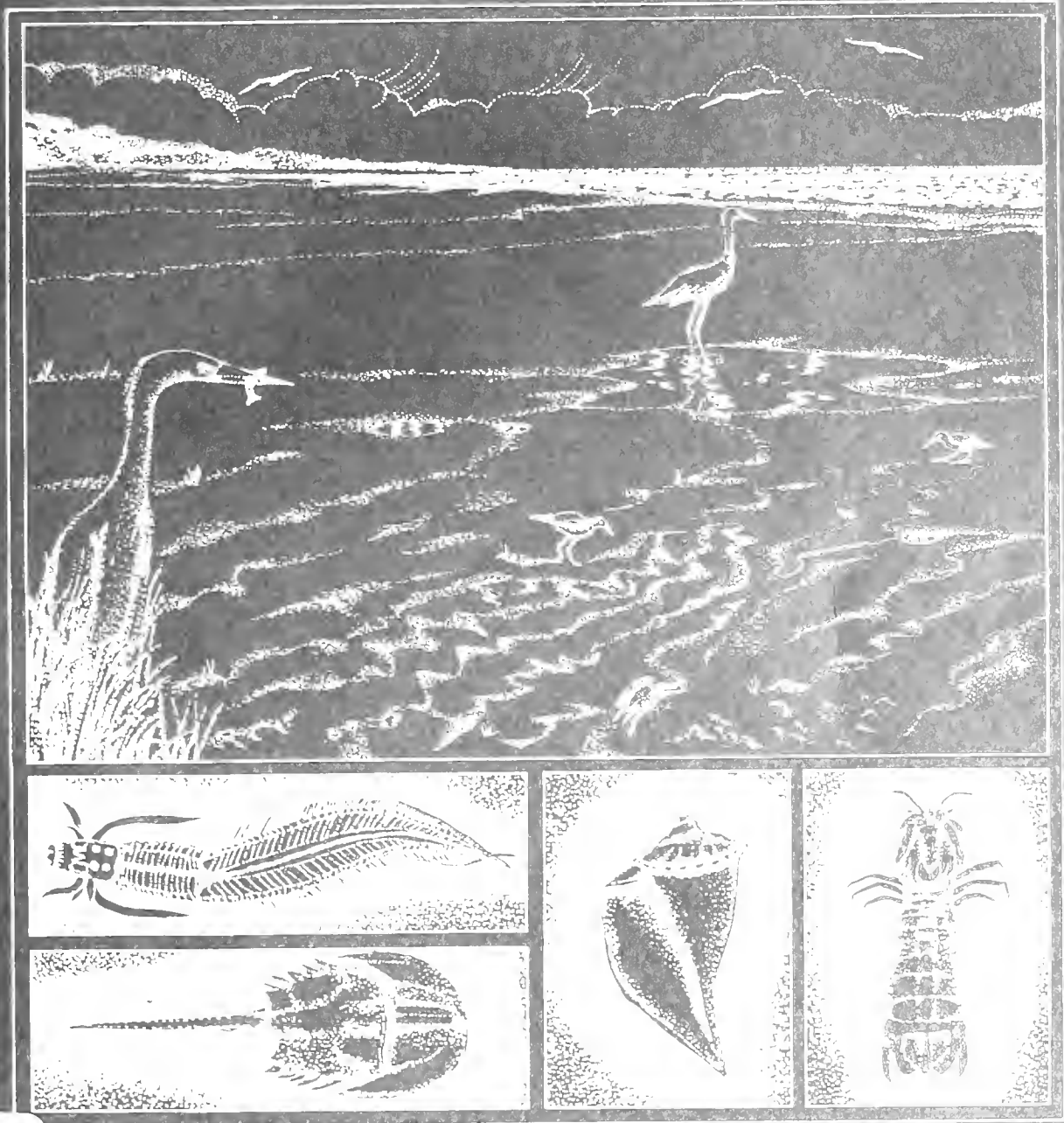


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November 1979

THE ECOLOGY OF INTERTIDAL FLATS OF NORTH CAROLINA: A COMMUNITY PROFILE



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UNITED STATES DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE

National Coastal Ecosystems Team
NASA/Slide11 Computer Complex
1010 Gause Blvd.
Slide11, Louisiana 70458

25 February 1980

The ecology of intertidal sand and mud flats is described in the enclosed report. Although examples of the ecological processes were drawn from coastal North Carolina, most of the functions and principles can be widely applied to intertidal shorelines of sounds, lagoons, estuaries and river mouths in temperate zones throughout the world.

Copies of FWS/OBS-79/39 are available from the U.S. Fish and Wildlife Service, 1010 Gause Blvd., Slide11, LA 70458 and the National Technical Information Service, Springfield, VA 22161.

Sincerely yours,

A handwritten signature in black ink, reading "Larry R. Shanks". The signature is written in a cursive style with a large initial "L".

Larry R. Shanks
Acting Team Leader

The Biological Services Program was established within the U.S. Fish and Wildlife Service to supply scientific information and methodologies on key environmental issues that impact fish and wildlife resources and their supporting ecosystems. The mission of the program is as follows:

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- 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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Cover design by Graham Golden



THE ECOLOGY OF INTERTIDAL FLATS OF NORTH CAROLINA:
A COMMUNITY PROFILE

by

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PREFACE

We have developed this community profile to serve as an introduction to the ecology of intertidal sand and mud flats. Our main goal is to describe the ecological processes that characterize a habitat which, at first glance, appears barren and almost devoid of life. We emphasize and draw all our examples from the intertidal flats of coastal North Carolina with which we are most familiar. To the degree that we are successful in describing general processes of ecosystem function on an intertidal flat, what we have to say can be widely applied to the intertidal shorelines of sounds, lagoons, estuaries, and river mouths in temperate zones throughout the world. We trust that our descriptions of the ecology of intertidal mud and sand flats will be useful to scientists and informed laymen alike. We especially hope that our text will provide much of the background needed by coastal planners and environmental scientists whose decisions will influence the future of many of our coastal systems. Intertidal mud and sand flats are classified as habitat types by the National Wetlands Inventory of the U.S. Fish and Wildlife Service and designated as E2FL3 and E2FL2, respectively.

Our text is organized on a taxonomic and a functional basis. After an introductory description of the physical environment of the intertidal soft-sediment habitat (Chapter 1), we describe the plants, the primary producers of most marine systems (Chapter 2). In succeeding chapters we discuss the benthic infauna and the mobile epibenthic invertebrates (Chapter 3), the fishes (Chapter 4), and the birds (Chapter 5). This progression is clearly taxonomic, but to a great extent it is also functional, reflecting the major pathways of energy flow through the intertidal flat system. The benthic infauna are largely herbivorous or detritivorous and form the prey of the mobile epibenthic invertebrates. Bottom-feeding fishes and shorebirds feed extensively on these mobile invertebrates, as well as on the benthic infauna. Some of the fishes fall victim to wading or diving birds. Consequently, our progression of chapters roughly corresponds to the flow of energy up the food chain of a coastal flat. In our final chapter (6), we address some specific applied problems that emerge in managing man's activities in the vicinity of intertidal flats.

Although this publication is explicitly con-

cerned with what occurs on an intertidal mud or sand flat, we are also compelled to describe important processes which happen elsewhere within the estuarine ecosystem. Breadth is forced upon us by the open nature of the intertidal flat environment: this is by no means a closed system ecologically. Inputs of organic matter, various inorganic particles, and even mobile animals are basic to the functioning of an intertidal flat. Only the benthic infauna are relatively fixed in position and restricted to completing their lives in a single habitat. The infauna of an intertidal flat are sustained by primary production which occurs in large measure outside this habitat and which is imported by water currents. The highest trophic levels, the birds and fishes, are extremely mobile. Most birds and fishes are merely seasonal visitors to the intertidal flat, later moving to other habitats within the estuarine system and then on to other entirely different systems. Consequently, it is not surprising that when one speaks of an intertidal mud flat community, one tends to think solely of the clams, worms, crustaceans, and other benthic invertebrates which can always be found there. Yet our goal is to unfold the complexity, both taxonomic and functional, that characterizes the entire ecosystem of a coastal mud or sand flat.

C. H. Peterson
N. M. Peterson

19 September 1979

Any questions or comments about, or requests for this publication should be directed to:

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Slidell, LA 70458

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The dendritic drainage pattern evident in this areal photograph is a result of the action of water movement over the substrate during ebbing and flooding tides. This pattern effectively increases the surface area of the interface between the sediments and the contiguous waters facilitating the exchange of nutrients, gases, and other materials. Photo by Wiley M. Kitchens, U.S. Fish and Wildlife Service.

CHAPTER 1. THE PHYSICAL ENVIRONMENT

1.1 DEFINITION OF AN INTERTIDAL FLAT

Intertidal flats represent one habitat among several that comprise an estuarine system (Figure 1). Although the other extensive habitats (i.e., salt marshes, seagrass beds, unvegetated subtidal bottoms, and the overlying water column) will not be directly described in this community profile, it will be necessary to compare the intertidal flats with these other estuarine habitats. Science is a comparative process such that data are only meaningful relative to other contrasting data. The intertidal flat habitat, like the estuarine ecosystem as a whole, is an open system physically and biologically, with the consequence that nutrients, organic particles, and living organisms move readily in and out of the habitat. An understanding of the ecology of an intertidal flat requires some knowledge of processes occurring elsewhere within the broader estuarine system.

Intertidal flats are defined as those portions of the unvegetated bottom of sounds, lagoons, estuaries, and river mouths which lie between the high and low tide marks, as defined by the extremes of spring tides. Intertidal flats occur along the shorelines of islands and of the mainland, but some emergent soft bottom also occurs in areas unconnected to dry land. Such bars and flood tidal deltas are not directly considered in this text, although these habitats share many of the characteristics of a true intertidal flat. An intertidal flat is unvegetated only in the sense that it lacks macroscopic plants such as grasses, shrubs, and seagrasses. Benthic microalgae, such as diatoms and blue-green algae, are usually very abundant. Intertidal flats are composed of sandy and muddy sediments in a wide range of relative proportions. Ocean beaches are specifically excluded from this definition of an intertidal flat.

1.2 SEDIMENTARY ENVIRONMENT

Soft sediments bear a clear stamp of the physical environment in which they are found. Coarser sediments (sands and even highly abraded shell fragments and pebbles) dominate in relatively high energy environments, whereas fine sediments (silts and clays) are indicative of environments of

lower physical energy (Sanders 1958, Warne 1971). Sediment texture reflects the physical environment because fine sediments are suspended and ultimately transported away from areas of high water turbulence and rapid velocities (high-energy locales), whereas these same silts and clays are deposited out of the water column in still waters of low turbulence (low-energy locales).

Tidal currents exhibit their highest velocities within channels in the immediate vicinity of inlets that connect the ocean with an estuary or lagoon (Figure 2). Tidal current velocities within an estuary or lagoon gradually decline with increasing distance from the inlet and with decreasing water depth. The inlet itself is an area of very high physical energy, characterized by relatively coarse sands and abraded shell fragments. Inlet sediments are extremely mobile; even coarse sands are transported readily by the strong currents. New sand flats are continually forming and old ones eroding. Such high substrate instability renders this environment inhospitable to nearly all species of benthic macrofauna. Densities of macrofaunal benthic invertebrates are so low on most intertidal flats in inlets that one might justifiably consider this environment almost devoid of benthos.

At some distance from the inlet or on semi-protected shallow flats not far from the inlet where tidal currents have slowed sufficiently, the intertidal flats are composed of finer, but still sandy, sediments which are stable enough to support a benthic community (Figure 2). In general, the silt and clay (i.e., mud) content of the sediments progressively increases on a gradient away from the inlet. Technically, clean sand sediments are considered to be those with a silt-clay fraction (particles <62 microns in diameter) smaller than 5% by dry weight. Muddy sands contain between 5% and 50% silt-clay. True muds are composed of greater than 90% silt-clay, while sandy muds possess a mud content of 50% to 90% (Folk 1974). These distinctions should require that one distinguish between intertidal sand flats on the one hand and mud flats on the other hand, although in practice all intertidal flats are often inaccurately termed mud flats. In this publication, this sedimentological distinction will be retained

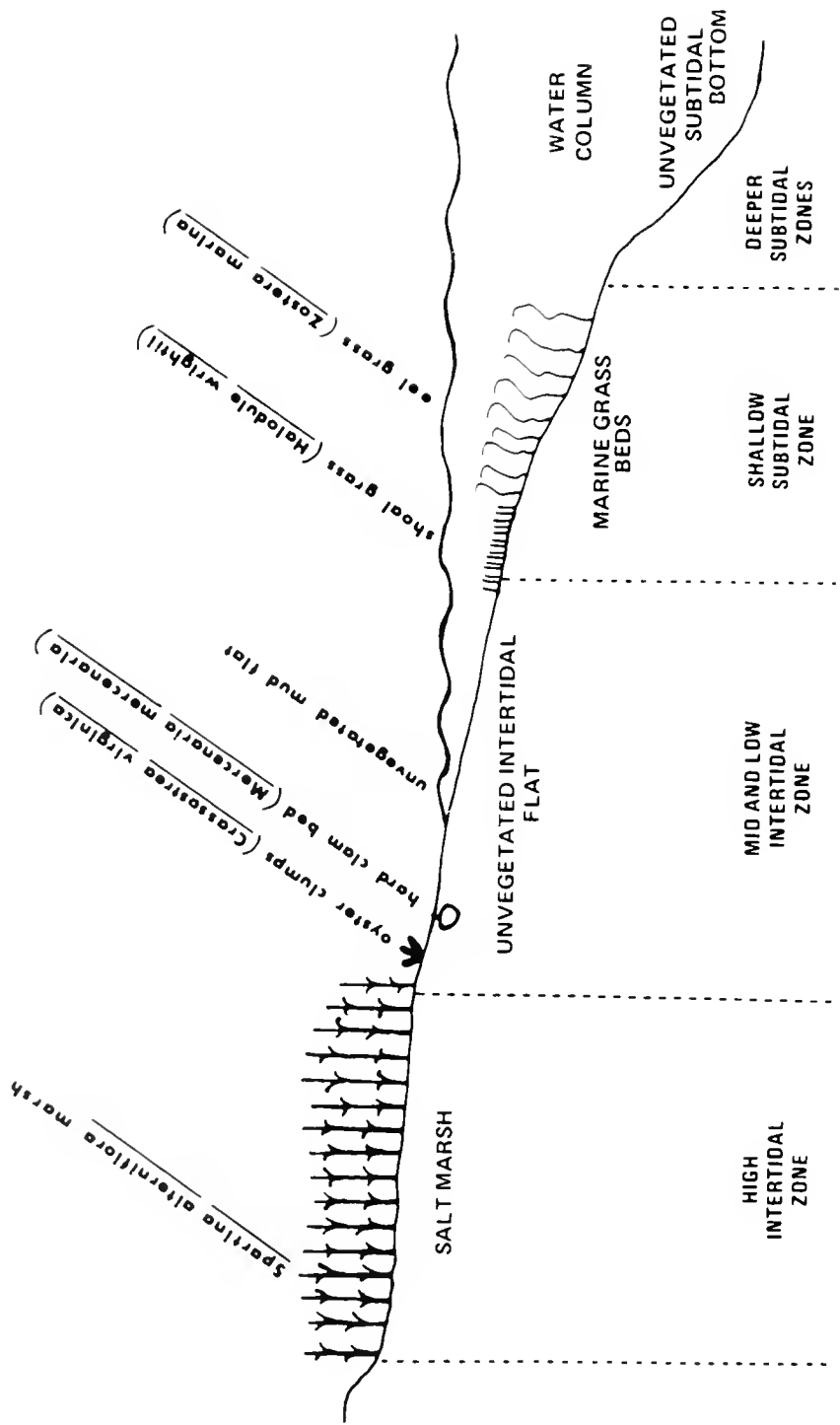


Figure 1. A diagrammatic profile of typical changes in benthic community types along a depth gradient on a semi-protected shoreline of a high-salinity sound or estuary in North Carolina. Along this gradient appears each of the five common habitats which together comprise an estuarine ecosystem: (1) the salt marsh, (2) the unvegetated intertidal flat, (3) the marine grass beds, (4) the unvegetated subtidal bottom, and (5) the water column. Slopes are exaggerated and not to scale. Benthic microalgae and infauna are not illustrated, with the exception of hard clams.

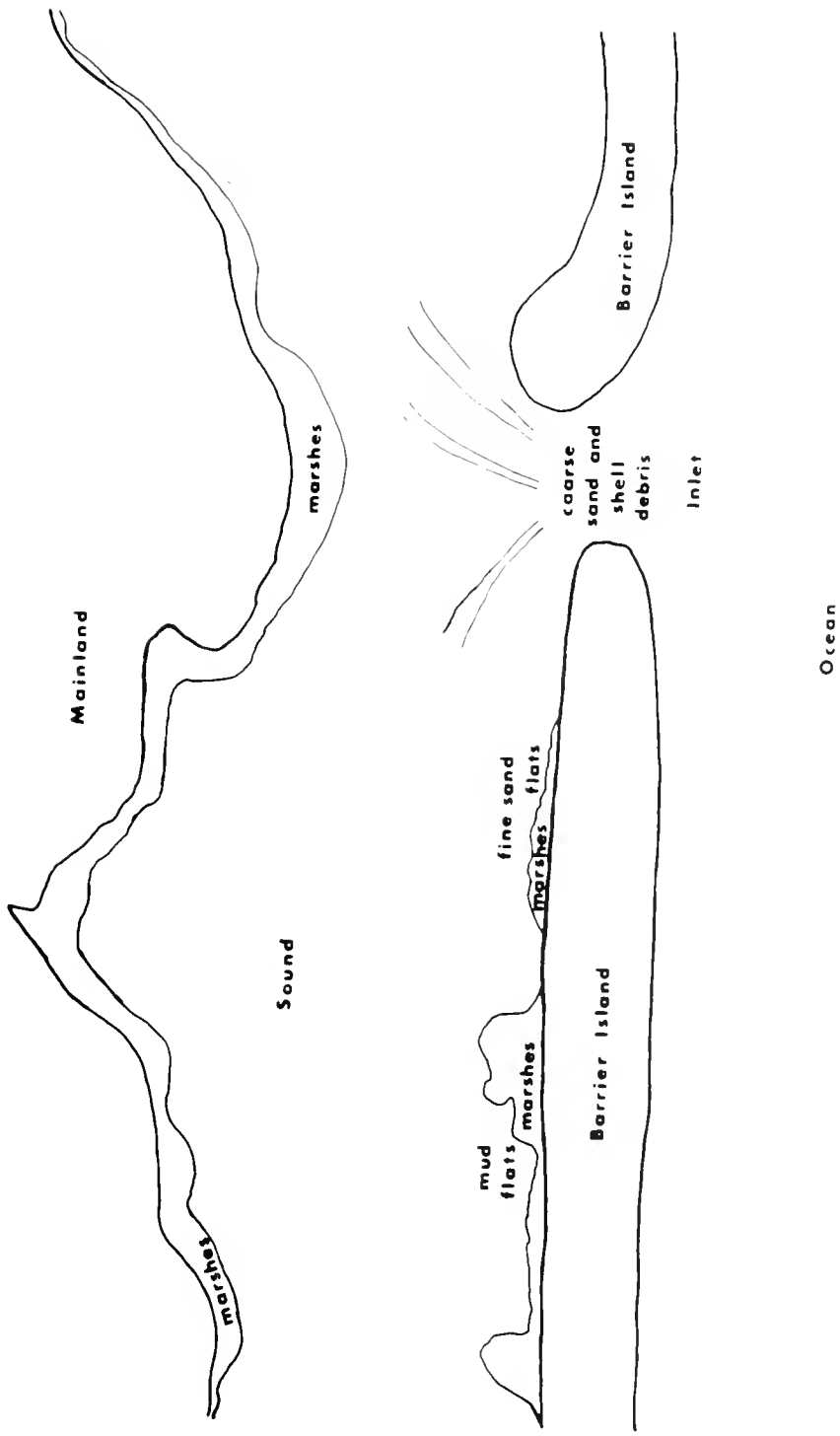


Figure 2. A generalized profile of sedimentary change in a North Carolina sound, illustrating the progression from coarse sediments in inlets to finer sediments as the distance from the inlet increases.

because both the animals and plants of benthic soft sediments are extremely sensitive to grain size differences and the associated chemical and biochemical differences between sands and muds. For instance, Brett (1963) documents how the molluscan fauna changes as a function of sediment type in a North Carolina sound.

Superimposed upon the pattern of gradual change in grain sizes along a gradient away from inlets are other patterns created in part by the second major energy source, wind-driven waves. Waves moving across a body of water have their greatest effect upon the bottom when they reach the shoreline. At the shoreline, even small waves can cause enough water turbulence to resuspend fine sediment particles in the water column. These particles are then transported into quieter areas of deposition, retained in suspension until the winds become calmer, or flushed out of the estuarine or lagoonal system into the ocean. This process, whereby waves expend their energy by breaking at the shoreline, produces the familiar gradient of increasing median particle diameters along a transect from subtidal to intertidal flats. The higher levels of the intertidal shoreline experience most of the wave action and are depleted of the silt-clay fraction. Lower levels of the shoreline less often feel the impact of wave action and are therefore able to retain a muddier sediment character. Most flats in coastal North Carolina, where sounds tend to be large and wave action significant, illustrate this change from sandy sediments in the high intertidal to muds in the shallow subtidal (Tenore 1972).

Wave action within enclosed embayments such as lagoons and estuaries varies with the size of the body of water. In relatively large bodies of water, the fetch is sufficient for substantial wave development, while the same wind speed would fail to produce appreciable wave action in a small tidal creek. The coastline along the North Carolina Outer Banks is characterized by relatively large sounds lying behind long barrier islands with comparatively few inlets to the ocean (Figure 3). Such coastal morphology is typical of a coastline where tidal range is small to moderate, with tides of approximately 1 m creating a so-called "microtidal coast" (Davies 1964, Hayes 1975). Further south in North Carolina (Figure 3), and especially along the coasts of South Carolina and Georgia, the coastal morphology is radically different (Williams et al. 1966, Schwartz and Chestnut

1973). The tidal range becomes larger (2 to 4 m), producing a "mesotidal" coast and, as a consequence, barrier islands are short, inlets numerous, marshes well-developed, and sounds and estuaries quite small (Davies 1964, Hayes 1975). In areas away from the inlets, most intertidal flats in South Carolina and Georgia are very muddy, whereas the intertidal flats along the North Carolina Outer Banks, even including those of Bogue, Back, and Core Sounds tend to be true sand flats (Figure 3). This geographical pattern in sediment size on intertidal flats is produced largely by the varying importance of wind-driven waves, which have a greater impact in larger bodies of water because the fetch is greater. In smaller estuaries and tidal channels, where waves are insignificant, the slowing of tidal currents in the shallows is of overriding importance and produces abundant sedimentation of fine particles on the tidal flats.

Although muddy areas are indicative of low-energy environments where sediment deposition is common, even mud-flat sediments are mobile. Because they are finer, less energy is needed to suspend and transport silts and clays than is required to move sand grains. Either tidal currents or wave energy can be sufficient to transport sediments on mud flats, as well as on sand flats. The activities of burrowing benthic animals also contribute to destabilization of soft sediments. Although sediment mobility is greater in high-energy sand environments, the mobility of unconsolidated, uncemented soft sediments is a universal characteristic of soft-sediment habitats.

The largest of the North Carolina sounds, the Pamlico, Albemarle, and Currituck, have negligible contact with the Atlantic Ocean (Figure 3). This feature produces very brackish waters and isolates these embayments from the influence of lunar tides (Riggs and O'Connor 1974). Except in the immediate vicinity of the few inlets (Ocracoke, Hatteras, etc.) where tidal influence is felt, there are few true intertidal flats or salt marshes along the shorelines of these major bodies of water. Persistently strong winds, operating over large expanses of water in these brackish sounds, create occasional wind tides which expose portions of the shorelines (Riggs and O'Connor 1974). These exposed shorelines are not true intertidal flats in that they are not regularly exposed and covered by lunar tides. Instead, they are usually covered by water and are only exposed at irregu-

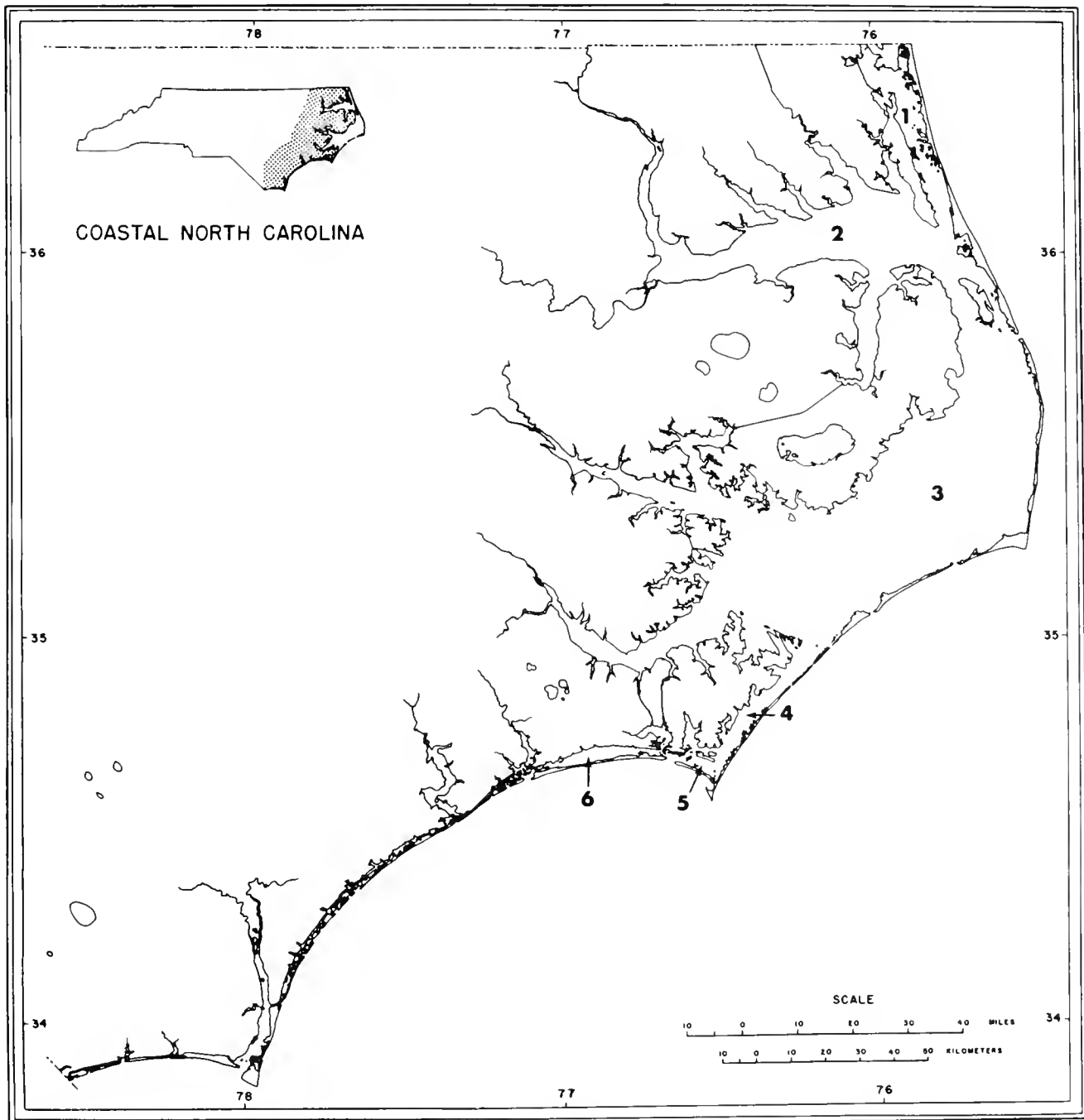


Figure 3. A map of eastern North Carolina, identifying by number the location of all the major sounds: (1) Currituck, (2) Albemarle, (3) Pamlico, (4) Core, (5) Back, and (6) Bogue.

lar intervals for up to days at a time until the wind direction shifts or the wind velocity declines greatly. Wind direction in coastal North Carolina varies strongly with the seasons. Winters are characterized by north, northwest, and northeast winds, while southwest winds prevail during summer months. In response to the seasonal shifts in wind direction different shorelines tend to be exposed at different seasons in these large sounds. Northern shorelines are frequently uncovered in the winter months, while southern areas are exposed during the strong winds of summer (Roelofs and Bumpus 1954).

1.3 CHEMICAL ENVIRONMENT

Geologists usually recognize a fairly distinct dichotomy among semienclosed coastal water bodies by distinguishing true estuaries from marine lagoons (Warne 1971). An estuary is an area where freshwater runoff from land meets the sea. Along its length an estuary exhibits a gradient in salinity, and usually includes large expanses of brackish waters in the middle of this salinity gradient. Estuaries usually extend in a direction more or less perpendicular to the coastline and are inhabited by euryhaline organisms, tolerant of brackish waters and variable salinities. Marine lagoons, on the other hand, tend to be fully saline with little freshwater input. They usually lie parallel to the shoreline behind a barrier island. A marine lagoon is populated by stenohaline organisms typical of marine waters and physiologically incapable of withstanding low salinities.

Although marine lagoons are characteristic of continental coastlines in desert and Mediterranean climates and of the coasts of islands where the land drainage basin is small, there are occasional marine lagoons along the coast of North Carolina. Bogue Sound, Back Sound, and to some extent even Core Sound (Figure 3) are marine lagoons. A number of true estuaries can be found on the North Carolina coast, such as the mouths of the Newport and Cape Fear Rivers.

Estuarine waters are characteristically variable in virtually all of their physico-chemical properties. For example, Rice and Ferguson (1975) describe the variability in temperature and salinity in the Newport River estuary in North Carolina. Animals and plants that inhabit estuaries must be able to tolerate this extreme environ-

mental variability. Much of the variability, in temperature and salinity especially, is on a very short time scale in that it is produced by the change of tides and the alternating influence of the sea and of terrestrial runoff (Roelofs and Bumpus 1954). Along the Atlantic coast of North America tides are semidiurnal, meaning that there are two low and two high tides daily. Consequently, every 6 hr or so, conditions within an estuary are likely to change radically. Water temperature and salinity within an estuary or lagoon vary with tidal movements. As the incoming tidal current penetrates the estuary, salinity rises. In winter, water temperature also rises abruptly on incoming tides; in summer, the ocean is colder and provides a cooling influence at high tide (Roelofs and Bumpus 1954). Because of these sudden changes in the physical conditions that recur with each tidal change, daily changes in many environmental variables in an estuary or marine lagoon are often a large fraction of the total annual variation. This renders the estuary a harsh physical environment for both plants and animals.

The movement of tidal currents through the complete ebb and flood cycle is rarely symmetrical in any sound or estuary. Inlets at the mouths of sounds and estuaries are usually either ebb-dominated or flood-dominated. In a system dominated by flood tides, the incoming tidal currents usually last a shorter period of time than the outgoing currents, but the incoming flood currents are much faster. Ebb-dominated systems possess the opposite pattern. In both ebb- and flood-dominated systems, the flow velocities vary through the tidal cycle. The alternating directions of flow produce short periods (up to 20 or 30 min) of slack water inside sounds and estuaries near the time of the change of the tides. During these periods turbidity drops to a minimum only to rise again with the resumption of tidal currents.

Turbidity of the water column is, in part, related to the degree of input from rivers into the coastal waters. Estuaries tend to be more turbid than coastal lagoons, where terrestrial input is negligible. Some estuaries like those along the Georgia-South Carolina coast experience greater freshwater flows and have higher turbidity levels than others, like the Newport River estuary in North Carolina. There is a general gradient of increasing turbidity from the central North Carolina estuaries and coastal lagoons to those of the south-

eastern states (Meade 1969). Turbidity is significant biologically in that sunlight penetration is so reduced in extremely turbid waters that phytoplankton productivity is inhibited and subtidal benthic algal production is nearly eliminated.

Physical changes in the water column are greatly buffered by the sediments, such that benthic infauna (animals living buried within the sediments) are sheltered from the extensive environmental variability of the overlying waters. This buffering action occurs for temperature (Johnson 1965), salinity (Reid 1930, 1932, Sanders et al. 1965, Johnson 1967), and other physico-chemical properties, and is especially significant for short-term variation such as is generated by the tidal cycle. The deeper one penetrates into the sediments, to a depth of approximately 10 cm, the greater is the buffering effect (Johnson 1965). An infaunal mode of living permits the avoidance of many of the rigors of the estuarine physical environment.

The intertidal zone is a physically rigorous place to live for any marine organism. Exposure to air, the sun's heat, and the wind during a portion of almost every tidal cycle is inevitable. This exposure can cause desiccation, overheating, and death for many marine organisms. Among the marine animals on an intertidal flat, feeding must cease whenever the overlying waters recede. Because the highest levels of the intertidal zone are exposed for longer periods than the middle and lower intertidal zones, there is a gradient of increasing intensity of physical rigor which runs from the subtidal to the top of the intertidal zone. The effects of this gradient in physical stress have been well described on rocky shorelines (Connell 1970), but there is very little information available on the impact of the varying degrees of aerial exposure on soft-sediment organisms. It seems likely that numerous species of plants and animals in soft sediments are restricted to subtidal habitats or at least to the lowest intertidal zones by the rigors of exposure. For instance, the seagrasses are almost certainly limited at the high margins of their distribution by such increased physical harshness. Many epifaunal species, which as a group do not possess a sedimentary buffer, are also limited to subtidal zones or to the low intertidal by physical stress. Infauna with protective outer skeletons or shells (such as clams) are probably not so greatly affected by such exposure to air.

Sandy sediments contain interstitial spaces among the sand grains which permit a great deal of diffusive exchange with the overlying water column. For this reason, the buffering effect of living at depth in the sediments is not quite as great in sands as it is in muds, although it is still a significant factor. Because of the large quantities of oxidizable organic matter (detritus) contained in the sediments of estuarine systems, the biological oxygen demand (BOD) is extremely high in the sediments. This demand produces anoxic conditions at depth in the sediment column of mud flats and sand flats. Because of the higher exchange rates with the overlying oxygenated waters and the lower concentrations of detritus in sandy sediments, the boundary between the oxygenated layer at the surface and the deeper anoxic sediments (the so-called "redox layer") occurs at a somewhat greater depth in sandy sediments than in muddy sediments (Figure 4).

Sandy and muddy sediments generally differ radically in their chemical environments as a direct consequence of their differing BOD levels. In muds, the supply rate and concentration of detritus are sufficient to use up all the oxygen available so that a reducing environment exists below the surface centimeter. Here anaerobic bacteria dominate the sediment chemistry and will produce reduced compounds which accumulate in the sediments (e.g., characteristically black iron sulfide and distinctively odoriferous hydrogen sulfide). This smell of "rotten eggs" is what many visitors best remember of a visit to a coastal mud flat. In contrast, detritus is supplied to a sand flat at a rate for which sufficient oxygen exists for oxidative decomposition reactions, and the chemical environment is far different. To emphasize this difference, Fenchel (1969) has coined two terms, defining the microbial community found on mud flats as a sulfuretum system and the sand flat community as an estuarine sand microbiocenosis.

In shallow estuaries and sounds, the sediments actually determine much of the water chemistry because of their frequent resuspension and great chemical activity. In some deeper areas, particularly where there is seasonal stratification of the water column and reduced mixing, the water column at depth can become anoxic as a result of the BOD of the sediments. Such anoxic conditions frequently occur during the summer in areas of

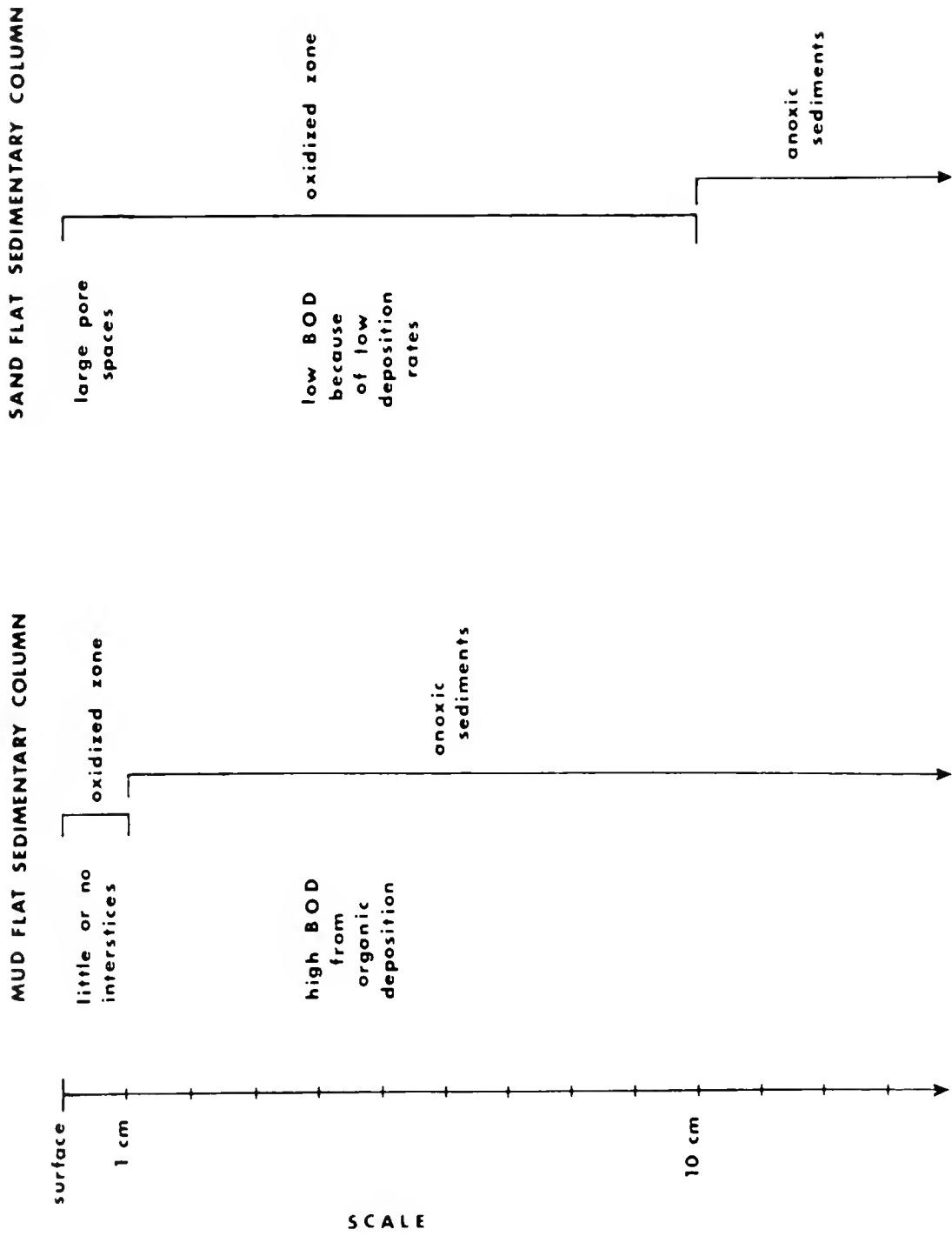


Figure 4. Diagrams of sedimentary columns from sand and mud environments.

North Carolina's Pamlico Sound (Tenore 1972), proving toxic for most benthic organisms and often causing extensive fish kills as well. Anoxia never develops in the water column and in the surface sediments of intertidal flats because of the surface mixing along the shorelines.

1.4 THE ESTUARY AS A NUTRIENT TRAP

Coastal lagoons and estuaries ordinarily possess far higher concentrations of nutrients than the sea itself or than the freshwaters running off from land. The high nutrient levels stimulate plant growth resulting in the high organic productivity that characterizes estuarine environments. In particular, nitrogen and phosphorus, the two most important nutrients required for plant growth, can be found in abundance in estuarine waters.

Estuaries act as nutrient sinks for at least three major reasons. First, and probably most important, is the effect of the sediments. Clay-sized sediment particles tend to adsorb nutrients and other chemicals (Rae and Bader 1960). When concentrations in the water column decline, the sediments give up their adsorbed nutrients in a classical chemical equilibrium reaction (Pomeroy et al. 1965). The sediments thus serve as a buffer for phosphates, nitrates, and other chemical species. When biological reactions occur to utilize available dissolved nitrates and phosphates, the nutrients deposited in the "sediment bank" are released into the water column, helping to maintain nutrient concentrations at high levels in estuarine waters.

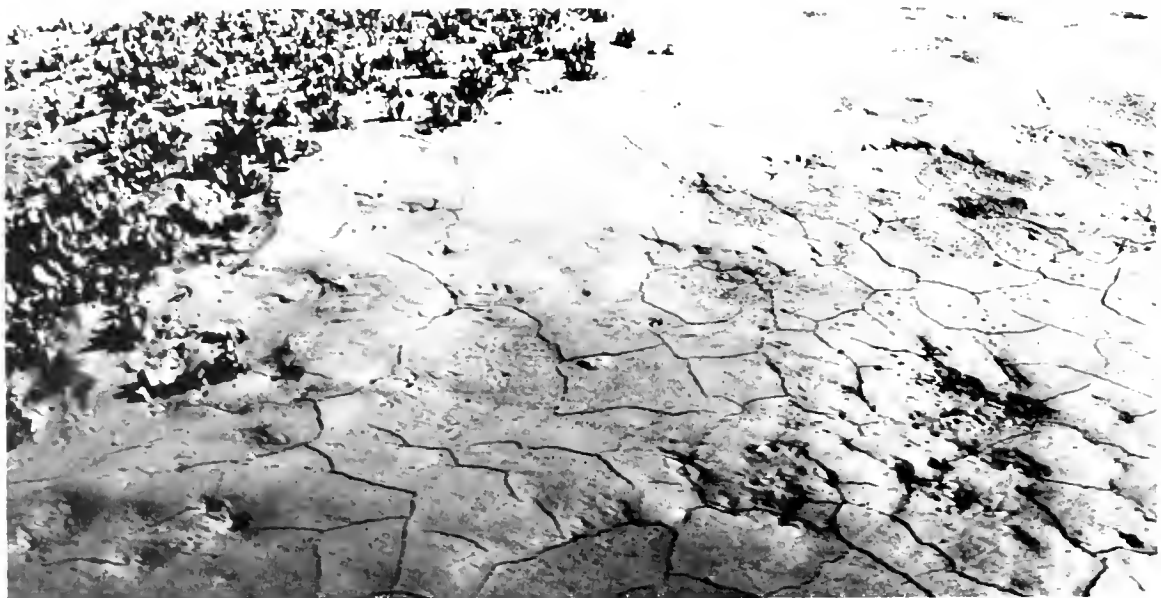
A second cause of high nutrient levels in estu-

arine systems is related to the basic circulation pattern of estuaries and lagoons. Lunar tides produce an ebb and flood of coastal waters with minimal net movement of particles and even water molecules. Physical oceanographers characterize estuaries and dissolved species of chemicals within them by their residence times in the system. Some chemicals have long residence times while others pass through more readily. In general, coastal waters are characterized by relatively long residence times as a consequence of the ebb and flood patterns of the estuary or lagoon. In well-stratified estuaries, it is easy to see how particles (including adsorbed nutrients) can be carried out toward the sea by the freshwater flow at the surface and then returned upstream by the tidal wedge below, which flows as a counter-current when the tide is rising.

The process of biodeposition also helps account for the nutrient-sink properties of estuarine systems. Large numbers of suspension-feeding molluscs and crustaceans in estuaries and lagoons remove suspended material from the water column and package it into feces and pseudofeces. These act as large particles (which they are, even though a conglomerate of smaller units) and sink to the bottom. There they become buried, but by no means are the nutrients bound within them lost. Subsequent erosion, sediment reworking by animals, and the uptake of deeper nutrients by macrophytic benthic plants maintain these nutrients in the estuarine system. Further discussions of the basic structure and biology of estuarine systems appear in a number of texts, including Barnes (1974) and Reid and Wood (1976).



Expansive intertidal flats often fringe the bays and sounds of the mid-Atlantic coast. Photo by Larry R. Shanks, U.S. Fish and Wildlife Service.



The intertidal habitat is subjected to physical extremes. In summer, the substrates often become desiccated between tides. Photo by Rhett Talbot, University of South Carolina.

CHAPTER 2. THE FLORA OF INTERTIDAL FLATS

2.1 MICROFLORA

To the untrained eye, an intertidal mud or sand flat usually appears barren and almost totally uninhabited by plants. Microalgae, however, are extremely abundant in and on the sediments of intertidal flats. These small plants can be best viewed and identified under a microscope, but they are frequently obvious to the naked eye as a conspicuous discoloration of the sediment surface. Benthic diatom films appear as brownish stains on the sediments, while green microalgae occasionally tint the sediments with bright greens.

Several different groups of microalgae are important on intertidal flats: benthic diatoms, benthic dinoflagellates, filamentous greens, and blue-green algae. Of these, the diatoms are usually the most numerous with pennate forms such as *Navicula* and *Nitzschia* predominant. Benthic diatoms such as *Navicula* occasionally form dense multilayered sheets on intertidal flats (Pamatmat 1968). Mats of blue-green algae are often obvious features of protected flats (Brenner et al. 1976, Polimeni 1976). These mats, composed of several blue-greens (*Lyngbya*, *Microcoleus*, and *Phormidium* in North Carolina) and also some diatoms, are located in the high intertidal zone. During low tides, they often dry into a hard black or blue-green crust that resembles asphalt. Although these blue-green mats in the high intertidal and the diatom mats in the lower intertidal are perhaps the most prominent examples of intertidal microalgae, even where they are not conspicuous, benthic microalgae are usually important primary producers on intertidal flats.

Benthic microalgae are of two types – mobile and attached. The attached forms tend to be relatively small and to adhere to the surfaces of sediment particles (Meadows and Anderson 1968). In some areas, mobile forms migrate vertically in the sediments. For instance, Pomeroy (1959) demonstrated vertical migration among the microalgae on an intertidal mud flat in Georgia. When the tide was out the algae lived on the sediment surface, whereas at high tide the densest concentra-

tion of benthic microalgae was lower in the sediments. In other systems, such as on the intertidal sand flats of False Bay, Washington (Pamatmat 1968), the algae apparently do not migrate vertically. Living algae can often be found to depths of 10cm, but the majority is usually located within the top centimeter of sediments. In turbulent areas and in places undergoing erosion, the biomass of benthic microalgae is much lower than on relatively protected flats.

2.2 MACROPHYTES

Although an intertidal flat contains, by definition, no marsh plants or seagrasses, macrophytic algae are often a conspicuous element of this environment. Attached to shell debris, pebbles, and other small fragments of hard substrate, large numbers of macrophytic marine algae can frequently be found. In North Carolina, which lies at the boundary of two major biogeographic provinces, the macrophytic algae of intertidal flats undergo an almost total turnover during the year. In winter (from around November through March) various species of *Ectocarpus*, a filamentous brown alga, are extremely common on intertidal sand and mud flats in areas of relatively high salinity. This alga is replaced in spring by equally massive amounts of the filamentous greens, *Enteromorpha* and *Cladophora*. These greens are abundant from around February through June on North Carolina flats. In summer (April – July) the leafy green alga, *Ulva*, is dominant in this environment. Only in the fall do macrophytic algae fail to be prominent in the intertidal zones of North Carolina's sand and mud flats. Although most of these macrophytes are attached to hard substrates, floating mats of actively growing and healthy *Enteromorpha* and other green filamentous algae are also common on many intertidal flats. These mats can occasionally be quite extensive, covering up to 50% or more of the total area of some intertidal flats during summer months.

2.3 BACTERIA AND FUNGI

Fungi and especially bacteria are extremely

abundant on the surfaces of sediment particles in intertidal flats. Smaller particles, because of their greater surface area, contain larger populations of microbes than coarser sediments (Zobell 1938, Newell 1970). As a result, bacteria and probably also fungi tend to be more abundant in the sediments of mud flats than in sand flats (Levinton 1972). Both bacteria and fungi play an important ecological role in converting dead organic matter to inorganic nutrients (a process termed mineralization), which are then available to support another cycle of primary (plant) and secondary (animal) production. Because this mineralization process occurs in the sediments, nutrients are made rapidly available to benthic plants, whereas planktonic algae, especially in deeper waters, are often severely limited by the slow return of nutrients to the water column. Fungi are commonly found on decomposing plant material, whereas bacteria are abundant decomposers of both plant and animal matter. Fungi tend to act inside the detrital particle by extending long hyphae, while bacteria are most commonly associated with the outer surfaces. Both fungal and bacterial decomposition are aided by the activities of various animals which serve to break up the detritus into progressively finer particles with larger and larger surface area.

In addition to their role as mineralizers of detritus, bacteria (and probably also fungi) play another extremely important part in the dynamics of estuarine systems. They also serve as a trophic intermediate between relatively indigestible plants (and plant fractions such as cellulose and lignin) and potential consumers of plant detritus (de la Cruz 1973, Tenore 1977). Many studies of marsh plants, including *Spartina* (cord grass), *Juncus* (needle rush), and *Salicornia* (saltwort), and of seagrasses, including *Zostera* (eelgrass), *Halodule* (shoalgrass), and *Thalassia* (turtle grass), in various estuarine systems around the world have demonstrated that very little of the primary production is grazed directly by herbivores (Teal 1962, Tenore 1977). Most of the plant matter dies and is shed into the water. A large fraction (probably exceeding 50% in most systems) of the dead plant material that is shed each year from marsh plants and seagrasses is carried away from the immediate area where the plants grew and is ultimately processed by decomposers and detritivores elsewhere within the estuarine or coastal marine ecosystem (Odum and de la Cruz 1967, de la Cruz 1973).

For the same reasons that render the living plant largely indigestible to herbivores, the dead

plant matter is not directly usable by most detritivores (Zobell and Feltham 1942, Newell 1965). The plants (especially *Spartina* and *Juncus*) contain high levels of carbon but few nutritious proteins. By growing on this relatively intractable detritus, protein-rich microorganisms provide a means of making some of that energy bound up in plant material available to consumers and higher trophic levels (de la Cruz 1973, Tenore 1977). Numerous studies have demonstrated that the consumption of detrital particles by various detritivores results in the assimilation of the bacteria but in little or no digestion of the detritus itself (Fenchel 1970, Newell 1970, but see also conflicting evidence in Adams and Angelovic 1970, Cammen et al. 1978). Passage through the gut often serves to aid the process of mechanical break-down of the detritus despite this lack of direct digestion of the detritus (Fenchel 1970). This explains why the reingestion of feces (termed coprophagy) is a commonly observed practice among many marine deposit feeders (detritivores) (Johannes and Satomi 1966, Frankenberg and Smith 1967). Fecal pellets are enriched in detritus but stripped of much of their bacteria and presumably fungi during passage through the animal's gut. After it is defecated, the fecal pellet is rapidly recolonized by microbes, which because of high bacterial growth rates quickly increase in abundance, such that after a sufficient lag time the fecal pellet is again suitable for consumption by detritivores (Newell 1965, Fenchel 1970, Hargrave 1970). Many researchers who study marine benthic deposit feeders believe that this process of microbial renewal on detritus is an important rate-limiting step which determines the abundances of various deposit-feeding species in marine benthic communities (Levinton 1972, Levinton and Lopez 1977). The best studied of these deposit feeders are snails of the genus *Hydrobia*, which live on intertidal mud flats.

In addition to their role as mineralizers and their role as trophic intermediates between detritus and its consumers, bacteria in marine systems have a third major function. Some bacteria are capable of growing on dissolved substances from the water column. Such activity essentially produces edible particulate matter (the bacteria) from substances that would otherwise be unavailable to higher-level consumers. Dissolved substances which some bacteria can utilize in this fashion are of two major types: (1) dissolved organic compounds, previously excreted or other-

wise released largely by plants, and (2) dissolved inorganic compounds. Bacteria that can grow on dissolved inorganics are termed chemo-autotrophs because they produce particulate organic matter without directly utilizing the sun's energy in photosynthesis. Instead, they utilize energy in the chemical bonds of certain inorganic compounds, notably hydrogen sulfide. Bacteria on marine soft sediments exhibit a broad range of functional strategies from 100% chemo-autotrophs to 100% utilizers of solar energy. Despite the importance of bacteria as chemo-autotrophs in oceans and the abundance of high-energy sulfur compounds in intertidal mud flats, this sort of production of particulate food is apparently not very significant on tidal flats, not even on mud flats. Primary production based upon photosynthetic pathways far outweighs the contribution from chemo-autotrophy in such a well-lighted environment.

Although most of the detritus upon which decomposers are operating is produced in other estuarine habitats, much of this detritus ultimately does reach the intertidal flat. Newly sloughed-off plant material usually rafts away from the immediate vicinity of its production (Odum and de la Cruz 1967), and, because it floats on the water surface, much of it is deposited by the wind and tides in the intertidal zone, especially along the most recent high-tide line. Here numerous animals fragment it, process it, and gradually work it into the sediments so that the detrital content of intertidal flats can be quite substantial (Odum 1970a). Food levels for detritivores can thus be high on intertidal flats, especially on mud flats (as shown by Ferguson and Murdoch 1975 for a North Carolina estuary). Decomposition (mineralization) of this detritus, which is derived from other habitats, helps to fuel the substantial rates of productivity by benthic microalgae on the intertidal flats and even by phytoplankton in the overlying water column. Rublee and Dornseif (1978) counted bacteria in sediments taken directly from an intertidal marsh in North Carolina and found that bacterial abundances declined significantly with depth in the sediments, suggesting that food levels for detritivores are far higher in surface sediments.

2.4 PHYTOPLANKTON

At high tide, when the intertidal flats are covered by flood waters, phytoplankton have the opportunity to grow and reproduce in intertidal

areas. In North Carolina's estuaries, various diatoms, especially *Skeletonema*, dominate (Carpenter 1971, Williams 1973). Winters are characterized by low levels of phytoplankton probably because of low light levels and low temperatures. Coastal waters are therefore quite clear in winters, except when clouded by silt in the runoff after heavy rains. Phytoplankton concentrations usually peak in spring and remain almost as high during summer, substantially increasing the turbidity of coastal waters. Intertidal flats contribute significantly to total phytoplankton production in estuarine systems because at high tide when the flood waters spread out across the flats the total area (and volume) of the euphotic zone (the zone where light levels are sufficient for net photosynthesis) is greatly increased, often by a factor of two or more (Figure 5). The degree to which the intertidal flats enhance phytoplankton production by increasing the euphotic zone at high tide can probably be approximated by the proportion of the estuarine bottom that is intertidal. However, no studies have yet been done to measure this effect quantitatively. Despite the relatively high levels of nutrients in estuaries, phytoplankton production is limited in North Carolina's estuaries by nitrogen concentrations (Williams 1966).

2.5 MEASUREMENTS OF PRIMARY PRODUCTIVITY

In a review of the data on the rate of production of plant matter (primary productivity) on intertidal flats, one must necessarily consider each of the major types of plant on the flats, namely (1) benthic macrophytes, (2) benthic microalgae, and (3) phytoplankton. Because the intertidal flats receive organic input from other wetland habitats, the productivity of other major elements of the whole estuarine system must also be described here. Fragments, large and small, of important producers, such as marsh plants (e.g., *Spartina*, *Juncus*) and seagrasses (e.g., *Zostera*, *Halodule*, *Ruppia*), are found abundantly on and in the sediments of intertidal flats. The intertidal flats are not a closed system ecologically, but rather rely upon organic inputs from other wetland habitats as well as their own *in situ* production.

The plants of the salt marsh have received a great deal of attention as a result of several studies

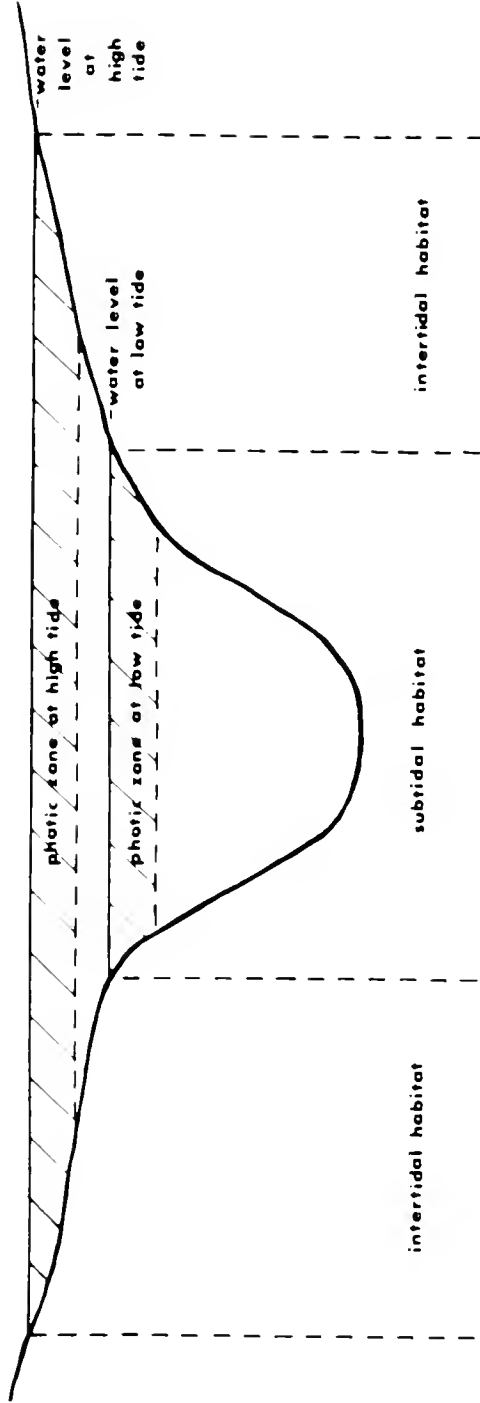


Figure 5. A diagrammatic cross-section of a sound, lagoon, estuary, or river mouth illustrating how high tide increases the extent of the euphotic zone. The increase is approximately proportional to the ratio of the area of intertidal flats to the area of subtidal bottom. An increase in the euphotic zone permits a corresponding increase in phytoplankton productivity. Notice that elimination of any of the intertidal flat habitat, for instance by dumping dredge spoils and thereby raising the sediment level, will reduce phytoplankton production accordingly.

which have demonstrated their high rates of primary production. Primary productivity is often measured in units of grams of carbon produced per square meter of ground per year or in grams dry weight per square meter per year. Since carbon makes up slightly less than one-half of the dry weight of these marine plants, one could multiply grams of carbon by approximately 2 to convert to grams dry weight. Well-known studies of the Georgia *Spartina alterniflora* marshes by Smalley (1959) and Odum and Fanning (1973) have produced productivity estimates as high as 3990 g dry wt/m²/yr. Keefe (1972) and Turner (1976) reviewed the various salt marsh productivity studies and concluded that production usually declines on a gradient from south to north along the east coast of North America. In North Carolina, primary productivity of *Spartina alterniflora* marshes usually falls in the range of 329 to 1296 g dry wt/m²/yr while *Juncus roemerianus* production lies between 560 and 1960 g dry wt/m²/yr (Keefe 1972). Stiven and Plotecia (1976) employed a multiple regression model to analyze the importance of several factors on marsh productivity using data from 23 east coast marshes. They found that along the east coast of North America, vegetational species, latitude, growing season, temperature range, and mean tidal height explained 69% of the variation in reported productivities.

Virtually all of these studies rely upon what is termed the harvest method of estimating net primary productivity. At the time of peak standing crop (usually in the fall), sample plots are harvested and the plants are dried and weighed. Assuming that marsh plants undergo incremental growth to a peak height without loss of any significant portions during the year, this peak biomass would represent the total production for the full year. Such an assumption obviously produces an underestimate of true productivity. Kirby and Gosselink (1976) demonstrated that the underestimate was large indeed in a Louisiana *Spartina alterniflora* marsh. By using the so-called Wiegert-Evans "old-field" method of estimating primary productivity, which involves estimating the death and loss of vegetation during the year, they demonstrated that true annual rates of primary production are about two and one-half times the harvest estimates. Although the published harvest estimates seem relatively high for marsh plants, actual values are even higher.

Just how great the primary production of marsh plants is has been discussed by Odum (1959). Most marshes are more productive than cultivated and highly managed terrestrial crops. The world's average production for corn fields is 412 g carbon/m²/yr, while rice is 497 g carbon/m²/yr (Odum 1959). In the U.S., hayfields are highly productive, but they average only 420 g carbon/m²/yr. The most productive parts of the seas occur in upwelling areas, such as off the coast of Peru (Ryther 1969); however, these upwellings too are not as productive on an areal basis as a salt marsh.

Seagrass beds also show relatively high productivities in many areas. Values for annual production of *Zostera* range from approximately 5 to 600 g carbon/m²/yr (Phillips 1974). In North Carolina, *Zostera* productivity has been measured near Beaufort at approximately 330 to 340 g carbon/m²/yr (Dillon 1971, Penhale 1977). Mixed in with the eelgrass in this area is another seagrass, *Halodule*, and a brown alga, *Ectocarpus*, which together contribute another 73 to 300 g carbon/m²/yr (Dillon 1971, Penhale 1977). If these estimates are representative of the subtidal seagrass beds in North Carolina's estuarine systems, then it is clear that an acre of a North Carolina seagrass bed is also more productive than rice, corn, and the other terrestrial crops listed by Odum (1959). In the sounds and estuaries of North Carolina, seagrass beds are prominent and clearly important producers of detritus, some of which is processed on mud and sand flats.

As is suggested by its low standing crop, the productivity of phytoplankton in estuarine systems has long been thought to be relatively low. For instance, Marshall (1970) estimated that phytoplankton contributed only 50 g carbon/m²/yr to New England's subtidal shoal waters, compared to a contribution of 125 g carbon/m²/yr for all macrophytes. In the Newport River estuary at Beaufort, North Carolina, Williams (1966) and Thayer (1971) estimated that phytoplankton produce about 110 g carbon/m²/yr. Ragotzkie (1959) measured oxygen uptake in light and dark bottles (a conventional means of estimating net phytoplankton productivity) in the Duplin River estuary of Georgia and found phytoplankton production to be negligible.

Despite this prevailing concept that phytoplankton contribute an insignificant fraction of total carbon to the estuaries and lagoons, more recent data provide support for a different viewpoint. Sellner and Zingmark (1976) found phytoplankton production as high as 350g carbon/m²/yr in shallow tidal creeks and estuaries of South Carolina. Haines (1977) has demonstrated that the majority of the detrital pool in a Georgia estuary has a ratio of stable carbon isotopes (termed the $\delta^{13}\text{C}$ ratio) appropriate for either phytoplankton or benthic microalgae and not for *Spartina*, *Juncus*, and seagrasses. This suggests that phytoplankton and benthic microalgal production in estuarine systems is far greater than past measurements indicate. Further research is necessary to resolve this issue. In North Carolina's sounds, and even in its estuaries, the summer turbidity tends to be low, suggesting that phytoplankton production could often be significant.

Very little work has been done to measure *in situ* primary production of benthic algae on intertidal sand and mud flats. There are no estimates of macrophyte productivity from these habitat types, despite the obvious abundance of macrophytes like *Ulva*, *Enteromorpha*, and *Ectocarpus*. Some estimates are available, however, for the benthic microalgae. Pomeroy (1959) measured microalgal productivity throughout the year on an intertidal mud flat in Georgia. He found that annual gross productivity of benthic microalgae was about 200g carbon/m²/yr. Net production (that quantity measured in macrophyte studies) is at least 90% of this figure. Pomeroy (1959) observed that benthic primary productivity remained nearly constant year-round on this mud flat. In summer, productivity was greatest at high tide, whereas in winter the algae were more productive when the tide was out. Four other studies have measured benthic diatom production on tidal flats year-round. Pamatmat (1968) found microalgal productivity on an intertidal sand flat in False Bay, Washington, to be about the same as measured on flats in the Danish Wadden Sea (Grøntved 1960), namely about 116 to 178g carbon/m²/yr. In intertidal flats of a southern California lagoon, microalgal productivity was estimated to be about 200g carbon/m²/yr (Onuf et al. 1980). Leach (1970) found microalgal productivity to be 31g carbon/m²/yr in the Ythan estuary in Scotland at latitude 57° N. Since latitude seems to explain much of the variability in these observations (lower productivity at high lat-

itudes where sunlight is more limited), the intertidal flats in North Carolina probably produce close to 200g carbon/m²/yr. The only available value for a North Carolina microalgal community (Bigelow 1977) is far lower (40g carbon/m²/yr), but that figure comes from a 6-month study of the Newport River estuary where turbidity is probably greater than in sounds and is probably not representative of North Carolina's intertidal flats in general.

2.6 FOOD CHAINS OF INTERTIDAL FLATS

The entire estuarine ecosystem is commonly viewed as a detritus-based system in which the vast majority of consumer food chains is based at the bottom level upon the consumption of detritus and its associated microflora. (See Nixon and Oviatt 1973 for an excellent and detailed analysis of energy flow in a New England estuary.) This viewpoint is supported by the numerous observations on (1) marshes and marine grass beds which demonstrate little *in situ* herbivory despite very high productivity, and (2) gut contents of consumer organisms which are frequently dominated by detrital particles (Teal 1962, Tenore 1977). Classic studies of the Georgia estuaries, where marshes cover a large proportion of the total estuarine acreage, have emphasized the tremendous importance of marsh plant detritus in the nutrition of the large majority of shrimp, crabs, and fishes of the estuarine ecosystem (Teal 1962, Odum and de la Cruz 1967).

Despite such conclusions about the importance of detritus in the energy flow of estuarine systems and in the fueling of the consumer food chains, it has remained difficult to confirm the quantitative importance of detritus and its associated microflora in the nutrition of any given species. Gut contents are not especially useful for determining the diets of detritivores and other consumers low in food chains because of difficulties in interpretation of such information. Often the gut contents cannot be identified because of their advanced state of decomposition. Even the basic distinction between marsh plant and diatom or seagrass detritus is usually impossible. Furthermore, what is found in the gut is not necessarily what is being digested and assimilated. The majority of the gut contents of a detritivore will usually pass through undigested. As a result, even the accurate identification of the source of the detritus in guts does not permit reasonable inferences

about the relative importance of various types of primary producers in the nutrition of the animal. Differential rates of digestion of those food sources which are actually ingested cause further difficulty in the interpretation of data on gut contents (Peterson and Bradley 1978). The most quickly digested items may be greatly diminished or even absent from most gut contents.

A recent technique has been developed which has the potential to circumvent all of these problems with interpretation of gut content data. Two different stable carbon isotopes exist in nature, ^{13}C and ^{12}C . The ratio of these two isotopes (the so-called $\delta^{13}\text{C}$ ratio) is constant in the atmosphere. However, photosynthesis does not draw its CO_2 randomly and can enrich the photosynthate (the plant's carbohydrates) in one or the other carbon isotope. Plants which utilize the Hatch-Slack (C_4) pathway of photosynthesis have a characteristic $\delta^{13}\text{C}$ ratio that differs greatly from the ratio incorporated by plants which utilize the Calvin (C_3) pathway. Grasses such as *Spartina* are C_4 plants, while most other vascular plants are C_3 plants. Benthic diatoms have predictably and consistently intermediate $\delta^{13}\text{C}$ ratios (Haines 1976a, b, Thayer et al. 1978). Distinctions can thus be drawn among the major types of primary producers in the estuary.

Haines and Montague (1979) have done feeding experiments in the laboratory to demonstrate that animals which consume plant material incorporate a $\delta^{13}\text{C}$ ratio that reflects that of their food. This appears to be true even if the plant detritus passes first through a microbial intermediate (Haines 1977, Haines and Montague 1979). As a result, the relative importance of certain major types of plants (marsh grass vs. seagrass vs. algae) in the diet of a detritivore can now be inferred by analyzing the detritivore's $\delta^{13}\text{C}$ ratio. This technique has a tremendous advantage over using gut content information in that it provides an integration of the animal's diet over quite a long (but undefined) period of time instead of yielding just an instantaneous picture of the most recent meal. Some results of this work are available (Haines and Montague 1979) which tend to contradict previous assumptions about the importance of marsh plant productivity to some of the detritivores that dominate the fauna of an estuarine system. The results reveal that algae (phytoplankton and benthic microalgae combined) are

far more important than expected in the nutrition of consumers in estuarine systems. Haines (1977) has also shown that the detrital pool of particles available for breakdown and subsequent incorporation by consumers in a Georgia estuary is largely derived from algal sources, not from marsh grasses. If it is true, however, that phytoplankton and benthic microalgae are more important producers of utilizable detritus than are the highly productive marsh macrophytes, a major question remains unanswered. Where does all of that marsh productivity go? Research is necessary to resolve this issue.

In estuarine systems of North Carolina, Virginia, and Maryland, and, to a lesser degree, elsewhere along the east coast of the United States, it is clear that the areal extent of the phytoplankton habitat is often far greater than the areal extent of the marshes and seagrass beds. Estuarine systems with large expanses of open water, such as are found in North Carolina, would be expected to support high phytoplankton production. Bigelow (1977) has constructed a summary table (Table 1) for the Newport River estuary in North Carolina, which presents the available data on the productivity of each major type of primary producer. In this table he also lists the areal coverage of each habitat and from these data calculates the relative importance of each type of plant in the total production of the entire estuary. Phytoplankton account for 49% of this estuary's total productivity, *Spartina alterniflora* 42%, while benthic microalgae contribute only 7.4%, and *Zostera* only 1.4% to the total. Bigelow had no data on the production of benthic macrophytes like *Ulva*, *Enteromorpha*, and *Ectocarpus*, so these plants are not included in these percentages.

There is more suitable phytoplankton habitat and often also more suitable habitat for benthic microalgae than there is marsh area in North Carolina estuaries. Thus, even though the per-unit-area productivity of phytoplankton and benthic microalgae may not be as great as the areal productivity of *Spartina*, the total amount of microalgae produced in the estuary may be higher. A large proportion of this estuarine phytoplankton production and essentially all of the benthic microalgal production is transformed into benthic invertebrates on intertidal and shallow subtidal flats. The benthic microalgae are probably far more important in this process than their

Table 1. Net annual primary productivity of each major source of plant production in the Newport River estuary (from Bigelow 1977).

Source of primary production	Effective area of habitat (km ²)	Productivity (g C/m ² /yr)		Reference
		Per unit area within its own habitat	Per unit area averaged over all estuarine habitats	
Phytoplankton	31	110	110	Williams (1966), Thayer (1971)
<i>Spartina alterniflora</i>	6.2	470	94	Williams and Murdoch (1969)
<i>Zostera marina</i>	0.3	330	3.18	Penhale (1977)
<i>Zostera</i> epiphytes	0.3	73	0.71	Penhale (1977)
Benthic microalgae	15.5	33.7	16.8 ^a	Bigelow (1977)

^aBased on data from June to December and multiplied by 2 to get annual production.

productivity indicates because of their close proximity to benthic consumers, making possible a high utilization efficiency on the part of the consumers. As will be developed in succeeding chapters, the intertidal flat thus serves as the habitat in which primary production from several estuarine habitats is transformed into benthic animals which provide the food resources for all probing shorebirds and many bottom-feeding fishes.

Although it is currently impossible to state unequivocally which sources of plant production are the most significant suppliers of nutrition to the consumers at the base of estuarine food chains, certain generalizations are possible. Several authors have recognized that the trophic status of an aquatic animal tends to be complex. In marine systems, most animals reproduce by using planktonic larval stages. Such larvae are generally small and become a part of the zooplankton. Some larvae feed in the water column (planktotrophic) and some do not feed until after metamorphosis (leicotropic). In either case, when the new animal first begins to feed it is usually orders of magnitude smaller than the eventual adult size. Its trophic status is likely to be entirely different from that of the adult or even the juvenile.

A progression of trophic changes through development as a function of increasing body size is common among marine animals. For instance, many predatory fishes of estuarine systems pass first through a planktivorous larval stage and then a detritivorous juvenile stage before becoming predaceous as adults. Even as adults, estuarine predators often switch to detritus as a supplement

ary food source when prey are scarce (Odum 1970a). Consequently, trophic relationships in estuaries and lagoons tend to be dependent upon available alternative food supplies as well as upon stages in the life cycles. Since most larval fishes and crustaceans in estuaries depend upon eating zooplankton during early weeks, the zooplankton of an estuarine system and the phytoplankton upon which most of them feed are far more significant than their small numbers may suggest (Odum 1970a). In North Carolina sounds, Williams et al. (1968) found relatively low zooplankton abundances and suggested that the high population levels of larval fishes may be partly responsible.

Another commonly recognized feature of estuarine food chains is their narrow base. Very few plant species are major contributors to the pool of organic detritus which fuels estuarine food webs. A wide diversity of consumer organisms is dependent upon the relatively simple base of primary production. This characteristic helps to distinguish estuarine food webs from those of terrestrial ecosystems where diversity is usually highest at lower trophic levels. In addition, within the system energy first fixed (i.e., transformed from light energy to chemical energy) by a single plant can flow up the food chain in several possible ways with several possible trophic end-points. The discussion of the fauna of intertidal flats will focus upon trophic relationships to illustrate the variety of top predators which exist at the ends of largely detrital-based food chains on the mud and sand flats of estuarine systems.

CHAPTER 3: THE BENTHIC INVERTEBRATES

3.1 BENTHIC EPIFAUNA

Benthic animals are those which live in close association with the bottom. This category includes animals which live in more or less fixed positions on top of the substrate (epifauna), those that live buried in the substrate (infauna), and those which move readily about the bottom foraging both on and in the sediments (mobile epibenthos). Marine epifauna and infauna are almost solely composed of invertebrate species, whereas both invertebrates and vertebrates are commonly represented among the mobile epibenthos.

On most sand and mud flats the epifauna is apparent, but sparsely distributed (Moore et al. 1968). In the intertidal flats of Europe and along the Pacific coast of North America, the blue mussel, *Mytilus edulis*, is the most apparent epifaunal species. Along the southeast Atlantic and Gulf coasts of North America, the oyster, *Crassostrea virginica*, is the most obvious epifaunal invertebrate. In North Carolina, oysters are often found in a dense band in the mid to high intertidal zone at the lower edge of the salt marsh (Figure 1). Below this band of oysters is usually an open mud or sand flat which may contain more oysters ("an oyster reef") at a lower level of the shoreline. In North Carolina, however, most of these oyster reefs tend to be subtidal.

Oyster beds contain numerous plants attached to the shell surfaces, and a whole community of associated animals. In North Carolina, the intertidal oyster shells are colonized by various marine algae and epifaunal invertebrates characteristic of intertidal hard substrates. Tunicates (such as *Styela*), branching bryozoans (*Bugula*), hydroids (*Pennaria*), barnacles (*Balanus eburneus* and *B. amphitrite*), encrusting bryozoans (*Schizoporella*), sponges (*Hymeniacidon*, *Cliona*), soft coral (*Leptogorgia*), and small gastropods (like *Bittium*) are common epifaunal elements associated with oyster beds.

Oysters feed upon suspended algae in the water column. Haines's (1976a) data demonstrate

this trophic link, as do numerous examinations of gut contents of adult oysters (Nelson 1921). The most important single source of energy is probably phytoplankton, but resuspended benthic diatoms and other microalgae may contribute a significant proportion. No study has successfully separated the planktonic and benthic components of the oyster's diet.

Occasional empty shells from dead clams or snails provide hard substrate for attachment by the local array of hard-surface epifauna. Except for these ephemeral substrates, there is no basis for firm attachment in a soft-sediment environment. As a result, the epifauna, other than oysters and mussels, are not important components of intertidal flat habitats. Oysters and mussels succeed in this environment, in part, by forming heavy clumps which are more stable than isolated individuals. A few other epifaunal species can be found in depressions on mud and sand flats where they have been carried by the currents. For instance, *Styela plicata* is often found in such depressions on the intertidal sand flats at Beaufort, North Carolina (Williams and Thomas 1967). Nevertheless, the oyster is the most common epifaunal resident of this habitat and certainly the most important commercially.

On relatively high-energy sand flats in North Carolina and elsewhere, various species of sea pansies (*Renilla*) are often abundant. These animals are common on sand flats at the mouths of inlets in North Carolina. They are colonial coelenterates which form a purple disk about the size of a silver dollar when fully developed. Sea pansies are not really epifaunal in that, although the disk is visible at the sediment surface, an appendage called the peduncle extends vertically into the sediments and anchors the colony in the sand. Some authors have called sea pansies semi-infaunal because of this. These colonial coelenterates are suspension feeders. They are most numerous on the ocean floor just outside the surf zone, but they are also typical inhabitants of the high-energy sand flats of sounds and lagoons.

3.2 BENTHIC INFAUNA

Soft substrates, because of their mobility, are most suitable for occupation by infaunal organisms. The infauna are usually subdivided into three groups: the microfauna, the meiofauna, and the macrofauna. The distinction between the groups is occasionally blurred, but basically the microfauna are the smallest benthic animals (passing through a 0.062 mm mesh); the meiofauna are small, but somewhat larger benthic animals (usually those which pass through a 0.5 mm mesh but are retained on a 0.062 mm mesh), while the macrofauna are larger (those retained on a 0.5 mm mesh). This size distinction also corresponds broadly with some major taxonomic size breaks, so that the operational definitions of microfauna, meiofauna, and macrofauna do not reflect a purely arbitrary decision. Among the meiofauna, those taxa which never grow large enough to be retained on a 0.5 mm mesh are termed the permanent meiofauna. Macrofaunal juveniles which are still small enough to be within the meiofaunal size range are termed the temporary meiofauna.

Microfauna include all protozoans. Ordinarily, the most numerous are foraminifera and ciliates; these groups can be extremely abundant on some intertidal flats, but their ecological roles are poorly understood. Because foraminifera produce a calcified test which is left behind at the animal's death, geologists and paleontologists have studied them more intensively than have marine biologists.

The meiofauna of intertidal sand flats differ considerably from the meiofauna of intertidal mud flats. Sands are by definition coarser, which means that larger interstitial spaces exist between adjacent particles. The meiofauna of sands are largely interstitial organisms, well-adapted to moving among these sediment grains. Gastrotrichs and turbellarians are essentially restricted to the sand environment (McIntyre 1969). The interstitial spaces in sands provide oxygenation to deeper sediments so that the meiofauna of sands are distributed over a broader range of sediment depths, extending in abundance to 10 cm or more. In mud flats, the meiofauna are restricted to surface sediments. Nearly all of the individuals occur within the top centimeter or in the oxygenated zone which may extend slightly deeper or shallower than 1 cm. Here, most of the meiofauna are epibenthic forms, found on top of the sediment surface, or burrowing forms found just below the

surface. These mud animals tend to have large, stocky bodies, whereas meiofauna from sands are smaller vermiform animals, adapted to moving among the grains (McIntyre 1969).

On the intertidal flats of North Carolina, nematodes are the most numerous meiofaunal taxon. This pattern of abundance is apparently typical of shallow marine sediments world-wide. Harpacticoid copepods are ordinarily the second most abundant meiofaunal taxon. Other meiofaunal taxa of importance in North Carolina flats are the gastrotrichs, turbellarians, and gnathostomulids. Coull and Fleeger (1977) in studying the meiofauna of sand and mud flats of South Carolina found that seasonal progressions of harpacticoids occurred regularly on the mud flats, whereas harpacticoids in a sandy habitat showed less predictable patterns of variation in abundance.

The ecological role of the meiofauna is not clear. At one time, most meiofauna specialists believed that these groups represented a trophic dead end in estuarine food chains. Several more recent studies have demonstrated that various consumers feed upon the meiofauna. For instance, grass shrimp, *Palaemonetes*, greatly reduce the abundance of nematodes and a meiofaunal polychaete probably because they are preying upon them (Bell and Coull 1978). *Balanoglossus*, a common macrofaunal species in North Carolina sand flats, consumes nematodes very effectively (B. Duncan, Univ. North Carolina, Chapel Hill, Pers. Comm.). Coull and Bell (1979) reviewed all studies that demonstrate that certain meiofauna do serve as food for higher-level consumers and found that most of these studies were done in muddy sediments. Attempts to demonstrate consumption of meiofauna in sands have almost always failed. Coull and Bell (1979) suggested that the meiofauna in muds are much more available to consumers because they are densely packed into the surface sediments where a consumer can gather them readily by merely ingesting the top centimeter of sediment. In sands, on the other hand, a consumer must process a large volume of sediments to harvest the sparsely distributed meiofauna. Not many organisms are adapted for this sort of sediment processing, which is energetically expensive. Sand meiofauna may often be a trophic dead end, whereas mud meiofauna may regularly be eaten by various consumers (normally by those considered to be detritivores or deposit feeders).

The macrofauna of intertidal flats contributes a much higher proportion to total community biomass than the meiofauna at any given time. Since macrofauna are also much larger and easier to study, a great deal more is known about their ecological function in soft-sediment systems. For North Carolina, several fairly complete studies of the macro-infauna of intertidal flats are available for the following groups: haustoriid amphipods (Dexter 1967), polychaetes (Gardner 1975), and the total invertebrate infauna (Lee 1974, Commito 1976, Wilson 1978). Although prepared to cover the South Carolina coastline, Zingmark's (1978) checklists are excellent for the southern half of North Carolina's coastline. Taxonomically, the macrofauna of an intertidal flat is usually dominated by polychaete worms, bivalve molluscs, amphipods, other crustaceans, enteropneusts, sipunculid (peanut) worms, nemertean worms, gastropod molluscs, and echinoderms. Trophically, the macrofauna is ordinarily subdivided into four categories: suspension feeders, deposit feeders, predators, and scavengers (Sanders et al. 1962, Levinton 1972). Distinctions among these trophic categories are often complicated by the great diversity of ways of making a living in soft-sediment communities. Nevertheless, differences among benthic species in modes of feeding and in diet justify an attempt to produce such a trophic classification.

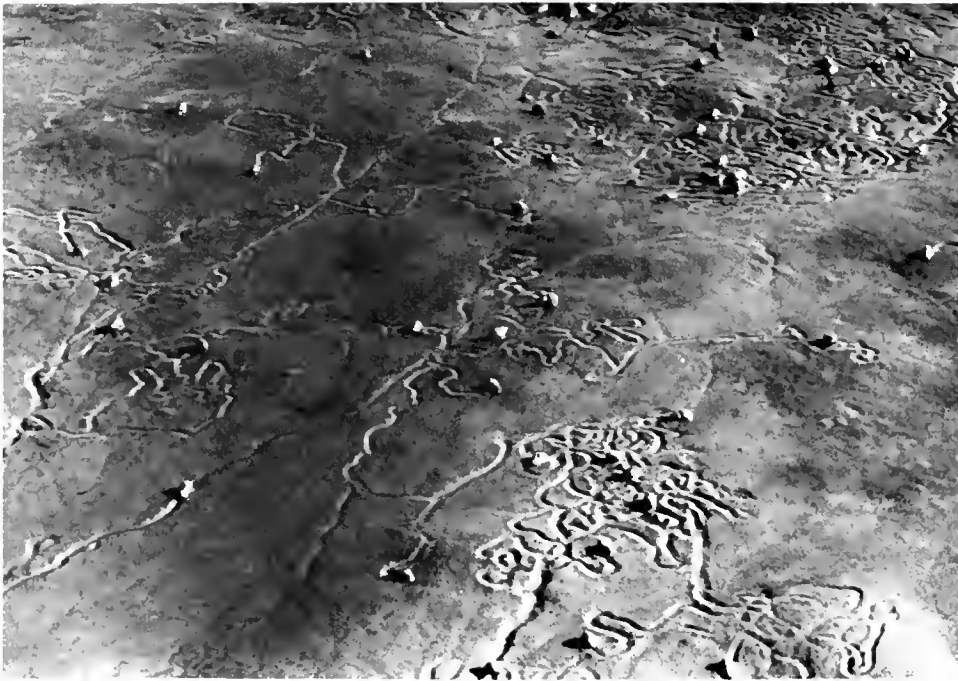
Suspension feeders take their food by capturing particles suspended in the water column. This typically requires the use of some sort of filter. Bivalve molluscs (clams) are probably the most common suspension feeders on most intertidal flats. Suspension-feeding clams pump a water current through the body cavity and past the gills, which serve as a food-collecting filter. Most suspension feeders are usually considered to be herbivores which consume phytoplankton. While it is surely true that phytoplankton contribute greatly to a suspension feeder's diet on an intertidal flat, many suspension feeders in this environment probably also capture and assimilate both resuspended benthic algae and to some extent detritus and its surface microbiota. The degree to which these possible additional sources of food contribute to the diet of intertidal suspension feeders is not known.

Deposit feeders are so named because of their general feeding mode. A deposit feeder ingests

sedimentary deposits and presumably assimilates the bacteria and fungi on detrital particles as well as the living microalgae. Many different types of benthic deposit feeders have been distinguished by researchers who study soft-sediment systems. Most deposit feeders harvest surface deposits, but some feed upon food sources at depth. Some are more selective of individual particle size and type, while others are apparently nonselective in their feeding (Sanders et al. 1962). One type of deposit feeder is termed a funnel feeder because it constructs feeding funnels in the surface sediments which it ingests. These funnel feeders and other deposit feeders can process and "turn over" large volumes of surface sediments on both sand and mud flats (Myers 1977a, b, Powell 1977, Reise 1978).

Because most deposit feeders ingest living organisms along with detritus, it is often difficult to distinguish between a predator and a deposit feeder in soft sediments. A pure predator is a species which selectively ingests individual living animals. Fauchald and Jumars (1979) have suggested that it might be better to distinguish between benthic feeding modes on the basis of relative prey size. One feeding type (which includes most pure predators) consumes prey which are large relative to the body size of the consumer. These can be called macrophages. Microphages, in contrast, take prey items which are small relative to their own body size. Microphages tend to be nonselective in their feeding because of the perceptual difficulties and excessive energetic costs of distinguishing among very small potential food particles. The true microphage is thus a deposit feeder in the classic sense. Infaunal species illustrate not only these extremes in food preferences, but also all the intermediate strategies as well. The macrophage-microphage distinction is, nevertheless, one that can often be drawn and that helps to explain differences in foraging strategies among the infauna. Common predators, or macrophages, on intertidal flats include polychaetes in the genus *Glycera* (bloodworms) and nemertean worms (ribbon worms).

Scavengers are relatively mobile species which can move to any source of dying or dead animal matter. Most infaunal scavengers in shallow marine substrates are gastropod molluscs, usually dominated by various species in the Nassariidae family. The common mud snail, *Ilyanassa obsoleta*, often



The tranquility of an intertidal flat as viewed from afar (above) belies the often frenzied biological activity obvious upon closer inspection, as demonstrated by the feeding of the mud snail, *Illyanassa obsoleta*, and the resultant bioturbation of the sediments (below). Photos by Wiley M. Kitchens, U.S. Fish and Wildlife Service.

feeds by scavenging. *Ilyanassa obsoleta* also ingests sediments and assimilates energy by this other feeding method. Like many trophic distinctions, that made between scavengers and deposit feeders is blurred by the diversity of feeding options actually employed in nature. A pure scavenger may not exist among the infauna of an intertidal flat.

3.3 CONTROLS ON INFAUNAL POPULATIONS

Infaunal species often interact strongly enough to set patterns of distribution and abundance on an intertidal flat. Such interactions can be either direct or indirect. The major form of indirect interaction among the infauna is what Rhoads and Young (1970) have termed "trophic group amensalism." They demonstrated that deposit feeders, because of their high level of mobility, tend to increase the water content of the sediments they occupy. This creates a loose, flocculent layer on the sediment surface which is easily resuspended and mixed into the water column with the slightest degree of water turbulence. Wave action and even the relatively slow motion of tidal currents are sufficient to produce such resuspension of silts and clays.

Large quantities of sediment suspended in the water column tend to clog up the filtering apparatus of suspension feeders. Consequently, wherever deposit feeders are abundant, suspension feeders tend to be eliminated. This process, involving one trophic group and the negative effects it produces upon another, is an example of trophic group amensalism. Deposit feeders are more common as a group in muddy sediments than in sands because the finer particles (muds) have greater surface area for microbial attachment and because some of these fine particles are detritus itself. In other words, food levels for deposit feeders are far higher in muds than in sands, and the density of deposit-feeding species increases accordingly. Because suspension feeders cannot feed or grow at normal rates where deposit feeders are abundant, only in sandy areas can one normally find high densities of suspension feeders. This pattern of complementary distribution of suspension feeders and deposit feeders has frequently been observed in natural infaunal distributions (Sanders 1958, Young and Rhoads 1971) and appears to be exhibited on the intertidal flats of North Carolina.

Brenchley (1978) has carried the ideas of Rhoads and Young (1970) a step further by recognizing that any species which moves around in the sediments will increase water content and stimulate resuspension of sediments. A mobile suspension feeder can produce this same effect; however, deposit feeders tend to be more active and mobile than suspension feeders, probably because most deposit feeders must forage for their food while suspension feeders need only sit and wait for water currents to carry in their meal. Usually, it is a deposit feeder which will induce high rates of sediment resuspension, as Rhoads and Young suggest. Brenchley (1978) also showed by laboratory experiments that stationary species tend to stabilize the sediments and that the total level of sediment instability produced by any assemblage is an additive result of all the various species inputs. Seagrasses, which baffle wave action and increase sedimentation rates, and large suspension-feeding clams such as cockles have a substantial stabilizing effect on the sediments which can lead to coexistence of suspension feeders and deposit feeders. Some long-lived and relatively large suspension-feeding bivalves like the stout razor clam (*Tagelus plebeius*) and the hard clam (*Mercenaria mercenaria*) may play this role in North Carolina flats.

In addition to interacting indirectly through effects on sediments, infaunal species can also interact directly. Adult infauna can and do feed upon the larvae of potential colonizers. Woodin (1976) has emphasized the importance of these "adult-larval interactions" in determining which types of species can coexist in marine infaunal communities. Suspension feeders often capture larvae of many infaunal invertebrates while they are still present in the water column and before settlement. Deposit feeders, on the other hand, have an effect upon larval survivorship just after settlement. Deposit feeders consume larvae directly as part of their diet and also cause mortality of new recruits by their physical activities in processing the sediments. Larvae that survive these "rites of passage" may then grow to adulthood in the community, if they avoid subsequent predator attacks. Woodin (1976) argues that these adult-larval interactions are strong enough in any dense infaunal assemblage to limit the membership of that assemblage to only a few of the species that could potentially live there. In other

words, the history of which species first abundantly colonize an infaunal area is extremely important and determines, in part, which species will continue to occupy that area.

In the intertidal sand and mud flats of North Carolina, infaunal densities are rarely high enough to produce exclusion of one type of species by the adults of another. The activities of adult infauna are nonetheless important in determining infaunal abundances on these intertidal flats. One group of deposit feeders, the funnel feeders, are extremely abundant on the high salinity flats of North Carolina. This group processes and turns over tremendous quantities of sediment, probably causing the mortality of vast numbers of colonizing larvae. On intertidal sand flats, the enteropneust *Balanoglossus aurantiacus* is the most common funnel feeder. Although its density is often only about one to four individuals per square meter, the worm is about 75 cm long and processes about 140 cm³ of sediment daily during the warm months (B. Duncan, Univ. North Carolina, Chapel Hill, unpub. data). The funnel feeders such as the *Balanoglossus* can be recognized by their cone-shaped feeding funnels on the sand flats and by the coiled extrusions of feces, which lie in mounds spaced at some distance away from the feeding funnels.

By sampling the sediments falling down the feeding funnels of *Balanoglossus* and the fresh fecal extrusions, Duncan (unpub. data) demonstrated that this enteropneust consumes the most abundant meiofaunal taxon, the nematodes, very efficiently. *Balanoglossus* probably also consumes larvae and other infaunal taxa, and it certainly causes the mortality of large numbers of other larval and juvenile forms which it does not digest. Such mortality effects are a common result of large-scale sediment processing (Myers 1977a, b). Partly as a consequence of this mortality, the infaunal densities on intertidal fine sand flats in North Carolina are kept very low. *Balanoglossus* is effectively excluding potential competitors while at the same time processing sediments for its own dietary needs. In addition to the funnel-feeding enteropneust, *Balanoglossus*, another major sediment processor coexists on intertidal sand flats in North Carolina. *Leptosynapta tenuis*, a vermiform deposit-feeding echinoderm, is also very abundant in this environment and has similar high rates of sediment processing. Powell (1977) estimated

Leptosynapta densities on one intertidal Bogue Sound, North Carolina, sand flat to be about one individual per square meter and its sediment processing rate to be 1600 cm³ per individual per year. This level of activity probably has a similarly high impact upon the survivorship of other colonizing infauna and helps to explain why the intertidal sand flats of North Carolina contain relatively low densities of infauna.

As the mud content of intertidal flats increases, two other large-scale sediment processors tend to replace *Balanoglossus* and *Leptosynapta*. Another funnel feeder, the lugworm *Arenicola*, and another enteropneust, *Saccoglossus*, are extremely common on most mud flats in North Carolina. *Arenicola* is well known world-wide for its high rates of sediment reworking and for its effects at limiting the abundances of most other infauna (Reise 1978). Again the high density of these deposit feeders may well help to explain the relatively low density of other infauna on the intertidal mud flats of North Carolina. *Arenicola*, like *Balanoglossus*, is large, up to 0.5 m in length, and also lives fairly deep in the sediments, usually below the 30-cm level. The feeding funnels of *Arenicola* are occasionally distinguished from those of *Balanoglossus* by the presence of *Arenicola*'s long gelatinous egg case, attached at one end to the burrow and trailing out into the currents.

The infauna of intertidal flats in North Carolina follows a very general pattern found broadly among the benthic infauna of shallow bottoms. The infauna on unvegetated flats is far less abundant than the infauna of marine grass beds at the same tidal height (Williams and Thomas 1967, Warne 1971, Thayer et al. 1975a, Orth 1977, Reise 1977a, C. H. Peterson unpub. data for Bogue Sound, North Carolina). This difference in infaunal abundances is usually very great, often up to two orders of magnitude. Three general explanations exist to explain this repeatable abundance pattern (Heck and Wetstone 1977). First, the infauna of grass beds may get more food because as the grass blades baffle and slow the passing currents, the rate of organic deposition increases. This organic matter is food for several species of suspension feeders while it is still suspended in the water column. After it is deposited on the bottom, it becomes available to the deposit feeders as an added food supply. Second, densities of

infauna may be greater inside of marine grass beds because the grass itself provides a qualitatively different and new habitat which permits the addition of new infaunal species that are dependent in some way on the presence of the seagrass. The third hypothesis suggested to explain why infaunal densities are higher in vegetated areas can be called the predation hypothesis. Predators may be less effective in grass beds because the rhizome and root mats of the grasses may inhibit their foraging and thus provide a refuge from predation for many infauna.

Although each of these three explanations may contribute somewhat to the pattern of lower infaunal density in unvegetated sediments, most authors seem to think that the predation hypothesis is the single most important (Heck and Wetstone 1977, Orth 1977, Reise 1977a). In North Carolina, experimental removal of shoalgrass (*Halodule*) resulted in 100% mortality of all size classes of the hard clam (*Mercenaria mercenaria*) on intertidal flats that also contained whelks (*Busycon* spp.) (C. H. Peterson, unpub. data). Reise (1977a, b, 1978) built cages on intertidal flats in the North Sea to exclude predators. Some cages were constructed on unvegetated flats, while others were located in adjacent grass beds. Caging and the resultant exclusion of large predators had no effect on the infauna of the grass bed, whereas infaunal densities outside of the vegetated area increased by 4 to 20 fold. This result, too, suggests that large predators control the abundance of infauna on unvegetated intertidal flats, but not in vegetated areas, where infaunal densities are accordingly far greater. Young et al. (1976) performed a similar set of caging experiments in grass beds in the Indian River estuary of Florida, where they, too, found that infaunal densities did not consistently increase following the exclusion of predators from the vegetated bottom.

While the results of these experiments seem to indicate that large mobile predators, such as are excluded by building a cage over the bottom sediments, often control the densities of infauna on intertidal flats, the experiments done in North Carolina have produced ambiguous results. Commito (1976) demonstrated a higher density of benthic infauna inside cages on a mud flat in the Newport River estuary. However, this higher abundance (three times the infaunal density on the uncaged flat) only existed during the March-

April season of heavy infaunal recruitment. By summertime, density of the infauna had declined inside the predator-exclusion cages as well as outside where predators had continuous access. Commito's results suggest that large mobile predators may not be very significant in controlling densities on North Carolina mud flats. However, these experiments did not test the impact of the major sediment processors, the funnel feeders, which are probably of great significance.

Other caging experiments done on intertidal and shallow subtidal sand flats in Bogue and Back Sounds in North Carolina (H. Stuart, North Carolina State Univ., Raleigh, unpub. data; H. C. Summerson, Univ. North Carolina, Chapel Hill, unpub. data) provide strong support for the contention that larger predators are important in controlling infaunal abundances on unvegetated flats in North Carolina. Since Woodin (1978, in preparation), working farther north on intertidal muddy sand flats off Assateague Island, Md., has convincingly shown that larger predators do help to control infaunal abundances in that environment, it is reasonable to expect that larger mobile predators in combination with large-scale sediment processors may be important determinants of infaunal densities on North Carolina flats also.

Because the infauna of North Carolina's soft sediments are controlled by predation and biological disturbance in general, the vast majority of infaunal species tend to be small, short-lived opportunistic species. Polychaetes in the families Spionidae, Capitellidae, and Nereidae, and ampeliscid and corophiid amphipods tend to dominate the fauna of intertidal flats. In the face of heavy predation pressure, the evolution of short-lived opportunists would be expected because these are the species which can live long enough to reach reproductive maturity, reproduce, and thereby persist.

As a consequence of these high rates of predation, which are most intense in the warmer summer months, the abundance of infauna on intertidal flats in North Carolina shows a distinct pattern of seasonal change. Densities are high in spring, which is the peak period of reproductive activity for the North Carolina infauna (Commito 1976). Infaunal abundance declines steadily through the summer and shows a second lower peak of abundance in the fall when preda-

tors have less impact and reproductive activity is again intense. Low infaunal densities characterize the coldest winter months.

Although these relatively small opportunistic polychaetes and amphipods are the numerically dominant macrofauna on North Carolina's intertidal flats, some of the less abundant but far larger species often contribute an overwhelming proportion to the biomass. On intertidal mud flats, the stout razor clam, *Tagelus plebeius*, often makes up 90% or more of the total community biomass (Holland and Dean 1977 present some South Carolina data). In muddy sand flats the mud shrimp, *Upogebia*, commonly dominates the community biomass, even though its density is not especially high. Despite their taxonomic dissimilarity, *Upogebia* and *Tagelus* are both suspension feeders that live in semipermanent burrows constructed in the sediments. Long-lived, tube-building polychaetes also contribute substantially to total infaunal biomass: *Amphitrite ornata* on mud flats and *Diopatra* spp. on sand flats. These tube builders are surface deposit feeders, although *Diopatra* also grazes on the epibiotic growth on its tube cap.

3.4 THE MOBILE EPIBENTHOS

In the mobile epibenthos category are included some larger, especially active deposit feeders, as well as a group of predators which forage on and in the sediments of intertidal flats. The most obvious of these epibenthic species are fiddler crabs of the genus *Uca*. These crabs roam the intertidal zone at low tide foraging for epibenthic algae and detritus, both of which they apparently ingest and assimilate (Haines 1976b, Haines and Montague 1979). Three species of fiddler crab are found on the intertidal flats of North Carolina: *Uca pugilator*, *U. pugnax*, and *U. minax*. In sandy areas where there is no emergent vegetation near the high tide line, *U. pugilator* is found alone. On intertidal flats where *Spartina* is found toward the high tide line, either *U. minax* or *U. pugnax* is usually present. *Uca minax* will be dominant where the root mats in the *Spartina* zone are most dense, whereas *U. pugnax* is found in areas of low or intermediate root density (Ringold 1979). All three species of fiddler crab construct burrows near the high tide mark. Often the round entry holes and piles of spherical droppings are a common sight when one first

steps out on the intertidal zone of a North Carolina estuary.

Only a limited number of the mobile epibenthic species forage from land out onto the intertidal zone at low tide like *Uca*. Nevertheless, several amphipod species exhibit this same behavioral trait and can be extremely abundant on intertidal flats in North Carolina and elsewhere. Gammaridean amphipods of the genus *Orchestia* are especially common grazers on blue-green algal mats in North Carolina. Blue-green algae are usually considered to be a poor food source and difficult for herbivores to digest. Yet assimilation studies on similar gammaridean amphipods have demonstrated efficient utilization of blue-greens (Brenner et al. 1976). Numerous insect larvae (often larval dipterans), mites, and nematodes are also found grazing both on blue-green algal mats and on the wrack, which is the dried detrital material cast up at the most recent high tide mark on the shoreline. For anyone who has visited the pristine shorelines of a North Carolina sound or estuary in summer, it should not come as a surprise that the larvae of flies are quite abundant somewhere along the shore!

While all these mobile epibenthic consumers that forage down into the intertidal zone from land are herbivores or detritivores, those that forage on the intertidal zone when the tide is in tend to be largely predatory. The single most important of these species is the blue crab, *Callinectes sapidus*. Vimstein (1977) used cages in the Chesapeake Bay to enclose and other cages to exclude blue crabs so that he could estimate their impact on the benthic infauna. These experiments demonstrated that blue crabs cause substantial mortality among the benthic infauna, especially among the shallow burrowers which can be most easily excavated and consumed by the crabs. The sediments offer the deep-burrowing species somewhat better protection against predation. Thin-shelled bivalves such as *Macoma balthica* and *Mulinia lateralis* and polychaete worms are the most susceptible species to blue crab predation, but even thick-shelled clams are susceptible as juveniles. When young, the hard clam, *Mercenaria mercenaria*, is heavily preyed upon by blue crabs (Carriker 1959, Menzel et al. 1976). Blue crabs cannot forage effectively in the presence of shell debris and other hard objects which inhibit their digging. Consequently, the abundance of hard

clams and other benthic fauna is usually far greater at the margins of oyster beds, even those occurring near the high intertidal zone (Figure 1). Clammers have long recognized this pattern and often exploit their knowledge by clamming most intensively in such locations.

Blue crabs are especially effective predators because of their great tolerance of reduced salinity. Most other predators, including those which prey upon commercially important shellfish, drop out rather rapidly along a gradient upstream toward lower salinities. For instance, oyster drills (*Urosalpinx*) and seastars (*Asterias*) cannot tolerate brackish waters, and their prey have some refuge from predation in the upper portions of the estuary. This is not true for the prey of blue crabs, which are abundant throughout the estuary. Because blue crabs dig into the sediments to depths of 6 to 8 cm both to forage and to hide, they actually kill more organisms than they consume (Virnstein 1977). This, too, adds to their influence on the abundance of benthic fauna. They act, to some degree, as sediment processors and cause physical as well as predatory mortality.

The blue crab is common in all of the sounds and estuaries of North Carolina. Intertidal flats contain more juvenile crabs than adults, which prefer deeper waters. At night and during the day in spring and fall, even adult crabs can be found foraging over intertidal areas. In warmer months, large blue crabs tend to remain relatively inactive in deeper waters during the day. Juvenile crabs remain active during summer days even in shallow waters. During winter, blue crabs migrate to deep channels, this time to escape the extreme cold of the shallows. Only from about mid-December to mid-March are blue crabs rare on intertidal flats in North Carolina.

Oyster reefs are not the only structures in soft-sediment environments that protect the infauna from blue crab predation. Numerous polychaete species build tubes which extend into the sediments. The tubes of some onuphid polychaetes are especially large and extend vertically up to 10 cm into the water column. Two species of tube builders, *Diopatra cuprea* and *Americanuphis magna*, are quite common on intertidal sand flats in North Carolina. Woodin (1978, in preparation) has demonstrated that infaunal densities are far higher in the immediate vicinity of a *Diopatra*

tube on intertidal flats at Assateague Island, Maryland. Abundance of infauna declines rapidly with distance away from a tube. By building cages to exclude blue crabs, Woodin was able to demonstrate that blue crab predation was lowest near the tubes where the structures inhibit digging and foraging but that at some distance away from the tubes the blue crab controlled infaunal community abundance. This pattern also appears to exist among the benthic infauna of North Carolina's intertidal flats and is probably produced by the very same mechanism. Blue crabs leave small pits up to 8 cm deep on intertidal flats where they have been foraging (Woodin, in preparation). These pits persist only 2 or 3 days; so the usual pock-marked surface of North Carolina's intertidal flats is an indication of the high activity rate of the blue crab there.

Woodin (in preparation) also performed experiments with another major mobile epibenthic predator of the infauna on intertidal flats, the horseshoe crab, *Limulus polyphemus*. These large crabs dig broader pits than those made by the blue crab, but the horseshoe crab pits are shallower — only about 4 cm deep. Woodin (in preparation) showed by experiment that *Limulus* has an effect on infaunal densities too but not nearly as great an effect as that of blue crabs. Because *Limulus* is abundant on the intertidal flats of North Carolina, it is doubtless having a substantial impact there, too. Horseshoe crabs are quite seasonal in North Carolina, with noticeable abundances in shallow water from about April through October. This corresponds to the period when large shallow pits are evident on many North Carolina mud and sand flats.

Another abundant group of mobile epibenthic invertebrates on North Carolina's mud and sand flats is whelks, composed of species of *Busycon* (Magalhaes 1948). Three species of these large gastropods are common at the lower margins of intertidal sand and mud flats. The channeled whelk (*Busycon canaliculatum*) feeds mostly upon carrion and is commonly captured in crab pots. The two other whelks, the knobbed whelk (*B. carica*) and the lightning whelk (*B. contrarium*), are voracious, feeding mostly on clams such as *Mercenaria mercenaria* and the dog clam, *Chione cancellata*. These predatory whelks feed by using the lip of their shells to rasp away at the margins of a clam until enough of a gap is created to

permit the insertion of the snail's shell margin. Once opened, the clam is quickly consumed, leaving a dead pair of articulated shells marked with a clear clue to the cause of the clam's demise.

Many species of marine epifauna, such as some barnacles on rocky shorelines (Connell 1970), possess a refuge from predation by gastropods and other predators in large size classes. Some sizes of prey are too large for the predator to handle. Such refuges are important in insuring the stability of prey populations in the face of what are often very efficient predators. Little work has been done to establish whether soft-sediment infaunal species generally possess an analogous escape from their predators as a result of growing to large sizes. Whelks, however, take all sizes of *Mercenaria* and *Chione*, even the largest. Although hard clams can grow large enough to become invulnerable to predation by blue crabs, whelks more than compensate for the decline in blue crab predation and can denude an unvegetated sand flat of its hard clams in short order. Whelks do not extend in distribution into the high intertidal zone or into brackish waters, so clams have a refuge there from whelk predation.

Other predatory gastropods can occasionally be found on the lower margins of intertidal flats in North Carolina. Tulip snails, including the true tulip (*Fasciolaria tulipa*) and the banded tulip (*F. hunteria*), are residents of tide flats. Both of these species prey upon the benthic infauna and possess extremely varied diets (Paine 1963). Other gastropod predators found in this environment include the baby's ear (*Sinum perspectivum*) and the moon snail (*Polinices duplicatus*). Moon snails in North Carolina also have a broad diet which includes some clam species. A moon snail consumes a clam by using its radula to rasp a circular hole near the umbo of the clam. These characteristic holes often mark the shells of dead clams and clearly indicate the cause of death.

In addition to the blue crab and the horseshoe crab, a number of additional types of crabs roam an intertidal flat at high tide. In North Carolina, perhaps the most abundant and evident of these remaining species are the hermit crabs (*Pagurus longicarpus* and *Petrochirus diogenes*), which carry on their backs the shells of moon snails, mud snails, and whelks. The larger the crab, the

larger the shell it carries, such that little *Pagurus longicarpus* is almost always found in the smallest gastropod shells, those from mud snails (Finn 1973). Hermit crabs are apparently omnivores, acting as both predators and scavengers in estuarine systems. Various small grapsid mud crabs are locally abundant predators on intertidal flats. As one moves closer and closer to the equator, the importance of xanthid crabs gradually increases. North Carolina has a number of tropical faunal elements, including several xanthid crabs, during the summertime.

One major group of mobile epibenthic invertebrates remains to be discussed: the shrimp. While shrimp are generally considered residents of slightly deeper waters where marine grasses are common, many shrimp do forage up on intertidal flats at higher tides. Grass shrimp (*Palaemonetes* spp.) probably remain fairly well restricted to vegetated habitats, but other shrimp types such as the penaeids, alpheidids, and mysids range widely. The brown shrimp (*Penaeus aztecus*) is the most common penaeid in North Carolina waters. Juveniles enter the estuaries in spring where they grow and develop in shallow nursery areas usually in relatively muddy habitats far up small tidal creeks. By the end of summer when they have grown and matured, they migrate into the deeper waters of the sounds and ultimately into the ocean (Williams 1955). Penaeid shrimp are apparently both predators on small shallow-burrowing infauna and also detritivores (Williams 1955). Most of their energy is presumably derived from consuming the microbial flora on *Spartina* and seagrass detritus. Mysid shrimp, especially *Neomysis americana*, are commonly found on intertidal flats south of Chesapeake Bay feeding on detritus (D. Allen, Pers. Comm. Univ. South Carolina, October 1979). Snapping shrimp (*Ilpheus* spp.) are often found over flats. They are strictly predatory.

A few other even more subtidal species of mobile invertebrates can occasionally be found in the lower intertidal zone of flats when the tide is in. For instance, in fine sand sediments the sand-dollar, *Mellita quinquesperforata*, can be an abundant deposit feeder. *Mellita* forages just below the sediment surface by plowing along at a relatively rapid rate. It presumably consumes benthic microalgae and organic deposits, but because of its large size and high activity rate it must also have an important impact on the juveniles of many

benthic infaunal species through bioturbation (biological disturbance of the sediments). Other mobile epibenthic invertebrates which are basically subtidal but which may occur at the very low end of the intertidal zone include the dwarf olive (*Olivella*), which is presumed to be a herbivore and detritivore; the heart urchin (*Moira*), which is a deposit feeder; the stone crab (*Menippe*), spider crabs (*Libinia* spp.); and stomatopods or mantis shrimp (*Squilla*). Mantis shrimp are voracious predators which live in permanent burrows extending fairly deep into the sediments. They

lurk in these burrows until they spot a potential prey item, whereupon they quickly emerge and snap up the prey with their powerful chelae, capable even of inflicting a substantial wound on the hand of an unsuspecting biologist. Mantis shrimp are extremely common in subtidal sandy areas in North Carolina's sounds, but, because of the depth at which they burrow into the sediments and their mobility, their density is ordinarily grossly underestimated by typical benthic grab sampling.



Many commercial species, including flounder and shrimp, depend upon intertidal flats for food. Photo by T. A. Klopp.

4.1 TROPHIC ROLES

Because tidal changes would leave them stranded during a portion of each day, few fishes are permanent residents of intertidal flats. Only in areas where relatively large burrows are common in the intertidal sediments or where tide pools are present can one find fishes which reside in the intertidal zone. In the intertidal sand flats of southern California lagoons, the ghost shrimp (*Callinassa californiensis*) can be extremely abundant. Its burrows extend up to 1 m beneath the sediment surface and remain filled with seawater even at low tide. Consequently, fishes (like the arrow goby, *Clevelandia ios*) survive this period by living inside the burrows. Other fishes, such as various blennies and gobies, are common tide pool residents along coasts with rocky shorelines. In North Carolina, gobies, blennies, and cling fish occur as permanent residents of the intertidal zone, but they are usually found in association with hard substrates and are not abundant on intertidal sand and mud flats.

Although those fishes which are permanent residents of intertidal flats are not important in North Carolina's estuaries, the unvegetated intertidal zone of sounds, lagoons, river mouths, and estuaries is an important environment for many coastal and marine fishes. Intertidal flats are important to these fishes in two major ways. First, numerous fishes live and feed on intertidal flats during high tide at some stage in their life cycles. Second, many other fishes are, at least in part, trophically dependent upon prey which have lived and foraged on intertidal sand and mud flats. Table 2 presents a list of those fishes which are direct utilizors of North Carolina's intertidal flats. In Table 3 appears a list of those fishes in North Carolina which depend indirectly upon intertidal flats because a substantial proportion of their prey feed there. Distinctions necessary to construct these tables required several rather arbitrary decisions, but an attempt has been made to include all of the major species in either Table 2 or 3. Rare and occasional species have been specifically excluded. Although Tables 2 and 3 include several species, this does not imply that intertidal flats are a critical habitat for all of them. As a general rule, the fishes and shorebirds have complementary distributions in estuarine systems,

with fishes foraging mostly in subtidal habitats and shorebirds in the intertidal zone. Because fishes have access to subtidal habitats, the elimination of intertidal flats would probably cause few fish extinctions in North Carolina, but it would result in drastic declines both in the populations of several fishes and in the total fish production of estuarine systems.

The fishes which forage on intertidal flats and those partially dependent upon prey that feed on intertidal flats can be subdivided into four broad trophic types: (1) planktivores, (2) detritivores, (3) predators on benthic infauna, epifauna and small mobile epibenthos, and (4) predators on fish and larger mobile epibenthic species. These categories are artificial in that species in the same category do not share exactly the same diet and in that several species take prey in multiple categories. For instance, planktivores will often ingest suspended detritus. Likewise, detritivores will often consume small benthic animals as well as detritus when they ingest bottom sediments. Furthermore, as will be described later in detail, virtually all fishes undergo major changes in their food habits as they grow, moving from one trophic category to another with age.

4.2 PLANKTIVORES AND DETRITIVORES

Of several common marine fishes in North Carolina that are partially dependent upon the production of intertidal flats, perhaps the most abundant are planktivores, including the anchovies (*Anchoa* spp.), menhaden (*Brevoortia tyrannus*), and other clupeids (such as *Opisthonema oglinum*). Menhaden filter the water column and consume mainly phytoplankton. Because they feed so low on the food chain, it is not surprising that menhaden are extremely abundant and form a higher percentage of the total poundage of commercial fish landings in North Carolina than any other single species. Although juvenile menhaden grow up in rivers and sounds, they often are found directly over intertidal flats. Production of their food, phytoplankton, is greatly enhanced by the increased euphotic zone available over intertidal flats at high tide (see Chapter 2). Two species of anchovies (*Anchoa hepsetus* and *A. mitchilli*) are also common planktivores found over tidal flats at high tide. Both feed largely on zooplankton, although they also

Table 2. Fishes utilizing North Carolina's intertidal flats at high tide (rare and occasional species not included).

Family and species	Seasons present	Abundance on flats	Information source	Diet	Information source
Dasyatidae (stingrays)					
<i>Dasyatis americana</i> (Southern stingray)	Spring-fall	Few	Hyle 1976	Clams, shrimp, annelids, small fishes and blue crabs	Radcliffe 1914
<i>Dasyatis sabina</i> (Atlantic stingray)	Spring-fall	Few	Hyle 1976, Schwartz and Dahlberg 1978	Crustaceans and fishes	Hildebrand and Schroeder 1927, Schwartz and Dahlberg 1978
<i>Gymnura micrura</i> (Smooth butterfly ray)	Summer	Few	Hyle 1976	Mainly fishes (including black sea bass); also molluscs (including <i>Solemya</i>), annelids, shrimp, and other small crustaceans	Linton 1904
Myliobatidae (eagle rays)					
<i>Rhinoptera bonasus</i> (Cownose ray)	Spring-fall	Locally numerous	Smith 1907, Radcliffe 1914	Mainly molluscs (including <i>Solemya</i> , <i>Mya</i> , oysters, and scallops)	Smith 1907, Radcliffe 1914, Orth 1975
Clupeidae (herrings)					
<i>Brevoortia tyrannus</i> (Atlantic menhaden)	Spring-fall	Common	Turner and Johnson 1973, Marshall 1976	Mainly phytoplankton; also zooplankton and resuspended detritus	Linton 1904, Hildebrand and Schroeder 1927, Darnell 1958
<i>Opisthonema oglinum</i> (Atlantic thread herring)	Spring-fall	Common	Tagatz and Dudley 1961, Hyle 1976	Zooplankton (copepods)	Hildebrand and Schroeder 1927
Engraulidae (anchovies)					
<i>Anchoa hepsetus</i> (Striped anchovy)	Spring Summer Fall	Few Common Few	Smith 1907, Adams 1976a, Hyle 1976	Annelids, foraminifera, copepods, zoea, small shrimp and other small crustaceans (zooplankton)	Linton 1904
<i>Anchoa mitchilli</i> (Bay anchovy)	Year-round	Abundant	Turner and Johnson 1973, Hyle 1976	Mainly small shrimp (including mysids and larval penaeids), and detritus; also zooplankton, small bottom-dwelling molluscs and crustaceans (including minute snails, clams, isopods, amphipods, ostracods, and copepods)	Darnell 1958, Adams 1976b

continued

Table 2. Continued.

Family and species	Seasons present	Abundance on flats	Information source	Diet	Information source
Synodontidae (lizardfishes)					
<i>Synodus foetens</i> (Inshore lizardfish)	Summer Fall	Common Few	Tagatz and Dudley 1961, Hyle 1976	Mainly fishes (including silver- sides and young weakfish); also annelids, shrimp, crabs, and urchins	Linton 1904, Hildebrand and Schroeder 1927
Batrachoididae (toadfishes)					
<i>Opsanus tau</i> (Oyster toad)	Year- round	Common	Hyle 1976, Ross 1977	Mainly small crabs (including mud, blue, spider, stone, hermit, fiddler crabs), other crustaceans (including shrimp, isopods, and amphipods), molluscs, (including small snails, scallops, and clams), and fishes (including gobies, silver- sides, and <i>O. tau</i> eggs); also ane- lids, anemones, urchins (<i>Arbacia</i>), and vegetation	Linton 1904, Hildebrand and Schroeder 1927, Schwartz and Dutcher 1963
Gadidae (codfishes)					
<i>Urophycis regius</i> (Spotted hake)	Fall-spring	Few	Hyle 1976	Mainly small crustaceans (including mysids, shrimp, crabs, amphipods, isopods, cumaceans) and fishes; also annelids and molluscs	Hildebrand and Schroeder 1927, Sikora et al. 1972
Ophidiidae (cusk-eels and brotulias)					
<i>Ophidion welschi</i> (Crested cusk-eel)	Year-round	Few	Hyle 1976, Ross 1977	Presumed similar to that of <i>Rissola marginata</i>	
<i>Rissola marginata</i> (Striped cusk-eel)	Year-round	Few	Adams 1976a, Zingmark 1978	Small crustaceans and small fishes (including gobies)	Hildebrand and Schroeder 1927
Exocoetidae (flying fishes and halfbeaks)					
<i>Hyporhamphus unifasciatus</i> (Halfbeak)	Spring-fall	Common	Smith 1907, Tagatz and Dudley 1961	Green algae (mainly <i>Ulva</i>) and zooplankton	Linton 1904
			continue 1		

Table 2. Continued.

Family and species	Seasons present	Abundance on flats	Information source	Diet	Information source
Cyprinodontidae (killifishes)					
<i>Cyprinodon variegatus</i> (Sheepshead minnow)	Year-round	Common	Kneib 1976	Detritus and filamentous algae	Kneib 1976
<i>Fundulus heteroclitus</i> (Mummichog)	Year-round	Abundant	Kneib and Stiven 1978	Mainly small crustaceans (including amphipods, isopods, tanaids, ostracods and copepods), polychaetes, detritus; also algae, insects, crabs, fishes, snails, and invertebrate eggs	Kneib and Stiven 1978
<i>Fundulus majalis</i> (Striped killifish)	Year-round	Abundant	Tagatz and Dudley 1961, Kneib 1976	Mainly small crustaceans (including amphipods, isopods, ostracods, tanaids, and copepods), detritus and fecal pellets, polychaetes, and insects; also small bivalves, eggs, and small crabs	Darnell 1964, Kneib 1976
Atherinidae (silversides)					
<i>Membras martinica</i> (Rough silversides)	Year-round	Common	Tagatz and Dudley 1961, Adams 1976a	Mainly small zooplankton crustaceans (including calanoid copepods, gammaridean and caprellid amphipods, small shrimp, megalops); also juvenile and larval fishes, insects, detritus, and small snails	Hildebrand and Schroeder 1927, Adams 1976b
<i>Menidia beryllina</i> (Tidewater silversides)	Year-round	Few	Tagatz and Dudley 1961, Ross 1977	Mainly small zooplankton crustaceans (including isopods, amphipods, calanoid copepods) and insects; also small shrimp, small snails, and algae	Hildebrand and Schroeder 1927, Darnell 1958
<i>Menidia menidia</i> (Atlantic silversides)	Year-round	Abundant	Smith 1907, Tagatz and Dudley 1961, Turner and Johnson 1973	Mainly small zooplankton crustaceans (including calanoid copepods, gammaridean and caprellid amphipods, small shrimp, megalops); also juvenile and larval fishes, insects, detritus, small snails, annelids, and algae	Linton 1904, Hildebrand and Schroeder 1927, Adams 1976b

continued

Table 2. Continued.

Family and species	Seasons present	Abundance on flats	Information source	Diet	Information source
Carangidae (jacks and pompanos)					
<i>Carnax hippos</i> (young) (Crevalle jack)	Summer-fall	Few	Tagatz and Dudley 1961, Hyle 1976	Mainly small crustaceans; also small fishes (including anchovies)	Linton 1904, Darnell 1958
<i>Selene vomer</i> (young) (Lookdown)	Spring-fall	Common	Smith 1907, Hyle 1976	Mainly shrimp and other crustaceans; also small molluscs	Linton 1904
Gerreidae (mojarras)					
<i>Eucinostomus argenteus</i> (Spotfin mojarra)	Summer-fall	Few	Tagatz and Dudley 1961	Presumed similar to that of <i>E. gula</i>	
<i>Eucinostomus gula</i> (Silver jenny)	Summer-fall	Common	Smith 1907, Tagatz and Dudley 1961	Mainly calanoid copepods and other small crustaceans; also annelids, diatoms, and detritus	Linton 1904, Adams 1976b
Pomadasyidae (grunts)					
<i>Orthopristis chrysoptera</i> (Pigfish)	Spring-summer	Common	Smith 1907, Hyle 1976, Marshall 1976	Adult: mainly annelids (including <i>AxiotHELLa</i> , <i>Diopatra</i> , <i>Rhyncobolus</i> , <i>Arenicola</i> , and <i>Pectinaria</i>), nemerteans (<i>Cerebratulus</i>), molluscs, crabs (including fiddler, horseshoe, hermit, and blue), shrimp, and other small crustaceans (including amphipods and isopods); also fishes and urchins	Linton 1904, Smith 1907, Adams 1976b
(young)	Winter-Spring-summer	Few Common		Young: mainly detritus, zooplankton, and small shrimp; also other small crustaceans (including gammaridcan amphipods, hapacticoid copepods, and small crabs), small molluscs, and annelids	

continued

Table 2. Continued.

Family and species	Seasons present	Abundance on flats	Information source	Diet	Information source
(<i>young</i>)	Year-round	Abundant		Young: mainly small epibenthic animals (including copepods, ostracods, amphipods, isopods, rotifers, and foraminifera), and detritus; also minute molluscs and annelids	al. 1975, mysids, and crabs), and detritus; also fish remains, algae, and insects Hyle 1976, Chao and Musick 1977, Virnstein 1977
<i>Menticirrhus</i> spp. (Kingfish)	Fall	Few	Hyle 1976	Mainly shrimp, crabs, and other small crustaceans; also fishes, and molluscs (including <i>Bulla</i> , <i>Urosalpinx</i> , and clams)	Linton 1904, Smith 1907, Hildebrand and Schroeder 1927
<i>Micropogonias undulatus</i> (Atlantic croaker) (<i>adult</i>)	Spring-summer	Abundant	Turner and Johnson 1973, Hyle 1976	Adult: mainly annelids (including <i>Arenicola</i>), enteropneusts (<i>Balanoglossus</i>), molluscs (including <i>Rangia</i> , <i>Solemya</i>), crabs (including mud and blue crabs), palaemonid and penaeid shrimp, small fishes (including anchovies, gobies, young croakers), and detritus; also insect larvae, algae, ascidians, and ophiurans	Linton 1904, Hildebrand and Schroeder 1927, Roelofs 1954, Darnell 1958, Stuckney et al. 1975, Hyle 1976, Chao and Musick 1977, Overstreet and Heard 1978a
(<i>young</i>)	Year-round	Abundant		Young: mainly small zooplankton crustaceans (including copepods, amphipods, mysids, isopods, ostracods, cumaceans, tanaids), insect larvae, and detritus; also foraminifera	
Ephippidae (spadefishes)					
<i>Chaetodipterus faber</i> (Atlantic spadefish) (<i>young</i>)	Summer-fall	Few	Smith 1907, Hyle 1976	Young: detritus and small crustaceans	Hildebrand and Schroeder 1927

continued

Table 2. Continued.

Family and species	Seasons present	Abundance on flats	Information source	Diet	Information source
Mugilidae (mullets)					
<i>Mugil cephalus</i> (Striped mullet)	Year-round	Abundant	Tagatz and Dudley 1961, Turner and Johnson 1973	Organic detritus, epiphytic algae, and littoral diatoms	Linton 1904 Darnell 1958, 1964, Odum 1970b
<i>Mugil curema</i> (White mullet)	Year-round	Few	Smith 1907, Ross 1977	Organic detritus, epiphytic algae, and littoral diatoms	Linton 1904, Hildebrand and Schroeder 1927
Uranoscopidae (stargazers)					
<i>Astroscoptes</i> spp. (Stargazers)	Year-round	Few	Smith 1907	Mainly fishes, also isopods	Hildebrand and Schroeder 1927
Gobiidae (gobies)					
<i>Gobionellus bolcosoma</i> (Darter goby)	Year-round	Few	Hyle 1976	Presumed similar to that of other gobies	
<i>Gobiosoma boscii</i> (Naked goby)	Year-round	Few	Smith 1907, Hyle 1976	Mainly small crustaceans (including gammaridean amphipods), and annelids; also fishes and eggs	Hildebrand and Schroeder 1927
<i>Gobiosoma ginsburgi</i> (Scaboard goby)	Summer-winter	Common	Ross 1977, Zingmark 1978	Mainly small crustaceans (including gammaridean amphipods)	Hildebrand and Schroeder 1927
<i>Microgobius thalassinus</i> (Green goby)	Year-round	Few	Smith 1907, Ross 1977	Small crustaceans (including gammaridean amphipods) and other invertebrates	Hildebrand and Schroeder 1927, Schwartz 1971
Triglidae (searobins)					
<i>Prionotus carolinus</i> (Northern searobin)	Year-round	Common	Hyle 1976	Mainly crustaceans (including mysids, amphipods, isopods, shrimp, and crabs)	Hildebrand and Schroeder 1927
<i>Prionotus evolans</i> (Striped searobin)	Winter-spring	Few	Hyle 1976	Small crustaceans (mainly mysids)	Hildebrand and Schroeder 1927
<i>Prionotus scitulus</i> (Leopard searobin)	Year-round	Few	Hyle 1976	Mainly small molluscs (including <i>Solemya</i> , <i>Batalla</i> , young <i>Olivia</i>), shrimp, crabs, and fishes; also	Linton 1904

continued

Table 2. Continued.

Family and species	Seasons present	Abundance on flats	Information source	Diet	Information source
<i>Prionotus tribulus</i> (Bighead scarobin)	Year-round	Common	Hyle 1976	small crustaceans (including ostracods, copepods, and cumaceans)	Linton 1904
Bothidae (lefteye flounders)					
<i>Ancylosetta quadrocellata</i> (Ocellated flounder)	Spring-fall	Few	Smith 1907, Hyle 1976	Mainly crabs and shrimp; also mysids, other crustaceans (including amphipods, copepods, cumaceans, and isopods), annelids, and fishes	Stickney et al. 1974
<i>Citharichthys spilopterus</i> (Bay whiff) (young)	Summer-fall	Few	Hyle 1976	Mainly mysids; also other crustaceans (including shrimp, crabs, copepods, amphipods), fishes, annelids	Stickney et al. 1974
<i>Etropus crossotus</i> (Fringed flounder)	Fall-winter Spring	Common Abundant	Hyle 1976	Mainly calanoid copepods and other small crustaceans (including cumaceans, amphipods, mysids, shrimp, crabs, isopods); also annelids, molluscs, and fishes	Linton 1904, Stickney et al. 1974
<i>Paralichthys dentatus</i> (Summer flounder) (adult)	Spring-summer	Few	Hyle 1976, Powell and Schwartz 1977	Mainly fishes; also squid, shrimp, crabs, mysids, small molluscs, sand dollars, annelids, and gammaridean amphipods	Smith 1907, Hildebrand and Schroeder 1927, Adams 1976b
(young)	Year-round	Common			
<i>Paralichthys lethostigma</i> (Southern flounder) (adult)	Spring-summer	Few	Hyle 1976, Powell and Schwartz 1977	Mainly fishes (including mullet, menhaden, shad, anchovies, pinfish, mojarra, young croakers); also crabs (including blue, mud, and stone crabs), mysids, molluscs, penaeid shrimp, and gammaridean amphipods	Darnell 1958, Adams 1976b
(young)	Year-round	Common			

continued

Table 2. concluded

Family and species	Seasons present	Abundance on flats	Information source	Diet	Information source
<i>Scophthalmus aquosus</i> (Windowpane)	Fall-winter Spring	Few Common	Hyle 1976, Shelton 1979	Mainly mysids; also other crustaceans (including copepods, amphipods, cumaceans, shrimp, and crabs), fishes, annelids, snails, and ascidians	Linton 1904, Hildebrand and Schroeder 1927, Stickney et al. 1974, Shelton 1979
Soleidae (soles)					
<i>Trinectes maculatus</i> (Hogchoker)	Spring-fall	Common	Tagatz and Dudley 1961, Hyle 1976	Mainly annelids, small crustaceans, (including amphipods), and detritus; also insect larvae, algae, and foraminifera	Hildebrand and Schroeder 1927, Darnell 1958
Cynoglossidae (tonguefishes)					
<i>Symphurus plagiusa</i> (Blackcheek tonguefish)	Spring-fall	Few	Hyle 1976	Mainly annelids, small crustaceans, detritus, diatoms, and small molluscs; also fishes, shrimp, and vegetation	Linton 1904, Hildebrand and Schroeder 1927
Balistidae (triggerfishes and filefishes)					
<i>Monacanthus hispidus</i> (Planchehead filefish)	Summer	Few	Smith 1907, Hyle 1976	Mainly detritus, bryozoans (<i>Bugula</i>), annelids, small crustaceans (including harpacticoid copepods, amphipods, hermit crabs), and small molluscs; also algae and small urchins	Linton 1904, Hildebrand and Schroeder 1927, Adams 1976b
Tetraodontidae (puffers)					
<i>Sphoeroides maculatus</i> (Norther puffer)	Spring-fall	Few	Hyle 1976	Mainly small crustaceans (including crabs, shrimp, isopods, amphipods); also small molluscs (including oysters, scallops, <i>Solenya</i> , <i>Mercenaria</i> , snails, and barnacles), annelids, urchins, bryozoans, ascidians, sponges, and algae	Linton 1904, Hildebrand and Schroeder 1927

Table 3. Fishes which prey upon species which feed on intertidal flats in North Carolina (rare and occasional species are not included).

Family and species	Abundance	Information source	Diet	Information source
Carcharhinidae (requiem sharks)				
<i>Carcharhinus milberti</i> (Sandbar shark)	Few	Ross 1977	Mainly fishes (including pinfish)	Hildebrand and Schroeder 1927
<i>Carcharhinus obscurus</i> (Dusky shark)	Common	Smith 1907, Ross 1977	Mainly fishes (including menhaden and butterfish)	Linton 1904, Radcliffe 1914
<i>Mustelus canis</i> (Smooth dogfish)	Few	Smith 1907, Ross 1977	Mainly crabs, lobsters, and other bottom invertebrates; also fishes (including menhaden)	Smith 1907, Hildebrand and Schroeder 1927
<i>Rhizoprionodon terraenovae</i> (Atlantic sharpnose shark)	Abundant	Radcliffe 1914, Ross 1977	Mainly fishes (including pigfish, silversides, menhaden); also crabs (including hermit, blue, and fiddler crabs), shrimp, annelids, and molluscs	Linton 1904, Smith 1907, Radcliffe 1914
Sphyrnidae (hammerhead sharks)				
<i>Sphyrna lewini</i> (Scalloped hammerhead)	Few	Smith 1907, Ross 1977	Mainly fishes and crustaceans	Hildebrand and Schroeder 1927
Elopidae (tarpons)				
<i>Elops saurus</i> (Ladyfish)	Few	Smith 1907, Tagatz and Dudley 1961	Mainly fish (including anchovies, pinfish, and shad) and penaeid shrimp; also crabs, squid, and other invertebrates	Darnell 1958
Anguillidae (freshwater eels)				
<i>Anguilla rostrata</i> (American eel)	Abundant	Smith 1907, Hyle 1976	Mainly crustaceans, annelids, fishes, echinoderms, molluscs, and eelgrass; also carrion	Smith 1907, Hildebrand and Schroeder 1927
Congridae (conger eels)				
<i>Conger oceanicus</i> (Conger eel)	Few	Smith 1907, Hyle 1976	Mainly fishes; also shrimp, and snails (<i>Urosalpinx</i>)	Linton 1904
Belonidae (needlefishes)				
<i>Strongylura marina</i> (Atlantic needlefish)	Common	Smith 1907, Tagatz and Dudley 1961, Hyle 1976	Mainly fishes (including anchovies, silversides, mullet); also shrimp, amphipods, annelids, and urchins (<i>Moira</i>)	Linton 1904, Hildebrand and Schroeder 1927
Percichthyidae (temperate basses)				
<i>Morone saxatilis</i> (Striped bass)	Abundant in northern estuaries	Hester and Copeland 1975	Mainly fishes, crustaceans, annelids and insects	Hildebrand and Schroeder 1927
Serranidae (sea basses)				
<i>Centropristis striata</i> (Black sea bass)	Few	Ross 1977	Mainly crabs (including hermit crabs), and fishes; also shrimp, molluscs, annelids, urchins (<i>Moira</i>), and small crustaceans (including isopods and amphipods)	Linton 1904, Smith 1907, Hildebrand and Schroeder 1927

continued

Table 3. Concluded

Family and species	Abundance	Information source	Diet	Information source
Pomatomidae (bluefishes)				
<i>Pomatomus saltatrix</i> (Bluefish) (young)	Abundant	Smith 1907, Ross 1977	Young: mainly fishes, (including anchovies, silversides, killifishes, menhaden, shad, and spotted seatrout); also shrimp, crabs, other small crustaceans, annelids, and small snails	Linton 1904, Smith 1907, Hildebrand and Schroeder 1927
Sciaenidae (drums)				
<i>Cynoscion nebulosus</i> (Spotted seatrout)	Common	Hyle 1976, Ross 1977	Mainly fishes (including spot, croaker, mullets, anchovies, silversides, gobies, menhaden, pinfish, pigfish), and penaeid and palaemonid shrimp; young also eat crustaceans	Linton 1904, Hildebrand and Schroeder 1927, Darnell 1958
<i>Cynoscion regalis</i> (Weakfish)	Common	Hyle 1976, Ross 1977	Mainly fishes (including anchovies, Atlantic thread herring, menhaden, pigfish, spot, and weakfish), and mysids; also crabs, annelids (<i>Nereis</i>), molluscs, and small crustaceans	Linton 1904, Smith 1907, Hildebrand and Schroeder 1927, Merriner 1975, Stickney et al. 1975
<i>Sciaenops ocellata</i> (Red drum)	Common	Ross 1977	Mainly crustaceans (including penaeid shrimp and blue crabs) and fishes (including mullet, menhaden, anchovies, killifishes, silversides, pinfish, spot); also molluscs (including bivalves and squid), and annelids	Linton 1904, Hildebrand and Schroeder 1927, Darnell 1958, Bass and Avault 1975, Overstreet and Heard 1978b
Stromateidae (butterfishes)				
<i>Peprilus</i> spp. (Butterfish, harvestfish)	Common	Smith 1907, Ross 1977	Probably small fishes, squid, crustaceans, annelids, and ctenophores	Hildebrand and Schroeder 1927

consume detritus, small shrimp, and other small crustaceans. As suggested by its common name, the bay anchovy, *A. mitchilli*, is common in brackish waters, whereas *A. hepsetus* is characteristic of fully saline environments. Along with silversides, the anchovies are the most numerous of the small baitfishes found in shallow waters along the North Carolina coast.

Like anchovies, juvenile silversides (*Menidia menidia*, *M. beryllina*, *Membras martinica*) are also planktivores, feeding largely on zooplankton (Darnell 1958). Silversides also show some habitat segregation along a salinity gradient, with *M. menidia* in fully saline waters and *M. beryllina* in brackish areas. As adults, silversides become more omnivorous, feeding on detritus and polychaetes, small shrimp, amphipods, and other small crustaceans. This omnivorous diet closely resembles the diet of another type of baitfish common on intertidal flats, the killifishes (*Fundulus majalis*, *F. heteroclitus*, *Cyprinodon variegatus*). Where deeper tide pools are found on the flats, *F. heteroclitus* and *C. variegatus* are year-round residents of shallow waters in North Carolina, although most individuals spend the winters in deep-water habitats. *Fundulus majalis* tends to be found in sandy sediments and in high salinities, while *F. heteroclitus* prefers muddier habitats and tolerates lower salinities. Some authors have suggested that *F. heteroclitus* feeds only in salt marshes at high tide (Vince et al. 1976). Even if *F. heteroclitus* also feeds on unvegetated tidal flats, *F. majalis* is by far the most important killifish in the unvegetated intertidal flat environment.

The mullets (*Mugil cephalus* and *M. curema*) represent the last baitfish group of importance remaining to be mentioned. *Mugil cephalus*, the striped mullet, is by far the most abundant mullet in North Carolina. Mulletts are almost pure detritivores, taking mouthfuls of surface sediments and digesting what they can. Juvenile mulletts grow up in shallow waters of sounds, estuaries, and lagoons along the North Carolina coast. In the fall, young mulletts form massive schools which migrate south. This mullet migration coincides with what is called a mullet blow in North Carolina, a shift of the winds into the north induced by the passage of a cold front. Schools of migrating mulletts, with each individual almost geometrically positioned and equally spaced from its nearest neighbors in the school, are a common

sight in the sounds of North Carolina during September and October. Although many mulletts join this southward migration in the fall, mulletts are still common in North Carolina's estuaries during the winter. *Mugil cephalus* is also known as the jumping mullet for its tendency to leap from the water, although the less common white mullet (*M. curema*) probably jumps also. Smaller mulletts clearly jump as a response to being disturbed or chased by predators. Larger mulletts also jump, and some authors have suggested that such leaping may help remove external parasites.

Other fishes occasionally consume detritus from the surface of North Carolina's intertidal flats. Of these, the pinfish (*Lagodon rhomboides*) is the most common. The pinfish is generally considered a grass-bed species when it occurs in estuaries. Its normal diet encompasses the encrusting fauna and flora found on firm substrates such as grass blades. Yet pinfish are so universally abundant in North Carolina's sounds and estuaries that they can be found feeding on all types of bottoms including unvegetated intertidal flats. The filefish (*Monacanthus hispidus*) feeds in a similar fashion in grass beds, and like the pinfish, can also be found feeding over intertidal flats. The filefish is much less abundant than pinfish, which is the most characteristic benthic feeder in North Carolina's estuaries.

4.3 PREDATORS ON BENTHIC FAUNA, MOBILE EPIBENTHIC INVERTEBRATES, AND FISHES

The vast majority of the fish species listed in Tables 2 and 3 are predators either (1) on the benthic infauna and small epibenthos or (2) on fishes and larger epibenthic animals. These two trophic categories include two groups of fishes which, along with some of the smaller baitfishes discussed above, are perhaps the most characteristic fishes of intertidal flat habitats worldwide: (1) the rays and skates and (2) the flatfishes.

Rays are prominent on intertidal flats around the world. They dig pits in the sediments in their search for clams and other buried infauna. Flapping their "wings," the fleshy parts of their extensive pectoral fins, enables rays to excavate substantial craters. The roots of marine grasses help to inhibit excavations by rays in the same way that they interfere with the activities of blue

crabs and horseshoe crabs. Consequently, the physical impact of skates and rays is ordinarily far greater on unvegetated flats than in nearby grass beds. Because of their relatively large size, most skates and rays prey upon fairly large benthic animals. Their extensive digging activities also cause widespread mortality even among the smallest of benthic organisms. Many smaller predatory species, such as the pinfish, follow the rays and skates in order to consume any smaller invertebrates which they may uncover but not consume. The excavation pits then undergo colonization by opportunistic species and succession proceeds back toward larger infaunal species (VanBlaricom 1978). This characteristic disturbance process makes rays an important determinant of the benthic infaunal abundances and community composition anywhere they are common.

In North Carolina, the most abundant ray, the Atlantic stingray (*Dasyatis sabina*) does not excavate pits, but a locally abundant ray, the cownose ray (*Rhinoptera bonasus*), does. In spring and fall, large schools of cownose rays often can be found around grass beds in North Carolina's sounds and in the Chesapeake Bay (Orth 1975). Here they damage grass beds somewhat by their digging for food. Cownose rays consume large quantities of commercially valuable shellfish, especially hard clams, scallops, and oysters. Because these rays are so large, their appetites are substantial, and their effects on the benthic communities are great. An attempt is now being made by some North Carolina researchers to develop an overseas market for cownose (and other) rays. In Europe the ray "wings" are cut into scallop-like pieces which are considered a delicacy. Developing this fishery in North Carolina would have the added benefit of freeing the hard clam, scallop, and oyster populations from one of their major predators in certain areas.

The other major category of predators which are most characteristic of intertidal flats is the flatfishes (flounders, soles, and tonguefish). Some flounders employ the tactic of lying buried just beneath the surface of the sediments with only their eyes protruding. While lying on the sediment surface, many flounders (mostly *Paralichthys* spp.) are masters of disguise, the chameleons of the ichthyological world. Here they are able to change not only their coloration to match their background but also the pattern of blotches and marks

on their skin (Mast 1914), concealing them from their unsuspecting prey. Flounders then dart up out of hiding to capture fish, shrimp, crabs, and other epibenthic species.

The most important of this flatfish group on the intertidal flats of North Carolina are the summer flounder (*Paralichthys dentatus*), the southern flounder (*P. lethostigma*), and the hogchoker (*Trinectes maculatus*). The *Paralichthys* species prey predominantly upon fish, usually silversides, anchovies, and other small fishes, and upon shrimp and crabs. The hogchoker is a small bottom-feeder that captures relatively small prey. Polychaetes and small crustaceans along with detritus make up the bulk of its diet.

The summer flounder and the southern flounder are the most important of these flatfishes in that they contribute to both the sport and commercial fisheries along the east coast. Juvenile flounders of both species are year-round residents of shallow waters in North Carolina, living in sounds, lagoons, and estuaries until they are 18 mo old (Powell and Schwartz 1977). They then leave through the inlets for the ocean for spawning. Some adults return to the sounds when the water warms, leaving again for ocean spawning each fall. Flounders weighing up to 8 to 10 lb are not uncommon in North Carolina's sounds. Because of the flounder's habit of lying on shallow flats to await its prey, fishermen often catch flounders by "gigging." This involves walking or poling a boat along in shallow water and using a barbed spear (or gig) to capture any flounder that is encountered. Flounder gigging is most frequently practiced at night when flounders are most often found on the shallow flats and when they are relatively inactive. This entire fishing methodology is dependent upon the flounders' affinity for shallow-water sand flats.

The hogchoker has been used in experiments to determine its influence on the benthic infaunal community. Virnstein (1977) enclosed hogchokers inside of mesh cages and after varying periods of time took core samples of the benthic infauna. By comparing these cores to cores taken inside cages which lacked all predators, he was able to test whether the hogchoker had a significant impact on the benthic infaunal community. Even though the hogchoker feeds upon benthic infauna, it appeared to have no significant impact on the

infaunal community in Virnstein's (1977) Chesapeake Bay experiments. Since the hogchoker density used (one per 0.25 m²) is much higher than usually prevailing hogchoker densities, it may be reasonable to conclude that the hogchoker has a relatively trivial impact on benthic infaunal systems as a consequence of its feeding activity. This result probably indicates that hogchokers, like flounders, do not excavate the sediments to the degree that is characteristic of many rays and skates and of the blue crab.

As juveniles, other species of bottom-feeding, predatory fishes frequently visit intertidal flats at high tide. Some of these species are so generally abundant in the sounds and estuaries of North Carolina that their presence on the intertidal flat is quite obvious. For instance, spot (*Leiostomus xanthurus*), Atlantic croaker (*Micropogonias undulatus*), silver perch (*Bairdiella chrysura*), and pigfish (*Orthopristis chrysoptera*) are all abundant during warm months. Because of their relatively large size, they have relatively high feeding rates. Virnstein (1977) measured the impact of spot on the benthic infaunal community inside cages in Chesapeake Bay and found that one spot per 0.25 m² significantly reduced the abundance and diversity of the infauna. Although this experiment was carried out in a subtidal habitat, the occasionally high abundance of juvenile spot in the intertidal zone suggests that they may have a similar impact there.

A few spot, Atlantic croaker, pigfish, and silver perch are year-round residents of shallow waters in North Carolina, but most adults of these species migrate offshore to spawn in fall and winter. All four of these species are commonly caught by sport fishermen, while spot and Atlantic croaker also contribute to commercial fisheries. Because each species feeds, at least occasionally, on intertidal flats, this habitat contributes to these important fisheries to some extent. However, the majority of the feeding of each of these species occurs outside of intertidal habitats. For this reason, the truly characteristic fishes of intertidal flats remain the baitfishes (silversides, anchovies, menhaden, killifishes, mullets, etc.), the rays and skates, and the flatfishes (flounders, sole, and tonguefish). If any fish species would be threatened with local extinction by the elimination of intertidal mud and sand flats, that species would come from this list. In North Carolina,

probably all the baitfishes, rays, and flatfishes would be seriously depleted by loss of intertidal flat habitat. The planktivores, which benefit from the increased production of phytoplankton over intertidal flats, and the piscivorous (fish-eating) predators would also suffer through depletion of their food.

Table 2 lists a few additional bottom-feeding, predatory fishes which, upon occasion, forage in the intertidal zone of estuaries, sounds, and lagoons in North Carolina. Some of these species, such as the lizardfish (*Synodus foetens*) and the oyster toad (*Opsanus tau*), are abundant, although the bulk of their feeding is undoubtedly done outside of the intertidal zone. Oyster toads commonly forage around hiding places in the subtidal zone, but this foraging often carries them up onto intertidal flats. Oyster toads are also known to excavate pits while feeding in the intertidal zone. Occasionally, an oyster toad can be found stranded in such a pit at low tide.

4.4 NON-RESIDENT FISHES INDIRECTLY DEPENDENT UPON INTERTIDAL FLATS

The fishes listed in Table 3 are only occasionally found over intertidal flats, but ordinarily consume some prey that have fed in intertidal environments. Most of these species are large, very mobile predators and fall into the fourth trophic category: consumers of fish and large epibenthic invertebrates. As such, these species tend to feed on a higher trophic level than those species which forage directly on the intertidal flat. Many of these larger predators, especially the sharks, remain in deeper water during the day and only approach the shallows during the cooler temperatures of night. Because these species are so large and mobile, they are rarely netted in otter trawls or seines, so that their abundance and importance in coastal systems are largely unknown.

Several of these larger predators are valuable to either commercial or sport fisheries in North Carolina. The weakfish (*Cynoscion regalis*) is probably the most important of these. Although less abundant, the spotted seatrout (*C. nebulosus*) and small red drum or "puppy drum" (*Sciaenops ocellata*) are prized game fishes in the sounds of North Carolina. The bluefish (*Pomatomus saltatrix*) is abundant and contributes greatly to the

sport and commercial fisheries of the State. Bluefish generally spend their first summer feeding and growing in sounds and lagoons before moving out into the ocean sometime in the fall. These young bluefish reach about 4 lb in size before they make this shift in habitat. The black seabass (*Centropristis striata*) is also an important contributor to the sport fishing industry of North Carolina. Although the Spanish mackerel (*Scomberomorus maculatus*) has not been included in the list of species partially dependent upon food species from intertidal flats, it sometimes leaves the ocean to venture into sounds and estuaries. When it does, it preys heavily on silversides and other baitfishes which may have been feeding on intertidal flats.

Among the sharks listed in Table 3, perhaps only the Atlantic sharpnose shark (*Rhizoprionodon terranova*) is often seen in shallow waters in the sounds and estuaries of North Carolina. Other sharks which are larger, more mobile, and nocturnal in their visits to shallow water, may be more involved with intertidal flats than is commonly recognized. Sharks represent one common terminus of food chains originating in the intertidal flat habitat.

4.5 ESTUARIES AS NURSERY GROUNDS FOR FISHES

One of the most widely quoted functions of estuaries and coastal lagoons is their role as nursery areas for many marine fishes. Many fish species which live or spawn at sea as adults utilize the estuary as postlarval forms and as juveniles. Presumably this split life history has developed in response to (1) the very high productivity of estuarine systems which can satisfy the early nutritional needs of the juvenile fishes and (2) the protection from predators provided by the shallow waters. Those species which utilize the estuaries as nurseries include most of the important commercial and sport species as well as most baitfishes in the coastal marine systems of North Carolina (Turner and Johnson 1973). The contribution of estuarine systems in general to marine fisheries is enormous, and the intertidal flat habitat makes its contribution to this pattern.

The dietary information presented earlier applies to juvenile and adult fishes. Most species of bony fishes undergo radical changes in their

trophic status as they grow and age. As larvae, most marine fishes are considered part of the plankton because of their small size. Even as postlarval forms, most marine fishes are very small. Both larval and early postlarval fishes feed upon zooplankton. This is true of species which are planktivorous as adults, as well as species which are predatory when older (Kjelson et al. 1975). Atlantic croaker, spot, striped mullet, and virtually all other larval and postlarval fishes in marine systems spend much time in small size classes which feed on the zooplankton. Because zooplankton are supported by a diet of phytoplankton, intertidal flats contribute indirectly to zooplankton production through the mechanism of increasing the area of the euphotic zone and supplying inorganic nutrients, both of which stimulate phytoplankton production (see Chapter 2). Intertidal flats also contribute directly to the success of larval and postlarval fishes in another way. Because of their vulnerability to predators, these postlarval fishes congregate in the shallowest waters of the estuarine system for protection against predatory fishes, which are ordinarily reluctant to risk the shallows. Many fishes which are strictly marine as adults can thus be found during their earliest life stages in the intertidal flat habitats. For instance, even some of the offshore reef fishes, various snappers and groupers, spend their larval and early postlarval days as planktivores in the shallows of estuaries and lagoons in North Carolina (Adams 1976a), although it is unclear how important these juveniles are to the total reproductive effort of the reef species.

Not only do marine fishes raised in estuaries demonstrate predictable changes in trophic status as they grow, but they also show unpredictable changes in feeding habits in response to varying abundances of preferred foods. Predatory fishes in estuaries commonly supplement their diets with detritus when their usual prey are scarce (Darnell 1964). Although growth rates on pure diets of detritus are quite low, this plastic feeding behavior at least permits the predators to survive periods of food scarcity. Detritus always is available as a dependable alternate source of energy in any estuarine system.

4.6 SEASONAL CHANGES IN THE FISH FAUNA OF INTERTIDAL FLATS

Seasonal variation in the fish fauna found over intertidal flats at higher tides is quite substan-

tial. Most estuarine and lagoonal fish species are not year-round residents in North Carolina. Many, like the bluefish, migrate south during the cold months. Others, like adult spot and Atlantic croaker, simply migrate into deeper oceanic waters for the winter, although they may also undergo some north-south migration. Even fishes which remain in enclosed sounds and estuaries during the cold months usually move into deeper waters where the temperature extremes are not so pronounced. For instance, those spotted seatrout and yearling spot and croakers which spend winters in North Carolina sounds are found congregated in deeper holes during cold months. These species are never seen foraging out over intertidal zones during winter.

In spring, the North Carolina flats remain populated by the characteristic silversides and killifishes. As the waters warm in March, April, and May, large schools of small postlarval and adult Atlantic croaker, spot, menhaden, and flounders will appear. Occasionally, the near-shore waters will be dark with schools of the young of these fishes. Juvenile striped mullet also appear during this period, but their numbers do not equal those of the juvenile spot, Atlantic croaker, and menhaden at this time of the year. By late spring large schools of juvenile silversides are also common. Small pinfish appear during the spring, but they are ordinarily restricted to grass-bed habitats during this stage of their life cycle. By late spring, species diversity of fishes has reached a high level that is exceeded only by the diversity in the fall. Species diversity of fishes in North Carolina estuaries is bimodal when plotted over the full year with a spring and a higher fall peak coinciding with the presence of fishes on their north-south migrations (F. J. Schwartz, Univ. North Carolina, Chapel Hill, Pers. Comm.).

Although fishes are common over North Carolina's tidal flats only during the warmer months of the year, most of the production of invertebrates and other prey types occurs then, too. The summer is characterized by high fish abundances. Species diversity of fishes is high in summer but not as high as the spring level. During the summer months the species described earlier are actively feeding. Baitfishes, flatfishes, and rays are the prominent members of the summer ichthyofauna on North Carolina's tidal flats, with several additional species occasionally visiting the flats to feed.

In the early fall, fish species diversity reaches its yearly maximum. Summer residents are still present and are joined by the early fall migrants to produce this high diversity. In late fall, many of the warm-water residents begin to leave the shallows for their migratory runs to deeper or more southerly waters. Small bluefish, rare on North Carolina's intertidal flats during the summer, invade in large schools that have come from sounds farther north. These feed on baitfishes over intertidal flats and in deeper waters before continuing their migration southward. Striped mullet begin to school up in preparation for their migration south. Spotted seatrout move into shallow waters during the fall, as do kingfish (*Menticirrhus* spp.). Flounders are still abundant in the fall, although the adults school up and move out the inlets by the end of October. The year-round residents of intertidal flats, killifishes and silversides, remain obvious on tidal flats throughout the fall.

This cyclic pattern of seasonal change in abundance and diversity is a universal characteristic of the fish fauna of east-coast estuarine systems. Partly responsible is the seasonal variation in abundance of all fish foods from plankton to marine invertebrates to smaller fishes. The physiological temperature tolerances of the fishes and breeding habits also may play a role in setting this pattern of seasonality.

In addition to seasonal patterns in fish abundances on intertidal flats, there are strong temporal cycles in abundance over shorter time periods. The most important of these are probably the patterns induced by the alternation of day and night. Most, but not all, fishes feed more actively at certain times of day, often early morning and late evening. Other behavioral patterns are also cued into day-night cycles. In particular, many smaller fishes appear to forage away from the cover of grass beds and other hiding places only under the protection of darkness. The unvegetated intertidal flats are often far more heavily visited by fishes, as well as crabs, during the night than in the daytime. Some of the larger predators follow a day-night pattern as well. It is no accident that almost all giggering for flounders on the North Carolina tide flats occurs at night, when flounders lie on these flats and are relatively inactive. Many of the sharks that play the role of top predators on the intertidal flats pay their summertime visits to shallow waters at night.



The common egret often feeds in small intertidal creeks where food organisms concentrate in the receding waters. Detritus, accumulated on the exposed mudbank, is in the process of degradation which is vital to its incorporation into the food web. Photo by T. A. Klopp.

5.1 THE VARIETY OF AVIAN ROLES ON INTERTIDAL FLATS

Most visitors to an estuary would probably associate intertidal flats with the various species of wading birds and shorebirds which are commonly seen there. Birds are certainly the most conspicuous element of almost any intertidal flat, in part because they are large and usually clearly visible. This subjective impression that many birds are intimately associated with intertidal sand and mud flats is supported by evidence. Fishes can always forage subtidally. Wading and sediment-probing shorebirds, however, can gather food only on intertidal and very shallow subtidal flats. Deeper subtidal habitats are largely inaccessible, except to some deep-diving ducks. Furthermore, because of their frequently high abundances and their substantial food requirements resulting from high metabolic rates, birds often have a substantial impact on the infaunal invertebrates of intertidal habitats (Schneider 1978).

Table 4 provides a nearly complete list of those species of birds which utilize the intertidal flats of sounds, lagoons, estuaries, and river mouths in North Carolina. This list is subdivided into six ecological categories, or 'guilds': (1) waders (including herons, egrets, ibises, yellowlegs); (2) shallow-probing and surface-searching shorebirds (sandpipers, plovers, knots, oystercatchers, etc.); (3) deep-probing shorebirds (godwits, willets, curlews); (4) aerial-searching birds (terns, gulls, skimmers, pelicans, kingfishers); (5) floating and diving water birds (ducks, grebes, geese, loons, cormorants, and a swan); and (6) birds of prey (ospreys, hawks, eagles, owls). Each of these guilds is ordinarily represented by at least one species on intertidal flats around the world. Certain guilds are clearly more diverse than others. For instance, the shallow-probing shorebirds are the most diverse on almost any shoreline including the flats of North Carolina. In contrast, there are few birds of prey that are important in intertidal systems.

Many (probably most) of these species of birds represent end-points in the consumer food chains of intertidal flats. Certainly adult waders are largely free of predation because of their large

body sizes, although eggs and nestlings are probably preyed upon by gulls, foxes, raccoons, and rats. As adults, terns and gulls are not ordinarily preyed upon by higher-order predators. Only the smaller probing shorebirds (sandpipers, etc.) and some of the ducks are likely to have natural enemies as adults. Even for these groups, most natural mortality probably occurs as a consequence of starvation or other factors unrelated to predation. Given that many of the species listed in Table 4 are end-points in the food chains of intertidal flats in North Carolina, an important pattern in the food chains of estuaries is clearly illustrated. The usual trophic pyramid is inverted; there are more numerically important consumer species at the top of the food web. This intertidal flat community organization differs radically from the organization of rocky intertidal benthic communities where distinct food webs, each headed by a limited number of 'top carnivores,' are the rule (Paine 1966). One implication of this difference is that any loss of primary production in an estuarine system will have widespread ramifications on the populations of top predators because they are all dependent upon the same narrow energy base. Because so many of these top predators are birds, it is the birds that would suffer most from such a hypothetical loss in primary production.

5.2 WADERS

Wading birds are characteristic components of the intertidal flat habitat. Table 4 lists all of the wading species that one would ever be likely to encounter feeding on the intertidal flats of North Carolina. Of these, three species are by far the most numerous in this habitat: the great egret, the snowy egret, and the Louisiana heron (Soots and Parnell 1975). These are also the three most abundant species in rookeries along the entire east coast (Custer and Osborn 1977). This correspondence underscores the importance of the intertidal flat habitat to wading birds.

The greater yellowlegs is also characteristic of sand and mud flats. The yellowlegs have been included in the wading bird guild because they act like miniature herons or egrets, wading in shallow water while searching for and ultimately catching

Table 4. Bird species which utilize intertidal flat habitats in North Carolina, subdivided into guilds of ecologically similar species.^a

Guild and species	Abundance ^b	Diet	Residency status in N.C.
1) WADERS			
Great Egret (<i>Casmerodius albus</i>)	FC(S); U(W)	Small fishes	Permanent resident
Snowy Egret (<i>Egretta thula</i>)	FC(S); U(W)	Small fishes	Permanent resident
Louisiana Heron (<i>Egretta tricolor</i>)	FC(S); U(W)	Small fishes	Permanent resident
Great Blue Heron (<i>Ardea herodias</i>)	U(S); FC(W)	Small fishes	Permanent resident
Little Blue Heron (<i>Egretta caerulea</i>)	FC(S); U(W)	Small fishes	Permanent resident
Green Heron (<i>Butorides striatus</i>)	FC	Small fishes	Summer resident
Black-crowned Night Heron (<i>Nycticorax nycticorax</i>)	FC	Small fishes	Permanent resident
Yellow-crowned Night Heron (<i>Nycticorax violacea</i>)	U	Crustaceans	Summer resident
White Ibis (<i>Eudocimus albus</i>)	FC (south of Cape Lookout)	<i>Uca</i> and other crustaceans	Permanent resident
Greater Yellowlegs (<i>Tringa melanoleuca</i>)	FC	Small fishes, crustaceans	Winter resident
2) SHALLOW-PROBING AND SURFACE-SEARCHING SHOREBIRDS			
Clapper Rail (<i>Rallus longirostris</i>)	FC	<i>Uca</i> and other crustaceans	Permanent resident
Piping Plover (<i>Charadrius melodus</i>)	U	Insects, amphipods, etc.	Winter resident
Semipalmated Plover (<i>Charadrius semipalmatus</i>)	FC + <u>C</u>	Insects, amphipods, etc.	Winter resident + <u>transient</u>
Wilson's Plover (<i>Charadrius wilsonia</i>)	U	Insects, amphipods, etc.	Summer resident
Killdeer (<i>Charadrius vociferus</i>)	U	Insects, amphipods, etc.	Winter resident
American Golden Plover (<i>Pluvialis dominica</i>)	R	Insects, amphipods, etc.	Transient
Black-bellied Plover (<i>Pluvialis squatarola</i>)	C	Insects, amphipods, etc.	Winter resident
Ruddy Turnstone (<i>Arenaria interpres</i>)	FC + <u>C</u>	Crustaceans, polychaetes	Winter resident + <u>transient</u>
Red Knot (<i>Calidris canutus</i>)	U(F); C(Sp)	Crustaceans, polychaetes	Transient
Dunlin (Red-backed Sandpiper) (<i>Calidris alpina</i>)	C	Insects, molluscs	Winter resident
Spotted Sandpiper (<i>Actitis macularia</i>)	FC	Invertebrates	Transient
White-rumped Sandpiper (<i>Calidris fuscicollis</i>)	U	Invertebrates	Transient
Least Sandpiper (<i>Calidris minutilla</i>)	U + <u>FC</u>	Invertebrates	Winter resident + <u>transient</u>
Western Sandpiper (<i>Calidris mauri</i>)	C	Invertebrates	Winter resident
Semipalmated Sandpiper (<i>Calidris pusilla</i>)	FC	Invertebrates	Transient
Short-billed Dowitcher (<i>Limnodromus griseus</i>)	U + <u>FC</u>	Polychaetes, other benthic invertebrates	Winter resident + <u>transient</u>
Long-billed Dowitcher (<i>Limnodromus scolopaceus</i>)	U	Polychaetes, other benthic invertebrates	Winter resident

continued

Table 4. (continued)

Guild and species	Abundance ^b	Diet	Residency status in N.C.
Sanderling (<i>Calidris alba</i>)	C	Polychaetes, other benthic invertebrates	Winter resident
American Oystercatcher (<i>Haematopus palliatus</i>)	FC	Large bivalves	Permanent resident
3) DEEP-PROBING SHOREBIRDS			
Marbled Godwit (<i>Limosa fedoa</i>)	U	Deep invertebrates	Fall transient (some winter)
Willet (<i>Catoptrophorus semipalmatus</i>)	C(S); U(W)	Crabs, etc.	Permanent resident
Long-billed Curlew (<i>Numenius americanus</i>)	R	Deep invertebrates	Fall transient
Whimbrel (Hudsonian Curlew) (<i>Numenius phaeopus</i>)	FC	Deep invertebrates	Transient
4) AERIAL-SEARCHING BIRDS			
Caspian Tern (<i>Sterna caspia</i>)	FC	Fishes	Fall transient (few summer, few winter)
Gull-billed Tern (<i>Gelochelidon nilotica</i>)	U	Insects over marshes	Summer resident
Forster's Tern (<i>Sterna forsteri</i>)	FC + <u>C</u>	Fishes	Winter resident + <u>fall transient</u>
Common Tern (<i>Sterna hirundo</i>)	FC	Fishes	Summer resident
Least Tern (<i>Sterna albifrons</i>)	FC	Fishes	Summer resident
Royal Tern (<i>Sterna maxima</i>)	FC(S); U(W)	Fishes (some offshore)	Permanent resident
Sandwich Tern (Cabot's Tern) (<i>Sterna sandvicensis</i>)	U	Fishes (some offshore)	Summer resident
Black Tern (<i>Chlidonias nigra</i>)	U	Fishes	Fall transient
Herring Gull (<i>Larus argentatus</i>)	C	Fishes, scallops, clams	Winter resident
Great Black-backed Gull (<i>Larus marinus</i>)	FC	Fishes	Winter resident
Ring-billed Gull (<i>Larus delawarensis</i>)	C	Fishes	Winter resident
Laughing Gull (<i>Larus atricilla</i>)	C(S); U(W)	Fishes	Permanent resident
Bonaparte's Gull (<i>Larus philadelphia</i>)	FC	Fishes	Winter resident
Fish Crow (<i>Corvus ossifragus</i>)	C	Fishes, molluscs	Permanent resident
Brown Pelican (<i>Pelecanus occidentalis</i>)	FC(S); U(W)	Fishes	Permanent resident
Black Skimmer (<i>Rynchops niger</i>)	C(S); U(W)	Fish (mullet)	Permanent resident
Belted Kingfisher (<i>Megasceryle alycon</i>)	FC(W); U(S)	Small baitfishes	Permanent resident
5) FLOATING AND DIVING WATER BIRDS			
Common Loon (<i>Gavia immer</i>)	C	Fishes	Winter resident
Red-throated Loon (<i>Gavia stellata</i>)	FC	Fishes	Winter resident

continued

Table 4 (concluded)

Guild and species	Abundance ^b	Diet	Residency status in N.C.
Horned Grebe (<i>Podiceps auritus</i>)	FC	Fishes	Winter resident
Pied-billed Grebe (<i>Podilymbus podiceps</i>)	FC	Fishes	Winter resident
Double-crested Cormorant (<i>Phalacrocorax auritus</i>)	C	Fishes	Winter resident (few summer)
Whistling Swan (<i>Olor columbianus</i>)	U	Herbivorous-omnivorous	Winter resident
Canada Goose (<i>Branta canadensis</i>)	C (north of Cape Hatteras)	Herbivorous-omnivorous	Winter resident
Brant (Black Brant) (<i>Branta bernicla</i>)	FC (only near Ocracoke Inlet)	Benthic macro-algae, seagrass	Winter resident
Snow Goose (<i>Chen caerulescens</i>)	C (around Bodie Island)	Herbivorous-omnivorous	Winter resident
Black Duck (<i>Anas rubripes</i>)	FC	Benthic mud flat algae, invertebrates	Winter resident
Redhead (<i>Aythya americana</i>)	U (C in Core Sound)	Herbivorous-omnivorous	Winter resident
Canvasback (<i>Aythya valisineria</i>)	U (C in Pamlico River)	Algae, invertebrates	Winter resident
Greater Scaup (<i>Aythya marila</i>)	U	Predominantly molluscs	Winter resident
Lesser Scaup (<i>Aythya affinis</i>)	FC (C in Neuse River)	Predominantly molluscs	Winter resident
Common Goldeneye (<i>Bucephala clangula</i>)	U	Predominantly molluscs	Winter resident
Bufflehead (<i>Bucephala albeola</i>)	FC	Predominantly molluscs	Winter resident
White-winged Scoter (<i>Melanitta fusca</i>)	U (north of Cape Hatteras)	Predominantly molluscs	Winter resident
Surf Scoter (<i>Melanitta perspicillata</i>)	FC (C in Neuse River and Pamlico Sound)	Predominantly molluscs	Winter resident
Common Scoter (Black Scoter) (<i>Melanitta nigra</i>)	C	Predominantly molluscs	Winter resident
Ruddy Duck (<i>Oxyura jamaicensis</i>)	C (Neuse River, Core Sound)	Molluscs and other invertebrates	Winter resident
Red-breasted Merganser (<i>Mergus serrator</i>)	C	Baitfishes	Winter resident
Hooded Merganser (<i>Lophodytes cucullatus</i>)	FC	Baitfishes	Winter resident
6) BIRDS OF PREY			
Osprey (<i>Pandion haliaetus</i>)	U	Large fishes	Summer resident
Bald Eagle (<i>Haliaeetus leucocephalus</i>)	R	Large fishes	Winter resident
Marsh Hawk (<i>Circus cyaneus</i>)	FC	Rodents, birds	Winter resident
Short-eared Owl (<i>Asio flammeus</i>)	U	Rodents, perhaps birds	Winter resident
Barn Owl (<i>Tyto alba</i>)	U	Rodents, perhaps birds	Winter resident

^aData for this list were assembled from Harper (1914), Simpson (1940), Pearson et al. (1942), Funderburg and Quay (1959), Palmer (1962), Robbins et al. (1966), Parnell and Soots (1978), Zingmark (1978), personal observations, and (predominantly) from John Fussell, III's observations.

^bAbundance categories: R = rare, U = uncommon, FC = fairly common, C = common. If abundance changes during period of presence in North Carolina season is given in parentheses.

small baitfishes (killifishes, silversides, anchovies). Although present in coastal North Carolina, the lesser yellowlegs is typically associated with impoundments and high marsh pools. Because it very rarely visits intertidal flats, it is excluded from Table 4. With the exception of the ibises and the yellow-crowned night heron, the waders are almost exclusively fish eaters. The white ibis feeds largely upon crustaceans, including in particular fiddler crabs (*Uca* spp.) on North Carolina's tidal flats. The yellow-crowned night heron consumes a variety of smaller crustaceans as well as some fishes. Some species of waders, such as the green heron and the great blue heron, are frequent foragers along the shorelines of ponds and other freshwater habitats. Since the cattle egret feeds almost entirely on insects taken from pastures and fields and since the glossy ibis feeds almost exclusively in ponds on the high marsh, neither species has been listed in Table 4 despite their obvious presence in coastal North Carolina.

Because the herons, egrets, and ibises are colonial nesters, breeding populations are easy to estimate. Parnell and Soots (1978, 1979) have made extensive studies of the rookeries of these waders in North Carolina, from which excellent population estimates are available. Almost all heron, egret, and ibis rookeries (usually called heronries for this group) occur on islands, probably because potential egg predators like foxes, raccoons, and rats are usually absent from islands. In North Carolina, 61% of estuarine islands are artificial, composed of dredge spoil. Of the heronries, 62% occur on such dredge-spoil islands, and those heronries on dredge-spoil islands are larger and contain 92% of all nesting waders (Parnell and Soots 1978). Parnell and Soots suggest that the dredge-spoil island is a preferred site because such islands are higher in elevation than natural islands and, therefore, less subject to overwash and flooding. Since most dredging is done near inlets where fish are abundant, the spoil islands are ideal locations for fish-eating waders.

The birds of any coastline can be divided into at least four groups based upon their seasonal occurrence: (1) summer (breeding) residents; (2) winter residents; (3) transients (passing through during either fall or spring migrations or both); and (4) permanent residents. All of the herons, egrets, and the ibis listed in Table 4 summer and breed in North Carolina, and most species spend

the winter as well. The greater yellowlegs is the only species in this guild which fails to breed in North Carolina; it is a winter resident. The year-round presence of wading birds is made possible by the permanent presence of small baitfishes over the tidal flats of North Carolina. Farther north, where small fishes are rare on flats during winter and where ice cover restricts access to those fishes which are present, waders cannot feed year-round.

5.3 SHALLOW-PROBING AND SURFACE-SEARCHING SHOREBIRDS

Like the waders, this guild is typical of intertidal habitats worldwide. It is also the most diverse and most abundant guild on many intertidal flats, including those of North Carolina. Not only is the species diversity of this guild high, but also the diversity of form and structure. Bill lengths and shapes vary widely, presumably correlated with differences in prey type. Recher (1966) has suggested that various species in this group possess such a wide diversity of bill structures and feeding habits as a means of coexistence in a habitat (the intertidal flat) which itself cannot be adequately partitioned because of its physical uniformity. In other words, perhaps these probing and searching species have specialized on certain food types and certain foraging strategies in order to avoid competitive exclusion because habitat segregation is nearly impossible.

The list of shallow-probing and searching shorebirds of North Carolina's intertidal flats (Table 4) includes all species that would ever be encountered in this habitat, with two exceptions (the pectoral sandpiper and the solitary sandpiper which feed almost exclusively on sandy beaches). Some of the species which appear on this list, such as killdeer, golden plover, and long-billed dowitcher, obtain only a small fraction of their food from intertidal flats. Killdeer often feed on insects in fields. The majority of species listed in this guild, however, depend upon the intertidal flat for most of their food requirements (Palmer 1962).

Shallow probers are extremely opportunistic in their feeding, taking what food items are most abundant. Diets of individual species differ radically over time and in different localities. Schneider (1978) constructed cages to exclude

migratory shorebirds (mostly shallow probers) from intertidal mud flats in Plymouth, Massachusetts, and learned that these shorebirds caused a huge decline in the density of invertebrate infauna on these mud flats during the 2-month (July-September) migratory period. The probers always tended to select the most abundant of the several prey species that made up their diet. This was true on each mud flat examined in the study even though the prey species which were most common varied from one flat to another. The only species which the shorebirds seemed to avoid was *Gemma gemma*, a small but relatively thick-shelled clam. They fed heavily on polychaetes, amphipods, other small crustaceans, and insects. The largest invertebrates were generally preyed upon more heavily than the smaller species. The most numerous species of shorebirds on Schneider's experimental flats were the sanderling, semipalmated sandpiper, short-billed dowitcher, and black-bellied plover, all of which occur on flats in North Carolina.

Shallow-probing and searching shorebirds differ among themselves in feeding strategies and, therefore, in diet. The plovers and smaller sandpipers feed by sight (Recher 1966) and, accordingly, prey upon surface fauna most heavily, including insects and surface amphipods. Most of the other species in this guild (except the American oystercatcher and perhaps the red knot) have intricately innervated bills which permit them to feed by touch. Feeding by these species is normally a subsurface process of true probing in the shallow layers of the sediments. These birds are thus more likely to take polychaete worms and other infaunal invertebrates in their diets. A study of two coexisting sandpipers in Sweden (Bengtson and Svensson 1968) demonstrated large differences in feeding habits and subsequent diets between two very similar shallow-probing shorebirds. Other studies (Wolff 1969) demonstrate how probing shorebirds in the same estuary possess different distributions to match the spatial patterns of their preferred prey.

Other clear behavioral and ecological differences occur among the shallow-probing and searching shorebirds. For instance, the ruddy turnstone will frequent hard-substrate outcroppings within the mud flat environment. This bird is commonly found feeding around rocks, pilings, and oyster clumps surrounded by

soft sediments. In Beaufort, North Carolina, the ruddy turnstone has been observed feeding upon the wharf roach, *Ligia exotica*, found on such hard substrates (Simpson 1940). The clapper rail, like all rails, is a secretive bird which hides high in the salt marsh. Rails are more often heard than seen. In feeding, clapper rails often venture out onto the mud flats at low tide, where they can be seen in North Carolina pursuing and capturing fiddler crabs (*Uca*) and other decapod crustaceans.

Oystercatchers differ substantially from the other shorebirds in this guild in that they feed upon large bivalves, such as clams and oysters. In a sense, an oystercatcher is a heavy-duty version of a probing shorebird, distinguished by its heavy bill which permits harvest of the large thick-shelled bivalves, which are sufficiently armored for protection against the probing shorebirds. Oystercatchers worldwide have the distinction of being able to harvest large bivalve molluscs of the intertidal zone. In Europe and on the west coast of North America, they consume large cockles and cockle-like clams from this habitat. The oystercatcher in North Carolina seems entirely restricted to, and therefore totally dependent upon, foraging in intertidal habitats at low tide.

Although both dowitchers listed in Table 4 possess long bills, they appear in the shallow-probing and searching guild because of their feeding habits. Only occasionally do dowitchers probe to the 8- to 10-cm depth made possible by their long bills. Dowitchers frequently use their bills to capture tube-building polychaetes like *Amphitrite*. By taking such polychaetes, their diets more closely resemble that of the shallow probers than that of the deep-probing shorebirds. This distinction is subtle and the dowitchers could easily be included in the deep-probing guild.

Most of the species in this shallow prober guild are only abundant in North Carolina during migrations. Some, like the clapper rail and American oystercatcher, are year-round residents, whereas other species spend either the winter (dunlin) or the summer (Wilson's plover) on North Carolina's tidal flats. Nonetheless, this is largely a migratory guild with high abundances in spring (March-May) and fall (July-November). The spring and fall migrations differ in length and intensity as well as in the direction of net movement of the birds. The fall migration tends to be

spread out over a relatively long period, perhaps as long as 4 to 5 months in Beaufort, North Carolina. Species are moving independently and peak abundances of various species are displaced in time. In spring, the migratory period is greatly compressed into 1 or 2 months. The shorebirds move through the area much faster and peak numbers of various species tend to coincide. As a result, total density of shallow-probing shorebirds can often be far higher during spring migration than during the fall migratory period. Recher (1966) has speculated that this difference may be a consequence of the lower tides during the spring months, which permit the birds a much greater feeding time to refuel for their continued journey. This tidal pattern holds true along the North Carolina coast, but, in addition, the densities of infaunal invertebrates on intertidal flats in North Carolina are far greater in the spring than in the fall (Commuto 1976). Consequently, refueling can be accomplished much more efficiently in a shorter period of time. If this refueling need is the determinant of the length of feeding delays during migration, then the difference in prey abundance as well as the difference in feeding time because of seasonal tidal variations may be causes of the short spring migratory season. This argument, along with Schneider's (1978) experimental results, helps to demonstrate the extreme importance of intertidal flats as feeding grounds for the migratory, shallow-probing and searching shorebirds.

5.4 DEEP-PROBING SHOREBIRDS

The deep-probing shorebirds have been separated from the shallow probers in Table 4 because of Recher's (1966) and Baker and Baker's (1973) analyses of feeding habits and diets among probing shorebirds. These deep probers are ecologically different from the birds of the shallow-probing guild. Deeper probing makes available a large group of deeper-burrowing and generally larger marine invertebrates. Furthermore, members of this deep-probing shorebird guild are most efficient when wading in water, so that they tend to forage at lower levels along the shoreline than the shallow probers which are largely restricted (with some exceptions) to the exposed portions of the flats.

Only four species of deep probers appear regularly on the intertidal flats of North Carolina:

the marbled godwit, willet, long-billed curlew, and whimbrel (Table 4). Not only are there few east-coast species in this guild, but also the abundance of deep probers on North Carolina's intertidal flats is quite low relative to similar habitats on the west coast of North America. This geographic difference may be related to a large difference in the invertebrate communities of the two coasts. On North Carolina's intertidal flats, the abundance of relatively large crustacean infauna (such as *Callianassa* and *Upogebia*) is low (Lee 1974, Commuto 1976, Wilson 1978). In contrast, these ghost shrimp and mud shrimp are extremely common in the intertidal flats of the west coast (Peterson 1977). Both *Callianassa* and *Upogebia* dig relatively deep burrows which protect them from shallow probers but not from deep-probing shorebirds. West coast abundances of other infaunal invertebrates are also far higher, permitting larger total densities of probing shorebirds. These prey differences between coasts probably explain why the deep-probing guild is relatively underrepresented on North Carolina's intertidal flats.

When deep probers are abundant along the North Carolina coast, they are often found feeding on ocean beaches. Willets, especially, are more often found feeding on sandy beaches, where they can gather the abundant mole crab (*Emerita*) during the warm months, than on intertidal sand and mud flats. Only during colder months when *Emerita* has migrated off the beach into deeper waters are willets likely to be found in abundance on intertidal flats. Among the shallow-probing guild only the sanderling seems to follow this pattern of strong preference for beach habitats during warm months, although it more often preys upon the beach hoppers (*Talorchestia* and *Orchestia*).

It is somewhat misleading to include the willet among the other shorebirds in the deep-probing guild. Although the willet is appropriately equipped with a comparatively long bill, it does not always use that bill for probing into the sediments. Willets are extremely aggressive and commonly follow other probing shorebirds around the flats, waiting for an opportunity to attack and pirate their catch before they can swallow it. Willets in North Carolina often rob from marbled godwits, sanderlings, and some of the smaller shallow-probing shorebirds. As a result, the willet's diet

will often resemble that of a shallow prober despite its ability to forage at depth. Willets also attack and consume small crabs on the sediment surface much more readily than do other deep probes. This, too, gives a different flavor to their diet.

Although the deep-probing guild is not especially important on the intertidal flats of North Carolina, some flats are especially attractive to this group. Specifically, those flats where any of the larger infaunal crustaceans, such as the ghost shrimp and mud shrimp, are abundant play an important role in the ecology of species in the deep-probing guild. Such flats may be of critical importance during winter when the mole crab is unavailable on the ocean beaches.

5.5 AERIAL-SEARCHING BIRDS

This guild includes all species of terns and gulls, as well as the single species of pelican, skimmer, kingfisher, and fish crow commonly found along the North Carolina coast. These birds feed predominantly on fishes, including (in North Carolina) silversides, mullets, and anchovies. The inclusion in Table 4 of all of the terns and gulls normally visible along the North Carolina coast overstates the importance of intertidal flats to this guild. Some species, like the sandwich tern and the royal tern, often fish in the ocean, and all of the others probably do most of their foraging outside of the intertidal zone. Nevertheless, even those birds fishing far away from intertidal habitats often take prey which have fed over intertidal flats, while other terns and gulls do a significant fraction of their feeding in the shallow waters overlying intertidal environments.

Both gulls and terns prey on fishes. Terns tend to hunt from the air, spotting their prey visually and diving to capture it. Gulls often employ this same foraging technique, but they also search for prey from a floating position. In body size, terns are slightly smaller than gulls and seem to capture somewhat smaller fishes. Both terns and gulls take advantage of feeding schools of piscivorous fishes by circling overhead and diving to harvest the left-overs, the injured and confused bait fishes. Terns are thought to feed almost exclusively on live prey, whereas gulls are not so choosy. Especially while floating, gulls often scavenge dead fish. Both terns and gulls feed most

heavily along shorelines where even bottom-feeding fishes are close to the surface and where land masses block the wind creating a flat water surface under which prey are most easily seen from the air. Many gulls have far broader diets than most terns as a partial consequence of their scavenging activities during low tide. Herring gulls can often be seen strutting about the intertidal flats of North Carolina scavenging dead fish and searching for scallops, clams, and other relatively large, shelled invertebrates which they carry aloft and drop upon the ground to crack open the shells. Many gulls are aggressive scavengers which chase various shorebirds in an occasionally successful attempt to pirate their catch. Fish crows scavenge dead fish and consume invertebrates along the shoreline at low tide in a fashion similar to the herring gull and other gulls.

Although some gulls and some terns remain in North Carolina waters year-round, there is an obvious seasonal replacement that occurs in both groups. Summers are characterized by high abundances of several species, including especially the least tern, common tern, and laughing gull. In winter these gulls and terns are replaced by an almost completely different set of common species, Forster's tern, the herring gull, and the ring-billed gull. Other species can be very abundant during migrations, such as the black tern, the caspian tern, and Bonaparte's gull. Although some birds from each of several species remain in North Carolina year-round, the dominant pattern is this seasonal replacement. Summer abundances of this guild are ordinarily somewhat higher than winter densities in North Carolina. This is probably a consequence of the seasonal variation in the abundance of the dominant prey, the smaller fishes. One major reason that winter abundances are as high as they are is that the herring gull, the most common winter gull, takes invertebrates in its diet, and is, therefore, not totally dependent upon fishes.

The black skimmer, belted kingfisher, and brown pelican are all fish eaters like the terns and gulls. Each of these three species is a year-round resident of North Carolina, although the abundances of skimmers and pelicans are much reduced during winter. Black skimmers fish by gliding over the water surface, often with their lower mandible trailing in the water. In North Carolina, they commonly fish in pairs along the

edges of sounds, estuaries, and river mouths. Black skimmers can also be found on ocean beaches fishing the surf zone. They virtually restrict their fishing to the intertidal zone in each habitat. The belted kingfisher is likewise restricted to fishing along the margins of shorelines, over intertidal areas when the tide is high and over shallow subtidal areas at other times. This restriction to shorelines is produced by the search habits of the belted kingfisher, which sits on a perch, usually a tree or shrub, to gain perspective on its potential prey. When the kingfisher spots a likely prey item, it dives from its perch to attack. Brown pelicans usually fish by gliding at low altitudes over the water surface in sounds and estuaries, as well as at sea. They are not restricted to feeding in shallow water like the belted kingfisher and black skimmer. Brown pelicans, which have been increasing in population in North Carolina in recent years, tend to aggregate on tidal deltas in the vicinity of inlets. It is around inlets that pelicans do most of their fishing.

The terns, gulls, pelicans, and skimmers are colonial nesters which build their nests on the ground on emergent land masses along the coast, particularly on barrier islands and dredge-spoil islands. Those species which summer and breed in North Carolina are quite easy to census because of their colonial nesting habits. Soots and Parnell (1975) have estimated the breeding abundance of several of these species in North Carolina and have studied the habitat selection of each species. Some species choose almost open beaches for nesting, while others prefer varying degrees of vegetative cover. In choosing its nesting site, the least tern avoids other species of terns (Jernigan et al. 1978) because it is small and less successful in aggressive encounters which often occur between least terns and common terns. Due to the increased human usage of barrier island beaches, the breeding habitats of many of these ground-nesting species are greatly threatened. Presumably, the decline of black skimmers in New Jersey is a consequence of the loss of breeding habitat. The need for protecting such habitats may result in restricting off-road vehicles from some ocean beaches. Dredge-spoil islands have provided valuable alternative nesting sites for these ground nesters.

5.6 FLOATING AND DIVING WATER BIRDS

The guild of floating and diving birds includes ducks of several types, loons, grebes, cormorants, geese, and a single swan species. Loons, grebes, and cormorants are usually found in fairly deep-water habitats but often fish in sounds and estuaries, occasionally even over intertidal flats. Virtually all of the birds in this guild (Table 4) are winter visitors to North Carolina waters. Only a few black ducks are present during the summer.

Although several different types of waterfowl are combined to form this guild on the basis of their common habit of foraging while floating on the water's surface, this remains a heterogeneous group of water birds. There are three identifiably different trophic types included: fish eaters, benthic mollusc eaters, and herbivores. The loons, grebes, mergansers, and cormorants prey upon fish, often relatively large ones. The scaup, scoters, bufflehead, common goldeneye, and to a lesser degree the ruddy duck, redhead, and black duck feed on benthic invertebrates, preferring clams found in shallow, occasionally intertidal habitats along shorelines. Most of the other ducks appear to be largely herbivores, including the geese, brants, swans, and canvasback. In consuming quantities of vegetation many of these species also ingest benthic invertebrates and should, therefore, be considered omnivorous (Pearson et al. 1942). The strict herbivorous are clearly not feeding on intertidal flats, where, by definition, there are no macrobenthic plants of significance. Several additional ducks are found in North Carolina during the winter, but these have not been included in Table 4 because they are extremely rare on tidal flats. Many of these prefer freshwater and all are largely herbivorous: the mallard, gadwall, pintail, green-winged teal, blue-winged teal, American wigeon, shoveler, wood duck, and ring-necked duck.

Despite the seasonal nature of this guild in North Carolina waters, the winter is an extremely stressful period for waterfowl. Adequate winter food supplies in a suitable habitat are critical to the continued persistence and health of most of the species in this guild. Wintering grounds in North Carolina and along the Chesapeake Bay are

extremely important. Most species in this guild ordinarily feed over shallow subtidal waters, but some feeding is carried out over intertidal flats. Many species seek particular characteristics in their wintering habitat, prime among these being suitable food densities. Certain shallow areas of the Pamlico Sound are noted for their high sculpin abundances, probably because of relatively dense populations of thin-shelled clams, *Mulinia lateralis*, *Macoma balthica*, and *Macoma phenax*. These three species of clams contribute significantly to the winter diet of most benthic-feeding ducks in brackish waters in North Carolina. Fortunately, the recruitment potential of these clams is high so that there are fairly predictable supplies each winter somewhere within the brackish waters of North Carolina (Williams 1978). Bufflehead, in contrast, seem to prefer the more saline waters of Bogue, Back, or Core Sounds, where they only rarely encounter high clam densities. Although many ducks congregate in multi-species flocks on their wintering grounds, some degree of habitat specificity remains, which, in combination with the mobility of these birds, can make accurate estimation of wintering populations difficult.

5.7 BIRDS OF PREY

The most obvious of the birds of prey along the shorelines of North Carolina's sounds, lagoons, estuaries, and river mouths is the osprey. These large predators can often be seen soaring at altitudes of up to 60 meters. From this height they plummet down to capture fish with their talons. Because of their large body size, they normally take relatively large fish, including adult mullet, bluefish, and eels. Ospreys nest along shorelines in coastal North Carolina and are fairly common in several localities. They often fish in shallow waters, occasionally over intertidal habitats, perhaps for the same reasons that terns concentrate their searching in these areas. Even bottom fishes can be captured in shallows, where land masses help block the wind, smoothing the water surface for clearer visibility. Although ospreys are not directly dependent upon intertidal flats, many of the fish which they consume have used the intertidal flat as a feeding ground.

The bald eagle is another bird of prey which lives almost exclusively on a diet of fish. There have been several confirmed sightings of bald eagles from coastal North Carolina, but this species is unquestionably rare. When it does appear in coastal North Carolina, sightings usually decrease during winter. The bald eagle fishes in shallow coastal waters, even over intertidal flats. It also scavenges dead fish.

Various hawks are known to take an occasional shorebird in their diets. One relatively abundant hawk during winter in coastal North Carolina, the marsh hawk, preys heavily upon rodents and sometimes on the smaller shorebirds. It is also possible that some small shorebirds fall prey to owls. The barn owl and the short-eared owl are often seen hunting near the marshes of North Carolina during the winter.

5.8 GENERAL COMMENTS

In the preceding analysis of the birds of intertidal habitats, one group whose members fly over intertidal flats has been omitted. Purple martins and other swallows are extremely common in coastal North Carolina during the summer. These birds are insectivorous and can be seen 'hawking' insects over intertidal flats. These species have been excluded from Table 4 because most of the insects captured over intertidal flats actually come from other environments, including especially the salt marsh (see Davis and Gray 1966 for an analysis of the insects of a North Carolina salt marsh). The link between intertidal flats and the swallows is weak and relatively insignificant.

For the birds of Table 4 as a group, the intertidal flat habitat is extremely important. For waders, and both the deep and shallow probers, this habitat is critical to their continued survival because they feed there almost exclusively. For the molluscivorous ducks, intertidal flats are almost as important. In contrast, if intertidal flats were eliminated by channelization or some other process, most species of fishes and invertebrates would survive by virtue of their utilization of subtidal environments.

CHAPTER 6. PRACTICAL PROBLEMS IN MANAGING INTERTIDAL FLATS

Now that a complete taxonomic and functional profile of an intertidal flat has been developed in earlier chapters, this chapter will address some practical problems of current concern in the management of intertidal flat habitats. Because the coastal zone is under such heavy and often competing pressures from various groups of users, decisions must often be made which will not please everyone. Needs for housing, recreation, navigation, and boat harbors are often not compatible with the maintenance of a pristine, natural estuarine ecosystem. To enable coastal zone planners to make informed decisions in managing estuarine systems, information on the ecology of various estuarine habitats must be available in a form that permits the merits of various competing, alternative uses to be weighed. The first five chapters include such needed information on the ecology of one estuarine habitat, the intertidal flat. To conclude this report two very specific problems in the management of intertidal flat habitats will be addressed: (1) what guidelines are needed to regulate the perturbation of this habitat; and (2) how valuable is this intertidal flat habitat compared with other habitats in an estuarine system. The final section of this chapter and of this report will summarize information presented in all previous chapters to provide a concise model of the role of intertidal flats in the functioning of estuarine systems.

6.1 RECOVERY OF INTERTIDAL FLATS FOLLOWING PERTURBATION

Because of the need to maintain sufficient depth in coastal navigation channels and the tendency of such channels to fill in with sediments, frequent dredging is necessary in estuaries. Disposal of the dredge spoil always presents a problem. Few studies have ever adequately tested whether the added turbidity resulting from dredging has any detrimental effects on estuarine systems. Because the dredging process obviously disturbs the seabottom in the vicinity of the dredging, as well as in areas where the spoil is

deposited, some of the data relating to the recovery of benthic communities following perturbation will be reviewed.

Presumably one need only study the benthic invertebrates in such unvegetated soft sediment systems to obtain an indication of the recovery potential of the intertidal flat community. These benthic invertebrates are the food for the shorebirds and bottom-feeding fishes and crabs. So it seems reasonable that a recovery in the benthic invertebrates would be accompanied by a recovery in the higher trophic levels also.

Some workers have studied the recovery of soft-sediment benthic communities from perturbations of various sorts. The recovery following a red tide in Florida (Dauer and Simon 1976, Simon and Dauer 1977) and after halting a pulp mill effluent in Sweden (Rosenberg 1976) have provided some data on the repopulation process in marine soft sediments in shallow waters. In an extensive series of field experiments in shallow waters of Long Island Sound, McCall (1977) examined the recolonization of defaunated mud which he placed in sediment trays on the bottom. Defaunation (i.e., killing all the macro-, meio-, and microfauna) was accomplished by drying natural sediments from the experimental area and then rinsing them with freshwater. In McCall's shallow-water site, these defaunated sediments were rapidly recolonized by opportunistic benthic species like the polychaetes *Streblospio benedicti* and *Capitella capitata* and the amphipod *Ampelisca abdita*. Opportunistic species are characterized by certain life history features held in common: rapid development, frequent reproduction, fast growth, high recruitment rates, and high mortality rates (McCall 1977).

Rhoads et al. (1978) reviewed these benthic recolonization studies and concluded that early colonists of disturbed sediments (the opportunistic species) share one important ecological characteristic: even though some are suspension feeders and others are surface-deposit feeders, all of the early colonists live at or on the sediment surface.

Immediately after disturbance, sediments rapidly become anoxic and inhospitable to infaunal organisms at even shallow depths below the surface. Only through time are the disturbed sediments utilized at depth by species which appear later during succession, after bioturbation by earlier colonists has irrigated the sub-surface sediments and has worked some usable organic material into deeper deposits (Rhoads et al. 1977). After perturbation, a true successional sequence occurs during the recolonization of muddy sediments in shallow waters. Early, short-lived opportunists colonize the surface zone and are replaced by long-lived species which can now live deeper in the sediments only after their preparation by the biological activity of the initial colonists (Rhoads et al. 1978).

Opportunistic species tend to have variable densities through time (Rhoads et al. 1978). Specifically, they show strong seasonality in most shallow-water sediments (McCall 1977). One possible explanation of the great seasonal fluctuation in abundance of opportunists in the soft-sediment benthos is their susceptibility to predation (McCall 1977, Rhoads et al. 1978). Many studies have shown that the shallow-burrowing benthic infauna are most subject to predation (Blegvad 1928, Virnstein 1977, Nelson 1978, Woodin 1978). Caging experiments in soft sediments have also demonstrated that opportunists respond most rapidly when released from predation (Young et al. 1976, Virnstein 1977, Lee 1978, Reise 1978). Such results suggest that opportunistic species may often be controlled by predation in the soft sediments of shallow marine waters and may be responsible for most of the energy flow from the benthic invertebrates to fishes, crabs, and shorebirds.

Although available data suggest that predators prey most heavily upon the opportunists among the benthic infaunal invertebrates, this conclusion must remain tentative. Cage artifacts obscure the results of virtually all of the caging experiments in soft substrates (Peterson 1979). Full cages, which are designed to exclude predators, also have the effect of slowing down water currents and thereby causing increased organic deposition. These organic-rich deposits represent food for many opportunistic deposit feeders. The great increase in opportunistic species inside full cages

may be a consequence of this organic enrichment rather than an indication that opportunists suffer the highest mortality from predators. Future research must be done to separate these two possibilities before it can be unequivocally stated that densities of benthic opportunists are controlled primarily by predation.

Given that opportunistic benthic infauna undergo large seasonal fluctuations in abundance in the sediments of shallow-water marine habitats and assuming that these species contribute substantially to the energy flow to higher trophic levels, Rhoads et al. (1978) suggested that careful seasonal timing of dredging activities in shallow waters can minimize the impact on natural estuarine systems. Dredging during winter months should have minimal impact on this entire system, in part because the new set of opportunistic species, upon which higher trophic levels are dependent, does not occur until springtime. Winter dredging will not interfere with that process unless the sediments are altered in some way which makes them unsuitable for colonization. This suggestion can only be tested by an *in situ* pilot experiment in the actual system in question. Such winter dredging would also cause minimal damage from increased turbidity because phytoplankton production is lowest during winter. Although this model of the impact of dredging on soft-sediment systems was developed to describe the shallow subtidal benthos of Long Island Sound, it possesses much broader applicability. Specifically, it can undoubtedly be extrapolated to the intertidal mud flats of North Carolina where seasonal pulses of recruitment by opportunistic infauna are evident (Commito 1976) and where predation on these species is substantial.

One reason that the intertidal benthic communities of tidal flats can be perturbed so greatly with relatively little damage to their ecological functioning is that they are extremely resilient systems (Boesch 1974). A resilient system is one which recovers quickly after perturbation. Although estuarine systems are characterized by relatively low species diversities and low persistence stabilities (i.e., possess quite variable population abundances and community composition), their resilience stability may be relatively great (Boesch 1974). The physical environment is so variable and predators and benthic disturbers are so common in the benthic communities of

estuarine habitats that the species which inhabit them must be well-adapted to recovery following disturbances. Such recovery capability implies that the system is capable of withstanding the impact of some carefully controlled, periodic dredging without substantial long-term ecological harm. This is probably a more accurate description of temperate-zone estuaries than it is of tropical systems where natural environmental variability is reduced (Copeland 1970).

6.2 THE SIGNIFICANCE OF AN INTERTIDAL FLAT

When one is asked to place a value on a habitat or upon an ecosystem, the answer requires some sort of value judgement which is necessarily subjective. Nevertheless, planners are often forced to make decisions which require the ranking of certain habitats or ecosystems on some basis of worth. Such comparative rankings are certainly easier to reach and more easily defended than absolute valuations.

The importance of intertidal flats to estuarine systems is addressed either implicitly or explicitly in almost every earlier section of this publication. For instance, the significance of the tidal flats to the shorebirds of a coastal wetland has been emphasized. It is clear that the majority of probing and wading shorebirds do virtually all of their feeding on intertidal flats. For those species and for the avian segment of estuarine ecosystems in general, the intertidal flat habitat is clearly of far greater significance than the salt marshes, the sea-grass beds, or any of the other estuarine habitats. However, it is not clear whether shorebird populations are limited by the extent of the intertidal flats available. Recent studies (Goss-Custard 1977) have addressed this question without reaching a definitive answer. Habitat availability is limiting to the populations of many other types of birds, so it would not be surprising to learn that shorebirds are similarly dependent upon the areal extent of intertidal flat habitat.

For the other large consumers in an estuarine ecosystem, the shrimp, crabs, and fishes, the relative importance of the intertidal flat habitat is not as clear. The relative importance of various estuarine habitats to species within these categories depends upon the relative contributions of the various types of primary producers to the food

chains upon which these consumers depend. In other words, more $\delta^{13}\text{C}$ data such as those generated by Haines and Montague (1979) and Thayer et al. (1978) are badly needed. These $\delta^{13}\text{C}$ ratios permit one to make inferences concerning the importance of marsh plants versus algae versus seagrasses in the nutrition of consumers, as is described in Chapter 2.

As an approximate evaluation of the relative importance of the various groups of primary producers in an estuarine ecosystem, one might simply total the annual production of each plant type in the system. This was done by Bigelow (1977) for the Newport River estuary in North Carolina, and the results appear in Table 1. This technique would imply that the salt marshes, for example, contribute 42% of the energy ultimately consumed by estuarine species. There are three serious drawbacks in utilizing primary productivity values in this fashion to represent the relative importance of various types of plants in estuarine food chains. First, it is not known how much of the annual primary production is actually utilized by consumers. Some of the plant material is carried out of the estuarine system by tidal currents and river flow. Some plant material is decomposed before it can be used by consumers, and some is buried too deeply in the sediments to be available to consumers.

The second problem with utilizing primary production data to estimate the relative importance of each plant type lies in the realization that consumers differ greatly from one another in diet. For a given species, one type of plant will be far more important and others far less important in its diet than is suggested by the relative contribution of that plant to the total primary production of the estuarine system. For example, the oyster feeds almost exclusively on algae, including various phytoplankters and probably also suspended benthic microalgae. One needs to know much more about the fate of each source of primary production before evaluation of the significance of various types of plants and various habitats can be appropriately made.

The third major reason for avoiding the use of simple productivity measures to estimate the relative importance of various types of primary producers is implicit in the earlier discussion of the role of bacteria in estuarine ecosystems. Because

salt marsh plants are composed largely of structural proteins (lignins, etc.), they are relatively poor in nitrogen and are not a nutritious food source (Tenore 1977). Many workers feel that only after the plant material has been colonized by bacteria is the plant's energy truly available to detritivores and higher level consumers in the food web. In other words, salt marsh detritus must ordinarily be transformed into bacteria before any consumer can derive benefit from consuming it. Such a conversion, by the second law of thermodynamics, is associated with a loss in energy available to the next trophic link. In contrast, algae are highly nutritious and are ordinarily consumed directly by various species in the estuarine system. Exactly how much one must depreciate the amount of marsh plant productivity to account for the energy loss involved in passing it through bacterial intermediates before it is consumed is not clear and needs further study.

Answers to these ecological questions are necessary before estuarine habitats can be accurately compared. In any event, it seems clear that intertidal sand and mud flats represent a very important habitat in an estuarine ecosystem. Since the lack of hard facts makes it virtually impossible to evaluate the worth of one acre of mud flat compared with one acre of salt marsh, it would seem prudent to protect and treasure both types of estuarine acreage. Disposal of dredge spoil should certainly not be accomplished by dumping it on unvegetated flats simply because they appear unproductive. They are indeed productive and their output is directly usable by consumers. Probably, the use of dry land habitat above the high tide line for disposal of spoil should be favored. There the spoil is rapidly colonized by land plants, which undergo a normal process of succession (Soots and Parnell 1975). Such spoil dumps on land are immediately useful as nesting habitat for many shorebirds, including several gulls and terns which prefer to nest on relatively unvegetated areas (Soots and Parnell 1975). Creation of spoil areas thereby helps to take the place of ocean beaches, many of which are now too disturbed to act as breeding sites for these ground-nesting birds.

6.3 THE ROLES OF INTERTIDAL FLATS IN ESTUARINE SYSTEMS

Because information on the function of intertidal flats is scattered throughout the earlier chap-

ters, a concise summary is presented here. The proportion of an estuary's total primary production that occurs in the sediments of intertidal flats is small relative to the contributions from salt marshes and from the water column. Water column production is enhanced by the presence of intertidal flats through increasing the euphotic zone and through rapid recycling of mineral nutrients. This enhancement is substantial in any estuary where intertidal flats cover a large proportion of the estuarine area. Despite the relatively low total primary production from intertidal flats, the algae produced there are directly utilizable by consumers.

The production of utilizable plant material is only one function of the intertidal flat habitat. A major role of the intertidal flat habitat is to serve as the substrate where primary production is consumed and thereby transformed into animal biomass. Studies of salt marshes and of seagrass beds emphasize a common characteristic: most of the primary production of both of those habitats is not utilized *in situ* but is instead carried away by water currents. This is not true of intertidal flat algae, which are directly consumed by deposit-feeding and suspension-feeding benthic invertebrates on the flat. More importantly, the intertidal flat habitat serves as the site where much of the exported production from salt marshes and seagrass beds is deposited and subsequently consumed by and transformed into benthic invertebrates. Intertidal sand and mud flats thus function not only as important producers of plant matter, but even more significantly as a major site of conversion of plant matter from all estuarine habitats into animal tissue.

The benthic invertebrates living on intertidal flats and utilizing both the locally produced and the imported plant material are themselves a major food source for higher level consumers. These higher level consumers include blue crabs, shorebirds, some shrimp, and larger bottom-feeding fishes. Predation from these sources is usually sufficient to keep the population densities of benthic invertebrates at low levels on intertidal flats. Such low densities belie the importance of the benthos in the transfer of energy to higher level consumers. Most shorebirds are totally dependent upon the intertidal flat as a feeding ground.

Intertidal flats serve not only as a primary site

for conversion of plant matter to benthic invertebrates but also as a major location for feeding by the baitfishes, which are planktivorous, herbivorous, or detritivorous. These baitfishes then contribute to another set of very important estuarine food chains. They are major prey for wading birds, aerial-searching birds, piscivorous ducks, and many predatory fishes. Many marine fishes are also dependent upon intertidal flats in critical postlarval stages because they need the shallows for protection from their predators.

Intertidal flats are important in their own right as producers of utilizable plant matter. But perhaps even more significant is their function as the primary estuarine habitat where plant production from other habitats of the estuary is con-

verted into animal biomass. Some of this animal biomass is commercially important and directly harvested (oysters, hard clams), but most of it fuels food chains that lead to important piscivorous vertebrates (wading birds, some diving ducks, several important sport and commercial fishes), or to bottom-feeding vertebrate and invertebrate predators (blue crabs, shorebirds, and several important benthic-feeding fishes). In other words, intertidal flats are most important for what consistently happens on them rather than what is permanently found on them. They are tremendously important to the functioning of the entire estuarine system. Without them, many of the valuable aspects of the estuarine system would be threatened, and the value of the estuary would be diminished.

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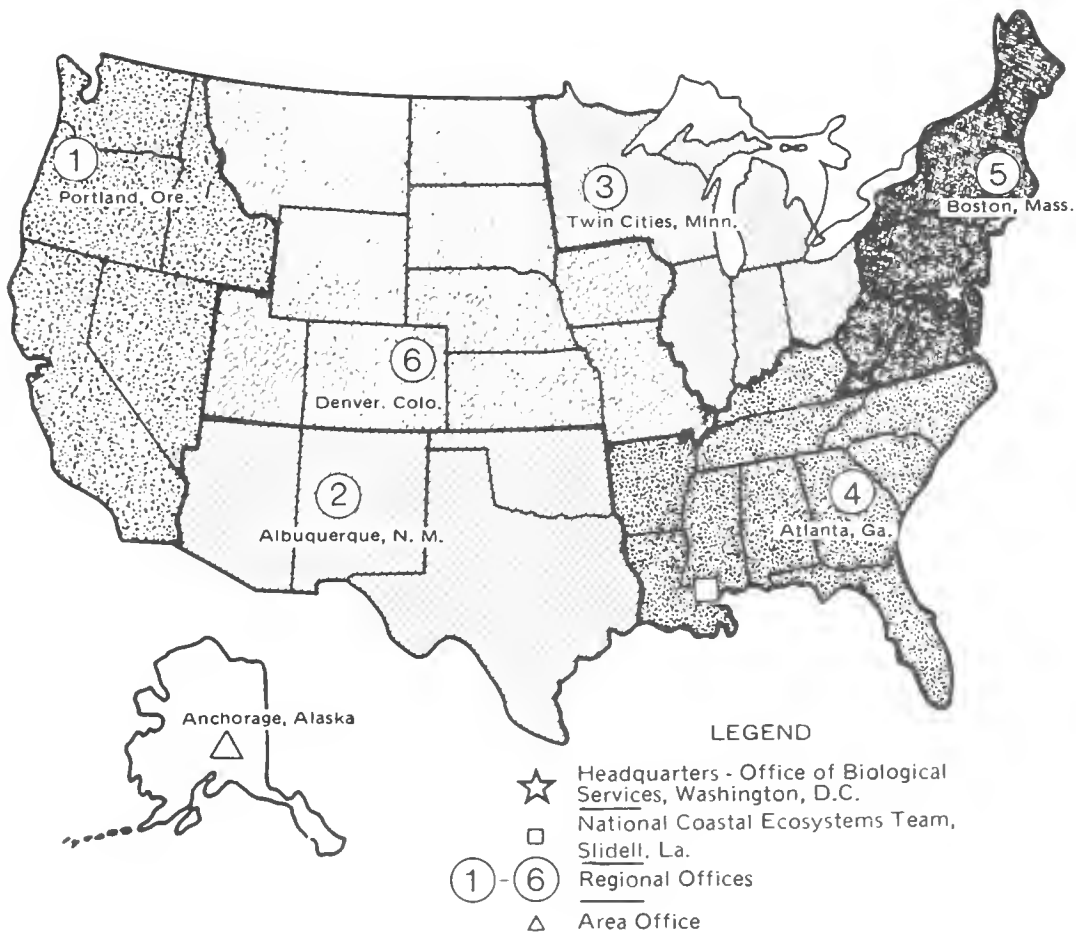
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