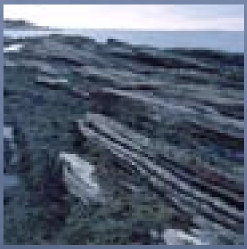
Gulf *of* Maine

Marine Habitat Primer



Gulf of Maine Council on the Marine Environment

Gulf *of* Maine

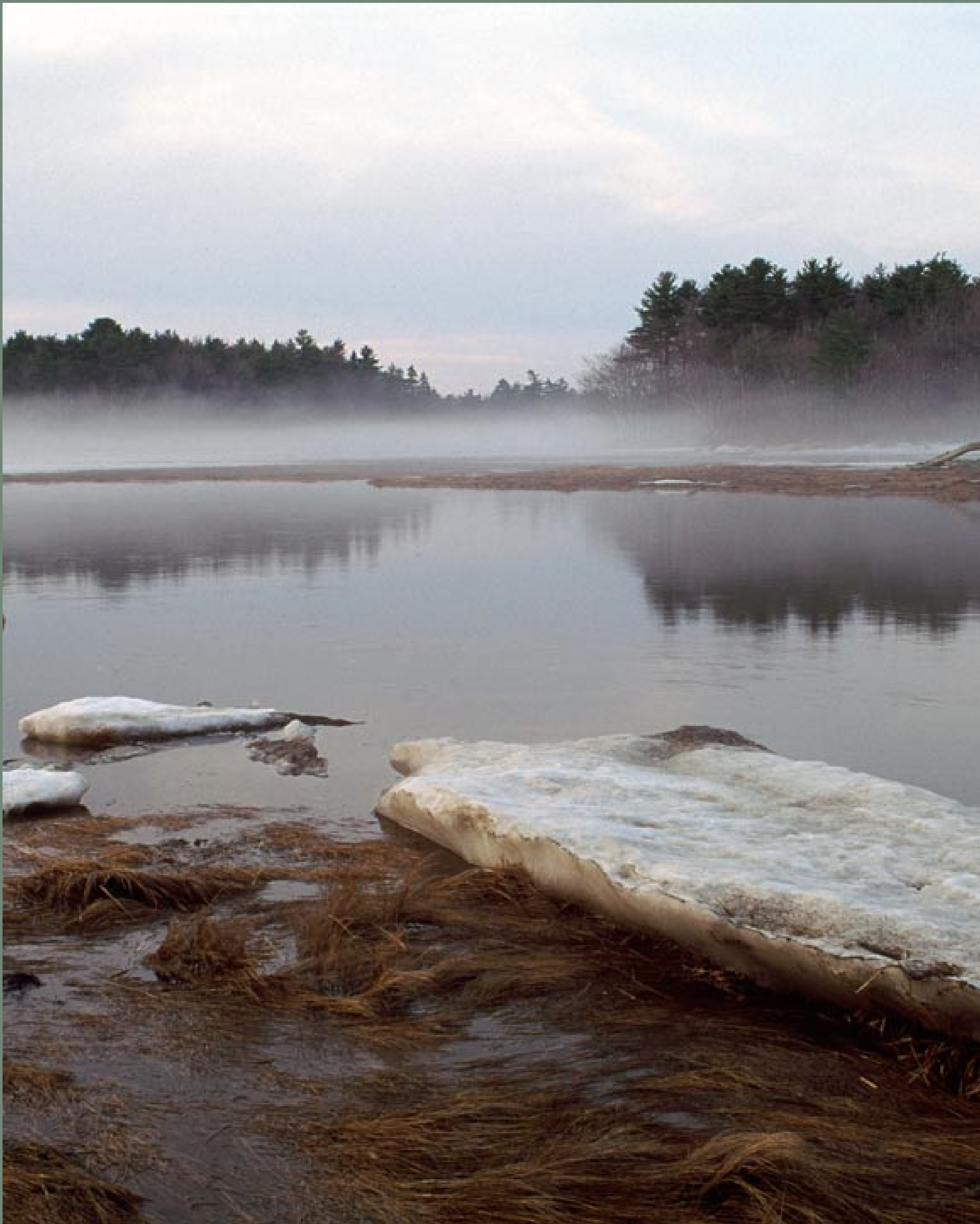
Marine Habitat Primer

Gulf of Maine Council on the Marine Environment
Habitat Conservation Subcommittee

Gulf of Maine Council Mission

"To maintain and enhance environmental quality in the Gulf of Maine and to allow for sustainable resource use by existing and future generations."

Gulf of Maine Council on the Marine Environment



Peter H. Taylor

Preface

The Gulf of Maine contains diverse habitats that are affected by many human activities. The *Gulf of Maine Marine Habitat Primer* is intended for everyone interested in learning more about the region's coastal and offshore habitats, especially resource managers and other coastal decision-makers in government and non-government organizations. A foundation of information regarding habitat types and their ecological relationships is essential for advancing ecosystem-based management and conservation.

The *Gulf of Maine Marine Habitat Primer* provides an overview of habitat characteristics, ecological functions, economic and recreational values, and management considerations. The *Primer*:

- enhances understanding of marine habitats in the Gulf of Maine;
- provides background needed to make more informed decisions on human uses, management, and conservation; and
- provides an initial step toward habitat conservation strategies for the Gulf of Maine developed in partnership with organizations around the Gulf.

The Habitat Conservation Subcommittee of the Gulf of Maine Council on the Marine Environment is working with partners in the region to develop and advance marine habitat conservation strategies. This primer is the first part of a process to determine: 1) habitat types and their ecological relationships, 2) activities impacting marine habitats, 3) the state of the science in understanding these impacts, and 4) management options for addressing the impacts. The project will culminate in Gulf of Maine marine habitat conservation strategies with findings and recommendations regarding science, policy, and management approaches.

Acknowledgments

The Gulf of Maine Council thanks the following organizations for financial support to print the *Gulf of Maine Marine Habitat Primer.*

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Massachusetts Office of Coastal Zone Management

Woods Hole Oceanographic Institution Sea Grant

Maine Coastal Program

Gulf of Maine Council on the Marine Environment

The Gulf of Maine Council (GOMC) thanks the many people who were involved in the preparation of this report. The author, Megan Tyrrell, wrote this document while working on a NOAA fellowship at the Massachusetts Office of Coastal Zone Management (CZM). Her knowledge of marine environments and effort to make the document factual and well-written as well as CZM's support of the project were invaluable contributions. GOMC also thanks members of its Habitat Conservation Subcommittee who volunteered to provide comments on the document. Subcommittee co-chairs Katie Lund and Marianne Janowicz served as project managers. In addition, a Scientific Advisory Panel reviewed portions or all of this report, provided figures and photographs, and engaged in helpful discussions. Finally, thanks to Peter Taylor and Ethan Nedeau, GOMC Science Translators, for their tireless work to edit, design, and provide layout for the Primer.

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Gulf of Maine Council on the Marine Environment
Science Translation Project
The Science Translation Project provides scientific information to state, provincial, and federal decision-makers to advance ecosystem-based management in the Gulf of Maine and its watershed. The project is supported by the National Oceanic and Atmospheric Administration (NOAA), Cooperative Institute for Coastal and Estuarine Environmental Technology (CICEET), Maine State Planning Office, Massachusetts Office of Coastal Zone Management, New Hampshire Coastal Program, Maine Sea Grant, Woods Hole Oceanographic Institution Sea Grant, and Environment Canada.

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To download a pdf copy of the *Marine Habitat Primer*, request printed copies, or become involved in development of Gulfwide habitat conservation strategies, go to www.gulfofmaine.org/habitatprimer.

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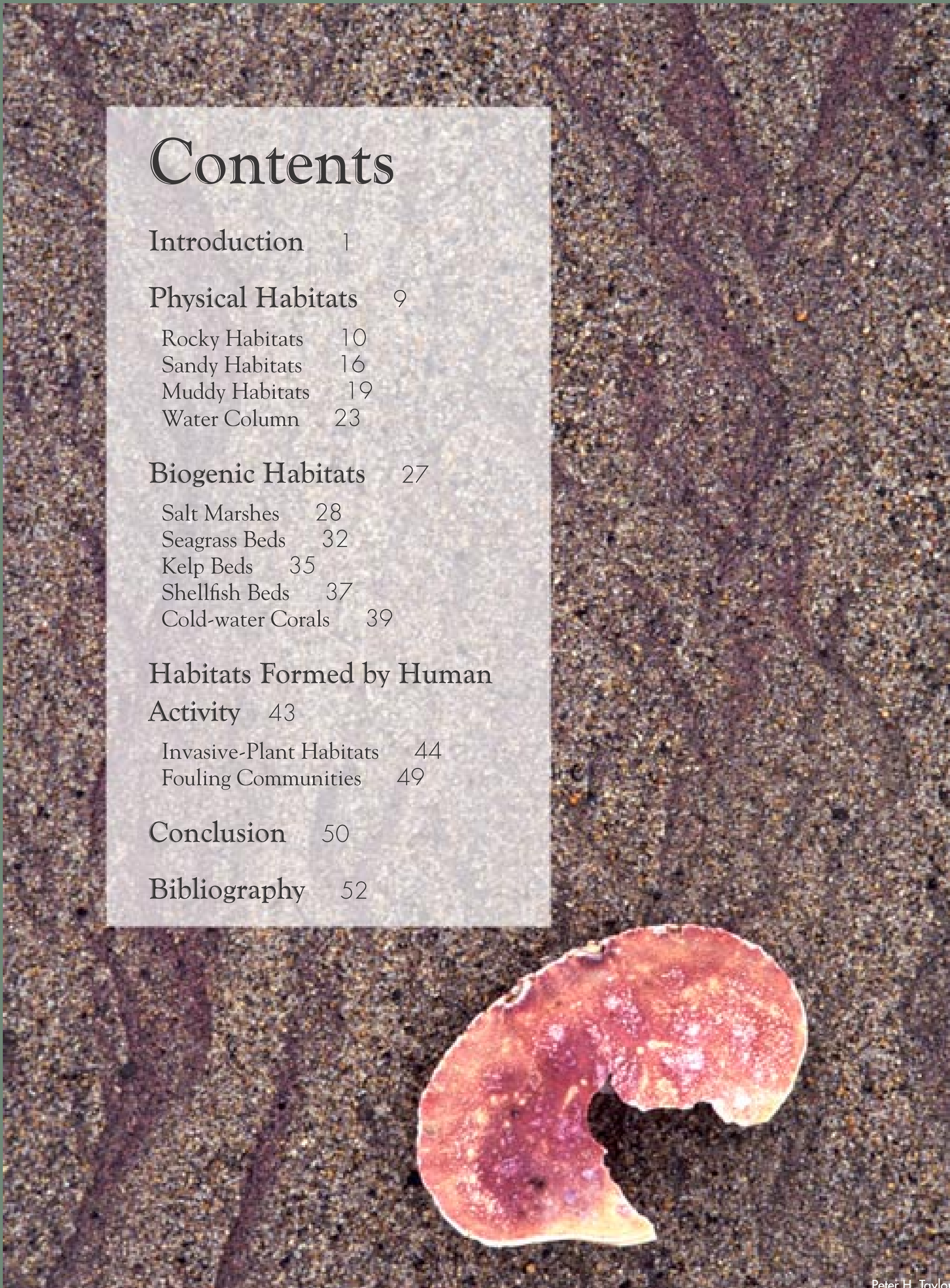
Cover photos: Fog and water background, sand ripples: Ethan Nedeau. Salt marsh pool, rocky shore: Peter H. Taylor. *Boltenia* tunicates and fish: Mike Strong and Maria-Ines Buzeta.

Contents



Peter H. Taylor


Ethan Nedeau

CHAPTER ONE

Introduction

Peter H. Taylor

Bordered by the northeastern United States and the Canadian Maritime Provinces, the Gulf of Maine is a semi-enclosed sea that is renowned as one of the world's richest marine ecosystems. Along the western and northern shores of the Gulf of Maine lie the cities, towns, and watersheds of coastal Massachusetts, New Hampshire, Maine, New Brunswick, and Nova Scotia, while the legendary fishing grounds of Georges Bank mark the southern and eastern boundary.

Salt marshes, seagrass beds, tidal mud flats, underwater rocky outcrops, kelp beds, and other marine and estuarine habitats are building blocks of the Gulf of Maine ecosystem. These habitats provide homes for the animals, plants, and microbes that inhabit the coastal and offshore waters, depending on each other and the environment for food, shelter, and the other necessities of life. Intact marine habitats in the Gulf of Maine support productive fisheries and serve a host of other functions such as cycling nutrients, filtering pollution, trapping sediments, storing carbon, buffering upland areas from storm damage, and providing recreation opportunities.

Tracy Hart/Maine Sea Grant

The Gulf of Maine has supported a long tradition of fishing, marine transportation, coastal development, and recreation, and these human activities have affected habitat integrity. Effective management and regulation is imperative for the continued functioning of the ecosystem and economic prosperity of the region, particularly given the growing variety and intensity of human uses. Existing and proposed uses of Gulf of Maine habitats include aquaculture, wind farms, fishing, sand mining, pipelines, cables, docks, piers, sewage outfalls, and discharge of pollutants—all of which can alter the natural functions of habitats.

Consequently, managing the natural resources of the Gulf of Maine and its coastline—whether at a municipal, state, provincial, regional, or federal level—requires a broad understanding of habitat types, distributions, ecological functions, and the potential human effects on habitat. This document introduces information about the Gulf of Maine's coastal and offshore habitats for coastal decision-makers involved in reviewing projects, siting special management areas, developing regulations and resource management plans, and targeting habitat restoration efforts.

Overview of Habitat Types

Some of the Gulf of Maine's habitats are relatively well known, and scientific understanding of them has expanded in recent years. Other habitats such as cold-water corals have only recently been explored. In this primer, habitats are categorized based on **substrate type and sediment grain size**, **water depth**, and presence of structure-forming plants and animals that create **biogenic habitat**. Each of these characteristics occurs along a continuum: small to large sediment grain size, shallow to deep water, and sparse to abundant habitat-forming species. As a result, the variety of habitats is nearly infinite, and any categorization system for habitat types is somewhat arbitrary. This primer categorizes Gulf of Maine habitats into twenty types according to substrate, depth, and biogenic structure.

Substrate type and sediment grain size have a strong influence on the types of plants and animals that can inhabit a given place. Substrates and sediment sizes range from tiny mud particles to fine sand to coarse sand to pebbles to cobbles to boulders to solid rock outcrop. To live on a hard substrate, animals and plants attach themselves to surfaces or dwell in crevices. To inhabit soft sediments, many animals burrow into the seafloor. Geologic history and oceanographic conditions determine the type of substrate in a given place. For example, muddy tidal flats tend to occur in sheltered embayments with weak currents and little wave action. These conditions allow fine mud particles to settle from the water and accumulate on the bottom. In turn, muddy bottoms tend to be oxygen-poor because the small particle size limits water flow through the sediment, meaning that species must be capable of tolerating oxygen-poor conditions or pumping oxygenated water into burrows.

Water depth also influences the types of species that inhabit a particular location. For example, animals and plants that live in the intertidal zone must endure exposure during low tide. Shallow waters tend to have more sunlight than deeper waters because of the attenuation of sunlight with depth. Seaweed and seagrass require sunlight for photosynthesis and can grow only in relatively clear, shallow water, not on

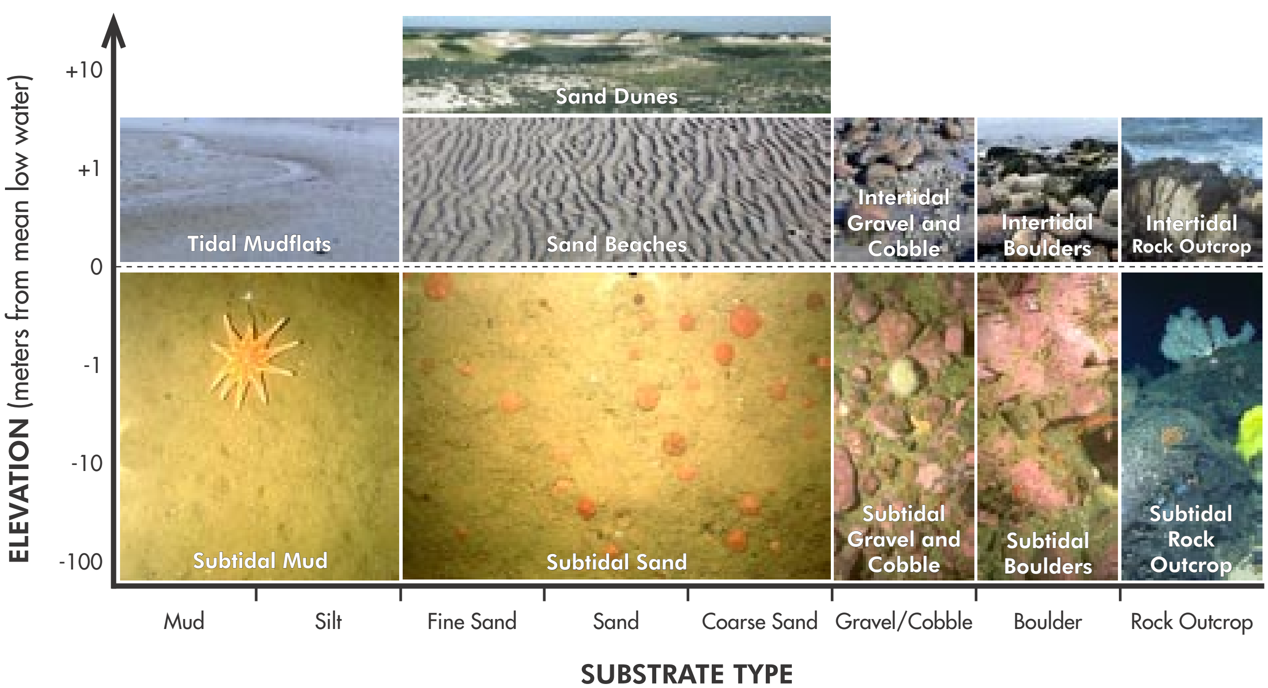


Figure 1. The distribution of physically defined habitats according to substrate type and elevation from mean low water. Sand dunes are formed primarily by wind and therefore extend above the intertidal zone into the supralittoral zone.
Figure concept: David Burdick, University of New Hampshire. Design: Ethan Nedeau.

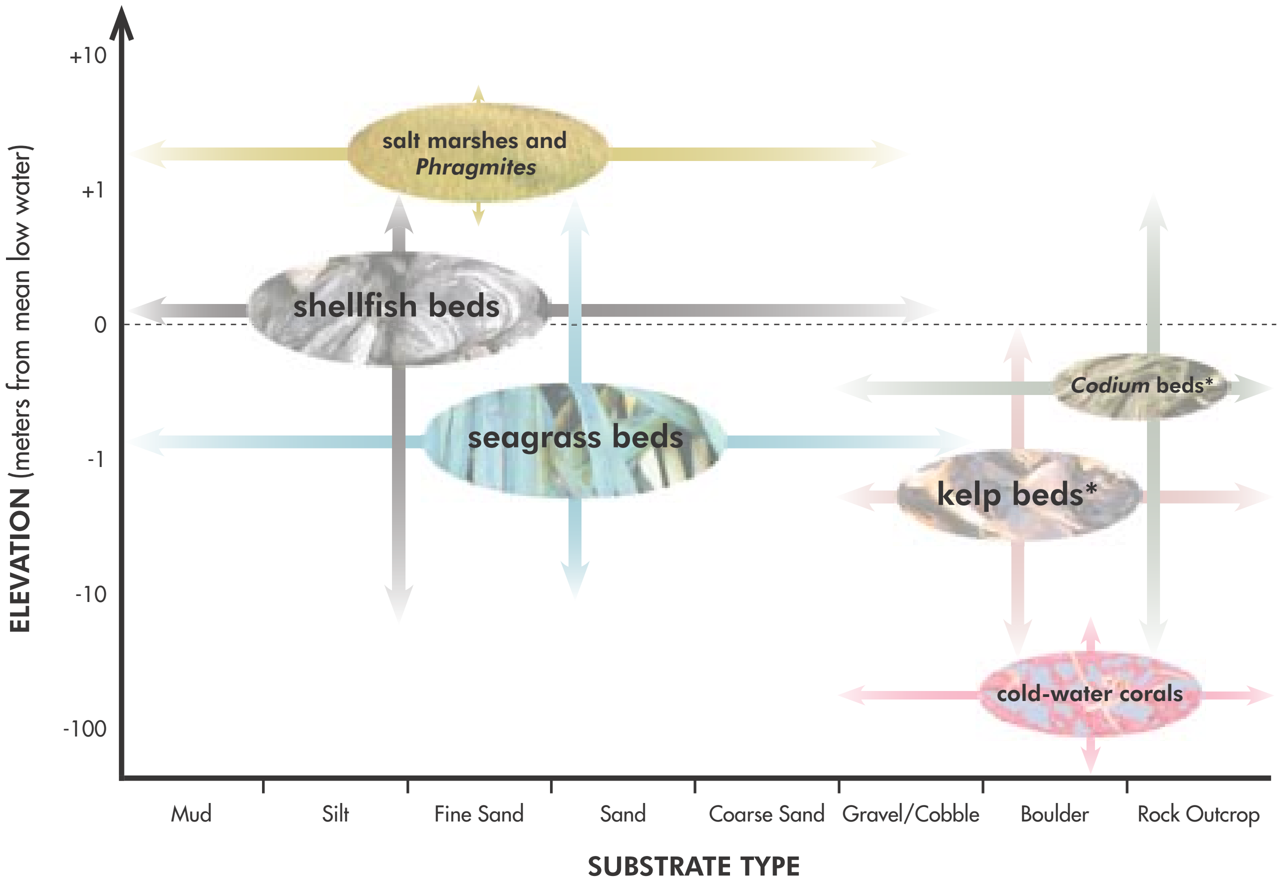


Figure 2. The distribution of biogenic habitats according to substrate type and elevation from mean low water. Depth distributions, particularly for lower depth limits, are approximate. * *Codium* and kelp can attach to a wide variety of substrates, including shellfish that occur in soft sediments, but neither algal species forms beds in soft sediments.
Figure concept: David Burdick, University of New Hampshire. Design: Ethan Nedeau.

the deep seafloor. Because seaweed beds serve as habitat for many animals and plants, it can be useful from an ecological perspective to define the lower limit of seaweed presence as the transition between shallow and deep habitats.

Biogenic habitats such as seaweed beds, seagrass beds, salt marshes, mussel beds, and cold-water coral thickets are distinguished by high densities of structure-forming species that substantially modify the physical environment and consequently host a distinct ecological community. Kelp beds, for example, are like undersea forests formed by the long blades of kelp that provide shelter and food for fish, lobsters, and other organisms. Typically, a structure-forming species must occur in great abundance to modify the environment enough to qualify as a distinct biogenic habitat. For example, a large, dense oyster reef provides hiding places for fish and invertebrates and slows the currents, which promotes the deposition of sediments. However, sparse oysters do not provide useful hiding places or substantially slow the currents, so they do not function as biogenic habitat. For similar reasons, small, isolated clumps of seagrass do not provide the same biogenic habitat value as dense, extensive seagrass beds. In some cases, the plants and animals of a biogenic habitat help to maintain the habitat type, such as when salt marshes accumulate sediment to match the rate of sea-level rise.

Habitat Complexity and Species Diversity

In general, habitats with more structural complexity, such as seagrass beds or cobble bottoms, support a greater diversity of species than relatively simple habitats, such as muddy or sandy bottoms. Each habitat has a different assemblage of species, so animals and plants found in a seagrass bed may not survive if that bed is transformed into a mudflat. Even habitats characterized by soft sediments can vary in their complexity. Waves and currents, for example, can shape the topography of a sandy bottom into ripples and ridges where fish hide to ambush prey. Similarly, some amphipods and other animals build tubes of sediment on the seafloor, creating structures among which other animals find shelter.

Glaciers up to one mile thick covered the Gulf of Maine region thousands of years ago, not unlike those seen today in Greenland, Alaska, and northern Canada.
NOAA Photo Library

Habitats Are Interconnected

Habitats of the Gulf of Maine do not exist in isolation. Myriad ecological relationships and oceanographic processes link them, and each habitat functions as part of the larger Gulf of Maine landscape. The movement of water plays a major role in the interconnection of habitats by transporting nutrients, food, larvae, sediments, and pollutants among them. Many marine species rely on different habitats in different parts of their life cycle. For example, lobsters begin life as larvae that drift in the water before settling onto the seafloor. Larval habitat is the top few meters of the water column, but juvenile habitat is a pebble or cobble seabed, where they can hide from predators. As adults, lobsters move into open habitats, such as sandy bottom or rocky outcrop, because large adults are less vulnerable to predators. The ecological linkages among marine habitats are unlike terrestrial habitats, and present a special challenge for resource managers and policy makers who must consider the Gulf of Maine ecosystem as a regional, interconnected system.

Regional Setting: The Gulf of Maine

Geologic History

The Gulf of Maine is within the cold-temperate Acadian biogeographic province. Although this province has relatively low species diversity, many of its species occur nowhere else. Glaciers scoured the Gulf of Maine 10,000 to 20,000 years ago, helping shape the wide variety of marine and estuarine habitats. During the last ice age, glaciers extended as far south as Cape Cod. Along the way, the ice sheets sculpted the bedrock and created the indented, rocky coast that characterizes much of the Gulf of Maine. The glaciers deposited huge quantities of sediment at Cape Cod to form extensive dunes, beaches, and sandy bottoms.

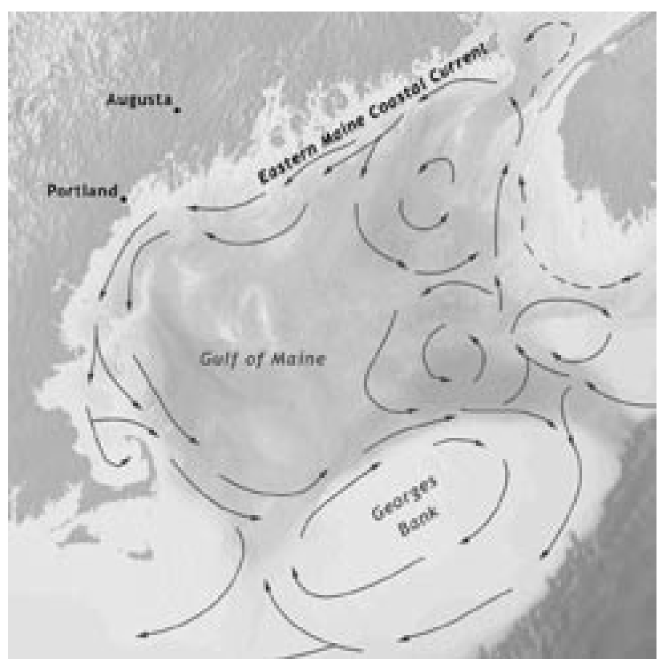
Physical Oceanography

Water in the Gulf of Maine generally flows counterclockwise with coastal currents sweeping from northeast to southwest from New Brunswick to Massachusetts. The deep Labrador Current dominates the oceanography of the Gulf of Maine and helps to drive the counterclockwise circulation. Its frigid waters enter the Gulf of Maine through the Northeast Channel to the south of Nova Scotia, after flowing southward along Nova Scotia's Atlantic Coast. The water exits the Gulf approximately three months later at the Great South Channel near Cape Cod. Warmer waters from the Gulf Stream sometimes enter the Gulf of Maine when eddies called warm-core rings spin off from that major current, carrying subtropical fish and other animals.

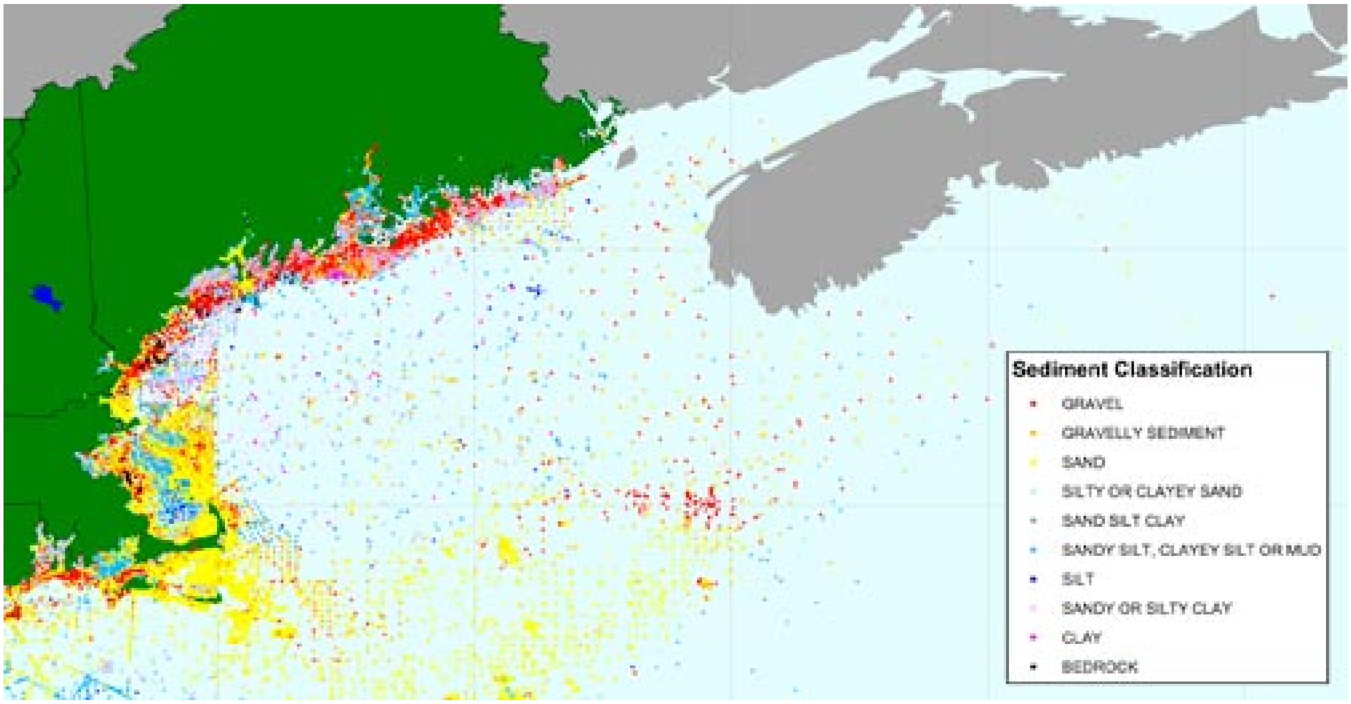
The Gulf of Maine's tidal range is relatively large. Strong tidal currents keep waters well mixed, increasing the availability of nutrients and fueling the ecosystem's biological productivity. In the northern reaches of the Gulf of Maine, the Bay of Fundy experiences the world's biggest tides.

Substrates: Rock, Sand, Mud

The Gulf of Maine has a wide variety of substrate types. Mud and sand accumulate in depositional areas such as



Direction of ocean currents in the Gulf of Maine.
Map by Chris Brehme. Redrawn from map by Neal R. Pettigrew.

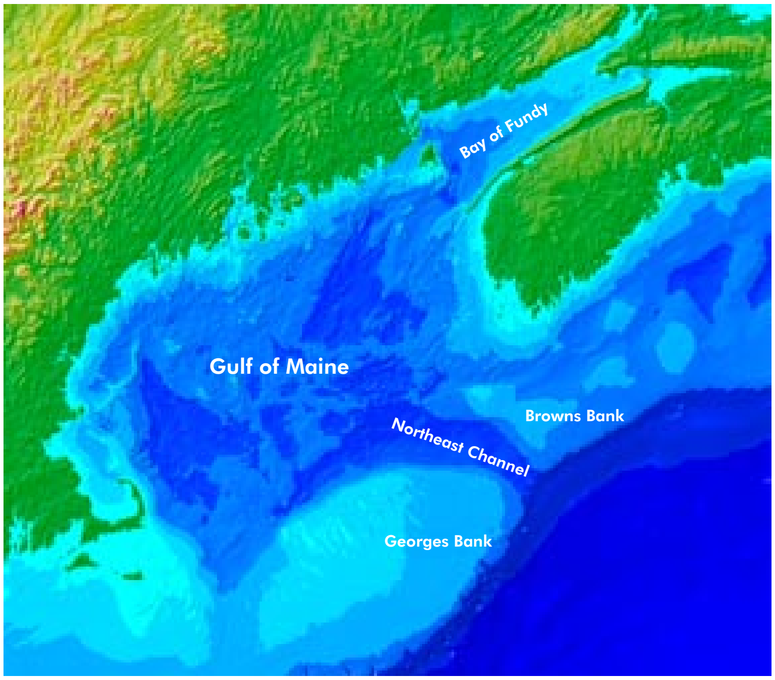


Distribution of sediments and bedrock in the Gulf of Maine. Source: U.S. Geological Survey

sheltered bays and deep offshore basins, which are common along subsiding coastlines such as North America's east coast. Solid rock outcrops, boulder fields, and cobble and pebble bottoms occur in places where fast currents or strong waves erode the finer sediments. The geographic pattern of substrate types in the Gulf of Maine ranges from soft sandstones and mud flats at the head of the Bay of Fundy to hard granite and basalt on the western shores of the Bay of Fundy into Maine, New Hampshire, and Massachusetts. At the southern edge of the Gulf of Maine, Cape Cod has glacial deposits of sand and gravel, and no bedrock. Within this broad geographic pattern, however, lies a mosaic of other substrate types, such as sandy pocket beaches along Maine's rocky coast.

Geographic Features

When glaciers scoured the region, they carved basins, channels, and banks. Banks, such as Georges Bank, are relatively shallow areas with a foundation of rock that resisted erosion. Basins are deep, depositional environments usually with muddy or sandy bottoms. Stellwagen Bank National Marine Sanctuary in Massachusetts Bay features a great variety of habitat types on top of banks, along their steeply sloped sides, and in basins. Similarly, the West Isles area between Maine and New Brunswick in the Bay of Fundy has steep zones, boulders, and ledges among areas of soft sediment. Complex topography, large tides, and tidal streams around the small islands result in high diversity of habitat types. Channels between banks allow deep, nutrient-rich water to circulate among basins. The Northeast Channel that separates Brown Bank and Georges Bank allows deep ocean water to move into the Gulf of Maine.



Geographic features, including basins (deep blue) and shallow banks (light blue), of the Gulf of Maine seafloor. USGS-Woods Hole Field Center

HABITAT CONSERVATION IS UNDERWAY

Many marine habitat conservation efforts have been implemented around the Gulf of Maine to address management concerns, as the following examples indicate. To facilitate a coordinated, regional approach, the Gulf of Maine Council on the Marine Environment is working with organizations to develop a habitat conservation strategy. One product is an inventory of habitat conservation tools and efforts.

To download the complete inventory and obtain more information about developing the strategy, visit:
www.gulfofmaine.org/habitatconservation

Examples of Habitat Conservation Efforts

Atlantic Reference Centre

Sponsored by the Huntsman Marine Science Center in St. Andrews, New Brunswick, and the Canadian Department of Fisheries and Oceans, the Atlantic Reference Centre has an extensive collection of marine life; conducts research in marine taxonomy, biodiversity, and ecology; and provides information for the Gulf of Maine Biogeographic Information System.
Web site: www.huntsmanmarine.ca/arc

Bay Area Management and Aquaculture Leases

New Brunswick has an aquaculture site allocation policy to ensure that aquaculture development is conducted in an environmentally-sustainable manner. A task force in Maine is investigating how to balance the range of potential uses of state waters and accommodate the growth of marine aquaculture, while considering scientific data, constraints, and opportunities.
Web site: www.state.me.us/dmr/aquaculture/aqtaskforce/aqtfhomepage.htm

Bay of Fundy Ecosystem Partnership

The Bay of Fundy Ecosystem Partnership, a virtual institute, is an inclusive, flexible, and multidimensional organization for encouraging communication and cooperation among all individuals and groups interested in the Bay of Fundy. It achieves on-the-ground progress through various working groups, focusing on topics such as *Corophium* as a keystone species, Minas Basin integrated management, salt marshes and restricted tidal systems, sublittoral ecology and habitat conservation, and communications.
Web site: www.bofep.org

Conservation Law Foundation (CLF) and WWF Canada Marine Conservation Project

A habitat-mapping project for the Gulf of Maine and Scotian Shelf is being conducted by the Conservation Law Foundation and World Wildlife Fund Canada. The project is using physical and biological data to determine priority areas for conservation.
Web site: www.wildsea.org

Cooperative Research Partners Initiative (CRPI)

The National Marine Fisheries Service is partnering with the New England Fisheries Management Council to produce better scientific information for fishery management decisions and to facilitate communication and collaboration among New England's commercial fishermen, marine scientists, and fishery managers.
Web site: http://coopresearch.nero.noaa.gov

Gulf of Maine Census of Marine Life (CoML)

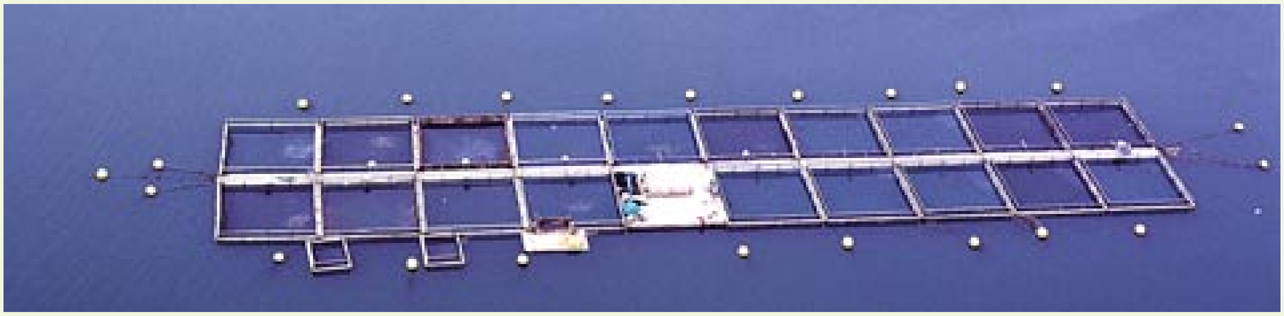
CoML is a global network of researchers in more than 45 nations engaged in a ten-year initiative to assess and explain the diversity, distribution, and abundance of marine life. Synthesis of this knowledge is intended to inform management decisions and improve predictions of change in species numbers and abundance over time.
Web site: www.usm.maine.edu/gulfofmaine-census

Gulf of Maine Council Habitat Restoration Strategy

The Council's Habitat Restoration Subcommittee developed a strategy that identifies important coastal habitat types in the Gulf, makes recommendations for enhancing restoration, provides background information on restoration techniques, and identifies regionally significant projects in states and provinces around the Gulf.
Web site: www.gulfofmaine.org/habitatrestoration

Gulf of Maine Mapping Initiative (GOMMI)

The Gulf of Maine Mapping Initiative is a multi-year project to map the entire sea floor of the Gulf of Maine. The maps will inform and improve decision-making



Aquaculture pens in New Brunswick Gilles Daigle

for management of ocean resources.
Web site: www.gulfofmaine.org/gommi

Gulf of Maine Ocean Observing System (GoMOOS)

GoMOOS is a national pilot program that conducts routine monitoring on weather and oceanographic conditions in the Gulf of Maine through a system of buoys and monitoring stations. The data function as a baseline for ocean parameters from which human-induced impacts and natural changes in the marine environment can be gauged.
Web site: www.gomoos.org

Gulfwatch

Gulfwatch is a chemical-contaminants monitoring program administered by the Gulf of Maine Council on the Marine Environment. Conducted and coordinated by scientists and managers from universities and agencies around the Gulf of Maine, the program uses blue mussels as indicators of habitat exposure to pollutants in coastal waters.
Web site: www.gulfofmaine.org/gulfwatch

Northeast Aquatic Nuisance Species Task Force

NEANS was established in 2001 by the Federal Aquatic Nuisance Species Task Force as one of six regional panels. Its mission is to "protect the marine and freshwater resources of the Northeast from invasive aquatic nuisance species through committed and coordinated action."
Web site: www.northeastans.org

Northeast Channel Coral Conservation Area

The Canadian Department of Fisheries and Oceans and the fishing industry are working to address the potential impacts of fisheries on deep-sea corals. Management measures, including restrictions on bottom-fishing gear, were implemented in 2002 to protect deep-sea corals in an area centered on Romey's Peak in the Northeast Channel.
Web site: www.mar.dfo-mpo.gc.ca

Regional Marine Research Program

The Gulf of Maine was the subject of one of the nine Regional Marine Research (RMR) Programs overseen by NOAA and the EPA. The goal of the Gulf of Maine Regional Marine Research Program was to produce models that collectively simulated how the Gulf of Maine ecosystem functions naturally and under stress.
Web site: http://woodshole.er.usgs.gov/project-pages/oracle/gomaine/regional.htm

Stellwagen Bank National Marine Sanctuary Mapping and Habitat Characterization

A partnership between the U.S. Geological Survey and the National Marine Sanctuary Program developed seabed maps to support management, research, monitoring, education, outreach, and enforcement in the National Marine Sanctuaries.
Web site: http://woodshole.er.usgs.gov/project-pages/stellwagen

Taunton and Great Salt Bay Closures

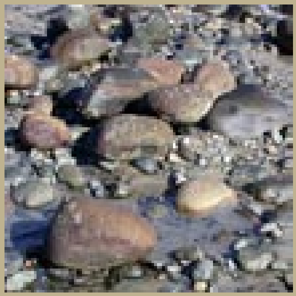
In Maine, a moratorium on dragging gear in Taunton Bay was established in response to public concern about habitat alteration and overfishing. Similarly, the Great Salt Bay marine shellfish preserve legislation, enacted in 2001, prohibits any harvesting activities resulting in bottom disturbance. The Taunton Bay legislation required the Department of Marine Resources to study the impacts of dragging and provide recommendations on whether to maintain the ban on dragging.
Web sites:
http://janus.state.me.us/legis/statutes/12/title12sec6961.html
http://janus.state.me.us/legis/statutes/12/title12ch627.pdf


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

CHAPTER TWO

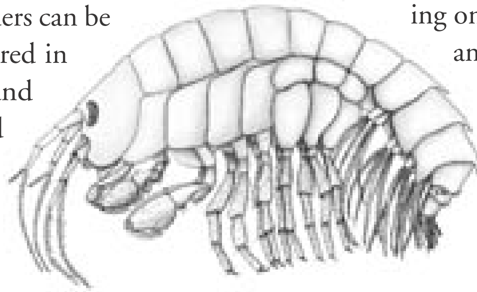
Rocky Habitats

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).



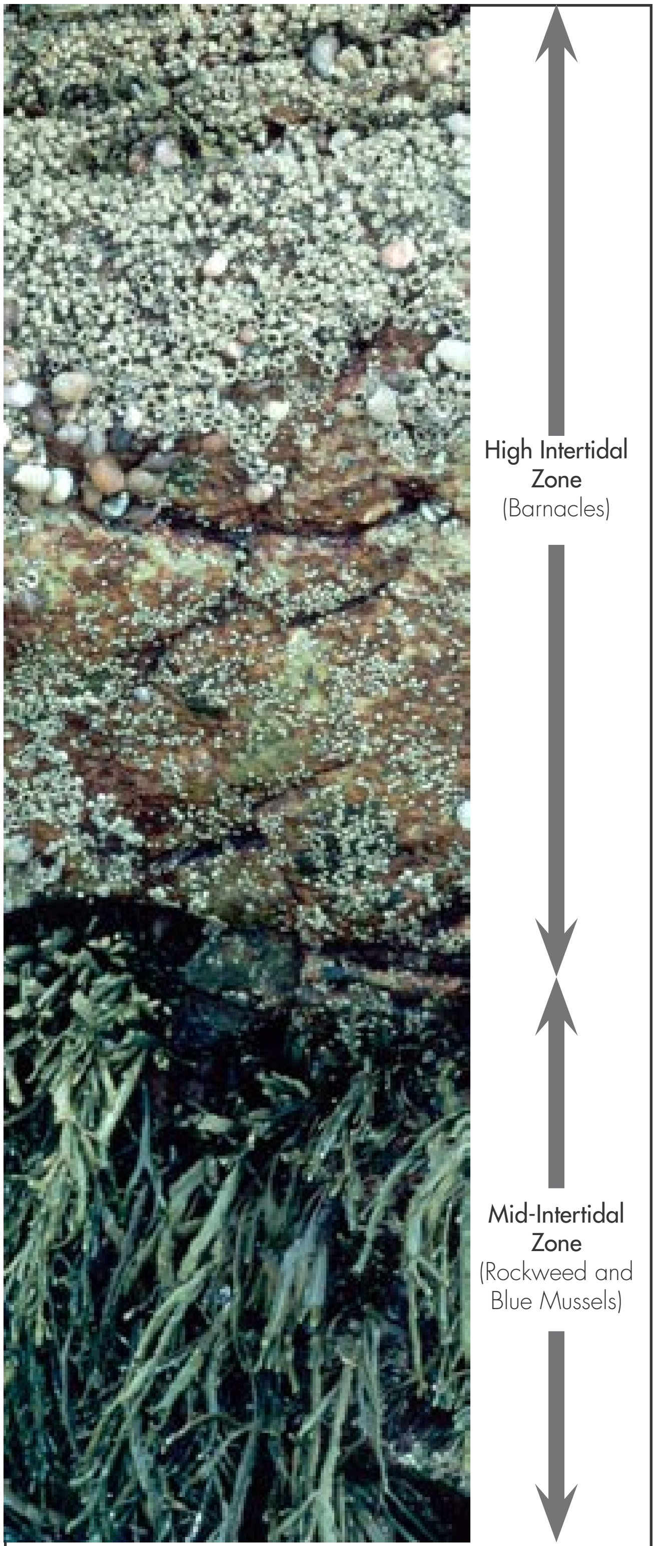
Amphipods are common in rocky habitats.
Ethan Nedeau

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

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



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

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

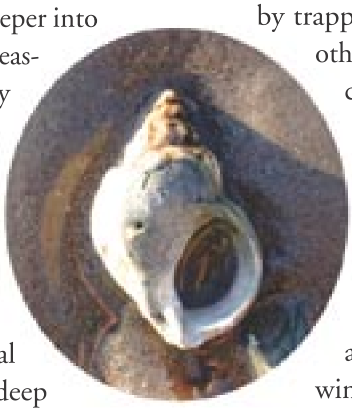
Sandy Habitats

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

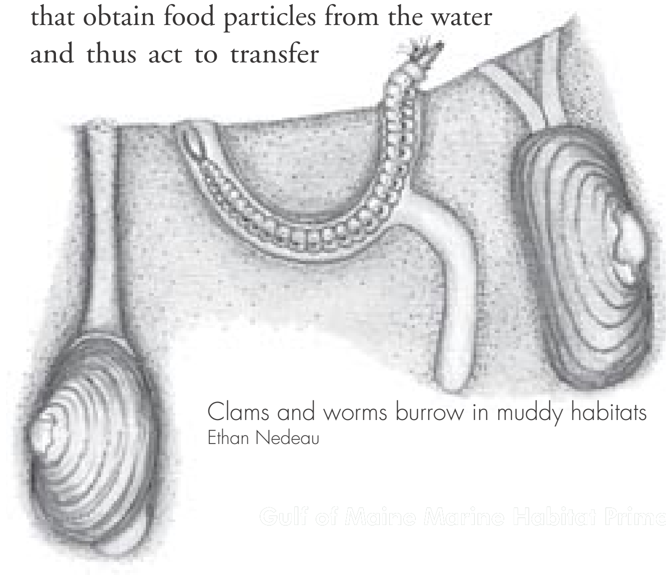
Greg Stott

General Description

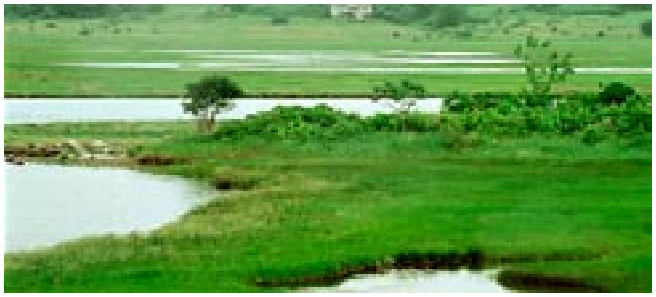
Muddy bottoms are areas of fine sediments that may be unvegetated or patchily covered with green algae and benthic diatoms. These habitats occur in calm, wave-sheltered, depositional environments in both the subtidal and intertidal zone, where they are commonly referred to as tidal flats. Grain size 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

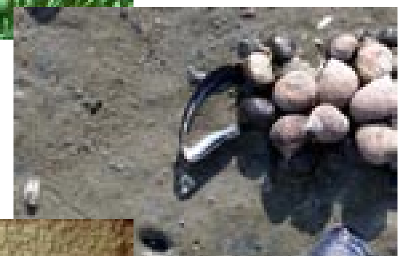


Clams and worms burrow in muddy habitats
Ethan Nedeau



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 *Ceranthid* 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

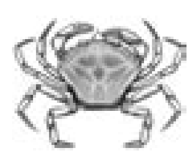
Intertidal mud flats are biologically productive environments that support important recreational and commercial fisheries for softshell clams, jackknife clams, quahogs, bloodworms, and sandworms (Roman *et al*. 2000). Muddy habitats play a role in sustaining the valuable fishery for winter flounder (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

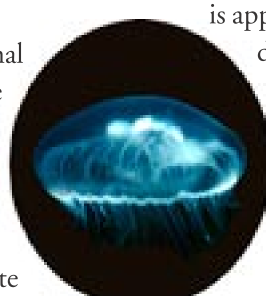
Water Column

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.

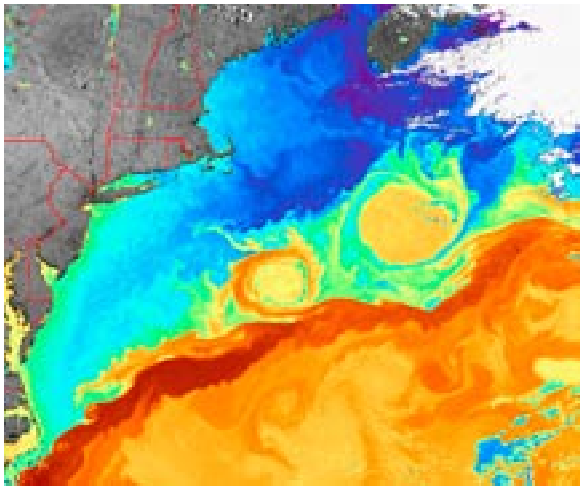


The top layer, called the photic zone, extends from the sea surface to the depth at which sunlight ceases to penetrate. The depth of the photic zone varies from place to place and over time depending on water clarity. Phytoplankton live in the photic zone and provide most of the water column's primary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

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

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.

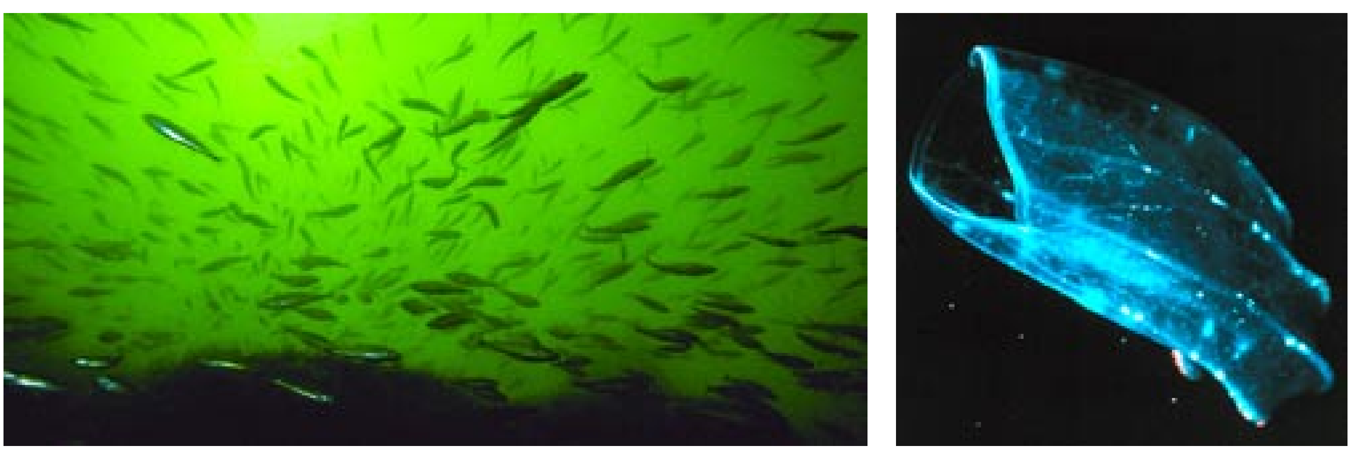
Organisms living in the water column display an extraordinary range of body sizes and lifestyles. Ultraplankton such as bacteria and phytoplankton measure only 0.005 millimeter in diameter, while some whales are tens of meters. Holoplankton spend their entire lives drifting in the water column, while 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.

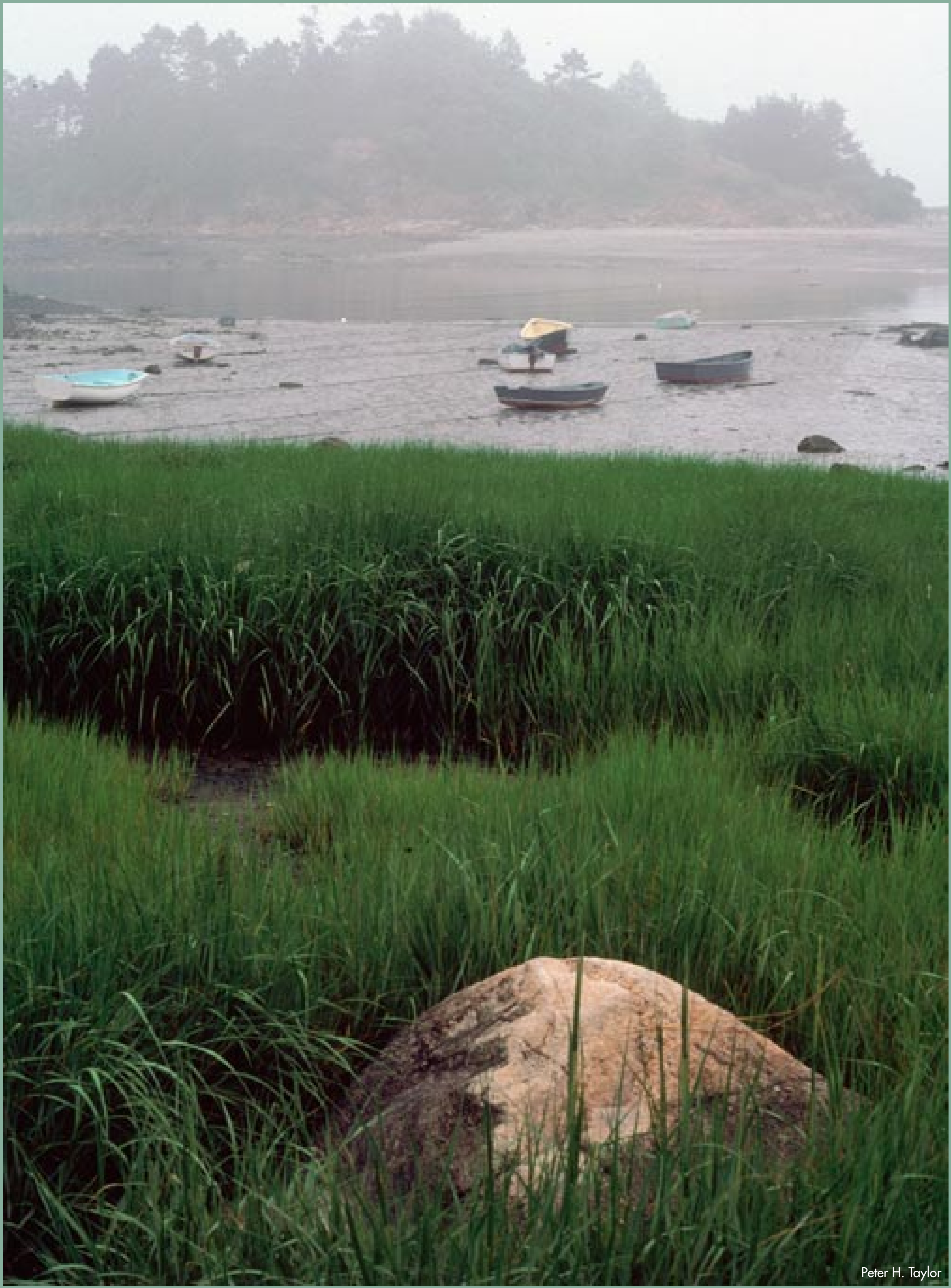
Management Considerations

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



Peter H. Taylor

Biogenic Habitats

Certain plants and animals grow in such a manner that they provide a unique environment and physical structure for other organisms. Habitats created by plants or animals are called biogenic. Biogenic habitats may offer space for attachment, hiding places from predators, and shelter from harsh environmental conditions. Examples of biogenic habitats in the Gulf of Maine include salt marshes, seagrass beds, kelp beds, shellfish beds, and cold-water corals. Each type can occur in a range of physical substrates and environmental conditions. For example, salt marshes develop primarily in muddy intertidal areas, but they also exist in some rocky and sandy intertidal areas. The biogenic character of a habitat depends on how dense the species are. Usually a sufficient density must be reached before an area is considered a true biogenic habitat. For example, a dense oyster bed is a biogenic habitat, but sparse oysters do not provide the same function and are not considered biogenic habitat.

Salt Marshes

Seagrass Beds

Kelp Beds

Shellfish Beds

Cold-water Corals

CHAPTER SIX

Salt Marshes

Peter H. Taylor

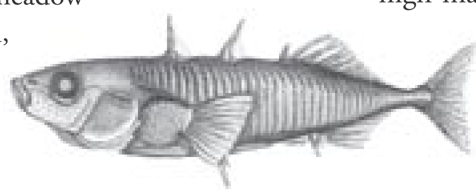
General Description

Salt marshes are grass-dominated habitats that extend from the low intertidal zone to the upper limits of the highest high tides. Salt marshes have gradients in elevation and soil salinity, with areas near inputs of surface water or groundwater being less saline. Salt marshes may grade into brackish and fresh tidal marshes along their upland and upriver edges.

Salt marshes generally have three distinct zones: low marsh, high marsh, and marsh fringe or border. Tall forms of salt marsh cordgrass (*Spartina alterniflora*) dominate the low marsh, which includes areas typically flooded by tides twice in a 24-hour period. The high marsh is flooded less often by tides, and dominant plants are saltmeadow hay (*Spartina patens*), black grass or rush, spike grass, and the short form of salt marsh cordgrass (Tiner 1987). The transition between salt marsh cordgrass and saltmeadow hay generally corresponds to the mean elevation of high tide. At the salt marsh upland border, plant diversity increases, and common species include marsh elder, seaside goldenrod, and switch grass. A non-native form of the common reed (*Phragmites australis*) is invading salt marshes throughout the northeastern United States, and drastically alters the habitat. Chapter eleven of this primer discusses *Phragmites* marshes as a distinct biogenic habitat.

Animals living in salt marshes of the Gulf of Maine include fish (mummichog, stickleback, Atlantic silverside, sheepshead minnow), ribbed mussels, snails, and fiddler crabs.

The two basic types of salt marsh in the Gulf of Maine region differ in their relative abundance of low- and high-marsh grasses. Fringing marshes form narrow bands along shorelines where protection from waves and winds is adequate but steep slopes and coarse sediments constrain the development of marsh peat and



Three-spine stickleback
Ethan Nedeau

sediment accretion. These narrow marshes can grow in areas of muddy, sandy, or rocky substrates and are dominated by the tall form of salt marsh cordgrass. They are more susceptible to erosion from waves and ice, and therefore the narrow bands of fringing marsh are more ephemeral than extensive marsh meadows.

As their name implies, salt marsh meadows are broad expanses of vegetation that form in calm areas along the coastline, such as behind barrier beaches, where they are protected from waves and strong winds. Inhabited mostly by high-marsh plants, meadow marshes typically have a greater variety of topography and ecological communities than fringing marshes. They have areas of high-marsh plants; border plants; marsh pannes and pools; low-marsh plants; and intertidal and subtidal creeks with muddy bottoms. Meadow marshes usually have a deep base of organic peat.

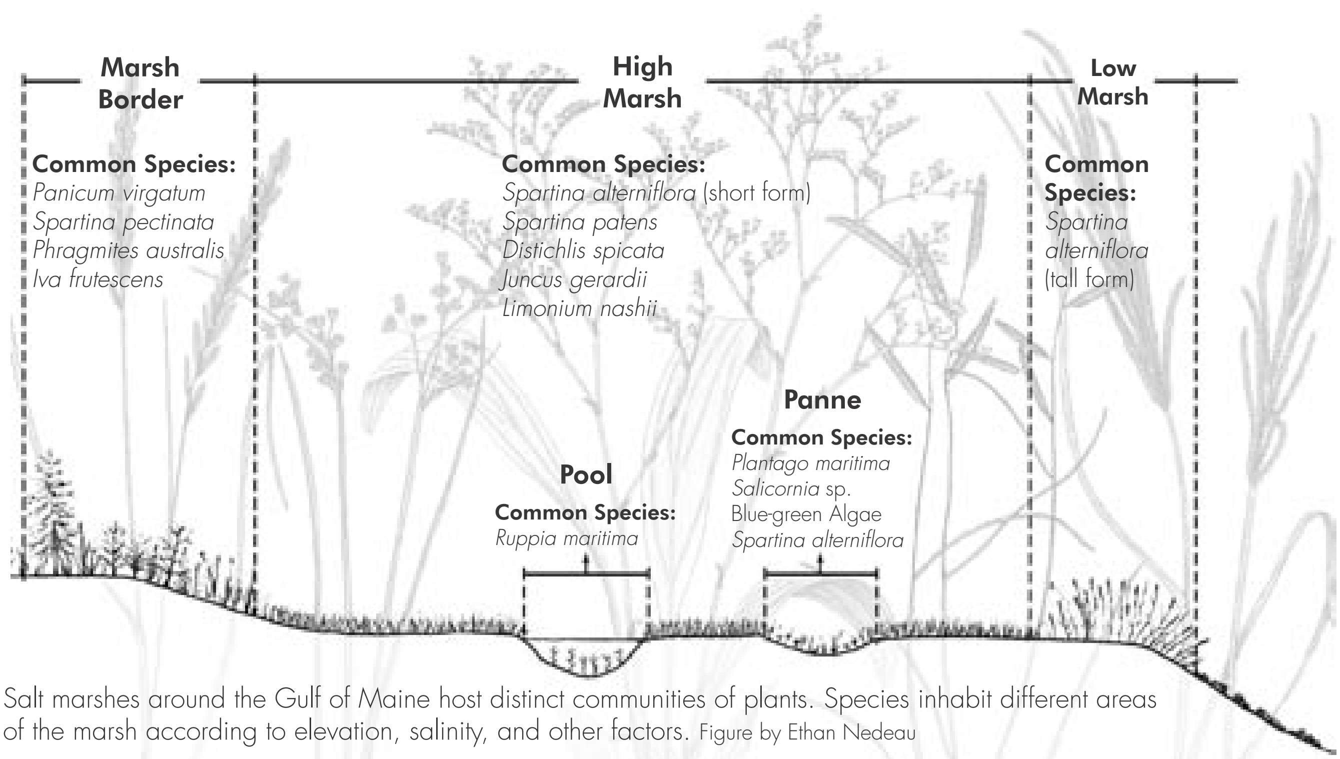
Distribution

Meadow and fringing salt marshes are found in bays and tidal rivers along the Gulf of Maine coastline. Some examples of expansive salt marshes are at the head of the Bay of Fundy; at the mouths of the Penobscot and Kennebec rivers and in Scarborough, Wells, and Ogunquit, Maine; in New Hampshire's Piscataqua River; on the north shore of Massachusetts and on the perimeter of Cape Cod.

Ecological Functions

Salt marshes are among the most biologically productive ecosystems in the world. In the Gulf of Maine, they help support rich coastal and estuarine food webs. Canada geese, deer, snow geese, voles, insects, snails, and crustaceans directly consume vegetation in the marsh, and farmers historically grazed their livestock on salt marsh grasses. However, most of the plant matter that grows in salt marshes enters the food web after it dies, rather than being eaten while alive. Microbes and worms break down the decaying plant material, or detritus, producing food particles that are swept away by the tides, transporting nutrients to other habitats. The detritus is eaten by crabs and shellfish and several species of fish that feed, breed, and find refuge in tidal channels or on the flooded marsh surface.

Salt marshes provide critical resting and feeding grounds for migratory birds and serve as nurseries for some young fish, shellfish, crabs, and shrimp because the physical structure of the grasses offers hiding places from predators. Some juvenile fish that live in salt marshes include menhaden, tomcod, and tautog. By laying eggs in the marsh before larvae enter



Salt marshes around the Gulf of Maine host distinct communities of plants. Species inhabit different areas of the marsh according to elevation, salinity, and other factors. Figure by Ethan Nedeau

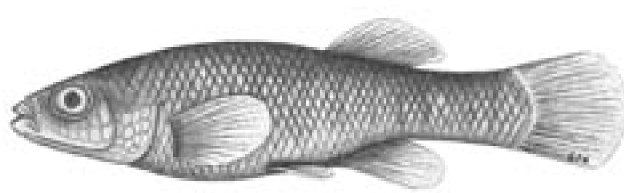
A clapper rail looks for food in a salt marsh.
Derek and Frances Richardson

Salt marshes serve as natural classrooms for students.
Peter H. Taylor

the water column, mummichogs and Atlantic silversides rely on salt marsh habitats for important parts of their life cycles. Many large predators rely on the small fish that are produced in salt marshes. Birds such as the clapper rail and salt marsh sparrow nest in salt marshes. Raptors hunt for small mammals among the grasses, while the American black duck and other waterfowl feed on invertebrates.

As they grow, salt marsh plants absorb atmospheric carbon dioxide, which is a major greenhouse gas. The carbon can be stored in the soil for thousands of years as the vegetation dies and is transformed into peat. The roots and stems of marsh plants improve water clarity by slowing water flow and trapping waterborne sediments, which block sunlight penetration, clog filter-feeding animals and fish gills, and may contain toxins or heavy metals. In addition, the grasses absorb excess nutrients that enter groundwater and surface water from fertilizers and sewage discharge. This reduces the risk of eutrophication in estuaries and nearby coastal waters.

Salt marshes protect uplands and prevent property damage by absorbing storm surge. Historically, marshes typically were able to accrete sediment fast enough to keep pace with rising sea levels. Old, buried tree stumps that are occasionally unearthed in salt marshes provide evidence of this accretion. However, increases in sea level could drown some marshes, causing the loss of productive habitat and protection of the uplands from storm surge.



Mummichog. Ethan Nedeau

Economic and Recreational Value

From an economic perspective, salt marsh habitats have enormous indirect value because commercial species depend on them during parts of their lives. These species find refuge in marshes as young, they feed in marshes as adults, and they depend on coastal food webs that are fueled by salt marsh detritus.

Salt marsh hay historically was used as livestock feed and for insulation, and today it is more commonly sold as high-grade mulch. A salt-marsh view can raise the value of residential or commercial real estate. Bird watching is a popular recreational activity in salt marshes, while kayakers and canoeists paddle the tidal channels, and recreational anglers catch fish that rely on salt marsh habitats. Educational programs for children and adults often visit salt marshes, which are convenient, accessible, and attention-grabbing natural classrooms for lessons in estuarine and coastal ecology.

Management Considerations

For centuries, salt marshes around the Gulf of Maine were filled, dredged, and drained for agriculture, urban and port development, and mosquito control. In Boston, for example, nearly four thousand acres of salt marsh were filled between 1643 and 1988 (Dalia 1998). Historically, materials from harbor dredging were disposed directly on the marsh surface, burying the vegetation and eventually transforming the marsh to upland. In practical terms, filled marshes are lost forever. However, the effects of some other human impacts, such as drainage ditches, can be countered through habitat restoration. In the 1600s, farmers dug ditches in

Road crossings and human-made ditches (visible as straight lines) intended for mosquito control and draining harm the health of many salt marshes around the Gulf of Maine. Massachusetts ACEC Program

salt marshes to increase drainage, promoting the growth of salt marsh hay that fed herds of livestock. This practice is no longer common, partly because people recognize the value of natural marsh habitats. People also dug ditches to drain the upper portions of the salt marsh—believed to be mosquito nurseries—in an attempt to reduce mosquito populations. This practice climaxed in the 1930s. Yet these "mosquito-control" ditches usually led to increased mosquito populations because draining the marsh forced minnows, which normally ate larval and adult mosquitoes, to leave. Ditches also lowered the water table and altered soil salinity, which shifted vegetation patterns and ultimately altered the quality of salt marsh habitat for birds, wildlife, and invertebrates (Roman *et al*. 2000).

Highways, roads, and railroads currently divide many salt marshes. These barriers fragment the habitat and reduce the natural tidal flushing of the marsh. Culverts allow for some flooding and draining, but many culverts are undersized, creating tidal restrictions and facilitating invasion by less salt-tolerant plants such as the common reed *Phragmites* (see Chapter 11). This hardy plant spreads rapidly when salinity is reduced, and it can out-compete other plants such as salt marsh hay. Stands of *Phragmites* lower biodiversity and degrade habitat quality for many species.

Salt marshes incur indirect and cumulative effects of human activities, such as non-point source pollution from upland development and sea-level rise due to climate change. Constructing roads, seawalls, and buildings along the upland border of salt marshes prevents the natural landward migration of the marsh and reduces the species diversity of upland plant communities (Bozek and Burdick 2003). Construction of seawalls or groins has led to erosion of salt marshes because the structures interrupt the natural sediment-transport processes that had supplied sediments to marshes. Dock and pier construction can shade and kill salt marsh plants if the structures do not allow enough light to reach the marsh surface. If erosion-prevention measures are not properly implemented in upland construction projects, excessive sedimentation can smother marsh flora and fauna and provide favorable conditions for invasion by *Phragmites*.

Tidal creek straightened to drain marsh and control mosquitoes. Ethan Nedeau

CHAPTER SEVEN

Seagrass Beds

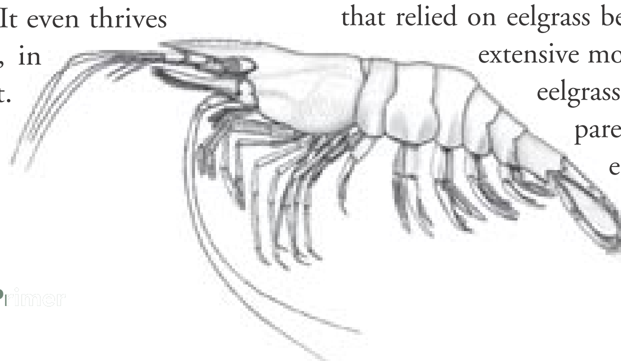
Seagrass beds grow in shallow, clear waters because they need plenty of sunlight. Seth Barker

General Description

Seagrass is a general term for flowering plants that live in low intertidal and subtidal marine environments. Roots anchor seagrass to the sediment, but unlike terrestrial plants, seagrass also absorbs nutrients from the water along the entire length of its blades, which can reach ten feet. Similar to horizontal stems, rhizomes connect the upright shoots.

Two species of seagrass live along the Gulf of Maine coast. Eelgrass (*Zostera marina*) is the dominant seagrass throughout the region, while widgeon grass (*Ruppia maritima)* is limited to low-salinity waters. Eelgrass tolerates a wide range of temperature (0–30°C) and salinity regimes (10–30 parts per thousand) and takes root on substrates from coarse sand to mud (Thayer *et al*. 1984). It even thrives among cobbles and boulders, in small patches of soft sediment. Eelgrass can live everywhere from tide pools along the shoreline to subtidal areas of several meters depth, as long as the water is relatively clear and allows sufficient light for growth. The most important factor in eelgrass survival and growth is light limitation.

Eelgrass beds are a critical habitat in the Gulf of Maine. Their connection to fisheries is especially valuable. Eelgrass also provides vital services to improve water quality by filtering suspended sediment and excess nutrients. The ecological importance of eelgrass beds along the Atlantic coast became clear after an outbreak of wasting disease in the 1930s. Caused by a slime mold that infects the leaves, the disease killed an estimated 90 percent of eelgrass in the region (Burdick *et al*. 1993). The die-off led to massive erosion and dramatic changes in water quality (Thayer *et al*. 1984). Scallops, American brant, and other animals that relied on eelgrass beds for food and shelter suffered extensive mortality (Thayer *et al*. 1984). The eelgrass limpet (*Lottia alveus*) even apparently went extinct due to the eelgrass die-off, which is the only documented extinction



Grass shrimp. Ethan Nedeau




Seagrass beds slow the movement of water. They provide shelter and hiding places for many species, such as scallops (lower left) and needlefish (far right). Top left: Fred Short, University of New Hampshire. All others: U.S. Geological Survey

of a marine invertebrate in North America (Carlton *et al.* 1991). Some commercially valuable species, such as scallops, also reportedly declined as eelgrass disappeared.

Distribution

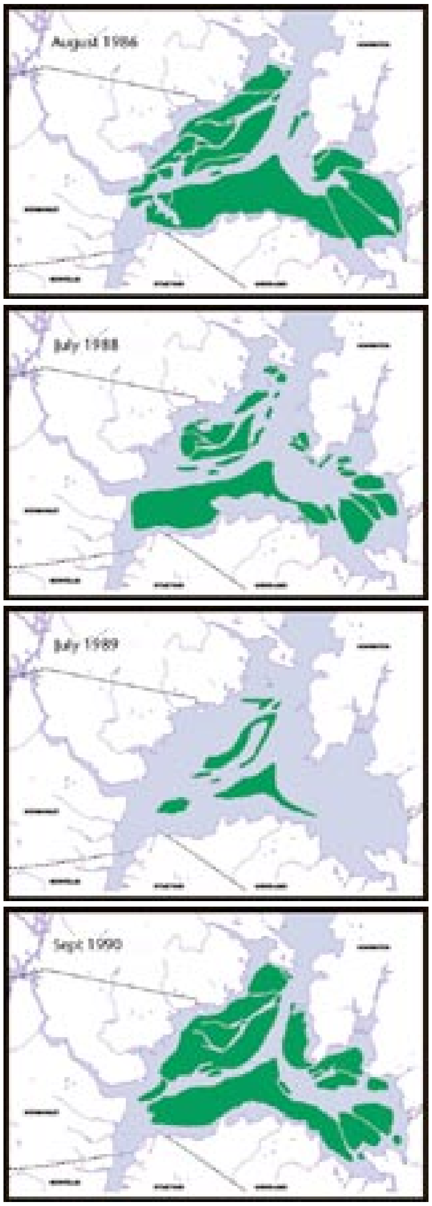
Seagrass usually lives in shallow (to a depth of 35 feet), clear waters where it receives ample sunlight. The beds often lie next to salt marshes or in harbors and inlets where they are protected from storms. Declining water clarity has caused eelgrass to disappear from many urban harbors. For example, eelgrass has been lost from Boston Harbor, Massachusetts; Portland Harbor, Maine; and Little Bay and much of the Piscataqua River in New Hampshire. In Maine, fishing practices impact eelgrass in many bays. These are losses of great ecological magnitude. Widgeon grass lives in salt marsh pools and shallow areas of brackish coves. Massachusetts, New Hampshire, and Maine conduct mapping programs to assess changes in the distribution of seagrass beds.

Ecological Functions

Seagrass beds are highly productive with photosynthetic rates approaching that of intensively farmed agricultural fields (Thayer *et al.* 1984). However, most of the productivity enters the food web as detritus, not as living plant tissue. Some suspension-feeding animals grow faster in seagrass beds compared to unvegetated habitats because of the greater availability of food particles (Lenihan and Micheli 2001). Seagrass blades make it difficult for predators to find and track their prey, so the beds act as refuges for small animals. The blades also slow the water, providing inhabitants a respite from currents and promoting sediment deposition. Seagrass produces oxygen through photosynthesis, which benefits the animals that inhabit the beds.

While the persistence of seagrass beds depends on clear water to ensure light penetration, the beds also help improve water quality by trapping suspended sediments and absorbing nutrients. In addition, seagrass beds stabilize sediments, which reduces erosion and maintains deeper channels. Like cobble beds and other structurally complex habitats, eelgrass beds support a greater diversity of bottom-dwelling animals than flat, open habitats (Deegan and Buchsbaum 1997). Seagrass beds are especially notable for their role as nurseries. Commercially valuable species such as bay scallop, cod, blue mussel, and winter flounder use seagrass habitats as juveniles, though not exclusively. Many algal and invertebrate species attach themselves to seagrass blades, including encrusting and upright bryozoans, tunicates, hydroids, and red and green epiphytic algae. Atlantic silversides and other species spawn in eelgrass beds. Other species that occur commonly

American brant feed in seagrass beds. U.S. Fish and Wildlife Service



Mapping of seagrass beds (green area) in Great Bay, New Hampshire, revealed contraction caused by an outbreak of the eelgrass wasting disease. Source: Fred Short, University of New Hampshire; http://ciceet.unh.edu/GBdata/

in seagrass beds are lobster, pipefish, tomcod, American brant, and European green crab.

Economic and Recreational Value

Seagrass beds can reduce property damage from coastal storms by absorbing waves and preventing erosion. These habitats are nurseries for commercially valuable species such as bay scallop, cod, and winter flounder, providing economic benefits for humans. Seagrass beds also provide recreational value for hunters and bird watchers by attracting waterfowl.

Management Considerations

Impaired water clarity due to turbidity, algal blooms, and improper disposal of dredged material present some of the biggest threats to seagrass beds. Water quality can degrade due to particulate matter in the runoff from areas of coastal deforestation or industrial development (Roman *et al.* 2000). Other factors that diminish water clarity include pollution from land use, dredging, boating, and turbid runoff from streets and exposed soil. Seagrass generally needs more light than phytoplankton, but water quality standards often are set at levels more amenable for phytoplankton.

Excessive nutrients and disease present two more threats to seagrass. Elevated nitrogen levels stemming from increased commercial and residential development leads to a decline in the relative abundance of seagrass compared to phytoplankton and macroalgae, including epiphytes (Roman *et al.* 2000). Phytoplankton blooms can shade seagrass beds, while growth of algae on the seagrass blades can render the plants more vulnerable to wave damage. High nutrient levels also make eelgrass more susceptible to disease. An especially severe outbreak of the naturally occurring slime mold wasting disease in the 1930s led to the decline of 90 percent of eelgrass along the Atlantic coast (Roman *et al.* 2000).

Fishing, boating, and dredging harms seagrass blades and roots. For example, turbid water from a propeller or dredging equipment can block transmission of sunlight (Deegan and Buchsbaum 1997). Docks, piers, and other structures shade seagrass and can fragment the beds (Burdick and Short 1999). Mussel dredging, trawling, and mooring chains scrape gaps in seagrass beds that heal slowly because of physical damage to the roots. Bare patches created by boat groundings and propeller scars recover slowly because of the sediment displaced by propeller wash. Dredging in harbors and navigation channels can bury or remove seagrass beds.

Several non-native species threaten seagrass beds. For example, the lacy crust bryozoan (*Membranipora membranacea*) and the orange colonial tunicate *Botrylloides violaceus* both attach to seagrass blades, while the green alga *Codium fragile* ssp. *tomentosoides* attaches to eelgrass blades and may compete for nutrients. The overgrowth by these and other attached organisms blocks light transmission and increases drag on the blade, potentially increasing its susceptibility to wave damage (Lambert *et al.* 1992).

CHAPTER EIGHT

Kelp Beds

Kelp beds provide habitat for many fish, invertebrates, and algae. Ian Skipworth

Kelp blade. Ethan Nedeau

General Description

Kelp beds form a distinct type of underwater habitat. While many different seaweeds live on rocky substrates in the Gulf of Maine, kelps are noteworthy because they are large and create underwater forests with physical structure and layering similar to that of a terrestrial forest.

Kelps in the Gulf of Maine tend to be much smaller than kelps found on the Pacific coast of North America, but they nonetheless form a very important habitat type. Kelps are brown algae that use root-like holdfasts to attach to hard substrates. Although their general morphology resembles terrestrial plants, kelps are quite different. For example, nutrient absorption occurs throughout the whole organism, not just through the holdfast. Kelp beds resemble forests on land in that the kelp blades form a canopy layer, fleshy algae such as Irish moss form an understory layer, and the crustose red algae that live on rocks are comparable to a forest's herb layer. This complex structure creates homes for many different species. Different species of kelp generally dominate at different water depths and wave-exposure conditions. For example, the strap-shaped blades of oarweed (*Laminaria digitata*) help to dissipate wave energy, while species with wide blades are common in wave-sheltered conditions.

Distribution

The most common species in this region are sugar kelp (*Laminaria saccharina*), oarweed, edible kelp (*Alaria esculenta*), and shotgun kelp (*Agarum clathratum*). The precise distribution and abundance of kelp beds in the Gulf of Maine are poorly known. In general, kelps require clear, cold water and a firm substrate for attachment. As a result, they are more common north of Cape Cod than to the south, where the water is warmer and soft sediment more widespread. Kelps can be found attached to rocks from the lower intertidal zone to about 40 meters depth if the water is very clear. Kelps also attach to human-made structures such as docks and piers.

Large kelp found washed ashore in Maine. Peter H. Taylor

Kelp holdfast attached to mussel. Ethan Nedeau

Ecological Functions

Kelp beds support higher species diversity than adjacent unvegetated habitats because of the structure provided by these large algae. Invertebrates and fish, especially juvenile fish such as cunner, find protection from predators and harsh environmental conditions, including ultraviolet radiation and strong currents, by inhabiting kelp beds. The holdfasts provide microhabitats for small invertebrates such as brittle stars, polychaete worms, snails, and juvenile mussels. Lobsters hide in kelp beds while molting (Harvey *et al*. 1995). Some invertebrates such as sea slugs, snails, bryozoans, and hydroids, as well as other algae, live attached to kelp blades and stipes.

Both living and dead kelp are important foods for echinoderms, mollusks, and crustaceans. When storms rip kelp from the rocks, the decaying algae may be deposited on nearby beaches, providing food and shelter for crustaceans and insects. In turn, shorebirds feed on these organisms. Kelp is also significant because its rate of primary productivity is among the highest in the world. It contributes to nutrient cycling by absorbing inorganic nutrients and then entering the food web as dead tissue, or detritus.

Economic and Recreational Value

Kelp beds provide habitat for many commercially valuable fish and invertebrates, as well as their prey. Kelp is the preferred food of green sea urchins, which began supporting an important commercial fishery in the late 1980s and 1990s. Extensive kelp beds reduce current speeds and buffer upland areas from erosion or storm damage.

Management Considerations

Herbivory can have a major effect on kelp beds. In the late 1980s and 1990s, population explosions of green sea urchins destroyed kelp beds in many parts of the Gulf of Maine (Witman 1987, Taylor 2004). Kelp is susceptible to overgrowth by several non-native species, including the lacy crust bryozoan and several introduced tunicates (e.g., *Botryllus schlosseri* and *Botrylloides violaceus*) that attach to kelp blades. Overgrowth by the lacy crust bryozoan slows kelp's growth rate by reducing light penetration and may make the kelp prone to dislodgement during storms by increasing drag on the blade (Lambert *et al*. 1992). In some areas in the Gulf of Maine, kelp beds are being replaced by beds of the non-native green alga *Codium fragile* ssp. *tomentosoides* (see Chapter 11) (Harris and Tyrrell 2001).

Coastal construction, boat anchors, and mobile fishing gear can damage kelp beds. Because kelp spores need hard substrates for settlement, construction projects on shore or underwater that cause excessive sedimentation may inhibit the successful establishment of young kelp. Turbidity also blocks light penetration and reduces growth rates of kelp.

If the frequency and intensity of storms increase because of climate change, the persistence of kelp beds could be threatened. Storms frequently dislodge kelp, especially kelp with holdfasts attached to mussel shells rather than solid rock surfaces. In addition, warmer waters caused by climate change might favor the growth of *Codium* beds rather than kelp beds.

CHAPTER NINE

Shellfish Beds

General Description

Some bivalve mollusks form large, dense aggregations called shellfish beds that function as distinct biogenic habitats. Small animals find refuge in the crevices among the shellfish, while others attach to the shells. Each species that forms shellfish beds has different environmental requirements, and therefore shellfish beds can be found in the intertidal and subtidal zone and from estuaries to far offshore.

The Gulf of Maine has three types of shellfish beds that are especially noteworthy as biogenic habitats. Mussels secrete strong, flexible threads that bind individuals together in clumps. Oysters settle onto the seabed in clusters, and as they grow, their shells attach permanently to the substrate, leading to formation of a calcareous reef. Scallops do not attach to each other or the substrate, but their dense aggregations are nevertheless referred to as shellfish beds. In some places, currents arrange the empty shells of dead shellfish into long rows, called windrows, on the seafloor, where fish hide to ambush prey, avoid predators, or escape currents.

A small bed of blue mussels in the intertidal zone.
Albert E. Theberge, NOAA Photo Library

Distribution

Blue mussels and oysters inhabit the intertidal to shallow subtidal zone, while scallops and horse mussels only live

Blue mussels (left), oysters (center), and bay scallops (right) can grow dense enough to create biogenic habitats. Ethan Nedeau

Oyster harvest. Gilles Daigle

in the deeper subtidal zone. Eastern oysters are largely restricted to estuaries, where they tolerate brackish water with relatively low salinities from 20 to 27 parts per thousand.

Ecological Functions

Shellfish are filter feeders that improve water quality by removing suspended material and particulate pollutants (Gili and Coma 1998). They are such effective filter feeders that sometimes they are stocked specifically to improve water quality. Large oyster reefs alter local flow conditions, and the slower flows promote deposition of particulates from the water. The improved water quality associated with shellfish beds benefits seagrass and seaweed. Mussel beds harbor greater biodiversity than adjacent bare substrates because many species of small animals live in the crevices among mussel shells. Calcareous oyster reefs provide protection for small reef-dependent fish, mollusks, polychaete worms, decapods, and other crustaceans.

Humans, crabs, lobsters, fish, predatory snails, and diving seabirds all consume large quantities of shellfish. Flocks of sea ducks such as common eider, long-tailed duck, and black scoter dive for shellfish near the coast, especially during the winter. Their feeding forays can leave large gaps in subtidal mussel beds, rendering the remaining mussels vulnerable to dislodgement by currents and waves.

Shellfish also provide an important function in the food web by transferring food from the water column to benthic habitats. These filter feeders convert water column productivity in the form of phytoplankton and zooplankton into their tissues, which then becomes available as food to animals higher in the food web, such as the birds, crabs, and fish that eat filter feeders.

The filter feeding of dense aggregations of shellfish can concentrate contaminants from the water column. Similarly, deposit-feeding bivalve shellfish accumulate pollutants in their tissues when feeding in contaminated sediments. Resource managers routinely use shellfish as bioindicators because the concentration of contaminants and toxins in their tissues can be monitored as indicators of water quality.

Economic and Recreational Value

Blue mussels, oysters, and scallops are harvested commercially and recreationally in the Gulf of Maine. Aquaculture businesses grow blue mussels and oysters in some locations along the coast. Many commercially valuable fish and invertebrates inhabit shellfish beds. Finally, large mussel or oyster reefs can help protect upland areas from storm damage.

Management Considerations

Shellfish beds face numerous threats. Declining water quality due to eutrophication, sedimentation, toxics, and rising water temperature is the biggest problem. Dredging, disposal of dredge materials, and increased freshwater run-off to coastal waters because of land development all can threaten shellfish beds.

Dense aggregations of shellfish are susceptible to outbreaks of disease, such as the parasites MSX and Dermo. Some non-native species threaten shellfish by attaching to their shells. For example, colonial tunicates can smother them, while the alga *Codium fragile* raises the risk of dislodgement by increasing drag on the shellfish.

Overharvesting can reduce or eliminate the filtering function of shellfish beds, which may lead to more turbid water and less light penetration for growth of seaweed and seagrass. Trawling gear can destroy the biogenic habitat that shellfish beds and reefs add to otherwise featureless bottoms. The gear can also resuspend sediments and contaminants into the water, potentially smothering the shellfish beds.

Many shellfish beds are closed to harvest because of high levels of fecal coliform bacteria resulting from inadequate sewage treatment. They are closed to protect human health, but contaminants of concern to humans may not harm the shellfish themselves. In fact, closures can benefit the shellfish by halting harvesting.

CHAPTER TEN

Cold-water Corals

A basket star wraps its arms around the soft coral *Gersemia*. Mike Strong and Maria-Ines Buzeta

General Description

Corals are suspension-feeding invertebrates with feathery tentacles that capture food particles from the water column. Corals living in the Gulf of Maine include horny corals (*Gorgonacea*), soft corals (*Alcyonacea*), and hard corals (*Scleractinia*). Horny corals have tree- or bush-like forms, soft corals resemble broccoli, and hard corals grow into a wide variety of shapes. The flexible skeletons of soft corals are composed mainly of proteins, unlike the fully calcified skeletons of hard corals. Many corals require a hard substrate for attachment, ranging from pebbles or boulders to solid rock outcrop. Some species can anchor in soft sediments, while others such as cup corals are free-living and do not attach to the substrate.

Historically, most people thought that reef-building corals only lived in the clear, warm waters of tropical oceans. However, recent deep-sea explorations have revealed important populations of hard corals off the coast of the northeastern United States and the Canadian Maritimes. Scientists already have discovered a *Lophelia* reef at the mouth of the Laurentian Channel off Nova Scotia and Newfoundland that qualifies as biogenic habitat; there are reports of *Lophelia* in the Jordan Basin, so perhaps such reefs exist in the Gulf of Maine, awaiting discovery (D. Gordon, personal communication). Gorgonians may grow densely enough in parts of the Northeast Channel to function as biogenic habitat (D. Gordon, personal communication).

In general, corals are long lived and slow growing. Studies of cold-water corals in Alaska indicate that some species grow only one centimeter per year (Krieger and Wing 2002), suggesting that corals may take centuries to attain several meters in height (Watling and Auster 2003). Fishermen in the Gulf of Maine who have found corals in their nets have referred to them as trees because of their large size.

The hard coral *Lophelia*. NOAA

The soft coral *Gersemia* (orange-yellow in center of photo), inhabiting a rocky ledge with urchins.
Mike Strong and Maria-Ines Buzeta

Distribution

Few data exist on the distribution of corals in the Gulf of Maine. Mortensen and Buhl-Mortensen (2004) recently published observations on the distribution and abundance of cold-water corals in the Northeast Channel between Georges Bank and Browns Bank. They reported finding three species of gorgonians that were more common along the shelf break and slope than on the inner part of the shelf. The highest densities of corals lived in areas less than 400 meters deep with a high proportion of cobble and boulder substrates and water temperature below 9.2° C. Other surveys in the Gulf of Maine have revealed soft corals at much shallower depths (MacKay *et al*. 1978) such as historical records of corals thirteen meters deep.

Ecological Functions

Cold-water corals can form a unique habitat that hosts a great diversity of species. Suspension-feeding invertebrates such as crinoids, basket stars, and anemones live on the corals, which improves their exposure to currents carrying food particles, protects them from some predators, and helps them avoid sedimentation. Fish, shrimp, and crabs swim or crawl among the corals, and some fish, sea stars, sea slugs, snails, and other invertebrates eat the soft tissues of corals.

Economic and Recreational Value

Although soft corals themselves currently have little direct economic value, scientists are exploring the potential for using them to produce pharmaceutical and cosmetic products. Deep-water coral habitats in the Gulf of Maine are not used for recreational activities such as scuba diving or ecotourism because they are inaccessible. However, some *Gersemia* and *Alcyonium* corals live in water shallow enough for recreational scuba divers to visit (L. Watling, personal communication).

Management Considerations

Cold-water corals in the Gulf of Maine are highly vulnerable to damage by fishing gear that scrapes the seafloor. Because of corals' slow growth rates, recovery from damage may take decades or centuries. In addition, because corals are non-mobile, larval dispersal is their only means of recolonizing after severe disturbance. Consequently, the abundance and distribution of coral habitats in the Gulf of Maine likely has declined because of damaging use of some types of fishing gear. Rising sea temperatures may further reduce the distribution and abundance of some cold-water corals. One study reported that the upper depth limit of three gorgonian corals was strongly influenced by high water temperatures (Mortensen and Buhl-Mortensen 2004). Non-native species also can pose a threat to corals. For example, populations of one octocoral species, *Alcyonium siderium*, in Massachusetts were severely threatened by predation by a non-native nudibranch, *Tritonia plebia* (Sebens 1999). Excessive sedimentation, pollution, and seafloor mining also can affect the persistence of corals as a habitat type.

The soft-coral *Gersemia* on a rock outcrop, among urchins and sponges.
Mike Strong and Maria-Ines Buzeta

Sponges in the Gulf of Maine can form biogenic habitat and provide similar ecological value as corals. This sponge has seastars and a basket star on it.
Mike Strong and Maria-Ines Buzeta


Ethan Nedeau

Habitats Formed by Human Activity

The habitats described in this section owe their existence to human activity. They include biogenic habitats formed by invasive species and physical habitat on the surfaces of docks, boat hulls, and other structures in the water. Many invasive species have become established in the Gulf of Maine. They arrive through a variety of human activities, such as shipping, aquaculture, and release of aquarium pets. Sometimes these invaders attain high enough densities to replace other habitats and cause profound ecological changes. Two notable habitat-modifying, invasive species in the Gulf of Maine are the common reed, *Phragmites australis*, and the green alga *Codium fragile* ssp. *tomentosoides*. Unlike the habitats described in the previous chapters, areas of invasive *Phragmites* and *Codium* are viewed generally as habitats to be contained or eliminated, rather than protected. Barnacles, mussels, and many other invertebrates and algae thrive attached to the underwater surfaces of human-made structures such as docks and boat hulls. These assemblages of species are called fouling communities. Fouling communities, which can include native and non-native organisms, may cause problems by exacerbating the spread of invasive species around the Gulf of Maine.

Invasive-Plant Habitats

Fouling Communities

CHAPTER ELEVEN

Invasive-Plant Habitats

A tall stand of non-native *Phragmites australis* invades a salt marsh, visibly altering the habitat. Ethan Nedeau

Common Reed (*Phragmites australis*)

General Description

The common reed, *Phragmites australis*, is a grass that grows up to five meters tall. It lives along the borders of rivers, lakes, and other freshwater environments, as well as salt marshes in areas of low salinity. A perennial species, its standing litter persists through the winter. The distribution and abundance of the common reed has increased dramatically along the Atlantic coast within the last 150 years (Saltonstall 2002). A non-native genotype of this species has displaced native strains and spread into areas where *Phragmites* did not historically occur (Saltonstall 2002). The invasive form has spread rapidly in degraded salt marsh habitats and areas with naturally low salinity, forming extensive monotypic stands.

Phragmites can spread in several ways. Its most common method of expansion is through underground rhizomes. To spread across barren surfaces, *Phragmites* produces stolons, or shoots that grow horizontally over the ground. It also produces small seeds that are carried by the wind. Often, small, isolated patches of *Phragmites* enlarge and coalesce into larger stands (Lathrop *et al*. 2003).

Low salinity and soil disturbance are factors that allow *Phragmites* to become established. Typically, tidal restrictions or increased runoff lower the salinity of a salt marsh. When salt marsh habitats are degraded or disturbed, *Phragmites* may outcompete native salt marsh vegetation, including salt marsh cordgrass (Burdick and Konisky 2003).

Various management methods have been used to control the spread of *Phragmites* along the Atlantic coast. One of the most effective and commonly used approaches is to restore tidal flow to the marsh by removing tidal restrictions or installing larger culverts (Blossey 2003). Prescribed burning, selective application of herbicide, and physical removal of plants have been used to wipe out or slow the spread of *Phragmites*. Attempts at biological control using the

The flowering structure of *Phragmites australis.* Ethan Nedeau

European beetle *Rhizedra lutosa*—a natural enemy—have not proved successful (Casagrande *et al*. 2003).

Distribution

Phragmites occurs in areas along the entire Gulf of Maine coastline. Its distribution has been mapped in some places, but the lack of a comprehensive mapping program makes it difficult to track its expansion. The areas most susceptible to invasion are the upper edges of salt marshes, especially marshes that have been disturbed by construction, fill, or tidal restriction.

Management Considerations

Increased sediment accumulation rates caused by dense stands of *Phragmites* may change marsh drainage patterns by eliminating some small intertidal channels. Eventually *Phragmites* expansion reduces tidal flooding and increases the proportion of high intertidal habitat. Organic matter produced by *Phragmites* may fill in the pools that mummichogs use for spawning and nurseries (Osgood *et al*. 2003, Raichel *et al*. 2003). Flow across *Phragmites*-dominated marshes becomes sheet-like because of the smooth surface, whereas in cordgrass-dominated marshes drainage occurs via rivulets and small creeks (Raichel *et al*. 2003). Because *Phragmites* grows taller than native salt marsh vegetation, it blocks sunlight needed by other plants, reducing their growth and survival (Burdick and Konisky 2003).

Phragmites has some positive ecological effects that arise from its high productivity, carbon storage, and erosion control (reviewed by Burdick and Konisky 2003). *Phragmites*-dominated marshes have such high rates of sediment accumulation—due to high production, lack of export of litter, and slow decay rates—that this invasive reed might help offset the problems that rapid sea-level rise poses to many coastal marshes (Rooth *et al*. 2003).

Unlike most salt marsh plants, *Phragmites* persists throughout the winter as standing litter. Some birds such as common yellowthroats, marsh wrens, salt marsh sparrows, and the imperiled least bittern may roost in *Phragmites* when other salt marsh vegetation has senesced (J. Smith, Massachusetts Bays Program, personal communication). Red-winged blackbirds and some wading birds nest in *Phragmites* stands (Parsons 2003).

The effects of *Phragmites* on the salt marsh food web are unclear. Replacement of native salt marsh vegetation by

Phragmites stands can be dense, and the persistent dead plants may be a fire risk throughout the year. Ethan Nedeau

Phragmites likely affects most marsh-dwelling herbivores and secondary consumers such as mummichogs (e.g., Raichel *et al.* 2003). One study found only the spotfin killifish in *Phragmites*-dominated marshes, suggesting that the diversity of marsh fish may be affected when *Phragmites* replaces cordgrass (Able *et al.* 2003). Similarly, species that live in tidal creeks, such as the grass shrimp, may decline as *Phragmites* fills in small creeks (Osgood *et al.* 2003). Thickets of *Phragmites* along creek banks may block non-resident fish and swimming crustaceans from entering the salt marsh. *Phragmites* also may inhibit the movement of other large animals, including the diamondback terrapin (Neider in Lathrop *et al.* 2003).

Habitat changes caused by *Phragmites* could harm commercially important species that use salt marshes as nurseries and feeding grounds. While the ecological and economic effects have yet to be quantified, these concerns have spurred efforts to remove *Phragmites* (Grothues and Able 2003).

Because it grows so tall, *Phragmites* obscures salt marsh views for coastal landowners, potentially reducing property values, and it hinders recreational bird watching. The standing, dry litter during winter is a significant fire risk. Higher rates of sedimentation brought on by *Phragmites* could degrade the recreational value of marshes for fishing and kayaking.

Deadman's Fingers (*Codium fragile* ssp. *tomentosoides*)

General Description

Deadman's fingers (*Codium fragile* ssp. *tomentosoides*) is a green alga that is native to Japan. It attaches to rock surfaces and mollusk shells, and it is one of the most invasive seaweeds in the world (Trowbridge 1998). In the early 1960s, *Codium* was introduced to southern Massachusetts attached to the shells of transplanted oysters from Long Island Sound (Carlton and Scanlon 1985). *Codium* has invaded many regions such as northwestern Europe, the Mediterranean, and New Zealand (Chapman 1999, Mathieson *et al.* 2003).

Codium lives in intertidal pools and in the subtidal zone as deep as fifteen meters (Chapman 1999), where it is found in both sheltered and wave-exposed environments. In some locations in the Gulf of Maine, *Codium* now dominates the algal community above seven meters depth; its abundance below this depth varies among sites (Harris and Mathieson 1999; Mathieson *et al.* 2003). The plant can grow very fast (Fralick and Mathieson 1973), reach heights of more than one meter, and thrive with relatively little light (Chapman 1999). Because *Codium* can reproduce through fragmentation, it can spread easily.

Invasive *Codium* can dramatically change the seafloor habitat, as shown here along Nova Scotia's coast. Alan Pinder

The bushy growth form of *Codium* creates a different biogenic habitat than the blades of kelp that it replaces. Alan Pinder

Codium frequently associates with, and sometimes replaces, kelp beds (see Chapter 8). This represents a major change in the seafloor habitat because *Codium* has a bushy growth form that is markedly different from the long stipes and blades of kelp. As a result, *Codium* beds support a very different ecological community than kelp beds. *Codium* has become prominent in some bays where eelgrass has declined, suggesting that *Codium* may flourish in the niche formerly occupied by eelgrass (Trowbridge 1998). When attached to shells, *Codium* increases drag, which can result in shellfish being ripped from the bottom. *Codium* can also attach to other plants, including coralline algae and various red and brown algae that are common in the understory. *Codium* blocks light penetration to these species and reduces their growth and survival.

Herbivory by the native sea slug *Placida dendritica* and overgrowth by the introduced lacy crust bryozoan may constrain the spread of *Codium*, especially in sheltered areas. In areas exposed to waves, strong storms dislodge *Codium* from the seafloor and help to clear space for other species to colonize.

Distribution

Codium was found at limited sites north of Cape Cod by the 1970s, presumably reaching these locations via dispersal through the Cape Cod Canal (Carlton and Scanlon 1985, Mathieson *et al*. 2003). Evidence suggests that nutrient-rich sites, such as bays that receive nutrient inputs from land-based activities, may be most susceptible to establishment of *Codium* (Trowbridge 1998 and references therein).

Management Considerations

Codium is eaten by a variety of native herbivores, including snails, sea slugs, and the green sea urchin (Freeman and Smith 1999). However, urchins prefer kelp and consume relatively little *Codium* under natural conditions, possibly due to its lack of chemical attractant (Prince and LeBlanc 1992).

The dense branches of *Codium* may shelter small animals from predators. However, *Codium* beds have less habitat value than kelp beds for larger organisms, such as juvenile cunner and other fish (Levin *et al*. 2002). *Codium*'s dense growth form also shades the understory, impeding the establishment of young kelp in *Codium* beds.

Codium is colonized by other introduced species, including the epiphytic red alga *Neosiphonia harveyi*, the lacy crust bryozoan, and the tunicates *Botrylloides violaceus* and *Diplosoma listerianum*. Drifting fragments of *Codium* may help to spread these other introduced species to new locations.

In *Codium*'s introduced range, its dense beds have negative economic effects. It attaches to shellfish, including commercially valuable blue mussels, bay scallops, and oysters. It may harm these species by increasing drag and buoyancy, making these species more susceptible to being ripped up and deposited on the beach during storms. *Codium* also clogs fishing gear, reducing the efficiency of the gear. Although people harvest and eat *Codium* in its native Asia, the alga is not harvested commercially in the Gulf of Maine.

The species may contain potentially valuable antibiotic, anticarcinogenic, and immunosuppressive compounds. Additional exploration of *Codium*'s properties could reveal other possible beneficial uses (Trowbridge 1998).

In the next few decades, other non-native species may attain sufficient densities to modify native habitats and qualify as distinct biogenic habitats. For example, the non-native red alga *Grateloupia turuturu*, which grows as long as two meters, occurs in southern Narragansett Bay. If it continues to spread along the east coast, this species could become a problem in the Gulf of Maine.

CHAPTER TWELVE

Fouling Communities

General Description

Piers, docks, wharves, shipwrecks, artificial reefs, bridge abutments, and other human-made structures provide habitat for a variety of marine animals and plants. The assemblages of seaweeds and invertebrates that attach to artificial substrates are called fouling communities. In the Gulf of Maine, fouling communities typically include blue mussels, barnacles, encrusting and upright bryozoans, sabellid and spirorbid worms, caprellid shrimp, tunicates, sponges, and a roster of other species. Many non-native species are found in fouling communities. In fact, surveys intended to find non-native marine and estuarine species often target docks and wharves because of their tendency to host invaders. By building structures in the water, humans may inadvertently help non-native species become established.

Wooden piling in Boston Harbor, Massachusetts, colonized by a fouling community. Ben Fertig

Top: Scientists analyze fouling communities on a permanently floating dock in Boston Harbor. Above: Organisms were scraped off from the underside of the dock and identified in a "rapid assessment survey" to detect the presence of non-native species. Peter Hanlon, Massachusetts Bays Program

Conclusion

Ecosystem-based management must balance many uses and impacts on marine and coastal habitats.
Images from Communications New Brunswick, except wind farm image from AMEC Border Wind

Currently, much public discussion, scientific research, and resource-management effort centers on the integrity of marine habitats in the Gulf of Maine and the impacts of human activities on these habitats. As coastal and fishery managers work to advance marine habitat conservation, restoration, and protection, a foundation of information regarding habitat types and their ecological relationships is essential.

Intact marine habitats support diverse ecological communities and productive fisheries. The physical structure provided by some plants and animals actually creates habitat for other organisms. Habitats in the Gulf of Maine serve many additional functions such as cycling nutrients, filtering pollution, trapping sediments, buffering upland areas from storm damage, and providing recreational opportunities.

Coastal and fisheries resource managers are frequently tasked with making decisions about projects or uses of the marine environment without sufficient knowledge of the habitat types that may be affected. Projects being proposed at sites around the Gulf of Maine include wind farms, natural gas facilities, aquaculture, sand mining, pipeline and cable installations, construction of docks and piers, and sewage outfalls. These projects can severely disrupt and degrade the natural functions of marine habitats. Pollutant discharges, nutrient loading, coastal development, fishing practices, dredging, sea-level rise, increasing water temperatures, and invasive species are most often cited as management concerns. The information about habitat characteristics and management concerns provided in the *Gulf of Maine Marine Habitat Primer* can help inform managers decisions about project reviews, special management area designations, restoration targets, and other issues under their jurisdiction.

Managers from around the region are working hard to protect marine habitats in the Gulf of Maine despite limited knowledge of where these habitats are, how sensitive they are to alteration, and the diverse functions they perform. As we learn more about marine habitats through scientific research as well as management experience, we can be more effective at protecting them from harmful human activities. Some examples of marine habitat management projects and organizations are listed on page six of this document. For more ideas about activities and organizations, visit the

Gulf of Maine Council's Web site at www.gulfofmaine.org. The Gulf of Maine Council's Habitat Conservation Subcommittee is working with partners in the region to develop and advance a range of marine habitat conservation strategies. This *Primer* is the first in a series of steps that focus on determining: 1) habitat types and their ecological relationships, 2) activities impacting marine habitats, 3) the state of the science in understanding these impacts, and 4) management options for addressing the impacts. In order to promote marine habitat management, the project will also seek to understand the current suite of legislative and regulatory tools and their varying effectiveness. Ultimately, the project will culminate in Gulf of Maine marine habitat conservation strategies with findings and recommendations regarding science, policy, and management approaches. The Subcommittee hopes this work will assist and be complementary to related habitat conservation efforts underway throughout the region.

Ethan Nedeau

Bibliography

Recommended Readings

Habitat Overviews

Gulf of Maine Knowledgebase. Gulf of Maine Council on the Marine Environment. www.gulfofmaine.org

Bertness, M. D. *The Ecology of Atlantic Shorelines*. Sunderland, Massachusetts: Sinauer Associates, Inc., 1999.

Bertness, M. D., S.D. Gaines and M.E. Hay, eds. *Marine Community Ecology*. Sunderland, Massachusetts: Sinauer Associates, Inc., 2001.

Conkling, P.W., ed. *From Cape Cod to the Bay of Fundy: An Environmental Atlas of the Gulf of Maine*. Cambridge, Massachusetts: MIT Press, 1995.

Mann, K. H. *Ecology of Coastal Waters: With Implications for Management*. Malden, Massachusetts: Blackwell Science, 2000.

Nybakken, J. W. and M. D. Bertness. *Marine Biology: An Ecological Approach (6th Edition)*. Benjamin Cummings, 2005.

Ray, G. C. and J. McCormick-Ray. *Coastal Marine Conservation: Science and Policy*. Malden, Massachusetts: Blackwell, 2004.

Rocky Habitats

Mathieson, A.C., C.A. Penniman and L.G. Harris. Northwest Atlantic rocky shore ecology. In A.C. Mathieson and P.H. Nienhuis, eds., *Intertidal and Littoral Ecosystems*, pp. 109-191. *Ecosystems of the World* Vol. 24. Amsterdam; Elsevier, 1991.

Mud Flats

Whitlatch, R.B. *The Ecology of New England Tidal Flats: A Community Profile*. Washington, D.C.: United States Fish and Wildlife Service, Biological Services Program, 1982.

Subtidal Habitats

Auster, P.J, K. B. Heinonen, and M. McKee 2003. Stellwagen Bank National Marine Sanctuary: An Underwater Tour. National Undersea Research Center for the North Atlantic and Great Lakes, University of Connecticut-Avery Point. CD-ROM.

Salt Marshes

Ward, A.E. 1999. *Maine's Coastal Wetlands: I. Types, Distribution, Rankings, Functions and Values.* Maine Department of Environmental Protection. 113 pp.

Seagrass Beds

Fonseca, M.S., W.J. Kenworthy and G.W. Thayer. 1998. Guidelines for the Conservation and Restoration of Seagrasses in the United States and Adjacent Waters. NOAA Coastal Ocean Program Decision Analysis Series No. 12. NOAA Coastal Ocean Office, Silver Spring, MD. 222 pp.

Phragmites australis (Common Reed)

Burdick, D.M. and R.A. Konisky. 2003. Determinants of expansion for *Phragmites australis,* common reed, in natural and impacted coastal marshes. *Estuaries* 26(2B):407-416.

Literature Cited

Able, K.A., S.M. Hagan and S.A. Brown. 2003. Mechanisms of marsh habitat alteration due to *Phragmites*: response of young-of-the-year mummichog (*Fundulus heteroclitus*) to treatment for *Phragmites* removal. *Estuaries* 26(2B):484-494.

Addessi, L. 1994. Human disturbance and long-term changes on a rocky intertidal community. *Ecological Applications* 4(4):786-797.

Albright, J.J.H. and R. Podolsky. 1995. Biodiversity: Animal, plant, and landscape diversity in the Gulf of Maine. In P.W. Conkling, ed., *From Cape Cod to the Bay of Fundy: An Environmental Atlas of the Gulf of Maine*. MIT Press, Cambridge, MA.

Allmon, R.A. and K.P Sebens.1988. Feeding biology and ecological impact of an introduced nudibranch *Tritonia plebia* in New England, USA. *Marine Biology* 99:375-385.

Auster, P.J., J. Lindholm, S. Schaub, G. Funnell, L.S. Kaufman and P.C. Valentine. 2003. Use of sand wave habitats by silver hake. *Journal of Fish Biology* 62(1):143-152.

Auster, P.J, K. B. Heinonen, and M. McKee. 2003. Stellwagen Bank National Marine Sanctuary: An Underwater Tour. National Undersea Research Center for the North Atlantic and Great Lakes. University of Connecticut-Avery Point CD-ROM.

Barry, J.P., C.H. Baxter, R.D. Sagarin and S.E. Gilman. 1995. Climate-related, long-term faunal changes in a California rocky intertidal community. *Science* 267:672-675.

Bozek, C.M. and D.M. Burdick. 2003. Impacts of seawalls on salt marsh plant communities in the Great Bay Estuary of New Hampshire. Report to the Great Bay National Estuarine Research Reserve, Durham, NH. Grant Number NA160R2395.

Brosnan, D. M. and L. L. Crumrine. 1994. Effects of human trampling on marine rocky shore communities. *Journal of Experimental Marine Biology and Ecology* 177(1):79-97.

Burdick, D.M., F.T. Short and J. Wolf. 1993. An index to assess and monitor the progression of wasting disease in eelgrass *Zostera marina*. *Marine Ecology Progress Series* 94:83-90.

Burdick, D.M. and F.T. Short. 1999. The effects of boat docks on eelgrass beds in the coastal water of Massachusetts. *Environmental Management* 23(2):231-240.

Burdick, D.M. and R.A. Konisky. 2003. Determinants of expansion for *Phragmites australis,* common reed, in natural and impacted coastal marshes. *Estuaries* 26(2B):407-416.

Carlton, J.T. and J.A. Scanlon. 1985. Progression and dispersal of an introduced alga: *Codium fragile* ssp. *tomentosoides* (Chlorophyta) on the Atlantic coast of North America. *Botanica Marina* 28:155-165.

Carlton, J.T., G.J. Vermeij, D.R. Lindberg, D.A. Carlton, and E.C. Dudley. 1991. The first historical extinction of a marine invertebrate in an ocean basin: the demise of the eelgrass limpet Lottia alveus. *Biological Bulletin* 180:72-80.

Carlton, J.T. and J. Hodder. 2003. Maritime mammals: terrestrial mammals as consumers in marine intertidal communities. *Marine Ecology Progress Series* 256:271-286.

Casagrande, R.A., G. Balme and B. Blossey. 2003. *Rhizedra lutosa*, a natural enemy of *Phragmites australis* in North America. *Estuaries* 26(2B):602-606.

Chapman, A.S. 1999. From introduced species to invader: what determines variation in the success of *Codium fragile* ssp. *tomentosoides* (Chlorophya) in the North Atlantic Ocean? *Helgolander Meeresunters* 52:277-289.

Chapman, A.R.O. and C.R. Johnson. 1990. Disturbance and organization of macroalgal assemblages in the Northwest Atlantic. *Hydrobiologia* 192:77-121.

Chapman, A.S., A.R. Chapman and J.E. Lindley. 2001. Killer alga? A case study on the infamous seaweed invader *Codium fragile* ssp. *tomentosoides*. (abs.) In: *Marine Biological Invasions: A Perspective on Atlantic Canada and New England*. Halifax, Nova Scotia. pp. 6-7.

Chavanich, S. 2001. Habitat ecology of the native subtidal snail, *Lacuna vincta*, in the Gulf of Maine and the impact of two introduced species. Dissertation, University of New Hampshire. 123 pp.

Collie, J.S. G.A. Escanero and P.C. Valentine. 1997. Effects of bottom fishing on the benthic megafauna of Georges Bank. *Marine Ecology Progress Series* 155:159-172.

Dalia, W. 1998. Losing Massachusetts' coastal salt marshes. University of Massachusetts Boston. http://site.www.umb.edu/conne/wendy/Boston.html

Deegan, L.A. and R.N. Buchsbaum. 1997. The effect of habitat loss and degradation on fisheries. In Buchsbaum, R.N., W.E. Robinson and J. Pederson, eds., *The Decline of Fisheries Resources in New England: Evaluating the Impact of Overfishing, Contamination and Habitat Degradation*. Massachusetts Bays Program, Boston, MA. 39 pp.

Fralick, R.A. and A.C. Mathieson. 1973. Ecological studies of *Codium fragile* in New England, USA. *Marine Biology* 19:127-132.

Gili, J.M. and R. Coma. 1998. Benthic suspension feeders: their paramount role in littoral marine food webs. *Trends in Ecology and Evolution* 13(8):316-321.

Grizzle, R.E., F.T. Short, C.R. Newell, H. Hoven and L. Kindblom. 1996. Hydrodynamically induced synchronous waving of seagrasses: 'monami' and its possible effects on larval mussel settlement. *Journal of Experimental Marine Biology and Ecology* 206:165-177.

Gutierrez, B.T., B. Butman and D.S. Blackwood. 2001. Photographs of the sea floor of Western Massachusetts Bay, offshore of Boston, Massachusetts: July 1999. US Geological Survey Open File Report 00-427. CD-ROM.

Harris, L.G. and A.C. Mathieson. 1999. Patterns of range expansion, niche shift and predator acquisition in *Codium fragile* ssp. *tomentosoides* and *Membranipora membranacea* in the Gulf of Maine. In J. Pederson, ed., *Marine Bioinvasions: Proceedings of the First National Conference*. Massachusetts Institute of Technology Sea Grant. January 24-27, 1999. p. 46-56.

Harris, L.G. and M.C. Tyrrell. 2001. Changing community states in the Gulf of Maine: synergism between invaders, overfishing and climate change. *Biological Invasions* 3:9-21.

Harris, L.G. and A.C. Jones. Changing distribution patterns in the invasive alga *Codium fragile* ssp. *tomentosoides:* Interplay of herbivores and hydrographic conditions in the Gulf of Maine. *Biological Invasions.* In press.

Harvey, J., K. Mann, R. Podolsky and P.W. Conkling. 1995. The Thin Edge Between Land and Sea. Pages 121-143 In P.W. Conkling, ed., *From Cape Cod to the Bay of Fundy: An Environmental Atlas of the Gulf of Maine*. MIT Press, Cambridge, MA.

Heikoop, J.M., D.D. Hickmott, M.J. Risk, C.K. Shearer and V. Atudorei. 2002. Potential climate signals from the deep-sea gorgonian coral *Primnoa resedaeformis*. *Hydrobiologia* 471(1-3): 117-124.

Institute for Man and Environment. 1976. Sensitivity analysis and priority ranking for coastal habitats. Publication No. R-76-11. Massachusetts Coastal Zone Management, Boston, MA. 90 pp.

Jennings, S., J.K. Pinnegar, N.V.C. Polunin and K.J. Warr. 2001. Impacts of trawling disturbance on the trophic structure of benthic invertebrate communities. *Marine Ecology Progress Series* 213:127-142.

Jivoff, P.R. and K.W. Able. 2003. Blue crab, *Callinectes sapidus*, response to the invasive common reed, *Phragmites australis*: abundance, size, sex ratio and molting frequency. *Estuaries* 26(2B):587-595.

Keser, M., J.T. Swenarton, J.M. Vozarik and J.F. Foertch. 2003. Decline in eelgrass (*Zostera marina)* in Long Island Sound near Millstone Point, Connecticut (USA) unrelated to thermal input. *Journal of Sea Research* 49:11-26.

Koslow, J.A., K. Gowlett-Holmes, J.K. Lowry, T. O'Hara, G.C.B. Poore and A. Williams. 2001. Seamount benthic macrofauna off southern Tasmania: community structure and impacts of trawling. *Marine Ecology Progress Series* 213:111-125.

Krieger, K.J. and B.L. Wing. 2002. Megafauna associations with deepwater corals (*Primnoa* spp.) in the Gulf of Alaska. *Hydrobiologia* 471(1-3):83-90.

Lambert, W.J., P.S. Levin and J. Berman. 1992. Changes in the structure of a New England kelp bed: the effects of an introduced species? *Marine Ecology Progress Series* 88:303-307.

Lathrop, R.G., L. Windham and P. Montesano. 2003. Does *Phragmites* expansion alter the structure and function of marsh landscapes? Patterns and processes revisited. *Estuaries* 26(2B):423-435.

Lenihan, H.S. and F. Micheli. 2001. Soft-sediment communities. Pages 253-288 In M.D. Bertness, S.D. Gaines and M.E. Hay, eds., *Marine Community Ecology*. Sinauer Associates Inc., Sunderland, MA. 550 pp.

Lercari, D. and O. Defeo. 2003. Variation of a sand beach macrobenthic community along a human-induced gradient. *Estuarine, Coastal and Shelf Science* 58(1):17-24.

Levin, P.S., J.A. Coyer, R. Petrik and T.P. Good. 2002. Community-wide effects of nonindigenous species on temperate rocky reefs. *Ecology* 83(11):3182-3193.

Lindholm, J.B., P.J. Auster and L.S. Kaufman. 1999. Habitat mediated survivorship of juvenile (0-year) Atlantic cod *Gadus morhua*. *Marine Ecology Progress Series* 180:247-255

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. *American Naturalist* 112:23-39.

MacKay, A.A., R.K. Bosien, and B. Wells. 1978. Bay of Fundy Resource Inventory Vol. 3. Deer Island - Campobello. Final report to the New Brunswick Department of Fisheries, Fredericton, New Brunswick. 233 pp.

Marston, M. and M. Villalard-Bohnsack. 1999. The use of molecular genetics to investigate the geographic origin and vector of an invasive red alga. In: J. Pederson, ed. *Marine Bioinvasions: Proceedings of the first National Conference.* Massachusetts Institute of Technology Sea Grant. January 24-27, 1999. p. 244-250.

MassGIS. 2003. DEP Eelgrass – July 1999. http://www.state.ma.us/mgis/eelgrass.htm

Mathieson, A.C., C.J. Dawes, L.G. Harris and E.J. Hehre. 2003. Expansion of the Asiatic green alga *Codium fragile* subsp. *tomentosoides* in the Gulf of Maine. *Rhodora* 105(921):1-53.

Mills, C.E. 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? *Hydrobiologia* 451:55-68.

Mortensen, P.B. and L. Buhl-Mortensen. 2004. Distribution of deep-water gorgonians in relation to benthic habitat features in the Northeast Channel (Atlantic Canada). *Marine Biology* 144(6): 1223-1238.

Ojeda, F.P. and J.H. Dearborn. 1989. Community structure of macroinvertebrates inhabiting the rocky subtidal zone in the Gulf of Maine: seasonal and bathymetric distribution. *Marine Ecology Progress Series* 57:147-161.

Parsons, K.C. 2003. Reproductive success of wading birds using *Phragmites* marsh and upland nesting habitats. *Estuaries* 26(2B): 596-601.

Pennings, S.C. and M.D. Bertness. 2001. Salt marsh communities. Pages 289-316 In M.D. Bertness, S.D. Gaines and M.E. Hay, eds., *Marine Community Ecology*. Sinauer Associates, Inc. Sunderland, MA. 550 pp.

Prena, J., P. Schwinghamer, T.W. Rowell, D.C. Gordon Jr., K.D. Gilkinson, W.P. Vass and D.L. McKeown. 1999. Experimental otter trawling on a sandy bottom ecosystem of the Grand Banks of Newfoundland: analysis of trawl bycatch and effects on epifauna. *Marine Ecology Progress Series* 181:107-124.

Prince, J.S. and W.G. LeBlanc. 1992. Comparative feeding preference of *Strongylocentrotus droebachiensis* (Echinoidea) for the invasive seaweed *Codium fragile* ssp. *tomentosoides* (Chlorophyceae) and four other seaweeds. *Marine Biology* 113:159-163.

Poppe, L.J., J.S. Schlee, B. Butman and C.M. Lane. 1989. Map showing distribution of surficial sediment, Gulf of Maine and Georges Bank. U.S. Geological Survey. Misc. Invest. Ser. Map. I-1986-A, scale 1:1,000,000.

Raichel, D.L., K.W. Able and J.M. Hartman. 2003. The influence of *Phragmites* (common reed) on the distribution, abundance and potential prey of a resident marsh fish on the Hackensack Meadowlands, New Jersey. *Estuaries* 26(2B):511-521.

Roman, C.T., N. Jaworski, F.T. Short, S. Findlay and R.S. Warren. 2000. Estuaries of the northeastern United States: Habitat and land use signatures. *Estuaries* 23(6):743-764.

Rooth, J.E., J.C. Stevenson and J.C. Cornwell. 2003. Increased sediment accretion rates following invasion by *Phragmites australis:* the role of litter. *Estuaries* 26(2B):475-483.

Saltonstall, K., 2002. Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. *Proceedings of the National Academy of Sciences of the United States of America* 99(4):2445-2449.

Scheibling, R.E. and S.X. Anthony 2001. Feeding, growth and reproduction of sea urchins (*Strongylocentrotus droebachiensis*) on single and mixed diets of kelp (*Laminaria* spp.) and the invasive alga *Codium fragile* ssp. *tomentosoides*. *Marine Biology* 139:139-146.

Schmidt, H., J.G. Bellingham, M. Johnson, D. Herold, D.M. Farmer and R. Pawlowicz. 1996. Real time frontal mapping with AUVS in a coastal environment. MIT Sea Grant College Program 97-4J, Oceans 96 MTS/IEEE, Fort Lauderdale, Florida.

Schoch, C.G. and M.N. Dethier. 1996. Scaling up: the statistical linkage between organismal abundance and geomorphology on rocky intertidal shorelines. *Journal of Experimental Marine Biology and Ecology* 201:37-72.

Sebens, K.P. 1986. Community ecology of vertical rocky walls in the Gulf of Maine, USA: small scale processes and alternative community states. Pages 346-371 In P.G. Moore and R. Seed, eds., *The Ecology of Rocky Coasts*, Columbia University Press, NY. 467 pp.

Sebens, K.P. 1999. Marine bioinvasions in the rocky subtidal zone (Massachusetts 1977-1998). (abs.) In J. Pederson, ed., *Marine Bioinvasions: Proceedings of the First National Conference*. Massachusetts Institute of Technology Sea Grant.

Simms, E.L. and J-M.M. Dubois 1999. Satellite remote sensing of submerged kelp beds on the Atlantic coast of Canada. *International Journal of Remote Sensing* 22(11):2083-2094.

Southward, A.J., Hawkins, S.J. and Burrows, M.T., 1995. Seventy years' observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. *Journal of Thermal Biology* 20:127-155.

Taylor, P. H. 2004. Green gold: Scientific findings for management of Maine's sea urchin fishery. Maine Department of Marine Resources. 32 pp.

Theroux, R.B. and R.L. Wigley 1998. Quantitative composition and distribution of the macrobenthic invertebrate fauna of the continental shelf ecosystems of the northeastern United States. U.S. Department of Commerce. NOAA Technical Report NMFS 140.

Thayer, G.W., W.J. Kenworthy and M.S. Fonseca. 1984. The ecology of eelgrass meadows of the Atlantic coast: a community profile. United States Fish and Wildlife Service FWS/OBS-84/02. 147 pp.

Tiner, R.W. 1987. *Coastal Wetland Plants of the Northeastern United States*. The University of Massachusetts Press, Amherst, MA.

Trowbridge, C.D. 1998. Ecology of the green macroalga *Codium fragile* (Suningar) Hariot 1889: Invasive and non-invasive subspecies. *Oceanography and Marine Biology: An Annual Review* 36:1-64.

Tupper, M. and R.G. Boutilier. 1995. Effects of habitat on settlement, growth and postsettlement survival of Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Science* 52:1834-1841.

Valentine, P. and D. Blackwood. USGS National Geologic Studies of Benthic Habitats, Northeastern United States. http://woodshole.er.usgs.gov/project-pages/stellwagen/stellwagenbank.html

Wahle, R. A. and R.S. Steneck. 1992. Habitat restrictions in early benthic life: experiments on substratum selection and *in situ* predation with the American lobster. *Journal of Experimental Marine Biology and Ecology* 157:91-114.

Watling. L. 1998. Benthic fauna of soft substrates in the Gulf of Maine. In E.M. Dorsey and J. Pederson, eds., *Effects of fishing gear on the seafloor of New England*. Conservation Law Foundation, Boston, MA. 160 pp.

Watling, L. and P. Auster. 2003. A preliminary summary of the distribution, status and ecological role of deepwater corals off the northeast coast of the United States. Unpublished manuscript.

Witman, J.D. 1985. Refuges, biological disturbance, and rocky subtidal community structure in New England. *Ecological Monographs* 55(4): 421-445.

Witman, J.D. and P.K. Dayton. 2001. Rocky subtidal communities. Pages 339-366 In M.D. Bertness, S.D. Gaines and M.E. Hay, eds., *Marine Community Ecology*. Sinauer Associates, Inc., Sunderland, MA. 550 pp.

Zajac. R.N., R.S. Lewis, L.J. Poppe, D.C. Twichell, J. Vozarik and M.L. DiGiacomo-Cohen. 2000. Relationships among sea-floor structure and benthic communities in Long Island Sound at regional and benthoscape scales. *Journal of Coastal Research* 16(3):627-640.

Gulf of Maine Council Mission

"To maintain and enhance environmental quality in the Gulf of Maine and to allow for sustainable resource use by existing and future generations."