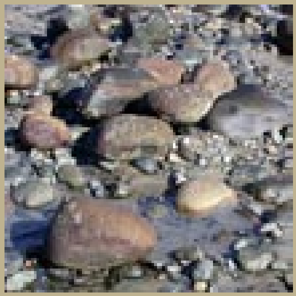

Peter H. Taylor

Physical Habitats

Physical habitats are defined primarily by substrate and water depth, which influence the species that can survive in a given place. The substrate can range from solid rock outcrop to sand or mud. Solid rocks provide secure places onto which animals and plants can attach, but they do not accommodate burrowing species. Conversely, soft substrates do not provide solid attachment but do allow burrowing, although mud and sand vary in how much oxygen-rich water can penetrate among grains to sustain life beneath the surface. Water column habitat is defined by a lack of substrate. Water depth affects the amount of sunlight reaching the seabed, which in turn influences the presence and abundance of vegetation. Below a certain depth, too little sunlight penetrates to sustain plants. Water can affect other environmental conditions. Along the coast, for example, waves pound against the shoreline, and intertidal habitats are exposed during low tide. Species must be adapted to survive these harsh conditions.

Rocky Habitats



Sandy Habitats

Muddy Habitats

Water Column

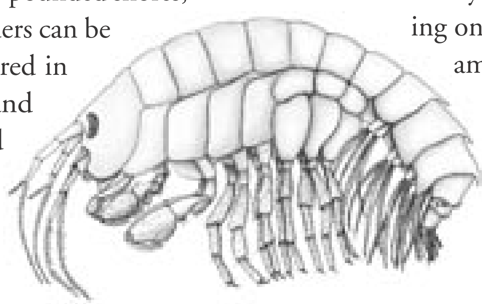
Rocky Habitats

Peter H. Taylor

General Description

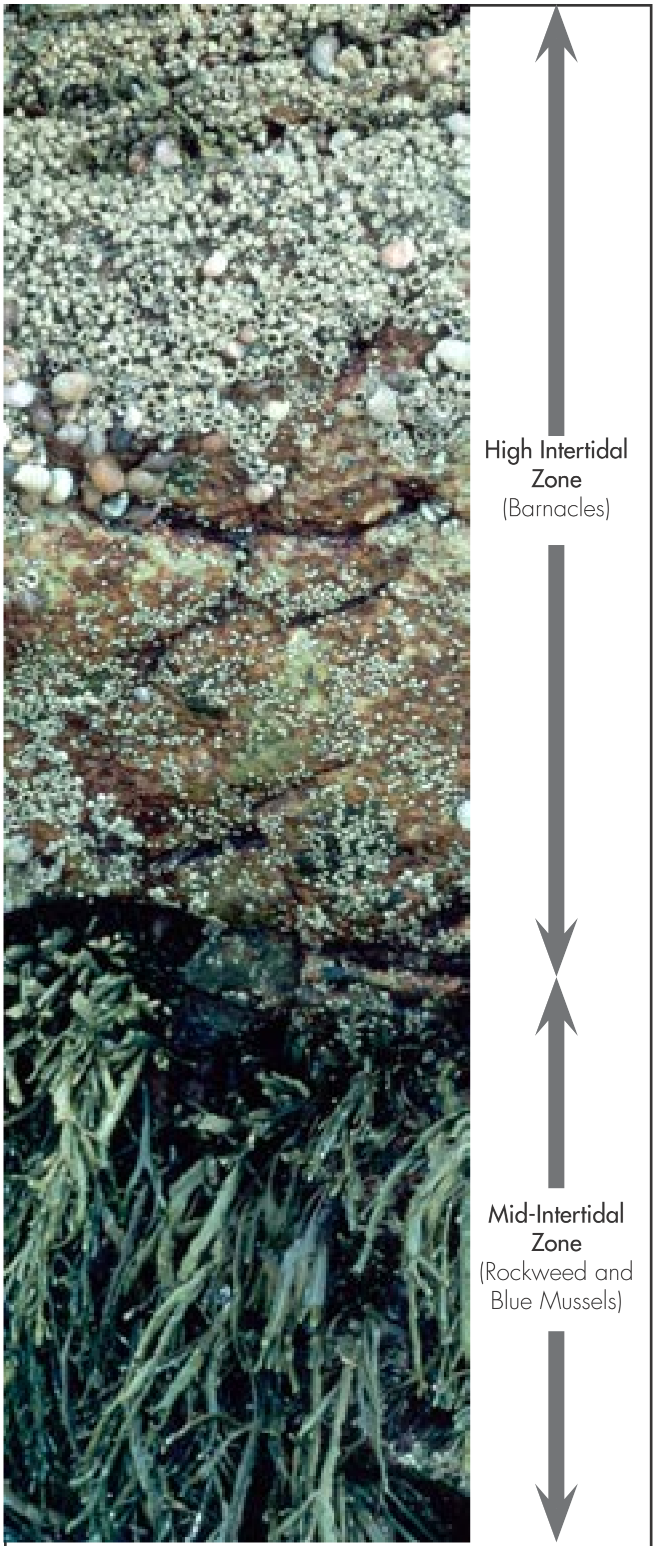
The Gulf of Maine region is known for its rocky shorelines, and its seabed also has rocky areas. Underlying much of the region are erosion-prone metamorphic rocks such as shale and schist. Metamorphic rocks form when sedimentary rocks such as sandstone and mudstone are transformed by extreme heat and pressure. Erosion-resistant granite, an igneous rock composed of solidified magma, often appears in exposed headlands. Most rocky habitats include a mixture of rock sizes, except for extremely wave-pounded shores, where rock outcrop dominates. Boulders can be scattered across the seafloor or clustered in piles, providing important hiding and living spaces for bottom-dwelling and swimming organisms.

Rocky habitats have distinct ecological communities because many of the species require a hard substrate for attachment. The structure formed by both the rock and the attached organisms, such as mussels and seaweeds, provide habitat for many smaller organisms, especially small invertebrates and juvenile fish (Lindholm *et al.* 1999). The precise mix of species inhabiting a rocky habitat is strongly affected by water depth, sunlight, wave exposure, and stability of the substrate. For example, many species inhabiting rocks in the intertidal zone have adaptations for avoiding desiccation and wave damage. Species on intertidal rocky outcrops, such as rockweed, anemones, barnacles and mussels, tend to be relatively large, long-lived, and securely attached to the rock, while species living on wave-tossed intertidal cobbles, such as amphipods and isopods, tend to be small, mobile, and short-lived. In general, stable rocks like bedrock, boulders, and partially buried cobbles have greater diversity of species than rocks that are frequently shifted by waves (Schoch and Dethier 1996).



Amphipods are common in rocky habitats.
Ethan Nedeau

Pounding surf and exposure at low tide make the rocky intertidal zone inhospitable for all but the hardiest marine animals. Peter H. Taylor



ROCKY INTERTIDAL ZONATION

Barnacles dominate the high intertidal zone and are preyed on by dog whelks. Rockweed dominates the mid-intertidal zone and shelters mussels and other invertebrates. Mussels may dominate the mid-intertidal zone at sites exposed to pounding waves that damage rockweed. The low intertidal zone (not shown) typically hosts red algae such as Irish moss and false Irish moss. Peter H. Taylor

Solid Rock Outcrop: Intertidal

In the Gulf of Maine, the wave-sheltered rocky intertidal zone is often inhabited by an abundance of brown seaweeds. At high tide, the algae form an underwater canopy similar to a kelp forest. When the tide is low, the algae lie on the rocks and protect snails, mussels, barnacles, and crabs from exposure to sun, wind, rain, and bird and human predators. In the Gulf of Maine, typical canopy-forming brown algal species are knotted wrack (*Ascophyllum nodosum*), bladder wrack (*Fucus vesiculosus*), and spiral wrack (*Fucus spiralis)*. Collectively, these species are referred to as rockweed or fucoid brown algae. Knotted wrack and bladder wrack are found in the mid-intertidal zone, and spiral wrack is found in the upper intertidal zone. Their abundance contributes to the high productivity of rocky intertidal shores.

On rocky shores, invertebrates and algae live in horizontal zones between the high and low tide marks. The zones reflect the varying abilities of species to tolerate the environmental conditions, predation, and competitive pressures at different heights. The highest zone is the splash zone, which is colored darkly by lichens that tolerate salt spray. Just below the splash zone, acorn barnacles inhabit the high intertidal zone. On wave-exposed shores, blue mussels often populate the middle and low intertidal zone with many small invertebrates living in crevices among them. At less wave-exposed sites, rockweeds may dominate the mid-intertidal zone, and tufts of red algae known as Irish moss and false Irish moss may cover the low intertidal zone. Tide pools

Subtidal boulder and rock outcrops near Deer Island and Campobello Island, also known as the West Isles area, with (a) sponges and dahlia anemones (*Tealia felina*), (b) finger sponge (*Haliclona oculata*), (c) dahlia anemone (*Tealia felina*), (d) field of stalked tunicates (*Boltenia ovifera*).
Mike Strong and Maria-Ines Buzeta

form in depressions in intertidal rock outcrops and provide homes for some animals and algae that otherwise might not survive exposure to air.

Solid Rock Outcrop: Subtidal

Shallow, rocky seabed often hosts kelp and other algae. Large, mobile animals such as lobsters, crabs, sea stars, whelks, green sea urchins, and fish such as cunner, Acadian redfish, and cod live in subtidal areas of rock outcrop. Anemones, bryozoans, mussels, tunicates, and even soft corals attach to the substrate. The angle of the rock outcrop substrate strongly influences the ecological community (Witman and Dayton 2001). Seaweeds generally dominate horizontal rocky surfaces that receive plenty of sunlight. In contrast, soft corals, brachiopods, mussels, tunicates, sponges, hydroids, and anemones typically prevail on vertical faces because these areas are less susceptible to sedimentation and relatively inaccessible to non-swimming predators such as urchins, crabs, and lobster (Chapman and Johnson 1990, Witman and Dayton 2001). On both horizontal and vertical rock outcrops, cracks and crevices provide refuge for small invertebrates and fish.

The abundance of green sea urchins (*Strongylocentrotus droebachiensis*), which eat kelp and other algae, helps to determine the amount of algae living in a given shallow subtidal area. Because kelp and other seaweeds require light for photosynthesis, they cannot thrive in deeper waters, where little or no sunlight penetrates. Deep rocky outcrops tend to be dominated by invertebrates rather than kelp beds. For example, horse mussels create dense beds at depths below approximately ten meters (Witman 1985). The interstices among their shells provide refuge from grazing and predation for smaller species. Many species of brachiopods, sponges, sea cucumbers, tunicates, and anemones also inhabit rocky outcrops in deep areas (Ojeda and Dearborn 1989, Witman and Dayton 2001).

Boulders: Intertidal

Boulders are rocks with a diameter greater than 256 millimeters (approximately 10 inches). Because they are not frequently overturned by waves due to their large size, boulders support similar species as rocky outcrops. Long-lived algae and animals can survive attached to them. In the intertidal zone, boulders provide a substrate for algae, mollusks, barnacles, hydroids, and other sessile organisms. In addition, boulders provide shelter from wind, sun, rain, and predators for small organisms that can take shelter underneath and beside them. Birds, mammals, and fish forage

Rocky habitat at high tide. The floating rockweed forms a canopy for organisms below it. Tracy Hart/Maine Sea Grant

less efficiently in boulder fields than on flat, rocky outcrops because the boulders offer hiding places for prey.

Boulders: Subtidal

Large, underwater piles of boulders known as boulder reefs provide an important habitat for algae, anemones, mollusks, and sponges that attach to the rock surfaces or dwell in crevices. Lobsters, crabs, and many fish associate with boulder reefs, including Acadian redfish, cunner, sculpin, cusk, and tautog. Some animals spawn on boulder reefs, such as squid that attach egg cases directly to rocks. Studies at Stellwagen Bank National Marine Sanctuary in Massachusetts Bay showed that cod spent considerable time at boulder reefs, indicating that this habitat is valuable to their growth and survival (Lindholm and Auster, unpublished).

Cobble and Pebble: Intertidal

Cobbles are rocks with a diameter of 64 to 256 millimeters (2.5 to 10 inches), and pebbles are 2 to 64 millimeters (0.1 to 2.5 inches). Cobble and pebble habitats tend to have higher species diversity than mud and sand because the rocks provide refuges for algae and small animals. Invertebrates and algae attach to cobbles or take shelter in crevices. Flat or partially buried cobbles often harbor the greatest diversity of species because these rocks are less frequently overturned by waves. In the wave-swept intertidal zone, cobble habitats are typically devoid of long-lived rockweed, but ephemeral algae such as sea lettuce or laver may colonize some relatively stable rocks. Rock barnacles often attach to cobbles, and the blue mussel's byssal threads can partially anchor cobble to the underlying substrate. Several gastropod species frequent this habitat type. Small native animals such as amphipods, isopods, worms, and gunnels, as well as the non-native European green crab and Asian shore crab, dwell among cobbles or pebbles.

Cobble and Pebble: Subtidal

Cobble and pebble habitats in the subtidal zone host many of the same species as boulder reefs. Some of the organisms that attach to cobble include anemones, tunicates, hydroids, soft corals, and sponges. In places where storm waves and other disturbances are infrequent, these organisms may become abundant and cover cobble substrates. Among the fish that commonly inhabit subtidal cobble and pebble bottoms are redfish, scup, ocean pout, and two species of shanny. Cobble and pebble habitats are important to fisheries because several species use this habitat during vulnerable stages in their lives. For example, laboratory and field experiments have demonstrated that juvenile cod survived at a higher rate in cobble habitats than in open habitats such as sand (Lindholm *et al.* 1999, Tupper and Boutilier 1995).

Distribution

The Gulf of Maine has more rocky intertidal habitats than other areas along the Atlantic coast (Roman et al. 2000). These habitats are most prevalent on the Gulf of Maine's northern shores, including Maine, New Brunswick, and Nova Scotia. The geographic distribution of rocky subtidal substrates is not well documented, but scientists are working to map substrates and habitat types of the entire Gulf of Maine seafloor. Subtidal bedrock habitat has been documented in waters north and south of Boston Harbor, and it occurs in other shallow areas. Subtidal cobble and pebble habitats occur along the New Hampshire and southern Maine coasts, as well as on Georges Bank and the southern coast of Nova Scotia.

Atlantic puffin posing on a rock. Brian Atkinson

Ecological Functions

The primary productivity of seaweed-dominated rocky shorelines is nearly ten times greater than that of the adjacent open ocean (Harvey *et al*. 1995) and helps fuel the marine ecosystem. Seaweeds sustain animals in other habitats, as fragments break off, drift away, and enter the food web.

Rocky habitats provide homes for many animals and plants. Both the physical structure provided by rock itself and the biogenic structure created by seaweeds, mussels, and other attached species offer important habitat for many organisms. Spawning fish such as herring and capelin use the rocky habitats to shield their eggs from currents and predators. Rock crevices protect algae and small animals such as snails, crabs, isopods, and amphipods from predators.

Rocky habitats provide food for many predatory animals. For example, gulls, diving ducks, and other birds feed on the abundant mollusks, fish, and crabs. Lumpfish, rockfish, cunner, Acadian redfish, and sculpin are some of the predatory fish that feed in rocky intertidal and subtidal habitats. Mammal predation can be significant (Carlton and Hodder 2003); rats, mink, and other small mammals forage in the Gulf of Maine's rocky intertidal zone.

Economic and Recreational Value

Historically, rockweed, Irish moss, and dulse were harvested in large quantities in the Gulf of Maine. Commercial harvesting of seaweed still occurs in New Brunswick, Nova Scotia, and Maine. Boulder reefs and cobble bottoms provide nursery habitat for valuable species such as lobster (Wahle and Steneck 1992), cod (Tupper and Boutilier 1995), and many other animals that hide from predators among the cobbles. Other commercially important species associated with rocky outcrops and boulders include blue mussels, rock crabs, green sea urchins, and sea cucumbers. Sea scallops live in high densities on subtidal pebble bottoms. Rocky shores can protect upland properties by absorbing the pounding of waves. Tourists, naturalists, and students explore rocky shores and tide pools as a recreational and educational activity. Recreational divers frequently visit subtidal rocky outcrops and boulder reefs.

Kayaking has become a popular recreational activity in the coastal Gulf of Maine. Peter H. Taylor

Management Considerations

Coastal development can affect rocky intertidal habitats, especially when breakwaters or other structures disrupt alongshore currents and cause sediments to accumulate. Runoff of oil, road salts, industrial chemicals, and other pollutants from the uplands can harm the species living in rocky intertidal habitats and other coastal habitats. Replacing cobbles and pebbles with sand to make a beach displaces species that need rocks for attachment and shelter. Studies in other regions show that climate change may be responsible for some recent shifts in the distribution and abundance of species that inhabit rocky shores (Barry *et al*. 1995, Southward *et al*. 1995).

Increasingly, people are harvesting mollusks, crabs, and other invertebrates on rocky shores (Addessi 1994; personal observation). Rockweed harvesting can dramatically affect the organisms that rely on shelter that rockweed provides. Trampling by people walking on rocky shores can harm invertebrates and seaweeds (Brosnan and Crumrine 1994). When curious explorers upturn rocks and do not replace them to their original position, many small animals fall victim to heat, desiccation, and predation.

Subtidal rocky habitats face a similar range of impacts from pollution and climate change. Coastal construction, disposal of dredged material, and even natural causes of sedimentation can overwhelm some animals by clogging their feeding tubes and gills. Food and waste from finfish aquaculture pens can bury plants and animals living on rocky bottoms, and the decomposition of these materials can lead to low levels of dissolved oxygen. Mining companies sometimes extract subtidal pebbles for use in construction and other activities.

Harvesting rockweed. Canada Department of Fisheries and Oceans

Fishing can also affect rocky habitats. For example, overfishing of sea urchins can allow kelp beds to become established in former urchin barrens. This shift in habitat type can influence the survival of many species—some positively, some negatively. Fishing trawls and other gear disturb rocky bottoms. Collie *et al*. (1997) examined the short-term effects of mobile fishing gear on pebble bottoms on Georges Bank and found that sites disturbed by the fishing gear had less biomass, species richness, and species diversity compared to the undisturbed sites.

CHAPTER THREE

Sandy Habitats

Brian Atkinson

General Description

The Gulf of Maine has a variety of sandy habitats, including dunes, beaches, and sandy subtidal bottoms. In this region, sand is composed primarily of quartz. As in cobble and pebble habitats, the sand particle size strongly influences which species can live in a given place. Small grains pack together tightly, making the sediment less permeable to overlying water and less susceptible to movement by waves. In contrast, coarse sand allows water to percolate downward between grains, bringing dissolved oxygen deeper into the substrate. Coarse sand can also shift more easily. Most burrowing animals can survive only in the upper few centimeters of sand, where they receive an adequate supply of oxygen.

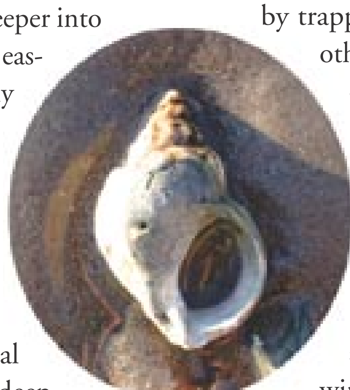
The dynamic nature of sandy habitats affects the abundance and types of species living there. Wave-swept areas host animals that can recover quickly from burial—or avoid burial altogether. Stable, sandy bottoms, such as deep areas that are not disturbed by storm waves, generally host a greater diversity of species than wave-swept sandy habitats.

Dunes

Sand dunes can develop when American beachgrass and other plants trap windblown sand. Many plants and animals inhabit dunes, despite the dryness, salinity, and erosion by waves and wind. Joining beachgrass on dunes are seaside goldenrod, bayberry, beach heather, and beach plum. Vegetation stabilizes dunes and helps them to expand by trapping more sand. Deer, rodents, insects, and other terrestrial animals live in dune habitats. To counteract human effects on dunes, various organizations have conducted re-vegetation and fencing projects.

Beaches

Sand beaches are constantly in motion. Their shape, size, and location shift continually due to wind, waves, and storms. During winter, beaches tend to have a steep profile and



Center: A subtidal whelk, *Buccinum undatum*. Ethan Nedeau

This path over the dunes disrupts the vegetation that helps retain sand. Massachusetts ACEC Program

American beachgrass reduces erosion of dunes. Its roots stabilize the sand, and the plant traps windblown grains. Massachusetts ACEC Program

coarser sand due to stormy conditions that carry fine sand into deeper waters. In summer, beaches flatten and have a broader intertidal zone composed of fine sand deposited by gentler waves. Like dunes, beaches are harsh environments. The highest reaches have few animals except for nesting shorebirds and ghost crabs. At the high tide mark, waves deposit seaweeds and other debris, providing an important source of food and refuge for isopods and amphipods. In turn, shorebirds eat these small crustaceans. Mole crabs, razor clams, and coquina clams inhabit the surf zone, where they filter food and are hunted by shorebirds.

Seaweed washed ashore, called wrack, shelters small invertebrates that are an important source of food for birds, invertebrates, and some terrestrial mammals. Ethan Nedeau

Subtidal Sandy Habitats

In shallow areas, storm-generated waves and currents shape sandy bottoms into ripples and ridges. In deeper water, storms don't affect the bottom topography, but currents can create sand waves or the bottom can be relatively featureless. Few animals live atop the sandy seafloor. Instead, they bury themselves in the sand to avoid predators, currents, and shifting grains. Among these burying species are predatory moon snails, whelks, sand dollars, lady crab, and American sand lance. Camouflage is a common adaptation in this environment of scant hiding places. For example, flounder, gobies, skates, and shrimp have cryptic coloring that makes them difficult to see. Other fish of sandy bottoms include sea robin, Atlantic halibut, and silver hake, which hide among sand ridges to ambush prey (Auster *et al*. 2003).

Distribution

Although sandy beaches and dunes are more common to the south of Cape Cod, they occur in every state and province along the Gulf of Maine coast. Cape Cod is notable for its prominent sandy beaches and dune systems, while subtidal sandy bottoms are prevalent in the nearby waters and on Georges Bank (Poppe *et al*. 1989).

Ecological Functions

Sandy environments tend to have comparatively low biological productivity and species diversity, but they have

Some animals that use sandy habitats are (a) winter flounder, (b) predatory moon snails, (c) silver hake, and (d) squid. Photos a, c, and d: Dann Blackwood and Page Valentine/U.S. Geological Survey. Photo b: Peter Auster

unique species assemblages. Few seaweeds grow in sandy areas because of a lack of solid substrates for attachment. Some filter- and deposit-feeding invertebrates thrive in sandy habitats, and fish hide among the ripples and ridges of subtidal sandy bottoms. Moon snails consume their bivalve prey while buried beneath the sand surface. Dunes provide nesting habitat for some imperiled birds, such as the roseate tern, northern harrier, piping plover, and least tern, and for the threatened diamondback terrapin.

Economic and Recreational Value

Some commercially valuable species such as the surf clam, quahog, winter flounder, summer flounder, and Atlantic halibut associate closely with sandy habitats. Dunes can protect inland areas from storm waves and wind, but human alterations of the shoreline frequently compromise this natural service. Sand beaches and dunes are prized for human recreation. The price of real estate along sandy shores reflects this value.

Management Considerations

Commercial and residential development on sand dunes is the most obvious impact on these habitats. Development along the landward edge of dunes also has negative effects by impeding the normal shifting movements of dunes. Construction of jetties, groins, and seawalls threatens beaches because they disrupt the alongshore currents that regulate the erosion and deposition of sediments. Pavement and other impervious surfaces near beaches can elevate the rate of erosion by promoting overland flow of rainwater. Trampling of dune vegetation by humans and livestock, as well as overgrazing by livestock, can lead to dune destruction. Off-road vehicles tear up beaches and dunes, crush burrowing invertebrates, and disturb nesting animals, including imperiled birds and the diamondback terrapin. Sand compaction by the weight of vehicles can make burrowing difficult or impossible for some animals. On some beaches, people remove large quantities of seaweed and other detritus from the wrack line to “clean up” the beach for recreation or tourism, eliminating a vital source of food and shelter for invertebrates and shorebirds.

Sandy habitats in deep waters incur less impact from human activities. Sandy bottoms probably are more resilient than other seabed habitats to disturbance by trawling and other fishing gear because they generally lack sponges, hydroids, and other organisms that provide biogenic habitat for other species. Nevertheless, scientific studies have shown that trawling changes the species composition and reduces the biomass of non-target species on sandy bottoms of the North Sea and the Grand Banks off Newfoundland (Jennings *et al.* 2001, Prena *et al.* 1999). Sand mining for beach renourishment projects threatens the integrity of subtidal sandy bottoms.

Jetties can cause erosion of beaches by disrupting the currents that transport and deposit sediments along the shore. Ethan Nedeau

CHAPTER FOUR

Muddy Habitats

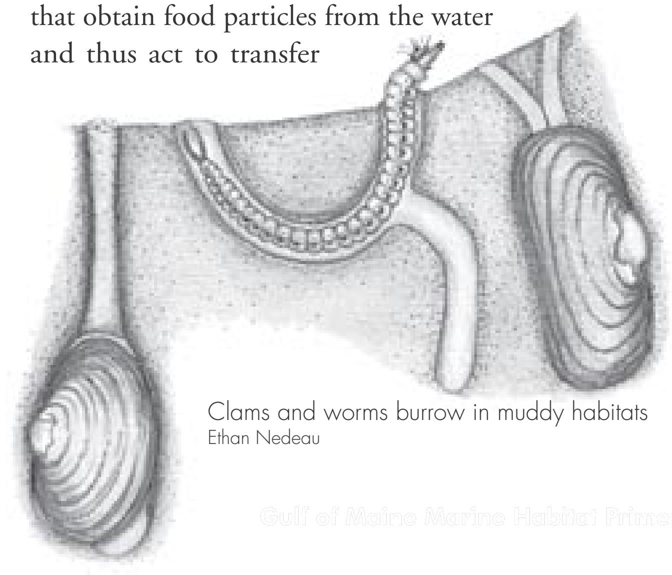
Greg Stott

General Description

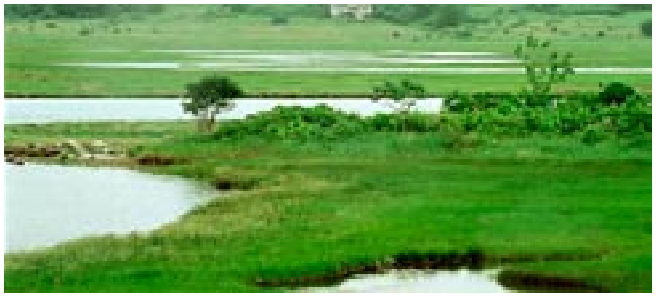
Muddy bottoms are areas of fine sediments that may be unvegetated or patchily covered with green algae and benthic diatoms. These habitats occur in calm, wave-sheltered, depositional environments in both the subtidal and intertidal zone, where they are commonly referred to as tidal flats. Grain size can range from pure silt to mixtures containing clay and sand. The sediments of muddy habitats boast a higher proportion of nutrient-rich, organic-mineral aggregates (detritus) than the sediments in sandy habitats (Whitlatch 1982). From a distance, tidal flats may appear relatively featureless, but they often have small ripples due to wave action and small depressions left by burrowing animals. Subtidal muddy bottoms have more bottom features including pits and mounds left by large burrowing animals, along with sea pens and anemones protruding from the seafloor. The cohesive nature of muddy sediments facilitates burrow construction by many types of invertebrates. Watling (1998) estimates that a thousand species of macroinvertebrates live in muddy habitats of the Gulf of Maine.

Intertidal Muddy Habitats

Tidal mudflats frequently occur next to eelgrass meadows and salt marshes. Many of the invertebrates in mud bottoms live near the mud's surface because oxygen typically becomes scarce within a few centimeters of the sediment surface. To adjust to the harsh, oxygen-deprived conditions, many organisms build and maintain burrows or tubes, while some have adaptations such as siphons or tubes for filter-feeding (Watling 1998). Some of the animals are suspension-feeders that obtain food particles from the water and thus act to transfer

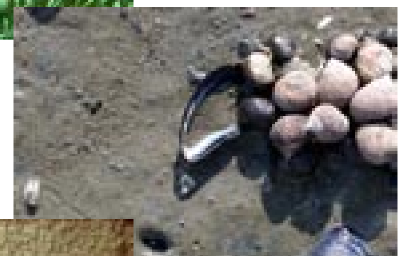


Clams and worms burrow in muddy habitats
Ethan Nedeau



In a tidal marsh, muddy banks and creek beds exposed at low tide (top) are feeding grounds for birds. At high tide (bottom), fish and invertebrates feed there. Peter H. Taylor

Tubes of *Ampelisca* amphipods. U.S. Geological Survey



Snails cluster near mussel shells. Ethan Nedeau

Shrimp in mud. U.S. Geological Survey

energy from the water column to the seafloor. In contrast, deposit-feeders ingest sediments and extract the organic material; this is another mode of feeding in muddy habitats. The tube-dwelling amphipod *Corophium volutator* is a deposit feeder and a filter feeder. Living in extraordinarily high densities in the Bay of Fundy—up to 120,000 per square meter (Hamilton *et al*. 2000)—it is a major food source for migrating birds that stop at mudflats to replenish their energy. Among the migratory birds that forage on tidal flats are the semipalmated sandpiper, least sandpiper, semipalmated plover, red knot, and short-billed dowitcher. Tidal flats are also feeding grounds for fish at high tide.

Subtidal Muddy Habitats

A variety of invertebrates and fish inhabit subtidal mud bottoms. Lugworms bury themselves in the mud, while parchment worms and snake blennies maintain burrows. Other species, including *Cerianthid* anemones and tube-dwelling amphipods, build tubes that protrude above the mud's surface. These tube structures provide shelter for a diverse community of invertebrates and fish such as the Acadian redfish (Auster *et al*. 2004). Mobile animals common on muddy bottoms include brittle stars, spider crabs, American eels, and red hake. In very deep, undisturbed basins, sea pens and other species may live on the muddy seabed (Watling 1998). Commercially important species on subtidal mud bottoms include northern shrimp, *Cancer* crabs, American lobster, and winter flounder.

Distribution

Mud habitats exist in many wave-protected areas along the Gulf of Maine coast, particularly at the heads of bays. The Bay of Fundy is well known for its highly productive tidal flats. In the subtidal zone, large areas of mud occur in deep waters off the coast of Massachusetts, including Cape Cod Bay and north of Georges Bank.

Subtidal muddy habitat with anemones (*Cerianthus borealis*). Mike Strong and Maria-Ines Buzeta.

Low tide exposes mud flats next to a tidal creek and salt marsh. Ethan Nedeau

Ecological Functions

Tidal flats are less biologically productive than salt marshes (Whitlatch 1982), but their role in the conversion of primary production (plant material) to secondary production (prey) is nonetheless a valuable ecosystem function. Mussels, clams, and other filter feeders provide a vital link between water column and seabed habitats by feeding on plankton and other waterborne particles. These consumers, in turn, are prey for animals higher in the food web.

Tidal flats are noteworthy for their value as shorebird feeding grounds. The high densities of crustacean and molluscan prey in tidal flats support vast numbers of shorebirds during migration. The piping plover, which is listed as federally endangered in the United States and Canada, and many herons and ducks look for food on tidal flats. Terrestrial mammals such as foxes and raccoons forage on mud flats at low tide (Lehihan and Micheli 2001).

Muddy habitats provide a home for many bottom-dwelling animals. Burrowers such as clams, crustaceans, and worms facilitate nutrient cycling in the seabed, and their burrowing helps to prevent the upper layer of sediments from becoming oxygen deprived, which benefits other mud-dwelling organisms. The fecal pellets produced by some inhabitants change the sediment grain size and stabilize the sediments. Species that live atop the soft sediments include mussels, horseshoe crabs, mud snails, skates, and flatfish. Spider crabs, horseshoe crabs, and polychaete worms gather in large numbers on muddy bottoms to spawn.

A clam digger on a tidal flat. Bob Semple

Semipalmated sandpipers and other shorebirds feed on the rich intertidal flats of the upper Bay of Fundy. Shirley Sloat

Economic and Recreational Value

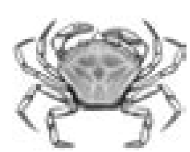
Intertidal mud flats are biologically productive environments that support important recreational and commercial fisheries for softshell clams, jackknife clams, quahogs, bloodworms, and sandworms (Roman *et al*. 2000). Muddy habitats play a role in sustaining the valuable fishery for winter flounder (Whitlatch 1982), as they are prime feeding grounds for these fish. Seasonal aggregations of migrating birds draw flocks of birdwatchers to mud flats.

Management Considerations

Because muddy habitats are located in areas where waves and currents are weak, they are especially susceptible to pollution. Calm waters allow contaminants to settle onto the bottom, rather than being swept away. Toxic chemicals and other hazardous substances deposited in mud bottoms tend to remain there. Excessive inputs of nutrients, especially nitrogen, from agriculture, sewage disposal, and other human sources can lead to population explosions of algae on mud bottoms. When the algae die, the decomposition leads to oxygen-deprived conditions that may harm animals and plants living in the mud or on its surface.

Like salt marshes, many tidal flats historically were filled for residential and commercial development. Disposal of dredged materials onto intertidal and subtidal mud bottoms can also dramatically alter the habitat. Construction of jetties and other structures to stabilize the shoreline can lead to erosion or excessive sedimentation of tidal flats because natural sediment transport processes are interrupted. Trawls and other fishing gear can resuspend sediments in the water, smothering sessile organisms, which cannot escape to clearer waters. Fishing gear also disturbs the organisms that live on the sediment surface, removing them and destroying the biogenic habitat that these species provide for smaller organisms.

Non-native species and aquaculture can have major effects on muddy habitats. For example, the European green crab, which is well established in the Gulf of Maine, can drastically reduce the abundance of soft-shell clams on tidal flats. In certain cases, shellfish aquaculture on tidal flats can result in decreased densities of non-target species and compromised foraging by birds and fish.



Green crab
Ethan Nedeau

CHAPTER FIVE

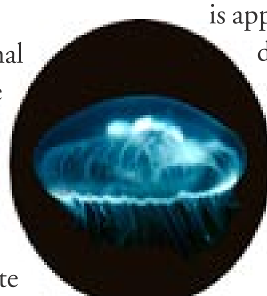
Water Column

Whales are the largest inhabitants of the water column. Communications New Brunswick

General Description

The liquid realm between the seafloor and the sea surface is referred to generically as the water column. All of the estuarine and marine waters in the Gulf of Maine are part of the water column. While the previous marine habitats discussed in this primer were categorized according to the substrate type—rock, sand, mud—the water column is characterized by a lack of solid substrate.

The water column is a dynamic, three-dimensional environment with distinct layers, which can be considered habitats unto themselves. Water masses with different temperature, salinity, and density exist within and among the depth zones. Organisms living in the water column are closely attuned to physical conditions, and many migrate vertically to stay in favorable conditions.

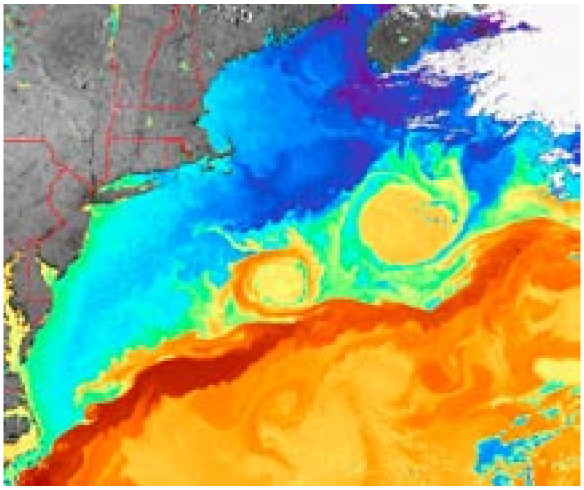


Center: A moon jelly drifts in the water column. U.S. Geological Survey

The top layer, called the photic zone, extends from the sea surface to the depth at which sunlight ceases to penetrate. The depth of the photic zone varies from place to place and over time depending on water clarity. Phytoplankton live in the photic zone and provide most of the water column's primary productivity. Through the food web, this productivity supports animals that live at greater depths.

In the ocean, the mesopelagic zone extends from the bottom of the photic zone to depths of a thousand meters, although it is truncated in the Gulf of Maine, where the deepest water is approximately five hundred meters. The food web in deep waters is fueled by the primary productivity of the photic zone. For example, some mesopelagic animals migrate upward to feed in the rich surface waters at night to avoid predators. During the day, they return to deeper, darker waters, where predators cannot see them. Other species consume organic particles, such as feces and dead plankton, that sink down from the photic zone.

Many factors influence the biological productivity of the water column. For example, the topography of underwater



This satellite image shows two warm-core rings (orange circles) spinning off the Gulf Stream (red and dark orange) near the Gulf of Maine.

Source: http://gulf.ocean.fsu.edy/~sturges/OCP5050/Gulf_Stream_Eddy_june11.gif

banks and ledges forces cold, nutrient-rich, deep currents toward the sea surface, fueling growth of phytoplankton. This upwelling supports abundant fish and other animals.

The boundary of two adjacent water masses, called a front, can affect the productivity of the water column by stimulating vertical mixing. One example of a front is the boundary between the warm, saline waters of the Gulf Stream and the colder, less saline waters of the Gulf of Maine, which shows up clearly in satellite images. The oceanographic environment may change dramatically over a short distance across a front and influence the types of animals and phytoplankton living in the water column. The location of some fronts move over time, while others are relatively stable.

Organisms living in the water column display an extraordinary range of body sizes and lifestyles. Ultraplankton such as bacteria and phytoplankton measure only 0.005 millimeter in diameter, while some whales are tens of meters. Holoplankton spend their entire lives drifting in the water column, while meroplankton drift for only part of their lives, often concentrated near shore or over shallow banks far offshore. Most meroplankton are fish and invertebrate larvae that eventually transform into larger swimming or sedentary adults. Plankton feature many adaptations to keep them afloat. Copepods, for example, are tiny crustaceans with long spines or feathery appendages that increase their surface-area-to-volume ratio, while the Portuguese man-of-war has gas-filled floats. Large gelatinous creatures such as jellies (commonly known as jellyfish) and ctenophores (comb jellies) are uniquely adapted to life in the water column, and they are consumed by sea turtles.

Distribution

The water column represents the most widespread habitat in the Gulf of Maine, extending from the intertidal zone to the open ocean.

Ecological Functions

Water column habitats in the Gulf of Maine are highly productive. Upwelling areas are notable for having especially high primary productivity stimulated by the mixing of nutrients from the bottom waters. One byproduct of the productivity is oxygen: Approximately 70 percent of oxygen in the atmosphere comes from photosynthesis of marine phytoplankton. The fronts that occur at boundaries of different water masses host abundant zooplankton that attract dense aggregations of pelagic fish such as Atlantic sea herring

A school of pollock (*Pollachius virens*) swims in the water column. Right: A comb jelly, or ctenophore, feeds on plankton.

Fish: Mike Strong and Maria-Ines Buzeta. Ctenophore: NOAA Photo Library and mackerel. In turn, larger fish, mammals, and birds such as storm petrels and shearwaters feed on the schools of fish.

The water column serves as the nursery habitat for most bottom-dwelling species—ranging from seaweeds to barnacles to sea urchins—because they spend their early lives drifting with the ocean currents. A variety of imperiled species live in the Gulf of Maine's water column habitats. The endangered northern right whale lingers in Cape Cod Bay during spring, feeding on copepods, and then travels north to the Bay of Fundy in summer. The leatherback turtle, known for its unusual habit of eating jellies as a major part of its diet, inhabits the southern Gulf of Maine.

Economic and Recreational Value

Throughout history, the economies of coastal towns have depended on fishing and other industries tied to the open waters of the Gulf of Maine. Because many marine species, including numerous commercially fished species, spend their whole life or a portion of their life cycle in the water column, this habitat type has enormous economic value. Many species such as squid, Atlantic sea herring, mackerel, bluefish, swordfish, bluefin tuna, and mako sharks live in the Gulf of Maine's water column. Clams, sea urchins, mussels, lobsters, and other bottom-dwelling invertebrates begin life as tiny larvae that drift in the water column. Filter feeders such as clams and mussels rely on the water column as a source of food after they settle onto the seafloor. Aquaculture in embayments and the open ocean is an increasingly valuable industry. Sport fishing for pelagic species such as tuna is also an important recreational activity.

Management Considerations

Nutrients, especially nitrogen and phosphorus, strongly influence the ecological condition of the water column. Excessive nutrients can lead to algal blooms and eutrophication, which occurs when the abundant, uneaten phytoplankton die and sink. Their decomposition results in oxygen-deprived water that harms animals of the water column and the seabed. Therefore, eutrophication affects both habitats. In the Gulf of Maine, sewage outfalls from some municipalities are located close to shore, which may raise the potential for eutrophication because of low dissipation of nutrients. Land use can affect water quality through runoff of nutrients, sediment, and toxic contaminants. Excessive sediment and other particulate material in the water column blocks light penetration, reducing primary productivity in the photic zone. Non-point source pollution from the uplands also affects water column habitats when toxic contaminants are transported to marine waters in runoff.

Harmful algal blooms, commonly known as red tides, are outbreaks of toxic plankton in the water. They are becoming more frequent and widespread along the world's coastlines. Toxic dinoflagellates (*Alexandrium* sp.) can accumulate in shellfish and cause paralytic shellfish poisoning in people who consume shellfish with high toxin concentrations. In the southeastern United States, beaches sometimes are closed because wind-borne toxins from certain red tides cause human respiratory problems and irritation of the nose, throat, and eyes.

Two important management considerations in water column habitats are overfishing and climate change. Overfishing may strongly influence the species in the water column. For example, dramatic increases in jellies in coastal waters may be linked to depleted fish stocks that would compete with jellies by feeding on zooplankton (Mills 2001). Climate change might alter circulation patterns, winds, and temperatures in the Gulf of Maine. Shifts in predominant winds could lead to the relocation or cessation of localized upwelling. Changes in the direction or strength of currents could affect the mixing of distinct water masses, leading to changes in nutrient supply and productivity in the water column.

Fishermen trawl for pollock and other fish. NOAA Photo Library