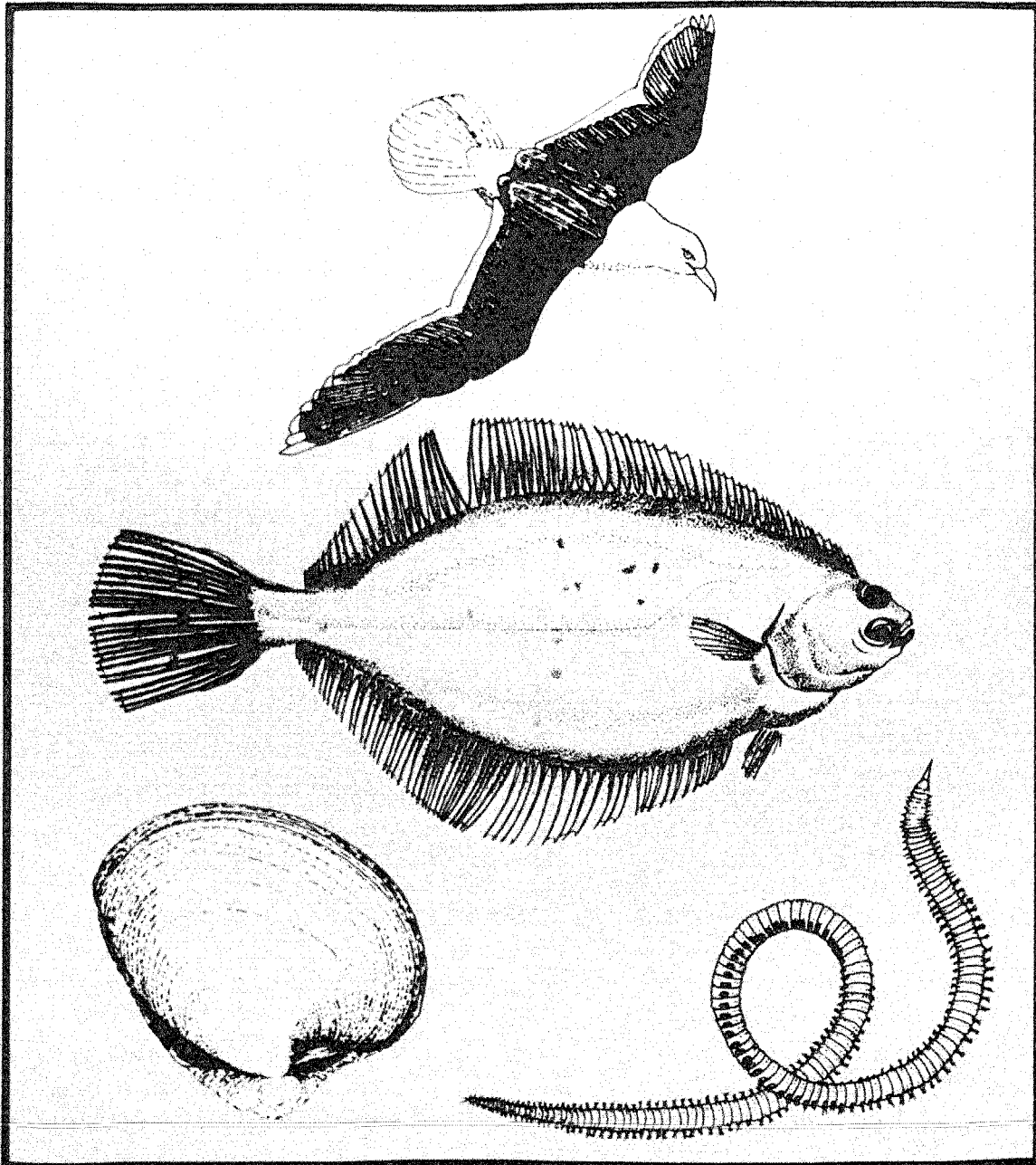


THE ECOLOGY OF NEW ENGLAND TIDAL FLATS: A Community Profile



Fish and Wildlife Service

U.S. Department of the Interior

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- To strengthen the Fish and Wildlife Service in its role as a primary source of information on national fish and wildlife resources, particularly in respect to environmental impact assessment.
- To gather, analyze, and present information that will aid decisionmakers in the identification and resolution of problems associated with major changes in land and water use.
- To provide better ecological information and evaluation for Department of the Interior development programs, such as those relating to energy development.

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FWS/OBS-81/01
March 1982

THE ECOLOGY OF
NEW ENGLAND TIDAL FLATS:
A Community Profile

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National Coastal Ecosystems Team
Office of Biological Services
Fish and Wildlife Service
U.S. Department of the Interior
Washington, D.C. 20240

Library of Congress Number 82-600534

This report should be cited as follows:

Whitlatch, R.B. 1982. The ecology of New England tidal flats: a community profile. U.S. Fish and Wildlife Service, Biological Services Program, Washington, D.C. FWS/OBS-81/01. 125 pp.

PREFACE

To many, the thought of walking along the coastline of New England produces visions of the rocky shores of Maine or the sandy beaches of Cape Cod. Intertidal sand and mud flats, conversely, are typically viewed as physically uninviting if not repellent habitats filled with sticky muds, foul odors, and singularly uninteresting organisms except, possibly, for the soft-shell ("steamer") clam. This view is probably due to a lack of understanding and appreciation of these habitats. While tidal flats appear at first glance to be rather inhospitable portions of the coastline, they play an important role as habitats for commercially and recreationally important invertebrates and fishes as well as serving as feeding sites along the New England coast for a variety of migratory shorebirds.

The purpose of this report is to provide a general perspective of tidal flats of New England, the organisms commonly associated with them, and the importance of tidal flats to the coastal zone viewed as a whole. The approach is taxonomically based although there is also attention paid to the flow of organic matter through the tidal flat habitat. The method of presentation is similar to that of Peterson and Peterson (1979) who have described the tidal flat ecosystems of North Carolina. The reader, therefore, has the opportunity of comparing and contrasting the physical and biological functioning of the two regions. Chapter 1 begins with a general view of the physical, chemical, and geological characteristics of tidal flat environments followed by a discussion of organic production and decomposition processes vital to these systems (Chapter 2). The next three chapters deal with the benthic invertebrates (Chapter 3), fishes (Chapter 4), and birds (Chapter 5) common to New England tidal flats. The coverage within each chapter reflects the published information avail-

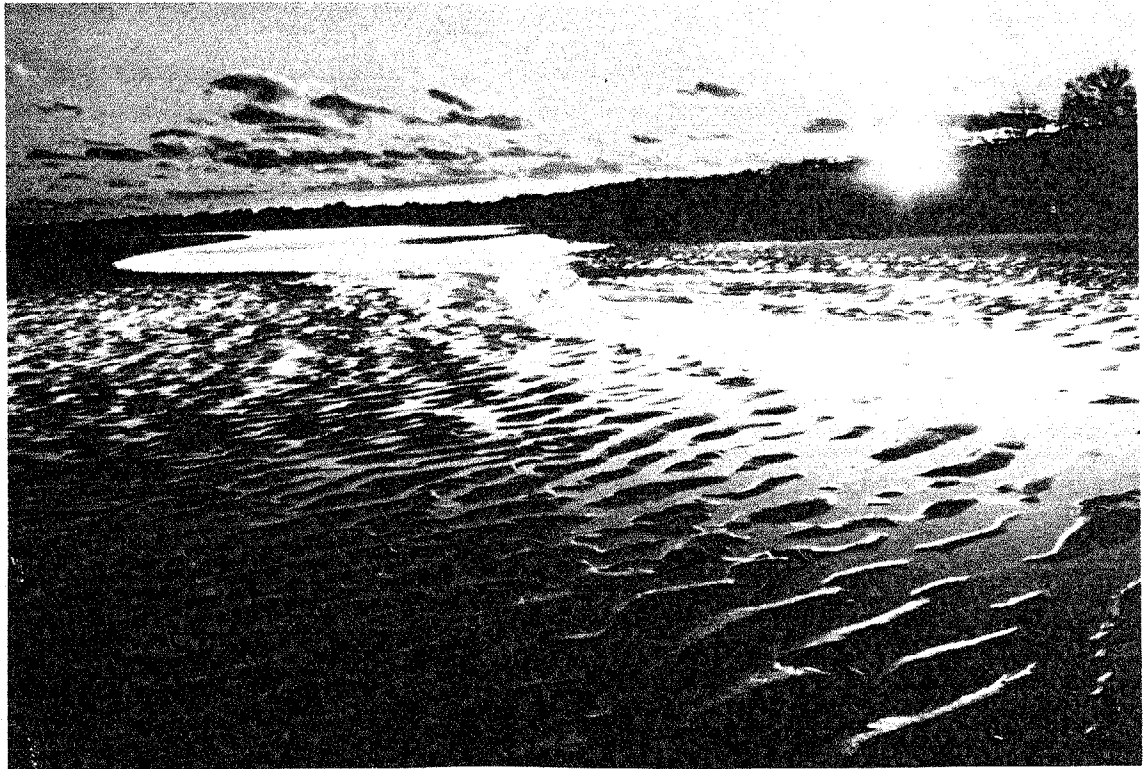
able at the time of writing in addition to the author's perception about the structure, function, and importance of each of the taxonomic groups to the overall tidal flat system. The last chapter (Chapter 6) considers the response of tidal flats to environmental perturbation as well as their value to the New England coastal zone.

The reader should be aware that this report is not intended to be an exhaustive survey of the literature pertaining to New England tidal flats. Rather, the approach and philosophy used has been to provide an overall impression of the characteristics of the various players and their roles within the habitat. If there has been a goal in the writing, it is to provide a better understanding and appreciation of these habitats.

This report is part of a series of "community profiles" of coastal habitats of the United States. Sand and mud flats are identified as habitats by the U.S. Fish and Wildlife Service, National Wetlands Inventory classification system (Classification of Wetlands and Deepwater Habitats of the United States, by Cowardin et al. 1979). Cowardin et al. placed flats in the "unconsolidated shore" class, the intertidal subsystem, of the marine and estuarine systems. These landforms are produced by erosion and deposition by waves and currents and are alternately exposed and flooded by tides (see Figure 1).

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Aside from their aesthetic value, tidal flats represent important areas in the coastal zone for a variety of invertebrate and vertebrate species. Photo by Robert E. DeGoursey, University of Connecticut.

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ACKNOWLEDGMENTS

I wish to thank a number of people for valuable assistance with this project. Robert DeGoursey and Peter Auster helped to collate much of the fish literature and served as sounding boards and reviewers of Chapter 4. Steven Malinowski gathered information on coastal birds and wrote the lion's share of Chapter 5. Members of the Manomet Bird Observatory, Manomet, Massachusetts, were instrumental in identifying pertinent references and in providing access to unpublished reports of their work. An informative conversation with Les Watling helped to clarify questions regarding the mud flats of Maine. Barry Lyons supplied information about mud flat chemistry. Steven Edwards and Barbara Welsh provided access to unpublished data on tidal flat macrophytes. Sarah Malinowski expertly drew all the figures from sketches and verbal descriptions of what benthic invertebrates, fish, and bird communities "really" look like. I appreciate the thoughtful and extensive reviews of Ralph Andrews, Bill Drury, Eric Mills,

Don Rhoads, and Peter Larsen. Martha Young initiated the project, provided editorial assistance and logistic support, and most importantly, allowed (relatively) unimpeded time to think and write. Joyce Lorensen typed portions of an early draft and Ann Whitlatch expertly typed, edited, and quietly suffered through the final draft. Preparation and publication of this report were supported by the U.S. Department of Interior, Fish and Wildlife Service, National Coastal Ecosystems Team. To all, I am grateful.

This report is dedicated to A.C. Redfield and H.L. Sanders. Dr. Redfield's pioneering studies provided the initial stimulus for my working in the most beautiful salt marsh-tidal flat system in New England. Howard Sanders not only provided the opportunity to undertake this project, but his encouragement and insightful and provocative outlook on marine ecology have been a constant source of professional stimulation.

CHAPTER 1

GENERAL FEATURES OF TIDAL FLATS

1.1 INTRODUCTION

Intertidal sand and mud flats are soft to semi-soft substrata, shallow-water habitats situated between the low and high tidal limits. Tidal flats are found where sediment accumulates and are, therefore, associated with coastal embayments, behind spits and barrier beaches, and along the margins of estuaries. The occurrence and extent of tidal flats varies according to local coastline morphology and tidal amplitude. These habitats are sometimes bordered landward by salt marshes and seaward by tidal channels and/or subtidal eelgrass (*Zostera marina*) beds (Figure 1). Tidal flats are common features of the New England coastline, especially in Maine, New Hampshire, and parts of Massachusetts where increased tidal amplitude exposes more of the tidal flats at low tide. For example, tidal flats represent about 48% of the intertidal habitats of Maine (Fefer and Schettig 1980).

Tidal flats are not static, closed ecological habitats, but are physically and biologically linked to other coastal marine systems. It is generally recognized, for example, that organisms inhabiting tidal flats rely heavily upon organic materials (e.g., plankton, detritus) imported from adjacent coastal, estuarine, riverine, and salt marsh habitats. In addition, many species of estuarine and coastal fishes migrate over tidal flats with the incoming tide to feed on the organisms found on and in the sediments.

1.2 THE NEW ENGLAND COASTAL ENVIRONMENT

Climatic conditions of the New England coastal region exhibit pronounced seasonal temperature fluctuations, a characteristic of temperate environments. Extremes in seawater temperatures, warmest in August through September and coolest in

December to March, are among the greatest in the world (Sanders 1968). The region is commonly divided, for convenience, into two areas: the Gulf of Maine extending from Cape Cod, Massachusetts, to the Bay of Fundy, Nova Scotia, Canada, and the areas south of Cape Cod ranging to western Connecticut including Long Island Sound (Figure 2). This division is based largely on differences in annual water temperature variation in the two regions. Waters in the Gulf of Maine are continually well-mixed by tidal, current, and wind action (Brown and Beardsley 1978) and in the summer do not become as warm as the waters south of Cape Cod. On the south side of Cape Cod, the influence of the Gulf Stream coupled with a shallower coastal plain produces more abrupt increases in summer temperatures. The net effect is that the annual range of seawater temperatures along the coast of New England is closely related to latitude (Figure 3). For instance, in the northern portion of the Gulf of Maine there is a 10°C (50°F) annual temperature range while in portions of Long Island Sound the annual range is about 20°C (68°F).

Cape Cod is a transition zone rather than a discrete physical barrier separating warm and cool New England coastal water masses. Water associated with embayment and estuarine environments is generally shallow and is more likely to be influenced by atmospheric and terrestrial conditions than deeper water areas. Spring runoff from rivers, thermal warming of mud and sand flats with subsequent heat transfer to shallow waters, and low flushing rates of water in some estuarine habitats all contribute to warmer water temperatures. Warm water embayments north of Cape Cod do occur (e.g., Barnstable Harbor, Massachusetts; upper reaches of some estuaries in New Hampshire and Maine), but in autumn shallow water habitats respond quickly to the cooler

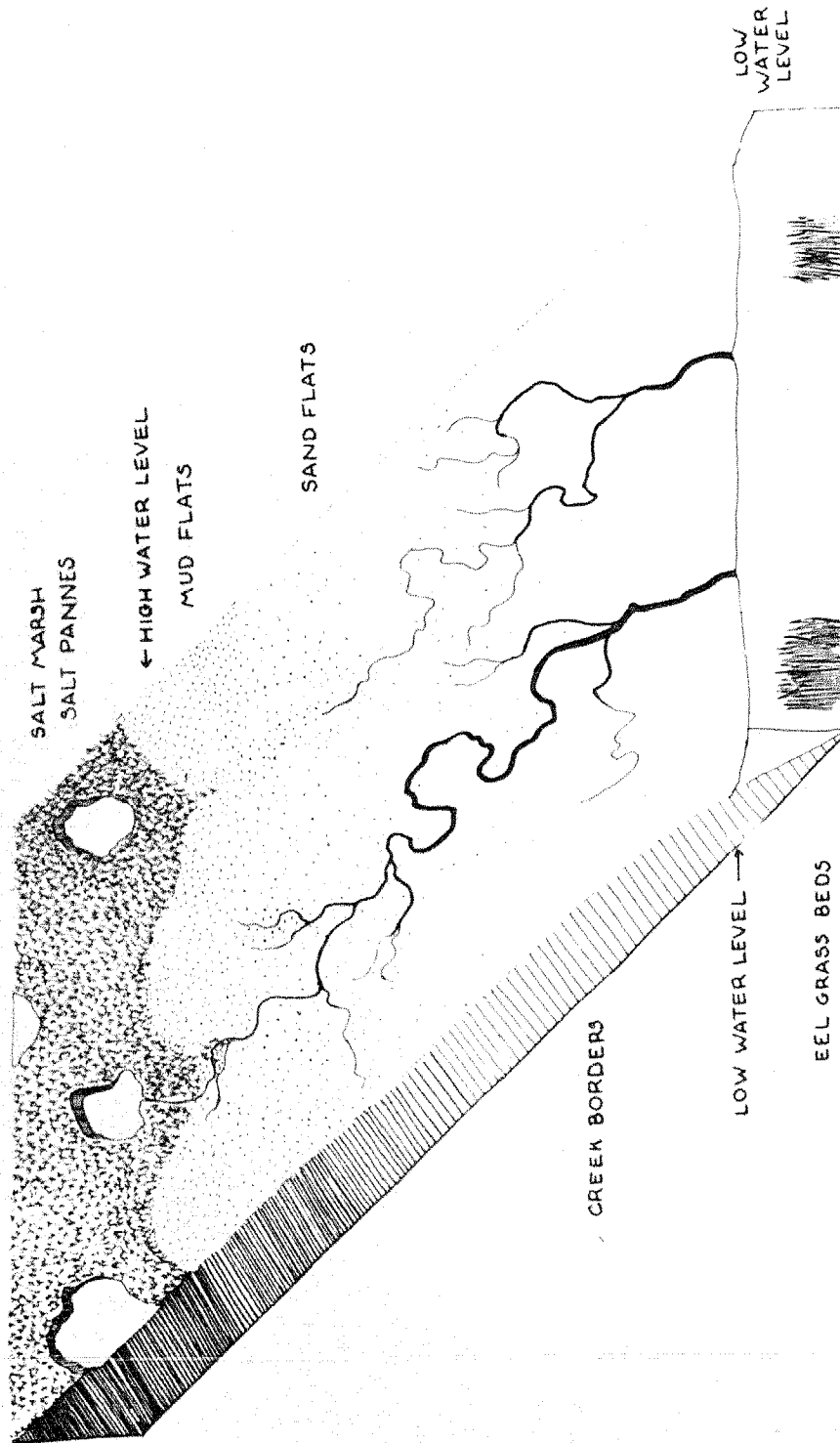


Figure 1. Diagrammatic representation of a tidal flat.

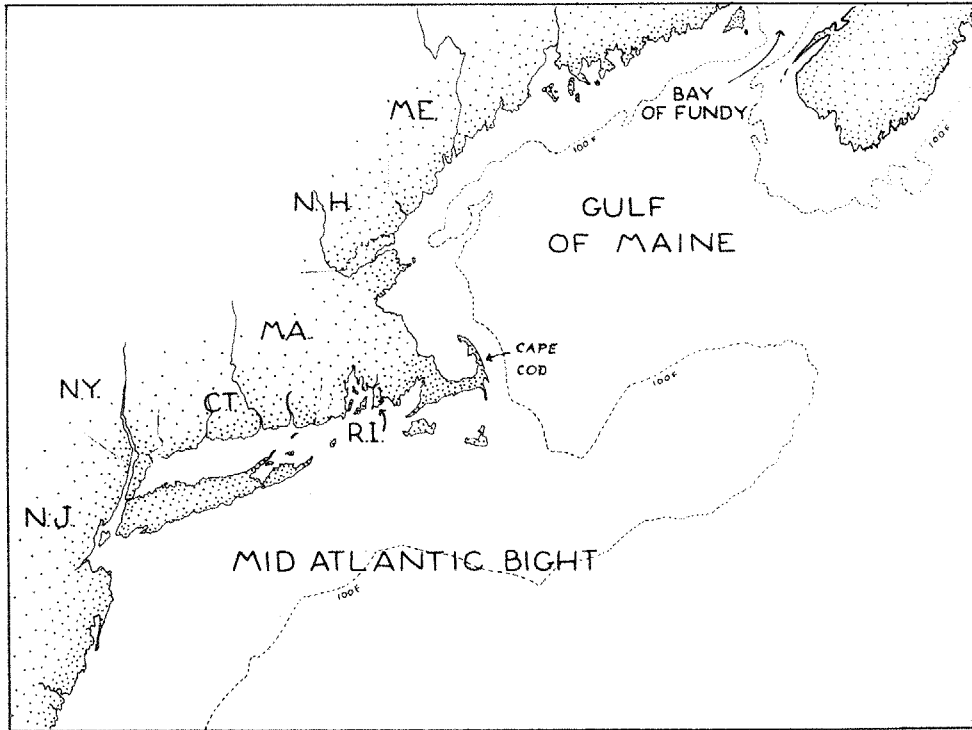


Figure 2. Map of the New England coast. The marine waters are often separated into two areas: Gulf of Maine (north of Cape Cod, MA) and Mid-Atlantic Bight (south of Cape Cod, MA).

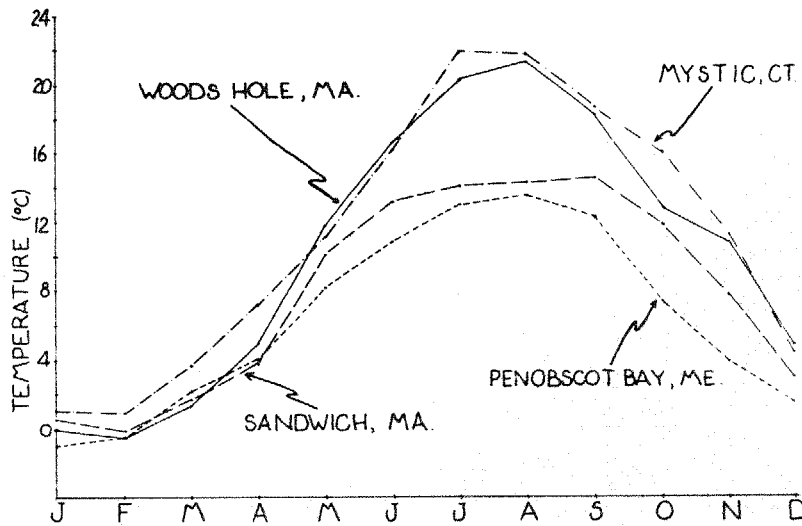


Figure 3. Monthly surface seawater temperatures at four localities along the New England coastline. Note differences in summer temperatures north (Sandwich, MA, and Penobscot Bay, ME) and south (Woods Hole, MA, and Mystic, CT) of Cape Cod, MA.

atmospheric conditions and influence of associated land masses, and the waters become cooler than nearby coastal waters.

Buildup of seawater ice on New England tidal flats, both north and south of Cape Cod, commonly occurs in winter. The appearance and extent of the ice is dependent upon tidal fluctuation, location, and severity of the winter. Because of tidal action, the ice moves back and forth across the flats resulting in appreciable geomorphological effects upon the sediment through accretion, erosion, and transport. Boulders weighing several tons have been transported considerable distances by ice at Barnstable Harbor (Redfield 1972). Salt marsh turf may also be transported onto tidal flats by ice movement. Shortly after breakup of the ice in early spring, erosional scars in the sediment are evident. Most of the scars are quickly removed by tidal and wave action. Although ice occurs regularly on New England tidal flats, relatively little is known about its effects on the biota. Ice scouring can remove or displace infaunal and epifaunal organisms. Freezing of the sediments to a depth of 5 to 10 cm (2 to 4 inches) may also occur, although little is known about what effect this has on the organisms living in the sediment. During periods of severe and prolonged ice buildup on tidal flats, birds that use the areas as feeding sites may have to forage elsewhere.

Storms that pass through New England also affect the sedimentary features of tidal flats. Both northern and southern New England normally experience three to five major storms each year, usually in fall and winter. Winds in New England are predominantly from the southwest but during winter are likely to shift to the west or northwest. Occasionally winds come from the northeast and are typically associated with the most severe storms (the classic "nor'easter"). Hurricanes occur in New England - the last major storm hit the coastline in 1954.

Fog is common in the coastal zone especially in northern New England. Fog occurs at any time of the year although dense fog is associated with the warmer, summer months. The presence of fog on

the tidal flats acts to insulate organisms living on or in the sediments from desiccation and allows less hardy organisms to survive in intertidal areas during periods of intense solar heating.

1.3 GEOLOGICAL, PHYSICAL, AND CHEMICAL CHARACTERISTICS OF TIDAL FLATS

On a geologic timescale, coastal marine environments of New England represent systems that have continually changed. Since the last Pleistocene glaciation episode, the coastline has slowly subsided and sealevel has progressively risen. The net effect is a slow migration of the sea into the lowlands, altering coastal habitats. Historical reconstructions of many New England estuarine systems show the transitional nature of tidal flat habitats. Flats develop as depositional features expanding at the expense of tidal channels and eelgrass beds and they in turn are invaded by the progression of salt marsh vegetation (Redfield 1967).

The formation of tidal flats and their sedimentary characteristics are primarily dependent upon the physical and biological environment (e.g., tidal currents, wave action, and biologically-induced sediment mixing), the nature and source of available materials, and the glacial history of New England. Vast deposits of coarse-grained sediments left by glacial activity are responsible for the general restriction of sand flats to Cape Cod and southward. Mud flats, more commonly found in northern New England, are derived from land-based sources, and transported by river systems. Sediments are also deposited on tidal flats by currents from offshore sources or through the erosion of adjacent tidal flats or shorelines.

Sediments of tidal flats can be characterized in various ways. Geologists prefer to use the bulk properties of the sediment (e.g., median grain size, percent silt-clay fraction). Sandy sediments are those having less than 5% of their weight composed of silt-clay-sized material (particles less than 62 μm in diameter), while muddy-sands and sandy-muds consist of 5% to 50% and 50% to 90% silt-clay,

respectively. Muds are sediments with greater than 90% silt-clay fraction. Biologists, on the other hand, have attempted to view sediments with a higher degree of resolution. Sediments are described by biologists according to their particulate constituents: these consist of a complex array of organic and inorganic forms, varying in size, shape, and qualitative nature (Table 1; Figure 4). Most of the sediments found in New England tidal flats are dominated by siliceous sands, clay minerals, and organic-mineral aggregates (detritus). The abundance and variety of particle types vary spatially and vertically within the sediment (Johnson 1974; Whitlatch 1981). A larger variety of particle types is usually found in the upper layers of the surface than in deeper layers. Muddy sediments have a greater proportion of organic-mineral aggregates than sandy sediments.

Examination of the surface of tidal flats reveals undulations and ripples formed by waves and currents sweeping over the flats. Large grains tend to accumulate on the front of the ripples while smaller grains tend to concentrate on the back side of the ripple marks. Sand and mud flats may or may not be dissected by channels. When they occur, the channels form meandering depressions roughly perpendicular to the creeks that border the flats and are more common on the lower portion of the flat (Figure 1).

Tidal action is responsible for sediment movement and control of sediment texture as currents continually resuspend and transport sediments. In exposed areas where there are high current velocities and turbulence, sediments are generally composed of coarse, unstable sands and cobble. In more protected areas, reduced

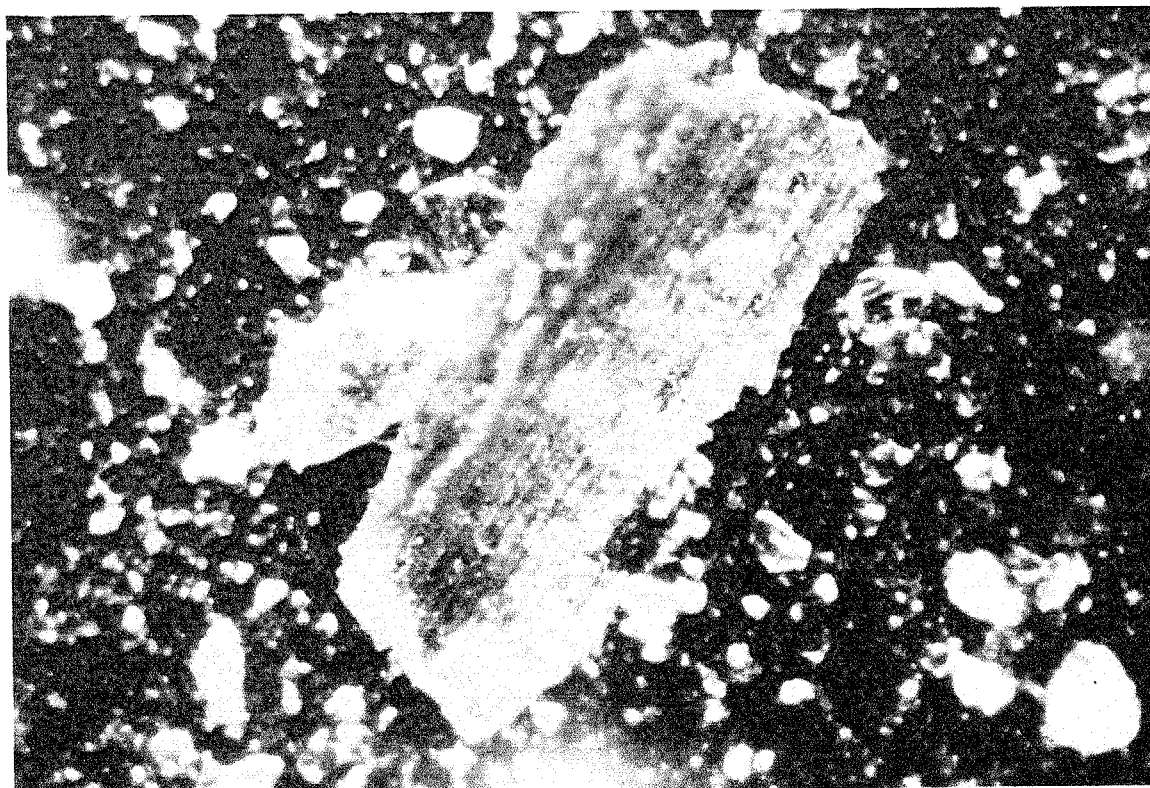


Figure 4. Viewed microscopically, tidal flat sediments are a complex array of organic and inorganic particulate material. The large (0.2 mm) plant fragment from cordgrass, *Spartina alterniflora*, is the source of much of the detritus entering many New England tidal flat ecosystems. Photo by R.B. Whitlatch, University of Connecticut.

Table 1. Different types and relative abundances of living and non-living particulates found in sands and muds of some New England tidal flat sediments (Whitlatch unpublished data, Alewife Cove, Connecticut).

Particle type	Sands (%)	Muds (%)
Organic-mineral aggregates (detritus)	11.3	41.2
Organic-encrusted mineral grains (e.g., bacterial films, diatoms, fungi)	28.2	16.7
Clean mineral grains	51.6	36.1
Vascular plant fragments (e.g., <u>Zostera marina</u> , <u>Spartina alterniflora</u>)	0.2	1.5
Diatoms	3.1	2.6
Algal fragments	0.7	0.1
Fecal material (fragments and pellets)	3.8	0.8
Meiofauna (e.g., copepods, nematodes)	0.1	0.1
Protozoans (e.g., ciliates, foraminiferans)	0.1	
Molluscan shells and fragments	0.2	0.5
Chitinous molts and fragments	0.3	0.1
Polychaete setae and tubes	0.1	0.1
Pollen, spores, and seeds	0.1	0.1
Rods, spines, and spicules	0.2	0.1

water flow results in the deposition of finer-grained, more stable sediments. On a larger scale, coarser-grained sandy sediments are found in channels, on beaches, and near the mouths of inlets, while finer-grained sediments are associated with increasing distance from the mouths of inlets and at higher intertidal elevations. Redfield (1972) described these sediment distribution patterns at Barnstable Harbor, Massachusetts, noting a decrease in grain size proceeding from the mouth of the harbor to the vegetated salt marsh.

Wind-generated waves and currents also affect mixing and redistribution of sediments on some tidal flats. The magnitude of wind impact is largely dependent upon the size and depth of the waterbody over which the wind passes. Large shallow embayments in some southern states, for example, can be influenced considerably by wind-generated waves (Peterson and Peterson 1979). In New England, embayments are comparatively smaller and shallower; wind action is generally less significant than tidal action. Most wind effects on tidal flats are probably concentrated in periods of storm activity when resuspension and redistribution of sediments occur.

The New England coast has semi-diurnal tides (e.g., two high and two low tides per tidal day). Channel constrictions and bottom topography alter the magnitude of the tidal range although the mean tidal range south of Cape Cod is about 1 to 1.5 m (3 to 5 ft) while mean tides north of Cape Cod range 3 to 4 m (10 to 13 ft). The twice daily inundation and exposure contributes in an important manner to the spatial and temporal complexity of the tidal flat habitat. When tidal flats are submerged, they share many of the same physical and chemical characteristics of the water found in adjacent coastal and/or estuarine systems. When exposed, tidal flats are affected by climatic variations of air temperature, precipitation, and wind. Organisms living in these environments, therefore, must be well adapted to the physically rigorous environmental conditions.

While the physical conditions of the water over the tidal flats may change considerably during a tidal cycle, physical features of the sediments are less variable. Even at low tide, small amounts of water are retained in the sediments; this helps prevent desiccation. Sediments also tend to buffer temperature and salinity fluctuations (Sanders et al. 1965; Johnson 1965, 1967). The net result is that organisms living within tidal flat sediments are normally able to withstand greater environmental fluctuation than exposed organisms attached to or living on the sediments (Alexander et al. 1955).

Chemical properties of the sediments vary vertically in tidal flats and it is possible to view this stratification by examining sediment samples in cross-section. In muddy sediments, two or three distinctly colored zones commonly exist. The uppermost is light-brown, extending 1 to 5 mm below the sediment surface. This is the zone of oxygenated sediment. Below this thin layer is a black zone where oxygen is absent and the sediments smell of hydrogen sulfide ("rotten egg" gas). The black color is due primarily to the presence of iron sulfides. In some muddy sediments a third, gray-colored zone may exist below the black zone due to the presence of iron pyrite.

The boundary between and position of the oxygenated and black anoxic zone (termed the redox potential discontinuity, or redox zone) varies with depth, depending on the amount of organic matter in the sediment, sediment grain size, and the activities of organisms burrowing through the sediment or disturbing the surface. Oxygen diffusion may extend 10 to 20 cm (4 to 8 inches) below the sediment-water interface in sandy sediments due to increased percolation of water through the sediments and small amounts of organic material. On many sandy flats it may be difficult to find a black zone and the sediments may not smell of hydrogen sulfide. In muddy sediments containing greater amounts of organic material, the redox zone is usually within several millimeters of the surface. Rhoads (1974) noted that activities of burrowing

organisms greatly increased the diffusibility of oxygen into muddy sediment and extended the redox layer further below the surface. Despite the lack of oxygen, black reducing sediments contain a variety of small organisms such as bacteria and

nematodes. Larger organisms (e.g., annelids) that also live in the anoxic zone tend to build tubes or burrows to the surface that bring oxygenated water to the organism.

CHAPTER 2

PRODUCERS, DECOMPOSERS, AND ENERGY FLOW

2.1 INTRODUCTION

Estuaries and coastal embayments are well-recognized for their high primary and secondary productivity. High production by New England tidal flats is reflected in their abundant and diverse populations of invertebrates (Chapter 3) and vertebrates (Chapters 4 and 5) that utilize the habitat as nursery grounds and feeding sites. In addition, many New England tidal flats support large populations of commercially and recreationally important shellfish and baitworms. The high productivity of tidal flats is attributed, in part, to the diverse variety of primary food types (e.g., benthic microalgae, phytoplankton, imported particulate organic materials - "detritus") that are available to the organisms of the flat.

2.2 PRODUCERS

2.2.1 Microalgae

New England tidal flats support a large and diverse microflora. These assemblages typically appear as brownish or greenish films or mats on the sediment surface and tend to be dominated by benthic diatoms, euglenoids, dinoflagellates, and blue-green algae.

The depth of microalgal distributions in tidal flat sediments is affected by the ability of light to penetrate the sediments. Fenchel and Straarup (1971) found that the photic zone (depth of light penetration) of fine sands was about half the thickness of that found in coarse sand. Although the majority of microalgae are concentrated in the upper several centimeters of the sediment, pigmented cells are commonly found below the photic zone. When exposed to light, these cells actively photosynthesize and it has been hypothesized that they provide a reservoir of

potential benthic primary producers if the upper several centimeters of the sediment are eroded by wave action (Van der Eijk 1979).

By virtue of their location, benthic microalgal species composition, abundance, and spatial distribution patterns are strongly influenced by near-surface physical, chemical, and biological processes. These groups of organisms exhibit pronounced spatial and temporal variation in abundance. Exposed tidal flats generally have lower abundances of microalgae than protected flats. Marshall et al. (1971) noted that benthic microflora were most abundant from May to August in several southern New England shallow estuaries probably as a result of temperature and illumination cycles. While summer peaks in abundance are typical throughout New England, Watling (L. Watling; University of Maine, Walpole; February 1981; personal communication) has observed dense surface films of diatoms on a tidal flat in Maine during winter, possibly a consequence of decreased grazing activities by benthic invertebrates at this time of the year.

Most of the academic study of the benthic microflora of tidal flats has been concentrated on the diatoms. Diatoms are ordinarily divided by specialists into two categories: the episammic (non-motile) and epipellic (motile) forms. Most studies have concentrated on the epipellic form since the method commonly used to collect diatoms (e.g., Eaton and Moss 1966) depends on the movement of microalgae into layers of fine netting placed on the sediment surface.

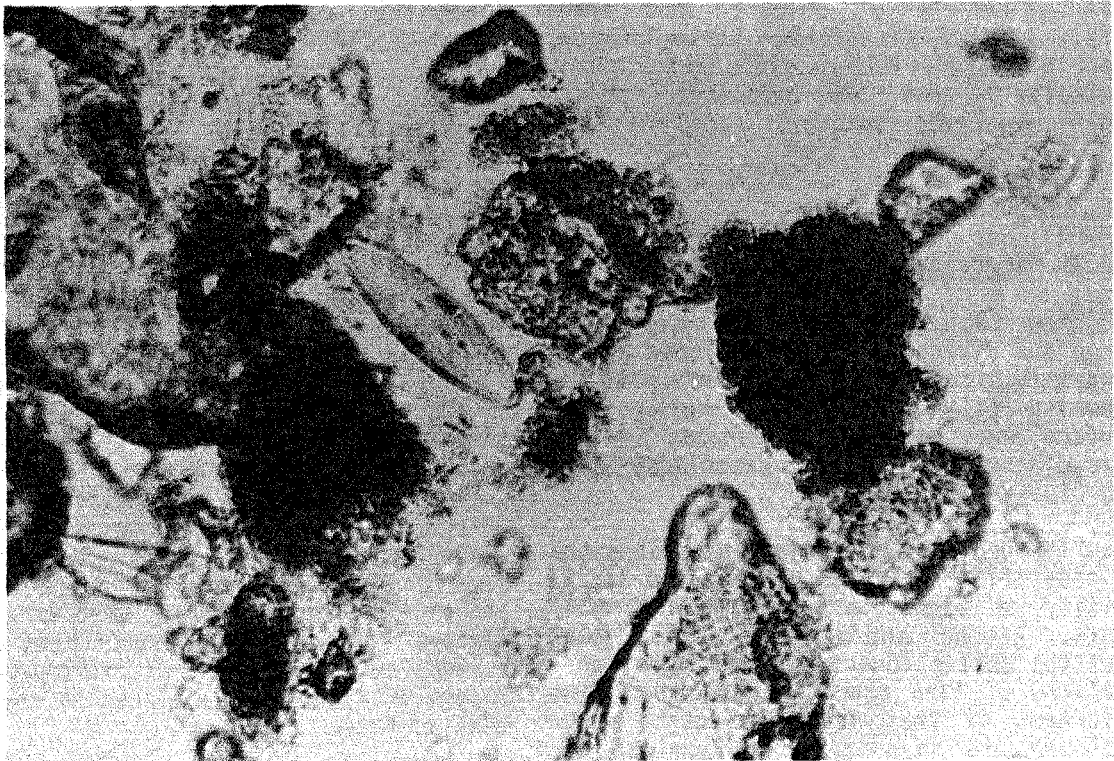
The benthic epipellic diatom tidal flat communities of New England are dominated by pennate forms such as Navicula, Hantzschia, and Nitzschia (Moull and Mason 1957; Connor 1980). These forms can migrate vertically through sediments by

extruding mucus threads. The extent of movement is variable and species-specific, ranging from diurnally migrating forms such as *Hantzschia* to relatively immobile forms such as *Amphora* (Round 1979). Vertical movements are thought to be dependent upon cycles of illumination with diatoms appearing at the sediment surface at low tide and burrowing into the sediment at flood tide (Palmer and Round 1967). The downward migration into the sediments is considered to be either an active response to compensate for displacement by tidal action or a mechanism for increasing nutrient availability (Pomeroy 1959). While the non-migratory forms are most commonly attached to sand grains, some species are capable of limited mobility.

Although episammic forms are not as intensively studied as the epipelagic

diatoms because they become more easily buried in unstable tidal flat sediments (Williams 1962; Sullivan 1975; Pace et al. 1979), these forms may be important benthic primary producers. Riznyk (1973) found that when sampling methods were used to collect both motile and non-motile forms, the latter group was more abundant on an Oregon tidal flat.

Occasionally algal mats are present in the higher elevations of tidal flat habitats. The mats consist of tightly intertwined groups of species of green and blue-green algae. The mats form a dark-green or blue-black crust on the sediment surface and are found in protected areas. The principle species found in a Massachusetts salt marsh by Brenner et al. (1976) were *Lyngbya aestuarii*, *Microcoleus chthonoplastes*, and *Calothrix contarenii*. In cross-section, many of the mats form



Epipelagic pennate diatoms (this specimen is approximately 0.2 mm long) are commonly seen in the upper several centimeters of tidal flat sediments. When very abundant, benthic diatoms form brownish films on the sediment surface. Photo by R.B. Whitlatch, University of Connecticut.

alternating layers of dark-green organic matter and lighter colored sediment 1 to 10 cm (0.4 to 4 inches) deep. Algal mats are known to accelerate rates of sediment accretion on tidal flats by mucilaginous trapping of fine-grained sediments.

The formation of algal mats is probably restricted to the high intertidal zone because of the reduced activities of grazing and burrowing organisms in these areas. Experimental removal of the surface-grazing periwinkle, Littorina littorea, and the mud snail, Ilyanassa obsoleta, from the mid-intertidal portions of a Barnstable Harbor, Massachusetts, sand flat resulted in the formation of a 1 to 2 mm thick algal mat within several weeks. Replacement of the snails in these plots resulted in the quick destruction of the mats (Whitlatch unpublished data). Other organisms such as amphipods and fish are also known to feed on the mats and probably help to control their distribution on tidal flats.

2.2.2 Macroflora

Because of the fine-grained and unstable nature of tidal flat sediments and their regular exposure to salt water at high tide and desiccation at low tide, macroalgae and rooted vegetation are relatively uncommon. While these factors may preclude the establishment of stable macrophytic communities on tidal flats, several species of ephemerals (short-lived species) are occasionally found in the New England region. These species (notably Ulva spp. - sea lettuce, and Enteromorpha spp. - green algae) are often associated with protected areas, the upper portions of sand flats, or with eutrophic conditions (e.g., sewage outfalls). They appear in early spring, continue to thrive throughout the summer, and rapidly decline during fall and winter.

In some parts of New England, dense populations of Ulva spp. have been documented. Welsh (1980) reported quantities up to 185 g/m² and several centimeters thick at the Branford Cove, Connecticut, mud flat. Edwards (S. Edwards; University of Rhode Island, Kingston; June 1980; personal communication) found that more than 75% of this same tidal flat was covered by Ulva during the summer. This

dense coverage resulted in the establishment of anaerobic conditions at the sediment surface and contributed to the reduction of microalgae through shading as well as decreased abundance of meio- and macrofauna. Others (e.g., Woodin 1974; Watling 1975) have also found that dense stands of Ulva can create anaerobic conditions at the sediment-water interface that alter infaunal species abundance and composition. Inhibitory effects of Ulva on tidal flat animal populations may also extend to fish species. In a series of laboratory experiments, Johnson (1980) demonstrated that mortalities of post-larval winter flounder (Pseudopleuronectes americanus) were greatly increased in the presence of Ulva. She offered the hypothesis that the increased fish mortality rates were the result of a harmful algal exudate.

Other species of large plants are commonly transported onto New England tidal flats from adjacent salt marshes (e.g., cordgrass-Spartina spp., rush-Juncus sp.), from eelgrass beds (Zostera marina), and from rocky coastlines (e.g., fucoids, Codium in southern New England). These species are most abundant on flats following storm activity or during the fall when they begin to die and decompose. When very abundant, these plant remains form strand or "wrack" lines on the higher elevations of the flats and provide food and protection for small crustaceans. Most of the biomass of these plants, however, is not used by herbivores but is broken down by microorganisms and by physical and biological fragmentation, becoming part of the tidal flat detritus-based food web (see section 2.3).

2.2.3 Phytoplankton

Phytoplankton are temporary tidal flat components and are present only when water is covering the flat. Phytoplankton are influenced by nutrient concentration, water temperature and circulation patterns, and by grazing; pronounced spatial and temporal variability in species composition and abundance exist along the New England coastline (see TRIGOM-PARC 1974 and Malone 1977 for reviews). Typically, phytoplankton concentrations are reduced during winter because of cold water temperatures and low light levels.

Growth rates increase in spring and may remain high throughout the summer in shallow waters. Primary production, therefore, tends to be higher in near-shore than oceanic waters because the shallower waters are continuously well-mixed and the phytoplankton have a constant supply of nutrients from the sediments. Growth rates are also higher in southern New England than northern New England probably due to higher water temperatures and the presence of larger amounts of anthropogenic nutrients in southern areas.

Phytoplankton species composition varies along the New England coast. Diatoms are most abundant in northern waters while the warmer, southern waters have higher concentrations of dinoflagellates. Hulbert (1956, 1963) found that several central New England shallow estuaries exhibited large concentrations of one or two species of phytoplankton and that species diversity was generally lower than in more oceanic waters. These patterns are assumed to reflect the more physically unstable inshore conditions that favor motile species (e.g., dinoflagellates) that do not sink to the bottom in shallow waters.

Occasionally, outbreaks of the dinoflagellate, *Gonyaulax excavata*, occur in New England nearshore waters. This "red tide" organism produces a toxin that is harmful to marine species when ingested (e.g., suspension-feeding clams, mussels). If the toxin accumulates in shellfish in sufficient quantities, it may be fatal to the host organism as well as to humans when contaminated shellfish are eaten. The intensity and duration of red tide outbreaks are variable in New England, but massive outbreaks create a severe health problem and economic impact upon the shellfish industry.

2.2.4 Photosynthetic and Chemosynthetic Bacteria

Although photosynthetic bacteria are commonly found in the sediments of New England tidal flats, relatively little is known about their ecology or role in the tidal flat food web. These organisms are restricted to the upper few millimeters of

the sediment and appear as purplish films especially during the warmer months of the year. Chemosynthetic bacteria, on the other hand, tend to be most abundant in the redox layer of tidal flat sediments and derive energy from the oxidation of inorganic compounds such as sulfide, nitrite, and ammonia. While relatively little is known about these bacterial types, recent studies in New Hampshire tidal flats (Lyons and Gaudette 1979) and a Massachusetts salt marsh (Howarth and Teal 1980) have shown that chemosynthetic bacteria may contribute significantly to primary production. How much of this energy is transferred to higher trophic levels within the tidal flat ecosystem is not known.

2.3 THE DECOMPOSERS

While considerable attention has focused on coastal embayments and estuaries as areas of high primary production, much of the organic material entering these systems is in the form of organic detritus (e.g., dead and decomposing salt marsh plants, eelgrass, phytoplankton). Recent evidence points to *in situ* utilization of the bulk of detritus (Haines 1977; Woodwell et al. 1977) as well as importation of additional detritus into shallow water from adjacent coastal water. Combining these organic inputs with those coming from terrestrial and aquatic sources and human activities (e.g., Kuenzler et al. 1977; Welsh et al. 1978), it appears that the utilization of detritus in inshore waters outweighs the consumption of the products of primary production.

Decomposition processes become increasingly important to the fauna on tidal flats because of (1) a high relative proportion of shallow water areas that promotes the occurrence of autochthonous (indigenous) detrital producers (e.g., benthic micro- and macroalgae), (2) low velocity current regimes that increase the probability of organic particles settling out from the water column, and (3) an increase in the ratio of length of shoreline to volume of water resulting in increased amounts of allochthonous (transported) detrital material entering from

freshwater, terrigenous salt marsh and eelgrass sources.

The organisms primarily responsible for the initial decomposition of detrital material on tidal flats are a wide variety of microorganisms, mainly fungi and bacteria. Fungi are associated with decomposing vascular plant material and breakdown cellulose by extending their hyphae into the detrital fragments. Fungi adhering to other particles, such as organic-encrusted mineral grains, are less common in tidal flat sediments (Johnson 1974). Bacteria are associated with the interstitial water found in sediments as well as the external surface of detrital particles and the concave surfaces of mineral grains (Johnson 1974). Studies have shown that bacterial standing stock is inversely correlated with particle size in marine sediments (e.g., Dale 1974). Presumably such a relationship exists because of the increased surface-to-volume ratio of the smaller particles resulting in increased area per unit volume of sediment for bacterial colonization and growth. Finer-grained sediments, therefore, have more abundant bacterial populations than coarser-grained sediments. Bacteria are also more abundant at the surface of sediments than at depth (Rublee and Dornseif 1978) probably because of the greater amount of detrital material found in near-surface sediment layers (Whitlatch 1981).

Decomposition rates of detritus are a function of the type and source of the organic substrate, physical and chemical conditions, and the density and type of organism feeding upon the matrix of living and non-living organic material. Detrital material entering tidal flats from terrestrial sources is more resistant to decomposition than much marine-derived detrital material. Terrestrial plants build more structural polymers (e.g., lignins) than marine plants and are much more resistant to bacterial decomposition (MacCubbin and Hodson 1980). Larger organisms (e.g., invertebrates) feeding upon detrital material have been shown to accelerate the decomposition process through the reduction of particle size, exposure of grazed surfaces to microbial activity, and selective foraging upon fast-growing microbial cells (Fenchel 1970, 1972; Fenchel and Harrison 1976; Lopez et al. 1977).

The decomposers perform several vital functions in marine coastal habitats. First, microbial decomposition of plant material serves as the primary link between primary and secondary production (Odum and de la Cruz 1967). Many studies have demonstrated that only small percentages of plant material are consumed while plants are living but that after death and physical-biological fragmentation, plant material serves as an energy source for the microbial and fungal populations in the sediment. The resultant microbial activity breaks down detritus and enhances its nutritive value as a food source for many other species of organisms. Second, during the decomposition process, the microbiota convert dead organic material into nutrients that can be utilized by primary producers. Loder and Gilbert (1980), for example, calculated that 7% of the dissolved phosphate entering Great Bay Estuary, New Hampshire, came from the estuarine sediments. Zeitzschel (1980) recently suggested that 30% to 100% of the nutrient requirements of shallow-water phytoplankton growth comes from the sediments. Release of nutrients from the sediment may also be important for tidal flat macroalgal production (B.L. Welsh; University of Connecticut, Avery Point, Groton; February 1981; personal communication). Bacteria can also convert dissolved organic materials from the water column into particulate biomass. While the importance of dissolved organic material in shallow-water marine environments is not fully understood, many types of marine invertebrates can utilize these substances as a food source (Stephens and Schinske 1961; Stephens 1975). Tidal flat invertebrates have well-developed digestive systems for the ingestion of particulate material and it is thought that bacteria can outcompete many of these organisms for dissolved organic material in marine sediments (Fenchel and Jørgensen 1977). Last, the net effect of having bacteria and fungi at the base of the decomposer food web is a stabilization of energy transfer to higher trophic levels within the tidal flat habitat. The availability of food for consumers is not restricted to the growing season of a temperate climate. The energy tied up in the primary detrital fraction is slowly released depending on the rate of microbial degradation to become available to higher trophic levels throughout the year.

2.4 ENERGY FLOW AND FOOD WEB RELATIONSHIPS

Organic materials in marine ecosystems are channeled through two types of food webs: one based on grazing, which starts with the utilization of the products of primary production; and another based on the consumption of detrital material and associated microbial populations. While these two food webs exist in tidal flat habitats, they are not well-defined. The trophic structure of New England tidal flats includes a number of primary food types and an intricately connected food web of generalized feeders. Many organisms interact and feed at different trophic levels at the same time and are able to utilize both living plant and detrital materials. Also, many tidal flat organisms change their trophic status with increasing size. Most fish, for example, begin their lives as planktivores, pass through a detritus-feeding stage, and finally become predaceous as adults.

Because detrital material is so conspicuous in the guts of many species associated with tidal flats (Whitlatch 1976; Tenore 1977), food webs in these habitats are considered to be detritally driven. The grazing food web apparently contributes less to tidal flat energy. One of the more striking examples of the lack of utilization of the products of primary production is the scarcity of organisms feeding on *Ulva* and *Enteromorpha*. While these macrophytes may densely carpet portions of New England tidal flats, only a few species (e.g., the snail, *Littorina*, nereid polychaetes, some gammaridean amphipods, and birds) feed upon them directly. Occasionally dense populations of birds or snails deplete these macrophytes locally, but probably 90% to 95% are consumed after death and entry into the detrital food web (Mann 1972). Grazing on microalgae by herbivorous snails and some tube-dwelling amphipods is more common although to what extent these organisms rely exclusively upon the microalgae as food has yet to be determined.

Although detritus appears to be the major food source of many tidal flat organisms, there are uncertainties regarding exactly what fractions of the detrital materials are utilized by detritivores.

The microbial portion (the "living" fraction) of the detrital particle is easier to digest and is more nutritious than the structural ("non-living") portion. Fungi, bacteria, and protozoans associated with detrital particles are efficiently removed by detritivores (Fenchel 1972; Hylleberg 1975; Lopez and Levinton 1978), and studies have shown that these living materials are more easily digested than the non-living fraction (Kofoed 1975; Wetzel 1977). When comparing the ingestion rates of various detritivores, Cammen et al. (1978) found that the microbial portion of detritus accounted for only about 10% of their metabolic demands. This apparent contradiction suggests some possibilities about the importance of the living versus the non-living fractions of detritus to detritivores. First, detritivores may be able to derive most of their nutrition from the non-living fraction. Second, energy obtained from other sources, such as dissolved organic materials or small meiofaunal organisms (see section 3.3) may figure significantly in a detritivore's nutritional requirements. Last, organisms may be selectively feeding on the living portion of the detrital particle. Selectivity for high organic food items has been shown in several species of detritivores (e.g., Whitlatch 1974; Connor 1980) and selective ingestion of microbially-enriched fecal material (termed coprophagy) is common (Johannes and Satomi 1966; Frankenberg and Smith 1967). While more information is needed to test the various alternative explanations, it is becoming increasingly apparent that inshore detrital food web dynamics are more complex than previously considered.

Many ecologists believe that tidal flat ecosystems are "energy subsidized", receiving the bulk of their energy from adjacent salt marshes, seagrass beds, estuaries, and coastal waters as detrital carbon. It has been difficult in actual practice to assign a relative importance to the contributions of organic material from primary producers and detrital decomposers and to identify from which source they are derived. Much of this uncertainty centers around a general lack of *in situ* estimates of primary production and decomposition on tidal flats. Some data are available on standing crops of

macroalgae, but photo- and chemosynthetic bacterial productivity have yet to be estimated. There are several estimates of benthic microalgal production in temperate, shallow-water habitats (Table 2), but only Marshall et al. (1971) deal specifically with the New England region. Table 2 shows large regional differences in primary production, probably dependent upon local biological, physical, and chemical conditions, and the time of the year of the measurements. In addition since it appears that microalgal production is lower at higher latitudes, the estimates by Marshall et al. (1971) cannot be used to generalize for the whole New England region. Phytoplankton productivity in several temperate estuarine environments is given in Table 3. As in the case of benthic microalgae, large regional differences in productivity exist for phytoplankton making general statements of little value. No estimate of phytoplankton production on New England tidal flats is available and conflicting evidence exists as to whether tidal flat production levels are higher or lower than production levels in deeper coastal waters. Phytoplankton productivity above the flats may be low because these areas are covered by water only a portion of the day and the water over the flats is turbid because of tidal action. Conversely, primary production may be stimulated by the increased warmth of water over the flat and the closer proximity of nutrients available in the sediments.

Few studies have attempted to determine organic sources and estimate input and utilization rates of organic matter in New England coastal environments. The few data available, while not specifically from tidal flat habitats, suggest that the flats rely on external sources of organics transported by tidal action. Nixon and Oviatt's (1973) comprehensive study on a small Rhode Island coastal embayment demonstrated that the system depended heavily on imports of organic matter from adjacent salt marsh grasses and microalgae. Welsh (1980) found a western Connecticut mud flat to be a nutrient importer in which mud flat sediment scavenged nutrients derived from both an adjacent salt marsh and tidal creek. In fact, the sediments were so effective in trapping passing nutrients that very little were transported to the adjacent

open estuarine environment. The periodic contribution of detrital material to the sediment of Barnstable Harbor, Massachusetts sand flats was related to the annual productivity-decay cycles of Spartina alterniflora (Whitlatch 1981). Other data support the view that detritus imported from salt marshes, eelgrass beds, and phytoplankton contribute significantly to the annual budget of organic matter entering shallow water estuarine systems (e.g., Day et al. 1973; DeJonge and Postma 1974; Wolff 1977).

Data are available that contradict the "energy subsidy" thesis. In a variety of southern New England coastal ponds and estuaries, Marshall (1970) found that most of the organic matter contributed to the sediment came from sources within the system (Table 4). While it is difficult to extrapolate directly from these data to tidal flat habitats, they do point to benthic micro- and macrophyte production as significant contributors of organic carbon. Marshall (1972) later pointed out that the rates at which organic matter was added to those systems he studied was less than the rates at which it was being utilized. He suggested that rapid recycling of organic materials within the habitats could explain the imbalanced carbon budget. In addition, there is a debate regarding the importance of salt marshes as energy subsidizers of estuarine and coastal environments (see Nixon 1980 for a review). Early studies suggested that marsh grasses were exported in large quantities to become the major contributor of detritus to the coastal zone. More recently, studies have indicated that much of the detritus associated with Georgian estuaries is not derived from marsh grass but comes from algal sources (e.g., Haines 1977; Haines and Montague 1979). Production of organic materials by chemosynthetic bacteria has been overlooked and may contribute appreciably to the tidal flat carbon budget (see section 2.2.4). In any event, it is obvious that more research carried out with a holistic (whole system) perspective will be needed to clarify this situation. The contribution of salt marsh organic materials to tidal flat habitats, for instance, may be determined by hydrographic characteristics (e.g., flushing rates, topographic conditions) of the individual systems and the proximity of the salt marshes to the tidal flats.

Table 2. Primary production by benthic microalgae in some temperate intertidal and shallow subtidal habitats.

Area	Production gC/m ² /yr	Reference
Danish Wadden Sea	115-178	Grøntved 1962
Dutch Wadden Sea	35-435	Cadée and Hegeman 1974
False Bay, Washington ^a	143-226	Pamatmat 1968
Ythan estuary, Scotland	31	Leach 1970
Southern New England shoals	81	Marshall et al. 1971

^aEstimated by oxygen method, all others ¹⁴C.

Table 3. Phytoplankton primary production in some temperate estuarine areas.

Area	Production gC/m ² /yr	Reference
Long Island Sound ^a	380	Riley 1956
St. Margaret's Bay, Nova Scotia	190	Platt 1971
Loch Etive, Scotland	70	Wood et al. 1973
Wadden Sea, Netherlands	100-200	Cadée and Hegeman 1974
Ems estuary, Netherlands	13-55	Cadée and Hegeman 1974
Grevelingen estuary, Netherlands	146-200	Vegter 1977
Marsdiep Inlet, western Wadden Sea, Netherlands	135-145	Cadée and Hegeman 1979

^aEstimated by oxygen method, all others ¹⁴C.

Table 4. Sources and contributions of organic carbon to some southern New England coastal ponds and estuaries (Marshall 1970).

Source	Production gC/m ² /yr	Percentage of total organic carbon
Macrophytes (e.g., eelgrass, macroalgae)	125	45-47
Benthic microalgae	90	33-34
Phytoplankton	50	18-19
Allochthonous materials (e.g., tidal marshes, terrestrial and coastal sources)	0-10	0-4
Dissolved organic materials	No estimate available	
Photosynthetic and chemosynthetic bacteria	No estimate available	

CHAPTER 3

BENTHIC INVERTEBRATES

3.1 INTRODUCTION

Living in close association with tidal flat substrata are a variety of benthic invertebrates. These organisms may be extremely abundant and play major roles in the tidal flat habitat. The benthos are, for instance, a major link in the coastal detritus-based food web. Many species feed on detrital materials and associated microorganisms and, by doing so, accelerate the decomposition of organic materials deposited on the sediment surface (see Chapter 2). Many of these same species then serve as food for bottom-dwelling fishes (Chapter 4), birds (Chapter 5), as well as commercially important species of crabs. In addition, as the mobile benthos forage on or burrow through the sediment, they promote sediment mixing (bioturbation) has the potential of greatly modifying the biological, physical, and chemical properties of the sediments. Such activities alter sediment stability, vertical profiles of sedimentary materials, movements of organic and inorganic materials across the sediment-water interface, and the distribution and abundance patterns of other benthic species. In a recent review, Zeitzschel (1980) estimated that between 30% to 100% of the nutrient requirements of shallow water phytoplankton populations were derived from sediments with the benthos playing a major role in promoting regeneration and recycling of inorganic nutrients from the sediments to the water column. And last, several benthic invertebrate species are commercially and recreationally important in New England (Chapter 6).

By convention, benthic invertebrates have been divided into generalized groups based upon life mode. Organisms living on the surface of the sediment are termed

epifauna and most are actively mobile members of the phyla, Arthropoda and Mollusca. The infauna consist of organisms that live in the sediments. These species include a taxonomically broader group of organisms ranging from small nematodes and ostracods to larger annelids, crustaceans, and molluscs. Categorization of benthic organisms as "infaunal" and "epifaunal" remains somewhat arbitrary. Many infaunal species spend certain portions of time foraging and reproducing on the sediment surface or have been found swimming in the water column in inshore areas (e.g., Thomas and Jolley 1972; Dean 1978a, b; Dauer et al. 1980). While the latter behavior may be related to reproductive and feeding activities or environmental cues (e.g., changes in salinity, temperature, and light), much of the migrational activity into and out of the sediments remains unexplained and may result from overcrowding or habitat degradation.

3.2 BENTHIC EPIFAUNA

Because of its general lack of suitable substrate for settlement of larvae, there are few permanently attached organisms living on tidal flats. Unlike some areas along the Atlantic coast (Bahr and Lanier 1981), extensive intertidal oyster (*Crassostrea virginica*) reefs do not occur in New England. Overexploitation coupled with pronounced environmental variability in New England probably control the upper limit of intertidal distribution of the oyster. The only significant populations of this bivalve are found in subtidal, commercially maintained areas. Blue mussel (*Mytilus edulis*) beds, however, are found throughout New England tidal flats (especially in Maine) and occur in the lower elevations of the intertidal zone in dense concentrations. Along some parts of the Maine coast, mussel densities are high

enough to be commercially harvested. The initial formation of these beds on tidal flats is dependent upon the existence of a hard substrate such as stones, mollusc shells, or other debris. After establishment, other mussels settle and the bed spreads laterally forming a complex mat of sediment, shell debris, and animals. The mussel beds provide a stable substrate upon which other sessile epifauna attach as well as serving as protection for mobile epifauna and infauna. Lee (1975) found many species of annelids, molluscs, and crustaceans associated with mussel beds in Long Island Sound. New England tidal flat mussel beds have not been well-studied and in some areas may be ephemeral features of the habitat. Field (1923) indicated that many beds in Long Island Sound only last two to three years. Because of the limited availability of firm substrate for attachment, physical disturbance such as ice, storm waves, and accreting sediment contribute to the temporal instability of mussel beds.

The mobile invertebrate epifauna comprise two taxonomic groups--arthropods and molluscs (Table 5). Both groups exhibit low habitat specificity although predatory gastropods are found in sandy areas where their preferred prey items (bivalve molluscs) reside. Distribution and activity patterns of these epifauna are affected by seasonal changes in water temperature. As water temperature declines in the fall, all the crustacean species migrate into deeper water where many burrow into the subtidal sediment and become semi-torpid. The gastropods are apparently less sensitive than arthropods to low temperatures and tend to remain on tidal flats until the beginning of ice formation. In relatively mild winters, some species do not migrate into deeper water.

The receding tide may reveal large populations of gastropods on New England tidal flats. In high intertidal areas, concentrations of common (Littorina littorea) and rough (Littorina saxatilis) periwinkles are often found. These gastropods are herbivorous and are often seen scraping the sediment surface for microalgae or grazing on pieces of Ulva and Enteromorpha. Another species found in this area is Hydrobia totteni. This minute gastropod browses upon sediment particles

consuming microalgae and associated microorganisms. Although abundant on many tidal flats, it is often overlooked because of its small (2 to 4 mm) size.

Extremely large and often dense aggregations of the mudsnail, Ilyanassa obsoleta, frequent New England tidal flats. This species displays catholic feeding behavior ranging from strict herbivory to carnivory (Brown 1969; Connor 1980). Aside from the snail's impact on the benthic microalgal community (Chapter 2), several authors have documented the effects of its feeding and sediment disruption upon the benthic infauna. Movements by Ilyanassa reduce the abundance of nematodes (Nichols and Robertson 1979) and the infauna associated with amphipod tubes (Grant 1965). Snail enclosure experiments conducted at Barnstable Harbor, Massachusetts, resulted in pronounced decreases in the infauna particularly newly settled juveniles of near-surface dwelling polychaetes (Whitlatch unpublished data). Boyer (1980) has shown that the mudsnail decreases stability of the sediment-water interface. Ilyanassa migrates into deeper waters during the winter and reappears each spring. Brenchley (1980) feels that this migratory pattern may be altered by the presence of Littorina littorea which may also interfere with the reproductive activities of Ilyanassa.

Several species of mollusc-eating gastropods are common in southern New England. The most abundant is the moon snail, Polinices duplicatus; this active predator leaves distinctive circular bore holes in the shells of its victims. Edwards and Huebner (1977) concluded that Polinices eats only living prey items and prefers the soft-shelled clam, Mya arenaria. Wiltse (1980) demonstrated the influence of the snail's foraging activities on the infauna using caging experiments in the field. When snails were excluded from cages, increased numbers and diversity of both prey (molluscs) and non-prey (annelids, sipunculids) species were found inside the cages. The snail's influence was both through direct consumption of prey items and indirect disruption of the upper few millimeters of the sediment surface as it plowed along in search of food. Boyer (1980) found that the foraging behavior of Polinices destroyed blue-green

Table 5. Common epifaunal invertebrates inhabiting New England tidal flats.

Species	Distributional range; habitat preferences	Feeding habits
Mollusca		
<u>Ilyanassa obsoleta</u> (mudsnail)	Throughout New England; ubiquitous, although usually most dense on mud flats.	Deposit feeder/scavenger/predator
<u>Littorina littorea</u> (periwinkle)	Throughout New England (introduced species); in higher intertidal areas.	Herbivore
<u>Polinices duplicatus</u> (Tobed moon snail)	Throughout New England (more common south of Cape Cod); mostly on sand flats.	Molluscivore
<u>Lunatia heros</u> (northern moon snail)	Throughout New England; most abundant subtidally.	Molluscivore
<u>Hydrobia totteni</u> (minute hydrobid)	Throughout New England; most abundant in muddy sediments.	Detritivore
<u>Haminoea solitaria</u> (paper-bubble)	Northward to southern Maine; seasonally abundant in muddy sediments.	Detritivore
<u>Busycon canaliculatum</u> (chambered whelk)	Chiefly south of Cape Cod; shallow subtidal sandy bottoms.	Molluscivore
<u>Mytilus edulis</u> (blue mussel)	Throughout New England; especially common on Maine mud flats.	Suspension feeder
<u>Crassostrea virginica</u> (common oyster)	Throughout New England; occasionally found intertidally on mud flats.	Suspension feeder
<u>Aequipecten irradians</u> (bay scallop)	Common in southern New England, occasionally in northern New England; most abundant near eelgrass beds.	Suspension feeder

continued

Table 5. (Continued).

Species	Distributional range; habitat preferences	Feeding habits
Mollusca (continued)		
<u>Littorina saxatilis</u> (rough periwinkle)	Throughout New England; in higher intertidal areas.	Herbivore
<u>Placopecten magellanicus</u> (deep-sea scallop)	Intertidally in some parts of Maine; mostly subtidal.	Suspension feeder
Arthropoda		
<u>Carcinus maenas</u> (green crab)	Throughout New England (introduced species); most abundant on mud and muddy sand sediments.	Molluscivore; deposit feeder; scavenger
21 <u>Callinectes sapidus</u> (blue crab)	Occasionally abundant in southern New England estuaries; on mud bottoms.	Molluscivore; deposit feeder; scavenger
<u>Limulus polyphemus</u> (horseshoe crab)	Throughout New England; seasonally abundant in spring-summer.	Bivalves and polychaetes
<u>Palaemonetes pugio</u> (grass shrimp)	Throughout New England; ubiquitous.	Deposit feeder; scavenger; predator on small invertebrates
<u>Crangon septemspinus</u> (sand shrimp)	Throughout New England; ubiquitous.	Similar to <u>Palaemonetes</u>
<u>Libinia emarginata</u> (spider crab)	Throughout New England; juveniles more common near eelgrass beds, adults on muddy sediments.	Omnivore
<u>Libinia dubia</u> (spider crab)	Throughout New England, but more common south of Cape Cod; possibly more estuarine than <u>L. emarginata</u> .	Similar to <u>L. emarginata</u>
<u>Cancer irroratus</u> (rock crab)	Throughout New England, more intertidal north of Cape Cod; ubiquitously distributed.	Omnivore

continued

Table 5. (Concluded).

Species	Distributional range; habitat preferences	Feeding habits
Arthropoda (continued)		
<u>Pagurus longicarpus</u> (long-armed hermit crab)	North to Massachusetts; ubiquitously distributed.	Omnivore
<u>Pagurus pollicaris</u> (flat-armed hermit crab)	To southern Maine, but more common south of Cape Cod; ubiquitously distributed, most common on subtidal sand sediments.	Omnivore
<u>Uca pugnator</u> (sand fiddler crab)	North to Cape Cod; sand flats and salt marshes.	Deposit feeder
<u>Uca pugnax</u> (mud fiddler crab)	North to Cape Cod; sand flats and salt marshes.	Deposit feeder
<u>Ovalipes ocellatus</u> (Tady crab)	North to Cape Cod; typically on sandy sediments.	Scavenger
<u>Cancer borealis</u> (Jonah crab)	Throughout New England; most common among rocks.	Omnivore

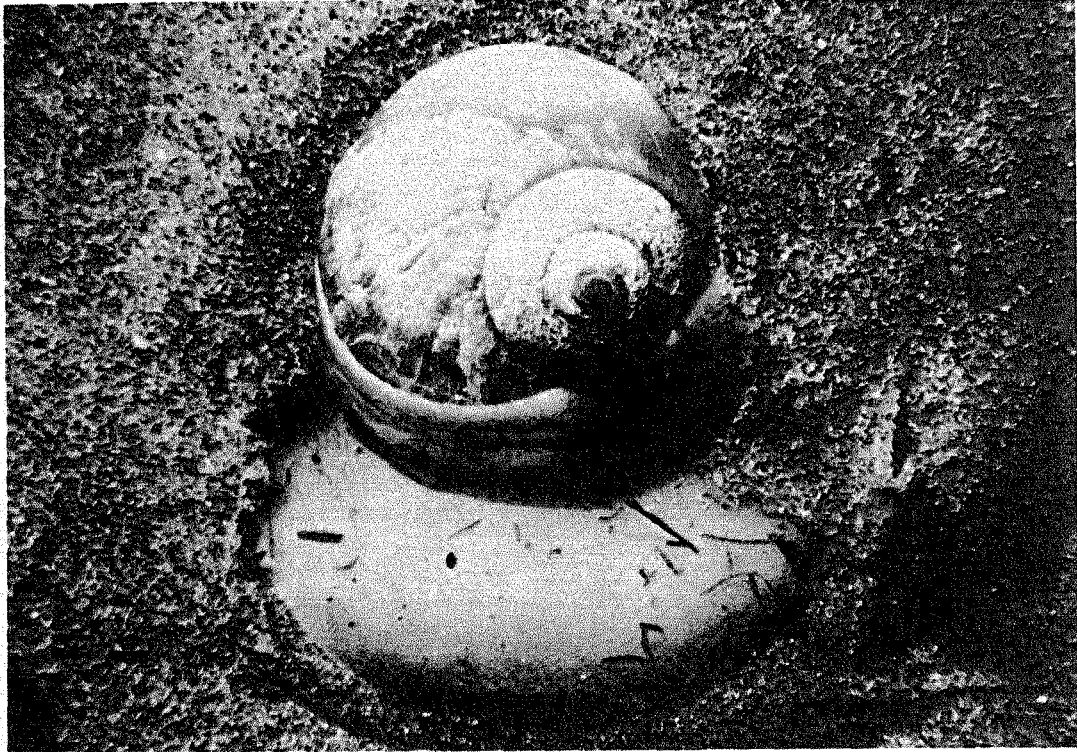


Dense aggregations of the mudsnail, Ilyanassa obsoleta, typically overwinter subtidally during New England winters. As water temperature increases in the spring, the snails begin mass migrations back onto tidal flats where they begin reproducing and feeding. Snails are approximately 2 cm in length. Photo by R.E. DeGoursey, University of Connecticut.

algal mats and microalgae, decreased sediment stability, and contributed to increased erosion of the sediment-water interface. Another species of naticid snail, Lunatia heros, is occasionally found on tidal flats in northern New England although it is more abundant in subtidal, sandy substrates. The whelk, Busycon canaliculatum, also forages intertidally in southern New England but is a rare inhabitant of tidal flats.

The mobile bay scallop (Aequipecten irradians) is sometimes seen on tidal flats. Settling juveniles prefer to attach themselves by threads to eelgrass (Zostera marina) or other subtidal macroalgae. As scallops grow, they drop to the sediment surface in the vicinity of eelgrass beds and may move onto tidal flats at high tide.

Several species of epifaunal arthropods are common to New England tidal flats. Unlike the gastropods, this group migrates on and off the flats with the tidal cycle. The most common species throughout New England is the green crab, Carcinus maenas. Like all large crabs, this species feeds by crushing its prey. Feeding rates and preferred prey are related to crab size (Elner and Hughes 1978; Elner 1980) with a tendency to specialize on bivalves (e.g., Mya arenaria, Mytilus edulis). Ropes (1968) noted that these crabs ingest annelids, detritus, and Spartina blades as well. Other large crab species are also present but are less abundant than the green crab. The blue crab, Callinectes sapidus, so very abundant in the middle and southern portions of the eastern seaboard, is less so in New England, found only south of Cape Cod.



The gastropod, Polinices duplicatus (shell approximately 8 cm in width), bulldozing through the sediments in search of molluscan prey. Photo by P. Auster, University of Connecticut.

This species is found in estuaries and its distributional pattern varies seasonally, with the sexes, and with the stage of development of the crab (Van Engel 1958). Virnstein (1977) has documented the impact of this species on the benthic infauna of Chesapeake Bay. Blue crabs are voracious predators as well as active diggers in the sediment and can significantly alter both species composition and abundance of the infauna. The rock (Cancer irroratus) and Jonah (C. borealis) crabs, commonly found in estuaries on mud bottoms and rocky outcrops respectively, are more often found intertidally in northern New England than in southern New England (MacKay 1943) and probably have similar effects upon the infauna as the blue crab.

In spring, Limulus polyphemus, the horseshoe crab, appears intertidally to initiate spawning activities. These crabs dig distinctive pits about 3 to 6 cm (1 to 2 inches) deep on the sediment surface

while searching for bivalves and polychaetes. Woodin (1978) demonstrated that this digging activity reduced the abundance of several infaunal invertebrates on a Maryland tidal flat. She noted that high spring-summer densities of Limulus resulted in feeding pits that covered 50% to 70% of her study site. New England populations of Limulus are not as large and tend to be more spatially variable than those described in Maryland. Occasionally this species is used as bait for eel fisheries and uncontrolled harvesting may have led to reduced population levels in some New England areas.

Several other species of crustaceans also frequent tidal flats. The grass shrimp, Palaemonetes pugio, is more often found in southern than in northern New England eelgrass beds. The sand shrimp, Crangon septemspinosus, in contrast, is the only common shallow-water species between Cape Ann and the Bay of Fundy.

This species can often be seen following the leading edge of flood tides over tidal flats feeding on resuspended detrital material and carrion. The hermit crabs, Pagurus longicarpus and P. pollicaris, are abundant locally. Pagurus longicarpus, found occupying Ilyanassa and Littorina shells, and P. pollicaris, preferring Polinices shells, are omnivores scavenging on living and non-living animal material as well as detrital material on the sediment surface. The lady crab, Ovalipes ocellatus, is frequently seen on the sand flats of Cape Cod where it hides buried in sand with only its eyestalks exposed. Spider crabs (Libinia emarginata and L. dubia) and fiddler crabs (Uca pugilator and U. pugnax) are also locally abundant, although the former two species are more characteristic of eelgrass beds, while the latter two species are in greatest abundance near or in salt marsh habitats. Various smaller amphipods and isopods also occur in both mud and sand flats. These species typically burrow slightly below the sediment-water interface and have been categorized as infaunal organisms (see Appendix I).

3.3 BENTHIC INFAUNA

Broad designations, based on organism size, are used to distinguish among groups of infaunal organisms. Confusion arises because of this approach although size groupings tend to correspond to taxonomic groupings. Organisms that pass through a 64 μm mesh sieve are termed microfauna, those retained on a 300 to 500 μm mesh are called macrofauna, and all others are designated as meiofauna. In addition to the arbitrariness of sieve-size selection in determining the various infauna groups, many organisms pass from the meiofaunal category to the macrofaunal category as they grow.

Because of the small size of micro- and meiofauna and difficulties in sampling them, our knowledge of these groups is fragmentary and speculative. Microfauna include the protozoans, especially the ciliates and foraminiferans. They are abundant, particularly in fine sands with strong reducing properties and numerous sulfur bacteria (Fenchel 1967). Most

microfauna are found within several centimeters of the sediment surface although Fenchel (1969) noted distinct species-specific vertical distribution patterns related to the redox-discontinuity layer. Relatively little is known about the role of microfauna in coastal ecosystems although Barsdate et al. (1974) found that detrital decomposition was apparently stimulated and phosphorus cycling increased in the presence of grazing protozoans. Other workers have questioned the overall importance of the microfauna in the recycling of detrital materials (Fenchel and Jørgensen 1977) recognizing that microfauna may be a food source for meio- and macrofauna.

Meiofaunal populations comprise a taxonomically broader group of organisms. Tietjen (1969), for example, found that nematodes, ostracods, harpacticoid copepods, and turbellarian flatworms were abundant in two shallow subtidal sites in southern New England. Meiofaunal distributions are apparently controlled by sediment composition. Turbellarians dominate coarser sandy sediments and nematodes are in greater numbers in muddy sediments, presumably because of the increased amounts of detrital material and microorganisms in muds. Most meiofauna occur in the upper, well-oxygenated layers of the sediment (Figure 5) although nematodes have been recorded at greater depths.

As more information accumulates on the marine meiofauna, biologists share a greater appreciation for the ecological importance of these organisms in soft-sediment environments. In addition to accelerating decomposition and recycling of detrital materials (see Chapter 2), these effects may be transmitted to higher trophic levels in the detritus-based food web (Tenore et al. 1977). A high degree of interest has focused on the trophic position of the meiofauna--questioning whether they represent a trophic dead end, are competitors with macrofauna for shared food materials, or are a major food source consumed by macrofauna. Recent evidence points to the last hypothesis. Gerlach (1978) estimated that foraminifera and meiofauna represent 12% to 30% of the living biomass in many marine sediments and

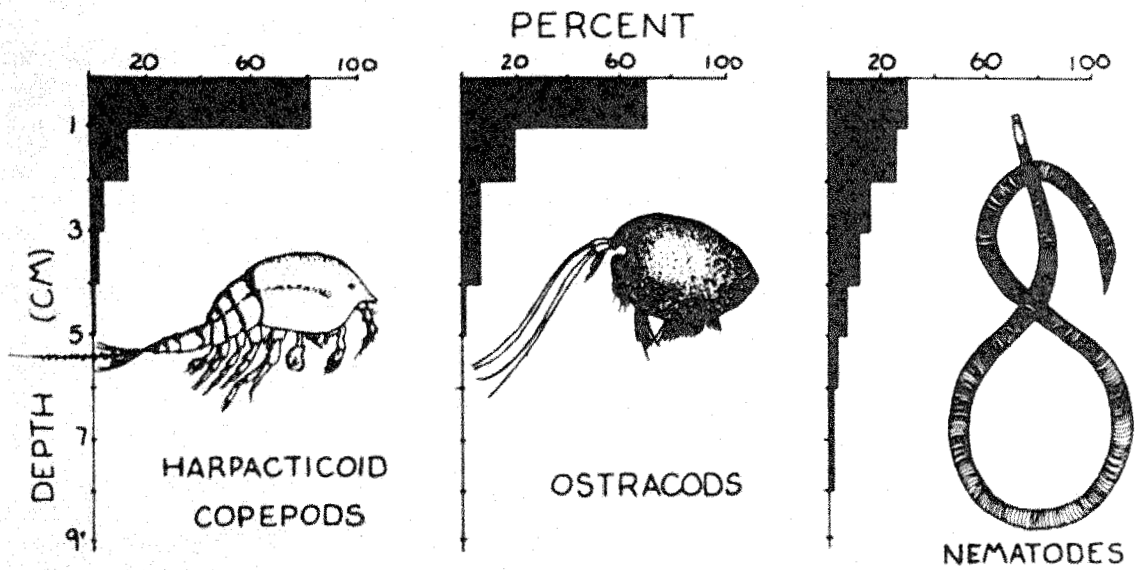
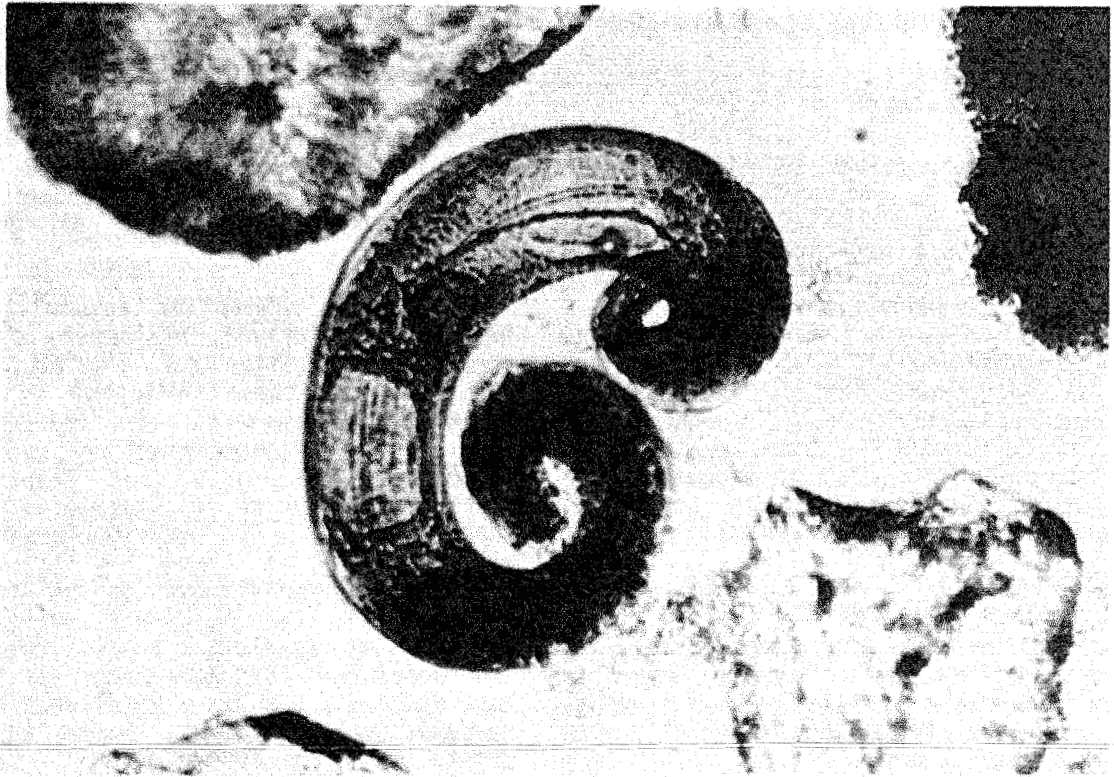


Figure 5. Vertical distributions of some dominant groups of meiofaunal organisms (from Tietjen 1969; Whitlatch unpublished data).



Nematodes (this specimen is approximately 0.3 mm in length) are very common members of the benthic meiofauna of New England tidal flats. Photo by R.B. Whitlatch, University of Connecticut.

are fed upon by a wide range of benthic macrofaunal invertebrates. Many species of juvenile fishes are also known to ingest large numbers of meiofauna (e.g., gobies, Smidt 1951; flatfish, Bregnballe 1961; salmonids, Feller and Kaczinski 1975). The transfer of meiobenthic biomass to higher trophic levels may be limited to areas where the meiobenthic densities are high enough to be readily consumed by bottom-feeding invertebrates and vertebrates (Coull and Bell 1979).

The macrofauna are the most well-studied group of infauna because of their relatively large size and the fact that several species are commercially and recreationally important along the New England coast (see Chapter 6). Annelid worms, bivalve molluscs, and amphipod crustaceans are usually the most numerous although other taxonomic groups such as echinoderms, hemichordates, sipunculids, and nemertean are also relatively common on tidal flats. The macrofauna are often divided into three generalized trophic groups: (1) suspension feeders, organisms that obtain food materials (e.g., planktonic diatoms, suspended sediment) from the overlying water column, (2) deposit feeders, organisms dependent upon the organic fractions within the sediment for food, and (3) scavenger-predators, organisms that feed mostly on dead and living animal materials. These trophic groupings are complicated by the feeding plasticity exhibited by most species of infauna (e.g., Sanders et al. 1962; Fauchald and Jumars 1979; Taghon et al. 1980). Many species tend to be generalized feeders whose diet is primarily limited by the size of the food particles they are able to ingest (Whitlatch 1980).

One feature of macrofaunal communities is the long recognized association of particular species or assemblages of species with particular sediment types. The scientific literature often refers to "mud" and "sand" communities rather than mentioning specific species names (see Figures 6 and 7). Spatial variation among such species assemblages is primarily correlated with sediment particle size (Sanders 1958; Fager 1964; Bloom et al. 1972). Other factors directly or indirectly influencing the composition of bottom sediments can also affect the

distribution patterns of macrofauna (e.g., sedimentation rates, sediment stability, food availability).

The intimate association of infaunal organisms with sediment features is a consequence of the animals' reduced mobility. Infauna rely on sediments not only for shelter, protection, and areas to reproduce, but also for food. Deposit feeders usually dominate in fine-grained muddy sediments because of the increased availability of detrital material and microorganisms. Suspension feeders, conversely, must retain contact with the sediment-water interface to feed and are usually found in stable sedimentary environments where there is less resuspended sediment to clog their filtering structures. This complementary trophic group separation of the benthic habitat by feeding type while apparently true of New England subtidal habitats (Sanders 1958; Rhoads and Young 1970), may be less so intertidally. While Whitlatch (1977) found trophic separation by sediment type in Barnstable Harbor, Massachusetts, Larsen et al. (1979) found deposit feeders to be abundant in both sand and mud flats in Maine. Only unstable sandy beach substrates were dominated by suspension-feeding amphipods.

In addition to conditions in the sediment, other physical factors limit the distribution of New England macrofauna. On a geographic basis, distribution patterns of macrofauna can be divided into three generalized categories: (1) species that occur throughout the New England coast, (2) species more restricted to the cold Gulf of Maine waters, and (3) species found in warmer southern New England waters (Appendix I). Cape Cod is recognized as a biogeographical boundary and several studies have noted distinct groups of subtidal benthic species occurring only north or south of Cape Cod (Yentsch et al. 1966). Nearshore, where water temperatures exhibit pronounced fluctuation, these categories are less distinct. North of Cape Cod, warm water embayments and estuaries do occur and one occasionally finds warm water species in these areas (e.g., the quahog, *Mercenaria mercenaria*). Representatives of the cold water group inhabit southern New England waters especially during winter. Depending upon

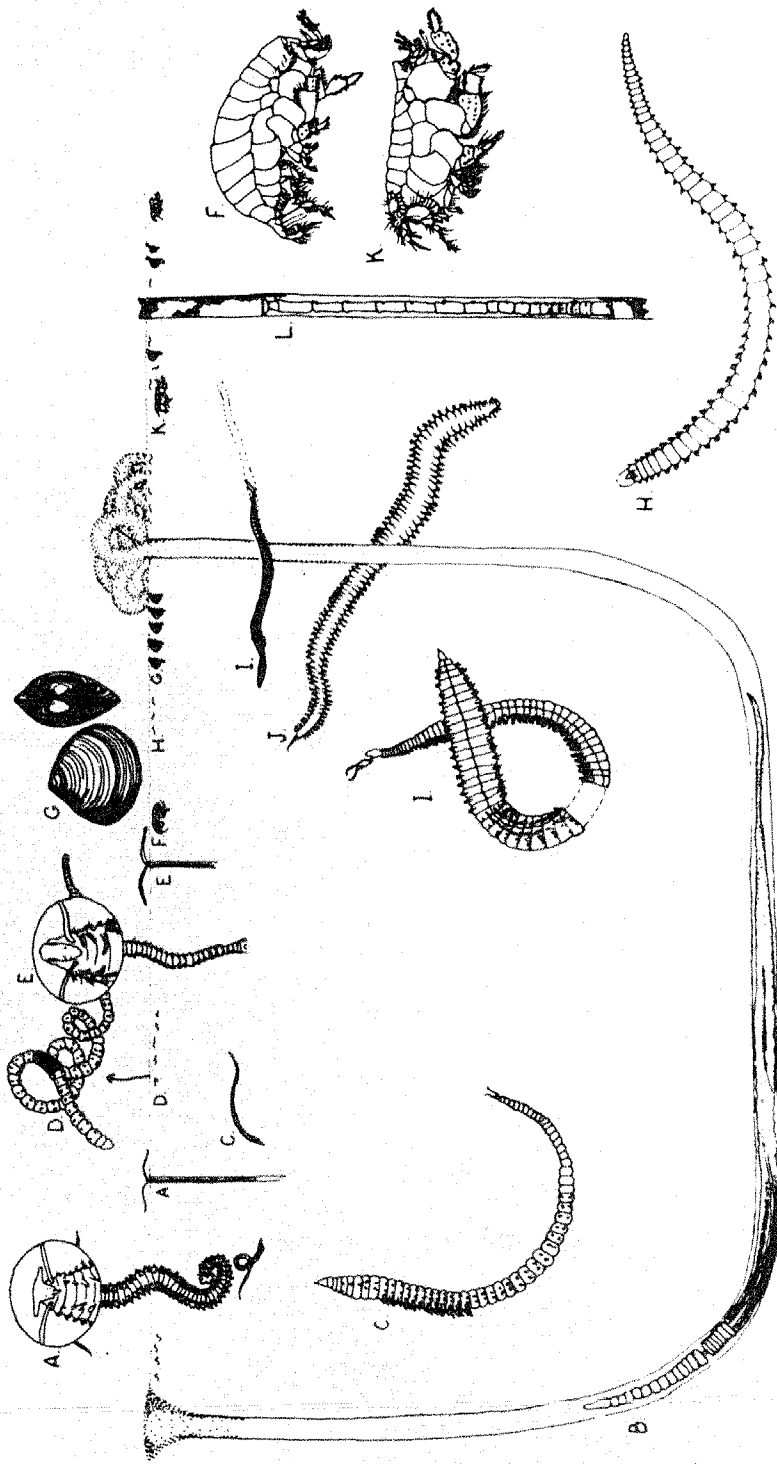


Figure 6. Some representative New England sand flat benthic invertebrates indicating general life habits.

Surface deposit feeders:

- A = *Spiophanes bombyx* (spionid polychaete)
- B = *Saccoglossus kowalewskyi* (protochordate)
- E = *Pygospio elegans* (spionid polychaete)

Burrowing deposit feeders:

- C = *Aricidea* sp. (paraonid polychaete)
- D = *Oligochaete*
- H = *Exogone hebes* (syllid polychaete)
- I = *Scoloplos* spp. (orbiniid polychaete)
- J = *Nephtys* spp. (nephtyid polychaete)

Suspension feeders:

- G = *Gemma gemma* (venerid bivalve)
- F = *Protohaustorius deichmannae* (haustoriid amphipod)
- K = *Acanthohaustorius millisi* (haustoriid amphipod)

Conveyor-belt deposit feeder:

- L = *Clymenella torquata* (malmanid polychaete)

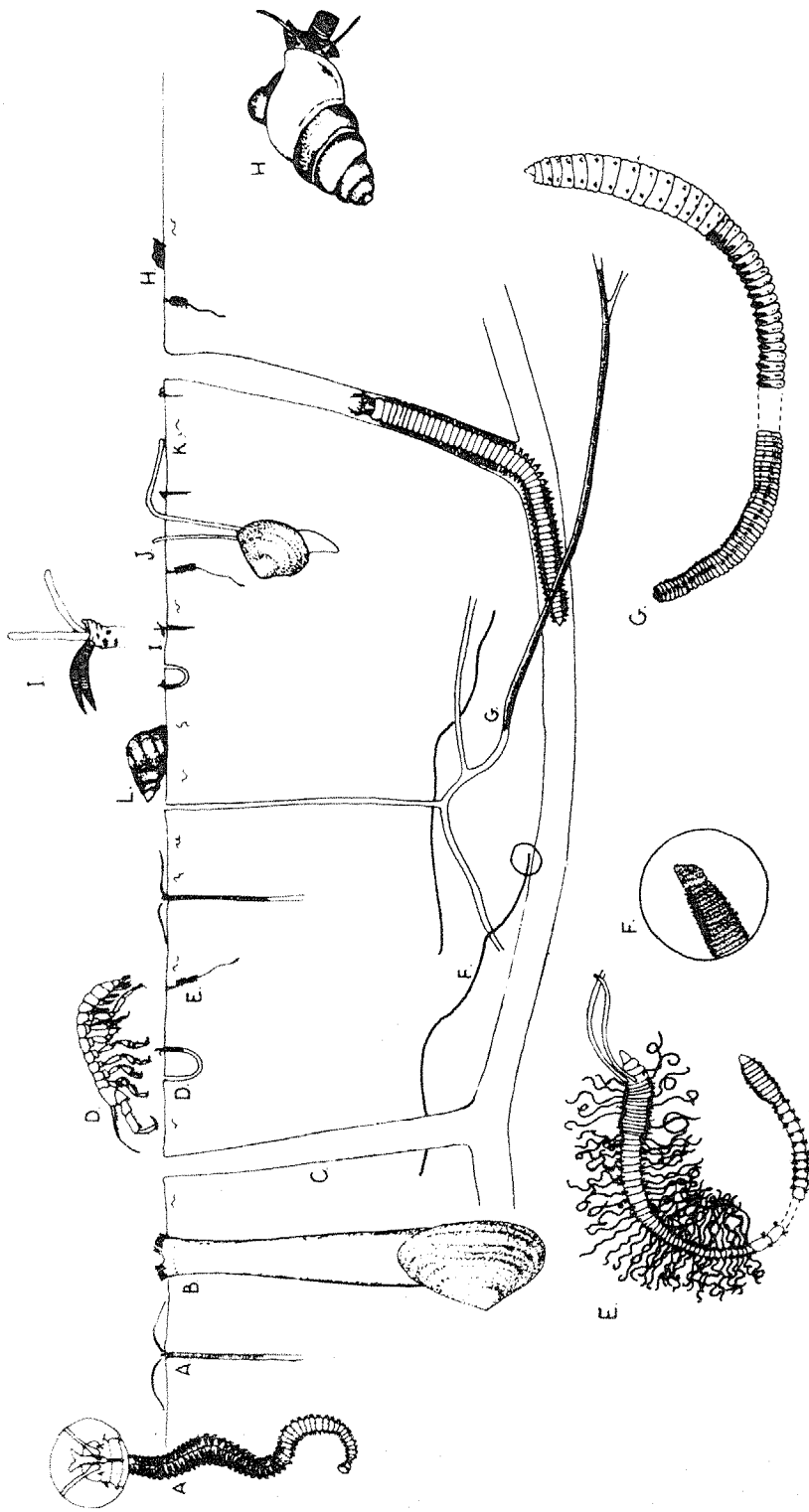


Figure 7. Some representative New England mud flat benthic invertebrates.

Suspension feeder:

B = Mya arenaria (soft-shelled clam)

Surface deposit feeders:

A = Polydora ligni (spionid polychaete)
 D = Corophium spp. (gammaridean amphipod)
 H = Hydrobia totteni (hydrobid gastropod)
 I = Streblospio benedicti (spionid polychaete)
 J = Macoma balthica (bivalve)
 L = Ilyanassa obsoleta (mudsnail)

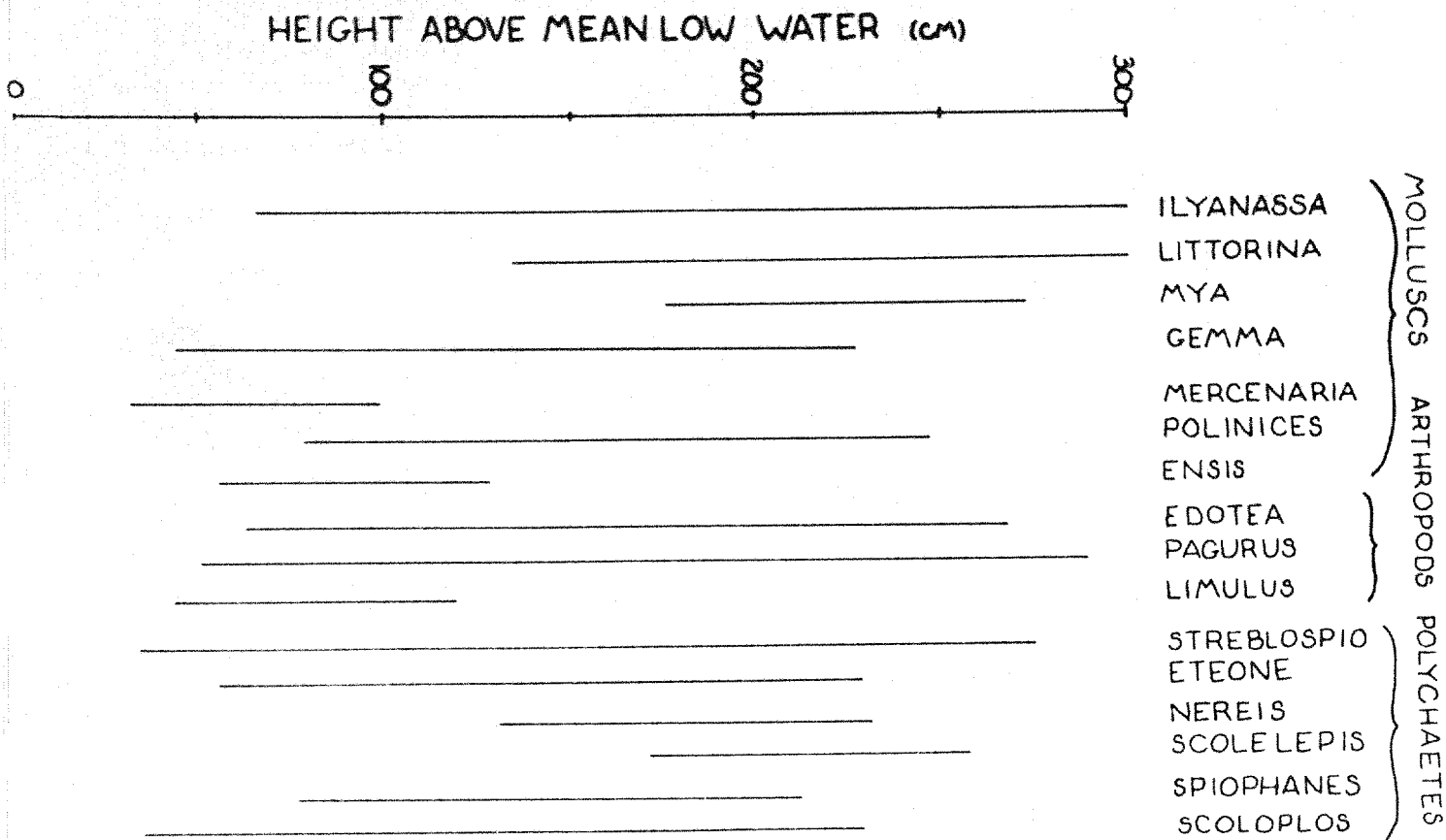
Burrowing omnivore:

C = Nereis virens (nereid polychaete)

Burrowing deposit feeders:

E = Tharyx sp. (cirratulid polychaete)
 F = Lumbrineris tenuis (lumbrinerid polychaete)
 G = Heteromastus filiformis (capitellid polychaete)
 K = oligochaete

Figure 8. Intertidal zonation patterns of major groups of benthic macrofauna inhabiting a New England muddy sand flat (Whitlatch unpublished data, Barnstable Harbor, MA, June 1975).



local environmental features, members of both groups may occupy the same habitat reproducing at different times of the year at water temperatures appropriate for each species (Whitlatch 1977). It has been hypothesized that a third biogeographic boundary exists northeast of Penobscot Bay, Maine, where boreal species are limited in their southern distribution by warm summer water temperatures (Bousfield and Laubitz 1972 cited in Fefer and Schettig 1980).

On a more local scale, the structure of New England tidal flat macrofaunal communities is also determined by temporal and spatial variations in temperature. Green and Hobson (1970) found that small differences in tidal range influenced the density of several species of infauna and affected the growth rate of the small bivalve, *Gemma gemma*. Since tidal flats are gently sloping habitats, zonation patterns are not as pronounced as those observed in rocky intertidal areas. Figure 8 shows an example of infaunal zonation on a muddy-sand flat in Massachusetts. Broadly defined, species-specific patterns are probably related to physiological tolerances, desiccation, and temperature as well as certain biological interactions (e.g., competition and predation). Larsen (1979) suggested the importance of temporally and

spatially variable hydrographic features affecting nearshore zonation of infauna. In northern New England regions, winter ice and spring thaw can alter patterns of salinity for brief periods. In areas with restricted water flow (e.g., glacially-incised estuaries), this yearly event may have profound effects on infaunal distribution patterns (Larsen 1979).

New England tidal flat macrofauna display high temporal and spatial variability; numbers of species and total numbers of organisms may vary by several orders of magnitude within and between years. This high degree of variability, coupled with the effects of latitudinal variation in physical properties of the region, make it difficult to describe a "typical" tidal flat infaunal association. Figures 6 and 7 and Appendix I illustrate some of the more common macrofaunal organisms found in sand flats and mud flats. Not all species will always occur together in any one particular habitat. Rather, the species are representative of those associated with the two different sediment types.

Most macrofauna live in the upper layers of the sediment, probably reflecting the greater amount of food and oxygen in this zone (Figure 9). Amphipods and

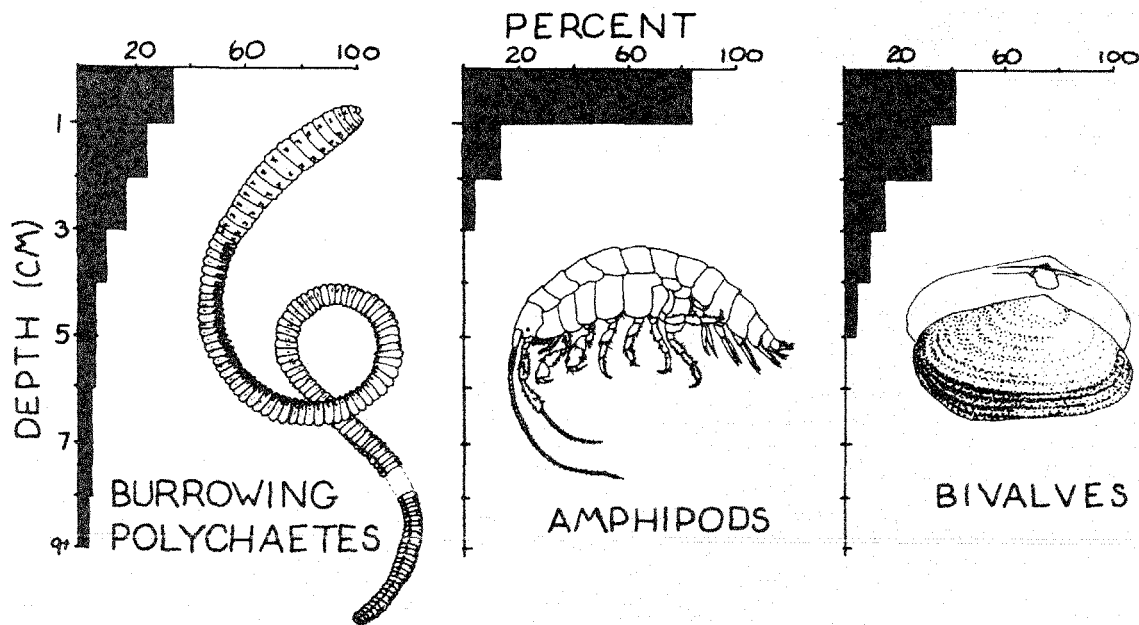


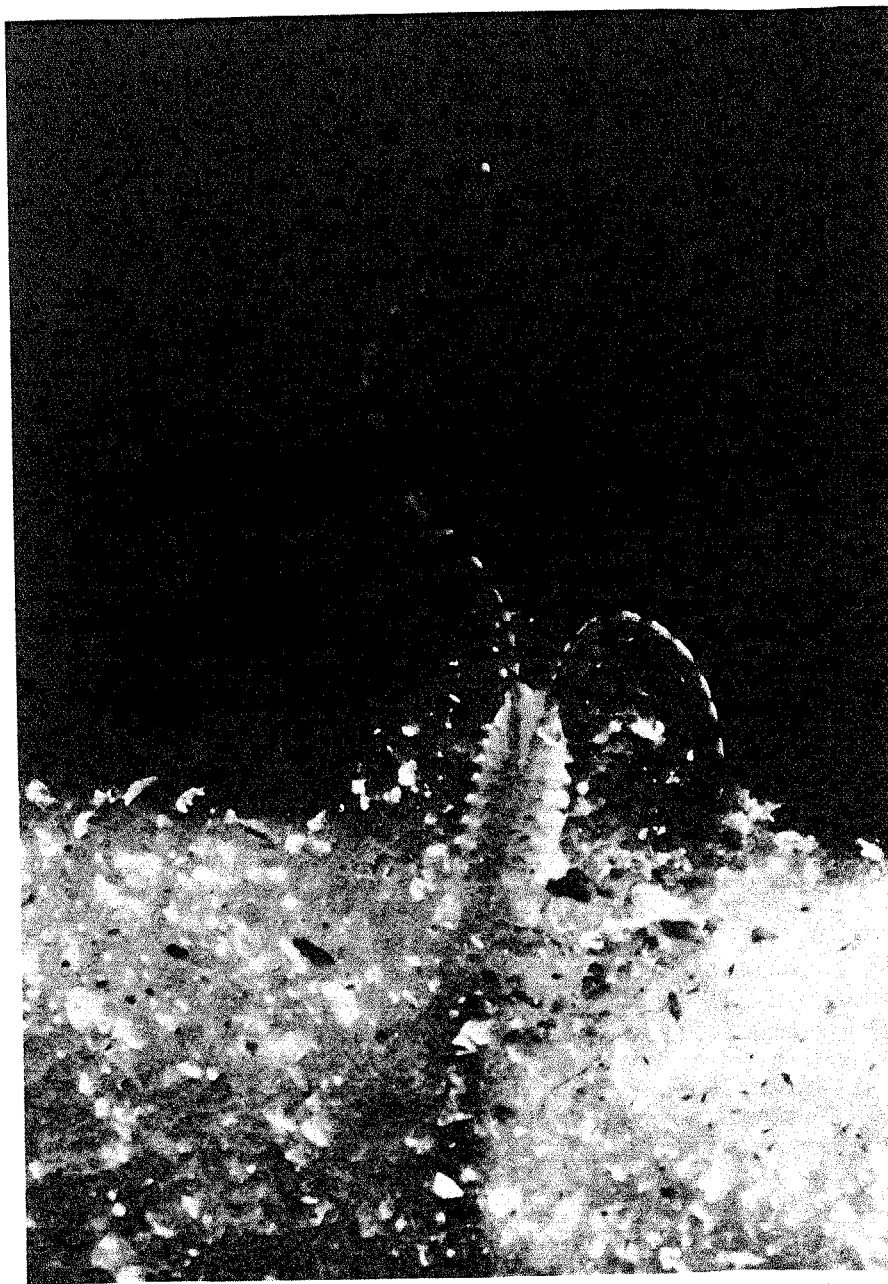
Figure 9. Vertical distributions of major groups of tidal flat macroinvertebrates (Whitlatch unpublished data, Barnstable Harbor, MA, 1974 to 1977).

bivalves are more restricted to the near-surface layers than are the burrowing annelids. The deposit feeders exhibit a wide range of feeding and mobility patterns although three general life styles or guilds are apparent. First is the surface-feeding species. These organisms either live in vertical tubes (e.g., spionid and terebellid polychaetes) or burrow slightly below the surface (e.g., some gammaridean amphipods) feeding with appendages on or slightly above the sediment-water interface. The deposit-feeding clam, Macoma balthica, an abundant species on northern New England mud flats, also feeds off the sediment surface with a long inhalent siphon. The surface-feeding guild is the most abundant group of organisms in tidal flat habitats. Second in abundance are the organisms that burrow through the sediment, much like earthworms. This group has the largest number of species (e.g., members of the polychaete worm families Capitellidae, Nereidae, Syllidae, Lumbrinereidae, Orbiniidae, Nephyidae). Several species build temporary burrow-like structures to the surface. Since many worms live in anaerobic sediments, the burrows aide in transport of oxygenated water to the organism from the sediment surface. Last are the "conveyor-belt species" (Rhoads 1974), organisms that live head down in the sediments (e.g., the polychaetes, Pectinaria gouldii and Clymenella torquata) feeding at depth and depositing egested sedimentary materials on the surface. While this feeding group is less diverse and abundant than the other two, the members are interesting because of their impressive bioturbation activities. Dense populations of Clymenella are known to completely bioturbate (turn over) sediments to a depth of 20 cm (8 inches) annually. One noticeable effect of this extensive feeding activity is described by Sanders et al. (1962) who state that the presence of Clymenella on the Barnstable Harbor, Massachusetts, tidal flats could be detected by walking over areas and feeling a spongy sediment underfoot.

Suspension-feeding organisms include bivalve molluscs and some species of amphipods and polychaetes. Probably the most abundant suspension feeder on New England tidal flats is the small bivalve, Gemma gemma. Densities exceeding 300,000 per m² have been recorded and individuals

are often found packed valve to valve in fine-grained tidal flats. Even though these are small organisms (about 3 mm), at these high densities they are able to effectively exclude other species of suspension-feeding bivalves and surface-feeding polychaetes from their habitats (Sanders et al. 1962; Whitlatch unpublished data). The clam, Mya arenaria, is also abundant, especially in Maine, New Hampshire, and parts of Massachusetts. This species tends to be associated with silty-sand sediments and is not usually found in areas dominated by G.gemma. The hard-shelled clam, Mercenaria mercenaria, is generally restricted to sand flats in southern New England. Abundant assemblages of suspension-feeding amphipods are found in northern New England (Croker 1977) where they are primarily associated with sandy beach habitats.

New England tidal flat infaunal associations are highly dynamic and many studies have noted pronounced seasonal changes in species occurrence and abundance (e.g., Whitlatch 1977; Dobbs 1981). Large fluctuations in population size are attributable to the short life span of most infaunal species (probably 1 to 3 years), seasonal reproductive cycles, predation by vertebrates and benthic invertebrates, and large-scale habitat heterogeneity. Seasonal patterns of population and community change are reflected as sudden rises in the densities of certain species or groups of species followed by declining densities over a period of weeks to months. Specific patterns of seasonal change in New England are tied to latitude, and increased infaunal abundance may be a response of benthic organisms to seasonally-induced variations in food supplies. Natural selection favors individuals that reproduce at about the time that food for juveniles (e.g., planktonic plants and animals) is increasing in abundance. The result of such a response is temporal acceleration of birth rates in response to seasonally-induced increases in the availability of prey and/or nutrients. Seasonal reduction in abundance of tidal flat benthos begins about July in Massachusetts (Green and Hobson 1970; Whitlatch 1977) and slightly later in Maine (L. Watling; University of Maine, Walpole; February 1981; personal communication) and Nova Scotia (Levings 1976). Seasonal decreases in benthic organism



Small spionid polychaetes (this species is Spio setosa, approximately 1 mm body width) are common inhabitants of New England tidal flats. They construct vertically positioned tubes in the sediment and feed on surface deposits with a pair of grooved, ciliated palps. Photo by K.W. Kaufman, Johns Hopkins University.

abundance begin before July south of Massachusetts (Duncan 1974; Dobbs 1981). These declines in population abundance are probably the result of biotic interactions such as competition for food and space and the seasonal appearance of vertebrate and invertebrate predators (e.g., fish, epifaunal gastropods, crabs, and birds).

While seasonal change in the physical and chemical components of benthic systems contributes to the highly variable spatial-temporal abundance of organisms in tidal flats, several studies have noted the existence of consistent year-to-year trends in benthic community structure in New England and elsewhere (Grassle and Smith 1976; Whitlatch 1977; Coull and Fleeger 1978). The cycle may be attributed to seasonally-programmed reproductive activities of organisms found in different geographic areas (Whitlatch 1977) or to the seasonal occurrence of benthic invertebrate and vertebrate predators (e.g., demersal fishes, epifaunal crustaceans and gastropods). Other studies have failed to find repeatable seasonal trends in community structure (e.g., Levings 1976; Dobbs 1981). The existence of such patterns may be the result of the specific characteristics of the local biotic and abiotic environment controlling the structure of the infaunal populations and communities.

Infaunal interactions result in alterations of their abundance and distribution patterns on tidal flats. These interactions may take several forms but may be conveniently separated into direct and indirect effects. The most common form of indirect interaction is habitat modification by one species or trophic group resulting in an adverse impact upon another species or trophic group. The best documented example of this type of interaction is called trophic group amensalism (Rhoads and Young 1970). First described in subtidal, muddy sediments of Buzzards Bay, Massachusetts, this phenomenon involves the destabilization of the surficial sediment by the burrowing and feeding activities of deposit feeders which results in increased sediment resuspension and subsequent interference with the filtering activities of suspension feeders. This type of interaction is most likely to occur in muddy sediments where

deposit feeders are abundant and fine sediments are easily resuspended, but Myers (1977a, b) has recently reported trophic group amensalism in a shallow water sandy habitat. Biological destabilization of the sediment-water interface by demersal fishes, large epifaunal invertebrates, and meiofauna has also been reported (e.g., Yingst and Rhoads 1978; Boyer 1980), but the predicted effect upon suspension feeders has yet to be determined.

Direct interactions can be either adult-adult or adult-larval effects. Adult-larval interactions occur when infaunal assemblages of adult organisms are dense enough to prevent or restrict recruitment of larvae. Woodin (1976) suggested that these interactions occur when suspension and deposit feeders ingest settling larvae or when deposit feeders, through their feeding activities, bury or smother settling larvae. Dense populations of infauna are common in New England tidal flats (e.g., Sanders et al. 1962; Whitlatch 1977; Dobbs 1981) and there is evidence that adult-larval interactions occur. At present, however, we lack controlled field studies to document the importance and magnitude of adult-larval interactions in the New England region.

Adult-adult interactions involve predatory interactions and infaunal organisms competing for either space (lateral or vertical) and/or food. Whitlatch (1980) found a general relationship between food and space overlap and sediment organic matter suggesting the importance of exploitive competition for food by deposit-feeding species. In habitats with high levels of organic matter, species that were similar in resource utilization were able to coexist and species numbers were high. In less productive habitats, ecologically similar species were excluded and species number declined. Grassle and Grassle (1974) documented intraspecific effects on egg production in the polychaete, *Capitella capitata*, related to competition for food. Other studies have noted the importance of exploitive interactions in limiting the distributional patterns of infaunal organisms (e.g., Levinton 1977; Weinberg 1979). Competition between species for space within sediments has been shown in a variety of suspension- and deposit-feeding species

(Woodin 1974; Levinton 1977; Peterson 1977; Peterson and Andre 1980). There are relatively few infaunal predators on the macrobenthos. Nemerteans and the predaceous polychaete annelids, Nereis virens and Glycera dibranchiata, are the most common species although the latter two species also supplement their diets by

deposit-feeding. The more important predators live outside the infaunal community. Epifaunal invertebrates, demersal fishes, and birds consume significant fractions of the infauna and can alter species distribution and abundance patterns (see Peterson 1979 for a review).

CHAPTER 4

FISHES

4.1 INTRODUCTION

Fishes migrate onto tidal flats during flood tides and retreat during ebb tides. A few species, such as sticklebacks and mummichogs, remain in tidal creeks during ebb tide. It is difficult, therefore, to identify which species of fish actually are representative of tidal flat habitats since they may utilize these areas only during portions of their life cycle (e.g., as a nursery ground), on a daily or seasonal basis for spawning or pursuing preferred prey items, or throughout their entire life span. In addition, tidal flats are not closed ecological systems; rather, they are bounded by and intricately linked to other coastal habitats such as salt marshes, estuaries, and eelgrass beds. Actively moving organisms such as fishes can and do readily move from habitat to habitat during the course of feeding and reproducing. Few species are exclusive inhabitants of tidal flats but are more often found in other habitats adjacent to tidal flats (e.g., deeper waters, rocky outcrops) that afford more protection. Generally, fish utilizing tidal flats are estuarine species, juvenile and adult fishes from deeper marine waters that use the sites as nursery grounds and feeding sites, and diadromous species that cross the habitat during migrations to and from spawning sites or wintering areas.

The approach taken to describe the fishes associated with New England tidal flats has focused on those representative species one would be most likely to encounter when sampling. Commercially important species (for which the most life history information is available) and non-commercial species (for which there are sporadic sampling and life history data) are viewed collectively. In many publications, the two groups have been treated separately.

Appendix II gives names and related life history information for fish species common throughout the tidal flats of the New England coastal zone. Species were selected from Bigelow and Schroeder (1953), Leim and Scott (1966), and Thomson et al. (1971) who provide extensive inventories for the regions they cover. Scientific and common names are those cited by Robins et al. (1980). Distributional patterns, spawning periodicity, and food habits have been accumulated for each species from several sources and are as general or specific as the cited authors have reported.

4.2 TROPHIC RELATIONSHIPS

A broad spectrum of trophic roles is displayed by fishes inhabiting the New England coastal zone and it is possible to divide them into generalized feeding categories (e.g., demersal feeders, predators, planktivores). Aside from menhaden (an exclusive herbivorous planktivore) and several species of omnivores and grazers, most fish appear to be carnivorous. Although Appendix II shows that many species display wide dietary preferences, several studies have demonstrated that food selection does occur on a community level. Demersal and pelagic fishes apparently select food by size and type as well as forage at different times or in different habitats (Richards et al. 1963; Tyler 1972; Maurer 1976). A change in food preference with age (size) appears to be the general rule (Appendix II) with many of the juvenile stages feeding as planktivores regardless of later dietary specialization. This feature is particularly germane to a discussion of trophic relationships on tidal flats because many fish inhabiting these areas are juvenile forms. There have been several explanations for age- or size-related changes in feeding behavior. Changing dietary

preference may reduce the effects of intra- and interspecific competitive interactions in food-limited habitats. Second, there are probably age- or size-related changes in the energy requirements of fish. Possibly the metabolic demands of species change with age, necessitating shifts in dietary preference. Many near-shore individuals are juveniles that, as they grow, tend to move into deeper waters (Haedrich and Hall 1976). Olla et al. (1974) described differences in habitat preference in the tautog. Large tautog foraged at greater distances from resting sites than small individuals. Also, older fish migrated offshore during colder months while younger fish remained near-shore and became torpid. Finally, broad dietary preference may reflect the unpredictable nature of food supplies in marine temperate environments. Pronounced seasonal and local variations in primary and secondary productivity may favor generalized feeding habits.

4.3 GEOGRAPHIC DISTRIBUTION PATTERNS

Fish communities north and south of Cape Cod show distinctive differences in species composition, apparently related to seasonal differences in water temperature (see Chapter 1). Fish communities north of Cape Cod tend to be dominated by boreal, non-migratory forms while those to the south primarily consist of warm-water, migratory species (Colton 1972; Colton et al. 1979). Species composition on a large scale, therefore, is determined by temperature.

Temperature effects on a more local scale have also been observed in northern Atlantic coast fish communities. Tyler (1971a), working in a deep, nearshore site in Passamaquoddy Bay, New Brunswick, and Maine, classified four broad types of demersal fish according to their residence patterns: year-round residents, winter residents, summer residents, and occasional species. The fish community reflected patterns of temperature fluctuation throughout New England. Areas exhibiting greater annual temperature fluctuation (e.g., south of Cape Cod) had more temporary residents and fewer year-round species (Figure 10).

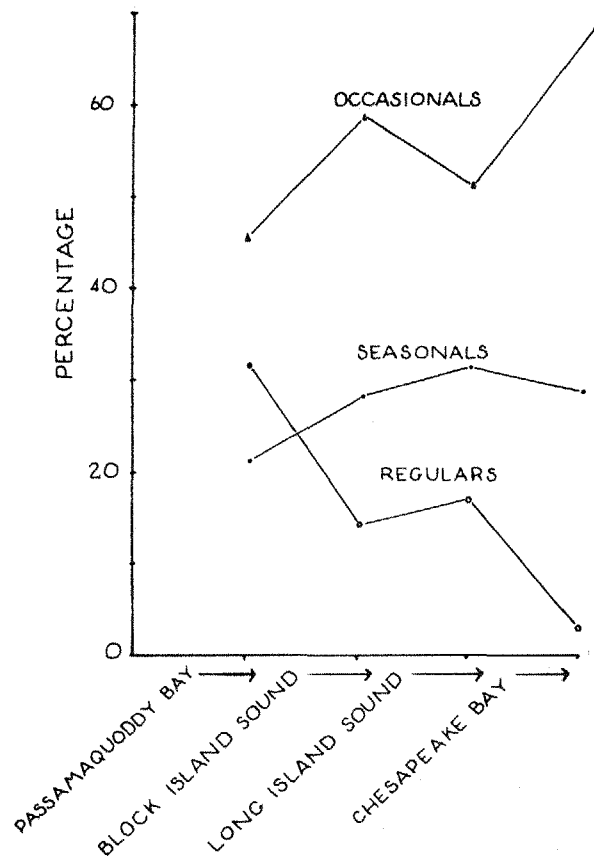


Figure 10. Percentages of different temporal components in fish species along the northeast Atlantic coastline (modified from Tyler 1971).

Recksiek and McCleave (1973), working in the Sheepscot River-Back River estuary at Wiscasset, Maine, found pelagic fish assemblages corresponding to Tyler's community structure groups. The relatively warm Back River estuary had a summer pelagic component consisting mostly of alewives, blueback herring, and Atlantic menhaden, while the relatively cooler and oceanic Sheepscot River estuary had a summer migrant pelagic component of Atlantic herring, Atlantic mackerel, and spiny dogfish. Rainbow smelt was the only year-round resident and Atlantic herring was the only winter resident species. It appears, therefore, that although pelagic and demersal fish assemblages can be divided into similar residency patterns, species composition varies with temperature regime both within and between latitudes along the New England coastline.

4.4 MIGRATORY PATTERNS

The structure of New England fish communities is dynamic and the species are, for the most part, constantly shifting position in the coastal zone. Many movements can be linked predictably to patterns of foraging, local and regional variations in water temperature, or reproductive activities. The frequency and magnitude of migrational activities, however, appear to be both species- and regionally-specific.

Species in the resident (non-migratory), nearshore fish assemblage make inshore-offshore movements over small distances, moving into slightly deeper water to avoid extremes in water temperature (e.g., tomcod). Movements are also linked to tidal cycles where fish move out of areas that are exposed at low tide or are very shallow and reoccupy the areas as the tide floods (e.g., mummichogs). Dusk feeding movements are also common to many species. Herring move to the surface to feed at dusk (Sindermann 1979a), juvenile pollock move inshore, and striped bass also rise to the surface to feed at dusk following their preferred prey items.

Coastal fish migrations occur on a regional scale in New England; Figure 11 summarizes these general patterns. Bluefish, mackerel, and menhaden are examples of spring-summer northward migrants. These species move along the coastline and inshore to southern New England and the Gulf of Maine as water temperature increases. The timing of these migrations is probably also a response to increasing food supplies since during the warm months pelagic and demersal food organisms are abundant in coastal areas. In fall and winter, the fish reverse direction in response to declining water temperature. Southward migrating fish do not always follow the coastline, but may move offshore to the warmer continental slope waters off southern New England (Figure 11). Many inshore migrant species (including red hake, silver hake, scup, butterfish, summer flounder, and goosefish) winter there (TRIGOM-PARC 1974). Some species, such as the winter flounder, reside in cooler offshore waters during the summer and move inshore in winter.

Because of differences in water temperature variation, southern New England contains few permanent fish residents and is characterized by a continuously shifting fish species composition. The Gulf of Maine, conversely, is typified by more resident species and less pronounced seasonality in species composition.

4.5 REGIONAL PATTERNS

Since New England coastal fish communities are strongly influenced by water temperature variation, more detailed community descriptions can be made by examination of both regional and seasonal differences using Cape Cod as a biogeographic boundary. Regional patterns of community structure have been separated into spring-summer and fall-winter periods. It is important to realize that within-region physical and biological conditions vary, and that these will in turn affect the distribution and abundance patterns of the fishes. The generalized patterns described below are intended to convey overall trends in seasonal shifts of species composition and not, necessarily, the dynamics of specific, localized fish community structure.

4.5.1 South of Cape Cod (Figure 12)

During spring, anadromous species such as lampreys, striped bass, and large schools of certain herring (e.g., alewives, bluebacks, and shad) begin ascending river systems to spawn in brackish and freshwater. Although larger rivers such as the Hudson, Connecticut, and Thames support major spawning runs, anadromous fish also enter many smaller rivers and streams. Lampreys, sturgeon, and herrings have spawning populations along the entire northeast coast while for the striped bass, the Hudson River marks the northern limit of a major spawning population. (Recent anadromous fish restoration projects to re-establish successful spawning populations of the Atlantic salmon and shad have been initiated in many New England rivers.) Adults of some species die following spawning (e.g., lampreys); others descend rivers and feed actively to regain body stores lost during spawning (e.g., herrings, striped bass). In southern New England, adults of most anadromous

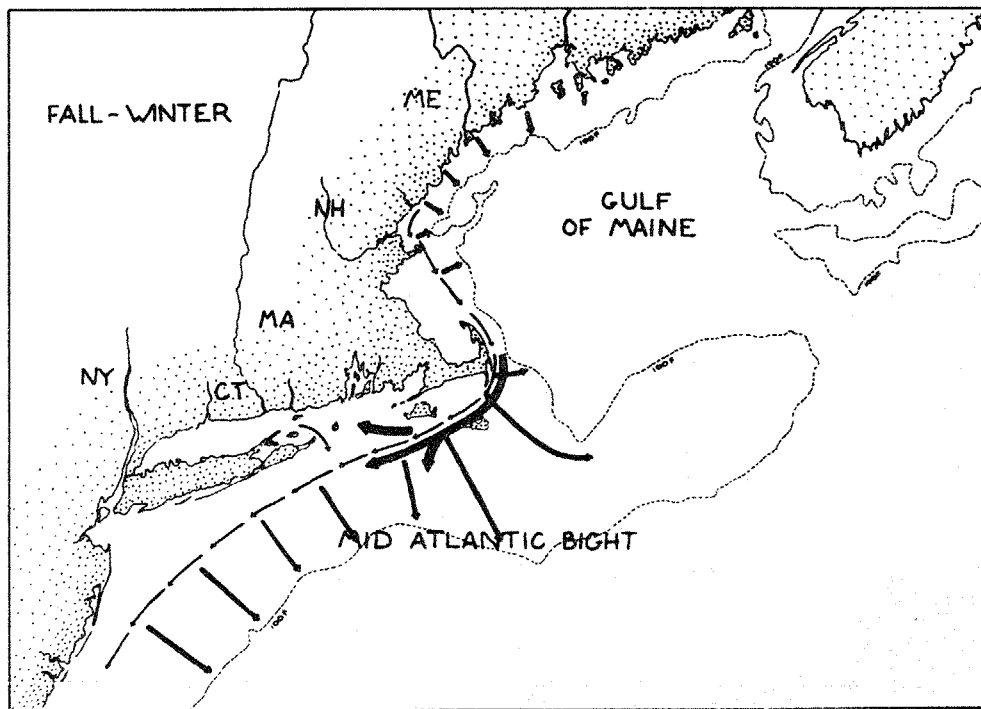
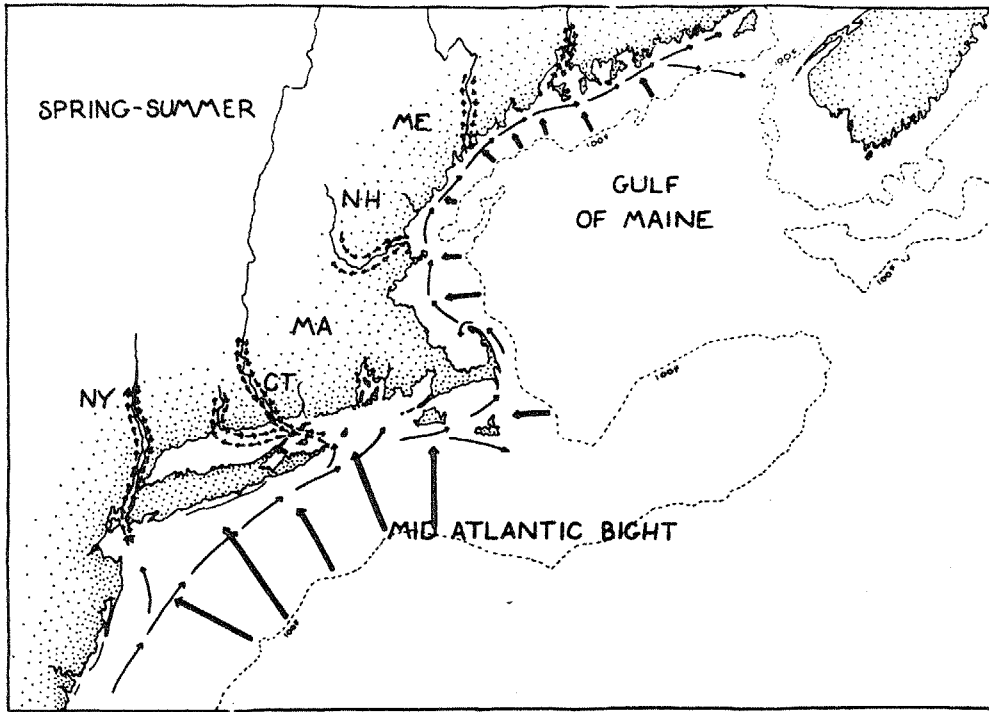


Figure 11. Seasonal migration patterns of New England coastal fish populations. See text for details (modified from TRIGOM-PARC 1974).

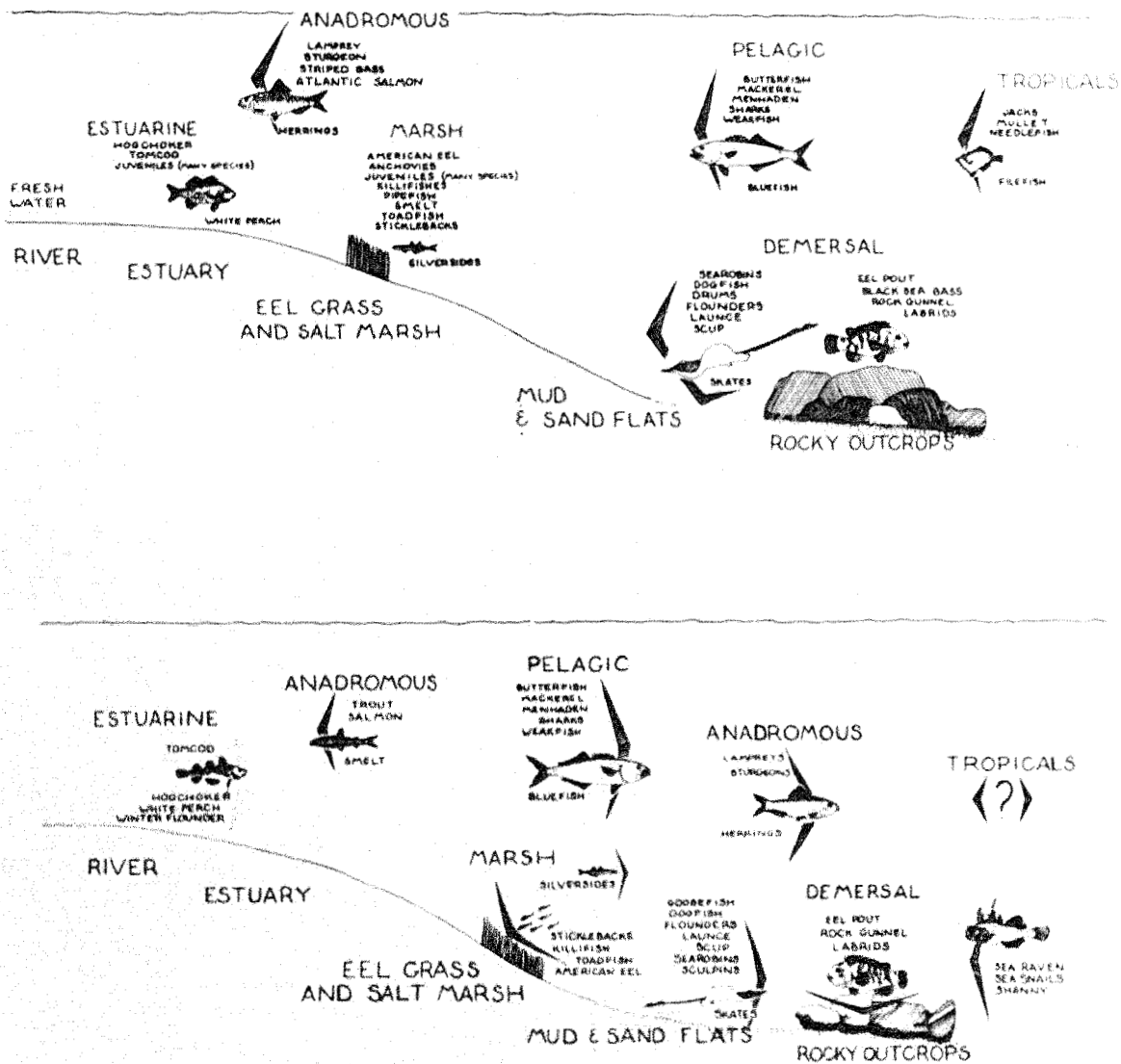
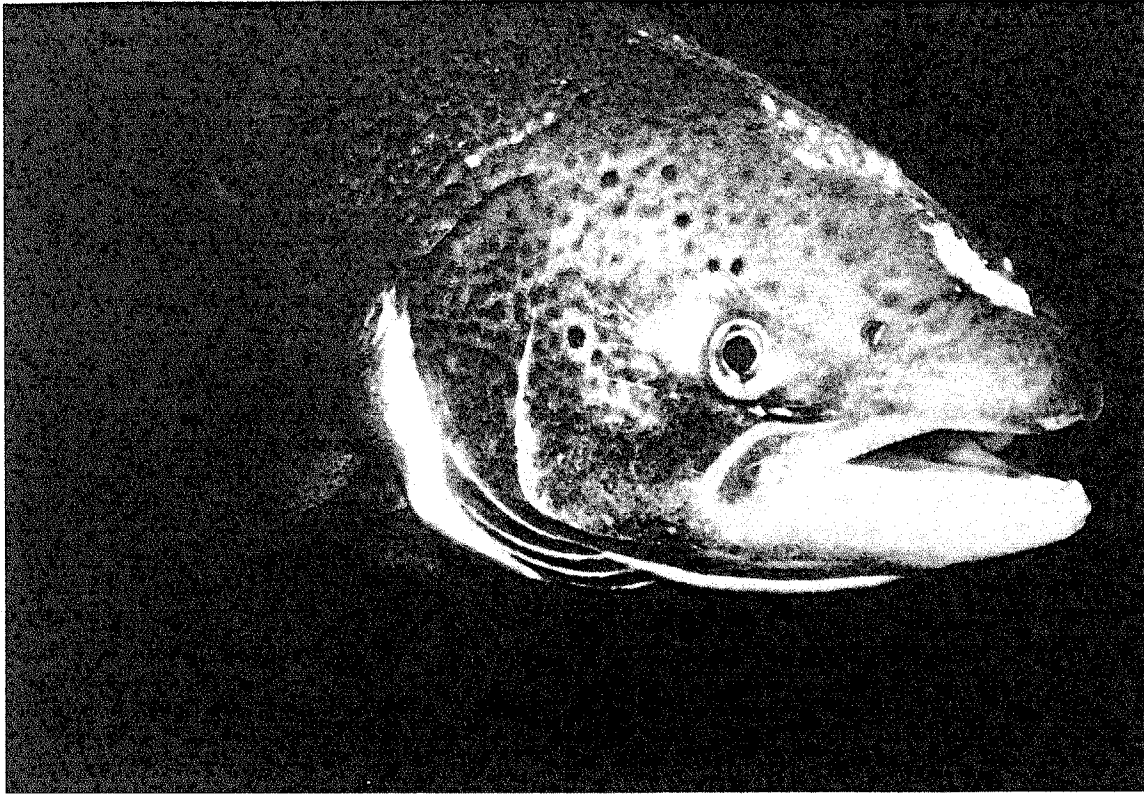


Figure 12. Examples of major groups of fish which occupy tidal flats and adjacent coastal habitats in southern New England. Upper figure refers to movements during the spring-summer period; lower figure refers to movements in fall-winter months. Arrows indicate direction of movement for fish that migrate. Fish depicted without arrows are either restricted in home range or undertake only localized movements, both moving alongshore and into the substrate. The figure depicts these groups for an extended period (approximately six months) and does not show the location of particular species at any one time. These individuals or groups are found at different times (for the most part sequentially, see text) throughout the period considered. The fish are typical representatives of groups found in each habitat.



An extensive restoration effort has been undertaken to re-establish populations of the anadromous Atlantic salmon, Salmo salar, in New England's major river systems. This individual (approximately 60 cm) was photographed during its spawning migration in the Salmon River, Connecticut. Photo by R.E. DeGoursey, University of Connecticut.

species have moved from nearshore areas by midsummer. Exceptions include striped bass that may remain in coastal waters until late October or early November, and fall spawners (e.g., salmon) that begin to move into the estuaries in late winter and early spring and are found in the river systems until early winter. Following spawning, adults return to the open ocean to overwinter. Rainbow smelt remains in the lower estuaries throughout the winter and ascends to freshwater to spawn as soon as the ice begins to break up on upper estuaries (usually February to March). Juveniles of most anadromous species occupy estuarine and nearshore water through late spring and summer, then move offshore with declining water temperatures in fall.

Another group of fish is more typically associated with estuarine conditions

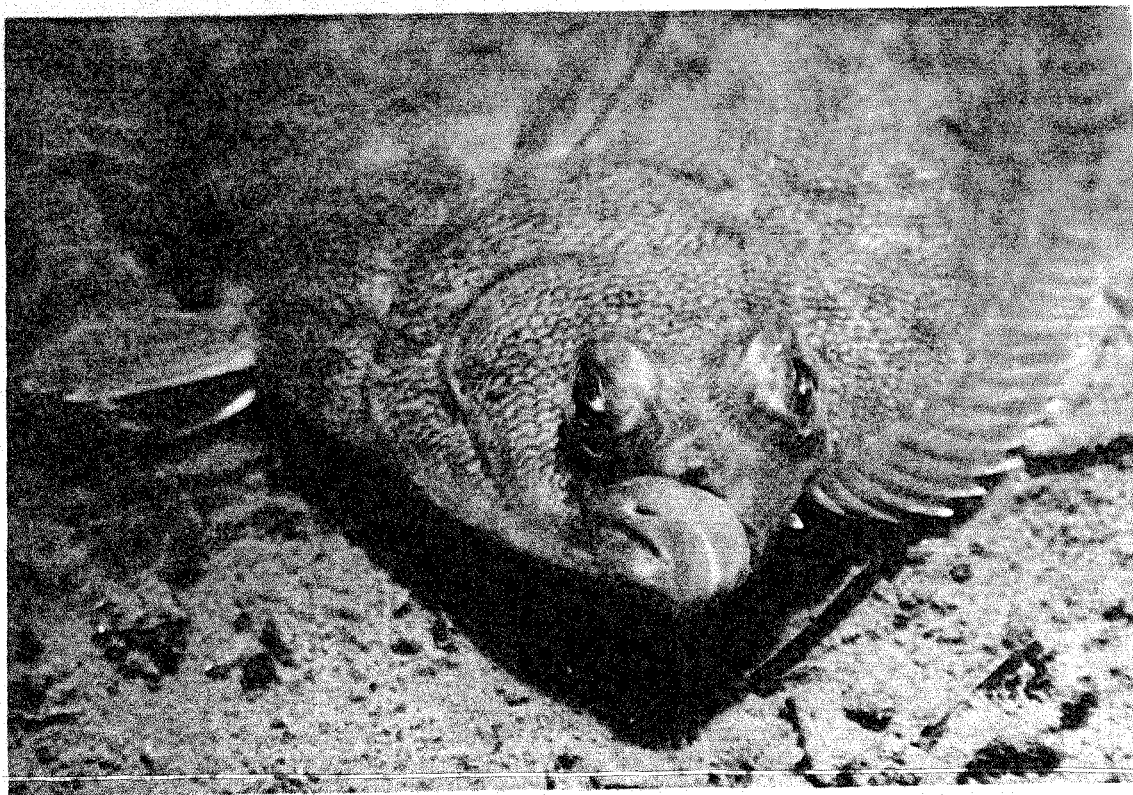
in southern New England. Tomcod are winter spawners that move from brackish to more saline waters in the spring. White perch and hogchokers move from the lower estuary where they overwinter to more brackish waters to begin feeding and spawning. They remain active in estuaries throughout the warmer months. Winter flounder are also found abundantly in estuaries and bays in early spring. They spawn in late winter and early spring in lower portions of the estuaries. Tyler (1971b) reported that this species concentrates feeding in soft substrate habitats of the intertidal zone. Adult winter flounder begin moving into deeper waters during the summer to avoid elevated water temperatures in the shallows, while juvenile fish remain in relatively shallow, heavily vegetated, muddy bottoms throughout the year where they feed on benthic invertebrates.

In early spring, fish communities of eelgrass beds and marsh tidal creeks consist of year-round residents (e.g., killifishes, sheepshead, sticklebacks, pipefish, and toadfish) that emerge from a torpid overwintering state and begin to feed actively in preparation for spawning in mid- and late spring and early summer. Schools of the planktivorous Atlantic silverside (*Menidia menidia*) also move into tidal wetlands and shallow bays to spawn in spring. The year-round residents and the juveniles of many spring spawners are found in wetlands and marshes throughout summer and early fall and are able to tolerate severe stress of heated water and reduced oxygen levels. These species are active until late fall and early winter when it is believed the majority hide beneath vegetation and some species burrow into mud to avoid extremely cold water temperatures. They also may move into

slightly deeper waters (e.g., eels, killifishes, and sticklebacks). Silversides are apparently an exception since they have been observed feeding and schooling in early winter and early spring in southern New England. Their whereabouts during the middle of winter has not been determined.

In late spring, anchovies (*Anchoa mitchilli*) move northward along the New England coast and into small, shallow bays and inlets where they often school in tremendous numbers. They remain in coastal waters throughout the summer and move southward and offshore during the fall. Although they are seasonally abundant, no commercial fishery for anchovies presently exists in southern New England.

Skates, dogfish, windowpane, and winter flounder are abundant on sand and mud flats in early spring. In late spring and



The winter flounder, *Pseudopleuronectes americanus*, is a common inhabitant of New England tidal flats. This demersal fish (actual size) consumes large amounts of benthic infaunal invertebrates. Photo by R.E. DeGoursey, University of Connecticut.

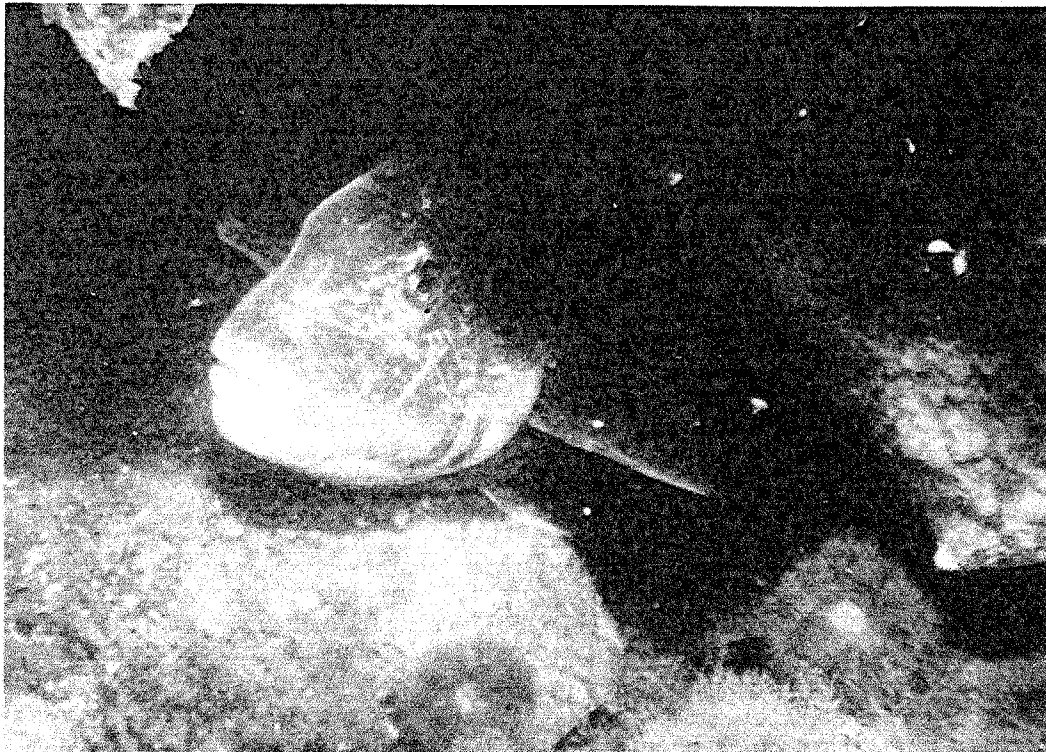
early summer (June to July), spawning aggregations of searobins, which inhabit sandy substrates, move into coastal waters. During the same period, schools of scup move from offshore waters into bays and inlets to spawn. Both scup and searobins begin to migrate offshore by October. Also during the summer months, dense schools of the sand lance are found inhabiting inshore sand flats, often burrowing into the sediment. This species is an important food item for many pelagic and demersal fish, as well as finback whales, porpoises, and terns. Most of these fish species begin moving offshore by mid- to late September and disappear from the coastal zone by mid-October. Only little skate and windowpane flounder remain through the fall and winter.

With declining fall temperatures some offshore species migrate into nearshore sand and mud flats. From October to December, sea ravens move inshore to spawn and are commonly observed in water 1 to

2 m (3.2 to 6.5 ft) deep. Goosefish enter coastal waters in October and November to feed, and sculpin, which are winter spawners, move inshore in late fall. The grubby sculpin is frequently found in very shallow water during this period.

Summer southern migrants that enter southern New England waters include the summer flounder, black seabass, and kingfish. Their occurrence is predictable but the overall abundance of each species varies from year to year, possibly because of the abundance of specific year-classes. In some years, a particular species may be abundant in certain areas while in succeeding years it may be scarce due to natural population fluctuations and/or increasing fishing pressure.

From May to October, rocky inshore habitats adjacent to tidal flats are dominated by two labrids, the tautog (Tautoga onitis) and the cunner (Tautoglabrus adspersus). Both species spawn in



A large 55 cm male tautog, Tautoga onitis, emerges from a rock crevice in the spring to resume actively feeding after overwintering in a torpid state. Tautog prefer rocky habitats and adults feed almost exclusively on the blue mussel, Mytilus edulis. Although tautog are most abundant south of Cape Cod, they also range into the Gulf of Maine. Strictly a coastal fish, they are seldom found more than 1-2 km from shore. Photo by R.E. DeGoursey, University of Connecticut.

the spring and remain in or directly adjacent to rocky outcrops, pilings, or debris to feed throughout summer and fall. They appear to have restricted territories and are seldom found more than a few kilometers from the coastline. The young of both species feed on small invertebrates while the adults feed mainly on mussels (*Mytilus edulis*). Other smaller, more cryptic species also inhabit these areas (Figure 12) and their abundance and occurrence may be more widespread than the current literature suggests. For example, gobies, rock gunnel, and juveniles of tropical migrants are missed by conventional fishing methods (R. DeGoursey; University of Connecticut, Noank; February 1981; personal communication; Munroe and Lobspeich 1979). In late October, the labrids occupy crevices in which they overwinter in a torpid state, or may move to slightly deeper areas. The rock gunnel, a winter spawner, remains active and in certain localities moves into shallower waters to spawn.

The pelagic component of fishes in southern New England is found strictly during the summer and is composed of schooling fishes that enter nearshore waters either as southern migrants (e.g., young weakfish, bluefish) or offshore species moving inshore from the continental shelf (e.g., mackerel, butterfish). Some species are oceanic spawners (e.g., bluefish and menhaden) that enter coastal waters in late spring to feed. Menhaden form tremendous schools that often can be seen moving in and out of bays and harbors. Since menhaden form such large aggregations and often enter shallow embayments in summer months, elevated water temperatures and low dissolved oxygen concentrations occasionally cause mass mortalities (e.g., in Long Island Sound).

Pelagic predators, such as the bluefish and weakfish, enter coastal waters in southern New England in late spring and early summer to feed. Young bluefish, known as "snappers", often form large schools that move through the coastal waters chasing prey such as silversides, sand lance, and juveniles of many other fish species. The Atlantic mackerel is usually the first to appear in coastal

waters in early spring to spawn, and also one of the first species to abandon those areas in mid- and late summer to overwinter offshore.

A group of warm water, tropical migrants also moves into coastal waters of southern New England and sometimes into the Gulf of Maine in mid- and late summer. These tropicals occur sporadically and in small numbers often first entering the shallow bays in Long Island Sound and eventually appearing in Connecticut and Rhode Island and further north in late summer. Primarily juveniles of most species have been collected although adults are sometimes recorded. No comprehensive study has been undertaken to determine the seasonal abundance and distribution of these tropical species, so existing data probably underestimate their numbers in southern New England. The more common migrants include the mullets, jacks, drums, triggerfish, filefish, and needlefishes. The behavior of these migrants during declining temperatures in the fall is not known. It is not known whether they move offshore, return to warmer southern waters during the winter, or whether a significant proportion experiences winter mortality. None of the tropical migrants have been collected in New England during the winter.

4.5.2 Gulf of Maine

Figure 13 shows that many of the seasonally-related movement patterns of fish that exist in southern New England also are found in the Gulf of Maine inshore waters. For example, the anadromous and resident marsh-eelgrass species are similar, although spawning activities of the former group occur later in spring. A major difference between the two New England regions is that fewer migratory species are found in the Gulf of Maine; this contributes to lower summer species diversity when compared to southern New England. In addition, a greater number of gadids (e.g., cod, hakes, pollock, tomcod, haddock) are found in the inshore Gulf of Maine waters. All but the hakes, which are summer migrants, are year-round residents of these waters. The tomcod is the most common inshore gadid found at the mouths of streams and estuaries.

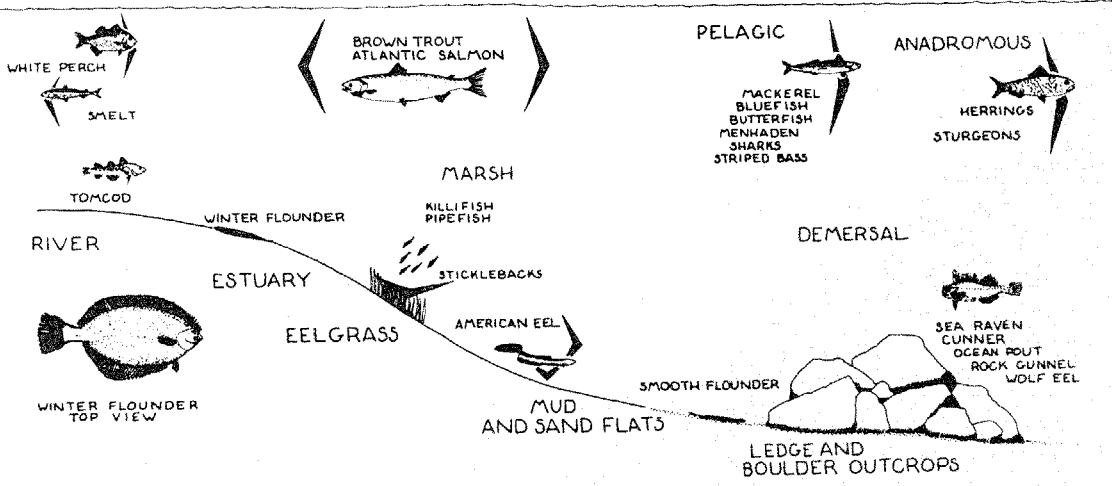
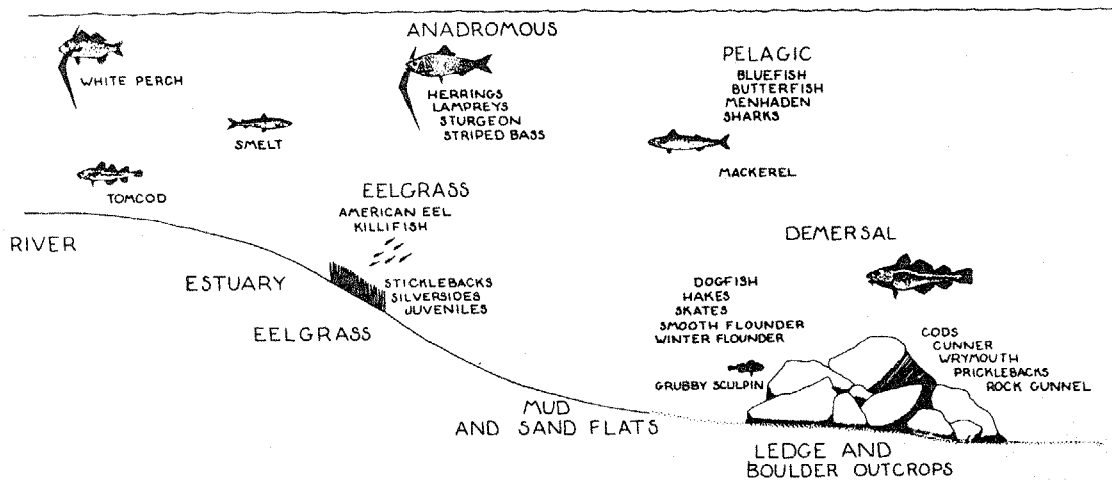
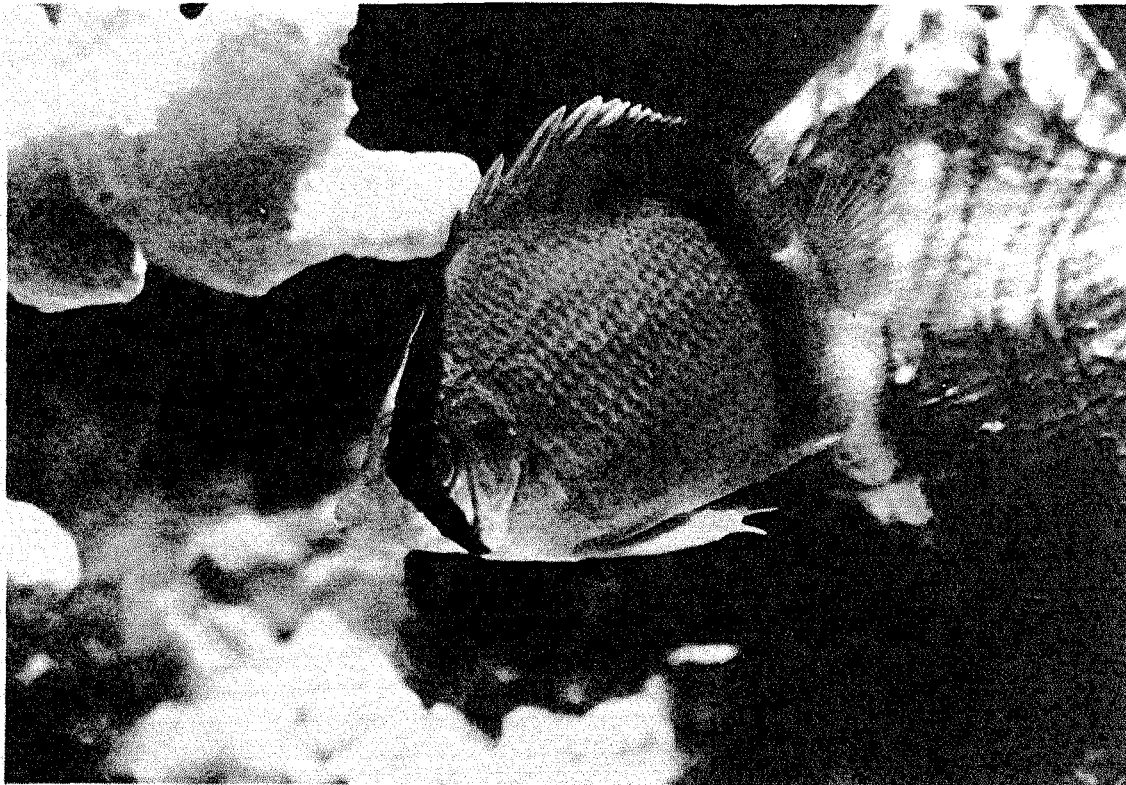


Figure 13. Seasonal movements of fish in the Gulf of Maine inshore environment; upper figure refers to movements in the spring-summer months; lower figure refers to fall-winter movements (see Figure 12 for further details).



The spotfin butterflyfish, Chaetodon ocellatus, is one of a group of tropical species which migrate northward along the east coast and enter New England waters during mid- and late summer. Many of these summer southern migrants (such as the fish pictured) are juveniles (about 4 cm). These fish probably perish with the onset of declining water temperatures. There is no evidence to suggest that they are capable of returning south or of overwintering in New England. Photo by R.E. DeGoursey, University of Connecticut.

As in southern New England, flounders and skates are the common demersal species found on muddy and sandy bottoms. Both groups feed actively on benthic invertebrates and the skates make noticeable depressions in the sediment surface as they forage for crustaceans, bivalves, and polychaete annelids. Flounders represent a major inshore groundfishery in the Gulf of Maine and winter flounder is the most abundant species. Other species of flounder are also found in the Gulf of Maine (see Appendix II), although the smooth flounder, windowpane, and American plaice are associated more with the bays and estuaries of northern New England.

Many species of pelagic fishes inhabit northern New England waters. The

pelagic predators are similar to those found in southern New England, although bluefish, weakfish, and striped bass are all reduced in number when compared to warmer New England waters. Striped bass is a popular sport fish, although spawning populations have not been located north of Cape Cod. All these species are summer migrants. The Atlantic herring, another member of the pelagic fish component, is commercially the most important fish in the Gulf of Maine. This species is found offshore during fall (when it spawns) and winter, but is seen in nearshore waters during summer (Targett and McCleave 1974). The tropical migrant species are only found sporadically in the Gulf of Maine, restricted to those summers with unusually warm water temperatures.

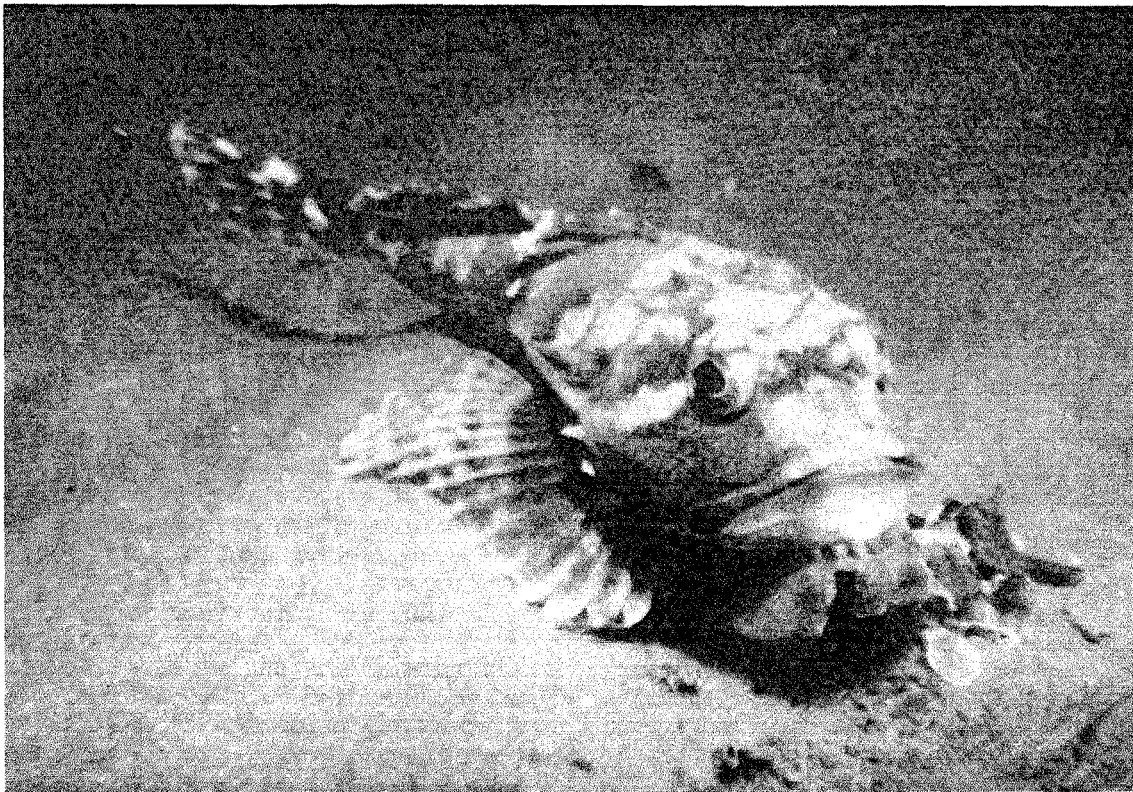
In winter, many species remain part of a year-round resident population (Figure 13). The winter and smooth flounder remain in the estuaries, with the winter flounder, in particular, moving into shallower parts of the area during fall and winter. White perch move from their habitat upstream in slightly brackish and freshwater to more brackish and oceanic conditions in estuaries during the winter. Some boreal-Arctic species (e.g., alligatorfish) migrate southward into these waters in the winter.

There are three major differences between the fish communities north and south of Cape Cod: a greater proportion of the fish in the Gulf of Maine are year-round resident species, so that during the summer, lacking migrants from the south, fish species diversity is generally lower

than in southern New England; gadids are more common to the inshore Gulf of Maine region, while in southern waters their distribution is largely restricted to offshore waters; migration and spawning activities tend to occur later in northern waters because Gulf of Maine water temperatures increase later than those in southern New England.

4.6 THE DEPENDENCE AND ROLE OF FISH ON TIDAL FLATS

Many fish utilize shallow-water coastal habitats as feeding and nursery grounds. The reproductive activities of these species coincide with periods of maximum food production, and predation rates on juvenile fish are apparently lower in shallow-water than adjacent deeper water areas. As the fish grow,



The longhorned sculpin, Myoxocephalus octodecemstinosus, (this specimen 20 cm long) is distinguished from the other western North Atlantic sculpins by a long, sharp spine on the preopercular bone. In the northern part of its range it is a year-round resident moving into deeper waters in cold weather and back inshore in spring. In the southern part of its range, it remains in deeper water during the warmer months and moves inshore with declining water temperatures. Longhorned sculpins are winter spawners in New England, laying adhesive egg clumps on vegetation. Photo by R.E. DeGoursey, University of Connecticut.

they begin moving into deeper waters. Haedrich and Hall (1976) hypothesize that these ontogenetic habitat shifts and the general absence of adults in an estuarine environment act as mechanisms to reduce competitive interactions within species as well as to allow the juvenile stages access to the more productive marine habitats.

Age-related changes in the use of inshore environments by fish and their subsequent effects on a tidal flat habitat is largely species- or group-specific (i.e., resident vs. migratory species). Those fish most dependent upon tidal flats for feeding are the demersal species (e.g., flatfishes, skates) and small baitfishes (e.g., silversides, killifishes, and menhaden), while most of the pelagic fishes are probably less dependent upon tidal flats for food items.

Juvenile fish dominate coastal waters and because of their abundance can consume large quantities of benthic invertebrates and have a conspicuous effect upon the structure of benthic communities. Many demersal fishes form schools (e.g., scup) or may be found in loosely aggregated populations (e.g., winter flounder) and have caused localized, short-term reductions in the population abundance of polychaetes, small crustaceans, and bivalves. The

reported seasonal population decline of infaunal invertebrates in a Massachusetts salt marsh habitat was probably due to the appearance of invertebrate predators (e.g., epibenthic crustaceans) and fish predators (Schneider 1978). Tyler (1971b) found that adult winter flounder fed over a Bay of Fundy intertidal flat and suggested that destruction of the habitat would reduce the productivity of the fish populations. Others have also noted the presence of large populations of demersal fishes associated with intertidal zones (Hancock and Urquhart 1965; Edwards and Steele 1968). Virnstein (1977) demonstrated experimentally that the effect of demersal fish on the benthos was highly species-specific. Some species like the hogchoker had a minimal effect on benthic population abundance while other species such as the spot (*Leiostomus xanthurus*) reduced both the abundance and species diversity of the infauna in a Chesapeake Bay subtidal site. The relative magnitude of such impact is dependent upon the degree of disturbance associated with foraging on the bottom (e.g., excavating activities) as well as feeding rates. Species such as skates that can disturb large areas of the bottom when foraging have more pronounced effects on the benthos (Van Blaricom 1978) than species that only browse on the sediment surface.

CHAPTER 5

BIRDS

5.1 INTRODUCTION

To the casual observer, the avifauna is the most conspicuous component of the tidal flat biota. Since birds are comparatively large bodied with high metabolic rates, their impact on the tidal flat as predators is often considerable (Schneider 1978). Collectively, coastal birds take on a wide variety of trophic roles and occupy numerous positions in the coastal food web (Figure 14), ranging from primary consumers that feed on vegetation, to top level carnivores that prey exclusively on fish. Few are themselves preyed upon and therefore, regardless of where each species or group fits into the food web, their trophic level is necessarily a terminal one in the tidal flat ecosystem.

Appendix III lists the species of birds that commonly use tidal flats in New England during some portion of their life history. The list is not exhaustive and does not include all those species that might be seen on a tidal flat or all species of coastal birds. The birds that have been included vary considerably in terms of their use of and dependence on the tidal flat environment. For some, such as the herons and shorebirds, tidal flats are an absolutely essential habitat, while for others such as the diving ducks, the tidal flat at high tide is just one of many potential foraging areas and often not even a primary one. The geographical ranges of most of New England's tidal flat avifauna extend beyond the boundaries of New England and much of what we know about their ecology is based on studies done elsewhere. This literature has been included because, in most cases, it applies to New England birds as well.

Various methods may be used to organize a discussion of this highly diverse assemblage of organisms. The following scheme is based on trophic groups and is

convenient since there are fairly consistent relationships within the taxonomic groups concerning ecology and distributional status. The major groups are: (1) shorebirds, which are largely migratory and feed on invertebrates, (2) gulls and terns, which feed on fish and large invertebrates and commonly breed in New England, (3) herons, which also breed in New England and consume small fish and large crustaceans, (4) waterfowl, cormorants, and diving birds, which are primarily migratory and as a group eat a wide variety of prey, and (5) raptors, which breed in New England and, while over the tidal flats, feed on fish and birds. In addition to these five major groups, the kingfisher and fish crow have been included in Appendix III. The kingfisher is a year-round resident of much of New England. The fish crow is a year-round resident of Connecticut and Rhode Island and feeds on intertidal invertebrates and the eggs of unguarded tern and heron nests.

The following is a group-by-group discussion elaborating on the functional roles and other important biological information about each of the five categories.

5.2 SHOREBIRDS

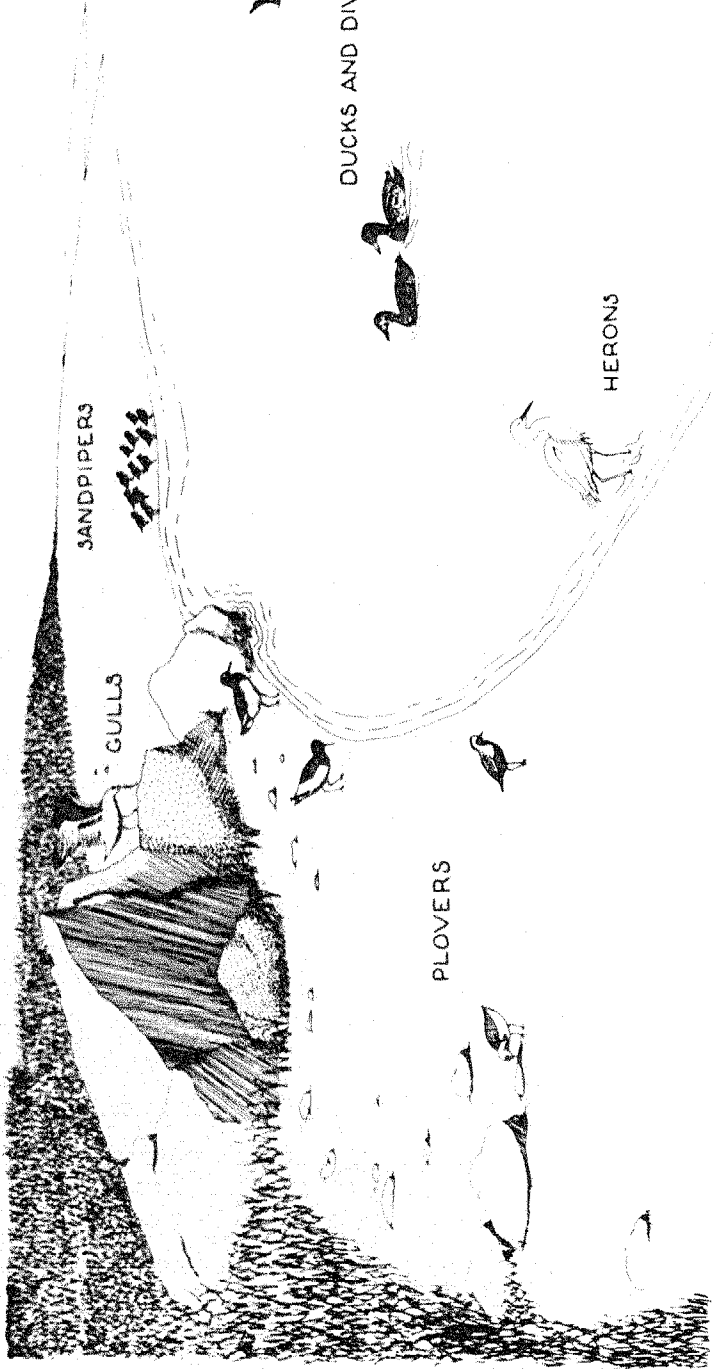
Shorebirds that appear on the New England coast belong to the families Charadriidae (plovers), Scolopacidae (sandpipers), and Haematopodidae (oystercatchers). Although several shorebird species breed and/or winter in New England (Appendix III), most are hemispheric travelers, appearing only during spring and fall migrations. The semipalmated sandpiper is the most abundant shorebird in North America. Because this species has a yearly migratory pattern characteristic of many migratory shorebirds, it will be used as an example of the typical



RAPTORS



TERNs



SANDPIPERS

GULLS

PLOVERS

DUCKS AND DIVING BIRDS

HERONS

Figure 14. New England tidal flat bird guilds showing general feeding positions of the various groups (see text for further explanation).

yearly schedule of events in the lives of shorebirds that frequent New England tidal flats. From its Arctic breeding range, which extends from Alaska to eastern Canada, the sandpiper migrates thousands of miles to its wintering grounds along the U.S. Gulf coast and the West Indies, south to northern Chile and Paraguay (Palmer 1967). During migrations, the birds stop at various resting and feeding areas along the eastern coast of North America. In Plymouth, Massachusetts, a minor staging area, peak counts of these birds occur in late July and early August with stragglers present until early October (Harrington and Morrison 1979). While at these stopover areas, the birds do little more than rest and eat, accumulating sufficient reserves of subcutaneous fat to fuel what may be a nonstop flight to the wintering areas in South America (McNeil and Burton 1973) where they remain for 6 to 7 months. In April, the birds start on a return migration to their breeding ranges (Palmer 1967), a trip that takes many to their fall stopover areas. Others take an inland route along the Mississippi Valley. The spring migration occupies less time than the fall migration and after arriving on their Arctic breeding ranges, they spend about a month producing young. They then accumulate in large flocks at major staging areas such as James Bay, Ontario, Canada, and Bay of Fundy, first adults and later juveniles. Soon they depart from the northeast coast and repeat this yearly cycle of events.

Shorebirds feed primarily on invertebrates (molluscs, crustaceans, polychaetes) that are captured on beaches and sand and mud flats. Their daily activity patterns and specific foraging sites are often dictated by the tides. During the early part of the ebb tide, foraging begins on the beaches and as the tide continues to recede, many species then move to tidal flats (Burger et al. 1977). Connors et al. (1981) related these movements to the peak availability of prey items in these two habitats. During high tide, the birds usually rest on adjacent beaches and upland areas (Harrington et al. 1974).

Although there are a few large sandpipers, the majority are among the smallest birds to frequent tidal flats. These exquisitely camouflaged shorebirds often

go unnoticed by even well-trained eyes. They are probers that often feed in small flocks. Many plovers are larger, may assume a more upright posture in alarm, frequently feed solitarily or in loose groups, and are considerably more active than most sandpipers. Only a single species of oystercatcher is found in New England. The American oystercatcher is conspicuous with a long, bright orange bill. As the name implies, these birds feed almost exclusively on large molluscs and are only infrequently seen.

A tidal flat may be exploited by a large number of shorebirds of many different species. Their effects may deplete prey populations (Schneider 1978). Since tidal flats appear to be a physically uniform habitat, severe competition for food between predator species may be expected. How is it that so many seemingly similar bird species can all exploit the invertebrates of the same tidal flats and continue to coexist? There are several possible explanations. Due to their migratory nature, shorebirds may not deplete resources to the critically low levels that would result in severe competition. When resources are severely depleted, however, we must look for alternative explanations. Among these is the possibility that a tidal flat may not be as physically uniform an environment as it appears. If the tidal flat actually represents a collection of discrete microhabitats, then different species may exploit different habitats with the result that competition is reduced. Differences in sediment grain size, patches of algae, depressions, shellfish beds, cobbles and larger rocks create surficial, horizontal discontinuities while segregation by depth of water and sediments of different prey items represents a vertical habitat diversity. Superimpose on these variables the temporal component of tidal fluctuations and there exists a wide variety of different habitats within a single tidal flat. If bird species differ in microhabitat preferences, then foraging individuals may be separated in either space or time, reducing direct competition. In addition, morphology (e.g., bill shape and size), feeding tactics, and prey preferences may prevent even those species that forage in the same areas simultaneously from actually competing for food.

There is evidence that bird species differ with respect to substrate preferences. Sanderlings prefer sandy substrates and dowitchers are more often found over siltier areas (Harrington and Schneider 1978) while ruddy turnstones most frequently forage on barnacle-covered rocks and in accumulations of tidal wrack (Groves 1978). Other species, such as black-bellied plovers, opportunistically feed in any of several habitats with no noticeably strong preferences (Harrington and Schneider 1978). Burger et al. (1977) found that larger species prefer muddier algal zones while smaller species frequent drier microhabitats.

Temporal segregation may occur as the tides recede--when a wave of species, each oriented to preferred distances from the water's edge, sequentially use the same areas of the tidal flat. Sanderlings and semipalmated sandpipers characteristically follow the water's edge as the tide ebbs while semipalmated plovers restrict their foraging to the middle areas of the tidal flats (Harrington et al. 1974). Knots and dunlins also follow the receding tide and

although they occur together, both spatially and temporally, competition is avoided since knots prefer molluscs while dunlins eat polychaetes (Evans et al. 1979). Dowitchers also follow the tide but feed deeper in the sediments. The form of the bill and leg length influence the type of potential prey items available to a species (Figure 15).

Temporal segregation may occur on a broader, seasonal scale. As shorebirds arrive in fall or spring, peak densities of different species may be staggered in time, reducing competition, particularly between ecologically similar species (Recher 1966). Even subtle differences in migration schedules may have profound effects on resource availability. Harrington and Schneider (1978) mention that shrimp that feed on the juveniles of infaunal invertebrates may not arrive on the flats until late in the shorebird migratory season. Shorebirds that prey on crustaceans, such as black-bellied plovers and sanderlings, are later fall migrants than short-billed dowitchers and semipalmated sandpipers that consume infaunal prey.

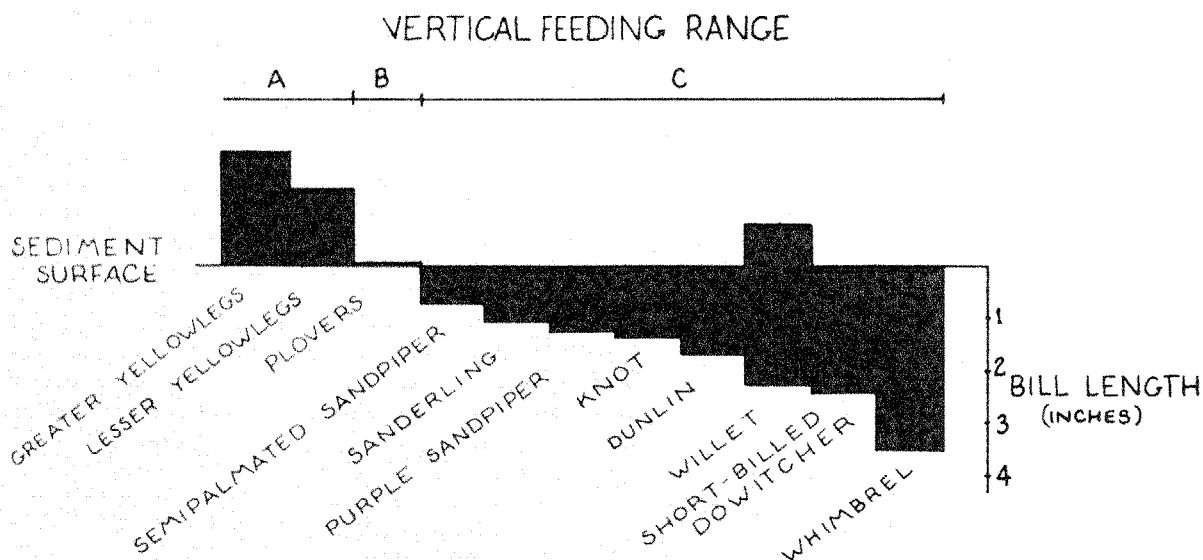


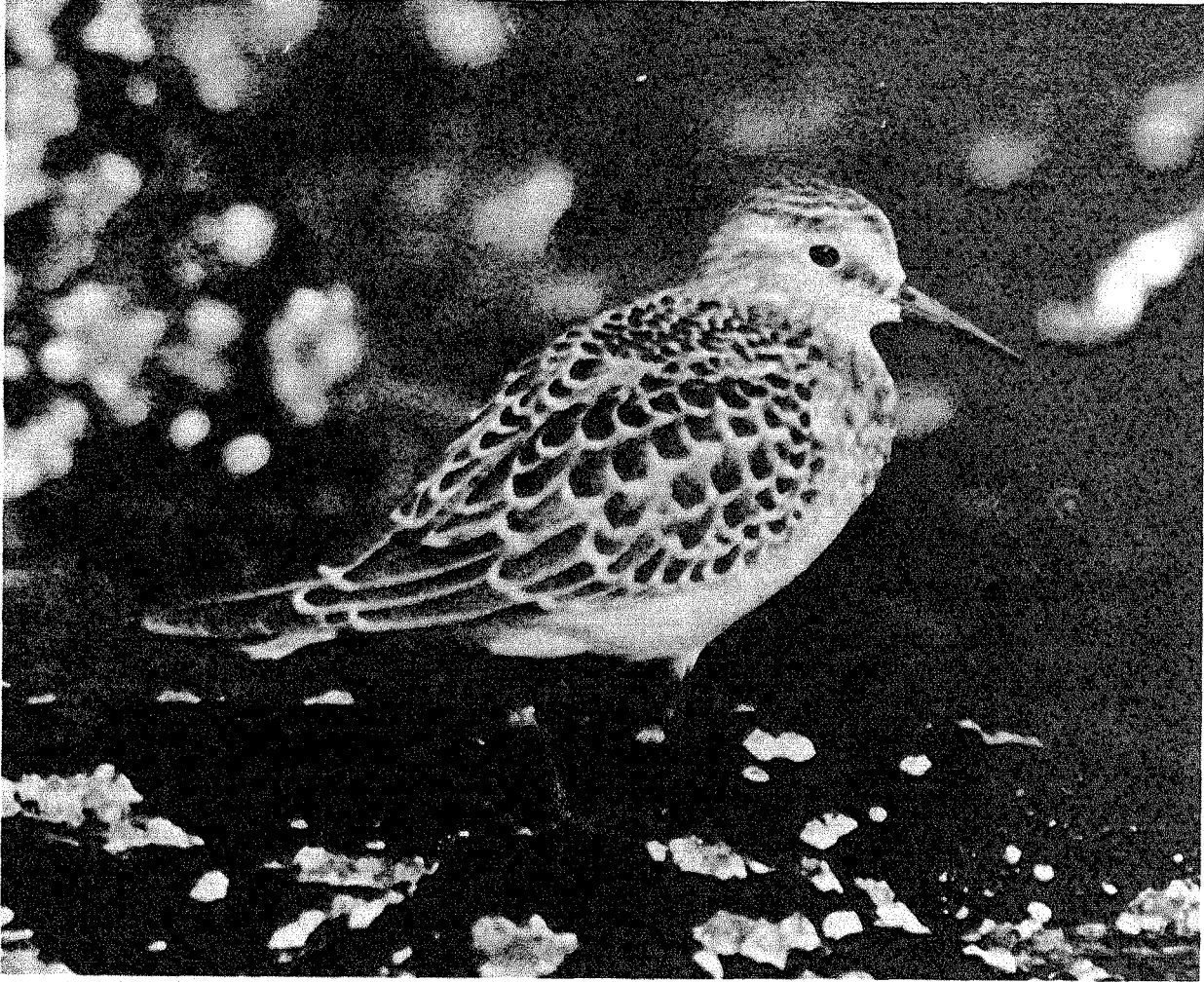
Figure 15. Vertical feeding depths of some common New England shorebirds (modified from Recher 1966). Bill lengths are an average of the ranges given by Palmer (1967). A = species foraging between the water and sediment surface (heights of bars refer to water depths); B = species primarily feeding on the sediment surface; C = species mainly feeding below the sediment-water interface (the willet feeds below the sediment surface as well as in shallow water).

In addition to habitat selection and bill and leg morphology, variability in foraging behaviors between bird species is also a critical factor in determining potential shorebird food resources (Baker and Baker 1973). Behavioral patterns may be stereotyped to the extent that not only may species identifications be possible by observations of behavior, but also it has been suggested that behavioral as well as morphological attributes may reflect evolutionary relationships (Matthiessen 1967). The erratic run and peck foraging behavior of the plovers easily distinguishes them from the slower, more methodical probing sandpipers. Pearson and Parker (1973) found behavioral uniformity within each group and an inverse relationship between bill length and stepping speed suggesting that birds that peck the surface for prey are more active than those that probe deeper in the sediments. The active audio/visual hunting by plovers requires increased activity, quick movements, and intermittent pauses for searching and stalking. The probing sandpipers locate their prey primarily by tactile methods, walking slowly and continually thrusting their bill into the sediment. These very different hunting techniques may result in the consumption of different prey species or different-sized individuals of the same species or a more efficient prey-capture time. For example, the semipalmated plovers that forage on the middle regions of the tidal flats search for prey in areas that have been previously exploited by the probing sanderlings and semipalmated sandpipers. All three species may consume the same species of prey but the later-arriving and visually hunting semipalmated plovers are more successful per unit time (Harrington et al. 1974). Most probing shorebirds will also respond to visual cues and peck at prey items. Often the pecking or probing alternative may be a function of habitat type and prey availability.

Since migrating shorebirds may often occur in high densities, aggressive interactions in the form of displays and chases are quite common among many species, particularly those that feed primarily by visually active hunting tactics (Burger et al. 1979). Probers frequently occur in foraging flocks and only rarely do aggressive interactions occur, as in the

case of knots that most commonly feed in tight groups (Bryant 1979). Species such as the sanderling that feed by both visual and tactile methods will show little aggression and feed in flocks but maintain intraspecific distances while foraging solitarily (Harrington et al. 1974). In general, among shorebirds, intraspecific aggressions are more frequent than interspecific interactions (Burger et al. 1979) and when interspecific aggression does occur, it is most common among similar species such as between the least and semipalmated sandpipers (Recher and Recher 1969b) that avoid each other by marked habitat segregation (i.e., mud flats vs. grassy marsh and seaweeds).

A remaining question is what role shorebirds play in the New England tidal flat community. Although the majority are transients, their role as major consumers of invertebrate production is a substantial one during migrations. They may be best described as removers. Other than the nutrients in their feces, no form of the energy they consume is returned to the tidal flats. During the fall migration, in just a few weeks they may deplete large portions of their prey populations. Schneider (1978) found the average harvest by foraging shorebirds was 50% and 70% of invertebrate populations during two successive years of study. In Massachusetts, dowitchers have been reported to remove nearly one half of available food resources during July and August (Harrington and Schneider 1978). Wintering species may have a more dramatic effect as seen in a study done in England where shorebirds were responsible for removing 90% of the Hydrobia (snail) population and 80% of the nereid polychaetes (Evans et al. 1979). Stomach contents of dunlins in Sweden revealed an average of 152 Nereis (polychaete worm) jaws per individual (Bengtson and Svensson 1968). Site selection among foraging shorebirds is not a random, passive process. Favorable feeding areas with a high density of prey can be recognized and exploited. Harrington and Schneider (1978) found that semipalmated plovers shifted their habitat usage to coincide with peak densities of nereid worms and that extremely high densities of knots could be correlated with an unusually heavy set of Mytilus (mussels).



Shorebirds, such as this semipalmated sandpiper, concentrate in large numbers on New England tidal flats in spring and fall. They consume great quantities of invertebrates to provide the necessary fat reserves for long migrations from Arctic nesting grounds to wintering areas in South America. (Photo by J.M. Greeny; courtesy U.S. Fish and Wildlife Service.)

Since shorebird predation may be intense and focused in areas where prey species are most abundant, these birds probably play an important, if temporary, role in structuring the invertebrate communities of tidal flat environments. On Long Island, New York, Schneider (1978) found that such predation resulted in wider spatial distributions of prey species. By concentrating their foraging on the most abundant prey, shorebirds prevent single species of invertebrates from dominating areas of the tidal flats at the expense of others.

5.3 GULLS AND TERNS

Eight species of gulls and six species of terns (family Laridae) occur commonly in New England. Seven of the fourteen species nest in colonies on the New England coast, and two species, the herring and great black-backed gulls, appear year-round. The distribution of nesting pairs of colonial waterbirds throughout New England is given in Table 6.

Gulls will drop to the surface from flight (plunge diving, Ashmole 1971) when

Table 6. Number of coastal nesting pairs of colonial waterbird species in 1977 (Maine-Connecticut), showing occurrence by state (from Erwin and Korschgen 1979).

Species	ME	NH	MA	RI	CT
Double-crested Cormorant <u>Phalacrocorax auritus</u>	15,333	24	1,760		
Great Blue Heron <u>Ardea herodias</u>	903				
Green Heron ^a <u>Butorides striatus</u>			1	2	15
Little Blue Heron <u>Florida caerulea</u>	4		19	35	1
Great Egret <u>Casmerodius albus</u>			6	22	20
Snowy Egret <u>Egretta thula</u>	90		459	180	50
Louisiana Heron <u>Hydranassa tricolor</u>	1		1		
Black-crowned Night Heron <u>Mycticorax nycticorax</u>	117		1,958	517	406
Glossy Ibis <u>Plegadis falcinellus</u>	75		112	160	10
Common Eider <u>Somateria mollissima</u>	22,390		1+		
Great Black-backed Gull <u>Larus marinus</u>	9,847	91	4,670	540	164
Herring Gull <u>Larus argentatus</u>	26,037	350	25,845	6,016	3,134
Laughing Gull <u>Larus atricilla</u>	231		200		
Common Tern <u>Sterna hirundo</u>	2,095		4,475	589	1,479
Arctic Tern <u>Sterna paradisaea</u>	1,640		73		
Roseate Tern <u>Sterna dougallii</u>	80		1,327		
Least Tern <u>Sterna albifrons</u>	21		1,551	47	120

^aIncluded only when found at mixed species heronries.

feeding on schools of small fish. More frequently they paddle slowly on the surface dunking their heads (surface dipping, Ashmole 1971), fly a few feet up from this position and make short plunges in shallow water (surface plunging, Ashmole 1971), or forage over exposed tidal flats or intertidal rocky substrates. Some of their feeding techniques show remarkable ingenuity. They paddle in shallow water, creating a current that moves away sediments to expose infaunal prey. It is not uncommon to see gulls cracking mollusc shells by dropping them from the air onto docks, boulders, parking lots, or any other large hard object.

Most New England terns are smaller than the gulls. Some kinds with forked tails are aptly called sea swallows. Their speed and flight patterns, particularly when being pursued by one of their own kind, are remarkable to watch. They are most famous for their group feeding "frenzies" when they plummet head first from the sky to capture schooling fish and crustaceans. More gracefully, on calm days they can swoop down and snatch a minnow without making a ripple. While searching for food, they may be seen hovering or "stilling". Their relatively small feet serve to orient them but prevent them from being good swimmers. Prey, usually small fish or crustaceans, are generally captured by plunge diving.

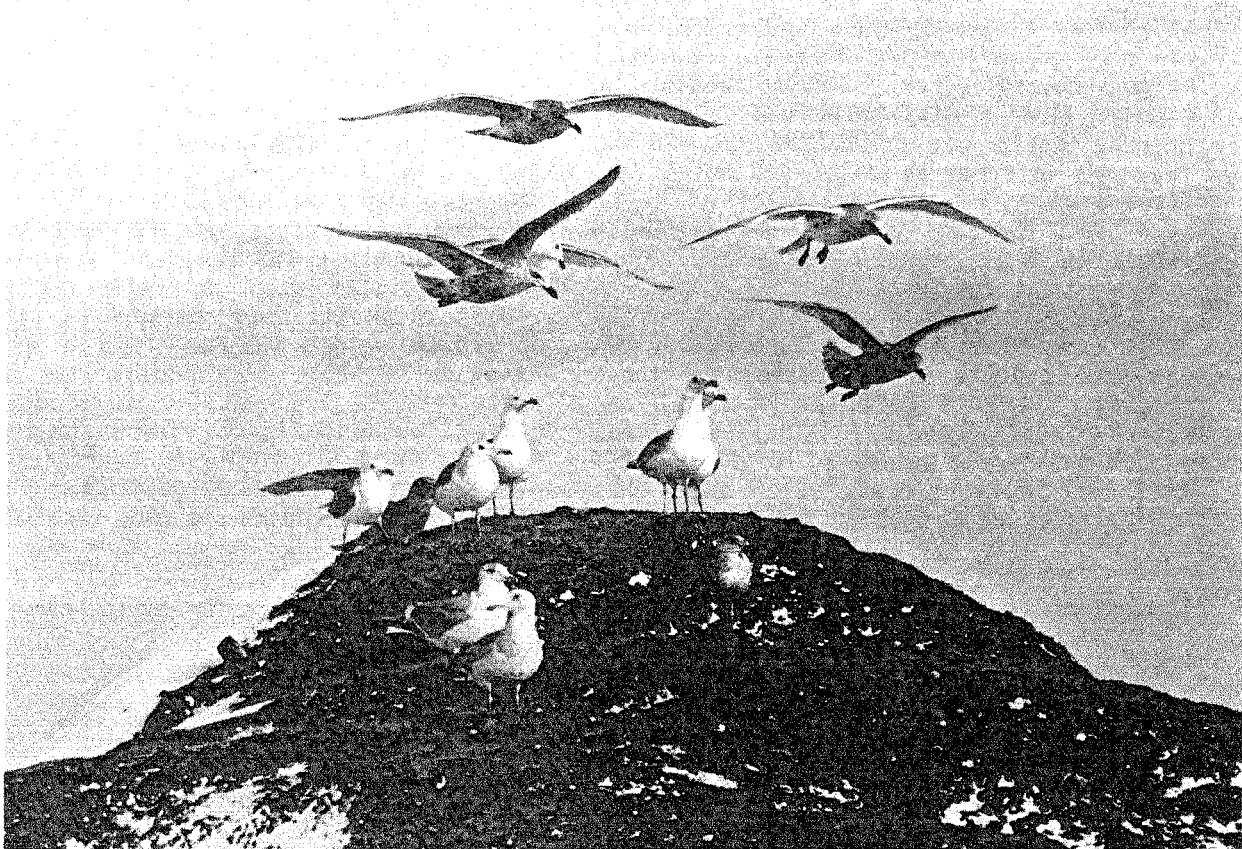
At the turn of the century, no one would have predicted that "sea gulls" would become a symbol of the New England seashore. During the last two hundred years, the breeding populations of New England gulls and terns have fluctuated greatly. Surveys have been made at frequent intervals during this century and there is good documentation for recent periods of both declines and expansions. The following discussion of the historical trends in these populations is summarized from Drury (1973) and Nisbet (1973).

During much of the 18th and 19th centuries, the larger gulls were exploited for their food value and nearly exterminated in New England, and in the later decades of the 19th century, the millinery trade inflicted hunting pressures on terns as well. By 1900, both gull and tern populations were at low levels, and some

conservationists feared these species were on the verge of disappearing from the New England coast. A conscious effort to save these birds resulted in the passage of several bird protection laws and the response of the bird populations has been good to spectacular for terns and gulls respectively.

The New England herring gull breeding population numbered only about 10,000 pairs at the turn of the century, with the great majority restricted to islands off the Maine coast. Both the number and range of gulls have increased tremendously in the last 75 years. From 1900 to the 1960's, the population appears to have increased by a factor of 15 to 30, doubling every 12 to 15 years (Kadlec and Drury 1968). As early as the 1920's, there was concern that the rapidly increasing herring gull population threatened farm and blueberry crops in eastern Maine as well as the continued survival of the terns; in the 1930's, a gull control program was initiated in the form of egg spraying. This was originally focused in Maine and the gulls responded in part by a southwestward expansion into Massachusetts (Kadlec and Drury 1968). During the 1940's to early 1950's, the control program was conducted on most colonies from Maine to Massachusetts, but was eventually abandoned as ineffective. Although gulls colonized islands at the eastern end of Long Island Sound by 1933, it was not until 1950 that herring gulls colonized the shores of Connecticut. By 1960, they had expanded their range as far south as North Carolina.

The common tern has been the most abundant tern nesting on the northeastern coast of the United States, although the Arctic tern may now be more numerous in Maine (W.H. Drury; College of the Atlantic; Bar Harbor, Maine; April 1981; personal communication). Historical population estimates indicate a period of increase early in this century followed by a more recent period of decline in population numbers. Peak populations occurred during the 1940's and since then, the population has been reduced by about one half. One author suggests that the decline of these birds may be due in part to decreased breeding success that has resulted from the displacement of breeding



Gulls of several species are the most abundant and conspicuous birds on New England tidal flats. They feed on a wide variety of fish and invertebrates and scavenge human waste. (Photo by L.C. Goldman; courtesy U.S. Fish and Wildlife Service)

birds from preferred areas by herring gulls (Nisbet 1973), and also from winter predation pressure by residents of the Guianas on the northern coast of South America (W.H. Drury; College of the Atlantic; Bar Harbor, Maine; April 1981; personal communication).

Most gulls and terns are highly gregarious. They are colonial breeders and often gather in large groups where food is concentrated. It is impressive to witness the accumulation of a group of feeding gulls. Initially only one or two may be within sight, but within a few minutes there may be one hundred or more. Group feeding techniques in gulls have been examined by Frings et al. (1955). They found that food finding and the accumulation of feeding groups resulted from the combination of auditory and visual cues.

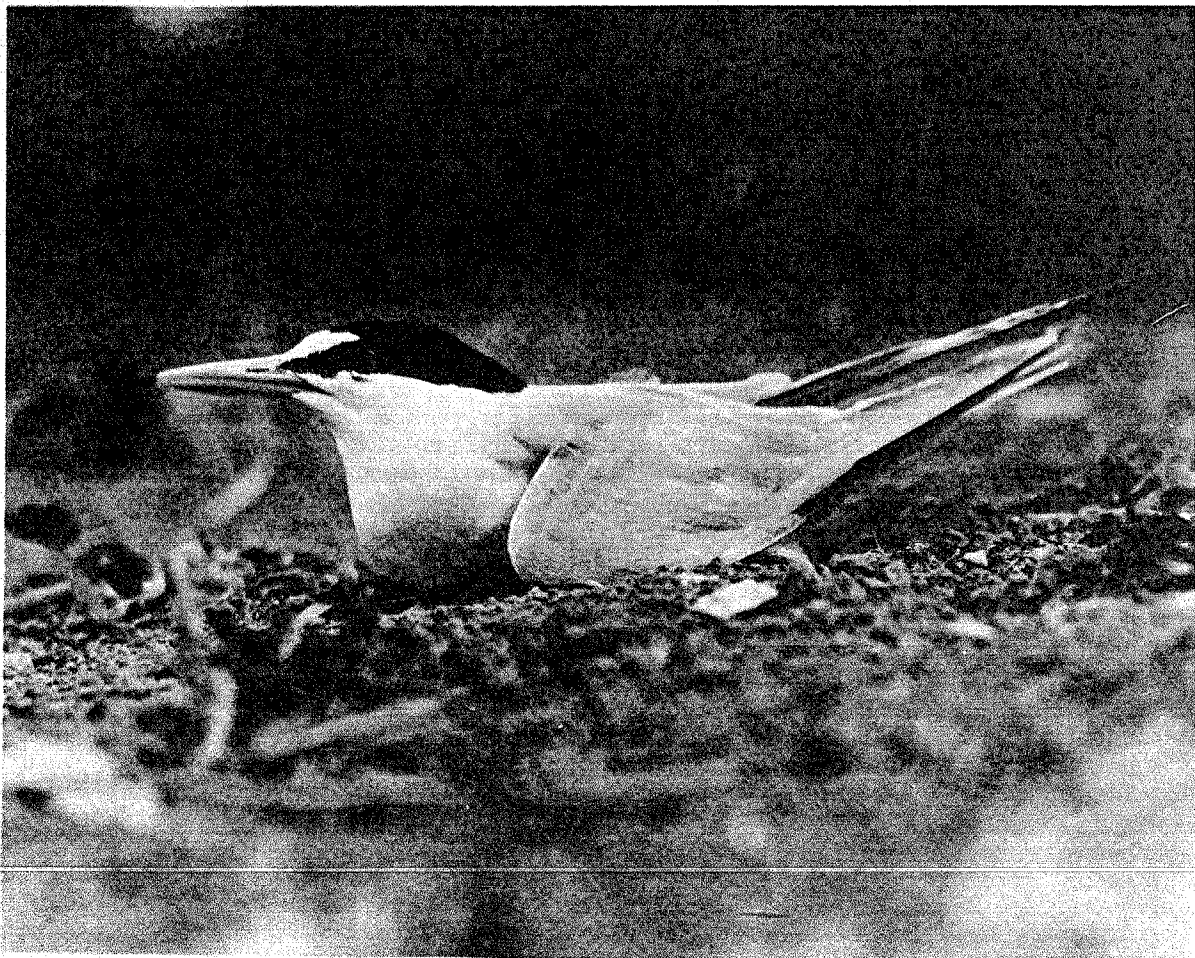
There is a constant visual surveillance of all parts of the coast by individuals or small groups of birds. A bird that has spotted food flies a characteristic figure eight flight pattern in an attempt at prey capture and emits a characteristic call. Gulls within sight respond to the flight pattern and those within earshot respond to the call. Terns may also form feeding groups via auditory and visual cues (Erwin 1977).

Colonies may serve as information centers and be an important aid in food finding, particularly for species that feed in groups on a patchy resource (Ward and Zahavi 1973; Erwin 1978). Davis (1975) found that the nests of gulls that consistently fed together at fish docks were not randomly dispersed in the breeding colonies, but were clumped, suggesting that

gulls may follow each other to foraging sites. Among different species of terns, Erwin (1978) suggests that those species which feed closer to the breeding colonies are more gregarious while feeding and have larger colony sizes. While feeding on exposed tidal flats where food is patchy, herring gulls may establish territories that are defended by calls and posturing. These territories may be maintained by the same birds for many years (Drury and Smith 1968).

The displacement of nesting terns by gulls can be explained in part by reviewing some aspects of the biology of these species. Herring gulls are general and opportunistic foragers. They will eat almost any large piece of organic material, living or dead, and have thus capitalized on a subsidy in the form of

tons of organic wastes produced each year by the northeastern coastal human population which has increased spectacularly during this century. The effect has been to tremendously increase the carrying capacity of their environment which has released the population growth rate of the gulls from dependence on food resources; the New England herring gull population is now dependent on human refuse. Perhaps the greatest impact on the species has been to increase the survival of wintering yearlings that feed on refuse. Harris (1965) estimated that in England as much as two-thirds of the food remains of herring gulls were attributable to human waste and Kadlec and Drury (1968) suggested that only 12% of New England gulls make an "honest" living by consuming food other than that generated by man. Hunt (1972) studied Maine islands of varying



The least tern is one of four species of terns that feed on small fish of the New England tidal flats and nest on nearby beaches and islands. (Photo by L.C. Goldman; courtesy U.S. Fish and Wildlife Service)

distances from refuse sources and observed that fledging success was greatest at the near islands. Since there is little difference between the fledging success of two and three egg clutches (Kadlec and Drury 1968), when chick mortality does occur, it is generally not because of insufficient food, but rather due to parental neglect (Drury and Smith 1968; Hunt 1972). If gull chicks are left unattended for long periods of time, they may wander into adjacent territories and may be attacked by neighboring adults (Hunt and McLoon 1975).

Another potential control on population growth is available breeding space. During the last 75 years of rapid expansion, the density of nests in herring gull colonies has remained unchanged (Kadlec and Drury 1968). As the number of birds in the New England gull population has grown, new nesting pairs have established new colonies, expanding the breeding range. Most breeding colonies occur on nearshore islands, the same type of islands used by breeding terns. Kadlec and Drury (1968) have estimated that approximately 15% to 30% of adult herring gulls are nonbreeders in any given year. There is a tendency for gulls that find no space in existing colonies to establish territories on islands that support tern colonies and, in time, to displace the terns (Drury 1974).

Terns are much more selective in their feeding than gulls, preferring small fish and crustaceans. Unlike the herring gulls, their population growth is food-limited. During the breeding season, adult males may hunt for food up to 14.5 hours per day (Nisbet 1973). There is evidence that the number of chicks that survive to fledging may be a function of food availability. LeCroy and Collins (1972) found that both roseate and common tern productivity in Long Island Sound, as measured by successful fledgings, fluctuated yearly, and the authors suggested that these fluctuations were related to food availability. These workers also examined the relationship between clutch size and chick survival. Common and roseate terns may lay either two or three egg clutches and, unlike the herring gulls, the survival from hatched egg to fledging is much greater in two egg clutches than three.

This evidence suggests that (1) during this century, we have increased the carrying capacity of New England for the herring and great black-backed gull populations, (2) tern populations are limited by natural controls, and (3) both groups overlap considerably in their preferred breeding areas. Collectively then, this evidence implies that the dense coastal human population of the northeast is threatening the continued coexistence of these two groups of birds.

5.4 HERONS AND OTHER WADING BIRDS

For many people, the most conspicuously beautiful and aesthetically pleasing birds that frequent tidal flats are the herons and egrets. These long-legged and slender-necked wading birds are elegant as they take off and land with broad wings beating in slow motion. At other times as they pursue prey with feet splashing, head jerking, and wings flapping, they seem clumsy. Like the gulls and terns, herons and other wading birds are colonial breeders that often nest on islands. Table 6 shows the relative abundance of coastal breeding herons in New England. Most species frequent the New England coast only during the warmer months, but the great blue and the black-crowned night herons may remain all winter. After young are fledged, there is a general dispersion northward and then a southward migration in the fall. In New England, herons are primarily tree nesters. Until the 1950's, most kinds of wading birds nested only in more southern states. Since then there has been a steady "invasion" into New England (R. Andrews; U.S. Fish and Wildlife Service, Newton Corner, Massachusetts; April 1981; personal communication). In the south, dense multispecies breeding and feeding assemblages frequently occur. Each species has a characteristic foraging behavior and the collective repertoire of the feeding behaviors of this group has been studied extensively.

Soon after arriving from wintering areas, pairs of herons establish well-defended breeding territories. At least one member of the pair always occupies the territory (Jenni 1969). Nest site selection is species-specific. Snowy egrets have a tendency to nest in exposed areas

around the periphery of the colony, while little blue herons prefer more protected locations (Jenni 1969).

Egg destruction occurs as the result of predators such as raccoons or crows (Teal 1965). During the first few weeks after hatching, chick mortality may be high. Jenni (1969) suggested that snowy egret chick loss was largely due to starvation. He found that mortality rates were 37% per nest of four, 23% per nest of three, and 10% per nest of two. In a mixed species heronry in Georgia, 10% of the nestlings died of starvation (Teal 1965). Nest success varies from species to species. Teal (1965) found that only black-crowned night herons fledged more than 50% of the eggs laid. He attributed this to pugnacious behavior of the chicks who vigorously defend their nest. He suggested that the smaller and less fierce species (snowy egret and Louisiana heron) were the least successful.

After fledging, high mortality rates may be sustained through the first year of life. Kahl (1963) found that 76% of the common egrets alive on July 1 died during their first year, and mortality rates of 71% (Owen 1959) were reported for the great blue heron. Most of the first year mortality for both common egrets and great blue herons occurs between July and December and may be due to the unfamiliarity of inexperienced young of the year with migratory territories (Kahl 1963). It takes time for young birds to become proficient hunters. Although feeding behaviors appear to be innate components of a heron's biology and similar techniques are used by both adults and juveniles, success rates are much higher for adult birds. Recher and Recher (1969a) found that for each minute spent foraging, adult little blue herons obtained more prey by weight than the juveniles. Similarly, adult great blue herons were found to be successful in 62% of strikes while juveniles captured prey in only 33% of their attempts (Quinney and Smith 1980).

While it appears that food is a limiting resource particularly during the breeding season, Teal (1965) concluded that there is a surplus of food, but this food is not sufficiently available to even the adult birds since they are relatively

inefficient predators. This is not surprising since the primary prey are mobile fish and large crustaceans, making food finding and foraging techniques critical factors in heron ecology.

The role of colonies as information centers has been studied extensively in heron breeding colonies. Krebs (1974) specifically addressed this problem in a study of the great blue heron. To illustrate the advantage of gregariousness, he showed that while the birds exploited a patchy food supply, individuals were not behaving independently, and birds that foraged in groups had a higher rate of food intake than those feeding solitarily. Feeding areas were highly variable from day to day and the colony tended to switch in unison from one feeding site to another. Departure from the breeding colonies to foraging areas generally occurred in groups and birds from neighboring nests frequently fed in the same areas. Finally, Krebs (1974), who put styrofoam models of foraging herons in the field, found individuals flying overhead were attracted to them, landed, and began foraging.

During foraging, the herons may be either solitary and defend feeding territories or gregarious and form small flocks. Great blue herons have their highest rate of feeding success at a flock size of about twenty birds and Krebs (1974) suggests that flocks may buffer the risk of birds being unsuccessful in feeding on the short term, which may be critical when rearing chicks. Even when great blues feed alone, colonies may still play a role as information centers in locating the position of food resources relative to the colony (Ward and Zahavi 1973).

As a group, the herons use a diverse array of foraging behaviors and within the tidal flat environment, may segregate themselves according to habitat preferences and morphology. As a result, the overlap in prey items between species may be reduced. In Florida, Meyerriecks (1962) has seen as many as nine species of herons feeding on the same shoal; he claims that their ability to coexist while using a common habitat results from their use of different feeding methods. Kushlan (1976) provides a good descriptive summary of heron feeding behaviors. The major

categories of foraging tactics are stand or stalk feeding, disturb and chase feeding, and aerial and deep water feeding. Within each of these major categories, there are several variations. The stand and wait feeding behavior is the most typical and is common to all species of herons (Allen 1962).

Depending on the habitat, which includes prey density, predator density, water depth, and plant cover, species use their own unique hunting tactics (Kushlan 1976). In his study of heron feeding in southern New Jersey, Willard (1977) summarized the foraging behaviors of many of the herons seen in New England. He found that great blue herons and common egrets hunt in deeper water than the smaller species. Great blue herons used stand and wait and slow wading techniques to the same extent. Active pursuit was rare, probably related to the large and highly mobile fish species in the diet. Great egrets also used slow wading techniques but their pace was faster than the great blue herons, and when feeding in flocks, they used the stand and wait technique. Snowy egrets showed the greatest variety of feeding behaviors and of habitat selection. They were the only species to frequent exposed mud flats where they would take large polychaetes. Slow wading was the most frequent hunting technique, but foot stirring and active pursuit were also common. The foot stirring behavior resulted in a larger portion of benthic crustaceans in the snowy egret's diet. The Louisiana herons also relied on active pursuit, but the most common feeding behavior was to crouch and strike horizontal to the water's surface. This was the only species in which slow wading was not the preferred technique. Little blue herons commonly waded slowly and peered around banks and vegetation. The green heron and black-crowned night heron were not studied by Willard (1977). Both these species can be commonly seen crouched overlooking the water's surface where they wait motionless for prey to wander by.

5.5 WATERFOWL AND DIVING BIRDS

This group is composed of a wide variety of families, including the loons

(Gaviidae), grebes (Podicipedidae), cormorants (Phalacrocoracidae), and the ducks, geese, and swans (Anatidae). The majority are migrants, present in New England only during spring and fall, or they are winter residents. Exceptions are the double-crested cormorant, common loon, gadwall, wood duck, and red-breasted merganser that breed in some areas of New England and the pied-billed grebe, Canada goose, black duck, mallard, and mute swan that are year-round residents. With only a few exceptions (the geese, swan, and dabbling ducks), all these birds dive for their food which is usually fish, molluscs, or crustaceans. Although many species are capable of dives to great depths (over 70 m or 230 ft for the common loon), most forage in shallower water, usually less than 10 m (33 ft) deep. Some have become extremely well-adapted to an aquatic existence, can barely walk on land, and can only take off from the water.

Two species of loons (common loon and red-throated loon) are often found along the New England coast during the winter. Although they do not concentrate their foraging on tidal flats, at high tide, they may be seen over these shallow areas diving for fish. Common loons are solitary, even during migrations, and occur singly or in pairs, while the red-throated loons accumulate in large flocks, particularly during migrations (Terres 1980). Because the loons require up to several hundred meters of water "runway" to become airborne, when approached, they will dive rather than fly as a means of escape.

Grebes, like the loons, may use tidal flats at high tide as one of several of their feeding areas. They are extremely well-adapted for their primarily aquatic existence where they feed, sleep, court, and carry their chicks on their backs in the water. Of the three species seen along the New England coast, the horned and red-necked grebes breed in Canada but winter in coastal New England. The pied-billed grebe breeds throughout New England and winters as far north as Massachusetts. Their diets consist of small fish and crustaceans.

Cormorants are related to pelicans and feed almost entirely on fish that they



Young double-crested cormorants in nest. Cormorants are specialists that feed on fish and have been increasing along the New England coast. (Photo by R.G. Schmidt; courtesy of U.S. Fish and Wildlife Service.)

capture by diving beneath the water's surface. Double-crested cormorants are colonial breeders, present in New England only from April to November. They nest on rocky islands, along the Maine and Massachusetts coast, although they have been reported to nest in trees at many locations in New England (Drury 1973). An historical review of the status of this species in New England has been provided by Drury (1973). After being completely extirpated on the New England coast during the last century, double-crested cormorants made a dramatic comeback during the early part of the 1900's. Between 1925 and 1945 the population grew to about 13,000 nesting pairs along the Maine coast and since then, has expanded its range along the New England coast as far south as the entrance to Long Island Sound (although the majority of breeding pairs occurs north of Boston, Massachusetts). In the mid 1940's, Maine fishermen declared this species a menace

to the commercial fishery and an egg spraying program was initiated by the U.S. Fish and Wildlife Service but was terminated in 1953. Since then, the population has continued to expand despite some indications that cormorants may have been affected by toxic chemical poisoning (Drury 1974).

As the double-crested cormorant leaves the New England coast each year during the fall migration, it is replaced by the larger and more northerly breeding great cormorant that is a winter resident. Both species consume fish that they pursue underwater. Double-crested cormorants appear to be the least wary and maritime of the two and frequently feed over tidal flats at high tide but can pursue fish to great depths. Feeding may occur solitarily or in groups. Bartholomew (1942) has reported observations of orderly flock-feeding on San Francisco Bay. During

flock-feeding, cormorants exploit schooling fishes. Active fishing is confined almost exclusively to the front line of birds, and as many as one quarter to one half of the birds may be underwater at one time.

Peak densities of wintering waterfowl on the Atlantic coast occur in the mid-Atlantic states, but large numbers of several species are found on the New England coast, some of which use tidal flats. North American migratory waterfowl that pass through or winter along the New England coast use the Atlantic flyway, which is one of the four great North American migratory flyway systems (Lincoln 1935, cited in Gusey 1977). Unlike the long, nonstop migratory flights of shorebirds, waterfowl often follow the coast, stopping occasionally to rest and feed. Flocks even take up residence in areas for extended periods. For example in Massachusetts, oldsquaw may appear during the middle part of October, remain until the middle of November, and then fly farther south (MacKay 1892).

Geese (Canada geese and brant) frequent the New England coast primarily during the winter, although a small number of introduced Canada geese breed in New England as well. As herbivores, Canada geese forage on submerged eelgrass (*Zostera marina*) and algae in shallow coastal areas by reaching down into the water with their long necks, often tilting their tails straight up in the air. Brant are true sea geese with well-developed salt glands that enable them to drink salt water. Although they are usually herbivorous, brant also eat crustaceans, molluscs, and polychaetes (Bent 1937). Before the 1930's, brant fed almost exclusively on eelgrass. After a blight destroyed much of the eelgrass in the northeast, the brant population declined dramatically. Since then, brant have switched their foraging preference to *Ulva* (sea lettuce) and although the population is reduced compared to that in the 1930's, its numbers have increased in recent years.

The majority of wintering ducks and mergansers in New England belong to only a few species. Diving ducks and mergansers use tidal flats at high tide as one of several habitats for catching small fish

and invertebrates, while the dabblers are more restricted to shallow coastal areas and may feed extensively on tidal flats at high and low tide. Stott and Olson (1972) found all wintering species in New Hampshire (scoters, goldeneye, red-breasted merganser, oldsquaw, and bufflehead) to be within 450 m (1,476 ft) of the shoreline. Competition between these wintering birds appears to be reduced as a result of species-specific habitat and food preferences. Many species of sea duck studied were consistent in their habitat usage from arrival in the fall until departure in the spring (Stott and Olson 1973). Within the study area, there were sandy beaches, rocky outcrops, and bays. The scoters preferred to feed in areas adjacent to the sand beaches, while goldeneyes and red-breasted mergansers most often foraged closer to the rocky headlands. Oldsquaws showed no consistent habitat preferences and buffleheads were almost exclusively restricted to the quieter bays. All these species are divers. Ninety percent of the scoter's diet consisted of molluscs of which the Atlantic razor clam (*Ensis directus*), Arctic wedge clam (*Mesodesma arctatum*), and blue mussel (*Mytilus edulis*) were the most abundant species. Although the goldeneyes and red-breasted mergansers overlapped in habitat preference, the goldeneyes ate small crustaceans, with some gastropods and polychaetes, while the mergansers were fish eaters, consuming killifish and silversides. Small sand shrimp comprised 90% by volume of the bufflehead's prey items. Nilsson (1969) found similar habitat segregation among wintering ducks in southern Sweden, but in his study he found goldeneyes to feed mainly over mud bottoms.

Waterfowl are the only group of coastal waterbirds that constitute a commodity harvested for recreational use. The bulk of each year's harvest in New England is dabbling ducks; the major species taken are black ducks, mallards, and geese. Eiders and oldsquaw are also taken in numbers along the coast of Maine (W.H. Drury; College of the Atlantic; Bar Harbor, Maine; April 1981; personal communication). The dabbling ducks are mainly herbivorous but omnivorous in that they eat whatever their feeding techniques catch in shallow submerged vegetation.

Both mallards and black ducks are year-round residents of New England. The black duck is currently more abundant, but there is evidence that it is hybridizing with and being replaced by the northward spread of the closely related mallard. Black ducks use tidal flats, especially in northern New England, more than any other species of this group. Breeding in freshwater swamps, marshes, and streams throughout New England, black ducks migrate to the coast in the fall and rely heavily on tidal flats during the winter. Winter feeding may be regulated by tidal rhythms and weather and although these ducks are mainly herbivorous, their diet includes intertidal invertebrates such as the blue mussel (*Mytilus edulis*), soft-shelled clam (*Mya arenaria*), and sand worm (*Nereis virens*) and various amphipods and isopods (Hartman 1963). During severe winter weather, black ducks remain in groups in open water kept free of ice by tidal currents (Spencer et al. 1980).

5.6 RAPTORS

As consumers of large fish and shore-birds, the hawks and eagles (family Accipitridae), and osprey (family Strigidae) occupy the highest level in the nearshore food chain. Of these raptors, the osprey, and bald eagle exceed all others in terms of their dependence on the coastal zone. Ospreys eat a variety of coastal pelagic fish and often hunt over shallow water where they can take more demersal varieties. Prey species weigh up to 2 kg (4 lb) (Bent 1937) and there have been reports of these birds being drowned while attempting to capture large fish. The osprey soars 30 m (100 ft) or more above the water, where with its keen eyesight, it may locate even the most camouflaged species such as flatfish. When prey is detected, the soaring is often interrupted by hovering which may last up to ten seconds and is usually followed by a spiral plunge into the water. Prey is captured with specialized talons and carried in flight always with the head pointing forward to reduce frictional drag (Terres 1980). Hovering is an important behavioral adaptation. Although an energetic cost is involved, dives from hovers are 50% more successful than those started from a glide (Grub 1977).

Ospreys nest along most of the Maine coast and at several locations in southern New England, often forming loose colonies. Telephone poles, trees, channel markers, duck blinds, chimneys, and man-made nesting platforms are all acceptable locations for their huge nests that may weigh up to 455 kg (1000 lb) (Abbott 1911, in Terres 1980). These birds are protected by law and although presently on the increase, their numbers in New England have reached precariously low levels during this century. The decline of the osprey is due to coastal development, human disturbance, and eggshell thinning and embryo mortality as a result of poisoning by DDT and other chlorinated hydrocarbons. Puleston (1975) reviewed the historical status of the species on Gardiner's Island in Long Island Sound. In 1932, there were 300 nests on the island, representing what was probably the world's greatest concentration of nesting ospreys. In the 1940's, the colony seemed to be in good health; the productivity of each nest averaged two fledglings. A decline began in 1948 so that by 1965 there were only 55 to 60 nests that were producing 0.07 young per nest. Since then and coinciding with a nationwide ban on many pesticides, fledging success has increased, and in 1974, a total of 26 young were produced from 34 nests. Puleston (1975) believes that the current modest increases in the New England osprey population will continue.

The bald eagle nests and winters in Maine. Coastal areas support 75% of the resident breeding and wintering populations and are used by spring and fall migrants (Famous et al. 1980). Most eagle nests are close to bays or estuaries where the birds can obtain their preferred diet of fish (tomcod, sculpin, alewives, blue-black herring, and American eels) (Famous et al. 1980). During the winter, eagles depend increasingly on birds as their major prey. The remains of 20 different species of seabirds have been recorded as eagle prey, of which black ducks and gulls constitute more than 50% (Famous et al. 1980). Like the ospreys, the terminal position of the eagle in the food chain has resulted in decreased breeding success due to toxic chemical poisoning. Studies of Maine bald eagle eggs from 1967 to 1979 indicated an average shell thickness 15% less than normal and no significant

reduction in the levels of DDE, PCBs, or mercury during this period. It is difficult to assess recent trends in bald eagle numbers in Maine, but the current levels of recruitment per nest remain below that necessary to sustain a stable population (Famous et al. 1980).

Several other raptors are included in Appendix III because they may consume shorebirds. Of these, the peregrine falcon preys most heavily on shorebirds and often follows migratory shorebird flocks (E.L. Mills; Dalhousie University, Halifax, Nova Scotia; April 1981; personal communication). In a study conducted on the west coast of the United States, Page and Whitacre (1975) found that raptors consume a large portion of wintering shorebirds. At the study site, a variety of hawks and owls removed 20.7% of the dunlins, 11.9% of the least sandpipers, and 13.5% of the sanderlings. New England tidal flats are migratory stopover areas for most shorebirds and such large removals do not occur. Most of the raptors studied on the west coast occur in New England also and occasionally consume shorebirds.

5.7 DEPENDENCE ON TIDAL FLATS

The major groups of coastal birds differ in their dependence on tidal flats. For the shorebirds that feed extensively on exposed flats and the wading birds that feed in shallow waters, tidal flats are essential sources of food. The migratory and winter habitat and feeding behavior among shorebirds and the feeding behavior of wading birds suggests a dependence relationship that has persisted on an evolutionary time-scale. Tidal flats differ in their importance as feeding sites, with those areas having dense populations of infaunal invertebrates being more attractive. Also, migration routes

differ among species of shorebirds and a relatively few coastal areas support large numbers of shorebirds (Morrison and Harrington 1979). The wading birds are more evenly distributed, especially in southern New England. Since many nest there, the ability to successfully fledge young is a function of how well tidal flats can provide energy for their metabolic demands.

The terns and particularly the gulls are the most persistent and common birds of New England tidal flats, but this habitat is only one of many used by this group. Deeper waters are suitable for hunting pelagic fishes and gulls feed as well in rocky intertidal areas and terrestrial refuse sites. Gulls make greater use of the exposed tidal flats than the fish-eating terns. This is true especially in winter when the terns migrate south and many fish leave the coastal area. Exposed flats become particularly important to wintering gulls that feed on sedentary invertebrates and organic materials left by the tides.

Although waterfowl and diving birds often forage over tidal flats at high tide, they are not restricted to these areas. Many species prefer rocky substrates and those that forage in or over soft substrates often do so in deeper water. Exceptions are the omnivores that do not dive, such as several species of dabbling ducks, geese, and the mute swan. For these species, foraging occurs in shallow water where they can reach benthic vegetation by "tipping up" without diving.

Raptors, other than the osprey and the eagle generally feed over terrestrial areas and, except for peregrines and merlins, only occasionally hunt shorebirds on tidal flats. Ospreys are especially dependent on the flats in the spring when pelagic schooling species of fish are rare.

CHAPTER 6

TIDAL FLATS: THEIR IMPORTANCE AND PERSISTENCE

6.1 INTRODUCTION

It has been recognized since the late 1950's that nearshore marine habitats, particularly estuaries and coastal embayments, are vitally important as nursery and spawning grounds for fishes and as habitats for shellfish. Tidal flats function in many of the same ways as deeper-water, coastal habitats in addition to providing resting and feeding sites for coastal birds. Because the coastal zone is heavily used for other land- and marine-based recreational and commercial purposes, tidal flats frequently are subjected to reversible and irreversible man-induced environmental impacts. Conflicting demands on the use of tidal flats necessitate legislative participation in the management of these areas and it is important to address questions such as: How valuable are tidal flats relative to other coastal habitats and how resistant or resilient are tidal flat organisms to environmental perturbation? In other words, can we afford to lose tidal flat habitats without experiencing unacceptable alterations in the productivity of marine biota?

6.2 RESPONSE OF TIDAL FLATS TO ENVIRONMENTAL PERTURBATIONS

The majority of man-induced impacts on tidal flats can be categorized as follows: (1) dredging and channelization to maintain navigable waterways and the construction and maintenance of water-dependent industries or businesses (e.g., marinas), (2) discharge of pollutants from waste disposal and industrial outfalls or non-point sources (e.g., sewage, chemicals, oil), (3) building of dams and jetties resulting in altered inorganic deposition, (4) spoil disposal for the creation of salt marshes, or landfill for residential and/or commercial purposes,

and (5) overexploitation of commercially important tidal flat shellfish.

The response of tidal flat organisms and their ability to recover from man's activities depends upon the type, magnitude, and frequency of the impact. Environmental impacts can be classified as those which are (1) destructive (e.g., dredging and spoil disposal) and result in changes in habitat quantity or (2) those that alter habitat quality (e.g., excessive organic pollution) and result in the degradation of the habitat.

The most easily detected effects upon tidal flats are those that lead to habitat destruction. Generally these impacts are incremental and vary widely. Dredging and spoil disposal, for instance, can result in dramatic changes in the physical, chemical, and biological nature of a tidal flat. When these perturbations are taken to extremes, the result is irreversible habitat loss or modification. Dredging eliminates feeding sites for shorebirds and spoil deposition destroys benthic invertebrates and feeding sites for vertebrates.

The response of tidal flat populations to severe habitat alteration has usually been studied by examining change in species composition and abundance following perturbation. Field studies may involve monitoring the patterns of repopulation by benthic organisms following spoil disposal (e.g., Rhoads et al. 1978) or after experimental elimination of the fauna in relatively small areas (e.g., Grassle and Grassle 1974; McCall 1977; Zajac 1981). Despite differences in the type of disturbance, environmental characteristics, and species composition considered, there are common trends in benthic community re-establishment and development. Early colonizers of a disturbed habitat are small species, predominately

polychaete worms. These species have similar life histories, such as prolific reproduction (often with several broods per year), early maturation, and high mortality rates (e.g., the classic pollution indicator species, the polychaete worms, Capitella capitata and Streblospio benedicti). These so-called "opportunists" are gradually replaced by slightly larger, taxonomically more diverse assemblages that typically exhibit slower growth rates, lower mortality rates, delayed reproduction, and reduced reproductive rates. Rhoads et al. (1978) have also noted changes in benthic infaunal life mode during the recolonization of disturbed subtidal soft-bottom habitats. Early colonists on spoil disposal sites tended to live in the upper layers of the sediment and to isolate themselves from the surrounding sediment through tube-building activities. As the sediments were increasingly affected by bioturbation, (e.g., by organisms burrowing and feeding), larger, subsurface burrowing animals invaded the spoil site.

Patterns of temporal change reported in the literature correlate recovery rates of disturbed shallow-water areas with habitat, type of disturbance, and the size and degree of isolation of the affected area. In one study, over 3 years were needed to establish a stable number of benthic species (Dean and Haskins 1964), while Sanders et al. (1980) found that complete recovery of a benthic community following a small oil spill had not occurred over a period of more than 5 years. On a smaller scale, recolonization may take weeks to months (Grassle and Grassle 1974; McCall 1977; Zajac 1981). Recruitment by benthic organisms into soft-bottoms can be accomplished by planktonic larval settlement as well as migration of adults from surrounding areas. This colonization is relatively rapid when compared to marine rocky substrate systems (Osman 1977) in which repopulation of disturbed sites is almost exclusively planktonic.

Life histories of infaunal species inhabiting New England tidal flats include a range of strategies. Many species display life histories characteristic of the earliest stages of recolonization. Temperate tidal flat environments are continually exposed to extremes of natural

physical and biological change (See Chapters 1 and 3). The organisms inhabiting flats, therefore, are well-adapted to withstand natural perturbations and persist by recovering rapidly. Other species have life histories more similar to those found in the later stages of recolonization. These organisms are more sensitive to disturbance and do not inhabit tidal flat areas that are continually exposed to environmental fluctuation. In Maine, dense populations of Mya arenaria are commonly found in areas that are not abraded by ice scouring (L. Watling; University of Maine, Walpole; February 1981; personal communication).

Fish and birds respond differently to habitat perturbations. They are more mobile and move from the impacted area. Fish and birds may not be affected by the loss of small portions of a tidal flat, but a bigger loss of that habitat would have an effect upon species abundance and composition. The remarkable recovery of many populations of New England coastal birds following near annihilation in the last century was almost certainly dependent upon the existence of undisturbed feeding and nesting sites. Inshore fish communities also appear resistant to small habitat losses or modifications (e.g., Nixon et al. 1978) but more pronounced alterations of these habitats would undoubtedly result in decreased abundance of certain fish species. Spinner (1969), for example, reported the decline in menhaden population abundance after loss of estuarine nursery areas in Connecticut.

The effects of more subtle habitat degradation can readily be seen on both a regional and historical basis in New England. The southern New England coastline is more heavily populated than northern New England and many tidal flats are exposed to residential, municipal, and commercial pollutant discharges. Increased pollution (e.g. from sewage, heavy metals, bacteria) has drastically reduced tidal flat shellfisheries in southern New England. In upper Narragansett Bay, Rhode Island, oyster populations were once so abundant that they were used to fatten pigs by early New England colonists. While the upper bay supported a viable oyster industry for many years (peaking in the early 1900's), no oysters have been

harvested there since 1957 primarily because of pollution and overfishing (Robadue and Lee 1980). The soft-shell clam fishery in upper Narragansett Bay is apparently experiencing a similar fate. In 1949, approximately 296,600 kg (650,000 lb) of clams were harvested while in 1979 commercial landings declined to about 3,650 kg (8000 lb). Abundant populations of clams have been reported in the upper bay but many areas have been closed to shellfishing because of organic pollution (Robadue and Lee 1980). In Connecticut, approximately 90% of tidal flats are closed to shellfishing because of pollution. Urbanization and its associated impacts on northern New England tidal flats have not yet been as severe. Although approximately 20% of Maine's tidal flats are closed annually to soft-shell clamming because of water pollution, over-exploitation of the shellfisheries may pose a greater threat to clam populations than habitat degradation (Doggett and Sykes 1980).

The effects of changing habitat quality extend to other groups of organisms using tidal flats. Haedrich and Hall (1976) suggested that the degree of seasonal change in New England fish communities (see Chapter 4) is a convenient indicator of estuarine environmental "health". Environments unaffected by pollution should exhibit high annual diversity of fish species and pronounced seasonal turnover in species composition. Where unfavorable habitat change has occurred, the most sensitive species will be eliminated and only those best-adapted to inhospitable conditions will remain. The net effect upon fish communities, therefore, is an overall reduction in the variety of species that utilize the habitat.

Other sources of pollution are also responsible for damage to New England tidal flats. One of the more severe and long-lasting impacts is from oil spills. In a well-documented study of a relatively small spill in Wild Harbor, Massachusetts, Sanders et al. (1980) observed an almost complete elimination of benthic organisms at several oiled sites. The effects of oil on the biota were still detectable at this site 5 years after the spill, in part because oil remained in the sediments and did not degrade or disperse.

Not all responses to environmental degradation are as dramatic as these. Sindermann (1979a), in reviewing pollution-associated diseases in fish, suggested that many effects are subtle (e.g., fin rot and fin erosion) and due to chronic exposure of fish to a polluted inshore environment. Since many fish inhabiting inshore waters are juveniles, they may be even more sensitive to these chronic effects than adults.

The New England region provides a well-documented historical case study of environmental degradation and destruction of tidal flats and their resident organisms. These changes in New England should provide an impetus for developing management criteria for tidal flat habitats. To begin such an undertaking, however, the tidal flat's importance to the coastal zone must be well-understood.

6.3 THE IMPORTANCE OF NEW ENGLAND TIDAL FLATS

In the past, legislation protecting marine coastal habitats was based on a series of suppositions regarding the role of these habitats in the overall coastal zone (e.g., Oviatt et al. 1977). The suppositions focused on a habitat's role as wildlife, fisheries, and storm-control areas in addition to its potential for exporting organic materials to stimulate or enhance production in adjacent marine systems. While much attention has been directed toward identifying the functioning of specific coastal habitats, it has been more difficult to assign a "value" to individual systems. Early efforts to evaluate habitats converted primary production values for salt marshes into average dollar value per calorie produced by the marsh (Gosselink et al. 1974). This approach remains subjective because many of the functions or roles of salt marshes lie outside recognized monetary systems and do not have an agreed monetary value (Shabman and Batie 1980). In addition, adequate evaluation of coastal zone habitats must include values associated with incremental changes (i.e., with time) in these habitats and not be restricted to the worth of an "average" salt marsh, tidal flat, or estuary. Alternative approaches to value assessment of coastal

zone habitats have been formulated (e.g., Kennedy 1980) although no generally accepted method presently exists.

Unlike salt marshes that are recognized for their potential for exporting the primary production of grasses to adjacent marine habitats, tidal flats function as sites for the conversion of plant production into animal biomass. The most tangible evidence of the value of New England tidal flats to human consumers is the shellfish and baitworm fisheries. All New England coastal states exploit tidal flat shellfish populations. The extent of these fisheries varies widely between states and harvestable catch is largely dependent upon habitat quality. In southern New England, urbanization of the coastal zone and associated pollution has resulted in the closure of many tidal flats to shellfishing. In Connecticut only a few hundred pounds of shellfish are harvested annually and virtually all of the common tidal flat shellfish (e.g., Mya arenaria and Mercenaria mercenaria) sold commercially are imported from outside the State. In northern New England, where coastal urbanization is not as extensive, tidal flat shellfish and baitworm fisheries are extremely important industries. In Maine soft-shell clam (Mya arenaria) and baitworm (Nereis virens and Glycera dibranchiata) fisheries rank third and fourth in economic value after the extensive lobster and (now diminished) shrimp fisheries. While soft-shell clams and baitworms are not restricted to tidal flat habitats, their abundance is greatest in these areas and destruction or degradation of these habitats would eliminate the fisheries. Other species of economically valuable invertebrates (e.g., crabs) are also found on New England tidal flats. Crabs do not depend entirely on flats, but use them as important feeding sites.

The value of tidal flats to coastal fish populations is more difficult to assess. Most fish frequenting flats are juveniles and are known to consume tidal flat food items (especially benthic invertebrates). Relatively little is known about the degree of dependence of juvenile fish on flats and about the contribution of these populations to commercial

catches. Probably demersal fishes (e.g., winter flounder) rely most heavily on tidal flats for feeding, but to what extent remains conjecture. Tyler (1971b) has suggested that the destruction of tidal flats in the Bay of Fundy would reduce the winter flounder populations. Shallow water coastal habitats provide juvenile fish a refuge from their predators in addition to serving as sheltered feeding areas.

Many species of shorebirds rely heavily (and some species exclusively) upon tidal flats for feeding and resting sites. Without productive benthic invertebrate populations on flats some bird species would probably suffer population declines. A recent study (Goss-Custard 1977) that has addressed the importance of tidal flats to shorebird populations, however, has failed to define the degree to which the birds are limited by tidal flat habitat availability. Other groups of birds (e.g., gulls, terns, waterfowl), while not as dependent on tidal flats for feeding sites, are commonly present and are known to consume benthic invertebrates.

One of the major difficulties in attempting to assign specific values to tidal flat habitats centers on the lack of information about the magnitude of their primary and secondary productivity and about how much of that production is channeled to higher trophic levels within the coastal food web. Examination of the sources and amounts of organic materials entering the flats from other systems, the rates at which these organics are utilized, and the amounts passed to different trophic levels requires detailed information about energy flow, life history characteristics of resident and transient organisms, as well as insight into abiotic and biotic processes affecting tidal flat populations. This lack of knowledge, of course, does not diminish the importance of tidal flats to the coastal zone. More information about ecological processes and interrelationships on tidal flats is required before planners, managers, and legislators will be able to develop a comprehensive and rational basis for the preservation, utilization, and management of tidal flats.

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Appendix I. Common infaunal invertebrates associated with New England tidal flats.

Taxonomic group	Species	Range ¹	Habitat ²	Living mode ³	Feeding mode ⁴
Crustacea					
Cumacea	<u>Oxyurostylis smithi</u>	C	Estuarine muddy sands	B	DF
	<u>Mancocuma stellifera</u>	C	Sands	B	DF
	<u>Almyracuma proximoculi</u>	V	Especially muddy sands	B	DF
	<u>Diastylis polita</u>	C	Sands	B	DF
Isopoda	<u>Edotea triloba</u>	C	Ubiquitous	B	DF
	<u>Cyathura polita</u>		Ubiquitous	B	DF/C
	<u>Chironotea coeca</u>	C	Primarily sands	B	DF/C
Amphipoda	<u>Gammarus mucronatus</u>	C	Estuarine muds	B	DF/G
	<u>Gammarus lawrencianus</u>	C	Sands, sandy muds	B	DF/G
	<u>Gammarus palustris</u>	C	Estuarine muds	B	DF/G
	<u>Gammarus oceanicus</u>	C	Estuarine muds	B	DF/G
	<u>Monoculodes edwardsi</u>	C	Sands	B	DF
	<u>Ampelisca macrocephala</u>	C	Sands	T-S	SF/DF(?)
	<u>Ampelisca abdita</u>	C	Fine sands and muds	T-S	SF/DF(?)
	<u>Ampelisca vadorum</u>	M	Coarse sands	T-S	SF/DF(?)
	<u>Unicola irrorata</u>	C	Sands	B	DF
	<u>Microdeutopus gryllotalpa</u>	C	Near eelgrass beds	T-S	DF
	<u>Microdeutopus anomalous</u>	V	Muds	T-S	DF
	<u>Leptocheirus pinguis</u>	C	Sands, sandy muds	T-S	DF
	<u>Leptocheirus plumulosus</u>	V	Estuarine muds	T-S	DF
	<u>Corophium insidiosum</u>	C	Sandy muds	T-S	DF/SF(?)
	<u>Corophium volutator</u>	B	Estuarine muds	T-S	DF/SF(?)
	<u>Corophium tuberculatum</u>	C	Sandy muds	T-S	DF/SF(?)
	<u>Corophium acutum</u>	V	Muds and sands	T-S	DF/SF(?)
	<u>Haustorium canadensis</u>	C	Common in sands	B	DF
	<u>Acanthohaustorius millisi</u>	C	Sands	B	DF
	<u>Pseudohaustorius caroliniensis</u>	V	Sands and muds	B	DF

Appendix I. (Continued).

Taxonomic group	Species	Range ¹	Habitat ²	Living mode ³	Feeding mode ⁴
Amphipoda (continued)	<u>Amphiporeia virginiana</u>	C	Estuarine sands	B	DF
	<u>Neohaustorius biarticulatus</u>	V	Sands	B	DF
	<u>Neohaustorius schmitzi</u>	V	Sands, especially beaches	B	DF
	<u>Protohaustorius deichmannae</u>	M	Fine sands	B	DF
	<u>Acanthohaustorius spinosus</u>	B	Sands	B	DF
	<u>Phoxocephalus holbolli</u>	C	Sands, sandy muds	B	DF
	<u>Trichophoxus epistomus</u>	C	Fine sands	B	DF
	<u>Psammonyx nobilis</u>	C	Sands	B	DF/S
	<u>Talorchestia megalophthalma</u>	C	Sands	B	DF
	<u>Talorchestia longicornis</u>	C	Fine sands	B	DF
	<u>Orchestia grillus</u>	C	Commonly under wrack	B	DF
	<u>Orchestia uhleri</u>	M	Commonly under wrack	B	DF
	<u>Melita nitida</u>	C	Estuarine muds		
	<u>Amphithoe valida</u>	C	Estuarine muds	T-S	G
<u>Amphithoe longimana</u>	V	Estuarine muds	T-S	G	
Tanaidacea	<u>Leptocheilia savignyi</u>	C	Muds, sandy muds	T-S	DF
Sipuncula	<u>Phascolopsis gouldii</u>	C	Primarily in sands	B	DF
Hemichordata	<u>Saccoglossus kowalewskyi</u>	M	Sands	U-B	DF
Nemertea	<u>Micrura leidyi</u>	C	Sands	B	C
	<u>Cerebratulus lacteus</u>	C	Sandy muds	B	C
	<u>Amphiporus ochraceus</u>	V	Sands and muds	B	C
	<u>Amphiporus griseus</u>	V	Sands and muds	B	C
	<u>Lineus</u> spp.	C	Muds and sands	B	DF
Bivalvia	<u>Mya arenaria</u>	C	Muddy sands, muds	S	SF
	<u>Macoma balthica</u>	C	Estuarine muds	S	DF
	<u>Mercenaria mercenaria</u>	V	Sands, sandy muds	S	SF

continued

Appendix I. (Continued).

Taxonomic group	Species	Range ¹	Habitat ²	Living mode ³	Feeding mode ⁴	
Bivalvia (continued)	<u>Gemma gemma</u>	C	Fine sands	S	SF	
	<u>Tellina agilis</u>	C	Sands	S	DF	
	<u>Arctica islandica</u>	B	Fine sands	S	SF	
	<u>Spisula solidissima</u>	C	Sands, mostly beaches	S	SF	
	<u>Lyonsia hyalina</u>	C	Fine sands, muddy sands	S	SF	
	<u>Solemya velum</u>	C	Fine sands	S	SF	
	<u>Laevicardium mortoni</u>	C	Fine sands, muddy sands	S	SF	
	<u>Montacuta elevata</u>	C	Commensal with <u>Clymenella torquata</u>	SS	SF	
	<u>Ensis directus</u>	C	Sands	S	SF	
	<u>Petricola photadiformis</u>	C	Common in peat	S	SF	
	<u>Myrella planulata</u>	C	Sands, muddy sands	S	SF	
	Holothuroidea	<u>Lyptosynapta tenuis</u>	C	Sands	B	DF
	Annelida					
		Capitellidae	<u>Capitella capitata</u>	Ubiquitous	B	DF
<u>Heteromastus filiformis</u>			Ubiquitous	B	DF	
<u>Mediomastus ambiseta</u>	Muds		B	DF		
Orbiniidae	<u>Scoloplos robustus</u>	C	Sands and muds	B	DF	
	<u>Scoloplos armiger</u>	B	Sands and muds	B	DF	
	<u>Scoloplos acutus</u>	C	Sands and muds	B	DF	
	<u>Scoloplos fragilis</u>	C	Sands and muds	B	DF	
	<u>Orbinia ornata</u>	C	Sands and muds	B	DF	
Nereidae	<u>Nereis virens</u>	C	Estuarine muds	B	0	
	<u>Nereis acuminata</u>	V	Sands and muds	B	0	
	<u>Nereis succinea</u>	C	Estuarine muds	B	0	
	<u>Nereis diversicolor</u>	B	Estuarine muds	B	0	
	<u>Nereis pelagica</u>	C	Ubiquitous	B	0	

continued

Appendix I. (Continued).

Taxonomic group	Species	Range ¹	Habitat ²	Living mode ³	Feeding mode ⁴
Chaetopteridae	<u>Spiochaetopterus oculatus</u>	V	Sands	T-S	SF/DF(?)
Dorvilleidae	<u>Protodorvillea gaspeensis</u>	C(?)	Muds and sands	B	0
	<u>Schistomeringos caecus</u>	V	Muds and sands	B	0
Eunicidae	<u>Marphysa sanguinea</u>	V	Muddy sands, mud	B	DF/0
Opheliidae	<u>Ophelina bicornis</u>	V	Sands	B	DF
Ctenodrilidae	<u>Ctenodrilus serrata</u>		Sands and sandy muds	B	DF
Polynoidae	<u>Harmothoe imbricata</u>	C	Muddy sands, muds	S	C/S
	<u>Lepidonotus squamatus</u>	C	Muddy sands, muds	S	C/S
Maldanidae	<u>Clymenella torquata</u>	C	Sands	T-SS	DF
Lumbrineridae	<u>Lumbrineris impatiens</u>	C	Sands and muds	B	DF/S
	<u>Lumbrineris tenuis</u>	C	Sands and muds	B	DF/S
	<u>Lumbrineris fragilis</u>	C	Muddy sands, muds	B	DF/S
	<u>Ninoe nigripes</u>	C	Sands and muds	B	DF/S
	<u>Eteone lactea</u>	C	Muddy sands	B	DF/0
Phyllodoceidae	<u>Eteone longa</u>	C	Muddy sands	B	DF/0
	<u>Eteone heteropoda</u>	C	Ubiquitous	B	DF/0
	<u>Phyllodoce mucosa</u>	C	Muddy sands	B	DF/0
	<u>Phyllodoce groenlandica</u>	C	Sands	B	DF/0
	<u>Phyllodoce arenae</u>	C	Sands	B	DF/0
	<u>Paranaitis speciosa</u>	C	Ubiquitous	B	DF/0
	<u>Eulalia viridis</u>	C	Sands and muds	B	DF/0
	<u>Eumida sanguinea</u>	C	Muds	B	DF/0

continued

Appendix I. (Continued).

Taxonomic group	Species	Range ¹	Habitat ²	Living mode ³	Feeding mode ⁴
Paraonidae	<u>Paraonis fulgens</u>	C	Sands	B	DF
	<u>Aricidea catherinae</u>	C	Sands and muds	B	DF
	<u>Aricidea quadrilobata</u>	B	Sands and muds	B	DF
Nephtyidae	<u>Nephtys picta</u>	C	Sands	B	C
	<u>Nephtys caeca</u>	C	Sands	B	C
	<u>Nephtys ciliata</u>	C	Muds and sands	B	C
	<u>Nephtys buccera</u>	C	Sands, muddy sands	B	C
Glyceridae	<u>Glycera dibranchiata</u>	C	Sands and muds	B	C/DF
	<u>Glycera capitata</u>	C	Sands and muds	B	C/DF
	<u>Glycera americana</u>	V	Sands and muds	B	C/DF
Hesionidae	<u>Microphthalamus szcelkowi</u>	C	Sands and muds	B	DF/G
	<u>Microphthalamus aberrans</u>	C	Sands	B	DF/G
	<u>Podarke obscura</u>	C	Muddy sands	B	DF/G
	<u>Gyptis vittata</u>	B	Shelly sands	B	DF
Pectinariidae	<u>Pectinaria gouldii</u>	V	Sandy muds	T-SS	DF
	<u>Pectinaria hyperborea</u>	B	Muddy sands	T-SS	DF
Sabellidae	<u>Sabella microphthalana</u>	V	Near <u>Zostera</u> beds	T-S	SF
	<u>Potamilla neglecta</u>	C	Near <u>Zostera</u> beds	T-S	SF
	<u>Fabricia sabella</u>	C	Near <u>Zostera</u> beds	T-S	SF
Arabellidae	<u>Drilonereis longa</u>	V	Sands and muds	B	DF
	<u>Drilonereis magna</u>	C	Ubiquitous	B	DF(?)
	<u>Arabella iricolor</u>	C	Mostly sands, muddy sands	B	DF(?)
Arenicolidae	<u>Arenicola marina</u>	C	Sandy muds, muds	U-B	DF

continued

Appendix I. (Continued).

Taxonomic group	Species	Range ¹	Habitat ²	Living mode ³	Feeding mode ⁴
Onuphidae	<u>Diopatra cuprea</u>	V	Sands and muds	T-S	C
Pilargiidae	<u>Sigambra tentaculata</u>	C	Shelly muds	B	0(?)
Syllidae	<u>Parapionosyllis longicirrata</u>	C	Muddy sands	B	0
	<u>Exogone hebes</u>	C	Sands, muddy sands	B	0
	<u>Exogone dispar</u>	C	Sands	B	0
	<u>Syllis cornuta</u>	C	Ubiquitous	B	0
	<u>Syllis gracilis</u>	C	Ubiquitous	B	0
	<u>Syllides longocirrata</u>	C	Primarily sands	B	0
	<u>Syllides verrilli</u>	B	Sands	B	0
	<u>Brania clavata</u>	C	Sands and muds	B	0
	<u>Brania wellfleetensis</u>	V	Muddy sands	B	0
	<u>Streptosyllis arenae</u>	V	Sands	B	0
	<u>Streptosyllis varians</u>	C	Sands	B	0
Cirratulidae	<u>Caulerliella</u> spp.		Sandy muds, muds	B	DF
	<u>Tharyx</u> spp.		Sands, muds with shell	B	DF
	<u>Chaetozone</u> spp.		Sands	B	DF
	<u>Cirriformia</u> spp.		Muds	B	DF
Magelonidae	<u>Magelona rosea</u>	V	Sands	B-S	DF
Ampharetidae	<u>Asabellides oculata</u>	M	Sandy mud, mud	T-S	DF
	<u>Melinna cristata</u>		Estuarine muds	T-S	DF
	<u>Ampharete arctica</u>	C	Muds	T-S	DF
	<u>Hobsonia florida</u>	M	Muds	T-S	DF
Spionidae	<u>Streblospio benedicti</u>	C	Ubiquitous	T-S	DF
	<u>Polydora ligni</u>	C	Ubiquitous	T-S	DF
	<u>Polydora caulleryi</u>	C	Muddy sands, muds	T-S	DF
	<u>Polydora aggregata</u>	ME	Muds between rocks	T-S	DF

continued

Appendix I. (Continued).

Taxonomic group	Species	Range ¹	Habitat ²	Living mode ³	Feeding mode ⁴
	<u>Polydora quadrilobata</u>	C	Sandy muds	T-S	DF
	<u>Polydora socialis</u>	C	Muds	T-S	DF
	<u>Scolecolepides viridis</u>	C	Estuarine muds	T-S	DF
	<u>Spio setosa</u>	C	Sands and muddy sands	T-S	DF
	<u>Scoletepis squamata</u>	C	Sands	T-S	DF
	<u>Spiophanes bombyx</u>	C	Sands	T-S	DF
	<u>Prionospio heterobranchia</u>	C	Sands, muddy sands	T-S	DF
	<u>Prionospio steenstrupi</u>	C	Muds	T-S	DF
	<u>Pygospio elegans</u>	C	Sands	T-S	DF
	<u>Dispio uncinata</u>	V	Sands	T-S	DF
	<u>Boccardia hamata</u>	V(?)	Muds	T-S	DF
	<u>Polycirrus eximius</u>	C	Muds	B-S	DF
	<u>Amphitrite ornata</u>	C	Muds	T-S	DF
	<u>Pista maculata</u>	C	Estuarine muds	T-S	DF
	<u>Nicolea zostricola</u>	C	Muds	T-S	DF
	<u>Enplobranchus sanguinea</u>	C	Muds	T-S	DF
	<u>Marionina spicula</u>	MA	Sands	B	DF
	<u>Marionina achaeta</u>	MA	Sands	B	DF
	<u>Marionina southerni</u>	MA	Sands	B	DF
	<u>Marionina preclitellochaeta</u>	MA	Sands	B	DF
	<u>Marionina subterranea</u>	MA	Sands	B	DF
	<u>Peloscolex benedeni</u>	C	Sands	B	DF
	<u>Peloscolex gabriella</u>	V	Sands and muds	B	DF
	<u>Phallosdrilus monospermathecus</u>	MA	Sands	B	DF
	<u>Lumbricillus lineatus</u>	B	Sands	B	DF
	<u>Paranais litoralis</u>	C	Sands	B	DF
Terebellidae					
	<u>Polycirrus eximius</u>	C	Muds	B-S	DF
	<u>Amphitrite ornata</u>	C	Muds	T-S	DF
	<u>Pista maculata</u>	C	Estuarine muds	T-S	DF
	<u>Nicolea zostricola</u>	C	Muds	T-S	DF
	<u>Enplobranchus sanguinea</u>	C	Muds	T-S	DF
Oligochaeta					
	<u>Marionina spicula</u>	MA	Sands	B	DF
	<u>Marionina achaeta</u>	MA	Sands	B	DF
	<u>Marionina southerni</u>	MA	Sands	B	DF
	<u>Marionina preclitellochaeta</u>	MA	Sands	B	DF
	<u>Marionina subterranea</u>	MA	Sands	B	DF
	<u>Peloscolex benedeni</u>	C	Sands	B	DF
	<u>Peloscolex gabriella</u>	V	Sands and muds	B	DF
	<u>Phallosdrilus monospermathecus</u>	MA	Sands	B	DF
	<u>Lumbricillus lineatus</u>	B	Sands	B	DF
	<u>Paranais litoralis</u>	C	Sands	B	DF

continued

Appendix I. (Concluded).

Taxonomic group	Species	Range ¹	Habitat ²	Living mode ³	Feeding mode ⁴
	<u>Enchytraeus capitatus</u>	MA	Sands	B	DF
	<u>Monopylephorus irroratus</u>	MA	Sands	B	DF

¹Range: C = found throughout New England; B = found primarily north of Cape Cod, Massachusetts; V = found primarily south of Cape Cod; M = found primarily south of central Maine; ME = Maine only; MA = Massachusetts only.

²Habitat: sediment type where species are most commonly found.

³Living mode: B = burrower; S = feeding on or slightly above sediment surface; T = tube-dweller; SS = subsurface feeder; U-B = U-shaped burrow.

⁴Feeding mode: DF = deposit feeder; SF = suspension feeder; C = carnivore; G = grazer; O = omnivore.

Appendix II. Coastal fishes of New England.

Name common/scientific	Distribution	Spawning period	Food preferences	Movements	References
Class Agnatha					
Order Petromyzontiformes					
Petromyzontidae - Lampreys					
Sea Lamprey <u>Petromyzon marinus</u>	West coast of Greenland to Florida.	Spring	Parasitic (adults) on mack- arel, anadromous herrings, cod, haddock, pollock, salmon, basking sharks, swordfish, hake, sturgeon, eels. Amphicoete larvae are filter feeders.	Anadromous spawner. Ascends rivers in spring; probably in shallow depths for remainder of year.	Bigelow and Schroeder (1953); Thomson et al. (1971).
Class Chondrichthyes					
Order Squaliformes					
Carcharhinidae - Requiem Sharks					
Smooth Dogfish <u>Mustelus canis</u>	Coastal waters from Uruguay and Brazil to Cape Cod and Passamaquoddy Bay as a stray.	Gestation about ten months; off southern New England young May to mid-July.	Chiefly large crustaceans (lobsters, crabs) and small fishes (menhaden, sculpins, tautog); also squid and razor clams.	Inshore in spring-summer; offshore in fall-winter.	Bigelow and Schroeder (1953); Thomson et al. (1971).
Squalidae - Dogfish Sharks					
Spiny Dogfish <u>Squalus acanthias</u>	Temperate and subarctic belt of North Atlantic.	Young born in winter November- January; second year.	Chiefly mackerel, herring, cod, haddock, squid regularly. Known to take worms, shrimps, crabs, and ctenophores.	Seasonal coastally. Inshore in southern New England in March-April and Gulf of Maine in May; offshore in southern New England in November and Gulf of Maine in October.	Bigelow and Schroeder (1953); Jensen (1965); Thomson et al. (1971).

continued

Appendix II. Continued.

Name common/scientific	Distribution	Spawning period	Food preferences	Movements	References
Order Rajiformes Rajidae - Skates					
Little Skate <u>Raja erinacea</u>	Southern side of Gulf of St. Lawrence and northern Nova Scotia to Virginia.	Eggs apparently laid year-round but most productive November-January and June-July.	Benthic invertebrates; chiefly crabs, shrimps, worms, amphipods, ascideans, bivalves, molluscs, squid, small fish including lance, herring, cunners, silversides, tomcod, and silver hake.	Prefers sandy or gravelly bottoms; wide temperature tolerance. Inshore in summer; offshore in winter.	Bigelow and Schroeder (1953); Richards et al. (1963); Leim and Scott (1966); Thomson et al. (1971).
Barndoor Skate <u>Raja laevis</u>	Banks of Newfoundland, Gulf of St. Lawrence, and outer coast of Nova Scotia and Nova Scotia banks to North Carolina.	Lay eggs in winter; hatch in spring.	Bivalves, worms, various crustaceans, (rock crabs, lobsters, shrimps), squid, and fish (dogfish, alewives, herring, menhaden, butterfish, sand lance, cunners, tautog, sculpins, silver hake, hake, flatfish, and probably cod, haddock).	Inshore in fall; offshore when water temperatures rise.	Bigelow and Schroeder (1953); Thomson et al. (1971).
Winter Skate <u>Raja ocellata</u>	Southern side of Gulf of St. Lawrence and southern part of Newfoundland banks to northern North Carolina.	Eggs collected off south-eastern New England April, May, August, November, February.	Rock crabs and squid favorite prey. Also take worms, amphipods, shrimp, razor clams, and any available small fish including skates, eels, herring, alewives, bluebacks, menhaden, smelt, lance, chub mackerel, butterfish, cunners, sculpins, silver hake, tomcod.	Found confined to sandy or gravelly bottoms in shoal water < 80 m in temperatures 18-19°C in southern New England.	Bigelow and Schroeder (1953); Thomson et al. (1971).

continued

Appendix II. Continued.

Name common/scientific	Distribution	Spawning period	Food preferences	Movements	References
Class Osteichthyes					
Order Acipenseriformes					
Acipenseridae - Sturgeons					
Atlantic Sturgeon <u>Acipenser oxyrinchus</u>	St. Lawrence River to Gulf of Mexico.	Anadromous; spawn in June-July in southern New England.	Worms and small molluscs, small fish, particularly sand lance. Juveniles feed mostly on amphipods and isopods. Adults do not feed while ascending rivers to spawn.	Anadromous--movements at sea not known.	Bigelow and Schroeder (1953); Leim and Scott (1966).
Order Anguilliformes					
Anguillidae - Eels					
American Eel <u>Anguilla rostrata</u>	West Greenland, eastern Newfoundland, Strait of Belle Isle, northern side of Gulf of St. Lawrence to Gulf of Mexico, Panama, West Indies.	Catadromous spawner; mid-winter spawning in Sargasso Sea.	Nocturnal feeder; omnivorous. Feeds on just about any animal matter; shrimps, crabs, lobsters, fish, crustaceans, bivalves, and worms.	Descend rivers and estuaries in fall and migrate to Sargasso Sea to spawn. Larvae migrate back to coastal waters.	Bigelow and Schroeder (1953); Leim and Scott (1966); Thomson et al. (1971); Wenner and Musick (1975).
Congridae - Conger Eels					
Conger Eel <u>Conger oceanicus</u>	Adults to north of Cape Cod; larval stages to off Nova Scotia. Southern limit may be to South American coast.	Spawn at sea in summer.	Chiefly on fish but also shrimp and molluscs.	Coastal individuals move offshore during summer spawning.	Olsen and Merriman (1946); Bigelow and Schroeder (1953); Leim and Scott (1966); Thomson et al. (1971).

continued

Appendix II. Continued.

Name common/scientific	Distribution	Spawning period	Food preferences	Movements	References
Order Clupeiformes Clupeidae - Herrings					
Blueback <u>Alosa aestivalis</u>	Southern New England and occasionally north to Cape Breton, Nova Scotia to St. John's River, Florida.	Ascend rivers to spawn in spring at 21-34°C mid-May to June; in southern New England July-September at Woods Hole.	Planktivore; chiefly on copepods, pelagic shrimp, small fish, lance.	Anadromous, schools at sea; movements not known.	Bigelow and Schroeder (1953); Loesch and Lund (1977).
Hickory Shad <u>Alosa mediocris</u>	Bay of Fundy to Florida.	Probably anadromous.	Lance, anchovies, cunners, herring, scup, silversides, squid, fish eggs, and small crabs.	More abundant in southern part of range; enters southern New England waters in summer.	Bigelow and Schroeder (1953); Thomson et al. (1971).
Alewife <u>Alosa pseudoharengus</u>	Gulf of St. Lawrence and northern Nova Scotia to North Carolina.	Ascend rivers to spawn in early spring at 13-16°C; April-May in southern New England.	Planktivore, copepods, amphipods, appendicularians, and small fish--herrings, eels, lance, cunners, and fish eggs.	Anadromous; ascend rivers; spring, adults return to ocean. Oceanic movements not known.	Bigelow and Schroeder (1953); Kissitt (1969).

continued

Appendix II. Continued.

Name common/scientific	Distribution	Spawning period	Food preferences	Movements	References
Shad <u>Alosa sapidissima</u>	Southeastern coast of Newfoundland and St. Lawrence to St. John's River, Florida.	Anadromous; initial and peak entry of shad to rivers 3-15°C in spring.	Planktivore; copepods, euphausiids, mysids, rarely small fish.	Oceanic migration. Prespawning adults enter coastal waters of Mid-Atlantic Bight from latitude 36-40°N + 90° north of south to natal rivers. In salt water shad caught most frequently 7-13°C. In summer all shad caught north of 40°N in two primary areas-- Gulf of Maine and south of Nantucket shoals. Leave Gulf of Maine by late autumn; caught between latitude 39° and 41°N in winter.	Bigelow and Schroeder (1953); Neves and Depres (1979).
Menhaden <u>Brevoortia tyrannus</u>	Nova Scotia to eastern Florida; northern Florida to Gulf of Maine.	Spawning probably occurs at sea June-August off southern New England and September-October.	Planktivore, small prey, diatoms, phytoplankton, small crustaceans.	Single population over-winters offshore of southeastern United States; moves northward in spring followed by southward fall migration; oldest and largest fish in northern areas, smallest and youngest farther south.	Bigelow and Schroeder (1953); Thomson et al. (1971); Nicholson (1978).
Atlantic Herring <u>Clupea harengus</u>	Northern Labrador and west coast of Greenland to Cape Cod and Block Island. Occasionally to Cape Hatteras in winter.	Late August-January.	Plankton feeder when first hatched; larval snails, crustaceans, diatoms, and peridiniums. Fish to 12 mm feed on copepods, > 12 mm feed on larger copepods, amphipods, euphausiids, shrimp and decapod larvae; small lance, silversides, capelin, herrings.	Extensive seasonal movements; late summer and early autumn spawning migration. Rapid post-spawning migration to warmer southern waters for overwintering in spring; early summer feeding migration.	Bigelow and Schroeder (1953); Leim and Scott (1966); Sindermann (1979b).

continued

Appendix II. Continued.

Name common/scientific	Distribution	Spawning period	Food preferences	Movements	References
Engraulidae - Anchovies					
Bay Anchovy <u>Anchoa mitchilli</u>	Maine to Texas chiefly west and south of Cape Cod.	Late spring to end of summer.	Chiefly mysids plus copepods and gastropods.	Schooling fish found mostly along sandy shores and mouths of rivers, muddy coves. Probably a year-round resident in southern New England with onshore and offshore movement.	Bigelow and Schroeder (1953); Thomson et al. (1971).
Order Salmoniformes Salmonidae - Trouts					
Atlantic Salmon <u>Salmo salar</u>	Formerly from northeastern Labrador to Housatonic River and possibly Hudson River.	Spawn in October-November; eggs hatch in spring.	Young feed on insects and insect larvae; adults do not feed in freshwater. During sea run, small fish, crustaceans, euphausiids, and pelagic amphipods.	Young in freshwater 2 to 3 years. Adults return to freshwater April-October to spawn after sea runs from 1 to 2 years. Adults that survive either return immediately to the sea or remain in freshwater until spring.	Bigelow and Schroeder (1953); Leim and Scott (1966); Thomson et al. (1971).
Brown Trout <u>Salmo trutta</u>	Introduced into streams from Newfoundland to New Jersey.	Spawn in fall.	Nocturnal feeder; invertebrates and fish.	Some populations in Nova Scotia are definitely anadromous. Sea run populations have also been established on the Avalon Peninsula, Newfoundland.	Thomson et al. (1971); Leim and Scott (1966).

continued

Appendix II. Continued.

Name common/scientific	Distribution	Spawning period	Food preferences	Movements	References
Brook Trout <u>Salvelinus fontinalis</u>	Coast of Labrador, west to Minnesota and south to Georgia along Allegheny Mountains.	Spawn in freshwater in summer.	Shrimps, gammaridean amphipods, small crustaceans, and fish.	On Cape Cod descend rivers to saltwater in November immediately following spawning to overwinter. Ascend rivers in April and back in freshwater by mid-May.	Bigelow and Schroeder (1953).
Osmeridae - Smelts					
Capelin <u>Mallotus villosus</u>	Boreal-Arctic seas, south to the coast of Maine.	June-August (6-10°C); spawn at night over sand and fine gravel.	Small crustaceans, particularly copepods, euphausiids, decapods, shrimp, and their larvae as well.	Pelagic schooling species moving inshore to spawn.	Bigelow and Schroeder (1953); Leim and Scott (1966); Janguard (1974)
Rainbow smelt <u>Osmerus mordax</u>	Eastern Labrador, Strait of Belle Isle and the Gulf of St. Lawrence to New Jersey.	Anadromous; spawns February to June.	Small crustaceans such as decapods, mysids, and gammaridean amphipods; also worms and small fish.	Adults gather in harbors and brackish estuaries in autumn; movements influenced by tidal cycles. Overwinter in these areas then move into fresh- or more brackish water in spring to spawn. Adults return to saltwater after spawning and remain in estuary or in the sea closeby.	Bigelow and Schroeder (1953); Mckenzie (1964); Leim and Scott (1966); Thomson et al. (1971).

continued

Appendix II. Continued.

Name common/scientific	Distribution	Spawning period	Food preferences	Movements	References
Order Myctophiformes Synodontidae - Lizardfish					
Inshore Lizardfish <u>Synodus foetens</u>	Massachusetts and Bermuda, through Caribbean to Brazil.	Spring spawner.	Piscivorous.	Regularly occurring inshore and in bays. Only lizardfish to enter brackish water. Summer migrant to southern New England.	Pearcy and Richards (1962); Hoese and Moore (1977).
Order Batrachoidiformes Batrachoididae - Toadfish					
Oyster Toadfish <u>Opsanus tau</u>	Cape Cod to Cuba.	Summer spawner.	Omnivorous; worms, amphipods, shrimps, crabs, molluscs, ascidians, squid, any small fish.	Shoal water, year-round resident. Sandy, muddy bottoms, eel grass beds, burrows under stones.	Bigelow and Schroeder (1953); Thomson et al. (1971).
Order Lophiiformes Lophiidae - Goosefishes					
Goosefish <u>Lophius americanus</u>	Southern and eastern Grand Banks of Newfoundland; north side of Gulf of St. Lawrence to North Carolina.	Spring, summer, and early fall.	Piscivorous; any fish available as well as various seabirds; invertebrates; crustaceans, squids, worms, molluscs, starfish, sand dollars, even eelgrass.	Bottomfish, on all bottom types. Estuarine to upper part of continental slope.	Bigelow and Schroeder (1953); Leim and Scott (1966); Thomson et al. (1971).

continued

Appendix II. Continued.

Name common/scientific	Distribution	Spawning period	Food preferences	Movements	References
Order Gadiformes Gadidae - Codfishes					
Fourbeard Rockling <u>Enchelyopus cimbrius</u>	West Greenland and northwest Gulf of St. Lawrence and northeastern Newfoundland to Narragansett Bay and Long Island Sound coastally to Gulf of Mexico in deeper water.	April to July in Gulf of Maine. Peak May and June; April to possibly November in Mid-Atlantic Bight.	Shrimps, isopods, amphipods, and other small crustaceans; worms and fish fry.	Bottom fish, working inshore and into shoal water in autumn. Moves offshore and deeper in spring.	Bigelow and Schroeder (1953); Leim and Scott (1966); Thomson et al. (1971); Cohen and Russo (1979); Colton et al. (1979); Langton and Bowman (1980).
Atlantic Cod <u>Gadus morhua</u>	West Greenland, Davis Strait, Resolition Island, and Hudson Strait south to near Cape Hatteras.	December to April.	Larval, post-larval--copepods, and other small crustacea; Juveniles--same as post-larval as well as amphipods, barnacle larvae, small crustaceans, worms; Large juveniles and adults--larger invertebrates: molluscs, crabs, lobsters, shrimps, echinoderms, tunicates, worms, squid; algae, small fish.	Some individuals stationary, others migrate extensively. Southern New England populations move west in winter and turn eastward and north in May. Northern populations exhibit an inshore movement in summer and offshore movement in winter.	Bigelow and Schroeder (1953); Leim and Scott (1966); Colton et al. (1979); Langton and Bowman (1980).

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Appendix II. Continued.

Name common/scientific	Distribution	Spawning period	Food preferences	Movements	References
Silver Hake <u>Merluccius bilinearis</u>	Newfoundland banks to South Carolina.	May to October-- Gulf of Maine; June to December --Mid-Atlantic Bight.	Voracious; prefer fish--herring, mackerel, menhaden, alewives, silversides. Also crustaceans, molluscs, and worms.	Year-round resident in Long Island Sound. In northern part of range, movements offshore in winter to either deeper water or to the south.	Bigelow and Schroeder (1953); Leim and Scott (1966); Thomson et al. (1971); Colton et al. (1979); Langton and Bowman (1980).
Atlantic Tomcod <u>Microgadus tomcod</u>	Gulf of St. Lawrence and northern Newfoundland to Virginia.	Spawn in shoal waters of estuaries in salt- or brackish water November-February; peak in January.	Small crustaceans, chiefly shrimps and amphipods. Also worms, molluscs, and fish fry.	Strictly inshore fish. Frequent at mouths of streams and estuaries. In Gulf of Maine--some stay in brackish water and move into freshwater in winter. South of Cape Cod--move out from shore to slightly deeper water in spring. Come into estuaries in autumn and winter.	Bigelow and Schroeder (1953); Leim and Scott (1966); Thomson et al. (1971).
Pollock <u>Pollachius virens</u>	Southeastern part of Gulf of St. Lawrence and northeastern Nova Scotia to New Jersey.	October-February in Gulf of Maine.	Small fish, pelagic crustaceans, mostly euphausiids, molluscs.	Bottom to surface according to food supply, often schooling. Young observed to be loosely segregated by size along the coast (size increasing to offshore). Also nocturnal, shift inshore to feed. ¹	Bigelow and Schroeder (1953); Leim and Scott (1966); Thomson et al. (1971); Colton et al. (1979); Langton and Bowman (1980).

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Appendix II. Continued.

Name common/scientific	Distribution	Spawning period	Food preferences	Movements	References
Red Hake <u>Urophycis chuss</u>	Coastal region from southern Labrador, Gulf of St. Lawrence and southern Grand Banks to North Carolina.	May-September in Gulf of Maine; peak June and July.	Shrimps, amphipods, other small crustaceans, squid, gadids, and other small fish, echinoderms, molluscs, worms.	Fry in very shallow water.	Bigelow and Schroeder (1953); Leim and Scott (1966); Thomson et al. (1971); Colton et al. (1979); Langton and Bowman (1980).
Spotted Hake <u>Urophycis regia</u>	Southern New England and New York to Cape Hatteras.	August-April; peak in October.	Crustacea, fish, molluscs, worms.	Adults move inshore in spring; offshore probably in fall.	Bigelow and Schroeder (1953); Leim and Scott (1966); Thomson et al. (1971); Colton et al. (1979); Langton and Bowman (1980).
White Hake <u>Urophycis tenuis</u>	Gulf of St. Lawrence and southern part of Grand Bank to North Carolina.	October-April in Mid-Atlantic Bight; peak December-February.	Small fish, crustaceans, molluscs, worms.	Probably same as red hake as both species receive similar treatment by many authors.	Bigelow and Schroeder (1953); Leim and Scott (1966); Colton et al. (1979); Langton and Bowman (1980).

continued

Appendix II. Continued.

Name common/scientific	Distribution	Spawning period	Food preferences	Movements	References
Zoarcidae - Eelpouts					
Ocean Pout <u>Macrozoarces americanus</u>	Strait of Belle Isle, Gulf of St. Lawrence, and southeastern Newfoundland; south to Delaware; common from southern Gulf of St. Lawrence to New Jersey.	September and October.	Echinoderms; sea urchins, sand dollars, ophiurids, crustaceans, amphipods, molluscs, worms, tunicates, small fish.	Adults may congregate through summer; autumn and early winter on rocky bottoms where eggs are deposited and guarded. They disperse again in winter to smoother ground where food is more abundant. Also autumn shift offshore to deeper water and spring movement to coastal regions.	Bigelow and Schroeder (1953); Leim and Scott (1966); Colton et al. (1979); Langton and Bowman (1980).
Order Atheriniformes Scomberesocidae					
Atlantic Saury <u>Scomberesox saurus</u>	Temperate parts of Atlantic north to southern Newfoundland and southern Nova Scotia; south to South Carolina, West Indies.	Fry caught between 11-40°N.	Primarily small pelagic crustaceans and on small fish.	Oceanic fish; only seen inshore June to October or November.	Bigelow and Schroeder (1953); Leim and Scott (1966).
Cyprinodontidae - Killifishes					
Sheepshead Minnow <u>Cyprinodon variegatus</u>	Cape Cod to Mexico.	April-September in shallow waters.	Omnivorous and aggressive feeder; known to be cleaning symbiont with <u>F. majalis</u> .	Resident species; confined to shallow waters in bays, inlets, and salt marshes often in brackish water.	Bigelow and Schroeder (1953); Thomson et al. (1971).

continued

Appendix II. Continued.

Name common/scientific	Distribution	Spawning period	Food preferences	Movements	References
Mummichog <u>Fundulus heteroclitus</u>	Gulf of St. Lawrence to Texas. Restricted to estuaries, marshes, embayments.	Spawn in April-August; courtship and spawning ritual.	Omnivorous, including detrital material, eelgrass, diatoms, forams, shrimps, small crustaceans, molluscs (particularly <u>Mya arenaria</u>), fish fry.	Resident coastal/marsh species; localized movements only. Resistant to low oxygen levels in autumn; probably move to water of reduced salinity to overwinter.	Bigelow and Schroeder (1953); Leim and Scott (1966); Thomson et al. (1971); Fritz and Lotrich (1975); Kelso (1979).
Striped Killifish <u>Fundulus majalis</u>	Southern Gulf of Maine to Florida.	Spawn late spring to late summer west and south of Cape Cod.	Small animals; molluscs, crustaceans, fish, insects and insect larvae, vegetable matter.	Resident coastal/marsh species; localized movements. Closer to saltwater in estuaries than <u>F. heteroclitus</u> .	Bigelow and Schroeder (1953); Thomson et al. (1971).
Rainwater Killifish <u>Lucania parva</u>	Massachusetts to Florida occurs in vegetated areas and algal communities.	Late spring-summer.	Small prey such as crustaceans; known to be cleaning symbiont to <u>C. variegatus</u> .		Bigelow and Schroeder (1953); Thomson et al. (1971); Hoese and Moore (1977).
Atherinidae - Silversides					
Atlantic Silverside <u>Menidia menidia</u>	Common on southern side of Gulf of St. Lawrence and outer Nova Scotia coast to Massachusetts Bay; very abundant south to Chesapeake Bay.	May-July in southern New England.	Omnivorous; copepods, mysids, shrimps, amphipods, cladocerans, fish eggs, squid, worms, molluscan larvae, insects, algae, diatoms.	Schooling fish; prefers sand and gravel shores into eelgrass, <u>Zostera</u> , and cordgrass, <u>Spartina</u> ; ventures into brackish waters. Resident with no known offshore-onshore migration.	Bigelow and Schroeder (1953); Leim and Scott (1966); Thomson et al. (1971).

continued

Appendix II. Continued.

Name common/scientific	Distribution	Spawning period	Food preferences	Movements	References
Inland Silverside <u>Menidia beryllina</u>	Cape Cod to South Carolina.	Spring and late summer in Long Island Sound.	Small crustaceans, molluscs, worms, and insects.	Probably more estuarine than <u>M. menidia</u> .	Bigelow and Schroeder (1953); Thomson et al. (1971).
Order Gasterosteiformes Gasterosteidae - Sticklebacks					
Fourspined Stickleback <u>Apeltes quadracus</u>	Southern side of Gulf of St. Lawrence and Nova Scotia to Virginia.	May-July at Woods Hole later in Gulf of Maine; nest builder to protect eggs.	Small crustaceans, primarily copepods. ²	Strictly an inshore resident, primarily in salt- and brackish water but occasionally into freshwater.	Bigelow and Schroeder (1953); Leim and Scott (1966); Thomson et al. (1971).
Threespined Stickleback <u>Gasterosteus aculeatus</u>	Circumpolar in northwest Atlantic from Hudson Bay and Baffin Island to Chesapeake Bay.	Spring in freshwater, brackish water in southern New England.	Small invertebrates, fish eggs, and fish fry.	Similar to <u>Apeltes</u> <u>quadracus</u> .	Bigelow and Schroeder (1953); Leim and Scott (1966); Thomson et al. (1971).
Blackspotted Stickleback <u>Gasterosteus wheatlandi</u>	Newfoundland to New York, less common south of Massachusetts.	Probably similar to <u>G. aculeatus</u> .	Probably similar to other sticklebacks.	Probably similar to other sticklebacks.	Bigelow and Schroeder (1953); Leim and Scott (1966); Thomson et al. (1971).

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Appendix II. Continued.

Name common/scientific	Distribution	Spawning period	Food preferences	Movements	References
<u>Ninespined Stickleback</u> <u>Pungitius pungitius</u>	Arctic seas to New York along North American coast Gulf of St. Lawrence to New Jersey.	Fresh- or brackish water in spring; guards eggs and fry.	Probably similar to other sticklebacks.	Strictly a shore fish.	Bigelow and Schroeder (1953); Leim and Scott (1966); Thomson et al. (1971).
Syngnathidae - Pipefishes					
<u>Northern Pipefish</u> <u>Syngnathus fuscus</u>	Southern side of Gulf of St. Lawrence and outer Nova Scotia at Halifax to South Carolina.	March-August in Mid-Atlantic Bight; eggs brooded in pouch.	Minute crustaceans, fish eggs and fry.	Strictly a coastal species; found in marshes, harbors, river mouths, and into brackish waters, prefers vegetative habitat; resident non-migrating.	Bigelow and Schroeder (1953); Leim and Scott (1966); Thomson et al. (1971).
Order Perciformes					
Percichthyidae - Temperate Basses					
<u>Striped Bass</u> <u>Morone saxatilis</u>	St. Lawrence River, Canada, as far west as Montreal to the St. John's River in northern Florida and along the Gulf of Mexico tributaries in western Florida, Alabama, Mississippi, and Louisiana.	Anadromous; spawn in brackish water May-June.	Voracious feeder on fish and invertebrates, e.g. alewife, anchovy, croakers, channel bass, eels, flounder, herring, menhaden, mummichog, mullet, rock eels, lance, sculpins, shad, silver hake, silversides, smelt, tomcod, weakfish, white perch, lobsters, crabs, shrimps, isopods, worms, soft clams, mussels.	Inshore fish, not usually found out beyond 6-8 km offshore; usually run up into river mouths and estuaries. Overwinter off New Jersey and Chesapeake Bay. In early spring move northeast perhaps as far as southern Canada; reverse migration occurs in fall. Small population may overwinter in Long Island Sound.	Bigelow and Schroeder (1953); Thomson et al. (1971); Setzler et al. (1980).

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Appendix II. Continued.

Name common/scientific	Distribution	Spawning period	Food preferences	Movements	References
White Perch <u>Morone americana</u>	Gulf of St. Lawrence.	April-June in New England; move into fresh- or brackish water to spawn.	Fish eggs, small fish fry, squid, shrimp, crabs, various other invertebrates.	Localized movements; restricted in its seaward range. Found in brackish bays, estuaries, river mouths. Move to slightly deeper waters to overwinter.	Bigelow and Schroeder (1953); Thomson et al. (1971).
Serranidae - Sea Basses					
Black Sea Bass <u>Centropristis striata</u>	Cape Cod to northern Florida, occasionally to Maine.	May-June.	Crabs, lobster, shrimp, various molluscs, fish fry; sometimes squid.	Strictly saltwater. Depths of few feet to moderately deep water. Prefer hard sandy bottoms inshore. Move inshore off New Jersey, Long Island Sound, and southern New England during mid-May and offshore in late October to early November (7-8°C). Preferred offshore movements may combine with southward migration off Virginia and North Carolina.	Bigelow and Schroeder (1953); Thomson et al. (1971); Briggs (1978).

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Appendix II. Continued.

Name common/scientific	Distribution	Spawning period	Food preferences	Movements	References
Pomatomidae - Bluefishes					
Bluefish <u>Pomatomus saltatrix</u>	Widely distributed in warmer seas to Cape Cod and occasionally to Nova Scotia.	Mid-May to mid-September peak July and August in Mid-Atlantic Bight; probably two separate spawning populations along east coast of United States.	Piscivorous; chiefly mackerel, menhaden, alewives, scup, weakfish, hake, butterfish, cunners, other small fish of all kinds. "Snappers" (15-20 cm) chiefly feed on copepods, crustaceans, molluscan larvae, fish fry.	Schooling species. Warm seasonal migration along coast; not found in numbers in water below 14-16°C. Adult fish enter bays and harbors along southern New England in late October to move offshore. Juveniles probably move southward along coast following warm water mass.	Bigelow and Schroeder (1953); Lund and Maltezos (1970); Thomson et al. (1971); Kendall and Walford (1979).
Sparidae - Porgies					
Scup <u>Stenotomus chrysops</u>	Cape Cod to North Carolina; occasionally in coastal Gulf of Maine.	May-August; peak in southern New England.	Bottom feeder, chiefly feeds on crustaceans (amphipods and copepods), worms, hydroids, sand dollars, squid, small fish fry, crustacean and molluscan larvae, appendicularians, and various other benthic invertebrates.	Migrate inshore in early May and withdraw from coastal waters in late October. A coastal fish found in bays and harbors, often schooling. Fish moving offshore appear to follow 70°C isotherms.	Bigelow and Schroeder (1953); Richards et al. (1963); Thomson et al. (1971).

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Appendix II. Continued.

Name common/scientific	Distribution	Spawning period	Food preferences	Movements	References
Sciaenidae - Drums					
Weakfish <u>Cynoscion regalis</u>	Massachusetts Bay to east coast of Florida.	May-October; peak in mid-May to mid-June. Spawn in larger estuaries or close to their mouths at night.	Feeds chiefly on crustaceans, molluscs, worms, and small fish (e.g., menhaden, butterfish, herring, scup, anchovies, silversides, mummichogs). Precise diet varies with locality and age.	Schooling species, few to thousands. Close inshore in summer found in shallow waters, open sandy shores and larger bays and estuaries. Moves north in spring and summer, south in fall and winter. Fish less than four years move south along coast. Fish more than four years move south and offshore to Cape Hatteras then inshore and north in spring.	Bigelow and Schroeder (1953); Leim and Scott (1966); Thomson et al. (1971); Merriner (1975); Wilk (1976).
Spot <u>Leiostomus xanthurus</u>	Massachusetts to Texas.	Late fall, early winter in Mid-Atlantic Bight; probably spawn at sea.	Small invertebrates and young fish.	Present in coastal waters. Often enters brackish water and freshwater. Mature fish move offshore to spawn.	Bigelow and Schroeder (1953); Thomson et al. (1971).
Northern Kingfish <u>Menticirrhus saxatilis</u>	Cape Cod to Florida.	June to August.	Various shrimps and crabs, other crustaceans, small molluscs, worms, small fish.	Coastal species, sometimes moving in schools. Inshore May to October.	Bigelow and Schroeder (1953); Thomson et al. (1971).

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Appendix II. Continued.

Name common/scientific	Distribution	Spawning period	Food preferences	Movements	References
Labridae - Wrasses					
Tautog <u>Tautoga onitis</u>	Outer coast of Newfoundland to South Carolina.	Mid-May to mid-August.	Invertebrates; chiefly univalve and bivalve molluscs; especially mussels and barnacles. Also crabs, sand dollars, scallops, amphipods, shrimps, isopods, and lobsters.	Coastal species--from tideline to approximately 20 m depth. Prefers ledges, submerged objects, boulder bottoms, and mussel beds. Larger fish migrate and overwinter offshore. Small fish remain nearshore. Overwinter in torpid state.	Bigelow and Schroeder (1953); Cooper (1965, 1966); Leim and Scott (1966); Thomson et al. (1971); Colton et al. (1979); Olla et al. (1974, 1979).
Cunner <u>Tautoglabrus adspersus</u>	Newfoundland and the Gulf of St. Lawrence. South to Chesapeake Bay.	May to August.	Omnivorous; feeds chiefly on amphipods, shrimps, young lobsters, small crabs, other crustaceans, univalve and bivalve molluscs, hydroids, worms, small fish, sea urchins, bryozoans, and ascidians. Also eelgrass and macroalgae.	Coastal year-round resident. Many move to deeper water in winter. May leave shoal waters to escape high temperature; overwinter in torpid state in crevices.	Bigelow and Schroeder (1953); Leim and Scott (1966); Thomson et al. (1971); Green (1975); Olla et al. (1979); Shumway and Stitkney (1975); Dew (1976); Colton et al. (1979).
Stichaeidae - Pricklebacks					
Snakeblenny <u>Lumpenus lumpretaeformis</u>	Arctic and north Atlantic to off-shore southern New England.	In Europe in autumn or winter. Fry caught in Gulf of Maine from March-May.	Amphipods, copepods, small crustaceans, starfish, bivalves; holothurians in European waters.		Bigelow and Schroeder (1953); Leim and Scott (1966).

continued

Appendix II. Continued.

Name common/scientific	Distribution	Spawning period	Food preferences	Movements	References
Daubed Shanny <u>Lumpenus maculatus</u>	Arctic Ocean to Cape Cod.	Probably in winter.	Worms and pelagic amphipods.	Off Europe, spends most of year in deep water and migrates to shallows to spawn.	Bigelow and Schroeder (1953); Leim and Scott (1966).
Radiated Shanny <u>Ulvaria subbifurcata</u>	Eastern Newfoundland, north shore of Gulf of St. Lawrence, northern Nova Scotia to Nantucket Shoals and southern New England.	Late spring through summer.	Juveniles less than 55 mm; prey on copepods. Larger fish prey primarily on amphipods and nereid worms.	Resident species restricted to a small home range (less than 3 m ²).	Bigelow and Schroeder (1953); Leim and Scott (1966); LeDrew and Green (1975); Green and Fisher (1977).
Pholidae - Gunnels					
Rock Gunnel <u>Pholis gunnellus</u>	Hudson Strait to off Delaware Bay.	December to February.	Amphipods, isopods, small decapods, bivalves, gastropods, worms, algae.	Year-round coastal resident. Leaves intertidal zone in winter.	Bigelow and Schroeder (1953); Leim and Scott (1966); Sawyer (1967).
Anarhichadidae - Wolffishes					
Atlantic Wolffish <u>Anarhichas lupus</u>	Davis Strait to Cape Cod.	In European waters from November to January.	Hardshelled molluscs, crustaceans, echinoderms.	Solitary, year-round resident.	Bigelow and Schroeder (1953); Leim and Scott (1966); Thomson et al. (1971).

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Appendix II. Continued.

Name common/scientific	Distribution	Spawning period	Food preferences	Movements	References
Cryptacanthodidae - Wrymouths					
Wrymouth <u>Cryptacanthodes maculatus</u>	Southern Labrador and the Grand Bank to off New Jersey.	Winter spawner in Gulf of Maine.	Gammaridean amphipods, shrimps, small fish.	Year-round resident below low water mark.	Bigelow and Schroeder (1953); Leim and Scott (1966).
Anmodytidae - Sand Lances					
American Sand Lance <u>Anmodytes americanus</u>	Labrador, Newfoundland, and Gulf of St. Lawrence to Cape Hatteras.	December to April in Gulf of Maine. December to February in Mid-Atlantic Bight.	Chiefly small crustaceans, especially copepods, and on fish fry and worms.	Travels in dense schools. Able to burrow into sand above low water mark and wait for next high tide.	Bigelow and Schroeder (1953); Leim and Scott (1966); Thomson et al. (1971); Colton et al. (1979); Meyer et al. (1979).
Gobiidae - Gobies					
Naked Goby <u>Gobiosoma bosci</u>	Massachusetts to Mexico.	June to August.	Crustaceans, worms, small fishes.	Probably year-round resident.	Hildebrand and Schroeder (1927); Dahlberg and Conyers (1973); Hoese and Moore (1977).
Seaboard Goby <u>Gobiosoma ginsburgi</u>	Virginia north to southern Massachusetts.	June to August.	Crustaceans, molluscs, worms, algae.	Probably year-round resident.	Hildebrand and Schroeder (1927); Dahlberg and Conyers (1973); Munroe and Lotspeich (1979).

continued

Appendix II. Continued.

Name common/scientific	Distribution	Spawning period	Food preferences	Movements	References
Scombridae - Mackerels					
Atlantic Mackerel <u>Scomber scombrus</u>	Northern side of Gulf of St. Lawrence and Strait of Belle Isle to North Carolina.	May to July in Gulf of Maine, April to June in Mid-Atlantic Bight.	Pelagic crustaceans, fish eggs, small fish, plankton.	Warm water migrant to nearshore areas of Gulf of Maine and southern New England. Overwintering offshore in warm waters at or near shelf break. Each spring a general northern migration occurs and fish move inshore as well.	Sette (1950); Bigelow and Schroeder (1953); Leim and Scott (1966); Thomson et al. (1971); Colton et al. (1979); Morse (1980).
Stromateidae - Butterfishes					
Butterfish <u>Peprilus triacanthus</u>	Gulf of St. Lawrence, and Newfoundland to North Carolina.	May to August in Gulf of Maine, May to October in Mid-Atlantic Bight.	Small fish, squid, crustaceans, worms.	Schooling fish; winter offshore and summer inshore migration.	Bigelow and Schroeder (1953); Leim and Scott (1966); Thomson et al. (1971).
Triglidae - Searobins					
Northern Searobin <u>Prionotus carolinus</u>	Bay of Fundy to South Carolina; chiefly west and south of Cape Cod.	May-November in Mid-Atlantic Bight. June-July in Long Island Sound.	Young-of-the-year feed primarily on copepods. Adults feed primarily on small crustaceans; occasionally on squid, bivalves, worms, small fish-herring, menhaden, winter flounder.	In southern New England move inshore in May or June to tideline, move offshore in October.	Bigelow and Schroeder (1953); Richards et al. (1963); Colton et al. (1979).

continued

Appendix II. Continued.

Name common/scientific	Distribution	Spawning period	Food preferences	Movements	References
Striped Searobin <u>Prionotus evolvans</u>	Cape Cod to South Carolina.	June-July in Long Island Sound.	Adults feed primarily on crustaceans. Young-of-the-year (3-6 cm) feed on copepods such as <u>Neomysis</u> , <u>Diastylis</u> , <u>Crangon</u> , <u>Hemiaris</u> . <u>P. evolvans</u> feeds more on nektonic species than <u>P. carolinus</u> which prefers benthic invertebrates.	Move inshore in April. Begin to move offshore after spawning and absent from southern New England waters by November.	Bigelow and Schroeder (1953); Richards et al. (1979).
Cottidae - Sculpins					
Sea Raven <u>Hemitripterus americanus</u>	Northern Gulf of St. Lawrence and Strait of Belle Isle on the Newfoundland side southward to Chesapeake Bay.	October-December in southern New England.	Bivalve and univalve molluscs, crustaceans, sea urchins, worms, various fish.	In southern New England, move into coastal waters in fall. Found on rocky hard sand or pebble bottoms.	Bigelow and Schroeder (1953); Thomson et al. (1971).
Grubby Sculpin <u>Myoxocephalus aeneus</u>	Strait of Belle Isle, southern Gulf of St. Lawrence, and Nova Scotia to New Jersey.	Spawns in winter in southern New England and through to June in Gulf of St. Lawrence.	Omnivorous, feeds chiefly on worms, shrimp, crabs, copepods, snails, nudibranchs, molluscs, ascideans, small fish including alewife, cunner, eel, mummichog, lance, silversides, sticklebacks, tomcod.	Resident nearshore. Moves to slightly deeper water in winter.	Bigelow and Schroeder (1953); Ennis (1969); Thomson et al. (1971).
Longhorn Sculpin <u>Myoxocephalus octodecemspinosus</u>	Eastern Newfoundland and Gulf of St. Lawrence south to New Jersey.	November-February. Peaks in December and January.	Omnivorous, feeds chiefly on shrimps, crabs, amphipods, hydroids, worms, mussels, other molluscs, squids, ascideans, fish fry.	Year-round resident of continental shelf waters. Onshore migration to southern New England in winter, offshore in summer, spring.	Morrow (1951); Bigelow and Schroeder (1953); Thomson et al. (1971).

continued

Appendix II. Continued.

Name common/scientific	Distribution	Spawning period	Food preferences	Movements	References
Shorthorn Sculpin <u>Myoxocephalus scorpius</u>	West Greenland and southern Labrador. Southward to southern New England.	November-February at Woods Hole.	Crustaceans, particularly crabs, shrimp. Also, sea urchins, worms, fish fry, rarely shellfish.	Cold water fish found in nearshore waters in Gulf of Maine.	Bigelow and Schroeder (1953).
Cyclopteridae - Snailfishes					
Lumpfish <u>Cyclopterus lumpus</u>	Gulf of St. Lawrence, Newfoundland, Labrador, Hudson Bay, Davis Strait, and west Greenland to New Jersey.	Probably April-June in Gulf of Maine.	Euphausiids, medusae, amphipods, caprellids, small fish.	Movement of adults into shoal water at spawning time and offshore movement following spawning.	Bigelow and Schroeder (1953).
Seasnail <u>Liparis atlanticus</u>	Northeastern Newfoundland, Gulf of St. Lawrence, and Grand Banks to southern New England.	Late winter and spring in Gulf of Maine.	Presumably small crustaceans, small shellfish, similar to European species.	Primarily coastal fish, rarely pelagic. Attach by sucker to stones, kelp, and other seaweeds. Probably inshore in winter to spawn. Winter migrant to southern New England waters.	Bigelow and Schroeder (1953).

continued

Appendix II. Continued.

Name common/scientific	Distribution	Spawning period	Food preferences	Movements	References
Order Pleuronectiformes Bothidae - Lefteye Flounders					
Summer Flounder <u>Paralichthys dentatus</u>	Maine to South Carolina, chiefly south of Cape Cod.	In Mid-Atlantic Bight, September-April, peaking in October. In Gulf of Maine probably October-April.	Predaceous--chiefly small fish, squid, crabs, shrimps, other crustaceans, small shelled molluscs, worms, and sand dollars.	Young move inshore during warmer months. Majority of population, especially larger fish, stay offshore.	Bigelow and Schroeder (1953); Thomson et al. (1971); Colton et al. (1979).
Fourspot Flounder <u>Paralichthys oblongus</u>	George's Bank to coast of South Carolina. Most abundant from southern New England to Delaware Bay.	May to mid-July.	Chiefly small fish and squid. Also on worms, shrimp, crabs, and other crustaceans.	Found in deeper water in Gulf of Maine. In southern New England adults are found inshore during warmer months. ³	Bigelow and Schroeder (1953).
Windowpane <u>Scophthalmus aquosus</u>	Gulf of St. Lawrence to South Carolina. Most abundant west and south of Cape Cod.	May to September.	Feeds primarily on mysids; also sand shrimp, amphipods, and small fish.	No migration evident. Year-round resident in coastal Gulf of Maine and Mid-Atlantic Bight.	Bigelow and Schroeder (1953); Thomson et al. (1971).

continued

Appendix II. Continued.

Name common/scientific	Distribution	Spawning period	Food preferences	Movements	References
Pleuronectidae - Righteye Flounders					
Smooth Flounder <u>Liopsetta putnami</u>	Virginia Bay, Labrador, Strait of Belle Isle, Gulf of St. Lawrence south to Massachusetts Bay.	December to March.	Amphipods, small molluscs, shrimp, crabs, worms.	Occurs close to shore over entire range. Found in estuaries, river mouths, bays, and harbors with mud bottoms.	Bigelow and Schroeder (1953).
Winter Flounder <u>Pseudopleuronectes americanus</u>	Strait of Belle Isle, Gulf of St. Lawrence, and Newfoundland to off North Carolina and Georgia.	Spawning occurs at different times in different parts of the range. March-May peaking in April in Boothbay Harbor, Maine, mid-February to April peaking in March in Mystic, Connecticut.	Omnivorous; chiefly feeds on isopods, copepods, amphipods, crabs, shrimp, worms, molluscs, snail eggs, and some seaweed.	Moves into deeper water in summer when temperature exceeds 15°C. Remain off-shore in 12-15°C isotherms until fall. Moves inshore to spawn during winter (3-4°C).	Pearcy and Richards (1962); Klein-MacPhee (1978).

continued

Appendix II. Concluded.

Name common/scientific	Distribution	Spawning period	Food preferences	Movements	References
Soleidae - Soles					
Hogchoker <u>Trinectes maculatus</u>	Atlantic and Gulf coasts of North America from Massachusetts to Panama. Most abundant south of Chesapeake Bay. Uncommon north of Cape Cod.	May to August.	Worms and small crustaceans.	Coastal fish confined to bays and estuaries. Sometimes found in freshwater.	Bigelow and Schroeder (1953); Koski (1978).
Order Tetraodontiformes					
Tetraodontidae - Puffers					
Northern Puffer <u>Sphoeroides maculatus</u>	Maine to Florida. Abundant south of Cape Code.	Early June through summer in southern New England. Spawns in shoal water close to shore.	Feeds almost exclusively on invertebrates; chiefly crustaceans, molluscs, and worms.	Coastal fish common in shoal waters during summer; probably moves to nearby deeper waters in winter.	Bigelow and Schroeder (1953).

1. P. Auster; University of Connecticut, Marine Research Laboratory, Noank, CT; February 1981; personal communication.
2. S. Sousa; University of Connecticut, Marine Research Laboratory, Noank, CT; February 1981; personal communication.
3. R. Defoursey; University of Connecticut, Marine Research Laboratory, Noank, CT; February 1981; personal communication.

Appendix III. Bird species that regularly utilize New England tidal flats.

	Residency status (Peterson 1980)	Diet (Terres 1980)
Shorebirds		
American Oystercatcher <u>Haematopus palliatus</u>	Breeds locally north to Massachusetts	Primarily bivalves, some crustaceans and echinoderms
Black-bellied Plover <u>Pluvialis squatarola</u>	Migrant; a few present in summer and winter	Crustaceans, polychaetes, molluscs
Lesser Golden Plover <u>Pluvialis dominica</u>	Migrant; rare	Molluscs, crustaceans
Ruddy Turnstone <u>Arenaria interpres</u>	Migrant; prefers rocky coasts	Crustaceans, polychaetes
Semipalmated Plover <u>Charadrius semipalmatus</u>	Migrant	Polychaetes, crustaceans, molluscs
Piping Plover <u>Charadrius melodus</u>	Breeds locally along New England coast in very small numbers	Polychaetes, crustaceans, molluscs
Killdeer <u>Charadrius vociferus</u>	Breeds throughout New England; generally inland; on flats in fall	Crustaceans, insects
Short-billed Dowitcher <u>Limnodromus griseus</u>	Migrant	Molluscs, crustaceans, polychaetes
Long-billed Dowitcher <u>Limnodromus scolopaceus</u>	Fall migrant	Molluscs, crustaceans, polychaetes
Willet <u>Catoptrophorus semipalmatus</u>	Breeds locally north to southern Maine and Nova Scotia; more common as migrant	Polychaetes, crustaceans, molluscs, some small fish
Greater Yellowlegs <u>Tringa melanoleuca</u>	Migrant; occasionally winters north to Massachusetts	Fish, molluscs, polychaetes, crustaceans
Lesser Yellowlegs <u>Tringa flavipes</u>	Migrant; uncommon in spring	Fish, molluscs, polychaetes, crustaceans
Stilt Sandpiper <u>Micropalma himantopus</u>	Migrant; rare in spring	Molluscs, crustaceans

continued

Appendix III. (Continued).

	Residency status (Peterson 1980)	Diet (Terres 1980)
Shorebirds (continued)		
Red Knot <u>Calidris canutus</u>	Migrant	Primarily molluscs, some crustaceans, polychaetes
Sanderling <u>Calidris alba</u>	Migrant	Primarily molluscs, some crustaceans, polychaetes
Pectoral Sandpiper <u>Calidris melanotos</u>	Migrant	Crustaceans
Spotted Sandpiper <u>Actitis macularia</u>	Fall migrant; breeds inland	Crustaceans
Dunlin <u>Calidris alpina</u>	Migrant; some winter north to southern Maine	Crustaceans, polychaetes, molluscs
Purple Sandpiper <u>Calidris maritima</u>	Migrant; some winter throughout New England; rocky areas	Crustaceans, molluscs
Least Sandpiper <u>Calidris minutilla</u>	Migrant	Crustaceans, polychaetes, molluscs
Semipalmated Sandpiper <u>Calidris pusilla</u>	Migrant	Molluscs, polychaetes, crustaceans
Western Sandpiper <u>Calidris mauri</u>	Migrant; may winter in very small numbers, rare in spring	Molluscs, polychaetes, crustaceans
White-rumped Sandpiper <u>Calidris fuscicollis</u>	Migrant; rare in spring	Polychaetes, molluscs
Hudsonian Godwit <u>Limosa haemastica</u>	Migrant	Molluscs, crustaceans, polychaetes
Marbled Godwit <u>Limosa fedoa</u>	Migrant	Molluscs, crustaceans, polychaetes
Gulls and terns		
Herring Gull <u>Larus argentatus</u>	Breeds on islands along New England coast; winters throughout New England	Fish, invertebrates, refuse, seabird chicks and eggs

continued

Appendix III. (Continued).

	Residency status (Peterson 1980)	Diet (Terres 1980)
Gulls and terns (continued)		
Ring-billed Gull <u>Larus delawarensis</u>	Migrant; winters along New England coast	Fish, refuse
Great Black-backed Gull <u>Larus marinus</u>	Breeds on islands along New England coast; winters throughout New England	Fish, invertebrates, refuse, seabird chicks and eggs
Laughing Gull <u>Larus atricilla</u>	Breeds locally along New England coast	Fish, tern eggs or chicks
Bonaparte's Gull <u>Larus philadelphia</u>	Migrant; winters locally along New England coast	Fish, invertebrates
Least Tern <u>Sterna albifrons</u>	Breeds north to central Maine	Fish, crustaceans
Arctic Tern <u>Sterna paradisaea</u>	Breeds south to Massachusetts	Fish, crustaceans
Common Tern <u>Sterna hirundo</u>	Breeds on coast throughout New England	Fish, crustaceans
Roseate Tern <u>Sterna dougallii</u>	Breeds locally through southern New England and Maine	Fish
Waterfowl and diving birds		
Common Loon <u>Gavia immer</u>	Breeds in interior New England lakes; winters along coast	Fish
Red-throated Loon <u>Gavia stellata</u>	Migrant; also winters along New England coast	Fish
Horned Grebe <u>Podiceps auritus</u>	Winters throughout New England	Fish and some shrimp
Red-necked Grebe <u>Podilymbus grisegena</u>	Winters locally along New England coast	Fish

continued

Appendix III. (Continued).

	Residency status (Peterson 1980)	Diet (Terres 1980)
Waterfowl and diving birds (continued)		
Double-crested Cormorant <u>Phalacrocorax auritus</u>	Migrant; breeds on islands along New England coast, mostly north of Cape Cod	Primarily fish, also crustaceans
Great Cormorant <u>Phalacrocorax carbo</u>	Winters along New England coast	Primarily fish, also crustaceans
Mute Swan <u>Cygnus olor</u>	Year-round resident inland and on coast in Connecticut, Rhode Island, and Massachusetts	Aquatic plants
Canada goose <u>Branta canadensis</u>	Migrant; also resident throughout New England	Primarily aquatic plants, also molluscs and small crustaceans
Brant <u>Branta bernicla</u>	Migrant; some winter north to southern Maine	Aquatic marine plants
Mallard <u>Anas platyrhynchos</u>	Resident; increasing due to stocking	Aquatic plants, seeds, grains
Black Duck <u>Anas rubripes</u>	Resident; most breed inland, winter along coast	Aquatic plants, some molluscs, crustaceans and polychaetes during winter
Gadwall <u>Anas strepera</u>	Breeds locally in New England; some winter	Aquatic plants, invertebrates
Canvasback <u>Aythya valisineria</u>	Migrant; especially spring in southern New England, some winter	Primarily aquatic plants, also some molluscs
Redhead <u>Aythya americana</u>	Migrant; especially spring in southern New England, some winter	Primarily aquatic plants, also some molluscs and crustaceans
Greater Scaup <u>Aythya marila</u>	Migrant; winters locally	Primarily molluscs, also aquatic plants
Lesser Scaup <u>Aythya affinis</u>	Migrant; a few winter north to Cape Cod	Primarily molluscs, also aquatic plants

continued

Appendix III. (Continued).

	Residency status (Peterson 1980)	Diet (Terres 1980)
Waterfowl and diving birds (continued)		
Common Goldeneye <u>Bucephala clangula</u>	Winters along New England coast	Molluscs and crustaceans
Bufflehead <u>Bucephala albeola</u>	Winters along New England coast	Primarily shrimp, also other crustaceans and molluscs
White-winged Scoter <u>Melanitta deglandi</u>	Migrant; locally common in winter	Primarily molluscs (especially blue mussel), some crustaceans
Surf Scoter <u>Melanitta perspicillata</u>	Migrant; locally common in winter	Primarily molluscs (especially blue mussel), some crustaceans
Black Scoter <u>Melanitta nigra</u>	Migrant; locally common in winter	Primarily molluscs (especially blue mussel), some crustaceans
Oldsquaw <u>Clangula hyemalis</u>	Migrant; winters locally offshore	Molluscs and crustaceans
Common Eider <u>Somateria mollissima</u>	Winters along New England coast, along Cape Cod and offshore islands	Primarily mussels
Harlequin Duck <u>Histrionicus histrionicus</u>	Winters locally along coast, prefers rocky areas	Molluscs and crustaceans
Red-breasted Merganser <u>Mergus serrator</u>	Breeds locally in northern New England; winters along New England coast	Primarily fish, some crustaceans
Wading birds		
Great Blue Heron <u>Ardea herodias</u>	Breeds locally on Maine coast and elsewhere in interior; occasionally winters north to southern Maine	Primarily fish, amphibians, some crustaceans, small mammals

continued

Appendix III. (Continued).

	Residency status (Peterson 1980)	Diet (Terres 1980)
Wading birds (continued)		
Little Blue Heron <u>Florida caerulea</u>	Breeds locally north to southern Maine	Fish, crustaceans
Great Egret <u>Casmerodius albus</u>	Breeds very locally north to Massachusetts	Primarily fish, and crustaceans
Snowy Egret <u>Egretta thula</u>	Breeds locally north to southern Maine	Fish, crustaceans, some polychaetes
Black-crowned Night Heron <u>Nycticorax nycticorax</u>	Breeds locally north to eastern Maine	Fish, crustaceans, amphibians, occasionally heron and tern chicks
Green Heron <u>Butorides striatus</u>	Breeds throughout New England, coast and interior	Fish, crustaceans
Glossy Ibis <u>Plegadis falcinellus</u>	Breeds along coast to southern Maine	Crustaceans
Raptors		
Bald Eagle <u>Haliaeetus leucocephalus</u>	Breeds locally in northern Maine; some winter on coast or interior throughout New England	Fish, carrion, birds
Osprey <u>Pandion haliaetus</u>	Breeds locally throughout New England, coast and interior, mostly in Maine	Fish
Marsh Hawk <u>Circus cyaneus</u>	Migrant; breeds locally in New England; winters north to Cape Cod	Small mammals, birds
Sharp-shinned Hawk <u>Accipiter striatus</u>	Migrant on coast; resident inland	Birds, small mammals
Rough-legged Hawk <u>Buteo lagopus</u>	Migrant; winters throughout New England	Small mammals, occasionally birds
Red-tailed Hawk <u>Buteo jamaicensis</u>	Breeds throughout New England; winters north to central Maine and Nova Scotia	Small mammals, occasionally birds

continued

Appendix III. (Concluded).

	Residency status (Peterson 1980)	Diet (Terres 1980)
Raptors (continued)		
Merlin <u>Falco columbarius</u>	Migrant; occasionally winters throughout New England	Birds, small mammals
Peregrine Falcon <u>Falco peregrinus</u>	Rare migrant	Birds
Others		
Belted Kingfisher <u>Megaceryle alcyon</u>	Breeds throughout New England; year-round resident north to northern Maine	Primarily fish, some crustaceans
Fish Crow <u>Corvus ossifragus</u>	Year-round resident Connecticut, Rhode Island, Massachusetts	Crustaceans, bird eggs

REPORT DOCUMENTATION PAGE		1. REPORT NO. FWS/OBS-81/01	2.	3. Recipient's Accession No.
4. Title and Subtitle The Ecology of New England Tidal Flats: A Community Profile		5. Report Date March 1982		6.
7. Author(s) Robert B. Whitlatch		8. Performing Organization Rept. No.		10. Project/Task/Work Unit No.
9. Performing Organization Name and Address University of Connecticut Department of Marine Sciences Marine Research Laboratory Noank, Connecticut 06340		11. Contract(C) or Grant(G) No. (C) (G)		13. Type of Report & Period Covered
12. Sponsoring Organization Name and Address National Coastal Ecosystems Team Office of Biological Services, Fish and Wildlife Service U.S. Department of the Interior Washington, DC 20240		14.		
15. Supplementary Notes				
16. Abstract (Limit: 200 words) The purpose of this report is to provide a general perspective of tidal flats of New England, the organisms commonly associated with them, and the importance of tidal flats to the coastal zone viewed as a whole. The approach is taxonomically based although there is also attention paid to the flow of organic matter through the tidal flat habitat. The method of presentation is similar to that of Peterson and Peterson (1979) who have described the tidal flat ecosystems of North Carolina. The reader, therefore, has the opportunity of comparing and contrasting the physical and biological functioning of the two regions. Chapter 1 begins with a general view of the physical, chemical, and geological characteristics of tidal flat environments followed by a discussion of organic production and decomposition processes vital to these systems (Chapter 2). The next three chapters deal with the benthic invertebrates (Chapter 3), fishes (Chapter 4), and birds (Chapter 5) common to the New England tidal flats. The coverage within each chapter reflects the published information available at the time of writing in addition to the author's perception about the structure, function, and importance of each of the taxonomic groups to the overall tidal flat system. The last chapter (Chapter 6) considers the response of tidal flats to environmental perturbation as well as their value to the New England coastal zone.				
17. Document Analysis a. Descriptors sand flats, mud flats, birds, fishes, benthic invertebrates b. Identifiers/Open-Ended Terms c. COSATI Field/Group				
18. Availability Statement Unlimited		19. Security Class (This Report) Unclassified	21. No. of Pages 125	20. Security Class (This Page)
			22. Price	

(See ANSI-Z39.18)

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(Formerly NTIS-35)
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