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AN ECOLOGICAL CHARACTERIZATION OF COASTAL MAINE
(North and East of Cape Elizabeth)

Stewart I. Fefer and Patricia A. Schettig
Principal Investigators

Volume 2

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Department of the Interior
U.S. Fish and Wildlife Service
Northeast Region
One Gateway Center, Suite 700
Newton Corner, Massachusetts 02158

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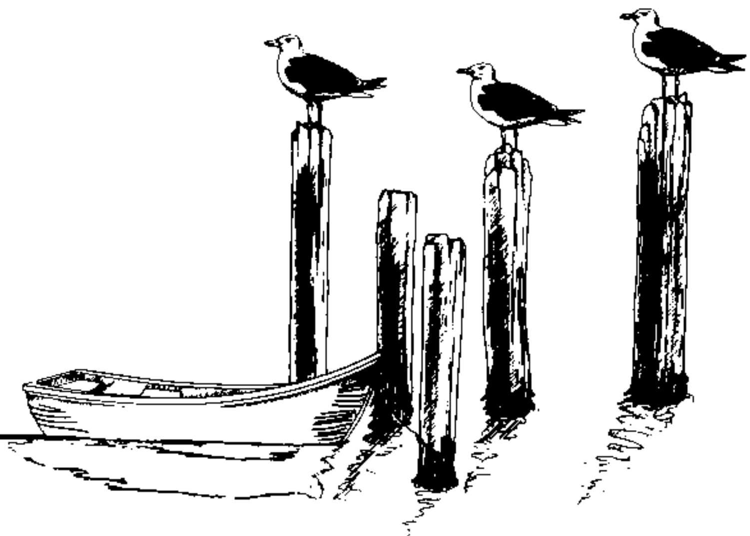
The Organization of the Characterization	Stewart Fefer	U.S. Fish and Wildlife Service
	Patricia Schettig	U.S. Fish and Wildlife Service
The Coastal Maine Ecosystem	Stewart Fefer	
	Edward Shenton	New England Coastal Oceanographic Group
	Barry Timson	Mahoosuc Corporation
	Dave Strimaitis	Environmental Research and Technology
Human Impacts on the Ecosystem	Stewart Fefer	
	Norman Famous	University of Maine at Orono
	Lawrence Thornton	N.J. Department of Environmental Protection
	Dr. Peter Larsen	Bigelow Laboratories for the Ocean Sciences
	Richard Lee	Bigelow Laboratories for the Ocean Sciences
The Marine System	Dr. Peter Larsen	
	Lee Doggett	Bigelow Laboratories for the Ocean Sciences
	Dr. Chris Garside	Bigelow Laboratories for the Ocean Sciences
	Dr. Jerry Topinka	Bigelow Laboratories for the Ocean Sciences
	Dr. Tim Mague	Bigelow Laboratories for the Ocean Sciences
	Charles Yentsch	Bigelow Laboratories for the Ocean Sciences
	Toby Garfield	Bigelow Laboratories for the Ocean Sciences
	Dr. Ray Gerber	Bowdoin College
The Estuarine System	Dr. Peter Larsen	
	Lee Doggett	
	Dr. Chris Garside	
	Dr. Jerry Topinka	
	Dr. Tim Mague	
	Toby Garfield	
	Dr. Ray Gerber	
	Stewart Fefer	
	Patricia Schettig	
	Lawrence Thornton	
The Riverine System	Russell McCullough	Maine Cooperative Fishery Unit, Orono
	Stewart Fefer	
The Lacustrine System	Dr. Ronald Davis	University of Maine at Orono
	Stewart Fefer	
	Meryl Freeman	University of Maine at Orono
The Palustrine System	Stewart Fefer	
The Forest System	Dr. Craig Ferris	University of Maine at Orono
Agricultural and Developed Land	Dr. Craig Ferris	
Fishes	Patricia Schettig	
	Stanley Chenoweth	Maine Department of Marine Resources
	Beth Surgens	U.S. Fish and Wildlife Service
Commercially Important Invertebrates	Lee Doggett	
	Susan Sykes	Bigelow Laboratories for the Ocean Sciences
Marine Mammals	Patricia Schettig	
	Cheryl Klink	U.S. Fish and Wildlife Service
Waterbirds	Norman Famous	
	Dr. Craig Ferris	
Waterfowl	Howard Spencer, Jr.	Maine Department of Inland Fisheries and Wildlife
	Dr. Kenneth Reinecke	U.S. Fish and Wildlife Service
	John Parsons	U.S. Fish and Wildlife Service
Terrestrial Birds	Norman Famous	
	Charles Todd	University of Maine at Orono
	Dr. Craig Ferris	

Terrestrial Mammals	Dr. Craig Ferris	
Reptiles and Amphibians	Dr. Craig Ferris	
	Sally Rooney	University of Maine at Orono
Commercially Important Forest Types	Dr. David Canavera	University of Maine at Orono
Endangered, Threatened, and Rare Plants	Norman Famous	
	Dr. Craig Ferris	
Atlas Introduction	Beth Surgen	
	Dean Johnson	U.S. Fish and Wildlife Service
Technical Guidance and Conceptual Framework	Curt Laffin	U.S. Fish and Wildlife Service
	Dr. James Johnston	U.S. Fish and Wildlife Service
Editor	Eileen Dunne	Consultant
Technical Editing	John Parsons	
	Kenneth Adams	U.S. Fish and Wildlife Service
	Norman Benson	U.S. Fish and Wildlife Service
	Carroll Cordes	U.S. Fish and Wildlife Service
	Carolyn French	U.S. Fish and Wildlife Service
	Wiley Kitchens	U.S. Fish and Wildlife Service
	Martha Young	U.S. Fish and Wildlife Service
Artwork and Layout	Eleanor Bradshaw	U.S. Fish and Wildlife Service
	Nancy Perry	U.S. Fish and Wildlife Service
	Lynn Bjorklund	U.S. Fish and Wildlife Service
Data Collection and Analysis	Beth Surgens	
	Cheryl Klink	
	Renata Cirri	University of Maine at Orono
	Peter Moberg	University of Maine at Orono
	Terry McGovern	University of Maine at Orono
	Porter Turnbull	University of Maine at Orono
	Jean Garside	Bigelow Laboratories for the Ocean Sciences
	Veronica Berounsky	Bigelow Laboratories for the Ocean Sciences
	Linda Cummings	U.S. Fish and Wildlife Service
Word Processing	Renata Cirri	
	Ruth Walsh	Consultant
	Peg Colby	Bigelow Laboratories for the Ocean Sciences
	Teve MacFarland	Bigelow Laboratories for the Ocean Sciences
	Doris Dombrowsky	Bigelow Laboratories for the Ocean Sciences
	Dot Dimetriff	Bigelow Laboratories for the Ocean Sciences
	Joyce Aiello	U.S. Fish and Wildlife Service
	Linda Cummings	
Data Source Appendix	Elaine McLaughlin	U.S. Fish and Wildlife Service
Cartography	Dean Johnson	
	Beth Surgens	
	Eleanor Bradshaw	
	Lynn Bjorklund	
	Nancy Perry	
	Liam O'Brien	U.S. Fish and Wildlife Service
	Carl Melberg	U.S. Fish and Wildlife Service
	Mike Fantasia	U.S. Fish and Wildlife Service
	Steve Gale	U.S. Fish and Wildlife Service
Production Manager	Renata Cirri	Consultant

Chapter 4
The Marine System



Authors: Bigelow Laboratories for Ocean Sciences

The marine system is the largest and most ubiquitous aquatic system in coastal Maine. Coastal Maine waters support many industries, including commercial fishing, transportation, waste disposal, and recreation. They sustain diverse food webs of organisms that directly and indirectly benefit people. Ultimately, the marine system receives waters that pass through all other systems in the coastal zone. This chapter will present some basic concepts and data on the functions of the marine system. Such information is essential if wise decisions balancing the various uses of the marine system are to be made.

The marine system is that area exposed to full-strength sea water (over 30 ppt salinity) between extreme high water of a spring tide and the 300-foot (100 m) depth contour. It is located along the shoreline in open embayments and seaward of the headlands and encompasses the overlying water as well as the substratum beneath the water (figure 4-1).

The habitats encompassed by the marine system include the water column and the major bottom substrata of unconsolidated sediments and rocky bottoms. Unconsolidated sediments include cobble, gravel, sand, and mud, as well as eelgrass or emergent wetland subhabitats growing on the sediments and streams flowing over the sediments. Rocky substrata are bedrock or boulder with algal beds (kelp) attached to the rock. The area between the tides (intertidal zone) is ecologically different from the area that is submerged at all times (subtidal zone), hence, the two zones and their habitats are discussed separately here.

The area of marine waters along the shoreline of the characterization area is 172,705 acres (69,921 ha; National Wetlands Inventory, preliminary data). The acreage of marine waters between the embayments and 300-foot (100 m) depth contour was not calculated by the NWI but amounts to more than the number of acres inshore. The specific locations of the marine system in the characterization area are depicted in atlas map 1.

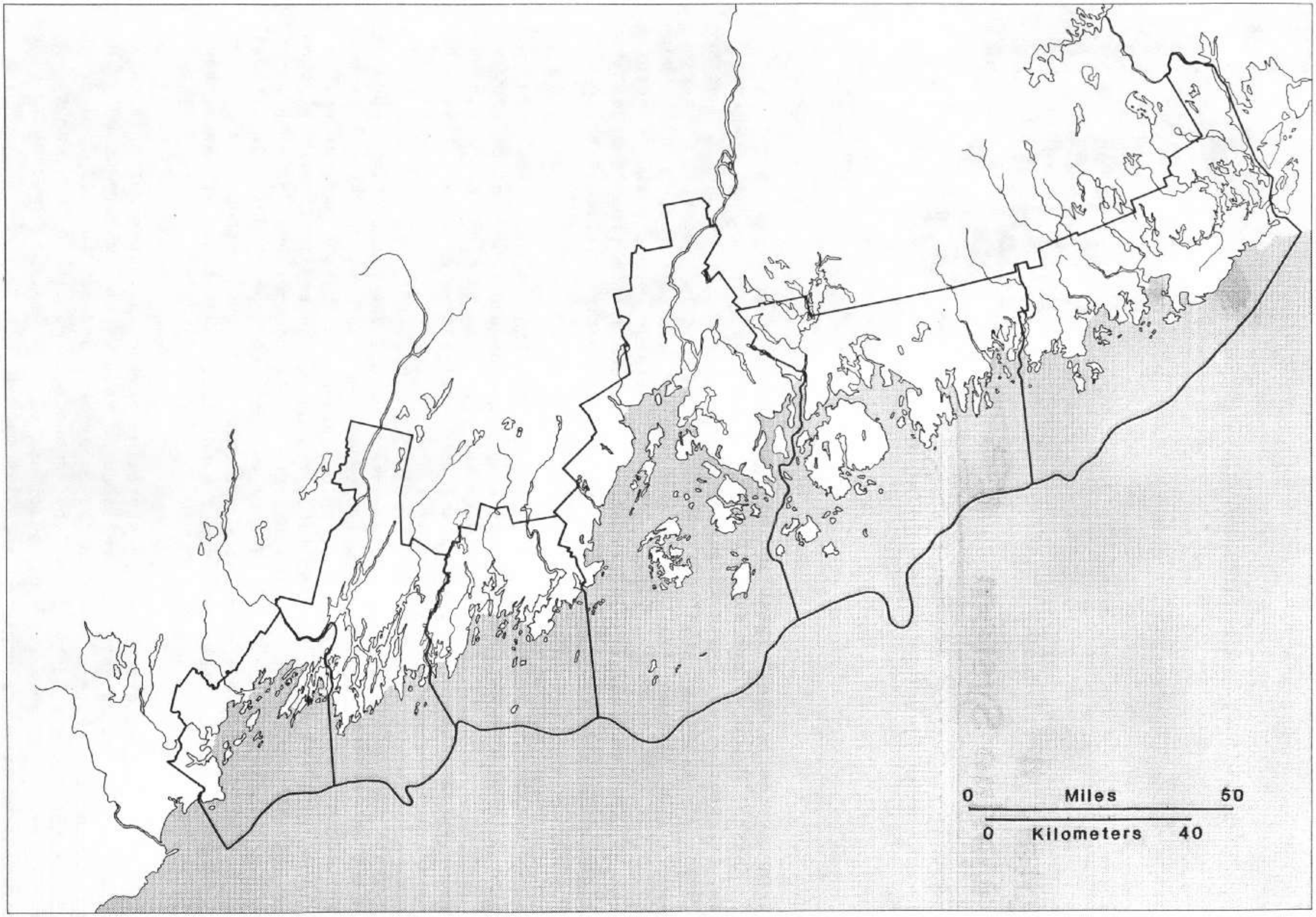


Figure 4-1. The Maine Coast Characterization Area Marine System.

The Maine marine system is characterized by salinities ranging between 30 and 32 ppt, a moderate seasonal temperature range (27° F; 15° C), wide seasonal variation in solar radiation, periods of fog, severe storms, large tidal amplitudes, and a poorly understood system of coastal currents. Zoogeographically, Maine can be considered boreal (cold temperate). On the North American continent the boreal zone is a narrow area extending from Cape Cod to Labrador and is ecologically similar to the broad boreal zone in northwestern Europe.

General descriptions of physical and biological factors related to the marine system are given in this chapter to illustrate the interrelationships and dynamic nature of the life-supporting processes in the marine environment. The abiotic physical factors addressed include geology, hydrography, and climate. The biotic factors discussed include biotic roles in the ecosystem, energy flow, and biogeochemical cycling. Finally, the marine system is examined as a hierarchical structure (figure 4-2) based on substrata, media, or vegetative forms. Abiotic and biotic compositions and functions of specific habitats found along the Maine coast are described. Common names of species are used except where generally accepted common names do not exist. Taxonomic names of all species mentioned in the text are given in the appendix to chapter 1. Data are scarce at the class level, yet it is here that information is most often needed for impact assessment.

DATA SOURCES AND COMPILATION OF DATA

This chapter synthesizes the existing environmental information on Maine's marine system. It draws on published and unpublished literature, preliminary results of the National Wetlands Inventory (NWI) of the U.S. Fish and Wildlife Service, personal communication with persons active in research or management of the system, and the experience of the authors. Information not otherwise documented has been supplied by the authors.

Sufficient reliable data are not available to characterize clearly many of the components of the marine system or to understand fully interactions among the components. To a certain extent this shortcoming has been overcome by using data generated in other similar areas (such as Nova Scotia, Canada, or northwestern Europe) that have been more fully studied, or by using general concepts that apply to Maine.

Data gaps are addressed at the end of this chapter. All literature used to produce this chapter is listed at the end of this chapter and in the Data Source Appendix (volume 5). Many other data sources were reviewed but not used directly, and these items also are included in the Data Source Appendix.

Many components of the marine system are similar to those of the estuarine system. All aspects of the marine system are discussed at the generic level but, for the sake of brevity, only those that are unique to the marine system are discussed at the class or habitat level. Habitats that have characteristics specific to the marine system include exposed rocky shore, boulder beach, and sand beach in the intertidal subsystem; and unconsolidated bottom and rock bottom in the subtidal subsystem. Not enough information is available on Maine aquatic beds to determine whether they differ between marine and estuarine systems.

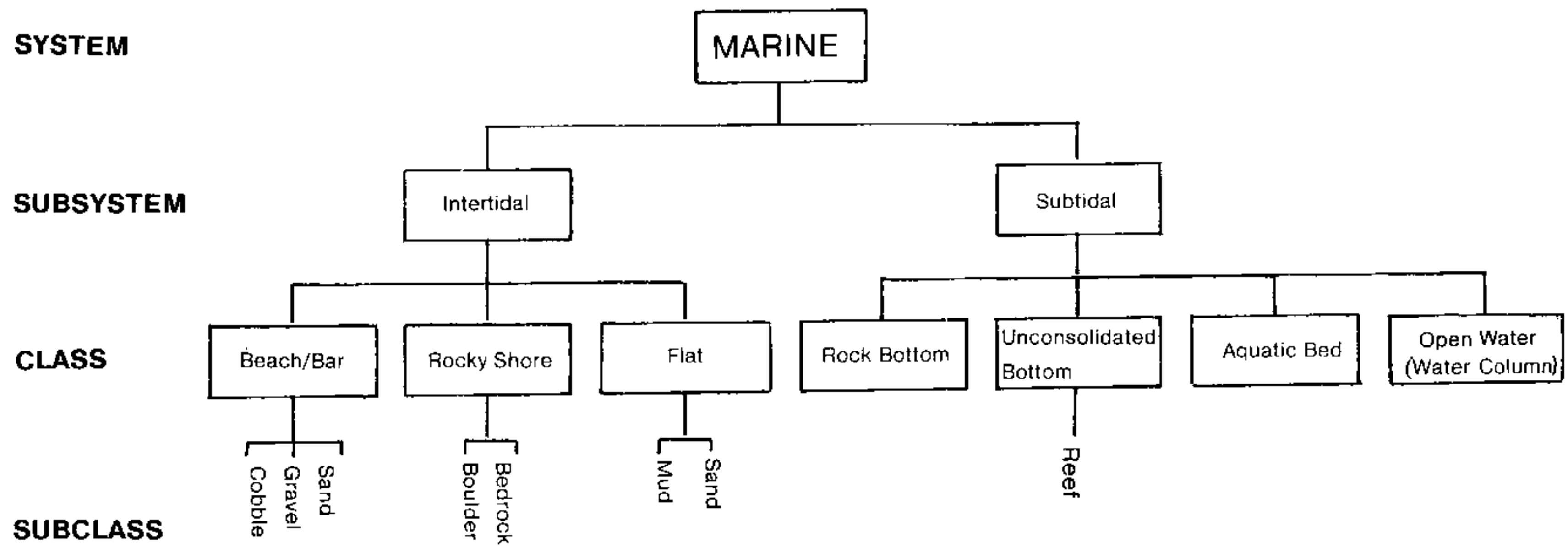


Figure 4-2. Hierarchical classification of the marine system of coastal Maine (Cowardin et al. 1979).

Information from the NWI on the location and extent of marine habitats is incorporated. Habitat units are mapped at a minimum resolution of about 3 to 5 acres (1 to 2 ha) in the NWI (personal communication from R. W. Tiner, U.S. Fish and Wildlife Service, Newton, MA; June, 1978). Thus, habitat areas smaller than 3 acres (1.2 ha) generally were not mapped. A particular marine habitat may contain more than one marine class and a particular marine class may contain areas of other marine classes smaller than 3 acres. For example, an area mapped as a 5-acre (2 ha) flat may consist of a sand or mud flat surrounded by emergent wetland and rocky shore with an aquatic bed or mussel reef in the lower intertidal area. If each of these habitat types (rocky shore, emergent wetland, reef, and aquatic bed) was 3 to 5 acres (1.2 ha to 2 ha) or larger they would be mapped as distinct units. Small-scale variations in abiotic factors affecting marine areas may result in several marine classes being found in the same area. These classes may intergrade into one another, adding to the difficulty of precise classification. The NWI provides the user with data on the distribution of marine habitats in the Maine coastal zone. These data provide a baseline against which the future status of marine habitats can be measured.

Marine classes identified by the NWI include aquatic bed, unconsolidated bottom, open water, and rocky bottom in the subtidal subsystem; and aquatic bed, beach/bar, flat, reef, and rocky shore in the intertidal subsystem (figure 4-2). Marine classes of rock bottom, unconsolidated bottom, and aquatic bed have been mapped mostly as open water, although a few areas have been designated as unconsolidated bottom; and, as much rock bottom is vegetated (principally by kelp), it is therefore classified as aquatic bed.

In classifying the intertidal zone, the NWI included the splash zone. An estimated 34% of the rocky intertidal acreage (personal communication from J. A. Topinka, Bigelow Laboratory, West Boothbay Harbor, ME; November, 1979) identified by the NWI is above the zone where macroalgae are found. Other intertidal classes include flats, beach/bars, aquatic beds, and reefs. Flats include both sand and mud flats and stream beds crossing the flats. Beach/bar encompasses cobble, gravel, and sand beaches. Both boulder beaches and bedrock are mapped as rocky shore. Intertidal and subtidal aquatic beds are principally eelgrass on mud sediments. Reefs are composed of mussels and usually are found on mud flats. Since many of these subhabitats (e.g., sand vs. mud) are ecologically distinct they will be addressed separately here. Lack of useful data prevents an in-depth discussion of each subhabitat.

DISTRIBUTION OF THE MARINE SYSTEM

The eastern regions of the characterization area (regions 4, 5, and 6) have greater areas of marine waters than those in the west (regions 1, 2, and 3; table 4-1). If the area of water to the 300-foot contour were included (rather than just that area enclosed by headlands as calculated by the NWI), the eastern regions would have an even higher percentage of marine waters. In these regions the 300-foot contour is farther offshore. Part of this discrepancy between regions is due to differences in size. Large bays are encompassed in region 1 (Casco Bay), region 4 (Penobscot Bay), region 5 (Frenchman Bay and Blue Hill Bay), and region 6 (Cobscook Bay), which account for the high acreage of subtidal and intertidal areas in these regions. Regions 2 and 3 encompass smaller segments of the coast and have more acres of estuarine waters than marine waters.

Table 4-1. Area (acres) of Marine Waters in Each of the Coastal Regions and Its Percentage Contribution to the total.

Region	Acres	Percentage
1	25,356	15
2	3863	2
3	4430	3
4	56,062	32
5	38,459	22
6	44,535	26
Total	172,705	100

Subtidal acreage, which is greatly underestimated (data seaward of the headlands were not calculated), is a much higher percentage of the total marine water area than intertidal acreage: 65% (112,130 acres; 45,397 ha) vs. 35% (60,576 acres; 24,525 ha), respectively. Open water covers the entire subtidal zone and, therefore, is equal in acreage to that zone. Unconsolidated bottom comprises 25% or 28,202 acres (11,418 ha) of the subtidal zone. However, as noted previously, most of the substratum under the open water is unconsolidated bottom.

The largest habitat acreages in the intertidal zone are flats [48% or 28,803 acres (11,661 ha)] and rocky shores [36% or 21,521 acres (8713 ha)] . Aquatic beds and beach/bars make up most of the remaining acreage with 10% (6202 acres; 2511 ha) and 6% (3897 acres; 1578 ha), respectively.

The distribution of marine habitats in each of the towns in coastal Maine is included in appendix A of chapter 2.

The marine system of coastal Maine is located between an estuarine system of much less acreage and a deepwater marine area of vast acreage. The three areas are contiguous and processes occurring in any area have the potential to affect the others.

ABIOTIC FEATURES

Abiotic factors are forcing functions that influence the biotic components of the ecosystem. This section addresses the geology, hydrography, and climate of nearshore areas.

Geology

Geology has a primary role in shaping the ecology of the marine system. The biological communities that comprise the marine system are often related to substrate types. NWI categories are often defined by substratum characteristics (figure 4-2). Since the marine system is composed of many varieties of deposits, the descriptions of the geologic substrata are found in the class level discussions below. The size distribution of substratum particles by habitat is given in figure 4-3. The composition and formation of the substrata in the marine system, and the primary abiotic forces affecting it, are summarized in table 4-2. A general discussion of coastal marine geology is contained in "Geology," page 2-35 in Chapter 2.

In coastal Maine, human activities may affect the marine system by altering the marine geology and associated erosion and sedimentation rates. Coastal developments in and adjacent to the marine system and dredging and filling are activities that could alter the marine geology. For a discussion of the extent of these activities and their potential impacts, see chapter 3, "Human Impacts on the Ecosystem."

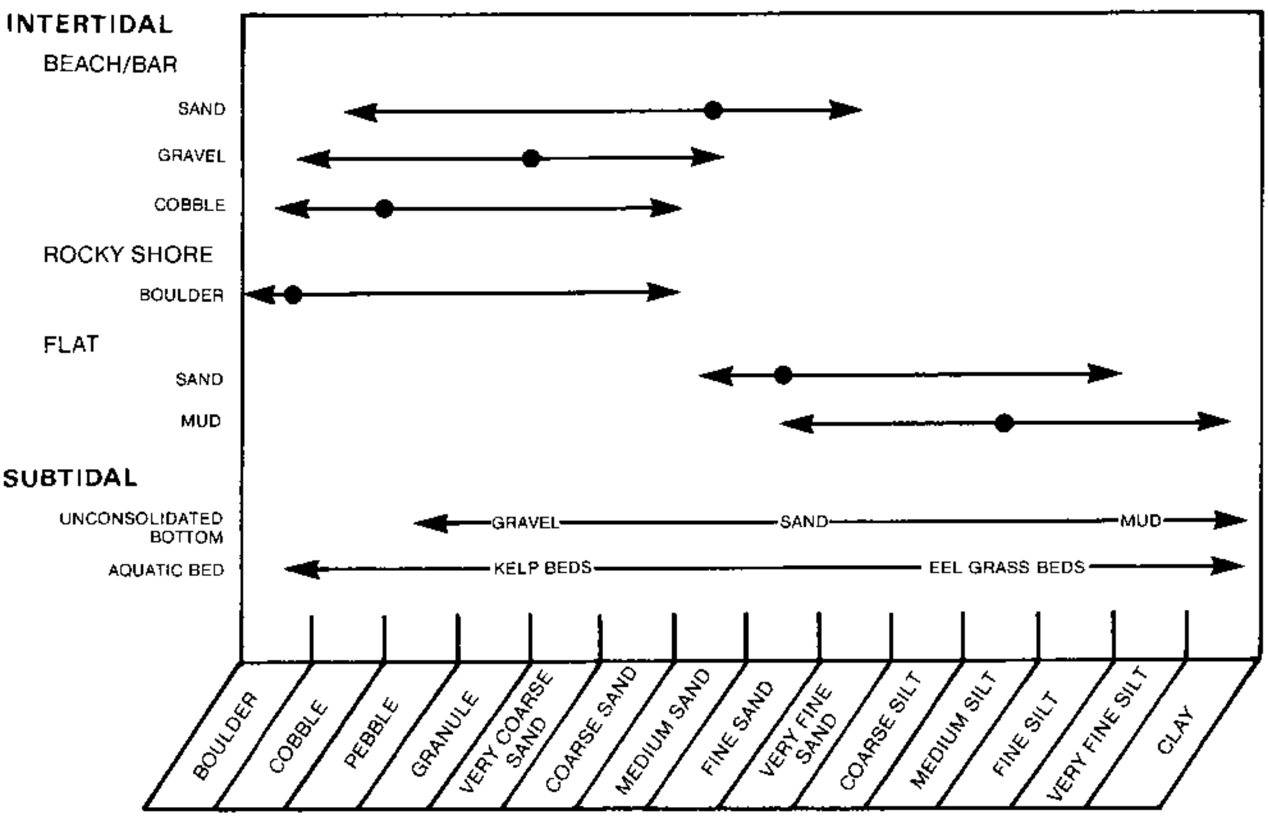


Figure 4-3. Size distribution of sediment particles in marine habitats of coastal Maine. Dots indicate dominant size; arrows indicate range.

Table 4-2. Composition, Formation and, Primary Abiotic Forces Affecting the Substrata of the Estuarine System and Subsystems.

Subsystem	Class	Origin or formation	Composition	Abiotic forces affecting substrata
Intertidal				
	Beach/bar			
	Gravel	Erosion of adjecent upland formed earlier and migrated landward with rise in sea level Growth from headland	Coarse pebble	Waves and wave-generated currents
	Cobble	Erosion of adjacent upland or shallow offshore deposits	Cobble	Waves
	Rocky shore			
	Ledge	Submergence of exposed bedrock	Bedrock	Waves, tidal currents and ice
	Flat			
	Sand	Erosion of adjacent upland Deposited from tidal channel from riverine or subtidal sources	Medium to very fine sand	Tidal currents and waves biogenic reworking

(Continued)

Table 4-2 (continued)

Subsystem	Class	Origin or formation	Composition	Abiotic forces affecting substrata
Intertidal (Cont.)				
	Flat (cont.)			
	Mud	Erosion of adjacent upland Suspended sediment deposition from riverine or offshore sources Sediment derived from other parts of flat	Coarse to medium silt	Tidal currents, waves biogenic reworking
Subtidal				
	Unconsolidated Bottom			
	Gravel	Lag deposits in tidal channel bottoms	Pebble to coarse sand	Tidal currents, waves
	Sand	Derived from erosion of shoreward beaches or submergence of sand flats	Very fine sand	Tidal currents, wave-generated currents biogenic reworking
	Mud	Deposition of suspended sediment from water column	Fine silt to clay	Tidal currents, wave-generated currents biogenic reworking

(Continued)

Table 4-2 (concluded)

Subsystem	Class	Origin or formation	Composition	Abiotic forces affecting substrata
Subtidal (cont.)				
	Ledge	Submergence of exposed bedrocks	Parent material	Tidal currents, wave-generated currents
	Aquatic bed			
	Eelgrass	See Intertidal and Subtidal Mud Flat	Silt	Tidal currents, wave-generated currents biogenic reworking
	Kelp beds	See Ledge and Gravel Unconsolidated Bottom		

Hydrography

The circulation patterns in the Gulf of Maine determine the distribution of much of the fauna of the marine system in coastal Maine. Density, Coriolis force pressure (the force due to the rotation of the earth on its axis), drag, and boundary configuration are the primary parameters controlling circulation. Temperature and salinity determine the density of marine waters. "Temperature (and probably salinity to a lesser extent)...in some way affects survival of whole populations of young fish, perhaps through affecting their food supply or rate of growth and, consequently, their resistance to adverse environmental conditions" (Taylor et al. 1957). Fluctuations in mackerel, lobsters, whiting, and yellowtail flounder abundance were found to be correlated with fluctuations in sea water temperature (Taylor et al. 1957). Other environmental factors have been correlated with catches of commercially important fisheries but temperature is the parameter most frequently used, in part due to the existence of long and continuous records (e.g., in the Gulf of Maine; Iselin 1939; Redfield 1939; Carruthers 1951; Templeman and Fleming 1953; Chase 1955; Colton and Temple 1961; Dow 1964a, 1964b, and 1977; Martin and Kohler 1965; Flowers and Saila 1972; Dickson and Lee 1972; Iles 1973; Gulland 1965; and Sutcliffe et al. 1977).

Long-term continuous temperature records have been maintained in Maine only at Boothbay Harbor (region 2), since 1906, and at St. Andrews, New Brunswick, Canada, (near region 6), since 1921. Short-term and intermittant data have been collected at other sites along the coast by various government agencies (e.g., Kangas 1974). Published mean monthly temperature records and seawater densities (from which salinity can be determined) are published for stations at Eastport (since 1930), Bar Harbor (since 1947), Pulpit Harbor (1945 to 1946), and Portland (1922 to 1945 and since 1956; U.S. Department of Commerce 1972). Salinity values have been obtained daily at Boothbay Harbor since 1966.

The most comprehensive physical oceanographic study of the Gulf of Maine was conducted by Bigelow (1927) from 1912 to 1925. Subsequent studies on the hydrography of the Gulf generally substantiate Bigelow's findings. Summaries of more recent studies are given in Colton (1964), Bumpus (1973), and Hopkins and Garfield (1979). Although a number of studies have been conducted in the Gulf of Maine, sufficiently detailed data to determine more than the broad generalized circulation patterns are not available. This scarcity of data precludes a more specific discussion.

Long-term temperature trends. Temperature has a major influence on the distribution of most organisms. The Gulf of Maine is subject to long-term temperature trends. These trends are particularly important in the characterization area, where many species are at the northern or southern limit of their ranges.

In inshore coastal areas, based on records from Boothbay Harbor, annual mean surface temperatures have varied over a 9°F (5° C) range since 1906. Mean annual temperatures recorded at Boothbay Harbor from 1906 through 1978 are illustrated in figure 4-4. The 5-year moving average of sea surface temperatures (figure 4-4) illustrates the fact that until the early 1940s mean annual water temperatures were generally below approximately 47° F (8.3 °C). Since this time, mean annual water temperatures have been above 47° F. During

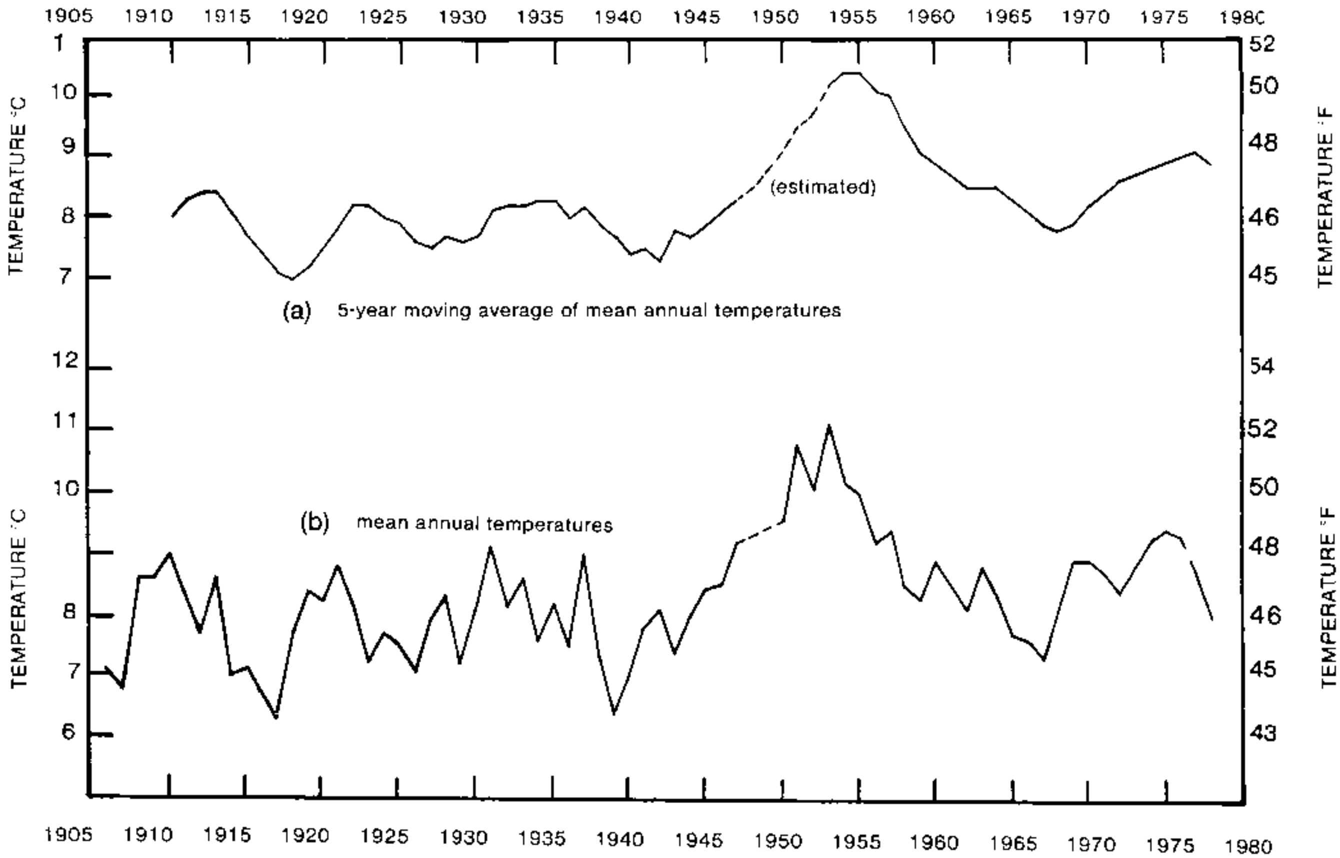


Figure 4-4. Mean annual sea surface temperatures recorded at Boothbay Harbor from 1906 to 1978 (a) and 5-year moving average (b) (Garfield and Welch 1978).

the warming trend beginning in the 1940s, warmer winter water temperatures accounted for most of the observed rise (Taylor et al. 1957). Warmer winters could affect plant and animal populations by decreasing icing, which causes mortalities in the intertidal zone, and allowing southern species to survive winter.

Atmospheric temperature variability is the main cause of fluctuations in sea water, but the formation of locally produced dense cold water in winter complicates the relationship. Similar long-term trends were found in the data from St. Andrews, New Brunswick. However, absolute temperatures differ between the two regions.

Seasonal changes in temperature and salinity. The temperate coastal waters of New England exhibit large seasonal variation in temperature compared to most oceanic waters. The seasonal range of water temperature in region 2 (i.e., Boothbay Harbor) is from 28° F (-2 °C) to about 73 °F (23 °C). Physiological processes of organisms can be markedly affected over this range.

Seasonal changes in coastal water off Boothbay Harbor, described below, are based on a time series of data from Apollonio and Applin (1972; appendix A). Although this time series represents the most comprehensive collection of data available, too few stations were sampled to draw more than general conclusions about nearshore temperature distribution. Small-scale temperature variability, due to turbulent mixing induced by currents, and irregular topography in this area make temperature distribution too complex to be deduced from such a limited number of stations.

As spring approaches, the atmosphere warms the surface waters of the ocean, making them less dense, and a distinct surface layer forms. This layer becomes thicker as warming continues and in Maine coastal waters reaches 100 feet (30 m) by August. Its depth is clearly defined by a rapid change in temperature of several degrees in a few meters and a correspondingly rapid increase (downward) in density. The density change lends a great deal of stability to this boundary, which is called a seasonal thermocline or pycnocline. From the time of its initial formation (May in Maine) the thermocline separates the ocean into two layers, each of which mixes relatively freely within itself but has only limited exchange with the other.

During the fall and winter months, when atmospheric temperatures are lower than sea surface temperatures, waters lose heat to the atmosphere and cool until they become sufficiently dense to sink. Continued cooling results in overturn of the entire water column, which results in water of uniform properties being distributed from surface to bottom or to approximately 300 to 500 feet (100 to 150 m) in deep water (late February).

A number of processes occur that can affect the seasonal cycle described above. They include storms, upwelling , and tidal currents. Seasonal fluctuations in salinity are greatest in areas adjacent to freshwater discharges. Changes in salinity in marine waters near the mouths of estuaries in the characterization area have not been monitored. The extent of influence of this runoff in marine waters is therefore unknown. The Kennebec estuary (region 2) and the Penobscot estuary (region 4) are expected to have the greatest effect on the salinity of adjacent marine waters.

According to records from Boothbay Harbor (region 2), the nearshore salinity cycle proceeds from a November maximum to a May minimum (figure 4-5). No significant correlation between salinity and precipitation has been recorded at Boothbay Harbor. Since the salinity recorder is below the depth of short-term surface mixing and away from areas of energetic tidal mixing, usually a period of a day or longer passes before a reduction in salinity due to precipitation occurs, if it occurs at all.

It is not possible to establish a strong correlation between river discharge and surface salinity either. Local currents and distance from gaged freshwater sources are two factors that obscure the relationship between salinity and land runoff.

In offshore waters at Boothbay Harbor (region 2), salinity data (Apollonio and Applin 1972) indicate that upwelling of deeper water may be taking place at certain times of the year and the boundary runoff may be diluting sea water at other times. As with temperature, the actual distribution is much more complex than can be represented by the number of stations sampled.

Below approximately 400 feet (120 m), neither temperature, salinity, nor density show much seasonal variation. Water below this depth is removed from direct atmospheric influences, and any short-term variability is caused by other factors, such as changes in the sea water outside the Gulf of Maine.

Spatial variability of coastal waters. Organisms have specific ranges of temperatures and salinities outside which they cannot survive or reproduce; therefore, variability among these parameters is significant. A great deal of alongshore (see figure 4-6 for station locations) variability in temperature and salinity was found by Speirs and coworkers (1976). Generally, temperature and salinity variability was greatest at the stations most exposed to river discharge and least at offshore stations. (The data from these stations are given in appendix B). Generally, river discharge, besides potentially carrying pollutants, creates a variable environment to which organisms must adapt.

In the characterization area temperature variability decreases from west to east (Graham 1970a). Summer salinities are generally lower than winter salinities, due to river discharge. In both summer and winter, surface salinity shows a trend of increasing values from west to east. Both the smaller temperature range and the higher salinities in the east are attributable to increased tidally induced mixing (see "Processes influencing coastal water" below) toward the Bay of Fundy (see also appendix C). This decreased environmental variability may allow for the development of more diverse biotic communities.

The 1975 summer distribution of surface temperature and salinity (Yentsch et al. 1976; see appendix D), indicates the same trends. A major difference in the eastern distribution of temperature is evident. In 1963 temperature decreased in the offshore direction, while in 1975 temperature increased in the offshore direction. The 1975 distribution is typical of an upwelling area (see "Processes influencing coastal waters" below), whereas Graham (1970a) states that the 1963 distribution is due to the presence of a tongue of cold water that exists in summer between warmer inshore and offshore waters.

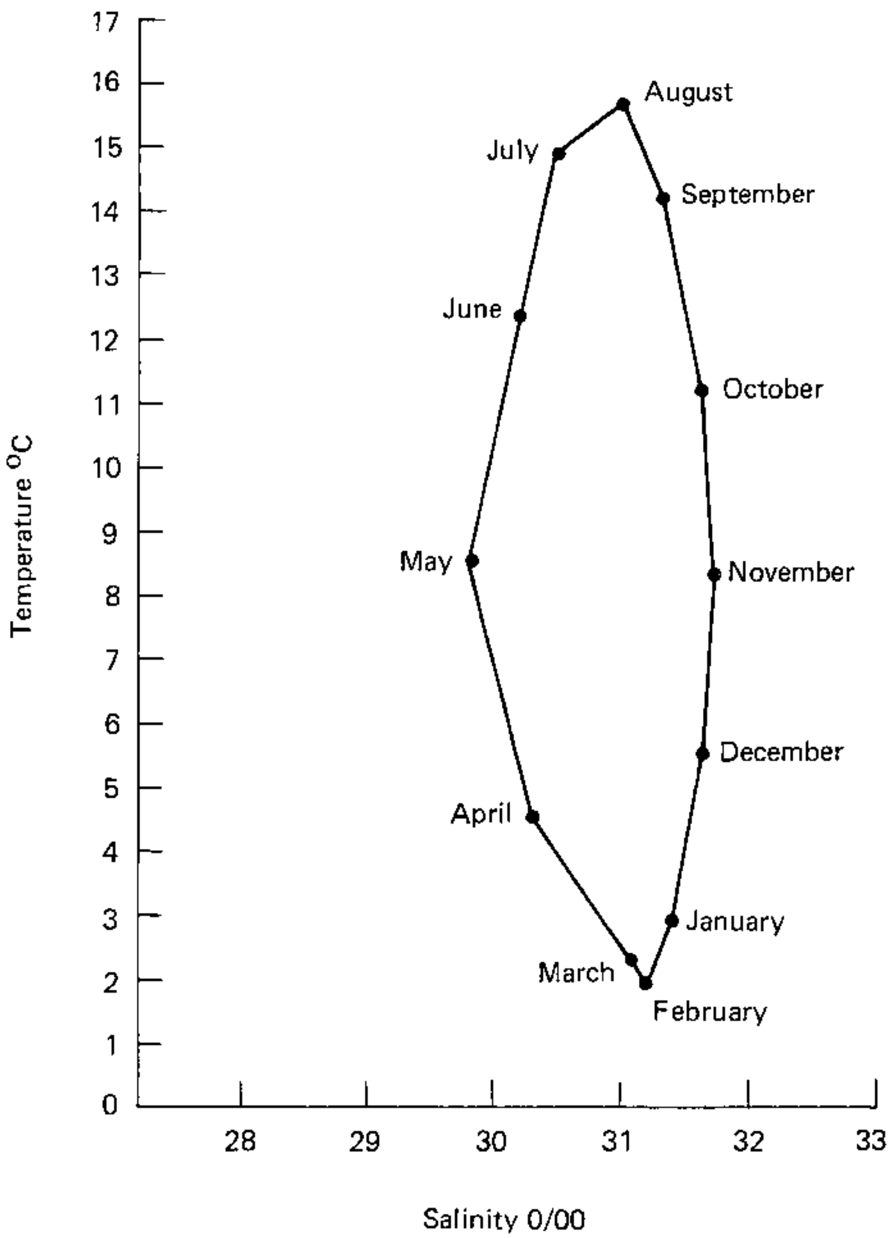


Figure 4-5. The annual temperature and salinity cycle at Boothbay Harbor (region 2; Garfield and Welch 1978).

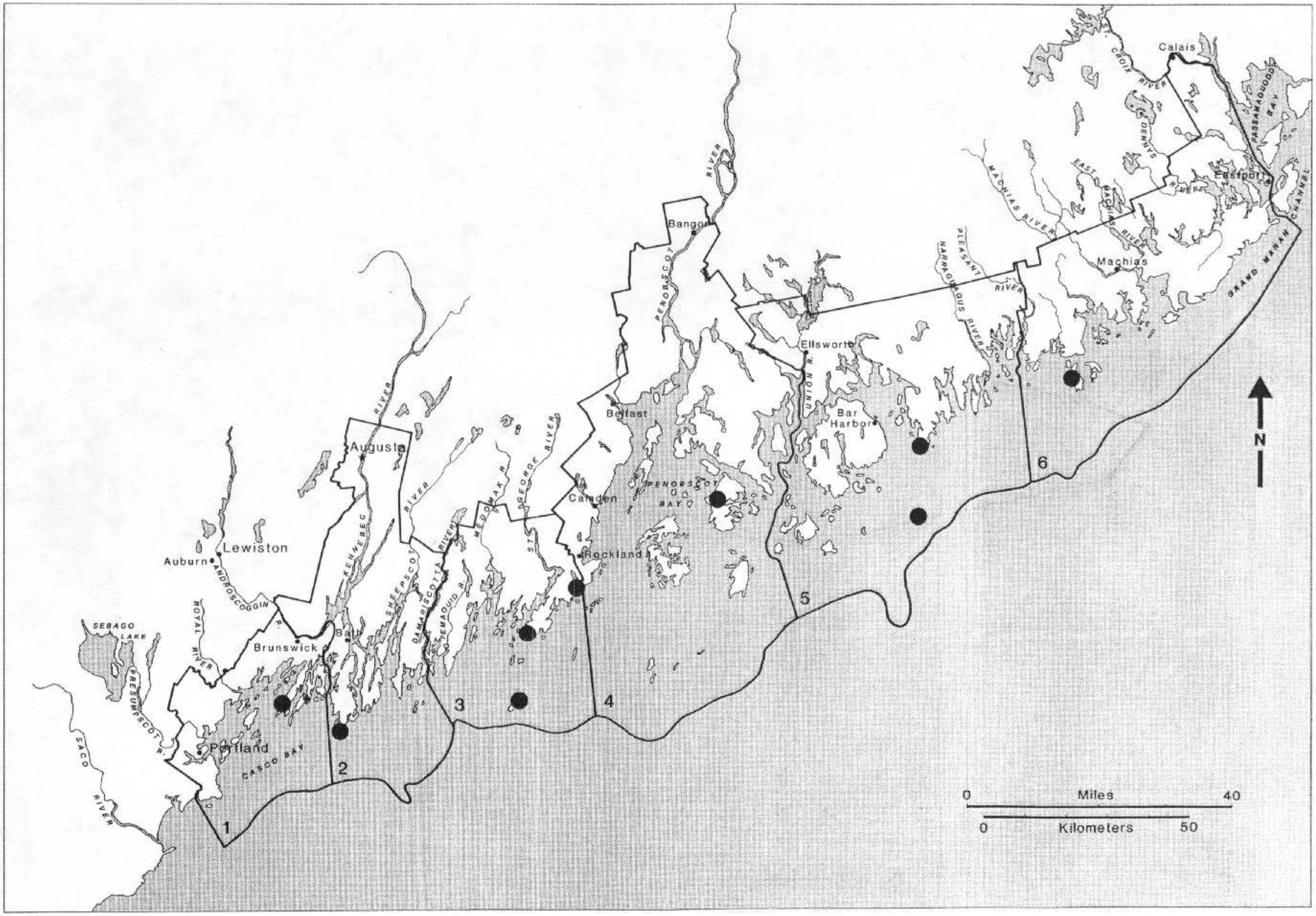


Figure 4-6. Location of stations sampled for temperature and salinity of sea water (Speirs et al. 1976).

Water masses. Coastal waters of Maine are not a uniform water mass experiencing gradual changes in temperature and salinity. Instead, the nearshore waters are composed of relatively discrete masses of water moving along the coast. The boundaries between these different water masses are often marked by precipitous changes in temperature and salinity. Species distribution may be linked to these masses.

Based on the distribution of temperature and salinity, Gulf of Maine water can be characterized as being composed of three water masses: Maine surface water (MSW), Maine intermediate water (MIW), and Maine bottom water (MBW; Hopkins and Garfield 1979). MBW commonly has salinities between 31 and 33 ppt and in the nearshore regions salinities may be <30 ppt. The temperature range of approximately 33 to 63°F (1 to 17°C) reflects the seasonal heating and cooling cycle. The surface temperature-salinity properties along the coast of Maine are influenced by the eastward increase in tidal mixing. Such tidal mixing tends to cause lower surface temperatures as well as higher salinities toward the east.

MIW is a low-salinity, minimum-temperature water. The salinities are too low to be of offshore origin and the water mass volume shows seasonal fluctuation; thus, local coastal formation is suggested. It may be that water from the Nova Scotian Shelf, in which salinity is lowered by discharge from the St. Lawrence River (Sutcliffe et al. 1976), or local coast of Maine water which is cooled during winter, or both comprise MIW (Bigelow 1927; Hopkins and Garfield 1979). MIW characteristics converge with MSW during the winter and the two water masses diverge during the spring as MSW is freshened and warmed. MIW is the remnant water mass from the previous winter. It is not destroyed during summer heating, because the mixing processes associated with cooling extend deeper than do those associated with warming. The MIW core is found between 160 and 400 feet (50 to 120 m), with the lower limit and volume dependent upon seasonal production. MIW is an envelope of water with temperature ranging from 34 to 43°F (1 to 6°C) and salinity from 32 to 33 ppt. These ranges will vary depending on the season, the year, and the location. These aspects are discussed in greater detail by Hopkins and Garfield (1979).

MBW is a warmer, higher salinity water than MIW. It occupies the depths between MIW and the bottom. Its water type is unaffected by air-sea interaction (because the direct effects are absorbed by MIW). The only offshelf exposure (below 250 feet; 75 m) occurs through the Northeast Channel, where the sill is about 800 feet (240 m). This permits entry of slope water (water from the continental slope) into the Gulf of Maine. The position of MBW, between the MIW and the slope water, implies mixing between these three water masses.

Using historical data Hopkins and Garfield (1979) have provided strong evidence for local water mass production during the winter along the coast of Maine. The production zone is a coastal zone that extends offshore, the area and depth of which vary with the winter cooling processes (i.e., heat loss to the atmosphere). During colder years (as in the mid-1960s) the zone may extend to Georges Bank and to depths of about 500 feet (150 m); and during warmer years (as in the early 1970s) the zone may extend 30 miles (50 km) offshore and to depths of 400 feet (120 m). The depth penetration depends on the heat content of the underlying waters. The water mass produced during the winter in this zone becomes a major constituent of MIW. It is assumed that the volume of MIW diminishes as it mixes with waters above and below it, especially as it leaves the Gulf of Maine via the Northeast Channel and the Great South Channel.

Bigelow (1933) labeled a cool, low-saline water mass found in the lower layer at the shelf edge of the Mid-Atlantic Bight as the "cold pool." He identified it as remnant winter water. More recent observations (e.g., Beardsley et al. 1976) have shown the cold pool to be moving to the southwest along bathymetric contours. Such a movement implies an upstream source and various possibilities have been suggested, among them the Gulf of Maine. Thus, MIW potentially may be a source for the subthermocline waters of the Mid-Atlantic Bight. The band of cooler water covers a large portion of the benthic regime. The exposure is roughly proportional to the vertical thickness of MIW, which may vary from zero to >50 m of any cross section. The geographic distribution of certain demersal fish stocks is influenced by annual trends in temperature (see chapter 11, "Fishes"). Colton (1972) has given evidence that detectable southward shifts occurred for the distribution of American plaice and butterfish associated with the cooling trend between 1952 and 1967. The 37 to 45 °F (3 to 7 °C) thermal bank of MIW coincides with the optimal spawning temperatures for stocks such as plaice and haddock; and since this range differs by several degrees from that of MSW, or even MBW, local variations in MIW availability could represent significant differences in thermal regulation of the duration of spawning populations. Similar relationships with other fish and shellfish have not been investigated but undoubtedly occur. Lack of nearshore hydrographic data prevents analysis of the role of MIW in coastal marine waters. For the same reason the nearshore seasonal distribution of MIW cannot be determined.

MIW has the potential to provide nutrients to the coastal zone. This is covered in "Nutrients," in chapter 5. This interaction is one of the major physical forcing functions in coastal Maine.

Tides. Tide, or the periodic rise and fall of the ocean, and accompanying tidal currents are caused by the gravitational effect of the moon and sun on the ocean. Observed tides are primarily the response to the greater attractive force of the moon. Tides vary in height during the month. Tidal terms are defined in table 4-3 and illustrated in figure 4-7. Tidal level and range are important in determining the location, quantity, and type of flora and fauna inhabiting the intertidal zone (see "Intertidal Subsystem," below). Tidal level is also important in predicting dispersal of pollutants (e.g., oil) in the intertidal zone. For example, an oil spill could impact higher tidal levels and a greater area during a spring tide than during a neap tide.

Because of the configuration of the Bay of Fundy, the tide in the Gulf of Maine and the Bay of Fundy assumes some characteristics of a standing wave. Two important consequences of this phenomenon are that the time at which the tide "turns" is nearly simultaneous along the outer coast and the range of the tide increases from west to east as the Bay of Fundy is approached. At Portland the mean tidal range is 9.0 feet (2.7 m), while at Eastport the mean tidal range is 18.2 feet (5.5 m). More intertidal area is available for colonization by organisms in areas of large tidal range.

Table 4-3. Tidal Terms and Definitions

Term	Definition
1) Mean high water	(MHW) the average height of all the high waters recorded over a 19-year period, or a computed equivalent period.
2) Mean low water	(MLW) the average height of all the low waters recorded over a 19-year period or a computed equivalent period.
3) Mean sea level	(MSL) the average height of the surface of the sea for all stages of the tide over a 19-year period, usually determined from hourly readings of tidal height.
4) Mean tide range	(Mn) the difference in height between mean high water and mean low water.
5) Mean tide level Mean water level	(MTL) the mean surface level determined by averaging the height of the water at equal intervals of time, usually at hourly intervals, over a considerable period of time.
6) Neap tide	tide of decreased range which occurs about every two weeks when the moon is in quadrature.
7) Spring tide	tide of increased range which occurs about every two weeks when the moon is new or full (syzygy).

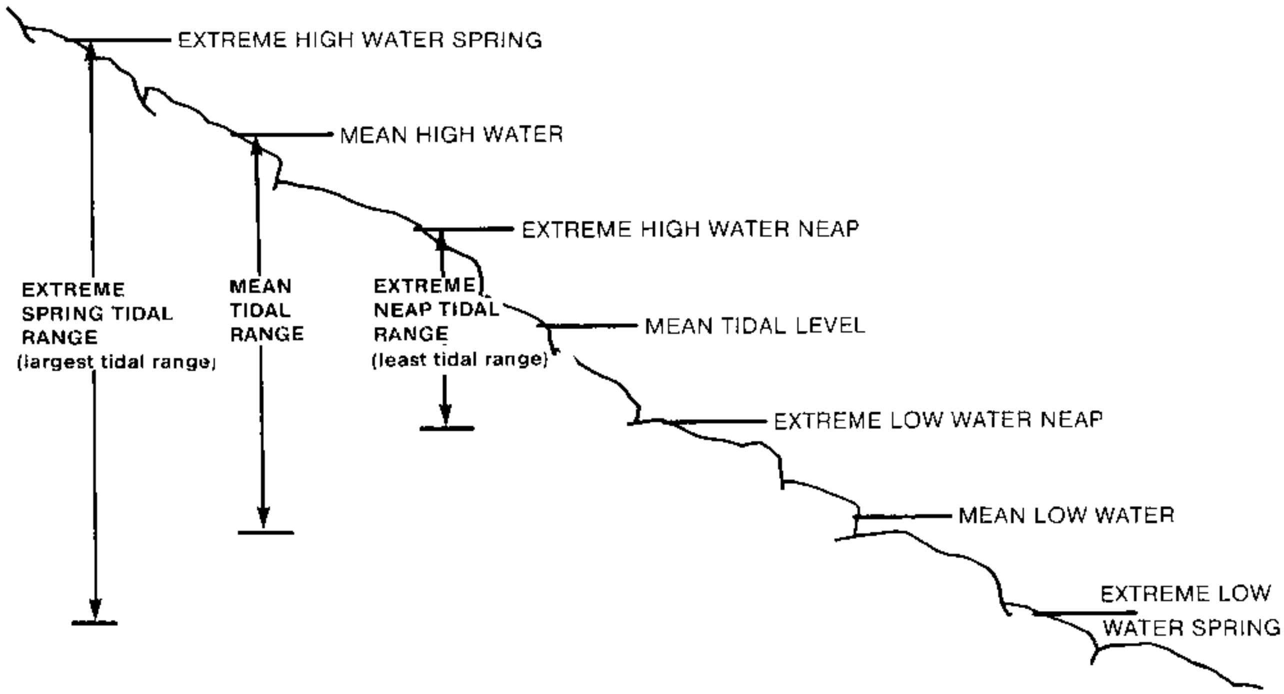


Figure 4-7. Tidal levels and ranges.

Daily predictions of the tide are published annually by the U.S. Department of Commerce in "Tide Tables, High and Low Water Predictions." Deviations in tidal predictions occur during storms with the associated winds.

Processes influencing coastal water. Besides being influenced by atmospheric temperature, temperature and salinity are affected by river discharge, indrafts of offshore waters (upwelling), storms, and currents. Water masses are moved by currents and upwelling. Tides are affected by storms. These dynamic processes are discussed below.

The discharge of fresh water via rivers and estuaries affects the salinity and temperature of marine waters in the coastal zone. Thirteen rivers in the characterization area have gaging stations where flow is recorded (see table 6-3 in chapter 6, page 6-7). Analysis of the effects of river discharge from the Penobscot, Sheepscot, and Kennebec-Androscoggin rivers on Boothbay Harbor nearshore marine waters revealed (through salinity distribution) that Penobscot River water traveling westward was the most likely major source of freshened water observed in Boothbay Harbor (figure 4-8). Discharge from the Sheepscot and Kennebec is carried to the west, away from the Boothbay region. Graham (1970a) calculated an average westward nontidal drift of 1.87 miles/day (0.07 miles/hour; 3 km/day; 0.12 km/hour) for coastal water between Bucksport and Boothbay Harbor. (The movement of riverine discharge in other rivers and streams in coastal Maine is not well known.)

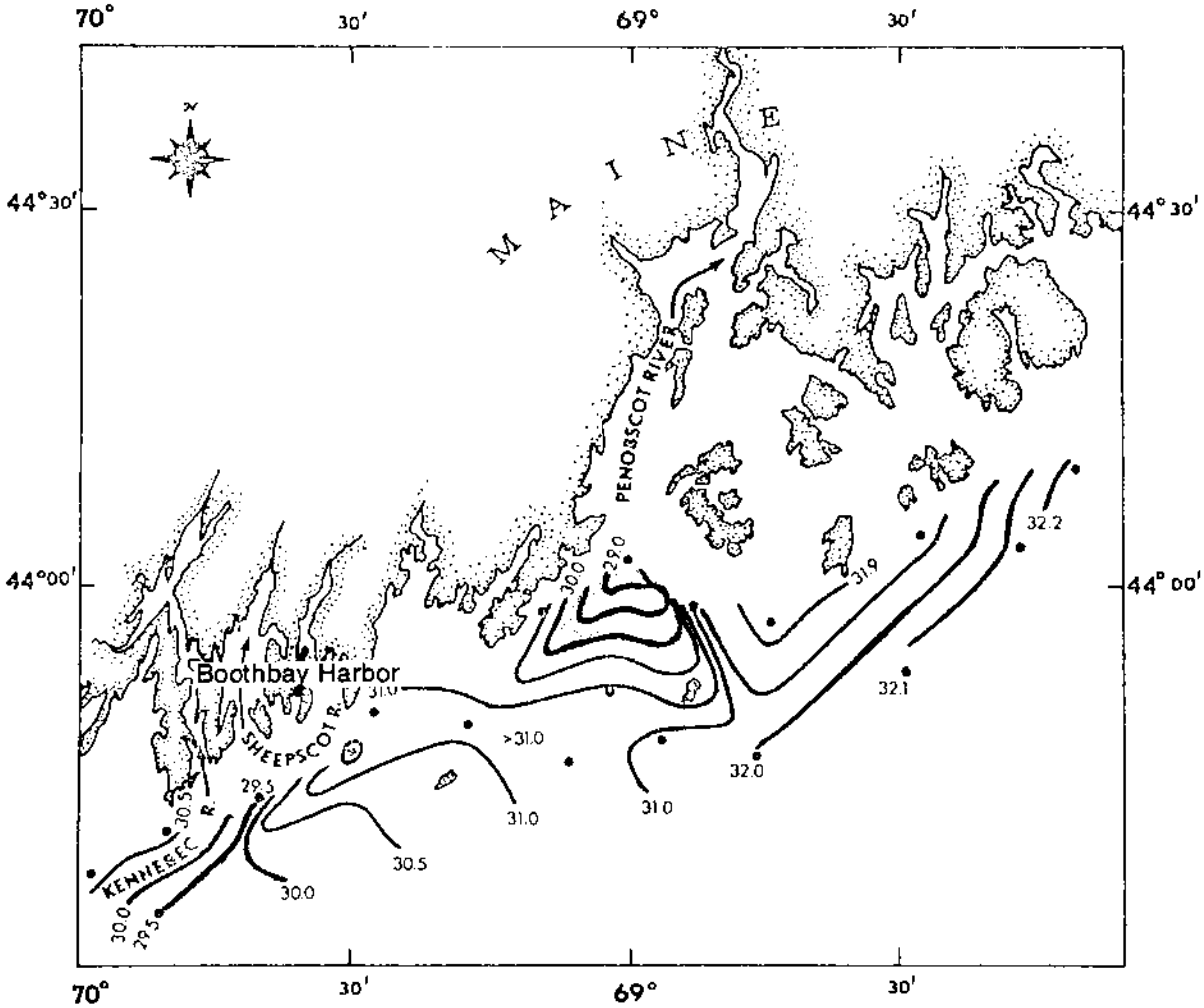


Figure 4-8. Coastal salinity (ppt) contours off the Penobscot, Kennebec, and Sheepscot Rivers during May 1965. Stippled areas have salinities <30 ppt (Graham 1970b).

In the northern hemisphere, the process of upwelling occurs when the predominant winds blow north along the coast. The wind-driven current, because of Coriolis force, is then to the right of the direction of the wind and consequently offshore. Water that is moved offshore is replaced by vertical movement of water from below. The probable source of marine water is MIW. The dominant wind direction of the Maine coast in summer is from the southwest, which is appropriate for establishing upwelling.

Upwelling regions have the most productive fisheries in the world. Upwelling appears to occur along the entire eastern part of the characterization area (regions 5 and 6; Yentsch et al. 1976, and Graham 1970b). Localized upwelling may occur in the deeper channel areas of Casco Bay (region 1; Hulbert and Corwin 1970), southeast of Monhegan Island in the summer (region 2; Yentsch and Glover 1977) and near Matinicus Island (region 4; Bertrand 1977).

Currents are a combination of tidal and nontidal currents. Tidal currents, the response to the gravitational attraction of the earth-moon-sun system, are oscillatory currents, producing no net displacement of water over a tidal cycle in offshore waters. At maximum ebb and flood, tidal current velocities are usually the strongest currents in coastal waters of the Gulf of Maine. Tidal-current prediction is done from long-term records of the velocity fields.

Nontidal currents, comprised of three types of circulation: wind-driven, geostrophic, and thermohaline (principally in estuaries); are a set of responses to meteorological and oceanographical conditions. These different types of circulation are interrelated and changes in one will affect the others. Unlike tidal currents, nontidal currents exhibit marked short-term variability in response to changing conditions and result in net displacements or transports of water. Storm surges are a general set of nontidal currents in response to wind events. The rate of river discharge or changes in offshore hydrography also influence the coastal water currents.

Water movements are significant because water transports material such as plankton, nutrients, or pollutants. Moving water supplies food, carries away wastes and distributes larval organisms. Nontidal currents determine the general transport of material but tidal currents greatly increase the total distance and area traveled.

Tables of tidal current predictions are published annually by the U.S. Department of Commerce as an aid to navigators. The following general description of Maine's tidal currents is taken from the U.S. Department of Commerce NOAA-NOS Atlantic Coast Pilot (1976):

> Along the coast of Maine eastward of Portland (region 1) the flood sets eastward and has greater velocity than the ebb which sets westward.
>
> With easterly or southeasterly winds the currents have a tendency to set toward the shore.
>
> At Portland Lighted Horn Buoy P the tidal current is weak, being on the average less than 0.3 knot at time of strength, setting 335° on the flood and 140° on

the ebb. Since the tidal current is weak, currents of 1 knot or more occur only with strong winds. The largest velocity likely to occur is about 1.5 knots.

Eastward of Mount Desert Island (region 5) the tidal currents along the coast are stronger and more regular than those farther west. Between Mount Desert Island and Portland there is a westward resultant drift along the coast.

In Grand Manan Channel (region 6) the average velocity at strength (i.e. maximum flood or ebb) of the current is about 2.5 knots. The current sets approximately parallel to the channel, the flood setting northeastward and the ebb southwestward.

The speed and direction of tidal currents changes constantly during the tidal cycle. In the offshore regions, tidal currents flow in rotary movement, with no period of slack water. Along the coast, the boundary compresses the rotary flow into an elongated ellipse with an apparent period of slack water.

The interaction between tidal currents and bottom friction results in turbulent mixing that tends to suppress the formation of a thermocline by keeping the water column well mixed. The rougher the bottom and the faster the currents, the more turbulence will be created. Turbulent energy declines more or less exponentially upwards through the water column. Only when the thermocline is within 33 to 66 feet (10 to 20 m) of the bottom will this process result in mixing across the thermocline. Mixing of the water column is important in supplying nutrients to surface waters thus increasing plankton production (see "Nutrient Cycle" and "Phytoplankton" below). Increased mixing also distributes pollutants in the water column more quickly. Increased tidal currents in eastern Maine (regions 5 and 6) cause increased turbulent mixing resulting in high surface salinities and lower surface temperatures from west to east.

Information on the nontidal drift in the Gulf of Maine has been obtained primarily by using surface drift bottles and seabed drifters (Bigelow 1927; Chevier 1959; Bumpus and Lauzier 1965; Graham 1970b; and Bumpus 1973). Some additional information has been obtained through current meters (Forrester 1959 and Vermersch et al. 1979) and geostrophic calculations (Bigelow 1927; Watson 1936; and Hopkins and Garfield 1979).

Whenever sufficient river discharge is entering a coastal area, a weak current system develops, with a flow parallel to the coast due to the relatively low density of the inshore waters (Iselin 1959). In Maine the flow is in a southerly direction along the coast. This flow is not steady but fluctuates with changes in river discharge and onshore movement of oceanic water. In addition, wind-induced currents can completely mask this current.

A schematic representation of the summer nontidal surface currents in the Gulf of Maine (deduced from returns of drift bottles) is illustrated in figure 4-9. Bumpus and Lauzier (1965) were able to show that the circulation pattern was most pronounced during spring and summer and least defined in fall and winter.

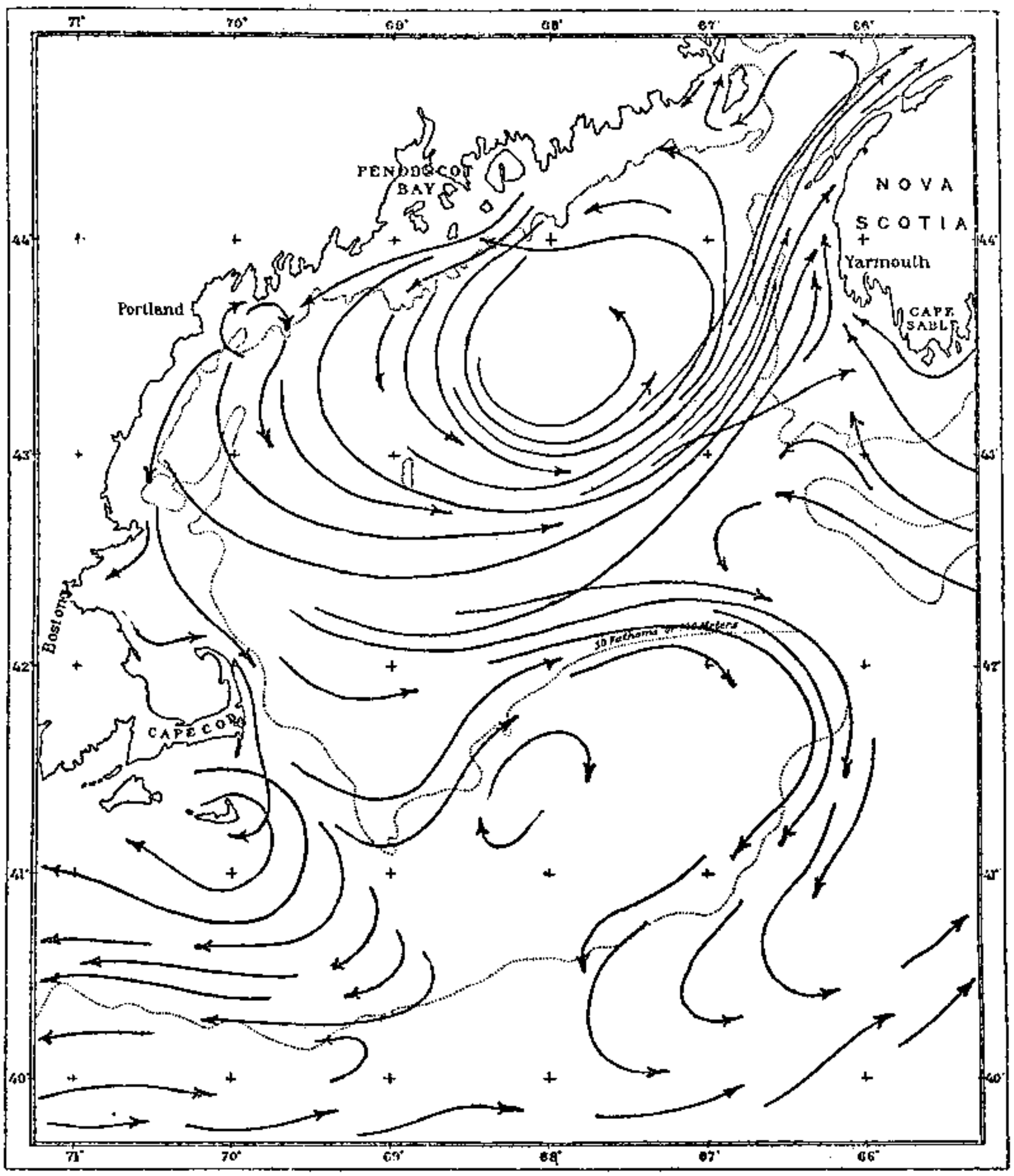


Figure 4-9. Schematic representation of the summer nontidal surface currents in the Gulf of Maine (Bigelow 1927).

Offshore currents were also examined by Vermersch and coworkers (1979). No surface currents were observed but at 100 feet (33 m) the currents were consistent with Bigelow's gyre (figure 4-8). The 100 feet (33 m) mean flow approximately parallels the bathymetric contours to the southwest and with depth the currents veer onshore. The authors note that these currents have only a very weak coherence with the local winds and they suggest that possibly the rough bottom topography interacts with the alongshore flow to produce eddies.

The major features of the nontidal circulation along the coast are summarized by Graham (1970b; figure 4-10 and table 4-4). The westward surface flow is more pronounced west of the Mt. Desert region (region 5) and more variable to the east, especially in Grand Manan Channel (region 6), where it often reverses. In the area just to the east of Penobscot Bay (region 4), the surface drift is often offshore. Along the bottom the nontidal flow is generally inshore, indicating that upwelling is the predominant feature of the coastal circulation. This representation is extremely general. In many areas, particularly the region between Grand Manan Island and Penobscot Bay, very little is known about the mean circulation and almost nothing about the short-term variability.

Except for the results of Hartwell (1976) in New Hampshire, and Naval Underwater Systems Center (NUSC; 1979) in Casco Bay (region 1), direct current measurements in the coastal area of the Gulf of Maine are largely lacking. Data from a current meter array located approximately 4.2 miles (7 km) northeast of the Portland Buoy are being analyzed. These data will provide additional local information on both the tidal and nontidal flow regimes.

Nearshore data (Naval Underwater Systems Center 1979, and Hartwell 1976) indicate that nontidal currents are correlated with meteorological events. Data from New Hampshire waters (south of the characterization area; Hartwell 1976) show summer currents to be weaker and more dominated by tidal currents than winter currents. In winter, currents quickly respond to winds associated with storms. If low pressure systems pass to the south of an area southward flows are produced and those passing to the north produce northward flows. In spring and fall this bimodal tendency decreases and increases respectively.

In summary, although general trends of currents in Maine's coastal waters can be surmised, small-scale variability is considerable. The many factors that affect coastal currents make predicting water movement and the accompanying dispersal of nutrients, phytoplankton, and pollutants (e.g., oil) difficult. Conditions (e.g., winds, and stage of tide) prevailing at a particular point in time are critical in determining where and how fast a water mass will move.

Climate

Meteorological factors influence both abiotic factors (e.g., hydrography and geology) and the biota.

Wind. Winds play an important role in moving surface waters. The effect depends on strength, duration, and fetch. The predominant winds in coastal Maine are from the southwest in summer and from the northwest in winter (see "Climate," page 2-9 in chapter 2). Splash and surge from waves produced by winds provide more moisture to the intertidal zone than a calm sea provides.

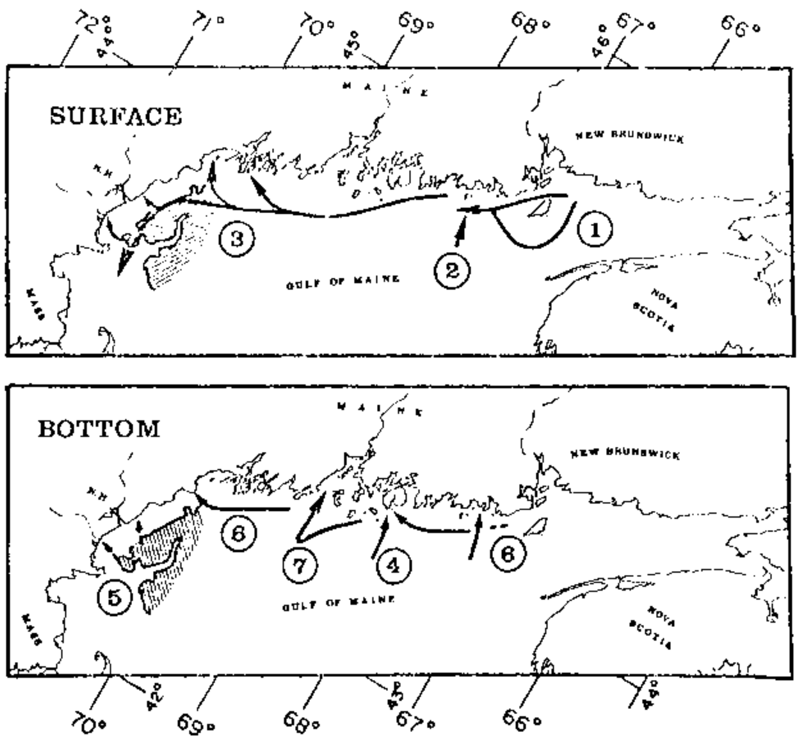


Figure 4-10. Major features of nontidal circulation along the Maine coast. Numbers 1 to 7 refer to table 4-4, which follows (Graham 1970b).

Table 4-4. Movements of Coastal Water[a]

Initial location		Movement	Destination	
Area	Depth		Area	Depth
1. Bay of Fundy	Surface	West of Grand Manan Island to Maine coast or to east side of the Island and then west to the coast of Maine. Primarily in spring, autumn, and winter (Chevier and Trites 1960)	Eastern sector of coast	Surface
2. Western Basin off the eastern sector of the coast	Surface	Inshore during winter	Inshore	Surface
3. Eastern sector of the coast	Surface	Westward along the coast, then offshore near Penobscot Bay and parallel to the western sector of the coast, finally inshore as a compensatory current or a current diverted by bottom topography. During autumn, spring and summer	Inshore	Surface
4. Western Basin off eastern and central coastal sectors	100m and deeper bottom	Inshore along the bottom. All seasons (Lauzier 1967)	Shore	Surface
5. Jefferys and Scantum Basins	100m and deeper, bottom	Inshore along the bottom. All seasons	Shore	Surface

[a] Graham 1970b.

(Continued)

Table 4-4. (Concluded)

	Initial location		Movement	Destination	
	Area	Depth		Area	Depth
6.	Coastal	30-100m bottom	From east to west along the bottom and then inshore. All seasons. Occasionally eastward into the Bay of Fundy	Shore	Surface
7.	Penobscot Bay	Bottom	Sinking during winter in a southerly direction to 150m and deeper (Bigelow 1927).	Offshore	100m
			Possible return along the bottom	Shore	Surface

This allows intertidal communities to develop higher in the intertidal zone than they would in protected areas.

Heat budget and precipitation. Sea temperature depends on the energy exchange processes occurring at the air-water interface, as well as the advective processes occurring below the sea surface. Salinity is affected by precipitation, which increases freshwater discharge of rivers, and by evaporation.

The influence of the Maine climate on the development of local plant and animal communities should not be underestimated. Many species need a minimal summer temperature to induce reproduction and, if it is not reached in a given year, no recruitment takes place. Species with southern affinities often face this problem in Maine. An example is the quahog, which only survives in localized pockets of warm water. Summer water temperatures are lower in the eastern part of the State than in the western section (Bousfield and Laubitz 1972), so some species with southern affinities may not be able to survive in regions 5 and 6. The seasonal nature of Maine's climate divides the year into a relatively dormant winter period and a productive summer period.

Fog. Fog affects the biota by protecting the intertidal organisms from desiccation and allowing less hardy (less adaptable) species to survive in the low intertidal zone.

Atmospheric pressure. Atmospheric "highs" and "lows" cause temporary changes in sea level and may temporarily affect the circulation by bringing dynamic forces into action.

The most extreme deviations on the Maine coast occur during extratropical cyclones producing "northeasters" and tropical cyclones producing "tropical storms" and "hurricanes." Coastal flooding and habitat destruction and/or alteration are often associated with these storms or low pressure systems. Mass mortalities of animals and "uprooting" of macroalgae may occur. The flushing action associated with flooding is particularly important in redistributing detritus from the high intertidal (emergent wetlands and wrack area) and terrestrial systems into the marine system. Flooding may also distribute pollutants (e.g., oil) into the high intertidal zone, where emergent wetlands and wrack communities may be impacted.

Storms affect the stability of the thermocline. Sufficiently severe storms can generate enough turbulent energy to cause some mixing across the thermocline. The energy of storm-induced mixing declines more or less exponentially with depth. Storms are also often a factor in influencing the timing of the fall overturn of the water column.

The direction and speed of currents are influenced by storms. The current direction is determined by whether the storm system passes to the north or south of a given area (see "Processes influencing coastal waters" above) and current speed is related to the intensity of the winds associated with the storm.

Ice formation. Ice formation may have major effects on biota, including marine invertebrates and waterbirds. Ice forms along the shore in protected areas (mostly estuarine) for varying lengths of time each winter. Ice movement may dislodge individuals. In extreme conditions the water may freeze all the way to the bottom and suffocate all the biota. During years of extensive ice formation, large areas of substrate, including biota, may be transported in ice rafts.

The freezing of mudflats may affect waterbirds, who traditionally "home" to specific flats in winter for feeding. Long periods of icing may result in the starvation of these species. Where tidal fluctuations are greatest (in eastern Maine; especially Cobscook Bay, region 6) icing is less likely to occur.

Additional information on climatic parameters is found in "Climate", page 2-9 in chapter 2.

BIOTIC FEATURES

Within the environment created by the abiotic features lives the biota of the marine ecosystem. It is divided by function into three interrelated groups: the producers, the consumers, and the decomposers.

Producers

Producers construct new organic material from inorganic matter. In the marine environment the major producers include the macroalgae, rooted macrophytes, phytoplankton, and benthic diatoms. To an undetermined extent certain microbes may be involved in the production mechanisms of the marine system. The major difference between the production of the marine and estuarine systems is that the productivity of the marine system is dominated by phytoplankton, whereas phytoplankton, macroalgae, and rooted aquatic plants dominate estuarine productivity. The components, habitat preferences, and potential fates of primary production will be described here.

Phytoplankton. Phytoplankton is a collective term for the several major groups of microscopic algae that are suspended in the water column. In Maine, diatoms occur more frequently and in larger numbers than the other groups. These organisms occur in chains and single cells and in bizarre shapes and sizes, ranging from about 10 to 100 μm. Their cell walls are composed of silica and they have very low motility. Chaetaceros, Skeletonema costatum, and Thalassiosira are dominant diatoms in temperate waters.

Dinoflagellates are the next most abundant group and they occur most frequently offshore and in waters south of Maine. They exist mostly as solitary cells; however, some species form chains. Their cell walls are cellulose and generally they have a flagellum used in active swimming. Their sizes range from about 30 to 100 μm and the blooms of one species are noted for occurring in swarms known as red tides (see "Red Tides," page 12-31 in chapter 12).

Another group of phytoplankton, coccolithophores, are more common to the open ocean than to the Gulf of Maine. Their cell wall is composed of calcium carbonate and they are smaller in size (10 to 15 μm) than diatoms or dinoflagellates. Another group of much smaller (about 5 μ m) phytoplankton occurs but very little is known about it. These organisms do not appear to take part in the massive seasonal changes common to the other forms.

Over vast expanses of ocean, phytoplankton are the only producers; hence, the size of higher trophic levels is limited by phytoplankton productivity.

Growth of phytoplankton is controlled by nutrient availability (see "Nutrient Cycle" below) water temperature, salinity, mixing of the water column, and availability of sunlight. These factors and their interrelationships are discussed in "Interactions affecting productivity and distribution of biota" below.

Phytoplankton are consumed by animals, such as zooplankton, which also occur in the water column. They also sink to the benthic environment, where phytoplankton cells are consumed by benthic invertebrates or remineralized in the sediments.

Macroalgae and rooted vegetation. Macroalgae, commonly called seaweeds, are the largest forms of algae and are found in great abundance in marine and estuarine areas along the coast of Maine. They range in size from minute plants to plants of 3 feet (1 m), such as the intertidal rockweeds, or several meters in length, such as the kelps. Seaweeds form the bands of attached nonrooted vegetation that extend from between tide marks to shallow waters (<60 ft; 20 m) along rocky coasts. Seaweeds are divided into three phyla, the brown algae (Phaeophyta), the red algae (Rhodophyta), and the green algae (Chlorophyta), based upon taxonomic considerations.

The brown algae dominate the biomass or bulk weight of rocky intertidal and subtidal plant communities. In intertidal areas the brown alga Ascophyllum and various species of Fucus (collectively call fucoids) commonly account for greater than 90% of intertidal plant weight. These plants are commonly known as rockweeds, bladderwrack, or knotted wrack.

In subtidal areas the brown algae, Laminaria and Agarum (collectively known as laminarians), often dominate biomass. These laminarians, or kelp, extend from low water marks to depths of approximately 30 to 60 feet (10 to 20 m).

Macroalgae require suitable stable surfaces, to which they attach themselves for support. The large rockweeds and kelp need large stones or rocks that are free of other flora and fauna for attachment. Areas lacking in stable surfaces for attachment, such as mud, sand, or gravel, are generally devoid of larger algae but may support relatively minor biomasses of small plants in wave-sheltered areas.

The convoluted rocky shore along much of the coast of Maine provides abundant habitat for macroalgae, resulting in large, dense beds of plants. Seaweed communities provide habitat for numerous marine and estuarine animals. The growth of macroalgae is controlled by water temperature, salinity and the availability of nutrients and sunlight, in addition to suitable substrata. Macroalgae are consumed by grazers, such as sea urchins (e.g., Strongylocentrotus droebachiensis), and fish. The amount of material consumed is unknown but in areas that have periodic high densities of sea urchins, such as Sheepscot Bay and Cobscook Bay, most plant material is consumed. Reestablishment of macroalgal populations may require many years.

Benthic diatoms. Benthic diatoms are similar in form to diatoms living in the water column. However, these organisms live on bottom substrate in intertidal and shallow subtidal areas. The size of the role this component plays in the productivity of the marine system is undetermined. Benthic diatoms on a mudflat in the Bristol Channel, England, had twice the productivity of the overlying phytoplankton on a square meter basis (personal communication from R. M. Warwick, Institute for Marine Environment Research, Plymouth, England; September, 1977). Whether this factor of 2 can be applied to similar habitats in other regions is not known.

Benthic diatom productivity is consumed by invertebrate deposit feeders and grazers, such as the common periwinkle and the mud snail. The degree of dependence of such species on this food source is unknown but, in some situations, it may be significant.

Microbial producers. Microbial producers are bacteria and other microorganisms that are suspended in the water column. They may be either photosynthetic (i.e., dependent on light for growth) or nonphotosynthetic. Little is known about the role or importance of these producers. It seems likely that the large numbers of bacteria in open ocean water (10^5 to 10^6 cells/ml) are being utilized as a food source by planktonic feeders (personal communication from T. Novitsky, Energy Resources Company, Cambridge, MA; December, 1977).

Consumers

Consumers are those animals that feed on the products of primary productivity, as well as on each other. The major marine consumer groups are zooplankton, benthic invertebrates, squid, fish, birds, and marine mammals.

This section describes each group, its habitat preference, and its role in the system.

Zooplankton. Zooplankton is the collective term for the diverse assemblage of animals that float or swim weakly in the water column and thus are carried by currents. The principal components of the zooplankton can be classified as follows: holoplankton, if all the life cycle is spent in the water column; and meroplankton, if only a portion of the life cycle is planktonic. The copepods are the most important members of the holoplankton. These small crustaceans are largely filter feeders, which remove particles, principally phytoplankton and detritus, from the water column. Larval stages of benthic invertebrates and fishes make up the meroplankton, a group that may outnumber the holoplankton for short periods, particularly in bays during spring.

The holoplankton are a principal trophic link between the primary producers, phytoplankton and detritus, and aquatic carnivores, such as jellyfish, comb jellies, arrow worms, larval fish, herring, mackerel, and menhaden. Grazing by zooplankton can be a significant control of phytoplankton populations. Detritus, from unused phytoplankton production or fringing salt marshes (Jeffries 1972), may be an important food source during periods of low phytoplankton production (Riley 1963). Certain zooplankton species may be part of more than one trophic level. For example, a filter-feeding herbivore, such as the copepod *Acartia clausi*, is to some extent carnivorous (Hodgkin and Rippingdale 1971), and even cannibalistic (Petipa 1966). Some meroplankton feed on phytoplankton, while others live off their own yolk supplies. A close connection may exist between food supply and the initiation of reproduction in zooplankton. This is especially true of copepods, where spawning and breeding times correlate closely with seasonal phytoplankton blooms (Marshall and Orr 1972). The general suitability of the phytoplankton as food, in terms of size, taste, and composition, is also a critical factor (Smayda 1973). As was observed in Narragansett Bay, Rhode Island (Martin 1965), there may be a delay between the onset of the phytoplankton bloom and the initiation of zooplankton reproduction. Zooplankton produce detritus, in the form of fecal pellets and molted exoskeletons, which sink to the bottom and provide food for benthic organisms. Their vertical movements in the water column bring some live animals near the bottom, also resulting in food for the benthos. Davies (1975) has indicated that the primary input to the benthos of a Scottish sea loch was in the form of sinking zooplankton fecal pellets and this rate of input was about one-third the primary production of the overlaying waters. The contribution of fecal pellets may be important in the shallow waters and estuaries of coastal Maine, where dense zooplankton populations occur. Zooplankton also may have an important role in the release of organic matter (see "Organic Matter Cycle" below), nutrients, nitrogen and phosphorus (see "Nutrient Cycle" below); and excretory products (Corner and Davies 1971), which then become available to phytoplankton for enhanced growth.

Benthic invertebrates. Benthic invertebrates live primarily in (infaunal) and on (epifaunal) the bottom substrata. Three groups, the annelids, molluscs, and crustaceans constitute the majority of animals in benthic communities in coastal Maine. Annelids are segmented worms. Molluscs, such as clams and snails, have shells and soft bodies. Crustaceans are crablike organisms. Fifteen hundred and eighty-two taxa have been reported from the characterization area. These species are listed by region in appendix E.

Communities of benthic invertebrates occupy an important position in the marine system. They take the direct and indirect products of primary production and convert them to animal protein, which is passed to higher trophic levels through predation.

The burrowing and feeding activities of the benthic invertebrates alter sedimentary structures and return to the water column nutrient materials that have been deposited or bound in the sediments. They are dependent on the overlying water to supply oxygen and food and to remove wastes. Food consists of phytoplankton (particulate organic material of plant origin), bacterial flora on detritus, benthic diatoms, living plants, and/or living animals. Some benthic invertebrates feed on one type of food only, while others feed on many types (Sanders et al. 1962). The feeding type of a particular species can change with its size and age (Sanders et al. 1962). Small individuals may be able to consume only one type of food but as they grow they become able to handle larger, more diverse food particles.

Benthic invertebrates live on all types of substrata and, thus are affected in some way by any type of habitat disruption. Up to 95% of these animals occur within 5 cm (2 in.) of the water-sediment interface (Stromgren et al. 1973), because organic material (i.e., food) is more concentrated there.

Many species which are considered to be infaunal leave the sediment at night and swim in the water column (i.e., bloodworms and sandworms; Dean 1978 a and b), and crustaceans, which are thought to be planktonic, enter the substratum during daylight hours (Thomas and Jelley 1972).

Larval stages of many benthic invertebrates live in the water column; usually up to 5 to 6 weeks in Maine (personal communication from E. L. Bousefield, National Museum of Canada, Ottawa, Canada; June, 1977). Other invertebrates such as predatory snails, amphipods, and isopods develop directly into small adults and never enter the water column. Invertebrates that have pelagic larvae have the ability to disperse widely at this stage in their development. Local or short-term perturbations have less effect on these populations than on animals that develop without the larval stage and carry out dispersal as adults. Natural mortality of pelagic larvae is high, possibly as high as 95% to 99%.

The primary factor influencing distribution and abundance of benthic species is the nature of the substratum. Pelagic larvae metamorphose into juveniles when they come in contact with a suitable substratum and some delay metamorphosis for a limited time until suitable substratum is located. The period of metamorphosis and settlement is probably the most critical in the life of a benthic species (Thorson 1966). Predation on newly settled juveniles is severe.

Substratum requirements are related to feeding type and mode of living. Detrital feeders are most abundant in fine sediments of silt and clay containing organic detritus. The detrital feeders pass the sediment through their bodies, digest the bacteria, and excrete fecal material, which is again colonized by bacteria and reconsumed (Young 1971).

Organisms that feed on suspended (filter feeders) material, either phytoplankton or detritus, exist almost anywhere that the currents are strong enough to provide a sufficient amount of food. They are found most commonly, however, in sandy or rocky environments, where deposit feeders are not as successful. Other requirements include shelter for animals (e.g., lobsters), hard substrates for nonmobile organisms (e.g., anemones), appropriate sediments for making tubes and algal substrates for some polychaetes and bryozoans. See chapter 12, "Commercially Important Invertebrates," for a complete description of nine important benthic invertebrates.

Squid. Although they have no shell, these invertebrates are related to clams and mussels. They live in the water column and are active swimmers that shoot backwards through the water. Squid are carnivores and feed on mackerel, herring, krill and shrimp and are preyed upon by other carnivores, such as large fish and whales.

Finfish. The marine system in Maine supports a slightly higher diversity of finfish species than the estuarine system (73 vs. 61). Seventeen species are strictly marine inhabitants. Temperature is a major factor determining the seasonal and local distribution of marine fish. Fish populations in the marine system of coastal Maine are dominated by resident demersal (bottom-dwelling) species (e.g., cod, pollock, flounders, sculpins, and skates; table 4-5). A number of summer migrants to coastal Maine add to the seasonal diversity of fish. Finfish are important components in the energy flow of both marine and estuarine systems due to their abundance (biomass) and representation on many levels of aquatic food chains; they are primary, secondary, and tertiary consumers. Fish support a wide variety of seabird and waterfowl populations.

Many researchers have held the belief that, in the context of the total ecosystem, organisms (fish or otherwise) could be considered as groups occupying defined feeding niches (Langton and Bowman 1978). These niches are defined according to the fishes' feeding habits and size or life stage. Finfish are discussed from an ecological perspective here, in terms of their feeding habits and habitats. A single species may utilize several different feeding strategies during its various life stages, from larvae through mature adult. Species that share the same feeding habits may be functionally but not taxonomically related.

Marine fish can be classified on the basis of their principal feeding habits as planktonic, nektonic, or demersal/semidemersal (figure 4-11). The marine system is dominated by demersal/semidemersal feeding finfish populations, followed by nektonic and then planktonic feeders. The cunner and Atlantic cod are both nektonic and demersal feeders. Planktonic feeders such as the herrings, (Atlantic herring, alewife, blueback herring and American shad) Atlantic menhaden, and American sand lance are water-column feeders that consume primarily pelagic crustaceans; copepods, mysids, euphausiids, and amphipods. The nektonic feeders utilize pelagic crustaceans and fish. These nektonic feeders include the majority of the Maine coast's summer migrants: bluefin tuna, the hakes (red, white, and silver), spiny dogfish, bluefish, Atlantic mackerel, and striped bass. The dominant demersal feeding fishes include most of the groundfish (e.g., cod, hakes, skates, and flounders), the sculpins, the ubiquitous American eel, the anadromous sturgeons, and the sticklebacks. Major food items are pelagic crustaceans, echinoderms, bottom fish, fish eggs, benthic diatoms, molluscs, and polychaete worms. See chapter 11, "Fishes," for a complete description of this group of animals.

Birds. Waterbirds, including seabirds, shorebirds, wading birds, and waterfowl, use the marine system (including terrestrial islands) for breeding, feeding (among all habitat classes), moulting, migrating, and wintering. Twenty percent of waterbirds are permanent residents. In addition, several raptors, including the resident endangered bald eagle utilize the marine system. Waterbirds are described in detail in chapter 14, "Waterbirds," chapter 15, "Waterfowl," and the bald eagle and other raptors in chapter 16, "Terrestrial Birds." Most species are high level consumers, preying on zooplankton, benthic invertebrates, squid, finfish, and invertebrates and vertebrates of the strand line. Marine waters are the primary breeding and feeding areas for petrels, terns, and alcids. Many pelagic seabirds (i.e., shearwaters, kittiwakes, fulmars, murres, and gannets) are indigenous to marine waters and rarely are found in estuaries.

The highest densities of waterbirds occur in late summer after the young have fledged and during the fall migration (which begins in early July). Waterfowl are most abundant during the fall and spring migrations; shorebirds during the fall migration; wading birds during the breeding season and fall migration; and seabirds during the summer and fall migration. Peak numbers of shorebirds and seabirds correspond with peak periods of invertebrate productivity. Bald eagles occur throughout the year. Peak seasonal abundance is during the spring and summer.

The role that waterbirds play in energy flow, nutrient cycling, and community structure in the marine system in Maine is unknown. Studies in Oregon on seabird population energy requirements indicated that some 22% of the fish production of the area was utilized by seabirds (Wiens and Scott 1975). In Scotland, Furness (1978) estimates that the total energy requirements of seabirds in a very large colony represents 29% of the mean estimate of the total annual fish production within a 28-mile (45-km) radius of the colony. This implies that seabirds, predatory demersal fish, and industrial fisheries are in direct competition for the energy flow from pelagic fish, so that any increase in the energy flow to one of these would result in a reduced energy availability to the others (Furness 1978). Both studies involved much larger breeding seabird populations than those of coastal Maine. Evans' analysis (1973) of energy flow through the avifauna of the North Sea; based on estimated summer and winter biomass totals of shorebirds, marine waterfowl, and seabirds; concluded that a minimum of 0.01% of the primary production was metabolized by the birds, representing a minimum of 10% of the energy input to the top carnivores (birds and predatory fish).

Table 4-5. Habitat, Abundance, and Seasonality of Fish Inhabiting the Marine System

Species	Habitat	Abundance	Seasonality
Atlantic hagfish	D	UC	R
Sea lamprey *	D	C	R
Spiny dogfish	P	C	SM
Thorny skate	D	C	R
Barndoor skate	D	UC	R
Smooth skate	D	UC	R
Little skate	D	C	R
Winter skate	D	C	R
Shortnose sturgeon * ES	D	R	R
Atlantic sturgeon * SC	D	R	R
American eel **	D	C	R
Conger eel	D	UC	R
Atlantic herring	P	C	R
Blueback herring *	P	C	SM
Alewife *	P	C	R
American shad *	P	R	SM
Hickory shad ***	P	UC	SM
Atlantic menhaden	P	C	SM
Atlantic salmon *	P	R	R
Rainbow smelt *	SD	C	R
Capelin	P	UC	R
Goosefish	D	C	R
Atlantic cod	D	C	SM
Atlantic tomcod	D	C	R
Haddock	D	C	SM
Fourbeard rockling	D	C	R
Silver hake	S	C	SM
Spotted hake	D	UC	SM
White hake	D	C	SM
Red hake	D	C	SM
American pollock	D	C	R
Cusk	D	C	R
Ocean pout	D	C	R
Atlantic silversides	P	C	R
Blackspotted stickleback	SD	C	R
Nine-spine stickleback	SD	C	R
Four-spine stickleback	SD	C	R
Three-spine stickleback	SD	C	R
Northern pipefish	D	C	R
White perch	SD	C	R
Striped bass ***	P	C	SM
Bluefish	P	C	SM
Scup	D	UC	SM
Cunner	D	C	R
Tautog	D	UC	SM

P = pelagic; D = demersal; SD = semidemersal; C = common; UC = uncommon; R = are.
* = Anadromous; ** = catadromous; *** = anadromous but does not spawn in Maine.
ES = endangered species; SC = species of special concern; I = introduced.
R = resident; SM = summer migrant; WM = winter migrant.

(Continued)

Table 4-5. (Concluded)

Species	Habitat	Abundance	Seasonality
Snakeblenny	D	C	R
Daubed shanny	D	UC	R
Radiated shanny	D	C	R
Rock gunnel	D	C	R
Wrymouth	D	C	R
American sand lance	P	C	R
Atlantic mackerel	P	C	SM
Bluefin tuna	P	C	SM
Butterfish	D	UC	SM
Redfish	D	C	R
Striped searobin	D	UC	R
Grubby	D	C	R
Shorthorn sculpin	D	C	R
Longhorn sculpin	D	C	R
Mailed sculpin	D	C	R
Moustache sculpin	D	UC	R
Arctic hookear sculpin	D	UC	R
Sea raven	D	C	R
Alligatorfish	D	C	R
Lumpfish	D	C	R
Sea snails	D	C	R
Windowpane	D	C	R
Witch flounder	D	C	R
American plaice	D	C	R
Atlantic halibut	D	UC	R
Yellowtail flounder	D	C	R
Smooth flounder	D	C	R
Winter flounder	D	C	R

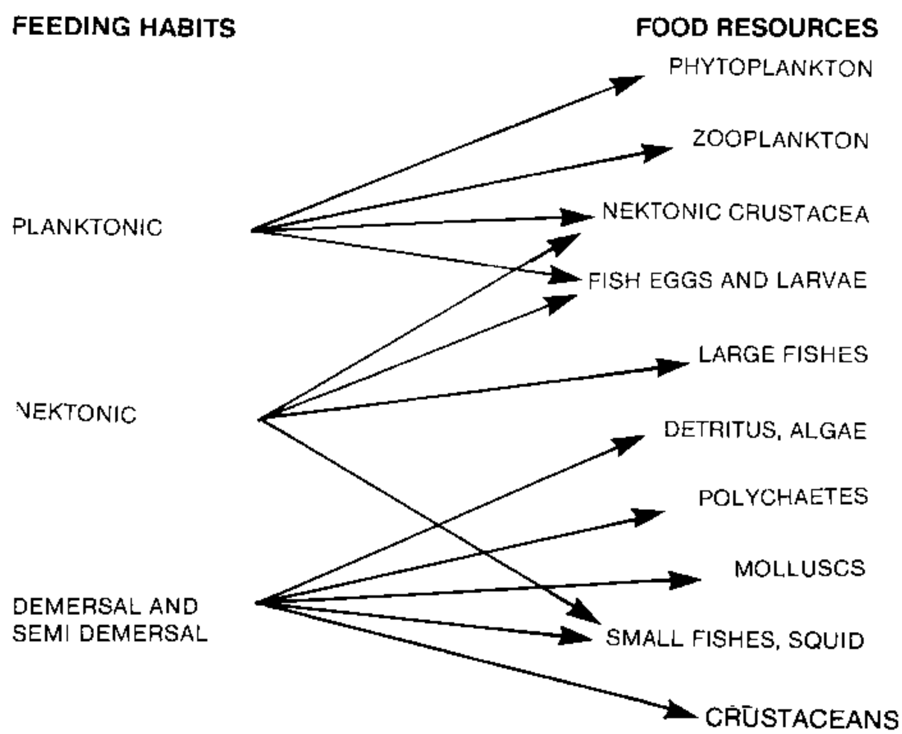


Figure 4-11. Food habits of marine fishes.

A recent study of waterbird food habits, conducted along the western approach to the Bay of Fundy, found that cormorants fed primarily on sculpin and herring, krill, refuse, plants, urchins, and mussels; eiders fed mostly on blue mussels and urchins; and purple sandpipers fed on smooth periwinkle, amphipods, pearly top shell, and blue mussels (Marine Research Associates 1979). A second study in the Head Harbor Passage area, off Eastport (region 6), found that herring gulls and great black-backed gulls took herring up to 25 cm (9.8 in.) long and ate large numbers of euphausiid shrimp (Gaskin et al. 1979). In the summer months herring gulls generally are associated with herring weirs and stop seines, where they exist in coastal Maine (primarily region 6). In the Head Harbor Passage study, it was found that Bonaparte's gulls fed mostly on euphausiids, terns on smaller herring and euphausiids, and northern phalaropes probably on copepods and smaller size classes of euphausiids. Bald eagles are an important predator in coastal Maine where they feed on fish, waterfowl, and seabirds.

In summary, the foods important to waterbirds include herring, sculpin, pollock, sand lance, euphausiids, shrimp, copepods, amphipods, mussels, urchins, and other invertebrates. Most of the waterbird food items or types listed in "Consumers," page 5-41 in chapter 5, are applicable to the marine system. The discussion on the role of waterbirds in energy flow, nutrient cycling, and community structure in the estuarine system also is applicable to the marine system.

Terrestrial islands in the marine system are used for nesting (e.g., bald eagles, ospreys, wading birds, gulls, eiders, and double-crested cormorants), rearing young (e.g., bald eagles, ospreys, eiders, black duck, common and roseate terns, laughing gulls, and wading birds), moulting (e.g., eiders and Bonaparte's gulls), roosting (most groups), wintering (e.g., bald eagles, black ducks, mallards, Canada geese, seaducks, purple sandpipers, gulls, loons, grebes, kittiwakes, and great cormorants), and as migratory stopover areas (e.g., shorebirds, brant, geese, dabbling ducks, peregrine falcon, bald eagles, ospreys, diving ducks, Bonaparte's gulls, and ring-billed gulls).

Marine mammals. This community is essentially opportunistic in feeding but major feeding methods may be clearly defined. Pinnipeds and cetaceans of the Gulf of Maine may be functionally classified according to their major feeding methods as planktonic, nektonic, or demersal/semidemersal feeders (figure 4-12). A certain degree of overlap exists, indicating flexibility and opportunism.

Plankton feeders utilize surface plankton and planktonic crustaceans (e.g., krill and copepods) as major food resources. These plankton feeders are represented exclusively by the baleen whales. Familiar species include the finback, minke , humpback, and right whales.

Nektonic feeders exploit the free-swimming species of the marine water column, such as gregarious fishes, euphausiids, squid, and some benthic fishes. This feeding group includes the toothed whales, the baleen whales, and the seals. All of these classes are nektonic feeders to a degree. For the toothed whales and seals, nektonic feeding is a major feeding method, while for the baleen whales it is a supplementary one. Representative nektonic feeders include the sperm whale, the pilot whale, the harbor porpoise, the beaked

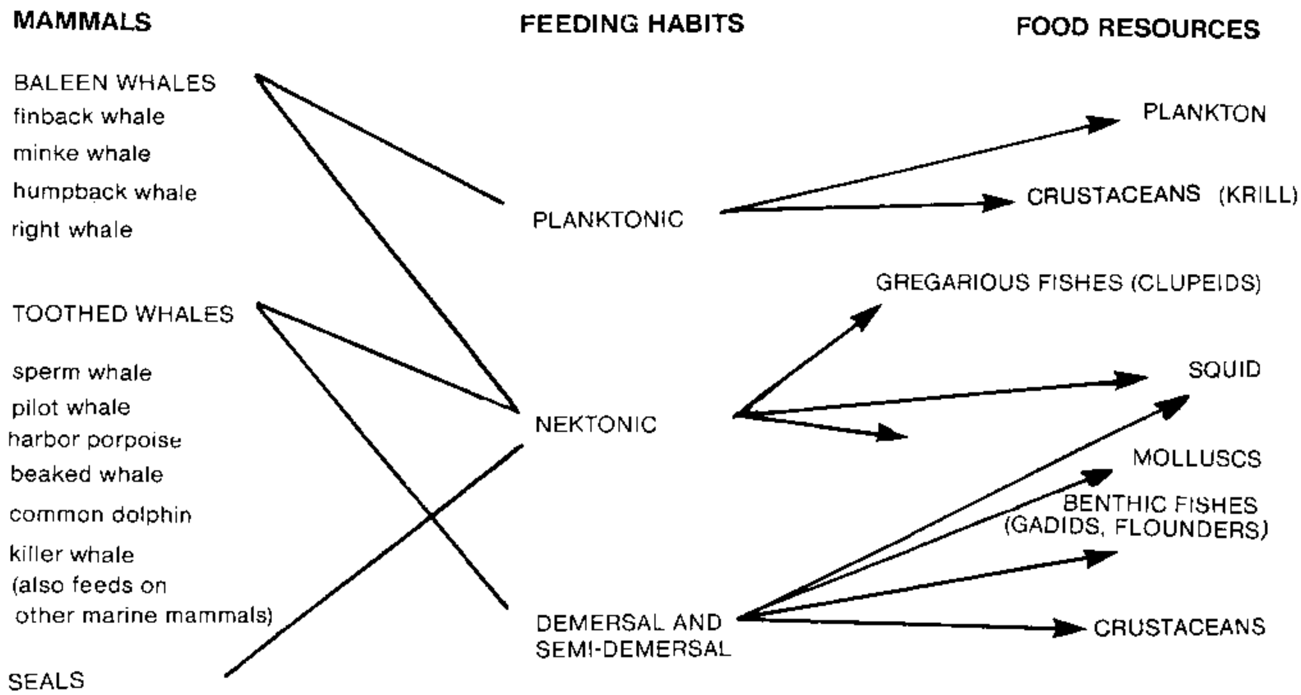


Figure 4-12. Food habits of marine mammals.

whales, the common dolphin, and the killer whale. The killer whale also feeds on other marine mammals.

The demersal and semidemersal feeders consume benthic fish (gadids, flounders, and skates), molluscs, and crustaceans. This feeding group is dominated by seals but also includes toothed whales to a lesser degree. Representative species include the harbor seal, the gray seal, the harbor porpoise, and the beaked whales. See chapter 13, "Marine Mammals" for a full description of this group of animals.

Decomposers

The decomposers are microbes, such as bacteria. Their function in the ecosystem is to break down dead organic matter and convert it to a form that can be recycled. In so doing these organisms enrich detrital particles (dead organic matter), making them suitable for some consumers.

Microbial decomposers have important roles in marine ecosystems. Bacterial and fungal degraders comprise the largest group of living organisms in the sea. In coastal waters, for example, from 10^5 to 10^6 bacteria/ml sea water can be found by direct counting techniques (Ferguson and Rublee 1976; and Watson et al. 1977). In coastal sediments, from 10^8 to 10^{10} bacteria/g dry weight sediment (Dale 1974; and Watson and Novitsky, unpublished) can be found. Not all of these bacteria are degraders or even living bacteria, but a large percentage are and this fact reflects their importance. The most prevalent genera are *Pseudomas*, *Vibrio*, *Flavobasterium*, *Anthrobacter*, *Caulobacter*, *Hyphomicrobriu*, *Cytophaga*, *Acinetobacter*, and *Photobacterium* (Sieburth 1971; and Leifson et al. 1964).

Two limited reports exist for the bacterial populations of the Gulf of Maine. Pratt and Reynolds (1973 and 1974) studied bacteria isolated on selective media from Schoodic Point, Maine. Populations at Schoodic Point ranged from 10 to 1500 cells/ml when counted on marine agar. Although no detailed taxonomic study was undertaken, the colonies isolated were probably representative of the genera listed above. Results of counting bacteria using culture media are usually several orders of magnitude lower than those found using direct counting techniques, so comparisons of published densities of bacteria must be made with caution.

FOOD WEBS

The biological components of the marine system are linked by food chains or food webs. Through food webs energy (food) is passed from the producers to the herbivores (plant-eating species), to secondary consumers (animal-eating species) and higher level consumers, and, ultimately, to the decomposers. Each step in this progression is called a trophic level. Organisms function at one or more trophic levels, i.e., a diatom is a primary producer, a filter-feeding clam is an herbivore and functions on the second trophic level, while crabs that eat both plant and animal material are both herbivores and carnivores.

From one trophic level to the next a loss of energy takes place: only a small part of the energy contained in one level is passed to the next. Maximum energy is contained in the primary producer level and subsequent trophic levels contain less and less. For example, a four trophic level pelagic food chain consists of phytoplankton, zooplankton, zooplankton-eating fish, and predaceous fish. Each trophic level feeds on the one below it and the predaceous fish are harvested by people. If we assume a 10% efficiency to the energy transfer between trophic levels, a great amount of energy is needed to support a top carnivore (e.g., bird, fish, or people). The transfer efficiency is probably higher than 10% to 12% at higher latitudes with discontinuous productive seasons (Gulland 1970). The Gulf of Maine may be in this category, although sufficient specific information to make generalizations about energy transfer efficiencies is not available. Using the 10% assumption, to produce a pound (.45 kg) of commercially utilizable fish, 10 lb (4.5 kg) of smaller fish are required as prey. The support of 10 lb of small fish requires 100 lb (45 kg) of zooplankton, which in turn consume 1000 lb (450 kg) of phytoplankton (figure 4-13). In other words, even a simple food chain must contain a large amount of energy at the lowest level in order to support the higher trophic levels, which have progressively less energy available.

A more realistic and still simple marine food web is shown in figure 4-14 from Mills and Fournier (1979). This model is based on the Nova Scotian fishery and shows yearly productivity levels for each component, as well as the pathway of energy flow among the components. It demonstrates the process by which the energy of primary production is transferred and utilized, so that only a small amount reaches the higher trophic levels where it can be utilized by people.

A sample series of food chains organized into a marine food web is shown in figure 4-15. The species included, which are representative of larger numbers of species, are arranged according to their approximate trophic level.

PHYSICAL/BIOGEOCHEMICAL/BIOLOGICAL INTERACTIONS

Energy Cycles

Marine productivity is higher in coastal areas than in offshore areas. Nutrients from land runoff and nutrient regeneration from the bottom can be utilized by the primary producers in shallow coastal waters. Largely for this reason the major fisheries of the world are located on continental margins.

In the following discussions material is used from studies conducted outside coastal Maine. In Maine, research has been limited to the study of primary production by phytoplankton, and no investigations have addressed energy flows or the energy requirements of higher trophic levels.

A schematic diagram of the functioning of the Maine marine system is shown in figure 4-16. This figure represents biological food webs but also integrate the abiotic forcing functions.

The two major productive elements in the Maine coastal marine system are the phytoplankton and macroalgae. Benthic diatoms may be locally important in some intertidal areas. Insufficient nutrients often limit the growth of these plants; therefore, importation and recycling of nutrients, especially nitrate, are necessary for high productivity.

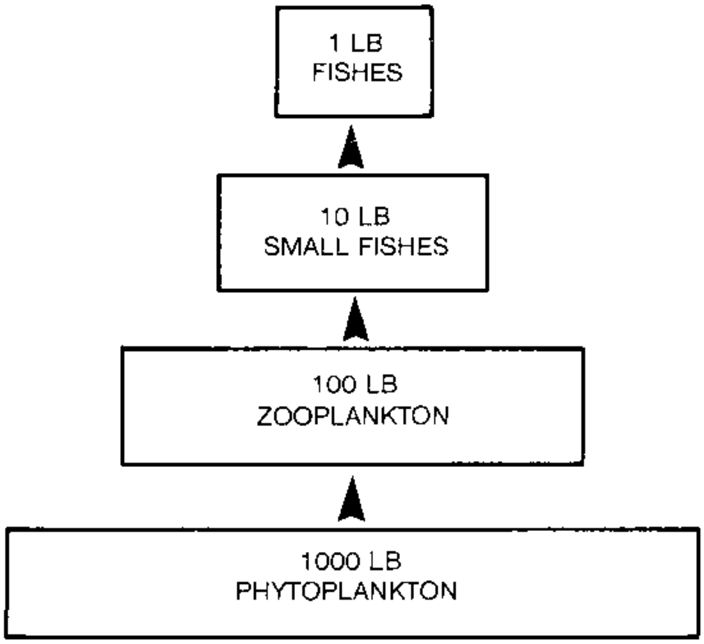


Figure 4-13. Simple representation of the energetic relationships between trophic levels.

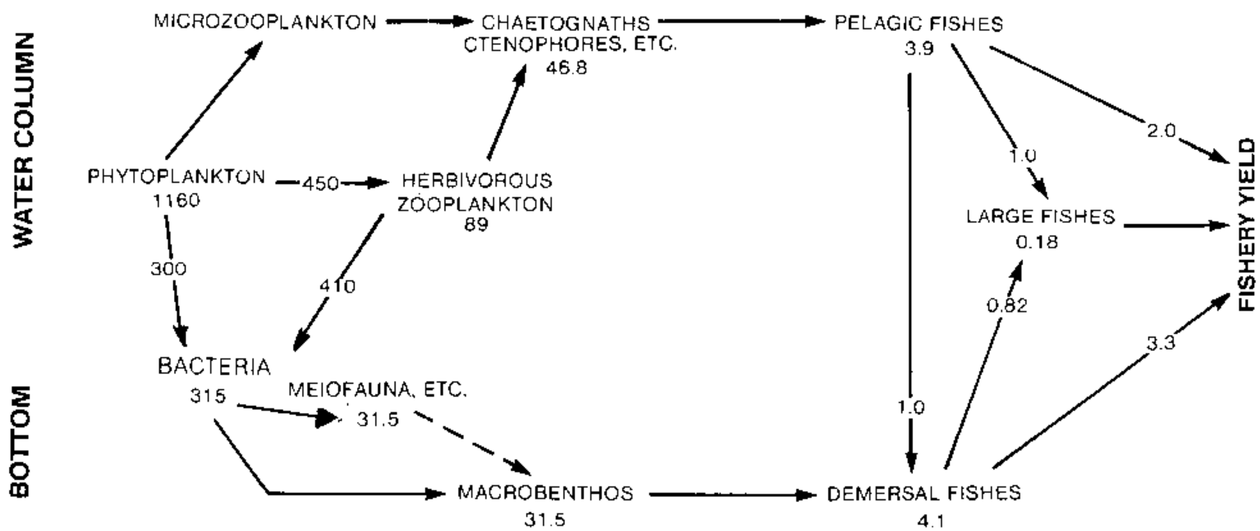


Figure 4-14. Marine food web for fishery centered on the southeast Nova Scotian shelf. Values are kcal/m^2/yr (adapted from Mills and Fournier 1979).

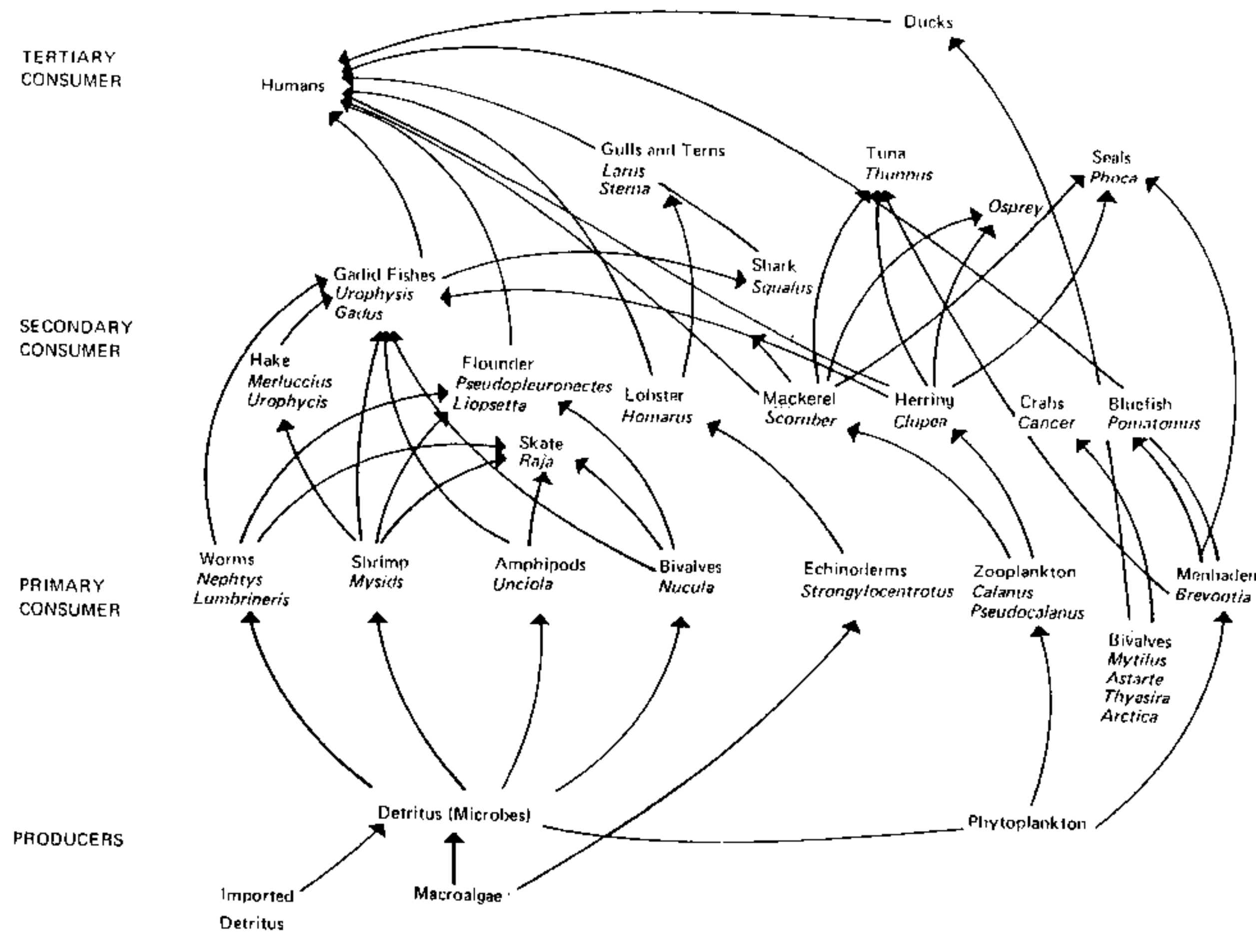


Figure 4-15. Genralized food web for the marine system of coastal Maine.

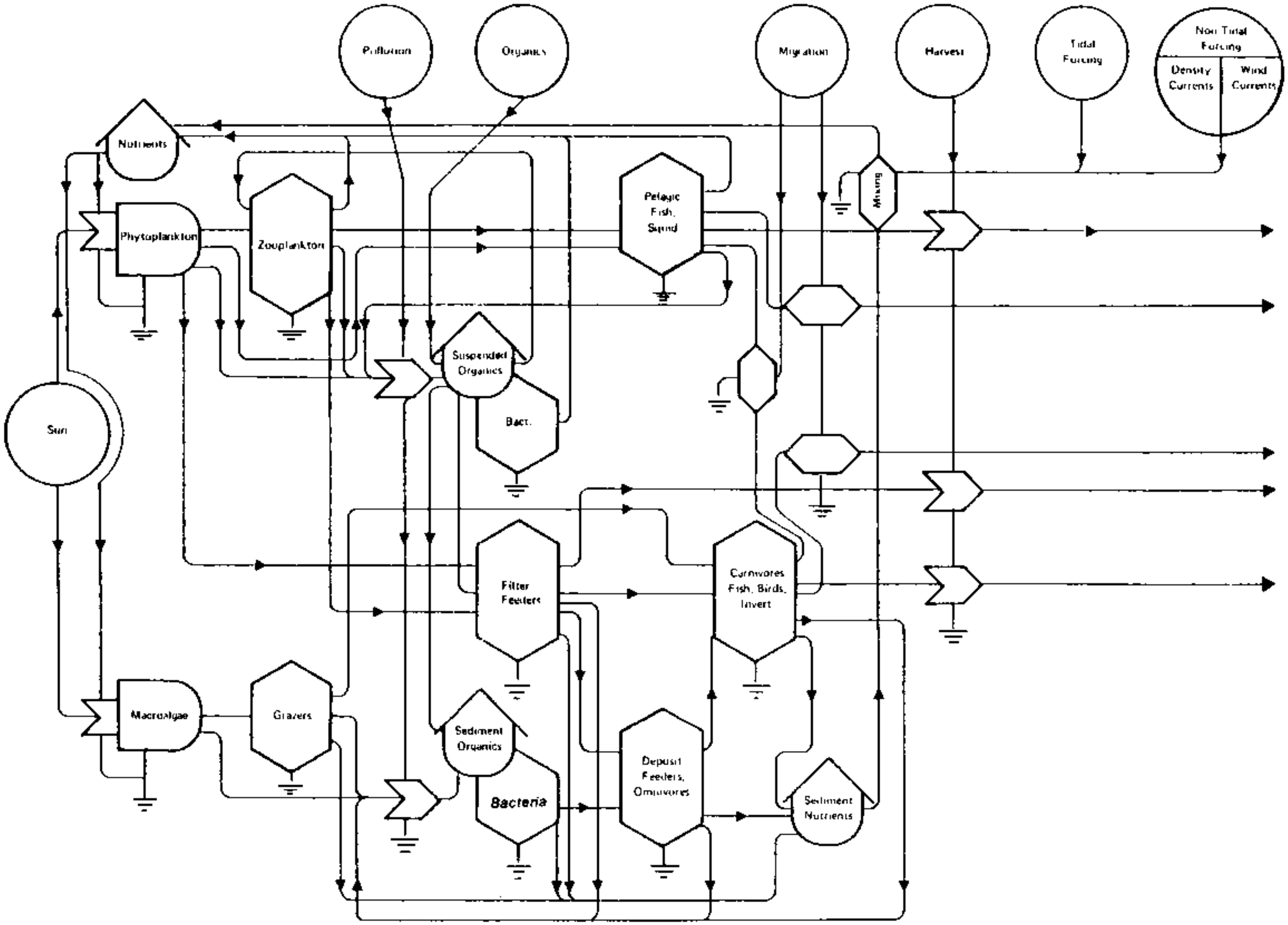


Figure 4-16. Energy flow model for the marine system in coastal Maine. The top half of the model refers to interactions within the water column and the bottom half to those that occur on or in the bottom.

As shown in figure 4-16 the energy bound in phytoplankton biomass can be utilized in five ways. Some is utilized by the plants themselves for growth and respiration. (This is indicated by a heat sink symbol in the figure.) The four other pathways of utilization of phytoplankton energy result in either direct or indirect energy transfers to higher trophic levels. Many plant cells are grazed directly by zooplankton, filter-feeding benthic organisms, and pelagic fishes. Some cells die and enter the pool of suspended organic material.

Zooplankton feed on living phytoplankton and suspended organic matter and its associated bacteria and, in turn, are devoured by certain pelagic fishes and filter-feeding benthic invertebrates. Through zooplankton death and normal metabolism these organisms, as well as all groups of consumers, recycle nutrients and contribute to the pools of nonliving organic material.

The top consumers of the pelagic system are the fishes and squid, that feed on one another as well as on species more closely associated with the bottom. These mobile carnivores import or export energy to or from the system by their migratory habits, and some of their biomass is removed from the system by fishing.

The suspended organic pool, with contributions from other systems, is utilized by bacteria, which remineralize much of the nutrients, and by benthic filter feeders. Another portion settles to the bottom, where it enters another part of the benthic food chain.

Much of the gross productivity of macroalgae is consumed by the macroalgae themselves via respiration. At low light levels, or in dense populations with little turnover, this value may be large. Net production in excess of respiratory demands may provide considerable food for higher trophic levels.

Benthic microalgae, including diatoms, in addition to small macroalgae, are often directly consumed by grazers (such as various snails, limpets, and sea urchins) and fishes. Large plants, especially their basal portions, also are eaten directly. Generally, it is thought that the direct ingestion of live, attached macroalgae accounts for a relatively small proportion of macroalgal consumption.

Marine macroalgae also may leach large amounts of dissolved organic matter into surrounding waters. Although the extent of this process has not been completely determined yet, the release of dissolved organic matter appears to be greatest in plants under stress conditions (e.g., desiccation and freezing). On a long-term basis, this might account for losses on the order of a few percent of net production. The epiphytic bacterial, algal, and invertebrate populations present on the surface of macroalgae are exposed to high concentrations of these organic materials as they are released and presumably use them as energy sources. Much of the dissolved organic matter that escapes epiphytic consumption may be consumed by the high populations of marine bacteria in coastal areas.

Most of the net production of marine macroalgae only becomes available to higher trophic levels after plants have been dislodged from their substrata by grazing, ice scouring, or storms, or have totally or partially decomposed. Although some of this plant material also becomes available for direct consumption by grazers, much macroalgal production is at least partially broken down by bacteria to form conglomerates of algal detritus and bacteria. Some algal detritus (called wrack) is temporarily washed up on shore, while most remains in subtidal marine waters. This material then forms a major food pathway to higher trophic levels. These conglomerates are consumed by omnivores and deposit-feeding (detrital) invertebrates. These invertebrates, as well as grazers, are consumed by other invertebrates, demersal fish, and waterbirds.

A similar type of energy dynamics applies to eelgrass beds. As with macroalgae, little of the net productivity of *Zostera marina* is consumed directly by grazers, although epiphytes may be heavily grazed. Much of the net production goes into formation of detritus. Areas populated by *Z. marina* are frequented by waterfowl species, including Canada geese and black ducks. These and many other birds graze directly on *Z. marina*, or the associated invertebrate community that *Z. marina* supports.

People remove energy from the benthic marine system by harvesting demersal fish, filter-feeding molluscs, and crustaceans, which support major commercial fisheries. Waterbirds, which are highly mobile, also remove energy from the system.

In the coastal zone, mixing of the water column is the major physical factor determining water quality and water chemistry. Mixing transports various nonmotile components, such as nutrients and organic materials, which allows their effective utilization and recycling. The principal forcing functions of the mixing process are ocean currents caused by tides, density gradients, and wind (see "Hydrography" and "Climate" above).

Biogeochemical Cycles

Many essential substances are cycled through the chemical, geological, and biological components of the marine system. Several such cycles have been described in the scientific literature, for example, those of nitrogen, organic matter, silica, phosphorus, and sulfur. One or more of these cycles may involve a rate-limiting step of primary production within a given system or subsystem.

Two cycles discussed below will be referred to throughout the chapter: the nutrient and organic matter cycles. The seasonal cycling of nutrients in the water column and processes that may affect nutrient levels will be described in the discussion of the nutrient cycle. The discussion of the organic matter cycle will address the different categories of organic matter in the marine environment and their cycling through biotic and abiotic segments of the marine system.

Nutrient cycle. Many nutrients are required for growth of phytoplankton and macroalgae; however, in the marine system, nitrogen in various forms is generally considered to be the limiting element. The same is also true in estuarine waters. There is, however, a major difference between coastal marine and estuarine waters with respect to the mechanisms of the supply of nutrients.

The nutrient cycle is linked to seasonal changes in coastal Maine waters. When the water column is mixed, in winter, nutrients are distributed throughout it. The low levels of phytoplankton growth at this time of year (see "Phytoplankton" below) often result in available nutrients not being utilized.

When the thermocline develops, in spring, (usually May in Maine) phytoplankton proliferate and use up the nitrogen in the surface layer. Since only limited exchange takes place across the thermocline, no further nitrogen can be supplied to the surface layer. Phytoplankton cells that die and fecal pellets produced by zooplankton are sufficiently dense that they sink out of the surface layer. This process transports the nitrogen that supported the spring bloom out of the surface waters, so that within a month surface nitrogen concentrations are undetectable. With the exception of processes described below no new nutrients are available for the rest of the summer and phytoplankton productivity remains low. This lack of nutrients in summer and early fall also may limit macroalgal production. When the thermocline begins to disappear, usually in September, nutrients, including nitrogen, are returned to the surface layer.

The nutrient data given in Apollonio and Applin (1972) from a transect from Cape Newagen (region 2) to 20 miles (32 km) offshore show the typical seasonal cycle of coastal waters described above. In December, 1969, the inshore waters out to 33 feet (10 m) were almost homogeneous in nitrate content (8 μM NO_3) over the entire depth (165 feet; 50 m), while deeper waters offshore retained some salinity stratification and surface waters contained about 6 μM NO_3. By January, 1970, overturn was complete over the entire transect; very little density structure remained and the upper 300 feet (100 m) of the water column contained 8 $\pm$ 1 μM NO_3. This condition persisted with a lens of higher nutrient (10 to 12 μM NO_3) water below 400 feet (120m) until early May, when the seasonal thermocline had become established in the upper 33 feet (10 m) of the water column. The upper 16 feet (5 m) of the water column had <1 μM NO_3 remaining, and 5 μM concentrations were found at 33 feet (10 m). By July and August the thermocline had deepened to 66 to 100 feet (20 to 30 m) and the upper 66 feet (20 m) had <1 μM NO_3. In September the thermocline was beginning to weaken, with 1μM NO_3 concentrations reaching the surface, and the 5 μM NO_3 concentration, which had been as deep as 165 feet (50 m) during the summer, was then at about 66 feet (20 m). By October, overturn was well under way and surface nitrate concentrations reached 5 to 7 μM. During the following May, stratification began to occur.

Within this general picture of the seasonal distribution of nutrients, a number of processes can occur that enhance the supply of nutrients to the surface layer and consequently result in higher primary productivity. Estuaries often supply nutrients to coastal waters. This comes about partly because of the natural circulation processes of estuaries (see chapter 5, "Estuarine System") and partly because nutrients are introduced to estuaries in sewage wastes. The latter process is not likely to be significant anywhere in Maine at the present time, with the possible exception of the area where sewage is dumped into Casco Bay (region 1), adjacent to the Fore and Presumpscot Rivers. An outflow of nutrients to coastal water due to natural circulation processes would be expected to be most significant in the vicinity of the mouth of the Sheepscot River, since it has the deepest entrance in the characterization area. In fact, it is extremely difficult to find evidence of nutrient enrichment at a station about 2 miles (3 km) south of the estuary (Garside, unpublished). Nevertheless, estuaries undoubtedly do provide some enhancement of the nutrient supply in their immediate vicinity.

A second factor that has recently been recognized as important in resupplying nutrients to the surface layer is storms (Walsh et al. 1978). Turbulent mixing associated with storms (see "Hydrography," above) causes mixing of surface waters and is most effective in resupplying nutrients when the thermocline is shallow, shortly after its formation. The timing of the fall overturn, which brings nutrients into surface waters, may be influenced by storms.

Upwelling and the interaction of tidal currents with the sea floor also produce turbulent energy that can cause mixing across the thermocline. The high nutrient concentrations found throughout the summer from Mt. Desert (region 5) to the Bay of Fundy (region 6; Apollonio and Applin 1972) may be maintained by these processes. A tongue of high nitrate water extends down the coast, with maximum values of 7 μM NO_3 close to the Bay of Fundy and 10 to 15 miles (16 to 24 km) offshore; with declining values inshore (to 4 μM) and offshore, as well as to the southwest, to <1 μM off Penobscot Bay (region 4).

Over the area within which upwelling seems to be taking place (regions 5 and 6), nutrients are not usually limiting to phytoplankton productivity. The potential production of such water is probably equivalent at least to the Sheepscot Estuary (150gm^{-2}y^{-1}; Garside et al. 1978) for a net yield of 1.3 million tons (1.8 million metric tons) of carbon fixed per year. The importance of such productivity to the Gulf of Maine fisheries cannot be ignored, but, unfortunately, little is known of the mechanisms influencing the nutrient supply that supports it.

Where depths are sufficiently shallow, the thermocline may reach the bottom. When this occurs, nutrients regenerated in the sediments can be released to the surface layer and become available for reuse. It may not be possible to detect an increased nutrient concentration, since nutrients often are used as fast as they are supplied, but productivity is increased as a consequence of the process. Such processes are restricted to water depths of 66 to 100 feet (20 to 30 m). Where these depths are found over extensive areas (such as Georges Bank), this regeneration can contribute significantly to maintaining high levels of productivity.

Organic matter cycle. Nearly all organic matter found in the natural environment has been derived from, or is a constituent of, living organisms. Since living organisms interact closely with abiotic organic matter in their environment, metabolically active compounds are passed rapidly from species to species, during feeding, assimilation, growth, and death. Other organic components include toxic substances that may profoundly affect growth in minute concentrations, and relatively inert compounds that may be transformed to active compounds by abiotic factors (e.g., wave action and salinity changes).

To illustrate the potential significance of dissolved organic substances in the oceans when compared to the sizes of living organisms, the organic carbon content of an open ocean water sample is plotted in figure 4-17 as a function

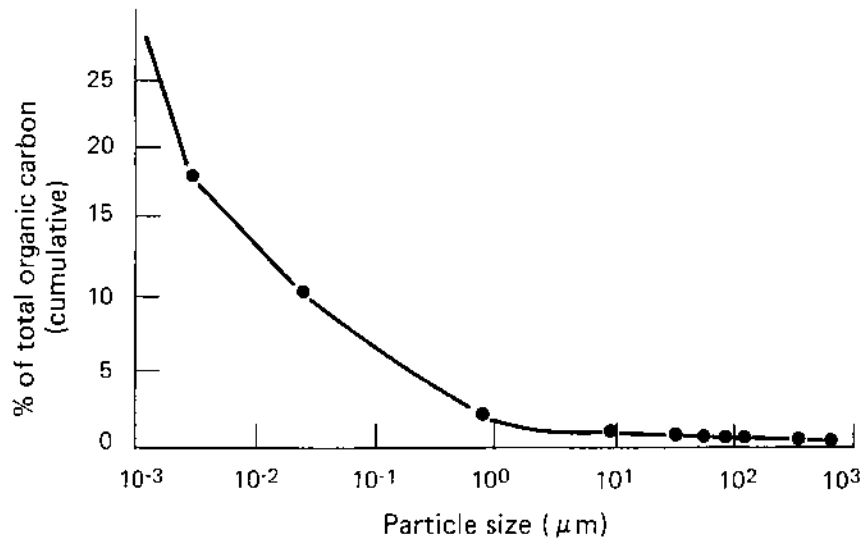


Figure 4-17. Size distribution of organic carbon particles in sea water (adapted from Sharp 1973).

of particle size. Although all living cells are contained in size fractions greater than approximately 0.5 μM they account for <5% of the total mass of carbon in the water column. In fact, it might be argued that any marine organism larger than a 10 μM phytoplankton cell is insignificant in the organic matter cycle in the oceans.

Three size groups of organic matter are present in sea water: particulate, intermediate, and dissolved. Particulate matter is any microbial organism or nonliving material that is large enough to be injested by a filter-feeding organism or to support bacterial attachment. Dissolved matter can be assimilated through cell membranes. The intermediate class of material is too small to be caught and digested but too large to assimilate through the cell membrane. In the following discussion, "biologically active" organic matter represents the larger and small-sized groups. Intermediate sized particles are ill-defined and are probably converted and transformed primarily by physical and chemical processes.

The original source of organic matter is plant photosynthesis. The primary source in nearshore areas and estuaries is terrestrial vegetation (introduced by freshwater runoff), emergent wetland plants, benthic diatoms, and attached algae. In the open ocean, phytoplankton is the most important source of organic matter. Concentrations of organic material are much more variable in coastal waters, due to local inputs, than in the open ocean.

Particulate matter is derived from decaying and fragmented plant material and algal cellular debris. Zooplankton play an important role in transforming particulate matter, through feeding and release of fecal pellets (larger animals are not considered here due to proportionately smaller input into the system). During conversion of particles, dissolved compounds are produced through extracellular release, protoplasm is released during death or breakage of cells, and feces are excreted by grazing animals. Some simple molecules can be reassimilated by phytoplankton.

The importance of bacteria in the cycling of organic matter is not fully understood. Bacteria assimilate dissolved compounds and release carbon dioxide and nutrients. Bacteria can attach to particles and living cells and hasten their decomposition by liberating enzymes. These colonized particles are eaten by filter-feeding and deposit-feeding animals. One current view suggests that the majority of organic cycling in the water column is accomplished by unattached bacteria that maintain the concentrations of readily-assimilated compounds (e.g., sugars and amino acids) at very low levels.

Components of the organic cycle that are unique to Maine are contributed by the pulp and paper industry and other point-source discharges of processed waste (see chapter 3, "Human Impacts on the Ecosystem").

A schematic diagram of the organic matter cycle in the marine system is given in figure 4-18.

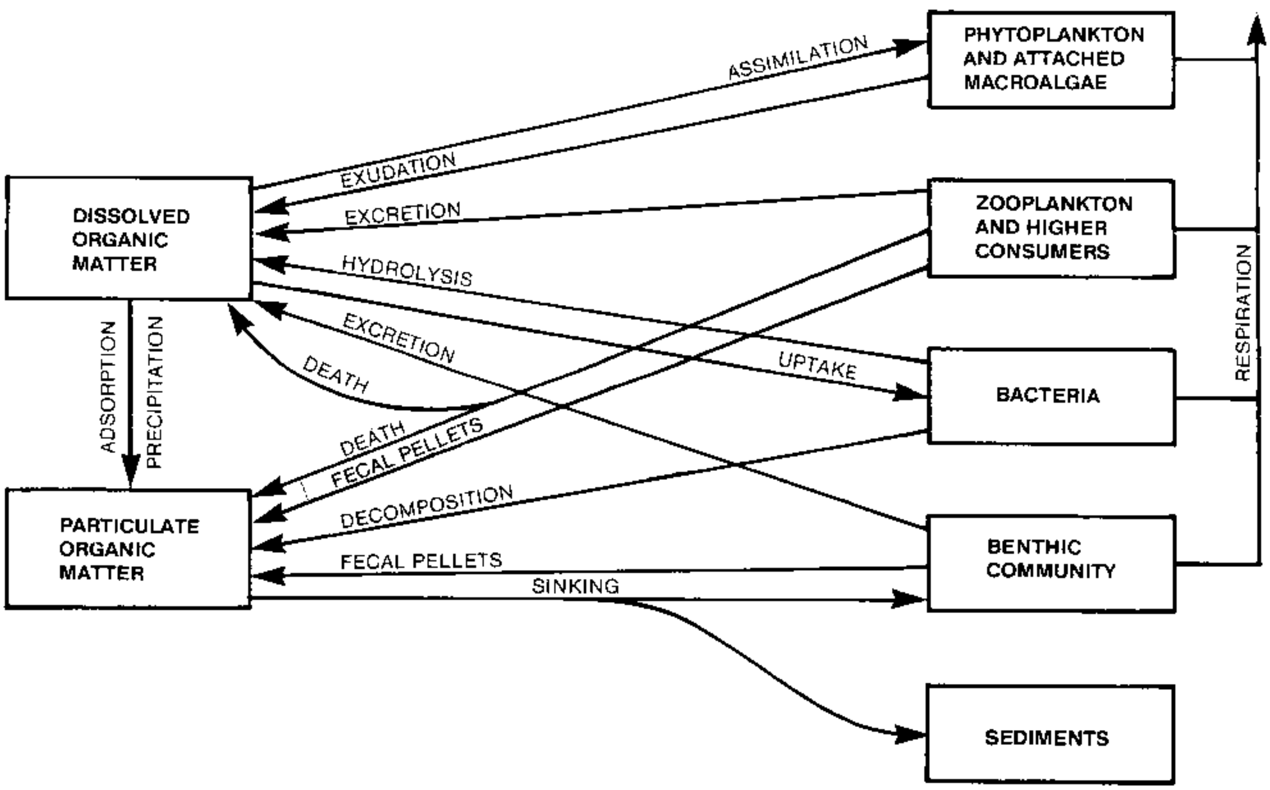


Figure 4-18. Schematic diagram of the organic matter cycle in the marine system.

Interactions Affecting the Productivity and Distribution of Biota

Phytoplankton. Phytoplankton require adequate sunlight, nutrients, and particular ranges of water temperature and salinity for optimal growth. Specific requirements vary with species; however, conditions occur in coastal Maine waters that affect whole phytoplankton populations. Currents determine the distribution of phytoplankton populations. Seasonal changes in the water column (see "Hydrography" and "Nutrients" above) control the growth of phytoplankton populations.

In winter the deep mixing of the water column (figure 4-19) may limit phytoplankton growth by carrying the phytoplankton below the level where sufficient sunlight is present to support growth. If the depth of the water is shallow phytoplankton cannot fall below the illuminated region of the ocean; the mixing action continuously carries them back to light intensities at which photosynthesis can take place. This "critical mixing depth" is considered to be about three times the depth of the photic zone (the depth of the level at which light intensity is reduced to 1% of its surface value). The critical depth of Maine coastal waters is about 130 to 200 feet (40 to 60 m; personal communication from C. S. Yentsch, Bigelow Laboratory, West Boothbay Harbor, ME; June, 1977).

Winter water temperatures also limit phytoplankton growth. With every change of approximately 18°F (10°C) in water temperature within the range of 32°F to 68°F (0 to 20°C), the photosynthetic rate is altered by about 50% (Yentsch et al. 1974). These authors conclude that the major effects of temperature would be felt and would be detectable in early winter; after this period temperature effects would be difficult to distinguish from other influences, such as the presence or absence of nutrients.

In summer, when the thermocline develops and waters become stratified (figure 4-19), the phytoplankton consume all or most of the nutrients available. Once all the nutrients are exhausted, growth of the phytoplankton is arrested and mass mortalities occur.

Optimal environmental conditions for phytoplankton growth, that is, the intermediate condition between vertical mixing and stability, occur in the spring and fall and give rise to spring and fall blooms (i.e., sharp increases in abundance) of algae.

When phytoplankton production in the characterization area is compared with that in other temperate regions, general trends can be noted. Mean annual cell densities and maximum cell densities of phytoplankton and chlorophyll concentrations are lower in Maine waters than in many bays and estuaries south of Cape Cod. The higher productivities in southern nearshore waters may be due to the following: water temperatures are higher for a longer period of time; the period of optimal light intensity is longer; and the nutrient levels are probably higher, because of runoff from the large population centers in these areas. Phytoplankton growth may not reach its full potential in these southern areas, however, because of increased turbidity from land-based discharges, which may limit light penetration. Although phytoplankton productivities in nearshore waters of coastal Maine are lower than those in southern waters, they are higher than those of the offshore Gulf of Maine for the above reasons.

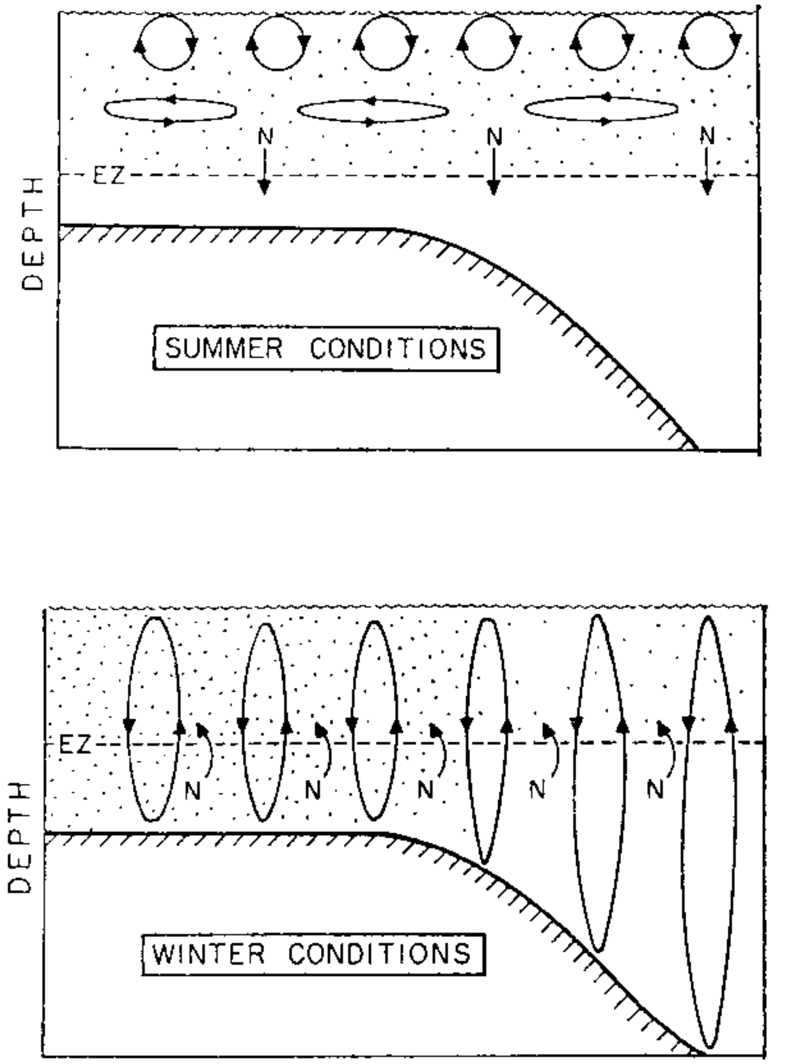


Figure 4-19. Physical conditions of the marine water column during summer (stratified) and winter (well mixed) which affect phytoplankton growth. Arrows indicate mixing; N= nutrients; dots are phytoplankton (C.S. Yentsch 1977).

Macroalgae. The physical and chemical factors that control macroalgal productivity are varied and may differ substantially between species, with most plants responding to several factors at one time. Factors governing the productivity of marine macrophyte communities are the availability of light and suitable substrata; suitable salinity levels and water temperatures, and an adequate nutrient supply. Tides carry life-sustaining compounds to intertidal macroalgal populations.

Growth of the dominant intertidal alga, Ascophyllum nodosum, is limited by low temperatures. Even high light levels (apparently necessary to approach photosynthetic saturation) do not initiate rapid growth below 50°F (10°C). Generally, higher summer water temperatures can be expected to yield greater productivity than lower winter temperatures. Also, stress associated with freezing during winter probably depresses growth. Increased grazing activity is an indirect effect of warmer summer water temperatures (approximately 68°F; 20°C) in Maine. Much of the coast of Maine has suitable substrata and salinity conditions for the development of A. nodosum.

Factors such as ice scouring, wave action, and grazing, which dislodge or consume A. nodosum, increase the rate of turnover of algae, thus, increasing net production. Wave action is also a factor in determining the distribution and abundance of macroalgal species. Certain species thrive in areas of increased wave action (e.g., Fucus sp.), while others are more abundant in protected areas (e.g., Ascophyllum sp.). Greater wave action and steeper shores promote the development of more ruggedly constructed plants that are resistant to wave drag and abrasion. Biomass per unit area also tends to be somewhat lower along the high-energy, wave-exposed shores at the headlands and islands in coastal Maine than in more protected areas. In the sublittoral zone wave action exerts influence only at the uppermost levels.

Populations of subtidal laminarians (the dominant subtidal alga) are restricted to areas of suitable substrata and relatively high salinity. Light availability greatly influences their growth as is true of many subtidal plants. Therefore, laminarians grow only in shallow subtidal areas (to 60 feet; 20 m), where light is most available. Clarity or turbidity of the water also affect their growth; algal penetration increases with clarity. High-intensity solar radiation in summer may discourage the growth of some light-sensitive plants, especially at shallow depths. In contrast to the intertidal fucoids, which grow better at high temperatures, laminarians grow quickly at low water temperatures and appear to show ill effects at higher temperatures, approximately 68 °F (20 °C). Their major growth period begins in winter and continues into spring. In addition to the possible stress of higher summer temperatures, lack of available nitrogen (see "Nutrient Cycle" above) may limit summer and fall kelp productivity.

Zooplankton. Temperature, along with food availability, is the principal factor responsible for the succession of zooplankton species that occurs in nearshore waters of coastal Maine. Each species has a particular temperature range in which growth, reproduction, and survival occur. As one group disappears, another appears and overall production is maintained throughout the year, despite annual temperature ranges far exceeding the reproductive tolerances of either group. In areas of freshwater discharge, such as upper Penobscot Bay, certain zooplankton species appear to be unable to reproduce or, in some instances, survive (Bertrand 1977). Water currents carry the zooplankton and determine their distribution.

Benthic invertebrates. Each benthic invertebrate species has certain physical and chemical requirements to survive. Chief among these are suitable temperatures, salinities, and substrata. Currents directly and indirectly affect benthic populations also.

The difference in water temperatures and temperature ranges between the eastern regions of the characterization area (5 and 6) and the western regions (1 to 4; see "Spacial Variability of Coastal Waters" above) is a major factor in determining which benthic invertebrate species inhabit these areas. Although it is not distinct and includes much overlap, a zoogeographic boundary (species' range limit) appears to exist in region 4. Many invertebrates in the northeast (regions 5 and 6) have northern affinities and do not occur or have reduced occurrences west of region 5. In the southwest (regions 1 to 4) many species have southern affinities and are not found or rarely are found northeast of region 4.

Many of the species with southern affinities need a certain minimum temperature to spawn and tend to occur only where these temperatures are reached with sufficient frequency. Maine has warm pockets of water, such as the upper Sheepscot estuary (region 2), where the summer water temperatures are high enough to support species such as the American oyster and xanthid crabs, which have their centers of abundance much farther to the south.

Less variable environmental conditions in the eastern regions (5 and 6) may allow for the development of diverse benthic communities. Eastern Maine and the Quoddy region are the most environmentally stable areas in the Northeastern United States.

Except at the mouths of large estuaries (e.g., Kennebec, region 2 and Penobscot, region 4), where freshwater discharge is present, salinity does not appreciably affect marine benthic communities. The effect in areas of runoff is described in chapter 5, "The Estuarine System."

Substrate requirements vary with species. Some species can live on a variety of substrates, while others are quite specific in their requirements. Bedrock and boulders are suitable habitats for animals that must attach to a stable surface. Sedimentary environments are inhabited by animals that burrow into the substrate.

Water currents supply food to the benthos through the transport of phytoplankton or detritus. They likewise supply respiratory gases, remove some waste material and act as a dispersing medium for pelagic larvae. Areas with currents often have increased productivity, probably because of the increased food supply (i.e., more phytoplankton passing by). Large numbers of mussels and associated animals are usually found in these high energy areas.

Benthic invertebrates living in the intertidal zone also have interactions with physical factors that are unique to life in this zone. Tides, the most important factor, bring life-supporting materials to the animals. They also remove wastes and disperse larvae.

Temperature is important to the survival of intertidal animals. High summer temperatures can create stress in the intertidal zone through desiccation, particularly in combination with wind. Maine's winter temperatures can freeze exposed organisms. Ice formation (see "Climate" above) can suffocate, dislodge, or freeze and displace animals. Some intertidal animals survive being frozen.

Fog and sunlight have opposite effects. Fog (see "Climate" above) protects animals from desiccation. Areas facing south receive more insolation than those facing north and hence are likely to be drier.

Reduced salinity may limit the development of invertebrate communities. In areas where streams cross the intertidal zone, or where fresh water seeps in from the water table, lowering salinity, those species that cannot tolerate salinity reduction are excluded.

Waves influence the penetration of animals into the intertidal zone. When waves are present, higher areas of the intertidal zone are wetted than are wetted during calm seas (see "Climate," above and "Class Level Discussions and Intertidal Subsystems" below). Waves also carry floating debris, such as logs that can grind across the shore and dislodge animals.

The nature of the substrate influences the distribution and abundance of intertidal animals. Sediments with finer consistencies (see table 4-2) have water remaining in the interstitial spaces at low tide and afford a degree of insulation against drying to intertidal animals. Cracks, crevices, undersides of rocks and tidepools are also areas that are less subject to drying. These areas support more diverse animal life than exposed surfaces.

The angle of the shore determines not only how far upwards a wave will surge before its energy is dissipated, but also how quickly water will drain off it. Water drains off flat wide shores very slowly and this lessens the threat of desiccation.

The area of tides also affects animal abundance and distribution. Large tides, as are found in the eastern region of the coastal zone, are important because they create large intertidal zones, which are potentially more diverse than smaller intertidal zones.

Squid. Little is known about the effects of physical and biogeochemical factors on squid. The two species (flying squid and long-finned squid) found in waters of coastal Maine have northern and southern affinities, respectively. The zoogeographic boundary described above (at region 4) appears to be applicable for these invertebrate species also.

Finfish, birds, and marine mammals. Interactions of finfish, waterbirds, and marine mammals with physical and biogeochemical factors are described in chapter 11, "Fishes," chapter 17, "Waterbirds," and chapter 13, "Marine Mammals."

Decomposers. Temperature strongly influences microbial processes. Even though bacteria have been shown to function at 32° F (0° C; Ingraham 1962), their growth and metabolic activity at low temperatures is extremely slow. Seasonal cycles of microbial activity are pronounced, with most activity occurring during spring, summer, and fall. While the greatest phytoplankton activity occurs in spring, decomposer activity probably peaks somewhat later (Novitsky and Passman, unpublished). Bacterial and fungal decomposers generally are able to function at lower temperatures than phytoplankton.

The geology of the Maine coast plays a significant role in controlling the size and type of microbial populations. Dale (1974) reported that the abundance of bacteria associated with sediments in an intertidal basin at Petpeswick Inlet, Nova Scotia, Canada, was highly correlated with grain size and other sedimentary properties. A fine silty or sandy bottom supported a large bacterial population but a rocky or cobble bottom would be expected to support a smaller population.

The upper intertidal pools that are present in coastal Maine harbor unique bacterial communities. Forsyth and his coworkers (1971) found that certain salt-tolerant and "salt-loving" bacteria could be isolated from tidal pools near St. Andrews, New Brunswick. They concluded that the increased salt concentration in these pools, which results from evaporation, was a factor in the natural selection of these "salt-loving" bacteria.

BIOLOGICAL PRODUCTIVITY

Primary Productivity

Primary productivity, or the rate of input of photosynthetically-fixed organic carbon, is fundamental to the maintenance of marine biological systems. Net productivity is that productivity stored as chemical energy after respiratory demands have been met. The net production is available to primary consumers (see "Food Webs" above).

Primary production in nearshore marine waters is discussed in chapter 5, "The Estuarine System." It is impossible to divide the discussion into estuarine and marine systems, because nearshore marine (intertidal and shallow subtidal) and estuarine production differ from production in deeper marine and estuarine waters respectively. The major source of production in deeper waters is phytoplankton, while in nearshore and estuarine waters macroalgae, phytoplankton, and emergent wetlands are important in maintaining production. The boundary, or depth, at which phytoplankton becomes the principal component of production is unknown.

Secondary Productivity

Secondary productivity refers to the production of animal tissue, that is, the growth of trophic levels above the primary producers. It is a measure of energy flow through the various faunistic components of the ecosystem. Unfortunately, no data exist on secondary productivity in the characterization area.

Biomass, or standing stock, is the weight or volume of animal tissue in a given area or sample(e.g., per m^2 or net tow of zooplankton) and it is often used as a crude indication of productivity, on the assumption that biomass and productivity are correlated. This is not necessarily true, of course, as a community of large, long-lived molluscs will have a high biomass but low productivity because the turnover rate is small. Conversely, a community dominated by small short-lived species, such as amphipods and polychaetes, will have a low biomass and high productivity. If, however, two communities are composed of the same types of organisms, biomass comparisons should reflect productivity differences. Biomass data for coastal Maine are limited. Sherman (1968) compared zooplankton biomass along the Maine coast and found reduced amounts in eastern Maine. Such a pattern is unexpected, because the biomass of other groups, benthos, birds, marine mammals, and herring, is high in region 6. Larsen (1979) presented biomass values for the shallow-water benthos of the Sheepscot River estuary that are comparable with other shallow-water areas (see "Estuarine Unconsolidated Bottom," page 5-81 in chapter 5). This suggests that, since other parts of the Sheepscot River are more densely populated than the estuary, the secondary productivity of the Sheepscot is high. Data on this subject are lacking, however.

CLASS LEVELS AND AN INTRODUCTION TO THE SUBTIDAL AND INTERTIDAL SUBSYSTEMS

Introduction

Two ecologically distinct but related subsystems make up the marine system: the subtidal and intertidal zones. The physical subtidal zone includes marine habitats extending beyond the extremes of low water. The area of the intertidal zone varies during the month (see "Hydrography" above). The physical boundaries of the zone are defined as the area between extreme high tide and extreme low tide.

The biological boundaries of the zones (which correspond to the NWI subsystem boundaries) often differ from their physical boundaries. The biological boundaries are defined by the grading of the biotic assemblages from subtidal to terrestrial areas, and the area between these boundaries is called the littoral zone. The difference between the physical intertidal zone and littoral zone (NWI intertidal zone) is shown schematically in figure 4-20. The littoral zone, is narrower than the physical zone in protected areas and is wider and higher than the physical zone in wave-exposed areas. Wave surge and spray wet higher intertidal levels and allow for the raised and widened development of intertidal communities. The subtidal subsystem and intertidal subsystems were calculated as making up 65% (112,130 acres; 45,397 ha) and 35% (60,576 acres; 24,525 ha), respectively, of the marine system. (Limitations of these calculations are discussed in "Data Sources and Compilation of Data" above.)

The Subtidal Subsystem

The marine subtidal zone is the area that is continually immersed by the ocean and has high constant salinities. Four types of habitats are found in the marine subtidal zone of coastal Maine: aquatic bed, rock bottom, water column, and unconsolidated bottom. These habitats, except aquatic beds, are discussed below. Aquatic beds are discussed in chapter 5, "The Estuarine System." The available information on this habitat is not sufficient to determine whether the beds differ between the estuarine and marine systems.

Eighty-five percent of the subtidal system in the characterization area is in the northeastern section. Regions 4, 5, and 6 have 40,167 acres (16,262 ha; 36%), 25,180 acres (10,194 ha; 22%), and 29,740 acres (12,040 ha; 27%) respectively. These regions are large and encompass large bays. The subtidal

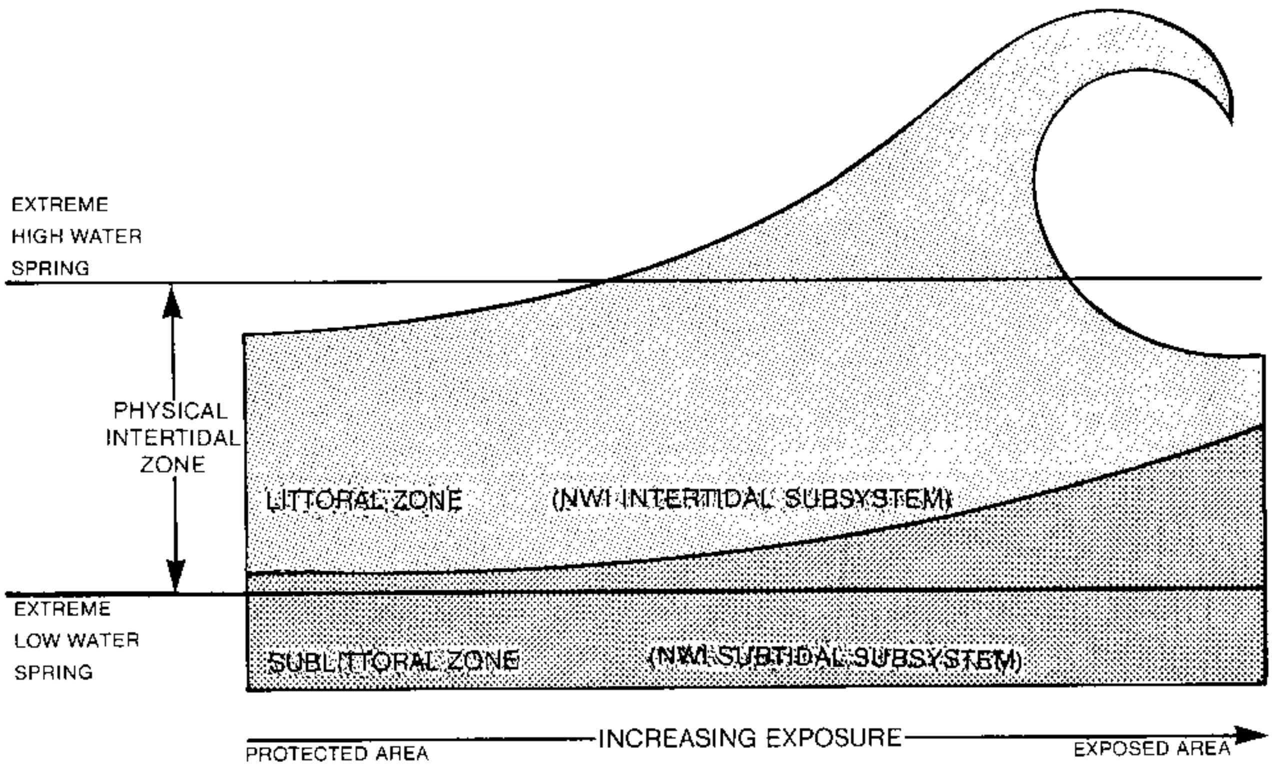


Figure 4-20. Comparison of the boundaries of the physical intertidal and subtidal zones and the littoral (biological intertidal) and sublittoral (biological subtidal) zone with increasing exposure to wave action (adapted from Lewis 1964).

area for these regions would be even larger than the southwestern regions if the area out to the 300-foot (100-m) contour were calculated. Regions 1, 2, and 3 have 13,730 acres (5559 ha; 12%), 2323 acres (940 ha; 2%), and 988 acres (400 ha; 1%) respectively. The total subtidal area in the characterization area is 112,120 acres (45,393 ha). The western regions also were not calculated to the 300-foot contour but the difference between the actual and calculated subtidal acreages in the western regions is not as large as that in the eastern regions.

The relative stability of the subtidal environment allows for the establishment of diverse, highly organized communities. In general, physical stability and biological diversity increase with depth (Gray 1974). The effects of seasons, waves, and currents, are felt less with increasing depth; therefore, communities are less vulnerable to physical disturbances. The principal physical factors that affect subtidal benthos are water temperature and temperature range, substratum type, salinity, and water currents. Phytoplankton, most zooplankton, pelagic fishes and many marine mammals spend most, if not all, of their lives within the water column. The bottom is occupied by benthic invertebrates and demersal fish and, in shallow water, macroalgal species, which are important producers. Marine birds utilize the surface or near-surface marine subtidal waters for feeding, molting (i.e., eider ducks), and resting.

Most of the ocean-derived food resources are harvested in the marine subtidal zone. In the Gulf of Maine these resources include pelagic fishes, such as herring and mackerel; demersal fishes such as haddock, cod, and flounder; and invertebrates, such as lobster, scallops, and shrimp. These and other commercial species depend on the energy base of the phytoplankton and macroalgae, as well as on the zooplankton, benthic invertebrates and other fishes at intermediate trophic levels (see "Food Webs" above, chapter 11, "Fishes," and chapter 12, "Commercially Important Invertebrates").

Levels of knowledge of the various biological groups occupying the marine subtidal zone vary considerably in Maine. Little research has been done on macroalgal and invertebrate communities in the Gulf of Maine. Environmental influences on the abundance and distribution of many species of plants and animals are not well understood.

Class: open water (water column). The water column is the environment of pelagic organisms, i.e., those that do not have regular contact with the bottom. These organisms include phytoplankton, zooplankton, squid, pelagic fish, birds, and cetaceans. Interaction takes place between the water column and the benthic environment in coastal waters. Some nutrients that support phytoplankton growth are recycled in bottom sediments, some zooplankton are larvae of benthic species, and pelagic fishes often lay their eggs on the bottom. The marine water column habitat is contiguous with the estuarine water column habitat. Organisms in the water column move, or are transported, extensively between marine and estuarine systems. Pollutants in the estuarine water column are transported into the marine water column. The water column extends over the entire subtidal zone and encompasses 100% of the subtidal area inland of the headlands. Also included in the water column habitat is the subtidal area from the headlands to the 300-foot (100-m) depth contour. The distribution of the water column by region is the same as that of the subtidal subsystem.

In the Gulf of Maine, phytoplankton production is not constant throughout the year. The first bloom of phytoplankton (chlorophyll-a photosynthetic pigment is used as an index of the abundance of algae) appears in the spring and is associated with physical and chemical factors (see "Hydrography" above). This bloom terminates because of the depletion of nutrients (see "Nutrients" above). The second bloom is in the fall after the overturn of water, when the nutrient supply is replenished.

The overall seasonal pattern is generally repetitive and predictable. The exact timing and number of peaks of the blooms, particularly the spring bloom, varies from year to year and with location (see figure 4-21). Usually, the spring bloom occurs earlier in southern regions and progresses northward across the Gulf of Maine and coastal waters of Maine from late February through May. The spring bloom is composed mainly of diatom species. The stratified warm waters of summer support dinoflagellates.

The general seasonal pattern described above may be altered when certain processes occur that enhance the supply of nutrients to the phytoplankton (see "Nutrient Cycle" above). The extent of this variability in the characterization area is unknown but it appears that higher phytoplankton production may be occurring in the eastern regions (5 and 6) than in the western regions (1 to 4), probably due to upwelling. Areas of localized upwelling (see "Hydrography" above) also appear to sustain phytoplankton production through the summer. High amounts of chlorophyll were found in patches at the surface (figure 4-22) before the fall overturn near Monhegan Island (Yentsch and Glover 1977). Also, the continued growth of diatoms through the summer was reported by Hulbert and Corwin (1970) for Casco Bay.

In temperate ocean waters, such as those of New England, the diversity of species generally increase with decreasing population size; that is, low chlorophyll concentrations are associated with high diversity. Seasonal changes in the diversity of phytoplankton populations are apparent. During the poorest growth season of the year (summer), no single species is very abundant and diversity is high. Conversely, when growth conditions become favorable (spring), species diversity decreases. This seasonal pattern has been noted by Petrie (1975) in the Damariscotta River estuary (region 3). The significance of diversity can be seen in the comparison of rich and poor areas for growth (figure 4-23). In nutrient-rich estuaries phytoplankton populations are much less diverse than in the relatively nutrient-poor ocean waters.

A succession of zooplankton species occurs in coastal Maine. Each species has a seasonal cycle of peaks in abundance followed by decreased numbers and the species composition changes with seasons. Within each species, propagation is initiated by a few individuals that have survived the seasonal mortality or by individuals hatched from resting eggs produced the previous year, as may be the case for the copepod Centropages hamatus (Fish and Johnson 1937). The life cycle of zooplankton species is controlled by food supply (quantity and quality) and physical factors (see "Physical/Biogeochemical/ Biological Interactions" above).

A limited number of zooplankton species are dominant (i.e., abundant) in coastal Maine waters. Reproduction and seasonal abundances vary greatly between species. The life cycles of dominant species (or taxa) in the characterization area (listed in table 4-6) are described in appendix F. In order to determine the potential effect of perturbations on species their seasonal cycles must be known. Much of the data in the appendix are based on two nearshore studies: the first by Bertrand (1977) in Penobscot Bay and the second by Sherman (1966 and 1968) in the coastal waters of Maine.

According to Sherman (1968), copepods generally accounted for over 70% of the zooplankton in coastal Maine waters (table 4-7), except infrequently when appendicularians (pelagic tunicates) became abundant. In addition to appendicularians, other zooplankton that appear in abundance periodically are comb jellies (Ctenophora), siphonophores and medusae jellyfish (Cnidaria), and arrow worms (Chaetognatha). Many of these species are important predators on zooplankton. Therefore, their density has a significant impact on zooplankton populations. Siphonophores have an impact on the fishing industry (see appendix F). Euphausiids (krill, shrimplike animals) are a small but relatively consistent proportion of the zooplankton in spring and summer (Sherman 1968).

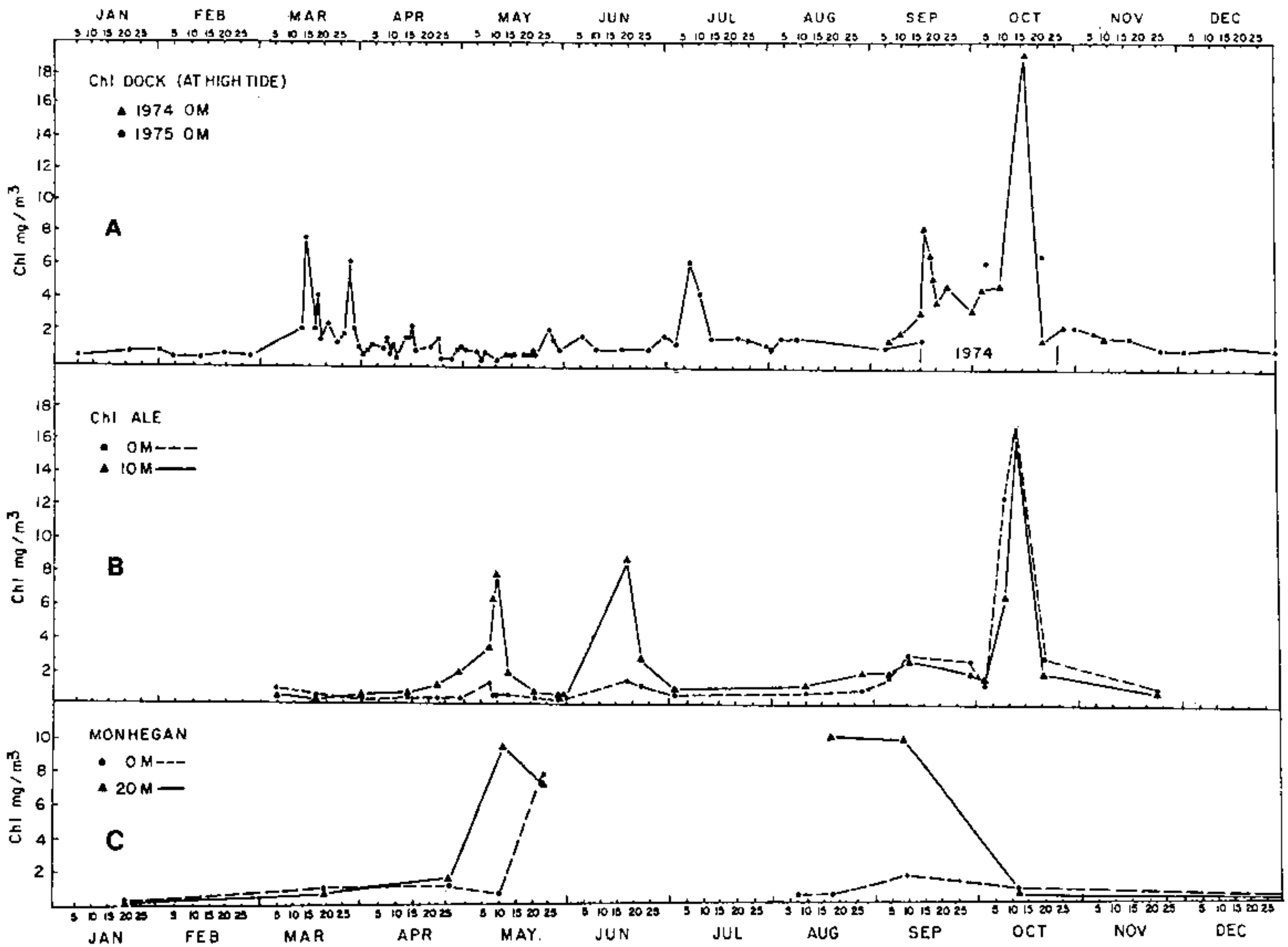


Figure 4-21. Seasonal variation in chlorophyll-a concentrations at Boothbay Harbor (A, region 2), approximately 8 miles south of the mouth of the Sheepscot estuary (B, region 2), and near Monhegan Island (C, region 3; Yentsch, unpublished).

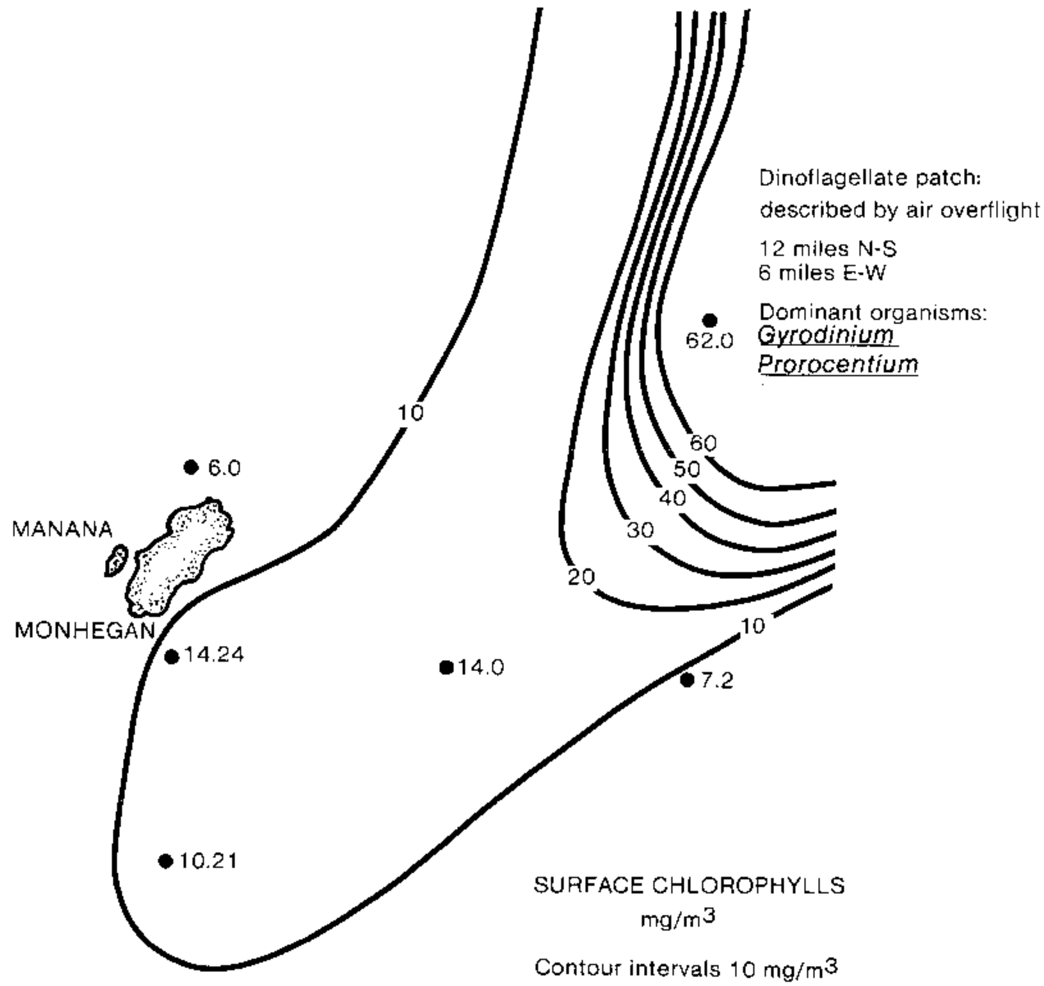


Figure 4-22. Contour map of surface chlorophyll concentrations off Monhegan Island (region 3) during the 1976 dinoflagellate bloom (Yentsch and Glover 1977).

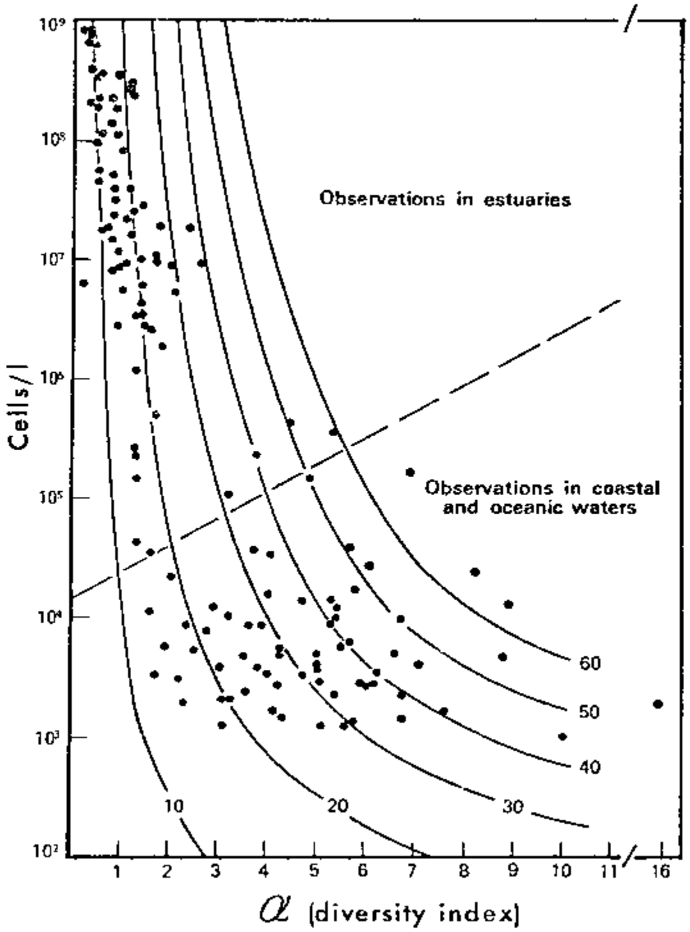


Figure 4-23. Relation of phytoplankton species diversity to phytoplankton population size in marine and estuarine waters (Hulbert 1963).

Table 4-6. Dominant Taxa of Zooplankton Found in the Characterization Area[a]

Taxonomic name	Common name
Calanus finmarchicus	copepod
Psuedocalanus minutus	copepod
Centropages typicus	copepod
Centropages hamatus	copepod
Microsetella norvegica	copepod
Temora longicornis	copepod
Oithona similis	copepod
Acartia sp.	copepod
Eurytemora herdmani	copepod
Cirripeds	barnacles
Cladocerans	crustaceans
Echinoderm larvae	starfish, sea cucumbers
Appendicularians	pelagic tunicates
Sagitta elegans	arrow worm
Coelenterate medusae	jellyfish
Ctenophores	comb jellies
Molluscan larvae	e.g., snails, clams
Polychaete larvae	worms

[a]These species are discussed individually in appendix F.

Table 4-7. Percentage Composition of Zooplankton Groups in Coastal Waters of the Gulf of Maine in 1965 and 1966[a]

Group	1965				1966			
	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall
Holoplankton	Percent	Percent	Percent	Percent	Percent	Percent	Percent	Percent
Amphipoda	P[b]	P	----	P	P	P	P	----
Appendicularia	----	2.1	1.6	P	----	3.7	27.4	1.4
Chaetognatha	1.3	P	1.1	2.1	1.9	----	P	1.5
Cladocera	P	2.6	P	2.1	P	1.6	1.9	12.1
Copepoda	96.9	74.4	71.4	91.6	97.3	72.4	35.4	76.8
Euphausiacea	1.3	4.6	6.2	P	P	4.6	3.4	1.5
Isopoda	P	----	----	----	----	----	----	----
Medusae	P	P	P	----	----	P	P	P
Pteropoda	P	----	P	1.0	P	P	P	P
Metroplankton								
Annelida larvae	P	P	P	P	P	P	P	P
Brachyura larvae	---	P	1.5	1.4	----	P	1.8	----
Cirripedia larvae	P	12.3	P	----	P	13.3	P	----
Crustacean eggs	----	P	10.9	P	P	P	15.1	3.5
Crustacean nauplii	----	----	----	P	----	P	P	P
Decapoda larvae	P	P	P	P	----	P	4.8	P
Echinodermata larvae	----	----	----	----	----	----	P	P
Fish eggs	P	1.1	6.1	P	P	1.7	8.1	P
Gastropoda larvae	----	P	P	----	----	P	P	P
Pelecypoda larvae	----	----	P	P	P	----	P	----
Pycnogonoida	----	P	----	----	----	----	----	----

[a]Sherman 1968.
[b]P = present, but representing <1% of the zooplankton in each season.

The copepod Calanus finmarchicus is the most abundant zooplankton species found in the Gulf of Maine, Bay of Fundy, and surrounding coastal waters, where it often makes up 35% to 70% of the total zooplankton population. It is noted for its importance as the chief diet of herring, shad, and mackerel (Bigelow 1926; Fish 1936; and Sherman 1970). This species is primarily a coastal species that is carried inshore by tidal currents.

In view of the observations of Bigelow (1926), Fish and Johnson (1937), and Sherman (1965, 1966, 1968, and 1970) on the enormous number of C. finmarchicus in the Gulf of Maine, it is likely that zooplankton grazing limits phytoplankton populations (Riley 1946 and 1947). Cushing (1968) has shown this to be the case in temperate waters where C. finmarchicus is the dominant zooplankton organism. It is proposed that during the spring phytoplankton bloom, Calanus lays its eggs; after the eggs hatch, the nauplii grow to adults and consume enough phytoplankton to decrease the standing stock. Sufficient data to test this hypothesis in the coastal areas of the Gulf of Maine are not available at present (Cohen 1975).

Mean volumes of zooplankton (figure 4-24) are primarily determined by abundances of C. finmarchicus (figure 4-25; Sherman 1968). An areal decline in zooplankton volumes and C. finmarchicus abundances from southwestern Maine to northeastern Maine is apparent. Sherman (1968) states that differences in hydrography in the three areas appear to account for this decline. The lower temperatures and unstable water column in the northeastern Gulf in combination with a lack of immigrants from the north and east has been hypothesized as the reason for lower populations in eastern Maine (Sherman 1968). The water column becomes increasingly stable and spring and summer temperatures become higher from northeast to southwest. These factors favor increased abundances of the zooplankton population (Sherman 1968). Based on nutrient data (above), and hydrographic data (above) it would be expected that zooplankton volumes would be higher in the northeastern part of the characterization area (regions 5 and 6), because of the potentially high phytoplankton production in this region. It is unknown why this has been found not to be true.

In Penobscot Bay (region 4) and probably in other bays along the coast, the seasonal cycle of zooplankton is somewhat different from that in the coastal and offshore waters. Copepods comprised more than 90% of the total zooplankton population in Penobscot Bay from August through early March (Bertrand 1977). From late March through July copepods accounted for <50% of the zooplankton. Balanus spp. (barnacle) larvae, cladocerans, and echinoderm larvae (e.g., starfish) made up most of the rest of the zooplankton. Relative percentages of copepod and noncopepod zooplankton in three areas of Penobscot Bay are given in figure 4-26.

In spring, cirriped (barnacle) larvae are a significant part of the zooplankton in coastal waters (Sherman 1968) but never reach abundances comparable to those in Penobscot Bay. This spring-summer pulse of principally meroplanktonic species is typical of bays and estuaries in coastal Maine.

The decreased copepod abundance in Penobscot Bay in spring and early summer may be due in part to predation (Bertrand 1977). Important predators present at this time are the ctenophores, Bolinopsis infunidbulum and Pleurobrachie pileus; the medusae, Cyanea capillata and Aurelia aurita; the chaetognath, Sagitta elegans; and the fishes, Atlantic herring and Atlantic menhaden.

Copepods are particularly affected by predation, and the copepod Microsetella norvegica was found to be part of the diet of the fishes. In Penobscot Bay, predation may be in part responsible for the fact that there was only one peak in copepod abundance (in late summer), rather than two (spring and fall) as has been reported by a number of investigators in other areas (Bigelow 1926; Marshall 1949; Deevey 1956; and Martin 1964).

Two species of squid, flying squid and long-finned squid, are found in the waters of coastal Maine. The flying squid is the more common of the two species and is found in large schools in nearshore waters during summer, particularly in the northeastern regions (5 and 6) of the characterization area. Long-finned squid, which is the most common inshore squid species in southern New England, is found in low numbers (relative to the flying squid) in Penobscot Bay, (region 4) and infrequently in the Bay of Fundy (region 6).

Nothing is known about the distribution or abundance of squid in Maine. Flying squid are important predators in the characterization area, because they seize fishes (herring and mackerel) and kill large numbers of individuals. These squid have been observed in bays and harbors of region 6 hurling themselves out of the water (sometimes landing on boats or the shore) in the frenzy of attacking fishes.

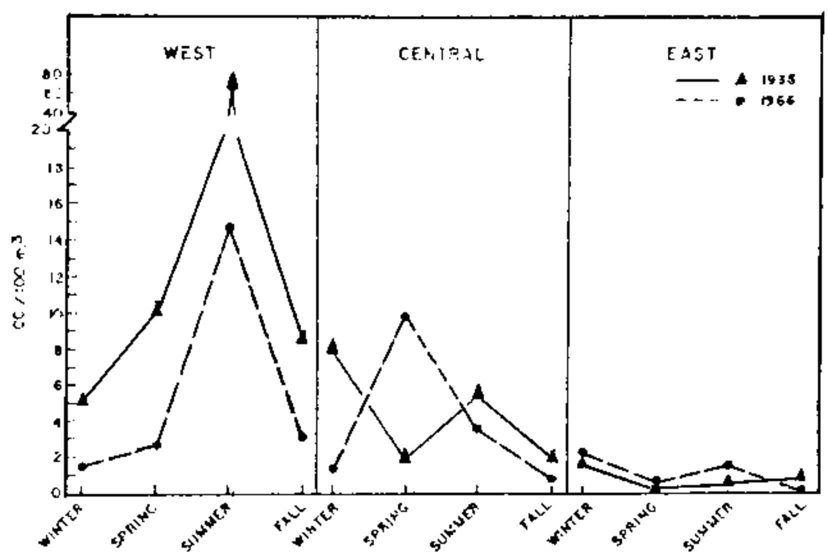


Figure 4-24. Mean seasonal volumes of zooplankton in Gulf of Maine coastal areas in 1965 and 1966 (Sherman 1968).

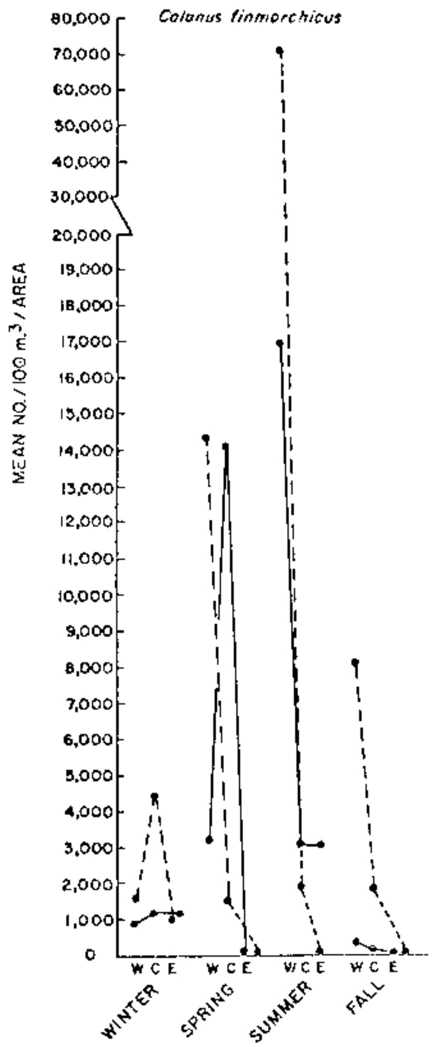


Figure 4-25. Mean number (by season) of dominant copepod species (per $100\,m^3$) in Gulf of Maine coastal waters in 1965 and 1966. W= western, C= central, and E= eastern (Sherman 1968).

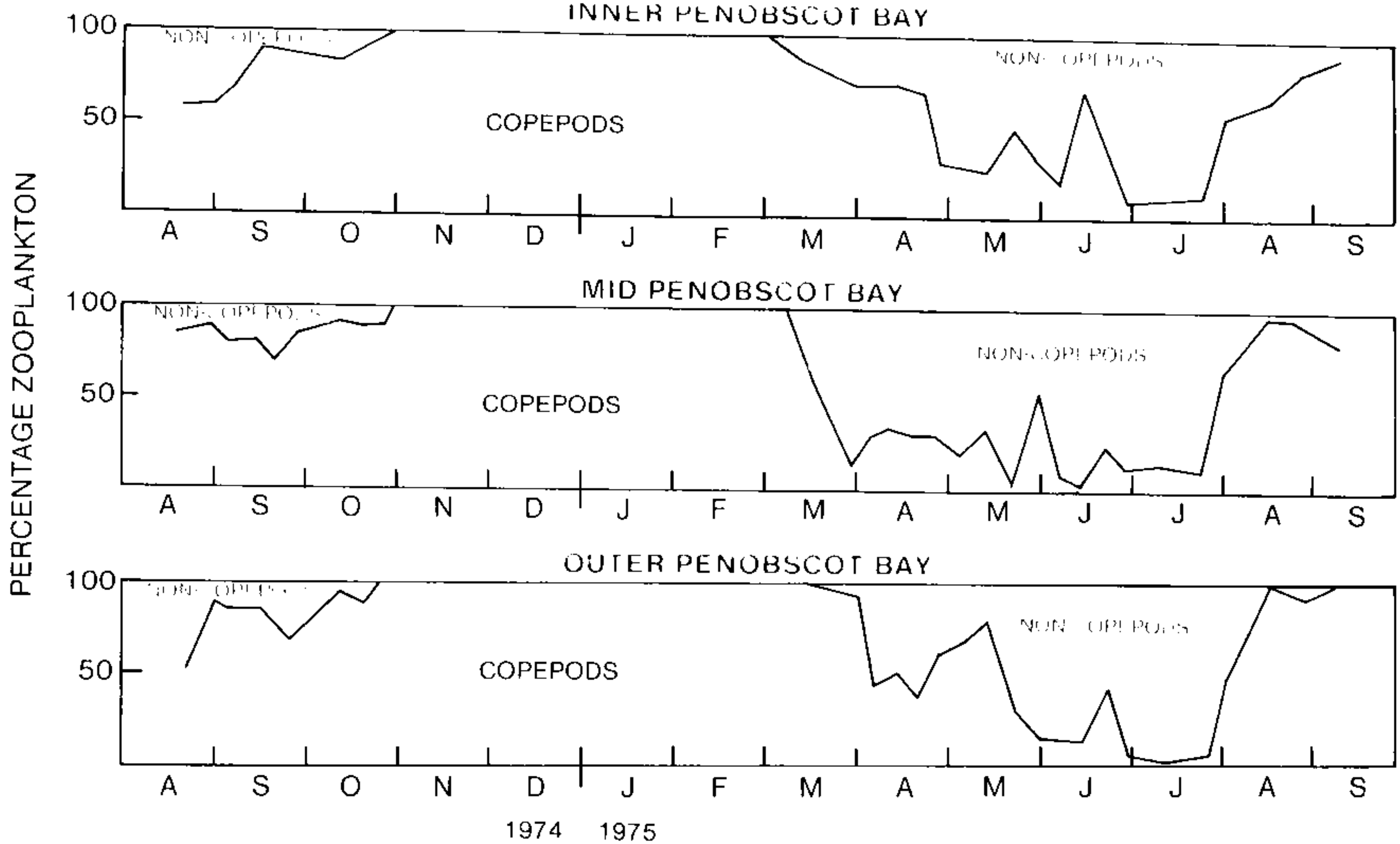


Figure 4-26. Seasonal variation in percentage composition of copepods and non copepods in Penobscot Bay in 1974 and 1975 (Bertrand 1977).

The majority of pelagic and semidemersal fish range freely throughout the water column. Planktonic and nektonic feeders feed primarily in the water column. Fishes are discussed in detail in chapter 11, "Fishes."

The primary waterbirds feeding in inshore open water are common terns, cormorants, eiders, guillemots, bay ducks, and sea ducks. Birds feeding in offshore water include kittiwakes (mostly winter), artic terns (summer), large alcids (throughout the year), phalaropes (migration), shearwaters (summer), fulmar (fall, winter, and spring), and petrels (summer). Common terns, large alcids, and shearwaters eat mostly fishes. Arctic terns, fulmars, and Bonaparte's gulls eat fishes, copepods, and euphausiid shrimps. Petrels and phalaropes feed mostly on copepods and the smaller-sized classes of euphasiids.

Large concentrations of seabirds occur in open water, especially near upwellings, tidal rips, and slicks. In August, concentrations of northern phalaropes number over 1 million in open water off Eastport (region 6), south of Grand Manan (region 6), and near Mt. Desert Rock (region 5). Phalaropes numbering in the hundreds of thousands have been reported near Machias Seal Island in spring. Large mixed flocks of Bonaparte's gulls, large gulls, shearwaters, fulmar, kittiwakes, and terns may occur over local food concentrations. The large seabird concentrations near Eastport feed on the euphausiid surface swarms and on herring and other finfish (see chapter 14, "Waterbirds").

Many waterfowl that feed on intertidal flats rest in 'rafts' (large groups) on open water, especially when the flats are inundated. Many of these rafts are located on the lee side of islands and ledges (see chapter 15, "Waterfowl").

Marine mammals are discussed in chapter 13, "Marine Mammals," and in this chapter.

<u>Class: unconsolidated bottom.</u> Unconsolidated bottoms are characteristic of the majority of the subtidal marine environment. In NWI terms, beach/bar, open water (i.e., unknown bottom), unconsolidated bottom, and flat habitats are all classed as unconsolidated bottoms.

Unconsolidated bottoms are sedimentary deposits of glacial or recent origin of which many types exist: gravelly sand, silty sand, and sand and mud. The gravelly sand and silty sand deposits are offshore from present-day beach and fluvial systems. The gravelly sands offshore are marginal to the larger island complexes in Knox and Hancock Counties (regions 4 and 5) and are probably relict glaciofluvial gravels. Marine mud sediments fall into two types (Schlee 1973). Veneering the offshore areas of the midcoast areas are pelagic deposits of sandy mud. Areas offshore from Hancock and Washington Counties (regions 5 and 6) have a smaller sand fraction and approach true silt-clay mixture muds.

Sediment composition of unconsolidated bottom deposits is dependent upon sediment sources. Gravel fraction compositions probably reflect onshore bedrock compositions, sand and silt fractions are most commonly dominated by quartz and feldspar minerals, while the clay fraction is composed mostly of illite, chlorite, and hornblende, reflecting the metamorphic bedrock terrain from which the clays were originally derived (Hathaway 1972). These deposits are subject to modification by waves and currents.

Except for an occasional large stone, unconsolidated bottoms do not provide suitable substrata for the development of large macroalgae. Hence, organic matter flux is largely determined by phytoplankton production and the inflow of detrital material. Microbial transformation of organic material depends upon the degree of anaerobiosis in the sediments, which, in turn, is related to the magnitude of organic deposition.

Subtidal unconsolidated bottoms often support a large number of animal species in varying densities. Since these animals are dependent on the influx of detritus and phytoplankton productivity, the density of individuals below the photic zone usually decreases with depth. At the same time diversity, or numbers of species, usually increases with depth, because of the increasing environmental constancy, which, over time, has allowed the species present to partition the environment more finely through evolution (Gray 1974).

Sediment type and particle size influences the structure of benthic communities. Unstable sediments are suitable only for those species that can burrow quickly and thereby maintain a proper contact with the sediment surface. Fine sediments are often dominated by deposit feeders, which glean organic matter from the substratum, and, in so doing, may prevent the establishment of suspension-feeding populations (Rhoads and Young 1970). Fine sand has the highest species richness, followed by a lowered number of species in coarse sand or gravel. Sediments that have high percentages of silt and clay appear to be generally poor in numbers of species. Sediments that have a high silt-clay content also often have very high percentages (over 85%) of polychaetes, often with high abundances of one or two species (Normandeau Associates 1974).

Information on the benthic communities of unconsolidated bottoms in the marine system in Maine is sparse relative to what is available in other geographic areas. The principal qualitative surveys include Verrill (1874) and Kingsley (1901) in Casco Bay (region 1), Procter (1933) in the Mt. Desert area (region 5), Webster and Benedict (1887) and Verrill (1872) in the Eastport area (region 6). Quantitative studies in the characterization area are largely the result of impact-related surveys. Normandeau Associates (1974), Rowe (1972 to 1973), and the U.S. Environmental Protection Agency (EPA; 1975) surveyed in Casco Bay (region 1). Dean (1977) studied a site off the mouth of the Kennebec River (region 2). Penobscot Bay sites were examined by Kyte (1974), Normandeau Associates (1975), and Dean and Schnitker (1971) (region 4). Larsen and Doggett (unpublished) sampled a few stations in Cobscook Bay (region 6), and Bilyard (1974) did research near Damariscove Island (region 2).

Cobscook Bay, the only place in region 6 where unconsolidated bottoms have been sampled, seems to be particularly diverse. Larsen and Doggett (unpublished) found the mean number of species per station (0.2m^2) to be 50 (range 28 to 70). The mean density in Cobscook Bay, 3788 individuals (m^{-2}) (range 880 to 12,970) is also relatively high for a nonenriched, boreal coastal area. Both the diversity and density of Cobscook Bay, and presumably eastern Maine in general, are a reflection of the unique hydrographic features of the area (see "Spacial Variability of Coastal Waters" and "Processes Influencing Coastal Waters" above).

Fishes are found primarily in the subtidal zone, but frequent intertidal areas at high tide or when sufficient water and food are present. Demersal fishes are more closely associated with specific bottom types than pelagic fish. A variety of fish are commonly found in subtidal unconsolidated bottom habitats (and intertidal flats and beaches at high tide) in inshore marine waters in Maine, including alligatorfish, American sand lance, wrymouth, lumpfish, Atlantic cod, the flounders, the skates, scup, the sturgeons, haddock, and silver hake. Fishes are discussed in detail in chapter 11, "Fishes."

Class: rock bottom. While subtidal rock bottoms are uncommon along the East Coast of the United States, they are relatively common in the characterization area. These areas were not specifically considered in the NWI. It may be assumed that, except for a band of varying width that parallels rocky shores, the total area of this habitat is relatively small and it occurs in an insular fashion, separated by unconsolidated bottom.

Subtidal rock bottoms are formed by the submergence of coastal areas underlain by bedrock. The surficial sediments are removed by waves, as the swash zone moves landward. Wave-generated subtidal currents, however, may continue to expose bedrock in water depths up to 66 feet (20 m), the depth limit of storm-wave influence along the Maine coast (Farrell 1972).

Subtidal rock bottom is the most important habitat along the Maine coast with regard to macroalgal biomass, because it provides the stable substratum required by these plants. Vegetated rock bottoms fall into the NWI aquatic bed class. This habitat probably accounts for the majority of macroalgal productivity in coastal Maine. Unfortunately, little attempt has been made yet to quantify the subtidal flora of Maine.

The subtidal vegetation of rocky bottoms is dominated by large brown laminarians (kelps), principally of the genus *Laminaria*. These plants, which appear to exert a stabilizing influence on sublittoral macroalgal populations, are perennials and live many years. While brown algae dominate the algal biomass, red and green algae are present in low biomass and the reds account for most of the species. Many of these species are annuals and may appear for only brief periods during the year. *Chondrus crispus* (Irish moss), however, may be locally abundant. In water deeper than 66 feet (20 m) smaller, slow-growing forms are dominant. Due to the paucity of information on subtidal macroalgae, geographic variations cannot be considered. Large scale variations do not appear to be present, however, and the above pattern remains the same from Cape Elizabeth to Eastport.

Few studies have been conducted on invertebrates of subtidal rock bottoms in the characterization area. Available information includes a qualitative study by Verrill (1874) in Casco Bay and impact-related studies in Casco Bay (Normandeau Associates 1974) and Penobscot Bay (Normandeau Associates 1975). In addition, Marine Research Associated (1979) conducted subtidal studies in the Passamaquoddy/Deer Isle area adjacent to region 6. Normandeau Associates (1974) describe the fauna of rocky outcrops of Casco Bay as sparse, with two species, the barnacle *Balanus crenatus* and the amphipod *Unciola irrorata*, being numerical dominants.

In Penobscot Bay, Normandeau Associates (1975) report that considerable variation exists in community composition. They think that the variation is related to location and substratum variability, rather than season. Of the 221 species and 20,000 individuals collected, the following eight species were dominant (i.e., most abundant; Normandeau Associates 1975):

Strongylocentrotus droebachiensis	sea urchin
Echinarachnius parma	sand dollar
Thyasira flexuosa	bivalve
Acmaea testudinalis	limpet
Alvania sp.	gastropod
Cerastoderma pinnulatum	bivalve
Astarte undata	bivalve
Leptocheirus pinguis	amphipod

Since some of the species listed above are infaunal (live in the bottom sediment) the hard substrate must have contained pockets of sediments.

High local abundances of sea urchins were reported in Penobscot Bay (Normandeau Associates 1975). High densities of sea urchins also have been observed in Cobscook Bay and at the mouth of the Sheepscot estuary (personal communication from L. F. Doggett, Bigelow Laboratory, West Boothbay Harbor, ME; June, 1977). Individuals of this species can pave the bottom and graze everything in their path, thereby modifying the nature of the bottom for several years. Subtidal rock bottom habitats are preferred feeding areas for eider ducks, other seaducks, loons, and grebes where they feed on benthic invertebrates.

Subtidal rock bottom habitat (and intertidal rocky shore areas at high tide) are preferred habitat for a number of fish species, including American eel, sea raven, sea snails, snakeblenny, rock gunnel, tautog, redfish, and ocean pout. Fishes are discussed in detail in chapter 11, "Fishes."

The Intertidal Subsystem

The physical intertidal zone is the area between extreme high and low tide marks (see "Hydrography" above). This zone is ecologically different from the subtidal zone, because of the alternative submersion and exposure of the substratum.

Eleven habitats occur in the intertidal zone of coastal Maine. They are mud flat, sand flat, sand beach, gravel beach, cobble beach, boulder beach, protected rocky shore, exposed rocky shore, emergent wetland, stream bed, and reef. Only those habitats that are specific to the marine system are discussed below. They are sand beach, exposed rocky shore, and boulder beach. The other habitats are discussed in chapter 5, "The Estuarine System," because the estuarine intertidal subsystem and marine intertidal subsystem are ecologically similar in coastal Maine.

The area of the intertidal marine subsystem in the characterization area is 60,576 acres (24,525 ha) and 71% of that acreage is in the eastern regions of the characterization area (4, 5, and 6). Regions 4, 5, and 6 have 26% (15,895 acres; 6435 ha), 22% (13,297 acres; 5383 ha), and 24% (14,795 acres; 5990 ha) of the total area, respectively. These regions have higher acreages because they are larger than the western regions and they encompass bays. Casco Bay (region 1) has the next highest area, 11,625 (4706 ha; 19% of the total area of the intertidal marine subsystem), among the six regions. Regions 2 and 3 account for only 3% (1540 acres; 623 ha) and 6% (3442 acres; 1394 ha), respectively, of the total intertidal marine acreage.

Acreages of the habitats of the intertidal marine subsystem are given in table 4-8. The NWI classification system grouped some of the 11 types of habitats listed above. The term "beach/bar" in the NWI system includes sand beach, gravel beach, and cobble beach. "Flats" encompass mud flats, sand flats, and stream bed. Boulder beaches and exposed and protected rocky shores are included in the NWI category of "rocky shore."

Flats and rocky shores are the dominant habitats in the characterization area and much of the area (86% and 87% respectively) of these habitats is in the eastern regions (4, 5, and 6). Aquatic beds (probably eelgrass) are most dominant in region 1. Region 2, which has only 3% of the total intertidal marine area, has 14% of the total beach/bar habitat. Most of the marine intertidal habitat in this area is sand beach.

Organisms inhabiting the intertidal zone live within biological boundaries; the area between these boundaries is called the littoral zone (see "Introduction to the Subtidal and Intertidal Subsystem" above). The permanent residents of this zone are principally macroalgae and benthic invertebrates. At high tide, fishes from the subtidal zone move in to forage and at low tide the zone is utilized by shorebirds, waterfowl, wading birds, and mammals. The permanent intertidal residents are mainly of marine origin and can be considered to be displaced from the subtidal zone.

Physical factors affecting the distribution of organisms of the intertidal zone are: tide, temperature, waves, nature and angle of substratum, available sunlight, fog, and size of the intertidal zone (see "Physical/Biogeochemical/Biological Interactions" above).

The intertidal zone can be considered a stress gradient, running from low stress near extreme low water spring tides to very high stress as extreme high water spring tides are approached. The distance that plants and animals penetrate upwards in the intertidal zone is determined to a significant degree by their resistance to the stresses there, which include extreme cold and heat, extreme drying by wind, and osmotic stress from heavy rain (i.e., fresh water).

Resistance to stresses of the intertidal zone varies among species. Few species can tolerate the upper levels of the intertidal zone. The ribbed mussel is an example of such a tolerant species in Maine. Some individuals of this species may be reached by the sea only during a few tides each month.

The lower limit of a species' distribution in the intertidal zone is set by biological factors, such as competition or predation. Although intertidal animals have adapted to stressful physical conditions in the intertidal zone, many are not able to avoid being preyed upon or to compete for space and food with the less adaptable but more specialized subtidal animals.

Table 4-8. Acreages and Percentages of Intertidal Marine Habitat Types in the Regions of the Characterization Area

Region		Habitat type					Total intertidal marine subsystem
		Aquatic bed	Beach/bar	Flat	Reef	Rocky shore	
1	Acres	3390	722	5223	6	2284	11,625
	%	55	19	18	6	11	19
2	Acres	----	562	168	----	810	1531
	%	----	14	1	----	4	3
3	Acres	279	20	1419	----	1724	3442
	%	4	1	5	----	8	6
4	Acres	855	926	6293	----	7814	15,895
	%	14	24	22	----	36	26
5	Acres	360	423	7753	78	4665	13,279
	%	6	11	27	74	22	22
6	Acres	1318	1245	7982	26	4225	14,795
	%	21	31	37	20	19	24
Total							
	Acres	6202	2897	28,827	108	21,521	59,566
	% of all regions	10	5	48	<1	36	100

The physical and biological interactions discussed above result in the distribution of intertidal biota into bands parallel to the water line (zonation). Zonation is a general feature along the intertidal zone of the characterization area and is most easily observed on a bedrock shore where all the organisms are on the substratum surface.

Many animals found in the intertidal zone are ubiquitous; that is, they are able to live in a variety of habitats and tidal heights and have a wide geographic distribution. They also tend to be more resistant to stress (both human-induced and natural) than other marine animals. Species distributed throughout the intertidal zone of marine subsystems of the characterization area at all tidal heights, in all habitats are listed in table 4-9 (Larsen and Doggett, *in press*).

Oligochaetes and nematodes are dominant species at all habitat types in the characterization area except the wave-battered bedrock headlands (Larsen and Doggett, *in press*). Oligochaetes had as many as 12,000 individuals/m^2 at a single cobble-beach station.

Class: rocky shore. The NWI indicates that 36% of the marine intertidal area in the characterization area is composed of rocky shore. The biotic communities on rocky shore vary according to the degree of wave exposure. That is, wave-battered headlands and islands support a different flora and fauna than is found in sheltered embayments and estuaries. For this reason the discussion will be in two sections: exposed rocky shores, including bedrock shores and boulder beaches, will be considered here and protected rocky shores will be addressed in chapter 5, "The Estuarine System," as they are most fully developed in estuaries and bays.

Table 4-9. Species Found in all Habitats and at All Tidal Heights in the Marine Intertidal Subsystem in the Characterization Area.

Taxonomic name		Common name
Aschelminthes	Nematoda	roundworms
Rhynchocoela:	Nemertea	ribbon worms
Annelida:	Oligochaeta	same group as earthworm
	Nereis virens	sandworms (polychaete)
	Eteone longa	polychaete worm
	Polydora sp.	polychaete worm
Mollusca:	*Littorina littorea*	common periwinkle
	Littorina obtusata	smooth periwinkle
	Mytilus edulis	blue mussel
	Modiolus modiolus	horse mussel
	Myra arenaria	soft-shelled clam
Arthropoda:	*Balanus balaniodes*	barnacle
	Jaera sp.	isopod (looks like sowbug)
	Gammarus oceanicus	amphipod (scud)
	Carinus maenus	green crab

The rocks along the coast north and east of Cape Elizabeth are folded and faulted igneous and metamorphic units that are locally invaded by granitic intrusion (plutons) and ring dike-volcanic complexes (a grouping of rocks arranged in a circle) up to a mile in diameter (TRIGOM 1974). All of these rocks are of Paleozoic and Mesozoic age. Paleozoic volcanic rocks occupy a portion of the coast in Washington County (Doyle 1967). The distribution of these rock types is a result of the tectonic history of the central New England uplands; one of folding, faulting, and intrusion during the late-Paleozoic coastal fracturing accompanying the opening of the North Atlantic basin and renewed tensional movements along the Fundian Rift Zone (Ballard and Uchupi 1972; TRIGOM 1974). The degree of folding, rock type, and fracture patterns of bedrock ledge determine the available area that can be inhabited by intertidal or subtidal biota.

Rocky shores provide a stable substratum for colonization. Unlike sand, gravel, and cobbles, boulders and bedrock substrata are not moved by wave action. Stable substratum is necessary for the development of abundant and dense populations of intertidal plants, and the intertidal rocky habitat is second only to subtidal rocky areas in production.

Intertidal macroalgae are physiologically hardy plants that can endure the stresses of intertidal existence. The intertidal vegetation of the rocky shores of Maine is dominated by large brown fucoid algae (rockweeds). Two genera of great importance are Ascophyllum and Fucus. While several species of Fucus can be found, Fucus vesiculosus is the most abundant. Similarly, while other forms of Ascophyllum may be found in upper estuaries, Ascophyllum nodosum dominates along much of the coast. Areas that are extremely wave-exposed support little macroalgal growth. Encrusting macroalgae are widely distributed on rocky shores. Their growth rates are slow and they contribute little in productivity.

Much of the organic matter produced by macroalgae can be released as soluble material, when the plants are stressed by exposure to desiccation or fresh water at low tide, or destroyed by violent wave action.

Microbial activity occurs where microorganisms attach to the surfaces of the macroalgae. The youngest (apical) parts of the plants are often free of bacteria, while the older (basal) parts support a dense layer of microheterotrophs, that is often so thick that it can serve as the staple diet of protozoa and rotatoria. The attached microheterotrophs find an abundant supply of amino acids, carbohydrates, and organic acids in the microenvironment of the algal surface. These materials are assimilated and regenerated into carbon dioxide (CO_2) and inorganic nutrients.

Exposed rocky shores support a dense and diverse assemblage of benthic invertebrates (Larsen and Doggett, in press). The solid substratum provides a secure foundation for the many epifaunal species that can anchor themselves to the rock and the crevices; tide pools and macroalgae provide additional habitat space for motile species. In addition, the rocks are constantly swept by sea water, which ensures fairly stable conditions of salinity, temperature, and moisture.

Larsen and coworkers (1979) present limited data on exposed rocky shore communities. They report up to 55 species at one station and densities of the barnacle Balanus balanoides up to 160,000/m^2. Compared to the other eight intertidal habitats sampled by this team, high energy rocky shores rank first in terms of both density and numbers of species.

Table 4-10 gives a qualitative assessment of the abundances of selected species of various exposed sites in Maine (Doggett et al. 1978). The blue mussel, Mytilus edulis, is often dominant in the low intertidal zone, commonly attached to the thallus of Irish moss, Chondrus crispus, forming a Mytilus-Chondrus mat. Predators (i.e., Thais lapillus, Asterias spp., Carcinus maenas, and Cancer borealis) and herbivores (i.e., Littorina littorea, Acmaea testudinalis, and Strongylocentrotus droebachiensis) are also present at most sites. More potential predators, such as starfish and crabs, are present in tide pools in exposed locations than in those in more protected locations. The amount of actual predation that occurs when the tide is high is unknown.

Some species are dependent on other species for protection and/or sustenance. Such is the case with oligochaetes and nematodes, which are usually found in association with mussels or in Irish moss mats. The mussels probably provide nourishment in the form of pseudofeces for these animals. The amphipod Hyale nilssoni dwells among mussels and sometimes barnacles, where it can avoid desiccation.

Algae provide substratum for a number of species. The polychaetes Spirorbis borealis and Fabricia sabella are often found attached to the macroalgae Ascophyllum or Fucus. Bryozoans and hydrozoans also attach to these algal species. The gastropod, Lacuna vincta, is often found grazing on sea lettuce (Ulva) or kelp (Laminaria).

Sponges, Halichondria panicea, and the holdfasts of kelp harbor a variety of species. Polychaetes, Lepidonotus squamata; brittle stars, Ophiopholis squamata; and the mussel Musculus niger are found in these protective habitats.

Suspension feeders represent the most abundant feeding type on rocky shores. The dominant barnacle, Balanus balanoides, and blue mussel are dependent on phytoplankton for food. The common green sponge, Halichondria panicea, is also a suspension feeder.

Other characteristic species of rocky shores are herbivores. The periwinkles, Littorina littorea, L. obtusata, and L. saxatilus, the limpet, Acmaea testudinalis, the gastropod Lucuna vincta, the chiton Tonicella ruber, and the sea urchin, Strongylocentrotus droebanchiensus, all graze on algae on the rock surface. The herbivore L. littorea grazes on ephemeral algae and in doing so allows irish moss to establish itself in the cleared space (Lubucheno and Menge 1978).

The principal predator on rocky shores is the whelk (Menge, 1976, 1978a, and 1978b; and Lubucheno and Menge 1978). Other invertebrate predators include the crabs, Carcinus maenas and Cancer irroratus, and the starfish, Asterias vulgaris. These species are found commonly on most of Maine's rocky shores. Other predators may move into the intertidal zone at high tide.

Table 4-10. Qualititive Assessment of Species Abundance in the Irish Moss Zone at 12 Exposed Headlands on the Maine Coast in August, 1977[a].

	Common name									
	Irish moss	Blue mussel	Barnacle	Periwinkle	Whelk	Starfish	Limpet	Sea urchin	Green crab	Rock crab
	Taxonomic name									
Location (Region)	*Chondrus crispus* % Cover	*Mytilus edulis*	*Balanus balanoides*	*Littorina littorea*	*Thais lapillus*	*Asterias* sp.	*Acmaea testudinalis*	*Strongylocentrotus droebachiensis*	*Carcinus maenas*	*Cancer borealis*
Hoyt Neck	60-100%	VC	--	VC	VC	VC	--	UC	UC	--
Two Lights(1)	C-M mat	A	VC	UC	VC	VC	C	UC	UC	--
Newagen (2)	70-100%	C	--	C-VC	C	VC	VC	UC	UC	UC
Ocean Point (2)	70-100%	C	UC	VC	C	C	C	C	C	C
Pemaquid (3)	C-M mat	A	UC	UC	VC	VC	VC	UC	--	--
Port Clyde (3)	40-50%	A	--	A	A	C	UC	--	--	--
Seal Harbor(4)	60-100%	UC	UC	--	UC	UC	C	--	--	--
Schoodic (5)	C-M mat	A	C	C	UC	--	C	--	UC	--
Petit Manan (5)	30-80%	C	C	VC	VC	UC	C	--	--	--
McClellan Pk.(6)	Sparse	VC	UC	UC	C	C	C	--	--	UC
Great Wass (6)	Rich 100%	--	--	UC	UC	UC	C	UC	--	--
Roque Bluffs (6)	C-50% Kelp	--	--	--	C	--	VC	--	--	--

A = abundant - extremely abundant and dominant and visually obvious
VC = very common - not dominant but readily apparent
C = common - readily found in a cursory examination
UC = uncommon - not readily found with a cursory examination but present regularly enough so that more than one individual can be located after a relatively thorough search
C-M = *Chondrus-Mytilus* mat - percent cover cannot be determined

[a]Doggett et al. 1978.

Zonation of the biota is easily observed on exposed rocky shores. The shore appears as a series of dark red, brown, white, and black, or gray bands (figure 4-27). The red is caused by the red alga, Irish moss, while the brown is the result of dominance by one of several brown algae from the genera Ascophyllum or Fucus. The white band is made up of a pavement of the barnacle B. balanoides. The next higher band, often called the black zone, is caused by a film of blue-green algae on the rocks.

Fauna of specific zones at 13 sites on Maine's exposed bedrock shores (Doggett et al. 1978; and Larsen and Doggett, in press) are listed in table 4-11.

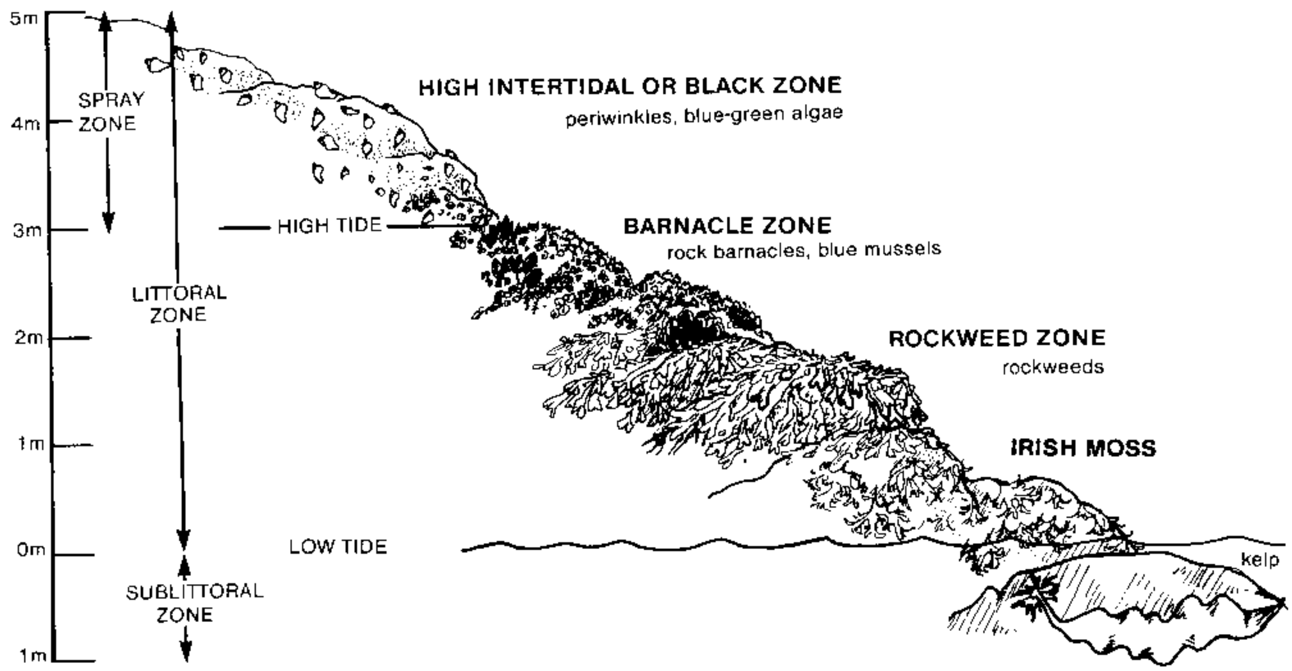


Figure 4-27. Schematic representation of the intertidal zonation patterns on exposed rocky shores in coastal Maine.

Table 4-11. Fauna of the Intertidal Zones on Exposed Bedrock Shore on the Maine Coast based on Data from 13 sites.

Zone	Taxa
High intertidal:	Littorina saxatilus (periwinkle) Anurida maritima (spring tail)
Barnacle:	Balanus balanoides (barnacle) Mytilus edulis (mussel) with the following associated animals: Hyale nilssoni (amphipod) Oligochaetes Nematodes
Rockweed:	Littorina littorea (periwinkle) Littorina obtusata (periwinkle) Acmaea testudinalis (Chinaman's hat) Thais lapillus (dog whelk) Mytilus edulis (blue mussel) with associated animals, oligochaetes and nematodes Modiolus modiolus (horse mussel) Balanus balanoides (barnacle)
Irish moss:	Halichondria panicea (green sponge) Encrusting bryozoans Tonicella ruber (chiton) Acmae testudinalis (Chinaman's hat) Littorina littorea (periwinkle) Lacuna vincta (gastropod) Hiatella arctica (arctic clam) Lepidonotus squamata (scaleworm). Mytilus edulis (blue mussel) Oligochaetes Nematodes Modiolus modiolus (horse mussel) Balanus balanoides (barnacle) Gammarellus angulosus (amphipod) Carcinus maenas (green crab) Asterias vulgaris (starfish)

Clumps of juvenile mussels may occur in damp places throughout the barnacle and rockweed zones. In the Chondrus zone, the limpet Acmaea testudinalis, and the starfish may be found. Other species commonly found in the Chondrus zone, although less frequently, are anemones, various nudibranchs (shell-less gastropods), Cancer irroratus (rock crab), Henrica sp. (blood starfish), Ophiopholis aculeata (brittle star), and Strongylocentrotus droebachiensis (sea urchin).

The ecological factors controlling zonation are complex and involve both physical and biological mechanisms. Interactions between dominant rocky shore species have recently been studied in Maine by Menge (1976) and Grant (1977).

Physical factors are especially important in the upper intertidal zone. Barnacles, which dominate the high intertidal zone of rocky shores, are controlled only by competition with each other and by environmental conditions, such as desiccation and wave action (Menge 1976). Recruitment is greatest in open areas that stay moist at low tide. Dense growths of the macroalgae Ascophyllum and Fucus inhibit barnacle settlement and survival (Menge 1976 and Grant 1977).

In the rockweed zone (lower in the intertidal zone), interspecific competition becomes important. On exposed shores the mussel always competes for space more successfully than the barnacle, although less quickly so on vertical surfaces than on horizontal surfaces (Menge 1976). The upper limit of the barnacle zone is set by a physical factor - desiccation. At slightly less-exposed sites, predation by the whelk, Thais lapillus, moderates the population growth of both mussels and barnacles and allows them to coexist. At very exposed sites the lower limit of the barnacle zone is controlled by competition with the mussel, which can compete more successfully than the barnacle but is less tolerant to exposure to the atmosphere, and therefore cannot penetrate to so high a level in the intertidal zone as the barnacle. This pattern is modified by predation on the mussel by the whelk, which prevents the absolute dominance of the mussel. The intertidal distribution of other species is undoubtedly controlled by similar mechanisms.

In early spring, filamentous algae (Ulothrix, Urospora, and Bangia) cover available space on rocky shores. Barnacles settle in May and June in space remaining after a die-off of the algae. High settlement density of barnacles is correlated with early mortality. If barnacles are as dense as $60/cm^2$, 90% mortality can be expected in 5 months. In summer, foliose algae Fucus establishes itself in any remaining free space. Mussels settle from June to September in areas occupied by barnacles, Fucus, or other mussels (Grant 1977).

By August through October, the mussels dominate the barnacles on the more horizontal surfaces of the midintertidal zone (Menge 1976). Clearing of space occurs in the fall and winter and is density dependent (i.e., the hummocks of elongated and weakly-attached barnacles produced by crowding and mats of mussels are prone to removal by winter surf). Space that is cleared in fall and winter remains clear until settlement by filamentous algae in the spring.

Normandeau Associates (1975) report a high degree of variation of biomass seasonally at intertidal sites on Sears Island in Penobscot Bay. This variation is a function of the presence and density of mussels.

NWI data indicate that boulder beaches (boulder rock shores) comprise about 6% of the intertidal area of the characterization area. Boulder beaches are limited to relatively short expanses and are usually adjacent to or associated with bedrock shores. Boulder shorelines provide relatively stable surface for attachment. Shelter is present between and under boulders and the sediment between and under the boulders provides habitat space for infaunal species.

Boulder beaches consist mostly of boulder-sized particles derived mainly from glacial till deposits or from jointed bedrock ledge exposed to very high energy wave conditions.

Productive elements on boulder beaches are identical to those of bedrock shores as discussed above. The one exception is that, since boulders provide more surface area per unit of shoreline, the absolute productivity on boulder beaches may be slightly higher.

The single study available on Maine boulder beaches (Larsen and Doggett, *in press*) showed that these beaches have a diversity comparable to exposed bedrock shores, although the density of individuals is not as high. Boulder beaches have many microhabitats which allow for the high diversity. No zonation studies have been conducted on boulder beaches but the sharp zonation of mussels and barnacles that is obvious on bedrock shores is not as well defined in boulder areas.

The species present on boulder beaches generally were found also on exposed bedrock shores (Larsen and Doggett, *in press*). The infaunal species of boulder beaches are similar to those found in pockets of sediment at protected rocky shore areas. The following species were present on six boulder beaches in Maine (Larsen and Doggett, *in press*):

Platyhelminthes	Flatworm
Nematodes	Roundworm
Nermerteans	Ribbon worm
Oligochaetes	
Acmaea testudinalis	Chinaman's hat
Littorina littorea	Common periwinkle
Littorina obtusata	Smooth periwinkle
Littorina saxatilus	Rough periwinkle
Thais lapillus	Dog whelk
Mytilus edulis	Blue mussel
Balanus balanoides	Rock barnacle
Jaera sp.	Isopod
Gammarus oceanicus	Amphipod
Marinogammarus stoerensis	Amphipod
Carcinus maenas	Green crab

Shorebirds and gulls are the two major groups of waterbirds that feed extensively on exposed rocky shores. Eiders feed mostly on benthic invertebrates in the intertidal and subtidal zones. Seaducks, loons, and grebes feed in these areas, also. In winter the purple sandpiper is the primary shorebird species using rocky intertidal areas, while ruddy turnstones and least sandpipers are the primary species during the fall and spring migrations. Other small sandpipers (peeps), black-bellied plovers, and pectoral sandpipers use rocky intertidal areas to a lesser extent. Rocky ledges are used as resting areas for semipalmated sandpipers, semipalmated plovers, short-billed dowitchers, yellowlegs, black-bellied plovers, and turnstones, especially where extensive flats are bordered by rocky shores (i.e., Indian River flats in Jonesport, region 6, and in the Harrington-Millbridge area, region 5). Preferred roosting sites [gravel and sand spits (bars) and beaches] are in short supply in these areas. Waterfowl and gulls use rocky shores and ledges as resting areas and nocturnal roosts.

The coast is the major wintering area in Maine for crows. Many crows feed on intertidal invertebrates of the rocky shore. Other passerines feed along the strand line and in the exposed algae along rocky shores (i.e., song sparrows and yellow-rumped warblers).

Harbor seals haul out on intertidal rocky ledges. Those areas are important to this species for resting and whelping. Intertidal rocky ledges, important to harbor seals, are included in atlas map 4.

Class: sand beach. Sand beaches form from the deposition of sand by wave swash and wind processes. The sand-sized particles are derived from wave erosion of coastal or submerged glacial and glaciofluvial deposits or from sediment transported to the shore by present-day rivers. The latter source, within the characterization area, is limited to the Kennebec River. According to preliminary NWI data sand beaches are scarce in Maine, making up <1% of the characterization area.

Three types of sand beaches exist: barrier beaches and spits, strandplain beaches, and pocket beaches. Barrier beaches separate estuaries, lagoons, and estuarine emergent wetlands form open marine waters. Barrier spits include inlets to enclosed lagoons or wetlands. Strandplain beaches are directly backed by the upland from which their sediment is derived. They occur largely along the landward margins of bays where glacial and glaciofluvial deposits are being eroded by waves. Sand from these deposits is added to the beach sediment during storm wave activity. Pocket beaches are small barrier beaches, spits, and strandplain beaches. Pocket beaches are to be distinguished from the other beach types by their total inclusion within small embayments; they derive their sand from submerged glacial deposits flooring the embayment (see atlas map 2).

The composition of sand beaches ranges from fine sand to coarse sand mixed with gravel. Many sand beaches are resting on gravel beach deposits; and sandy beaches may have significant amounts of gravel on their surfaces as storm-lag deposits or from the throwing of gravel from submerged glacial deposits onto the beach by storm waves. Particle sizes on sandy beaches range from 0.125 mm to 16 mm (0.004 in. to 0.6 in.). Beach sands are very well sorted and are composed mainly of quartz and feldspar minerals but also contain minor amounts of metamorphic rock fragments and common heavy minerals, such as garnet and amphibole.

Waves, tides, and winds are the major physical forces that control the beach environment. Beaches exhibit seasonal changes during the winter months. When northeast storms occur, beaches are eroded. Their faces are steepened and become featureless. After storms and during spring, summer, and fall, beaches become accretional (i.e., build up material) and form berms and ridges on their upper and lower faces, respectively.

Waves move sand laterally along the beach at variable rates of transport, varying according to sediment size, direction of wave approach, orientation of the beach, tide stage, and other factors. Rates of longshore transport are not well established on Maine beaches except Wells beach, which is outside the characterization area but is under the same wave influence as many exposed Maine sand beaches. Byrne and Zeigler (1977) estimated gross littoral transport rates at Wells to be 35,000 to 55,000 cu yds/year to the north and

17,000 to 25,000 cu yds/year toward the south, indicating a net northerly drift rate of from 18,000 to 30,000 cu yds/year. Other Maine beaches exhibit long-term growth to the south, however, and the data from Wells should only be considered as an indication of possible drift rates.

Tides influence the vertical range over which waves act on a sand beach, hence the thickness of beach deposit. Within the characterization area, mean tide ranges vary from 9.0 feet (2.7 m) at Portland to 18.2 feet (5.5 m) at Eastport (U.S. Department of Commerce, Yearly).

Winds play a major role in moving sand on the back beach and dune areas. Depending upon a number of factors (grain size, sorting, plant cover), winds begin to transport dry sand at velocities of about 11 mph (18 km/hour) (Bagnold 1954). The greatest amount of sand moved by wind occurs on desiccated portions of the beach and vegetated dunes.

Sand is transported by wind from the top of the beach berm to the foredune and accumulates as a wedge against the foredune scarp (Timson and Kale 1977). Continual movement and accumulation occurs during the summer and fall months, increasing the width of the foredune and, in some areas, the height. Most of this accumulation occurs under the influence of southerly winds.

Timson (unpublished) has found that some landward transport of sand occurs during the northeast or east northeast winds onto and beyond the foredune. Sand transport behind the foredune is relatively minor where dune vegetation occurs; but devegetated areas are heavily affected by northwest winds. Deflation of bare areas by northwest winds creates parabolic dunes, which enlarge and migrate seaward towards the foredune ridge. Continued growth of the parabolic dune and transport of sand may force the dune to breach in the foredune ridge, through which storm waves may overwash and intrude into the dune field.

Sand beaches have only a very limited primary production. Due to the fine grain size on sand beaches and wave action that continually moves the sediments, macroalgal vegetation does not develop. A discussion of the unique plant communities associated with sand beaches and dunes is found at the end of this chapter. Depending upon the degree of exposure of the beach microalgal colonization of pebbles and interstitial spaces below the surface may be a source of organic matter production. Other heterotrophic microorganisms (bacteria and fungi) coexist and provide a sink for organic matter produced by photosynthesis.

Low organic carbon and total nitrogen concentrations are reported by Croker and coworkers (1975) on western Maine and New Hampshire beaches. These authors also found unsystematic (i.e., without a pattern) seasonal differences in the mean concentrations of these elements. The high values of the carbon/nitrogen ratios indicate a large percentage of plant material, in the form of shredded and detached macrophytic algae and smaller algae, is attached to sand grains (Croker et al. 1975). This work suggests that imported material and diatoms are the sources of energy (i.e., food) for the invertebrate faunas of sand beaches.

Information on the benthic invertebrates of Maine's sand beaches comes from the work of Larsen and Doggett (in preparation) mainly within the characterization area and Croker and his students (Croker et al. 1975; and Croker 1977) just to the south of the characterization area in southern Maine and New Hampshire.

The results of Larsen's and Doggett's study indicate that the benthic macrofauna inhabiting the sand beaches of Maine cannot be considered a single community. This fact can be illustrated in two ways. First, the percentage composition of higher taxa changes along the coast from crustacean-dominated beaches in the south to annelid-dominated beaches in the north (figure 4-28). Secondly, a complex, computer classification of the data identifies four faunal communities (table 4-12), three of which are characteristic of three geographically distinct segments of the coast (figure 4-29). The most significant discontinuity occurs in the area of Boothbay Harbor and separates the southwestern beaches (site-group A) from the more northeasterly beaches (site-groups B and C).

The most likely explanation for the above distribution involves differences in summer water temperature. Bousfield and Laubitz (1972) suggest that the coast of Maine may be divided into two zoogeographic zones: zone A, northeast of Penobscot Bay, where summer water temperatures are $<53^{o}F$ ($12^{o}C$); zone B, the southwestern area where temperatures reach $61^{o}F$ ($16^{o}C$). Species requiring warm temperatures for reproduction are excluded from the northeast, and warm-sensitive species cannot compete in the southwest.

Although the zoogeographic boundary hypothesized by Bousfield and Laubitz (1972) does not coincide exactly with the major discontinuity identified by the Larsen and Doggett data analysis, this may simply be a function of time of sampling combined with the cyclic temperature changes that the Gulf of Maine is known to undergo (Hopkins and Garfield 1979; and Taylor et al. 1957).

The separation of the five northeastern beaches into site groups B and C is more difficult to explain. Garfield (Bigelow Laboratory, West Boothbay Harbor, ME; personal communication; March, 1979) believes that other, as yet undefined, oceanographic features (i.e., high nutrients, tidal fluctuations, temperature, salinity, and upwelling systems) may be responsible, but the possibility exists that physical and/or biological factors too subtle to be recognized from the existing data are responsible.

Besides water temperature, Dahl (1953) lists ice action, air temperature, food conditions, interspecific competition, and wave action as factors important to intertidal organisms. Of these, the latter three are most important in Maine.

Interspecific competition has been noted between two species of amphipods (Bousfield 1973). Orchestia platensis is a colonizer of upper beaches that is excluded by species of the more specialized amphipod genus Talorchestia. Competition between amphipod species is presently being investigated in southern Maine by Drs. Croker and Hatfield of the University of New Hampshire, Durham, NH.

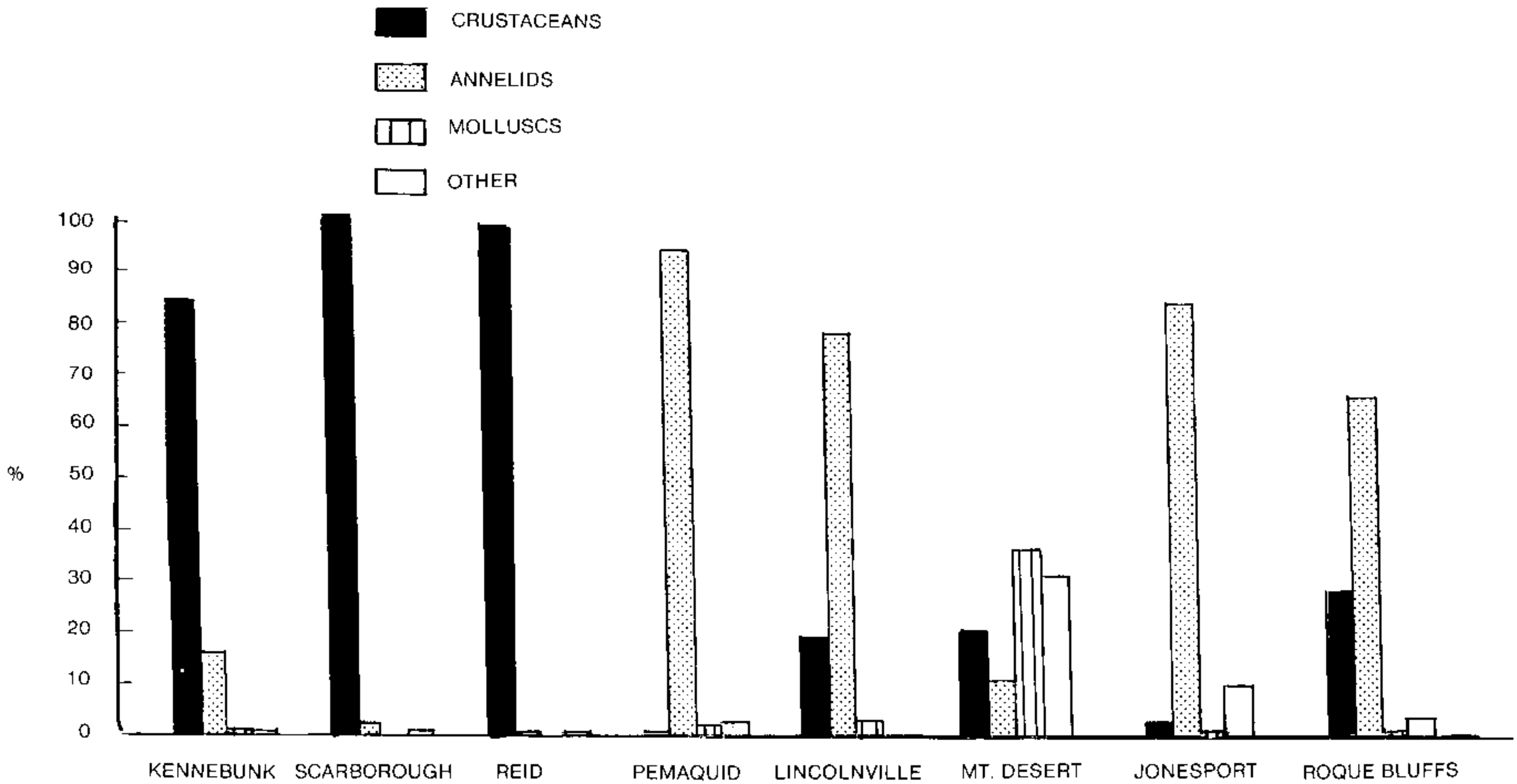


Figure 4-28. Percentage composition by taxa of invertebrates on sand beaches in Maine (Larsen and Doggett, *in preparation*).

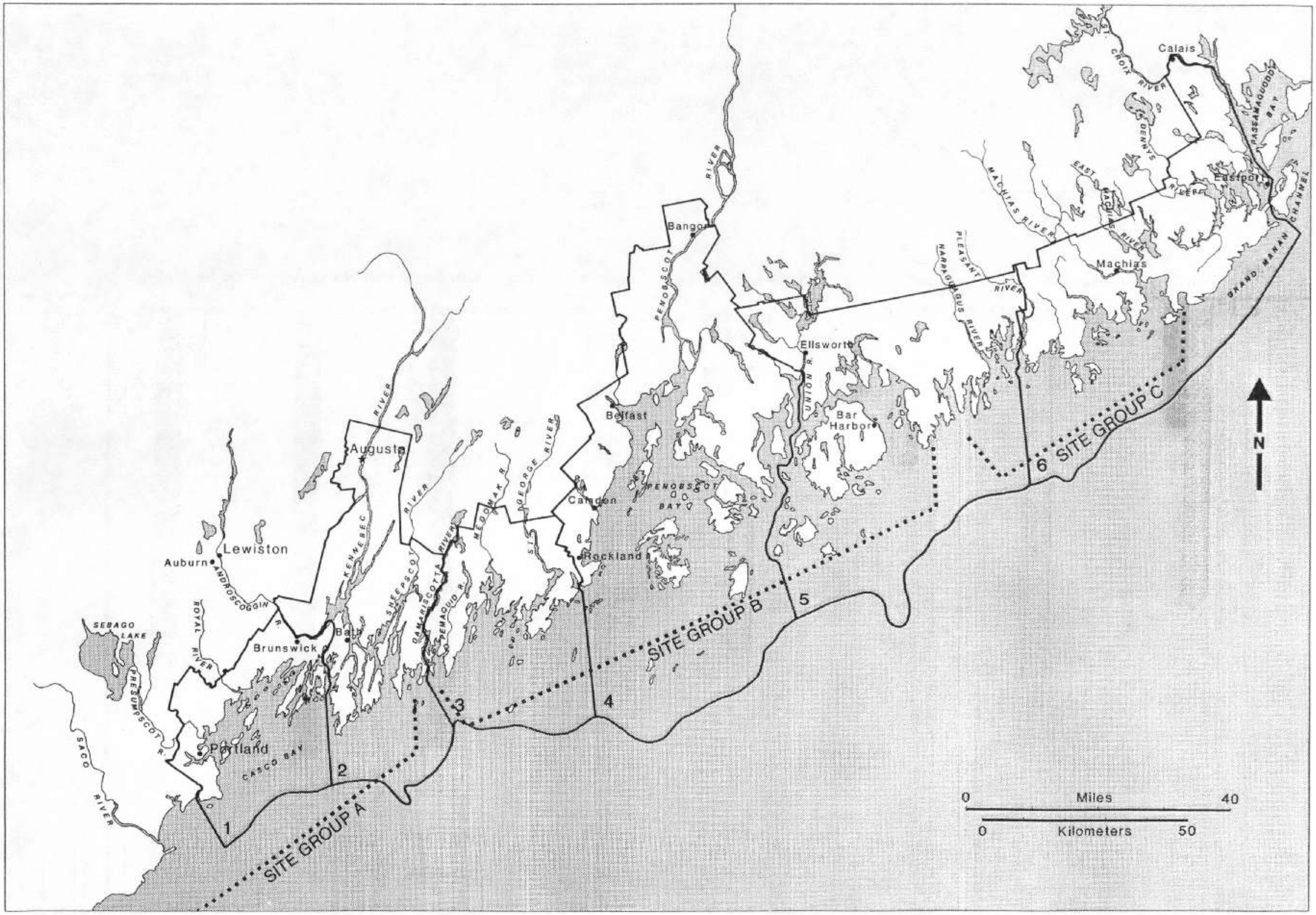


Figure 4-29. Geographic distribution of site groups sampled on the coast of Maine (Larsen and Doggett, in press).

Table 4-12. Species Composition of the Four Defined Faunal Communities.

Faunal Community	Species	Common name	Site-group association
I	Insecta pupae		none
	Polychaeta unidentified		
	Coleoptera adult	beetle	
	Anurida maritima	springtail	
II	Nemertea unidentified		A
	Nephtys bucera	polychaete	
	Haustorius canadensis	amphipod	
	Acanthodhaustorius millsi	amphipod	
	Amphiporeia virginiana	amphipod	
	Scolelepis squamata	polychaete	
III	Oligochaeta unidentified		C
	Nematoda unidentified		
	Psammonyx nobilis	amphipod	
	Arachnida unidentified	spider	
	Insecta adult		
	Insecta larvae		
	Odostomia sp.	gastropod	
	Talorchestia megalophthalma	amphipod	
IV	*Lacuna vincta*	gastropod	B
	Nephtys caeca	polychaete	
	Paraonis fulgens	polychaete	
	Littorina littorea	gastropod	
	Orchestia platensis	amphipod	
	Mya arenaria	soft clam	
	Mytilus edulis	blue mussel	
	Balanus balanoides	barnacle	
	Glycera dibranchiata	bloodworm	
	Carcinus maenus	green crab	
	Chironomid larvae	insect	

[a]Larsen and Doggett, *in preparation*.

In the Larsen and Doggett study (in preparation) no relationship between sediment parameters (including interstitial salinity) and biotic parameters could be discerned, with the exception of the Mt. Desert site. The beach at Mt. Desert is most similar to the one at Reid State Park in terms of exposure and sediment grain size, while in terms of density and species diversity the two are dissimilar. The difference is that the sediments at Mt. Desert are composed largely of shell fragments, which limit faunal development (Stephen 1930, and Hedgpeth 1957).

The degree of wave exposure is a major ecological factor on sand beaches (Seed and Lowry 1973). The fauna of extremely exposed beaches is limited (Stephen 1930; and Scott 1960). With decreasing exposure, amphipods become abundant, followed by polychaetes, and finally molluscs on the most sheltered beaches. Increasing shelter cannot explain the distribution of fauna observed by Larsen and Doggett (in preparation). An example of the faunal differences between an exposed and neighboring less-exposed sand beach is presented in table 4-13. The exposed beach is dominated by amphipods, while in the less-exposed location polychaetes and molluscs are more abundant. The number of species and biomass also increase with decreasing exposure (McIntyre 1970).

Sand beaches exhibit a high degree of variability in faunal density, as is shown by the large ranges in density in table 4-14. The highest densities recorded by Larsen and Doggett (in press) occurred at the lower intertidal regions of amphipod-dominated western beaches composing site group A. The more eastern beaches in site groups B and C, which are dominated by polychaetes, have much lower faunal densities. In general, the mean densities on sand beaches are not exceptionally high, as has been stated often (Hedgpeth 1957). Indeed, of the nine intertidal habitats sampled in Maine (Larsen and Doggett, in press) sand beaches had the lowest mean species density.

Sand beaches are populated by very few species relative to other marine habitats. This is because of the stress associated with the constantly shifting sediments. The range of species found at individual sites (table 4-14) is fairly typical for boreal and temperate sand beaches. The high total number of species reported by Larsen and Doggett (in preparation) from the western site-group A beaches largely confirms the summer zonation pattern presented by Croker and coworkers (1975). The lower intertidal zone was dominated by the haustorid amphipod *Amphiporeia virginiana*, the mid-intertidal regions at these sites were inhabited by other haustorid amphipods, such as *Acanthohaustorius millsi* and *Haustorius canadensis*, and the polychaete *Scolelepis squamata*, while the amphipod *Talorchestia megalophthalma*, a species related to *Orchestia platensis*, was the most abundant animal in the upper intertidal area. This pattern is similar to that proposed by Dahl (1953) and modified by Fincham (1971) for the north temperate regions with the exception that no cirolanid isopod belt was found in the mid-intertidal region of the beaches, a situation previously reported by Colman and Segrove (1955).

A different pattern of zonation was observed by Larsen and Doggett (in preparation) at the eastern Maine beaches sampled. In each case, the lower intertidal zone contained the polychaetes *Nephtys caeca*, *Paraonis fulgens* and/or the amphipod *Psammonyx nobilis*. Croker and coworkers (1975) found the latter species intertidally only in the winter in western Maine. Apparently, summer water temperatures are cool enough in the eastern part of the study area for the species to survive on the beaches in this season. Polychaetes,

Table 4-13. Fauna of Sandy Beaches of Two Exposure Levels in Decreasing Order of Relative Abundance[a]

Hendrick's Head, Southport (region 2) less exposed pocket beach (Stickney 1959)			Reid State Park, Georgetown (region 2) very exposed (Larsen and Doggett, *in press*)		
Taxa	Group	Relative Nos. Indiv./m^2	Taxa	Group	Relative no. indiv./m^2
Nereis virens	polychaete	300	*Amphiporeia virginiana*	amphipod	24,152
Polydora ligni	polychaete	100	*Tolorchestia megalopthalma*	amphipod	40
Capitella capitata	polychaete	60	Oligochaeta		24
Mya arenaria	bivalve	20	Nematoda		24
Nephtys caeca	polychaete	20	*Haustorius canadensis*	amphipod	12
Macoma balthica	bivalve	occasional	*Chaobrus* sp.	insect	12
Pectinaria hyperborea	polychaete	occasional	*Littorina obtusata*	gastropod	8
			Scolelepis squamata	polychaete	4
			Chiridotea coeca	isopod	4

[a]Density levels are maxima of semiquantitative data.

Table 4-14. Mean Density, Range, Total Number of Species per Study, and Range of Species Encountered per Study in Sand Beach Investigations in Northern New England

Investigation	No. of sites sampled	Sieve size (mm)	Density mean	Range (m^{-2})	Species	
					No.	Range
Larsen and Doggett, *in prep.*	8	1.0	1222	0-24,160	59	10-22
Croker et al. 1975	5	0.5	5000	288-12,368	31	5-22
Croker 1977	2	0.5	3100[a] 500[b]			

[a]Semiexposed.
[b]Semiprotected.

Scoloplos sp., Ophelia bicornis, and oligochaetes are dominant at mid-intertidal heights at Pemaquid (region 3), Jonesport (region 6), and Roque Bluffs (region 6), respectively. The sparsely populated Lincolnville (region 4) and Mt. Desert (region 5) beaches have no clear dominants in the mid-intertidal region of the beach. Talitrid amphipods remain present at high intertidal heights with Orchestia platensis at Lincolnville and Mt. Desert and Talorchestia megalophthalma at the two most eastern beaches.

Very few species are present above mean tidal level (MTL) in the winter (figure 4-30). By moving seaward during the fall and winter, the animals are able to decrease the exposure time and stabilize the temperatures to which they must be exposed during low tide. The dominant amphipod on western Maine beaches, Amphiporeia virginiana, does not exhibit this seasonal shift (Croker et al. 1975).

Croker and coworkers (1975) found that the haustorid amphipod, Amphiporeia virginiana, made up more than 50% of the biomass at more exposed sandy beaches in southern Maine. Because A. virginiana does not migrate appreciably on a seasonal basis (Croker et al. 1975), there would be only minor differences in seasonal biomass. As Croker and coworkers (1975) pointed out, seasonal differences in biomass and abundance may become more pronounced on beaches that are more sheltered and not dominated by A. virginiana.

Energy flow through a sand beach system is less complex than in other intertidal habitats. The sand beach is completely dependent on imported energy for the maintenance of its resident populations; that is, the sand beach fauna utilize the primary production of other systems as supplied by waves and currents. Odum and coworkers (1974) describe the sand beach system as follows:

> The beach, with its sand fauna, forms an extensive food filtering system taking from the rushing water nutrients in the form of detritus, possibly dissolved materials, and plantonic or larger organisms.

Odum and coworkers (1974) divide the fauna of a sand beach into three components: epipsammon, endopsammon, and mesopsammon. The epipsammon are those species that occur above the sand surface and usually prey on the endopsammon, or those species that live in the sand. Epipsammon is composed principally of shorebirds and fish; whereas, in the characterization area, the edopsammon is dominated by haustorid amphipods, especially Amphiporeia virginiana. This species of amphipod is known to be preyed upon by shorebirds (Croker 1972).

The mesopsammon group is defined as those flora and fauna that live between sand grains. Figure 4-31 illustrates the relations of these components to each other and the oceanic system. Imported material is used by the infaunal constituents, which either export directly to the marine system or provide energy to the next highest trophic level.

Gulls, terns, shorebirds, and waterfowl are the dominant birds using beaches. Most birds using sand and gravel beaches, bars, and spits use them more for resting than for feeding. Least terns and piping plovers use beaches for nesting and are the major exception to this usage pattern. Sand beaches are the most important roosting area for shorebirds. Concentrations of more than 10,000 birds have been reported from sand beaches in region 6. Gulls and terns roost in large numbers on sand and gravel beaches. Sanderlings feed extensively on sand beaches and flats throughout the coastal zone. Semipalmated plovers, black-bellied plovers, red knots, and semipalmated sandpipers feed on sand and gravel flats. Sand and gravel flats that are covered with seaweed are utilized extensively by ruddy turnstones, which forage primarily by turning over algal fronds, stones, and pebbles. Many large gulls feed extensively on sand and gravel flats, especially those that are mussel-covered. They often can be observed dropping mussels from the air onto stones in order to break the shells.

BEACH DUNE PLANT COMMUNITIES

Sand beach and sand dune communities are found on sand and gravel substrata above the mean high tide line. A series of five plant communities has been described for coastal Maine (Trudeau 1977; and Nelson and Fink 1978). They include a foredune community, a dunegrass community, a dry dune slack community, a shrub community, and a dune forest community. The dominant plant associations in these communities have been described for the Phippsburg-Georgetown area (region 2) by Trudeau (1977) and for all of the coast by Nelson and Fink (1978).

Predominant ecological factors influencing the distribution of the plant species in the sand beach and sand dune communities include salt spray, soil moisture, soil temperature, nutrient availability, soil salinity, and air moisture. The five communities intergrade and represent a series of successional communities starting with the pioneering annuals in the foredune community and terminating with the dune forest community.

The foredune community is composed of two major associations: seasonal berm and perennial berm. The seasonal berm is flooded by spring high tides and winter storms. The substratum is very unstable because it is subject to frequent storm-related erosion. Rapidly growing, fecund annuals [i.e., sea rocket (Cakile edentula) and saltworth (Salsola kali)] are the only plant species able to repopulate this habitat. The perennial berm or eolian ramp is a recently accreted area of wind-deposited sand above the spring and storm tides. The community is dominated by American beachgrass (Ammophila breviligulata), beach pea (Lathyrus japonicus), and dusty miller (Artemisia stelleriana). Strand wheat (Elymus arenarius) replaces or coexists with beachgrass on the more rocky and cobble beaches in regions 4 to 6.

The dunegrass community is dominated by American beachgrass. It runs from the frontal dune ridge inland to a shrub community. Its habitat contains no soil and only a limited amount of nutrients. It receives excessive salt spray. Species diversity is low in this community (Nelson and Fink 1978). Several subassociations have been described by Trudeau (1977) and Nelson and Fink (1978). Rapid growth after burial is an important adaptation for plants in the perennial berm, the dunegrass, and the dry dune slack communities.

The dry dune slack community is found on dry dunes inland from the dunegrass community in region 2. Salt spray and sand burial rates are lower than in the above communities. This community is dominated by beach heather (Hudsonia tomentosa), which reaches its northernmost distribution in the United States in the Reid State Park area (region 2). Common associates include pinweed (Lechea maritima), pinweed aster (Aster linariifolius), joint weed (Polygonella articulata), a rush (Juncus greenei), and two sedges (Carex silicea and C. pensylvanica). Lichens (Cladonia spp.) are an important component of this community. Their presence reflects the maritime climate of coastal Maine. They are generally absent from dry dune slack communities farther south (Nelson and Fink 1978). The above associates may comprise the community in the absence of beach heather.

The shrub community is dominated by bayberry (Myrica pensylvanica), Virginia rose (Rosa virginiana), meadow sweet (Spiraea latifolia), and raspberry (Rubus idaeus). This community may be intermixed with either the dry slack dune community or the dunegrass community, or it may form a homogeneous community on the landward side of the above communities. This community is present in regions 3 to 6, where the dry dune slack community is absent. The rugosa rose (Rosa rugosa) and gooseberry (Ribes spp.) are important components of this community in regions 4 to 6. Bayberry occurs infrequently east of Penobscot Bay.

The dune forest community is found on nutrient deficient inactive parabolic dunes. The shrub community intergrades into this community. Pitch pine (Pinus rigida) is the dominant species where salt spray is high. Red maple (Acer rubrum), white birch (Betula papyrifera), aspen (Populus tremuloides), and juneberry (Amelanchier spp.) are common associates on more developed soils where nutrient levels are higher. A well-developed herbaceous layer may exist in the more nutrient-rich areas.

RESEARCH NEEDS

Since the marine and estuarine systems are contiguous and generally similar ecologically, data gaps in both are discussed in chapter 5, "The Estuarine System."

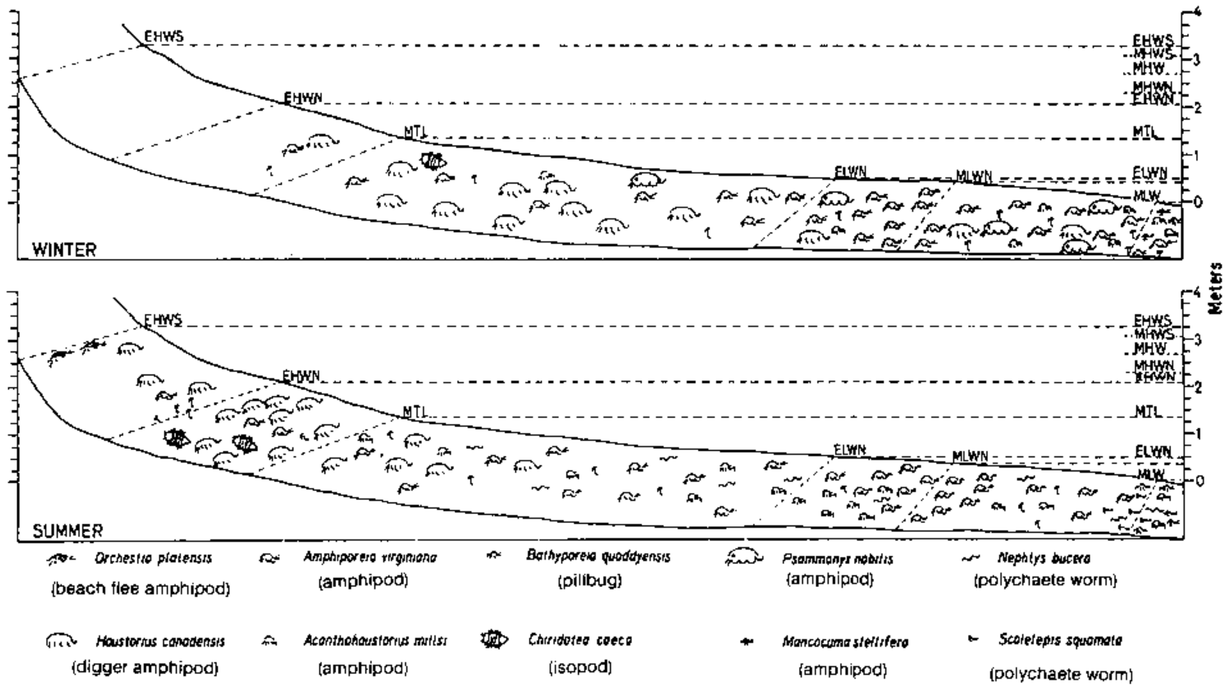


Figure 4-30. Distribution of a typical marine intertidal invertebrate community in moderately exposed New England sand beaches during winter and summer (from Croker et al. 1975).

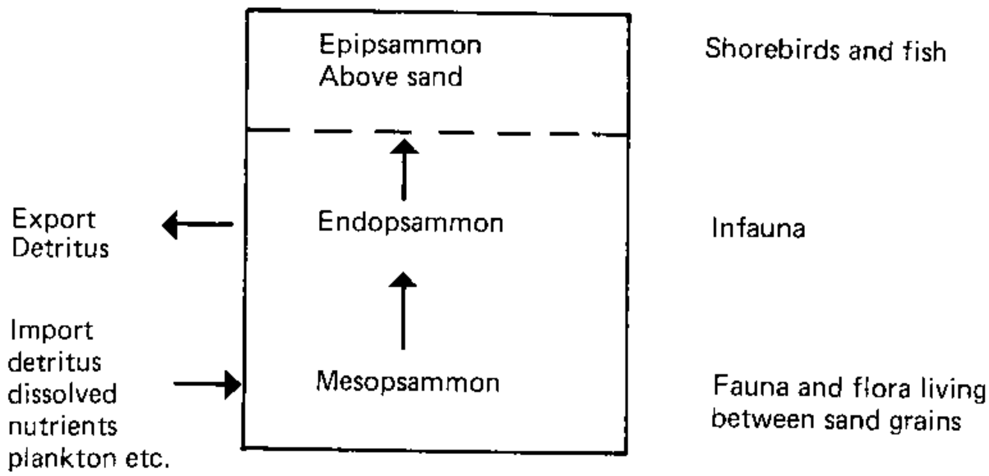


Figure 4-31. Relations among the major biotic components of the sand beach class (adapted from Odum et al. 1974).

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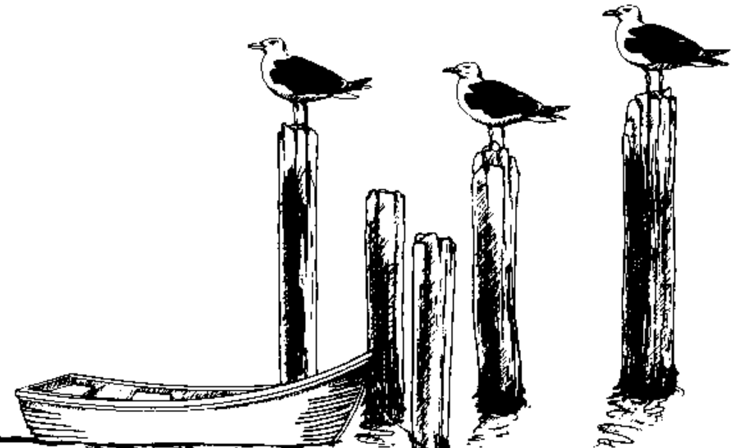
Chapter 5
The Estuarine System



Authors: Peter Larsen, Lee Doggett, Chris Garside, Jerry Topinka, Tim Mague, Toby Garfield, Ray Gerber, Stewart Fefer, Patricia Shettig, Lawrence Thornton

Estuaries are the major link between the sea and fresh water and terrestrial environments. Cities and towns historically have been built on estuaries, consequently, estuaries have been used as major transportation corridors and waste disposal systems. Estuaries also receive the flow of rivers, which is comprised of runoff from the landmass and includes pollutants from upstream developments. They are used as finfish spawning and nursery grounds, shellfish habitats, migratory bird feeding and breeding areas, and recreational areas. This chapter examines the basic concepts and information on the functions of the complex estuarine system of coastal Maine.

The U.S. Fish and Wildlife Service (FWS; Cowardin et al. 1979) defines the estuarine system as "deepwater tidal habitats and adjacent wetlands which are usually semi-enclosed by land but have open, partially obstructed, or sporadic access to the open ocean and in which ocean water is at least occasionally diluted by freshwater runoff from the land." Furthermore, "estuaries extend upstream and landward to the place where ocean-derived salts measure <0.5 ppt during the period of annual low flow. The seaward limit of the estuarine system is: 1) a line closing the mouth of a river, bay or sound; 2) a line enclosing an offshore area of diluted sea water with typical estuarine flora and fauna; or 3) the seaward limit of wetland emergents, shrubs or trees where these plants grow seaward of the line closing the mouth of a river, bay or sound." Since estuaries most often are semienclosed by land they are somewhat protected from marine influence and are a low-energy environment compared to the marine system. Tides and riverine inputs are the dominant physical factors within estuaries, although currents and wind also may be important (Cowardin et al. 1979).

Table 5-1. Major Estuarine Systems of Coastal Maine and Their Sizes (acres)

Region	Estuarine System	Acres
1	Fore River	1690
1 and 2	Presumpscot River/Back Cove	2148
1	Royal River/Cousins River	1568
1	New Meadows River Complex	13,489
2	Kennebec R./Sheepscot R./Back River/Sasanoa River Complex	27,952
3	Damariscotta River	7627
3	Johns River/Johns Bay	1360
3	Pemaquid River	432
3	Medomak River/Hockomock Channel	4740
3	St. George River	3801
3 and 4	Weskeag River	913
4	Passagassawakeag River	303
4	Penobscot/Orland Rivers	10,631
4	Bagaduce River	3958
5	Union River/Union Bay	794
5	Jordan River	467
5	Somes Sound	1880
5	Raccoon Cove	639
5	Skillings River	2600
5	Taunton Bay/Hog Bay	3772
5	Steuben Harbor/Tunk Stream	1023
5	Narraguagus River	1440
5	Back Bay/Beaver Meadows Brook	1397
5	Harrington River/Mill River	4186
6	Pleasant River	2481
6	Indian River/West River	1732
6	Chandler River/Mason Bay	1866
6	Little Kennebec Bay	569
6	Machias Bay/Machias River and East Machias	2986
6	Cobscook Bay Complex: Dennys River/Dennys Bay/ Orange River/Whiting Bay	11,667

Coastal Maine includes 30 major estuarine systems. These are listed along with their areal extent (where available) as determined by the FWS National Wetlands Inventory (NWI) in table 5-1. The major estuarine systems comprise more than 92% (120,111 acres; 48,628 ha) of the total estuarine system in coastal Maine (130,075 acres; 52,662 ha). Twenty-three of these major systems are >1000 acres (405 ha) in size; four are >10,000 acres (4049 ha) in size. The locations of the major estuarine systems and their limits (riverine/estuarine upper limit and marine/estuarine lower limit), as determined by the NWI, are illustrated in figures 5-1 to 5-6. The locations of specific areas are given in atlas map 1. The estuarine system is located between a relatively small riverine system and a much larger marine system. Since the three systems are contiguous, processes occurring in one area are likely to affect the others.

The estuarine system in Maine includes areas with considerable freshwater inflow (e.g., Kennebec-Androscoggin, and Penobscot estuaries) and areas with relatively little freshwater inflow (e.g., Somes Sound, Little Kennebec Bay, and New Meadows Rivers). Specific estuaries in Maine are often contiguous (e.g., Kennebec-Sheepscot, and Machias-East Machias) and receive freshwater flow from more than one riverine source.

Only the Sheepscot, Damariscotta, and Penobscot estuaries and the Passamaquoddy/Cobscook Bay system have been the subject of detailed hydrographic studies. Hydrographic data from these studies are examined under "Hydrography" in this chapter. Little sampling of hydrographic data is available for other estuaries. However, freshwater flow data on 11 rivers in the characterization area are available from United States Geological Survey (USGS). Using these data, tidal range data from the National Ocean Survey and topographic data from nautical charts, a semiquantitative model is employed to describe the hydrographic features of those 11 estuaries (Ketchum 1951). Limitations of the model are discussed under "Hydrography." The hydrography of the remaining estuaries is not discussed here because of the lack of data.

The estuarine system in coastal Maine as discussed here consists of subsystems and classes that have been identified by the NWI. The area exposed at low tide (intertidal subsystem) is ecologically different from the area that is submerged at all times (subtidal subsystem); for this reason, the two habitats are discussed separately here. Estuarine classes identified by the NWI include aquatic beds, unconsolidated bottoms, open water and rocky bottoms in the estuarine subtidal subsystem and aquatic beds, beach/bars, flats, reefs, rocky shores, emergent wetland, and streambeds in the estuarine intertidal subsystem (figure 5-7).

Intertidal and subtidal aquatic beds are principally eelgrass on mud sediments. Unconsolidated bottoms are comprised of cobble, gravel, sand, and mud. Vegetation may include eelgrass or emergent wetland species. Rocky bottoms consist of substrata of bedrock and/or boulder. Vegetation is principally algal beds (kelp). Beach/bar habitats encompass cobble, gravel, and sand beaches. Flats include both sand and mud flats and streambeds crossing the flats. Reefs are composed of mussels and usually are found on mud flats. Atlas map 1 depicts the location of all estuarine systems, subsystems and classes identified by the NWI in coastal Maine.

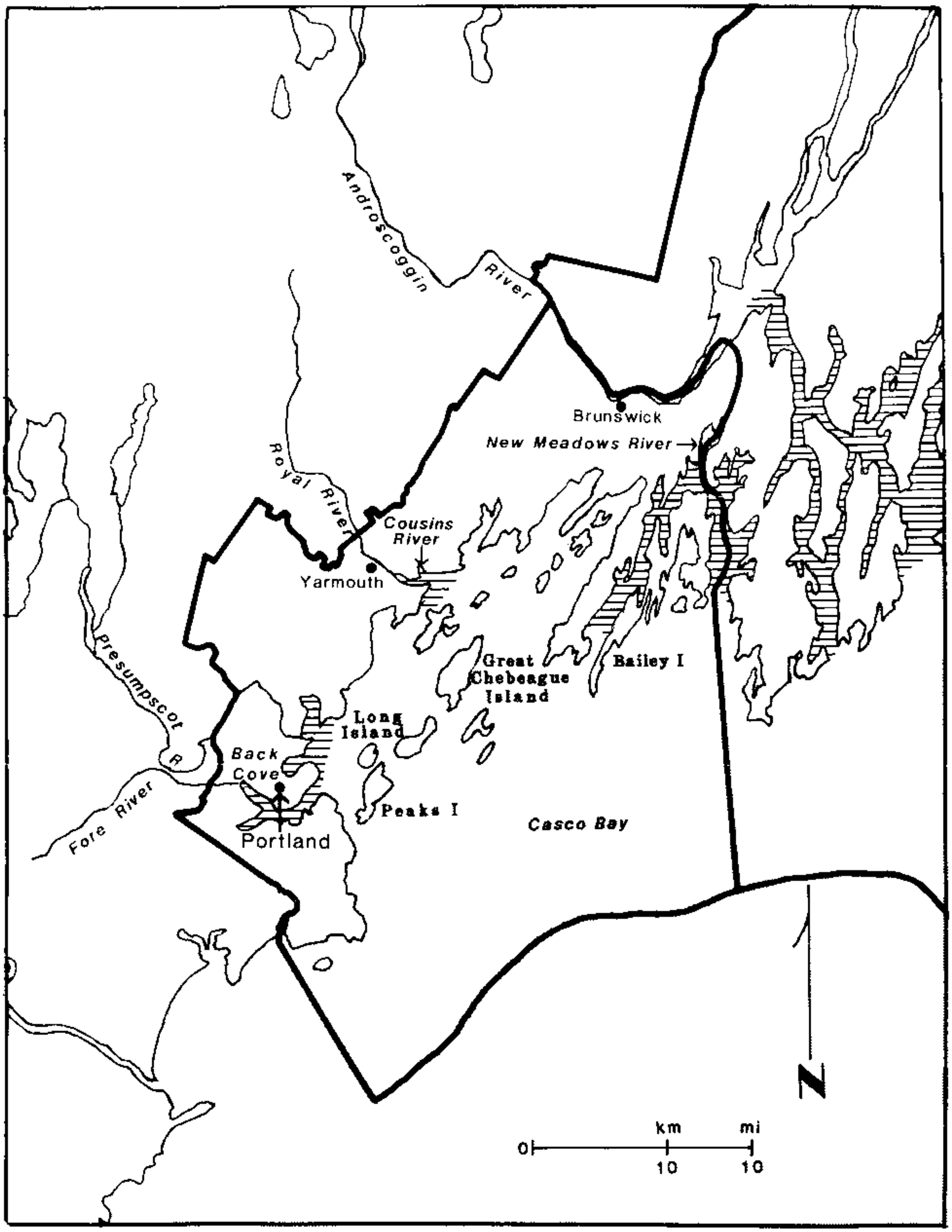


Figure 5-I. The major estuarine systems in region 1 of the characterization area as listed in table 5-1 and as delineated by the National Wetlands Inventory (Cowardin et al. 1979).

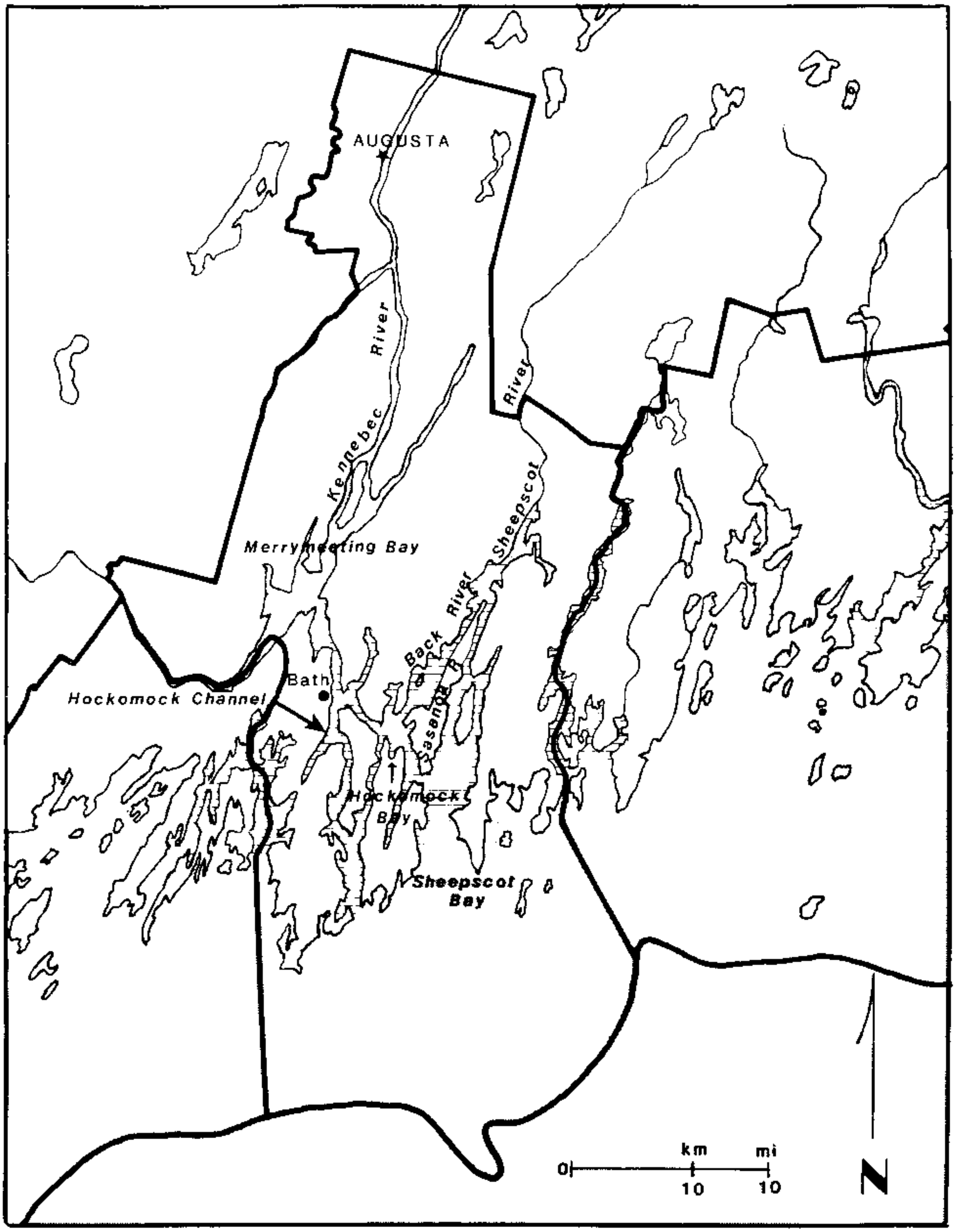


Figure 5-2. The major estuarine systems in region 2 of the characterization area as listed in table 5-1 and as delineated by the National Wetlands Inventory (Cowardin et al. 1979).

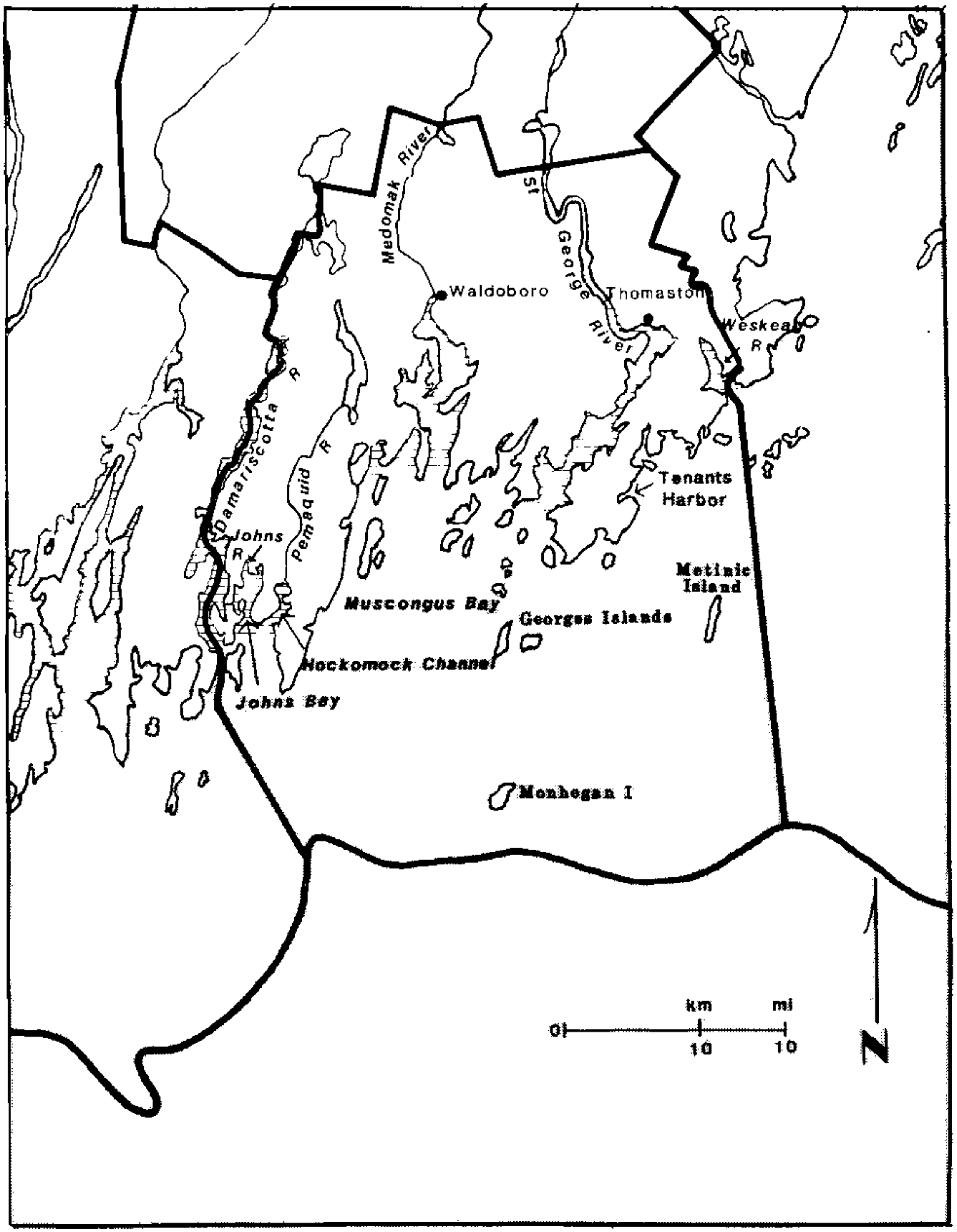


Figure 5-3. The major estuarine systems in regions 3 of the characterization area as listed in table 5-1 and as delineated by the National Wetlands Inventory (Cowardin et al. 1979).

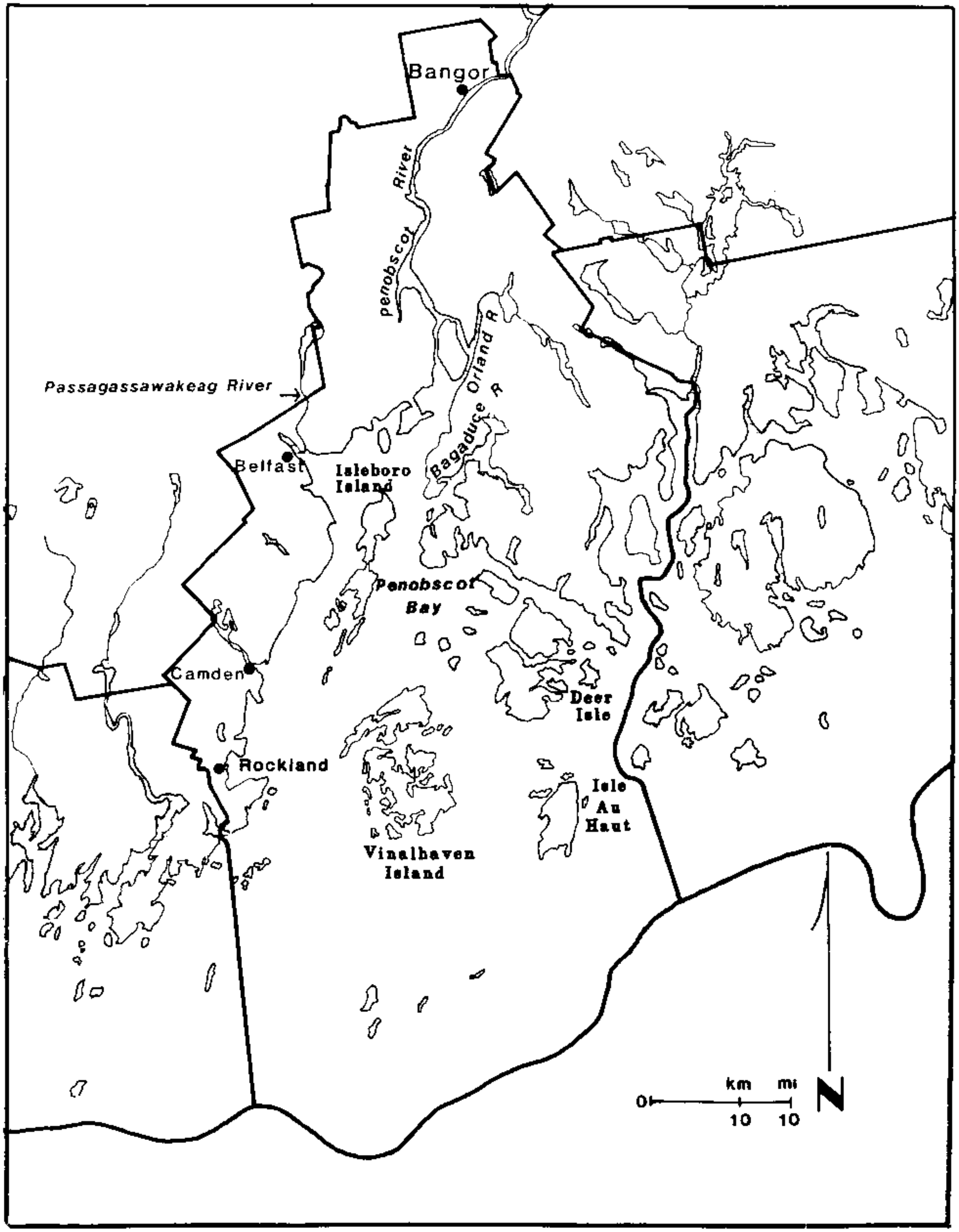


Figure 5-4. The major estuarine systems in region 4 of the characterization area as listed in table 5-1 and as delineated by the National Wetlands Inventory (Cowardin et al. 1979).

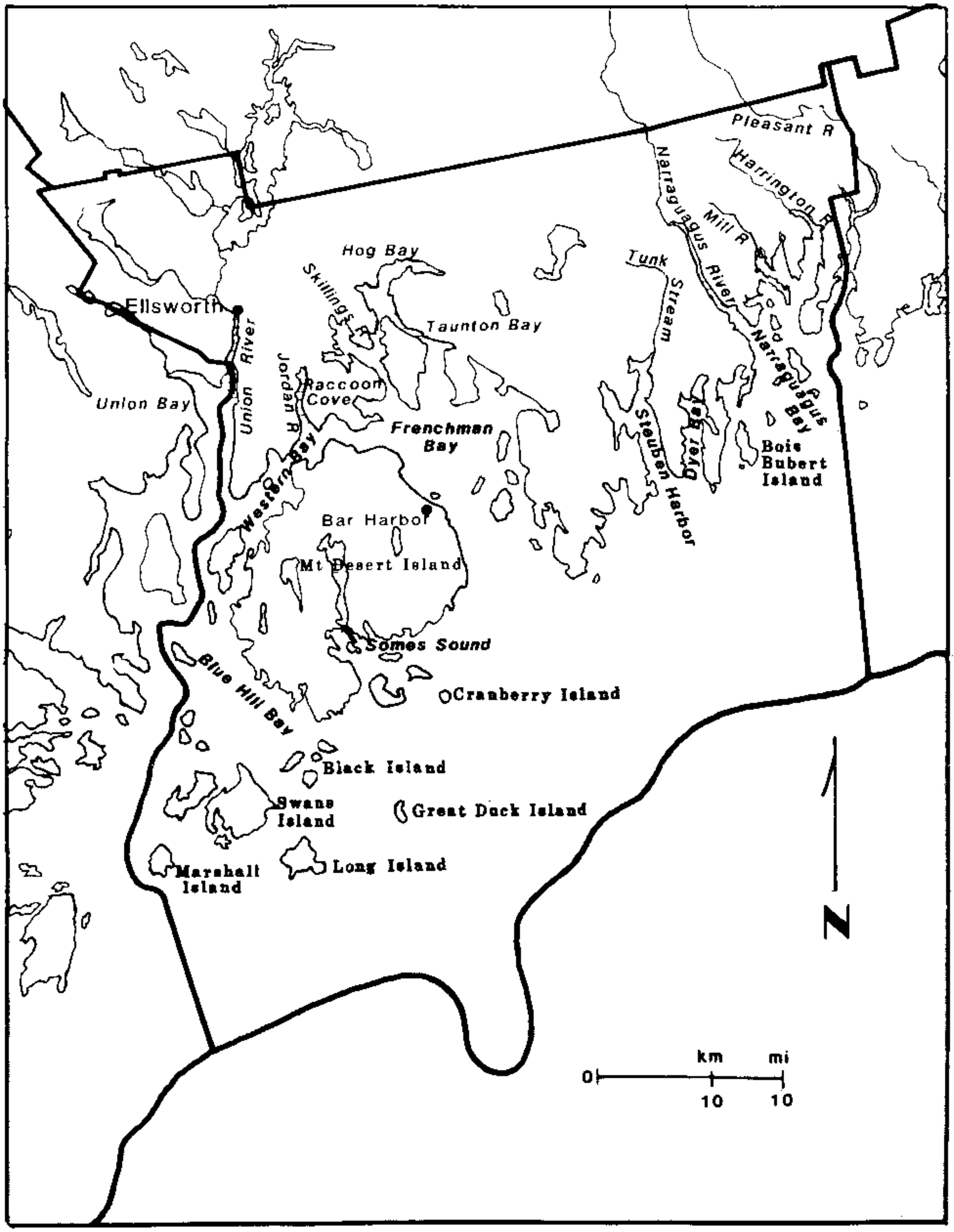


Figure 5-5. The major estuarine systems in region 5 of the characterization area as listed in table 5-1 and as delineated by the National Wetlands Inventory (Cowardin et al. 1979).

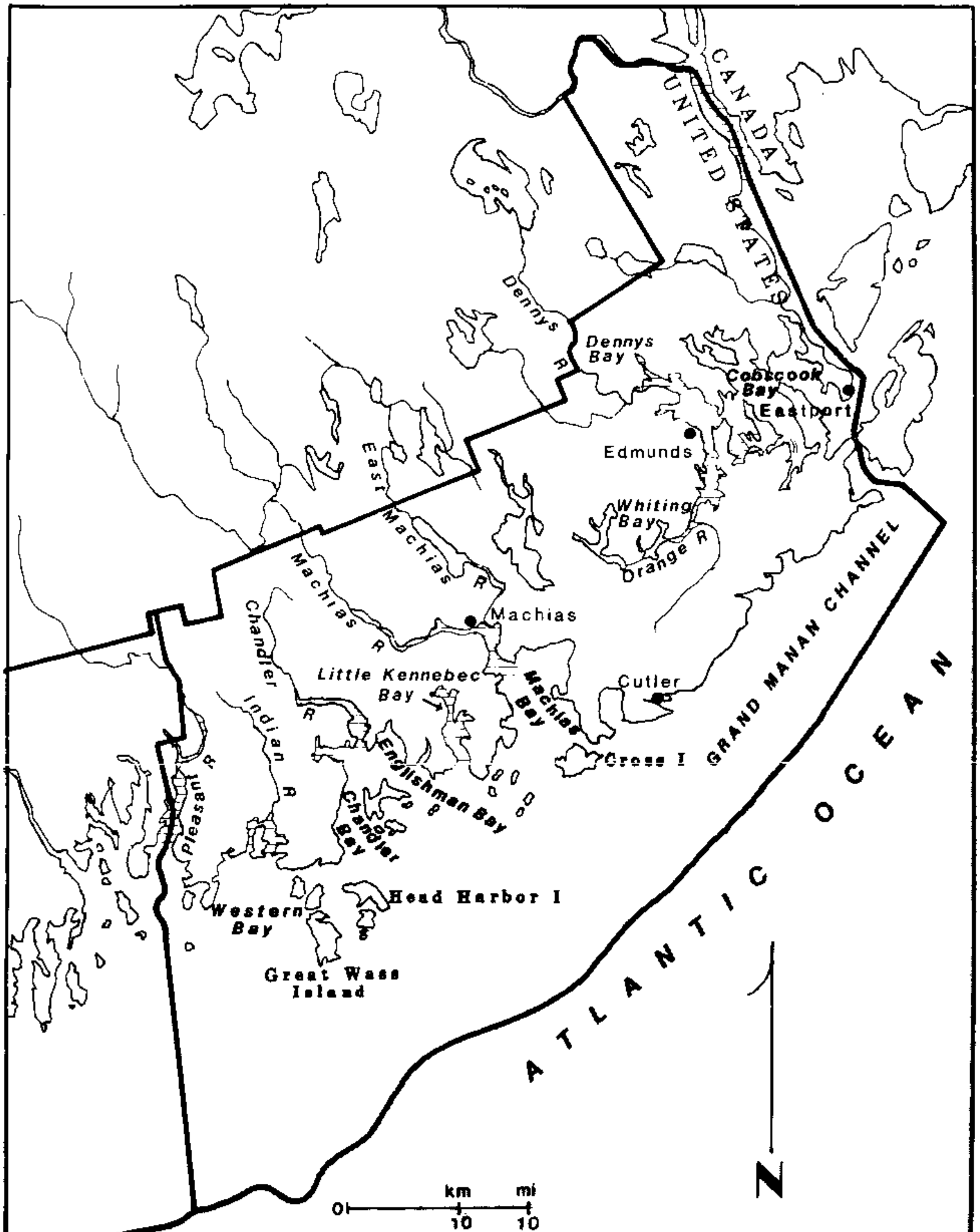


Figure 5-6. The major estuarine systems in region 6 of the characterization area as listed in table 5-1 and as delineated by the National Wetlands Inventory (Cowardin et al. 1979).

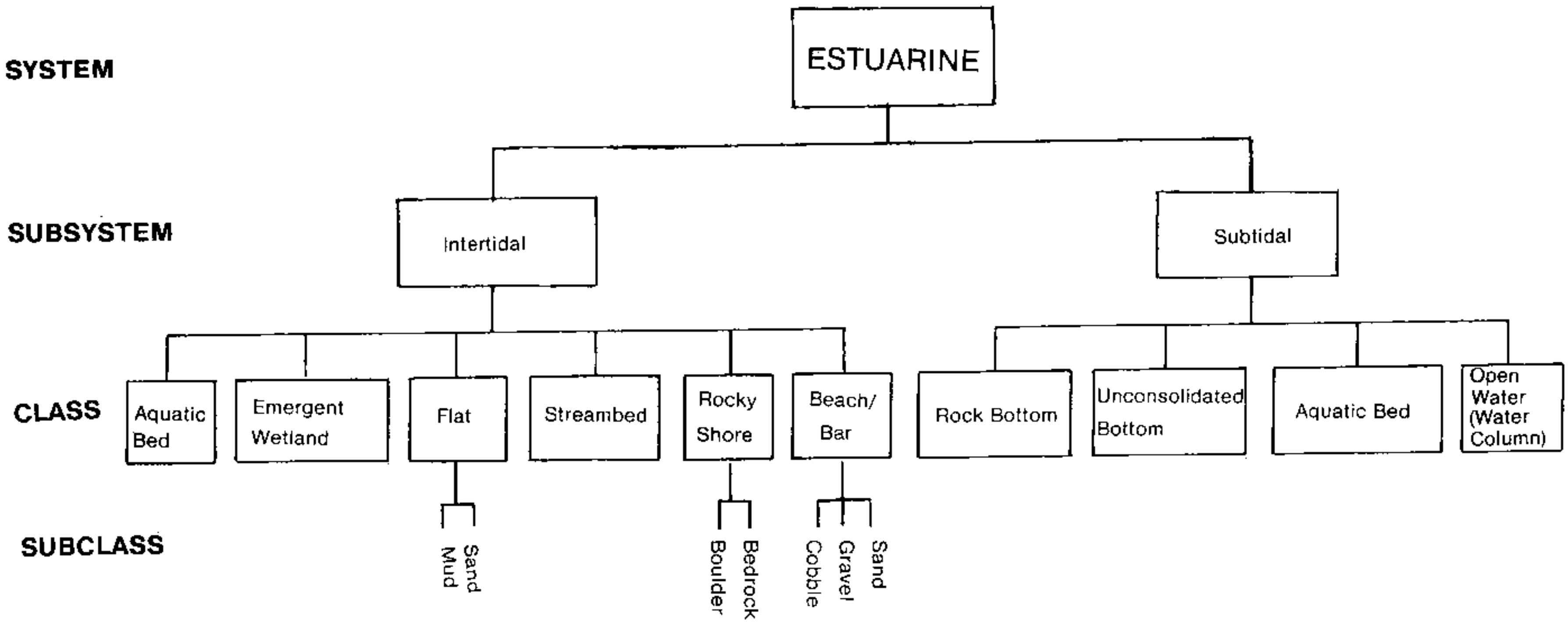


Figure 5-7. Hierarchical classification of the estuarine system of coastal Maine (Cowardin et al. 1979).

This chapter describes the general physical and biological features of the estuarine system in coastal Maine and details the characteristics of the subsystems and classes that comprise the system. Abiotic physical factors addressed are geology, hydrography, and climate. The biological features are introduced in the estuarine system level discussion and a general description of biotic roles in the ecosystem is included. The biota are described further in the specific subsystem (e.g., subtidal and intertidal) and class level (e.g., flat, rocky shore, and emergent wetland) discussions. Biological features described include the producers (phytoplankton, macroalgae, rooted aquatics, benthic diatoms, and microbes), consumers (zooplankton, benthic invertebrates, and fish and birds) and decomposers (bacteria and fungi).

The interactions of characteristic components of the different trophic levels are described under "Food Webs." The interactions of the biota with physical factors are discussed under "Energy Flow." Primary production is examined under "Primary Productivity." Biogeochemical cycling is illustrated in a description of the role of nitrogen and the organic matter cycle in Maine estuaries. Following the system level discussions, the subsystems and classes comprising the estuarine system are described. Detailed descriptions of the physical features and communities found in the varied estuarine habitats identified in coastal Maine are described at this level.

The descriptions of estuarine systems, subsystems, and classes presented in this chapter apply generically to the various individual estuarine systems (e.g., Machias River estuary and Penobscot River estuary) in coastal Maine unless a specific estuary is cited.

Many components (e.g., phytoplankton, zooplankton, invertebrates, fish, birds, and marine mammals) of the estuarine system are similar to those of the marine system. All aspects of the estuarine system are discussed in this chapter on the general level but, for the sake of brevity, all habitats except those that are unique to the marine system are discussed later on the class level. Habitats discussed in the estuarine intertidal subsystem include protected rocky shores, streambeds, gravel and cobble beaches, and sand and mud flats. Habitats with characteristics unique to the estuarine subtidal subsystem include unconsolidated bottoms, rock bottoms, and aquatic beds. The remaining classes are discussed in chapter 4, "Marine System."

Common names of species are used here except where accepted common names do not exist. Taxonomic names of all species mentioned are given in the appendix to chapter 1.

DATA SOURCES AND COMPILATION OF DATA

This chapter synthesizes the existing environmental information on Maine's estuarine system. It draws on published and unpublished literature, preliminary results of the National Wetlands Inventory (NWI) of the U.S. Fish and Wildlife Service, personal communication with persons active in research or management of the system, and the experience of the authors.

Sufficiently reliable data are not available to characterize many of the components of the estuarine system or to understand fully interactions between the components. To some extent, this shortcoming has been overcome by using data generated in other similar areas, such as Nova Scotia or northwestern Europe, which have been more fully studied, or by applying general concepts true for Maine.

Research needs are addressed at the end of the chapter. All literature used to produce this chapter is listed under "References" at the end of the chapter and in the Data Source Appendix (volume 4). In addition, many other data sources were reviewed but are not cited. These are included in the Data Source Appendix.

Information on the location and extent of estuarine habitats compiled by the NWI is incorporated. NWI has mapped habitat units at a minimum resolution of about 3 to 5 acres (1 to 2 ha; personal communication from R. W. Tiner, Jr., U.S. Fish and Wildlife Service, Newton Corner, MA; March, 1979). Habitats <3 acres (1.2 ha) generally were not mapped. A particular estuarine habitat may contain more than one class and a particular estuarine class may contain areas of other classes <3 acres. For example, an area mapped as a 5-acre (2 ha) flat may consist of a sand or mud flat surrounded by emergent wetland and rocky shore with an aquatic bed or mussel reef in the lower intertidal area. If each of these habitat types (rocky shore, emergent wetland, reef, and aquatic bed) were 3 to 5 acres or larger, they would be mapped as distinct units. Small-scale variations in abiotic factors affecting estuarine areas may result in several estuarine classes being found in the same area. These classes may intergrade into one another, adding to the difficulty of precise classification.

In the intertidal classification, all reflective areas were considered part of the intertidal zone. An estimated 34% of the rocky intertidal acreage classified by NWI is above the zone where macroalgae are found (personal communication from J. Topinka, Bigelow Laboratory for Ocean Sciences, West Boothbay Harbor, ME; December, 1979). Other intertidal classes include flats, beach/bars, emergent wetlands, aquatic beds, and reefs.

The NWI provides the user with the most detailed data to date on the distribution of estuarine habitats of coastal Maine. These data provide a baseline against which the future status of estuarine habitats can be measured.

DISTRIBUTION OF THE ESTUARINE SYSTEM

The total area (130,075 acres; 52,662 ha) and distribution of the estuarine system in the six regions of the characterization area are given in table 5-2. Major estuaries for each region are mapped in figures 5-1 to 5-6. Estuarine systems are most abundant in regions 2 (33,419 acres; 12,530 ha) and 6 (28,103 acres; 11,378 ha). Region 2 is dominated by the interconnected Kennebec/Sheepscot/Back River estuary complex and region 6 is dominated by Cobscook Bay and the St. Croix River estuary. Complete data on the St. Croix River are not available. The estuarine system is divided about equally between subtidal and intertidal areas. The majority of open water habitat (bottom type undetermined) probably is underlain by unconsolidated bottom. Rock bottom and aquatic beds account for a small percentage of the identified subtidal habitat. Flats occupy the largest area of any single intertidal class and account for 66% of the intertidal area and 32% of the total estuarine area. With the exception of the beach/bar class, most of the intertidal classes are distributed evenly among the regions. The beach/bar

Table 5-2. Acreages of the Estuarine System and Its Component Subsystems and Classes in Each of the Characterization Area, by region.

Region	Estuarine total	Subtidal total	Aquatic Bed	Open water	Unconsolidated bottom	Rock bottom	Intertidal total	Aquatic bed	Beach/bar	Emergent	Emergent/OW	Emergent/UB	Flat	Flat/EM	Flat/SS	Reef	Rocky shore	Scrub/shrub
1	14,098	5908	209	5437	262	--	8190	387	7	1921	286	9	5411	5	47	43	74	--
2	33,419	18,711	718	17,993	--	--	14,708	163	--	4975	--	--	9432	-	--	--	130	8
3	18,119	10,382	138	10,244	--	--	7737	326	7	1084	190	--	5841	-	--	74	215	--
4	19,690	10,709	135	10,446	128	--	8981	722	648	980	--	--	6021	-	--	--	610	--
5	16,646	6820	--	5310	1510	--	9826	602	12	2179	23	397	6135	-	--	21	457	--
6	28,103	14,163	4	12,938	1162	59	13,940	569	415	2663	--	--	8809	-	--	--	1425	58
Total	130,075	66,693	1204	62,368	3062	59	63,382	2769	1089	13,802	499	406	41,650	5	47	138	2911	66

class is most common in region 4 (60%) and region 6 (38%). Estuarine emergent wetlands represent a high proportion of total estuarine areas in region 1 (14%) and 2 (15%), respectively, and comprise 23% and 34% of the estuarine intertidal habitat. Region 5 also has a relatively large amount of emergent marshes (13%). The distribution of estuarine habitats in each town is included in appendix A of chapter 2. The distribution of estuarine systems, subsystems, and classes is depicted on atlas map 1.

ABIOTIC FACTORS

Abiotic factors influence the biotic composition of an ecosystem. The geology, hydrography, and climate of estuarine areas are addressed below.

Geology

The biological communities that comprise the estuarine system often are related to substratum types. NWI categories often are defined by substratum characteristics (figure 5-7). Since the estuarine system is composed of many varieties of substrata, the geological substrata (e.g., mud, cobble, and sand) are described in the class level discussion. The size distribution of sediment particles (e.g., sand, mud, cobble, and gravel) by habitat is given in figure 5-8. The composition of, formation of, and primary abiotic forces (e.g., currents) affecting the substrata of the estuarine system are summarized in table 5-3. A general discussion of coastal estuarine geology is found under "Geology," page 2-35 in chapter 2.

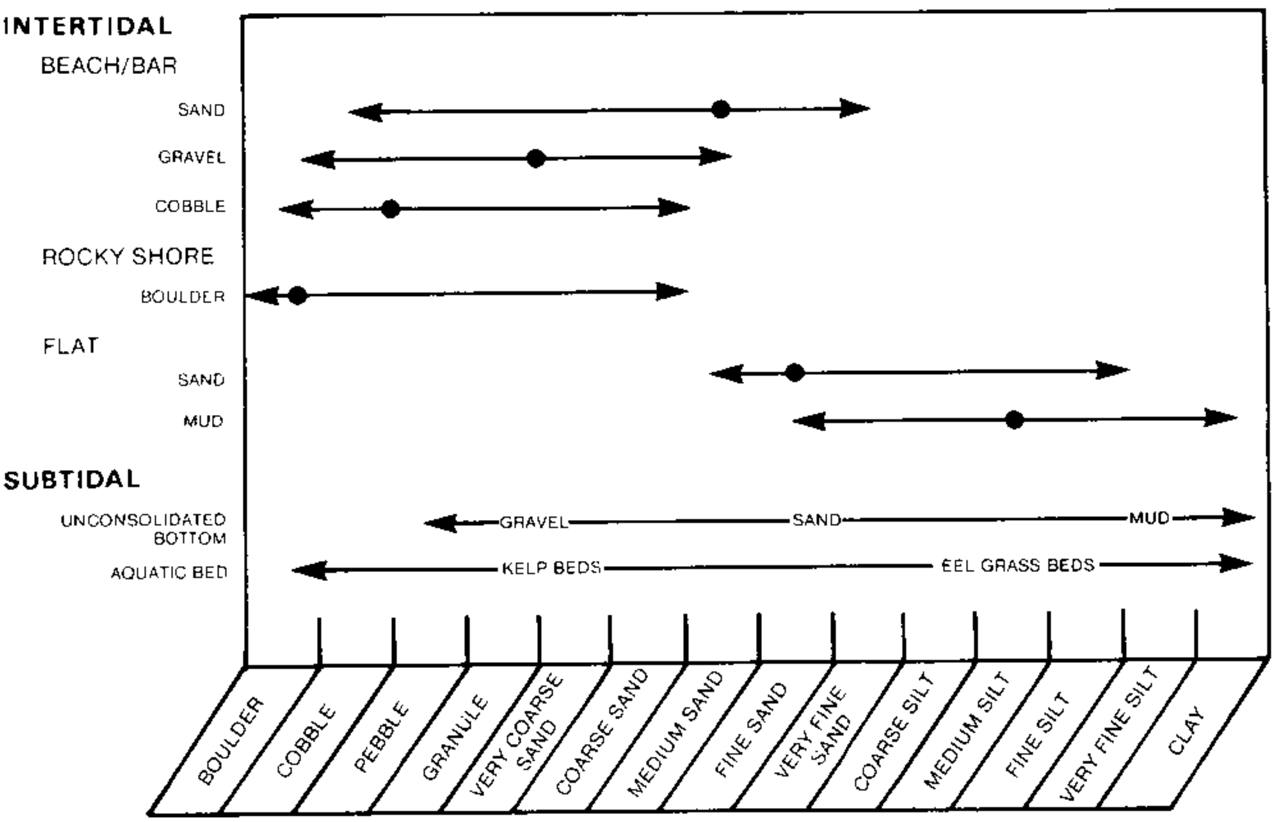


Figure 5-8. Size distribution of sediment particles in estuarine habitats of coastal Maine. Dots indicate dominant size, arrows indicate range.

Table 5-3. Composition, Formation and, Primary Abiotic Forces Affecting the Substrata of the Estuarine System and Subsystems.

Subsystem	Class	Origin or formation	Composition	Abiotic forces affecting substrata
Intertidal				
	Beach/bar			
	Gravel	Erosion of adjecent upland formed earlier and migrated landward with rise in sea level Growth from headland	Coarse pebble	Waves and wave-generated currents
	Cobble	Erosion of adjacent upland or shallow offshore deposits	Cobble	Waves
	Rocky shore			
	Ledge	Submergence of exposed bedrock	Bedrock	Waves, tidal currents and ice
	Flat			
	Sand	Erosion of adjacent upland Deposited from tidal channel from riverine or subtidal sources	Medium to very fine sand	Tidal currents and waves biogenic reworking

(Continued)

Table 5-3. (Continued)

Subsystem	Class	Origin or formation	Composition	Abiotic forces affecting substrata
Intertidal (Cont.)				
	Flat (cont.)			
	Mud	Erosion of adjacent upland Suspended sediment deposition from riverine or offshore sources Sediment derived from other parts of flat	Coarse to medium silt	Tidal currents, waves biogenic reworking
Subtidal				
	Unconsolidated Bottom			
	Gravel	Lag deposits in tidal channel bottoms	Pebble to coarse sand	Tidal currents, waves
	Sand	Derived from erosion of shoreward beaches or submergence of sand flats	Very fine sand	Tidal currents, wave-generated currents biogenic reworking
	Mud	Deposition of suspended sediment from water column	Fine silt to clay	Tidal currents, wave-generated currents biogenic reworking

(Continued)

Table 5-3. (Concluded)

Subsystem	Class	Origin or formation	Composition	Abiotic forces affecting substrata
Subtidal (cont.)				
	Ledge	Submergence of exposed bedrocks	Parent material	Tidal currents, wave-generated currents
	Aquatic bed			
	Eelgrass	See Intertidal and Subtidal Mud Flat	Silt	Tidal currents, wave-generated currents biogenic reworking
	Kelp beds	See Ledge and Gravel Unconsolidated Bottom		

In coastal Maine, human activities may impact the estuarine system by altering the estuarine geology and associated erosion and sedimentation rates. Certain upstream and coastal developments and associated dredging and filling alter estuarine geology. The extent of these activities and their potential impacts are covered in chapter 3, "Human Impacts on the Ecosystem."

Hydrography

From the hydrographic standpoint estuaries are areas where fresh water mixes with ocean water. (A discussion of marine hydrography is found on page 4-11 in chapter 4, "The Marine System.") This mixing is influenced by many factors, including freshwater flow, winds, basin topography, and tidal exchange. Consequently, areas defined as estuarine change and are not constrained geographically by their enclosing points of land. In fact, Bigelow (1927) considered the entire Gulf of Maine to be an extended estuary; however, the geographical approach used by the NWI will be used here.

Sufficient data are not available for hydrographic comparisons of the estuarine systems in coastal Maine. Among the many schemes for characterizing estuaries, the Ketchum (1951) flushing model requires data only on fresh water flow, tidal height, and topography to provide a semiquantitative description of the major features of estuarine hydrography. This model will be used as a basis for comparison with specific data on selected estuaries.

An estuary is a semienclosed coastal body of water that has a free connection with the open sea and within which sea water is diluted measurably with fresh water derived from land drainage (Cameron and Pritchard 1963). The vertical circulation of the water in estuaries is a result of the interaction of salt water and fresh water, which is determined by local topography, freshwater flow, tidal exchange, and local winds. These factors vary on time scales of hours to years and circulation varies accordingly. They are examined individually below.

Freshwater flow. The principal factor determining the circulation in estuaries is the inflow of fresh water from rivers. Fresh water is less dense than sea water, and when it flows into an estuary it floats on the surface and is separated from the sea water underneath by a strong density interface that inhibits mixing. It floats above the sea water and across the surface towards the open sea, and in the absence of mixing would flow as an intact layer, as an extension of the river. In the absence of mixing, the circulation would exist as a surface flow underlain by a layer of salt water and as the estuary widened downstream the seaward velocity would decrease (figure 5-9).

In practice, the boundary between the flowing fresh water and static sea water would have to be frictionless for the above conditions to be realized, and it is not. However, in estuaries where the freshwater flow is the dominant flow, estuarine circulation approximates the above description and such estuaries are termed "salt wedge" or "highly stratified" estuaries.

Tidal exchange (see also "Tides," page 4-18 in chapter 4, "The Marine System"). Tidal exchange is the major factor providing mixing energy to estuaries. Few estuaries are large enough to have their own tides, and Maine estuaries experience an extension of the oceanic tide. The tide enters an estuary as a long period wave that moves progressively up the estuary, so that

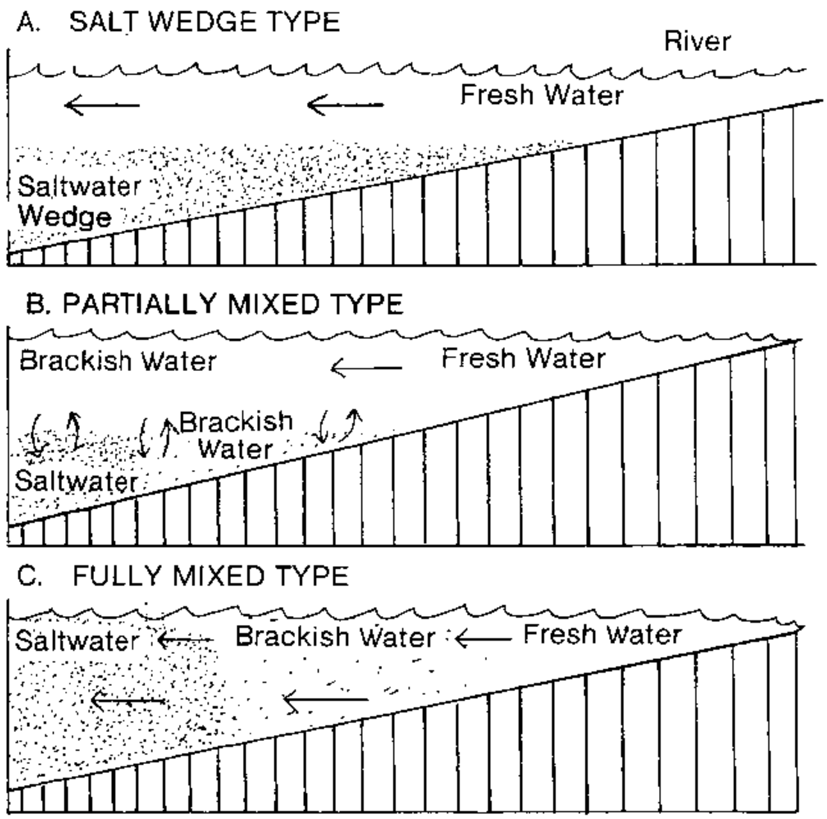


Figure 5-9. Cross-sectional diagrams of generalized estuarine types found in coastal Maine.

high tide occurs later upstream than at the mouth. In an estuary with parallel sides and uniform depth, the tide distributes energy throughout and the tidal amplitude decreases towards the riverine end. In estuaries that become narrower towards the riverine end, the tidal wave is narrowed and becomes higher as it moves upriver. If the tidal wave is high enough, or if the bottom is shallow enough, the tide begins to interact with the bottom and friction slows the wave. The same friction causes turbulence in the water column and results in mixing. If the tide is high enough and the bottom shallow enough, the tidal wave breaks and moves up the estuary as a tidal bore.

When bottom friction on the tidal exchange is low, turbulence is only sufficient to push salt water up into the layer of fresh water. This process, called entrainment, results in the surface layer becoming increasingly salty as it flows to the sea. (The term brackish water is used to describe this water, which has a lower salinity than coastal sea water.) The underlying sea water is not diluted with fresh water and is saline but moves up the estuary to replace the salt water lost by entrainment. With increased tidal friction, entrainment becomes a two-way process: fresh water mixes downward into the bottom layer and salt water mixes upward into the surface layer. In estuaries in which two-way entrainment takes place, called "partially mixed" or "partially stratified" estuaries, both the surface and bottom layers have decreasing salinities toward the riverine end, and the flow is seaward at the surface and landward at the bottom (figure 5-9).

When bottom friction becomes extreme, mixing from surface to bottom occurs and the water column becomes homogeneous from top to bottom. Estuaries of this type are termed "vertically homogeneous" or "fully mixed" estuaries, and salinity decreases from the oceanic to the riverine end of the estuary but is uniform throughout the water column. Water moves towards the oceans at all depths and the salinity of the estuaries is maintained by horizontal mixing or diffusive processes (figure 5-9).

Topography. Although tides provide the energy for mixing, topography determines where that energy is translated into mixing. An estuary with a deep wide mouth will not restrict the entering tide and may approximate the "salt wedge" estuary at that point. As the estuary narrows and becomes shallower, the topography begins to increase the tidal height and mixing, and increasing bottom friction will result in the estuary becoming partially stratified. Still further toward the riverine end, the shallower water and greater bottom friction creat a well-mixed and homogeneous estuary. Thus, all estuarine types and gradations between them can occur in a single estuary, depending on topography. Likewise, spring and neap tides and changes in seasonal freshwater flow can cause a given portion of an estuary to change from one type to another.

Winds. Prevailing winds affecting large estuaries can modify circulation and tides. Tidal ranges can be altered by winds blowing along the axis of the estuary, and crosswinds in sufficiently large estuaries can result in the seaward flow being moved to one side of the estuary and accelerated greatly or diminished, depending upon the direction of the wind. Storm winds creating surface waves can cause intense vertical mixing. These effects last only as long as the winds, and relaxation is rapid afterwards. However, such wind events are frequent enough that they introduce many short-term variations into estuarine circulation, so that it becomes difficult to establish a typical, or average, circulation for any estuary. Eliot (1978), for example, found that the Potomac estuary was two-layered and partially mixed during 40% of the time during which it was studied. During the remaining 60% of the time, any one of five flow regimes existed as a result of meteorological influences.

General Hydrographical Characteristics of Maine Estuaries

Most Maine estuaries are drowned river valleys, formed as a result of the rise in sea level over the recent geological past. Maine estuaries exhibit all estuarine types, often within the same estuary. For example, the upper part of the Sheepscot estuary is vertically homogeneous; below Wiscasset to Five Island and Townsend Gut it is partially stratified, and below that region it becomes almost a "salt wedge" type (although these boundaries change seasonally and are approximate). Most Maine estuaries have considerable tidal exchange relative to fresh water flow, so that all experience mixing. The extreme "salt wedge" type is rare. Most estuaries in Maine have a partially mixed character over much of their length, with the upper segment being well mixed to homogeneous.

Because the circulation of estuaries is principally a function of fresh water flow, topography, and tidal exchange, these parameters have been used by scientists and engineers to characterize and compare estuaries. One of the most widely applied methods is Ketchum's (1951) modified tidal prism method. This method uses topographic and tidal height data and fresh water flow data (available for most major rivers from the USGS).

The method is described in detail in Dyer (1973; which also includes a comprehensive treatment of general estuarine hydrography); the following description is intended only to indicate the results obtained and some of their limitations. The method hypothetically divides the estuary into a number of segments that are about 2 miles (3.2 km) long in most estuaries in Maine. It then calculates an average salinity, a flushing time, and tidal and nontidal currents for each segment.

The model operates on the assumption that the contents of each segment are thoroughly mixed by each tide and measures the salinity accordingly. In most Maine estuaries, only a surface layer of 10 to 15 m thickness approximates well mixed conditions and, consequently, the model has been applied only to this layer. Both the segmentation and the salinity distribution change as fresh-water flow changes, so for comparative purposes the 10-year mean flow from USGS water resource data for each estuary was used. These data were adjusted for drainage basin area, since the gaged flow is only for that part of the total drainage basin upstream of the gage (see chapter 6, "The Riverine System"). The predicted salinity distribution is only the average surface salinity and in the Sheepscot estuary, for example, where comparable field data are available, the predicted salinity is usually within 1 ppt of the observed surface salinity. It must be noted though that salinity below the surface is always higher than it is at the surface. Changes in freshwater flow can alter the salinity distribution greatly. Freshwater flow in Maine estuaries varies seasonally between 33% and 300% of the mean.

The flushing time of a segment of an estuary is the average length of time that water spends in that segment. In the reports of flushing time given here, the data corresponds to the cumulative flushing time. That is, the segment nearest the sea flushes in, for example, five tides; the next segment flushes in five tides also, but to flush to the ocean it must flush through the lower segment, taking an additional five tides. Hence, this segment flushes completely to the ocean in 10 tides. The data are presented in this way on the assumption that reader interest will focus on questions of the type "If something is spilled here how long will it take to be diluted out of the estuary?" Two points must be made about flushing time: (1) the flushing times reported here probably are low, because the complete mixing assumed in the model does not occur and because only the surface layer is treated in the model and (2) since the flushing time is the average time water spends in the estuary, it represents the time required for at least half, but not all, of a pollutant to be flushed out of the estuary.

The terms "tidal and nontidal flows" are simply a convenient way of separating the two components of the estuarine water flow. In the absence of tides, estuarine waters would flow steadily seawardas rivers do, and would vary as fresh water flow varies. This current is nontidal flow. Superimposed on this flow is a tidal flow, which flows in opposite directions between high and low tides. The average velocity of this flow can be computed. Obviously, tidal currents vary from zero at low or high tide to a maximum at half tide, which is approximately 150% of the mean flow. Local topography can cause extreme changes in the currents.

The flushing model has been applied to provide some basis for comparison. The reader is cautioned that the model output is only a reasonable facsimile of average values under mean flow and is intended only for comparative purposes. These are not field data and should not be viewed as such. In the discussions below on the hydrography of individual Maine estuaries, information derived from the Ketchum model will be integrated with data from published reports. Thus, the amount of information reflects the amount of study the estuary has received.

Casco Bay/Portland Harbor/Fore River. According to Hulbert (1968 and 1970) a cold bottom water inflow and upwelling are the major nontidal flows in Casco Bay. Strong tidal mixing around shoals and around the island of the bay prevents the establishment of a summer thermocline, which has formed elsewhere in the Bay. At a station in the mouth of Portland Harbor, Normandeau Associates (1974) observed spring (March) and neap (April) currents. In both instances, flood currents were uniform regardless of depth. This is typical of a partially mixed estuary. More data (including data on a greater number of years) are necessary to support a general conclusion. The flushing model was not applied to this estuary.

Presumpscot and Royal estuaries. The Ketchum model was applied to these estuaries, which are highly atypical (figures 5-10 and 5-11). Both are bounded by barriers (Presumpscot Falls and Yarmouth Dam, respectively) at their upper end within a few kilometers of the ocean. Each comprises only a single segment and according to the model would be flushed by a single tide. The model predicts a mean salinity for each, but this is misleading, as complete flushing would result in salinities ranging from zero to full oceanic levels during each tide. No data exist for these two estuaries.

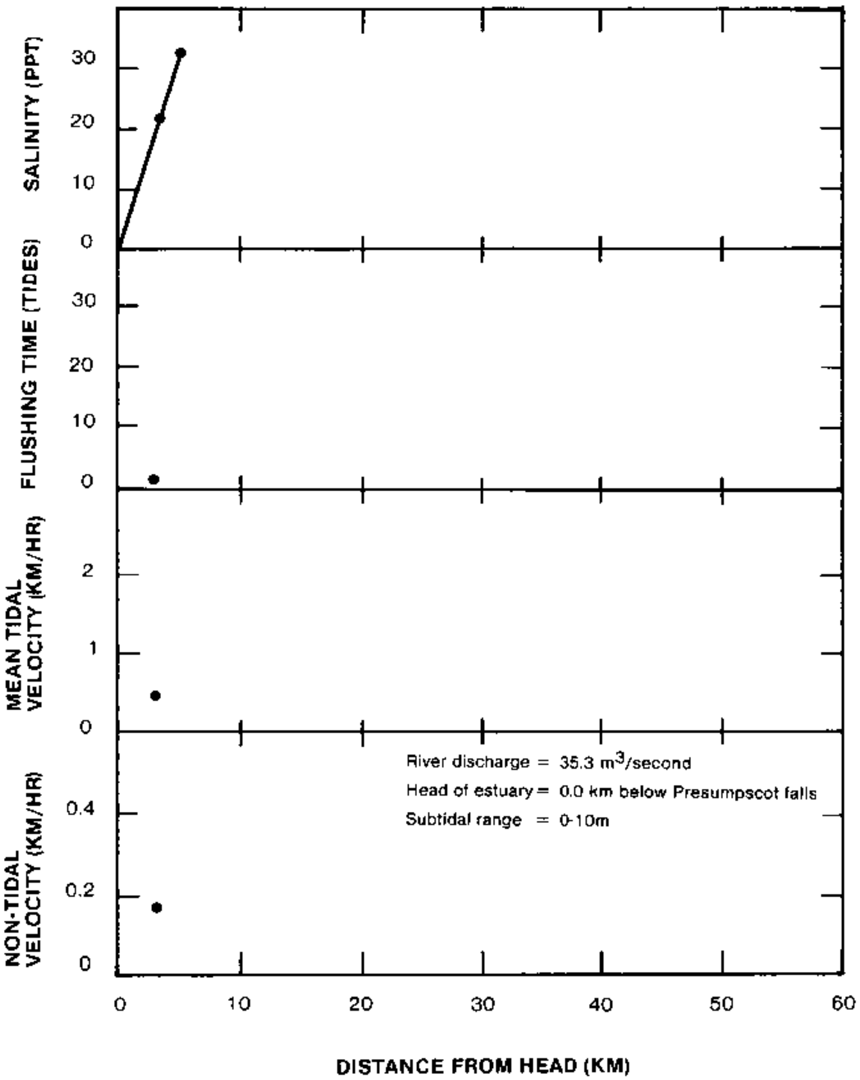


Figure 5-10. Salinity (ppt), flushing time (number of tides), mean tidal velocity (km/hr), and non-tidal velocity (km/hr) as predicted by the Ketchum estuarine flushing model for the Presumpscot estuary. Data are plotted from the head of the estuary (0 km) downstream to the point of predicted oceanic salinity.

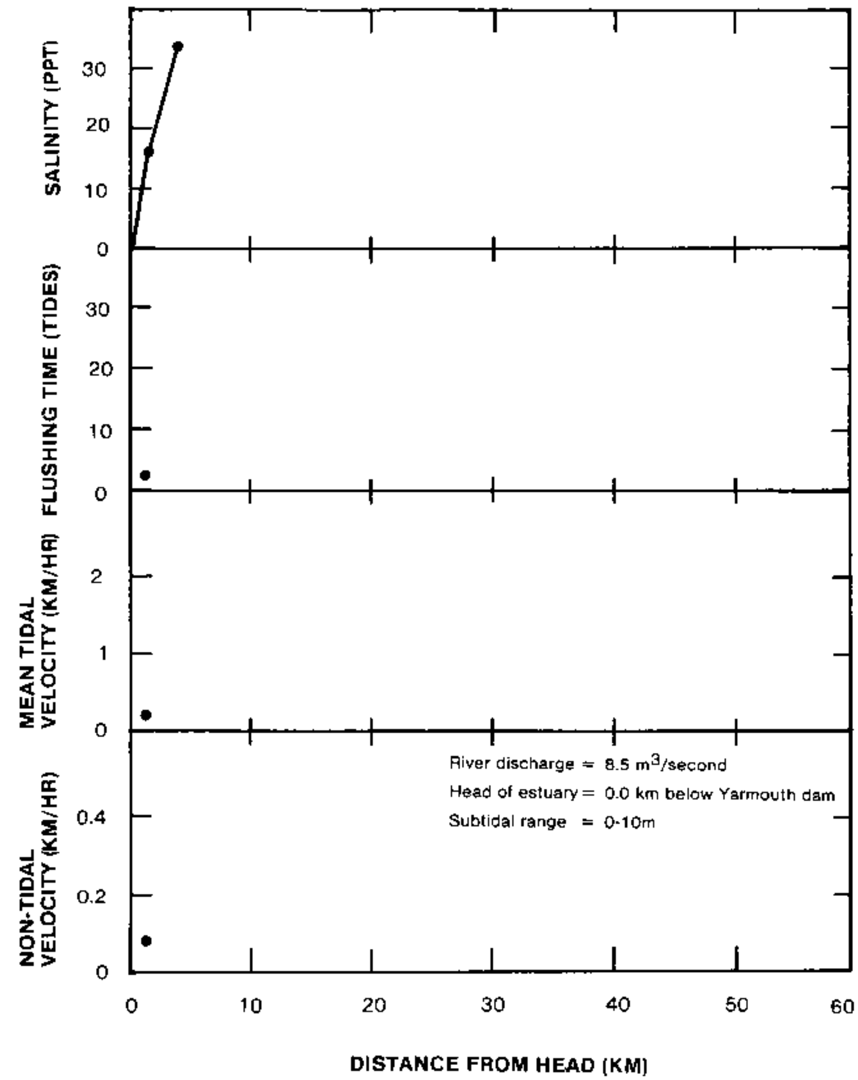


Figure 5-11. Salinity (ppt), flushing time (number of tides), mean tidal velocity (km/hr), and non-tidal velocity (km/hr) as predicted by the Ketchum estuarine flushing model for the Royal estuary. Data are plotted from the head of the estuary (0 km) downstream to the point of predicted oceanic salinity.

Kennebec estuary. The few data available for the Kennebec estuary support the results of the Ketchum model. The estuary is comprised of only two segments as a result of its shallow, narrow topography and considerable freshwater inflow (figure 5-12). Consequently, the model predicts a short flushing time with strong nontidal and extremely strong tidal currents. The strong current regimes and constricted topography should result in intense mixing.

Francis and coworkers (1953) sampled this estuary below Bath during a fall period of low flow and found it to be stratified only slightly. In one area, ("Doubling Bends") they observed great turbulence that was not noted elsewhere and that should cause intense vertical mixing. Because of their observation of slight vertical salinity gradients, they concluded that this mixing was not complete. Stommel (1953), commenting on the data above, described the Kennebec as having such intense vertical mixing that vertical salinity differences were only a small fraction of the horizontal differences. He attributed the mixing to strong tidal and nontidal currents interacting with the rough bottom.

Sheepscot estuary. The Sheepscot is one of the most complex of Maine's estuaries. The upper part is somewhat isolated by a rock-ledge reversing falls below Sheepscot Village. Between the falls and Wiscasset the estuary is shallow with extensive mud flats, and below Wiscasset it is narrow and more deeply bounded by rock ledge. From Barters Island southward, the estuary deepens further and has several interconnections: through Goose Rock passage to Wiscasset via Montsweag Bay, via the Sasanoa River to the Kennebec, through Ebenecook Harbor via a complex of small islands to Townsend Gut and Boothbay Harbor, and several back waters, such as Cross River and Back River (see atlas map 1 and figure 5-2 for locations). Each of these contributes in a complicated manner to the circulation, on which data are scarce. The Ketchum model cannot account for much of this complexity but illustrates a number of the major features of the estuary that have been documented (figure 5-13).

Stickney (1959) hypothetically divided the estuary into an upper and lower section at Wiscasset. Unpublished data by Larsen refer only to the upper section and Garside and coworkers (1978) provided additional data on the lower section, so that Stickney's framework is adopted for modeling.

According to Ketchum's model, the upper portion of the estuary, because of its shallowness, experiences a rapid tidal exchange and flushes quickly (figure 5-13). The effect of riverflow into this small volume results in rapidly changing salinity. The shallowness of the region can be expected to result in strong tidal mixing and, consequently, small vertical salinity gradients. This is supported by June, 1974, tidal cycle data at the Sheepscot Village bridge (figure 5-14). The salinity range is from 0 to 15 ppt with little surface to bottom variabiity, and the curve is asymmetrical (Stickney 1959). At stations farther up the estuary, the asymmetry becomes more pronounced (because of the influence of the falls; figure 5-15) with salinity increasing rapidly on the flood tide and decreasing slowly on the ebb tide.

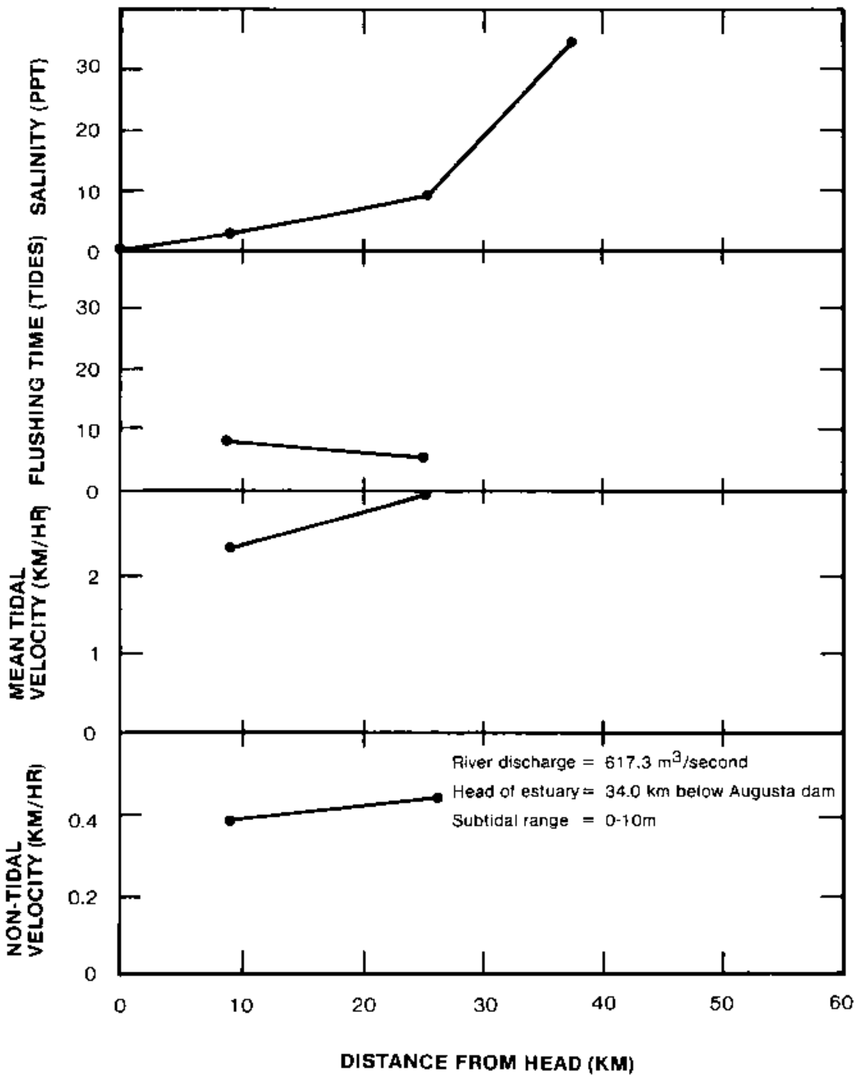


Figure 5-12. Salinity (ppt), flushing time (number of tides), mean tidal velocity (km/hr), and non-tidal velocity (km/hr) as predicted by the Ketchum estuarine flushing model for the Kennebec estuary. Data are plotted from the head of the estuary (0 km) downstream to the point of predicted oceanic salinity.

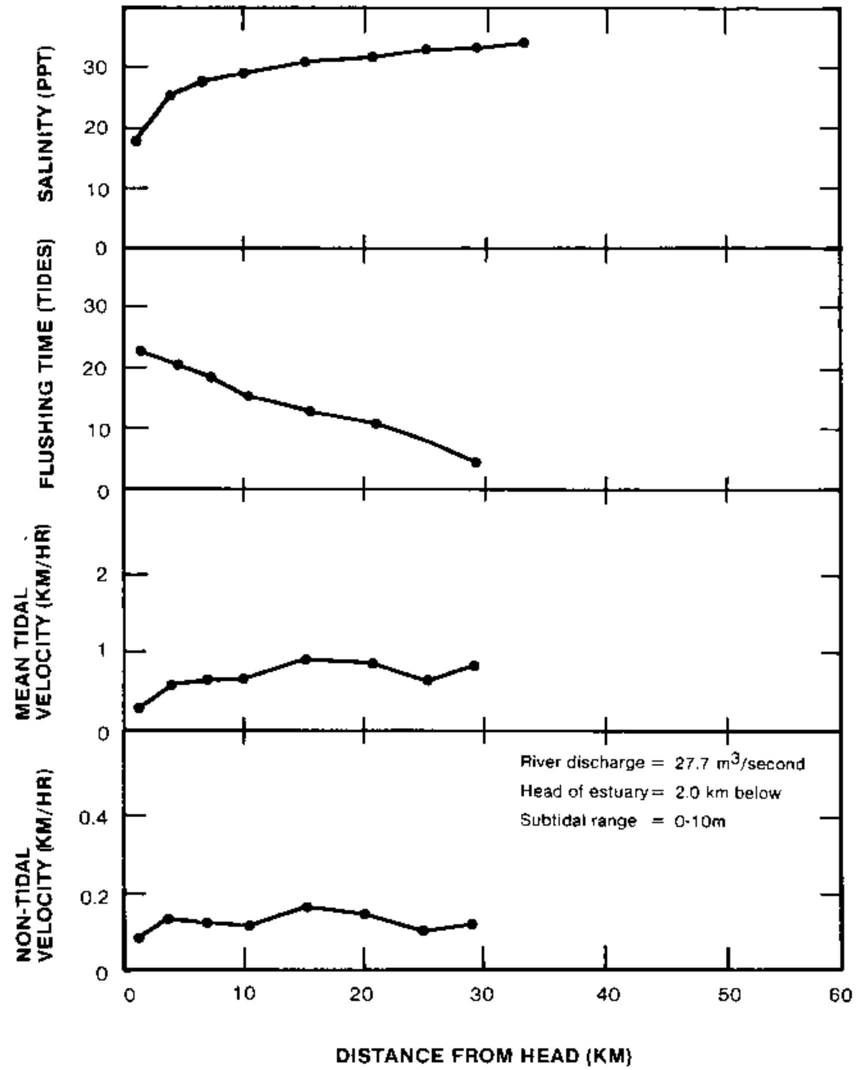


Figure 5-13. Salinity (ppt), flushing time (number of tides), mean tidal velocity (km/hr), and non-tidal velocity (km/hr) as predicted by the Ketchum estuarine flushing model for the Sheepscot estuary. Data are plotted from the head of the estuary (0 km) downstream to the point of predicted oceanic salinity.

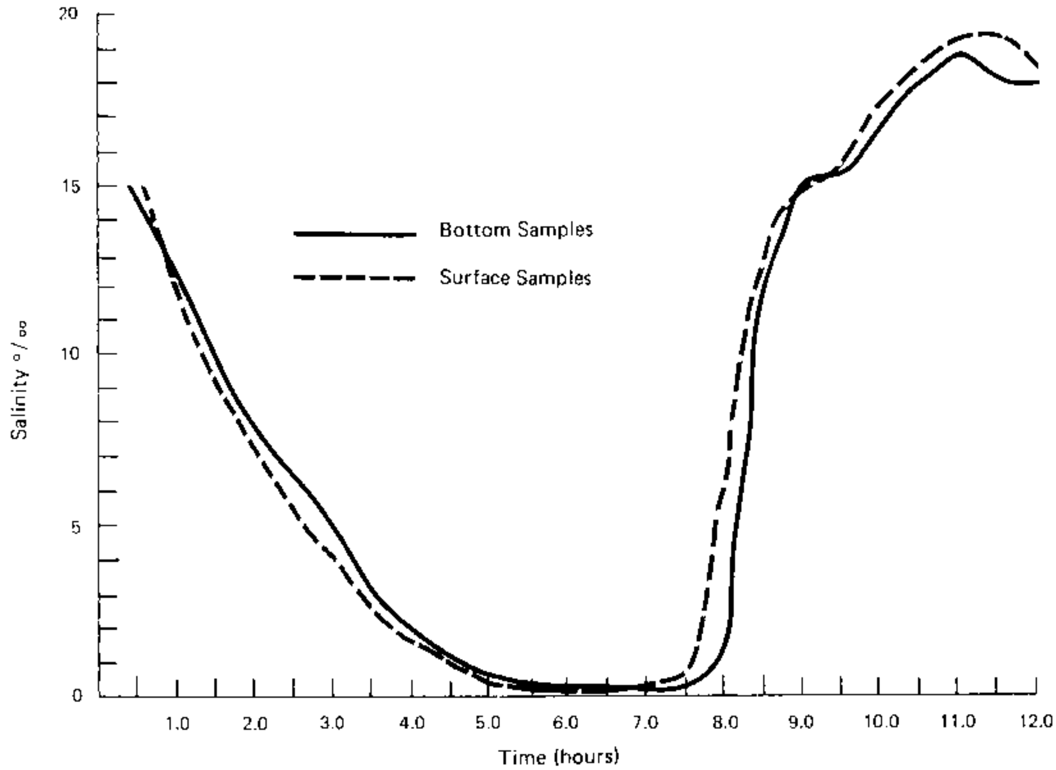


Figure 5-14. Surface and bottom salinity in the upper Sheepscot estuary during a tidal cycle in June 1974 (Larsen, unpublished).

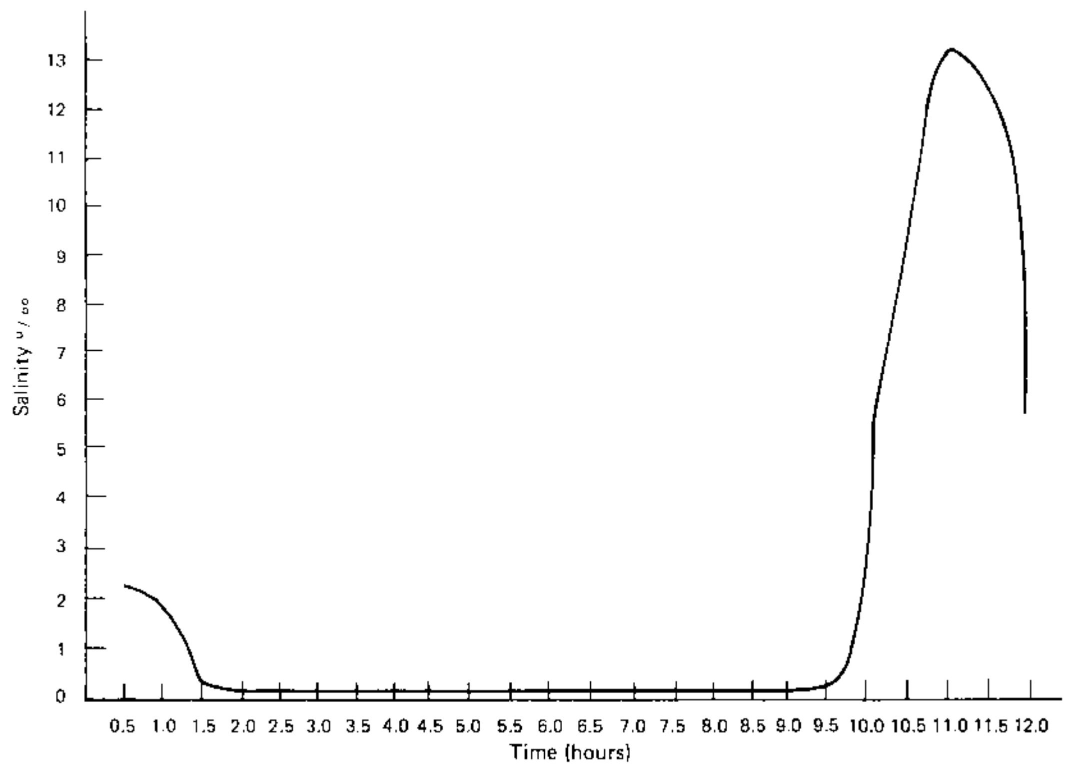


Figure 5-15. Salinity over a tidal cycle in the upper Sheepscot estuary in June 1974 (Larsen, unpublished).

The model predicts that the lower part of the estuary will have high salinities, approximating oceanic salinity, with maximum tidal velocities in the lower estuary just south of Wiscasset. The narrow rocky channel should have a considerable degree of mixing and may be an important factor in determining the upper extreme of the two-layered flow regime. This is evident in the steepening of the isopycnals (lines of equal density; figures 5-16 and 5-17) in both summer and winter (Garside et al. 1978). The lower estuary has a permanent pycnocline, which in summer depends on both temperature and salinity and in winter on salinity alone, and which has an inverse temperature structure (lower temperature at the surface and towards the head of the estuary). Stickney (1959) concluded that the uniform vertical temperature structure in the fall resulted from vertical mixing but this is probably not so, as the salinity stratification still remains then.

The mixed water from the narrow channel south of Wiscasset flows southward and to some extent is diluted further by fresher water entering from Goose Rock passage. This fresher water stays to the west of the estuary and flows southward into the Gulf of Maine (Stickney 1959). Below the surface layer (10 m deep), water having relatively high salinity enters the estuary (Stickney 1959) and Garside and coworkers (1978) identified the oceanic source of this water as Maine Intermediate Water, based on its nutrient content (see "Hydrography," page 4-11 in chapter 4).

The surface tidal excursion of 2.8 miles (4.5 km) measured off mid-Barters Island compares well with the mean tidal current (0.5 mile/hour or 3 miles/tide; 0.8 km/hr or 5 km/tide) predicted by the model. These same current measurements and associated salinity measurements are typical of patterns in partially stratified estuaries and are confirmed by extensive measurements of the salinity distribution (Garside et al. 1978).

Hockomock, Montsweag, and Nubble Bays. These irregularly shaped bays lie between the Kennebec and Sheepscot Rivers and connect with them at Wiscasset, Goose Rock Passage, and the Sasanoa River, respectively. These connections provide for a cross exchange of water between the two estuaries. According to Stickney (1959), water enters from the Sheepscot on the rising tide and leaves on the ebb; the reverse is true for the Kennebec. Considerable mixing occurs within the bays, so that the salinity of water returning to the estuaries has been modified by the waters of the bays. Higher salinity water should be returned to the Kennebec and lower salinity water to the Sheepscot.

The inflow and outflow of the bays are not in phase with the estuarine tides. Water flows into the Sheepscot from Hockomock for about an hour after the start of its flood and the maximum flow out of Hockomock occurs about 3 hours after the start of the ebb on the Sheepscot (Stickney 1959). The Maine Department of Environmental Protection (DEP; 1979) conducted a survey to examine the distribution of Kennebec River Water (KRW) in these bays and in the Sasanoa River. They concluded, based on surface salinity measurements, that some of the KRW was impounded in Montsweag Bay on each tide and the remainder was discharged to the Sheepscot. They observed also a surface (8 ppt) to bottom (20 ppt) salinity gradient at Preble Point (junction of Kennebec and Sasanoa rivers). This highly saline water could only originate in the Sheepscot and suggests a two-layered flow, west to east at surface and east to west at deeper levels, throughout the Sasanoa River.

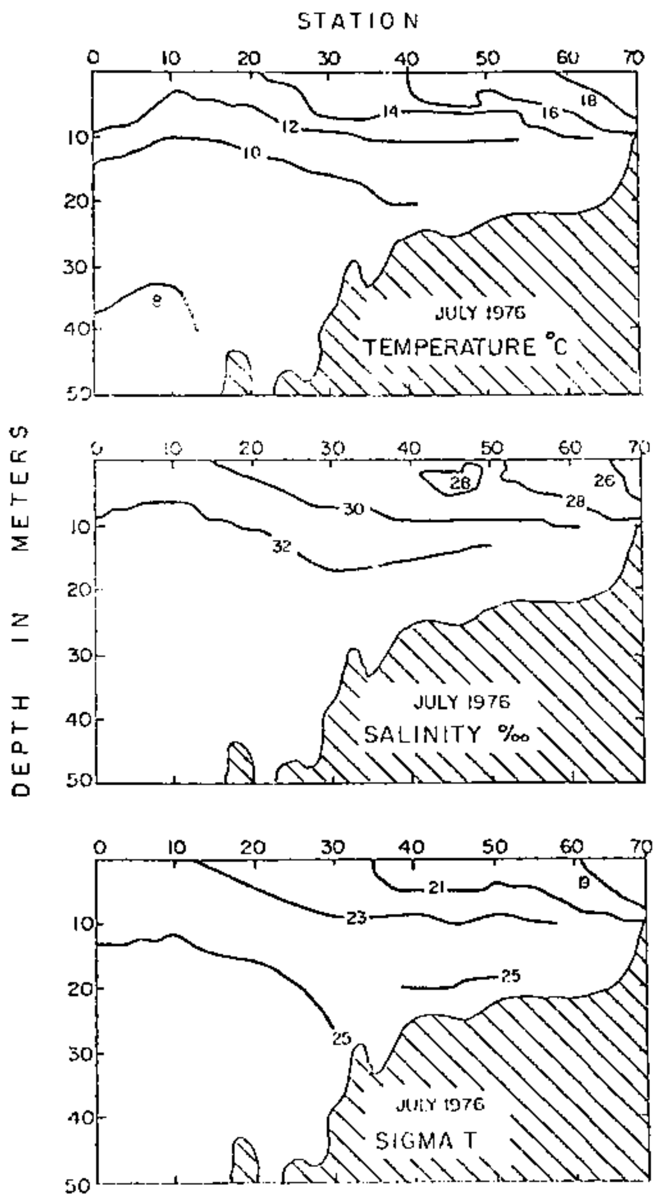


Figure 5-16. Cross-sectional representation of lower Sheepscot estuary and corresponding distribution of temperature, salinity, and density isoclines during July 1976 (Garside et al. 1978).

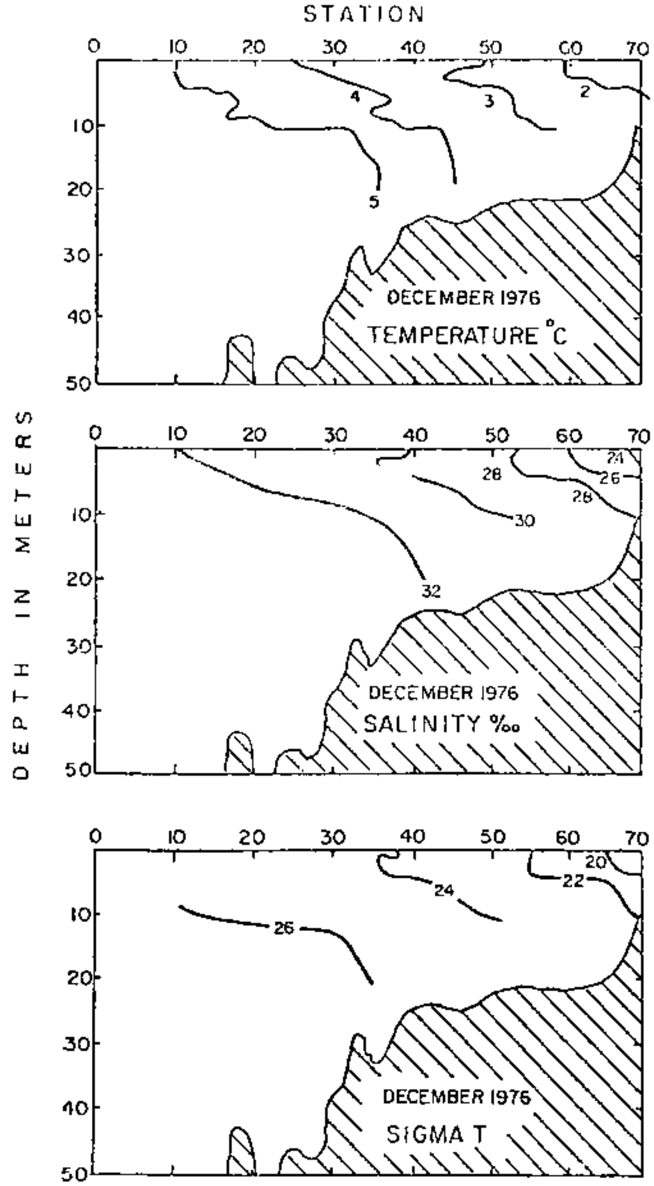


Figure 5-17. Cross-sectional representation of lower Sheepscot estuary and corresponding distribution of temperature, salinity, and density isoclines during December 1976 (Garside et al. 1978).

Thompson (1978) has collected temperature and salinity data since 1969 in conjunction with the installation of the Cowseagan Narrows Causeway and the Maine Yankee Atomic Power Company plant. These data do not facilitate identification of potential effects of the power plant and causeway on estuarine hydrography, since they were collected during low and high river runoff, which could obscure any other effects.

Damariscotta River estuary. Although the Damariscotta estuary is narrow and relatively shallow in comparison to the Kennebec estuary, its flow regime is quite different, because of its very low fresh water inflow. This appears in the Ketchum flushing model results, which indicate long flushing times, generally low nontidal flow, and high salinity throughout most of its length (figure 5-18). Tidal currents are not as strong as in the Kennebec, so that some thermal stratification can be expected in the summer due to the long residence time of marine waters in the estuary. Nontidal velocities are very low. The model represents mean flow and it should be noted that under high flow the increased fresh water discharge could modify the salinity regime and flushing characteristics substantially. Most of the hydrographic data for this estuary are contained in a report by McAlice (1977) and some additional data are contained in Hulburt (1968). The following synopsis is taken largely from the former.

The Damariscotta estuary is an embayment with a small fresh water flow entering from Damariscotta Lake via Salt Bay. The estuary is stratified near the head but approaches well-mixed conditions towards the mouth, with some stratification in both temperature and salinity present over most of the year. The temperature stratification is maximal in summer, with warmer water towards the head and surface, but is weak and reverses itself in winter, with cooler water at the head.

Strong vertical mixing occurs in the floodtide waters upstream of the Fort Island and Fitch Point constrictions. The flow is two-layered. The tide enters progressively and is 18 minutes later at the head than at East Boothbay. The basins between the constrictions at Fitch Point, Fort Island, and the head tend to fill sequentially; the ebb is similarly 24 minutes later there than that at East Boothbay. Drifter studies have revealed that tidal currents are basically longitudinal, with local variations. The ebb is constrained to the channel, while the more diffuse flood is less so, but local eddies are present in the ebb south of the Newcastle bridge, Hall Point, Merry Island, and Wentworth Point. The estuary is partially mixed above Wentworth Point and approaches well-mixed conditions south of that point.

Penobscot River estuary. The boundaries of the Penobscot estuary are difficult to define. The upper limit of salt water varies seasonally between 2 miles (3.2 km) south of the Bangor Dam (Bangor-Hampden region) and 9 to 11 miles (14 to 18 km) south of the dam (almost to Winterport; Haefner 1967). The downstream oceanic limit is similarly difficult to define, as the estuary widens gradually from Sandy Point and divides into two channels at North Haven. In terms of salinity, 30 ppt water occurs at the surface as far up as Sears Island and 31.9 ppt at the mouth of the bay (Seiwell 1932). For the purposes of the model, the upper boundary was set at 8 miles (13 km) below the dam and the lower boundary at a line connecting Rockport, North Haven, and Stonington.

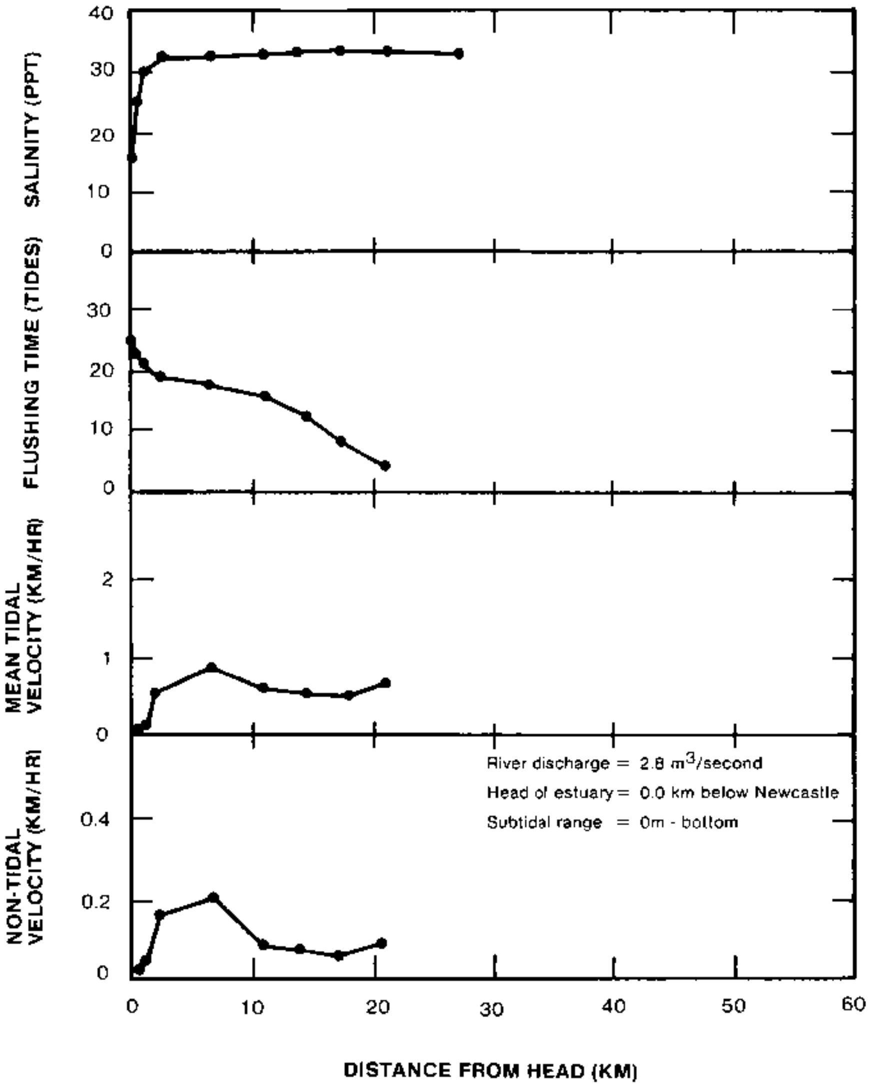


Figure 5-18. Salinity (ppt), flushing time (number of tides), mean tidal velocity (km/hr), and non-tidal velocity (km/hr) as predicted by the Ketchum estuarine flushing model for the Damariscotta estuary. Data are plotted from the head of the estuary (0 km) downstream to the point of predicted oceanic salinity.

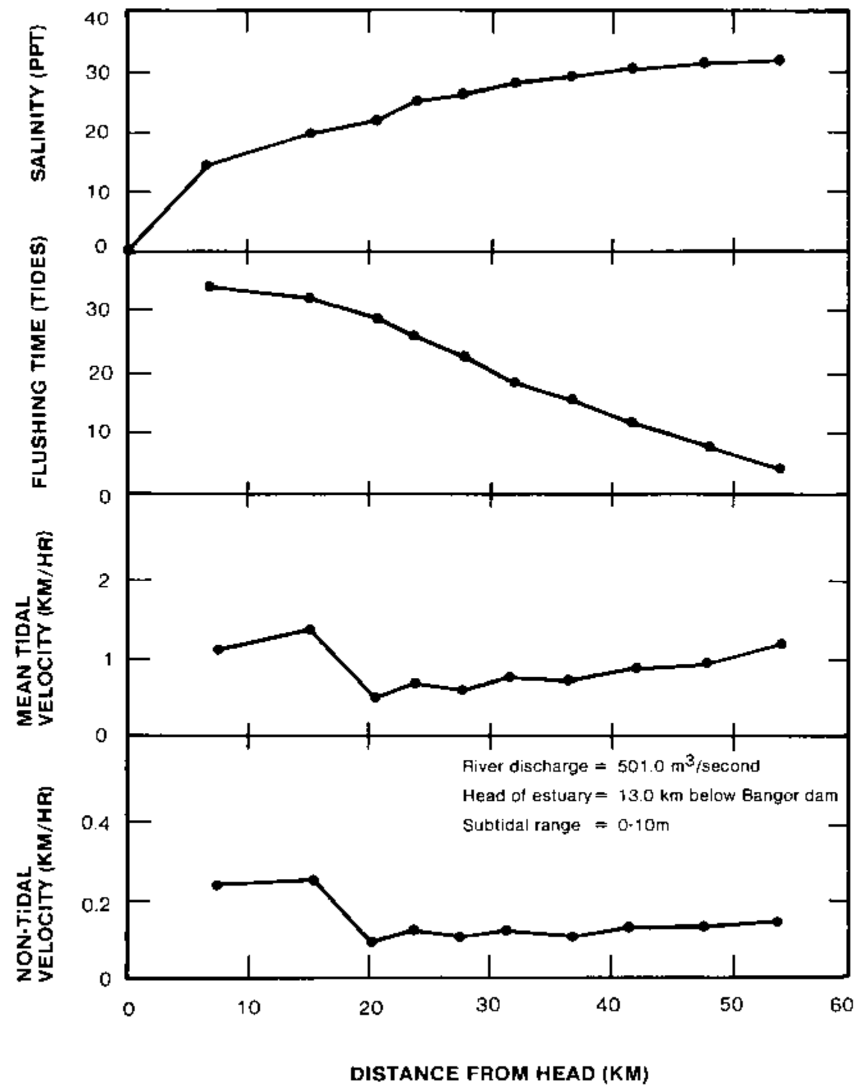


Figure 5-19. Salinity (ppt), flushing time (number of tides), mean tidal velocity (km/hr), and non-tidal velocity (km/hr) as predicted by the Ketchum estuarine flushing model for the Penobscot estuary. Data are plotted from the head of the estuary (0 km) downstream to the point of predicted oceanic salinity.

The model indicates that high salinity water (30 ppt) should be present throughout the lower estuary from Northport/Harborside southward (figure 5-19), which compares well with Siewell's data. Salinity decreases rapidly from the region of Sandy Point northward with 15 ppt at Bucksport, which agrees well with an observed 14 ppt (Garside, unpublished), especially since large tidal excursions are to be expected based on the high tidal currents predicted for the upper narrow section of the estuary. The nontidal currents are weak in the lower part of the estuary and give rise to flushing times that are extremely long when the high fresh water input is considered.

According to data collected by Haefner (1967), the seasonal temperature cycle of the Penobscot estuary probably is typical of Maine estuaries. Warming of the fresh water inflow and the surface results in a seasonal thermocline (layer of water separating warmer, lighter water and colder, heavier water) forming in April and persisting until October. Temperatures decrease with depth and distance downstream, with the highest temperatures (68 to 72° F; 20 to 22° C) in the upper part of the estuary in August. In winter the freeze begins in December and persists until March in the upper estuary. In April uniformly cold (39 to 41°F; 4 to 5°C) water exists at all depths from Bangor to Bucksport, with the coldest (36°F; 2°C) water in the bottom downstream from Verona Island.

The Center for Natural Areas (1978) has compiled a summary of hydrographic data on Penobscot Bay that corresponds to the lower part of the Ketchum model of the estuary. Water column temperature ranges were highest in shallow coves and protected embayments in April (36 to 43°F; 2 to 6°C) and in August (55 to 72° F; 13 to 22°C) with a lower range in deeper open waters. During winter months, temperatures were uniform at 36°F (2°C) in the upper 39 feet (12 m).

In summer the temperature at 1m reached a seasonal maximum of 64°F (18°C) in July and at 10m, 54°F (12°C) in September. A distinct thermocline usually occurs from May to late August. The thermocline forms when surface temperatures are about 46°F (8°C) and disappears in the fall when surface temperatures are about 57 to 61°F (14 to 16°C).

During periods of high runoff, the upper 10m of the water column has diminished salinity (as low as 20 ppt) underlain by 30 ppt water. Under low flow, vertical salinities are much more uniform, with 28 to 30 ppt throughout the water column.

Density stratification varies in response to both temperature and fresh water flow, so that warming temperatures and high flow in the spring give highest stratification while low temperatures and low flow in winter result in least stratification. Haefner (1967) considers the density structure in the Penobscot to be typical of a partially mixed or moderately stratified estuary.

Currents in both the upper estuary and Penobscot Bay (lower estuary) are dominated by tidal flows. The high tidal flow in the upper estuary (figure 5-19) under low fresh water flow conditions could provide the energy for the complete vertical mixing noted by Haefner (1967). Tidal flows in the lower estuary are much less, and in the deeper water will contribute less mixing energy and allow stratification to be maintained. Nontidal flow affects flushing in the upper estuary, where the first 12 miles (20 km) flushes in 2 to 3 days. In the lower estuary, flushing is slow due to the large volume and low nontidal currents.

Union River estuary. No hydrographic data are available for the Union River but the Ketchum model has been used, with the upper limit of the estuary set at the Ellsworth dam and the lower limit at the end of Union River Bay. The model shows that, except for the river and the upper part of the bay, the estuary will have close to oceanic salinities (figure 5-20). This, in turn, results in long flushing times at the upper end of the estuary and indicates that materials discharged there would have a long residence time and high accumulation in the bay. Further, the tidal velocities are low and thus exchange of water due to tidal excursion (water leaving the lower part of the bay on the ebb and being replaced by different water on the flood) would contribute minimally to flushing.

The low velocities in the upper narrow 4-mile (6 km) section and the rapid change in salinity horizontally suggest that little vertical mixing occurs and that vertical salinity stratification will occur at all times. In the bay, stratification is likely to be similar to that in Penobscot Bay.

Somes Sound. This estuary, Maine's only fjord, was studied in August, 1969, by Folger and coworkers (1972). Maximum depths within the Sound reach 50 m, and exchange of these waters with the adjacent coastal water is restricted by 10 to 20 m depths at the mouth.

In a typical fjord, this poor exchange would result in persistent thermal stratification during the summer months and depletion of oxygen in bottom waters as the result of decay of organic matter. However, Folger's data do not show evidence of this. Some thermal stratification (7 °F;4 °C) over the upper 33 feet (10 m) occurs but dissolved oxygen concentrations are not low. Salinity approximated oceanic levels throughout, with lower salinity occurring only close to small streams near the head. Although this estuary is a fjord morphologially, high tidal exchange results in sufficient mixing that precludes its functioning as a fjord.

A lack of fresh water flow data precludes application of the Ketchum model to this estuary.

Narraguagus River estuary. No hydrographic data exist for the Narraguagus estuary, but the Ketchum flushing model can be applied (figure 5-21). Although slightly larger than the Presumpscot and Royal estuaries, this estuary is very similar to both. The entire salinity range from fresh to oceanic is contained in the segment between Cherryfield and Milbridge (5 miles; 8 km). The volume is small and both tidal and nontidal currents are high. The estuary probably is mixed well throughout and the residence time is extremely short, so that the estuary ought to be well flushed.

Machias River estuary. The Machias estuary is very similar to the Narraguagus. No hydrographic data exist and the model predicts great similarity between them (figure 5-22). Most of the salinity regime is contained in the first 4 miles (7 km) of the estuary, tidal and nontidal currents are high. This estuary ought to be mixed well and has short residence times and rapid flushing.

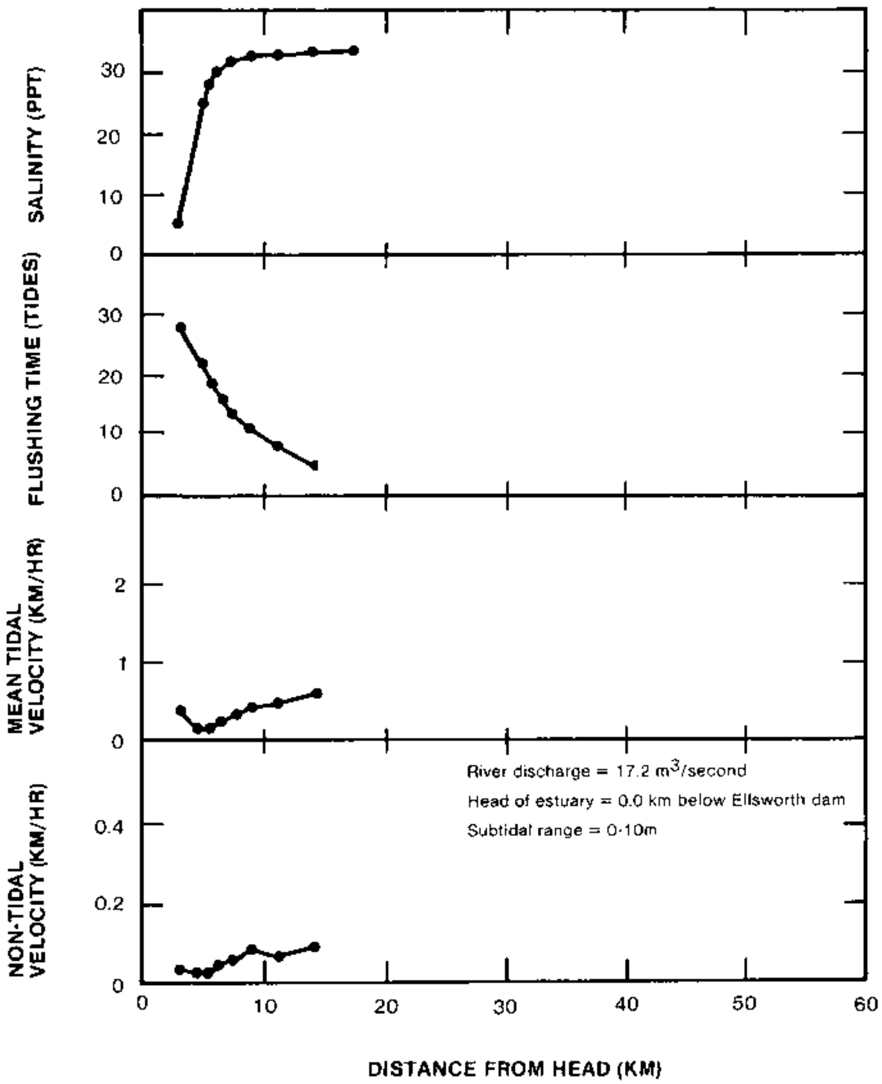


Figure 5-20. Salinity (ppt), flushing time (number of tides), mean tidal velocity (km/hr), and non-tidal velocity (km/hr) as predicted by the Ketchum estuarine flushing model for the Union estuary. Data are plotted from the head of the estuary (0 km) downstream to the point of predicted oceanic salinity.

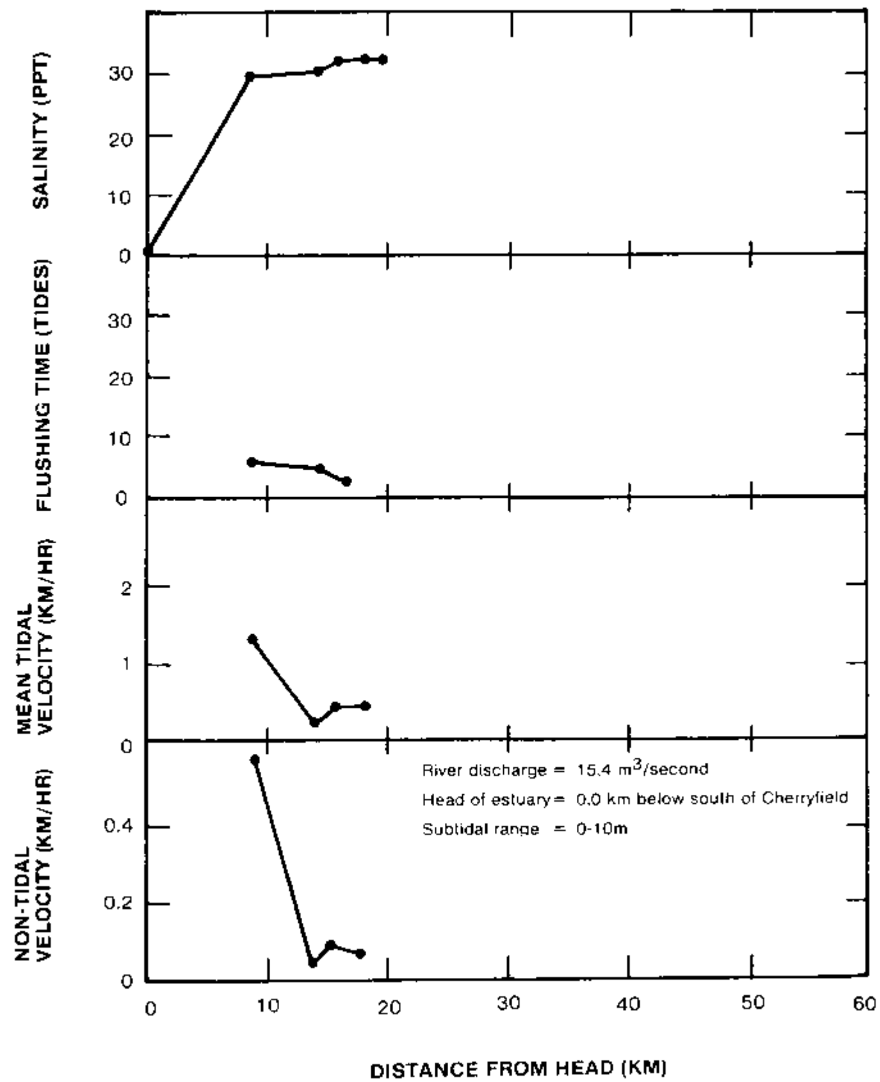


Figure 5-21. Salinity (ppt), flushing time (number of tides), mean tidal velocity (km/hr), and non-tidal velocity (km/hr) as predicted by the Ketchum estuarine flushing model for the Narraguagus estuary. Data are plotted from the head of the estuary (0 km) downstream to the point of predicted oceanic salinity.

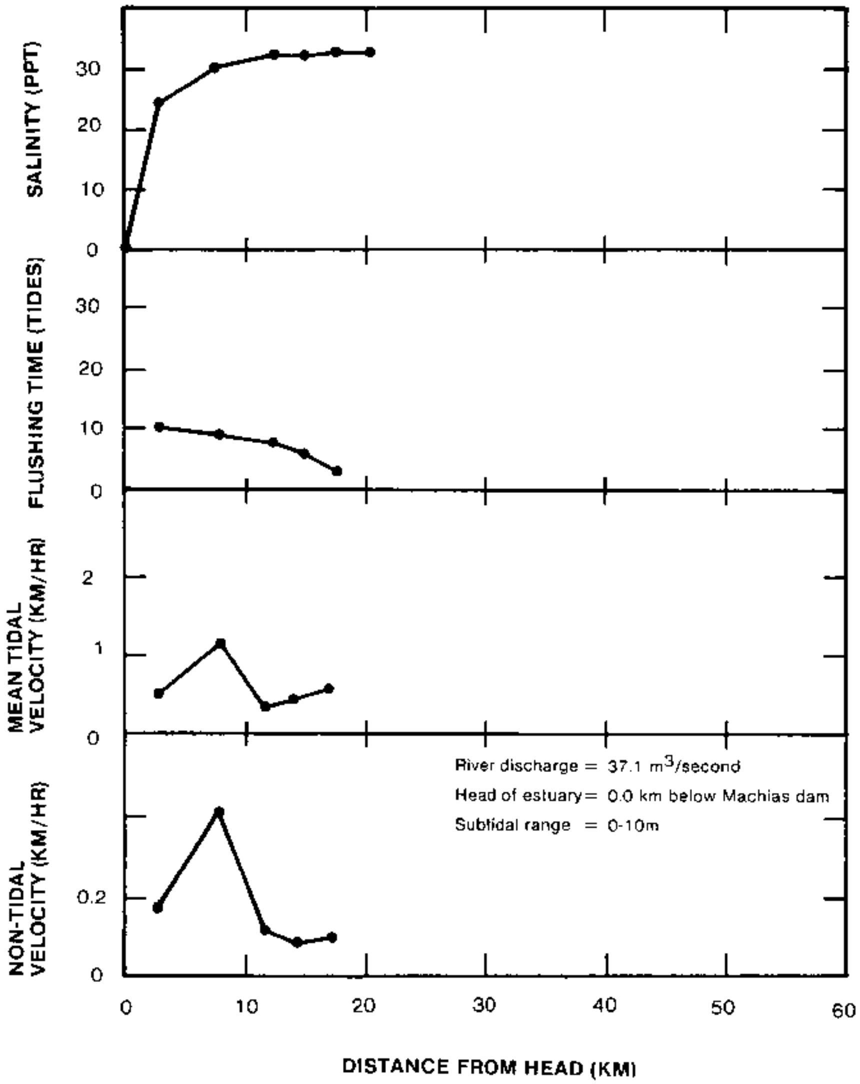


Figure 5-22. Salinity (ppt), flushing time (number of tides), mean tidal velocity (km/hr), and non-tidal velocity (km/hr) as predicted by the Ketchum estuarine flushing model for the Machias estuary. Data are plotted from the head of the estuary (0 km) downstream to the point of predicted oceanic salinity.

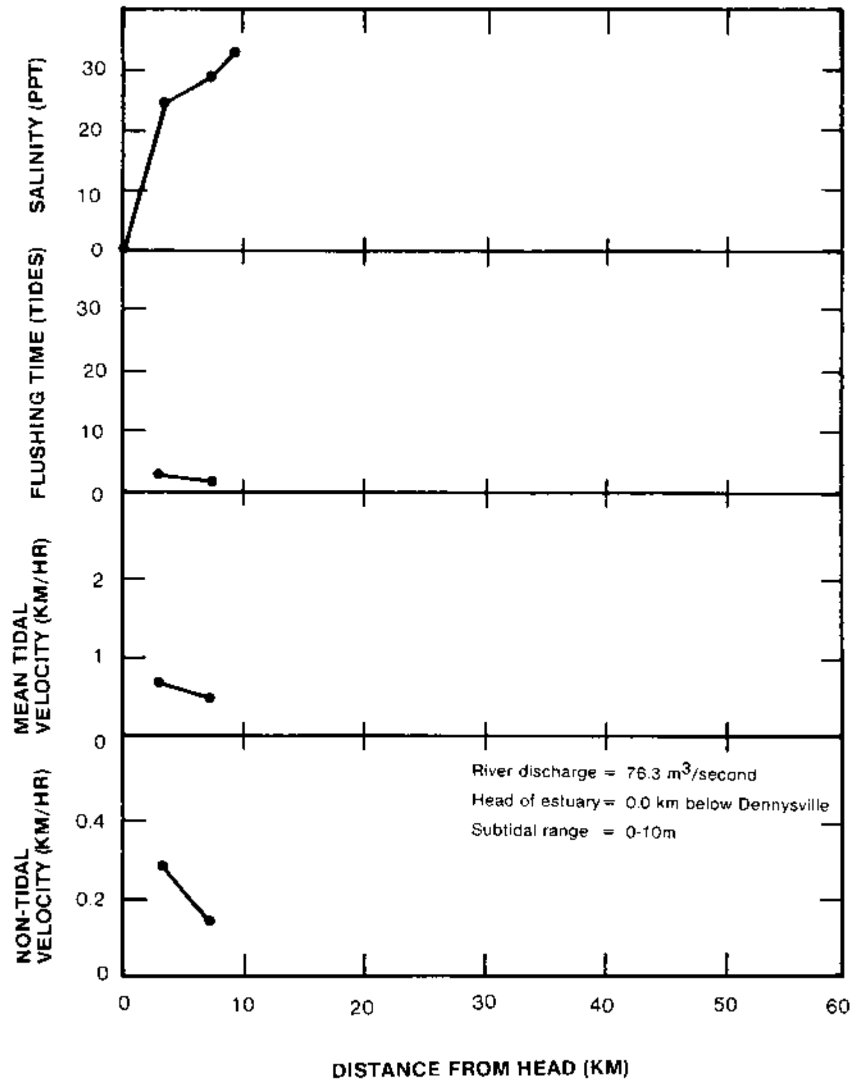


Figure 5-23. Salinity (ppt), flushing time (number of tides), mean tidal velocity (km/hr), and non-tidal velocity (km/hr) as predicted by the Ketchum estuarine flushing model for the Dennys estuary. Data are plotted from the head of the estuary (0 km) downstream to the point of predicted oceanic salinity

Dennys River estuary. The Dennys River is the major fresh water inflow to Cobscook Bay but no hydrographic data on it exist. The Ketchum model has been applied to this estuary between the upper boundary at Dennysville and the lower boundary at the constriction between the inner and outer parts of the Bay, across from Cobscook State Park. This estuary is similar to the Narraguagus and Machias and probably is mixed well and flushed well as a reult of the high tidal and nontidal flows (figure 5-23).

St. Croix River estuary. The Ketchum model has been applied to this estuary (figure 5-24). The upper boundary was set at the Calais Road Bridge and the lower boundary at the point where the estuary widens rapidly in the vicinity of Robbinston on the United States side and St. Andrews on the Canadian side. The model results indicate that only the upper segment, the first few kilometers below Calais, will have salinities below oceanic levels. The low fresh water flow into the rapidly widening estuary results in this section flushing fairly slowly, but the high tidal range and exchange farther down the estuary will result in this portion flushing rapidly. Ketchum and Keen (1953) computed a flushing time of 8 days for the estuary above St. Andrews, compared to 6 days in our application of the model. Both the Dennys and St. Croix Rivers discharge into the Passamaquoddy Bay/Cobscook Bay complex. It is evident from the salinity distribution (figures 5-23 and 5-24) that this area would not be defined as estuarine on the basis of its salinity but it will be discussed briefly below, nevertheless.

Passamaquoddy and Cobscook Bays. This complex system of bays and interconnecting channels has been the focus of study, at least in part, because of potential oil refinery and marine terminal sitings and tidal power development. The most complete study of the region, summarizing work up to 1959, is appendix 1 of the International Passamaquoddy Fisheries Board Report to the International Joint Commission (Bumpus 1959). The reader is referred to this detailed source, which has been used in preparing this brief summary.

Cobscook Bay has a mean depth of 26 feet (8 m) at low tide. A narrow channel about 66 to 98 feet (20 to 30 m) deep exists in the lower bay. The bay bottom is regular and slopes to the channel, has little relief, and is a submerged valley. Passamaquoddy Bay was probably shaped by glacial and ice sheet action, the latter forming the shallow, gently sloping northern part of the bay and the former the deep steeply sloping region from the northern side of Deer Island to Midjik Bluff. The average low water depth is 79 feet (24 m).

Tidal exchange of water establishes extremely strong currents and mixing. Fresh water input from the St. Croix, Magaguadavic, Digdeguash, and the Dennys Rivers is small compared to the tidal exchange and contributes little to the current regime. For example, the intertidal volume of Cobscook Bay is 490 million cubic meters while during half tide (6 hrs and 12 min) the Dennys River mean discharge is slightly under 2 million cubic meters. About 20% of the water in Passamaquoddy Bay and 50% of the water in Cobscook Bay exchange on each tide.

Forrester (1959) presents tidal current data and maps for the Passamaquoddy Bay and mouth of Cobscook Bay region at hourly tide stages. These current patterns are complex and the reader is referred to the source for specific information.

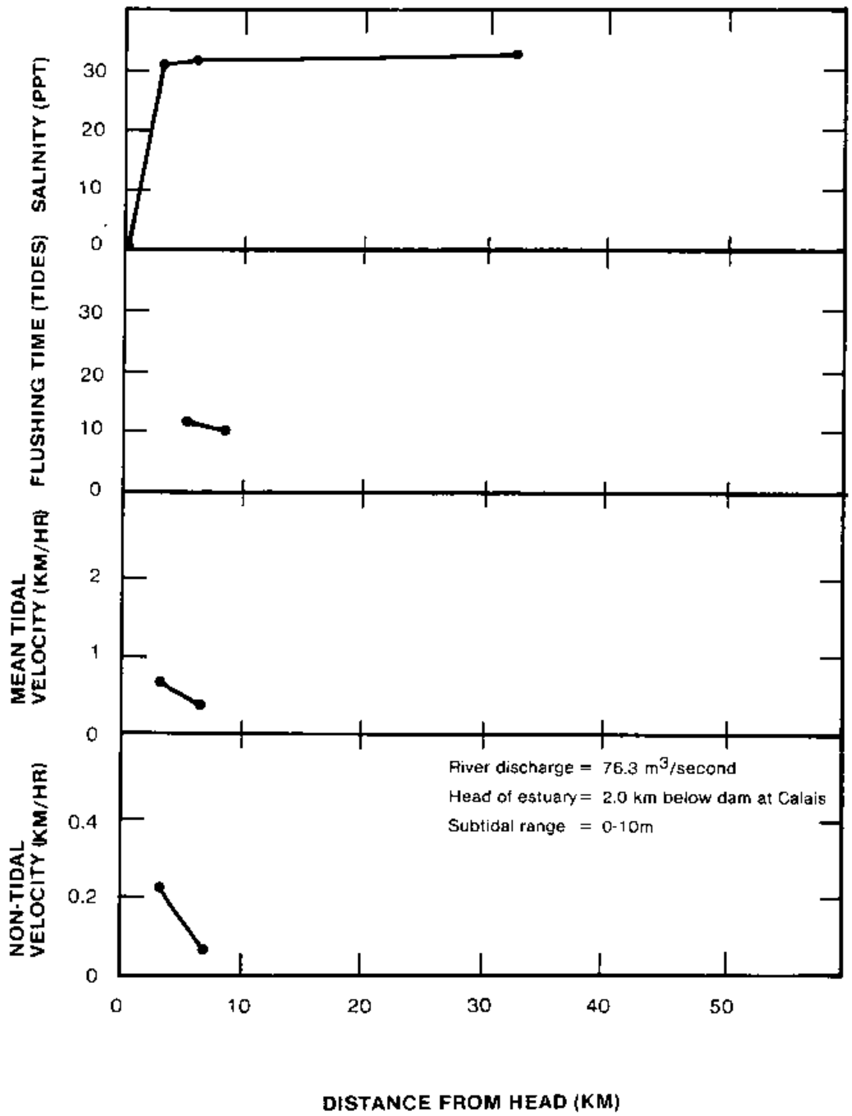


Figure 5-24. Salinity (ppt), flushing time (number of tides), mean tidal velocity (km/hr), and non-tidal velocity (km/hr) as predicted by the Ketchum estuarine flushing model for the St. Croix estuary. Data are plotted from the head of the estuary (0 km) downstream to the point of predicted oceanic salinity.

While tidal currents are extreme and dominate flow, significant residual nontidal flows occur. Chevier (1959) measured these monthly throughout 1957, using drift bottles and radar-tracked drift poles. He concluded that wind speed and direction were very effective in determining the residual flow. Summer winds from the south tend to confine surface waters to Passamaquoddy Bay, while winter northwest winds remove them. Cobscook Bay tended to have an outward residual flow at all times. Monthly drift bottle trajectories are presented in Chevier (1959).

Forgeron (1959) presents seasonal temperature and salinity data measured at the surface and near bottom at 10 stations within this region. With only rare exceptions, very little difference exists between surface and bottom temperatures and salinities. Maximum temperature differences of 6 °F (2° C) between surface and bottom occurred at the deeper [131 feet (40 m)] stations and maximum differences in salinity of 1 to 3 ppt were found only during high freshwater flow (April or May). Seasonal water temperatures varied sinusoidally from extreme winter lows of 32 to 36°F (0 to 2°C) to summer highs of 54 to 57°F (12 to 14°C). Comparable salinity variations were small, with maximum variations from 29.5 to 32.5 ppt and a smaller range for many individual stations. These observations reflect the generally oceanic nature of these waters and the extreme vertical mixing in them that results from tides. Tidal variations reflect both tidal excursion and lateral gradients. The tidal excursions are large but lateral gradients are small, so the resultant tidal variations also are small.

Climate

Meteorological factors that influence the other abiotic factors (hydrography and geology) as well as the biota are described below.

Wind. Winds play an important role in moving surface waters (see "Hydrography" above). Their effect depends on strength, duration, and fetch (the extent of their influence). The predominant winds in coastal Maine are from the southwest in summer and from the northwest in winter (see "Climate," page 2-9 in chapter 2). Wave action produced by wind provides moisture to the intertidal zone at levels higher than a calm sea provides. This added moisture allows intertidal communities to develop higher in the intertidal zone than they would in protected areas (e.g., inner bays; see "Introduction to the Subtidal and Intertidal Subsystems" below). Winds associated with storms are discussed below.

Heat budget and precipitation. Water temperature in estuaries depends on the degree of heat interchange at the air-water interface, the temperature of fresh water inflow, and tidal currents. The level of salinity in an estuary is determined partly by the amount of precipitation and surface evaporation.

Water temperatures sometimes are critical to the biota, because many plants and animals need a minimal summer temperature to induce reproduction, and if it is not reached in a given year little or no recruitment takes place. Some species in Maine are at the northern edge of their ranges, are scarce, and cannot reproduce because of low temperatures. An example is the quahog, which survives only in small pockets of warm water. Summer water temperatures are lower in the northeastern part of the State (regions 4 to 6) than in the southwestern section (regions 1 to 3; Bousfield and Laubitz 1972), so species requiring warmer temperatures may not be able to survive in abundance in regions 5 and 6.

Fog. Fog affects the biota by insulating the intertidal organisms from desiccation and allowing less hardy (less adaptable) species to survive in low intertidal areas. Eastport has more fog (1 day in 3) than Portland (1 day in 5), which may be one reason why the Cobscook Bay intertidal fauna is richer than that of Portland.

Atmospheric pressure. Atmospheric "highs" and "lows" cause temporary changes in sea level and may affect the water levels or circulation in estuaries temporarily, through coastal storms or ice formation and movement. The most extreme climatic variations that occur on the Maine coast are extratropical cyclones producing "northeasters," and tropical cyclones producing "tropical storms" and hurricanes. Coastal flooding, habitat destruction, and alteration are often associated with these storms. Mass mortalities of animals and "uprooting" of macroalgae may occur. The flushing action associated with flooding is particularly important in redistributing detritus from the high intertidal area (emergent wetlands and wrack area) and terrestrial system into the marine system. Flooding can also distribute pollutants (e.g., oil) into the high intertidal zone, where emergent wetlands and wrack communities may be impacted.

Ice formation sometimes has major effects on biota, especially estuarine invertebrates and waterbirds. Ice forms along the shore in protected areas (mostly estuaries) for varying lengths of time each winter. Ice movement may dislodge species such as clams and other burrowing invertebrates. Under extreme conditions, the water can freeze all the way to the bottom and kill all the biota. During years of extensive ice formation, large areas of shallow substratum, containing biota, may be transported in ice rafts. Disturbances during winter (clamming) dislodge animals, making them more susceptible to icing and freezing temperatures.

The freezing of mudflats may harm waterbirds that traditionally inhabit specific flats in winter. Long periods of icing may result in the starvation of some birds. Where tidal fluctuations are greatest (in eastern Maine, especially Cobscook Bay; region 6), icing is less likely to occur at a given winter temperature because of the relatively forceful tidal currents.

Additional information on climate parameters is found in chapter 2, under "Climate," page 2-9 .

BIOTA

The living components of estuaries may be divided into producers, consumers, and decomposers, based on their function in the food web. These groups, their habitats, and their roles in the estuarine system are discussed below. Communities of organisms found in the specific estuarine subsystem and classes are described. Food web and energy flow interactions between these components are described in subsequent sections of this chapter.

Producers

Producers construct new organic material from solar energy and inorganic matter. In the estuarine system, the major producers include the macroalgae, rooted macrophytes, phytoplankton, and benthic diatoms. To an undetermined extent, certain microbes may be involved in the biological production of the estuarine system. The major difference between the production of the marine and estuarine systems is that the productivity of the marine system is dominated by phytoplankton, whereas in estuarine areas productivity is shared by several components, i.e., phytoplankton, macroalgae, benthic diatoms, and rooted aquatic plants.

Phytoplankton. Phytoplankton is a collective term for the several major groups of microscopic algae that are suspended in the water column. In Maine, diatoms occur most frequently and in the largest numbers. These organisms occur in chains and single cells in bizarre shapes and sizes ranging from about 10 to 100 microns. Their cell wall is composed of silica and they have very low motility. The genus *Chaetaceros*, along with *Skeletonema costatum* and *Thalassiosira*, are dominant diatoms in temperate waters.

Dinoflagellates, the next most abundant group, are more abundant offshore and in waters south of Maine. They exist mostly as solitary cells; however, some species form chains. Their cell wall is cellulose, and they generally have a flagellum for active swimming. Sizes range from about 3 to 100 microns and the blooms of one species in particular are noted for occurring in swarms known as red tides (see "Red Tide," page 12-31, chapter 12).

Phytoplankton growth is controlled by estuarine hydrography and climate; specifically, sunlight, nutrients, salinity, temperature, rainfall (and the accompanying river discharge), water transparency, and wind speed and direction. These factors and their interrelationships are discussed with interactions affecting phytoplankton productivity, below.

Estuarine phytoplankton are grazed upon by animals, including species of zooplankton and fishes. Those not consumed in this way sink to the bottom when they die and either decompose or are consumed by benthic invertebrates.

Macroalgae and rooted vegetation. Macroalgae, commonly referred to as seaweeds, are the largest forms of algae and are found in great abundance in marine and estuarine areas along the coast of Maine. They range in size from minute plants (e.g., *Polysiphonia* spp.) to plants several meters in length, such as the kelps. Seaweeds along rocky coasts form the band of attached, nonrooted vegetation that can be seen between the intertidal zone and shallow waters. Seaweeds are divided into three phyla: the brown algae (Phaeophyta), the red algae (Rhodophyta) and the green algae (Chlorophyta). Rooted vegetation include the plants of the emergent wetlands (*Spartina* spp. and *Juncus* spp.) and eelgrass beds (*Zostera marina*).

The brown algae dominate the biomass or bulk weight of rocky shore intertidal and subtidal plant communities. In intertidal rocky shore habitats the brown alga *Ascophyllum* and various species of *Fucus* (collectively called fucoids) commonly account for >90% of intertidal plant weight. These plants commonly are known as rockweeds, bladderwrack, or knotted wrack.

In subtidal rocky shore areas, the brown algae, Laminaria and Agarum (collectively known as laminarians), dominate biomass. These laminarians, or kelp, extend from low-water marks to depths of approximately 30 to 60 feet (10 to 20 m).

Macroalgae require adequate light and suitable stable surfaces for attachment. The large rockweeds and kelp need large stones or rocks for attachment. Unstable surfaces, such as mud, sand, or gravel, are generally devoid of the larger algae and may support only relatively minor quantities of small plants and then only in wave-sheltered areas. The growth of macroalgae also is controlled by water temperature, salinity, and the availability of nutrients.

The convoluted rocky shore along much of the coast of Maine, including its estuaries, provides large areas of dense beds of plants. Rocky shore seaweed communities provide habitat for numerous marine and estuarine animals. Macroalgae are consumed by grazers, such as sea urchins and fish. The amount of material consumed is unknown but in areas that have periodic high densities of sea urchins, such as the Sheepscot River estuary and Cobscook Bay, large quantities of plant material are consumed. Reestablishment of seriously depleted macroalgal populations may take many years.

Benthic diatoms. Benthic (bottom-dwelling) diatoms are similar to diatoms living in the water column (see "Phytoplankton" above), but they live on bottom substrata in intertidal and shallow subtidal areas. Their contribution to productivity in the estuarine system is undetermined. Benthic diatoms on an intertidal mudflat in the Bristol Channel (Great Britain) had twice the productivity of the phytoplankton in the ovelying water column on a square meter basis (personal communication from R. M. Warwick, Institute for Marine Environment Research, Plymouth, England; April, 1979). Whether this relationship applies to similar habitats in other regions is not known.

Benthic diatoms are consumed by invertebrate deposit-feeding and grazing species, such as the common periwinkle and the mud snail. The degree of dependence of such species on this food source is unknown but in localized situations it may be significant.

Microbial producers. Microbial producers are bacteria and other microorganisms that are suspended in the water column. They may be either photosynthetic (i.e., dependent on light for growth) or nonphotosynthetic (e.g., chemosynthetic). Although little is known about their role in the food chain or their importance as producers, J. Teal (personal communication; Woods Hole Oceanographic Institute, Woods Hole, MA; May, 1980) points out that these organisms are closely related to the cycling of sulfur and carbon in New England salt marshes.

Consumers

Consumers are animals that feed on the products of primary production as well as on each other. The major groups are zooplankton, benthic invertebrates, fish, birds, and marine mammals.

Zooplankton. Zooplankton is the collective term for the diverse assemblage of animals that float or swim weakly in the water column. The principal components of zooplankton are holoplankton (all the life cycle of which is spent in the water column) and meroplankton (only a portion of the life cycle is planktonic). The copepods are the most important members of the holoplankton. These small crustaceans are largely filter feeders and remove particles from the water column. Meroplankton in estuaries consist largely of larval stages of benthic invertebrates and fishes that may outnumber the holoplankton for short periods, particularly in the spring.

The holoplankton are a principal trophic link between the primary producers (phytoplankton and detritus) and aquatic carnivores (e.g., herring). Grazing by zooplankton controls, to a certain degree, the abundance of phytoplankton. Detritus, from dead phytoplankton, emergent wetland vegetation, and macroalgae, (Jeffries 1972) may be an important food source for zooplankton during periods of low phytoplankton production (Riley 1963). Certain zooplankton species may be part of more than one trophic level. For example, filter-feeding herbivores, such as Acartia clausi, are to some extent zooplanktivorous (Hodgkin and Rippingdale 1971) and even cannibalistic (Petipa 1966). Some meroplankton (e.g., soft-shelled clam larvae) feed on phytoplankton. Other macroplankton (e.g., fish fry) live on yolk supplies in their egg sacs.

A close connection may exist between food supply and the initiation of reproduction in zooplankton. This is especially true of copepods, whose spawning and breeding times correlate closely with seasonal phytoplankton blooms (Marshall and Orr 1972). For the most part, zooplankton in estuaries are dependent upon phytoplankton for food (Smayda 1973). In some areas, (e.g., Narragansett Bay, Rhode Island) a delay takes place between the onset of phytoplankton blooms and the initiation of zooplankton reproduction (Martin 1964).

Benthic organisms receive food through (1) the vertical movements of live zooplankton in the water column, (2) the sinking of detritus in the form of fecal pellets, dead organisms, and molted exoskeletons, plus phytoplankton and detrital plant material. Davies (1975) indicates that the primary input to the benthos of a Scottish sea loch is in the form of sinking zooplankton fecal pellets, and this rate of input is about one-third the primary production of the overlying waters. The contribution of fecal pellets may be important in the shallow waters and estuaries of coastal Maine, where dense zooplankton populations are present. Zooplankton also may have an important role in the release of organic matter (see "Organic Matter Cycle," below) and nutrients, including nitrogen and phosphorus (see also "Nutrient Cycle," page 4-48 in chapter 4), which then become available to phytoplankton for growth.

Benthic invertebrates. Benthic invertebrates are either infaunal (live in the bottom sediments; e.g., clams and worms) or epifaunal (live on the bottom; e.g., mussels and scallops). Three groups, the annelids, molluscs, and crustaceans, constitute the majority of estuarine benthic invertebrates in Maine. Annelids are segemented worms; molluscs, such as clams and snails, have shell-enclosed soft bodies; and crustaceans are crablike organisms. Fifteen hundred and eighty-two taxa have been found in coastal Maine. These species are listed by region in appendix E of chapter 4. The commercially important invertebrates (e.g., clams, scallops, and lobsters) are described in detail in chapter 12, "Commercially Important Invertebrates."

Communities of benthic invertebrates occupy an important position in the estuarine system. They convert the direct and indirect products of primary production to animal protein, which is passed to higher trophic levels through predation.

The burrowing and feeding activities of benthic invertebrates alter sedimentary structures and return to the water column nutrient materials that have been deposited or bound in the sediments. These activities also disturb bottom sediments, which sometimes make the area unsuitable (excessively turbid) for animals that feed by filtering. Benthic invertebrates are dependent on the overlying water for oxygen and food and to remove wastes. Major foods are phytoplankton, particulate organic material of plant origin, bacterial flora on detritus, benthic diatoms, living plants, and living animals. Of these food sources, particulate organic matter and detritus are particularly important to benthic invertebrates in estuaries. Some feed on only one type of food, whereas others feed on many types (Sanders et al 1962). The food consumed by a particular animal may change with the animals' size or age (Sanders et al. 1962). A small individual may be able to consume only one type of food, but as it grows it may eat larger and more diverse food particles.

Benthic invertebrates live on all types of substrata and are affected in some way by most types of habitat disruption. Most (nearly 95%) of the animals occur within 5 cm (2 in.) of the water-sediment interface (Stromgren et al. 1973), because organic material (i.e., food) is more concentrated there.

Many species that are considered infaunal leave the sediment at night and swim in the water column (e.g., bloodworms and sandworms; Dean 1978a and b) and crustaceans that are thought to be planktonic (e.g., amphipods) enter the substratum during the daylight hours (Thomas and Jelley 1972).

Larval stages of many benthic invertebrates live in the water column, (see "Zooplankton" above) usually up to 5 to 6 weeks in Maine (personal communication from E. Bousefield, National Museum of Canada, Ottawa, Canada; June, 1977). Other invertebrates, such as predatory snails, amphipods and isopods, develop directly into small adults and rarely enter the water column. Pelagic larvae have the ability to disperse widely. However, natural mortality of pelagic larvae is high, possibly as high as 95% to 99%. Invertebrates with pelagic larvae produce large numbers of young, thus ensuring the survival of their species.

The primary factor influencing the distribution and abundance of benthic species is the nature of the substratum. Pelagic larvae metamorphose into juveniles when they come in contact with a suitable substratum and some (e.g., clams and mussels) can delay metamorphosis for a limited time until a suitable substratum is located. The period of metamorphosis and settlement is probably the most critical period in the life of a benthic organism (Thorson 1966). Predation on newly settled juveniles sometimes is severe.

Substratum requirements are related to feeding type and mode of living. Deposit feeders (e.g., clams) are most abundant in fine sediments of silt and clay containing organic detritus. The deposit feeders pass the sediment through their bodies, digest the bacteria on it, and excrete fecal material which is colonized again by bacteria and reconsumed (Young 1971). Organisms that feed on suspended material (filter feeders, e.g., mussels) usually live where the currents are strong enough to provide a sufficient amount of food. They are found most commonly in sandy or rocky environments, where deposit feeders are relatively scarce. Other requirements include shelter, hard substrates for nonmobile organisms (e.g., anenomes), appropriate sediments to make cases, and algal substrates for some polychaetes and bryozoans.

Fish. The estuarine system supports a slightly lower diversity of fish species than the marine system. Fishes of coastal Maine are discussed in detail in chapter 11, "Fishes." Temperature and salinity are major factors determining the seasonal and local distribution of fish in estuaries. Fish populations in Maine's estuarine systems are dominated by resident demersal (bottom-dwelling) species, such as the Atlantic tomcod, flounders, sculpins, skates, cunner, rock gunnel, and sea raven. The estuaries also host a variety of fishes on a seasonal basis, including the anadromous fishes (alewife, American shad, blueback herring, sturgeons, Atlantic salmon, sea lamprey, and rainbow smelt), Atlantic herring, Atlantic menhaden, hakes, and the catadromous American eel. The rainbow smelt is perhaps the only year-round resident in the upper estuaries. Most fish leave the estuaries for deeper, warmer waters in winter.

Fish are important components in the energy flow of the estuarine system because of their abundance (biomass) and representation on many levels of aquatic food chains (primary, secondary, and tertiary consumers). Many fish utilize the estuaries as primary spawning or nursery areas (wrymouth, rock gunnel, sculpins, sea snails, snakeblenny, sticklebacks, mummichog, tomcod, silversides, winter flounder, and Atlantic herring).

Estuarine fish are classified on the basis of their principal feeding habits as planktonic, nektonic, or demersal/semidemersal (figure 5-25). Estuarine systems are dominated by demersal/semidemersal-feeding finfish populations, followed by nektonic feeders, and then planktonic feeders. The cunner and Atlantic cod are both nektonic and demersal feeders. Planktivores, such as the herrings (Atlantic herring, blueback herring, alewife, and American shad), Atlantic menhaden, and American sand lance are water column feeders that feed on pelagic crustaceans, mostly (copepods, mysids, euphausiids, and amphipods). Nektonic feeders consume pelagic crustaceans and fish. These active feeders include the majority of the area's summer migrants (the hakes, spiny dogfish, bluefish, Atlantic mackerel, and striped bass) as well as rainbow smelt, Atlantic salmon and white perch. The dominant demersal-feeding fishes are flounders, codfish, and skates, the sculpins, the ubiquitous American eel, Atlantic tomcod, the anadromous sturgeons, and the sticklebacks. Major food items are crustaceans, echinoderms, bottom fish, fish eggs, benthic diatoms, molluscs, and polychaete worms.

Birds. Waterbirds, including seabirds, shorebirds, wading birds, and waterfowl, use the estuarine system for breeding (mostly the islands), feeding (all habitat classes), moulting, migrating, and wintering. Twenty percent of waterbirds are permanent residents. In addition, several raptors, including the resident endangered bald eagle, utilize the estuarine system. Waterbirds are described in detail in chapters 14 and 15, "Waterfowl" and "Waterbirds" respectively. The bald eagle and other raptors are described in chapter 16, "Terrestrial Birds." Most estuarine bird species are high level consumers. Seabirds feed on zooplankton, benthic invertebrates, cephalopods, finfish, and

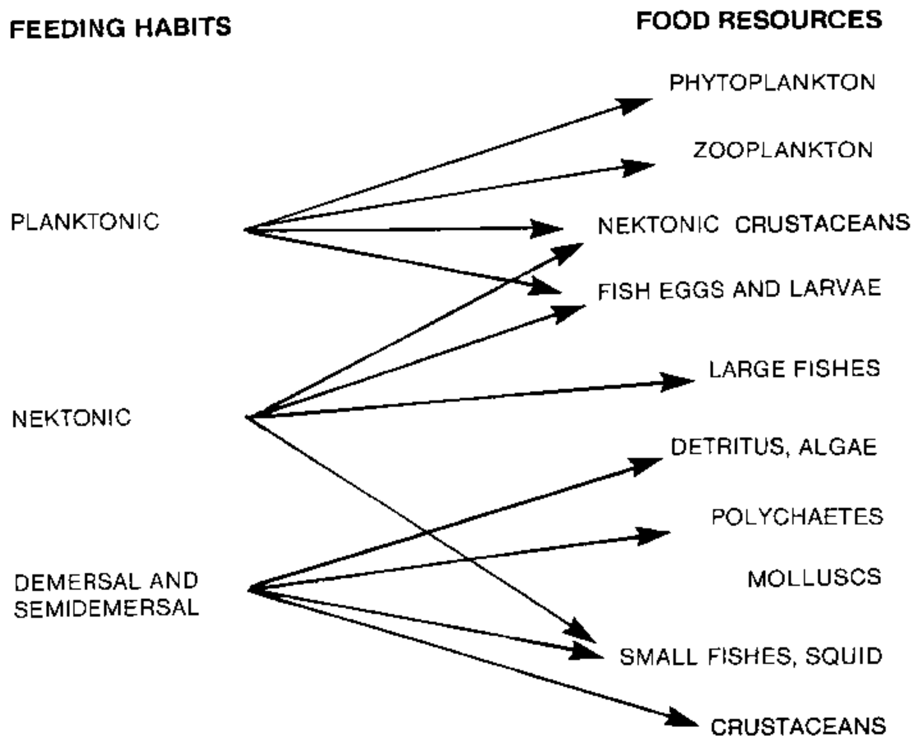


Figure 5-25. Feeding habits of estuarine fishes.

invertebrates and vertebrates of the strand line (the supratidal zone where a community develops on the macroalgae that washes ashore). Shorebirds eat mostly intertidal mudflat invertebrates (i.e., oligochaete and polychaete worms, amphipods, and the Baltic clam), squid, other invertebrates, finfish, zooplankton, and strand line invertebrates. Wading birds prey on reptiles, amphibians, finfish, insects, benthic invertebrates, birds, small mammals and some plant materials. Waterfowl feed mostly on benthic and other invertebrates, fish, and plant material. Brant are important herbivores, feeding on intertidal and subtidal algae (e.g., Ulva), vascular plants (e.g., eelgrass), and the invertebrate fauna associated with these communities. Ospreys are primarily fish eaters. Bald eagles in coastal Maine feed mostly on fish, waterfowl, and seabirds.

Islands in estuaries are used for nesting (e.g., bald eagles, ospreys, wading birds, gulls, eiders, and double-crested cormorants), rearing young (e.g., bald eagles, ospreys, eiders, black duck, common and roseate terns, laughing gulls, and wading birds), moulting (e.g., eiders and Bonapartes gulls), roosting (most groups), wintering (e.g., bald eagles, black ducks, mallards, Canada geese, seaducks, purple sandpipers, gulls, loons, grebes, kittiwakes, and great cormorants), and as migratory stopover areas (e.g., shorebirds, brant, geese, dabbling ducks, peregrine falcon, bald eagles, ospreys, diving ducks, Bonaparte's gulls, and ring-billed gulls).

The highest densities of waterbirds occur in late summer after the young have fledged and during the "fall" migration (which begins in early July). Waterfowl are most abundant during the fall and spring migrations, shorebirds during the fall migration, wading birds during the breeding season and fall migration, and seabirds during the summer and fall migrations. Peak numbers of shorebirds and seabirds correspond with the peak periods of invertebrate production. Bald eagles are present throughout the year. Peak abundance occurs during spring and summer.

The role of waterbirds in energy flow, nutrient cycling, and community structure in the estuarine system is little known. Studies in Massachusetts and in Europe have shown that shorebirds [oystercatcher, red knot, red shank (Goss-Custard 1977), black-bellied plover (Schneider 1978), and purple sandpiper (Feare 1966)] are important predators on selected prey items (i.e., amphipods, Baltic clams, mud shrimps, bamboo worms, sandworms, and other polychaetes). Studies on wading birds in Florida have shown that they remove most prey from temporary pools of water (Kushlan 1976). Eiders and other seaducks may influence benthic community structure (as yet not studied in Maine) while geese can affect plant community structure and composition in salt marshes (Jefferies et al. 1979). Changes in eelgrass populations were significantly reduced during the 1930s due to a "wasting disease" (the actual cause of which is questionable), which in turn reduced east coast populations of brant to very low numbers. They are now making a recovery. Their diet has changed from eelgrass to sea lettuce.

The amount of energy passing through estuarine food webs that involve birds is unknown. Because of their numerical abundance and large biomass, gulls, eiders, and cormorants probably process the greatest prey biomass. Shorebirds and waterfowl are the next group in importance. The remaining waterbird groups process lesser amounts. In general, waterbirds in Maine are most abundant at the same time that Maine invertebrates and fish (primary prey items) are at peak densities (August to September) and less abundant when prey are either at lower densities or physically unavailable (December to April). For example, peak densities of shorebirds correspond to peak densities of the amphipod Corophium (personal communication from P. Hicklin, Canadian Wildlife Service, Sackville, New Brunswick, Canada; March, 1979). The Baltic clam is the prey of medium- and longer-billed shorebirds (e.g., red knot, willet, sanderling, and black-bellied plovers) in summer, when it has burrowed below the reach of most shorebirds (reach is determined by bill length; Reading and McGrorty 1978). In New Jersey, sanderlings have been reported to spend more time feeding at midtide levels of sand beaches than on lower and upper portions of the beach (Burger et al. 1977). Amphipods are also most abundant in this same zone on Maine sand beaches. Research is needed to determine if sanderling use of these midlevel beach areas in Maine is similar to that of New Jersey.

Migratory waterbirds (especially those that remain in coastal waters for extended periods of time) represent an important energy loss from the estuarine system. Shorebirds, for example, arrive in Maine with minimal fat reserves. They remain for 2 to 4 weeks, during which time their weight increases about 50% to 100%. Without these added fat reserves (the energy for their long transatlantic migrations), they could not successfully complete the 2500-mile flight from coastal Maine to the Lesser Antillies and northern South America.

Marine mammals. Marine mammals are found principally in the marine system and therefore are discussed in chapter 4, "The Marine System" and in chapter 13, "Marine Mammals."

Decomposers

The decomposers are microbes, such as bacteria and fungi. They break down dead organic matter and convert it to a form that can be recycled. These organisms attach to, live on, and enrich detrital particles (dead organic matter), making it nutritious for some consumers.

Microbial decomposers have important roles in estuarine ecosystems. Bacterial and fungal degraders comprise the largest group of living organisms in the sea. In coastal waters, for example, from 10^5 to 10^6 bacteria/ml of sea water can be found by direct counting techniques (Ferguson and Rublee 1976; and Watson et al. 1977). In coastal sediments, from 10^8 to 10^{10} bacteria/g dry weight sediment (Dale 1974; and Novitsky and Watson, unpublished) can be found. Not all of these bacteria are decomposers or even living bacteria but a large percentage of them contribute to the energy flow.

In the estuary as well as in the open ocean, the most prevalent decomposers are *Pseudomas*, *Vibrio*, *Flavobasterium*, *Anthrobacter*, *Caulobacter*, *Hyphomicrobriu*, *Cytophaga*, *Acinetobacter*, and *Photobacterium* (Sieburth 1971; and Leifson et al. 1964).

Bacterial populations at Schoodic Point ranged from 10 to 1500 cells/ml on marine agar (Pratt and Reynolds 1973 and 1974). Although no detailed taxonomic study was undertaken, colonies isolated probably were representative of the genera listed above. Results of counting bacteria using culture media are usually several orders of magnitude lower than those found using direct counting techniques, so that comparisons of published densities of bacteria must be made with caution.

FOOD WEBS

The biological components of the estuarine system are linked to one another through food chains or food webs. In this way, energy (food) is passed from the producers (plants) to the herbivores (plant eaters) to secondary consumers (animal eaters) to tertiary and higher consumers, and ultimately to the decomposers. Each step in this progression is called a trophic level. Organisms function at one or more trophic levels, i.e., a diatom is a primary producer, a filter-feeding clam is a herbivore and functions on the second trophic level, and crabs that eat both plant and animal material are both herbivores and secondary consumers.

From one trophic level to the next energy is lost; only a small part of the energy contained within one level is passed to the next. In other words, maximum energy is contained in the primary producer trophic level and subsequent levels contain less and less. If we assume a 10% efficiency in the energy transfer between trophic levels a great amount of energy from lower levels is needed to support a top carnivore (e.g. bird, fish, or person). The transfer efficiency is probably higher than 10% to 12% at higher latitudes with discontinuous productive seasons (Gulland 1970). The Gulf of Maine could fall into this category, although no specific information is available to support generalizations about energy transfer efficiencies there. Retaining the 10% assumption, 10 pounds of smaller fish are required as prey to produce 1 pound of commercially utilizable fish. The support of 10 pounds of small fish requires 100 pounds of zooplankton, which in turn requires 1000 pounds of phytoplankton (figure 5-26). In other words, even a simple food chain must contain a large amount of energy at the lowest level to support the higher trophic levels, to which energy is progressively less available.

A sample series of food chains organized into a Maine estuarine food web is shown in figure 5-27. The species shown, which are representative of a larger number of species, are arranged in the illustration to show their approximate trophic level. Energy fixed by estuarine diatoms (primary producers) is transferred via feeding to zooplankton (primary consumers), Atlantic herring (secondary consumers), and terns (tertiary consumers). The detrital-based food web is the dominant avenue of energy transfer in Maine estuarine system.

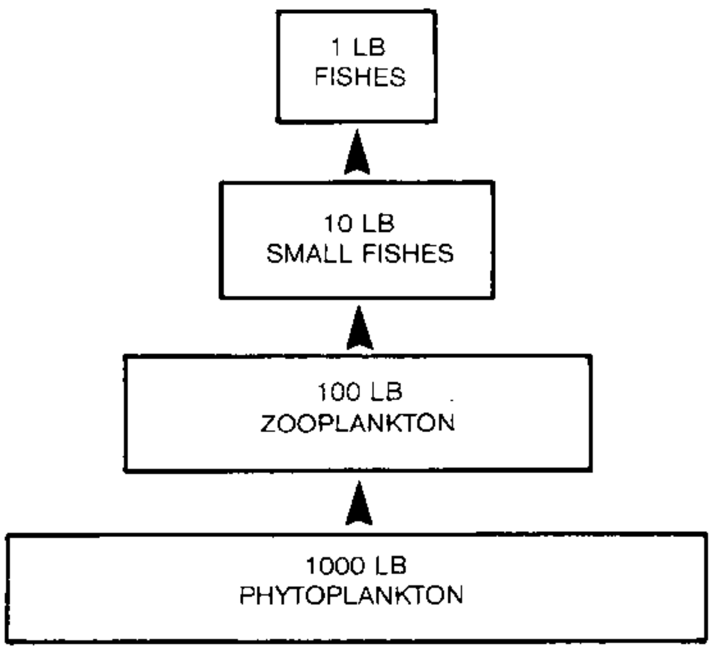


Figure 5-26. Simple representation of the energetic relationships between trophic levels.

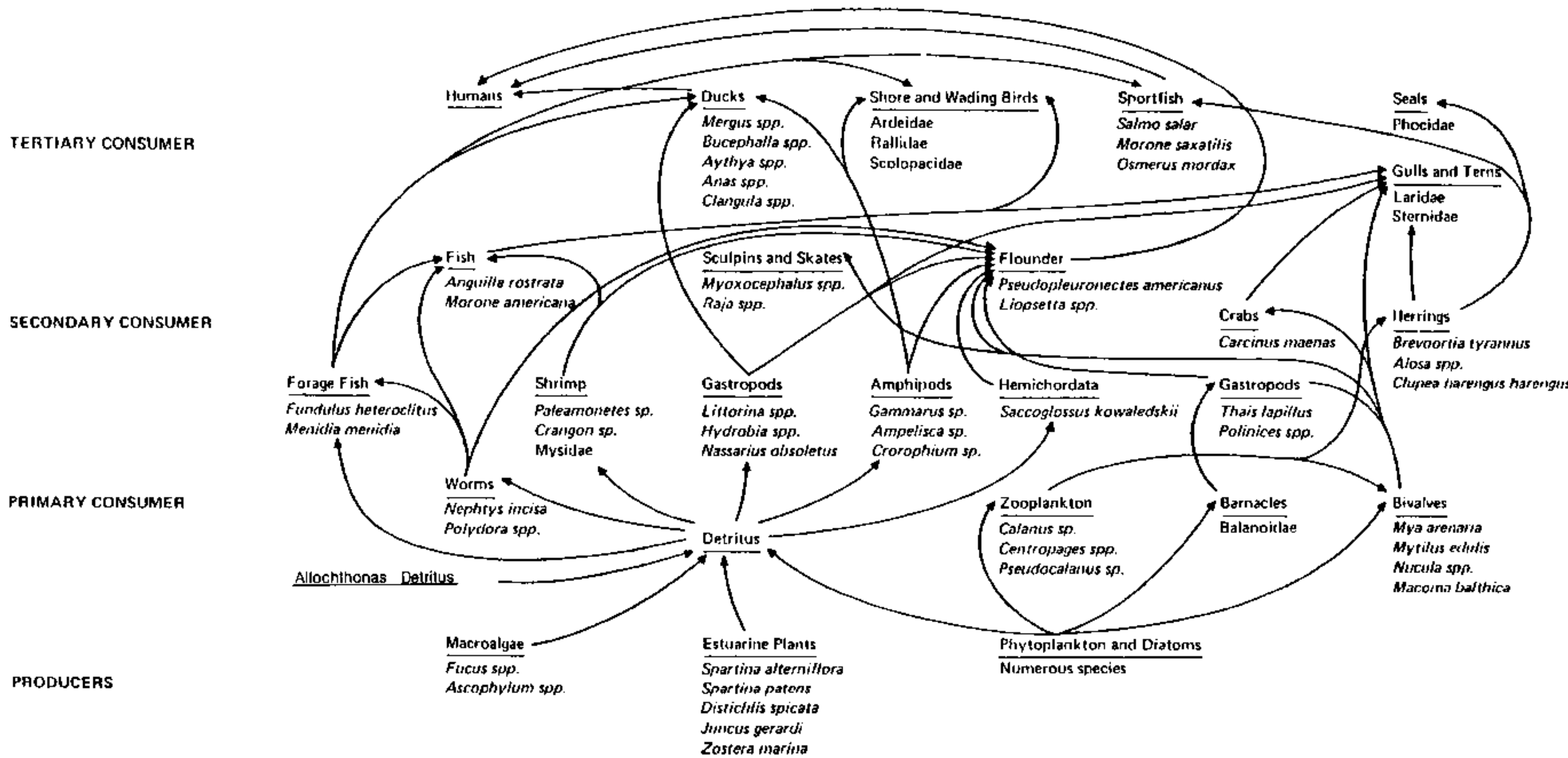


Figure 5-27. Generalized food web for the estuarine system of coastal Maine.

ENERGY FLOW

Among all ecological systems throughout the world, rates of primary production (primary productivity) are highest in estuaries (figure 5-28). The high rate of primary productivity by estuarine phytoplankton, macroalgae, and rooted macrophytes is supported by high nutrient levels from land runoff, influx from deep nutrient-rich ocean water, and rapid regeneration from the bottom. Research on energy flow in Maine estuaries has been limited to the study of production by phytoplankton and emergent vegetation. No investigations have addressed energy flows through or energy requirements of higher trophic level organisms.

Energy flow in the estuarine system is driven primarily by hydrologic and climatic processes, as these forcing functions control primary production. Hydrologic factors control the mixing of fresh water with sea water. This mixing transports materials, such as nutrients essential for plant production, into estuaries from adjacent marine and terrestrial systems. Climatic factors, such as temperature and insolation, influence the rate of photosynthesis.

A generalized schematic diagram of the functioning of the Maine estuarine system is presented in figure 5-29. Growth of primary producers (phytoplankton, macroalgae, rooted macrophytes, and benthic diatoms) is influenced by nutrient supply, insolation, and temperature.

COMPARATIVE PRODUCTION RATES OF THE GENERALIZED ECOSYSTEM TYPES IN THE WORLD

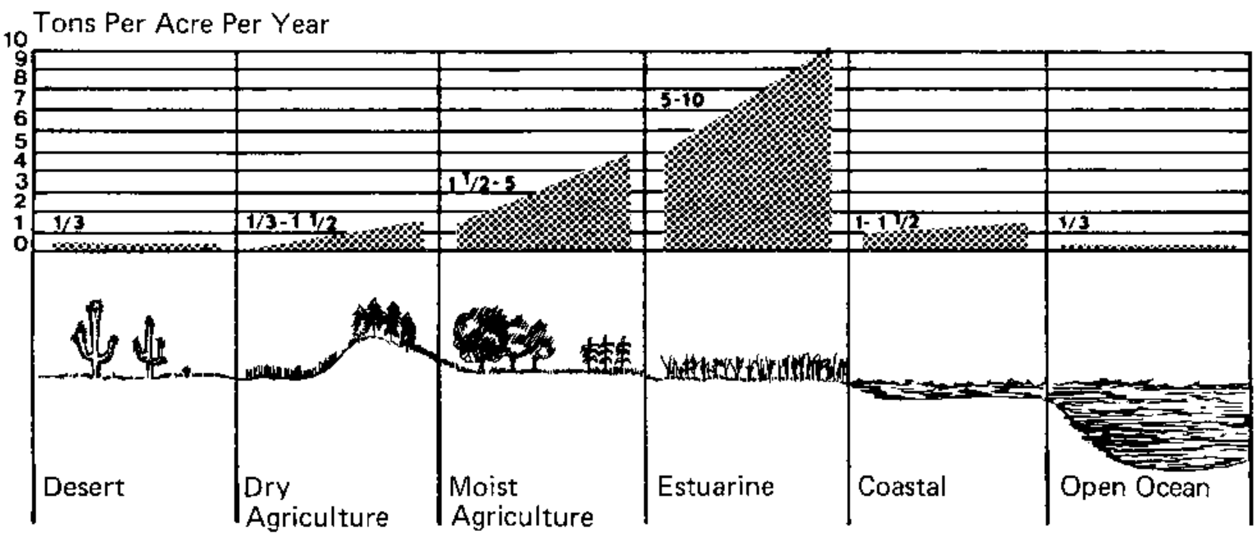


Figure 5-28. A comparison of the primary productivity (tons of dry weight produced per acre per year) for different types of terrestrial and aquatic sytems in the world. Shaded bars indicate general ranges (Teal and Teal 1969).

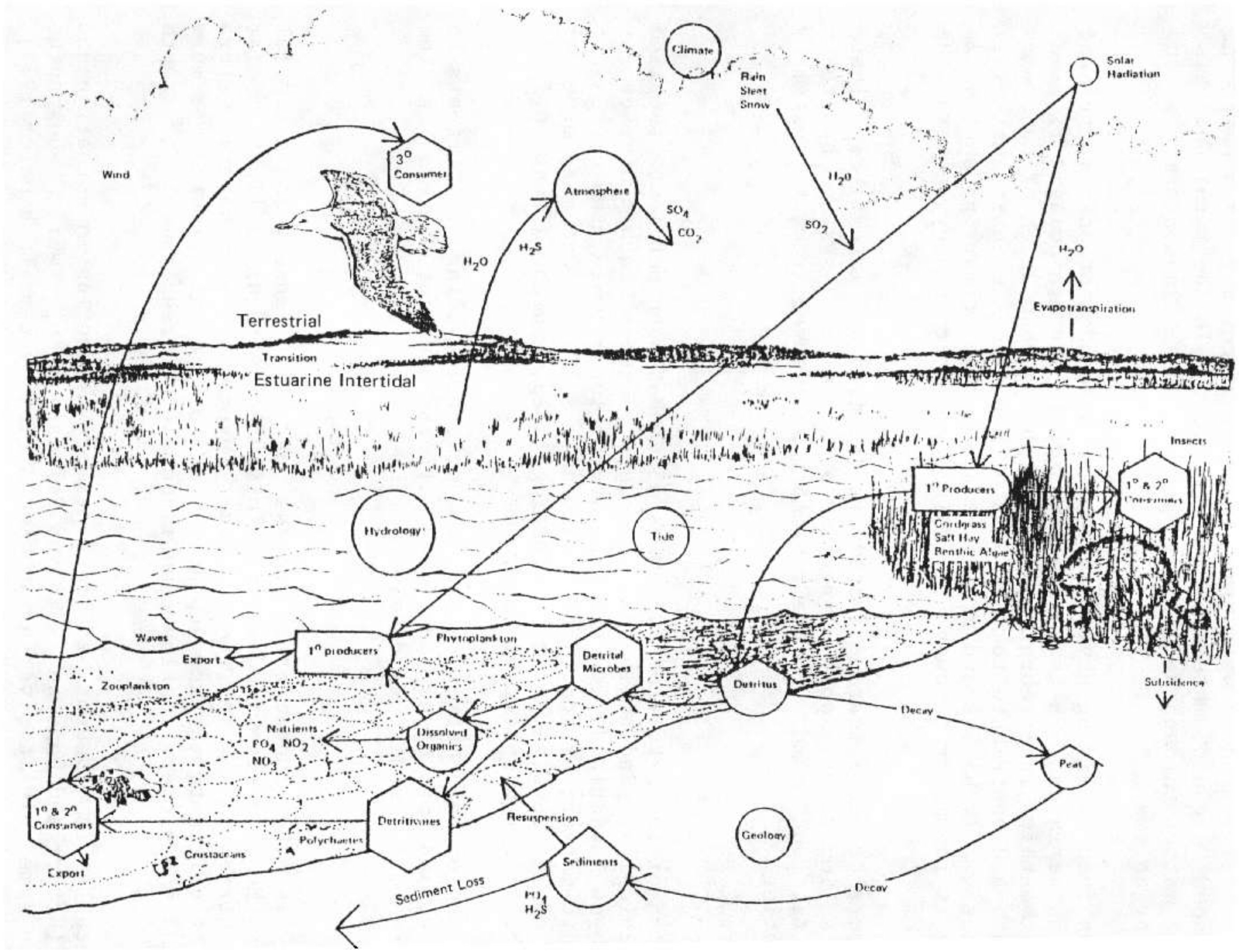


Figure 5-29. Simplified energy flow model for an estuarine system in Maine.

The energy bound in producer biomass is utilized in many ways. Some is utilized by the plants themselves for growth and respiration. The other pathways result in energy transfers to higher trophic levels, either directly through grazing on plants or indirectly through the detrital chain. Many plant cells are grazed directly by zooplankton, filter-feeding benthic organisms (e.g., clams), and pelagic fish. Some plant cells die and enter the pool of suspended organic material and detritus. The detrital pool also receives organic matter through decay, resuspension of peat and sediments, and death of other organisms.

The zooplankton feed on living phytoplankton and suspended organic matter and its associated bacteria and, in turn, are devoured by certain pelagic fish and filter-feeding benthic invertebrates. Excretion by and death of consumers recycle nutrients and contribute to the pools of nonliving organic material. Detritivores (e.g., polychaetes and crustaceans) consume primary production as detritus. This is the major pathway in which producer energy enters the estuarine system.

The top consumers of the estuarine system are the fish and waterbirds. These mobile carnivores import or export energy to or from the system by their migratory habits, and some of their biomass is removed from the system by fishing and hunting.

BIOGEOCHEMICAL CYCLES

The maintenance of the estuarine system is dependent upon nutrients supplied by chemical, geological, and biological processes. Several such processes or cycles have been described in the literature; for example, the cycling of nitrogen, organic matter, silica, phosphorus, and sulfur. One or more of these cycles could involve a rate-limiting step, which affects primary production within a given system or subsystem.

The nutrient and organic matter cycles, the seasonal cycling of nutrients in the water column, and processes that may affect nutrient levels in the estuarine environment are discussed below.

Plant Nutrients

Photosynthesis is the fundamental process by which energy and essential nutrients enter the estuarine food chain. This process requires light (solar energy) and nutrients. In the surface layers of most natural waters sufficient light exists to varying depths to support plant growth (primary production), and the process continues until some other requirement for growth is exhausted.

Nitrogen generally is thought to limit primary production in estuarine and marine waters (Ryther and Dunstan 1971; and Goldman 1976), while phosphorus may fulfill the same role in riverine and lacustrine systems (Schindler 1971). A meager supply of either of these nutrients limits productivity, whereas a plentiful supply usually produces large quantities of plant material. Although the concept of a limiting nutrient is not new (Liebig 1840) it is difficult to determine which element is potentially limiting and, under natural conditions, the extent to which a limitation exists.

Evidence suggests that nitrogen is a potentially limiting nutrient in estuarine and coastal marine waters in Maine during the summer (active growth) months. The atomic ratio of nitrogen to phosphorus (N:P ratio) in marine waters is generally 15:1 (Armstrong 1965). The uptake ratio for the two elements during phytoplankton growth is higher than this, so that nitrogen could be expected to be exhausted before phosphorus and, thus, nitrogen would be the potentially limiting nutrient. In the discussions of nitrogen supply in Maine estuaries below, the N:P ratios are given. As these N:P ratios are generally much lower than 15:1 in Maine estuaries, nitrogen is considered limiting.

A similar conclusion can be drawn by examining the distribution of the two elements within a given area. In the New York Bight, for example, concentrations of the two elements decrease seaward from the mouth of the Hudson River estuary because of dilution and biological uptake. A plot of nitrogen concentration versus phosphorus concentration indicates that nitrogen would be exhausted first and ultimately would limit production (Garside, unpublished). It is apparent that nitrogen can be expected to limit productivity even in marine and estuarine areas that are heavily polluted by sewage wastes.

Ambient nutrient concentrations do not represent the nutrient status of a natural phytoplankton population necessarily, because phytoplankton growth is a dynamic process. That is, the ambient concentration of a nutrient is a static property, whereas the dynamic process of phytoplankton growth may depend more on the rate of supply of nutrients rather than the instantaneously measured concentrations. In this regard, two further arguments can be made to support the contention that nitrogen limits phytoplankton growth in marine and estuarine waters of coastal Maine.

The resupply of nutrients in a body of water often depends on regeneration as a result of *in situ* heterotrophic activity, such as zooplankton grazing. Bacterial processes are not necessary because merely breaking the cell wall is sufficient to release phosphate. Phytoplankton cells themselves contain the necessary enzymes to bring about phosphate release. By contrast, organic nitrogen compounds are far less labile and usually are regenerated by bacterial activity at a slower rate. Consequently, the resupply of phosphorus generally can be expected to be greater than that of nitrogen, making the latter more likely to limit phytoplankton growth. For a more detailed discussion of nutrient regeneration see Raymont (1963).

A second aspect of phosphorus supply is inferred from the observation that in temperate estuaries phosphorus supplies near the bottom are higher during summer than they are in any other location at any time (Taft and Taylor 1976). Many workers have noted that estuarine muds contain large quantities of bound phosphorus. Jitts (1959) showed that river mud adsorbs more phosphate as the ratio of iron to organic matter increases. Taft and Taylor (1976) support the hypothesis that phosphorus probably precipitates as ferric phosphate during winter oxygenated conditions and is released during summer months. The release mechanism involves the development of anoxic conditions in the sediment as organic detritus from primary producers decomposes. Ferric phosphate is reduced to ferrous phosphate, which is soluble and mobilized from the sediment. This storage/release mechanism that provides phosphate during the period of peak phytoplankton production has no counterpart in nitrogen cycling.

Nitrogen. The sources of nitrogen for phytoplankton growth and the processes by which nitrogen is supplied are complex and may vary among estuaries in Maine. Data are insufficient to support definitive statements about specific estuaries, so the following generalizations on nutrient supply are based on the authors' experience with estuarine systems in Maine.

The supply of nitrogen in any estuary depends to a large extent on the unique circulation patterns of that body of water (see "Hydrography" above; Dyer 1973). The three major external sources of inorganic nitrogen to an estuary are inorganic nitrate nitrogen that is introduced in the bottom flow of saline water from the ocean, nitrate (and possibly ammonia) that enters from agricultural land runoff in the freshwater flow, and sewage-derived nitrogen (both nitrate and ammonia). Although it is not a source of "new" nitrogen, regeneration within an estuary also can be an important source of nitrogen for plant growth. The principal export of nitrogen from an estuary is in the surface outflow, in the form of inorganic nitrogen, detritus, phytoplankton, zooplankton, and migrations of fishes and birds. Annually there is probably little accumulation of nitrogen in Maine estuaries, so that the export to local waters will equal the inputs to the individual estuaries. This export may represent an important source of nutrients to local coastal waters.

In most estuaries, salinity increases from surface to bottom and much of the input of coastal water is contained in a net nontidal upstream bottom flow. The nutrient cycle in nearshore waters follows the seasonal pattern described in chapter 4, "The Marine System." Nutrient distribution is related directly to density structure of the waters. Surface water is not as rich in nutrients as the denser waters below it (figure 5-30). The amount of nutrients in the saline water inflow depends on the depth from which that saline water comes (source waters). This is illustrated for the Kennebec and Sheepscot Estuaries in figure 5-30. An estuary that is shallow or has a shallow sill at its seaward end obtains sea water from near the surface. The Kennebec is an example of such an estuary. If the depth from which water is drawn into the estuary is above the seasonal thermocline very little import of nutrients will take place. Conversely, an estuary that is deep at its mouth will draw enriched water from below the thermocline; the Sheepscot is an estuary of this type.

Under certain circumstances, it is possible to determine the nutrient content of this oceanic water supplied to an estuary. In fall as day length decreases, estuarine phytoplankton production and nutrient uptake decline (Garside et al. 1978). Consequently, nutrient and salinity distribution are similar (as determined by the proportion of fresh and saline water and the concentration of nutrients). In summer, lower nutrient concentrations are expected because of the high uptake of nutrients by primary producers. In winter, the thermal structure breaks down in coastal waters and all estuaries, regardless of depth, receive similar concentrations of nutrients as the nutrient concentration of offshore waters becomes more uniform (see Apollonio and Applin 1972). However, in early fall during the brief period when primary production is low but the offshore thermocline structure remains, the distribution of nutrient concentrations with respect to salinity can be used to identify the nutrient concentration in the coastal water that has been

THE EFFECT OF DEPTH OF THE MOUTH OF AN ESTUARY HAVING A TWO LAYER FLOW REGIME ON NUTRIENT SUPPLY FROM OFFSHORE WATERS IN SUMMER

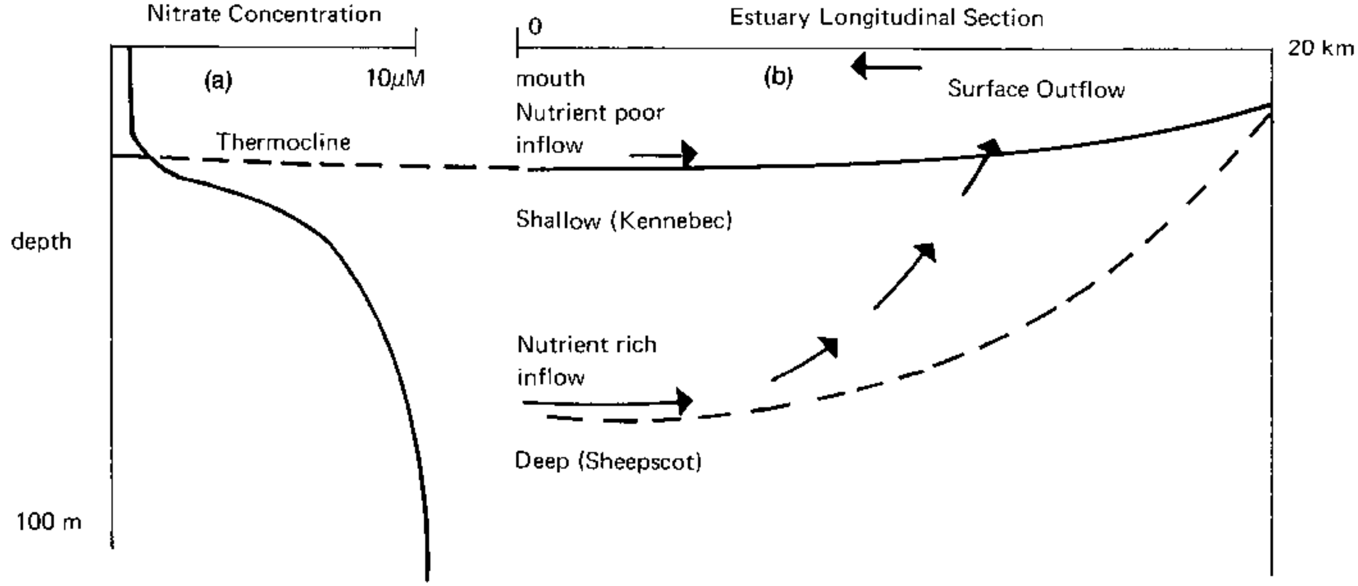


Figure 5-30. The relationship between depth of water and nitrate concentration (a), and the subsequent nutrient character of the marine waters entering the Sheepscot and Kennebec estuaries (b) (Garside, unpublished).

entering the estuary during the summer months. The winter nutrient concentration has little influence on the estuary or its phytoplankton productivity, as phytoplankton productivity is low in winter. In the Sheepscot estuary, for example, winter production is only 10% of that in the summer and nutrients are not likely to be limiting at that time in Maine estuaries (Garside et al. 1978).

The distribution of nitrate versus salinity in the Sheepscot Estuary in September 1976 is shown in figure 5-31. Extrapolation of a line through these data points to the maximum salinity expected close to the mouth of the estuary (32.8 ppt) indicates a source water containing just over 9 μM nitrate. This water was tentatively identified by Garside and coworkers (1978) as Maine Intermediate Water, and described by Hopkins and Garfield (1979) as having a salinity of 32.5 ± 0.5 ppt and a temperature of 4.5 ±1.5 C. It is a rich source of oceanic nutrients that is available to the Sheepscot Estuary because of its relatively deep entrance. In coastal Maine a concentration of 9 μM nitrate is considered a relatively high concentration.

Since the relationship between nutrient concentration and salinity can be expected to be linear in the early fall only a pair of nutrient/salinity values would be needed to describe the distribution and determine the nutrient concentration in ocean water entering any Maine estuary. Data gathered in September, 1978, in a number of Maine estuaries (Presumpscot, Kennebec, Sheepscot, Damariscotta, Penobscot, Machias, Cobscook Bay, and the St. Croix)

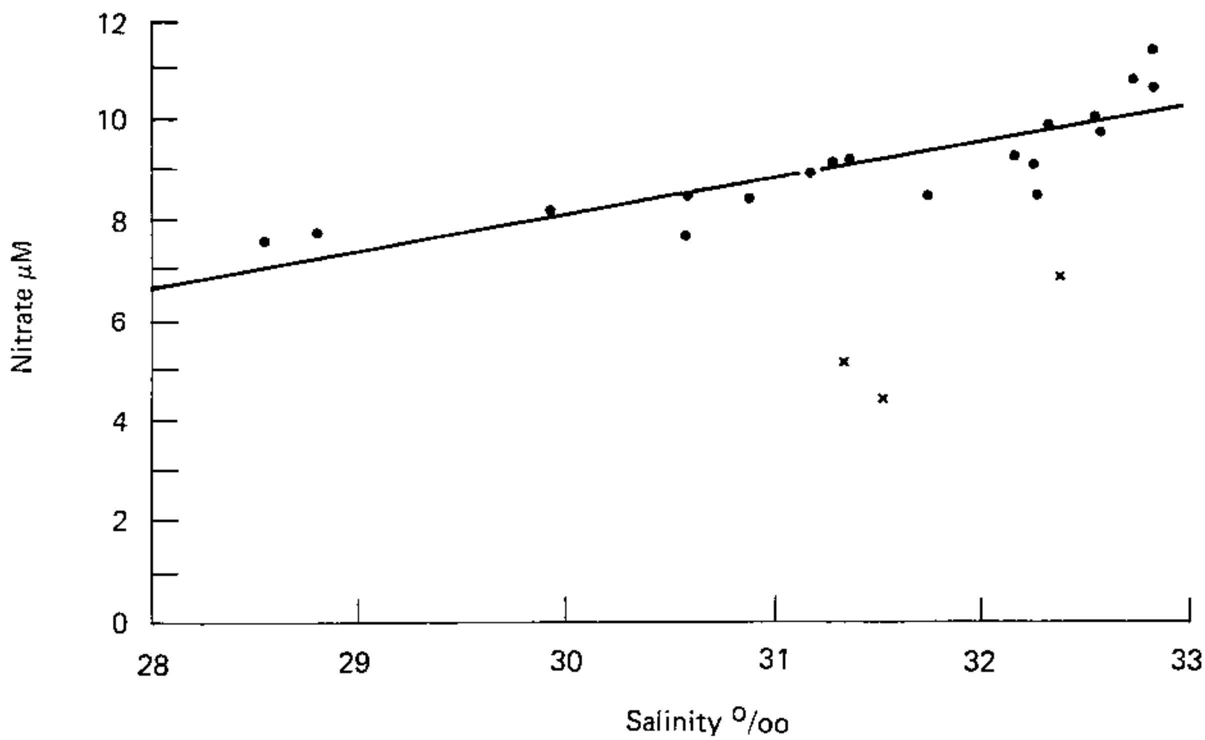


Figure 5-31. Nitrate concentration (μM) and salinity (ppt) in the Sheepscot estuary in September 1976 (Garside et al. 1978).

are discussed below in terms of the depth of the entrance of each estuary and the expected offshore nutrient distribution (Garside, unpublished).

Land surface runoff and river flow are potentially significant sources of nutrients to estuaries. When large areas of cultivated land lie within an estuary's watershed substantial quantities of nutrients from fertilizers applied to agricultural land can be carried to the estuary by surface runoff. This nutrient source is not likely to be very important in Maine estuaries, because only a small proportion of the land in estuarine watersheds is used agriculturally. Nevertheless nutrients in river flow from natural systems (wetlands and lakes) cannot be ignored and should be examined on the basis of measured nitrogen concentration in river water.

The United States Geological Survey (USGS) maintains flow gage and water quality monitoring stations on a number of major rivers in the State. Nitrogen concentrations were measured as nitrate (NO_3, the most oxidized form of organic nitrogen) and Kjeldahl nitrogen. The latter term refers to all forms of nitrogen determined by the Kjeldahl technique and includes ammonia (NH_3 or NH_4^+, the most reduced forms of inorganic nitrogen) and both dissolved organic nitrogen (DON) and particulate organic nitrogen (PON) if the sample was not filtered before analysis. Ammonia and nitrate nitrogen are directly available to phytoplankton (Dugdale and Goering 1967), but most other forms of organic nitrogen first must be broken down by bacteria before they can be used for plant growth.

Of the rivers for which data are available (Androscoggin, Kennebec, Penobscot, and St. Croix) all have higher Kjeldahl nitrogen in winter than in summer, although some have low values during certain winter months and high values during some summer months. It is difficult to be precise in this analysis and much of the scatter in the data may be attributable to methodology. However, if the general summer/winter trend is significant it is probable that high Kjeldahl nitrogen when temperatures are low represents high DON rather than NH_3. Temperatures sufficient to allow bacterial conversion of organic nitrogen to ammonia probably also would allow the bacterial oxidation of ammonia to nitrate.

During summer months, it is not possible to make such clear distinctions, since heterotrophic activity can supply ammonia rapidly (Garside et al. 1978). Summer concentrations of nitrate or ammonia plus DON are small in most instances. Nitrate concentrations do not exceed 13 μM during the summer months and are often 1 μM to undetectable and ammonia concentrations are not likely to double the total nitrogen concentration.

For the Sheepscot estuary using a mean summer daily flow of 2.7×10^5 m^3/d (USGS 1967 to 1976 data) and assuming 10 μM (based on data for the Kennebec watershed) this source would supply 37.5 kg/N day. Assuming that phytoplankton assimilate 1 g C/m^2/day and have a carbon to nitrogen assimilation ratio of 6:1 (by atoms) this production would require 0.194 g N/m^2/day (Garside et al. 1978). Thus, the total river supply would support primary production over an area of about 0.2 km^2. The Sheepscot estuary south of Wiscasset has an area of about 50 km^2, so that land runoff can support only about 0.4% of the total estuarine production.

Supporting data are given in figure 5-31. The inference can be drawn that as NO_3 concentration even at times of low production is zero at salinites below the freshwater regime (<0.5 ppt), very little of the nitrate in the freshwater flow ever reaches the estuary. The difference between what is required to support estuarine production and the potential riverine/land run-off supply is so great that it is probably safe to suggest that this source is unlikely to be important to production in Maine estuaries. Specific data for individual estuaries are discussed below.

Sewage-derived nitrogen can represent a major nitrogen source to an estuary and can even lead to the production of excessive blooms (excessive abundance) of phytoplankton in the summer months (Carpenter et al. 1969). The siting historically, and the present potential development of major population centers on estuaries, make the disposal of sewage nitrogen for these urban centers a potentially serious problem. The New York/New Jersey metropolis on the lower Hudson River estuary, for example, has a population of 16 million, and discharges 160 t (180 tons) of nitrogen daily, enough to have a measurable effect not only on the estuary but also on the productivity of adjacent coastal waters to a distance of 16 miles (25 km) from the mouth of the estuary (Garside et al. 1976.). Except for areas of major population centers, little impact of sewage disposal on nitrogen concentration can be expected in most Maine estuaries except in specific locations (see chapter 3, "Human Impacts on the Ecosystem").

Regeneration of nutrients by heterotrophic activity combined with the unique circulation patterns in estuaries may serve as a means by which nutrients, once within the estuarine system, may pass repeatedly through the food chain (Schelske and Odum 1961). This mechanism, often termed a "nutrient trap," has the potential to provide high primary production for a given supply of nutrients. The nutrient trap functions in the following way. Nutrients in the surface layer are consumed by phytoplankton. Phytoplankton are transported downstream by the surface flow and either die and sink or are grazed. Resultant detrital material settles to the bottom layer or to the bottom. Once within the bottom layer the detrital particles in most Maine estuaries are transported upstream (layered tidal inflow) and decompose, or do so in the sediments. In either instance the regenerated nutrients eventually are released to the bottom flow and are transported upstream, during which time they are progressively mixed back into the surface layer. Once in the surface layer they are again available for the growth of more phytoplankton. This mechanism helps enhance the productivity of estuaries.

The nutrient recycling processes described above function to some degree in all estuaries, yet the biological and physical parameters often are extremely difficult to measure and where measurements have been made, they are only incidental to the study, such as benthic regeneration (Nixon and Oviatt 1972) and zooplankton excretion (Smith 1978), and food habits of the pelagic menhaden, mackerel, and herring (Oviatt et al. 1972). Although such studies are of value in providing some general insight into specific processes or locations, opinions of the relative importance of nutrient regeneration are often diametrically opposed and preclude direct application to Maine estuaries. For example, Martin (1968) considered benthic nutrient regeneration to be capable of supplying all of the nutrient requirements of phytoplankton in Narragansett Bay in August, whereas Carpenter et al. (1969)

concluded that benthic regeneration in Chesapeake Bay was insignificant as a nutrient source for overlying primary production.

It cannot be concluded that any single nutrient regeneration process is applicable to any of the estuaries of coastal Maine. In some estuaries one process will be dominant and in others, others may dominate. Thus, predicting the importance of regeneration or even more specifically which components of regeneration are important in Maine estuaries cannot be undertaken. Some specific statements based on actual measurements in the Sheepscot estuary are made below but more information is needed before any more general or specific statements on nitrogen regeneration in Maine can be made.

Nevertheless, insofar as certain parts of the biosphere are potentially important in the recycling of nutrients in estuaries their vulnerability to perturbation must be considered. Changes in uses of estuaries that may have direct impacts on populations with no apparent commercial or recreational value also may have indirect impacts on total estuarine productivity, by virtue of the key position of such populations in maintaining the estuarine nutrient cycle.

<u>The Role of Flushing</u>

The importance of land runoff and ocean water in supplying nutrients to an estuary has been discussed above. Land runoff and tidal exchange are important in the flushing of estuarine systems and help determine the distribution and residence time of nutrients in estuaries. The concepts of flushing are discussed more fully above under "Hydrography," but the following considerations apply specifically to nutrients in Maine estuaries.

Fresh water inflow drives estuarine circulation. A large freshwater inflow results in lower salinities further down the estuary and more rapid flushing of the estuary. Small freshwater inflow results in higher salinities further up the estuary and longer residence times for water in the estuary. Since most of the nutrients in many Maine estuaries are supplied by the ocean rather than freshwater input, low freshwater inflows result in nutrient-rich ocean water influencing a larger part of an estuary. Additionally, longer residence time of water helps assure that the processes of uptake and regeneration have sufficient time to occur and that more of the nutrients entering an estuary are retained and regenerated. The reverse is true in estuaries with disproportionately higher freshwater flows. Consequently, fresh water inflow (especially as a fraction of the volume of the estuary) in Maine is inversely related to the nutrient supply and productive potential of an estuary.

Tidal exchange, the fraction of the volume of an estuary that is moved in and out of the estuary on each tide, also is important in this regard. Tidal exchange contributes only slightly to the circulation but in smaller estuaries it is especially important for flushing. On each tide, fresh water enters the estuary, principally at the surface. It mixes with water in the estuary and a slightly larger volume of water leaves the estuary on the falling tide. If these tidal volumes are large compared to the low tide volume of the estuary, the estuary will be well flushed and nutrients may not be resident in the estuary for sufficient time to contribute to the productivity of the system.

These ideas cannot be translated quantitatively into rates of nutrient supply or potential productivity but can be used for the following comparative purposes. The important volumes to consider are the fresh water inflow volume (V_F), the low tide volume (V_L), and the tidal exchange (intertidal) volume (V_T). The relative proportions of these will determine qualitatively the magnitude and nature of estuarine flushing. Two parameters:

$F = 100V_F/(V_F + V_L + V_T)$ (F = percentage of total volume changed by fresh-water flow)

$T = 100V_T/(V_F + V_L + V_T)$ (T = percentage of total volume changed by tidal flow)

describe the percentage of the total volumes involved in fresh water and tidal flushing, respectively. A third parameter:

$L = 100V_L/(V_F + V_L + V_T)$ (L = percentage of total volume remaining in estuary at low tide)

brings the sum of F, T, and L to 100 and is a function of the unflushed volume.

These parameters can be calculated for Maine estuaries and plotted. The position of an estuary on the plot indicates, relatively, the type of flushing (and hence nutrient supply) that might be expected (figure 5-32). Thus, the Presumpscot is well flushed; most of the volume is represented by fresh water flow and tidal exchange. Neither the supply of nutrients nor their residence time might be expected to favor high uptake and productivity. Comparatively, the Sheepscot has a relatively slow flushing rate, and what exchange of water does occur is mostly tidal. Such an estuary might be expected to have a larger supply of nutrients and a longer residence time allowing for their uptake and retention. Reference will be made to these parameters in the following discussion of nitrogen availability in the coastal estuaries of Maine.

Fore estuary. Only one source of data (Normandeau Associates 1974) is available on nutrients in the Fore River estuary. These data (May 1974) show a nitrate distribution with values of about 6 μM NO_3 at the I-295 bridge in the estuary and 1.8 μM at the mouth of the estuary in Casco Bay. This report also gives values for ammonia concentrations, which show maximum values in the upper half of the estuary (10 μM), and particulate nitrogen which is about 0.6 μM and is distributed rather uniformly. Much of the ammonia is probably derived from sewage; certainly a source internal to the estuarine system is implied by the high value of 10 μM in the upper half of the estuary. Nevertheless, these concentrations are insufficient to cause eutrophication, and flushing precludes the accumulation of nutrients.

Presumpscot estuary. The Presumpscot has the shallowest entrance (2 m) of all the estuaries in the study area that remain flooded at low tide. The Presumpscot only has access to surface coastal sea water and therefore would not be expected to have a rich nutrient source.

Samples collected in September, 1978, at the route 9 and route 1 road bridges had salinities of 2.3 and 31.59 ppt and nitrate concentrations of 6.7 and

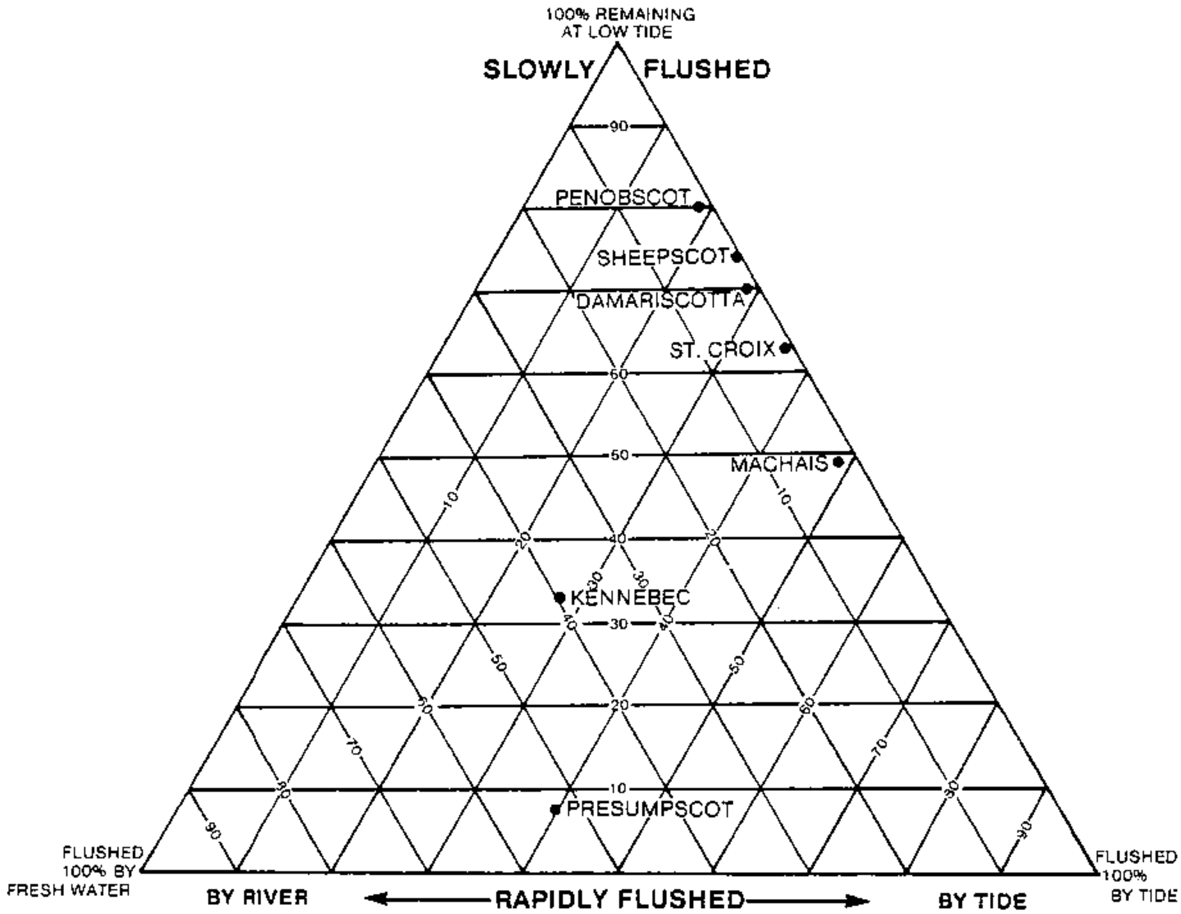


Figure 5-32. Factors controlling flushing in seven Maine estuaries, based on application of the model described on page 5-59. For example, in the Kennebec estuary 40% of the estuary's volume is provided by river flow, about 28% by tidal input, and 32% is residual at low tide.

3.6μM respectively. The corresponding N:P ratios were 2.5:1 and 1.4:1 indicating that nitrogen would be the potentially limiting nutrient, as the ratio of N:P taken up by phytoplankton is much higher than this. The nitrate concentrations in the fresh and saline source waters are 6.9 and 3.5 μ M, respectively. Since the estuary's nitrate concentration ranges between 3.6 and 6.7 μM it is probable that nutrient loading from sewage in the river has elevated nutrient concentrations throughout the estuary by about 1 to 2 μM.

Flushing of this estuary by tidal exchange and runoff is very rapid (figure 5-32). The salinity distribution supports this conclusion. The two sampling sites, which are less than 2 miles (3.2 km) apart, span a wide salinity range (2.3 to 31.6 ppt). Apparently, ocean water does not penetrate far into the estuary and the large tidal exchange relative to subtidal volume ensures that the nutrients in the estuary will be flushed rapidly to the coastal waters. No other nutrient data are available for this estuary.

Kennebec estuary. The entrance to the Kennebec is about 35 feet (11 m) deep and thus may have a low supply of nitrate from sea water. The Kennebec also receives a supply of salt water from the Sheepscot via the Sasanoa River (a net exchange of fresh water in the opposite direction takes place; see "Hydrography" above). As a result, the actual nitrate concentration in the saline source is expected to be somewhere between 1.7 μM, (on the basis of the sill depth) and 9.2 μM if all the saline water were to enter from the Sheepscot estuary via the Sasanoa River.

Measurements made in September, 1978, indicate that at Bath and Phippsburg salinities were 5.26 and 23.38 ppt and nitrate concentrations were 18.7 and 8.7 μM, respectively. The N:P ratios were 17:1 and 7.3:1, respectively, which suggests that nitrogen is the potentially limiting nutrient over most of the estuary. The coastal source water would have an expected nitrate concentration of 4.0 μM and the fresh water would have an expected concentration of 21.5 μM (Garside, unpublished). The high value of nitrogen in fresh water may be attributable to the local sewage outfall rather than to all the fresh water entering the estuary. The complexity of the sources of seawater and freshwater exchange between the Sheepscot estuary and the Kennebec estuary makes a simple application of a mixing model less than satisfactory.

Because the Kennebec has both a large fresh water flow and a large tidal exchange relative to its low tidal volume nutrients from the ocean water would not be expected to penetrate far into the estuary and rapid flushing would tend to minimize the residence time of nutrients from the fresh water in the estuary. On this basis the Kennebec is not expected to be a highly productive estuary; however, the complex circulation and nutrient source distribution may increase the productivity of this estuary. Three sources of nutrient data on the Kennebec system are available. The USGS's gaging and water quality station at Bingham reports nitrate plus nitrite nitrogen, as well as Kjeldahl nitrogen. Mean nitrate plus nitrite was 8 μM with a seasonal high in winter and low in summer ranging from 13.6 to 5 μM, respectively. Total Kjeldahl nitrogen was about twice that of the mean inorganic nitrogen with no seasonal trend. This input would be an insignificant source of support for primary production in the estuary.

Nitrates were measured at Dix Island within a half-mile of the mouth of the estuary on 17 August 1970. Measurable nitrate was present at all depths and all nutrient concentrations at the surface were much higher than those near the bottom. In fact, surface nitrate concentrations were similar to those in the Sheepscot (3 μM) but deep water values are much lower (1 μM) in the Kennebec than at a comparable location in the Sheepscot.

Sheepscot estuary. The Sheepscot has the deepest entrance of any Maine estuary (50 m) and as a consequence has access to nutrient-rich deep water throughout the year. Based on samples taken in September, 1976, Garside and coworkers (1978) identified the oceanic source water as Maine Intermediate Water with a nitrate content of 9.2 μM (figure 5-31). No nitrate from the freshwater flow reaches the lower part of the estuary so that the estuary is almost totally dependent on the oceanic source for its supply of nutrients. These authors tentatively concluded, based on a limited time series analysis of ammonia, that the regeneration of nitrogen as ammonia during darkness and its subsequent uptake in the light represents a major potential supply of nitrogen in the estuary. In fact, recent calculations (Garside, unpublished) suggest that probably only 20% of the measured primary production could be supported by nitrate supplied in the inflow of deep coastal water. This suggests that regeneration is essential to the maintenance of high productivity in the Sheepscot and probably all Maine estuaries.

The large subtidal volume of this estuary, relative to its freshwater flow and tidal exchange, suggests that its circulation rate is slow. Garside and coworkers (1978) have shown that the Sheepscot always has a two-layered structure as far north as Wiscasset, where it becomes vertically well mixed. Thus, deep coastal water and nutrients will be supplied to the entire lower estuary and will have a residence time sufficient for their uptake and retention. Garside and coworkers (1978) have reported that nutrient concentrations throughout the lower estuary at all times of the year were sufficient so that phytoplankton productivity would not be expected to be limited by lack of nutrients. Nitrate concentrations had minimum values in the 2 to 3 μM range, and similar concentrations were found for ammonia. Nutrient concentrations increased with depth, with 6 to 8 μM nitrate in the deep inflowing water. Other nutrient measurements have been conducted in the Sheepscot estuary (Maine Department of Marine Resources, unpublished; Maine Yankee Power Company 1970 to 1976). The former data are in general agreement with those presented above. The latter are not directly comparable as they represent minimum values.

Damariscotta estuary. The Damariscotta estuary is shallow (7.5 m) near its mouth and the inflow of nutrient-rich sea water is reduced. In September, 1978, one sample was taken at the Damariscotta/Newcastle Bridge; its salinity was close to that of sea water. Salinity was 32.33 ppt and the nitrate concentration was 1.7 μM with a N:P ratio of 0.9:1. Thus, nitrate potentially limits productivity in this estuary, since the oceanic surface water, that is the source water, also would be low in nutrients. The high salinity at the town of Damariscotta at the head of the estuary indicates that, except during high spring fresh water inflow, the estuary probably functions more like a shallow, poorly flushed arm of the sea. McAlice (1970 to 1977) presents nitrate, phosphate, and silicate data for the period from December, 1969, to May, 1971, and nitrate concentrations were near zero from mid-May to early

August. This estuary is probably nitrogen-limited during most of the summer months and probably is not as productive as the Sheepscot estuary.

Penobscot estuary. The Penobscot, like the St. Croix, has no clearly defined seaward boundary, but the depth is only 13 m near its mouth and the inflow of enriched sea water is relatively small because of it. Unlike the St. Croix, the offshore waters of the Penobscot are not particularly rich in nutrients during the summer. Measurements of water taken in September, 1978, were as follows:

	S ppt	NO_3 µM	N:P
Bangor	1.37	3.0	2.7:1
Bucksport	20.41	7.0	3.0:1
Searsport	29.27	2.9	1.7:1

These data indicate that the estuary is potentially nitrogen-limited. The fresh-water source contains 2.9 µM NO_3 and the oceanic source 1.4 µM NO_3. The relatively high nitrate concentration at Bucksport indicates some local internal source, possibly sewage waste.

The estuary is not very rapidly flushed, especially the lower portion south of Verona. Due to a lack of a rich nutrient supply, it is probably not very productive compared to the Sheepscot.

Pleasant, Narraguagus, and Union estuaries. No specific data are available for any of these estuaries, but they are probably similar to the Machias. Because of their small size, tidal exchange in these estuaries is probably important.

Machias estuary. The Machias River estuary is fed by the Machias and East Machias Rivers and has an entrance depth of 6 m. Two samples were taken in September, 1978, on the Machias below the falls, (S=8.51 ppt, NO_3=3.6 µM) and at the confluence of the Machias and East Machias Rivers (S=25.73 ppt, NO_3=4.4 µM). The N:P ratios were 3.6:1 and 3.4:1, respectively. Nitrogen is also potentially limiting in this estuary. The nitrate content of fresh water was 4.7 µM and even though the sill is shallow the oceanic source is probably a more important source of nutrients than fresh-water inflow. Ocean waters in this region of coastal Maine are well mixed and rich in nutrients. According to the model the estuary flushes fairly rapidly above the confluence of the two rivers and tidally below them.

Cobscook Bay. Cobscook Bay is fed by the Dennys River. The river flow is extremely small compared to the tidal exchange. Shroeder (1977) describes the area as having intense vertical mixing. Tidal exchange is so extreme that although a constant supply of nutrients is ensured, no phytoplankton population specific to the bay is expected, rather it is expected to be typical of the adjacent coastal waters. The rapid exchange of highly productive waters in the estuary should ensure high benthic and fixed algal production. This would be an important consideration if this exchange were to be restricted as a consequence of tidal power development.

St. Croix estuary. It is difficult to define the seaward boundary of this estuary but a sill depth of 10 m probably restricts the offshore supply to the surface layer. Nevertheless, samples taken in September, 1978, at the International bridge (S=2.18 ppt) and on the southern side of St. Croix Island (S=27.05 ppt) contained 3.5 and 3.7 μM NO_3. Nitrogen to phosphorus ratios were 2.5:1 and 4.1:1, respectively. Nitrogen would thus be expected to be the limiting nutrient. Both freshwater (3.5 μM) and oceanic (3.7 μM) sources of nitrate are implied, although the oceanic source is quantatively likely to be more important. The high offshore nutrient concentration in surface water in the northeastern coastal regions of Maine (as compared to areas in southwestern Maine) results from mixing of nutrients into the surface layer from deep water in the Gulf of Maine (see chapter 4, "The Marine System") and is probably the major factor in supplying relatively high concentrations of nutrients to the estuary.

Flushing of the St. Croix is moderate and most of the exchange of water in the estuary is tidal (figure 5-32), partly because of the high tidal range. Nutrient resident times in the system are sufficient for uptake. No specific data for the estuary are available.

Organic Matter Cycle

Nearly all organic matter found in the natural environment has been derived from or is a constituent of living organisms. Metabolically active compounds are passed rapidly from species to species during feeding, assimilation, growth, and death. Other organic components include toxic substances that may affect growth profoundly in minute concentrations and relatively inert compounds that may be transformed to active compounds by abiotic factors (wave action and salinity changes).

To illustrate the potential significance of dissolved organic substances in oceans, when compared to the sizes of living organisms, the organic carbon content of an open ocean water sample is plotted in figure 5-33 as a function of particle size. Although all living cells are contained in the size fractions greater than approximately 0.5 μm, they account for <5% of the total mass of carbon in the water column. In fact, it may be conjectured that any marine organism larger than a 10 μm phytoplankton cell is totally insignificant in the organic cycle in the oceans.

There are three size groups of organic matter in sea water: particulate, intermediate, and dissolved. Particulate matter is any microbial organism or nonliving material that is large enough to be ingested by a filter-feeding organism or to support bacterial attachment. The intermediate class of material is too small to catch and digest but too large to assimilate through the cellular membrane. Dissolved matter can be assimilated through cellular membranes. In the following discussion "biologically active" organic matter represents the larger and smaller size groups. Intermediate size particles are ill defined and probably are converted and transformed primarily by physical and chemical processes.

The primary source of organic material in nearshore areas and estuaries is terrestrial vegetation (introduced by fresh water runoff), emergent wetland plants, benthic diatoms, and attached algae. In the open ocean, phytoplankton is the most important source of organic matter. Concentrations of organic material are much more variable in estuaries, because of localized inputs, than in the open ocean.

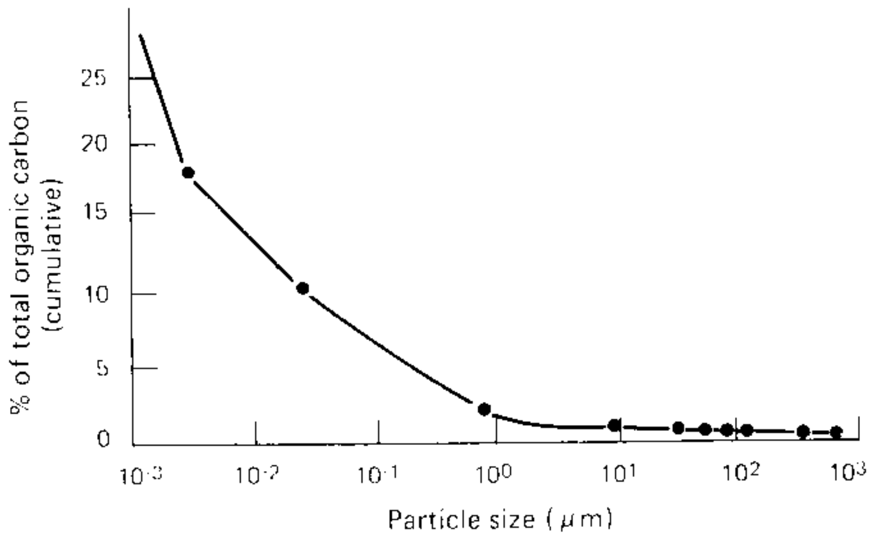


Figure 5-33. Generalized size distribution of organic carbon particles in seawater (adapted from Sharp 1973).

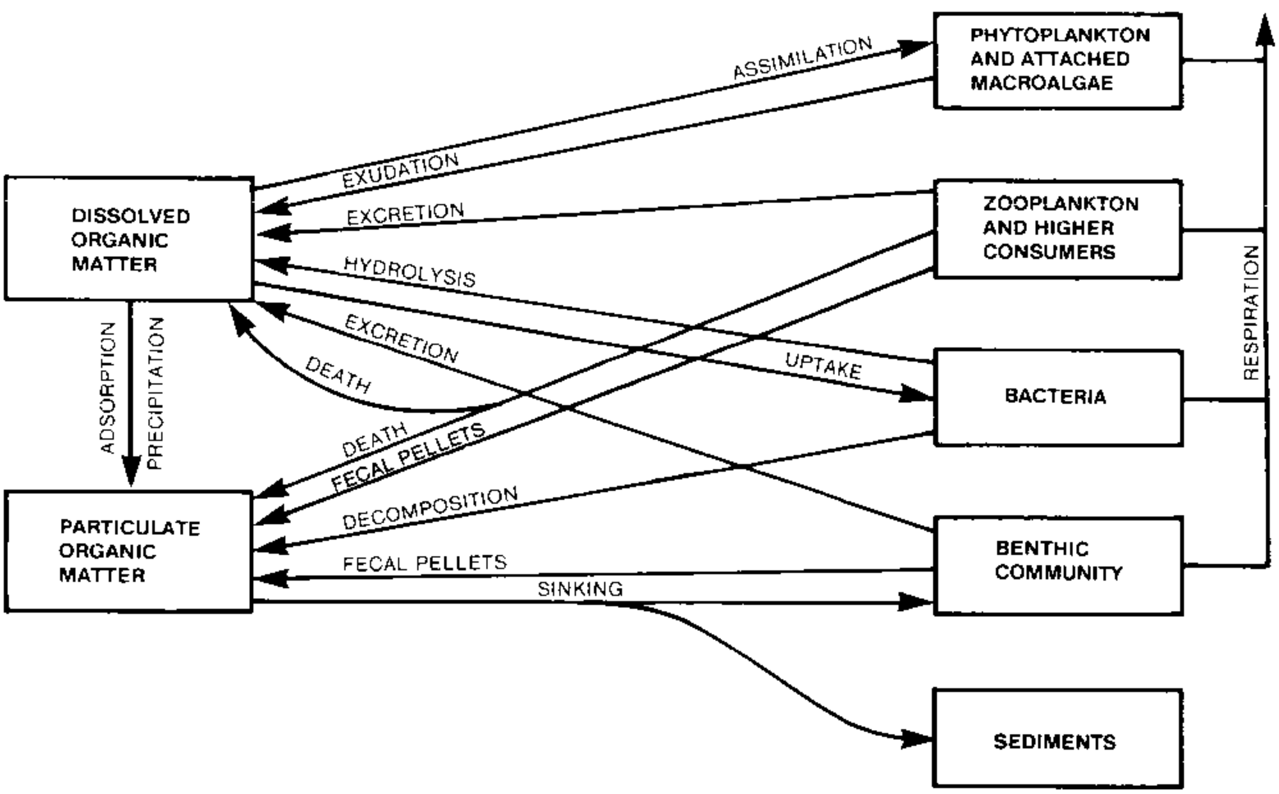


Figure 5-34. Schematic diagram of the organic matter cycle in the estuarine system.

Particulate matter (detritus) is derived from decaying and fragmented plant material. Zooplankton play an important role in transforming particulate matter through feeding and the release of fecal pellets. During conversion of pesticides, dissolved compounds are released through the liberation of protoplasm (during death or breakage of cells) and excretions. Some simple molecules can be reassimilated by phytoplankton.

The importance of bacteria in the cycling of organic matter is not understood fully. Bacteria assimilate dissolved organic compounds and release carbon dioxide and other nutrients. Bacteria attach to particles and living cells and hasten their decomposition by liberating enzymes. These colonized particles are eaten by filter-feeding and deposit-feeding animals.

A schematic diagram of the organic matter cycle of the oceans is presented in figure 5-34.

INTERACTIONS AFFECTING PRODUCTIVITY AND DISTRIBUTION OF BIOTA

The interactions of the biota with physical environment associated with Maine estuaries are described below. The interactions associated with fish and birds are described in detail in chapter 11, "Fishes," chapter 14, "Waterbirds," chapter 15, "Waterfowl," and chapter 16, "Terrestrial Birds." In addition, interactions associated with commercially important invertebrates are discussed in chapter 12.

Phytoplankton

Phytoplankton require adequate sunlight, nutrients, water temperatures, and salinity for optimal growth. The specific requirements vary with the species. Seasonal changes of the above factors in the water column (see "Hydrography" and "Nutrients" in chapter 4) largely control the species compositon and biomass of the phytoplankton populations.

In winter, the deep mixing of the water column (figure 5-35) may limit phytoplankton growth by carrying the phytoplankton below the level where sufficient sunlight exists to support growth. If the depth of the water is shallow, phytoplankton usually do not fall below the level of light penetration and constantly are mixed back up into the photosynthetic zone. This "critical mixing depth" is considered to be about three times the depth of the photic zone (the depth of the level at which light intensity is reduced to 1% of its surface intensity). The critical depth in Maine coastal waters is about 130 to 200 feet (40 to 60 m). Some areas of coastal Maine estuaries are this deep (e.g., the Sheepscot).

Winter water temperatures also limit phytoplankton growth. For about every 18° F (10°C) change in water temperature between 32 to 68°F (0 to 20° C), the photosynthetic rate is changed by about 50% (Yentsch et al. 1974). These authors conclude that the major effects of temperature would occur in early winter but after that the effects of changes in temperature would be difficult to distinguish from other factors such as nutrient availability.

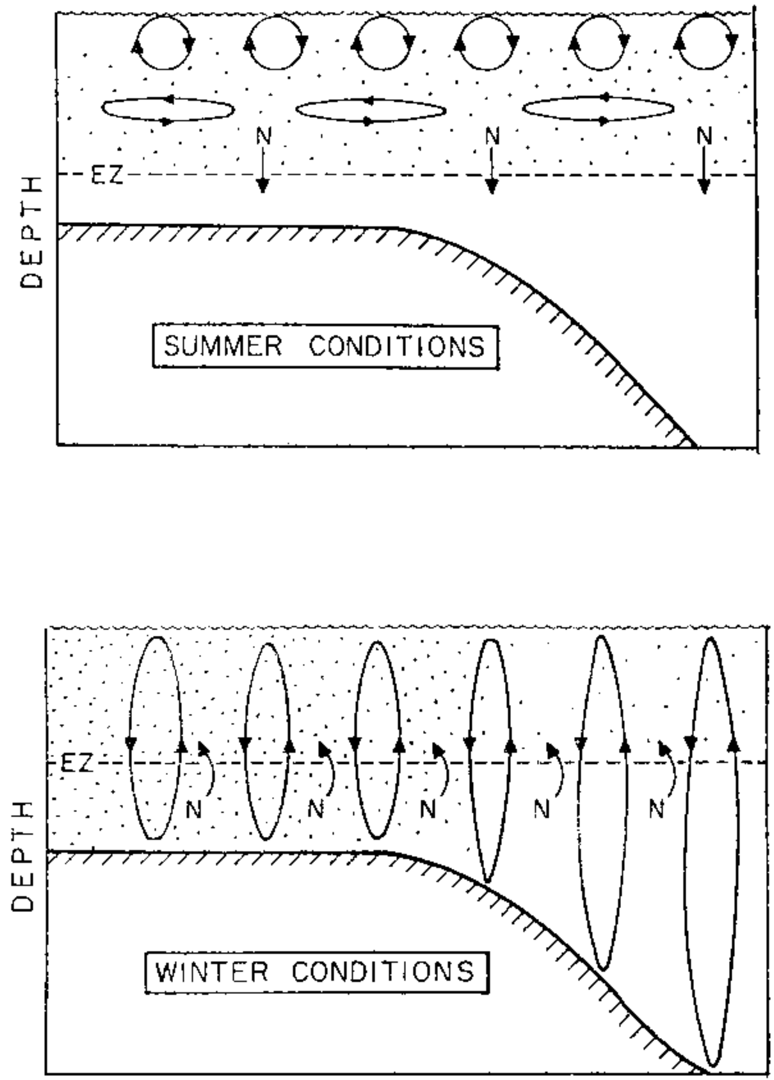


Figure 5-35. Physical conditions of the estuarine water column during summer (stratified) and winter (well mixed) which affect phytoplankton growth. Arrows indicate mixing; N= nutrients; dots are phytoplankton (Yentsch 1977).

In summer, when the thermocline develops and waters become stratified (figure 5-35), the phytoplankton consume all or most of the nutrients available. Once the supply of nutrients is exhausted, growth is arrested and mass mortalities occur.

Optimal environmental conditions for phytoplankton growth (i.e., the intermediate condition between vertical mixing and stability) occur in spring and fall and give rise to spring and fall blooms of algae.

When phytoplankton production in the characterization area is compared with other temperate regions, general trends are noted. Mean annual and maximum cell densities of phytoplankton and chlorophyll concentrations are higher in many bays and estuaries south of Cape Cod than in Maine waters. The higher productivities in southern New England nearshore waters may be due to the following: water temperatures are higher for a longer period of time, the period of optimal light is longer, and the nutrient levels are probably higher due to municipal sewage in the runoff from the large population centers in these areas. In summary, the limited light intensities (due to higher latitudes) combined with low water temperatures and generally low levels of land-based nutrient inputs result in phytoplankton productivities in nearshore waters of the characterization area that are lower than those of southern waters but higher than those of the Gulf of Maine.

Estuaries have higher productivity than coastal marine waters. Generally, the maxima of production are similar but production is maintained over a longer time period in estuaries, because of mixing. For most estuaries, it is a combination of the following factors that make estuarine waters richer in terms of phytoplankton production than coastal waters or waters of the Gulf of Maine:

1. Nutrient enrichment associated with inflow of fresh water;
2. Updraft of nutrient-rich deep water because of displacement of surface water by freshwater inflow;
3. High rate of nutrient regeneration associated with shallow water sediments;

4. Mixing processes associated with tidal energy.

Macroalgae

The physical and chemical factors that control macroalgal productivity are varied and may differ substantially between species. The factors governing the productivity of marine macrophyte communities are the availability of light, availability of suitable substrata, suitable salinities and water temperatures, and an adequate nutrient supply. Tides carry life sustaining oceanic compounds to intertidal macroalgal populations.

Growth of the dominant intertidal alga, rockweed (Ascophyllum nodosum), is limited by low water temperatures (below 50°F; 10°C). Generally, the warmer the water the greater the productivity and biological activity in Maine estuaries. In winter the stress associated with surface freezing probably depresses growth. An indirect effect of warmer (summer) water temperatures (around 68°F or 20°C) in Maine is that grazing activity would increase.

Factors such as ice scouring, wave action, and grazing, which dislodge or consume the rockweed increase the rate of turnover of algae, thus increasing net growth. Wave action is also a factor in determining distribution and abundance of macroalgal species. Certain species (e.g., *Fucus* spp.) thrive in areas of increased wave action, while others (e.g., rockweed) prefer more protected areas. Greater wave action and steeper shores promote the development of more hardy plants (e.g., *Fucus* spp.) which are resistant to wave drag and abrasion. Biomass per unit of area also tends to be somewhat lower in the high energy, wave-exposed shores along the headlands and islands of the characterization area than in more protected areas. In the sublittoral zone wave action influences productivity only at the uppermost levels.

Populations of subtidal laminarians, or kelp (the dominant subtidal algae), are restricted to areas of suitable substrata and relatively high salinity and, therefore, are limited to the seaward end of estuaries. As with many subtidal plants light availability greatly influences laminarian growth. Therefore these algae only grow in shallow subtidal areas (to 20 m). In areas of high light penetration algae grow at greater depths, whereas in turbid areas growth is confined to shallower depths. In summer, when solar radiation is highest, some light-sensitive algae do not grow in shallow water. In contrast to the intertidal fucoids, which grow best at high temperatures, laminarians grow fastest at low water temperatures and appear to grow least when temperatures reach about 68 $^{\circ}$F (20 $^{\circ}$C). Their major growth period is winter and spring. In addition to the possible stress of higher summer temperatures, lack of available nitrogen (see "Nutrient Cycle," page 4-48 in chapter 4) may limit summer and fall kelp production.

Zooplankton

Tidal flushing exports and imports various marine species of zooplankton to estuaries. Certain zooplankton species that live in the offshore waters are introduced into Maine estuaries and become a temporary component of these ecosystems. In estuaries where the circulation is restricted, zooplankton populations are more endemic, but the composition is dependent largely on the distribution of salinity and temperature for a given estuary (Jeffries and Johnson 1973). These two factors have far greater seasonal ranges in estuaries than in the open coastal waters but the accompanying biological phenomena in both habitats bear much in common.

Temperature is largely responsible for regulating the species composition of zooplankton that occur in the estuaries. Each species has particular temperature requirements for growth, reproduction, and survival. As one group appears another disappears and production is maintained throughout the year, despite annual temperature ranges that sometimes exceed the reproductive tolerances of all the groups. Within each group, annual propagation is dependent upon overwinter survivors or the maturation of new individuals from resting eggs produced the previous year. Temperature, along with food supply (quantity and quality), also controls the rate of growth of zooplankton.

The concentration of salt in an estuary forms a fresh- to salt-water gradient that limits the distribution and abundance of various species of zooplankton. This factor separates estuarine from offshore or coastal populations of zooplankton. The interactions of temperature and salinity have very specific effects on certain estuarine species. They largely control the distribution and seasonal abundance of many species.

Jeffries (1967) has classified copepods into five groups according to their ability to reproduce along a salt-concentration gradient: (1) fresh water species; (2) true estuarine (brackish water) species; (3) estuarine-marine species (widely distributed in an estuary and to a limited extent in open coastal waters); (4) euryhaline-marine species (coastal and mouths of estuaries); and (5) stenohaline marine species (open water). Representatives from each group form a chain of overlapping species populations along the salt gradient from fresh water to fully marine conditions. The exact relations to salinity are determined in part by the specific nature of the embayment and its flushing mechanisms. Correlations between salinity and species distribution often are not immediately clear, because the density of a planktonic population in an estuary also is influenced by conditions up and downstream from the point of observation (Jeffries and Alzara 1970).

Benthic Invertebrates

Each benthic invertebrate species has certain physical and chemical requirements for survival. Chief among these are suitable temperatures, salinities, substrata, and currents.

The differences in water temperatures and ranges of water temperature between the northeastern part of the characterization area (regions 5 and 6) and the southwestern regions (1 to 4; see "Hydrography," page 4-11in chapter 4) is a major factor controlling which species inhabit these areas. Although much overlap exists and the boundary is not distinct, a broad zoogeographic boundary appears to exist in the area of region 4. Many invertebrates in the northeast (regions 5 and 6) have northern affinities and do not occur or have reduced occurrences west of region 5. In the southwest (regions 1 to 4) many species have southern affinities and are not found or rarely are found north of region 4.

Many of the species with southern affinities need a certain minimum temperature to spawn and occur only where these temperatures are reached with sufficient frequency. Maine has certain warm-water pockets, such as the upper Sheepscot Estuary (region 2), where summer water temperatures are high enough to support populations of species such as the American oyster and xanthid crabs, which have their centers of abundance much farther to the south. Less variable environmental conditions in the eastern regions (5 and 6) may allow for the development of diverse benthic communities. Eastern Maine and the Quoddy region are the most environmentally stable areas in the northeastern United States.

Salinity has a profound effect on the distribution of estuarine benthic invertebrates. This is discussed in detail below in the class level discussion of unconsolidated bottom but, in general, species diversity decreases from the mouth of the estuary upstream to fresh water.

Substratum requirements vary among species. Some species live on a variety of substrata, while others are quite specific in their requirements. Bedrock, boulders, and mollusc shells, are suitable habitats for animals that must attach to a stable surface. Sedimentary environments are inhabited by animals (e.g., clams and worms) that burrow into the substratum.

Water currents supply food to the benthos by transporting phytoplankton or detritus. They likewise supply respiratory gases, remove some waste material, and act as a dispersing medium for pelagic larvae. Water areas that have curents have relatively high productivity, probably because of the increased food supply (i.e., more phytoplankton passing by). Large numbers of mussels and associated animals usually are found in these high energy areas.

Relatively high summer temperatures in areas exposed during low tide sometimes cause desiccation, particularly if strong winds are blowing. Ice formation (see "Climatology" above) sometimes suffocate, dislodge, freeze, or displace benthic animals. Some intertidal animals (clams and worms) survive short periods of freezing.

Fog and sunlight have opposite effects. Since areas facing south receive more solar energy than those facing north, they are likely to be warmer and drier. Heavy fog (see "Climatology" above) sometimes protects animals from desiccation.

Waves are a factor in determing the penetration of animals into the intertidal subsystem. During periods of heavy waves, areas higher in the intertidal subsystem are wetter than during calm seas (see "Climatology" above and "Introduction to Subtidal and Intertidal Subsystems," below). Waves also carry floating debris which can grind across the shore and dislodge animals.

The physical nature of the bottom influences the distribution and abundance of animals. For example, benthos that live in intertidal sediments are protected somewhat from desiccation because sediments with finer consistencies (see table 5-3) retain more water in their interstitial spaces at low tide. Cracks, crevices, undersides of rocks, and tidepools also are areas that are less subject to drying. These areas support more diverse animal life than the more exposed surfaces.

The angle of a beach-like shoreline determines not only how far up the beach a wave will surge before its energy is dissipated but also how quickly the water will drain from it. The water drains off flat, wide, sandy or muddy shores very slowly and this lessens the threat of desiccation. Tidal area also affects animal abundance and distribution. Large tides in the northeastern coastal region of the characterization area (see "Hydrography," page 4-11 in chapter 4) create larger intertidal zones and potentially higher benthic diversity than those in southwestern coastal Maine.

Decomposers

Temperature strongly influences microbial processes. Even though bacteria have been shown to function at $32^{\circ}F$ ($0^{\circ}C$; Ingraham 1962), their growth and metabolic activity at low temperatures is extremely slow. Seasonal cycles of microbial activity are pronounced, with most of the activity occurring during spring, summer, and fall. The largest phytoplankton populations usually occur in spring but the abundance of decomposers peaks somewhat later (Novitsky and Passman, unpublished). Bacterial and fungal decomposers generally are able to function at lower temperatures than phytoplankton.

The geology of the Maine coast plays a large role in controlling the size and type of decomposers. Dale (1974) reported that the abundance of bacteria associated with sediments in an intertidal basin at Petpeswick Inlet, Nova Scotia, was correlated highly with grain size and other sedimentary properties. A fine silty or sandy bottom supported a large bacterial population and a rocky or cobble bottom supported a smaller population.

The upper intertidal pools in the characterization area harbor unique bacterial communities. Certain "salt-tolerant" bacteria were found in tidal pools in nearby St. Andrews, New Brunswick, Canada (Forsyth et al. 1971). They concluded that the increased salt concentrations in these pools, resulting from evaporation, supported these bacteria.

BIOLOGICAL PRODUCTIVITY

Primary Productivity

Primary productivity, the rate of input of photosynthetically fixed organic carbon, is fundamental to the maintenance of marine and estuarine biological systems. While plant communities provide many potentially important requirements of other organisms (e.g., food, nest sites, shelter, and roosting sites), their relative importance to marine or estuarine systems may be measured best by comparing their primary productivity. All references to production here refer to net production, which is that production stored as chemical energy after respiratory demands have been met.

Although too little data are available to predict accurately marine or estuarine primary productivity in Maine, it is possible to estimate the primary productivity of some of the important plant groups. Such estimates facilitate comparisons between the primary productivity in various plant groups characteristic of specific habitats. These comparisons aid in understanding plants' functional relationships in coastal Maine. Those plant groups that have measurable primary production, based on biomass, carbon content, carbon assimilation, and habitat coverage, are phytoplankton, intertidal macroalgae, and the taxonomically higher plants of emergent wetlands, which are described below. The productivity of other plant groups, such as those algae that inhabit mudflats and salt marshes, are so poorly understood that annual productivity estimates cannot be made. Input of organic matter from land drainage and rivers is yet another source of production not adequately addressed.

Measurements were made of intertidal macroalgal biomass and the substrata generally suitable for colonization by large seaweeds [e.g., stones greater than approximately 2.5 inches (6.4 cm) in diameter] at 46 randomly selected sites throughout Lincoln County (region 2; Topinka and Tucker, unpublished). The wet weight biomass on suitable rocky substrata averaged 18 pounds (8 kg) of macroalgae/m^2. Over 90% of the biomass was rockweed. Previous studies of this species suggested that approximately 10.3% of its wet weight was carbon. On this basis the quantity of macroalgal carbon per unit area of suitable rocky area was determined to be 823 g C/m^2. This is the standing stock of carbon and will serve as a point of reference in subsequent productivity estimates.

In productivity estimates, it is assumed that the intertidal seaweed biomass is turned over once a year. Rough approximations of seaweed productivity are commonly made by assuming one biomass turnover per year (Luning 1968). One cycle of intertidal seaweed carbon per year therefore yields a productivity of 823 g C/m^2 /yr . MacFarlane (1952) and Westlake (1963) reported a similar productivity of 640 to 840 g C/m^2/year in rockweed populations in Nova Scotia.

An examination of wetlands identified by the NWI shows that the area of dense intertidal macroalgal colonization may be approximated by summing marine and estuarine intertidal rocky shore areas. The assumption is made that this area is equivalent to that designated as suitable substrata [composed of stones greater than 2.5 inches (6.4 cm) in diameter] that would support dense populations of intertidal fucoid seaweeds. Data from 99 randomly selected sampling sites in Lincoln County indicate the rocky shore habitats identified by the NWI included reflective areas above the seaweed zone as part of intertidal areas. To correct for this situation, the estimated area of seaweed habitat was estimated to be 56% of the identified rocky shore habitat (Topinka, unpublished). Based upon adjusted NWI habitat data and the above productivity data, intertidal seaweed productivity values were calculated (table 5-4). Intertidal seaweed contributes about 40% of total estuarine primary production, and dominates estuarine primary production in regions 3, 4, and 5.

Table 5-4. Estimate of Net Annual Primary Production (kgC/y X 10^6) by Region and Percentage Contribution to the Total Productivity of Producers Found in the Estuarine System.[a]

	Region						
	1	2	3	4	5	6	All regions
Intertidal seaweed	5.2	2.1	8.7	18.6	11.3	12.5	58.4
%	32	8	45	53	51	41	39
Estuarine emergent marsh	4.4	10.0	2.2	1.9	4.4	5.4	28.3
%	27	37	12	6	20	17	19
Estuarine phytoplankton	6.7	15.0	8.2	14.4	6.5	12.8	63.6
%	41	55	43	41	29	42	42
Total production	16.3	27.1	19.1	34.9	22.2	30.7	150.3
%	100	100	100	100	100	100	100

[a]Topinka, unpublished.

Although few estimates of estuarine primary production by phytoplankton exist, phytoplankton dominate total estuarine primary production. Estuarine phytoplankton productivity in Maine has been estimated at approximately 150 g C/m^2 /year by standard C_{14} assimilation techniques. Although productivity varies considerably among estuaries, this estimate represents a value between gross and net primary productivity, which is suitable for rough estimates of estuarine phytoplankton production. The above estimate of productivity is applied below to the estuarine areas identified by the NWI.

NWI data on the total estuarine subtidal area have been employed in estimating the extent of subtidal phytoplankton habitat. Phytoplankton, however, are also present in waters overlying intertidal regions. The intertidal zone represents a large percentage (40% to 60%) of total estuarine area among the regions. The phytoplankton productivity of waters overlying intertidal bottoms was assumed to be approximately 40% of that in deep estuarine regions. This productivity in intertidal areas represents a large percentage (27%) of total estuarine phytoplankton productivity. Estuarine phytoplankton is the dominant estuarine producer in regions 1 and 2 and accounts for a large percentage (42%) of total estuarine production (table 5-4).

Emergent wetland areas are often highly productive. Productivity per unit area is examined under "Emergent Wetlands" below. Emergent wetlands that were measured in the NWI included both salt marsh and brackish water marsh. For the sake of productivity determinations, salt marsh represents the major type of marsh and is dominated by cordgrass (Spartina alterniflora). It is possible therefore to make salt marsh productivity estimations based on emergent wetland area data from the NWI and productivity data for cordgrass.

Maximum biomass data give a minimum average productivity of 1216 g dry weight/m^2/year for cordgrass in Maine (Vadas et al. 1976). Assuming that 40.77% of this dry weight is carbon (Burkholder and Bornside 1957) annual carbon production is 496 g/m^2. Salt marsh production is presented in table 5-4 and accounts for about 20% of estuarine production. Salt marsh productivity in Maine will be discussed further below. In regions 1 and 2, salt marsh production accounts for approximately one-third of the total production (table 5-4).

In comparison with the estuarine phytoplankton habitat, intertidal seaweed beds and salt marshes occupy relatively small areas. Areas supporting intertidal seaweeds and salt marshes are nevertheless important because their productivity per unit area is great. This is in contrast to estuarine phytoplankton which occupy large areas but the productivity per unit area of which is relatively low.

Although it is clear that the phytoplankton, intertidal seaweeds, and salt marshes all make important contributions to estuarine production, other plant groups, such as the subtidal benthic algae, salt marsh algae, mudflat algae, and eelgrass populations also may be important contributors to primary production. Much research needs to be done before estuarine and inshore coastal productivity can be better defined.

Secondary Productivity

Secondary productivity applies to the production of animal tissue, that is, the growth of trophic levels above the primary producers. It is a measure of energy flow through the various components of the ecosystem. Data on secondary productivity in coastal Maine estuarine systems are lacking.

Biomass or standing stock is the weight or volume of animal tissue in a given area (e.g., per square meter) and it is often used as a crude indication of productivity, on the assumption that biomass and secondary productivity are correlated directly. This is not necessarily true because communities of large, long-lived molluscs have a high biomass but low secondary productivity because of their small turnover rate. Conversely, a community dominated by small, short-lived species, such as amphipods and polychaetes, has low biomass and high productivity. If, however, two communities are composed of the same types of organisms, biomass comparisons ought to reflect differences in productivity. Limited biomass data are available on animals in the characterization area. Sherman (1968) compared zooplankton biomass along the Maine coast and found lesser amounts in northeastern Maine (region 6). Such a pattern is unexpected, because the biomass of other groups, benthos, birds, marine mammals and herring, is assumed to be high in region 6. Larsen (1979) presents biomass values for the shallow water benthos of the Sheepscot River estuary, which are similar to those of other shallow water areas (see "Estuarine Unconsolidated Bottom" below).

CLASS LEVEL DISCUSSIONS WITH INTRODUCTION TO THE SUBTIDAL AND INTERTIDAL SUBSYSTEMS

Estuaries consist of subtidal and intertidal subsystems that are separated by physical boundaries. The intertidal subsystem is that area between extreme high and extreme low tides that varies during the month (lunar cycle; see chapter 4, page 4-18). The subtidal subsystem extends into the estuary beyond the extremes of low water.

The biological boundaries of the intertidal subsystem, which often differ from the physical boundaries, enclose the area called the littoral zone where the biotic assemblages grade from the subtidal to terrestrial environment. The difference between the physical intertidal zone and the littoral zone is shown schematically in figure 5-36. The width of the littoral zone is greater than the width of the physical zone in wave exposed areas. Waves and their spray wet the higher intertidal levels and allow for the development of intertidal communities in these areas. The areas of subtidal subsystem and intertidal subsystem were calculated as comprising 51% (66,693 acres; 27,001 ha) and 49% (63,382 acres; 25,661 ha), respectively, of the estuarine system in coastal Maine, based on NWI measurements.

The Subtidal Subsystem

The estuarine subtidal subsystem is permanently flooded by ocean waters but has lower salinities (<30 ppt) than offshore coastal waters. The four types of habitats in the subtidal area are the water column, rock bottoms, unconsolidated bottoms, and aquatic beds. Fifty percent of the subtidal area of coastal Maine is in regions 2 (28%; 18,711 acres; 7575 ha) and 6 (22%, 14,163 acres; 5734 ha). Regions 1, 3, 4, and 5 have 5908 acres (239 ha; 9%),

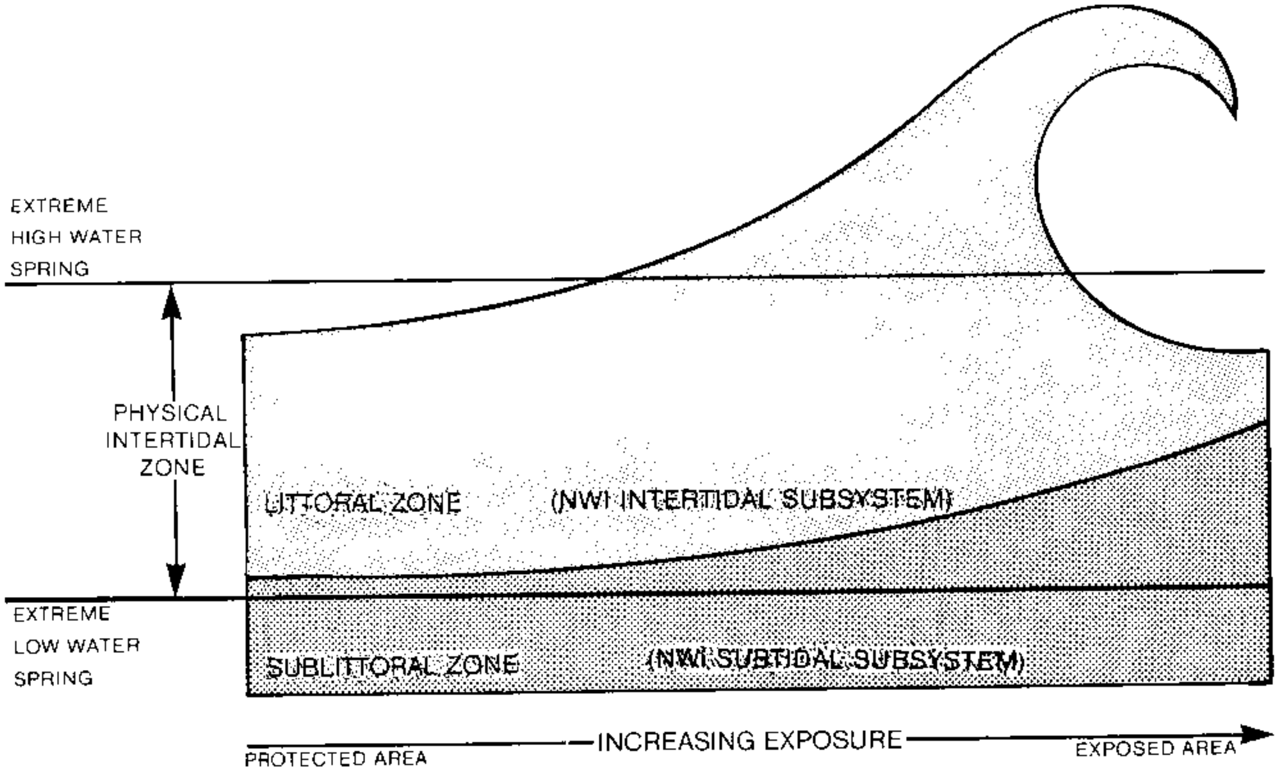


Figure 5-36. Comparison of the boundaries of the physical intertidal zone and the littoral (biological intertidal) zone with increasing exposure to wave action (adapted from Lewis 1964).

10,382 acres (4203 ha; 15%), 10,709 acres (4336 ha; 16%), and 6820 acres (2761 ha; 10%), respectively.

The relative physical stability of the subtidal environment allows for the establishment of diverse, highly organized communities. Ecological factors that affect the biota sometimes are quantitatively different in estuaries than in marine systems. Since the biota present in the brackish waters of estuaries are usually of marine origin, in order to survive they must physiologically adapt to estuarine conditions, such as reduced or highly variable salinities and temperatures. Areas that have greatly reduced and/or variable salinities have the fewest species (see "Estuarine Unconsolidated Bottoms" below). In subtidal subsystems tidal currents that carry suspended sediments and detritus are an important component of the subsystem. Estuarine productivity is dependent largely on attached macroalgae, macrophytes, benthic diatoms, and land-derived detritus, whereas marine systems are dependent largely on phytoplankton productivity.

In general, pollution loads are greater in estuarine areas than in nearby coastal waters because of their higher human populations. Estuarine organisms generally are more adaptable to a wide range of environmental conditions and are more tolerant of perturbations than their marine relatives. Indeed, some of the species characteristic of upper estuarine areas are also characteristic of polluted water (Boesch 1973). Increased nutrient levels in estuaries due to sewage favor macroalgae with greater nutrient demands, such as sea lettuce (Ulva lactuca) and the green algae, Enteromorpha sp.

Turbidity may influence plant distribution. Turbidity is usually greater in estuaries than in coastal waters, so plant growth (e.g., macroalgae) in estuaries is limited to shallower waters.

Phytoplankton, most zooplankton, and pelagic fish spend most, if not all, of their lives within the water column. The bottom is occupied by benthic invertebrates and demersal fish and, in shallow water, macroalgal species, which are important producers. Waterbirds utilize the surface or near surface estuarine subtidal waters for feeding and resting.

Subtidal marine benthic invertebrates are of direct and indirect commercial importance. Lobsters, scallops, and crabs, which are found in high salinity subtidal areas of estuaries, have all supported major shell fisheries and a significant portion of Maine's economy is dependent on these species. Clams and worms are common in subtidal areas of estuaries and, although they are rarely harvested there, their reproduction probably helps to replenish depleted intertidal populations. The smaller invertebrates, such as amphipods and worms, comprise the major food source of flounder and other bottom-feeding fishes.

Little research has been done on the subtidal estuarine benthic communities of rock bottoms or aquatic beds in coastal Maine; therefore, the data presented here are sparse. Two relatively detailed studies of estuarine unconsolidated bottom sediments (Larsen 1979; and Larsen and Doggett 1978b) provide insight into the effects of salinity on benthic invertebrate communities.

Subtidal water column. The open water column is the habitat of pelagic organisms, that is, those that do not have regular contact with the bottom. These organisms include phytoplankton, zooplankton, pelagic fish, birds, and marine mammals.

The water column and the benthic environment interact. Some nutrients that support phytoplankton growth are recycled in bottom sediments; some zooplankton are larvae of benthic species, and pelagic fish often lay their eggs on the bottom. The marine water column habitat is contiguous with the estuarine water column habitat. Organisms in the water column move or are transported extensively between marine and estuarine systems. Pollutants in the estuarine water column are transported into the marine water column.

In the Gulf of Maine, phytoplankton production is not constant throughout the year, but the pattern is not necessarily similar between estuarine and coastal waters. Those differences are due to the characteristics of the individual estuaries. In Maine, only Casco Bay and the drainage areas of the Penobscot and Kennebec Rivers possibly would have significant organic discharge. Possibly the continued summer-fall peaks of chlorophyll-a in upper Penobscot Bay (figure 5-37) rather than the spring and fall peaks that are typical of coastal waters are a result of high nutrient concentrations. This summer-fall peak has also been reported in Great Bay, New Hampshire (Normandeau Associates 1974). However, in Penobscot Bay the source of nutrients may be either freshwater inflow or upwelling from nutrient-rich deeper waters in the Gulf of Maine (see "Plant Nutrients" above).

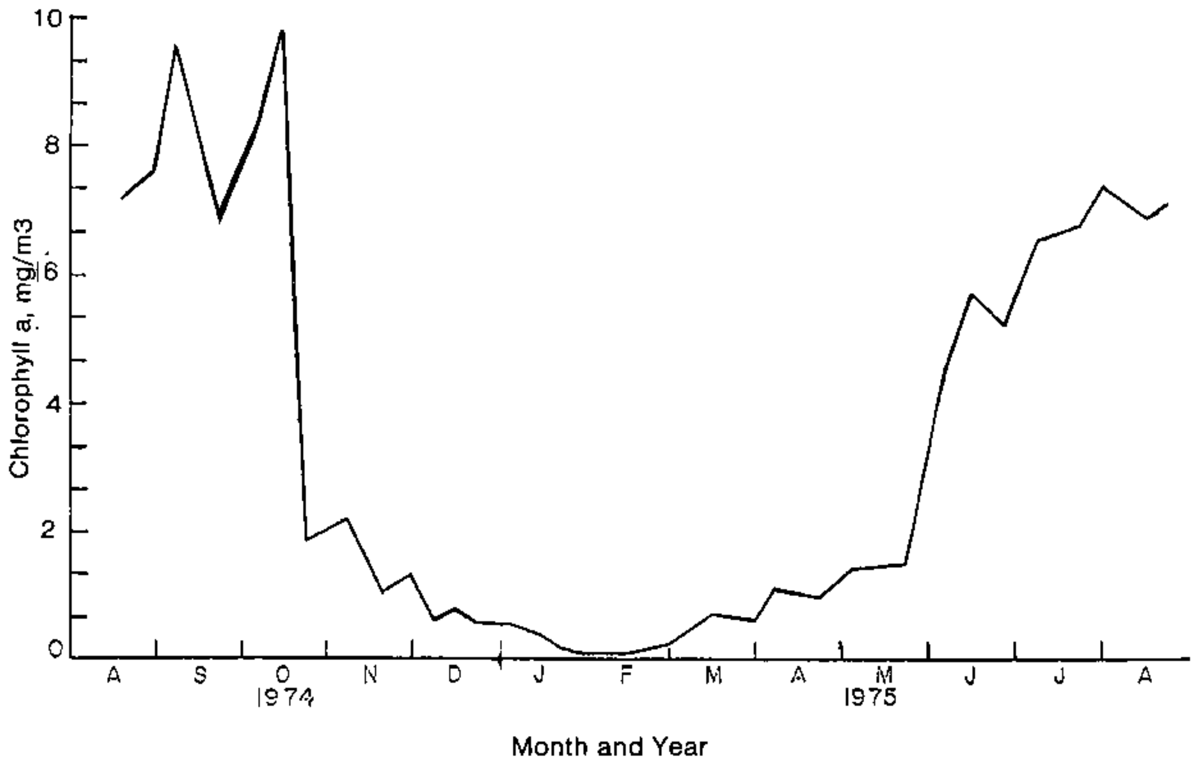


Figure 5-37. Monthly measurements of chlorophyll-a concentrations (mg/m^3) in upper Penobscot Bay for 1974 to 1975 (Bertrand 1977).

In the Damariscotta River estuary, nutrient (nitrates) levels are related inversely to cell densities of phytoplankton. In this estuary, the spring and fall peaks in productivity are similar to those in coastal waters. Apparently, nutrients are not available continuously at high enough levels to sustain phytoplankton productivity throughout the summer.

Much of the supply of nutrients in the Sheepscot River estuary is thought to be due to the inflow of nutrient-rich sea water (Garside et al. 1978; see "Plant Nutrients" above). Phytoplankton in this estuary are not nutrient limited and populations may be limited by heavy grazing (Garside et al. 1978).

Many nearshore sediments are rich in phosphorus and nitrogen compounds. These nutrients show concentrations 10 to 100 times higher in the interstitial spaces in sediments than in the water column (Yentsch, unpublished). Periodic mixing of the sediments (i.e., resuspension) may be an important mechanism for adding nutrients to the water column. As an example, tidal currents that mix the water column bring nutrient-rich water into the euphotic zone and prevent thermal stratification; however, Petrie (1975) believes that nutrients in the Damariscotta estuary probably are mixed to the surface. This mixing also entrains some phytoplankton down below the photic zone, reducing productivity.

Tidal currents also probably help to retain the sediment load in the water column. Increased turbidity due to tidal currents, which are particularly prevalent in shallow bays, may have an inhibitory effect on phytoplankton productivity. McAlice and coworkers (1978) found that the biomass of phytoplankton was lower in Montsweag Bay than in the Sheepscot Estuary. The lower phytoplankton biomass is attributed to higher turbidity in the shallow bay.

Tidal fluctuations also may be responsible for changes in phytoplankton composition, particularly in the upper estuary. Phytoplankton samples at the uppermost estuarine station in the Damariscotta River estuary show that species composition of phytoplankton changes with the tides (Petrie 1975). Changes in species composition in Penobscot Bay (Burkholder 1933) and the Bay of Fundy (Gran and Braarud 1935) also have been attributed to tidal fluctuations.

The only study in Maine which examines phytoplankton communities along the estuarine gradient was conducted by Petrie (1975) in the Damariscotta River estuary. This estuary differs from most in Maine because relatively high salinities were recorded throughout its length, with the exception of the uppermost station. At the other stations, phytoplankton composition was about the same along the estuarine gradient from June to November. In winter, increased spatial heterogeneity is noted.

A predominance of diatoms rather than dinoflagellates (as in the Gulf of Maine) during the summer in the Damariscotta River estuary probably is due to the availability of ample nutrient supplies (Petrie 1975). Petrie cites Margalef's statement (1963) that the turbulence (in estuaries) overcomes the competitive advantage of being motile and allows the nonmotile diatoms to take advantage of the nutrients. The St. Croix River had a more pronounced diatom abundance than Passamaquoddy Bay (Davidson 1934). Davidson felt the higher nutrient levels in the estuary partly were responsible.

In temperate areas, such as the waters of New England, the number of species (diversity) generally increases with a decrease in population size, that is, low chlorophyll concentrations would be associated with high diversity. Seasonal changes in the diversity of phytoplankton populations are apparent. During the slow growth season (summer) no single species is very abundant and diversity is high. Conversely, when growth conditions become favorable (spring) species diversity sharply decreases. This seasonal pattern (corresponding to the nitrogen cycle) has been noted by Petrie (1975) in the Damariscotta River estuary (region 3). The significance of diversity can be seen when growth in rich and poor areas is compared (figure 5-38). In the southwestern regions of coastal Maine the nutrient-rich estuaries generally support phytoplankton populations that are much less diverse than those in the relatively nutrient-poor offshore surface waters. In northeastern Maine (regions 5 and 6) estuaries probably support phytoplankton populations similar to those in the marine system because ocean waters, by which the estuaries in these regions are well flushed, are well mixed and relatively homogenous.

A succession of zooplankton occurs in estuarine waters of the characterization area. Each species has a seasonal cycle of peaks in abundance followed by decreased numbers. The peaks are not synchronous among species; therefore, the seasonal composition of species is variable. Within each species, propagation is initiated by a few individuals that have survived the winter or by maturation of individuals developing from resting eggs produced the previous year, as may be the case for the copepod Centropages hamatus (Fish and Johnson 1937). The life cycle of various species is controlled by food supply (quantity and quality) and physical factors (see below).

Only a few species of zooplankton are either dominant or abundant in the coastal waters of Maine. The seasonal abundance and time of reproduction of 11 species of copepods and seven groups of meroplanktonic species are discussed in appendix F of chapter 4. The zooplankton Calanus finmarchicus is not dominant in the estuaries of Maine; however, it is abundant in coastal waters of Maine. Meroplanktonic zooplankton, which are addressed in appendix F of chapter 4, are characterized as being (1) dominant (i.e., abundant); (2) important to the benthic population (e.g., barnacles, molluscs, or polychaetes); (3) important as predators (i.e., coelenterates or Sagitta elegans); or (4) dominant in marine populations and included for comparison (i.e., Cladocerans).

Data on zooplankton species composition come from studies reported by McAlice (1970 to 1977) on the Montsweag Bay area of the Sheepscot River estuary and by Lee (1974) on the Damariscotta River estuary. Gross estimates of the relative abundance of zooplankton in 1975 to 1976 are given for the Montsweag Bay area in the Sheepscot River estuary (McAlice et al. 1978; table 5-5). Copepods and tintinnids dominate zooplankton populations in the upper Sheepscot estuary.

Fishes are found primarily in the subtidal zone. Demersal fishes are more closely associated with specific bottom types (classes) than pelagic fishes. The majority of pelagic and some semidemersal fishes range freely throughout the water column and are dependent on estuarine open water habitat for at least part of their life cycle. These fishes include the rainbow smelt, striped bass, spiny dogfish, bluefish, Atlantic mackerel, the herrings (Atlantic herring, blueback herring, alewife, American shad, and Atlantic menhaden), and some trout (Atlantic salmon, brook trout, and brown trout). Fishes are discussed in detail in chapter 11, "Fishes."

A number of bird species use estuarine open water for feeding and resting. Large concentrations of waterfowl inhabit estuarine open water. The most abundant species are eiders, scoters, oldsquaw, scaup, mergansers, goldeneyes, and bufflehead. They are primarily migrants and wintering species. They may feed on a variety of substrates. Dabbling ducks and the above mentioned bay ducks and sea ducks often rest on open water. Large numbers of gulls use estuarine open water both for feeding and resting. Cormorants feed in large numbers on benthic and pelagic estuarine fish. Ospreys, bald eagles, and kingfishers also feed in estuarine open water. Chapter 14, "Waterbirds," chapter 15, "Waterfowl," and chapter 16, "Terrestrial Birds," contain more detailed information on these birds.

Subtidal unconsolidated bottom. In Maine estuaries, unconsolidated bottoms are the predominant habitat type. The preliminary data from NWI indicate that only 5% of the identified estuarine subtidal subsystem consists of unconsolidated bottom. However, the vast majority of the estuarine areas underlying estuarine open water in coastal Maine (subtidal open water comprises more than 90% of the identified subtidal area) is actually unconsolidated bottoms. This habitat probably comprises most of the estuarine floor along with a relatively small area of aquatic beds.

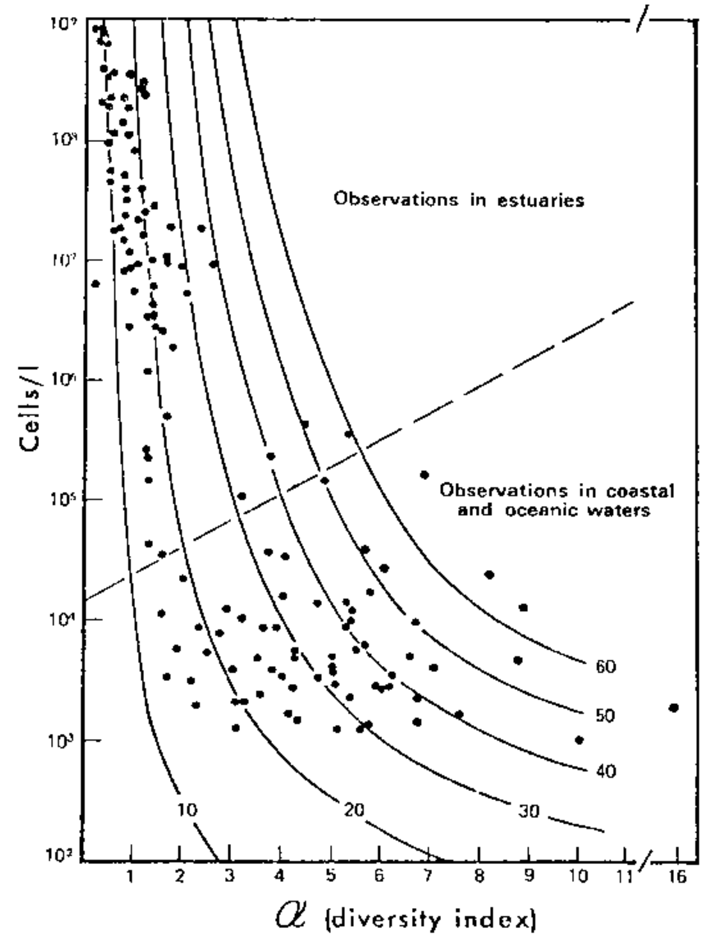


Figure 5-38. Relation of phytoplankton species diversity to phytoplankton population size in marine and estuarine waters (Hulburt 1963).

Table 5-5. Relative Abundance of Major Zooplankton Species in the Sheepscot Estuary (Montsweag Bay) From January, 1975, to December, 1976[a].

Taxa	Individuals/m³
Copepods	21,600
Microsetella norvegica	17,345
Acartia tonsa	2660
Oithona similis	666
Acartia clausi (*A. hudsonica*)	274
Acartia longiremis	207
Temora longicornis	131
Pseudocalanus minutus	117
Eurytemora herdmani	116
Centropages hamatus	56
Centropages typicus	28
Tintinnids	56,145
Rotifers	18,997
Polychaete larvae	6629
Bivalve larvae	2548
Nematodes	1655
Cirriped larvae	987
Gastropod larvae	532
Bryozoan larvae	82
Sagitta elegans	69
Cladocerans	58

[a]Adapted from McAlice et al. 1978.

The unconsolidated bottoms of estuaries are submerged glacial deposits, glacial deposits presently undergoing modification by existing marine processes, deposits originating from present day marine processes (Swift et al. 1971), and/or deposits originating from the fresh water inflow. In general, unconsolidated bottoms in the estuarine system are similar to the sand and mud bottoms discussed in the marine system (chapter 4). These bottoms consist of sediments ranging from pebbly gravel to mud, depending upon the velocity of associated currents. Some channels, where channel bottom velocities exceed 150 to 200 cm/sec, contain gravel (Timson, in preparation) but generally gravelly sand predominates. These channels result either from headward erosion of erosion gullies in tidal flats or from modification of ancestral riverine channels that were submerged during the Holocene Transgression (Kraft et al. 1974).

Macroalgal populations are poorly developed on subtidal unconsolidated bottoms due to lack of suitable substrata for attachment. At greater depths or in other areas where water movement is greatly reduced large stable stones may support minor populations of small plants. Flux of organic matter on unconsolidated bottoms is determined mainly by impact of detritus and organisms from the water column.

The vast majority of research on estuarine benthic invertebrates in Maine has focused on unconsolidated bottoms in the Sheepscot and Penobscot River estuaries. Studies on the Sheepscot include Stickney (1959), Hanks (1961, 1964), Dean and Ewart (1978), Larsen and Doggett (1978b), and Larsen (1979). The benthos of the Penobscot has been examined by Haefner (1967), Dean (1970), Ayer (1971), and Shorey (1973). The Sheepscot studies are the most comprehensive.

From the mouth of the estuary toward upstream, the salinity becomes progressively lower and the fluctuation of salinity and temperature increases until fresh water is reached. These changes produce a natural stress gradient for the fauna and species with limited tolerances are restricted to the oceanic end of the estuary. The more tolerant a marine species is, the further it can penetrate towards fresh water. As a result of these hydrographic conditions, fewer species are present in the upper estuary. This was illustrated for a German estuary by Remane (1934) in figure 5-39. The number of species is lowest at the upper end of the estuary, before fresh water is encountered (salinity = 5 to 10 ppt) and increases both toward the ocean and toward fresh water as environmental conditions become more stable. However, the brackish water invertebrate species of marine origin that can live at the reduced salinities in the middle reaches of estuaries flourish because of the absence of severe competition and predation by more specialized marine species. The species diversity and abundance of benthic invertebrates in subtidal unconsolidated bottoms in Maine estuaries are described below.

In the study of the Sheepscot estuary along an estuarine salinity gradient from oceanic salinity to tidal fresh water Larsen and Doggett (1978b) found species numbers to approximate the shape of Remane's classic illustration (figure 5-39 and 5-40). Differences between the two illustrations are caused by abrupt hydrographic changes in the Sheepscot and the limited sampling in the riverine (freshwater) system in the Sheepscot gradient study. Most individuals found in the area of the "species minimum" in the upper Sheepscot are members of typical intertidal or estuarine species. The amphipod

Gammarus oceanicus and the isopod *Jaera* sp. are examples of the former and the amphipods *Corophium lacustre* and *Gammarus tigrinus* and the isopod *Cyathura polita* are examples of the latter.

The number of species at a particular location depends on the season, substratum, water column stability, pollutional stress, productivity, and salinity. In silt-clay sediments in shallow areas of the Sheepscot estuary Hanks (1964) found 104 species of invertebrates and Larsen (1979) later found 94 species. Over 450 species were found in the deeper, sandier portions of the estuary (Larsen and Doggett 1978b). This translates to 19 species per station in the shallow silt-clay areas and 51 species per station in the deeper sandy areas. Comparative data are not available for other Maine estuaries or for coastal marine waters. Only 27 species of invertebrates were identified by Haefner (1967) in the Penobscot estuary, but it is not known whether this low diversity of species is a natural condition or the result of pollution.

It appears that the Sheepscot estuary supports a diverse fauna. It is not known whether this is typical of Maine estuaries or what factors are important in maintaining this diversity, i.e., limited seasonal temperature and salinity variation, high productivity, habitat diversity, etc. Densities of organisms vary throughout estuaries in response to several ecological factors. Larsen (1979) reports only 771 individuals/m^2 in the shallow silt-clay areas of the lower Sheepscot River estuary, whereas a mean of 4928 individuals/m^2 was found in a more comprehensive study comparing a mixture of shallow and deep water areas by Larsen and Doggett (1978b). Highest densities of individuals (over 20,000 /m^2) were found in the area where species diversity was lowest (upper estuary; see figures 5-39 and 5-40). In these areas of reduced competition and predation, the few species that are able cope with variable conditions are able to proliferate.

The Sheepscot Estuary is productive as well as diverse relative to other temperate and boreal estuaries (table 5-6). It is not known if the same is true of other Maine estuaries.

Biomass (the weight of living animals) values for invertebrates in Maine are available in Larsen's report (1979) of his shallow water survey. This survey covers a low density area. The values (mean at all stations = 3.18 g/m^2 ash-free dry weight; range = 0.59 to 12.4 g/m^2) compare closely with the 0.1 to 4.0 g/m^2 range reported in Chesapeake Bay by Mountford and coworkers (1977) and the mean value of 4.25 g/m^2 found by O'Connor (1972) in stations in Moriches Bay, New York. European values also fall in the same general range; Raymont (1947) 4 g/m^2; Buchanan and Warwick (1974) 3.98 g/m^2 in 80 m mud, and 3.7 g/m^2 (dry weight) in a shallow sandy sea loch (McIntyre and Eleftherious 1968).

Biomass levels in higher density areas (e.g., Sheepscot River and Mystic River, Massachusetts; table 5-6) are undoubtedly considerably higher than those listed above, especially in the species minimum area, where the organisms are larger as well as more abundant. This is indicative of a high secondary productivity and suggests that the potential exists for the support of large populations on even higher trophic levels.

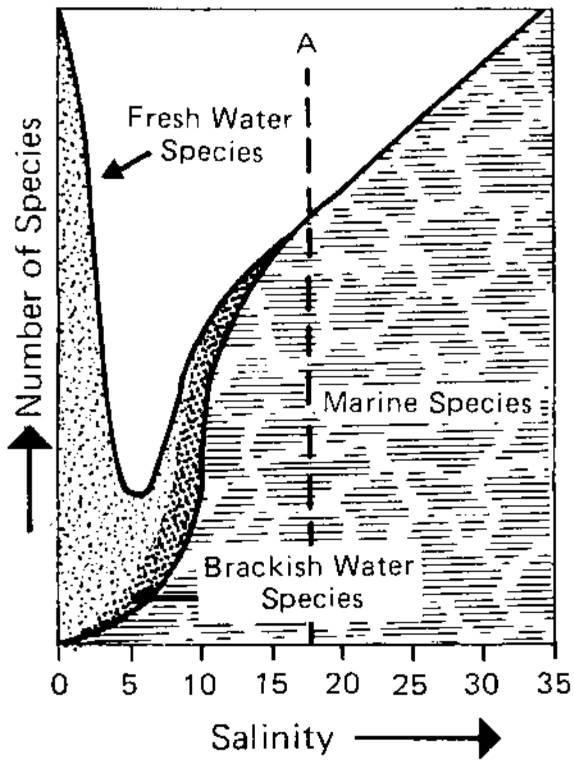


Figure 5-39. The comparative distribution of marine, brackish, and freshwater species along a salinity gradient in a German estuary (after Remane 1934).

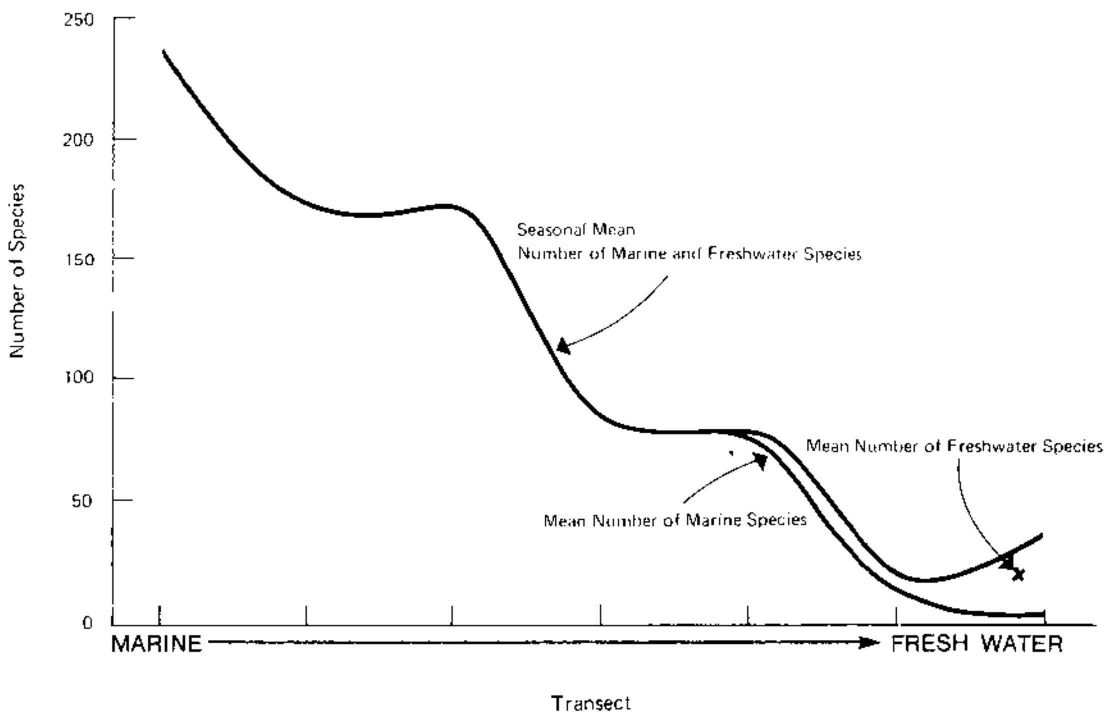


Figure 5-40. Number of marine and freshwater invertebrate species from the mouth to the head of the Sheepscot River estuary (Larsen and Doggett 1978b).

Table 5-6. Average Density of Estuarine Invertebrates in Unconsolidated Sediments of Temperate and Boreal Estuaries and Bays[a]

Location	Mean number individuals/m^2 (sieve size 1mm)	Source
Sheepscot River Estuary, Maine USA		
Gradient Study	4928	Larsen and Doggett (1978b)
Shallow Water Study	771	Larsen (1979)
Mystic River, Massachusetts USA	3000	Rowe et al. (1972)
Moriches Bay, New York USA	1300	O'Connor (1972)
Delaware Bay, Delaware USA	722	Maurer et al. (1978)
False Bay, South Africa	2220	Field (1971)
Gullmarsfjord, Sweden	4198	Rosenberg (1973)
Lambert Bay, South Africa	1153	Christie (1976)

[a]Modified from Maurer et al. 1978 a & b.

Seasonal variations in invertebrate density along the estuarine gradient are minimal at the oceanic end, where environmental factors are most stable, and increase upestuary where physical conditions vary more seasonally. The few species that dominate in the upper estuary undergo extreme seasonal population fluctuations. For example, near the head of the Sheepscot Estuary, the crustaceans Gammarus tigrinus, Corophium lacustre, and Cyathura polita account for over 90% of the individuals present. Their density is 19,603/m^2 in the summer. This drops to 13,140/m^2 in the fall, and to 713/m^2 in the spring. Spring is the time of lowest salinities and lowest temperatures.

Larsen (1979) compared a 1973 survey in the lower Sheepscot with one done by Hanks (1961 and 1964) in 1955. During the intervening 18 years significant changes appeared to occur in mean density, dominant species, species composition, and distribution of species within the study area (Larsen 1979). It is not known if these apparent changes are associated with a long-term environmental trend or if they are simply random fluctuations around a mean condition.

Most of the above discussion is based on the Sheepscot estuary as data are available. As stated in the hydrography and nutrients discussions, considerable difference exist among the physical characteristics of Maine estuaries. Many of these characteristics, such as flow rate, tidal exchange, sill depth, low tide volume, intertidal area, and suspended load, govern the nature of the benthic invertebrates in unconsolidated bottoms. For this reason definitive statements on the other estuaries must await further study.

A variety of fish commonly are found in subtidal unconsolidated bottom habitats (and intertidal flats and beaches at high tide) in Maine estuarine systems. Representative fishes include American sand lance, alligatorfish, wrymouth, lumpfish, Atlantic cod, Atlantic tomcod, the flounders, the skates, sturgeon, and silver hake.

Rock bottom. Subtidal rock bottoms in estuaries are not as extensive as they are in the marine system. The NWI places <1% of estuarine bottom in this class, although much of the rock bottom habitat was classified as open water and the bottom type was not specificed.

Subtidal rock bottoms originated from the submergence of exposed bedrock. Most bedrock bottoms are relatively clear of sediment because most of it has been removed by ocean waves. Wave-generated subtidal currents may continue to remove surficial sediment from as yet uncovered bedrock in depths up to about 20 m, which is the limit of storm wave depth influence along the Maine coast (Farrell 1972).

Rock bottoms in the higher salinity portions of estuaries provide stable substrata for macroalgal attachment. These bottoms are similar to marine rock bottoms and are very productive (see chapter 4). The vegetation is dominated by the perennial brown laminarians (kelps), principally of the genus *Laminaria*. Red and green algae also are present, although the red algae are limited to the lower portions of estuaries. Irish moss (*Chondrus crispus*) may be abundant locally. Little attempt has been made to quantify the subtidal flora of Maine, but subtidal flora would be expected to account for the majority of estuarine macroalgal biomass and production. Due to a paucity of information on estuarine subtidal macroalgae, no attempt will be made to consider their geographic variations. Large-scale variations do not apear to exist in marine flora between Cape Elizabeth and Eastport. The character of the flora is consistent, with fucoids dominating intertidal rocky areas and laminarians dominating subtidal areas.

In rocky areas not colonized by macroalgae the magnitude of organic matter flux depends chiefly upon input of organic matter (detritus) from elsewhere. In areas scoured clean by currents, films of microorganisms on the surfaces of rocks interact principally with dissolved organic material in the water. Undisturbed areas receiving sinking detritus and excreta from resident fauna support larger microheterotrophic populations than do the wave-scoured areas.

Investigations of the invertebrates of rock bottoms in the characterization area are limited to those of Stickney (1959; table 5-7). He examined subtidal rock surfaces from both high salinity and low salinity areas of the Sheepscot Estuary. On the rocks in the high salinity portions he found 32 species including sponges, coelenterates, polychaetes, molluscs, crustaceans, echinoderms, and chordates. In low salinity areas he found only half as many species belonging to the coelenterates, molluscs, and crustaceans. Three of these, the American oyster and two species of xanthid crabs (*Rhithropanopeus harrisi* and *Neopanope texana*), are considered by many researchers to be "relict" populations of more southern species that only occur in warm-water pockets in Maine.

Table 5-7. The Most Common Invertebrates Collected from, or Recorded on, Subtidal Rock Bottoms in the Sheepscot Estuary.[a]

Species found in salinities from 28 to 30 ppt		Species found in salinities from 0 to 27 ppt	
Taxonomic name	Common name	Taxonomic name	Common name
Sponges:		Coelenterates:	
Halichondria sp.	dead man's fingers	*Obelia longissima*	
Chalina oculata		*Cordylophora lacustris*	
Coelenterates:		Molluscs:	
Metridium dianthus	sea anemone	*Crassostrea virginica*	oyster
Urticina crassicornis	sea anemone	*Mytilus edulis*	mussel
Obelia spp.		*Odostomia bisuturalis*	
Sertularia spp.			
Polychaete worms:		Crustaceans:	
Harmathoe imbricata	scaled worm	*Balanus improvisus*	barnacle
Lepidonotus squamatus	scaled worm	*Rhithropanopeus harrisi*	mud crab
Spirorbis borealis		*Neopanope texana*	mud crab
Molluscs:		*Jaera marina*	
		Leptochelia rapax	
		Aeginella longicornis	
Hiatella arctica		*Gammarus annulatus*	beach flea
Anomia simplex	jingle shell	*Gammarus tigrinus*	beach flea
Anomia aculeata		*Carinogammarus mucronatus*	beach flea
Ischnochiton ruber		*Corophium lacustre*	
Aeolidia papillosa		*Melita nitida*	
Odostomia bisuturalis			
Crustaceans:			
Balanus crenatus	barnacle		
Idothea baltica			

(Continued)

Table 5-7. (Concluded)

Species found in salinites from 28 to 30 ppt		Species found in salinites from 0 to 27 ppt	
Taxonomic name	Common name	Taxonomic name	Common name
Crustaceans (Cont.):			
<u>Aeginella longicornis</u>			
<u>Gammarus marinus</u>	beach flea		
<u>Gammarus annulatus</u>			
Echinoderms:			
<u>Asterias vulgaris</u>	common starfish		
<u>Asterias forbesi</u>	purple starfish		
<u>Henicia sanguinolenta</u>	blood starfish		
<u>Ophiopholis aculeata</u>	brittle star		
<u>Gorganocephalus arcticus</u>	basket star		
<u>Cucumaria frondosa</u>	sea cucumber		
<u>Strongylocentrotus droehbachiensis</u>	sea urchin		
Protochordates:			
<u>Boltenia echinata</u>	sea squirt		
<u>Amaroucium</u> sp.			
<u>Didemnum albidum</u>			
<u>Dendrodoa carnea</u>			

a. Stickney 1959.

A variety of fish commonly are found in subtidal rock bottom habitat. These include the American eel, the sea raven, the sea snails, the snakeblenny, the rock gunnel, the ocean pout, and the redfish.

Subtidal aquatic beds. Aquatic plant beds in Maine's coastal marine and estuarine systems are either eelgrass or kelp. Preliminary NWI data indicate that aquatic beds comprise 4% of subtidal bottom in the marine system and 2% of the subtidal estuarine system. What is known of kelp beds in Maine is discussed under "Rock Bottom" above, because these beds are indigenous to rock bottoms.

Eelgrass beds are found in shallow subtidal areas of the Maine coast (Timson 1977) and are increasing in areal extent since their virtual disappearance in 1931 as a result of a "wasting disease" (Phillips 1974). In Maine, eelgrass colonizes mostly muddy substrates, ranging from muddy gravels to pure mud, and is found at levels from mean low water to several meters deep. Colonization on gravel or sand surfaces is patchy or nonexistent (Tutin 1938). The criterion for eelgrass colonization appears to be protection from strong wave surges or current activity (Ostenfeld 1908), rather than substrate particle size.

Strong current velocities apparently prevent colonization by eelgrass, but it has been observed in Puget Sound (Phillips 1974) that moderate currents may enhance eelgrass growth. In Maine, eelgrass beds appear to flourish on broad subtidal mud flats adjacent to flood- and ebb-dominated tidal channels.

Information is lacking on marine subtidal aquatic beds in the characterization area. These habitats have been studied elsewhere (e.g., Chesapeake Bay), particularly in estuarine areas, and have been shown to support dense and diverse assemblages of benthic invertebrates that are different from those on surrounding bottoms (Orth 1973; Marsh 1973; and Thayer and LaCroix 1971).

Eelgrass beds are abundant enough in coastal Maine to warrant detailed study. These beds are a productive element of the coastal ecosystem that provide habitat surface, nutrient regeneration, sediment stability, primary production, and feeding areas for waterbirds.

Kelp beds also provide detritus and habitat surface to estuaries. As with eelgrass beds, the benthic invertebrate fauna of kelp beds is qualitatively different from that of surrounding areas, especially in the plant holdfasts (structures that attach them to rocks; Jones 1973). The uniqueness of the fauna of kelp holdfasts has been confirmed in Maine by the authors.

Subtidal aquatic bed areas (and intertidal aquatic bed and emergent classes at high tide) are preferred habitat for most sculpins, red and white hake, sticklebacks, mummichog, Atlantic silversides, cunner, and northern pipefish.

The Intertidal Subsystem

The intertidal subsystem is the area between extreme high and low tides. This area is ecologically different from the subtidal area because of the daily submersion and exposure of the substratum. The intertidal subsystem comprises 49% of the estuarine system in the characterization area.

The 11 habitat types in the intertidal zone of the characterization area are: mud flats, sand flats, sand beaches, gravel beaches, cobble beaches, boulder beaches, protected rocky shores, aquatic beds, exposed rocky shores, emergent wetlands, streambeds, and reefs. The habitat types that are most characteristic of the estuarine system are gravel and cobble beaches, sand and mud flats, protected rocky shores, streambeds, and emergent wetlands. The other habitat types are discussed in chapter 4, "The Marine System," because those habitats are unique to that system.

The area of the intertidal subsystem is 66,382 acres (26,875 ha; see "Introduction" for limitations of data). Acreages of the habitats of the intertidal subsystem are given in table 5-2. The NWI class levels have grouped some of the 11 habitats listed above. Beach/bar includes sand beach, gravel beach, and cobble beach. Flats encompass areas of mud, sand, and streambeds. Boulder beaches and exposed and protected rocky shores are included in the NWI rocky shore class.

Flats are the dominant (66%) intertidal habitat in the characterization area. With the exception of the beach/bar habitats most of the other intertidal habitats are distributed evenly among the regions. The beach/bar habitat is more common in regions 4 and 6 than it is in the other regions. These areas have many gravel and cobble beaches.

Macroalgae and benthic invertebrates are the principal permanent residents of the intertidal zone. At high tide fish from the subtidal zone move in to forage and at low tide the intertidal zone is utilized by shorebirds, waterfowl, wading birds, and mammals. The permanent intertidal residents are mainly of marine origin.

Physical factors affecting the distribution of organisms of the intertidal subsystem are: tide, temperature, waves, nature and angle of substratum, available sunlight, fog, and size of the intertidal zone. The intertidal habitat is subject to a wide range of habitat conditions, ranging from extreme low water spring to extreme high water spring (see "Hydrography," page 4-11 in chapter 4). The upward limit to which plants and animals can thrive in the intertidal zone is determined by their capacity to adapt to periodic exposure to extreme cold and heat, extreme drying action by the wind, and exposure to fresh water (rain).

The different tolerances of intertidal biota are indicated by their distribution in bands parallel to the water line (zonation). Zonation is a general feature within the intertidal zone of the coastal area and can be observed easily on a bedrock shore where all the organisms are attached to the substrate surface. Few species tolerate the upper levels of the intertidal zone. The ribbed mussel, for example, thrives so far up the intertidal area that they are inundated only during a few high tides each month.

Many invertebrate animals found in the intertidal zone are ubiquitous, that is, widely distributed and able to live in a variety of habitats and tidal heights. They also tend to be more resistant to human-induced and natural stress. Invertebrate species common to estuarine intertidal areas of coastal Maine are given in table 5-8. Oligochaetes and nematodes are dominant species in all estuarine habitat types in the characterization area (Larsen and

Doggett 1978a). As many as 12,000 oligochaetes/m^2 have been found at a single cobble beach station.

The estuarine intertidal zone differs from the marine intertidal zone largely in the upper reaches of estuaries where the salinity of the overlying waters at high tide is much lower than that of sea water. Two examples of the effects of estuarine hydrography on the distribution of intertidal benthic invertebrates are given. In estuaries with high tidal volumes and low freshwater input, benthic invertebrate species live farther upestuary in the intertidal subsystem than in the subtidal subsystem. This is because during low tide the benthic invertebrates, which prefer waters of higher salinity, in the intertidal zone would not be covered by fresh waters coming down the estuary from the river (Milne 1940; and Sanders et al. 1965). In estuaries that have high freshwater inputs, it is hypothesized that any intertidal species may occur progressively lower in the intertidal zone as the head of the estuary is approached. This is because of stratification of the water column. Fresher water floats on top, so that the surface waters, those that will contact the intertidal invertebrates at high tide, are less saline toward the head of the estuary.

The differences between the epifaunal and infaunal distribution of benthic invertebrates in estuarine areas parallels those in the subtidal marine benthos. On rocky substrata, the distance upestuary in which a species can survive is limited by the salinity regime. Epifaunal animals in the upper

Table 5-8. Invertebrate Species Common to All Estuarine Intertidal Areas of Coastal Maine[a]

Order	Taxonomic name	Common name
Nematoda		round worms
Nemertea		ribbon worms
Annelida	Oligochaetes	same group as earthworms
	Nereis virens	sand worm (polychaete)
	Eteone longa	polychaete worm
	Polydora sp.	polychaete worm
Mollusca	*Littorina littorea*	common periwinkle
	Littorina obtusata	smooth periwinkle
	Mytilus edulis	blue mussel
	Modiolus modiolus	horse mussel
	Mya arenaria	soft-shelled clam
Arthropoda	*Balanus balaniodes*	barnacle
	Jaera sp.	isopod (looks like sowbug)
	Gammarus oceanicus	amphipod (scud)
	Carcinus maenas	green crab

[a]Larsen and Doggett 1978a.

reaches of estuaries are exposed to the full fluctuations in salinity because they are exposed to saltwater due to flooding tides and fresh water due to riverine flow and ebbing tides (Bassindale 1943). In unconsolidated substrata, the infaunal species live farther upestuary than epifaunal species because of the dampening effect of the sediment on salinity fluctuations (Alexander et al. 1935). The extent of this dampening was shown by Boyden and Little (1973) to be great in the tidally dominated Severn Estuary in England. These investigators demonstrated that the nature of the substrata is more important than the salinity regime in controlling the upestuary habitation of intertidal infaunal species. Flats near the head of the estuary were capable of harboring as many species as flats near the mouth, because the sediment protected infaunal organisms from the salinity fluctuations.

Intertidal rocky shore. Rocky shores are not as predominant in Maine estuaries as they are in coastal marine waters. The preliminary NWI data indicate that 5% of the estuarine intertidal area is comprised of rocky shore. Rocky shore areas border many flats and emergent wetlands in intertidal areas but were not delineated as areal features by NWI because of the linear nature of rocky shores.

The geologies of estuarine and marine rocky shores are nearly identical, that is, the substrata of both consist of folded and faulted igneous and metamorphic rocks locally invaded by granitic intrusions (plutons) and ring dike complexes (a grouping of rocks arranged in a circle) of volcanic origin up to a mile in diameter (TRIGOM 1974). All of these rocks are of Paleozoic and Mesozoic age. Paleozoic volcanic rocks also occupy a portion of the coast of Washington County (Doyle 1967).

Primary production on rocky shores is dependent on macroalgae (see "Rocky Shore" page 4-78, in chapter 4). Density of the brown algae knotted wrack (*Ascophyllum nodosum*) and various other species of rockweed (*Fucus* spp.) is great. Estuarine rocky shores generally support the largest individual plants. Areas that are exposed to heavy waves support little macroalgal growth, however, sheltered areas are subject to severe freezing and ice abrasion that may reduce macroalgal populations. Wave action is minimal in estuaries compared to marine systems. The area and width of the intertidal zone in estuaries is less than at exposed coastal rocky shores; total productivity is reduced.

The types of benthic invertebrates encountered on protected rocky shores are basically the same as those on exposed shores, but the number of species is lower on protected rocky shores, presumably because of reduced habitat diversity and higher environmental variability; that is, warmer temperatures in summer, colder in winter, greater turbidity, and more variable salinity. Ice formation may dislodge or destroy the fauna in some locales. Protected rocky shores often have a layer of silt coating the surface of the rocks and attached macroalgae. Grant (1977) observed that the trapped silt may smother barnacles. The total number of benthic individuals in protected rocky areas is much less than in exposed rocky areas, mainly because the barnacle habitat is reduced in comparison to exposed areas.

The size (slope and vertical height) of the intertidal subsystem in protected rocky areas is smaller than that of the intertidal subsystem in exposed rocky areas and the zones are not analogous. The upper intertidal subsystems generally are covered with algae and are dominated by barnacles, but in some areas, particularly those with large tidal amplitudes, rough periwinkle and mites are the only species present at the highest tidal level. Lower intertidal rocky areas usually are covered by a dense growth of algae, which is grazed by the common and smooth periwinkles and the limpet. Crustaceans common to the algae-covered lower zones are isopods, amphipods, and green crab. Pockets of mussels are found in association with oligochaetes, nemerteans, and nematodes. Mites, chironomid larvae, and the predatory whelk are characteristic of these zones. Irish moss and its associated animals notably are absent in these protected areas.

Suspension feeders are the most abundant feeding type on rocky shores. The dominant rock barnacle and the blue mussel are dependent on phytoplankton for sustenance. Other common species are the herbivorous periwinkles (common, smooth, and rough) and the limpet, all of which graze on algae on rock surfaces. Lubucheno and Menge (1978) state that the limpet, which has the potential to control algal populations, generally is too scarce to have any effect.

The principal predator on protected rocky shores is the whelk (Menge 1976, 1978a, 1978b; and Lubucheno and Menge 1978), which preys upon other intertidal animals (e.g., blue mussels and barnacles). The dense algal canopy at protected sites reduces desiccation stress and provides more habitat for the snail to graze on than that at exposed sites. The whelk and another common predator, the green crab, commonly are found on most of Maine's protected rocky shores. Other predators (e.g., fish) may move into the intertidal zone at high tide. No information is available on the extent and composition of this mobile component.

Intertidal streambeds. The streambed environment has not been studied in Maine. The biota of streambeds is unquestionably different from that of surrounding intertidal areas because the sediments of streambeds are different, they are exposed to water of low salinities, and they are not exposed at low tide.

Eelgrass is often abundant in streambeds, as are mud shrimps, hermit crabs, soft-shelled clams, and mummichogs. Factors such as currents, sediment stability, sediment type, and salinity determine which plants or animals dominate.

Intertidal beach. Beaches in Maine are composed of sand, gravel, and cobble. Sand beaches are predominantly marine and therefore are discussed in chapter 4, "The Marine System." Gravel and cobble beaches, which are more widespread in estuaries, are reviewed below.

Most beaches originate from the reworking of submerged glacial deposits by waves. They are composed of either one particle type or mixed types. The most common mixtures are gravel-cobble and gravel-sand. Boulders also may be scattered on gravel or cobble beaches. In fact, beaches composed of "pure" cobble or gravel are rare in Maine. The low intertidal and midintertidal areas of estuarine beaches have a mud, sand-gravel, or cobble matrix under the surface layer of pure gravel or cobble. Gravel and cobble beaches are relatively harsh environments for organisms, although they are not as harsh as sand beaches. The movement of gravel or cobbles, particularly during storms, hinders many attached species (such as mussels and barnacles) from establishing themselves and surviving more than 1 year.

Estuarine beaches are not subject to extensive wave action. Current velocity, particularly during spring runoff and storms, is more important in determining the particle size of the sedimentary material.

The production of organic matter in situ is low for beaches because of the absence of suitable substrata for macroalgal attachment. The largest source of organic matter for beaches is uprooted macroalgae and other estuarine vegetation (eelgrass, sea lettuce, and cordgrass) deposited by tidal and wave action. Depending upon the degree of exposure of the beach macroalgal colonization of pebbles and interstitial spaces below the surface may be a source of organic matter production. Bacteria and fungi living in the interstitial spaces consume organic matter produced by photosynthesis.

Several invertebrate species are able to survive the rigors of living on estuarine beaches in Maine (Larsen and Doggett 1978a). The only study of the invertebrate fauna of the cobble and gravel beaches of Maine (Larsen and Doggett 1978a) indicates the species composition is similar. Indeed, seven of the eight most abundant species in each habitat are shared between them and the top four species have similar abundances in both habitats (table 5-9). All of the abundant invertebrate species on cobble and gravel beaches are ubiquitous and none are unique to these habitats (Larsen and Doggett 1978a). The oligochaetes and nematodes are by far the most abundant groups. They inhabit the sand underlying the gravel and cobbles and also are found in association with rotting wrack and the blue mussel.

Most of the rock barnacles on the gravel and cobble beaches are small, indicating that they had set the previous spring. The absence of adults suggest that they had been dislocated, probably during the winter.

Filter-feeding blue mussels usually congregate in the lower intertidal zone. They wrap byssal threads around each other and around rocks which renders them less vulnerable to displacement by wave action.

Other important species inhabiting intertidal beaches include the common periwinkle and the amphipod Orchestia platensis. The periwinkle grazes microscopic algae, while the amphipod feeds in the wrack line. The periwinkle undoubtedly becomes dislodged by waves but is motile and can reestablish its position. The only common carnivore is a nemertean worm. Of the nine types of intertidal habitats investigated by Larsen and Doggett (1978a), gravel and cobble beaches ranked eighth and seventh, respectively, in the mean number of invertebrate species per station. Each habitat averaged about 10 invertebrate species per station, and the only habitat with a lower species diversity was the sand beach.

Gravel and cobble beaches differed most in the density of organisms (Larsen and Doggett 1978a). Gravel beaches supported about 5000 individuals/m^2, while cobble beaches supported 8000/m^2. As many as 87,096 barnacles/m^2 and 21,836 oligochaetes/m^2 were present at individual station locations on cobble beaches. Differences in substratum stability may explain this difference in density. In terms of density of invertebrate organisms at the nine intertidal

Table 5-9. Invertebrates Common to Gravel and Cobble Beaches in Maine Estuaries and Relative Scores of Abundance[a].

Gravel (highest possible score - 280)		Cobble (highest possible score - 320)	
Oligochaetes	243.5	Oligochaetes	222.0
Nematodes	155.5	Nematodes	128.5
Balanus balanoides	68.0	*Balanus balanoides*	78.0
Littorina littorea	42.5	*Littorina littorea*	63.5
Mytilus edulis	40.5	*Orchestia platensis* platensis	59.0
Nemertea	39.5	*Mytilus edulis*	48.25
Orchestia platensis	37.5	*Marinogammarus stoerensis*	34.0
Mite	20.5	Nemertea	34.0

[a]Larsen and Doggett 1978.

habitats sampled by Larsen and Doggett (1978a), gravel and cobble beaches ranked seventh and fifth respectively.

Gulls, terns, shorebirds, and waterfowl are the dominant waterbirds utilizing beaches. Most waterbirds utilizing sand and gravel beaches and bars and spits use them more for resting than for feeding. Sand beaches are the most important roosting areas for shorebirds. Concentrations of more than 40,000 semipalmated sandpipers on a sand beach in Harrington (region 5) have been reported while more than 10,000 have been observed at beaches in Cutler (region 6) and Lubec (region 6; see atlas map 4 for specific locations). Roosts of more than 5000 have been observed on beaches in Perry (region 6), Eastport (region 6), Lubec (region 6), and Phippsburg (region 2).

More than 2400 semipalmated plovers also have been reported resting on a Harrington beach (region 5). Gulls and terns roost in large numbers on sand and gravel beaches. Up to 5000 gulls have been reported to roost on a gravel bar in south Lubec (region 6), while concentrations of 2000 gulls are not uncommon throughout coastal Maine.

The least tern and piping plover breed and feed along sand beaches in region 2 (Popham Beach and Morse River Beach). Sanderlings feed extensively on sand beaches and flats throughout coastal Maine. Semipalmated plovers, black-bellied plovers, red knots, and semipalmated sandpipers feed on sand and gravel flats. Many large gulls feed extensively on sand and gravel flats.

Intertidal flats. Intertidal flats are the most characteristic habitat of the estuarine system in Maine. The preliminary NWI data show 66% (41,650 acres; 16,862 ha) of the intertidal estuarine subsystem of the characterization area is composed of flats. In Maine, intertidal flats are principally sand or mud, with some cobble/gravel.

Mud flats develop in relatively sheltered waters where suspended sediments are deposited during slack (high or low) tide periods. Most intertidal flat sediments originate from offshore, from coastal river sediment loads, or from other flats (Schnitker 1974; see "Geology" above.)

Sand flats are found in areas that are exposed to greater tidal and wave energy than mud flats. Sand flats are caused by deposition of sand carried by tidal or wave-generated currents. The sand flats at Sagadahoc Bay and Heal Eddy, Georgetown (region 2) are good examples of areas exposed to wave and current action. Areas just a short distance away in the Kennebec Estuary are less subject to waves and currents and are composed of mud.

Stable macroalgal communities do not develop on intertidal flats because of the lack of suitable substratum. Ephemeral algae, however, such as the sea lettuce, Ulva, and the green algae, Enteromorpha, sometimes bloom on flats, but their contribution to the total production of the system is unknown.

The principal difference between sand and mud flats is that mud is more anaerobic than sand. The production of "new" organic matter usually is limited to benthic diatom productivity on the flats, yet the influx of organic matter from the water column or from shore and its modification by benthic fauna is relatively large. Metabolic wastes of the fauna and buried plant material provide a rich substratum for microheterotrophic growth. In fact, certain species of diatoms found in surface layers of the sediment appear to have acquired partial heterotrophic capabilities. During their growth, microheterotrophs (certain diatoms, bacteria, and fungi) may cause aggregation of particles, which helps to stabilize bottom sediments. Through decomposition by bacteria and fungi, much of the organic matter in the flats is broken down and remineralized. In areas that do not receive much organic matter, microbial activity may be at a level high enough to prevent the accumulation of organic matter. More frequently, however, an excess of organic matter is present on the flats and the vigorous microbial consumption of oxygen often leads to the formation of anaerobic zones where fermentation as well as desulfurication occur. The latter reaction has a lasting effect on sediment diagenesis, that is, the hydrogen sulfide released during sulfate reduction combines with iron to form ferrous sulfide, and black "sulfide mud" is produced. Anaerobic decomposition of proteins also leads to the production of ammonia. This ammonia may diffuse out of the sediments and contribute a nutrient source to the water column or may be oxidized to form N (denitrification) which cannot be used by producer organisms. In regions bordering on aerobic zones sulfur-oxidizing bacteria again may contribute to the oxidation of sulfides.

Flats are especially important environments, not only because of the rich and diverse fauna that they support but also because several of the invertebrate species that live there are utilized commercially. The harvest of clams, sandworms, and bloodworms, among the State's most valuable fisheries, is centered on flats (see chapter 12, "Commercially Important Invertebrates" for a description of these species; also atlas map 4). In addition, flats are a major feeding ground for several species of fishes, waterbirds, and waterfowl.

Because flats have a low grade the bands of infaunal animals are broad. Since the grade is so slight, often irregular, and the sediment is fine, some water remains in the sediment between tides. Since desiccation is probably a major factor affecting the distribution of invertebrate species and most invertebrates present are infaunal, precise delineation of specific zones in a flat is difficult. Sagadahoc Bay (region 2) is a good example of a low grade sand flat. Here tides with an amplitude of about 3 m cover a flat that is almost 4000 m (over 2 miles; 1.2 km) long (Bradley and Cooke 1959).

In addition to tidal height a number of other factors determine species distribution. Animals in these low grade areas respond strongly to the type and stability of sediments, currents, wave action, salinity, and availability of food (Odum et al. 1974; Sanders et al. 1962). Some of these factors are related in varying degrees to tidal heights. The habitat requirements of some species (e.g., amphipods and polychaetes) are so specific that the species can only live on sand "waves" (Sanders et al. 1962).

On flats some animal species are scattered throughout (exclusion), whereas others tend to congregate into groups or patches (clumping). Exclusion means that individuals are separated spatially, whereas clumping means the individuals are grouped together spatially, often quite densely (Little and Boyden 1976). The Baltic clam is an example of a species that exhibits exclusion (Segerstrale 1965). Since the Baltic clam is a deposit feeder, it excludes other species by eating almost anything organic (including clam larvae) that comes within range of its siphon.

Clumping is exhibited by a number of species. Some larvae select the type of substratum on which to settle and/or settle near animals of their species. Other animals brood their young, which accounts for their presence in the vicinity of others of the same species.

Migration of adults may play an important role in species distribution. Dauer and Simon (1976) found that adult polychaetes accounted for over 90% of the intertidal populations in an area that had been essentially devoid of fauna. Dean (1978 a and b) has noted mass migrations of bloodworms and sandworms in the Damariscotta River estuary. These migrations were in winter and not related to the reported reproductive periods of these species. Yeo and Risk (1979) report that adult baltic clams can migrate laterally to repopulate ice-scoured or storm-damaged areas.

Almost all of the infaunal species that live in the flats, with the exception of burrowing forms such as large soft-shelled clams and adult sandworms, are present in the upper 6 inches (15 cm) of sediment. Stromgren and coworkers (1973) found on a Norwegianflat that within the upper 6 inches (15 cm), most of the species were present in the top few centimeters. Many were located near the surface because the availability of food was greater on the diatom-detritus rich surface. Some were known to migrate to the sediment surface when the tide was high. The larger forms were either mobile (sandworms) or had long siphons that reach to the surface (soft-shelled clams).

Seasonal changes in faunal abundance on intertidal flats are believed to be due to life history events, such as mortality and recruitment, since little evidence of active seasonal migration has been found among most infaunal species (Little and Boyden 1976; and Stromgren et al. 1973). Passive transport of infaunal animals by ice, waves, or on the surface film, may occur to a limited extent.

In a study of intertidal mud flats in the Sears Island area of Penobscot Bay (region 4) the highest number of individuals per m^2 (table 5-10) was present in fall and the lowest in spring (Normandeau Associates 1975). Winter mortality due to low temperatures and ice probably accounted for the differences.

The density of natural populations fluctuates widely over time. Dean and Ewart (1978) have noted annual variations in the density of several common mud flat species, including the Baltic clam, the gastropod, Hydrobia totteni, the polychaetes Heteromastus filiformis,, Scoloplos sp., and Streblospio benedicti in Montsweag Bay (region 2). Some densities varied between years by a factor of twenty. Dauer and Simon (1976) found that although great fluctuations occurred in the density of sand flat animals over time the species composition remained relatively constant.

Deposit feeders were the most abundant feeding type on both the mud and sand flats surveyed in Maine by Larsen and Doggett (1978a). Exceptions to this

Table 5-10. Numbers of Individuals/m^2 Collected on Intertidal Flats in Upper Penobscot Bay (Region 4)[a]

Transect	Summer	Fall	Spring
1	6572	35,967	2144
2	20,987	4945	13,574
3	26,202	47,555	23,296
Totals	53,761	88,467	39,014

[a]Normandeau Associates 1975.

generalization occured in sand flats with unstable sediment surfaces, which were characterized by pronounced sand waves. At Heal Eddy, a sand flat in Georgetown (region 2), Larsen and Doggett (1978a) found that sand wave areas were dominated by the amphipods Acanthohaustorius millsi, a suspension feeder, and Psammonyx nobilis, an omnivore (Croker 1977). Deposit feeders are uncommon in areas with ripples, because the instability of the sediment prevents the establishment of unicellular algae (Sanders et al. 1962).

Predators on Maine's intertidal flats include the green crab, the moon snail, the sand shrimp, and the sandworm. At high tide the flats are utilized by bottom-feeding fish. Shorebirds feed on the exposed flats (low tide) especially during fall migration.

The primary waterbird groups feeding on intertidal flats include shorebirds, gulls, wading birds, and waterfowl (dabbling ducks, geese, and brant). Herring gulls, great black-backed gulls, and black ducks use flats throughout the year. Estuarine flats are especially important habitat for migratory and wintering black ducks. Shorebirds, Bonapartes gulls, and ring-billed gulls, are more abundant on intertidal flats in fall rather than in spring. In contrast, brant are most abundant during spring migration. Wading birds use mudflats throughout spring, fall, and summer.

Flats are critically important for shorebirds because of their almost obligate dependence on the coastal habitats as refueling and resting areas during their long migration from the Arctic to South America. Shorebirds occur there in very large numbers in relatively small areas, which makes them susceptible to environmental contaminants and habitat deterioration.

Mud and sand flats along the southwest New Brunswick and eastern Maine (regions 5 and 6) coasts are especially important to migrating semipalmated plovers. Numbers between 1000 and 2400 have been reported in many areas in this region. These same flats are important feeding areas for semipalmated sandpipers migrating in fall (see sand beaches above for a discussion of their preferred roosting areas). Large numbers of short-billed dowitchers and black-bellied plovers feed on Maine flats.

Sand flats usually occur seaward of sand or gravel beaches in which active erosion of shore deposits supplies sand to the intertidal zone. Isolated, irregularly shaped sand deposits may occur as flats adjacent to tidal channels, as levee deposits, or as bar deposits in the insides of channel bends.

The composition of sand flats ranges from medium sand to silty sand (Timson, unpublished), but some areas also may have some pebbly sands (gravel) and coarse sands toward the shoreward end of the sand flat. Sediments of sand flats are generally poorly sorted. Muds are periodically deposited over the sand during low wave activity, or coarser particles are moved seaward over fine-grained deposits during storms. Intertidal organisms also mix sediment layers after deposition. Under conditions of a rising sea level, such as exists on the Maine coast, sand flats migrate shoreward as beaches recede and mud deposition covers the seaward margins of the sand flat.

Sand flats of the bar variety occur adjacent to tidal channels in which current velocities are strong enough to transport sand as bedload. The sand may be derived from the channel bottom or from the shore immediately adjacent to the channel. Sand sediment is deposited at channel bends, either on adjacent flats on the outsides of bends or as bar deposits on the insides of bends, where current velocities decrease and drop their bedload. Sand flats of the bar type are more well sorted than sheet deposits. Generally, bar type sand flats are under the constant influence of unidirectional, or bidirectional tidal currents that are of similar magnitude at high and low tide and consist of fine to very fine sand. Over time these sand flat environments also migrate landward, as nearshore deposits shift landward in response to sea level rise (Timson, in preparation). The surface of these bar deposits is mobile at all times in response to tidal current variability. Sediments to depths of up to 8 inches (20 cm) may be mobilized and transported several meters by tidal currents (Boothroyd and Hubbard 1975).

Large sand flats in Maine are relatively few. Along the eastern coast of the United States south of Maine low energy intertidal flats commonly are composed of sand. In the characterization area, most of the source material for low energy systems is silt and clay, which contribute to the extensive mud flats found along the coast. The major sand flat areas in the characterization area are Sagadahoc Bay and Heal Eddy near Georgetown (region 2), Sprague Neck bar in Machias Bay (region 6), Bailey's Mistake at Trescott (region 6), the spit of South Lubec (region 6), and Clam Cove at Rockport (region 4).

The benthic marine flora supported by sand flats is small in terms of biomass and productivity in comparison with the rocky shore environment. Much of the sand bottoms along the coast are not stable enough to support large macrophyte populations. In areas that are extremely stable, small macroalgal populations may appear for brief periods on sediment surfaces, such as small stones or shells. Only small plants develop under these conditions and species diversity is low.

Invertebrate species living on sand flats in Maine include representatives from sand beaches and mud flats (Larsen and Doggett 1978a). The species listed in table 5-11 are the 12 most abundant species on sand flats, as determined by a rank score analysis. Oligochaetes and nematodes are most abundant and polychaetes and amphipods are relatively common. Two species that are commercialy valuable and common to both sand and mud flats are the bivalve soft-shelled clam and the polychaete sandworm. These species are found in abundance, (up to 404 and 272 individuals/m^2, respectively) in many locations.

Larsen and Doggett (1978a) identified 71 species of invertebrates on the six sand flats in the characterization area. At the 48 stations sampled, the number of species varied from 0 to 21, with a mean of approximately 12. In species diversity sand flats rank fifth among the nine intertidal habitats sampled by Larsen and Doggett (1978a). The mean faunal density on sand flats is low but widely variable (Larsen and Doggett 1978a). The mean density is 1510 individuals/m^2 and the range is 0 to 16,840/m^2. Sand flats in the characterization area are therefore only slightly more densely populated than sand beaches and rank eighth among the nine types of intertidal habitats investigated.

Table 5-11. The Relative Abundance of Invertebrate Species Commonly Taken in Samples of Maine's Sand Flats, as Determined by Rank Score Analysis[a]

Taxonomic name	Score (highest possible score 100)	Common name
Oligochaeta	52	Oligochaete
Acanthohaustorius millsi	42	amphipod
Nematoda	39	Nematodes
Pygospio elegans	37	polychaete
Spiophanes bombyx	31	polychaete
Nereis virens	30	sand worm
Protohaustorius deichmannae	29	amphipod
Psammonyx nobilis	29	amphipod
Mya arenaria	24.50	soft-shelled clam
Exogone hebes	22.50	polychaete
Scolecolepides viridis	20	polychaete
Chirodotea coeca	15	isopod

[a]Larsen and Doggett 1978a.

Mud flats are the dominant intertidal habitat in the estuaries of coastal Maine. They are the fine-grained equivalent of sand flats, originating from the deposition in the intertidal zone of sand, silt, and clay particles by rivers and offshore waters (Schnitker 1974), and through the erosion of adjacent shorelines.

Mud flats consist primarily of silt particles with some fine sand and clay intermixed. The sediments and their clay mineral compositions are derived from subaerial and subtidal glacio-marine clays and silts of the Presumpscot Formation (Bloom 1963; and Timson, in preparation). Mud flats also contain a small amount of organic detritus but generally <5% by weight (Timson, unpublished). The organic fractions of a mud flat are usually bound to fecal pellets, agglomerates, and flocculates. Agglomerates are clay particles, irregular in shape, that are bound by organic material. Flocculates are clay particles bound primarily by electrostatic forces (Zabawa 1978).

Grain size over the mud flat surface generally decreases landward, unless significant volumes of sediment have been contributed by shoreline erosion. Grain size decreases from tidal channels toward the periphery of the flat. This distribution is caused by the movement of water traveling over tidal flats during a tidal cycle (Postma 1967; and Van Straatan and Kuenan 1957).

Transport by suspension is the primary process of sedimentation on the flats and much of the suspended sediments are derived directly from the flats themselves (Anderson 1973; and Schnitker 1974). What is eroded from the flats at high water usually is redeposited elsewhere on the flat by the ensuing ebb tide. Currently, mud flats in Maine probably are accreting at a rate of 1.9 to 2.8 cm/year (Schnitker 1972).

Sediment transport and deposition within tidal channels that border or drain mud flats occurs through suspension and bedload transport. The most coarse sediments (fine to very fine sand) in mud flats are found on the floor of tidal channels. Coarser sediments also are found in association with mussel banks flanking large tidal channels that border on mud flats. Significant quantities of sand and shell particles compose sediments that act as a substratum for the banks (Timson, unpublished).

The dominant natural processes affecting mud flats are tidal currents, local wave conditions, and biological activities such as the burrowing of invertebrates. Tidal currents and waves suspend and redistribute particulate matter over the flat surface. The activities of organisms on the sediment surface mix sediment layers directly on the flats.

Mud flats do not provide a stable substratum for the attachment of the large macroalgae, but protected waters often may permit the seasonal development of highly productive small plants, including green algae such as *Enteromorpha*. Dense populations of dinoflagellates and diatoms also may appear. Stable substrata permit the occasional development of isolated larger plants, but in general and excepting the benthic microflora the habitat depends on imported organic material to support its rich fauna.

Mud flats support a diverse population of invertebrates and many species develop large populations only in this habitat (Larsen and Doggett 1978a).

The following species were found at all or almost all of the flats surveyed by the authors:

Worms:	Nemertea
	Nematoda
Gastropods:	Hydrobia sp.
	Littorina littorea (common periwinkle)
Bivalves:	Macoma balthica (baltic clam)
	Mya arenaria (soft-shelled clam)
	Mytilus edulis (blue mussel)
Polychaetes:	Eteone longa
	Nephtys caeca
	Nereis virens (sandworm)
	Heteromastus filiformis
	Polydora sp.
	Streblospio benedicti
	Scoloplos sp.
	Tharyx acutus
	Oligochaeta
Crustaceans:	Balanus balanoides (rock barnacle)
	Ampelisca abdita
	Corophium volutator
	Gammarus mucronatus
	Carcinus maenas (green crab)

These species are present over the entire characterization area on mud flats composed of different proportions of sand, silt, and clay. The more common genera of the flats of Montsweag Bay (based on size, diversity, and frequency of occurrence) are the polychaete, Heteromastus, the baltic clam, and the polychaete, Scoloplos (Dean and Ewart 1978). The gastropod Hydrobia and the polychaete Streblospio are dominant species listed by Dean and Ewart (1978). Of 116 species collected on intertidal mud flats in the Sears Island area of Penobscot Bay (region 4) the following species accounted for 73% of the total (Normandeau Associates 1975):

Gastropod	Hydrobia totteni
Rough periwinkle	Littorina saxatilis
Soft-shelled clam	Mya arenaria
Baltic clam	Macoma balthica
Polychaetes	Heteromastus sp.
	Tharyx sp.

Of these species only the periwinkle was not reported by Larsen and Doggett (1978a); the study by Normandeau Associates (1975) may have included a high rocky intertidal area.

Table 5-12 lists the 12 most abundant species found on mud flats in coastal Maine by Larsen and Doggett (1978a). All but one, the gem clam, are found characteristically on mud flats. Gem clams are high on the list in table 5-12, mainly because of their abundance (up to 23,652 individuals/m^2) at one site. These 12 species account for about 95% of the invertebrate individuals on Maine's mud flats, indicating that the community is homogeneous throughout the characterization area (Larsen and Doggett 1978a).

Some of the species listed for mud flats have particular requirements that affect their distribution. For instance, the rock barnacle must have substratum on which to attach. It is only found in association with mussels, rocks, and other firm substrata. The common periwinkle also is found most commonly in association with mussels or rocks. Blue mussels tend to aggregate with other mussels and may form mussel reefs.

The mean number of species per station encountered by Larsen and Doggett (1978a) is 17, which ranks mud flats behind only exposed rocky shores and boulder beaches in species diversity. A total of 75 species was identified on mud flats. The mean number of individuals/m^2 was 7345; however, at some stations certain species had very high densities. As many as 24,848 oligochaetes, 23,652 gem clams, and 16,660 gastropods, *Hydrobia* sp., were found per m^2 at individual station locations.

Since intertidal mussel reefs are found usually on mud flats they are considered as a subhabitat of mud flats. The number and location of mussel reefs varies from year to year. Field (1923), in his study in Long Island Sound, New York, found mussel reefs to be ephemeral, lasting only 2 to 3 years. Storm waves, floating ice, suffocation by sand and gravel deposits,

Table 5-12. The Relative Abundance of the Invertebrate Species Commonly Taken in Samples of Maine's Mudflats as Determined by Rank Score Analysis[a]

Taxonomic name	Score (highest possible score 195)	Common name
Oligochaeta	119.5	Oligochaete
Hydrobia sp.	89.0	gastropod
Macoma balthica	57.5	Baltic clam
Streblospio benedicti	48.5	polychaete
Nereis virens	41.5	polychaete
Corophium volutator	30.5	amphipod
Gemma gemma	29.0	gem clam
Scoloplos sp.	24.5	polychaete
Nematoda	24.0	Nematode
Heteromastus filiformis	20.0	polychaete
Mya arenaria	15.5	soft shelled clam
Polydora sp.	14.5	polychaete

[a]Larsen and Doggett 1978[a].

and high temperatures are factors that damage or destroy the reefs. In Maine, action by storm waves and floating ice are more severe than in Long Island Sound, so the life of some Maine intertidal mussel reefs is likely to be shorter.

The formation of the reefs begins with dense sets of mussels on stones, shells, or other debris. When the first mussels become established other mussels set upon them. The reef is not dependent on the underlying sediment. In fact, the reefs may modify the chemical and physical characteristics of the underlying sediments (Newcombe 1935). The soft-shelled clam is smothered by overlying mussel reefs (Newcombe 1935). Other infaunal species may be affected similarly.

Species living in association with mussels include worms: nematodes, nemerteans, and oligochaetes. The rock barnacle and the common periwinkle use the mussels as a substrate on which to attach (barnacles) or graze (periwinkles). Lee (1975) found a number of polychaetes, such as *Eteone longa*, *Harmothoe imbricata*, *Polydora ligni*, and *Spio setosa*, in association with mussel reefs in Long Island Sound. Also present were species of the crustacean genera *Jaera*, *Corophium*, *Gammarus*, *Melita*, and *Pagurus*. Potential predators included the green crab and the starfish *Asterias* sp. Although communities associated with mussel reefs have not been studied in Maine many of the species reported by Lee (1975) occur in Maine.

Feeding types on mussel bars, in addition to the suspension feeding mussels, include herbivores, carnivores, and deposit feeders (Lee 1975). Nematodes, oligochaetes, and other deposit feeders, such as the polychaetes *Nereis succinea*, *Polydora ligni*, *Spio setosa*, and the amphipod *Corophium*, thrive on the pseudofeces produced by mussels. Carnivores include nemerteans, some polychaetes (*Harmothoe*) and crabs. Species such as *Jaera* sp. and the common periwinkle graze the surfaces of the substrate. Scavengers on mussel reefs include the crustaceans *Pagurus*, *Gammarus*, and green crab.

Emergent wetland. Intertidal emergent wetlands (e.g., salt marshes) are productive elements of coastal areas worldwide. Because of their productivity they are widely studied and data on many areas including southern New England and some regions of coastal Maine are available.

The east coast of the United States south of Cape Elizabeth, Maine, is an almost entirely sedimentary environment of the type that encourages emergent wetland development. In the characterization area, however, conditions are such that expansive intertidal emergent wetlands are not numerous. However, significant areas of intertidal emergent wetlands are narrow and fringe on protected flats. These were not delineated as areal features by NWI due to their linear nature. This class constitutes <3% of the total (fresh-water and saline) wetland habitat and approximately 11% of the estuarine system in coastal Maine (table 5-2). The southwestern regions of the characterization area (1, 2, and 3) have more (in total acres and percent of total area) estuarine emergent wetland than the eastern regions (4, 5, and 6). Of all the estuarine classes identified by NWI, this is among the least abundant. The extensive information regarding this wetland type, however, allows for a disproportionately thorough discussion of this type of habitat relative to the others.

An understanding of the functions of the intertidal emergent wetlands of the estuarine system is valuable to the overall understanding of the ecology of the Maine coast ecosystem. Estuarine emergent wetlands represent a fragile and highly productive community.

In Maine, estuarine emergent wetlands are dominated by three persistent species: salt marsh cordgrass (Spartina alterniflora), salt hay (Spartina patens), and black rush (Juncus gerardii). Intertidal emergent wetlands that are characterized by these species are called salt marshes. The term salt marsh can be subdivided into two categories: (1) low marsh, generally dominated by the regularly inundated cordgrass; and (2) high marsh, irregularly flooded areas dominated by salt hay and black rush.

The importance and roles of the estuarine intertidal emergent wetlands and the estuarine intertidal subsystem in areas outside Maine have been well documented (Odum 1961; Teal 1962; Niering 1966; Cooper 1969; Redfield 1972; Gosselink et al. 1974; Wiegart et al. 1975; and Chapman 1977). Only a few researchers (Vadas et al. 1976; Linthurst 1977; Linthurst and Reimold 1978; Keser et al. 1978; and McGovern et al., in press) have attempted to characterize the ecology of salt marshes in Maine. Consequently, when reviewing the characteristics and interactions of Maine's intertidal wetlands it is often necessary to draw from research on similar intertidal wetland systems in other New England States.

Descriptions of the physical and biological features and physical/biological interactions in Maine's estuarine emergent wetlands are given below.

The two physical features which most influence the natural history of the estuarine intertidal salt marsh habitat are geology and hydrography. The contributed effects (e.g., icing and storm tides) of climate are discussed above.

Coastal Maine possesses a unique geological history that is reflected in its distinctive physiographic structure. Glaciation helped create a coastal ecosystem characterized by long, deep, steep shores and rocky headlands. The geological foundation, formation, evolution, and overall physical structure of the intertidal salt marsh in Maine is discussed under "Geology" above.

Hydrographic parameters are important in determining the distribution of intertidal salt marshes. Tidal inundation, frequency, and duration, and salinity are the most important hydrographic parameters that influence salt marshes. The process driving succession and the effects of both geology and hydrology on plant distribution are discussed below.

The physical features of the characterization area are much different from those of southwestern coastal Maine, New Hampshire, and other States in New England. In general, the steep nearshore-to-upland relief, lack of suitable sedimentary material (usually deposited by rivers), and relatively high energy tidal currents, limit the formation of intertidal wetlands. In Maine, intertidal wetlands tend to be small, contiguous, fringing in nature, and located in drowned sediment-filled valleys of estuaries, as in the Sheepscot River drainage (Vadas et al. 1976; see atlas map 1).

Maine salt marshes have developed on a coastline forged by glaciation. They are built on marine peat, marine silt, sand, gravel, cobbles and, in some instances, over the remains of fresh water bogs in which stumps of old pine trees (Pinus strobus) can be found (Chapman 1940a; and Thompson 1976). Redfield (1972) discovered in his examination of the salt marsh peat in Barnstable Marsh, Massachusetts, that the upper and lower peat fringes of the marsh sediments were dominated by the heavier material (sand) but that the peats within the marsh were composed of fine-grained silty material. The sediment distribution indicates that the salt marsh acts as a buffer against wave energy by absorbing it and slowing the movement of the waters. As the wave energy is dissipated in the grass, the small silt and clay particles no longer held in suspension by the wave are deposited on the marsh surface. Thus, marshes absorb energy and act as buffers for upland systems, while at the same time capturing fine-grained material to maintain themselves.

Salt marshes have two major requirements for existence: a source of sediment (sand and peat) and a sheltered (low energy) location. Salt marshes cannot form without the accumulation of depositional material. In Maine, the hard rocky coast is relatively resistant to marine erosion (consequently, a major source of sediments is lacking) and marsh development depends upon the highly limited quantities of silt from rivers and from decayed plant material (peat). In northeastern Maine, particularly, the numerous drowned river valleys and inlets have not accumulated an abundance of sediment material suitable for salt marsh formation. Most of the fine clays and silts (which are little) transported by rivers are not trapped in the estuaries but move into the deep water of the Gulf of Maine. These factors limit the availability of suitable substrate for salt marshes in Maine.

Salt marshes in Maine require natural protective structures if they are to be maintained. Since salt marshes usually form on fibrous marine peat they cannot exist in high-energy situations (characterized by waves). Sandy barrier beaches and islands are the most common protective structures for salt marsh formation but the scarcity of sand and sand sources in Maine limits the formation of such protective structures.

In areas in Maine where sediment supplies and protective structures exist (sand spits or barrier beach structures), protected intertidal sand flats may become colonized with cordgrass. Salt marsh vegetation may become established by seeding, lateral growth of rhizomes, and by rafting by ice (Redfield 1972).

Salt marsh plant propagation by lateral growth of rhizomes and by seeding is common. Ice rafting is a unique colonization feature of northern latitude salt marshes. Ice, which moves in and out of intertidal regions during winter and spring, is capable of transporting plants or plant particles frozen in it to locations far from the parent source. Salt marsh turfs 10 feet (3 m) in diameter that rafted high into the marsh in Barnstable Marsh, Massachusetts, were observed by Redfield (1972) and smaller blocks were observed stranded on bare sand flats. Cordgrass rafted to unvegetated sand flats potentially could initiate marsh development.

If sedimentation rates continually exceed the rise in sea level over time cordgrass may spread over the accumulated sediment and accrete laterally over formerly open-water areas as depicted in figure 5-41 (Chapman 1960; and Redfield and Rubin 1972). Areas in which cordgrass previously grew will accumulate decaying vegetation and elevate to high marsh, outstripping sea water rise and sediment compaction. Redfield (1972) reported that the marsh surface on which cordgrass became colonized rose 1 foot (30 cm) in 6 years due to sedimentation but gradually slowed as the marsh surface approached high water. The deposition of sediments changes inundation patterns and salinity regimes and may induce successional patterns in the marsh vegetation as other higher marsh plants, such as salt hay and black rush, invade the area.

In higher energy situations salt marshes and protective barrier structures may transgress inland as high energy waves breach the protective sand structures pushing the marsh inland (figure 5-42). Two geological processes are responsible for transgression; the actual rise in sea level (eustatic rise) caused by melting ice caps and the compaction of sediments, which causes the near shore land surface to subside gradually.

From a geological point of view salt marshes are very recent formations and undergo change very rapidly. For example, the peat in the Barnstable Marsh is 25 feet deep due to the relative rise of the sea compared to the land (Redfield 1972). Radiocarbon dating showed that the oldest peats 25 feet below the present sea level were approximately 4000 years old (Post Quaternary). Unlike geological features such as mountains or rocky headlands, salt marshes are modified through accretion, erosion, and transgression over a period of a few years rather than hundreds or thousands of years. Thus, they are relatively fragile geological entities.

The daily ebb and flow of the tide is the prime regulatory factor in coastal salt marsh ecosystems (Miller and Egler 1950). Salts and nutrients are introduced to and removed from the marsh with the twice-daily tides. Salt marsh floristic zonation is dependent upon the frequency and duration of tidal inundation (Adams 1963). Tidal inundation affects all the physical regulatory parameters cited by Penfound (1952) as influencing plant distribution in estuarine emergent wetlands.

The relationship between the vertical range of the tide and the distribution of the three dominant emergent species in a Maine salt marsh has been determined by Linthurst (1977; table 5-14). These vertical ranges become meaningful when compared with inundation patterns derived by Chapman (1940a) for a Massachusetts salt marsh. Inundation patterns as a function of height above mean low water are similar in Massachusetts and Maine (table 5-13).

The lower limit of growth for cordgrass was determined to be 7.6 feet (2.3 m) above mean low water (MLW) in a Maine salt marsh. This translates into approximately 690 inundations/year (about 2/day) with a submergence time of 6 hours/day. No other emergent species can compete with cordgrass and tolerate the physical and chemical stresses associated with the submergence pattern.

Salt hay begins to intergrade at 9 feet (2.7 m) above MLW. Salt hay in Maine is characterized by an average of 200 inundations per year, with a submergence time of about 2 hours/day. The vertical range of distribution for salt hay is quite restricted, <1 foot (30 cm).

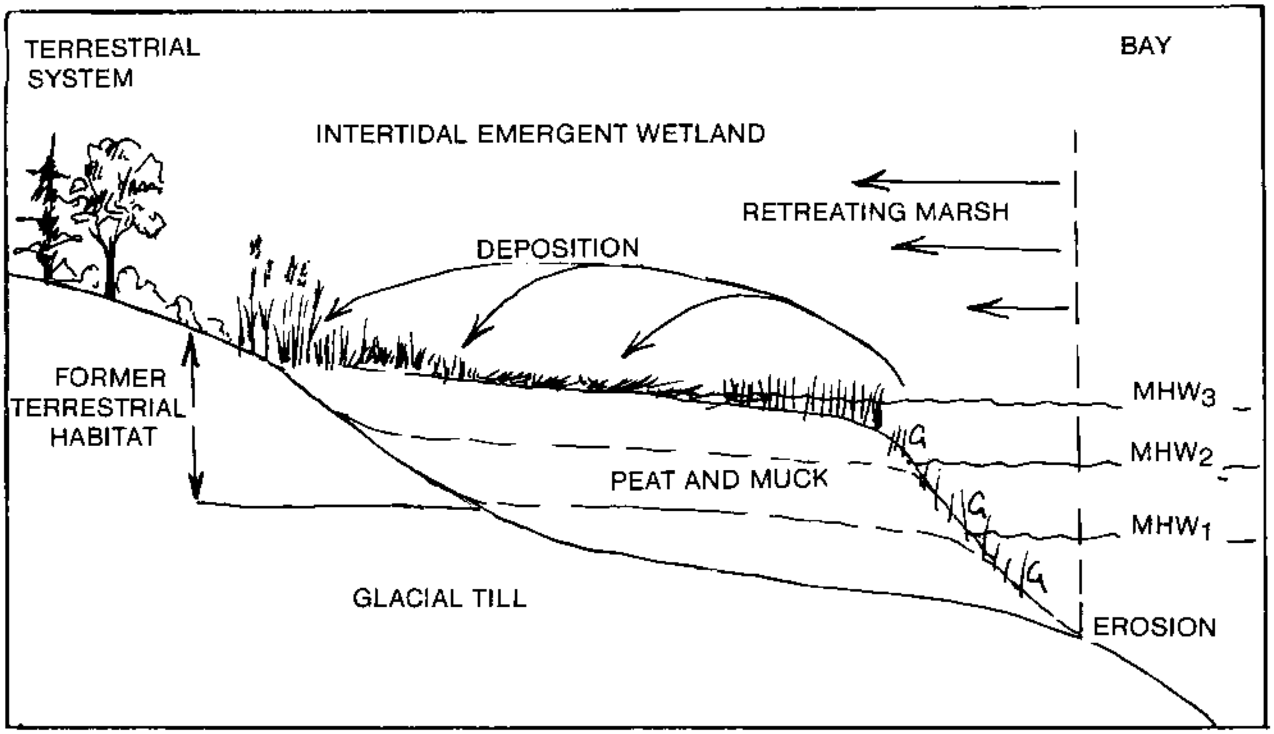


Figure 5-41. The process of salt marsh progradation (adapted from Redfield 1972).

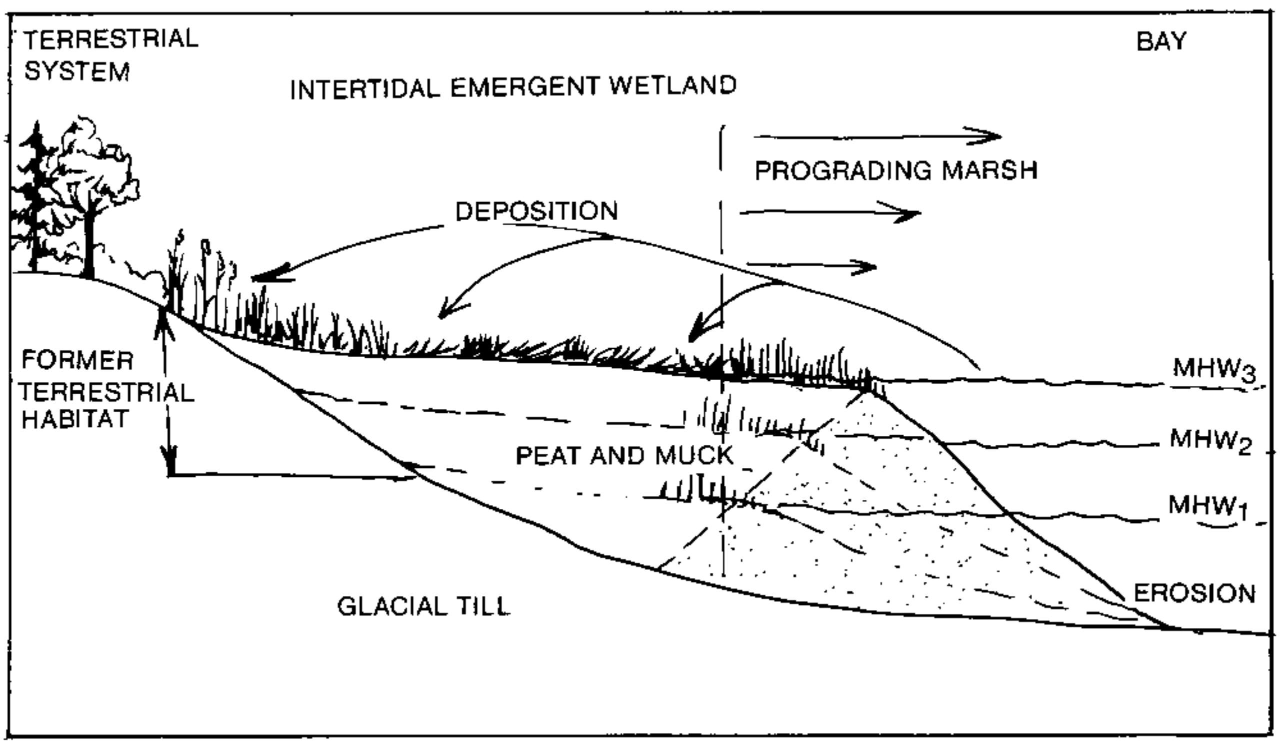


Figure 5-42. The process of salt marsh transgression.

Table 5-13. Inundation Patterns as a Function of Height Above Mean Low Water (MLW) in a New England Salt Marsh[a]

Species and vertical range	Feet Above MLW Level	Number of Submergencies/yr.	Number of Submergencies/growing season (May-Oct.)	Av. hours Submerged /d/y	Av. hours exposed /d/y
	12.6	0	0	0	24
	12.3	0	0	0	24
	12.0	0	0	0	24
	11.6	7	5	0.01	23.99
	11.3	31	18	0.06	23.94
	11.0	59	33	0.16	23.84
Black rush	10.84	72	39	0.22	23.76
	10.74	82	43	0.27	23.73
	10.60	101	55	0.37	23.63
Approximate MHW in the Maine Coastal Zone	------	------	------	------	------
	10.42	115	62	0.47	23.3
	10.3	144	81	0.59	23.41
	10.15	161	87	0.7	23.3
	10.0	198	105	0.94	23.4
	9.75	245	131	1.5	22.5
Salt hay	9.5	318	168	1.7	22.3
	9.3	372	193	2.1	21.9
	9.15	416	210	2.15	21.85
	9.0	451	233	2.96	21.04
	8.6	564	292	3.87	20.13
Cordgrass	8.35	599	308	4.78	19.22
	8.0	674	344	5.7	18.3
	7.81	683	350	6.3	17.7
	7.0	705	355	8.0	16
	6.0	705	355	10.2	13.8
	4.9	705	355	12.0	12
	4.0	705	355	13.7	10.3
	3.31	705	355	15.3	8.7
	2.0	705	355	18.4	5.6
	1.0	705	355	21.25	2.73
	0.0	705	355	23.27	0.53

[a]Vertical ranges from Linthurst (1977); inundation patterns from Chapman (1940a).

Table 5-14. The Relationship of Vertical Range of the Three Principal Salt Marsh Emergents in the Franklin and Salisbury Cove Salt Marsh Near Ellsworth, ME.[a]

Species	Maximum level (ft. above MLW)	Minimum level (ft. above MLW)	Range (ft.)
Cordgrass	9.2	8.0	1.2
Cordgrass (creekbank)	9.9	7.6	2.3
Salt hay	10.2	9.4	0.9
Black rush (high marsh)	13.0	9.6	3.3
Black rush (creekbank)	12.8	11.6	1.2

[a]Linthurst 1977.

High marsh black rush exhibits the widest vertical range of distribution, some 3.3 feet (1 m) in a Maine salt marsh. This is not unusual for high marsh species. As submergence time and number of inundations decrease more widely adapted species invade the high marsh, increasing competition and diversity. The critical level below which black rush does not grow appears to be the optimum habitat for salt hay.

The period of submergence of the high marsh is only about 1.5% at 10.6 feet (3.2 m) above MLW, which is the approximate mean high water mark in coastal Maine. At 8.6 feet (2.6 m) above MLW, the cordgrass zone, submergence time is at least 11.9%.

Although inundation is important, the dissolved salts in tidal water are critical in determining the type, vigor, and distribution of plant life. Plants in salt marshes have different salinity tolerances (Chapman 1940a; figure 5-43). For instance, high soil-sediment salinities may reduce the growth of cordgrass (Mooring et al. 1971; and Broome et al. 1973).

In New England, a distinct zonation pattern based on dominant vegetation exists in coastal salt marsh ecosystems (Miller and Egler 1950; Niering 1961; and Fiske et al. 1966). As in other coastal areas the vegetative zonation is a reflection of the hydrographic, chemical, and biologial factors influencing coastal emergent salt marshes. Penfound (1952) listed the following physical parameters as important factors affecting the plant distribution in the

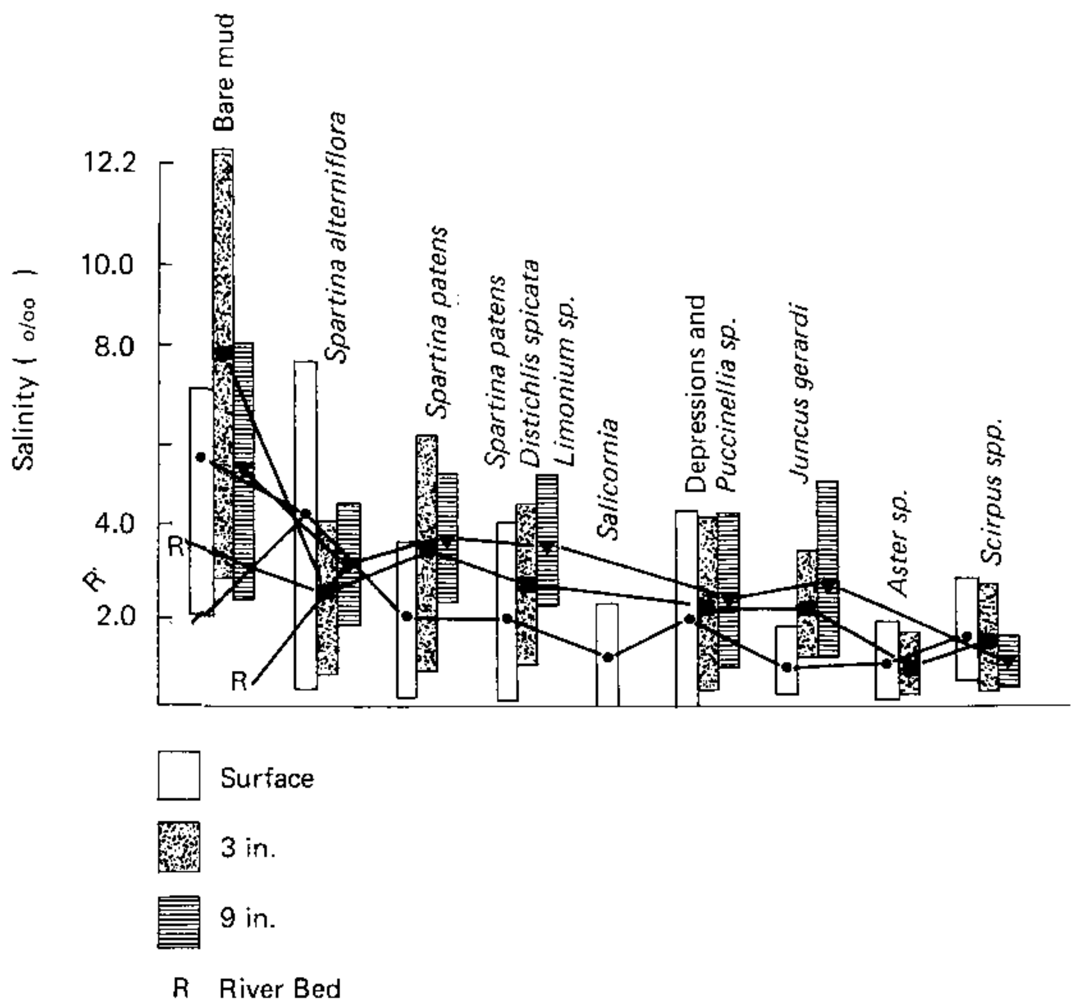


Figure 5-43. Salinity ranges of the bottom sediments underlying the different marsh communities in New England salt marshes (adapted from Chapman 1940a).

emergent salt marsh: (1) water content, (2) water table, (3) fluctuation of water levels, (4) soil types, (5) aeration, (6) nutrients, (7) acidity, (8) salinity, (9) temperature, (10) light, and (11) chemistry. Biotic forces include animal actions, plant competition, and human activities.

In Maine the sharp physiography between subtidal and terrestrial habitats tends to compact the salt marsh and enhance zonation. Two zones can be characterized (figure 5-44); (1) the low marsh, which is regularly flooded by the tides and dominated by smooth cordgrass; (2) the high marsh, which is irregularly flooded by the tides and dominated by salt hay, with black rush dominating along the highest fringe of the marsh. Above the black rush zone a variety of transitional and terrestrial species may be found as the influence of tidal inundation and salinity becomes markedly reduced. The macrophytes most commonly found in Maine salt marshes and their habitat preferences are listed in table 5-15.

The low intertidal marsh zone in Maine is dominated by salt marsh cordgrass. Smooth cordgrass is a stout marsh grass with long, smooth, tough leaf blades and strong creeping rhizomes. It usually grows in dense stands in the low marsh. It tends to occur in a tall form near the water edge, followed by a shorter "dwarf" form farther up the marsh.

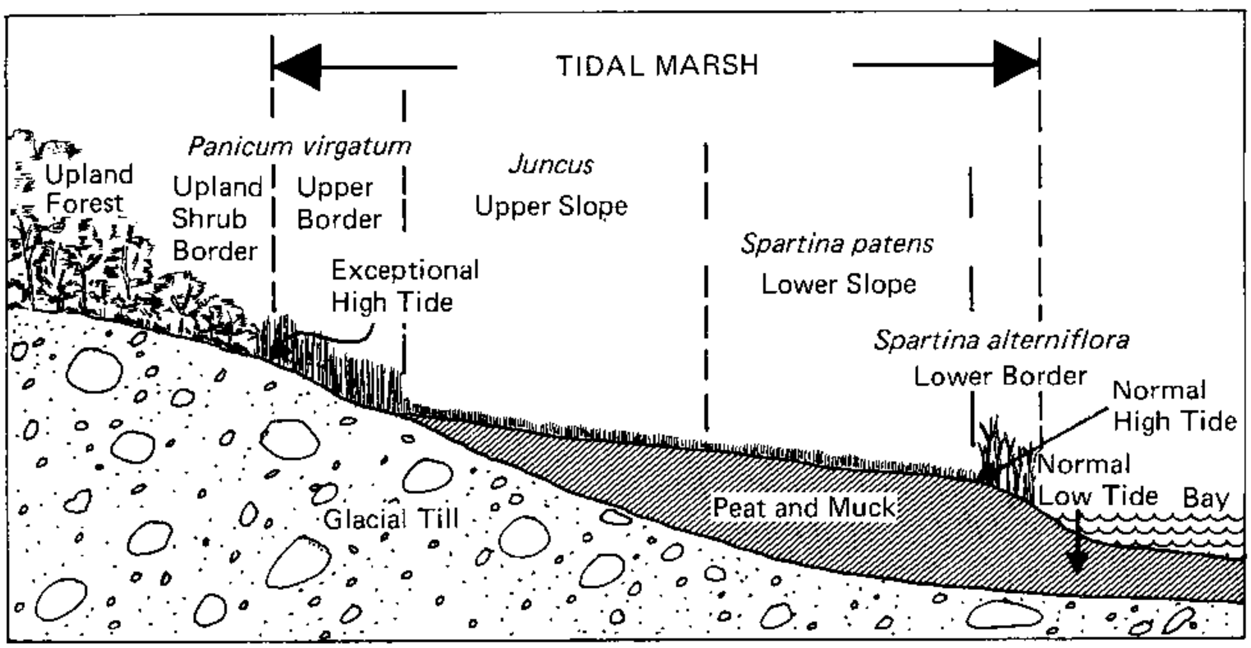


Figure 5-44. Cross section of an upland-to-bay sequence in a New England salt marsh showing intertidal high and low marsh (adapted from Miller and Egler 1950).

Table 5-15. Emergent Vegetation Associated with Salt Marshes in Maine[a]

Species	Common name	Characteristics	Habitat preference
Spartina alterniflora	Smooth cordgrass	10 cm-2 m high, high protein production	Intertidal zone, borders all salt marshes, covers the low marsh, grows best in wet, high salinity soil regularly flooded
Spartina patens	Salt meadow grass, salt hay, marsh grass	15-75 cm	High marsh, grows best in drier parts of marsh, typically forms a mat as it dies seasonally, irregularly flooded
Distichlis spicata	Spike grass	10 cm-1.2 m, perrenial	Grows in clumps around edges of tide pools along tidal creeks and where there is considerable salt, irregularly flooded
Juncus gerardii	Black rush or Black grass	15-80 cm, June-Sept. main growth	Round in high marsh in drier soil, grows luxuriantly toward the upland, irregularly flooded
Typha latifolia	Cattail	1-2.5 m, May-July main growth, perennial	Indicates fresh water in upland portions of the marsh

[a]Adapted from TRIGOM 1974.

(Continued)

Table 5-15. (Concluded)

Species	Common name	Characteristics	Habitat preference
Phragmites australis	Reedgrass	1-4 m tall, perennial	Commonly grows along ditches, irregularly flooded
Salicornia europea	Glasswort, chicken claws	1-10 cm. tall, Aug-Nov. annual, turns red in fall	Grows well in salt pannes or depressions in marsh, irregularly flooded
Limonium Nashii	Sea lavender, marsh rosemary	15-60 cm, July-Oct.	High marsh plant
Solidago sempervirens	Seaside golden rod	20 cm-2 m high, July-Nov.	Upland fringe
Scirpus maritimus	Bulrushes	30 cm-1 m high, July-Oct. perennial	Above high tide mark

Linthurst (1977) found that cordgrass in Maine grew at elevations of 7.6 feet (2.3 to 3.0 m; creek bank) and 8 to 9 feet (2.4 to 2.8 m; higher marsh) above mean low water (MLW). (In Maine, mean high water approximates 10.5 feet, 3.2 m, and mean low water 0.0 feet.) Generally, creek bank cordgrass reaches a maximum height of 4 to 6 feet (1 to 2 m) at peak standing crop (July and August). Farther into the marsh, as elevation increases, cordgrass may become dwarfed, attaining 0.5 (0.25 m) to 1 feet (0.5 m) in height. The following species occassionally are found in association with cordgrass in Maine: salt marsh aster (Aster novibelgii), sea lavender, (Limonium nashii), saltwort (Salicornia europea) and salt hay.

Maine salt marshes are dominated by high intertidal marsh (salt meadows). Salt meadows (salt hay and spike grass Distichlis spicta) grow at elevations that are irregularly flooded by tides (exceed the mean high tide level). Linthurst (1977) found that salt hay grew at an elevation of about 9.8 feet (3 m) above MLW. Species that may associate with salt hay are: salt marsh aster, orach (Atriplex patula hastata), seaside gerardia (Gerardia maritima), salt marsh pink (Stellaria stellaris), marsh alder (Iva frutescens), panic grass (Panicum virgatum), sea-meadow grass (Puccinellia sp.), silverweed (Potentilla quinquefolia), sea lavender, saltwort, salt marsh cordgrass, black rush, and arrowgrass (Triglochin maritima).

Salt hay grows from 6 inches to 2.4 feet (15 to 75 cm) in height in dense yellowish green mats and often resembles a meadow with swirls or "cowlicks." Spike grass is darker green and grows in association with salt hay but may occur in dense, erect, pure stands.

The black rush community often is found immediately above the salt haymeadow. In Maine, black rush grows from 10 to 13 feet (3 to 4 m) above MLW on creek banks and on high marshes (Linthurst 1977). This area defines the upper slope of the intertidal salt marsh. Salt hay intergrades with black rush on the lower marsh edge, while black rush, which appears on a pure thin grassland, grades into the transitional and terrestrial communities on the upland side. Species that may intergrade with black rush include: salt marsh aster, orach, spike grass, sea lavender, common reed (Phrogmites communis), seaside goldenrod (Solidago sempevirens), dwarfed spikerush (Eleocharis parvula), alkali bulrush (Scirpus paludosus), common three-square (Scirpus americanus), salt marsh bulrush (Scirpus robustus), prairie cordgrass (Spartina pectinata), saltmarsh sedge (Carex paleacea), saltwort, and cattail (Typha augustifolia).

No research has been done on the transitional marsh but most of the species found in the black rush zone are probably in the transitional marsh as well.

An interesting phenomenon of New England salt marshes is the existence of numerous salt pannes (irregularly flooded flats) and pond holes (depressions with unconsolidated sediments). A salt panne usually refers to a slight depression in the intertidal marsh surface, generally circular or oval, in which no vegetation grows. These depressions trap standing salt water, which kills most forms of vegetation because evaporation increases the salinity beyond the limits tolerable to most plant species. Pannes in high marsh areas may be referred to as pond holes.

Pond holes may be of variable depth. They may be derived from relics of intertidal pannes or they may be the result of blocked creeks or decay of the marsh surface turf (Redfield 1972). Pond holes in the middle of high (salt hay) marshes are characteristic of newly formed high marsh and, in older high marshes, may exist in several developmental forms. Pond holes that have been drained as the result of erosion or ditching are invaded by stands of cordgrass.

Little data are available on the size, floristic composition, and frequency of salt pannes in Maine. Gore (1965) and Rasar (1968) discuss the occurrence in Maine and function of widgeon grass pools (Ruppia maritima), which are flooded forms of salt pannes.

Ecological succession may be defined as "...an orderly process of community development that involves changes in species structure and community processes with time" (Odum 1971). In the intertidal salt marsh, successsion culminates in change in the biotic structure of the flora (figure 5-45). However, the floristic changes are triggered most often by (1) changes in the height of the marsh surface relative to mean sea level; (2) changes in tidal range and inundation; (3) changes in the drainage pattern across the marsh; and (4) change of the salinity regime in the marsh.

Changes in the height of the marsh surface are most often the result of accumulation of sediment in the marsh (sedimentation). Human activities can also influence marsh elevation (e.g., ditching and filling). As salt marsh grasses slow the velocity of tidal flow, particles in the water are more apt to become deposited on the marsh. As the height on the marsh floor increases, the inundation patterns change and species that require less inundation become established. Primary succession in a New England salt marsh with increasing elevation proceeds with cordgrass giving way to salt hay (figure 5-42).

Retrogressive succession, in which high marsh becomes progressively wetter due to subsidence of the marsh floor or a rise in the level of sea water causes salt hay to be replaced by cordgrass. Any natural or artificial disturbance (e.g., ditching or canals) of drainage across the marsh, tidal regime, sedimentation, or salinity can accelerate or reverse salt marsh succession.

Keser and coworkers (1978) studied the effect of removing the Cowseagan Narrows Causeway (Montsweag Bay, region 2) on the intertidal community of cordgrass. The causeway had for many years acted as a restraint to tidal waters flowing up and down the bay. Its removal initiated retrogressive succession in the neighboring causeway salt marsh. The physical parameters of the upper bay changed overnight:

> "After removal of the causeway in the fall of 1974, the average tidal range increased by 0.34 m reflecting greater water flow in and out of Montsweag Bay. The average high tide was 0.06 m higher and the average was 0.27 m lower. The resultant average tidal range, 2.88 m, exposed an additional 109 to 168 ha (269 to 415 acres) of mud flat during each tide" (Anonymous, in Keser et al. 1978).

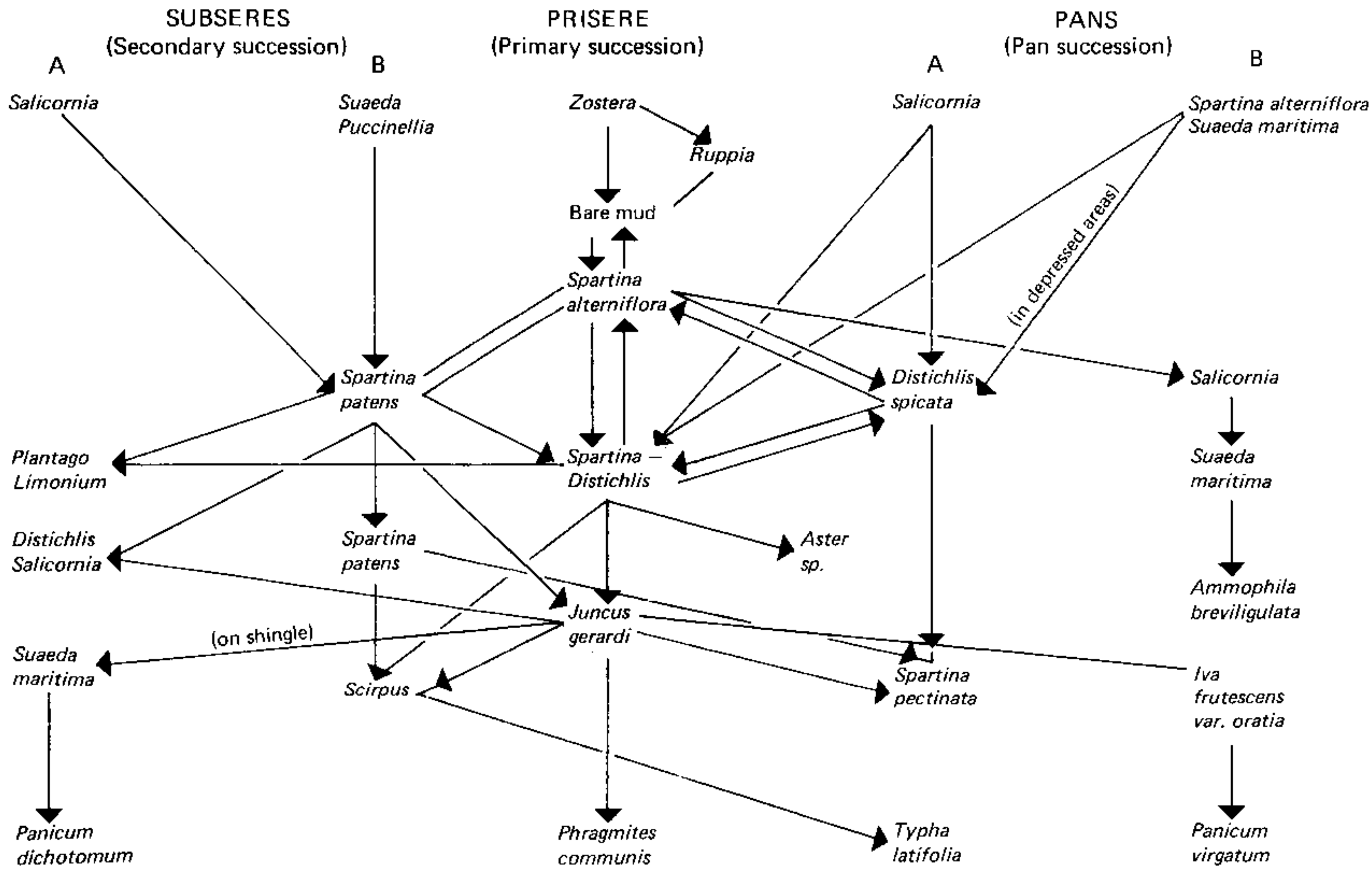


Figure 5-45. Succession of plant communities on New England salt marshes (adapted from Chapman 1940b)

Average salinities during 1975 to 1977 increased 4.2 ppt at the surface and 3.4 ppt at a depth of 3^{o}m (Keser et al. 1978) and average temperatures were 1.3^{o} C (2.3^{o}F) lower at 0.15 m and 2.1^{o}C (3.8^{o}F) lower at 3 m. These changes were due to increased exchange between bay waters and the colder, more saline waters of the Sheepscot River when the causeway was removed.

Two years after the causeway was removed changes in the cordgrass community were observed. The mean number of shoot densities sharply decreased in 1975 to 1977 because of the increased salinity and colder water (Keser et al. 1978). Plants 20 to 30 inches (50 to 75 cm) tall did not flower after the causeway was removed. Between 1975 and 1977 average biomass decreased to 58% of that of the previous years. Increased tidal amplitude, higher salinity, and lower temperatures reduced vigor and fecundity in the lower marsh and eventually will lead to its destruction.

The primary producers in estuarine emergent salt marshes are phytoplankton, the benthic and epiphytic algae of the mud surfaces, and emergent vegetation. The relative contributions of each of these producer groups to estuarine intertidal marsh production is not known. In Maine, scientists have concentrated on establishing the level of production of the emergent vegetation and the role it plays in supplying energy to the estuarine system primarily through the detrital cycle. Data that characterizes salt marsh phytoplankton and algae are scarce.

Although phytoplankton contributes to wetland productivity, it is much more important in the open estuary (see "Phytoplankton" above). Nixon and Oviatt (1973) found that in a Rhode Island salt marsh the diatoms Asterionella, Thalassiosera, Nityochia, Skeletonema, and Chaetocerus dominated the larger phytoplankton except during late summer when dinoflagellates were more abundant.

Epiphytic algae are small plants that grow on exposed mud surfaces and on stems of emergent and submergent plants. Although detailed information on their contribution to the productivity of Maine salt marshes is lacking the importance of these small but numerous plants is heightened by the knowledge that they are very productive during the fall and winter months, when the grass communities lie senescent. Chapman (1940a) identified the algae of a Massachusetts salt marsh and found that algal associations were correlated with the emergent grass communities and the degree of inundation. Redfield (1972) working in a Massachusetts salt marsh reported that the dwarf cordgrass zone is covered almost completely with a thin layer of filamentous algae during summer, principally Lyngbia sp. and Vaucheria sp. (see "Macroalgae and Rooted Vegetation" above).

Little, if any, research has been conducted concerning the epibenthic productivity of salt marshes in Maine; however, researchers have found that in Massachusetts, epibenthic marsh productivity exhibits a seasonal variation. Production in Great Sippewisset Marsh, Falmouth, Massachusetts, was found to be low during summer and early winter but peaked in the spring (115 mg C/m^2 /yr) and in the fall (60 mg $C/m^2/yr$). Epibenthic production was as high as or higher than the marsh phytoplankton production (Van Raalte et al. 1976).

The most visible biotic component of the marsh, the emergent vegetation, dominates the salt marsh and is the principal contributor to salt marsh production. In Maine, cordgrass and salt hay dominate the emergent salt marsh flora. Research in Maine salt marshes has concentrated on characterizing the intertidal emergent cordgrass community.

Causeway Marsh, a cordgrass marsh in Montsweag Bay, was studied in detail over a 5-year period by Vadas et al. (1976) and Keser et al. (1978). Linthurst (1977) made a comprehensive study of Maine salt marsh productivity in Franklin and Salisbury Cove near Ellsworth, Maine. McGovern (1978) looked at above- and below-ground biomass, net productivity, elemental composition, and elemental release of cordgrass at Herrick Bay near Brooklin, Maine. The following is based largely on their work.

In Maine, cordgrass shows two distinct peaks of plant density (figure 5-46) during the growing season (Vadas et al. 1976; and Keser et al. 1978). A high density appears in spring when young plants first appear. In late spring and early summer, densities decrease as intraspecific competition for light, nutrients, and space increases (Vadas et al. 1976). In late August or September an increase in density is produced by a new crop of small plants from tillers and rhizomes of mature plants. At Causeway Marsh stem densities per square meter in late summer ranged from 1676 in 1972 to 1306 in 1974. Spring densities were 1541 in 1972 and 2035 in 1974.

Linthurst (1977) reported the following stem densities for three dominant species of salt marsh emergent vegetation in Maine salt marshes:

Species	Location	Stem densities (no./m^2)
Black rush	Creek bank	8680 ± 684
	High marsh	3880 ± 294
Cordgrass	Creek bank	3206 ± 664
	High marsh	1804 ± 129
Salt hay		12,880 ± 2438

Stem densities for salt hay in Maine are far higher than those in Delaware (5900 ± 574) or Georgia (2900 ± 484; Linthurst 1977). Shoot densities for cordgrass not growing on creek banks are remarkably similar (Linthurst 1977; and Vadas et al. 1976).

In June, the new spring growth of cordgrass is approximately 8 to 24 inches (20 to 60 cm) high. Most plants are tallest (7 feet; 2 m) in July. By August a second growth of small plants begins. The second crop rarely grows higher than 1 foot (30 cm; figure 5-46; Vadas et al. 1976).

Vadas and coworkers (1976) observed that cordgrass plants over 3 feet (1 m) tall usually begin to flower in August. A maximum net estimate of biomass (peak standing crop) was 1419 g dry wt/m^2 in 1974 at Causeway Marsh, according to Vadas et al. (1976). Maximum biomass usually occurs between July and September and often is followed by a decrease of 40% to 50% within a month after the maximum biomass is attained (Vadas et al. 1976). The maximum living and dead biomass of cordgrass in the Franklin and Salisbury Cove area is 863 ± 140 g dry wt/m^2 for creek bank cordgrass (Linthurst 1977). The biomass of cordgrass near Herrick Bay peaked at 508 g dry wt/m^2 (McGovern 1978).

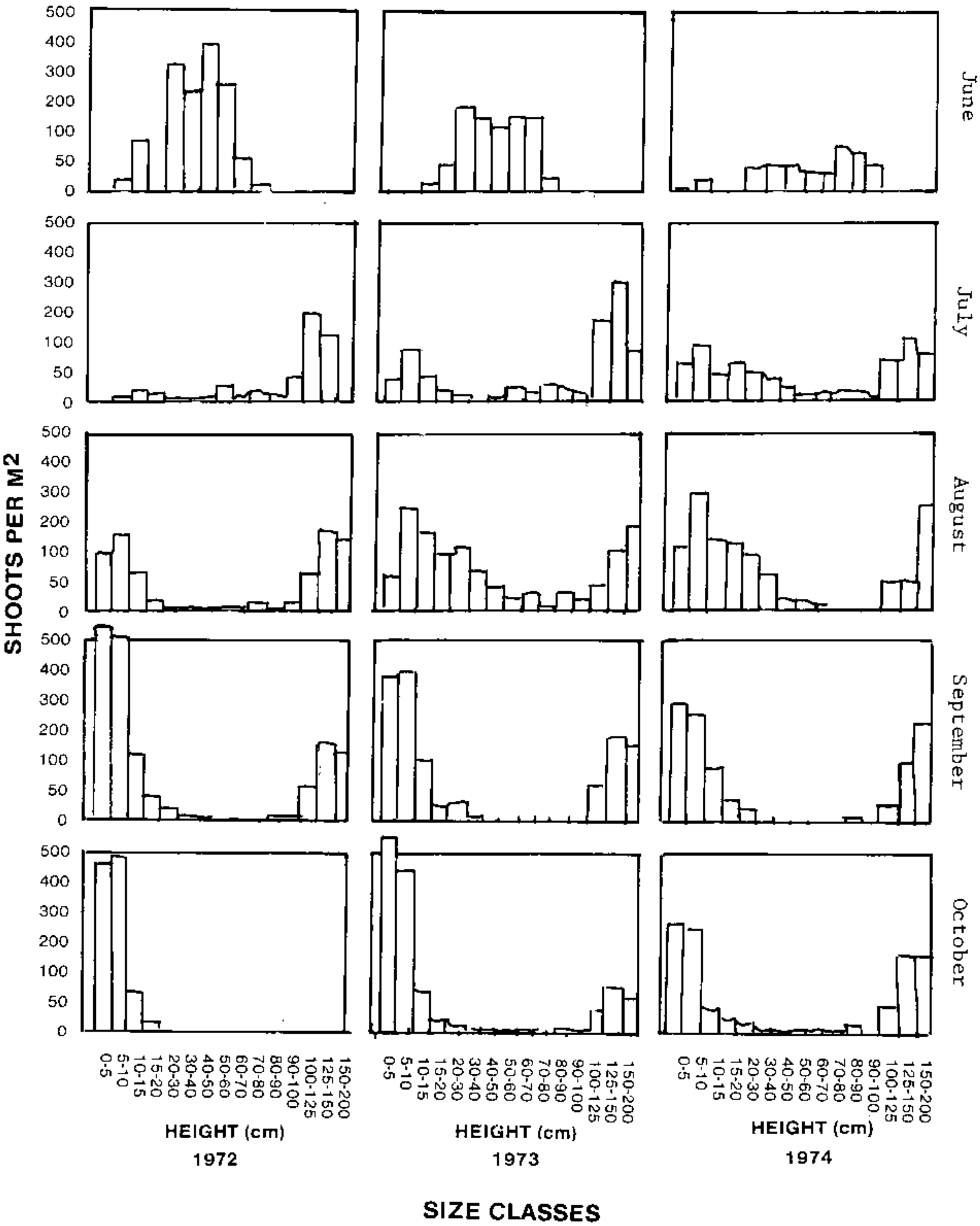


Figure 5-46. Monthly (June to October) density (number of shoots per square meter) of cordgrass in the Causeway marsh, Montsweag Bay, from 1972 to 1974 (Vadas et al. 1976; and Keser et al. 1978).

A maximum living and dead biomass of salt hay for Maine marshes approached 3036 ± 506 g dry wt/m^2 (Linthurst 1977). Values for Delaware and Georgia marshes showed lower maximum biomass values (2000 g dry wt/m^2). Above-ground production of salt hay in Rhode Island at the end of the growing season was 430 g dry wt/m^2 (Nixon and Oviatt 1973).

Creek bank black rush had a maximum living and dead biomass in Maine of 1694± 190 g dry wt/m^2. High marsh black rush possessed a somewhat lower maximum biomass of 676± 90 g dry wt/m^2(Linthurst 1977).

Estimates of productivity attempt to reflect the production of a standing crop of vegetation over an entire growing season, rather than the biomass at peak standing crop. The net aerial primary productivity (NAPP) of the three dominant species of emergent salt marsh vegetation in Maine was determined by Linthurst (1977; table 5-16). NAPP was calculated by methods used by Smalley (1959) and Weigart and Evans (1964). Linthurst (1977) used a combination of these methods in estimating NAPP in the estuarine intertidal wetland. The NAPP of salt hay in Maine was approximately double that of Delaware and also higher than that reported for Georgia (table 5-16).

NAPP values for creek bank black rush were much higher in Maine than in Delaware; however, the NAPP for high marsh black rush in Maine was much lower than that in Delaware (table 5-16).

The annual above ground net productivity of cordgrass was 619 g/m^2/year (McGovern 1978). Of this, at least 223 g/m^2 of organic material was later stored as below ground tissue and at least 396 g/$m^2$was left above ground as detritus each year.

The turnover rate of cordgrass in Maine was higher than that of Delaware and Georgia, primaily because of the greater loss of dead plant material due to greater tidal activity (Linthurst 1977). Maine salt marshes apparently supply more energy per unit area of marsh to the estuarine ecosystem through the detrital cycle than salt marshes further to the south.

The below ground biomass of cordgrass at Herrick Bay salt marsh in Brooklin, Maine (McGovern 1978), was 1422 g/m^2 when first sampled in April but decreased to a low of 909 g/m^2 in August and then increased to 1646 g/m^2 in December (McGovern 1978).

Because below ground biomass was 223 g/m^2 greater in December than in April, Herrick Bay cordgrass marshes required 223 g/m^2 organic matter for respiration and senescence of tissue during the winter. Since net above-ground productivity was determined to be 619 g/m^2, McGovern (1978) estimated that at a maximum, 396 g/m^2 (2 tons/acre) of organic tissue potentially would become detritus each year. This indicates a very productive system, one of the most productive natural systems in the world (Teal and Teal 1969).

Below-ground productivity makes a special contribution to salt marsh productivity by providing primary production to infaunal organisms and microbes. In addition, the below ground parts of plants help ward off erosion and stabilize the marsh peats and bordering uplands.

Table 5-16. Net Aerial Primary Productivity (NAPP) $g/m^2/yr$ of Species in Salt Marshes at Different Locations[a].

Species	Location	Productivity[b]
Maine		
Black rush	Creekbank	3000
Black rush	High marsh	600
Cordgrass	Creekbank	1300
Cordgrass	High marsh	1300
Salt hay	High marsh	4600
Delaware		
Salt hay		2000
Black rush		1200
Georgia		
Salt hay		3000

[a]Linthurst 1977.
[b]Values are interpreted from a bar graph (Linthurst 1977).

A wide variety of organisms are found in and around the intertidal emergent salt marsh because of its high productivity. The consumers in the salt marsh are herbivores (organisms that consume algae and green plants), detritivores (organisms that consume dead plant and animal particles as their chief source of nutrients), and the predators (organisms that actively search for prey).

Invertebrate communities in salt marshes are dominated by the hard-shelled bivalves or shellfish, gastropods (snails), crustaceans, and soft-bodied worms or polychaetes.

Invertebrates are a primary source of food for higher consumers. Data on the nature of the invertebrate population of the Maine salt marshes are scarce.

Unfortunately little is known about the population dynamics, distributions and life histories of benthic invertebrates in the intertidal salt marshes in Maine. In a Cousins River, Yarmouth, salt marsh, the benthic mud-dwelling invertebrates of the intertidal marsh are dominated by the deposit- and suspension-feeding annelids (segmented worms), particularly the oligochaetes (Larsen, unpublished). Bivalves include the deposit feeding baltic clam and the filter-feeding soft-shelled calm. Gastropods are represented by the rough periwinkle and the common mud snail. The crustaceans are represented by the isopod Edotea triloba and amphipod Orchestia grillus (Larsen, unpublished).

The presence of forage fish in salt marshes is one of the primary reasons that the larger commercially important carnivorous species at sometime in their life history utilize wetland areas to feed. Small fishes inhabiting the intertidal wetlands, such as the ubiquitous mummichog and the silverside, are preyed upon continually by striped bass, winter flounder, and eels. Small fish that feed in the marsh during high tides represent an integral link in the estuarine food web between the primary producers and the higher consumers. Intertidal wetlands are also valuable nurseries for larval and juvenile fishes (see chapter 11, "Fishes," for more detailed information).

Small mammals that frequent the marsh are the meadow mouse and the muskrat. Muskrats not only consume the leaves and stems of cordgrass and bulrush (Scirpus spp.) but then also use the grass blades for hutch building. Upland species that occasionally comb the marsh in search of food are raccoons, opposums, and woodchucks. Weasels, red and gray foxes, deer, and rabbits, also frequent the emergent marshes. They utilize the marshes for food and sometimes are preyed upon by other animals.

Nixon and Oviatt (1973) reported occasional small mammals including mice, voles, muskrats, and raccoon in Bissel Cove salt marsh in Rhode Island. The impact by small mammals on salt marsh systems was considered slight, except for the building of hutches by muskrats. No studies to date have described the use of the intertidal salt marsh by small mammals in Maine.

Various waterfowl, shorebirds, wading birds, and terrestrial birds inhabit the low cordgrass marsh, where they find food and cover. Red-winged blackbirds and sharp-tailed sparrows consume cordgrass seeds. Both black ducks and green-winged teals eat the root and rhizomes of cordgrass, although they prefer the invertebrates in the associated bottom materials seasonally. Black ducks and mallards consume mud snails found in wetlands. Geese consume the leaves and stems of cordgrass and feed extensively on bulrush when it is available. Least sandpipers, godwits, and semipalmated plovers feed on worms in or contiguous to the low areas of salt marshes. Great blue herons feed on fish in the salt marsh.

The seed and root stocks of salt hay are eaten by ducks and geese. The dense growth occasionally is used as nesting cover by waterfowl. Black ducks raise young in this area of the marsh. Sharp-tailed sparrows, savannah sparrows, and the spotted sandpiper nest in the salt hay marsh. Salt pannes in the upper areas of marshes in Maine support large production of widgeon grass and invertebrates which are important food for a variety of waterfowl and shorebirds (Gore 1965; and Rasar 1968).

Other species found feeding in and around the salt marshes are great blue herons, long-billed marsh wrens, snowy egrets, Louisiana herons, and glossy ibises (see chapter 14, "Waterbirds," and chapter 16, "Terrestrial Birds," for further information). The last three species are more commonly found in the southwestern regions of coastal Maine.

Detrital microbes play an important role in the production of food for detritivores. On the coast of Maine the decomposition by microbes of cordgrass is of great importance. Bacterial species (usually Cytophaga) contain active cellulolytic enzyme systems for consuming detritus, but very little is known specifically about microbes because of their extremely small size and relatively nondescript morphology. In Georgia, most microbial activity in the salt marsh water column was associated with detrital particles <3 μM in size (Hanson and Wiebe 1977). In salt marshes, microbial activity is greatest at ebb tide and lowest at slack low water and high tide. In Maine no studies have been made concerning the decomposition rates of detritus or the microbial activity associated with decomposition.

The usually high productivity associated with intertidal salt marshes and particularly cordgrass is unique among natural systems. In Maine, productivity (annual biomass turnover) approaches 2 tons/acre ($396 g/m^2$). The fact that much of this productivity then is transported to the estuarine water column where it is a basic unit of the primary production upon which the consumers and decomposers thrive is an added dimension of wetland productivity. Although cordgrass is near the northern limit of its distribution in Maine it appears to be no less productive than it is in the South and mid-Atlantic States. The fact that salt marshes are small and relatively uncommon in Maine in comparison with other States reinforces their importance to Maine. Many consumers inhabit or frequent intertidal salt marshes. Diverse birds and fishes are the most visible consumers, yet a host of invertebrates species (insects, worms, molluscs and shellfish) also thrive in salt marshes. People benefit from wetland productivity through commercial and sport fishing, game hunting, and bird watching.

In estuarine intertidal emergent salt marshes the physical environment interacts with the biological community to form the basic characteristics of the habitat. Energy flow, food webs, and nutrient and biogeochemical cycling are examples of interaction between the biological and physical spheres.

Symbolic representations of the major components and interactions of energy flow in estuarine intertidal wetlands are given in figure 5-47 (see chapter 1 for a detailed description of energy and symbolic energy-flow diagrams). In intertidal salt marshes primary producers (plants) capture the energy of the sun and produce biomass through photosynthesis. Much of the energy produced by photosynthesis is consumed in plant respiration. In marshes the energy produced by photosynthesis is greater than that consumed by respiration, so organic matter accumulates and becomes available to the system as a source of energy for consumers.

In the salt marshes of Maine, primary producers are the phytoplankton, algae, and emergent vegetation (figure 5-47). Emergent vegetation in the forms of cordgrass, salt hay, and black rush dominates the primary productivity. Primary production in the form of plants is ingested directly by herbivores. In wetland habitats, phytoplankton and, to some extent, algae are consumed by a variety of filter-feeding invertebrates and larvae. Leaf loss to herbivores was about 23.3% in a northern population of cordgrass (Hatcher and Mann 1975), but no significant population of grasshoppers or other herbivorous insects was observed in a Rhode Island salt marsh (Nixon and Oviatt 1973).

Most of the primary production of salt marshes enters the food web as detritus, but some is stored in the sediments as peat. As emergent plants die, much of their above-ground biomass is transported from the marsh surface to the water column by tides and exported to the adjacent estuary. In Maine, scoring of the intertidal marshes removes virtually all of the cordgrass. (McGovern, 1978, found no unsenescent above-ground cordgrass in December and April). Dead vegetation (detritus) is colonized by microbes which decompose the vegetation to particulate form. As detrital particles are further decomposed, they are converted into an enhanced nutritious food source which includes the colonizing microbes (figure 5-48) and is consumed by a variety of filter- and deposit-feeding organisms.

Salt marshes may import energy from the terrestrial habitats that border them, the riverine systems that flow into them, the atmosphere, and the estuarine open water systems that are contiguous to them. Litter from bushes, trees, and grasses may be transported to salt marshes by rain, runoff, and wind. Some terrestrial consumers (e.g., mice and rabbits) browse the salt marsh vegetation and leave nutrient-rich fecal droppings.

Runoff from rain potentially can carry a variety of inputs into the upper areas of marshes. Natural items (e.g., litter, debris, and sediment) may be transported into the marsh, but non-natural inputs, such as heavy silt from construction activities, oil and grease from highways or parking lots, and pesticides from fields also can be transported into the salt marsh.

The riverine system carries organic material, dissolved nutrients, fresh water animals, and potential pollutants (pesticides, sewage, heavy metals, and hydrocarbons) from the inland systems to the estuarine salt marshes. It is extremely difficult to quantify the amounts of these materials entering the wetland system. However, it is clear terrestrial and riverine systems have a direct, if not well-understood, relationship with the intertidal wetland habitats. Most researchers agree that estuarine intertidal wetlands export more energy than they import (Teal 1962; and Nixon and Oviatt 1973).

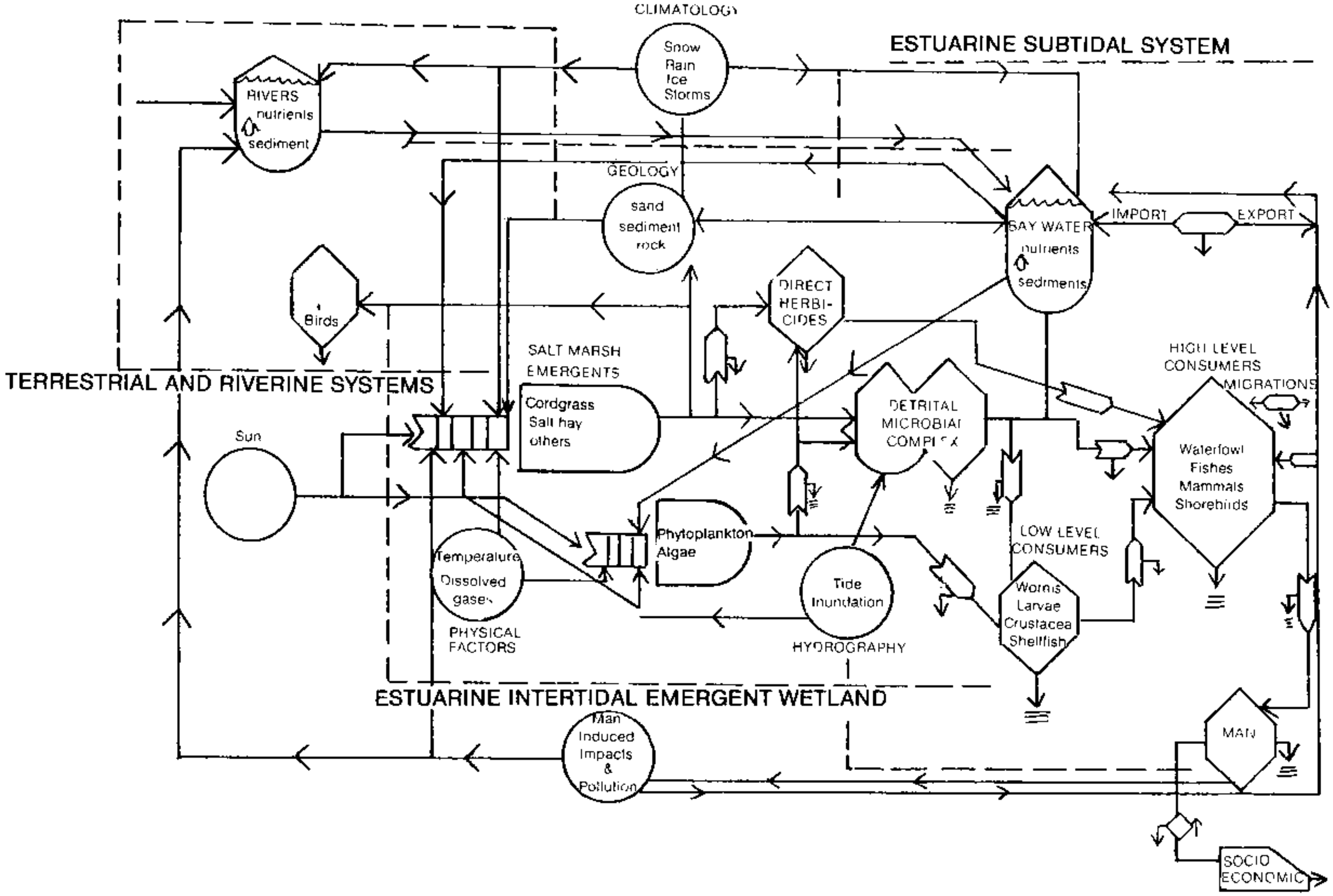


Figure 5-47. Energy flow in an estuarine intertidal emergent wetland, showing the relationship between the terrestrial, riverine, and estuarine systems.

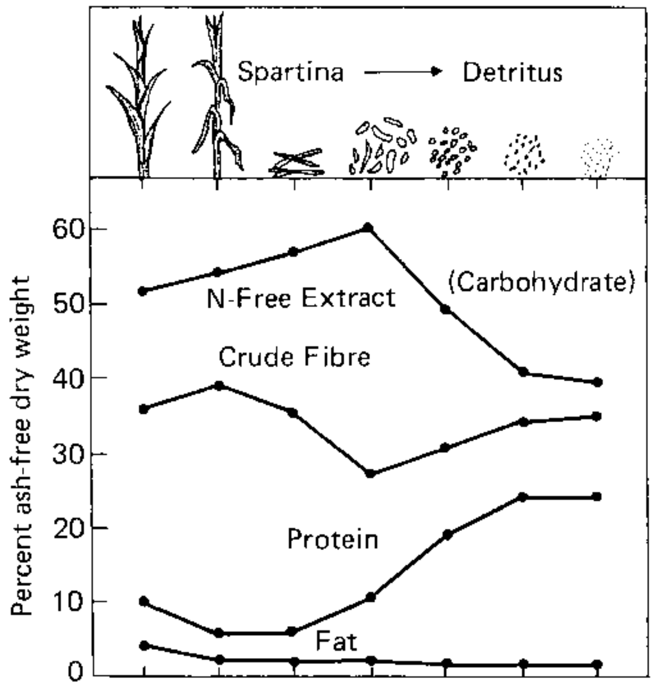


Figure 5-48. Protein enrichment of Spartina detrital particles resulting from microbial colonization (after Odum and de la Cruz 1967).

Energy flow also may be traced through a system through the examination of a food web (see chapter 1, "The Conceptual Framework of the Characterization" for a discussion of food webs). The estuarine intertidal and subtidal food web (figure 5-27) is dominated by the detrital food chain, in which dead vegetation colonized with microbes is ingested as detritus. However, zooplankton, barnacles, and bivalves, for example, may feed directly on phytoplankton and diatoms. Consumers of primary production in the detrital and grazing food chains include, for example, forage fish, such as the mummichog, the shrimp (Crangon sp.), the worms (Nepthys incisa and Scolecolepides viridis), the amphipods (Gammarus spp. and Ampelisca spp.), the molluscs (soft-shelled clam, Baltic clam, and Hydrobia spp.), and many species of zooplankton and grazing fishes. The larvae of many of these species and families also are primary consumers in the estuarine food web.

Secondary and tertiary consumers, energy-intensive organisms, are dominated by fish, waterfowl, and mammals. These species require high energy inputs from the lower trophic levels to maintain themselves, grow, reproduce, and migrate. Examples of high level consumers in Maine estuaries include the hakes, winter flounder, harbor seal, and mergansers. People are high level consumers also.

An important feature of the salt marsh habitat is the fact that the primary producers (the green plants) are the primary energy sources. The energy fixed through photosynthesis in the green plants is consumed directly (as leaves) or indirectly (as detritus) by the higher consumers. Ultimately, the highest consumers, which are significant economic resources in coastal industry in Maine, depend upon the primary production of the salt marsh grasses.

Impacts, such as destruction of wetlands by dredging and filling, on the energy flow in salt marsh habitats ultimately will affect those plants and animals that depend upon salt marsh production for their energy requirements. Similarly, the overharvesting or destruction of any components of the food web will affect the species that depend upon those components as a food source.

Energy flow models and food webs aid in understanding the complex interrelationships in an ecosystem. Managers must be cognizant of the intricate patterns of energy flow from the primary producers to the highest consumers in order to assess adequately the impacts of particular activities on estuarine intertidal salt marshes.

Globally, estuarine intertidal wetlands have been postulated to have critical roles in maintaining and controlling the cycles of sulfur and nitrogen (Deevey 1970). On a regional level, tidal marshes exhibit an excess of stored phosphorus in the sediments yet lack the vital nitrogen component for maximum growth. Since salt marsh sediments contain enough phosphorus in the upper 33 feet (10 m) to promote normal plant growth for 500 years salt marshes do not appear to be phosphorus-limited (Pomeroy et al. 1969).

Little research has been done on biogeochemical cycling in Maine salt marshes. McGovern and coworkers (<u>in press</u>; and 1978) studied salts secreted by cordgrass and the elements in the leaves of cordgrass that potentially could enter the estuarine detrital food web.

Reimold (1972) reported that cordgrass in Georgia is a vehicle to translocate phosphorous from salt marsh sediments to estuarine waters. McGovern and coworkers (<u>in press</u>) found that a stand of cordgrass with a biomass of 1.0 kg/m^2 could export 1.0 g P/m^2/hour.

Although it appears that cordgrass in Maine may not contribute as much phosphorous to the estuarine system as populations farther south, the high productivity of Maine's salt marsh cordgrass and the export of almost all of the above-ground senescent biomass to the water column yield a large quantity of nutrients. McGovern (1978) determined the elemental composition of cordgrass and subsequently the amounts of these nutrients that enter the estuarine water column annually in a Maine salt marsh. They were nitrogen, 0.993 g-atoms/m^2; phosphorous, 0.075 g-atoms/m^2; potassium, 0.218 g-atoms/m^2; calcium, 0.144 g-atoms/m^2; magnesium, 0.330 g-atoms/m^2; iron, 0.030 g-atoms/m^2; boron, 1681.0 g-atoms/m^2; copper, 281.0 g-atoms/m^2; and manganese, 2634.0 g-atoms/m^2. This represents a significant contribution to the estuary from the cordgrass of the intertidal emergent wetland habitat. No data are available concerning the contribution of other salt marsh species (salt hay and black rush) to the estuarine water column.

Little data are available on nutrient levels in the salt marsh peats and in the contiguous water column in Maine. It generally is agreed that nitrogen is the key nutrient limiting growth in the salt marsh plants (Pomeroy et al. 1969; and Sullivan and Daiber 1974). Nitrogen, applied to the marsh in the form of urea or ammonium nitrate, caused increased production of almost all plants in a Massachusetts salt marsh (Valiela and Teal 1974).

Forms of nitrogen found experimentally in salt marshes include nitrate, ammonia, and nitrite. Nitrate concentrations are high in winter and low or undetectable in summer. Ammonia is the dominant form of nitrogen in tidal creeks in summer. Nitrite concentrations rarely exceed 1.5 μ g-atoms/l and showed no discernible seasonable patterns in a Delaware salt marsh (Aurand and Daiber 1973).

The import of nutrients from other systems fertilizes wetlands. Sewage and fertilizer from terrestrial sources, transported to the wetland via the riverine system or by direct runoff into the intertidal wetland, may increase production greatly. There is a limit, however, to the amount of nutrient loading and physical alteration that these wetlands can handle and still maintain their critical functions.

The role that tides play in transporting vital nutrients to intertidal salt marshes generally is known. Some researchers have suggested that the action of the tides 'subsidizes' the intertidal marsh (Odum and Riedenburg 1976). Increased nutrient loads, aeration, and other environmental factors controlled by the tides are cited as giving creek bank cordgrass (which grows more vigorously than cordgrass in other physiographic locations) a greater growth potential. Odum (1971) stated "...the higher the tidal amplitude the greater the production potential..." In Maine, the high tidal amplitude and twice-daily tides could play a critical role in expanding the hypothetical role of 'tidal subsidy' in supplying nutrients needed for growth and carrying away waste products.

RESEARCH NEEDS

In comparison with other estuaries on the east coast of the United States, such as Chesapeake Bay, Long Island Sound, and the New York Bight, estuaries in coastal Maine are poorly studied. Major data gaps exist in virtually every scientific discipline. Knowledge of estuarine hydrography is embryonic. Data are needed on coastal currents and circulation, both tidal and nontidal. Upwelling and frontal processes need to be investigated, especially in eastern Maine (region 6) where such processes may be responsible for maintaining high biological productivity. Information on circulation in estuaries and water exchanges between estuaries and coastal marine waters of the Gulf of Maine is lacking almost completely. Annual and interannual trends in water temperature and salinity need investigation, as does spatial and seasonal variability in water masses, in order to facilitate more accurate delineation of estuarine habitats.

Present data on nutrients are random and patchy. Monitoring of nutrient distributions spatially and temporally is a high priority. The nutrients in estuaries need to be sampled at fixed stations at frequent time intervals, monthly or more often. A combined study of hydrography, nutrient distribution, and primary productivity in both coastal and estuarine waters is the most efficient way of filling the data gaps in these areas. Pollution levels in Maine coastal waters, especially estuaries, are little known.

Surveys of heavy metals, hydrocarbons, and pesticides, in water, sediments, and organisms would provide a baseline against which future improvements or declines in environmental quality could be measured. Presently, the amount of these substances entering the environment and the location of their accumulation is little known. Information on the pathways and rates of movement of these pollutants through the ecosystem also is needed.

The relative and absolute importance of the various sources of primary production in estuaries is not well understood. Information on the contributions of phytoplankton, intertidal and subtidal macroalgae, benthic diatoms, emergent wetlands, eelgrass beds, and river inflow would enable researchers to identify the systems most in need of consideration by management. Secondly, it is important to understand the ecological factors, such as shelter, habitat type, and nutrient requirements, which control the distribution and abundance of these plants. Using the data of the NWI, researchers may now be able to quantify the production contributions of the various habitat types and hence estimate the total productivity of the coastal system. Eelgrass beds need investigation from the point of view of providing habitat space for several groups of organisms.

As an adjunct to the productivity research needs mentioned above, research also is needed on carbon pathways through the ecosystem: the fate of primary productivity needs to be known. Specific questions would involve the food and feeding of the primary consumers, benthos, and zooplankton and the utilization of these species by fish, birds, and marine mammals.

Many large data gaps exist concerning the fauna of the characterization area. Data are lacking on the distribution, abundance, and biomass of the subtidal benthos of marine and estuarine areas. Most estuaries and much of the coast have not been sampled, so no baseline exists for impact assessment. No data are available on the natural variability of the fauna and no studies of the secondary productivity of zooplankton or benthos have been carried out. The biology of many ecologically and commercially important species is not fully understood. For example, the early life histories of the bloodworm and the sea scallop are not known and regulation is, therefore, difficult. Little is known about the ecological factors controlling most intertidal and subtidal species, and almost nothing is known about species interactions. Why such a high diversity exists in the Sheepscot estuary and whether high diversity is a general characteristic of the characterization area are questions that remain unanswered.

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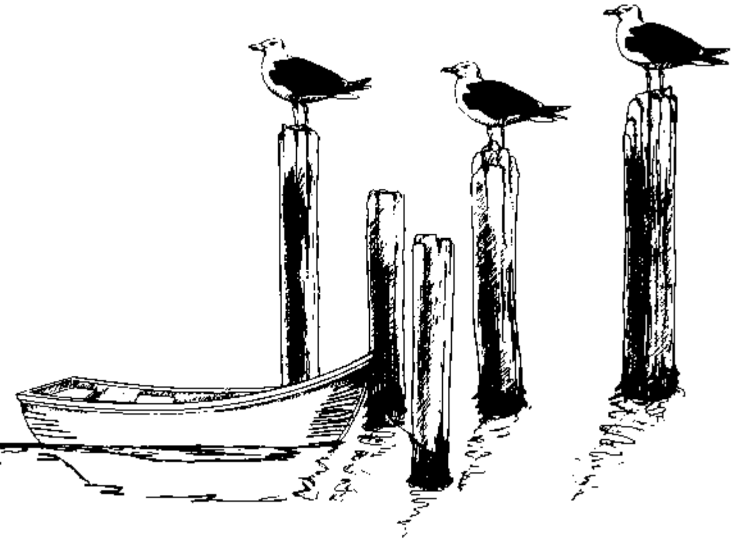
Chapter 6
The Riverine System



Authors: Russell McCullough, Stewart Fefer

This chapter characterizes the riverine system of coastal Maine. The riverine system includes all bodies of fresh flowing water: streams, rivers, brooks, tributaries, and creeks. The term "stream" is used to refer to all of these bodies. The term "river" is used to refer to those streams commonly known as rivers. Streams are among the most conspicuous and valuable natural features of coastal Maine. Approximately 381 streams are named on U.S. Geological Survey (USGS) maps of the characterization area (atlas map 1). The four largest rivers in Maine (Penobscot, Kennebec, Androscoggin, and St. Croix) flow through the coastal zone and the lower portions of their drainage basins are located there. Major portions of several intermediate-sized rivers (e.g., Fore, Presumpscot, Pleasant, Chandler, Sheepscot, Pemaquid, St. George, Union, Narraguagus, Machias, E. Machias, Orange, Dennys, and Pennamaquan) and their drainages are located within the coastal zone, also. These rivers are among the most heavily used natural resources in coastal Maine. For many years Maine's streams have been used for waste disposal, power generation, log transport, and navigation. These uses have caused disruption of natural riverine functions and frequently have interfered with the uses of streams for water supply and recreational purposes.

The National Wetlands Inventory (NWI) of the U.S. Fish and Wildlife Service (FWS; Cowardin et al. 1979) classifies riverine systems hierarchically, according to physical and biological features (figure 6-1). Riverine systems include four subsystems: tidal (segments influenced by tidal rise and fall); lower perennial (segments having a slow current and water in the streambed year-round); upper perennial (segments having a rapid current and year-round water); and intermittent (segments where the streambed is dry part of the year). The named streams on USGS maps of coastal Maine include both riverine and streamside palustrine systems. The specific areas identified as riverine systems by the NWI are included in atlas map 1. Common names of species are used except where accepted common names do not exist. Taxonomic names of all species mentioned are given in the appendix to chapter 1. This chapter details the distribution of riverine systems in coastal Maine and presents some of the basic concepts and available data on riverine function.

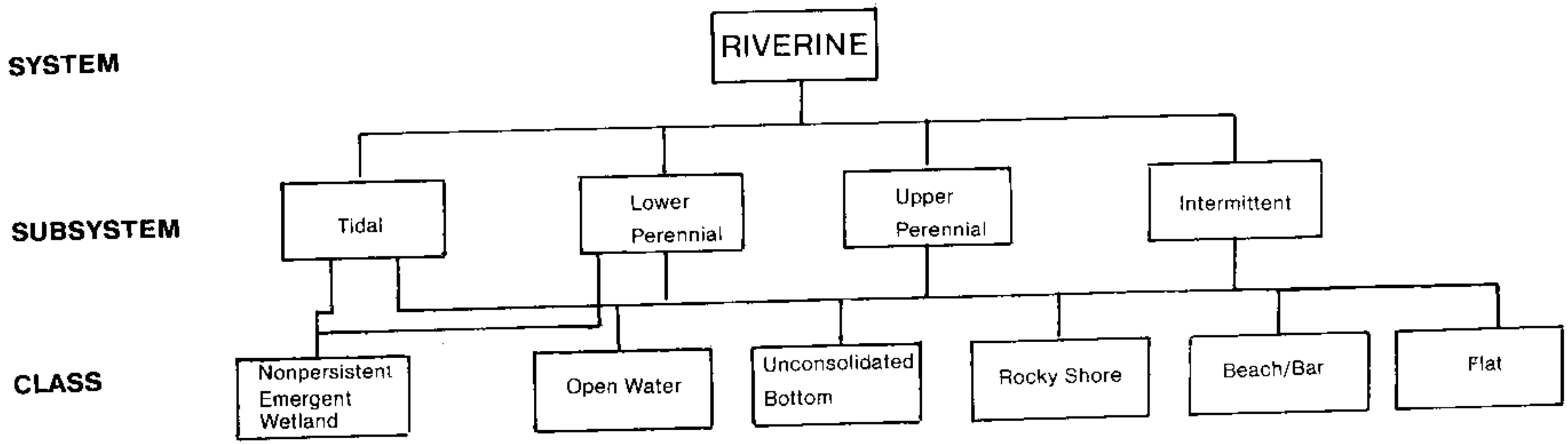


Figure 6-1. Hierarchical classification of the riverine system of coastal Maine (Cowardin et al. 1979).

DATA SOURCES AND COMPILATION OF DATA

Sources used in composing this chapter include pertinent scientific literature, unpublished theses and reports, the preliminary results of the National Wetlands Inventory (NWI), and personal communications. The NWI does not delineate small (<40 feet; 12 m wide) rivers, streams, and brooks. Some are identified as linear features (no area measurements possible). Intermittent stream subsystems also are not delineated by the NWI, but intermittent streams are identified on USGS quads as dashed lines. Preliminary data on the acreage of river and stream habitat acreage are conservative, especially with regard to the upper perennial subsystem. Additional information on certain individual river systems (primarily those in eastern Maine, regions 5 and 6) has been collected by the Atlantic Salmon Commission of Maine Department of Marine Resources, but is not presently available.

GEOGRAPHICAL CHARACTERISTICS

NWI data indicate that a variety of riverine habitat types exist in coastal Maine and that their abundance varies regionally (tables 6-1; see also atlas map 1). The rivers of the coastal zone comprise a total area of approximately 16,136 acres (6533 ha), which constitutes <1% of the land and freshwater area of the coastal zone. Riverine systems occupy the least area of the aquatic systems in coastal Maine and the major portion of riverine area is tidal (13,190 acres; 5340 ha, or 82%). Most of the riverine habitat in the coastal zone is located in region 2; 11,631 acres (4510 ha) or 72% (table 6-1). Only 180 acres (73 ha), or about 1% of the riverine habitat in the coastal zone, is located in region 3 (table 6-1). Region 2 has the only extensive riverine emergent wetland habitat in coastal Maine (Merrymeeting Bay area), as well as the largest area of riverine tidal flat and beach/bar habitat. The major portion of mapped lower and upper perennial riverine habitat is in region 6 (725 acres and 535 acres; 294 ha and 217 ha, respectively). A total of 381 streams are named on USGS topographic quads of the coastal zone. The length of riverine subsystems in these named streams is given in table 6-2. Fifteen percent of the linear riverine habitat was classified in the NWI as tidal, 51% as lower perennial, and 34% as upper perennial. The areal and linear measurements indicate that the riverine tidal habitat represents a relatively large acreage but relatively few linear miles; and lower and upper perennial represent relatively few acres but many miles. Palustrine wetlands occupy 44% of the total length of the named streams in coastal Maine. The State water quality classification of named streams within the characterization area is given in appendix B of chapter 3. The habitat mileages, tributaries, and townships of named streams are listed in appendix A of this chapter.

PHYSICAL CHARACTERISTICS

The size of drainage basins in Maine riverine systems is presently being examined by the USGS Water Resources Division and the Maine Department of Environmental Protection. Data on drainage basin size and amount of discharge on rivers gaged by the USGS are given in table 6-3. The drainage basin size given is only that of the area upstream of the gaging station. Thus, the size of the drainage basin of the entire riverine system is larger than that given. (The site of the gaging stations are not necessarily within the coastal zone.) The Penobscot River (8570 sq miles; 22,196 sq km) has the largest drainage basin of any of the riverine systems in Maine, followed by the Kennebec (5780 sq miles; 14,970 sq km), Androscoggin (3450 sq miles; 8936 sq km) and St. Croix (1635 sq miles; 4235 sq km). As is to be expected, the Penobscot River also has the largest average discharge (11,817 cu feet/sec; 335 cu m/sec) followed by the Kennebec (4436 cu feet/sec; 126 cu m/sec), Androscoggin (3707 cu feet/sec; 105 cu m/sec) and St. Croix (2692 cu feet/sec; 76 cu m/sec). Other rivers in coastal Maine have smaller drainage basins (<700 sq miles; 813 sq km) and an average flow of <1000 cu feet/sec (28 cu m/sec). Bodies of water with drainage basins (if they are larger than 25 acres) are shown in atlas map 3.

Riverine systems of coastal Maine do not exhibit an orderly progression of subsystems environments from mouth to head (tidal to intermittent subsystems). Only the larger rivers of the characterization area (Penobscot, Kennebec, Androscoggin, and St. Croix) exhibit any type of progression and within these only the two lower subsystems, tidal and lower perennial, are present within the coastal zone. Smaller streams may not contain the tidal or intermittent habitats. Small streams account for the majority of the acreage of upper perennial riverine habitat in coastal Maine. Many other rivers in the system originate in lakes and ponds and enter the estuarine system over bedrock falls that exceed the vertical tidal range height.

The four subsystems of the riverine system are defined on the basis of river morphology and geology. A compilation of the habitat types found within each named stream in coastal Maine is given in appendix A (see also atlas map 1). The tidal subsystem is that portion of the river streambed where daily water level and flow fluctuates under the influence of tides. Flow may reverse in this subsystem during periods of spring tides and low river discharge. The tidal subsystem in Maine coastal riverine systems may be as long as 19 miles (30 km), as it is in the Kennebec River, or absent entirely. The Penobscot River is the other river having a substantial section of freshwater tidal habitat. The river channel gradient of the tidal subsystem is the lowest gradient within the riverine system. Gradients are commonly as low as .015% (Kennebec River from Augusta to Bowdoinham), meaning that over a given distance (e.g., 10 miles), the gradient or slope of land is .015% of that distance (e.g., .0015).

The morphology of the tidal subsystem is variable and dependent upon a number of factors, including river discharge, channel slope, sediment load, and the surficial or bedrock geology of the lower river basin. The larger river basins contain relatively wide, straight river valleys cut into bedrock or surficial deposits. These valleys, from 99 to 216 feet (30 to 65 m) deep and up to 1.6 miles (2.5 km) wide, were cut during post-glacial rebounding (see "Geology," in chapter 2). The riverine tidal basins originated from the lower perennial subsystem prior to its drowning by a rise in sea-level approximately 7000 years ago (Schnitker 1974). With the reduction in the river channel gradient that resulted from this drowning of the lower perennial subsystem, sedimentation occurred within the channel sections. Deposition on channel bottoms formed channel beach/bars, flats, and emergent wetlands. Upson and Spencer (1964) found up to 13.3 yards (12 m) of estuarine-riverine sediments below the active channel bottom in the Kennebec River at Bath and <3 feet (1 m) at Augusta (figure 6-2). Their investigations in the Fore, Sheepscot, Penobscot, and St. Croix Rivers also indicate channel aggradation in the tidal subsystem portions of these waterways.

Table 6-1. Area (acres) and Percentage Contribution (in parenthesis) of Riverine Subsystems and Classes in coastal Maine and for each Region[a].

Region	Riverine Habitat Total	Tidal total	Beach/bar	Nonpersistent Emergent Wetland	Open water	Flat	Unconsolidated bottom	Rocky shore	Lower perennial total	Open water	Emergent	Upper perennial total
1	1122 (7)	882 (7)	278	52	552	0	0	0	119 (6)	119	0	121 (12)
2	11,631 (72)	11,140 (84)	1102	3133	5682	1211	12	0	353 (19)	353	0	138 (13)
3	180 (1)	0 (0)	0	0	0	0	0	0	163 (9)	163	0	17 (2)
4	1270 (8)	871 (7)	0	0	808	62	0	1	175 (9)	175	0	224 (21)
5	374 (2)	0 (0)	0	0	0	0	0	0	371 (19)	371	0	3 (<1)
6	1557 (10)	297 (2)	0	7	97	193	0	0	725 (38)	646	79	535 (51)
Total	16,136	13,190	1380	3192	7139	1466	12	1	1906	1827	79	1038

[a]Percentages given in parentheses.

Table 6-2. Length (miles) of Riverine Subsystems in the Named Riverine Systems of Coastal Maine, by Region

Regions	Tidal	Lower perennial	Upper perennial	Total
1	<1	20	9	29
2	52	36	23	111
3	0	7	9	16
4	8	32	54	94
5	0	67	6	73
6	<1	47	38	86
Total	61	209	139	409

Table 6-3. Drainage Area (square miles) and Discharge (cu.ft./sec) of Gaged Maine Streams at Most Downstream Gage Stations[a]

Basin	Stream	Site of gage station	Drainage area[c] sq. miles	Period of record (years)	Discharge cu feet/sec Max	Min	Aver	Temp °C Max	Min	°F Max	Min
Fore River Basin	Stroud Water River	Portland, ME	28		1160	3					
Presumpscot River Basin	Presumpscot River	West Falmouth, ME	590 (648)[c]		12,500	39		29	0	84	0
Royal River Basin	Royal River	Yarmouth, ME	142	28	11,500	4	274				
Androscoggin River Basin	Androscoggin River	Brunswick, ME	3410 (3450)					27	0	81	0
	Androscoggin River[b]	Rumford, ME	2067	85	74,000	625	3707				
Kennebec River Basin	Cobbosseecontee Stream	Gardiner, ME	217	75	5020		339				
	North Branch Tanning Brook	Manchester, ME	<1	13	195	<1	2				
	Kennebec River[b]	Bingham, ME	2720 (5870)	49	58,800	110	4436				
Sheepscot River Basin	Sheepscot River[b]	North Whitfield, ME	148	39	6420	5	245				
Pemaquid River Basin	Tributary near Damariscotta	Damariscotta, ME	<1	3.5	no flow						
Penobscot River Basin	Penobscot River[b]	West Enfield, ME	6670 (8570)	75	153,000	1630	11,817				
Union River Basin	Garland Brook[b]	Mariaville, ME	10 (497)	13	1230	<1	22				
Narraguagus River Basin	Narraguagus River	Cherryfield, ME	232	29	10,400	20	495				
Machias River Basin	Machias River	Whitneyville, ME	457	64	14,800	4	939				
Dennys River Basin	Dennys River	Dennysville, ME	92	22	3930	8	192				
St. Croix River Basin	St. Croix River	Baring, ME	1370 (1635)	18	23,500	262	2692				
	St. Croix River	Milltown, ME						28	0	82	0

[a]USGS 1978.
[b] River in coastal zone, gage station outside coastal zone.
[c]Figure in parentheses total area of drainage basin (TRIGOM 1974).

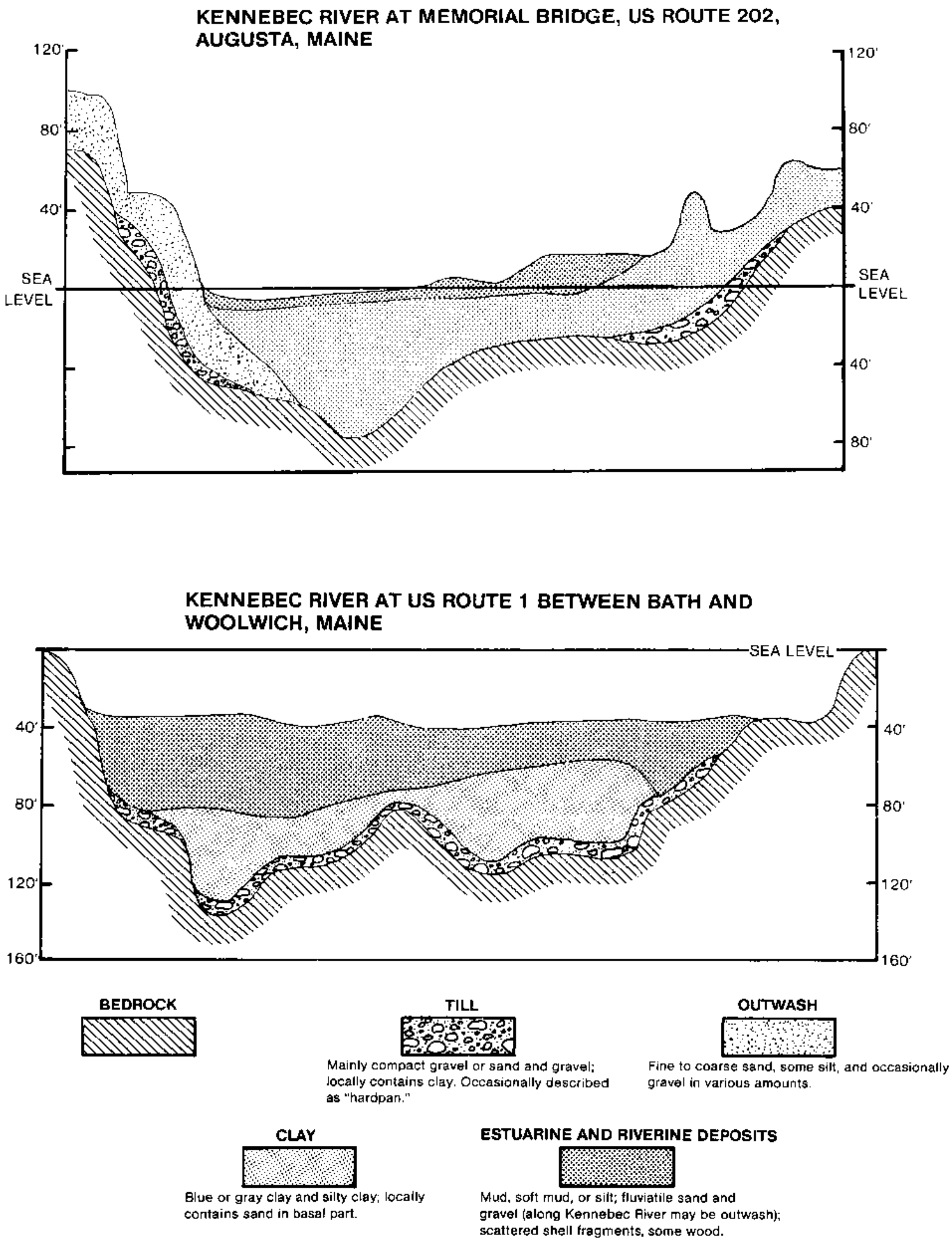


Figure 6-2. Cross-section of deposits filling the tidal portion of the Kennebec River (adapted from Upson and Spencer 1964).

The NWI includes the following classes within the tidal subsystem in coastal Maine: open waters, unconsolidated bottom, flat, rocky shore, beach/bar, and nonpersistent emergent wetland (figure 6-1). While most rivers exhibit at least one of these classes within their tidal sections, only the larger ones contain all of the classes. Merrymeeting Bay (region 2), the confluence of the tidal reaches of the Androscoggin, Kennebec, Cathance, Abbagadasset, and Muddy rivers, has all of the above classes. The main streambeds of the Kennebec and Androscoggin rivers are open water, with unconsolidated or rock bottoms. Unconsolidated bottoms probably erode during spring freshet peaks and aggrade as discharge decreases. Most bottom sediment ranges probably from silt to medium sand.

Bordering the tidal streambeds are partially subaqueous bars, including mid-channel, lateral (parallel alongside) and point (sticking out from the land) bars of relatively clean fine sand, or partially submerged mud-flats that rise gently in slope to emergent wetlands covered with nonpersistent fresh-water aquatic plants. Flat and bar environments are submerged constantly during periods of high river discharge but may be uncovered daily during low flows and low tides. Beaches and rocky shores also comprise shoreline areas of the tidal subsystems of larger rivers. The origin and composition of sediment in all tidal classes is discussed in chapter 5, "The Estuarine System." Tidal subsystems of smaller rivers and streams generally exhibit a zonation of classes from open water stream bed to flat to emergent wetland or rocky shoreline.

The lower and upper perennial subsystems of rivers and streams within the characterization area may be juxtaposed or intermixed (atlas map 1), depending upon the geologic substrate over which the channel flows. The lower perennial subsystem is that part of the stream where the channel gradient is low; flow is slow; the channel substrate consists predominantly of sand and mud; and the floodplain is relatively wide. The upper perennial subsystem is that channel segment where the channel gradient is high; flow is fast; the channel substrate consists of sand, gravel, and cobbles; and little or no floodplain is present. The larger river systems (Androscoggin, Kennebec, Penobscot, and St. Croix) all exhibit typical lower perennial subsystems above the tidal stretches throughout their courses within the characterization area. The floodplains of these are not very wide and some channel sections may flow over bedrock or contain substrates of gravel. However, substrates are predominantly depositional and vegetated lateral and point bars have built up on the inside of channel bends. Smaller rivers such as the Dennys, Machias, East Machias, Presumpscot, St. George, Fore, Sheepscot, and Narraguagus have sections of lower perennial channels separated by upper perennial segments.

Lower perennial segments flow through low terrains such as broad valley bottoms, and glaciated terrains whose drainage has been blocked locally by moraines or other ice-contact deposits. Channel segments are generally sinuous, meandering with local subaqueous bars and lateral nonpersistent emergent wetlands, or may flow through palustrine wetlands, with the channel bounded on three sides by palustrine deposits. Upper perennial reaches are generally straight and can be broken down into pools and riffles. Pools are relatively low-flow segments of a reach where the depth of the channel is greater than in other reaches. The channel bottom still may consist of sand, gravel, cobbles, and boulders deposited during periods of high flow; these sediments may be covered with mud, which settles from the water column during low flow. Riffles are reaches where flow is rapid and the channel gradient is high. Depth of water during average flow is low and the channel is usually covered with cobbles and boulders. Streams with smaller drainage areas (<77 sq miles; <200 sq km) may be composed of either or both upper or lower perennial subsystems. The intermittent subsystem of a river or stream consists of channel segments over which water flows only during portions of the year, usually during spring freshets or just after periods of high precipitation. Otherwise, the channel is dry or contains small pools of still water.

CHEMICAL CHARACTERISTICS

The continuing compilation of water quality records by the USGS serves as a valuable long-term record of general chemical variability in certain Maine streams. Mairs (1968), Hutchinson (1968), and Taylor (1973) have provided water quality data for certain streams in Maine. Recent data on chemical characteristics are given in appendix B, tables 1 to 7. The following is a summary of water quality parameters. A discussion of the functions of water chemistry parameters is presented in "Water Chemistry Parameters" below.

In all riverine systems measured in coastal Maine, pH levels are highly variable and no consistent trends are evident. Maine rivers rarely exceed pH 7.0 (see appendix B, tables 2 and 3). Frequently, pH levels in Maine streams are at the lower end of the scale. Dissolved oxygen is variable in those rivers where O_2 has been measured (see appendix B, table 4). The concentration of dissolved oxygen in measured Maine rivers ranged from 5.3 mg/l (St. Croix River in summer) to 14.2 mg/l (St. Croix River in spring). Maine rivers show fluctuating, relatively low levels of alkalinity (appendix B, table 5). Low alkalinity and extremely low levels of calcium and magnesium are responsible for the "softness" of fresh waters. Maine streams show variations in concentrations of phosphorus. Nitrate is one of the most variable and unpredictable constituents measured. Natural levels of phosphorus and nitrates are normally relatively low and highly susceptible to influence by pollution. No sharp maximum or minimum specific conductance has been seen in Maine rivers. Most tended toward a spring minimum under conditions of heavy spring runoff (see appendix B, tables 6 and 7).

Major cations in order of abundance are calcium, sodium, magnesium, and potassium, while the order of abundance of anions is sulfate, bicarbonates, chloride, and nitrate. Rather wide seasonal variability is found among trace elements phosphorus, aluminum, iron, manganese, zinc, copper, and boron. No high concentrations of heavy metals were detected in the water sampled in the stream systems listed in appendix B table 1.

ABIOTIC FACTORS AFFECTING THE RIVERINE SYSTEM

Abiotic factors determine the composition of biota prevailing at a particular site. Considered below are climatic, geologic, and physicochemical factors, the effects of which usually cannot be separated.

Climate

Climatic factors are major determinants of the physical and biological characteristics of streams through their control of air and water temperature and the amount and pattern of precipitation.

Temperature. Air temperature has a direct effect on the freeze-up and break-up of streams. Freezing may occur in two ways: surface ice forms when air temperature drops to freezing levels at the air-water interface; anchor bottom ice is formed when climatic conditions (i.e., cool temperatures and clear skies) allow radiational cooling of rocks, logs, or other immersed objects to the extent that ice forms around them. Surface ice interferes with the exchange of gases between air and water, and reduces the amount of light penetrating the surface (especially if snow covers the ice). Anchor ice around objects prevents organisms from attaching to them and may trap organisms, causing deaths. Scouring of the substrate may occur when anchor ice breaks up, resulting in dislodgment of organisms and disturbance of sediments.

Air temperature, in conjunction with light-intensity, tree-canopy cover and current velocity, also influences year-round water temperatures. Water temperature has a major influence on the rates of production, respiration, and decomposition of stream organisms; thereby affecting nutrient and energy cycling within the stream system. Temperature also affects the distribution of stream organisms. For example, in Maine streams brook trout and other salmonids require cool temperatures (65°F; 11°C), while smallmouth bass grow and reproduce best under warmer conditions.

Air temperature affects stream conditions indirectly, also, through its influence on evapotranspiration (loss of water by direct evaporation at the surface and through plant use). Evapotranspiration is a factor determining the percentage of entering precipitation that remains in streams. High temperatures increase evapotranspiration rates.

The southwest to northeast air temperature gradient along the Maine coast results in warmer water temperatures and earlier ice breakup in southern areas, cooler temperatures and later ice breakup in northern areas (Lautzenheiser 1972; Fobes 1974; and Davis 1966).

Precipitation and flow levels. Water in streams may come from direct precipitation, surface runoff, through-flow (lateral movement of water through the soil) or ground-water discharge. The primary source of all these waters is atmospheric precipitation. Therefore, the amount and pattern of precipitation in an area are the ultimate determinants of the amount (i.e., flow) and pattern of stream flow in that area.

Annual precipitation in Maine (see "Climate," page 2-9in chapter 2) is greater than that in much of the United States and is sufficient to maintain comparatively large rivers with moderate-sized drainage basins.

The flow pattern of a river is frequently equally or more important than the amount of flow in relation to physical and biological processes. For example, most channel-cutting erosion occurs during peak flow periods, and a stream with a very irregular pattern of flow may erode its channel much more quickly than a stream with comparable mean flow but a less variable flow (Beaumont 1975). Unregulated streams that have irregular flow patterns are more likely to cause flood damage and erosion than those with regular flow patterns. Variations in flow may influence animal behavior. Upstream migrations of fish such as Atlantic salmon, an important Maine sport fish, are cued by peak flows. Along the Maine coast, as in most of New England, maximum flows occur in early spring (coinciding with snow melt) and minimum flows in late summer and early autumn (Langbein and Wells 1955).

Pollutant transport. In addition to temperature and precipitation, transportation of pollutants, particularly nutrients, acids, and heavy metals, has important effects on streams. Acid precipitation and associated heavy metal contamination are of particular concern in Maine (Davis et al. 1978; and Norton et al. 1978), where most natural waters have a low buffering capacity (i.e., low resistance to changes in acidity). Under conditions of extremely low buffering capacity (more likely to be encountered in lakes than in rivers) acidification and metal contamination may interfere with fish reproduction (Beamish 1976). Airborne acids and metals are usually the result of fuel combustion, while nutrients are normally dust particles raised by wind, farming, building construction, and similar dust-producing activities. The extent of atmospheric pollutant problems in rivers of coastal Maine is not known, but the general problems of acid precipitation are discussed in chapter 3, "Human Impacts on Coastal Maine."

Geology-Hydrology

The riverine system in coastal Maine lowlands originated after the Wisconsinan deglaciation of about 11,000 to 13,000 years ago (Stuiver and Borns 1975). Most streams are dependent upon or controlled by the geologic structure of their channels or by the form and slope of the channels' surface. The channel courses developed in the glacially-created terrain in response to sea-level withdrawal and post-glacial upland uplift (Sayles 1938).

Three stream course types based upon origin are present in the characterization area:

1. Large streams conforming to pre-Wisconsinan channels;
2. Smaller streams following late glaciation meltwater stream courses;
3. Smaller streams developing independent courses on the uplifted coastal upland.

The first type includes the tidal and lower perennial portions of the major rivers (Kennebec, Androscoggin, Penobscot, and St. Croix), although portions of these rivers were diverted from their pre-Wisconsinan channels by glaciation (Gerber 1979).

The second type includes many streams in regions 5 and 6 that developed on the low topography of coastal lowlands. Here, water flows in a southeasterly direction, parallel to the flow of glacial ice and meltwater streams. Water courses are interrupted frequently by lacustrine and palustrine systems and are diverted locally by marginal ridges that block their direct flow to the ocean.

The third type of stream has developed in regions 1 through 4, in the marine clay valleys and low plains. Stream courses are variable here, sometimes controlled by glacial topography, regional slope and, where downcutting has intersected the bedrock surface, by the bedrock structural grain (from NE to SW).

Landform and chemical composition of bedrock exert a major influence on stream hydrology. Landform (e.g., relief, elevation, and soil development) determines the shape and size of the drainage basin and modifies the amount and pattern of stream flow in conjunction with precipitation. Chemical composition of bedrock and soils is a major influence on water chemistry. Bodies of water in the coastal zone with their drainage basins (if they are larger than 25 acres) are shown in atlas map 3.

Landform. Among the effects of geology on stream hydrology perhaps the most basic is that of regional topography on the size of drainage basins. Larger drainage basins not only collect more water for a given regional rainfall but, because of the local and scattered nature of storms, provide a more regular input of water from precipitation than smaller basins. Topography also influences the developmental pattern of stream channels. This, in turn, influences flow patterns, since highly-branched channel systems tend to have a more regular flow than less-branched systems (Beaumont 1975). Irregular or variable flow increases a stream's vulnerability to erosion and affects behavior of some stream organisms (see "Precipitation," above).

Topography, particularly slope, and the geological history of an area, especially glaciation history, have a strong influence on the way water from precipitation enters a stream. In areas with steep slopes and a history of glaciation, (e.g., the headwaters or source areas of many Maine streams) soil development generally is limited and bedrock is present near the surface. Under these conditions percolation of water through the substrate into groundwater is minimal and most precipitation reaches the stream by surface runoff or through-flow (Beaumont 1975). In downstream reaches, where slopes are more moderate and peat and soil development is more extensive, groundwater discharge is greater (Beaumont 1975). Current velocity, which is dependent on slope, channel geometry, and substrate roughness, tends to decrease along the upstream to downstream gradient. Current velocity is an important factor in determining substrate type (high velocity results in large particles), amount of erosion (high velocity increases erosion), stream load (high velocity transports more material), and degree of mixing within the water column and between the water and the air (high velocity creates greater turbulence and mixing). These phenomena are significant biologically and contribute to the development of biological communities along the length of a stream.

Bedrock composition. Chemical composition of the bedrock and soils within the drainage basin is normally the most dominant factor in determining water chemistry within a stream system, although airborne pollutants, runoff pollutants from developed areas, and pollutants dumped directly into the water may be dominant factors in some areas. Calcareous bedrock (e.g., limestone) and soils derived from it usually are associated with streams that have high levels of inorganic plant nutrients, reflected in high conductances and alkalinities. Calcareous deposits within the coastal zone are extremely limited and, therefore, geologic contributions of nutrient ions to Maine rivers are relatively slight. Peaty soils, common in Maine lowlands, may contribute substantial quantities of dissolved organic material to stream waters, causing yellow-brown water color.

Water Chemistry Parameters

Chemical constituents of freshwater systems are derived from material that runs off, is eroded, leached, and/or dumped into the surrounding drainage basin and material that is transported via the atmosphere and falls out with precipitation. These constituents exist in the aquatic system as dissolved or particulate inorganic matter, dissolved or particulate organic matter, or dissolved gases. The chemical and biological interactions of these constituents are similar in all freshwater systems (see "Water Chemistry," above). However, because water is present in a given section of a stream for only a short period of time, the chemical composition of flowing water tends to vary more and be less affected by local conditions than that of standing water over both time and distance. Chemical composition is particularly sensitive to seasonal changes in flow rate and material input (Golterman 1975).

Inorganic plant nutrients. Nitrogen (N), a major plant nutrient that may limit plant growth when in short supply (Reid 1961) is derived originally from the atmosphere as molecular nitrogen (N_2). It may be fixed by bacterial or algal oxidation into nitrite (NO_2) and nitrate (NO_3) within a body of water or may be carried into the water as nitrate or amnonia (NH_3) by precipitation or runoff (Reid 1961). Decomposition of organisms, organic debris, and metabolic wastes by bacteria and fungi helps to recycle nitrogen within the aquatic system. Most nitrogenous compounds must be converted to nitrate (usually by bacterial action) before they can effectively be used by plants. The world average concentration of nitrate in fresh water is 0.3 ppm (Reid 1961). Some values of nitrogen concentration in Maine rivers are presented in appendix B table 1. Values of nitrogen in Maine rivers for which data are available are somewhat higher than the world average, probably as a result of human imputs.

Phosphorus (P) is a plant nutrient that is frequently in short supply in fresh water aquatic systems and whose absence sometimes limits plant growth (Hynes 1970a). Phosphorus generally enters the water via runoff. Major storage reservoirs are sedimentary bedrocks or soils derived from them (Golterman 1975). The forms of phosphorus that are most important to freshwater organisms are soluble ionic phosphate (PO_4), soluble organic phosphorus and particulate organic phosphorus. Ionic phosphate is the form most available to plants and is absorbed rapidly wherever plants are growing (Hynes 1970b). In the particulate organic form, phosphorus is not easily available to plants. This form may serve as a reservoir from which phosphorus is released gradually. Concentrations of phosphates in rivers are normally higher than those in lakes in similar areas, because less absorption by algae and emergent vegetation takes place in rivers. Typical values of phosphorus in Maine rivers range from about 0.01 to 0.27 ppm.

Potassium, another major plant nutrient, is common in most bedrocks and soils, and rarely limits plant growth in freshwater systems (Hynes 1970b).

High concentrations of plant nutrients in the proper proportions may lead to rapid and dense plant growth (eutrophication), which may have undesirable effects. This is usually a problem in sluggish or still waters. The precise amounts and proportions of nutrients required to cause eutrophication in any stream segment depends on local conditions. These include pattern and amount of rainfall, size and shape of drainage basin, size and shape of stream channel, current velocity, light penetration, and plant species present.

Other inorganic ions. Inorganic materials also play important roles in stream chemistry. The concentration of dissolved inorganic ions, particularly of calcium (Ca), magnesium (Mg), potassium (K), sodium (Na), chloride (Cl), bicarbonate (HCO_3), and silicon dioxide (SiO_2) determine the electrical conductance of stream water (Golterman 1975). These materials are normally derived from runoff or airborne dust particles and sea spray. Ionization of calcium and magnesium carbonates ($CaCO_3$, $MgCO_3$; derived primarily from sedimentary rock such as limestone) is the primary source of "hardness" in natural waters (Reid 1961). Conductance and hardness have few known direct effects on stream organisms. However, both of these factors may be indicative of the amount of plant nutrients available and hence the potential productivity of the stream system. Conductivity and hardness also may determine the suitability of stream water for domestic and industrial uses.

Carbonates in conjunction with carbon dioxide (CO_2) are responsible for buffering capacity (the ability to resist violent changes in levels of acidity) in aquatic systems (Hynes 1970b). Well-buffered systems tend to be more stable and frequently support more diverse biological communities than those that are poorly buffered.

Since most of the Maine coast is underlain by igneous and metamorphic rocks the natural contribution of inorganic ions to stream water is probably minimal (appendix B, tables 1, 5, 6, and 7; Golterman 1975).

Organic matter. Organic matter is present in water in solution, and in the form of organisms and organic debris. Most organic matter (other than organisms) in streams is derived from external (allochthonous) sources, such as fallen leaves. Dissolved portions of this material are consumed by some bacteria (Reid 1961). Particulate organic material is a source of energy for many invertebrate and some vertebrate detritivores (see "Energy Flow," below). In addition, organic material leached from peat or other shallow water plant debris is responsible for the yellowish-brown color common in the upper reaches of many Maine streams (Reid 1961).

Dissolved gases. Oxygen (O_2) and carbon dioxide are the major dissolved gases involved in the water chemistry and biological activity of streams. Nitrogen (N_2) is also present in streams as a dissolved gas but has little chemical or biological significance in this form.

Oxygen, essential for plant and animal respiration, usually enters the stream by diffusion from the atmosphere or as a byproduct of photosynthesis. In the upper reaches (upper perennial) of a stream system aquatic plant growth is usually limited, but turbulence enhances diffusion of oxygen to such an extent that dissolved oxygen is maintained in the water at or slightly above saturation levels (Golterman 1975). In autumn, when large amounts of leaf-litter enters the stream and begins to decompose, oxygen levels may decline due to microbial activity, but severe oxygen depletion is unlikely. In the lower, deeper, and slower-moving sections of the stream (lower perennial, tidal) aquatic vegetation plays a larger role in introducing oxygen into the water. In these areas significant depletion of oxygen may occur if winter ice blocks gas exchange between the water and the air and if snowcover on the ice interferes with light penetration and, thus, reduces photosynthesis. Low rates of flow may reduce oxygen replenishment from upstream and exacerbate the depletion problem. In addition, oxygen depletion may occur in bottom waters when large amounts of decaying vegetation or other organic matter (e.g., domestic or industrial wastes) are present and decomposer organism activity consumes oxygen. Saturation levels of oxygen in fresh water at sea level range from 14.6 ppm at 32°F (0°C) to 7.6 ppm at 86°F (30°C) (temperatures in excess of 86°F, or 30°C, are unusual in Maine streams).

Carbon dioxide from deep rock formations enters the stream via groundwater discharge. Decomposition of organic matter in the soil produces carbon dioxide that enters the stream via surface runoff or throughflow. Organic decomposition and plant and animal respiration within the stream itself also yields CO_2 (Golterman 1975). Dissolved carbon dioxide is essential for photosynthetic activity in submerged plants. In combination with carbonates it plays a major role in regulating the pH (acidity) of streams. In addition to direct diffusion into the atmosphere, buffering and photosynthesis are the primary means through which carbon dioxide is removed from the aquatic system.

ENERGY FLOWS

In forested regions such as the State of Maine, shading by the forest canopy limits the growth of aquatic vegetation (primarily attached algae and aquatic mosses) to the extent that only about 10% of the organic matter supply of headwater (upper perennial, intermittent) streams is derived from instream photosynthesis (Cummins and Spengler 1978). The major energy source in these streams is coarse particulate organic material (e.g., leaves, twigs) derived from trees and other streamside vegetation. The use and breakdown of this coarse material into fine, particulate, and dissolved material involves considerable biological activity. The role of an organism in the structure of the stream community is largely determined by its role in organic matter processing (table 6-4, figure 6-3).

The first step in the processing of coarse organic material is a primarily physical process, in which leaves or other material loses dissolved components through leaching. Thirty to 40% of the dry weight of some types of leaves may be lost in this manner (Cummins and Spengler 1978). These dissolved organic compounds are a source of nutrients for stream bacteria. The leached leaves then are colonized by stream bacteria and fungi. Hyphomycete fungi are particularly important, since they are capable of breaking down cellulose and, in some cases, lignin, which are major components of leached leaves and woody debris (Cummins and Spengler 1978). Different types of organic debris are colonized at different rates. Material from deciduous trees usually is colonized more rapidly than that from conifers (Cummins and Spengler 1978; and Marzolf 1978). Invertebrates that feed on leafy or woody debris are referred to as shredders. These animals frequently select the most heavily colonized debris as food, presumably because the bacteria and fungi add to the available protein (Cummins and Spengler 1978; and Marzolf 1978). Typical shredders in Maine streams include cranefly larvae, caddisfly larvae, and stonefly nymphs. Microbial metabolism, shredder feeding, and mechanical breakage serve to convert coarse particulate organic matter into fine particles and dissolved compounds (Cummins and Spengler 1978). Fine particles also may be derived

Table 6-4. Feeding Habits and Major Fauna in Different Habitat Classes[a]

General category based on feeding mechanism	General particle size range of food (microns)	Sub-divisions based on feeding mechanisms	Subdivision based on dominant food	Rock bottom	Unconsolidated bottom	Aquatic beds
Shredders	$>10^3$	Chewers and miners	Herbivores feeding on vascular plant tissue	Trichoptera (Phryganeidae, Leptoceridae)	Trichoptera (Phryganeidae, Leptoceridae)	Lepidoptera Diptera (Chironomidae, Ephydridae)
			Large particle detrivores feeding on decomposing vascular plant tissue		Turbellaria Plecoptera (Filipalpia) Trichoptera (Limnephilidae, Lepidostromatidae) Diptera (Tipulidae, Chironomidae) Isopoda Amphipoda	Turbellaria Trichoptera (Limnephilidae, Lepidostromatidae) Diptera (Chironomidae) Isopoda
Collectors	$<10^3$	Filter or suspension feeders	Herbivore-detritivores feeding on algal cells and decomposing organic matter	Ephemeroptera (Siphlonuridae) Trichoptera (Brachycentridae) Diptera (Simuliidae)	Ephemeroptera (Siphlonuridae) Trichoptera (Philopotamidae, Psychomyiidae, Hydropsychidae, Brachycentridae) Diptera (Chironomidae) Pelecypoda	Trichoptera (Hydropsychidae) Diptera (Chironomidae, Culicidae) Pelecypoda

[a]Cummins 1973.

(Continued)

Table 6-4. (Continued)

General category based on feeding mechanism	General particle size range of food (microna)	Sub-divisions based on feeding mechanisms	Subdivision based on dominant food	Rock bottom	Unconsolidated bottom	Aquatic beds
Collectors (cont.)						
		Sediment or deposit (surface) feeders	Fine particle detrivores feeding on decomposing organic matter		Ephemeroptera (Ephemeridae, Leptophlebiidae, Baetidae, Ephemerellidae, Heptemereliidae) Diptera (Chironomidae) Isopoda Amphipoda	Annelida (Oligochaeta, Hirudinea) Ephemeroptera (Caenidae, Ephemeridae, Leptophlebidae) Coleoptera (Hydrophilidae) Diptera (Chironomidae, Ceratopogonidae) Isopoda Amphipoda
Scrapers	$<10^3$	Mineral scrapers	Herbivores feeding on algae and associated material (periphyton)	Ephemeroptera (Heptageniidae, Baetidae, Ephemerellidae) Trichoptera (Glossosomatidae, Helicopsychydae, Molannidae) Coleoptera (Psephenidae) Gastropoda	Ephemeroptera (Heptageniidae, Baetidae, Ephemerellidae) Trichoptera (Glossosomatidae, Helicopsychydae, Molannidae) Coleoptera (Elimidae, Psephenidae) Diptera (Chironomidae, Tabanidae) Gastropoda	

(Continued)

Table 6-4. (Concluded)

General category based on feeding mechanism	General particle size range of food (microna)	Sub-divisions based on feeding mechanisms	Subdivision based on dominant food	Rock bottom	Unconsolidated bottom	Aquatic beds
Scrapers (cont.)						
		Organic scrapers	Herbivores feeding on algae and associated material (periphyton)		Ephemeroptera (Leptophlebiidae, Heptageniidae, Baetidae) Trichoptera (Leptoceridae) Diptera (Chironomidae) Gastropoda	Ephemeroptera (Coenidae, Leptophlebiidae) Hemiptera (Corixidae) Diptera (Chironomidae) Gastropoda
Predators	$>10^3$			Plecoptera (Perlidae) Trichoptera (Rhyacophilidae)	Plecoptera (Perlidae) Odonata Megaloptera Trichoptera (Rhyacophilidae)	Coleoptera (Dytiscidae) Odonata Hemiptera (Notonectidae, Belostomatidae) Annelida (Hirudinea)
				Osteichthyes (Salmonidae, Cyprinidae)	Osteichthyes (Salmonidae, Cyprinidae, Catostomidae, Anguillidae)	Osteichthyes (Cyprinidae, Centrarchidae, Percichthyidae, Percidae, Catostomidae, Anguillidae)

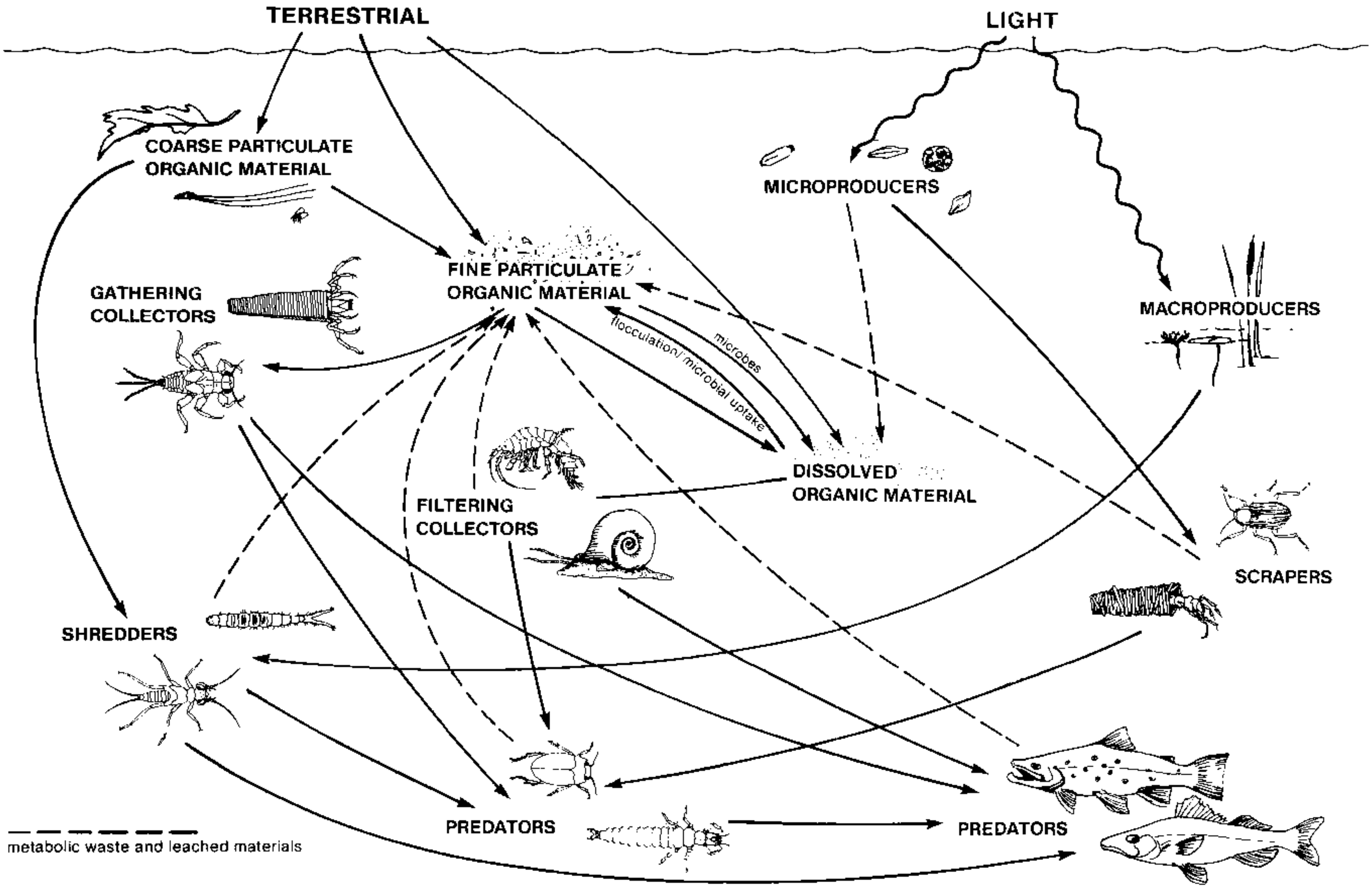


Figure 6-3. Organic matter processing in upper perennial stream communities(adapted from Cummins and Spengler 1978).

from the feces of various organisms and by flocculation (clumping together) of dissolved compounds.

Fine particulate organic matter and the bacteria which colonize it are eaten by invertebrates known as collectors, which either filter the particles from the water or gather it from the sediments (figure 6-3). Typical Maine collectors (table 6-4) include larval blackflies (filter feeders), and larval chironomid midges (gatherers). Collectors generally select their food on the basis of size and do not specifically select bacteria-enriched particles (Cummins and Spengler 1978).

Metabolic wastes of shredders, collectors, and other organisms, along with material leached directly from aquatic debris and the terrestrial environment, contribute to the supply of dissolved organic matter. This material is an important source of nutrients, including nitrogen and phosphorus. In upper perennial reaches, most of these nutrients support growth of bacteria and fungi. Photosynthetic activity in streams is limited by forest canopy shading. Invertebrates that are dependent upon the limited food supply provided by aquatic plants in upper perennial regions are referred to as scrapers (e.g., snails; table 6-4).

Stream predators include vertebrates, primarily fish (table 6-5 ; e.g., sculpins and brook trout) and invertebrates, such as some stoneflies and caddisflies. These predators consume shredders, collectors, grazers, and other predators. Terrestrial predators including many birds (e.g., waterfowl, herons, kingfishers, and ospreys) and some mammals (e.g., otters) also prey on stream organisms. People consume some fishes (i.e., resident sport fish). Human consumption accounts for <1% of the total biomass of the stream animals in the upper reaches of the stream (Cummins and Spengler 1978).

The biological community in the lower reaches (lower perennial, tidal) of streams is less dependent on direct organic inputs from the terrestrial environment and more dependent on instream photosynthesis and import of fine organic particles from upstream (Marzolf 1978).

Aquatic plants, including planktonic algae (e.g., the brown alga Dinobryon) and rooted vegetation (e.g., the river bulrush Scirpus) are more common in lower reaches and require greater inputs of nutrients (e.g., nitrogen, phosphorus) either directly from terrestrial sources (e.g., leaching) or from dissolved material processed by the upstream community. Since plants are more dominant in the lower perennial reaches of stream systems so are grazers, (equivalent to upstream scrapers) which feed on them (figure 6-4). The lower reaches of streams have a well-developed zooplankton community (primarily collectors) that feed on planktonic algae. Most zooplankton are collectors, although some of the larger copepods may be predatory. Fishes that feed on zooplankton (e.g., alewives) and fish predators (e.g., chain pickerel) are more important in the lower reaches of streams than in the upper reaches.

In contrast to that of standing water systems much of the organic matter (living and nonliving) in stream systems is exported downstream from its point of origin for varying distances before being consumed. Very coarse particles, such as leaves, are normally trapped by obstructions within 300 feet (100 m) of the point where they enter the stream (Cummins and Spengler 1978). Benthic macroinvertebrates, which are frequently swept up by the current, normally

Table 6-5. Common and Scientific Names and Biological Characteristics of Some Typical Maine Stream Fishes

Common name	Taxonomic name	Life cycle[a]	Spawning site[b]	Food[c]
Lampreys				
Sea lamprey	*Petromyzon marinus*	A	G	D-P
Sturgeons				
Atlantic sturgeon	*Acipenser oxyrhynchus*	A	G	D
Herrings				
Alewife	*Alosa pseudoharengus*	A	PL	I
American shad	*Alosa sapidissima*	A	G	I
Salmonids				
Atlantic salmon	*Salmo salar*	A	G	I-F
Landlocked salmon	*Salmo salar sebago*	R(L)	G	I-F
Brown trout	*Salmo trutta*	R(L)	G	I-F
Rainbow trout	*Salmo gairdneri*	R(L)	G	I-F
Brook trout	*Salvelinus fontinalis*	R(L)	G	I-F
Smelt				
Rainbow smelt	*Osmerus mordax*	A(L)	G,S,V	I-F
Suckers				
White sucker	*Catastomus commersoni*	R(L)	G	I,D
Longnose sucker	*Catastomus catostomus*	R(L)	G	I,D
Minnows				
Longnose dace	*Rhinichthys cataractae*	R	G	I
Blacknose dace	*Rhinichthys atratulus*	R	G	I
Finescale dace	*Chrosomus neogaeus*	R	unknown	I
Pearl dace	*Semotilus margarita*	R	GS	I
Fallfish	*Semotilus corporalis*	R	G	I
Creek chub	*Semotilus atromaculatus*	R	G	I-F
Golden shiner	*Notemigonus crysoleucas*	R	G	I
Common shiner	*Notropis cornutus*	R	G	I
Blacknose shiner	*Notropis heterolepis*	R	S	I
Bridled shiner	*Notropis bifrenatus*	R	P	I

[a]A - anadromous; C - catadromous; R - resident; L - lake run.
[b]G - gravel; S - sand; V - vegetation; Db - debris; PL - palustrine or lacustrine.
[c]D - detritus; P - parasite on fishes; I - invertebrates; F - fishes; () indicates change as fishes grow.

(Continued)

Table 6-5. (Concluded)

Common name	Taxonomic name	Life cycle[a]	Spawning site[b]	Food[c]
Catfish				
Brown bullhead	*Ictalurus nebulosus*	R	S	D,I,F
Pike				
Chain pickerel	*Esox niger*	R	PL	F
Eels				
American eel	*Anguilla rostrata*	C	-	I-F
Cod				
Burbot	*Lota lota*	R(L)	-	I-F
Sea bass				
White perch	*Morone americanus*	R(L)	G,V,Db	I-F
Perch				
Yellow perch	*Perca flavescens*	R(L)	V,Db	I-F
Sunfish				
Smallmouth bass	*Micropterus dolomieui*	R	G	I-F

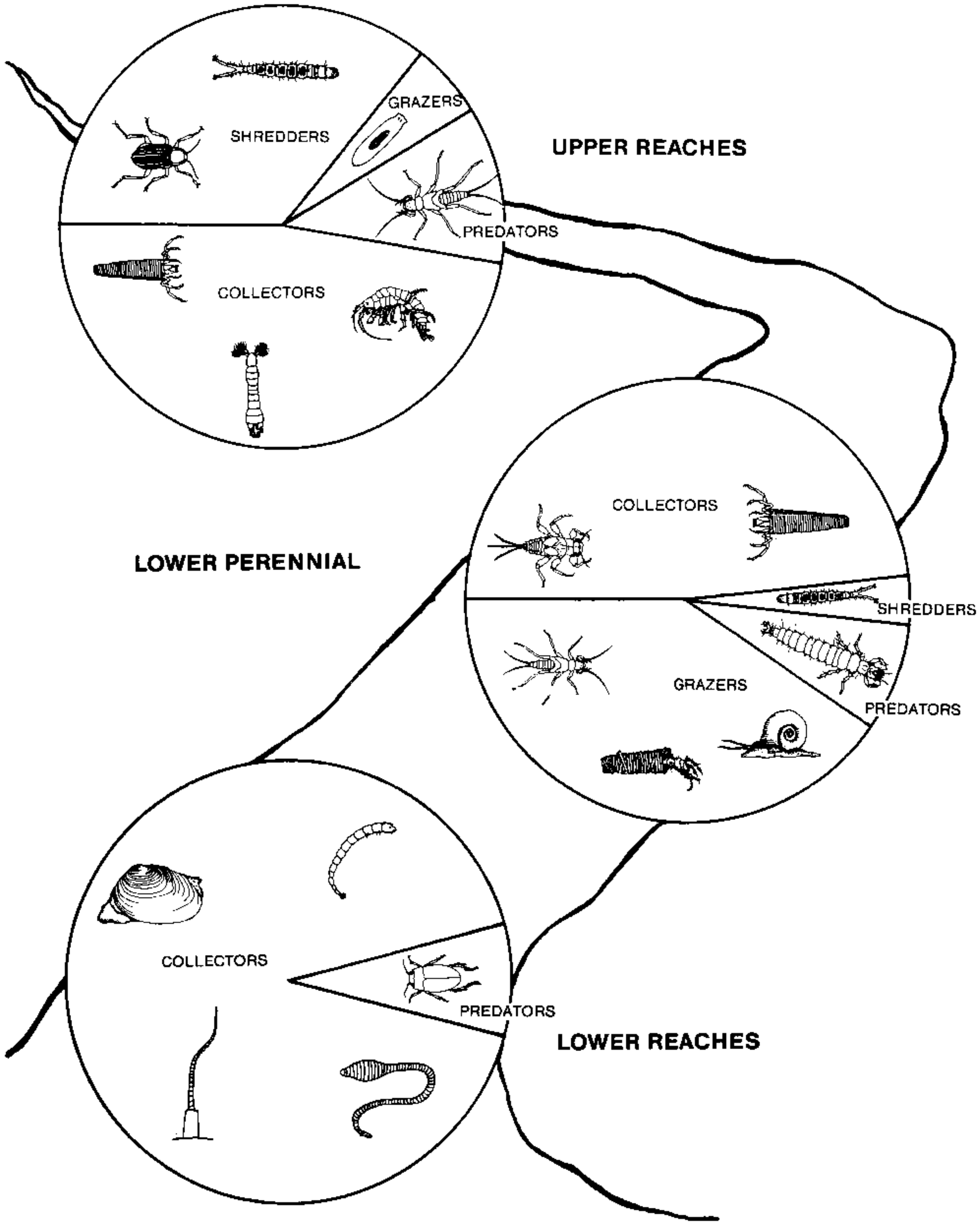


Figure 6-4. Trends in the composition of invertebrate communities along an upstream-downstream gradient (adapted from Marzolf 1978).

settle quite rapidly. However, planktonic organisms, fine particles, and dissolved compounds may be carried long distances, frequently into estuaries. The emergence of immature aquatic insects that have terrestrial adult forms is a significant form of energy and nutrient export that is common to both standing and flowing water systems. Thus, energy and nutrient cycling at any point along the stream's course is affected by export downstream and to the terrestrial system. Much of this loss is compensated for by the input of organic matter from terrestrial vegetation in the headwaters and the input of organic and inorganic nutrients through runoff, throughflow, and leaching along the entire water course.

BIOTA

The types of organisms that inhabit riverine systems vary according to biotic and abiotic factors. In the upper perennial or intermittent subsystems the biota is characterized by the dominant decomposers of organic matter and their predators. Aquatic producers and primary consumers play a minor role in these subsystems. Lower stream subsystems (tidal, lower perennial) are characterized by a producer community of aquatic plants and their consumers, including zooplankton, fishes that feed on zooplankton, and predators on fishes.

Producers

Aquatic plants of riverine systems in Maine include phytoplankton, algae, mosses, and nonpersistent emergent plants. Phytoplankton are not considered integral to the riverine system even though they make an energy contribution to the system. Their presence is usually dependent on a lacustrine/palustrine source upstream and is a function of time, passage of nutrients, light, and temperature. Attached plants in the riverine system include periphyton and rooted, vascular plants. Attached plants may have local importance if conditions for growth are suitable. The habitation zone of the periphyton is restricted to the immediate water-substrate interface at high current velocities. Periphyton algae may form a green cover that is several cells thick on rocks and other objects. Rooted vegetation may occur in areas of reduced flow and shallow depth. Linear-leaved forms (e.g., *Sparganium* spp., *Carex* spp., *Zizania* sp., and *Scirpus* spp.) and mosses are most predominant. Vegetation in the Merrymeeting Bay riverine tidal wetland subsystem is described in detail by Spencer (1959, 1960, and 1965). Physical factors, especially shear stress, limit development of persistent vegetation. Palustrine systems in which aquatic plants grow occur within rivers and streams as islands of persistent vegetation (see chapter 8, "The Palustrine System").

Consumers

Invertebrates typical of riverine systems and their role in the food web are discussed under "Energy Flow" above (table 6-4). Invertebrate consumers include collectors, scrapers, shredders, and predators. It is difficult to confine any organism to only one classification. Feeding habits may change with development of organisms (Cummins 1973). Fishes serve as primary and secondary consumers in the food web, and as parasites on other fishes and decomposers (table 6-5). The distribution of fishes in Maine rivers is poorly understood and data are incomplete. Those fishes that have been recorded in certain Maine rivers are listed in table 6-6. Certain fishes may occur in streams included in table 6-6 but are not listed as their occurrence has not been reported (see also "Fishes," chapter 11).

Waterbirds, mammals, reptiles, and amphibians also inhabit the riverine system. Several species of waterbirds, including waterfowl, shorebirds, and wading birds utilize riverine systems for feeding, resting, breeding, and/or rearing habitats (see chapter 14, "Waterbirds," and chapter 15, "Waterfowl"). Mammals, including mink, otter, muskrat, beaver, raccoon, fox, deer, and moose also utilize riverine habitats for their feeding (see "Terrestrial Mammals," chapter 17). Birds, mammals, reptiles, and amphibians that inhabit riverine systems also utilize palustrine habitats as these systems are often interspersed. The occurence of these species in coastal Maine is given in the appendices to chapter 8, "The Palustrine System".

Decomposers

The significance of detritivores in the riverine system has been discussed under "Energy Flow," in this chapter. The abundance of allochthonous material supports a significant cycle within this group. Organic matter is consumed, excreted, re-colonized by microbes, re-consumed, and so on. Breakdown of the detritus is especially important to filter feeders because they are dependent on the limited supplies of plankton and microparticles of detritus for their food. The existing decomposer fauna of riverine systems in coastal Maine is not precisely known; however, assumptions may be made regarding those present in some substrate habitats (see table 6-4).

NATURAL FACTORS AFFECTING DISTRIBUTION

Many factors influence the distribution of aquatic organisms. The overriding factors that determine the types of organisms that compose the biological stream community include water chemistry, light and related temperature, current speed, and related substrate factors (including detritus and sedimentation).

Water Chemistry

Dissolved oxygen levels can be limiting to aerobic organisms if they become extremely low, although this is a rare occurrence in most Maine streams. Reduced levels of dissolved oxygen can be a problem primarily in lower perennial and tidal reaches of streams. The U.S. Environmental Protection Agency (EPA) has encountered difficulty in setting water quality standards for dissolved oxygen, because of lack of definitive data on fish oxygen requirements (Everhart et al. 1975). It is generally agreed that dissolved oxygen levels of less than 5 to 6 ppm would be too low for long-term survival of coldwater fishes (e.g., salmonids). Many factors could cause fish oxygen requirements to be higher than this level (Everhart et al. 1975), however. Factors involved in determining actual oxygen requirements of fishes at any specific site include current velocity, water temperature, age of fishes, growth rate of fishes, spawning condition, migration, predation pressure, exposure to pollutants or disease organisms, and exposure to varying water chemistry (e.g., acidity). Under conditions where moderately low oxygen levels recur frequently, as in shallow bays, areas with sluggish current where large amounts of vegetation collect and decay, or waters receiving large

Table 6-6. Fishes Known To Occur in Some Maine Stream Systems[a].

Fish	Presumpscot	Crooked	Royal	Androscoggin	Kennebec	New Meadows	Sheepscot	Damariscotta	Pemaquid	Medomak	St. George	Passagassawakeag (Belfast)	Penobscot River Drainage	Union	Narraguagus	Pleasant	Machias	E. Machias	Dennys
<u>Game Fishes</u>																			
Atlantic salmon	x	x	x	x	x		x					x	x	x	x	x	x	x	x
Landlocked salmon		x	x	x	x				x										x
Brook trout	x	x	x	x	x		x	x	x	x		x	x	x	x	x	x	x	x
Brown trout	x		x	x	x		x	x	x	x		x		x		x			
Rainbow trout				x	x														
Lake trout					x		x												x
White perch					x		x		x	x		x							x
Striped bass					x		x				x	x			x				
Smallmouth bass	x		x	x	x		x		x	x									x
Largemouth bass					x														x
American shad				x	x		x						x		x			x	x
Alewife			x	x	x		x	x	x		x	x			x	x		x	x
Smelt			x		x	x	x	x		x	x	x			x	x			x
Chain pickerel	x		x	x	x		x		x	x		x			x				x
<u>Nongame Fishes</u>																			
Hornpout (bullhead)			x		x		x			x		x							x
Yellow perch					x		x			x		x							x
Pumpkinseed sunfish			x		x		x			x		x							x
Red breasted sunfish					x														
American eel			x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
White sucker			x		x		x			x					x				x
European carp				x	x														
Burbot					x														
9 spine stickleback					x					x									x
3 spine stickleback					x														x
Brook stickleback					x														

[a]Streams are arranged from south to north.
[b]x - present; r - rare.

(Continued)

Table 6-6. (Concluded)

Fish	Presumpscot	Crooked	Royal	Androscoggin	Kennebec	New Meadows	Sheepscot	Damariscotta	Pemaquid	Medomak	St. George	Passagassawakeag (Belfast)	Penobscot River Drainage	Union	Narraguagus	Pleasant	Machias	E. Machias	Dennys
<u>Nongame Fishes</u> (cont.)																			
Slimy sculpin					x														
Longnose sucker					x														
Banded killifish					x		x					x						x	
Mummichog					x														
Minnows																			
Fallfish			x		x		x					x						x	
Common shiner			x				x			x									
Golden shiner			x		x		x			x		x							
Blackchin shiner										x									
Blacknose shiner					x										x				x
Creek chub			x									x							
Lake chub					x					x									
Fathead minnow					x														
Red belly dace			x							x		x							x
Black nose dace			x		x		x			x		x							
Pearl dace			x		x														
Longnose dace					x														
Red sided dace																			
Finescale dace					x														x
Northern red dace					x														
Sea lamprey					x		x								x				x

amounts of organic pollutants, communities must be capable of withstanding chronic oxygen shortage. Many of the species composing such communities are typical of standing water systems (lacustrine and palustrine), where low oxygen conditions are more common (Hynes 1970a). Some stream invertebrates are capable of tolerating low and varying oxygen conditions. Typical of this type of organism in Maine are some chironomid midge larvae and some aquatic worms (e.g., Tubificidae).

Low dissolved-nutrient levels may limit the growth of aquatic plants and animals. Submerged plants (e.g., aquatic mosses) and floating plants (e.g., duckweed, Potamageton) are frequently dependent on dissolved nitrogen, phosphorus, and potassium, and low levels may limit growth. Effects of nutrient supply on aquatic plants are difficult to document (Westlake 1975) and quantitative information on these effects in running water is extremely rare (Hynes 1970a). Available information differs on the levels at which nutrient supply may become limiting in any given running water plant community. Animals that use calcium carbonates in their exoskeletons, including crustaceans (e.g., amphipods and crayfish) and molluscs (e.g., snails and clams), are sensitive to deficiencies in these nutrients and are generally less common in soft water, where these nutrients are less abundant (Hynes 1970a). At least one freshwater snail (Ancylus fluviatilus), cannot tolerate waters with less than 2 mg/l of calcium (Maitland 1966). The notable absence of amphipods from many apparently suitable Maine streams (personal communication from C. F. Rabeni, University of Maine, Orono, ME; March, 1979) may be related to the low level of calcium carbonate in Maine waters. Acidity (pH) may influence plant growth. Acid waters tend to favor the growth of algae such as the conjugales (e.g., Spirogyra) and mosses (Westlake 1975). Very acidic water may endanger animal populations through interference with feeding and reproduction. Extremely high acidities may be directly lethal. Exact levels at which these problems occur vary according to species and local conditions. However, in Maine, problems are most likely to occur at pH <5. A discussion of the effects of acid rain is presented in chapter 3, "Human Impacts on the Ecosystem."

Light and Temperature

Light has a direct effect on the type and amount of vegetation present in any given stream community. Aquatic mosses, for example, prefer low light levels and are frequently the predominant vegetation (along with encrusting algae) in shaded streams. Emergent vegetation is usually more common in streams in summer. The total amount of vegetation present generally increases with the amount of light reaching the stream. The type and amount of vegetation, in turn, determines the relative dominance of scraper-grazer types of organisms in the animal community.

The amount of light penetrating water influences its temperature. Stream sources (e.g., spring or pond) also influence water temperature. Many stream organisms have definite temperature requirements. Stoneflies, an important food source for game fish in many Maine streams, are generally limited to cool headwaters (Hynes 1970a).

Current and Substrate

Many aquatic organisms have distinct current-speed requirements. Planktonic algae and zooplankton require relatively still waters, since they have little or no capacity for resisting currents. Other organisms require water that moves at higher velocities, because of food-capturing or respiratory requirements. Net-spinning caddisflies, important collectors, depend on water currents to carry food into their nets. Many insects (stoneflies and mayflies) and fishes depend primarily on water currents to move water over their gills to allow exchange of respiratory gases.

Current also affects the distribution of stream organisms through its effect on substrate. Substrates of larger particles (e.g., stones) are normally associated with more rapid current. Smaller particles (e.g., sand and silt) are carried away and deposited in areas with slower currents. Among stream plants, mosses and encrusting algae are associated primarily with stony substrates, while emergent vegetation may require softer substrates for rooting. Many benthic invertebrates exhibit substrate preferences (table 6-4). Rabeni and Gibbs (1977) found that silt and detritus concentrations, along with current (which controls the deposition of this material), are major factors controlling the distribution of benthic invertebrates in the Penobscot River. Most stream fishes show little direct preference for substrate types during most of the year, although some (e.g., chain pickerel; table 6-5) may be associated with vegetation, which is limited to certain substrate types. Many fishes do have specific requirements for spawning substrates, however. For example, salmonids require clean gravel and rapid current for spawning beds (table 6-5 and chapter 11, "Fishes").

RESEARCH NEEDS

Virtually all aspects of Maine riverine systems require more research for management and impact assessment. Water quality is of primary concern. Data are needed on the amounts of toxic materials (heavy metals, pesticides, herbicides, oil, and PCB's) present in Maine streams and their effects (short and long term) on populations of organisms.

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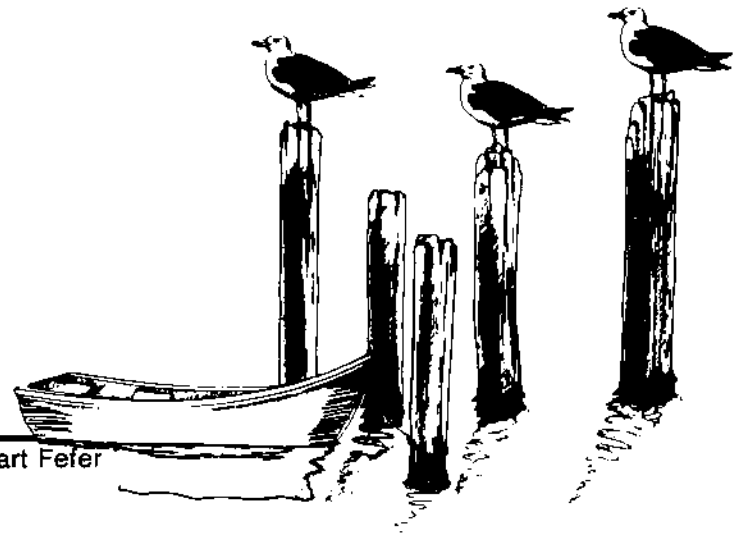
Chapter 7 The Lacustrine System



Authors: Ronald Davis, Meryl Freeman, Stewart Fefer

This chapter describes the freshwater bodies (lacustrine system) of the Maine coast, including natural lakes, natural lakes with water control structures, deep ponds, abandoned quarries that have become flooded, flooded gravel pits, reservoirs, and impounded streams and rivers. Data are not available for all the lacustrine water bodies. The lacustrine system of the coastal zone of Maine comprises slightly less than 3% of the zone's total land and freshwater area.

Natural lakes that are larger than 10 acres (4 ha) are, according to Maine law, owned by the public. However, the adjacent lands often are owned privately and public access is highly limited. Most of the lakes are used for recreation, water supplies, and/or scenic backgrounds for residential (mostly seasonal cottages) developments.

Lacustrine systems are bodies of fresh water that have depths >7 feet (>2 m) at low water (bodies of water having depths <2 m are classified as palustrine). Where data on depth are not available lacustrine systems include those freshwater bodies that are larger than 20 acres (8 ha), are not contained within a channel, and are without persistent vegetation. The lacustrine system has been classified hierarchically, based upon depth and bottom characteristics (figure 7-1). The limnetic subsystem is the deep-water part of the lake (>2 m in depth), while the littoral subsystem is the shallow section of the lacustrine system. Each subsystem has component classes. It should be noted that lacustrine systems are often bordered by palustrine systems (defined by the presence of persistent emergent plants, e.g., *Scirpus* spp.), but they are classified separately by the National Wetlands Inventory (NWI). Specific locations of lacustrine systems are included in atlas map 1.

The definitions of the terms lacustrine, littoral, and limnetic, used by the National Wetlands Inventory, differ from those used by many limnologists. Those definitions conform to the system of Cowardin and coworkers (1979) which provides the framework for chapters on wetland and aquatic systems. This framework is described in chapter 1. Common names of species are used except where accepted common names do not exist. Taxonomic names of all species mentioned are given in the appendix to chapter 1.

Lacustrine systems are ecological components of the coastal ecosystem and they and their interaction with other habitats must be considered in the long-range planning, development, and management of the renewable natural resources of coastal Maine.

DATA SOURCES AND COMPILATION OF DATA

Locational data on the lacustrine system were derived primarily from the preliminary results of the National Wetlands Inventory (NWI) of the U.S. Fish and Wildlife Service (FWS). The lakes of the coastal zone are mapped on atlas map 1. Locations of lakes that supply municipal water were obtained from Maine Department of Human Resources.

Biological and physical data on the named lakes were derived from the following sources. Lake identification numbers ("MIDAS numbers"), and elevation-above-sea-level data were acquired from Maine Department of Inland Fisheries and Wildlife (MDIFW; MIDAS computer file 906Z) . Data on fisheries and water quality also were obtained from MDIFW files. MDIFW (1975) lake-survey leaflets for 172 lakes provided bathymetric maps, lists of fish species, and statements on fisheries management. Fisheries appraisals for 151 lakes were obtained from Hutchinson (1977a, b, and c), Hutchinson and Spencer (1975a, b, c, and d), and Spencer and Hutchinson (1974a, b, c, and d). Maps of the presence of anadromous fish species were acquired from the Maine State Planning Office (MSPO; 1977). That office also provided maps of lake management capabilities, recreational facilities and activities, and land cover types around the lakes. Water-quality information for 37 lakes was obtained from Maine Department of Environmental Protection (DEP; Division of Lakes and Biological Studies). These data had come from several sources, including the Cobbossee Water District (CWD) and the DEP Lay Monitoring Program. Additional data for region 2 came from Cortell and coworkers (1973); data for Branch, Green and Brewer lakes from Cowing and Scott (1975, 1976, 1977, and <u>in preparation</u>), and additional data for Branch Lake from Dewick (1973). The files of the Maine Pesticide Control Board provided information on pesticide (e.g., algicide) use in and around the lakes. Information on areas of the coastal region sprayed for spruce budworm control was acquired from the Maine Bureau of Forestry at Old Town. Data collected in 1938, 1941, and 1942 for 59 of the lakes in regions 2 to 5 were obtained from Cooper (1939 and 1942) and Fuller and Cooper (1946). In addition to temperature and oxygen profiles, and pH and phosphorus data, the Cooper references provided data on plankton and benthos, plus extensive fisheries information, including growth rates of fishes.

DISTRIBUTION OF THE LACUSTRINE SYSTEM

The lacustrine system of the coastal zone comprises a total area of approximately 57,537 acres (23,294 ha; table 7-1). A total of 215 lacustrine systems are named on U.S. Geological Survey (USGS) quadrangle sheets or quads (atlas map 1). These comprise >98% of the area of the lacustrine system. (Available physical data on named lakes are given in tables 7-2 and 7-3 and appendix table 1. Available data on chemical characteristics of named coastal zone lakes are given in table 7-4 and in appendix table 2.)

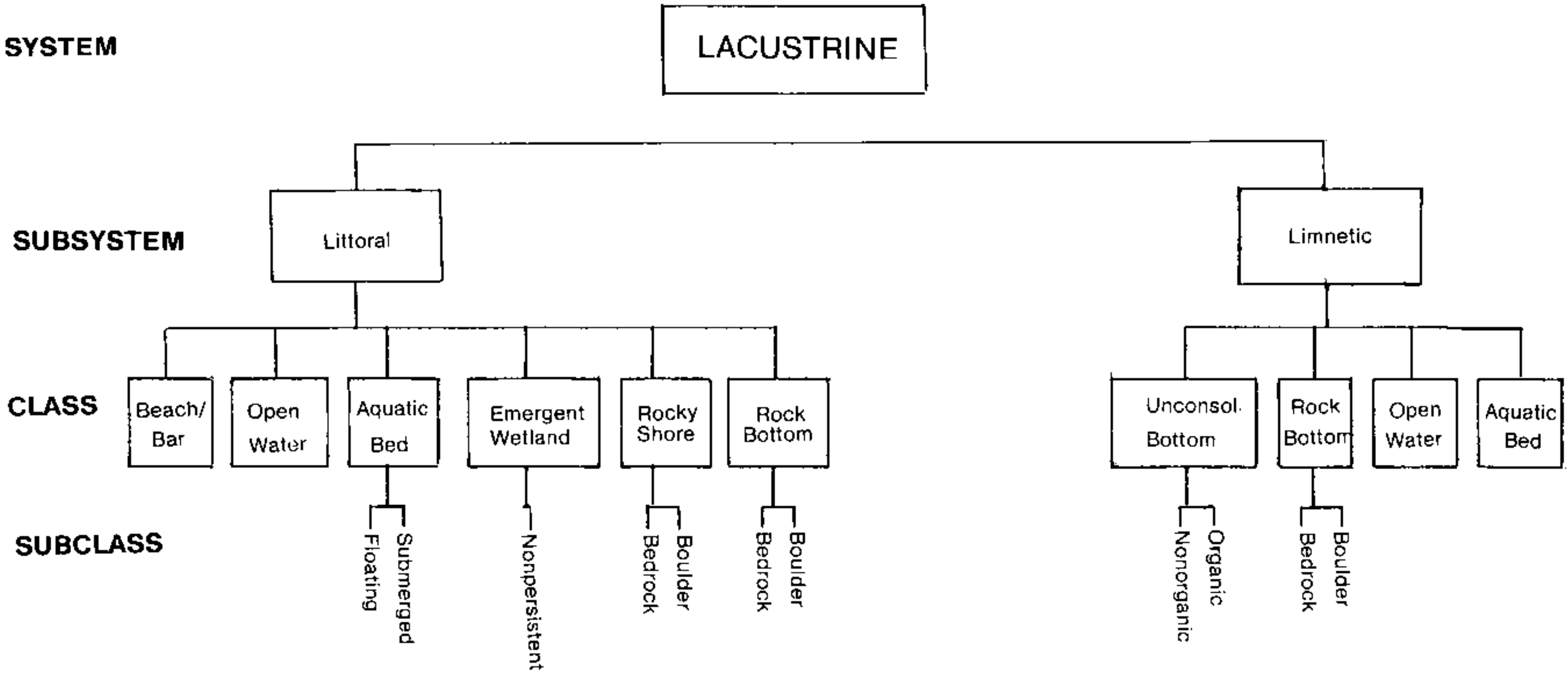


Figure 7-1. Hierarchical classification of the lacustrine system of coastal Maine (Cowardin et al. 1979).

Table 7-1. Area in Acres and Percentage Contribution (in parentheses) of the Lacustrine System, for Each Region.

Region	Total lacustrine
1	426 (21)
2	4199 (7)
3	7219 (13)
4	12,900 (22)
5	19,567 (34)
6	13,226 (23)
Total	57,537

Table 7-2. Physical Characteristics of Named Coastal Zone Lakes[a]

	Regions 1	2	3	4	5	6	Total
Number of lakes	4	34	26	58	56	37	215
Area of lakes (acres)	385	3786	6917	12,869	19,387	13,138	56,483
Average area[c]	96	111	266	222	346	355	263
Percent of coastal zone area occupied by lakes	1	1	4	2	5	3	3
Average summer surface temperature °F(°C)	78°(25°) [2][b]	73°(23°) [31]	72°(22°) [20]	72°(22°) [45]	72°(22°) [49]	71°(22°) [26]	73°(23°) [173]
Percent thermally stratified in the summer:							
None	50 [1]	32 [10]	35 [7]	35 [17]	26 [14]	41 [11]	33 [60]
Epilimnon & metalimnion only	0	45 [14]	30 [6]	29 [14]	21 [11]	30 [8]	29 [53]
Tripartte strat. including Hypolimnion only	50 [1]	23 [7]	35 [7]	35 [17]	53 [28]	30 [8]	38 [68]
Secchi disc transparency in summer: average in meters	9.1 (1)	4.0(8)	4.2 (8)	5.0 (17)	6.3 (18)	4.5 (4)	5.5 (56)
Number of lakes used for municipal water supply	1	4	2	9	10	1	27
Number of lakes with dams at outlets	0	3	4	3	11	5	26

[a]Lakes for which data are unavailable are not included.
[b]number of observations.
[c]of individual lakes (acres)
[d]incomplete data

Table 7-3. Sizes (acres) and Maximum Depths (meters) of Lakes in Coastal Maine and Percentage of Total (in parenthesis).

	Regions						
	1	2	3	4	5	6	Total
Surface area (acres) (215 lakes)							
<1	0	0	0	0	1 (2)	0	1 (21)
1- 10	0	3 (9)	1 (4)	3 (5)	1 (2)	1 (3)	9 (4)
10- 100	3 (75)	22 (65)	13 (50)	29 (50)	31 (55)	23 (62)	121 (56)
100- 1000	1 (25)	9 (27)	10 (39)	23 (40)	18 (32)	8 (22)	69 (32)
1000+	0	0	2 (8)	3 (5)	5 (9)	5 (14)	15 (7)
Total	4	34	26	58	56	37	215
Maximum depth (meters) (180 lakes)							
<5	1 (50)	10 (32)	5 (23)	16 (35)	11 (21)	5 (19)	48 (27)
5- 10	0	13 (42)	6 (27)	12 (26)	15 (29)	10 (37)	56 (31)
10- 15	0	4 (13)	7 (32)	10 (22)	12 (23)	8 (30)	41 (23)
15- 20	0	2 (6)	3 (14)	4 (9)	3 (6)	4 (15)	16 (9)
20- 25	1 (50)	1 (3)	0	3 (7)	1 (2)	0	6 (3)
25- 30	0	0	0	0	3 (6)	0	3 (2)
30- 35	0	1 (3)	1 (5)	0	1 (6)	0	3 (2)
35- 40	0	0	0	1 (2)	3 (2)	0	4 (2)
40+	0	0	0	0	3 (6)	0	3 (2)
Total	2	31	22	46	52	27	180

Table 7-4. Chemical Characteristics of Coastal Maine Lakes from 1938 to 1978, by Region[a]

	Regions 1	2	3	4	5	6	Total
Conductance (umhos/cm at 25°C)							
surface average	42 (1)[b]	43 (5)	37 (3)	32 (4)	31 (6)		37 (19)
bottom average	- - -	41 (1)	40 (2)	28 (3)	30 (4)		35 (10)
pH							
surface median	6.5 (8)	6.7 (31)	6.4 (21)	6.8 (45)	6.6 (51)	6.4 (25)	6.6 (175)
bottom median	6.0 (2)	6.1 (24)	6.1 (21)	6.2 (44)	6.0 (52)	5.9 (52)	6.0 (169)
Alkalinity (ppm $CaCO_3$)							
surface average	6.0 (1)	7 (11)	8 (8)	9 (17)	7 (33)	8 (4)	8 (74)
bottom average		8 (6)	13 (4)	13 (13)	9 (25)	12 (4)	11 (52)
Phosphorus (total; ppb)							
surface	10 (1)	16 (12)	9 (10)	12 (24)	7 (18)		11 (63)
bottom	- - -	23 (7)	36 (4)	12 (6)			24 (22)
Chlorophyll-a (ppb)	5 (1)	6 (6)	9 (3)	7 (6)	2 (6)		6 (22)
Percent of lakes with "brown" water	50 (2)	44 (23)	47 (15)	9 (38)	13 (38)	17 (23)	28 (133)
Percent of lakes with less than 4.0 ppm free oxygen at bottom	- - -	68 (17)	64 (14)	58 (26)	47 (24)	50 (13)	48 (94)

[a]Cooper (1939, 1942); Fuller and Cooper (1946); Maine DEP; Davis et al. 1978a; Cobbossee Water District 1977 a & b.
[b]number of lake sampled.

The number of named lacustrine systems in each of the six coastal regions ranges from 4 (region 1) to 58 (region 4; table 7-2). The total surface area of all lacustrine systems, named and unnamed, in each of the regions ranges from 426 acres (170 ha) in region 1 to 19,567 acres (7827 ha) in region 5 (table 7-1), while the average lacustrine area ranges from 96 acres (38 ha) in region 1 to 355 acres (145 ha) in region 6 (table 7-2). The percentage of land and freshwater area occupied by lakes ranges from <1% (region 1) to 5% (region 5) of the total. These data clearly indicate that the lakes and ponds in regions 1 and 2 are much smaller than those in regions 3 to 6, and that their total surface area and percentage of total regional land and freshwater area are also less.

PHYSICAL CHARACTERISTICS

Physical characteristics other than size data and habitat type of lacustrine systems are available only for those lakes named on USGS quads. Eighty-four (39%) lakes in the coastal zone exceed 100 acres (40 ha) in area (table 7-3) and the largest, Gardner Lake (region 6) is 3694 acres (1495 ha). The largest lakes in individual regions are: Highland Lake, in region 1, 261 acres (106 ha); Togus Lake, in region 2, 640 acres (259 ha); Damariscotta Lake, in region 3, 2034 acres (823 ha); Toddy Pond, in region 4, 2412 acres (976 ha); Graham Lake, in region 5, 3278 acres (1327 ha); and Gardner Lake, in region 6, 3694 acres (1495 ha). (The parts of individual lakes lying outside the coastal zone are not included in acreages above or in table 7-3.) Of the 27 municipal water supply lakes (see table 7-2 for regional distribution), 14 are smaller than 247 acres (100 ha) and 13 are larger (range 348 to 2275 acres; 139 to 910 ha). Region 4 contains the greatest number of lakes. Twenty-six lakes have dams at their outlets (see table 7-2 for regional distribution). However, these data are incomplete. The surface areas of 15 of these lakes exceed 1000 acres (400 ha). Thirteen of the dams are equipped with fish ladders and four are equipped with fish screens (these data also are incomplete; see atlas map 4).

The average summer surface temperatures of the lakes are almost uniform (71 to 78°F; 22 to 25°C; table 7-2). The percentages of named lakes that are not thermally stratified (33% of the total), that are stratified without a hypolimnion (29%), or that are stratified and have a hypolimnion (37%), differ among the regions. Descriptions of stratified lakes are given later in "Lacustrine Limnology."

The transparency of named lakes, based upon Secchi disc visibility in meters in summer, ranged from 4 m (13.2 ft; region 2 mean) to 6.3 m (21 ft; region 5 mean), and averaged 5.5 m (18 ft) for 56 lakes (table 7-2). The one observation of 9.1 m (30 ft) in region 1 is insufficient for comparison. Differences in transparency show no consistent trends among regions. Further physical data are given in appendix tables 1 and 2.

Maximum depths of 180 coastal zone lakes are known (table 7-3; appendix table 1). Region 5 has the greatest number of deep lakes; 20% of the 52 lakes that were surveyed there are deeper than 25 m (83 ft). The deepest lake in coastal Maine, Tunk Lake (68 m;224 ft), is in region 5. Average surface tempertures, average water transparency levels, and ratios of thermally unstratified to thermally stratified named lakes vary slightly among regions.

CHEMICAL CHARACTERISTICS

Measurements of some of the major chemical characteristics of lakes in the coastal zone were made from 1938 to 1978, between late July and early September (table 7-4). Although all the data are not comparable, because of sampling deficiencies, major characteristics and some trends are clear.

Differences among average alkalinity levels in the regions show no trends. In Maine lakes the common range of alkalinity (as ppm $CaCO_3$) is 5 to 30, with most of the larger lakes nearer the low point of this range (Davis et al. 1978a). These alkalinity levels are very low by worldwide standards. Low alkalinity is characteristic of soft water and is consistent with low pH. The pH of lake waters among the regions varies little but differences between surface water (pH 6.6) and bottom waters (pH 6.0) are apparent (table 7-4). Specific conductances (as μmhos/cm3 at 25°C) are low in Maine lakes, commonly between 20 and 80, with most of the larger lakes <50. In the coastal zone lakes the conductance of water showed little difference between near-bottom or near-surface waters but a general decrease from 43 to 30 in surface waters (41 to 28 in bottom waters) from western regions (regions 1 to 3) to eastern regions (regions 4 to 6) was apparent. The alkalinity range for lake surface waters was 0 to 19 (n=74), and the conductance range was 7 to 52 (n=19) in the coastal zone.

In Maine lakes that do not receive a significant input of nutrients from industrial wastes alkalinity and conductance ranges clearly parallel concentrations of natural nutrients (phosphorus in particular; Davis et al. 1978a). However, this relationship is not observed among the 30 coastal zone lakes for which both alkalinity and total phosphorus readings are available. Alkalinity levels are controlled by the chemistry of watershed bedrock and surficial deposits, and by the acidity of precipitation. Phosphorus levels, in addition to being controlled by the latter factors, also are affected by lake morphometry. Since these factors vary among the 30 coastal zone lakes the relationship between alkalinity and total phosphorus is obscured.

The total phosphorus averages for all lakes range from 7 to 16 ppb for surface waters and from 12 to 36 ppb for bottom waters. Concentrations of total phosphorus in Maine lakes that are not severely polluted range from 2 to 15 ppb (Davis et al. 1978a; Cowing and Scott 1975, 1976, 1977, and <u>in preparation</u>). In the absence of significant agricultural acreage, excessive shoreline residential development, or other sources of pollution, total phosphorus concentrations are usually less than 10 ppb (Davis et al. 1978a). Surface waters of 63 coastal lakes (table 7-4; appendix table 1) average 11 ppb total phosphorus and range from a trace to 30 ppb. The higher values suggest that anthropogenic enrichment is taking place at certain lakes (appendix table 1). Five of the lakes with high phosphorus levels are in the Cobbossee Watershed District in region 2. Studies of these lakes indicate that excessive phosphorus is a result of agricultural and residential development in the watersheds (Gordon 1977; Cobbossee Watershed District 1977a and b).

Measurements of chlorophyll-a concentrations (table 7-4) are generally low among the regions (2 ppb to 9 ppb) and in the coastal zone as a whole (6 ppb) but range as high as 24 ppb in some lakes. Such high chlorophyll is indicative of eutrophic (nutrient-rich) conditions. A majority of mid-to large-size lakes in Maine are meso-oligotrophic (moderately nutrient-poor) and oligotrophic (nutrient-poor); only a small percentage are eutrophic. Available data on chlorophyll-a, epilimnetic total phosphorus, and Secchi disc transparency in coastal Maine lakes indicate slightly more productive conditions (still mesotrophic for most lakes) in the coastal zone than in Maine lakes in general.

"Brown water" is a term that is often used to define water conditions in Maine. It usually indicates low pH. Of the 133 lakes in the coastal zone with color information, 22% are brown-water lakes. More than 40% of the lakes in regions 1 to 3 and <17% in regions 3 to 6 are brown-water lakes. Most brown water lakes have contiguous areas of acidic wetland or peat bog. The brown dissolved organic matter that accounts for the water color contributes to the depletion of oxygen in the stratified deep water.

Oxygen profiles are available from the 68 coastal zone lakes that have hypolimnia. Nineteen percent of these had no oxygen near the bottom by August or September and 68% had <4 ppm (unsuitable for cold water fishes). Of the 94 coastal zone lakes for which some oxygen data are available, regardless of whether sustained thermal stratification is present in summer, 48% had <4 ppm free oxygen in the hypolimnia.

Cyclical salt (salts carried to the sea by rivers and returned to the land in precipitation and dry fallout) levels are most significant in lakes close to the sea. Adams Pond (Boothbay), Southport reservoir (unnamed) and Long Pond (Isle au Haut), three lakes that are near the sea, had sodium concentrations of 4.4 to 6.7 ppm, 14 ppm, and 17.7 ppm, respectively. Sodium concentrations in Maine lakes that are farther inland and which have similar conductances are only 2 to 3 ppm, approximately (Davis et al. 1978a). Lakes near the sea may have relatively high conductances in relation to their alkalinities (appendix table 2). For example, Jordan Pond in region 5 had an alkalinity of only 3.0 ppm as $CaCO_3$ but had a conductance of 41 micromhos/cm, probably due mostly to sodium chloride (appendix table 2).

Data on chemical parameters other than those discussed above (e.g., nitrogen, silicon) are available for too few coastal zone lakes to warrant discussion but are included in appendix table 2.

The above data indicate that the general chemical characteristics of lakes are almost uniform among regions and that the slight differences found cannot be interpreted. The coastal zone lakes are not highly productive, as indicated by low conductance, low pH, and low alkalinity, total phosphorus, and chlorophyll-a, and are typical of lakes in forested areas of Maine. Atypical lakes generally are those that are affected significantly by human input of nutrients.

THERMAL STRATIFICATION AND LAKE ZONATION

Certain limnological characteristics are typical of the freshwater lakes of coastal Maine. For the sake of clarity, the coastal lakes are described in this section on the basis of water temperture, principally as it relates to thermal stratification, and aspects of biological function that are determined by light penetration and zones of production.

Temperature Characteristics.

A majority of lakes in coastal Maine are too shallow to exhibit summer stratification with a deep-water hypolimnion. In summer, waters of shallow lakes mix well from the surface to the bottom, because of wind and current action. Consequently, temperatures and oxygen levels are nearly uniform at all depths. In moderately deep lakes (many small natural lakes in Maine fit into this category) the surface and bottom waters do not mix well and the water stratifies into a warmer layer near the surface and a cooler one near the bottom. In deep lakes, thermal stratification is well developed. Warmer water temperatures persist near the surface (the epilimnion), a metalimnion (strata where temperatures decline rapidly with depth) forms in mid-water, and colder water temperatures persist to the bottom (hypolimnion). Stratified lakes have little vertical movement of water in their metalimnia and hypolimina during summer, which often results in oxygen depletion near the bottom and limitation in biological activity and productivity in the epilimnion. Graphic descriptions of thermal stratification and its effects are given in figure 7-2.

Thermal stratification, or its absence, in lakes is largely determined by depth, surface area, exposure to wind, and climate. Temperature profiles are available for 181 of the named lakes in the coastal zone of Maine, as determined from the data in appendix table 1. Of the 181 lakes, 121 (67%) have some thermal stratification during summer. The duration of stratification in lakes with no hypolimnion may be short and may vary considerably with the weather from year to year.

Only 68 (38%) of the named coastal zone lakes (appendix table 1), possess a hypolimnion. Temperature data are not available for most of the small natural lakes, which are shallow and would not be expected to be stratified. Because most of the small, shallow unnamed lakes are not included in the data for stratified and nonstratified lakes in table 7-2, the true percentage of stratified lakes with hypolimnia is considerably less than is indicated in the table.

The spatial and temporal patterns of water temperatures in lakes have major effects on free oxygen levels, nutrient recycling, biological productivity, and species composition of fishes and other biota. Many of the nutrients in lakes are released into the aquatic system by the decomposition of organic materials on or near lake bottoms. As a result, nutrients become available throughout the aquatic system of shallow, well-mixed lakes, making them more productive than deep stratified lakes (Richardson 1975). In well stratified lakes much of the nutrient release from decomposition may accumulate near the bottom and is largely unavailable to the trophogenic zone. A comparison of total phosphorus in the epilimnion (surface layer) and the hypolimnion (bottom layer) of eight thermally stratified lakes in the coastal zone of Maine during summer illustrates this point. A mean value of 8 ppb (range: trace to 12 ppb) near the surface and of 33 ppb (range 10 to 95 ppb) near the bottom is indicative of how thermal stratification potentially can affect biological productivity. In addition, high rates of decomposition in these waters may result in severe oxygen depletion during mid- and late summer.

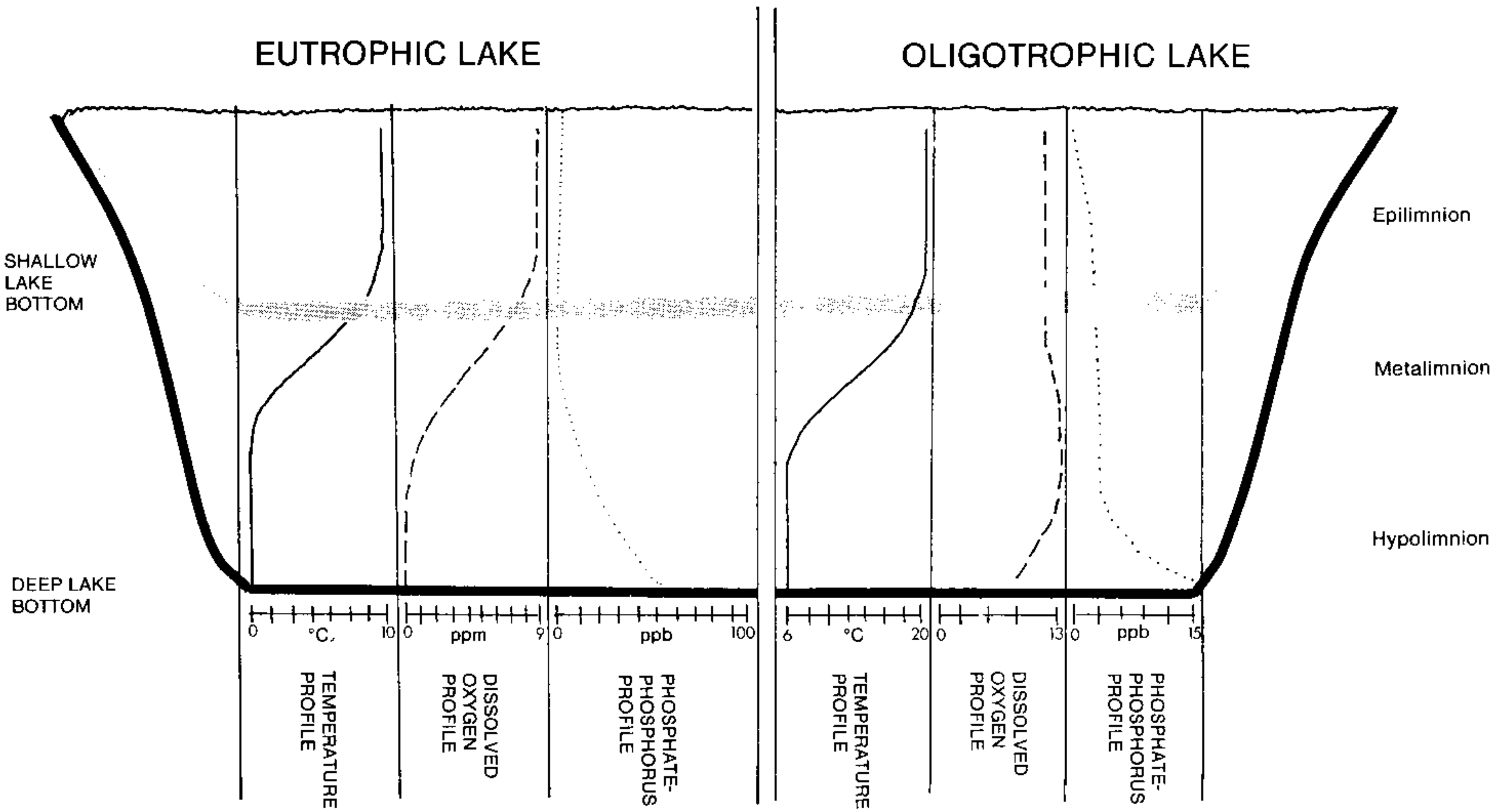


Figure 7-2. Comparison of summer conditions of temperature, oxygen, and phosphate-phosphorus at different depths in shallow and deep eutrophic lakes (fertile) and oligotrophic lakes (infertile).

Biological Characteristics

Meaningful functional attributes of a lacustrine system have been described by Hutchinson (1967) and Wetzel (1975). A cross section of a typical moderately deep mid-sized oligo-mesotrophic coastal zone lake is given in figure 7-3. This diagram is based on biological function and is not to be confused with the habitat classification system used by the NWI. Thus, the functional littoral zone in Maine lakes is 10 to 15 m (33 to 50 ft) while the NWI littoral zone is <2 m (7 ft). Major components are the littoral zone (where emergent, floating, or submerged vegetation grow), and the limnetic (pelagial) zone (where the bottom is at depths too great to possess enough light for supporting macrophytes). The littoral zone is trophogenic. The trophogenic zone is separated from the tropholytic zone (deeper water) by the "compensation level" where the rates of photosynthesis (determined by light penetration) and respiration are equal. Depending upon weather conditions, the depth of the compensation level may change somewhat from day to day.

In clear, oligotrophic lakes the deepest attached plants are usually nonvascular (algae or bryophytes). Below the compensation level, metabolism is mostly heterotrophic and detritus-based. Because decomposition of organic matter exceeds production of organic matter (by photosynthesis) there, the deeper water of deep lakes is called tropholytic, in contrast to the near-surface trophogenic zone where net production of organic matter occurs. Eutrophic lakes have a shallow compensation level compared to clear, oligotrophic lakes, because heavy plankton populations in eutrophic lakes greatly reduce light penetration. Mesotrophic lakes have characteristics that are intermediate between oligotrophic and eutrophic lakes. The littoral zone has been described for only a few Maine lakes (Davis, unpublished) and none of these are in the coastal zone.

The interaction of factors that ultimately determine the composition and quantity of biota, the rates at which nutrients are recycled, and the general productivity of lakes are highly complex (figure 7-4). For example, lake morphology (lake depth, area, and contours, etc.) affects light penetration, heat distribution, and oxygen distribution, all of which in turn affect the trophic status of lakes and the biota present in them.

ABIOTIC FACTORS AFFECTING THE LACUSTRINE SYSTEM

Several major factors affect the productivity of Maine lakes. Some are applicable to all lakes and some are particular to coastal zone lakes. Most Maine lakes are infertile in comparison to average temperate zone lakes. Climatic, other atmospheric, hydrological, geological, and other physical factors that affect lakes, will be considered here. These factors work in combination and their combined effects usually cannot be separated. Topography may affect local climate (e.g., alters wind), climate may affect edaphic factors (e.g., weathering and leaching of soils), people may alter edaphic factors (e.g., soil erosion), etc. Lake hydrology, which has a major influence on biological productivity, is determined by climate and other factors including lake morphology and watershed size. Some of the complex interrelations among these factors are illustrated in figure 7-4.

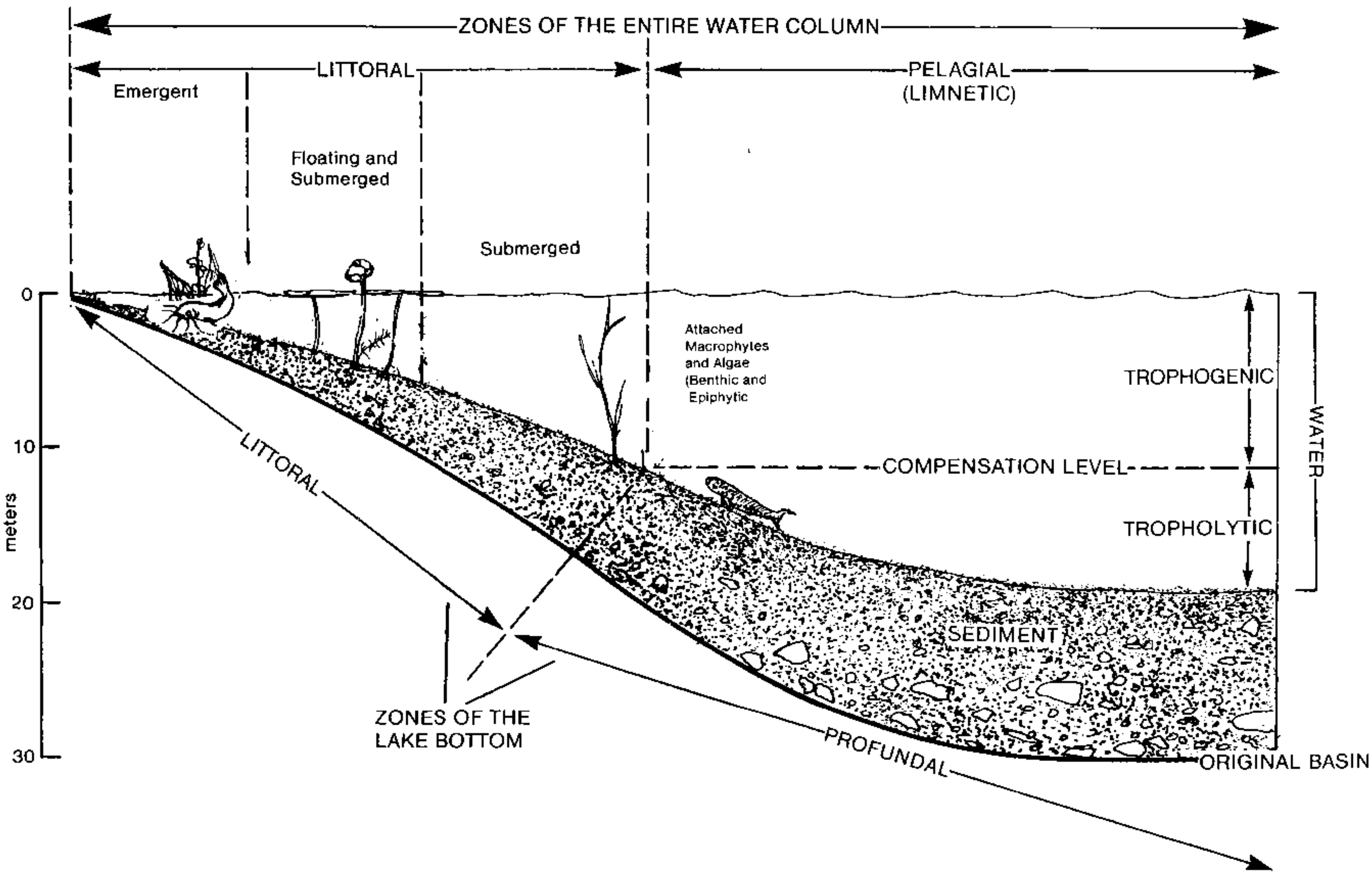


Figure 7-3. Lake zonation based on biological function. Example given is a moderately deep oligo-mesotrophic Maine lake.

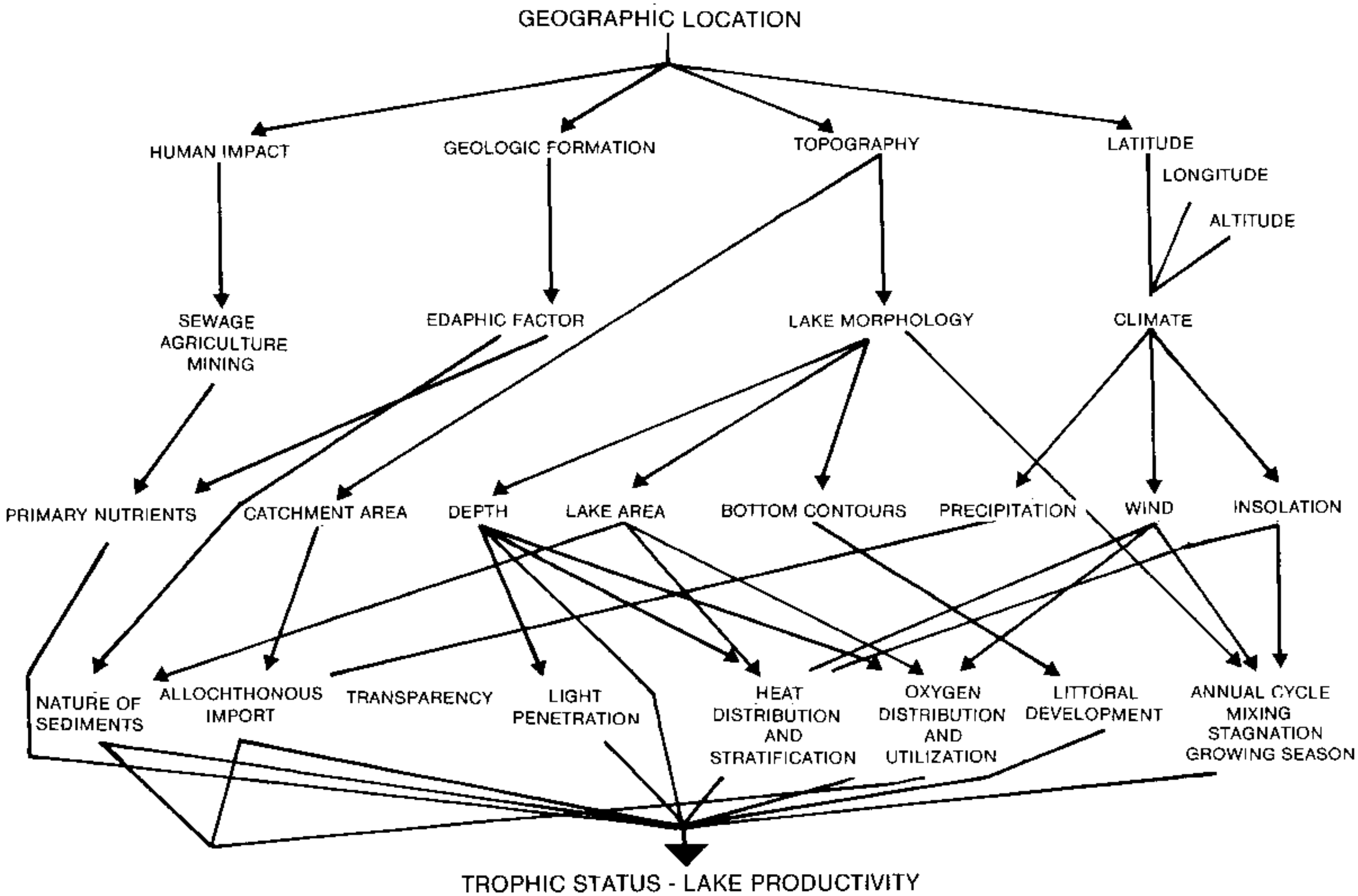


Figure 7-4. Factors and interactions that determine lake characteristics (modified from Rawson 1939 by Cole 1975).

Climate

Climatic factors play major roles in determining biological productivity and types of biota in lakes, especially on a world-wide scale (Brylinsky and Mann 1973). However, within relatively restricted regions with "one climate," nonclimatic factors, such as lake morphometry (Richardson 1975) and rock chemistry, are more influential in determining variations between lakes. While it is true that within the coastal zone of Maine there are climatic gradients (see chapter 2, "The Coastal Maine Ecosystem"; Davis 1966 and Lautzenheiser 1972), the ranges of these gradients are not great enough to affect within-zone variation in lacustrine productivity to the degree that nonclimatic factors do. Nevertheless, some differences attributable to climatic gradients are perceivable between the lakes of the various regions. For example, summer surface-water temperatures, when averaged by region (table 7-2), roughly parallel the southwest to northeast gradient of July air temperatures (Lautzenheiser 1972). Also, the ice-clearing dates for the coastal zone lakes in the southwest (early April) have averaged a week or more earlier than in the northeast (mid-to late April) during the past several decades (Fobes 1974). The southwest to northeast climate gradient is clearly reflected in the terrestrial vegetation of the coastal zone (Davis 1966) but present data on lake biota do not indicate an unequivocal correlation between biota and climate differences. Within the coastal zone, differences in the biota and productivity of lakes seem to be caused mainly by nonclimatic factors.

Other Atmospheric Factors

The atmosphere affects lakes significantly by its input of pollutants, including nutrients, acids, and heavy metals. The latter two pollutants originate mostly in the burning of fossil fuels and the smelting of sulfide ores. Acidic precipitation (and the resultant decreasing pH of lakes) and associated heavy metal inputs are of growing concern in Maine (Davis et al. 1978b and Norton et al. 1978). In other, similar regions (e.g., Adirondack Mountains, New York; southern Norway) important negative impacts on lake systems have already been documented (Schofield 1976 and Braekke 1976).

Atmospheric inputs of phosphorus may constitute major portions of the phosphorus budget of lakes with relatively undisturbed watersheds where edaphic inputs are low (Peters 1977).

The "average" hydrogen ion concentration (pH) in Maine lakes possessing pH data showed a decline from a pH of 6.8 in 1937 to pH 6.0 in 1974 (Davis et al. 1978b). Due to the logarithmic nature of the pH scale, this decrease in the "average pH" may be caused by only a small percentage of lakes where major increases in hydrogen ion concentrations have taken place. In the summer of 1978 a sampling of pH at 37 Maine lakes that were selected for susceptibility to acidification (due to low alkalinity water) resulted in a pH range from 5.7 to 6.7. Thirty-two had decreased in pH (median decrease 0.4, maximum 1.1) since about 1940 (Davis et al. 1979). Lakes in the coastal zone, although often of very low alkalinity and therefore of low acid-buffering capacity, are probably somewhat more resistant to the effects of acidic precipitation than lakes farther inland. This resistance is created by small amounts of buffering substance in the cyclical salts that coastal zone lakes receive via the atmosphere from the nearby ocean. Nevertheless, lakes in the vicinity of the coastal city of Halifax, Nova Scotia, have declined in pH during the past two decades due to atmospheric inputs of sulphur originating in sulphur emitting-industrial plants in the Halifax area (Watt et al. 1978). The changes in pH of Maine lakes are currently under further investigation by R. B. Davis and S. A. Norton of the University of Maine at Orono.

Fallout of heavy metals from the atmosphere may be a serious problem. Norton and his coworkers (1978) found that zinc content in the sediments of Maine lakes has doubled since the late 1800s. The authors ascribe this increase to atmospheric inputs of zinc that originated in urban and industrial air pollution. Whether the rate of accumulation of zinc is or will be serious has not been determined yet.

Hydrology

Hydrologic factors affect lake productivity principally through rates of flushing (the time it takes to fill a lake with ambient flow) and mixing and flow patterns. Rivers and streams may carry nutrients into or out of a lake and add or remove nutrients to degrees that might affect basic productivity. Nutrient-laden streams enrich recipient lakes and, in extreme cases, may accelerate eutrophication and cause severe oxygen depletion especially in thermally-stratified lakes. Streams also may flush out pollutants from lakes. These and other aspects of the hydrology of Maine lakes are discussed by Davis and coworkers (1978a), and hydrology, nutrients, and eutrophication are reviewed by Vollenweider and Dillon (1974) and Dillon (1975).

The use of hydrologic models in the formulation of lake restoration plans has recently been investigated by Uttormark and Hutchins (1978). Hydrologic information is available for only a few lakes in the coastal zone. One of these is Little Pond in region 3, where Mower (1978) calculated phosphorus loadings. Hydrologic retention times were calculated for Highland Lake in region 1, Brewer Lake in region 4, and Branch and Green lakes in region 5, using information from nearby stream gauges (Royal, West Branch Union, and Narraguagus rivers; Cowing and Scott, in preparation). The retention times for these lakes were 1.1 to 1.4 years (range of three methods of calculation), 1.2 to 1.5 years, 2.0 to 2.3 years, and 1.4 to 1.6 years, respectively. The significance of these flushing rates were not disclosed. Outside the coastal zone, at culturally eutrophic Lake Sebasticook, Hannula (1978) modeled the phosphorus cycle on the basis of hydrologic and other information to provide a basis for management decisions in controlling nuisance algal blooms. He concluded that substantial reduction in external P loading by "... removal of known point sources will have little impact on the lake until the magnitude of the summer sediment release is reduced" and he indicated that an extended fall drain down would reduce "...the phosphorus pool at the top of the sediment."

Geology

Most lakes in coastal Maine originated during deglaciation and after marine submergence (about 12,000 years ago; Stuiver and Borns 1975). Many of the lake basins originated from glacial sub-ice abrasion that modified topography. The three main types of lakes, with regard to basin geology, have been recognized along the Maine coast (Davis et al. 1978a). Lake basins scoured into the metamorphic rocks of the tightly-folded structural belt along the coast southwest of Penobscot Bay (regions 1,2, and 3) are elongated in a south-southwesterly direction (Damariscotta and St. George lakes for example).

Lakes elongated in a south-southeasterly direction, parallel to apparent glacial ice-flow, are common to the east of Penobscot Bay (regions 5 and 6). Scouring developed apparently along lines of high ice-flow, along preglacial drainage lines, and along structural weaknesses (joint planes) within igneous bodies (Gardner, Beddington, and Green lakes for example; Davis et al. 1978a). Smaller lakes occupy depressions within glacial sediments that were created during ice-stagnation. Ice blocks surrounded or covered by glacial sediment subsequently melted, forming depressions called kettles. Kettle lakes (the third lake type) are abundant in Washington County (region 6), where glaciodeltaic sedimentation was prominent.

Lake substrates. Lake basins within the coastal zone are underlain by bedrock, glacial till, or glaciomarine clay-silt substrates. Deglaciation was sufficiently rapid along the Maine coast that the sea lavel rose faster than rebound could occur (Stuiver and Borns 1975). Inundation of low-lying areas (up to elevations of about 150 m; 495 ft) by marine waters left extensive deposits of marine silt and clay (Presumpscot Formation). The spillways of many lake basins were below sea level for a short period of time, allowing the silt and clay to be deposited on lake basin floors and margins (Davis et al. 1978a).

Lacustrine sedimentation. Lake sedimentation can be differentiated between limnetic (pelagial-profundal; figure 7-3) sedimentation and littoral sedimentation. Generally, sediments that are deposited in profundal environments are derived from littoral sediments or have passed through the littoral zone. Lacustrine sediments are mostly derived from lake watersheds and delivered to the basin by overland flow, or from erosion of shore deposits by waves. The amount of sediment delivered annually to a lake depends upon several factors: precipitation, runoff volume, watershed soil distribution and type, watershed vegetation, watershed agricultural activity, and local wind and lake wave action. High levels of precipitation and runoff, agricultural activity, extensive use of motor boats, construction in the watershed, and stronger winds all increase sedimentation within the lake basin.

Sediments delivered to the deeper lake portions are limited to silts and clays, which remain in suspension for up to tens of days. The sediment in deep sections of lakes also contains varying amounts of fine organic debris derived from the surrounding watershed, and the littoral and pelagial zones. Essentially, these sediments are a fine-grained mud. Only rarely is this sediment layered or graded; such structure is destroyed by mixing of sediment brought about by resuspension during overturn (and more frequently in lakes too shallow to stratify), and by the activities of animals burrowing within the upper few centimeters of sediment.

Geologic formations in the littoral environments can be broken down into different morphological units. These units are rocky shores, beaches and spits, littoral flats and deltas. Rocky littoral areas are common on the margins of lakes that are carved into bedrock or situated in glacial boulder tills. Little sediment can accumulate on these shores, because of a lack of sediment input to the lake or because the shores are moderately steep. These shores are stable and are affected little by changes in water levels.

Beaches and spits of sand or mixed sand and gravel occur along lake shores in which the shore substrate consists of glaciofluvial sands and gravels. These features commonly occur on the eastern shores of lakes, as prevailing southwesterly winds create waves of sufficient magnitude to erode shoreline banks and transport material along the beach.

Mud flats (vegetated and unvegetated) may occur along lake shorelines, but are found infrequently, except where lake levels are lowered artificially. Littoral flats may occur lakeward of beach and spit shorelines or may occur unassociated with such features in sheltered shallow coves of lakes with high mud-content sediment input. Littoral flats also may be associated with deltas that form at the mouths of streams entering a lake.

A more common depositional feature of coastal Maine lakes is delta deposits at the heads of lakes. While generally of small areal extent (10s of hectares) they indicate the first step of lake infilling by sediments delivered in streams. They are usually sand deposits that are capped by mud sediments and are deposited after spring freshets or during winter months. Delta surfaces usually are vegetated with freshwater aquatic vegetation and upland emergent plant species. The deposits are irregular in shape and often have a straight channel in the center, leading from the stream to the open lacustrine tract. The distal (outer) margins of the delta may be rimmed by sandy beaches and spits. Beaches and spits are common where sediment-input sand volume is high.

Deltas extend into the lake depths by deposition of sand on the prodelta face below the delta channel mouth (progradation). Sand deposited in this way (extending laterally into the lake) forms three types of beds (bottomset, foreset, and topset beds). Mud accumulates on the surface of the delta, entrapped by aquatic and emergent plants during high spring runoff and flood water levels. Thus, delta surfaces are built up over time. No studies have been undertaken to ascertain delta progradation or accretion (vertical growth) rates. Present rates of lake infilling or lake delta progradation within the characterization area are unknown but it can be assumed that these rates are highly variable.

The areal extent and processes of littoral deposit are determined by the rate of sediment input, by lake water levels, and by waves. Lake levels fluctuate due to watershed runoff input or as a result of manipulation by people. Unless there is a rapid input of sediment from alongshore, a raising or lowering of the water level by more than several tens of centimeters either will cover existing littoral deposits or leave them stranded subaerially, respectively. In the latter case, these deposit surfaces will become colonized by upland plant vegetation.

Soils

The primary influence that the geology and soils of the coastal zone have on lake ecosystems derives from their effect on the chemistry of runoff waters from watersheds. If rock chemistry is such that high concentrations of nutrients are released into the runoff waters the effect will be an increase in biological productivity. The structure, depth, and permeability of the deposits also influence the chemistry of the runoff. These factors in Maine lakes are discussed by Davis and coworkers (1978a).

The coastal zone is underlain by a variety of bedrock types. Region 1 is predominantly metasedimentary, with some calcareous content in the rocks slightly inland from Casco Bay. Region 2, also, is underlain by metasediments, largely gneiss, quartzite, schist, and phyllite, with minor calcareous content in a few areas. Areas of granite also occur in region 2, especially in the northern area. Region 3 has metasediments in some areas and granite in others. Region 4 contains a variety of metasedimentary rocks, some with minor calcareous content (e.g., around Hammond Pond). A large area of granite occurs at the eastern part of the region (around Craig Pond). Region 5 is predominantly granite, diorite, and gabbro (e.g., around Narraguagas Lake) but also includes areas of metasediments (especially schist) in the west (around Ellsworth), and slate, metasandstone, and quartzite in the east (around Columbia). Region 6 has a complex pattern of volcanic rocks (rhyolite and basalt flows, and tuff; e.g., around Rocky Lake), granite, diorite, and gabbro, metasedimentary rocks (e.g., phyllite and schist), and areas of interbedded metavolcanic and metasedimentary rocks. Bedrock geology maps of the coastal zone are available (Maine Geological Survey 1978).

Bedrock in the uplands of the coastal zone is overlain by thin glacial till, except in occasional areas on ridges, where it is exposed. The till is composed largely of rocks derived from within a few kilometers of the site of deposition and therefore reflects the nature of the bedrock nearby that was in the path of the glacial flow. Peat deposits frequently occur in the lowlands. They are often contiguous with lakes, or streams draining into lakes, and the dissolved organic matter they release creates a yellowish or brownish color in the water of the lakes. Much of the lowland is covered by a deposit of glaciomarine silt-clay; for example, in the north and west areas of region 2 and near Rockland in region 4 (Smith and Anderson 1974). Maps of the surficial geology of the coastal zone are available showing the above-mentioned deposits (Maine Geological Survey 1977).

Calcareous sedimentary and metasedimentary rocks generally yield waters with higher concentrations of critical biogenic nutrients than waters of predominantly siliceous rocks. Because rocks with calcareous content occupy only a small fraction of the coastal zone the runoff (where unpolluted) from most of the watersheds is a relatively dilute, infertile solution, as is suggested by the low alkalinities of coastal zone lakes. The alkalinity of lake surface waters in the coastal zone averages only 8.0 ppm as $CaCO_3$, with no great difference from region to region, except for a small number of lakes on relatively calcareous rock in region 4 that have alkalinities of 15 to 26 ppm (table 7-4; appendix table 2). However, the direct relationship of watershed rock and runoff chemistry to lake productivity is sometimes obscured. Two reasons for this are: (1) lake morphology has a major influence on productivity; (2) the edaphically fertile watersheds are those whose agricultural acreage is greatest, and the effect of agriculture on soil is to increase nutrient runoff and resultant inputs to surface water. Data for coastal zone lakes are inadequate to definitively attribute productivity differences from lake to lake to edaphic causes. However, Cowing and Scott (in preparation) found that among the 43 Maine lakes they studied those surrounded by relatively calcareous deposits had slightly greater productivities than the others. Studies by Davis and coworkers (1978a) at 17 Maine lakes are in agreement.

Morphometry

Data on the morphometry of coastal zone lakes are discussed under "Distribution of the Lacustrine System," above. The effect of morphometry on productivity is discussed under "Temperature Characteristics" above. The shallowness of most coastal zone lakes has an important influence on their productivity, or trophic state (Richardson 1975). The relationship may be illustrated by an analysis of coastal zone lakes for which relevant data are available. Phosphorus (total), chlorophyll-a, and plankton (especially algae) concentrations are used as indices of biological productivity (Davis et al., 1978a) in Maine lakes. For Maine lakes with low water color, Davis and coworkers (1978a) observed that total phosphorus concentrations in near-surface waters, chlorophyll-a concentrations in near-surface waters, and the inverse of Secchi disc transparency (an approximate index of plankton or seston concentrations) were all correlated. Data for these parameters in shallow lakes (<18 m; 60 ft) and deep lakes (>18 m; 60 ft) in the coastal zone indicate that the shallower lakes are more productive on a per unit volume basis (table 7-5).

Table 7-5. Comparison of Trophic Indicators for Shallow (<18 m) versus Deep (≥18m) Coastal Maine Lakes with Low Water Color [a,b].

Trophic indicator		Shallow	Deep
Secchi disc transparency (m)	$\bar{x}$	4.0	8.0
	min-max	1.3-5.8	4.0-12.0
	n	28	18
Total phosphorus (ppb)	$\bar{x}$	13.6	7.5
	min-max	T-30	T-20
	n	15	14
Chlorophyll-a (ppb)	$\bar{x}$	8.5	2.9
	min-max	2.5-24.0	1.5-5.5
	n	9	8

[a]n=number of lakes; T=trace
[b]Lakes for which data are unavailable are not included.

BIOGEOCHEMICAL CYCLES AND BUDGETS

The effects of biological uptake and sedimentation on available phosphorus, nitrate, and silica in Maine lakes are described by Davis and coworkers (1978a). Ordinarily nitrogen rarely is a factor limiting production in lakes because it is readily available from the atmosphere, and is fixed by some aquatic algae. However, in summer low levels of dissolved, fixed nitrogen, the result of biological uptake, favor certain phytoplankton forms, especially the nitrogen-fixing, bloom-forming, blue-green algae. Silica rarely affects lake productivity but its scarcity or abundance may have a considerable effect on the abundance of some organisms. For example, low silica favors nonsiliceous algae instead of silica-demanding diatoms.

The availability of phosphorus probably has the greatest single effect on lake productivity (Wetzel 1975), although the availability of certain trace elements (e.g., molybdenum) can have an effect on a short-term basis (Thurlow et al. 1975). Phosphorus budgets or cycles have been estimated for only two of the coastal zone lakes, Pleasant Pond in region 2 (Gordon 1977) and Little Pond in region 3 (Mower 1978). The closest approaches to complete phosphorus budgets (including in-lake cycling) for Maine lakes are those developed for Haley Pond (Scott et al. 1977) and for Lake Sebasticook (Hannula 1978), both outside the coastal zone. The major sources of phosphorus input in lakes are (1) biological input: for example, bird and insect droppings and animal and plant detritus; (2) dry and wet atmospheric fallout; (3) surface runoff and inflowing streams; (4) ground water; and (5) pollution (human and industrial wastes). Losses of phosphorus from lakes may be caused by (1) emerging insects, and food consumed by birds and animals; (2) outlet streams; (3) ground water loss, and (4) binding of phosphorus to sediment. In internal cycling of phosphorus in a lake system phosphorus may be transferred by (1) biological and chemical decomposition in the water column and sediment-water interface, and by animal excretions; (2) uptake from water and sediment by algae and macrophytes; or (3) consumption by herbivores and carnivores. In the open water epilimnion (warm, shallow water) the internal cycling of phosphorus is extremely rapid. Complete turnover between the phytoplanktonic algae and water is measured in minutes, but for the epilimnion as a whole turnover is measured in days or weeks (Wetzel 1975). Large quantities of phosphorus are replaced in lakes by residential and municipal sewage. Sewage may significantly alter the concentrations and flux of phosphorus in lakes and, thereby, increase productivity to the point of causing obnoxious algal blooms and related detrimental phenomena.

BIOTA

How organisms live and interact is important in understanding the significance of the biology of lakes. The following is a general description of some of the major forms of biota and the methods of classifying them.

Benthic organisms live on the bottom, in bottom sediments, or attached to surfaces protruding from the bottom (e.g., macrophytes). Planktonic organisms live in the water column and possess limited or no power of locomotion. Neustonic organisms live at the air-water interface (e.g., water striders). Organisms in Maine lakes sometimes are sorted on the basis of their littoral, profundal, and pelagial distribution (figure 7-3). Lacustrine organisms can also be grouped on the basis of their nutritional habits: primary producers (e.g. phytoplankton), consumers, (e.g., fish), and decomposers (e.g., bacteria). Consumers and decomposers both contribute to the degradation of organic matter, and many consumers feed on organic detritus, all of which falls under heterotrophic nutrition.

Data on the biota (except fishes) of the coastal zone lakes generally are too sparse to be representative. Data of Cooper (1939 and 1942) on net plankton are not suitable for meaningful comparisons. The most complete biological data on coastal zone lakes are those for Highland, Brewer, Branch, and Green lakes. These lakes were included by Cowing and Scott (1975 to 1977) in their report on 3 years' data from 43 Maine lakes. The authors calculated trophic state indices for these lakes, indicating that Green Lake (region 5) is oligotrophic, Branch (region 5) and Highland (region 1) oligomesotrophic, and Brewer (region 4) mesotrophic.

The abundance and biomass of organisms in Maine lakes have been correlated to the lakes' trophic status by Cowing and Scott (1975 to 1977) and Davis and coworkers (1978a). The annual mean phytoplankton density in Maine lakes ranges from about 100 cells/ml to at least 30,000 cells/ml, and annual mean phytoplankton biomass (as total volumes of cells) ranges from about 20,000 to >2 million μm^3/ml (Davis et al. 1978a). Summer phytoplankton in relatively oligotrophic lakes (e.g., Green and Branch) are dominated by small flagellates and diatoms, whereas relatively eutrophic Brewer Lake is dominated by blue-green algae _Aphanizomenon flos-aquae_ and _Gomphosphaeria aponina_. Elsewhere in the coastal zone the blue-green algae genus _Anabaena_ has been found to predominate the summer plankton of relatively eutrophic lakes (e.g., Togus and Pleasant Ponds in region 2; Cobbossee Watershed District 1977a and 1977b). Outside the coastal zone, small blue-green algae (_Merismopedia tenuissima_), several diatoms (especially _Tabellaria_ spp.) and small unicellular flagellates dominated the summer phytoplankton in relatively oligotrophic lakes. Under eutrophic conditions the summer phytoplankton was dominated by _Anabaena_ spp., _Oscillatoria_ spp., and _Gomphosphaeria_ spp. In addition to these the taxa _Anacystis_, _Asterionella_, _Cyclotella_, _Chromulina_, and _Ochromonas_ occur commonly in Maine lakes (Davis et al. 1978a).

Genera of macrophytes that occur commonly in Maine lakes include: (1) emergents, _Scirpus_, _Eleocharis_, _Typha_, _Pontederia_, and _Sparganium_; (2) the floating-leaved plants, _Nuphar_, _Brasenia_, _Nymphaea_, and _Valisneria_; and (3) the submerged plants, _Eriocaulon_, _Potamogeton_, _Myriophyllum_, _Utricularia_, and _Osoetes_ (Cowing and Scott 1975, 1976, and 1977). A complete list of aquatic vascular plant species that occur in Maine coastal counties encompassed in the characterization area is given in appendix A of chapter 8.

The abundance and biomass of the benthos in March is also related to the trophic status of Maine lakes. _Phaenopsectra_ (_Tribelos_) spp. and _Micropsectra_ spp. were found in the relatively oligotrophic lakes and _Chironomus plumosus_ in the relatively eutrophic lakes (Cowing and Scott 1975 to 1977; and Davis et al. 1978a). _Ericaulon septangulare_ is a common macrophyte of the relatively oligotrophic lakes.

Based on plankton biomass calculations coastal zone lakes (mean 9.2 cm^3/m^3; min-max 1.8 to 39.3 cm^3/m^3) are more productive in summer than Maine lakes as a whole (mean 4.8 cm^3/m^3; min-max 0.7 to 10.9 cm^3/m^3; Cooper 1939, 1942; Fuller and Cooper 1946; Davis et al. 1978a). These data also suggest that lakes in the southwestern region of the coastal zone are more productive than other areas of the coastal zone. Unfortunately, no data are available for regions 1 and 6.

The coastal zone lakes support anadromous, catadromous, and resident sport fish species. The most widespread and common species of warm-water sport and pan fishes (excluding sunfishes) in these lakes are yellow perch, chain pickerel and smallmouth bass. Brook trout and rainbow smelt are the most common coldwater game and pan fishes. The fisheries in coastal zone lakes (n=59) have been evaluated by Cooper (1939 and 1942) and Fuller and Cooper (1946). The fisheries at 151 of the coastal zone lakes were appraised in the 1970s (Spencer and Hutchinson 1974a, b, c, and d; Hutchinson 1977a, b, and c; and Hutchinson and Spencer 1975a, b, c, and d). Data organized by individual lakes are given in appendix table 3 and summarized in table 7-6. The freshwater fishery of the coastal zone is a mix of coldwater and warmwater fisheries. Fisheries differ from region to region. Regions 1 to 4 contain mostly warmwater fisheries, and the percentages of lakes with coldwater fisheries in these regions increase from southwest to northeast. In region 5, coldwater fisheries predominate but warmwater fisheries remain important. The fishery in region 6 is mixed, although data on it are sparse.

Coastal zone lakes serve as breeding and feeding areas for a number of waterbirds (e.g., loons), waterfowl (e.g., mergansers, black ducks, wood ducks), and raptors (e.g., bald eagles, ospreys). Information on these groups of species is presented in chapter 14, "Waterbirds," chapter 15, "Waterfowl," and chapter 16, "Terrestrial Birds."

ENERGY FLOW AND FOOD WEBS

Trophic Structure, Energy Flows, and Budgets

The energy entering a lake is direct-solar (light) and indirect-solar (heat from substrate, from atmosphere, and from entering streams). Most of this energy (including about 99% of the direct energy) is consumed by heating the water. Only a minute percentage (<1%) of the light is used by the phytoplankton in photosynthesis. A slightly higher percentage may be used in the shallow parts of the littoral zone, due to the presence of attached plant communities. A diagram of the energy flow through the biota of the pelagial part of a large, deep lake is given in figure 7-5. A general, but less complete, diagram of a Russian lake is given in figure 7-6. These relationships have not been studied in any lakes in Maine. Allochthonous inputs (from outside the lake) of organic detritus to the food web of small lakes are substantial. However, in a typical medium-to large-size mesotrophic or oligotrophic Maine lake (figure 7-5) it is doubtful that the allochthonous detritus chain would be as important or that the Protozoa and *Asplanchna* would appear as prominently as they do in figure 7-6.

Table . Fisher. of Coastal Maine Lakes [a]

Region	Number of lakes surveyed	Number of lakes																								
		Coldwater fishery [b]										Warmwater fishery [b]										Fishery type [c]				
		Existing					Potential					Existing					Potential									
		high	moderate	low	nil	unknown	high	moderate	low	nil	unknown	high	moderate	low	nil	unknown	high	moderate	low	nil	unknown	warm water	cold water	mix	none	unknown
1	4	0	0	0	1	3	0	0	0	1	3	0	1	0	0	3	0	1	0	0	3	1	0	1	0	2
2	34	0	3	5	21	5	1	4	4	20	5	7	10	11	1	5	8	12	8	1	5	22	2	7	0	3
3	26	1	8	2	6	9	1	9	1	5	10	2	9	3	3	9	2	11	1	2	10	9	2	7	1	7
4	58	0	12	12	17	17	1	5	4	2	46	4	25	8	2	19	6	1	3	1	47	30	7	8	1	12
5	56	2	17	21	0	16	12	20	8	0	16	4	9	28	0	15	5	12	24	0	15	8	24	11	2	11
6	37	0	1	9	0	27	0	7	3	0	27	0	0	10	0	27	1	5	4	0	27	7	10	6	0	14
Entire coastal zone	215	3	41	49	45	77	15	45	20	28	107	17	54	60	6	78	22	42	40	4	107	77	45	40	4	49

Region		Percent of lakes														
		Coldwater fishery					Warmwater fishery					Fishery type				
		high	moderate	low	nil	unknown	high	moderate	low	nil	unknown	warm water	cold water	mix	none	unknown
1	E/P [d]	0/0	0/0	0/0	25/25	75/15	0/0	25/25	0/0	0/0	75/75	25	0	25	0	50
2	E/P	0/3	9/12	15/12	62/59	15/15	21/24	29/35	32/24	3/3	15/15	65	6	21	0	9
3	E/P	4/4	31/35	8/4	23/19	35/39	8/8	35/42	12/4	12/8	35/39	35	8	29	4	27
4	E/P	0/2	21/9	21/7	29/3	29/79	7/10	43/2	14/5	3/2	33/81	52	12	14	2	21
5	E/P	4/21	30/36	37/14	0/0	29/29	7/9	16/21	50/43	0/0	27/27	14	43	20	4	20
6	E/P	0/0	3/19	24/8	0/0	73/73	0/3	0/14	27/11	0/0	73/73	19	27	16	0	38

(Continued)

Table 7-6. (Concluded)

	Percent of lakes														
	Coldwater fishery					Warmwater fishery					Fishery type				
	high	moderate	low	nil	unknown	high	moderate	low	nil	unknown	warm water	cold water	mix	none	unknown
Entire coastal zone	1/7	19/21	23/9	21/13	36/50	8/10	25/20	28/19	3/2	36/50	36	21	19	2	23

[a]More complete data are shown in appendix table 3.
[b]According to fishery appraisals by Hutchinson and Spencer (Various references)
[c]Present or desired management, according to files of Maine Dept. of Inland Fisheries and Wildlife.
[d]E = existing; P = potential.

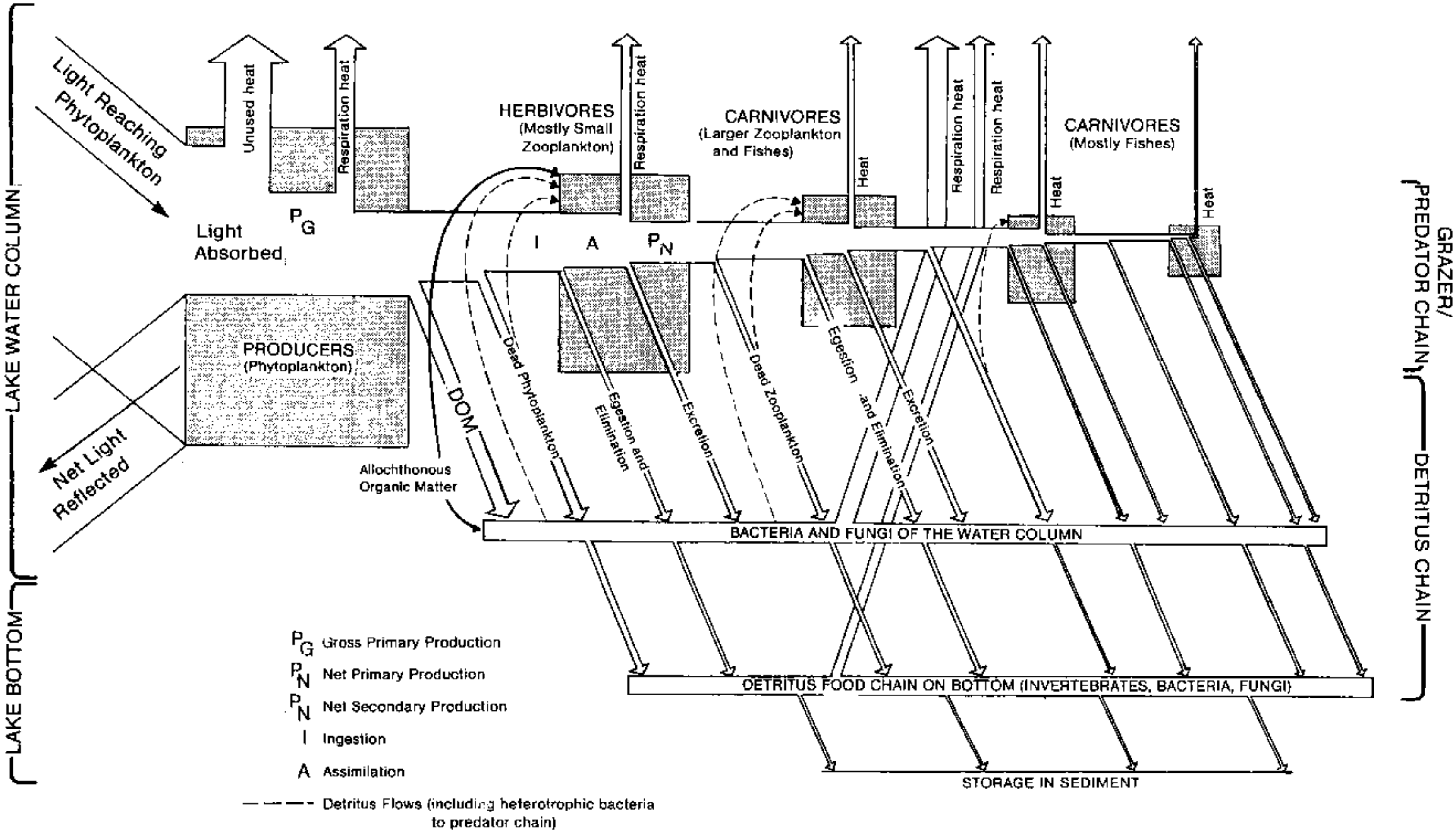


Figure 7-5. Idealized energy flow diagram for the pelagic portion of a large, deep lake.

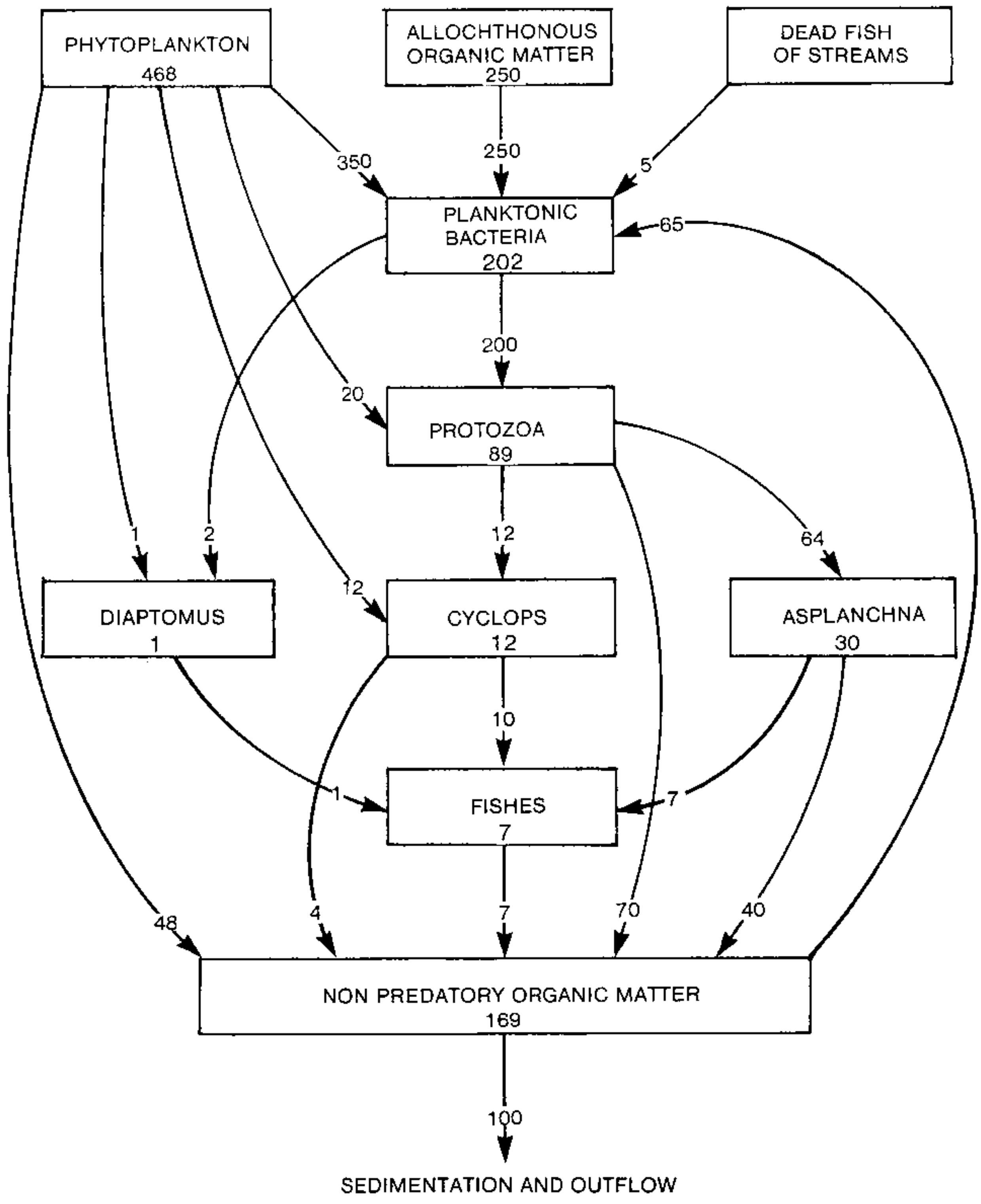


Figure 7-6. Energy flow diagram for a particular lake. Generalized relationships of the average energy flow in the pelagic zone of Dalnee Lake, Kamchatka, USSR, during the month of July. Data expressed in calories per square meter per 30 days (from Wetzel 1975; Sorokin and Paveljeva 1972).

An energy-flow model for a typical littoral zone would be similar to that in figure 7-5, except that (1) attached plants would dominate the producer level (phytoplankton would be present, also); (2) a much larger proportion of the net primary productivity (mostly macrophytes and attached algae) would be invested in detritus food chains on the bottom; (3) inputs of allochthonous organic detritus would be greater; (4) the biomass of detritus-feeding invertebrates (and associated predators) would be greater than that in the pelagial zone.

Food Webs

A general food web for the pelagial plankton community of a Maine lake is given in figure 7-7. The generic examples given in the web are known to occur commonly in Maine lakes (Davis et al. 1978a and Cowing and Scott 1975, 1976, and 1977). Feeding relationships among the plankton have not been studied in Maine lakes. The base of the web consists of phytoplankton and allochthonous organic matter, which are fed upon by herbivorous (and detritus-feeding) zooplankton and heterotrophic bacteria. The herbivorous zooplankton are fed upon by the predatory zooplankton and planktivorous fishes. Many organisms occupy more than one trophic (feeding) level. The zooplankton that feed on detritus may ingest autochthonous as well as allochthonous detritus and the bacteria and fungi associated with both types of detritus. That is, a portion of detritus is recycled within the pelagial plankton food web itself. The remainder of the detritus is carried out by the outlet stream or falls to the bottom where it becomes the food for a benthic food web (not included in figure 7-7). In the profundal zone the web includes various detritivorous and deposit-feeding chironomids (e.g., Chironomous), tubificid oligochaetes (e.g., Limnodrilus), and the fingernail clam Pisidium, the predatory chironomids (e.g., Procladius), and the predatory phantom midge Chaoborus (Davis et al. 1978a). Detailed information on the pelagial biota of 17 Maine lakes is given by Davis and coworkers (1978a). Cowing and Scott give information for 43 other Maine lakes (1975, 1976, 1977, and in preparation).

The littoral zone food web (figure 7-8) is much more complex than the pelagial plankton food web. No thorough descriptions have been done of the littoral parts of lake systems in Maine. Davis and coworkers (1978a) and Cowing and Scott (1975, 1976, 1977, and in preparation) sampled the plankton and macrozoobenthos in the deepest parts of Maine lakes whose entire areas were littoral. Cowing and Scott (1975, 1976, and 1977) surveyed the common vascular plants in 43 Maine lakes, four of which (Brewer, Branch, Green, and Highland) are in the coastal zone. The base of the web consists of macrophytes and other producers.

Algal epiphytes on vascular plants may account for a significant portion of littoral productivity (Wetzel 1975). Food for subsequent parts of the littoral web includes allochthonous organic matter, as well as organic matter produced in the littoral zone itself. The consumer populations (herbivores and carnivores) are dominated by many different kinds of arthropods (especially insects and crustaceans) and fishes. The heterotrophic bacteria and fungi occupy a central position in the littoral food web in that feces, dead organisms, and dissolved organic matter from various sources ultimately serve as a food source for these decomposers, which, in turn, may be ingested by consumers.

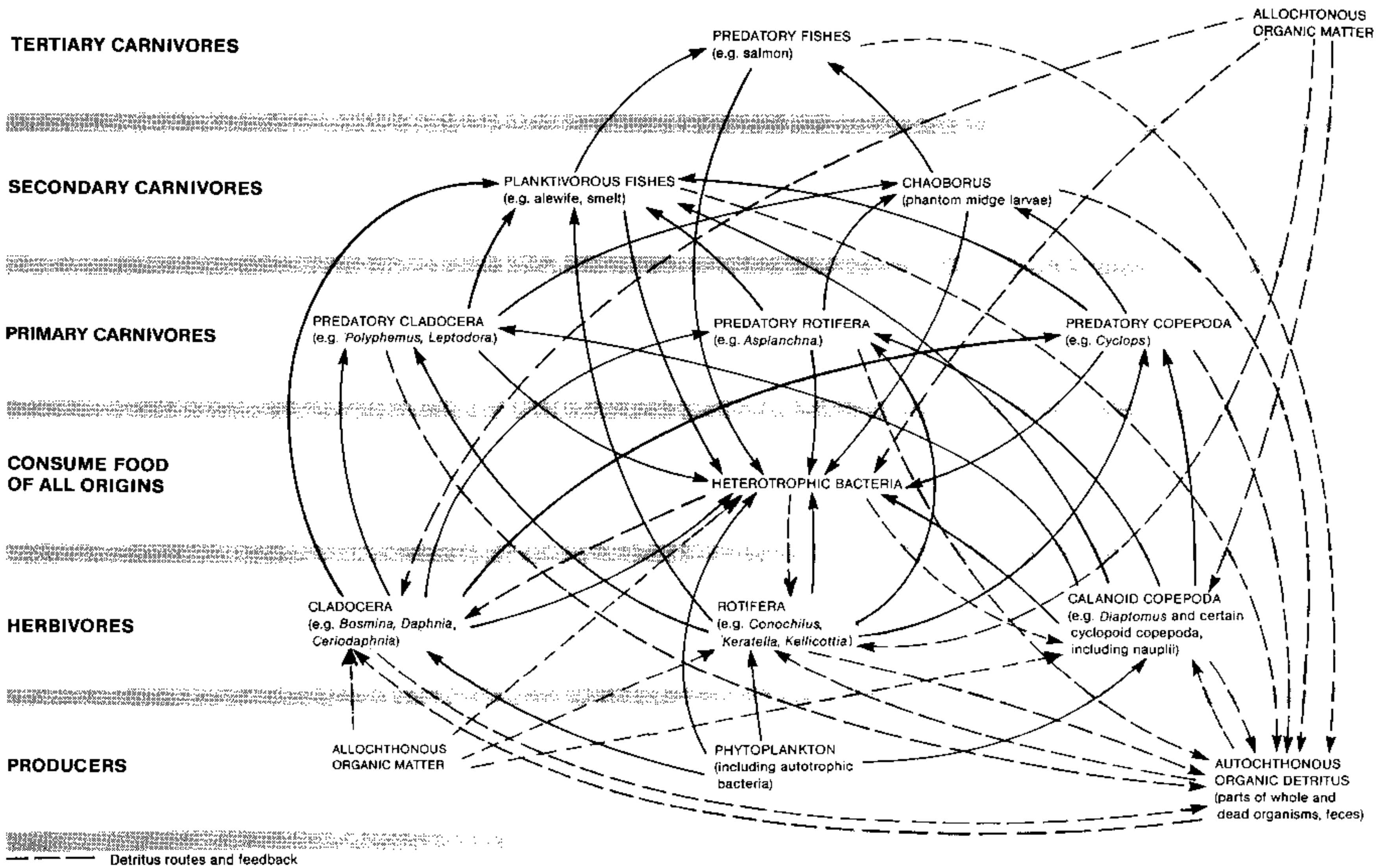


Figure 7-7. Generalized pelagial plankton food web for a Maine lake (based on Davis et al. 1978a; and Wetzel 1975).

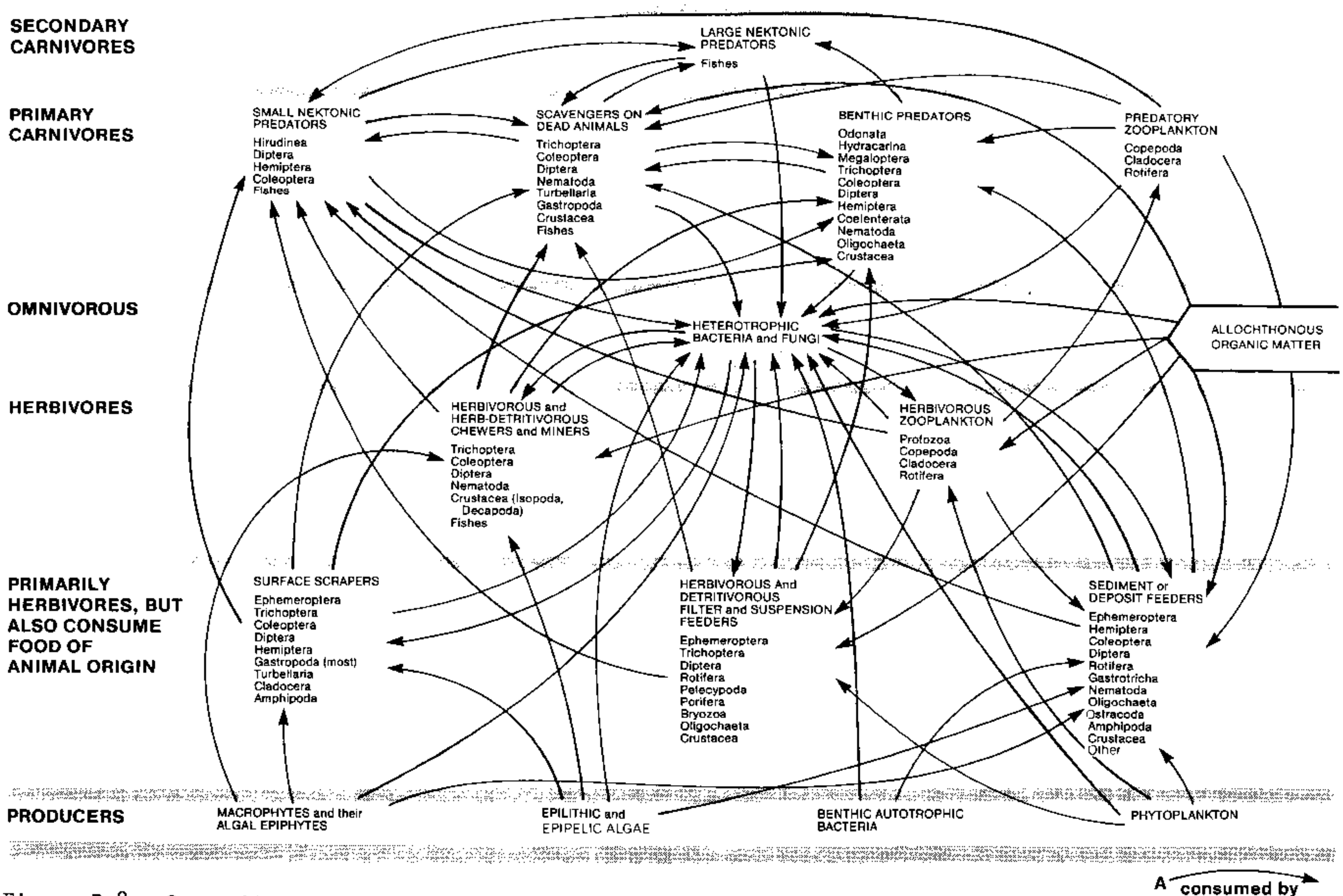


Figure 7-8. Generalized food web for the littoral zone of a lake, based on Cummins (1973), Pennak (1953), Wetzel (1975), and R.B. Davis (unpublished). Only certain species of those taxonomic groups listed would be present.

Most coastal zone lakes have extensive shallows with abundant growth of macrophytes. However, the abundance of macrophytes and associated animal life is greately reduced in the more oligotrophic Maine lakes (e.g., Jordan Pond in region 5), which often have rocky and gravelly bottoms in their shallow areas. The diversity of invertebrates (as shown in figure 7-7) is much greater in littoral zones (especially those associated with macrophytes) than in pelagial zones.

Lake food webs are closely integrated with lands or waters adjacent to lake systems. Food-chain energy and materials are lost by lakes in the emergence of insects and the departure of vertebrates that temporarily occupy the lake, and much food energy is gained from the influx of organic matter from terrestrial ecosystems. Terrestrial and wetland vertebrates (e.g., swallows, mink, and some waterfowl) may obtain much of their food from lakes and associated wetlands.

LACUSTRINE SUCCESSION

Lake basins gradually become shallow through accumulation of biotic (plant and animal remains) and abiotic (mineral) sediments. The accumulation of sediments is often accompanied by the encroachment of palustrine areas on the original basin. Eventually, lacustrine systems pass through the process of palustrine succession (see chapter 8, "The Palustrine System," page 8-6).

LAND USE

Landcover maps published by the Maine State Planning Office (1977) were used to identify land use practices adjacent to the lakes named on U.S. Geological Survey maps. The land-use survey included all lands within 0.5 km of the shorelines.

A large proportion of the area surrounding the named lakes and ponds in the coastal zone is dominated by forests. They give stability to the physical and biological characteristics of lakes and contribute significantly to lake energy cycles.

Recreational and Municipal Use

Except among some of the larger lakes in the coastal zone, recreational opportunities are limited largely to shoreline residents; consequently, few are managed in the public interest. Recreational uses include swimming, boating, fishing, picnicking, camping, hunting, and golf. Parks, campgrounds, playing fields, and playgrounds are associated with only 9% (about 15% in regions 3 and 4) of the lakes named in USGS maps, according to the Maine State Planning Office (1977). Swimming beaches exist on only 4% of the lakes, and marinas, boat harbors, or docks on only 9% of the lakes.

Summer cottages occupy much of the shoreline on a large percentage of the coastal zone lakes. Although lakes of 10 acres (4 ha) and larger are considered public waters in Maine, only a small percentage of the lakes have public access. Public access to coastal zone lakes is greatest in Acadia National Park.

Twenty seven lakes in the coastal zone are used as municipal water supplies. Waters derived from these lakes are routinely sampled for water quality by the Maine Department of Human Services and records are kept on file in Augusta. Water from Craig Pond and Green Lake is used in Atlantic salmon hatcheries.

Dams and Water Control Devices

Dams and water control devices, common to the larger lakes of coastal Maine, have had a significant effect on lakes and streams, yet few of these effects have been studied or evaluated. These dams serve, or once served, to stabilize water levels for ice production, for operating grain mills, and for power production. Hydroelectric dams, or dams at lake outlets that control flow for downstream hydroelectric facilities or for other purposes, can affect lakes by periodically altering water levels and downstream flows. Biota and fish-spawning areas in the littoral zone are especially affected. Relatively serious water level problems exist at present at Branch Lake in region 5, and Alamoosook and Silver Lakes and Toddy Pond in region 4. Some of the dams on coastal zone lakes have fishways to facilitate the passage of fish to upstream areas. Numerous dams have fallen into disrepair, because the original purposes of the dams no longer exist and laws are inadequate to enforce maintenance or removal. These dams are matters of State and local controversy. Waterflow control agencies, boaters, fishermen, and shoreline cottage owners have different opinions on desired water levels at most dams.

LAKE MANAGEMENT and FISHERIES

According to the Maine State Planning Office (1977), 67% of the coastal zone lakes are in "lake management capability category A," covering lakes "extremely vulnerable to water-quality degradation" from shoreland development. All but one of the lakes not in category A are in categories B and C; that is, capable of supporting without degradation "light intensity" development (16% of the lakes) or "medium intensity" development (16% of the lakes), respectively. Lakes and water bodies are also classified into categories based on maximum acceptable levels of pollutants (e.g., coliform bacteria). The criteria for the State Water Quality Classification scheme are presented in chapter 3, appendix B. Ninety-six percent of the coastal zone lakes are placed in categories A (12%) and B1 (84%). The water quality permitted by Maine law is acceptable for recreational purposes, including water contact recreation.

At present, at least five State agencies administer laws and regulations that directly affect lakes in the coastal zone. These agencies are the departments of Environmental Protection, Inland Fisheries and Wildlife, Human Services (Division of Health Engineering), and Agriculture (Abandoned Dams Act), and the Land Use Regulation Commission. Activities of several other State agencies indirectly affect lakes (e.g., the Department of Transportation, and the Bureau of Forestry). The U.S. Fish and Wildlife Service and the National Park Service have jurisdiction over lakes in Moosehorn National Wildlife Refuge and Acadia National Park, respectively.

Fish and wildlife in or near most of Maine's coastal freshwater lakes are managed largely by regulatory controls. Most fishing controls relate to seasons, size, or bag and creel limits, and other special considerations. These regulations are meant to help control populations, or rate of cropping, rather than protect the environment. Exceptions are water supply lakes, which are usually managed to maintain clean water, and wildlife management areas and parks, which attempt to maintain high quality environments, plant and animal populations, and high aesthetic values.

Appendix table 3 lists the named lakes in each region and other information on each lake, including fishery appraisals; known existence of dams (data incomplete), fishways, and screens; lake reclamation; stocking records; and the occurrence of aquatic pesticides, hydrogen sulfide, siltation, and water level problems.

Although coastal zone lakes generally support good sport fishing, commercial fishing is restricted to the collection of immature eels (elvers). Most lakes support both coldwater and warmwater fishing but the trend is for warmwater species to dominate the western regions and for coldwater fishes to dominate the eastern regions (see "Biota" above).

Little has been documented on how coastal zone lakes are managed by private landowners. Some public lakes are managed by the Maine Department of Inland Fisheries and Wildlife by stocking lakes with fish, principally sport fish. In the last several decades fish have been stocked in 109 lakes (some are repeated stockings) as determined from data in appendix table 3. Most of the plantings (74%) were in regions 4 to 6, and 43% were in region 5. More than half of the plantings were brook trout and Atlantic salmon, which were planted largely in the deep, cold lakes of regions 5 and 6.

From 1955 to 1973, nine lakes in the coastal zone were reclaimed by killing the fish with chemicals. Of the nine lakes, two were reclaimed in each of regions 4 and 6, and five were reclaimed in region 5 (appendix table 3). The lakes were relatively small, 10 to 232 acres (4 to 94 ha), and all were stocked with brook trout.

RESEARCH NEEDS

More detailed information on ecology, plant communities, fish and wildlife, and fishing and hunting on public lakes in the coastal zone is needed. Present data on lake water levels and downstream temperatures and flow are insufficient. More data are needed to establish an ecologically sound basis for removing or modifying abandoned or nonfunctional dams, when applicable, and for controlling water levels and discharges of functional dams, in order to improve fish and wildlife habitat and the environment as a whole.

Since lake watersheds in coastal Maine are principally forested, additional information is needed on how such operations as clearcutting and insect control affect silt, nutrient and toxic runoff, and lake productivity and biotic composition. Cause and effect studies would assist in planning and managing lakes and forests as integral parts of the coastal ecosystem.

Data are needed, also, to better classify lakes on the basis of water temperature, depth, light penetration, watershed boundaries and flow patterns, and productivity, in order to better determine management options and priorities for habitat protection and for fishery management policies.

Monitoring studies on the chemical, physical, and biological components of several representative lakes in each region would be beneficial for establishing baseline data, against which current differences and future changes can be measured.

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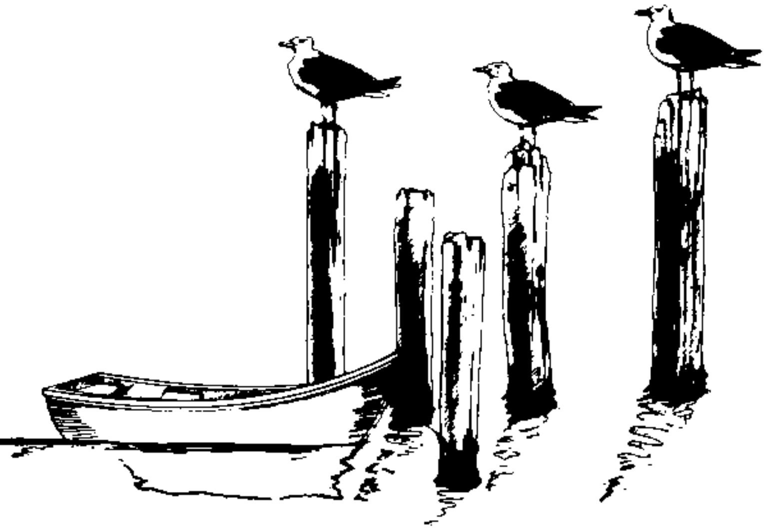
Chapter 8 The Palustrine System

Author: Stewart Fefer



The coastal zone of Maine has many types of freshwater vegetated wetlands and these comprise most of the palustrine system. Major types are bogs, marshes, wooded swamps, and small, shallow, permanent, or intermittent ponds. Most palustrine wetlands are discrete units; often they are near or connected to lakes, river channels or estuaries, or on river flood plains and slopes; some are islands of shallow areas in lakes or rivers (Cowardin et al. 1979), where vegetation persists throughout the year. The palustrine wetlands of the characterization area constitute an area of approximately 189,702 acres (75,881 ha) or about 9% of the total land and freshwater area. Palustrine wetlands are the dominant wetland type in coastal Maine comprising 34% of the aquatic system according to preliminary National Wetlands Inventory (NWI) data. Most palustrine wetlands are privately owned and have limited public access.

Palustrine areas are valuable to the ecology of coastal Maine partly because their hydrological characteristics aid in controlling floods, recharging groundwater supplies, and maintaining minimum stream flows. The accumulation and export of energy and nutrients by palustrine areas can have profound effects on neighboring habitats. Many species of fish and wildlife depend on wetlands during certain phases of their life cycles. Certain bogs in coastal Maine are unique in that they are not found in such abundance elsewhere on the U.S. Atlantic coast. Palustrine wetlands also have recreational, educational, aesthetic, and economic value. The impact of human activities on palustrine areas is often destructive.

The palustrine wetland classification system developed by Davis (1906; table 8-1) is generally applicable to the coast of Maine. It illustrates the complexity of palustrine wetlands. The NWI classifies palustrine wetlands according to standardized definitions of palustrine classes (habitat types). This method of classification results in a hierarchical system based upon dominant vegetative life forms (figure 8-1). Marshes and bogs are the two major types of palustrine wetlands in coastal Maine. This chapter details the distribution of palustrine wetlands in coastal Maine and describes their components and functions. The specific locations of palustrine wetlands in coastal Maine are detailed in atlas map 1. Common names of species are used except where accepted common names do not exist. Taxonomic names of all species mentioned are given in the appendix to chapter 1.

SOURCES OF AND COMPILATION OF DATA

The data sources used for characterizing the palustrine system include pertinent scientific literature, unpublished theses and reports, personal communications, and preliminary results of the NWI of the U.S. Fish and Wildlife Service (FWS). Information on the location and extent of wetlands mapped by the NWI project has been incorporated. NWI has mapped wetland units at a minimum resolution of about 3 to 5 acres (1 to 2 ha; personal communication from R. W. Tiner, Jr., U.S. Fish and Wildlife Service, Newton Corner, MA, September, 1978). Thus, palustrine areas smaller than 3 acres (1 ha) generally were not mapped. A particular palustrine wetland may contain more than one palustrine class and a particular palustrine class may contain areas <3 acres (1 ha) of other palustrine classes. For example, an area mapped as a 5 acre (2 ha) scrub/shrub wetland may consist of an area of open water surrounded by a floating mat of emergent vegetation mixed with hummocks of moss/lichen vegetation, with the general scrub/shrub cover intergrading occasionally into forested wetlands. If each of these habitat types (scrub/shrub, open water, emergent, forested) were 3 to 5 acres (1 to 2 ha) or larger, they would be mapped as distinct units. This complexity exists primarily because of small-scale variations in abiotic factors affecting palustrine areas. In combination with phenomena of plant ecology such as competition and succession, these small-scale variations in abiotic factors often result in several palustrine classes comprising the same wetland (figure 8-2). These classes may intergrade into one another, also, adding to the difficulty of precise classification. The NWI provides the user with the most detailed data to date on the distribution of wetlands in the Maine coastal zone. These data provide a baseline to which the future status of palustrine wetland habitats can be compared.

Twelve palustrine classes (and mixed classes) were identified by NWI (figure 8-1 and atlas map 1): aquatic bed, unconsolidated bottom, forested wetland, forested scrub/shrub wetland, forested emergent wetland, forested/open water wetland, scrub/shrub wetland, scrub/shrub emergent wetland, scrub/shrub/open water wetland, emergent wetland, emergent/open water wetland, and open water wetland. Mixing of wetland classes occurred when 30% of the area was covered by the upper canopy of the dominant vegetation. Palustrine flats and moss/lichen wetlands occur in the coastal zone but these areas are overshadowed by higher canopy vegetation or are below the size resolution for mapping. Palustrine classes of rock bottom, unconsolidated bottom, and aquatic bed have been mapped mostly as open water (atlas map 1), although a few areas have been designated as unconsolidated bottom and aquatic bed.

Most bogs are classified as forested and scrub/shrub wetland. Relatively few scientific studies have been made on the ecology of palustrine areas in coastal Maine. The shortage of useful data is sufficient to require a review of research needs.

Table 8-1. Systems for the Classification of Palustrine Areas[a]

Wetlands Classified According To the Form of The Land Surface Upon Which They Have Become Established
I. Depressed surfaces or hollows:
A. Lake basins of the tarn type
B. Shallow lake basins of the ordinary type
C. Hollows not permanently filled with water
D. Hollows in sand dunes
E. Hollows formed by dams of various sorts
II. Surfaces not hollowed out:
A. Poorly drained till plains
B. Broad divides
C. Floors of glacial drainage valleys
D. Lake and stream terraces
E. Deltas of streams
F. Slopes over which seepage spring waters flow
G. Northern bogs in which peat forms on slopes ("climbing bogs") often called raised bogs

Wetlands Classified According To the Manner In Which Their Peat Deposits Have Developed
I. Those built up by successive generations of plants, starting from what is now the bottom of the peat
II. Those which have been formed by growth at the sides or at the top of the basin or both:
A. Inwash of dead and decaying vegetation from the shores into the deeper parts of the lake basin
B. Drifting of such materials from tributary streams
C. Vegetation may grow out from shores to form floating mats, which ultimately cover entire water surface
D. Floating, rootless plants which may develop abundantly at or near water surface

[a]Adapted from Davis 1906.

(Continued)

Table 8-1. (Concluded)

Wetlands Classified According to Dominant Vegetative Cover	
I.	Elm/red maple and black ash swamps
II.	Tamarack swamps and bogs
III.	Cedar (arbor-vitae) swamps or bogs
IV.	Spruce swamps or bogs
V.	Willow and alder swamps
VI.	Heath (blueberry, cranberry, and *Chamaedaphne*) swamps, marshes, or bogs
VII.	Grass and sedge marshes and bogs
VIII.	Rush marshes (cattail and bulrush marshes)
IX.	Moss bogs (including sphagnum bogs)
X.	Open water vegetation

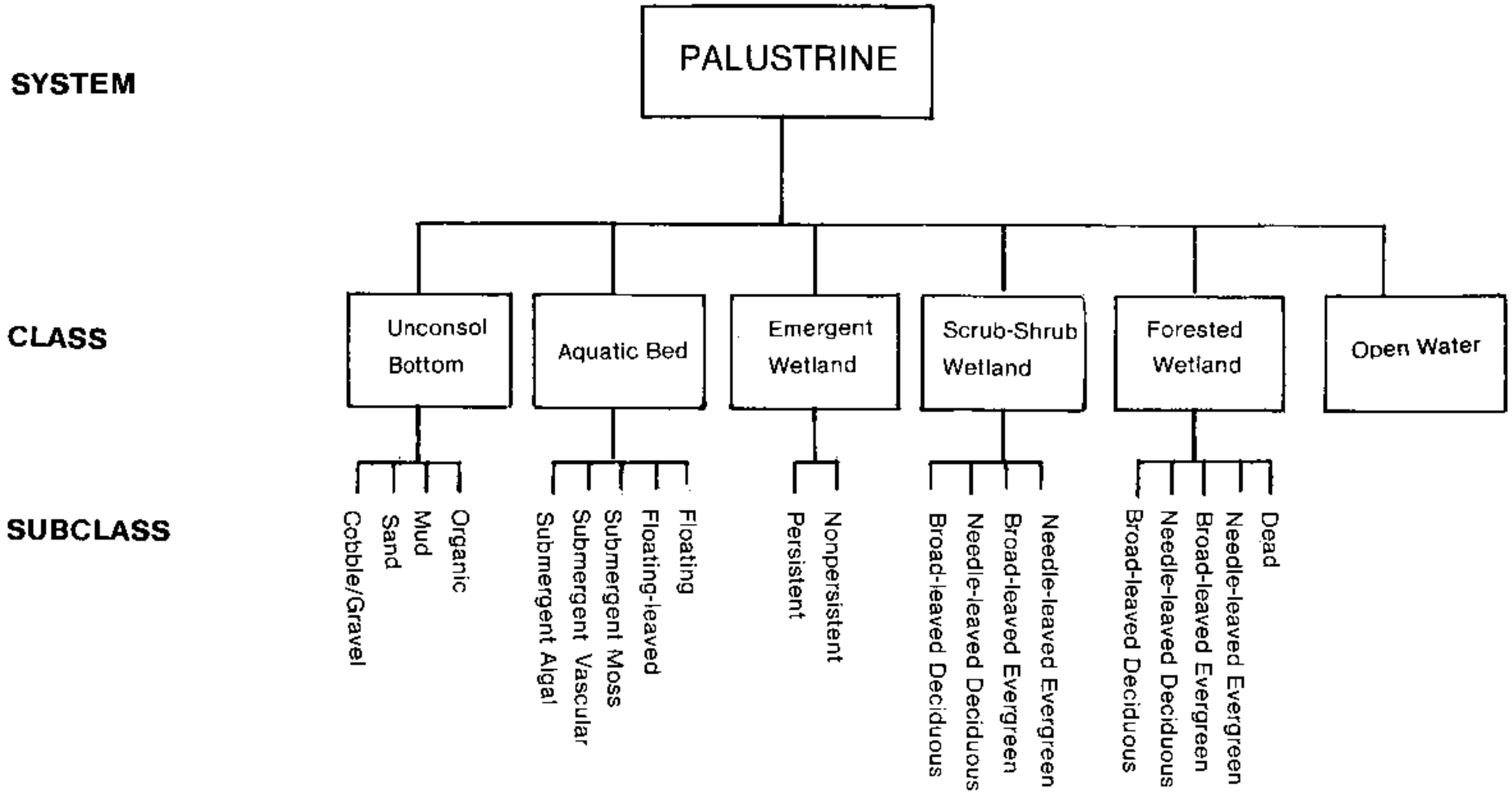


Figure 8-1. Hierarchical classification of the palustrine system in coastal Maine (Cowardin et al. 1977).

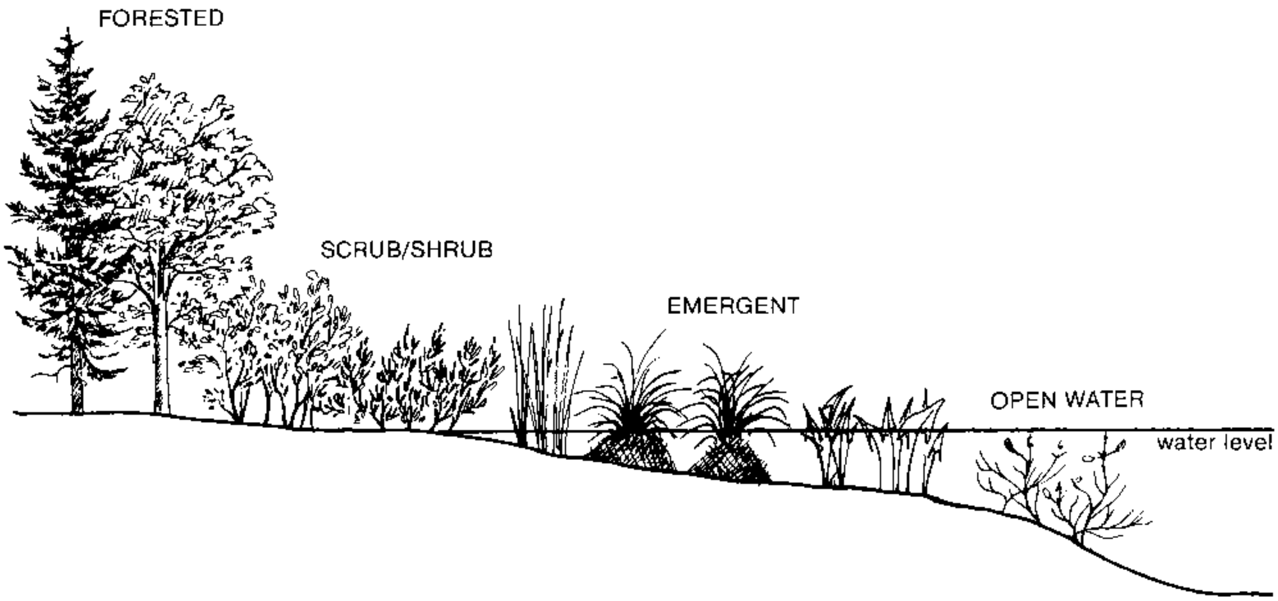


Figure 8-2. Distribution of palustrine wetland classes along a continuum from the upland environment to deep water.

DISTRIBUTION OF THE PALUSTRINE SYSTEM

Palustrine wetlands comprise a total area of approximately 189,702 acres (75,881 ha), or about 9% of the land and freshwater area of the coastal zone (table 8-2). A total of 13,650 palustrine wetland units have been identified by the NWI project in the characterization area (table 8-3). The number of palustrine wetland units in each of the six coastal regions (which vary greatly in size) ranges from 758 (region 1) to 3323 (region 4). Their total surface area by region ranges from 57,831 acres (23,132 ha) in region 6 to 7096 acres (2838 ha) in region 1 (table 8-2). The palustrine wetlands comprise between 4% and 13% of the total upland and freshwater area in regions 1 and 6, respectively. Forested wetlands represent 56% of the area of palustrine wetlands in the coastal zone. They are the most numerous, are generally the largest, and occupy the greatest area in each of the regions. Scrub/shrub wetlands comprise 25% of the palustrine wetlands in the coastal zone. Forested, scrub/shrub, and forested/scrub/shrub mixed wetlands together comprise more than 88% of the total area of palustrine wetlands in coastal Maine. As these classes in Maine are primarily bogs, the figures reveal the prevalence of bogs in coastal Maine.

The distribution of palustrine wetland classes in each of the towns in coastal Maine is included in appendix A of chapter 2.

Table 8-2. Area (acres) and Percentage Contribution of Palustrine Classes in the Palustrine System for Each Region[a].

Region		Palustrine total	Emergent	Forested	Forested shrub	Scrub/shrub	Open water	Shrub emergent	Emergent open water	Forested emergent	Forested open water	Shrub open water	Unconsolidated bottom	Aquatic bed
1	Acres	7096	1113	3261	650	1458	362	201	25	19	5	2	--	--
	%[b]	100	16	46	9	21	5	3	<1	<1	<1	<1	--	--
2	Acres	24,134	1938	10,321	1941	7884	561	1481	7	3	--	--	--	--
	%	100	8	43	8	33	2	6	<1	<1	--	--	--	--
3	Acres	19,349	891	11,320	1670	4436	418	614	--	--	--	--	--	--
	%	100	5	58	9	23	2	3	--	--	--	--	--	--
4	Acres	40,303	1719	22,768	4013	8165	1013	2360	13	141	39	8	52	12
	%	100	4	56	10	20	3	6	<1	<1	<1	<1	<1	<1
5	Acres	40,989	1634	20,301	4652	9596	575	3646	69	437	58	21	--	--
	%	100	4	50	11	23	1	9	<1	1	<1	<1	--	--
6	Acres	57,831	1688	38,737	802	15,737	520	269	--	33	--	--	--	45
	%	100	3	67	1	27	<1	<1	--	<1	--	--	--	<1
Characterization Area Total		189,702	8983	106,708	13,728	47,276	3449	8771	114	633	102	31	52	57
		100	5	56	7	25	2	5	<1	<1	<1	<1	<1	<1

[a]Preliminary NWI data 1979.
[b]Percent of region occupied.

Table 8-3. Number of Units of Palustrine Classes, Percentage Contribution and Average Size (acres) in Coastal Maine[a]

Region		Palustrine total	Emergent	Forested	Forested shrub	Scrub/shrub	Open water	Shrub emergent	Emergent open water	Forested emergent	Forested open water	Shrub open water	Unconsolidated bottom	Aquatic bed
1	# of units	758	107	262	42	170	147	19	6	3	1	1	–	–
	% of units	100	14	36	6	21	20	3	<1	<1	1	<1	–	–
	Avg. size	7	8	12	16	9	3	11	5	6	5	2	–	–
2	# of units	2424	233	855	168	785	282	96	2	1	2	–	–	–
	% of units	100	10	35	7	32	12	4	<1	<1	<1	–	–	–
	Avg. size	10	8	12	11	10	2	15	3	3	20	–	–	–
3	# of units	1848	111	768	178	538	217	36	–	–	–	–	–	–
	% of units	100	6	42	10	29	12	1	–	–	–	–	–	–
	Avg. size	11	8	15	9	9	2	17	–	–	–	–	–	–
4	# of units	3323	469	1309	299	786	307	127	2	14	5	3	1	1
	% of units	100	14	39	9	24	9	4	<1	<1	<1	<1	<1	<1
	Avg. size	12	4	17	13	10	4	19	7	10	8	3	52	12
5	# of units	2584	117	1150	324	526	189	188	9	60	15	6	–	–
	% of units	100	5	45	13	20	7	7	<1	2	1	<1	–	–
	Avg. size	16	14	18	14	18	3	19	8	7	4	4	–	–
6	# of units	2713	156	1408	75	944	109	18	–	3	–	–	–	–
	% of units	100	6	52	3	35	4	<1	–	<1	–	–	–	–
	Avg. size	21	11	28	11	17	5	15	–	11	–	–	–	–
Characterization Area, Total		13,650	1193	5752	1086	3749	1251	484	19	81	23	10	1	1
		100	9	42	8	27	9	4	<1	<1	<1	<1	<1	<1
		14	8	19	13	13	3	18	6	8	4	3	52	12

[a]Preliminary NWI data 1979.

CHARACTERISTICS OF PALUSTRINE WETLANDS

Wetland Development

Palustrine wetlands develop (1) where water tables are higher than the surrounding topography, resulting in hydric (moist) soils, (2) where lake basins have become shallow through accumulation of biotic (plant and animal remains) and abiotic (mineral) sediments, and (3) where beaver have blocked drainage. Palustrine wetlands are not necessarily permanent features of the landscape. Over a period of hundreds of thousands of years palustrine wetlands may occupy a site that develops from open water to an emergent wetland to scrub/shrub wetland to forested wetland to upland forest. This process is termed succession. The type of palustrine community (whether a marsh or bog) and the duration of each of the vegetation stages depend on prevailing abiotic conditions (below). Furthermore, all palustrine wetlands do not necessarily pass through the complete successional sequence. Certain factors (e.g., fire and beaver dams) may cause wetlands to regress to an earlier condition. Thus, a scrub-shrub wetland may be flooded by beaver resulting in conditions favoring an open water emergent wetland.

The patterns of palustrine succession outlined in figure 8-3 illustrate that marshes and bogs are the two basic sequences of seral (successional) stages occurring in coastal Maine freshwater wetlands. These types are classified by their dominant vegetative cover. Differences between these types are described in table 8-4 and in "Biota", below.

The development of a typical coastal Maine boglike palustrine wetland may begin with deposition of organic sediment from floating plant types (such as algae and pondweeds) over the inorganic clay bottom of a lake. This organic sediment eventually builds up the lake bottom to a depth where rooted plants (such as pond lilies and bulrushes) are capable of growing. The pond eventually is filled completely with sediment and the pond lilies and bulrushes are replaced by grasses, sedges, and sphagnum moss, which forms dense mats. At this stage the organic deposit builds up and out beyond the original limits of the unfilled water body. The water table also rises with the elevation of organic deposit, thus allowing further growth of the moss into domes and/or plateaus and allowing for a perched water table above the land surface margins of the bog. Figure 8-3 depicts these stages of bog development.

Marsh wetlands in coastal Maine develop similarly but usually do not form dense floating mats of vegetation; rather, vegetation is rooted into the mineral substrate. As organic matter accumulates it mixes with the mineral sediments. This gradually fills the basin from the bottom upwards resulting eventually in an upland forest system. Under natural conditions, the successional sequence may occur over a period of hundreds or thousands of years.

Physical Characteristics

No comparative data base, other than the size information discussed in the preceding section, is available on the physical characteristics of individual wetlands in coastal Maine. Data on temperature and transparency of individual wetlands are lacking. Certain physical characteristics of bog wetlands in Maine have been described by Cameron (1975). She recognized five basic types of peat deposits (figure 8-4) which are significant in commercial peat extraction.

Type 1 (figure 8-4) bogs occur in valleys occupied by streams. The stream flows over peat composed chiefly of decayed marsh and forest plants. One or more heath-covered domes of moss peat may extend along the stream. Groundwater enters the deposit as seepage along the valley walls above the basal clay deposit, and moves toward the stream and down the valley. Type 1 bogs may range in size from 30 to 320 acres (12 to 130 ha) and range in thickness from 7 to 21 feet (2.1 to 6.4 m).

Type 2 (figure 8-4) bogs form in a closed basin. Floating mats of moss peat extend over open water of the vestigial lake or pond. The vegetation cover is scrub/shrub surrounded by tall forest, grading inward to stunted trees and shrubs. Water enters the basin as rainfall or from seepage from basin walls. Most bogs of this type are found in sink holes in the limestone terrain of Aroostook County but several occur in Washington County in large kettle holes. Type 2 bogs are small (5 to 15 acres; 2 to 6 ha) and shallow (<12 ft; <3.8 m).

Type 3 (figure 8-4) bogs are plateau-like domes developed on gentle surfaces of sand, gravel, or clay. Surface drainage is diverted around the margins of the bog. Growth of the deposit is maintained by rainfall and groundwater that flows up through the sand and gravel deposit below the bog. The edge of the bog is invaded by trees from the sloping margins. Bogs of this type range widely in size and thickness. An example of this type is Runaway Pond Heath in region 6 (Washington County). Plateau bogs are found only near the coast in regions 5 and 6.

Type 4 (figure 8-4) are domed bogs that contain ponds arranged in concentric rings. Water gathers in pockets of undulating surfaces in the bog and the ponded depressions are made larger by oxidation of exposed peat. Bogs of this type are generally very large (1000 to 4000 acres; 400 to 1600 ha) and reach depths of up to 25 feet (7.6 m). The Great Heath in Cherryfield is an example of this type of bog.

Type 5 (figure 8-4) bogs, the most complex, are those in which domes of moss peat coalesce over divides that separate basins containing peat developed above and below the original pond surfaces. The divides are most likely areas of groundwater exchange between the deposit and the rock. The Meddybemps Heath is an example of this type of bog.

Peat bog stratigraphy. Cameron (1975) described the general stratigraphy of Maine coastal peat deposits. Physiographic forms reflect the stratigraphy of a peat deposit, and quality factors, especially ash content, reflect the deposit. For purposes of discussion, the deposit may be divided into two parts: (1) the part below the level of the original pond surface and (2) the part above that level. The basal zone (bottom) of Part 1 is clay and peaty clay containing more than 50% ash. Ash content in the overlying clayey peat ranges from >25% to <75%, depending on the pond environment. Algae and pond weeds living in clear water produce peat with low ash content; a clayey peat layer low in ash may have been produced in a pond obliterated by floating mats of marsh and moss vegetation, which continually sink and mix with pond sediments until the surface level of the original pond is reached.

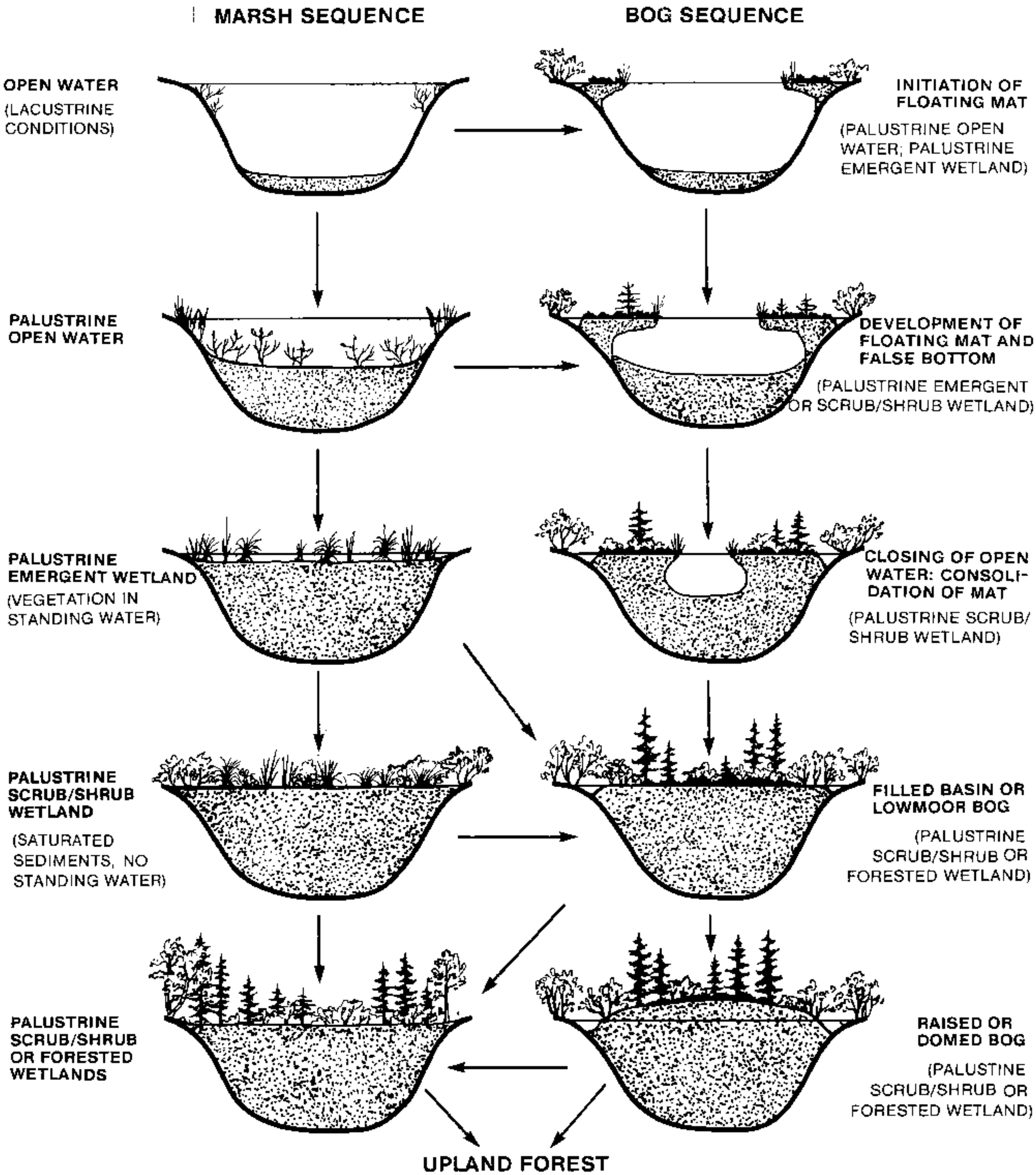


Figure 8-3. Two patterns of palustrine succession in coastal Maine (adapted from Wetzel 1975 and Dansereau and Segadas-Vianna 1952).

Table 8-4. The Contrasting Characteristics of Bog and Marsh [a]

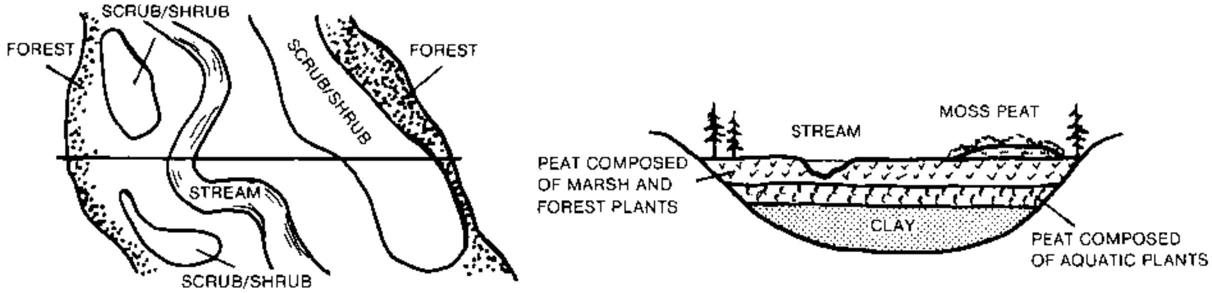
Bog	Marsh
Physiography	
Blocked drainage causes an indefinite accumulation of organic materials; a small quantity of mineral soil is introduced by seepage, inwash, and atmospheric agents.	Drainage pattern does not allow a considerable accumulation of organic materials; the shallow substratum and seepage permit a thorough mixture of organic and mineral sediments.
Drainage is further congested by the growth of a bog; several small bogs can unite and modify the drainage pattern over a fairly large expanse. This process is reversed only in the very late stage, when trees cover the area.	Drainage is gradually, if slowly, improved by the growth of swamp vegetation and the corresponding sedimentation.
Open water is invaded by a floating mat and pools are filled in from top as well as from bottom.	Open water is invaded mostly by non-floating vegetation and filling-in is from bottom upwards.
Physical Conditions	
Water table reaches the surface in the spring and is below the surface during the rest of the year. Often water level is just below the surface in the spring and considerably lower in midsummer.	Water table well above the surface in the spring and just at surface or slightly below it during the rest of the year.
Adjacent open water generally brownish (dystrophic).	Adjacent open water generally turbid, olive-green or dark green (eutrophic).
Substratum cohesive, resilient, can uphold considerable weight (e.g., man).	Substratum soft, will absorb heavy objects, will not resist pressure.
Substratum almost 100% organic and always in the form of peat; mineral content low.	Substratum has variable percentage of organic materials, usually not peat; mineral content high.
A false bottom forms in open water, owing to accumulation of colloids.	No false bottom.

[a] Dansereau and Segadas-Vianna 1952.

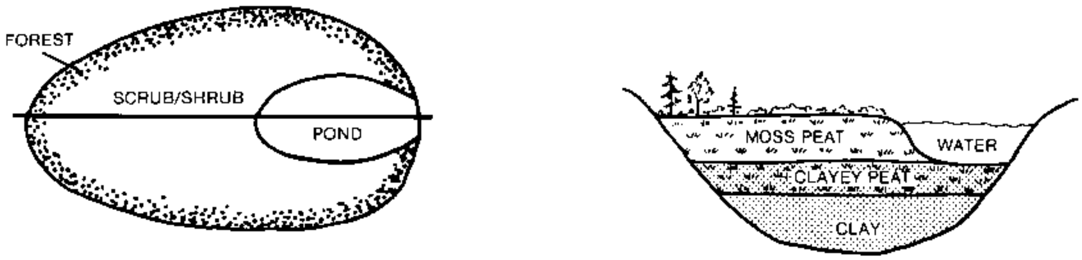
(Continued)

Table 8-4. (Concluded)

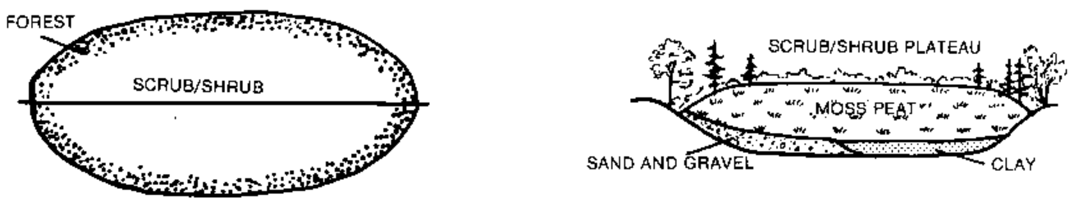
Bog	Marsh
	Chemical Conditions
Predominance of strongly acid reaction. Percentage of saturation low. Large quantity of colloids in suspension.	Acid or alkaline reaction. Percentage of oxygen saturation high. Small quantity of colloids in suspension.
Potassium and nitrogen deficient in soil (some nitrogen-fixing bacteria present).	Potassium and nitrogen sufficient.
	Vegetation
Presence (at some time) of a floating mat usually dominated by ericoid plants.	Mat, when present, composed of graminoid plants.
Physiognomic dominance of curvilinear contours: much-branched shrubs, cushionlike tufts of herbs and mosses, curved surface of raised bogs.	Physiognomic dominance of rectilinear contours: graminoid herbs, flat surface of soil.
On the whole, a bog is a large cushion.	On the whole, a swamp is a wet prarie.
Dominance of the ericaceous type in many of the pioneer stages.	Dominance of the graminoid type in the pioneer stages.
Dominance of needle-leaved types in the subclimax stages.	Dominance of broad-leaved types in the subclimax stages.
Vegetal cover continuous, uneven, forming cushions, eventually parklike.	Vegetal cover discontinuous, in tufts or isolated individuals, eventually thicketlike.
Mosses (mostly Sphagnum)always forming the lowest layer.	Mosses (at least Sphagnum) generally absent.
	Fauna
Animal life scarce, both in numbers of species and of individuals.	Animal life abundant. Both in species and individuals.



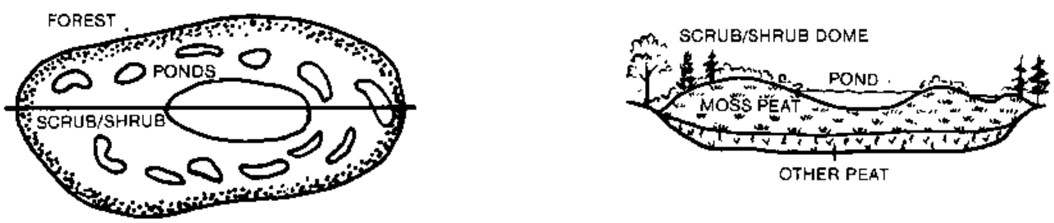
1) Valley occupied by stream.



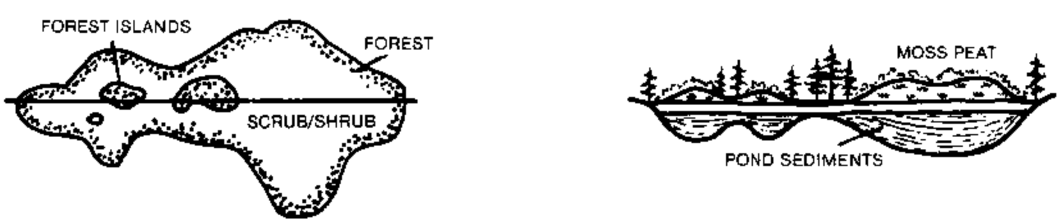
2) Closed basin. Remnant of the initial pond or may not be present.



3) Plateau-like dome on gentle surface of clay, sand or gravel.



4) Domes and ponds. Ponds are secondary, developing on moss peat.



5) Coalesced domes over deposit occupying several basins.

Figure 8-4. Five peat bog types recognized by Cameron (1975) as existing in coastal Maine.

The basal zone of Part 2 usually contains <25% ash, unless a period of oxidation and decay has interrupted plant growth, and consists of a variety of plant communities such as marshes, mosses, heaths, and perhaps forest growth. Because moss becomes the dominant plant type as the dome increases in height, ash content decreases to <2%, the percent of fibers that are 0.15 mm (0.016 inches) long increases to >67%, and water-holding capacity increases to several thousand percent. However, as soon as oxidation begins to destroy peat, a layer of humus develops at the surface, especially near the margin of the dome where oxygenated water moves most freely. As humus develops, ash content increases, fibers become shorter, water-holding capacity decreases, and forest invades the heath from the margin and migrates toward the center of the dome.

Chemical Characteristics

No specific comparative data base exists on the chemical parameters of palustrine wetlands in the characterization area. Specific conductance, alkalinity, and ion concentration in Maine wetlands are much lower than those in prairie potholes (Swanson et al. 1974, cited in Reinecke 1977) and are probably much lower than those in other temperate wetlands. Relatively nutrient poor, acidic waters are characteristic of bog wetlands. In areas of nutrient-rich soils (agricultural areas) and/or water, or in areas where nutrient-rich water flushes palustrine wetlands, nutrient levels are higher and vegetation is characteristic of marshes. This flushing occurs on a regular basis by riverine waters and irregularly by marine and estuarine waters (once or twice a year during storms).

ABIOTIC FACTORS AFFECTING PALUSTRINE SYSTEMS

The composition of any palustrine system depends upon a combination of abiotic conditions prevailing at its site. In general, Maine palustrine systems are relatively infertile compared to most temperate zone palustrine wetlands. Due to different abiotic conditions, certain palustrine systems have developed into marshes and others into bogs. Climatic, hydrologic, and geologic factors that affect palustrine wetlands are considered here. These factors work in combination and their combined effects usually cannot be separated. As palustrine and lacustrine systems are closely related, a review of the abiotic factors in the lacustrine system provides additional information (see chapter 7, "The Lacustrine System").

Climate

The climate of the characterization area and its gradients are discussed in chapter 2. The effects of climate on the palustrine system generally are similar to those on the lacustrine system (see chapter 7, "The Lacustrine System"). The relatively cold waters of the Maine coastal zone contribute to the formation of bogs. In combination with other abiotic factors cold waters restrict the activity and numbers of decomposer organisms. Thus, much of the organic matter formed in palustrine wetlands is not broken down for use by other organisms but is stored as peat.

Ice and frost action affect the palustrine system by breaking up peat mats and the accompanying flora. Climate also affects the growing season and floral composition of palustrine systems.

Hydrology

Hydrological factors affecting palustrine areas include:

1. Water chemistry;
2. Water flow and its characteristics of import, export, and retention time;
3. Water temperature;
4. Water level and its fluctuation extremes.

Water flow transports animals, organic matter, nutrients, and other chemical compounds through palustrine wetlands. Inflowing water can provide nutrients to organisms in palustrine areas and outflowing water exports food to organisms downstream. Where blocked drainage occurs in combination with other abiotic factors, organic matter may accumulate, resulting in the formation of peat, a characteristic of bogs in coastal Maine. Drainage is further congested by the growth of bogs.

As mentioned above, the low water temperature characteristic of coastal Maine contributes to the formation of bogs. Water levels vary in palustrine wetlands. The relationship of the water table to the wetland surface is one factor contributing to the type of wetland a basin develops (table 8-4).

Palustrine species are very vulnerable to fluctuations in water levels. In spring, for example, fluctuating water levels may affect the use of wetlands by waterfowl. Water that is too high at critical periods during the breeding season can result in lower waterfowl populations and lower production: (1) through direct losses when nests are flooded; and (2) indirectly, by making the environment less attractive to waterfowl (flooding food supplies and nests) and therefore less extensively used (Mendall 1958). When water levels decrease during the breeding season, terrestrial predators on waterfowl nests may gain access to nesting areas that would otherwise have been inaccessible.

Geology

Deglaciation 12,000 years ago modified the topography of the Maine coast and thereby altered drainage patterns, mainly through the deposition of glacial or glacially-derived sediments. In many areas previously well-drained surfaces were dammed by glacial deposits, or previously well-drained soils were stripped and replaced by relatively impervious surficial materials (lodgment till and marine silt-clay deposits). Palustrine wetlands developed behind moraines, in blind valleys, and in kettle depressions (figure 8-5) where water table levels were higher than the surrounding topography. Heeley and Motts (1976) found that most wetlands in Massachusetts are underlain by stratified drift, till, or bedrock. Similar substrates generally can be expected for wetlands on the Maine coast although marine clays are also prevalent.

The chemistry of runoff waters is dependent upon the character of bedrock and surficial deposits. Variations in concentrations of nutrients (phosphate, nitrates, potassium) in waters flowing into palustrine areas affect their productivity and species composition. The scarcity of biogeochemicals in watersheds of siliceous bedrock may result in wetlands of low productivity.

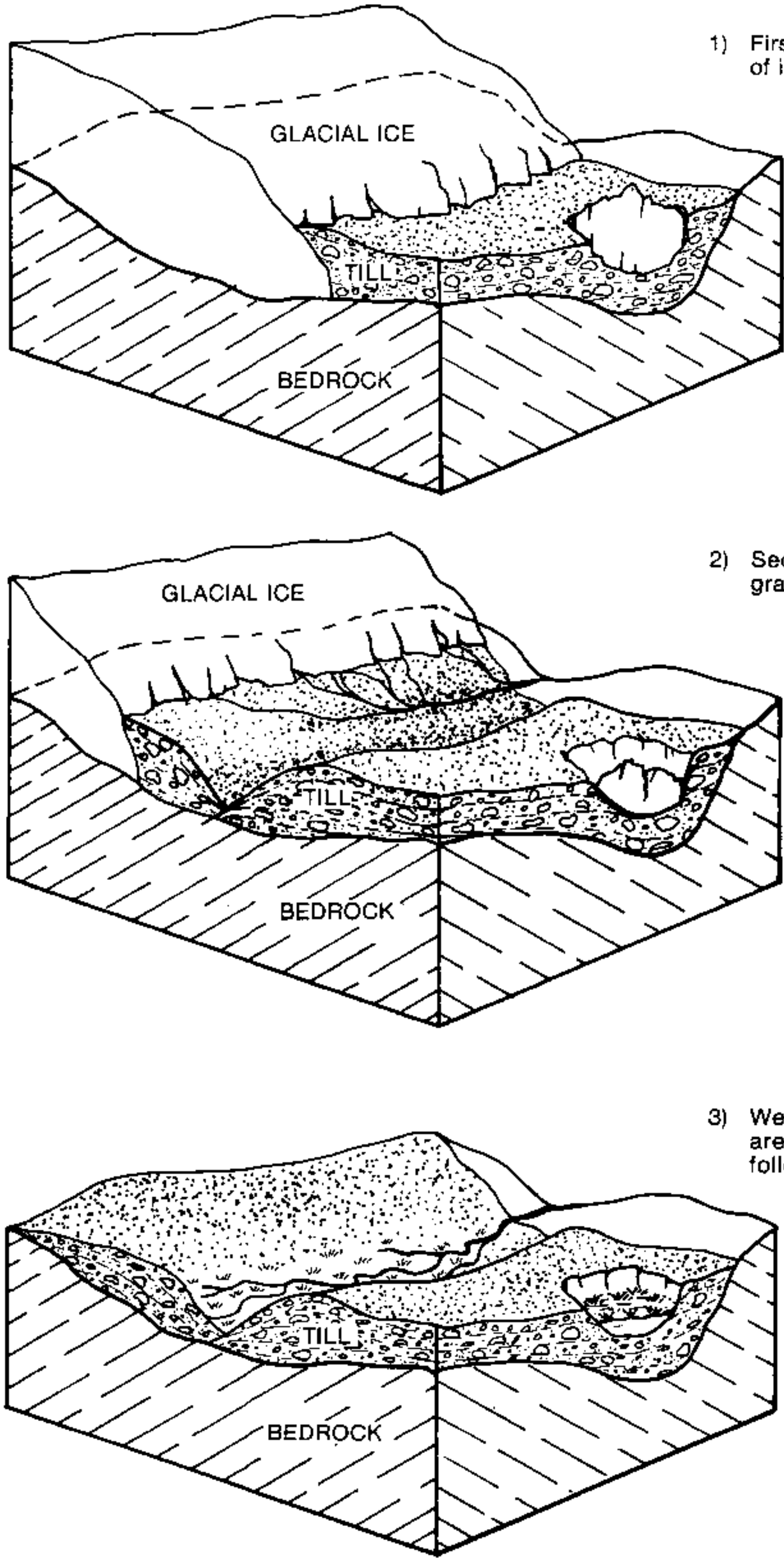


Figure 8-5. Development of palustrine wetlands on glacial terrain (adapted from Heeley and Motts 1976).

Variations in organic matter, mineral fractions, and waterlogging (saturation of sediments) determine palustrine soil types, which in turn determine plant species. At present there are no data available detailing soil types in palustrine wetlands in coastal Maine.

BIOGEOCHEMICAL CYCLES AND BUDGETS

Biogeochemicals (e.g., nitrogen, phophorus, potassium) are those substances derived from the earth's crust, hydrosphere, and atmosphere that are essential to life processes. Because the supply of biogeochemicals is limited sometimes, the availability of these substances to organisms is dependent upon continuous cycling. Low availability of biogeochemicals (nutrient limitation) usually results in low populations of organisms and low biological productivity.

Peat, which is formed in many coastal Maine palustrine wetlands, has an exceptionally high water absorption and ion exchange capacity (Moore and Bellamy 1974). Biogeochemical ions from palustrine waters are bound to the peat and held strongly by physiochemical forces. These ions, once bound, are not easily leached. As peat formation progresses the bound ions may be buried below the reach of plant roots and become fossilized.

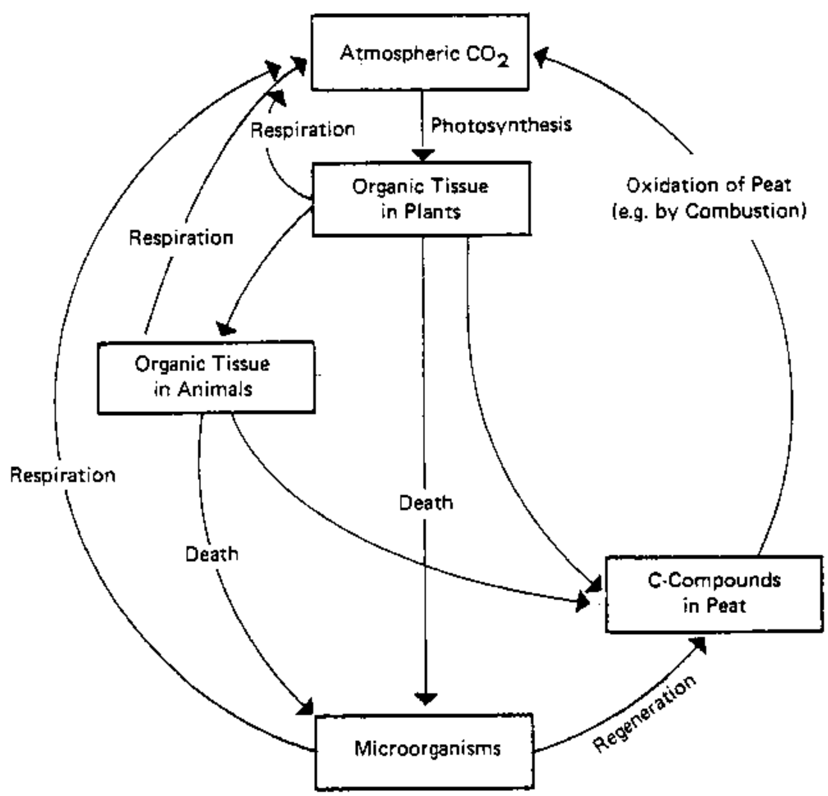


Figure 8-6. Cycling of carbon in a palustrine wetland (Moore and Bellamy 1974).

Some biogeochemicals, particularly carbon, may be present in abundance and readily available from the environment. Storage of these elements in peat does not seriously affect their availability as new sources are continually formed. Figure 8-6 illustrates the cycling of carbon in a palustrine wetland. The supply of other biogeochemicals may be affected significantly when they are incorporated into peat, depending upon:

1. How much of the element is locked up in a given quantity of peat;
2. How fast the peat is being formed;
3. The rate at which a new supply of the element enters the system (Moore and Bellamy 1974).

Shortages of phosphorus and nitrogen for plant nutrition are likely to develop in palustrine areas where rapid peat deposition occurs. These areas are isolated from nutrient-bearing groundwaters by the peat "barrier." Plants growing on peat deposits are largely dependent upon rainwater (or sources such as dust and captured insects) for nutrients; consequently their growth is limited. The nitrogen budget is of particular interest in the study of palustrine biogeochemicals. Elemental nitrogen is abundant in the atmosphere but plants require a reduced form of nitrogen, such as nitrates. This reduction of nitrogen is accomplished chiefly through the action of nitrogen-fixing bacteria. In many palustrine areas of coastal Maine nitrogen-fixing bacteria, which live symbiotically with the bog myrtle (Myrica gale) and speckled alder (Alnus rugosa), seem to be important to the nutrient budget (Sculthorpe 1967). Conditions of rapid peat deposition and a deep peat substrate do not favor the growth of these two plants and the supply of nitrogen is further limited. A model of phosphorus and nitrogen flow in a palustrine wetland is presented in figure 8-7. Many plants commonly found in bogs are adapted to the acid, low nutrient environment.

In summary, the slow rate of decomposition in palustrine wetlands of coastal Maine results in nutrients being bound in peat. Thus, nutrient cycling is limited, which results in deficiencies in already nutrient-poor ecosystems. The slow-moving waters of many palustrine areas render their biogeochemical cycles closed compared to those of lotic (swiftly moving) waters. In Maine wetlands the greatest period of nutrient exchange occurs during the spring, when palustrine systems usually are flushed by high water.

BIOTA

The organisms inhabiting palustrine areas have evolved over billions of years and each is fitted to the its available supply of biogeochemicals, and the flow of energy within ecosystems. The biota of palustrine systems can be divided into three groups: the producers, the consumers, and the decomposers. The producers include most plants and certain forms of bacteria that synthesize organic matter from inorganic materials. The consumers are animals (e.g., beaver) that feed on producers (living or in some stage of decomposition) and/or other consumers. The decomposers (largely bacteria and fungi) transform dead organic matter into recyclable constituents. Data on the biotic component of palustrine systems in the Maine coastal zone are sparse. A review of information concerning the composition and function of palustrine trophic levels follows.

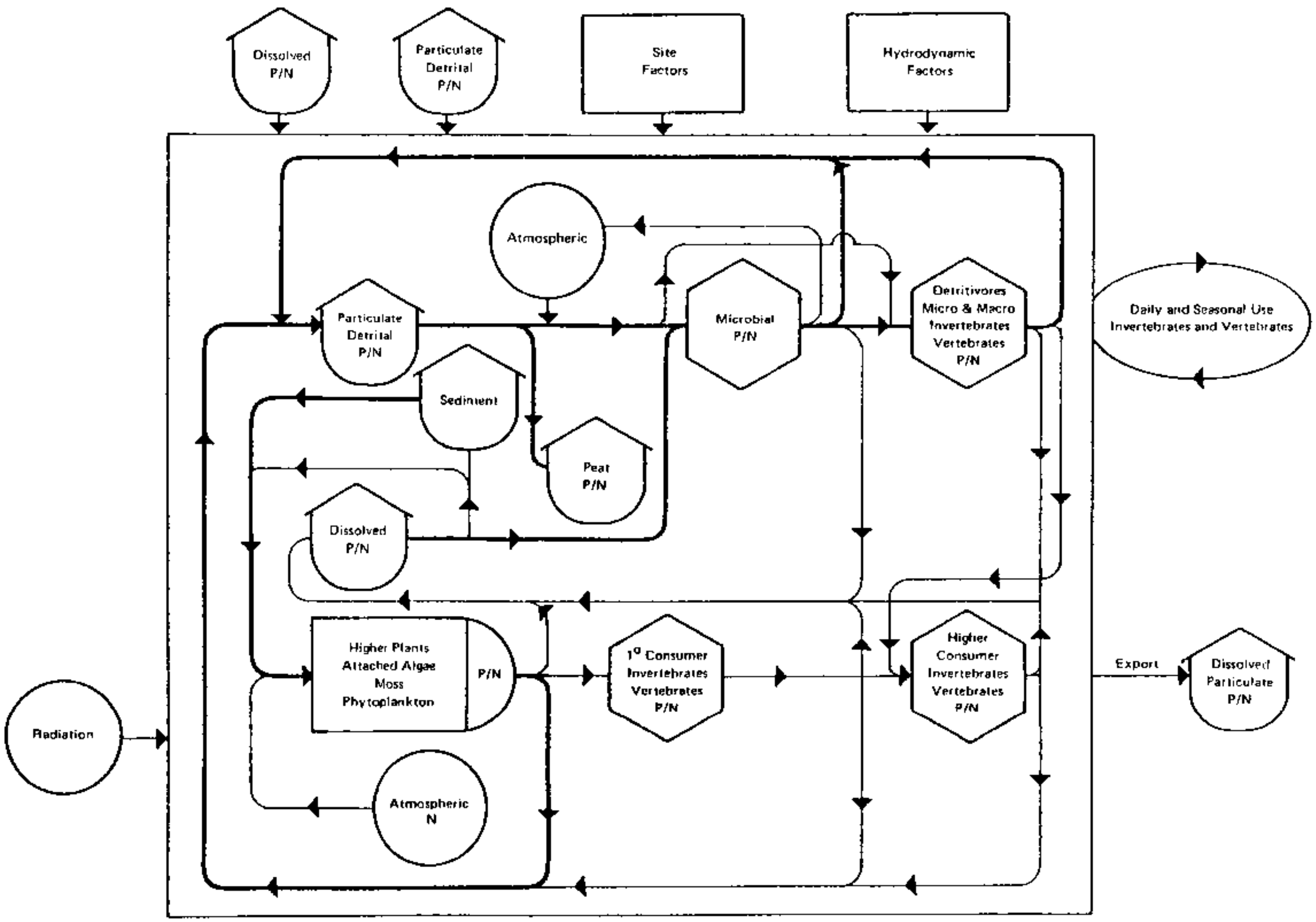


Figure 8-7. Model of phosphorus and nitrogen flow in the palustrine system.

Producers

Plant species characteristic of palustrine classes in coastal Maine are listed by vegetation type (table 8-5). Palustrine classes are illustrated in figure 8-2. It should be noted that emergent perennials growing from substrate usually covered with shallow water are typical of marsh wetlands, whereas emergent perennials forming dense mats are characteristic of bogs.

A complete list of vascular plant species likely to occur in palustrine areas is given in appendix A. The species composition and distribution of algae, mosses, and other nonvascular plants occurring in palustrine areas have not been studied adequately, nor have the bacterial producers.

Among the plants characteristic of bogs in coastal Maine are some species of special interest. Sphagnum moss species grow well when nutrient supply is low because they have an ability to accumulate ions necessary for growth from the water. Some plant species supplement their mineral intake by trapping and digesting insects. Carnivorous plants in the Maine coastal zone include the pitcher plant (Sarracenia purpurea), sundew (Drosera spp.), and bladderwort (Utricularia spp.).

Plants supply the food energy necessary for the existence of other palustrine organisms (see "Food Webs" below). Vegetation types (which are grouped into classes comprising the palustrine system) differ greatly in their annual production of organic matter. No data are available on the productivity of palustrine wetlands in coastal Maine. That information at present must be inferred from data on similar vegetation types in other areas. The primary productivity reported for bogs (scrub/shrub, moss/lichen, and certain emergent wetlands) varies greatly (table 8-6). The expected range of productivity for bog systems in coastal Maine is 300 to 1900 g/m^2/year dry weight (Moore and Bellamy 1974). A major factor responsible for the low productivities of bogs is the incorporation of available chemicals into peat making them unavailable for plant productivity (see "Energy Flow" below). Emergent wetlands that have developed as marshes are probably the most productive palustrine vegetation type occurring in the characterization area. Forested wetlands are highly variable in productivity, depending on species composition, but in general can be expected to be lower in productivity than terrestrial forests. Trees of forested wetlands do not grow as well as trees of the same species in terrestrial environments. Curtis (1944 and 1946) found this true of northern white cedar in Maine. Ahlgren and Hansen (1957) found that conifers in northern Minnesota were less flood tolerant than deciduous trees. The productivity of phytoplankton and submersed macrophytes contribute to the productivity of palustrine open waters. Productivities ranging from 200 to 1600 g/m^2/year may be expected for the palustrine open water class. As a whole, palustrine wetlands compare favorably with the productivity of temperate forests.

Plants have important functions in addition to food production. They are often used by animals to build nests and dens. Forested wetlands provide nesting sites for many species of hole-nesting birds (e.g., wood ducks, hooded mergansers, woodpeckers).

Table 8-5. Common Plants Characteristic of Palustrine Systems in Coastal Maine

Common name	Taxonomic name
Open water vegetation: floating aquatics, nonrooted	
Small duckweed	*Lemna minor*
Big duckweed	*Spirodela polyrhiza*
Open water vegetation: floating aquatics, rooted	
Watershield	*Brasenia schreberi*
Spatterdock	*Nuphar* spp.
White water lily	*Nymphaea odorata*
Water smartweed	*Polygonum amphibium*
Pondweeds	*Potamogeton* spp.
Open water vegetation: submersed aquatics, rooted	
Coontail	*Ceratophyllum demersum*
Waterweed	*Elodea* spp.
Water milfoil	*Myriophyllum* spp.
Bushy pondweed	*Najas flexilis*
Stonewort	*Nitella* spp.
Pondweeds	*Potamogeton* spp.
Water bulrush	*Scirpus subterminalis*
Bladderwort	*Utricularia* spp.
Wild celery	*Vallisneria americana*
Emergent vegetation: perennials growing from substrates usually covered with shallow water	
Sweet flag	*Acorus calamus*
Water willow	*Decodon verticillatus*
Three-way sedge	*Dulichium arundinaceum*
Spikerush	*Eleocharis* spp.
Horsetail	*Equisetum fluviatile*
Bayonet rush	*Juncus militaris*
Reed	*Phragmites communis*
Pickerel weed	*Pontederia cordata*
Arrowhead	*Sagittaria latifolia*
Threesquare	*Scirpus americanus*
Great bulrush	*Scirpus validus*
Bur-reed	*Sparganium* spp.
Cattail	*Typha* spp.
Wild rice	*Zizania aquatica*

(Continued)

Table 8-5. (Continued)

Common name	Taxonomic name
Emergent vegetation: perennials and mosses forming dense mats	
Blue-jointgrass	*Calamagrostis canadensis*
Water arum	*Calla palustris*
Sedges	*Carex* spp.
Water hemlock	*Cicuta bulbifera*
Sundews	*Drosera* spp.
Wild millet	*Echinochloa* spp.
Grasses	*Eriophorum* spp.
Bedstraws	*Galium* spp.
Manna grass	*Glyceria* spp.
Marsh st. john's wort	*Hypericum virginicum*
Blue flag	*Iris versicolor*
Soft rush	*Juncus effusus*
Rice-cut grass	*Leersia oryzoides*
Water horehound	*Lycopus uniflorus*
Swampcandle	*Lysimachia terrestris*
Purple loosestrife	*Lythrum salicaria*
Bogbean	*Menyanthes trifoliata*
Reed canary grass	*Phalaris arundinacea*
Arrow-leaved tearthumb	*Polygonum sagittatum*
Marsh cinquefoil	*Potentilla palustris*
Mermaid weed	*Prosperpinaca palustris*
Arrowhead	*Sagittaria latifolia*
Bulrush	*Scirpus atrovirens*
Woolgrass	*Scirpus cyperinus*
Water parsnip	*Sium suave*
Sphagnum moss	*Sphagnum* spp.
Marsh speedwell	*Veronica scutellata*
Scrub/shrub vegetation: shrubs	
Speckled alder	*Alnus rugosa*
Bog rosemary	*Andromeda glaucophylla*
Buttonbush	*Cephalanthus occidentalis*
Leatherleaf	*Chamaedaphne calyculata*
Black huckleberry	*Gaylussacia baccata*
Dwarf huckleberry	*Gaylussacia dumosa*
Sheep laurel	*Kalmia angustifolia*
Pale-laurel	*Kalmia polifolia*
Labrador tea	*Ledum groenlandicum*
Sweetgale	*Myrica gale*
Willows	*Salix* spp.
Meadow-sweet	*Spiraea latifolia*
Large cranberry	*Vaccinium macrocarpon*
Small cranberry	*Vaccinium oxycoccus*

(Continued)

Table 8-5. (Concluded)

Common name	Taxonomic name
Forest or scrub/shrub vegetation: trees	
Red maple	*Acer Rubrum*
Gray birch	*Betula populifolia*
Tamarack	*Larix laricina*
Black spruce	*Picea mariana*
Red spruce	*Picea rubens*
White pine	*Pinus strobus*
Northern white cedar	*Thuja occidentalis*
Amercian elm	*Ulmus americana*
Yellow birch	*Betala alleghenicisis*
Balsam fir	*Abies balsamla*
Eastern hemlock	*Abies balsamla*

Table 8-6. Net Plant Productivity in Palustrine Systems

Ecosystem	Net plant productivity Dry g/m²/year
Forested bog[a]	340
Emergent bog[b]	635
Emergent/Scrub/shrub bog[c]	1943
Emergent cattail marsh[d]	2900
Emergent bulrush marsh[d]	4600

[a] Rodin et al. 1972
[b] Forrest 1971
[c] Reader and Stewart 1971
[d] Westlake 1963

Consumers

Consumers in palustrine systems of coastal Maine include invertebrate (appendix B) and vertebrate species (appendix C). The diversity of invertebrates inhabiting palustrine areas is considerable and varies greatly between different palustrine classes. Reinecke (1977) characterized the invertebrates of beaver ponds in central (noncoastal) Maine (appendix B). Similar invertebrate composition is expected in palustrine open water habitats in coastal Maine. In peat bogs the abundance and diversity of invertebrate organisms are much less than in a marsh wetland habitat.

Invertebrates in palustrine systems are especially important links in fish and wildlife food chains. The larvae of insects are a highly nutritious food source necessary for the successful reproduction and growth of vertebrates, including fish and waterfowl. The migrational behavior of certain bird species (e.g., swallows) can be viewed as a response to the seasonal availability of invertebrates.

Palustrine wetlands support a diversity of vertebrate species including reptiles, amphibians, fish, mammals, and birds. Appendix C summarizes the requirements of wetland vertebrates.

Palustrine wetlands support a greater number and diversity of reptile and amphibian species than any other wetland system in coastal Maine (see chapter 18, "Reptiles and Amphibians"). These species support food chains necessary for the survival of other vertebrate species. Snapping turtles are present in certain wetlands in coastal Maine where they may feed upon young waterfowl and other waterbirds.

Most of the fish inhabiting areas of palustrine open water (ponds) are warmwater species such as pickerel, bass, sunfish, perch, and minnows (see chapter 11, "Fishes"). Brook trout inhabit cold, spring-fed palustrine open water systems as well as some palustrine systems created by beaver.

Palustrine wetlands are among the most important habitat types for mammals (see chapter 17, "Terrestrial Mammals"). Several species utilize palustrine wetland for feeding areas, breeding areas, and/or shelter (i.e., muskrats, raccoon, deer, moose, red fox, mink, otter, black bear, and beaver). Wetlands supply all the requirements of muskrats. Forested wetlands provide important winter habitat for deer. Beavers impound streams, thereby creating palustrine habitats. An estimated 1000 active beaver flowages exist in the wildlife management units that enclose the characterization area (Hunt and Boettger 1975).

A wide diversity of birds frequent wetlands for breeding and/or feeding during nesting and migratory periods. Palustrine wetlands support waterbirds and waterfowl as well as terrestrial birds (see chapters 14, 15 and 16). Approximately 100 species of birds breed in palustrine wetlands, many of them exclusively (e.g., ring-necked duck, common snipe, marsh wrens, and marsh hawks; appendix C). The black duck, the most important waterfowl species in Maine in terms of sport, breeds in palustrine wetlands. Densities of one pair of black duck per 20 acres (8 ha) are common in scrub/shrub emergent wetlands of Maine (Coulter and Miller 1968). Densities of other species have not been investigated. The palustrine avifauna is migratory. Peak densities of birds occur during the breeding season (May to July). Most palustrine wetland-inhabiting birds are insectivorous during the breeding season even if they are otherwise mostly herbivorous. Waterfowl, for example, feed on invertebrates during the breeding season but in late summer and fall revert to seeds and fruit for the greater portion of their diet.

Waterfowl production on small palustrine wetlands in Maine was evaluated by Spencer (1963). He found that among small wetlands producing ducks those in the coastal zone and those in the 5 to 10 acre (2 to 4 ha) size range produced more young birds than inland and larger wetlands. Forested wetlands are especially important for hole-nesting species of waterfowl, including wood ducks and mergansers. Bog wetlands support a unique community of passerine birds including palm warblers, Wilson's warblers, and Lincoln sparrows. Uncommon species of birds in Maine found exclusively breeding in a variety of palustrine habitats include short-billed marsh wren (sedge-dominated emergent wetland), least bittern (emergent wetland), willow flycatcher (willow dominated scrub/shrub wetland), and marsh hawk (emergent wetland). During the migration period palustrine wetland inhabiting-species from other areas concentrate in Maine wetlands for feeding and resting.

Decomposers

Organic matter produced in palustrine areas is: (1) degraded into its recyclable constituents, such as nitrogen and phosphate, by bacteria and fungi; (2) stored as peat; or (3) exported from the system by water flow. The relationship between the rate of organic matter accrued and the rate of decomposition determines the rate of peat formation (see below). No data exist on decomposer species composition and rates of decomposition in wetland systems in coastal Maine.

Food Webs

A generalized food web for the community of a Maine palustrine wetland is given in figure 8-8. The generic examples listed are known to occur commonly in palustrine wetlands in coastal Maine. The base of the web consists of the lower plants and vascular plants. These are fed upon by fish, mammals, invertebrates, and zooplankton. These, in turn, are fed upon by fish, birds, mammals, invertebrates, reptiles, and amphibians. Many organisms occupy more than one trophic level. The heterotrophic bacteria and fungi ingest feces, dead organisms, and dissolved organic matter from various sources. These may, in turn, be ingested by consumers. However, much of the organic matter is stored as peat due to the slow rate of decomposition in Maine wetlands.

Feeding relationships based on specific paths of energy through organisms have not been studied in Maine palustrine wetlands.

ENERGY FLOW

In most biological systems the reduced compounds and organic material entering the food chain are broken down, stored, and respired by organisms. Eventually these organisms decompose. Much of the energy is dissipated in each of these steps. In the palustrine system of coastal Maine, however, the activity of decomposer organisms may be too slow to effect complete decomposition because of low temperature, low pH, and waterlogging. Fungal decomposers are not well adapted to a waterlogged environment. Biomass of fungi in palustrine systems is generally expected to be low. Bacterial decomposers are not well adapted to water with a low pH, such as that found in most Maine palustrine wetlands. Other decomposers (invertebrates) are not well adapted to the low oxygen tension found in wetlands. As a result organic matter accumulates in Maine palustrine systems.

The generalized scheme of energy flow through an ecosystem must be modified for the palustrine system (figure 8-9). Not all the solar energy rendered usable by the primary producers (plants) is liberated by the respiration of the component organisms in the palustrine system. Full utilization is preventd by physical conditions that limit the activity and number of decomposers. Crossby (1963) found that most of the production in a peat-producing system went into peat; about 5% was consumed by herbivores.

IMPORTANCE TO HUMANITY

Palustrine wetlands support diverse food chains and play an important role in pollution control and the hydrologic cycle. The water storage capacity of palustrine wetlands helps slow runoff and reduce runoff from snow melts and heavy rains. The low, flat surfaces of wetlands store runoff from adjacent uplands and slowly release the water to streams, reducing peak flood flows. After wetlands are flooded they may recharge aquifers (water-bearing formations) for several weeks and augment the low flow of streams for an even longer period. Wetlands have the capacity to store peak flood waters temporarily which can result in a reduction in the volume and severity of a flood. If the water level in a 10 acre (4 ha) wetland is raised 6 inches (15 cm), 1.5 million gallons of water have been stored (Niering 1966).

Two geologically different wetland basins near Boston were studied by O'Brien (1977). Groundwater accounted for 93% of the total annual discharge from both wetlands. In late summer the wetlands underlain by peat deposits recharged the regional groundwater body. Estimates suggest that during the summer groundwater recharge may be several orders of magnitude greater than surface runoff (O'Brien 1977).

Palustrine wetlands affect the quality and quantity of water in downstream aquatic systems. For example, in a chain of lakes that receives excess nutrients, the first lake in the chain may become a bog or marsh (depending on the interrelationship of abiotic factors) and entrap nutrients in the peat or sediments of its basin, thereby helping to slow eutrophication in the other lakes of the chain. The dense vegetative cover characteristic of palustrine areas traps sediment by slowing water velocity. In their function as sediment traps palustrine areas enhance the habitat of fish and wildlife in downstream aquatic systems.

Wetlands also play a significant role in the lives of people. They are valuable as open space, offer diverse groupings of plant and animal species, and add to the diversity of the landscape. They support many forms of recreation: bird watching, nature photography, hiking, camping, canoeing, hunting, fishing, berrypicking, trapping, skating, skiing, and picnicking.

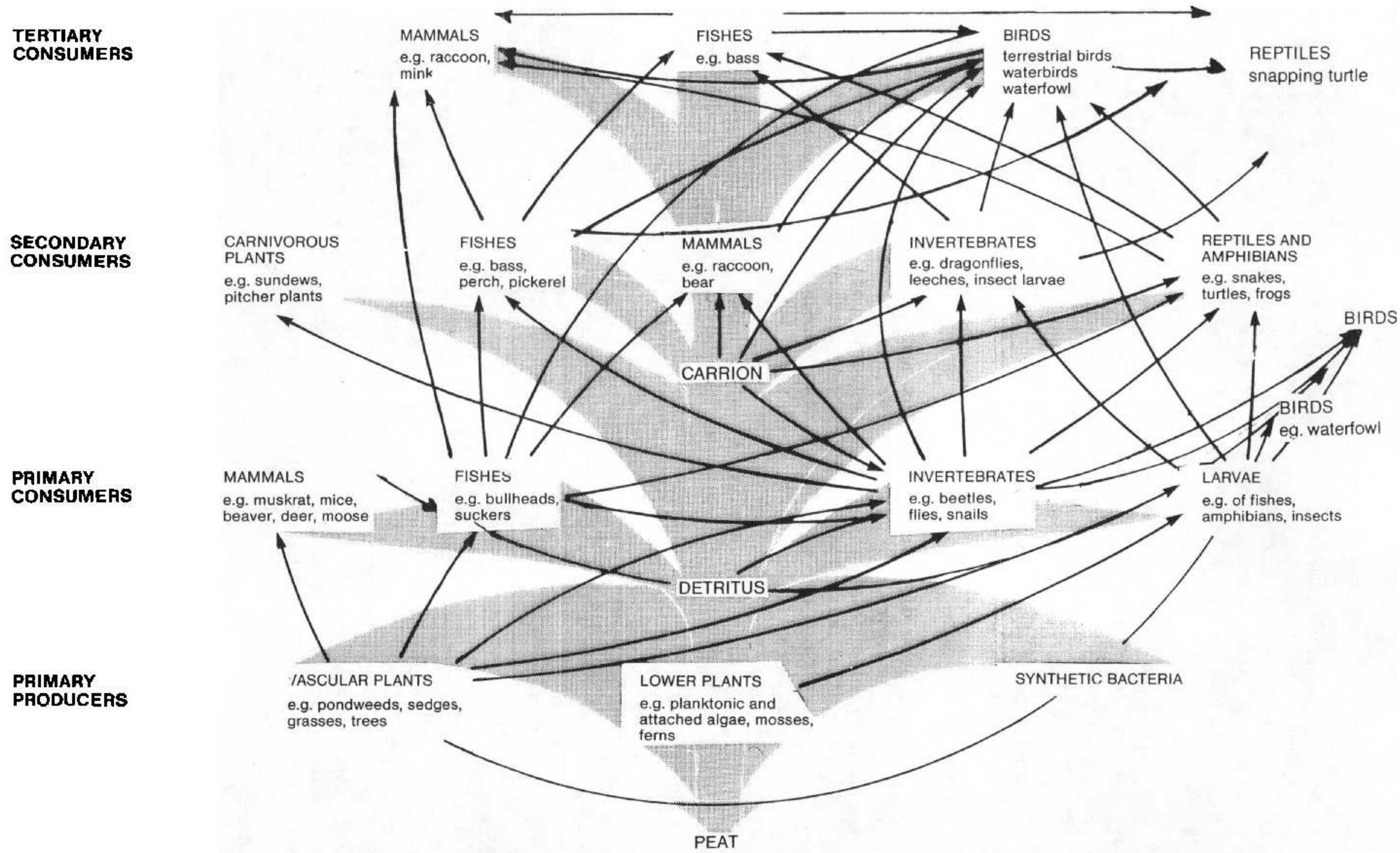


Figure 8-8. Food web of the forested, scrub/shrub, emergent and open water palustrine wetlands.

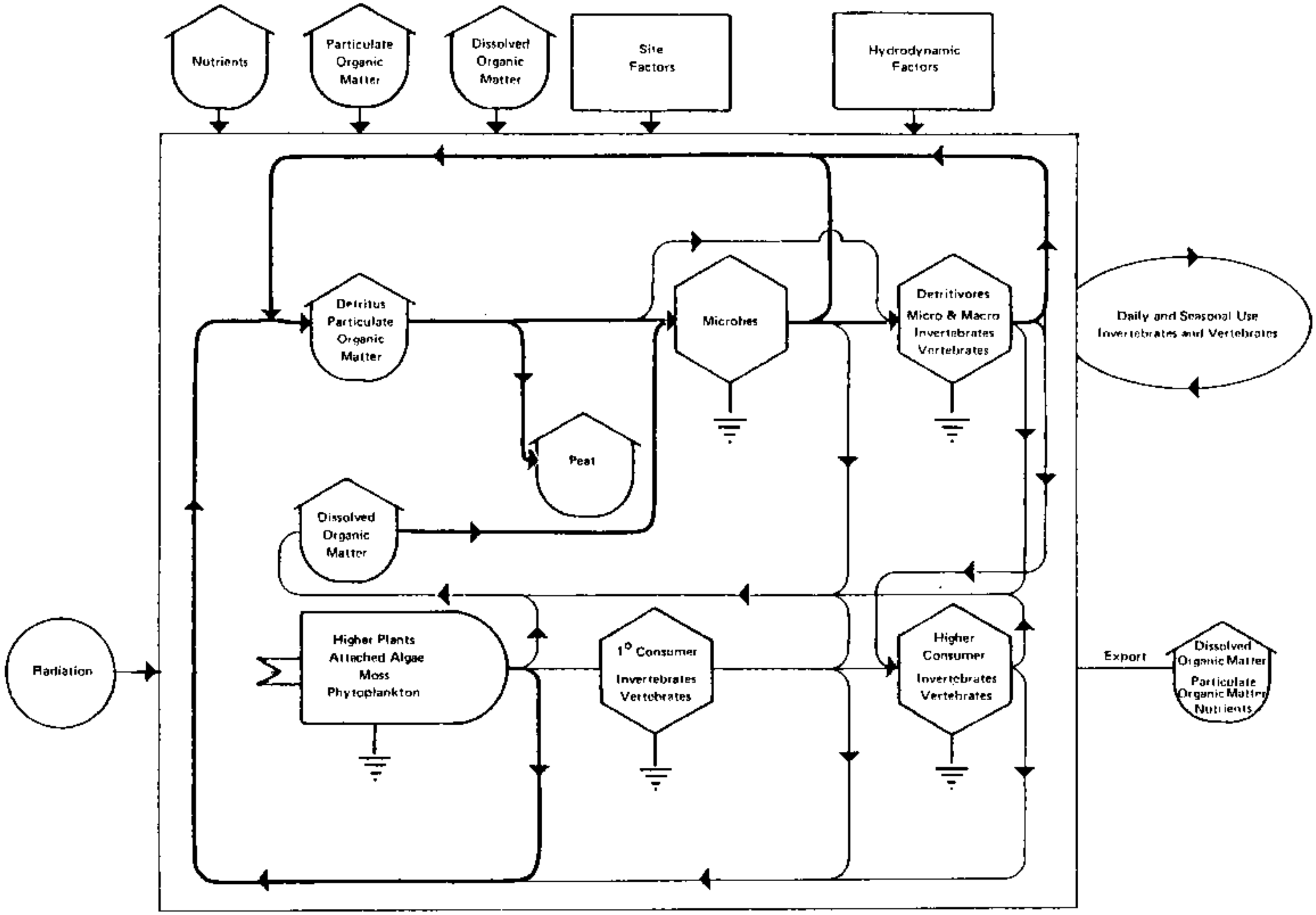


Figure 8-9. Model of energy flow in the palustrine system.

Peat As A Commercial Resource

Peat is mined at several bogs in Maine for use as a soil conditioner and as horticultural material. Two types of peat are harvested commercially, sphagnum peat and peat humus.

Sphagnum moss peat contains a minimum of 67% fiber by weight, has a low ash content (<10%), and has a minimum water-holding capacity of 800% by weight. It is the principal material mined from Maine bogs.

Peat humus is decomposed moss peat, has a low water-holding capacity and a medium-to-high nitrogen content. Minor amounts of this material are mined at some operations that normally extract moss peat.

Recent interest in energy resources has spawned interest in Maine peat as a source of energy, either by direct burning or conversion to gas. Recent tests by the U.S. Bureau of Mines indicate that some Maine bogs may yield peat which, when dried and burned, will release up to 9000 BTU/lb (personal communication from W. A. Anderson, Maine Geological Survey, Augusta, ME.; March, 1979).

Over 31 million short tons of commercial peat resources have been surveyed within the coastal counties from Cumberland to Washington Counties (atlas map 3). More reserves exist but are unsurveyed.

PALUSTRINE MANAGEMENT

In Maine there are limited direct Federal and State controls over palustrine wetland areas. These are discussed in chapter 3. This section describes habitat management programs in palustrine wetlands in coastal Maine.

MDIFW owns and manages some palustrine wetland areas in coastal Maine. Wetlands under MDIFW ownership are ensured protection. MDIFW protects and manages beaver populations for production. Beaver management is indirectly related to wetland management as beavers, by impounding streams, create productive wetland areas. An estimated 1000 active beaver flowages exist in the wildlife management units that encompass the characterization area (Hunt and Boettger 1975). Hodgdon and Hunt (1966) noted that increases in waterfowl numbers in Maine coincided with beaver increases. Ruffed grouse and woodcock feed in the small openings in the woods created by beavers.

MDIFW and the U.S. Fish and Wildlife Service (Moosehorn National Wildlife Refuge) have been involved in marsh management programs in Maine intended to improve habitat for waterfowl. These experimental programs have managed specific local areas comprising a very small percentage of palustrine wetlands in coastal Maine. Small marshes were created and various management techniques (drawdown, water level reduction, water level control, plant control, fertilization, fire, and waterfowl food plantings) were applied. A study evaluating the small wetland construction program of the MDIFW was conducted by Spencer (1963). Fefer (1977) evaluated the palustrine wetland management program at Moosehorn National Wildlife Refuge. Detailed studies documenting management techniques and their effects in coastal Maine are lacking.

Management can improve cover, increase the quantity and quality of aquatic food, and improve the interspersion of vegetation and water for waterfowl. Detailed descriptions of waterfowl habitat development and management practices are available in Anderson (1966) and Atlantic Waterfowl Council (1972).

RESEARCH NEEDS

This characterization of the coastal palustrine system in Maine contains little specific information about its ecology because very little research on this subject has been done. Trends in wetland abundance and impacts in relation to human activity need further investigation. In addition, knowledge of the productivity of particular plant and animal communities would be valuable.

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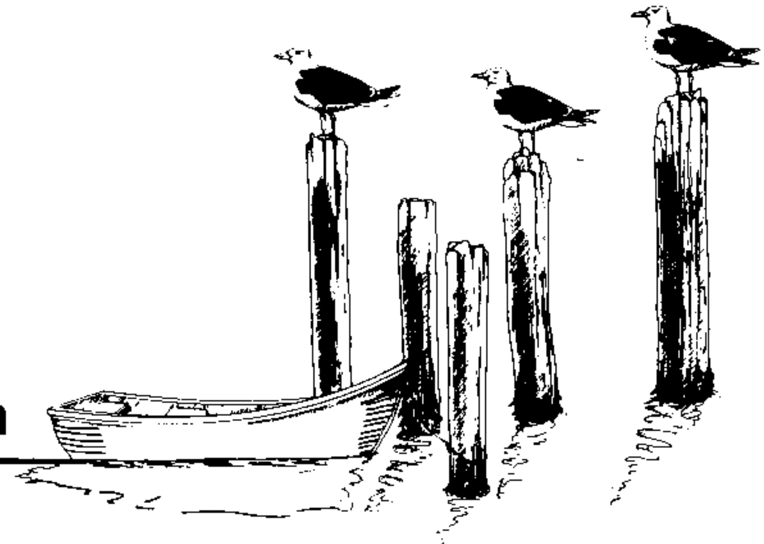
Chapter 9
The Forest System



Author: Craig Ferris

Forests, the major terrestrial habitat in Maine, comprise about 85% of the coastal land area (table 9-1). They largely determine the characteristics of the hydrology, microclimate, soil structure, nutrient flow, and animal composition of the terrestrial habitats of coastal Maine.

In ecological terms forests are systems. They are somewhat independent of other ecosystems but require sufficient nutrients and minerals from the soil, nutrient inputs from precipitation and the atmosphere, and energy from the sun. Mature forests have a large standing biomass of plant tissue, extensive root systems and a large photosynthetic surface area. Forests are among the most productive terrestrial habitats and support numerous and diverse forms of animal life, including insects and other invertebrates, reptiles (snakes), amphibians (frogs, toads, and salamanders), birds, and mammals. In spite of the abundance of above-ground animal life, nearly all of the annual production of plant material in forest systems falls to the forest floor where it becomes the source of energy for a complex detritus-based food web.

Although forests tend to be independent of other ecosystems their output sometimes strongly influences other systems. The nutrients transported out of forest systems in surface and underground runoff represent very small amounts of the annual productivity. Although this loss is insignificant to the forest system it may form the primary energy source for streams that receive runoff from forest land. Forest vegetation also moderates the flow of water out of forest systems, reducing the peak flows in streams. Herbicides or pesticides applied to a forest and carried in the runoff could pollute the streams.

Major disturbances or perturbations to forest systems include fire, logging, wind storms, and insect damage. Normally forests recover rather quickly from these perturbations, because regrowth of herbaceous and woody vegetation and trees usually repopulate the area within a year or two. After 40 to 60 years a disturbed area may support a mature forest. On the other hand, excessive disturbance resulting from severe fire or careless forestry practices may result in erosion of both organic matter and mineral soil, which exposes infertile soils on which forest recovery is slow.

Table 9-1. Amount of Forest Land (thousands of acres) in Coastal Maine by Forest Sampling Unit

Forest sampling unit	Forest land	Land total	% Forest
Capital [a]	1288	1721	75
Hancock	909	984	92
Washington	1510	1635	92
Totals	3707	4340	85

[a] Includes Sagadahoc County.

Forest systems also are important for economic, recreational, and aesthetic reasons. Forests in the coastal counties of Maine account for 20% of the State's forests and provide approximately 17% of all timber harvested in the State. Maine's timber is used for pulp and paper, sawlogs, veneer, pilings, posts, turnings, and other products. The total value of manufactured goods resulting directly or indirectly from Maine's forests accounted for approximately 40% of the State's total manufacturing output in 1975, and its associated industries employed about 25% of the State's work force. Recreational and aesthetic values of forest systems include photography, hunting, camping, snowmobiling, skiing, sightseeing, hiking, and trapping.

The major threat to Maine's coastal forests is real estate development. The spread of urban and suburban areas, accompanied by industrial plants, shopping centers, roads, and powerlines, results in the permanent loss of forest habitat that will not be replaced. This loss of forest land sometimes seriously damages the river systems flowing through and from the forests. Water flow may be seriously altered. Heavy rains may produce excessive flooding and soil erosion; during low precipitation rivers may exhibit unusually low flows. In industrial areas pollution may become severe.

The purpose of this chapter is to describe coastal forest ecosystems, forest composition, the functions of forests, their importance, and data gaps. A detailed discussion of forest management is found in chapter 19, "Commercially Important Forest Types." Chapter 19 describes important tree species and forest types, the management strategies employed for each, and problems associated with timber harvest operation. Also included are discussions of important diseases and pests. Atlas map 2 details land cover types for specific areas in coastal Maine. Common names of species are used except where accepted common names do not exist. Taxonomic names of all species mentioned are given in the appendix to chapter 1.

DATA SOURCES AND COMPILATION OF DATA

Most of the data used to prepare this report came from books, published research reports, and unpublished theses. In cases where data on Maine's forests were not available, information from other areas with forests similar to Maine's was used. Much of the descriptive data on forest systems along the coast was derived from the U.S. Department of Agriculture (USDA) forest inventory conducted between 1968 and 1970 (Ferguson and Kingsley 1972). Data from this forest inventory were summarized by sampling units that correspond with county boundaries. The three sampling units that encompass the majority of the characterization area are the Capital unit, Hancock unit and Washington unit (figure 9-1). The data are for the most part representative of the coastal area and discrepancies will be pointed out where they exist. The Capital unit includes Knox, Lincoln, Waldo, and Kennebec Counties and is representative of regions 2, 3, and part of 4. The Hancock and Washington units correspond to the coastal counties of the same names and are representative of regions 5 and 6 respectively.

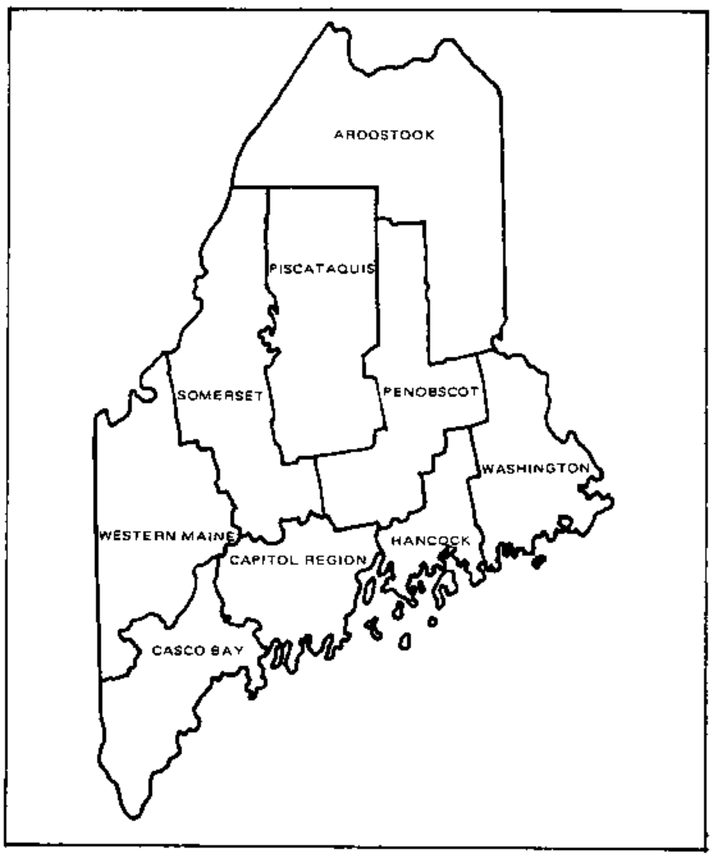


Figure 9-1. Geographic sampling units of the 1968 to 1970 forest inventory in Maine (Ferguson and Kingsley 1972).

CLASSIFICATION OF FOREST SYSTEMS

Two sets of terms will be used to discuss forest systems in this chapter. The first will be used to describe the functional aspects of the forest system, such as energy flow, nutrient cycles, and food webs, and the other will serve to group forests according to "forest types."

Functionally, forests can be considered softwood, hardwood, or mixed. Softwood stands are those in which two-thirds or more of the trees comprising the canopy are softwood or coniferous (e.g., spruce, fir, and pine), whereas in hardwood stands at least two-thirds of the canopy trees are hardwood or deciduous (e.g., maple, birch, oak, and aspen). Mixed stands have neither a predominance of hardwoods nor softwoods. This grouping is considered functional since, with some exceptions, similar environmental conditions and associated plant and animal life are found in stands dominated by softwood or hardwood trees, regardless of the tree species composition, and generalizations can be made about nutrient cycles and energy flow in both. Along the coast of Maine there is a continuum from pure coniferous to pure deciduous stands but the amount of forest land occupied by each of these functional groups has not been quantified.

Forests also can be separated into forest "types" as proposed by the Society of American Foresters (1964). Forest types indicate tree species that "singly or in combination make up the plurality (>50%) of the stands." This nomenclature system recognizes that certain associations of tree species occur repeatedly under similar conditions of topography, climate, soil type, and moisture.

For the purposes of this report, the three major forest types are spruce-fir, white pine-hemlock-hardwood, and beech-birch-maple. These three types incorporate the seven major types described by Ferguson and Kingsley (1972) and include 19 local types (table 9-2).

DISTRIBUTION OF FOREST TYPES

Spruce-Fir

Spruce-fir is the most abundant forest type in coastal Maine, making up 46% of the commercial forest land (table 9-3). Spruce (red, white, or black) and balsam fir, singly or in combination, dominate. Other tree species commonly associated with this type are northern white cedar, eastern hemlock, eastern white pine, tamarack, red maple, paper birch, aspen, white ash, American beech, sugar maple, and yellow birch.

Spruce-fir forests in Maine represent the southern extensions of the northern boreal forest. This type is commonly found in low areas with poorly drained soils (locally called spruce-fir swamps or flats), on thin soils at higher elevations (spruce balds) and on islands, peninsulas, and coastal headlands. These areas, called primary softwood sites (Westveld 1941), usually have a colder microclimate than surrounding upland areas and indicate the adaptations of these conifers for cold temperatures and shallow soils. Spruce-fir also is found on the better drained soils at moderate elevations (secondary softwood sites) but here competition from hardwoods is more intense and hardwoods usually dominate.

Table 9-2. Major Forest Types and Local Subtypes Found within the Coastal Zone of Maine[a]

Spruce-fir	White pine-hemlock-hardwood	Maple-beech-birch (Northern hardwood)
Balsam fir	Jack pine	Red maple
Black spruce	White pine	Black ash-elm-red maple
Red spruce-balsam fir	White pine-hemlock	Sugar maple-beech-birch
Northern white-cedar	White pine-red oad-white ash	Black cherry
Tamarack	Northern red oak	Aspen
White spruce	Mixed hardwood	Paper birch
		Gray birch

[a]Ferguson and Kingsley 1972.

Table 9-3. Amount of Commercial Forest Land (thousands of acres) in Maine's Coastal Units (percentage contributions to the total in parentheses) by Forest Type[a]

Forest sampling unit	Forest type			
	Spruce-fir	White-pine hemlock hardwood	Beech-birch-maple	Total
Capitol	336 (30)	348 (30)	449 (40)	1133
Hancock	472 (55)	127 (14)	264 (31)	863
Washington	850 (59)	133 (9)	455 (32)	1438
Totals	1658 (46)	608 (17)	1168 (32)	3434

[a]Ferguson and Kinglsey 1972.

Spruce-fir forests are most abundant in the eastern coastal areas, comprising between 55% and 60% of the commercial forest land (table 9-3; figure 9-2). Along the immediate coast east of Penobscot Bay (regions 5, 6, and part of 4) spruce-fir type dominates the shoreline (Davis 1966). Areas that are not spruce-fir are usually successional stages, primarily aspen-birch, that if given sufficient time will develop into spruce-fir forests (see "Forest Succession" below). East of Machias, spruce-fir is the dominant forest type both inland and along the coast but from Machias west to Penobscot Bay it is replaced inland by northern hardwood types. South and west of Penobscot Bay (regions 2, 3, and part of 4) spruce and fir comprise a smaller percentage of the forest types (25%; see table 9-2). Where it is present in this area in uniform stands it usually occurs on the tips of peninsulas and offshore islands. South and west of Casco Bay (region 1), spruce-fir forests give way to white pine-hemlock-hardwood forests.

The presence of spruce and fir along the immediate coast and on offshore islands is not correlated with either bedrock or soil type but seems to be due to the cold, damp, microclimate created by the marine exposure (Davis 1966). Competition from hardwoods is minimized because the soils are generally shallow. Mature stands of spruce-fir along the coast are dominated by red spruce because it is slightly more tolerant and long-lived than fir or other spruces. Balsam fir and white spruce survive in openings and white spruce often forms a narrow border along the immediate shoreline (Davis 1966).

White Pine-Hemlock-Hardwood

This forest type is one in which either eastern white pine or eastern hemlock predominate. Many species of hardwoods are associated with this type but none are particularly characteristic. Species associated with this type are red pine, aspen, birch, maples, red oak, and elm. This type includes the oak and oak-pine types described by Ferguson and Kingsley (1972).

White pine-hemlock-hardwood type is most abundant along the southwestern coast of Maine, where it comprises 26% of the forest land (table 9-2; figure 9-2). Typical white pine sites are those with dry, sandy, infertile soils, which are common in this area. On these sites white pine may form a climax association with oaks. White pine is found also in areas that have been burned in the past, but is replaced in these areas by other forest types. Many of the pine forests in southern Maine are thought to be present because of fires which favor the establishment of pine (see "Effects of Fire" below). Without recurring fires, which kill competing hardwood trees, these stands will succeed to northern hardwoods, the climax (dominate) association in this area. Other sites suitable for white pine forests are oldfields, barrens, and dunes, where white pine competes successfully during the early stages of succession. Other species of pine (pitch, jack, and red) also are found in these situations.

Hemlock is adapted to a wide variety of edaphic and physiographic conditions. It is found often in scattered groves along ravines and in less well-drained areas but rarely along the immediate coast (Fowells 1965). Hemlock is normally associated with the beech-birch-maple type.

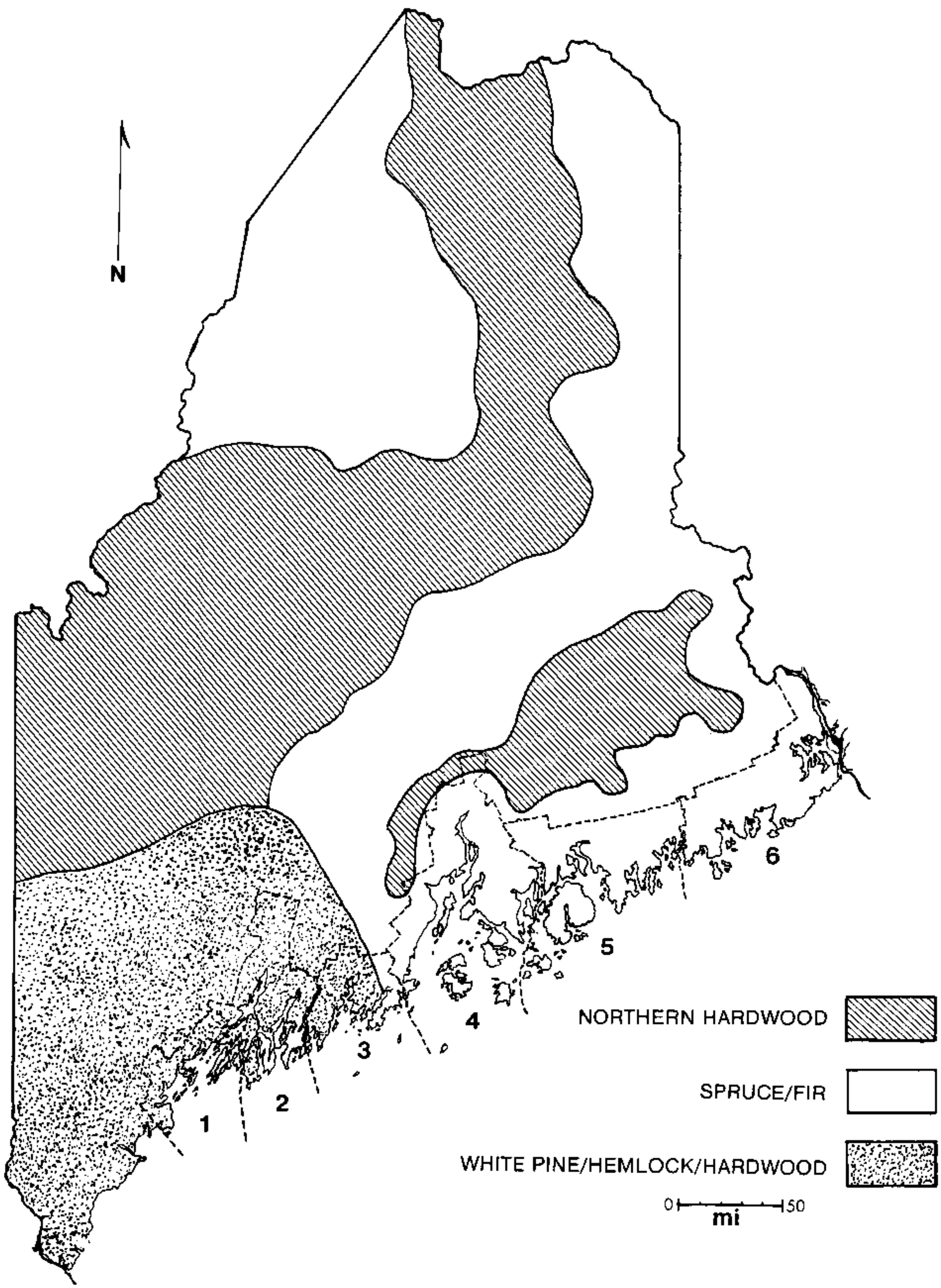


Figure 9-2. Approximate distribution of major forest types in Maine.

Beech-Birch-Maple

This forest type, which is also known as the northern hardwood type, is characterized by American beech, yellow birch, and sugar maple. Other common associates are basswood, red maple, red oak, white ash, eastern white pine, balsam fir, cherry, paper birch, gray birch, American elm, slippery elm, hophornbeam, red and white spruce, and hemlock.

Northern hardwoods are normally found in areas with deep (over 20 inches; 51 cm), moist, well-drained soils. In Maine this type is most common in the western and central regions of the State but occurs on mid-elevation sites in eastern Maine as well (figure 9-2). In coastal Maine this type is found mixed with spruce and fir in the mid-coast areas (Casco to Penobscot Bays) and is found inland from the coastal stands of spruce and fir east from Penobscot Bay to Machias.

This type includes the aspen-birch subtype described by Ferguson and Kingsley (1972), which is an important association on forestland recently disturbed by logging or fire. This is a successional type, however, and gives way to either northern hardwood or spruce-fir, depending on the site.

SUCCESSION OF FOREST SYSTEMS

The development of forest vegetation on an area follows a somewhat predictable sequence of changes in plant communities known as succession. Temporary plant communities (grasses, shrubs, and aspen-birch trees) in this process are known as seral stages. Each seral stage modifies the environment in such a way that it becomes more suitable for the invasion of another plant association, which then succeeds the previous one. A plant association that ultimately dominates is known as the climax association. In Maine the climax associations on all land and fresh water habitats are forests.

Maine's original forests developed after the last glaciation through primary succession on exposed rock, glacial till (soil), or water (figure 9-3). Early seral stages of primary succession (lichens, mosses, and herbs) result in the accumulation of organic matter and mineral soil so that shrubs and then trees eventually are able to survive. The order in which different species of trees invade a site depends on the "tolerance" of each species (table 9-4), as well as on site conditions. Tolerance refers to the ability of a plant, especially a young plant, to survive in an understory (under a tree canopy). A tolerant tree is one that can compete successfully with other plants for moisture and nutrients and can grow well under low light intensity (Spurr 1964). Intolerant trees, such as birches, aspens, and pines, comprise the first seral stage dominated by trees. Intolerant trees grow rapidly in full sunlight and can outgrow and overtop more tolerant species that are present. Intolerant trees usually have open canopies, which allows more tolerant species to invade underneath the canopy.

In some areas tolerant tree species (table 9-4) such as red spruce, balsam fir, sugar maple, and American beech, often invade as an understory and form the climax plant association as the overstory trees die out. These species usually succeed themselves because their seedlings survive under the dense shade of closed canopies. Tolerant tree seedlings do not necessarily grow rapidly under heavy shade; they are merely able to survive until they can be

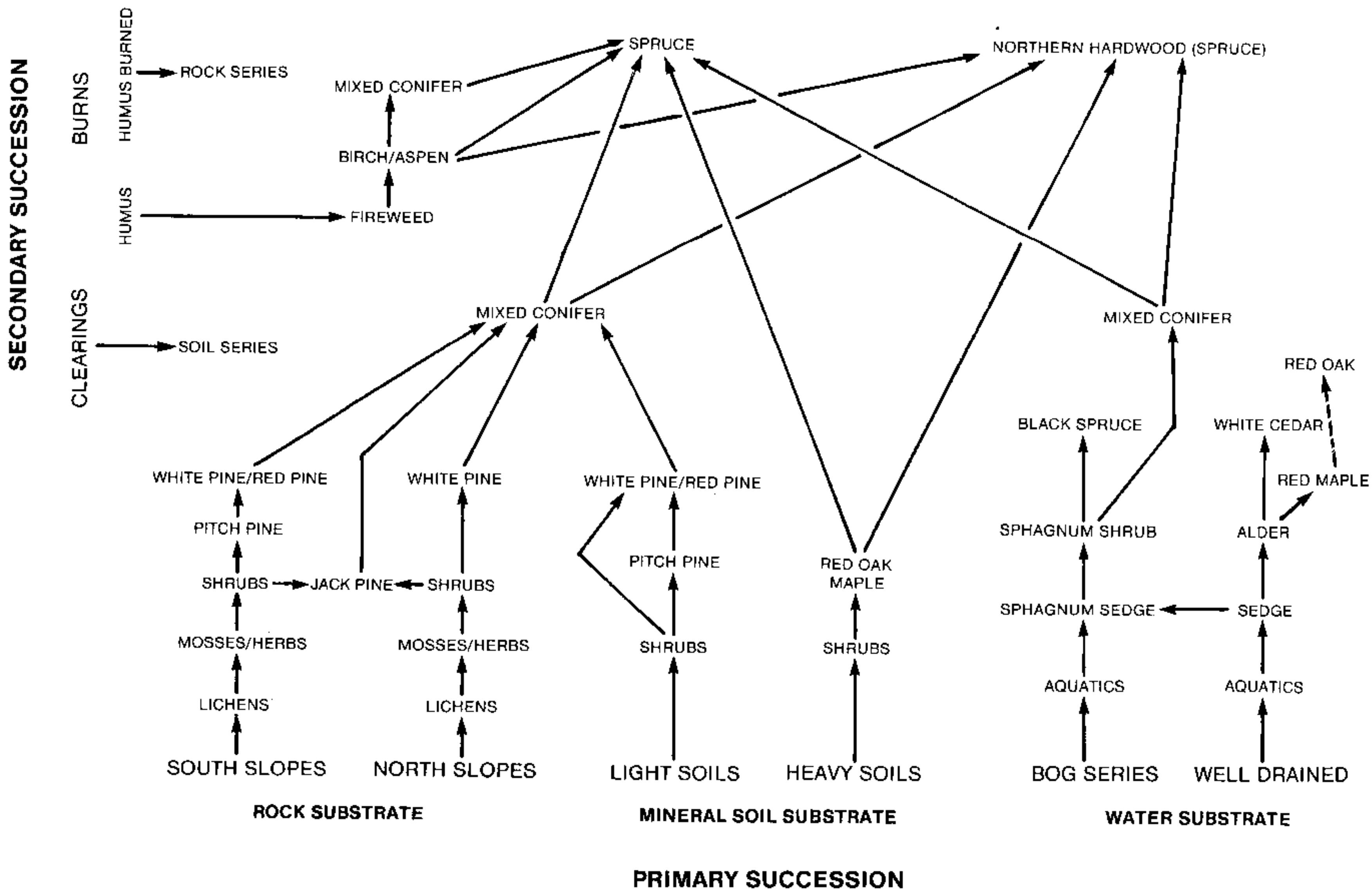


Figure 9-3. Patterns of primary and secondary succession under different substrate conditions along the coast of Maine.

Table 9-4. Tolerance Levels of Major Tree Species of Coastal Maine

Intolerant	Intermediate	Tolerant	Very tolerant
Paper birch	White ash	Black spruce	Balsam fir
Quaking aspen	American elm	Red maple	White spruce
Northern red oak	Eastern white pine	Sugar maple	Red spruce
Jack pine		Yellow birch	Eastern hemlock
Pitch pine		American beech	
Tamarack		Northern white cedar	
Red pine			

released as the overstory is removed or as trees die. If large openings are created in the canopy, by lumbering for example, conditions may be suitable for intolerant species to propogate and grow. Without major disturbance, however, climax associations are capable of dominating a site indefinitely. In the characterization area two forest types are considered climax associations: the spruce-fir and the northern hardwood types. Spruce-fir is the climax association on wet lowland and shallow soils, and on coastal islands, headlands, and peninsulas. The hardwoods are dominant on deep, well-drained soils. White-pine can sometimes form a climax community with oak on sandy, infertile sites but it is usually considered a seral stage and is succeeded by northern hardwoods. Common forest subtypes that are important seral stages include aspen-birch, elm-ash-red maple, northern white cedar, gray birch-paper birch, and pin cherry.

A climax community usually persists unless a major disturbance destroys a large section of forest. Natural disturbances, such as wind storms, fire, and insect defoliation, are known to have occurred in Maine's forests prior to settlement. The relative importance of each of these types of disturbance to Maine's forests is not known. Fire is thought to have been generally common in the northern boreal forest (occurring approximately every 100 years; Heinselmann 1971) but is not thought to have been common in Maine's spruce-fir forests (Little 1974). Fire was relatively uncommon in northern hardwood forests in New Hampshire (Bormann and Likens 1979), and this probably is true of Maine's northern hardwoods as well. Indians along the southern coastal region may have used fire to keep forests open and are thought to have been responsible for establishing the white pine forests found in that area (Little 1974).

Wind storms are not uncommon in Maine and mature spruce-fir stands are particularly susceptible to windthrow because they have shallow root systems. Examples of windthrown spruce-fir stands are at Otter Point, on Mt. Desert Island (region 5), and Hog Island (region 3). Spruce-fir stands are also susceptible to periodic outbreaks of spruce budworm, which are thought to occur every 40 to 70 years. Since the time of settlement, logging and fire have become the most damaging disturbances to Maine's forests. Historically, most forested areas have been logged two or three times.

Secondary Succession

As a result of fire and logging most of Maine's forests are not virgin stands but have developed through secondary succession following a major disturbance. The pattern of secondary succession and the rate at which forest vegetation is reestablished on the site depends on the severity of the disturbance, the residual vegetation present, the degree to which the organic matter and the soil structure have been destroyed, and available seed sources. Under conditions of severe fire or in which careless forestry practices have been used, the organic matter and mineral soil may be destroyed or eroded, setting succession back to bare rock or mineral soil (figure 9-3). Since the organic matter and mineral soil must be built up again recovery is very slow. Normally, however, recovery is very rapid. Initial growth of herbaceous vegetation is rapid because fire and logging release nutrients stored in the soil by exposing the soil to higher surface temperatures and higher soil moisture (which increases decomposition). While some of these nutrients are lost by leaching, they also serve to assist the regeneration of the site. The major difference between the effects of fire and logging is that fire usually kills all the above-ground vegetation, whereas logging allows residual vegetation to remain. Consequently, the first plants that occur on burned areas are those that sprout from roots or stumps or germinate from seeds that are dormant in the soil, blown in by the wind, or carried by animals. After logging the first plants are usually the woodland herbs and tree saplings and seedlings left after logging. Because most residual species grow slowly in full sunlight and some may die, logged sites are usually quickly invaded by the same intolerant species that occur on burned sites and the sequence of changes is similar. Intolerant trees invade disturbed areas within a year or two and succession to the climax stage involves a series of even-aged stands of first intolerant, then midtolerant and finally tolerant trees that form the climax (Bormann and Likens 1979).

Secondary succession also occurs on abandoned farmland (see chapter 10, "Agricultural and Developed Land"). The pattern of succession here differs from that following logging or fire because no native residual vegetation exists. After years of cultivation, herbicides, and harvesting, the seeds and root systems of native vegetation are gone. In addition, the natural soil structure has been changed by plowing and a cover of sod that inhibits the invasion of native species is usually present. Shrubs and trees may not invade the site for 10 to 15 years.

BIOTA

The biota of forest ecosystems can be classified according to the role of organisms in the transfer of energy through the ecosystem. Four basic functional groups, or trophic levels, exist:

1. The primary producers, green plants: trees, wood shrubs, nonwoody higher plants, ferns, and mosses.
2. The decomposers: fungi, bacteria, and microorganisms (smaller soil insects, worm phyla, and other small invertebrates)
3. The primary consumers, herbivores: many insects and plant-eating vertebrates and invertebrates.
4. The secondary consumers, the carnivores and insectivores: many insects and vertebrates.

Energy flow from one level to another is shown in figure 9-4. Sunlight is converted to plant tissue (carbohydrates, fats, and protein) by green plants. This constitutes primary production which then is consumed by herbivores (primary consumers) or falls to the forest floor, where it is utilized by decomposers and other primary consumers. Primary consumers and decomposers then become food for higher level consumers (insectivores and carnivores). The increase in animal tissue as a result of growth or reproduction is termed secondary production. A more detailed discussion of the various trophic levels follows.

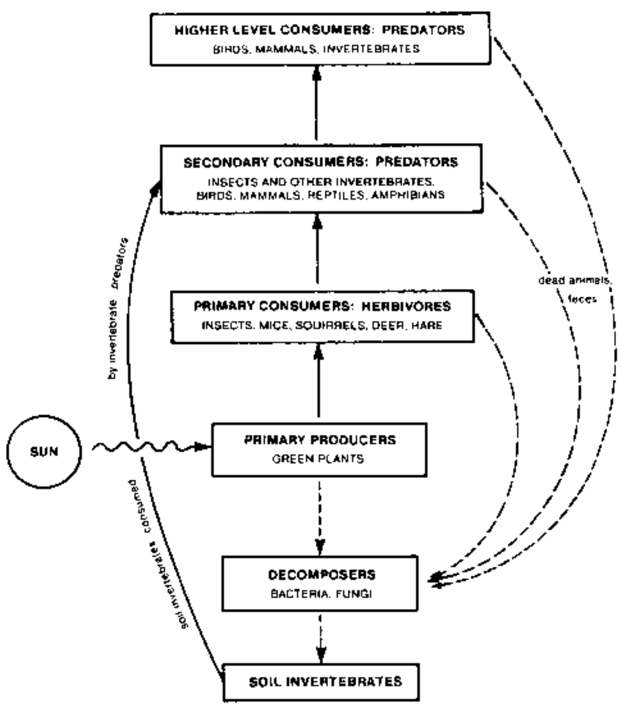


Figure 9-4. Generalized trophic structure of a forest system showing major pathways of energy transfer (solid lines are "grazing" pathways, broken lines are "decomposer" pathways).

Primary Producers

Trees that make up the canopy of a forest are the dominant producers, sometimes accounting for 98% or more of the above-ground biomass and net productivity (Ovington 1965). The relative abundance of the important softwood and hardwood tree species (>6 inches; 15 cm dbh) for each of the three forest units along coastal Maine is listed in table 9-5. In the Capitol unit (which represents regions 2, 3, and 4) softwoods slightly outnumber hardwoods (56% and 44% respectively); balsam fir is the most abundant species (18%), followed by the soft maples (red and silver, combined 16%), and white pine (11%). The abundance of pine in this region reflects the importance of the pine-hardwood-hemlock forest type along the southwest coast of Maine. The species composition of forests in the Washington and Hancock units (representative of regions 5 and 6) is similar, where about 75% of the commercial trees are softwoods. The most abundant species are red spruce (27%), balsam fir (20% to 23%), and soft maples (10% to 12%).

Forest vegetation beneath the canopy consists of immature or overtopped trees (understory), shrubs, nonwoody vascular plants, ferns, mosses, grasses, and lichens. The extent to which these plants are present depends on the density of the canopy, which controls the amount of light reaching the understory. For example, the open canopy characteristic of aspen and birch stands allows for the growth of a well-developed understory that usually is comprised of young spruce and fir (that may eventually become dominant), shrubs, grasses, ferns, and other herbaceous plants. Pine stands also have open canopies with understories of hardwoods (often oak). Stands dominated by beech-birch-maple are usually too dense for development of good herbaceous layers but seedlings and saplings of overstory trees sometimes survive. In dense spruce-fir stands the only vegetation beneath the canopy, if any, is a sparse growth of mosses and lichens on the forest floor (Davis 1966).

Forest biomass. Forest biomass, as the term is used here, refers to the weight of the living vegetation on an area. This includes both above-ground portions (stems, trunks, and leaves) and below-ground portions (roots) of all plants. Biomass is usually represented on a dry-weight basis, which is roughly equivalent to 50% of fresh weight.

Fully stocked, mature, second growth forests in Maine support between 56 to 85 tons/acre (125 to 190 t/ha) of dry weight biomass (above and below ground; Young et al. 1976). A survey of over 64,220 acres (26,000 ha) of forest land in northern Maine indicates that second growth and mature softwood stands have the greatest biomass, 78 to 84 tons/acre (175 and 188 t/ha), respectively, followed by mixed stands, 63 and 78 tons/acre (141 and 175 t/ha) for second growth and mature respectively and hardwoods, 56 and 70 tons/acre (125 and 157 t/ha; table 9-6; Young et al. 1976). Young stands support about one-third of the biomass of older stands, and young hardwood biomass (26 tons/acre; 58 t/ha) is greater than for either softwoods (24 tons/acre;54 t/ha) or for mixed species (13 tons/acre;29 t/ha). In a typical Maine forest nearly all (98%+) of the living plant biomass is in the trees; the remainder is in shrubs and herbs (table 9-7; Young et al. 1976).

Table 9-5. Percentage Contribution of Major Tree Species to the Number of Trees and Volume (in board feet) of the Total in Three Units in Coastal Maine[a].

	Capital unit		Hancock unit		Washington unit	
	No.	Vol.	No.	Vol.	No.	Vol.
Softwoods						
White pine	11	18	2	4	1	4
White spruce	4	4	4	4	4	3
Red spruce	8	8	27	33	27	31
Balsam fir	18	12	20	12	23	17
Hemlock	8	10	7	9	7	8
Northern white cedar	6	4	14	11	9	7
Other softwoods	<1	1	1	1	2	2
Subtotal	56	57	73	75	74	72
Hardwoods						
Red oak	3	4	2	2	1	1
Yellow birch	2	2	1	1	1	1
Paper birch	5	5	8	5	6	5
Sugar maple	3	4	2	2	1	1
Soft maple	16	14	10	10	12	13
Beech	1	1	2	2	1	1
White ash	3	3	1	2	1	1
Aspen	4	3	1	2	3	4
Other hardwoods	6	7	<1	<1	<1	<1
Subtotal	44	43	27	25	26	28

[a]Ferguson and Kingsley 1972.

Table 9-6. Total Biomass (above and below ground) of Some Representative Forest Communities in Maine[a]

Forest communities	Biomass (metric tons/ha)
Immature (regenerating)	
Softwood	54
Mixed	29
Hardwood	58
Second growth	
Softwood	175
Mixed	141
Hardwood	125
Mature	
Softwood	188
Mixed	175
Hardwood	157

[a]Young et al. 1976.

Table 9-7. The Percentage Contribution of Commercial, Noncommercial and Shrub Species to the Biomass of Maine Forests

Forest component	Diameter Breast Height		Total
	<5 feet	>5 feet	
Commercial tree species	9.7	87.3	97.0
Noncommercial tree species	1.0	1.4	2.4
Shrubs	0.6	0.0	0.6
Totals	11.3	88.7	100.0

In general, about 55% of a tree's biomass is found in the merchantable bole, 25% is in the top (leaves and branches), and 20% in the roots (Young et al. 1976). Bark, which is included in both bole and top figures, accounts for about 14% of total biomass. Coniferous trees have a greater percentage of their biomass in leaves (needles; 11%) than do deciduous trees (4%).

Although much of the forest land along the coast of Maine is capable of supporting biomasses comparable to those described above (i.e., 67 to 78 tons/acre; 150 to 175 t/ha), the actual average biomass is considerably less (table 9-8). The 3,309,800 acres (1,340,000 ha) of commercial forest land in the three sampling units in coastal Maine support an average of 16 tons/acre (35 t/ha) of merchantable timber (trees >6 inches; 15 cm dbh) or 32 tons/acre (72 t/ha) when total biomass of trees above and below ground is included (Ferguson and Kingsley 1972). The latter figure is about half what is expected. The reason for the discrepancy is that much of the forest land contains immature and understocked forest stands on which forest biomass is much lower than in mature fully stocked stands. Average biomass of merchantable timber is highest in the Washington unit (17 tons/acre; 39 t/ha) followed by the Hancock (15 tons/acre; 33 t/ha) and Capitol units (14 tons/acre; 31 t/ha). This is because the Washington unit has a higher percentage of its commercial forest land (63%) in pole-sized or sawtimber-sized stands, compared to the Hancock (57%) and Capitol (38%) units (table 9-9), and the higher percentage of pole- and sawtimber-sized stands is reflected in higher biomass values.

Primary productivity. Primary productivity is the amount of solar energy that is converted to plant tissue on a unit of area during a unit of time; it is expressed, therefore as a rate. Production is measured by either the weight of plant material grown on a unit of land or by the energy equivalent (kcal) of that tissue when oxidized. In this chapter the terms "forest productivity," "net primary productivity," and "productivity" will be synonomous and will refer to the increment in forest biomass (wt/unit area) during 1 year.

Forests are more productive than most terrestrial habitats because they support a large biomass and have a large photosynthetic surface. The extensive root systems rapidly absorb moisture and nutrients from the soil and make them available to the photosynthetic process.

The productivity of Maine's forests is below that of most North American forests, because Maine's soils are unusually shallow and low in nutrients. Productivity estimates for forest types similar to those found in Maine range from 3 to 5 tons/acre/year (6 to 11 t/ha/yr; Whittaker and Woodwell 1968), whereas in Maine forest productivity ranges from 1 to 3 tons/acre/year (3 to 7 t/ha/yr; Young 1971).

The distribution of forest productivity among the layers of a forest community reflects the distribution of biomass. In a New Hampshire hardwood forest 97% of the total above-ground production was due to the trees, 0.7% was due to shrubs, and 2.7% by herbs (Bormann and Likens 1979). This pattern is similar to that reported in other studies (Whittaker and Woodwell 1968, and others).

Table 9-8. Volume (millions cubic feet) and Biomass (t/ha) of Merchantable Timber in Commercial Forests in the Capital, Hancock, and Washington Sampling Units[a].

Sampling unit and forest type	Area of forestland (thousands)	Timber volume (millions cu.ft.)	Cu. ft./ha	Biomass (t/ha)
Capital				
Softwood		601.8	1296	18
Hardwood		454.6	979	13
Subtotal	1114 ac. (464 ha)	1056.4	2275	31
Hancock				
Softwood		641.5	1806	25
Hardwood		216.8	610	8
Subtotal	853 ac. (355 ha)	858.3	2416	33
Washington				
Softwood		1191.8	2054	28
Hardwood		457.1	788	11
Subtotal	1392 ac. (580 ha)	1648.9	2842	39
Total	3359 ac. (1400 ha)			

a Ferguson and Kingsley 1972.

Table 9-9. Percentage of Forest Land in Each Sampling Unit by Stand Size Class[a].

Stand size class	Unit		
	Capital	Hancock	Washington
Sawtimber and pole	38	53	63
Sapling-seedling and nonstocked	62	47	37

[a]Ferguson and Kingsley 1972.

The pattern of stand productivity at different ages was examined after clearcutting a 55-year old hardwood stand in New Hampshire. Within 2 years productivity was 38% of that before cutting, and by 6 years productivity exceeded that of the mature forest (Bormann and Likens 1979). Following this, a slight decrease in net productivity took place; the transition from one stage of succession to another generally is not smooth. Young and coworkers(1979) simulated stand productivity over time (15 to 55 years) for softwood and hardwood stands on dry, meso, and wet sites. They found a steady decline in productivity in all stands with the exception of hardwoods on dry sites, which showed a steady increase.

Stand productivity also varies with the level of soil moisture of the site. For both hardwoods and softwoods, at all ages, stands on meso (moderately wet or dry) sites are more productive than those on either dry or wet sites (Young et al. 1979). Hardwoods on dry sites are initially less productive (15 years) than those on wet sites but at 55 years they are more than twice as productive and almost equal those on meso sites. Softwoods are also more productive initially on wet sites but at 55 years they are only slightly more productive.

The forest industry is concerned with productivity of merchantable wood, which accounts for about 35% of the total productivity of a forest. The net annual growth of merchantable timber volume (biomass) for the three forest units sampled along the coast is summarized in table 9-10. Net production of commercial products ranges from 0.4 tons/acre/year (0.9 t/ha/yr) in the Hancock unit to 0.5 tons/acre/year (1.1 t/ha/yr) in the Capitol unit. The greater productivity of the latter may be due to the higher percentage of immature stands as described under "Biomass" above.

Table 9-10. Productivity of Forests in Three Units Sampled Along the Maine Coast[a].

Unit	Growing stock biomass (t/ha)	Average annual growth (t/ha/yr)	Percentage of growing stock
Capitol			
Softwood	18	0.84	5
Hardwood	13	0.29	2
Total	31	1.13	4
Hancock			
Softwood	25	0.73	3
Hardwood	8	0.16	2
Total	33	0.89	3
Washington			
Softwood	28	0.92	3
Hardwood	11	0.12	1
Total	39	1.04	3

[a]Ferguson and Kingsley 1972.

Decomposers and Consumers

Of the total energy fixed by green plants (net primary production), some is stored in the community as woody tissue and the rest is used by the consumer and decomposer organisms of the system. More energy flows through the detrital pathway (decomposers) than the grazing pathway (consumers) in forest systems. For example, in a mature stand of northern hardwoods in New Hampshire 99% of the nonwoody net production passed through the detrital pathway (Bormann and Likens 1979). In addition, much of the energy that flows through the grazing pathway ultimately ends up in the detritus food chain (e.g., feces and dead animals). The importance of the detrital chain is often overlooked, however, because the animals comprising the grazing pathway are more important and more visible to people.

Decomposers. There are two major groups of decomposer organisms: the soil microflora, which include bacteria, fungi, and protozoa, and the soil invertebrates, which include nematodes, earthworms, mites, snails, isopods, springtails, dipteran larvae, Enchytraeidae, diplopods, and coleopteran larvae (Edwards et al. 1970). Decomposers break down the organic matter and release nutrients, which are absorbed by plants. The actual chemical decomposition is accomplished by the microorganisms (bacteria, fungi, and protozoans), which possess enzymes necessary to hydrolize cellulose and lignin. This process is aided by the soil invertebrates (primarily earthworms, enchytreaid worms, diplopods, isopods, dipteran larvae, collembolas, and mites), which consume the litter and break it down mechanically. This increases the surface area that is exposed to further invasion by microorganisms and is considered the most important contribution to litter breakdown (Edwards et al. 1970). Very little chemical change takes place in the litter as it passes through soil invertebrates. These organisms receive their nourishment from the microflora and other small invertebrates that are gleaned from the litter. After litter breakdown soil invertebrates also serve to mix the organic material into the soil and form soil aggregates.

The soil invertebrates form the base of an entire food chain consisting primarily of predaceous invertebrates but also small mammals (moles, shrews, and voles), birds, reptiles, and amphibians.

Rate of decomposition. Temperature, moisture, pH, and type of litter determine the rate of decomposition. Decomposition is most rapid in a warm, moist environment. In acid soils, common to coniferous forests, fungi are the dominant decomposers, whereas in neutral or alkaline soils (most common in hardwood stands) bacteria are the most abundant decomposer organisms. In acid soils fewer soil invertebrates are present to break down and mix organic matter and, as a result, decomposition is slower than in neutral and alkaline soils (see "Soils," below).

Woody tissue (branches and trunks) may take several decades to decompose completely, whereas leaves, fruits, and buds usually decay completely in a few years. Leaves of yellow birch, sugar maple, and beech are 95% decomposed in 5, 9, and 11 years respectively (Bormann and Likens 1979).

Consumers. Consumer organisms include herbivores (primary consumers), insectivores, and carnivores (secondary or higher level consumers). In forest systems important primary consumers are insects and other invertebrates, mammals (deer, hare, squirrels, mice, and voles) and some birds (finches). Secondary consumers include predaceous invertebrates, birds (e.g., warblers, vireos, and thrushes), mammals (shrews, mice, weasels, minks, foxes, and bobcats), and reptiles and amphibians (frogs, toads, snakes, and salamanders). Gosz and coworkers (1978) listed the consumers in a New Hampshire deciduous forest in the following order of importance: chipmunks, mice, foliage-eating insects, birds, deer, and hares.

The biomass of invertebrate consumers is miniscule compared to the total plant biomass. In a pine plantation in England the biomass of foliage-feeding invertebrates ranged from .00004 to .002 ton/acre (.0001 to .005 t/ha), whereas plant material biomass was 67 tons/acre (150 t/ha; Ovington 1962). Despite these major differences invertebrates form the major food source for most species of birds, reptiles, amphibians, and some species of mammals.

Of the invertebrate consumers found in forest systems insects are most important. Herbivorous insects are divided into seven groups based on their feeding habits (table 9-11; Franklin 1970). Foliage-feeding insects are the most abundant group but under normal circumstances the foliage consumed is not damaging to the forest. Insect consumption of deciduous leaves in southern Ontario by forest insects was estimated to be 5% to 10% of the leaf surface area, which represented only 1.5% to 2.5% of total net primary productivity (Bray 1961 and 1964). As small as this seems Reichle and coworkers (1973) consider it an overestimate. Under normal circumstances the effect of insects as mortality factors in Maine's forests is insignificant. Total annual mortality of trees averaged <1% of total growing stock between 1960 and 1970 and insects accounted for about 3% of this (Ferguson and Kingsley 1972). However, overpopulation of insect herbivores has occurred in Maine's forests and the results can be serious. Defoliating insects, such as spruce budworm, gypsy moth, saddled prominent caterpillar, and satin moths sometimes reach high enough populations to cause complete defoliation of host trees. Most trees can withstand this defoliation for a few years but if insect populations remain high the trees die.

The most destructive defoliator in Maine forests is the spruce budworm, which attacks primarily balsam fir and spruce. A major outbreak of spruce budworm occurred in Maine between 1910 and 1919 (Pistell and Harshberger 1979). The infestation covered the entire state and in all an estimated 27 million cords of wood were killed. The severity of the infestation varied among areas but in some cases up to 95% of the fir and 85% of the spruce was killed over areas of several thousand acres.

Maine's forests are currently experiencing an outbreak of budworm that began in 1972. By 1979, 6 to 7 million acres (about 40% of Maine's forestland) were infested to some degree. Approximately 3 million acres were seriously infested, with tree mortality approaching 40%. Pesticides (including carbaryl, trichlorfan, and aciphator) are used to control budworm numbers. The spray program peaked in 1976 when 3.5 million acres were sprayed (Pistell and Harshberger 1979). In 1977 and 1978 about one million acres, and in 1979 over 2.5 million acres, were sprayed.

Outbreaks occur in stands of overmature balsam fir under certain weather conditions (warm, dry days in late May and early June). Trees begin to die after 5 years of defoliation and mortality is nearly complete after 8 years

Table 9-11. Foods of Forest Insect Orders[a]

Insects	Food items						
	Foliage	Bud, twig terminal shoots	Seeds	Bark	Sap	Wood	Roots
Lepidoptera (moths and butterflies)	X	X	X	X	-	X	-
Hymenoptera (wasps, bees and ants)	X	-	X	-	-	X	-
Orthoptera (grasshoppers and crickets)	X	-	-	-	-	-	-
Diptera (flies and mosquitoes)	X	-	X	X	-	-	-
Coleoptera (beetles)	X	X	X	X	-	X	X
Hemiptera (bugs)	-	-	-	-	X	-	X

[a]adapted from Franklin 1970.

(Belyea 1952). Large numbers of dead trees are conducive to fire, which often follows in budworm-killed stands. Succession following fire leads to mature spruce-fir stands in 50 or 60 years in which conditions are again conducive to outbreaks.

Insect defoliation may have serious ramifications for forest systems exclusive of the consumption of energy. Decreased leaf surface area reduces the energy available to other consumers and lowers the rates of transpiration and nutrient uptake. The result is increased loss of nutrients in streamflow, which increases when leaf surface area is reduced (Hibbert 1967). Other destabilizing effects of insect defoliation on forest systems are: (1) populations of soil invertebrates that feed on newly fallen leaves decreases; (2) increased solar radiation to the forest floor increases the rate of decomposition and subsequent nutrient loss (Bormann and Likens 1979).

Insects also damage trees by boring into the bark and wood (Coleoptera, Lepidoptera, and Diptera) and sucking the sap (Hemiptera). These insects weaken trees and create openings where disease can enter. Other insect pests in Maine's forests include the white pine weevil and balsam wooly aphid. While these insects are not important as mortality factors they result in reduced wood quality.

Forest communities along the coast of Maine support abundant and diverse bird populations. Warblers, vireos, thrushes, finches, flycatchers, and woodpeckers are the most important groups and 100 or more species may be found. A large part of the forest avifauna is migrants. Peak densities of birds occur during the breeding season (May to July), when populations of breeding adults in Maine's forest average 13 to 20 birds/ha for softwood stands and 15 to 16 birds/ha in hardwoods. Winter lows have not been accurately determined in Maine but in New Hampshire deciduous forests, populations of two to three birds/ha were recorded. Winter densities of birds should be higher in softwood stands. Seed-eating finches are abundant in softwood stands, which have more benign microclimate for insectivorous species as well (e.g., chickadees, nuthatches, and woodpeckers).

Most birds found in Maine forests are insectivorous during the breeding season and are classified as secondary or higher level consumers. However, the insects consumed by birds may be more closely tied to the detrital food chain than to the grazing pathway (Bormann and Likens 1979). During most years the summer diet of birds in a New Hampshire deciduous forest consists of adult Diptera (whose larvae are detritivores in soil and streams), adult Coleoptera (whose larvae prey on soil invertebrates), and adult Hymenoptera (secondary and tertiary consumers). When an outbreak of saddled prominent caterpillars occured birds switched to this source of food and became part of the grazing pathway. In late summer, fall, and winter, seeds and fruits make up a large portion of the diet of birds.

Birds consume only 0.1% of the net primary production of deciduous forests in New Hampshire (Holmes and Sturges 1973); however, this figure is not indicative of the role of birds in forest systems. Between 1960 and 1970 the yellow-bellied sapsucker was responsible for 2% and 5% of the total annual mortality of softwood and hardwood trees respectively in Maine (Ferguson and Kingsley 1972). This species of woodpecker drills holes in the bark of trees and returns later to eat the sap and especially insects which are attracted to it. These holes become avenues for disease and insects and occasionally a tree is completely girdled. Birds also can affect tree reproduction, by consuming seeds and nipping the buds from young trees. The mobility of birds makes them important in seed dispersal and as vectors of various diseases (Shugart et al. 1975; and Warner 1976). Woodpeckers were considered a major factor in the spread of the chestnut blight and birds have been implicated as important long-distance vectors of the parasite Arceuthobium vaginitum (dwarf mistletoe) in Colorado (Hudler 1976). [A morphologically similar congener (A. pusillum) occurs in the characterization area.]

Cedar waxwings (often called cherry birds) and other fruit-loving species disperse seeds of pin cherries (Prunus pennsylvanica) and raspberries (Rubus spp.). Both are important pioneering species in secondary plant succession (Marks 1974). Insectivorous birds (e.g., warblers, vireos, and thrushes) can be effective in preventing or delaying the outbreak of spruce budworm populations, by consuming sufficient numbers of insects while populations are low. Once the budworm population has erupted, however, birds are capable of consuming only a small fraction of the budworm population (George and Mitchell 1948).

Mammals found in Maine's forests are either primary or secondary consumers or both. Major herbivores are deer, moose, hares, mice, chipmunks, and squirrels. Secondary consumers are foxes, weasels, fishers, coyotes, minks, bobcats, shrews, and bats.

The influence of herbivorous mammals on forest vegetation is, for the most part, insignificant. Only 2.5% of total net production in a pine-oak forest on Long Island was consumed by herbivores, only a small portion of which was due to mammals (Woodwell and Whittaker 1968). However, browsing by deer and hares sometimes removes significant portions of the vegetation (see "Terrestrial Mammals," chapter 17). Deer and hares can inhibit regeneration by consuming seedlings and growing tips of saplings. Squirrels and mice can destroy up to 90% of a forest's seed crop (Baker 1950); the extent to which this is a problem in Maine is not known. On some large coastal islands where hunting is restricted (Mt. Desert Island and Isle au Haut) deer populations sometimes severely inhibit forest regeneration (Baird 1966). Concentrations of deer in winter yarding areas can lead to overbrowsing of the vegetation in the wintering area. White cedar, a preferred winter food, is particularly vulnerable.

ABIOTA

Forest vegetation influences its environment by affecting the penetration of solar radiation, the interception of precipitation, and wind and temperature profiles. The degree of its influence depends on the density of the forest canopy. As a rule, tolerant trees (i.e., sugar maple, beech, hemlock, and red spruce) form dense crowns and intolerant trees (such as aspen, paper birch, and pines) have more open canopies; consequently trees exert an increasing influence over the forest environment as succession progresses.

Solar Radiation

The amount of light penetrating a forest canopy is a major factor affecting plants in the understory and on the ground. Under dense canopies as little as 1% to 2% of the total solar radiation reaches the forest floor (Vezina 1961). Only highly tolerant plant species survive under these low light conditions (such as mosses and lichens). The conical shape of spruce and fir allows sunlight to penetrate deeper into the canopy but on the ground light levels may still be only about 3% of those in the open (Vezina 1961; and Vezina and Pech 1964). Red and white pines have less dense canopies and as much as 10% to 15% of incident solar radiation may reach the ground (Spurr 1964). The sunlight that many species of understory plants receive in early spring, before the trees develop leaves, gives them the energy to survive for the remainder of the year. In addition, small patches of direct sunlight reaching the forest floor through holes in the canopy (called sunflecks) are important to understory plants. Although sunflecks are small, changes in the angle of the sun causes flecks to move across the forest floor and provide direct sunlight to most of the ground vegetation for at least part of the day.

Temperature

Air temperatures in a forest are somewhat stratified, because of the amount of solar radiation reaching each stratification level and the degree of air circulation permitted by the vegetation. In deciduous stands in summer, maximum temperatures are reached just below the top of the canopy, where solar radiation is most intense and air circulation is reduced. Air temperatures in the canopy of coniferous stands are usually less than those in hardwood stands, because the open canopy of coniferous allows more air circulation. Minimum temperatures in forests are found near the ground (Geiger 1965).

Temperature extremes are much greater in open ground than in forests. During the day the canopy intercepts solar radiation, which reduces maximum temperatures beneath the canopy. At night the canopy traps thermal radiation from the ground and reduces wind velocity, thus increasing nighttime temperatures. Forests usually reduce daytime maximum temperatures more than they increase nighttime temperatures (Kittredge 1948 and Spurr 1957). In deciduous forests in winter, these differences in temperatures are much reduced (Spurr 1964).

Wind

Wind velocity is reduced by friction with forest vegetation and is deflected up and over the canopy. The degree of interference is dependent on the density of vegetation. In tall dense stands wind velocity may be only 20% of that in the open (Fons 1940). In stands with dense understory, wind velocity decreases near the ground, whereas stands with more open understories have higher wind velocities.

Water

Precipitation falling on a forest may be either intercepted by the vegetation (interception) or fall directly to the ground (throughfall). Precipitation that is intercepted is either absorbed by the leaves, evaporated into the atmosphere, or drained down the stem to the ground (stemflow; Zinke 1967; Geiger 1965; and Kittredge 1948). During light rains nearly all of the precipitation may be intercepted by the canopy, whereas in heavy, prolonged rains interception may be as little as 10% (Voight 1960). Dense canopies intercept more rainfall than open canopies and coniferous trees intercept more than deciduous trees.

During an average growing season about 80% to 90% of the incident precipitation that falls on a forest reaches the ground (Likens et al. 1977). Stemflow averages about 5% of the incident precipitation, although it may be as high as 10% to 16% for smooth-barked species (beech) or as low as 1% for rough-barked species (sugar maple; Horton 1919; and Geiger 1965). Much of the water reaching the ground is held in the soil by organic matter, absorbed in the tree roots and transpired through the leaves. About 60% of the rain falling on a deciduous forest in New Hampshire becomes runoff. The remainder is either evaporated or transpired. Following deforestation, streamflow may increase 25% to 40%. This not only affects the water supply in the soil but also causes increased loss of nutrients and soil particles as well (see "Logging Effects" below).

Soils

Forest soils consist of four basic layers (also called horizons). The most important of these ecologically is the organic layer, or forest floor, which consists of fresh or partially decomposed organic matter. Below this is the A horizon, which consists of mineral soil to which organic matter has been added by leaching and mixing and from which clay, iron, and aluminum have been removed by leaching. The B horizon has concentrations of clay, iron, aluminum, and humus leached from the A horizon. Finally, the C horizon consists of weathered material, which may or may not resemble the bedrock (depending upon whether or not it has been transported by water, glaciers, or wind).

The formation of soils under Maine's softwood stands is strongly influenced by the acidity of the foliage. As a result of this acidity the main decomposer organisms are fungi, which also produce acid and depress the activity of soil organisms (see "Decomposers" above). Slow decomposition and poor mixing of the organic matter into the soil results in large accumulations of litter, which rest on top of the mineral horizons. These are the so-called "mor" soils. The mineral soil is also affected by the acidity, which causes a greater leaching of clay, organic matter, iron, and aluminum from the A horizon, which is deposited in the B horizon; a process known as "podzolization."

Under hardwood stands the lower acidity of the litter results in an organic layer formed under different circumstances. Bacteria replace fungi as the major decomposer organisms and animal activity, which is closely tied to bacterial activity, increases and nitrification is accelerated. Decomposition is rapid and much of the organic matter is rapidly and thoroughly mixed with the top layers of mineral soil by soil invertebrates and through leaching, so that only a thin layer of litter rests on top of the soil. These are the so-called "mull" soils. Organic matter content of the mineral soil is higher than in softwood stands and leaching of elements is reduced somewhat.

BIOGEOCHEMICAL CYCLES

Some 30 to 40 elements are essential to plant and animal organisms (Smith 1966). The 18 essential elements for plants have been divided into macronutrients (those needed in large quantities) and micronutrients (e.g., trace elements and minerals). The macronutrients include carbon, hydrogen, oxygen, nitrogen, phosphorous, potassium, sulfur, magnesium, and calcium. The micronutrients are iron, sodium, chlorine, boron, maganese, zinc, copper, molybdenum, and cobalt (Gauch 1972).

The movement of nutrients within an ecosystem involves uptake or assimilation of nutrients by plants from the available nutrient pool in the soil, or by absorption from the atmosphere (figure 9-5). These elements may be incorporated into long-term storage in woody tissue or released to the system through leaf-fall, herbivore consumption, plant respiration, or leaching from plant tissue. Subsequent breakdown of litter by decomposers in the soil makes the nutrients available to plants again. Weathered soil and minerals contribute to the nutrient pool; some elements may be redeposited as secondary minerals.

Nutrients enter and leave a forest system by meteorological, geological, or biological processes. Meteorological inputs or outputs exist in the form of atmospheric gasses (e.g., CO_2 and O_2), dissolved substances in rain or snow, and wind-blown particulate matter. Geological movements include those elements dissolved or suspended in surface or subsurface drainage and movement of colluvial materials. Biological movement is the transfer of animal material from one ecosystem into another. The nutrient budget for a northern hardwood forest in New Hampshire was studied extensively (Likens et al. 1977) and the conclusions listed below probably apply to most of Maine's forests (table 9-12):

1. precipitation and gasses are the major source of sulfur, nitrogen, chlorine, and phosphorus;
2. weathering is the major source of calcium, magnesium, potassium, iron and sodium;
3. photosynthesis and nitrogen fixation play a major role in carbon and nitrogen inputs;
4. ecosystems show net gains of nitrogen, sulfur, phosphorus, and chlorine and net losses of silicon, calcium, sodium, aluminum, magnesium, and potassium.

Most of the loss is in surface and underground runoff, for which weathering somewhat compensates.

In undisturbed forest systems the nutrients available through meteorologic and geologic sources are usually adequate to support forest vegetation. In some areas deficiencies of certain elements or toxic levels of others may exist but this is unusual. Problems concerning biogeochemical cycles arise when people alter the flow of nutrients through ecosystems by air pollution, lumbering, fire, and increased erosion. These problems will be discussed below.

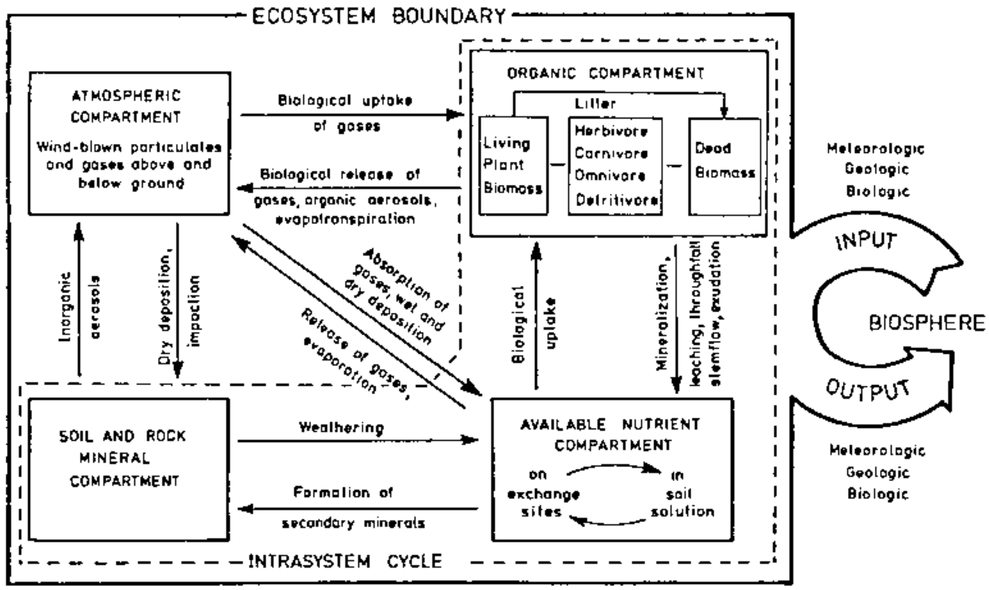


Figure 9-5. Major storage compartments and flows of nutrients within the forest system (from Bormann and Likens 1979).

Table 9-12. Percentage Contribution of Nutrients from Several Sources in a New Hampshire Deciduous Forest[a]

Nutrient	Precipitation	Gas or aerosol	Weathering
Iron	<1	<1	100
Calcium	9	--	91
Potassium	11	--	89
Magnesium	15	--	85
Sodium	22	--	78
Nitrogen	31	69[b]	<1
Sulfur	65	31	4

[a]Bormann and Likens 1979.
[b]nitrogen fixation.

PERTURBATIONS

More or less permanent and serious disturbances of forests usually are caused by the destruction of forest lands for urban or suburban development and for roads, power lines, and other industrial and commercial developments. Determination of the rate at which forests are destroyed along the coast is a necessity in Maine. The amount of forest land in Maine actually increased slightly (3%) between 1960 and 1970 (Ferguson and Kingsley 1972), because old farmland was abandoned and succeeded to forest at a faster rate than new forest land was cleared.

Developed areas also affect forests indirectly by the chemical pollutants they release into the water and air. A detailed study of nutrient inputs into a deciduous forest in New Hampshire has revealed a wide array of airborne pollutants entering the ecosystem, even though the area is remote from any large source of pollution. These include sulfuric acid, nitric acid, oxidates (ozone), heavy metals (Pb), and pesticides (DDT; Borman and Likens 1979).

Acid precipitation is common throughout much of the Northeastern U.S. (Likens and Bormann 1974; and Likens 1976). The effects of these pollutants on forest systems are hard to determine, since the biogeochemical relationships are complex, but some of the direct consequences are the leaching of nutrients from foliage and the soil (Wood and Bormann 1974; and Abrahamsen et. al 1976), erosion of the cuticles of leaves, increased susceptibility of trees to disease, failure of germination and establishment of conifer seedlings, alteration of the nitrogen availability in the soil, and decreased rate of decomposition.

Forest systems also absorb heavy metals from the atmosphere. Siccamma and Smith (1978) found that 98% of the lead entering a forest system was retained. Other metals that show increasing levels in the forest included aluminum, gold, chromium, nickel, lead, antimony, and vanadium (Galloway and Likens 1977). While these studies were conducted in the Adirondack Mountains and in New Hampshire, the same levels probably exist in Maine. The long-term effects of metals and the extent to which they can continue to be accumulated are not known.

Forest systems are also affected by logging, fire, and insect and wind damage. These disturbances, particularly that of logging, affect a greater amount of Maine's forest land each year than does urban or suburban development. Their effects are not permanent and forest systems recover from them. Wind affects forests in ways similar to those of logging. These effects and those of fire are discussed below.

Effects of Logging

The common cutting and logging practices employed in Maine are discussed in chapter 19, "Commercially Important Forest Types." The two main types of practices are selective cutting and clearcutting. Management of uneven-aged stands employs selective cutting, which strives to simulate the conditions in a steady-state forest, removing only selected, mature trees that would normally be lost through natural mortality. This type of system is best for regenerating tolerant tree species, because it maintains a closed canopy at all times. Selective cutting usually does very little damage to forest systems. The forest floor and understory vegetation is somewhat disturbed by heavy machinery, road construction, and use. The forest system largely remains intact and tends to function normally.

Clearcutting simulates conditions in a forest that follow a major disturbance, such as fire or wind storms (Bormann and Likens 1979) and regrowth is principally intolerant species. Major destruction of a forest system alters the water and nutrient cycles and interrupts the pattern of productivity and biomass accumulation, decomposition, and mineralization. Quantitative data concerning these effects on Maine's forests are lacking but research in northern hardwood stands in New Hampshire are applicable (Bormann and Likens 1979).

Removal of the forest canopy allows increased solar radiation to reach the ground, causing higher soil temperatures. Removal of trees reduces the rate at which water is removed from the soil by plants and transpired, thus, increasing soil moisture. Higher soil temperature and moisture content promotes more rapid nitrification and decomposition of litter, which releases more nutrients for plant and animal use. The control that the forest vegetation previously had over the flow of water through the systems is partially lost, resulting in accelerated runoff and erosion and greater annual extremes in high and low flow. Increased runoff causes accelerated particulate matter loss and soil erosion. The decomposition of the residual organic matter, such as logging slash, reduces these effects for up to 2 years, at which point vegetation may cover the site sufficiently to prevent further losses.

After cutting, the nutrients removed from the forest in the harvestable stems must be replaced. To prevent nutrient deficiencies following future cuttings (Bormann and Likens 1979) harvest rotations must be based on the time it takes for these nutrients to be replenished from atmospheric, geologic, or meteorologic sources (see "Biogeochemicals" above). The northern hardwood stands studied in New Hampshire would require approximately 65 years to replenish nutrients removed by stem-only harvesting. Other forms of logging that are becoming popular, such as whole-tree (all above-ground portions) or complete tree (includes roots) logging, have been found to remove two to four times as much nitrogen as stem-only harvesting (Hornbeck 1977). The other nutrients would be expected to be decreased comparably. More time must be allowed between rotations to replenish nutrients, following these more intensive harvesting practices. In addition, these practices result in greater disturbance to the forest floor, increasing decomposition and erodability of the forest floor and delaying revegetation.

An estimated nutrient budget based on sustained yield practices in Maine's forests indicated that levels of nitrogen, sulfur, phosphorus, and potassium could become deficient after a few rotations of complete-tree harvesting. In order for this type of harvesting practice to continue profitably nutrients and organic matter must be replenished; otherwise, high productivity is a short-term benefit only.

The extent to which forest systems are affected by tree removal depends on the care with which logging is carried out. Excessive disturbance of the forest floor and residual understory vegetation from heavy machinery may expose the soil to erosion and delay regeneration. For example, improperly placed roads can cause excessive erosion and result in soil compaction. Cutting too close to streams may cause bank erosion and higher water temperature (because of increased sunlight). Large clearcut areas may not have an adequate seed source nearby if adequate seed sources are not present in the duff, which they usually are not in Maine's spruce-fir stands (Frank and Safford 1974). Cutting on steep slopes with shallow soils also may lead to erosion and delayed regeneration. Since peak runoff is increased by clearcutting, a watershed approach to cutting patterns (selective cutting or block cutting) is most desirable; that is, only a certain portion of a watershed is harvested at any one time to prevent serious soil, nutrient, and runoff problems.

Other practices that may affect the forest system are spraying herbicides and pesticides and piling and burning slash. Herbicides are used to kill woody deciduous trees and shrubs and herbaceous plants (such as raspberry, cherry, birch, and aspen) that often dominate clearcut sites for many years after cutting. These species outgrow the commercially desirable species in much of Maine's forest land, which delays the rotation time of merchantable species. Selective herbicides are used to kill these "weed" species when adequate regeneration is present or prior to planting seedlings. The long term effect of removing this stage of succession from a regenerating forest system is not known (Bormann and Likens 1979). These species are adapted to rapid growth and their presence is important to the prevention of long-term degradation following human disturbance. Deciduous species have lower acidity in their litter, which promotes greater soil fertility. Their loss would affect many wildlife species that are important to humanity and to ecosystem functions. They also provide valuable food and cover, and when compared with uniform stands of softwoods support more numerous and diverse wildlife populations. In addition, the long-term toxic effects of herbicides on plants and animals is uncertain. The effects of logging on birds and mammals are discussed further in chapters 16 and 17, "Terrestrial Birds," and "Terrestrial Mammals" respectively. Briefly, some species are benefitted by habitat changes after logging, while others are adversely affected.

Pesticides are used in forest systems to control insect defoliators, primarily the spruce budworm. The chemicals currently used, such as Sevin, are relatively short-lived and break down rapidly. Consequently, they are not concentrated in animal or plant tissue as were some of the pesticides (e.g., DDT) that were used in the past. On the other hand, nontarget insects may be killed by spray and reduce the abundance of insects as food for most birds and small mammals.

During clearcut logging, slash is often piled and sometimes burned. This is done because slash inhibits the growth of tree seedlings. However, slash has been shown to be important during the immediate postcutting period. Slash can reduce the effects of rainfall and erosion, shade the ground, reduce soil temperatures, and release nutrients as it decomposes (Bormann and Likens 1979). Excessive disturbance of the forest floor when slash is piled also can result in increased decomposition and leaching of nutrients.

Roads are necessary for access to forest stands. In New Hampshire roads occupied between 2% and 10% of the forests being cut (Bormann and Likens 1979). Roads reduce productivity, because of disturbance and compaction of the soil, removal of organic matter, and the directing of the flow of water by drainage ditches associated with roads.

Effects of Fire

The severity of a fire largely determines its effects on forest systems. Light surface fires destroy only the surface litter and ground vegetation, whereas severe surface and crown fires may kill all the vegetation and destroy the organic matter. As a result, the modifying influence of the forest canopy over the forest environment is lost and changes occur in the water and nutrient cycles, and the plant and animal life. Many of these effects are similar to those following logging and are discussed above. Other aspects unique to disturbance during or after a fire are discussed below.

The amount of humus is reduced after fire because humus burns and because the rate of decomposition increases after fire. Decomposition is increased by higher soil temperatures and increased ash (alkaline) from burned plant materials (see "Decomposition" above).

Soil nutrients increase immediately after fires because nutrients in dead and living plant material are released by burning. Initially these nutrients may be leached from the soil but vegetation (especially grasses or herbs) quickly recolonize the burned area and absorb the available nutrients. Since these plants are short-lived, the nutrients are rapidly released again.

Fire may result in large losses of nitrogen from the soil but it has been found that the nitrogen lost is in a form that is unavailable to plants. On the other hand, fire simultaneously increases the level of mineralized nitrogen that is available to plants.

The abundance of bacteria in soil sharply declines immediately following fire and then rapidly increases to above pre-fire levels within a few months. Only those bacteria in the top 1 to 2 inches (3 to 5 cm) of soil are killed by fires and repopulation from lower layers is rapid. The increased nutrients and decreased acidity promote high bacterial populations.

The abundance of fungi is related to temperatures, acidity, and nutrient sources. High temperatures reduce spore viability but reintroduction from areas around the burned areas is rapid. Changes in pH affects the species composition of fungi present, since species have different preferences.

For the most part, the soil fauna is not usually hurt by fires, because they can escape underground. The major exceptions are the mites and collembolans. The soil fauna are adversely affected by the loss of organic matter (humus), which provides both food and habitat for soil organisms. The xeric conditions on the forest floor following fire also are not conducive to soil organisms. Data on the organisms that have been studied so far indicate that earthworms are reduced significantly following fire, primarily because of the loss of soil moisture; spiders are drastically reduced because they inhabit the uppermost soil layers; centipedes and millipedes are reduced because of a lack of prey populations; and mites and collembolans are reduced by high temperatures but recover in 3 to 4 years.

Most fires do not seem to cause a considerable amount of direct mortality to vertebrates, since animals are able to escape severe temperatures by burrowing underground, or by moving to residual patches that are not burned, or into water, or simply by outrunning the fire. The indirect effects are more important. On-site climate is modified by burns; air temperature extremes are greater, air moisture is lower during the day, wind velocity is higher, and snow depths are greater. Vegetation structure is the most important change following forest fires. Fires rarely burn evenly and, thus, create a mosaic of old and new habitats. Burns create edges and interspersion of habitats, which are beneficial to species requiring a variety of resources. Fire also alters the plant species available as food; grasses, herbs, woody shrubs, and browse, particularly increase. In addition to the quantity, the quality of food may be improved as well. A slight increase in the protein or nutrients available may occur.

INTERACTIONS WITH OTHER SYSTEMS

Forest systems are important to other systems (primarily aquatic) as a source of nutrients and energy, and as a moderating effect on the flow of water from terrestrial to aquatic systems. Many of the brooks and streams that drain forest habitats in Maine are relatively infertile and rely on nutrients and organic matter inputs from forests, upon which a detritus-based trophic structure is built (see chapters 6, 7, and 8, "The Riverine System," "The Palustrine System," and "The Lacustrine System" respectively for more detailed discussions). The output of nutrients and organic matter from Maine's forests is not known but is currently being studied.

Forests have an equally important impact on aquatic systems because they moderate the discharge of water (surface or underground runoff) to aquatic systems. Precipitation is held in trees and vegetation in forests, and in the organic matter in the soil. Much of the water is absorbed by the roots and transpired or evaporated directly from the plant surfaces. This reduces the amount that reaches streams, rivers, or lakes. The vegetation and organic matter on the forest floor reduces surface runoff, which increases the time it takes for water to reach streams, and distributes the runoff over a longer period of time. As a result, flooding in streams and rivers draining forest land is less severe than in those draining agricultural or developed lands, where runoff is more rapid. The "insulative" protection of forest vegetation delays the melting of snow in the spring, a time when flooding is usually most severe. In addition, the ground under forests is usually not frozen (as is the case in open areas such as agricultural land) and much melting snow can be absorbed and further delayed as it filters underground to streams. Moderation of runoff is important not only to the water bodies directly receiving this discharge but to all the aquatic systems it subsequently reaches (e.g., large rivers, lakes, estuaries).

IMPORTANCE TO HUMANITY

One of the greatest values of Maine's forests is economic: the commercial use of timber products. Maine's timber resources are used for pulp and paper, sawlogs, veneer logs, cooperage, pilings, posts, poles, and fuelwood (Ferguson and Kingsley 1972). Maine's forest products accounted for 41% of the total value of the State's manufacturued products in 1975 ($11.5 billion) and the industry employed 25% of Maine's work force with a combined payroll of $201 million (30% of the State total). A major share of Maine's economy is dependent on the forest system. Coastal Maine has 20% of the State's commercial forest land and accounted for 17% of the State's total timber harvest in 1970 (Ferguson and Kingsley 1972). Many of the primary wood processing plants that manufacture goods from timber are located along the coast, mainly in the midcoast and southern coastal regions.

The use of wood to heat homes and other buildings is becoming increasingly important to Maine. The increased demand on Maine's forests for the less desirable hardwoods that are used for heating (such as red maple and gray and paper birch) could adversely affect the functioning of forest systems. As pointed out earlier, these species, most of which are early successional species, are important to the reorganization of forest systems after disturbance from logging and help to regain control over the site and rebuild the store of nutrient and organic matter in the forest floor. Cutting these stands at short rotations could deplete the sites and not allow them to replenish nutrients and organic matter.

In addition to the economic values associated with Maine's forests, these systems are perhaps the most important habitats for outdoor recreation in Maine. Forests are used for numerous outdoor activities, which include camping, hiking, snowmobiling, hunting, trapping, skiing, and sightseeing. Maine's forests also help to maintain the quality of the streams and rivers that drain forest land and which support recreation, including fishing and canoeing. The unspoiled, remote nature of the State's forest systems draw many tourists each year.

RESEARCH NEEDS

Extensive studies have been conducted recently on several forest systems outside of Maine and the general conclusions concerning forest functions can be applied to Maine's forests. However, because differences in topography, drainage patterns, climate, soils, and plant species composition influence ecological functions, studies of productivity, biomass, nutrient and mineral cycles, and hydrology need to be conducted in Maine. In addition, the influence of fire and cutting practices on these processes needs to be determined.

Of more immediate concern is the need for more detailed inventories of forest systems along the Maine coast. Inventories of forest types, age classes, cutting practices being employed, herbicides and pesticides being used, and rate of harvest are needed. To determine changes in the amounts of forest land it would be necessary to repeat these inventories periodically.

Also of importance is the role of coastal forests in determining water flow to major rivers and estuaries. The degree to which Maine's forests are being affected by air pollution (acid rain and heavy metals) needs to be investigated.

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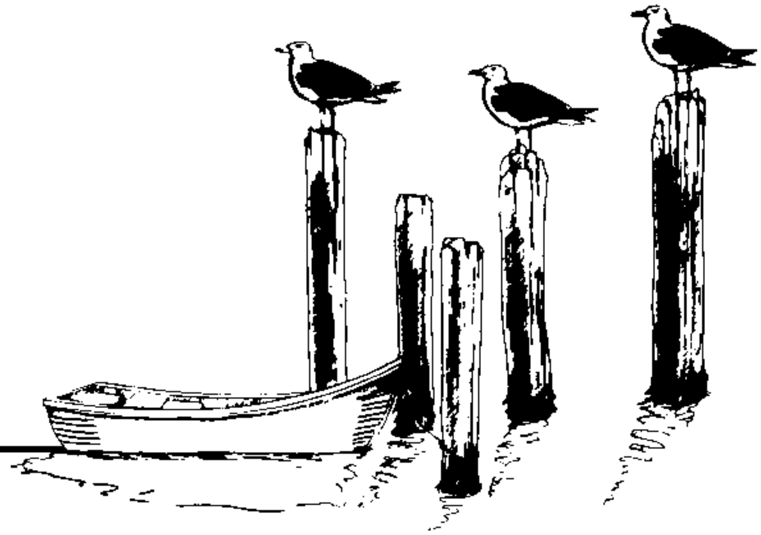
Chapter 10 Agricultural and Developed Lands

Author: Craig Ferris



Fifteen percent of the land in coastal Maine has been developed as real estate or has been or is used presently for farming. Of this, agricultural lands (croplands, pasture land, and blueberry barrens) presently comprise about 4% of the coastal area. Developed lands (urban, suburban, and industrial lands, parks, roads, and utility rights-of-way) make up 9%, and oldfields (abandoned agricultural lands usually in the process of reverting to forests) make up 2%.

Agricultural and developed lands are highly valued lands. They are also natural environments that have been altered extremely and are a source of pollutants (agricultural, municipal, and industrial wastes) in the ecosystem. Oldfields, on the other hand, are nature's attempt to reestablish climax vegetation in a denuded area.

The principal value of oldfields is wildlife habitat. The natural mosaic of cover types resulting from vegetative succession on oldfields provides valuable "edge" habitats that support an abundance of wildlife, including many game species (e.g., deer). Revegetation of oldfields helps to stabilize the hydrological and biogeochemical cycles of the area and benefits the riverine system. However, oldfields may be reclaimed easily for agriculture or industrial and urban development.

This chapter discusses separately the three types of land use, their contributions and special problems in the coastal area, and some functional aspects of their plant and animal life in the ecosystem. Management considerations and data gaps also are reviewed at the end. Common names of species are used except where accepted common names do not exist. Taxonomic names of all species mentioned are given in the appendix to chapter 1.

AGRICULTURAL LANDS

Farmland along the coast of Maine is used for tilled crops (hay, potatoes, corn, and vegetables) and for orchards, pasture, and blueberry culture. Farming reached its peak in Maine in 1880, when over 1.4 million acres

(551,181 ha) were cultivated on 64,000 farms. Acreage declined steadily until 1969 when only 0.7 million acres (275,591 ha) on 8000 farms were under cultivation. The trend in Maine and elsewhere in the U.S. was toward fewer but larger farms. Since 1969 the decline in acreage under cultivation has slowed (Bureau of Census 1977).

Currently the coastal counties of Maine contain an estimated 360,000 acres (141,732 ha) of farmland, which comprise 8.3% of the total land area (Bureau of Census 1977). About half (52.7%) is classified as farm woodland and does not qualify technically as farmland as defined here. When the acreage of woodland is subtracted the coastal counties contain only 147,000 acres (57,874 ha) of farmland, which accounts for 3.4% of the land area (table 10-1). Of the 147,000 acres (57,874 ha), 55% (87,773 acres; 34,556 ha) is in harvested crops and 16% is pasture. The remaining 30% includes woodland pasture, house lots, barn lots, roads, wasteland, ponds, and range land. Of the harvestable crops (table 10-2), hay accounts for the largest area (62%), followed by blueberries (4%), and field corn (8%). Over 75% of the blueberry production is in Washington County. Sorghum, wheat, potatoes, vegetables, and orchard fruit make up the other 6.5%.

Farmland provides a significant economic benefit for coastal Maine. The market value of all agricultural production from the coastal counties in 1974 was $71 million (table 10-3). Waldo County (region 4) was highest, accounting for about 43% of the total.

Table 10-1. Total Area (acres), Agricultural Area (acres) and Percentage Contribution of Farmland Types to the Total for Each County and for All Counties Combined[a]

County	Region	Total area (acres)	Agricultural area (acres)	% of total area	Percentage of farmland		
					Crop-land	Past-ure	Other
Cumberland	1	564,185	34,946	6.2	58	17	25
Sagadahoc	2	165,299	7552	4.6	57	17	25
Lincoln	3	292,100	13,244	4.5	56	19	25
Knox	4	235,775	12,730	5.4	45	26	29
Waldo	4	472,704	40,036	8.5	52	18	30
Hancock	5	989,163	8726	0.9	43	11	47
Washington	6	1,625,327	29,674	1.8	61	6	33
		4,345,553	146,908	3.4	55	16	30

[a]Bureau of Census 1977

Table 10-2. Area (acres) of Crops in the Coastal Counties of Maine[a]

County	Region	Hay	Blue-berries	Field corn	Potatoes	Vege-tables	Orchard fruits	Sorghum	Wheat
Cumberland	1	15,871	233	2286	1234	710	769	130	4
Sagahadoc	2	3771	1	377	--	196	20	115	--
Lincoln	3	6032	702	389	131	114	71	--	--
Knox	4	4312	1055	178	11	141	90	--	--
Waldo	4	16,476	929	2878	694	171	187	140	1
Hancock	5	1332	2132	19	82	92	92	--	--
Washington	6	3024	14,640	267	86	51	29	18	1
Totals		50,828	19,292	6394	2238	1435	1218	403	6
Percentage		(62)	(24)	(8)	(3)	(2)	(2)	(1)	(1)

[a]Bureau of Census 1977.

Table 10-3. Market Value (thousands of dollars) of Farm Products Produced in the Coastal Counties of Maine in 1974[a].

County	Region	Market value (thousands of dollars)
Cumberland	1	16,080
Sagadahoc	2	3354
Lincoln	3	4128
Knox	3	8700
Waldo	4	30,248
Hancock	5	2644
Washington	6	5895
Total		71,049

[a]Bureau of Census 1977.

Plants and Animals

The diversity of plant and animal life on agricultural lands is low because of the dominance of crops and livestock. Although all three basic trophic levels (producers, consumers, and decomposers) are present on agricultural lands, each is represented by only a few species, which results in short food chains and simple food webs.

Native plant species that compete with crops for nutrients, water, and light, for the most part are destroyed by cultivation and herbicides. Pastures and orchards have a higher density and diversity of native plants than cultivated cropland. Oldfields have a wide variety of plants. In agricultural areas native species are most abundant in small patches along fences and roadsides, in corners of fields, and in low wet areas. Some important native plant species are spirea, dogwood, alder, crabapple, goldenrod, asters, and white pine.

The biomass of living vegetation on agricultural land also is small, because the plants are harvested at short intervals, usually every year, and plant biomass is not allowed to accumulate in woody tissue from one year to the next. No data are available on total biomass of plants on agricultural land in Maine. For the sake of comparison, however, the 1974 above-ground production of hay (207,480 acres; 84,000 ha) in Maine was 0.8 ton/acre (1.9

t/ha; Bureau of Census 1977). This is far lower than the 67 to 85 tons/acre (150 to 190 t/ha) of biomass in Maine's forests.

In spite of their low plant biomass, agricultural lands produce as much plant material (weight/unit area) each year as forest land (Lieth 1963). On a world-wide basis mechanized agriculture is 1.5 times more productive than moist temperate forests and 4 times more productive than boreal coniferous forests. The energy and nutrient subsidies provided in the form of machinery, fertilizers, pesticides, herbicides, and irrigation make the high productivity of farms possible. Without mechanization farmland is only about equally productive as boreal forests and less than half as productive as moist temperate forests. No data are available on the productivity of Maine's agricultural land. Farm productivity is measured in bushels or pounds of usable product and does not include roots and unmerchantable stems or leaves.

The plant material produced on agricultural land is utilized primarily by people or domestic livestock. A hypothetical energy budget constructed for a field of soy beans indicated that 43% of the net primary production was used by people (Odum 1971). Decomposition accounted for 44% (compared to nearly 99% in forest systems), insect and invertebrate pests consumed nearly 7%, and beneficial symbiotic organisms utilized the remaining 7%.

To maximize the plant material harvested from farmland, the primary consumers that feed on crops are controlled. The most important consumers are invertebrate and insect pests which are controlled with chemical pesticides. As a rule, vertebrate consumers cause only local problems in Maine. Some vertebrates that can be pests on agricultural lands are red-winged blackbirds, grackles, robins, sparrows, starlings, mice, woodchucks, hares, deer, bears, and raccoons.

Higher level consumers found on farmland are those that feed primarily on invertebrates and small vertebrates. These include songbirds, raptors (hawks and owls), shrews, weasels, foxes, and coyotes. For the most part these species utilize the edges of farmland, where it intersperses with forests, wetlands, and oldfields, because agricultural land lacks consistent food and cover throughout the year.

Abiotic Factors

The vegetation on farmland is generally sparse and may be absent for much of the year; consequently, it exerts very little influence over microclimatic features, such as rainfall, temperature, wind, and solar radiation. These variables fluctuate more widely on agricultural land than in forests.

Growing seasons along the Maine coast range between 130 and 160 days in length (table 10-4). They are influenced by the marine climate throughout the characterization area and differences in growing season are due to local topography. Mean frost data for several locations along the coast also are shown in table 10-4. Because agricultural lands lack the protective vegetation of forest lands, spring frosts may occur up to 14 days later and fall frosts 15 to 40 days earlier on agricultural lands than in forests (Sartz 1957).

Table 10-4. Average Length of Growing Seasons (days) and Mean Frost Dates for Five Locations in Coastal Maine

Location	Growing season	Mean frost dates	
		Last spring frost	First fall frost
Portland	136	13 May	26 Sept.
Brunswick	163	2 May	12 Oct.
Gardiner	133	16 May	26 Sept.
Augusta	159	2 May	8 Oct.
Rockland	143	10 May	30 Sept.

Precipitation is fairly evenly distributed throughout the year in Maine. During the growing season, approximately 2 to 4 inches (5 to 9 cm) of rain falls each month.

Problems Associated with Agricultural Lands

The most significant consequence of sparse vegetation cover on farmland is uncontrolled surface runoff. For example, surface runoff from two cultivated fields was about 15% of precipitation, while on a woodland site, runoff was only 0.2% of precipitation (Dreibelbis and Post 1941). Even the small vegetation cover afforded by a pasture greatly reduced the surface runoff.

High surface runoff from agricultural land causes erosion of soil, and runoff carries sediments, minerals, chemicals, and nutrients from farmland to downstream areas. These transported products can cause serious problems for those systems receiving runoff from farms. The effects of sediment nutrients and chemicals on aquatic systems (palustrine, lacustrine, riverine, marine, and estuarine) are discussed in chapter 3, "Human Impacts on the Ecosystem."

DEVELOPED LANDS

Developed lands encompass approximately 9% of the coastal zone (table 10-5). On a regional basis this ranges from about 5% to 6% in regions 3, 4, and 6 to 31% in region 1 (Portland and South Portland). An approximate breakdown of the amount of land in each of the various categories of developed lands is given in table 10-6. Urban areas occupy approximately 50% of the developed system, ranging from 16% in northeastern Maine to 62% in southeastern Maine. Residences, which include seasonal and year-round residences and farmsteads, occupy 33% of the developed system. Roads account for about 12%, and railroads only about 1% of coastal Maine.

Biota

In addition to people, the biota of developed land consists mainly of exotic (non-native) species of plants and animals that have been introduced intentionally (garden plants, trees, dogs, and cats) or accidentally (weeds, pigeons, rats, and mice). The trophic structure of developed systems is simple. The primary producers in suburban areas, golf courses, city parks, and rural residences are lawns, gardens, and shade trees that are maintained by watering, pruning, fertilizing, mulching, and by poisoning their competitors. Although no data are available the productivity of these plants is probably high because of the intensive care that is given them. Primary consumers (most of which are considered pests) are insects or other invertebrates whose populations are controlled by spraying with pesticides, as well as some vertebrates, including mice, voles, rabbits, hares, and woodchucks. Important secondary consumers are songbirds, such as the robin, house sparrow, song sparrow, starling, catbird, northern oriole, cardinal, mockingbird, as well as mice, cats, dogs, and perhaps raccoons and skunks.

In highly developed urban areas, essentially no primary production takes place. Vacant lots may support a few species of weeds and small lawns may exist but generally the concrete and buildings reduce the productivity to near zero. The animals that do exist are able to do so because of the presence of people. Pigeons, starlings, rats, mice, dogs, and cats exist on the food or garbage provided by people, or in isolated small patches of habitat such as are found in vacant lots.

There is probably a well-developed decomposer system in suburban areas. High levels of organic matter (grass clippings, leaves, and garden residue) and nutrients (mulch and fertilizer) are added to the soil to promote fertility, which also enhances decomposer activity. This is nearly nonexistent in cities, however. In general, decomposer activity is unable to handle the excess waste produced by people, and additional sewage treatment facilities and sanitary land fills are needed to properly dispose of this material.

Abiotic Features

The local climate in urban areas is modified by the presence of concrete and buildings and particulate matter added to the air (LeBlanc and Rao 1973). Temperatures in cities are slightly warmer than those in nearby vegetated areas because of the absorptive and radiative properties of concrete. Wind velocity is also approximately 20% to 30% lower in cities than in open areas, which also helps to maintain slightly higher temperatures. Particulate matter in the air may be up to 10 times higher in cities than in rural areas. This causes a 15% to 20% reduction in solar radiation and, because the particles serve as nuclei for raindrop formation, precipitation is increased 5% to 10%.

Table 10-5. Amount (acres) and Percentage Composition (parentheses) of Developed Land in Each Region of the Maine Coastal Characterization Area[a]

Region	Residential	Non-residential	Parks	Total
Region 1				
Cumberland County	44,100 (9)	54,542 (12)	1707 (1)	100,349 (22)
Coastal towns only	16,037 (16)	13,767 (14)	1130 (1)	30,934 (31)
Region 2				
Sagadahoc County	--	-- (nonforest, nonfarm)	--	22,537 (14)
Regions 3 and 4				
Coastal towns only	--	--	--	13,943 (5)
Region 5				
Hancock County	36,924 (5)	7973 (1)	38,539 (5)	83,436 (11)
Coastal towns only	33,762 (6)	6742 (1)	38,451 (7)	78,955 (14)
Region 6				
Washington County	--	--	--	94,900 (6)

[a]Bureau of Census 1977.

Table 10-6. Percentage of Different Types of Developed Land in Coastal Maine[a]

Section	Dwellings			Farm-steads	Roads	Rail-roads	Other
	Urban	Year-Round	Seasonal				
Southeastern Region 1	62	14	4	9	8	1	2
Midcoast Regions 2, 3, and 4	34	24	6	12	19	1	5
Northeastern Regions 5, 6	16	38	8	3	23	3	8
Average for entire Characterization area	50	19	5	9	12	1	3

[a]From Anderson et al. 1975.

Because of the lack of vegetation and exposed ground and the general lack of interception and reevaporation in cities, most rain or snow becomes runoff. In Maine the runoff carries chemicals and particulate pollutants as well as nutrients to streams, rivers, palustrine, lacustrine, or estuarine habitats, which are absorbed by these ecosystems. Water used by urban systems usually is imported from other nearby ecosystems but is then exported to downstream ecosystems after nutrients, chemicals, pesticides, herbicides, and other impurities have been added. This cycle, in a much less severe form, is also applicable to suburban and rural communities.

Problems Associated with Developed Areas

Developed lands produce large amounts of waste products that cannot be processed by the natural decomposers of urban ecosystems. When these wastes are transported out of the urban system they may overtax the ability of natural ecosystems to filter, break down, and/or assimilate these organic and inorganic chemicals and particles. These waste products include industrial emissions, such as sulfur dioxide, hydrogen sulfide, and particulates; automobile fumes containing nitrous oxide, carbon monoxide, hydrocarbons; and particulate matter and fumes from dumps and incinerators. Environmental problems are caused in cities by these pollutants; high plant mortality, health problems in people, and contamination of natural ecosystems. These problems exist throughout coastal Maine and are more severe where population densities are highest. Specific sources of contamination are detailed in chapter 3, "Human Impacts on the Ecosystem", as well as the overall effects of these on aquatic systems.

OLDFIELDS

Oldfields do not occupy a large area of land in coastal Maine but they are ecologically important. The amount of oldfield habitat in Maine is difficult to determine, partly because its regrowth superficially resembles the regrowth on recently logged or burned areas. On the other hand, for the first few years after abandonment oldfields resemble pasture land or idle farmland and may be classified as such. The only data available on oldfield habitat are for region 6, in which 18% of the farmland is brush land, or waste land. This amounts to less than 1% of the total land area in Washington County.

The amount of oldfield habitat present at any one time depends not only on the rate at which farmland is abandoned but also on the rate at which formerly abandoned farmland is reclaimed for agriculture or development. Neither of these rates in Maine are known but until 1969 the amount of farm land was decreasing, and oldfields were increasing. Presently the two about balance.

The ecological value of oldfields stems from their importance as wildlife habitat and their role in rehabilitation of disturbed ecosystems. A high diversity of plant life is present during succession from farmland to forests. This provides abundant food and cover for many species of insects and invertebrates, birds, mammals, and some reptiles and amphibians. Usually the growth of plants (density and composition) is not uniform and cover types are patchily distributed. The mosaic of habitats and edges is conducive to wildlife. Many important game species, such as hares, grouse, and deer, are sometimes abundant in oldfields. Through the process of succession in oldfields plant biomass and soil organic matter accumulate and soil structure is slowly restored. This process serves to rehabilitate disturbed ecosystems.

Succession

The process of succession from active farmland to forest involves a series of changes in plant communities. The first stage consists of annual grasses, such as fescue, panic grass, *Agrostis* spp., orchard grass, witch grass, and bluegrass. The second stage is perennial herbs, such as goldenrod, hawkweeds, asters, and ragweed. The third stage is woody shrubs that gain a foothold and spread from isolated clumps. Common shrubs in Maine oldfields are dogwood, spirea, willow, alder, wild apple, and juneberry. The fourth stage is trees, usually the more intolerant species of aspen, birch, pine, white cedar, and cherry. The invasion of trees is relatively slow but when the overstory or canopy finally closes the area once more becomes a forest.

Succession on oldfields is slow because cultivation and the application of herbicides has destroyed most remnants of native vegetation and altered the soil structure. In addition, the grasses develop a cover of sod that later hampers the establishment of woody plants. Even after trees begin to invade they do so in isolated clumps and it may be many years before a complete cover of trees is established. A study of oldfield ecology in Michigan indicated that after 50 or 60 years large areas of grasses and only isolated clumps of trees and shrubs were present (Weigert and Evans 1964). The sequence of changes in plant communities was documented on a series of oldfields in New

Jersey (Pearson 1959). After 7 years the area was dominated by herbaceous plants, such as asters and goldenrod, and by broomsedge. Woody plants, which included cedar, dogwood, bayberry, and sumac, were present only as seedlings. After 16 years of abandonment broomsedge still occupied 75% of the area and goldenrod-aster cover and trees and shrubs accounted for the other 25%. After 46 years trees and shrubs were more abundant, but broomsedge still occupied most of the area. After 66 years shrub and tree cover was extensive but patches of herbaceous vegetation still grew between them. Forest succession on abandoned farmlands is much slower than on burned over or logged forest lands because of more numerous and slower stages of succession.

Plants and Animals

Oldfields support a wide variety of grasses, herbaceous plants, shrubs, and trees but the dominant form depends on the stage of succession. The biomass of vegetation increases as succession proceeds, because more and more perennial and woody species become established. Biomass in early successional stages may be as low as 1.1 tons/acre (2.5 t/ha; Odum 1960). The biomass sharply increases once woody vegetation begins to invade, and by the time immature forests are present biomass is about 44.5 tons/acre (100 t/ha).

Although biomass of abandoned fields is initially low, productivity (annual growth increments) may be as high or higher than in forests. Values of 2.2 to 2.9 tons/acre/year (4.9 to 6.5 t/ha/year) have been reported for oldfields in the eastern United States (Bazaaz and Metzgar 1973; and Golley 1965). Productivity is usually higher the first year or two after abandonment, after which it declines slightly. As each new seral stage or plant life form becomes dominant, another sharp, but smaller, increase occurs in productivity.

The most important consumers in oldfields are invertebrates (Weigert and Evans 1964), although they consume only a small portion of the available net productivity. A study of the trophic structure of an oldfield in Georgia indicated that grasshoppers, which accounted for 91% of the invertebrate biomass, consumed only 7% of the net production (Odum et al. 1962). They estimated that all invertebrates would consume no more than 20%.

Other primary consumers in oldfields are mice, hares, deer, woodchucks, and some seed-eating birds (e.g., sparrows and other finches). Mice and birds were found to consume as much as 50% of the annual seed crop in a Georgia oldfield but this represented only 1% to 2% of the net annual primary productivity (Odum et al. 1962).

Secondary consumers include birds (e.g., red-winged blackbirds, meadow larks, sparrows, warblers, and hawks), snakes, toads, and mammals (e.g., shrews, weasels, and fox).

MANAGEMENT PRACTICES

The management of agricultural, developed, and abandoned lands for fish and wildlife and for environmental protection in Maine is exercised in a number of ways by several authorities. Some programs are mandated by law, while others are only guidelines and compliance is voluntary.

The two practices that are most important for environmental protection on farmlands are crop rotation and other soil erosion control, and application of biocide chemicals. State soil conservationists and agricultural extension agents encourage strip cropping, contour plowing, crop rotation, and cover crops to reduce soil erosion and increase production. Ultimately, of course, soil conservation is controlled by farmers.

The use of agricultural chemicals (e.g., pesticides and herbicides) is regulated by Federal legislation and by the Maine Pesticide Control Act of 1975. Enforcement of the regulations is carried out by the Department of Agriculture. Pesticides dangerous to fish and wildlife and to human life must be applied by a licensed operator who has demonstrated ability to use them safely. Safe use of farm chemicals is provided in guidelines issued by the USDA Cooperative Extension Service. An integrated pest management program has been underway in Maine since 1974. The object of this program is to reduce the need for pesticides by carefully monitoring insect populations to eliminate excessive spraying if applicable, and to eliminate alternate host plants for some insect pests. One of the most important Federal acts was the 1974 ban on the use of organochlorides as pesticides (the residues of which are still present at upper trophic levels).

The amount of agricultural chemicals applied to farmland is being reduced by applying conservation practices aimed at reducing surface runoff, soil erosion, and chemical dispersion. Proper disposal of chemical containers is one aspect of this problem.

Safe methods of storage and disposal of raw manure are reasonably well known but not always practiced. An extension service bulletin entitled "Maine Guidelines for Manure and Manure Sludge Disposal on Land" is available from the USDA Cooperative Extension Service. The U.S. Soil Conservation Service has suggested Federal cost-sharing assistance for construction of costly manure storage facilities.

A number of Federal and State agencies have recommended that farming methods be modified to benefit fish and wildlife. Suggestions made were to reduce the size of the individual fields, to grow farm woodlots, and to increase the abundance of weed and brush patches, by providing greater areas of fencerows, roadsides, woodlots, and other areas of natural vegetation that provide food and nesting cover.

No program exists for managing abandoned farmlands for fish and wildlife. Attempts to reclaim abandoned farmlands for agriculture would not favor most wildlife. Some conservation groups have bought and successfully managed abandoned farmlands for wildlife.

Many of the sewage disposal programs of urban and suburban areas, and industrial sites, are aimed at protecting public health, fish and wildlife resources, and natural habitats in the air, land, and waters of the cities and nearby natural habitats. City parks, parkways, recreation areas, and similar types of municipal lands sometimes are managed for natural vegetation and various forms of wildlife and provide natural areas and nature trails.

The value of the fish and wildlife and natural environments in the agricultural and developed land of coastal Maine is and will be determined largely by the degree of control of, and practices exercised by, existing agencies, regulations, and guidelines. The help of coastal planners may be needed to establish the means and motivation to make environmental protective measures on these lands more effective.

RESEARCH NEEDS

A lack of resource inventories is a major data gap for coastal Maine. The size, abundance, and distribution of agricultural and developed land must be better known. To do that the criteria for distinguishing two of the land types (farmland and abandoned) must be better established and corresponding surveys must be conducted periodically to determine their statuses and changes.

The current uses of biocides, their chemical composition, method of dispersal, and their potential and actual ecological effects in coastal Maine need to be better known, especially as they relate to surface and ground water supplies. A systematic and periodic survey that would provide data on actual and projected levels of contamination throughout each region is needed.

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