrin slowly degraded in place just as DDT does in anoxic sediments. Aldrin disappeared from the sludge after its use was banned in 1972; fiddler crab populations returned to pre-aldrin levels within about 1 year (Teal et al. 1982).

Information is also available on the effects and persistence of other organic pollutants, particularly petroleum. In 1969, 2,000 barrels of No. 2 fuel oil from the barge *Florida* were spilled in Wild Harbor at West Falmouth, Massachusetts. In the most heavily affected areas, the oil persisted in sediments for as long as 12 years, although over 90% of the area

recovered within about 6 years. "Recovery" was measured in terms of a lack of either killing *Spartina alterniflora* or preventing its regrowth (Teal and Howarth 1983). Hydrocarbons from the spill reduced population levels of *Uca pugnax* much as aldrin had (Krebs and Burns 1977). Post-spill levels of more than 100 µg of the lighter hydrocarbons per gram of mud killed both *Spartina* and fiddler crabs (Burns and Teal 1979; Hampson and Moul 1979).

The persistence of oil in the sediments acted like a predator or trap for the crabs. Resident crabs in contaminated sediments died; in response to their absence, neighboring populations expanded into the contaminated areas and the invading individuals died in turn. Overwintering young crabs were the most sensitive, probably because they were in intimate contact with the contaminated sediments in their burrows (Krebs and Burns 1977).

There are also studies of the persistence of hydrocarbons contained in the sewage sludge added experimentally to Great Sippewissett Salt Marsh. These hydrocarbons are those that survived both the sewage treatment and sterilization necessary before the sludge is sold. Preliminary studies indicate that there is little buildup of these hydrocarbons in treated marsh sediments or in untreated nearby sediments (J.M. Teal, unpubl. data); this suggests that the hydrocarbons must degrade quite rapidly.

6.3.3. Nutrients

Marshes have been considered for use in the treatment of sewage. In fact, one of the highest economic values placed on marshes is arrived at considering them in this context (Gosselink et al. 1973). It is, therefore, important to know what the effects of such use would be. The Great Sippewissett Salt Marsh fertilization experiments were designed partly to study these effects and will be used as an example.

The experiments of Great Sippewissett Salt Marsh measured the marsh's retention of nutrients to evaluate the possible eutrophication of the waters associated

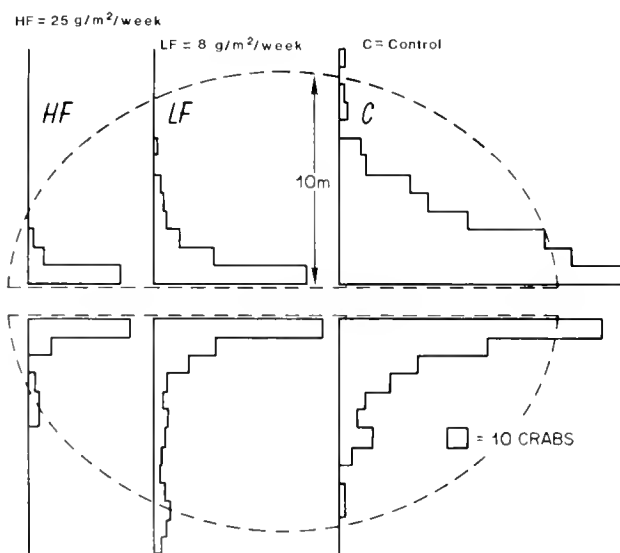


Figure 27. Distribution of fiddler crabs (*Uca pugnax*) in marshes receiving sewage sludge. The duplicate censuses are shown extending back from the creek next to one another for comparison although all were made in the center of the respective plots (the size of the plots is indicated by the dashed line) (from data of Krebs and Valiela 1977).

with the marsh. Nutrients were added once every 2 weeks as sewage sludge solids. During the summer, when the grasses were actively growing, only 6% to 20% of the applied nitrogen and 6% to 9% of the applied phosphate were lost in tidal waters (Valiela et al. 1973). When nutrients were added as a dilute solution via a spray irrigation system, about 90% of both nitrogen and phosphorus were retained during the growing season; in spring and fall, 25% to 40% were lost to ebbing tidal waters.

The biggest effect of the addition of sewage to this salt marsh was the stimulation of marsh productivity by nitrogen. The increased production of grasses and algae stimulated production of the herbivores, detritivores, and the rate of plant decomposition. There were also changes in marsh structure. *Spartina alterniflora* plants changed from the short to the tall form. The stems became thicker and the plants more widely spaced--features characteristic of the tall form of the grass that grows on creek banks (Valiela et al. 1978a). This change made the surface of the marsh more accessible to predatory fishes which were then better able to maneuver between the more widely spaced stems.

Added nitrogen also increased the nitrogen content of grass tissues by about 1% (Figure 28; Vince et al. 1981). This was enough to make the grass leaves more attractive as food for geese and voles. In fertilized plots, voles cut off as much as 30% of the *Spartina*, although they ate only a little of the base of each piece cut. Their effects were nearly absent in control plots (Valiela et al. 1985). There were even more dramatic increases in the abundance of insect herbivores in the fertilized plots (Figure 29). The detritus formed was also enriched in nitrogen and increased the production of detritivores (e.g., marsh amphipods and snails) by 2 to 5 times (J.M. Teal, unpubl. observ.). In Great Sippewissett Salt Marsh, even the largest additions of nitrogen (2.5 g N/m²/week) did not seem to damage the marsh system. However, there was a change in the relative abundance of *Spartina* and *Distichlis*. (Figure 30). *Spartina alterniflora* exhibited maximum production at relatively low N levels,

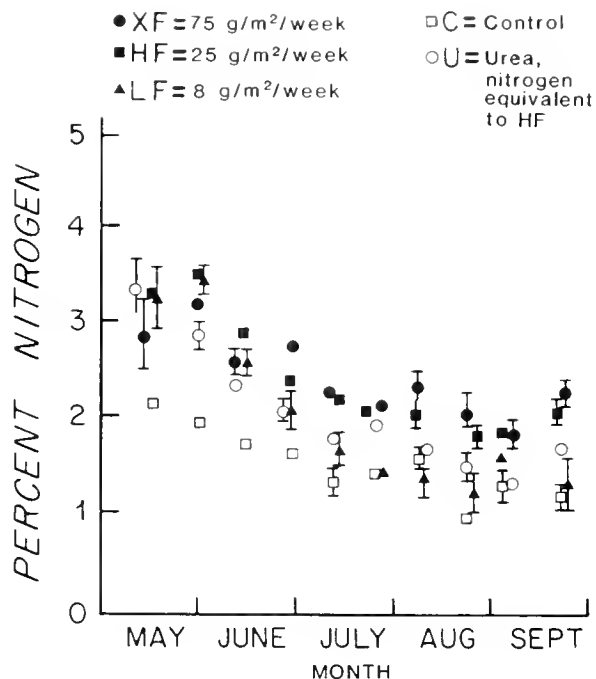


Figure 28. Total nitrogen content of *Spartina alterniflora* grown in experimental plots at Great Sippewissett Salt Marsh through the growing season. Values are mean percent dry weight \pm standard error.

while *Distichlis spicata* continued to increase production as the nitrogen addition rate was increased.

Spartina production increased over time, but there was a relative decrease in standing crop after the first 4 years (Figure 31). Valiela et al. (1985) suggested that this decrease may have been caused by increased water loss by transpiration of the more vigorous plants which led in turn to increased soil salinity, or by increased herbivory in fertilized plots. Both processes might also have led to the formation of the patches of glasswort, *Salicornia europaea*. *Salicornia* is an opportunistic annual plant species that became a conspicuous part of the marsh in the second and third years following high levels (c. 2,000 kg/ha/yr) of nitrogen addition. This species disappeared as it was selectively

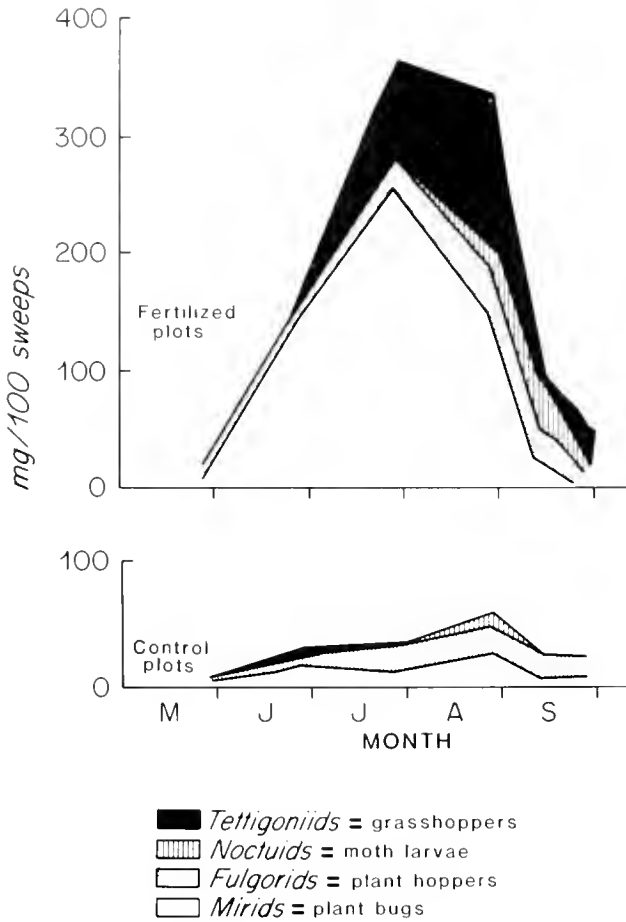


Figure 29. Abundance of herbivorous insects in Great Sippewissett Salt Marsh control and fertilized plots. Samples were taken with a sweep net (data from Vince 1979).

fed upon by a chrysomelid beetle, *Erynephala maritima*, and was replaced by invading rhizomes from the surrounding *Spartina* (Figure 32; Valiela et al. 1982). Interestingly, the *Salicornia* could survive at the lowest tidal levels because the beetle does not do well if submerged too much.

Probably most New England salt marshes are polluted to some extent, if only by pollutants carried in the air and coastal waters. In the vicinity of cities, some are heavily polluted. But aside from repeated heavy oiling, digging, and filling-in, salt marshes seem to survive most human insults rather well. In all of the experiments in Great

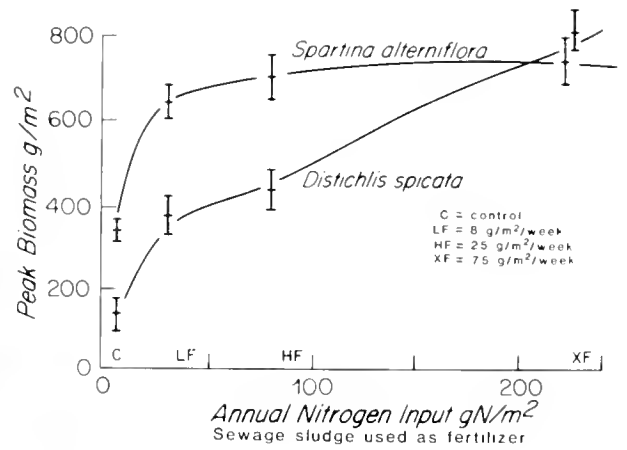


Figure 30. Responses of two species of marsh grass to rates of nitrogen fertilization. The response of *Spartina* levels out at about the dosage used in LF plots, while the response of *Distichlis* continues to rise to the highest rates of N addition used in XF plots. (Valiela and Teal, unpubl. data, Great Sippewissett Salt Marsh, MA).

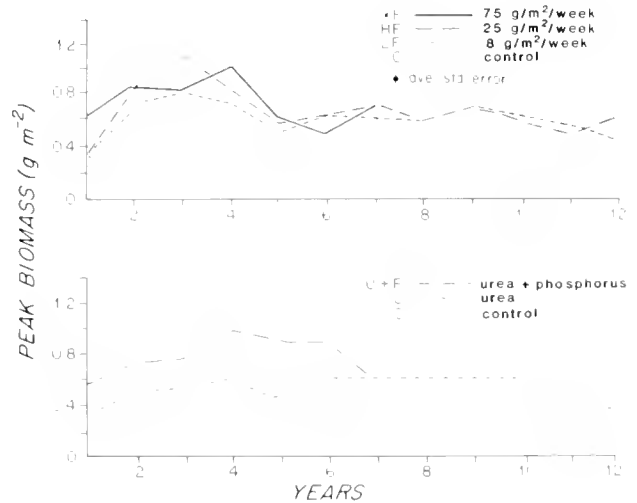


Figure 31. Long-term effects of fertilization regimes on the annual aboveground peak biomass of *Spartina alterniflora*. Standard errors omitted for clarity. Control: sewage sludge fertilizers, LF and HF; and urea at nitrogen level equal to HF were started in 1970; XF in 1974; and U+P at a level equal to HF in 1975. All are graphed according to years from initiation of experiment to facilitate comparisons (Teal and Valiela, unpubl. data, Great Sippewissett Salt Marsh, MA).

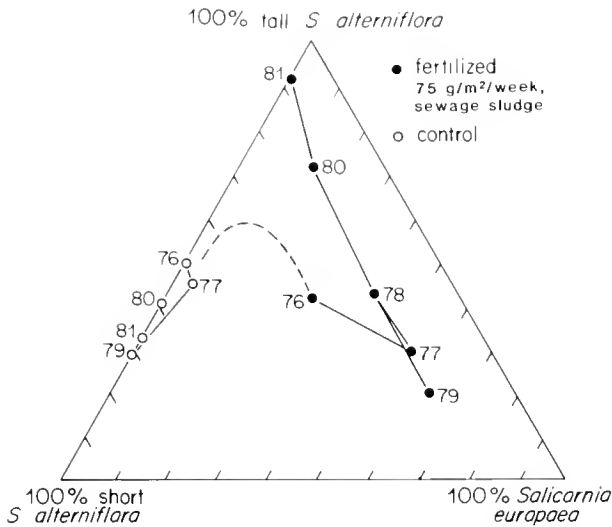


Figure 32. Distribution of percent cover between the three major plant types in Great Sippewissett Salt Marsh regularly flooded areas between 1976 and 1981. Dashed line shows presumed trend of fertilized plot based on other observations. There has been little change in the control area but great changes in vegetation cover in plots highly enriched in nitrogen.

Sippewissett Salt Marsh, no clearly detrimental effects of sewage sludge on marsh plants were demonstrated, in spite of the heavy metals in the sludge. The observed changes in the marsh ecosystem were mainly the results of changes in nitrogen relations within the marsh

system. Nitrogen first affected plant production and structure, with consequent changes in animal feeding and plant decomposition. The marsh ecosystem itself seems not to have suffered any degradation.

On the other hand, some of the marsh products we are interested in (such as shellfish), may show elevated levels of heavy metals in polluted New England salt marshes. This certainly affects their value to human society and reduces it to zero if the shellfish grounds must be closed. If the marsh pollution includes pathogens, shellfish may become contaminated with the pathogens and have to be depurated in cleaner waters to make them safe for human consumption. However, marshes may, in fact, reduce pathogens. Many details about the function of these systems and of their reactions to abuse are still not well understood. Marshes are remarkably resistant and the fact that a salt marsh is polluted is not a reason to write it off as lost or even as without considerable value.

As our knowledge of the functioning of these rich intertidal grasslands has grown, we have learned better how to appreciate them. If we have been overenthusiastic about some aspects of their role in coastal ecology, we have surely been less appreciative of some of their other characteristics. On balance, salt marshes remain of considerable value to us and are well worthy of both our concern and our protection.



Common egret (*Casmerodius albus*) feeding in salt marsh. Photo by B.L. Howes, Woods Hole Oceanographic Institution.

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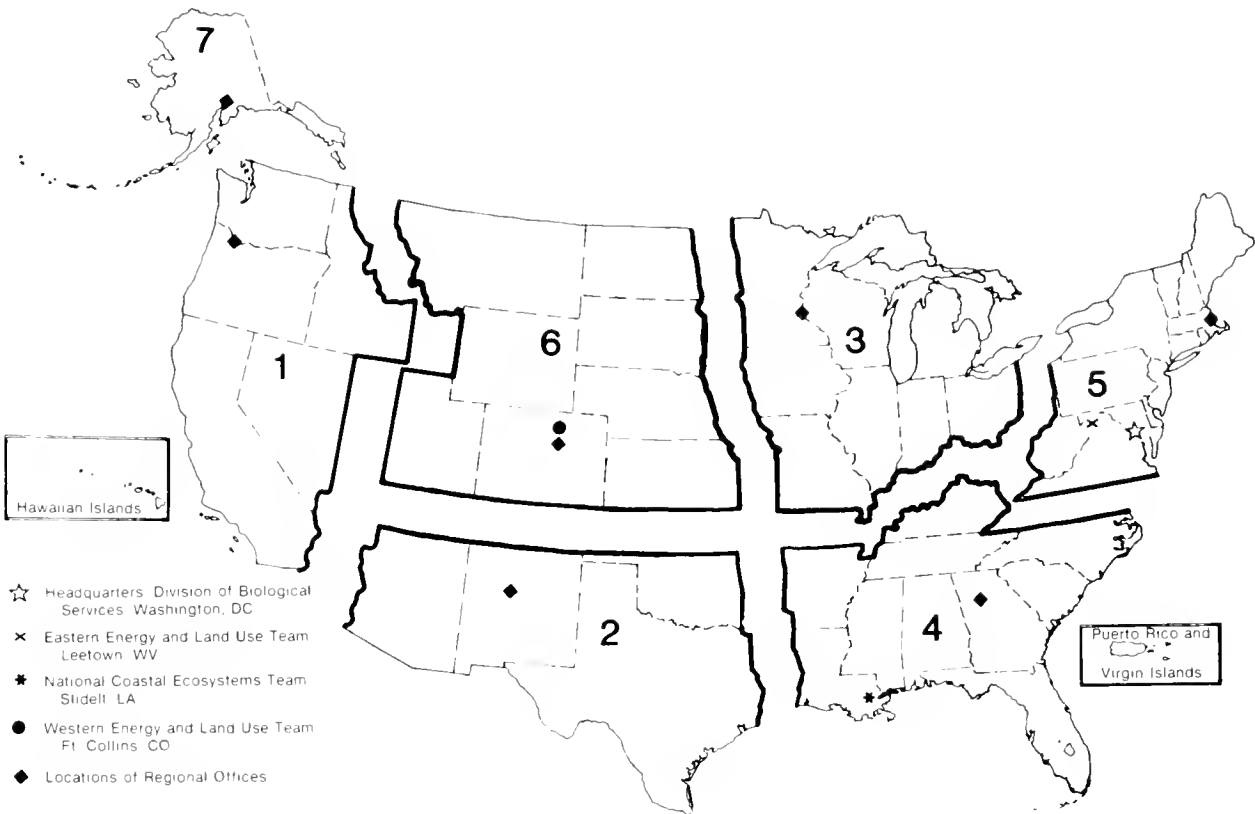
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16. Abstract (Limit: 200 words) The report summarizes and synthesizes information on the ecology of intertidal, regularly flooded <i>Spartina alterniflora</i> marshes in New England. The report focuses on the Great Sippewissett Salt Marsh in Falmouth, Massachusetts, where the author and other scientists have investigated the basic structure and functions of these wetlands. Marsh plant productivity and decomposition and the related processes of bacterially mediated cycling of nitrogen, phosphorus, sulfur, and carbon through the marsh are discussed in this profile. These marshes are dominated both vegetationally and ecologically by a single emergent plant species, <i>Spartina alterniflora</i> . Dead decomposed <i>Spartina</i> , associated bacteria, benthic algae, and fungi on the marsh surface support large populations of a few dominant species of macroinvertebrates, such as bivalve mollusks and fiddler crabs, and small fish, such as mummichogs and striped killifish. Salt marshes have value as possible exporters and transformers of biogenic materials. Studies at the Great Sippewissett Marsh have considered the role of marshes as processors of human-derived materials such as petroleum products, heavy metals, and nutrients in sewage sludge.				
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