Ann. Rev. Ecol. Syst. 1988. 19:147–76

COMPARATIVE ECOLOGY OF TIDAL FRESHWATER AND SALT MARSHES

William E. Odum

Department of Environmental Sciences, Clark Hall, University of Virginia, Charlottesville, Virginia 22903

INTRODUCTION

After several decades of intensive research in salt marshes, both community structure and basic ecological processes are reasonably well understood (44, 50, 78, 88). Further up the estuary, however, the often extensive tracts of tidal freshwater wetlands (Figure 1) are not so well researched (52, 99, 113). Historically, tidal freshwater environments have been ignored by limnologists because of the presence of oceanic tidal influence, and neglected by marine ecologists because they are bathed by freshwater and inhabited primarily by freshwater organisms.

Objectives

This review compares the modest amount of information concerning physical and biological aspects of tidal freshwater wetland systems with the more substantial literature about salt marsh systems in order to answer several fundamental questions. (*a*) What are the community and ecosystem-level effects of greatly lowering concentrations of dissolved salts and sulfur while maintaining similar tidal amplitudes? (*b*) Are there, as a result, significant differences in community structure? (*c*) Do the same taxonomic groups function in the same way in tidal freshwater marshes and in salt marshes? (*d*) Are the basic ecological processes such as primary production and decomposition similar in the two environments?

In analyzing these points we must remember that estuaries are complex and dynamic gradients, not always linear (43). Variables such as salinity, tem-

0066-4162/88/1120-0147$02.00

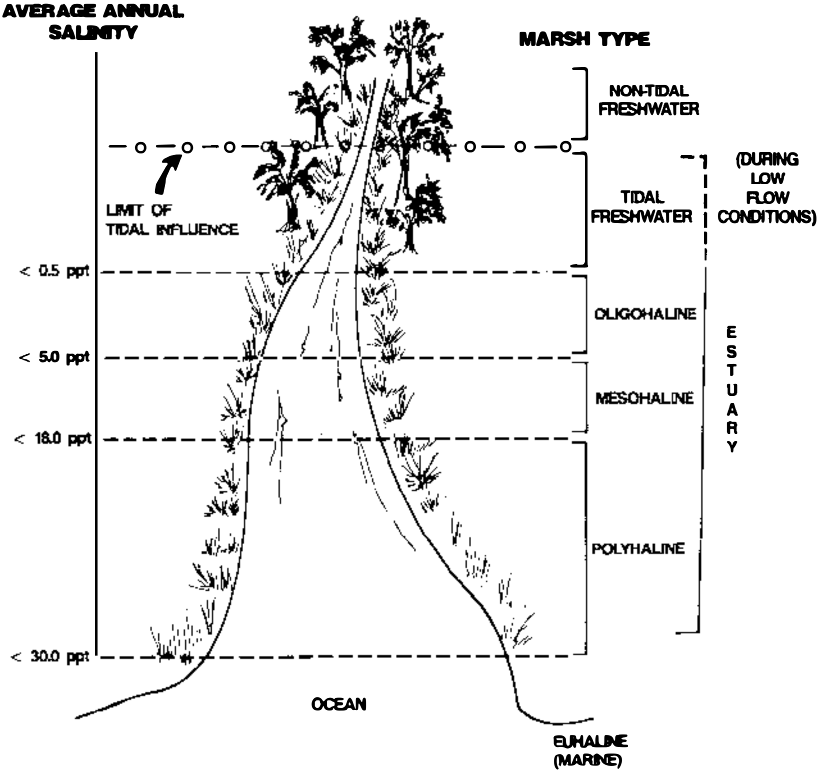

Figure 1 The relationship between marsh type and average annual salinity (values are approximate only). Terminology is based on Cowardin et al (24). From Odum et al (99).

perature, and dissolved oxygen vary spatially and temporally in often confusing three-dimensional patterns.

For simplicity, I have chosen the ends of the salinity gradient (tidal freshwater and salt marshes) and largely ignored the oligohaline and mesohaline wetlands that lie in the middle. This choice was made partly because the latter are so little-studied and partly because the physical conditions in the center of the gradient are even more complex and ever-changing than at the ends.

Finally, many of the ideas discussed here are both preliminary and hypothetical and require considerable testing. Moreover, most of the data reviewed comes from the Gulf and east coasts of North America at temperate latitudes. It remains to be seen whether the present hypotheses adequately explain conditions on other continents or at higher and lower latitudes.

COMPARISON OF PHYSICAL CHARACTERISTICS

Understanding coastal wetland ecology requires a firm grasp of the physical processes that ultimately control biological interactions. In Table 1, I have compared selected physical characteristics of tidal freshwater and salt marshes. Many other useful comparisons (e.g. evapotranspiration, subsurface hydrology) exist for which there are insufficient comparative data.

Geographical Distribution

Both tidal freshwater and salt marshes are distributed worldwide (23). In fact, their distributions are similar, except that tidal freshwater marshes usually occur in association with large river systems (e.g. the Delaware, Hudson, Potomac, and St. Lawrence in North America; the Rhine and Thames in

Table 1 Comparison of physical characteristics between tidal freshwater marshes and salt marshes

	Tidal freshwater marsh	Salt marsh
Location	Head of the estuary (above the oligohaline zone)	Mid and lower estuary
Geographical distribution	Worldwide, usually associated with rivers	Worldwide, not always associated with rivers
Salinity	Annual average below 0.5 ppt	Annual average between 18.0 and 35.0 ppt
Tidal range	Ocean-derived lunar tide, often greater amplitude than nearby salt marshes	Ocean-derived lunar tide
Sediments	Silt-clay, high organic content, low-moderate root and peat content	More sand, lower organic content, higher peat and root content
Sediment erodability	High erodability (particularly in the low marsh)	Generally lower erodability
Streambank morphology	Low gradient, little undercutting	Steeper gradient, more undercutting
Stream channel morphology	Low sinuosity	Moderate to high sinuosity
Dissolved sulfur	Trace (approximately 1 ppm)	Very high (approximately 2500 ppm)
Sediment redox potential	Moderate to strongly reducing (multiple redox pairs)	Strongly reducing (sulfur redox pairs most important)
Reduced iron-sulfur compounds	Rare or absent	Plentiful
Dissolved and particulate organic carbon	High concentrations	Moderate to low concentrations

Europe; the Ganges and Yellow Rivers in Asia). While both types of marshes reach their greatest extent at temperate latitudes, similar types of wetlands occur from the subarctic to the equator (23, 49, 97). For example, in the tropics, mangrove forests largely replace salt marshes at the mouth of the estuary, while tropical forests with ferns, Nepa palms, and herbaceous plants dominate tidal freshwater.

Salinity

By definition (24) the tidal freshwater environment occurs where the average annual salinity is below 0.5 ppt (Figure 1); salinity may rise above this concentration periodically during droughts. Salt marsh salinities have been variously defined, but for the purposes of this comparison they will be limited to the range of 18.0 to 35.0 ppt. Between the two are the oligohaline (average 0.5–5.0 ppt) and mesohaline (average 5.0–18.0 ppt) regions (24). Inherent in all classifications is recognition that the salinity regime of estuaries is highly variable both seasonally and between years. Seasonal incursions of water of higher salinity into tidal freshwater marshes are likely to have a significant effect on both animal and plant communities (e.g. 12, 13).

Tidal Range

Both types of wetlands are subject to ocean-derived lunar tides. In certain locations it is not unusual to have a greater tidal range at the head (the tidal freshwater marsh) than at the mouth of the estuary (the salt marsh). For example, at the mouth of the Potomac River the tidal range is approximately 70 cm, while 100 km upstream in the tidal freshwater marshes near Washington, DC the tidal range exceeds one meter (99). This can be attributed largely to the constricting of the tidal water mass as it moves upstream in a continually narrowing river channel.

Sediment Composition

Although few comparative studies exist, fundamental differences in sediments appear in the two types of marshes. Tidal freshwater marshes typically are high in materials derived from upriver and terrestrial sources, such as clays, silt, and fine organic matter, with minor amounts of sand. Frequently, these marshes are located near the section of the estuary with the highest rates of sedimentation of fine, river-borne materials (75, 83).

Salt marsh sediments, in contrast, typically contain more fine sands and clays from marine sources (89, 106). They often have a lower organic carbon content than those from tidal freshwater marshes, presumably due to the greater annual inputs of riverine and terrestrial carbon to the latter (92). In a series of samples from the east coast of North America, I found the average organic content of salt marsh sediments to range from 10% to 40% by weight (mean = 15%) while the average in tidal freshwater sediments ranged from 20% to 70% (mean = 35%). Also there appeared to be more fibrous, peat-like material in salt marsh sediments. These are general tendencies; a great deal of site-to-site and within site variability clearly exists in both types of marsh.

Sediment Erodability and Streambank Morphology

Tidal freshwater marsh sediments, particularly in the lower part of the marsh, may be more erodable than are salt marsh sediments (48). This may be related to several factors, including the lower biomass of plant root material per unit area in the freshwater marsh sediments, the lesser amounts of plant litter on the sediment surface during the winter and spring, and the finer mean particle size (and lower sand content) of the freshwater sediments. (The first two points are discussed later. Garofalo (48) has further suggested that this greater susceptibility to erosion, particularly in the winter, results in low profile stream banks and tidal creeks in tidal freshwater with less sinuosity compared to those in higher salinity marshes.

Serodes & Troude (109) report an extreme annual erosion cycle from a tidal freshwater section of the St. Lawrence River near Quebec. They documented an annual variation of more than 20 cm in marsh surface elevation due to high erosion rates in spring and fall that are initiated by heavy grazing of the marsh vegetation by snow geese. While intense grazing by snow geese occurs in some salt marshes (117), the annual erosion cycle is much more modest.

Garofalo's observations (48) of high erodability come from midlatitude tidal freshwater marshes. In some locations at higher latitudes sedges (*Carex* spp.) and other peat-forming plants dominate, and plant decomposition rates are slower; these may not exhibit high erodability and resulting geomorphological differences from salt marshes.

Dissolved Sulfur

The water that inundates salt marshes is not only saltier but differs considerably in its elemental composition from tidal freshwater (78). For example, seawater has approximately three orders of magnitude more dissolved sulfur than freshwater. As a result, sulfur reduction is an important anaerobic decomposition process in salt marshes but is of less significance in tidal freshwater (99).

Sediment Redox Potential

Aerobic (oxidized) and anaerobic (reduced) sediments are contrasted by the availability of oxygen for chemical and biological processes. Redox potential (Eh) measurements are useful indicators of the intensity of oxidation or reduction (46). In spite of theoretical limitations and methodological difficulties, redox potential of saturated wetland soils is of great interest to ecologists, since it affects a variety of processes ranging from the depth to which infauna can penetrate the sediment to the availability of nutrients to plants (78).

Unfortunately, it is not easy to compare the redox potential of tidal freshwater and salt marshes. Salt marsh sediments have strongly reducing conditions (62) as reflected by generally low Eh values ranging from −100 to −250 mV. The redox couples are principally sulfide and sulfate sulfur (46).

In tidal freshwater, understanding of redox conditions is much more difficult. Sulfur couples are not important because of the generally low amounts of sulfur. Instead there are many potential redox couples including ferrous and ferric iron, nitrite and nitrate nitrogen, and many organic compounds (46). As a result, measured Eh estimates of +50 to +150 mV from tidal freshwater sediments (22) are probably inaccurate since Eh probes do not work well with multiple redox couples (46). Tidal freshwater marsh sediments probably are moderately to strongly reducing, at least within microsites, since rates of methanogenesis are high (31) and methanogenic bacteria require strong reducing conditions (140).

Reduced Iron-Sulfur Compounds

In most salt marshes the combination of plentiful sulfate and iron and the activity of anaerobic sulfur–reducing bacteria leads to quantities of stable pyrites and iron monosulfides in the sediments (61). The biological significance of these reduced iron-sulfur compounds is that they are plentiful energy sources for sulfur oxidizing bacteria wherever sediments or pore waters are exposed to oxidizing conditions, such as along creek banks (60). The sulfur oxidizers, in turn, may provide an energy source for estuarine bactivorous consumers.

In tidal freshwater, reduced iron-sulfur compounds are generally rare or nonexistent because of the scarcity of sulfur. This lack of pyrite provides a useful indicator of the paleoecological origin of tidal freshwater versus salt marsh sediments, peat, and coal (R. Ellison, personal communication).

Subsurface Hydrology

The movement of water and dissolved substances through the interstitial spaces in wetland sediments and soils is referred to as subsurface hydrology. These transport processes significantly affect a wide range of other processes below the sediment surface including redox potential, fluxes of nutrients and toxic compounds such as sulfide, and even influence the distribution of plants, their physiological state and the magnitude of primary production.

Over the past decade, much has been learned about nutrient concentrations in soil pore waters (88) and exchanges between pore waters and tidal creeks (63). Evapotranspiration has been shown to be important in the vertical flux of water from marsh soils (26, 58, 91). Replacement of this water has been demonstrated to occur (*a*) from inflow from tidal creek banks (55, 63), (*b*) from vertical infiltration of flooding tidal water and precipitation (57, 91, 138), and (*c*) from upland ground water (19, 128).

Synthesis of this information suggests that for expansive coastal wetlands, irregularly flooded by tidal water, the critical pathway of pore water exchange is via vertical flux mediated by evapotranspiration (26, 58, 91). This means that subsurface water in these marshes may become stagnant, with high concentrations of toxic substances such as sulfides and greatly reduced redox conditions. The result is stressed and stunted plants (64).

In contrast, along narrow marshes or near the tidal creek banks of expansive marshes, the critical exchange of pore water is horizontally through the creek bank (55, 63, 138). This leads to higher fluxes of pore water, lower sulfide concentrations, higher turnover rates of nutrients and less stressed plants, with higher primary production along the creek banks (64).

Virtually no published information on subsurface hydrology exists for tidal freshwater marshes. Research in progress by J. W. Harvey, R. M. Chambers, and myself suggests that the current hypotheses from salt marshes probably apply to tidal freshwater marshes, with modifications due to (*a*) the generally finer texture of sediments, (*b*) the low concentrations of sulfide, (*c*) the influence of upland groundwater at many sites, and (*d*) the more uneven distribution of plant roots in tidal freshwater.

Dissolved and Particulate Organic Carbon

Odum (92) reviewed data suggesting that concentrations of both dissolved and particulate organic carbon in the water column tend to be higher in tidal freshwater by a factor of two or three than further down the estuary at higher salinities. This apparently results from the high inputs of terrestrial and riverine carbon at the head of the estuary and the gradual dilution at higher salinities by seawater, which is typically lower in organic carbon concentrations.

COMPARISON OF COMMUNITY STRUCTURE

In comparing aspects of community structure between tidal freshwater marshes and salt marshes (Table 2 and 3), a number of fundamental differences are apparent. While these seem to be related to differences in mean annual salinity, other factors may be involved.

Vascular Plant Community Composition

Many factors affect the distribution of vascular plant species along the estuarine gradient, but decades of research have established that water salinity is the dominant factor (1, 32, 42, 43). A number of other factors including

Table 2 Comparison of vascular plant community structure between tidal freshwater marshes and salt marshes.

	Tidal freshwater marsh	Salt marsh
Community composition	Freshwater species	Marine and estuarine species
Species diversity	High species diversity, low dominance by single species	Low species diversity, high dominance by single species
Intertidal distribution	Entire intertidal zone	Upper two thirds of intertidal zone
Zonation and habitat overlap	Zonation present, but not always distinct; much habitat overlap	Pronounced zonation; little habitat overlap
Seasonal sequence of dominant species	Pronounced	Absent or minor
Life history strategies	Reproduction both sexual and asexual, seed banks very important	Reproduction principally asexual (through dispersal of pieces of rhizomes), seed dispersal secondary, seed banks not as important
Tree distribution	Present at least to latitude 45°	Disappear north of latitude 30°

time of inundation (32), sulfide concentrations (18), and substrate composition may play important roles.

With this in mind, it is not surprising to find that the plant communities at either end of the salinity gradient are almost totally different in species composition. In tidal freshwater marshes, almost all of the vascular plants are species most commonly restricted to freshwater or low salinities (99). The salt marsh, in contrast, is populated with species able to tolerate estuarine and marine conditions through specialized physiological adaptations (78). For example (99), on the east coast of the United States, the tidal freshwater marsh community is dominated by a variety of freshwater plants including (*a*) broad-leaved emergent perennial macrophytes, (*b*) herbaceous annuals, (*c*) annual and perennial sedges, rushes, and grasses, (*d*) shrubform herbs, (*e*) a few hydrophytic shrubs, and (*f*) a few hydrophytic trees. In contrast (77), the salt marsh community is composed of relatively few estuarine and marine halophytic gramminoid, shrub and herbaceous species.

Vascular Plant Species Diversity

In addition to significant differences in the species composition of the two types of wetlands, a pronounced contrast exists in species diversity in the regularly flooded sections of the two marsh types, with a relatively low diversity in salt marshes and a much higher diversity in tidal freshwater (Figure 2). For example, tidal freshwater marshes on the east coast of the

United States usually have 25–40 species growing intertidally and over 100 species growing in sections of the marsh that are flooded frequently (99). Single species rarely dominate the marsh throughout the year, and it is not unusual to have combinations of a dozen or more dominant species of annuals and perennials (113), a situation reminiscent of nontidal freshwater wetlands (78).

With the additional stress of saline conditions, salt marshes rarely have more than 10 species growing in the regularly flooded marsh and 30 or 40 species in the area of the marsh that is flooded monthly (77, 89, 102, 139). Even more striking is the almost total domination of the intertidal "low" salt marsh by single species such as smooth cordgrass *(Spartina alterniflora)* on the east and Gulf coasts of the United States (78). Even the irregularly flooded

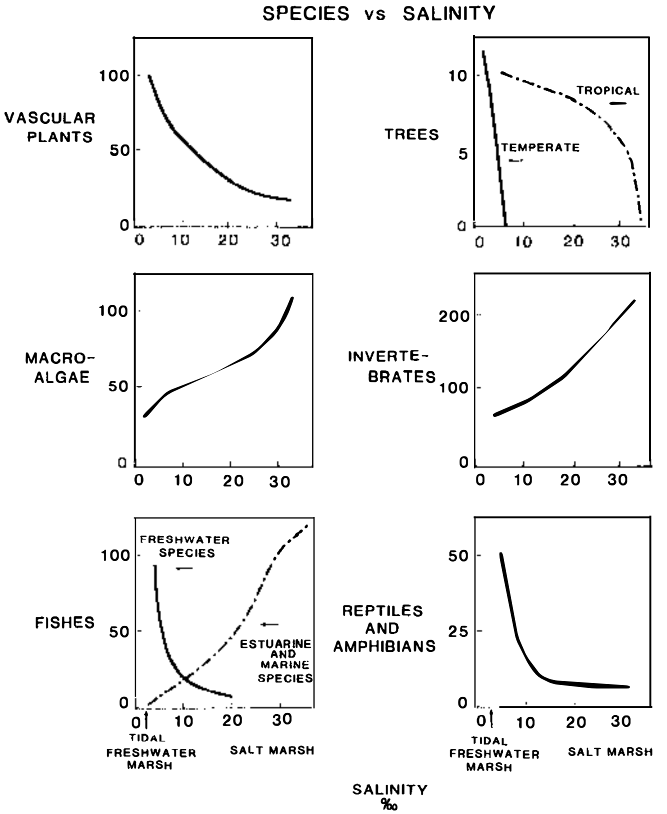

Figure 2 Hypothetical trends in total species numbers versus mean annual salinity along the estuarine gradient. Exact shapes of curves, particularly at intermediate salinities, require much more data.

"high marsh" is usually dominated by only three or four species (78). Exceptions to this pattern such as the higher diversity have been reported from the sporadically flooded salt marshes of Southern California which receive highly variable amounts of freshwater inputs (139).

Vascular Plant Zonation and Habitat Overlap

Salt marshes are characterized by relatively distinct zonation into a regularly flooded low marsh with low species diversity and an irregularly flooded high marsh with a slightly higher number of vascular plant species present (1, 87, 90, 105). The dividing line between the two zones coincides with mean high tide. Extensive habitat overlap between zones usually does not occur, as species tend to be restricted to a specific zone in the marsh (77). Apparently, distinct zonation results from the combined effects of concentrations of salts and sulfide, soil pore water movement and evaporation, regular inundation, and interspecific competition mediated by differences in physiological tolerances of the plant species (96).

In tidal freshwater marshes, distinct zonation is rare, because considerable habitat overlap occurs (59) and, ultimately, because the physical factors that cause zonation in salt marshes are not present. Although patterns of domination may occur, most species are found in most habitats (133). Certain plants along the US middle Atlantic coast, such as wild rice *(Zizania aquatica)* and arrow-arum *Peltandra virginica)* may dominate at many points along the marsh elevational gradient (99). Significant differences in vascular plant species composition occur at the lowest and highest points along the tidal gradient, but the transition along the gradient is gradual and relatively indistinct. As a result, there is no distinct "low" or "high" marsh in tidal freshwater. One exception to this tendency toward indistinct zonation occurs on very gradual elevational gradients where spatter-dock, *Nuphar luteum,* may form a band at the lowest elevation, and the cattail, *Typha latifolia,* or the common reed, *Phragmites australis,* exists in a dense stand in the higher marsh.

Vascular Plant Distribution in the Intertidal Zone

A cross-sectional comparison of the two marsh types reveals an apparent fundamental difference in the lower extent of macrophyte distribution. In the salt marsh, vascular plants typically are found only in the upper two thirds of the intertidal zone (106); the lower one third is usually devoid of emergent marsh plants and consists of bare mud and, at times, a layer of micro and macro algae. This lack of colonization is probably a result of the combined stress of exposure to salt water and duration of flooding (96). Exceptions to this general pattern appear to occur where the tidal amplitude is very slight, as along the northern coast of the Gulf of Mexico. Here marsh plants such as *Spartina alterniflora* grow virtually to mean low tide (40).

In contrast, Hoover's research in Virginia (59) suggests that tidal freshwater plants typically are able to colonize all of the intertidal zone if slope, exposure, and sediment characteristics are suitable. Odum & Hoover (96) hypothesized that the complete colonization of the intertidal zone in tidal freshwater is due to the lack of salt stress and the resulting larger pool of emergent and floating-leaved vascular plant species which can grow there.

Seasonal Sequence of Dominant Macrophytes

In undisturbed salt marshes, the same macrophyte species usually dominate throughout the growing season (90). Certain minor species flourish later in the growing season, but the dominants remain—usually perennial gramminoids with extensive underground rhizome systems such as *Spartina alterniflora.*

Tidal freshwater marshes, at least on the mid-Atlantic coast of North America, undergo a pronounced seasonal change in dominant vegetation (37, 93, 111, 133). Perennials such as *Peltandra virginica* and *Acorus calamus* reach peak biomass in late June to early July in Virginia (137) and then give way to annuals such as *Zizannia aquatica* and *Impatiens capensis* which reach peak biomass in late August. A third dominance peak may occur in mid-September when other annuals such as *Polygonum arifolium* and *Bidens laevis* become dominant in terms of biomass (133).

This complex seasonal succession in tidal freshwater appears to result from minimal salt stress and the resultant lack of domination by perennial gramminoids with extensive rhizome structures (96). Instead a large species pool generates complicated seasonal sequences of both perennial and annual species (113). Because of the importance of annuals particularly later in the growing season, considerable interannual differences in the dominant species may exist at a particular site (99). For example, it is not uncommon for wild rice, *Zizonia aquatica,* to be extremely abundant at a location one year and rare the next.

Life History Strategies

As I mentioned previously, undisturbed salt marshes tend to be dominated by perennial gramminoids with extensive rhizome systems, e.g. *Spartina alterniflora.* While seeds are produced and do germinate, reproduction and colonization are often asexual and mediated through dispersal of pieces of rhizome. Plants such as the sedge *Scirpus americanus* colonize disturbed, burned, or bare areas quickly by seed dispersal, but they tend to be replaced over time by the perennial gramminoids with extensive rhizomes (117).

Because tidal freshwater marshes are composed of complex assemblages of both perennial and annual species, many life history strategies are important (96). Perennial gramminoids with rhizomes are present (e.g. *Typha* spp., *Zizanopsis*), but almost all the plants produce large quantities of seeds that accumulate as extensive seed banks in tidal freshwater marsh sediments (67, 68). This seed bank plays a much more important role in tidal freshwater marshes than in salt marshes in determining community composition (68). From an applied standpoint, this means that it is much easier to create or rebuild tidal freshwater marshes than salt marshes; planting of seeds or nursery stock are not necessary in the former (47).

Distribution of Trees

Little has been published concerning the comparative distribution of trees in saline and tidal freshwater wetlands. Lugo et al (in press) have hypothesized some fundamental differences along the salinity gradient, including increased structural complexity in freshwater communities and increased litter fall and export of organic matter in salt water.

Odum & Hoover (96) noted that trees occur at higher latitudes in tidal freshwater wetlands than in saline environments (Figure 2). They hypothesized that while tree species have evolved mechanisms to deal with the dual stresses of daily fluctuations in water levels and salinity, the additional stress of subfreezing temperatures has proven insurmountable.

In fact, mangroves (a nontaxonomic term that includes most tree species that grow in saline habitats; 97) never occur at latitudes higher than the climatological point where subfreezing temperatures are common nor where the mean temperature of the coldest month is below 20°C (97). In tidal freshwater, in contrast, trees such as bald cypress, *Taxodium distichum,* and gums, *Nyssa sylvantica* var. *biflora* and *N. aquatica,* extend into the north temperate zone; the Atlantic white cedar, *Chaemaecyparis thyoides,* can be found in tidal freshwater at least as far as latitude 45°N (personal observation). Brinson et al (12) have observed that when saline water intrudes into tidal freshwater during extended droughts at temperate latitudes, trees experience increased mortality.

Benthic MacroAlgae

Included in this category are filamentous and other forms of green, blue-green, red, and brown algae, but not benthic diatoms and dinoflagellates for which there are insufficient comparative data. The work of P.H. Nienhuis (e.g. 84, 85; personal communication) in Dutch estuaries suggests significantly more species of benthic algae in salt marshes than in tidal freshwater (Figure 2). This trend probably results from the loss of many marine species in the upper estuary even though this loss is offset somewhat by the gain of freshwater species. Although reduced in species numbers, macroalgae probably play an important role in tidal freshwater wetlands as in salt marshes (45, 131) since they cover extensive areas of the marsh surface during the autumn, winter, and early spring when vascular plant cover is reduced (134).

Invertebrates

Clear differences exist in the invertebrate communities of tidal freshwater marshes versus those of salt marshes, in response to adaptability to salt stress and other factors. On the east coast of the United States the dominant benthic macrofauna in tidal freshwater marshes are oligochaetes, chironomid midge larvae, freshwater snails, and a few crustaceans including amphipods (34, 98). Few bivalves exist, although the Asiatic clam *(Corbicula fluminea)* has spread into this environment in an explosive fashion in the past 15 years (36). Salt marshes, in contrast (29), have numerous bivalve species along with polychaetes and many different types of crustaceans (e.g. crabs, isopods, many species of amphipods, caridean and penaeid shrimp).

The benthic microfauna of tidal freshwater is characterized principally by the camoebinids while foraminifera dominate in salt marshes (41). In fact, the demarcation in distribution between these two groups provides a convenient geological record of the historical boundaries between tidal freshwater and oligohaline conditions.

The zooplankton in tidal freshwater creeks are dominated by rotifers, cladocerans, and one or two species of estuarine copepods (70). Zooplankton in salt marsh creeks are typically copepods and larval stages of bivalves, crustaceans, and fishes. Insects are not well enough studied in tidal freshwater marshes to make a meaningful comparison. However, larval aquatic stages (e.g. chironomid and dragonfly larvae) appear to be much more numerous in tidal freshwater than in salt marshes.

Invertebrate Species Diversity

The number of species of both benthic macrofauna and microfauna (Figure 2) appear to be lower in tidal freshwater habitats than in either salt marsh or nontidal freshwater habitats (34, 41). Diaz & Boesch (35) attribute this phenomenon to a general lack of habitat diversity, since most habitats in tidal freshwater have a silty mud substrate similar to those that occur in many eutrophic lakes. Remane (107) and others (30) have suggested species impoverishment as a result of salinity effects. They hypothesize that few marine and estuarine species are able to penetrate the low salinity end of the estuary because of physiological difficulties, while the converse holds for freshwater species. At the present time the small amount of comparative data makes it impossible to validate either the lower number of invertebrate species in tidal freshwater or the reasons for this.

Fishes

The community of fishes present in tidal freshwater is markedly different from that associated with either oligohaline or salt marshes (Figure 2). Odum et al (98) compared published data from 13 tidal freshwater sites on the east

Table 3 Comparison of animal community structure between tidal freshwater marshes and salt marshes

	Tidal freshwater marshes	Salt marshes
Invertebrates (other than insects)	Lower species diversity, predominantly freshwater species	Higher species diversity, estuarine and marine species
Fishes	Freshwater and oligohaline species; larvae, juveniles and spawning adults of anadromous species; juvenile marine species	Marine and estuarine species
Reptiles and amphibians	High species diversity	Low species diversity
Fur-bearing mammals	High species diversity, high density	Low-moderate species diversity, moderate densities
Waterfowl	High species diversity, high, but spotty densities	Moderate species diversity, moderate densities

coast of the United States between the Hudson River, New York, and the Altamaha River, Georgia. They found that of the numerically dominant species, 60% were freshwater species, 20% were anadromous, 13% were estuarine, and 7% were marine species. They also compared data from four oligohaline sites. The oligohaline fish community, which geographically may be very close to tidal freshwater, was dominated by estuarine and marine species. A similar species composition has been reported for salt marsh fish communities (74), with an apparently higher species diversity in salt water than tidal freshwater (28, 33).

These data suggest that marine and brackish water fish species are better able to exploit the lowered salinity conditions in oligohaline waters than the almost totally freshwater conditions in tidal freshwater. Conversely freshwater species appear to have difficulty penetrating very far into higher salinities. These observations are consistent with Deaton & Greenberg's (30) conclusions that the most severe changes in ionic ratios, possibly a limiting factor to invading species, occur in the range of 0–2 ppt rather than in the range between 5 and 8 ppt suggested by Klehbovich (66).

Reptiles and Amphibians

Not surprisingly, tidal freshwater environments have many more species of reptiles and amphibians than do salt marshes (99) (Figure 2). Salamanders, frogs and toads, turtles, lizards, and snakes thrive in most tidal freshwater wetlands, but only a few can tolerate the osmotic problems presented by salt water.

Waterfowl and Shorebirds

Mitsch & Gosselink (78) have suggested that tidal freshwater marshes support the largest and most diverse populations of birds of any wetland type. While this is probably true (99), a lack of comparative quantitative data makes it difficult to test this hypothesis.

It is well established, however, that certain species prefer one habitat over the other. In general, dabbling ducks (e.g. mallard, black, greenwinged teal, wood duck), Canada geese, and whistling swans appear to prefer tidal freshwater habitat while diving ducks, mergansers, snow geese, clapper rails, and sea ducks prefer salt marsh associated habitat (86, 99, 110). These distributions are determined largely by the distribution of preferred foods.

Mammals

Complete inventories do not exist of large and small mammals in the contrasting wetland types. While a number of species with commercially valuable pelts are found in both types of marshes (e.g. otter, mink, muskrat, nutria, raccoon), the diversity and density of mammals using tidal freshwater appear to be higher than those that use salt marshes (99).

ECOSYSTEM PROCESSES

Significant differences in physical characteristics and community structure between tidal freshwater and salt marshes suggest possible differences in ecological processes such as primary production and decomposition. These possible differences are explored in Table 4 and the following sections.

Annual Net Primary Production of Vascular Plants

Tidal freshwater marshes are likely to support a higher net primary production for several reasons. First, lowered primary production of *Spartina alterniflora* in response to increasing mean annual salinity has been reported (103, 132). Lowered photosynthesis occurred at higher salinities in three salt tolerant plants from California (101). Deschenes & Serodes (32) found lower biomass of *Scirpus americanus* at higher salinities from the St. Lawrence River. Ewing (43) found no drop in productivity with increasing salinity for the same species from the Fraser River delta but did find declines for *S. validus* and *Carex lyngbyei*. While Ewing reported a decline in total community primary production with increasing salinity, he cautioned against generalizations because of the complex interacting factors present in estuaries.

From a physiological standpoint, vascular plants in salt water invest more energy than do freshwater plants to exclude or extrude salts and sulfides (76), energy that might otherwise be stored as net primary production. Cavalieri & Huang (20, 21) report, for example, that high salt levels stimulate the

Table 4 Comparisons of ecological processes between tidal freshwater marshes and salt marshes

	Tidal freshwater marsh	Salt marsh
Net primary production	Theoretical and sampling difficulties prevent a meaningful comparison. There appears to be more investment in belowground biomass in salt marshes.	
Decomposition		
1. Decomposition rates	Intertidal marsh plants = extremely rapid; high marsh plants = slow to moderate	Slow to moderate for all vascular plants
2. Detritus quality	Intertidal marsh material = high quality (low C/N ratio, low crude fiber content)	Intertidal marsh material = low to moderate quality (higher C/N ratio, high crude fiber content)
3. Benthic litter layer	Missing or much reduced in most intertidal marshes in later winter and spring	Present all year except on lower creek banks
4. Anaerobic decomposition	Methanogenesis and fermentation predominate	Sulfur reduction and fermentation predominate
5. Biogenic gas	Large amounts of methane and CO_2, low amounts of sulfur gases, magnitude of nitrous oxides unknown	Large amounts of sulfur gases and CO_2, low amounts of methane, magnitude of nitrous oxides unknown
Nutrient flux	Controlled by presence or absence of litter layer. May be pronounced spring uptake of NO_2, NO_3, PO_4 and large autumn release of reduced compounds	More even processing and release (conversion of oxidized to reduced forms) throughout the year
Energy Flow		
1. Primary consumers	Insects, oligochaetes, amphipods, muskrats	Insects, crustaceans, polychaetes, molluscs
2. Direct grazing	Variable (5–40%)	Low (less than 5%)
3. Food web base	Comparable (vascular plant detritus, benthic microalgae, phytoplankton); may be more terrestrial carbon in tidal freshwater	

synthesis of nitrogen-containing solutes (proline and glycine betaine) in *Spartina alterniflora*. While these solutes aid in salt tolerance, they represent a drain on both nitrogen and energy that would normally be used for growth.

Additionally, salt can affect growth of *S. alterniflora* throught the action of sodium as a competitive inhibitor of ammonium uptake (54). Although plants such as *S. alterniflora* have a variety of ways to reduce the toxicity of sulfide found in salt marsh soils (18), this too represents an energy drain. Sulfide concentration in marsh soils has been shown to be an important factor in reducing salt marsh primary production (64).

A few factors may enhance net primary production in salt marshes in comparison to tidal freshwater: (*a*) Extensive burrowing activity by fiddler crabs in salt marshes (80, 121) can aerate the sediment and may reduce sulfide stress. (*b*) In salt marshes, *Spartina alterniflora* is a C^4 photosynthetic pathway plant, while almost all of the plants in tidal freshwater are C^3 (99). This may give *S. alterniflora* a physiological advantage under certain conditions of flooding, high temperatures, or CO_2 concentration. (*c*) Oxidized conditions (e.g. around the plant roots) may cause phosphorous to be complexed with the large amounts of iron and aluminum often present in tidal freshwater (22). This could reduce the availability of phosphorous to tidal freshwater plants and lower primary production. While this might also happen in salt marshes, usually phosphorous is plentifully available (78).

Given the uncertainty of theoretical arguments, comparative field data are disappointingly scarce. Unfortunately, meaningful comparisons of mean annual primary production between salt marshes and tidal freshwater marshes are difficult because of two intractable problems.

First, while a tremendous amount of effort has been expended studying primary production in salt marshes, temporal and spatial variability limits generalizations. Morris (81) has demonstrated a 200–300% variability between years in the aboveground net primary production of *S. alterniflora* within the same permanent quadrats. Spatial variability of 300–500% has been reported on transects from creek banks to "short form" *Spartina* marshes (78). Given this sort of variability, how can you generate a representative "average" for the marsh?

Second, and even more vexing, estimates of annual net primary production from most tidal freshwater communities are almost impossible to obtain. As discussed previously, these are highly diverse, mixed communities with complex patterns of seasonal succession, interannual variation, many "dominant" species, and rare monospecific stands. Maximum annual standing crop and annual production of single species have little meaning in terms of annual net community production. Even worse, underground biomass is unevenly distributed (99); this makes it virtually impossible to estimate belowground production using conventional salt marsh random coring techniques (108, 127).

Since salt marsh plants typically invest more into belowground production than aboveground (108, 116, 127) and accurate estimates of above and belowground production have not been made in tidal freshwater communities, how is it possible to make a meaningful comparison? Estimates and comparisons have been made (37, 99, 113), but they are based on peak seasonal standing crop and do not include belowground biomass.

Decomposition Rates of Intertidal Vascular Plants

Although many factors influence the decomposition rate of wetland plants (14), there appears to be a significant difference between rates of intertidal plants in tidal freshwater and salt marshes (95). Salt marsh vascular plants such as species of *Spartina* generally decompose at a moderate rate (e.g. 51, 71, 79). This moderate rate is a function of a number of factors including a relatively low nitrogen content of salt marsh plants (71) and typically high amounts of resistant materials such as cellulose, hemicellulose, and lignin, along with large concentrations of inorganic ash (129).

In contrast, vascular plants from the low and middle elevations of the tidal freshwater marsh generally decompose at a rapid rate (95). These plants (e.g. *Peltandra virginica, Bidens laeuis, Nuphar luteum, Sagittaria latifolia,* and the leaves of *Zizania aquatica* and *Hibiscus moscheutos*) have relatively high amounts of nitrogen ranging from 2% to 4% of total dry weight (38) and relatively low amounts of resistant compounds such as cellulose (130). During the warm summer months, a dead leaf of one of these plants may lose 30% to 40% of its dry weight in one week and completely decompose in 4 weeks or less (95, 123).

Tidal freshwater vascular plants growing in the higher portion of the marsh (e.g. *Typha* spp., *Carex* spp., *Phragmites communis* and the stems of *Zizania aquatica* and *Hibiscus moscheutos*) resemble the typical salt marsh plants in their content of both nitrogen and resistant compounds, and they decompose at a much slower rate than do plants lower in the intertidal zone (99).

Detritus Quality

The decomposing remains of many salt marsh macrophytes such as *Spartina* spp. have only low to moderate palatability and growth potential for detritivore consumers (122). The less than maximal food value of salt marsh organic detritus can be traced to generally low nitrogen content, high crude fiber content, and the presence of unpalatable substances such as cinamic acids (125).

Detritus derived from the vascular plants growing in the low and middle elevations of tidal freshwater marshes appears to have high nutritive quality due to its high nitrogen content and low crude fiber content. Dunn (38) and Smock & Harlowe (118) have shown that the decomposing remains of plants such as *Peltandra virginica, Nuphar luteum,* and *Zizania aquatica* are selected as much more palatable than *Spartina* detritus by detritus consumers such as the amphipod *Gamarus fasciatus* and the isopod *Asellus forbesi.*

Benthic Litter Layer

Because of the moderate rate of macrophyte decomposition, salt marshes usually have at least a partial litter layer on the marsh surface throughout the year (44). There may be bare spots in certain locations (i.e. stream banks, lower intertidal zone, ice-sheared areas), but standing dead and fallen marsh grass litter is normally present over much of the marsh surface.

In contrast, the lower and middle elevations of most tidal freshwater marshes are characterized during the late winter and spring months by extensive expanses of bare mud with little standing or fallen litter (113). This results from the rapid decomposition rates of the plants that grow in this zone (95). The higher portions of the tidal freshwater marsh and some northern marshes (8, 10) with slower decomposing species (e.g. *Typha* spp.) often have large amounts of litter present throughout the year, in a way similar to most salt marshes.

Anaerobic Decomposition

A fundamental difference in anaerobic decomposition below the marsh surface exists between the two wetland types. In salt marshes the principal pathway of anaerobic decomposition is through fermentation and sulfur reduction (5, 27, 124, 136). In tidal freshwater marshes, methanogenesis and fermentation predominate (4, 5, 31, 120). Acetate and hydrogen plus CO_2 are used as terminal electron acceptors by both methanogens and sulfate reducers (15). Since both compounds are present in limited quantities in the sediments, a highly competitive relationship exists between the two groups of bacteria (72, 124).

If sufficient sulfate is present, sulfate-reducing bacteria will out-compete the methanogenic bacteria for available acetate and hydrogen plus CO_2 (72, 124). This leads to the observation that methane and sulfate are inversely related in sediment pore water concentrations (4, 5).

As a general principle, this means that sulfate reduction predominates in the salt marsh and methanogenesis predominates in tidal freshwater. But, like many general principles, there are modifiers that must be considered. For example, if sulfate becomes depleted at some depth below the surface of the salt marsh, there may be significant methanogenic activity (25). Conversely, if saline water penetrates the tidal freshwater environment, as often happens in the late summer, some sulfate will be imported, sulfate reduction will occur in the shallow sediments, and methanogenesis may decline significantly (5). All of these observations have implications for comparison of biogenic gas emissions.

Biogenic Gas Emissions

Comparative data of biogenic gas emissions can provide important clues for understanding biogeochemical processes in wetlands (78). Furthermore, on a global scale it is well documented that wetlands are important sources of gases such as methane, CO_2, NO_x, and sulfide that play critical roles in atmospheric chemical and radiation transfer processes (39, 53, 69, 73).

The preceding review of anaerobic decomposition provides a basis for hypotheses concerning the comparative release of certain biogenic gases from tidal freshwater and salt marshes. On an annual basis salt marshes should

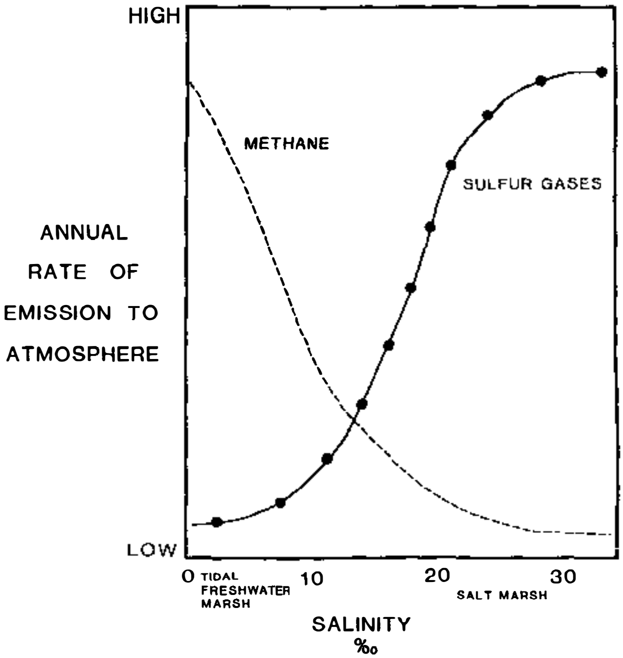

Figure 3 Hypothetical trends in annual rates of gas emissions of wetlands along the estuarine salinity gradient. Exact shapes of curves, particularly at intermediate salinities, require more data.

release principally sulfur gases, and tidal freshwater marshes should release methane (Figure 3). There is no reason to expect CO_2 release to vary between the two environments (81, 82).

Data summarized by Bartlett et al (5) (Figure 4) support the methane portion of the hypothesis. Annual methane emission rates of 100–200 g CH_4 m^{-2} yr^{-1} have been estimated from tidal freshwater (31), and rates of 1–5 g CH_4 m^{-2} yr^{-1} have been estimated from salt marshes (5, 6, 65), with intermediate amounts from oligohaline marshes (5).

Unfortunately, almost no data exist for sulfur gases from tidal freshwater. Brock et al (15) point out that sulfide emissions can occur from freshwater marshes but at much reduced annual rates, compared to salt marshes. The data of Bartlett et al (5) suggest that some sulfur reduction occurs in low salinity marshes, particularly in the late summer.

On the other hand, significant releases of sulfide from salt marshes are well documented (27, 124, 136). Furthermore, Dacey et al (27) have found significant quantities of dimethyl sulfide (DMS) released from salt marshes. Unlike sulfide, which is released primarily across the sediment surface, DMS

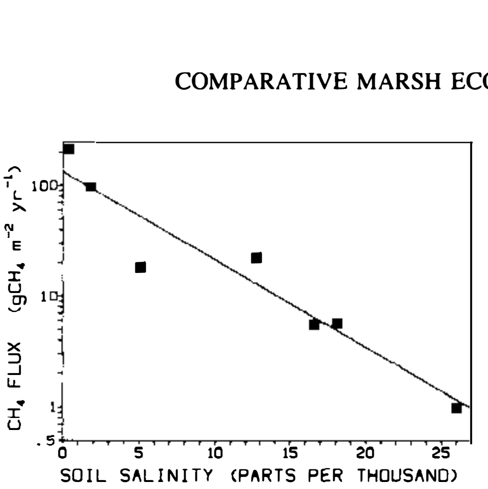

Figure 4 Field estimates of annual methane flux versus average soil salinity. Figure by permission from Bartlett et al (5) summarizing data from several publications.

arises from physiological processes within the leaves of higher plants, principally *Spartina alterniflora* (27). This means that sulfide emissions from salt marshes and even oligohaline marshes probably occur somewhat independently of the presence of vegetation, but DMS release is closely linked to the presence of *Spartina alterniflora*.

There are other important biogenic gases, such as ammonia, nitrogen gases resulting from denitrification, and CO and CO_2 resulting from anaerobic decomposition in wetlands. Unfortunately, data for these gases are insufficient for any comparisons between tidal freshwater and salt marshes.

Nutrient Flux of Elements Other Than Carbon

The general model of estuarine nutrient flux (88, 126, 128) (Figure 5) suggests that salt marshes act primarily as transformers of nutrients by importing dissolved oxidized inorganic forms (nitrite, nitrate, phosphate) and exporting dissolved and particulate reduced forms (ammonium, forms of organic nitrogen and phosphorous compounds). Salt marshes may function as either sinks or sources of nutrients depending upon a variety of factors including the successional age of the marsh, salinity and redox characteristics, presence of upland sources of nutrients, tidal energy input, presence of human inputs of nutrients, presence of a litter layer, and the magnitude and stability of nutrient flux in the estuary to which the marsh is coupled (119). Salt marshes tend to have a net import of nutrients at the beginning and during the growing season and a net export in the autumn and winter (88).

Nutrient flux characteristics of tidal freshwater marshes are probably similar to salt marshes (7, 9, 56, 114, 115, 119). One possible difference is that in marshes which lose their winter plant and litter cover, the characteristic seasonal nutrient exchange is more pronounced. In these marshes a large uptake of nitrite, nitrate, and phosphate appears to occur in the spring, and a

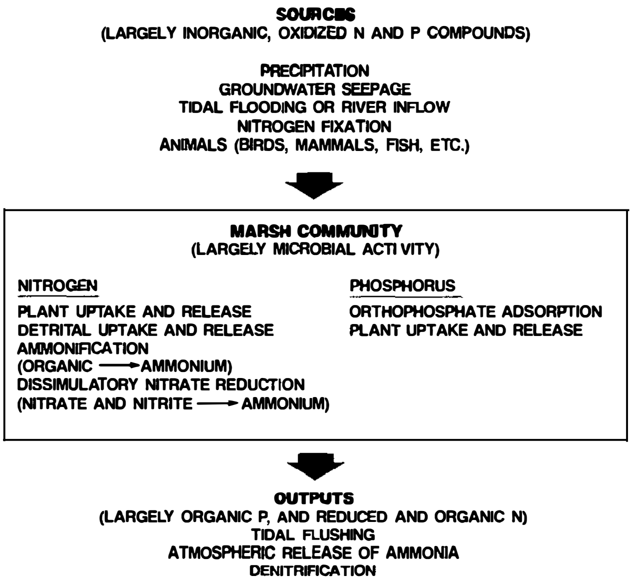

Figure 5 A general model of nutrient fluxes in coastal marshes. Based on Valiela & Teal (128) and Nixon (88). From Odum et al (99).

considerable export of reduced nitrogen and phosphorous in the late autumn and winter, due to the rapid disappearance of dead and dying plant material from the lower sections of the marsh (135).

Bowden (11) describes a very different situation in a Massachusetts tidal freshwater marsh in which *Typha, Carex,* and *Calamagrostis* littler persists on the marsh surface all winter. He found a tight internal nitrogen cycle based on the following: (*a*) Microbes on the litter immobilize nitrogen under aerobic conditions and mineralize nitrogen under anaerobic conditions. (*b*) Fresh, aerobic litter acts like a cap on the marsh, preventing nitrogen loss from the high-N sediment pore water to the low-N river water, and it may even extract nitrogen from the latter. (*c*) Eventually this aerobic litter is compacted, forms anaerobic peat, and becomes a net source of nitrogen available for plant uptake. The effect is to buffer the system against short-term deficiencies of nitrogen. Similar tight internal nitrogen cycling are probably characteristic of the higher portions of tidal freshwater marshes further south which are dominated by plants such as *Typha* and *Zizaniopsis*.

No estimates of nitrogen fixation and denitrification from tidal freshwater marshes have been published; therefore, comparisons with salt marshes are not possible. Given the methodological difficulties with estimating both processes (11), it may be some time before meaningful comparisons are available.

Organic Carbon Flux

Apparently, tidal freshwater marshes function as net importers or exporters of organic carbon on an annual basis in response to the same factors that control this process in salt marshes (see 88 and 94 for discussions of the latter). These factors include but are not limited to tidal range, basin geomorphology, successional age of the marsh, relative amount of marsh versus open water, and amount of freshwater input to the marsh system. Studies by Axelrad et al (3) and Adams (2) found significant export of carbon from tidal freshwater marshes in Virginia. In both cases the bulk of export appeared to be in the form of dissolved carbon compounds rather than particulate material. Heinle & Fleming (56), on the other hand, found neither export nor import in poorly flooded low salinity marshes in Maryland.

Energy Flow

A basic foodweb structure appears to be common to both salt marshes (29, 90, 121) and tidal freshwater marshes (99). In both types of ecosystems the principal sources of energy come from a combination of marsh macrophytes, benthic microalgae, phytoplankton, and terrestrial organic material (100). Although the relative importance of different energy sources varies from one location to the next, organic detritus originating from both marsh and terrestrial sources along with autochthonous micro and macroalgae are probably the most important basic energy sources for consumers in both types of wetlands.

Minor differences appear in the manner in which basic sources of energy are processed in the two systems. For example, although comparative estimates of insect herbivory have not been made, direct grazing of marsh macrophytes seems to be more important in tidal freshwater where leaf-grazing and seed-eating birds and mammals (e.g. muskrats and nutria) are more prevalent (78). This fact may be related to the typically higher palatability (higher nitrogen content, lower crude fiber) of tidal freshwater as compared to salt marsh vegetation (38) and to the greater number of seed-bearing plant species (99). Whereas direct grazing in salt marshes is generally thought to account for less than 5% of total net primary production (100), the figure for tidal freshwater ranges from 5–40% (17, 99) and can be 100% in areas of muskrat "eat outs" (78).

Within the marsh system (marsh surface and small marsh creeks) the roles of primary consumers appear to be played by different organisms in the two wetland types. Important consumers in salt marshes and mangrove swamps include crustaceans such as crabs, amphipods, and caridean shrimp, along with polychaetes, molluscs, and adult insects (29, 97). In tidal freshwater marshes both larval and adult insects play a key role along with oligochaetes and a few crustaceans such as amphipods and caridean shrimp (99).

SUMMARY

At the beginning of this review, I posed a series of questions formulated around a single central issue. Do the contrasting physical conditions in tidal freshwater and salt marshes, including major differences in the ionic composition of the water flooding the marshes, lead to substantial differences in community structure and ecological processes? Having completed the review it is apparent that while the basic structure and processes are the same in the two environments, significant differences do exist in species numbers and composition and in the patterns, rates, and end products of many of the processes.

For example, the extreme difference in sulfur concentrations in the two types of wetlands influences the composition of the anaerobic microbial communities; along with fermentors, methanogens predominate in tidal freshwater and sulfur reducers in the salt marsh. This affects both the redox potential and the emission of biogenic gases; methane is generated by tidal freshwater marshes and sulfur gases by the salt marsh. Anaerobic decomposition occurs in both types of wetlands, but differences in operational details may have global significance.

Numbers of intertidal vascular plant species declined dramatically between tidal freshwater and salt marshes, a decline accompanied by a decrease in palatability (higher crude fiber, lower nitrogen content), a possible greater investment in belowground production, and a prevalence of asexual reproduction. These changes, in turn, lead to slower aerobic decomposition rates for many salt marsh plants. Rapid decomposition of many intertidal freshwater marsh plants results in a reduced or missing litter layer in the winter, a phenomenon which may affect how "tight" nutrient cycles are at that time. In addition, decreased palatability and lower seed production mean generally lower densities and fewer species of herbivorous mammals and waterfowl in salt marshes.

Taxonomic groups such as vascular plants, reptiles, and amphibians that have evolved primarily in terrestrial and freshwater habitats show a trend of declining species numbers from tidal freshwater to salt marshes, presumably because of osmotic difficulties with salt water. Other groups, however, such as macroalgae, invertebrates, and fishes that have a long evolutionary history in both freshwater and salt water have a different pattern. They show high species numbers in salt marshes (and possibly in nontidal freshwater) and a somewhat reduced number in the tidal freshwater-oligohaline region.

The cause of this sag in species numbers is probably complex and involves several possible factors: (*a*) Low salinities present osmotic difficulties for both freshwater and marine species (30, 107). (*b*) The area of available habitat is much reduced by the narrowing of the estuary so that species/area considerations become critical (16). (*c*) From a geological and evolutionary perspective, the low salinity portion of the estuarine gradient has always been restricted and dynamic (112). In fact, in lower stands of sea level, this region may have been almost nonexistent. (*d*) Substrates in tidal freshwater are typically muddy and soft (35). This presents problems for many invertebrate and most macroalgae species that require a firmer substrate.

In conclusion, salinity has been shown to play an important role in most of the differences between tidal freshwater and salt marshes I have discussed. However, in almost every case there are other factors (e.g. sulfide, species/area relationships) that operate in a synergistic fashion and cannot be dismissed.

ACKNOWLEDGMENTS

Research supported by NSF Grant (No. DEB-8109674) and Virginia Sea Grant (No. NA81AA-D-00025) contributed to this review. Phyllis Taylor and Judith Peatross were a great help with technical aspects. I would like to thank the students whose thoughts and hard work have contributed most of the new ideas presented here: Katherine Brosemer, Randolph Chambers, Jeff Drifmeyer, Michael Dunn, Jonathan Frye, Judson Harvey, Mary Ann Heywood, John Hoover, Beth Hussey, Debra Marsh, Carole McIvor, Barry Nash, Samuel Patterson, James Pickral, Lawrence Rozas, David Scott, Rebecca Schneider, DeWitt Smith, Thomas Smith III, Katherine Turner, Nancy Van Dyke, and Thomas Wolaver.

Literature Cited

1. Adam, D. A. 1963. Factors influencing vascular plant zonation in North Carolina salt marshes. *Ecology* 44:445–56
2. Adams, D. D. 1978. *Habitat development field investigations Windmill Point marsh development site, James River, Virginia:* Appendix F: Environmental impacts of marsh development with dredged material: sediment and water quality: Vol. II: Substrate and chemical flux characteristics of a dredged material marsh. *US Army Waterways Exp. Stn. Tech. Rep. D-77-23.* 72 pp.
3. Axelrad, D. M., Moore, K. A., Bender, M. E. 1976. *Nitrogen, phosphorus and carbon flux in Chesapeake Bay marshes. Va. Water Resour. Res. Cent. Bull.* 79. 182 pp.
4. Bartlett, K. B., Bartlett, D. S., Harriss, R. C., Sebacher, D. I. 1987. Methane emissions along a salt marsh salinity gradient. *Biogeochemistry* 4:183–202
5. Bartlett, K. B., Harriss, R. C., Sebacher, D. I. 1985. Methane flux from coastal salt marshes. *J. Geophysical Res.* 90:5710–20
6. Bertness, M. D., Ellison, A. M. 1987. Determinants of pattern in a New England salt marsh plant community. *Ecol. Monogr.* 57:129–47
7. Bowden, W. B. 1982. *Nitrogen cycling in the sediments of a tidal, freshwater marsh.* PhD Thesis. NC State Univ., Raleigh, NC
8. Bowden, W. B. 1984. Nitrogen and phosphorus in the sediments of a freshwater tidal marsh. *Estuaries* 7:108–18
9. Bowden, W. B. 1984. A nitrogen-15 isotope dilution study of ammonium production and consumption in a marsh sediment. *Limnol. Oceanogr.* 29:1004–15
10. Bowden, W. B. 1986. Nitrification, nitrate reduction and nitrogen immobilization in a tidal freshwater marsh sediment. *Ecology* 67:88–99
11. Bowden, W. B. 1987. The biogeochem-

istry of nitrogen in freshwater wetlands. *Biogeochemistry* 4:313–48

12. Brinson, M. M., Bradshaw, H. D., Jones, M. N. 1985. Transitions in forested wetlands along gradients of salinity and hydroperiod. *J. Elisha Mit. Sci. Soc.* 101:76–94
13. Brinson, M. M., Brinson, L. J., Lugo, A. E. 1974. The gradient of salinity, its seasonal movement and ecological implications for the Lake Izabal-Rio Dulce ecosystem, Guatemala. *Bull. Mar. Sci.* 24:533–44
14. Brinson, M. M., Lugo, A. E., Brown, S. 1981. Primary production, decomposition and consumer activity in freshwater wetlands. *Annu. Rev. Ecol. Syst.* 12:123–61
15. Brock, T. D., Smith, D. W., Madigon, M. T. 1984. *Biology of Microorganisms.* Englewood Cliffs, NJ: Prentice-Hall. 847 pp.
16. Bulger, A. J. 1987. *A critical evaluation of the paradigm used to illustrate the effect of salinity on species richness in estuaries.* Pap. pres. Ninth Int. Estuarine Res. Conf., New Orleans
17. Cahoon, D. R. 1982. Community production and biomass allocation of *Hibiscus moscheutos*, a brackish marsh dominant. PhD Thesis. Univ. Md., College Park, Md. 144 pp.
18. Carlson, P. R., Yarbro, L. A. 1987. Physical and biological control of mangrove pore water chemistry. In *Ecology and Management of Wetlands*, ed. D. D. Hook et al, pp. 112–32. London: Croom Helm
19. Carr, A. P., Blackley, M. W. L. 1986. The effects and implications of tides and rainfall on the circulation of water within salt marsh sediments. *Limnol. Oceanogr.* 31:266–76
20. Cavalieri, A. J., Huang, A. H. C. 1979. Evaluation of proline accumulation in the adaptation of diverse species of marsh halophytes to the saline environment. *Am. J. Bot.* 66:307–12
21. Cavalieri, A. J., Huang, A. H. C. 1981. Accumulation of proline and glycinebetaine in *Spartina alterniflora* in response to NaCl and nitrogen in the marsh. *Oecologia* 49:224–28
22. Chambers, R. 1987. *Iron reduction and Eh determinations in a tidal freshwater marsh.* Pap. pres. at Ninth Int. Estuarine Res. Conf., New Orleans
23. Chapman, V. J. 1960. *Salt Marshes and Salt Deserts of the World.* New York: Interscience
24. Cowardin, L. M., Carter, V., Golet, F. C., Laroe, E. T. 1979. *Classification of wetlands and deepwater habitats of the United States. U.S. Fish and Wild. Ser. Biol. Serv. Program. FWS/OBS-79/31.* 103 pp.
25. Crill, P. M., Martens, C. S. 1983. Spatial and temporal fluctuations of methane production in anoxic coastal marine sediments. *Limnol. Oceanogr.* 28:1117–30
26. Dacey, J. W. H., Howes, B. L. 1984. Water uptake by roots controls water table movement and sediment oxidation in short *Spartina* marsh. *Science* 224:487–89
27. Dacey, J. W. H., King, G. M., Wakeman, S. G. 1987. Factors controlling emission of dimethylsulphide from salt marshes. *Nature* 330:643–45
28. Dahlberg, M. D. 1972. An ecological study of Georgia coastal fishes. *Fish. Bull.* 70:323–53
29. Day, J. W. Jr., Smith, W. G., Wagner, P. G., Stowe, W. C. 1972. *Community structure and carbon budget of a salt marsh and shallow bay estuarine system in Louisiana. Center for Wetland Resources, La. State Univ. Publ. LSU-SG-72-04*
30. Deaton, L. E., Greenberg, M. J. 1986. There is no horohalinicum. *Estuaries* 9:20–30
31. DeLaune, R. D., Smith, C. J., Patrick, W. H. 1983. Methane release from Gulf coast wetlands. *Tellus* 35B:8–15
32. Deschenes, J., Sérodes, S. B. 1985. The influence of salinity on *Scirpus americanus* tidal marshes in the St. Lawrence River estuary, Quebec. *Can. J. Bot.* 63:920–27
33. Dias, R. K., Merriner, J. V., Hedgepeth, M. 1978. Part III. Aquatic biology - nekton. In *Habitat development field investigation. Windmill Point marsh development site, James River, Virginia:* Appendix D: Environmental impacts of marsh development with dredged material: botany, soils, aquatic biology, and wildlife. *US Army Waterways Exp. Sta. Tech. Rep. D-77-23*, pp. 55–78
34. Diaz, R. J. 1977. *The effects of pollution on benthic communities of the tidal James River, Virginia.* PhD Thesis Univ. Va., Charlottesville, Va. 149 pp.
35. Diaz, R. J., Boesch, D. F. 1977. *Habitat development field investigations Windmill Point marsh development site, James River, Virginia:* Appendix C: Environmental impacts of marsh development with dredged material: acute impacts on the macrobenthic community. *US Army Waterways Exp. Stat. Tech. Rep. D-77-23.* 122 pp.
36. Dresler, P. V., Cory, R. L. 1980. The

Asiatic clam, *Corbicula fluminea*, in the tidal Potomac River, Maryland. *Estuaries* 3:150–51

37. Doumlele, D. G. 1981. Primary production and seasonal aspects of emergent plants in a tidal freshwater marsh. *Estuaries* 4:139–42
38. Dunn, M. L. 1978. *Breakdown of freshwater tidal marsh plants*. MS Thesis. Univ. Va., Charlottesville, Va. 87 pp.
39. Ehhalt, D. H. 1985. On the rise---Methane in the global atmosphere. *Environment* 27:6–12, 30–33
40. Eleuterius, L. 1984. Autecology of the black needlerush, *Juncus roemerianus*. *Gulf Res. Rep.* 7:339–50
41. Ellison, R. L., Nichols, M. M. 1976. Modern and holocene foraminifera in the Chesapeake Bay region. *Mar. Sed. Spec. Publ.* No. 1:131–51
42. Ewing, K. 1983. Environmental controls in Pacific northwest intertidal marsh plant communities. *Can. J. Bot.* 61:1105–16
43. Ewing, K. 1986. Plant growth and productivity along complex gradients in a Pacific northwest brackish intertidal marsh. *Estuaries* 9:49–62
44. Frey, R. W., Basan, P. B. 1978. Coastal salt marshes. In *Coastal Sedimentary Environments*, ed. R. A. Davis, pp. 101–169. New York: Springer Verlag
45. Gallagher, J. L., Daiber, F. C. 1974. Primary production of edaphic algal communities in a Delaware salt marsh. *Limnol. Oceanogr.* 19:390–95
46. Gambrell, R. P., Patrick, W. H. Jr. 1978. Chemical and microbiological properties of anaerobic soils and sediments. In *Plant Life in Anaerobic Environments*, ed. D. D. Hook, R. M. M. Crawford, pp. 375–423. Ann Arbor, Michigan: Ann Arbor Sci.
47. Garbisch, E. W. Jr., Coleman, L. B. 1978. Tidal freshwater marsh establishment in upper Chesapeake Bay. In *Freshwater Wetlands*, ed. R. E. Good, D. F. Whigham, R. L. Simpson, pp. 285–98. New York: Academic Prcss
48. Garofalo, D. 1980. The influence of wetland vegetation on tidal stream channel migration and morphology. *Estuaries* 3:258–70
49. Glooschenko, W. A., Clarke, K. 1982. The salinity cycle of a subarctic salt marsh. *Nat. Can. (Rev. Ecol. Syst.)* 109:483–90
50. Gosselink, J. G. 1984. *The ecology of delta marshes of coastal Louisiana: a community profile. Fish Wildlife Serv. FWS/OBS-84/09*. 134 pp.
51. Gosselink, J. G., Kirby, C. J. 1974. Decomposition of salt marsh grass, *Spartina alterniflora*. *Limnol. Oceanogr.* 19:825–32
52. Grant, R. R., Patrick, R. 1970. Tinicum marsh as a water purifier. In *Two Studies of Tinicum Marsh*. Washington, DC: Conservation Found. 121 pp.
53. Guthrie, P. D. 1986. Biological methanogenesis and the greenhouse effect. *J. Geophys. Res. Atmos.* 91:847–51
54. Haines, B. L., Dunn, E. L. 1976. Growth and resource allocation of *Spartina alterniflora* to three levels of NH_4-N, Fe, and NaCl in solution culture. *Bot. Gaz.* 137:224–30
55. Harvey, J. W., Germann, P. F., Odum, W. E. 1987. Geomorphological control of subsurface hydrology in the creekbank zone of tidal marshes. *Est. Coast. Shelf Sci.* 25:677–91
56. Heinle, R. R., Fleming, D. A. 1976. Flows of materials between poorly flooded tidal marshes and an estuary. *Mar. Biol.* 35:359–73
57. Hemond, H. F., Burke, R. W. 1981. A device for the measurement of infiltration in intermittently flooded wetlands. *Limnol. Oceanogr.* 26:795–800
58. Hemond, H. F., Fifield, J. L. 1982. Subsurface flow in salt marsh peat: a model and field study. *Limnol. Oceanogr.* 27:126–36
59. Hoover, J. K. 1984. Spatial and temporal niche relationships in a tidal freshwater macrophyte community. MS Thesis. Univ. Va., Charlottesville. 85 pp.
60. Howarth, R. W., Giblin, A., Gale, J., Peterson, B., Luther, G. 1983. Reduced sulfur compounds in the pore waters of a New England salt marsh. *Ecol. Bull.* 35:135–62
61. Howarth, R. W., Teal, J. M. 1979. Sulfate reduction in a New England salt marsh. *Limnol. Oceanogr.* 24:999–1013
62. Howes, B. L., Howarth, R. W., Teal, J. M., Valiela, I. 1981. Oxidation-reduction potentials in a salt marsh: spatial patterns and interactions with primary production. *Limnol. Oceanogr.* 26:350–60
63. Jordan, T. E., Correll, D. L. 1985. Nutrient chemistry and hydrology of interstitial water in brackish tidal marshes of Chesapeake Bay. *Est. Coast. Shelf Sci.* 21:45–55
64. King, G. M., Klug, M. J., Wiegert, R. G., Chalmers, A. G. 1982. Relation of soil water movement and sulfide concentration to *Spartina alterniflora* production in a Georgia salt marsh. *Science* 218:61–63
65. King, G. M., Wiebe, W. J. 1978. Methane release from soils of a Georgia

salt marsh. *Geochim. Cosmochim. Acta* 42:343–48
66. Klehbovich, V. V. 1969. Aspects of animal evolution related to critical salinity and internal state. *Mar. Biol.* 2:338–45
67. Leck, M. A., Graveline, K. J. 1979. The seed bank of a freshwater tidal marsh. *Am. J. Bot.* 66:1006-15
68. Leck, M. A., Simpson, R. L. 1987. Seed bank of a freshwater tidal wetland: turnover and relationship to vegetation change. *Am. J. Bot.* 74:360-70
69. Levine, J. S., Allario, F. 1982. The global troposphere: biogeochemical cycles, chemistry and remote sensing. *Environ. Monitor. Assess.* 1:263–306
70. Lippson, A. J., Haire, M. S., Holland, A. F., Jacobs, F., Jensen, J., Moran-Johnson, R. L., Polgar, T. T., Richkus, W. A. 1979. *Environmental Atlas of the Potomac Estuary.* Washington, DC: Williams & Heintz Map Corp. 280 pp.
71. Marinucci, A. C., Hobbie, J. E., Helfrich, J. V. K. 1983. Effect of litter nitrogen on decomposition and microbial biomass in *Spartina alterniflora. Microb. Ecol.* 9:27–40
72. Martens, C. S., Berner, R. A. 1974. Methane production in the interstitial waters of sulfate-depleted marine sediments. *Science* 185:1167–69
73. McCormac, B. M. 1973. *Physics and Chemistry of Upper Atmospheres.* New York: Reidel. 473 pp.
74. McHugh, J. L. 1967. Estuarine nekton. In *Estuaries*, ed. G. H. Lauff, pp. 581–620. Washington, DC: Am. Assoc. Ad. Sci. Publ. No. 83
75. Meade, R. H. 1972. Transport and deposition of sediments in estuaries. In *Environmental Framework of Coastal Plain Estuaries*, ed. B. W. Nelson, pp. 91–120. Washington, DC: Geol. Soc. Am. Memoir 133
76. Mendelssohn, I. A., Burdick, D. M. 1987. The relationship of soil parameters and root metabolism to primary production in periodically inundated soils. See Ref. 18, pp. 398-428
77. Miller, W. B., Egler, F. E. 1950. Vegetation of the Wequetequock-Pawcatuck tidal marshes, Connecticut. *Ecol. Monogr.* 20:143–72
78. Mitsch, W. J., Gosselink, J. G. 1986. Wetlands. New York: Van Nostrand Reinhold. 539 pp.
79. Montagna, P. A., Ruber, E. 1980. Decomposition of *Spartina alterniflora* in different seasons and habitats of a northern Massachusetts salt marsh, and a comparison with other Atlantic regions. *Estuaries* 3:61–64
80. Montague, C. L. 1980. A natural history of temperate western Atlantic fiddler crabs (Genus *Uca*) with reference to their impact on the salt marsh. *Cont. Mar. Sci.* 23:25–55
81. Morris, J. T. 1987. Pathways and controls of the carbon cycle in salt marshes. See Ref. 18, pp. 497–510
82. Morris, J. T., Whiting, G. J. 1986. Emission of gaseous CO_2 from salt marsh sediments and its relation to other carbon losses. *Estuaries* 9:9–19
83. Nichols, M. M. 1972. Sediments of the James River estuary, Virginia. See Ref. 75, pp. 169–213
84. Nienhuis, P. H. 1978. Dynamics of benthic algal vegetation and environment in Dutch estuarine salt marshes studied by means of permanent quadrats. *Vegetatio* 38:103–12
85. Nienhuis, P. H. 1987. Ecology of salt-marsh algae in the Netherlands. In *Vegetation Between Land and Sea*, ed. C. Blom, J. Rozema, pp. 66–83. Dordrecht: Junk
86. Niering, W. A., Warren, R. S. 1977. Salt marshes. In *Coastal Ecosystem Management*, ed. J. R. Clark, pp. 697–702. New York: Wiley
87. Niering, W. A., Warren, R. S. 1980. Vegetation patterns and processes in New England salt marshes. *Bioscience* 30:301–7
88. 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. In *Estuarine and Wetland Processes*, ed. P. Hamilton, K. B. MacDonald, pp. 437–525. New York: Plenum
89. Nixon, S. W. 1982. *The ecology of New England high salt marshes: a community profile. U.S. Fish and Wild. Serv. FWS/OBS-81/55.* 70 pp.
90. Nixon, S. W., Oviatt, C. A. 1973. Ecology of a New England salt marsh. *Ecol. Monogr.* 43:463–98
91. Nuttle, W. K. 1986. *Elements of salt marsh hydrology*. PhD Thesis Mass. Inst. Technol., Cambridge, Mass. 282 pp.
92. Odum, W. E. 1984. Dual-gradient concept of detritus transport and processing in estuaries. *Bull. Mar. Sci.* 35:510–21
93. Odum, W. E., Dunn, M. L., Smith, T. J. 1978. Habitat value of tidal freshwater wetlands. In *Wetland Functions and Values: The State of Our Understanding*, ed. J. R. Clark, J. E. Clark, pp. 248–55. Minneapolis, Minn: Am. Water Resour. Assoc.
94. Odum, W. E., Fisher, S. J., Pickral, J. C. 1979. Factors controlling the lux of

particulate organic carbon from estuarine wetlands. In *Ecological Processes in Coastal and Marine Systems*, ed. R. J. Livingston, pp. 69–80. New York: Plenum
95. Odum, W. E., Heywood, M. A. 1978. Decomposition of intertidal freshwater marsh plants. See Ref. 47, pp. 89–97
96. Odum, W. E., Hoover, J. K. 1987. A comparison of vascular plant communities in tidal freshwater and salt water mashes. See Ref. 18, pp. 526–34
97. Odum, W. E., McIvor, C. C., Smith, T. J. 1982. *The ecology of the mangroves of south Florida: a community profile. US Fish and Wild. Serv. FWS/OBS-81/24*. 144 pp.
98. Odum, W. E., Rosze, L. P., McIvor, C. C. 1987. A comparison of fish and invertebrate community composition in tidal freshwater and oligohaline marsh systems. See Ref. 18, pp. 561–69
99. Odum, W. E., Smith, T. J., Hoover, J. K., McIvor, C. C. 1984. *The ecology of tidal freshwater marshes of the United States east coast: a community profile. US Fish Wild. Serv. FWS/OBS-83/17*. 177 pp.
100. Odum, W. E., Zieman, J. C., Heald, E. J. 1973. The importance of vascular plant detritus to estuaries. In *Coastal Marsh and Estuary Management*, ed. R. H. Chabreck, pp. 91–114. Baton Rouge: La. State Univ. Press
101. Pearcy, R. W., Ustin, S. L. 1984. Effects of salinity on growth and photosynthesis of three California tidal marsh species. *Oecologia* 62:68–73
102. Pemadasa, M. A., Balasubramaniam, S., Wijewansa, H. G., Amarasinghe, L. 1979. The ecology of a salt marsh in Sri Lanka. *J. Ecol.* 67:41–63
103. Phleger, C. F. 1971. Effect of salinity on growth of a salt marsh grass. *Ecology* 52:908–11
104. Pomeroy, L. R., Wiegert, R. G. 1981. *The Ecology of a Salt Marsh*. New York: Springer-Verlag. 271 pp.
105. Ranwell, D. O. 1972. *Ecology of Salt Marshes and Sand Dunes*. London: Chapman & Hall
106. Redfield, A. C. 1972. Development of a New England salt marsh. *Ecol. Monogr.* 42:201–37
107. Remane, A. 1934. Die Brackwasser fauna. *Verh. Dtsch. Ges.* 36:34–74
108. Schubauer, J. P., Hopkinson, C. S. 1984. Above- and belowground emergent macrophyte production and turnover in a coastal marsh ecosystem, Georgia. *Limnol. Oceanogr.* 29:1052–65
109. Serodes, J. B., Troude, J. P. 1984. Sedimentation cycle of a freshwater tidal flat in the St. Lawrence estuary. *Estuaries* 7:119–27
110. Shaw, S. P., Fredine, C. G. 1956. *Wetlands of the U.S. US Fish and Wild. Serv. Circ. 39*. 69 pp.
111. Shima, L. J., Anderson, R. R., Carter, V. P. 1976. The use of aerial color infrared photography in mapping the vegetation of a freshwater marsh. *Chesapeake Sci.* 17:74–85
112. Shubel, J. R., Hirschberg, D. J. 1978. Estuarine graveyards, climatic change and the importance of the estuarine environment. In *Estuarine Interactions*, pp. 285–302. New York: Academic Press
113. Simpson, R. L., Good, R. E., Leck, M. A., Whigham, D. F. 1983. The ecology of freshwater tidal wetlands. *Bioscience* 33:255–59
114. Simpson, R. L., Good, R. E., Walerk, R., Frasco, B. R. 1981. *Dynamics of nitrogen, phosphorous, and heavy metals in Delaware River freshwater tidal wetlands. Tech. Rep. E.P.A. Grant R-805908 (Corvallis)*. 192 pp.
115. Simpson, R. L., Whigham, D. F., Walker, R. 1978. Seasonal patterns of nutrient movement in a freshwater tidal marsh. See Ref. 47, pp. 243–58
116. Smith, K. K., Good, R. E., Good, N. F. 1979. Production dynamics for above- and belowground components of a New Jersey *Spartina alterniflora* tidal marsh. *Estuarine Coastal Mar. Sci.* 9:189–201
117. Smith, T. J. III, Odum, W. E. 1981. The effects of grazing by snow geese on coastal salt marshes. *Ecology* 62:98–106
118. Smock, L. A., Harlowe, K. L. 1983. Utilization and processing of freshwater wetland macrophytes by the detritivore *Asellus forbesi*. *Ecology* 64:1556–65
119. Stevenson, J. C., Heinle, D. R., Flemer, D. A., Small, R. J., Rowland, R. A., Ustach, J. F. 1977. Nutrient exchanges between brackish water marshes and the estuary. In *Estuarine Processes*, ed. M. Wiley, pp. 219–40. New York: Academic
120. Swain, F. M. 1973. Marsh gas from the Atlantic coastal plain. *Adv. Org. Geochem. Proc. 6th Cong. Org. Geochem.* pp. 673–87
121. Teal, J. M. 1962. Energy flow in the salt marsh ecosystem of Georgia. *Ecology* 43:614–24
122. Tenore, K. R., Cammen, L., Findlay, S. E. G., Phillips, N. 1982. Perspectives of research on detritus: do factors controlling the availability of detritus to macroconsumers depend on its source? *J. Mar. Res.* 40:472–90

123. Turner, C. S. 1978. Decay of two freshwater tidal marsh plants. MS Thesis. Univ. Virginia, Charlottesville
124. Valiela, I. 1984. *Marine Ecological Processes.* New York: Springer-Verlag. 546 pp.
125. Valiela, I., Koumjian, H., Swain, T., Teal, J., Hobbie, J. E. 1979. Cinnamic acid inhibition of detritus feeding. *Nature* 280:55–57
126. Valiela, I., Teal, J. M. 1979. The nitrogen budget of a salt marsh ecosystem. *Nature* 280:652–56
127. Valiela, I., Teal, J. M., Persson, N. Y. 1976. Production and dynamics of experimentally enriched salt marsh vegetation: below ground biomass. *Limnol. Oceanogr.* 21:245–52
128. Valiela, I., Teal, J. M., Volkman, S. B., Shafer, D., Carpenter, E. J. 1978. Nutrient and particulate fluxes in a salt marsh ecosystem: tidal exchanges and inputs by precipitation and groundwater. *Limnol. Oceanogr.* 23:798–812
129. Valiela, I., Wilson, J., Buchsbaum, R., Rietsma, C., Bryant, D., Foreman, K., Teal, J. 1984. Importance of chemical composition of salt marsh litter on decay rates and feeding by detritivores. *Bull. Mar. Sci.* 35:261–69
130. Van Dyke, N. L. 1978. *Oxygen demand of decaying freshwater and salt marsh vegetation.* MS Thesis, Univ. Virginia, Charlottesville
131. Van Raalte, C., Valiela, I., Teal, J. M. 1976. Production of epibenthic salt marsh algae: light and nutrient limitation. *Limnol. Oceanogr.* 21:862–72
132. Webb, J. W. 1983. Soil water salinity variations and their effects on *Spartina alterniflora*. *Cont. Mar. Sci.* 26:1–13
133. Whigham, D. F., McCormick, J., Good, R. E., Simpson, R. L. 1978. Biomass and primary production in freshwater tidal wetland of the middle Atlantic coast. See Ref. 47, pp. 3–20
134. Whigham, D. F., Simpson, R. L. 1976. The potential use of freshwater tidal marshes in the management of water quality in the Delaware River. In *Biological Control of Water Pollution,* ed. J. Tourbier, R. W. Pierson, pp. 173–86. Philadelphia: Univ. Penn Press
135. Whigham, D. F., Simpson, R. L., Lee, K. 1980. The effect of sewage effluent on the structure and function of a freshwater tidal marsh ecosystem. *Tech. Compl. Rep., US Dept. Int., Office Water Resourc. Tech. Proj. B-60-NJ.* 159 pp.
136. Wiebe, W. J., Christian, R. R., Hansen, J. A., King, G. 1981. Anaerobic respiration and fermentation. See Ref. 104, pp. 137–60
137. Wohlgemuth, M. 1987. *Net aerial primary production estimates of* Peltandra virginica *(L.) using harvest and tagging techniques.* Pap. pres. Ninth Int. Estuarine Res. Conf., New Orleans
138. Yelverton, G. F., Hackney, C. T. 1986. Flux of dissolved organic carbon and pore water through the substrate of a *Spartina alterniflora* marsh in North Carolina. *Estuarine Coastal Shelf Sci.* 22:255–67
139. Zedler, J. B. 1977. Salt marsh community structure in the Tijuana estuary, California. *Estuarine Coastal Mar. Sci.* 5:39–53
140. Zeikos, J. G. 1977. The biology of methanogenic bacteria. *Bacteriol. Rev.* 41:514–41

Annual Review of Ecology and Systematics
Volume 19, 1988

CONTENTS

INSECT SEASONALITY: WHY?, *H. Wolda* 1

MARINE PLANKTON FOOD CHAINS, *Tom Fenchel* 19

SYSTEMATICS OF THE *RANA PIPIENS* COMPLEX: PUZZLE AND PARADIGM, *David M. Hillis* 39

VARIATION IN INTERSPECIFIC INTERACTIONS, *John N. Thompson* 65

NUTRIENT LIMITATION OF NET PRIMARY PRODUCTION IN MARINE ECOSYSTEMS, *Robert W. Howarth* 89

MARINE PLANT-HERBIVORE INTERACTIONS: THE ECOLOGY OF CHEMICAL DEFENSE, *Mark E. Hay and William Fenical* 111

COMPARATIVE ECOLOGY OF TIDAL FRESHWATER AND SALT MARSHES, *William E. Odum* 147

PARENT-OFFSPRING CONFLICT, SIBLING RIVALRY, AND BROOD SIZE PATTERNS IN PLANTS, *R. Uma Shaanker, K. N. Ganeshaiah and Kamaljit S. Bawa* 177

THE EVOLUTION OF ECOLOGICAL SPECIALIZATION, *Douglas J. Futuyma and Gabriel Moreno* 207

MACROEVOLUTIONARY COMPARISONS OF HOST AND PARASITE PHYLOGENIES, *Daniel R. Brooks* 235

HYDROPHILOUS POLLINATION, *Paul Alan Cox* 261

ENVIRONMENTAL HETEROGENEITY AND THE COEXISTENCE OF DESERT RODENTS, *Burt P. Kotler and Joel S. Brown* 281

EL NIÑO-SOUTHERN OSCILLATION 1982–1983: NEARSHORE POPULATION, COMMUNITY, AND ECOSYSTEM RESPONSES, *Peter W. Glynn* 309

DIPTEROCARP BIOLOGY AS A WINDOW TO THE UNDERSTANDING OF TROPICAL FOREST STRUCTURE, *Peter S. Ashton* 347

(*continued*)

MASS MORTALITY OF *DIADEMA ANTILLARUM* IN THE CARIBBEAN: WHAT HAVE WE LEARNED?, *H. A. Lessios* 371
THE PROCESSES OF EVOLUTION: TOWARD A NEWER SYNTHESIS, *John A. Endler and Tracy McLellan* 395
THE EVOLUTION OF ESS THEORY, *Thomas L. Vincent and Joel S. Brown* 423
PHYLOGENIES AND QUANTITATIVE CHARACTERS, *Joseph Felsenstein* 445
THE CONTRIBUTION OF POPULATION AND COMMUNITY BIOLOGY TO CONSERVATION SCIENCE, *Daniel Simberloff* 473
VICARIANCE BIOGEOGRAPHY, *E. O. Wiley* 513
THE ECOLOGY OF KIN RECOGNITION, *Bruce Waldmann* 543
THE UNDERGROUND IN GRASSLANDS, *N. L. Stanton* 573
INDEXES
Subject Index 591
Cumulative Indexes of Contributing Authors, Volumes 15–19 603
Cumulative Indexes of Chapter Titles, Volumes 15–19 605