FWS/OBS-83/17
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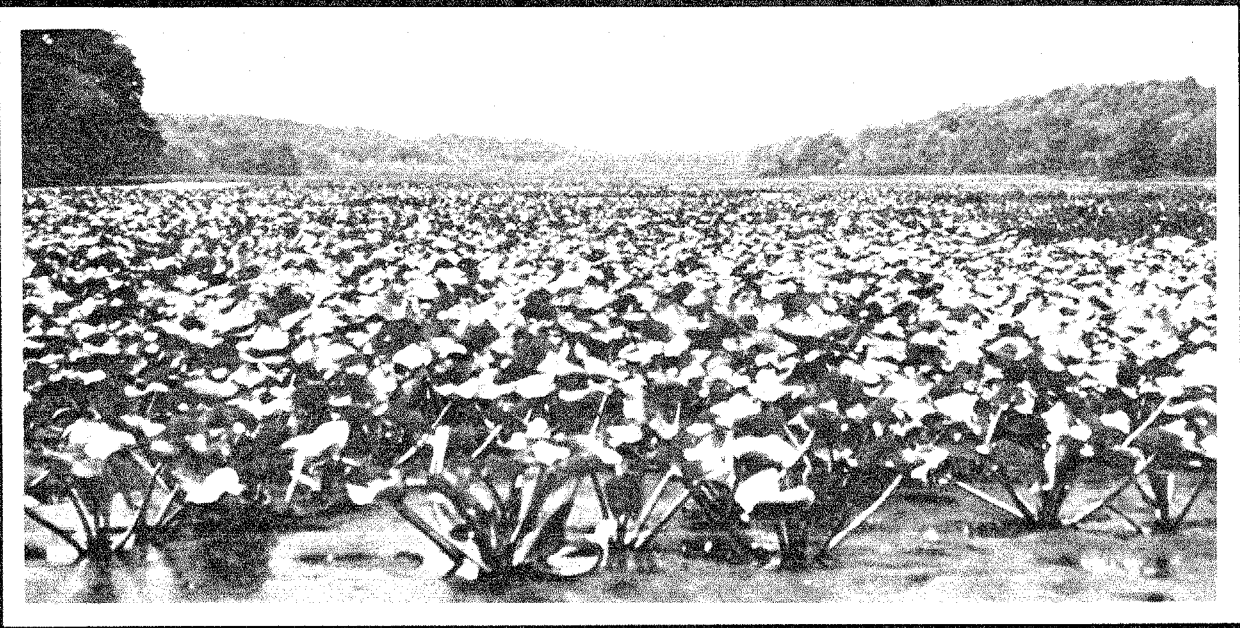
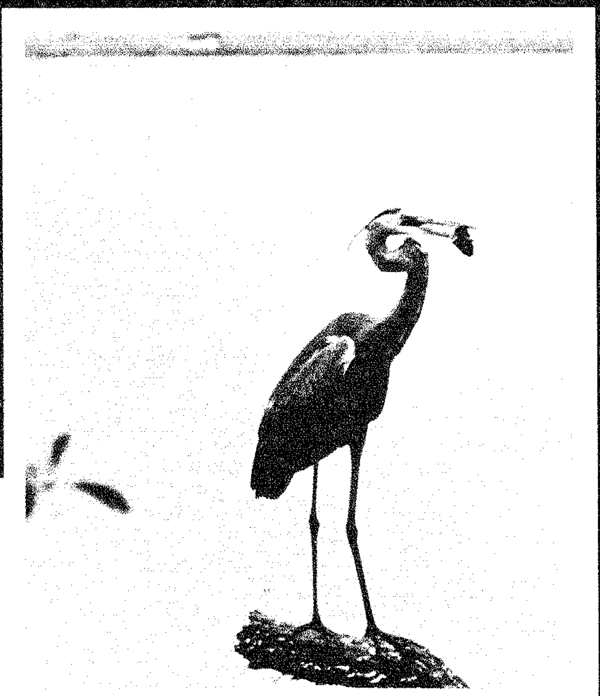
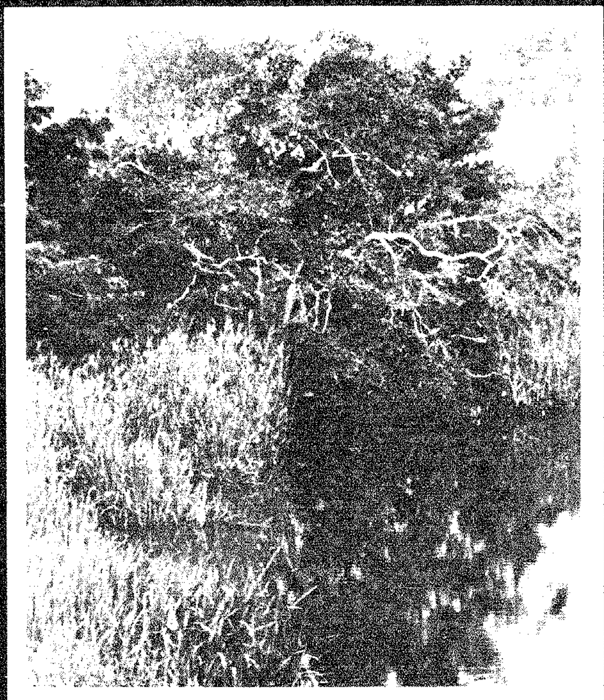
THE ECOLOGY OF TIDAL FRESHWATER MARSHES OF THE UNITED STATES EAST COAST: A Community Profile







Fish and Wildlife Service

U.S. Department of the Interior

FWS/OBS-83/17
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THE ECOLOGY OF TIDAL FRESHWATER MARSHES OF THE UNITED STATES EAST COAST: A COMMUNITY PROFILE

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Division of Biological Services
Research and Development
Fish and Wildlife Service
U.S. Department of the Interior
Washington, DC 20240

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Library of Congress Card Number: 83-600579

This report should be cited as:

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.

PREFACE

This report is part of a series of community profiles produced by the Fish and Wildlife Service to provide up-to-date information on coastal ecological communities of the tidal freshwater marsh community along the Atlantic coast from southern New England to northern Florida.

Tidal freshwater marshes occupy the uppermost portion of the estuary between the oligohaline or low salinity zone and nontidal freshwater wetlands. By combining the physical process of tidal flushing with the biota of the freshwater marsh, a dynamic, diverse, and distinct estuarine community has been created. The profile covers all structural and functional aspects of the community: its geology, hydrology, biotic components, and energy, nutrient and biomass cycling.

A major purpose of the community profile series is to gather and synthesize the diverse bits of ecological information existing on each community and, further, to condense this information into a coherent and practical habitat guide. The following discussion has been a true synthetic effort on the part of the authors. Their careful compilation and analysis of available data represent an extensive compendium of knowledge of this important natural resource and wildlife habitat.

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

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ACKNOWLEDGMENTS

This publication owes its existence to a number of individuals and organizations. Significant contributions of information, unpublished data, and helpful advice came from J.B. Birch, Glen Carawam, Bob Christian, Domenic Ciccone, Tom Curtis, Charlene D'Avanzo-Van Raalte, Michael Dunn, Larry Gerry, Bob Harriss, Dan Holder, Marjorie Holland, Erik Kiviat, Roy Lewis III, Harold Olson, Nick Roark, Steve Ross, Fairfax Settle, Catherine Turner, Nancy Van Dyke, Mike Weinstein, Tom Wolaver, and Patricia Young.

We particularly appreciate the unselfish help of Ed Pendleton, Wiley Kitchens, and the staff of the National Coastal Ecosystems Team of the U.S. Fish and Wildlife Service. The draft manuscript was reviewed for scientific content by Ralph Andrews, Breck Bowden, Glenn Kinser, James Kirkwood, John Organ, Gene Silberhorn, Robert Simpson, Ralph Tiner, Dennis Whigham, and Bob Zepp. All of these reviewers provided information as well as critical comments.

We would like to especially thank David Brime of the Virginia Game and Fish Commission. Without his help and support our research on the tidal freshwater wetlands of the Chickahominy Wildlife Management area would not have been possible. It is this research which provided the basis for much of this book.

Factual errors and faulty conclusions are the sole responsibility of the authors. Carole McIvor has taken primary responsibility for Chapter 5; Tom Smith for Chapters 6, 7, and 8; John Hoover for Chapter 2 and Section 3.1; and Bill Odum for the remainder of the book, including general organization. Unless otherwise noted, photographs and figures were produced by the authors.

Final copy of this manuscript was prepared by the staff of the National Coastal Ecosystems Team. Barbara Carney, Daisy Singleton, and Nonie Wilson typed the profile. Charlotte Willett edited the report, and Rae Ann Martin proofread it. Graham Golden drew several of the final figures and designed the cover. Sue Lauritzen prepared the final layout of the camera-ready manuscript.

CONVERSION FACTORS

Metric to U.S. Customary

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

U.S. Customary to Metric

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

CHAPTER 1. INTRODUCTION

1.1 DEFINITION AND LOCATION

Tidal freshwater wetlands are a distinctive type of ecosystem located upstream from tidal saline wetlands (salt marshes) and downstream from nontidal freshwater wetlands (Figure 1). They are characterized by (1) near freshwater conditions (average annual salinity of 0.5 ppt or below except during periods of extended drought), (2) plant and animal communities dominated by freshwater species, and (3) a daily, lunar tidal fluctuation.

In a classification system based on salinity, these wetlands lie between the oligohaline zone and nontidal freshwater (Figure 1). The lack of dominance by estuarine marshgrasses (Spartina) differentiates tidal freshwater marshes from oligohaline and higher salinity marshes. Oligohaline estuarine marshes tend to be dominated by big cordgrass (S. cynosuroides) and saltier estuarine marshes by saltmeadow hay (S. patens) and smooth cordgrass (S. alterniflora). Tidal freshwater marshes, on the other hand, are characterized by a large and diverse group of broad-leafed plants, grasses, rushes, shrubs, and herbaceous plants (see Table 4, Appendix A).

This wetland type has been variously classified as tidal freshwater (Odum et al. 1978; Lippson et al. 1979), freshwater tidal (Whigham et al. 1978), transition marsh combined with arrow-arum and pickerelweed marsh (Daiber et al. 1976), coastal shallow fresh marsh (Shaw and Fredine 1956), fresh marsh combined with intermediate marsh (Chabreck 1972), estuarine river marsh (Stewart 1962), and palustrine emergent wetland (Cowardin et al. 1979). All of these terms are basically synonymous. We have chosen to use tidal freshwater marsh because it is convenient and widely used.

In the U.S. Fish and Wildlife Service's classification system of wetlands (Cowardin et al. 1979), tidal freshwater marshes are classified as either of the following: (1) system: palustrine; class: emergent wetland; subclasses: persistent and nonpersistent, or (2) system: riverine; class: emergent wetland; subclass: nonpersistent. Water regime modifiers for either classification are: permanently flooded-tidal, regularly flooded, or seasonally flooded-tidal. The system selected depends on the position of the marsh with respect to the river channel. High back marshes with persistent vegetation are more properly termed palustrine; fringing low marshes along river edges are properly classified as riverine.

1.2 GEOGRAPHICAL DISTRIBUTION

The most extensive development of tidal freshwater marshes in North America occurs on the United States east coast between Georgia and southern New England. The two regions with the greatest area of this type of wetland are in the mid-Atlantic States and South Carolina and Georgia (Table 1).

The distribution of extensive tracts of tidal freshwater marshes follows an interesting pattern (Figure 2). They appear to be best developed in locations which have (1) a major influx of freshwater, usually a river, (2) a daily tidal amplitude of at least 0.5 m (1.6 ft), and (3) a geomorphological structure which constricts and magnifies the tidal wave in the upstream portion of the estuary.

In southern New England, where large river systems are relatively scarce, ex-

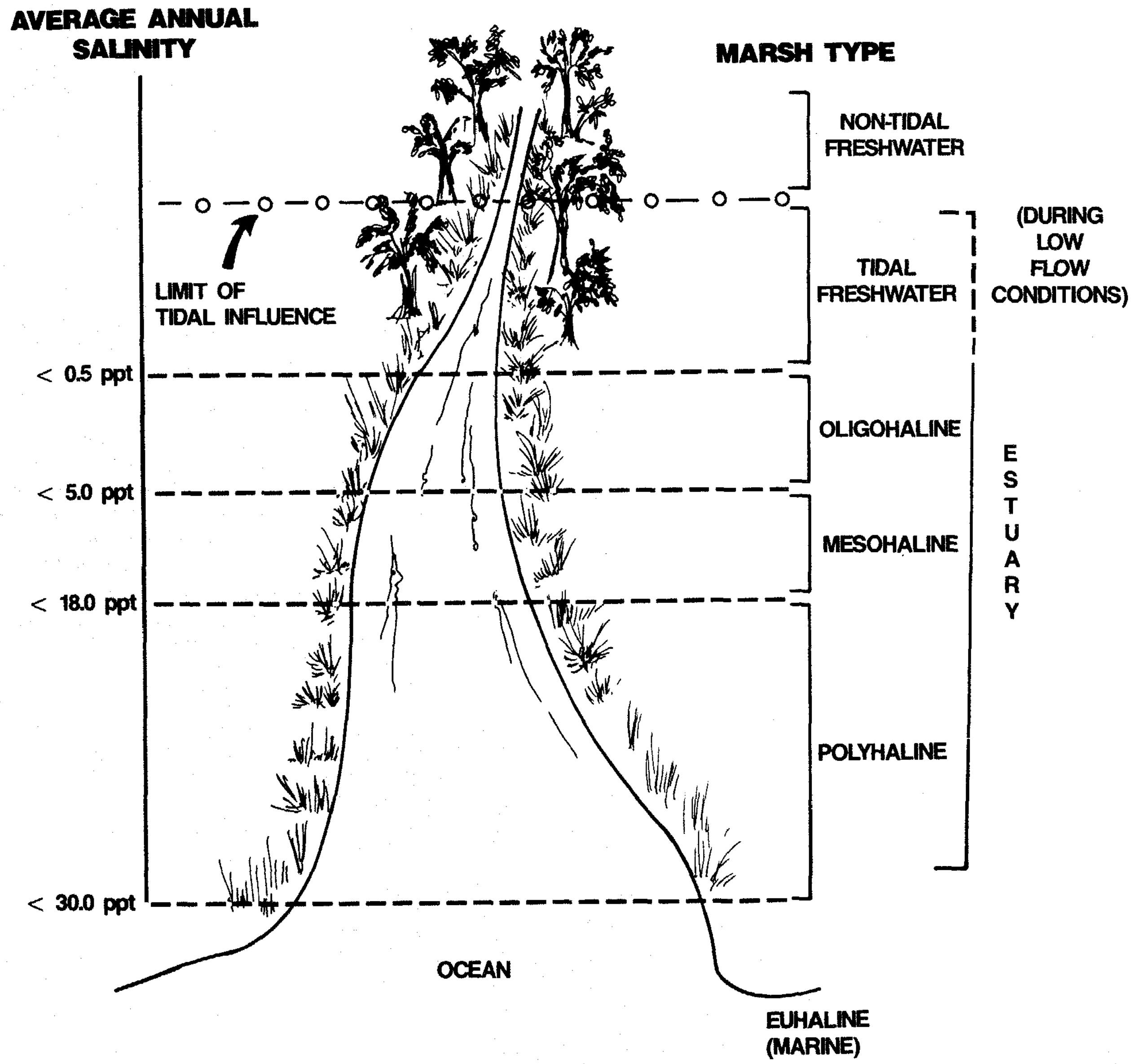


Figure 1. The relationship between marsh type and average annual salinity (values are approximate only). Terminology is based on Cowardin et al. (1979).

tensive tidal freshwater marshes are uncommon. They occur along the Hudson River, Connecticut River, and a few smaller rivers such as the Mystic and the North Rivers. In northern New England and much of eastern Canada, geomorphological conditions (steep, rocky coastlines) are not conducive for tidal freshwater marsh development on a large scale. One exception is the St. Lawrence River system which has a tidal freshwater zone with marsh areas as large as 400 ha (1,000 acres) (Reed 1978).

From New Jersey south to Virginia and throughout the Chesapeake Bay region, tidal freshwater marshes are abundant and often extensive in size. A noteworthy gap in the distribution occurs through much of North Carolina (Figure 2). In this region most estuaries lie behind closely spaced barrier island systems (e.g., the Outer Banks). This results in a greatly dampened tidal amplitude within the lower

Table 1. Conservative estimates of acreages of tidal freshwater marshes on the United States east coast. Figures in parentheses are hectares.

State	Estimated area ha (acres)	References	Comments
Florida	No reliable estimate or observations available		
Georgia	19,040 (47,047)	Wilkes (1976) Mathews et al. (1980)	Estimate may include some tidal swamp and non-tidal freshwater marsh
South Carolina	26,115 (64,531)	Tiner (1977)	South Carolina also has 28,511 ha (70,451 acres) of "coastal impoundments" which contain considerable acreage of tidal freshwater marsh
North Carolina	1,200 (3,000)	U.S. Army Corps of Engineers (1979); Wilson (1962)	18,600 ha (46,000 acres) of "shallow fresh marsh" reported by Wilson are not tidal freshwater by our definition; reported area is on the Cape Fear River
Virginia	16,000 (39,000)	Gene Silberhorn (unpublished data) (1954)	Precise estimate based on the Virginia wetlands inventory
Maryland	10,345 (25,563)	McCormick and Somes (1982)	Appears to be an excellent estimate and an improvement on earlier State and Federal estimates
Delaware	823 (2,033)	Daiber et al. (1976)	There are an additional 4230 ha (10,452 acres) of "transition marsh" which is very similar to tidal freshwater marsh
Pennsylvania	400 (1,000)	Our observations	Rough estimate; located along the Delaware River
New Jersey	89,000 (220,000)	Simpson et al. (1983)	Very rough estimate, may be too high
New York	400 (1,000)	Our observations	Rough estimate; located along Hudson River
Connecticut	444 (1,097)	Metzler and Rosza (1982)	421 ha (1,040 acres) associated with the Connecticut River and 23 ha (57 acres) along the Housatonic River
Rhode Island	40 (100)	Our observations	Very rough estimate
Massachusetts	400 (1,000)	Our observations	Along the North and Merrimack Rivers
New Hampshire and Maine	No estimate or observation available		
TOTAL	164,000 (405,000)		(an imprecise estimate)

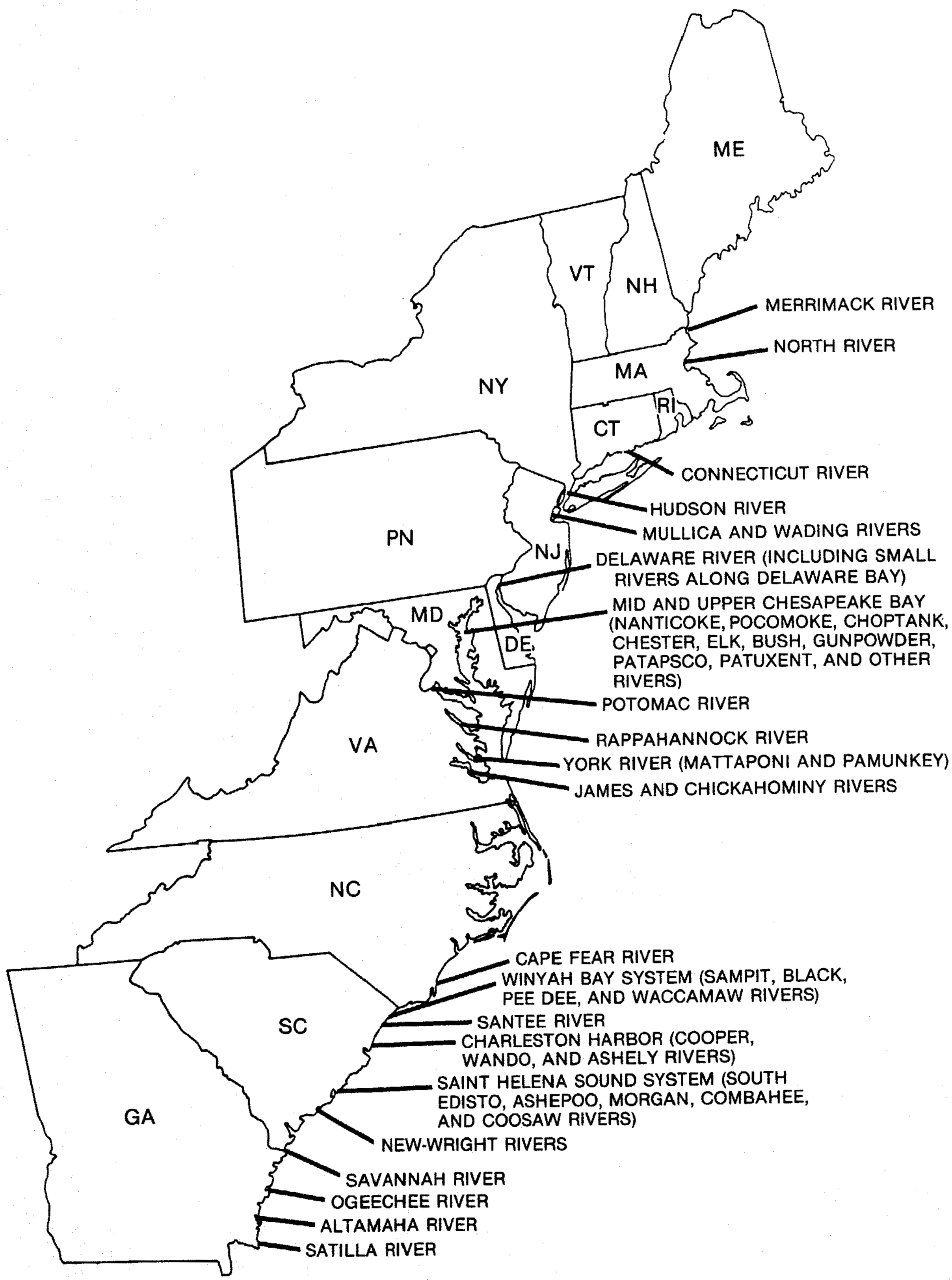


Figure 2. Representative areas with more than 200 ha (500 acres) of tidal freshwater marsh.

reaches of coastal rivers such as the Neuse and Pamlico. As a result, almost all North Carolina coastal river systems have sections which are both tidal and freshwater. However, the tidal range is slight; and tides are irregular, and greatly affected by the wind. Therefore, in North Carolina the types of plant communities typical of most east coast tidal freshwater sites (see Chapter 2) are restricted in size and are replaced by tidal swamps. The one major exception in North Carolina is the Cape Fear River system. It empties directly into the Atlantic Ocean, has a one-meter tide, and has extensive areas of typical tidal freshwater marshes.

South Carolina and Georgia contain numerous and often extensive tidal freshwater marshes. Many of these marshes and associated swamps were diked, impounded, and converted to ricefields during the 18th and first half of the 19th centuries. Some of these impoundments remain virtually intact. However, in others the dikes have broken and the impoundments have reverted to tidal marsh. A difficult management decision needs to be made as to whether the intact impoundments should be managed for waterfowl or should be allowed to revert to tidal marsh (discussed in Chapter 9).

The most southern major river system on the coast, the St. Johns River in Florida, has tidal influence for over 160 kilometers (99 mi) inland (L. Gerry, Jacksonville Water Control District, Palatka, Florida; pers. comm.). Due to its unusual morphology (narrow mouth, broad upper reaches), the tidal amplitude in the tidal freshwater stretch is minor, and typical plant communities are absent or restricted to small areas.

Tidal freshwater environments (including some mangrove areas) exist in south Florida. However, they are generally too restricted in size or too seasonal in occurrence (e.g., the Everglades estuary) to be included in this report.

Similar types of tidal freshwater marshes occur on other coasts of the United States. For example, Louisiana has extensive stretches of tidal, freshwater wetlands. However, these wetlands have a tide that is irregular, of low amplitude, and wind driven. This makes both the community structure and ecosystem processes appear to be somewhat different (Chabreck 1972; Hopkinson et al. 1978). Tidal freshwater marshes are relatively rare on the Pacific coast. They do occur extensively, however, in Alaska (McRoy and Goering 1974), in California in association with several large river systems including the Sacramento (Kelley 1966), and between Washington and Oregon in association with the Columbia River. (Clairain et al. 1978).

1.3 VISUAL APPEARANCE

Tidal freshwater marshes look strikingly different from either salt marshes or nontidal freshwater marshes. Plant diversity is much higher than that found in higher salinity estuarine marshes. The result is a highly heterogeneous plant assemblage (Figure 3) quite different in appearance from the almost monospecific *Spartina* marshes found nearer the mouth of the estuary. Zonation is present (discussed in Chapter 2) but is not as sharply defined as in salt marshes. The so-called low marsh is dominated by a few broad-leaved, fleshy plants such as spatterdock (*Nuphar luteum*) and pickerelweed and by wild rice (*Zizania aquatica*) and giant cutgrass (*Zizaniopsis miliaceae*). The higher sections of the tidal freshwater marsh contain more species than the low marsh and may be dominated by a variety of plants including cattail (*Typha* spp.), smartweeds (*Polygonums* spp.), rose-mallow (*Hibiscus moscheutos*), sweet flag (*Acorus calamus*), and burmarigold (*Biden* spp.). Certain species such as arrow-arum are found throughout the marsh.

The tidal freshwater marsh has plants in flower through much of the spring and summer. In the spring wild iris (*Iris* spp.) blooms in the high marsh. In early summer, pickerelweed sends up a spike of purple flowers. Rose-mallow, jewelweed (*Impatiens capensis*), and the spectacular yellow flowers of burmarigold bloom later in the summer.

One of the most striking features of the tidal freshwater marsh is the pronounced seasonal sequence of vegetation

Figure 3. Tidal freshwater marsh on the Chickahominy River, Virginia, during midsummer.

(discussed at length in Chapter 2). The low marsh undergoes particularly extreme changes. There is a period of virtually bare mud in late winter and early spring. Then there is a period of domination by broad-leaved plants (e.g., arrow-arum) in the late spring, and finally in late summer there is a period dominated by grasses and herbaceous plants (Figures 4a,b).

Conspicuous organisms in the tidal freshwater marsh include freshwater snakes and turtles, adult and larval insects, ducks and geese, and muskrats. A casual examination of the fauna of the tidal freshwater marsh reveals few bivalves, crustaceans, or polychaetes, organisms which dominate the higher salinity marshes in the lower estuary.

In summary, the tidal freshwater marsh appears superficially different from the nearby salt marshes. In Chapter 10 we discuss whether these apparent differences actually exist and whether they include aspects of community structure and ecosystem processes.

1.4 HORIZONTAL, TEMPORAL, AND REGIONAL VARIATIONS

Tidal freshwater ecosystems form a complex gradient with freshwater on one side and oligohaline and higher salinity esturine conditions on the other side. Concentrations of dissolved oxygen, particulate and dissolved carbon, dissolved heavy metals, nitrite, nitrate, ammonia, and other chemical and physical water and sediment parameters change dramatically as salinities increase from 0.1 to 1.0 ppt (Morris et al. 1978). Fish, plant, and invertebrate communities change significantly as the salinity rises above 1 ppt. Rarely are conditions homogeneous over a very great distance. For this reason, general statements about tidal freshwater marshes and associated bodies of water must always be made with gradient conditions in mind.

Tidal freshwater wetlands vary temporally as well as spatially. Daily, seasonal, and long-term changes may occur at a given site in response to tidal or wind influences and as a result of annual or

Figure 4a. Tidal freshwater marsh on James River in early spring.

Figure 4b. Tidal freshwater marsh on James River in late summer.

longer-term variations in freshwater runoff. A marsh that experiences higher salinities during periods of drought may switch to tidal freshwater characteristics after prolonged rains. A slight increase in salinity during one summer may change the plant composition of a tidal freshwater marsh for several years. Tidal freshwater marshes lie in a dynamic transition zone between freshwater and saltwater.

Although we treat the tidal freshwater marsh as a general wetland type on the Atlantic coast, there are clear regional differences in flora, fauna, and physical characteristics. For example, New England marshes appear to have more peat than mid-Atlantic marshes. The muskrat is a plentiful herbivore in mid-Atlantic marshes but is absent in the coastal marshes of South Carolina and Georgia (discussed in Chapter 8). The brackish water fiddler crab (Uca minax) occurs throughout tidal freshwater in South Carolina and Georgia (J. Birch, Institute of Ecology, University of Georgia, Athens; pers. comm.), but is usually found in oligohaline and higher salinities in the Chesapeake region (Kerwin 1971, and our personal observations). The bowfin and the pirate perch are plentiful members of the fish communities throughout tidal freshwaters of South Carolina and Georgia, but are generally restricted to nontidal freshwater in the Chesapeake region (see Section 5.7).

1.5 GEOLOGICAL HISTORY

It is difficult to generalize about the geological history of tidal freshwater environments on the Atlantic coast because considerable variability exists from one region to the next. New England river systems such as the Connecticut and Hudson are incised into highly resistant Paleozoic and Lower Mesozoic bedrock. (Frey and Basan 1978). Clay minerals are in relatively short supply. Further south, along the coasts of South Carolina and Georgia, coastal river systems have cut into bedrock which is mainly Upper Mesozoic and Cenozic. Thick, well-developed saprolites (mineral soils) of the southern Piedmont provide abundant clay for redistribution into both tidal freshwater and estuarine marshes along the coast.

In general the river systems of the mid-Atlantic and south Atlantic Coastal Plains tend to be more numerous, more extensive, and fed by greater quantities of runoff. For these reasons, the tidal freshwater marshes in Maryland, Virginia, Georgia, and South Carolina are much vaster than the states north of New Jersey.

For a variety of reasons (e.g., slower decomposition rates, freezing of marsh surfaces during the winter, and differences in vegetation), most New England coastal marshes tend to have more peat than southern coastal marshes (Frey and Basan 1978). Southern marshes, on the other hand, have sediments with a higher clay and silt content.

In spite of these regional differences in geology and sediments, the recent geological history of east coast tidal freshwater marshes is similar. Virtually all contemporary marshes are very recent in origin (Holocene). They lie in river valleys which were cut during Pleistocene periods of lowered sea level. As sea level rose during the post-Wisconsin period of the Holocene (5,000 to 15,000 Before Present [BP]), both tidal freshwater and estuarine marshes expanded rapidly as the lower stretches of drowned river systems were inundated (Ellison and Nichols 1976). There is excellent evidence (Froomer 1980a, 1980b) which suggests that coastal marsh expansion has continued at a relatively rapid rate to the present. In fact, Froomer (1980b) concluded that the rate of coastal marsh building in the mid-Atlantic region has been accelerated over the past three centuries due to increased soil runoff associated with man's activities. He reported an average vertical growth in marsh sediments of 27.4 cm/century for estuarine and tidal freshwater marshes in the northern portion of Chesapeake Bay. Because of these high rates of deposition, many tidal freshwater marshes have started and have grown to considerable extent in only the last few centuries.

The recent geological history of tidal freshwater marshes can be demonstrated by examining a vertical profile taken from corings through a contemporary marsh. A typical sequence through a mid-Atlantic marsh could show (1) a hard bottom consisting of a Pleistocene erosion surface (bedrock) cut during a glacial period of lowered sea level; (2) varying layers of river, estuarine, and marsh sediments; and (3) a cap of recent tidal freshwater marsh sediments varying in thickness from less than 1 m (3 ft) to more than 10 m (30 ft). Of course, very young marshes might be underlain by layers of sand or clay and have only a thin layer of marsh sediments on the top.

Even though contemporary tidal freshwater marshes are generally less than 15,000 years of age and most are much younger, this does not mean that this type of wetland did not exist in earlier geological periods. Certainly, during Pleistocene periods of reduced sea level, all types of coastal marshes were relatively reduced in extent. There is ample evidence from coal deposits, however, which shows that early equivalents of our present-day tidal freshwater marshes existed hundreds of millions of years ago.

1.6 MARSH DEVELOPMENTAL STAGE

In the same way that all wetlands pass through various stages of development, tidal freshwater marshes have certain geomorphological and ecological characteristics which tend to reflect their geological age. Frey and Basan (1978) have classified coastal estuarine marshes into three categories: (1) young marshes which are largely low or intertidal marsh, (2) mature marshes which are a mixture of low and high marsh, and (3) old marshes which are largely high marsh.

We feel that this classification system, while somewhat simplistic, is equally useful in studying tidal freshwater marshes. Young tidal freshwater marshes, of a few hundred years of age or less, are typically low-lying, largely intertidal, and dominated by vegetation of the low marsh (spatterdock, arrow-arum, and wild rice). Old marshes are generally all high marsh (except along creek banks and around depressions), may not be flooded at all by neap tides, and are dominated by high marsh vegetation (e.g., cattails, marsh mallow, and iris). Mature marshes are intermediate in appearance and have a mixture of low and high marsh plants and geomorphology.

Of course, the apparent age of a specific marsh is influenced by more than its time of existence. Factors such as local physiography, latitude, rates of local subsidence, rates of local sea level change, degree of wave and current action, suspended sediment loadings, vegetation type, alterations by man (e.g., conversion to rice fields in South Carolina), and local rates of net primary production all influence the stage or age of the marsh. Taking these factors into consideration and remembering that apparent chronological age may be misleading, it is still convenient to use the concept of young, mature, and old in describing the visual state of a specific marsh.

1.7 SUBSTRATES

Sediments underlying most tidal freshwater marshes are typically dark-colored and sticky with a high content of silt and clay. Usually, the marshes are located in the section of the estuary with the highest rates of sedimentation (Nichols 1972). This accreting material, largely clays and silts, combines with large quantities of organic detritus to form a dark, mucky soil. From the viewpoint of the U.S. Fish and Wildlife Service (Cowardin et al. 1979), the low marsh can generally be regarded as having a mineral soil (less than 50% organic matter) and the high marsh a mixture of mineral soils and organic soils (greater than 50% organic matter), depending on the location within the marsh.

Peat may be present in the <u>Typha</u>-dominated high marsh in northern New England marshes and in the giant cutgrass marshes of the Southeast. However, it is not as common as in salt marshes. Because tidal freshwater marsh sediments have a lower biomass of plant roots and peat (particularly in the low marsh), they are more erodable than estuarine marsh sediments (Garofalo 1980). Areas covered with arrow-arum and spatterdock appear to be particularly vulnerable to winter erosion. Because of their erodible banks, tidal freshwater creeks tend to have lower meander amplitudes (sinuosity) than salt marsh creeks (see Chapter 10).

Generally, tidal freshwater marsh sediments have a high organic content which may vary considerably with depth and locations. Whigham and Simpson (1975) found that the marsh soils along the tidal freshwater portion of the Delaware River varied from 14% to 40% organic matter on a dry weight basis. Organic content was lower in the arrow-arum-dominated low marsh (14% to 30%) compared to the sweet flag-cattail-dominated high marsh (30% to 40%). Volatile solids (a parameter related to organic content) from a James River marsh ranged from 10% to 20% (Lunz 1978). In other Virginia tidal freshwater marshes, we have found a range in soil organic matter from 20% to 50%. The highest values were found in the high marsh (Hoover 1983). Bowden (1982) reported that the soils of the North River marsh in Massachusetts had from 50% to 75% organic matter; this difference from more southerly marshes may reflect either a dominance by different plant species or a slower annual rate of decomposition.

Water content tends to parallel organic content. For example, the James River marsh soils typically contain 50% water (Lunz 1978). On the other hand, water may compose as much as 88% of the fresh weight of North River marsh soils (Bowden 1982).

The combination of ample organic matter and iron along with at least some sulfur produces sediments which are usually anaerobic just below the surface. The degree of reducing conditions in tidal freshwater marsh sediments is difficult to determine. Since the reaction pairs for the oxidation-reduction reactions are not as obvious as the sulfur reduction reactions in salt marshes, classical redox (Eh) estimates have little obvious meaning for tidal freshwater sediments. The scant evidence which is available from our own research (presence of methanogens, negative Eh readings) has led us to conclude that tidal freshwater marsh sediments are moderately to strongly reducing.

Typical pH values for tidal freshwater sediments range from 6.0 to 6.5 (Schwartz 1976, Lunz et al. 1978). Wetzel and Powers (1978) measured the cation exchange capacity of sediments from a James River marsh and found values ranging from 39.6 to 67.3 meg x 100 g dry weight. This is a relatively high value compared to coastal plain and piedmont soils, but typical for highly organic, high clay wetland sediments (personal observation). These high values of cation exchange capacity also indicate a young, slightly weathered sediment with high nutrient availability.

A range of sediment nutrient concentrations is shown in Table 2. It should be noted that these limited data come from polluted sites. It is possible that unpolluted sediments might have lower nutrient concentrations.

As in other wetland sediments, ammonium is the most abundant form of inorganic nitrogen (Table 2). Nitrate and nitrite usually do not accumulate in anaerobic soils. This is because nitrification proceeds slowly while denitrification proceeds rapidly. Bowden (1982), who worked in the tidal freshwater marshes of the North River, Massachusetts, found that the amount of ammonium that is free in the interstitial water is often less than the amount of ammonium adsorbed loosely onto sediment particles. Consequently, the pool of available ammonium is probably much greater than the pool of free ammonium. Bowden also presents evidence that the amount of ammonium in tidal freshwater marsh sediments may be highest in midsummer and lowest in late spring, coincident with heavy demands for nitrogen from new vegetation. He found the highest concentrations near the surface (3.7 mg/l). Lower concentrations were found at 20-cm (8-inch) depth (0.9 mg/l), and an increase (2.0 mg/l) was found at 60-cm (24-inch) depth.

In summary, from limited information it appears that the sediments of tidal freshwater marshes typically have (1) a high organic content, (2) a pH in the 6.0 to 6.5 range, (3) moderate to strong reducing conditions, (4) a high cation exchange capacity, and (5) interstitial nutrient concentrations which are high in ammonium and low in nitrate and nitrite. Sediment and water nutrients are discussed further in Section 3.3.

Table 2. Concentrations of chemicals in the soils and interstitial water of three tidal freshwater marshes. na = not available, ± = one standard deviation.

Location and reference	Soil		Interstitial water		
	Total N (% dry wt.)	Total P (% dry wt.)	NH^{1} (g/l)	NO + NO (g/l)	Total dissolved P (g/l)
Herring Creek Marsh, James River, Va. (Lunz et al. 1978)	1.5±0.8	0.7±0.4	1600±1200	100±50	180±100
North River Marsh, Mass. (Bowden 1982)	1.6±1.9	0.1-0.3	900-3700	0-170	na
Hamilton and Woodbury Creek marshes. Delaware River (Simpson et al. 1981)	0.5-1.0	0.04-0.2	na	na	na
Hamilton marshes, Delaware River (Whigham et al. 1980)	1.03-1.64	0.12-0.35	na	na	na

1.8 HYDROLOGY AND WATER QUALITY

The hydrology of tidal freshwater marshes and associated streams and rivers is poorly studied. Presumably, this environment is more strongly influenced by the effects of inflowing riverine freshwater than the lower part of the estuary which, in most cases, is strongly influenced by oceanic tides. We have observed that changes in wind direction and velocity appear to have a greater effect on the daily tides at tidal freshwater sites than further down the estuary.

Certainly, more information is needed on the relative effects on tidal freshwater environments of upstream floods, droughts, ocean-induced tides, and wind. Perhaps most important of all, we need to know the extent to which the tidal freshwater marsh zone is able to absorb and buffer inputs of floodwater from upstream.

Water quality data from a variety of tidal freshwater sites are shown in Table 3. Unfortunately, all but one of these locations are highly eutrophic. The one exception, the Ware Creek marshes on the York River in Virginia, is a relatively pristine site, but has salinities slightly higher (annual average = 7 ppt) than a typical tidal freshwater marsh. However, the Ware Creek data have been included since the vegetation in these marshes contains many freshwater species.

Comparison of the nitrogen and phosphorous data in Table 3 with the criteria presented by Wetzel (1975) suggests that these tidal freshwater sites range from eutrophic (Ware Creek) to hypereutrophic (the remaining sites). Certainly, there are more than adequate nutrient levels to support high phytoplankton production. The generally high chlorophyll concentrations (Table 3) give further proof of a eutrophic environment. Unpublished data (T. Wolover, University of South Carolina, Georgetown, pers. comm.) confirm that even

Table 3. Water quality parameters from a variety of tidal freshwater locations arranged in approximate order of increasing eutrophication. DOC = total dissolved organic carbon, POC = total particulate organic carbon, TKN = total Kjehldahl nitrogen. TP = total particulate and dissolved phosphorous, DO = dissolved oxygen, na = not available. Where two values are given, one above the other, the upper value = summer, the lower value (in parentheses) = winter.

Location and reference	pH	DO (mg/l)	Chlor. A (g/l)	Alkalinity (meq/l)	DOC (mg/l)	POC (mg/l)	NH[1] (g/l)	NO +NO (g/l)[3]	TKN (g/l)	PO (g/l)	Total P (g/l)
Ware Creek Marsh, York River (Axelrad et al. 1976)	na	na	2.2-23.6	na	5-10	1-5	15-20	20-30	na	na	40-60
Hamilton and Woodbury Creek marshes, Delaware River (Simpson et al. 1981)	na	4-6 (10-12)	na	na	na	na	40-80	40-300	na	5-20	5-50
Herring Creek Marsh, James River (Adams 1978)	7.3 (8.0)	6.9 (12.3)	13.9 (0.9)	na (0.39)	3.8 (9.1)	na (1.5)	470 (460)	500 (1600)	4200 (3300)	40 (30)	160 (180)
Tinicum Marsh, Delaware River (Grant and Patrick 1970)	na	0.6-11.2	na	0.8-2.0	na	na	500-6000	300-1000	na	na	na
Potomac River (Lippson et al. 1979)	na	4-6 (12-13)	50+	na	na	na	200-800	350+	na	na	400-700

unpolluted tidal freshwater sites have high levels of dissolved nitrogen and phosphorous compounds during much of the year.

Since dissolved nutrient levels are more than adequate to support high phytoplankton production, the factor limiting production is probably water clarity. In fact, most tidal freshwater regions are considerably more turbid than nearby upstream freshwater areas (authors' personal observations). This relatively great turbidity can be largely attributed to high suspended sediment loads and high phytoplankton standing crops. Adams (1978) reported suspended solid values of 25-27 mg/l for water flushing the Herring Creek Marsh on the James River. Ellison and Nichols (1976) give a range of 5.7 to 93.0 mg/l for suspended sediment in Virginia tidal freshwater regions. They also reported typical Secchi disc readings of 0.2 to 1.2 m (0.7 to 3.9 ft).

Examination of Table 3 also shows relatively high concentrations of dissolved and particulate organic carbon. The combined effects of high suspended sediment loads, high organic content sediments, high nutrient levels, and high phytoplankton production can cause low dissolved oxygen values in the summer (Table 3). Our observations suggest that it is not unusual to have dissolved oxygen (DO) values below 2 ppm in pristine stretches of small tidal freshwater creeks during the early morning hours of summer months. Even lower concentrations can occur in locations in which pollutants add further biological oxygen demand (BOD) loadings (e.g., Tinicum Marsh near Philadelphia, Grant and Patrick 1970). This suggests that conditions may be limiting for many fishes in tidal freshwater marshes at times during the summer.

The limited data summarized above indicate that mid-Atlantic tidal freshwaters are generally (1) eutrophic or hypereutrophic, (2) contain high levels of suspended sediments, and (3) may have depressed oxygen concentrations during the summer.

CHAPTER 2. COMMUNITY COMPONENTS: PLANTS

2.1 INTRODUCTION

The physical characteristics which distinguish tidal freshwater wetlands (see Section 1.1) exert considerable influence on plant community development. Nearly all of these wetlands are riverine. The lack of stressful salinity levels facilitates utilization of this habitat by many more plant species than are found in coastal or inland brackish marshes. Such high diversity produces a complex and seasonally variable mixture of life forms. Unlike nontidal riparian wetlands where marsh vegetation is confined to a narrow band paralleling channels, regular inundation in tidal freshwater regions serves to laterally extend habitat boundaries. Plant communities visibly stratify across this broadened niche space, although distinct zonation is not readily apparent.

No known plant species appears exclusively in the tidal freshwater habitat. Most marshes are dominated by a combination of annuals and perennials, the majority of which are common to freshwater wetlands over much of North America (Fassett 1957, Cowardin et al. 1979; Silberhorn 1982). Latitudinal differences in climate as well as local variation in physiography and geology produce distinct heterogeneity within tidal freshwater marshes. Marshes in respective regions of the Atlantic coast differ markedly in plant species composition, relative diversity, and community structure as a result of this variation. Although tidal freshwater marshes share much in common with other wetlands as a whole, only a limited amount of available information pertains specifically to the flora and ecology of this habitat.

The discussion which follows will focus upon those plant species which most commonly occur in tidal freshwater marshes. Emphasis will be placed on descriptions of community structure and those physical and ecological processes influencing plant demography and succession. Habitat variability on a regional basis will be discussed, although in most instances the tidal marshes of the mid-Atlantic States will serve as a general model. Plant species are addressed by common names in the text; scientific names are listed in Appendix A.

2.2 GENERAL SPECIES/HABITAT DESCRIPTIONS

The bulk of tidal freshwater marsh flora consists of (1) broad-leaved emergent perennial macrophytes (spatterdock, arrow-arum, pickerelweed, arrowheads), (2) herbaceous annuals (smartweeds, tearthumbs, burmarigolds, jewelweed, giant ragweed, water-hemp, water-dock), (3) annual and perennial sedges, rushes and grasses (bulrushes, spike-rushes, umbrella-sedges, rice cutgrass, wild rice, giant cutgrass), (4) grasslike plants or shrubform herbs (sweetflag, cattail, rosemallow, water parsnip), and (5) a handful of hydrophytic shrubs (button bush, waxmyrtle, swamp rose) (Whigham et al. 1976; Tiner 1977; McCormick and Somes 1982; Metzler and Rosza 1982; Silberhorn 1982).

Regional variations in species composition and diversity persist, but have never been described comparatively. Marshes of the mid-Atlantic and Georgia Bight regions can contain as many as 50 to 60 species at a single location, and are comprised of a number of codominant taxa (Odum 1978; Sandifer et al. 1980). Among the more conspicuous species occurring in both regions are arrow-arum, pickerelweed, wild rice, and cattails. However, there are notable differences between the tidal freshwater marshes of these respective regions. Briefly, vegetation communities in South Carolina and Georgia are often either a nearly monospecific stand of giant cutgrass or a mixed community dominated by one or more of the aforementioned species plus sawgrass, alligatorweed, plumegrass, giant cordgrass or soft-stem bulrush. In Virginia, Maryland, and New Jersey, giant cutgrass becomes less prevalent, and plants such as spatterdock, various smartweeds and tearthumbs, sweetflag, rice cutgrass, and burmarigolds become more prolific.

The vegetation communities in New England tidal marshes generally harbor fewer species with perennial sedges and grasses becoming more conspicuous constituents. Important components of these northern marshes include reed bentgrass, various rushes and sedges, arrowheads, cattails and spiked loosestrife (Kiviat 1978a; Bowden 1982; Metzler and Rosza 1982).

Tidal freshwater swamps prevail along many tidal rivers from Virginia south, and are often closely associated with tidal freshwater marsh. Occurring primarily landward of the marsh, these forested areas are dominated by trees such as bald cypress, red maple, black gum, and tupelo gum (Silberhorn 1982). In addition, tidal swamps typically harbor an understory of emergent herbs and shrubs, many of which occur in the marsh. Some of these species include arrow-arum, jewelweed, royal fern, lizard's tail, Asiatic spiderwort, wax-myrtle, and alder.

In areas where salinities periodically extend into oligohaline ranges (0.5 to 5 parts per thousand [ppt]), species such as big cordgrass, common threesquare, narrow-leaved cattail, various smartweeds, arrow-arum, wild rice, marsh mallow, and water-hemp become the most prevalent community components (Phillip and Brown 1965; Sandifer et al. 1980; Ferren et al. 1981; Silberhorn 1982).

A survey of the literature on vascular plant populations in tidal freshwater marshes indicates an inherent variability in the composition and spatial distribution of plant communities. However, several dozen species occur consistently at many locations on the Atlantic Coastal Plain. A listing of common tidal freshwater wetland species plus their general characteristics and habitat preferences are given in Table 4. A more extensive listing of common and rare species appears in Appendix A.

2.3 COMMUNITY STRUCTURE

Species Composition

Plant communities can be classified by a number of characteristics including growth form dominance, species dominance, and species composition. Generally these characteristics define arbitrary boundaries between community types, but nevertheless are useful in describing vegetation patterns (Whittaker 1975). Although tidal freshwater marsh flora is not particularly well-suited to such a classification scheme due to its unusually high diversity, many attempts have been made to describe marshes in this manner (McCormick 1970; McCormick and Ashbaugh 1972; Whigham and Simpson 1975; Shima et al. 1976; Doumlele and Silberhorn 1978; McCormick and Somes 1982). In most instances, species dominance has been used as a primary means of classification, usually because vegetation units represented by nearly pure stands of a species are easily mapped. Our synthesis of this information has resulted in the classification of eight major floristic associations occurring in tidal freshwater wetlands from Massachusetts to northern Florida. Each of these associations, or community types, presumably results from reponse to a specific set of environmntal conditions or seasonal changes (see Sections 2.4 and 2.5) and can be described as follows:

1) Spatterdock Community type - Spatterdock can be found in distinctly pure stands (Figure 5), especially in late spring, in areas of the marsh adjacent to open water. Generally these areas are below the level of mean low water; therefore, during high tide, spatterdock stands are submerged rather deeply. Each period of inundation can be extensive. Sprouting from thick underground rhizomes, this species forms dense clonal colonies often covering submerged point bars on tidal creek meanders. As the growing season

Table 4. Common species of vascular plants occurring in the tidal freshwater habitat.

Species	General characteristics	Habitat preference	Salinity tolerance	Associated species
Acorus calamus (Sweetflag)	Grows in dense colonies propagating mainly by rhizome; stemless plants up to 1.5 m with stiff, narrow basal leaves; cylindrical inflorescence emerges from side of stem (open spadix); aromatic.	Shallow water or wet soil; channel margins	Fresh	Peltandra virginica Polygonum spp. Impatiens capensis
Alternanthera philoxeroides (Alligatorweed)	Hollow stems with simple branches bearing opposite, lance-shaped leaves; forms dense mats; flowers on long panicles; perennial.	Extremely adaptable; often emersed	Fresh to oligohaline	-------
Amaranthus cannabinus (Water-Hemp)	Erect, fleshy and stout; up to 2 m; leaves lanceolate with blades as long as 20 cm; not conspicuous until mid-summer when it towers above other marsh forbs.	Common to levee sections of the tidal marsh habitat; tolerates periodic inundation	Fresh to mesohaline	Peltandra virginica Polygonum spp. Bidens spp.
Asclepias incarnata (Swamp milkweed)	Tall, leafy, pink-flowered herb growing solitary or in small, loose groups; lance-shaped, opposite leaves; reproduces via seeds or rhizomes.	Cosmopolitan; grows in many wetland situations; high marsh species	Fresh to oligohaline	High marsh herbs
Bidens coronata Bidens laevis (Burmarigold)	Annual plants up to 1.5 m tall, solitary or in small scattered groups; loosely branched above with opposite leaves; leaf shape variable but generally toothed or lanceolate; impressive yellow bloom late in the growing season.	Cosmopolitan, growing in the upper two-thirds of the intertidal zone on wet mud or in shallow water	Fresh	Polygonum spp. Amaranthus cannabinus other Bidens spp.
Calamagrostis canadensis (Reed-bentgrass)	Slender grass up to 1.5 m, generally forming dense colonies; long, flat leaves; loose, ovoid panicle with purplish color; perennial.	Wet meadows and thickets	Fresh?	Typha spp. Acorus calamus
Carex spp. (Sedges)	Grasslike sedges, culms mostly 3-angled, bearing several leaves with rough margins; up to 2 m tall and usually in groups; perennial from long, stout rhizomes.	Low areas with frequent flooding or damp soil	Fresh	-------
Cephalanthus occidentalis (Buttonbush)	Branched shrub up to 1.5 m tall with leathery smooth opposite leaves and white flowers crowded into dense, spherical, stalked heads; flowers June through August; leaf petioles reddish.	Upland margins and raised hummocks of tidal freshwater marshes; wet soil	Fresh to oligohaline	Hibiscus spp. Cornus amommum
Echinochloa walteri (Water's millet)	Grass up to 2 m, solitary or in small groups; long, moderately wide leaf blades; flowers in a terminal panicle which is ovoid, greenish purple, and appears in July/August.	Shallow water; moist areas, disturbed sites	Fresh to oligohaline	-------

(continued)

Table 4. (Continued).

Species	General characteristics	Habitat preference	Salinity tolerance	Associated species
Hibiscus spp. Kosteletzkya virginica (Mallows)	Shrubform herbs up to 2 m, scattered or in large colonies; leaves wedge-shaped or rounded and alternate; large, showy pink or white flowers appearing in midsummer; perennial.	Freshwater marshes or the upland margin of saline marshes with freshwater seepage	Fresh to mesohaline	Typha spp. Spartina cynosuroides Polygonum spp. Impatiens capensis
Eleocharis palustris E. quadrangulata (Spikerushes)	Perennials with horizontal rootstocks; culms stout, slender, and cylindrical or squarish with a basal sheath; flowers crowded onto terminus of spikelet; between .5 and 1.5 m.	Channel margins or stream banks in shallow water; muddy, organic substrates	Fresh to oligohaline	Pontederia cordata Scirpus spp. Juncus spp. Leersia oryzoides
Impatiens capensis (Jewelweed)	Annual plants up to 2 m with succulent, branched stems with swelling at the joints; colonial; leaves alternate and ovate or elliptic with toothed margins; flowers orange and funnel-like, appearing in July/August.	Same as Bidens spp.; also grows in shaded portions of marshes	Fresh	Bidens spp. Typha spp. Polygonum spp.
Iris versicolor (Blue flag)	Flat, swordlike leaves arising from a stout creeping rhizome; large, purplish-blue flowers emerge in spring from a stiff upright stem; perennial.	High, shaded portions of the intertidal zone in damp soi; will not tolerate long inundations.	Fresh	None in particular
Leersia oryzoides (Rice cutgrass)	Weak slender grass growing in dense, matted colonies; leaf sheaths and blades very rough; emerges from creeping rhizomes and often sprawls on other vegetation.	Mid-intertidal zones of marshses; high diversity vegetation patches	Fresh to oligohaline	Many; none in particular
Lythrum salicaria Decodon verticillatus (Loosestrife)	Shrubform herbs forming large, dense colonies; aggressive; up to 1.5 m in height with lanceolate leaves opposite or whorled; upper axils branched with small purplish-pink flowers; terminal spikes pubescent; annual.	Moist portions of marshes; high intertidal or upland areas	Fresh to oligohaline	Hibiscus spp. Convolvulus spp.
Mikania scandens (Climbing hempweed)	Long, herbaceous vine forming matted tangles over other emergent plants; heart-shaped leaves; dense, pinkish flower clusters; slender stem; propagates by both seed and rhizome; perennial.	Open, wooded swamps and marshes; shrub thickets	Fresh to oligohaline	-------
Myrica cerifera (Wax-myrtle)	Compact, tall, evergreen shrub with leathery alternate leaves; spicy aroma; waxy, berry-like fruits; forms extensive thickets.	Most all coastal habitats; border between intertidal zone and uplands	Fresh	Acer rubrum Nyssa spp. Taxodium distichum
Nuphar lutecum (N. advena) (Spatterdock)	Plant with floating or emergent leaves and flowers attached to flexible underwater stalks; rises from thick rhizomes imbedded in benthic muds; flowers deep yellow, appearing throughout the summer.	Constantly submerged areas up to 1.5 m depth, or if tidal, near or below mean low water in deep organic muds	Fresh	Usually in pure stand

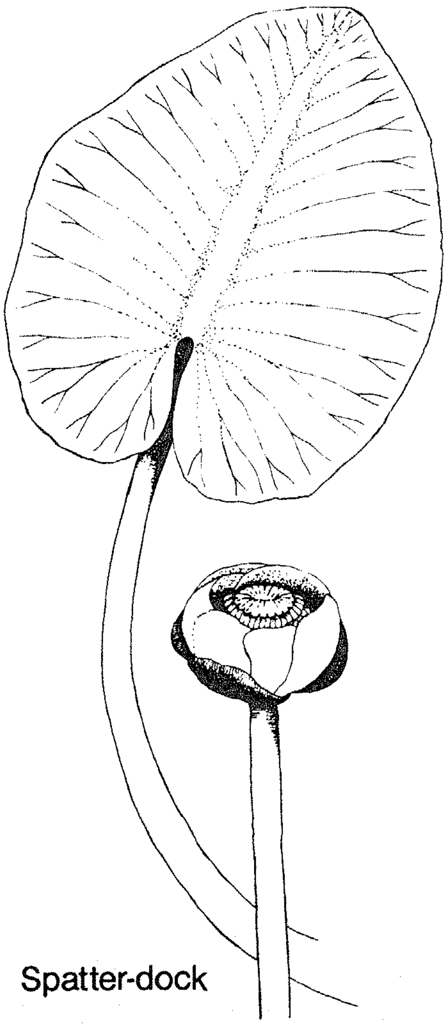
Nyssa sylvantica Nyssa aquatica (Gum)	Medium-sized tree (10 m) with numerous horizontal, crooked branches; leaves crowded at twig ends turning scarlet in fall; flowers appear in April/May.	Marsh/upland borders	Fresh	Acer rubrum Myrica cerifera Alnus spp.
Panicum virgatum (Switchgrass)	Perennial grass 1-2 m in height in large bunches with partially woody stems; nest of hairs where leaf blade attaches to sheath; large, open delicately branched seed head produced in late summer; rhizomatous.	Dry to moist sandy soils or the mid-intertidal portions of tidal freshwater marshes; disturbed areas	Fresh to mesohaline	Hibiscus spp. Scirpus spp. Eleocharis palustris
Peltandra virginica (Arrow-arum)	Stemless plants, 1-1.5 m tall, growing in loose colonies; several arrowhead-shaped leaves on long stalks; emerge in rather dense clumps from a thick subsurface tuber; flowers from May to June.	Grows predominantly as an emergent on stream margins or intertidal marsh zones on rich, loose silt	Fresh to oligohaline	Pontederia cordata Zizania aquatica many other species
Phragmites australis (Common reed)	Tall, coarse grass with a feathery seed head; 1-4 m in height; grows aggressively from long, creeping rhizomes; perennial; flowers from July to September.	Extremely cosmopolitan, growing in tidal and nontidal marshes and often associated with disturbed areas	Fresh to mesohaline	Spartina cynosuroides Zizania aquatica
Polygonum arifolium Polygonum sagittatum (Tearthumbs)	Plants with long, weak stems up to 2 m tall, usually leaning on other vegetation; leaves sagitate in shape and alternate; leaf midribs and stems armed with recurved barbs; flowers small and appearing in late summer; annual.	Shallow water or damp soil; middle to upper intertidal zone	Fresh to oligohaline	Bidens spp. Hibiscus spp. Impatiens capensis
Polygonum punctatum Polygonum densiflorum Polygonum hydropiperoides (Smartweeds)	Upright plants growing from a fibrous tuft of roots; narrowly to widely lanceolate leaves with stalks basally enclosed within a membranous sheath; up to 1 m; flowers at spike at end of stalk.	Upper three-quarters of intertidal zone in freshwater marshes on wet or damp soil	Fresh to oligohaline	Many species
Pontederia cordata (Pickerelweed)	Rhizomatous perennial growing in dense or loose colonies; plants up to 2 m tall; fleshy, heart-shaped leaves with parallel veins and emerging from spongy stalks; flowers dark violet-blue, appearing June to August.	Lower intertidal zone of tidal freshwater marshes	Fresh to oligohaline	Nuphar luteum Peltandra virginica Sagittaria latifolia
Rosa palustris (Swamp rose)	Shrub up to 2 m growing in loose colonies; stems lack prickles except for those occurring at bases of leaf stalks; pinnately compound leaves with fine serrate margins; showy, pink flowers appearing July/August.	High intertidal zones or wet meadows	Fresh to oligohaline	Cephalanthus occidentalis
Rumex verticillatus (Water dock)	Erect, robust annual with dark-green, lance-shaped leaves; stem swollen at nodes; attains heights over 1.5 m and grows solitary or in loose colonies; flower head is evident in late spring and can be 50 cm in length.	Wet meadows or pond margins on mud or in shallow water	Fresh to oligohaline	-------

(continued)

Table 4. (Concluded).

Species	General characteristics	Habitat preference	Salinity tolerance	Associated species
Sagittaria latifolia (Duck-potato) Sagittaria falcata (Bultongue)	Perennial herbs; stemless, up to 2 m in height and emerging from fibrous tubers; leaves arrowhead-shaped or lanceolate with white flowers in whorls appearing on a naked stalk in July/August.	Borders of rivers or marshes in low intertidal zones on organic, silty mud	Fresh to oligohaline	Peltandra virginica Pontederia cordata
Scirpus validus (Soft-stem bulrush) Scirpus cyperinus (Woolgrass) Scirpus americanus (Common three square)	Medium to large rushes with cylindrical or triangular stems; inconspicuous leaf sheaths; usually grow in small groups; bear seed clusters on end or side of stem; perennial.	Brackish to fresh shallow water or low to middle intertidal zones on organic clay substrates	Fresh to mesohaline	Other rushes Typha spp.
Sparganium eurycarpum (Great burread)	Stout upright forbs up to 1 m with limp, underwater, emergent leaves attached basally and alternating up the stem; towards the terminus, stems zig-zag bearing sphere-like clusters of pistillate and staminate flowers.	Partially submerged, shallow water marsh areas; lower to middle intertidal zones	Fresh	Zizania aquatica Leersia oryzoides Polygonum spp.
Spartina cynosuroides (Big cordgrass)	Perennial grass attaining heights in excess of 3 m, having long, tapering leaves and growing from vigorous underground rhizomes; found in dense monospecific or mixed stands.	Channel and creek margins in tidal oligohaline marshes	Fresh to mesohaline	Phragmites australis Typha spp.
Taxodium distichum (Bald cypress)	Tall tree with straight trunk (40 m), conifer-like but deciduous; light porous wood covered by stringy bark; unbranched shoots originating from roots as knees.	Marsh/upland borders	Fresh?	Nyssa spp. Acer rubrum
Typha latifolia Typha domingensis Typha angustifolia (Cattails)	Stout, upright reeds up to 3 m forming dense colonies; basal leaves, long and sword-like, appearing before stems; yellowish male flower disintegrates leaving a thick, velvety-brown swelling on the spike; rhizomatous; perennial.	Very cosmopolitan, occurring in shallow water or upper intertidal zones; some disturbed areas	Fresh to mesohaline	Many associates
Zizania aquatica (Wild rice)	Annual or perennial aquatic grass, 1-4 m tall, usually found in colonies; short underground roots, stiff hollow stalk, and long, flat, wide leaves with rough edges; male and female flowers separate along a large terminal panicle in late summer.	Fresh to slightly brackish marshes and slow streams, usually in shallow water; requires soft mud and slowly circulating water	Fresh to oligohaline	Peltandra virginica many other species
Zizaniopsis mileacea (Giant cutgrass)	Perennial by creeping rhizome; culms 1-4 m high; long, rough-edged leaves geniculate at lower nodes; large, loose terminal panicles appearing in midsummer; aggressive.	Swamps and margins of tidal streams	Fresh?	-------

References: Fassett 1957; Fernald 1970; Beal 1977; Tarver et al. 1979; Magee 1981; Silberhorn 1982.



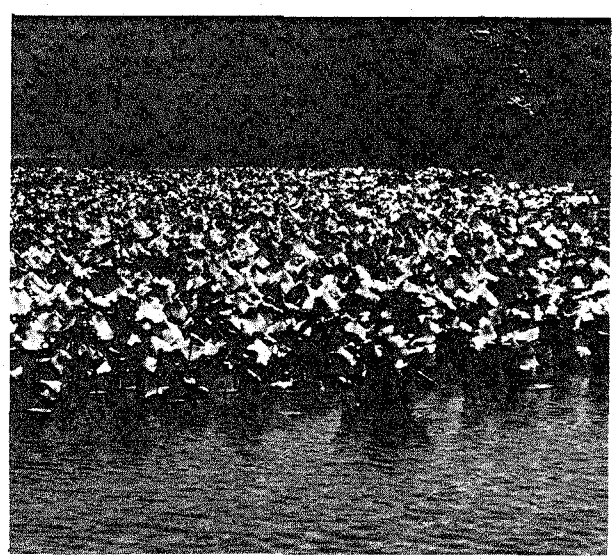


Figure 5. Spatterdock community type.

progresses, some plants will be overtopped by other species commonly inhabiting the low intertidal zone such as arrow-arum, pickerelweed, and wild rice.

2) Arrow-arum/Pickerelweed Community Type - Arrow-arum is an extremely cosmopolitan species growing throughout the intertidal zone of many marshes. This species forms its purest stands in the low intertidal portions of the marsh in spring or early summer. Pickerelweed, a common associate, is equally as likely to dominate or codominate this lower marsh zone (Figure 6), although its distribution is usually more clumped than arrow-arum. Both species tolerate long periods of inundation. Other species associated with this community type, especially in more elevated sections of the marsh, include burmarigolds and wild rice, and less frequently, arrowhead, sweetflag, and smartweeds.

3) Wild Rice Community Type - Wild rice is conspicuous and widly distributed throughout the Atlantic Coastal Plain. This annual grass can completely dominate a given marsh, producing plants which attain heights in excess of 4 m (13 ft) in August and September (Figure 7). Wild rice is not noticable until midsummer when it begins to overtop a discontinuous canopy generally composed of arrow-arum, pickerelweed, spatterdock, arrowhead, smartweed, and burmarigolds.

4) Cattail Community Type - Cattails are among the most ubiquitous of wetland plants and are principal components of many tidal freshwater marshes. The cattail community type (Figure 8), which includes several species of Typha in the mid-Atlantic region, is mostly confined to the upper intertidal zone of the marsh. Cattails are usually found with one or more common associates---arrow-arum, rosemallow, smartweeds, jewelweed, and arrowhead---but will also form dense monospecific stands. Cattail communities are also prevalent in disturbed areas, where they often are associated with common reed.

5) Giant Cutgrass Community Type - Giant cutgrass, also known as southern wild rice, is an aggressive perennial confined predominantly to wetlands south of Virginia and Maryland. This species dominated

Pickerelweed Arrow-Arum

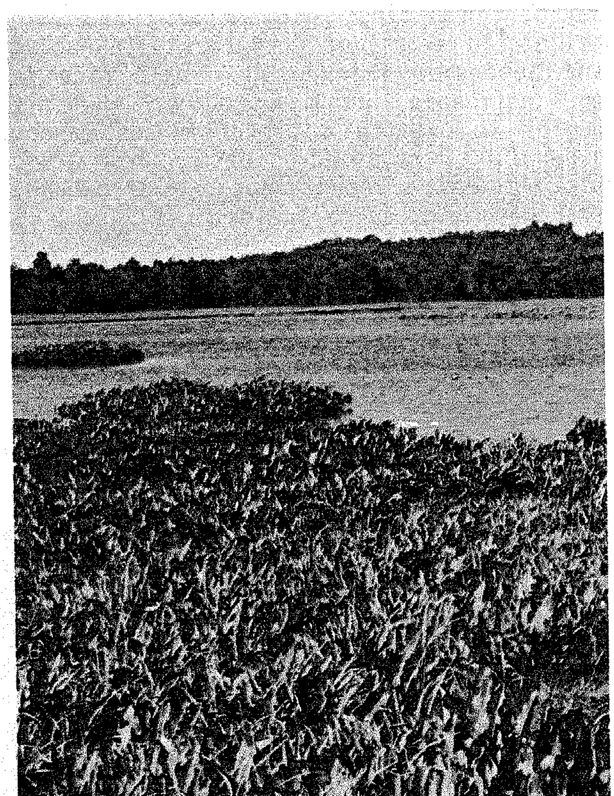


Figure 6. Arrow-arum/pickerelweed community type.

Wild Rice

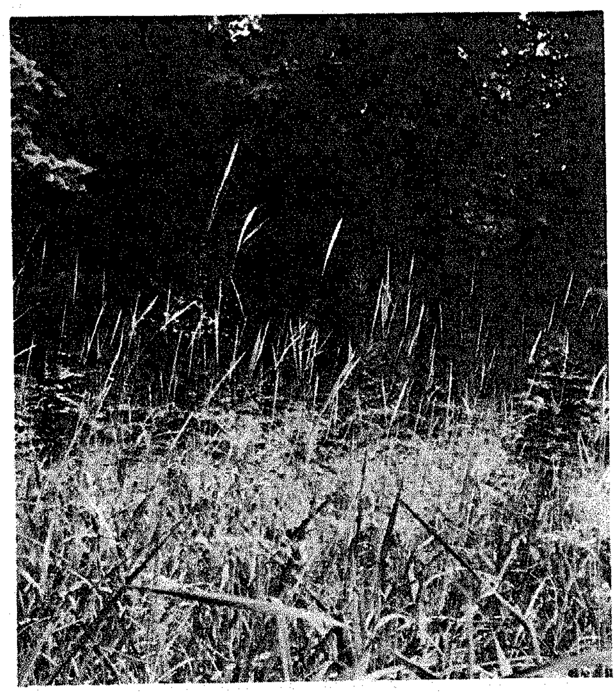


Figure 7. Wild rice community type.

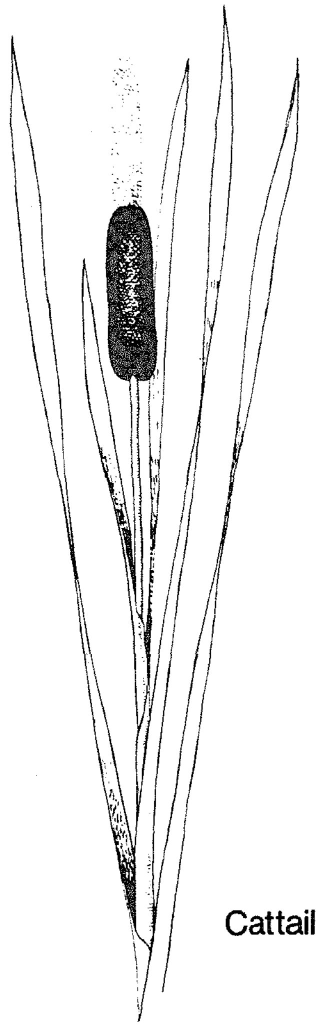


Figure 8. Cattail community type.

many of the tidal freshwater marshes of this region, often competing with other plants to their exclusion. When not in pure stands, this grass associates with a variety of other emergent macrophytes including sawgrass, cattails, wild rice, alligator weed, water parsnip, and arrow-arum (Figure 9).

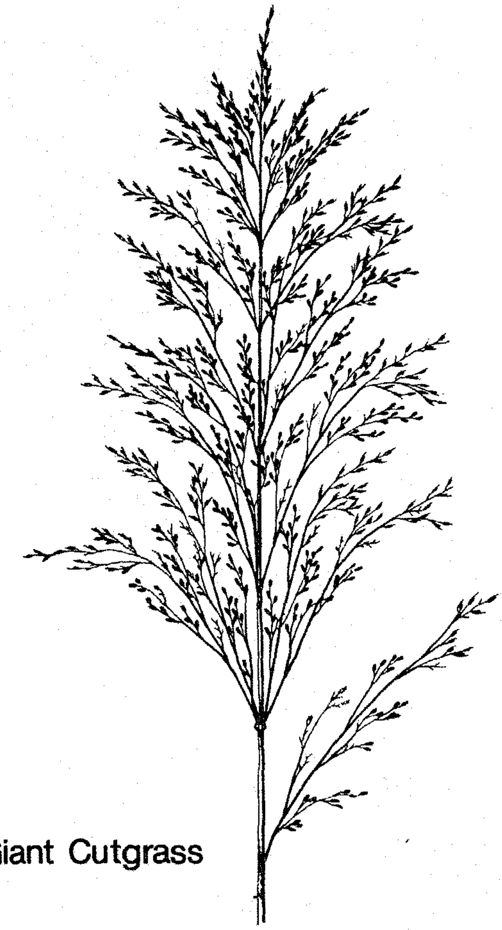
6) Mixed Aquatic Community Type - The mixed aquatic community consists of an extremely variable conglomeration of freshwater marsh vegetation (Figure 10). Generally occurring in the upper intertidal zone of the marsh, it is composed of a number of codominant species which form an intricate mosaic over the marsh surface. Important species include arrow-arum, rose-mallow, smartweeds, water-hemp, burmarigolds, sweetflag, cattails, rice cutgrass, loosestrife, arrowhead, and jewelweed. Certain components of the mixed aquatic type dominate on a seasonal basis.

7) Big Cordgrass Community Type - Big cordgrass is often seen growing in nearly pure stands in narrow bands along tidal creeks and sloughs, or on levee portions of oligohaline marshes (Figure 11). Arrow-arum and pickerelweed are associated with big cordgrass in these locales, but when stands extend further up onto the marsh, this species will intermix with cattails, common reed, rice cutgrass, and wild rice.

8) Bald Cypress/Black Gum Community Type - The bald cypress/black gum type (Figure 12) generally represents an ecotonal community forming the boundary between the marsh itself and wooded swamp or upland forest. Situated in the most landward portions of the tidal freshwater marsh at approximately the level of mean high water, this community consists of a mixture of herbs, shrubs, and trees. Other overstory species include tupelo gum, red maple, and ash, as well as shrubs such as wax-myrtle and buttonbush. Understory species include typical marsh plants, although their diversity and density is reduced because of shading.

<u>Zonation</u>

The presence of reoccurring groups of species which form recognizable patterns in many wetland habitats has encouraged



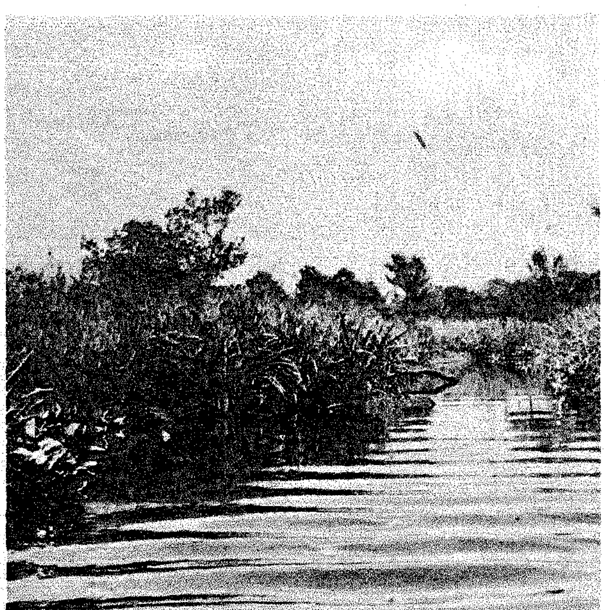


Figure 9. Giant cutgrass community type. Photograph by Charles Hopkinson.

the description of plant species distributions in terms of zones. Zonation in tidal freshwater marshes is less distinct than in many other aquatic or wetland environments. This is partially a function of the complexity of the major tidal freshwater community types. A number of species consistently form pure or mixed stands which do not necessarily occur in regular patterns from marsh to marsh (Whigham et al. 1976, Odum 1978). In some instances, individual species or groups of species have little or no organizational pattern, appearing to be distributed in a random fashion over the marsh surface.

The existence of zonation is supported by some studies. In Virginia tidal marshes on the Chickahominy River, cattails and rose-mallow regularly appear in the landward half to one-third of the marsh profile. Precise surveying of some of these areas indicates that this natural vegetation boundary coincides with a 20 to 30 cm (8 to 12 inch) rise in the marsh surface (Hoover 1983). Parker and Leck (1979) described two major zones in a New Jersey marsh dominated by annuals. The low marsh zone contained water smartweed, clearweed, and water-hemp, and the high marsh zone contained tearthumb, bur-marigold, and jewelweed. Seedling transplant studies indicated that high marsh species could not tolerate prolonged periods of inundation in the low marsh zone. Concurrently, competitive interactions seemingly contributed to the exclusion of the low marsh dominates from the high marsh zone.

Whigham (Chesapeake Bay Center for Environmental Studies, Edgewater, Maryland, pers. comm.) notes that a variety of annual species tend to congregate in the upper intertidal reaches of mid-Atlantic coast marshes. He postulates that the ability of many of these species to produce adventitious roots above the marsh substrate may be a mechanism allowing greater species packing. As such, plants with this adaptation (e.g., bur-marigold) can avoid anaerobic substrate conditions yet exploit a low, humid, and densely shaded layer just above the marsh surface.

In a freshwater marsh habitat influenced by artificial water level fluctuations on the Connecticut River, van Raalte

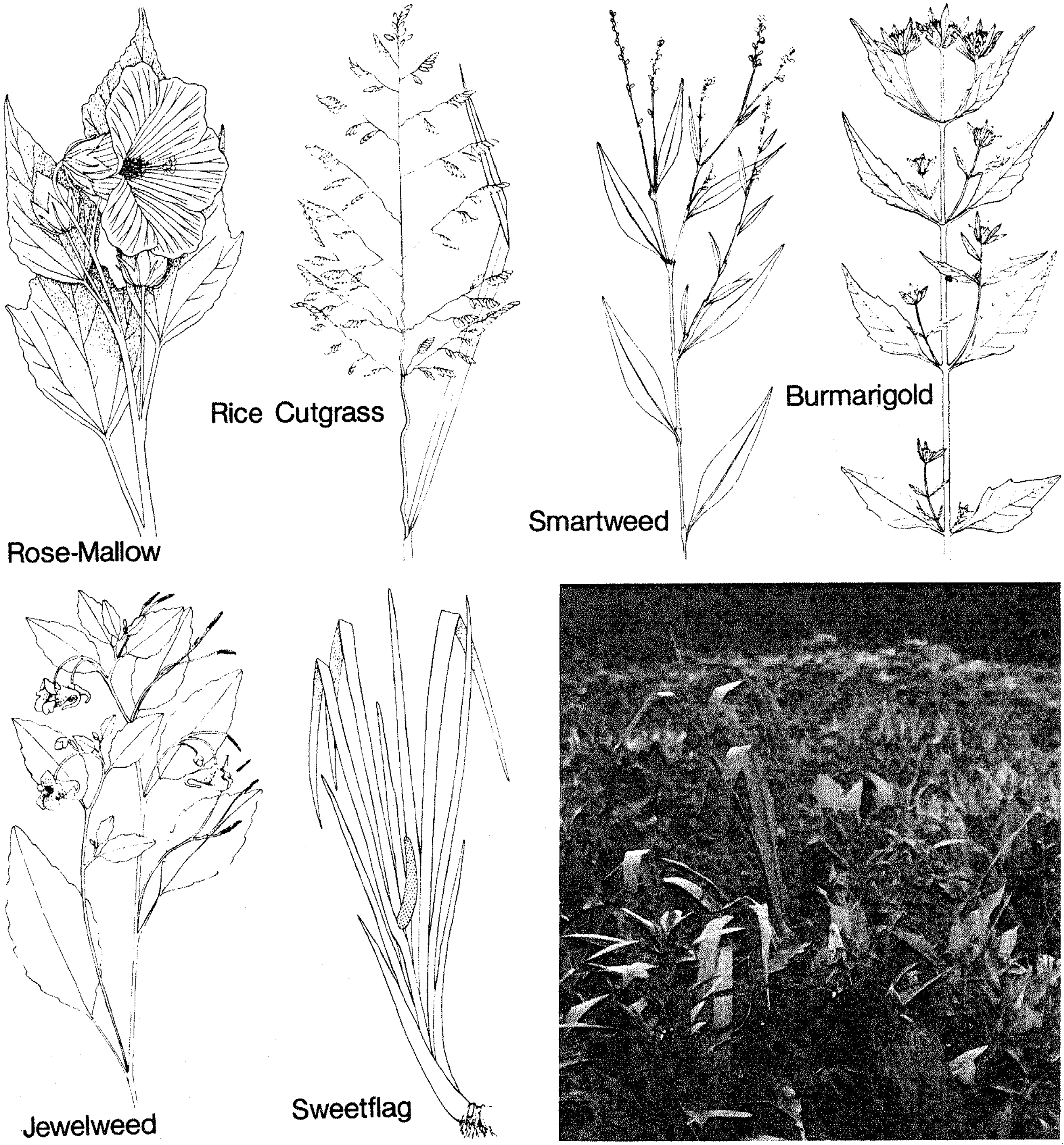
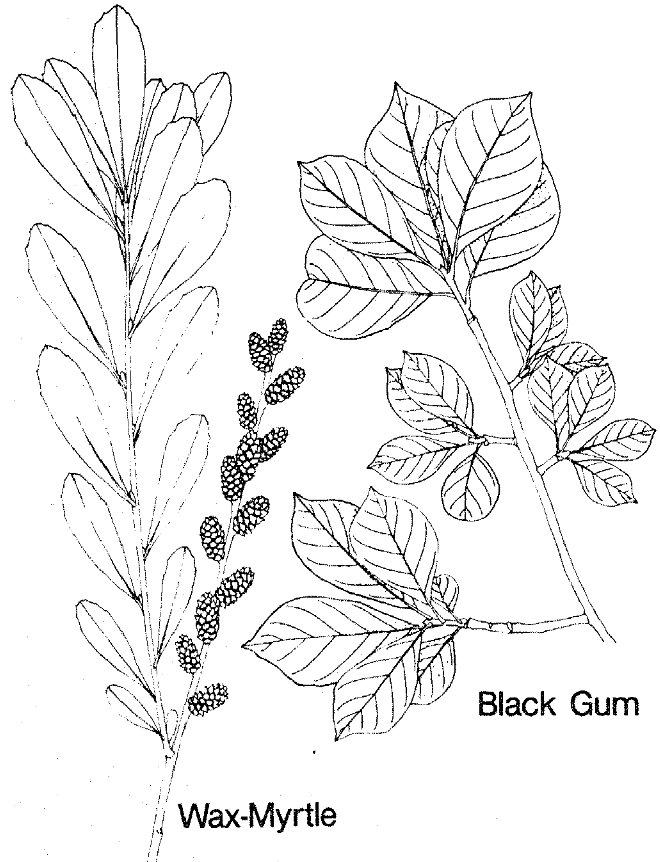


Figure 10. Mixed aquatic community.

(1982) found that plants grew in distinct zones. Pickerelweed dominated the low intertidal zone followed by more landward bands of arrowhead and rice cutgrass. Transplant experiments indicated that elevation, interspecific competition, and herbivory all contributed to this obvious zonation pattern. Cahoon (1982) discovered that the biomass allocation pattern of individual rose-mallow plants was influenced by salinity, water depth, and soil temperature. The existence of vari-



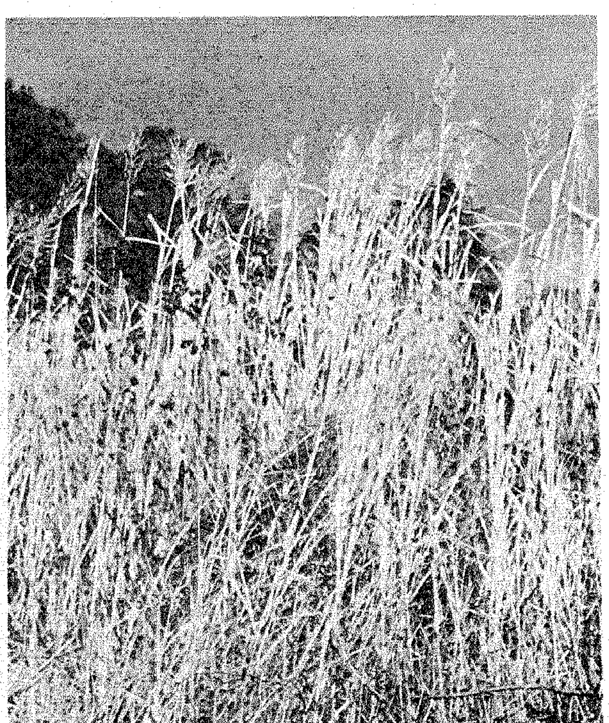


Figure 11. Big cordgrass community type.

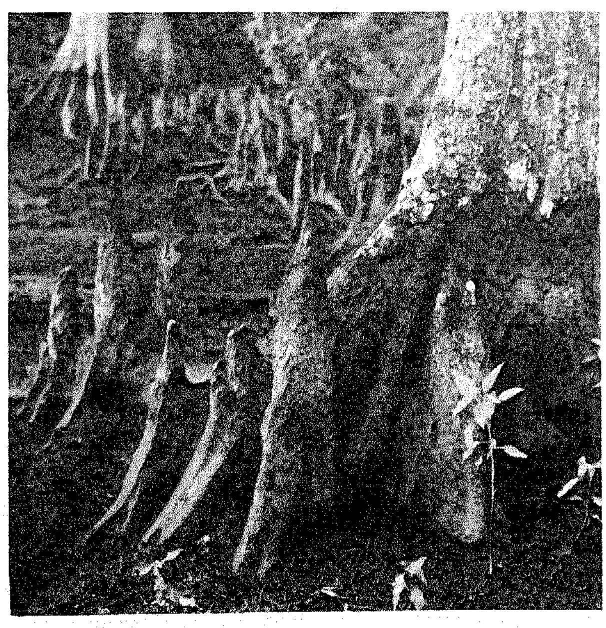


Figure 12. Bald cypress/black gum community type.

able physiognomies in this species might be considered analogous to the height forms of smooth cordgrass which delineate zones in salt marshes.

Where zonation, as an organizational expression of species distributions, actually exists in the tidal freshwater marsh habitat, it is probably controlled by a combination of physical variables and ecological processes. Preliminary evidence suggests that there may be a certain degree of consistency in the zonation found in tidal freshwater marshes. However, the extent of this patterning with respect to various community types, as well as its regularity from location to location, is unknown.

The Marsh Profile

Except for the most obvious community types, it is difficult to place a given species within a general structural framework for tidal freshwater wetlands. As a first approximation to community structure within this habitat, most of the commonly occurring vegetation falls into one of the following categories: (1) submerged or floating-leaved plants, (2) emergent plants with basal leaves and/or leafless stems, (3) emergent or damp soil herbs with stems bearing alternate or opposite leaves, (4) grasslike or rushlike plants, and (5) broad-leaved shrubs and trees (Magee 1981). By recognizing the approximate modal distributions of common plant species or community-type indicator species within these structural subgroups, a typical marsh profile can be visualized and described.

The marsh profile depicted in Figure 13 is most characteristic of mid-Atlantic tidal marshes. Beds of submerged, rooted aquatic plants (see Section 2.6) make up

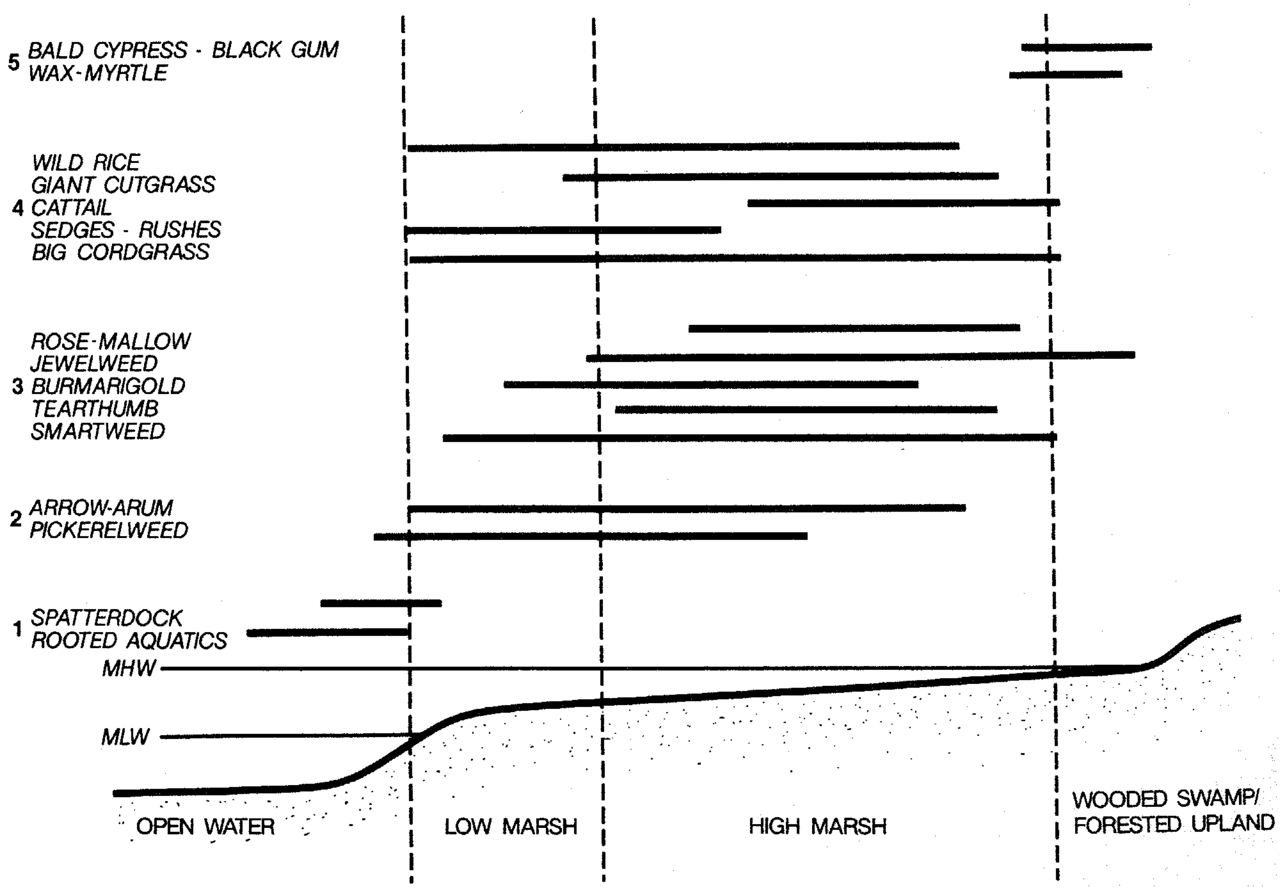
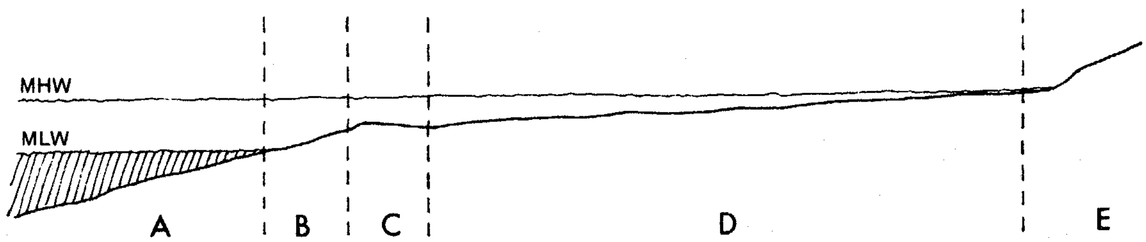


Figure 13. Characteristic profile of mid-Atlantic tidal freshwater marsh.

an invisible, suspended mat of vegetation at the foot of the marsh where inundation is constant. Merging with this subtidal layer and extending variable distances up onto the muck surface of the marsh are a host of fleshy-leaved, emergent macrophytes: spatterdock, arrow-arum, pickerelweed, and arrowhead. These species, plus wild rice, big cordgrass, and numerous sedges and rushes, comprise the bulk of low marsh vegetation. The transition from low to high marsh is generally marked by an increase in species number, presumably due to reduced periods of inundation. The predominant components of the high marsh zone include low swards of tangled grass (rice cutgrass), erect or sprawling herbaceous thickets (burmarigold, tearthumb, jewelweed, smartweed), tall grasses or grasslike plants (giant cutgrass, wild rice, cattail, sweetflag), and shrublike thickets (rose-mallow, swamp rose, loosestrife). The most landward extent of the marsh usually coincides with the mean high water mark and is indicated structurally by a dense wall of shrubbery (wax-myrtle) and associated overstory (bald cypress, black gum, red maple) and understory (jewelweed, Asiatic spiderwort) species.

Variations on this scheme are numerous, and are often associated with the physiographic characteristics of the marsh profile. One physiographic feature consistently found in the tidal freshwater habitat is an elevated levee forming the crest of the channel bank. This feature creates a niche for facultative hydrophytes or less water-tolerant species within the low marsh zone. Plant species commonly taking advantage of the levee-niche in Virginia are water-hemp, common threesquare, squarestem spike-rush, rose-mallow, giant ragweed, and other high marsh herbs. Similarly, subsidence areas within the high marsh zone can create a niche for obligate hydrophytes. This phenomenon can usually be attributed to geologic maturation of riverine and estuarine wetlands (see Section 1.6).

Metzler and Rosza (1982) describe a marsh profile for northeastern Atlantic coast tidal freshwater wetlands. For comparison, it is presented in Figure 14. The definition and extent of zones is quite similar to that described for mid-Atlantic marshes, although there are significant differences in species composition.



ZONE	DESCRIPTION	SPECIES CHARACTERISTICS
A	SUBTIDAL	PONDWEEDS, WATERWEED, HORNWORT
B	LOWER INTERTIDAL	ARROWHEADS, SEEDBOX, BULRUSHES
C	MID-TIDAL MARSH BORDER	BULRUSHES, WATER HEMP, WATER PARSNIP, SNEEZEWEED, SMOOTH BURMARIGOLD, WILD RICE, PICKERELWEED, ARROWHEADS
D	HIGH MARSH	SWEETFLAG, CATTAIL, SWAMP ROSE, REED BENTGRASS
E	UPLAND	RED MAPLE, WATER WILLOW, ARROW-WOOD

Figure 14. Northeastern marsh profile. Modified from Metzler and Rosza (1982).

2.4 FACTORS CONTROLLING PLANT DEMOGRAPHY

The distribution of plant species populations in any natural situation reflects the response of individual species to specific environmental parameters. In wetland habitats these parameters are especially varied, primarily due to the influence of water on habitat gradients. Biologically-mediated interactions between plant species further complicate the perception of physical gradients. Much of the information concerning the causes for observed spatial distributions of vascular flora in these marshes is anecdotal, although enough exists to warrant a general discussion.

Inundation

There seems to be a general consensus among researchers investigating plant demography in the tidal freshwater habitat that the frequency and duration of flooding is the primary factor governing species distributions (Kiviat 1978a; Doumlele and Silberhorn 1978; Ferren et al. 1981; McCormick and Somes 1982). Despite the fact that the vast majority of plants occurring in these marshes must experience flooding on a daily basis, species vary greatly in their ability to withstand inundation. For some species, extensive flooding seems to be a physiological requirement for subsistence, whereas for others, it can be a detriment to normal growth and development. Sculthorpe (1967) notes that numerous terrestrial plants are able to survive long periods either completely or partially submerged. It is conceivable that facultative hydrophytes have evolved in order to avoid competition or to exploit open niches in habitats such as these.

In the progression from open water channels to the marsh-upland boundary, the species composition of vascular flora changes noticeably, even over almost imperceptable variation in marsh surface elevations (Hoover 1983). It is known that common and narrow-leaved cattails will segregate along a gradient of water depth in nontidal habitats, the latter species found in deeper water (Grace and Wetzel 1981). Common reed and wild rice also respond to varying inundation, each species producing fewer and somewhat stunted progeny in deep-water experimental plots (Yamisaki and Tange 1981). Many other researchers working in salt marsh, mangrove swamp, and freshwater lake environments have concluded that inundation effectively contributes to segregation of plant species populations along an elevational gradient (Mandossian and McIntosch 1960; Adams 1963; Sculthorpe 1967; Kerwin and Pedigo 1971; Odum 1971). As yet, this phenomenon has not been quantitatively determined for tidal freshwater marshes. However, evidence from other wetland situations suggests that tidal freshwater plant communities segregate along inundation gradients as well.

Substrate

The soil in tidal freshwater marshes can be described as a waterlogged organic muck with varying amounts of sand, silt, and clay (see Section 1.7). Differences in soil stability, soil moisture retention, and soil nutrient availability are all related to the physical characteristics of a given substrate and may influence species distributions directly. The spatial heterogeneity of substrate characteristics is not sufficient to explain distributions or species performance (Whigham and Simpson 1975; Wetzel and Powers 1978). Wetzel and Powers (1978) concluded that substrate characteristics affect plant demography only in localized zones within the marsh, and then, these subtle differences are largely obscured by major environmental gradients acting to produce species distributions (e.g., elevation and tidal inundation). In our opinion, this is an area which needs considerably more research.

Current Flow

Low-gradient river courses of the Atlantic Coastal Plain tend to flow rather sluggishly except during extreme storm or flood events. Aside from channel discharge, however, the daily ebb and flood of tidal water onto and off the marsh surface can produce significant current velocities. Much of this water becomes channelized into dendritically-shaped creeks within the marsh. These creeks deliver ground water from high marsh to low marsh to channel long after the tide has ebbed (Hoover 1983). Concentrated water movement may (1) impair the ability of seeds, seedlings, or adult plants to grow and develop and (2) may confine the dispersion of particular seeds to portions of the marsh with little or no water flow.

Several studies provide evidence to support these ideas. Whigham et al. (1979) noted that arrow-arum seedlings, which develop uniformly throughout most sections of the marsh, were absent from streambank areas. Higher rates of water movement along the streambank apparently prevented seeds from establishing themselves, since seeds collected from these same areas were found to be physiologically capable of germination. In contrast, pickerelweed is known to prefer streambank locations, taking advantage of greater soil surface temperatures on the exposed mud as well as reduced competitive pressures in this area (Garbisch and Coleman 1978).

Salinity

The variability and complexity of wetland plant communities increases with decreasing salinity. Anderson et al. (1968), studying a 25-mile stretch of the Patuxent River estuary in Maryland, illustrated this fact by quantifying plant species' diversity at sites with different salinity regimes (Table 5). By definition, the tidal freshwater habitat should not encounter average water salinities greater than 0.5 ppt. However, this boundary between tidal fresh and oligohaline waters has been seen to migrate considerable distances over the course of a year in response to drought and flood periods. Marshes which intermittently come into contact with elevated water salinities may harbor slightly less diverse plant communities dominated by facultative halophytes (see Section 2.2). Freshwater species which appear to drop out of the plant communities in these areas include spatterdock, sweetflag, blueflag, various sedges, and giant cutgrass.

Physiological Capability/Anaerobic Toxins

Preliminary evidence suggests that tidal freshwater marsh soils are not as reduced as some salt marsh substrates, at least in the surface horizon (see Section 1.7). Presumably, the extent of oxygen deficiency is not homogeneous over the entire marsh profile, being less intense in those areas which drain regularly with each tidal cycle. Nevertheless, soils and associated microbial populations shift their predominant metabolic pathways under anoxic conditions, affecting both inorganic and organic soil constituents --- this can have important consequences for wetland plant life.

The bioavailability of most nutrients and toxins responds to the oxidation-reduction conditions of wetland soils (Gambrell and Patrick 1978). Increased levels of soluble iron and managanese in some reduced soils are reported to be toxic to plants (Armstrong 1975), and furthermore, may facilitate the formation of inorganic-oxide layers around roots which potentially impedes the transport of nutrients from soil to plant (Armstrong and Boatman 1967; Howeler 1973). Extremely reduced soils with appreciable organic carbon may develop toxic sulfide compounds.

Many wetland plants have adapted to these extreme conditions, developing means of metabolizing anaerobically and excluding toxins from roots. The provision of air-space or aerenchymatous tissue is one mechanism enabling plants to transport atmospheric gas to anoxic rhizospheres. The functioning of this pressurized, flow-through system has been documented in detail for spatterdock (Dacey 1980), a species which typically thrives in the most waterlogged portions of the marsh. Other emergent macrophytes which possess aerenchymatous tissue include arrow-arum, pickerelweed, and even certain grasses and sedges. Most of these species will be found in the lower intertidal zones in tidal freshwater marshes.

Competition

From an ecological point of view, the diverse flora indigenous to tidal freshwater wetlands would seem to have a high potential for species-species interactions. A conspicuous feature of many plant communities that is often considered evidence of competitive displacement is the segregation of species along a habitat gradient. Although species segregations

Table 5. Species composition of five marshes along the Patuxent River in Maryland. The marshes have been designated by their respective salinity regimes. This table is modified from Anderson et al. (1968).

Species	Salinity regimes				
	10-17 ppt	6-10 ppt	3-7 ppt	0.5 ppt	0.2 ppt
Aster tenuifolius	*				
Distichlis spicata	*				
Fimbristylis castlanea	*				
Juncus gerardi	*				
Lythrum lineare	*				
Atriplex patula	*	*	*		
Iva frutescens	*	*			
Scirpus robustus	*	*			
Spartina patens	*	*			
Spartina alterniflora	*	*	*		
Pluchea camphorata	*	*	*		
Spartina cynosuroides	*	*	*		
Teucrium canadense	*	*	*		
Meliotus alba		*			
Baccharis halimifolia	*	*	*		
Panicum virgatum		*	*	*	
Sarurus cernuus		*			
Althaea officinalis		*	*		
Carex crinita		*		*	
Elymus virginicus		*	*		
Myrica gale		*	*		
Rumex crispus		*	*		
Typha angustifolia		*	*		
Eleocharis palustris		*	*	*	
Cephalanthus occidentalis		*	*	*	
Amaranthus cannabinus		*	*	*	*
Asclepias incarnata		*	*	*	*
Boehmeria cylindrica		*	*	*	*
Cicuta maculata		*	*	*	*
Hibiscus moscheutos		*	*	*	*
Peltandra virginica		*	*	*	*
Phragmites australis		*	*	*	*
Rosa palustris		*	*	*	*
Scirpus americanus		*	*	*	*
Apios americana			*		
Eupatorium serotinum			*		
Juncus acuminatus			*		
Rumex verticillatus			*		
Vernonia noveboracencis			*		
Cassia fasciculata			*		*
Commelina communis			*		
Galium tinctorium			*		*
Lycopus americanus			*		*
Mentha arvensis			*		*
Scirpus cyperinus			*	*	
Scirpus validus			*	*	
Cornus amomum			*	*	*
Echinochloa walteri			*	*	*
Impatiens capensis			*	*	*

(continued)

Table 5. Concluded.

Species	Salinity regimes 10-17 ppt	6-10 ppt	3-7 ppt	0.5 ppt	0.2 ppt
Mikania scanoens			*	*	*
Pontederia cordata			*	*	*
Polygonum arifolium			*	*	*
Polygonum punctatum			*	*	*
Polygonum sagittatum			*	*	*
Ptilimnium capillaceum			*	*	*
Alnus serrulata				*	*
Carex lurida				*	*
Carex stipata				*	*
Decodon verticillatus				*	*
Dulichium arundinaceum				*	*
Eupatorium perfoliatum				*	*
Gratiola virginiana				*	*
Hypericum dissimulatum				*	*
Leersia oryzoides				*	*
Lobelia caroinalis				*	*
Ludwigia palustris				*	*
Nuphar luteum				*	*
Pilea pumila				*	*
Sagittaria latifolia				*	*
Sparganium eurycarpum				*	*
Typha latifolia				*	*
Zizania aquatica				*	*
Acer rubrum				*	
Carex alata				*	
Carex albolutescens				*	
Carex annectens				*	
Carex comosa				*	
Carex lupulina				*	
Galium obtusum				*	
Geum canadense				*	
Juncus effusus				*	
Lactuca canadensis				*	
Lythrum salicaria				*	
Myosotis laxa				*	
Rorippa palustris				*	
Scirpus fluviatilis				*	
Acorus calamus					*
Aster calamus					*
Bidens frondosa					*
Bidens laevis					*
Cyperus strigosus					*
Cyperus refractus					*
Irls versicolor					*
Ludwigia alterniflora					*
Lycopus virginicus					*
Orontium aquaticum					*
Slum suave					*
Zizaniopsis miliacea					*
Species Totals	14	29	45	55	52

of some form (e.g., major community types) are apparent in most tidal freshwater habitats, ascribing such a phenomenon to competition per se is difficult.

The mechanisms involved in competitive plant interactions are varied. Only a few studies have experimentally demonstrated the importance of competitive displacement in maintaining wetland plant distributions. Grace and Wetzel (1981) showed that populations of common and narrow-leaved cattails segregate according to water depth, the former competitively superior in shallow water due to its greater leaf surface area. However, narrow-leaved cattail has the potential to grow in deeper water than common cattail, a capacity facilitated by phenotypic traits such as taller, narrower leaves and greater rhizome storage. Cahoon (1982) also noted phenotypic responses in two tidal freshwater species with overlapping distributions. Rose-mallow was found to respond to the presence of narrow-leaved cattail by increasing its leaf size. However, the consequence of such a strategy was a concomitant reduction in reproductive output. Buttery and Lambert (1965) found that manna-grass dominated a particular portion of a habitat gradient strictly through its ability to opportunistically outcompete another species, the common reed. Without further studies, it is difficult to accurately ascertain the importance of competition on species distribution patterns. The evidence available thus far, however, suggests that competitive pressures act in conjunction with physical factors to produce species niches.

Allelopathy

Chemicals derived from one plant which have inhibitory effects on the growth and development of another plant are termed allelochemics. The concentration in the soil of alleleochemics from a dominant plant may exclude many other plant species from the community (Whittaker 1975). McNaughton (1968) suggested that cattails have allelopathic effects on other aquatic species. Bonasera et al. (1979) compared the allelopathic potential of four species common to tidal freshwater habitats --- giant ragweed, arrow-arum, burmarigold, and common cattail. Experiments with leaf and petiole extracts, as well as soil extracts, showed that these species vary in their ability to affect the germination of bioassay species, suggesting that similar interactions may occur between marshland species.

2.5 SEASONAL SUCCESSION

A unique aspect of tidal freshwater marshes is the continually changing appearance of the vegetation over the course of the growing season (Figure 15)

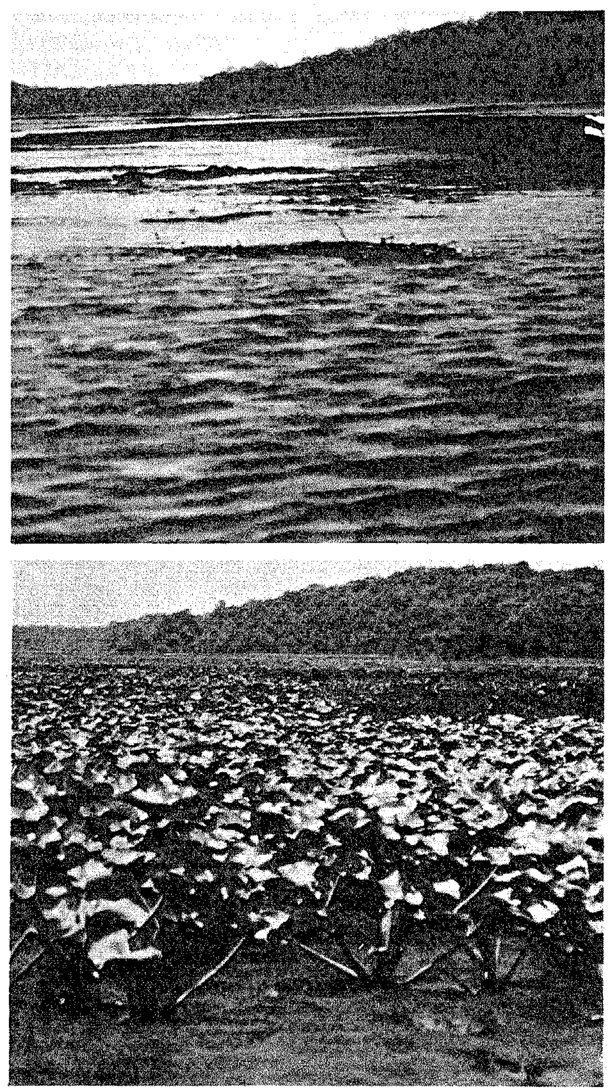


Figure 15. Winter and early summer scenes at the same location on tidal freshwater Potomac River. Photographs by Michael Dunn.

(Shima et al. 1976; Whigham et al. 1976; McCormick and Somes 1982; Silberhorn 1982). In the mid-Atlantic region, the first real evidence of renewed plant life in tidal freshwater marshes is the emergency of spatterdock in the low intertidal zone. Shortly thereafter, as temperatures begin to rise, the spike-like projections of arrow-arum and pickerelweed poke through the muck surface from underground rhizomes. Interspersed among these emerging perennials are large numbers of annual seedlings, largely comprised of wild rice, burmarigolds, tearthumbs, and smartweeds. By early May, arrow-arum, pickerelweed, and spatterdock completely dominate the intertidal zone, forming a dense low canopy over the other species; in places, this canopy is overtopped by the tall, sword-like leaves of cattail and sweetflag.

Many other species will have germinated by early summer, but remain largely obscured by the vegetation canopy. However, it is not long before grasses such as wild rice and giant cutgrass begin to overtop the layer of flesh-leaved perennials, reaching heights in excess of 3 meters (10 ft) by mid-July. As other species follow suit (e.g., rose-mallow, burmarigolds, tearthumbs, water-hemp, jewelweed), the diversity of the marsh becomes noteworthy, often as many as 30 to 50 species appearing in a single marsh location.

By late July the leaves of arrow-arum and sweetflag start to yellow, beginning a dieback caused by the intense summer heat, the increased abundance of herbivores feeding on succulent plant parts, and the tangled mat of vegetation now sprawling over the former canopy. August brings a surge in the growth of the flower-bearing stalks of giant cutgrass, wild rice, and other grasses. Pickerelweed, somewhat indistinguishable from arrow-arum until now, produces conspicuous purplish flowers. By September brilliant yellow flowers of burmarigold bloom and outline the dense thickets this species forms. Cardinal flower, swamp milkweed, water parsnip, and ironweed also display their exotic flowers.

After this intense display of flowering, the entire marsh shows signs of the coming fall: deep reddish hues appear in the leaves and stems of tearthumb; wild rice stands topple under the force of strong winds and rain; the dense clumps of arrow-arum become reduced to stubby, mud-covered sprigs. The killing frosts of November eliminate any remaining greenery. All that is left by winter is a mat of tangled, dead stems which gradually break up and disperse under tidal influence leaving a largely barren mudflat until springtime.

2.6 OTHER AQUATIC VEGETATION

Largely ignored in the existing floristic studies of tidal freshwater marshes are (1) species of aquatic vascular plants characteristically growing beneath the water surface, (2) phytoplankton within the water column, and (3) benthic or soil algae residing on muddy substrates or epiphytic on emergent plant parts. Each of these taxonomic groups is inherently less visible than emergent marsh macrophytes, yet their importance to the overall ecology of the tidal marsh habitat must not be overlooked.

Aquatic Vascular Plants

Submerged vascular flora generally grow in a zone extending approximately from the level of mean low water to depths up to several meters depending upon the clarity of the water (see Figure 13). This zone typically lies adjacent to emergent low marsh, and in the case of small shallow creeks, can encompass the entire channel. Most of these aquatic plants establish roots in soft benthic muds, perennially giving rise to herbaceous outgrowths. The density and extent of stands are extremely variable, and many species are subject to drastic fluctuations in their populations from year to year, or in some cases, within a given season (Southwick and Pine 1975; Bayley et al. 1978).

At the genus level, waterweeds, pondweeds, and watermilfoils (Figure 16) are some of the more prevalent components of tidal freshwater wetlands of the Atlantic coast (Wilson 1962; Tiner 1977; McCormick and Somes 1982; Metzler and Rosza 1982). In Virginia, some fresh subtidal aquatic beds are composed of various

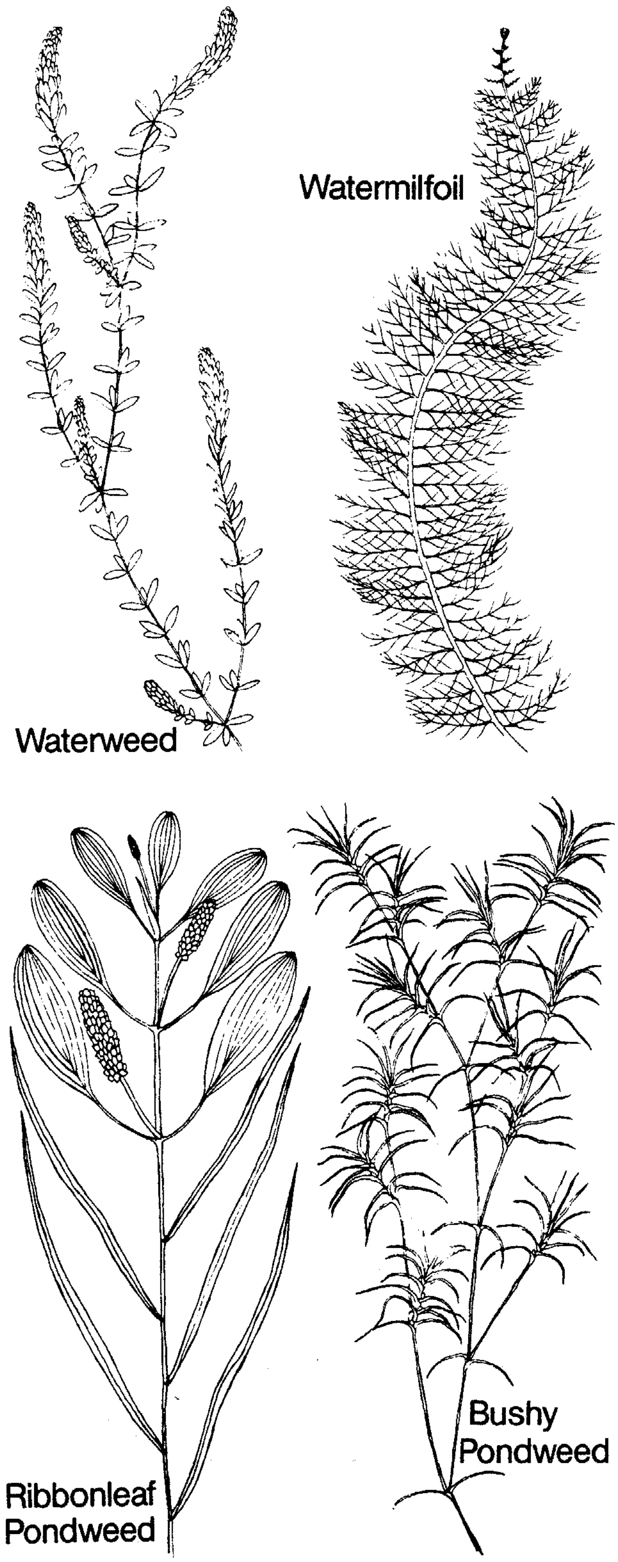


Figure 16. Common submerged aquatic plants found in Atlantic coast tidal freshwater marshes.

naiads, wild celery, and dwarf arrowhead, the latter species situated approximately at the level of mean low water on gently sloping channel banks (Hoover 1983). The Connecticut River has been described specifically as having a rooted aquatic zone codominated by waterweeds, pondweeds, and wild celery, with less common species such as hornwort, pygmyweed, and mud-plantain in association (Metzler and Rosza 1982). Often, macroscopic algae are found growing amidst these vascular aquatic plants including species of the genera Nitella, Spirogyra and Chara (Lippson et al. 1979; McCormick and Somes 1982).

Ecologically, aquatic vascular plants are important in several respects. Dense stands of aquatic plants can represent a significant fraction of the overall autotrophic productivity in tidal freshwater marshes. Many species are primary foodstuff for migrating and nesting waterfowl (see Chapter 7), and may also serve as habitat for various fishes and aquatic invertebrates (Chapter 4). It is possible that these plants act to bind substrates with their dense root networks and may even encourage sediment deposition by baffling water movement. However, these effects are not yet quantified.

As with emergent vegetation, the diversity of rooted vascular aquatics increases as water salinities decrease. Stewart (1962), working in estuaries of the Chesapeake Bay region, showed the dramatic increase in species composition between brackish and fresh salinity regimes (Table 6). However, in certain instances, the natural historical distribution of these types of aquatic plants has been altered by the multiple impacts of human population growth and activity within the estuarine watershed. Haramis and Carter (1983), in an extensive survey of submersed aquatic macrophytes in the Potomac River, found that the tidal freshwater portions of the river were essentially devoid of plants. Apparently, long-term enrichment of the river water has caused massive and persistent algal blooms which have altered the competitive balance between phytoplankton and macrophytes, resulting in the decline of the latter.

Table 6. Salinity tolerances of various submerged aquatic plants common to estuaries of the mid-Atlantic coast. Modified from Stewart (1962).

Species	Salinity Regimes				
	Marine	Poly-haline	Meso-haline	Oligo-haline	Tidal Fresh
Brown algae	*				
Ulva lactuca	*	*	*		
Enteromorpha spp.	*	*	*		
Zostera marina	*	*	*		
Red algae	*	*	*	*	
Ruppia maritima		*	*	*	
Zannichellia palustris		*	*	*	*
Potamogeton pectinatus			*	*	*
Potamogeton perfoliatus			*	*	*
Myriophyllum spicatum			*	*	*
Elodea canadensis			*	*	*
Chara spp.				*	*
Potamogeton crispus				*	*
Vallisneria americana				*	*
Najas quadalupensis				*	*
Potamogeton pusillus				*	*
Ceratophyllum demersum				*	*
Elodea nuttaillii					*
Potamogeton nodosus					*
Potamogeton amplifolus					*
Potamogeton foliosus					*
Potamogeton epihydrus					*
Potamogeton robbinsii					*
Potamogeton gramineus					*
Myriophyllum pinnatum					*
Myriophyllum tenellum					*
Najas gracillima					*
Zosterella dubia					*
Nitella spp.					*
Spirogyra spp.					*
Najas flexilis					*
Species Totals	5	6	10	14	25

Phytoplankton

Phytoplankton are an extraordinarily diversified group of organisms floating freely in the water column as single cells or as small multicellular colonies. Seasonal and spatial population dynamics of this taxonomic group result from a large and constantly changing array of environmental parameters interacting with physiological characteristics of the organisms. Salinity is a major factor influencing the geographical distribution of phytoplankton, creating a distinct community in tidal fresh water which is comprised, for the most part, of riverine taxa (Lippson et al. 1979). Light, temperature, and water turbidity exert considerable influence on photosynthesis and other metabolic processes such as reproduction. These factors interact with cycling nutrients, especially nitrogen and phosphorus, to govern the seasonal blooms and successions of phytoplankton populations. In undisturbed tidal freshwater locales this successional periodicity is fairly constant from year to year; however, biotic transitions may be muted in southern Atlantic coastal regions where climatic changes are less drastic (Sandifer et al. 1980).

Generalizations concerning seasonal abundances and periodicities of phytoplankters in fresh water are difficult to make, especially if unnatural nutrient loading occurs in the estuary (Wetzel 1975). One of the few existing quantitative assessments of tidal freshwater phytoplankton communities was compiled for the Potomac River in Virginia and Maryland (Lippson et al. 1979). These algal populations were largely characterized by (1) species of green algae (Chlorophytes) which are moderate to high in abundance year around, (2) diatoms (Bacillariophytes), which are extremely prevalent in all seasons except midsummer and early fall, and (3) moderate numbers of blue-green phytoplankters (Cyanophytes) predominating in the summer and fall months.

Chlorophyta account for as much as one-third of the total tidal freshwater phytoplankton community in the Potomac. Over 100 species have been recorded from this area with no single species dominating. J. Fourqurean and D. Childers (Department of Environmental Sciences University of Virginia, Charlottesville; pers. comm.) found that desmids and filamentous Chlorophytes comprised over 50 percent of a Virginia tidal freshwater phytoplankton community in late fall. Species commonly found in both of these studies include Micractinium spp., Pedlastrum spp., Scenedesmus spp., Spirogyra spp., and Microspora spp.

The most ubiquitous and abundant of all phytoplankters are the Bacillariophytes. Many of these species are actually epibenthic algae which become entrained in the water column via tidal currents. Peak diatom biomass often exceeds one million cells per liter (Lippson et al. 1979); however, no information is available concerning the genera most consistently encountered in tidal fresh waters.

The remaining phytoplanktonic components include various Cyanophytes, euglenoids, and dinoflagellates. Freshwater species of blue-green algae are strongly inhibited by salinities greater than a few parts per thousand and generally do not exceed densities over one-hundred thousand cells per liter. Common genera include Anabaena, Anacystis and Oscillitoria. Populations of euglenoids are transient, and occur only during midsummer in the Potomac. Densities do not exceed 10,000 cells per liter. During late summer the most prevalent genera are Euglena and Trachelmonas. The dinoflagellate, Peridinium, was found to be an abundant constituent of phytoplankton communities in the James River in Virginia (Fourqurean and Childers, pers. comm.).

Benthic/Mud Algae

Epibenthic algae grow wholly or partially submerged on a variety of surfaces. They occur as microscopic unicells or larger colonial forms, with many species residing only temporarily on the benthos. Planktonic forms commonly settle onto benthic or marsh surface substrates to complete the reproductive or resting stages of their life cycles. The benthic algal communities of tidal freshwater marshes are not well studied, and like phytoplankton, are subject to complex blooms and successions which make it difficult to give general demographic descriptions. The limited information available suggests that Cyanophytes, Bacillariophytes, and Chlorophytes dominate epibenthic algal communities' tidal freshwater habitats. Many of these communities are comprised of riverine species which are intolerant of saline conditions.

Summer communities in tidal freshwater portions of the Potomac River are typified by the blue-green algae Shizothrix spp. and Chromulina paschrei and by green algae such as Cosmarium spp. and Clostreium spp. (Lippson et al. 1979). In contrast, late fall benthic algal counts in a tidal freshwater tributary of the James River showed centric (Cyclotella sp., Stephanodiscus sp., Coscinodiscus sp.) and pennate (Naviculales sp.) diatoms to be the dominant community constituents (Fourqurean and Childers, pers. comm.).

In a year long study of soil algae in a New Jersey tidal freshwater marsh, a total of 84 species, exclusive of diatoms, were cataloged (Whigham et al. 1980). Algal diversity peaked prior to the beginning of the growing season. It peaked again in September after commencement of the macrophyte dieback. Chlorophytes strongly dominated this marsh surface community, followed by Cyanophytes and then Xanthophytes.

Whigham et al. (1980) maintain that summer growth of emergent macrophytes reduces the algal density on muddy marsh substrates. Whigham and Simpson (1975) assessed the productivity of mud algae in various macrophyte community types. Soil type appeared to influence productivity most significantly; the silty-sand soils and low organic content of low marsh-spatterdock zones provided the best substrate for algal growth. In contrast, silty-clay soils and high organic contents found in mixed-herbaceous high marsh areas and cattail communities produced lower algal productivities. Presumably, edaphic characteristics act in conjunction with light, temperature, and nutrient concentrations to produce these differences in standing crop. As with phytoplankton, nutritive sewage effluent is known to significantly increase algal standing crops in tidal marshes (Whigham and Simpson 1975).

Mud algae can often be seen forming a dark-greenish band on exposed channel banks of tidal areas. Peak biomass for this taxa is estimated to be two to three orders of magnitude less than peak biomass for vascular plants (Wetzel and Westlake 1969). Mud algae remain as functioning producers throughout the entire year, however, and may contribute more to total annual production than might be expected.

CHAPTER 3. ECOSYSTEM PROCESSES

3.1 PRIMARY PRODUCTIVITY

Introduction

The primary productivity of an ecological system, community, or any part of such a system, is defined as the rate at which various organisms, chiefly green plants, assimilate and synthesize gaseous and dissolved inorganic substances into organic matter. The total amount of organic matter produced by green plants during a particular time interval is termed gross primary production. The rate of storage of organic matter in plant tissues in excess of the respiratory utilization by plants during the period of measurement is known as net primary production.

The organic matter produced by vascular plants, phytoplankton, and benthic algae in the tidal freshwater habitat serves as an energy source for various heterotrophic organisms. Much live material can be consumed in situ by various herbivores. Microbial populations decompose and utilize a large fraction of the dead plant material on the marsh surface. Detritivores further fragment decomposing plant remains. Although a significant portion of this organic matter is utilized and stored within the marsh habitat, a large fraction may be exported out of the system. Tidal currents and wind encourage the entrainment and transport of organic carbon to downstream estuarine locations. Migrating consumers may feed within the habitat and then move on. It is estimated that salt marshes export about one-half of the net primary production to adjacent tidal waters (Teal 1962, Odum and Skjei 1974); however, a comparable figure is not available for tidal freshwater marshes.

Production Estimates

The biomass and primary production of tidal freshwater wetlands have been reported to be very high (Odum 1978). Numerous estimates of standing crop and annual aboveground net production exist for the dominant species of vascular plants occurring within this habitat (Table 7); however, there are only a few estimates of total net community production (Whigham et al. 1976, Doumlele 1981). The existing data on biomass and production show a great deal of variability both within and between vegetation types, yet it appears that the total net community production of these marshes generally ranges from 1,000 to over 3,500 $g/m^2/yr$ (Odum 1978). Productivity measures reported for saline wetlands fall within the same range as those for tidal freshwater marshes, within a given latitudinal zone (e.g., mid-Atlantic); the biomass production of fresh tidal wetlands may be greater than higher salinity communities (Whigham et al. 1976).

Obtaining accurate estimates of net production in tidal marshes, either on a per-species or community basis, is difficult because of (1) seasonal patterns of biomass allocation, (2) the heterogeneity in plant community composition, (3) seasonal biomass turnover due to leaf mortality, decomposition, and herbivory, and (4) the inherent problems in measuring the production of belowground plant parts (Whigham et al. 1978). Traditionally, investigators have compared the productivity of tidal wetland vegetation by measuring peak aerial standing crops. However, there is no objective way of pinpointing the exact moment at which the peak crop exists; therefore, the potential for error with single harvest methods is high (McCormick and Somes 1982). By restrict-

Table 7. Peak standing crop and annual production estimates for common tidal freshwater vegetation types. Data are largely generated from mid-Atlantic tidal freshwater marshes. Values are in grams per m² dry weight. Average values are not necessarily a function of table entries, but represent best estimates from selected literature values. This table is an extension of those produced by Whigham et al. (1978) and McCormick and Somes (1982).

Vegetation type	Peak standing crop			Annual production	State	Source
	Tops	Roots	Dead			
Spatterdock	514*	-	-	-	MD	12
	245	-	-	-	VA	15
	743*	-	-	863*	NJ	10
	516	-	-	-	NJ	11
	605	1146	-	-	NJ	5
	529*	-	-	-	NJ	16
	-	4799	-	780	NJ	16
	1175	-	-	-	PA	9
Average	627			780		
Arrow-arum/ pickerelweed	459	-	-	-	VA	3
	648*	-	-	-	MD	12
	988	-	-	-	MD	4
	1286	2463	-	-	NJ	6
	594*	-	-	-	NJ	11
	587*	-	-	-	NJ	16
	-	-	-	650	NJ	16
	667	-	-	1126	NJ	10
	553	-	-	-	NJ	9
Average	671			888		
Wild rice	2091*	-	-	-	MD	12
	1178*	-	-	-	MD	4
	560	-	-	-	VA	15
	1390	-	-	-	NJ	11
	1600	721	-	-	NJ	5
	866*	-	-	1589	NJ	16
	1346	-	-	1520	NJ	10
	1117	-	-	-	PA	9
Average	1218*			1578		
Giant cutgrass	1039	518	-	2048	GA	1
Smartweed-rice cutgrass	2142*	-	-	-	MD	12
	1547	-	-	-	VA	15
	116	-	-	-	VA	3
	769	507	-	-	NJ	5
	523	-	-	-	PA	9
Average	1207					

(continued)

Table 7. Continued.

Vegetation type	Peak standing crop Tops	Roots	Dead	Annual production	State	Source
Rose-mallow	1713*	-	-	-	MD	12
	569*	-	-	-	MD	2
	-	-	-	489	MD	13
Average	1141			869		
Cattail	2338	-	167	-	MD	7
	1190*	-	300	-	MD	4
	966	-	-	1868	MD	8
	987	-	-	-	NJ	11
	850	1800	-	-	NJ	5
	1007*	1371	-	-	NJ	6
	-	-	-	956	NJ	13
	1297*	-	-	1320	NJ	16
	1199	-	-	1534	NJ	10
	804	5053	-	-	NJ	14
	1310*	-	-	-	PA	9
Average	1215			1420		
Burmarigold	1026	-	-	910	NJ	16
	1109	-	-	1771	NJ	10
	900	-	-	-	PA	9
Average	1017			1340		
Sweetflag	1174*	-	-	-	MD	12
	605	-	-	-	NJ	11
	819*	-	-	-	NJ	16
	623	-	-	1071	NJ	10
Average	857					
Duck-potato	649	-	-	1071	NJ	10
	214	-	-	-	NJ	6
Average	432					
Water-hemp	1112	-	-	1547	NJ	10
	678	560	-	-	NJ	6
Average	960					
Giant Ragweed	1160	-	-	1160	NJ	16
	1227*	-	-	-	PA	9
Average	1205					

(continued)

Table 7. Concluded

Vegetation type	Peak standing crop: Tops	Roots	Dead	Annual production	State	Source
Common reed	3999*	-	-	-	MD	12
	-	-	-	3900	MD	13
	1367	-	347*	-	MD	4
	1451	-	-	1678	MD	8
	1727	-	-	-	NJ	11
	1493	-	-	2066	NJ	10
	1074	-	-	-	NJ	14
	654	-	-	-	PA	9
Average	1850			1872		
Big cordgrass	3543*	-	-	-	MD	12
	951	-	241	-	MD	4
	1207	-	-	1572	MD	8
Average	2311					
Spiked-loosestrife	2104	-	-	2100	NJ	16
	1373	-	-	-	PA	9
Average	1616					
Swamp rose	699**	-	-	-	MD	12
Red maple/ash	522**	-	-	-	MD	12
Bald cypress	344**	-	-	-	MD	12
Mud algae	4*	-	-	-	NJ	16

*Value generated from more than one estimate
**Leaves of woody plants; no wood is included

List of Sources:

1-Birch and Cooley 1982
2-Cahoon 1982
3-Doumlele 1981
4-Flemer et al. 1978
5-Good and Good 1976
6-Good et al. 1975
7-Heinle et al. 1974
8-Johnson 1970
9-McCormick 1970
10-McCormick 1977
11-McCormick and Ashbaugh 1972
12-McCormick and Somes 1982
13-Stevenson et al. 1976
14-Walker and Good 1976
15-Wass and Wright 1969
16-Whigham and Simpson 1975

ing the sampling effort to just one point during the growing season, those plant tissues which develop after sampling and those that senesce or are consumed by insects before sampling are missed. Given the dramatic seasonal successional changes that are known to occur in almost all tidal freshwater vegetation communities, estimates of total community production are likely to be inaccurate and underestimated unless multiple harvests are made.

Density of vegetation and species composition also greatly influence production estimates. Doumlele (1981) noted that peak biomass values for arrow-arum from a number of different studies ranged from 67 to 1,286 g/m^2. These drastic differences were attributed to the degree of spacing between individuals at various locations and to the relative pureness of the predominant vegetation type within a given stand. Pure stands of any given species are uncommon in tidal freshwater marshes, especially at higher elevations. Total biomass production estimates of mixed tidal freshwater marsh communities are strongly dependent on species composition. A diversified community can contain a variable proportion of prolific producers (e.g., common reed or wild rice) or species with inherently lower biomass production (e.g., arrow-arum or spatterdock) (Whigham et al. 1978; Doumlele 1981).

Inspection of the peak standing crop and annual net production estimates compiled in Table 7 clearly reveals the high variability between species. Marshes dominated by tall reeds and grasses such as wild rice, common reed, giant cutgrass, big cordgrass, or cattail produce the greatest quantities of biomass, generally in the range of 1,500 to 2,000 g/m^2/yr. Considering the potential heights and densities attained by these species, such extraordinary production rates are not surprising. Early in the growing season, many marshes are dominated extensively by fleshy-leaved macrophytes (arrow-arum, pickerelweed, spatterdock) and would seemingly show high rates or biomass accumulation. However, all these species show maximum peak standing crops of less than 700 g/m^2/yr. In reality, all of these emergent perrenials produce aerial leaves and stems composed primarily of water and air-filled aerenchymatous tissue.

Other vegetation producing significant quantities of biomass on an annual basis include burmarigold (1,340 g/m^2), water-hemp, giant ragweed, rose-mallow (869 g/m^2), and sweetflag. In addition, shrubs and hydrophytic trees may supply 300 to 700 g/m^2 of leaf material onto the marsh surface.

No satisfactory method exists for quantifying belowground production in wetland habitats. Belowground production measurements, however, are essential to the accurate assessment of per-species or community productivity. Whigham et al. (1978) suggested that belowground production can be quite high for some species. Data for cattail, spatterdock, and arrow-arum show impressive underground production capability (see Table 7), but as perrenials, these values do not represent biomass accumulation from a single growing season. In order to account for changes in belowground biomass on a yearly basis for either annual or perrenial species, production rates need to be calculated over short, repeated intervals. Although largely unquantified, the rates of belowground production in these species are thought to be high.

Unfortunately, the peak standing crop production information in Table 7, from studies spanning a number of years and locations, is not conducive to making between-marsh comparisons of productivity. If seasonal changes in community biomass per marsh unit were quantified (e.g., Doumlele 1981), our understanding of the factors influencing marsh productivity would be greatly enhanced.

Biomass Partitioning

The partitioning of net primary production between aboveground and belowground structures of tidal freshwater macrophytes can provide insight into the life history strategies of species populations. Whigham and Simpson (1978) noted that yearly production in annual species including grasses (wild rice) and herbs (burmarigold, jewelweed, smartweed, water-hemp) was largely allocated to aboveground shoot production except during early stages of growth. At peak standing crop, the ratio of belowground (roots) to aboveground (stems) biomass (R:S) averaged less than 0.5 for all annual species measured. Perennials exhibited more variation in patterns of biomass allocation, but generally partitioned greater amounts of biomass to belowground plant parts. Arrow-arum provides the most extreme example of this trend, allocating up to 90% of its total biomass to roots and rhizomes (R:S much greater than 1.0).

Differences in biomass partitioning are most likely related to reproductive strategies, survival strategies, or physiological adjustments associated with exploitation of stressful portions of a habitat gradient (Whigham and Simpson 1976; Ferren and Schuyler 1980). Annual seedlings allocate more biomass to rooting structures during establishment phases, then convert to a rapid phase of shoot growth. Anaerobic conditions prevailing in low marsh substrates demand physiologic adaptations for survival. The deep underground tubers produced by arrow-arum are adapted to cope with such stresses, but the energy expenditure required to maintain such structures is great.

3.2 DECOMPOSITION AND LITTER PRODUCTION

Decomposition of marsh plant material (reviewed by Brinson et al. 1981) varies greatly in response to a variety of factors. These include ambient temperatures, moisture, periodicity of flooding, nutrient availability from external sources, presence or absence of oxygen, consumer activity, and a range of plant substrate characteristics including nitrogen and crude fiber content. In spite of this variability, there are several general trends associated with tidal freshwater plant material which we have identified.

Tidal freshwater vascular plants can be placed into two general groups based on the rate at which they decompose (Table 8). One group, generally found in the low and mid sections of the marsh, decompose extremely rapidly (Odum and Heywood 1978) (see Figure 17). These plants have relatively low amounts of resistant compounds (e.g., hemi-cellulose, cellulose, lignin) and relatively high amounts of nitrogen (2% to 4% of total dry weight according to Dunn 1978). They also have the highest rates of oxygen consumption (BOD) during decomposition (Van Dyke 1978). During the warm summer months, these plants may lose 30% to 40% of their dry weight in one week

Table 8. Two groups of tidal freshwater vascular plants based on rates of decomposition under similar conditions are arranged in approximate order of rate of decay with the most rapid at the top. Other plants in the marsh lie between these two groups. Decay rates are of aboveground material only.

Species	Reference
RAPID DECOMPOSERS	
Spatterdock, Nuphar luteum	Van Dyke (1978)
Arrow-arum, Peltandra virginica	Odum and Heywood (1978)
Burmarigold, Bidens laevis	Sickels et al. (1977)
Pickerelweed, Pontedaria cordata	Our unpublished data
Arrowhead, Sagittaria latifolia	Our unpublished data
Hibiscus (leaves), Hibiscus moscheutos	Cahoon (1982)
Wild rice, Zizania aquatica	Our unpublished data
SLOW DECOMPOSERS	
Sedges, Carex spp.	Bowden (pers. comm.)
Broad-leaf cattail, Typha latifolia	Brinson et al. (1981)
Narrow-leaf cattail, Typha angustifolia	Brinson et al. (1981)
Common reed, Phragmites australis	Our unpublished data
Hibiscus (stems), Hibiscus moscheutos	Cahoon (1982)

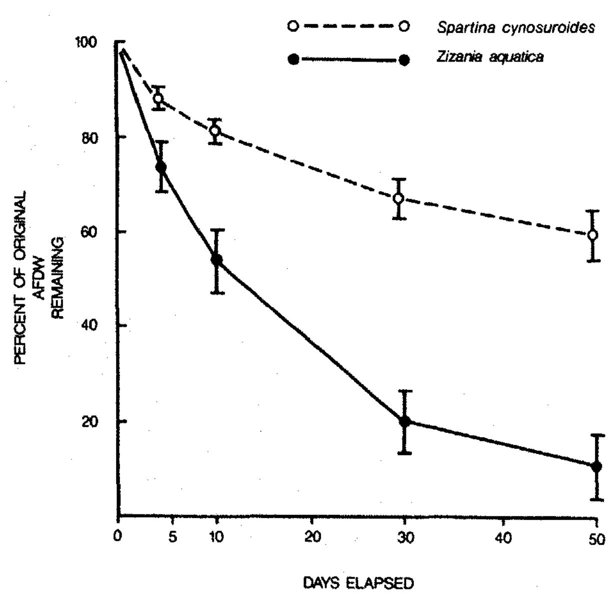


Figure 17. Typical decomposition curves for high marsh plants (e.g., Spartina cynosuroides) and low marsh plants (e.g., Zizania aquatica) subject to similar environmental conditions. From Turner (1978).

and completely decompose in 4 to 6 weeks (Van Dyke 1978, Turner 1978).

The second ground of tidal freshwater plants (Table 9) are found in the higher sections of the marsh and have much slower rates of decomposition (Figure 17). In general, they contain high concentrations of resistant compounds and lower concentrations of nitrogen than the first group of plants (Dunn 1978). Consumption of this type of plant material by detritivores is significantly lower than from the first group (see Section 3.5).

Plants that decompose rapidly dominate the low marsh in tidal freshwater (see Chapter 2). The low marsh has a modest litter layer during the summer months and very little litter during the winter and spring. This contributes to the high erodibility of the low marsh (Section 1.6) and the tendency to release nutrients into tidal waters during the winter and spring (Section 3.3). The high marsh with its slower decomposing plants retains a significant litter layer throughout the year (personal observation). In some northern marshes, such as the North River Marsh in Massachusetts which is dominated by species of _Calamagrostis_, _Carex_, and _Typha_, and where decomposition rates are generally slower, much of the marsh retains a significant litter layer during all seasons (Bowden 1982). The same situation exists in southeastern marshes dominated by giant cutgrass which has an extensive rhizome system and produces a thick peat layer.

Table 9. Typical zooplankton to be expected in mid-Atlantic tidal freshwater. Data from Lippson et al. (1979) for the Potomac River, and from Van Engel and Joseph (1968) for the York River.

Jellyfish	
	winter jellyfish, _Cyanea capillata_
Copepods	
	Eurytemora affinis
	Mesocyclops edax
	Acartia tonsa
Mysid	
	Neomysis americana
Amphipods	
	Corophium lacustre
	Monoculodes edwardsi
	Gammarus spp.
Cladocerans	
	Daphnia
	Sida crystallina
	Leptodora kindii
	Bosmina longirostris
Rotifers	
	Keratella cochlearis
	Brachionus calciflorus
Benthic invertebrate larvae	
	Rhithropanopeus harissii (mud crab)

Not only do the rapidly decomposing plants have a high nitrogent content, but during the early stages of decomposition the nitrogen and phosphorous content may increase (Odum and Heywood 1978; Turner 1978) (see Figure 18). Sickels et al. (1977) and Whigham et al. (1980) showed that tidal freshwater marsh litter is capable of concentrating both phosphorus and nitrogen from sewage effluent released onto the marsh surface. This nutrient concentration has implications for understanding nutrient flux (Section 3.3).

It appears that the low marsh, with its seasonal litter layer, may serve as a nutrient sink only during the summer and fall months while the high marsh may have a greater year-long nutrient uptake capacity.

In summary, the low and high marsh plants of the tidal freshwater marsh decompose at dramatically different rates. This leads to differences in the thickness and duration of the litter layer, erosion rates, and nutrient retention capacity in different sections of the marsh. As a result, depending upon the relative proportions of high and low marsh vegetation, these marshes may vary in their capacity to absorb excess loads of nutrients (i.e., sewage effluent).

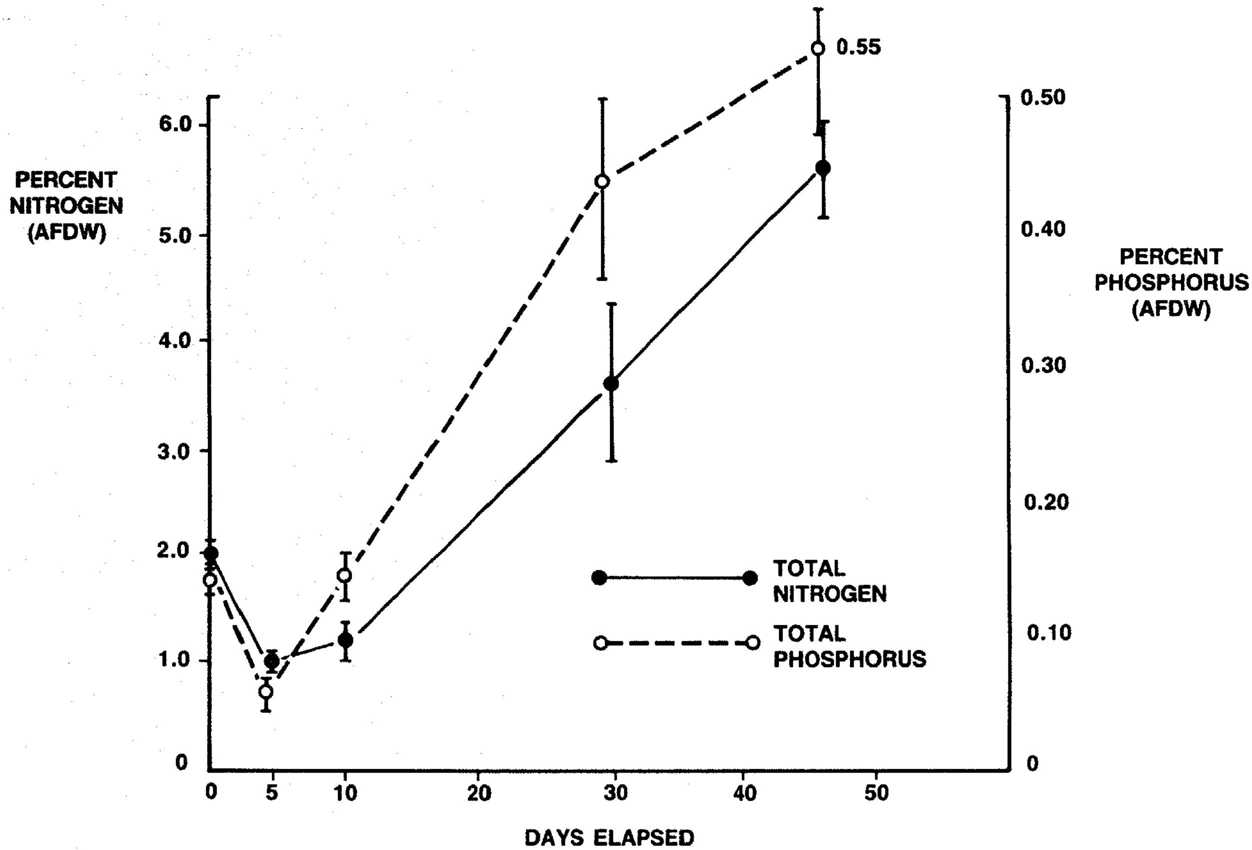


Figure 18. Changes in total nitrogen and phosphorus content of decaying wild rice, *Zizania aquatica*, expressed as percent of the remaining ash-free dry weight. Plotted values are mean ± 1 S.E. From Turner (1978).

3.3 NUTRIENT CYCLING (OTHER THAN CARBON)

The general model of nutrient cycling in estuarine marshes is based on a number of studies (e.g., Axelrad et al. 1976; Valiela and Teal 1979; Nixon 1980). This model appears to apply in principle to tidal freshwater marshes. Certain details, however, may be different.

The general estuarine model (Figure 19) indicates that coastal marshes act primarily as transformers of nutrients, particularly nitrogen and phosphorus; in addition they may function as either sinks or sources of nutrients depending upon a variety of conditions. As transformers they import dissolved oxidized inorganic forms (nitrite, nitrate, phosphate) and export dissolved and particulate reduced forms (ammonium, forms of organic nitrogen and phosphorous compounds). There is a tendency for coastal wetlands to have a net import of nutrients at the beginning and during the growing season and to have a net export in the autumn and winter. Whether a specific marsh is a net importer or exporter of nutrients depends on a number of factors including: (1) successional age of the marsh, (2) salinity and redox characteristics, (3) presence or absence of upland sources of nutrients, (4) presence or absence of human inputs of nutrients, (5) tidal energy input, and (6) magnitude and stability of nutrient flux in the estuary to which the marsh is coupled (Stevenson et al. 1977).

Tidal freshwater marshes apparently function in a similar fashion (Heinle and Flemer 1976; Stevenson et al. 1977; Adams 1978; Simpson et al. 1978; Simpson et al.

SOURCES
(LARGELY INORGANIC, OXIDIZED N AND P COMPOUNDS)

PRECIPITATION
GROUNDWATER SEEPAGE
TIDAL FLOODING OR RIVER INFLOW
NITROGEN FIXATION
ANIMALS (BIRDS, MAMMALS, FISH, ETC.)

↓

MARSH COMMUNITY
(LARGELY MICROBIAL ACTIIVITY)

NITROGEN	PHOSPHORUS
PLANT UPTAKE AND RELEASE	ORTHOPHOSPHATE ADSORPTION
DETRITAL UPTAKE AND RELEASE	PLANT UPTAKE AND RELEASE
AMMONIFICATION (ORGANIC → AMMONIUM)	
DISSIMULATORY NITRATE REDUCTION (NITRATE AND NITRITE → AMMONIUM)	

↓

OUTPUTS
(LARGELY ORGANIC P, AND REDUCED AND ORGANIC N)
TIDAL FLUSHING
ATMOSPHERIC RELEASE OF AMMONIA
DENITRIFICATION

Figure 19. A general model of nitrogen and phosphorus nutrient cycling in coastal marshes. Based on Valiela and Teal (1979) and Nixon (1980).

1981; Bowden 1982). One possible difference, however, is that the characteristic seasonal nutrient exchange tendencies are more pronounced in tidal freshwater marshes, probably due to a lack of winter plant and litter cover. In these marshes there appears to be a clear pattern of nitrite, nitrate, and phosphate import from river water to the marshes at the beginning of the growing season. This is metabolized by bacteria into forms more useful to plants (i.e., ammonium) and stored during the summer months in both plant tissues and the litter layer on the surface of the marsh. Whigham et al. (1980) demonstrated the importance of the litter layer in holding both nitrogen and phosphorus temporarily during the summer and early autumn. Later in the autumn there is considerable export of reduced nitrogen and phosphorus due to the rapid disappearance of dead and dying plant material from the lower sections of the marsh. During the winter nutrients continue to be exported, but at a slower rate.

The preceding discussion remains hypothetical. There is a lack of studies on processes involved in the cycling of nitrogen and phosphorus in tidal freshwater marshes. Whether the spring and autumn peaks of nutrient flux are more pronounced than in salt marshes remains to be demonstrated conclusively.

The importance of nitrogen fixation in tidal freshwater wetlands is not certain. Excessive shading by the broad-leaved plants (arrow-arum, pickerelweed, spatterdock) may limit the activity of blue-green algae to creek banks during the early spring and late autumn.

Bowden (1982) has emphasized the importance of ammonium in tidal freshwater marshes. In a mass balance study of the North River, Massachusetts, he found the gross ammonium production by microbes to be 53.5 g $N/m^2/yr$. This production rate was sufficient to supply all of the nitrogen required to support plant production (estimated to be 22.3 g $N/m^2/yr$), microbial assimilation (measured as 17.9 g $N/m^2/yr$), and nitrification (measured as 11.6 g $N/m^2/$ yr). The ammonium production rate was supported by efficient internal recycling of nitrogen in litter, by microbial immobilization of ammonium and nitrate, and by sedimentation of allochthonous organic matter from the adjacent river. This marsh imported inorganic nitrogen during the plant growing season. Unlike many southern marshes, an extensive litter layer persists all year and may retard nitrogen export even during the winter.

Most other studies (e.g., Axelrad et al. 1976; Heinle and Flemer 1976; Stevenson et al. 1977; Adams 1978; Simpson et al. 1981) have concluded that tidal freshwater marshes are net exporters of both nitrogen and phosphorus on an annual basis. This may reflect the fact that all of these studies were done in eutrophic or hypereutrophic locations. Under these conditions, the marsh sediment-plant complex can become saturated with both nitrogen and phosphorus, at least in the low marsh. Without a permanent litter layer or significant amounts of peat, there may be no mechanism for excessive nutrient storage and the marsh functions as a net source of nutrients. This suggests that many tidal freshwater wetlands probably do not have a great assimilative capacity for either sewage effluent or heavy metals (discussed in Chapter 9).

In summary, the overall pattern of nutrient cycling in tidal freshwater marshes appears to be similar to the pattern hypothesized for estuarine marshes. Simply stated, oxidized nitrogen and phosphorous compounds are processed within the marsh and reduced compounds are released back into the river. In tidal freshwater marshes the spring influx of oxidized compounds and the autumn release of reduced compounds may be more pronounced than in estuarine marshes. In addition, most tidal freshwater marshes which have been studied appear to be net exporters of both nitrogen and phosphorus.

3.4 CARBON FLUX

As in the case with most wetland ecosystems, knowledge of carbon flux in tidal freshwater marshes is incomplete. Several studies have addressed this topic (e.g., Axelrad et al. 1976; Heinle and Flemer 1976; Adams 1978), but no more than hypotheses can be presented at this time.

Sources (or inputs) of organic carbon for the marsh include: (1) primary production within the marsh, (2) dissolved and particulate carbon flowing into the marsh on the rising tide, (3) dissolved carbon in rainwater, and (4) dissolved carbon in groundwater. Outputs from the marsh include: (1) export of dissolved and particulate carbon on the outgoing tide, (2) permanent burial of carbon in the marsh sediments, and (3) release of methane and carbon dioxide to the atmosphere. The most significant inputs are most likely primary production in the marsh and carbon imported on the flooding tide. The latter probably includes considerable amounts of terrestrial carbon brought from upstream in the river water (Biggs and Flemer 1972). Significant outputs are probably tidal export and burial. Regardless of the net carbon flux (net import or net export) from an individual marsh, it is important to note that there is an approximate 100% turnover of the aboveground biomass on an annual basis.

Individual tidal freshwater marshes function as net importers or exporters of organic carbon in response to the same factors which control this process in estuarine marshes (discussed by Odum et al. 1978 and Nixon 1980). These factors include, but are not limited to, tidal range, basic geomorphology, relative amount of marsh versus open water, and amount of freshwater input to the system. Studies by Axelrad et al. (1976) and Adams (1978) found significant export of carbon from tidal freshwater marshes on the York and James Rivers in Virginia. In both cases the bulk of export appeared to be in the form of dissolved carbon compounds rather than particulate matter. But Heinle and Flemer (1976), on the other hand, found neither export nor import in poorly flooded oligohaline marshes on the Patuxent River in Maryland.

With only a handful of studies completed, it is difficult to conclude much beyond the following hypotheses. Tidal freshwater marshes that (1) are relatively young (see Section 1.7), (2) do not have an outer berm or natural dike, (3) have significant iceshearing of the vegetation during the winter, and (4) have a significant tidal range, probably export significant quantities of both particulate and dissolved carbon. Older marshes that are more developed both geologically and ecologically (i.e., have a large area of high marsh) probably do not export significant quantities of particulate carbon (Heinle and Flemer 1976); they may, however, export quantities of dissolved organic carbon. This last point is far from resolved.

Methanogenesis is one aspect of carbon flux which deserves close study in tidal freshwater marshes. As pointed out by Swain (1973), there is a gradient of methane loss in progressing from freshwater to marine wetlands. Under freshwater conditions, methanogenesis is an important pathway of anaerobic decomposition; under marine conditions it is relatively minor because sulfate reduction replaces methanogenesis. Since SO_4 is not typically abundant in freshwater, this means that methane release from freshwater environments should be much higher than from seawater environments. There is considerable evidence to support this hypothesis (Robert Harriss, NASA, Hampton, Virginia; pers. comm.), although King and Wiebe (1973) reported relatively high methane release rates from Georgia coastal salt marshes.

Following current theories, tidal freshwater marshes should release significant amounts of methane. This can occur through (1) direct release to the atmosphere from the marsh surface, (2) release from plants such as cattails (Sebacher and Harriss, in press), or (3) release from dissolved methane in creek water (Harriss et al. 1982). Lipschultz (1981) measured the release of methane from a tidal freshwater marsh dominated by *Hibiscus moscheutos*. He estimated an annual loss of 10.7 g $CH_4/m^2/yr$, a value more similar to freshwater conditions than marine. On the other hand, this loss was less than 1% of annual net primary production in this marsh and, therefore, appears unimportant. Robert Harriss (pers. comm.) suggested, based on preliminary measurements, that rates of methane release from tidal freshwater may be much higher than indicated by Lipschultz's (1981) estimate. More work is needed in this area.

3.5 ENERGY FLOW

Any attempt to describe energy flow in tidal freshwater marshes will be speculative since no complete study exists for this habitat. We can, however, present a hypothetical model based on a few partial studies and our experience in the field.

Our hypothetical model (Figure 20) is based on functional groups. In some cases these represent a single group (i.e., juvenile fishes) while others, such as benthic fauna, may include many taxa. Several preliminary but important observations can be derived from this model.

(1) There appear to be three principal sources of energy to support food webs--marsh macrophytes, terrestrial organic material, and phytoplankton. Benthic microflora within the marsh may be of some importance, but there is presently no information to confirm this. The relative

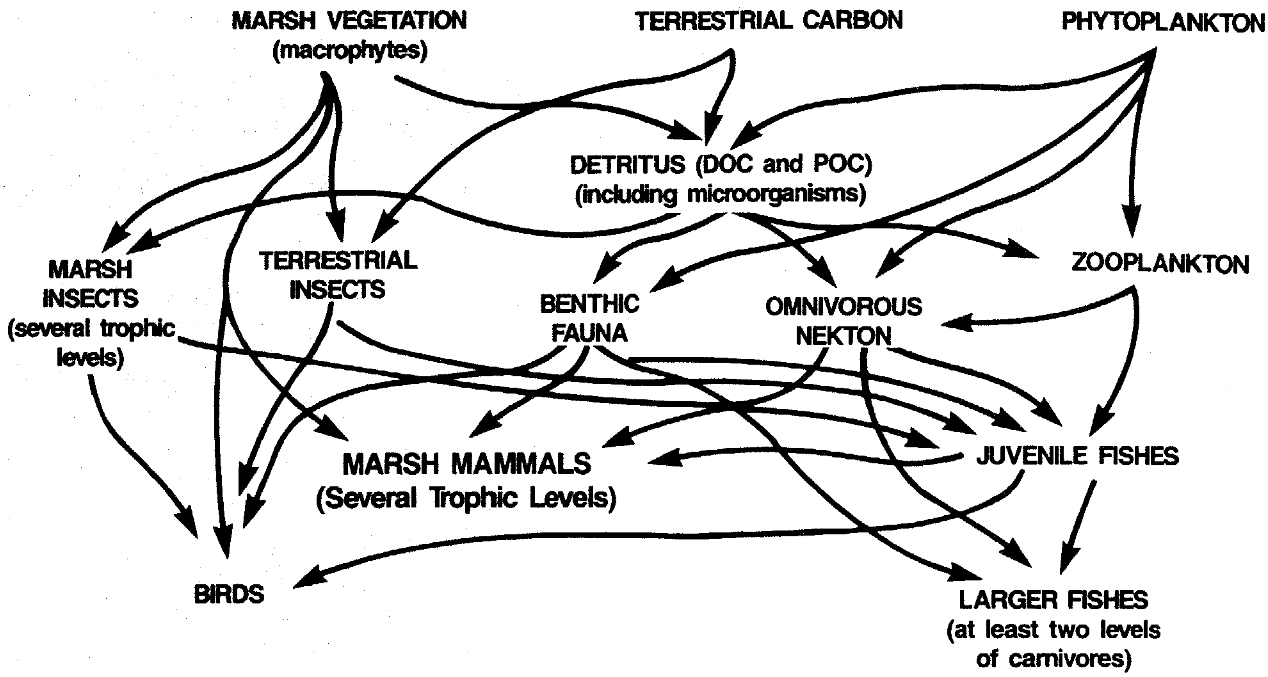


Figure 20. Hypothetical pathways of energy flow in a tidal freshwater marsh ecosystem. Not all possible pathways have been drawn. For example, benthic microflora in the marsh may provide carbon for consumers; however, evidence is lacking at this time.

importance of the three major sources of energy is unknown. We suspect that marsh plant detritus and associated microorganisms are most important in well-flushed marsh systems, that terrestrial material is of importance where large river systems bring quantities of organic carbon from upstream sources, and that phytoplankton plays a key role in certain situations (see number 3 below).

(2) In general, we suspect that tidal freshwater wetlands are primarily detritus-based ecosystems, although this is unproven. Dunn (1978) showed that a number of benthic invertebrates will readily consume vascular plant detritus from tidal freshwater marshes (Figure 21). Large quantities of particulate and dissolved carbon are flushed out of these marshes and also from upstream sources (see Section 3.4). At certain times of the year (late summer, autumn, winter), large quantities of particulate detritus are present on the marsh surface and on the bottom of the marsh creeks (personal observations). The relative importance of dissolved versus particulate detritus is totally unknown at this time. Water draining tidal freshwater marshes typically contains 5 to 10 times as much dis-

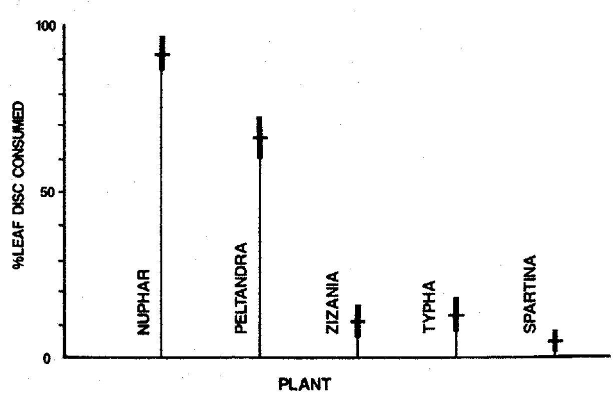


Figure 21. Percent leaf disc consumed (ODW) by amphipods, Gammarus fasciatus, during 96-hr feeding tests. Plotted values represent the mean of three samples ± 1 S.E. From Dunn (1978).

solved carbon as particulate carbon. There are, however, significant quantities of particulate material available for the benthos. Associated with this particulate material are large numbers of bacteria and fungi (Marsh and Odum 1979), suggesting that it has an enhanced food value.

(3) The food chain consisting of phytoplankton/detritus-zooplankton-larval and juvenile fishes is of considerable interest and importance to man because of the commercial fisheries involved. The data of Van Engel and Joseph (1968) in the York and Pamunkey Rivers documented the key role of zooplankton as a dietary component for a wide variety of larval, postlarval, and juvenile fishes, many of commercial importance. They found that the most common zooplankters in fish stomachs were the mysid, Neomysis americana; the copepods, Acartia tonsa and Eurytemora affinis; four or five species of cladocerans; and several species of amphipods. These zooplankters, in turn, have been shown to ingest both phytoplankton and organic detritus (Heinle et al. 1977).

(4) Within the marsh system (marsh surface, small marsh creeks), terrestrial and aquatic insects along with the benthic fauna appear to be important in the diets of omnivorous fishes. Van Engel and Joseph (1968) found the crab Rhithropanopeus harissii and the shrimps Crangon septemspinosa and Palaemonetes pugio to be important components of the diets of a variety of fishes. Dias et al. (1978) emphasized the importance of the aquatic larvae of terrestrial insects as a food source for tidal freshwater fishes, while Diaz and Boesch (1977) mentioned the significant contribution of benthic fauna (oligochaetes, chironomid larvae, the Asiatic clam) in the diets of benthic feeding fishes such as catfish, striped bass, carp, perch, eel, and cyprinodont minnows (see Chapter 5 for more on this subject).

(5) Direct usage of marsh plant material (leaves, seeds) appears considerably important in tidal freshwater marsh systems, in fact, probably more important than in salt marshes. Muskrats, beaver (during the summer), and nutria consume quantities of fresh plant material (see Chapter 8); other mammals including whitetail deer ingest smaller quantities (personal observation). Birds utilize the seed production of tidal freshwater marshes extensively in the late summer, fall, and early winter (see Chapter 7). Insects graze certain marshplants heavily (i.e., Hibiscus) while other plants such as Phragmites are scarcely touched.

In summary, our knowledge of energy flow in tidal freshwater wetlands is almost totally speculative. We hypothesize that foodwebs are generally detritus-based with a variety of omnivorous benthic fauna serving as the intermediary link to fishes. Zooplankton apparently play a key role in supporting larval and juvenile fishes. Direct grazing and seed consumption by mammals, birds, and insects are probably more significant than in higher salinity estuarine marshes farther downstream.

CHAPTER 4. COMMUNITY COMPONENTS: INVERTEBRATES

4.1 ZOOPLANKTON

The zooplankton community of tidal freshwater is dominated by a combination of freshwater rotifers and cladocerans along with estuarine copepods. Typical examples of the different phyla are shown in Table 9. Although the numbers of species represented are far less than further downstream, there is some evidence that total numbers (density) of zooplankton in tidal freshwater are significantly greater than in contiguous nontidal freshwater or estuarine water (Van Engel and Joseph 1968).

At any particular location the plankton may be dominated by rotifers, cladocerans, or copepods depending upon the season. Lippson et al. (1979) reported typical concentrations of zooplankton from the tidal freshwater section of the Potomac River as: (a) rotifers (80 species), 5,000 to 20,000/m^3 with a peak in spring and summer; (b) cladocerans (approximately 8 species), 5,000 to 100,000/m^3 with peaks in spring and fall; and (c) copepods (approximately 9 species), 1,000 to over 100,000/m^3 with a characteristic late summer peak. In the York River, Van Engel and Joseph (1968) found the dominant zooplankton in terms of volume to be the mysid, Neomysis americana, the copepods, Eurytemora affinis and Acartia tonsa, several species of amphipods, and a number of species of cladocerans.

The zooplankton in tidal freshwater provide an important food source for the larvae and postlarvae of anadromous fishes such as striped bass and shad. There is some evidence that the copepods derive a significant portion of their diet from particulate plant detritus (Heinle and Felemer 1976). It has been hypothesized that the amount of particulate detritus available in the early spring controls zooplankton production and that this, in turn, may influence year class strength in fishes such as white perch and striped bass (Joseph Mihursky, Chesapeake Biological Laboratory, Solomons, Maryland; pers. comm.).

Based on limited data of our own, it appears that the mysid, Neomysis americana, and several species of amphipods provide the greatest biomass of food for larval and juvenile fishes in tidal freshwater. The two species of copepods, the cladocerans, and the rotifers apparently are the most important food sources for recently hatched larvae and postlarvae (Ed Houde, Chesapeake Biological Laboratory, Solomons, Maryland; pers. comm.).

4.2 BENTHIC INVERTEBRATES

Comprehensive documentation of the benthos in tidal freshwater is scarce. An early study of the Hudson River, New York (Townes 1937), characterized the benthos of tidal freshwater as composed of freshwater snails, oligochaetes (Limnodrilus spp.), chironomids, and the amphipod, Gammarus fasciatus. This amphipod seems to be characteristic of many tidal freshwater locations. Dunn (1978) found it to be abundant in plant and algal mats in Virginia while Calder et al. (1977) mention it as common in South Carolina freshwater tidal marshes.

Studies of southern tidal freshwater benthos are relatively rare. Dorjes (1977), quoted in Sandifer et al. (1980), found the dominant macrobenthic invertebrates in the tidal freshwater areas of the Ogeechee estuary, Georgia, to be the amphipod, Lepidactylus dytiscus, and the polychaete, Scolecolepides viridus. In South Carolina, Calder et al. (1977) found these two species to compose 60% by number of the macrobenthos from tidal freshwater stretches of the South Edisto River.

One of the most complete studies of tidal freshwater benthos is that of Diaz (Diaz and Boesch 1974; Diaz 1977; Diaz et al. 1978). His studies concentrated on the tidal James River, a typical, although highly eutrophic, tidal freshwater river in Virginia. The marsh macrobenthos was dominated qualitatively and quantitatively by tubificid oligochaetes and larval chironomid insects. Oligochaetes were most abundant and chironomids were most diverse. Dominant species included a chironomid, Chironomus tanypus, and an oligochaete, Limnodrilus spp. Also highly abundant was the introduced Asiatic clam, Corbicula fluminea (formerly C. manilensis) which is discussed below.

These studies also showed that the number of benthic macrofauna species in tidal freshwater is considerably lower (69 according to Koss et al. 1974; 49 according to Diaz 1977) than further upstream in nontidal freshwater (between 150 and 200 species according to Kirk 1974). This relatively simple community structure in tidal freshwater was attributed to a lack of diverse habitats; the most available habitat was a silty mud bottom (Diaz and Boesch 1977). Diaz (1977) likened tidal freshwater benthic communities to those found in large lakes, such as the Great Lakes, or the profundal zone of smaller lakes, polluted harbors, or the vicinity of river mouths. Furthermore, he concluded that there is no species of benthic animal which is specialized for exclusive existence in tidal freshwater. Most species which are present appear to be eurytopic (wide range of tolerance) with few species exhibiting qualitative preference for a particular substrate type.

Diaz et al. (1978) found the macrobenthic diversity (H^1) in the James tidal freshwater marshes to be relatively low, ranging from 2.0 to 2.2. Mean densities were 1800-4000/m^2; 85% to 97% lived in the top 10 cm of marsh sediment. Annual production was estimated (in dry g/m^2/yr) as 4 g to 7 g of oligochaetes, less than 1 g of chironomids, approximately 1 g of nematodes (the major component of the microbenthos), and 1 g to 2 g of the Asiatic clam.

The Asiatic clam, introduced earlier in the century, is well established throughout tidal freshwater environments in the Southeastern States (Sandifer et al. 1980). It entered the southern tributaries of Chesapeake Bay about 1968 (Diaz 1977) and has since spread northward at least as far as the Potomac River where it was established by 1975 and now reaches densities as great as 665/m^2 (Dresler and Cory 1980). Diaz and Boesch (1977) have noted that the ease with which the Asiatic clam has populated tidal freshwater may be a clue to the extent to which benthic communities are structured by physical rather than biological processes in this environment. Presumably, if interspecific competition and competitive exclusion were intense, the spread and proliferation of the Asiatic clam would not have been as dramatic.

Penaeid shrimp do not appear to occur in tidal freshwater habitats in high densities, although they are very common at slightly higher salinities (personal observation). However, the caridean shrimp, particularly Palaemonetes pugio, has been reported commonly in tidal freshwater from Georgia (Sandifer et al. 1980) to Virginia (personal observation). In South Carolina and Georgia, the freshwater shrimp, Macrobrachium ohione and M. acanthurus are common in tidal freshwater (Sandifer et al. 1980).

A general and preliminary list of representative benthic macrofauna from tidal freshwater marsh systems is shown in Table 10. It is probable that certain groups such as crayfish and amphipods are even more important than indicated but have been poorly sampled in past studies. In addition, more mobile estuarine organisms are known to stray in fair numbers (personal observations) into tidal freshwater (e.g., the blue crab, Callinectes sapidus, the mud crab, Rhithropanopeus harissii, the caridean shrimp, Palaemonetes pugio, and, in the southern part of its range, the brackish water fiddler crab, Uca minax). Except for the work of Diaz, our knowledge of the tidal freshwater macrobenthos is very preliminary.

Table 10. Representative benthic macrofauna from mid-Atlantic tidal freshwater environments. Data from Lippson et al. (1979) for the Potomac River, Grant and Partick (1970) for the Delaware River, and Diaz (1977) and Diaz and Boesch (1977) for the James River.

Sponges

- Spongilla lacustris and other species

Hydra

- Hydra americana
- Protohydra spp.

Bryozoans

- Barentsia gracilus
- Lophopodella sp.
- Pectinatella magnitica

Leeches

- Families Glossiphoniidae, Piscicolidae

Oligochaetes

- Families Tubificidae, Naididae

Insects

- Dipteran larvae (especially family Chironomidae)
- Larvae of Ephemeroptera, Odonata, Trichoptera, and Coleoptera

Amphipods

- Hyallela azteca
- Gammarus fasciatus
- Lepidactylus dytiscus (southeastern States)

Crustaceans

- Crayfish
- Blue crab, Callinectes sapidus
- Caridean shrimp, Palaemonetes paladosus

Mollusks

- Fingernail clam, Pisidium spp.
- Asiatic clam, Corbicula fluminea (formerly C. manilensis)
- Brackishwater clam, Rangia cuneata
- Pulmonate snails (at least six families)

The microbenthos in tidal freshwater is more thoroughly documented than the macrobenthos thanks to the work of Robert Ellison and Maynard Nichols (summarized in Ellison and Nichols 1976). They have described a sharp demarcation in the distribution of the microbenthos which occurs at the border between tidal freshwater and estuarine conditions (Figure 22). In the tidal freshwater marshes the dominant group is the thecamoebinids (a group of amoeba with theca or tests); the foraminifera, common in estuarine salinities, are absent. Dominant species of thecamoebinids are Centropyxis arenata, C. constrictus, Difflugia constricta, and D. pyriformis. Density often reaches 2,000/20 ml of sediment. Just downstream, in the oligohaline zone of the estuary, the thecamoebinids disappear and are replaced by the Ammoastuta fauna. This is a group of foraminifera dominated by Ammoastuta salsa and including Astrammina rara and Miliammina earlandi. Different groups of forams predominate at locations further downstream in the estuary at higher salinities (Ellison and Nichols 1976).

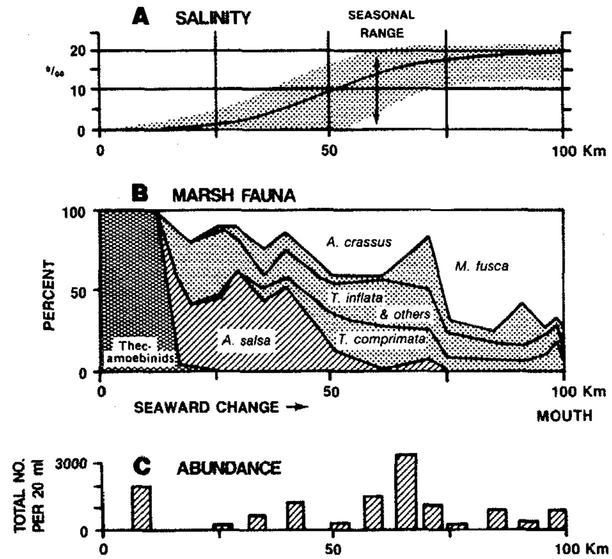


Figure 22. Seaward change in (a) salinity, (b) species composition, and (c) total numbers of microfauna of the marshes along the Rappahannock Estuary, Virginia. From Ellison and Nichols (1976).

The demarcation between thecamoebinids and forams provides a convenient geological and ecological indicator of the extent of tidal freshwater wetlands in the recent geological record. Using the occurrence of these organisms in marsh cores, Ellison and Nichols (1976) concluded that the tidal freshwater environment moved downstream in the James River basin during the most recent period of relative sea level stability (past 6000 years) perhaps due to sediment deposition and marsh building throughout the estuary.

4.3 MARSH PLANT INSECT COMMUNITY

Published information dealing with the insect community associated with vascular plants of tidal freshwater is very inadequate. One exception is the study of Simpson et al. (1979) that describes the insects associated with three plants: burmarigold, arrow-arum, and jewelweed. In general, they found both low densities of insects and low species diversity. Insects from 32 families and 6 orders were collected; only 11 families were found on all three species of plants. The Coccinellidae (ladybird beetles) were the most ubiquitous. Other common families were the Curculionidae (snout beetles), the Lampyridae (fireflies), the Lagnuridae (lizard beetles), the dipteran family Dolichopodidae (long-legged flies), the Otitidae (picture-winged flies), the Syrphidae (flower flies), the Tachinidae (deer and horse flies), the hemipteran Anthocoridae (minute pirate bugs), and the homopterans Aphidae (plantlice) and Cicadellidae (leafhoppers). Additional families were found only on specific plants.

Simpson et al. (1979) found little evidence of herbivorous insects or of herbivory in general and concluded that tidal freshwater marshes, like coastal _Spartina_ marshes, are only lightly grazed. Cahoon (1982), on the other hand, found grazing rates on _Hibiscus_ to be as high as 20% to 30% in certain locations in Maryland tidal freshwater marshes. We have recorded grazing rates on a mixture of tidal freshwater marsh plants as high as 12% to 15% in discrete patches of marsh, but less than 10% for the marsh as a whole (unpublished data). At this time, with little data in hand, we must agree with Simpson et al. (1979) that grazing rates by insects on most plants in tidal freshwater are low, _Hibiscus_ excepted.

Although direct grazing rates may be low, it should be emphasized that insects apparently play an important role in energy flow in the tidal freshwater marsh system (see Section 3.5). In particular, the aquatic larvae of terrestrial insects appear to be an important food source for the postlarvae and juvenile fishes which utilize this habitat as a nursery area (see Chapter 5).

CHAPTER 5. COMMUNITY COMPONENTS: FISHES

5.1 INTRODUCTION

The tidal freshwater portion of Atlantic coast estuaries is a transitional zone between a typically freshwater fish fauna found above tidal influence and fauna characteristic of the oligohaline portion of the estuary. No fish species is known to be restricted to the tidal freshwater habitat. Instead, the fish community of tidal freshwater (summarized in Appendix B) is a complex and seasonally variable mixture of freshwater forms tolerant of low salinity conditions, typical estuarine residents, anadromous fishes on spawning runs and their juveniles, juvenile marine fish using the area as a nursery ground, and adult marine fish best considered seasonal transients (Figure 23).

Because the unconsolidated sediments and dense vegetation make sampling within the marsh difficult, most of our information on fishes of the tidal freshwater reaches of the estuary comes from trawl surveys in the main channels and beach seining in unvegetated shallows. As a result, much of the following discussion concerns the fishes of tidal freshwaters in general and is not restricted to those fishes that use the marsh directly. Where direct use has been observed, this distinction is made.

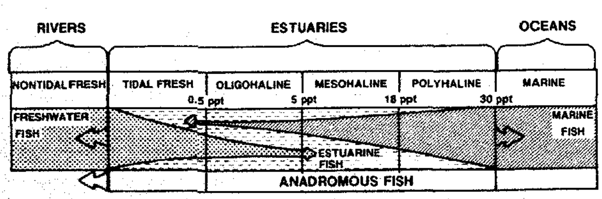


Figure 23. Distributions of different types of fishes by salinity zones. Modified from Lippson et al. (1979).

5.2 THE FAUNA: AFFINITIES AND NATURAL HISTORY OF IMPORTANT SPECIES

Freshwater Fishes

In tidal freshwaters, fish of freshwater affinity are particularly common. In fact, up to a salinity of approximately 3.5 ppt, freshwater fish often outnumber estuarine, anadromous, and marine species combined (Keup and Bayliss 1964). Species of freshwater fish found in tidal freshwaters generally occupy lentic (slow-flowing) habitats, such as lakes, ponds, and river backwaters, in nontidal freshwaters. In tidal freshwaters, freshwater forms are more often associated with shallows and vegetation than with deeper channels. Freshwater species characteristic of lotic habitats with fast flowing water and gravel substracts rarely extend their range into tidal freshwaters (Lippson et al. 1979).

The three families with the most species and individuals in tidal freshwater are the cyprinids (minnows, shiners, carps), centrarchids (sunfishes, crappies, bass), and ictalurids (catfishes). While a relatively large proportion of the cat-fish and sunfish populations in a given geographic area extends into tidal freshwater habitats, this is not the case for the minnows. As a group, minnows are much more common above the Fall Line in non-tidal habitats.

Minnows are small, often schooling species, most abundant in the shore zone. Of this group, the spottail shiner, silvery minnow, satinfin shiner, and golden shiner are the most common. Many of the other smaller members of this group listed in Appendix B are best considered strays in tidal freshwaters because their occurrence there is sporadic. As a group the minnows occupy midwater and benthic habitats. The carp and goldfish have been introduced widely from Asia and may be locally common in tidal freshwaters. Both species have broad niches; they are omnivorous in feeding habits and have wide tolerances for variations in dissolved oxygen, turbidity, and salinity.

As a group the sunfishes are most common in shallow, still waters containing some cover. The smaller members of the family in the genera Enneacanthus and Elassoma are invariably associated with vegetation and are most abundant in tidal and nontidal swamps (Wang and Kernehan 1979, Lee et al. 1980). The bluegill and largemouth bass are common in tidal freshwaters throughout the mid- and southeast Atlantic regions. The pumpkinseed is more common in the mid-Atlantic, while the redbreast and redear sunfishes, warmouth, and black crappie reach peak abundance in tidal freshwaters in the southeast. Juveniles of all these species are most abundant in the shallows, and larger fishes are found in deeper water. All but the smallest sunfishes are important to sports fishermen. As a result of their recreational value, many species have been introduced to areas outside their native range (see Appendix B).

Catfishes are bottom oriented and well adapted to feeding in turbid waters which often occur in tidal freshwater habitats. Here they locate their prey primarily by nonvisual means (i.e., by tactile and olfactory stimuli). They also tolerate conditions of low dissolved oxygen. Of the larger members of the genus Ictalurus, the white catfish, channel catfish, brown bullhead, and yellow bullhead are common. The smaller members of the genus Noturus are known as madtoms and are more abundant in nontidal freshwaters. Only the tadpole madtom is common in tidal freshwaters.

A number of other species of freshwater fish are resident in tidal freshwaters and are important there either because of their numerical abundance or their role as predators. Of the smaller species, the mosquitofish is particularly abundant along creek edges, in backwaters, and on the marsh surface. One or more of the darters and suckers are often common. The darters reside in the shallows, the suckers in slightly deeper water. The pirate perch is locally common in the upper tidal freshwater habitat, particularly where the marsh and swamp are in close proximity. Gars, pickerels, and bowfin are resident predators whose abundance and activities probably affect the population structure of the smaller fish species using the tidal freshwater habitat.

Estuarine Fishes

The estuarine component of the tidal freshwater fish assemblage is composed of resident species that complete their entire life cycle in the estuary. These species are generally most abundant in lower, more saline portions of the estuary, but several extend their ranges into tidal freshwaters.

The cyprinodontids or killifishes are very abundant in tidal freshwater marshes where they occur in schools in the shallows and on the marsh surface at high tide. At low tide these small fishes congregate along marsh edges and also on the marsh surface in rivulets and tide pools. The two most common species in tidal freshwaters are the banded killifish and the mummichog (Raney and Massmann 1953; Hastings and Good 1977; Virginia Institute of Marine Science 1978; Lippson et al. 1979). These two species feed opportunistically, taking food items in proportion to their relative abundance in the environment (Baker-Dittus 1978; Virginia Institute of Marine Science 1978). Their diets are very similar and they sometimes even feed in mixed schools (Baker-Dittus 1978). While their niches appear broadly overlapping, the two species may reach peak abundance in different habitat patches. Hastings and Good (1977) suggested that the mummichog shows a preference for muddy substrate and the banded killifish for sandy areas. Killifishes are often used as bait by sports fishermen and are important forage fishes for numerous larger fishes which are of commercial or sport importance. Killifishes are also an important food item for most species of wading birds (see Chapter 7).

The bay anchovy and tidewater silverside, small pelagic schooling fishes, are important forage species for larger fishes of recreational or commercial interest. The tidewater silverside is most abundant spring through fall and is often more abundant in tidal freshwaters where it may breed than in salt water (Raney and Massmann 1953; Virginia Institute of Marine Science 1978; Lippson et al. 1979). Bay anchovy juveniles and adults enter tidal freshwater in spring to feed. In late spring adults return downstream to spawn in areas of >10 ppt salinity. Newly hatched larvae move upstream to oligohaline and tidal freshwater nursery areas in summer (Dovel 1971, 1981). Most anchovies return to the lower estuary to overwinter (Lippson et al. 1979; Dovel 1981).

Hogchokers and naked gobies are bottom-oriented estuarine residents whose young use tidal freshwater and oligohaline nursery grounds. Spawned in mesohaline portions of the estuary in midsummer, young of both species are transported upstream in the salt wedge to the upper estuary where they are common in the shallows through autumn. The species differ in their use of this habitat in cold weather. Hogchoker adults and juveniles may overwinter here, while naked gobies return downstream to adult habitat in the middle and lower estuary (Van Engel and Joseph 1968; Dovel et al. 1969; Lippson et al. 1979).

Anadromous Fishes

Anadromous fishes are those which ascend from an oceanic habitat to freshwater to spawn. Like the anadromous fishes, semianadromous forms ascend to freshwaters to spawn, but spend most or all of their lives within the estuary rather than the ocean. Many of these fishes are of considerable commercial importance in Atlantic coast estuaries. Characteristics of these fishes are summarized in Table 11.

Of the anadromous fishes, the clupeids (herrings and shad) are of major commercial importance. These fishes are captured on the upstream spawning runs in gill nets operated in tidal fresh and brackish waters. Except for hickory shad, the peak abundance of young of these species is in tidal freshwaters. In this nursery area, the juveniles feed heavily on small invertebrates before migrating to the lower estuary or out to sea by late fall or early winter. While in the nursery area, these juveniles are important forage fishes for striped bass, white perch, catfishes, and others. Considerable research on the biology of the anadromous clupeids has been conducted by the various state agencies responsible for fisheries management and is summarized in their progress reports (Adams 1970; Sholar 1975; Loesch and Kriete 1976; Hawkins 1980; Curtis 1981; Loesch et al., undated).

The two species of sturgeons, once important commercially in east coast estuaries, were badly overfished and their numbers decimated by the turn of the century (Reiger 1977). In addition to declines due to overexploitation, small sturgeons of no economic value were purposely destroyed when they became entangled in and damaged the gill nets of herring and shad fishermen (Ryder 1890; Brundage and Meadows 1982). The shortnose sturgeon, probably never common, is now designated an endangered species, and the Atlantic sturgeon is relatively rare (Ryder 1890; Bigelow and Schroeder 1953; Reiger 1977). Because sturgeons are rare, relatively little is known of their specific habitat preferences for spawning and nursery areas. Both species of sturgeons spawn in nontidal and tidal freshwaters and the juveniles may remain in freshwater for several years (Vladykov and Greeley 1963; Brundage and Meadows 1982). Small commercial fisheries still exist for the Atlantic sturgeon in New York and the Carolinas (Reiger 1977).

Of all the fishes occupying tidal freshwaters at some time in their lives, probably none has received greater attention than the striped bass, a species of major commercial and sport importance (Figure 24). Though present along the entire Atlantic coast of the United States, spawning is largely restricted to three estuaries. Major tributaries of Chesapeake Bay account for approximately 90% of the striped bass spawned on the east coast, while the Hudson River, New York, and the Roanoke River, North Carolina, account for the remainder (Berggren and Lieberman 1977). In the mid-Atlantic, adult striped bass overwinter in the lower

Table 11. Characteristics of anadromous and semianadromous fishes of the Atlantic coast.

Fish	Spawning area	Spawning temperature °C	Nursery ground	Residence time of juveniles in tidal freshwater	Commercial use	Reference
Anadromous						
Alewife	Small nontidal freshwater streams, also tidal fresh; primarily tributaries, on bottom	12-22.5	Tidal freshwater & oligohaline areas	Until late fall	Fertilizer	Wang & Kernehan 1979; Lippson et al. 1979
Blueback herring	In mid-Atlantic; tidal fresh & low brackish (to 2 ppt) tributary streams. In Southeast; river floodplains & backwaters, abandoned ricefields, main stream & tributaries	15-24	Within 5 nautical miles of spawning areas	Until late fall	Fertilizer; live-bait fishery	Adams 1970; Christie & Walker 1982; Wang & Kernehan 1979
American shad	Nontidal & tidal freshwater in main stream; on shallow flats with relatively swift currents	12-20	Same general area as spawning area, or slightly downstream	Until late fall	Food fish; eggs for caviar	Massmann et al., 1952; Sholar 1977; Hawkins 1980
Hickory shad	Mid-Atlantic; tidal freshwater mainstream & lower portion of some tributaries on shoals. Southeast Atlantic; tributary streams, lakes & river floodplains	13-21	Brackish & marine waters	Little; juveniles move to sounds & offshore waters soon after hatching	Food fish	Adams 1970; Wang & Kernehan 1979; Hawkins 1980
Sea lamprey	Nontidal freshwater streams in rapidly flowing water; will use tidal freshwater if passage blocked	11-24 14-15.6 (peak)	Natal freshwater streams	3-4 years as ammocoete larvae	None; a pest species	Wang & Kernehan 1979
Atlantic sturgeon	Nontidal & tidal freshwaters, also oligohaline waters	14-18	Freshwater	Up to 8 years	Food fish; eggs for caviar	Vladykov & Greeley 1963
Shortnose sturgeon	Nontidal & tidal freshwaters	8-19	Upper estuary	Up to 4 years	Once used as food fish; endangered, cannot be legally harvested	Heidt & Gilbert 1981; Brundage & Meadows 1982

(continued)

Table 11. Concluded.

Fish	Spawning area	Spawning temperature °C	Nursery ground	Residence time of juveniles in tidal freshwater	Commercial use	Reference
Rainbow smelt	Nontidal freshwater streams, brooks; tidal freshwater if progress blocked; main stream & tributaries	8.9-18.3	Brackish & marine waters	Little; juveniles move rapidly to sea	Food fish	Scott & Crossman 1973; Kirchels & Stanley 1981
Tomcod	Nontidal & tidal Freshwater streams	0-3.9	Oligohaline areas	Little; mainly use brackish waters	Food fish, recreational use only	Scott & Crossman 1973
Striped bass	Tidal fresh & oligohaline (to 2 ppt) in mainstream; waters 2 m depth	10-23 15-18 (peak)	Same as spawning area, also associated tributaries	Until late summer	Major food fish	Wang & Kernehan 1979; Lippson et al. 1979
Atlantic salmon	Nontidal freshwater	Oct.-Dec. in New England & Canada	Nontidal freshwater	None; juveniles only migrate through tidal freshwater	Food fish; recreational	Scott & Crossman 1973
Threespine stickleback	nontidal & tidal freshwater, oligohaline waters	10-?	Tidal fresh & oligohaline	Throughout summer	None	Scott & Crossman 1973; Wang & Kernehan 1979
<u>Semianadromous</u>						
White perch	Tidal fresh & oligohaline (to 2 ppt), tributaries & main stream; shallows; also nontidal freshwater	10-20 14-18 (peak)	Shallows downstream of spawning areas; mouths of tributary creeks & main stream, tidal freshwater	Slight downstream movement in summer, but may remain & overwinter in deeper channels	Food fish	Wang & Kernehan 1979; Lippson et al. 1979
Yellow perch	Mainly tidal fresh & oligohaline (to 2 ppt); less in nontidal fresh; tributaries	6.8-12.5	Downstream of spawning area; lower portions & mouths of tributaries & main stream	Probably through fall	Food fish	Wang & Kernehan 1979; Lippson et al. 1979
Gizzard shad	Mainly tidal freshwater, main stream & tributaries; also nontidal freshwater	10-25 15-25 (peak)	Tidal fresh & oligohaline, in shallows	Probably through fall	Little; considered a trash fish	Wang & Kernehan 1979; Lippson et al. 1979

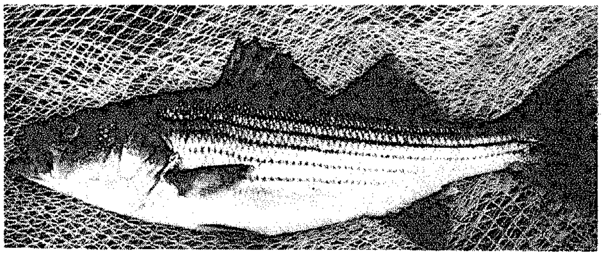


Figure 24. Striped bass, the most important sport and commercial fish utilizing tidal freshwater environments. Photograph by Dennis Allen, Belle W. Baruch Institute for Marine Science and Coastal Studies, University of South Carolina, Georgetown.

estuary and open ocean, returning to their natal streams in spring to spawn (Lippson et al. 1979). In Georgia, striped bass are entirely riverine, never entering coastal waters (Hornsby 1980). We have chosen to classify striped bass as anadromous because in the mid-Atlantic, the area of peak abundance, some proportion of the spawning population overwinters in the ocean.

Spawning occurs in tidal fresh and oligohaline waters in the main watercourse when temperatures exceed 10°C (50°F) early April at the latitude of Chesapeake Bay. Most adults return to estuarine waters after spawning. Juvenile striped bass preferentially inhabit nearshore zones within the tidal freshwater and oligohaline nursery area where food is denser than in channels and deeper waters (Boynton et al. 1981). Juveniles move gradually downstream as they grow.

Detailed studies on survival of juvenile striped bass and variation in year-class strength have demonstrated that the critical period is the larval stage. It is hypothesized that variation in food densities, primarily rotifers and copepod nauplii within the tidal freshwater and oligohaline nursery zone, may be the critical factor in determining year-class strength (Atlantic States Marine Fisheries Commission 1981). Apparently, strong year classes are correlated with cold winters and high spring runoff. It is thought that high runoff contributes nutrient and detrital influxes which favor high zooplankton densities, and thus high larval striped bass survival (Lippson et al. 1979).

The only catadromous fish species in estuaries in this geographic area is the American eel. Eels spend nearly all their lives in fresh or brackish water, returning to the ocean in the region of the Sargasso Sea off Bermuda to spawn. Young eels return to the coast and enter estuaries, some ascending into nontidal freshwaters. Eels are ubiquitous throughout the estuary and are very common in the tidal freshwater reaches. They readily enter tidal marsh creeks and may move onto the marsh itself (Virginia Institute of Marine Science 1978, Kiviat MS; Lippson et al. 1979).

Marine Fishes

Marine fishes spawn at sea and spend most of their lives in the marine habitat. They use estuaries either as nursery areas, in which case they are estuarine dependent, or as seasonal feeding grounds as adults. Many more marine fishes use the lower estuary than tidal freshwaters. Atlantic menhaden, spot, croaker, silver perch, weakfish, spotted seatrout, black drum, and the summer flounder are marine species whose young occupy nursery areas extending into tidal freshwater reaches during the warmer months (Massmann et al. 1952; Dovel 1971; Thomas and Smith 1973; Markle 1976; Virginia Institute of Marine Science 1978). In Georgia and Florida, snook and tarpon are dependent upon tidal freshwater and oligohaline nursery areas (Rickards 1968). Generally, these young-of-the-year, and adults of marine species as well, leave the estuary as temperature declines in the fall.

We have attempted to summarize these diverse patterns of habitat use in Table 12. The more common species for which adequate life history information is available are arranged by affinity group on the basis of their use of tidal freshwaters.

5.3 COMMUNITY STRUCTURE

Relative Abundance

The relative abundance of fish species in tidal freshwaters is best

Table 12. Patterns of use of tidal freshwater habitat by fishes.

Affinity group	Pattern of habitat use	Examples
I. Freshwater	Resident	Pumpkinseed Tessellated darter Redfin pickerel Longnose gar Largemouth bass
	Spawn elsewhere	Some catfish Most suckers
II. Estuarine	Resident	Mummichog Tidewater silverside
	Nursery area	Hogchoker Naked goby
III. Anadromous	Nursery area	American shad Alewife Striped bass
	Migratory only	Hickory shad Rainbow smelt
IV. Marine	Nursery area	Spot
	Feeding ground for adults	Mullet

assessed from comparable data collected at a series of sites. In Table 13 the most common fishes from ten studies are arranged by rank abundance. The eight species lsited for each study account for between 80% and 99% of all fishes captured in these investigations. While differences exist in sampling methodology and proportion of the annual cycle covered, some generalizations are possible. Overall, freshwater species outnumber all others. Estuarine and migratory forms (anadromous and semianadromous) are about equally abundant. Marine fishes are the least common group in tidal freshwaters.

The coverage in this table on a latitudinal basis is relatively complete except for North Carolina. Only the Cape Fear, New, and White Oak Rivers in the southern portion of this state have tidal freshwater marshes comparable to those of the other states. Unfortunately, the survey data from the tidal freshwater portion of these three river systems are inadequate to include in this table. Biogeographic observations from Table 13 are discussed in Section 5.7.

Diversity

Seasonal diversity in tidal freshwaters in the mid-Atlantic generally peaks in late summer and early fall when the young of freshwater, estuarine, anadromous, and marine forms are still on the nursery ground (Merriner et al. 1976, Lipton and Travelstead 1978). In the southeast, the diversity peak appears to be later - in fall or winter (D. Holder, Department of Natural Resources, Georgia Game and Fish, Waycross, pers. comm.; Hornsby 1982). Few data sets exist from which to compare diversity of fishes along a salinity gradient. The data of Merriner et al. (1976) from bimonthly trawl samples in the Pinakatank River, Virginia, showed more species at the saline end of the gradient (20 species, mean salinity 16.3) than at the oligohaline-seaonally fresh end (11 species, mean salinity 4.3). Similarly, Dahlberg (1972) found a decrease in fish species richness from the mouth of the Newport River, Georgia, as his sampling extended into freshwater. No readily discernable differences existed in the diversities of collections of fishes made at two times by beach seine in mesohaline (H^1 = 1.80, 1.62) and tidal freshwater reaches (H^1 = 2.20, 0.94) of the James River, Virginia (Lipton and Travelstead 1978). In summary, it appears that the tidal freshwater fishes are less diverse than in more saline portions of the estuary.

5.4 FUNCTION OF TIDAL FRESHWATER MARSH FOR FISHES

Spawning Location

The tidal freshwater marsh itself is a spawning ground for several species of fishes (Table 14). The shallow water marsh edges, channels, and tidal impoundments are spawning areas for a large number of other species. The only obligate marsh spawners are the two killifishes, the banded killifish, and mummichog (Table 14). These two species also breed in higher salinity marshes. The use of the marsh as a spawning site is a facultative use by the remaining marsh spawners; they also breed in the shallows in both tidal

Table 13. Numerically dominant fishes in tidal freshwaters, New York to Georgia.

Rank	Hudson R. NY	Woodbury Ck., NJ	Delaware R. tributaries	Potomac R. VA	Rappahannock River, VA	Pamunkey R., VA	James River VA	Winyah Bay drainage, SC	Savannah R. oxbow, creek	Savannah R. mainstream	Altamaha R. oxbow	Altamaha R. mainstream
1	blueback herring	mummichog	white perch	white perch	Atlantic menhaden	blueback herring	spottail shiner	largemouth bass	striped mullet	striped mullet	black crappie	channel catfish
2	white perch	banded killifish	mummichog	Atlantic menhaden	blueback herring	satinfin shiner	spot	pirate perch	redbreast sunfish	redbreast sunfish	bluegill	hogchoker
3	tesselated darter	silvery minnow	banded killifish	gizzard shad	mummichog	spottail shiner	white perch	warmouth	spotted sucker	gizzard shad	redbreast sunfish	redbreast sunfish
4	banded killifish	alewife	tidewater silverside	threadfin shad	tidewater silverside	tesse-lated darter	threadfin shad	banded killifish	redear sunfish	spotted sucker	warmouth	flathead & small cat-fish
5	spottail shiner	blueback herring	hogchoker	brown bullhead	white perch	American shad	tidewater silverside	yellow bullhead	bluegill	bowfin	pirate perch	brown bullhead
6	goldfish	pumpkin-seed	bay anchovy	alewife	satinfin shiner	banded killi-fish	mummichog	bowfin	gizzard shad	largemouth bass	tadpole madtom	carpsucker species
7	pumpkin-seed	brown bullhead	pumpkinseed	spot	striped bass	alewife	gizzard shad	striped mullet	bowfin	American shad	Florida gar	white catfish
8	American shad	white perch	bluegill		banded killifish	tide-water silver-side	striped bass	brown bullhead	largemouth bass	bluegill	gizzard shad	bluegill
sam-ple size	9,260	12,143	41,025	4,546	1,500	6,000	6,319	464	unknown	unknown	4,140	11,611
sam-ple period	Sum	Sum, Fall	Spr-Fall 1969-1970	Spr-Fall 1976	Sum-Fall, 1951	Summers, 1949-1951	seasonally 1976-1951	Spr-Sum 1982	seasonally	seasonally	11-31-79	10-4-80
place	shore zone	shore zone	shore zone	channel	shore zone	shore zone	shore zone & marsh interior	entire width creeks, ditches	shore zone	shore zone	entire oxbow	entire river width, 4.3 ha
sam-ple method	seine	seine	seine	gill net, fyke net, D-traps	seine	seine	seine, fyke net, minnow traps	gill net, plankton net, rotenone	electro-shock	electro-shock	rotenone	rotenone
number species	18 +	17	43	26	32	36	37	39	33	29	45	39
source	Perl-mutter et al. 1967	Hastings & Good 1977	Smith 1971	Powell 1977	Massman et al. 1952	Massmann et al. 1952	VIMS 1978	N. Roark pers. comm.	Hornsby 1982	Hornsby 1982	D. Holder pers. comm.	Holder 1982

*N. Roark, S.C. Wildlife and Marine Resources Department, Charleston, SC.

Table 14. Fishes reported to spawn in tidal freshwater. (Compiled from Lippson et al. 1979; Wang and Kernehan 1979; Christie and Walker 1982; Curtis 1982; Anonymous.)

Marsh	Shallows	Channels or shoals away from shore	Tidal impoundments
Banded killifish	Golden shiner	American shad	Largemouth bass
Mummichog	Satinfin shiner	Blueback herring[c]	Northern pike
Mosquitofish	Spottail shiner	Alewife	Blueback herring[b]
Eastern mudminnow	Silvery minnow	Hickory shad[c]	20 others[b]
Bluegill	Tessellated darter	Striped bass	
Pumpkinseed	Tidewater silverside	Gizzard shad	
Carp	Yellow perch		
Redfin pickerel	White perch		
Chain pickerel	Hickory shad[b]		
	Blueback herring[b]		
	Atlantic needlefish[a]		

[a]Reported to spawn in this habitat in Potomac River, Virginia. Generality of tidal freshwater spawning unknown.
[b]in the southeast region
[c]in mid-Atlantic region

and nontidal freshwaters. Those species using the shallows may spawn just off the edge of the marsh, often in association with submerged vegetation. The presence of marshes is probably of little consequence for the breeding activities of the channel spawners. The relative importance of tidal impoundments as spawning locations is poorly known. These habitats are rather common from the Cape Fear River, North Carolina, south through Georgia. Since Curtis (1982) reported the finding of the eggs of 20 species in an abandoned ricefield on the Cooper River, South Carolina, it is likely that these habitats will be important spawning locations.

Primary Habitat for Resident Species

The tidal freshwater marsh and associated shallows and waters provide year-round food and shelter for adults and juveniles of resident species. Resident fishes are primarily freshwater species and may or may not spawn in tidal freshwaters. This group includes the following common fishes: longnose gar, American eel, redfin and chain pickerels, carp, goldfish, silvery minnow, golden shiner, satinfin shiner, spottail shiner, white and creek chubsuckers, white and channel catfish, brown bullhead, banded killifish, mummichog, mosquitofish, redbreast sunfish, pumpkinseed, bluegill, largemouth bass, black crappie, and tessellated darter.

Nursery Zone and Juvenile Habitat

The role as a nursery zone for the young of nonresident adults (Table 15) is a particularly important function of tidal freshwater marshes and associated shallows. The broad zone at the tip of the salt wedge (i.e., the freshwater-saltwater interface) is often the region of maximum primary and secondary productivity within the estuary (Dovel et al. 1969; Cronin and Mansueti 1971). The hydraulics of the salt wedge can act to concentrate the larval stages within the upper portion of the estuary near the tidal freshwater zone. In addition, it is in this same river reach that tidal freshwater and oligohaline marshes occur. The often extensive vegetated zone of these marshes provides shelter to small fishes and an additional feeding ground rich in benthic invertebrates, algae, and detritus.

Dovel (1971, 1981), in studying the

Table 15. Fishes using tidal freshwaters as nursery grounds.

Species	Affinity group Anad-romous	Ma-rine	Estu-arine
Alewife	+		
American shad	+		
Atlantic menhaden		+	
Atlantic sturgeon	+		
Bay anchovy			+
Blueback herring	+		
Gizzard shad	+		
Hogchoker			+
Naked goby			+
Shortnose sturgeon	+		
Southern flounder		+	
Spot		+	
Striped bass	+		
Tidewater silverside			+
White perch	+		
Yellow perch	+		

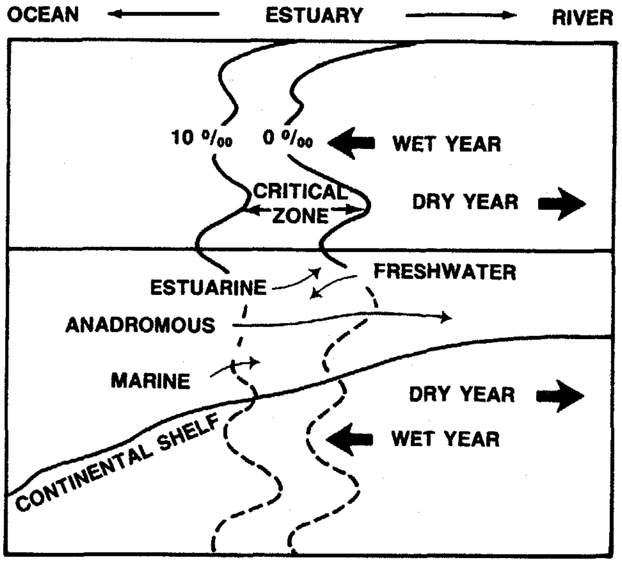


Figure 25. Concept of movement of estuarine-dependent fish larvae through the low-salinity critical zone and toward the ocean as the fish grow. The movements of individual fish (*) show a gradually changing relationship to the salt front, which results in a downstream shift of nursery zones for succeeding stages of development (from Dovel, 1981).

ichthyoplankton of the Patuxent River, Maryland, and the Hudson River, New York, formulated the concept of the critical zone of the estuary, an area encompassing that portion of the estuary with salinities between 0 and 10 ppt (Figure 25). Dovel considered this region critical since it is within this area that the survival and strength of each year class of most species of anadromous fishes is determined. Dovel further pointed out that this critical zone is variable in location and extent since it is affected by both freshwater runoff and tidal changes.

The tidal freshwater marsh and associated shallows are also important habitat for the juveniles of resident freshwater species listed in the previous section. The South Carolina Wildlife and Marine Resources Department compared three sets of abandoned ricefields and adjacent tidal creeks during two summers. On an areal basis, over 80% of all fish collected were taken in ricefields. Ninety-two percent of 0- to 4-inch gamefish (largemouth bass, redbreast sunfish, warmouth, pumpkinseed) were captured in ricefields. Larger fish, six inches and greater, were more numerous in the creeks (Curtis 1982).

Estuaries are believed to be important nursery grounds because they are (1) rich in food and (2) low in predators. The second portion of this explanation is not entirely accurate for tidal freshwaters. While tidal freshwaters lack large marine predators, freshwater predators are abundant (see Section 5.5 below). Tidal freshwaters may act as an important nursery ground because juveniles are found in the extreme shallows and larger predatory fishes in deeper waters, as suggested from the South Carolina data above. Juveniles may also select habitats with high stem densities (marsh surface and/or vegetated shallows) where the foraging efficiency of fish predators is reduced (Vince et al. 1976, Crowder and Cooper 1979).

5.5 TROPHIC ASSOCIATIONS

The diets of fishes recorded from tidal freshwater marshes are given in

Appendix B. Wherever possible, published information was sought from studies undertaken in this habitat. The dietary information appears in as much detail as was given in the orginal citation, and dietary items are listed in order of decreasing importance for a species.

A number of generalizations are possible from these data. First, most fish pass through several ontogenetic feeding stages. The striped bass is a good example. The postlarvae are planktivorous. Juveniles begin to take larger food including a range of benthic invertebrates. Adults continue to take some invertebrates, but are mainly piscivorous (see Appendix B). Such changes are a function of both growth and maturation of the feeding apparatus and capabilities as well as changes in habitat. Secondly, many fish are opportunistic, without strict food preferences. Instead, they tend to feed on locally and seasonally abundant food resources within an appropriate size range, switching to other items as food availabilities change.

The tidal freshwater marsh has an abundance of small crustaceans, immature insects, and annelid worms (see Chapter 4). Crustaceans (including amphipods, ostracods, cladocerans, mysids, and copepods) and insect nymphs and larvae are important foods for nearly all the smaller fishes and many of the larger ones that use this habitat. Annelid worms (oligochaetes) are apparently not a major dietary item in this habitat, possibly because they tend to be infaunal rather than epibenthic. Alternatively, they may be more important than they appear to be due to a lack of hard chitinous parts which would appear in gut contents. They may be thus underestimated in food habit studies.

Depsite the abundance of algae and plant detritus in this habitat, few species of fish feed directly on these resources. Those whose guts do contain appreciable quantities of these items include gizzard shad, striped mullet, silvery minnow, golden shiner, blacknose dace, marsh killifish, and hogchoker (Appendix B). More generally, these abundant resources of detritus and algae are made available to fish through intermediate steps in the food chain, specifically through the small crustacea and immature insects.

The most abundant fishes which prey on small fishes in tidal freshwater marshes include largemouth bass, longnose gar, American eel, redfin pickerel, chain pickerel, bowfin, warmouth, black crappie, and striped bass. Wading birds, kingfishers, certain ducks, terns, and gulls take small fishes in the shallows. Ospreys feed both on the marsh at high tide and in less turbid waters next to the marsh where they take larger fishes from coves, tidal creeks and the mainstream (see Chapter 7 and Appendix D).

It appears from these observations that the abundant primary production of the marsh system is channeled through a host of small invertebrate consumers of plant detritus and algae to numerous small and medium-sized fishes and then to a smaller number of top predators, including predaceous fishes, birds (Chapter 7), and mammals (Chapter 8).

5.6 SEASONALITY

The trophic patterns described above are seasonal in nature. The anadromous and semianadromous fishes are among the earliest spawners. Their young begin to use the tidal freshwater nursery area early in the spring, often before the freshwater fishes spawn. Other early arrivals are the juveniles of winter spawning marine fishes including the croaker and spot. As the waters warm, the freshwater species begin their reproductive season and more juveniles are found in the shallows. The resident killifishes spawn in midsummer. Thus, there are sequential arrivals of juveniles in this nursery area. Invariably, the greatest number of individuals and of species are observed in summer and fall in the mid-Atlantic (Merriner et al. 1976; Lipton and Travelstead 1978).

As temperatures decline in the late fall in this region, fish populations decline. The juveniles of the anadromous, marine, and estuarine species (except for the killifishes) move downstream to overwinter in the lower estuary or to return to the ocean. The freshwater residents tend to move to deeper waters where the temperatures are slightly higher and less variable. Some resident killfishes may burrow in silty sediments within the marsh (Kiviat MS) or move to deeper waters (Fritz et al. 1975). In the mid-Atlantic the shallows are largely deserted in the winter, and ice may cover the marsh. Despite species-specific variations in the relative abundance, community-wide population levels are less variable seasonally in the southern portion of our geographic coverage (Figure 26).

5.7 BIOGEOGRAPHY

The geographic area covered by this community profile is large, and there are evident differences in the fish communities in the northern and southern portions. Marine biogeographers have long recognized that on the Atlantic coast Cape Cod, Massachusetts, and Cape Hatteras, North Carolina, are boundary areas separating coastal regions with distinguishable water masses, floras, and faunas (Marshall 1951; Pielou 1979; Whitlatch 1982). Similarly, North Carolina seems to be a transition area in the distribution patterns of freshwater fishes, with a number of species terminating either northern or southern ranges at this latitude

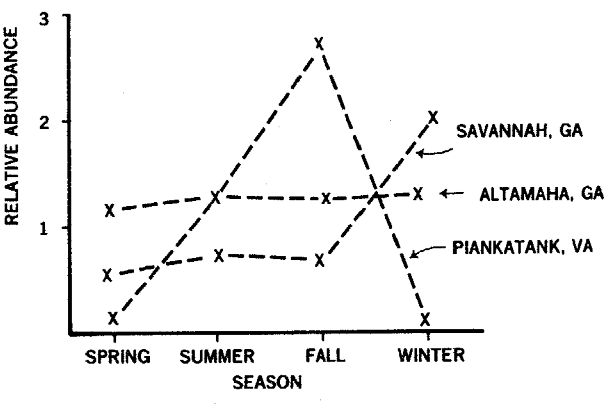


Figure 26. Comparison of seasonal variation in total fish numbers in three river systems. (Relative abundance in arbitrary units because of difference in sampling methods. Data from Holder, pers. comm.; Hornsby 1982; Merriner et al. 1976).

(Jenkins et al. 1971; Lee et al. 1980). Examination of Table 13 suggests real differences in the fish communities of the mid-Atlantic (Hudson River to James River) and the Southeast (South Carolina and Georgia). Based on Appendix B, Table 11, and Table 13, the following generalizations regarding latitudinal differences in fish communities in tidal freshwaters can be made:

1. Some species, largely restricted to nontidal freshwaters in the mid-Atlantic, are common in tidal freshwaters in the Southeast (bowfin, warmouth, pirate perch, banded sunfish).

2. Some species present in both areas use different spawning habitats in the two regions (hickory shad, blueback herring).

3. Juvenile sciaenids (drums) extend into tidal freshwaters in the mid-Atlantic, but apparently not in the Southeast.

4. There is a greater tendency for some marine species to penetrate freshwater in the Southeast (striped mullet, southern flounder).

5. There is less pronounced seasonal change in fish density in the Southeast.

6. As a result of human modification of the environment, there exists in the Southeast a rather unique habitat (the abandoned ricefield, analogous to a tidal impoundment) which appears to be intensively used as spawning and juvenile habitat.

CHAPTER 6. COMMUNITY COMPONENTS: AMPHIBIANS AND REPTILES

Much literature exists concerning the amphibians and reptiles of freshwater lakes, ponds, rivers, streams, swamps, and marshes. This literature, however, rarely mentions tidal freshwater wetlands as a habitat for these two groups of organisms. For example, Behler and King (1979) list a total of 283 species of amphibians and reptiles for North America. Only one of these is listed as inhabiting tidal freshwater marshes. We feel that this represents the fact that many biologists fail to recognize tidal freshwater wetlands as a distinct community type, and not the fact that there is an absence of fauna in this community.

Included in our compilation are 102 species: 22 salamanders, 28 frogs and toads, 18 turtles, 6 lizards, and 28 snakes (Appendix C). Two reasons account for this large number of species: (1) the large geographic region covered and (2) the many reptiles and amphibians using nontidal freshwater habitats that can also use tidal freshwater habitats. Many species of amphibians, especially those which live in the terrestrial environment as adults, must breed in permanent water and also spend their larval stages there. These species have not been included in Appendix C because the literature did not specifically identify them from tidal freshwater habitats.

6.1 SPECIES COMPOSITION

Salamanders are generally rare or uncommon in tidal freshwater wetlands. Mudpuppies, sirens, and amphiumas are uncommon in northern marshes, becoming more common to the south. Frogs and toads are much more common in tidal freshwater wetlands than salamanders.

River turtles (e.g., painted turtle, river cooter, Florida cooter) are by sight the most conspicuous members of the herpetofauna of tidal freshwater wetlands. These turtles are abundant in almost all river drainages in the Southeastern United States. The turtles reported from mid-Atlantic tidal freshwater wetlands are a diverse group, ranging from very rare species such as the false map turtle, introduced at the Tinicum marshes near Philadelphia, to the ubiquitous snapping turtle. The wood turtle is a northern species, occasionally found in the high marsh. Arndt (1977) stated that in the wet sedge meadows he surveyed along the Delaware Bay the bog turtle was the most common reptile found. Once considered an endangered species, the bog turtle is now recognized as being secretive rather than rare (Arndt 1977). Eastern box turtles are usually considered to be terrestrial. We have found a surprising number of references which record box turtles as being found occasionally to commonly in tidal freshwater wetlands (McCormick 1970; Arndt 1977; Mckenzie and Barclay 1980).

Diamondback terrapins are brackish and salt water turtles. They often enter the tidal freshwater reaches of estuaries. Once hunted extensively for food, the populations of these turtles were rapidly decimated (McCauley 1945). Between 1880 and 1900 approximately 23,000 kg (50,000 lb) of meat were harvested annually from Maryland alone. By 1920 the harvest was 373 kg (823 lb). With legal protection from indiscriminate harvesting, the take increased to 2,600 kg (5,800 lb) by 1935 (McCauley 1945). A major factor in the continued increase in this species has been the loss of a market due to changing public tastes (McCauley 1945). Currently terrapin is considered a high-priced delicacy in many parts of Maryland; however, overall public demand is still low.

Lizards and lizard-like reptiles are the least common group of reptiles in the tidal freshwater wetlands. Those species listed in Appendix C are most often found in tidal swamps, shrub marshes, and high marsh where vegetation is high enough for them to escape inundation. The American alligator was once abundant throughout coastal plain rivers and marshes in the Southeast. Their populations declined drastically due to over exploitation. Following protection, alligator populations have increased rapidly, but the species remains on the list of threatened species (Federal Register 1980). Alligators are found in tidal freshwater marshes and swamps from North Carolina to Florida. They are more common in the southern portion of this range. Although alligators use tidal freshwater wetlands, they are found in a variety of other wetland habitats.

Three species of watersnakes, Nerodia (formerly Natrix), appear to be the most abundant snakes in tidal freshwater wetlands. These snakes (plain-bellied, northern, and banded watersnakes) make use of the low marsh, high marsh, and tidal swamps. They also use a wide variety of other wetland habitats. Cottonmouth moccasins are found from the south shore of the James River southward. The many reports of this species from other portions of the Chesapeake Bay are proabably sightings of Nerodia which are mistaken for the cottonmouth (McCauley 1945).

There are no species of amphibians or reptiles included here which are confined solely to tidal freshwater wetlands. All are capable of using a wide variety of wetland and terrestrial habitats.

6.2 LATITUDINAL DISTRIBUTION

Chesapeake Bay is a region where many species reach their distributional limits and can be used as a dividing line for distinguishing a northern and southern herpetofauna. Southern species (e.g., cottonmouth moccasin) are at the northern edge of their range, and northern species (e.g., bog turtle) are at the southern edge of their range. Musick (1972a) lists 41 species which reach their northern distributional limit around the Chesapeake Bay and another nine species which reach their southern limit.

Reasons for this separation are based on the change in winter climate between northern and southern areas. Tidal freshwater wetlands in New England, Delaware Bay, and Chesapeake Bay are subjected to much more severe winters than tidal freshwater wetlands from North Carolina southward. The northern marshes are often frozen and covered by snow for prolonged periods. Freezing temperatures are infrequent and of short duration along the southern Atlantic coast. Reptiles and amphibians, being both ectothermic (cold-blooded) and incapable of long distance migration, are the vertebrate group most affected by this latitudinal change in climate. As a result we see that the species diversity of this group is greatly reduced in northern regions in comparison to southern regions. Of the species listed, 25 are reported from tidal freshwater wetlands in New England and 83 are given for the wetlands of Georgia.

6.3 DAILY AND SEASONAL VARIABILITY

The temporal variability exhibited by amphibians and reptiles is probably greater than that shown by birds and mammals. This temporal variation is manifested as daily and seasonal activity cycles. Most amphibians and reptiles hibernate during the winter months, often seeking a hibernaculum which may be located some distance from the nearest wetland (Cagle 1942, 1950; Gibbons 1970; Ernst 1971, 1976). Kiviat (1978b) cataloged the following species of tidal freshwater reptiles which commonly use muskrat lodges or burrows for their winter quarters: snapping turtle, musk turtle, mud turtle, spotted turtle, bog turtle, wood turtle, false map turtle, pond slider, painted turtle, and northern water snake. In southeastern Pennsylvania, Ernst (1971, 1976) found that most turtles using wet, nontidal sedge meadows along the Susquehanna River are active only from April to September. Daily activity cycles are also well developed and are dependent on air and water temperature (Cagle 1942, 1950; Ernst 1971, 1976; Arndt 1977). Turtles, especially those in the genera Chrysemys and Clemmys are rarely active until the ambient temperature reaches 10° C or higher. If the temperature goes above 34° C, many of these same turtles will become inactive, seeking cool areas. Similar patterns of winter and daily activity are noted for frogs, toads, and snakes (Noble 1954; Orr 1971). Salamanders of the family Plethodontidae are adapted to cold waters with high oxygen levels and hence might be more active in the winter than the other species of reptiles and amphibians listed in Appendix C.

6.4 ECOLOGICAL RELATIONSHIPS

Most tidal freshwater amphibians and reptiles are primary or secondary carnivores. They feed on a wide variety of animal matter from tiny insects to medium-sized mammals and birds (Appendix C). One important exception to this generalization are the turtles in the genus Chrysemys. While young, these turtles are carnivorous. As they mature, they switch to a diet which is almost completely vegetable matter (Ernst and Barbour 1972). This change in diet may cause the total biomass of these species' populations to reach very high values, on the order of 200 to 500 kg/ha (Table 16). Only fish and the tiger salamander have population biomass densities which exceed those of herbivorous turtles (Iverson 1982). Most carnivorous mammals and birds have population standing stock biomasses which are 10 to 100 times less than that of these turtles (Table 17). Although these estimates are based on studies done

Table 16. Population densities (numbers/ha) and standing stock biomass (kg/ha) of selected species of turtles and various other vertebrate groups. Data are modified from Iverson (1982), Tables 1 and 2. O = Ominivorous, C = Carnivorous, H = Herbivorous.

Species or group	Habitat	Food habits	Density	Population biomass
Snapping turtle	marsh	C	1.2	9.1
Snapping turtle	pond	C	59	181
Mud turtle	creek	O	81+	26
Musk turtle	pond	O	80	8.4
Musk turtle	lake	O	150	10.2
Painted turtle	lake	O	49	11.2
Painted turtle	pond	O	571-591	28-102
Spotted turtle	pond	O	40-80	3.2-8.7
Bog turtle	bog	O	123	10.9
Bog turtle	swamp	O	140	12.9
Chicken turtle	pond	O	40	8.2
River cooter	spring	H	170	384
Florida cooter	spring	H	154	311
River cooter	pond	H	5.2	4.0
Pond slider	pond	O	58-361	27-283
Pond slider	river	O	190	40
Softshell	river	C	42	19
Large mammals	-	H	-	280
Small mammals	-	H	-	100
Large mammals	-	C	-	1
Small mammals	-	C	-	1
Birds	-	O,C	-	1
Snakes	-	C	-	5
Frogs	-	C	-	27
Salamanders	-	C	-	21
Fish	-	C	-	477

Table 17. Efficiency of secondary production by various species of animals. Data adapted from Pough (1980), Table 3.

Species	Efficiency (%) Gross	Net
Warm-blooded		
Cottontail rabbit	0.74	0.83
Deer mouse	0.98	1.09
Meadow vole	2.10	3.00
Savannah sparrow	-	1.10
Long-billed marsh wren	0.35	0.50
Cold-blooded		
Red-backed salamander	39	48
Southern toad	-	49
Northern watersnake	20-35	-
Corn snake	-	86

in ponds, streams, and nontidal freshwater marshes, they are probably comparable to the value in tidal freshwater wetlands.

High population biomass does not necessarily imply that the energy flow through the population is also large. A result of ectothermy is that high biomass can be supported with a low level of energy flow if the organisms are efficient at utilizing what they consume (Pough 1980). It has been shown that the gross and net efficiency of secondary production (i.e., the efficiency of an organism in converting what it eats into body mass) of amphibians and reptiles is 10 to 100 times greater than that of birds and mammals (Table 17). Hence the biomass of herbivorous turtles may become large and be supported by a low level of energy flow through the entire population. A management consequence of this point is that it may take a long time for the populations to reach high levels. If the populations are exterminated from an area, it will take many years for them to recover (Iverson 1982). The effect of amphibian and reptile populations on the structure, function, and energy flow within wetlands is poorly understood and should be studied more in the future.

CHAPTER 7. COMMUNITY COMPONENTS: BIRDS

7.1 INTRODUCTION

Tidal freshwater wetlands provide a varied habitat for birds. Of the different types of coastal wetlands, tidal freshwater wetlands are among the most structurally diverse. Structural diversity is provided by the broad-leaved plants characteristic of the low marsh, tall grasses of the high marsh, the intermediate canopy provided by the shrub zone, and the high canopy found in tidal freshwater swamps.

Tidal freshwater wetlands harbor a higher diversity of birdlife than structurally simpler wetland types such as salt or brackish water marshes. Low marsh and adjacent exposed mudflats are used by shorebirds and rails. The grasses and sedges characteristic of higher elevations in the marsh are similar to grassland or savanna habitats and support an abundance of seed-eating species. Tidal channels and pools provide habitat for wading birds. Waterfowl use the open water areas in addition to the marsh surface itself. Shrubs and trees found in the high marsh and along the upland-marsh ecotone provide habitat for a large number of arboreal birds. These arboreal birds can often be found feeding in or over the marsh proper.

The few surveys which have been conducted in tidal freshwater wetlands reveal a diverse assemblage of birds. Kiviat (1978a) observed 142 species of birds which used the tidal freshwater marshes along the Hudson River. The Hamilton marshes on the Delaware River in New Jersey supported 64 species of birds during the summer (Hawkins and Leck 1977). McCormick (1970) reported 246 species from the region of the Tinicum marshes near Philadelphia. Wass (1972) listed 109 species as being found in the freshwaters and swamps from the lower Chesapeake Bay. He did not, however, refer directly to tidal freshwater marshes. Domenic Ciccone (Refuge Manager, Mason Neck National Wildlife Refuge, Lorton, Virginia; pers. comm.) cited 76 bird species from the tidal freshwater marshes at Mason Neck on the upper Potomac River. An additional three species were listed as upland species which frequently entered the marsh. Wass and Wilkins (1978) found 129 species using a tidal freshwater marsh which had been built by the Army Corps of Engineers on dredgespoil in the James River. Harold Olson (Refuge Manager, Presquile National Wildlife Refuge, Hopewell, Virginia; pers. comm.) stated that 83 species of birds are commonly seen in the tidal freshwater marshes at Presquile. P. E. Young (Outdoor Recreation Planner, Georgia Coastal National Wildlife Refuge Complex, Savannah, Georgia; pers. comm.) provided an exhaustive list of 215 species which are known to utilize tidal freshwater wetlands in Georgia. Of these species, 64 are mostly limited to tidal marshes; the remaining 151 species use the tidal swamps and upland forests which border the tidal marsh. Sandifer et al. (1980) listed 76 birds which inhabit the palustrine, nonforested wetlands of the South Carolina and Georgia coasts. They also listed 122 species from forested palustrine wetlands.

Based on information obtained from the literature and limited field surveys conducted by T. J. Smith, we have compiled a list (Appendix D) of 280 species of birds which use tidal freshwater wetlands for feeding, breeding, roosting, or other activities. We have included rare and abundant species. The most common species, or those which are most dependent on tidal freshwater wetlands, are discussed here.

The birds of tidal freshwater wetlands have been divided into seven groups for the purposes of this volume. The distinction as to group membership was made on the basis of trophodynamics or on the method employed by a particular species in procuring its food (hawking, diving, probing). The seven groups are: floating and diving waterbirds, wading birds, rails and shorebirds, birds of prey, gulls and terns, arboreal birds, and ground- and shrub-dwelling birds. These groups are not meant to represent guilds in an ecological sense, rather they are intended to show very general affinities between groups and provide for ease of discussion.

7.2 FLOATING AND DIVING WATERBIRDS

This group of 44 species is comprised primarily of members of the waterfowl family (Anatidae) plus gallinules, coot, pelicans, grebes, double-crested cormorant, and anhinga. Because of their economic and recreational importance, waterfowl are the most studied and best understood of the wetland avifauna, but characterization of their utilization of wetland habitats remains difficult. Shaw and Fredine (1956) inventoried the wetlands of the United States and rated them according to their value to this group. Many areas rated as having high waterfowl use at that time no longer support even small populations. An example is the greatly reduced use of the Susquehanna Flats region of the upper Chesapeake Bay during the past 20 years. This can be related to a dramatic decrease in the amount of submerged aquatic vegetation (Bayley et al. 1978). Lynch (1968) stated ". . . cases of consistently heavy exploitation of these coastal wetlands (referring to all types of wetlands) by waterfowl are almost overshadowed by instances of their partial or intermittent use or even casual abandonment."

As an example of the variable nature of waterfowl use of differing wetland types and of different wetlands of the same type, we present three years of annual mid-winter waterfowl survey data for Virginia (Table 18). This survey is conducted in early January, across the entire country to provide baseline data on trends in waterfowl populations and on changes in habitat use. Virginia is divided into 19 survey units which we have arranged along a gradient of saline to freshwater. Patterns of use between years, between differing salinities, and among units of the same salinity are striking (Table 18). The Pamunkey, Mattaponi, and Chickahominy Rivers all have large acreages of tidal freshwater marshes and swamps. Only the Pamunkey is used substantially by geese, often having more than 10,000 individuals, while the Chickahominy has less than 100. The greatest use by dabbling ducks of tidal freshwater marshes also occurs along the Pamunkey but is highly variable. Over a three-year period, January populations in the Pamunkey fluctuated by a factor of four. The Mattaponi River marshes, which are less than five kilometers from the Pamunkey, receive little use by dabbling ducks. Tidal freshwater marshes along these two rivers appear, visually, to be identical (T. J. Smith, personal observation). Causes for disparities in usage are unknown but may be related to subtle habitat differences, historical factors, microclimatological differences between sites, disturbance, or some other causes.

These data also indicate other important points in the use of wetlands by waterfowl. Dabbling ducks and geese (especially Canada geese) appear to be most closely tied to tidal freshwater wetlands (Figure 27). Diving ducks and mergansers are found in tidal freshwater habitats but are much more common in oligohaline and brackish wetlands. Sea ducks are almost never found in tidal freshwaters, being most abundant in brackish and saline environments. In more northerly areas where tidal freshwater wetlands are in closer proximity to brackish and salt marshes, the diving and sea ducks occur more regularly in the freshwater areas.

Of the various types of coastal marsh and wetland habitats, Shaw and Fredine (1956) rated shallow, tidal freshwater marshes as the most important habitat for ducks, geese, and swans. Stewart (1962) provided one of the most comprehensive discussions of wintering habitat use by waterfowl. In the upper Chesapeake Bay region, thirteen wetland habitats were delineated, two of which were tidal freshwater marsh systems. These two habitat types (estuarine river marshes and fresh

Figure 27. Late autumn mixed assemblages of Canada geese and ducks in tidal freshwater marshes of the Pamunkey River, Virginia. This photograph was taken from an aircraft approximately 200 feet in the air.

estuarine bay marshes) comprised only 4.82% of the entire study area. Dabbling ducks were obviously selecting tidal freshwater marshes in place of other available wetland habitats (Table 19), especially early in the autumn. Green-winged teal were the most selective; in some months one quarter of these birds were found in tidal marshes comprising only one-twentieth of the total wetland area. Mallards, American black ducks, and American wigeon were also selective, but not to the extent of green-winged teal (Table 19).

Diving ducks such as canvasback, redhead, scaup, bufflehead, common goldeneye, and ruddy ducks were highly selective for freshwater and oligohaline estuarine bay habitats (Stewart 1962). These species do utilize tidal freshwater marshes but were not as common there as in the open-water bays (Stewart 1962).

The seasonal pattern of waterfowl use in tidal freshwater marshes is most likely determined by a combination of food availability, food quality, and weather conditions. The vegetation of tidal freshwater marshes provides an abundant source of high energy foods when waterfowl need them most, i.e., immediately following their southward migration when energy stores are depleted and prior to the northward flight when energy reserves must be built up. During the winter months when a bird's maintenance requirements must be met, lower quality foods available in brackish and saline environments are suitable. Additionally, at northern locations tidal freshwater wetlands freeze over in the winter and food plants are not available; the waterfowl are forced to move to more brackish wetlands or to migrate to areas further south.

The seeds and rhizomes of annual and perennial sedges, rushes, grasses, and broad-leaved herbs appear to be favored foods of most waterfowl. Those species most commonly eaten include threesquare, softstem bulrush, saltmarsh bulrush, rice cutgrass, knucklegrass, halberdleaf tearthumb, dotted smartweed, Walter's millet, dwarf spikerush, squarestem spikerush, fragrant umbrellasedge, and wildrice. It appears that these middle to upper intertidal marsh species are more important food items than are the seeds and rhizomes of the broad-leaved species of the low marsh (Stewart 1962; Conrad 1966; Kerwin and Webb 1971; Perry and Uhler 1981). However, exceptions to the above generalization do occur. Perry and Uhler (1981) reported that approximately one third of the food by volume of the wood ducks from the James River in Virginia was arrow-arum. They also stated that Canada geesse occasionally fed on pickerelweed. Stewart (1962) listed arrow-arum as important in the diets of Canada geese, mallards, black ducks, and wood ducks from the upper Chesapeake region. Yellow waterlily is an important food of ring-necked ducks in the upper Chesapeake Bay (Stewart 1962).

The great diversity of foods available to and eaten by waterfowl in tidal freshwater wetlands indicates the value of this habitat type to them (Perry and Uhler 1981). A notable feature of the food habits of waterfowl is the opportunistic

Table 18. Distribution of waterfowl in various regions of Virginia during early January 1978-1980. Regions are arranged on a gradient of salinities, from tidal saline to tidal freshwater. Data provided by Fairfax H. Settle, District Biologist, Virginia Commission of Game & Inland Fisheries. TR = Trace.

			Saline					Brackish	
	Mobjack	*Chincoteague*	*Virginia barrier islands*	*Lower eastern shore, bayside*	*Upper eastern shore, bayside*	*Poquoson*	*Hampton Roads*	*Lower James River*	*York River*
Whistling swan									
1978	711	1100	TR	TR	400	0	0	0	169
1979	464	900	TR	100	200	0	0	25	77
1980	461	300	0	200	900	0	0	0	46
Canada geese, snow geese, and brant									
1978	317	11700	17000	7700	3800	515	249	460	318
1979	260	2300	8800	7100	1700	10	114	204	187
1980	460	5600	7800	6600	2400	358	363	34	51
Dabbling ducks									
1978	492	9400	14900	1100	1700	546	322	61	983
1979	346	11900	10400	1100	1200	255	6482	166	231
1980	309	8600	5400	2200	3200	461	710	286	309
Diving ducks									
1978	10666	1400	11100	3100	3700	585	2972	1804	5332
1979	10585	1000	4600	3100	4200	588	2963	356	2496
1980	2700	300	2700	4800	10500	1031	2253	1050	2007
Sea ducks									
1978	1903	200	2000	100	800	22	101	220	21
1979	1035	300	1000	1000	100	5	5	0	5
1980	819	100	1000	600	600	1067	88	10	24

Table 19. Percentage of total species population present in the upper Chesapeake Bay, observed in tidal freshwater habitats, estuarine river marshes, and fresh estuarine bay marshes. (Tabulated from data in Stewart 1962.) NR = Not reported.

Species	Oct.	Nov.	Dec.	Jan.	Feb.	March
Whistling swan	0	3	TR	0	NR	1
Dabbling ducks						
Mallard	13	17	14	12	NR	9
Black duck	16	9	4	4	NR	6
Green-winged teal	52	30	24	16	NR	36
American wigeon	4	15	TR	0	NR	TR

Lower Rappa-hannock River	Reedville	Back Bay	Hog Island	Upper James River	Presquile	Freshwater Chicka-hominy River	Pamunkey River	Mattaponi River	Upper Rappa-hannock River
383	555	2490	0	35	0	27	0	1	986
611	224	5048	0	50	0	0	0	1	706
158	330	3810	30	35	0	29	0	0	531
4978	420	12380	3968	8013	7857	0	12072	1091	12584
2250	0	22935	1750	1619	2953	60	6425	1100	16232
1250	563	25790	3134	5104	9495	0	6790	185	15179
387	291	21135	5493	1578	2658	4482	17432	139	4319
201	193	3162	1318	2396	102	5123	5031	1036	3739
1126	272	20975	3466	6583	4342	7250	20284	512	6104
6701	2244	440	0	160	722	5176	14	57	56
11022	583	0	100	270	0	2506	0	0	25
9773	1212	340	0	167	87	3246	61	18	35
22	244	0	0	0	0	0	0	0	0
512	30	0	0	0	0	0	0	0	0
1084	550	0	0	0	0	0	0	0	0

feeding and consequently the wide diversity of items eaten. Perry and Uhler (1981) examined 116 gizzards from eight species of waterfowl and found 136 different food items. Ten American black ducks ate 51 types of food while five American wigeon consumed 21 different foods (Table 20). Other examples of marsh omnivores are the American coot, common gallinule, and purple gallinule which feed on the leaves and seeds of sedges, rushes, spikerushes, wildrice, and pondweeds. They also take a large number of aquatic insects, tadpoles, snails, frogs, and small fish.

Perry and Uhler (1981) reported that two hooded mergansers taken from the upper James River, Virginia, fed exclusively on alewives. Johnny darters and American eels are eaten by the hooded merganser in the upper Chesapeake Bay (Stewart 1962). Common mergansers were reported to feed on pumpkinseed sunfish and yellow perch along the tidal freshwater wetlands of the Potomac River, Virginia (Stewart 1962). Loons, pelicans, cormorants, and anhingas are also fish eaters. Gallinules and grebes consume a broad range of aquatic invertebrates and vertebrates. During the fall, grebes and gallinules will eat the seeds of numerous marsh plants such as wildrice, sedges, and rushes (Terres 1981).

Few waterfowl breed in tidal freshwater wetlands of the mid- and south Atlantic coasts. Only wood ducks, and to a lesser extent American black ducks and mallards, commonly use these wetlands for breeding habitat. Stotts and Davis (1960) found that 65% of the nests of American black ducks were located in upland areas often hundreds of yards from the nearest water. Only 17% of the nests were in the marsh and these were located on elevated sites above the high-tide line. Once the

Table 20. Breadth of diet of selected species of waterfowl from tidal freshwater wetlands. Calculated from data presented in Stewart (1962) and Perry and Uhler (1981).

Species	Number examined	Number of animal foods	Number of plant foods	Food items/ bird
Canada goose	3	0	11	3.67
Wood duck	8	1	25	3.25
American wigeon	5	3	18	4.20
Green-winged teal	29	10	46	1.93
Mallard	38	10	68	2.05
Black duck	10	11	40	5.10
Pintail	20	7	48	2.75
Northern shoveler	1	3	5	8.00
Hooded merganser	2	1	0	1.00

eggs have hatched, the brood moves to the nearest wetland. Although brood rearing may occur in a number of habitats, it seems that sedge, cattail, and bulrush marshes are favored (Bellrose 1976). Availability of cover is the most important criterion for brood-reading areas since ducklings feed on aquatic insects, not vegetation. Wood ducks are tree-cavity nesters and their breeding activity is restricted to freshwater swamps (tidal and nontidal) and wooded uplands. They will often nest over one mile from the nearest water. Favored species which provide suitable cavities include cypress, sycamore, sweet gum, willow, and red maple. Once the eggs have hatched, the brood is immediately lead to the nearest marsh. The tidal freshwater wetlands along the western shore of the Chesapeake Bay, such as along the Pamunkey and Mattaponi Rivers in Virginia, are used extensively for brood rearing by this species (Smith, personal observation), as are similar areas throughout the mid- and south Atlantic (anonymous reviewer).

Loons, grebes, pelicans, gannet, mergansers, cormorant, anhinga, and gallinules comprise the remainder of the floating and diving waterbird group. Of these, only the common and hooded mergansers, pied-billed grebe, gallinules, coot, and anhinga are found with regularity in tidal freshwater marshes and swamps (Stewart 1962; Perry and Uhler 1981). The remaining species are most abundant in tidal freshwater when it lies in the vicinity of large areas of brackish or salt marsh. Pied-billed grebes, gallinules, and coots occasionally nest in the marsh, choosing high marsh sites with plentiful sedges and reeds for constructing their floating nests.

7.3 WADING BIRDS

Fifteen species of herons, egrets, ibises, and bitterns make up this familiar group of marsh birds. These species are commonly seen during the summer throughout the Atlantic coastal region. Only the limpkin and wood stork are restricted in range, being found south of South Carolina. The great blue heron (Figure 28) is the only species found during winter in the northern parts of the Atlantic coast. The other species migrate southward in the winter. Along the southern portions of the coast, waders are present year-round. These birds make heavy use of the tidal channels, creeks, and ponds found throughout the low and high marshes. They are also found commonly along the banks of watercourses in tidal swamps and salt marshes.

Fish, from small minnows and silversides to catfish, are preferred prey.

Figure 28. The great blue heron feeds in tidal freshwater marshes throughout the year.

Other food items include: crayfish, snails, frogs, lizards, and snakes. Occasionally herons and bitterns consume some warm-blooded prey items such as mice and shrews or even young birds. Limpkins have have a highly specialized diet consisting almost entirely of snails.

Green herons and bitterns nest in tidal freshwater marshes. Green herons build nests of sticks in vegetation low to the ground. Bitterns use sedges and grasses to construct nests low over the water. Breeding colonies of herons use a wide variety of trees and shrubs to support their nests, and sometimes nest on the ground in dense vegetation. The actual location of the nest site is not critical to these birds as they will fly long distances between heronry and feeding grounds (Kushlan 1977; Maxwell and Kale 1977). During the summer when these waders are raising young, their fish prey is most abundant within the marsh (see Chapter 5). The food which the waders gather from tidal freshwater marshes is undoubtedly important to the maintenance of adults and to the growth and survival of their young.

7.4 RAILS AND SHOREBIRDS

At least 35 species of shorebirds and rails make extensive seasonal use of the high marsh, low marsh, and especially of the associated tidal flats. Hawkins and Leck (1977) observed killdeer, spotted sandpiper, sora rail, and American woodcock in tidal freshwater marshes in New Jersey during the summer. The woodcock was confirmed as nesting in the wildrice/arrow-arum zone of this wetland. The other three species were believed to have nested but nests were never found. McCormick and Somes (1982) observed a number of species of sandpipers and rails at Oldmans Marsh, also in New Jersey. Greater yellowlegs were observed year-round, common snipes and dunlins during winter and in migration, king rails in the summer, and large numbers of least sandpipers, pectoral sandpipers, and Virginia rails during summer and migrations. Lesser yellowlegs were seen only during migration. Fifty percent or more of the total sightings of these eight species, summed over all habitats surveys, were made in tidal freshwater marshes (McCormick and Somes 1982). King rails are one of the few species of birds to be active during winter months in the tidal freshwater wetlands of the upper Chesapeake Bay (Meanley 1975). King rails remain active despite snow and ice covering the marsh surface. Peak abundance of soras occurs during fall migration at tidal freshwater wetlands along the entire Atlantic coast (Webster 1964, Meanley 1965).

Primary foods of these species include freshwater worms, crayfish, snails, and mollusks. In fact, they will eat almost any invertebrate organisms found in the upper few centimeters of the sediment surface (Baker and Baker 1973; Schneider 1978). During their fall migrations, surprising numbers of shorebirds make extensive use of the seeds of marsh plants such as wildrice, three-square, halberdleaf tearthumb, dotted smartweed, redroot sedge, rice cutgrass, and many other marsh plants. Many shorebirds are present only during the fall migration when the seed supply is maximum. An interesting note is the utilization of wildrice by rails. During autumn migration large numbers of soras (and possibly other rails) gather to feed on the seeds of this abundant marsh plant (Webster 1964; Meanley 1965). We have observed flocks of several hundred soras feeding on wildrice seeds in tidal freshwater marshes along the Chickahominy River (Smith, personal observation). During the month-long period in the fall when wildrice seeds are ripening, they may comprise 90% of the sora's diet (Webster 1964).

7.5 BIRDS OF PREY

Hawks, falcons, eagles, osprey, owls, vultures, and the loggerhead shrike form this group of 23 predatory or carrion-eating birds. These species are at the top of the wetlands' food pyramid and so were never abundant. Recently, some species of birds of prey have suffered rapid and drastic declines in population size because of pollution, habitat loss, and, most importantly, chlorinated hydrocarbon pesticides (Henny et al. 1974). Of this group the southern bald eagle and peregrine falcon are officially listed as endangered (Federal Register 1980). Swallow-tailed kites and Cooper's hawks are proposed for inclusion on South Carolina's endangered and threatened species lists, respectively (Gauthreaux et al. 1979, quoted in Sandifer et al. 1980). Additionally, the barn owl, great-horned owl, merlin, Mississippi kite, and loggerhead shrike are proposed for special-concern status by South Carolina. All of these species have suffered large declines in population size in the South Carolina coastal zone in recent years.

Southern bald eagle populations appear to have stabilized in the past decade. Breeding eagles are found along tidal freshwater stretches of the Potomac River (Lippson et al. 1979). In South Carolina, areas of impounded marsh, many of which are tidal freshwater habitats, are apparently very important for nesting eagles (Sandifer et al. 1980).

Northern harriers (marsh hawks) and American kestrels are common in tidal freshwater marshes, especially in winter. Red-shouldered and red-tailed hawks are common permanent residents. Cooper's hawks are more likely to be found in river swamps. American swallow-tailed kites prefer the ecotone between forested and nonforested habitats. They are most often found in the region where the tidal freshwater marsh grades into upland forest or tidal swamp.

Populations of osprey are recovering from their pesticide-caused declines of the 1960's. Ospreys are common along many stretches of the Atlantic coast. Breeding ospreys use tidal freshwater wetlands around the Delaware Bay (Hawkins and Leck 1977), Chesapeake Bay (Henny et al. 1974), and along the Georgia Bight (Sandifer et al. 1980). Henny et al. (1974) reported the observation that nesting ospreys use man-made structures (e.g., navigation buoys, towers) almost as much as natural structures. This habit appears to be more prevalent in the Maryland portions on the bay. In Virginia, ospreys are more prone to use trees such as cypress to hold their nests (Henny et al. 1974).

Ospreys and bald eagles are highly dependent on tidal marshes for the production of fish, their primary prey. Marsh hawks are also very dependent on tidal wetlands. All three of these raptors can use wetlands along the entire estuarine salinity gradient, and so are not restricted to tidal freshwaters. Of the other birds of prey in this group none are completely dependent on tidal freshwater marshes since they all can exploit a variety of other habitats, both wetland and upland.

7.6 GULLS, TERNS, KINGFISHERS, AND CROWS

Included in this group of 20 species are gulls, terns, crows, and kingfishers. Gulls are present during winter and during migration. Common and Forster's terns are present in the summer and during migration. Fish and American crows, laughing gulls, ring-billed gulls, and the belted kingfisher can be found year-round. Herring gulls and great black-backed gulls are common winter residents of coastal saltwater areas which often range up the estuary to tidal freshwater regions. Glaucous and Iceland gulls are reported from the vicinity of the Tinicum Marsh near Philadelphia, Pennsylvania. McCormick (1970) reported that these gulls are attracted by garbage dumps which are close to these marshes. This may not reflect true use of the tidal freshwater wetlands by these species.

Tidal creeks, channels, and pools in the marsh are used for hunting fish. The belted kingfisher, American crow, and fish crow breed in tidal freshwater wetlands.

7.7 ARBOREAL BIRDS

This is the largest group, comprising 90 species. Flycatchers and swallows are the most important species in this group. Stewart and Robbins (1958) reported that flocks of swallows numbering into the tens of thousands could be seen over tidal freshwater marshes in the upper Chesapeake Bay during fall and spring migrations, evidently feeding on the abundant insect fauna of the marsh. Sandifer et al. (1980) noted that swallows were important to tidal freshwater wetlands in South Carolina and Georgia for similar reasons. We have commonly observed flycatchers feeding over tidal freshwater wetlands in Virginia (Hoover and Smith, personal observations). Species such as eastern kingbirds and great-crested flycatchers will perch in trees or shrubs along the upland border of the marsh in search of prey. When an insect is spotted flying over the marsh, the bird darts out to capture it. Both swallows and flycatchers are important insectivores in the marsh. Many of the other species listed in this group are birds of the ecotonal community between the marsh and upland. The wood warblers have mostly been reported from tidal freshwater marshes and swamps during migration. While these warblers are in transit between summer and winter quarters, these wetlands may provide important temporary habitat. The arboreal birds as a group are the least dependent on tidal freshwater marshes for their survival.

7.8 GROUND AND SHRUB BIRDS

Fifty-three species of birds are included in this group which is composed of the emberizids and fringilids (sparrows, juncos, finches, blackbirds, wrens, and several other species). The seeds of the high marsh plants which are important to other groups are also the staple diet of these species. Ten species are recorded as breeding in tidal freshwater marshes, including ring-necked pheasant, red-winged blackbird, American goldfinch, rufous-sided towhee, savannah sparrow, grasshopper sparrow, tree sparrow, chipping sparrow, field sparrow, swamp sparrow, and song sparrow (Meanley and Webb 1963; Hawkins and Leck 1977). Large flocks of red-winged blackbirds, dickcissels, and bobolinks create a spectacular sight in wildrice marshes when they congregate during early autumn. Flocks numbering into the tens of thousands are common. The timing of the arrival of these large flocks coincides with seed set by the wildrice. It takes only a few days for these birds to consume most of the crop and then move to another marsh. Bobolinks were referred to as ricebirds in the last century by plantation owners in Georgia and South Carolina. These birds with their voracious appetites inflicted heavy losses on the rice crops.

Of the birds in this group, marsh (long-billed) wrens and sedge (short-billed marsh) wrens are most dependent on tidal freshwater marshes. Short-billed marsh wrens are most abundant in brackish and saline environments, though they are common in tidal freshwater marshes. Short-billed marsh wrens are considered a regionally endangered species in New Jersey (Hientzleman 1971).

7.9 ENERGY FLOW AND AVIAN COMMUNITY DYNAMICS

Wiens (1973) suggested three possible roles for birds in ecosystems: (1) they may directly effect the ecosystem by influencing the flow of nutrients and/or energy, (2) by acting as controlling factors, they may help maintain stability in the ecosystem without playing a major role in nutrient and/or energy flows, and (3) they may simply be frills living off the excess production of the ecosystem and having no influence on it whatsoever. There have been few studies on the role of birds on energy and nutrient flows in ecosystems of any type to test Wien's ideas.

The role of birds in nutrient cycling has not been studied in tidal freshwater wetlands. Bedard et al. (1980) examined the effects of seabirds on nutrient concentrations within the St. Lawrence River estuary. The effect of importing nutrients to the estuary from outside sources by seabirds was negligible compared to the amount of nutrients already present in the system. Manny et al. (1975), McColl and Burger (1976), and Onuf et al. (1977) presented data to show that on a localized scale birds may be quite important. In these three studies, birds (Canada geese, Franklin's gulls, and herons, respectively) were shown to be important by importing nitrogen, phosphorus, potassium, and organic carbon to wetland systems. Manny et al. (1975) and Onuf et al. (1977) were able to show that the imported nutrients led to increased levels of primary production. Onuf et al. (1977) presented additional evidence to show elevated secondary production in regions receiving nutrient inputs by herons. The input of nutrients led to increased nitrogen content of the plants (mangroves in this instance) which made them more palatable to herbivores. On a local scale then, birds can be an important vector in nutrient flow.

In tidal freshwater marshes migratory waterfowl and shorebirds and the large flocks of blackbirds and rails could possibly act as nutrient exporters since they feed in the wetlands and then leave. If colonially nesting species were to develop a colony in or near a marsh, this could certainly provide for an input of nutrients.

The role of birds in the energy flow of marhes has likewise received little attention. Hawkins and Leck (1977) examined the breeding bird fauna in three tidal freshwater marsh habitats in New Jersey. These included a cattail marsh, high marsh, and low marsh. Breeding bird biomass in these marsh habitats was estimated to be 0.012-0.017, 0.006, and 0.007 g dry wt/m^2, respectively. The energy flow through the breeding bird component of this system was estimated using measured weights of birds present in the marsh and converting to energy using standard metabolic equations. Energy flow was reported as 0.037-0.050, 0.015, and 0.021 kcal/m^2/day in each of the wetland types studied, respectively. Over the 60-day breeding season this represented 2.82-3.00, 0.90, and 1.26 kcal/m^2. Day et al. (1973) examined the energy flow of the entire salt marsh/ shallow bay region of Barataria Bay in Louisiana. These authors reported an average yearly standing crop of 0.044 g dry wt/m^2 for the avian component of the system. This value is slightly higher than what Hawkins and Leck reported for only the common breeding birds in a tidal freshwater marsh. When the nonbreeding birds, uncommon breeding birds, and the juvenile birds which are produced are included in the calculations, the annual biomass of birds in tidal freshwater marshes will probably be higher than in salt or brackish marshes. Day et al. (1973) reported that total consumption by the birds amounted to 7.33 g dry wt/m^2 for the year. A portion of the bird's consumption is returned to the marsh surface as feces. This amounted to 2.20 g dry wt/m^2/yr. Respiration accounted for 5.11 g dry wt/m^2/yr, and the remaining 0.022 g dry wt/m^2/yr was production by the birds. Day et al. (1973) state that certain groups of birds, especially the dabbling ducks, may be ten times more abundant in nearby freshwater marshes. Energy flow through the avifauna of tidal freshwater marshes may be somewhat higher than in brackish and salt marshes.

Although the flow of energy through the avian component of tidal freshwater wetlands represents only a small portion of the overall energy flow, birds can exert other influences on the system. Reed (1978) studied the effect of grazing by snow geese on tidal freshwater marshes along the St. Lawrence River in Canada. He found that increasing grazing pressure resulted in greater primary production by three-square, the dominant plant. Hence grazing facilitated energy flow through the entire system. Along the mid-Atlantic coast, however, snow geese are much more common in salt marshes. They can drastically reduce primary production and cause changes in species composition of the marsh vegetation (Lynch et al. 1947; Smith and Odum 1981; Smith 1983). Canada geese have been reported to cause temporary, local loss of vegetation from tidal freshwater wetlands through overgrazing (Smith, personal observation). Thus, organisms which account for only small fractions of the total energy flow may have more important impacts on the system than energy flow alone would suggest.

CHAPTER 8. COMMUNITY COMPONENTS: MAMMALS

8.1 SPECIES OCCURRENCE

The 45 species of mammals that we have found to be reported from tidal freshwater marshes (Appendix E) range from abundant, almost ubiquitous species such as the Virginia opossum, to relatively rare or localized species such as the nine-banded armadillo. In this section we have chosen to focus only on the common or ecologically important species. Due to the lack of published studies restricted to tidal freshwater marshes, regional occurrences listed in Appendix E should not be construed as comprehensive.

A variety of mammals utilize the tidal freshwater marsh as year-round residents (Table 21a). All of these species have the following characteristics: (1) they are capable of obtaining all of their nutritional needs from within the tidal freshwater habitat (note that these species are either herbivorous or omnivorous), (2) they have a fur coat which is relatively impervious to water, and (3) they have the ability to nest (and hibernate in more northern areas) within the marsh either in a submerged lodge or a nest elevated on vegetation. A variety of other species are unable to exist in the tidal freshwater marsh habitat on a permanent basis, but make periodic feeding forays into the marsh (Table 21b).

Of the species listed in Appendix E and Tables 21a and 21b, those which appear to be most dependent upon the tidal freshwater marsh habitat include the river otter, muskrat, nutria, mink, eastern raccoon, marsh rabbit, and marsh rice rat. This does not imply, of course, that these species do not use alternate habitat such as swamps, river bottom floodplains, and freshwater streams.

Table 21a. Examples of mammals commonly found in tidal freshwater marshes as year-round residents.

Star-nosed mole	Meadow vole
Marsh rabbit	Nutria
Beaver	Eastern raccoon
Marsh rice rat	River otter
Muskrat	Mink

Table 21b. Examples of mammals which make forays into tidal freshwater marshes for feeding purposes, but which are not considered permanent residents.

Virginia opossum	Red and gray fox
Least and short-tailed shrews	Striped skunk
Big brown bat	Bobcat
House mouse	White-tailed deer
Norway rat	

Comparisons of mammal species diversity between tidal freshwater marshes on one hand and saline marshes, nontidal freshwater marshes and swamps on the other, have generally not been made. We suspect that species diversity is significantly higher in tidal freshwater marshes than in saline marshes; however, data for comparison with nontidal freshwater and upland habitats are generally lacking for the east coast.

8.2 ROLES IN MARSH ECOLOGY

Unfortunately, not much is known about the ecological interactions between the various species of mammals in tidal freshwater marshes. Most information which is available comes from research in the wetlands of Louisiana or the oligohaline stretches of east coast marshes. Neither habitat is directly comparable to tidal freshwater marshes. For this reason much of the information which follows in this section should be regarded as either extrapolations or guesswork based on information from better studied habitats.

In reviewing the following material two points should be remembered. (1) The process of herbivory is probably important both directly as an impact on the structure of the tidal freshwater plant community and indirectly through its effect on substrate morphology and integrity. (2) The higher trophic levels (predators) are probably not as important to the structure and functioning of the tidal freshwater marsh community.

Herbivores

Weller (1978) states that the activity of herbivorous animals is the most important factor, after fluctuations in water level, in structuring plant communities in nontidal freshwater wetlands. In tidal freshwater wetlands this is also probably true with only tidal action itself being more important. A large number of the mammals which are found in tidal freshwater wetlands are herbivorous (Appendix E). Small mammals such as mice in the genus Peromyscus fall into this trophic category. The white-tailed deer also feeds on the leaves and stems of wild rice, cattails, and other wetland plants (Figure 29). However, herbivorous muskrats, nutria, and beavers influence wetland vegetation to the greatest extent.

Muskrats are found in a variety of marsh types; from nontidal freshwater marshes of the Midwest to tidal saltmarshes of the Atlantic and Gulf coasts. Tidal freshwater marshes dominated by sweetflag, arrow-arum, and wild rice are considered favored habitat for muskrats along the Atlantic coast (McCormick and Somes 1982). Threesquare and cattail marshes along the eastern seaboard are also considered prime muskrat habitat (McCormick and Somes 1982). Wass and Wilkins (1978) reported high muskrat

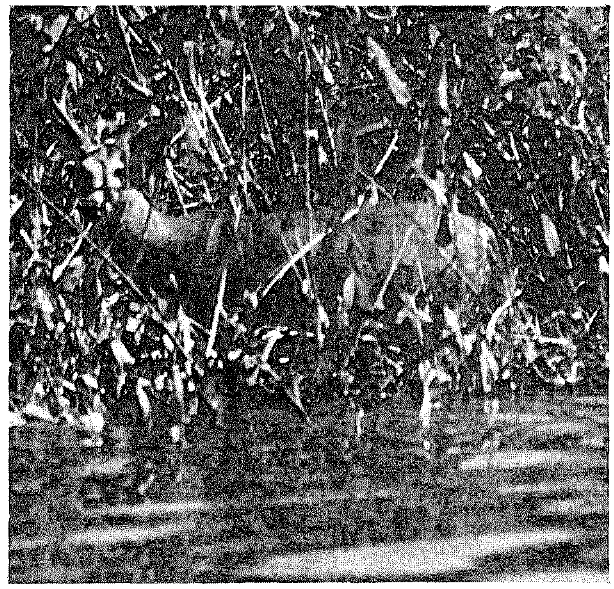


Figure 29. White-tailed deer feeding in a Virginia tidal freshwater marsh. Photograph by Michael Dunn.

densities (2.25 active houses/ hectare) in a tidal freshwater marsh dominated by burmarigold on the James River. In Louisiana muskrats appear to be most abundant in brackish and oligohaline marshes in which threesquare rushes (Scirpus americanus and S. olneyi) are the dominant plants (Palmisano 1972).

Surprisingly, the muskrat is not found in the coastal marshes of Georgia and most of South Carolina, although it occurs in the piedmont regions of both states. The more southern distributed muskrat, the round-tailed muskrat (Neofiber alleni), occurs inland in south Georgia (as close to the coast as the Okeefeenokee Basin). It would not be surprising to find this muskrat eventually extending its range into the tidal freshwater habitat along the Georgia coast.

Muskrats feed extensively on the shoots, roots, and rhizomes of threesquares, cattail, sweetflag, arrow-arum, and other marsh plants. These plants may represent almost 80% (by weight) of the muskrat diet. The young shoots, which are high in nutrients, especially nitrogen, and older stems are favored in the spring and summer, respectively (Weller 1981).

Leaves of marsh plants are seldom, if ever, consumed. During the winter months roots and rhizomes comprise almost 100% of the muskrat diet (Stearns and Goodwin 1941). The activity of muskrats in digging up roots and rhizomes can have deleterious effects on marsh soils. Roots and rhizomes of marsh plants are the fibers which bind the marsh substrate. When muskrats remove these plant organs, the substrate lacks cohesiveness and is easily resuspended and may be washed away by storms and even normal tidal action (Lynch et al. 1947). Muskrats harvest a larger mass of above-ground plant parts (leaves and stems) than below-ground plant parts. Above-ground portions of the vegetation are used in construction of their houses and feeding platforms. Muskrat houses may be 2-3 m (6-10 ft) wide at the base and 2 m (6 ft) tall. Often mud and sticks are worked into the house to strengthen it. It is common to see upland vegetation sprouting from the tops of those muskrat houses which are not inundated by tides.

The muskrats' practices of digging up roots and rhizomes for food and of clearing large areas of above ground vegetation for houses could potentially cause denuding and disruption of large areas of marsh (Lay and O'Neil 1942; Lynch et al. 1947; Weller 1981). The practices of snow geese have similar effects on salt marshes (Smith and Odum 1981, Smith 1983). Areas of the marsh which are heavily grazed and disrupted by muskrats (or geese) are referred to as eat-outs by marsh managers. Eat-outs may range up to several square kilometers in area (Lynch et al. 1947). Generally, the influence of muskrats on the vegetation is not this severe. Initially a small clearing is created immediately around the house. If there are many muskrat families present in a given marsh, this will result in many small openings in the vegetation. Numerous small open areas actually benefit a variety of other wetland species including waterfowl, grebes, and herons (Weller and Spatcher 1965, Weller and Fredrickson 1974). Continued muskrat activity may enlarge and deepen these initial excavations. Arrowheads, arrow-arum, and spatterdock may become established in the small ponds which open around muskrat lodges (Meanley 1975). When the muskrat population grows to high densities, these small openings are enlarged and may be joined to other openings nearby. It is estimated that if the muskrat population reaches densities greater than 75 individuals per hectare (30/acre), losses of vegetation and accompanying population crashes are likely (Dozier et al. 1948, Errington 1963, Wilson 1968, Weller 1981). Eat-outs are usually revegetated within several years depending on climatic conditions and the severity of the eat-out (Lynch et al. 1947). In cases where little vegetation remains or storms have washed away the marsh soils, revegetation may not occur for 10-15 years. Lynch et al. (1947) and Weller (1981) presented excellent discussions of the various successional pathways which may be followed after marshes have been grazed by muskrats (or geese). Unfortunately, their work deals with brackish marshes and nontidal freshwater marshes, respectively. In a general manner their results probably hold for tidal freshwater marshes as well.

Along the Atlantic coast, nutria are common in Maryland and North Carolina (Evans 1970), especially in Dorchester and Somerset Counties, Maryland. The distribution of nutria in Virginia is not well known. Evans (1970) presents distribution maps showing that tidal freshwater reaches of the James, Chickahominy, Pamunkey, Mattaponi, and Rappahannock Rivers are inhabited by nutria. Wass (1972) stated that nutria are abundant in the oligohaline marshes around Back Bay, Virginia, but did not mention their occurrence in any of Virginia's tidal river marshes. These marshes abound with muskrats and would seem to be ideal nutria habitat also. Lippson et al. (1979) stated that nutria are present in moderate numbers along the Potomac River.

Nutria are ecologically similar to muskrats. A small difference is that nutria feed more heavily on leaves of marsh plants than do muskrats. Leaves may make up 20% of their diet at certain times of the year (Willner et al. 1979). During most of the year, roots and rhizomes comprise the bulk (70%) of the nutria's diet (Willner et al. 1979). Because their habitats and feeding habits are similar, nutria and muskrats may be competitors. Interactions between these two species have not been directly studied. Studies in Louisiana indicate that nutria have a greater preference for freshwater marshes than do muskrats (Wilson 1968, Palmisano 1972). Along the Atlantic coast nutria and muskrats appear to be found in the same types of marshes, ranging from oligohaline threesquare marshes to tidal freshwater wetlands at the heads of estuaries (Evans 1970, Lippson et al. 1979).

Direct field experiments will be required to fully understand the ecological relationships between nutria and muskrats.

Nutria are not tolerant of cold temperatures and are often killed by hard freezes. (Willner et al. 1979). During the winter of 1976-1977 substantial nutria mortality was noted by Willner and coworkers in the marshes of Dorchester County, Maryland. They reported it common to find dead nutria with extensive frostbite damage to feet and tails. It is not likely that nutria will expand their range northward. However, they could easily move into tidal wetlands in South Carolina and Georgia.

Beavers are becoming more common, especially in the tidal freshwater marshes at the headwaters of the tributaries to Chesapeake Bay. Often beavers will dam the upper reaches of a tidal freshwater stream, cutting off the influence of the tide (Figure 30). We have observed the activities of beavers on a tributary of the Chickahominy River in Virginia. Wild rice was growing on both sides of the dam. The only noticeable difference was that on the upstream side the wild rice was much more open and generally less dense than on the downstream side. The influence of beavers in other habitats is well known and they obviously can have an impact on tidal freshwater marshes. The nature of the effect of beavers needs to be studied in detail.

Carnivores

From an economic standpoint, the most important carnivorous mammals in tidal freshwater marshes are the raccoon, mink, and river otter. These species are very important to the fur trade in the United States (Chabreck 1979). Raccoons prey heavily on juvenile muskrats and may play a role in controlling the size of muskrat populations. Predation by raccoons may keep muskrat populations below the levels where they will damage marsh vegetation and/or where it is feasible to harvest them (Wilson 1953). Mink and river otter occasionally prey on muskrats (Wilson 1954). For the mink, however, mice, voles, and small birds are more important food items. River otter feed primarily on fish, taking only small amounts of other foods (Wilson 1954).

Except for the relation between raccoons and their muskrat prey, the relationships between mammalian predators and their prey in wetlands are poorly under-

Figure 30. Beaver dam on a tidal freshwater marsh stream near the Potomac River, Virginia.

stood. We do not know if any carnivores are acting as keystone predators, keeping their prey populations in check. The role of carnivores on nutrient and energy flows within wetlands is not understood.

8.3 ECONOMIC VALUE

While it is clear that a number of mammals of the tidal freshwater marsh have valuable pelts (e.g., otter, mink, muskrat, nutria, and raccoon) and that pelts from this habitat enter the commercial market, the magnitude of this fur production is not known. This is because detailed harvest records are not available; the origin of muskrat pelts from tidal freshwater, oligohaline, and estuarine habitats is not differentiated by most of the State and Federal agencies which keep fur production records. Louisiana is one exception and records from this state offer some insight into the relative importance of tidal freshwater marshes as fur producers.

Data gathered by Palmisano (1972) and Chabreck (1979) are summarized in Table 22. As shown by this table, freshwater marshes are most important for nutria; oligohaline marshes for muskrats; and swamps for mink, raccoon, and river otter. The harvest of muskrats is greater in freshwater marshes than in swamps and is at least comparable to that of brackish and oligohaline marshes. Harvest of all other species is greatest in the freshwater wetlands (marshes and swamps) than in the other categories. In terms of dollars, the freshwater marshes are second in value to swamps. Swamps gain their value based on the large catch of river otter, valued at close to $50 per skin.

Of course, this data cannot be extrapolated directly to east coast tidal marshes. Louisiana fresh marshes are often nontidal or affected only by irregular, wind-driven tides; as a result, the vegetation is considerably different from east coast tidal freshwater marshes. Nevertheless, the Louisiana data suggest that muskrat harvest from tidal freshwater marshes on the east coast must be substantial and that harvest of beaver, mink, otter, and nutria is probably greater from tidal freshwater than that from areas of higher salinties. Our personal observations from Virginia and Maryland tend to support this speculative hypothesis.

Table 22. Mean number of aquatic furbearers harvested per 400 hectares 988 (1000 acres) according to marsh type. Data originally from Palmisano (1972) and Chabreck (1979).

Species	Marsh type			
	Brackish	Oligohaline	Fresh	Swamp
Muskrat	84	97	78	42
Nutria	86	285	513	341
Mink	1	1	2	73
River otter	3	1	6	98
Raccoon	1	1	1	2
Total Value ($/400 ha)	$1124	$2752	$4564	$5040

CHAPTER 9. VALUES, ALTERATIONS, AND MANAGEMENT PRACTICES

9.1 VALUE TO MAN

In reviewing the material presented in the first eight chapters, it becomes clear that tidal freshwater wetland ecosystems have a considerable inherent value to man. Both direct and indirect values are involved. Unfortunately, both categories of values tend to defy conventional economic analysis, and it is very difficult to place an economic value on these wetlands. After examining the following listing, we have concluded that tidal freshwater wetlands are best regarded as "priceless".

Fisheries

A number of species of freshwater, estuarine, marine, and anadromous fishes use tidal freshwater at some stage in their life histories (see Chapter 5). This results in extensive sport and commercial fisheries in most tidal freshwater rivers. As an example, the Potomac River supports a commercial fishery worth several million dollars. A relatively small portion of the Potomac catch actually comes from tidal freshwater (Table 23a). However, close examination of the total river catch (Table 23b) reveals that the leading eight species spend part of their life cycle in tidal freshwater even though they may be captured further downstream. There are also fish not represented in Table 23a, that utilize tidal freshwater as a nursery area, invade or pass through as juveniles or adults, and may be eventually caught at a distant location. The Atlantic menhaden and striped bass are examples.

Sport fisheries' catches from tidal freshwater are not well documented but are apparently high (personal observation).

Table 23a. Commercial fish harvest from the tidal freshwater portion of the Potomac River. Values are in pounds/year averaged for the period 1964-1971. From Lippson et al. 1979.

1.	Catfish (brown bullhead, white and channel catfish)	138,872
2.	Striped bass	34,211
3.	American eel	28,028
4.	American shad	18,203
5.	White perch	5,449
6.	Carp	5,064
7.	Alewife and blueback herring	1,121
8.	Yellow perch	754
9.	Crappies	187
10.	Hickory shad	22
	Total	231,911

Table 23b. Commercial fish harvest from the entire tidal Potomac River. Values are in pounds/year averaged for the period 1964-1971. From Lippson et al. 1979.

1.	Alewife and blueback herring	7,044,637
2.	Atlantic menhaden	3,952,136
3.	Striped bass	1,117,248
4.	Spot	422,691
5.	American shad	366,495
6.	American eel	340,738
7.	White perch	191,327
8.	Catfish (same as Table a)	161,088
9.	Flounders	47,309
10.	Bluefish	44,356
	Total	13,688,025

Important sport fishes include striped bass, largemouth bass, white perch, several species of catfish and sunfish, crappie, pickerel, and yellow perch. The quality of sportfishing can be excellent. For example, the Chickahominy River provides some of the most consistent and productive fishing in the state of Virginia.

Trapping

As discussed in Chapter 8, tidal freshwater marshes provide excellent habitat for a variety of mammals including valuable fur bearers such as beaver, nutria, muskrat, raccoon, and otter. A significant, but undocumented portion of the fur production of Virginia, Delaware, Maryland, and New Jersey comes from these marshes.

Birds

We have attempted to emphasize the diversity of birds found in tidal freshwater marshes in Chapter 7. This habitat provides an important location for breeding, feeding, and stopovers during migratory movement. Resident and visiting birds include those of considerable recreational importance (ducks and geese) as well as birds of interest to birdwatchers.

Endangered Species

We have been unable to identify any endangered animal species which is solely dependent upon tidal freshwater. There are several endangered and threatened animals, however, which use these areas extensively. These include the peregrin falcon, the American bald eagle, the American alligator (south of Virginia), and the short nose sturgeon.

Ferren and Schulyler (1980) mentioned that a number of rare plant species occur in tidal freshwater wetlands. Furthermore, they have documented the extirpation (local eradication) of six plant species from tidal freshwater sections of the Delaware River, seven from the Schuylkill River and, possibly, five or more species from the Raritan River. Factors considered responsible for the extirpations include dumping of dredge spoil, landfill, and refuse as well as bulkheading, damming of tributaries, and diking of wetlands.

Aesthetic Value

Considerations of aesthetic value are complicated by extreme subjectivity and lack of easily quantifiable variables. In spite of this, tidal freshwater wetlands appear to have a broad appeal to many types of people. The combination of (1) diverse plant communities, (2) plentiful wildlife, (3) diversity of landscape types (forest, marsh, waterways) in close juxtaposition, (4) broad expanses of open land, (5) numerous flowering plants, and (6) a diversity of plant types ranging from broadleaf to grasses and ferns produces an area with a great deal of appeal for artists, sportsmen, naturalists, scientists, and others. Further amplifying this high aesthetic appeal is the occurrence of many tidal freshwater wetlands in close proximity to major urban areas, such as Boston, New York City, Philadelphia, and Washington, D.C.

Value as a Buffer

As pointed out by Simpson et al. (1983) tidal freshwater marshes lie in an intermediate position between coastal waters and marshes on one side and upland land and streams on the other. Pollutants (heavy metals, nutrients) and suspended sediments from upstream sources can be at least partially intercepted and processed in the tidal freshwater system. Sediments are trapped by reduced flows on top of the marsh surface with the result that downstream loadings on the estuary are reduced. As shown by Grant and Patrick (1970), eutrophic river water is processed in the tidal freshwater marsh by a combination of sediments, bacteria, algae, and vascular plants. The result is that reductions may occur in nutrient concentrations, BOD (biological oxygen demand), COD (chemical oxygen demand), and sediment loads. In certain cases marsh plants may raise the dissolved oxygen concentration of the river water flowing through the marsh on the rising tide. The net result is that the tidal freshwater marsh can act as a partial filter to improve the water quality of freshwater flowing into the head of the estuary. The magnitude of this cleansing action is not well documented. Certainly, it must vary from one estuary to the next depending upon relative inputs of river and tidal water, the degree of eutrophication of inflowing water, the extent of tidal freshwater wetland, and the time of year.

9.2 CONNECTIONS WITH ADJACENT ECOSYSTEMS

In any consideration of the management of tidal freshwater wetland ecosystems, it is important to recognize that these are extremely open ecosystems and are coupled with a variety of nearby systems. By "open" we mean that significant flows of nutrients, including carbon, move between tidal freshwater wetlands and nearby systems such as terrestrial upland forests, tidal swamp forests, nontidal and tidal freshwater rivers, and downstream oligohaline marshes. For example, as we discussed in Chapter 3, inputs of nitrogen and phosphorus to tidal freshwater marshes can come from the adjacent river water as well as from upland terrestrial sources. This means that attempts to manage tidal freshwater wetlands must also include considerations of human activities in nearby associated systems. There are many situations similar to the Tinicum Marsh on the Delaware River (Grant and Patrick 1970). The marsh itself thas been preserved with no direct alterations. However, it has been badly degraded by activities (sewage and waste dumping) further upstream.

9.3 ALTERATIONS BY MAN

Historical Aspects

Since the arrival of the first colonists at Jamestown, Virginia, tidal freshwater wetlands have undergone a continuing progression of alterations and changes, resulting from human activities. Almost all of this habitat on the Atlantic coast is in the 13 original colonies; much of it lies adjacent to major cities. Most tidal freshwater wetlands are connected to rivers whose watersheds have been dramatically altered over the past three centuries. Poor farming practices combined with extensive forest clearing and land development have produced heavy loads of sediments and dissolved nutrients in the freshwaters flowing into tidal freshwater regions. Local inputs of sewage and other wastes have exacerbated the problem. The results are manifold: (1) rapid sediment deposition rates on the wetland surfaces (Chapter 1), (2) hypereutrophication at many sites (Chapter 3), and (3) alteration of plant and animal community composition.

In colonial times in the Northeast and mid-Atlantic States, mill ponds were constructed across the upper ends of many tidal freshwater sites. In most cases, these unused ponds remain, partially filled with sediment, and covering sites of former tidal freshwater marshes.

Ricefield Conversions

In the Southeast during the 18th and first half of the 19th centuries, slave labor converted thousands of hectares of freshwater tidal marsh and swamp to diked ricefields (Figure 31). Some of these diked areas, particularly in South Carolina, are now managed for waterfowl, trapping, and even aquaculture (Sandifer et al. 1980). Many other former ricefields still exist. These ricefields are in disrepair and have perforated dikes which allow the tide to rise and fall normally. These areas are covered with a typical freshwater marsh plant community dominated by giant cutgrass. Management options for these old ricefields range from continued control for waterfowl production to complete abandonment and a return to tidal freshwater marsh. Correct management decisions for individual locations are usually difficult to reach. Often, the answer is determined by site-specific characteristics such as the number of waterfowl supported in the managed marsh versus the amount of juvenile fishes supported by the natural marsh.

Twentieth Century Problems

The pattern of alterations begun in colonial times continues unabated in the late twentieth century. High sedimentation rates in tidal freshwater marshes still occur because of poor land use practices upstream. Interruption of freshwater input from upstream sources is caused by diversions for irrigation and navigation purposes and is widespread. Two recent large diversions in the Southeast, the Santee-Cooper diversion in South

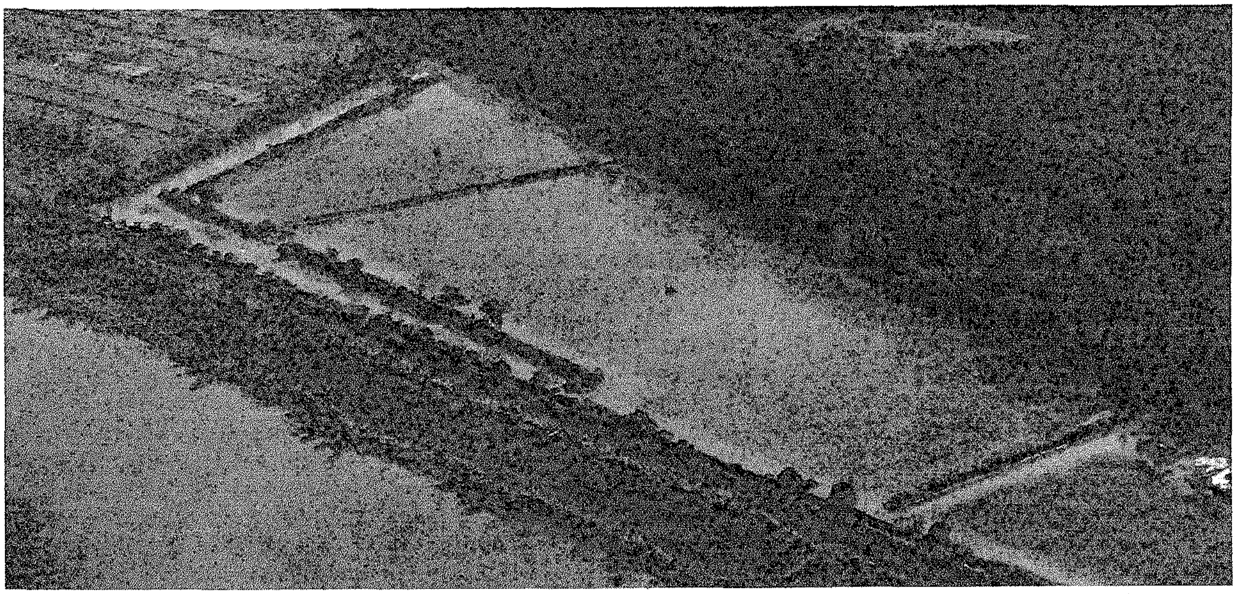


Figure 31. Abandoned ricefields. Photograph by Dennis Allen.

Carolina for facilitating hydroelectric power generation and the partial diversion of the Savannah River between South Carolina and Georgia for navigation concerns, have caused upstream salinity increases and conversion of tidal freshwater wetlands to oligohaline wetlands.

Diking, dredging, and filling of tidal freshwater wetlands have occurred throughout the Northeast and mid-Atlantic States. Some of the most damaging episodes have occurred on the Connecticut, Hudson, Delaware, and Potomac Rivers (personal observation). A characteristic sign of this type of alteration is the profusion of monotypic stands of the common reed (Phragmites australis) on many of these sites.

As mentioned in Chapter 3, eutrophication of tidal freshwater is a widespread and persistent problem at many locations. On many of the tidal freshwater stretches of the Potomac and Delaware Rivers, eutrophication, in combination with significant heavy metal inputs, has led to drastically lowered dissolved oxygen concentrations and to simplified animal communities (fewer species).

Pesticide contamination of tidal freshwater wetlands does not appear to be generally well documented. However, the most serious kepone contamination from the Allied Chemical spill occurred in the tidal freshwater zone of the James River, Virginia (Drifmeyer et al. 1980). Even today, many years after the event, many fisheries remain closed in the tidal freshwater James River because of continuing contamination.

Alteration of tidal freshwater wetland ecosystems is a problem which began in colonial times and has become even worse in the twentieth century. The close proximity of this habitat to large urban areas, shipping channels, and industrial sites has produced a multitude of problems ranging from direct impacts such as diking to more subtle changes resulting from eutrophication.

9.4 POTENTIAL FOR SEWAGE ASSIMILATION

Grant and Patrick (1970), in one of the earliest holistic studies of a tidal freshwater marsh, concluded that considerable potential existed to assimilate and process nutrients contained in raw or partially treated sewage. Whigham and Simpson (1978) confirmed that these marshes could take up nutrients, at least on a seasonal basis (see discussion in

Section 3.3). Simpson et al. (1981) further demonstrated a capacity to remove metals from river water flowing across the marsh.

Recently, however, Whigham et al. (1980) directly tested the ability of tidal freshwater marshes to accumulate nutrients from secondary treated sewage. They concluded that the marsh can assimilate nutrients from sewage during the spring and summer growing season, but that there is a tendency to release nutrients in the fall and winter. Evidently, the lack of a permanent litter layer or extensive peat deposits, along with certain other sediment chemistry characteristics (e.g., pH), limits the capacity of this type of marsh to process and assimilate large quantities of partially treated sewage.

In summary, it appears that tidal freshwater marshes may be useful in improving the water quality of hypereutrophic rivers such as the James, Potomac, and Delaware, at least on a seasonal basis. On the other hand, their use as direct receivers of treated sewage seems unfeasible.

9.5 BEST MANAGEMENT PRACTICES

Clearly, tidal freshwater marshes have great value to man. The wisest management plan appears to be protection and preservation. Controlled hunting, trapping, and fishing are compatible with this plan. Dumping of pollutants and sewage is destructive. Diking or impounding these marshes is not advisable. Part of their unique character and their high productivity can be traced to the daily tidal pulse (Odum et al. 1983). Most evidence suggests that insects (mosquitoes and biting flies) are a minimal problem in tidal freshwater that is flooded daily (Daiber et al. 1976); therefore, mosquito ditching or diking is not necessary or cost effective.

While preservation of tidal freshwater marshes is desirable, construction or building of new marshes with expensive plant propagation programs does not seem to be necessary. Lunz et al. (1978) concluded that the vegetation of tidal freshwater marshes can become established very rapidly on new sites (e.g., spoil disposal islands) without much help from humans.

Although much of the tidal freshwater acreage on the east coast does not lie in preserved tracts, virtually all States protect this habitat with the same laws which protect other tidal wetlands. In addition, there are significant areas of tidal freshwater marsh which are located in Federal and State refuges and wildlife management areas. Private organizations have also played a role in preserving these wetlands. For example, the Nature Conservancy recently acquired Chapman's Pond, the largest tract of tidal freshwater marsh on the Connecticut River (Nature Conservancy 1982).

CHAPTER 10. COMPARISON OF TIDAL FRESHWATER MARSHES AND SALT MARSHES

10.1 A GENERAL COMPARISON

In Chapter 1 (Figure 1) we show that estuaries consist of a gradient of conditions from tidal freshwater at the head of the estuary to near marine conditions at the mouth. Throughout this profile we have mentioned apparent differences between tidal freshwater wetlands and the Spartina-dominated salt marshes closer to the ocean. To facilitate this comparison, we have prepared a table of physical and biological characteristics of the two types of ecosystems (Table 24). This table is based upon earlier attempts to contrast the two wetland types (Odum 1978, Odum et al. 1978). In considering these characteristics, two points should be remembered. (1) The estuary is a gradient from freshwater to marine conditions. (2) Characteristics at any given location may fluctuate daily, seasonally, or from year to year.

10.2 PHYSICAL COMPARISONS

All of the physical characteristics presented in Table 24 are also discussed in Chapter 1. Essentially, there are two significant differences in the two types of ecosystems. First, the sediments in tidal freshwater are high in clay, silt, and organic matter, but generally low in peat (see exceptions in Section 1.6) and in total plant root biomass. This results directly in a higher susceptibility to erosion, low profile stream banks, and tidal creeks with low sinuosity (Garofalo 1980) compared to higher salinity estuarine marshes which generally have greater percentages of sand, peat, and plant root material. These differences in substrate can be traced to sediment sources and the types of plants growing in the two environments. Tidal freshwater sediments are derived primarily from upstream river sources (clays, silt, fine organic matter); in addition, much of the organic content probably comes from autochthonous plant production. The plants in tidal freshwater marshes generally have a relatively low root/shoot ratio (see Section 3.1) leading to less root and peat material in the sediments. Salt marsh sediments are derived from a variety of sources including some sand from downstream (marine) sources. In addition, the salt marsh plants tend to have a higher root/shoot ratio.

The second great difference in the physical characteristics of the two environments concerns water chemistry. Salt marshes are flooded by water containing significant quantities of seawater; water flooding tidal freshwater marshes is largely river water. As a result salt marsh water is not only saltier but differs considerably in its elemental makeup. For example, seawater has approximately three orders of magnitude more dissolved sulfur than freshwater. For this reason, the process of sulfur reduction is important in salt marshes under marine conditions but probably is of less significance in freshwaters. See Morris et al. (1978) for a discussion of the chemical differences in marine and freshwater and the zone of transition between the two.

10.3 BIOLOGICAL COMPARISONS

Characteristics of the vascular plant community are discussed at length in Chapter 2. The significant differences in diversity, zonation, seasonal succession, and root/shoot ratios are summarized in Table 24. Benthic algal production appears to be relatively low in tidal freshwater wetlands (less than 1% of total

Table 24. Hypothetical comparisons of ecosystem characteristics between tidal freshwater marshes and higher salinity, Spartina-dominated salt marshes (based on Odum 1978, Odum et al. 1978).

Characteristics	Tidal freshwater marsh	Salt marsh
Physical		
Location	Head of estuary (above oligohaline zone)	Mid and lower estuary
Salinity	Average below 0.5 ppt	Average above 8.0 ppt and below 35 ppt (approx.)
Hydrology	Riverine influence and tidal influence	Largely tidal influence
Sediments	Silt-clay, high organic content, low root and peat content	More sand, lower organic content, higher peat and root content
Sediment redox potential	Moderate-strongly reducing (redox pairs unkown)	Strongly reducing, (due to sulfur reduction)
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 senuosity	Moderate to high sinuosity
Dissolved oxygen (water column)	Very low (summer)	Low (summer)
Dissolved sulfur	Trace (1 ppm)	Very high (2500 ppm)
Biological		
Macrophytes	Freshwater species	Marine and estuarine species
Macrophyte diversity	High species diversity	Low species diversity
Macrophyte zonation	Present, but not always distinct	Pronounced
Seasonal sequence of dominant macrophytes	Pronounced	Absent or minor
Macrophyte root/shoot	Low (generally below 2.0)	High (generally above 5.0)

(continued)

Table 24. Continued.

Characteristics	Tidal freshwater marsh	Salt marsh
Biological		
Above-ground annual primary production	Comparable (?)	
Benthic algal production	Very low (less than 1% of Net community primary production)	Moderate (may be as High as 30% of net community primary production)
Phytoplankton	Comparable (?)	
Decomposition rate of intertidal vascular	Low marsh plants = extremely rapid, high marsh plants = moderate to slow	Moderate to slow for all plants
Anaerobic decomposition	Methanogenesis and fermentation probably predominate	Sulfur reduction predominates
Nutrient cycles	Pronounced spring uptake of NO, NO, PO large autumn release of reduced compounds	More even processing and release (conversion from oxidized to reduced forms throughout the year)
Sewage assimilative capacity	Low	Moderate
Primary consumers	Larval and adult insects, oligochaetes, amphipods	Adult insects, crustaceans, polychaetes, mollusks
Direct grazing	Variable (5-15%), higher on *Hibiscus*	Low (5%)
Detritus quality	High (low C/N ratio low crude fiber)	Low to moderate (higher C/N ratio, high crude fiber)
Invertebrates (other than insects)	Low species diversity, freshwater species	Moderate species diversity, estuarine and marine species
Insects	Both aquatic larval insects and terrestrial species	Mostly adult terrestrial species
Fishes	Freshwater and oligohaline species, and larvae, juveniles, and spawning adults of anadromous species	Marine and estuarine species

(continued)

Table 24. Concluded.

Characteristics	Tidal freshwater marsh	Salt marsh
Biological		
Reptiles and amphibians	High species diversity	Low species diversity
Waterfowl	High species diversity, high but spotty densities	Low to moderate species diversity, moderate densities
Furbearers	High species diversity, moderate densities	Low to moderate species diversity, moderate densities

net community primary production according to Whigham and Simpson 1976). The data of Gallagher and Daiber (1974), on the other hand, show that benthic algal production can contribute as much as 30% of the net community primary production in some salt marshes. The lower contribution from tidal freshwater may reflect the extensive shading from broad-leaved tidal freshwater plants. Phytoplankton production may be similar in the tidal creeks of the two ecosystems. Good comparative data are generally lacking, but Axelrad et al. (1976) found similar rates of primary production (5 to 15 mg C/m^3/hr in the two environments. Conversely, in the North River, Massachusetts, higher chlorophyll concentrations were found in tidal freshwater and oligohaline locations than downstream in the estuary proper (J. Hobbie and B. Peterson, Ecosystems Center, Woods Hole, Massachusetts; pers. comm.).

In Chapter 3 we discussed differences in decompsoition, decomposition rates, detritus, nutrient cycling, and consumers. Invertebrates are discussed in Chapter 4, fishes in Chapter 5, waterfowl in Chapter 6, amphibians and reptiles in Chapter 7, and furbearers in Chapter 8. Sewage assimilative capacity and fisheries are covered in Chapter 9. The significant differences in these aspects of the two wetland types are summarized in Table 24.

In addition to the differences discussed in Chapters 3 through 8 and those noted in Table 24, several additional points should be made. Unlike the vascular plant community, most components of the tidal freshwater marsh animal community are much less diverse than in salt marshes. For example, Diaz et al. (1978) found that the benthic macrofauna in the tidal freshwater portion of the James River was less diverse than further downstream in the high salinity zone. In the same river, Ellison and Nichols (1976) reported a lower diversity of benthic microfauna in tidal freshwater. Similarly, the fish community in the James River had its lowest diversity in the tidal freshwater section (Dias et al. 1978). In the case of macrofauna and fishes, the number of species increased downstream toward the estuary mouth and upstream in nontidal freshwater. We suspect that the same pattern also holds for zooplankton (personal observation).

Not all animal species, however, appear to follow this pattern of reduced species diversity in tidal freshwater. Mammals, waterfowl, and insects are probably more diverse in tidal freshwater marshes than in salt marshes, presumably because of the higher diversity and food value found in freshwater plant species.

10.4 COMPARISON WITH NONTIDAL FRESHWATER MARSHES

Few researchers have directly compared tidal and nontidal freshwater marsh ecosystems which lie in close proximity. There are intriguing questions associated with such a comparison since in one case tidal energy is present and in the other it is absent. One could hypothesize that the presence of tidal energy might encourage higher primary production in tidal freshwater marshes than in nontidal freshwater marshes (Odum 1971). Odum et al. (1983) compared the annual net production of giant cutgrass, *Zizaniopsis miliacea*, in the two environments separated by a dike and found 38% greater production in tidal freshwater. As with all comparisons, variability in factors other than tidal amplitude (e.g., substrate type, nutrient supply) creates difficulties. It seems, however, that carefully controlled comparisons of tidal freshwater and nontidal freshwater may reveal a great deal about the ecological importance of tidal energy.

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APPENDIX A

Plants of the Tidal Freshwater Marsh

Family and species list of characteristic plants occurring in tidal freshwater marshes of the Atlantic coastal region. Scientific nomenclature conforms with the National List of Scientific Plant Names (Soil Conservation Service 1982). Common names conform with Gray's Manual of Botany (Fernald 1971).

Osmundaceae	
Osmunda regalis	Royal Fern
Polypodiaceae	
Onoclea sensibilis	Sensitive Fern
Thelypteris thelypteroides	Marsh Fern
Salviniaceae	
Azolla caroliniana	Water Fern
Pinaceae	
Taxodium distichum	Bald Cypress
Typhaceae	
Typha latifolia	Common Cattail
Typha angustifolia	Narrow-leaved Cattail
Typha glauca	Blue Cattail
Typha domingensis	Southern Cattail
Sparganiaceae	
Sparganium eurycarpum	Great Burreed
Sparganium americanum	Branching Burreed
Potomogetonaceae	
Potamogeton spp.	Pondweeds
Zannichnellia palustris	Horned Pondweed
Najadaceae	
Najas spp.	Naiads
Alismataceae	
Alisma subcordatum	Mud-plantain
Sagittaria subulata	Dwarf Arrowhead
Sagittaria falcata	Bultongue
Sagittaria latifolia	Duck-potato
Hydrocharitaceae	
Elodea spp.	Waterweeds
Elodea nuttallii	Nuttall Waterweed
Vallisneria americana	Tapegrass
Limnobium spongia	Frogbit
Gramineae	
Phragmites australis	Common Reed
Elymus virginicus	Wild Rye Grass

Gramineae continued:	
Calamagrostis canadensis	Reed-Bentgrass
Cinna arundinacea	Wood-Reedgrass
Spartina cynosuroides	Big Cordgrass
Spartina alterniflora	Smooth Cordgrass
Spartina pectinata	Freshwater Cordgrass
Phalaris arundinacea	Reed-Canarygrass
Leersia virginica	Whitegrass
Leersia oryzoides	Rice Cutgrass
Zizaniopsis miliacea	Giant Cutgrass
Zizania aquatica	Wild Rice
Panicum virgatum	Switchgrass
Echinochloa crusgalli	Barnyard Grass
Echinochloa walteri	Walter's Millet
Arundo donax	Giant Reed
Cyperaceae	
Cyperus spp.	Umbrella-sedges
Cyperus strigosus	Strawcolor Umbrella-sedge
Cyperus esculentus	Yellow Nutgrass
Eleocharis obtusa	Blunt Spike-rush
Eleocharis palustris	Creeping Spike-rush
Eleocharis quadrangulata	Squarestem Spike-rush
Dichromena colorata	Star Rush
Fimbristylis autumnalis	Autumn Sedge
Scirpus americanus	Common Threesquare
Scirpus robustus	Stout Bulrush
Scirpus smithii	Smith's Bulrush
Scirpus validus	Soft-stem Bulrush
Scirpus cyperinus	Woolgrass
Scirpus fluviatilis	River Bulrush
Rhynchospora macrostachya	Horned Rush
Cladium jamaicense	Saw-grass
Carex spp.	Sedges
Carex lurida	Sallow Sedge
Carex crinita	Fringed Sedge
Carex vulpinoidea	Foxtail Sedge
Carex stricta	Erect Sedge
Carex alata	Broadwing Sedge
Carex squarrosa	Spreading Sedge
Araceae	
Peltandra virginica	Arrow-Arum
Orontium aquaticum	Goldenclub
Acorus calamus	Sweetflag
Lemnaceae	
Lemna spp.	Duckweeds
Commelinaceae	
Commelina virginica	Dayflower
Murdannia keisak	Asian Spiderwort

Pontederiaceae		
	Pontederia cordata	Pickerelweed
	Zosterella dubia	Waterstargrass
Juncaceae		
	Juncus spp.	Rushes
	Juncus acuminatus	Sharpfruit Rush
	Juncus bufonius	Toad Rush
	Juncus effusus	Soft Rush
Iridaceae		
	Iris versicolor	Blue Flag
	Iris virginica	Southern Blue Flag
	Iris pseudoaorus	Yellow Iris
Saururaceae		
	Saururus cernuus	Lizard's Tail
Salicaceae		
	Salix spp.	Willows
	Salix caroliniana	Swamp Willow
Myricaceae		
	Myrica cerifera	Wax-Myrtle
Betulaceae		
	Carpinus caroliniana	American Hornbeam
	Alnus serrulata	Tag Alder
Urticaceae		
	Pilea pumila	Clearweed
	Boehmeria cylindrica	False Nettle
Polygonaceae		
	Rumex verticillatus	Water Dock
	Polygonum virginianum	Jumpseed
	Polygonum densiflorum	Southern Smartweed
	Polygonum pensylvanicum	Pinkweed
	Polygonum amphibium	Swamp Smartweed
	Polygonum hydropiper	Common Smartweed
	Polygonum persicaria	Lady's Thumb
	Polygonum punctatum	Water Smartweed
	Polygonum hydropiperoides	Mild Water-pepper
	Polygonum sagittatum	Sagittate Tearthumb
	Polygonum arifolium	Halberd-leaved Tearthumb
Amaranthaceae		
	Amaranthus cannabinus	Water-Hemp
	Alternanthera philoxeroides	Alligatorweed

Ceratophyllaceae	
Ceratophyllum demersum	Hornwort
Nymphaeaceae	
Nuphar luteum macrophyllum	Spatterdock
Nuphar luteum variegatum	Bullhead Lily
Nymphaea odorata	White Water Lily
Brasenia schreberi	Water-Shield
Ranunculaceae	
Clematis crispa	Blue Jasmine
Rosaceae	
Rosa palustris	Swamp Rose
Rosa multiflora	Multiflora Rose
Leguminosae	
Gleditisa aquatica	Water Locust
Cassia fasciculata	Partridge Pea
Amorpha fruticosa	Indigo-Bush
Apios americana	Groundnut
Strophostyles umbellata	Pink Wild Bean
Aeschynomene virginica	Sensitive-joint Vetch
Aceraceae	
Acer rubrum	Red Maple
Balsaminaceae	
Impatiens capensis	Jewelweed
Malvaceae	
Kosteletzkya virginica	Seashore-Mallow
Hibiscus moscheutos palustris	Swamp Rose
Hibiscus moscheutos	Mallow Rose
Hibiscus laevis (militaris)	Halberd-leaved Rose
Guttiferae	
Hypericum mutilum	St. John's Wort
Elatinaceae	
Elatine americana	Waterwort
Lythraceae	
Decodon verticillatus	Swamp Loosetsrife
Lythrum lineare	Linear Loosestrfe
Lythrum salicaria	Spiked Loosestrife
Cornaceae	
Nyssa aquatica	Cotton Gum
Nyssa sylvatica	Black Gum

Onagraceae	
<u>Jussiaea repens</u>	Creeping Primrose-Willow
<u>Ludwigia palustris</u>	Water-purslane
Halorrhagidaceae	
<u>Myriophyllum spp.</u>	Water-Milfoils
Umbelliferae	
<u>Eryngium aquaticum</u>	Marsh Eryngo
<u>Cicuta maculata</u>	Water Hemlock
<u>Sium suave</u>	Water Parsnip
<u>Ptilimnium capillaceum</u>	Mock Bishop's Weed
Clethraceae	
<u>Clethra alnifolia</u>	Sweet Pepperbush
Oleaceae	
<u>Fraxinus pennsylvanica</u>	Red Ash
Asclepiadaceae	
<u>Asclepias incarnata</u>	Swamp Milkweed
Convolvulaceae	
<u>Convolvulus arvensis</u>	Field Bindweed
<u>Calystegia sepium</u>	Hedge Bindweed
<u>Cuscuta compacta</u>	Swamp Dodder
<u>Ipomoea coccinea</u>	Morning Glory
Labiataceae	
<u>Lycopus virginicus</u>	Water-Horehound
<u>Lycopus europaeus</u>	European Horehound
Bignoniaceae	
<u>Campsis radicans</u>	Trumpet Flower
Scrophulariaceae	
<u>Gratiola virginiana</u>	Hedge-hyssop
<u>Linderina dubia</u>	False Pimpernel
Lentibulariaceae	
<u>Utricularia spp.</u>	Bladderworts
Rubiaceae	
<u>Galium tinctorium</u>	Stiff Bedstraw
<u>Cephalanthus occidentalis</u>	Buttonbush
Caprifoliaceae	
<u>Viburnum recognitum</u>	Arrowwood
<u>Viburnum dentatum</u>	Southern Arrowwood
Campanulaceae	
<u>Lobelia cardinalis</u>	Cardinal Flower

Compositae	
Vernonia noveboracensis	Ironweed
Eupatorium perfoliatum	Boneset
Eupatoriadelphus fistulosus	Joe-Pye-Weed
Mikania scandens	Climbing Hempweed
Aster spp	Asters
Aster subulatus	Annual Marsh Aster
Baccharis halimifolia	Groundsel Tree
Pluchea purpurascens	Marsh Fleabane
Iva frutescens	Marsh Elder
Ambrosia trifida	Giant Ragweed
Bidens spp.	Burmarigolds
Bidens laevis	Smooth Burmarigold
Bidens connata	Swamp Beggarticks
Bidens comosa	Leafybract Beggarticks
Bidens frondosa	Black Beggarticks
Bidens coronata	Tickseed Sunflower
Cosmos bipinnatus	Spanish Needles
Helenium autumnale	Sneezeweed
Senecio spp.	Ragworts

APPENDIX B
FISH OF TIDAL FRESHWATERS
Introduction

The geographic region on which we have concentrated in our account is the Hudson River, NY through southern Georgia. We make occasional references to areas north or south of these boundaries where information is available on given species, even though surveys of the entire community were unavailable. The species included in this tabulation are limited to documented observations from tidal freshwaters. The sources of information include published accounts, master's theses, government reports, and personal communication from fisheries workers with various state agencies. These sources are numbered in the Appendix with a key given at the end. Nomenclature follows Robins et al. (1980). We have neither included hybrids nor subspecies in this list.

Relative abundance refers to the abundance in tidal freshwaters only. This assessment does not apply over the whole geographic range, nor over all habitats occupied by the species.

Explanation of categories and abbreviations

<u>Geographic range</u>

Compass directions expressed in lower case (n,s,e,w). State and province abbreviations are capitalized and are standard postal ones given in Carlander (1969) and Lee et al. (1980). Unless otherwise noted Gulf coast refers to the Gulf of Mexico.

US STATES

Alabama	AL	Ohio	OH
California	CA	Oklahoma	OK
Connecticut	CT	Pennsylvania	PA
Delaware	DE	South Carolina	SC
Florida	FL	Texas	TX
Georgia	GA	Virginia	VA
Illinois	IL	CANADA	
Louisiana	LA	British Colombia	BC
Maine	ME	New Brunswick	NK
Maryland	MD	Newfoundland	NF
Massachusetts	MA	Nova Scotia	NS
Mississippi	MS	Labrador	LB
Missouri	MO	Ontario	ON
New Hampshire	NH	OTHER	
New Jersey	NJ	Great Lakes	GL
New York	NY	Mexico	MEX
North Carolina	NC	Atlantic	ATL
		Pacific	PAC

<u>Comments</u>

Information is provided on affinity group, range of habitats, preferred habitat, seasonality of use, differences in juvenile and adult use of habitat.

<u>Relative abundance</u>

R - rare. Seldom seen, likely a stray from an adjacent habitat.
END - endangered. Threatened with extinction.
U - uncommon. Infrequently encountered.
O - occasional. Seen frequently enough to be considered a regular member of the community.
C - common. Encountered on nearly every sampling trip during the appropriate season.
LC - locally common. Present in appreciable numbers, but restricted to particular habitats or localized areas.
A - abundant. Conspicuous by its presence. Encountered in appreciable numbers on every sampling trip during the appropriate season.
UNK - unknown. Insufficient data to assess abundance in tidal freshwaters.

<u>Salinity range</u>

fw = < 0.5 ppt.
brackish = > 0.5 ppt.

<u>Food habits</u>

Food items listed in decreasing order of frequency of occurrence.

APPENDIX B. Fishes of tidal freshwaters of the mid and south Atlantic coast.

Name	Geographic range	Salinity range ppt	Relative abundance	Food habits	Comments	Source
Petromyzontidae - lampreys						
Lampetra aepyptera least brook lamprey	upper OH drainage, ATL coast-PA to NC	fw - 1.5	U	filter-feeders; adults non-parasitic	Restricted to small streams. Burrows in sediment.	33,35
Lampetra appendix American brook lamprey	upper OH drainage, ATL coast-NH to Roanoke River, NC	fw	R	filter-feeders; adults non-parasitic	As previous species.	33,35
Petromyzon marinus sea lamprey	ATL coast-LB to FL, also GL	fw - 35	C	Young to four years nonparasitic, feeding on minute organisms. Adults parasitic, feeding on the blood of other fishes.	Anadromous; ascends fw streams in spring to spawn. Young stay 3-4 years in freshwaters.	33,35
Acipenseridae - sturgeons						
Acipenser brevirostrum shortnose sturgeon	NK to St. John's River, FL	fw - 35	R, END	A bottom feeder. Young: algae, protozoa, crustaceans, small insects Adults: benthic organisms, small plants	Anadromous; small populations exist in Canada, Maine, the Hudson, Delaware & Altamaha Rivers. Extirpated or threatened throughout much of its range.	5,6,46, 52
Acipenser oxyrhynchus Atlantic sturgeon	LB to ne FL	fw - 35	R	A bottom feeder. Young in fw; aquatic insects, amphipods, oligochaetes, *Pisidium* clams. In marine environments; gastropods, shrimp, amphipods, other benthic invertebrates, small fish (launce).	Anadromous; young remain in fw a year, in estuary up to 4 years.	6,33,46
Lepisosteidae - gars						
Lepisosteus osseus longnose gar	much of e half of US	fw - 33	C	Young to 50 mm; small crustaceans, insect larvae Adults; almost entirely fish taken in the water column.	Of fw affinity, but very tolerant of higher salinities.	6,33
Lepisosteus platyrhincus Florida gar	FL & GA	fw	LC	mostly fish, also crustaceans, insects	Recorded from Altamaha & Savannah Rivers, GA	26,27

Name	Geographic range	Salinity range ppt	Relative abundance	Food habits	Comments	Source
Amiidae - bowfins						
Amia calva bowfin	MS, OH Gulf & GL drainages, ATL coast-CT to FL	fw	LC	Nocturnal feeders on fish, crayfish, insects, molluscs, earthworms, frogs, leeches.	Inhabitant of sluggish, clear often vegetated low-land waters. More common in tidal fw's in s. portion of its range.	26,33, 46,50, 51
Elopidae - tarpons						
Megalops atlanticus tarpon	ATL coast- SC to Brazil	fw - 35	R	Juv; fish, copepods, ostracods, shrimp, insects Adults; almost exclusively fish.	Spawns offshore. Young inhabit headwaters of brackish & fw streams. Adults marine. Recorded from Altamaha, GA, St. John's, FL	26,27, 33
Anguillidae - freshwater eels						
Anguilla rostrata American eel	ATL coast-Gulf of St. Lawrence to West Indies	fw - 35	A	In fw: Young; benthic macroinvertebrates (insect nymphs & larvae, oligochaetes, cladocerans) Older fish; crayfish, tadpoles, fish, fewer invertebrates. In brackish water: soft blue crabs, bivalves, polychaetes.	Largely nocturnal feeders & highly opportunistic. Burrow in mud in winter. Have been captured on fw tidal marsh surface; catadromous.	9,64,67
Ophichthidae - snake eels						
Myrophis punctatus speckled worm eel	ATL coast-NC to Brazil	18 - 35	R	In brackish water; polychaete worms, sand crabs	A stray from the lower estuary. Recorded only infrequently from tidal fw's.	3,11,57
Clupeidae - herrings						
Alosa aestivalis blueback herring	ATL coast- NS to St. John's River, FL	fw - 35	C-A	Juv; feed at surface on cladocerans (primarily bosmids), copepods, crustacean eggs, chironomid larvae (as drift)	Anadromous; spawn in fast flowing water over hard substrate. Juveniles use tidal fw & low salinity nursery areas until autumn.	15,16, 33,37

Name	Geographic range	Salinity range ppt	Relative abundance	Food habits	Comments	Source
Alosa mediocris hickory shad	ATL coast- ME to FL	fw - 35	O	chiefly small fish	Anadromous; least common species of this genus. Peak abundance Chesapeake Bay & NC. Juveniles spend little time in tidal fw nursery.	1,22,65
Alosa pseudoharengus alewife	GL, NF to SC	fw - 35	C	Juv in tidal fw; cladocerans, copepods, crustacean eggs, insects (various dipterans)	Anadromous; spawn in slower moving water than blueback herring. Juveniles use fw tidal & low salinity nursery areas until autumn.	15,37,65
Alosa sapidissima American shad	Gulf of St. Lawrence to FL, peak abundance CT to NC; introduced on US west coast	fw - 35	C-A	Juv; feed somewhat opportunistically both at the surface & beneath the surface on cladocerans (primarily daphnids), chironomid larvae (as drift), water boatmen, terrestrial insects (flies, gnats, ants), fish larvae	Anadromous; spawn primarily in main channels over sand shoals in areas of perceptible currents. Juv. use fw tidal & low salinity nursery areas until mid to late autumn.	15,16,65
Brevoortia tyrannus Atlantic menhaden	NS to FL	fw - 33	C-A	filter-feeders:small crustaceans, especially copepods, annelid worms, rotifers, unicellular plants	Spawn at sea. Juveniles are estuarine dependent.	24,35,46
Dorosoma cepedianum gizzard shad	MA to MEX, MS basin & GL	fw - 29	C-A	Juv; protozoa, copepods, ostracods Adults; microscopic plants, phytoplankton, algae, detritus	Spawns in fw. Young inhabit fw & low brackish nursery areas. Prefers quiet waters of lakes large rivers, estuaries. Young are important forage for several species of game fish.	45,46
Dorosoma petenense threadfin shad	native to lower MS & Gulf coast drainages; widely introduced elsewhere	fw - 17	O-C	principally plankton, also dipteran larvae (Chaoborus, chironomids)	Spawns in fw, juveniles enter estuarine waters.	6,35,46
Engraulidae - anchovies						
Anchoa mitchilli bay anchovy	MA to MEX	fw - 35	C-A	Feeds pelagically on zooplankton; copepods, insect larvae, mysids, shrimps, larval fishes, gastropod larvae, crab zoeae. Feeds on benthic organisms when zooplankton are scarce.	Important forage species for larger species of commercial importance. Most abundant at salinities less than 20 ppt.	33,46

Name	Geographic range	Salinity range ppt	Relative abundance	Food habits	Comments	Source
Salmonidae - trouts						
Salmo salar Atlantic salmon	Hudson Strait to CT River; Arctic Circle to Portugal, s Greenland	fw - 35	UNK	Juv; mayflies, chironomids, caddisflies, stoneflies, cladocerans, dipterans, molluscs, fish fry (suckers)	Anadromous; spawn in non-tidal fw in Oct-Dec. Fry inhabit riffles, spending 2-3 years in nontidal fw. Adults & young migrate through tidal fw's. Major commercial & sport importance.	55
Osmeridae - smelts						
Osmerus mordax rainbow smelt	GL, LB to NJ	fw - 35	U	Young: copepods, cladocerans, Adults in fw lake: insect larvae, copepods, amphipods, small molluscs, fish (shiners)	Anadromous; spawn in non-tidal fw at night. Juveniles move rapidly to sea.	6,30,32
Umbridae - mudminnows						
Umbra pygmaea eastern mudminnow	ATL coast-Long Island to FL	fw - 4	U	In fw stream: copepods, caddisfly larvae	Inhabits small, sluggish muddy stream & weed beds. Burrows in soft, silty substrates.	6,46
Esocidae - pikes						
Esox americanus redfin pickerel	ATL coast-s ME to FL. Also Lake Champlain drainage	fw - 8.7	O	Fry; plankton Juv;cladocerans, amphipods, immature insects Adults; fish, crayfish, dragonfly nymphs	Inhabits sluggish streams, weed beds, swamps.	6,46,50
Esox lucius northern pike	n Europe, Asia & N Am s to e NY, also n MS basin	fw - 1.6	UNK	A diurnal feeder. fry; microcrustaceans, fish larvae <40 mm;insects, small crustaceans >65mm; primarily fish, also salamanders, crayfish, mayflies	Inhabits weedy lakes, ponds, rivers. Breeds in Chapman's Pond, a tidal lake on the Connecticut River. Important game species.	6,33
Esox niger chain pickerel	ATL coast - NS to FL, MS drainage	fw - 22	O-C	Young; invertebrates including amphipods, chironomids, daphnids Adults; fish (minnows, sunfish), frogs, crayfish	Adults feed nocturally in shallows, rest in deeper water by day.	6,19,44

Name	Geographic range	Salinity range ppt	Relative abundance	Food habits	Comments	Source
Cyprinidae - minnows, carps						
Carassius auratus goldfish	introduced from Asia; present throughout US	fw - 17	LC	Omnivorous with preference for phytoplankton. Young feed more on zooplankton & insect larvae.	Primarily inhabits still often oxygen deficient waters with thick vegetation.	33,46
Cyprinus carpio common carp	introduced from Asia; widely distributed in ATL coast drainages	fw - 17.6	C	An omnivorous bottom-feeder taking vegetation, insects, worms.	Inhabits streams, rivers, ponds, impoundments; both clear & turbid waters. Often considered a pest due to habit of stirring up bottom sediments during feeding.	33,46
Hybognathus regius eastern silvery minnow	St. Lawrence & ON drainages; ATL coast s to Altahama, GA	fw - 14	O-C	Feeds in large schools near bottom on diatoms, desmids, filamentous algae.	More abundant in channel than in coves.	46,50
Nocomis raneyi bull chub	James, Chowan, Roanoke, Neuse & Tar Rivers, VA & NC	fw	R	benthic insects, crayfish, snails, fish, filamentous algae	New species described in 1971. More common above fall line.	33,64
Notemigonus crysoleucas golden shiner	NS to TX	fw - 5.1	LC	Omnivorous; algae, macrophytes, amphipods, molluscs, detritus, insects	Prefers quiet vegetated water with access to extensive vegetated shallows.	19,33,46
Notropis amoenus comely shiner	NY s through Cape Fear River, NC	fw	R		Typically found in nontidal freshwaters in channels. A schooling mid-water form.	33,50
Notropis analostanus satinfin shiner	Hudson River & Lake ON drainages s to Peedee River, SC	fw - 2	LC	In fw stream; insect larvae (mayflies, caddisflies, stoneflies)	Preferentially inhabits weedless streams, straying into tidal fw's.	19,33,46
Notropis bifrenatus bridle shiner	MA to Neuse River, NC	fw - 11.8	U	small invertebrates, algae, macrophytes	Inhabits sluggish streams over areas of mud, silt, detritus in slackwater areas with moderate to abundant vegetation.	33,46

Name	Geographic range	Salinity range ppt	Relative abundance	Food habits	Comments	Source
Notropis chalybaeus ironcolor shiner	ATL & Gulf coast NY to TX; MS basin n to Iowa	fw	R-U	Feeds on surface or in midwater on small crustaceans, aquatic & terrestrial insects.	Recorded from tidal fw's only in s. portion of its range.	6,26,33, 65
Notropis cornutus common shiner	ATL coast ME to VA; upper MS & GL drainages	fw	U	Omnivorous; algae, rotifers, small crustaceans, insects	More common in moderate to swift weedless streams.	33,46
Notropis emiliae pugnose minnow	Edisto River, SC to Altahama River, GA; Gulf coast & MS drainages	fw	U	chironomid larvae, minute crustaceans	Usually in clear, sluggish, often weedy waters.	26,33,59
Notropis hudsonius spottail shiner	CT to Altamaha, GA; also St. Lawrence & GL to nw Canada	fw - 10.7	LA	small molluscs (*Corbicula manilensis*), crustacea (cladocerans, ostracods, copepods), plant seeds (*Saggataria* sp., *Panicum*), insects (chironomid larvae, ceratopogonid larvae), fish eggs	Inhabits mainstream & sluggish weedy necks, creeks, swamps.	33,46,64
Notropis petersoni coastal shiner	s NC into AL, c & w FL	fw - 4.5	U	insects, crustaceans	Inhabits small & large streams & lakes with sandy substrate.	3,26,33
Rhinichthys atratulus blacknose dace	NS to GA; also upper MS drainages	fw	R-U	In stream; 64% of diet microscopic plants & vegetative matter, remainder insects	More likely to enter tidal fw's in n portion of its range.	19,33,58 65
Semotilus atromaculatus creek chub	most of e N AM	fw	O-C	Omnivorous sight feeder; insects, cladocerans, algae, higher plant tissues.	Absent from coastal plain in SE states.	33,35
Semotilus corporalis fallfish	NK, Canada to James River, VA. James Bay, Lake ON & St. Lawrence drainages	fw	R-U	Probably aquatic & terrestrial insects, crustaceans, fish	More abundant in nontidal fw's.	33,35,46, 50,55

Name	Geographic range	Salinity range ppt	Relative abundance	Food habits	Comments	Source
Catostomidae - suckers						
Carpiodes cyprinus quillback	St. Lawrence River; DE drainage to Altamaha, GA; MS basin & Gulf coast	fw - 10.7	R	A benthic feeder on insect larvae & other organisms found in bottom sediments.	Inhabits turbid rivers and clear lakes.	33,35,46
Catostomus commersoni white sucker	Arctic Circle s to New Mexico & GA	fw - brackish	LC	Insects, molluscs, worms, copepods, cladocerans, ostracods, microscopic plants	Inhabits larger streams, ascends small creeks in spring to spawn.	19,33
Erimyzon oblongus creek chubsucker	ME to Altamaha, GA; w Gulf coast & MS basin	fw	C	Largely crustaceans (cladocerans, ostracods, copepods), also chironomid larvae, nematodes, molluscs, diatoms	Inhabits quiet waters with thick growths of submergent vegetation.	33,46,64
Erimyzon sucetta lake chubsucker	s VA to Lake Okeechobee, FL; Gulf & MS drainages	fw	U	Young; copepods, cladocerans, chironomids	Occupies ponds, oxbows, sloughs, impoundments. Prefers clear water & aquatic vegetation.	6,26,33, 41
Hypentelium nigricans northern hog sucker	MS, OH & GL basins; upper ATL coast drainages s to n GA	fw - brackish	R-U	bottom fauna	More abundant above fall line.	6,32,33, 46,54
Minytrema melanops spotted sucker	Cape Fear River to s GA; MS & Gulf drainages	fw - brackish	LC	A benthic feeder on insect larvae (particularly chironomids), crustaceans (cladocerans, copepods), oligochaete worms.	Inhabits larger streams, oxbows, impoundments. Intolerant of turbid waters.	6,26,27, 33,68
Moxostoma macrolepidotum shorthead redhorse	Hudson River, NY to Santee River, SC; MS & St. Lawrence basins, GL, Hudson Bay drainage	fw - 5	O-C	molluscs, microcrustaceans, immature insects	Inhabits large rivers & small tributaries. Readily enters brackish waters.	33,35,50, 54
Ictaluridae - catfishes						
Ictalurus brunneus snail bullhead	NC to n FL	fw	LC	Omnivorous benthic feeder; molluscs, insect larvae, small fish, filamentous algae.	More abundant in nontidal fw's. Recorded from Altahama, GA	26,33

Name	Geographic range	Salinity range ppt	Relative abundance	Food habits	Comments	Source
<u>Ictalurus catus</u> white catfish	NY to FL; widely introduced	fw - 14.5	C-A	4-57 cm; an opportunistic feeder; amphipods, isopods, decapods, copepods, cladocerans, mysids, cumaceans, chironomid larvae, polychaete worms, small clams, larval & adult insects, fish	Minor sport importance. Most tributaries, mainstream.	23,33,46, 63
<u>Ictalurus furcatus</u> blue catfish	native to MS basin s to MEX	fw - ?	R	Young; zooplankton Adults; insect larvae, crayfish, fish, detritus	Introduced into James & Rappahannock Rivers, Va. Characteristic of deep rivers & swift currents.	6,33,46
<u>Ictalurus melas</u> black bullhead	native to MS drainage & & n MEX	fw	R	Young; isopods, small crustaceans, insect larvae Adults; insects, small crustaceans, plant debris, fish, frogs	Recorded from a tributary of Potomac River Va. & Winyah Bay drainage, SC. Inhabits ponds, pools, swamps.	6,33,49, 51
<u>Ictalurus natalis</u> yellow bullhead	native to e & c US	fw	O-C	In stream; decapod crustaceans (palaemonid shrimp, crayfish), mayfly nymphs, annelid worms, beetles	Inhabits swamps, ditches, sluggish streams.	19,33,46, 51
<u>Ictalurus nebulosus</u> brown bullhead	native to e half of US & s Canada	fw - 8	A	insect larvae (dipterans, mayflies, caddisflies, dragonflies), molluscs, algae, fish (spottail shiner, elvers), polychaete worms, zooplankton	Inhabits sluggish oxbows, backwaters, impoundments. Minor sport importance.	33,39,46
<u>Ictalurus platycephalus</u> flat bullhead	NC to s GA	fw	LC	Juv; insects Adults; fish, insects, annelids, molluscs, bryozoans	Juveniles inhabit small clear streams. Adults inhabit slow moving waters of large rivers.	26,33,51
<u>Ictalurus punctatus</u> channel catfish	native to Gulf & MS drainages; introduced elsewhere	fw - 15.1	A	insect larvae (chironomids, dipterans), terrestrial insects, spiders, crustaceans (cladocerans, harpacticoid copepods, ostracods), plant material (berries, grasses, <u>Sagittaria</u> seeds), molluscs, fish & fish eggs	Inhabits mainstream. Rests in deep water by day, moves to shallows at night to feed.	46,64
<u>Noturus gyrinus</u> tadpole madtom	ATL, Gulf & MS drainages	fw	LC	In lake; cladocerans, ostracods, isopods, chironomids & detritus	Inhabits quiet waters with extensive vegetation. Best considered a stray in tidal fw's, except in Altahama where it is relatively common.	6,11,26, 33,35,46

Name	Geographic range	Salinity range ppt	Relative abundance	Food habits	Comments	Source
<u>Noturus</u> <u>insignis</u> margined madtom	NY to GA	fw	O	In stream; insect larvae (dipterans, stoneflies), fish	More abundant above fall line.	19,33,46
<u>Noturus</u> <u>leptacanthus</u> speckled madtom	SC to LA	fw	R		Occupies areas of moderate current.	33
<u>Pylodictus</u> <u>olivaris</u> flathead catfish	native to MS basin & into MEX; sparingly introduced	fw	R	100 mm; insect larvae (mayfly & caddisfly nymphs) 100-200 mm; insect larvae, fish, crayfish	Inhabits large rivers. Recorded from Winyah Bay drainage, SC.	6,33,50
Aphredoderidae - pirate perches						
<u>Aphredoderus</u> <u>sayanus</u> pirate perch	NY to TX; Gulf coast & MS basin	fw	LC	an opportunistic feeder; Juv; mostly crustaceans (ostracods, amphipods, cladocerans) Adults; mostly insect larvae (dragonflies, damselflies, mayflies, dipterans, hemipterans)	Inhabits quiet ponds, oxbows, swamps, sluggish lowland streams. Usually associated with dense vegetation. More common in tidal fw's in the SE.	11,20,26, 33,51,65
Gadidae - codfishes						
<u>Microgadus</u> <u>tomcod</u> Atlantic tomcod	Gulf of St. Lawrence to VA	fw - 31.4	UNK	shrimp, amphipods, worms, snails, immature fish	Anadromous; spawns in fw in winter. Larvae move to low salinity waters during first year. Does not spawn in Chesapeake system. Minor sport importance.	18,32,46 55
Belonidae - needlefishes						
<u>Strongylura</u> <u>marina</u> Atlantic needlefish	ME to Brazil	fw - 35	LC	In low brackish estuary; small fishes, insects, shrimp, small amounts of vascular plant material & algae	A marine form which readily enters fw. Best considered a summer transient. May breed in tidal fw's in Potomac, Va.	13,33,35, 36,46
Cyprinidontidae - killifishes						
<u>Cyprinodon</u> <u>variegatus</u> sheepshead minnow	ME to MEX, also Bahamas	fw- 32.8	R	In higher salinities; detritus, filamentous algae, nematodes, small crustaceans	More common in higher salinity areas. Inhabits shallows. Winters in channels or low salinity ponds buried in mud.	33,35,40, 46,47
<u>Fundulus</u> <u>confluentus</u> marsh killifish	s VA to TX	fw - 24.4	U	larval & adult mosquitoes, shrimp, copepods, annelids, plant material	Inhabits bayous, mangrove swamps, tidal streams, fw rivers and streams.	11,33

Name	Geographic range	Salinity range ppt	Relative abundance	Food habits	Comments	Source
<u>Fundulus diaphanus</u> banded killifish	NF to SC	fw - 20	LC	small crustaceans, insects, molluscs, annelid worms, detritus	More likely to occur in fw than most others of genus. Common in bays, rivers, coves in low salinity areas, extending into freshwater.	33,36,46
<u>Fundulus heteroclitus</u> mummichog	s NF to ne FL	fw - 32	C	In tidal fw; crustaceans (ostracods, cyclopoid copepods), insects (dipterans, homopterans), fish eggs, grass seeds (<u>Panicum</u> sp.), gastropods, spiders	Inhabits muddy marshes, grassflats, channels, pools in marsh interior in summer. May burrow in silt in winter.	11,26,33, 40,46,64
<u>Fundulus lineolatus</u> lined topminow	s VA to Dade Co., FL	fw	R		Found in clear streams, backwaters, ponds. Recorded from Altahama, GA	26,33
<u>Fundulus majalis</u> striped killifish	NH to ne FL	fw - 32	R	In brackish waters; small crustaceans, detritus, polychaete worms, insects, small bivalves, eggs, small crabs	Inhabits tidal creeks, sandy flats, grass beds. More common in lower estuary.	35,48,65
<u>Lucania goodei</u> bluefin killifish	SC to se AL	fw - 10.3	U	epiphytes, vascular plants	In heavily vegetated ponds & streams in areas of little or no current. Tolerates very low dissolved oxygen content.	10,33
<u>Lucania parva</u> rainwater killifish	Cape Cod to MEX	fw - 31.2	U	copepods, mosquito larvae	Inhabits weed beds, muddy coves. More common at higher salinities.	33,35
Poeciliidae - livebearers						
<u>Gambusia affinis</u> mosquitofish	NJ to FL; s MS basin	fw - 34	LC-A	Feeds primarily near surface. In fw stream; insects (hemipterans, dipterans) In brackish waters; amphipods, chironomid larvae, mites, copepods, snails, ants, adult insects, polychaete worms, ostracods, mosquito pupae, algae	Inhabits tidal pools, coves & backwaters. Readily follows flood tide onto marsh surface. May remain in marsh pools during low tide.	11,19,33, 42,46,47, 50
<u>Heterandria formosa</u> least killifish	Cape Fear River, NC to LA	fw - 30	R-U	In brackish waters; insect larvae, small crustaceans, filamentous algae, diatoms	Inhabits weedy pond and stream margins.	11,33,47

Name	Geographic range	Salinity range ppt	Relative abundance	Food habits	Comments	Source
Poecilia latipinna sailfin molly	SC to MEX	fw - 34	U	algae, vascular plants, detritus, mosquito larvae	Recorded from low salinity creeks in GA	11,33
Atherinidae - silversides						
Labidesthes sicculus brook silverside	SC to s FL; GL, MS & Gulf drainages; widely introduced	fw	R	A specialized feeder near surface on cladocerans, terrestrial insects, *Chaoborus* larvae	Inhabits clear vegetated and unvegetated warm waters.	26,33
Membras martinica rough silverside	NY to MEX	3 - 24	U	In brackish waters; zooplankton crustaceans, juvenile and larval fishes, insects, detritus, small snails	An estuarine species. Young occasionally enter low salinity reaches of estuary.	46,48,64, 65
Menidia beryllina tidewater silverside	MA to Mex	fw - 31	C	copepods, mysids, isopods, amphipods, insects	Estuarine resident; readily enters fw. May spawn in tidal fw. Inhabits tidal creeks & grassflats in summer, channels in winter.	46,48,50, 58
Menidia menidia Atlantic silverside	NF to s FL	fw - 31	U	crustaceans, annelid worms, molluscs, fish eggs, plants, insects	Collected well above brackish water in James, Rappahannock, Pamunkey rivers in VA, but more common in lower estuary.	33,40,46, 50
Gasterosteidae - sticklebacks						
Apeltes quadracus fourspine stickleback	Gulf of St. Lawrence to to Trent River, NC	fw - 26	U	small crustaceans, mainly amphipods. In fw; chironomid & mayfly larvae, cladocerans	Estuarine resident. Occupies shallows in summer, channel & channel edges in winter.	32,33,40, 46
Gasterosteus aculeatus threespine stickleback	n Europe & N AM; Hudson Bay to VA; also PAC coast of N AM	fw - 35	LC	An opportunistic feeder; aquatic & terrestrial insects, worms, fish eggs & fry, algae	Anadromous; in Chesapeake Bay area inhabits small tributaries during breeding season, rare or absent rest of year.	6,33,46, 55

Name	Geographic range	Salinity range ppt	Relative abundance	Food habits	Comments	Source
Centropomidae - snooks						
Centropomus undecimalis snook	FL to Brazil	fw - 35	UNK	Juv. in brackish waters; caridean shrimp, small killifishes, gobies, mojarras	Young inhabit oligohaline & tidal freshwater nursery areas. Strays north to Cape Fear River during warm periods. Very sensitive to low temperatures.	33,34,47
Percichthyidae - temperate basses						
Morone americana white perch	NS to SC	fw - 25	A	Juv; copepods, cladocerans, rotifers, amphipods, insect larvae (ceratopogonids & dipterans), small molluscs, mysids Adults; larger crustaceans (*Crangon septemspinosa*, *Paleomonetes pugio*, *Rithropanopeus harrisii*), small fish (eels, spottail shiners, *Fundulus* spp.)	Semianadromous; juveniles inhabit shallows, moving to deeper water in winter. Minor sport & commercial importance. Peak abundance Hudson River to Chesapeake Bay.	21,33,35, 46,49,58, 64
Morone saxatilis striped bass	St. Lawrence to St. John's River, FL, Gulf of MEX; introduced into Oregon, CA	fw - 35	C-A	Postlarvae; zooplankton Juv. 25-100mm; flexible nonselective feeders on insects (dipteran larvae & pupae, mayfly larvae), amphipods, *Palaemonetes* shrimp, other decapods, mysids, fish & fish larvae (*Gobiosoma bosci*, *Lepomis gibbosus*, *Notropis hudsonius*, *Menidia* spp.), polychaetes Adults in tidal fw; 84% of diet clupied fish (*Brevoortia tyrannus*, *Alosa aestivalis*, *A. pseudoharengus*, *Dorosoma cepedianum*), 4% spiny-rayed fish, 3% invertebrates (amphipods, mayfly & dipteran larvae, blue crabs, palaemonid shrimp)	Anadromous; peak spawning in tidal freshwaters. Adults move downstream after spawning, juveniles move downstream as they grow. Inhabit deeper water by day, move into shallows at night to feed. Overwinter in deeper channels. Major sport & commercial importance.	2,4,35, 38,64

Name	Geographic range	Salinity range ppt	Relative abundance	Food habits	Comments	Source
Centrarchidae - sunfishes						
Acantharchus pomotis mud sunfish	coastal plain se NY to n FL	fw	R		Inhabits sluggish. heavily vegetated swamplike waters. Very secretive.	29,33,64
Ambloplites rupestris rock bass	native to MS basin; introduced into ATL coast drainages	fw	R	Young; copepods, insects, crustaceans, chironomids, amphipods Adults; fish, crayfish. molluscs, worms	More abundant above fall line. Best considered a stray into tidal reaches.	7,32,33
Centrarchus macropterus flier	VA to FL; MS basin n to s IL	fw - 7	R	cladocerans, insects (chironomid larvae, water boatmen)	Inhabits sluggish lowland areas with clear. heavily vegetated waters. May be more common in wooded swamps than in marshes.	7,11,29, 26,33,46, 51
Elassoma evergladei Everglades pygmy sunfish	Cape Fear River, NC to s FL; Gulf coast to Mobile Bay. AL	fw	R	copepods, cladocerans	Prefers quiet vegetated waters below the fall line.	11,33
Elassoma zonatum banded pygmy sunfish	NC to c FL; Gulf drainages MS basin n to IL	fw - 2.17	U	small crustaceans. chironomid pupae	Inhabits swamps, weedy ponds. sluggish streams below fall line.	7,26,29, 33
Enneacanthus chaetodon blackbanded sunfish	coastal plain NJ to c FL; also w FL	fw	U	aquatic insects, gammarid amphipods, filamentous algae. plant leaves	Most abundant in heavily vegetated swamplike waters of low pH, & in cypress lowlands.	7,20,33. 46,65
Enneacanthus gloriosus bluespotted sunfish	se NY to FL	fw - 12.9	LC	In fw stream; 55% diet crustaceans (copepods, crayfish, amphipods, cladocerans). Also insect larvae (dipterans, hemipterans, dragonflies)	Associated with submerged weedbeds in tidal fw. A common inhabitant of sluggish streams, acid ponds, swamps. More abundant in coves than in mainstream.	19,42,46, 50
Enneacanthus obesus banded sunfish	s NH to w FL	fw - 3.33	U	similar to E. gloriosus.	Most common in sluggish streams. swamps of low pH & ditches over mud substrates. Often associated with bluespotted sunfish, but less abundant.	7,29,33, 46,50,65

Name	Geographic range	Salinity range ppt	Relative abundance	Food habits	Comments	Source
Lepomis auritus redbreast sunfish	NK to c FL; Gulf coast to TX	fw - 3	LC	In fw stream; 88% diet insects (dipteran larvae, coleopterans), also cladocerans, copepods, decapods, fish	Mainstream & tributaries. May spawn in tidal waters.	11,19,25, 27,35,50, 65
Lepomis cyanellus green sunfish	native to MS basin; introduced into ATL coast drainages	fw	R	Young; zoplankton Adults; fish (crappies, gizzard shad, mosquitofish, sticklebacks, largemouth bass fry), fish eggs, crayfish, insects	Primary habitat is nontidal freshwater.	7,33,35
Lepomis gibbosus pumpkinseed	NK to n GA; upper MS basin; introduced elsewhere	fw - 18.2	C	Primarily a benthic feeder. In fw stream; 63% diet dipteran larvae. Also other insects & insect larvae, crustaceans (copepods, ostracods, amphipods), snails, fish	Prefers quiet water with abundant vegetation. Spawns in tidal fw portion of the Potomac River, VA. & Hudson River, NY. Major sport importance.	19,21,32, 33,46,48, 58
Lepomis gulosus warmouth	ATL coast-MD to s FL; much of e US	fw - 4.1	LC	Young; small crustaceans Adults; insects, crayfish, fish. More piscivorous than others of genus.	Inhabits ponds, lakes & streams. Often associated with weedy areas, swamps. Withstands low dissolved oxygen levels. More common in tidal fw's in the SE.	7,11,26, 33,51
Lepomis macrochirus bluegill	much of US; entire e coast	fw - 18	C-A	In fw stream; an opportunistic feeder on insects (dipterans, hemipterans, mayfly nymphs), crustaceans (copepods, cladocerans), filamentous algae	Juveniles readily follow flood tide onto fw marsh surface where they forage in dense vegetation. Major sport importance.	11,19,25, 27,33,42, 46
Lepomis marginatus dollar sunfish	NC to TX; n through c MS basin	fw - 3.33	U	insects	Inhabits swamps, sluggish streams. Recorded from low salinity waters of the Neuse River, NC.	7,26,29, 33
Lepomis megalotis longear sunfish	e & c N AM w of Appalachians; introduced into Chesapeake Bay drainages & into NY	fw	R	Young; aquatic insects, small crustaceans Adults; fish eggs, terrestrial insects, snails, small crayfish, oligochaete worms, isopods	Primary habitat is nontidal freshwaters. Intolerant of large amounts of silt, salinity.	7,33

Name	Geographic range	Salinity range ppt	Relative abundance	Food habits	Comments	Source
Lepomis microlophis redear sunfish	NC to FL, w to TX & s MO & OH; introduced into OK, CA, VA, PA, IL	fw - 12.3	C	snails, insect larvae (chironomids, mayflies), cladocerans, isopods. Seldom feeds on surface.	Most common in large warm rivers, bayous & lakes. Often associated with vegetation, submerged stumps or logs.	7,10,26, 33,51
Lepomis punctatus spotted sunfish	NC to s FL; s MS & Gulf drainages	fw - 11.8	O	In brackish water: variety of crustaceans (amphipods, mysids, xanthid crabs), sponge (*Ephydatia fluviatilis*), insects (chironomid larvae, ants)	Occupies swamps, sloughs, floodplain lakes.	7,11,26, 33,51,69
Micropterus dolomieui smallmouth bass	NF to VA; MS basin; introduced into ATL coast drainages	fw - 7.4	R	Young; copepods, cladocerans, rotifers, chironomid larvae, mayfly nymphs, larval fish Adults; crayfish, fish (alewives, centrarchids), tadpoles	More abundant above the fall line. Prefers clear fast flowing waters.	7,32,46, 64
Micropterus salmoides largemouth bass	native to MS drainage & ATL coast drainage n to SC; widely introduced elsewhere, including ATL coast drainages	fw - 12.9	LC-A	In fw: young; microcrustaceans, insects, cladocerans, amphipods, decapods, small fish Adults; large insects, fish (small centrarchids, gizzard shad), crayfish, frogs In brackish water; blue crabs, shrimp, fish, insects	Inhabits sluggish streams, weed beds; prefers creeks & coves to river proper. Spawns in fw tidal portion of Potomac River, Va. Major sport importance.	7,11,27, 33,35,46, 50
Pomoxis annularis white crappie	native to MS drainage; introduced elsewhere including most ATL coast drainages NY to FL	fw - 1.5	U	Young; zooplankton during first year, later amphipods, insect larvae (chironomids, *Chaoborus*, mayflies) Adults; fish (cyprinids, threadfin shad, darters, centrarchids, catfish)	Quite intolerant of turbidity & siltation. More common in nontidal fw's.	7,33,46
Pomoxis nigromaculatus black crappie	native to MS, Gulf & ATL coast drainages n to VA; introduced elsewhere, including most ATL coast drainages	fw - 1.5	O-C	Young; cladocerans, copepods, chironomid larvae, *Chaoborus* larvae, ostracods, oscillatorial algae, insects, forage fish Adults; cladocerans, terrestrial insects, fish (shiners, threadfin & gizzard shad, largemouth bass, striped bass, white catfish, channel catfish, centrarchids)	Associated with abundant aquatic vegetation. Does not readily enter brackish water.	7,26,32, 33,46,56

Name	Geographic range	Salinity range ppt	Relative abundance	Food habits	Comments	Source
Percidae - perches						
Etheostoma fusiforme swamp darter	ME to TX	fw - 1.3	R	insect larvae (chironomids, mayflies), crustaceans (amphiphipods, copepods, cladocerans, ostracods)	Inhabits swamps, backwaters of sluggish streams, ponds. Often associated with dense vegetation, mud or organic substrate.	20,26,33, 46,65
Etheostoma olmstedi tessellated darter	St. Lawrence to Altahama, GA	fw - 13	O-C	microscopic crustaceans, small insects, detritus	Inhabits shallows & low gradient rivers. Spawns in nontidal fw streams, swamp runs.	32,33,46, 66
Perca flavescens yellow perch	native NS to Santee River, SC & upper MS basin; widely introduced	fw - 13	C-A	Young; zooplankton, later small insects Adults; insects, crayfish, small fish	Spend most of year in low salinity portions of estuary. Adults migrate upstream to spawning areas in early spring. Very adaptable species. Most abundant in clear open water with moderate vegetation.	33,35,46, 48,50,66
Percina nigrofasciata blackbanded darter	Edisto River, SC to c FL; also Gulf drainages	fw	R	diurnal visual subsurface feeder on immature insects (dipterans, mayflies, caddisflies)	Most common over gravel or sand in nontidal fw's.	26,33
Carangidae - jacks						
Caranx hippos crevalle jack	NS to Uruguay	fw - 35	R	mainly fish	Marine species, but juveniles occasionally enter fw in s. portion of range. Recorded from Altamaha River, GA	26,33
Gerreidae - mojarras						
Eucinostomus argenteus spotfin mojarra	NJ to Brazil	fw - 35	R	In estuarine waters; ostracods, copepods, polychaetes, bivalves, insect larvae	Recorded from fw's only in s. portion of range, Ga, FL & LA	27,33

Name	Geographic range	Salinity range ppt	Relative abundance	Food habits	Comments	Source
Haemulidae - grunts						
Orthopristis chrysoptera pigfish	Cape Cod to MEX; more common s of Cape Hatteras, NC	fw - 35	R	In brackish water; shrimp, polychaetes, molluscs, amphipods	Reported from Altahama River, GA; autumn only. More common in lower estuary.	26,33
Sciaenidae - drums						
Bairdiella chrysoura silver perch	MA to TX	fw - 35	U	Larvae; copepods, larval fish (tidewater silversides) Juv; largely mysids, also shrimp, fish (bay anchovy), mysids, grass shrimp	Marine form, spawned at sea. Juveniles present in estuary into tidal fw in summer, fall. More abundant in lower estuary. Apparently less likely to enter tidal fw's in SC & GA	8,33,46, 47,63
Cynoscion nebulosus spotted seatrout	Cape Cod to MEX	fw - 35	R	In brackish water; 50 mm; copepods, planktonic crustaces 50-274 mm; wide variety of fish.	Present in tidal fw's in spring, summer, fall, but more common in lower estuary. Winters in deep channels in estuary or in inshore marine waters. Not recorded from tidal fw's in SC or GA	8,33,40, 47,60
Cynoscion regalis weakfish	MA to GA	fw - 35	U	In low salinity nursery ground; 20-40 mm; largely mysids, also penaeid shrimp, fish (bay anchovies, naked gobies, clupeids, spot, pigfish). Adults primarily piscivorous.	A marine form. spawned at sea. Juveniles present in estuary in spring, summer, fall. Some enter tidal fw reaches.	8,28,43
Leiostomus xanthurus spot	MA to TX	fw - 35	LC	A benthic feeder: juveniles in low brackish water; harpacticoid copepods, amphipods, polychaete worms, nematodes, mysids, ostracods, isopods, chaetognaths, bivalves, snails	A marine form, spawned at sea. Juveniles arrive in Chesapeake Bay in April, use estuary as a nursery area, leave in Dec. Fw tidal reach is upper portion of nursery area.	8,57,63, 64

Name	Geographic range	Salinity range ppt	Relative abundance	Food habits	Comments	Source
Micropogonias undulatus Atlantic croaker	MA to Argentina	fw - 35	LC	Juveniles feed in water column, adults feed on bottom. In low brackish water juveniles feed principally on mysids & gammarid amphipods, also on copepods & polychaete worms.	A marine form, spawned at sea, juveniles present spring through fall. Inhabit channels in fw tidal areas, though more common in lower portion of estuary. Suffer high mortality in severe winters. Peak abundance s. of Cape Hatteras.	8,28,35, 57
Pogonius cromis black drum	MA to Argentina & Gulf of MEX	fw - 35	U	A bottom feeder. 180 mm juveniles in low salinity waters; small bivalves (*Mulinia lateralis*) & polychaete worms, also mysids, amphipods, blue crabs.	Adults enter DE Bay mid-late April on spawning runs, leave early June. Young-of-the-year collected in June in 0-6 ppt tidal marsh creeks. Young leave bay in October.	13,46,61, 63
Mugilidae - mullets						
Mugil cephalus striped mullet	NS to Brazil; most common Chesapeake Bay south; circumtropical	fw - 35	O-C	plant material, detritus & associated fauna, plankton	Often enters fw's, particularly in s. portion of its range.	11,27,33, 47,51
Gobiidae - gobies						
Gobionellus hastatus sharptail goby	NC to Brazil	fw - 29	R-U		A marine form occasionally taken in freshwater. Most common at 20-24 ppt salinity.	3,56
Gobionellus shufeldti freshwater goby	Newport River, NC to c FL; Gulf coast to TX		U	From oligohaline waters; copepods, ostracods, nematodes, chironomid larvae, forams	Prefers low salinity marshes and upper estuaries.	11,33,52
Gobiosoma bosci naked goby	MA to MEX	fw - 27	O	Larvae; zooplankton Adults; mainly small crustaceans including gammaridean amphipods. Also annelid worms fishes, fish eggs, dying oysters.	Estuarine resident, spawns in moderate salinity areas, pelagic larvae move upstream to low salinity nursery areas. Adults occupy oyster bar community, only young extend into tidal fw's.	11,12,17, 33,46,63

Name	Geographic range	Salinity range ppt	Relative abundance	Food habits	Comments	Source
Bothidae - lefteye flounders						
Citharichthys spilopterus bay whiff	NJ to Brazil	fw - 35	U	mysid shrimp, crabs, copepods, amphipods, fish, annelids	Juveniles regularly enter fw's in central America. Recorded from tidal fw's in NE Cape Fear River, NC & Newport River, GA	11,33,48, 62
Paralichthys dentatus summer flounder	ME to FL	6 - 35	R	In brackish water; fish, shrimps, crabs, mysids, small molluscs, sand dollars, annelids, amphipods	Rarely recorded from tidal fw's. More common in lower estuary.	40,46
Paralichthys lethostigma southern flounder	VA to n FL; Gulf coast	fw - 35	U	mainly fish, also crabs, mysids, molluscs, penaeid shrimp, amphipods	A marine form with a tendency to enter tidal fw's in s. portion of its range.	11,14,33, 64
Soleidae - soles						
Trinectes maculatus hogchoker	MA to Panama & Gulf of MEX	fw - 32	C	A benthic feeder on small crustaceans including amphipods & mysids, also annelids, isopods, detritus, insect larvae (chironomids), algae, forams	Estuarine resident inhabiting channel edges, mud bottoms. Nursery zone extends into tidal fw's.	11,13,17, 46,47,64

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THE VERTEBRATE FAUNA (except fish) OF TIDAL FRESHWATER WETLANDS
Introduction to Appendices C, D, and E.

The geographic region covered in our literature search was centered on the mid-Atlantic coast, but references to estuaries from Maine to northern Florida have been included. References to vertebrate species (except fish, see Appendix B) from this region had to satisfy one of three criteria before that species was included in Appendices C, D, or E: 1) direct reference to the use of "tidal freshwater marshes", "tidal rivers", "freshwater tidal estuaries", or similar wording, 2) reference to the species occurence in a specific geographical locale (e. g. Pamunkey River marshes, Gunpowder River) which we know, from other sources, to be tidal freshwater habitats, or 3) reference to the use of permanent bodies of fresh water such as "swamps", "marshes", "head-waters of estuaries", "riverine marshes", which do not explicitly state tidal freshwater, but imply that tidal freshwater habitats could be used. Application of these criteria has led to the production of rather extensive species lists since we have included rare as well as abundant species. Nomenclature follows AOU (1982) for birds Jones et al. (1979) for mammals, and Collins et al. (1978) for amphibians and reptiles.

A key to the abbreviations used is given below. The heading Region refers to the areas (State or bay) along the Atlantic coast from which the species has been reported. Our estimate of regional occurrence should not be construed as being comprehensive at this time. Under Status we give an estimate of the relative abundance of each species. This estimate is for that species abundance in tidal freshwater wetlands only. It does not apply over a species entire geographical range or for all of the various habitats it may use. Thus, for example, the eastern box turtle is listed as rare to uncommon in tidal freshwaters. It is a common species in pine woods habitat. Where possible our estimate of status is based on reports from the primary literature. When these sources were not available we used the gray literature and species lists provided to us by various National Wildlife Refuges in the region. Under Habitat we list in a general way the types of tidal freshwater wetlands which are used. An estimate of the time of year during which a species is present is given under Season. These latter two categories apply only to Appendix D: Birds.

Appendices C-E

REGION

NE - New England, particularly the Hudson and Connecticut estuaries.
DEL - Delaware River and Bay, including its tributaries.
CH - Major tributaries of the Chesapeake Bay including the Susquehanna, Patuxent, Potomac, Rappahannock, Mattaponi, Pamunkey, Chickahominy, and James Rivers on the western shore and the Nanticoke and Pocomoke Rivers on the eastern shore.
NC - North Carolina, particularly the Cape Fear River and estuary.
SC - South Carolina, with special reference to the Waccamaw lower Pee Dee, Combahee, South Edisto, Santee, and Savannah Rivers.
GA - Georgia. Especially the Altamaha, Satilla, and Oconee Rivers.
FL - Florida, the Saint Marys and upper Saint John's Rivers.

STATUS

A - Abundant. A species which is very conspicuous, being seen on almost all visits during the appropriate season.
C - Common. Species seen in good numbers during appropriate seasons but not on every visit.
FC - Fairly Common. Seen in moderate numbers at the proper season, and/or on 1/2 to 2/3 of the visits.
UC - Uncommon. A species which is observed infrequently (on 1/3 to 1/2 of the visits) or in low numbers.
OC - Occasional. A species seen on 1/4 to 1/3 of the visits or in small numbers during the proper season.
R - Rare. A species seen very infrequently (<1/10 of the visits) or in very small numbers, during the proper season.
L - Locally. A modifier used in conjunction with the Abundant and Common classifications. Refers to a species which is usually UC to OC but which may become concentrated in certain small geographic regions or for short periods of time.

REFERENCES

Numbers refer to references listed at the end of each appendix.

Appendix D.

HABITAT

TS - tidal swamps, including shrub marshes
HM - high marsh
LM - low marsh

SEASON

S - Spring, April - June.
SU - Summer, July - September.
F - Autumn, October - December.
W - Winter, January - March.
P - Permanent, year-round resident.
T - Transient, during both spring and autumn migrations.

APPENDIX C:
Amphibians and reptiles of tidal freshwater wetlands along the Atlantic coast

Family / Species	Region	Status	Food habits	References
Proteidae - waterdogs				
Dwarf waterdog (*Necturus punctatus*)	CH,NC,SC, GA,FL	R	Molluscs, crustacens, aquatic insects, amphibians	1
Mudpuppy (*N. maculosus*)	NE	R-UC	aquatic insects, mollusks, amphibians	9
Sirenidae - sirens				
Greater siren (*Siren lacertina*)	CH,NC,SC,GA	UC	crustaceans, mollusks, worms, aquatic insects, small vertebrates	1,3,14
Dwarf siren (*Pseudobranchus striatus*)	GA,FL	UC-C	crustaceans, aquatic insects, salamanders, frogs, freshwater oligochaetes	13,14
Ambystomidae - mole salamanders				
Marbled salamander (*Ambystoma opacum*)	CH,NC,SC,GA	UC-C	insects, ants, worms	6,13,14,25
Mole salamander (*A. talpoideum*)	SC,GA	LC-C	small snails, spiders, worms	14,25
Mabee's salamander (*A. mabeei*)	NC,SC	LC-A	small insects and snails	14,15,25
Eastern tiger salamander (*A. tigrinum*)	SC,GA	LC-A	worms, snails, small aquatic insects	14,25
Spotted salamander (*A. maculatum*)	SC,GA	LC-A	small aquatic insects, worms	14,25
Salamandridae - newts				
Eastern newt (*Notophthalmus viridescens*)	NE,DEL,CH, NC,SC,GA	UC-LC	oligochaetes, insects, mollusks, fish and amphibian eggs	13,14,18,24
Striped newt (*N. perstriatus*)	SC,GA	R	fish and amphibian eggs, oligochaetes, mollusks	14,25
Amphiumidae - amphiumas				
Two-toed amphiuma (*Amphiuma means*)	CH,NC,SC,GA	UC-C	crayfish, mollusks, fish, frogs, amphibians, small snakes	1,13,14, 18,24

Family / Species	Region	Status	Food habits	References
Plethodontidae - lungless salamanders				
Southern dusky salamander (*Desmognathus auriculatus*)	CH,NC,SC,GA	UC-C	insect larvae, sowbugs, worms	14,25
Northern dusky salamander (*D. fuscus*)	DEL,CH	R-UC	worms, insect larvae	1,15,25
Two-lined salamander (*Eurycea bislineata*)	NE,DEL,CH, SC,GA	UC-C	small invertebrates	6,14,21
Three-lined salamander (*E. longicauda guttolineata*)	CH,NC,SC,GA	R-UC	small invertebrates	1,3,14,21
Dwarf salamander (*E. quadridigitata*)	NC,SC,GA,FL	UC-C	small invertebrates	14,18
Four-toed salamander (*Hemidactylium scutatum*)	DEL,CH	R	small invertebrates	6,15
Red-backed salamander (*Plethodon cinereus*)	NE,DEL,CH,NC	R	earthworms, ants, bugs	6,15,26
Slimy salamander (*P. glutinosus*)	SC,GA	UC	ants, bugs, earthworms	13,14,18
Many-lined salamander (*Stereochilus marginatus*)	CH,NC,SC,GA	R	aquatic insects	1,13
Mud salamander (*Pseudotriton montanus*)	SC,GA	UC	aquatic invertebrates, small insects	13,14
Bufonidae - toads				
American toad (*Bufo americanus*)	NE,DEL,CH	OC-C	small insects	1,2,9, 10,26
Woodhouse's toad (*B. woodhousei*)	DEL,CH	C	small insects	1,2,7
Oak toad (*B. quercicus*)	CH,NC,SC,GA	UC-C	small insects	3,13
Southern toad (*B. terrestris*)	SC,GA	C	small insects	14
Hylidae - treefrogs				
Northern cricket frog (*Acris crepitans*)	DEL,CH,NC,SC	UC-C-north R-south	small insects	1,14,25
Southern cricket frog (*A. gryllus*)	NC,SC,GA	C-A	small insects	1,13,14,25

Family / Species	Region	Status	Food habits	References
Green treefrog (*Hyla cinerea*)	CH,NC,SC, GA,FL	C-A	small insects	1,2,11, 13,18
Spring peeper (*H. crucifer*)	NE,DEL,CH,NC, SC,GA,FL	C	arthropods, small insects	1,9,13,26
Cope's gray treefrog (*H. chrysoscelis*)	SC,GA	LC	insects, spiders	14,25
Common treefrog (*H. versicolor*)	SC,GA	C	small invertebrates	12-14,25
Pine-woods treefrog (*H. femoralis*)	CH,NC,SC,GA	LC	insects	1,13,18,25
Squirrel treefrog (*H. squirella*)	CH,NC,SC, GA,FL	LC	insects	1,25
Barking treefrog (*H. gratiosa*)	CH,NC,SC, GA,FL	UC	insects	5
Bird-voiced treefrog (*H. avivoca*)	SC,GA	C-Savannah River drainage only	small insects	14,25
Little grass frog (*Limnaoedus ocularis*)	CH,NC,SC,GA	UC-C	insects	1,13
Brimley's chorus frog (*Pseudacris brimleyi*)	CH,NC,SC,GA	C-A-north R-south	insects	1,14
Striped chorus frog (*P. triseriata*)	DEL,CH,NC,SC	R-C	insects	1,3,6,14
Southern chorus frog (*P. nigrita*)	NC,SC,GA	UC	insects	24,25
Ornate chorus frog (*P. ornata*)	NC,SC,GA	UC	insects	24,25
Microhylidae - narrow-mouthed toads				
Eastern narrowmouth toad (*Gastrophyrne carolinensis*)	CH,NC,SC,GA	R	ants and other small insects	1,14
Ranidae - true frogs				
Bullfrog (*Rana catesbeiana*)	NE,DEL,CH,NC, SC,GA,FL	C-A	crayfish, aquatic insects, small vertebrates	1,3,6,7,9, 10,14,19,26
Pigfrog (*R. grylio*)	SC,GA,FL	C-A	small vertebrates, insects, crayfish	12,13,14, 19,20

Family / Species	Region	Status	Food habits	References
Green frog (R. clamitans)	NE,DEL,CH, NC,SC,GA	C-A	arthropods, snails, freshwater oligochaetes	1,3,6,7,9, 14,19,26
Carpenter frog (R. virgatipes)	CH,NC,SC,GA	UC-C	arthropods, snails, spiders, crustaceans	13,14,20, 24,25
River frog (R. heckscheri)	NC,SC,GA,FL	C	snails, insects, crustaceans	13,14,21,25
Wood frog (R. sylvatica)	NE,DEL,CH	R	insects, crustaceans, spiders	3,26
Pickerel frog (R. palustris)	NE,DEL,CH, NC,SC	LC-north R-south	insects, spiders, other artropods	6,9,10, 14,25,26
Southern leopard frog (R. sphenocephala)	CH,NC,SC, GA,FL	C-LC	small insects	1,6,7,13 13,14,19
Chelydridae - snapping turtles				
Snapping Turtle (Chelydra serpentina)	NE,DEL,CH,NC, SC,GA,FL	C-A	aquatic invertebrates, fish, reptiles, carrion, aquatic plants, birds	1,4-6,9,10, 13,14,26
Kinosternidae - mud turtles				
Stinkpot (Kinosternon subrubrum)	NE,DEL,CH,NC, SC,GA,FL	R-north C-south	insects, mollusks, carrion	1,4-6,10, 13,14
Eastern musk turtle (Stenotherus odoratus)	NE,DEL,CH,NC, SC,GA,FL	UC-C	insects, snails, carrion	1,4-6,10 13,14
Emydidae - pond turtles				
Painted turtle (Chrysemys picta)	NE,CH,DEL,NC, SC,GA,FL	C	young-tadpoles, amphibians, mollusks adults-aquatic plants	1,4-7,9,10, 12-14,26
Slider (C. scripta)	CH,NC,SC, GA,FL	UC-C	young-aquatic insects, mollusks, carrion, adults-aquatic plants	1,14,18,24
Cooter (C. floridana)	CH,NC,SC, GA,FL	UC-C	algae, aquatic plants	1,12-14
River cooter (C. concinna)	CH,NC,SC, GA,FL	C	algae, aquatic plants	1,4,13,14
Redbelly turtle (C. rubriventris)	DEL,CH,NC, SC,GA,FL	R-north C-south	snails, crayfish, tadpoles, aquatic plants	1,4,5, 7,10,14
Chicken turtle (Deirochelys reticularia)	NC,SC,GA,FL	LC	crayfish, fish, snails, carrion	12-14,18
Spotted turtle (Clemmys guttata)	NE,DEL,CH, NC,SC,GA	LC-north R-south	aquatic plants, small invertebrates, carrion	1,4-7,10, 11,26

Family / Species	Region	Status	Food habits	References
Wood turtle (*C. insculpta*)	NE,DEL	R-UC	algae, berries, insects, mollusks	9,10
Bog turtle (*C. muhlenbergi*)	NE,DEL,CH	LC	tadpoles, slugs, snails, insects, oligochaetes	6
Map turtle (*Graptemys geographica*)	DEL,CH	R	crayfish, mollusks	9
False map turtle (*G. pseudogeographica*)	DEL	R	crustaceans, mollusks, insects, aquatic plants	10
Diamondback terrapin (*Malaclemys terrapin*)	DEL,CH,NC, SC,GA,FL	OC-C	clams, snails, worms	1,7,10,13
Eastern box turtle (*Terrapene carolina*)	DEL,CH,NC, SC,GA,FL	UC	slugs, earthworms, mushrooms	1,6,7,10 11,13,14
Trionychidae - softshell turtles				
Florida softshell (*Trionyx ferox*)	SC,GA,FL	C	fish, frogs, snails, amphibians	13,14
Spiny softshell (*T. spiniferus*)	SC,GA	UC	frogs, snails, fish, amphibians	13,14
Crocodilidae - alligators				
American alligator (*Alligator mississippiensis*)	NC,SC,GA,FL	UC-C	fish, snakes, amphibians	8,14,18,24
Iguanidae - iguanas				
Green anole (*Anolis carolinensis*)	SC,GA,FL	UC-C	insects	8,14
Scincidae - skinks				
Blue-tailed skink (*Eumeces fasciatus*)	DEL,CH,NC, SC,GA.FL	C	insects, spiders, worms, small mice, crustaceans	7,8,25
Five-lined skink (*E. inexpectatus*)	CH,NC,SC, GA,FL	R-LA	insects, spiders, small crustaceans	1,12,25
Broadhead skink (*E. laticeps*)	CH,NC,SC,GA	UC	pupae of wasps and bees, other insects	1,16,25
Anguidae - glass lizards				
Eastern glass lizard (*Ophisaurus ventralis*)	NC,SC,GA	R-UC	ground insects, lizards, frogs, small mammals	16,24

Family / Species	Region	Status	Food habits	References
Colubridae - snakes				
Rat snake (_Elaphe obsoleta_)	DEL,CH,NC, SC,GA,FL	A	mice, voles, birds and their eggs	1,5-7,14
Corn snake (_E. guttata_)	SC,GA	R	lizards, frogs, small mammals	14
Eastern mud snake (_Farancia abacura_)	CH,NC,SC, GA,FL	UC-C	sirens, amphiumas, salamanders	1,12,14, 15,18
Rainbow snake (_F. erytrogramma_)	CH,NC,SC,GA	LC	young-salamanders, tadpoles, frogs adults- American eels	1,4,14,15
Common kingsnake (_Lampropeltis getulus_)	DEL,CH,NC, SC,GA	C	water snakes, mice, birds	1,4,5, 13,14
Plain-bellied water snake (_Nerodia erythrogaster_)	DEL,CH,SC, GA,FL	C-A	_Gambusia_, frogs, tadpoles	1,7,14,27
Northern water snake (_N. sipedon_)	NE,DEL,CH, NC,SC,GA	A	small fish, frogs, salamanders crustaceans	1,4-7,10, 11,13,14,26
Southern water snake (_N. fasciata_)	NC,SC,GA,FL	LC-A	frogs, tadpoles, _Gambusia_	14,15,24,27
Green water snake (_N. cyclopion_)	SC,GA,FL	LC	_Gambusia_, _Lepomis_, _Micropterus_, Centrarchids, frogs, aquatic insects	12-14,27
Brown water snake (_N. taxispilota_)	CH,SC,GA	C	fishes. frogs	1,9,11,14, 15,24
Black swamp snake (_Seminatrix pygaea_)	NC,SC,GA,FL	UC	leeches, small fish, worms, tadpoles, dwarf sirens, salamanders	13-15,18
Racer (_Coluber constrictor_)	NE,DEL,CH, NC,SC,GA,FL	C	large insects, frogs, lizards, small rodents, birds	7,14,26
Rough green snake (_Opheodrys aestivus_)	DEL,CH,NC, SC,GA,FL	C	grasshoppers, crikets, spiders, caterpillars	13-15
Glossy crayfish snake (_Regina rigida_)	CH,NC,SC, GA,FL	UC-LC	crayfish, sirens, frogs, small fish, salamanders	1,15,18, 22,23
Queen snake (_R. septemvittata_)	DEL,CH	R-OC	crayfish	1,4-6,15
Brown (deKay's) snake (_Storeria dekayi_)	NE,DEL,CH,NC, SC,GA,FL	OC	oligochaetes, snails, slugs	10,12,25
Redbelly snake (_S. occipitomaculata_)	SC,GA	R-UC	slugs, earthworms, insects	14,25

Family / Species	Region	Status	Food habits	References
Eastern ribbon snake (*Thamnophis sauritis*)	NE,DEL,CH,NC, SC,GA,FL	C	frogs, salamanders, small fish	1,4,5,7, 10,12-14
Common garter snake (*T. sirtalis*)	NE,DEL,CH,NC, SC,GA,FL	OC-C	toads, frogs, salamanders, earthworms	1,4-7,10, 12-14,26
Worm snake (*Carphophis amoenus*)	SC	R-UC	worms, soft-bodied insects	14,15
Ringneck snake (*Diadophis punctatus*)	DEL,CH,NC, SC,GA,FL	R-UC	salamanders, earthworms, frogs, small snakes	14,15
Eastern earth snake (*Virginia valeriae*)	SC,GA	R-UC	worms, slugs, snails, frogs	14,25
Crotalidae - pit vipers				
Copperhead (*Agkistrodon contortrix*)	NE,DEL,CH, NC,SC,GA	UC	mice, voles, frogs, caterpillars	12,14,24
Cottonmouth (*A. piscivorus*)	CH,NC.SC, GA.FL	OC-A	fish, amphibians, small mammals, sometimes waterbirds	1,12,14
Pygmy rattlesnake (*Sistrurus miliarius*)	SC,GA,FL	R-UC	mice, lizards, frogs, small snakes	15,16
Eastern diamondback rattlesnake (*Crotalus adamanteus*)	SC,GA,FL	R	small mammals, frogs, other snakes	12,14
Timber rattlesnake (Canebrake) (*C. horridus*)	CH,NC,SC, GA,FL	R	rodents, rabbits, small birds	14,15

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APPENDIX D:
Avifauna of tidal freshwater wetlands

FLOATING AND DIVING WATERBIRDS

Family / Species	Region	Season	Status	Habitats	Food Habits	References
Gaviidae - loons						
Common loon (*Gavia immer*)	NE,DEL,CH, NC,SC,GA	W,T	UC-A	LM	Fish, crabs, mollusks, frogs	6-9,12, 15,17
Red-throated loon (*G. stellata*)	NE,DEL,CH	W,T	UC	LM	Molluscs, fish, crabs, frogs,	5-7,9
Podicipedidae - grebes						
Horned grebe (*Podiceps auritus*)	NE,DEL,CH, NC,SC,GA,FL	W,T	LC-C	LM,HM	aquatic insects, fish, mollusks crustaceans	5-10, 15
Red-necked grebe (*P. grisegena*)	NE,DEL,CH, NC,SC,GA	W,T	R-UC	LM	Fish, mollusks, aquatic insects	6,7,9
Pied-billed grebe (*Podilymbus podiceps*)	NE,DEL,CH, NC,SC,GA, FL	SU,T-north P-south	A	LM,HM	crayfish, aquatic insects, mollusks, fish	1,5-9, 11,14, 15,17
Pelecanidae - pelicans						
American white pelican (*Pelecanus erythrorhynchos*)	SC,GA,FL	W,T	R	LM	fish	17
Brown pelican (*P. occidentalis*)	SC,GA,FL	P	R-UC	LM	fish	17
Sulidae - boobies and gannets						
Northern gannet (*Sula bassanus*)	NE	W	UC	LM	fish	7
Phalacrocoracidae - cormorants						
Double-crested cormorant (*Phalacrocorax auritus*)	NE,DEL,CH, NC,SC,GA, FL	W,T-north P-south	UC-C	LM	fish	5-10,15, 17,22
Anhingidae - anhingas						
Anhinga (*Anhinga anhinga*)	CH,NC,SC, GA,FL	SU-north P-south	R-north C-south	LM,HM,TS	*Mugil*, *Lepomis*, frogs, aquatic insects, crustaceans	5,12,14, 17,18

Family / Species	Region	Season	Status	Habitats	Food Habits	References
Anatidae - swans, geese, and ducks						
Mute swan (*Cygnus olor*)	NE,DEL,CH	W,T	R-UC	LM,HM	*Scirpus*, *Cyperus*, *Potamogeton*	5-7,22
Whistling swan (*C. columbianus*)	NE,DEL,CH, NC,SC,GA	W,T	A-north R-south	LM,HM	*Scirpus*, *Eleocharis*, *Cyperus*	3-10, 12,15
Canada goose (*Branta canadensis*)	NE,DEL,CH, NC,SC	W,T	UC-LA	LM,HM	*Cyperus*, *Echinochloa*, *Panicum*, *Polygonum*, *Scirpus*, *Peltandra*, *Pontederia*, *Potamogeton*	2,3-10,12, 14,15,17, 22
Brant (*B. bernicla*)	NE,DEL	W,T	R	LM	*Vallisneria*, *Scirpus*, *Cyperus*	6,7
Snow geese (*Anser caerulescens*)	NE,DEL,CH, NC,SC,GA	W,T	C-north R-south	LM,HM	roots and rhizomes of *Spartina*, *Cyperus*, *Scirpus*, *Eleocharis*	5-8, 10,12, 14,17
Fulvous whistling duck (*Dendrocygna bicolor*)	CH,NC,SC, GA,FL	W	R	LM,HM,TS	*Scirpus*, *Panicum*, *Cyperus*	5,12,17
Mallard (*Anas platyrhynchos*)	NE,DEL,CH, NC,SC,GA, FL	P-north W,T-south	A	LM,HM,TS	*Scirpus*, *Setaria*, *Cyperus*, *Leersia*, *Cephalanthus*, *Panicum*, *Polygonum*, *Peltandra*, *Lachnanthes*, *Corbicula*	1,2,4-10, 12,14-17, 19,20,22
Mottled duck (*A. fulvigula*)	GA,FL	P	UC	LM,HM	*Panicum*, *Polygonum*, *Cyperus*, *Eleocharis*, aquatic insects	14
America black duck (*A. rubripes*)	NE,DEL,CH, NC,SC,GA, FL	P-north W,T-south	A	LM,HM,TS	*Carpinus*, *Aneilema*, *Leersia*, *Cephalanthus*, *Panicum*, *Pontederia*, *Polygonum*, *Zizania*, *Sparganium*, *Peltandra*, *Corbicula*	2,4-10, 12,14-17, 19,20,22
Gadwall (*A. strepera*)	NE,DEL,CH, NC,SC,GA, FL	W,T	UC-C	LM,HM,TS	*Scirpus*, *Chara*, *Najas*, *Potamogeton*, *Panicum*, *Polygonum*, *Cyperus*, *Lachnanthes*	4-9,12, 14,16,17, 19,20
Northern pintail (*A. acuta*)	NE,DEL,CH, NC,SC,GA, FL	W,T	UC-A	LM,HM,TS	*Aneilema*, *Cephalanthus*, *Panicum*, *Cyperus*, *Leersia*, *Peltandra*, *Zizania*, *Polygonum*, *Corbicula*	2,4-10, 12,14-17, 19,20
Green-winged teal (*A. crecca*)	NE,DEL,CH, NC,SC,GA, FL	W,T	C	LM,HM,TS	*Cyperus*, *Panicum*, *Polygonum*, *Eleocharis*, *Scirpus*, *Zizania*, *Fimbristylis*	2,4-9, 12,14-17, 19,20
Blue-winged teal (*A. discors*)	NE,DEL,CH, NC,SC,GA,	W,T	C-A	LM,HM,TS	*Cyperus*, *Panicum*, *Polygonum*, *Scirpus*, *Echinochloa*, *Zizania*,	4-10,12, 14-17, 19,20
American wigeon (*A. americana*)	NE,DEL,CH, NC,SC,GA,	W,T	UC-C	LM,HM	*Cephalanthus*, *Cyperus*, *Ruppia*, *Echinochloa*, *Scirpus*, *Leersia*, *Myriophyllum*, *Lachnanthes*	2,4-10, 12,14-17, 19,20

Family / Species	Region	Season	Status	Habitats	Food Habits	References
Northern shoveler (A. clypeata)	NE,DEL,CH, NC,SC,GA, FL	W,T	UC-C	LM,HM,TS	Aneilema, Cyperus, Scirpus, Panicum, Lachnanthes, Corbicula, Corixidae, Zygoptera	2,4-9, 12,14-17, 19,20
Wood duck (Aix sponsa)	NE,DEL,CH, NC,SC,GA, FL	P	A	LM,HM,TS	Carpinus, Cephalanthus, Nyassa, Cornus, Peltandra, Quercus, Toxicodendron, Scirpus, Zizania	1,2,4-10, 12,14-20, 22
Redhead (Aythya americana)	NE,DEL,CH, NC,SC,GA, FL	W,T	UC-LA-north R-UC-south	LM,HM	Scirpus, Zizania, Potamogeton, Najas, Ruppia	4-10,12, 15,17
Ring-necked duck (A. collaris)	NE,DEL,CH, NC,SC,GA, FL	W,T	UC-C	LM,HM,TS	Scirpus, Nuphar, Cyperus, Najas, Vallisneria, Polygonum, Panicum, Brasenia	4-9,12, 14-17, 19,20
Canvasback (A. valisineria)	NE,DEL,CH, NC,SC,GA, FL	W,T	UC-C	LM,HM	Sagittaria, Potamogeton, Ruppia, Vallisneria, Ephemerioptera	4-10,12, 15,17
Greater scaup (A. marila)	NE,DEL,CH, NC,SC,GA	W,T	O-UC	LM,HM,TS	Zizania, Scirpus, Potamogeton, Vallisneria, Panicum, Polygonum, Eleocharis, Gastropoda, Pelecypoda	4-8,12, 15,19, 20
Lesser scaup (A. affinis)	NE,DEL,CH, NC,SC,GA, FL	W,T	UC-C	LM,HM,TS	Sagittaria, Cyperus, Eleocharis, Potamogeton, Scirpus, Vallisneria, Najas, Panicum, Pelecypoda Gastropoda	4-10,12, 14,15,17
Common goldeneye (Bucephala clangula)	NE,DEL,CH, NCSC,GA	W,T	O-UC	LM	Decapoda, aquatic insect larvae, Potamogeton	4-9,12, 15,17
Bufflehead (B. albeola)	NE,DEL,CH, NC,SC,GA	W,T	UC-LA	LM,HM,TS	Zizania, Isopoda, Gastropoda, Pelecypoda, Gammaridae	4-8,10, 12,15-17
Oldsquaw (Clangula hyemalis)	NE,DEL,CH, NC,SC,GA, FL	W,T	UC-north R-south	LM	Amphipoda, Decapoda, Pelecypoda	4,6,7,9
Surf scoter (Melanitta perspicillata)	NE,DEL,CH, NC	W	R	LM	Scirpus, Cyperus, bivalves, Amphipoda	7,9,15
White-winged scoter (M. fusca)	NE,DEL	W,T	R-UC	LM	crustaceans, mussels	6,7,15
Black scoter (M. nigra)	NE,DEL	W,T	R-UC	LM	mussels, esp. Mytilus edulis, barnacles, caddisfly larvae	6,7,15
Ruddy duck (Oxyura jamaicensis)	NE,DEL,CH, NC,SC,GA, FL	W,T	UC-C	LM,HM,TS	Scirpus, Najas, Potamogeton, Vallisneria, Gastropda, chironomids	4-10,12, 14-17

Family / Species	Region	Season	Status	Habitats	Food Habits	References
Hooded merganser (*Lophodytes cucullatus*)	NE,DEL,CH, NC,SC,GA, FL	W,T	UC-FC	LM,HM,TS	*Fundulus*, *Ictalurus*, *Anguilla*, *Etheostoma*, *Alosa*	2,4-9,12, 15-17,22
Common merganser (*Mergus merganser*)	NE,DEL,CH, NC,SC,GA	W,T	FC-C-north UC-south	LM	fish	5-10,14, 15
Red-breasted merganser (*M. serrator*)	NE,DEL,CH, NC,SC,GA, FL	W,T	UC-FC	LM,HM,TS	fish	1,5-9,12, 14-16
Rallidae - gallinules, coots, and rails						
Purple gallinule (*Porphyrula martinica*)	CH,NC,SC, GA,FL	SU-T	R-north UC-south	LM,HM	*Zizania*, *Scirpus*, *Eleocharis*, aquatic insects, snails, frogs	5,6,9,12, 16-18
Common moorhen (Common gallinule) (*Gallinula chloropus*)	NE,DEL,CH, NC,SC,GA, FL	SU-north P-south	FC	LM,HM	*Zizania*, *Cyperus*, *Scirpus*, grasshoppers, aquatic insects	1,5-7,9, 12,14-18
American coot (*Fulica americana*)	NE,DEL,CH, NC,SC,GA, FL	P	UC-A	LM,HM	*Scirpus*, *Zizania*, *Cyperus*, *Eleocharis*, *Potamogeton*, small fish, tadpoles, snails	1,4-10, 12,14-17

WADING BIRDS

Family / Species	Region	Season	Status	Habitats	Food Habits	References
Ardeidae - herons and bitterns						
American bittern (*Botaurus lentiginosus*)	NE,DEL,CH, NC,SC,GA, FL	SU,T-north P-south	C	LM,HM,TS	fish, aquatic insects, frogs, mice, shrews	5-7,12-17
Least bittern (*Ixobrychus exilis*)	NE,DEL,CH, NC,SC,GA, FL	SU,F-north P-south	FC	LM,HM	fish, aquatic insects, amphibians, crustaceans	1,5-7, 12-15, 17,18
Black-crowned night heron (*Nycticorax nycticorax*)	NE,DEL,CH, NC,SC,GA, FL	SU,T-north P-south	A	LM,HM,TS	crayfish, fish, crabs, mice, frogs	5-7, 9,10, 14-18
Yellow-crowned night heron (*N. violaceus*)	DEL,CH,NC, SC,GA,FL	SU,T-north P-south	C	LM,HM,TS	snails, aquatic insects, fish, crayfish, crabs	5,6,10, 12,14, 16-18
Green-backed heron (*Butorides striatus*)	NE,DEL,CH, NC,SC,GA, FL	SU,T-north P-south	C	LM,HM,TS	small fish, crayfish, aquatic insects	1,6,7,9, 10,12-18, 22
Cattle egret (*Bubulcus ibis*)	CH,NC,SC, GA,FL	SU,T-north P-south	R-north A-south	LM,HM	grasshoppers, crickets, spiders	10,12,17
Little blue heron (*E. caerulea*)	NE,DEL,CH, NC,SC,GA, FL	SU,T-north	C P-south	LM,HM,TS	fish, crayfish, Orthoptera, amphibians	5-7,9,12, 14-18
Tricolored heron (Louisiana heron) (*E. tricolor*)	DEL,CH,NC, SC,GA,FL	SU,T-north P-south	UC-north C-south	LM,HM,TS	fish, snails, lizards, frogs	6,10,12, 14-18
Snowy egret (*E. thula*)	NE,DEL,CH, NC,SC,GA, FL	S,SU-north P-south	C	LM,HM	fish, crayfish, crabs, aquatic insects	6,7,10, 12,14-18
Great egret (*Casmerodius albus*)	NE,DEL,CH, NC,SC,GA, FL	S,SU-north P-south	C	LM,HM,TS	aquatic insects, fish, crayfish, crabs, snails	5-7,10, 12,14-18
Great blue heron (*Ardea herodias*)	NE,DEL,CH, NC,SC,GA, FL	P	C	LM,HM,TS	mice, amphibians, fish, crayfish	1,5-7,9,10, 12,14-18, 22
Ciconiidae - storks						
Wood stork (*Mycteria americana*)	SC,GA,FL	P	FC-summer UC-winter	LM,HM	snails, aquatic insects, fish	12,14, 16,17

Family / Species	Region	Season	Status	Habitats	Food Habits	References
Threskiornithidae - ibises						
Glossy ibis (*Plegadis falcinellus*)	NE,DEL,CH, NC,SC,GA, FL	S,SU-north P-south	R-north C-south	LM,HM,TS	snails, crayfish, fish, aquatic insects, crabs	6,7,12, 14,16-18
White ibis (*Eudocimus albus*)	DEL,CH,NC, SC,GA,FL	SU,T-north P-south	R-north A-south	LM,HM,TS	crabs, aquatic insects, crayfish	5,6,12, 14,16-18
Aramidae - limpkins						
Limpkin (*Aramus guarauna*)	GA,FL	SU	R	LM,HM,TS	snails	14,16

RAILS AND SHOREBIRDS

Family / Species	Region	Season	Status	Habitats	Food Habits	References
Rallidae - rails and gallinules						
King rail (*Rallus elegans*)	NE,DEL,CH, NC,SC,GA, FL	P	C	LM,HM	seeds of: *Zizania*, *Polygonum*; Orthoptera, worms, spiders, snails, crayfish, small fish	5-7,9-12, 14-18
Virginia rail (*R. limicola*)	NE,DEL,CH, NC,SC,GA, FL	SU,T-north W,T-south	C	LM,HM	seeds of: *Zizania*, *Cyperus*, *Polygonum*; worms, slugs, snails, small fish	5-7,9,10, 12,14-17
Sora (*Porzana carolina*)	NE,DEL,CH, NC,SC,GA, FL	SU,T-north W,T-south	UC (A in migration)	LM,HM	seeds of: *Zizania*, *Cyperus*, *Scirpus*; aquatic insects, worms, spiders, snails	1,5-7,9, 10,12, 14-17
Yellow rail (*Coturnicops noveboracensis*)	DEL,CH,NC, SC,GA,FL	SU,T-north W,T-south	R	LM,HM	seeds of: *Cyperus*, *Polygonum*, *Zizania*, *Setaria*; worms, snails, spiders	5,6,9,14, 16,17
Black rail (*Laterallus jamaicensis*)	DEL,CH,NC, SC,GA,FL	SU,T	R (FC in migration)	LM,HM	worms, snails, spiders, also seeds of: *Scirpus*, *Zizania*, *Cyperus*	5,6,9,11, 16,17
Charadriidae - plovers and turnstones						
Killdeer (*Charadrius vociferus*)	NE,DEL,CH, NC,SC,GA, FL	SU,T-north P-south	C	LM,HM	Coleopotera, Orthoptera, Hymenoptera	1,5-7,9, 10,12,15, 17,22
Semipalmated plover (*C. semipalmatus*)	NE,DEL,CH, NC,SC,GA, FL	W,T	FC-C	LM	crustaceans, mollusks, freshwater worms, seeds of *Polygonum*	6,7,9,10
Lesser golden plover (*Pluvialis dominica*)	NE,DEL,CH, NC,SC	T	UC-C	LM	worms, snails, crustaceans, grasshoppers	6,7,12,17
Black-bellied plover (*P. squatarola*)	NE,DEL,CH, NC,SC,GA, FL	W,T	C	LM	crustaceans, freshwater worms, mollusks, grasshoppers, beetles	6,7,10,12
Scolopacidae - snipe, woodcock, and sandpipers						
Ruddy turnstone (*Arenaria interpres*)	NE,DEL,CH, NC,SC,GA, FL	W,T	C	LM	crustaceans, grasshoppers mollusks	6,7,10
Common snipe (*Gallinago gallinago*)	NE,DEL,CH, NC,SC,GA,FL	SU,T-north P-south	UC-C	LM,HM	aquatic Coleoptera, snails, worms, seeds of: *Scirpus*, *Polygonum*	6,7,9,10, 12,14,15
American woodcock (*Scolopax minor*)	NE,DEL,CH, NC,SC,GA,FL	SU,T-north P-south	UC-C	LM,HM	earthworms, larvae of: craneflies, horseflies, snipe flies	1,5,6,9,10, 12,15,16, 22

Family / Species	Region	Season	Status	Habitats	Food Habits	References
Upland sandpiper (*Bartramia longicauda*)	NE,DEL,CH, NC,SC	T	R-UC	LM,HM	freshwater worms, snails, centipedes, millipedes, aquatic insects, seeds of: *Setaria*, *Cephalanthus*	6,10,11
Spotted sandpiper (*Actitus macularia*)	NE,DEL,CH, NC,SC,GA, FL	SU,T-north P-south	C	LM,HM	nymphs of: caddisflies, mayflies, dragonflies; mollusks, worms, grasshoppers, crickets	1,5-7, 9-12, 15-17
Solitary sandpiper (*Tringa solitaria*)	NE,DEL,CH, NC,SC,GA, FL	T	UC-C	LM,HM	mollusks, worms, Hymenoptera, Orthoptera, small frogs, nymphs of: caddisflies, mayflies, dragonflies	5,6,9, 11,12, 15,17
Greater yellowlegs (*T. melanoleuca*)	NE,DEL,CH, NC,SC,GA, FL	W,T	C-A	LM,HM	aquatic insects, worms, mollusks, small fish	5-7,9,10, 12,14, 15,17
Lesser yellowlegs (*T. flavipes*)	NE,DEL,CH, NC,SC,GA, FL	W,T	UC-C	LM,HM	aquatic insects, snails, worms	5-7,9,10, 12,14, 15,17
Willet (*Catoptrophorus semipalmatus*)	NE,DEL,CH, NC,SC,GA, FL	SU,T-north W,T-south	R-UC	LM,HM	aquatic insects, worms, crabs, mollusks, small fish, seeds of: *Cyperus*, *Scirpus*, *Polygonum*	6,9, 12,15
Short-billed dowitcher (*Limnodromus griseus*)	NE,DEL,CH, NC,SC,GA, FL	W,T	UC-C	LM,HM	fly larvae, worms, snails, seeds of: *Scirpus*, *Polygonum*, *Potamogeton*, *Cyperus*	5-7,10-12, 14
Stilt sandpiper (*Calidris himantopus*)	DEL,CH,NC, SC,GA,FL	T	UC	HM	clamworms, mollusks, aquatic insects, seeds of: *Cyperus*, *Scirpus*, *Eleocharis*	5,6,9, 11,12
Dunlin (*C. alpina*)	NE,DEL,CH, NC,SC,GA, FL	W,T	UC-FC	LM,HM	worms, mollusks, insects	6,7,9,10
Red knot (*C. canutus*)	NE,DEL,CH, NC,SC,GA,FL	W,T	UC	LM,HM	snails, periwinkles, worms, seeds of: *Scirpus*, *Potamogeton*, *Cyperus*	10,17
Least sandpiper (*C. minutilla*)	NE,DEL,CH, NC,SC,GA,FL	W,T	R-UC	LM,HM	worms, mollusks, aquatic insects, seeds of *Scirpus*, *Panicum*	5-7,9-11, 15
White-rumped sandpiper (*C. fuscicollus*)	NE,DEL,CH, NC,SC,GA,FL	T	R-UC	LM,HM	insects, clamworms, small fish, snails, grasshoppers	5,6
Pectoral sandpiper (*C. melanotos*)	NE,DEL,CH, NC,SC,GA, FL	T	UC	HM	aquatic insects, worms, mollusks, seeds of: *Cyperus*, *Panicum*	5-7,9,10, 14
Semipalmated sandpiper (*C. pusilla*)	NE,DEL,CH, NC,SC,GA, FL	T-north W,T-south	FC-C	LM,HM	larvae of: caddisflies, mayflies, dragonflies; clamworms, mollusks, seeds of: *Scirpus*, *Potamogeton*	6,7,9,10, 17
Baird's sandpiper (*C. bairdii*)	DEL,CH	T	UC	HM	amphipods, beetles, weevils, mosquitoes, craneflies	10,11

Family / Species	Region	Season	Status	Habitats	Food Habits	References
Western sandpiper (C. mauri)	NE,DEL,CH, NC,SC,GA,FL	T-north W,T-south	FC	LM,HM	aquatic insects, beetles, mollusks, seeds of: Potamogeton, Scirpus	5,6,9,10, 17
Sanderling (C. alba)	NE,DEL,CH, NC,SC,GA,FL	W,T	UC	LM,HM	flies and their larvae, mollusks, worms	6,7,9,10
Ruff (Philomachus pugnax)	DEL,CH	T	UC	LM,HM	aquatic insects, worms, mollusks, flies	5,6,11
Buff-breasted sandpiper (Tryngites subruficollis)	DEL,CH	T	UC	LM,HM	beetles and their larvae, flies, seeds of: Potamogeton, Scirpus	5,6
Red-necked phalarope (Phalaropus lobatus)	DEL,CH	T	R	LM,HM	snails, midges, fly larvae	5,6,9
Wilson's phalarope (P. tricolor)	DEL,CH,NC, SC,GA	T	R-UC	LM,HM	larvae of: caddisflies, mayflies, dragonflies; seeds of: Cyperus, Scirpus, Potamogeton	5,6,9-11, 14
Recurvirostridae - avocets and stilts						
American avocet (Recurvirostra americana)	DEL,CH,NC, SC,GA,FL	SU,T-north T-south	R-UC	LM,HM	clamworms, aquatic insects, seeds of: Scirpus, Potamogeton	5,6,14
Black-necked stilt (Himantopus mexicanus)	DEL,CH,NC, SC,GA	SU,T	R	LM,HM	aquatic insects, snails, small fish	5,6,12,14

DIURNAL AND NOCTURNAL BIRDS OF PREY

Family / Species	Region	Season	Status	Habitats	Food Habits	References
Cathartidae - vultures						
Turkey vulture (*Cathartes aura*)	NE,DEL,CH, NC,SC,GA FL	P	C	HM,TS	carrion	1,6,7,9, 10,12, 16-18
Black vulture (*Coragyps atratus*)	CH,NC,SC, GA,FL	P	UC	HM,TS	carrion	9,10,12, 16-18
Accipitridae - kites, hawks, and eagles						
Mississippi kite (*Ictinia mississippiensis*)	SC,GA,FL	SU,T	UC-FC	HM,TS	lizards, frogs, snakes, large insects	12,16,17
American swallow-tailed kite (*Elanoides forficatus*)	SC,GA,FL	SU,T	UC-FC	HM,TS	snakes, lizards, frogs	12,16,17
Cooper's hawk (*Accipiter cooperii*)	NC,DEL,CH, NC,SC,GA,FL	SU,T-north P-south	UC	LM,HM,TS	small passerines, mice, voles	6,12,16, 18
Sharp-shinned hawk (*A. striatus*)	NE,DEL,CH, NC,SC,GA,FL	P-north W,T-south	UC-FC	LM,HM,TS	mice, voles, small passerines	6,9,10, 12,16
Northern harrier (Marsh hawk) (*Circus cyaneus*)	NE,DEL,CH, NC,SC,GA, FL	SU,T-north P-mid W,T-south	C	LM,HM,TS	mice, voles, rats, amphibians, snakes, small passerines	6,7,9, 10,12, 14-17
Red-tailed hawk (*Buteo jamaicensis*)	NE,DEL,CH, NC,SC,GA, FL	P	C	LM,HM,TS	mice, shrews, voles, rabbits, muskrats, gallinules, rails, small passerines	1,6,7,9, 10,12,13, 15-18,22
Red-shouldered hawk (*B. lineatus*)	NE,DEL,CH, NC,SC,GA, FL	P	UC-C	HM,TS	rails, small owls, mice, voles, small passerines	6,9,10,12, 13,16,18
Broad-winged hawk (*B. platypterus*)	NE,DEL,CH, NC,SC,GA, FL	SU,T-north W,T-south	UC	HM,TS	lizards, mice, snakes, frogs, voles, large flying insects	1,6,9,16
Rough-legged hawk (*B. lagopus*)	NE,DEL,CH	W,T	UC	HM,TS	voles, mice, snakes, frogs, small passerines	6,7,9
Southern bald eagle (*Haliaeetus leucocephalus*)	NE,DEL,CH, SC,GA,FL	P	R	LM,HM,TS	fish, waterfowl, rodents, carrion	1,6,7,9, 10,12, 15-18

Family / Species	Region	Season	Status	Habitats	Food Habits	References
Osprey (Pandion haliaetus)	NE,DEL,CH, NC,SC,GA, FL	SU,T-north P-south	FC-C	LM,HM,TS	fish	1,6,7,9,10, 12,14-18,, 22
Falconidae - falcons						
Peregrine falcon (Falco peregrinus)	DEL,CH,NC, SC,GA,FL	W,T	R	LM,HM	waterfowl, shorebirds, coots, gallinules, swifts, kingbirds, and small passerines	6,9,12, 14,17
Merlin (F. columbarius)	DEL,CH,NC, SC,GA,FL	W-T	UC-FC	LM,HM,TS	waterfowl, passerines, voles, mice, frogs, snakes	6,10,12, 16,17
American kestrel (F. sparverius)	NE,DEL,CH, NC,SC,GA, FL	P	C	LM,HM,TS	mice, voles, frogs, bats, insects, small passerines, lizards	1,6,7,9, 12,16,17
Tytonidae - barn owls						
Common barn owl (Tyto alba)	NE,DEL,CH, NC,SC,GA, FL	P	UC-FC	LM,HM,TS	mice, voles, small passerines	6,7,9
Strigidae - typical owls						
Eastern screech owl (Otus asio)	NE,DEL,CH, NC,SC,GA, FL	P	C	LM,HM,TS	mice, voles, frogs, small passerines, large insects	1,6,7,12
Great horned owl (Bubo virginianus)	NE,DEL,CH, NC,SC,GA,FL	P	FC	LM,HM,TS	shrews, voles, mice, rats, shorebirds, small passerines, bitterns, herons, waterfowl, hawks, other owls	7,9,10, 12,18
Barred owl (Strix varia)	DEL,CH,NC, SC,GA,FL	P	UC-FC	LM,HM,TS	mice, voles, small passerines, shorebirds, waterfowl	5,6,9,10, 12,15, 17,18
Short-eared owl (Asio flammeus)	NE,DEL,CH, NC,SC,GA,FL	W,T	C	LM,HM	mice, esp. Microtus, voles, small passerines, large flying insects	6,9,12,14
Northern saw-whet owl (Aegolius acadicus)	DEL,CH,NC	W,T	FC	LM,HM,TS	large flying insects, also mice, voles, shrew, small passerines	6,9,21
Laniidae - shrikes						
Loggerhead shrike (Lanius ludovicianus)	DEL,CH,NC, SC,GA,FL	P	R-UC	LM,HM	mice, voles, small passerines, large insects	6,12

GULLS, TERNS, KINGFISHERS, AND CROWS

Family / Species	Region	Season	Status	Habitats	Food Habits	References
Laridae - gulls and terns						
Glaucous gull (Larus hyperboreus)	NE,DEL,CH	W,T	R-UC	LM,HM	fish, mollusks, ducks, carrion	6,9
Iceland gull (L. glaucoides)	NE,DEL,CH	W	R-UC	LM,HM	fish, crustaceans, garbage, carrion	6,9
Great black-backed gull (L. marinus)	NE,DEL,CH	W,T	UC	LM,HM	fish, carrion, garbage	6,7,9,10
Herring gull (L. argentatus)	NE,DEL,CH	W,T	C	LM,HM	fish, crustaceans, mollusks, some insects	6,7,9,10, 22
Ring-billed gull (L. delawarensis)	NE,DEL,CH	P	A	LM,HM	fish, Coleoptera, Orthoptera, mollusks, crustaceans, rodents	5-7, 9,10
Laughing gull (L. atricilla)	NE,DEL,CH	P	UC	LM,HM	small fish, earthworms, carrion, crustaceans, garbage	1,6,7, 9,10
Bonaparte's gull (L. philadelphia)	NE,DEL,CH	W,T	UC-FC	LM,HM	fish, insects, worms, crustaceans, carrion, garbage	7,9,10
Black-legged kittiwake (Rissa tridactyla)	NE	W	R-UC	LM,HM	small fish, crustaceans, mollusks	7
Gull-billed tern (Sterna nilotica)	CH	T	R-UC	LM,HM	dragonflies, caddisflies, frogs, small fish, earthworms	6
Forster's tern (S. forsteri)	DEL,CH,NC, SC,GA,FL	W,T	UC	LM,HM	dragonflies, caddisflies, frogs, some small fish	6,9-11,
Common tern (S. hirundo)	NE,DEL,CH, NC,SC,GA,FL	SU,T-north W,T-south	UC	LM,HM	pipefish, menhaden, alewives	6,7,9,10
Least tern (S. antillarum)	DEL,CH	SU,T	R-UC	LM,HM	small fish and crutaceans	6,9,10
Royal tern (S. maximus)	CH	SU	UC	LM,HM	fish	8
Sandwich tern (S. sandvicensis)	NC,SC,GA,FL	SU	R-UC	LM,HM	fish	12
Caspian tern (S. caspia)	NE,DEL,CH,	SU,T	UC-FC	LM,HM	small fish, particularly menhaden, mullet, suckers	5-7, 9,10
Black tern (Chilodonias niger)	NE,DEL,CH,	T	UC	LM,HM	caddisflies, mayflies, dragonflies, moths, caterpillars, small fish	5-7,9
Black skimmer (Rhynchops niger)	CH	SU,T	UC	LM	small fish, crustaceans	10

Family / Species	Region	Season	Status	Habitats	Food Habits	References
Alcedinidae - kingfishers						
Belted kingfisher (*Ceryle alcyon*)	NE,DEL,CH, NC,SC,GA, FL	P	C	LM,HM,TS	fish, crayfish, crabs, mussels, newts, snails, frogs, toads, turtles, grasshoppers, beetles	5-8,22
Corvidae - crows and jays						
Fish crow (*Corvus ossifragus*)	NE,DEL,CH, NC,SC,GA, FL	P	C	LM,HM,TS	fish, crayfish, carrion, *Cornus*, *Smilax*, *Zizania*	1,5-7,
American crow (*C. brachyrhynchos*)	NE,DEL,CH, NC,SC,GA, FL	P	C	LM,HM,TS	fish, grasshoppers, beetles, amphibians, reptiles, small birds, carrion *Toxicodendron*, *Cornus*	1,6,7,10, 22

ARBOREAL BIRDS

Family / Species	Region	Season	Status	Habitats	Food Habits	References
Cuculidae - cuckoos						
Yellow-billed cuckoo (Coccyzus americanus)	NE, DEL, CH, NC, SC, GA, FL	SU, T	UC-C	LM, HM, TS	hairy caterpillars, crickets, dragonflies, grasshoppers	1,6,7,9, 12,13,16,
Black-billed cuckoo (C. erythropthalmus)	NE, DEL, CH, NC, SC, GA, FL	SU, T-north T-south	UC-C	HM, TS	grasshoppers, crickets, dragonflies, hairy caterpillars	6,7,12,13
Caprimulgidae - goatsuckers						
Common nighthawk (Chordeilus minor)	NE, DEL, CH, NC, SC, GA, FL	SU, T	C	LM, HM, TS	flying ants, beetles, grasshoppers, mosquitoes	6,7,9,14
Chuck-will's-widow (Caprimulgus carolinensis)	CH, NC, SC, GA, FL	SU, T	UC-FC	HM, TS	moths, flies, mosquitoes, grasshoppers, small passerines	9,12,16,18
Whip-poor-will (C. vociferous)	DEL, CH, NC, SC, GA, FL	SU, T-north W, T-south	C	LM, HM, TS	mosquitoes, moths, flies, grasshoppers	6
Apodidae - swifts						
Chimney swift (Chaetura pelagica)	NE, DEL, CH, NC, SC, GA, FL	SU, T	C	LM, HM	caddisflies, mosquitoes, mayflies, beetles, wasps, ants	1,6,7,9, 10,12,16
Trochilidae - hummingbirds						
Ruby-throated hummingbird (Archilochus colubris)	NE, DEL, CH, NC, SC, GA, FL	SU, T	UC	HM, TS	Hibiscus, Impatiens, Ipomoea, Tecoma	5-10,12,16
Picidae - woodpeckers						
Pileated woodpecker (Dryocopus pileatus)	NE, CH, NC, SC, GA, FL	P	R-UC-north UC-FC-south	TS	ants, larvae of wood boring beetles, Toxicodendron, Sassafras, wild grape	5,7,9,10, 12,16-18
Red-bellied woodpecker (Melanerpes carolinus)	CH, NC, SC, GA, FL	P	UC-FC	HM, TS	seeds of: Quecus, Fraxinus, Alnus, Myrica	9,10,12, 13,16,18
Red-headed woodpecker (M. erythrocephalus)	NE, DEL, CH, NC, SC, GA, FL	P	UC	HM, TS	beetles and their larvae, ants, caterpillars, grasshoppers, sedds of: Quercus, Myrica	6,7,16
Yellow-bellied sapsucker (Sphyrapicus varius)	DEL, CH, NC, SC, GA, FL	W, T	UC-FC	HM, TS	sap and wood of: Quercus, Acer	6,9,10, 12,16

Family / Species	Region	Season	Status	Habitats	Food Habits	References
Hairy woodpecker (*Picoides villosus*)	NE,DEL,CH, NC,SC,GA, FL	P	UC	TS	beetle larvae, ants, spiders, millipedes, *Toxicodendron*, *Cornus*	6,7,9,12, 13,16,17, 22
Downy woodpecker (*P. pubescens*)	NE,DEL,CH, NC,SC,GA, FL	P	UC	HM,TS	beetle larvae, moths, ants, snails, caterpillars, *Cornus*, *Toxicodendron*	1,6,7,10, 12,16-18, 22
Tyrannidae - tyrant flycatchers						
Eastern kingbird (*Tyrannus tyrannus*)	NE,DEL,CH, NC,SC,GA, FL	SU,T	C-A	LM,HM,TS	various Hymenoptera and Orthoptera	1,6,7,9, 10,12,13
Great-crested flycatcher (*Myiarchus crinitus*)	NE,DEL,CH, NC,SC,GA, FL	SU,T-north T-south	UC	LM,HM,TS	Lepidoptera, caterpillars, beetles, dragonflies	1,6,7,12, 13,16,18
Eastern phoebe (*Sayornis phoebe*)	DEL,CH,NC, SC,GA,FL	SU,T-north W,T-south	C	LM,HM,TS	grasshoppers, crickets, dragonflies, wasps, bees	5,6,9,10, 12,13,16, 18
Acadian flycatcher (*Empidonax virescens*)	DEL,CH,NC, SC,GA,FL	SU,T	C	LM,HM,TS	beetles, bees, wasps	5,6,9 12,16
Willow flycatcher (*E. traillii*)	NE,DEL,CH, NC,SC,GA	SU,T-north T-south	UC	LM,HM,TS	beetles, moths, caterpillars, bees, wasps	1,5-7, 9,13
Eastern wood pewee (*Contopus virens*)	NE,DEL,CH NC,SC,GA	SU,T	R-UC	LM,HM,TS	flies, beetles, treehoppers, grasshoppers, wasps, bees	1,6,7,10, 12,13
Hirundinidae - swallows						
Barn swallow (*Hirundo rustica*)	NE,DEL,CH NC,SC,GA, FL	SU,T-north P-south	C-A	LM,HM	grasshoppers, crickets, dragonflies, moths, mosquitoes	1,5,6,9, 10,12,14, 16,18,22
Cliff swallow (*H. pyrrhonota*)	NE,DEL,CH, NC,SC,GA, FL	SU,T	UC	LM,HM	beetles	6,7,9,14, 16
Northern rough-winged swallow (*Stelgidopteryx serripennis*)	DEL,CH,NC, SC,GA,FL	SU,T	C	LM,HM	wasps, bees, dragonflies, beetles	1,5,6,9, 10,14-16 18
Bank swallow (*Riparia riparia*)	NE,DEL,CH, NC,SC,GA, FL	SU,T	C-A	LM,HM	termites, ants, damselflies, dragonflies, aphids, beetles	1,5-10, 14-16,22
Tree swallow (*Tachycineta bicolor*)	NE,DEL,CH, NC,SC,GA, FL	SU,T-north W,T-south	A	LM,HM	beetles, flies, wasps, bees, seeds of: *Myrica*, *Scirpus*, *Polygonum*, *Cyperus*	1,6,7,9,10, 12,14-17, 22

Family / Species	Region	Season	Status	Habitats	Food Habits	References
Purple martin (*Progne subis*)	NE, DEL, CH, NC, SC. GA, FL	SU, T	C	LM, HM	beetles, wasps, bees, dragonflies, damselflies	1,6,7,9, 10,12, 14,16
Paridae - Chickadees and titmice						
Black-capped chickadee (*Parus atricapillus*)	NE, DEL	P	UC-C	HM, TS	moths, plant lice, spiders, katydids, *Toxicodendron*	6,7,13,22
Carolina chickadee (*P. carolinensis*)	DEL, CH, NC, SC, GA, FL	P	C	LM, HM, TS	eggs of insects, beetles, caterpillars, *Myrica*, *Toxicodendron*	6,10,12, 13,16-18
Tufted titmouse (*P. bicolor*)	DEL, CH, NC, SC, GA, FL	P	UC	LM, HM. TS	caterpillars, wasps, ants, *Myrica*	1,6,9,10, 12,13,16, 18
Sittadae - nuthatches						
White-breasted nuthatch (*Sitta carolinensis*)	NE, DEL, CH, NC, SC, GA, FL	P	UC-FC	HM, TS	bees, wasps, moths, caterpillars	5-7,9,12, 16,22
Red-breasted nuthatch (*S. canadensis*)	NE, DEL, CH, NC, SC, GA	W, T	R-UC	HM, TS	twig and bole insects	6,12,13
Brown-headed nuthatch (*S. pusilla*)	CH, NC, SC, GA, FL	P	UC	HM, TS	bole and twig insects	5,9,12
Certhiidae - creepers						
Brown creeper (*Certhia americana*)	DEL, CH, NC, SC, GA, FL	W, T	UC-FC	HM, TS	spiders, beetles, ants, caterpillars, *Panicum*	6,9,12,16
Mimidae - mockingbirds and thrashers						
Northern mockingbird (*Mimus polyglottos*)	NE, DEL, CH, NC, SC, GA, FL	P	UC	LM, HM, TS	beetles, ants, wasps, bees, grasshoppers, *Smilax*, *Toxicodendron*	1,6,7,10, 12,22
Muscicapidae - thrushes, gnatcatchers, and kinglets						
Wood thrush (*Hylocichla mustelina*)	DEL, CH, NC, SC, GA, FL	SU, T	UC	LM, HM, TS	beetles, ants, caterpillars, spiders	1,6,9,12, 13,16,17
Hermit thrush (*Catharus guttatus*)	DEL, CH, NC, SC, GA, FL	T	UC-FC	HM, TS	beetles, ants, caterpillars, *Smilax*, *Toxicodendron*	6,9,12,16
Swainson's thrush (*C. ustulatus*)	DEL, CH, NC, SC, GA, FL	W, T-north T-south	UC	HM, W, TS	ants, beetles, caterpillars,	6,9,12,13, 16,17
Gray-cheeked thrush (*C. minimus*)	DEL, CH, NC, SC, GA. FL	T	UC	HM, TS	caterpillars, beetles, ants, *Smilax*, *Toxicodendron*	6,9,12, 16,17

Family / Species	Region	Season	Status	Habitats	Food Habits	References
Veery (*C. fuscescens*)	NE,DEL,CH, NC,SC,GA, FL	SU,T-north T-south	UC	HM,TS	beetles, ants, wasps, bees,	6,7,9,12, 16,17
Eastern bluebird (*Sialia sialis*)	NE,DEL,CH, NC,SC,GA, FL	SU-north P-south	UC-C	LM,HM	weevils, grasshoppers, crickets, *Myrica*, *Smilax*	6,9,12,
Blue-gray gnatcatcher (*Polioptila caerulea*)	NE,DEL,CH, NC,SC,GA, FL	SU,T-north P-south	C	HM,TS	flies, caddisflies, gnats	5-7,9,10, 12,16-18
Golden-crowned kinglet (*Regulus satrapa*)	NE,DEL,CH, NC,SC,GA, FL	W,T	UC-C	HM,TS	wasps, flies, beetles, plant lice	6,7,9, 12,16
Ruby-crowned kinglet (*R. calendula*)	DEL,CH,NC, SC,GA,FL	T-north W,T-south	UC-FC	HM,TS	flies, beetles, *Toxicodendron*	6,7,9,12, 13,16
Bombycillidae - waxwings						
Cedar waxwing (*Bombycilla cedrorum*)	NE,DEL,CH, NC,SC,GA, FL	SU-north T-mid W,T-south	UC-C	LM,HM	*Smilax*, *Myrica*, *Cornus*, berries	6,7,9,12, 16,17
Vireonidae - vireos						
White-eyed vireo (*Vireo griseus*)	NE,DEL,CH, NC,SC,GA, FL	SU,T	UC-C	HM,TS	moths, beetles, ants, wasps	1,5-7,9, 10,12,13,
Yellow-throated vireo (*V. flavifrons*)	DEL,CH,NC, SC,GA,FL	SU,T	UC	HM,TS	eggs and caterpillars of moths and butterflies, dragonflies	6,9,12,18
Solitary vireo (*V. solitarius*)	DEL,CH,NC, SC,GA,FL	T-north W,T-south	R-UC	LM,HM,TS	dragonflies, damselflies, bees, wasps, crickets	6,12,16
Red-eyed vireo (*V. olivaceus*)	DEL,CH,NC, SC,GA,FL	SU,T	FC-A	LM,HM,TS	beetles, ants,wasps, moths	6,9,10, 12,16,18
Warbling vireo (*V. gilvus*)	DEL,CH	SU,T	R-UC	HM,TS	caterpillars, beetles	6,9

Family / Species	Region	Season	Status	Habitats	Food Habits	References
Emberizidae - wood warblers, blackbirds, tanagers, grosbeaks, buntings, and sparrows						
Black and white warbler (*Mniotilta varia*)	DEL,CH,NC, SC,GA,FL	T-north W,T-south	C	HM,TS	ants, moths, flies, aphids, spiders	5,6,9,10, 12,13,16, 17
Prothonotary warbler (*Protonotaria citrea*)	CH,NC,SC, GA,FL	SU,T	C-A	HM,TS	aquatic insects, mayflies, caterpillars	5,9-12, 15-18
Blue-winged warbler (*Vermivora pinus*)	NE,DEL,CH, NC,SC,GA, FL	T	R-UC	HM,TS	beetles, ants, spiders	5-7,9,12, 16
Golden-winged warbler (*V. chrysoptera*)	DEL,CH,NC, SC,GA,FL	T	R-UC	HM,TS	inch worms, spiders	5,6,9,10, 12
Tennessee warbler (*V. peregrina*)	DEL,CH,NC, SC,GA,FL	T	R-UC	HM,TS	beetles, weevils, scale insects, aphids	6,9,12, 13,16
Nashville warbler (*V. ruficapilla*)	DEL,CH	T	C	HM,TS	leafhoppers, aphids, flies, grasshoppers	6,9
Orange-crowned warbler (*V. celata*)	SC,GA	W,T	FC	HM,TS	leafhoppers, aphids, spiders	12
Bachman's warbler (*V. bachmanii*)	SC,GA	T	R	TS	little known, probably similar to other warblers	14
Northern parula (*Parula americana*)	DEL,CH,NC, SC,GA,FL	SU,T	UC-FC	HM,TS	beetles, cankerworms, spiders	5,6,9,10, 12,13,16,18
American redstart (*Setophaga ruticilla*)	DEL,CH,NC, SC,GA,FL	SU,T-north T-south	C-A	HM,TS	craneflies, leafhoppers, moths, beetles, *Myrica*	5,6,9,10, 12,13,16
Yellow warbler (*Dendroica petechia*)	CH,NC,SC, GA,FL	SU,T-north T-south	FC	HM,TS	mosquitoes, aphids, spiders, cankerworms, weevils	1,6,7,9, 12-14,16
Magnolia warbler (*D. magnolia*)	DEL,CH,NC, SC,GA,FL	T	UC	HM,TS	moths, scale insects, aphids, leafhoppers	6,12,13
Black-throated blue warbler (*D. caerulescens*)	DEL,NC,SC, GA,FL	T	C	HM,TS	moths, flies, beetles	6,12,13, 16,17
Black-throated green warbler (*D. virens*)	DEL,CH,NC, SC,GA,FL	SU,T	C	HM,SU,TS	beetles, ants, caterpillars, spiders	5,6,16-18
Yellow-throated warbler (*D. dominica*)	CH,NC,SC, GA,FL	SU,T	FC	TS	beetles, moths, aphids, spiders, mosquitoes	5,9,10, 12,16
Prairie warbler (*D. discolor*)	DEL,CH,NC, SC,GA,FL	SU,T	C	HM,TS	insects, spiders	5,6,12
Cape May warbler (*D. tigrina*)	DEL,CH,NC,	SU,T	UC	HM,SU,TS	bees, wasps, crickets, dragonflies, moths	6,13

Family / Species	Region	Season	Status	Habitats	Food Habits	References
Blackburnian warbler (*D. fusca*)	DEL	T	UC	HM,TS	bees, caterpillars, craneflies	6
Yellow-rumped warbler (*D. coronata*)	NE,DEL,CH, NC,SC,GA, FL	T-north W,T-south	A	LM,HM,TS	flies, beetles, ants, *Toxicodendron*, *Myrica*	5-10, 13,16
Chestnut-sided warbler (*D. pensylvanica*)	DEL,CH,NC, SC,GA,FL	T	UC	HM,TS	cankerworms, beetles, grasshoppers, caterpillars	6,12
Pine warbler (*D. pinus*)	DEL,CH,NC, SC,GA,FL	T	UC	TS	ants, wasps, bees, *Panicum*, *Toxicodendron*, *Cornus*	6,12
Bay-breasted warbler (*D. castenea*)	DEL,CH,NC, SC,GA,FL	T	UC	HM,TS	flies, moths leafhoppers	6,12
Palm warbler (*D. palmarum*)	DEL,CH,NC, SC,GA,FL	SU,T-north W,T-south	C	HM,TS	mosquitoes, beetles, flies, *Myrica*, *Rubus*	6,12,16
Blackpoll warbler (*D. striata*)	NE,DEL,CH, NC,SC,GA, FL	SU,T-north T-south	UC	HM,TS	aphids, scale insects, gnats	6,7,13,16
Yellow-breasted chat (*Icteria virens*)	DEL,CH,NC, SC,GA,FL	SU-north P-south	C	HM,TS	ants, wasps, beetles	6,9,12,13
Hooded warbler (*Wilsonia citrina*)	DEL,CH,NC, SC,GA,FL	SU,T	UC-FC	HM,SU,TS	caddisflies, moths, aphids, wasps, bees	5,6,9,12, 16-18
Wilson's warbler (*W. pusilla*)	DEL,CH,NC, SC,GA	T	UC	HM,TS	leafhoppers, scale insects, ants, aphids	6,12
Orchard oriole (*Icterus spurius*)	DEL,CH,NC,	SU,T	C	LM,HM	grasshoppers, ants, spiders, beetles	6,9,10,12
Northern oriole (*I. galbula*)	NE,DEL,CH, NC,SC,GA	SU,T-north	C	LM,HM,TS	spiders, ants, beetles, caterpillars	1,6,7,9, 12,13,22
Brown-headed cowbird (*Molothrus ater*)	NE,DEL,CH, NC,SC,GA, FL	SU,T-north P-south	C-A	LM,HM	*Polygonum*, *Echinochloa*, *Paspalum*	6-9,12,22
Thraupidae - tanagers						
Scarlet tanager (*Piranga olivacea*)	DEL,CH,NC, SC,GA,FL	SU,T-north T-south	C	HM,TS	beetles, bees, wasps, caterpillars	6,9,12
Summer tanager (*P. rubra*)	CH,DEL,NC, SC,GA,FL	SU	C	HM,TS	caterpillars, wasps, bees, beetles	12,13

Family / Species	Region	Season	Status	Habitats	Food Habits	References
Northern cardinal (*Cardinalis cardinalis*)	NE, DEL, CH, NC, SC, GA, FL	P	C	LM, HM, TS	grasshoppers, beetles *Polygonum*, *Cyperus*, *Toxicodendron*	1, 6-9, 12, 13, 16-18, 22
Rose-breasted grosbeak (*Pheucticus ludovicianus*)	NE, DEL, CH, NC, SC, GA	SU, T-north	UC	HM, TS	beetles, ants, wasps, bees, *Polygonum*	6, 7, 12
Blue grosbeak (*Guiraca caerulea*)	DEL, CH, NC, SC, GA, FL	SU, T	C	HM, TS	grasshoppers, beetles, weevils, *Panicum*, *Cyperus*, *Scirpus*, *Myrica*	6, 12
Evening grosbeak (*Coccothraustes vespertinus*)	DEL, CH, NC, SC, GA	T	R-UC	HM, TS	beetles, caterpillars, *Toxicodendron*, *Cornus*	6, 12
Indigo bunting (*Passerina cyanea*)	NE, DEL, CH, NC, SC, GA, FL	SU, T	UC	LM, HM	caterpillars, grasshoppers, beetles	1, 6-10, 13, 18
Painted bunting (*P. ciris*)	SC, GA, FL	SU, T	UC	HM, TS	*Myrica*, *Panicum*, beetles, caterpillars, grasshoppers	12, 16
American tree sparrow (*Spizella arborea*)	NE, DEL	W, T	UC-C	HM, TS	*Panicum*, *Cyperus*, *Amaranthus*, *Leersia*, *Setaria*, beetles, ants	6, 7, 13
Fringillidae - finches						
Purple finch (*Carpodacus purpureus*)	DEL, CH, NC, SC, GA	W, T	UC-FC	HM, TS	*Bidens*, *Myrica*, *Toxicodendron*, *Cornus*	6, 9, 10, 12,
House finch (*C. mexicanus*)	DEL	W, T	R-UC	HM, TS	*Myrica*, *Bidens*, *Toxicodendron*, *Cornus*	13
Pine siskin (*Carduelis pinus*)	DEL, CH, NC, SC, GA	W, T	UC	HM, TS	caterpillars, aphids	6, 9, 12
Common redpoll (*Acanthis flammea*)	DEL	W	R	HM, TS	*Polygonum*, *Setaria*, *Cyperus*	6
American goldfinch (*C. tristis*)	NE, DEL, CH, NC, SC, GA, FL	SU, T-north W, T-south	C	LM, HM, TS	seeds of: *Scirpus*, *Polygonum*, *Setaria*, *Zizania*, *Amaranthus*; aphids, caterpillars	1, 5-10, 12, 13, 16, 22

GROUND AND SHRUB DWELLING BIRDS

Family / Species	Region	Season	Status	Habitats	Food Habits	References
Phasianidae - quail and pheasant						
Northern bobwhite (_Colinus virginianus_)	NE,DEL,CH	P	UC	HM,TS	_Polygonum_, _Zizania_, _Panicum_, _Quercus_	9,10,22
Ruffed grouse (_Bonasa umbellus_)	NE	P	C	HM	_Zizania_, _Panicum_, _Polygonum_, _Scirpus_, _Echinochloa_,	22
Ring-necked pheasant (_Phasianus colchicus_)	NE,DEL	SU,T	C	LM,HM	seeds of rushes, grasses, sedges	1,6,22
Columbidae - doves and pigeons						
Mourning dove (_Zenaida macroura_)	NE,DEL,CH, NC,SC,GA, FL	SU,T-north P-south	C	LM,HM,TS	seeds of: _Scirpus_, _Zizania_, _Cyperus_, _Panicum_, _Echinochloa_	1,6,7,10, 12,16,22
Common ground dove (_Columbina passerina_)	SC,GA,FL	P	C	HM,TS	seeds of: _Scirpus_, _Cyperus_, _Zizania_, _Echinochloa_	12,14
Rock dove (_Columba livia_)	CH	P	C	LM,HM	seeds of: _Zizania_, _Scirpus_, _Polygonum_, _Cyperus_, _Panicum_	10
Picidae - woodpeckers						
Northern flicker (_Colaptes auratus_)	NE,DEL,CH, NC,SC,GA, FL	SU,T-north P-south	UC-C	HM,TS	caterpillars, beetles, grasshoppers, _Toxicodendron_, _Cornus_	1,6-8,10, 12,13,16, 18,22
Alaudidae - larks						
Horned lark (_Eremophila alpestris_)	NE,DEL,CH	W,T	C	LM,HM	seeds of: _Polygonum_, _Zizania_, _Cyperus_, _Scirpus_	6,9
Corvidae - jays and crows						
Blue jay (_Cyanocitta cristata_)	NE,DEL,CH, NC,SC,GA, FL	P	C	LM,HM,TS	seeds of: _Toxicodendron_, _Smilax_, _Scirpus_, _Myrica_, _Quercus_	6,7,9,10, 12-14,18, 22
Troglodytidae - wrens						
House wren (_Troglodytes aedon_)	NE,DEL,CH, NC,SC,GA,	SU,T-north W,T-south	UC-C	LM,HM	grasshoppers, crickets, beetles, ants, wasps, bees	1,6,7,12, 13,16
Winter wren (_T. troglodytes_)	NE,DEL,CH, NC,SC,GA	SU-north W,T-south	R-UC	LM,HM,TS	leaf beetles, weevils, spiders, caterpillars	5-7,9,10, 12,16
Carolina wren (_Thryothorus ludovicianus_)	NE,DEL,CH, NC,SC,GA, FL	P	A	LM,HM,TS	beetles, wasps, leafhoppers, spiders, snails, small lizards and frogs, _Toxicodendron_, _Myrica_	1,6,7,9, 10,12,13, 16,18

Family / Species	Region	Season	Status	Habitats	Food Habits	References
Marsh wren (Long-billed marsh wren) (*Cistothorus palustris*)	NE,DEL,CH, NC,SC,GA, FL	SU,T-north P-south	C	LM,HM	aquatic insects, snails, craneflies, dragonflies, mosquito larvae	1,5-12,14, 16,18,22
Sedge wren (Short-billed marsh wren) (*C. platensis*)	NE,DEL,CH, NC,SC,GA,FL	SU,T-north W,T-south	R-UC	LM,HM	beetles, moths, caterpillars, ants, grasshoppers	1,5,6,9, 12,16
Mimidae - mockingbirds and thrashers						
Gray catbird (*Dumetella carolinensis*)	NE,DEL,CH, NC,SC,GA, FL	SU,T-north P-south	A	LM,HM,TS	*Smilax*, *Myrica*, *Toxicodendron*	1,5-7,9,12, 13,16,18, 22
Brown thrasher (*Toxostoma rufum*)	DEL,CH,NC, SC,GA,FL	SU,T-north P-south	UC	HM,TS	beetles, ants, grasshoppers, *Smilax*, *Toxicodendron*, *Myrica*	6,10,12,18
Muscicapidae - thrushes, gnatcatchers, and kinglets						
American robin (*Turdus migratorius*)	NE,DEL,CH NC,SC,GA, FL	SU,T-north W,T-south	A	LM,HM,TS	caterpillars, beetles, worms, *Smilax*	1,6,7,9, 10,12, 16,18
Motacillidae - pipits						
Water pipit (*Anthus spinoletta*)	DEL,CH,NC, SC,GA,FL	W,T	UC-C	LM,HM	beetles, flies, caterpillars, crickets, *Panicum*	6,9,12
Sturnidae - starlings						
Starling (*Sturnis vulgaris*)	NE,DEL,CH, NC,SC,GA, FL	P	C-A	LM,HM,TS	beetles, grasshoppers, millipedes, *Toxicodendron*, *Myrica*	1,6,7,9, 12,18
Emberizidae - wood warblers, blackbirds, tanagers, groabeaks, buntings, and sparrows						
Worm-eating warbler (*Hermitheros vermivorus*)	DEL,CH,NC, SC,GA,FL	T	UC	LM,HM,TS	grasshoppers, walking sticks, span worms, weevils, spiders	6,9,12, 16,17
Swainson's warbler (*Limnothlypis swainsonii*)	CH,NC,SC, GA,FL	SU,T-north T-south	R-UC	LM,HM,TS	ants, bees, spiders, small caterpillars	5,9,11,12, 16,18,21
Ovenbird (*Seiurus aurocapillus*)	NE,DEL,CH, NC,SC,GA, FL	SU,T-north W,T-south	UC	LM,HM,TS	snails, slugs, worms, crickets, ants, spiders	1,6,7,12, 13,16
Northern waterthrush (*S. noveboracensis*)	NE,DEL,CH, NC,SC,GA, FL	SU-T	UC-C	LM,HM,TS	water beetles, damselflies, moths	5,7,9,11-13, 15,16

Family / Species	Region	Season	Status	Habitats	Food Habits	References
Louisiana waterthrush (*S. motacilla*)	DEL, CH, NC, SC, GA, FL	SU, T-north T-south	UC-FC	LM, HM, TS	dragonfly and cranefly larvae, killifishes, mollusks	5,6,9-12, 15-17
Common yellowthroat (*Geothlypis trichas*)	NE, DEL, CH, NC, SC, GA, FL	SU, T-north P-south	C-A	LM, HM, TS	grasshoppers, dragonflies, beetles, damselflies, spiders	1,5,7-14, 16-18
Mourning warbler (*Oporornis philadelphia*)	DEL	T	UC	HM, TS	insects, spiders	6,11
Connecticut warbler (*O. agilis*)	DEL, CH, NC, SC, GA	T	R-UC	HM, TS	spiders, bark insects	6,12
Kentucky warbler (*O. formosus*)	DEL, CH, NC, SC, GA, FL	SU, T	FC-C	HM, SU, TS	moths, caterpillars, grubs, aphids	5,6,9-12, 16,17
Canada warbler (*Wilsonia canadensis*)	DEL, CH	SU, T	R-UC	HM, TS	beetles, mosquitoes, flies, moths	5,6,9,13
Bobolink (*Dolichonyx oryzivorus*)	NE, DEL, CH, NC, SC, GA, FL	SU, T-north T-south	UC (LA in migration)	LM, HM	*Zizania*, *Panicum*, *Polygonum*, grasshoppers, caterpillars	5-9,12, 16,17
Eastern meadowlark (*Sturnella magna*)	NE, DEL, CH, NC, SC, GA, FL	P	C-A	LM, HM	*Myrica*, *Polygonum*, crickets grasshoppers	6-8,12, 16
Red-winged blackbird (*Agelaius phoeniceus*)	NE, DEL, CH, NC, SC, GA, FL	SU, T-north P-south	A	LM, HM, TS	seeds of: *Zizania*, *Polygonum*, *Panicum*, *Scirpus*, *Cyperus*	1,5-10,12, 12,14-18, 21,22
Rusty blackbird (*Euphagus carolinus*)	NE, DEL, CH, NC, SC, GA, FL	W, T	FC	HM, TS	*Zizania*, *Panicum*, aquatic insects, beetles	5-7,9,12, 13,16,17
Brewer's blackbird (*E. cyanocephalus*)	SC, GA, FL	W, T	R-UC	LM, HM	ants, grasshoppers, spiders	12
Boat-tailed grackle (*Quiscalus major*)	NE, DEL, CH, NC, SC, GA, FL	SU, T-north P-south	C-A	LM, HM	*Zizania*, *Quercus*	12,17,22
Common grackle (*Q. quiscula*)	NE, DEL, CH, NC, SC, GA, FL	SU, T-north P-south	C	LM, HM	bees, grasshoppers, crickets, earthworms, crayfish, *Zizania*, *Quercus*	6-10,12, 13,16,18, 22
Passeridae - sparrows						
House sparrow (*Passer domesticus*)	DEL, CH, NC, SC, GA, FL	P	A	LM, HM, TS	*Echinochloa*, *Panicum*, *Paspalum*, *Scirpus*, *Eleocharis*	1,6,12

Family / Species	Region	Season	Status	Habitats	Food Habits	References
Fringilidae - finches						
Rufous-sided towhee (Pipilo erythrophthalmus)	NE,DEL,CH NC,SC,GA FL	P-north W,T-south	C	HM,TS	seeds of: Panicum, Polygonum, Cyperus, Myrica	1,6,7,9, 10,12,13, 16,18
Savannah sparrow (Passerculus sandwichensis)	NE,DEL,CH, NC,SC,GA,	W,T	C	LM,HM	Echinochloa, Polygonum, Panicum, Cyperus	6-10,12,16
Grasshopper sparrow (Ammodramus savannarum)	DEL,CH,NC, NC,SC,GA	SU,T-north W,T-south	UC-FC	LM,HM	Polygonum, Panicum, grasshoppers, caterpillars	6,12
Henslow's sparrow (A. henslowii)	DEL,CH,NC, SC,GA	T	UC-FC	LM,HM	Panicum, Polygonum, beetles, grasshoppers	6,12,16
Le Conte's sparrow (A. leconteii)	SC,GA	W,T	UC	LM,HM	Panicum, Polygonum, grasshoppers, beetles	16,17
Sharp-tailed sparrow (A. caudacutus)	NE,DEL,CH NC,SC,GA	W,T	UC	LM,HM	Zizania, Panicum, leafhoppers	5,7,10
Vesper sparrow (Pooecetes gramineus)	DEL,CH,NC, SC,GA	W,T	UC	LM,HM	Polygonum, Panicum, beetles, grasshoppers	6,12
Slate-colored junco (Junco hyemalis)	DEL,CH,NC, SC,GA,FL	W,T	A	LM,HM	Polygonum, Panicum, Cyperus, Toxicodendron, beetles, caterpillars	6,12,16
Chipping sparrow (Spizella passerina)	NE,DEL,CH, NC,SC,GA, FL	SU,T-north P-mid W,T-south	C	LM,HM	grasshoppers, caterpillars, Setaria, Panicum, Amaranthus, Polygonum	1,6,7,12
Field sparrow (S. pusilla)	NE,DEL,CH NC,SC,GA, FL	P-north W,T-south	UC	LM,HM	Panicum, Amaranthus, Setaria, beetles, grasshoppers	6-8,10, 12,16
White-crowned sparrow (Zonotrichia leucophrys)	DEL,CH,NC, SC,GA,FL	W,T	C	LM,HM	Panicum, Polygonum, Setaria, Amaranthus, spiders, bees, wasps	6,7,9,10, 12
White-throated sparrow (Z. albicollis)	NE,DEL,CH, NC,SC,GA, FL	W,T	C-A	LM,HM	Polygonum, Setaria, Cyperus, Panicum, Amaranthus, ants, bees	6-10,12, 13,16
Fox sparrow (Passerella iliaca)	DEL,CH,NC, SC,GA,FL	W,T	UC	LM,HM	Polygonum, Setaria, Toxicodendron, millipedes, beetles	6,9,12, 13,16
Swamp sparrow (Melospiza georgiana)	NE,DEL,CH, NC,SC,GA, FL	W,T	C	LM,HM,TS	Cyperus, Polygonum, Panicum, Leersia, Setaria, beetles crickets, grasshoppers	1,5-9,12, 13,16

Family / Species	Region	Season	Status	Habitats	Food Habits	References
Song sparrow (*M. melodia*)	NE,DEL,CH, NC,SC,GA, FL	P-north W,T-south	A	LM,HM,TS	*Polygonum*, *Panicum*, *Cyperus*, *Amaranthus*, beetles, crickets	1,5-7,9, 12,13,16, 22
Snow bunting (*Plectrophenax nivalis*)	DEL,CH	W	UC	LM,HM	*Festuca*, *Setaria*, *Cyperus*, *Panicum*, fly larvae and pupae	6,10

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APPENDIX E:
Mammals of tidal freshwater wetlands of the Atlantic coastal region

Family / Species	Region	Status	Food habits	References
Didelphidae - opossums				
Virginia opossum (*Didelphis virginiana*)	NE,DEL,CH, NC,SC,GA	C	insects, fruits and berries, small mammals, birds	1,2,7, 14,15
Soricidae - shrews				
Masked shrew (*Sorex cinereus*)	DEL,CH	R	insects, crustaceans, mollusks	12
Southeastern shrew (*S. longirostris*)	CH,NC,SC,GA	C	spiders, slugs, snails	1,2,10
Short-tailed shrew (*Blarina brevicauda*)	NE,DEL,CH, NC,SC,GA	C	insects, crustaceans, annelids, mollusks	1,2,7,8, 14,15
Southern short-tailed shrew (*B. carolinensis*)	CH,NC,SC,GA	UC	crustaceans, insects, mollusks, annelids	1,9
Least shrew (*Cryptotis parva*)	CH,NC,SC,GA	A	grasshoppers, moths, beetle larvae, and other insects	1,9,12,13
Talpidae - moles				
Star-nosed mole (*Condylura cristata*)	NE,DEL,CH, GA	C	caddis fly larvae, midges, leeches, aquatic oligochaetes, small fish	1,8,9, 12,13,17
Eastern mole (*Scalopus aquaticus*)	DEL,CH,NC, SC,GA	UC	terrestrial and aquatic oligochaetes	1,8,9,14
Vespertilionidae - bats				
Silver-haired bat (*Lasionycteris noctivagans*)	NE,DEL,CH, NC,SC,GA	R-UC	flying insects	1
Big brown bat (*Eptesicus fuscus*)	NE,DEL,CH NC,SC,GA	C	Coleoptera, Hymenoptera	2,15
Seminole bat (*Lasiurus seminolus*)	NC,SC,GA,FL	C	crickets, large flying insects	3-5
Dasypodidae - armadilloes				
Nine-banded armadillo (*Dasypus novemcinctus*)	GA,FL	UC	beetle and their larvae, snails, slugs, centipedes	1,8

Family / Species	Region	Status	Food habits	References
Leporidae - rabbits				
Marsh rabbit (Sylvilagus palustris)	CH,NC,SC, GA,FL	R-north A-south	leaves, stems, roots of aquatic emergent plants	1-3,8,11
Eastern cottontail (S. floridanus)	NE,DEL,CH,NC, SC,GA,FL	LC	grasses, sedges, twigs of shrubs	1-3,7,14, 15,16
Sciuridae - chipmunks and squirrels				
Eastern chipmunk (Tamias striatus)	CH	UC	small birds, snakes, mice, slugs	3
Gray squirrel (Sciurus carolinensis)	NE,DEL,CH, NC,SC,GA,FL	UC	nuts, seeds, berries	1,2,8,15
Fox squirrel (S. niger)	CH,NC,SC,GA	R	seeds, berries, nuts	2,8
Southern flying squirrel (Glaucomys volans)	NC,SC,GA	R	berries, nuts, insects, small birds	2,3,8,15
Woodchuck (Marmota monax)	NE,DEL,CH	UC	perrenials, grasses, sedges	1,14,16
Castoridae - beavers				
Beaver (Castor canadensis)	NE,DEL,CH	LC	woody and aquatic plants - sweet gum, alder, willow, Peltandra, Pontederia, Nuphar, sedges, grasses	1,7,8, 12,13
Cricetidae - mice and rats				
Marsh rice rat (Oryzomys palustris)	DEL,CH,NC, SC,GA	A	seeds, esp. Zizania, grasses, sedges, insects	1,2,8,9, 13,15
Eastern harvest mouse (Reithrodontomys humulis)	CH,NC,SC, GA,FL	UC	moth larvae, seeds of grasses, esp. Setaria	3,9
White-footed mouse (Peromyscus leucopus)	NE,DEL,CH	A	insects, grasses, sedges, seeds of Impatiens	2,7,13,15
Cotton mouse (P. gossypinus)	NC,SC,GA,FL	C	grasses, sedges, insects	1,2,8
Deer mouse (P. maniculatus)	NE	C	rushes, grasses, sedges, berries, nuts	16
Eastern wood rat (Neotoma floridana)	SC,GA	C	grasses, sedges, seeds, nuts	1
Meadow vole (Microtus pennsylvanicus)	NE,DEL,CH	C	rushes, sedges, grasses	7,15

Family / Species	Region	Status	Food habits	References
Muskrat (*Ondatra zibethicus*)	NE,DEL,CH	C-LA	roots and rhizomes of: *Scirpus americanus*, *Saggitaria*, *Typha*, *Leersia*, *Zizania*, *Pontederia*, *Cyperus*, *Panicum.*, and many others	1-3,7,8,12, 13,15,16
Southern bog lemming (*Synaptomys cooperi*)	CH	UC	grasses, sedges	12,13
Hispid cotton rat (*Sigmodon hispidus*)	SC,GA,FL	A	crayfish, insects, grasses, sedges	1-3,9
Muridae - old world mice				
House mouse (*Mus musculus*)	NE,DEL,CH, NC,SC,GA,FL	C	seeds, esp. *Setaria*, beetle and butterfly larvae	1,14
Norway rat (*Rattus norvegicus*)	DEL,CH,NC,SC	UC	seeds, small mammals and birds	3,7,14,15
Zapodidae - jumping mice				
Meadow jumping mouse (*Zapus hudsonius*)	NE,DEL,CH,NC	UC	beetles, cutworms, berries, seeds, esp. *Impatiens*	3,13,14
Capromyidae - nutrias				
Nutria (*Myocastor coypus*)	DEL,CH,NC	UC-LA	stems and leaves of: *Typha*, grasses, rushes, sedges	12,15
Canidae - foxes				
Red fox (*Vulpes vulpes*)	NE,CH,SC,GA	UC	rabbits, mice, voles, birds, snakes	1,7,8,15,16
Gray fox (*Urocyon cinereoargenteus*)	NE,NC,SC,GA	UC	mice, voles, shrews, rabbits	2,7-9,15
Ursidae - bears				
Black bear (*Ursus americanus*)	NC,SC,GA	R	omnivorus	2,9
Procyonidae - raccoons				
Eastern raccoon (*Procyon lotor*)	NE,DEL,CH,NC, SC,GA,FL	C	fish, crayfish, frogs, mussels, birds, reptiles, muskrats	1,2,12,13, 15,16,18

Family / Species	Region	Status	Food habits	References
Mustelidae - weasels				
Long-tailed weasel (*Mustela frenata*)	NE,DEL,CH, NC,SC,GA	R	mice, rabbits, rats, shrews	6,8,10,14
Mink (*M. vison*)	NE,DEL,CH, NC,SC,GA,FL	UC	mice, voles, frogs, small birds, muskrats	1,2,6-9, 12,13,15
Striped skunk (*Mephitis mephitis*)	NE,DEL,CH,NC, SC,GA,FL	UC	mice, beetles, berries, crickets, nuts amphibians	2,3,8, 15,16
River otter (*Lutra canadensis*)	NE,CH,NC, SC,GA,FL	LC	crayfish, frogs, turtles, fish	1,2,6-8,12 13,15
Felidae - cats				
Bobcat (*Felis rufus*)	CH,NC,SC, GA,FL	UC-LC	marsh rabbits, muskrats, squirrels, mice	2,8
Cervidae - deer				
White-tailed deer (*Odocoileus virginianus*)	NE,DEL,CH, NC,SC,GA,FL	UC	sedges, grasses, esp. *Zizania*	1,2,7-9, 12,14,15,16
Delphinidae - dolphins				
Common dolphin (*Delphinus delphis*)	NE	UC	fish	7

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50272-101

REPORT DOCUMENTATION PAGE	1. REPORT NO. FWS/OBS-83/17	2.	3. Recipient's Accession No.

4. Title and Subtitle
The Ecology of Tidal Freshwater Marshes of the United States East Coast: A Community Profile

5. Report Date
January 1984

6.

7. Author(s) William E. Odum, Thomas J. Smith III, John K. Hoover and Carole C. McIvor

8. Performing Organization Rept. No.

Authors' Affiliation
University of Virginia
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10. Project/Task/Work Unit No.

11. Contract(C) or Grant(G) No.
(C)
(G)

12. Sponsoring Organization Name and Address
U.S. Fish and Wildlife Service
Division of Biological Services
Department of the Interior
Washington, DC 20240

13. Type of Report & Period Covered

14.

15. Supplementary Notes

16. Abstract (Limit: 200 words)

Tidal freshwater marshes are a distinctive type of estuarine ecosystem located upstream from tidal saline marshes and downstream fron non-tidal freshwater marshes. They are characterized by freshwater or nearly freshwater conditions most of the time, flora and fauna dominated by freshwater species, and daily lunar tidal flushing. This report examines the ecology of this community as it occurs along the Atlantic seaboard from southern New England to northern Florida.

This marsh community is heavily influenced by river flow, which maintains freshwater conditions and deposits sediments high in silt and clay. The plant assemblage in tidal freshwater marshes is diverse both in numbers of species and structural plant types. Plant community structure is markedly diverse spatially and seasonally, and reflects the dynamic processing of energy and biomass in the marsh through high productivity, rapid decomposition and seasonal nutrient cycling.

The diverse niches in this heterogeneous environment are exploited by a very diverse animal community of as many as 125 species of fish, 102 species of amphibians and reptiles, 280 species of birds, and 46 species of mammals over the community's broad range. Although fewer species are permanent residents or marsh breeders, use of this community for food and cover is high. This use, coupled with the marshes' capacity to be natural buffers and water filters, argue for their high value as natural resources.

17. Document Analysis a. Descriptors

Ecology, primary biological productivity, decomposition, invertebrates, fishes, amphibia, reptiles, birds

b. Identifiers/Open-Ended Terms

Tidal freshwater marsh, ecological succession, plant demography, nutrient cycling, carbon flux, energy flow

c. COSATI Field/Group

18. Availability Statement	19. Security Class (This Report)	21. No. of Pages
Unlimited	Unclassified	ix + 176
	20. Security Class (This Page)	22. Price
	Unclassified	

(See ANSI-Z39.18)

OPTIONAL FORM 272 (4-77)
(Formerly NTIS-35)
Department of Commerce

☆U.S. GOVERNMENT PRINTING OFFICE: 1984-771-783