
Biological Report 85(7.29)
September 1990

Tidal Salt Marshes of the Southeastern Atlantic Coast: A Community Profile



Fish and Wildlife Service
U.S. Department of the Interior

Biological Report

This publication series of the Fish and Wildlife Service comprises reports on the results of research, developments in technology, and ecological surveys and inventories of effects of land-use changes on fishery and wildlife resources. They may include interpretive bibliographies and proceedings of workshops, technical conferences, or symposia.

Copies of this publication may be obtained from the Publications Unit, U.S. Fish and Wildlife Service, 1849 C Street, N.W., Mail Stop 130—ARLSQ, Washington, DC 20240, or may be purchased from the National Technical Information Service (NTIS), 5285 Port Royal Road, Springfield, VA 22161.

Biological Report 85(7.29)
September 1990

Tidal Salt Marshes of the Southeast Atlantic Coast: A Community Profile

By

Richard G. Wiegert and
Byron J. Freeman

*Department of Zoology and
Institute of Geology
University of Georgia
Athens, Georgia 30602*

U.S. Department of the Interior
Fish and Wildlife Service
Washington, D.C. 20240



Conversion Table

Metric to U.S. Customary

<i>Multiply</i>	<i>By</i>	<i>To Obtain</i>
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters (m)	3.281	feet
meters (m)	0.5468	fathoms
kilometers (km)	0.6214	statute miles
kilometers (km)	0.5396	nautical miles
square meters (m ²)	10.76	square feet
square kilometers (km ²)	0.3861	square miles
hectares (ha)	2.471	acres
liters (L)	0.2642	gallons
cubic meters (m ³)	35.31	cubic feet
cubic meters (m ³)	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (t)	2205.0	pounds
metric tons (t)	1.102	short tons
kilocalories (kcal)	3.968	British thermal units
Celsius degrees (°C)	1.8 (°C) + 32	Fahrenheit degrees

U.S. Customary to Metric

inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
statute miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft ²)	0.0929	square meters
square miles (mi ²)	2.590	square kilometers
acres	0.4047	hectares
gallons (gal)	3.785	liters
cubic feet (ft ³)	0.02831	cubic meters
acre-feet	1233.0	cubic meters
ounces (oz)	28350.0	milligrams
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
pounds (lb)	0.00045	metric tons
short tons (ton)	0.9072	metric tons
British thermal units (Btu)	0.2520	kilocalories
Fahrenheit degrees (°F)	0.5556 (°F-32)	Celsius degrees

Contents

	Page
Conversion Table	iii
Preface	viii
Chapter 1. Formation and Distribution of Tidal Marshes	1
Uniqueness of Intertidal Communities	1
The Salinity Gradient and Community Boundaries	2
Definition and Distribution of Tidal Salt Marshes	3
Salt Marsh Formation	4
Tidal Effects on Marshes	4
Community Types	4
Chapter 2. Common Characteristics of Salt Marshes	9
Water: Physical and Chemical Factors	9
Soil and Sediment Formation and Marsh Development	9
Soil Composition	10
Soil Structure and Biogenic Effects	10
Salinity Gradients	12
Plant Adaptations	13
Tidal Salt Marsh Animals	13
Chapter 3. The <i>Spartina alterniflora</i> Salt Marsh	15
Description and Geographic Importance	15
<i>Spartina</i> Hybrids	15
Development of the <i>Spartina alterniflora</i> Community	15
Macrophytic Plants and Algae	16
Resident Terrestrial Animals	21
Aquatic Animals	24
Chapter 4. The <i>Juncus roemerianus</i> Community	27
Distribution and Pattern of the <i>Juncus</i> Community	27
The Primary Productivity of <i>Juncus</i>	27
Fauna of the <i>Juncus</i> Community	29
Chapter 5. Side Issues: Salt Pans, <i>Salicornia</i>, and Marsh	
Edge Communities	33
Community Composition in the High Marsh	33
Formation of the Salt Pans or Barrens	33
Higher Plant Communities of the Salt Flats	34
Chapter 6. Brackish-Water Tidal Marshes	37
Plant Communities	37
Productivity of <i>Spartina cynosuroides</i>	37
Chapter 7. Nutrient Cycles and Energy Flows	41
Trophic Structure of <i>Spartina alterniflora</i> Marshes	41
Aerial Primary Production and Grazing	41
Production of Roots and Rhizomes	42
Productivity of Benthic Algae and Phytoplankton	43
Aquatic Macroheterotrophs	44
Marsh–Estuarine Interaction: Outwelling	44
Chapter 8. Modeling the Dynamics of Salt Marshes	47
The Uses of Simulation Models	47
Model Structure and Function	47
Is the Marsh a Carbon Sink or a Source?	48
Chapter 9. Values of Tidal Marshes	51
Tidal Marshes as Wilderness	51
Commercial Uses of Intertidal Marshes	51
Noncommercial Uses of Intertidal Marshes	52

The Present	52
The Future	53
Acknowledgments	54
References	54
Appendix A. Selected List of Vascular Plants in Tidal Salt Marshes of the Southeastern Atlantic Coast	59
Appendix B. A Selected List of Invertebrates (Excluding Insects and Arachnids) in Tidal Salt Marshes of the Southeastern Atlantic Coast	61
Appendix C. A Selected List of Insect and Arachnid Families in Tidal Salt Marshes of the Southeastern Atlantic Coast	63
Appendix D. Selected List of Fishes in Tidal Salt Marshes of the Southeastern Atlantic Coast	65
Appendix E. Selected List of Reptiles in Tidal Salt Marshes of the Southeastern Atlantic Coast	67
Appendix F. Selected List of Birds in Tidal Salt Marshes of the Southeastern Atlantic Coast	68
Appendix G. Selected List of Mammals in Tidal Salt Marshes of the Southeastern Atlantic Coast	70

Figures

1.1. Distribution and shape of protective barrier islands along the southeastern Atlantic coast of the United States	2
1.2. The relation of intertidal community type to salinity	3
1.3. Drainage patterns of typical young and mature lagoonal <i>Spartina alterniflora</i> marshes in the Duplin River drainage, Doboy Sound, Georgia	5
1.4. Cross section of a barrier island and associated intertidal marsh on the southeastern coast of the United States showing major morphological features and vegetation types	5
1.5. Cross section of a levee in a Georgia <i>Spartina alterniflora</i> marsh showing the areas of creek bank (tall), intermediate, and short grass zones	6
1.6. Communities dominated by smooth cordgrass (<i>Spartina alterniflora</i>): (a) tidal creek with tall creek bank vegetation in foreground; (b) view from within the creek bank vegetation with hammock in the background	6
1.7. A stand of black needlerush (<i>Juncus roemerianus</i>)	7
1.8. Vegetation of the high marsh. Very short cordgrass in the foreground grades into areas dominated by glasswort (<i>Salicornia</i>)	7
1.9. A fringing stand of meadow cordgrass (<i>Spartina patens</i>)	8
1.10. A salt pan in the marsh at Sapelo Island, Georgia	8
2.1. Major intertidal marsh areas and tidal amplitudes on the southeastern coast of the United States, by State	10
2.2. Cross-sectional view of the sedimentary development of an intertidal salt marsh	11
2.3. Relation of depth to the composition of salt marsh soils on a gradient from creek bank to land	11
2.4. Graph of the difference in the Eh gradient with depth in a heavy clay, poorly drained site and a sandy site with more drainage between tides	12
2.5. Cross section of the stem of smooth cordgrass (<i>Spartina alterniflora</i>) showing pathways for gas transport	13
3.1. Distribution of the maritime and interior species complexes of <i>Spartina</i> in North America	16
3.2. Aerial view of triangular patches caused by death of <i>Spartina</i> after deposition of dead stems in rafts (wrack)	17
3.3. A dredge-spoil island that is becoming colonized by terrestrial woody plants and <i>Spartina</i> marsh	17
3.4. Aerial view of a tidal <i>Spartina alterniflora</i> marsh showing the distinct zonation between the tall plants on the creek banks and levees and the shorter plants in the mid- to high marsh	18

3.5. Factors that directly or indirectly affect the growth of cordgrass (<i>Spartina alterniflora</i>)	19
3.6. Mud flats are covered with a film of benthic diatoms and other algae	20
3.7. One of the common benthic diatoms in the marsh, <i>Cylindrotheca</i>	20
3.8. The genus <i>Skeletonema</i> , one of the more common forms of pelagic diatoms in the tidal creeks of the southeastern tidal marshes	21
3.9. (a) The filamentous brown alga <i>Ectocarpus</i> , abundant in the tidal marshes of North Carolina during the winter, and (b) the macrophytic green alga <i>Ulva</i> , which is abundant in summer	21
3.10. The salt marsh grasshopper (<i>Orchelimum fidicinium</i>), an important grazer on smooth cordgrass (<i>Spartina alterniflora</i>)	22
3.11. Nest of the marsh wren (<i>Cistothorus palustris</i>) in tall-form smooth cordgrass (<i>Spartina alterniflora</i>)	23
3.12. The marsh rice rat (<i>Oryzomys palustris</i>) is the only year-round resident mammal in the tidal <i>Spartina alterniflora</i> marshes of the east coast of the United States	23
3.13. Abundant snails inhabit the marsh: (a) the algal-feeding mud snail (<i>Ilyanassa obsoleta</i>), and (b) the aufwuchs-feeding periwinkle snail (<i>Littorina irrorata</i>)	24
3.14. The abundant mud fiddler crab (<i>Uca pugnax</i>) feeds on benthic microorganisms within the tidal <i>Spartina alterniflora</i> marsh or on the surface of the extensive mud flats bordering the tidal creeks	25
4.1. Small, isolated stands of <i>Juncus roemerianus</i> often are found on the slight elevations marking the sites of old mussel beds or other depositions	28
5.1. The relation of the salt flat's interstitial salinity and its vegetation	34
5.2. A mud barren or "borrow pit" at Sapelo Island, Georgia	35
5.3. Growth forms of some common saltflat species: glasswort (<i>Salicornia virginica</i>), saltwort (<i>Batis maritima</i>), and sea oxeye (<i>Borrichia frutescens</i>)	35
5.4. The sand fiddler crab (<i>Uca pugilator</i>)	36
5.5. A stand of salt grass (<i>Distichlis spicata</i>)	36
6.1. The dominant plant in the brackish-water intertidal marshes, big cordgrass (<i>Spartina cynosuroides</i>)	38
6.2. Three zones of the estuary of the Altamaha River, Georgia: (a) upper estuary with tidal freshwater vegetation; (b) middle estuary with mixtures of salt- and brackish-water vegetation; and (c) lower estuary with typical salt marsh	38
7.1. Diagrammatic representation of the three zones of a typical intertidal <i>Spartina alterniflora</i> community	42
7.2. Seasonal changes in the standing stock of the roots and rhizomes of <i>Spartina alterniflora</i>	43
7.3. An expanded trophic diagram of a <i>Spartina alterniflora</i> community	45
7.4. The outwelling concept, in which flood tides bring dissolved nutrients onto the salt marsh and the ebbing tides remove particulate organic carbon	46
8.1. The definitions of structure and function found in ecology versus systems science	47
8.2. A 14-component carbon-flow model of a coastal <i>Spartina alterniflora</i> salt marsh	48
8.3. Hypothesis proposed to explain the transport and transformation of carbon in a coastal Georgia <i>Spartina alterniflora</i> salt marsh	49
9.1. The impact of a causeway—changing the tidal exchange patterns can result in the replacement of cordgrass (<i>Spartina</i>) by needlerush (<i>Juncus</i>), glasswort (<i>Salicornia</i>), or salt pan	54
9.2. Filling the marsh for industrial, commercial, or residential development causes the complete destruction of the intertidal system	54

Tables

3.1. Productivity of smooth cordgrass (<i>Spartina alterniflora</i>) in creek bank and high-marsh zones	18
3.2. Effects of nitrogen fertilization experiments on the growth of <i>Spartina alterniflora</i>	19
4.1. Productivity of stands of black needlerush (<i>Juncus roemerianus</i>)	28
4.2. Relative densities of insect orders based on sweep samples in four intertidal community types in North Carolina	30
4.3. Trophic relations of common invertebrates from four intertidal marsh communities in North Carolina	31
6.1. Relationships of plant species to salinity in the intertidal estuary of the Altamaha River, Georgia	39

Preface

This report is part of a series of community profiles produced by the U. S. Fish and Wildlife Service on the ecology of wetland and marine communities. Within this series there have been a number of profiles of tidal marshes on the Atlantic, Pacific, and Gulf coasts. This profile considers those tidal salt marshes of the southeastern Atlantic coast, from northern North Carolina south to northern Florida.

These tidal salt marshes occupy the protected areas behind the coastal barrier islands and within the estuaries, in the tidal zone from neap (low) to spring (high). They graduate to freshwater tidal marshes where there is a significant riverine input. The profile considers all dynamic processes in these tidal communities, emphasizing both commonalities and differences among marshes in different latitudinal zones.

The community profile series synthesizes information about diverse representations of a basic community type into a coherent and practical guide for those working in the community or those concerned with its management. In this report we have tried to follow this guideline and present a condensed but accurate picture of the physical and biological dynamics of this extensive and important community type.

Questions or comments concerning this publication or others in the profile series should be directed to:

Information Transfer Specialist
National Wetlands Research Center
U.S. Fish and Wildlife Service
NASA-Slidell Computer Complex
1010 Gause Boulevard
Slidell, LA 70458

Chapter 1. Formation and Distribution of Tidal Marshes

Uniqueness of Intertidal Communities

Alone among the ecosystems of our earth, coastal communities are subjected to a bidirectional flooding occurring (in most regions) about twice every day. This periodic, predictable inundation is at once the most striking physical attribute of these systems and one of the most important influences on the successional development, species composition, stability, and productivity of these marine and brackish-water ecosystems.

Wherever the coastal physical environment permits the establishment of seedlings, a community develops that is dominated either by mangrove species (mangrove) or by nonarboreal, salt-tolerant plant species (salt marsh). In general, mangrove is found wherever the low winter water temperature does not drop below 20° C and the mean annual range in water temperature is not more than 10° C, although in Florida the black mangrove (*Avicennia germinans*) tolerates a winter temperature of 12.7° C (Chapman 1977). Conversely, the development of salt marsh vegetation is limited in its southward extension (northward in the Southern Hemisphere) because winters are too warm.

On the southeastern coast of the United States the transition between salt marsh and mangrove associations occurs at about 30° N in northern Florida (Odum et al. 1982). From that point north, the most common vegetational association on low-energy coasts and sheltered intertidal areas is the salt marsh, dominated for the most part by cordgrasses (*Spartina* spp.).

Salt marshes sometimes occur fronting the ocean when tides and wave energy are low. Such habitat is common along the Gulf coast, but rare along the southeastern coast of the United States. Here, much of the area suitable for the development of salt marsh is the extensive, shallow, sedimenting area between the Pleistocene barrier islands and the coast. Extensive intertidal *Spartina* marshes form in these areas. To the north (North Carolina) and the south (northern Florida), the barriers become long and narrow. In the center they are wider and shorter (Fig. 1.1).

Because coastal salt marshes develop in such low-lying sedimented depressions, a primary influence on their development and function is the tidal regime. On the southeastern coast of the United States, these basins are subjected to frequent (often twice daily) tidal flooding with water of moderate to high salinity. The high osmotic gradient produced creates a physiological perception of scarcity of water. In effect, these communities are a kind

of salt desert. Perhaps, not surprisingly, they exhibit attributes of both terrestrial and aquatic communities.

On the landward side, many of the species, especially the macrophytic plants, are terrestrial species, siblings of those found in the salt deserts of the continental interior. The deposited sediments, under the influence of the vegetation (and some bioturbating animals), change and begin to develop layered horizons much as a true soil in a terrestrial community. This process is most pronounced in the upper intertidal zone. The rooted macrophytes, once established, create what is perhaps best described as periodically flooded grassland, with an herbivorous fauna of terrestrial insects supporting a typical predator–parasitoid food web. Because it is free of water during part of each day, the intertidal zone is in contact with the atmosphere and is influenced directly by rain. Evapotranspiration is high enough, however, to remove interstitial water from the soil at such a rate that the salinity in this zone is commonly much higher than that of the overlying water. This contributes even more to the desert analogy.

In addition to these terrestrial attributes, there are equally important aquatic ones. Only in a salt marsh can one see a terrestrial organism such as the salt marsh grasshopper (*Orchelimum*) coexisting on the same stem of *Spartina* with a marine snail (*Littorina*). Clearly, the salt marsh water is the active medium of circulation of organic and inorganic nutrients, and it is the medium in which most organisms live, including the terrestrial type plants. Because of the intimate connection of salt marshes with the sea through the daily tides (and often with rivers at the upper end of the estuary), the biogeochemical processes in the marsh more closely resemble those in aquatic than in terrestrial ecosystems.

Flow in terrestrial watersheds is unidirectional, influenced by gravity. Flow onto and off the marsh watershed is bidirectional; the movement of water through the interstitial pore space of the sediment is driven by gravity and the tides, which are, of course, a consequence of the interacting gravitational forces of the earth, the sun, and the moon. Even where there is substantial input of fresh water from a headwater river, the contribution of the ocean to the inward flux of material to the salt marsh is seen in the high salinity, commonly 20 ppt or more and often virtually identical to that of seawater.

The sediments of the subtidal zones are closer to the sediments of lakes than to terrestrial soils. Even in the intertidal zone, with its rudimentary horizontal layering, the characteristic highly reduced anaerobic soil is typical

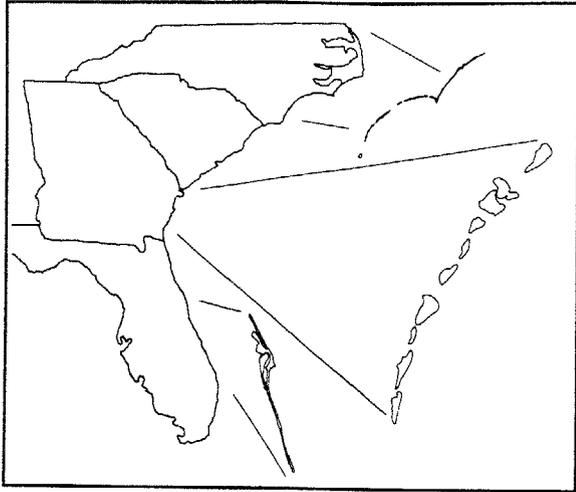


Fig. 1.1. Distribution and shape of protective barrier islands along the southeastern Atlantic coast of the United States.

of (interstitially) stagnant aquatic systems such as freshwater tidal marshes (Odum et al. 1984). The water in the subtidal creeks abounds with aquatic organisms, from plankton to porpoises; many of these organisms are migrants, moving with the tides to forage in the intertidal creeks during high tide, and in some instances moving onto the marsh itself (Vetter 1983).

The successional development of salt marshes is a process of interaction among vegetation, sediment, and water. This development requires protection from the full brunt of a high-energy coast. Thus, the salt marshes of the southeastern United States are almost without exception found in the shallow sedimentary lagoons behind barrier islands, or in protected estuaries. Perhaps the need for protection comes primarily in the seedling stage. Once established and mature, *Spartina*-dominated marshes modify the physical regime to a considerable degree and resist erosion. Frey and Basan (1978) described a *S. alterniflora* marsh that was able to withstand the full force of waves along the exposed shore of Cape Cod once the grass was firmly rooted in the substrate. Apparently, once the marsh has developed in a protected environment, subsequent shifts in barrier sandbars and exposure to the open sea need not result in the immediate destruction of the marsh. It may persist for decades or centuries and become an example of a relict community that was not formed through a change in climate (Wiegert et al. 1981).

Intertidal marshes are characteristically highly productive. Where they have not been physically disturbed (by dredging, causeways, etc.), they remain possibly the least affected of any ecosystem by the actions or results of human agriculture and industry. We will return to this point in Chapter 9.

The Salinity Gradient and Community Boundaries

The subject of this report is the plant and animal community that develops in the tidally influenced salt marsh, where salinity ranges from less than 1 ppt to that of seawater (30 ppt or more). Within this zone Cowardin et al. (1979) distinguished three kinds of tidal salt marsh: oligohaline (0.5–5 ppt), mesohaline (5–18 ppt), and polyhaline (18 ppt to seawater). This gradient, together with the depth and duration of inundation, largely determines the type of community that develops. At salinities less than 0.5 ppt, the communities are considered freshwater tidal marsh (Fig. 1.2). With increasing salinity (0.5–2 ppt; Johnson et al. 1974), the communities come to be dominated by big cordgrass (*S. cynosuroides*). In the southeastern United States, many organisms live within this salinity range. Although not complete, the floral and faunal lists of Appendixes A through G will give the reader an idea of the number of taxa found in tidal salt marshes.

Although the salinity gradient is virtually continuous, the boundaries of the various communities are sharp. This is thought to be an example of competitive interaction within a continuous gradient, but has not been intensively studied in any of the southeastern salt marsh communities. Nevertheless, the indirect evidence is compelling. For example, in laboratory trials, smooth cordgrass (*S. alterniflora*) actually grows better under very low salinities, yet it is found only rarely in such situations. Thus, although it seems to be physiologically stressed when exposed to 25 ppt or more salinity, it apparently does better than any of its competitors and survives as the dominant plant in this environment.

Within the polyhaline region, the dominant marsh species is *S. alterniflora*, but, depending on the inundation depth, frequency, and duration, other associations can be locally dominant, particularly black needlerush (*Juncus roemerianus*) and *Salicornia*–*Distichlis*. Here again the boundaries are usually sharp, although the distribution of the underlying physical causative agent is continuous.

However, the salinity gradient can have direct effects as well as indirect effects mediated through competition. For example, reefs of the Virginia oyster (*Crassostrea virginica*) are common in the southeastern polyhaline marshes. Unlike the situation in the more northern marshes, such as those in the Chesapeake Bay region, southeastern oysters are almost all intertidal. The reason for this is that two predators of the oyster, the oyster drill (*Urosalpinx cinerea*) and the boring sponge (*Cliona*), can live in the subtidal region because of the warmer southern winter temperatures. However, they cannot tolerate low salinities, while subtidal oysters can and do, usually locating in the upper tidal creeks where surface runoff lowers the salinity or in the upper part of those estuaries that have

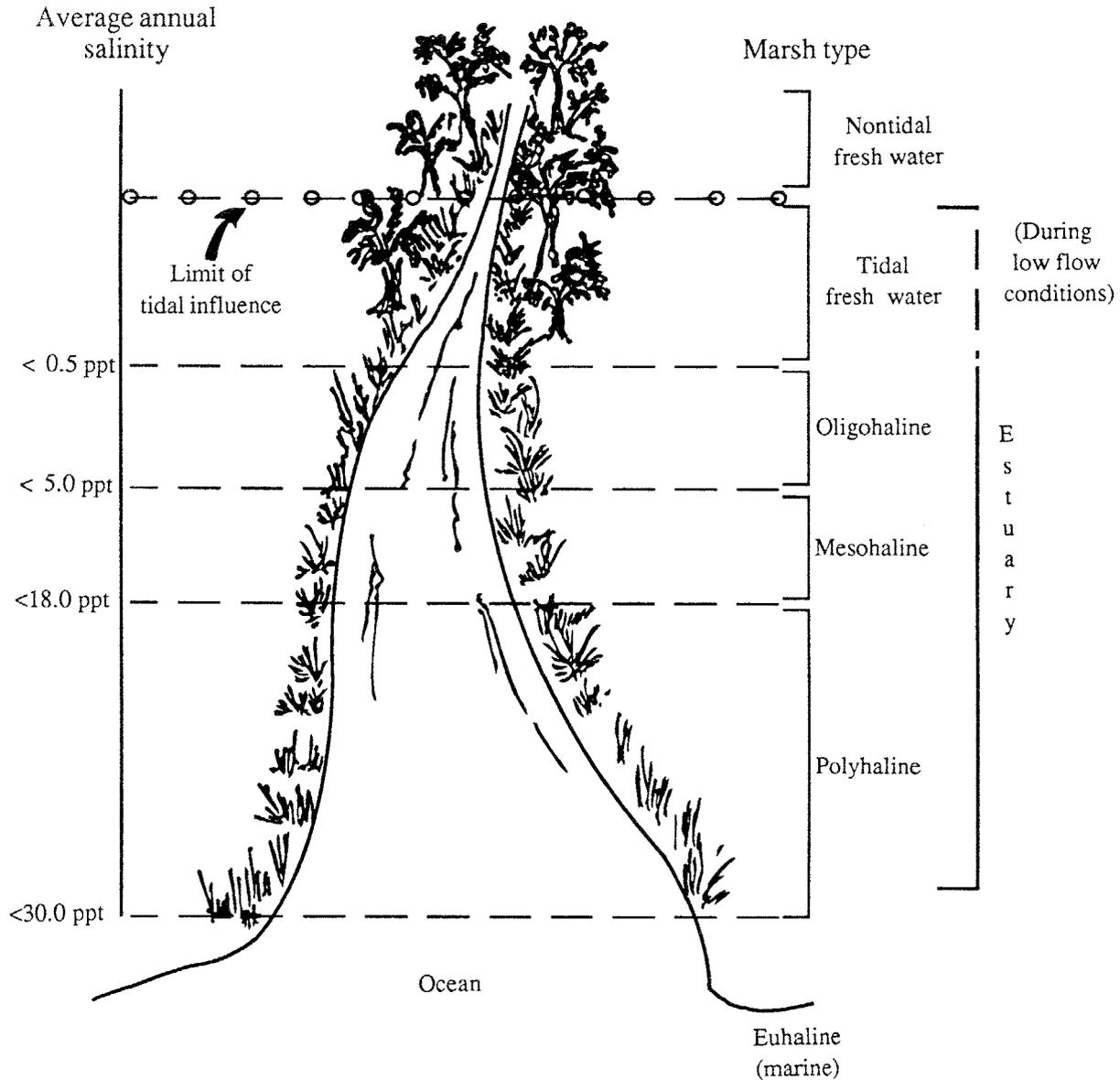


Fig 1.2. The relation of intertidal community type to salinity (redrawn from Odum et al. 1984).

a significant input of fresh water from rivers. Intertidal oysters are also protected by the inability of the predators to withstand the drying between tides.

Definition and Distribution of Tidal Salt Marshes

Tidal salt marshes along the southeastern Atlantic coast of the United States are located from Norfolk, Virginia, south to northern Florida. Tidal conditions are relatively low in the north, increase with decreasing latitude to a peak on the Georgia coast, and then decrease again to the point where salt marsh is replaced by mangrove in Florida. Although the marshes within this range are in some re-

spects quite distinct, as we will discuss, within a given salinity range and community type they all share a similar flora and fauna and together comprise 82% of the extant marshes on the east coast of the United States (Reimold 1977). Georgia, with only about 160 km of coastline, has 33% of the total area of east coast tidal marsh. It is followed by South Carolina with 30%, North Carolina with 11%, and Florida with 8%, although, because Reimold's computations for Florida included mangrove, the percentage for tidal salt marsh alone would be considerably smaller. In the transition zone in northern Florida, because of relatively low tides, the vegetational mosaic can become quite complex compared to the marshes farther north. Where tides are infrequent, areas may be dominated by clumped cordgrass (*S. bakerii*). For a more detailed dis-

cussion of this situation, see Montague and Wiegert (in press).

The salt marshes of the North, although less extensive historically than those of the Southeast, have also been reduced to a much greater extent by human activities such as dredging, filling, and polluting. Indeed, some of the marshes in South Carolina and Georgia are so pristine as to justify using the term wilderness, a topic discussed in Chapter 9.

Salt Marsh Formation

The majority of the southeastern marshes are lagoonal or deltaic types (Wiegert et al. 1981); that is, they have formed in the shallow, sedimentary area between a barrier island and the mainland, or in the protected delta areas of a large river. A typical lagoonal marsh showing two stages of drainage development is mapped in Fig. 1.3. The areas heavily dissected by tidal creek drainage are in an earlier stage of development than are those in which many of the drainage channels have been filled. Several theories have been proposed to account for the formation of the strings of barrier islands found along the coasts of Georgia and South Carolina (Hoyt 1967). The following is a summary of the prevailing view modified from Wiegert (1979) and Wiegert et al. (1981). All during the Pleistocene and up to the present time, sea level has varied widely. The combined action of wind, waves, and tides sometimes caused large dunes to form. With subsequent rises in sea level, these dunes were partly submerged and cut off from the shore. The lagoon that formed between these dunes and the mainland began to fill with fine sediments and, in effect, the dunes became barrier islands. As the accumulation of fine sediment continued, the lagoon became shallower and was invaded by salt-tolerant grasses.

We are now in such an interglacial period, and sea level continues to rise. In the coastal plain of Georgia, a number of earlier barrier island and salt marsh lagoonal episodes can be traced. The barrier islands are now worn down to ridges (Hails and Hoyt 1969). Except for a few small islands or extensions of islands of more recent (Holocene) origin (e.g., Sea and Blackbeard islands in Georgia), all of these, including the present barrier islands, are of Pleistocene age.

The coastal islands of Georgia and South Carolina are several kilometers offshore, with their long axes parallel to the coast. Between the islands and the coast proper, the salt marshes fill the lagoons wherever the depth is suitable (*Spartina* is almost totally submerged at high spring tides and the sediment is exposed during low tide). North along the North Carolina coast the islands become elongated barrier beaches enclosing large sounds (e.g., Pamlico and Albemarle), and the marshes occupy a smaller proportion of the protected water area. South into Florida, elongated barrier beaches also occur, but they hug

the coast, with only a narrow band of water and marsh to landward. Figure 1.4 is a cross section through a typical barrier island along the Georgia coast.

Tidal Effects on Marshes

Because tides are responsible for sedimentation in marshes and because the development of vegetation interacts with the tides, we can expect some topographical differences in *Spartina* marshes developing in areas of low, compared to high, tidal amplitude. The tidal amplitude on the southeastern Atlantic coast reaches a maximum of 2–3 m approximately in the middle of the Georgia coast at Sapelo Island, the site of the University of Georgia Marine Institute, and decreases both north and south of this point.

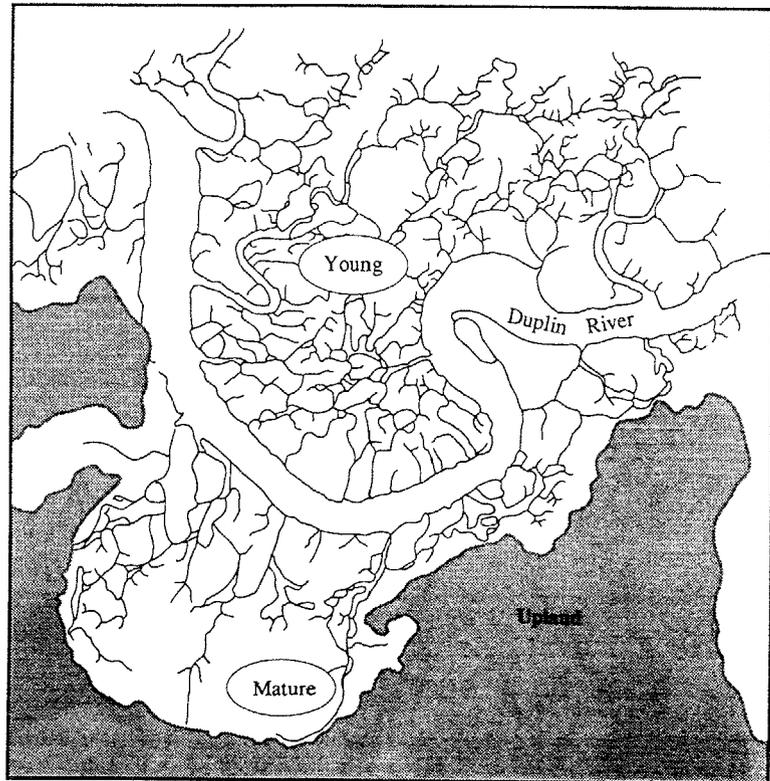
The most notable and important effect of a high tidal amplitude is the formation of pronounced natural levees. As the flood-tide water begins to spread over the marsh, it quickly loses velocity and drops the coarser material at the edge of the creek. Over time this process creates a levee in the same manner as a floodplain river (Fig. 1.5). As the levees grow, they reach a height where they are overtopped only by the higher tides. This has a profound effect on the way in which water moves over the surface of the marsh. Instead of rising out of the creek and flowing directly onto the marsh, the water is channeled by the levee system to central distribution points at the heads of the tidal creeks; from there it flows back and around to the landward sides of the levees.

The reverse process occurs on the ebb tide, but some water is trapped behind the levees. Much of this flows out during low tide through fiddler crab burrows that extend through the levee edge, or by gravitational flow (Wiegert et al. 1983). Enough water remains to create a permanent supply of anaerobic groundwater in the central part of any large expanse of salt marsh (Nestler 1977a, 1977b). In South Carolina, North Carolina, and Florida salt marshes, the smaller tidal amplitude results in little or no levee formation. The greatest effect of these differences in tidal height and drainage patterns would be expected to show up in the microbial processes in the marsh soils, particularly those occurring in the anaerobic zones.

Community Types

Within the salinity regime and geographic region under discussion, the vegetative communities can be cast into five more or less distinct categories plus a sixth, unvegetated, salt pan area. The most common (in area) and most productive is the community dominated by smooth cordgrass (*S. alterniflora*; Fig. 1.6). Figure 1.6a shows a view from the landward side with a tidal creek and tall creek bank vegetation in the foreground. Figure 1.6b is a

Fig. 1.3. Drainage patterns of typical young and mature lagoonal *Spartina alterniflora* marshes in the Duplin River drainage, Doboy Sound, Georgia (redrawn from Wadsworth 1979).



view from within the tall creek bank vegetation. A small wooded island (hammock) is seen in the background. Both views emphasize the great extent of the *Spartina*-dominated marshes in the area between barrier island and mainland.

This is an almost pure monospecific plant community if only macrophytes are considered, and not algae (see Chapter 3). Within the southeastern Atlantic region, this community develops wherever the salinity ranges between about 2 ppt and that of seawater, providing the tidal regime (depth, frequency, and duration of inundation) is suitable. Spinner (1969) found this community type to occupy 73% of all the coastal marsh area. Although there is some uncertainty as to the reliability of his actual areas,

this certainly gives some idea of the quantitative importance of this association.

Spartina alterniflora has very different morphological and productivity characteristics depending on the site within the marsh. This species reaches its greatest aboveground height and biomass and the greatest overall rate of net production on the levees and creek banks. The intermediate zone between the creek bank or levee and the high marsh, where the duration of inundation is several hours, contains vigorous plants and constitutes the largest zone of this community type. At higher elevations in the marsh, where the duration of tidal inundation drops to 1–2 h, the *S. alterniflora* is very short (whether this is a genetic or ecotypic adaptation will be discussed in Chap-

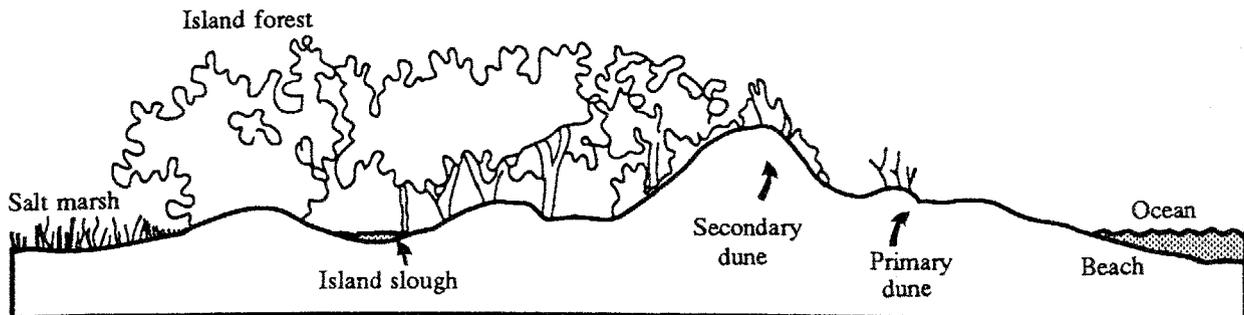


Fig. 1.4. Cross section of a barrier island and associated intertidal marsh on the southeastern coast of the United States showing major morphological features and vegetation types (redrawn from Wiegert 1979).

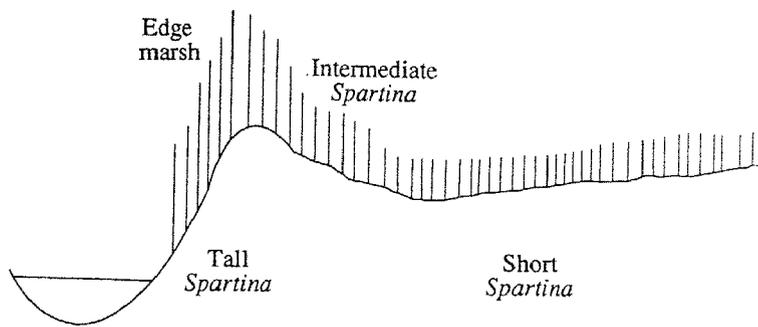


Fig. 1.5. Cross section of a levee in a Georgia *Spartina alterniflora* marsh showing the areas of creek bank (tall), intermediate, and short grass zones (redrawn from Wiegert 1979).



Fig. 1.6. Communities dominated by smooth cordgrass (*Spartina alterniflora*): (a) tidal creek with tall creek bank vegetation in foreground (U.S. Forest Service photograph); (b) view from within the creek bank vegetation with hammock in the background (photograph courtesy of E. Odum).



ter 3). For many reasons, the plants in these areas are highly stressed and production is low.

At still higher elevations, where flooding does not occur on every tide, other types of communities develop.

For example, 19% of the total coastal marsh of Georgia is dominated by black needlerush (*J. roemerianus*; Spinner 1969). The belief is that this plant dominates whenever a lower interstitial salinity prevails in the hydrological

regime, but data in support of that belief are scarce. Certainly the interstitial salinity should be lower in many of the large stands of *Juncus* that are flooded irregularly. Furthermore, *Juncus* is also commonly found in a narrow band shoreward of high-marsh *S. alterniflora* where flooding may occur every day (but only briefly) and soil interstitial salinity is reduced by rainfall runoff from the adjacent land. Even such a subtle change in local relief as that provided by the sedimentation and elevation (about 15 cm) of an old mussel bed can cause *J. roemerianus* to develop (Fig. 1.7).

If the irregular flooding still results in a high interstitial salinity, then instead of *Juncus* the developing vegetation will most likely be some combination of glasswort (*Salicornia* spp.), salt grass (*Distichlis spicata*), or

sea-lavender (*Limonium*; Fig. 1.8). These associations also often develop where an area of cordgrass has been killed by a persistent raft of wrack (dead cordgrass stems from the previous growing season). The community can persist for years in such a case.

The community dominated by meadow cordgrass (*S. patens*) is widespread and important in the northern tidal salt marshes (Nixon 1982), but in the southeastern tidal salt marshes it is relatively uncommon and usually confined to small patches or to a narrow fringing band shoreward of *S. alterniflora* (Fig. 1.9).

The salt pan communities are not really vascular plant communities at all (they have algae but no macrophytes). They are notable for high interstitial salinities and the absence of vascular plants (Fig. 1.10). The method of

Fig. 1.7. A stand of black needlerush (*Juncus roemerianus*).

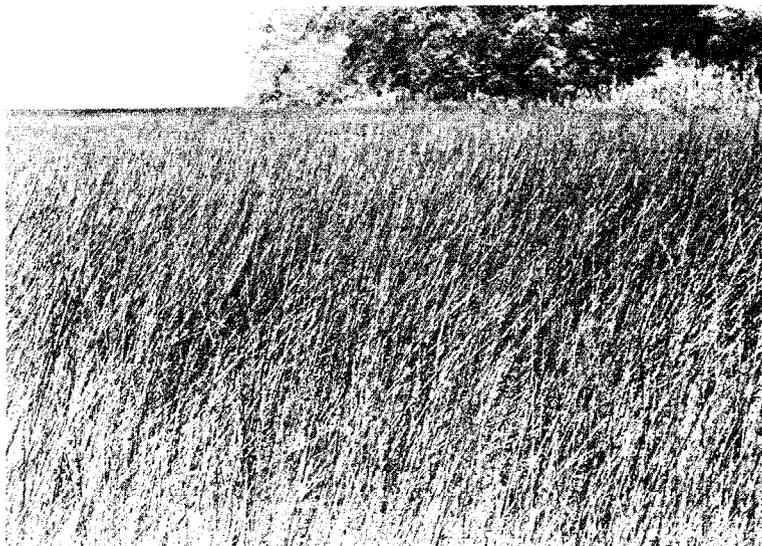


Fig. 1.8. Vegetation of the high marsh. Very short cordgrass in the foreground grades into areas dominated by glasswort (*Salicornia*).





Fig. 1.9. A fringing stand of meadow cordgrass (*Spartina patens*).



Fig. 1.10. A salt pan in the marsh at Sapelo Island, Georgia.

formation is not clear, but once formed they are clearly too saline for colonization by macrophytes. They generally form in slight depressions where the further evaporation of water during low tide accentuates the interstitial salinity.

Finally, farther up the estuary, where the salinity drops to around 2 ppt, the dominant *S. alterniflora* gives way to big cordgrass (*S. cynosuroides*) and, to a lesser degree, salt marsh bulrush (*Scirpus robustus*).

Chapter 2. Common Characteristics of Salt Marshes

Water: Physical and Chemical Factors

The dominant influence on the physical and chemical attributes of the water flooding the tidal salt marsh is, of course, the ocean, particularly when the marsh is physically close to the sea, or the estuary does not have major rivers flowing into its upper end. Thus, the farther up the estuary the marsh is found, the less important is the sea, and the tidal water begins to assume the characteristics of the riverine inputs. Where this occurs depends very much on the tidal amplitude.

On the southeastern coast, the highest tides, about 3 m, are found in the middle of the coast of Georgia, primarily because of the focusing effect of the gently concave shoreline forming what is known as the Georgia Bight (Wiegert et al. 1981). At this magnitude, the tides cause the formation of levees in the tidal salt marsh and may influence the salinity inland for several kilometers. The actual distance upstream reached by water in the salinity range of 0.5–2.0 ppt varies greatly, depending not only on the tidal amplitude, but also on the volume of fresh water discharged and the morphology of the estuary. Figure 2.1 shows the change in area of marsh, tidal amplitude, and water temperature along the north to south gradient from North Carolina to northern Florida.

We are concerned with salinities ranging from about 0.5 ppt to that of the open ocean (30–32 ppt). At the center of the Georgia coast, the approximate midpoint of the southeastern distribution of tidal salt marshes, the climate can be described as almost subtropical, with an annual soil temperature range of 11–26°C and an annual precipitation of 133 cm distributed quite evenly throughout the year (Schubauer and Hopkinson 1984).

The rather large tidal amplitude of the Georgia coast prevents extensive development of deltas, even though the watersheds drained by rivers such as the Altamaha are some of the largest on the East Coast and the water is heavily laden with sediment (Schubauer and Hopkinson 1984). Instead, much of this sediment is deposited between the river mouths and the barrier islands. This material is constantly being reworked, transported, and re-deposited until it is partly stabilized by the development of *Spartina* marshes. When added to the relatively large amount of organic detritus and dissolved humic materials, it causes considerable turbidity in the water. At the center of distribution of the southeastern tidal marshes, light penetration is seldom more than 0.6–0.9 m and is less in summer than in winter. Light penetration improves some-

what to both the north and the south so that heavy bottom covers of macroalgae can develop in the Florida and South Carolina tidal creeks; only the occasional individual of such plants is found in the coastal Georgia marshes (Pomeroy et al. 1981).

Soil and Sediment Formation and Marsh Development

The standing stock and productivity of rooted plants are largely a reflection of processes occurring within or mediated by the substrate. Tidal salt marshes, despite the daily inundations, are not exceptions. Whether the substrate is regarded as a true soil or as sediment is of little consequence, but the organisms and materials being transported and transformed within it determine and control much of the marsh dynamics (Pomeroy and Wiegert 1981a). Differential water velocities result in the size fractionation of sediment during the creation of levees, sandbars, mud flats, and, ultimately, a substrate suitable for colonization and stabilization by the *Spartina* marsh.

The process of marsh development from establishment (youth) through maturation and into old age was discussed in detail by Frey and Basan (1985). The following is a summary of their model (Fig. 2.2), which was based on the development of the more seaward marshes in Georgia, that is, those marshes associated with the barrier islands. Farther inland, where the influence of fresh water and other factors causes different plant associations (see sections on *Spartina cynosuroides* and *Juncus roemerianus*) to become dominant, some modifications in the model are necessary.

In the youthful stage, *S. alterniflora* marshes occupy from 100% (establishment) to more than 50% of the area when invasion of other species occurs. Zonation is not apparent. The high-marsh vegetation, if present at all, is restricted to the fringing terrestrial areas.

The drainage patterns are well developed early on, with pronounced meandering and erosion of tributaries at the headward end. This meandering and erosion become much less important in middle to late youth, as the drainage patterns become stabilized.

Sedimentation is very rapid in early development, and the marshes quickly accrete both vertically and laterally until further lateral growth is inhibited by erosion at the edges of the sounds and estuaries. During middle and late youth the marsh accretion is mainly vertical and slows

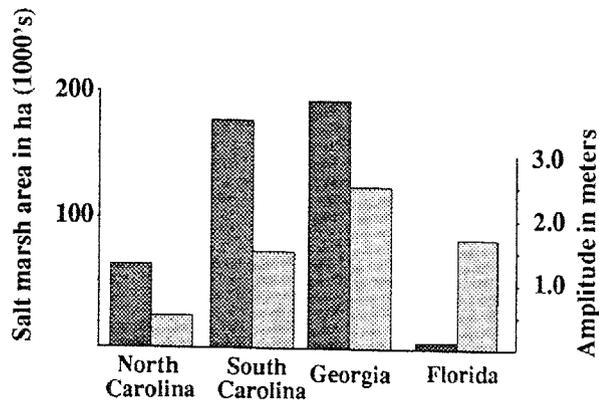


Fig. 2.1. Major intertidal marsh areas and tidal amplitudes on the southeastern coast of the United States, by State.

as the marsh nears equilibrium in the interaction of topography, tidal hydraulics, and sediment supply. This sequence can occur as the end result of the total filling of open lagoons and estuaries, but often is simply a thin layer of Holocene sediment over a base of Pleistocene sands, the remnants of old barrier islands.

At maturity, low and high marsh areas are approximately equal. The low marsh is a virtual monoculture of *S. alterniflora*. The high marsh contains various mixtures and mosaics of *S. alterniflora* and associations of *Salicornia* spp., *Distichlis*, and *Juncus*. Good drainage areas remain, but in the high marsh some of the channels are filling in. There is much erosion and slumping of creek banks, but (as mentioned previously) because of the daily reversal of the tidal flow, little net change in the position of the tidal creeks occurs. Deposition is relatively slow at this stage, with sedimentation restricted mainly to the low marsh. The high marsh is little affected except by catastrophic events such as unusual storms that can erode or deposit large quantities of material in a short time.

In old age, substantially more than 50% of the area is high marsh, and in late old age there may be substantial invasion of the marsh by typically terrestrial plants. They develop concentric zones of the plant associations mentioned in the mature stage, as well as more shoreward zones dominated, in the marshes of coastal Georgia, by such genera as *Sporobolus*, *Borrichia*, and *Batis*. The tall or creek bank form of *Spartina alterniflora* is restricted to the margins of the drainage channels.

Drainage in this stage is largely by surface runoff; most of the channels are filled, and the marsh appears more or less uniform in elevation. Deposition is extremely slow, tidal processes are correspondingly less important, and the marsh is beginning the transition to a terrestrial environment.

Frey and Basan (1985) point out that such a model serves only as a guide to the most probable course of development. In specific instances, marsh development

may be slowed or stopped for long periods. Thus, the transition to old age may be inhibited if there is a pronounced tidal amplitude and energy (pulse stability of Odum 1971) or if the area available for the growth of the marsh is restricted by the confines of a bay or estuary.

Soil Composition

The soils of the Atlantic Coastal Plain marshes, in contrast to the marshes of New England, contain little peat. The reasons for this continue to be debated. Probably, as Frey and Basan (1985) have recently concluded, it is due to a combination of factors, among which are tidal flushing, rapid degradation of plant detritus because of higher annual temperatures, and a very slow rate of coastal submergence.

The soil and sediment in the southeastern marshes contain substantial amounts of organic carbon. Much of this probably originates in place because of the growth of roots and rhizomes (see Chapter 3). The inorganic substrate is composed of a mixture of sand, silt, and clay. The proportions vary greatly with position on the gradient from creek to high marsh, but vary little with depth (Fig. 2.3). In Georgia marshes the soil at the creek bank averages 50% clay and almost 20% sand (the influence of the coarser material deposited in the creek bottom and on the levee), whereas at the high end of the marsh it is almost entirely sand.

Soil Structure and Biogenic Effects

With the emergence of new barrier islands or the destruction of areas of existing marsh, colonization of either *Spartina* or *Juncus* must occur either rapidly (in the sense of area occupied) by growth from seed, or more slowly by vegetative propagation from zones of remaining marsh. Large amounts of viable seed are produced by these plants each year, and seedlings can usually be found colonizing any suitable patch of exposed soil or sediment. But the usual method whereby the marsh expands into new areas, particularly smaller patches, is the growth of rhizomes. Just as it does in terrestrial ecosystems, colonization by plants exerts a profound effect on the structure of the sediment, ultimately transforming it into a soil with distinct zonation.

Although the soil of the tidal salt marsh is flooded each day, the interstitial water is virtually stagnant. Exchange in most parts of the marsh is by diffusion, bioturbation, or slow seepage from the creek bank at low tide. Aerobic microbial processes use up free oxygen faster than it can be supplied at depth, resulting in a soil containing relatively high levels of H_2S and organic matter with low pH (Pomeroy and Wiegert 1981a). Oxygen penetration from the soil-water interface is intercepted within the

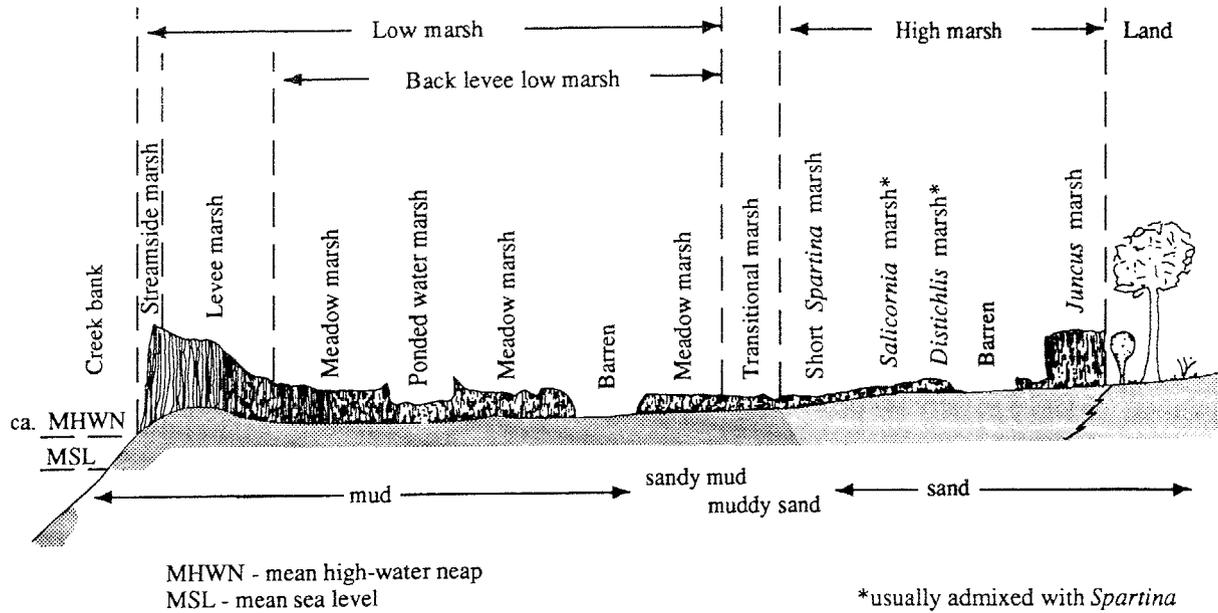


Fig. 2.2. Cross-sectional view of the sedimentary development of an intertidal salt marsh, based on the model of Frey and Basan (1985).

first 1–2 mm of the stagnant zone and removed by the action of sulfide oxidizers, methane oxidizers, etc. Thus, within the soil there is not only a biological oxygen demand created by the end products of anaerobic microbial processes such as fermentation, but also a considerable chemical oxygen demand (Teal and Kanwisher 1961, 1966; Frey and Basan 1985). However, although all the

soil below the first few millimeters is anaerobic, the degree of reduction (and therefore the total oxygen demand) is variable. Reduction (measured in a general way by the oxidation–reduction potential, or Eh) is least where there is some interstitial movement of water influenced by the tides (Fig. 2.4). Therefore, the soil of the creek bank or tall *Spartina* community seldom has the noticeable sulfide

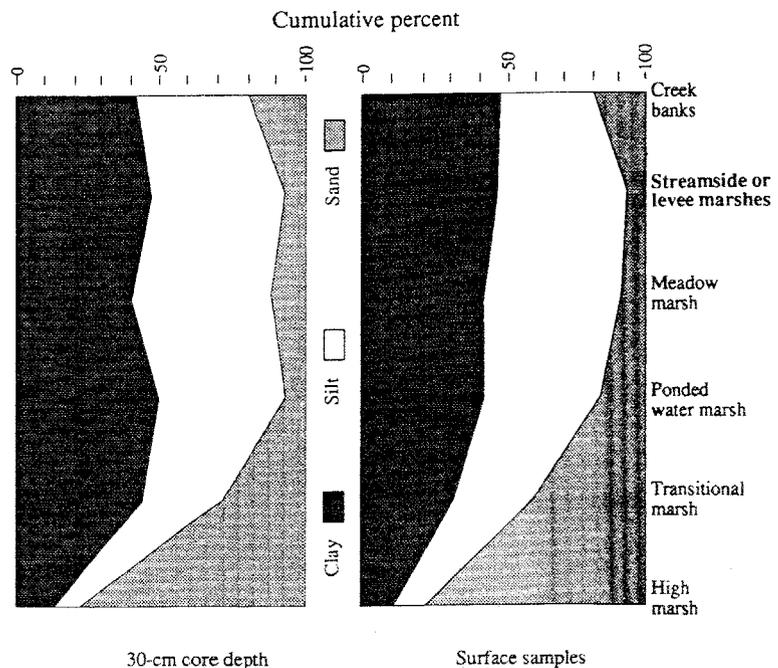


Fig. 2.3. Relation of depth to the composition of salt marsh soils on a gradient from creek bank to land, from Frey and Basan (1985).

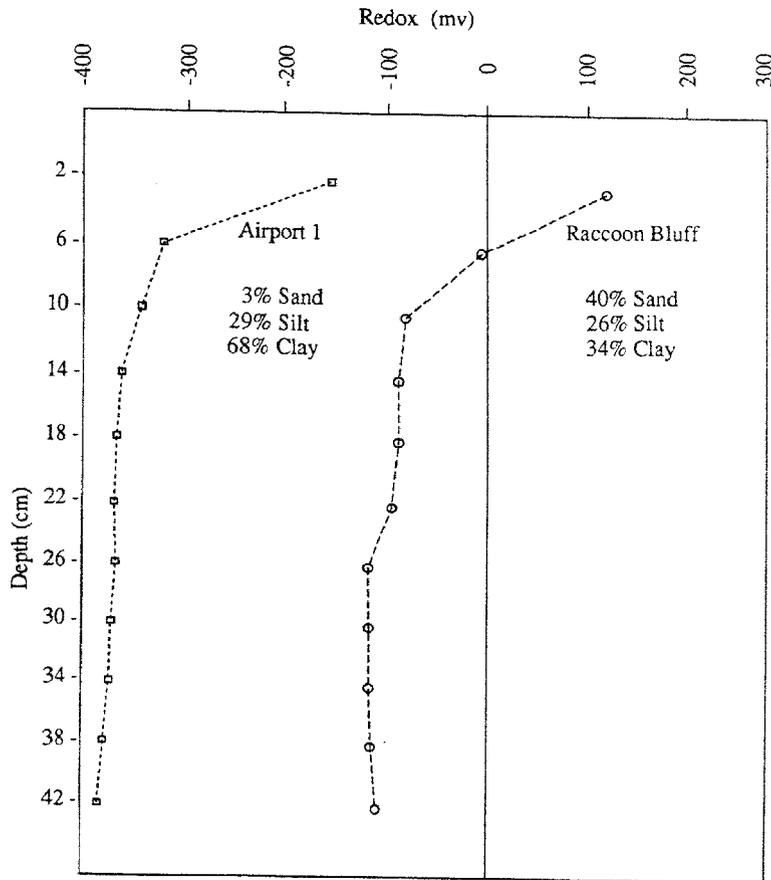


Fig. 2.4. Graph of the difference in the Eh gradient with depth in a heavy clay, poorly drained site (Airport 1), and a sandy site with more drainage between tides (Raccoon Bluff). Data are from Sapelo Island, Georgia (Chalmers et al., unpublished data).

odor of the soil beneath the shorter *Spartina* of the high marsh, even though both soils have a similar gray, reduced appearance. But the stems and rhizomes of *S. alterniflora* are hollow (Fig. 2.5), and around the roots and rhizomes of the marsh plants the soil shows evidence, in the form of a distinct reddish-brown zone, of the effect of oxygen diffused from the stem down and out into the soil (Teal and Kanwisher 1961, 1966; see also Chapter 3).

The physical effect of both marsh plants and animals on the process of sediment accretion and soil formation is probably large, but has been relatively little studied. Frey and Basan (1985) in summarizing the scant literature, made the following eight points: (1) The emergent grass has a damping effect on wind-generated waves, thus changing the transport-sedimentation regime from that of open, unprotected areas. (2) Near the soil-water interface, stems and leaves slow water velocity and thus promote sedimentation. (3) The presence of stems of marsh grass is often thought to influence deposition by creating turbulent flows (Christensen 1976), but Imberger et al. (1983), in contrast, found that in the absence of wind, tidal flow onto and off of the marsh was surprisingly close to true laminar flow. (4) Changes caused by plants in the surrounding water chemistry, particularly in salinity, are suspected of influencing the deposition of clays. (5) Roots and rhizomes help ensure the stability of the soil and its resistance

to hydraulic erosion. (6) Algal, bacterial, and diatom films help trap fine sediments and stabilize them against resuspension, particularly in summer when these microorganisms are most active. (7) Colonial animals influence deposition and soil structure with either their bodies, dwellings, or both. Mussels enhance substrate coherence by means of their byssal threads, and oyster rafts directly influence current velocity and thus deposition. Although they are not considered by Frey and Basan in this model, burrowing animals such as fiddler crabs also influence soil structure directly by bioturbation. (8) Macroinvertebrates trap enormous quantities of suspended detritus, ultimately depositing it as feces or pseudofeces.

Salinity Gradients

Besides the interaction between the sea and the fresh-water rivers in determining the salinity regime of the salt marshes, many other physical and biogenic factors of the marsh proper contribute to salinity gradients within both the tidal water flooding the ecosystem and the interstitial water of the soil.

An obvious factor in establishing an interstitial salinity gradient is water movement through the sediment under the influence of the hydraulic head created by the

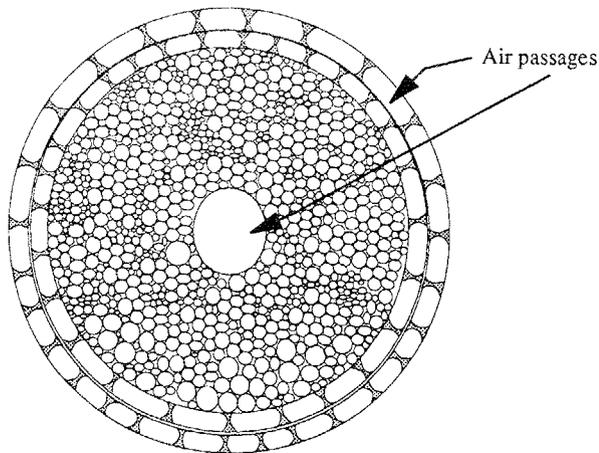


Fig. 2.5. Cross section of the stem of smooth cordgrass (*Spartina alterniflora*) showing pathways for gas transport.

receding water at low tide. Usually, the rate of water movement through the soil and out into the tidal creeks is related to the horizontal distance to the nearest creek bank and, in the case of levees, the vertical distance above the low water level. Usually, we find a gradient in the rate of interstitial water flow or exchange in the soil of the salt marsh from relatively rapid within the levees or near the creek bank to virtually stagnant farther away (Reideburg 1975; Nestler 1977a; Mendelssohn and Seneca 1980; Pomeroy and Imberger 1981). The steepness of this gradient is determined by a number of additional factors such as the height of the preceding tide, the period of tidal inundation, the degree of influence by groundwater movement from the land, and the character of the soil itself, as well as the underlying bedrock (Frey and Basan 1985). This gradation in the degree of movement of interstitial water then sets the stage for still further changes in interstitial salinity due to variability in the rates of evaporation and transpiration in parts of the marsh where exchange with the overlying tidal water is slow. The factors determining evapotranspiration, in addition to the kinds of plants present, are temperature, air movement, and humidity.

In any particular marsh, salinities in the soils of the creek bank and levees are close to that of the overlying water. The interstitial salinity increases landward because of the decreasing exchange with tidal water and the increasing effect of concentration by evapotranspiration, the point of inflection occurring where dilution and leaching due to freshwater runoff from the land balance the salinity-increasing factors (Frey and Basan 1985).

Within the so-called porous sand barrens (see Chapter 3) of the southeastern marshes, interstitial salinities may exceed 100 ppt (Basan and Frey 1977). But the high salinities in porous sand barrens are exceptions, often barren of any plants except algae and diatoms; the common range of salinity in the interstitial water is not more

than 10–20 ppt above that of seawater. This range, however, is enough to stress some of the dominant plants and thus is a factor in plant distribution.

Plant Adaptations

The plants inhabiting tidal salt marshes (except the most terrestrial forms just making it to the edge of the marsh) clearly have to be adapted to the three major physiological stresses found in their particular environment. The first of these is the frequent flooding by saline or brackish water, resulting in direct exposure of the above-ground parts to the water, alternate wetting and drying, and erosion by the moving water. Second, the composition of the water and the effects of evapotranspiration expose the plant roots and rhizomes to higher salinities (in most instances) than that of the tidal water. Third, the constantly waterlogged soil requires the plants to maintain their roots and rhizomes in an anaerobic environment.

In response to the first of these attributes of the tidal environment, marsh plants have had to develop mechanisms to close their stomatal openings when flooded, develop extensive root and rhizome structure to anchor them to the substrate (at least for those subjected to tidal currents), and be able to survive with leaf surfaces that support a well-developed aufwuchs.

In general, adaptations to the second factor take the form of maintaining an increased level of hypertonicity in the plant fluid and developing physiological mechanisms for excreting unwanted salt. This is done at the cost of increased maintenance energy needs; the consequences in specific cases will be discussed in the following chapters.

Rooted macrophytes growing in habitats where the interstitial water is stagnant or turns over very slowly have evolved either a toleration for an anaerobic environment for the roots and rhizomes or an ability to transport oxygen to the roots. The most common mechanism of the latter instance is the presence of hollow stems or rhizomes, or both coupled with some sort of diffusion pump.

Appendix A lists many of the plant species found in and around the tidal salt marshes.

Tidal Salt Marsh Animals

The animal communities of the tidal salt marshes comprise both terrestrial forms (i.e., those intolerant of submersion) and aquatic forms that may spend their entire time submerged or be periodically flooded by the tides. Within each of these categories are residents and migrants, making up specific communities that all share some common characteristics.

The resident terrestrial animals are primarily the arthropod consumers of the dominant macrophytes and some of their predators (Appendix C). During high tides,

most of these seek refuge in the highest parts of the plant. Some live in the hollow stems of the plants, however, and remain protected during the high water. This resident terrestrial component also includes the predaceous spiders and parasitoids that feed on the plant's primary consumers (Appendix C), as well as some resident birds (Appendix F) and a few omnivorous small mammals (Appendix G).

Migrant or nonresidential terrestrial animal forms are mostly the birds that fly into the marsh to forage at low tide, particularly several species of heron, egret, and ibis. The bald eagle (*Haliaeetus leucocephalus*) is occasionally seen foraging over the marshes and tidal creeks, but the graceful osprey (*Pandion haliaetus*) is more common, often nesting in the tops of the power-line poles in the marsh (Appendix F).

Aquatic animals are by far the most abundant species making up the tidal salt marsh fauna. Resident species

range in size from the microfauna and meiofauna in the interstitial water to the occasional predaceous alligator (Appendix E) or herbivorous manatee. Resident benthic infauna are abundant, particularly polychaete worms. Oysters, mussels, and fiddler crabs are all found in greater or lesser numbers, depending on latitude, salinity, and tidal amplitude (Appendix B).

The migrant aquatic species that move with the tides range in size from zooplankton to large predaceous fish (Appendix D). As with the residents, abundance varies with many factors of the marsh environment, including latitude, season, tidal amplitude, and salinity. Small killifish and grass shrimp are abundant in most marshes. Often during high tide the marsh is host to juvenile white shrimp and blue crabs. During spring tides, larger predaceous fish will move into the marsh seeking fiddler crabs and other prey.

Chapter 3. The *Spartina alterniflora* Salt Marsh

Description and Geographic Importance

Intertidal marshlands around the world are dominated by species belonging to the genus *Spartina* (Fig. 3.1). Smooth cordgrass (*Spartina alterniflora*) is the dominant macrophyte in tidal marshes from northern Florida to Maine (Reimold 1977), but this community reaches its greatest development from North Carolina southward, the region considered in this report. On the coast of Georgia, *S. alterniflora* marshes constitute approximately 79% of the total tidal marsh (Johnson et al. 1974, citing data in Spinner 1969). The remaining area supports glasswort (*Salicornia*) or salt grass (*Distichlis*) communities, each comprising about 0.1%; saltmeadow cordgrass (*Spartina patens*); about 0.2%; or black needlerush (*Juncus roemerianus*), 20.6%.

Within this range, smooth cordgrass exhibits considerable heterogeneity in height and productivity. The highest rates of production are found associated with the greatest tidal amplitude, that is, in the central Georgia coast, with the net production decreasing northward (Reimold 1977). The data on primary production of *S. alterniflora* in Florida are insufficient to say whether net production decreases southward from the Georgia node as well. There are indications that some of the latitudinal variation in productivity and other growth characteristics is genetic, as collections from various locations on the East Coast of the United States do show some differences when cultivated under the same conditions (Professor C. H. Chung, University of Nanjing, People's Republic of China, personal communication).

The major difference in growth form and productivity within populations of *S. alterniflora* is seen when the grass on the creek banks and levees is compared with that growing in the high marsh. Although this difference could have some genetic basis, it is mainly a function of the environmental conditions under which the plants are growing.

Spartina Hybrids

Smooth cordgrass is native to North America; indeed, the genus is thought to have originated in North America long before the advent of Europeans and their ships. Only one species, *Spartina maritima*, was found outside North America; it was thought to have migrated

via Iceland when the climate was warmer than at present (Chapman 1977). But in about 1860–70, *S. alterniflora* was introduced to several locations in Britain and Europe where the native species is *S. maritima*. A crossing of the two parent species sometime during this decade produced a male-sterile primary hybrid at Southampton Water in Britain. The sterile hybrid, named *S. townsendii*, expanded slowly by means of vegetative propagation at the expense of the parent populations. By doubling the chromosomes the primary hybrid produced a fertile amphidiploid, which was named *S. anglica* (Beefink 1977). One or the other of these hybrids has been introduced into many parts of the world, most notably into China (Chung 1982, 1983, 1985). In many areas, the plant is introduced only to stabilize tidal mud flats or dredge-spoil islands. The Chinese also use it for pasture, cooking fuel, and other purposes (Chung 1982 and personal communication).

Development of the *Spartina alterniflora* Community

Smooth cordgrass may colonize a bare substrate resulting from the natural deposition of new silt and sand, a bare patch occurring as a result of the death of the previous stand of grass, or a substrate resulting from dredging operations. In each case the process consists of substantially the same kinds of processes, either seed germination and establishment, or the gradual expansion of a nearby established stand.

Ranwell (1972) has reported the death of *Spartina* from litter deposited on the surface; we have observed the same phenomenon occurring in the marshes at Sapelo Island, Georgia (Fig. 3.2). These patches can often be quite large, reaching areas of hundreds of square meters, although they are usually much smaller. Sometimes these patches will revegetate with developing seedlings the following year, but in other cases they remain bare until regrowth from the edges fills them in. Little is known about the factors that decide which of these two scenarios will take place. Such patches can, in fact, remain bare for extended periods, forming salt pans (Ranwell 1972). Generally, these salt pans are very poorly drained and maintain salinities much higher than can be tolerated by cordgrass. Once formed, salt pans remain unvegetated unless some physical perturbation improves the drainage and reduces the interstitial salinity.

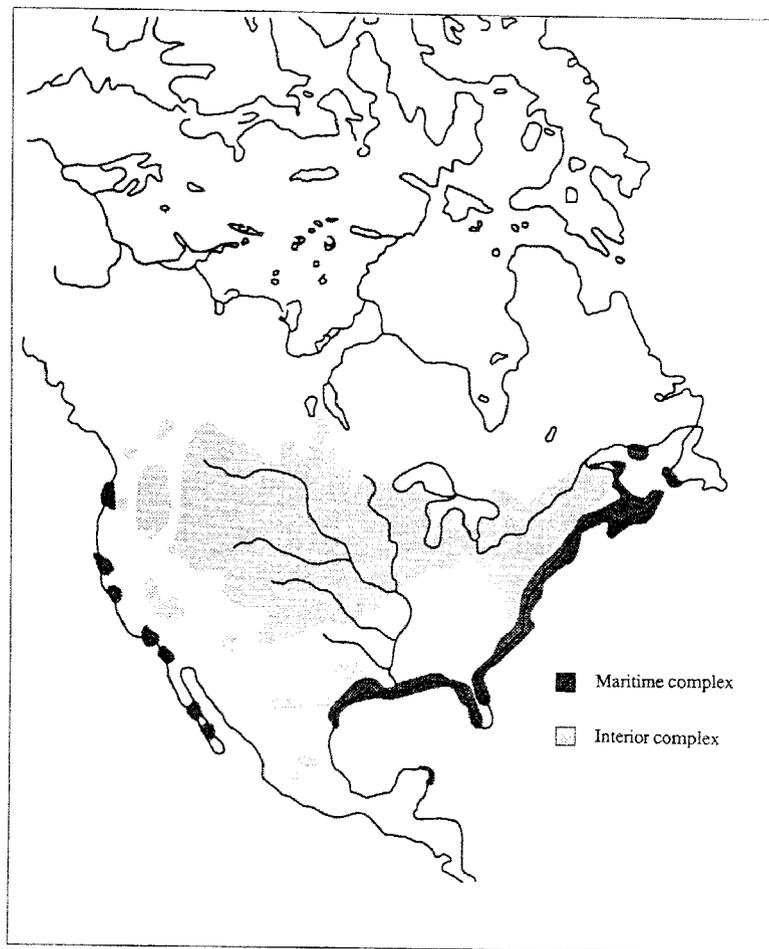


Fig. 3.1. Distribution of the maritime and interior species complexes of *Spartina* in North America (from Chapman 1977).

Dredge-spoil islands are often created during the process of dredging and maintaining navigational channels. In the United States, there has been much interest by the U.S. Army Corps of Engineers in developing the techniques for either transplanting or promoting natural development of *S. alterniflora* on these islands to stabilize them against erosion and the redeposition of material into the channel. Once established, such stands quickly begin to trap additional sediments and grow in height and extent, sometimes quite rapidly (Fig. 3.3). In China, such marshes are eventually diked and reclaimed as agricultural land. In less than 10 years from the time the transplants were put out, one such site accumulated more than 80 cm of sediment and was diked in the ninth year (Chung 1982). The natural reseeding and regrowth of marsh are slower, but quite variable depending on characteristics such as size, location, tidal regime, and amount of sediment carried by the water.

Macrophytic Plants and Algae

Spartina alterniflora is the only rooted macrophyte of importance in this community. It occurs in vast

stands that give the appearance, at least at a distance, of great uniformity. Despite the monotypic nature of the stand, however, closer observation reveals considerable heterogeneity, not only at the scale of the individual culms, which is expected, but also in terms of height, biomass (both aboveground and belowground), and productivity. On the banks of the tidal creeks and on levees built up by tidal deposition, the shoots may be up to 3 m in height, and the productivity is very high compared to the plants in the high marsh (away from the creeks), where the height of the stems is less than 0.5 m and productivity may be only one-half to one-third that of the taller stands (Table 3.1; Fig. 3.4). The tall plants also have a lower stem density (30–50 stems/m²) and a lower shoot-to-root-plus-rhizome biomass ratio (1.4:1) than the short plants growing in the high marsh. Here one finds up to 300 stems/m² and a biomass ratio ranging from 10:1 to almost 50:1 (Gallagher 1974; Gallagher et al. 1980; Chalmers 1982).

The plant dynamics of the smooth cordgrass community consist almost entirely of intraspecific interactions and environmental variables whose interplay regulates plant growth and primary productivity to produce the observed differences between stands. The following summary is based on an experimental demonstration of the

Fig. 3.2. Aerial view of triangular patches caused by death of *Spartina* after deposition of dead stems in rafts (wrack). The wrack has subsequently been removed by the tide, leaving the light-colored bare areas bordering the creek in the lower right-center of the photo.



effect of interstitial water movement (Wiegert et al. 1983) and a review by Chalmers (1982).

Some earlier workers had suggested that stand differences were largely genetic, a view that had some support in the taxonomic distinction between different forms of *S. alterniflora*. But more recent studies using electrophoretic techniques and reciprocal transplants have been unable to substantiate these views. (However, J. L. Gallagher, University of Delaware, Lewes, personal communication, has some ongoing transplant studies that do support the idea of a genetic component in plants from a Delaware marsh.) Seed germination and seedling growth studies have shown little evidence of genetic differences. There are, however, some genetic differences in latitudinal forms (Chung, personal communication; Anderson and Treshow 1980).

If the difference is not wholly or even largely genetically based, which seems reasonable on the face of current evidence, then environmental factors must be responsible. To date, only two kinds of direct field manipulation experiments have produced any shift of short plants toward characteristics of plants on the creek banks and levees. These are increased interstitial drainage of an intermediate stand of *S. alterniflora* (Wiegert et al. 1983) and fertilization with nitrogen (a number of the latter studies are summarized in Table 3.2). Increased interstitial movement of water, however, could result in increased movement of nitrogen to the roots and rhizomes of the plants as well as being the proximal cause of most of the other environmental factors that have been implicated as possible causes for the difference between creek bank or levee

Fig. 3.3. A dredge-spoil island that is becoming colonized by terrestrial woody plants (left foreground) and *Spartina* marsh (upper background).



Table 3.1. Productivity of smooth cordgrass, *Spartina alterniflora*, in creek bank and high-marsh zones (tall = creek bank, short = high marsh). From Schubauer and Hopkinson (1984).

Sampling locale	Height form	Net primary production (g dry mass · m ⁻² · yr ⁻¹)			Reference
		Aboveground	Belowground	Total	
Nova Scotia	Not reported	803	1,051	1,854	Livingstone and Patriquin (1981)
Massachusetts	Not reported	420	3,500	3,920	Valiela et al. (1976)
New Jersey	Short	500	2,300	2,800	Smith et al. (1979)
North Carolina	Short	650	460	1,110	Stroud and Cooper (1969)
	Tall	1,300	500	1,800	Stroud (1976)
Georgia	Short	1,350	2,020	3,370	Gallagher and Plumley (1979)
	Tall	3,700	2,110	5,810	Gallagher et al. (1980)
	Medium	2,840	4,780	7,620	Schubauer and Hopkinson (1984)

and high-marsh plants. Figure 3.5 summarizes the multiplicity of edaphic factors that could interact to determine the height, biomass, and productivity of *S. alterniflora*. Chalmers (1982:239–240) discusses the complexity of these interactions:

Field and laboratory studies have shown that salinity is one factor which can influence *S. alterniflora* growth, but there are marshes in which both tall and short forms occur in the absence of salinity gradients.

Fertilization experiments have demonstrated that growth of tall *S. alterniflora* is not nitrogen limited but that productivity of the short form can be increased by nitrogen additions. . . . Other studies have shown that the apparent nitrogen limitation in the short form is not due to a shortage of available nitrogen, but to an alteration in nitrogen uptake kinetics. Salinity stress-caused diversion of nitrogen to the production of osmotica can also reduce the nitrogen available for growth.

High sulfide concentrations and consequent low oxidation-reduction potentials in the rhizosphere can

affect nitrogen uptake kinetics. These factors and anoxia can also cause structural damage or alterations in the roots which could affect nutrient uptake. Soil drainage, iron concentrations, oxygen diffusion from *S. alterniflora* roots, and plant productivity itself can all affect sulfide concentrations and redox. In order to understand the controls of *S. alterniflora* productivity, it is essential that the effect of these factors on nitrogen uptake and utilization be demonstrated in the field. Laboratory or hydroponic culture studies are also necessary to elucidate the mechanisms by which nitrogen metabolism is altered. Finally, similar studies in marshes in various geographical areas will be needed to determine if the same factors control the within-marsh heterogeneity in height and productivity of *S. alterniflora*.

Unlike the monotypic stands of smooth cordgrass, the epibenthic and epiphytic algae of this community are very diverse, but rather poorly known ecologically. In the Georgia salt marshes, the algal flora comprises several hundred species of diatoms that together form 75 to 93%



Fig. 3.4. Aerial view of a tidal *Spartina alterniflora* marsh showing the distinct zonation between the tall plants on the creek banks and levees and the shorter plants in the mid- to high marsh.

Table 3.2. Effects of nitrogen fertilization experiments on the growth of *Spartina alterniflora* (from Chalmers 1982).

Site	Fertilizer, rate of application	Control (g/m ²)	Fertilized (g/m ²)	Reference
Massachusetts	urea, 290 g N · m ⁻² · yr ⁻¹	424	834	Valiela et al. (1976)
Delaware	ammonium nitrate, 240 g N · m ⁻² · yr ⁻¹	772 ^a	2,104 ^a	Sullivan and Daiber (1974)
North Carolina	ammonium sulfate, 67.2 g N · m ⁻² · yr ⁻¹	450	1,800	Broome et al. (1975)
Georgia	ammonium nitrate, 20 g N · m ⁻² · yr ⁻¹	471	803	Gallagher (1975)
Georgia	sewage sludge, 100 g N · m ⁻² · yr ⁻¹	396	650	Chalmers et al. (1976)
Louisiana	ammonium sulfate, 20 g N · m ⁻² · yr ⁻¹	1,666	1,916	Patrick and Delaune (1976)

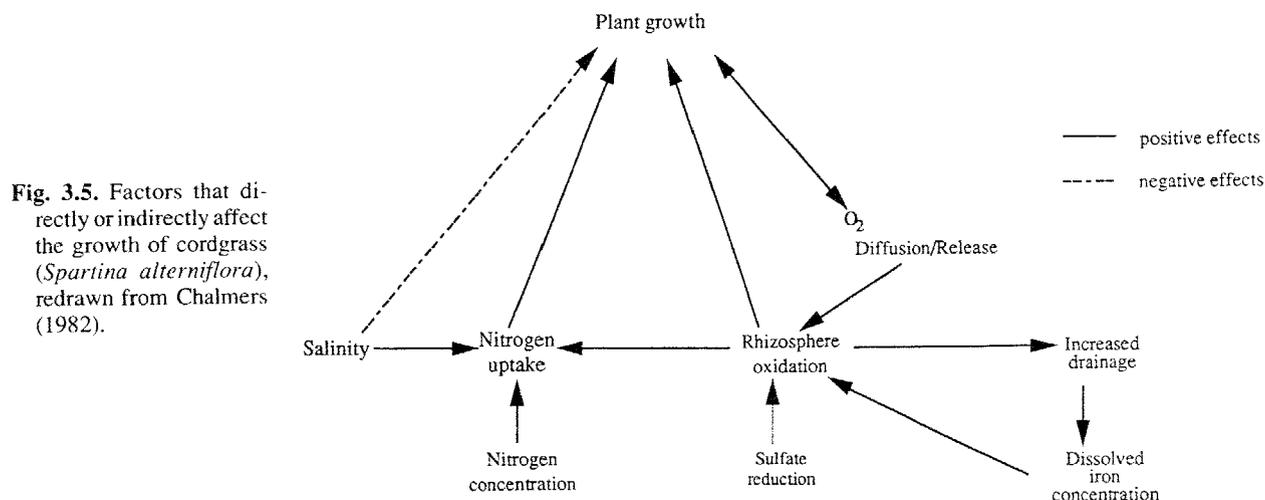
^ag fresh wt/m²; all others are g dry wt/m².

of the benthic algal biomass (Williams 1962). Most of the remainder of these benthic primary producers belong to three species of filamentous cyanobacteria (*Anabaena oscillarioides*, *Microcoleus lyngbyaceus*, *Schizothrix calcicola*) and a single species of *Euglena* (Pomeroy et al. 1981). Some of these are also found on the substrate provided by the standing dead remains of the cordgrass. In addition, small macroscopic red algae (*Caloglossa* and *Bostrychia*) are also found during the summer (Chapman 1971). Pomeroy et al. (1981) also stated that some *Ectocarpus confervoides* develop on the stems of streamside cordgrass in the winter months.

Williams (1962) found that the mud near creek banks and levees had the highest population densities of benthic diatoms (Fig. 3.6). The diatom assemblage was dominated by four genera (*Cylindrotheca*, *Gyrosigma*, *Navicula* and *Nitzschia*), which together accounted for 90% of the cells (Fig. 3.7). The density of the epibenthic flora decreases both toward the creek bottom and into the macroflora-dominated marsh. This corresponds in general to the de-

creased light available because of turbidity at high tide in the former instance and shading in the latter. In winter, cell densities in the vegetated portion of the marsh were about 10 times the summer values. Sudden decreases in standing stock were related to erosion by rain (Williams 1962).

In the shallow, turbid southeastern estuaries serving the tidal salt marshes, phytoplankton production was usually described as inconsequential because of poor light penetration (Ragotzkie 1959). Although light is probably the most important limiting factor, the current view is that phytoplankton are a significant source of organic carbon for the food web characteristic of the estuary (Thomas 1966; Pomeroy et al. 1981). Zingmark and Satcher (1984) reported the long-term productivity of the phytoplankton in a South Carolina estuary. They found similar values from year to year and ranked the controls on primary production, in order of importance from greatest to least, as solar insolation, depth of the euphotic zone, temperature, available nutrients, and salinity.



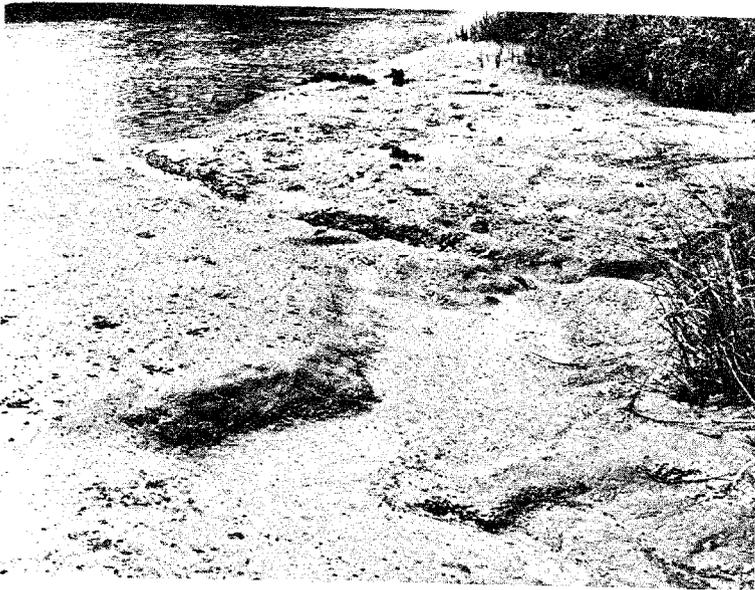


Fig. 3.6. Mud flats are covered with a film of benthic diatoms and other algae.

The species composition of the North and South Carolina estuaries has been described by Hustedt (1955) and Zingmark (1978) and is similar to the composition of the community in the Georgia marshes (Pomeroy et al. 1981). Pelagic diatoms are dominant (e.g., *Skeletonema*, *Rhizosolenia*, *Asterionella*, and *Coscinodiscus*), but benthic forms are always present as well, probably as a result of resuspension from the substrate during ebb and flood tides (Fig. 3.8). Several species of green flagellates and dinoflagellates are also present in the estuaries and tidal creeks

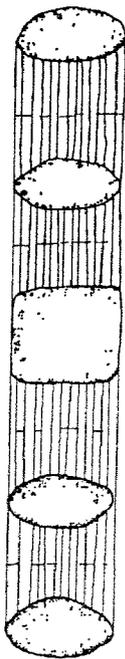


Fig. 3.7. One of the common benthic diatoms in the marsh, *Cylindrotheca*.

of the Georgia marshes; the dinoflagellates bloom periodically (Pomeroy et al. 1981).

At the seaward or estuarine side, the *Spartina alterniflora* community abuts the sharply differentiated tidal mud flat, defined by the absence of rooted macrophytes. In the northern part of the southeastern Atlantic coast (North Carolina), such habitat is much more extensive because of local topography and a much lower mean tidal amplitude. But in this more northern mudflat habitat, macrophytic algae are, during certain times of the year, very abundant (Peterson and Peterson 1979). These authors reported no data on the contribution of these macrophytic algae to total primary production of the tidal mud flats. The macrophytes are usually attached to some sort of hard particle, but in summer, floating mats of filamentous green algae such as *Enteromorpha* are often present on the tidal mud flats of North Carolina. The mats may cover as much as 50% of the total area of the flats.

The macrophytic algae, according to Peterson and Peterson (1979), show a striking seasonal change in species. From November through March, species of a filamentous brown alga (*Ectocarpus*) are common on the intertidal flats where salinity is high. In spring the filamentous green algae become prominent, continuing through the summer, when the leafy macrophytic green alga (*Ulva*) also becomes abundant (Fig. 3.9). There are few of these algae in the fall.

In the Georgia marshes the bare intertidal zone is reduced in most localities to relatively small areas of creek bank and small zones of active deposition that are soon colonized by *S. alterniflora*. Macroscopic algae are not well represented. Small patches of blue-green algae are seen occasionally on the mud, but the large mats of filamentous green algae described for North Carolina do not develop in Georgia marshes. Examples of the genera *Rhizoclonium*, *Ulva*, and *Enteromorpha* are found occa-

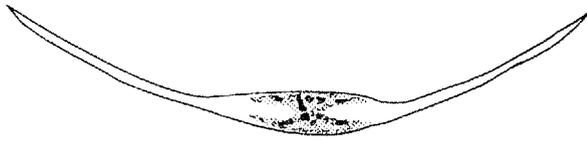


Fig. 3.8. The genus *Skeletonema*, one of the more common forms of pelagic diatoms in the tidal creeks of the southeastern tidal marshes.

sionally, especially in winter when the water is clearer and cooler. This scarcity of macroscopic algae is probably due to the normally very turbid water (low light), the accompanying rapid sedimentation, and the desiccation and high temperatures experienced at low tide on the mud flats. The motility of the diatoms, filamentous cyanobacteria, and euglenoids permits them to maintain themselves in the euphotic zone (Pomeroy et al. 1981).

Resident Terrestrial Animals

Because the dominant vegetation of the community is a grass that is emergent during all but the highest of spring tides, the associated fauna can be classified as terrestrial in the sense that it does not tolerate prolonged submersion. The diversity of this assemblage, largely arthropod, is low in terms of absolute numbers of species (relative to the area of habitat involved). But the diversity of species is high relative to the number of species of higher plants found in the community. Since the only primary producer of consequence in this community is *S. alterniflora*, it supports a diverse food web. However, the quantity of plant material that finds its way into this web is low (Teal 1962; Wiegert and Evans 1967) relative to the overall net primary production. This perhaps accounts for the rather few recent studies of this group, following a relatively active period of study during the 1950's and 1960's (Pfeiffer and Wiegert 1981).

Herbivorous insects of 109 species have been identified from the *S. alterniflora* marshes of North Carolina, South Carolina, and Georgia (Appendix C). They represent 9 orders and 43 families. However, relatively few of these species are abundant. In the Georgia marshes, for example, the two dominant herbivores are the salt marsh grasshopper, *Orchelimum fidicinium*, and the tiny planthopper *Prokelisia* (Fig. 3.10). Despite the small (less than 10%) fraction of the net primary production of smooth cordgrass that is grazed, the total net primary production of the plants is so high (relative to other grasslands) that the secondary production by the primary consumers of green plant material is one of the largest of any terrestrial system studied (Wiegert and Evans 1967). This is discussed further in Chapters 7 and 8. Here we want to point out some of the other potential consequences of herbivory that are not

directly related to quantity of energy or material flow.

Because they remove part of the mechanism of production as well as the product of photosynthesis, grazers can have a direct effect on the plant that is quite different from the less direct effect of primary consumers feeding on detritus (Wiegert and Owen 1971). In addition, grazers, particularly the sap-sucking species, can directly transmit pathogens to plants (Carter 1973). Salivary secretions can damage plant tissues and cause plugging of xylem and phloem (Miles 1968; Dixon 1971; Carter 1973).

Herbivory need not be regarded as solely detrimental to the plants; several authors have discussed the potential coevolution of relationships between the plant and herbivore in which the plant regulates the herbivore and vice versa (Mattson and Addy 1975; Owen and Wiegert 1976, 1987; Pfeiffer and Wiegert 1981).

The marsh wren (*Cistothorus palustris*), formerly the long-billed marsh wren, is one of the most common insectivorous birds in this community (Fig. 3.11). In the same habitat one also finds the seaside sparrow (*Ammodramus maritima*), but the two species seem to search and feed from distinctly different levels in the marsh. Kale (1965) found that the seaside sparrow foraged primarily on the marsh surface, whereas the wren searched



Fig. 3.9. (a) The filamentous brown alga *Ectocarpus*, abundant in the tidal marshes of North Carolina during the winter, and (b) the macrophytic green alga *Ulva*, which is abundant in summer.

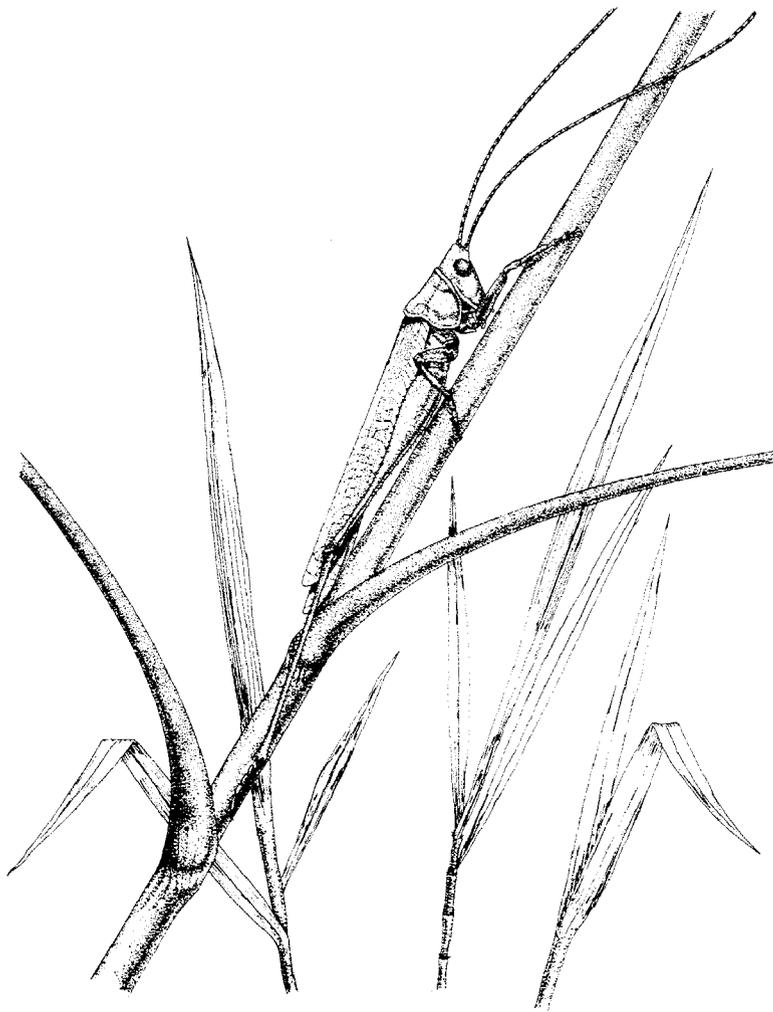


Fig. 3.10. The salt marsh grasshopper (*Orchelimum fidicinium*), an important grazer on smooth cordgrass (*Spartina alterniflora*).

the canopy. Kale wrote, "I have never collected a marsh wren with muddy feet, or a seaside sparrow with clean feet." He found that the marsh wren fed primarily on insects, but took some small mollusks, spiders, and other miscellaneous arthropods. Thus, this species has an effect on both the herbivores and the first-order predators in the terrestrial food web of the marsh. The seaside sparrow's food habits have not been studied so intensively in the southeastern marshes. Sprunt (in Bent 1968) listed foods that imply a somewhat larger intake of benthic marine organisms, along with insects. This would seem consistent with its benthic foraging preferences, but in a *Spartina* marsh in New York, 99.5% of the food items brought to nestlings were insects (Post 1974).

A number of other birds frequent the marsh at times and feed on herbivorous and predaceous arthropods. Swallows, overwintering sparrows, red-winged blackbirds (*Agelaius phoeniceus*), and gulls are a few examples (Pfeiffer and Wiegert 1981).

The only rodent that is a permanent resident of the *S. alterniflora* community is the marsh rice rat (*Oryzomys*

palustris); it generally is found in the tall grass where it uses abandoned nests of the marsh wren or builds its own (Sharp 1967). It feeds on Lepidoptera larvae and small crabs, but is ordinarily too scarce and localized in distribution to have a significant effect on the primary consumers of the marsh (Fig. 3.12). Other mammalian predators living in or using the marsh at low tide include raccoons (*Procyon lotor*) and mink (*Mustela vison*). There are no studies of the effect of these animals on the resident and migrant aquatic animals of the marsh, but they are unlikely to have any appreciable direct effect on terrestrial forms such as insects and arachnids.

A number of predaceous insects are present in this marsh community. Mirid bugs prey on the eggs of homopterans such as *Prokelisia*; they are present in both North Carolina marshes (Davis 1978) and Georgia marshes (Kale 1964). There are several species of parasitic flies and wasps as well as a number of generalist predators (Pfeiffer and Wiegert 1981) in these marshes.

Spiders and mites are the most numerous predators in the community, the former preying mostly on the

Fig. 3.11. Nest of the marsh wren (*Cistothorus palustris*) in tall-form smooth cordgrass (*Spartina alterniflora*).



herbivorous insects and the latter feeding on the microarthropods found on the dead cordgrass. The spider assemblages have been studied in North Carolina marshes (Barnes 1953) and in Georgia marshes (Pfeiffer and Wiegert 1981). The species composition of the two areas was very similar.

The marsh surface is inhabited mainly by the cursorial wolf and fishing spiders. There is little litter accumulation on the surface of the tidal salt marsh (compared with the typical grassland) and this may account for the lower density of this group in the salt marsh community. The majority of the predaceous spiders live in the above-ground vegetation, where the furled dead leaves, leaf sheaths, and hollow stems of *Spartina* provide refuge both from predators and from water during tidal inundation.

In the marshes of Sapelo Island in Georgia, the tall creek bank stands of grass had the highest biomass and

density of spiders; more than 80% of which were species in three dominant genera, *Grammonota*, *Paisochelifer*, and *Clubiona* (Pfeiffer and Wiegert 1981). The two major mechanisms regulating spider density in this community seem to be juvenile mortality, particularly due to cannibalism and starvation during periods of prey scarcity, especially those induced by the extreme fluctuations in planthopper densities from one generation to the next.

The reactions and adaptations to tidal inundation of these primarily terrestrially adapted consumer species vary greatly. Very mobile species that are intolerant of submersion must, of course, leave the marsh during high tide. Many of the insects and arachnids can tolerate lengthy periods of submersion (Arndt 1915). Indeed, the salt marsh grasshopper will often resort to hiding underwater when pursued, although it presumably cannot tolerate continued long-term immersion. The abundant small

Fig. 3.12. The marsh rice rat (*Oryzomys palustris*) is the only year-round resident mammal in the tidal *Spartina alterniflora* marshes of the east coast of the United States.



planthoppers in the marsh move up the vegetation during high tide. During extreme spring tides they may often be pushed off the vegetation by the rising water and then float on the surface in rafts of thousands until they again encounter leaves with the recession of the water. During this time they are preyed upon by a variety of aquatic predators, particularly the killifish (*Fundulus*).

Aquatic Animals

The aquatic macroconsumers supported in the *Spartina alterniflora* community range from protozoa and meiofauna through small copepods and polychaete worms to snails and large fish. The classification we have adopted is that "aquatic" denotes those animals that are either continually submerged or which carry out their normal physiological activities when submerged and which have adapted to survive periodic emergence and (some-

times) drying and heating during low tide. The food webs leading to these forms, in contrast to those discussed in the previous section, generally begin either with benthic algae or phytoplankton (grazing) or with the microorganisms colonizing detritus. In a few instances, such as with the marsh crab *Sesarma*, living cordgrass shoots, roots, or rhizomes are the initial food.

More common grazing pathways begin with the aufwuchs on the stems of living and dead *Spartina*, which are used by the periwinkle snail (*Littorina irrorata*), or with the benthic algae, which are grazed on by mud snails (*Ilyanassa obsoleta*) or fiddler crabs (Figs. 3.13 and 3.14). Two abundant species of fiddler crab are the mud fiddler (*Uca pugnax*), found in both the high and low marsh, and the sand fiddler (*U. pugilator*), which occurs in great numbers near the landward edges of the marsh and wherever the marsh meets the seaward beach.

Appendix B summarizes the species found in the

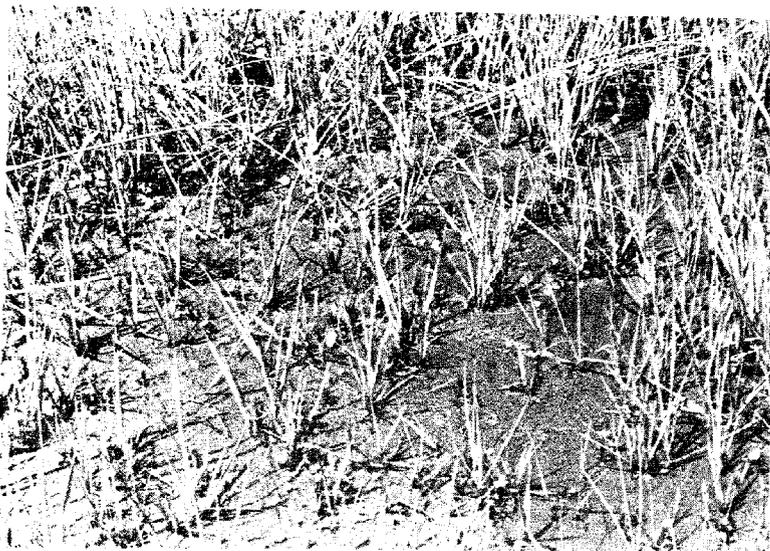
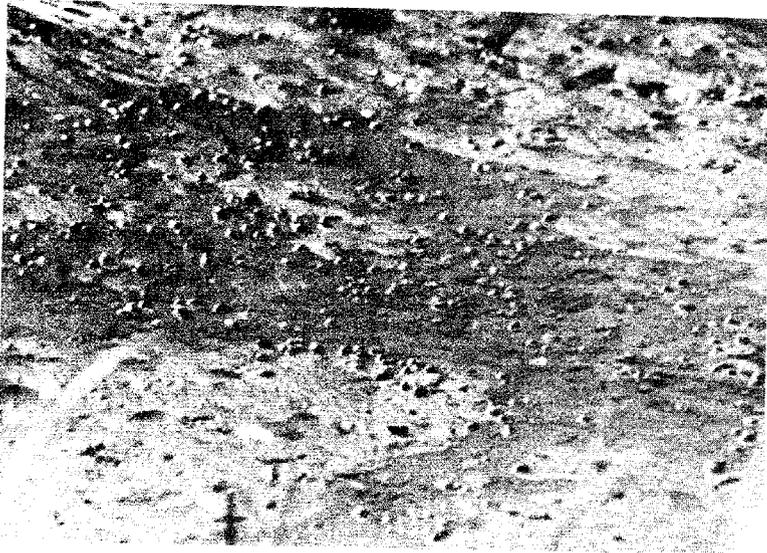


Fig. 3.13. Abundant snails inhabit the marsh: (a) the algal-feeding mud snail (*Ilyanassa obsoleta*), and (b) the aufwuchs-feeding periwinkle snail (*Littorina irrorata*).

Fig. 3.14. The abundant mud fiddler crab (*Uca pugnax*) feeds on benthic microorganisms within the tidal *Spartina alterniflora* marsh or on the surface of the extensive mud flats bordering the tidal creeks.



community. There is little difference in the species list from north to south within the region of tidal marshes under consideration. Note that individuals of a species are often abundant and biomass is large, but overall the diversity of species is relatively low (Montague et al. 1981). Much literature exists on the macroconsumers of the salt marsh. The preceding account is largely a summary of the 1981 review and discussion by Montague et al., with addi-

tional references that either were not cited by them or were published later. Despite the implication in Teal's 1962 summary of salt marsh energy flow that macroconsumers were not important in a quantitative sense, more recent information suggests that such a conclusion was unwarranted. Presently, there seems to be a reemphasis on the study of the effect of macroconsumers on the structure and function of salt marshes (see Chapters 9 and 10).



Chapter 4. The *Juncus roemerianus* Community

Distribution and Pattern of the *Juncus* Community

The *Spartina alterniflora* community is replaced in some places with virtually pure stands of the black needlerush (*Juncus roemerianus*). In the intertidal marshes of the southeastern coast this community type occupies 10% of the total area of marsh (Eleuterius 1976); at Bodie Island, North Carolina, *Juncus*-dominated marshes represent 9% of the vegetative cover (Waits 1967). This community is generally found in the more shoreward, irregularly flooded locations within the high marsh and in the lower reaches of creeks and rivers, or on the fringes of brackish embayments (Marshall 1974).

On the Atlantic coast the stands of *Juncus* are often small, commonly forming a narrow band adjacent to the shore of both the barrier island and mainland sides of the marsh. But sometimes the areal extent of *Juncus* is very large, comprising hundreds of hectares, particularly where human activity (or, occasionally, nature) has interfered with the normal action of the tides. Occasionally one finds small patches of *Juncus* appearing haphazardly within large, uniform stands of *Spartina*; often these patches will be found to be established on the slight mounds (local relief of 20 cm or less) that were the former sites of horse mussel (*Geukensia*) beds (Fig. 4.1).

In general, the common factor among *Juncus* stands seems to be a somewhat lowered interstitial salinity. The *Juncus* stands are usually found in the irregularly flooded sections of the intertidal marsh, those in which flooding occurs only during the spring-tide period of the tidal cycle. In the interim, rains reduce the interstitial salinity below that of the regularly flooded *S. alterniflora*-dominated sections of the marsh. In a study of the interstitial salinity along transects from creek bank to shore, Adams (1963) found that salinity increased from tall *Spartina* through the high marsh to the limit of the regularly flooded zone. But after this limit was crossed, the interstitial salinity began abruptly to decline through the *Juncus* and the *S. patens* communities to the more shoreward expressions of communities dominated by salt grass (*Distichlis spicata*).

In Gulf coast marshes, where *Juncus* often occupies the marsh zones dominated by *S. alterniflora* on the Atlantic coast, the interstitial salinity in the needlerush community can be greater than that of the cordgrass (Hackney and de la Cruz 1978), but the actual salinity is so low (usually less than 10 ppt) that it imposes no significant stress on

either species. At the very edge of the shore or the barrier island, runoff from the land could be a factor in lowering interstitial salinity.

Protection from the full sweep of the more saline tidal water, coupled with the fresh water from river mouths or mainland groundwater seepage, may account for some or all of the extensive stands of needlerush often associated with marshes that are traversed by causeways or are otherwise disturbed. The small patches on mussel beds may be taking advantage of lower average interstitial salinity caused by the drainage from the slightly higher elevation and the washout of salts caused by rain on the marsh at low tide, together with the less frequent inundation as a result of the higher elevation.

Whatever the causes leading to the displacement of *S. alterniflora* by *Juncus*, the fact is that the border between the two community types is invariably sharp, suggesting that there is a definite competition because the gradients of physical factors, including interstitial salinity, are much more gradual and continuous. Some observations suggest that these borders in marshes are not constant but shift, depending on the changing balance of the factors responsible for the competition. Waits (1967) reported cores of peat that showed the expansion of *Juncus* at the expense of both *Spartina* species during the decade before his study of the North Carolina marshes around Bodie Island. He speculated that it might have been the result of disturbance by grazing on *Spartina* more than a decade before, just at the time the expansion began. Unfortunately, there are no experimental demonstrations in support of the conclusion, drawn from empirical observation, that *Juncus* and *Spartina* are in competition.

The Primary Productivity of *Juncus*

The virtually monotypic stands of black needlerush are very productive, rivaling in most instances all but the most productive creek bank stands of smooth cordgrass. Indeed, Wise (1970), in a study of *Juncus* stands at Back River, Virginia, found black needlerush to have the highest production of all of the types of vegetation studied during 1966 and 1967. Unlike smooth cordgrass, one of its main competitors, *J. roemerianus*, is evergreen, maintaining a significant standing stock of living mass throughout the year. Productivity varies a good deal geographically, although what part of the wide reported range is due to variation and error in measurement methodology is at

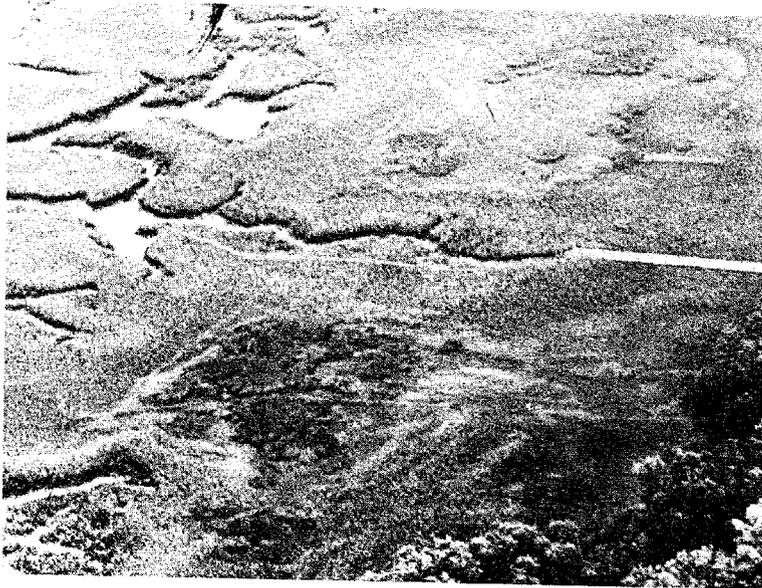


Fig. 4.1. Small, isolated stands of *Juncus roemerianus* are often found on the slight elevations marking the sites of old mussel beds or other depositions (upper right quadrant of photo).

present unknown. In a review of marsh productivity, Keefe (1972) reported annual net production (grams dry weight per square meter) in North Carolina ranging from a low of 560 g to a high of 1,360 g; a single value of productivity from Florida marshes reported by Keefe was intermediate at 849 g (Table 4.1). In the Georgia marshes black needlerush is more productive; the 2,160 g dry wt · m⁻² · yr⁻¹ reported by Gallagher et al. (1980) rivals that of the most productive creek bank stands of tall *S. alterniflora*. On the Gulf coast, stands of black needlerush can produce as much as 3,257 g dry wt · m⁻² · yr⁻¹ according to Gosselink (1984), but the study cited by Gosselink used Wiegert and Evans (1964) technique, which was not designed to be used in tidally flooded grasslands and has been shown to sometimes give inflated calculations of net primary productivity under such conditions.

Plants exhibit three quite different photosynthetic pathways (known respectively as C3, C4, and CAM) depending on the enzymes employed in carbon fixation and the physical location of the pathways. In carbon fixation, the CO₂ is first reduced and then the intermediary compounds are used to form sugars. In the C3 pathway, also called the Calvin cycle after one of its discoverers, both of

these reactions take place in mesophyll cells. The intermediate is a three-carbon compound. Although this fixation uses the energy in ATP and does not require light, light is required to activate the necessary enzymes, so C3 plants cannot fix CO₂ in the dark. Plants possessing a second pathway of carbon fixation produce a four-carbon intermediate and are known as C4 plants. In these plants, the site of CO₂ reduction is physically separated from the site of decarboxylation and sugar production. Reduction takes place in mesophyll cells while decarboxylation and sugar production occur in the bundle sheath cells. Compared to C3 plants, C4 plants have a lower CO₂ compensation point, lose less water per unit of photosynthate produced, grow faster, and are more salt-tolerant. Plants faced with greater water stress have evolved yet a third mechanism for carbon fixation. Because this mechanism was first investigated in the Crassulaceae, it is called the crassulacean acid metabolic, or "CAM," pathway. CAM plants are typically succulents belonging to 18 different families, including the Euphorbiaceae and the Cactaceae. They take in CO₂ during the night, store the products of CO₂ reduction, and then decarboxylate them during the day, keeping the stomata closed. Thus, they are remarkably efficient at

Table 4.1 Productivity of stands of black needlerush (*Juncus roemerianus*; from Keefe 1972).

Locale	Biomass (aerial parts) g(dry)/m ²	New production (aerial) g(dry) · m ⁻² · yr ⁻¹	Source
Florida	232	849	Heald (1969)
North Carolina	—	560	Foster (1968)
North Carolina	1,173	796	Stroud and Cooper (1969)
North Carolina	786	1,360	Waits (1967)
North Carolina	340	850	Williams and Murdoch (1968)
Virginia	650		Wass and Wright (1969)

water conservation and have a CO₂ compensation point even lower than C4 plants, at the cost of a much lower photosynthesis rate than either C4 or C3 plants.

Giurgevich and Dunn (1978) studied the physiological responses of *J. roemerianus*, a C3 plant, to variation in environmental factors such as temperature and light. But despite some of the inherent limitations of the C3 pathway in competition with C4 plants such as *S. alterniflora*, black needlerush, because it is an evergreen, manages to equal or exceed the annual net primary production of its major competitor. In the marshes of Sapelo Island, Georgia, *Juncus* shows no response to enrichment with nitrogen (Gallagher 1975). Giurgevich and Dunn (1978) found no significant light saturation, even though their measurements of photosynthesis were made with the leaves in a horizontal position. Because the leaves of *J. roemerianus* are normally almost vertical, they concluded that in nature (at least in the Georgia marshes where their measurements were made) photosynthesis in this species is light-limited.

The conclusions of Giurgevich and Dunn (1978) about the physiological responses of *J. roemerianus* to seasonal changes in its physical environment are summarized in the following six points: (1) Being evergreen permits a much higher annual production per unit of live biomass than would be achieved by deciduous species. (2) The species responds to increased light by increasing the rate of photosynthesis in all seasons. (3) The temperature optimum for photosynthesis shifted toward the prevailing daytime temperature, but not completely enough to totally avoid heat stress during the warmer months. (4) Internal resistance to diffusive uptake of CO₂ was always larger than stomatal resistance, but the importance of the latter in the total resistance increased with increasing temperature. (5) This increased stomatal resistance at higher temperatures helps prevent excessive rates of water loss that could lead to stress. (6) The efficiency of water use in photosynthesis is relatively high except under the highest summer temperatures.

Fauna of the *Juncus* Community

Because of the sparse literature on the faunal components of the *J. roemerianus* communities of the Atlantic coast intertidal areas, there is some question about the extent to which it boasts a "separate" group of organisms. Such doubts are reinforced when the largely patchy or ribbonlike nature of many of the *Juncus* areas is considered. On the Gulf coast, where large contiguous areas of *Juncus*-dominated intertidal marsh occur, the faunal component is well reviewed in the community profile by Stout (1984). Many of the same species, particularly the larger vertebrates, are found in both *Spartina*-dominated and *Juncus*-dominated Atlantic intertidal zones. The larger invertebrates are generally common to both types

of vegetation as well, any differences being confined to relative densities rather than presence or absence.

Like the smooth cordgrass-dominated marshes, the black needlerush community is a detritus-type system in which most of the net primary production goes to the saprophagous detritus food chain; a relatively small percentage is ingested by herbivores feeding on the living plants. Nevertheless, the high absolute net primary production per unit area ensures that this small percentage supports diverse and numerous terrestrial-type insects and their parasitoids and arachnid predators, just as the high absolute production of *S. alterniflora* supports such a group (Wiegert and Evans 1967). The herbivores, because they are small and, more importantly, feed directly from the living plant, might be expected to differ between stands of *Spartina* and *Juncus*, even when the latter occur in relatively small patches.

Davis and Gray (1966) studied the insect fauna of several intertidal marsh sites in North Carolina for 15 months during 1959. They characterized the study sites by means of three distinct zonal sequences: (1) comparatively steep slopes along the boundaries of sounds and estuaries, where the vegetation graded from *S. alterniflora* to *S. patens*; (2) a sequence of *S. alterniflora* to *J. roemerianus* to high marsh dominated by *Distichlis spicata*; and (3) in low salinity situations, a sequence of *S. cynosuroides* to *J. roemerianus* with little or no development of high marsh. Generally, the *S. alterniflora* marsh is flooded twice each day; the stands of *Juncus* are flooded irregularly, and the high marsh is reached only in the spring tides. Even in the low marsh, however, complete submergence of the vegetative shoots occurs only rarely, during the highest spring or storm tides, and then only for short periods, a fact important to terrestrial species living in these zones.

Davis and Gray used sweep net sampling because it provides a reasonably good quantitative comparison of relative densities, samples from a large area (thus minimizing distribution-related errors), and consumes less time than cage sampling. They went through considerable effort to standardize the seasonal samples to minimize the effects of time of day, temperature, tidal inundation, and structure of the vegetation. Table 4.2 summarizes their data from several locations within each of four types of vegetation. Here we discuss only the *S. alterniflora*-*J. roemerianus* comparison. Both communities showed similar dominance by Homoptera, with Diptera a distant second in frequency of occurrence. The range values show much variation between locations within each of the vegetational types. The absolute densities of insect per sample were almost seven times as great in the smooth cordgrass as in the needlerush. Whether this represents a real absolute difference in density per unit area depends on how successful Davis and Gray were in standardizing sweep sampling between vegetational types. When one considers

Table 4.2 *Relative densities of insect orders based on sweep samples in four intertidal community types in North Carolina (from Davis and Gray 1966).*

Plant association	Percentage composition						Other orders	Insects/sample \bar{X} (range)
	Homoptera	Diptera	Hemiptera	Orthoptera	Coleoptera	Hymenoptera		
<i>Spartina alterniflora</i>	78.8 (53-90)	13.4 (3-52)	3.9 (0.2-12)	2.7 (0.1-8)	1.0 (0.2-3)	0.73 (0.2-2.5)	0.24 —	411 (265-11,095)
<i>Juncus roemerianus</i>	72.2 (17-86)	9.9 (5-50)	2.8 (1-20)	11.1 (5-22)	0.79 (1-11)	2.8 (1-11)	0.4 —	63 (18-132)
<i>Distichlis spicata</i>	57.3 (38-61)	18.7 (10-41)	19.2 (9-30)	1.2 (0.4-2.4)	2.0 (0.5-3.5)	0.91 (0.6-1.2)	0.07 (0.06-0.09)	1,345 (1,130-1,782)
<i>Spartina patens</i>	30.4 (20-44)	43.9 (25-61)	8.8 (5-17)	3.0 (2-4.4)	4.4 (2-9)	8.8 (3-11)	1.0 (0.5-1.5)	196 (115-245)

all vegetational zones, Homoptera decrease in importance as the marsh zone elevation increases and the difference is made up by proportional increases in the remaining orders. One of the anomalies is the increase in the importance of the Orthoptera in the rush community. Davis and Gray explained this on the basis of the ability of grasshoppers to better exploit the open nature of the vegetation and the tough leaves of both the cordgrass and black needlerush (the densities per unit area seem similar in the two vegetational types).

There were considerable differences as well between cordgrass and needlerush communities in species within the orders. There was a nearly complete separation in the frequency and density of the most common homopteran species between the cordgrass and needlerush communities (Davis and Gray 1966). The *Juncus* stands had only two of the dipteran species common in *S. alterniflora* and these were found at very low densities. The single hemipteran species in *Juncus* was not found in the cordgrass stands. Similarly, the black needlerush communities shared only one orthopteran species and no coleopteran species with *S. alterniflora*. Table 4.3 illustrates another dimension of this comparison by separating the characteristic species of each community according to the kind of material they ingest. Again, the differences between the

Spartina and *Juncus* communities are clear.

The situation is different with respect to the spiders that prey on these herbivorous species. Some 13 years before the study of Davis and Gray, Barnes (1953) had sampled the spider populations in the same general area of North Carolina in Carteret County on the Outer Banks. Barnes sampled in several ways: by using sweeping, pitfall traps, and hand sampling. He collected 139 spider species belonging to 24 families. The results of the density frequency analyses showed no substantial difference between the spider fauna of the *Juncus* and *S. alterniflora* communities except that the former had very low densities (consistent with findings that suggest a much lower density of prey) and fewer total species. All of the 11 species found in the sweeps from *Juncus* were also found in the smooth cordgrass community. The constancy of the spider fauna, in both species presence and density, from stand to stand and through time, provided a striking contrast to the herbivorous insect fauna of the *S. alterniflora* zone. In general, Barnes found an increasing number of species with increasing proximity to the climax maritime community represented by the woody terrestrial vegetation. This was explained by the increase in structural diversity and niche availability.

Table 4.3. Trophic relations of common invertebrates from four intertidal marsh communities in North Carolina (from Davis and Gray 1966).

Feeding habits	Food	Dominant plants			
		<i>Spartina alterniflora</i>	<i>Spartina-Salicornia-Limonium</i>	<i>Juncus roemerianus</i>	<i>Distichlis spicata</i>
Herbivorous	Plant tissues	<i>Orchelimum fidicinium</i> <i>Conocephalus</i> spp. <i>Mordelistaena</i> spp.	<i>Orphulella olivacea</i>	<i>Paroxya clavuliger</i> <i>Conocephalus</i> spp.	<i>Orphulella olivacea</i> <i>Conocephalus</i> spp. <i>Clinocephalus elegans</i> <i>Nemobius sparsalsus</i>
	Plant sap	<i>Prokelisia marginata</i> <i>Sanctanus aestvarium</i> <i>Draeculacephala portola</i> <i>Ischnodemus badius</i> <i>Trigonotylus uhleri</i>	<i>Prokelisia marginata</i> <i>Sanctanus sanctus</i>	<i>Keyflana hasta</i> <i>Rhynchomitra microrrhina</i>	<i>Amphicephalus littoralis</i> <i>Spangbergiella vulnerata</i> <i>Delphacodes detecta</i> <i>Tumidagena terminalis</i> <i>Neomegamelanus dorsalis</i> <i>Trigonotylus americanus</i> <i>Rhytidolomia saucia</i> <i>Cymus breviceps</i> <i>Conioscinella infesta</i> <i>Oscinella ovalis</i>
	Plant secretions	<i>Chaetopsis apicalis</i> <i>Chaetopsis fulvifrons</i> <i>Conioscinella infesta</i>	<i>Chaetopsis apicalis</i> <i>Chaetopsis fulvifrons</i> <i>Conioscinella infesta</i>		
Carnivorous	Animal tissue	<i>Isohydnocera tabida</i> <i>Collops nigriceps</i>	Spiders	<i>Erythrodiplax berenice</i>	<i>Naemia serriata</i> Spiders
	Animal body fluids	<i>Dictya oxybeles</i> <i>Hoplodictya spinicornis</i> Spiders	<i>Dictya oxybeles</i> <i>Hoplodictya spinicornis</i> Spiders	Reduviids Asilids Spiders	<i>Tomösvaryella coquilletti</i> Reduviids Culicids Asilids Spiders
Omnivorous	Detritus	Ephydriids Dolichopodids <i>Littorina irrorata</i>	Ephydriids Dolichopodids		Ephydriids Dolichopodids
Parasitic	Plant tissues and sap	Dipterous larvae	Dipterous larvae		Dipterous larvae
	Animal tissues and body fluids	Larvae of parasitic Hymenoptera	Larvae of parasitic Hymenoptera	Larvae of parasitic Hymenoptera	Larvae of parasitic Hymenoptera



1
1

1
1

Chapter 5. Side Issues: Salt Pans, *Salicornia*, and Marsh Edge Communities

Community Composition in the High Marsh

The macrophytic vegetation of the creek banks and low- to midtidal salt marshes of the southeastern United States is virtually a monotypic stand of *Spartina alterniflora*. As the elevation increases landward (whether coastline or barrier island), the community diversity increases as well. Extensive stands of black needlerush (*Juncus roemerianus*) can develop when the interaction between freshwater runoff and tidal flow is changed such that the interstitial salinity is reduced. However, in these high marsh areas, where flooding is less and less frequent and of shorter duration, the influence of land runoff may not be sufficient to counteract the effects of evaporation and transpiration and the interstitial water becomes more, not less, salty.

Within this more diverse physical mosaic in the high marshes, the dominant plant may still be a short form of *S. alterniflora*, provided the interstitial salinity is not too high. But particularly high interstitial salinities are characteristic of the sandy soils and low elevational gradients that are commonly found between the high *Spartina*-dominated marsh and the shoreward *Juncus* zones. This is the zone termed a salt flat by Kurz and Wagner (1957). In the southeastern tidal salt marshes, salt flats cover extensive areas in both natural zones and those disturbed by humans. Tidal flooding is less frequent in these areas and the sediment is often exposed, particularly where plants are scarce or absent (areas variously termed salt barrens, salt pannes, or salt pans). Drying takes place to a greater depth and more rapidly because of the porous nature of the sandy substrate. Exceptions are the mud barrens (Frey and Basan 1985), which are shallow ponds in the salt-flat zone. The fine silt seems to provide enough of a seal to retain water, which becomes progressively more saline through evaporation.

Outside of these barren areas, large or small patches of vegetation are found, including pure stands or various mixtures of such species as *Distichlis spicata* (salt grass), *Batis maritima* (saltwort), and *Salicornia virginica* (perennial glasswort). Figure 5.1 shows an idealized diagram of the salt flat's interstitial salinity and its vegetation as related to the other regions of the tidal salt marsh. Compared to areas with dominant monotypic species, relatively little is known about the saltflat environment or its

vegetation. The following short sections discuss the barrens and the three major species of southeastern marshes.

Formation of the Salt Pans or Barrens

In the marshes on the Georgia coast, salt barrens or pans are very common adjacent to some forms of human disturbance such as levees or areas where free tidal movement has been blocked by roads across the high marsh with only one or two culverts providing drainage. Although little is known about exactly how the salt pan arises, the reduced amplitude of high tide landward from the barrier, together with the porous nature of the soil, results in increased soil salinity to the point where no rooted plants can survive. These sand barrens are commonly covered with thin films of blue-green algae (Frey and Basan 1985).

When these sandy barrens occur naturally, they probably result from the shifting geomorphology of the particular site. Near the sounds and the seaward margins of the southeastern barrier islands, the marshes are often subjected to much higher tides and swifter currents during storms and even during normal onshore winds. This can produce sandy substrate and block the access of tides, thereby leading to the formation of sand barrens. But such barrens should also be the most transient because the factors that produced them may often alter circumstances enough to give access once again to the tidal inundations that reduce the high interstitial salinity. Barrens produced by human activities, if the speculation is correct, should be much more permanent. Some interesting research could be done with experimental manipulations involving the placement and removal of tidal barriers.

The mud barrens mentioned by Frey and Basan (1985) are also of two kinds, those related to human activities and those that are natural. The former are usually found as small permanent ponds that resulted from excavation (borrow pits) along a road or other type of levee at high elevations where the tidal exchange of water is infrequent (Fig. 5.2). If the ponds are very shallow, evaporation presumably keeps the water sufficiently saline to prevent the growth of rooted macrophytes. Where the water is too deep, *Spartina* will not grow. In either instance, the permanent flooding, even if it is of only normal estuarine salinity, may be sufficient to prevent growth of macrophytes.

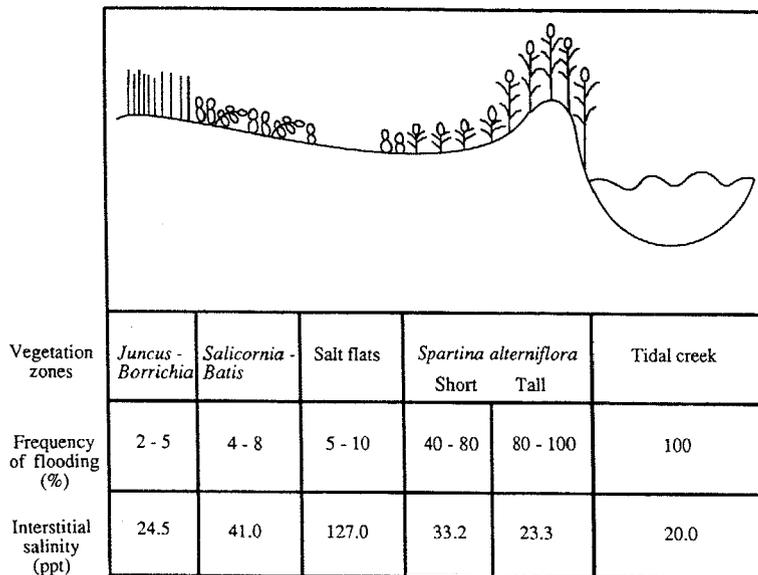


Fig. 5.1. The relation of the salt flat's interstitial salinity and its vegetation (redrawn from Antlfinger and Dunn 1979).

The second kind of mud barren is an area, in either the low or high marsh, which has obviously been recently vegetated by *S. alterniflora*, but now is barren. The dead stubble is still present and may remain so for some time. In many, and perhaps all of these instances, the cause of vegetational death can be traced to a patch of *Spartina* wrack (large stems and leaves) that overlies the area for long enough to kill the plants (see Fig. 3.2). When the wrack is subsequently removed by tidal action, often during a severe storm, the barren area remains. Depending on the location, particularly the schedule of tidal inundations, the area will either quickly revegetate with *Spartina*, lie barren for some time, or, in a few instances, be revegetated with *Salicornia* or *Batis*. If the area were extremely marginal for *Spartina* in the first place, with a pronounced sandy substrate and infrequent flooding, it could go directly to a sand barren that might remain indefinitely.

There seems to be no experimental demonstration of the above scenario, but at Sapelo Island, *Spartina* has been experimentally killed in the high marsh by mowing in June for 2 successive years, and the result was recolonization of the area by *Salicornia*, which persisted for years (Pomeroy and Wiegert 1981a). In the low marsh we have observed the almost immediate (within 1-2 years) recolonization of bare areas by *Spartina* after the removal of large rafts of wrack. In these areas the twice-daily flooding probably keeps the interstitial salinity low enough for rapid growth of *Spartina*.

Higher Plant Communities of the Salt Flats

None of the salt flat communities has been studied in a holistic manner as complete ecosystems. At best, the literature contains scattered references to the plant and

animal biota, species occurrences, a bit of life history and occasionally some process measurements, most often measurements of photosynthesis and respiration of the primary producers. Usually these data are obtained in the course of more extensive study of the *Spartina* or *Juncus* association.

Two types of plants occur in the salt flat habitat: the succulents (*Salicornia*, *Batis*, and *Borrichia*) and salt grass (*Distichlis spicata*). The available data on the primary productivity of *Salicornia virginica* are so variable that about all that can be said is that its productivity per square meter is only 1-10% of that of high-marsh short *Spartina alterniflora*. Underground production of *Salicornia* was reported as 140 g/m² by Gallagher and Plumley (1979). But Antlfinger (1976) and Antlfinger and Dunn (1979), using infrared gas analyzer measurements of total CO₂ exchange, reported only 6.8 mg CO₂ · m⁻² · h⁻¹. Even assuming that this rate is the same all year (they stated that rates were lower in winter), the annual production is only 16 g C · m⁻² · yr⁻¹. Thus, questions about the annual productivity maxima and minimum, as well as about the spatial variability in production, remain only partially answered at best.

Salicornia, *Batis*, and *Borrichia*, being succulent plants growing in a hypersaline environment where water is difficult to obtain and retain, would naturally be presumed to be C4 or maybe even CAM plants (Fig. 5.3). But the photosynthesis measurements of Antlfinger and Dunn (1979) showed that less than 20% of fixed CO₂ was lost through dark respiration, and all three genera showed inefficient water use with high rates of transpiration both summer and winter. They concluded that the plants were in the C3 category, a conclusion in agreement with the stable-carbon isotope ratios measured for these three genera by Haines and Montague (1979).

Salicornia apparently has a much lower ligno-



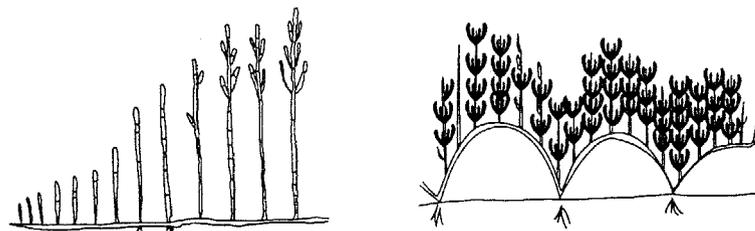
Fig. 5.2. A mud barren or "borrow pit" at Sapelo Island, Georgia.

cellulose content than either *Spartina* or *Juncus* because it is degraded by decomposers at a much higher rate (Haines and Hanson 1979). But the decomposer community is virtually unstudied in these saltflat systems.

The animals of the succulent communities are strongly influenced by the fauna of the extensive borders of either *Spartina* or *Juncus*. *Salicornia* and *Batis* are seldom extensive enough or offer enough cover to form the exclusive habitat of larger animals. The ubiquitous fiddler crabs are present in large numbers, particularly the sand fiddlers (Fig. 5.4). Although these communities are submerged almost completely during high spring tides, they support large numbers of insects and spiders. Barnes (1953) found great similarities in the species composition

of spiders in mixed saltflat communities (*Salicornia-Distichlis*) and in a pure *Spartina alterniflora* stand. During the summer there was a substantial population of cursorial hunting spiders. The density of insect populations in the *Salicornia* stands was much lower than that of *Spartina alterniflora*, but the percent composition by insect order was very similar in the two communities.

The salt grass (*D. spicata*) community forms virtually pure stands in the salt flat, often as a zone just seaward of extensive stands of black needlerush (Fig. 5.5). The species is also found in mixed border zones. Although short, the grass forms a dense cover and its primary production is very high. Linthurst and Reimold (1978) reported an aerial production of $1,900 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ and



Salicornia virginica

Batis maritima

Fig. 5.3. Growth forms of some common saltflat species: glasswort (*Salicornia virginica*), saltwort (*Batis maritima*), and sea oxeye (*Borrichia frutescens*), redrawn from Eleuterius (1980).



Borrighia frutescens



Fig. 5.4. The sand fiddler crab (*Uca pugilator*).

Gallagher and Plumley (1979) found the underground production (of a different stand) to be $420 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$. These harvest methods have some arguable assumptions in them, but if substantiated by gas analyses, these figures show the productivity of *D. spicata* to be similar to high-marsh short *Spartina alterniflora*. Salt grass is a C4 plant, in contrast to the succulent species of the salt flat. This is probably a major reason for its higher net production.

Partly because of this high production, but mainly because it offers good cover, the animal fauna of the *Distichlis* community is dense. Davis and Gray (1966) sampled five examples of this community in North Carolina and found remarkably little variation in relative density (mean number per sweep sample) from site to site.

They reported a mean of 1,344 individuals with a range of 1,130 to 1,782. This compares with their samples from smooth cordgrass (mean 2,528, range 265–11,095), black needlerush (mean 63, range 18–132), and the one sample from mixed *Spartina-Salicornia-Limonium* (mean 411). Although the *Distichlis* insect community is similar to that of cordgrass in density, the species composition is quite different. Homopteran species are less abundant in *Distichlis*; there are about 50% more dipteran species, and the orthopteran species account for ten times the percentage composition of the total insect fauna. Furthermore, the total number of insect species collected from *Distichlis* was higher than that of *S. alterniflora*.



Fig. 5.5. A stand of salt grass (*Distichlis spicata*).

Chapter 6. Brackish-water Tidal Marshes

Plant Communities

On the southeastern Atlantic coast, wherever rivers supply a significant input of fresh water into the upper end of the estuary, a broad band of brackish-water tidal marshes will develop. The dominant salt-tolerant plants of the southeastern tidal marshes can develop in brackish-water habitats as well. But another species, big cordgrass (*Spartina cynosuroides*), forms extensive stands where local salinity conditions are suitable (Fig. 6.1). Schubauer and Hopkins (1984) found good stands of this species where interstitial salinities were within the range of 2–14 ppt. Other brackish-water species such as bulrush (*Scirpus americana*) and pickerelweed (*Pontederia cordata*) are found in smaller stands mixed with the more extensive areas of big cordgrass (Gallagher and Reimold 1973). In these brackish tidal areas, local changes in currents, channels, and the associated salinity regimes will produce changes in dominant species rather than changes in biomass and productivity of the same species as is the case in the more saline marshes. In those, as we saw earlier, change in elevation produces only a change in the form of the dominant *Spartina alterniflora* and attendant changes in the biomass and productivity.

Along the southeastern Atlantic coast, the tendency is for big cordgrass to dominate the brackish tidal marshes wherever conditions permit it to replace *S. alterniflora* and *Juncus roemerianus*. Odum et al. (1984) reviewed the distribution of the mesohaline plants in the mid-Atlantic tidal marshes. To the south, the barrier island chain of coastal Georgia is breached at several points by the estuaries of major rivers, forming extensive areas of brackish tidal marsh. A typical example of this community type is the estuary of the Altamaha River, whose mouth is immediately to the south of Doboy Sound, the blind estuary bounding the southern end of Sapelo Island and the Duplin River marshes (Fig. 6.2). At times of high discharge from the Altamaha River (late fall to early spring), the fresh water can significantly lower the salinity of the tidal water on the southern Sapelo salt marshes.

The plant distribution in the delta of the Altamaha River was surveyed by using infrared aerial photography coupled with ground-truth sampling during high river flow in April and low flow in August (Gallagher and Reimold 1973). These investigators divided the Altamaha Delta area into three zones: the lower estuary with typical tidal salt marsh, the middle estuary with brackish and salt marsh vegetation, and the upper estuary with tidal fresh-

water vegetation (Fig. 6.2). Three species were dominant in the midestuary zone: *S. alterniflora*, *J. roemerianus*, and *S. cynosuroides*. Smaller numbers of other species were found, depending on the salinity at the sampling station (Table 6.1 and Fig. 6.2). Bulrush (*Scirpus americana*) was almost always mixed in with short *Spartina alterniflora*. Pickerelweed (*P. cordata*) was found in small pure stands or mixed with cordgrass.

Physically and hydrologically, the various areas of the estuary show no consistent change with respect to the three zones of Fig. 6.2, nor do the soils vary in composition with respect to zone. Gallagher and Reimold (1973) found silty clay predominating throughout the estuary, with little variation from site to site. Thus, virtually all the differences in the kinds of dominant vegetation reflect the fresh-water influence of the Altamaha River.

Productivity of *Spartina cynosuroides*

Unfortunately, the ecology of the brackish tidal marshes of the southeastern United States is poorly known. Most of the studies of big cordgrass, for example, were made on the more extensive stands found on the Gulf coast. On the southeastern Atlantic side, *S. cynosuroides* stands occupy substantially less area because the deltas are smaller. Accurate figures on the area occupied by big cordgrass are not available, but because the total of tidal fresh- and brackish-water areas together are only slightly more than 10% of the tidal salt marsh on the Georgia coast (Johnson et al. 1974), a reasonable assumption is that big cordgrass stands are significantly less than 10% of the area of saline tidal marsh.

The most recent extensive measurements of standing stock and productivity of big cordgrass stands is that of Schubauer and Hopkins (1984). The following discussion is based on their findings except where otherwise noted. *Spartina cynosuroides* had a somewhat different seasonal pattern of changes in standing stock than smooth cordgrass. Maximum aboveground biomass (1,234 g dry wt/m²) was reached in October instead of July and died back completely in the winter; *S. alterniflora* commonly has some live biomass aboveground all year. Aboveground dead standing stocks were inversely correlated with the live biomass and were about three times those of the *S. alterniflora*. This is due in part to the higher aboveground productivity of big cordgrass and in part to the greater diameter and rigidity of the stems, which permit it to stand for a longer period and thus exhibit a lower rate of



Fig. 6.1. The dominant plant in the brackish-water intertidal marshes, big cordgrass (*Spartina cynosuroides*).

degradation than that of *S. alterniflora* (McKee and Seneca 1982; Schubauer and Hopkinson 1984). The overall live-to-dead ratio of aboveground biomass was 0:24.

As is the case with *S. alterniflora*, Schubauer and

Hopkinson (1984) found large standing crops of belowground organic matter, of which about 80% was dead. Belowground live biomass peaked during the period of lowest aboveground biomass, in late fall to early winter.

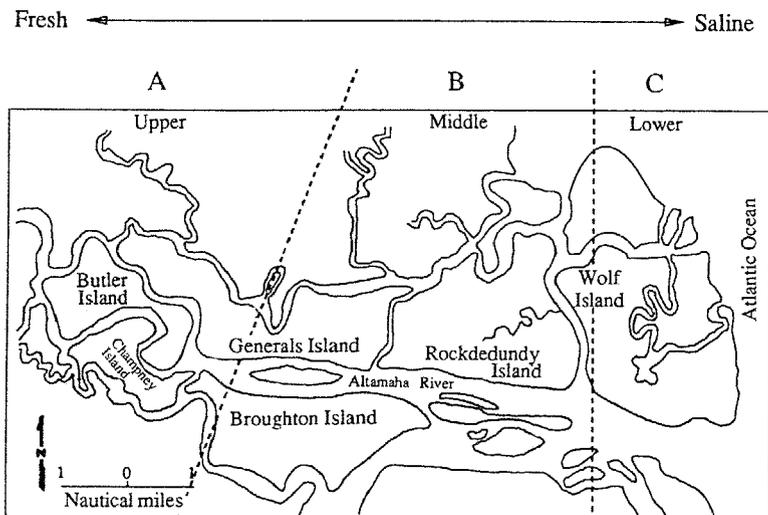


Fig. 6.2. Three zones of the estuary of the Altamaha River, Georgia: (a) upper estuary with tidal freshwater vegetation; (b) middle estuary with mixtures of salt- and brackish-water vegetation; and (c) lower estuary with typical salt marsh (redrawn from Gallagher and Reimold 1973).

Table 6.1. Relationships of plant species to salinity in the intertidal estuary of the Altamaha River, Georgia (from Gallagher and Reimold 1973).

Species	Stations																																				
	Atlantic Ocean										→																								Fresh water		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34			
<i>Spartina alterniflora</i>	+	+	+	+	+	+		+			+		+		+						+	+	+	+	+												
<i>Juncus roemerianus</i>							+	+	+									+	+																		
<i>Spartina cynosuroides</i>							+						+	+					+			+	+		+	+				+							
<i>Scirpus americanus</i>							+	+				+	+	+	+						+	+			+	+	+										
<i>Pontederia cordata</i>											+												+	+	+					+	+	+					
<i>Zizaniopsis miliacea</i>																							+				+					+	+				
<i>Zizania aquatica</i>																								+	+	+				+	+						
<i>Scirpus validus</i>																						+	+		+								+				
<i>Peltandra virginica</i>																						+							+								
<i>Eleocharis albida</i>																																	+				
<i>Typha domingensis</i>																																	+	+			

As with *S. alterniflora*, this stored material is rapidly mobilized and transferred to the shoots during spring growth.

Net aerial production was approximately 3,000 g · m⁻² · yr⁻¹. However, this estimate was based on unpublished turnover rates of 5.35 (production/mean biomass), which are higher than those found in other vegetational types (Wiegert and Evans 1964). The corresponding

estimated belowground production of roots and rhizomes was 4,628 g dry wt/m². This was higher than the only other measurement of belowground productivity, 3,560 g dry wt/m² (Gallagher and Plumley 1979). Schubauer and Hopkinson (1984) point out the problems encountered in the measurement of belowground production and the need for caution in comparing results based on differing methodologies.



Chapter 7. Nutrient Cycles and Energy Flows

Trophic Structure of *Spartina alterniflora* Marshes

Our discussion of the dynamic behavior of the marsh ecosystem is based on the smooth cordgrass (*Spartina alterniflora*) community for two reasons. First, from an areal standpoint, it is the dominant vegetative association of the southeastern tidal salt marshes, and second, much more is known about this system than any of the other vegetative communities of the southeastern intertidal zone. Known data on the process rates of the other salt marsh communities are included as well.

An ecological process, as we use the term here, encompasses transformations of matter or energy initiated by living organisms and modified or controlled in some way by physical factors in their environment, or by interactions with other organisms or abiotic materials (Wiegert et al. 1981). Here we will restrict our discussion to processes involving the transformation and transfer of carbon. Processes important in the salt marsh ecosystem include primary and secondary production, respiratory catabolism, predation, and seasonal mortality. These processes generate fluxes of carbon within and through the ecosystem.

We regard the marsh ecosystem as divisible into three interacting yet semiautonomous subsystems: processes active in the air (e.g., the emergent shoots of grass and their dependent organisms), processes active in the tidal water (e.g., the swimming and surface benthic resident organisms), and processes active in the soil or sediment (e.g., the benthic infauna, meiofauna, and the anaerobic and aerobic microorganisms). In the emergent shoots, terrestrial-type processes and organisms predominate. In the tidal creeks and in the water flowing over the marsh at high tide, aquatic organisms and predominantly aerobic processes are encountered. The soils and sediments exhibit both aerobic and anaerobic microbial and meiofaunal processes, and thus have attributes of both terrestrial soils and aquatic sediments. These divisions are of course oversimplified, but they do serve to make the important distinction between the intertidal ecosystem and most other ecosystems: in the latter the air-water and sediment-water interfaces form the boundaries between distinct systems. But in the intertidal system, these boundaries are compressed into such a highly interactive relation that they are hard to separate, even to allow description and study. The degree of spatial or temporal separation

between the three subsystems depends on the process under study.

Figure 7.1 is a diagrammatic representation of the three subsystems, showing the major flows of carbon involved. As an example, consider the fate of the annual net primary production of cordgrass. Since the marsh is a detritus system, very little of the net annual production is eaten while living; most dies and is transformed into detritus, ultimately becoming organic material assimilable by detritivores. These transformations are mediated by various microorganisms. The residence time of these transformation products in the water varies widely, ranging from minutes to millenia (Williams et al. 1969; Sottile 1974; Hanson and Wiebe 1977). The importance of any ecological process associated with these transformations is defined either by the magnitude of the flow or by the amount of influence it exerts in controlling other flows. For example, the aerobic microorganisms associated with the thin aerobic layer of flocculent particulate organic matter on the surface of the marsh represent a relatively small part of the total microbial standing stock in the marsh. Yet the rate at which they process carbon may be extremely important in determining many of the other flows and processes there (Wiegert 1986). Similarly, those organisms that graze on these bacteria and fungi may exert a strong controlling function on the marsh.

Aerial Primary Production and Grazing

There are three components to the primary producer array in a salt marsh. The first, and usually the most important in terms of total fixed carbon, is the suite of rooted plants. In the *Spartina alterniflora* community, this comprises only the single species. The second is a characteristic algal assemblage present on the surface of the mud between the stems of the macrophyte wherever there is sufficient light at low tide. The third, the tidal water itself, carries a population of phytoplankton; the latter are to a degree interconnected with the benthic algae, depending on the level of resuspension during flood and ebb tides and deposition during slack tides.

Because of the physical domination by the above-ground parts of smooth cordgrass in this salt marsh community, the casual observer might be pardoned the assumption that the algal production was of little consequence. However, that assumption is unwarranted

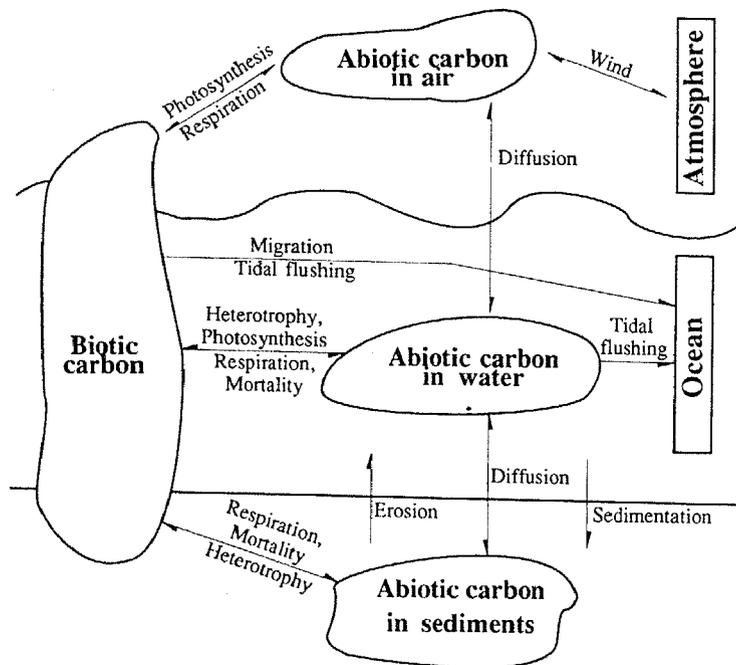


Fig. 7.1. Diagrammatic representation of the three zones of a typical intertidal *Spartina alterniflora* community (redrawn from Wiegert and Wetzel 1979).

because of the potentially high turnover rate of the microproducers.

Most studies of productivity by *S. alterniflora* have emphasized the division between plants growing on the creek bank and levees (where they are well developed) and plants in the poorer drained high marsh. The former are characterized by a higher aboveground biomass, a higher productivity, and a lower root and rhizome biomass than that of the high-marsh plants (Gallagher 1974; Gallagher et al. 1980).

The major physiological problem that must be overcome by salt marsh plants is to obtain CO_2 without losing too much water vapor through transpiration. Pomeroy et al. (1981) made the analogy between such plants and desert plants. In the case of the salt marsh species, there is clearly enough water in the absolute sense, but to use it the plant must separate it from the salt, a process costly in energy terms. Thus, a plant growing with its roots in salt water finds that it is not energetically efficient to open its stomata, yet without open stomata it cannot receive the CO_2 necessary for the fixation of solar energy. The water-use efficiency of the plant thus represents the degree to which the plant has evolved an ability to solve these conflicting demands.

In the Georgia marshes, allowing for open water and the surface areas occupied by mud banks, the productivity of smooth cordgrass (*S. alterniflora*) is $1,539 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$. About one-half of this total is produced aboveground (calculated from Gallagher et al. 1980; Giurgevich and Dunn 1982) and the remainder comprises production of roots and rhizomes. In the high marsh, the productivity (about $1,350 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) could be controlled by a

number of factors, including high interstitial salinity, sulfides, scarcity of iron, and lack of nitrogen (Chalmers 1982). On the creek bank, the tall *Spartina* produces much more, about $2,500 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, and the limitation seems to be self-shading (Giurgevich and Dunn 1982). These estimates of the aboveground production do not include the material removed by leaching, primarily soluble carbohydrates, nor do they include the amount taken by grazing herbivores. The former amounts to only about $6 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (Gallagher et al. 1976); this is negligible when compared to the net shoot production alone.

The food web of grazers and their predators found in the emergent shoots of *Spartina* are primarily terrestrial in origin. The two dominant grazers are the planthopper (*Prokelesia marginata*) and the salt marsh grasshopper (*Orchelimum fidicinum*) (Smalley 1960; Teal 1962; Pfeiffer and Wiegert 1981). The actual carbon flow through this grazing food chain to the predators of the grazers is substantial, but only because of the large absolute production by the plant (Teal 1962; Wiegert and Evans 1967). As a percentage of the net primary production, the amount grazed is small, less than 5%, making the aerial portion of the salt marsh ecosystem truly a detritus-type food web.

Production of Roots and Rhizomes

The underground biomass of cordgrass exceeds the shoot biomass (Gallagher 1974), and the productivity of the roots and rhizomes constitutes 68% of the total net production (Schubauer and Hopkinson 1984). The

production is seasonal: rhizomes store a large amount of energy during the winter; this energy is used to produce the very rapid aboveground growth in the spring. Figure 7.2 shows the seasonal distribution of *S. alterniflora* roots and rhizomes. In the fall, the root-rhizome material made up 78% of the total live biomass; by spring this had decreased to 53% (Schubauer and Hopkinson 1984). The greatest biomass of roots and rhizomes was found 10–30 cm below the surface. Living roots and rhizomes peaked at 10–20 cm; nonliving organic matter was most abundant slightly deeper at 20–30 cm. Dead material dominated at all depths, tending to mask the annual changes in living biomass.

The factors governing the productivity of roots and rhizomes, as well as the seasonal depth and distribution of this production, are poorly known. Schubauer and Hopkinson (1984) mentioned some possible explanations, such as growth inhibitors (H_2S , or increased salinity), but the topic needs further research. Because of the dominance of belowground production, these factors need to be elucidated.

Most of the belowground production that is not remobilized during the spring burst of shoot growth dies in place and must be degraded within the sediment. However, the burrowing of fiddler crabs, which cut through all but the largest rhizomes, can result in a substantial portion of this belowground production being returned to the surface (Montague et al. 1981).

Productivity of Benthic Algae and Phytoplankton

The epibenthic and epiphytic algae of the Georgia salt marsh, despite their low standing stocks relative to the macrophytes, contribute significantly to the net primary production of the marsh. By far the most important group of algae is the pennate diatoms, which form 75 to 93% of the total algal biomass (Williams 1962). In addition, there are several species of filamentous cyanobacteria and a single species of *Euglena* (Pomeroy et al. 1981).

The productivity of benthic algae differs in many ways from that of the macrophytes. They are small, with a low standing stock, but have a much higher turnover rate. Because of the much higher potential specific rates of photosynthesis, the algae respond much faster than do the macrophytes to changes in environmental factors that influence realized rates of productivity. In addition, the seasonality of the benthic algal production differs from that of *Spartina alterniflora*, being greatest in the winter when light attenuation at the surface is lower (Gallagher and Daiber 1974).

As Pomeroy et al. (1981) pointed out, these algae occupy a stratum (the surface few millimeters) that is poised "between a dark, nutrient-rich, anaerobic sediment

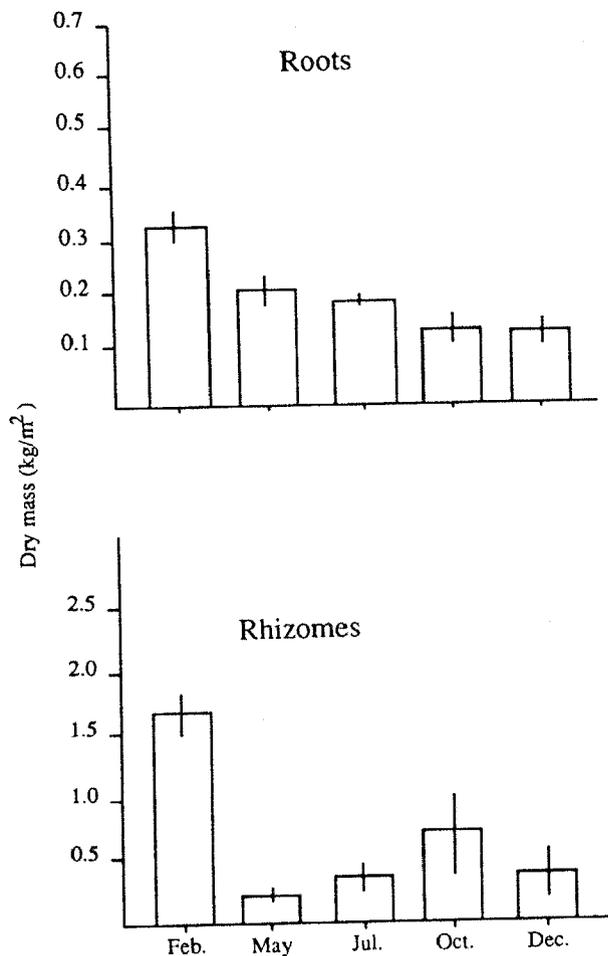


Fig. 7.2. Seasonal changes in the standing stock (mean \pm 1 standard error) of the roots and rhizomes of *Spartina alterniflora* (redrawn from Schubauer and Hopkinson 1984).

and either an illuminated, aerobic, comparatively nutrient-poor water column or, at ebb tide, the atmosphere." Thus, the habitat of the algae is subjected to very rapid changes in light, temperature, pH, salinity, and nutrients that can have correspondingly rapid effects on the photosynthetic rate. An additional factor that can interfere with diurnal rates of photosynthesis is the propensity of the diatoms in the low marsh to retreat into the sediment at flood tide, thus reducing the light they receive (Palmer and Round 1967; Brown et al. 1972).

In the Sapelo Island marshes, benthic productivity was estimated to be $200 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, gross, and 180 g C , net, from field measurements under both high and low tidal conditions (Pomeroy 1959). This is about 12% of the net primary production of the macrophytes in the marsh. About 75% of this production occurs during ebb tide and the bare creek banks are the most productive parts of the marsh (Pomeroy et al. 1981).

The tidal waters that inundate the southeastern salt

marshes are very turbid, particularly in the summer. Consequently, scientists who first studied the productivity of these marshes and estuaries tended to discount the phytoplankton production, reasoning that the photic zone must be so shallow as to severely limit algal photosynthesis. Typical of these early studies was that of Ragotskie (1959), who measured photosynthesis in the deeper parts of the Duplin River and concluded that net production by the phytoplankton on an annual basis was negative. But Ragotskie's results were probably biased by his sampling locations. More recent studies, summarized in Pomeroy et al. (1981), point to phytoplankton as a significant source of fixed organic carbon used by pelagic heterotrophs.

Aquatic Macroheterotrophs

The aquatic macroheterotrophs of the marsh include both resident and nonresident (migrant) species. The former remain on the marsh continually; the latter come and go with the tides, some being present in all their life stages, others (using the marsh during high tide) for only part of their life cycles. The most conspicuous and important of these migrants are juvenile brown and white shrimp and the smaller forms of several fishes. For the Georgia marshes, Montague et al. (1981) documented the considerable densities of organisms that may subsist as resident consumers. Biomass may exceed 15 g C/m^2 , consisting of 80–200 mud fiddler crabs (*Uca pugnax*), 400–700 periwinkle snails (*Littorina*) or mud snails (*Ilyanassa*), and 7–8 ribbed mussels (*Geukensia*). Other snails, clams, and polychaete worms contribute to the total biomass.

Despite the high densities of consumers, early studies of tidal salt marsh energetics tended to show a very small percentage of the total energy flow associated with macroconsumers. This comparatively low importance was, in part, a result of the extremely high net primary production. Although primary consumers used only a small percentage of the net primary production in absolute terms (energy/m²), these tidal salt marshes have one of the highest secondary productivities per unit area of any ecosystem in the world (Wiegert and Evans 1967).

The resources available to these macroconsumers include a variety of forms of organic carbon, including live vascular plants, dead *Spartina*, microorganisms, algae, particulate and dissolved carbon compounds, and other consumers, both living and dead. Of these resources, only living *Spartina* is little used, the marsh crab (*Sesarma reticulatum*) being the only aquatic grazer (Jackewicz 1973; Kraeuter and Wolf 1974).

The relative utilization of the remaining resources available to the macroheterotrophs can be ranked in order of increasing availability as macrodetritus, particulate organic carbon (POC), dissolved organic carbon (DOC), bacteria, algae, and animal material, both living and dead.

Although there have been many studies of the assimilation rates of detrital carbon by animals, there is no evidence that animals use the macrodetritus and POC to a significant extent. The refractory cellulose and lignocellulose components of the vascular plant detritus is broken down by bacteria and fungi. The latter seem to be important agents of the initial stages of weathering, particularly in the case of the standing dead material from *Spartina* (Newell et al. 1985).

Because a relatively small percentage of the vascular plant biomass is grazed, the two major bases for the food webs of the salt marsh ecosystem are the benthic algae-phytoplankton base and the POC and DOC detrital pool. Consumers of algae and of microorganisms are the two major links between these two sources of fixed energy and the higher trophic levels. This relation is illustrated in Fig. 7.3. The amounts of carbon involved in these transfers and transformations, when finally known with some degree of certainty, will help answer the question of whether the marsh is functioning as a source or a sink for fixed carbon.

Marsh–Estuarine Interaction: Outwelling

Tidal marshes on the Atlantic coast can be likened to terrestrial grasslands that are inundated by water twice each day. Then the question naturally arises: What are the mutual results of this interactive coupling between the marsh and the sea? How does the marsh differ in operation from a terrestrial grassland, and how does this difference influence the nearshore or down-estuary water that recedes from the marsh at ebb tide?

Very early in the development of an explanation of Georgia tidal salt marsh dynamics, the dominance of the detrital pathways leading to the higher trophic levels was recognized. The excess of net primary production over measured heterotrophic respiration was obvious (see, for example, the early summary of energetics in Teal 1962). Speculating on the ultimate fate of all this apparently excess carbon led to an answer to the question posed above that is, in hindsight, perhaps somewhat simplistic but which seemed at the time to be reasonable and logical. The tides, being an energy subsidy, physically move inorganic nutrients onto the marsh and remove the net product of community metabolism in the form of particulate organic carbon compounds. These are exported to the estuary or nearshore area. Nixon (1980), in an extensive and excellent review of salt marsh ecology as it stood at the end of the 1970's, pointed out that the last sentence of Teal's 1962 paper contained the interesting, but at the time unsupported, statement that 45% of the net production of the marsh was removed from the marsh to the estuaries by the tides, thus supporting an abundance of estuarine and nearshore animals.

This idea was quickly adopted by many researchers

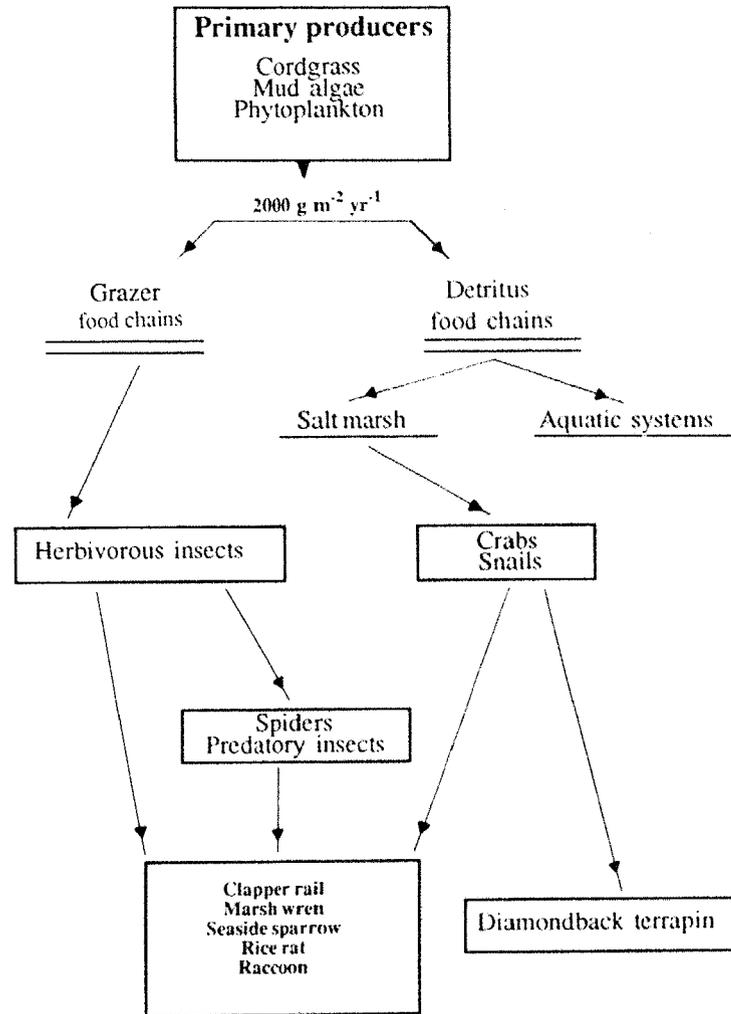


Fig. 7.3. An expanded trophic diagram of a *Spartina alterniflora* community (redrawn from Wiegert 1986).

in salt marsh ecology and became incorporated into the idea of outwelling, as opposed to the upwelling, of nutrients from deeper ocean water (Odum 1968). The concept is illustrated in Fig. 7.4. The twice daily influx of the tide brings dissolved inorganic nutrients onto the marsh where they are incorporated into energy-rich organic carbon compounds by the productive cordgrass. Much of this material is subsequently washed off of the marsh surface, and its decomposition fuels the estuarine and nearshore food chains, leading to commercially valuable populations of animals.

Nixon (1980) was properly critical of Odum and others who adopted this concept for not clearly labeling it for what it was, the outwelling hypothesis—an interesting mechanism, but one which was, at the time, unsupported by any direct measurements. Indeed, Nixon pointed out that if an earlier statement of the hypothesis by Kalber (1959) had had wider recognition, data might have been obtained sooner. But the outwelling concept may have been so useful to those seeking a reason to curtail the then

rampant destruction of tidal salt marshes that little could have stood in the way of its uncritical acceptance. If marshes did indeed export large quantities of energy-rich material to supplement the estuarine and nearshore fisheries, then they must be preserved. Moreover, an actual dollar value could be, and often was, applied to the marshes (e.g., Gosselink et al. 1974).

In the two decades since Odum proposed the outwelling concept (and almost a decade after the latest paper cited in Nixon's review), many measurements relevant to this hypothesis have been made. One of the clearest messages to emerge is that, although tidal *Spartina*-dominated marshes share many similarities, they can be very dissimilar in the mechanisms of import and export, primarily because of different latitudinal locations and differing hydrologic regimes. In the next chapter we summarize the state of our knowledge with respect to Georgia marshes, the place where salt marsh research and paradigms began.

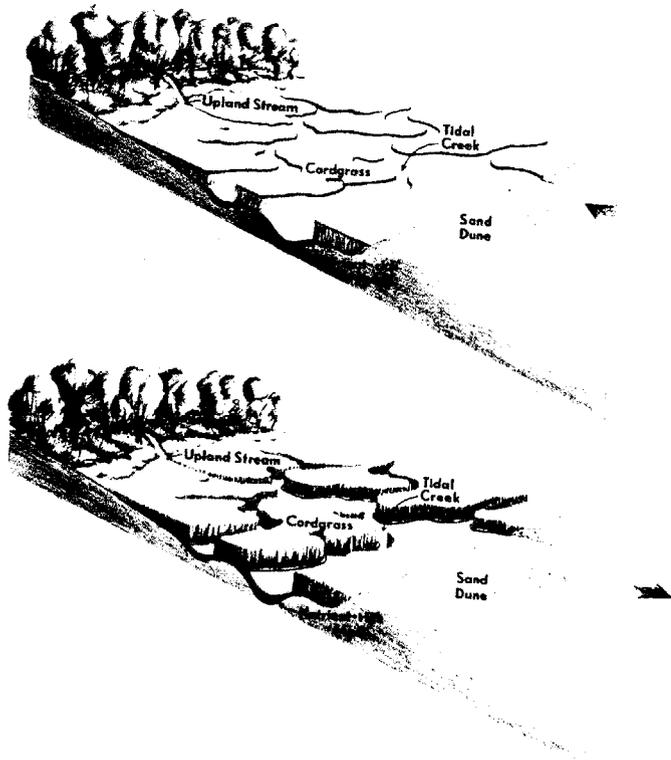


Fig. 7.4. The outwelling concept, in which flood tides bring dissolved nutrients onto the salt marsh and the ebbing tides remove particulate organic carbon (redrawn from Hitchcock 1972).

Chapter 8. Modeling the Dynamics of Salt Marshes

The Uses of Simulation Models

In modern ecology, simulation models are most useful tools for improving the efficiency with which research is conducted. As the system of interest grows larger, models become more and more indispensable adjuncts to the research effort; as the system grows larger, so does the known data base, and the digital simulation model is without peer as a means of storing data and testing the consequences of hypothetical relationships proposed by researchers. This brief review presents the types of models that are useful in this context, describes how they are constructed and used, and illustrates this use by showing how an ecosystem model was used in conjunction with field and laboratory research to construct an explanation of carbon transformation and transport in the coastal *Spartina* marshes of Georgia.

A model must, because of the complexity of even the simplest of living systems, be some abstraction of reality. It must also, however, preserve some aspects of the real system that are commensurate with the model objectives. Usually, prediction of altered states following a perturbation is involved. If that were all, and given a set of data on the responses of similar systems to a range of severity of the perturbation, then the indicated type of model would be some form of correlative fit of parameters to the data, often referred to as an empirical model. Such models are easy to construct (given the existence of the data sets), and within the variability and range of the data, they are good predictors. But because the parameters of such models are chosen entirely on the basis of improving the fit of the model to the data, they have no explanatory content; that is, they are nonmechanistic, containing no hypothetical relationships.

The kinds of model and the applications considered in this chapter focus on the implementation of the research, that is, on the discovery of mechanisms. In this use, the predictions *per se* are of secondary interest, the major focus being on pinpointing gaps in knowledge of the system and determining the sensitivity of the mechanistic parameters in the model. Because we are considering an ecosystem, the tidal salt marsh, the focus is on ecosystem level models. Any system is defined as some collection of parts, and their interaction, the whole displaying some defined unitary behavior (Miller 1965). Another way to define a system model is to say that the structure of the model interacts with the functional attributes of the parts to produce model behavior.

Model Structure and Function

In systems science the words “structure” and “function” are used differently than they are in ecology. In fact, a diagrammatic representation of this difference shows a symmetrical two by two classification (Fig. 8.1). To the field ecologist, the structures *in* the system include the organisms, trees, and animals, and the inanimate rocks, soil, and water. The functional attributes reside in the pathways of interaction and the dynamic processes such as matter–energy flow (Odum 1971). To the systems ecologist, a more useful way of dividing up structure and function is to think in terms of the abstract structure *of* the system, including both the potential niches (boxes) and the pathways (arrows), interacting with the functional attributes of the occupants. Thus, one can describe the political structure of a city or country, specifying all the offices and their paths of interaction, without reference to the functions of the particular occupants of the political offices. Thus, in general, system structure is more conservative in character than is function. The occupants of the system, and thus their functions, can change more often than the structure.

The first step in the construction of a model of an

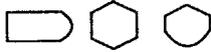
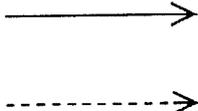
Ecology		Systems
Structure	Function	
		Structure
<i>Spartina alterniflora</i> Grazers POC	Flux of matter Flux of energy Controls	Function

Fig. 8.1. The definitions of structure and function found in ecology versus systems science (redrawn from Wiegert et al. 1981).

ecosystem is to specify the structure of the model, the compartments, and the pathways of matter, energy, or information transfer. Next, the ecological modeler must decide how to aggregate the multiple species in the system that share the characteristics of each of the structural compartments, set up the mechanisms by which they interact and are controlled, evaluate the parameters, and, finally, run the model and compare its output with independent data sets to provide some validation. At this point the mechanistic model is ready to be used to suggest conclusions, which are, of course, the consequences of the hypothetical mechanism built into the functional attributes of the compartment occupants.

Is the Marsh a Carbon Sink or a Source?

In Chapter 7 we described the controversy about whether the marsh should be regarded as a source of fixed carbon or as a sink for organic matter imported from the estuary and the nearshore. To investigate this problem, the first version of a simulation model of the Duplin River marshes was constructed in the mid-1970's. We began with the original division of the marsh ecosystem into air, water, and sediment sections and further subdivided the biotic components into 14 interacting compartments (Fig. 8.2).

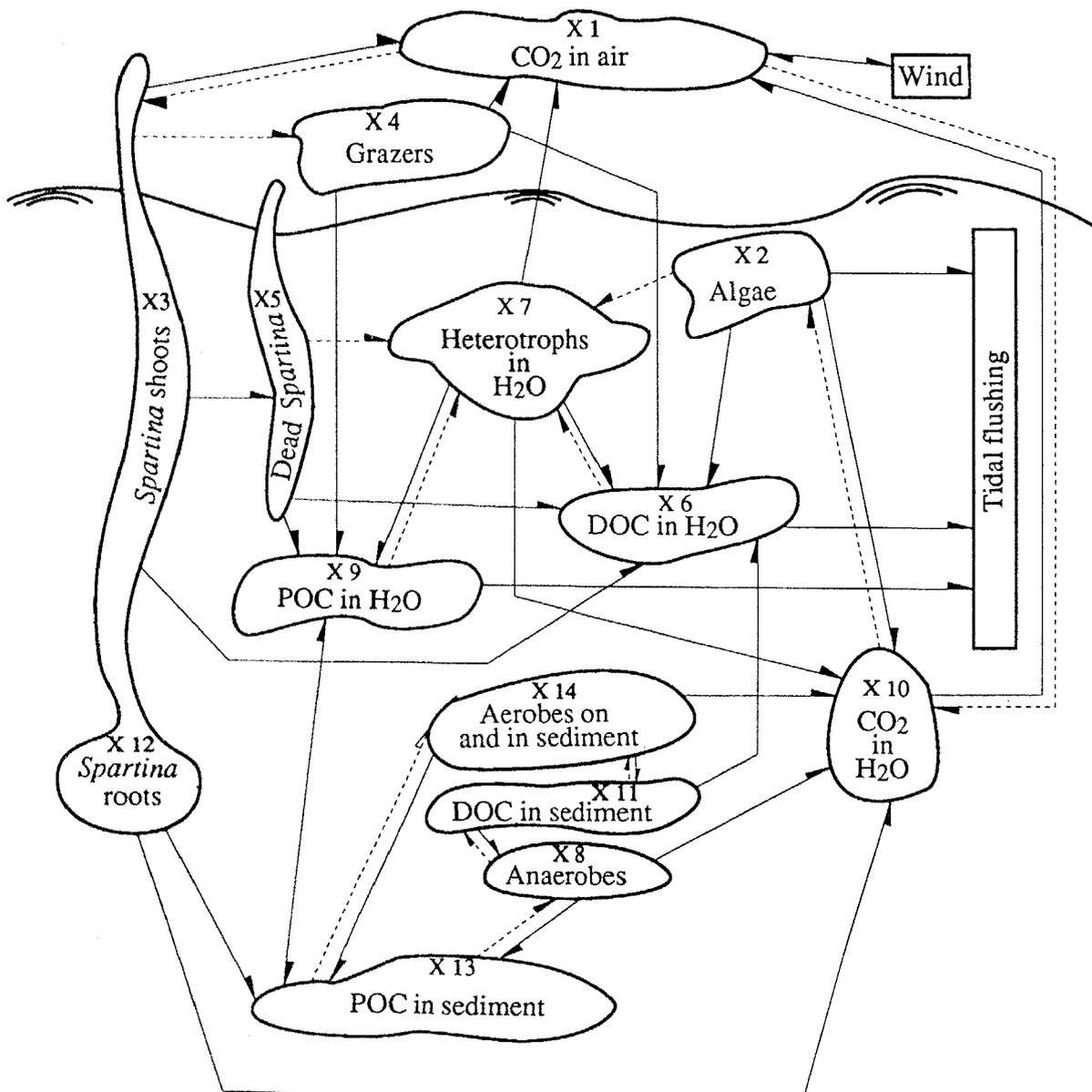


Fig. 8.2. A 14-component carbon-flow model of a coastal *Spartina alterniflora* salt marsh (redrawn from Wiegert and Wetzel 1979).

The algae (X2) comprised both phytoplankton and benthic algae, the latter dominated by diatoms, but with cyanobacteria as well. Because more information existed on the dynamics of the major producer (*Spartina alterniflora*) than was available for the other biotic components, it was modeled as three compartments: shoots (X3), roots and rhizomes (X12), and standing dead material (X5). The latter included the microbial colonizers, but in the first version of the model (Wiegert et al. 1975) the standing dead compartment was given no respiratory rate.

Compartment X4, the grazers of *Spartina*, comprised a number of insect species, the most important being members of the sucking bugs (Homoptera) and an abundant endemic grasshopper (*Orchelimum fidicinum*).

The dissolved organic carbon (DOC) in the water (X6) as well as the particulate carbon (POC-X9) included both refractory and labile forms. The same was true of the analogous compartments in the sediment (POC-X13) and in the interstitial water (DOC-X11).

Compartment X7 included all heterotrophs in the water, from microbes to fish. The parameters, however, were heavily weighted to simulate the behavior of the microbes. Other microbial compartments in the model were the aerobes at the surface of the sediment (X14) and the anaerobes in the sediment (X8). Gaseous carbon in the water (X10) and in the air (X1) completed the 14-compartment array of functional components.

Although extremely crude and simplified, simulations with this first model showed that nothing short of extraordinary (and biologically unrealistic) manipulations of some parameter values would prevent the marsh as a whole from acting as a source of fixed carbon (Wiegert et al. 1975). Subtracting total degradation from net primary production left a net budget accrual of several hundred

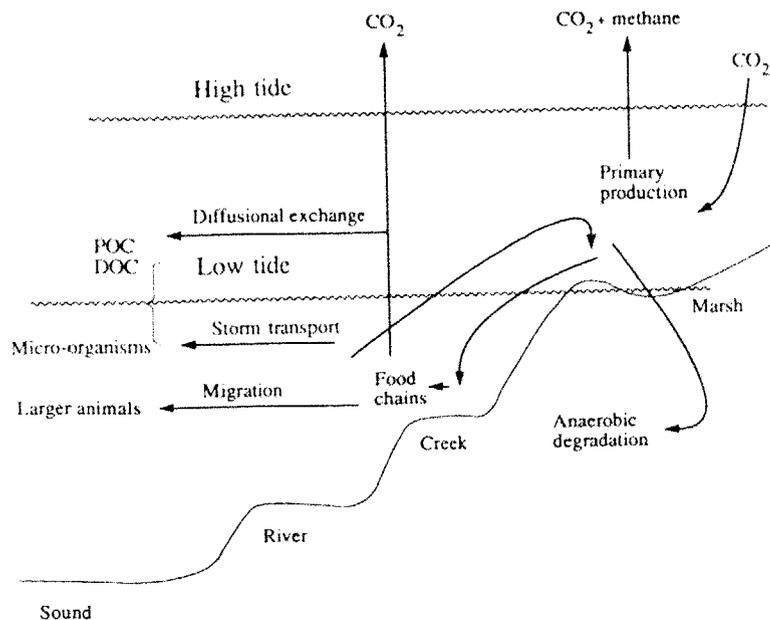
grams of carbon per square meter. Because no measured level of net deposition for the marsh exceeded a few tens of grams annually, the research for the next few years focused on solving the problem of the missing carbon. Either the current information on the overall degradation rate was in error, or the estimate of transport of carbon from the marsh to the estuary was low ($115 \text{ g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, derived by Wiegert 1979 from data of Odum and de la Cruz 1967).

During the next 5 years, a number of field and laboratory research efforts, together with simulations made with revised and expanded versions of the salt marsh model, resulted in a picture of the Duplin River marshes as an ecosystem that was indeed exporting significant quantities of organic carbon to the estuary (summarized in Pomeroy and Wiegert 1981b), but several hundred grams of carbon fixed as net production still were not accounted for.

The first step toward the solution of this remaining puzzle was taken by obtaining a much more detailed picture of the seasonal variation in the POC and DOC concentrations in the Duplin River (Chalmers et al. 1985). This permitted a major revision of the model parameters and some structural changes. Simulations with this revised model and concurrent studies of the depositional regime as water moved on and off the marsh resulted in support for a radically revised hypothesis about the transport of carbon within the marsh and its availability to microbial degraders and their consumers (Chalmers et al. 1985).

Figure 8.3 diagrams the elements of this new hypothesis. The major departure from previous views was based on the idea that material is either moved off the marsh in the guts of nonresident feeding migrants or deposited on the marsh, not eroded by every high tide but washed back into the upper tidal creek by rains falling on the marsh at

Fig. 8.3. Hypothesis proposed to explain the transport and transformation of carbon in a coastal Georgia *Spartina alterniflora* salt marsh (after Chalmers et al. 1985).



low tide (Chalmers et al. 1985). This latter mechanism in particular forced yet another major revision of the model (Wiegert 1986).

Simulations with this latter version showed a somewhat reduced export of POC through tidal exchange. But the most striking prediction of the model was that the marsh could exhibit at least two locally stable steady states with respect to carbon degradation and export. In the one—which seems from past data to be the nominal one for most of the marsh, most of the time—aerobic microbes that are degrading the flocculent layer moving up on the marsh with every high tide are controlled by their consumers. There is a considerable surplus of undegraded carbon that is being exported. The marsh itself is very

slowly accreting at a level that just approximates the annual rise in sea level. In the other locally stable steady state, the microbes escape from control by their consumers and increase the degradation of carbon to the point of exceeding the surplus left from the annual net primary and secondary production. The marsh is thus importing carbon and acting locally as a carbon sink. Thus, as a result of simultaneous field and laboratory research and ecological modeling, the story of the Georgia salt marshes has gradually unfolded. The current focus is now on the questions of when and under what circumstances the sink condition of the marsh occurs. If this latest prediction of the model is supported, then a further revision will be in order.

Chapter 9. Values of Tidal Marshes

Tidal Marshes as Wilderness

Intertidal marshes in general, but particularly the extensive *Spartina alterniflora*-dominated marshes of the southeastern coast of the United States, can be likened in many ways to wilderness in that they have been relatively little affected by human activities. These ecosystems, although impressively vast when one is in the midst of some of the larger ones, are small compared with the marshes of the Gulf coast. They are virtually insignificant in area when compared with the remainder of the continental land mass. Yet, unless they have been seriously affected or destroyed by direct physical perturbation such as dredging, filling, or draining, the original ecosystem remains largely intact, much as it must have been for eons before the invasion by humans, or indeed, even before the evolution of humans.

These intertidal marshes were not the primary home of, nor were they seriously affected by, the large vertebrates whose numbers were subsequently reduced or who became extinct because of humans. This is the major respect in which the intertidal marshes differ from the forest, grassland, and desert ecosystems making up the bulk of the continent and which were home to many species of large vertebrate herbivores. The subsequent extinction or severe reduction in the numbers of these dominant consumers produced a drastic change in the vegetational composition and productivity of these systems. Those few large vertebrates, such as deer, that used the margins of the marsh remain today in much the same densities as before. These marshes, with their soft substrates and twice-daily tides, are simply not very suitable habitats for large grazing vertebrates and their predators.

For somewhat the same reasons, the intertidal habitat was not immediately disrupted by the arrival in North America of the early European colonists because this habitat is not suitable for agriculture, at least not without extensive and expensive modification. In many areas of Europe and Asia, intertidal marshes have been destroyed by such modification; they have been reclaimed by means of dikes and tide gates, yielding rich agricultural land. Such reclamation projects usually require some combination of the following elements: a shortage of agricultural land in which to expand, high technology for reclamation, and cheap labor. Only the last of these was characteristic of colonial America. During the 19th century, considerable modification of intertidal marshes was made as marshland at the mouths of the major rivers

was extensively diked for rice growing. During the peak of the rice-producing period, 1850–1860, Georgia alone had almost 9,300 ha under cultivation (Johnson et al. 1974). Most of this development for rice production has now been abandoned and, because most of the diked areas were reclaimed cypress intertidal swamp; this kind of modification never seriously threatened the saline intertidal area supporting the extensive communities of *S. alterniflora*.

Intertidal marshes have retained their characteristic vegetation because they were relatively undisturbed by agriculture, and because the dominant species responsible for the productivity of the system were not seriously depleted. Along with the vegetation, the ecosystem within which the remaining consumer and decomposer species have evolved was also retained. Furthermore, the intertidal system, because of the stress imposed on plant growth by high salinity, is not an easy system for extraneous plants or animals to invade.

For these reasons, marshes that have avoided physical destruction have very few weed or invader species, either plant or animal. Such ecosystems are valuable extant communities for the study not only of marsh biology, but also of coevolutionary processes in general. Thus, the many thousands of hectares of intertidal salt marsh on the coast of the southeastern United States can be regarded in a sense as wilderness, even though they are traversed by relatively large numbers of people in search of recreation and commercial returns.

Commercial Uses of Intertidal Marshes

In the early decades of this century, the marshes of the southeastern coast supported a large industry centered on the oyster *Crassostrea virginica* (Stevens 1983). But overexploitation and the failure to replace shell led to the collapse of this industry, and at present only a handful of commercial oyster houses remain in operation. Presently, the only significant direct commercial use of the tidal salt marshes of the southeastern coast of the United States is by crabbers seeking the blue crab (*Callinectes sapidus*). This effort, although small compared with the crabbing industry of Chesapeake Bay, provides an important economic factor to the coastal areas of Georgia and the Carolinas. Although some of the trapping takes place off of the

beaches, the vast majority of the crabs are taken in the sounds and smaller tidal creeks associated directly with the marshes. In any case, all the crabs use the marshes and tidal creeks as habitat during their juvenile and subadult stages.

The marshes are also vital in the maintenance of the coastal shrimp (*Penaeus*) fishery, a multimillion dollar industry on the Georgia coast alone. In addition to the modest subsidy that the marshes provide to the nearshore zone where shrimp make most of their adult growth (see Chapter 8), the marshes and tidal creeks provide both the food and protection necessary for the survival of the juvenile shrimp population (Vetter 1983).

Noncommercial Uses of Intertidal Marshes

Although the relation between marshes and the nearshore fishery may be difficult to prove, as we saw above, the value of the fishery can be easily quantified in economic terms. However, the noncommercial uses of the marsh do not lend themselves so easily to quantitative evaluation. How does one measure aesthetic values? Even recreational and educational values can be expressed only partly in economic terms.

Coastal intertidal marshes, like all wetlands, have figured prominently in human artistic and aesthetic considerations for ages (Reimold et al. 1980; Daiber 1986). Aesthetic appreciation of the marsh is, of course, not the sole prerogative of the artistically talented; everyone can experience the joy and exhilaration that come with the sight of a sea of waving cordgrass stretching to the horizon or the swift swoop of the hunting osprey. Naturalists, birders, and others who venture into the marshes often have only such aesthetic values in mind. Others, however, combine aesthetic values with more concrete recreational benefits.

Recreational uses of intertidal marshes run the gamut from totally nonconsumptive to consumptive, either of the produce of the marsh (fishing) or of part of the system itself (marinas, for example). In addition to considering the aesthetic values of such recreational pastimes as fishing and boating, we can go a bit further in evaluating the worth of marshes. Recreational pursuits have an economic side simply because one has to bear some cost to engage in them. Although some of these costs may be well hidden, others are relatively easy and straightforward to compute.

People are spending an increasing amount of money on the pursuit of marine recreational fishing. Reimold et al. (1980) reported that a 1977 report of the National Marine Fisheries Service placed the total economic benefit from 1975 marine recreational fisheries at \$2.9 billion. Although most of these fish are caught in open water, most

of them require the presence of coastal intertidal wetlands as nursery grounds for their juvenile stages.

Reimold et al. (1980) also used the example of waterfowl hunting as a recreational use of tidal marshes that can be partly evaluated in economic terms. The average waterfowl hunter spends \$730 a year on the sport. At this rate Reimold et al. estimated the value of each acre of coastal hunting marsh at \$100 per year. Similar computations can be applied to other recreational uses (e.g., boating) of marshes and estuaries. Because more than 50% of the United States population now lives within coastal counties (Ketchum 1972), users of the marshes are not just vacationing visitors, but also local residents.

Educational values are yet another noncommercial category of salt marsh use. Marshes are often simpler than other ecosystems with respect to species diversity and pathways of energy and nutrient dynamics; this makes them excellent examples to study in order to learn more about the operation of the natural world. States, the Federal government, and numerous private foundations annually spend billions of dollars financing marsh and estuarine research, both basic and applied (Reimold et al. 1980).

The Present

People have finally begun to respond to the accelerating destruction of coastal zone ecosystems. As Daiber (1986) pointed out, "Humans have used tidal marshes in ways that have not, in general, been based on informed understanding or consideration for the resources they contain." Until very recently, many people involved in using or deciding the fate of marshes had very little appreciation of the range and variety of values possessed by the resource they so causally took for granted or dismissed out of hand. Until the National Environmental Policy Act (NEPA) was passed by Congress in 1969, the only policy governing the consumptive exploitation of coastal wetlands involved determining how much economic benefit could accrue from their development; no thought was given to the possibility that marshes could be worth far more left as they were (Daiber 1986). Consequently, we have lost much of the original acreage of intertidal marshes. On the east coast of the United States this destruction has been most complete in the Northeast, where the pressures of industry and development began as early as the late 19th century. In the Southeast we have been somewhat more fortunate; the intertidal salt marshes of the southeastern United States are still extensive and in good condition, relative to many other types of ecosystem. Partly because of the immense original extent of the marshes and partly because of less pressure on the southern marshes by commercial and industrial development and pollution, there is still time to ensure the preservation

of a significant fraction of the original area of this valuable ecosystem.

Although the terrestrial acreage on many of the coastal barrier islands has been developed by both private and governmental interests, the development has been largely of a residential or recreational nature and has often had minimal effect on the marshes themselves. In the 19th century there was extensive diking of the marshes to convert them for rice culture. With the decline in this kind of agriculture in the decades after the Civil War, deliberate or accidental breaching of the dikes has led to the restoration of much of the acreage to a community similar in most respects to the original, whether fresh, brackish, or saline. Presently, the biggest impoundment threat to the "natural" saline tidal marshes is diking to control mosquitos or for waterfowl management. About 11% of the southeastern marshes are diked, largely in South Carolina and Florida (Montague et al. 1987). An additional negative effect has been the conversion of thousands of acres of *Spartina alterniflora* marsh into black needlerush community by the building of causeways that disrupt the tidal regime (Fig. 9.1). Although such modifications result in large changes in the nature of the intertidal system, filling and draining the marshes, along with subsequent development, destroy the entire ecosystem (Fig. 9.2). In Georgia, many of the barrier islands themselves have been preserved, some relatively permanently, as part of the National Park System (Cumberland Island), as a National Marine Sanctuary (Sapelo Island), or as a federally owned wildlife sanctuary (Blackbeard Island). Many of the remaining larger islands have been only minimally affected by residential use and are being protected by the private owners with a view to permanent protection under Federal or State control. The latter, unfortunately, is no absolute guarantee of protection, however, as pressure from short-

sighted, developers can be a potent force in opposition to conservation of the barrier islands and marshes. One example of overdevelopment and subsequent negative effects on the intertidal marshes of the southeastern coast is that of Jekyll Island, which has been a Georgia State Park since the 1940's. The causeways built to give easy access to the island have drastically changed the character of the intertidal marsh.

With the change in our attitude toward the use and development of natural systems has come the appreciation that the value of these systems cannot entirely be expressed in economic terms; sociocultural values are involved as well (Reimold et al. 1980), and these may well prove to be of overwhelming importance, justifying wise management, use, and conservation of a valuable resource (Daiber 1986). Such sociocultural values are commonly characterized as aesthetic, recreational, and educational, although there are no hard and fast boundaries between such largely qualitative categories. Given the relatively new awareness of the multiplicity of values attached to the coastal wetland, what are the prospects for the future with respect to the fate of the intertidal zones of the southeastern United States?

The Future

Coastal marshes will continue to have great aesthetic, recreational, educational, and commercial value in the future. The importance and varied uses of the intertidal marshes discussed in this review have documented the desirability of conserving these valuable expressions of one of our last remaining truly natural ecosystems. Intertidal salt marshes are valuable in both the aesthetic and the economic sense. Unfortunately, as in all instances of the

Fig. 9.1. The impact of a causeway—changing the tidal exchange patterns can result in the replacement of cordgrass (*Spartina*) by needlerush (*Juncus*), glasswort (*Salicornia*), or salt pan.





Fig. 9.2. Filling the marsh for industrial, commercial, or residential development causes the complete destruction of the intertidal system.

protection and conservation of nature, though battles can be won, the war goes on. Moreover, an ecosystem once lost to development or industrialization can seldom, if ever, be restored. This is particularly true of coastal systems, in which the developmental process invariably affects the physical factors responsible for the development of the system in the first place. The conservation and wise management of our valuable coastal wetlands require a high level of informed action, ranging from the management of water levels in duck ponds to the protection against, and cleanup of, oil and other toxic spills. For an informative and detailed consideration of the management side of tidal marshes, the reader is referred to *Conservation of Tidal Marshes* by F. C. Daiber (1986).

As the human population increases in the next few decades, the pressure on all aesthetically desirable land will increase as land becomes even more important for recreation or commerce. In addition, there will be more pressure to replace marsh with residential housing, industries, or such ancillary structures as airports. Our task for the future, then, is to manage our recreational and commercial resources in a way that will prevent such use from destroying the very qualities that make such areas desirable in the first place. The beaches of the coastal barrier islands are highly desirable recreational resources; they must be managed to permit their use by the maximum number of individuals, but without destroying the very attributes that make them desirable: the dunes, the sand, and, to a degree, the sense of wildness and isolation. The intertidal marshes that are protected by these barrier beaches are absolutely vital as the nursery grounds for the larvae and juveniles of many marine species of commercial and sporting importance. Use of the marshes and their associated tidal waterways must be managed to ensure the survival of these ecosystems that represent some of the last and best expressions of a still largely undisturbed wild nature.

Acknowledgments

We thank our many colleagues, both at the University of Georgia and elsewhere, who have taken the time to answer queries during the long course of preparing this manuscript. Three associates at the University of Georgia, A. Chalmers, L. R. Pomeroy, and W. S. Wiebe, have been particularly instrumental in improving our knowledge of the salt marsh and its processes. We have also profited from the suggestions of successive project officers with the U.S. Fish and Wildlife Service's National Wetlands Research Center: W. Kitchens, E. Pendleton, W. Duffy, and R. Howard.

For help with the drawings and photographs used in the figures we are indebted to a number of individuals. The photographs used for Figs. 1.7, 1.8, and 5.4 were taken by L. Gassert; those for Figs. 3.11 and 3.12 were provided by E. Odum; and that used in Fig. 3.4 was taken by W. Wiebe. The original drawing for Fig. 3.10 was done by T. R. Melton and the drawing used in Fig. 7.4 was made by L. H. Barrett. All remaining photographs were taken by the senior author and remaining drawings were made by the junior author. The invertebrate appendixes (B and C) were prepared by D. Bishop.

References

- Adams, D. A. 1963. Factors influencing vascular plant zonation in North Carolina salt marshes. *Ecology* 44:445-456.
- American Ornithologists' Union. 1983. Check-list of North American Birds. 6th ed. 877 pp.
- Anderson, C. M., and M. Treshow. 1980. A review of environmental and genetic factors that affect height in *Spartina alterniflora* Loisel (salt marsh cordgrass). *Estuaries* 3:168-176.
- Antfingler, A. E. 1976. Photosynthetic and water-use strategies of three salt marsh succulents. M.S. thesis, University of Georgia, Athens. 76 pp.

- Antlfinger, A. E., and E. L. Dunn. 1979. Seasonal patterns of CO₂ and water vapor exchange of three salt-marsh succulents. *Oecologia* (Berl.) 43:249-260.
- Amdt, D. T. 1914. Some insects of the between tides zone. *Proc. Indiana Acad. Sci.* 323-336.
- Barnes, R. D. 1953. The ecological distribution of spiders in non-forest maritime communities at Beaufort, North Carolina. *Ecol. Monogr.* 23:315-337.
- Barnes, R. D. 1980. Invertebrate zoology. 4th ed. Saunders College/Holt, Rinehart & Winston Inc., San Diego. 1,089 pp.
- Basan, P. B., and R. W. Frey. 1977. Actual-paleontology and neoichnology of salt marshes near Sapelo Island, Georgia. *J. Geol. Spec. Issue* 9:41-70.
- Beal, E. O. 1977. A manual of marsh and aquatic vascular plants of North Carolina with habitat data. N.C. Agric. Exp. Stn. Tech. Bull. 247. 298 pp.
- Beeftink, W. G. 1977. The coastal salt marshes of western and northern Europe: an ecological and phytosociological approach. Pages 109-149 in V. J. Chapman, ed. *Ecosystems of the world I: wet coastal ecosystems*. Elsevier Science Publishing Company, New York.
- Bent, A. C. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. Part 2. Dover, New York. pp. 603-1248.
- Broome, S. W., W. W. Woodhouse, Jr., and E. D. Seneca. 1975. The relationship of mineral nutrients to growth of *Spartina alterniflora* in North Carolina. 2: The effects of N, P, and Fe fertilizers. *Soil Sci. Soc. Am. Proc.* 39:301-307.
- Brown, D. H., C. E. Gibby, and M. Hickman. 1972. Photosynthetic rhythms in epipellic algal populations. *Br. Phycol. J.* 7:37-44.
- Carter, W. 1973. Insects in relation to plant disease. John Wiley & Sons, Inc., New York. 759 pp.
- Chalmers, A. G. 1982. Soil dynamics and the productivity of *Spartina alterniflora*. Pages 231-243 in V. S. Kennedy, ed. *Estuarine comparisons*. Academic Press, New York.
- Chalmers, A. G., E. B. Haines, and B. F. Sherr. 1976. Capacity of a *Spartina* marsh to assimilate nitrogen from secondarily treated sewage. Tech. Completion Rep., USDI/OWRT Project A-057-Ga.
- Chalmers, A. G., R. G. Wiegert, and P. L. Wolf. 1985. Carbon balance in a salt marsh: interactions of diffusive export, tidal deposition and rainfall-caused erosion. *Estuarine Coastal Shelf Sci.* 21:757-771.
- Chalmers, A. G., R. G. Wiegert, and W. J. Wiebe. 1989. Effects of increased drainage in a short *Spartina alterniflora* marsh. [unpublished manuscript]
- Chapman, R. L. 1971. The macroscopic marine algae of Sapelo Island and other sites on the Georgia coast. *Bull. Ga. Acad. Sci.* 29:77-89.
- Chapman, V. J. 1977. Introduction. Pages 1-29 in V. J. Chapman, ed. *Ecosystems of the world I: wet coastal ecosystems*. Elsevier Science Publishing Company Inc., New York.
- Christensen, B. A. 1976. Hydraulics of sheet flow in wetlands. Pages 746-759 in *Inland waters for navigation, flood control and water diversions*. Proceedings of a symposium of the American Society of Civil Engineers, University of Colorado, Boulder.
- Chung, C. H. 1982. Low marshes, China. Chapter 6 in R. R. Lewis III, ed. *Creation and restoration of coastal plant communities*. CRC Press, Boca Raton, Fla.
- Chung, C. H. 1983. Geographical distribution of *Spartina anglica* (C. E. Hubbard) in China. *Bull. Mar. Sci.* 33:753-758.
- Chung, C. H. 1985. The effects of introduced *Spartina* grass on coastal morphology in China. *Z. Geomorph. N.F.* 57:169-174.
- Cowardin, L. M., V. Carter, F. C. Golet, and E. T. LaRoe. 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Fish Wildl. Serv., FWS/OBS-79/31. 103 pp.
- Dahlberg, M. D. 1975. Guide to coastal fishes of Georgia and nearby States. University of Georgia Press, Athens. 186 pp.
- Daiber, F. C. 1986. Conservation of tidal marshes. Van Nostrand Reinhold Company Inc., New York. 341 pp.
- Davis, L. V. 1978. Class Insecta. Pages 196-220 in R. G. Zingmark, ed. *An annotated checklist of the biota of the coastal zone of South Carolina*. University of South Carolina Press, Columbia.
- Davis, L. V., and I. E. Gray. 1966. Zonal and seasonal distribution of insects in North Carolina salt marshes. *Ecol. Monogr.* 36:275-295.
- Dixon, A. F. G. 1971. The role of aphids in wood formation, 1: The effect of the sycamore aphid, *Drepanosiphum platanoides* (Schr.) (Aphididae), on the growth of sycamore, *Acer pseudoplatanus* (L.). *J. Appl. Ecol.* 8:165-179.
- Duncan, W. H. 1982. The vascular vegetation of Sapelo Island, Georgia. Botany Department, University of Georgia, Athens. 75 pp.
- Duncan, W. H., and M. B. Duncan. 1987. Seaside plants of the Gulf and Atlantic coasts. Smithsonian Institution Press, Washington, D.C. 409 pp.
- Eleuterius, L. N. 1976. The distribution of *Juncus roemerianus* in the salt marshes of North America. *Chesapeake Sci.* 17:289-292.
- Eleuterius, L. N. 1980. An illustrated guide to tidal marsh plants of Mississippi and adjacent States. Miss-Ala. Sea Grant Consortium MASGP-77-039. 130 pp.
- Forsythe, D. M. 1978. Birds. Pages 277-295 in R. G. Zingmark, ed. *An annotated checklist of the biota of the coastal zone of South Carolina*. University of South Carolina Press, Columbia.
- Foster, W. A. 1968. Studies on the distribution and growth of *Juncus roemerianus* in southeastern Brunswick County, North Carolina. M.S. thesis, North Carolina State University, Raleigh. 72 pp.
- Fox, R. S., and E. P. Ruppert. 1985. Shallow-water marine benthic macroinvertebrates of South Carolina: species identification, community composition and symbiotic associations. University of South Carolina Press, Columbia.
- Frey, R. W., and P. B. Basan. 1978. North American coastal salt marshes. Pages 101-169 in R. A. Davis, Jr., ed. *Coastal sedimentary environments*. Springer-Verlag Inc. New York, New York.
- Frey, R. W., and P. B. Basan. 1985. Coastal salt marshes. Pages 225-301 in R. A. Davis, Jr., ed. *Coastal sedimentary environments*. 2nd ed. Springer-Verlag Inc. New York, New York.
- Gallagher, J. L. 1974. Sampling macro-organic matter profiles in salt marsh plant root zones. *Soil Sci. Soc. Am. Proc.* 38:154-155.
- Gallagher, J. L. 1975. Effect of an ammonium nitrate pulse on the growth and elemental composition of natural stands of *Spartina alterniflora* and *Juncus roemerianus*. *Am. J. Bot.* 62:644-648.
- Gallagher, J. L., and F. C. Daiber. 1974. Primary production of edaphic communities in a Delaware salt marsh. *Limnol. Oceanogr.* 19:390-395.
- Gallagher, J. L., W. J. Pfeiffer, and L. R. Pomeroy. 1976. Leaching and microbial utilization of dissolved organic matter from leaves of *Spartina alterniflora*. *Estuarine Coastal Mar. Sci.* 4:467-471.
- Gallagher, J. L., and F. G. Plumley. 1979. Underground biomass profiles and productivity in Atlantic coastal marshes. *Am. J. Bot.* 66:156-161.

- Gallagher, J. L., and R. J. Reimold. 1973. Tidal marsh plant distribution and productivity patterns from the sea to fresh water—a challenge in resolution and discrimination. Pages 165–181 in S. A. Cooper, R. L. Vadas, and S. E. Manzer, eds. Proceedings 4th biennial workshop on color aerial photography. American Society Photogrammetry, Falls Church, Va.
- Gallagher, J. L., R. J. Reimold, R. A. Linthurst, and W. J. Pfeiffer. 1980. Aerial production, mortality, and mineral accumulation-export dynamics in *Spartina alterniflora* and *Juncus roemerianus* plant stands. *Ecology* 61:303–312.
- Gibbons, J. W. 1978. Reptiles. Pages 270–276 in R. G. Zingmark, ed. An annotated checklist of the biota of the coastal zone of South Carolina. University of South Carolina Press, Columbia.
- Giurgevich, J. R., and E. L. Dunn. 1978. Seasonal patterns of CO₂ and water vapor exchange of *Juncus roemerianus* (Scheele) in a Georgia salt marsh. *Am. J. Bot.* 65:502–510.
- Giurgevich, J. R., and E. L. Dunn. 1982. Seasonal patterns of daily net photosynthesis, transpiration and net primary productivity of *Juncus roemerianus* and *Spartina alterniflora* in a Georgia salt marsh. *Oecologia (Berl.)* 52:404–410.
- Gosner, K. L. 1971. Guide to the identification of marine and estuarine invertebrates. John Wiley & Sons Inc., New York. 693 pp.
- Gosselink, J. G. 1984. The ecology of delta marshes of coastal Louisiana: a community profile. U.S. Fish Wildl. Serv., FWS/OBS-84/09. 134 pp.
- Gosselink, J. G., E. P. Odum, and R. M. Pope. 1974. The value of the tidal marsh. Center for Wetland Resources, Louisiana State University, Baton Rouge. 30 pp.
- Hackney, C. T., and A. A. de la Cruz. 1978. Changes in interstitial water salinity of a Mississippi tidal marsh. *Estuaries* 1:185–188.
- Hails, J. R., and J. H. Hoyt. 1969. An appraisal of the evolution of the lower Atlantic coastal plain of Georgia, USA. *Trans. Inst. Br. Geogr.* 46:53–68.
- Haines, E. B., and R. B. Hanson. 1979. Experimental degradation of detritus made from the salt marsh plants *Spartina alterniflora* Loisel, *Salicornia virginica* L., and *Juncus roemerianus* Scheele. *J. Exp. Mar. Biol. Ecol.* 40:27–40.
- Haines, E. B., and C. L. Montague. 1979. Food sources of estuarine invertebrates analyzed using ¹³C/¹²C ratios. *Ecology* 60:48–56.
- Hanson, R. B., and W. J. Wiebe. 1977. Heterotrophic activity associated with particulate size fractions in a *Spartina alterniflora* (Loisel) salt marsh-estuary, Sapelo Island, Georgia, and the continental shelf waters. *Mar. Biol.* 42:321–330.
- Heald, E. J. 1969. The production of organic detritus in a south Florida estuary. Ph.D. thesis, University of Miami. 110 pp.
- Heard, R. W. 1982. Guide to common tidal marsh invertebrates of the northeastern Gulf of Mexico. Miss-Ala. Sea Grant Consortium MASGP-79-004. 82 pp.
- Hitchcock, S. W. 1972. Can we save our salt marshes? *Na. Geogr. Mag.* 141:729–765.
- Hoyt, J. H. 1967. Barrier island formation. *Geol. Soc. Am. Bull.* 78:1125–1136.
- Hustedt, F. 1955. Marine littoral diatoms of Beaufort, North Carolina. *Duke Univ. Mar. Stn. Bull.* 6:1–67.
- Imberger, J., T. Berman, R. R. Christian, E. B. Sherr, D. E. Whitney, L. R. Pomeroy, R. G. Wiegert, and W. J. Wiebe. 1983. The influence of water motion on the distribution and transport of materials in a salt marsh estuary. *Limnol. Oceanogr.* 28:201–214.
- Jackewicz, J. R. 1973. Energy utilization in the marsh crab, *Sesarma reticulatum* (Say). M.S. thesis, University of Delaware, Newark. 61 pp.
- Johnson, S. A., H. O. Hillestad, S. F. Shanholtzer, and G. F. Shanholtzer. 1974. An ecological survey of the coastal region of Georgia. U.S. Natl. Park Serv., Sci. Monogr. Ser. 3. 233 pp.
- Kalber, F. A., Jr. 1959. A hypothesis on the role of tide-marshes in estuarine productivity. *Estuarine Bull.* 4:3.
- Kale, H. W., III. 1964. Food of the long-billed marsh wren, *Telmatodytes palustris griseus*, in the salt marshes of Sapelo Island, Georgia. *Oriole* 29:47–66.
- Kale, H. W., III. 1965. Ecology and bioenergetics of the long-billed marsh wren, *Telmatodytes palustris griseus* (Brewster), in Georgia salt marshes. *Nuttall Ornithol. Club Publ.* 5. Cambridge, Mass. pp. 589–591.
- Keefe, C. W. 1972. Marsh production: a summary of the literature. *Contrib. Mar. Sci.* 16:163–181.
- Ketchum, B. H., editor. 1972. The water's edge: critical problems of the coastal zone. MIT Press, Cambridge, Mass. 393 pp.
- Kraeuter, J. N., and P. L. Wolf. 1974. The relationship of marine macroinvertebrates to salt marsh plants. Pages 449–462 in R. J. Reimold and W. H. Queen, eds. *Ecology of halophytes*. Academic Press, New York.
- Kurz, H., and D. Wagner. 1957. Tidal marshes of the Gulf and Atlantic coasts of north Florida and Charleston, South Carolina. *Fla. State Univ. Stud.* 24:1–168.
- Linthurst, R. A., and R. J. Reimold. 1978. An evaluation of methods for estimating the net aerial primary productivity of estuarine angiosperms. *J. Appl. Ecol.* 15:919–931.
- Livingstone, D. C., and D. G. Patriquin. 1981. Belowground growth of *Spartina alterniflora* Loisel: habit, functional biomass and non-structural carbohydrates. *Estuarine Coastal Shelf Sci.* 12:579–588.
- McKee, K. L., and E. D. Seneca. 1982. The influence of morphology in determining the decomposition of two salt marsh macrophytes. *Estuaries* 5:302–309.
- Marshall, H. L. 1974. Irregularly-flooded marsh. Pages 150–170 in H. T. Odum, B. J. Copeland, and E. A. McMahan, eds. *Coastal ecosystems of the United States*. Vol. 2. The Conservation Foundation, Washington, D.C.
- Mattson, W. J., and N. D. Addy. 1975. Phytophagous insects as regulators of forest primary production. *Science* 190:515–522.
- Mendelsohn, I. A., and E. D. Seneca. 1980. The influence of soil drainage on the growth of salt marsh cordgrass, *Spartina alterniflora*, in North Carolina. *Estuarine Coastal Mar. Sci.* 2:27–40.
- Miles, P. W. 1968. Insect secretions in plants. *Annu. Rev. Phytopathol.* 6:137–164.
- Miller, J. G. 1965. Living systems: basic concepts. *Behav. Sci.* 10:193–411.
- Montague, C. L., S. M. Bunker, E. B. Haines, M. L. Pace, and R. L. Wetzel. 1981. Aquatic Macroconsumers. Chapter 4 in L. R. Pomeroy and R. G. Wiegert, eds. *The ecology of a salt marsh*. Springer-Verlag Inc., New York, New York.
- Montague, C. L., and R. G. Wiegert. 1990. Salt marshes in ecosystems of Florida. Pages 481–516 in R. L. Myers and J. J. Gwel, eds. *Ecosystems of Florida*. University of Central Florida Press, Orlando, Fla.
- Montague, C. L., A. V. Zale, and H. F. Percival. 1987. Ecological effects of coastal marsh impoundments: a review. *Environ. Manage.* 11:743–756.
- Nestler, J. 1977a. A preliminary study of the sediment hydrography of a Georgia salt marsh using rhodamine WT as a tracer. *Southeast. Geol.* 18:265–271.
- Nestler, J. 1977b. Interstitial salinity as a cause of ecophenic variation in *Spartina alterniflora*. *Estuarine Coastal Mar. Sci.* 5:707–714.
- Newell, S. Y., R. D. Fallon, R. M. Cal Rodriguez, and L.C. Groene. 1985. Influence of rain, tidal wetting and relative humidity on release of carbon dioxide by standing-dead salt-marsh plants. *Oecologia (Berl.)* 68:73–80.

- Nixon, S. W. 1980. Between coastal marshes and coastal waters—a review of twenty years of speculation and research on the role of salt marshes in estuarine productivity and water chemistry. Pages 437–525 in P. Hamilton and K. B. MacDonald, eds. *Estuarine and wetland processes*. Plenum Press, New York.
- Nixon, S. W. 1982. The ecology of New England high salt marshes: a community profile. U.S. Fish Wildl. Serv., FWS/OBS-81/55. 70 pp.
- Odum, E. P. 1968. A research challenge: evaluating the productivity of coastal and estuarine water. Pages 63–64 in E. Keiffer, ed. *Proceedings of the second Sea Grant conference*. University of Rhode Island, Kingston.
- Odum, E. P. 1971. *Fundamentals of ecology*. W. B. Saunders Company, Philadelphia. 574 pp.
- Odum, E. P., and A. A. de la Cruz. 1967. Particulate organic detritus in a Georgia salt marsh-estuarine ecosystem. Pages 383–388 in G. H. Lauff, ed. *Estuaries*. Am. Assoc. Adv. Sci. Publ. 83.
- Odum, W. E., C. C. McIvor, and T. J. Smith, III. 1982. The ecology of the mangroves of south Florida: a community profile. U.S. Fish Wildl. Serv., FWS/OBS-81/24. 144 pp.
- Odum, W. E., T. J. Smith, III, J. K. Hoover, and C. C. McIvor. 1984. The ecology of tidal freshwater marshes of the United States east coast: a community profile. U.S. Fish Wildl. Serv., FWS/OBS-83/17. 177 pp.
- Opler, P. A., and G. O. Krizek. 1984. *Butterflies east of the Great Plains*. The Johns Hopkins University Press, Baltimore and London. 273 pp.
- Owen, D. F., and R. G. Wiegert. 1976. Do consumers maximize plant fitness? *Oikos* 27:488–492.
- Owen, D. F., and R. G. Wiegert. 1987. Leaf eating as mutualism. Chapter 4 in P. Barbosa and J. S. Schultz, eds. *Insect outbreaks*. Academic Press, New York.
- Palmer, J. D., and F. E. Round. 1967. Persistent vertical-migration rhythms in benthic microflora. 6. The tidal and diurnal nature of this rhythm in the diatom *Hantzchia virgata*. *Biol. Bull. (Woods Hole)* 132:45–55.
- Patrick, W. H., Jr., and R. D. Delaune. 1976. Nitrogen and phosphorus utilization by *Spartina alterniflora* in a salt marsh in Barataria Bay, Louisiana. *Estuarine Coastal Mar. Sci.* 4:59–64.
- Peterson, M. C., and N. M. Peterson. 1979. The ecology of intertidal flats of North Carolina: a community profile. U.S. Fish Wildl. Serv., FWS/OBS-79/39. 73 pp.
- Pfeiffer, W., and R. G. Wiegert. 1981. Grazers on *Spartina* and their predators. Pages 87–112 in L. R. Pomeroy and R. G. Wiegert, eds. *Ecology of a salt marsh*. Springer-Verlag New York Inc., New York.
- Pomeroy, L. R. 1959. Algal productivity in salt marshes of Georgia. *Limnol. Oceanogr.* 4:386–397.
- Pomeroy, L. R., W. M. Darley, E. L. Dunn, J. L. Gallagher, E. B. Haines, and D. M. Whitney. 1981. Primary production. Pages 39–67 in L. R. Pomeroy and R. G. Wiegert, eds. *Ecology of a salt marsh*. Springer-Verlag New York Inc., New York.
- Pomeroy, L. R., and J. Imberger. 1981. The physical and chemical environment. Chapter 2 in L. R. Pomeroy and R. G. Wiegert, eds. *Ecology of a salt marsh*. Springer-Verlag New York Inc., New York.
- Pomeroy, L. R., and R. G. Wiegert. 1981a. Ecology of a salt marsh. *Ecological Studies Series*. Vol. 38. Springer-Verlag New York Inc., New York. 271 pp.
- Pomeroy, L. R., and R. G. Wiegert. 1981b. The salt marsh ecosystem: a synthesis. Pages 219–252 in L. R. Pomeroy and R. G. Wiegert, eds. *Ecology of a salt marsh*. Springer-Verlag New York Inc., New York.
- Poole, K. T. 1978. Fishes. Pages 236–259 in R. G. Zingmark, ed. *An annotated checklist of the biota of the coastal zone of South Carolina*. University of South Carolina Press, Columbia.
- Post, W. 1974. Functional analysis of space-related behavior in the seaside sparrow. *Ecology* 55:564–575.
- Ragotzkie, R. A. 1959. Plankton productivity in estuarine waters of Georgia. *Publ. Inst. Mar. Sci. Univ. Tex.* 6:146–158.
- Ranwell, D. S. 1972. *Ecology of salt marshes and sand dunes*. Chapman and Hall Ltd., London. 258 pp.
- Reideburg, C. H. 1975. The intertidal pump in a Georgia salt marsh. M.S. thesis, University of Georgia, Athens. 87 pp.
- Reimold, R. J. 1977. Mangals and salt marshes of eastern United States. Pages 157–164 in V. J. Chapman, ed. *Wet coastal ecosystems of the world*. Elsevier Science Publishing Co. Inc., New York.
- Reimold, R. J., J. H. Phillips, and M. A. Hardiskey. 1980. Socio-cultural values of wetlands. Pages 79–89 in V. S. Kennedy, ed. *Estuarine perspectives*. Academic Press, New York.
- Robbins, C. R., R. M. Bailey, C. E. Bond, J. R. Brooker, E. A. Lachner, R. N. Lea, and W. B. Scott. 1980. A list of common and scientific names of fishes from the United States and Canada. *Am. Fish. Soc. Spec. Publ.* 12. 174 pp.
- Sanders, A. E. 1978. Mammals. Pages 296–308. in R. G. Zingmark, ed. *An annotated checklist of the biota of the coastal zone of South Carolina*. University of South Carolina Press, Columbia.
- Schubauer, J. P., and C. S. Hopkinson. 1984. Above- and belowground emergent macrophyte production and turnover in a coastal marsh ecosystem, Georgia. *Limnol. Oceanogr.* 29:1052–1065.
- Sharp, H. F., Jr. 1967. Food ecology of the rice rat, *Oryzomys palustris* (Harlin), in a Georgia salt marsh system. *J. Mammal.* 48:557–563.
- Silberhorn, G. M. 1976. Tidal wetland plants of Virginia. *Va. Inst. Mar. Sci. Educ. Ser.* 19. 86 pp.
- Smalley, A. E. 1960. Energy flow of a salt marsh grasshopper population. *Ecology* 41:672–677.
- Smith, K. K., R. E. Good, and N. F. Good. 1979. Production dynamics for above- and belowground components of a New Jersey *Spartina alterniflora* tidal marsh. *Estuarine Coastal Mar. Sci.* 9:189–201.
- Sottile, W. S. 1974. Studies of microbial production and utilization of dissolved organic carbon in a Georgia salt marsh-estuarine ecosystem. Ph.D. dissertation, University of Georgia, Athens. 153 pp.
- Spinner, G. P. 1969. The wildlife wetlands and shellfish areas of the Atlantic coastal zone. Plates 1–17 in Wilfred Webster, ed. *Serial atlas of the marine environment*, Folio 18. American Geographical Society, New York.
- Stevens, S. A. 1983. Ecology of intertidal oyster reefs: food, distribution and carbon/nutrient flow. Ph.D. dissertation, University of Georgia, Athens. 195 pp.
- Stout, J. P. 1984. The ecology of irregularly flooded salt marshes of the northeastern Gulf of Mexico: a community profile. U.S. Fish Wildl. Serv., *Biol. Rep.* 85(7.1). 98 pp.
- Stroud, L. M. 1976. Net primary production of belowground material and carbohydrate patterns in two height forms of *Spartina alterniflora* in two North Carolina marshes. Ph.D. thesis, North Carolina State University, Raleigh. 140 pp.
- Stroud, L. M., and A. W. Cooper. 1969. Color-infrared aerial photographic interpretation and net primary productivity of a regularly-flooded North Carolina salt marsh. *Univ. N.C., Water Resour. Res. Inst. Rep.* 14. 86 pp.
- Sullivan, J. J., and F. C. Daiber. 1974. Response in production of cordgrass, *Spartina alterniflora*. *J. Exp. Bot.* 17:355–361.
- Teal, J. M. 1962. Energy flow in the salt marsh ecosystem of Georgia. *Ecology* 43:614–624.

- Teal, J. M., and J. Kanwisher. 1961. Gas exchange in a Georgia salt marsh. *Limnol. Oceanogr.* 6:388-399.
- Teal, J. M., and J. Kanwisher. 1966. Gas transport in the marsh grass, *Spartina alterniflora*. *J. Exp. Bot.* 17:355-361.
- Thomas, J. P. 1966. Influence of the Altamaha River on primary production beyond the mouth of the river. M.S. thesis, University of Georgia, Athens. 88 pp.
- Valiela, I., J. M. Teal, and N. Y. Persson. 1976. Production and dynamics of experimentally enriched salt marsh vegetation: belowground biomass. *Limnol. Oceanogr.* 21:245-252.
- Vetter, E. F. 1983. The ecology of the white shrimp (*Penaeus setiferus*): habitat selection, carbon and nitrogen metabolism and simulation modeling. Ph.D. dissertation, University of Georgia, Athens. 151 pp.
- Wadsworth, J. R., Jr. 1979. Duplin River tidal system: Sapelo Island, Georgia. Map reprinted in Jan. 1982 by The University of Georgia Marine Institute, Sapelo Island, Georgia.
- Waits, E. D. 1967. Net primary productivity of an irregularly flooded North Carolina salt marsh. Ph.D. dissertation, North Carolina State University, Raleigh. 113 pp.
- Wass, M. L., and T. D. Wright. 1969. Coastal wetlands of Virginia. Interim report to the Governor and General Assembly. Applied Marine Science and Ocean Engineering. Va. Inst. Mar. Sci. Spec. Rep. 10. 154 pp.
- Wiegert, R. G. 1979. Ecological processes characteristic of coastal *Spartina* marshes of the south-eastern U.S.A. Pages 467-490 in R. L. Jefferies and A. J. Davy, eds. Ecological processes in coastal environments. Blackwell, Oxford, England.
- Wiegert, R. G. 1986. Modeling spatial and temporal variability in a salt marsh: sensitivity to rates of primary production, tidal migration and microbial degradation. Pages 405-426 in D. A. Wolfe, ed. Estuarine variability. Academic Press, New York.
- Wiegert, R. G., A. G. Chalmers, and P. F. Randerson. 1983. Productivity gradients in salt marshes: the response of *Spartina alterniflora* to experimentally manipulated soil water movement. *Oikos* 41:1-6.
- Wiegert, R. G., R. R. Christian, J. L. Gallagher, J. R. Hall, R. D. H. Jones, and R. L. Wetzel. 1975. A preliminary ecosystem model of coastal Georgia *Spartina* marsh. Pages 583-602 in L. E. Cronin, ed. Estuarine research. Vol. 1. Academic Press, New York.
- Wiegert, R. G., and F. C. Evans. 1964. Primary production and the disappearance of dead vegetation on an old field in south-eastern Michigan. *Ecology* 45:49-63.
- Wiegert, R. G., and F. C. Evans. 1967. Investigations of secondary productivity in grasslands. Pages 499-518 in K. Petruszewicz, ed. Secondary productivity of terrestrial ecosystems. Polish Academy of Sciences, Cracow.
- Wiegert, R. G., and D. F. Owen. 1971. Trophic structure, available resources and population density in terrestrial vs. aquatic ecosystems. *J. Theor. Biol.* 30:69-81.
- Wiegert, R. G., L. R. Pomeroy, and W. J. Wiebe. 1981. Ecology of salt marshes: an introduction. Pages 2-19 in L. R. Pomeroy and R. G. Wiegert, eds. Ecology of a salt marsh. Springer-Verlag New York Inc., New York.
- Wiegert, R. G., and R. L. Wetzel. 1979. Simulation experiments with a fourteen-compartment model of a *Spartina* salt marsh. Pages 7-39 in R. Dame, ed. Marsh estuarine system simulation. University of South Carolina Press, Columbia.
- Williams, P. M., H. Oeschger, and H. Kinney. 1969. Natural radiocarbon activity of the dissolved organic carbon in the northeast Pacific Ocean. *Nature (Lond.)* 225:256-258.
- Williams, R. B. 1962. The ecology of diatom populations in a Georgia salt marsh. Ph.D. dissertation, Harvard University, Cambridge. 146 pp.
- Williams, R. B. and M. B. Murdoch. 1968. Compartmental analysis of production and decay of *Juncus roemerianus*. *Assoc. Southeast. Biol. Bull.* 13:59.
- Wise, E. A. 1970. A study of energy fixation and net production of plant communities in salt marshes of Back River, Va. Ph.D. dissertation, University of Illinois, Champaign. Abstracted in Coastal marsh productivity: a bibliography. 1977. U.S. Fish Wildl. Serv., FWS/OBS-77/3. 300 pp.
- Zingmark, R. G. 1978. An annotated checklist of the biota of the coastal zone of South Carolina. University of South Carolina Press, Columbia. 364 pp.
- Zingmark, R. G., and G. Satcher. 1984. Long-term patterns of phytoplankton standing crop and productivity in a salt marsh estuarine system. *J. Phycol.* 20 (suppl.):13.

Appendix A. Selected List of Vascular Plants in Tidal Salt Marshes of the Southeastern Atlantic Coast

Macrophytes

- Order Pandanales
 Family Typhaceae
Typha angustifolia L.—narrowleaf cattail
T. domingensis Persoon—southern cattail
- Order Alismales
 Family Juncaginaceae
Triglochin striatum R. and P.—arrowgrass
 Family Alismataceae
Sagittaria subulata Buch.
- Order Graminales
 Family Poaceae
Distichlis spicata (L.) Greene—saltgrass
Paspalum distichum L.—knotgrass
Polypogon monspeliensis (L.) Desf. rabbitfoot grass
P. maritimus Willd.
Setaria magna Grisebach—giant foxtailgrass
Spartina alterniflora Loisel—smooth cordgrass
S. bakeri Merr.
S. cynosuroides (L.) Roth—big cordgrass
S. patens (Aiton) Muhl.—saltmeadow cordgrass
Sporobolus virginicus (L.) Kunth—coastal dropseed
Zizania aquatica (L.)—wildrice
Zizaniopsis miliaceae (Michaux) Doell and Ascherso—southern wildrice
- Family Cyperaceae
Cladium jamaicense Crantz—sawgrass
Cyperus filicinus Vahl—umbrella sedge
Cyperus haspan L.—leafless sedge
Eleocharis albida Torrey—spikerush
E. flavescens (Poir.) Urban
Fimbristylis castanea (Michaux) Vahl
Scirpus americanus Persoon—chairmaker's rush
S. americana Gray—Olney three-square
S. robustus Pursh—salt marsh bulrush
- Order Liliales
 Family Juncaceae
Juncus marginatus Rostk.
J. roemerianus Scheele—black needlerush
- Order Caryophyllales
 Family Polygonaceae
Polygonum glaucum Nutt.—seaside knotweed
 Family Chenopodiaceae
Atriplex arenaria Nutt.—sea-beach atriplex
A. patula L.—sea-beach atriplex
Salicornia europaea L.—glasswort
S. virginica L.—glasswort
Salsola kali L.—Russian-thistle
- Suaeda linearis* (Ell.) Moq.—sea-blite
S. maritima (L.) Dum.
 Family Amaranthaceae
Amaranthus cannabinus L.—waterhemp
 Family Caryophyllaceae
Spergularia marina (L.) Griseb.—sand spurrey
- Order Batidales
 Family Bataceae
Batis maritima L.—batis
 Family Brassicaceae
Cakile edentula (Bigelow) Hooker—sea rocket
- Order Malvales
 Family Malvaceae
Hibiscus mosheutos L.—rosemallow
Kosteletzkya virginica (L.) Presl—seashore mallow
- Order Myrtales
 Family Lythraceae
Lythrum lineare L.—loosestrife
- Order Primulales
 Family Plumbaginaceae
Limonium carolinianum (Walt.) Britt.—sea-lavender
L. nashii Small—sea-lavender
- Order Gentianales
 Family Gentianaceae
Sabatia stellaris Pursh—marsh-pink
S. dodecandra (L.) B.S.P.—large marsh-pink
- Order Apocynales
 Family Asclepiadaceae
Cynanchum angustifolium Pers.—sand-vine
- Order Polemoniales
 Family Boraginaceae
Heliotropium curassavicum L.—seaside heliotrope
- Order Asterales
 Family Asteraceae
Aster novi-belgii L.—New York aster
A. subulatus Michx.—annual saltmarsh-aster
A. tenuifolius L.—perennial saltmarsh-aster
Baccharis angustifolia Michx.—false willow
B. halimifolia L.—groundsel tree
Borrichia frutescens (L.) DC.—sea oxeye
Iva frutescens L.—marsh-elder
Solidago sempervirens L.—seaside goldenrod

Common Trees

- Family Aquifoliaceae
Ilex vomitoria Ait.—yaupon
- Family Cupressaceae
Juniperus silicicola (Small) Bailey—southern red cedar

Family myricaceae

Myrica cerifera L.—waxmyrtle*M. pensylvanica* Loisel—bayberry

Schult.—cabbage palm

Family Rutaceae

Zanthoxylum clava-herculis L.—Pricklyash**Less Common Trees**

Family Oleaceae

Forestiera segregata (Jacq.) Krug and urban—

Florida privet

Family Palmae

Sabal palmetto (walt.) Lodd. ex. Schult. and**Shrub Vines**

Family Vitaceae

Ampelopsis arborea (L.) Koehne—peppervine

Family Vitaceae

Vitis aestivalis Michx.—summer grape

Appendix B. Selected List of Invertebrates (Excluding Insects and Arachnids) in Tidal Salt Marshes of the Southeastern Atlantic Coast^a

Phylum Cnidaria

Class Anthozoa

- Order Actinaria
- Family Edwardsiidae
- Nematosella vectensis*

Phylum Rhynchocoela

Class Anopla

- Order Paleonemertea
- Family Carinomidae
- Carinoma tremaphoras*
- Order Heteronemertea
- Family Lineidae
- Lineus socialis*

Class Enopla

- Order Hoplonemertea
- Family Amphiporidae
- Amphiporus ochraceus*

Phylum Annelida

Class Oligochaeta

- Order Tubificida
- Family Enchytraeidae
- Enchytraeus* spp.
- Family Naididae
- Paranais frici*
- Family Tubificidae
- Monopylephorus evertus*
- Tubificoides brownae*

Class Polychaeta

Subclass Errantia

- Order Eunicida
- Family Arabellidae
- Drilonereis magna*
- Family Lumbrineridae
- Lumbrineris tenuis*
- Family Onuphidae
- Diopatra cuprea*
- Order Phyllodocida
- Family Glyceridae
- Glycera americana*
- Family Nereidae
- Laenonereis culveri*
- Namalycastis abiuma*
- Neanthes succinea*

- Family Phyllodocidae

Subclass Sedentaria

- Order Capitellida
- Family Capitellidae
- Capitella capitata*
- Heteromastus filiformis*
- Family Maldanidae
- Branchioasychis americana*
- Order Orbiniida
- Family Orbiniidae
- Haploscoloplos robustus*
- Scoloplos fragilis*
- Order Sabellida
- Family Sabellidae
- Manayunkia aestuarina*
- Order Spionida
- Family Spionidae
- Streblospio benedicti*
- Order Terebellida
- Family Ampharetidae
- Hobsonia florida*
- Family Pectinariidae
- Cistenides gouldii*
- Family Terebellidae
- Amphitrite ornata*

Phylum Mollusca

Class Gastropoda

Subclass Prosobranchia

- Order Archaeogastropoda
- Family Neritidae
- Neritina usnea*
- Order Mesogastropoda
- Family Assimineidae
- Assiminea succinea*
- Family Hydrobiidae
- Hydrobia* spp.
- Littoridinops tenuipes*
- Onobops jacksoni*
- Family Littorinidae
- Littorina irrorata*
- Family Potamididae
- Cerithidea costata*
- C. scalariformis*
- Order Neogastropoda
- Family Nassariidae
- Ilyanassa obsoleta*

- Subclass Pulmonata**
 Order Basommatophora
 Family Ellobiidae
Decracia floridana
Melampus bidentatus
- Class Bivalvia**
Subclass Pteriomorpha
 Order Mytiloida
 Family Mytilidae
Amygdalum papyrium
Geukensia demissa
Iscahdium recurvum
 Family Ostreidae
Crassostrea virginica
- Subclass Heterodonta**
 Order Veneroida
 Family Corbiculidae
Polymesoda caroliniana
 Family Cyrenoididae
Cyrenoida floridana
 Family Mactridae
Mulinia lateralis
 Family Solecurtidae
Tagelus plebeius
 Family Veneridae
Gemma gemma
- Phylum Arthropoda**
Subphylum Crustacea
Class Cirripedia
 Order Thoracica
 Family Chthamalidae
Chthamalus fragilis
- Class Malacostraca**
 Order Decapoda
 Suborder Pleocyemata
 Infraorder Caridea
 Family Alpheidae
Alpheus heterochaelis
 Family Palaemonidae
Palaemonetes pugio
P. vulgaris
 Infraorder Brachyura
 Family Grapsidae
Sesarma cinerium
S. reticulatum
 Family Ocypodidae
Uca minax
U. pugnator
U. pugnax
 Family Pinnotheridae
Pinnixia chaetoptera
 Family Portunidae
Calinectes sapidus
 Family Xanthidae
Eurypanopeus depressus
Eurytium limosum
Panopeus obesus
Rithropanopeus harrisi
 Superorder Peracarida
 Order Tanaidacea
 Family Paratanaididae
Hargeria rapax
 Order Isopoda
 Family Anthuridae
Cyathura polita
 Family Bopyridae
Probopyrus pandalicola
P. pugio
 Family Idoteidae
Edotea montosa
 Family Munnidae
Munna reynoldsi
 Family Sphaeromidae
Cassidinidea ovalis
 Order Mysidacea
Neomysis americana
 Order Amphipoda
 Family Aoridae
Grandidierella bonnieroides
 Family Gammaridae
Gammarus mucronatus
G. palustris
 Family Hyalidae
Parhyale hawaiiensis
 Family Melitidae
Melita nitida
 Family Talitridae
Orchestia grillus
O. platensis
O. uhleri

*Gosner 1971; Barnes 1980; Heard 1982; Fox and Ruppert 1985; D. Bishop, University of Georgia, personal communication; G. Thomas, University of Georgia, personal communication.

Appendix C. Selected List of Insect and Arachnid Families in Tidal Salt Marshes of the Southeastern Atlantic Coast^a

Class Arachnida

- Order Pseudoscorpionida
 - Family Cheliferae
- Order Araneae
 - Family Dictynidae
 - Family Gnaphosidae
 - Family Clubionidae
 - Family Thomisidae
 - Family Salticidae
 - Family Pisauridae
 - Family Lycosidae
 - Family Theridiidae
 - Family Araneidae
 - Family Tetragnathidae
 - Family Micryphantidae
- Order Acarina
 - Family Trombidiidae

Class Insecta

Subclass Apterygota

- Order Collembola
 - Family Isotomidae
 - Family Entomobryidae
 - Family Sminthuridae
 - Family Exopterygota

Subclass Terygota

- Order Odonata
 - Family Aeschnidae
 - Family Libellulidae
 - Family Agrionidae
- Order Dermaptera
 - Family Forficulidae
- Order Orthoptera
 - Family Mantidae
 - Family Gryllidae
 - Family Tetrigidae
 - Family Acrididae
 - Family Tettigoniidae
- Order Hemiptera
 - Family Scutellaridae
 - Family Corimelaenidae
 - Family Pentatomidae
 - Family Coreidae
 - Family Neididae
 - Family Lygaeidae
 - Family Reduviidae

- Family Nabidae
- Family Miridae
- Family Hydrometridae
- Family Mesoveliidae
- Family Gerridae
- Family Saldidae
- Family Belostomatidae
- Family Corixidae

Order Homoptera

- Family Cicadidae
- Family Membracidae
- Family Cercopidae
- Family Cicadellidae
- Family Cixiidae
- Family Derbidae
- Family Acanaloniidae
- Family Dictyopharidae
- Family Issidae
- Family Delphacidae
- Family Aphidae
- Family Pysyllidae
- Family Pseudococcidae
- Family Diaspididae

Order Thysanoptera

- Family Thripidae
- Family Phloeothripidae

Endopterygota

- Order Neuroptera
 - Family Mantispidae
 - Family Myrmeleonidae

Order Coleoptera

- Family Cicindellidae
- Family Dytiscidae
- Family Gyrinidae
- Family Hydrophyllidae
- Family Staphylinidae
- Family Scarabaeidae
- Family Eucinetidae
- Family Buprestidae
- Family Elateridae
- Family Cantharidae
- Family Lampyridae
- Family Cleridae
- Family Melyridae
- Family Mordellidae
- Family Oedemeridae
- Family Languriidae

- Family Coccinellidae
- Family Orthoperidae
- Family Chrysomelidae
- Family Phalacridae
- Family Anthribidae
- Family Curculionidae

Order Lepidoptera

- Family Pyralidae
- Family Geometridae
- Family Noctuidae
- Family Lycaenidae
- Family Hesperidae

Order Diptera

- Family Tipulidae
- Family Culicidae
- Family Ceratopogonidae
- Family Chironomidae
- Family Sciaridae
- Family Tabanidae
- Family Asilidae
- Family Empididae
- Family Dolichopodidae
- Family Phoridae
- Family Pipunculidae
- Family Conopidae
- Family Syrphidae
- Family Otitidae
- Family Platystomatidae
- Family Tephritidae
- Family Sciomyzidae
- Family Ephydriidae
- Family Chamaemyiidae
- Family Chloropidae
- Family Anthomyiidae
- Family Muscidae
- Family Callophoridae
- Family Sarcophagidae

Order Hymenoptera

- Family Braconidae
- Family Ichneumonidae
- Family Eulophidae
- Family Encyrtidae
- Family Eupelmidae
- Family Pteromalidae
- Family Eurytomidae
- Family Chalcididae
- Family Elasmidae

Family Cynipidae
Family Scelionidae
Family Formicidae
Family Chrysididae

Family Tiphiidae
Family Multillidae
Family Vespidae
Family Pompilidae

Family Sphecidae
Family Halictidae
Family Apidae

^aDavis 1978; P. A. Opler 1984; A. Hurn, University Georgia, personal communication.

Appendix D. Selected List of Fish in Tidal Salt Marshes of the Southeastern Atlantic Coast^a

Subphylum Vertebrata

Superclass Pisces

Class Chondrichthyes

Order Rajiformes

Family Dasyatidae

Dasyatis americana Hildebrand and Schroeder—southern stingray

D. sabina (Lesueur)—Atlantic stingray

Class Osteichthyes

Order Elopiformes

Family Elopidae

Elops saurus L.—ladyfish

Order Anguilliformes

Family Anguillidae

Anguilla rostrata (Lesueur)—American eel

Family Ophichthidae

Myrophis punctatus Lütken—speckled worm eel

Order Clupeiformes

Family Clupeidae

Brevoortia smithi Hildebrand—yellowfin menhaden

B. tyrannus (Latrobe)—Atlantic menhaden

Dorosoma cepedianum (Lesueur)—gizzard shad

D. petenense (Günther)—threadfin shad

Harengula jaguana Poey—scaled sardine

Opisthonema oglinum (Lesueur)—Atlantic thread herring

Family Engraulidae

Anchoa hepsetus (L.)—striped anchovy

A. mitchilli (Valenciennes)—bay anchovy

Order Batrachoidiformes

Family Batrachoididae

Opsanus tau (L.)—oyster toadfish

Order Gadiformes

Family Ophidiidae

Ophidion marginatum (DeKay)—striped cusk-eel

Order Atheriniformes

Family Belontiidae

Strongylura marina (Walbaum)—Atlantic needlefish

Family Cyprinodontidae

Cyprinodon variegatus Lacepède—sheepshead minnow

Fundulus confluentus Goode and Bean—marsh killifish

F. diaphanus (Lesueur)—banded killifish

F. heteroclitus (L.)—mummichog

F. luciae (Baird)—spotfin killifish

F. majalis (Walbaum)—striped killifish

Lucania parva (Baird)—rainwater killifish

Family Poeciliidae

Gambusia affinis (Baird and Girard)—mosquitofish

Poecilia latipinna (Lesueur)—sailfin molly

Family Atherinidae

Membras martinica (Valenciennes)—rough silver-side

Menidia beryllina (Cope)—inland silverside

M. menidia (L.)—Atlantic silverside

Order Gasterosteiformes

Family Syngnathidae

Syngnathus louisianae Günther—chain pipefish

Order Perciformes

Family Centropomidae

Centropomus undecimalis (Bloch)—snook

Family Serranidae

Centropristis striata (L.)—black sea bass

Mycteroperca microlepis (Goode and Bean)—gag

Family Pomatomidae

Pomatomus saltatrix (L.)—bluefish

Family Carangidae

Caranx hippos (L.)—crevalle jack

C. latus Agassiz—horse-eye jack

Chloroscombrus chrysurus (L.)—Atlantic bumper

Oligoplites saurus (Schneider)—leatherjacket

Selene vomer (L.)—lookdown

Trachinotus carolinus (L.)—Florida pompano

T. falcatus (L.)—permit

Family Lutjanidae

Lutjanus griseus (L.)—gray snapper

L. synagris (L.)—lane snapper

Family Gerreidae

Diapterus auratus Ranzani—Irish pompano

D. plumieri (Cuvier)—striped mojarra

Eucinostomus argenteus Baird—spotfin mojarra

E. gula (Quoy and Gaimard)—silver jenny

E. melanopterus (Bleeker)—flagfin mojarra

Family Haemulidae

Orthopristis chrysoptera (L.)—pigfish

Family Sparidae

Archosargus probatocephalus (Walbaum)—sheepshead

Lagodon rhomboides (L.)—pinfish

Family Sciaenidae

Bairdiella chrysoura (Lacepède)—silver perch

Cynoscion nebulosus (Cuvier)—spotted seatrout

C. nothus (Holbrook)—silver seatrout

C. regalis (Bloch and Schneider)—weakfish

Larimus fasciatus Holdbrook—banded drum

Leiostomus xanthurus Lacepède—spot

Menticirrhus littoralis (Holbrook)—gulf kingfish
M. saxatilis (Bloch and Schneider)—northern kingfish
Micropogonias undulatus (L.)—Atlantic croaker
Pogonias cromis (L.)—black drum
Sciaenops ocellatus (L.)—red drum
Stellifer lanceolatus (Holbrook)—star drum
 Family Mugilidae
Mugil cephalus L.—striped mullet
M. curema Valenciennes—white mullet
 Family Ehippidae
Chaetodipterus faber (Broussonet)—Atlantic spadefish
 Family Uranoscopidae
Astroscopus y-graecum (Cuvier)—southern stargazer
 Family Blenniidae
Chasmodes bosquianus (Lacepède)—striped blenny
Hypsoblennius hentzi (Lesueur)—feather blenny
H. ionthas (Jordan and Gilbert)—freckled blenny
 Family Eleotridae
Dormitator maculatus (Bloch)—fat sleeper
 Family Gobiidae
Gobionellus boleosoma (Jordan and Gilbert)—darter goby
G. hastatus (Girard)—sharptail goby
Gobiosoma bosci (Lecepède)—naked goby
G. ginsburgi Hildebrand and Schroeder—seaboard goby
 Family Stromateidae
Peprilus alepidotus (L.)—harvestfish

P. triacanthus (Peck)—butterfish
 Family Scorpaenidae
Scorpaena plumieri Bloch—spotted scorpionfish
 Family Triglidae
Prionotus evolans (L.)—striped searobin
P. tribulus Cuvier—bighead searobin
 Order Pleuronectiformes
 Family Bothidae
Ancylosetta quadrocellata Gill—ocellated flounder
Citharichthys spilopterus Günther—bay whiff
Etropus crossotus Jordan and Gilbert—fringed flounder
E. rimosus Goode and Bean—gray flounder
Paralichthys albigutta Jordan and Gilbert—Gulf flounder
P. dentatus (L.)—summer flounder
P. lethostigma Jordan and Gilbert—southern flounder
Scophthalmus aquosus (Mitchill)—windowpane
 Family Soleidae
Trinectes maculatus (Bloch and Schneider)—hogchoker
 Family Cynoglossidae
Symphurus plagiusa (L.)—blackcheek tonguefish
 Order Tetraodontiformes
 Family Balistidae
Aluterus schoepfi (Walbaum)—orange filefish
Monacanthus hispidus (L.)—planehead filefish
 Family Diodontidae
Chilomycterus schoepfi (Walbaum)—striped burrfish

^aDahlberg 1975; Poole 1978; Robbins et al. 1980; S. Hale, University of Georgia, personal communication.

Appendix E. Reptiles in Tidal Salt Marshes of the Southeastern Atlantic Coast^a

Class Reptilia

Order Testudines

Family Kinosternidae

Kinosternon subrubrum subrubrum (Lacepède)—eastern mud turtle

Family Emydidae

Malaclemys terrapin centrata (Latreille)—Carolina diamondback terrapin

Order Crocodylia

Family Alligatoridae

Alligator mississippiensis (Daudin)—American alligator

Order Squamata

Suborder Serpentes

Family Colubridae

Elaphe obsoleta quadrivittata (Holbrook)—yellow rat snake

Nerodia fasciata fasciata (L.)—banded water snake

Family Viperidae

Agkistrodon piscivorus piscivorus (Lacepède)—eastern cottonmouth

^aGibbons 1978.

Appendix F. Selected List of Birds Occurring in Tidal Salt Marshes of the Southeastern Atlantic Coast^a

Class Aves

- Order Ciconiiformes
 Family Ardeidae
Botaurus lentiginosus (Rackett)—American bittern
Ixobrychus exilis exilis (Gmelin)—least bittern
Ardea herodias L.—great blue heron, great white heron
Casmerodius albus egretta (Gmelin)—great egret
Egretta thula thula (Molina)—snowy egret
Egretta caerulea caerulea (L.)—little blue heron
Egretta tricolor ruficollis (Gosse)—tricolored Louisiana heron
Egretta rufescens rufescens (Gmelin)—reddish egret
Butorides striatus virescens (L.)—green-backed heron
Nycticorax nycticorax hoactli (Gmelin)—black-crowned night-heron
N. violaceus violaceus (L.)—yellow-crowned night-heron
 Family Threskiornithidae
Eudocimus albus (L.)—white ibis
Plegadis falcinellus falcinellus (Linnaeus)—glossy ibis
Ajaia ajaja (L.)—roseate spoonbill
 Family Ciconiidae
Mycteria americana L.—wood stork
 Order Anseriformes
 Family Anatidae
Cygnus columbianus (Ord)—tundra swan
Chen caerulescens (L.)—snow goose
Branta bernicla hrota (Müller)—brant
Anas crecca carolinensis (Gmelin)—green-winged teal
A. rubripes Brewster—American black duck
Bucephala clangula americana (Bonaparte)—common goldeneye
B. albeola (L.)—bufflehead
 Order Falconiformes
 Family Cathartidae
Coragyps atratus (Bechstein)—black vulture
Cathartes aura septentrionalis Wied—turkey vulture
 Family Accipitridae
Pandion haliaetus—Osprey
Circus cyaneus hudsonius (Linnaeus)—northern harrier
Haliaeetus leucocephalus—bald eagle
 Family Falconidae
Falco sparverius L.—American kestrel
Falco columbarius L.—merlin
Falco peregrinus anatum Bonaparte—peregrine falcon
 Order Gruiformes
 Family Rallidae
Coturnicops noveboracensis noveboracensis (Gmelin)—yellow rail
Laterallus jamaicensis jamaicensis (Gmelin)—black rail
Rallus longirostris Boddaert—clapper rail
Porzana carolina (Linnaeus)—sora
 Order Charadriiformes
 Family Charadriidae
Pluvialis dominica dominica (Müller)—lesser golden-plover
Charadrius wilsonia wilsonia Ord—Wilson's plover
C. vociferus vociferus L.—killdeer
 Family Haematopodidae
Haematopus palliatus palliatus Temminck—American oystercatcher
 Family Recurvirostridae
Himantopus mexicanus mexicanus (Müller)—black-necked stilt
Recurvirostra americana Gmelin—American avocet
 Family Scolopacidae
Tringa melanoleuca (Gmelin)—greater yellowlegs
T. flavipes (Gmelin)—lesser yellowlegs
Catoptrophorus semipalmatus (Gmelin)—willet
Actitis macularia (L.)—spotted sandpiper
Arenaria interpres morinella (L.)—ruddy turnstone
Calidris pusilla (L.)—semipalmated sandpiper
C. minutilla (Vieillot)—least sandpiper
C. alpina (L.)—dunlin
Limnodromus griseus (Gmelin)—short-billed dowitcher
 Family Laridae
Larus atricilla L.—laughing gull
L. delawarensis Ord—ring-billed gull
Sterna nilotica aranea (Wilson)—gull-billed tern
S. caspia Pallas—Caspian tern
S. maxima maxima Boddaert—royal tern
S. sandvicensis acuflavidus (Cabot)—Sandwich tern

Sterna antillarum (Lesson)—least tern
Chlidonias niger surinamensis (Gmelin)—black tern
Rynchops niger niger L.—black skimmer
 Order Strigiformes
 Family Strigidae
Asio flammeus flammeus (Pontoppidan)—short-eared owl
 Order Coraciiformes
 Family Alcedinidae
Ceryle alcyon alcyon (L.)—belted kingfisher
 Order Passeriformes
 Family Corvidae

Corvus ossifragus Wilson—fish crow
 Family Troglodytidae
Cistothorus platensis stellaris (Naumann)—sedge wren
C. palustris (Wilson)—marsh wren
 Family Emberizidae
Geothlypis trichas (L.)—common yellowthroat
Ammodramus leconteii (Audubon)—LeConte's sparrow
A. caudacutus (Gmelin)—sharp-tailed sparrow
A. maritimas (Wilson)—seaside sparrow
Agelaius phoeniceus (L.)—red-winged blackbird
Quiscalus major Vieillot—boat-tailed grackle

^aForsythe 1978; nomenclature follows. The A.O.U. check-list of North American Birds, 6th edition.

Appendix G. Selected Mammals in Tidal Salt Marshes of the Southeastern Atlantic Coast^a

Class Mammalia

Order Insectivora

Family Soricidae

Cryptotis parva parva (Say)—least shrew

Family Talpidae

Scalopus aquaticus howelli (Jackson)—eastern mole

Order Primates

Family Hominidae

Homo sapiens L.—human

Order Lagomorpha

Family Leporidae

Sylvilagus palustris palustris (Bachman)—marsh rabbit

Order Rodentia

Family Muridae

Microtus pennsylvanicus pennsylvanicus (Ord)—meadow vole

Oryzomys palustris palustris (Harlan)—marsh rice rat

Peromyscus gossypinus gossypinus (LeConte)—cotton mouse

Sigmodon hispidus hispidus Say and Ord—cotton rat

Rattus norvegicus norvegicus (Berkenhout)—Norway rat

Order Carnivora

Family Procyonidae

Procyon lotor solutus Nelson and Goldman—raccoon

Family Mustelidae

Lutra canadensis lataxina F. Cuvier—river otter

Mustela vison lutensis (Bangs)—mink

Order Cetacea

Family Delphinidae

Tursiops truncatus (Montague)—bottle-nosed dolphin

Order Sirenia

Family Trichechidae

Trichechus manatus L.—manatee

Order Artiodactyla

Family Cervidae

Odocoileus virginianus virginianus (Zimmerman)—white-tailed deer

^aSanders 1978.