Chapter 1

The Setting

An understanding of Atlantic shoreline communities must begin with an appreciation of the historical and hydrodynamic forces that have shaped and will continue to shape them. Intertidal habitats are dynamic over a wide range of temporal and spatial scales. At large scales, shoreline features of entire continents have been shaped by geological events that occurred over hundreds of millions of years. Continental drift and the positions of continental margins relative to the shifting plates that move over the earth's semi-liquid interior have played a large role in establishing the types of intertidal habitats that dominate particular continental margins. Equally important in dictating the nature of current shoreline habitats at high latitudes, however, have been the glacial ice sheets that have scoured shorelines, deposited rocks and sediments, and changed sea levels by binding large amounts of the earth's water. The effects of global climatic cycles occur on temporal scales of thousands to tens of thousands of years. Superimposed on the effects of continental drift, climatic effects set the stage for modern shoreline habitats.

At smaller scales, shorelines are equally dynamic. Driven by gravitational interactions between the earth's water mass and the moon and sun, daily tides subject shorelines to predictable cycles of submersion in seawater and exposure to atmospheric conditions. Wind and tidal forces acting on water masses also generate waves and currents that sculpt intertidal habitats by eroding and depositing sediments on shorelines, while also influencing the delivery of food to organisms and the dispersal of their larvae.

This chapter examines the physical forces that have shaped and continue to shape the shoreline habitats of the Atlantic coast of North America. I begin by considering geological history as it relates to today's shoreline habitats and the kinds of organisms that occupy them. I then examine the importance of introduced species on western Atlantic shorelines and the influence of water movement on intertidal habitats and organisms.

CONTINENTAL DRIFT AND THE AGE OF THE EAST COAST

The east and west coasts of North America are strikingly different. The west coast is characterized by young, rugged coastal mountain ranges, wave-exposed rocky outcrops, and wave-swept, high-energy sand beaches. In contrast, the east coast is characterized by ancient, highly eroded mountain ranges and extensive marshes and sedimentary shorelines at lower latitudes. Understanding these differences requires a historical perspective and an understanding of continental drift, the dynamic movement of continents over the earth's surface.

The discovery of the fluid movement of continents over the earth's surface was one of the greatest scientific advances of the twentieth century. Prior to this time, the continents were thought to be fixed in position, even though early explorers and cartographers noted that the continents fit together like pieces of a puzzle. Alfred Wegener proposed the first serious theory of continental drift in 1912. He theorized that all the modern continents were initially part of one large supercontinent, Pangea. In Wegener's initial scheme, North America and Eurasia were at first joined to form Laurasia, or the northern portion of Pangea, while present-day South America, Africa, India, Antarctica, and Australia were joined to form the southern portion, Gondwanaland. Laurasia and Gondwanaland were separated by the Tethys (mother) Sea (Fig. 1.1). Wegener hypothesized that the modern distribution of continents resulted from the separation and migration of these huge landmasses over the earth's surface. Wegener amassed volumes of biological and geological evidence for his theory, but was unaware of a plausible mechanism for movement of the continents. Incorrectly, he proposed that gravitational pull from the moon was responsible for continental movement.

After nearly 50 years of ridicule, Wegener's ideas were confirmed and given a believable mechanism. In the 1950s and 1960s, geologists discovered that the crust of the earth is divided into a number of plates, both with and without continents (Fig. 1.2). These plates move over the fluid inner mantle (aesthenosphere) of the earth as molten material flows from the earth's core. As this fluid mantle material comes to the surface at the seams between plates, their spreading edges grow, and their leading edges are pushed together. This movement causes violent seismic activity, the buckling of continental margins, and the birth and growth of mountain ranges.

Continental drift largely explains the large-scale geomorphology of the east and west coasts of North America, as well the rest of the world. The North American continental plate has its margins in the middle of the Atlantic Ocean and along the west coast of North America (Fig. 1.3). Seafloor spreading at the mid-Atlantic ridge pushes the North American plate

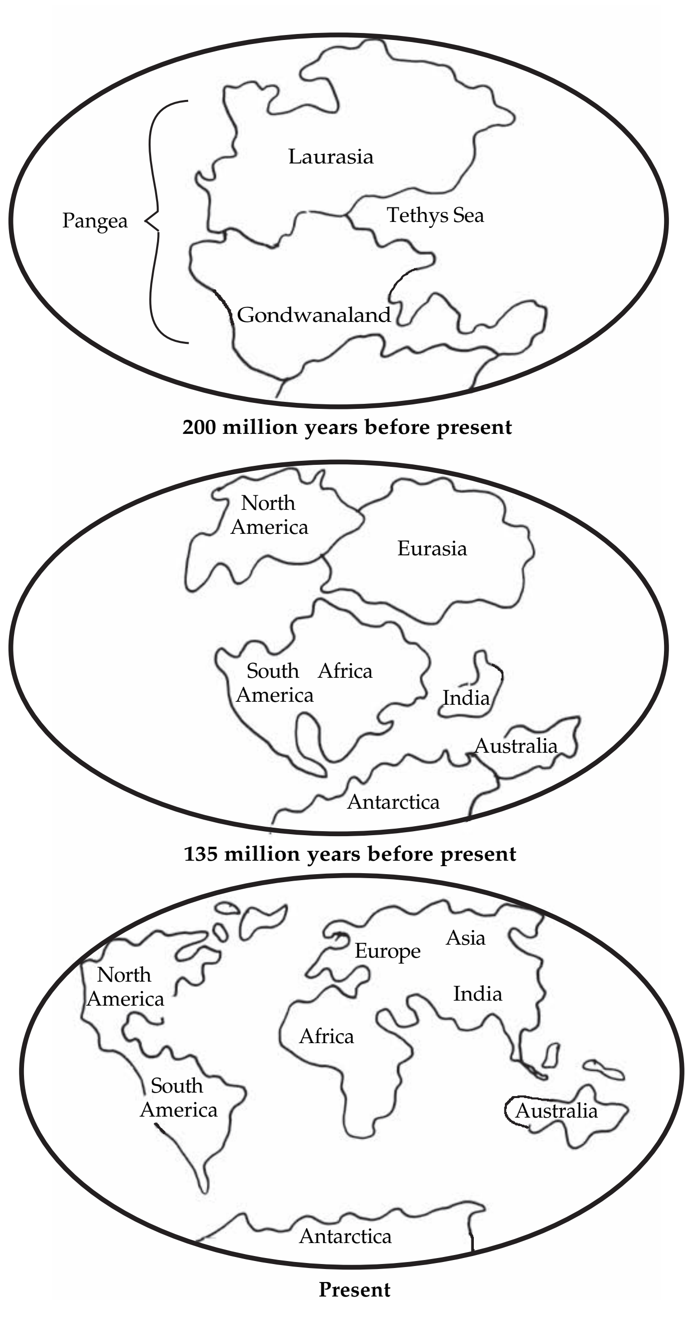

Fig. 1.1 Formation of the present continent configuration from the supercontinent Pangea over the past 200 million years.

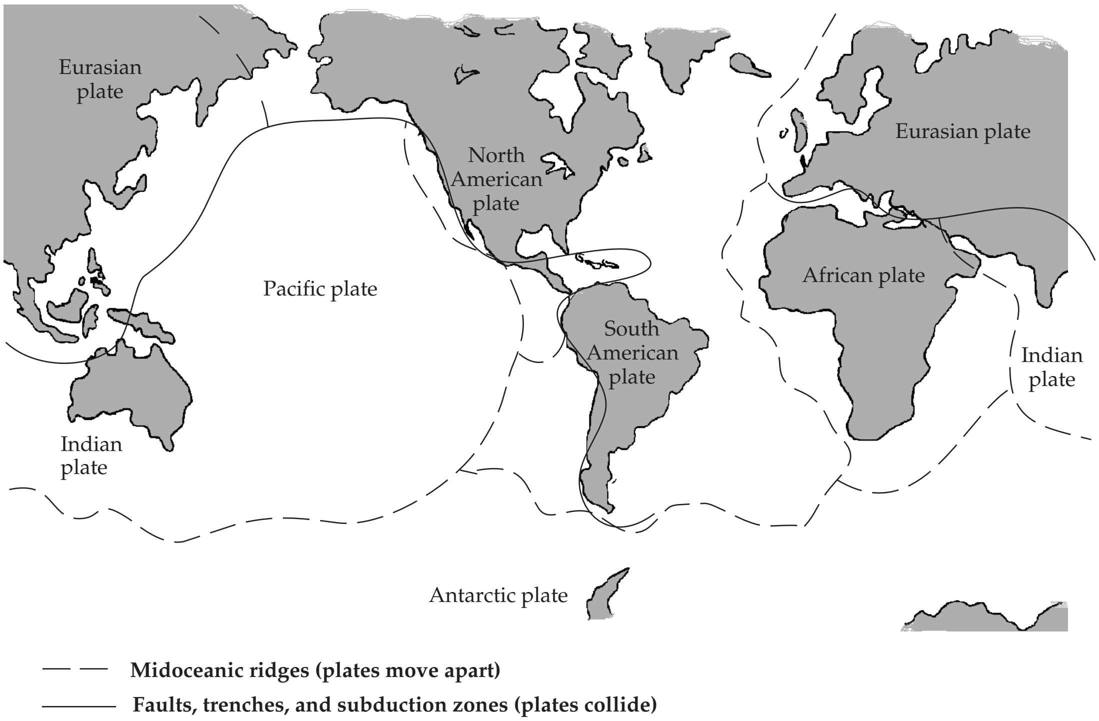

Fig. 1.2 Arrangement of the continental plates, ridges where plates are moving apart, and faults, trenches, and subduction zones where plates are colliding.

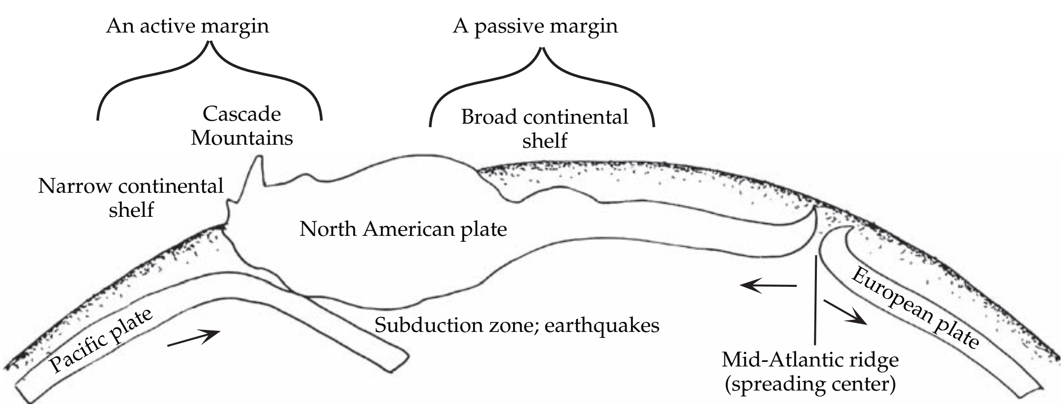

Fig. 1.3 Movement of the North American plate by seafloor spreading at the Mid-Atlantic ridge. Collision with the Pacific plate has given rise to the Cascade and Rocky Mountains. The Atlantic coast of the plate, however, has been stable for over 100 million years.

westward, where its western edge collides with the Pacific plate. The collision of these plates results in high seismic activity, subduction of the Pacific plate, and the uplifting of the North American plate to form coastal mountain ranges. Conversely, the position of the east coast, set far back from the spreading edge of the North American plate, explains many of its unique features. Like the east coasts of South America and Africa, the east coast of North America is geologically ancient, having been stable for more than 100 million years. Over this time, the coastline has eroded, wearing down mountain ranges such as the Appalachian and Smoky Mountains. This erosion has left wide continental margins of accumulated sediment, often bound by extensive marshes south of New England. North of New England, however, ice sheets have scoured the coast of accumulated sediment.

SEA LEVEL CHANGE

In addition to the history of continental movement, changes in global sea level and the scars left by glaciers are important determinants of the geomorphology of modern shorelines. Sea level has fluctuated markedly in the past, largely as a consequence of variation in climate (Fig. 1.4). Global climate is sensitive to the distance and angle between the sun and the earth, variation in solar radiation, and variation in the earth's atmosphere. Cooler temperatures lower sea level by shrinking the volume of water on the globe as large proportions of the earth's oceans become bound in polar ice sheets (Fig. 1.5).

During the last major Ice Age, which started 120,000 years ago and lasted 100,000 years, over 30 percent of the North American land mass was covered by ice sheets over 2 kilometers thick. These ice sheets lowered the global sea level 120 meters, exposed the coastal margins of North America, and scoured northern latitudes down to bare rock. They also deposited massive amounts of sediment and glacial debris at their bases and compacted landmasses by their sheer weight.

Over the last 20,000 years, temperatures have increased, the ice sheets have retreated, and the sea level has risen. The effect of this recent sea level change on modern landscapes and shorelines is dramatic. The Pleistocene ice sheet scraped bare the northern portion of the east coast of North America, leaving New England with a rugged rocky shoreline stripped of sediments and coarse rock debris. Narragansett Bay and Long Island Sound, just south of the glaciers' farthest reaches, are remnants of large river basins filled with coarse glacial debris and sediments deposited over nearly 100,000 years. Similarly, the Great Lakes formed at the foot of the ice sheet as the ice melted into large drainage basins. Long Island and Cape Cod are glacial moraines, essentially piles of debris that were pushed and deposited by the Pleistocene glaciers.

The entire east coast of North America has been strongly affected by the 120-meter sea level rise over the last 20,000 years. Coastal islands such as Long Island and Martha's Vineyard, once part of the mainland, were cut off

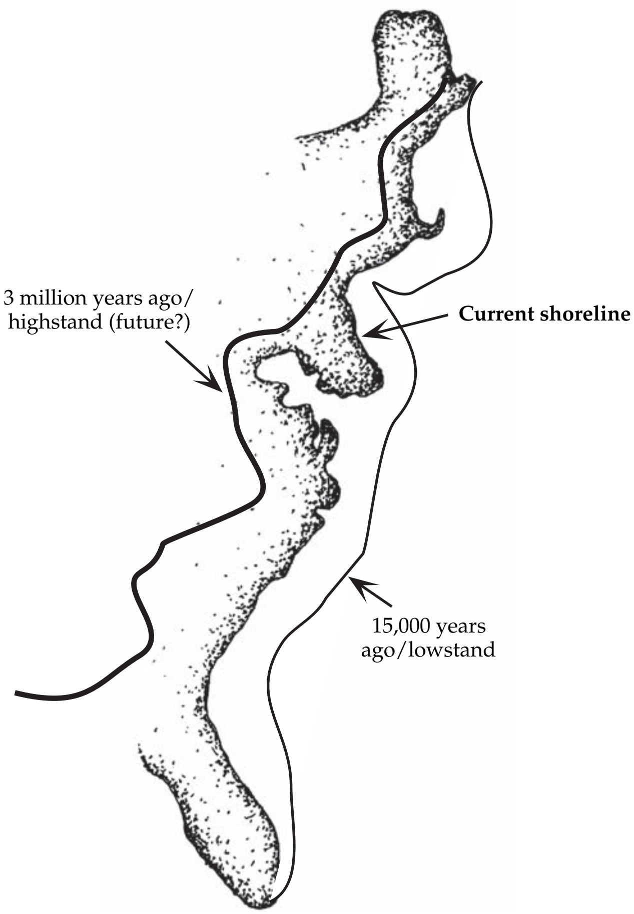

Fig. 1.4 Current Atlantic coastline of the United States, compared with the coastline during the last great glaciation, 15,000–20,000 years ago, and the coastline 3 million years ago, when ice cover was minimal and ocean volume was much higher than today.

from the coast during this period. Riverbeds created by the melting of glaciers were flooded, creating shallow soft-sediment bays like Narragansett Bay and Long Island Sound. Southward from where the Pleistocene glaciers had direct consequences, accumulated sediments on the continental margin were flooded, leaving a broad, shallow continental shelf and offshore barrier islands.

Sea level rise is now increasing at an unprecedented pace fueled by global warming. Global warming resulting from human use of fossil fuels is leading to the melting of the polar ice caps and the thermal expansion of the world's oceans. This will result in substantial increases in global sea level over the next few centuries. The current forecasts of expected sea level rise predict that sea level will increase by 50–100 cm over the next century (Church et al. 2001). This will have massive consequences on shorelines around the world, particularly where shoreline development prevents or limits shorelines from naturally migrating landward. It is also unknown whether shoreline habitats that are built by their inhabitants, like salt marshes, mangroves, and coral reefs,

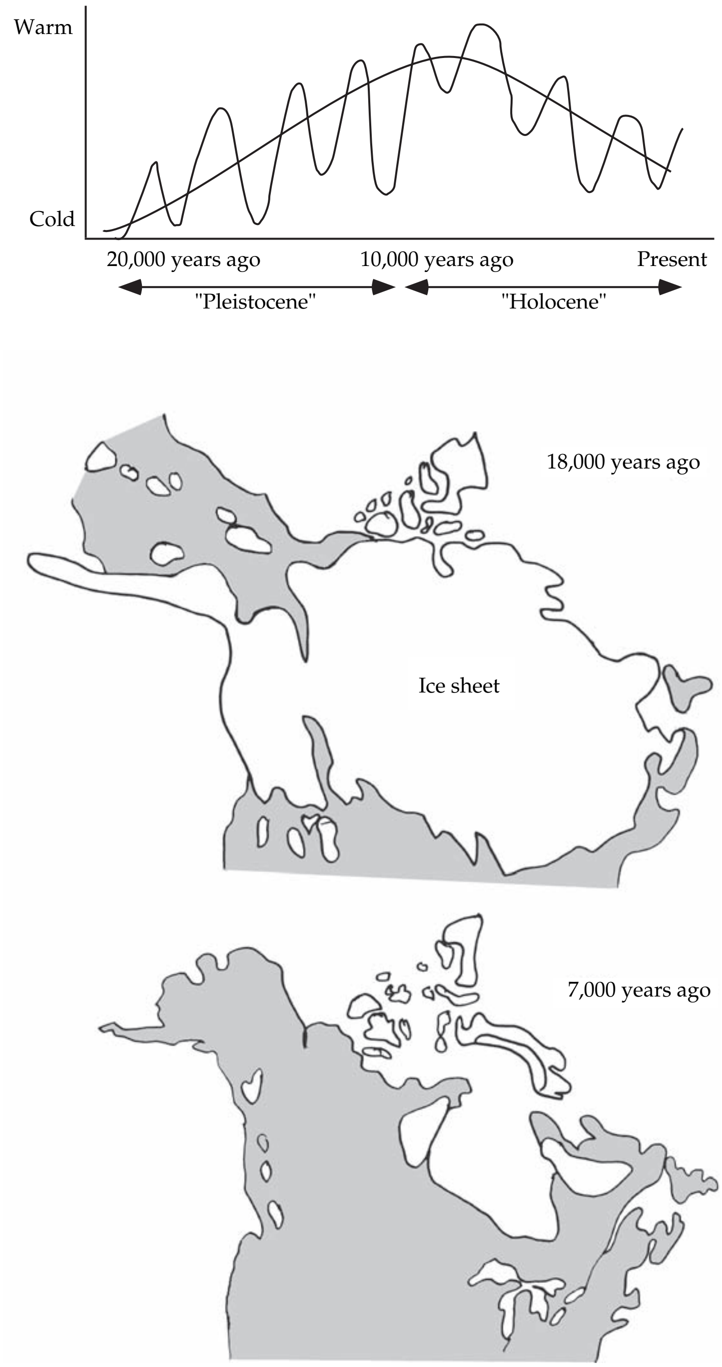

Fig. 1.5 Variation in global temperature over the past 20,000 years and its consequences for North American ice cover.

will be able to keep pace with elevated sea level rise or whether they will be destroyed.

WINTER ICE

Whereas severe Ice Age conditions were largely responsible for eroding and sculpting the rocky shores of the east coast of North America, ice continues to be a powerful influence on northern Atlantic shorelines (Stephenson and Stephenson 1971). The damaging effects of ice on shoreline organisms include freezing, crushing, abrasion, and ripping organisms from the substrate. While ice damage is most common in polar and subpolar regions (Neushul 1960; Zaneveld 1966), ice may also have important effects on north temperate shorelines and the organisms that live there (Mathieson et al. 1982). Canadian shorelines are particularly affected by ice.

Along the coast, ice can be either frozen to the shore or free-floating in the sea. The fringe of ice attached to the shore, often referred to as the **ice foot**, can be over a meter thick and can completely cover the intertidal habitat (Dinsmore 1972). While fringe ice can sometimes protect shoreline organisms from ice scour, when it thaws, it can rip plants and sessile invertebrates from the substrate (Mathieson et al. 1982) and abrade shorelines as it is moved up and down by tides. This scouring can leave a characteristic barren belt of rock in shoreline habitats, such as the ones north of Nova Scotia (Stephenson and Stephenson 1971).

Free-floating ice in the sea originates when ice from glaciers falls into the sea (**icebergs**), the sea freezes (called **sea ice**), or rivers or estuaries freeze (called **freshwater ice**) (Dinsmore 1972). The main effect of free-floating ice on shoreline organisms occurs when ice contacts the shore and scours the substrate, removing plants and animals from intertidal habitats (Bergeron and Bourget 1986; Minchinton et al. 1997).

The extent of the damage to shoreline habitats and organisms from ice is variable and depends on latitude, exposure, and a variety of other local factors (see Stephenson and Stephenson 1971; Minchinton et al. 1997). In the northwestern Atlantic from the Arctic to 45°N latitude (Halifax, Nova Scotia), conditions are conducive to the annual formation of ice (Dinsmore 1972) (Fig. 1.6). In the Arctic, scouring by sea ice is often severe enough to limit the colonization of shoreline organisms to only a few months of the year (Wilce 1959). At the southern limit of the formation of sea ice, near Nova Scotia, Canada, sea ice is relatively thin and restricted to sheltered inlets and bays. Rare ice scouring events can occur at these latitudes when arctic sea ice drifts southward (see Stephenson and Stephenson 1971; Minchinton et al. 1997). Farther south, ice effects are limited to inland bays and estuaries, but can be substantial there. In New Hampshire, for example, fringe ice can be responsible for killing up to 50 percent of the shoreline seaweed in protected bays (Mathieson et al. 1982), and ice often damages inland salt marshes as far south as Rhode Island (Bertness 1984b).

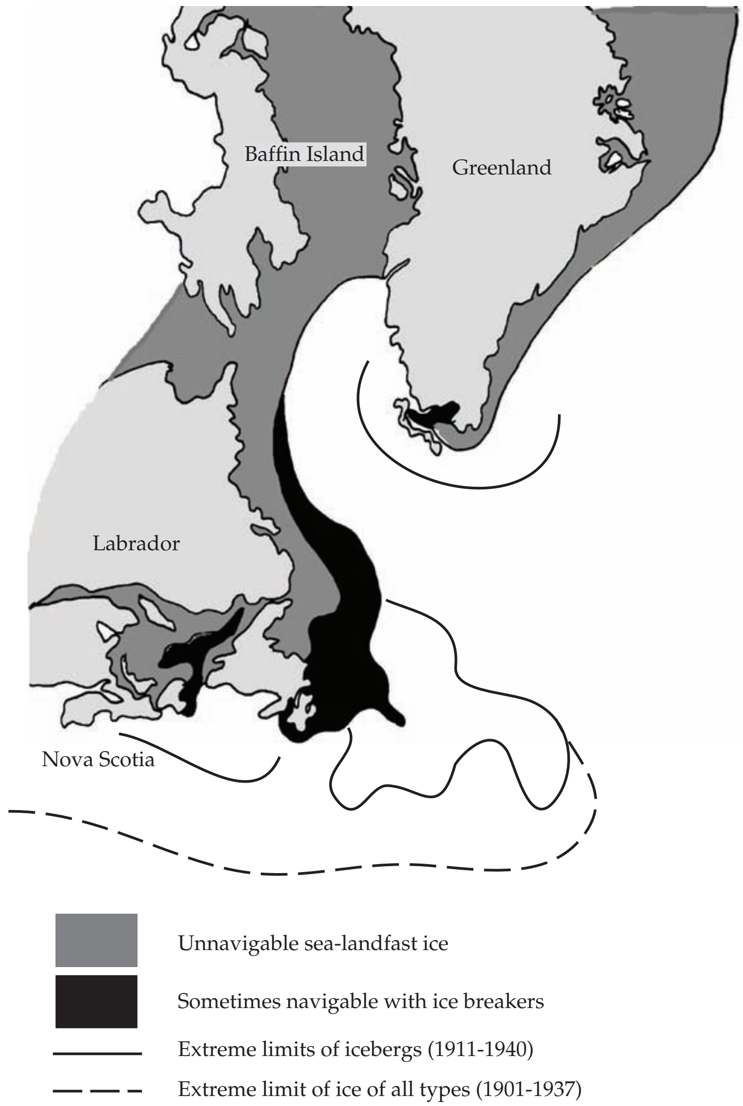

Fig. 1.6 Common extent of winter ice on the Canadian coast of North America. (After Stephenson and Stephenson 1971.)

BARRIER ISLANDS

South of Canada and New England, barrier islands are one of the most characteristic features of the east coast of North America. Barrier islands are a product of the age and stability of the east coast and its sea level history. They are common from the coast of Long Island to the Atlantic coast of Florida. They are not common north of Long Island because Pleistocene glaciers scoured sediments from these shores, leaving only bare rock or glacial debris. South of Long Island, however, the position of the shore far from a tectonic plate border, combined with over a hundred million years of sediment erosion from the continental margin, has left a massive accumulation of sediments. Barrier islands form when ocean waves, tides, and wind act together to pile up sediments on shorelines, creating large dunes stabilized by vegetation. When the sea level rises, these dunes are partly submerged and cut off from the shore. Some remain as long, uninterrupted barrier islands, whereas others break into smaller pieces, fragmented by storms and rip currents that erode channels through the obstructive barriers.

Because sea level has fluctuated markedly over the past 3 million years, and the east coast of North America has a large sediment load, dynamic barrier island formation, migration, and loss is a characteristic feature of the history of the east coast. Ancient barrier islands that formed when the sea level was at its highest 3 million years ago are now located 60 kilometers inland. The current barrier islands off the Atlantic coast are largely the result of melting global ice sheets and increasing sea level over the past 18,000 years. Typically, contemporary barrier islands on the east coast result from a single thin barrier complex on the coast of Holocene (Recent) origin. Off the coast of Georgia, however, amplified tides have led to the development of larger, wider barriers, built by both Holocene and earlier Pleistocene events (Fig. 1.7).

Barrier islands are dynamic structures that affect local water movement patterns and are constantly being eroded and reshaped by water movement and sediment deposition. The lagoons that form between barrier islands and the mainland fill with sediments and become shallow-water habitats that are invaded by salt-tolerant plants, promoting the formation of salt marshes. In contrast, the seaward edges of barrier islands are wave-swept, high-energy habitats characterized by constantly shifting sand dunes and spits. The shapes of barrier islands are continually changing. On the east coast of North America, coastlines are exposed to currents moving north to south, parallel to the coast, as a result of global ocean circulation patterns. The effect of these currents on barrier islands is usually to erode the northern ends while building up sediment on the southern ends. The southern ends of barrier islands often have a characteristic drumstick shape caused by these predictable accretion patterns. As longshore currents reach barrier islands, they bend inward toward the land masses (see below for explanation) and curl around the islands. This leads to sediment piling up on and around the southern end of the barrier island. The southern end of the island expands, and soft sediment conducive to marsh development accumulates on its landward edge. Longshore development of barrier islands can also lead to complicated patterns of islands running into one another, merging, and forming high sediment deposition areas between them, which grow together to form marsh habitats (Fig. 1.8).

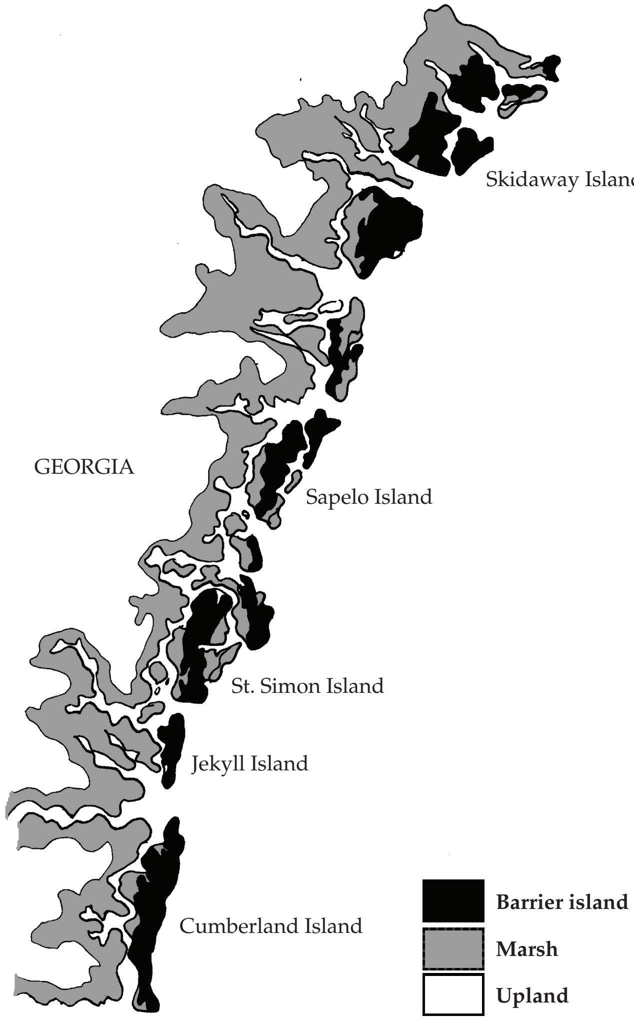

Fig. 1.7 Barrier islands off the coast of Georgia developed when shoreline dunes from previous Ice Age low water stands were flooded, creating offshore islands. Sediment accumulation on the landward side of the barrier islands has led to extensive marsh development.

SPECIES ORIGINS AND INVASIONS

The geological history of North America has also left its signature on the species composition of shoreline communities on the east coast. Over the past 3 million years, changes in sea level and climate have molded the communities of these shores. Changes in sea level have dictated the movement of species within the region as well as between the east coast and other biogeographical provinces. Past climatic extremes, especially Ice Age events, drove many species to extinction and limited the distributions of others.

Ice Age events over the past 3 million years decimated the fauna and flora of the western Atlantic and appear to have caused more species extinctions

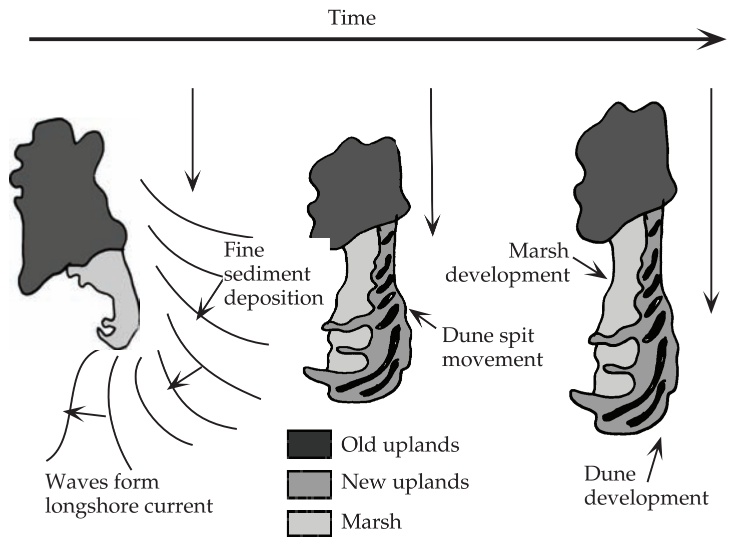

Fig. 1.8 Barrier islands are typically exposed to longshore currents that lead to characteristic sediment deposition patterns and island growth and morphology.

and displacements there than on many other coastlines (e.g., the eastern Pacific or Atlantic; see Vermeij 1991). The Pleistocene ice sheets displaced organisms dependent on rocky shores, as they left no suitable hard-substrate habitats to the south. Pleistocene Ice Age conditions also strongly affected shorelines far south of New England. Steven Stanley (1986) has shown that massive species extinctions due to cold Ice Age conditions occurred as far south as Florida and the Bahamas.

Following these Ice Age extinctions, the east coast of North America was invaded by species from other biogeographic regions. Geerat Vermeij (1989, 1991) has shown that much of this reinvasion came from the trans-Arctic migration of taxa with Pacific origins. He has suggested that Pacific taxa successfully colonized the Atlantic because of the ecological opportunities created by the Ice Age decimation of North Atlantic fauna and flora. Relatively few Atlantic taxa successfully invaded the Pacific when geological opportunities occurred, possibly because the Pacific coast biota experienced fewer Ice Age extinctions, and thus offered fewer ecological opportunities for invaders. Following Ice Age extinctions and subsequent climatic warming, migrants from eastern and southern waters also colonized the northwestern Atlantic Ocean (Franz and Merrill 1980a,b).

Changes in sea level have also dramatically influenced the shape of shorelines and opportunities for dispersal. For example, when little water was frozen in ice caps during the Pliocene highstand, 3 million years ago, the peninsula of modern Florida was flooded, Cuba was a set of islands rather than a single island, and the Isthmus of Panama was submerged. This situation allowed the exchange of organisms between the Atlantic and Pacific Oceans and movement of organisms between the Gulf of Mexico and the east coast of North America. Conversely, during the extensive Pleistocene

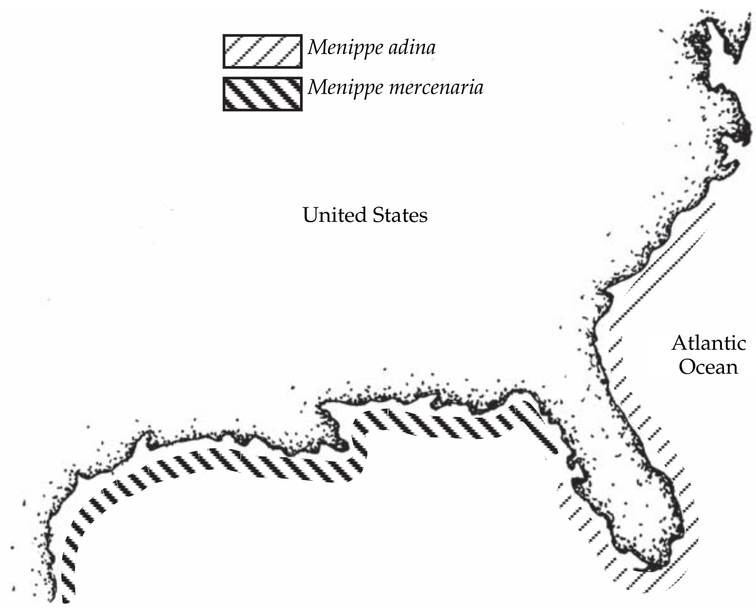

Fig. 1.9 Atlantic and Gulf coast stone crabs differentiated from a common ancestor after the emergence of the Florida land mass 3 million years ago. (After Bert 1986.)

glaciations 20,000 years ago, biotic exchange between the Atlantic and Pacific was precluded, and the continental barrier between the east and west coasts of Florida was more formidable than it is currently. The establishment of these dispersal barriers led to isolated populations and speciation events. The Atlantic stone crab *Menippe mercenaria*, for example, is one of many species shown to consist of two subspecies that diverged 3 million years ago when the sea level dropped and established the Florida peninsula (Bert 1986) (Fig. 1.9).

INTRODUCED SPECIES

An important and until relatively recently often overlooked component of shoreline communities in the western Atlantic is the recently introduced species that have come to North America due to human activities. Since Charles Elton's seminal book on the biology of invasions in 1958, ecologists have been aware of the effects that intentional and inadvertent introductions of species have had on terrestrial communities. It is only in the last few decades, however, that ecologists have come to realize the pervasiveness of introduced species in marine habitats. Ironically, the failure of marine ecologists to recognize the importance of introduced species was partially because the exotic nature of many common taxa had not been suspected.

Global introduction of exotic species has a long history. The past 500 years have been particularly important as Europeans have colonized the New World and engaged in long-distance commerce. The resulting spread of non-native species has led to the breakdown of traditional faunal boundaries and the homogenization of the world's fauna and flora in what Elton has called the largest biological crisis in history. Whereas the effects of introduced species have received the most attention in terrestrial habitats, particularly on islands such as Hawaii and Australia (which until European contact had relatively unique fauna and flora), shallow-water coastal habitats are also greatly affected by human-assisted invaders. James Carlton (1987, 1992) has conservatively estimated that over 1000 conspicuous marine invader species have been documented worldwide, and suggests that this number would be much larger if it included less conspicuous and poorly described organisms.

The widespread, human-assisted invasion of shallow coastal waters began in the fifteenth century and continues to this day. The large wooden ships used by early explorers in the fifteenth through the nineteenth centuries were ideally equipped to move shallow-water species around the globe. The hulls of these ships have been described as "floating biological islands." Ships sat in ports, where they were colonized by local fauna and flora. They then set sail, and at the end of a journey that could take as long as 3 months, the surviving organisms would colonize new shores. Seaweeds, barnacles, tunicates, bryozoans, and other **fouling organisms** often covered the bottoms of these ships in dense assemblages up to a meter thick (Carlton 1992). Moreover, wood-boring clams (teredos) and isopods (woodlice) typically riddled wooden ships, often forcing them out of service. These borers left ship hulls honeycombed with passages that collected sediment and sediment-inhabiting organisms, and also provided living space for crabs and other mobile organisms (Fig. 1.10). In addition to these formidable fouling communities on their hulls, pre-twentieth-century vessels also carried **ballast** to weigh down their hulls for rough oceanic voyages. This ballast was typically beach rocks, sand, or scrap iron. Ships would take on ballast for the trip at one port and then dump it at the journey's end to reduce their weight for maneuvering in shallow coastal waters. Cobbles and sand used as ballast may have transported entire assemblages from one port to another.

Since the early twentieth century, fast-moving, metal-hulled ships coated with toxic antifouling paint have replaced wooden ships and are not used by boring organisms. They also move fast enough to limit the development of large fouling communities, so that the pre-twentieth-century movement of "islands of shoreline" from coast to coast has ceased. However, contemporary ships use water as ballast, which is taken into their hulls at one port and jettisoned at the next. James Carlton (1985) and his colleagues have shown that ballast water often teems with planktonic larvae, and that these larvae can survive movement across the Atlantic and Pacific Oceans. They have suggested that ballast water movement may result in a constant inoculation of the shallow-water harbors of the world with non-native propagules. The larvae of segmented worms, crustaceans, flatworms, and molluscs are all commonly found in ballast water, suggesting that ballast water may be a relatively nonselective transport vector for moving entire coastal plankton assemblages across oceanic basins into similar habitats.

This five-century process of transporting shallow-water fauna and flora

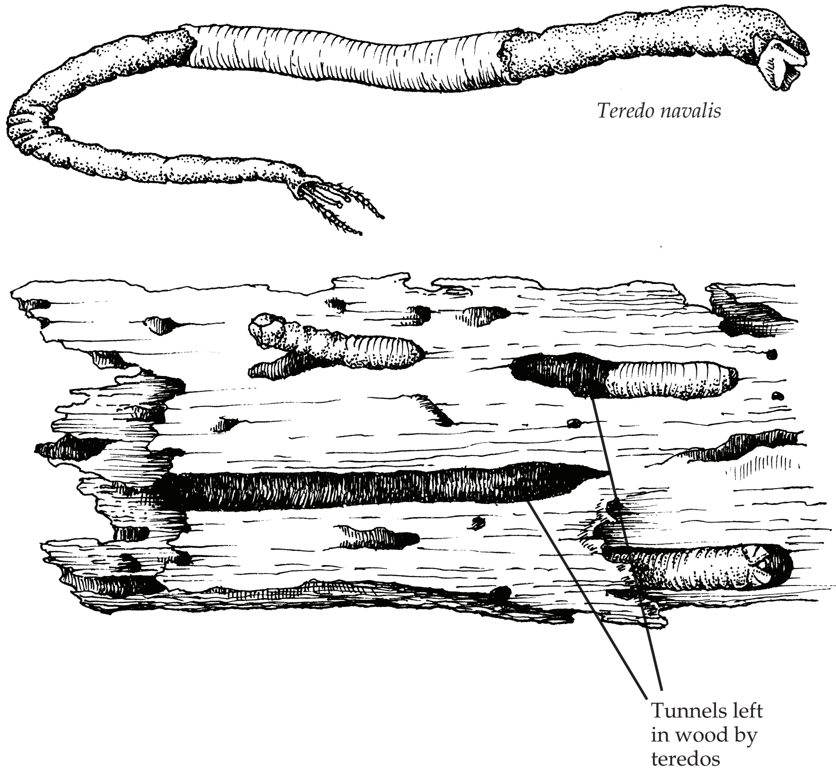

Fig. 1.10 *Teredos* (shipworms) were a serious problem for shipping in the sixteenth through nineteenth centuries. These wood-boring clams can riddle wooden ships with shell-lined tunnels and turn them into habitats for many fouling organisms.

around the globe has led to considerable homogenization of the world's shallow-water assemblages. The success of invaders has been particularly high in geologically young areas such as New England, where the fauna and flora have not fully recovered from recent climatic extinction events, presenting ecological opportunities for potential invaders (Vermeij 1991) (Fig. 1.11). The most striking aspect of the species that have successfully invaded shallow-water habitats on the east coast of North America is not their number, but how dominant some of them have become. For example, one of the dominant predators on western Atlantic shorelines, the green crab (*Carcinus maenus*), is an introduced species. It was probably transported from Europe to southern New England in the late eighteenth century with rock ballast, and in 200 years has become one of the most dominant omnivorous consumers on hard- and soft-substrate shorelines from southern Canada to the Chesapeake (Glude 1955) (Fig. 1.12).

There are also examples of invasions by seaweeds and sessile invertebrates. The Japanese seaweed *Codium fragile* spp. *tomentosoides*, or dead man's fingers, was initially introduced to Europe in the early twentieth century,

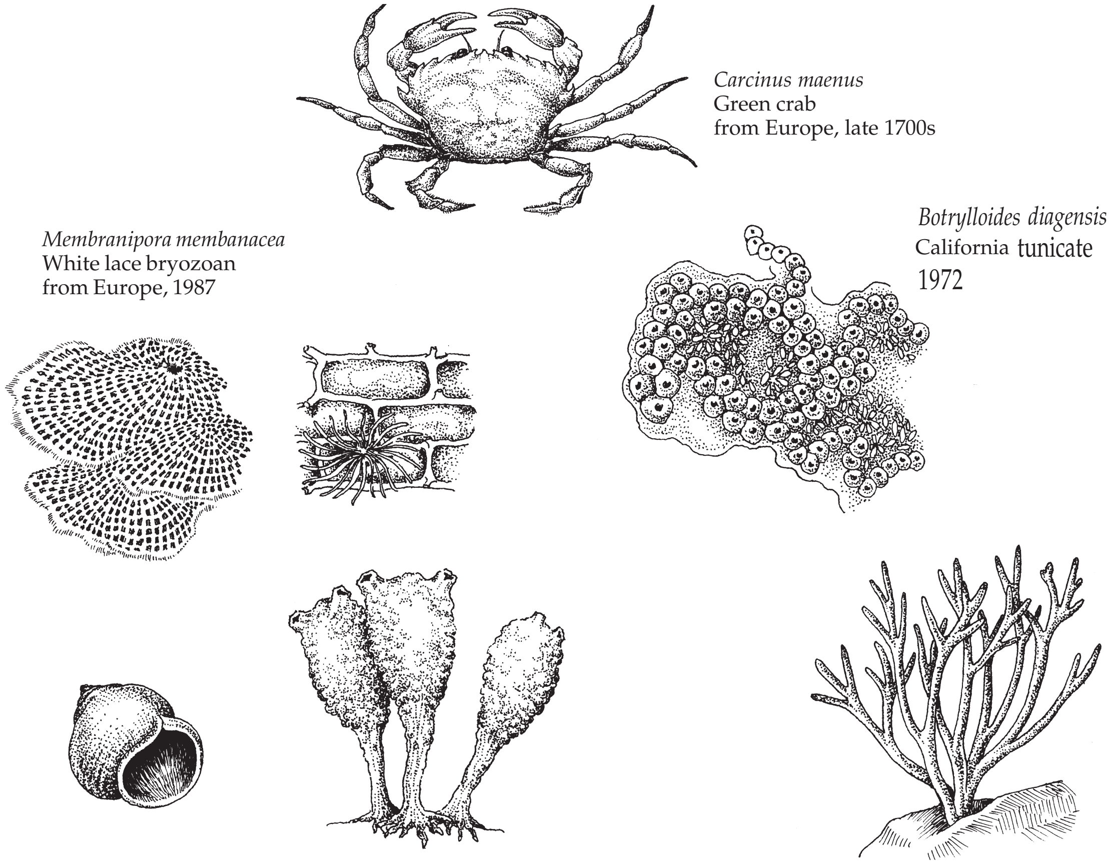

Fig. 1.11 Some successful invaders that have become dominant species on the east coast of North America.

either as a fouling organism or on oyster spat. In the mid-1950s it was introduced to New York Harbor, probably as a hitchhiker on fouled boats (Carlton and Scanlon 1985). In the past 40 years, *Codium* has rapidly moved north to Maine and Canada, and has moved more slowly against prevailing coastal currents south to the Carolinas (Fig. 1.13). The introduced tunicates *Botrylloides diagensis* and *Styela clava* are also conspicuous invaders in New England, where they can dominate shallow subtidal habitats and displace native organisms (Mathieson et al. 1991). In the past few decades, the white lacy bryozoan *Membranipora* has become a conspicuous invader in New England waters, with immediate repercussions. *Membranipora* settles on large

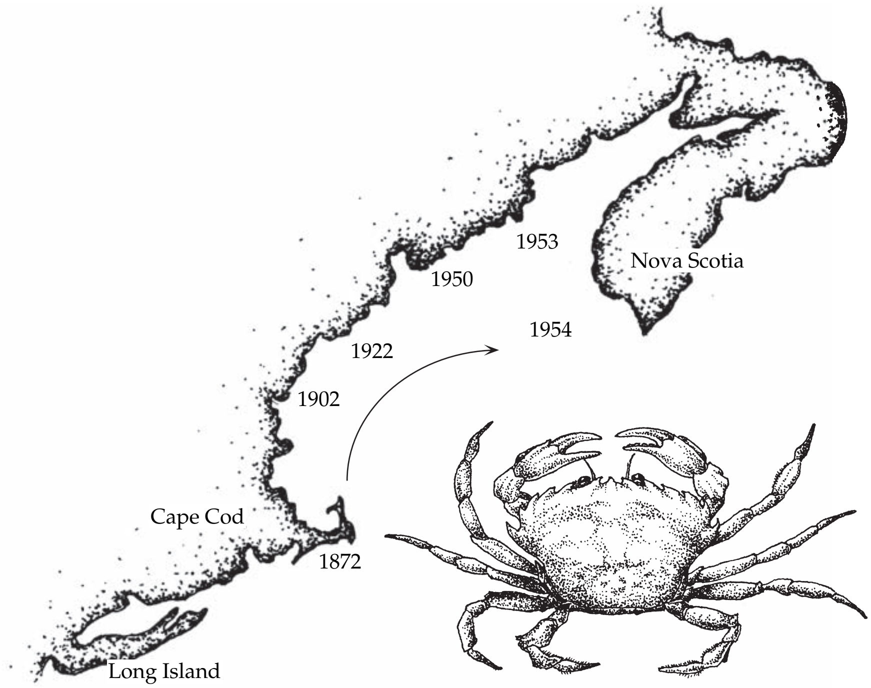

Fig. 1.12 The invasion history of the European green crab in northern New England.

seaweeds, and without natural predators, this encrusting bryozoan covers and kills large portions of shallow-water kelp forests (Levin et al. 2002).

New England salt marshes and freshwater marshes across North America are also being invaded by an exotic genotype of the common reed, *Phragmites australis* (Saltonstall 2002, Bertness et al. 2002a). This exotic genotype is much more aggressive than native genotypes, leading to *Phragmites* invading new marsh habitats and entirely displacing native marsh species and the entire native marsh landscape (Silliman and Bertness 2004).

Understanding the invasion history of marine shoreline organisms is tricky business. Until recently the common rocky shore periwinkle, *Littorina littorea*, the dominant intertidal herbivore on rocky shores from New England to Chesapeake Bay, was thought to have been introduced to North America either in rock ballast or as food in Nova Scotia in the mid-nineteenth century (Carlton 1982). Recent molecular evidence, however, has shown that *Littorina* likely did not go extinct during the last Ice Age but persisted in a warm water refuge in Nova Scotia (Wares et al. 2002). Thus, the invasion of the North American coastline by *Littorina* was a range expansion of North American snails, not the introduction of exotic European snails. Introduced species are clearly a pervasive feature of western Atlantic shorelines that need to be taken into account in considering any aspect of the ecology, history, or evolution of these assemblages.

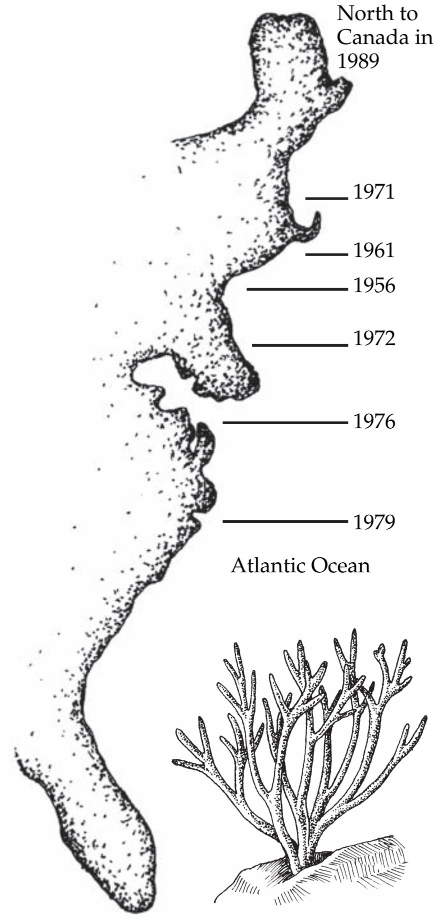

Fig. 1.13 The invasion history of *Codium fragile* spp. *tomentosoides* on the east coast of North America.

TIDES

The rise and fall of the tides is one of the most characteristic features of all shoreline habitats. Tides (from the Old English word for time) are complicated but highly predictable consequences of the gravitational pull of the moon and sun on the earth's water masses. The tidal heights at a particular location, however, can be modified by a wide variety of local, regional, and global factors. Tides play an extremely important role in shaping the abundance and distribution patterns of shoreline organisms.

Tides are caused by the gravitational forces of the moon and sun as well as the centripetal force of the earth–moon system spinning around a common center of mass. The moon exerts the strongest gravitational pull on the earth. While the moon is smaller than the sun, the sun is much farther from the earth. Consequently, the gravitational pull of the moon on the earth's oceans is twice that of the sun. The moon's pull on the earth's oceans causes

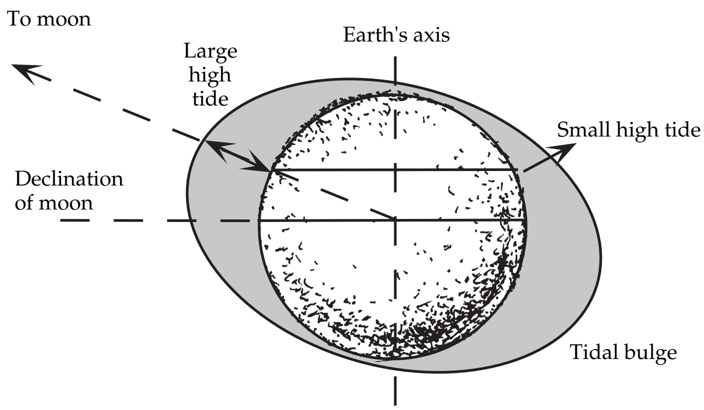

Fig. 1.14 Tidal bulges (greatly exaggerated in this drawing) on the earth's water mass caused by the gravitational pull of the moon and sun and the centripetal forces of the earth.

the oceans to bulge toward the moon. Opposing this gravitational pull, however, are centripetal forces caused by the earth–moon system's rotation. These centripetal forces cause the tidal bulge to form a roughly elliptical envelope of water around the globe (Fig. 1.14).

Tides are caused by the movement of these large bulges as standing waves of water across the earth. The earth rotates on its axis every 24 hours, and as it rotates, the tidal bulges move over its surface. If the globe were perfectly smooth and without continents, these bulges would be approximately 0.5 meters high and would travel at a speed of about 700 kilometers per hour over the earth's surface (Davis 1994). A wide variety of factors, however, complicate the magnitude and timing of tides.

Most shorelines on the earth, and all shorelines on the east coast of North America, have two tides a day, with the timing of low and high water shifting forward every day by 50 minutes. Fifty extra minutes of rotation are needed each day for the earth to catch up to the orbiting moon, which is moving in the same direction. Typically the high and low tides each day are not identical in magnitude, and are called **mixed tides** (Fig. 1.15). The difference is caused by the relationship between the axis of the earth's rotation and the angle of the gravitational distortion of the earth's water mass. As the

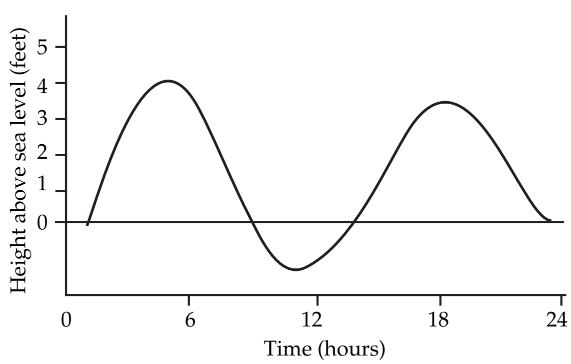

Fig. 1.15 Mixed semi-diurnal tides, in which two high and two low tides of different magnitudes occur each day, are found on the entire Atlantic coast of North America.

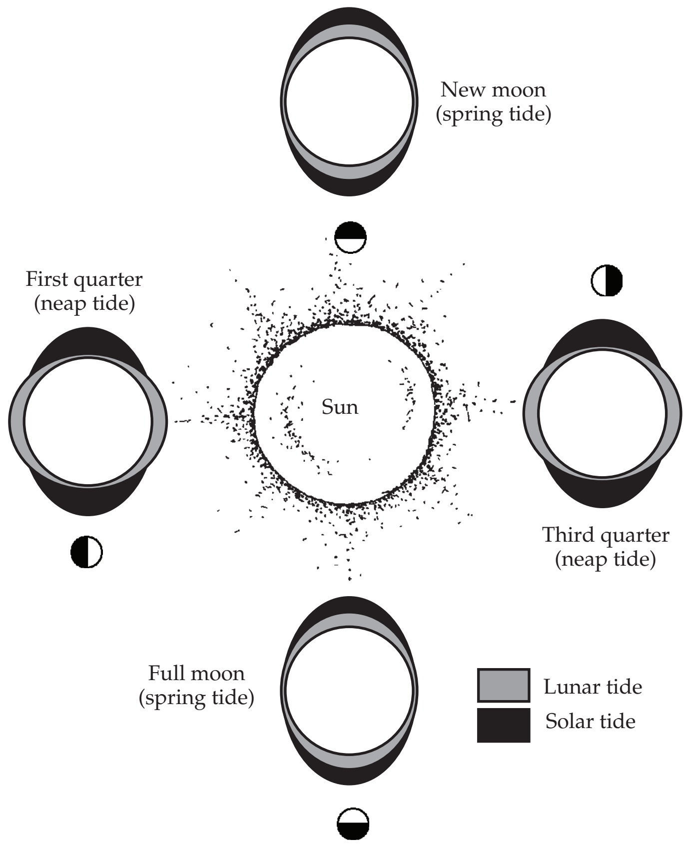

Fig. 1.16 The monthly tidal cycle. Maximum, or spring, tides occur when the gravitational forces of the moon and sun act together. Minimum, or neap, tides occur when the gravitational forces of the moon and sun oppose each other.

earth rotates around its axis, a particular location on its surface will encounter a tidal bulge or high tide every 12.5 hours, but at most locations on the globe, these high tides will be of different magnitudes. Conversely, low tides occur when the earth rotates through the troughs between tidal bulges.

The pronounced monthly cycles in the magnitude of the tides are largely the result of interactions between the gravitational pull of the moon and the sun. When the gravitational forces of the sun and moon act together to form the tidal bulge, the gravitational distortion of the earth's oceans is at its peak, and high and low tides are their greatest. This occurs twice monthly at new moons and full moons, and the resulting extreme tides are referred to as **spring tides** (though this has nothing to do with the season "spring"). Monthly minimal tidal excursions occur when the gravitational forces of the sun and moon oppose each other. These minimal tides also occur twice monthly as the moon passes its quarter phase, and the resulting tides are referred to as **neap tides** (Fig. 1.16).

Along the east coast of North America there are always two high and two low tides each day, with each daily tidal excursion differing in magnitude due to the position of the Atlantic coast relative to the global tidal bulges

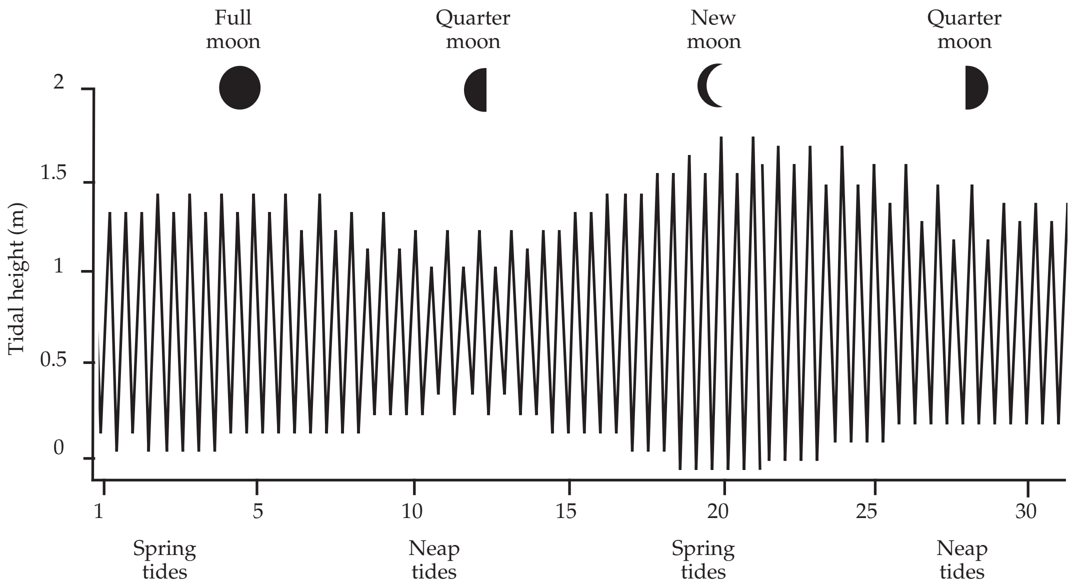

Fig. 1.17 Lunar tidal cycle for Prudence Island, Rhode Island, January 2003.

and the daily rotation of the earth. This is the most common type of tidal pattern and is called a **semi-diurnal tide**. Other coastlines, due to their position on the globe and other factors, can have other types of patterns (for example, a single tide a day, or days with either one or two tides) (Fig. 1.17).

In addition to this predictable monthly variation in the tides, annual variation in the intensity of tides occurs due to the position of the sun in relation to the earth. Twice a year, at the solar equinoxes (September 21 and March 21), the sun is directly over the equator and closest to the earth. At these times annual maximum tidal fluctuations occur. Conversely, at the two solar solstices (June 21 and December 21), the sun is farthest from the earth and equator, and annual minimum tidal fluctuations occur.

The exact timing and intensity of tides at a particular location is dependent on a variety of factors. Along the Atlantic coast of North America, the greatest tidal amplitudes are found in New England and the Canadian Maritime Provinces because of their global position in relationship to the tidal bulges. On mid- and southern Atlantic shores, tidal fluctuations decrease with latitude, both because of the global position of the tidal bulges and because of the standing wave patterns of the Atlantic Ocean as a whole. South of Cape Hatteras, however, the tides in Georgia are amplified by the funnel shape of the coastline. As a consequence, the tidal range in Georgia is 3 meters, while in North Carolina and on the Atlantic coast of Florida, the tidal ranges are less than 1 and 2 meters, respectively (Fig. 1.18). The timing of tides in particular locations is largely a product of shoreline and bottom topography and the time at which the tidal bulges reach particular locations.

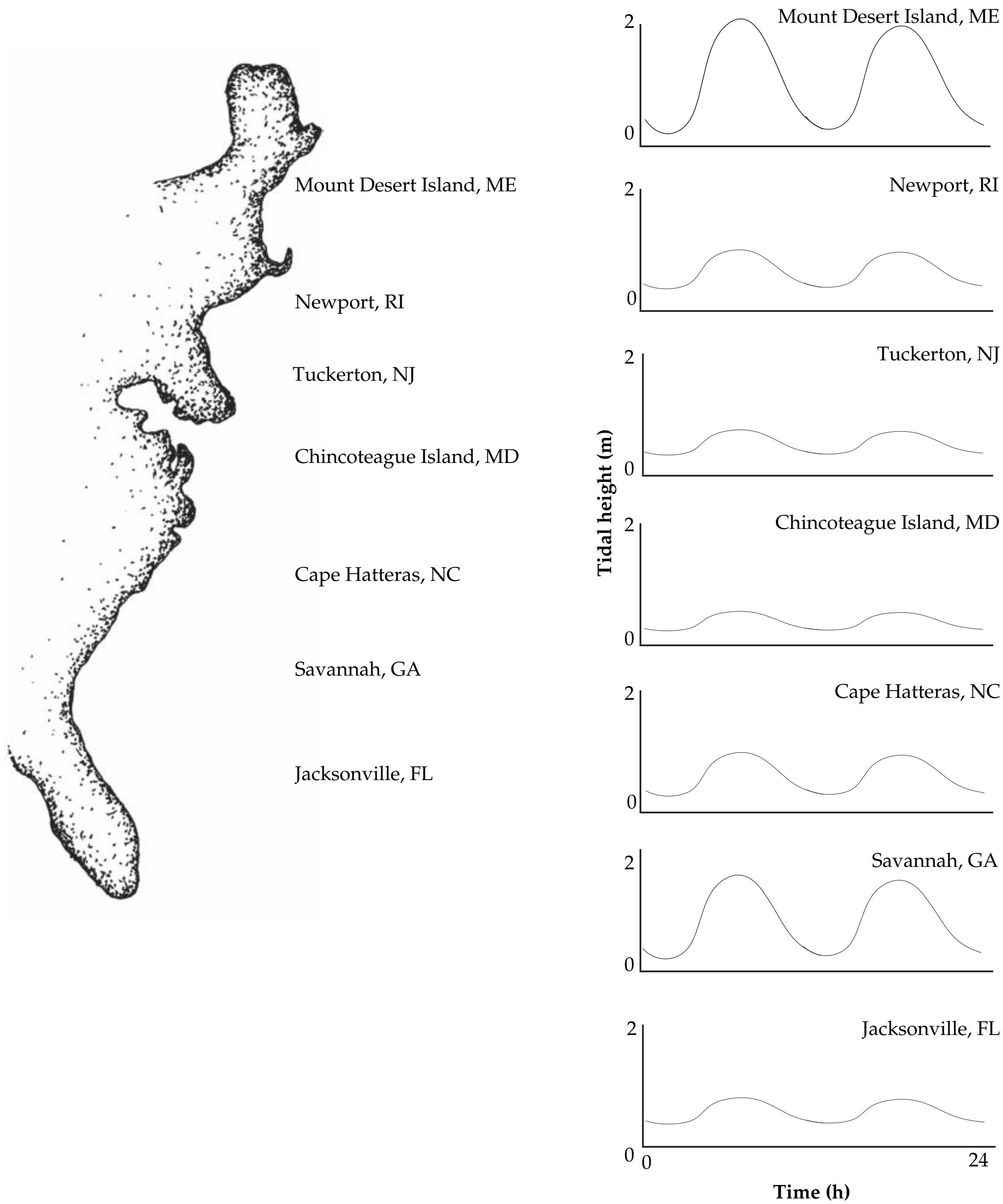

Fig. 1.18 Variation in tidal amplitude on the Atlantic coast. Maximum amplitudes are found in New England, due to the latitude of the tidal bulge, and in Georgia, due to the funnel shape of the coastline.

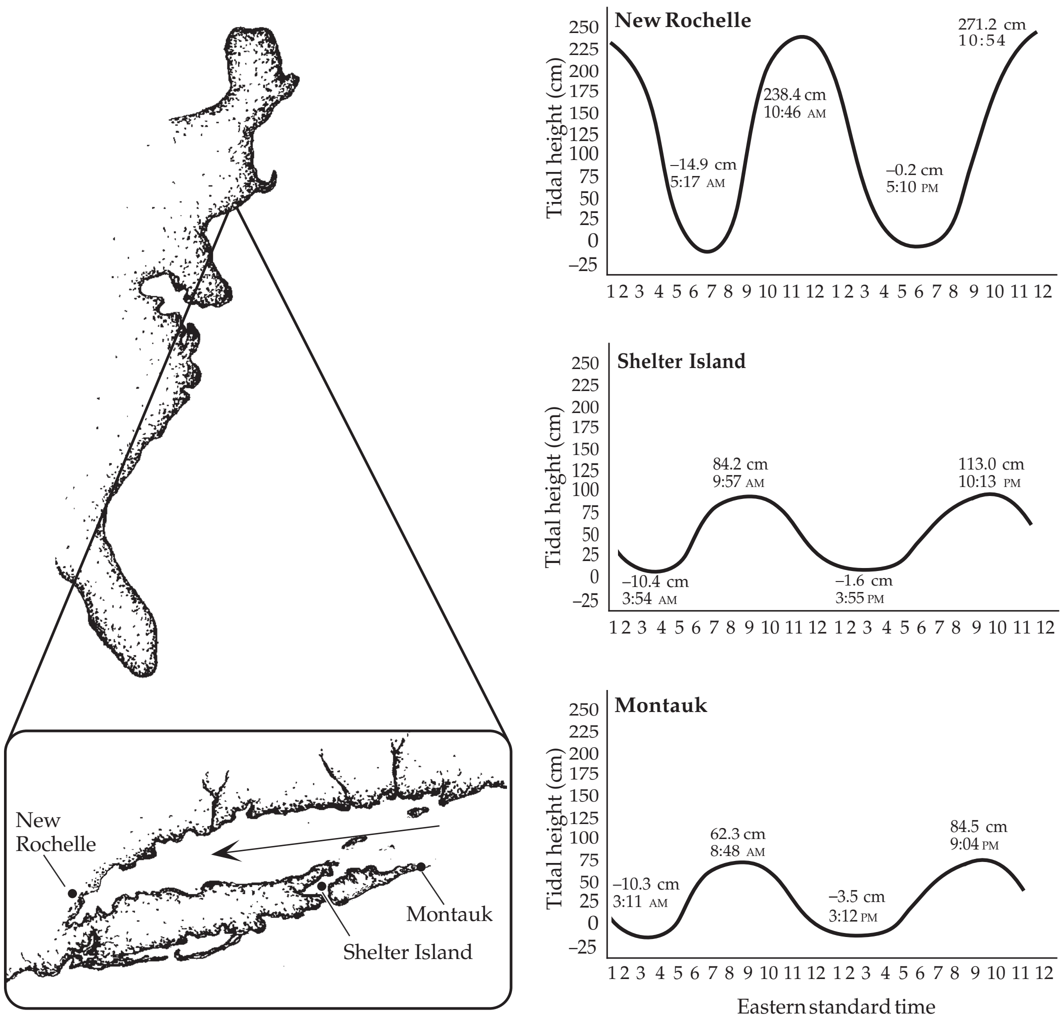

Fig. 1.19 Amplification of tides as they enter a funnel-shaped bay such as Long Island Sound. Note the temporal staggering of the tides as they enter the Sound.

Locally, the magnitude of tides can also be strongly influenced by shoreline morphology. As oceanic tidal bulges hit wide continental margins, the amplitude of tides can be magnified. Mid-oceanic islands without continental margins, for this reason, typically have very small tides. Bays and estuaries can also magnify the intensity of tides. Funnel-shaped bays, in particular, can dramatically alter tidal magnitude. The Bay of Fundy in Nova Scotia is the classic example of this effect, and has the highest tides in the world (over 15 meters). These prodigious tides are caused by the latitudinal position of the tidal bulge and the funnel shape and size of the bay (Fig. 1.19).

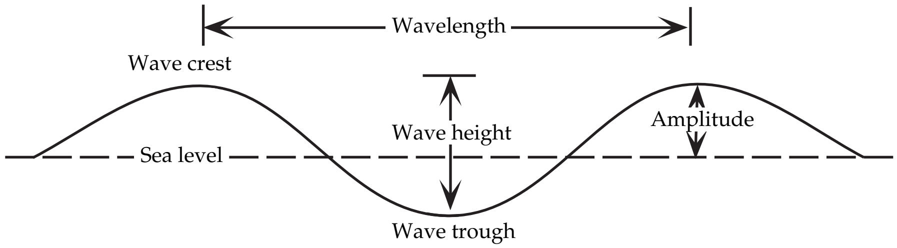

Fig. 1.20 Wave terminology.

Local wind and weather patterns can also affect tides. Strong offshore winds can move water away from coastlines, exaggerating low tide exposures, whereas onshore winds, by piling up water on shorelines, can virtually eliminate low tide exposures. Particularly in small, shallow bays, wind-driven water movement can deflect predicted tidal heights by as much as 1 meter. Changes in barometric pressure can also affect local tides by as much as 0.3 meters (Little and Kitching 1996). High-pressure systems can depress sea levels, leading to clear sunny days with exceptionally low tides. Conversely, low-pressure systems associated with cloudy, rainy conditions are typically associated with tides that are higher than predicted.

WAVES AND WATER MOVEMENT

In addition to the tides that predictably submerge and expose shoreline habitats, waves and nearshore flows also play an important role in shaping both shoreline habitats and the organisms that live there. Most nontidal water movement in shoreline habitats is the result of wind-generated waves. Although the precise mechanism whereby winds pass energy to bodies of water is uncertain, the friction and pressure of wind moving over water initiates surface waves. Waves can differ greatly in magnitude, but all can be described with the same simple terminology. The high point of a wave is its **crest**, and the low point is its **trough**. The **height** of a wave is the vertical distance from the trough to the crest, and the length of a wave, from crest to crest, is its **wavelength** (Fig. 1.20). The **steepness** of a wave determines its stability, and is defined as the ratio of its height to its wavelength (H/L). When a wave reaches a steepness of 0.6–1.5, it becomes unstable and collapses or breaks. The movement of a wave is referred to as its **period**, defined as the time it takes one wavelength of a wave to move past a reference point.

The magnitude of wind-generated waves depends on three factors (Bascom 1980): the speed of the winds, the **fetch**, or distance over which the winds act on the water, and the length of time a wind has to generate a given wave force. The light winds that produce small ripples in calm, protected bays demonstrate the same process that generates large oceanic waves and swell. In the open ocean, strong winds of 10–25 meters per second generated by severe weather patterns, operating over hundreds or thousands of kilometers and many days, can routinely produce waves 2–8 meters in height.

When waves are associated with the winds that generated them, they are referred to as **wind waves**. In heavy winds such waves have whitecaps, since the winds often blow their crests off. Some waves, however, continue long after the winds that generated them have subsided. Oceanic waves that persist independently of their original winds are termed **swell**. Waves in the open ocean, therefore, are a mix of long-wavelength swell, dissipating and coalescing from harsh weather conditions, often far away, and smaller-scale, locally wind-generated waves.

When a wave is in deep water, its surface water does not advance forward, but rather moves in a circular orbit with the diameter of the wave height. This seemingly counterintuitive motion is obvious once you think about it. If wind waves moved horizontally over the surface of the ocean, they would sweep floating objects with them. Instead of being swept across the sea, however, floating objects bob up and down in a gentle circular motion following the water's path. Floating in the surf, you can feel yourself surge slightly forward riding up the peak of a wave, and then surge back the same distance as you slip into a wave trough (Fig. 1.21).

The circular motion of water molecules in waves decreases with water depth, and stops altogether at a depth equal to half the wavelength of the wave on the surface. Below the surface, water moves in circular orbits of decreasing size until that depth is reached. This means that large oceanic swells with wavelengths of up to 300 meters are not detectable at depths of more than 150 meters, and that the effects of wind-generated waves in coastal habitats with wavelengths of 2–6 meters penetrate only 1–3 meters into the water column. Water affected by all these waves, however, does not move appreciably in a net horizontal direction until the shore is reached.

WAVES HITTING THE SHORE

When waves are in deep water, they are not affected by the sea bottom. When waves approach the shore, however, the bottom influences their structure, and ultimately causes them to become unstable and break, a process called **shoaling**. As a wave enters shallow water, the friction of the bottom makes it travel more slowly, particularly near the bottom. This decreases the wavelength of the wave, increases its height, and squeezes the orbital paths of its water molecules into elliptical paths (Fig. 1.22). At the same time, bottom friction causes the wave to slow more at the bottom than at the top. As a result of all these forces, waves encountering the shoreline become unstable and break. Broken waves, however, have not entirely lost their energy, and will reform and break again in shallower water until all their energy is dissipated.

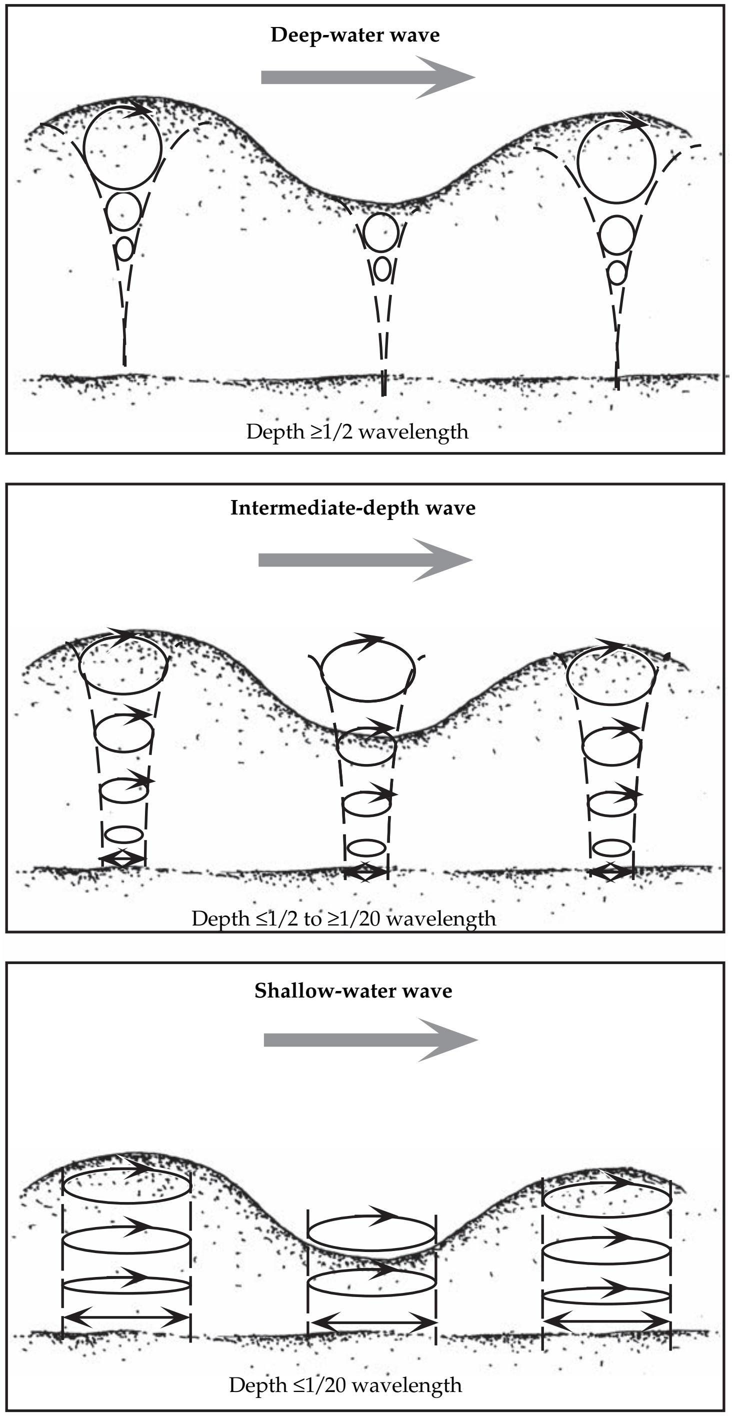

Fig. 1.21 Movement of water molecules in waves as a function of depth.

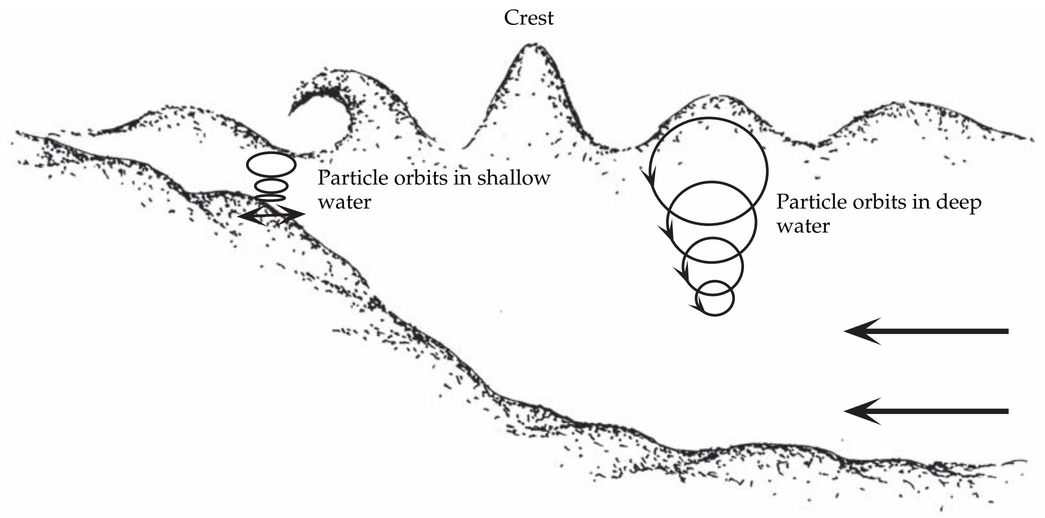

Fig. 1.22 A wave approaching the shore encounters the sea bottom, which compresses the orbits of its water molecules and slows its movement near the bottom. This increases the height of the wave until it becomes unstable and breaks.

Waves break differently on shorelines depending on their wavelength as they approach the shore and the slope of the bottom (Denny 1987, 1988). Long-wavelength oceanic swell develops into the classic **plunging breakers** that surfers in Hawaii and southern California enjoy. Shorter-wavelength, wind-generated waves that hit shallow slopes result in **spilling breakers**, which are taller waves that behave much like water spilling out of a container. As the steepness of the bottom increases, both long- and short-wavelength waves take the shape of **collapsing breakers**, relatively tall waves that develop rapidly and collapse rather then break (Fig. 1.23).

EFFECTS OF SHORELINE TOPOGRAPHY ON WAVES

Waves are also influenced by the shape of the shore and the angle at which they approach it. Waves rarely approach land with their crests parallel to the shoreline, but as they near landfall, they usually bend into the shoreline so that as they reach it, their crests are nearly parallel to the shore. This bending, or refraction, of waves is caused by the slowing of the waves by the bottom as they encounter the coast. As a wave enters shallow water at an angle, the part that first encounters shallow water is slowed, while that still in deeper water continues to move rapidly. Thus, slowing occurs at different times along a wave crest, causing it to bend into the shore.

Because of this bending of waves into shorelines, as waves meet complex shorelines, their forces are not distributed evenly across the shore. Waves converge at headlands or points, concentrating their energy at these

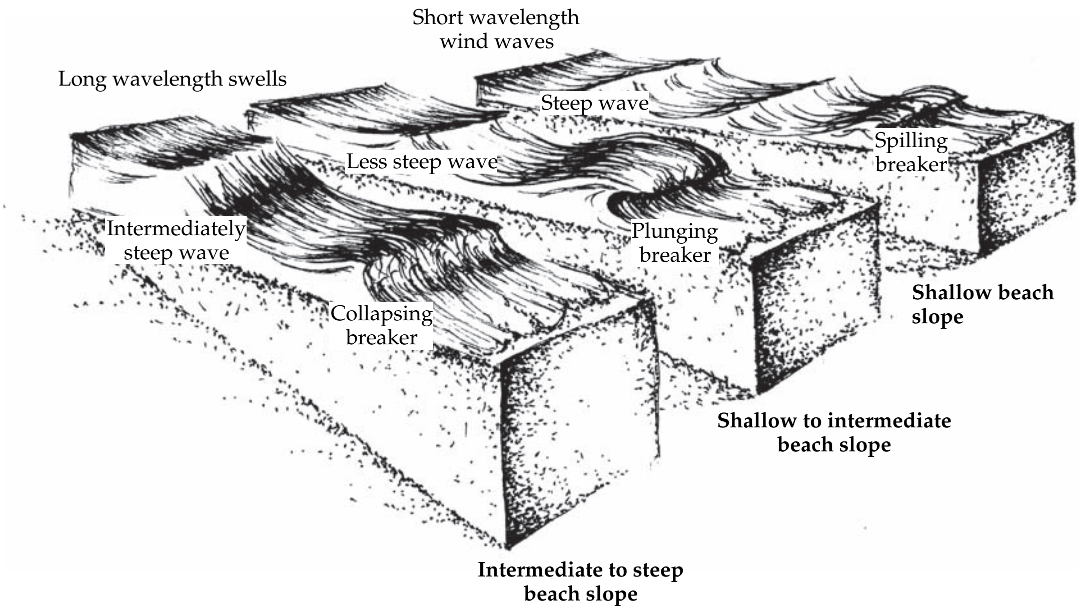

Fig. 1.23 Types of waves hitting shorelines.

exposed projections. This refraction of wave energy into headlands reduces the wave energy that enters adjacent embayments. As waves enter a bay, they also spread into the shape of the bay because of refraction. This further reduces the wave energy that reaches the shore of the bay (Fig. 1.24).

When waves encounter shorelines, they can generate impressive longshore currents, which run parallel to the shore and play an important role in transporting food, larvae, and sediments. Although wave crests bend as they approach shore, they still tend to hit shorelines at an angle. When this occurs, some of the water moves back into deep water (the undertow), and some of it moves parallel to the shore (Fig. 1.25). The amount of water in this longshore current typically depends on the angle at which waves hit the shore: in general, the greater the angle, the faster water moves along shore. Longshore currents are very predictable components of many shoreline habitats and have velocities ranging from 10 to over 100 centimeters per second.

WAVE EFFECTS ON SHORELINES

While shorelines strongly influence waves and nearshore water movement, waves and the currents they generate also play a major role in shaping shorelines. As waves are concentrated at headlands and dissipated in bays by refraction, headlands are eroded away while sediments are deposited in bays. Over long periods of time, typically measured in centuries, this pro-

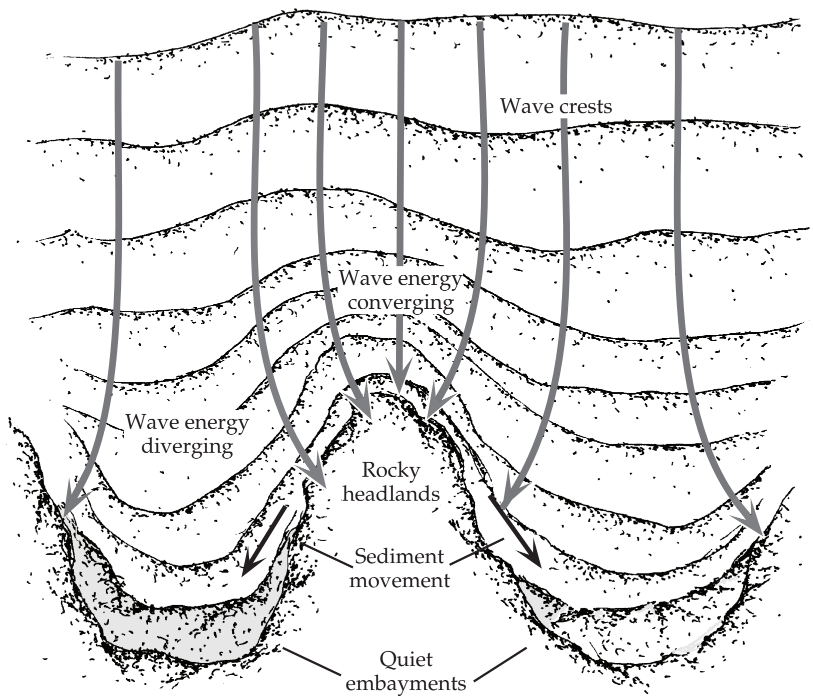

Fig. 1.24 Convergence of waves on headlands results in wave energy being focused on headlands and dissipated in adjacent bays.

cess generally leads to exposed headlands consisting of hard rocks and soft-sediment-dominated embayments.

On both short and long timescales, the action of waves and longshore currents on soft-sediment shores leads to the development of sandbars and barrier islands. As waves pound soft-sediment shorelines, the orbital movement of water hitting the shore churns up sediments, leaving them vulnerable to erosion by longshore currents. Deposition of sediments on the edges of longshore currents, where their velocity is reduced, leads to the formation of sandbars running parallel to the shore, punctuated by channels where water (piled onshore by waves) flows back out to sea. On a larger spatial scale, this same process, coupled with rising sea level and the stabilization of sediments by vegetation, is responsible for generating the barrier islands that are a dominant feature of the southeastern coast of North America.

Seasonal variation in the intensity of wave energy often leads to seasonal patterns in the morphology of sediment beaches on wave-exposed shores. Winter conditions typically lead to high seas, high wave energy hitting the coast, and the erosion of beach sediments. This erosion often exposes bedrock as sediments are moved offshore, and leads to beaches having a shallower profile in the winter than they do in the summer. During calmer spring and summer conditions, however, beaches that were eroded

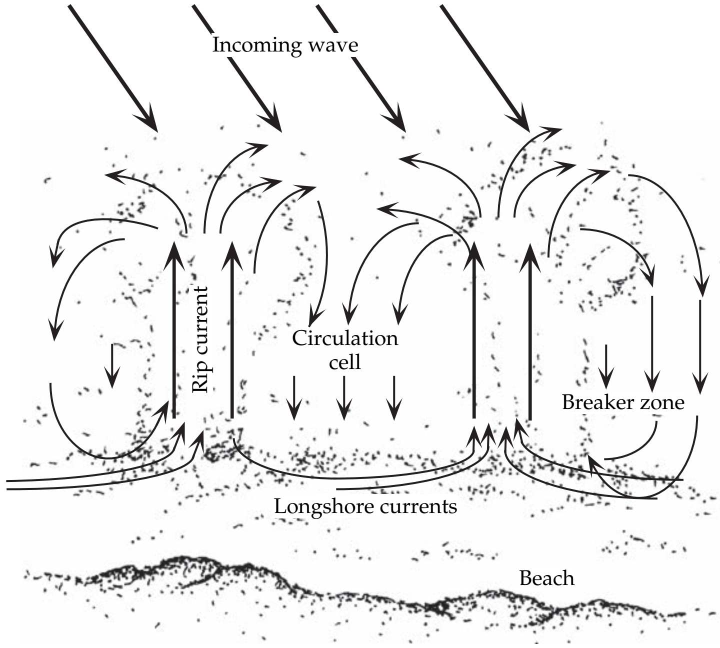

Fig. 1.25 As waves approach the shoreline at an oblique angle, a longshore current is produced. Rip currents form from the waves flowing back to the sea, completing a circulation cell.

away during the winter commonly experience heavy sedimentation. These seasonal shifts in wave energy can lead to dramatically different shoreline morphologies over the course of a year (Fig. 1.26).

WATER MOVEMENT: EFFECTS ON SHORELINE ORGANISMS

Water movement over shoreline habitats also has profound effects on intertidal organisms, populations, and communities. These effects have only recently begun to be fully appreciated. On wave-exposed shores, waves crashing into shorelines continually move and restructure intertidal habitats composed of sand and cobbles, often precluding organisms from inhabiting these highly disturbed habitats or limiting their inhabitants to rapidly colonizing species that are specifically adapted to live in unstable habitats. Surf clams, for example, migrate up and down high-energy sandy beaches with the tide, taking advantage of intertidal water movement to move and feed. Razor clams, in contrast, burrow deep into the substrate to escape shifting sediments. On wave-exposed rocky shorelines, the major adaptive challenge is typically not shifting substrate, but rather the intense force of waves hitting the shore. Strong attachments, streamlined morphology, and living in groups in which neighbors buffer one another from wave stresses are typical solutions to the problems of living on wave-exposed rocky shorelines (Denny et al. 1985). These issues are discussed further in chapter 5.

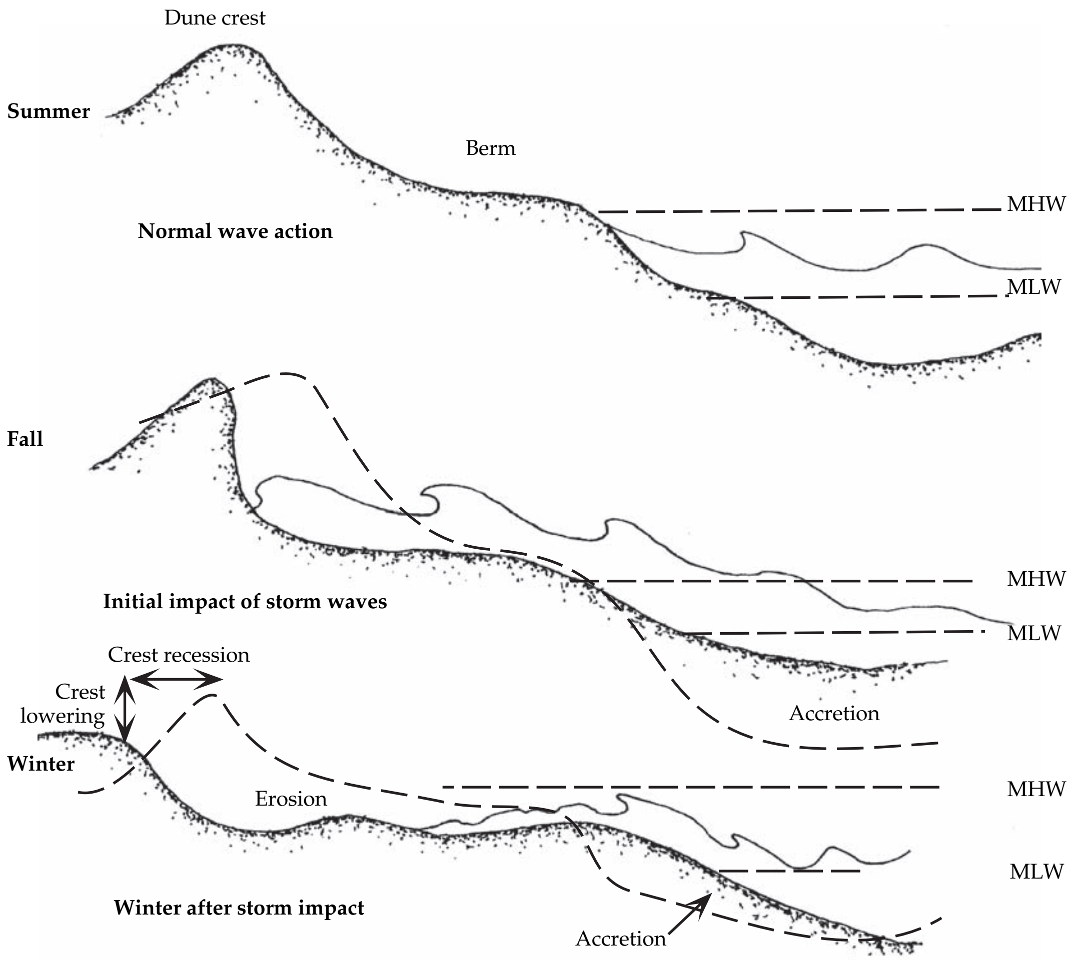

Fig. 1.26 Seasonal changes in a typical beach profile. Sand is accumulated in the summer when waves are small, forming a berm. The berm and beach can almost completely move offshore in the winter due to high waves and erosion. MHW, mean high water; MLW, mean low water.

Not all effects of water movement are negative. Water movement over shorelines is crucial in delivering food and nutrients to intertidal organisms, and plays a major role in the dispersal of the gametes and propagules of many intertidal inhabitants. Filter-feeding organisms that rely on water movement to deliver food to them (e.g., barnacles and mussels) are particularly dependent on high rates of flow to feed and grow (Sanford et al. 1994). Algal growth is also enhanced by high rates of flow, due to increased gas exchange efficiency (Gerard 1987). Because of these strong positive effects of water movement on intertidal producers, high-flow habitats typically

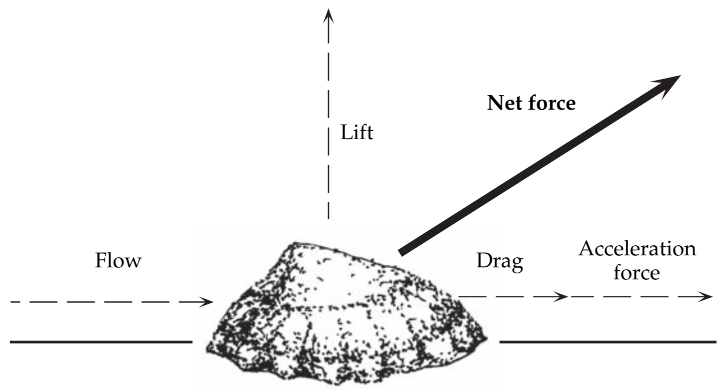

Fig. 1.27 Hydrodynamic forces on sessile organisms.

support more productive and diverse food webs than low-flow habitats (Leonard et al. 1998a).

Intertidal organisms are exposed to both wave and tidally generated water movement. In open-coast habitats subject to oceanic swell and wind-driven waves, wave forces dominate the water movement patterns experienced by intertidal organisms. In protected bays and estuaries, incoming and outgoing tides typically generate long, spatially and temporally predictable periods of unidirectional flow.

The hydrodynamic forces generated in exposed open-coast shoreline habitats when oceanic swell hits shorelines can be enormous. Water velocities of 10–20 meters per second and acceleration forces often exceeding 100 square meters per second are common (Denny et al. 1985). These high water velocities and accelerations result from waves breaking in shallow water, and expose intertidal organisms to drag, lift, and acceleration forces (Fig. 1.27). **Drag** is proportional to the area of an object, results from pressure differences on the sides of an object, and acts to pull an object parallel to and in the same direction as flow. Drag can be minimized by having a low, streamlined profile. **Lift** is also proportional to the area of an object, but acts perpendicular to flow. Lift is caused by pressure differences between an object and fluid moving over the object, and is the relative force responsible for blowing the roofs off buildings in storms. Since drag is maximized by having a low profile, the importance of lift increases for organisms that live in wave-exposed habitats. **Acceleration**, in contrast to lift and drag, results from the presence of an object's mass in flows, and is proportional to an object's volume, not its area.

Tidally generated hydrodynamic forces typically differ quantitatively and qualitatively from wave-generated forces. Tidally generated forces are generally much smaller than wave-generated forces, and acceleration forces are dramatically less in tidal flows. In bays and estuaries where tidal flows dominate, the hydrodynamic forces experienced by intertidal organisms will run landward during incoming tides and seaward during outgoing tides, punctuated by relatively calm periods at low and high tide. The tidal

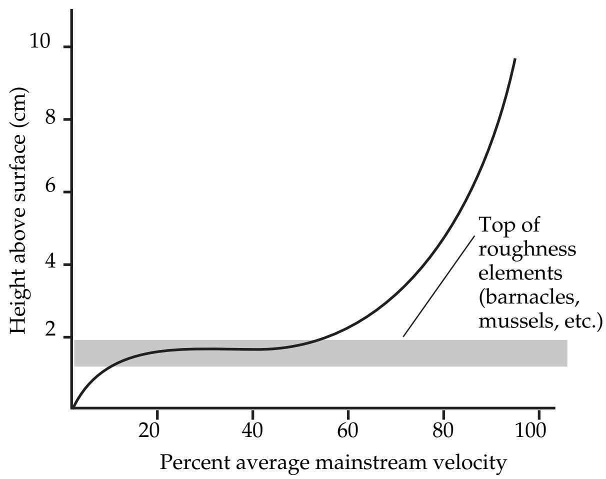

Fig. 1.28 Velocity gradient for a fluid flowing over a surface, showing the low-velocity boundary layer near the surface.

flows experienced by bay and estuarine organisms are largely predictable, based on the geomorphology of basins. Any constriction, such as the mouth of a bay, an island that occludes tidal flow, or a shallow bottom, will predictably increase tidal flows and their consequences on intertidal organisms. This is in contrast to the bashing wave flows seen by open coast organisms.

Because of friction with the seafloor, water velocities are typically lower nearer the bottom, resulting in a layer of slower-moving water called the **boundary layer**. As a consequence, small organisms on the seafloor experience a flow environment that is often very different from that higher in the water column. Very small organisms live in a boundary layer of relatively slow-moving water (Fig. 1.28). Boundary layers, however, are minimized by fast-moving near-bed flows and irregular surface topography. As a result, boundary layers are thinner in high wave energy or tidal flow habitats, and on rocky shores, where uneven topography generates turbulent flow conditions near the bottom. In contrast, boundary layers are more important in tidal mud and sand flats in estuaries and bays, where constant unidirectional flows over relatively flat surfaces are common.

SUMMARY

Understanding the ecology of shorelines requires an appreciation of geological history and of the intimate relationship between shorelines and oceanographic processes. The east coast of North America lies far from the edge of the North American plate, which carries the continent over the earth's surface. Seafloor spreading has slowly pushed the plate westward for the past 150 million years. This movement has resulted in the rugged mountains characteristic of the west coast of North America, as the western edge of the plate is pushed against the Pacific plate, and an old, geologically stable eastern margin characterized by massive sediment accumulation.

On a much shorter timescale, over the past few million years, changes in sea level have also left dramatic imprints on the east coast of North America. During past glaciations, the most recent of which ended only 20,000 years ago, large ice caps covered much of North America, extending as far south as New England. These ice caps scoured sediments from Canadian and northern New England shorelines, leaving behind rugged rocky shores and large depositional basins such as Narragansett Bay and Long Island Sound. The barrier islands that characterize the east coast of North America south of New England are another conspicuous signature of the coast's history of fluctuating sea levels. When the sea level was over 40 meters lower during the most recent glaciation, waves deposited large amounts of sediment on the shore, and as the sea level rose, these shorelines were flooded, leaving the barrier islands.

The dynamic geological history of the east coast of North America has also left its mark on the organisms that live there. Glaciations over the past 3 million years, in particular, led to the extinction of rocky shoreline organisms unable to retreat south of New England, as well as many other shoreline organisms unable to cope with cold Ice Age conditions. Consequently, much of the fauna and flora of the east coast of North America has only relatively recently colonized or recolonized the coastline. In New England, most of the reinvading organisms have come from Europe and the northern Pacific, whereas in the southern Atlantic, most colonizers have come from lower latitudes. The recent history of disturbance and the relatively depauperate fauna and flora of the east coast of North America have also made it particularly vulnerable to invasion by introduced species. In the past 300 years, since colonization by Europeans, introduced species from Europe and around the globe have come to dominate shorelines on the east coast of North America. Introduced species are so pervasive that any discussion of shoreline ecology must take into account the recent and artificial nature of relationships among many shoreline organisms.

Patterns of water movement shape shoreline habitats and determine the sizes and shapes of organisms that live there. Shoreline organisms are tightly linked to these patterns, which determine their exposure to terrestrial conditions and dictate the movement of their gametes, larvae, and food. Tides are one of the most fundamental organizing forces in shoreline habitats, since they generate predictable gradients of physical stress across shorelines. Water movement also shapes shorelines by eroding high-wave-energy habitats and depositing sediments in low-wave-energy habitats.

FURTHER READING

Carlton, J. T. 1992. Blue immigrants: The marine biology of maritime history. *Mystic Seaport Museum Publication* 44: 31–36. A semipopular account of the history of marine invasions.

Davis, R. A. 1994. *The Evolving Coast*. Scientific American Books, New York. An elegant, simple overview of coastal geology.

Denny, M. W. 1988. *The Biology and Mechanics of the Wave-swept Environment*. Princeton University Press, Princeton, NJ. A must-read for any aspiring marine intertidal ecologist.
Pethick, J. 1984. *An Introduction to Coastal Geomorphology*. Arnold Press, London. A very readable and insightful look at the dynamics of coastlines.
Vermeij, G. J. 1991. Anatomy of an invasion: The trans-arctic interchange. *Paleobiology* 17: 281–307.
Vogel, S. 1996. *Life in Moving Fluids*. Princeton University Press, Princeton, NJ. A delightfully written primer of hydrodynamics for biologists.