Ecology And Management Of Maine's Eelgrass, Rockweeds, And Kelps

Gail S. Wippelhauser, Ph. D.
Maine Natural Areas Program
Department of Conservation

June 1996

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EXECUTIVE SUMMARY

The purpose of this project, initiated by the Maine Coastal Program, was to determine whether three types of marine benthic vegetation, namely eelgrass (*Zostera marina*), kelps (*Alaria esculenta*, *Agarum cribrosum*, *Laminaria digitata*, *L. longicruris*, *L. saccharina*, and *Saccorhiza dermatodea*), and rockweeds (*Ascophyllum nodosum*, *Fucus vesiculosus*, *F. evanescens*, *F. distichus*, and *F. spiralis*), should specifically be protected in Maine, and to develop management guidelines if protection was warranted. The Maine Natural Areas Program was contracted by the Maine Coastal Program 1) to conduct a literature search on eelgrass, rockweeds and kelps to assess ecological requirements, ecological functions, and threats, 2) to convene a panel of experts to evaluate the importance of these species in Maine, and 3) to develop management guidelines for eelgrass, rockweed and kelp habitat if appropriate.

The three types of benthic vegetation have different ecological requirements, and are found in different habitats. Rockweeds grows primarily in the intertidal zone, and can tolerate exposure and desiccation during low tide. Eelgrass and kelps grow primarily in the subtidal zone, and are intolerant of desiccation. Rockweeds and kelps are found on rock, boulder, or cobble substratum, while eelgrass grows in mud, sand, or gravel. Rockweeds and kelps are algae, lacking true roots, stems or leaves. As a result, they must absorb nutrients from the water column. Eelgrass, a vascular plant, possesses true roots, stems and leaves. Because it has roots, eelgrass can stabilize and bind soft substrates, and can absorb nutrients from the substrate. Unlike the kelps, rockweeds and eelgrass have a high light requirement for growth.

These three types of benthic vegetation make similar contributions to the ecosystem, that is, they fulfill similar ecological functions. They are primary producers, capable of synthesizing organic material using the sun's energy. They are highly productive and contribute large amounts of organic matter to the nearshore environment. Relatively few animals consume living eelgrass and kelps. Instead, the organic matter produced by these three types of vegetation enters marine food webs as detritus. Rockweeds and kelps, however, become available as detritus more quickly than eelgrass. By absorbing nutrients, including inorganic waste products released by animals, and producing new organic matter, these three types of vegetation contribute to nutrient cycling. All three types of benthic vegetation add structural complexity to the habitat and increase the amount of substrate available for other species of plants and animals. As a result, species abundance and diversity is high in habitats supporting eelgrass, rockweeds and kelps when compared to unvegetated habitats. A number of commercially important species have been found to associate with all three types of benthic vegetation. Finally, eelgrass and kelps have been shown to reduce water currents by frictional forces. Although there is no evidence, rockweeds probably slows water currents as well.

The three types of benthic vegetation are vulnerable to different threats. Eelgrass and kelps face natural biological threats that cause enormous fluctuations in their abundance. Eelgrass is sporadically decimated by a wasting disease for which there is no cure, and kelps are consumed by large populations of grazing sea urchins. These natural biological threats are exacerbated by changes in the physical environment, which are often of anthropogenic origin. Eelgrass is vulnerable to reductions of light levels, physical disturbance, and overharvesting. Rockweeds are vulnerable to reductions of light levels, overharvesting, effluent from pulp mills, thermal discharges, petroleum hydrocarbons, and competition from non-native species. Kelps are vulnerable to overharvesting, effluent from pulp mills, petroleum hydrocarbons, and competition from non-native species. Reductions of light levels in most cases result from sediment loading, nutrient loading, and shade-producing structures.

A panel of scientists, planners, and representatives from regulatory agencies reviewed information on the three types of marine benthic vegetation, helped identify threats to them, and made management recommendations. Currently, eelgrass is specifically protected as a special aquatic site only at the federal level, whereas rockweeds and kelps are not specifically protected at either the federal or state level. The panel recommends that consideration be given to 1) inclusion of rockweeds and kelps in the Army Corps of Engineers list of special aquatic sites, 2) development of a State of Maine policy for protection of eelgrass, rockweed, and kelp habitat that incorporates Natural Resources Protection Act standards and water quality standards, and 3) support of education initiatives and research regarding these species.

INTRODUCTION

The purpose of this project, initiated by the Maine Coastal Program, was to determine whether 12 common species of marine benthic vegetation, namely eelgrass (*Zostera marina*), kelps (*Alaria esculenta, Agarum cribrosum, Laminaria digitata, L. longicruris, L. saccharina*, and *Saccorhiza dermatodea*), and rockweeds (*Ascophyllum nodosum Fucus vesiculosus, F. evanescens, F. distichus*, and *F. spiralis*) should specifically be protected in Maine, and to develop management guidelines if protection was warranted.

The project was initiated for a number of reasons. First, benthic vegetation is generally considered to be an important source of food, in the form of detritus, for the marine animals that live in shallow coastal waters (Teal 1962; Mann 1973; Newell 1984; Simestad and Wissmar 1985). Second, benthic vegetation adds structural complexity to the habitat in which it lives, making the habitat attractive to a greater variety of marine organisms (e.g., MacDonald et al. 1984; Olney and Boehlert. 1988; Heck et al. 1989). Third, comprehensive information about the ecological requirements and ecological functions of this group of primary producers has never been compiled in a single document. The Gulf of Maine is an unique body of water along the eastern coast of the United States. It has a great diversity of substratum and habitat types (Emery et al. 1965; Brown 1993) that support a diverse group of benthic plants, and it is part of a fauna-rich zoogeographic zone that extends northward from Cape Cod (Larsen 1979). The relative importance of these 12 species of primary producers and their ecological function within the Gulf of Maine ecosystem has not been addressed previously. Finally, the distribution of eelgrass is being mapped for the Oil Spill Response Committee, and the ecological information compiled here may be of use to the Committee.

Inclusion of *A. nodosum*, *L. digitata*, and *Z. marina* on the list of priority species compiled by the Gulf of Maine Council on the Marine Environment (GOMCME) is further indication of their importance. The GOMCME identified 161 priority species in the Gulf of Maine and ranked them by twelve criteria that included their environmental, scientific, and commercial importance, abundance, vulnerability to population decline, and life-history characteristics. Using these criteria, *A. nodosum*, *Z. marina*, and *L. digitata* were ranked 4, 12, and 45, respectively.

Eelgrass, rockweeds, and kelps are all found in nearshore areas, and are particularly susceptible to human activities. Point and non-point sources of pollution, structures such as piers and docks, dredging and mining projects, aquaculture activities, harvesting, and fishing practices all have the potential to impact these types of benthic vegetation to varying degrees. Development of a management policy for these types of benthic vegetation before more severe losses occur makes sense ecologically and economically.

The Maine Natural Areas Program was contracted by the Maine Coastal Program 1) to conduct a literature search on eelgrass, rockweeds and kelps to assess ecological requirements, ecological functions, and threats, 2) to convene a panel of experts to evaluate the importance of these species in Maine, and 3) to develop management guidelines for eelgrass, rockweed and kelp habitat if they were deemed necessary.

The panel of experts that participated in discussions and reviewed this document included scientists and representatives of planning, resource, and regulatory agencies. The panel included: Seth Barker (Department of Marine Resources), Richard Bostwick (Department of Transportation), Dr. Susan Brawley (University of Maine), Doug Burdick (Department of Environmental Protection), Phil Colarusso (US Environmental Protection Agency), Pat Corr (Department of Inland Fisheries and Wildlife), Dr. Michelle Dionne (Wells National Estuarine Research Reserve), Lee Doggett (Casco Bay Estuary Project), Jon Kurland (National Marine Fisheries Service), Dr. Linda Mercer (Department of Marine Resources), Josie Quintrell (State Planning Office), Dr. Fred Short (University of New Hampshire), Laurie Steams (University of Maine), Dr. Robert Steneck (University of Maine), Laura Taylor (State Planning Office), Dr. Robert Vadas (University of Maine), Robert Van-Riper (Department of Transportation), and Dr. Gail Wippelhauser (Department of Conservation).

SUMMARY OF THREATS

Threats to eelgrass, rockweeds, and kelps are summarized in the following table. The threats were verified by a review of the literature and by consultation with experts. Other threats may exist, but have not been documented. With one exception, these threats are the result of human activities. In most cases, a particular activity can impact more than one type of benthic vegetation.

Threat	Eelgrass	Rockweeds	Kelps
Reduction of light by nutrient loading	√	√	
Reduction of light by sediment or shading	√	√	
Episodic reduction of population by natural causes	√		√
Physical disturbance	√		
Local overharvesting	√	√	√
Chlorate effluent from pulp mills		√	√
Thermal discharge from power plants		√	
Reproductive interference by petroleum hydrocarbons		√	√
Competition from non-native species		√	√
Heavy metals			√

CURRENT PROTECTION

Federal

The United States Army Corps of Engineers (ACOE) regulates, by issuing permits, the discharge of dredged or fill material and the placing of pilings into the navigable waters and wetlands of the United States under Section 404 of the Clean Water Act. The ACOE also regulates temporary (seasonal) and permanent structures or work in or affecting navigable waters under Section 10 of the Rivers and Harbors Act. Three federal resource agencies, the Environmental Protection Agency (EPA), the National Marine Fisheries Service (NMFS) of the National Oceanic and Atmospheric Administration (NOAA), and the U.S. Fish and Wildlife Service (USFWS) evaluate the proposed projects and assess potential impacts to natural resources, including habitat.

Especially valuable types of marine habitats, termed "special aquatic sites," are defined under the Clean Water Act §404(b)(1) Guidelines (for implementing the Act) as "geographic areas, large or small, possessing special ecological characteristics of productivity, habitat, wildlife protection, or other important and easily disrupted ecological values. These areas are generally recognized as significantly influencing or positively contributing to the general overall environmental health or vitality of the entire ecosystem of a region." Mud flats, vegetated shallows (permanently inundated, rooted aquatic vegetation), and wetlands are three specific special aquatic sites that are mentioned in the Guidelines. Eelgrass is a type of rooted aquatic vegetation, but algae, such as rockweeds and kelps, are not.

The EPA regulates, by issuing permits, the discharge of any pollutant from a point source into the waters of the United States under Section 401 of the Clean Water Act. Municipal sewage treatment plants, industrial wastewater, and stormwater originating from certain classes of activities are all regulated under this system. Nonpoint sources of pollution are not directly regulated at the federal level. However, in accordance with section 6217 of the Coastal Zone Act Reauthorization and Amendments of 1990, the Maine Coastal Nonpoint Source Control Program (State Planning Office and Department of Environmental Protection 1995) was submitted to NOAA and EPA. This program, which has not yet been approved by EPA, calls for the implementation of Best Management Practices in all towns that have land areas draining directly into coastal waters. Funding for demonstration projects and training programs that address the reduction of non-point sources of pollution are available from EPA.

State of Maine

The Natural Resources Protection Act (NRPA) of Maine requires permits to be issued by the Department of Environmental Protection (DEP) for any dredging, bulldozing, removal of material, draining or dewatering, filling, and construction, repair or alteration of any permanent structure that affects coastal wetlands, defined as all tidal and subtidal lands, and other regulated areas. Structures that are not permanent (not in a fixed location in on or over the water for a period exceeding seven months each year) are not regulated. Proposed activities fall into two categories, Permit-By-Rule and Full Permit. Permit-By-Rule are specific activities (e.g., construction of an individual pile-supported pier) that should not significantly affect coastal wetlands when carried out according to DEP prescribed standards. Full permit activities have a greater potential for affecting coastal wetlands, and to these DEP applies the standards of avoidance, minimum alteration, compensation, and no unreasonable impact. Applicants for a Full Permit must demonstrate that there will be "no meaningful loss of the wetland's function and values based on the nature of the activity." The functions to be considered include food chain support, fisheries, wetland plant habitat, aquatic habitat and wildlife habitat, but there is no standard methodology for assessing functions and values of coastal wetlands (Doug Burdick pers. comm.).

Federal and state permitting may be more closely aligned in the future. The Army Corps of Engineers has recently initiated a three-category resource assessment policy for tidal and navigable waters. Category I activities are those with little potential to affect special aquatic sites, and have no equivalent under NRPA at present. Category II and Individual Permit activities are equivalent to DEP Permit-By-Rule and Full Permit activities, respectively.

The DEP regulates, by issuing permits, the discharge of pollutants from point sources into Maine waters under the Maine Protection and Improvement of Water Act. Under Maine's Water Classification Program (Title 38, Article 4-A, §464-470), estuarine and marine waters were placed into one of three classes (SA, SB, or SC). Each class of water is suitable for specific activities, and has designated standards for dissolved oxygen, bacterial content, and discharge of pollutants. Class SA waters, for example, "shall be of such quality that they are suitable for the designated uses of recreation in and on the water, fishing, aquaculture, propagation and harvesting of shellfish and navigation and as habitat for fish and other estuarine and marine life." Specific protection for marine benthic vegetation would require defining some of these terms (Lee Doggett pers. comm.).

Nonpoint sources of pollution are indirectly addressed through state laws that are administered by the DEP (Site Location of Development Act, Natural Resources Protection Act), and by municipalities (Municipal Subdivision Law and Land Use Regulation Act). Recommendations for reducing nonpoint sources of pollution have been made in the Maine Coastal Nonpoint Source Control Program (see CURRENT PROTECTION - Federal).

The Department of Marine Resources (DMR) regulates impacts on benthic marine plants in two ways. First, it requires purchase of a license for the harvesting and selling of seaweeds. Second, it requires applicants requesting suspended, net pen, or bottom aquaculture leases to assess the resources, including the submerged vegetation beds, in the lease tract. In addition, DMR inspects the proposed aquaculture site prior to the initial lease agreement and prior to lease renewals.

The Maine Seaweed Council, formed in 1993, is a coalition of seaweed industry representatives, seaweed farmers, researchers, educators, and government representatives. One objective of the Maine Seaweed Council is to protect and promote the sustainable use of macroalgae harvested from and grown in Maine's coastal waters. The Council is working to develop industry standards and to educate the public about the value of this resource. The Council is located at 7 Industrial Park, Brunswick, Maine, 04011.

DEVELOPMENT OF STATE OF MAINE GUIDELINES

The State of Maine needs to develop specific guidelines for the protection of eelgrass, rockweed, and kelp habitat. Research has shown these types of benthic vegetation are important because they help stabilize

sediments and control erosion, contribute to nutrient cycling, provide food to grazers and detritus feeders, help maintain water quality, and attract numerous species of invertebrates and vertebrates by adding structural complexity to the water column and substratum. The goals of the protection guidelines should be to:

- evaluate existing statutes to determine their applicability to eelgrass, rockweed, and kelp habitat,
- coordinate federal, state and local efforts to protect eelgrass, rockweed and kelp habitat,
- describe suitable activities, suitable water quality characteristics, and suitable methods for assessing the functions and values of eelgrass, rockweed and kelp habitat,
- reduce point and non-point sources of pollution near eelgrass, rockweed or kelp habitat,
- avoid placement of coastal projects in eelgrass, rockweed or kelp habitat whenever possible,
- minimize impacts if a coastal project must occur in eelgrass, rockweed or kelp habitat,
- compensate for unavoidable impacts due to coastal projects in eelgrass, rockweed or kelp habitat,
- incorporate into the permitting process consideration of the cumulative and temporal impacts of coastal projects on eelgrass, rockweed or kelp habitat,
- address the exclusion of non-permanent structures from the permitting process, and
- address the problem of introduced or non-native species.

RECOMMENDED STANDARDS FOR EELGRASS, ROCKWEED AND KELP HABITAT UNDER NRPA

The standards outlined below are recommended for Permit-By-Rule and Full Permit activities under NRPA, that is, activities which include any dredging, bulldozing, removal of material, draining or dewatering, filling, and construction, repair or alteration of any permanent structure (including aquaculture) that affects eelgrass, rockweed or kelp habitat.

1. Avoid placing coastal development projects in eelgrass, rockweed and kelp habitat when possible. Permit-By-Rule and Full Permit activities should not occur in areas with eelgrass, rockweed or kelp habitat.

The applicant, with assistance from resource and regulatory agencies, should determine whether eelgrass, rockweeds or kelps occurs at the location of proposed project. If one or more of these species is present, the project should be relocated if possible.

A. Eelgrass habitat in Maine is in the process of being mapped. For activities with little potential for affecting eelgrass (ACOE Category I), consult the digital files of eelgrass distribution available through the DEP regional offices (for areas that have been surveyed recently) or the Coastal Marine Geology Maps (for areas not surveyed) available through the Natural Resources and Information Mapping Center, Department of Conservation. For activities with a high potential to affect eelgrass (ACOE Category II or III; NRPA Permit-By-Rule and Full Permit), conduct an on-site, in-water survey by snorkeling, SCUBA diving, underwater video or other means.

B. Rockweed habitat has not been mapped. For activities with a high potential to affect rockweeds (ACOE Category II or III; NRPA Permit-By-Rule and Full Permit), conduct an on-site, on-foot survey of the intertidal zone.

C. Kelp habitat has not been mapped. For activities with a high potential to affect kelps (ACOE Category II or III; NRPA Permit-By-Rule and Full Permit), conduct an on-site, in-water survey by snorkeling, SCUBA diving, underwater video or other means.

2. Minimize the impact of coastal development projects through site design and mitigate for loss of functions and values.

If there is no practical alternative to placing a coastal development project in eelgrass, rockweed or kelp habitat, then the project should be designed to minimize its impact on the habitats, and mitigation for lost functions and values of these habitat should be included in the project.

A. The applicant should incorporate the following into the site design as appropriate:

1) The amount of dredging and filling that must occur should be minimized.

2) Structures over eelgrass, rockweeds, or kelps should be supported by piers, and should be as high as possible, as narrow as possible, and oriented as close to north-south as possible to reduce shading. Specifically, boat docks should be 1 m wide and oriented to within 10° of north-south with the base of the decking at least 3 m above the marine bottom (Burdick and Short in prep.). If the orientation is beyond the 10° limit, then 0.2 m should be added to the height for each 10° increment; if the dock is wider than 1 m, then 0.2 m should be added to the height for every 0.5 m increment in width (Burdick and Short in prep.).

3) Current velocity and wave energy in and around eelgrass, rockweed or kelp beds should be determined prior to initiation of the project, and should be maintained by careful placement of fill, designing pier structures with maximum spacing between pilings (width of free flow:total width = 0.86:1) (Colarusso pers. comm.), use of rip rap slopes rather than bulkheads, and preservation of the natural contour of the shoreline.

Mitigation or replacement for lost functions and values of should be incorporated into the permit. However, the level of mitigation should depend on the type of impact. Standards should describe when mitigation is required, how mitigation is to be accomplished, and how mitigation success is to be evaluated.

1) Mitigation for eelgrass involves transplanting eelgrass to another site. Methodology for the transplanting process has been studied and evaluated in several places on the east coast of the United States (e.g., Fonseca et al. 1982). The level of mitigation required would depend on the type of impact. Creation of new substrate for transplanting eelgrass would be required for the most severe case of mitigation, for example, permanent loss of eelgrass habitat. Transplanting onto existing substrate, would be required for temporary losses of eelgrass.

2) No mitigation methodology exists for algal vegetation, and requiring mitigation before a methodology exists would be inappropriate. Development of a methodology, perhaps as a small scale pilot project, should be considered. A possible method of mitigation does exist for kelps. Adult kelps can be removed from their natural substrate, affixed with wires to an artificial substrate (cement block), and transplanted to a new habitat (described in Bologna and Steneck 1993). Transplanted kelps would provide habitat for benthic organisms, and would serve as a source of propagules.

3. Compensate for loss of eelgrass, rockweed or kelp habitat due to coastal projects. Avoidance of eelgrass, rockweed and kelp habitat and minimization of impact should always be fully pursued before compensation is considered.

Standards should describe when compensation is required, how compensation is to be accomplished, and how compensation success is to be evaluated. Compensation standards have been developed at the federal level for eelgrass, but no compensation standards exist for rockweeds and kelps. The EPA often requires replacement of eelgrass in a ratio of 3: 1 as compensatory mitigation for projects that destroy eelgrass, and for losses greater than 3 acres, mitigation must be completed and must be proven successful before construction is allowed.

4. The Department of Environmental Protection should evaluate, as part of the permitting process, the cumulative and temporal impacts of coastal projects on eelgrass, rockweed, and kelp habitat.

The cumulative and temporal impacts of coastal projects on the three types of vegetation need to be addressed. Although an individual project, for example a single dock, may have little impact on benthic vegetation, the cumulative impacts of numerous docks may be sufficient to destroy the vegetation. A dredging project that will suspend sediments for months will be more damaging to these three types of vegetation than a dredging project that will be completed in a week.

5. The Department of Environmental Protection should evaluate the impact of non-permanent structures on eelgrass, rockweed and kelp habitat, and should include in the permitting process the structures that have a large impact on eelgrass, rockweed and kelp habitat.

RECOMMENDED WATER QUALITY STANDARDS

The standards outlined below are recommended for the purpose of reducing both point and nonpoint sources of pollution in areas with eelgrass, rockweed or kelp habitat. Water quality has been identified as important for maintaining healthy populations of these three types of benthic vegetation. High levels of sediments and nutrients decrease the amount of light that reaches benthic vegetation, stimulate the growth of species that compete with benthic vegetation, and reduce available oxygen. In addition, a number of chemicals are toxic to some life history stages of eelgrass, rockweeds and kelps. As the human population along the coast grows, maintaining good water quality will become increasingly important for the conservation of these three types of benthic vegetation. The standards recommended below can be incorporated into state laws, town ordinances, town and regional comprehensive plans, and watershed management plans.

1. Minimize point sources of pollution by developing water quality requirements for eelgrass, rockweed and kelp habitat and incorporating them into the State's Water Classification Program. Water quality requirements should include light attenuation coefficient, secchi depth, total suspended solids, chlorophyll a, dissolved inorganic nitrogen, dissolved inorganic phosphorus, heavy metals, chlorate, and biological oxygen demand.

2. Minimize the impact of nonpoint sources of pollution on eelgrass, rockweed and kelp habitat by:

A. Implementing Best Management Practices (available for erosion and sediment control and stormwater management) in land areas that drain directly to coastal water and that have new or significant existing sources of nonpoint pollution. Best Management Practices will reduce nonpoint sources of sediment, nutrients and toxic substances.

B. Eliminating overboard discharges from vessels by increasing the number of pumpout stations and publicizing their locations.

C. Requiring proper maintenance of septic systems and domestic overboard discharges.

RECOMMENDED RESEARCH AND EDUCATION

Eelgrass

1. Develop educational material for the public that describes the ecological requirements and ecological functions of eelgrass.

2. Dedicate funds to complete the eelgrass survey/mapping project and to provide for periodic upgrades. By 1997 most of the coast will have been surveyed and the distribution of eelgrass mapped. When the coast

has been completely mapped, developers will be able to review sites early in the planning stages. Data should be provided to each DEP regional office.

3. Develop a GIS data layer of coastal structures (docks, dredge projects, fill projects) that could be combined with the data layer of eelgrass habitat to assess the scope of cumulative impacts.

4. Develop a monitoring program to assess efficacy of site design standards, mitigation activity, and compensation activity.

5. Determine whether a minimum distance should be maintained between eelgrass and the footprint of a development project to avoid indirect impacts such as sediment-induced shading and alteration of the physical environment. If minimum distances are necessary, develop a research/monitoring program to determine the minimum buffer distance that should be maintained between eelgrass and a project footprint, and assess efficacy of the buffer.

6. Research and test eelgrass mitigation techniques in Maine to develop feasible methodologies for compensating for unavoidable impacts.

7. Research mitigation policies developed by other states that might serve as a model for Maine, determine the success of these mitigation policies, and develop a mitigation policy for eelgrass in Maine.

8. Conduct seasonal, site-specific surveys to assess the use of eelgrass by marine organisms and wildlife.

9. Develop water quality standards, methods for assessing functions and values, conditions and standards for mitigation, and conditions and standards for compensation for eelgrass.

Rockweeds

1. Develop educational material for the public that describes the ecological requirements and ecological functions of rockweeds.

2. Dedicate funds to initiate and complete a rockweed survey/mapping project and to provide for periodic upgrades.

3. Conduct seasonal, site-specific surveys to assess the use of rockweeds by marine organisms.

4. Conduct research to determine the effects of harvesting protocols on the ability of rockweeds to recolonize and on the benthic community associated with rockweed habitat.

5. Research mitigation policies developed by other states or countries that might serve as a model for Maine, determine the success of these mitigation policies, and develop a mitigation policy for rockweeds in Maine.

6. Develop water quality standards, methods for assessing functions and values, conditions and standards for mitigation, and conditions and standards for compensation for rockweeds.

Kelps

1. Develop educational material for the public that describes the ecological requirements and ecological functions of kelps.

2. Dedicate funds to initiate and complete a kelp survey/mapping project and to provide for periodic upgrades.

3. Conduct seasonal, site-specific surveys to assess the use of kelps by marine organisms.

4. Conduct research to determine the effects of harvesting protocols on the ability of kelps to recolonize and on the benthic community associated with kelp habitat.

5. Develop water quality standards, methods for assessing functions and values, conditions and standards for mitigation, and conditions and standards for compensation for kelps.

General

1. Research methods for preventing introduction of non-native species.

2. If managers feel diversity is important, use comparative techniques and scale to analyze diversity in each habitat.

3. Develop standards for using each of the three types of benthic vegetation as indicators of water quality.

4. Expand study of ecological role of habitat types to include unvegetated habitats.

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EELGRASS

IDENTIFICATION AND DESCRIPTION

Eelgrass (*Zostera marina* L.) is one of approximately 47 species of seagrasses, flowering plants which complete their entire life cycle in seawater (Thayer et al. 1984). Like all seagrasses, eelgrass has leaves and an extensive underground system of roots and rhizomes (Thayer et al. 1984). The epidermis of the leaves contains a high concentration of chloroplasts and is the principal site of photosynthesis (Sculthorpe 1967; Tomlinson 1980). The roots and rhizomes anchor the plants in the substrate, and like the leaves, absorb nutrients and gases. In common with its terrestrial relatives, eelgrass has a functioning vascular system (xylem and phloem tissue) which allows transport of substances through the plant. Eelgrass exhibits both vegetative expansion (by the underground roots and rhizomes) and sexual reproduction (by seed). Vegetative reproduction is important for the maintenance of eelgrass meadows (Tomlinson 1980). Seeds are important for colonizing unvegetated areas, and for genetic adaptation.

An individual plant consists of a rhizome which bears 2-5 linear strap-shaped leaves (Thayer et al. 1984). The leaves are enclosed at the base by a sheath that forms a stem-like structure. Younger leaves are subtended by older leaves giving the shoot a laterally compressed appearance. The leaves are approximately 0.3-0.7 cm wide and are rounded at the tip. Most eelgrass is perennial, but annual populations have been described in Maine.

DISTRIBUTION

Eelgrass has a wide geographical distribution. It is found on the east coast of North America from Hudson Bay to the Carolinas (33-65°N), in northern Europe from Spain to Finland and the Barents Sea, on the west coast of the United States from Baja California to Alaska, and along the coasts of Japan, North Korea and South Korea (Thayer et al. 1979; Thayer et al. 1984). In many areas eelgrass is the dominant species of submerged aquatic vegetation (Thayer et al. 1984).

Eelgrass grows in shallow coastal water in a variety of substrates in salinities ranging from 0 to 30 ppt and in water temperatures ranging from less than 0°C to greater than 30°C (Thayer et al. 1984). Eelgrass is limited to relatively shallow water primarily by the availability of light (Thayer et al. 1984). In Maine, eelgrass is found from the intertidal zone to a depth of approximately 11 m (Short pers. comm).

The geographical distribution and relative abundance of eelgrass along the Maine coast currently is being mapped for the Oil Spill Response Committee by Seth Barker of the Department of Marine Resources, and will be available as a GIS data layer. The distributional maps are based on interpretation of aerial photographs at a scale of 1:12000 (1 in = 1000 ft) and subsequent site visits to assess the accuracy of the interpretation (groundtruth). The areas with the greatest probability of experiencing an oil spill were mapped first. Provisional maps have been completed for Casco Bay, Cobscook Bay, Penobscot Bay, and the Piscataqua River. Information will soon be available for the mid-coast region (Small Point to Pemaquid Point), Machias Bay, and the St. Croix River. Photography recently has been acquired for the coast from York to Cape Elizabeth and Pemaquid Point to Owl's Head, and maps of these areas should be available in 1996. For the areas mapped to date, Casco Bay has the greatest area of eelgrass (Table 1; Figs. 1-6).

LIFE CYCLE

The generalized life cycle of eelgrass can be described in four stages (Setchell 1929). The seed germinates (stage 1); the first shoot develops, new leaves are added, and roots and rhizomes form (stage 2); there is further development of existing shoots and addition of new ones by vegetative reproduction (stage 3); some of the oldest shoots develop into erect flowering stalks (stage 4). Growth occurs at the meristem in the basal area of the leaf, and can involve an increase in the length of the primary shoot, the number of leaves per shoot, or the number of shoots per original seedling (Thayer et al. 1984). Leaf growth

Table 1. Number and area of eelgrass beds by percent cover for seven coastal regions, total area of eelgrass beds by region, and total area of eelgrass beds for all regions (data provided by Seth Barker). In the Penobscot Bay region, eelgrass beds were coded by percent cover near Vinalhaven and Northhaven, but were not coded by percent cover elsewhere. In Machias Bay, a percent cover could not be assigned to the five uncoded eelgrass beds.

Region	Percent cover	Number	Area by cover (m^2)	Area by region (m^2)	(acres)	(hectares)
Piscataqua River	0-10	22	151,521.3			
	10-40	41	170,532.9			
	40-70	46	518,419.7			
	70-100	30	317,488.8			
				1,157,962.6	286	1152
Casco Bay	0-10	201	3,687,447.8			
	10-40	393	4,982,218.8			
	40-70	529	5,513,694.5			
	70-100	307	14,372,432.3			
				28,555,793.4	7056	2855
Mid-Coast (Small Point to Pemaquid Point)	0-10	70	757,641.9			
	10-40	122	1,026,437.4			
	40-70	211	1,423,699.3			
	70-100	94	995,252.0			
				4,203,030.6	1038	420
Penobscot Bay	0-10	31	360,997.0			
	10-40	63	241,322.6			
	40-70	88	473,944.5			
	70-100	132	724,451.9			
	uncoded	381	10,464,684.1			
				12,265,380.1	3030	1226
Machias Bay	0-10	32	2,126,930.2			
	10-40	86	2,408,884.4			
	40-70	51	1,786,837.2			
	70-100	24	243,791.5			
	uncoded	5	224,714.6			
				6,791,157.9	1678	679
Cobscook Bay	0-10	70	548,841.4			
	10-40	173	1,442,128.2			
	40-70	208	2,226,190.3			
	70-100	44	468,833.7			
				4,685,993.61	1157	468
St. Croix	0-10	6	35,261.6			
	10-40	9	114,638.6			
	40-70	5	47,246.8			
	70-100	2	24,397.5			
				221,544.6	54	21
Total				57,880,862.7	14299	6821

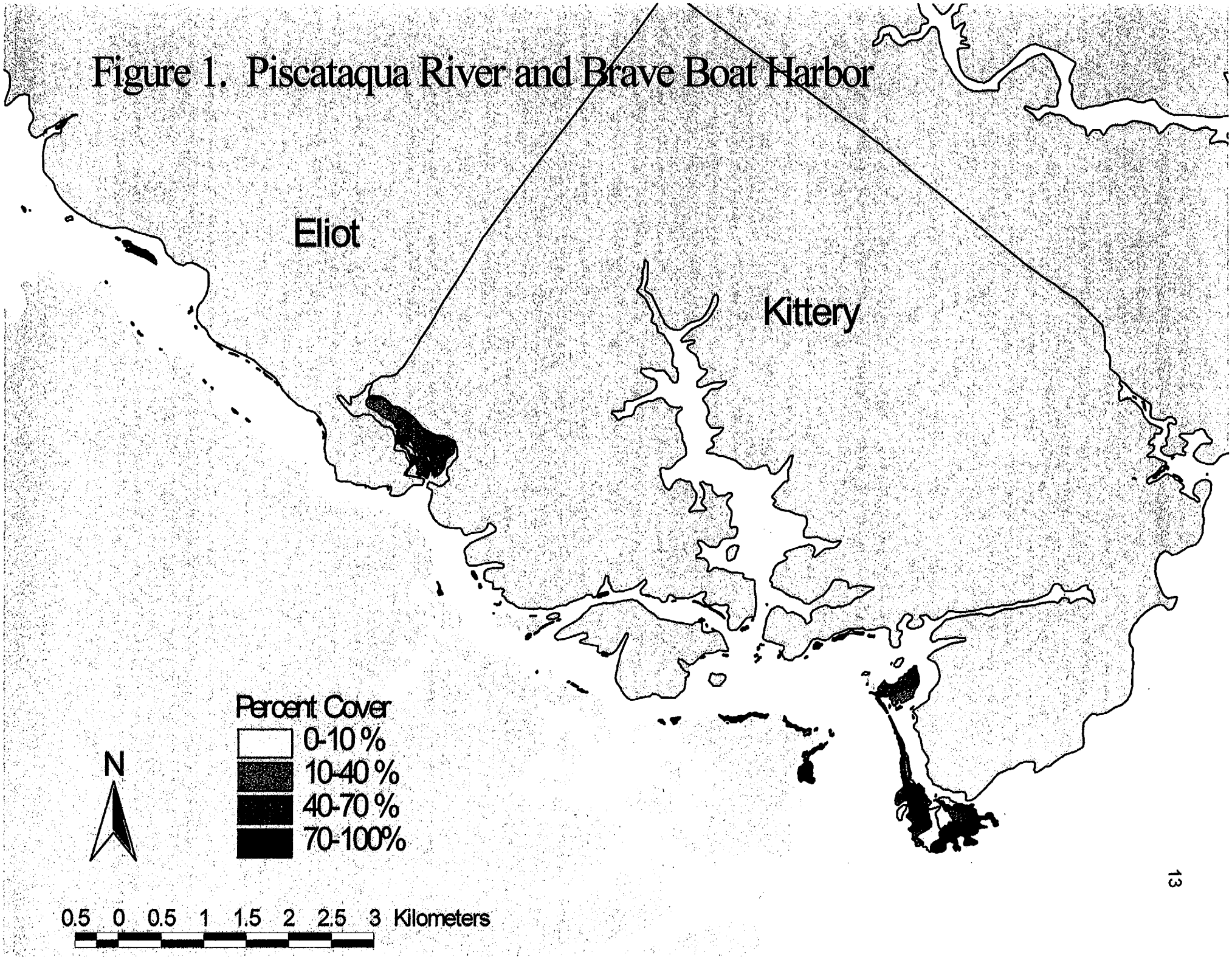


Figure 1. Piscataqua River and Brave Boat Harbor

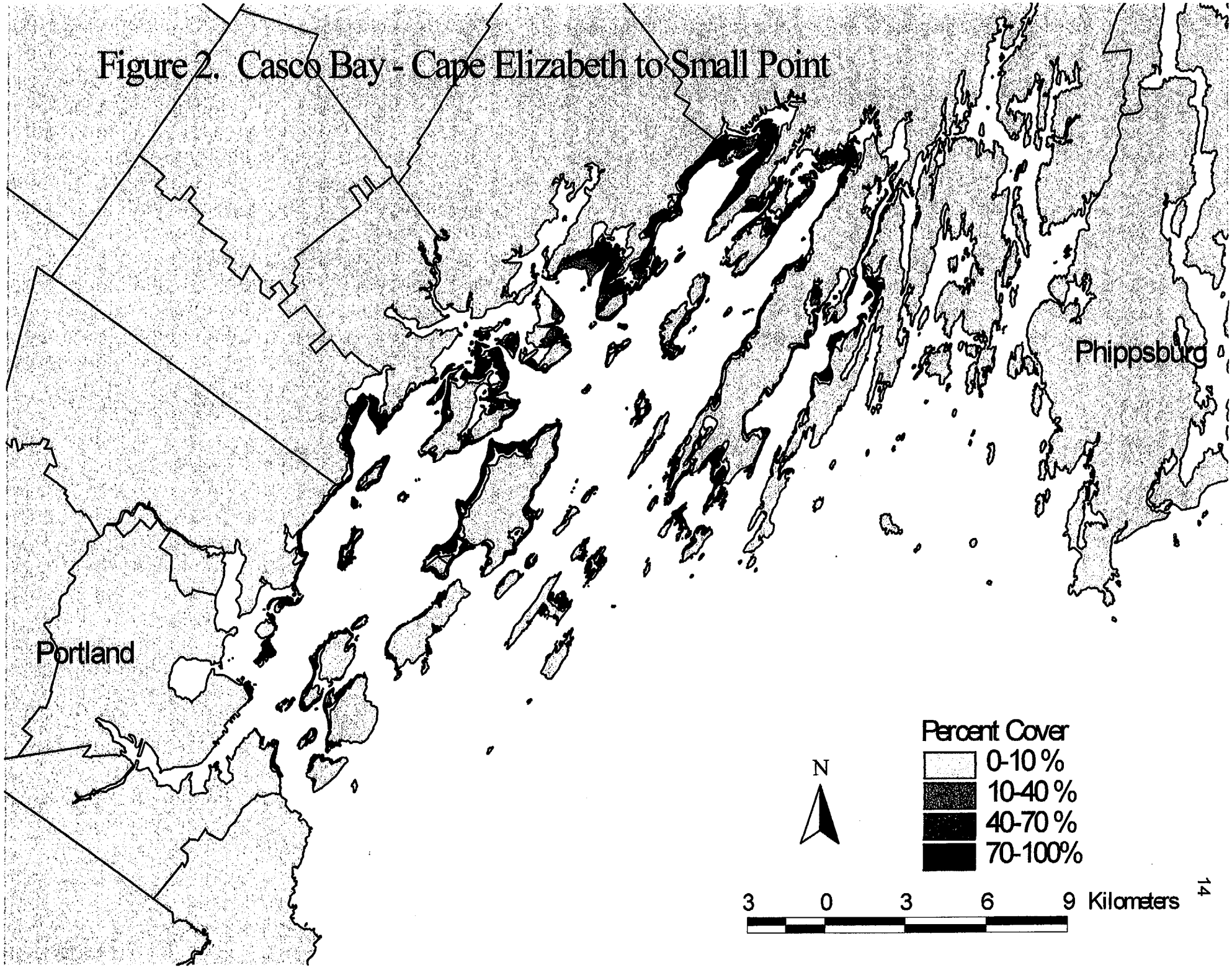


Figure 2. Casco Bay - Cape Elizabeth to Small Point

Figure 3. Midcoast - Small Point to Pemaquid Point

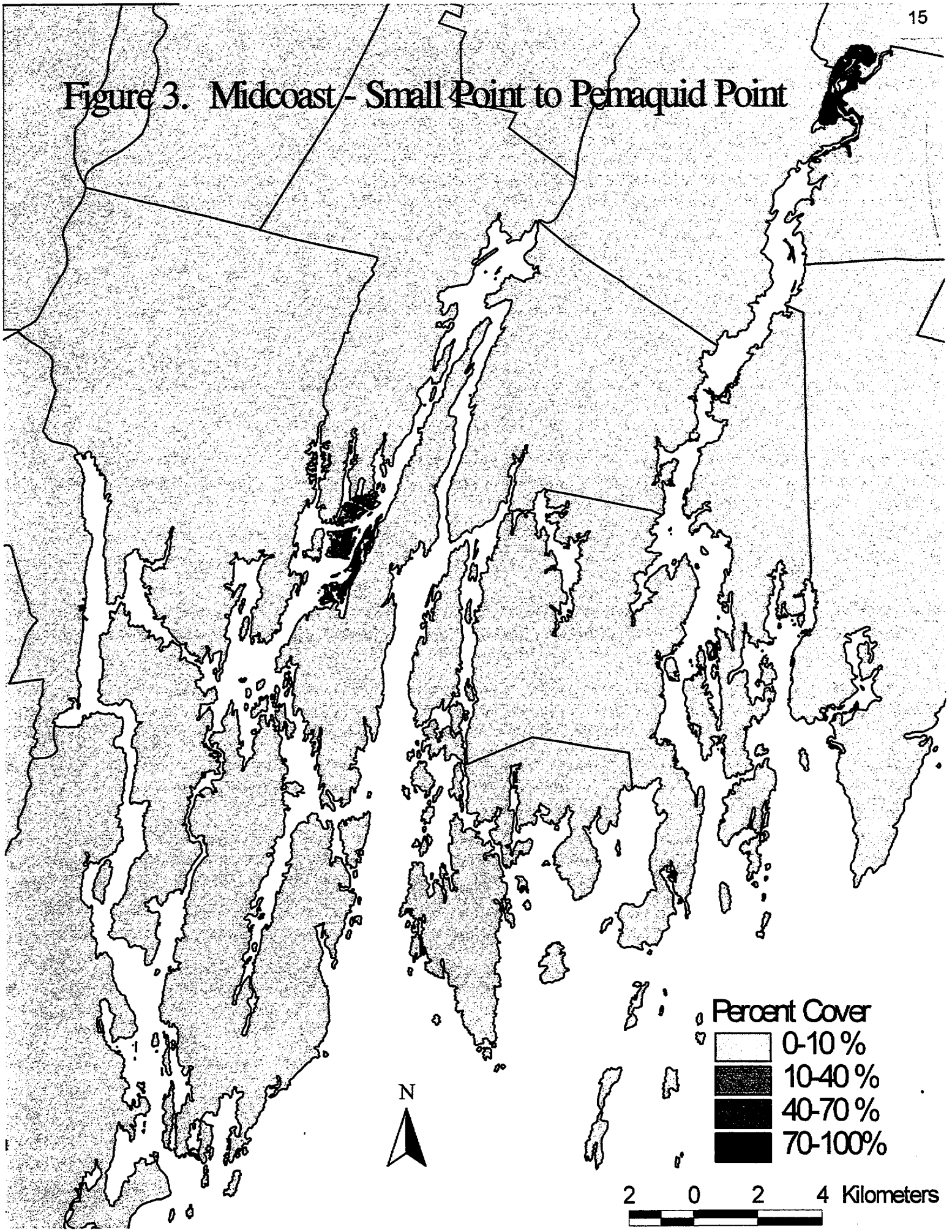


Figure 4 . Penobscot Bay - Owls Head to Stonington

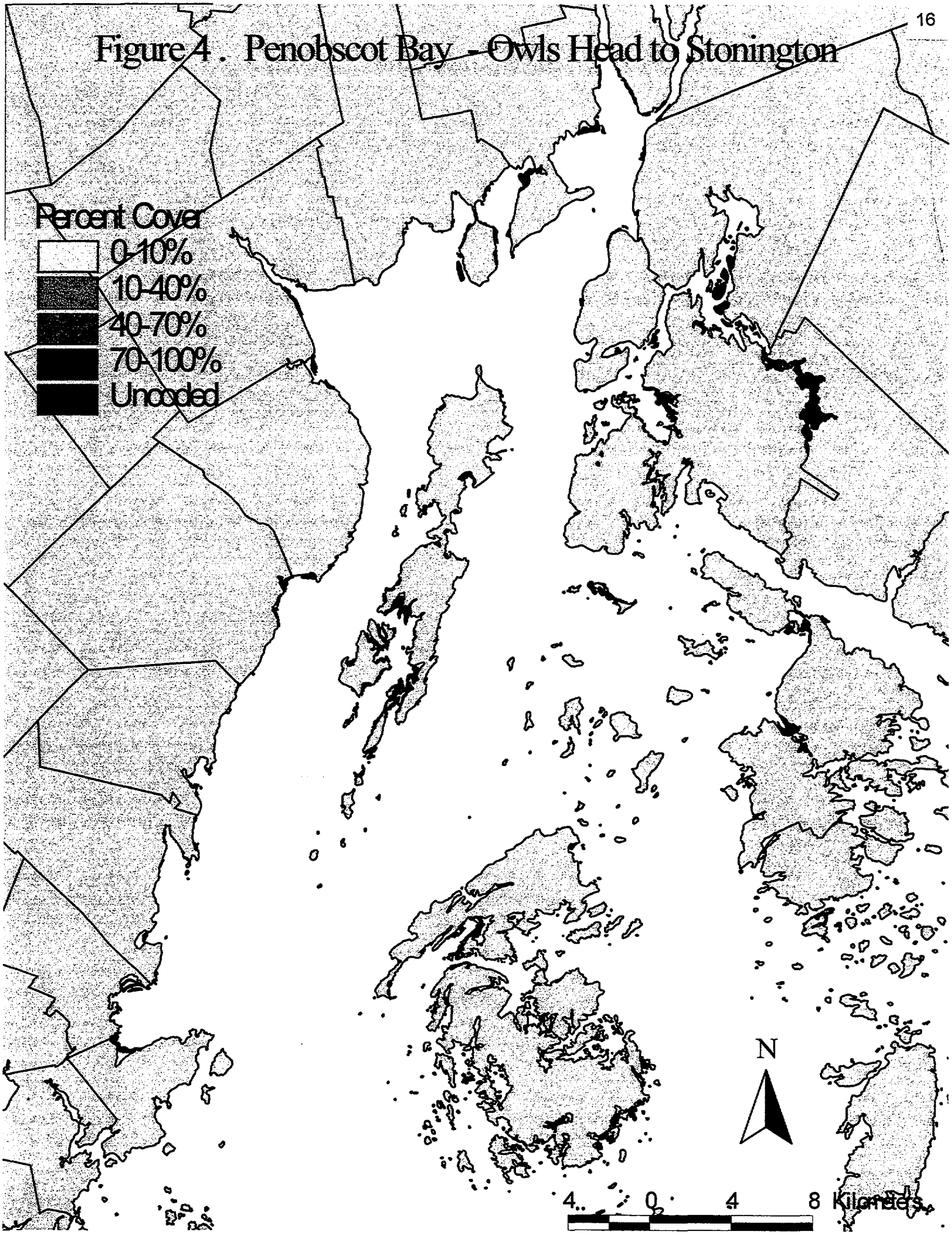


Figure 5. Machias and Little Machias Bays

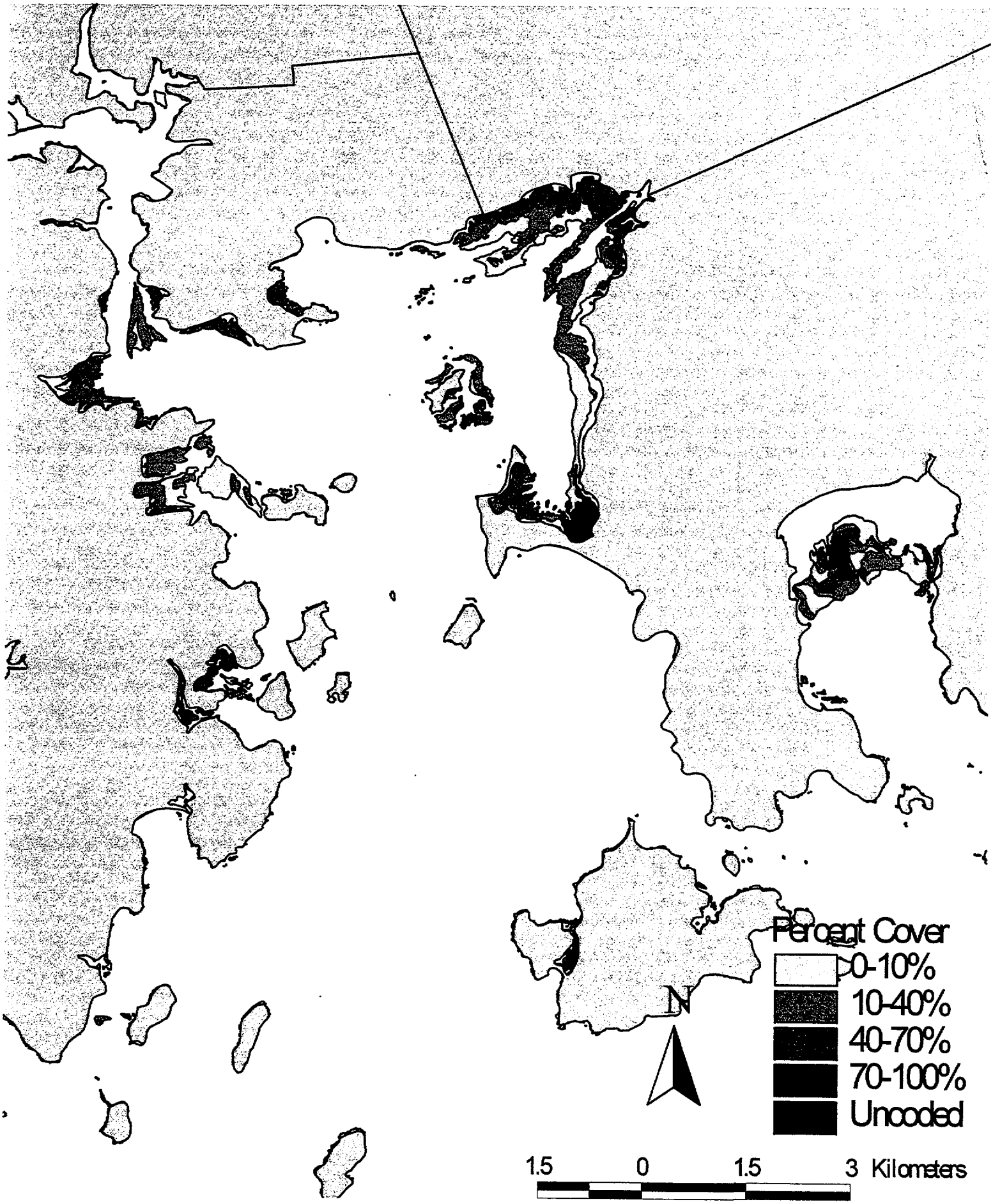
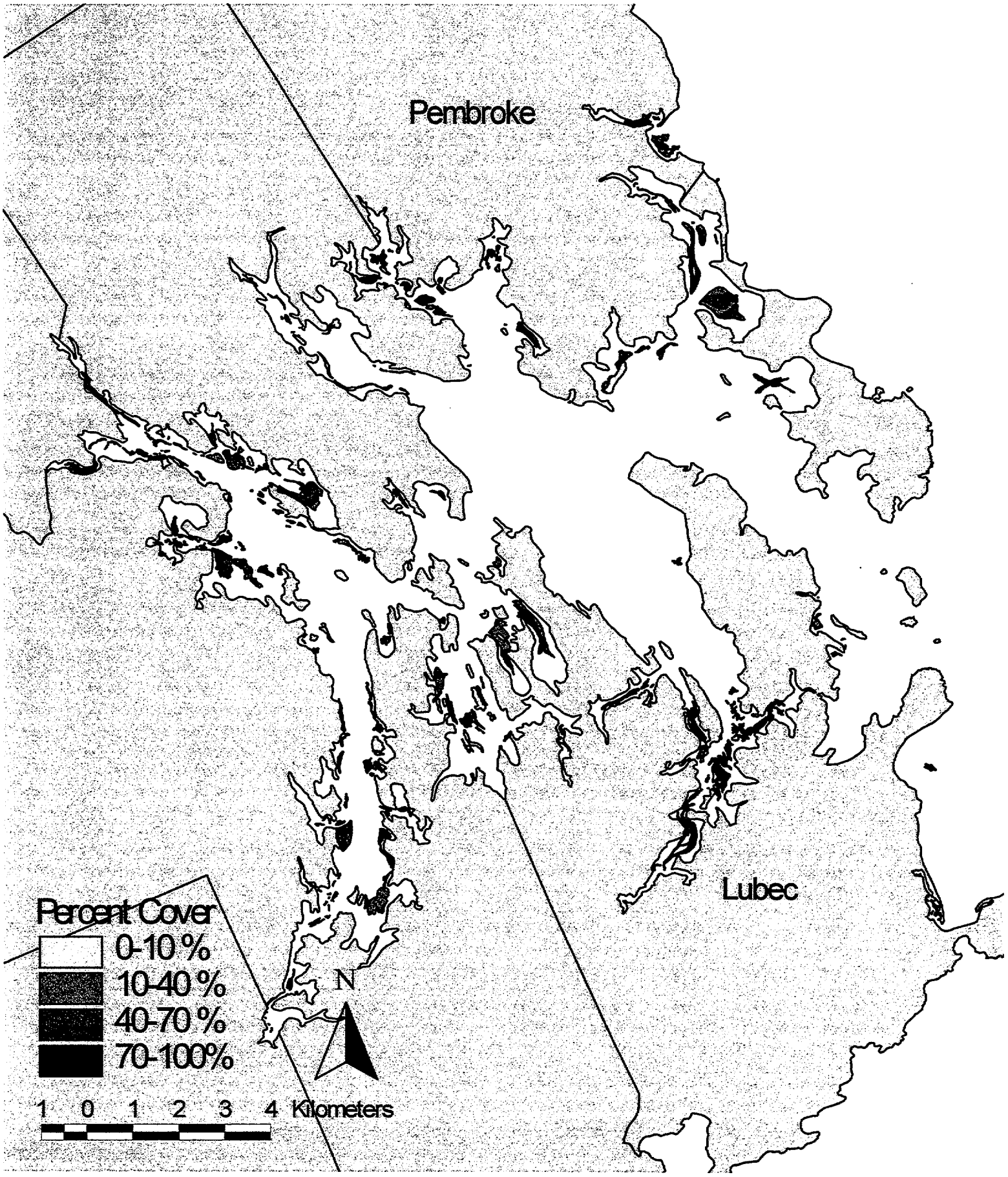


Figure 6. Cobscook Bay and Vicinity



is fastest just after it emerges and decreases with age. Eventually the oldest leaf is sloughed off and replaced by a young rapidly growing leaf.

Flowering shoots develop from the vegetative plants in the second season of growth (Setchell 1929), and the time of flowering is strongly influenced by water temperature. The flowering process requires 30-60 days, and occurs later in the season and lasts longest in the north (Phillips et al. 1983b). Pollination occurs entirely underwater. Cross pollination is normal (DeCock 1980), but self pollination can occur. Pollination depends in part on water movement, perhaps explaining the 14-72% range of successful pollination that has been reported (Churchill and Riner 1978; Orth and Moore 1983a; Kenworthy et al. 1980).

The contribution of seeds to the abundance of eelgrass depends on the abundance of flowering shoots, the number of seeds produced and the rate of seed germination. All of these can vary widely, although there may be a trend towards increased flowering in disturbed sites (Thayer et al. 1984). Unlike seeds deposited in quiescent areas, those deposited in open-water, high-energy habitats with strong currents and considerable wave action may not become established (Fonseca et al. 1982a). In high energy habitats, growth may be restricted to vegetative reproduction.

From New York to Nova Scotia, eelgrass seeds mature between June and July (Silberhorn et al. 1983). In New York, seeds collected in July germinated from October to December; seedling growth and development occurred in autumn and spring but not through the winter (Churchill 1983). Throughout its range, eelgrass biomass peaks in the summer and sharply declines in winter. In northern latitudes shoots produced in early spring will reproduce vegetatively through the summer and early fall.

In Nova Scotia, Maine, and Rhode Island an annual form of eelgrass has been described, although differences in the two forms are ascribed to nongenetic factors (Gagnon et al. 1980). In regions where ice forms in winter, the annual form grows intertidally and in shallow water and the perennial form grows in deeper water (Robertson and Mann 1984). Beds that recolonize by seed each year may not be evident early in the growing season.

POPULATION TRENDS

Disease

Between 1930 and 1933 a "wasting disease" destroyed approximately 90% of the eelgrass throughout its range (Tutin 1942). At the time it was suggested, but never proven, that a marine slime mold was the causative agent. Bacteria, fungi, commercial fish harvesting, pollution, competing organisms, and unusual climatic conditions including reduced light levels were also postulated as the causative agent of the wasting disease (Thayer et al. 1984).

Extensive recolonization by eelgrass over its range did not occur until after 1945 and full recovery, when it occurred, took 30 to 40 years (Rasmussen 1977). Eelgrass in salinities less than 12 to 15 ppt apparently was immune to the wasting disease and eventually formed the stocks for recolonization (Rasmussen 1973). In Chesapeake Bay (Orth and Moore 1981, 1982b) and in Cape Ann, Massachusetts (Dexter 1985) large scale oscillations in abundance, perhaps due to the wasting disease, have occurred since the 1930s. In other areas, eelgrass still has not returned (Thayer et al. 1984).

In the early 1980s, a new outbreak of disease and localized declines in eelgrass abundance occurred on both sides of the Atlantic (Short and Mathieson 1985; Short et al. 1986; Short et al. 1988). The cause of the decline, documented in the laboratory and in mesocosm experiments, was a marine slime mold (*Labyrinthula zosterae*) (Muehlstein et al. 1991) which produced symptoms similar to those of the 1930s wasting disease (Short and Mathieson 1985; Short et al. 1986; Short et al. 1987; Short et al. 1988; Muehlstein et al. 1988; Muehlstein 1989). Burdick et al. (1993) have developed an index, based on visual determination, for assessing and monitoring the progress of the disease.

It is impossible to determine whether the decline of eelgrass in the 1930s resulted in an overall decline in commercially important fish and invertebrates because quantitative data was not available on the fauna that utilize eelgrass beds (Thayer et al. 1984). Biological and geomorphological changes were reported in some places. After eelgrass beds were lost in Denmark, the substrate became coarser and deposits of fine mud adjacent to eelgrass beds changed from anoxic to oxidized sediments (Rasmussen 1973, 1977). In Woods Hole, overall species abundance decreased when eelgrass beds were lost (Stauffer 1937), but similar changes were not seen in Denmark (Rasumssen 1973, 1977). These seemingly contradictory results may reflect differences in sampling technique or differences in eelgrass function with geographic location.

In the United States, catastrophic declines were documented for the Atlantic brant (*Branta bernicla hrota*) and the bay scallop (*Argopecten irradians*) following the 1930s decline of eelgrass; a more limited decline was documented for the Canada goose. Prior to the wasting disease, brant geese fed almost exclusively on eelgrass (Cottam 1934; Cottam et al. 1944; Cottam and Monroe 1954; den Hartog 1977). The decline of the population was exacerbated by hunting and poor reproductive success (Corr pers. comm.). Following the wasting disease, the abundance of bay scallops declined precipitously in North Carolina and Chesapeake Bay. All stages of the bay scallop, which do not occur in Maine, feed on eelgrass-derived detritus (Kirby-Smith 1972; Kirby-Smith and Barber 1974) and the postlarvae settle on eelgrass leaves (Gutsell 1930; Thayer and Stuart 1974). Recovery to commercially harvestable quantities never occurred in Chesapeake Bay and required nearly 30 years in North Carolina (Orth and Moore 1982b).

ECOLOGICAL REQUIREMENTS

Light

Sunlight is the most fundamental requirement for eelgrass because light energizes the reactions of photosynthesis. As light passes through water and the substances dissolved and suspended in it, different wavelengths of light are selectively absorbed, causing the total amount of available light and the range of available wavelengths to decrease with depth. The depth at which eelgrass can grow is limited by the amount of light that reaches the leaf canopy.

A number of experiments using shading devices have shown that reductions in light cause significant decreases in plant density (Backman and Barilotti 1976; Burkholder and Doheny 1968; Short 1975; Short et al. 1993). The density of plants grown in reduced sunlight (63% reduction) was 5% that of plants grown in full sunlight after nine months (Backman and Barilotti 1976). Mesocosm experiments conducted in New Hampshire (Short et al. 1993) demonstrated a logarithmic decline in shoot density and biomass productivity of eelgrass with a decrease in light intensity after five months. Shading appears to have the greatest effect on plants growing in minimal light (Dennison and Alberte 1982).

Temperature

Eelgrass tolerates a wide range of temperatures (0°C to 30°C), but temperature extremes in combination with other factors can have detrimental effects (Thayer et al. 1984) In southern latitudes, exposure and desiccation are a threat, while in northern areas ice moving with winds and tides can scour the bottom and uproot plants. In one winter in Rhode Island, shoot density declined from 4000 to 400/m^2 due to ice (Short 1975).

Salinity

Eelgrass has been reported growing at salinities from nearly fresh (0 ppt) to full strength seawater (35 ppt) or higher (Thayer et al. 1984). An optimum salinity has never been determined. However, salinity may affect seed germination which has been reported to increase as salinity decreases (Lamounette 1977; Phillips et al. 1983a).

Water motion

Several researchers (Phillips 1972; Conover 1964; Short 1975) have noted that the most luxuriant eelgrass beds are usually in areas of moderate to high current speed. Water currents of increased velocity may make nutrients more available to the leaves (Conover 1964, 1968), perhaps accounting for the luxuriant growth. Conover (1964) and Fonseca and Kenworthy (1987) suggested there may be an optimum current speed between 20-40 cm/sec below which metabolism may be limited by diffusion, and above which growth may decline as a result of physical disruption. Higher current velocities and wave action can erode sediments, plants and seeds, prevent deposition, or deposit large amounts of sediment.

Substrate

Eelgrass grows on substrates varying from firm sand to fine mud (Ostenfeld 1908; den Hartog 1970) and occasionally on cobble in New England (Riggs and Fralick 1975; Thayer et al. 1984). Eelgrass distribution apparently is not limited by substrate type as long as the roots and rhizomes can penetrate the substrate (Kenworthy et al. 1982).

Nutrients

Eelgrass can absorb inorganic compounds containing carbon, nitrogen, phosphorus, and trace metals from the sediments via the roots and from the water column via the leaves (McRoy and Barsdate 1970; McRoy and Goering 1974; Penhale and Thayer 1980; Brinkhuis et al. 1980; Short 1981; Thursby and Harlin 1982). The ability to absorb nutrients from either the water column or the sediment contributes to the high productivity that has been documented for eelgrass.

Eelgrass may be nitrogen limited under certain circumstances (Short 1981, 1983a, b; Iizumi et al. 1982). If nitrogen in the water column is insufficient, eelgrass may have to compete with microorganisms for nitrogen in the sediments (Iizumi et al. 1982; Thayer et al. 1984). However, nitrogen regeneration in organic-poor sediments may be inadequate for eelgrass growth (Short 1983a).

ECOLOGICAL FUNCTION

Effect on water motion and sediment dynamics

Several papers have discussed the role of eelgrass in slowing current and promoting sedimentation and sediment stability (Petersen 1918; Marshall and Lukas 1970; Orth 1977; Kenworthy et al. 1982; Fonseca et al. 1982b, 1983). In the laboratory, water currents cause the eelgrass leaf canopy to bend into a compact layer over the substrate, and current speed is reduced in the leaf canopy due to drag forces (Fonseca et al. 1982b; Gambi et al. 1990; Ackerman and Okubo 1993). The reduced velocity near the bottom should enhance the deposition of fine particles and reduce scour (Fonseca et al. 1982b). The network of roots and rhizomes helps to bind sediment, reduce erosion, and preserve the sediment microfauna.

The patterns of water motion and sediment dynamics in an eelgrass meadow are dependent on a number of variables including the size of the meadow, the density of the eelgrass, current velocity, wave energy, the interaction between currents and waves, water depth, fetch, and proximity to inlets, channels, and sediment sources (Thayer et al. 1984). Eelgrass can tolerate current velocities of 120-150 cm/sec, but the configuration of the meadow and percent of fine particles and organic matter in the surface sediment varies with current velocity (Fonseca et al. 1983). Meadows in high current areas (>90cm/sec) may be sources and those in low current areas (<50 cm/sec) may be sinks of eelgrass-based organic matter (Fonseca et al. 1983).

Waves, particularly shallow water waves (water depth:wave length < 1:2), can generate lift forces as a wave trough passes that suspends sediment into the water column (Thayer et al. 1984). Seagrasses are as effective as emergent marsh plants in damping out waves, providing the seagrass canopy extends to the surface of the water. Under these conditions, both seagrasses and marsh plants dampen out wave energy

approximately 1 m into the vegetation (Wayne 1975; Knutson et al. 1982; Fonseca and Cahalan 1992) and may prevent erosion.

Nutrient Cycling

Chemical elements in an ecosystem cycle back and forth between the living organisms and the physical environment in a series of transfers termed biogeochemical cycles. The cycles involving carbon, nitrogen, phosphorus, and the trace metals are extremely important because these elements are vital to the maintenance of life. These elements make up the biomass of living organisms, and also exist in the sediment and water column as inorganic compounds, particulate organic matter, and dissolved organic matter.

Primary producers (autotrophs) alone absorb inorganic carbon, nitrogen, phosphorus, and trace metals, and use the sun's energy to convert them into living organic matter (biomass). Important primary producers in the Gulf of Maine include single-celled organisms (e.g. bacteria, diatoms, dinoflagellates) that drift in the water column as plankton or are associated with the substrate, macroalgae (e.g. rockweed, kelp, Irish moss) that usually are attached to a substrate, and flowering plants (e.g. salt marsh grasses and eelgrass) that are rooted in the substrate and inundated to various degrees. Biomass synthesized by primary producers is the ultimate source of nutrients and energy for heterotrophs (bacteria, other single-celled organisms, and multi-celled animals). Heterotrophs in turn excrete waste products containing inorganic nutrients which are absorbed and utilized by primary producers.

Eelgrass meadows are important in the cycling of nutrients because they 1) can produce large quantities of organic matter, 2) tend to be depositional areas where organic matter is retained, 3) harbor a diverse community of tightly-coupled heterotrophs that consume organic matter and release inorganic nutrients, and 4) are able to absorb nutrients from the water column or the sediment (Thayer et al. 1984). Research in different geographical areas has shown that sediments in eelgrass meadows have a higher concentration of organic matter when compared to sediments in adjacent unvegetated areas (Marshall and Lucas 1970; Thayer et al. 1975; Orth 1977; Kenworthy et al. 1980).

In the sediment, dissolved and particulate organic matter are consumed by heterotrophs ranging from anaerobic bacteria to large invertebrates that require oxygen. These organisms excrete inorganic waste products (ammonium and phosphate). Compared to unvegetated areas, sediments in eelgrass meadows have greater concentrations of ammonium and phosphate (Kenworthy et al. 1982; Billen 1978; Blackburn 1979; Iizumi et al. 1982; McRoy et al. 1972). Other bacteria in the sediment convert nitrogen gas to usable nitrates and nitrites. In addition, eelgrass beds, with their high rates of sedimentation, may act as sinks for metallic elements, and the activity of anaerobic bacteria can make them available for absorption (Wolfe et al. 1976).

In the water column, dissolved and particulate organic matter are consumed by aerobic heterotrophs. These organisms then excrete inorganic waste products containing ammonium and phosphate into the water column.

Eelgrass is able to absorb nitrogen (as ammonium or nitrate) and phosphorus (as phosphate) through its roots, rhizomes, and leaves (Penhale and Thayer 1980; Iizumi et al. 1982; Iizumi and Hattori 1982; Thursby and Harlin 1982; Short and McRoy 1984; Brix and Lyngby 1985). Recent evidence suggests that eelgrass does not significantly contribute to cycling of phosphorus between the sediment and water column (Brix and Lyngby 1985). Eelgrass also is able to absorb elemental metals (cadmium, zinc, iron, copper, manganese, lead, vanadium, and nickel) through its leaves and root/rhizome complex (Faraday and Churchill 1979; Driftmeyer 1980; Driftmeyer et al. 1980; Brinkhuis et al. 1980; Penello and Brinkhuis 1980; Lyngby and Brix 1982; Kurata et al. 1979; Lyngby et al. 1982; Brix et al. 1983).

Food Source

Grazing on live eelgrass

Few organisms feed directly on living eelgrass, perhaps because of the reduced availability of nitrogen compounds, the indigestible structural components of the cell wall, or the presence of toxic or inhibitory compounds (Thayer et al. 1984). Living plant material (eelgrass leaves, shoots, and seeds) reportedly is eaten by approximately 80 species of annelid worms, molluscs, crustaceans, echinoderms, fishes, reptiles, and birds (McRoy and Helfferich 1980; Thayer et al. 1984). American brant, which declined dramatically following the decline of eelgrass in the 1930s used to feed exclusively on eelgrass. In Maine, eelgrass meadows are important winter feeding areas for migratory populations of Canada geese and other waterfowl (Corr pers. comm.).

Grazing on epiphytes

Eelgrass leaves support a large number of epiphytes, organisms that grow on the leaves (use them as a substrate), and that may or may not derive nutrition from the eelgrass (Kikuchi and Peres 1977; Harlin 1980). Epiphytes on eelgrass include bacteria, fungi, microalgae, and macroalgae (Harlin 1980). Epiphytic bacteria utilize organic carbon derived from actively photosynthesizing leaves (Kirchman et al. 1984). Thayer et al. (1978) estimated that 50% of the carbon in the epiphytes may be derived from carbon released by the eelgrass leaf.

Epiphytes are an important source of food for many species of invertebrates, fishes, and birds, some of which are commercially important (Ewald 1969; Caine 1980; Howard 1982; Van Montfrans et al. 1982; Robertson and Mann 1982; Thayer et al. 1984; Van Montfrans et al. 1984). The biomass of the epiphytes may be comparable to the biomass of the eelgrass leaves themselves (Penhale 1977) and their productivity may approach 20% that of eelgrass leaves. In addition to obtaining nutrition, grazing herbivores may enhance the productivity of the eelgrass by cleaning the leaves; excessive epiphytes can reduce eelgrass photosynthesis by shading and perhaps by decreasing diffusion (Sand-Jensen 1977; Van Montfrans et al. 1984; see THREATS).

Consumption of eelgrass-derived detritus

Detritus refers to dissolved organic matter, particulate organic matter, and the assemblage of decomposing bacteria and fungi that inhabits the organic matter (Zieman 1982; Thayer et al. 1984). Dissolved organic matter includes soluble carbohydrates and proteins (Zieman 1982); particulate organic matter includes dead Primary producers or autotroph debris, dead heterotroph or heterotroph debris of any size, fecal pellets, and combinations of these items (Cousins 1980).

As part of the natural life cycle, old eelgrass leaves break away from the base of the shoot and fall to the bottom or are carried away by water currents (Phillips 1984). Whole leaves probably become fragmented by the shredding action of herbivorous invertebrates and by physical factors such as desiccation and ice grinding (Robertson and Mann 1980). In the laboratory, intact green leaves are consumed and shredded by several species of crustaceans, resulting in the production of small detrital particles that are released in the faeces (Robertson and Mann 1980). The intact leaves and leaf fragments become colonized by bacteria and fungi which begin to decompose the eelgrass.

The processes of particle size reduction and microbial colonization and decomposition are essential to the detrital food web,and have been described in detail by Zieman (1982). Particle size reduction is important because some organisms are able to ingest only fine particles, and the greater surface to volume ratio of fine particles allows greater colonization by microbes. The microbes enzymatically break down plant material that most organisms cannot digest, and convert it to microbial biomass which can be assimilated. Microbes also enrich the detritus by taking up nitrogen and phosphorus from the surrounding medium and incorporating it into microbe biomass. Organisms that consume eelgrass-derived detritus obtain most of their nutrition, especially nitrogenous compounds, from the microbes (Zieman 1982). During growth and decomposition, seagrasses release substantial amounts of dissolved organic carbon which is quickly

assimilated by microorganisms. Dissolved organic carbon becomes available to animals only after conversion to microbial biomass (Zieman 1982).

Eelgrass roots and rhizomes are a substantial source of organic matter into the sediment (Thayer et al. 1984; Kenworthy and Thayer 1984). The production and decay of roots and rhizomes contribute large quantities of dissolved and particulate organic matter into the sediments which decays more slowly than leaf material (Thayer et al. 1984). Unlike decomposition in the water column, decomposition in the sediment is largely anaerobic.

Habitat

An eelgrass meadow adds structural complexity to the substrate and water column and offers a variety of habitats for flora and fauna of all sizes. Leaves of varying age and size extend into the water column, and change their orientation with passing waves and as current changes. Epiphytes on the leaves add additional complexity. The dense interwoven roots and rhizomes that penetrate the substrate provide additional unique structure.

Researchers working in different places have reported a greater diversity and abundance of species in eelgrass meadows than adjacent unvegetated areas (Kikuchi 1966; Orth 1973; Thayer et al. 1975; Orth and Heck 1980; Weinstein and Brooks 1983; Stoner 1983; Summerson and Peterson 1984; Bell and Pollard 1989; Heck et al. 1989; Thayer and Chester 1989; Heck and Thoman 1984). However, few comparisons have been made between eelgrass and other vegetated areas (e.g. Sogard and Able 1991).

A functional classification of the flora and fauna of Japanese eelgrass beds (Kikuchi 1966, 1980; Kukuchi and Peres 1977) probably is valid for Maine and includes: 1) epiphytic organisms on eelgrass blades (macroalgae, microalgae and their associated microfauna and, meiofauna; sessile fauna attached to the blades; mobile fauna crawling on the leaves; swimming fauna that rest on the leaves; 2) biota that attach to blade stem and rhizomes, 3) mobile fauna that swim within and over the leaf canopy (includes diurnal or seasonal transients or permanent residents), and 4) epibenthic and infaunal invertebrates that dwell on or within the sediments. Harlin (1980) has compiled a list of 124 species of animals that have been reported on eelgrass blades.

The benthic and epibenthic fauna associated with eelgrass varies with latitude because there is a wide variation in temperature, other physical factors, and biological factors over the range of eelgrass (Thayer et al. 1984). Cape Cod and Cape Hatteras, divide the eastern United States into three zones that differ in climate, physiography, and hydrography. The species associated with eelgrass in each area also differs (Thayer et al. 1984). Species composition may even change within the same estuary or within a particular eelgrass meadow depending on salinity, sediment grain size, hydraulic regime, degree and type of physical disturbance (Thayer et al. 1984).

Many researchers have demonstrated that eelgrass meadows are nursery areas for commercially or recreationally important species or for species which are important as food for fish and birds (Thayer et al. 1984). Research conducted in Chesapeake Bay, North Carolina and other temperate areas showed, in general, that the density and diversity of the fish and decapod assemblage associated with eelgrass meadows was greater than that of unvegetated areas, and that the assembly displayed diel, tidal, and seasonal changes in abundance and composition (reviewed in Thayer et al. 1984). However, species of fishes that are common in eelgrass beds also are characteristic of other vegetated habitats (Weinstein and Brooks 1983). The large mobile animals found in seagrasses can be placed into four functional groups: permanent residents, seasonal residents, transients, and casual species (Kikuchi 1980).

In the southern Gulf of Maine, 40 species of fishes and 9 species of invertebrates have been collected from eelgrass beds (Table 2). These collections have been made in Hingham Harbor, Nahant Harbor and Gloucester Harbor, Massachusetts (Colarusso pers comm.); Great Bay, New Hampshire (Short 1992); the Nauset Harbor area, Massachusetts (Heck et al. 1989); and Jordan River, Maine (Newell et al. 1991). Some of the species are commercially important (e.g. Atlantic cod and American lobster), some are important forage species (Atlantic silversides and sand shrimp), and others are top-level predators (wolffish).

Stomachs of many of the larger fish (striped bass, cod, pollack, hake, tautog, and flounders) contained invertebrates which are more abundant in eelgrass beds than in adjacent unvegetated areas (Colarusso pers. comm.).

Eelgrass beds at the mouths of some estuaries in Maine are the sites of extensive primary settling by drifting blue mussel (*Mytilus edulis*) larvae (Hidu et al. 1988; Newell et al. 1991). The baffling effect caused by the undulation of eelgrass in response to rapid tidal currents (the "honami" effect) may serve to trap the larvae (Thayer et al. 1984; Hoven et al. 1991).

Several researchers have demonstrated the use of eelgrass beds by juvenile American lobsters (*Homarus americanus*). Barshaw and Bryant-Rich (1988) conducted an 8-month study on the behavior, growth, and survival of early juvenile American lobsters in three habitats: mud, rock with algae, and eelgrass. Rock and eelgrass were better habitats for the creation and maintenance of burrows, but lobster in eelgrass had a lower mortality rate than lobsters in rock or mud. In a Cape Cod estuary, the abundance of juvenile lobsters was greater in eelgrass beds than in adjacent unvegeated areas (Heck et al. 1989). Short et al. (in press) found that juvenile lobsters (average carapace length of 50 mm) were residents of eelgrass beds in the Piscataqua River, New Hampshire and Maine.

CONCLUSION

Extensive studies of eelgrass have been conducted along the east coast of the United States (specifically North Carolina, Chesapeake Bay, and the Gulf of Maine), the west coast of the United States, in Europe and in Japan since the 1970s. These studies collectively have shown that eelgrass 1) helps stabilize sediments and control erosion, 2) contributes to nutrient cycling, 3) directly provides food to grazers and indirectly provides food to detritus feeders and epiphyte grazers, 4) helps maintain water quality, and 5) provides habitat for numerous species including commercially and recreationally important species.

THREATS

The major verified threats to eelgrass include reductions of light levels due to eutrophication, degradation of water quality, and physical structures; episodic outbreaks of the wasting disease; physical disturbance; and overharvesting. In addition, a number of chemical substances may affect eelgrass, but cannot be considered as verified threats at this time. For example, the literature is ambiguous concerning the effects of petroleum hydrocarbons on eelgrass, but this ambiguity could be explained by eelgrass being differentially sensitive to the various types of hydrocarbons (Fred Short pers. comm.). Little data are available regarding the effects of pesticides, herbicides, chlorine, CCA (chromated copper arsenate) pressure-treated wood, and heavy metals have on eelgrass, especially in areas with strong tidal mixing. Future research may reveal these chemicals to be a threat to eelgrass.

Reduction of light levels due to degradation of water quality by nutrient loading is one of the greatest threats to eelgrass (Dennison et al. 1993). Nutrient loading can result from point sources such as wastewater treatment facilities and aquaculture sites and from non-point sources such as runoff from agriculture, animal wastes, and fertilized lawns (Short 1992). Excessive nutrients promote the rapid growth of phytoplankton in the water column, epiphytes on eelgrass leaves, and entangling macroalgae, all of which can reduce amount of light reaching the eelgrass, and thus destroy the eelgrass beds (Orth and Moore 1983b; Kemp et al. 1983; Twilley et al. 1985; Dennison 1987; Dennison et al. 1989).

Reduction of light levels due to sediment loading also is one of the greatest threats to eelgrass. Sediment loading can result from point and nonpoint sources of upland runoff and from resuspension of sediment by tidal currents, wave action, dredging, filling, boating activity, and fishing activity (Short 1992; Colarusso pers. comm.). Sediment suspended in the water column reduces the amount of light that penetrates the water, thus reducing the light that reaches eelgrass rooted on the bottom (Dennison 1987). The impact of suspended sediment in the vicinity of eelgrass may vary with hydrographic conditions, sediment grain size, time of year, distance from the sediment, health of the rockweeds, and a host of other variables. As

Table 2. Species of fishes and invertebrates collected from eelgrass beds in the southern Gulf of Maine.

Species/Reference	Common name	Season of use	Frequency of occurrence
Fishes			
Alosa aestivalis [1]	Blueback herring	spring	common
Alosa pseudoharengus [1,2]	Alewife	spring	common
Alosa sapidissima [2]	American shad		
Ammodytes americanus [3]	Sandlance		
Anarhichas lupus [1]	Wolffish	spring	rare
Anguilla rostrata [3]	American eel		
Apeltes quadricus [2,3]	Four-spine stickleback		
Brevoortia tyrannus [1]	Menhaden	spring, summer, fall	common
Centropristis striata [3]	Rock sea bass		
Clupea harengus harengus [3]	Herring		
Cyclopterus lumpus [1,2,3]	Lumpfish adults; juveniles	spring; summer, fall	occasional; common
Fundulus heteroclitus [2,3]	Mummichog		
Fundulus majalis [1]	Killifish		
Gadus morhua [1]	Atlantic cod	summer, fall	common
Gasterosteus aculeatus [1,2,3]	Three-spine stickleback	spring, summer, fall	common
Macrozoares americanus [1]	Ocean pout	spring	common
Menidia menidia [1,2,3]	Atlantic silverside	spring, summer, fall	common
Microgadus tomcod [1,2,3]	Atlantic tomod	summer, fall	common
Morone saxitilis [1]	Striped bass	spring, summer, fall	common
Myxocephalus aenaeus [1,3]	Grubby	spring, summer, fall	common
Myxocephalus scorpio [1]	Shorthorn sculpin	spring, summer, fall	common
Odontaspis taurus [1]	Sand tiger shark	summer	rare
Osmerus mordax [1,2]	Rainbow smelt	occasional	spring
Paralichthys dentatus [1]	Summer flounder	occasional	spring
Pholis gunnellus [1]	Rock gunnel	occasional	summer
Pomatomus saltatrix [1]	Bluefish	occasional	summer
Pollachius virens [1,3]	Pollock	spring, summer	common
Prionotus carolinis [1]	Searobin	spring	rare
Pleuronectes americanus [1,2,3]	Winter flounder	spring, summer, fall	common
Raja erinacea [1]	Little skate	spring, summer, fall	common
Raja ocellata [1]	Winter skate	spring, summer, fall	common
Scomber scombrus [1]	Atlantic mackerel	spring	occasional
Pungitius pungitius [2]	Nine-spine stickleback		
Scopthalmus aquosus [1]	Windowpane flounder	spring	occasional
Syngnathidae fuscus [1,2,3]	Northern pipefish	spring, summer, fall	common
Stenotomus chrysops [3]	Scup		
Stichaeus punctatus [3]	Arctic shanny		
Tautogolabrus adspersus [1,2,3]	Cunner	spring, summer, fall	common
Tautoga onitus [1,3]	Tautog	spring; summer	occasional; rare
Urophycis chuss [3]	Red hake		
Urophycis tenuis [1]	White hake	spring, summer	occasional
Invertebrates			
Crangon septemspinosa [3]	Sand shrimp		
Carcinus maenas [3]	Green crab		
Cancer irroratus [3]	Rock crab		
Hippolyte zostericola [3]			
Homarus americanus [3]	American lobster		
Libinia dubia [3]			
Mytilus edulis (larvae) [4]	Blue mussel		
Pagarus acadianus [3]			
Palaemonetes vulgaris [3]	Grass shrimp		

1 = Colarusso pers comm.; 2 = Short 1992; 3 = Heck et al. 1989; 4 = Newell et al. 1991.

eelgrass beds decline or are eliminated, their capacity for stabilizing the sediment is reduced or eliminated. The sediment may be more easily resuspended, making regrowth of eelgrass problematic. Unstable sediments result in communities with reduced abundance and reduced diversity. Reduction of light levels also occurs when physical structures such as docks and piers are placed over or in the vicinity of eelgrass beds.

Presently there are no treatments that can prevent the wasting disease or relieve its deleterious effects. For example, between 1981 and 1989, most of the eelgrass in the Piscataqua River and approximately 80% of the eelgrass in Great Bay, New Hampshire, was lost due to the wasting disease (Short et al. 1993). In addition, the loss of eelgrass from the wasting disease is exacerbated by reduction of light levels and physical disturbances (Short et al. 1991). If these other stresses are reduced then eelgrass may be better able to survive or recover from an outbreak of wasting disease.

Direct physical disturbances include the burying and uprooting of eelgrass. Indirect physical disturbances include alteration of the current velocity, wave action, substrate or depth where eelgrass plants are growing. Filling projects can cover eelgrass with large amounts of sediment. Dredging, fishing and boating activity can uproot eelgrass plants and resuspend sediments. Dredging and filling projects which alter the physical environments by changing current velocity, wave activity, substrate composition, and depth to the bottom can prevent eelgrass from maintaining itself through vegetative and sexual reproduction.

Overharvesting is a potential threat to eelgrass. In Canada, eelgrass currently is harvested and made into a natural, non-toxic insulation (Fred Short pers. comm.). If this new industry is profitable, harvesting of eelgrass could easily arise along the coast of Maine.

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ROCKWEEDS

IDENTIFICATION AND DESCRIPTION

Five species of brown fucoid algae, *Ascophyllum nodosum* (and its unattached *scorpiodes* form), *Fucus vesiculosus*, *F. evanescens* (formerly *F. distichus* subsp *evanescens* and subsp *edentatus*), *F. distichus*, and *F. spiralis* are found along the Maine coast. In terms of biomass and percent cover of substrate, *A. nodosum*, *F. vesiculosus*, and *F. evanescens* are the most important species (Vadas, pers. comm.). *F. distichus* is described as a small tidepool species, however, a non-tidepool member of the complex has been reported in southern Maine (Sideman and Mathieson 1983) and Nova Scotia (C. Bird pers. comm). *F. spiralis* has a limited distribution in the high intertidal zone.

Algae are relatively simple in structure. They lack well-developed tissue systems, and have no true roots, stems or leaves. The five species of fucoid algae described here, commonly referred to as rockweeds, range in color from dark brown to olive green due to the presence of fucoxanthin, a brown xanthophyll accessory pigment which tends to obscure the greenish chlorophyll (Lüning 1990). Rockweeds attach to the substrate by an expanded holdfast. The thalli or fronds of the algae have dichotomous or pinnate strap-shaped branches, usually with buoyant air bladders (Taylor 1957). The branches of the four *Fucus* species have a thickened midrib, whereas the branches of *A. nodosum* do not (Taylor 1957).

DISTRIBUTION

The five species of rockweeds occur primarily in the Cold Temperate North Atlantic marine biogeographic region, limited by the 10°C summer/0°C winter isotherms in the north and by the 15°C summer/10°C winter isotherms in the south, and to a lesser extent in the Arctic region (Lüning 1990). *A. nodosum* and *F. vesiculosus* are found on both sides of the Atlantic Ocean from Greenland to Virginia and from the Barents Sea to Portugal, i.e., from approximately 71°N to 38°N (Lüning 1990). Scattered populations of *F. vesiculosus* occur father north along Baffin Island and south on the northwest coast of Africa (Lüning 1990). A small, introduced population of *A. nodosum* also exists in San Francisco Bay (P. Silva pers. comm.). *F. spiralis* occurs from Newfoundland to Delaware (50°N to 38°N), from Finland to northwest Africa (70°N to 20°N), and sporadically along the coast of Washington, British Columbia, and Alaska (Lüning 1990). *F. evanescens* and *F. distichus* range from Greenland and Iceland (80°N) to Delaware (38°N) and the English Channel (50°N) (Lüning 1990). Members of the *F. distichus* Powell complex also occur on the Pacific coast (Lüning 1990).

In the Gulf of Maine, the rockweeds typically occur in the intertidal zone at a particular height, and these striking patterns of vertical zonation have received a great deal of attention (Norton 1986). *F. spiralis* is found in the upper intertidal zone, *F. vesiculosus* and *A. nodosum* in the mid-intertidal zone, *F. evanescens* in the low-intertidal zone, and *F. distichus* in tidepools in the intertidal zone (Taylor 1957; Mathieson and Guo 1992). Desiccation and overheating (see Ecology) and biological interactions have been identified as critical factors controlling the zonation of intertidal fucoid algae. The experimental removal of algal competitors and animal grazers allowed some species of rockweeds to expand upshore and downshore of their normal range (Burrows and Lodge 1951; Menge 1975; Schoenbeck and Norton 1980; Hawkins and Hartnoll 1985).

The rockweeds can grow in the subtidal zone (e.g., Lubchenco 1980; Serrão et al. 1996), although some appear to be better suited to the intertidal zone. In Rhode Island, plant density was greater in an intertidal population of *A. nodosum* (91 plants/m^2) than a subtidal population (50 plants/m^2), and the intertidal plants had a higher capacity for photosynthesis and nitrate uptake (Peckol et al. 1988).

In many areas, the distribution and abundance of the species of rockweeds varies with exposure to waves and currents. Menge (1976) examined the effect of exposure on the rocky intertidal community at six sites in Maine and Massachusetts. He reported that at the most exposed site (Pemaquid Point), *F. evanescens*

covered less than 10% of the substrate; at the third most exposed site (Chamberlain), *F. evanescens* covered 50 to 90% of the substrate; at the fifth most exposed site, *F. vesiculosus* covered 50 to 90% of the substrate; at the most protected site (in Massachusetts), *A. nodosum* covered 50 to 90% of the substrate. However, in the Bay of Fundy, *A. nodosum* dominated the intertidal zone with high biomass under all conditions of exposure, and *F. vesiculosus* was common, but its distribution was unrelated to exposure (Thomas 1994).

A. nodosum is the most abundant intertidal alga in the Gulf of Maine, and *F. vesiculosus* ranks second in abundance (Keser et al. 1981). On moderately exposed and sheltered shores in the Damariscotta-Pemaquid region of Maine, *A. nodosum* accounts for 50 to 90% of the substrate cover with average densities ranging from 390 to 521 plants/m^2 (Keser et al. 1981). Estimates of *A. nodosum* biomass in this region were 3 to 6 kg dry weight/m^2 depending on the exposure (Vadas 1972; Vadas et al. 1976). In Cedar Point, New Hampshire, *A. nodosum* (plus its unattached form) and *F. vesiculosus* accounted for an average of 98.3% of the intertidal algal biomass each month of a 15-month study, and maximum summer biomass was 1.36 to 1.68 kg dry weight/m^2 (Chock and Mathieson 1983).

LIFE CYCLE

The generalized life cycle of the five species of fucoid algae is rather simple. The gametes are released into the water column where fertilization occurs. The resulting embryos quickly sink to the substratum, and attach within several hours after fertilization as adhesive cell wall materials accumulate (Evans et al. 1982). Embryos of summer and winter reproducing species may take four hours to two days to attach, respectively, because the accumulation of adhesive material is temperature dependent (Bird and McLachlan 1974). The microscopic embryos begin to grow, becoming visible at a length of approximately one millimeter. Growth involves an increase in thallus length and the number of branches. Typically, each *A. nodosum* shoot forms an air bladder or vesicle each year, a growth pattern that has been used to estimate age and productivity (Cousens 1984). During the year, portions of the thallus may be torn off as a result of wave action or ice scouring, and vegetative propagation may occur from the holdfast. Eventually the adult plant develops reproductive structures where gametes are produced.

The time of reproduction varies with each species. *A. nodosum* reproduces in late spring and early summer, *F. vesiculosus* principally in autumn but also in early winter and spring to early summer in Maine, *F. evanescens* in autumn and spring, *F. spiralis* in summer and *F. distichus* principally in winter (Mathieson and Guo 1992; Brawley and Johnson 1992). The release of gametes in *A. nodosum* is correlated with specific temperatures (Bacon and Vadas 1991), and has a lunar or possibly a semilunar periodicity in estuaries (Lambert and Brawley 1993). Fucoid algae do not release gametes when hydrodynamic conditions are turbulent, even when other factors are favorable (Serrão et al. 1996a)

The tiny zygotes are passively dispersed and probably come into contact with substrate as a result of downward turbulence (Norton 1986). Survival "depends on settlement and attachment in an appropriate place because the zygotes are not equipped for dormancy like seeds," they are probably not able to actively select an appropriate substrate, and they cannot move if conditions later become unfavorable (Norton 1986). Most zygotes settle within a few meters of the parent plant, but Burrows and Lodge (1950) reported *Fucus* plants arising more than 60 m away from the nearest group of parent plants.

Mortality is high for the microscopic, early post-settlement stages (zygotes and embryos). Vadas et al. (1992) reviewed 23 factors and/or processes that have been reported to affect mortality in these stages. These factors and processes include grazing by herbivores, canopy effects (e.g. cover, sweeping and reduced light), turf effects (barrier to settlement), desiccation, water motion, competition by faster growing ephemeral algae, sediment/silt, and scour. Research has established that 90 to 100% of *F. vesiculosus* zygotes die within 17 days of settlement (Bray and Norton unpublished data) and that the mean life expectancy of newly settled *A. nodosum* zygotes is 10 days (Miller and Vadas 1984).

For some species (e.g., *F. gardneri* on the west coast of Canada), new recruits to the population arise only from zygotes (Ang 1991), but for others, populations may be maintained by vegetative propagation from the holdfast. Vadas and Wright (1986) observed no sexual recruitment in over 20 years in a population of *A. nodosum* on exposed shores in Maine; all the new shoots arose from vegetative sprouting. This lack of recruitment of *A. nodosum* in exposed areas is probably due to its slow growth and inability to settle when exposed to energetic wave action and high flow rates. Vegetative regrowth and canopy regeneration may be reduced if the holdfast is damaged. McCook and Chapman (1992) found only 20 to 30% of experimentally damaged holdfasts of *F. vesiculosus and F. evanescens* sprouted large numbers of shoots.

Growth rates vary with species, developmental stage, location, and season. Young *A. nodosum* grow very slowly compared to the four species of *Fucus*, and may reach only 1 to 2 mm at one year of age (Chapman and Johnson 1990). Growth rates of adult *A. nodosum* plants in Canada range from 5 to 20 cm/year, and are temperature dependent (CAFSAC 1992). The growth of species of *Fucus* was highly variable within and among sites in Connecticut (Keser and Larsen 1984), but the general pattern consisted of slow to moderate growth during winter and early spring and rapid growth through summer and autumn (Brinkhuis 1977; Brinkhuis and Jones 1976; Chock and Mathieson 1976; Mathieson et al. 1976). In Norway, the apical growth of *F. evanescens* (*F. distichus spp edentatus*) was greatest in July, but growth in March at 4 to 4.2°C was 45% of growth in July (Strömgren 1985).

The five species of fucoid algae are perennial plants with very different life spans. Keser et al. (1981) and Vadas (unpublished data) counted the number of vesicles (air bladders) on the longest unbroken shoot of plants in mid-coast Maine and estimated that shoots of *A. nodosum* plants may reach 16 to 18 years of age. The holdfasts may be a great deal older (Vadas pers. comm.). In Monsweag Bay and at Pemaquid Point, 98 to 99% of the *A. nodosum* shoots were 0 to 6 years old, while in the Damariscotta estuary 98% of the shoots were 0 to 13 years old (Keser et al. 1981). In contrast, the life span of *F. vesiculosus* in the region was 2 to 4 years (Keser et al. 1981).

There are a number of productivity estimates for adult *A. nodosum*. Cousens (1984) estimated the net productivity in Canada to range from 0.61 to 1.9 kg dry weight/m^2/year. Chock and Mathieson (1979) estimated productivity in New England at 1.5 kg/m^2/year by measuring standing crop on two dates. Keser (1978) estimated the productivity of harvested areas in Maine to be 1.86 kg/m^2.

POPULATION TRENDS

No overall trends have been reported for the rockweeds, but there are some regional trends in Europe. *A. nodosum* and *F. vesiculosus* disappeared from the inner part of the Oslofjord (Bokn and Lein 1978), but recently populations of these species have reappeared (Bokn et al. 1992). The depth penetration of *F. vesiculosus* decreased in the Baltic Sea from 11.5 m in 1943-44 to 8.5 m in 1984 at 10 of 11 stations (Kautsky et al. 1986; Kautsky 1991). Near Kiel, Germany, *Fucus* currently occurs no deeper than two meters, and there has been a 95% decline in biomass since the 1950s (Vogt and Schramm 1991). In the Archipelago Sea in Finland, there has been a decline in biomass of *F. vesiculosus* (Roennberg et al. 1985; Kangas et al. 1982; Haahtela 1984). In each case, the changes have be attributed, in part, to increased nutrient levels and eutrophication, which have changed the competitive balance between fucoid algae, ephemeral green algae, and grazers.

ECOLOGICAL REQUIREMENTS

Light

Sunlight is a fundamental requirement for the five species of rockweeds because light energizes the reactions of photosynthesis. However, the amount and spectral characteristics of available light varies with latitítude, season, water type, and depth (reviewed in Lüning 1990). As light passes through water and the substances dissolved and suspended in it, different wavelengths of light are selectively absorbed, causing

the total amount of available light and the range of available wavelengths to decrease with depth. Dring (1987) developed a model of the light environment in the intertidal zone to overcome the difficulties of making intertidal measurements. The model incorporated surface integrated light values, constantly changing water levels, water clarity, and the interactions of tidal and solar cycles.

The relationship between photosynthesis and light intensity (irradiance) is described by a parabolic curve (Lüning 1990; Chapman 1995b). The compensation irradiance (I_c) is the minimum amount of light needed for the plant to survive, i.e., at this light level the rate of photosynthesis equals the rate of respiration. As light intensity increases above the compensation irradiance, the photosynthetic rate first increases in a linear fashion, then plateaus as photsynthetic enzymes become light-saturated, and finally may decrease due to photoinhibition (Lüning 1990; Chapman 1995b). For a particular plant, the photosynthesis-versus-light relationship is the result of genetic adaptation and acclimation (Ramus 1981). Saturation irradiances for growth were estimated to be 90 to 100 W/m^2 for *A. nodosum* and 60 to 70 W/m^2 for *F. vesiculosus* and *F. spiralis* from the west coast of Sweden in a natural daylight regime in September (Strömgren and Nielsen 1986). Strömgren and Nielsen (1986) also reported that maximum growth rate occurred early in the morning and declined throughout the remainder of the day. However, at this site, tides are almost nonexistent, and growth patterns would differ in the intertidal zone.

Insufficient irradiance in turbid water has been posited as controlling the lower limits of intertidal fucoid algae (Dring 1984). Ramus et al. (1977) found decreased growth in excised pieces of *A. nodosum* and *F. vesiculosus* grown at various depths in the turbid waters of Long Island Sound when compared with pieces grown at the surface; despite an increase in light-harvesting pigments at depth. In addition, the maximum photosynthetic capacity of *F. vesiculosus* was about twice that of *A. nodosum* (Ramus et al. 1977).

Fucoid algae may be more sensitive to light quality than to light quantitity. They can survive in the dark for long periods, and they are protected against damage at high light levels (summarized in Chapman 1995b). Young fucoid plants die after exposure to yellow-green or orange light at photon fluence rates of 100μmol/m/s for 4 to 6 weeks (McLachlan and Bidwell 1983). These are the colors of light that penetrate best in turbid coastal waters. Under normal conditions, however, young fucoid plants have plenty of full spectrum light at and near low tide, even in turbid waters.

Light also may be used as an environmental signal to synchronize growth and reproduction to the seasonal cycle. For *A. nodosum* the onset of reproduction is under the control of short daylengths (Terry and Moss 1980).

Water

The rockweeds that occur in the intertidal zone can grow and thrive under conditions of continual submergence in water, however, they are physiologically adapted to periodic emersion in air during low tide and the subsequent stress of desiccation (Chapman 1995b). Schonbeck and Norton (1979a) showed that *F. spiralis* grew best when submerged, and grew rapidly only if illuminated while submerged. Hydrated *F. evanescens* and *A. nodosum* photosynthesized faster in air than in water, perhaps because of better illumination or the higher diffusion rate of CO_2 (inorganic carbon is required for photosynthesis) in air than water (Johnson et al. 1974; Johnston and Raven 1986), but photosynthesis began to shut down as the plants became dehydrated (Dring and Brown 1982). Photosynthesis in air was not greater for *F. vesiculosus* (Bidwell and McKachlan 1985).

The rockweeds have no mechanisms to prevent or slow water loss when exposed to air, they simply tolerate desiccation (Norton 1986). The species differ in their ability to tolerate desiccation and then resume photosynthesis, and these differences in tolerance are related to their vertical position in the intertidal zone (Schonbeck and Norton 1978). For example, *F. spiralis* survived four times longer than *F. vesiculosus* and *A. nodosum* under similar drying conditions (Schonbeck and Norton 1978). The rate and extent of recovery of phosphate uptake following severe desiccation and resubmergence increased with height on the shore (Hurd and Dring 1991). For five species of brown algae from different tidal heights along the shores of Ireland and Helgoland, photosynthesis increased as up to 25% of tissue water was lost, then photosynthetic

rate decreased with further desiccation (Dring and Brown 1982). Recovery from severe desiccation took about two hours in all species, but the extent of recovery from a given degree of desiccation was greatest in upper shore species. *F. spiralis* showed complete recovery from 80 to 90% water loss and *F. vesiculosus* from 70%.

Desiccation tolerance varies as a result of previous experience (hardening) and season, being maximal in summer and declining in winter (Schonbeck and Norton 1979b). It is likely that the smallest stages in the life history are more susceptible to desiccation than large plants. Brawley and Johnson (1993) showed that mortality of zygotes and embryos was highly correlated with desiccation as measured by agarose bead hydration, a technique that should facilitate study of these microscopic stages.

Temperature

Temperature tolerance is considered a major determinant of seaweed distribution (van den Hoek 1975; Lüning 1990). The rockweeds tolerate a wide range of water temperatures from 0 to 28°C (Lüning 1990), although high summer temperatures in combination with desiccation represent potential lethal stress to intertidal rockweeds (Norton 1986). In mid-coastal Maine, *A. nodosum* and *F. vesiculosus* grew where the water temperature ranged from 0° to 4°C in winter and 12° to 22°C in summer (Keser et al. 1981). In northern Europe, *A. nodosum* survived from 0° to 25°C when collected in winter, but survived to 28°C when collected in summer; *F. spiralis* and *F. vesiculosus* survived from 0° to 28°C (Lüning 1984). When several species of fucoid algae were grown at temperatures from 2.5°C to 35°C, a temperature optimum below 17.5°C was indicated, and high temperatures of 30° to 35°C were lethal to all species (Strömgren 1977). In other experiments, summer plants were more tolerant of high temperature and had a higher temperature optimum than winter plants, but winter plants had a higher net rate of photosynthesis at 5° to 30 C than summer plants (Niemeck and Mathieson 1978). Thermal discharges from the Maine Yankee Atomic Power Plant in Monsweag Bay raised water temperatures 7° to 15°C, and resulted in decreased biomass and percent cover of *A. nodosum* and *F. vesiculosus* near the discharge channel (Vadas et al. 1976).

Low winter temperatures also represent potential lethal stress to intertidal rockweeds (Davison et al. 1989; Pearson and Davison 1993). Experiments show that the species do not differ in the freezing point of their tissue during slow cooling, but they do differ in their freezing tolerance (Pearson and Davison 1993). Overall, laboratory experiments on fucoids from Maine shows that freezing tolerance is often correlated with vertical position in the intertidal zone (Davison et al. 1989; Pearson and Davison 1993; reviewed in Chapman 1995b). The freezing points of nine species of red and brown algae from the coast of Maine were similar, however, the recovery of photosynthetic capacity following freezing and thawing was related to tidal height, and species lower on the shore recovered slower (Pearson and Davison 1993). However, the importance of stress itolerance n determining the community structure of intertidal algae in nature is not well understood (reviewed in Davison and Pearson 1996).

In Nova Scotia, most species of *Fucus* reproduce in winter (Chapman 1995b) and low temperatures may negatively impact gametes, zygotes, and embryos. Bird and McLachlan (1974) tested the cold hardiness of these life history stages of *Fucus* and found reduced mortality for zygotes at and below -10 C. Older embryos were more resistant to cold, and full cold hardiness was achieved by *F. evanescens* after 2 days of age.

Salinity

It is generally believed that salinity is a major determinant of algal distribution because it can place osmotic stress on the cells (Bäck et al. 1992 a,b; Chapman 1995b), but there has been little experimental work to substantiate the idea. High salinity can potentially result in water loss, and low salinity can cause cells to swell and/or burst. In the rockweeds, intracellular inorganic (K, Cl) and organic (mannitol) substances are used to regulate osmotic potentials of cells. In Maine, adult rockweed plants have been studied in Monsweag Bay and the Damariscotta River Estuary where salinities ranged from 10 to 33 ppt (Keser et al. 1981). It has been suggested that salinity stress may be especially inhibiting to successful fertilization (Brawley 1992) and embryonic growth (Wright and Reed 1990). Polyspermy, multiple fertilizations which

are lethal, increases when sodium is limiting (Brawley 1991, 1992). However, sperm lack negative phototaxis under brackish conditions (Serrão et al. 1996b) which may reduce the sperm:egg concentration in the water column. Although this may reduce the susceptibility to polyspermy, it should decrease fertilization success. Hence, *A. nodosum* populations in estuaries are probably restricted by spring reproduction when run-off is high and salinity is low (S. Brawley pers. comm.).

Water motion

The intertidal rockweeds generally are found in areas that are protected or partially protected from wave action and tidal currents. Studies of several habitats in New Hampshire indicated that *A. nodosum* and *F. spiralis* were absent or stunted in mid-channel areas where the maximum current was 5.5 knots (Mathieson et al. 1983).

Several investigators have tested the hypothesis that differences in adult plant distributions may be explained by differences in hydrodynamic tolerance of early post-settlement stages. In a series of field and laboratory experiments, Vadas et al. (1990, 1992) demonstrated that wave action and currents are a major source of mortality to recently settled zygotes. Pottery substrates were seeded with zygotes and exposed in the field to 100 waves or quiet water for an equivalent period of time; the number of zygotes remaining was 0.4 to 0.5% when exposed to waves and 68 to 83% for quiet water (Vadas et al. 1990). The survival of *A. nodosum* and *F. evanescens* zygotes was compared when exposed to currents between 0 and 25 cm/sec in a flow tank (Vadas et al. 1992). Survival of *F. evanescens* was 30 to 100 times greater than survival of *A. nodosum* at speeds above 7.5 cm/s. Chapman (1995a) made pairwise comparisons to determine the resistance of 1-day zygotes to hydrodyamic forces. He found the survival of *A. nodosum* to be much reduced compared to *F. vesiculosus* at the highest water pressure tested, but no difference in survivorship of the different *Fucus* species.

Substrate

Along the Maine coast, the five species of rockweeds have been found attached to rock (>3m diameter), boulder (10 inches to 3 m diameter), and cobble (2.5 to 10 inches diameter) substrate in the intertidal and shallow subtidal zone (Brown 1993).

Nutrients

Uptake of nutrient ions varies with the ion, algal species, individual tested, life history stage, temperature, and light (Chapman 1995b). McLachlan (1977) made a general survey of minerals required for the growth of *F. evanescens* embryos. Deficiencies in the media of nitrogen, phosphorus or iron retarded growth rates of the embryos, and an increase in iron together with nitrogen and phosphorus stimulated growth; boron and bromine additions stimulated growth but vitamins had no effect. A requirement for zinc, copper and manganese was not demonstrated, although these essential metals were probably sufficiently available as contaminants.

Hurd and Dring (1990) reported that the rate of phosphorus uptake by three species of rockweeds was related to their normal zonation with uptake rate in *F. spiralis* > *F. vesiculosus* > *A. nodosum*. However, plants lower on the shore have a longer period to take up phosphorus, thus the total amount of phosphorus taken up was about the same for the three species when uptake rate and time for uptake were considered. The differences in uptake within a species may be related to development of hairs such as those found in *Fucus* species in Europe (Hurd et al. 1993).

A. nodosum and *F. vesiculosus* collected from Rhode Island were able to store nitrate (Asare and Harlin 1983), but Topinka and Robbins (1976) showed that fucoids are commonly nitrogen limited during the summer and that *F. spiralis* plants receiving supplements of either nitrate or ammonium showed a great increase in growth. In winter, supplements of nitrogen produce no growth enhancement (Rosenberg et al. 1984).

ECOLOGICAL FUNCTION

Nutrient cycling

Chemical elements in an ecosystem cycle back and forth between the living organisms and the physical environment in a series of transfers termed biogeochemical cycles. The cycles involving carbon, nitrogen, phosphorus, and the trace metals are extremely important because these elements are vital to the maintenance of life. These elements make up the biomass of living organisms, and also exist in the sediment and water column as inorganic compounds, particulate organic matter, and dissolved organic matter.

Autotrophs alone absorb inorganic carbon, nitrogen, phosphorus, and trace metals, and use the sun's energy to convert them into living organic matter (biomass). Important autotrophs in the Gulf of Maine include single-celled organisms (e.g. bacteria, diatoms, dinoflagellates) that drift in the water column as plankton or are associated with the substrate, macroalgae (e.g. rockweeds, kelps, Irish moss) that usually are attached to a substrate, and flowering plants (e.g. salt marsh grasses and eelgrass) that are rooted in the substrate and inundated to various degrees. Autotrophic biomass is the ultimate source of nutrients and energy for heterotrophs (bacteria, other single-celled organisms, and multi-celled animals). Heterotrophs in turn excrete waste products containing inorganic nutrients which are absorbed and utilized by autotrophs.

Rockweeds are important in the cycling of nutrients because they 1) can produce and release large quantities of organic matter, 2) harbor a diverse community of heterotrophs that consume organic matter and release inorganic nutrients, and 3) are able to absorb nutrients from the water column. Following experimental dehydration and rehydration, *A. nodosum* released 2 to 10 mg C/100 g dry weight into the water, and *F. vesiculosus* released 10 to 50 times more (Moebus et al. 1974). Aerobic heterotrophs that are attached to rockweed shoots or the substrate or that are in the water column consume dissolved and particulate organic matter and excrete inorganic waste products (ammonium and phosphorus) into the water column. Rockweed plants are able to absorb macronutrients like nitrogen (as ammonia, ammonium, or nitrate) and phosphorus, and micronutrients like elemental metals (cadmium, zinc, iron, copper, manganese lead, vanadium, and nickel) through the thallus. Rockweeds, with their high rates of accumulation, may act as a sink for metallic elements.

Uptake of pollutants

The tissues of rockweeds tend to accumulate many metal ions. *F. vesiculosus* accumulates silver, (Ag), arsenic (As), cadmium (Cd), cobalt (Co) copper (Cu), lead (Pb), manganese (Mn) and zinc (Zn) (Floc'h 1982; Bryan 1983; Luoma et al. 1982; Munda and Hudnick 1986; Holan and Volesky 1994) and *A. nodosum* accumulates Mn, Pb, and Zn (Floc'h 1982; Holan and Volesky 1994). Accumulation of Cd, Co, Mn, and Zn in *F. vesiculosus* is greatest in the vegetative shoots and is temperature dependent (Munda 1986).

Accumulation of metal ions may be a passive process. Holan et al. (1993) demonstrated the biosorption of cadmium by nonliving dried brown algae. Polyphenols extracted from *A. nodosum* and *F. vesiculosus* chelated a number of heavy metals in weakly acidic solution in the laboratory (Ragan et al. 1979). Ragan et al. (1980) noted that exudates from brown algae may contribute to the natural chelating capacity of nearshore water, important because some phytoplankton are very sensitive to heavy metals.

Bryan (1983) suggested that *F. vesiculosus* is a good indicator of bioavailable forms of Ag, Cd, Cu. Pb, and Zn. Luoma et al. (1982) reported that concentrations of Ag, As, Cu, Pb, and Zn in the tissue of *F. vesiculosus* correlated significantly with concentrations in the sediment. Within 57 days of being transplanted from an unpolluted to a polluted site, the concentration of Zn and Cu in the tissue of *A. nodosum* and *F. vesiculosus* had increased by at least a factor of 10 (Ho 1984).

Some metals inhibit the growth of rockweeds. Munda and Hudnik (1986) studied the effects of heavy metals (singly or in dual combinations at total concentrations of 2.5 and 5 ppm) on the growth of *F.*

vesiculosus. The inhibitory sequence was Cu > Ni > Cd > Zn > Co > Mn (with Cu lethal and Mn favorable for growth), and was not consistent with the sequence of accumulation. Some metals reduced the inhibitory effects of other metals or decreased their accumulation. Studies by Strömgren (1980b) demonstrated decreased growth of *F. spiralis*, *F. vesiculosus*, and *A. nodosum* when exposed to 810g/l Pb, 450g/l Cd and more than 10 g/l Hg. According to Strömgren (1980a), resistance to copper was greatest in *A. nodosum*, midrange in *F. vesiculosus* and least in *F. spiralis*, however, Smith et al. (1985) stated that *Fucus* species have a relatively high tolerance to high environmental levels of dissolved copper.

Food source

Grazing on live rockweeds

Grazing activity by herbivores appears to be the greatest source of mortality to the early post-settlement phases of many species of algae, although the effect depends on the species involved, developmental stage, height on the shore, interactions with other biological factors, and the experimental design (Menge and Farrell 1989; Vadas et al. 1992; McCook and Chapman 1993; Chapman 1995b). Gastropod snails (*Littorina littorea*, *L. obtusata*, and *Lacuna vincta*) and gammarid amphipods are the most common grazers in the intertidal zone. Lubchenco (1978, 1983) hypothesized that grazers remove ephemeral algae, which are able to outcompete the fucoid algae for space, thus allowing fucoid algae to establish iteself. In two-way choice experiments using adult plants, *L. littorea* prefered ephemeral green algae (*Ulva* and *Enteromorpha*) over *Ascophyllum* and *Fucus* (Lubchenco 1978; Watson and Norton 1985) while *L. obtusata* preferred *Ascophyllum* and *Fucus* over ephemeral green algae (Watson and Norton 1987). When recently-settled plants (germlings) were used in two-way choice experiments, *L. littorea* also preferred *Ulva* over *Ascophyllum* and *Fucus* (Watson and Norton 1985). However, when presented with germlings of a single species of *Fucus*, *L. littorea* consumed 70 to 100% and *L. obtusata* consumed 20 to 50% of the indivduals (Barker and Chapman 1990). Other multiple choice experiments demonstrated the preference of gammarid amphipods in Nova Scotia for *F. vesiculosus* (Denton and Chapman 1991). Under natural conditions in New Brunswick, Canada, *F. evanescens* was heavily grazed by the gastropod *Lacuna vincta* (Thomas and Page 1983). When the mean maximum number of snails was 280/m^2, grazing removed 79% of the net production of *F. evanescens*, which averaged 61 g dry weight/m^2/day.

Differences in the concentration of phlorotannins (Denton et al. 1990) and polyphenols (Geiselman and McConnell 1981) may inhibit the herbivores. *F. gardneri* responded to grazing damage by increasing its polyphenol content (Van Alstyn 1988) and *A. nodosum* responded by increasing the toughness of its tissue (Lowell et al. 1991).

Grazing on epiphytes

There is no comprehensive study of rockweed epiphytes in the Gulf of Maine. One of the most important epiphytes on *A. nodosum*, on both sides of the Atlantic Ocean, is the red alga *Polysiphonia lanosa* (Pearson and Evans 1990) which is probably resistant to grazers. In the Baltic Sea, *F. vesiculosus* was found to have 26 species of epiphytic algae that were distributed over the entire length of the thallus, but decreased toward the holdfast and at the growing tips (Colina 1981). In the Baltic Sea and in northern New Zealand, diatoms epiphytic on *F. vesiculosus* were found to contribute 1 to 10 mg C/m^2/host/h (Booth 1987).

Consumption of rockweed-derived detritus

Detritus refers to dissolved organic matter, particulate organic matter, and the assemblage of decomposing bacteria and fungi that inhabits the organic matter (Zieman 1982; Thayer et al. 1984; Mann 1988). Dissolved organic matter includes soluble carbohydrates and proteins (Zieman 1982; Mann 1988); particulate organic matter includes dead autotrophs or autotroph debris, dead heterotroph or heterotroph debris of any size, fecal pellets, and combinations of these items (Cousins 1980; Mann 1988).

As part of the natural life cycle, rockweed blades are eroded at the end by wave action or ice scouring and fall to the bottom or are carried away by water currents. Whole fronds probably become fragmented by the

shredding action of herbivorous invertebrates and by physical factors such as desiccation and ice grinding. The intact blades or fragments become colonized by bacteria and fungi, which begin to decompose the algae.

The processes of particle size reduction and microbial colonization and decomposition are essential to the detrital food web,and have been summarized in detail for algae by Mann (1988). Particle size reduction is important because some organisms are able to ingest only fine particles, and the greater surface to volume ratio of fine particles allows greater colonization by microbes. The microbes enzymatically break down plant material that most organisms cannot digest, and convert it to microbial biomass which can be assimilated. Microbes also enrich the detritus by taking up nitrogen and phosphorus from the surrounding medium and incorporating it into microbe biomass.

Macroalgae like the rockweeds make an important contribution to the detrital cycle. Josselyn and Mathieson (1980) conducted an 18-month study in Great Bay Estuary system and the adjacent open coast to determine the seasonal contribution and detrital processing of plant litter that is locally derived (*Spartina alterniflora*, *Zostera marina*, *A. nodosum*, and *F. vesiculosus*). Rockweed litter accounted for 35 to 85% of the total strand line throughout the year, and contained 1 to 3 times as much detrital material as the vascular plants within the estuary and 50 times as much on the open coast. Seaweeds decomposed 3 to 10 times faster than the vascular plant litter under similar conditions. Decomposition rates and changes in nutrient content of litter were dependent on surrounding environmental conditions, and were maximal in spring and summer.

Smith and Foreman (1984) assessed litter and detrital decomposition and nitrogen composition of decomposing litter for 10 important species of seaweeds in British Columbia, Canada. The decomposition rate for *F. gardneri* was about 70 days. As decomposition proceeded there was an accelerating increase in the nitrogen:dry weight ratio of the remnant litter.

Habitat

The rockweeds provide habitat for a variety of species by adding structural complexity to the water column when the plants are submerged in water and by ameliorating the extremes of temperature and desiccation when they are emersed in air (Vadas and Elner 1992). Using a functional approach, the flora and fauna associated with intertidal rockweeds include: 1) epiphytes on the thallus), 2) biota that attach to the holdfast and thallus, 3) mobile fauna that move on or swim over the thallus and 4) biota that dwell on or in the underlying substrate.

Researchers working in the Baltic Sea, where rockweeds are the dominant subtidal vegetation on hard bottoms, have reported a greater biomass of macroscopic animals in the *F. vesiculosus* zone than in shallow areas with soft bottoms (reviewed in Lehtinen et al. 1988). In addition to being important source of food and shelter for fish and invertebrates, the rockweed beds in the Baltic Sea are important as a spawning area for some species of pelagic fishes, especially herring, *Clupea harengus* (Aneer 1989).

During a 13-month study of epifauna on *A. nodosum* and *F. vesiculosus* in Nova Scotia, the total density of epifauna declined by two orders of magnitude between summer and winter (Johnson and Scheibling 1987). Harpacticoid copepods and their nauplii, nematodes and halacarid mites were numerically the most abundant species during the study, but considerable numbers of young annelid worm and gastropods also were present (Johnson and Scheibling 1987). Density of most of the epifaunal taxa was positively correlated with epiphytic algal biomass (Johnson and Scheibling 1987).

At a site in Scotland, experimental evidence showed that the species diversity and abundance of individuals settling on the substrate was greater under a canopy of *A. nodosum* than outside of the canopy (Hruby and Norton 1979). The authors attributed this to the greater humidity found under the *A. nodosum* when the tide was out. However, shelter from water motion and predation may contribute to the increase of settling species.

Table 1 lists the species of fishes and invertebrates that have been collected from the rockweed zone in southwestern Nova Scotia (Black and Miller 1991; Rangeley 1994), Passamaquoddy Bay (Thomas et al. 1983; Rangeley and Kramer 1995a,b), and the Sheepscot River Estuary (Tort 1993). Black and Miller (1991) obtained evidence that the fishes were feeding on amphipods, isopods, *Littorina* sp., green crabs, and young fish, all of which associate with *A. nodosum* in the intertidal zone.

Commercial uses

Salts of alginic acid (alginates) occur in all brown algae as structural components of the cell walls. Alginates are commercially extracted from *Macrocystis pyrifera*, *A. nodosum*, and *Laminaria* sp., and are used for their thickening, stabilizing, film forming and gel producing properties (Whyte 1988). The products are used extensively in the baking industry and as a stabilizer in the manufacture of ice cream. Extracts of *A. nodosum* have been used alone or with other ingredients as a biostimulant for field grown bedding plants (Poincelot 1994) and hydroponically grown barley (Steveni et al. 1992). In Maine, rockweeds are collected for use as packing material for live lobsters (L. Mercer pers. comm.). In some parts of Europe, *F. vesiculosus* is sold as a health food (S. Brawley pers. comm.).

Small quantities of *A. nodosum* are harvested in Maine, but large-scale commercial harvesting in Nova Scotia, Canada, has been active for 35 years (Sharp et al. 1994). Harvesting in Canada is traditionally done by raking from a boat or by cutting at low tide with a sickle (Sharp et al. 1994). However, suction cutters, if used properly, cause the least damage to the holdfast (R. Vadas pers. comm.).

CONCLUSION

Studies of the rockweeds have been conducted on both sides of the northern Atlantic Ocean. Many of these studies have concentrated on the causes of the striking patterns of vertical zonation that occur in the intertidal zone. Few studies have examined the ecological functions of these species, but collectively they have shown that the five species of rockweeds 1) contribute to nutrient cycling, 2) provide food to grazers and detritus feeders, 3) help maintain water quality, and 4) provide habitat for numerous species including commercially and recreationally important species.

THREATS

The major threats to rockweeds include reductions of light levels due to degradation of water quality or physical structures; reproductive inhibition due to petroleum hydrocarbons; local overharvesting; chlorate effluent from pulp mills; competition from nonnative species; and thermal discharges from power plants.

Reduction of light levels due to degradation of water quality by nutrient loading is a threat to the rockweeds. Nutrient loading can result from point sources such as wastewater treatment facilities and aquaculture sites (Roennberg et al. 1992) and non-point sources such as runoff of animal wastes and fertilizers from lawns (Short 1992). Excessive nutrients promote the rapid growth of phytoplankton in the water column and epiphytes on the rockweed thallus, both of which can reduce amount of light reaching the rockweeds. In the Baltic Sea, unlike the Gulf of Maine, *F. vesiculosus* grows subtidally and is the dominant coastal vegetation (Lehtinen et al. 1988). Increased inshore nutrient levels in the Baltic Sea (both nitrate, nitrite and phosphate) have been accompanied by increased blooms of plankton and filamentous algae, decreased water transparency, decreased depth penetration of *F. vesiculosus*, increased deposition of organic matter on the bottom, decreased oxygen in bottom waters, and reduced bottom fauna (Lainianen et al. 1989; reviewed by Cederwall and Elmgren 1990; Kautsky 1991). The disappearance of *A. nodosum, F. vesiculosus*, and *F. evanescens* from the inner part of Oslofjord was attributed to the increased discharge of sewage (Bokn and Lein 1978). Surveys conducted in 1988 to 1990 indicated that fucoid algae have recovered in many parts of Oslofjord, and this recovery corresponds to improved sewage treatment and discharge practices (Bokn et al. 1992).

Table 1. Species of fishes and invertebrates collected from intertidal fucoid algae and fucoid algae habitat in the Gulf of Maine.

Species	Common name
Fishes	
Alosa pseudoharengus [1, 2, 3]	Alewife
Ammodytes americanus [2]	Sandlance
Anguilla rostrata [1]	American eel
Clupea harengus [2]	Herring
Cyclopterus lumpus [2]	Lumpfish
Fundulus heteroclitus [1, 3]	Mummichog
Fundulus majalis [2]	Killifish
Gadus morhua [2]	Atlantic cod
Hemitripterus americanus [1]	Atlantic sea raven
Menidia menidia [2, 3]	Atlantic silverside
Microgadus tomcod [1, 2, 3]	Atlantic tomcod
Myxocephalus aenaeus [1]	Grubby
Myxocephalus octodecemspinosus [1]	Longhorn sculpin
Myxocephalus scorpius [1]	Shorthorn sculpin
Osmerus mordax [1, 2, 3]	Rainbow smelt
Pholis gunnellus [2]	Rock gunnel
Pollachius virens [1, 4]	Pollock
Pleuronectes americanus [1, 2, 3]	Winter flounder
Scomber scombrus [1]	Atlantic mackerel
Pungitius pungitius [3]	Nine-spine stickleback
Tautogolabrus adspersus [1]	Cunner
Tautoga onitus [1]	Tautog
Urophycis tenuis [1, 2]	White hake
Invertebrates	
Carcinus maenas [6]	Green crab
Flustrellida hispida [5]	Bristly bryozoan
Gammarus oceanicus [5]	Amphipod
Littorina obtusata [5]	Smooth periwinkle
Nucella lapillus [5]	Dogwinkle
Potamilla neglecta [5]	Fan worm
Sertularia pumila [5]	Hydroid

1 = Black and Miller 1991; 2 = Rangeley 1994; 3 = Tort 1993; 4 = Rangeley and Kramer 1995a, b; 5 = Thomas et al. 1983; 6 = Maria Tort pers comm.

Reduction of light levels can also be caused by sediment loading. Sediment suspended in the water column reduces the amount of light that penetrates the water, thus reducing the light that reaches rockweeds on the bottom. Suspended sediments result from point and nonpoint sources of upland runoff and from resuspension of sediment by tidal currents, wave action, dredging, filling, boating activity, and fishing activity (Short 1992; Colarusso pers. comm.). The impact of suspended sediment in the vicinity of rockweeds may vary with hydrographic conditions, sediment grain size, time of year, distance from the sediment, health of the rockweeds, and a host of other variables.

The reproductive stages of rockweeds are especially sensitive to oil pollution. In laboratory experiments, minute quantities of crude oil, No. 2 fuel oil, and two jet fuels killed *Fucus* sperm being released from receptacles, and fuel oil and jet fuels at a concentration of 20 ppm completely killed *Fucus* zygotes (Steele 1977, 1978). A shoreline survey conducted after No. 2 fuel oil was spilled in Narragansett Bay revealed little impact on adult *Fucus*, but sexual reproduction was inhibited due to mortality of gametes and/or embryos for approximately three weeks (Thursby et al. 1990). In *A. nodosum,* as well as other species of brown algae, unsaturated hydrocarbons serve as pheromones, attracting male to female gametes (Müller 1981). It has been suggested, but not demonstrated, that petroleum hydrocarbons could interfere with normal functioning of these pheromones (Maier and Müller 1986).

Overharvesting is a potential threat to fucoid algae, particularly to the slow growing *A. nodosum*. Large amounts of rockweeds are harvested in Canada, but the harvest is partially subsidized by the government (Inka Milewski pers. comm.). The harvest in Maine is small by comparison, but if the price for rockweeds increases sufficiently, harvesting would probably increase.

A study conducted in mid-coastal Maine to determine the regrowth of *A. nodosum* and *F. vesiculosus* following harvest demonstrated that regrowth varied with site, exposure, and harvest method (Keser et al. 1981). When *A. nodosum* was harvested to the holdfast, recovery to average pre-cut biomass required 2 to 3 years at protected sites and more than 3 years at moderately exposed sites. When *A. nodosum* was harvested by cuts at heights of 15 or 25 cm, recovery was faster at sheltered sites than exposed sites, and was faster than when the algae was harvested to the holdfast.

Few studies have addressed the ecological impact of rockweed harvesting. Only one study, conducted in Nova Scotia where harvests exceeded 20, 000 tons in 1989, has investigated the use by fishes of intertidal habitats where *A. nodosum* was dominant or had been harvested (Black and Miller 1991). However, sampling bias (Rangeley 1994) and the use of nets with a large mesh, which would not have captured juvenile fishes, make the results of this study inconclusive.

In the Baltic Sea, the abundance and biomass of fucoid algae declined regionally after cellulose pulp mills started releasing chlorate (CLO_3^-) in their effluent (reviewed in Lehtinen et al. 1988 and Kautsky 1992). The chlorate is formed as a by-product in the bleaching of chemical pulp (Lehtinen et al. 1988). Laboratory tests indicated that chlorate, effective at 10 to 20 μg/L, was the main causal agent for the decline of *F. vesiculosus* (Rosemarin et al. 1985). Other species of brown algae were highly sensitive to chlorate, while cyanobacteria, green algae, red algae, and *Zostera* had much lower sensitivities (Rosemarin et al. 1985; 1994). Transplantation experiments, quantitative surveys along transects, and mesocosm experiments were used to investigate the effect of chlorate. Briefly, these experiments revealed that the abundance, biomass and depth distribution of *F. vesiculosus* and the abundance, biomass and diversity of macroinvertebrates increased with increased distance from the chlorate source (Lehtinen et al. 1988; Kautsky 1992). Kautsky (1992) noted that reduction of chlorate effluent has resulted in the partial recovery of *F. vesiculosus* in the effluent receiving area.

The native species of rockweeds may be outcompeted by introduced or nonnative species. *F. serratus*, a species of fucoid algae that occurs in Europe, has been introduced into Nova Scotia. Its spread has been rapid in some areas but slow in others (Dale 1982). A study of the phytosociological structure of the seaweed community in Nova Scotia has found evidence that the spread of this species into new areas is not slowed by competition from *Chondrus crispus* but competition by *F. evanescens* is an important factor (Dale 1982).

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KELPS

IDENTIFICATION AND DESCRIPTION

Seven species of brown laminarian algae (*Agarum cribrosum*, *Alaria esculenta*, *Chorda filum*, *Laminaria digitata*, *L. longicruris*, *L. saccharina*, and *Saccorhiza dermatodea*) are found in the Gulf of Maine, and are the dominant fleshy macrophytes (Vadas and Elner 1992). *A. cribrosum*, *L. digitata*, and *L. longicruris* are the most important species in terms of biomass and percent cover of substrate. An aerial survey and supporting groundtruth surveys of kelps in southwestern Nova Scotia revealed an average biomass of 42.2 t/ha that was 60% *L. longicruris* and 40% *L. digitata* (Sharp and Carter 1986). In St. Margaret's Bay in Nova Scotia, *A. cribrosum*, *L. digitata*, and *L. longicruris* accounted for at least 72% of the total biomass of intertidal and subtidal seaweeds (Mann 1972a).

Algae are relatively simple in structure. They lack well-developed tissue systems, and have no true roots, stems or leaves. The seven species of laminarian algae described here, commonly referred to as kelps, are dark brown due to the presence of fucoxanthin, a brown xanthophyll accessory pigment which tends to obscure the greenish chlorophyll (Lüning 1990).

Six of the species of kelps are plants of moderate to large size with a holdfast (which attaches to the substrate), stalk, and greatly expanded flattened blade of various forms (Taylor 1957). *A. esculenta* has a midrib, lateral bladelets below the main blade, and a costate (ribbed) main blade; *A. cribrosum* has a midrib and a perforated blade; *L. digitata* has no midrib and a wide blade that is split into 5 to 30 straplike fingers; *L. longicruris* has no midrib, a stalk which is distally hollow and expanded, and a solid blade; *L. saccharina* has no midrib, a solid stalk and a solid blade; *S. dermatodea* has a cuplike holdfast, no midrib, and a solid blade with tufts of hairs on its surface (Taylor 1957). *C. filum*, a slender whiplike plant without branches, is not discussed further.

DISTRIBUTION

The six species of kelps occur primarily in the Arctic and cold temperate marine biogeography regions; detailed maps of their distribution, the basis for this section, have been compiled by Lüning (1990). *A. cribrosum* is found along the western Atlantic Ocean from Greenland (80 N) to Cape Cod (42 N) and in the Pacific Ocean from British Columbia to Korea. *A. esculenta* occurs on both sides of the Atlantic Ocean from Greenland (78 N) to Cape Cod (42 N) and from the Barents Sea to the English Channel; it also is found sporadically in the Pacific Ocean. *L. digitata* is restricted to both sides of the Atlantic Ocean from Greenland (78 N) to Cape Cod (42 N) and from the Barents Sea to France. *L. longicruris* is endemic to the eastern coast of North America. *L. saccharina* occurs in the Atlantic Ocean from north of 80 N to Long Island Sound and Portugal (40 N) and in the Pacific Ocean from British Columbia to Korea. *S. dermatodea* is restricted to the Atlantic Ocean and occurs from Greenland (70 N) to Cape Cod (42 N), along the coast of Norway, and sporadically in the Barents Sea.

Kelp beds flourish in the Bay of Fundy and offshore island and ledges in the Gulf of Maine (Vadas and Steneck 1988; Vadas and Elner 1992). Nearshore refuge areas that are free of seas urchins contain numerous patches of kelps (Steneck 1986).

Recent review articles have reported clear vertical zonation of communities on subtidal rocky substrate around the British Isles and in the Gulf of Maine, with a zone of kelps beginning in the subtidal fringe (level of lowest spring tide to 1 m above) and extending to varying depths (Hiscock 1986; Sebens 1986). *A. esculenta* often forms a band from the subtidal fringe to just below the low-water (Hiscock 1986; Edelstein et al. 1969; Mann 1972a; Lüning 1990). The slow-growing long-lived *L. digitata* and fast-growing short-lived *L. longicruris* are found at intermediate depths (Lüning 1990). *L. saccharina* grows farther south and in more protected areas (Lüning 1990). *A. cribrosum* is found at the greatest depths (Edelstein et al. 1969; Mann 1972a; Vadas and Steneck 1988; Lüning 1990). Boden's (1979) quantitative survey off Appledore Island,

Maine, confirmed this zonation pattern. *L. digitata* dominated from 0 to 1 m, *L. saccharina* from 2 to 8 m, and *A. cribrosum* below 11m. However, in other studies, the vertical distribution of the six species of kelps often showed considerable overlap when found at the same site (Edelstein et al. 1969; Mathieson 1979; Mann 1972a; Sebens 1986; Vadas and Steneck 1988).

The depth distribution and species mix of kelps in the Gulf of Maine depends, in part, on available light, available substrate, exposure, and the presence of sea urchins (Mathieson 1979). In the southern Gulf of Maine (Massachusetts), a zone of *L. saccharina*, *L. digitata*, *A. esculenta*, and *A. cribrosum* extended from the sublittoral fringe to a depth of 1 to 3 m where sea urchins were present, but extended to at least 15 m where urchins were scarce (Sebens 1986). At exposed sites in the Gulf of Maine, *L. digitata* and *L. saccharina* dominated at 4 to 8 m, and removal experiments indicated they were limited to these depths by sea urchins (Witman 1987). Near Halifax, Canada, a zone of mixed *L. saccharina*, *L. longicruris*, *L. digitata*, *A. esculenta*, and *S. dermatodea* extended to 15 m only where the substrate was stable and consisted of rock and large boulders (Edelstein et al. 1969). In St. Margaret's Bay, Nova Scotia, Mann (1972a) recognized four subtidal zones that were characterized by kelps. At exposed sites there was a mix of *L. digitata* and *L. longicruris* from 3 to 13 m; at sheltered sites there was a bed of *L. longicruris* from 4 to 18 m; a mix of *L. longicruris* and *A. cribrosum* occurred from 8 to 18 m, and *A. cribrosum* was found at 15 to 20 m (Mann 1972a).

LIFE CYCLE

The life cycles of the six species of kelps are similar, and alternate between a large asexual (sporophyte) stage and a microscopic sexual (gametophyte) stage. The sporophyte cells are diploid, i.e., they contain two of each type of chromosome characteristic of the species. At maturity, the sporophyte produces and releases haploid spores, which contain one of each type of characteristic chromosome. After being released into the water, each spore quickly attaches to the substrate and germinates into a microscopic gametophyte. The gametophyte produces either eggs or sperm. Sperm are released into the water, and are attracted to egg-containing gametophytes. In *L. digitata*, the release of male gametes is triggered by pheromones secreted by the female gametes (Maier 1982). Fertilization of the egg results in an embryonic sporophyte. Growth of the sporophyte occurs at the base of the blade where it joins the stipe, and involves an increase in thallus length, width, and thickness (Mann 1972b). During the year, portions of the thallus may be torn off as a result of wave action or ice scouring.

A single study of kelp reproduction, survival of early stages, and longevity has been conducted in the Gulf of Maine in southern Nova Scotia (Chapman 1984). The study showed that the average density of *L. digitata* ($3.22/m^2$) was 2.5 times greater than that of *L. longicruris* (1.24/m2), and yearly spore production of *L. digitata* (20.02×10^9) was 2.3 times greater than that of *L. longicruris* (8.9×10^9). Spore production occurred over a protracted period, but was greatest in October for both species. Recruitment of microscopic plants onto a substrate occurred year round, but was greatest from February to April. Yearly recruitment success of microscopic plants was 10 times greater for *L. longicruris* (8.89×10^6) than for *L. digitata* (0.98×10^6), and recruitment of visible plants was enhanced for both species by removal of red algal turf species. Mortality rate of macroscopic plants, although constant through time for each species, was greater in *L. longicruris*. When a mixed assemblage of plants was examined, the maximum ages of *L. longicruris* and *L. digitata* were approximately 2 and 4 years old, respectively (Chapman 1984). In a more recent study, in which a single cohort was followed through time, some *L. longicruris* lived to 4 years of age (Chapman 1986).

Kelp reproduction patterns in Long Island Sound, the southern limit of kelp distribution on the east coast of the United States, may or may not be similar to patterns in the Gulf of Maine. For instance, *L. longicruris* reproduced in the late fall with the highest percentage of fertile plants occurring from October to December (van Patten and Yarish 1993), similar to the pattern described for Nova Scotia. However, *L. saccharina* plants appeared to be primarily annuals, reproducing in early spring with maximum spore release in May (Lee and Brinkhuis 1986) and disintegrating between August and September (Lee 1984).

Seasonal growth patterns of kelps have been shown to vary and to be affected by external factors such as light, nutrients, and to a lesser extent, temperature. Recent experiments with *L. digitata* from the North Sea demonstrated that seasonal growth patterns are controlled by an endogenous circannual clock that is synchronized by daylength cycles (Schaffelke and Lüning 1994).

A characteristic growth pattern of kelps in the North Atlantic is rapid growth in late winter and early spring followed by a quiescent period in late summer and early fall (Chapman and Lindley 1980). *A. cribrosum, L digitata*, and *L. longicruris* in St. Margaret's Bay, Nova Scotia, demonstrated this characteristic pattern of increasing growth rate from October to May and decreasing growth rate from May to October (Mann 1972b). The same pattern was reported for *L. longicruris* in Long Island Sound (Egan and Yarish 1990), *L. saccharina* in Rhode Island (Brady-Campbell et al. 1984), and rope-cultured *L. saccharina* in Long Island (Brinkhuis et al. 1983). Field observations and laboratory experiments have shown that summer growth of *L. longicruris* in Nova Scotia is severely limited by the low nitrate availability (Chapman and Craigie 1977, 1978).

Irradiance and nitrogen have been proposed as factors limiting kelp growth at different times during the year (Brinkhuis et al. 1984). The growth of *L. digitata* and *L. saccharina* collected from the North Sea off Scotland and cultured in the laboratory in nutrient enriched seawater in April to May (15μM nitrate; 3 μM phosphate), June to July (7.5 μM nitrate; 1.8 μM phosphate) and September (7.5 μM nitrate; 3 μM phosphate) was about twice that of plants cultured without enriched seawater or growing in their natural habitat (Conolly and Drew 1985b). However, in January the growth rate of *L. saccharina* cultured under increased daylength (17.5 versus 7.5 h) was 3 to 4 times higher than plants cultured under conditions of higher temperature or nutrient enrichment (Conolly and Drew 1985b). The growth rate of a different population of *L. digitata* in the North Sea was nitrogen-limited between June and October, and was light-limited with a possible temperature effect for the remainder of the year (Davison et al. 1984).

A different growth pattern may occur in areas where nutrient levels are generally high. In the Gulf of St. Lawrence, growth of *L. longicruris* was maximal in June and minimal from December to February when ice cover limited light levels (Anderson et al. 1981). In Cobscook Bay, where nutrients levels are high all year and tidal energy prevents ice cover, growth of kelp continues year round, but is greatest in summer (Vadas unpublished data). Similarly, blade and stipe growth of *L. longicruris* at two depths in Quebec did not appear to be nitrogen limited, and showed an annual cycle characterized by a June peak (Gendron 1989). The growth rate of mature *L. saccharina* at Appledore Island in Maine, transplanted to 7 depths between 1 and 21 m, was maximal at 9 m in July (Boden 1979). The growth of transplants at 1 and 3 m and in undisturbed plants on shore at 0 m was 40% of the growth at 9 m and was attributed to low levels of nitrate and high temperatures near the surface and attenuated light at depth (Boden 1979).

In some studies, growth rate is apparently unrelated to a single environmental factor. Machalek and Davison (1992) studied a population of *L. digitata* growing in tidepools at Schoodic Point, Maine, and found no apparent correlation between photosynthesis irradiance parameters and growth rate. However, nutrients were not measured. In the North Sea, *L. digitata* and *L. saccharina* transplanted to three depths reduced or ceased growth at different times of the year under otherwise identical conditions of temperature, nutrients, light intensity or light quality suggesting that none of these factors actually trigger their seasonal growth behavior (Lüning 1979).

Numerous studies in St. Margaret's Bay, Nova Scotia, have produced an understanding of the internal storage capacity of *L. longicruris,* resulting in an ability to extend its growth period when light energy or dissolved nitrogen are in short supply (Hatcher et al. 1977; Chapman and Craigie 1978; Gagne and Mann 1981; Gagne et al. 1982). From late winter to early spring when ambient nitrate levels were high, *L. longicruris* grew rapidly and created an internal store of nitrogen. In the beginning of this growth phase, the carbon produced in new tissue exceeded that fixed by photosynthesis, and carbon reserves (mannitol and laminarin) were used for carbon and energy, but from January to May, growth was sustained by photosynthesis. During and after the spring plankton bloom when ambient nitrate levels were low, kelp grew at a decelerating rate and used up internal reserves of nitrate. During the summer when nitrate was not available and photosynthetic rates were high, carbon reserves were built up and stored in the blade tissue.

Of the annual net assimilation of carbon, approximately 45% appeared as new blade tissue, 8% as new stipe tissue, 12% as storage products (mannitol or laminarin) and 35% was assumed to be lost as dissolved organic carbon (Hatcher et al. 1977).

POPULATION TRENDS

Two alternate community states exist in the rocky subtidal zone of the Gulf of Maine and the Atlantic coast of Nova Scotia: highly productive kelp beds dominated by *L. longicruris* (Johnson and Mann 1988) and an unproductive sea urchin-coralline alga community. Initially, the kelp beds are heavily grazed by populations of sea urchins (*Strongylocentrotus droebachiensis*) that can increase dramatically in southwestern Nova Scotia (Johnson and Mann 1988), but that increase more gradually elsewhere in the Gulf of Maine (Robert Steneck pers. comm.). The sea urchin-coralline alga community then becomes dominant. Eventually, disease induced mortality of green sea urchins (Johnson and Mann 1988) or urchin harvesting (Steneck et al. 1995; Vadas and Steneck 1995) decreases the urchin population, reduces grazing pressure, and allows regrowth of the kelp community.

Urchins destructively grazed kelps along the coast of Nova Scotia during the 1970s (reviewed in Vadas and Elner 1992), however, *A. cribrosum*, a defended algae, was able to coexist with urchins in deeper zones (Vadas and Elner 1992). In St. Margaret's Bay, Nova Scotia, natural and experimentally induced regeneration of kelps was destroyed by sea urchins under normal grazing pressure within 10 months (Chapman 1981). Apparently, benthic microalgae with a mean biomass of 2.2 g C/m^2 and productivity of 15 g $C/m^2/y$ supported a population of sea urchins large enough to suppress kelp regeneration, and re-establishment of kelp beds seemed unlikely (Chapman 1981). Removal of sea urchins from a heavily grazed site in Conception Bay, Newfoundland, initially resulted in an increase in the biomass of macroalgal, but urchins grazed away all algae except *A. cribrosum* when urchin removal ceased (Gordon and Sand-Jensen 1990).

Ultimately, an urchin die-off in the early 1980s provided an opportunity to study the ability of *L. longicruris* to recover its former dominant status and to compete with other seaweeds and when perturbed by storms and grazers other than urchins. Recovery of seaweeds following overgrazing by urchins was studied extensively in St. Margaret's Bay, Nova Scotia. Rates of recolonization of *L. longicruris* depended on the proximity to a refugial source of spores (Johnson and Mann 1988), resulting in the rapid re-establishment of a canopy at some sites but not at others. Recovery by understory species also was rapid (Johnson and Mann 1993), and the recolonized communities resembled those documented at the same sites prior to the destructive grazing (Edelstein et al. 1969; Johnson and Mann 1993).

Miller (1985) and Elner and Vadas (1990) reviewed the hypotheses relating to the destruction of kelp beds by sea urchins that emerged, often with very little supporting data, during the 1970s and 1980s. Elner and Vadas (1990) summarized four scenarios that were proposed during this time period. Briefly, two scenarios predicted irreversible degradative spirals, ultimately resulting in a decline of system productivity and predators. Two other scenarios predicted cycles which involved dramatic growth of the urchin population, decimation of kelp beds by urchin grazing, decline of the urchin population, and recovery of the kelp beds. In retrospect, a cyclic scenario was correct. Kelp populations were repressed for nearly 15 years, but recovered quickly when urchin populations declined due to disease, changing environmental conditions, or a combination of both factors.

Kelps also are affected by a "stipe blotch" disease, caused by *Phycomelaina laminariae*. This disease was studied in infected *L. saccharina* population off Gloucester, Massachusetts. Susceptibility to infection appeared to be part of the aging process, as infections occurred primarily in the larger (older) size groups (Schatz 1984).

ECOLOGICAL REQUIREMENTS

Light

Sunlight is a fundamental requirement for the six species of kelps because light energizes the reactions of photosynthesis. However, the amount and spectral characteristics of available light varies with latitude, season, water type, and depth (reviewed in Lüning 1990). As light passes through water and the substances dissolved and suspended in it, different wavelengths of light are selectively absorbed, causing the total amount of available light and the range of available wavelengths to decrease with depth. Lüning and Dring (1979) made continuous measurements of underwater light at different depths for over a year in the North Sea, and related the available light to the lower limits of algal zones.

The relationship between photosynthesis and light intensity (irradiance) is described by a parabolic curve (Lüning 1990; Chapman 1995). The compensation irradiance (I_c) is the minimum amount of light needed for the plant to survive, i.e. at this light level the rate of photosynthesis equals the rate of respiration. As light intensity increases above the compensation irradiance, the photosynthetic rate first increases in a linear fashion, then plateaus as photosynthetic enzymes become light-saturated, and finally may decrease due to photoinhibition (Lüning 1990; Chapman 1995). For a particular plant, the photosynthesis-versus-light relationship is the result of genetic adaptation and acclimation (Ramus 1981). The saturation irradiance for photosynthesis was estimated to be 150 μmol photon/m^2/s for *L. saccharina* and *L. digitata* transplanted to three depth in the North Sea (Lüning 1979). Fortes and Lüning (1980) estimated the saturation irradiance for growth of *L. saccharina* cultured in the laboratory to be 70 μmol photon/m^2/s, and noted reduced growth at higher light levels. Growth rates of small *L. digitata* plants in the laboratory increased with increasing irradiance up to 50 μmol photon/m^2/s, at which point they became light saturated (Davison 1988). These values are typical for shade plants (Lüning 1990). For young *L. digitata*, the light saturated rate of photosynthesis was 50 to 100% higher in blue light than in red light, but at low irradiances the photosynthetic rates were slightly higher in red than in blue light (Dring 1989).

Experiments have confirmed ecotypic differences in light-related traits. *L. saccharina* plants from turbid Long Island Sound grew faster under light-limiting and saturating daily irradiances, had higher photosynthetic capacity and efficiency, low respiration rates, and higher surface area:weight ratios than plants from shallow and deep habitats along the Atlantic coast of Maine (Gerard 1990).

Temperature

Experiments on young *L. longicruris* under crossed gradients of light (5 to 70 μmol photon/m^2/s) and temperature (5° to 25°C) indicated that temperature was the primary factor regulating reproduction and vegetative growth and that the plants demonstrated seasonal acclimation responses (Egan et al. 1989). Germination of spores at 5°C was greater in January than in July, but at 25°C was greater in July. Optimal growth of gametophytes occurred at 10° to 15°C in March and 15° to 20°C in July. Growth of sporophytes was optimal at 10° to 15°C in all months (Egan et al. 1989). Other experiments on juvenile *L. longicruris* under crossed gradients of temperature (5° and 15°C) and nutrient concentrations demonstrated significantly greater growth at 15°C than 5°C at all nutrient concentration (Penniman et al. 1988).

L. saccharina on rope culturing systems in Long Island Sound grew slowly in winter when temperature ranged from -1° to 4°C (Brinkhuis et al. 1983). In one study, Davison (1987) demonstrated almost constant photosynthetic rate in *L. saccharina* grown at temperatures between 0° and 20°C, and in a later study reported that *L. saccharina* grown at 15 °C contained significantly more chlorophyll and had increased photosynthetic efficiencies than similar plants grown at 5°C (Davison et al. 1991).

Gerard (1988) reported that genetic variation among populations of *L. saccharina* exists in relation to several environmental factors, including light and temperature, and as a result of this variation, plants from different populations exhibit differential rates of carbon assimilation, growth, and survivorship under common garden conditions.

Salinity

It is generally believed that salinity is a major determinant of algal distribution because it can place osmotic stress on the cells (Chapman 1995), but there has been little experimental work to substantiate the idea. High salinity can potentially result in water loss, and low salinity can cause cells to swell or burst. In *L. digitata*, intracellular inorganic (Na, K, CL, NO_3) and organic (mannitol) substances are used to regulate osmotic potentials of cells (Davison and Reed 1985).

Water motion

Mechanical stress imposed by currents and waves may result in hydrodynamic streamlining of blade morphology without effecting productivity. Laboratory grown *L. saccharina* subjected to mechanical stress in the form of constant longitudinal tension had significantly narrower blades and higher rates of blade elongation than plants grown with no stress, however, the rates of biomass production were similar for the two groups (Gerard 1987)

Blade elongation was compared in two populations of *L. longicruris* in Nova Scotia; one population was exposed to and the other was sheltered from high intensity water movement. The maximum and minimum elongation rates were similar for the two populations, but the sheltered plants grew more rapidly during 8 months of the year. Low concentrations of dissolved nutrients in summer and low levels of illumination in fall and winter were more limiting to growth at the exposed site than the sheltered site (Gerard and Mann 1979).

Substrate

Along the Maine coast, the six species of kelps have been found attached to rock (>3m diameter), boulder (10 inches to 3 m diameter), and cobble (2.5 to 10 inches diameter) substrate in the subtidal zone (Brown 1993).

Nutrients

Kelps take up nutrients through the mature blade because they do not have a root system. The nutrients are transported to the meristem and used for growth or are stored in an internal pool for later use. In a population of *L. digitata* growing in Scotland, approximately 70% of the nitrogen demand of the meristem was supplied by nitrogen taken up by the blade and transported to the meristem (Davison and Stewart 1983). *L. longicruris* absorbed exogenous nitrate under both summer and winter conditions (Harlin and Craigie 1978). Translocation of iodine occurs in *L. saccharina* and follows a "source-to-sink" pattern i.e. it is translocated from the blade to the meristem, or if located at the meristem it stays there (Amat and Srivastava 1985).

The rate of uptake of nitrate (NO_3) and phosphate (PO_4) by *L. digitata* and *L. saccharina* collected from the North Sea off Scotland and maintained in laboratory increased with increasing nutrient concentration up to about 20 μM NO_3 and 10 μM PO_4 (Conolly and Drew 1985b). At these concentrations, uptake rates were approximately 24 μgN/g dry weight/h and 8 μgP/g dry weight/h (Conolly and Drew 1985b). Nitrite, ammonium and urea were also taken up, independently of each other, and supported growth (Conolly and Drew 1985b). Other laboratory experiments conducted on young *L. saccharina* from the North Sea confirmed the apparent saturation between 10 and 20 μM NO_3 and the development of internal reserves of nitrate at external concentrations above 20 μM NO_3^- (Chapman et al. 1978).

Studies of *L. longicruris* from nitrogen-poor (St. Margaret's Bay) and nitrogen-rich (Bay of Fundy) regions of Nova Scotia indicated genetic differences in the populations. Plants from the nitrogen-poor site had lower half-saturation values for growth, higher maximum specific growth rates, higher maximum uptake rates, and a greater capacity to accumulate nitrogen in an internal tissue pool than plants from the nitrogen-rich site (Espinoza and Chapman 1983).

ECOLOGICAL FUNCTION

Effect on water motion

In shallow water, dense canopies of macrophytes like kelps greatly reduce water movements throughout the water column and increase sedimentation (Neushul 1972).

Nutrient cycling

Chemical elements in an ecosystem cycle back and forth between the living organisms and the physical environment in a series of transfers termed biogeochemical cycles. The cycles involving carbon, nitrogen, phosphorus, and the trace metals are extremely important because these elements are vital to the maintenance of life. These elements make up the biomass of living organisms, and also exist in the sediment and water column as inorganic compounds, particulate organic matter, and dissolved organic matter.

Autotrophs alone absorb inorganic carbon, nitrogen, phosphorus, and trace metals, and use the sun's energy to convert them into living organic matter (biomass). Important autotrophs in the Gulf of Maine include single-celled organisms (e.g. bacteria, diatoms, dinoflagellates) that drift in the water column as plankton or are associated with the substrate, macroalgae (e.g. rockweed, kelp, Irish moss) that usually are attached to a substrate, and flowering plants (e.g. salt marsh grasses and eelgrass) that are rooted in the substrate and inundated to various degrees. Autotrophic biomass is the ultimate source of nutrients and energy for heterotrophs (bacteria, other single-celled organisms, and multi-celled animals). Heterotrophs in turn excrete waste products containing inorganic nutrients which are absorbed and utilized by autotrophs.

Kelp beds are important in the cycling of nutrients because they 1) can produce large quantities of organic matter, 2) harbor a diverse community of heterotrophs that consume organic matter and release inorganic nutrients, and 3) are able to absorb nutrients from the water column. Aerobic heterotrophs that are attached to kelp blades or the substrate or that are in the water column consume dissolved and particulate organic matter and excrete inorganic waste products (ammonium and phosphorus) into the water column. Kelp plants are able to absorb macronutrients including nitrogen (as ammonia, ammonium, or nitrate) and phosphorus, micronutrients (e.g., elemental metals), and other elements such as bromine and iodine (Pedersen and Romans 1983) through the blade. Kelp beds, with their high rates of accumulation, may act as sinks for nitrogen.

Kelps may be useful in reducing nutrient loading because of its high nitrogen requirements for growth. Subander et al. (1993) reported that kelp grown in the effluent of salmon aquaculture pens removed 26 to 40% of the incoming dissolved inorganic nitrogen during light periods. Uptake was greatest at the highest flow rates and at the lowest kelp density where no shading occurred. Conolly and Drew (1985a) studied the effect of a coastal eutrophication gradient (dissolved nitrate, nitrite, ammonium and phosphate on the growth and tissue composition of *L. digitata* and *L. saccharina* in St. Andrews, Scotland. The growth rates were considerably enhanced at the eutrophic stations in spring and summer.

Toxic accumulations

There is little information available regarding accumulation of toxics by kelps. All the tissues of *L. longicruris* collected from Long Island Sound had consistently lower concentrations of cadmium than copper for all months of the year-long study, and new blade tissue had significantly higher trace metal concentrations than other tissues for the months of June and October (Shimshock et al. 1992).

Food source

Several investigators have made estimates of kelp productivity. An annual net carbon budget, determined for a typical mature *L. longicruris* plant in Canada, revealed annual net assimilation was 6 to 8 mg C/cm^2 of blade surface or 71 cal/cm^2 (Hatcher et al. 1977). A seasonal carbon budget for a *L. saccharina* population in Scottish showed net annual production in excess of 120 g C/m^2/y (Johnston et al. 1977). Miller et al.

(1971) estimated that the production of seaweeds in St. Margaret's Bay was greater than 7000 kcal/m^2/yr, and that it far exceeded the ingestion rate by herbivores. In Long Island Sound, *L. longicruris* production was 10.6 kg fresh weight/m^2 in 1986, and was estimated to have been 46 to 50 kg/m^2 in 1987 (Egan and Yarish 1990).

Grazing on live kelp

The most important and destructive grazer on living kelp in the Gulf of Maine is the green sea urchin, *S. droebachiensis*. In the early 1970s, population increases of sea urchins resulted in intensive grazing of kelp and the conversion of kelp forests into coralline barrens along the Atlantic coast of Nova Scotia (Mann 1977). In 1968, the rocky floor of St. Margaret's Bay was covered with a dense bed *L. longicruris*, *L. digitata*, and *A. cribrosum* to a depth of approximately 20 m (Mann 1982). The average urchin biomass in the kelp was 150 g/m^2, but there were barren patches where kelp had been completely removed and urchin biomass averaged 1200 g/m^2 (Mann 1982). These barrens expanded due to urchin grazing, and by 1978 only 10% of the original cover of kelp remained (Mann 1982).

After sea urchin populations declined in the rocky subtidal area of the Gulf of Maine and dense beds of canopy-forming *L. longicruris* grew back, the major grazers on the kelps were snails (Lacuna vincta) (Johnson and Mann 1986) and perhaps amphipods (Robert Steneck pers. comm.). Johnson and Mann (1986) also reported that limpets and chitons grazed on kelps, but Steneck (1982) has shown that limpets graze on coralline algae. The presence of anti-herbivore chemicals in the tissue and variations in toughness and nutritional quality of tissues may have reduced grazing by snails (Johnson and Mann 1986).

Studies of carbon isotope ratios can be used to determine the importance of marine autotrophs in coastal food webs. A study of animals occurring in eelgrass and kelp beds in St. Mary's Bay, Nova Scotia, indicated that most herbivores, the filter feeders, and their predators derived their carbon from kelps, and only the herbivorous gastropod *L. vincta* utilized eelgrass more (Stephenson et al. 1984; Stephenson et al 1986).

Consumption of kelp-derived detritus

Detritus refers to dissolved organic matter, particulate organic matter, and the assemblage of decomposing bacteria and fungi that inhabits the organic matter (Zieman 1982; Thayer et al. 1984; Mann 1988). Dissolved organic matter includes soluble carbohydrates and proteins (Zieman 1982; Mann 1988); particulate organic matter includes dead autotrophs or autotroph debris, dead heterotroph or heterotroph debris of any size, fecal pellets, and combinations of these items (Cousins 1980).

As part of the natural life cycle, kelp blades are eroded at the end by wave action and fall to the bottom or are carried away by water currents (Mann 1972b). Whole blades probably become fragmented by the shredding action of herbivorous invertebrates and by physical factors such as ice grinding. The intact blades or fragments become colonized by bacteria and fungi which begin to decompose the algae.

The processes of particle size reduction and microbial colonization and decomposition are essential to the detrital food web, and have been described in detail for algae by Mann (1988). Particle size reduction is important because some organisms are able to ingest only fine particles, and the greater surface to volume ratio of fine particles allows greater colonization by microbes. The microbes enzymatically break down plant material that most organisms cannot digest, and convert it to microbial biomass which can be assimilated. Microbes also enrich the detritus by taking up nitrogen and phosphorus from the surrounding medium and incorporating it into microbe biomass.

Carbon budgets have been developed for various populations of kelps, and permit estimates of the amount of biomass that enters the detrital cycle. Hatcher et al. (1977) estimated that 35% of the annual net carbon of *L. longicruris* in Nova Scotia and was lost as dissolved organic carbon. Johnston et al. (1977) estimated that over 13% of gross carbon production was lost as extracellular secretions, and 40 to 45% was lost by distal decay and entered detrital food chains. Miller et al. (1971) estimated the production of seaweeds in St. Margaret's Bay and the ingestion rate of herbivores, and concluded that most of the seaweed production was exported out of the coastal system in the form of suspended particulate matter.

Habitat

All types of macroalgae, including kelps, add structural complexity to the substrate and water column and offer a variety of habitats for flora and fauna of all sizes (Hacker and Steneck 1990). Blades of varying age and size extend into the water column, and change their orientation with passing waves and as current changes. Epiphytes on the blades add additional complexity. Using a functional approach, the flora and fauna associated with intertidal rockweeds include: 1) epiphytes on the thallus), 2) biota that attach to the holdfast and thallus, 3) mobile fauna that move on or swim over the thallus and 4) biota that dwell on or in the underlying substrate.

There is very little data regarding the use of *A. esculenta*, *A. cribrosum*, *L. digitata*, *L. longicruris*, *L. saccharina*, and *S. dermatodea* habitat by invertebrates and fishes on the east coast of the United States. However, on the west coast of the United States the giant kelp (*Macrocystis pyrifera*) forms dense forests, and use of this habitat has been documented. Research has shown that many species of fishes use giant kelp habitat (Feder et al. 1974). The abundance and diversity of fish species declined after experimental removal of the plants (Bodkin 1988), and the density of many fishes, especially early life stages, were significantly and positively related to plant density (De Martini and Roberts 1990). The presence of giant kelp enhanced the local abundance of some species of temperate reef fishes and reduced the abundance of others (Carr 1989).

In the Gulf of Maine, 12 species of fishes and 51 species of invertebrates have been collected from kelp beds or have been observed in kelp beds (Table 1). Sampling was conducted in Passamaquoddy Bay (Logan et al. 1983) and near Pemaquid Point (Robert Steneck pers. comm). Logan et al. (1983) termed the area they sampled a subtidal crustose-coralline algae community because the encrusting coralline algae often covered 100% of the hard substrate. However, several species of kelps (*Agarum*, *Alaria*, and *Laminaria*) were listed as abundant or common, and the natural community they described is a kelp community.

In Maine, habitats with low disturbance potential (i.e., low herbivore grazing) and high productivity potential (i.e., well mixed water and sufficient light) are dominated by kelps and have high algal biomass and functional group diversity (Steneck 1994). Habitats with higher disturbance potential or lower productivity potential are dominated by crustose algae and have low algal biomass and functional group diversity (Steneck 1994).

Bologna and Steneck (1993) investigated the use of kelp beds by the American lobster (*Homarus americanus*) in mid-coast Maine. Lobster population density and biomass were significantly higher in plots of real and artificial (plastic) kelp than in adjacent non-kelp control plots, and the change in lobster density was apparent the day following the beginning of the experiment (Bologna and Steneck 1993). Early benthic stage lobsters are also found in kelp beds (Wahle and Steneck 1991).

One clear habitat-related use of macroalgae is as a substrate for numerous epifauna (Himmelman and Lavergne 1985; Himmelman et al. 1983). Some fish, such as herring (*Clupea harengus*), use macroalgae as egg-deposition sites (Cooper et al. 1975; Aneer 1989). Finally, juvenile Atlantic cod (*Gadus morhua*) may be more abundant among kelp beds (Keats et al. 1987).

Commercial uses

Salts of alginic acid (alginates) occur in all brown algae as structural components of the cell walls. Alginates are commercially extracted from *Macrocystis pyrifera*, *A. nodosum*, and *Laminaria* sp., and are used for their thickening, stabilizing, film forming and gel producing properties (Whyte 1988). The products are used extensively in the baking industry and as a stabilizer in the manufacture of ice cream. In Maine, kelp may dragged for sea urchin feed (L. Mercer pers. comm.).

Table 1. Species of fishes and invertebrates collected from kelp beds and kelp habitat in northern and mid-coastal Gulf of Maine.

Species	Common name	Species	Common name
Fishes		**Invertebrates**	
Anarhichas lupus [1]	Wolffish	*Halocynthia pyriformis* [3]	Sea squirt
Cyclopterus lumpus [1]	Lumpfish	*Harmothoe* sp. [3]	Scale worm
Gadus morhua [2]	Atlantic cod	*Henricia sanguinolenta* [3]	Sea star
Hemitripterus americanus [3]	Sea Raven	*Hiatella arctica* [3]	Boring clam
Myxocephalus aenaeus [1]	Grubby	*Homarus americanus* [3]	Lobster
Myxocephalus scorpio [1]	Shorthorn sculpin	*Hyas* sp. [3]	Toad crab
Myxocephalus octodecemspinosus [1]	Longhorn sculpin	*Iophon pattersoni* [3]	Sponge
Pholis gunnellus [1]	Rock gunnel	*Ischnochiton* spp. [3]	Chiton
Pollachius virens [1]	Pollock	*Lacuna vincta* [5]	Chink shell
Prionotus carolinis [1]	Searobin	*Lepidonotus* sp. [3]	Scale worm
Stichaeus punctatus [1]	Arctic shanny	*Littorina littorea* [4]	Periwinkle
Ulvaria subbifurcata [1]	Radiated shanny	*Obelia sp* [3].	Hydroid
Invertebrates		*Onchidorus* sp. [3]	Nudibranch
Acanthodoris pilosa [3]	Nudibranch	*Margarites* sp. [3]	Gastropod
Acmaea testudinalis [3, 4]	Limpet	*Metridium senile* [3]	Sea anenome
Alcyonium digitatum [3]	Octocoral	*Modiolus modiolus* [3]	Horse mussel
Amphitrite johnstoni [3]	Terebellid worm	*Molgula* sp. [3]	Sea squirt
Asterias sp. [3]	Blood star	*Mytilus edulis* [3]	Blue mussel
Balanus sp. [3]	Barnacle	*Myxicola infundibulum* [3]	Fanworm
Boltenia sp. [3]	Sea squirt	*Neptunea decemcostata* [3]	Whelk
Buccinum undatum [3]	Whelk	*Pagurus* sp. [3]	Hermit crab
Cancer sp. [3]	Rock crab	*Pandalus montagui* [3]	Boreal red shrimp
Caprella sp. [3]	Skeleton shrimp	*Potamilla* sp. [3]	Fanworm
Carcinus maenas [3]	Green crab	*Psolus fabricii* [3]	Sea cucumber
Chlamys islandicus [3]	Iceland scallop	*Solaster endeca* [3]	Sea star
Colus stimpsoni [3]	Whelk	*Spirontocaris spinus* [3]	Caridean shrimp
Coryomorpha pendula [3]	Hydroid	*Spirorbis* sp. [3]	Tubeworm
Coryphella sp. [3]	Nudibranch	*Strongylocentrotus droebachiensis* [3, 4]	Sea urchin
Cucumaria frondosa [3]	Sea cucumber	*Tealia felina* [3]	Sea anenome
Dendronotus sp. [3]	Nudibranch	*Tonicella rubra* [4]	Chiton
Gersemia rubiformis [3]	Soft coral	*Tubularia* sp. [3]	Hydroid
Haliclona sp. [3]	Sponge		Bryozoans [3]
Halichondria sp. [3]	Sponge		

1 = Robert Steneck pers. comm.; 2 = Keats et al. 1987; 3 = Logan et al. 1983; 4 = Schleibling and Raymond 1990; 5 = Johnson and Mann 1986.

CONCLUSION

Studies of the kelps have been conducted on both sides of the North Atlantic Ocean, and a great deal of work has been done in Nova Scotia, particularly St. Margaret's Bay. Few studies have examined the ecological functions of these species, but collectively they have shown that the five species of rockweed 1) contribute to nutrient cycling, 2) provide food to grazers and detritus feeders, 3) help maintain water quality, and 4) provide habitat for numerous species including commercially and recreationally important species.

THREATS

The major threats to kelps are destructive overgrazing by sea urchins, reproductive inhibition due to petroleum hydrocarbons, competition from nonnative species, chlorate effluent from pulp mills, local overharvesting, and toxic effects of heavy metals.

Destructive overgrazing of kelps by sea urchins appears to be sporadic problem that can last for at least 15 years. In Maine, sea urchins are harvested commercially, and in the past 10 years urchins have become the state's second most valuable marine harvest. However, in the past two years the catch has declined steadily, an indication of overfishing. A sustainable sea urchin harvest would not only provide jobs for fishermen, but would be a means of protecting kelp habitat.

The reproductive stages of *Laminaria* are especially sensitive to oil pollution. In laboratory experiments, more than 20 ppb of No. 2 fuel oil prevented *Laminaria* spores from germinating, and growth of male gametophytes was decreased by 64% in the presence of 2 ppb (Steele 1978). Petroleum products had less effect on female gametophytes and gametophytes more than 21 days old (Steele 1978). There was no evidence that adult *L. saccharina* and *L. digitata* were detrimentally affected by the release of No. 2 fuel oil following the grounding of the tanker *World Prodigy* on Brenton Reef (Peckol et al. 1990). However, *in situ* primary production of *L. saccharina* was significantly inhibited by all types and concentrations of oil tested in Canada including crude oils and the oil dispersant Corexit (Hsiao et al. 1978).

Now that populations of kelps in the Gulf of Maine have recovered from overgrazing by sea urchins, they are threatened by a non-native species of lacy crust bryozoan (*Membranipora*). The bryozoan colonizes and can completely cover a kelp blade during the growing season. The encrusting bryozoan makes the kelp blade inflexible and more likely to break when water motion increases (Robert Steneck pers. comm.).

In the Baltic Sea, the abundance and biomass of brown (fucoid) algae declined regionally after cellulose pulp mills started releasing chlorate (CLO_3^-) in their effluent (Lehtinen et al. 1988; Kautsky 1992). The chlorate is formed as a by-product in the bleaching of chemical pulp (Lehtinen et al. 1988). Laboratory tests indicated that chlorate, effective at 10 to 20 μg/L, was the main causal agent for the decline of the algae (Rosemarin et al. 1985). All species of brown algae tested were highly sensitive to chlorate, while cyanobacteria, green algae, red algae, and *Zostera* had much lower sensitivities (Rosemarin et al. 1985, 1994).

Overharvesting is a potential threat to kelps and their habitat. Current harvesting in Maine is minimal, but if the price for kelps increases sufficiently, harvest would probably increase. In Canada, harvesting of macroalgae, including *Laminaria*, by the dragrake method resulted in a by-catch of associated biota and alteration of the abiotic structure of the habitat (Pringle and Sharp 1980). Unfortunately, there is little data regarding the impact of harvesting on kelp recruitment, kelp regrowth, and on the assemblage of organisms that use kelp habitat. Population variables and the understory community composition were monitored before and after an experimental total harvest of *L. longicruris* and *L. digitata* in Nova Scotia. Both plots were characterized by high kelp standing crop that had not been affected by recent sea urchin grazing. In the deeper plot (3 to 4 m below MSL), *L. longicruris* attained maximum observed abundance within one year, and both species required two years to mature to pre-harvest population characteristics (Smith 1985).

Copper, a heavy metal, appears to have an effect on kelps. *L. saccharina* plants were cultured in various concentrations of copper. The release of spores was reduced at concentrations greater than or equal to 50 μg/l, development of early stages was delayed in concentrations greater than or equal to 5 μg/l, and growth of adult plants was inhibited at concentrations greater than 10 μg/l (Chung and Brinkhuis 1986)

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