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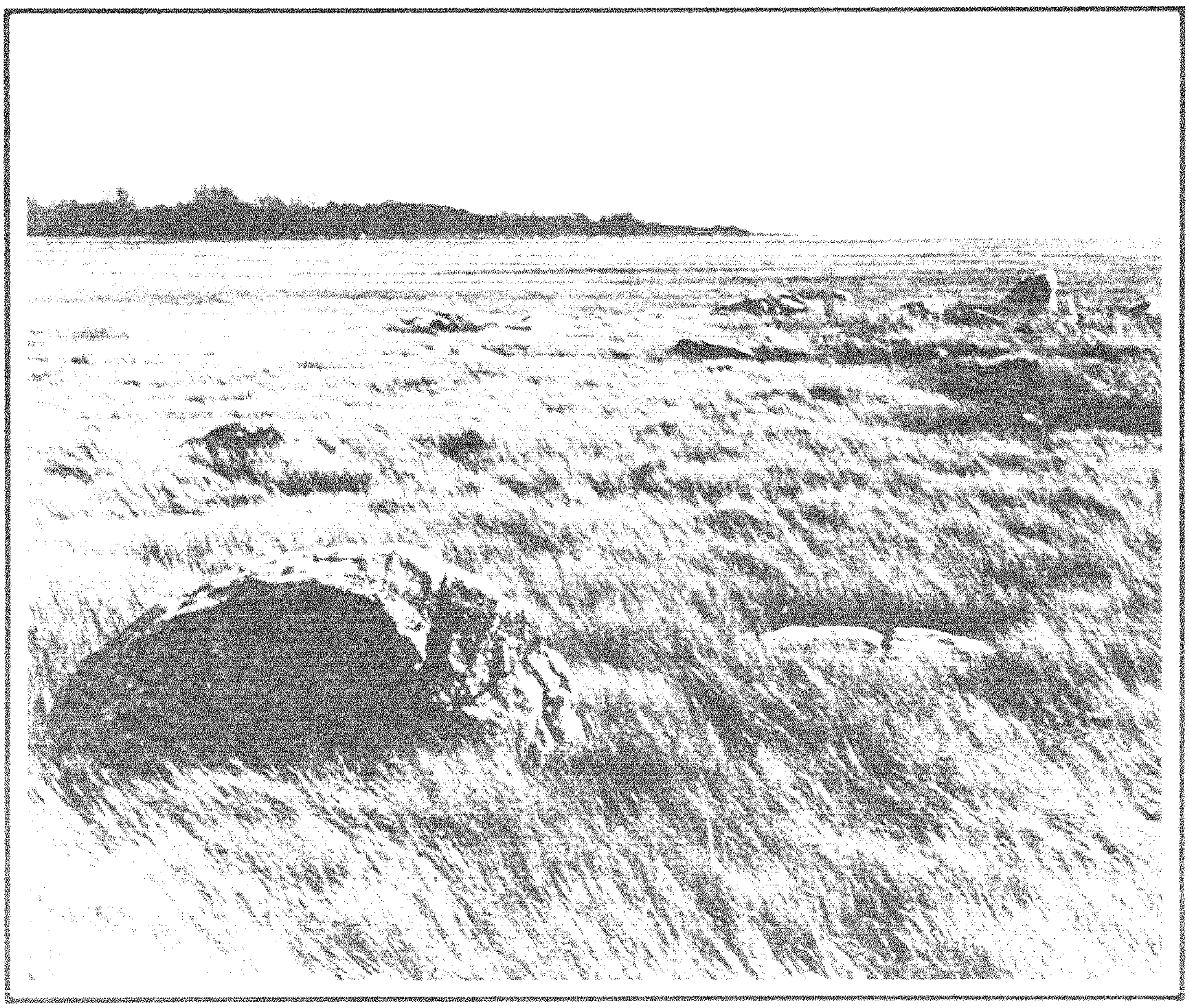
THE ECOLOGY OF NEW ENGLAND HIGH SALT MARSHES: A Community Profile



Fish and Wildlife Service

U.S. Department of the Interior

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THE ECOLOGY OF NEW ENGLAND HIGH SALT MARSHES:

A Community Profile

by

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PREFACE

In his classic description of the New England shoreline, Douglas Johnson (1925) recognized the coastal salt marshes found from Maine through Long Island as a type distinct from those to the north ("Fundy Type") or south ("Coastal Plain Type"). His distinction is still considered useful, and I have tried to confine this community profile to observations, measurements, and experiments which have been made in New England Type marshes. Although it is widely recognized that New England marshes are characterized or distinguished by a higher organic content of the marsh peats, to my knowledge no one has yet shown rationale for not extrapolating many of the concepts gleaned from the much more extensively researched Coastal Plain marshes to this area.

The focus of this profile is primarily on the high marsh in New England rather than the low, creekbank, or regularly flooded areas which have received most of the attention in the ecological literature. All of the marsh is intertidal, and it must be understood and managed as a geomorphological and ecological unit. I hope it will be useful to those working in coastal planning, management, and research to bring together much of the information that has been developed on this less frequently discussed, but important area of the marsh.

While the high marsh is commonly thought of as lying between mean high water and spring high water, the profile drawn here has not always followed such strict, and somewhat arbitrary, limits. Similarly, the major emphasis is on the *Spartina patens*-*Distichlis spicata* community, but in several cases I have included information from the stunted *S. alterniflora* zone. The development of marshes and the zonation of different species, especially plant, receive more attention in this profile than do animal populations or community metabolism. This largely reflects the relative abundance of information rather than my own biases. I can only hope that the gaps which are so evident in this profile might stimulate future work in these areas.

Salt marshes of the New England Type comprise less than 2% of the marsh area along the Atlantic coast of the United States (Reimold 1977), and the high marsh may amount to only 25% to 50% of that 2%. The ratio of people to wetland, however, is the highest in the country (Gosselink and Baumann 1980), and there is a long tradition in New England of using and valuing the marshes. I hope this profile will contribute to that tradition.

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Kingston, Rhode Island
June 1980

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I am grateful to a number of reviewers who read and criticized earlier drafts of this profile, including Virginia Lee, Wiley Kitchens, Ed Pendleton, John Gallager, Frank Daiber, Joseph Ustach, Rick Linthurst, Curt Laffin, Ralph Andrews, and Ralph Tiner. Their help eliminated errors and obscure passages. For those that remain, I am responsible. Germaine Webb typed and retyped the manuscript with her usual skill, patience, and good humor, and I thank her for it.

Rocks in the high marsh at Wequetequock-Pawcatuck, Connecticut, where Miller and Egler (1950) carried out their benchmark study of zonation on a New England salt marsh during the late 1940's.

CHAPTER 1

ORIGIN AND DEVELOPMENT OF THE MARSHES

It may seem odd to begin with an observation about rocks, but they were the first things I noticed when I went out across a New England salt marsh. They seemed out of place; marshes were sedimentary environments, not high energy places like sea cliffs or cobble beaches. But my images had been formed in Coastal Plain marshes to the south, where larger supplies of sediment from the rivers developed mineral soils around the grasses and helped to build the marshes outward across accreting shoals. The northern marshes filled with peat were different, and they made some processes that were operating all along the coast more conspicuous. There had been other oddities, like tree stumps, in many marshes I had seen, but for some reason the rocks caught my attention more forcefully. They were a dissonant note--cold, inorganic, gray, and unmoving amidst all that green and windblown grass. It was a useful lesson to see them in the middle of a *Spartina* meadow, and a reminder of the complexity of marsh development.

Since the present-day marshes are still responding to the forces that produced them, it is of more than historical or academic interest to investigate marsh development in some detail, particularly with respect to the Northeastern United States. The story of how the rocks came to be there, or rather of how the marsh grass came to grow around the rocks, is an interesting one that began as a formal scientific inquiry at least 125 years ago.

EVOLVING CONCEPTS OF MARSH DEVELOPMENT

Subsidence and Sea Level Rise--the Mudge Model

In 1857, B.F. Mudge (1862) presented a paper to the Essex, Connecticut, Institute in which he described his findings from a core taken in the Romney Marsh, near Lynn, Massachusetts, at a site "about one foot above ordinary high water mark and only overflowed by the higher spring tides." The remarkable feature of this core was that it showed the roots and rhizomes of the marsh grass extending down uniformly to a depth well below normal low tide. Because the grasses grew only above the normal high water level, Mudge concluded that the marsh had been subsiding and that the subsidence had been counter-balanced by a upward accretion from grass growth and subsequent sediment deposition. The process responsible for the subsidence of the marsh was not known at that time, and Mudge speculated that it might be due to erosion beneath the marsh caused by a "current of water in the diluvium under the clay."

As more cores were examined from many marshes, however, it became clear that Mudge's findings were too common to be explained by such a local phenomenon (Johnson 1925). The growing acceptance of glacial theory and sea level rise soon provided a more satisfactory general explanation for the thick deposits of marsh peat (Davis 1910). The development of ^{14}C dating techniques shortly after the Second World War made it possible to begin study of the quantitative relationship between marsh development, sea level rise, and land subsidence since the last glaciation--the Holocene Transgression.

Using radiocarbon-dated material from present-day salt marsh peat as well as from relic peat deposits and other materials on the continental shelves, workers have developed curves relating sea level to the land over the past 35,000 years. While there is some uncertainty in the data and various versions of the curve are offered from time to time (see Emery and Uchupi 1972), the general picture suggests a rapid fall in sea level which began about 20,000 years ago and continued for some 5,000 years. This rapid fall was followed by a rapid rise in sea level until about 7,000 or 8,000 years ago when the rate of rise began to slow appreciably (Figure 1). Virtually all present-day marshes found in the Northeastern United States appear to have become established only during the past 3,000 to 4,000 years (Redfield 1972; Rampino and Sanders 1980). The average rate of relative sea level rise during this recent period of marsh building has been about 1 mm/yr in this region (Table 1), and it is commonly thought that marsh development can only take place when the rate of sea level rise is slow. But relic salt-marsh peat has also been found on the continental shelf ranging in age from 5,000 to 11,000 years; a period when the average rate of sea level rise may

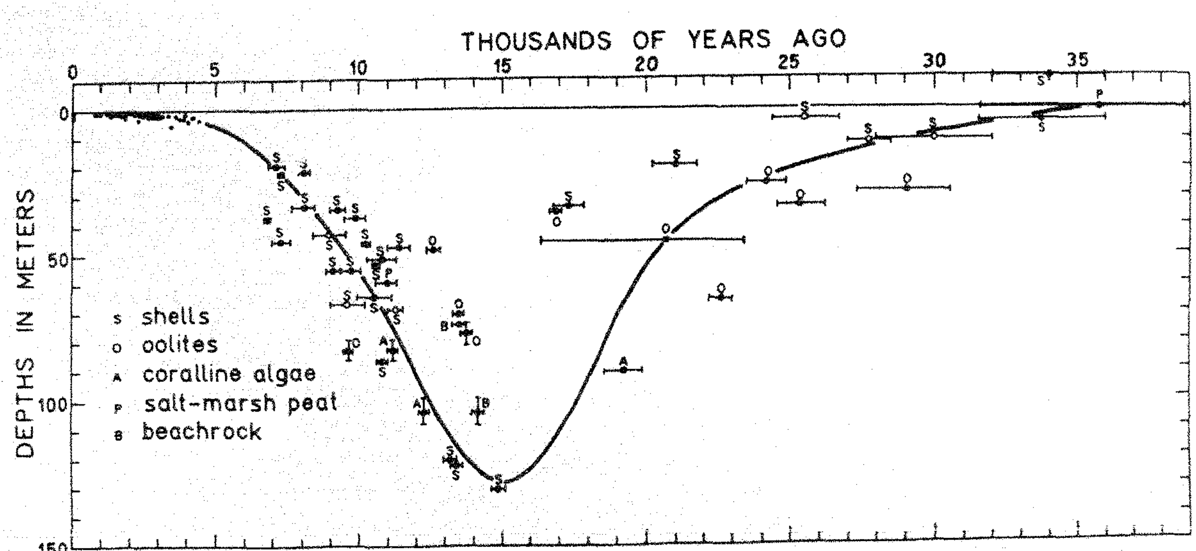


Figure 1. Sea level relative to the present level on the Atlantic continental shelf during the past 36,000 years (Emery and Uchupi 1972, based on Emery and Milliman 1971).

Table 1. Rates of sea level rise relative to the land in the Northeastern United States.

Long-term rates for the past 2000 to 3000 years estimated from age-depth curves for ^{14}C-dated material in marshes and continental shelf sediments (Bloom and Stuiver 1963; Redfield 1967; Keene 1971; Oldale and O'Hara 1980; Rampino and Sanders 1980)

	mm/yr	inches/100 yr
New Hampshire	1.1	4.3
Northeastern MA[a] (probably also NH and ME)	0.8	3
Southeastern MA[a]	1.0	3.9
Cape Cod to Virginia	1.1	4
Connecticut	0.9	3.5
Long Island, NY	1.0	3.9

Short-term rates for the past 35 years (1940-75) from tide gauge records (Hicks 1978)

	mm/yr
Eastport, ME	3.5
Portland, ME	2.0
Portsmouth, NH	1.8
Boston, MA	1.5
Woods Hole, MA	2.9
Newport, RI	2.5
New London, CT	2.6
New York, NY	3.1

[a]The published value of 0.01 m/100 yr is a typographical error in Oldale and O'Hara 1980 (Charles O'Hara, personal communication).

have been 16 mm/yr (Emergy and Uchupi 1972).

At least two possible explanations exist for this apparent discrepancy. The first is that marsh development is possible during times of more rapid sea level rise than has been experienced, on the average, during the past several thousand years. The second is that there have been times when sea level rise was much slower than it has been on the average, and that those periods were times of marsh development.

Analyses of tide gauge records (Hicks 1978) have shown that the relative rise of sea level along the Northeastern United States during the past 35 years has been two to three times the recent long-term average (Table 1). Studies of salt-marsh accretion rates in this area have shown that the marshes are capable of "keeping up" with this rate of rise (Table 2), and Redfield (1972)

Table 2. Estimates of accretion rates in salt marshes along the Northeastern United States

Location	Vegetation type		Accretion (mm/yr)
Barnstable Marsh, Cape Cod MA[a]	*Spartina alterniflora*	"Young marsh"	18.3
		"Older marsh"	1.5-2.7
Barn Island, CT[b]	*S. patens*		2.0
Great Island, CT[b]	*S. patens*		3.8
Hammock River, CT[b]	*S. patens*-*Distichlis spicata*		3.6
	Phragmites communis		17
Stony Creek, CT[b]	*S. patens*-dwarf *S. alterniflora*		6.6
Nells Island, CT[b]	*S. alterniflora* → *S. patens*		6.0
Farm River, CT[c]	*S. patens* (mean for top 14 cm)		3.0
Flax Pond, Long Island, NY[d]	*S. alterniflora*		2.5

[a]Redfield (1972).
[b]Harrison and Bloom (1977).
[c]McCaffrey (1977).
[d]Flessa et al. (1977).

found that a young, actively growing portion of the marsh at Barnstable, on Cape Cod, Massachusetts, increases in elevation at a rate exceeding 50 mm/yr. A detailed comparison of accretion rates and sea level rise over time was carried out by McCaffrey (1977) on the high marsh at Farm Creek, near New Haven, Connecticut, by using a Pb^{210}-dated core. The results showed that sea level rise was closely matched by marsh accretion, and that accretion continued even during short periods of relative sea level fall (Figure 2). However, the more rapid recent rates of sea level rise along the northeast coast are still considerably slower than the average 16 mm/yr that may have occurred during earlier marsh development.

Along the Louisiana coast, where recent subsidence rates have been about 12 mm/yr, extensive measurements by Baumann (1980) have shown that streamside marshes have had sedimentation rates of 15 mm/yr, but that more inland marsh areas have had rates of only 9 mm/yr. As a result, there has been a substantial loss of wetland. It is hard to know if this suggests a natural upper limit of about 10 to 12 mm/yr beyond which marshes cannot, on the average, keep pace. The more correct conclusion may be that, given an adequate sediment supply, the marsh grasses themselves are capable of dealing with rapid rates of sea level rise. I do not know how the past sediment supply on the northeast coast compares with the present day supply along the Gulf of Mexico; tidal

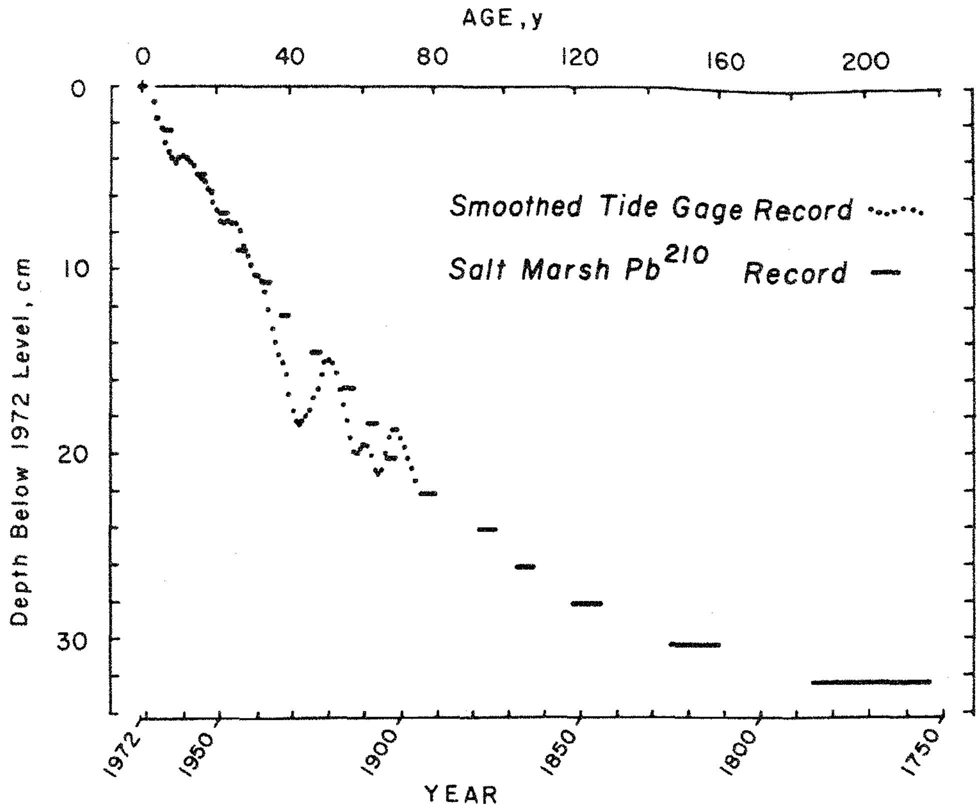


Figure 2. Variation in apparent sea level at New York City as shown by a smoothed tide gauge record and the elevation of a Spartina patens marsh in New Haven, Connecticut, calculated from the distribution of Pb^{210} in the sediment (McCaffrey 1977).

regimes are very different in the two areas. Harrison and Bloom (1977) found a positive correlation between tidal range and accretion rates in Connecticut marshes; Baumann (1980) found greatest sedimentation in Louisiana marshes during winter, when the wetlands were innundated for less time than they were during summer.

The second explanation for past marsh-building has been developed recently by Rampino and Sanders (1980), who suggested that marsh development in the Northeastern United States has been episodic during the last 10,000 years, taking place only when relative sea level remained constant for a time or went through a transient lowering in response to shorter-term climatic events. Sea level has risen over the past 15,000 years with different average rates of increase for different time increments (Figure 1). These data and other information have also been interpreted as showing oscillations in sea level, and the available information is apparently not detailed enough now to resolve the question. On the basis of ^{14}C-dated peat samples from the inner continental shelf, Rampino and Sanders (1980) concluded that there were six previous periods of marsh growth about 1,000 years apart, the most recent of which began some 4,700 years ago.

Changes in relative sea level (see Figure 1 and Table 1) are thought to reflect two components: isostatic processes that raise or lower the land surface and eustatic processes due to changes in the volume of the ocean from glacier formation and melting. The relative contribution of these components to the observed sea level change varies from place to place, but Redfield (1967) and Emery and Uchupi (1972) were able to use ^{14}C-dated peat from salt marshes along the Atlantic and Gulf of Mexico coasts to arrive at an estimate of about 0.8 mm/yr for the eustatic rise in sea level during the past 4,000 years (Figure 3). Thus, most of the change in sea level observed in the Northeastern United States during the last 2,000 to 3,000 years (Table 1) appears to be due to an absolute increase in the level of the sea rather than to land subsidence.

<u>Aggradation and Accretion--the Shaler Model</u>

About 30 years after Mudge offered his explanation for the thick salt-marsh peat accumulation he observed, N.S. Shaler (1886) developed a model for marsh formation based on a different set of observations. Shaler emphasized the gradual accumulation of sediments in shallow coastal waters, particularly where seagrasses might accelerate the depositional process. As the water became shallower, the seagrass beds would be replaced by mud flats which would, in turn, be colonized by <u>Spartina alterniflora</u>, the only grass to survive in the low intertidal zone. The presence of the grass would further enhance sediment deposition, and the roots and rhizomes would contribute to peat formation. This process would continue until the sediment accumulated almost to the limit of the high tide. By this process, the marsh would build up and out from the shore as sediments were redistributed along the coast.

In his classic description and analysis of the New England coastline, Johnson (1925) discussed the problem of salt marsh formation in some detail, and established "criteria for testing the Mudge and Shaler Theories." According to Mudge, sections through the marsh should show

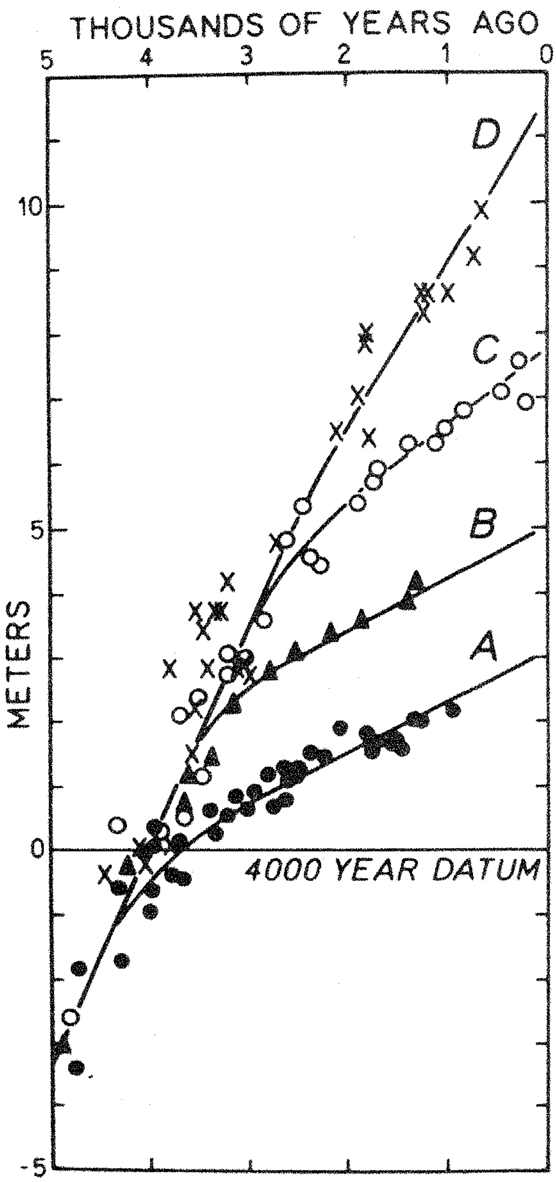


Figure 3. Age and depth of salt-marsh peat in different areas: A (Cape Hatteras to Mexico plus Bermuda), B (Cape Cod to Cape Hatteras), C (eastern Massachusetts), D (Bay of Fundy). In area A, the last 3,500 years are assumed to reflect the eustatic rise in sea level, so that the deviation of each of the other curves from A is due to local land subsidence. For example, in area C local subsidence continued until about 2,500 years ago at a rate of 0.3 mm/yr. When combined with the eustatic rise of 0.8 mm/yr, the result is the 1.1 mm/yr of relative rise shown (Redfield 1967, as modified by Emery and Uchupi 1972).

deep, relatively uniform accumulations of high marsh Spartina patens peat. The Shaler model, however, (which did not invoke a relative sea level change because many people at the time thought that the rise in sea level due to deglaciation had been completed long before) called for a relatively thin layer of high marsh peat over a layer of S. alterniflora peat over a mud flat deposit in a clear and regular sequence. The type of peat could be distinguished by the roots and rhizomes it contained (Figure 4). Johnson (1925) concluded, based on these criteria, that:

> "My own studies and those of my assistants, involving the making of many hundreds of sections through our coastal marshes from Prince Edward Island to Florida, amply confirm the essential points in the conclusions of Mudge and Davis. Marsh sections showing the theoretical sequence of deposits described by Shaler do exist, however, but they seem clearly to represent local departures from the normal sequences of marsh development...."

The Barnstable Marshes - Redfield's Synthesis

In 1934, J.B. Knight described the stratigraphy of a marsh near Branford, Connecticut, and suggested a mechanism by which the Mudge and Shaler theories might be reconciled. It appeared from Knight's work that the marsh had first formed as Shaler proposed, but that once the Spartina

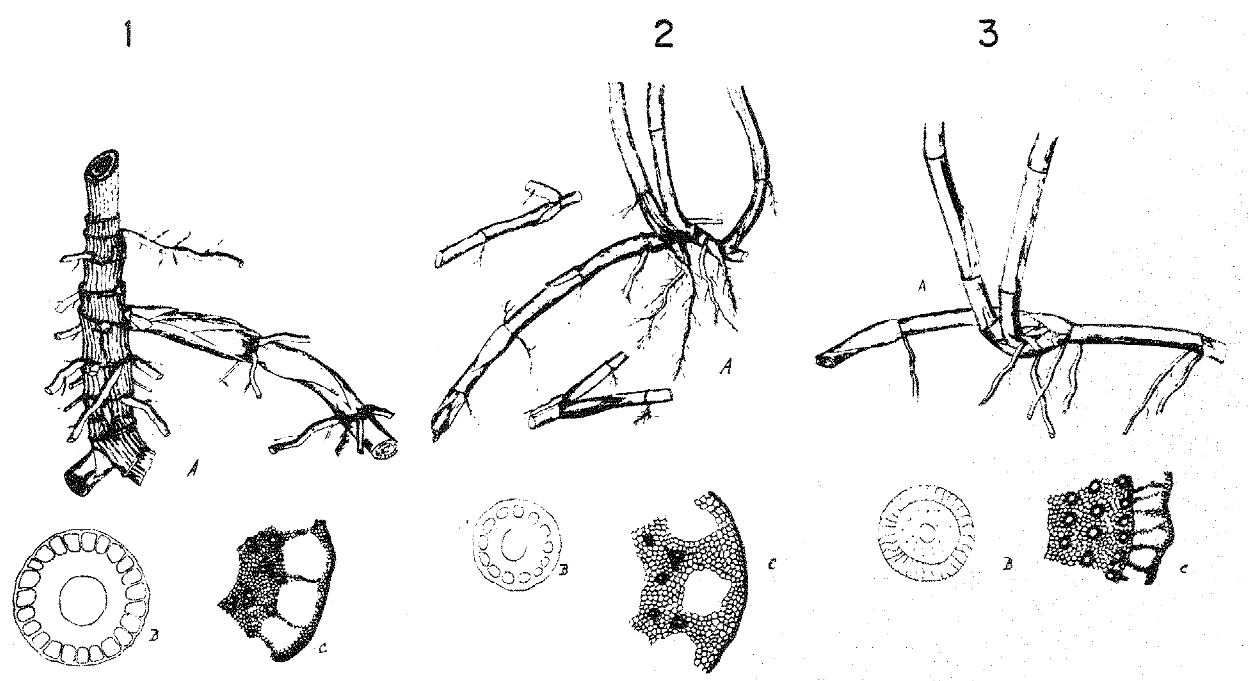


Figure 4. Characteristics used by Johnson (1925) to distinguish between salt marsh peat deposits containing low marsh plants (1) Spartina alterniflora, and high marsh plants (2) Spartina patens and (3) Distichlis spicata. Drawings by G.B. Reed in Johnson (1925). (A) culm bases, rhizomes, and roots, (B) cross section of rhizome, and (C) enlarged cross section of rhizome.

patens had become established, the high marsh peat kept accreting in response to rising sea level. Thus, a thick section of S. patens peat lay over a thin layer of S. alterniflora peat which was underlain by a mud flat deposit. It was not until A.C. Redfield (1972) carried out his extensive studies of the Barnstable Marsh in Cape Cod that a well-documented and comprehensive picture of marsh development on the northeast coast emerged.

Data collected from the Barnstable marsh confirmed the model proposed earlier by Redfield (1965; Redfield and Rubin 1962) in which the sequence of events described by Shaler was placed in the context of a rising sea level. It was clearly shown that the different views of Mudge and Shaler arose, at least in part, because Mudge had focused on the upland side of the marsh while Shaler had been looking primarily at the seaward side. With a rising sea level and a sufficient sediment supply, Redfield (1972) found that the intertidal S. alterniflora peat extended progressively out from shore and at an upward slope over an aggrading sand and mud deposit. The high marsh peat then formed over the intertidal peat as a wedge which thinned as it expanded toward the upland and toward the seaward edge of the marsh (Figure 5). Cores taken in areas where the marsh had overgrown the upland in response to rising sea level would contain only a uniform deposit of high marsh peat, as reported by Mudge, while cores from the outer portions of the marsh would appear as described by Schaler. Despite all his care and efforts, the many cross sections examined by Johnson (1925), and which confirmed only Mudge's views, happened to come from areas in the marshes that had formed over old upland sites or from marshes in which erosion had removed areas of recent marsh accretion.

The marshes are growing out and over the sand and mud flats as well as up and around the rocks.

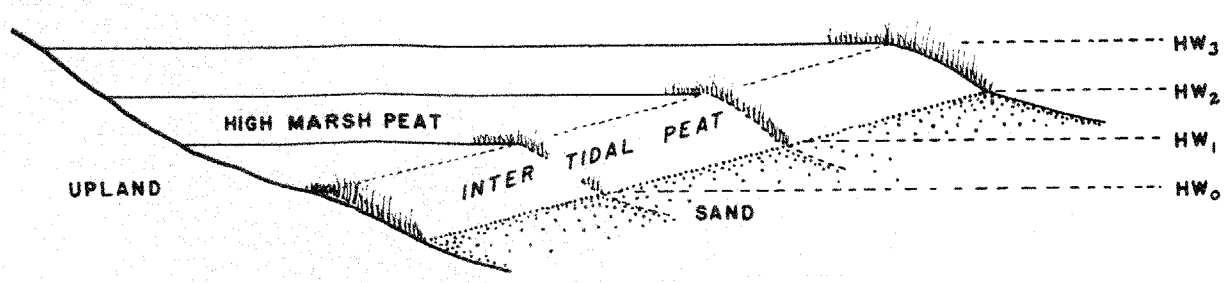


Figure 5. Redfield's model for salt-marsh development over accumulating sediment on a sand flat and over the upland under the influence of rising sea level (Redfield 1972). HW refers to mean high water at various times during development.

CHAPTER 2

WATER LEVELS, SEDIMENT DEPOSITION, AND THE FORM OF THE MARSH

FLUCTUATIONS IN WATER LEVEL

While the long-term secular rise in sea level due to glacial melting and land subsidence has played an important role in salt-marsh development, other processes influence water levels along the coast. Although people often think of sea level as a fixed datum, continuous water level records (such as those obtained from tide gauges) have shown that sea level varies on virtually every time scale. There are wind-generated waves which may have periods of seconds or minutes, as well as semidiurnal or diurnal tidal waves. The passage of atmospheric fronts with different barometric pressures and wind fields influences coastal water levels for hours or days. Seasonal and yearly changes in temperature, salinity, and barometric pressure influence the density and volume of coastal waters, making them rise and fall relative to the land. And changes in coastal geomorphology that may take place relatively rapidly (dredging, breachway opening) or over a number of years (development of a barrier spit), may influence water levels and tidal ranges. The name "tidal marsh" reflects the widely recognized importance of this component of water level changes, and it will receive particular attention in the next section. First, it is worthwhile to consider some other processes that influence water levels in the marsh on time scales longer than a tidal cycle but considerably shorter than the melting of glaciers.

Short-term Changes in Mean Sea Level

Sea level is usually calculated as the arithmetic mean of hourly water level measurements collected over the period of interest. Usually, water level data are taken from tide gauges that are designed to filter out short period changes due to waves. The elevation of the gauge itself is usually leveled to U.S. Geological Survey bench marks on land which can, in turn, be related to the zero elevation of the National Geodetic Vertical Datum (Hicks 1978).

Examinations of water level data reveal a bewildering array of nontidal changes, some of which are irregular while others appear to be cyclical. It is well known that there is a rise in sea level associated with storms which may reach 3 to 5 m (10 to 16 ft) above normal tide in the extreme case of a hurricane. More commonly, the effect of winter storms along the northeast coast will increase water levels by less than a meter. This increase is due to a short-term "surge" of water moving into the area because of the low barometric pressure associated with the passage of the storm front (the "inverse barometer effect," Smith 1979) and to a longer-term accumulation of water against the coast due to wind stress. Miller (1958) studied these two processes on the New England coast and found that there was a time lag of 1 to 14 hr with an average of 5 to 6 hr, between maximum wind and maximum "set-up" or water rise. A quantitative understanding of the wind, however, was limited by the complications of local geography at each site. A more general result was that the theoretical relationship of 1 cm change in sea level per 1 millibar (mb) change in barometric pressure appeared to be correct in this area. Since pressure drops of 20 to 30 mb are not uncommon, this is an important component of storm effects. However, Miller (1958) pointed out that "surge is a rapid rise in water level with a duration of several hours or less, while set-up appears to be a relatively slow rise or fall of water level with durations of hours or days...."

It is less widely realized that there is a seasonal cycle in sea level which passes through a minimum in winter and a maximum during summer (Figure 6). Along the northeast coast, the annual range in monthly mean sea level appears to increase from about 5 cm (2 inches) at Eastport, Maine, to over 15 cm (6 inches) at New York (Emery and Uchupi 1972). About 9 cm (3.5 inches) or less of this seasonal variation may be attributed to a seasonal cycle in barometric pressure, and seasonal changes in the wind may also play a role (Emery and Uchupi 1972; Kjerfve et al. 1978), but in general, the remainder is due largely to changes in the in situ density of the sea water. In areas with little freshwater input and a large annual temperature range, much of this density change may be due to heating and cooling (Kjerfve et al. 1978), but for most of the northeast coast the density of the water appears to be more strongly regulated by freshwater discharge (Figure 6) (Emery and Uchupi 1972). Changes in freshwater input also appear to be responsible for much of the variation in annual mean sea level (Figure 7), though there must be other factors operating, including secular rise and longer-period oscillations (Hicks 1968, 1972; Emery and Uchupi 1972). Still other, more permanent changes in water level may result from the dredging of breachways or passes through barrier spits (Lee 1980) or natural coastline changes such as the expansion or contractions of barrier spits or the shoaling of channels (Johnson 1925; Redfield 1972).

The magnitude of these various short-term changes in sea level appears deceptively large compared with the long-term secular rise of only 1 mm/yr discussed earlier. In the Northeastern United States, it may take about 100 years for the secular rise to equal the seasonal variation in any one year, but the seasonal variation is taking place around an annual mean which is increasing (on the average) throughout the 100-year period. Moreover, on geological time scales the variation due to glaciation is much larger than any of the short-term processes. Nevertheless, the daily, seasonal, and yearly variations in mean sea level (around which the still shorter-term tidal variations must act) may influence the distribution of organisms and sediments on the marsh, as well as chemical exchanges between the tidal waters and the surface of the marsh. The potential for such an effect was described by Kjerfve et al. (1978) in a careful study of a South Carolina marsh where the seasonal range in monthly mean sea level was 26 cm (10 inches).

One consequence of this variation was that the marsh was innundated 42% of the time during October, but only 27% of the time in January. Such a difference may well influence the growth rates of small fish or other animals that feed on the marsh surface (Valiela et al. 1977), but it does not necessarily follow that all water-marsh interactions will be greatest during the times of maximum sea level.

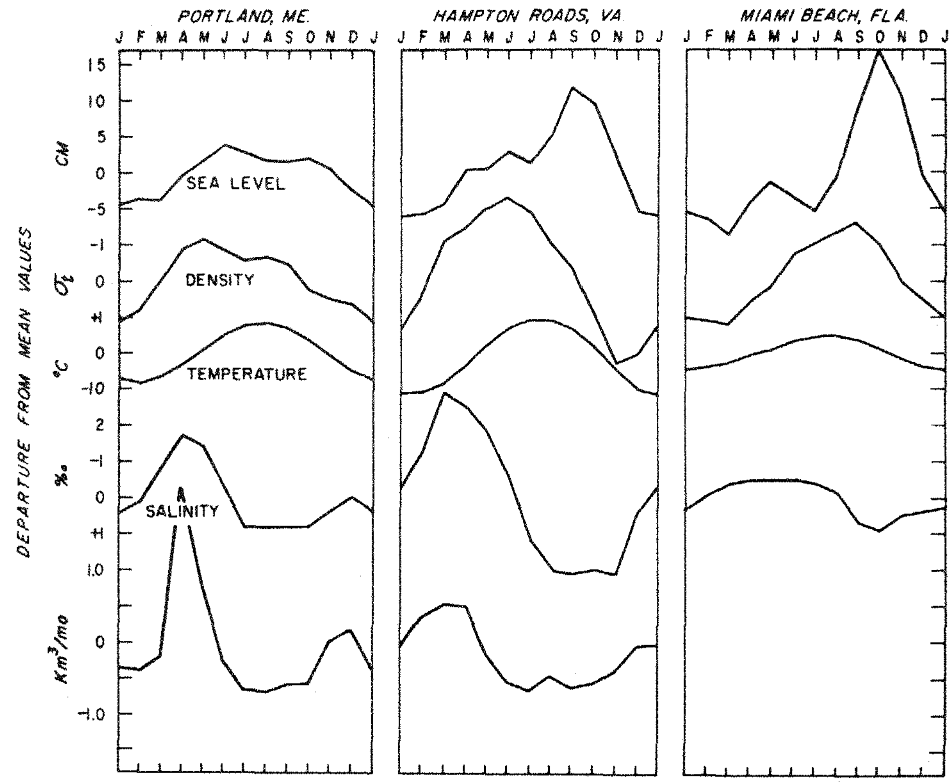


Figure 6. Departure from the annual mean of average monthly sea level, water density, temperature, and salinity at three primary tide stations (Emery and Uchupi 1972). Departures from the monthly mean for nearby river discharge (bottom line) are given for comparison.

In a detailed study of sedimentation on a Louisiana marsh, Baumann (1980) found that sediment deposition was not correlated with mean sea level or duration of submergence, but with the concentration of sediment in the flooding water. It is likely that many marsh-water interactions are variable and complicated, and that the strength of any particular coupling may not be a simple function of the duration of submergence.

Tides

In contrast to water level changes discussed earlier, variations caused by the tides are remarkably regular and their influences are thought to be "the most significant environmental factors responsible for the segregation of salt-marsh vegetation" (Redfield 1972). Tides along the Atlantic coast of the United States are semidiurnal and symmetrical with a period of 12 hr 25 min, in marked contrast to those of the Gulf of Mexico and Pacific coasts (Figure 8). The tides along the northeast and much of the southeast coast are also of considerably greater range (1 to 3 m or 3.3 to 10 ft) than those along the Gulf of Mexico coast (Figure 9). There is a substantial and regular variation in the tidal range, not only with the lunar cycle as shown in Figure 8, but over the annual cycle as well. While the tidal range is greatest during full and new moon, the highest and lowest tides occur nearest

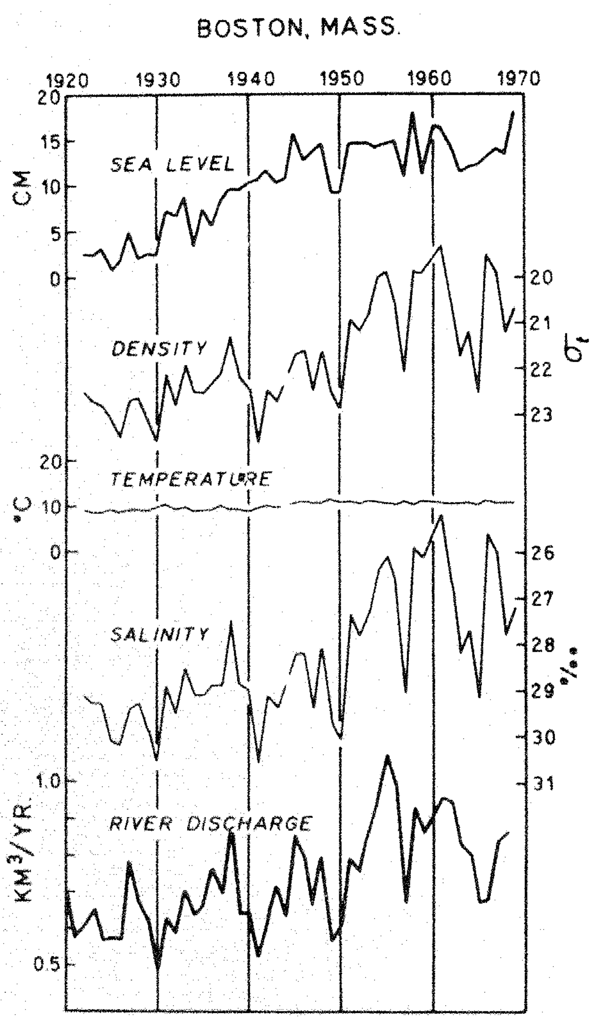


Figure 7. Annual variation in mean sea level at Boston, Massachusetts, compared with mean annual water density (inverted scale), temperature, and salinity at the tide gauge station, plus annual discharge of the Charles River including urban waste water (Emery and Uchupi 1972).

the summer and winter solstices (Figure 10). As Emery and Uchupi (1972) pointed out, there is also a "fortunate circumstance" such that the times of lowest low tide come during the night or early morning, so that animals and plants accustomed to life below the tide line are not exposed to excessive heating and desiccation (Figure 10).

While the National Ocean Survey (NOS), National Oceanic and Atmospheric Administration, publishes annual predictions of the daily tide heights and times for many primary and secondary locations along the coast, the tidal pattern found in a marsh may often be quite different from that observed or predicted at the nearest reference station. Generally, the tidal signature found inside a narrow opening, behind a barrier spit, or up a winding tidal creek will show a reduced tidal range and a delayed time of high water; flood tide will be shorter than ebb with a faster mean current speed.

The tide heights published in the NOS tables are given with reference to mean sea level, an elusive datum we have spent some time discussing in earlier sections. To eliminate or at least reduce much of the short-term variability in sea level measurements, the NOS uses a 19-year average of hourly tide gauge records for most of its tidal work. The choice of this averaging interval has some astronomical significance and represents a practical choice, given the lengths of records available for most stations and the level of variability in the yearly data (Hicks 1968). Sea level, however, is often estimated by NOS from a tidal record that is only 1 month to 1 year long by comparing it to a nearby station with a 19-year record and similar tidal characteristics. Similarly, it is relatively easy to develop yearly tidal predictions

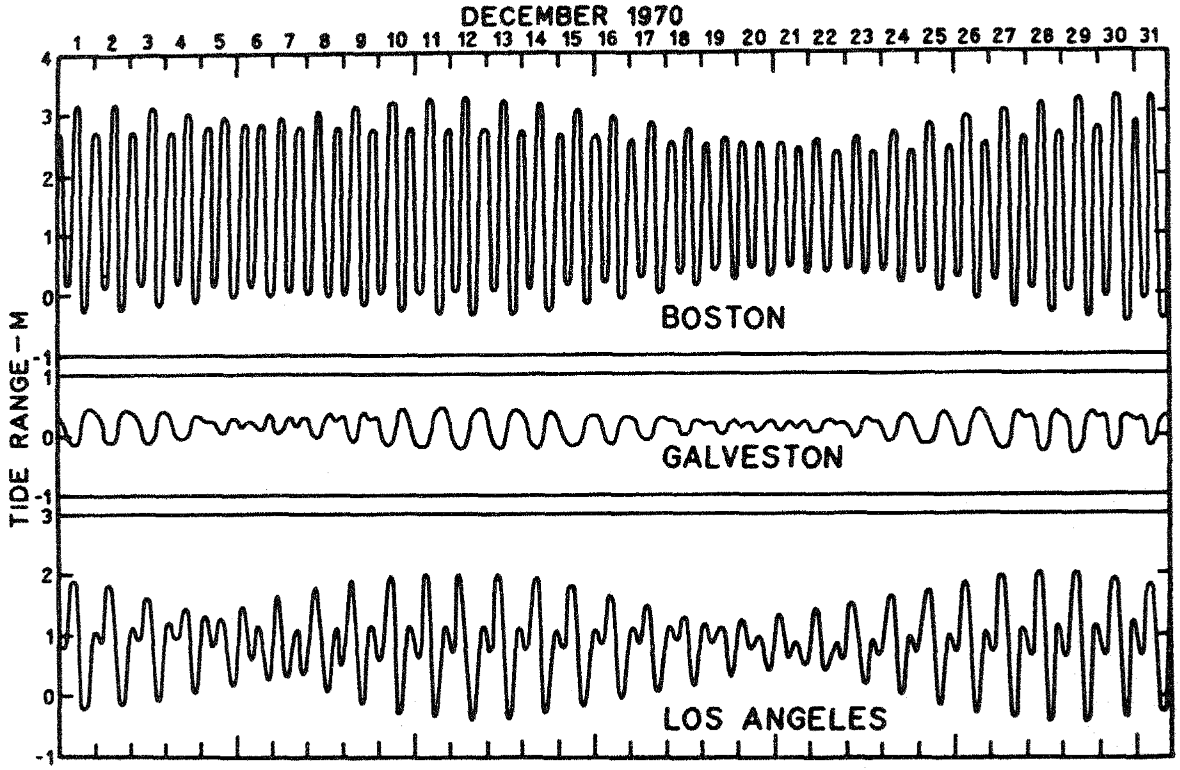


Figure 8. Typical curves of the predicted daily tide during December 1970 for stations on the Atlantic, Gulf of Mexico, and Pacific coasts of the United States (Emery and Uchupi 1972).

for a particular marsh area by using a measured tidal record as short as 15 days (Palmer et al. 1980).

Despite our long-standing ability to predict the tides with reasonable accuracy (except when winds, barometric pressure, or fresh water influences dominate), it is difficult to predict water level in a salt marsh or other coastal embayment because water level results from a complex set of interactions. Water level, especially as affected by tides, has traditionally been considered the major influence in determining marsh ecology. Water level also has been used often for classifying wetlands in inventories and in legal descriptions protecting or regulating various portions of the coastal environment, particularly descriptions of wetlands (Kavenagh 1980). There may be good ecological reasons, however, for doubting that marsh vegetation is finely tuned to the tides and water levels (Lagna 1975) because concepts like mean sea level, mean high water, and mean low water are arbitrary simplifications that depend on the time interval chosen. The relative position of the land-water-air interface over a defined time interval is a physical reality; it can be readily measured, and its importance in the marsh has been a central theme in coastal ecology for at least 50 years.

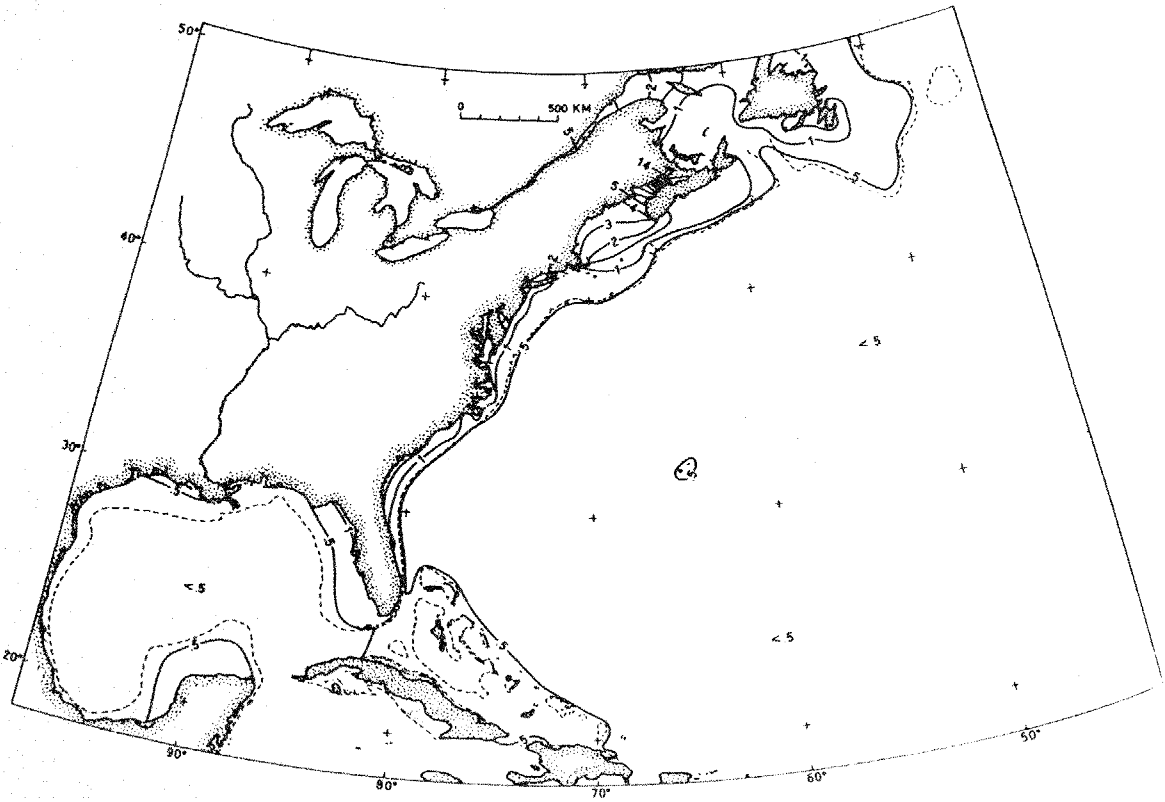


Figure 9. Height of mean spring tides offshore along the Atlantic and Gulf of Mexico coasts of the United States (Emery and Uchupi 1972). Contours are in meters with extra contours for 0.5 and 1.5 m.

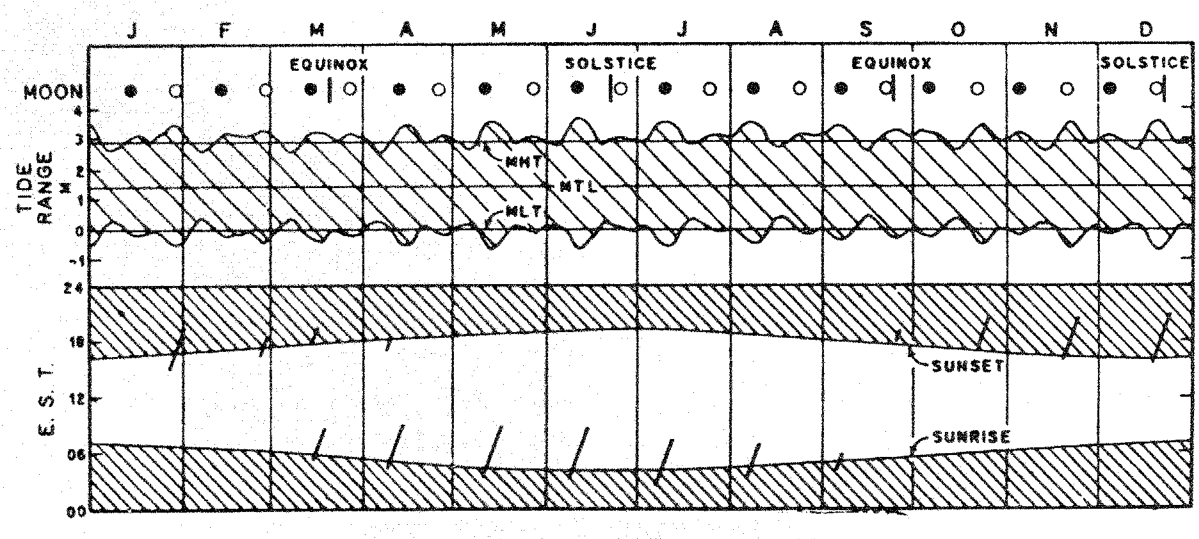


Figure 10. Relation of the tide range at Boston, Massachusetts, to the phases of the moon over an annual cycle (Emery and Uchupi 1972). Upper envelope encloses the daily tidal range with levels of mean high tide, mean tide level, and mean low tide shown. Lower portions show the relation of tides lower than -30 cm (wide diagonal lines) with respect to the time of sunrise and sunset.

THE FORM OF THE MARSH

The shape and appearance of each marsh result from unique and complex interactions of local topography and bathymetry, sea level rise, tides, sediment supply, and vegetation. While practical considerations force us to consider each of these subjects in turn, it is their interaction that makes a marsh. For example, the salt-marsh plants play a major role in trapping and stabilizing inorganic sediments as well as in producing the organic matter that forms the marsh peat. But marsh vegetation, especially its zonation and productivity, has received much study and a separate chapter will be devoted to this problem after a brief discussion of the development and form of the marsh substrate.

Marsh Development, Topography, and Morphology

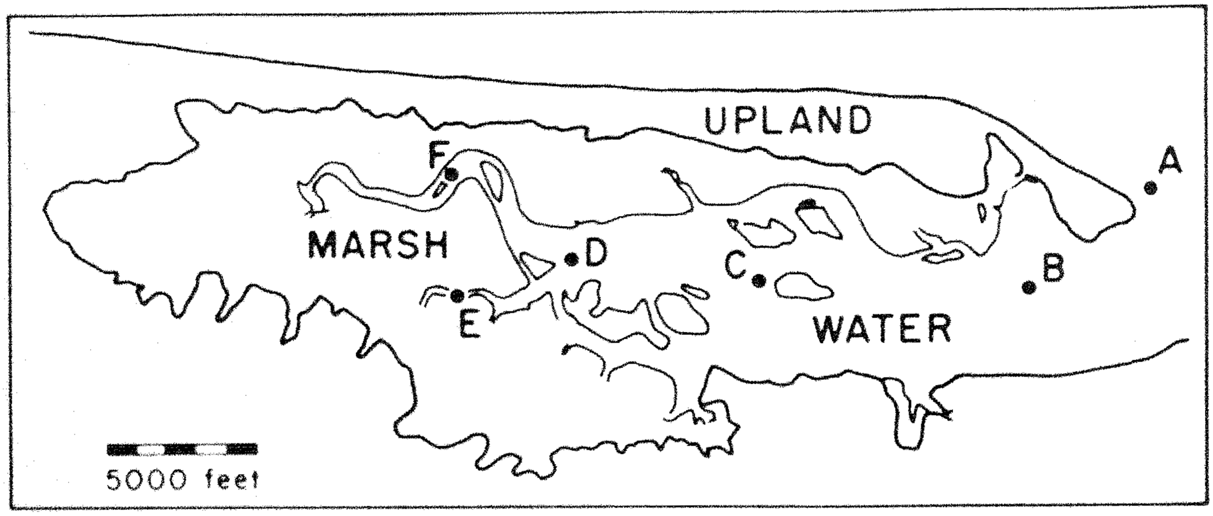
Marshes usually develop behind barrier spits or in the mouths of tidal river estuaries where there is some protection from waves. The major problem with waves appears to be that they prevent the sediments from forming a stable substrate, rather than mechanically damage the marsh grasses (Redfield 1972). As tidal currents carry water and sediments into these areas, they become progressively slower due to constrictions and bottom friction. As a result, their ability to keep particles in suspension decreases, so that sands become deposited near the mouth of the embayment with silts and clays toward the head of tidal creeks and meanders (Figure 11). Redfield (1972) distinguished between marshes that developed on sloping foreshores, in which the distribution of sediment had been relatively uniform and the drainage at low tide was reasonably complete, and those that developed across sand or mud flats where:

> "The pattern of development appears to have depended on the vagaries of the sedimentary processes which built up the sand flats to the critical level above which S. alterniflora can grow. The drainage pattern of the high marsh has been fixed by that of the channels which finally drained the flats in the broad sounds enclosed by the developing marsh. Such channels shift their position continually until stabilized by the turf of the marsh, which then fixes their final position."

In the former case, the resulting marsh has a more or less uniform appearance, and the sloping surface of the landform makes it possible for the high marsh to develop independently of the intertidal Spartina alterniflora. If the marsh accretes and aggrades across flats, however, its appearance is more interesting and its development follows the general pattern described by the Shaler model.

In spite of its appearance on casual inspection, the surface of the high marsh is not absolutely flat, but is elevated slightly toward its inner and older portions because of the longer period over which this area has been able to accumulate sediment and peat (Figure 12). Low natural levees, perhaps 5 to 15 cm (2 to 6 inches) high and several meters wide, sometimes occur along the major marsh creeks; these levees develop because a relatively larger amount of sediment is deposited there when the rising tidal water first overflows the creek banks and slows down as it spreads out across the marsh.

The greater elevation of the older marsh means that it will be less frequently flooded by tides, that it will be submerged for shorter periods of time, and that less water will need



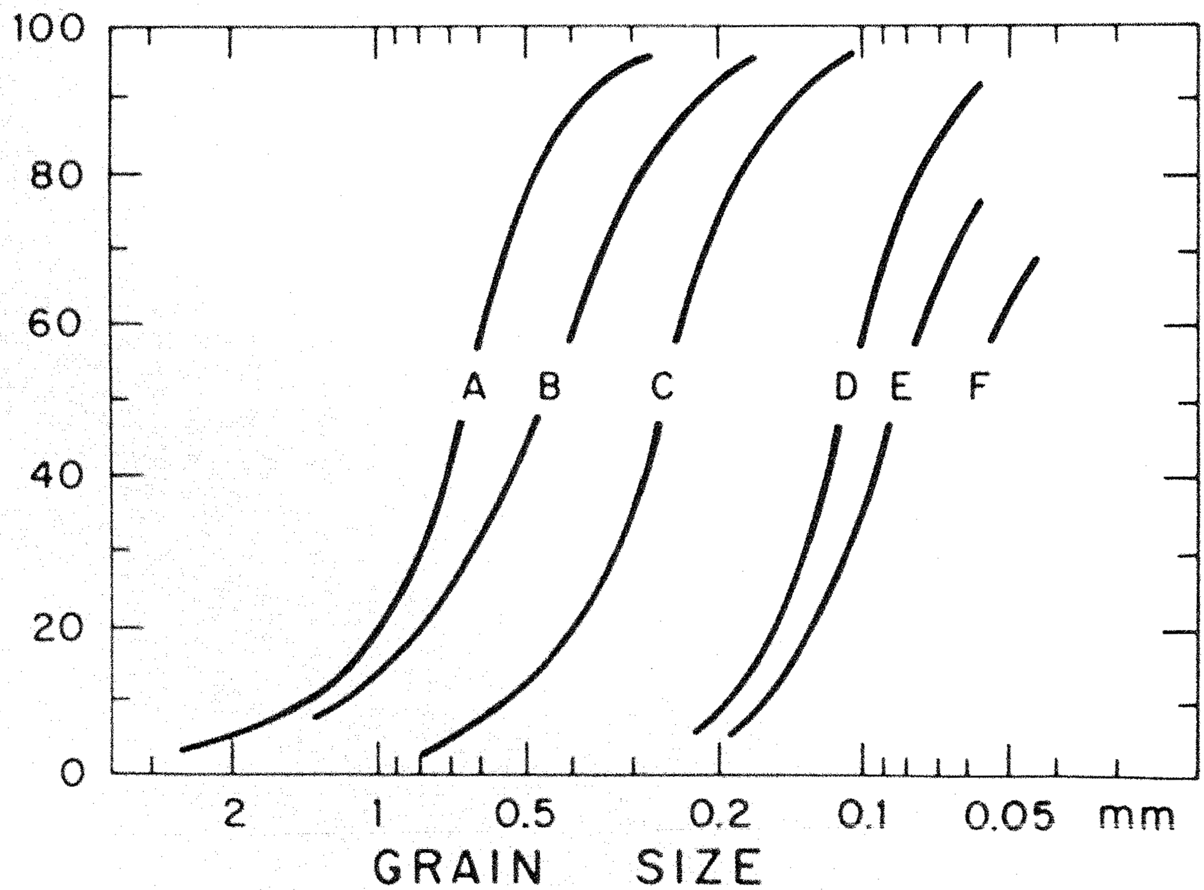


Figure 11. Cumulative distribution of grain size in the sediments from the mouth to the head of Barnstable Harbor and marsh (Redfield 1972). Coarser materials drop out quickly as currents slow inside the barrier spit.

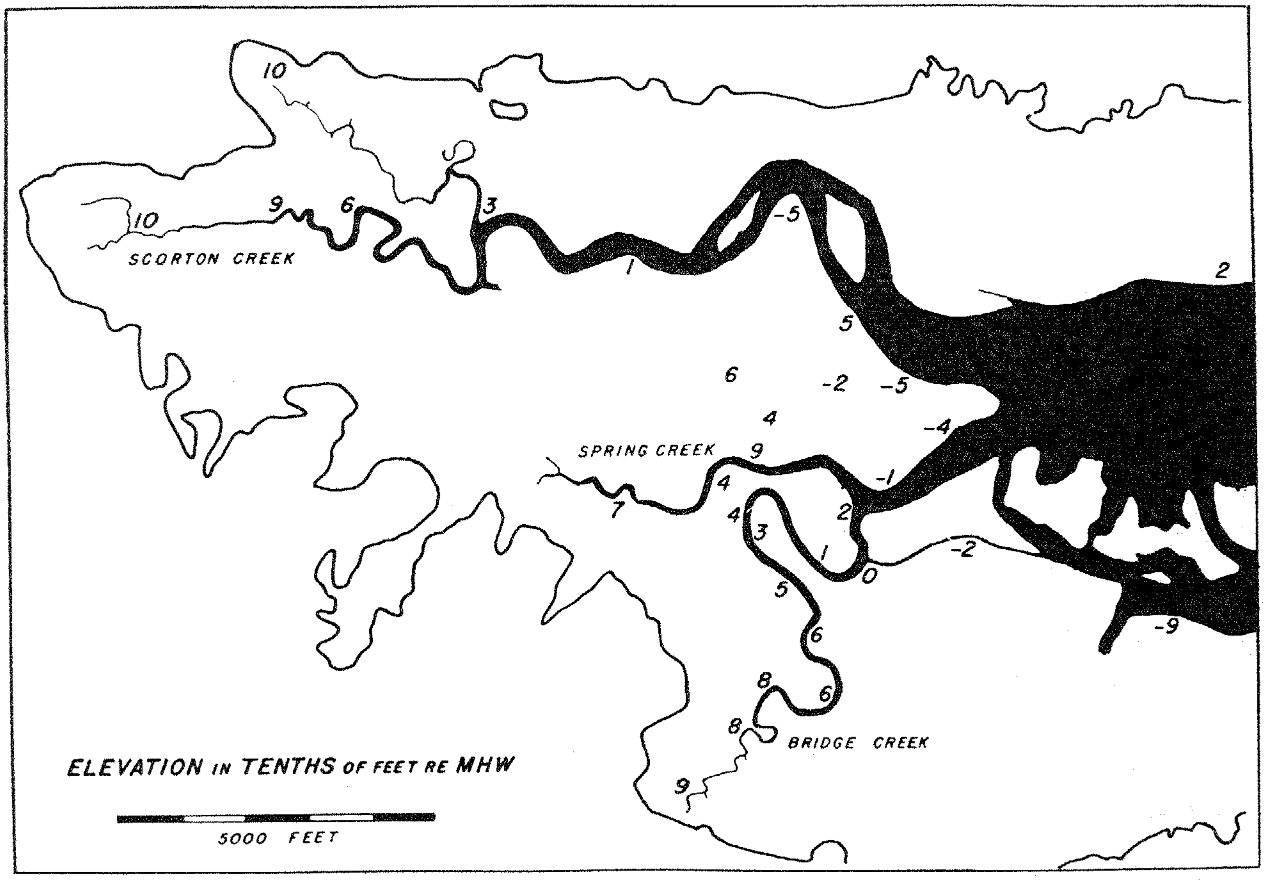


Figure 12. Elevations in tenths of feet of the high marsh surface relative to mean high water (MHW) at Barnstable, Cape Cod (Redfield 1972). Older portions of the marsh are higher.

to be drained from its surface (Table 3). As a result, there will be progressively fewer and smaller drainage creeks, pond holes, and "rotten spots" (Figure 13). The reduced amount of water reaching the high marsh will also bring in less sediment, so that the rate of vertical accretion will decline relative to the young portions of the marsh (Johnson 1925; Redfield 1972; Harrison and Bloom 1977; Baumann 1980).

The pannes and pond holes or "rotten spots" shown in Figure 13 are common features of the New England marshes which have been studied in detail (Miller and Egler 1950; Chapman 1960; Redfield 1972). Sometimes the pannes or shallow depressions of the marsh surface may be quite large and represent areas within the marsh which, for various reasons, did not receive enough sediment to shoal sufficiently for Spartina to grow. Many of the pannes contain round, shallow holes or small pools ("primary pannes"), with a depth somewhat greater than the thickness of the Spartina turf. They are filled by the higher tides, though some may even have small drainage systems. The lack of a peaty turf in more southern marshes may explain the absence of deeper pools in those areas (Redfield 1972). In other pannes the standing

Table 3. Annual marsh flooding at various elevations, volume of water, and period of submergence (Redfield 1972).

Elevation of marsh		Number of flooding tides per year	Volume of flood water (ft^3/ft^2 per year)	Period of submergence	
re MLW (ft)	re MHW (ft)			(hours per year)	(% of year)
9.5	0	316	198	500	5.7
10.0	0.5	170	173	240	2.7
10.5	1.0	83	114	115	1.3
11.0	1.5	43	80	48	0.55
11.5	2.0	18	38	8	0.14
11.7	2.5	1	2.3	0	0

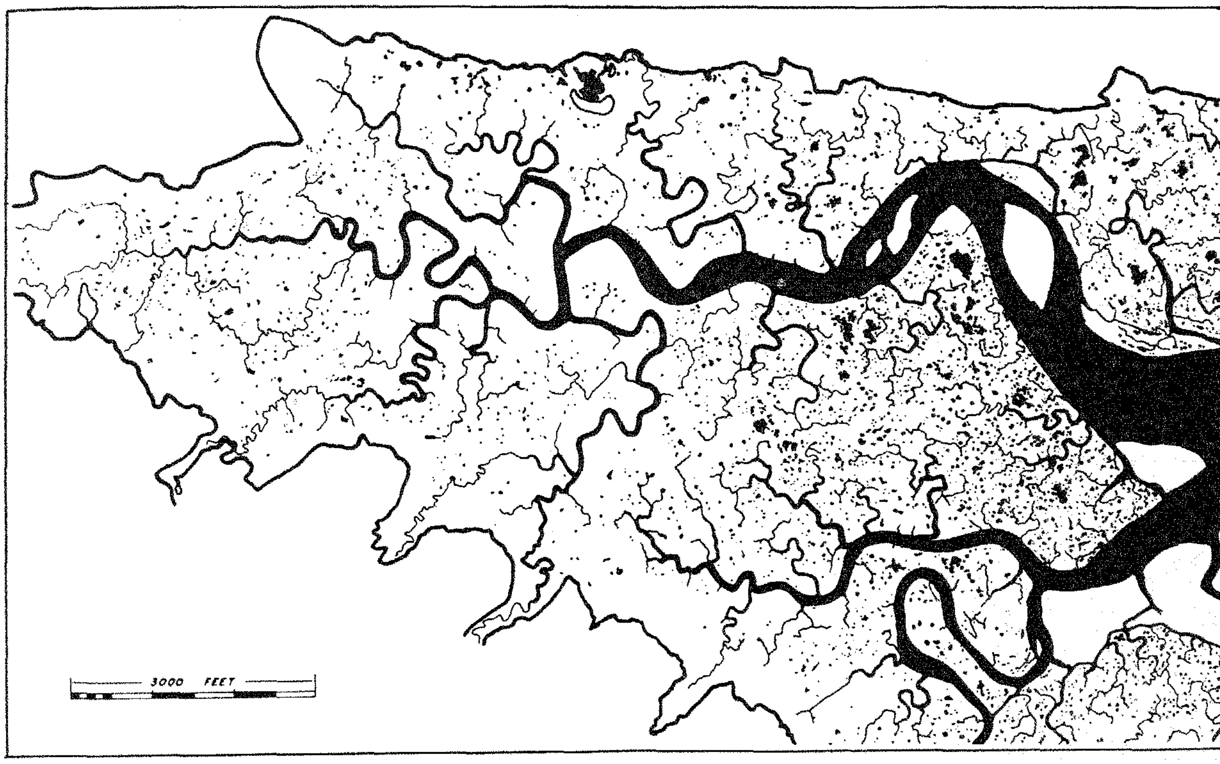


Figure 13. Dark areas represent the distribution of pond holes or pannes and tidal creeks on the high marsh at Barnstable, Cape Cod (Redfield 1972). The marsh on the left and in the foreground where fewer of these features are found is older accord to ^{14}C dating.

water may evaporate, leaving salt deposits that limit the vegetation. Several processes may be responsible for these features, including the blockage of drainage creeks by slumping of the banks, the evolution of high marsh from patches or lines of slough marsh growing together, the decay of surface turf because of poor drainage ("rotten spots"), and the accumulation of "trash." The pond holes appear to be relatively stable over the short term because the depth of standing water in them (0.5 to 1 m or 1.6 to 3.2 ft) is usually great enough to prevent the spread of Spartina rhizomes (Redfield 1972), but their disappearance from the older portions of the marsh (Figure 13) suggests that most of them are an ephemeral part of the marsh (Chapman 1960).

MARSH SEDIMENTS

Marshes along the Atlantic coast may receive sediment from rivers, from the nearshore zone, and from relic mud deposits on the continental shelf (Mead 1969; Phleger 1977). The latter sediment source is particularly important for many of the coastal marshes along the Northeastern United States, where the supply of new terrigenous sediment is low. The mechanism responsible is a landward flow of bottom water across the shelf. In areas where marshes have formed behind barrier spits, large amounts of sand may also be carried onto the marsh by wind and storm overwash. A recent review by Frey and Basan (1978) gave a detailed description of the mechanisms responsible for the movement and deposition of sediment in marshes, and I have drawn comparisons between some aspects of the chemical composition of marsh sediments and those of fresh water and nearshore marine waters (Nixon 1980).

Usually high marsh sediments consist of a fine, silt-like inorganic fraction and a coarse organic fraction made up largely of Spartina roots and rhizomes. As McCaffrey (1977) pointed out, the organic content of marsh soils is only slightly higher than that of many estuarine and nearshore sediments, although their bulk density is much lower. On a dry weight basis, the bulk density of Farm Creek marsh was only 0.2 g/cm (1.01 g/cm wet), while that of the adjacent Long Island Sound sediment was about 0.6 g/cm (McCaffrey 1977). Despite the use of the term "peat" in connection with New England salt marshes, the organic content is much lower than freshwater peat bogs, and it would be a cold home that tried to burn high marsh peat in the fireplace. Nevertheless, the dense growth of the Spartina patens roots and rhizomes greatly accelerates the vertical accretion of the marsh through their own volume as well as through sediment trapping; where dense tussocks of the grass develop, the microrelief of the marsh surface is affected (Figure 14). The continual input of new sediment onto the marsh is critical not only for the system to keep up with rising sea level, but nitrogen, phosphorus, and other elements associated with the sediment fertilize the vegetation to maintain the remarkable productivity (DeLaune et al. 1979; Nixon 1980). Though less spectacular than the annual flooding of the great river systems like the Nile or the Mississippi, the daily rise of the tides and the sediments they carry may be just as important for the productivity of these systems as those riverine sediments were for man's early floodplain agriculture.

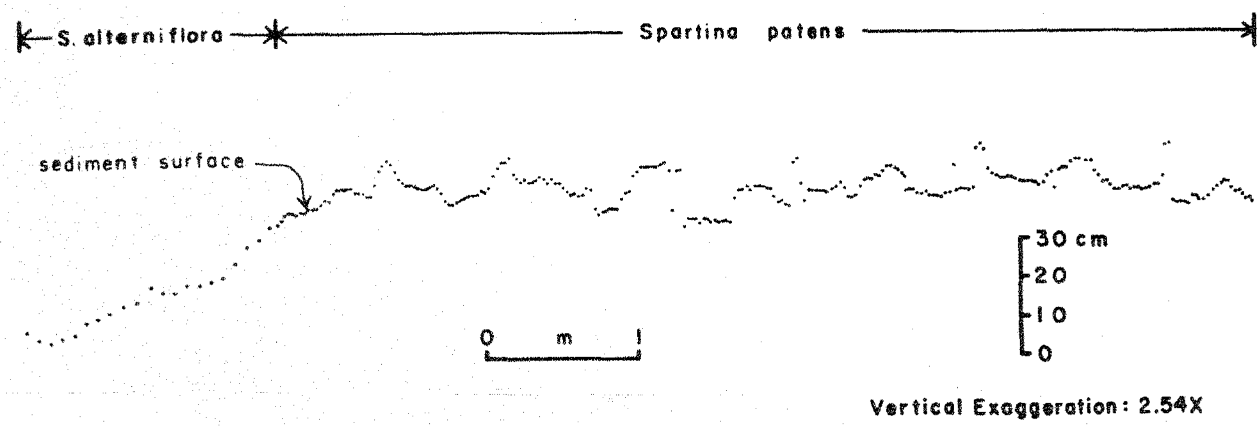


Figure 14. Surface microrelief across the transition from low to high marsh at Farm Creek, near New Haven, Connecticut (McCaffrey 1977). Note the effect of Spartina patens tussock development on sediment surface.

CHAPTER 3

ZONATION ON THE MARSHES

Striking patterns of plant zonation on the New England marshes attracted the attention of coastal ecologists and, beginning with the classic studies of Johnson and York (1915), there has been a continuing effort to understand the mechanisms responsible for the distribution and groupings of higher plants, as well as algae and animals, on these marshes (e.g., Nichols 1920; Johnson 1925; Taylor 1938; Chapman 1940; Miller and Egler 1950; Webber 1967; Daiber 1977). Most of the early efforts were descriptive, and we now have a reasonably complete picture of the various marsh species (for example, a taxonomic guide for the Northeastern United States was prepared by Moul 1973). Progress has also been made in understanding the significance (or lack of it) of various plant groupings and in appreciating the other factors in addition to tides that influence marsh vegetation (Niering and Warren 1980).

HIGHER PLANTS

The working definiton of a New England high marsh is often a taxonomic one, encompassing the area dominated by salt marsh hay or fox grass (*Spartina patens*) and spike grass (*Distichlis spicata*), in contrast to the regularly flooded marsh on which cordgrass (*Spartina alterniflora*) is virtually a monospecific dominant. Along the upland border, the high marsh often develops large areas of black grass (*Juncus gerardi*) and switch grass (*Panicum virgatum*), although where fresh water enters the marsh, cattails (*Typha* spp.) or reeds (*Phragmites*) often dominate (Figure 15). But the situation is complicated. As Redfield (1972) observed, "The distinction between high marsh and the upper levels of the intertidal marsh cannot be clearly drawn." Many writers seem to consider at least a portion of the stunted *S. alterniflora*, which grows away from the creekbanks, as belonging to the high marsh, and the characterization of any portion of the marsh as "intertidal" may be ambiguous. While it has often been reported that *S. alterniflora* grows up to the level of mean high water, and that this should define the "intertidal" marsh, a careful analysis of this proposition by Lagna (1975) has shown that it has little merit except as a rough approximation. Because the level of MHW is an arbitrary datum based on a 19-year record, it would be a remarkable coincidence if MHW was a finely tuned botanical indicator.

Our model of salt marsh vegetation must include a certain amount of overlap in boundaries. Factors other than tidal range may also influence the vegetation patterns. The more prominent factors have recently been summarized by Niering and Warren (1980), including salinity (Taylor 1938; Adams 1963; Parrondo et al. 1978), nutrients (Adams 1963; Mendelssohn 1979), and soil oxygen (Linthurst 1979). All factors contribute in varying degrees

Figure 15. Some common higher plants of the New England marshes. (a) Smooth cordgrass, Spartina alterniflora (b) Saltmeadow grass, Spartina patens (c) Blackgrass, Juncus gerardi (d) Spikegrass, Distichlis spicata.

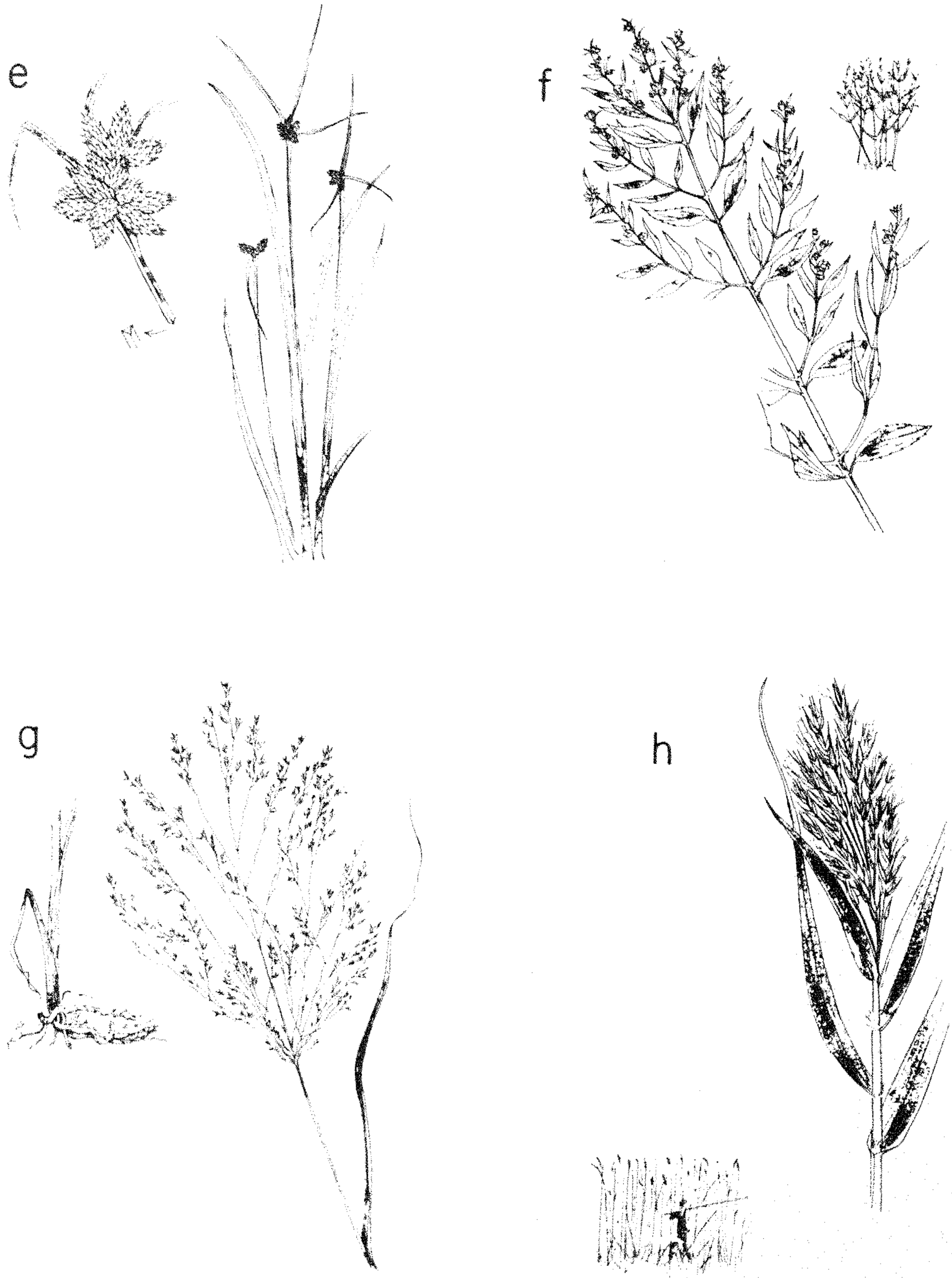


Figure 15. (Continued). (e) Saltmarsh bulrush, Scirpus robustus (f) Marsh elder, Iva frutescens (g) Switchgrass, Panicum virgatum (h) Common reed-grass, Phragmites communis. Drawings from Tidal Marshes of Old Lyme, Connecticut, published by the Old Lyme Conservation Commission, 1968.

to the height differences between tall creekbank S. alterniflora and the stunted form on the more poorly drained back marsh. The greater oxygenation of pore waters by the tides may also be the mechanism responsible for the correlation between creekbank S. alterniflora production and tidal range reported by Steever et al. (1976). On the high marsh, however, the situation is even more complex; no simple or direct relationship has yet been found between the distribution and abundance of high marsh species and a particular environmental variable. In spite of some exciting advances in our understanding of marsh zonation and marsh plants, Miller and Egler's (1950) comment still seems appropriate:

> "One is tempted to feel that this remarkable mosaic should be interpreted in terms of ecologic factors. If so, our present knowledge is yet far from sufficient. It is very likely that contemporary concurrently acting factors are only partly responsible for present distributions. In other words, simple abnormal catastrophic factors may have produced effects lasting into the present; and general past conditions may have been such that the vegetation still reflects them."

The picture developed by Miller and Egler (1950) from their work in Connecticut is probably the most useful general model of vegetation on the New England salt marshes. In their studies of the Wequetequock-Pawcatuck marshes, Miller and Egler found some 150 species of higher plants distributed in five belts or zones classified roughly according to elevation. The number of species was greater, and there were more common species (80% occurrence in test quadrats), on the upper borders and slopes of the marsh than on the lower portions or on the creekbanks (Figure 16). Their general upland-to-bay sequence consisted of a Panicum virgatum Upper Border, a Juncus gerardi Upper Slope, a Spartina patens Lower Slope, and a Spartina alterniflora Lower Border. But Miller and Egler also devoted considerable attention to the shallow pannes and pond holes on the marsh surface. Many pannes were characterized by stunted Spartina alterniflora or by colorful forbs such as Limonium carolinianum, Triglochin maritima, Aster tenuifolius, and Plantago decipiens which grew around their edges. Toward the inner portions of the pannes, evaporation and poor drainage produced areas with salt accumulation that were colonized by succulents such as Salicornia europea or remained unvegetated. Pond holes with the submerged macrophyte, Ruppia maritima, and various algae occurred in other areas.

The extent of these zones varies considerably in individual marshes. In general, the Panicum Upper Border and the Juncus Upper Slope are narrow and separate the marsh proper from upland trees and shrubs. The high marsh, consisting of Spartina patens, Distichlis spicata, and short S. alterniflora in various combinations of pure stands and mixtures, appears to comprise the largest area of most unfilled marshes. The regularly flooded or low marsh consisting of the tall form of S. alterniflora often amounts to 10% to 20% of the area of emergent grasses (Table 4). In the past, the coverage of the high marsh S. patens, Juncus, and Distichlis may have been even greater. In comparing their more recent marsh surveys on Long Island with those made 34 years earlier by Taylor (1938), O'Connor and Terry (1972) noted that:

> "Taylor described Spartina patens as 'by far the most common grass

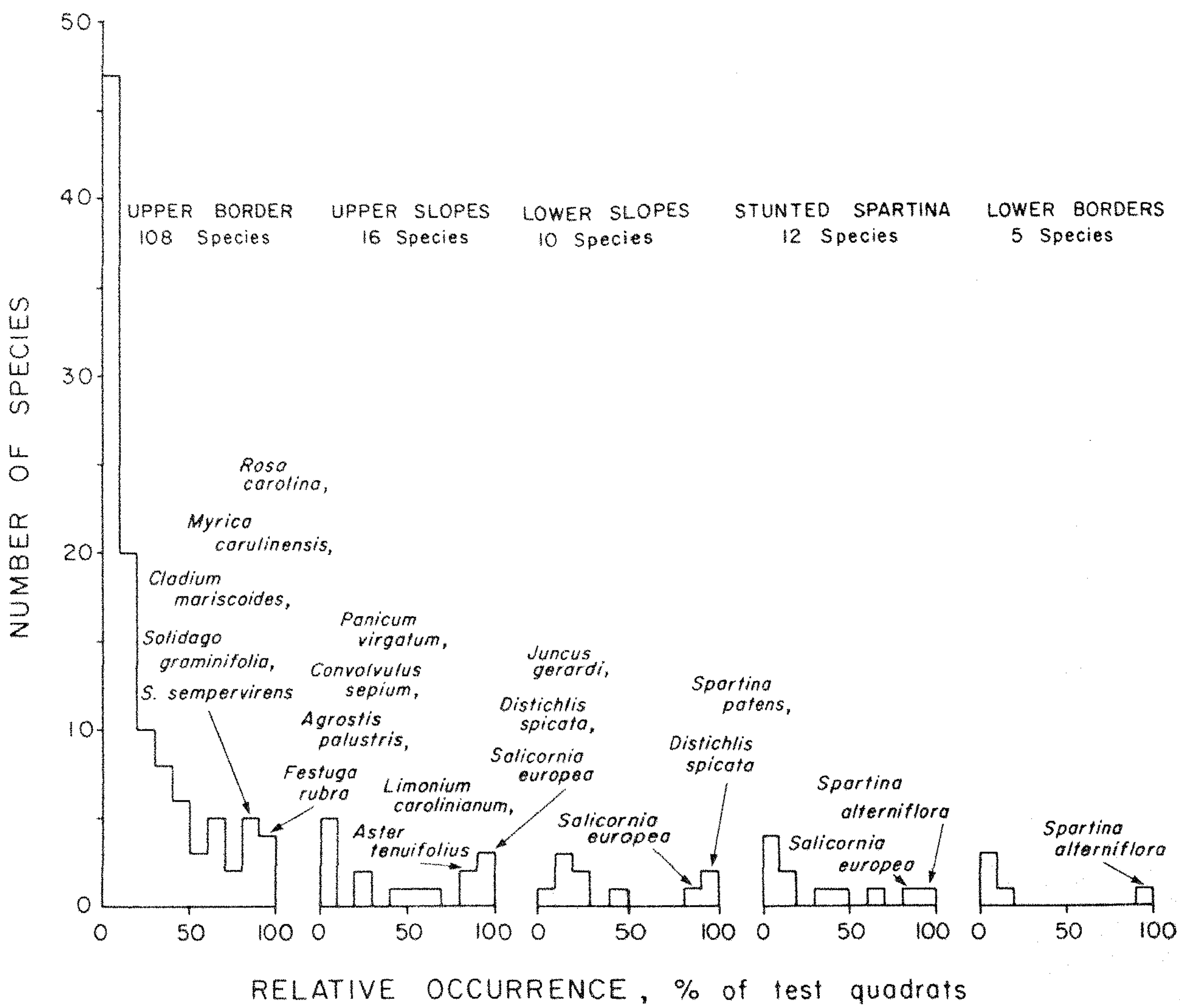


Figure 16. Relative diversity, dominance, and major species composition of vegetation zones described by Miller and Egler (1950) at the Wequetequock-Pawcatuck marshes in Connecticut. In each zone, species listed are those present in 80% to 90% or 90% to 100% of the sample quadrats. For example, in the upper border 108 plant species were found; 5 species occurred in 80% to 90% of the quadrats sampled, and 4 species occurred in 90% to 100% of all quadrats. Almost 50 species were rare and only found in 1% to 10% of the quadrats.

on the marshes' whereas we now estimate it covers only 16 percent of the marshes, or is less than one-quarter as common as S. alterniflora. Taylor also described Juncus gerardi as 'undoubtedly the next most prominent plant...,' whereas there now appears to be fewer than 30 acres of J. gerardi."

The loss of high marsh appears to be due to its susceptibility to filling and development, and it may be the lack of man's influence as much as any feature of geography that is responsible for the relative abundance of high marsh in northern New England (Table 5). In their recent summary of wetland loss in the United States, Gosselink and Baumann (1980) reported

Table 4. Relative amount (%) of coverage of high and low marsh in various New England salt marshes.

Marsh location	Tall *Spartina alterniflora*	Short *S. alterniflora*	Mixed *S. patens* and *Distichlis*
Barnstable, MA[a]	...32...	...11...	53
Barnstable, MA[b]	8	...92...	
Bissel Cove, RI[c]	7	72	19
Cottrell Marsh, CT[d]	...45...		65
Hempstead Bay, L.I.[e]	10	67	23
Flax Pond, L.I.[f]	...60...		
Iron Point, L.I.[f]	...50...		
Nassau & Suffolk, L.I.[g]	14	45	23

[a]Blum (1968).
[b]Redfield (1972) % of emergent marsh.
[c]Nixon and Oviatt (1973a).
[d]Steever (1972).
[e]Udell et al. (1969).
[f]Lagna (1975).
[g]O'Connor and Terry (1972), average for virtually all of the marshes in the two counties, except it is not clear if the marshes of Hempstead and south Oyster Bays were excluded as being "atypical."

Table 5. The ratio of high marsh (*S. patens*, *Distichlis*, *Juncus*) to low marsh (*S. alterniflora*) along the Atlantic coast. The extent of each wetland type was reported by Spinner (1969) based on 1954 U.S. Bureau of Sport Fisheries and Wildlife data and by the Maine Department of Inland Fisheries and Game.

State	High marsh/low marsh
Maine	11.1
New Hampshire	14.1
Massachusetts	4.3
Rhode Island	2.1
Connecticut	3.3
New York	2.1
New Jersey	7.2
Delaware	1.1
Maryland[a]	7.4
Virginia[a]	0.5
North Carolina[a]	1.7
South Carolina[a]	0.3
Georgia	0.3
Florida (east coast)[a]	3.3

[a]Includes *Juncus* marsh.

that the rates of loss in Maine and New Hampshire during 1954-74 (and presumably earlier) were much lower than for most of the other Northeastern States.

Marsh vegetation, however, changes in response to many other factors besides those related to human development. For example, Niering and Warren (1980) described shifts that have taken place during the past 25 years on the Wequetequock-Pawcatuck marshes, including a loss of the Juncus belt and a replacement of the S. patens by short S. alterniflora. After studying more than 100 marshes on Long Island Sound, Niering and Warren felt that while:

> "the Miller and Egler pattern was found to be generally valid ... tidal marsh vegetation is highly dynamic, and our field observations and peat core studies have shown that traditional successional concepts are of limited value in terms of interpreting vegetation changes."

As a result of their work, they developed a revised version of the often reproduced generalized cross section of the vegetation on a New England salt marsh that was first published by Miller and Egler (1950). The resulting diagram (Figure 17) illustrates the complex distribution that may result from a sequence of changes that Chapman (1940) tried to represent with an involved web of potential vegetation sequences on the New England marshes. After struggling to understand salt-marsh succession, Chapman commented with understatement:

> "This scheme may appear somewhat bewildering as it is very complex, but the present author has been forced to the conclusion that salt marsh succession is by no means the simple phenomenon seen by earlier authors, and that it can only be represented

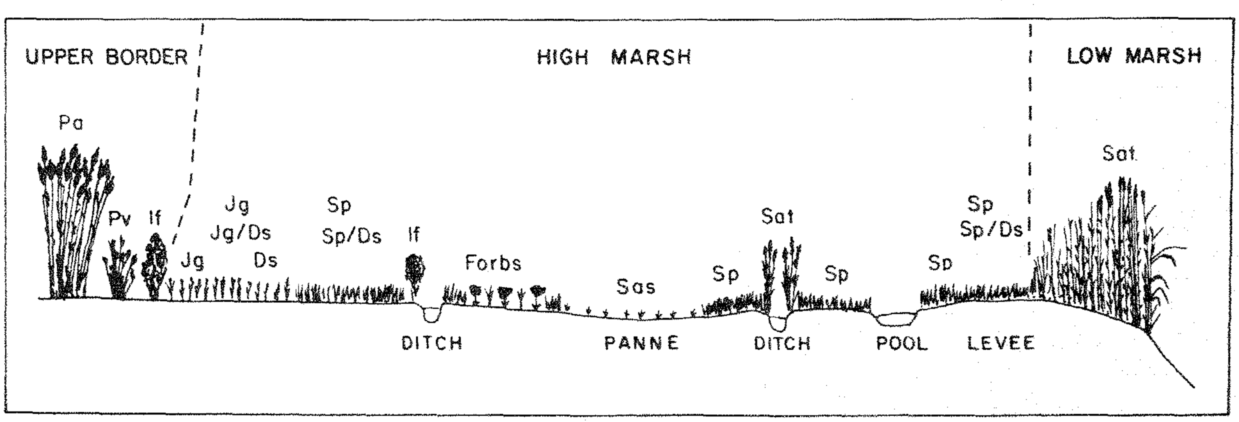


Figure 17. Generalized transect from the uplands to the low intertidal in a "typical" New England salt marsh showing the common vegetation types. Key to symbols: Sat = tall Spartina alterniflora; Sp = Spartina patens; Ds = Distichlis spicata; Sas = short Spartina alterniflora; If = Iva frutescens; Jg = Juncus gerardi; Pv = Panicum virgatum; Pa = Phragmites australis. From Niering and Warren (1980).

schematically by a complex diagram."

I think few would disagree with such a conclusion, but Miller and Egler put it another way:

> "... the present mosiac may be thought of as a momentary expression, different in the past, destined to be different in the future, and yet as typical as would be a photograph of moving clouds."

EPIBENTHIC ALGAE

Species composition and distribution patterns of epibenthic algae on the marsh surface are not well known. Algae are not as conspicuous as flowering plants and have received less attention; the lower plants are shorter-lived and have less specialized growth requirements.

In addition to his investigations on the succession of grasses on Romney Marsh, near Boston, Chapman (1940) also identified algal communities which he recognized on the basis of species composition, tidal range, and season. Attempts to impose taxonomic order on the marsh algae, however, were not very convincing or useful. As recently as 1967, Webber noted that no specific accounts of New England marsh algae had been published in the 27 years following Chapman's paper. Her own work on the blue-green algae of a marsh at Ipswich, Massachusetts, identified over 30 species that appeared to be associated with the various higher plants (3 with _Juncus_, 13 with _Spartina patens_, 10 with _S. alterniflora_, and 4 from the sublittoral), although no algal communities or zones were really defined. Within a year of Webber's publication, John Blum's (1968) monograph, "Salt Marsh Spartinas and Associated Algae," appeared. While recognizing that many of the dominant algae identified by Chapman were characteristic of the marshes, Blum concluded that: "most species of salt marsh algae appear to grow in miscellaneous mixtures with other species. Observations of numerous marshes impresses me with the paucity of mixed communities which are constant in make-up." General observations, however, could be made about the algae on the Cape Cod marshes. For example, the algal layer under the tall creek-bank _S. alterniflora_ consisted mainly of diatoms growing on the mud surface, while the high marsh stunted _S. alterniflora_ was associated with filamentous algae (Table 6) that grew upward on the grass leaves and culms to a height where the humidity became too low to support algal growth. High marsh algae also were found associated with other plants such as _Limonium_, _Plantago_, and _Salicornia_ and in unvegetated pannes. With the exception of _Calothrix_, which grows up on the _S. patens_ mat, there was virtually no algal layer below the high marsh _S. patens_ and _Distichlis_.

The lack of algal cover over the high marsh dominated by these species is due to the shading of the marsh surface by the dense _S. patens_ mat (Blum 1968). On a spring day only 2% to 3% of the incident light reached the soil beneath the _S. patens-Distichlis_ mat studied by Blum, while 50% to 55% reached the algal layer under stunted and creek-bank _S. alterniflora_. The growth of epibenthic algae under _S. alterniflora_ is light dependent and appears to be greatest during spring and fall when the grass cover is not as dense (Sullivan and Daiber 1975; Van Raalte et al. 1976). High light intensities appear to favor the growth of filamentous algae whereas diatoms dominate in low light areas (Sullivan 1974; Sullivan and Daiber 1975).

MARSH ANIMALS

In the sea, the density and kinetic energy of the water provide

Table 6. Principal epibenthic algal species on the Cape Cod marshes (Blum 1968)[a].

Lyngbya aestuarii (Mert.) Liebm.
L. semiplena (Ag.) Ag. _f. ex_ Gom
Vaucheria coronata Nordst.
V. arcassonensis Dang.
V. compacta (Collins) Collins
Symploca hydnoides Kutz
Microcoleus chthonoplastes Thur
Ulothrix flacca Thur
U. laetvirens (Kutz) Collins
Anabena tortulosa Lagerh.
A. variabilis Kutz
Hydrocoleum sp.
Rhizoclonium sp.
Cladophora sp.
Calothrix sp.

[a] A detailed description of edaphic diatoms in a stunted _Spartina alterniflora_ marsh in Delaware is given by Sullivan (1974).

the vertical structure for the plankton ecosystems that develop (Odum 1975). Phytoplankton expend little energy for storage or structure; their microscopic size removes them from our awareness, and we focus on the occasional fish or mammal whose concentrated biomass stands out against the formless water. The marsh is more like a terrestrial environment than the sea, however. Marsh plants spend most of their time in the air where they must provide their own structure and lift themselves into the vertical dimension to use light energy as efficiently as possible. It is the grasses that capture the attention of scientist and poet alike. Sidney Lanier's vision of the Georgia marshes in "The Marshes of Glynn" as "a league and a league of marsh-grass, waist-high, broad in the blade" is shared by us all, though on a more modest scale in New England.

Because few large conspicuous animals are found in the marsh, the discussion of marsh is usually preoccupied with the vegetation. In his recent review of salt-marsh animals, F.C. Daiber (1977) pointed out some characteristics of salt-marsh animals:

> "Salt-marsh animals find themselves in a particularly harsh intertidal zone. They must possess structural, physiological or behavioral capabilities that enable them to adjust to or avoid wide-ranging levels of salinity, temperature, humidity, desiccation and innundation. They must also adapt to the physical and chemical nature of the substrate .... Few species have tolerance limits broad enough to accommodate such variable conditions."

The widespread impression that animals are "not important" on the marshes may be traced back to the well-known pioneering studies in marshes at Sapelo Island, Georgia. This marsh work was among the first to emphasize ecological energetics in ecosystem analysis. While the New England marshes had been the focus of earlier work on the geological development of marshes and of more traditional analyses of plant communities, the "new ecology" of rates and processes on the marsh came largely from the South (Odum 1959). The Georgia salt-marsh work served for many years as the most frequently cited example of this "new ecology," and one of its major early findings was that little (less than 10%) of the live *Spartina alterniflora* was eaten on the marsh (Smalley 1960; Teal 1962). One consequence of this finding was an evolving concept of marshes as detritus-based systems in which microbial food chains rather than grazing food chains were important (Odum 1968). Most discussions of marshes and animals have emphasized the potential role of detritus in feeding estuarine and nearshore animals (the "outwelling hypothesis": Odum 1968, 1980; Nixon 1980) rather than on animals actually feeding on the emergent high marsh.

Despite this preoccupation, recent reviews by Daiber (1974, 1977) have shown that our knowledge of salt-marsh animals has been increasing, and that, "There are distinctive plant-animal relationships existing in tidal marshes." Such relationships have been described in detail for at least one New England high marsh by Tiner (1974). In studying Cottrell Marsh in Connecticut, Tiner found over 100 species of invertebrates, with at least 10 species associated with *Spartina patens*, 13 species with *Distichlis spicata*, 9 with *Juncus gerardi*, and 6 with *Iva frutescens* and *Juncus gerardi* mixed vegetation (Table 7). While grazing animals (with the occasional exception of some geese and domestic cattle and horses) may not consume much of the vegetation, the presence of animals on the marsh has had a substantial and varied impact (Kraeuter and Wolf 1974; Shanholtzer 1974). Much of the interest in the preservation of marshes is due to their value as waterfowl and wildlife habitat, while the presence of another group, the insects (i.e. mosquitoes), has been responsible for ditching, one of man's major impacts on the marshes.

Insects

The long-standing reputation of salt marshes as breeding grounds for mosquitoes is widespread and deeply rooted. Recognition of the specific interaction between vegetation zones and mosquito distribution seems to date from the work of J.B. Smith (1902) on the marshes of New Jersey. Subsequent study, much of it also in New Jersey, has confirmed that high marsh *Spartina patens* and *Distichlis spicata* are the areas with the largest salt marsh mosquito populations (Table 8). As Daiber (1974) put it, "as one proceeds in a *Spartina alterniflora* marsh from the frequently innundated tall form toward the less frequently flooded higher elevations, there is an increase in the number of salt marsh mosquito species, particularly *Aedes sollicitans*. Along with this increase in mosquitoes, there is a tendency to find greater numbers of biting flies." Moreover, the *Aedes* spp. which breed on the high marsh travel farther and feed more voraciously (at least on man and his domestic animals) than species which breed in areas that are more or less permanently flooded.

The reason for this zonation has not been clearly identified, but Connell (1940) reported that *Aedes* larvae did not appear in areas of the marshes in Delaware that were flooded more than 25 days each month, and that most breeding was limited to areas where the frequency of tidal inundation was less than 8 days per month. A common explanation is that predation takes place during flooding and that the thick mat of the grasses of the high marsh also makes predation

Table 7. Dominant[a] macroinvertebrates[b] in different vegetation zones on a high marsh near Stonington, Connecticut (Tiner 1974).

Spartina patens zone

Melampus bidentatus
Philoscia vittata (isopod)
Ceraticelus emertoni (spider)
Cornicularia sp. (spider)
Erythraeid mites
Orchestia grillus
Ceratozetes sp. (mite)
Delphacid nymphs
Clubiona spp. (spider)
Fieberiella florii (planthopper)

Distichlis spicata zone

Melampus bidentatus
Alderia modesta
Philoscia vittata
Modiolus demissus
Orchestia grillus
Exigonidae (spider)
Camisia sp. (mite)
Delphacid nymphs
Ceraticelus emertoni
Lycosidae (wolfspiders)
Nematodes
Cornicularia sp.
Coleoptera #1 (unidentified beetle)

Juncus gerardi zone

Philoscia vittata
Melampus bidentatus
Orchestia grillus
Alderia modesta
Cornicularia sp.
Ceraticelus emertoni
Lycosidae
Hemiptera #1 (unidentified plant bug)
Ceratozetes sp.

Iva frutescens - *Juncus gerardi* zone

Dactynotus sp. (aphid)
Philoscia vittata
Melampus bidentatus
Ceratozetes sp.
Orchestia grillus
Ceraticelus emertoni

[a] Ranked in order of abundance.
[b] Greater than 2 mm; infauna less than 1 mm.

Table 8. Average number of *Aedes* mosquito larvae per dip of water on the marshes of Egg Island, New Jersey (Ferrigno 1958).

Vegetation	Species		Total
	A. cantor	*A. sollicitans*	
S. patens	0.3	7.0	7.3
S. patens-*S. alterniflora* mix	0.3	2.4	2.7
S. alterniflora	0.0	0.4	0.4

difficult, even when these areas are flooded. In the case of the greenhead flies (Tabanidae), it appears that the larvae drown if they are subjected to more than 2 days of submergence.

With the exception of Dexter's (1947) monograph on the intertidal animals of Cape Ann, Massachusetts, and Tiner's (1974) thesis on a marsh near Stonington, Connecticut, there appears to have been little work on insects or other animals in New England marshes. The most extensive general study of insects on a salt marsh was carried out in North Carolina by Davis and Gray (1966), who found a marked zonation that correlated with vegetation, particularly on the high marsh. In general, both *S. alterniflora* and *Distichlis* had more insects than did *S. patens* or *Juncus roemerianus*. Because most insects can escape the tide by flying or hopping, it is likely that the abundance of insects on the marsh is regulated more by food and shelter than by the hydroperiod.

Crabs and Snails

Several crab species live in marshes; most inhabit the lower *S. alterniflora* zone rather than the high marsh. On the Farm Creek, Connecticut, marsh studied by McCaffrey (1977), the density of fiddler crab (*Uca pugnax*) burrows declined from 254 ± 40 ($\bar{x} \pm s$)/m^2 in the creek-bank *S. alterniflora* to $64 \pm 20/m^2$ at a site 2 m (6.6 ft) inland in *S. patens* to $2 \pm 3/m^2$ in the middle of the *S. patens* zone. The relative lack of crabs and burrowing animals on the high marsh may be due directly to the lower frequency of flooding (especially for those species which are active only under water, Teal 1959) as well as to the dense root and rhizome mat of *S. patens* (Daiber 1977; Frey and Basan 1978). One consequence is that there is considerably less bioturbation or mixing of the high marsh sediments (McCaffrey 1977).

While most of the work on marsh crabs has been performed in southern marshes, Dexter (1942, 1944, 1945) published a series of detailed studies on the molluscs of Cape Ann, Massachusetts, including those of the marshes. In contrast to the distribution of crabs, he found that high marsh *S. patens* was the most important habitat for the common coffee bean snail, *Melampus bidentatus*. Dexter (1947) identified a *Spartina patens*-*Melampus*-*Orchestia* (amphipod, beach flea) association as one of the seven major marine communities of the Cape Ann region. The common marsh snails, *Littorina littoria* (periwinkle) and *L. saxatilis*, were also abundant on the high marsh.

Tiner (1974) found that gastropods were the most common invertebrates on a high marsh in Connecticut where *Melampus* alone comprised about 44% of the total macrofauna. However, the second most abundant invertebrate associated with *Spartina patens* was an isopod, *Philoscia vittata* rather than *Orchestia* (Table 7). Together, *Melampus* and *Philoscia* accounted for over 57% of the invertebrates observed. The abundance of *Melampus* and other species varied markedly throughout the year. Crustacea reached their maximum in fall while gastropods were most abundant from early spring through midsummer.

Fish

Fish are excluded from most of the high marsh surface except during very high tides, although *Fundulus heteroclitus* (the common mummichog), *F. majalis* (striped mummichog), and *Cyprinodon variegatus* (sheepshead) may be permanent residents of the larger pond holes or pools.

Birds

After reviewing the literature, Daiber (1977) concluded, "There is a definite relationship between bird distributions in a salt marsh and the interplay between vegetational zonation, tidal flooding and salinity as it affects feeding and reproductive activities." Working at Cape Ann, Dexter (1947) identified 17 species of birds with the high marsh, including some from upland areas as well as shorebirds (Table 9). His list is not a complete inventory of the birds to be found in this part of the marsh.

Table 9. Birds on the high marsh at Cape Ann, Massachusetts (Dexter 1947).

Least sandpiper (*Pisobia minutilla*)
Semipalmated plover (*Charadrius semipalmatus*)
Crow (*Corvus brachyrhynchos*)
Red-shouldered hawk (*Buteo lineatus*)
Marsh hawk (*Circus hudsonius*)
Spotted sandpiper (*Actitis macularia*)
Kingbird (*Tyrannus tryannus*)
Tree swallow (*Iridoprocne bicolor*)
Barn swallow (*Hirundo erythrogaster*)
Catbird (*Dumetella carolinensis*)
Starling (*Sturnus vulgaris*)
Meadowlark (*Sturnella magna*)
Redwing (*Agelaius phoeniceus*)
Bronzed grackle (*Quiscalus quiscula*)
Sharp-tailed sparrow (*Ammospiza caudacuta*)
Song sparrow (*Melospiza melodia*)
Black duck (*Anas rubripes*)

For example, the clapper rail (Rallus longirostris) is often conspicuous by its familiar call in southern New England marshes during summer, and other birds including great black-backed gulls (Larus marginus), herring gulls (L. argentatus), laughing gulls (L. atricilla), common terns (Sterna hirundo), and least terns (S. albifrons) also use the high marsh for nesting (Lucid 1971; Nixon and Oviatt 1973a; Burger and Shisler 1978). The relatively high diversity of birds on the high marsh is largely due to the "edge effect" of the marsh-upland ecotone where shorebirds and water birds mix with field and forest species. Because many species appear to nest in areas with little or no tidal flooding, the high marsh may also be considerably more attractive as a nest site than the S. alterniflora zone. Berger and Shisler (1978) pointed out, however, "Despite the extensive recent work on shorebirds, little information exists either on general habitat preferences, or on specific nest-site preferences." Their particular study was concerned with nest-site selection by the willet (Catoptrophorus semipalmatus), a common marsh bird often associated with Spartina patens. While willets did build their nests from S. patens, the important environmental variable in nest-site selection was elevation rather than vegetation.

While few, if any, birds are confined to the high marsh habitat, many species use the high marsh for one or more activities: feeding, cover, nesting, or rearing young. The following habitat use-species associations in New England high marsh were provided by Ralph Andrews and colleagues of the U.S. Fish and Wildlife Service in Massachusetts.

Nest and feed in high marsh:

Sharp-tailed sparrow
Long-billed marsh wren (Typha or Phragmites)
Meadowlark
Savannah sparrow (highest areas)
Marsh hawk
Short-eared owl (local)
Black rail (rare)

Nest in high marsh, but feed in pools of S. alterniflora zone:

Clapper rail
Willet
Black duck
Blue-winged teal
Canada goose
Seaside sparrow

Nest in high marsh, but feed in open water:

Gulls
Terns

Nest in upland edge, but feed in high marsh:

Yellowthroat
Song sparrow
Catbird
Kingbird
Redwing
Grackle

Nest on woody islands; feed in the marsh:

Herons
Egrets
Glossy ibis

Nest elsewhere; feed on insects over marsh:

Swallow
Chimney swift

It is difficult to quantify the importance of different marsh plants and plant parts in the diets of the various bird species. Most waterfowl and shorebirds eat a great variety of plant or animal material or both, and their gut contents may reflect relative food abundance at a particular time rather than food preference or requirement (Cronan and Halla 1968).

Mammals

Although no large grazing animals live on the New England salt marshes as they do (or did) on prairies and savannas, many smaller mammals feed or live there or both (Daiber 1977). The dense mat of Spartina patens and Distichlis spicata provides excellent habitat for the meadow or field mouse (Microtus pennsylvanicus); other small mammals frequent or live in the high marsh including the meadow jumping mouse (Zapus hudsonius), the white-footed mouse (Peromysus leucopus), the house mouse (Mus musculus), and the masked shrew (Sorex cinereus).

Larger animals such as raccoon (Procyon lotor), mink (Mustela vison), skunk (Mephitis mephitis), and weasel (Mustela sp.) feed on the shellfish, bird eggs, and mice of the marsh, although their homes are usually in upland trees (raccoon), upland dens (skunk), or under fallen logs or in hollow stumps (mink and weasel). One of the most conspicuous animals on many marshes is the muskrat, Ondatra zibethica, whose diet consists almost entirely of vegetation, including roots and tubers. The muskrat favors lower salinity marshes with less tidal variation. Many New England muskrats use bank dens or burrows rather than the familiar large "house" made from marsh vegetation. The average house is a mound from 1 to 2 m (3 to 7 ft) in diameter and 0.5 to 1.5 m (1.5 to 5 ft) high. Generally, the mammals of the New England high marsh remain invisible to all but the very patient or fortunate observer, although many will leave some tracts of their passing in the soft mud.

CHAPTER 4

COMMUNITY METABOLISM

Marshes have attracted the attention of systems ecologists who are interested in the transfers of energy and matter in natural systems. The salt marshes of Georgia were among the first ecological systems to be studied as systems; Teal (1962) synthesized information from studies conducted at Sapelo Island under the overall guidance of E.P. Odum. The work of the Georgia group and others studying the mid-Atlantic, southeast and Gulf of Mexico coasts of the United States has dominated our thinking about wetlands, and only recently have results of ecosystem-level studies become available from the New England marshes (Nixon and Oviatt 1973a; Woodwell et al. 1977; Valiela and Teal 1979; Welsh 1980; Howarth and Teal 1980). No one yet has compared systematically the different types of marshes. Probably the differences in tidal signature (Figure 8), tidal range (Figure 9), freshwater inflow (Nixon 1981) and sediment type (Hill and Shearin 1970; Cotnoir 1974) along the coast will influence the metabolism as well as the species composition of marshes. Reviews of the amount of new aboveground production by Spartina alterniflora have already described north-south gradients correlated with solar energy input (Turner 1976) and tidal range (Steever et al. 1976). Most of the work on ecological energetics and nutrient cycling has emphasized the regularly flooded S. alterniflora zone (low marsh), but some information is available on the New England high marsh.

PRIMARY PRODUCTION

The marsh in summer is a great sward of green; productivity of the grass is high. Ever since R.M. Harper (1918) made what appears to be the first measurements of Spartina growth on the marshes of Long Island, countless quadrats of vegetation have been clipped and weighed all along the U.S. coast (see reviews by Keefe 1972; Turner 1976; and a bibliography compiled by the U.S. Fish and Wildlife Service 1977). While researchers in New England have not been as busy with productivity measurements as their colleagues to the south, even on the high marsh (which has been less intensively studied than the creek-bank areas) enough measurements have been made to establish that an impressive amount of carbon is fixed each year during the relatively short New England growing season (Table 10).

But production, measured by harvesting the grass, is an underestimate of the total energy or carbon fixed by the plants. Some growth will have been eaten; some will have been lost as leaf fall, seed dispersal, and organic exudates. All will be missed in an end-of-the-season harvest. There are various ways to try to account for such losses (see Turner 1976), and some of them have been used by those working in New England. Unfortunately, it appears from a comparative study of commonly used techniques that the choice of a method for estimating production will have a large influence on the results

Table 10. Estimates of aboveground primary production (g dry weight/m^2/yr) of vascular plants on New England high marshes.

Vegetation	Location					
	Long Island[a]	Conn.[b]	Rhode Island[c]	Cape Cod[d]	N. Mass.[e]	Maine[f]
Spartina alterniflora (short)	510	250	430	510	480	705
Spartina patens	500 990[g]	300	430		1,100	2,740
Salicornia europea					240	
Distichlis spicata	650	360			990	
S. patens - D. spicata mix		440	680			
Juncus gerardi		570			450	425
Typha latifolia	1,360[g]		690		580	
Phragmites communis	2,690[g]		900			

[a]Udell et al. 1969 (from end-of-the-season total biomass).

[b]Steever 1972 (from sequential measurements of live and dead standing vegetation).

[c]Nixon and Oviatt 1973a (from end-of-the-growing season total biomass).

[d]Valiela et al. 1975 (from sequential measurements of live and dead standing vegetation).

[e]Ruber et al. 1981 (from sequential harvests of live and dead vegetation and assumed corrections for grazing and decomposition. Data reported as ash-free weight; values given here have been increased by 10%).

[f]Linthurst and Reimold 1978 (mean of five techniques).

[g]Harper 1918 (from end-of-the-growing season total biomass, probably air dried).

(Linthurst and Reimold 1978). Grazing losses are small on marshes, and the relatively short and distinct growing season for Spartina in the Northeast makes the harvest technique more appropriate there than along the southern coast where grass grows continuously. But even in the Great Sippewissett Marsh on Cape Cod a 3-year analysis of production and standing crop showed that annual aboveground production may be as much as twice the maximum standing crop (Valiela et al. 1975). The greatest difference between total primary production and the harvest of green vegetation appears to be due to belowground growth, however.

In 1976, Valiela et al. published the results of the first measurements of the underground production of S. alterniflora and S. patens roots and rhizomes on a New England marsh. Their remarkable finding at Great Sippewissett, Massachusetts, was that belowground production on the high marsh was about four times greater than the green aboveground production. In addition to the 630 $gdw/m^2/yr$ produced above ground, they calculated a production of some 1,610 $gdw/m^2/yr$ of rhizomes and 910 $gdw/m^2/yr$ of roots (Table 11). Most of this production took place in the first 5 cm (2 inches) below the marsh surface (Figure 18), began earlier in the season, and proceeded faster than leaf growth (Figure 19). The high ratio of belowground to aboveground growth is surprising, but it may reflect the fact that Spartina is water stressed. As Valiela et al. (1976) noted, the plants on the marsh appear greener and show increased growth following heavy rainfall.

In addition to the production of the higher plants, some carbon and energy is fixed by the marsh algae growing on the sediment surface. This must be a very small amount under the dense S. patens mat, but in the lower portions of the high marsh there is a significant amount of production by algae in the stunted S. alterniflora zone. The algal productivity is more

Table 11. Effect of nitrogen[a] (N) additions on the production (g dry weight/m^2/yr) of high marsh and low marsh vegetation at Great Sippewissett Marsh, Cape Cod (after Valiela et al. 1976).

Marsh type and biomass compartment	N application rates		
	No N addition (control)	+0.8 g $N/m^2/wk$	+2.5 g $N/m^2/wk$
Low Marsh			
Aboveground	420	960	1,320
Rhizomes	3,290	5,490	2,940
Roots	210	150	370
Total	3,920	6,600	4,630
High Marsh			
Aboveground	630	1,380	1,260
Rhizomes	1,610	3,400	3,380
Roots	910	210	160
Total	3,150	4,990	4,800

[a]The sewage sludge fertilizer used also contained phosphorus and other materials, but additional experiments demonstrated that nitrogen was the effective ingredient.

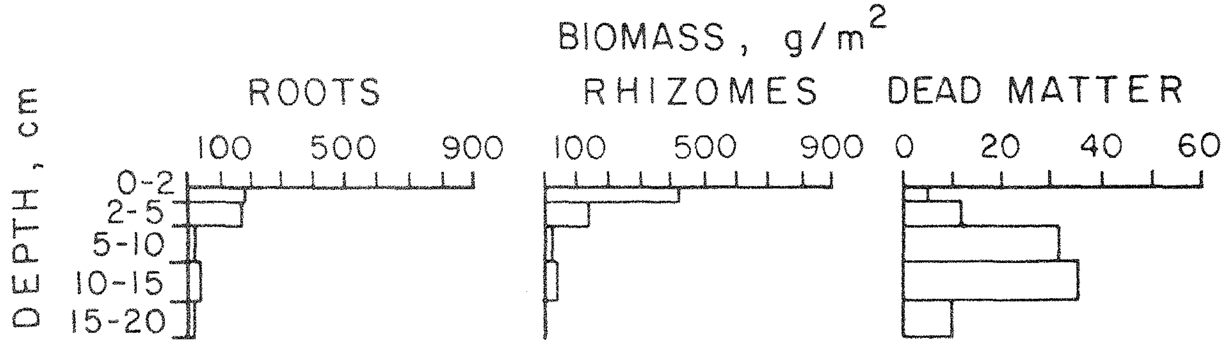


Figure 18. Vertical distribution of roots, rhizomes, and dead matter on the high marsh at Great Sippewissett Marsh on Cape Cod (Valiela et al. 1976). Most of the living material is found within 5 cm (2 inches) of the marsh surface.

difficult to measure than that shown above ground by grasses, and Great Sippewissett Marsh is the only site in New England that has been studied for this aspect (Van Raalte et al. 1976). There is some uncertainty in the results, but it appeared that algal production was greatest in spring, before the grass canopy shaded the sediment, with a secondary peak in fall. When integrated over the year, algal production amounted to some 100 gdw/m^2 or about 20% of the average aboveground S. alterniflora production. A similar value for epibenthic and epiphytic algae was also found in a Long Island marsh (Woodwell et al. 1979).

There is also some production in marsh pools by phytoplankton, macroalgae, and, in some cases, rooted macrophytes such as widgeongrass, Ruppia maritima. This aspect of marsh ecology has not been adequately studied, though recent measurements of phytoplankton and Cladophora mats in pools on a northern Massachusetts marsh showed production of about 550 gdw/m^2/yr (Ruber et al. 1981). Because pools usually cover a small portion of the marsh, however, their contribution to total marsh production will be considerably lower.

All these production figures are rough approximations that vary considerably according to the method used for measurement (Linthurst and Reimold 1978) as well as from year to year and from place to palce, even within a restricted area. For example, in three consecutive years at the Great Sippewissett Marsh, Valiela et al. (1975) calculated the following values for the high marsh:

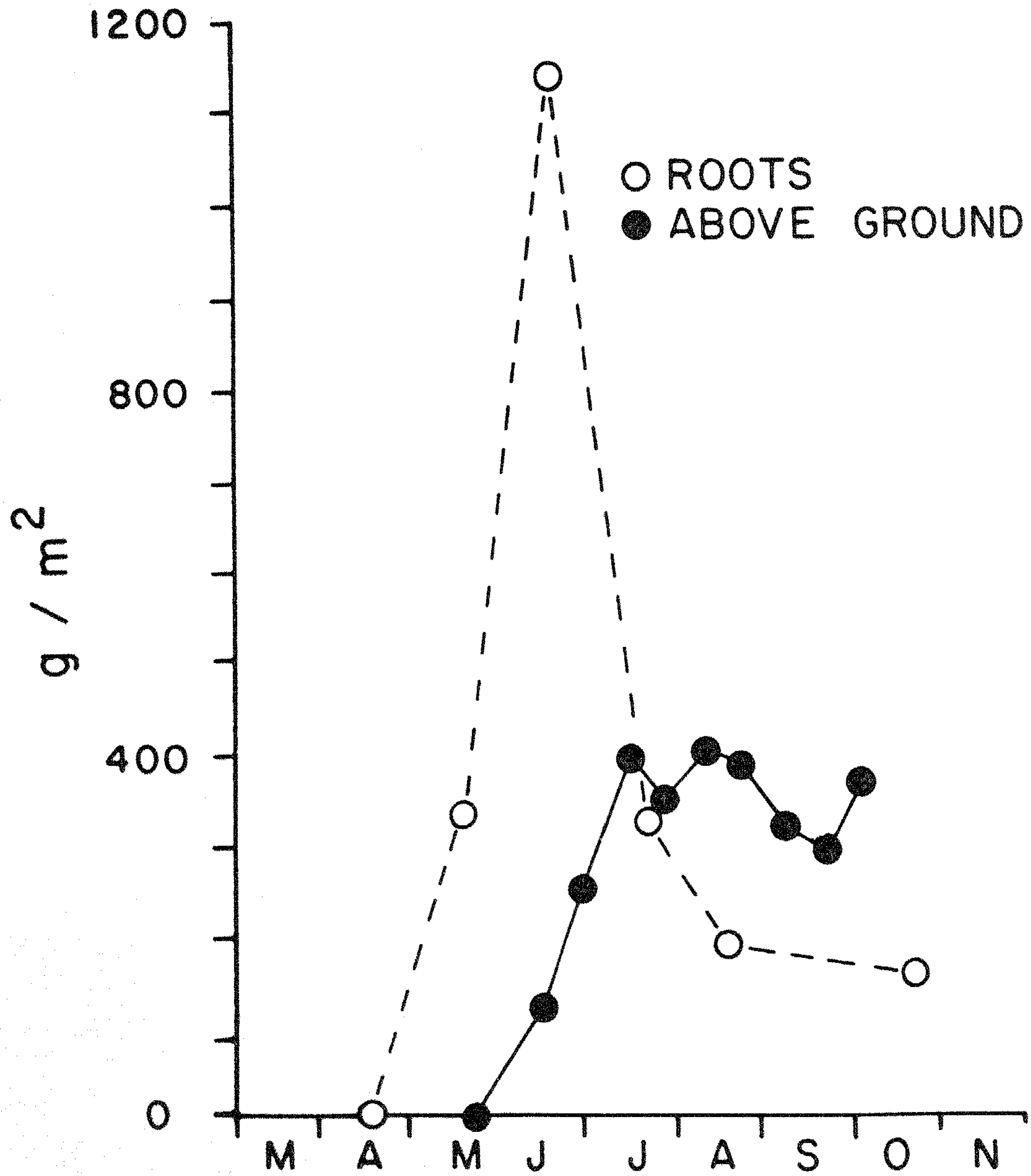


Figure 19. Amounts of aboveground vegetation and roots from April through November on the high marsh at Great Sippewissett Marsh on Cape Cod (Valiela et al. 1976).

Year	Peak biomass gdw/m^2	Net aboveground production $gdw/m^2/yr$
1971	440 ± 60	620 ± 110
1972	350 ± 10	540 ± 170
1973	540 ± 120	730 ± 250
3-year mean	440 ± 50	630 ± 50

Although the authors concluded that the differences among the years were not statistically significant, a simple estimate of the maximum standing crop of grasses may appear to vary by over 40% of the overall mean during just 3 years of sampling. In comparing the end-of-the season biomass of creek-bank S. alterniflora during one year on 12 marshes in Rhode Island (a very small area), we found a range in that one year from 430 to 1,380 gdw/m^2 (Nixon and Oviatt 1973b).

NUTRIENTS AND PRIMARY PRODUCTION

Of all the environmental parameters that may influence primary production on the New England high marsh (see Chapter 3; Valiela and Teal 1974; Niering and Warren 1980), the most convincing evidence concerns the importance of nitrogen as a limiting factor. In replicated field fertilization experiments carried out over a number of years at Great Sippewissett Marsh, Teal, Valiela, and their coworkers have developed data which show that nitrogen additions at least as low as 0.8 g N/m^2/week during the growing season more than double the aboveground production of S. patens and Distichlis on the high marsh. A similar effect was observed with the low marsh S. alterniflora (Valiela and Teal 1974; Valiela et al. 1975, 1976). Phosphorus additions had no effect on the production of any of the species. In terms of belowground production, the addition of nitrogen reduced the development of roots by about 75%, but more than doubled the production of rhizomes (Table 11). Overall, the production of low and high marsh appeared remarkably similar.

Since the fertilizer input was maintained for about 6 months out of every year, the total nitrogen supplement in the Sippewissett Marsh experiments amounted to about 20 g $N/m^2/yr$ and 60 g $N/m^2/yr$ for low and high treatment experimental plots, respectively, on both regularly flooded and high marsh. These inputs are large compared with other nitrogen sources and sinks on the marsh. Bacterial nitrogen fixation on the high marsh at Sippewissett is less than 5 g $N/m^2/yr$ (Teal et al. 1979), but there is a net loss of nitrogen to the atmosphere of about 4 g $N/m^2/yr$ from denitrification (Kaplan et al. 1979).

FATE OF THE PRIMARY PRODUCTION

Discovering the fate of the organic carbon and associated nitrogen, phosphorus, and other materials that are fixed on the high marsh each year is not simple. Since there appear to be few grazers feeding on the grass, little is transferred directly into secondary production of terrestrial animal tissue. Usually, the primary production either accumulates in the sediments as peat, decomposes in the marsh, or is exported by the tides to more open estuarine and coastal waters.

Accumulation in the Sediments

Surprisingly, few studies of the sediments and peat found on New England high marshes have been conducted. With the notable exception of McCaffrey's (1977; McCaffrey and Thomson 1980) analysis of Spartina patens peat at Farm Creek Marsh in Connecticut, the limited information available is based largely on studies of the stunted S. alterniflora zones of two marshes on Cape Cod. Because the composition of marsh sediment appears to be somewhat higher in organic carbon and nitrogen than nearshore subtidal sediments (Table 12), some fraction of the biologically accumulated carbon and nitrogen on the marsh must also be buried along with the mineral and organic material deposited by the tidal waters. The role of phosphorus is not as clear because there is some suggestion that this element may be released by anoxic marsh sediments. The remobilized phosphorus may then be exchanged across the sediment-water interface and removed from the marsh on ebb tides (Nixon 1980).

Based on a reasonable range in density and chemical composition of salt marsh sediment, and the range of accretion rates summarized in Table 2, somewhere between 75 to 400 g C/m^2/yr and 5 to 20 g N/m^2/yr may be accumulated in marsh peat (Figure 20). A consideration of the composition of estuarine sediment suggests that some 35 to 75 g of the carbon and 2 to 4 g of the nitrogen may be associated with the material that is removed from the tidal water. The remaining 0 to 365 g C/m^2/yr and 1 to 18 g N/m^2/yr would then be due to the burial of Spartina and marsh algae, though the contribution of the latter must be very small.

It seems apparent that the source of this organic matter is the large amount of belowground production of roots and rhizomes, although it is still not clear what is happening below the marsh surface.

Table 12. Comparison of sediments found on the high marsh at Farm Creek, Connecticut, with those of Long Island Sound and a short S. alterniflora marsh at Barnstable, Massachusetts. Data from McCaffrey (1977) and Redfield (1965).

	S. patens marsh, Conn.[a]	L.I.Sound	S. alterniflora marsh, Mass.
Wet bulk density g/cm^3	1.011		1.15
Dry bulk density g/cm^3	0.2	0.65	0.25
Inorganic matter g/cm^3	0.135	0.624	0.19
Organic content g/cm^3	0.056	0.04	0.06
Organic content, % dw	28	6	5.2

[a]Averaged over 1 m.

[b]Averaged over 5 m.

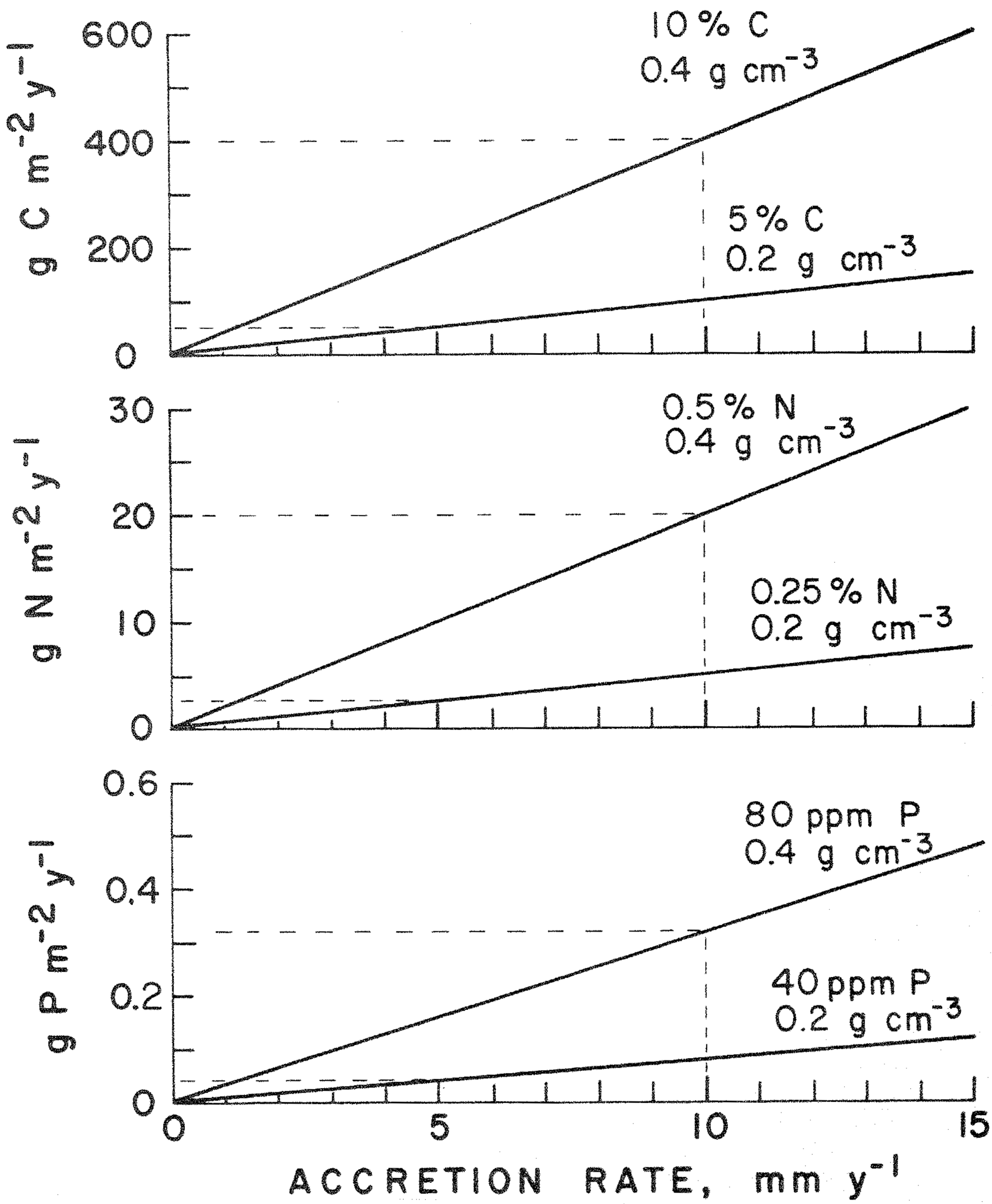


Figure 20. The accumulation of organic carbon, total nitrogen, and inorganic phosphorus in the sediments of a marsh calculated for different accretion rates, sediment densities, and sediment compositions (Nixon 1980). The upper and lower lines represent approximately maximum and minimum estimates based on the literature.

The belowground processes may also vary in different areas of a marsh, depending on water table and groundwater flow, tidal inundation, or sediment input. In analyzing a 1-m (3.3-ft) long core from the S. patens zone, McCaffrey (1977) found a remarkably uniform organic content with depth and a varying inorganic component. Similarly, Redfield (1965) reported on a 5-m (16.4-ft) core from the S. alterniflora zone in which the organic content of the peat was relatively constant with depth while the ash content varied by a factor of 10. Neither of these authors concentrated on the fine structure of the top 10 cm (4 inches) or so, where the production of Spartina roots and rhizomes is greatest and most variable (Figure 18; Valiela et al. 1976).

If the underground production rates measured by Valiela et al. (1976) on Cape Cod are representative of other New England marshes, less than a third of the belowground production is buried. In the S. alterniflora zone of the Great Sippewissett Marsh, it appears that only about 5% of the total Spartina production (~7% of belowground production) is accumulated in peat; the larger part is consumed aerobically on the marsh surface or through sulfate reduction in the anoxic sediment.

Decomposition

It is not surprising that most of the organic matter put below ground by the Spartina does not remain to form peat. If it did, Valiela et al. (1976) calculated that it alone would raise the level of Great Sippewissett low marsh by about 1 cm each year. Moreover, the distribution of organic matter with depth in the sediment (Figure 18) suggests that much of the organic matter produced near the marsh surface is not buried. At first, the removal of such a large annual increment in belowground organic matter seemed difficult to explain. As Valiela et al. put it in 1976:

> "We did not expect the marked decay in dead matter...., since we supposed that decomposition in anoxic sediments would be slow. However, dead parts still attached to the living plant would be supplied with oxygen from the plant's air spaces..., so that aerobic oxidation could occur."

Later work at Great Sippewissett, however, showed that sulfate reduction by the microbial community in the peat appeared to oxidize some 1,800 g C/m^2/yr in the S. alterniflora zone, an amount roughly comparable to the belowground production (Howarth and Teal 1980). It is also possible that belowground production measurements can be confounded by the overwintering storage of organic matter in basal portions of grasses. In work with S. alterniflora, Lytle and Hull (1980) found that a large fraction of late-season photosynthate was translocated to rhizomes and that this material was then used in spring to support much of the growth of the plants through the fourth or fifth leaf stage. Even in midsummer, "new rhizomes were regenerated largely using energy stored in over-wintered rhizomes." Unfortunately, similar studies are not yet available for the S. patens high marsh, nor do we yet have direct measurements of the decomposition rate in the S. patens zone.

The aboveground primary production can be decomposed on the marsh surface or it can be carried off the marsh. If it is carried off the marsh, it may accumulate on the bottom of marsh creeks and embayments or it may remain suspended in the water column and, perhaps, be transported into adjacent estuarine and nearshore waters. In general, the high marsh _S. patens_ is not usually thought of as contributing significantly to the export of organic matter from the marsh. There are at least three reasons for this opinion: the high marsh is much less frequently exposed to the tidal waters, the grasses are farther from tidal creeks, and _S. patens_ forms a dense interwoven mat rather than an open stand of vegetation (Blum 1968). In general, decomposition of the high marsh vegetation appears to be relatively slow. This may be true not only because decomposition is usually slower on the ground than in water, but because marsh plants (with the exception of _Salicornia_, a succulent) are relatively resistant to decay compared with a number of other marine and terrestrial plants (Figure 21).

Organic Export

Salt marshes are often valued more for their contribution to other environments than for their intrinsic value. Nowhere is this more evident than in the "outwelling" concept developed by E.P. Odum (1968, 1980), in which the export of organic matter and/or nutrients to coastal waters from marshes has often been considered a major part of wetlands valuation (Gosselink et al. 1974). The reality, magnitude, and significance of "outwelling" and its role in valuation have been reviewed by Walker (1973), Haines (1979), W.E. Odum et al. (1979), E.P. Odum (1980), Nixon (1980), and Shabman and Batie (1980), and little will be gained by doing so again here. The high marsh is not usually considered an important source of organic or nutrient exchange with the tidal waters. Upper portions of the intertidal zone with stunted _S. alterniflora_ may show variable uptake or release of nutrients (Lee 1979), and some of the aboveground production of the grass may be carried off the emergent marsh into tidal creeks. It would be difficult, however, to make a convincing argument that the export of organic matter or nutrients from high marshes in general plays an important role in the ecology of New England coastal waters.

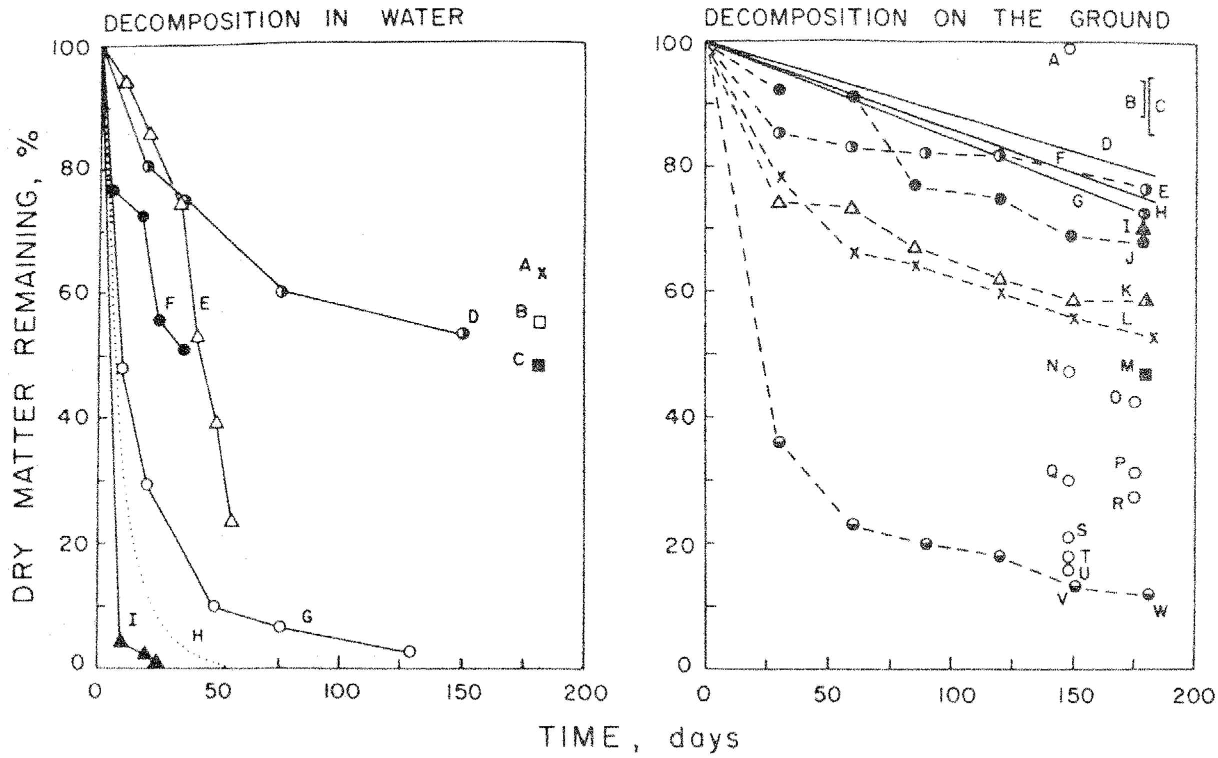


Figure 21. Decomposition of various kinds of plant material on the ground or submerged in water at different sites. Individual points are from single measurements while lines are shown for sequential measurements.

In water:
- A = Spartina cynosuroides
- B = Distichlis spicata
- C = Scirpus (A-C from de la Cruz 1975)
- D = Spartina alterniflora (Wood et al. 1969)
- E = Zostera marina (Burkholder and Doheny 1968)
- F = Juncus roemerianus (de la Cruz and Gabriel 1974)
- G = Peltandra virginica (Odum and Heyword 1978)
- H = marine plankton (Garber 1981)
- I = Ulva lactuca (Burkholder and Doheny 1968)

On land:
- A = filter paper
- B = fern (Pteridium, data of Frankland 1966 in Frankland 1974);
- C = coniferous leaf litter (data of Mikola in Millar 1974)
- D = sedge (Carex)
- E = Juncus (de la Cruz and Gabriel 1974)
- F = willow leaves (Salix)
- G = birch leaves (Betula) (Chamie and Richardson 1978)
- H = Spartina cynosuroides
- I = Distichlis spicata
- J = Juncus roemerianus (H,I,J from de la Cruz 1975)
- K = Distichlis spicata (Odum and de la Cruz 1967)
- L = S. alterniflora (Odum and de la Cruz 1967)
- M = Scirpus americanus (de la Cruz 1975)
- N = willow
- O = rhododendron
- P = oak
- Q = ash
- R = oak
- S = birch
- T = maple
- U = elm
- V = alder (N-V tree leaves from mull sites, Bocock 1964)
- W = Salicornia (Odum and de la Cruz 1967)

CHAPTER 5

HUMAN IMPACT ON THE HIGH MARSH

Lying between the tide line and the upland, the high salt marshes have been pushed in both directions by human activities. Since the mid 1600's, the marshes in New England have been flooded or drained, impounded or diked, ditched or filled. They have been converted into fresh or brackish water meadows as well as landfills, parking lots, and housing developments. They have been praised for growing hay that saved livestock and damned for breeding mosquitoes that brought discomfort and disease. Human activities have polluted them with metals, oil, chemicals, and trash. Recently they have been protected and preserved with environmental legislation. It is an interesting pattern of changing perceptions and values. In this environment, perhaps more than in any other marine ecosystem, man has been both manager and manipulator.

SALT MARSH HAY

Before the salt marshes were considered wastelands in need of "reclamation," and even longer before they were elevated to the rank of a "sacred cow" in the environmental movement, the marshes were clearly, and intimately, a part of the early New Englander's "life support system."

While the cutting of Spartina patens or salt marsh hay is a recent enough activity to be part of the boyhood memories of many present-day New England coastal farmers, it is difficult to appreciate the importance of this resource in the first 100 years or so of the agricultural economy of the area. In the recent past, salt marsh hay was a supplement used more for animal bedding, mulching, and "topping" hay stacks to keep field grasses dry, than as a staple feed. But at one time the marsh hay was a major food source which made the keeping of livestock possible and practical. And it was livestock that formed the mainstay of New England agriculture in the early years (Russell 1976).

The presence, at least in southern coastal New England, of large areas of land cleared by the Indians helped the first colonists greatly, as did the open freshwater meadows along the river floodplains. But it was difficult to obtain suitable forage for a large number of animals, and predators, especially wolves, were a great problem (Wood 1634; Russell 1976). As Bidwell and Falconer noted (1925) in their classic History of Agriculture in the Northern United States 1620-1860:

> "A condition of prime importance for the successful raising of livestock is of course an abundant supply of native forage plants. In this respect the North American continent was strikingly deficient. The Indians of the region kept no herbivorous domestic animals and hence had developed no forage plants.... In the face of such

difficulties it was a noteworthy accomplishment of New England and the Middle Colonies in the seventeenth century to have become not only independent of outside sources of supply, but even to have developed a surplus of cattle, horses, and meat products for export."

The use of salt-marsh hay contributed substantially to this success and helped to determine the pattern of settlement along the New England coast. In describing the history of New England agriculture, Russell (1976) has shown that the presence of fresh and salt hay marshes was a major factor in site selection of many towns settled before 1650 (Figure 22). As he described it:

> "All along the winding Massachusetts Bay shore, wherever salt grass caught the eye, exploring stockmen were petitioning the General Court to be allowed to set up new townships. The adjoining upland might be only moderately fertile, even chiefly ledges and woods, yet cattlemen brought up amid England's grassy vales and tidal marshes coveted the salt hay in the lowlands. In Plymouth Colony the same magnet drew ambitious men toward new locations. Reluctantly the Plymouth authorities permitted their neighbors to leave the close-knit mother town and its scant fertility and set up new and distant farmsteads beside inviting hay lands. Duxbury, Green Harbor (Marshfield), and Hingham, their tidal marshes rich in salt hay, drew planters northward. The miles of green salt meadow on the Cape Cod shore and Indian fields there open for tillage beckoned still others to plant Sandwich, Barnstable, and Yarmouth, and to move inland to Taunton at the head of Mt. Hope Bay."

On Long Island, and perhaps in other areas as well, the "salt meadows" were owned by the town and the right to mow and carry off the hay was auctioned off early in the spring of each year (Kavenagh 1980). The same practice probably applied to "thatch grass" or S. alterniflora. It is hard to know if this species was really used as thatch or as feed, bedding, or something else. Present-day farmers I have interviewed never recall any use for it, and Kavenagh (1980) concluded that it was probably not used for roofing:

> "Very early in the colonial experience in both Plymouth and Boston the colonists found to their sorrow that thatch grass for roofing quickly dried in this climate, in contrast to Old England with its more moist climate and ability to keep the outer grass damp and less fire-prone. Here wood and mud chimneys caught fire easily, sparks flew, and a dried thatch roof did not last very long. Ordinances were soon passed to prohibit them."

By 1700, "English grasses" had been introduced and spread throughout New England for pasture (Bidwell and Falconer 1925), but salt-marsh hay continued to be used in large quantity throughout the coastal region until the early 1900's. Russell (1976) described the situation as it was in the late 1700's:

> "Countless staddles (wood underpinning) for salt hay still dotted seacoast marshes from southern Maine to Cape Cod, along the shores of the Sound, and up the Connecticut and similar estuaries. In the fall,

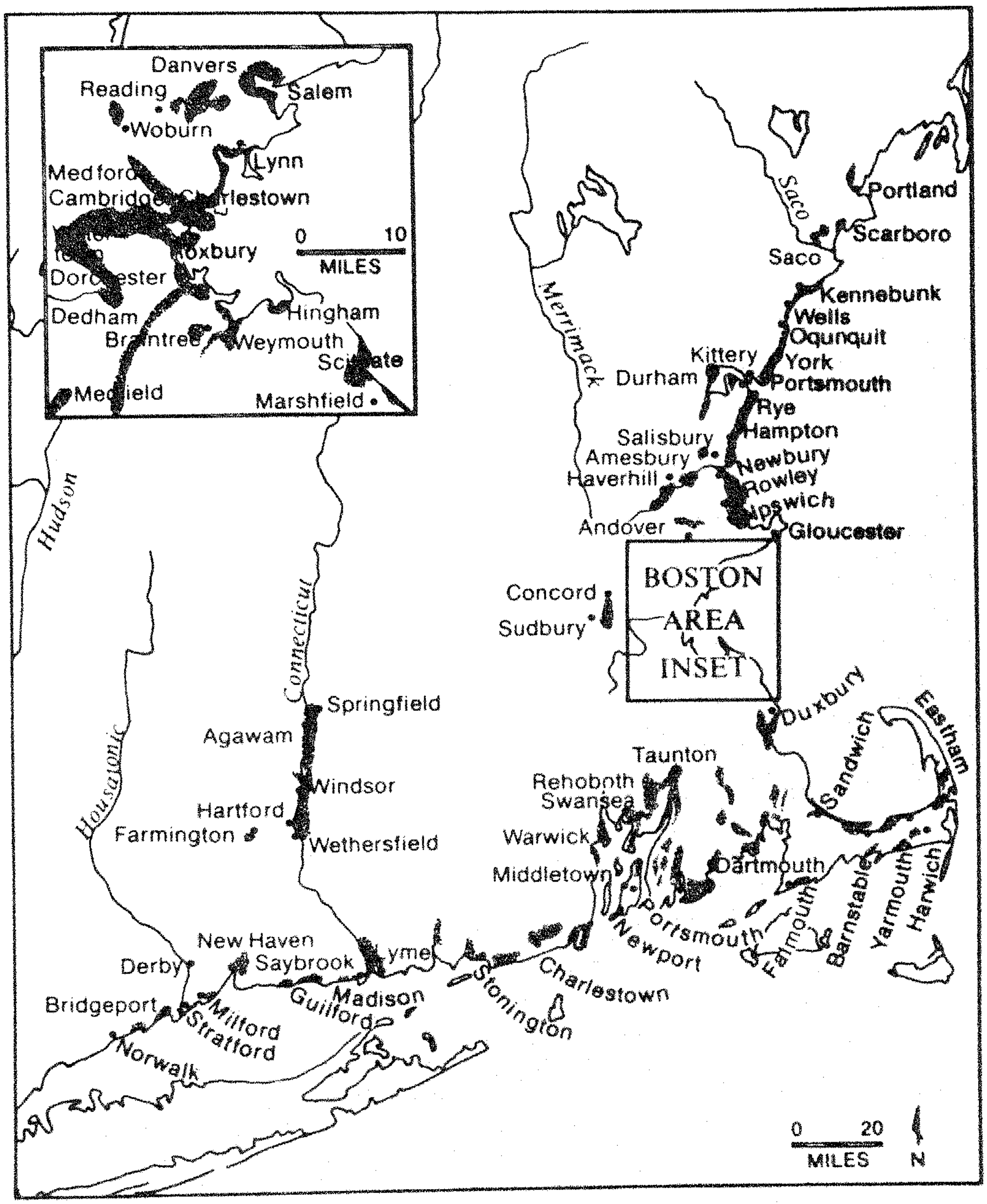


Figure 22. Locations of New England towns that were settled by 1650 adjacent to fresh or salt hay marshes (Russell 1976).

gundalows ferried the hay up every salt creek to the home farm. On such provender thousands of cattle and horses were wintered every year. The resulting manure, supplemented where possible from other sources, nourished merchantable crops of corn, potatoes, tobacco, flax, onions and other produce."

Staddles and gundalows (gondola) were still in use in Maine where they were photographed in the late 1800's (Figure 23). Moreover, the value of the high marsh black grass (Juncus gerardi) had been discovered, and this species was also being harvested (Russell 1976):

> "Salt hay from the thousands of acres of coastal marshes retained its importance. This 'harvest of the sea' actually improved in quality, as the nutritious 'black grass,' good fodder even for milkers, spread more widely. Black grass, cutting about a ton per acre, made up half the crop along Massachusetts Bay's North Shore."

The continuing importance of salt hay through the 1800's is reflected in its inclusion in the agricultural census data for the New England States. For example, in 1875 farmers in Rhode Island cut 1,717 tons of salt hay from 2,506 acres of marsh, for an average yield of 0.7 tons/acre or 160 g/m^2 (Anonymous 1867). The yield was comparable to conventional hay fields at the time, but low, relative to modern measurements of the production of high marsh vegetation (see Table 10). Some of this discrepancy may be due to differences in harvest technique, or because salt hay was usually harvested early in the season, before it bent over and formed a mat that was hard to cut (Kavenagh 1980). Even by 1875, the value of salt hay harvested in Rhode Island was only $16,000 compared with a seaweed fertilizer harvest (from drift on the beaches) of $60,000 and a marine fishery of almost $450,000. The importance of salt hay declined along with the fortunes of New England farming as agriculture moved west.

CHANGES IN THE AMOUNT OF HIGH MARSH

For a time, the attraction of salt hay may have drawn some coastal farmers to try to increase the acreage of high marsh. In his 1748 Essays upon Field Husbandry in New England, Jared Eliot (1748) described his successful effort to convert a "wholly unprofitable" low-lying piece of swamp into a salt meadow, and suggested that others might do the same since he had seen "sundry such places upon the Sea Coast."

> "Last Fall I began upon it and drew [dug] a Ditch of four Foot wide from a large Salt Creek, and carried it up in the middle of the Cove seventy Rods, in order to turn it into Salt Meadow, that being the best that I could do with it: It so far answers the design, that the Tide flows regularly into it, to the upper end of it; the Tide now flowing, where I suppose it never reach'd before."

It seems impossible to determine how much high salt marsh might have been created in this way, but it must have been a very small amount. The more common procedure was for farmers to dike the marshes in an attempt to convert them to fresh meadow or with the hope of draining them for growing traditional crops.

The expanding maritime economy of New England during the 1700's and the impact of the industrial revolution during the 1800's must have resulted in more widespread filling of coastal marshes, particularly in southern

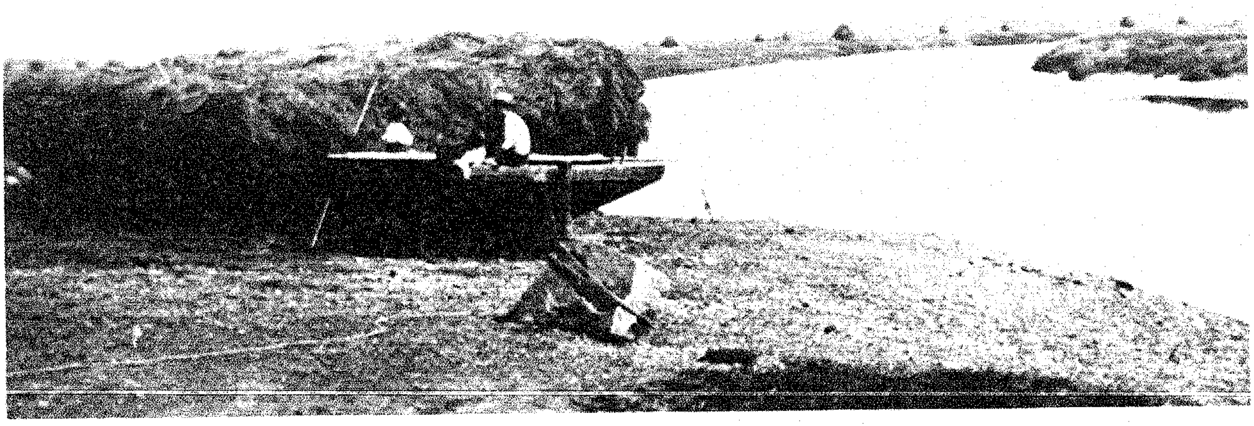


Figure 23. Top: Salt hay on staddles to keep it above the tide. Bottom: Gundalow loaded with salt hay to be floated out on the flood tide. (Courtesy of the Society for the Preservation of New England Antiquities, Boston, Mass.)

parts of the region. But no systematic inventory appears to have been compiled, and it may be impossible to make one. Some appreciation for the extent of wetland loss can usually be gained by examining detailed maps of coastal urban areas at various times in the past. The filling involved in the creation of harbors (using dredge spoil) as well as mill and factory sites, roads, railways, and housing is usually dramatic.

Data for more recent years are available from various sources listed by Spinner (1969) and Gosselink and Baumann (1980). According to the latter authors, wetland loss in New England since 1886 was greatest from 1922 to 1954 (Figure 24), "probably [as] a result of public works projects of the 1930's, the construction of major airports, the increase in military installations during World War II, and a post-World War II housing boom." As discussed in Chapter 3, it appears that a disproportionate part of this loss involved high marsh areas since they are less often flooded, easier to fill, and close to the uplands (O'Connor and Terry 1972). Much of the remaining marsh land is in public ownership, however, and legislation in the New England States now protects salt marshes, so it is likely that the rate of wetland loss due to human activities will continue to slow. But the dynamic nature of the marshes will continue to result in vegetation changes and in shifts of size and shape of the coastal wetlands.

MOSQUITO DITCHES

Among the most conspicuous signs of human activity on the New England marshes are the characteristic patterns of straight parallel ditches running from the upland edge of the marsh or from old pond holes

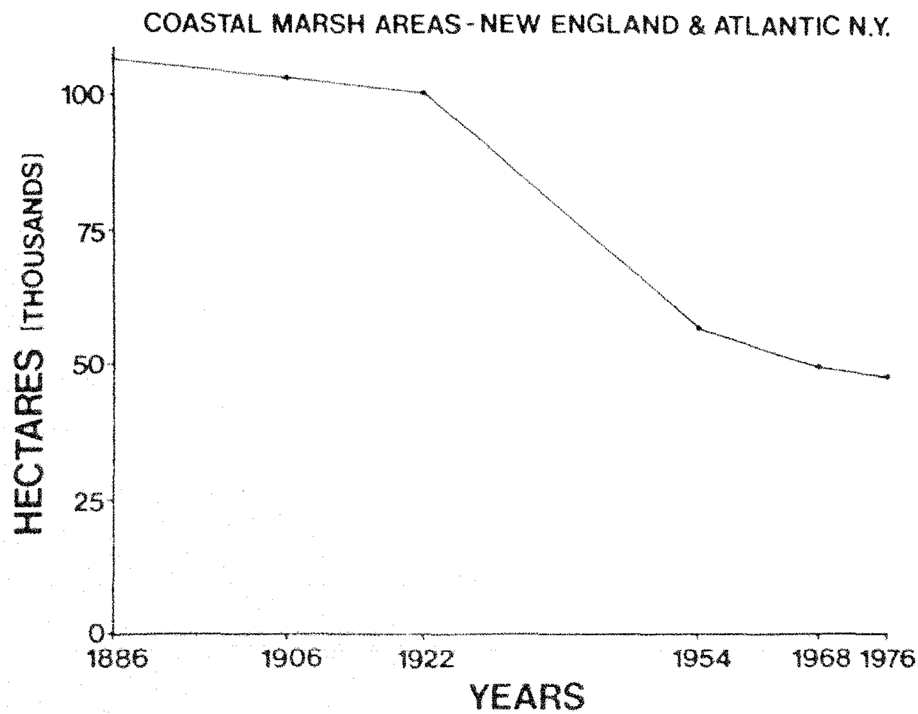


Figure 24. Amount of coastal wetlands in the Northeastern United States. (Gosselink and Baumann 1980.)

to the larger tidal creeks. Spaced 35 to 70 m (115 to 230 ft) apart, the shallow, narrow ditches were designed to remove pools and standing water from the marsh and thereby prevent the breeding of mosquitoes. Ditching as a method of mosquito control appears to have begun in New Jersey at the turn of the century (Smith 1902, 1907), but it was practiced most widely during the Depression years of the 1930's with support from the Works Progress Administration and the Civilian Conservation Corps. This attempt at "managing" the marshes was so thorough that by 1938 almost 90% of the tidal wetlands between Maine and Virginia had been ditched (Bourn and Cottam 1950).

The ecological impact of such a widespread alteration of the marshes is surprisingly difficult to describe with any certainty (Daiber 1974). Much of the early literature appears to be based on casual impressions and anecdotal information and often reflects the biases of "mosquito controllers" or conservationists. The findings of a widely cited study of ditching effects in a Delaware marsh by Bourn and Cottam (1950) may have been influenced by dredging in a nearby river (Lesser et al. 1976).

Information is lacking about the effects of ditching on New England high marsh; most of the work on this problem has been done in Delaware and New Jersey, though one of the better early studies on the effect of ditching on shorebirds and waterfowl was carried out in the Duxbury, Massachusetts, marshes (Bradbury 1938). In Duxbury, the marshes had supported abundant and diverse waterfowl before mosquito control operations were completed, but after ditching, the marshes became "dry and devoid of birds" (Daiber 1974).

Ditching can enhance the growth of high marsh plants at the expense of Spartina alterniflora, although the tall creek-bank S. alterniflora often grows along the banks of the ditches if the spoil from ditch construction has not been left there. Where S. alterniflora does develop, the nesting and production of clapper rails (Rallus longirostris) may be enhanced (Stewart 1951; Ferrigno 1966; Shisler and Shulze 1976). Where spoil is deposited, high marsh grasses or woody vegetation such as Iva fructescens and Baccharis halimifolia become established (Miller and Egler 1950; Daiber 1974). These species are generally of low value, but some birds (e.g. boat-tailed grackle, Cassidix mexicanus; red-winged blackbird, Agelaius phoeniceus) may use them for nesting (Meanley and Webb 1963; Post 1974). Because the ditches are often dug to drain pond holes and other shallow depressions, submerged aquatic plants such as Ruppia are usually eliminated. The loss of these plants as well as the protected open water makes the marsh less attractive to waterfowl and other birds.

Bradbury's (1938) study of the Duxbury marshes suggests that many of these changes can be reversed. Daiber (1974) summarized it in his review as follows:

> "The technique of restoration was based on the premise that mosquito larvae would be eaten by Fundulus heteroclitus, the mummichog minnow. The job was to create a habitat where fish could live at low tides and high temperatures. Former potholes were restored by damming outlets with sod. Care was taken to keep the water level about nine inches below the marsh surface, thus, keeping it free of water. Some potholes were deepened to assure sufficient water for Fundulus to live in during dry periods. Controlled burning of salt hay made a variety of insects

available for shore birds and it helped control mosquitoes by enhancing standing water evaporation. Ditches were partially blocked so water was retained but did not flow out over the marsh surface. Bird use was reported to immediately increase without any loss in mosquito control.

Some of these techniques form part of "open marsh water management" (OMWM), an alternative to parallel ditching and insecticides for mosquito control that has been developed by the New Jersey Department of Environmental Management (Ferrigno and Jobbins 1968; Ferrigno et al. 1975). Using this approach involves selective ditching of major mosquito breeding depressions, filling shallow depressions on the marsh surface, and carefully constructing some ditches to collect water in ponds that are deep enough at all times to contain small fish which feed on mosquito larvae. Studies have been carried out to document the effectiveness of OMWM in controlling mosquitoes and in enhancing the wildlife value of the marsh (Ferrigno 1979; Ferrigno et al. 1975). This contrasts with traditional parallel or grid ditching--a practice that has been of questionable value in controlling mosquitoes and that is thought to have had varying (and often undesirable) impacts on overall marsh ecology (Daiber 1974).

POLLUTION

Because the high marshes are above mean high tide, most of the time they are exposed to the atmosphere rather than to tidal waters (Figure 25). As a result, deposition of particulate matter from the air or in precipitation can be major pathways for pollutant inputs. Metals, toxic

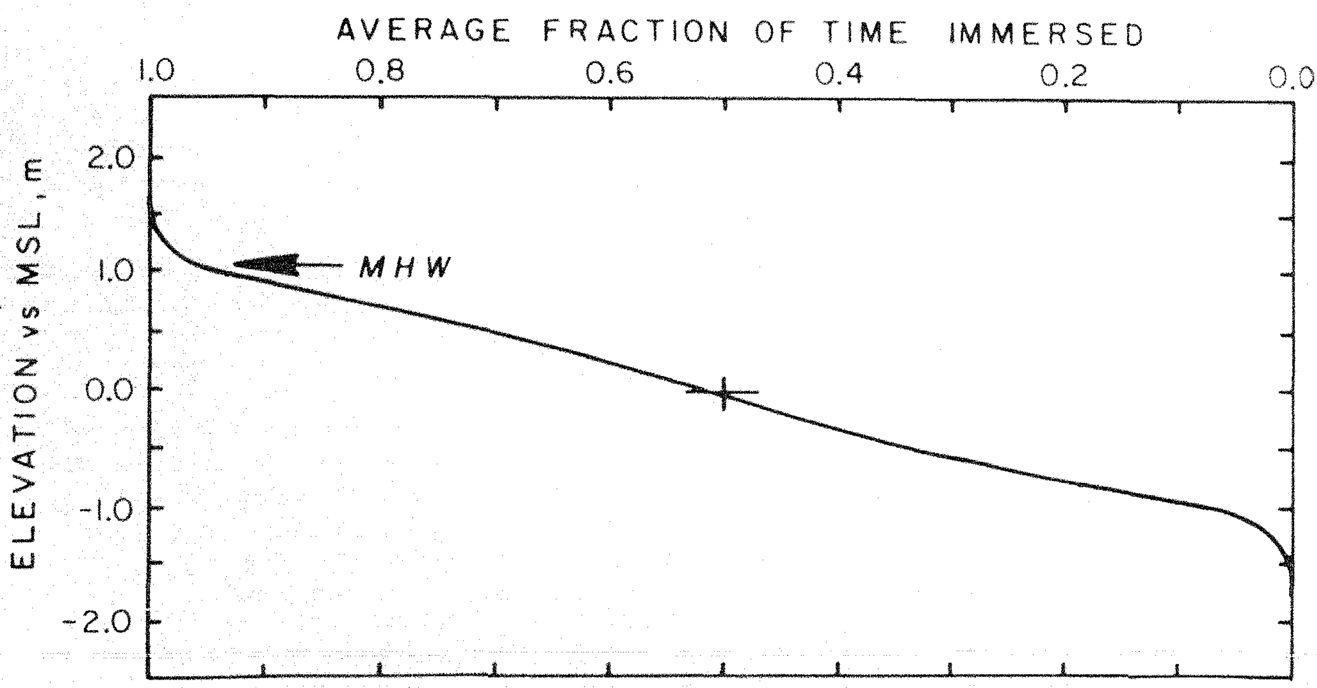


Figure 25. Amount of time the grasses and surface sediments at Farm Creek, Connecticut, are exposed to the atmosphere at different elevations across the marsh (McCaffrey 1977).

organics, petroleum hydrocarbons, and just plain junk also may be brought onto the high marsh each month with the highest tides. Junk is often evident along the drift line at the upland edge of the marsh; when large amounts accumulate the vegetation may be smothered and the visual quality of the area decreased. The accumulation and effects of other anthropogenic materials are usually more subtle.

Petroleum Hydrocarbons

Of the various oil spill incidents in New England compiled by Hyland (1977), few appear to have had a major impact on salt marshes in general or on the high marsh in particular. Nevertheless, the potential is there. Because urban sewage effluents are the major source of petroleum hydrocarbons in coastal waters (Van Vleet and Quinn 1977), many marshes in more developed estuarine areas must be exposed to tidal waters with elevated concentrations of dissolved and particulate petroleum compounds. The effects of chronic, relatively low-level (compared to spills) concentrations of these materials on marshes have never been assessed, however. The few marsh-oil studies which are available have been concerned with the impact of single or repeated oil spills, and most of this work has been carried out in Europe or the Southern United States (Cowell 1971; Bender et al. 1977; Baker 1979). The only major study of the impact of an oil spill on a New England salt marsh appears to be the work of Hampson and Moul (1978), who documented the impact of No. 2 fuel oil on a marsh in Buzzards Bay, Massachusetts. Their observations indicated that, in general, perennial plants such as *Spartina* and *Distichlis* were more resistant than annuals like *Salicornia*. But even for *S. alterniflora*, the biomass, height, and number of plants were markedly reduced in oiled areas 3 years after the spill. As might be expected, they also found that plants higher up in the marsh recovered more quickly because their exposure to the oil was less. However, petroleum compounds vary widely in composition and toxicity, and their impact must also be a function of other factors including temperature and season. At this point, it is impossible to make a very useful speculation about the response of the New England high marsh community to oil spills or to a large number of other possible perturbations.

Heavy Metals

Numerous researchers have investigated the various aspects of abundance, distribution, biological uptake, and effects of heavy metals in New England high marsh communities (Nixon 1980). Because there are few burrowing animals living under the dense *Spartina patens* mat, there is little bioturbation and the sediments appear to provide a relatively undisturbed record of metal input to the marsh surface. The higher concentrations usually found near the surface may reflect an anthropogenic influence (Figure 26) or may be the result of remobilization of the material at depth. For example, in the case of Mn it appears that manganese oxide is reduced in the anoxic sediments, and the soluble Mn is lost from the solid phase by diffusing through the pore waters and across the sediment water interface (Figure 27, McCaffrey 1977; Lord 1980). For metals like Cu, Zn, and Pb, which are relatively stable in the sediments, it is possible to combine their vertical distribution with measurements of the sediment accretion rate to gain an estimate of the history of anthropogenic inputs (Figure 28). It is also possible to compare the accumulation rates of different metals with estimates of their input rates to calculate the degree to which the

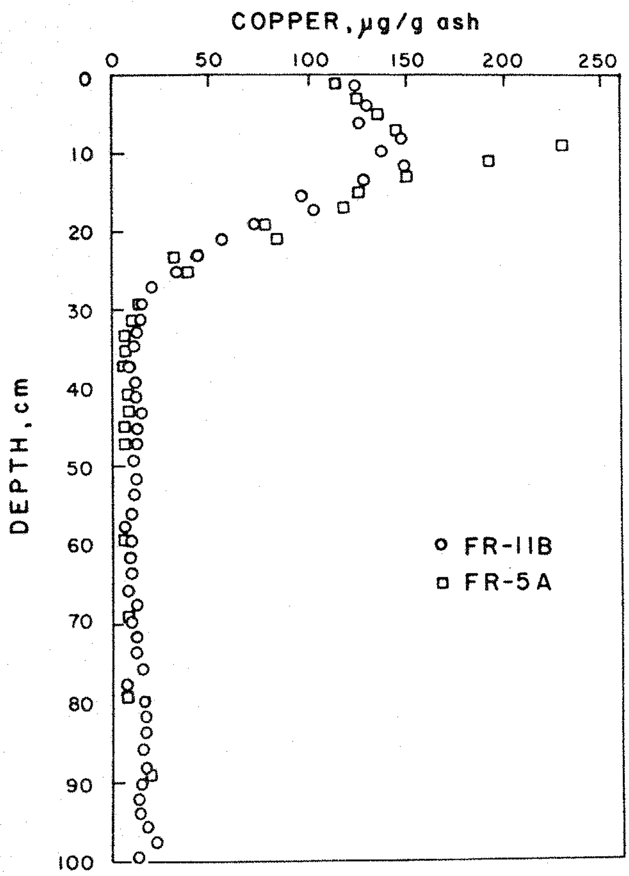


Figure 26. Concentrations of copper at various depths in the sediment under Spartina patens at Farm Creek Marsh, Connecticut. The increase from 30-cm depth to the surface is due to anthropogenic inputs, largely from the atmosphere (McCaffrey 1977).

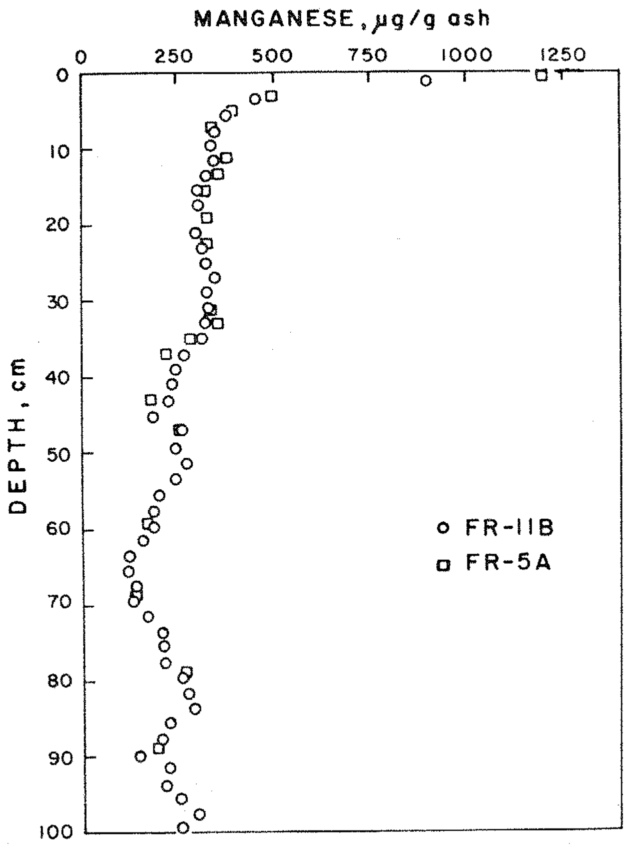


Figure 27. Concentrations of manganese at various depths in the sediment under the Spartina patens at Farm Creek Marsh, Connecticut. The rapid increase at the surface is largely due to a remobilization at Mn at depth and its subsequent loss across the sediment-water interface (McCaffrey 1977).

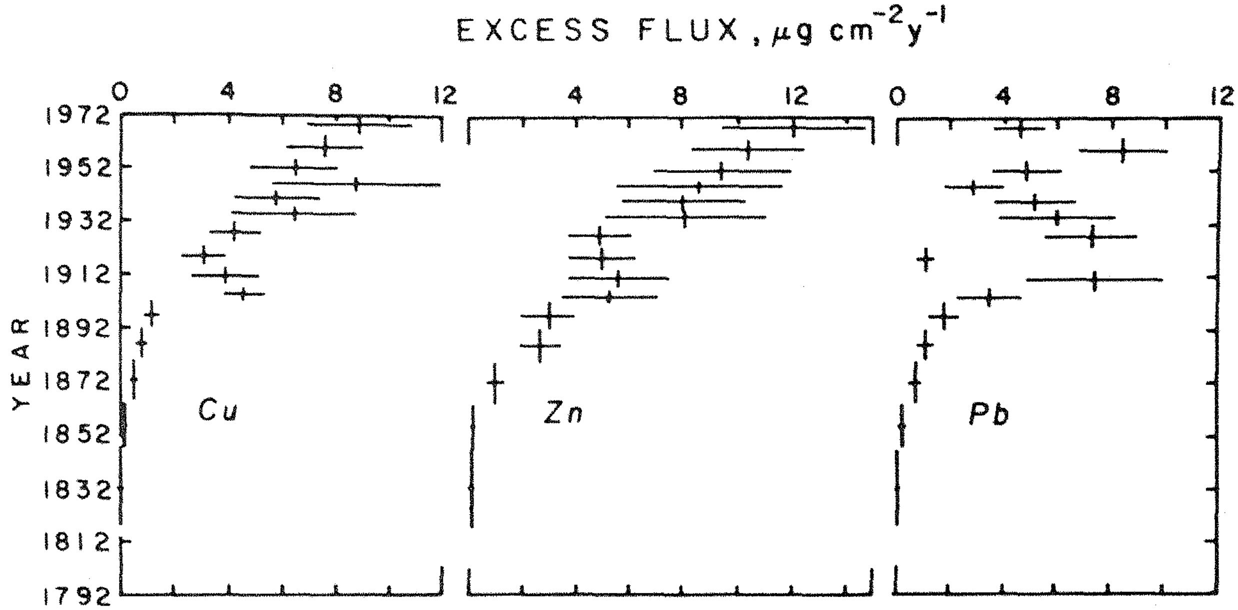


Figure 28. Historical variation in the anthropogenic fluxes of copper, zinc, and lead recorded in the high marsh sediments at Farm Creek, Connecticut (McCaffrey 1977).

marsh functions as a sink for various pollutants. Generally, it appears that Pb, Cu, and Fe are held very tightly in the high marsh, with Mn, Zn, and Cr showing only about 50% retention and Cd somewhat less (Siccama and Porter 1972; Banus et al. 1974, 1975; McCaffrey 1977; Giblin et al. 1980). The retention of metals by the lower intertidal marsh may be considerably less complete (Giblin et al. 1980).

In addition to providing us with a record of pollution inputs, it also has been suggested that marshes might serve as "biological filters" for urban sewage. To explore the ecological consequences of this idea, a long-term experimental study of the effects of nutrient enrichment and heavy metals was conducted at Great Sippewissett Marsh on Cape Cod by groups at Woods Hole Oceanographic Institution and The Marine Biological Laboratory at Woods Hole. Much of that work has been cited throughout this community profile.

The experiment involved the application of metals in commercial sewage sludge fertilizer (Table 13) and in dissolved form without associated nutrients (Fe = 650 mg/m^2/week; Cu and Cr = 20 mg/m^2/week) to plots of low and high marsh. In both treatments, the metals did not appear to have any effect on the growth of *Spartina patens* or *S. alterniflora* (Figure 29) according to Giblin et al. (1980). However, both grasses became enriched in Cd, Cr, Cu, and Zn in plots treated with large doses of the sludge mixture (Table 14). The fate of these metals is still uncertain and, as Giblin et al. (1980) concluded at the end of their paper, "The role of the grasses in making metals available to marsh organisms is presently being investigated."

In 300 years we seem to have come full circle, from viewing the New England marshes as a source of food to exploring their value as sewage treatment plants. I suppose it is

Table 13. Metal (in sewage fertilizer) added to each plot and amount of each element found in the top 2 cm of marsh sediments (Giblin et al. 1980).

Metal	Treatment plot[a]	Amount added to plot (mg/m^2)	Amount detected[b]	
			Low marsh	High marsh
Cd	C		8	8
	XF	490	94	152
Cr	C		50	54
	XF	10,300	2,150	4,750
Cu	C		46	63
	XF	2,010	1,120	2,270
Fe	C		26,200	18,800
	XF	110,000	105,000	158,000
Pb	C		187	187
	XF	1,740	1,090	1,750
Mn	C		207	218
	XF	1,320	890	940
Zn	C		146	78
	XF	6,820	1,450	2,760

[a] C=control plot; XF = metal-containing sewage sludge plot.

[b] Amounts in mg/m^2, average of 5 samples.

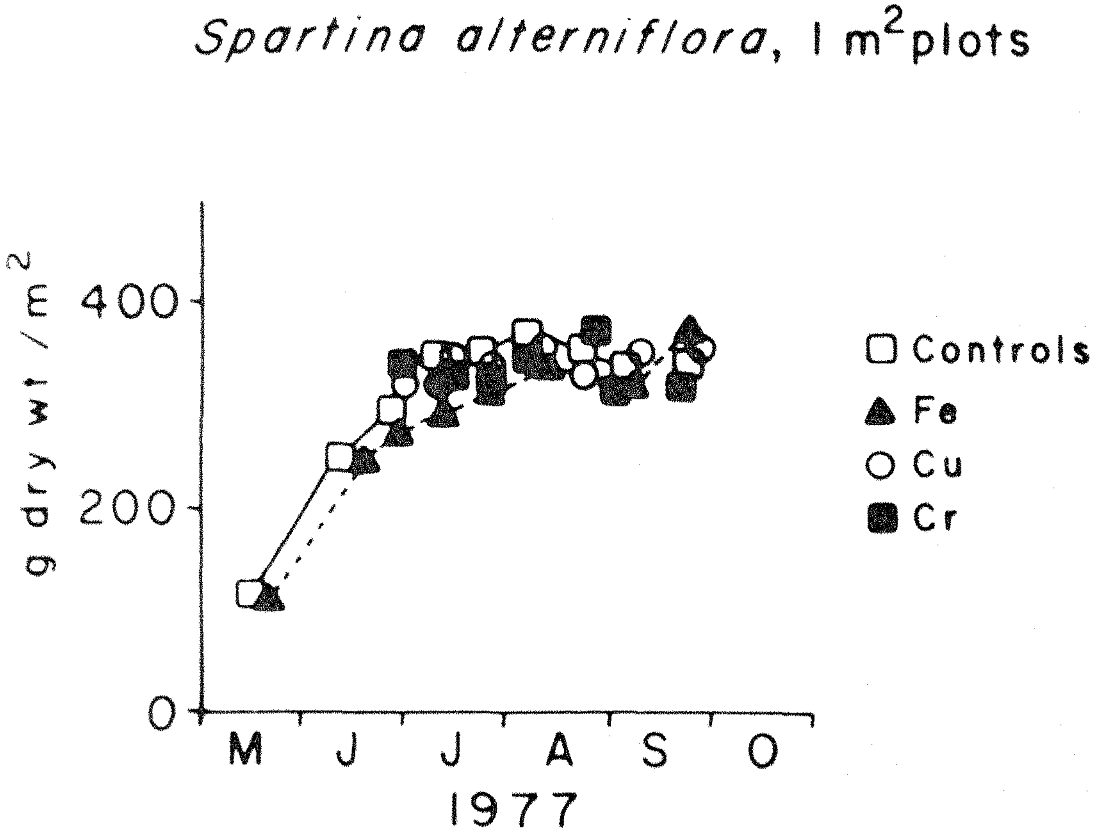


Figure 29. Aboveground biomass (g dry wt/m^2) of Spartina alterniflora in experimental plots treated with soluble iron, copper, and chromium at Great Sippewissett Marsh, Cape Cod (Giblin et al. 1980).

closed-system agriculture of a sort, though with a long time lag; sewage treatment is as much a part of our present "life support system" as salt hay production ever was. Perhaps someday, after a hundred years or so of nostalgia have accumulated, New Englanders may look at photographs of spray nozzles standing in the marshes with the same feelings we have now in looking at the old salt hay staddles and gundalows. Perhaps they will be as puzzled as I was when I came from the south and first saw the rocks sitting out in the grass of a New England marsh.

Table 14. Metal concentrations (ppm, oven dry weight) of live *Spartina alterniflora* and *S. patens* (Giblin et al. 1980).

Metal	Treatment plot[a]	*S. alterniflora*[b]	*S. patens*[c]
Cd	C	0.15	0.12
	XF	23.00	23.00
Cr	C	4.40	2.30
	XF	44.00	31.00
Cu	C	3.00	3.10
	XF	13.00	26.00
Fe	C	2,500.00[d]	80.00[d]
	XF	1,700.00[d]	65.00[d]
Pb	C	26.00[d]	25.00[d]
	XF	20.00[d]	21.00[d]
Mn	C	48.00[d]	37.00[d]
	XF	47.00[d]	50.00[d]
Zn	C	31.00	30.00
	XF	150.00	110.00

[a]C=control plot; XF = metal-containing sewage sludge plot.

[b]Mean of four replicates (each replicate being a pool of three samples).

[c]Mean of four replicates (each replicate being a pool of six samples).

[d]C and XF means are not significantly different at the 0.05 level.

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16. Abstract (Limit: 200 words)

The high salt marshes of New England have evolved in response to sea-level rises through accretion of sediments entrapped by marsh vegetation. Early theories of marsh development are traced and are reconciled in Redfield's synthesis accounting for marsh growth by aggradation over sand and mud flats as well as by accretion on existing marsh surfaces.

The shape and appearance of high marshes result from unique, complex interactions of local topography and bathymetry, sea-level rise, tides, sediment supply and vegetation. These factors, particularly the major influences of tides and short-term changes in sea-level, are incorporated in short-term processes that define and mold the ecology of the high marsh.

Short- and long-term mechanisms have produced approximate zonation of vegetation in the high marsh. High marshes are contrasted to Spartina-dominated low marsh in terms of plant and animal species and the relative importance of the dynamics of production, export, decomposition, and accumulation of materials in the sediments.

High marshes have been subjected to man's activities since earliest English settlement. The history of New Englanders' impact on this community is traced from their use of marshes as hay fields to depositories of pollutants. Habitat management considerations today include mosquito control and sewage sludge treatment.

17. Document Analysis a. Descriptors

Ecology, salt marsh, coastal wetlands, sedimentation, halophytes, tides

b. Identifiers/Open-Ended Terms

High salt marsh, New England

c. COSATI Field/Group

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