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Eelgrass in Estuarine Research Reserves Along the East Coast, USA

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EELGRASS IN ESTUARINE RESEARCH RESERVES ALONG THE EAST COAST, USA

PART I: DECLINES FROM POLLUTION AND DISEASE
AND
PART II: MANAGEMENT OF EELGRASS MEADOWS

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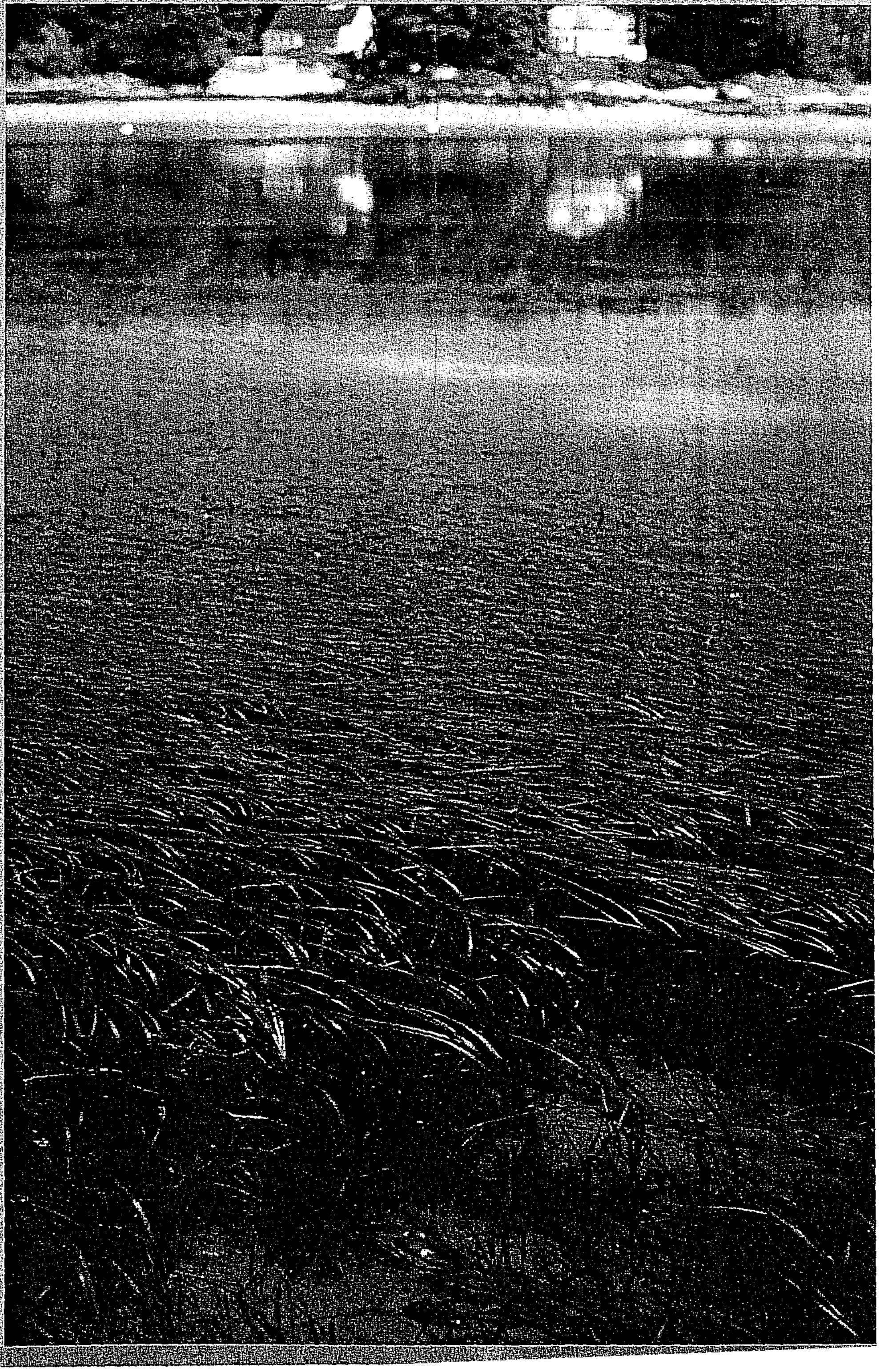

Jackson Estuarine Laboratory - UNH

NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION
U.S. DEPARTMENT OF COMMERCE

We dedicate this volume to Dr. John Sutherland, Program Manager of the Estuarine Habitat Research Program of the National Oceanic and Atmospheric Administration's Coastal Ocean Program. We appreciate his encouragement and support of our estuarine research program.

Cover Photograph shows a healthy eelgrass meadow off Gerrish Island, Maine in the Great Bay Estuary. Photo by Dr. David Porter, University of Georgia, Athens, GA.

Eelgrass in Estuarine Research Reserves Along the East Coast, U.S.A.,

Part I: Declines from Pollution and Disease

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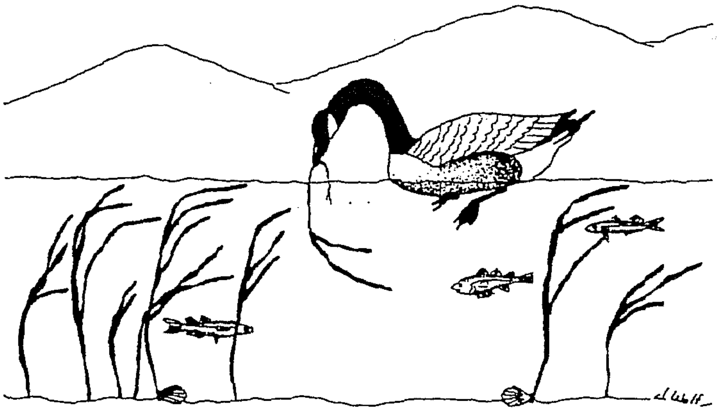

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National Estuarine Research Reserve Program and Coastal Ocean Program

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Declines of Eelgrass in Estuarine Research Reserves Along the East Coast, U.S.A.: Problems of Pollution and Disease

SUMMARY

Eelgrass, *Zostera marina* L., is a submerged marine vascular plant that provides the basic structure of an extensive and important estuarine and coastal ecosystem. Currently, eelgrass populations around the world are declining dramatically due primarily to two causes: human pollution and a disease. The extensive loss of eelgrass threatens major alterations to the coastal environment and to the waterfowl and fish that depend on these plant communities. However, the eelgrass declines represent natural experiments that provide an opportunity to investigate a disease's impact on an ecosystem, the characteristics of pollution-related declines, and finally, how declines from both causes can be diminished or mitigated.

The eelgrass ecosystem extends along the East Coast of the United States in large underwater meadows and small disjunct beds. It provides a breeding ground and nursery for coastal fish and for lobsters, crabs, and scallops. In addition, eelgrass is a food for American brant, Canada geese, black ducks and other birds, all of which can be seen feeding in estuaries with healthy eelgrass populations. Eelgrass also functions to hold coastal sediments in place and to filter suspended particles and nutrients from the water. And finally, eelgrass itself, as it dies and detaches in its annual cycle, provides a large quantity of organic material which is an important basis of the estuarine food web.

It should be clear that healthy eelgrass populations are of considerable economic value to commercial and recreational fisheries, recreational hunting of waterfowl, and to the tourism industry of coastal towns that depend upon salt water recreational resources. In addition, there are more subtle but equally important values of the eelgrass ecosystem, as it is of fundamental importance to estuarine environments now threatened by human development.

Our study presented here enhances our understanding of the physiology and ecology of eelgrass, and of the coastal ecosystems where it plays such a critical role. We have identified the status of eelgrass declines in some Estuarine Research Reserves along the East Coast and documented the progression of eelgrass declines, thereby laying the basis for follow-up restoration efforts that may lessen the impact that large-scale declines from disease or pollution might have on populations of migratory waterfowl, commercial fish and threatened species.

The eelgrass disease, discovered in eelgrass beds along the East Coast of the U.S. in 1984, has recently been named *Labyrinthula zosterae*. Disease symptoms first appear as small black spots on

eelgrass leaves. The spots spread and coalesce until finally the disease causes the plant to die. In the Great Bay Estuary on the Maine-New Hampshire border, many eelgrass beds disappeared in the 1980s due to this disease. In 1986, evidence of the disease was found as far south as Beaufort, NC and as far north as Nova Scotia, Canada. Infected eelgrass plants also have been found in Roscoff, France and in Puget Sound, WA. The symptoms and progress of the disease are similar to descriptions of a major eelgrass decline in the 1930s which was called the "wasting disease." In the 1930s, eelgrass beds from North Carolina to Newfoundland and along the coast of Europe succumbed to the wasting disease.

In addition to the wasting disease, eelgrass populations face the threat of increasing human pollution along our coastlines. Pollution-related causes of eelgrass decline include eutrophication, herbicides, dredging, and run-off from coastal land stripped of vegetation by development. Therefore, eelgrass faces a double threat: human pollution and development activities, and the recurrence of the wasting disease. Our results provide information on the status of eelgrass along the East Coast in relation to this double threat, thus establishing the background information necessary for management decisions to preserve this valuable resource.

The first major objective of our study was to determine the present status of eelgrass populations in several National Estuarine Research Reserves on the East Coast and compare the ecological conditions in the different types of estuaries. The second objective was to assess the extent of declines of eelgrass populations and determine the cause of these declines (human activity or a wasting disease) in different locations. Third, through the use of mesocosm cultures (outdoor growing tanks), the effects of disease and human-induced environmental changes on the survivorship and physiology of the plants were examined. Of particular interest were the effects of salinity, temperature, light, and nutrients in declining eelgrass beds.

Field research was conducted initially at the four National Estuarine Research Reserves on the East Coast. A fifth area, Great Bay (NH), was designated as a Reserve in 1989; a limited program of sampling was performed in this estuary from 1987 through 1989, supported by other sources (New Hampshire Waterfowl Association and New Hampshire Fish and Game). The Estuarine Research Reserve sites at Wells (ME), Great Bay (NH), Waquoit Bay (MA), Narragansett Bay (RI) and Beaufort (NC) represent a diversity of estuarine types that includes a large range of eelgrass habitats. To compare the suitability of each site for sustaining eelgrass growth and proliferation, ecological and environmental assessments of eelgrass meadows at each Research Reserve were made. Eelgrass growth, density, biomass, morphology, depth limit, phenology, and estuarine distribution were measured at each site. Field sampling was done during peak growth and peak biomass periods in different years. Additionally, environmental characteristics including water column light penetration, temperature, salinity, and depth as well as sediment organic content, porosity, pore water nutrients, and nutrient regeneration rates were measured at each location. At the Wells Reserve, where eelgrass no longer exists, the study emphasized sampling for historic eelgrass populations using seed cores and eelgrass transplanting tests. The eelgrass populations at the Research Reserves were also surveyed to determine the presence and extent of the wasting disease infection and its rate of progress.

The effect of nutrient enrichment is a conversion to algal-dominated communities, as we show in our mesocosm experiments. Examples of these community changes due to eutrophication have been documented over the last five years in estuaries along the New England coast, including Waquoit Bay. In the Waquoit Bay Research Reserve, epiphytic algal populations became dominant in Eel Pond, macroalgal blooms covered eelgrass beds in Hamblins Pond, and phytoplankton populations eliminated eelgrass in parts of Great River and Jehu Pond.

Disease is an important factor in Great Bay; causing long term loss of entire beds in the lower portions of Great Bay Estuary. Between 1981 and 1989, disease eliminated 15 of 17 beds in the Piscataqua River and Little Bay (about 99% of the original area was lost); two new beds appeared in 1991. The eelgrass population in Great Bay proper reached a low point in 1989; eelgrass is now recovering although it faces continuing losses to disease. In North Carolina, this study found only moderate disease levels (1987-1989), but in 1990 eelgrass die-offs were attributed to disease. Disease is present at high levels in Narragansett Bay and thins the beds, thereby reducing production. Waquoit Bay, with many scattered eelgrass beds separated by uplands, usually exhibits low infection by disease, even in the lower estuary, but pollution threatens upper estuarine eelgrass populations.

The mesocosm experiments were used for controlled examination of the effects of specific environmental factors on eelgrass growth and stature. For the mapping study of Research Reserves, aerial surveys, photographs and maps were examined in conjunction with ground truth checks to document the annual status of the decline and provide a permanent record for evaluating its progression or recovery. Eelgrass has been established as a valuable coastal habitat and an important part of many National Estuarine Research Reserves. Our evaluation of these habitats and the overall ecology and distribution substantially contributes to the ability to manage these estuarine systems as well as other estuarine areas.

RESEARCH DESCRIPTION

The research described is a multi-Reserve study to investigate declines in eelgrass populations. The three year project, "Decline of Eelgrass in Estuarine Research Reserves Along the East Coast, U.S.A.: Problems of Pollution and Disease" and a one year follow up study "Developing Guidelines for the Management of Eelgrass Populations Within Estuarine Research Reserves" were funded by NOAA 1987 through 1989, and 1990, respectively. During the study, eelgrass populations were surveyed within the five Estuarine Research Reserves, and areas of pollution, disease and decline were documented. Historical data on eelgrass distribution was collected and reviewed in year two. Eelgrass mesocosm experiments were run during each year of the project. Additional eelgrass populations were monitored at each Reserve to document changes due to pollution or disease. Data collected was analyzed and synthesized separately for each Reserve, and evaluated collectively with the mesocosm experimentation.

The research reported here for the North Carolina, Narragansett Bay (RI), Waquoit Bay (MA), and Great Bay (NH) Estuarine Research Reserves provides a time-course evaluation of pollution-related and disease-related declines of eelgrass over a large latitudinal range. The work includes an annual survey of eelgrass populations, a comparative analysis of eelgrass ecophysiology at the different sites, the completion of the mesocosm experiments, a synthesis of the three years of data and, finally, our management recommendations.

INTRODUCTION

The disappearance of eelgrass, *Zostera marina* L., from the coastal waters of North America and Europe in the early 1930s has been described as a major natural catastrophe (Milne and Milne 1951; reviews: Johnson and Sparrow 1961, Rasmussen 1977, den Hartog 1987). The actual cause of this so-called "wasting disease" was never determined, but the impact of that decline on the Great Bay Estuary in New Hampshire, among other places, indicated that eelgrass functions as a filter of sediments and pollutants (Jackson 1944) and promotes a healthy, productive estuary (Short and Short 1984). Eelgrass meadows form the basis of many estuarine and coastal ecosystems (see reviews: Phillips 1984, Thayer et al. 1984). These seagrass communities are best known for their roles as nurseries and breeding grounds for coastal fish and invertebrate populations, and as supporters of complex trophic food webs, by virtue of both their physical structure and their primary production (Thayer et al. 1975, Short and Short 1984).

Recently, seagrass declines resulting from environmental pollution and human activities in the coastal zone have been reported around the world. Decline is defined as chronic dieback of significant portions of seagrass beds with no reestablishment from perenniating organs. The loss of eelgrass in the Chesapeake Bay has been variously attributed to eutrophication, herbicide runoff, and increased turbidity from development (Jones and Tippie 1983, Kemp et al. 1983, Orth and Moore 1983). A seagrass decline in southwestern Australia was linked to industrial expansion and alteration of harbor circulation (Cambridge and McComb 1984). Analysis of eelgrass decline within a tidally restricted area in Holland suggests that increased nutrient loading produced toxic sediment conditions (Nienhuis 1983). Ongoing studies of lagoons on the southeast Massachusetts (USA) coast have shown that human development activities are responsible for the decline in eelgrass in the upper end of these estuaries (Costa 1988).

Major declines of eelgrass populations have been detected in the Great Bay Estuary, NH (Short et al. 1986) and on Cape Ann in Massachusetts (Dexter 1985, Short et al. 1987). Similar to the declines of the 1930s, but unlike the current pollution-related losses, this loss of eelgrass populations is caused by a disease. Detailed examinations of eelgrass from both Great Bay and Cape Ann confirm that the same symptoms of infection were associated with both declines. The current eelgrass disease has also been observed as far north as Nova Scotia, Canada and as far south as North Carolina (Short et al. 1987). Additionally, the disease has been found on eelgrass in Roscoff, France and Puget Sound, WA (Short et al. 1988). Surveys of eelgrass in the Research Reserves during this project have documented the extent of the wasting disease as well as the status of existing eelgrass populations and of present declines (see below).

We have recently discovered the organism responsible for causing the wasting disease (Short et al. 1987). Through the completion of Koch's Postulates we have shown that the protozoan *Labyrinthula* is the causal organism producing the eelgrass infection (Muehlstein et al. 1988). We have isolated the organism from infected eelgrass in New Hampshire, North Carolina, and Washington. Subsequent studies of the disease organism has shown that only one species of *Labyrinthula* is responsible for causing the wasting disease, and this species has been named *Labyrinthula zosterae* (Muehlstein et al. 1991). Knowledge of the causal organism now allows us to distinguish pollution-related declines from disease phenomena.

The characteristic symptoms of eelgrass infection begin as small black lesions on the healthy growing leaves. The necrotic spots quickly spread along the leaves and coalesce, eventually turning the entire leaf black. The extent of this infection on individual leaves has been quantified using an index of infection. A "Wasting Index" (Fig. 1) was developed to determine the infected area of an actively growing shoot. Using the index, it is possible to quickly determine the extent of infection in any eelgrass population or, with subsequent measurements, to determine the rate of spread of the disease. Controlled outdoor cultures of eelgrass maintained in mesocosm tanks (Short 1987) are also being used to investigate the progressive spread of this infection. The mesocosm cultures provide the opportunity to examine the effect of one altered condition while maintaining other factors constant or the same as the controls. Eelgrass shoots monitored over time in an infected mesocosm demonstrated progressive increases in infected areas and plant death (Fig. 2).

The present decline in the Great Bay Estuary represents a virtual disappearance of eelgrass from the outer estuary in a manner similar to the 1930s decline. Monitoring of the Piscataqua River and Little Bay, where abundant eelgrass grew in 1981, revealed no viable eelgrass beds in 1984 (Short et al. 1986). During 1985-89, the eelgrass decline continued to spread into the central part of Great Bay (Short, per. obs.). Since 1989, eelgrass has begun to recover throughout the estuary, although there are ongoing losses to disease. In the project reported here, we have examined eelgrass populations in the Estuarine Research Reserves of the East Coast and have laid the framework for following the progression of the wasting disease over this large geographic area.

WASTING INDEX METHOD

Introduction: The purpose of the wasting index method is to provide a rapid procedure to quantify the disease on an eelgrass shoot. Shoots are collected to represent the population under study, and should be rinsed with fresh water to halt disease spread.

A. Enter the date the shoots were collected under "Date", the location and site of the collection at under "Site", and the person collecting the eelgrass and measuring the disease under "Person".

B. Select a terminal, vegetative shoot and number it. Enter the number on the data sheet under "Shoot #".

C. Measure the shoot width in millimeters (e.g. 3.2) and enter under "Width".

D. Measure the height of the youngest visible sheath (usually encloses the youngest two to three leaves) from the youngest root node in centimeters (e.g. 14.7) and enter under "Sheath".

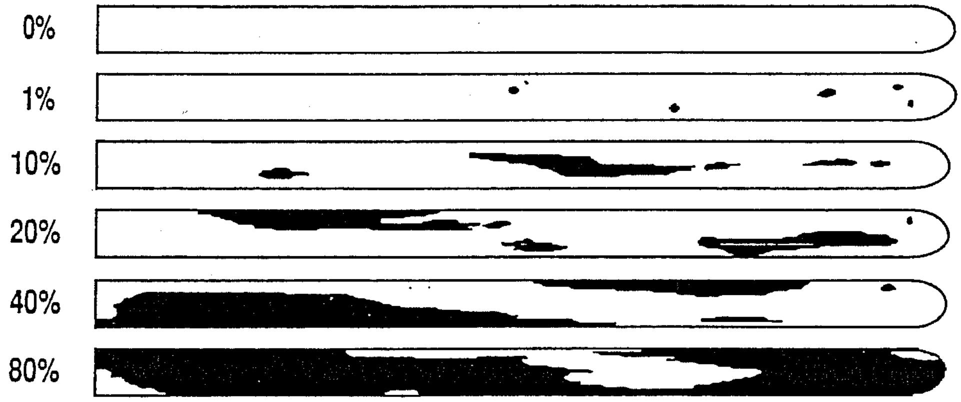
E. Number the leaves of each shoot from youngest to oldest.

F. Measure the length of each leaf from the youngest root node to the tip in centimeters (e.g. 54.9) and enter under "Length". If the tip is broken, measure to the break and write "BT" next to the measurement.

G. Enter the percentage of disease on the leaf under "Index". The percentage of disease on a leaf is estimated by examining the portion of the leaf from the top of the sheath to the tip, then comparing the disease areas on the leaf to the "Wasting Index Key". The diseased areas for 0, 1, 10, 20, 40, and 80% infection are shown. Interpolate if the leaf appears to have a percentage of disease between the numbers on the key (e.g. 3% or 65%).

H. Enter noteworthy observations under "Comments".

WASTING INDEX KEY



EELGRASS WASTING INDEX DATA ANALYSIS															
Date:		Site:			Person:										
	Width	Sheath	Leaf #1		Leaf #2		Leaf #3		Leaf #4		Leaf #5		Leaf #6		Comments
Shoot#	(mm)	(cm)	Length	Index %	Length	Index %	Length	Index %	Length	Index %	Length	Index %	Length	Index %	
1															
2															
3															
4															
5															
6															
7															
8															
9															
10															

Figure 1. Procedure to determine the Wasting Index, an objective and comparable measure of the area of disease infection by *Labyrinthula zosterae*.

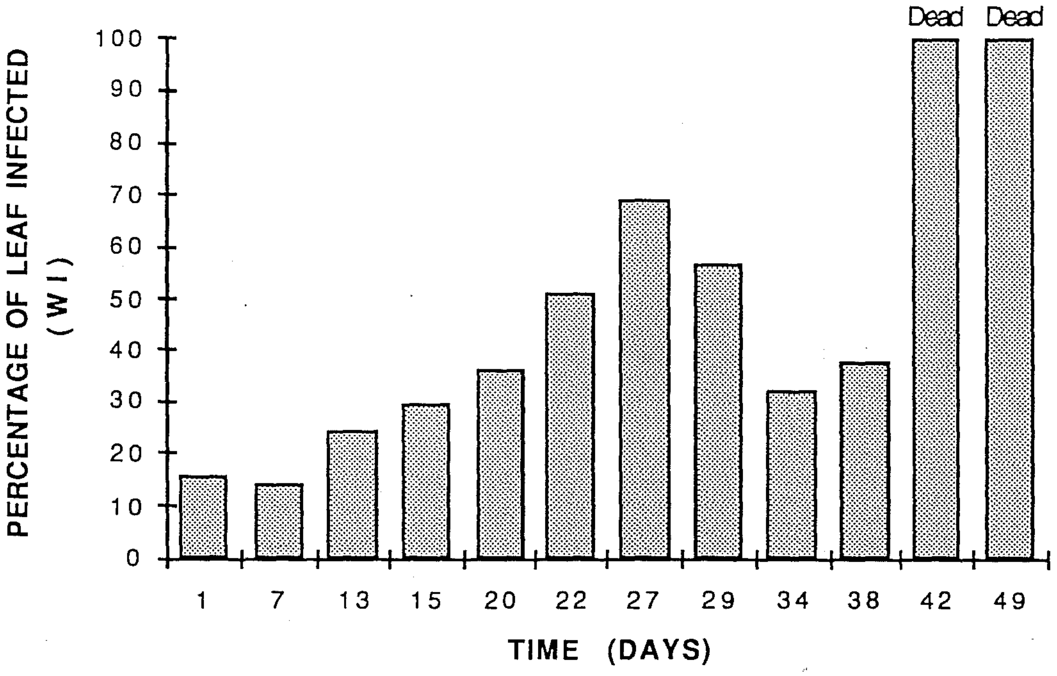


Figure 2. Progression of the wasting disease as measured by the Wasting Index on ten plants. Plants were maintained in 1.5 m^2 mesocosms at 12 to 15 ppt salinity and shaded to exclude 90% of the sunlight. The salinity was allowed to return to ambient levels (24-28 ppt) and at Day 0, diseased plants were introduced to the tank.

The declines represent a major threat to estuarine ecology, water quality, and commercially-important species. The most immediate impact of a widespread eelgrass decline will be, as in the 1930s (Dexter 1947), on the migratory birds that depend heavily upon the eelgrass community for their subsistence, such as Canada geese, American brant, black duck, and blue heron. The long range impacts will dramatically affect populations of fish, shellfish, and crustaceans (winter flounder, tom cod, lobster, crabs, scallop, blue mussel, oyster, and clams) that depend on the eelgrass habitat for food, protection, reproduction, and rearing of young.

Given the importance of eelgrass ecosystems and the double threat now facing them from both pollution and disease, it was important to establish baseline information for eelgrass beds along the East Coast. The first step was to establish the geographical distribution of present eelgrass populations, the habitats that they provide, and the varying environmental conditions where eelgrass is found. The second step was to investigate eelgrass ecology as it relates to the two types of decline that are threatening this ecosystem. The geographic locations of the National Estuarine Research Reserves and the types of estuarine environments that they include were ideal for investigating the eelgrass problem.

The research we report on below provides an integration of the following approaches: field surveys and mapping of eelgrass meadows, geographic analysis of population declines, and mesocosm experiments to investigate disease resistance and test for the direct and interactive effects of environmental stress. The research products included in this report are a synopsis of experimental research findings, a series of maps showing past and present eelgrass status in the study sites, and a document enabling coastal managers to recognize eelgrass declines and determine their probable causes.

OBJECTIVES

The goal of this project was to develop a comprehensive understanding of current eelgrass declines, providing the knowledge of eelgrass ecology necessary for management of this critical estuarine habitat. In addressing the current decline of eelgrass populations in estuaries and coastal areas of the East Coast, three major research objectives evolved. The first was to determine the present status of eelgrass populations in the National Estuarine Research Reserves of New England and North Carolina, and to compare their ecology in the different types of estuaries. The second objective was to further assess the extent of the decline of eelgrass populations and determine the causes of the decline, human activity or wasting disease, in various locations.

A third objective was to clarify the effects of natural and anthropogenic environmental factors on eelgrass physiology and its susceptibility to disease (Short 1987). The effects of salinity and light on eelgrass populations were examined using mesocosm tanks in years one and two. Mesocosm investigations in year three addressed the problem of nutrient pollution in estuarine waters and direct and indirect effects on eelgrass production and susceptibility to disease. In year four, reduced light treatments were combined with a nutrient enrichment treatment to investigate their interactive effect on eelgrass populations and plant susceptibility to disease. The mesocosms also served to provide a controlled source of plant stock for observations and experiments.

Finally, data from four years of work (1987-1990), resulting from field studies and mesocosm experiments, are combined in an overall analysis. A synthesis of the entire data base forms the basis for a management document with quantitative guidelines for sustaining eelgrass populations in coastal estuaries.

METHODS

Field Studies

Research was conducted at the four established Estuarine Research Reserves and the new Great Bay Research Reserve in New Hampshire (Fig. 3). The Estuarine Research Reserve sites at Wells (ME), Great Bay (NH), Waquoit Bay (MA), Narragansett Bay (RI), and Beaufort/Rachel Carson (NC) represent a diversity of estuarine types. Included are the shallow embayments of Wells that are dominated by salt marshes, the shallow mudflats and riverine system of Great Bay, the larger lagoon of Waquoit Bay with fringing marshes, the large deepwater Narragansett Bay, and an area of shallow open flats in North Carolina. These estuaries represent a matrix of decline conditions: areas having less eelgrass than expected (ME); areas impacted by human pollution (MA); areas that were heavily infected by the wasting disease (NH), and areas with wasting disease but that had no apparent active decline from either disease or pollution (RI and NC).

Ecological and environmental assessments of eelgrass meadows at each Research Reserve provided a basis for comparison within Reserves over time, and between Research Reserves, in order to distinguish pollution and disease related declines. Eelgrass growth, density, biomass, morphology, depth distribution, phenology, elemental composition (C:N:P), wasting disease infection, and areal distribution (see Table 1 for specific methods) were measured at Back Sound, NC, Waquoit Bay, MA, and Narragansett Bay, RI. Environmental characteristics of the water column (light penetration, temperature, salinity, current and depth), and the sediments (organic content, porosity, pore water nutrients, and nutrient regeneration) were measured at each location (Table 2). When light penetration was measured concurrently at two sites in a Reserve, the attenuation rate of the overlying waters was compared using an attenuation coefficient, k_r. The equation used was: $k_r = (\ln I_o - \ln I_z)/Z$, where I_z is the measured light averaged over nine hours (0800 to 1700), I_o is the average daily solar radiation at the Earth surface for the month of sampling and the Reserve location (Office of Meteorological Research and Office of Climatology 1964) divided by nine, and Z is the average depth over the day.

Twelve sediment cores to a depth of 10 cm were taken in modified 60 cc centrifuge tubes from each Estuarine Research Reserve location, and the cores incubated under anoxic conditions at 20°C for 0, 1, 2, and 4 days. The cores were removed (3 per day) and centrifuged to separate the water from the sediment. The pore water was then extracted, filtered and analyzed colorimetrically for ammonium (NH_4^+) and phosphate (PO_4^{3-}). Sediment porosity was measured on triplicate cores. Nutrient concentrations for regeneration rates were calculated on a sediment volume basis, and then regressed over time. The rate of nutrient production in the sediments (regeneration rate) is a measure of how fast ammonium and phosphate are being released into the sediment pore water and becoming available for uptake by eelgrass roots. The pore water content of the sediments was obtained from each of the core samples collected for the nutrient regeneration study. Core samples were weighed wet and again after drying at 80° C for 48h (or until constant wt.). The percent organic content in the sediment was also

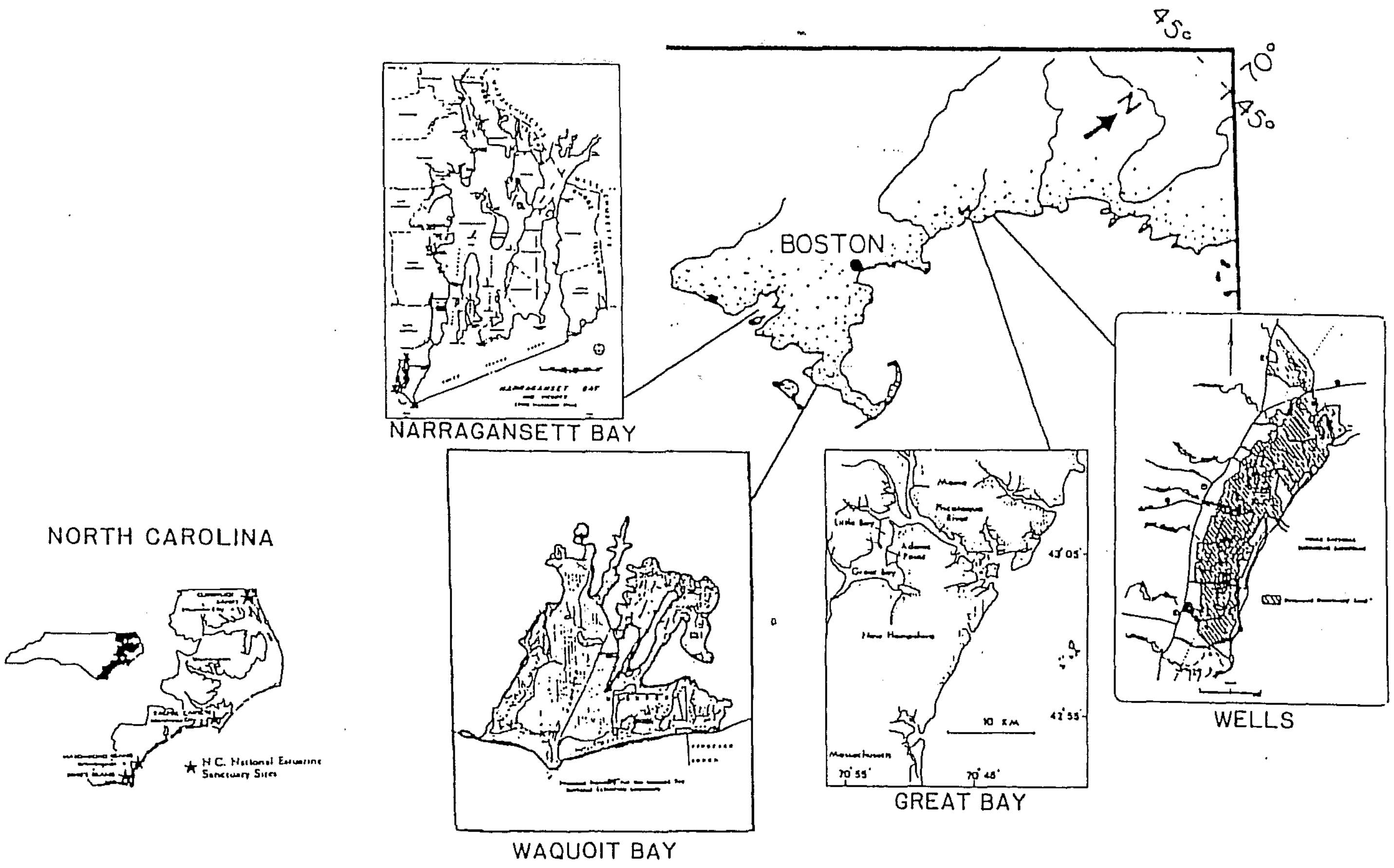


Figure 3. National Estuarine Research Reserves of the East Coast that were included in this study.

determined from these cores by combusting the dried sediment in a 500°C furnace for 24 h. The sediment samples were weighed before and after combustion. The difference in the two weights is due to the organic material having been burned off; the percent organic content of the sediment is calculated. Six replicate cores at each Research Reserve site were analyzed.

Table 1. Eelgrass ecological methods used at each of the sampling sites.

SAMPLE		UNITS	METHOD
Biomass	Shoot, rhizome, root	g dry wt./m^2	1/16 m^2, 24h @ 80°
Density	Shoots	#shoots/m^2	1/16 m^2, counts
Morphology	Shoot		Short, 1987
	Leaf length	cm	maximum for 10 shoots
	Leaf width	mm	maximum for 10 shoots
	Number of leaves	#/shoot	count for 10 shoots
Phenology	Reproductive/vegetative	#shoots/m^2	1/16 m^2, counts
Growth	Leaf length	cm/cm/d; cm/d/shoot	Zieman, 1974 leaf marking
Disease Infection	Shoot	% leaf area infected Wasting Index	Burdick et al. 1993
Elemental Composition	Leaf, rhizome, root	% C, N, P; C:N; C:P	Short, 1990
Distribution	Shoot	Areal distribution at 1:10,000 scale	aerial and ground surveys as needed

Each year the main sampling effort focused on data collection from eelgrass habitats at each Reserve that appeared to be comparable in terms of mean water depth, sediment organic matter, and current regime. The 1987 and 1989 data were collected from habitats having organic-rich sediments, whereas the 1988 samples (and a set of 1989 samples from Waquoit and Narragansett Bays) were collected from habitats having organic-poor sediments (Fig. 4). These data were analyzed on a latitudinal basis for each year (1987-1989).

The standing stock of eelgrass is often highly variable, making quantification of density and biomass a major project. For example, eelgrass density in any particular locale can vary from a few shoots per square meter to over 2,000. Measurements of biomass can have a large seasonal variation

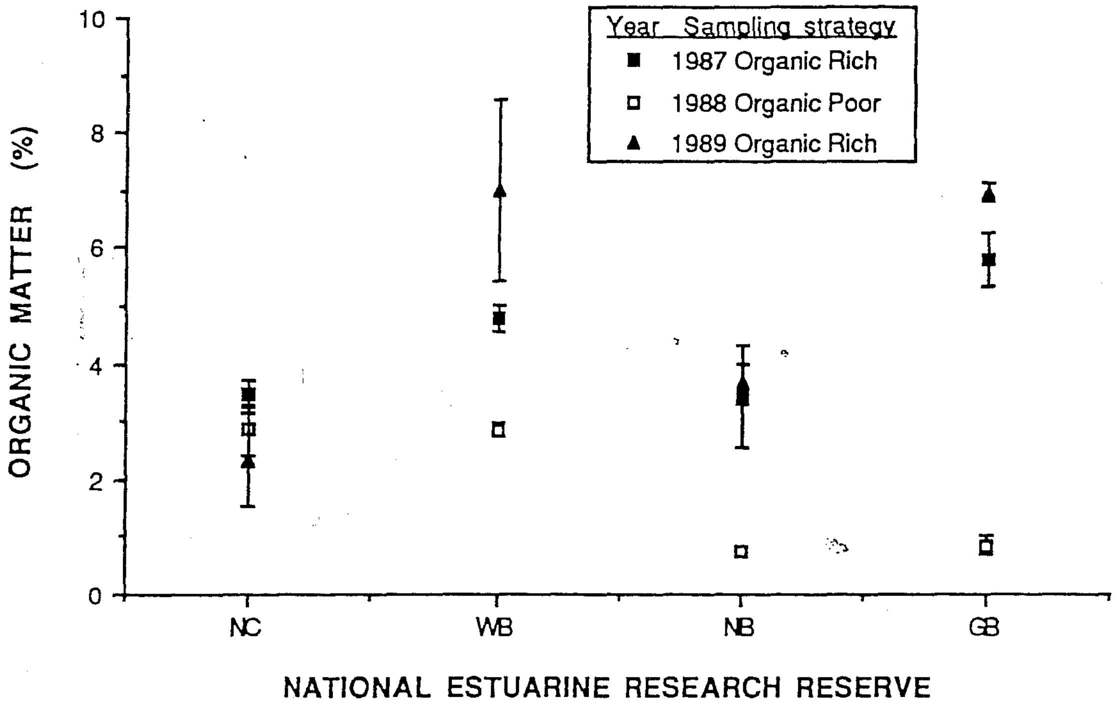


Figure 4. Organic matter in the top 15 cm of sediment in the areas sampled for eelgrass. In 1987 and 1989, the sampling strategy was to sample eelgrass in areas with organic-rich sediments. In 1988, the strategy was to sample areas with organic-poor sediments. Values are the means +/- standard error of three (1987) to six (1988, 1989) replicates.

as well. The timing of the field sampling at each Reserve was devised so that measurements would be made at comparable times in the growing season, since most of the important eelgrass characteristics have strong seasonal cycles. A compilation of data from seasonal studies of eelgrass shoot biomass published in the past 20 years indicates a trend of maximum standing crop later in the season with increasing latitude, as would be expected (Fig. 5). Field sampling in 1987 was done during the peak biomass period in July/August, when the wasting disease is usually widespread. This period probably yielded the best estimates of maximum standing stock, but following the first year of measurements it was concluded that the period of rapid vegetative growth (just prior to the July/August biomass maxima), would yield the most comparable data in terms of growth and elemental composition, while still yielding comparable data on standing stock and disease characteristics. Therefore, field sampling in 1988-89 for environmental and plant characteristics was done during the rapid growth period (May for North Carolina, late June for Narragansett Bay and Waquoit Bay, and July for Great Bay).

Table 2. Environmental characteristics monitored at each of the sampling sites.

SAMPLE	UNITS	METHOD
Water Column		
Light	µE/m^2/h	Estuarine Sensor and Profiler*
Temperature	°C	"
Salinity	ppt	"
Depth	m	"
Sediment		
Porosity	% vol.	wt. H_2O/vol. sediment
Organic content	% wt.	Combustion loss at 500°C
Pore water N	µM NH_4^+	sippers (Short et al. 1985)
Pore water P	µM PO_4^{-3}	sippers (Short et al. 1985)
NH_4^+regeneration	µmol/cm/d	incubation (Short 1987)
PO_4^{3-}regeneration	µmol/cm/d	incubation (Short 1987)

*The Estuarine Sensor and Profiler is an underwater monitoring unit deployed for two week periods to continuously record environmental data.

Eelgrass leaf biomass was measured on six 1/16 m^2 quadrats collected at each Research Reserve site. Number of leaves as well as length and width of the longest leaf for each shoot were measured for ten plants per sample. Samples of belowground material were taken with 1/50 m^2 cores

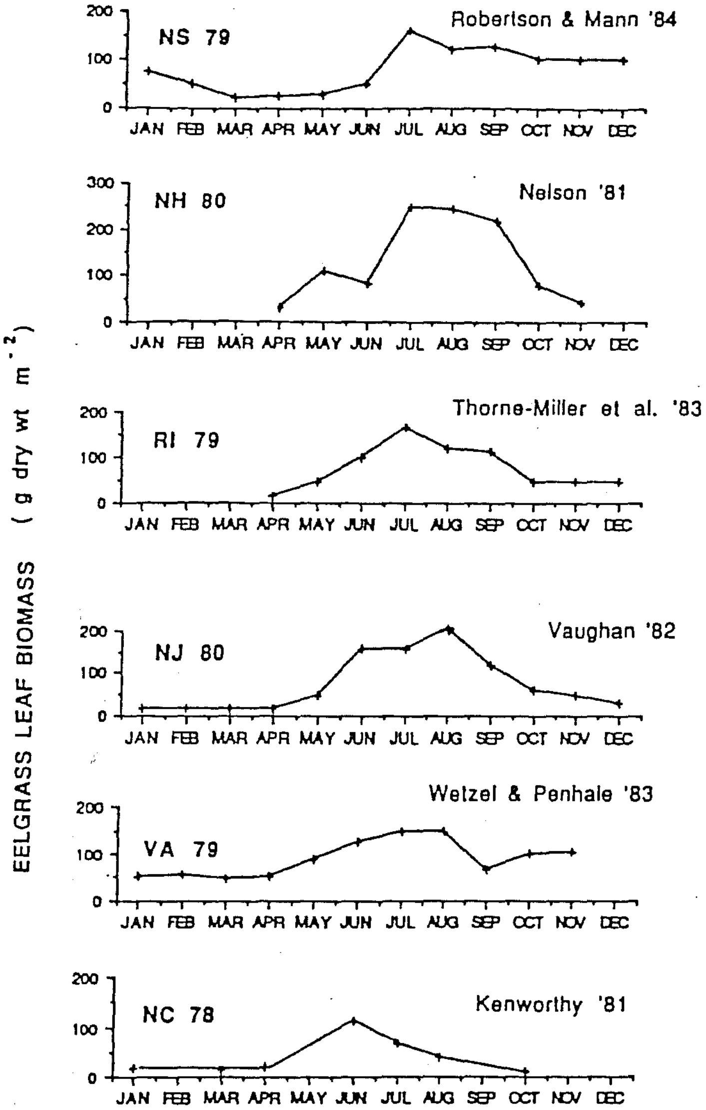


Figure 5. Seasonal patterns of eelgrass leaf biomass along the latitudinal gradient from North Carolina to Nova Scotia. The period of maximum upward slope, indicating maximum growth rate, is April to June in the southern half, and June to July in the northern half, of its range.

within the six quadrats at each location. All eelgrass plant material was washed from each core on a 1 mm screen. Roots and rhizomes were weighed separately, and the rhizome lengths measured.

Twenty to thirty eelgrass shoots were marked for growth at each National Estuarine Research Reserve site. The plants were marked *in situ* by means of a 21 gauge hypodermic needle inserted through the leaf bundle at a location just below the top of the leaf sheath. After 10 to 14 days, the marked plants were collected and measured. Leaf growth was determined by measuring the distance between the pin hole in the sheath and the hole in each individual leaf. Measurements were made for each leaf of each shoot. New growth was recorded in terms of increased length. Eelgrass growth per shoot (cm/day) and specific growth (cm/cm/day) were calculated for each site.

Eelgrass shoots were examined for the extent of infection by the wasting disease by collecting ten to twenty shoots from each Research Reserve location. Measurements were made for length and width of each leaf and the sheath length for each plant. The diseased area for each leaf was estimated by means of a "Wasting Index key" (Fig. 1). The key pictures various degrees of leaf infection ranging from 0 to 100% affected. An estimate of the percentage infected for each leaf is arrived at by comparing the individual leaves to the Wasting Index key. The Wasting Index is the percent infection on the most infected leaf for each plant, averaged for all the shoots indexed. The Whole Shoot Wasting Index is a measure of the amount of infection on all the leaves of a shoot, averaged for the sample of shoots.

Eelgrass populations at the Estuarine Research Reserves were surveyed to determine the extent of the disease infection and its rate of progress. Eelgrass samples taken during the field survey (Table 1) were rated using the "Wasting Index" (see Fig. 1) in order to quantify the degree of infection. Using this method, eelgrass shoots were analyzed to assess and compare the impact of the disease on populations of eelgrass at different locations and under different environmental conditions. In addition, the Wasting Index can document the progression of the disease at specific locations over a time course, such as was done in the mesocosms (Fig. 2).

At the Wells Reserve, where no persistent populations of eelgrass were found, sediment cores were collected to assess the historic record of eelgrass occurrence. Additionally, eelgrass was transplanted (using the method of Fonseca et al. 1982) into test plots at two sites of historic eelgrass beds to determine if the habitat is still suitable for eelgrass growth.

Mesocosm Experiments

The mesocosm tanks represent a mechanism for controlled examination of factors affecting eelgrass that were studied in the field. Using an array of mesocosms, effects of specific environmental factors can be elucidated (Short 1985, 1987). The advantage of the mesocosm approach is that one factor can be manipulated and examined while all other variables are maintained similarly in both the treatment and the control. The mesocosm apparatus consists of 1.5 meter square tanks supplied with running seawater. These outdoor tank cultures have been established with natural light regimes and ambient temperature conditions. Since higher salinities promote rapid eelgrass decline from the wasting disease (Fig. 6), salinity was used to control infection in the mesocosms. In the preinfection phase of the experiment, when the effects of light and nutrients on population characteristics were measured, the salinity was held at 12 to 15 ppt. Then the salinity was allowed to rise to the levels of the ambient Great Bay water to determine light and nutrient effects on the spread of the wasting disease.

Mesocosm research throughout the four years of the project provided the opportunity to examine and compare the two main causes of eelgrass decline (light attenuation and disease) simultaneously. Since eelgrass growth is largely a function of light and nutrients (Thayer et al. 1984), these factors were manipulated in the year four mesocosms to assess the impact of pollution-induced stresses on the spread of the disease (Table 3). In years one and two, irradiance was reduced to levels below eelgrass light saturation using neutral density screens positioned above the tanks. In year three, levels of nitrogen and phosphorus available to the plants were altered by addition of N and P to the water column. In year four, two nutrient levels were combined with three light levels in a factorial treatment arrangement with two replicates for each treatment combination (Table 3).

Table 3. Environmental and climatic factors established in the control and experimental mesocosms. The shade treatment indicates the percentage of light reaching a depth of 1 cm relative to that at the water surface. A "c" indicates that the environmental factor is the same as the control.

ENVIRONMENTAL FACTORS	CONTROL	SHADE EXPERIMENT (1988)	NUTRIENT EXPERIMENT (1989)	SHADE AND NUTRIENT EXP. (1990)
Irradiance	94%	11,21,41,61%	c	11,41%
Photoperiod	Natural	c	c	c
Seawater Nutrients	Low	c	6X N and P	6X N and P
Temperature	Ambient	c	c	c
Salinity	Regulated at <15 ppt	c	c	c
Seawater Flow	20 L/d	c	c	c
Current	2-20 cm/sec	c	c	c
Substrate	Mud/sand (1/1)	c	c	c
Water Depth	20 cm	c	c	c

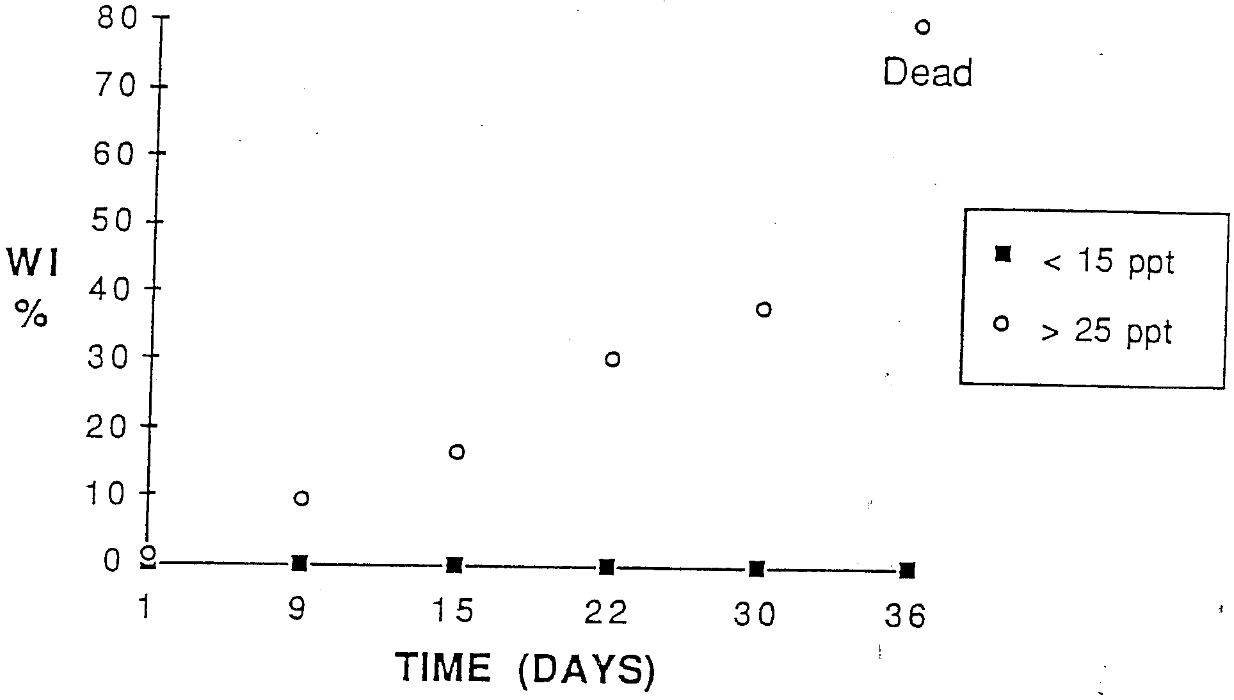


Figure 6. Infection of eelgrass by wasting disease at two contrasting salinities, followed through time on ten plants per tank using the Wasting Index (WI). The experiment was conducted in mesocosm tanks and began July 12, 1988.

Mapping

The extent of historical documentation of eelgrass distribution varies among the five Research Reserves. At Wells and Narragansett Bay, the extent of past populations of eelgrass is poorly known, whereas historical eelgrass distribution records in Waquoit Bay and Beaufort were made available. Our development of methods to determine current eelgrass distribution led to the realization that the historical distribution records for these two Reserves was of limited value. Coverage was incomplete for Waquoit Bay (Fig. 9), and lack of ground truthing to verify species distributions at both Reserves further decreased the utility of these limited data. The best records exist for Great Bay, and although they do not extend far back in time, they appear to be accurate.

The current status of eelgrass distribution was determined for the five Reserves. Aerial surveys employing color photography, existing photographs, maps, and ground truth checks have documented the current status of eelgrass, and the extent of decline (Waquoit Bay and Great Bay), and provided a permanent record for evaluating the continuing progression of eelgrass decline, or an eelgrass recovery when and if this trend reverses. Additional aerial surveys were made when existing documentation was not adequate or where rapid change in eelgrass distribution had occurred. Samples taken during ground truth surveys were analyzed to assess and document the impact of pollution and the wasting disease on various populations of eelgrass at different locations.

RESULTS AND DISCUSSION

Research Reserve Eelgrass Status

Mapping

The distribution of eelgrass in the Estuarine Research Reserves (Great Bay, Waquoit Bay, Narragansett Bay, and North Carolina) was mapped for 1989 in order to document and examine habitat loss. Composite maps constructed from aerial photographs and ground truth surveys provide an excellent record of present distribution. They also serve to document the extent of eelgrass decline, as shown for Great Bay and Waquoit Bay. Although no eelgrass is currently found in the Wells Reserve, the survey found another seagrass, *Ruppia maritima*, in the deep salt marsh pannes and drainage channels throughout the estuary.

The North Carolina Reserve at the Rachel Carson site is a series of islands within an embayment called Back Sound. Two previous studies of the seagrass distribution were made for the Research Reserve in this decade (Carraway and Priddy 1983, Kirby-Smith 1987) but both were incomplete assessments (e.g. Fig. 7a). However, at the time of the present study two other projects were ongoing mapping seagrass in this area of Back Sound (R. Ferguson, NMFS, Beaufort, NC, pers. comm.; Jose Rivera, NMFS, Beaufort, NC, pers. comm.). Because of the seagrass mapping projects underway in North Carolina, we concentrated our efforts in the seagrass area in and adjacent

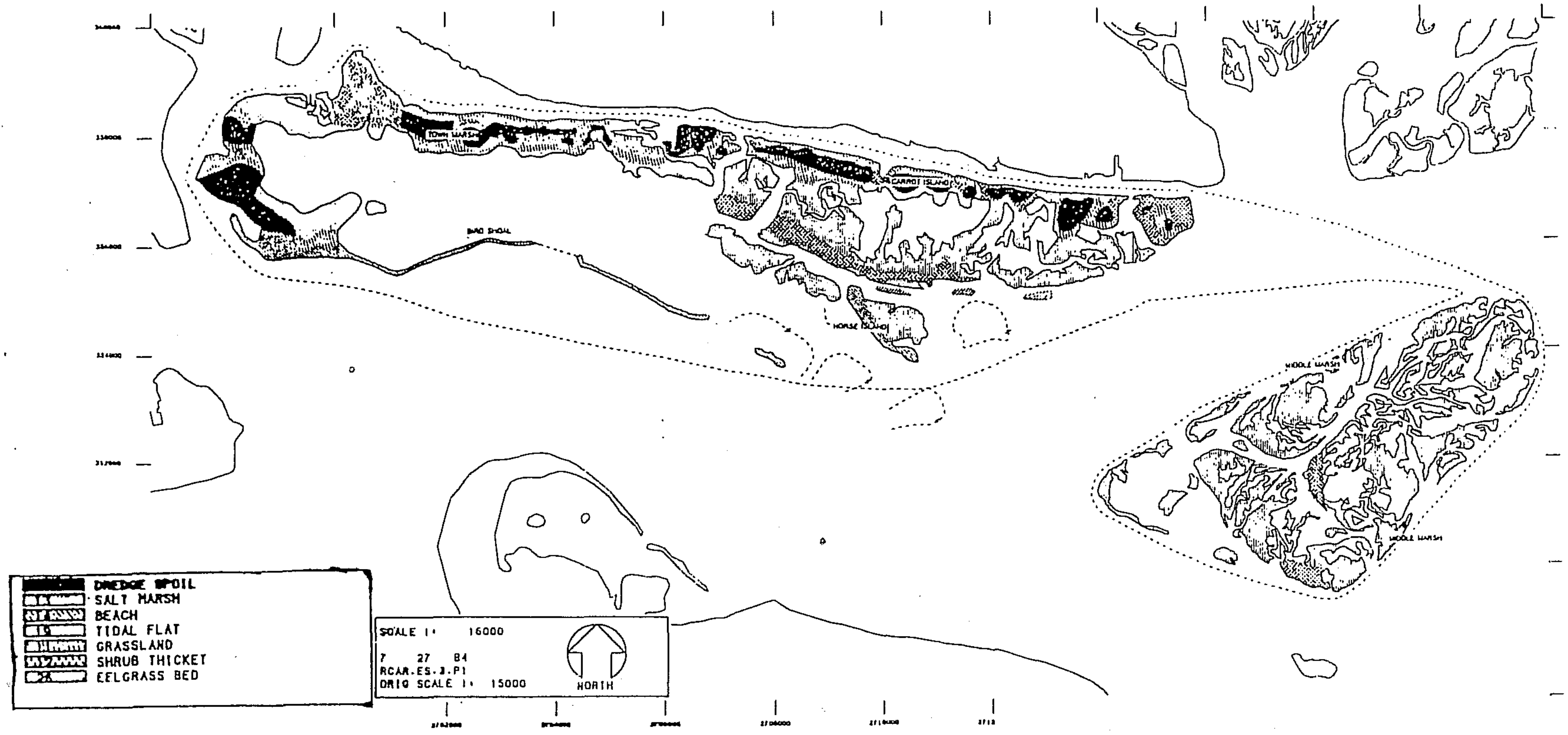


Figure 7. Eelgrass status in the Rachel Carson site of the North Carolina Reserve. a. Seagrass distribution in the Research Reserve determined by Carraway and Priddy (1983).

to the south side of Middle Marsh. There are three important seagrasses found in the Reserve (Fig. 7b): eelgrass (*Zostera marina*), shoal grass (*Halodule wrightii*), and widgeon grass (*Ruppia maritima*). The most extensive area of eelgrass was in the semi-enclosed embayment comprising the southeast corner of Middle Marsh (Fig. 7c). Monitoring this location throughout the project revealed no evidence of eelgrass decline. Many other smaller patchy and fringing beds are found throughout Middle Marsh and on the adjacent shoals, as well as along the southeast side of Carrot Island (Fig. 7b). An additional extensive and healthy eelgrass bed is found west of Middle Marsh adjacent to the shallow shoal south of Carrot Island.

Narragansett Bay Research Reserve includes the waters around Hope Island, Patience Island, and the north end of Prudence Island. However, throughout this project the eelgrass mapping area included all of Prudence Island (Fig. 8). The historical distribution of eelgrass within this study site had no scientific documentation, although anecdotal information suggests that eelgrass was previously found extensively all along the east side of Prudence Island, from shore to shore in the shallow areas between Prudence and Patience Islands, and on the shallow flats in the middle of the western shore. Local islanders contend that eelgrass on the east side of Prudence Island was wiped out by the 1938 hurricane, eroding the bottom and washing away all the soft mud.

The current distribution of eelgrass is relatively small, but stable. Within the Reserve, the largest bed of eelgrass was on the west side of Prudence Island in the embayment called Eelgrass Cove, where a healthy population persists (Fig. 8). The only other eelgrass bed found within the Reserve was a collection of large patches (>2 m diameter) on the east side of Hope Island. On the southern and southeastern sides of Prudence Island extensive beds are found fringing the shore (3 to 20 m wide) to a depth of about 3 m below Mean Low Water. We sampled the historical distribution of eelgrass using sediment cores. The presence of eelgrass seed husks in the sediment suggests that eelgrass formerly grew in Potters Cove on the east side, in Sheepshead Cove on the west side, and in the broad cove in the middle of the island's west side (Fig. 8).

Waquoit Bay Research Reserve has had more documentation of historic eelgrass distributions than any of the other Reserves we studied. The status of eelgrass populations for the central basin of Waquoit Bay was mapped by J. Costa in the early 1980s (J. Costa, Buzzards Bay Project, MA, pers. comm.) from historic photography spanning several decades (Fig. 9). His work suggests a dramatic decline in eelgrass in the central Bay over the previous thirty years. Unfortunately, his study area only covered the east side of the central basin, and excludes all areas where eelgrass beds occur today. Our monitoring of eelgrass distribution from 1987-89 has shown the persistence of a large bed in the lower basin, while documenting dramatic declines in many of the other eelgrass beds (Fig. 10 a,b,c). However, large changes in the size and shape of the lower basin bed are also evident. The greatest loss of eelgrass between 1987 and 1989 has occurred in areas adjacent to the central bay, including Eel Pond, Great River, Jehu Pond, Little River, and Hamblins Pond (Fig. 10d). The areas showing the least decline are the ponds to the south and the Eel Pond side of Washburn Island. Unfortunately, water color conditions in

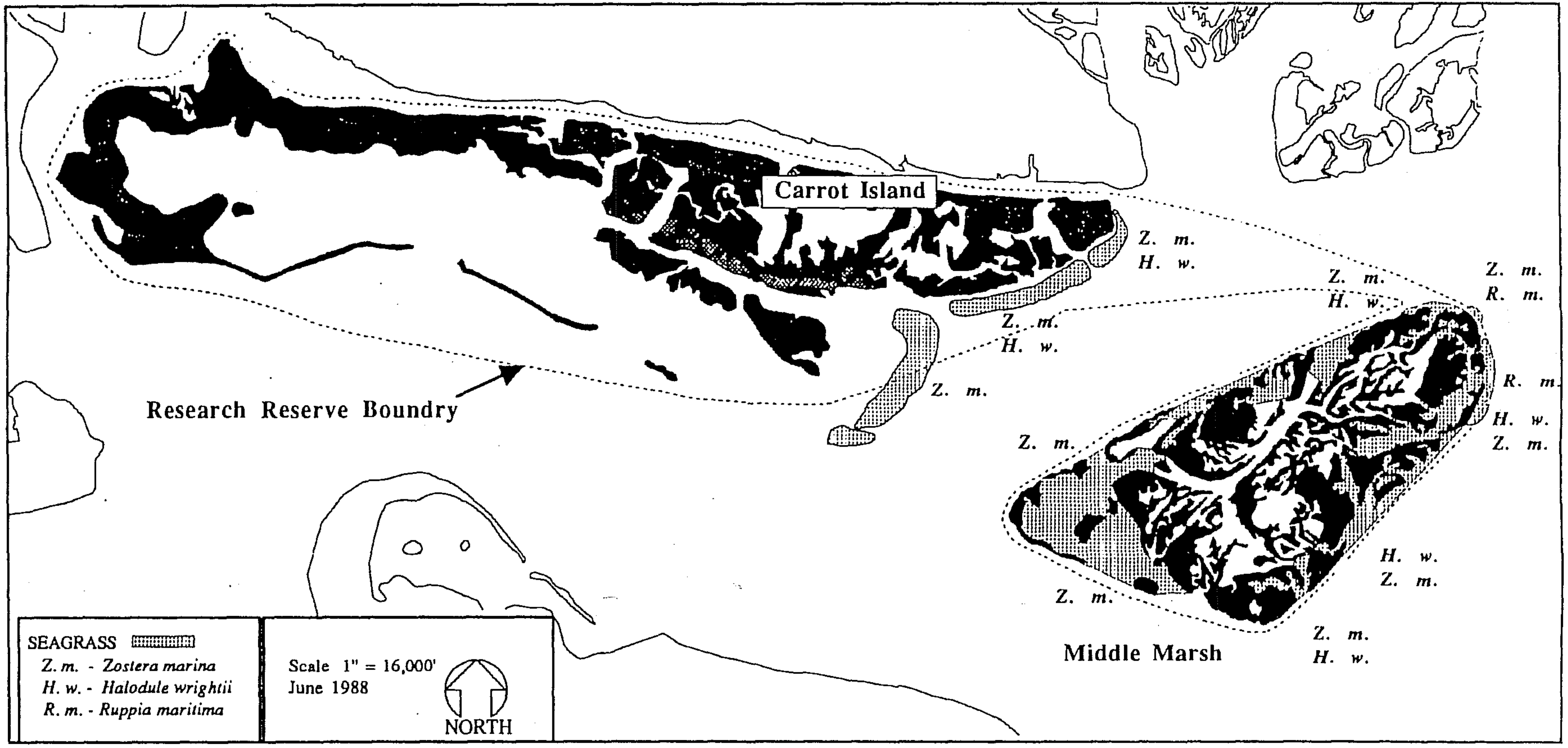


Figure 7b. Seagrass status in the Rachel Carson site of the North Carolina Reserve showing species associations for June 1988.

MIDDLE MARSH - NORTH CAROLINA NATIONAL ESTUARINE RESEARCH RESERVE
BEAUFORT, NORTH CAROLINA

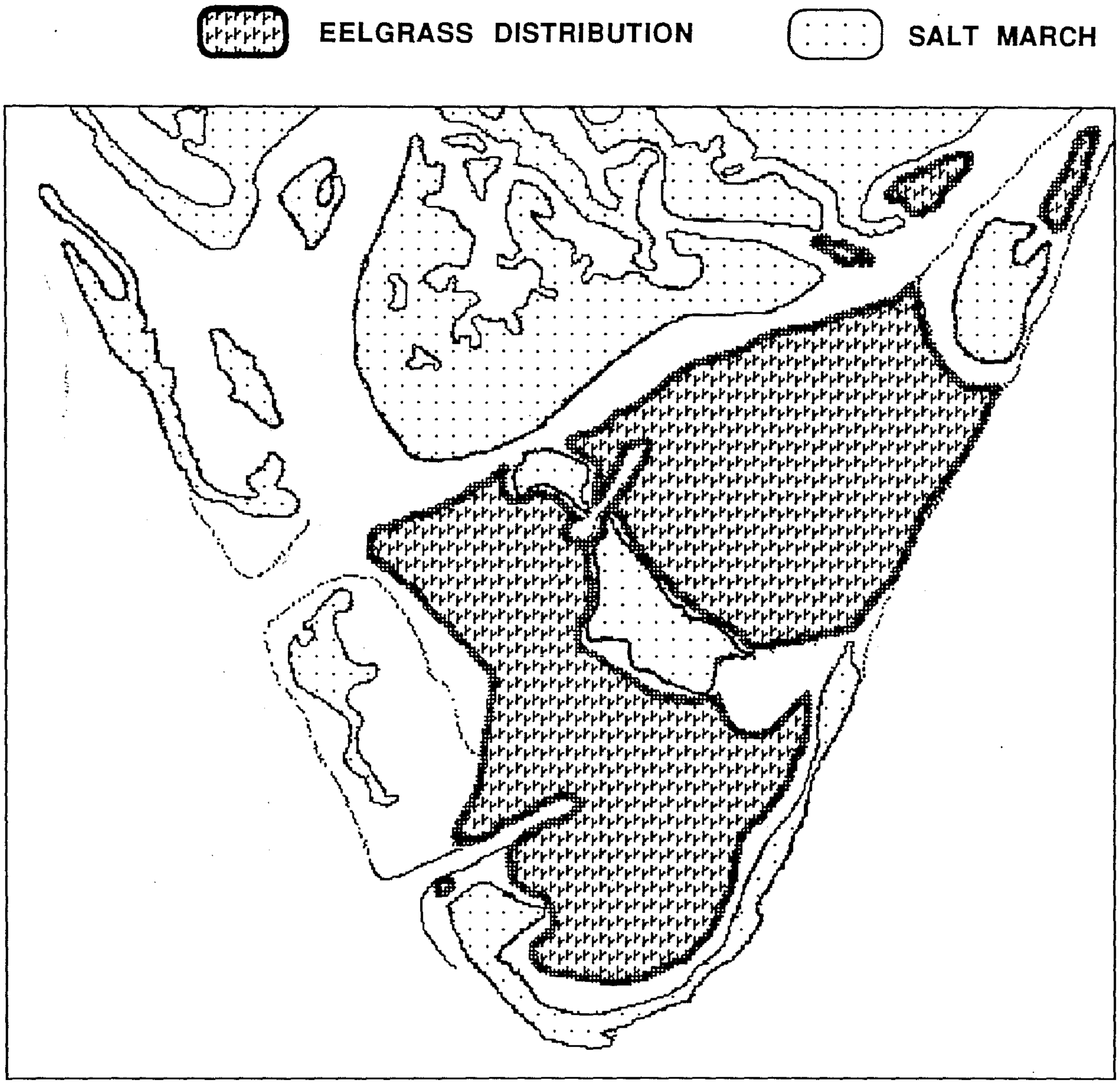


Figure 7c. Eelgrass status in the Rachel Carson site of the North Carolina Reserve. Detailed map of eelgrass distribution and study sites in Middle Marsh.

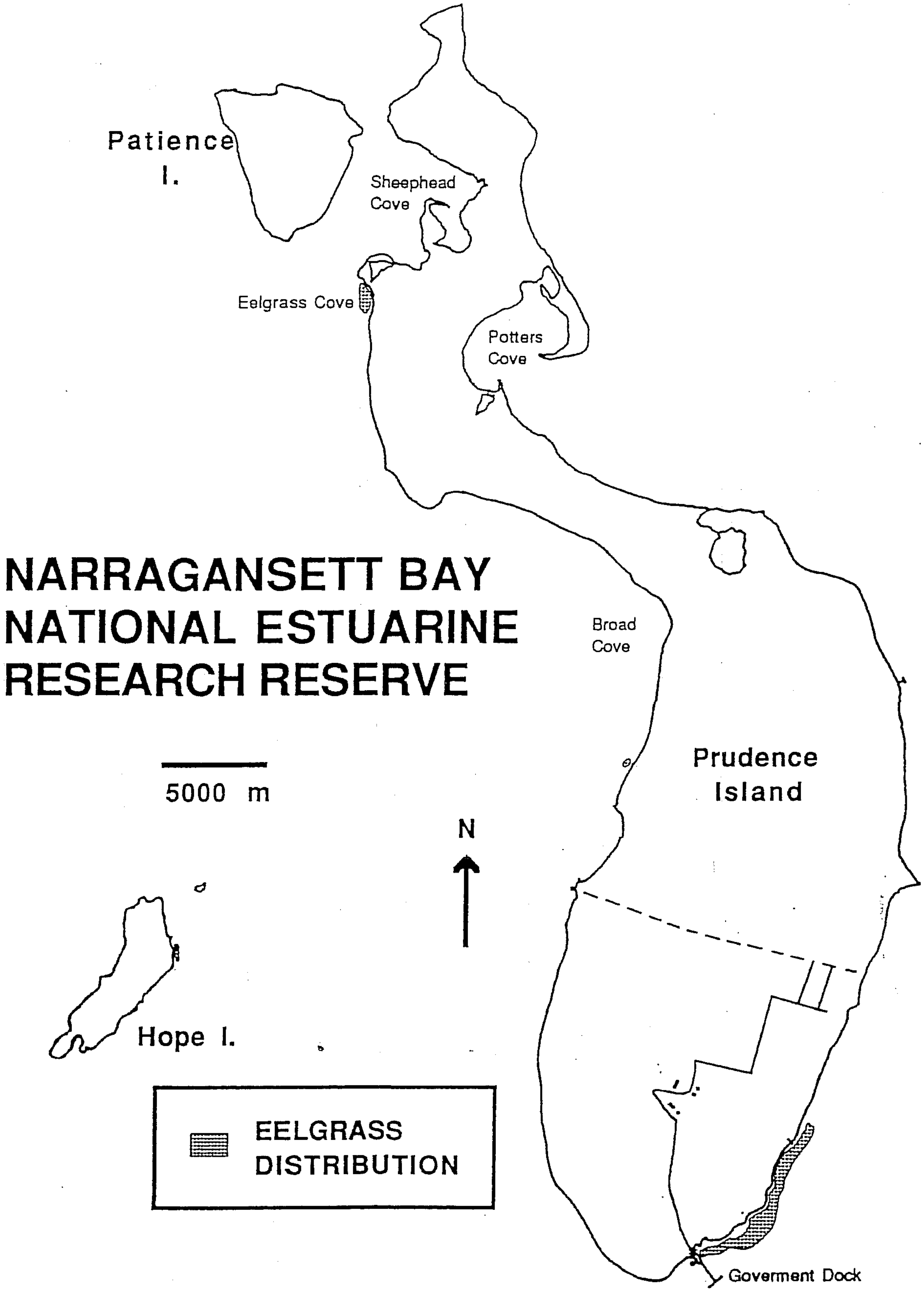


Figure 8. Eelgrass status in the Narragansett Bay Reserve, including all of Prudence Island.

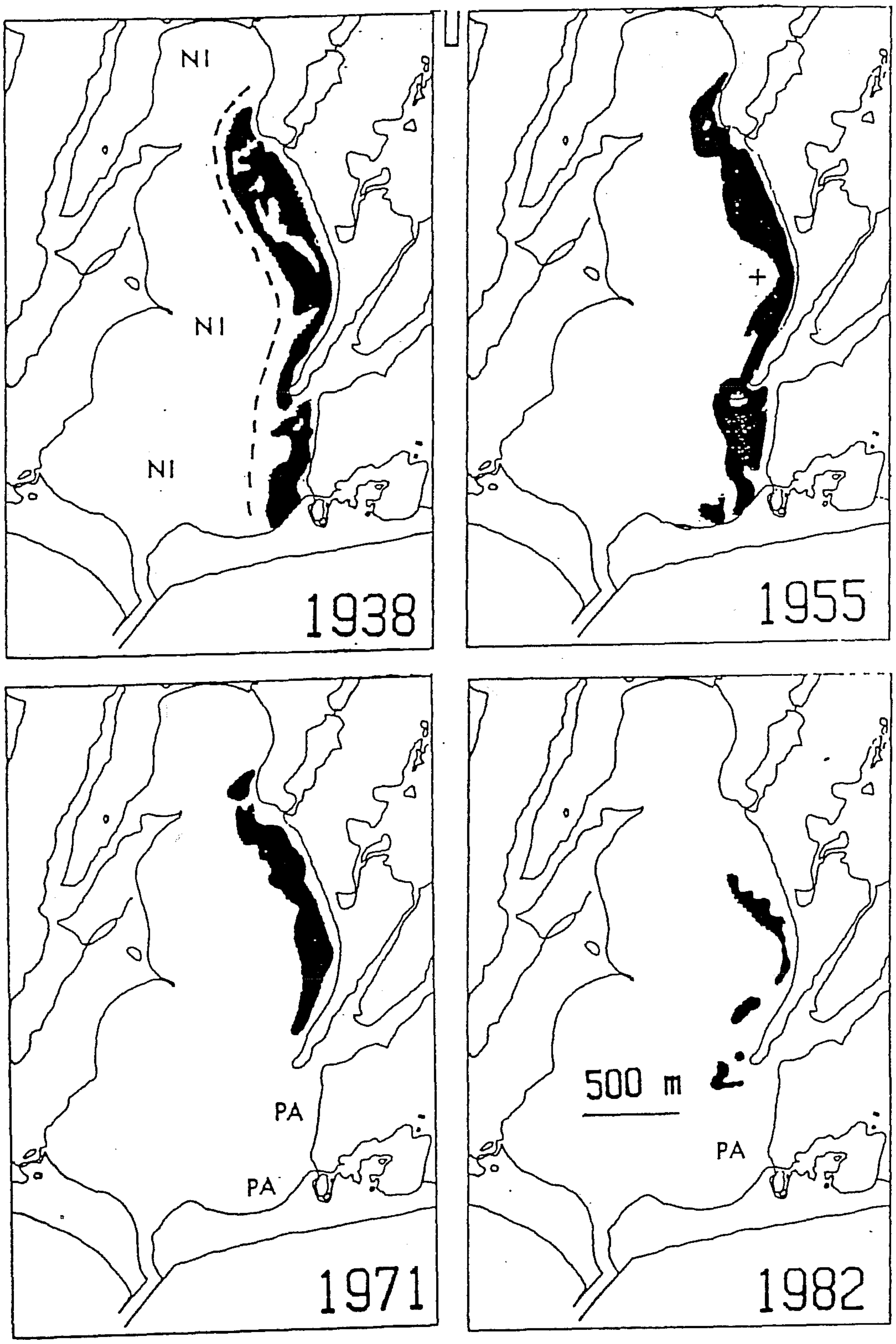


Figure 9. Historical distribution of eelgrass in the eastern half of Waquoit Bay from 1938 to 1982 (Costa 1988). Dotted line on 1938 survey indicates boundary of survey area for entire study.

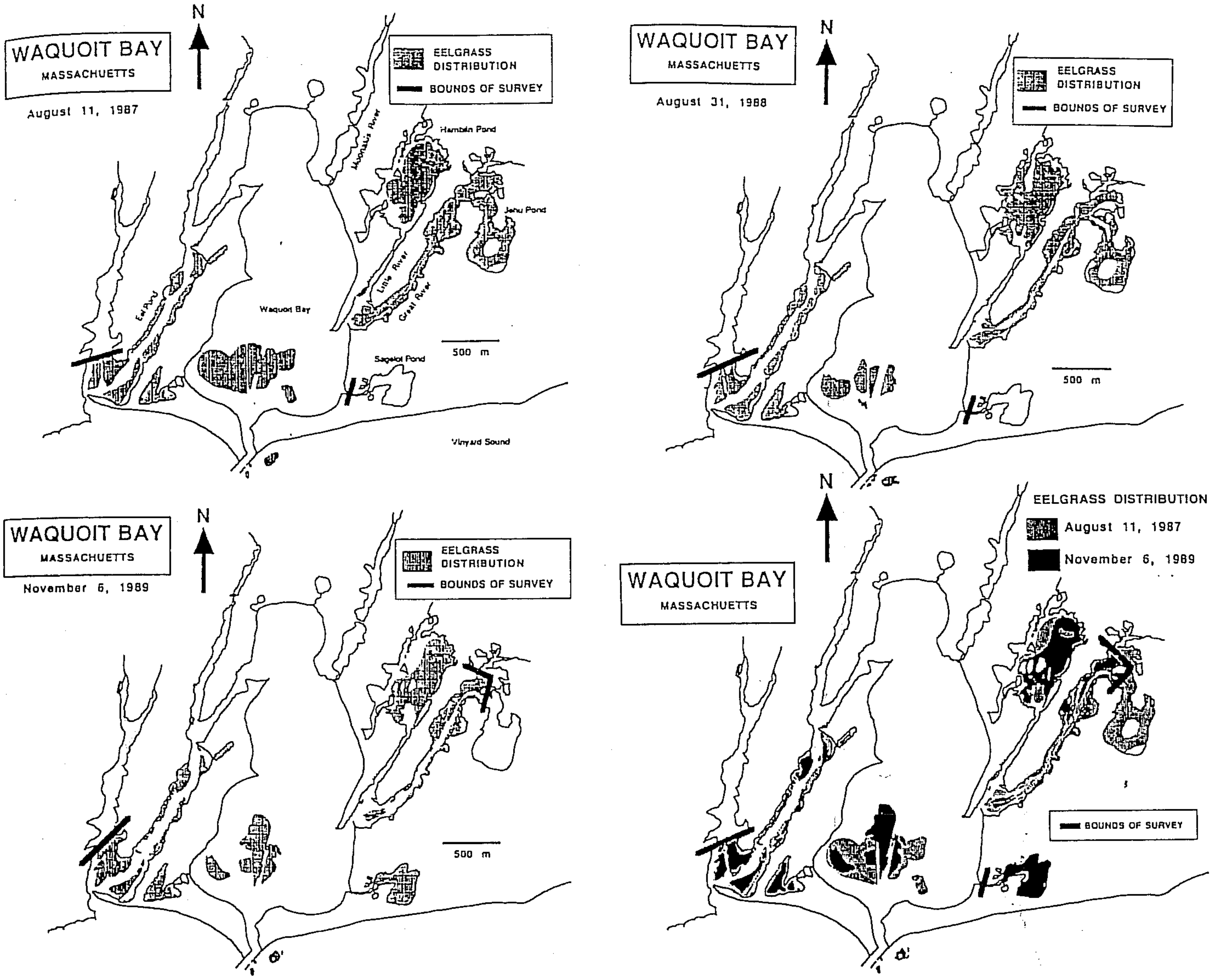


Figure 10. Eelgrass status in Waquoit Bay Reserve as determined by aerial photographs and ground truthing. a. Status in 1987. b. Status in 1988. c. Status in 1989. d. Composite of 1987 and 1989 eelgrass maps, illustrating the areas of eelgrass decline. Note bounds of survey, i.e. Sagelock Pond was not included in 1987 and 1988 surveys and Jehu was not included in 1989 survey due to poor water clarity.

Sagelock Pond made aerial documentation of the eelgrass distribution unreliable, but ground truthing performed in 1989 and 1991 has confirmed the presence of eelgrass throughout this pond (Fig. 10c).

Great Bay Estuary experienced severe eelgrass losses in the past decade, due to epidemic outbreaks of the wasting disease caused by *Labyrinthula zosterae*. The oldest quantitative survey of the eelgrass populations of Great Bay Estuary, done in 1981, showed eelgrass meadows throughout the estuary (Nelson 1981, Short et al. 1986). Since then several surveys, including those supported by this research, have shown dramatic losses, although recently there has been some recovery. By 1984, only a handful of small colonies remained seaward of Great Bay in Little Bay and the Piscataqua River (Fig. 11a). As in the wasting disease epidemic of the 1930s, eelgrass growing in higher salinity waters was more susceptible to the disease. Between 1984 and 1989, eelgrass beds in Great Bay were virtually destroyed by the disease (Fig. 11b). Within Great Bay, die-offs of as much as 80% of the eelgrass during each year were followed by partial recovery the following spring when eelgrass grew from seed (Fig. 11c). Since the low point in eelgrass population in 1989, eelgrass has spread rapidly and reestablished new beds in Great Bay; eelgrass in the seaward end of the estuary shows little recovery.

With most of the beds seaward of Great Bay destroyed, the epidemic proportions of the disease appear to have decreased, though there are still some examples of large scale mortality in Great Bay. The rhythm of bed destruction by disease and recovery by growth from seed in Great Bay suggests reestablishment of eelgrass in the face of a continuing disease threat.

Wells Research Reserve is currently without any eelgrass populations and has proven to be a non-productive site, unable to sustain transplanted eelgrass populations. The eelgrass population that was reported in the Webhannet River in 1986 was not found in 1987 or subsequent surveys we conducted (Fig. 12). However, a different seagrass, widgeon grass (*Ruppia maritima*), was found growing extensively in both the Webhannet estuarine system to the south and the Little River Estuary to the north, inhabiting many of the shallow ponds on the marsh surface and some tidal creeks (Fig. 12). Evidence that natural eelgrass beds once existed in the Webhannet system has previously been limited to personal accounts, but seed remains were found in one sediment core taken in 1988 from this estuary. A modest restoration effort (1200 plants over 120 m^2 in 1987, and 3525 plants over 353 m^2 in 1988) resulted in no permanent, self-sustaining beds. As the restoration experiment progressed, eelgrass plants died rapidly. At the first site in 1987, (Fig. 12) eelgrass plants died of exposure and dessication due to high temperature and burning sun conditions at the low tide periods associated with the large tidal range at Wells. The second site was planted in 1988 in a channel of the Webhannet where sun exposure was reduced, but prolonged periods of brown colored fresh water during the long low tide period prevented vegetative expansion of the transplants.

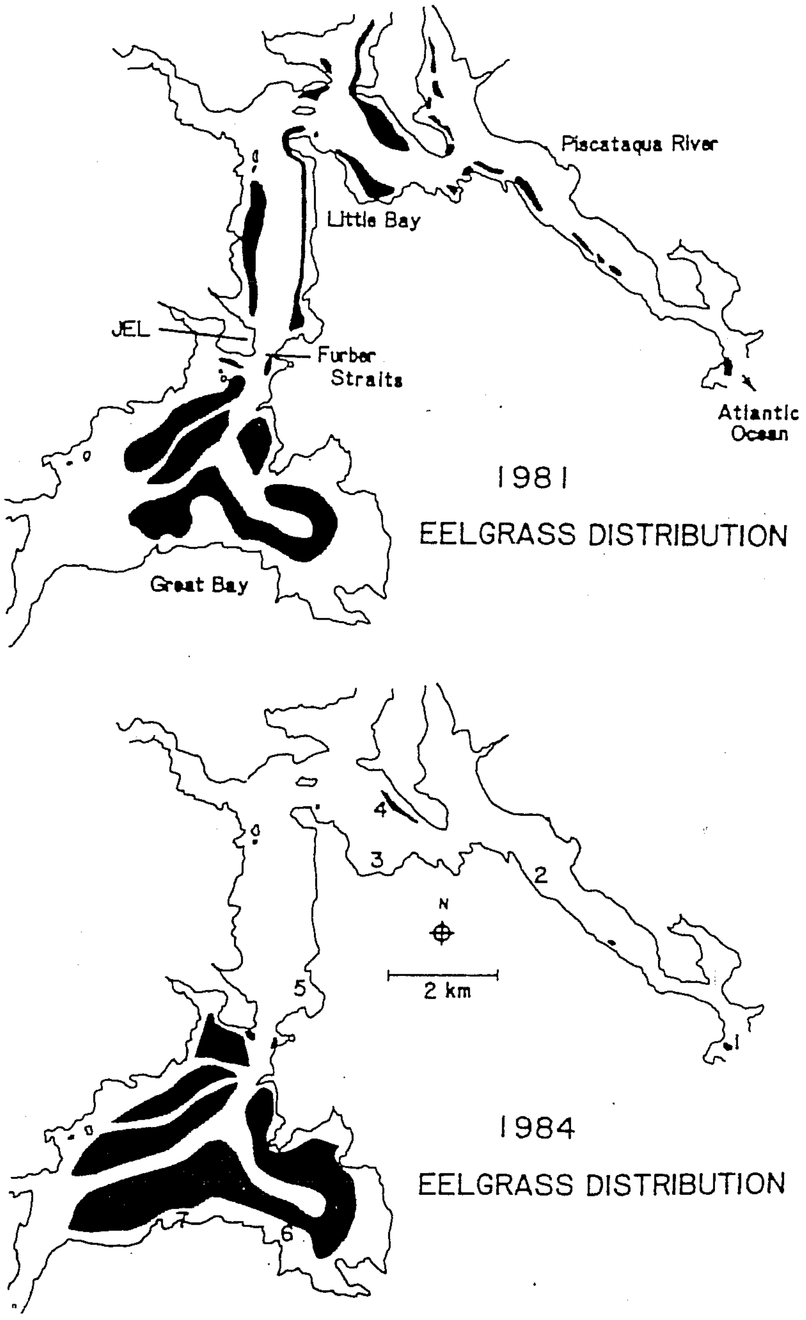


Figure 11a. Eelgrass status in Great Bay Reserve as determined by aerial photography and ground truthing. Eelgrass distribution and decline in the Great Bay Estuary, 1981 to 1984, after Short et al., 1986.

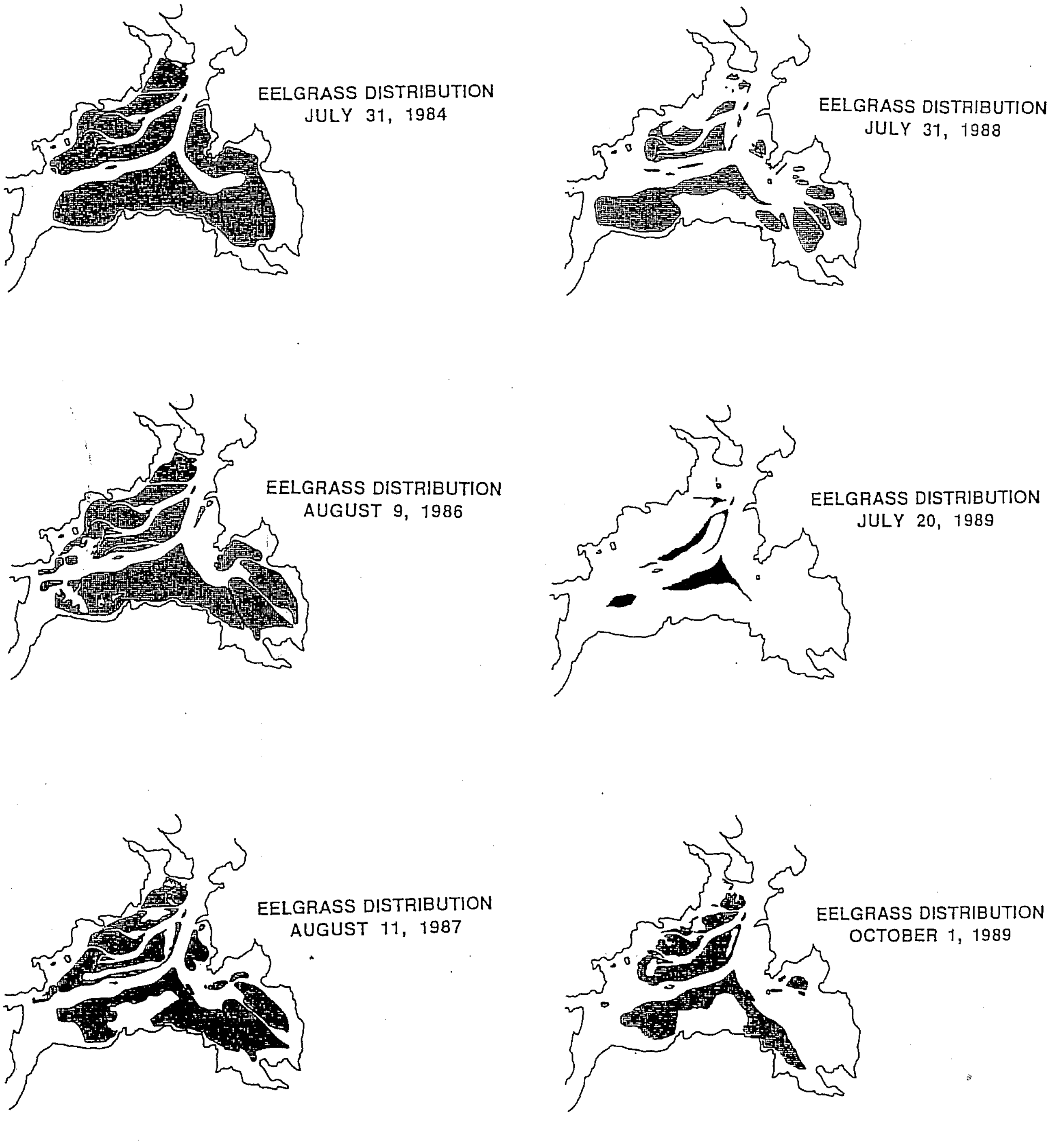


Figure 11b. Eelgrass status in Great Bay Reserve as determined by aerial photography and ground truthing. Eelgrass distribution in Great Bay, 1984 through 1989.

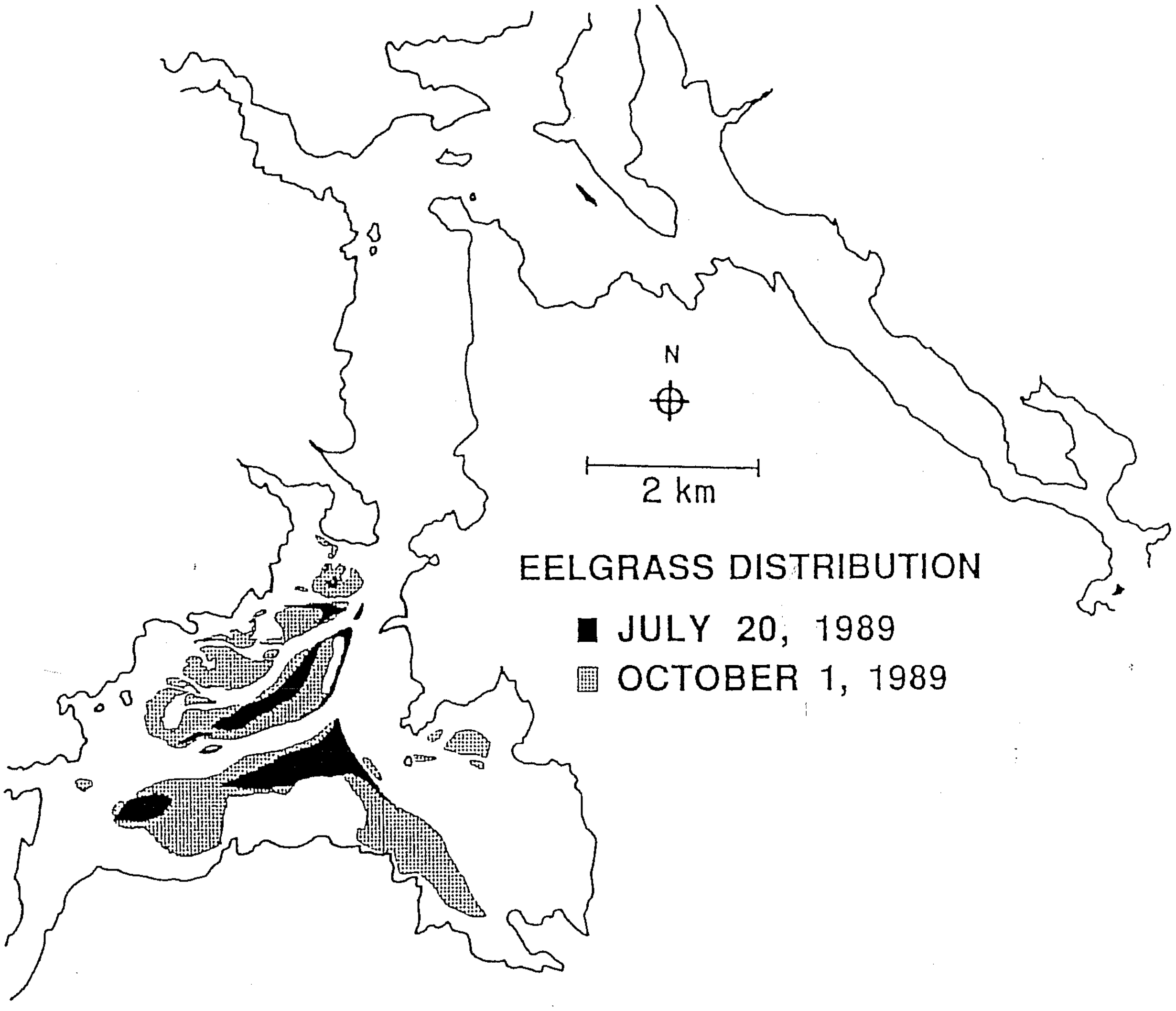


Figure 11c. Eelgrass status in Great Bay Reserve as determined by aerial photography and ground truthing. Composite map comparing eelgrass distribution in Great Bay within one year, from July to October, 1989.

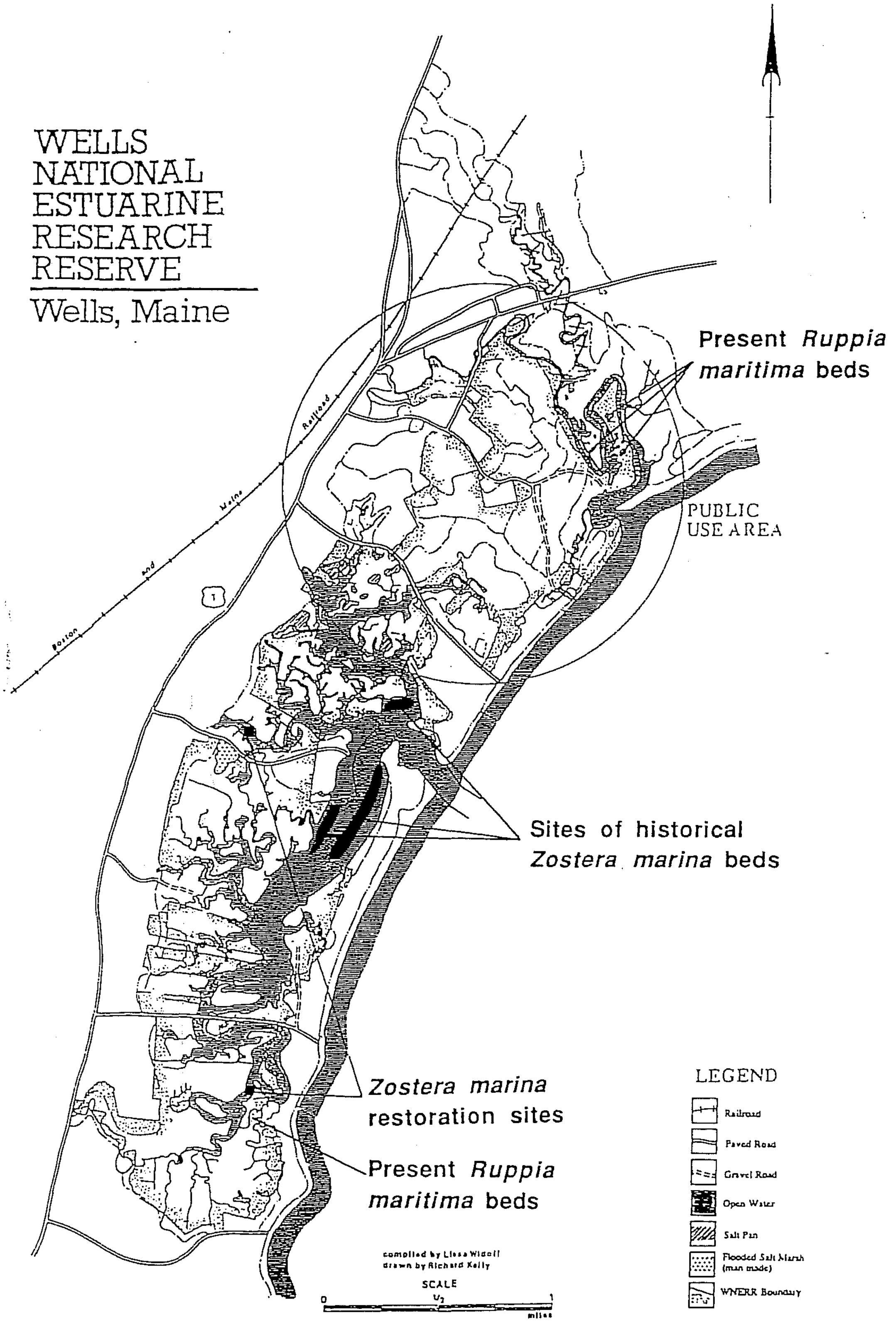


Figure 12. Seagrass status in Wells Estuarine Reserve, showing presence of *Ruppia maritima* beds that are common in large pannes of the salt marsh, areas of historical *Zostera marina*, and unsuccessful *Zostera marina* transplant sites.

Ecology

The results concerning eelgrass ecology are those which relate the capacities and limitations of eelgrass plants to their Research Reserve habitats; we discuss the major stresses that limit eelgrass production and distribution. Eelgrass has adapted to life under water as a rooted vascular plant. As such, it requires sunlight to reach the bottom where it begins life from seed, limiting the vertical distribution of this plant to less than 11 m depth along our coasts (3 m in most estuaries). Conversely, it cannot withstand prolonged exposure to air, and has an upper bound which approximates mean low water (but can be higher if afforded protection from dessication in tide pools). Thus, this species has rather narrow requirements with respect to depth, which are further restricted by water components that reduce light transmission. On the other hand, this species tolerates wide variations in temperature and salinity, allowing it to assume a position of importance and often dominance among the primary producers of an estuary. The root systems of seagrasses are unique among subtidal plants, and the fairly consistent nutrient supply of sediments frees them from dependence on nutrient concentrations in the water column. The rather unique ecological niche available to eelgrass was characterized in the five Research Reserves by physical measurements in the water column, the sediment of past and present eelgrass habitats, and characteristics of current populations.

Water Column

Selected water column data for each Reserve was collected using continuously monitoring sensors (Estuarine Sensor and Profilers). The data sets for each Reserve and year were reduced, and the important features are summarized in Table 4. Some notable points are unique to each estuary.

In the eelgrass habitat in North Carolina, strong diurnal increases in water temperature (up to 30°C) were due to insolation (Fig. 13). Salinities were stable (31 to 33 ppt). Tides were relatively small (less than 1 m tidal range) and semi-diurnal, with a small diurnal component. In this broad shallow bay, both temperature and salinity are likely to be strongly influenced by meteorological events occurring on a larger temporal scale than we measured. Although the beds were very shallow (approximately 0.5 m depth), only moderate light levels were measured (Fig. 13).

Water column data were collected in 1987 and 1988 in the eelgrass beds of central Waquoit Bay and in 1988, off the mouth of the Moonakis River where beds may have once existed, but are absent today (Figs. 14a and b). Temperature and salinity regimes were fairly stable in Waquoit Bay, but higher temperatures and lower salinities were consistently recorded off the mouth of the Moonakis River (Fig. 14b). Tides in Waquoit Bay were similar to those of North Carolina, but the diurnal component that overlays the relatively small semi-diurnal tide was larger. The stronger diurnal component may result from water levels being controlled by two inlets. At approximately 144 hours into the tidal record (Fig. 14a), this factor, perhaps in association with wind stress, eliminated the low tide and resulted in very low light levels reaching the seagrass that day, (possibly further decreased by cloudiness). Although light levels were consistently low in 1987

Table 4. Hourly means of water column characteristics at eelgrass habitats in the National Estuarine Research Reserves. The light meter was 26 cm above the sediment surface and data were excluded if mean water depth was less than 15 cm over the light sensor. Only means from 0900 to 1700 hours were reported for light data. An extinction coefficient, k_r, calculated for the entire sampling period using estimates of the average surface light for the sample month and geographic region as described in the methods.

Reserve Site/year	# hours (n)	Temperature (^oC)			Salinity (ppt)			Depth (cm)			Light ($E/m^2/h$)		
		Mean	Max	Range	Mean	Max	Range	Mean	Max	Range	Mean	Max	k_r
Back Sound, NC													
Middle Marsh '88	120	24.2	29.2	10.5	32.0	32.9	1.5	70	108	91	3.8	6.1	1.8
Middle Marsh '89	86	21.8	24.7	5.5	32.5	34.0	9.9	76	123	106	4.7	7.1	1.3
Waquoit Bay, MA													
Lower Bay N6 '87	385	23.0	24.1	2.8	29.7	30.1	1.5	181	227	76	1.9	3.8	0.96
Lower Bay N4 '88	143	20.1	21.9	3.0	30.9	31.2	1.4	98	131	56	4.5	7.1	0.90
Upper Bay '88	143	22.9	25.3	4.3	29.8	31.0	3.1	75	107	53	3.4	6.7	1.5
West of N4 '89	92	22.2	23.8	2.4	31.0	31.4	1.9	126	168	70	3.0	5.1	1.0
Great River '89	92	23.9	26.2	4.2	28.7	30.2	2.7	90	136	75	4.1	6.6	1.1
Narragansett Bay, RI													
S. Prudence I.'87	498	20.8	23.3	4.1	30.5	30.8	1.4	212	314	216	1.1	2.7	1.1
N. Prudence I.'88	116	15.8	18.3	4.5	30.0	30.3	0.5	167	245	147	3.1	6.2	0.75
S. Prudence I.'88	103	15.0	18.7	5.4	29.8	30.2	1.1	212	287	136	3.9	6.9	0.48
N. Prudence I.'89	140	20.1	22.1	4.4	28.0	29.7	3.2	175	250	139	2.0	3.9	0.97
Potter's Cove '89	139	20.5	24.7	6.2	26.4	27.6	3.5	155	233	151	2.1	4.5	1.1
Great Bay, NH													
Seal Rock '87	492	18.4	24.6	9.2	29.5	30.7	6.4	171	301	247	1.5	4.8	1.2
Fishing I. '88	164	14.0	18.4	8.0	28.5	31.2	6.5	246	403	302	3.9	7.8	0.43
Seal Rock '89	497	22.4	25.7	5.6	25.5	27.1	4.4	152	269	252	1.2	4.8	1.5
Lower Bay N6 '89	552	22.0	25.6	6.1	25.7	27.7	5.9	184	311	244	1.7	5.7	1.0
Wells Bay, ME													
Town Pier '87	235	12.6	17.2	8.5	30.8	31.3	10.2	254	391	322	2.7	7.1	0.57

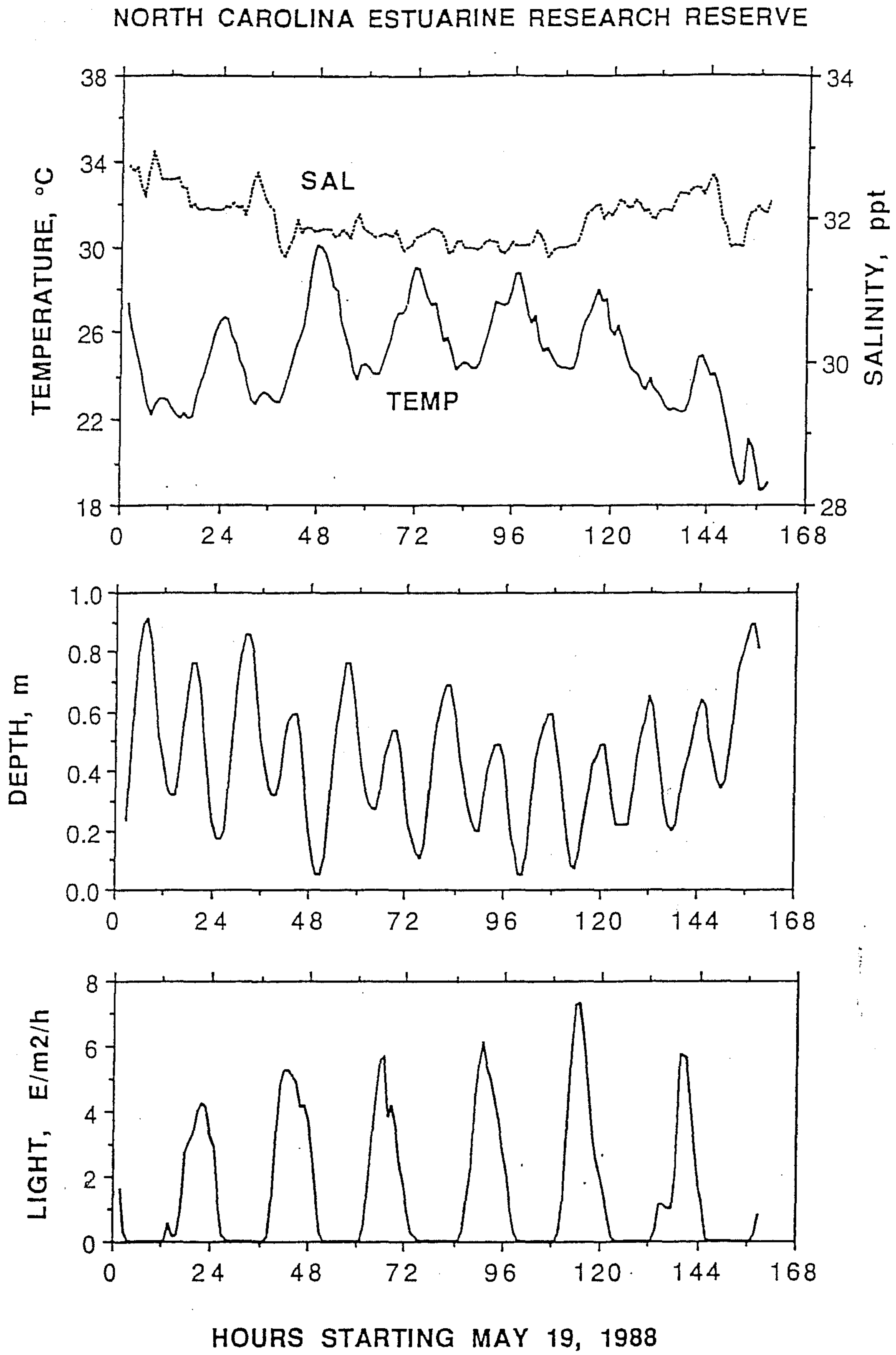


Figure 13. Water column data for the North Carolina Reserve collected with the Estuarine Sensor and Profiler (ESP) May 19-25, 1988.

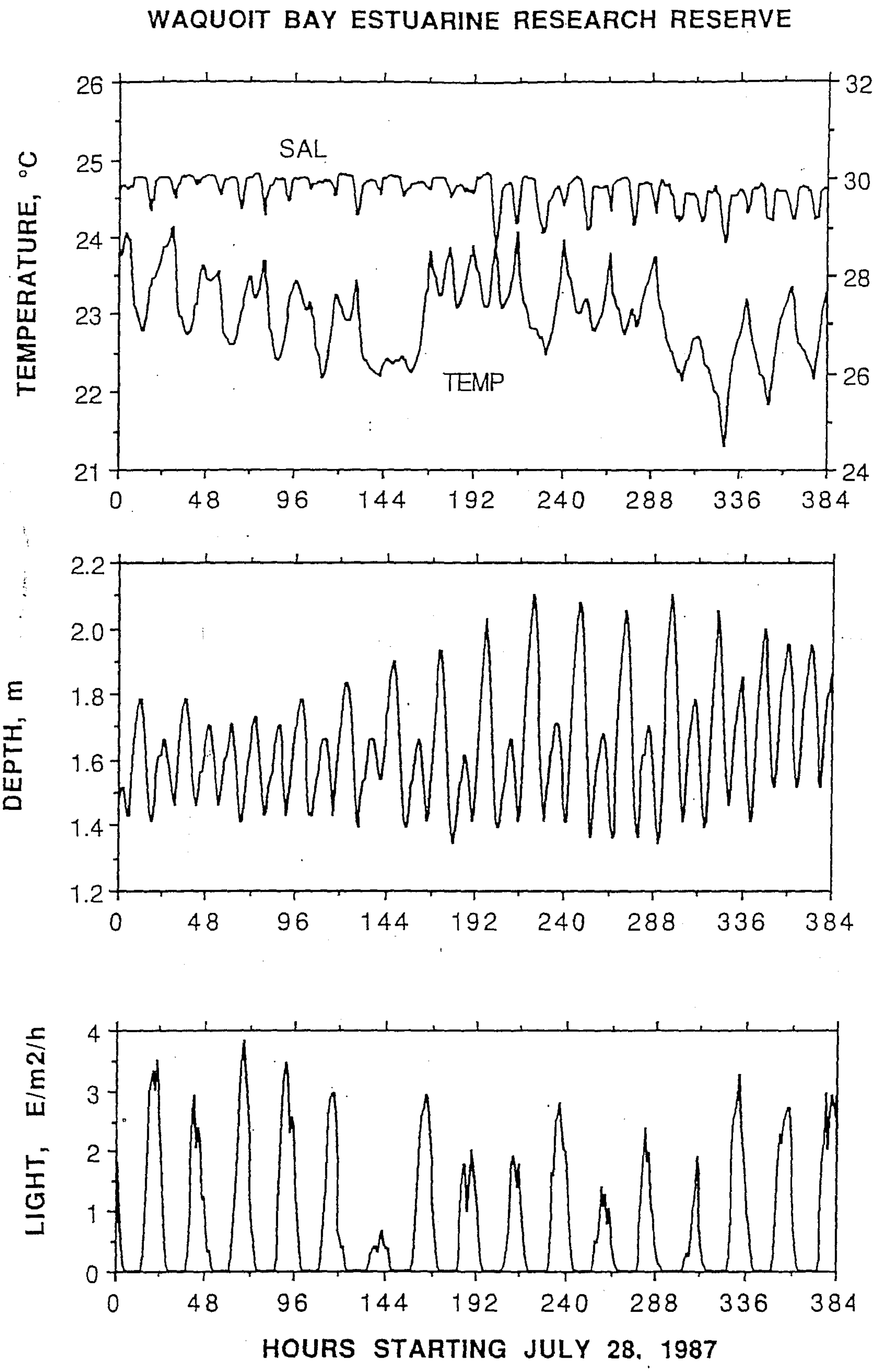


Figure 14a. Water column data for the Waquoit Bay Reserve collected with the Estuarine Sensor and Profiler (ESP). Central Bay, July 28 to August 12, 1987.

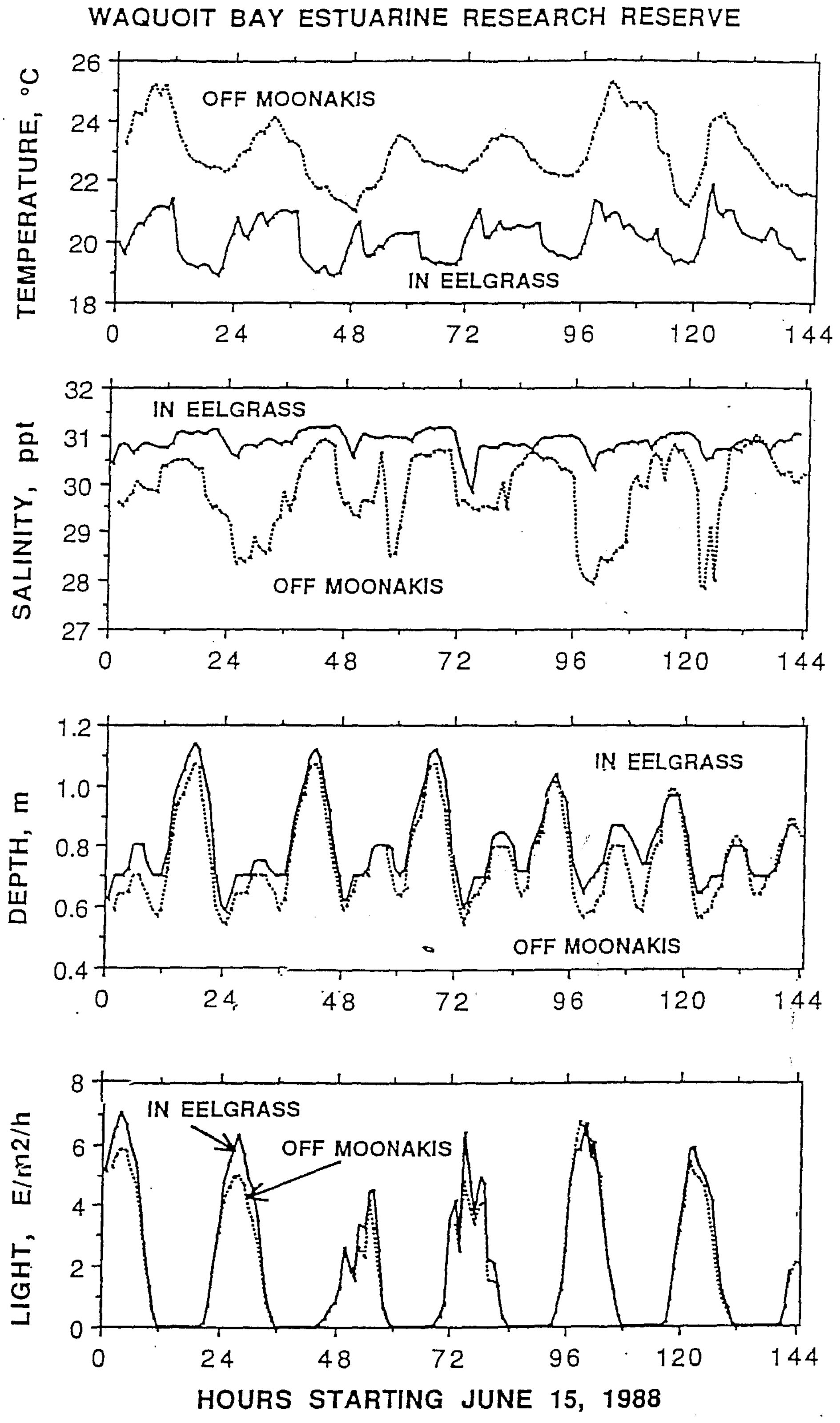


Figure 14b. Water column data for the Waquoit Bay Reserve collected with the Estuarine Sensor and Profiler (ESP). Water column conditions in lower bay eelgrass beds compared with former eelgrass habitat at the mouth of the Moonakis River in the upper bay, June 15-20, 1988.

(Fig. 14a), the depth of the beds was over a meter greater than in North Carolina. In 1988, light levels in a shallower area of Waquoit Bay were moderate (Fig. 14b). Although in slightly deeper water, more light reached the ESP in the center of the bay than off the Moonakis River in 1988 .

In 1987 an ESP was deployed adjacent to eelgrass beds on the south side of Prudence Island, and in 1988 water column conditions at this site and another on the north side of the island were monitored (Figs. 15a and b). Narragansett Bay has a greater tidal range than North Carolina or Waquoit Bay, with little diurnal component. Salinities were very consistent in Narragansett Bay, with small declines at the South Prudence site associated with the incoming tides (Fig. 15b). Water temperatures were fairly low due to the larger basin depth of this estuary, but still showed daily increases from sunlight. The South Prudence site was deeper, yet slightly greater light levels were recorded than at the North Prudence site (Fig. 15b).

Great Bay had very variable light levels during the measurement period in 1987, resulting from greater tidal range and wind driven resuspension of sediments (Fig. 16a). In 1988, an ESP was deployed near the mouth of the estuary where greater light was measured even though the site was slightly deeper and subject to greater tides than the Research Reserve sites further south (Fig. 16b). Salinity pulses were regulated by tidal influences at both ends of the Great Bay Estuary, but rainfall events can drive the salinity in Great Bay to very low levels.

The ESP instrument located at the town pier in Wells was occasionally exposed at low tide, as seen by the flattened troughs of the depth curve (Fig. 17). The dotted line in Figure 17 shows values during instrument exposure, which were edited from the data set used to make the solid line. When exposed at low tide, the light levels became extremely high and were matched by temperature peaks. The solid curve on Figure 17 has these data removed, and indicates a moderate environment with respect to sunlight and salinity. The environmental extremes measured at low tide were likely to have made this habitat unsuitable for eelgrass survival. Note that five days into the record, the water temperature declined dramatically (Fig. 17), likely in response to a cold front.

Sediment

Sediment characteristics can vary widely between eelgrass beds within one estuary (Table 5). Recall that the 1987 and 1989 sampling efforts were directed toward habitats with organic-rich sediments, whereas the 1988 sampling took place in habitats with sediments that appeared to have relatively low organic contents (Fig. 4). (However, in 1989, samples were also taken in habitats with organic-poor sediments at Waquoit and Narragansett Bays.) Most sites were chosen successfully with respect to this strategy, though the lack of variability with respect to sediment organic content in North Carolina made this Reserve the exception. Habitats having organic-poor sediments were sampled in Great and Narragansett Bays, but appeared to be unavailable in North Carolina and Waquoit Bay (Table 5). This is likely due to the particular sedimentary environments of these estuaries as controlled by geomorphology and hydrography. Sediment porosity closely followed organic matter content ($r^2 = 0.76$), as expected.

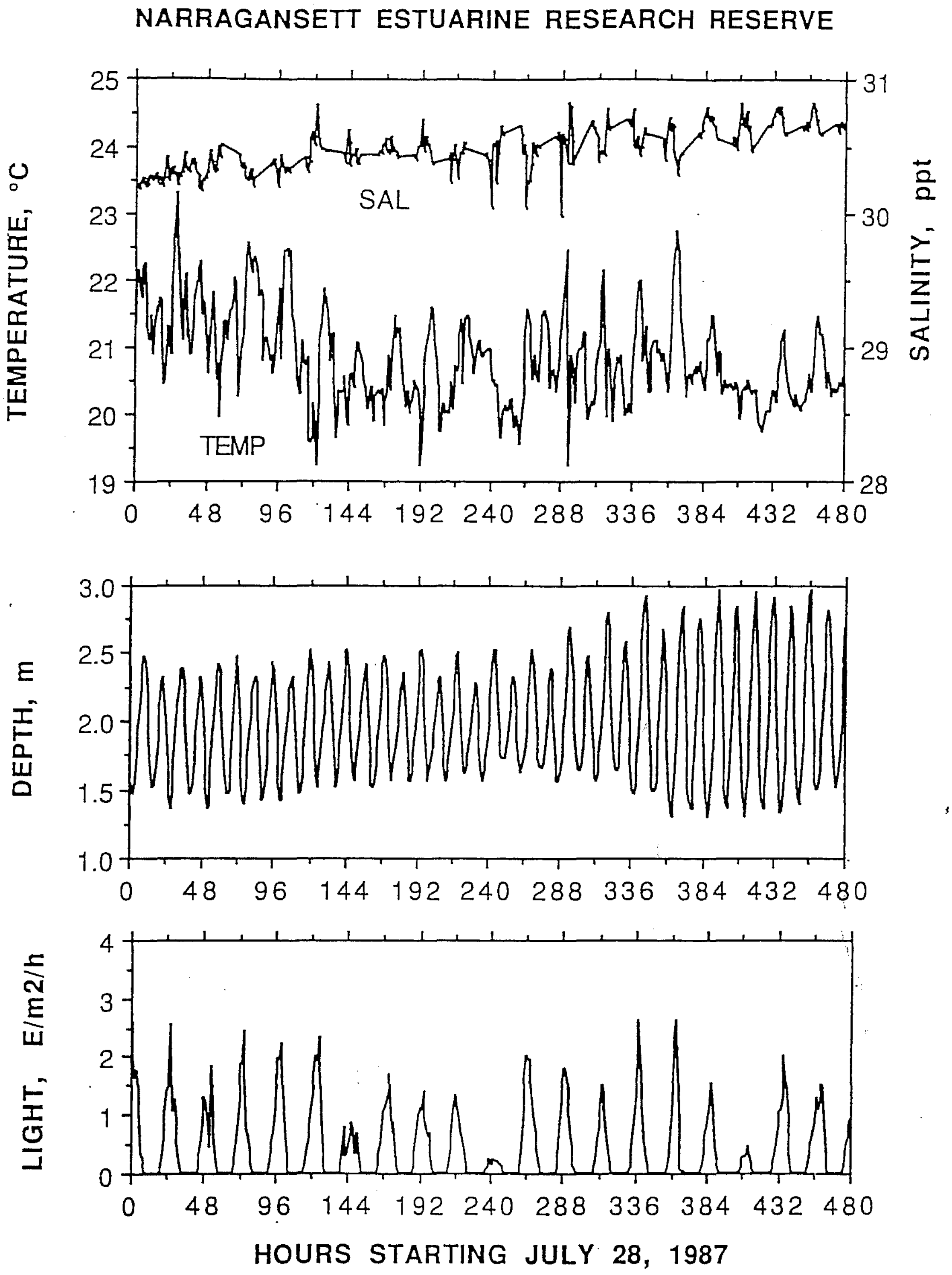


Figure 15a. Water column data for the Narragansett Bay Reserve collected with the Estuarine Sensor and Profiler (ESP). South Prudence Island, July 28 to August 16, 1987.

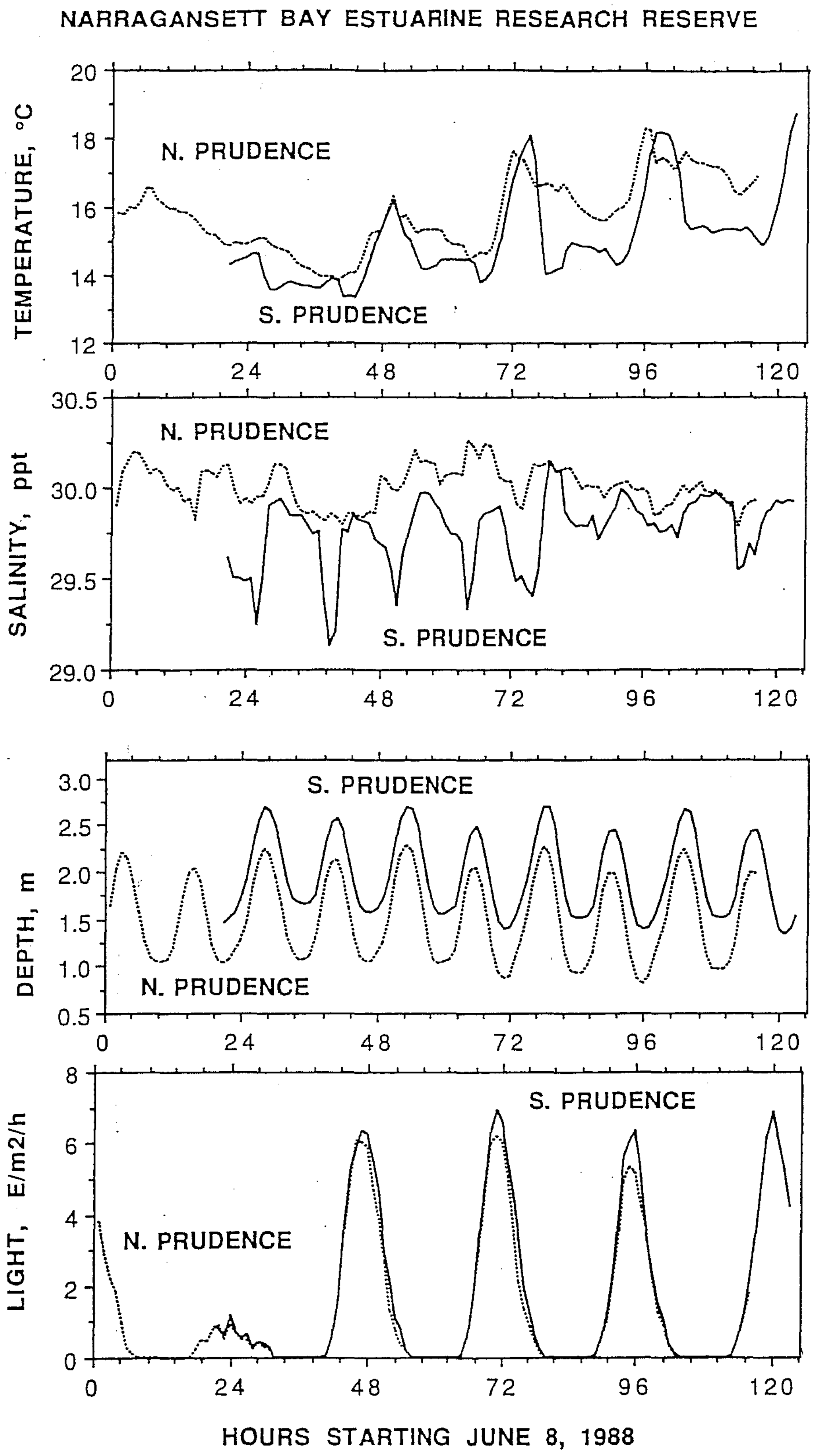


Figure 15b. Water column data for the Narragansett Bay Reserve collected with the Estuarine Sensor and Profiler (ESP). Comparison of water conditions in North versus South Prudence Island eelgrass habitats, June 8-12, 1988.

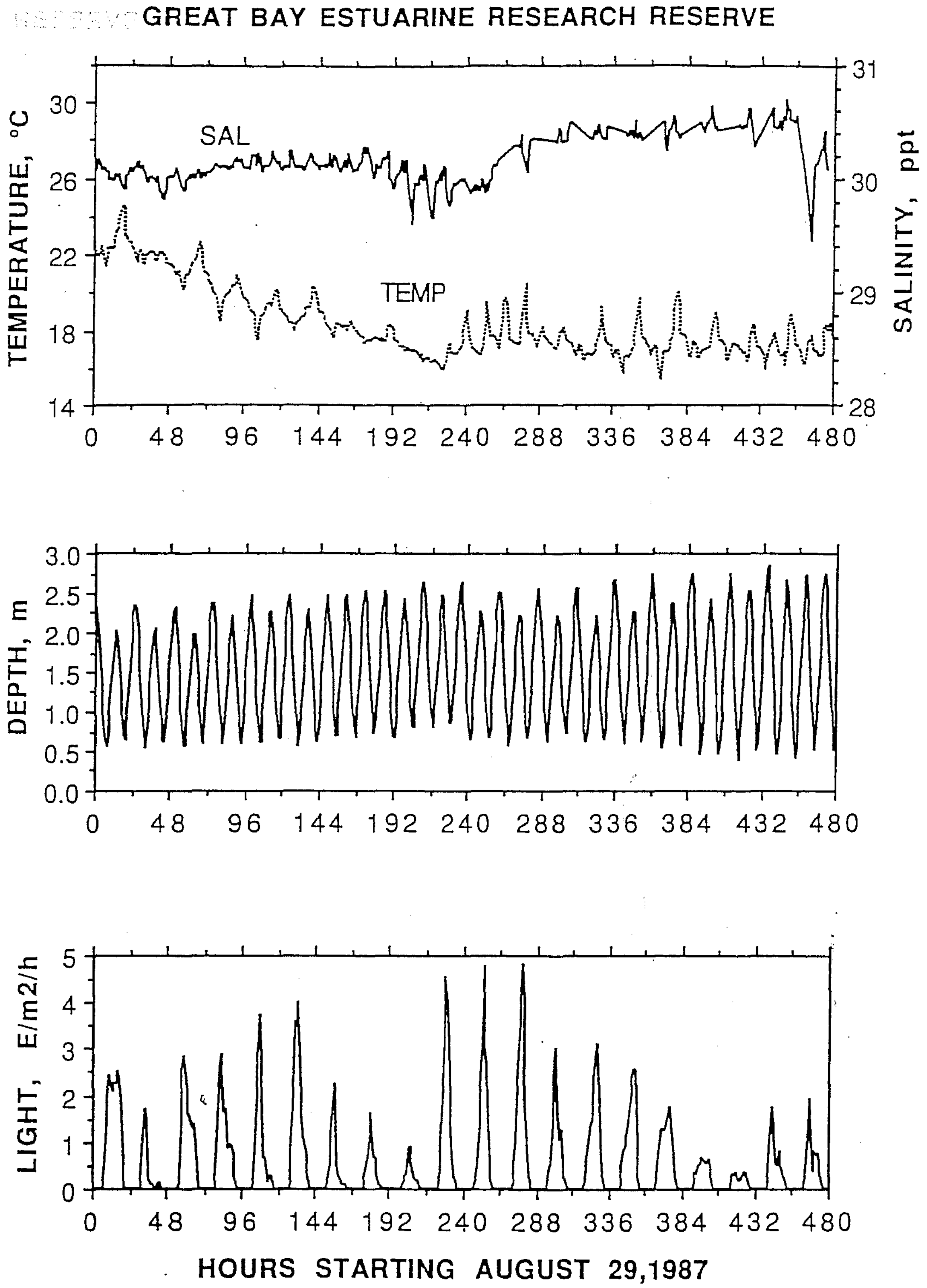


Figure 16a. Water column data for the Great Bay Reserve collected with the Estuarine Sensor and Profiler (ESP). Water column conditions at Seal Rock, August 29 to September 17, 1987.

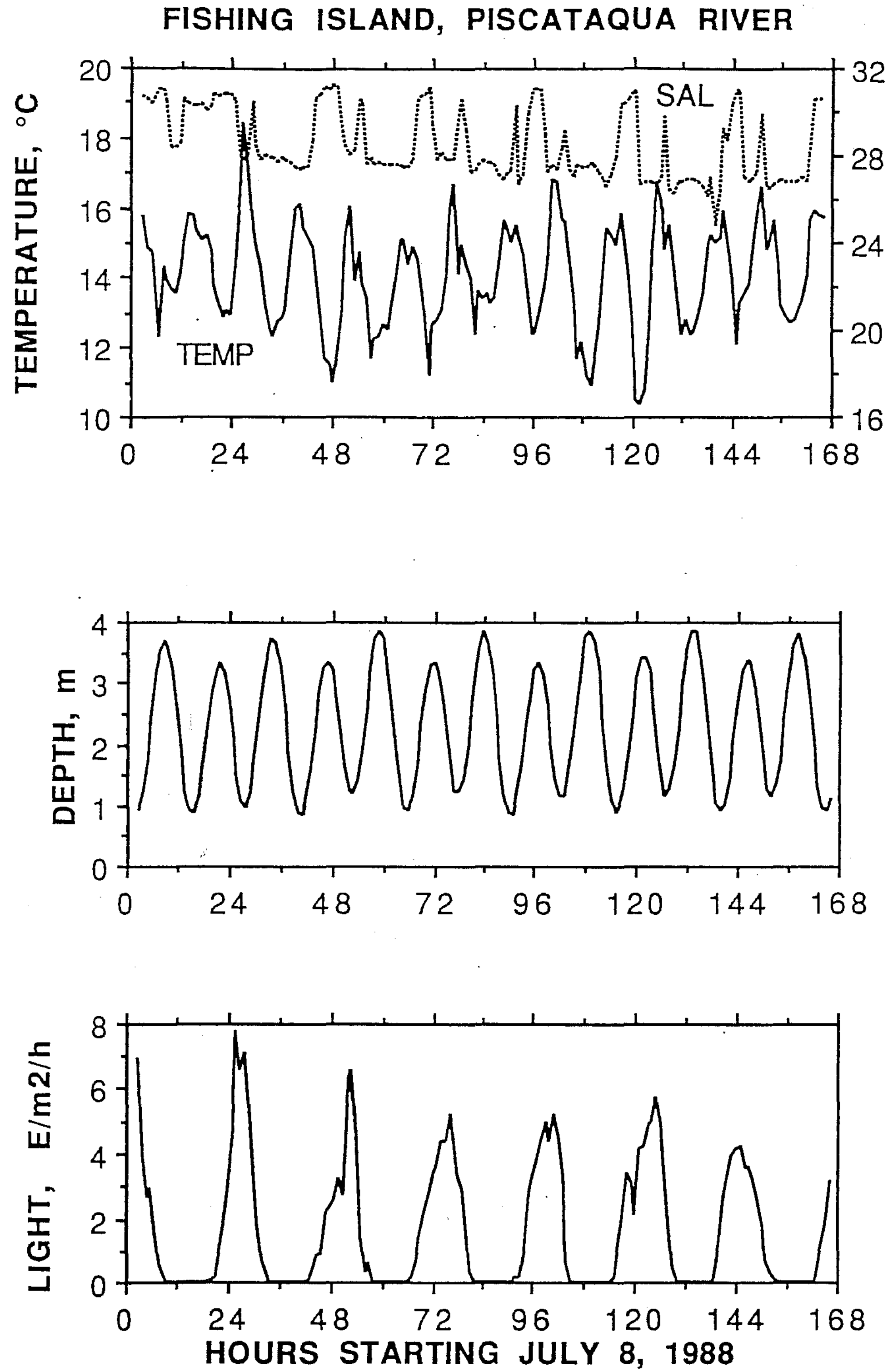


Figure 16b. Water column data for the Great Bay Reserve collected with the Estuarine Sensor and Profiler (ESP). Water column conditions at Fishing Island near the mouth of the Piscataqua River, July 8-14, 1988.

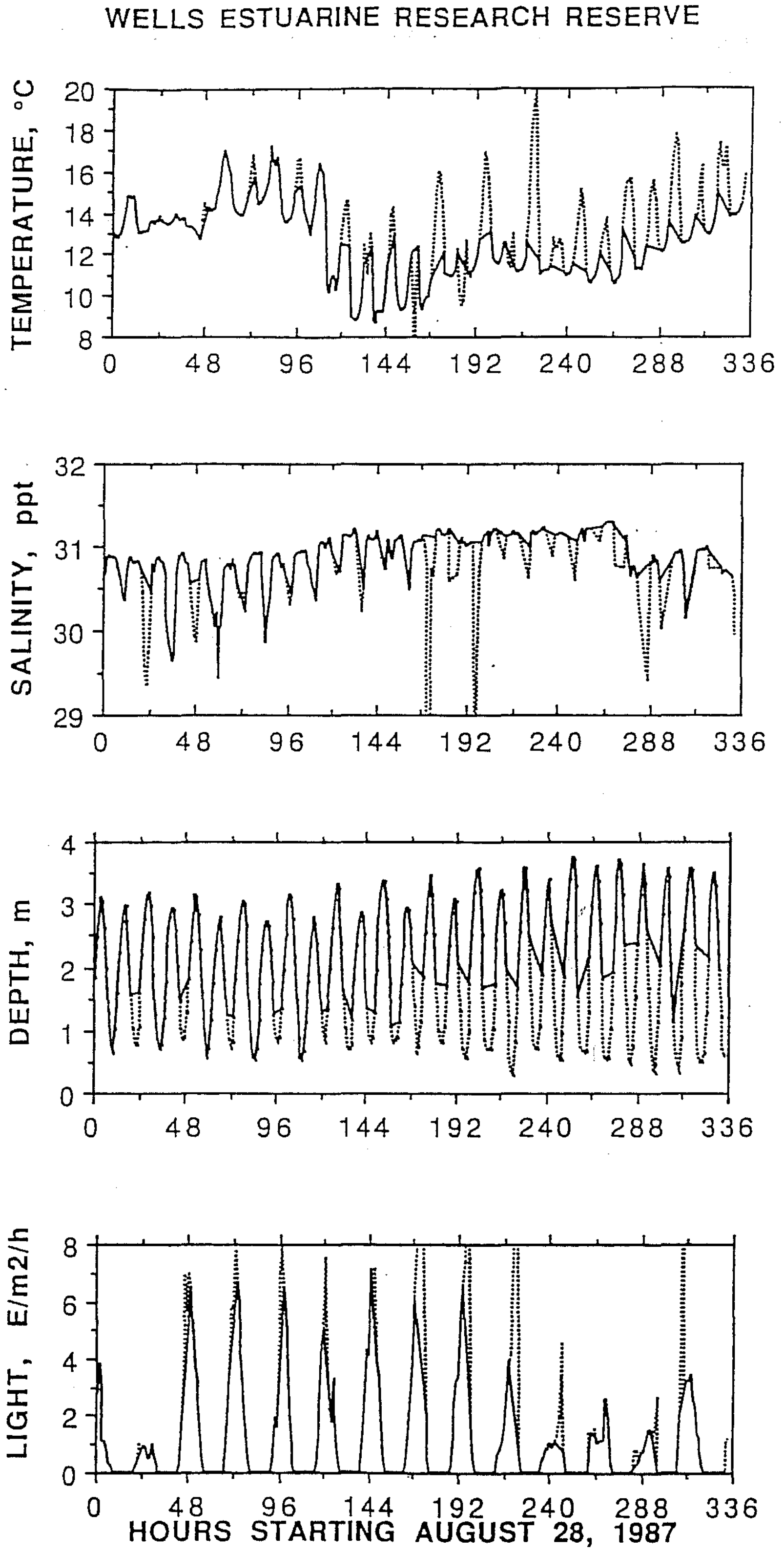


Figure 17. Water column conditions for the Wells Estuary Reserve collected with the Estuarine Sensor and Profiler (ESP) at the Wells Town Pier, August 28 to September 11, 1987.

Table 5. Sediment characteristics at selected eelgrass habitats in the National Estuarine Research Reserves show general differences within and among reserves. Habitats with organic-rich sediments were sampled in 1987 and 1989, while habitats with organic-poor sediments were sampled in 1988 at all reserves and at Waquoit Bay and Narragansett Bay in 1989. Sediment organic matter (OM) and interstitial water nutrient concentrations are means of 3 to 4 replicates, nutrient regeneration rates are slopes of predictive equations from least squares regressions of 3 replicates over three sampling times (time zero and following two incubation periods). Values were averaged over years where statistical analyses indicated no differences between years.

RESERVE Site	YEAR	OM (%)	[NH4] (µM)	NH4 RATE (nmoles/cc/d)	[PO4] (µM)	PO4 RATE (nmoles/cc/d)
NORTH CAROLINA						
Middle Marsh	1987	3.63	96	99	42.0	9.5
Middle Marsh	88/89	2.26			7.6	2.8
WAQUOIT BAY						
Hamblins Pond	1987	16.41	534	--	127.5	--
Central Bay/Gr. River	87/89	6.47	111	68	15.5	2.9
Central Bay	88/89	3.12	108	33	10.8	2.2
NARRAGANSETT BAY						
South Prudence	87/89	3.69	129	73	14.7	1.0
North Prudence	88/89	0.69	212	140	33.3	6.2
GREAT BAY						
Seal Rock	1987	7.57	294	38	110.0	7.2
Red Nun	1987	6.10	226	--	54.5	--
Red Nun	1989	6.80	391	14	87.4	2.9
Fishing Island	1988	0.75	212*	109	10.2*	7.4

* Interstitial nutrient concentrations estimated from least squares regressions of regeneration rates.

-- Not available.

Overall, both ammonium and phosphate concentrations in interstitial water of sediments were greater in eelgrass habitats with greater organic matter ($r^2 = 0.50$, $r^2 = 0.52$, respectively), and were correlated with each other ($r^2 = 0.72$). Ammonium concentrations were generally greatest in Great Bay, though the regeneration rate for this nutrient was highest in Narragansett Bay sediments, indicating relatively high availability in this eelgrass habitat as well (Table 5). At specific sites with low (<1%) sediment organic content in Narragansett and Great Bays, ammonium regeneration rates were relatively high. Interestingly, both these low organic matter sites were close to nutrient discharges (Providence, RI, sewage treatment plant, and Portsmouth, NH, primary treatment plant) in comparison to the other sites. Phosphate concentrations in the interstitial water were generally similar among Reserves, but greater in organic-rich sediments, especially Waquoit and Great Bays (Table 5). Phosphate regeneration rates did not appear to follow the organic content of sediments, but were generally higher in sediments with greater interstitial water phosphate concentrations.

Population

Characteristics of eelgrass populations at the different sites within Research Reserves are presented in Table 6. Eelgrass densities ranged from 300 to over 1200 shoots/m^2 and were positively correlated with leaf and total biomass. Total biomass ranged from 56 to over 500 g/m^2, but the lowest value represented an area recovering from a die-off caused by wasting disease (Seal Rock, Great Bay). Generally, the leaves comprised most of the biomass, with contributions by the roots and rhizomes varying in significance (Table 6). All biomass components were significantly correlated with total biomass (Table 7); leaves of vegetative shoots exhibited the closest association (r^2=0.90). Leaves were generally shortest in North Carolina and longest in Great Bay (excluding Seal Rock, Great Bay 1988). All leaf morphological characters that were measured correlated positively with total biomass, and the number of leaves were greater in samples with more reproductive biomass (Table 7). Leaf length was negatively correlated with root biomass and leaf width was negatively correlated with shoot density. Furthermore, tissue nitrogen was positively correlated with leaf length and width, and negatively correlated with root biomass and plant density. We suggest that less dense eelgrass beds supported plants with wider blades, and taller plants had less root biomass because there was better nitrogen nutrition at these sites (nitrogen deficient plants allocate greater biomass to their roots (Short 1987)).

Leaf nitrogen content varied between 1 and 3.2 % dry weight (Table 6). Variation within sites was similar to variation between sites and years, and no clear differences between Reserves was observed. However, leaf nitrogen tended to be lowest in Waquoit Bay and greatest in Great Bay. In addition, leaf nitrogen was positively correlated with organic matter content of the sediment (Table 7). Leaf phosphorus content was also similar among Reserves, but tended to decline through time. In 1987, phosphorus levels in the leaves were much higher than in the following two years (Table 6), perhaps as a result of sampling at the time of maximum shoot biomass. Since the 1988 and 1989

Table 6. Eelgrass standing stock, population characteristics, and nutrient composition in the four Estuarine Research Reserves having eelgrass. The number of subsamples was three for 1987 and six for 1988 and 1989 (density, biomass, morphology and nutrient composition) based on 1/16m2 quadrats, and 10-20 for wasting index.

RESERVE Site Year	DENSITY #/m2	BIOMASS Shoots	 Roots	g/m2 Rhizomes	 Total	MORPHOLOGY Length cm	 Width mm	 #Leaves #/shoot	SHOOT NUTRIENTS N	 P %	 N/P	MAXIMUM WASTING INDEX %
Back Sound, NC												
Mid Marsh '87	450	106	4.5	19	130	35	3.5	3.7	1.7	.39	4	20.7
Mid Marsh '88*	1275	209	53	40	302	52	4.4	5.0	1.8	.30	6	5.6
Mid Marsh '89*	664	121	90	57	268	56	4.0	3.8	1.8	.09	21	20.2
Waquoit Bay, MA												
Red Nun 6 '87*	304	149	11	36	196	91	4.8	3.6	1.9	.33	6	9.7
Hamblins Pond '87	320	124	52	199	375	64	5.2	3.5	2.0	.34	6	6.9
Red Nun 4 '88*	469	231	45	48	324	70	5.0	4.9	1.0	.25	4	3.8
Red Nun 4-6 '88	1059	189	67	72	328	42	4.3	4.4	1.1	.21	5	2.6
West of RN 4 '89*	581	343	54	38	435	78	4.8	4.5	1.4	.13	11	3.5
Hamblins Pond '89	397	278	74	133	485	59	5.6	4.2				24.5
Eel Pond '89	376	196	32	32	260	77	5.4	4.1				
Narragansett Bay, RI												
S. Prudence I.'87	763	155	189	54	398	47	4.4	4.2	1.5	.40	4	16.9
S. Prudence I.'87*	528	156	26	24	206	67	5.7	3.7	2.6	.37	7	20.7
N. Prudence I.'88*	525	96	47	28	171	52	3.7	4.3	1.3	.20	7	10.1
S. Prudence I.'88*	931	186	196	138	520	55	4.5	4.5	1.1	.24	4	29.0
N. Prudence I.'89*	552	118	66	51	235	45	3.9	4.4	1.7	.19	9	27.6
S. Prudence I.'89	379	135	37	41	213	67	5.0	4.6	2.0	.17	12	37.4
Great Bay, NH												
Red Nun 6 '87	427	197	21	45	263	114	5.0	4.7	3.2	.38	9	16.6
Fishing I. '88*	888	244	124	138	506	74	4.0	5.2	1.6	.17	9	22.8
Middle Bay '88	368	133	10	29	172	95	4.4	4.5	2.7	.28	10	17.9
Seal Rock '88	339	25	7.7	23	56	33	3.9	4.5				27.3
Red Nun 6 '89*	504	249	15	113	377	125	5.2	4.8	2.0	.21	10	43.5

* Site of ESP deployment for water column measures.

Table 7. Correlations between population characteristics of eelgrass at the Research Reserves 1987 to 1989. Correlation coefficients (r) shown indicate significant associations at the 0.05 level if in plain type and at the 0.01 level if underlined; n varied from 83 to 108.

	DENSITY	BIOMASS					SHOOT MORPHOLOGY: LEAF		
		Vege. Sh.	Repro. Sh.	Roots	Rhizomes	Total	Length	Width	Number
	shoots/m^2			g/m^2			cm	mm	#
BIOMASS									
Vegetative Shoots	.25								
Reproductive Shoots	.27	-							
Roots	.46	-	.28						
Rhizomes	.24	.44	-	.55					
Total	-	.32	.95	.32	.24	.42			
MORPHOLOGY									
Leaf Length	-	.51	-	-.24	-	.48			
Leaf Width	-.20	.56	-	-	.28	.51	.46		
Leaf Number	-	.22	.24	-	-	.29	.24	-	
NUTRIENT COMPOSITION									
Carbon	-.31	-.27	-.46	-	-	-.41	-	-	-.27
Nitrogen	-.33	-	-.37	-.44	-	-	.52	.22	-
Phosphorus	-	-	-	-	-	-	-	-	-.23
C/N	.26	-	.40	.41	-	-	-.45	-	-
N/P	-	-	-.21	-	-	-	-	-	-

samples were taken at the time of maximum vegetative growth, differences in leaf phosphorus may have been more pronounced for these years. Although the reason for the phosphorus decline is not known, the decline did not seem to influence plant characteristics, as indicated by the paucity of significant correlations (Table 7). Lower P levels in leaves were found at higher latitudes in 1988 when sediments with low organic matter content were sampled in Great Bay, NH and Narragansett Bay, RI. In 1988, root and rhizome C, N, and P tissue levels were determined. Rhizome P followed that of the leaf tissue closely, and at about the same level, while no differences in root P were found between Reserves. No differences in root or rhizome N were found between Reserves.

Growth rates ranged from 0.7 to almost 20 $g/m^2/d$ on an areal basis, and 0.7 to 8.4 cm/day for an average shoot (Table 8). In 1987, when sampling of eelgrass was done during the estimated period of maximum standing crop, growth rates were slower than in subsequent years when sampling was done during periods of rapid vegetative growth. Specific growth, the rate of growth adjusted for the size of the plant, varied less than the other two growth measures reported and showed lower rates in 1987. However, no pattern of growth differences were found among Reserves, and growth measures were not significantly correlated with any population characteristic.

Effects of sediment and the water column on eelgrass distribution and population characteristics were examined using correlation matrices and linear regressions. Where nitrogen regeneration in the sediment was high, leaf biomass and plant size were low (Table 9). In a system that is nitrogen limited (N/P is generally below 20, Table 6), this relationship seems counterintuitive. However, the sites of high nitrogen regeneration (North Prudence Island, Narragansett Bay and Fishing Island, Great Bay Estuary) were low in organic matter and near sewage outfalls, suggesting these areas may not have been nutrient limited and another factor, such as competition from phytoplankton, may have been strongly influencing leaf biomass and plant size.

Eelgrass samples generally had more reproductive shoot and root biomass at low organic sites where greater light reached the bottom (Table 9). On the other hand, plant leaves were larger at sites with greater organic matter, and their shoots had greater nitrogen content. Interestingly, eelgrass blades were likely to be smaller in low organic matter sediments where phosphorus in sediment pore water and nitrogen regeneration were high.

Wasting Disease Status

The recent recurrence of the eelgrass wasting disease (Short et al. 1986) adds a complication to the investigation of eelgrass declines due to human activities, since the disease accelerates and intensifies the demise of eelgrass populations in many estuarine and coastal environments. Losses of eelgrass due to the wasting disease may eliminate eelgrass from environments where its survival has been marginal, producing changes in the habitat that will decrease water clarity, thereby creating conditions that are even less conducive for the natural revegetation of eelgrass.

Table 8. Aboveground growth rates of eelgrass in the four Estuarine Research Reserves that have natural eelgrass populations.

RESERVE Site Year	AREAL GROWTH g/m2/day	SHOOT GROWTH cm/day	SPECIFIC GROWTH cm/cm/day
Back Sound, NC			
Mid Marsh '87	0.7	0.7	.006
Mid Marsh '88	9.0	4.4	.024
Mid Marsh '89	5.8	4.9	.026
Waquoit Bay, MA			
Red Nun 6 '87	1.6	1.9	.015
Red Nun 4 '88	10.0	7.1	.031
Red Nun 4-6 '88	5.6	4.5	.027
Red Nun 2-4 '88	8.8	4.3	.032
West of Red Nun 4 '89	5.1	6.9	.024
Great River '89	3.3	3.5	.043
Hamblins Pond '89	4.3	3.9	.022
Eel Pond '89	8.1	6.2	.033
Washburn Pond '89	2.4	3.2	.030
Narragansett Bay, RI			
S. Prudence I.'87	4.5	2.9	.020
N. Prudence I.'88	4.3	5.2	.024
S. Prudence I.'88	2.2	1.8	.018
N. Prudence I.'89	5.9	6.1	.031
N. Prudence I.'89	9.0	6.5	.034
S. Prudence I.'89	6.0	8.2	.028
S. Prudence I.'89	4.6	7.0	.033
Great Bay, NH			
Seal Rock '88	1.4	4.4	.050
Fishing I. '88	12.6	7.5	.027
Fishing I. '88	19.1	8.3	.027
Red Nun 6 '89	8.8	8.4	.029

Table 9. Correlations between means of eelgrass population characteristics and sediment and water column parameters at the Research Reserves, 1987 to 1989. Correlation coefficients (r) shown indicate significant associations at the 0.05 level if in plain type and at the 0.01 level if underlined; n varied from 11 to 16.

	YEAR	LATITUDE	SEDIMENTS					WATER COLUMN	
PLANT CHARACTERS			Organics %OM	[NH4] µmolar	N Regen. nmol/cc/d	[PO4] µmolar	P Regen. nmol/cc/d	Light $E/m^2/hour$	Salinity Range, ppt
BIOMASS, g/m^2									
Vegetative Shoots	-	-	-	-	-.72	-	-	-	-
Reproductive Shoots	-	-	-.58	-	-	-	-	.61	-
Roots	-	-	-.73	-	-	-	-	.62	-
Rhizomes	-	-	-	.56	-	-	-	-	-
MORPHOLOGY									
Leaf Length	-	.61	.77	-	-.69	-	-	-	-
Leaf Width	-	-	.63	-	-.73	-	-.80	-	-
WASTING INDEX									
Maximum, % on leaf	-	-	-	-	-	-	-	-	-
NUTRIENT COMPOSITION									
Nitrogen, %	-	-	-	-	-	-	-	-.69	-
Phosphorus, %	-.90	-	-	-	-	-	-	-	-.63

Among the Reserves, the wasting indices were not significantly correlated with any other plant, soil, or water column measure. Eelgrass beds in the Great Bay and Narragansett Bay Reserves have exhibited relatively high indices of wasting disease that averaged significantly higher than disease in Waquoit Bay over the study period (Fig. 18). In fact, the high level of disease in Great Bay has led to numerous incidents of mass mortality, accounting for extensive eelgrass decline (Figs. 11a,b). Die-off from disease has also occurred in North Carolina (M. Fonseca, NMFS, Beaufort, NC, pers. comm.). In contrast, no mass mortality has been observed recently in Narragansett Bay. Waquoit Bay Reserve has eelgrass populations with consistently low levels of infection by the wasting disease (except in Hamblins Pond, 1989).

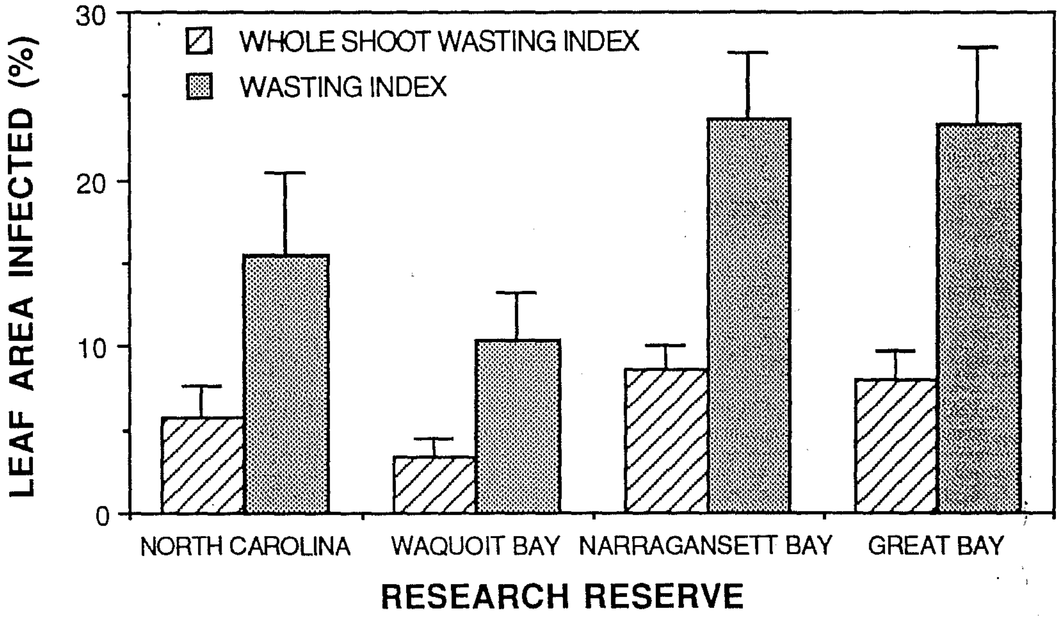


Figure 18. Eelgrass infection by wasting disease at the four Research Reserves. Whole Shoot Wasting Index is the percentage of leaf area of the whole plant that is necrotic, whereas Wasting Index is the percentage of necrotic area of the most infected leaf of each plant. Values are the means +/- standard error of three (NC), five (GB), and six (WB, NB) replicates.

Pollution Status

Water clarity, a measure of the ease with which light may pass through water, is a major problem affecting estuarine and coastal benthic plant communities since these primary producers need light to photosynthesize and grow. Suspended particles in the water effectively reduce water clarity, a process that reduces the depth to which light can penetrate into the water (Dennison 1987). Thus, decreases in water clarity limit the depth to which benthic plants, like eelgrass, can grow in an estuary.

Elevated nutrient levels entering estuarine systems generally lead to increased primary production, but loadings that exceed certain levels for a specific system will result in large scale changes in the plant community which, in turn, affect the animal community. The entire process of stimulating production by increasing the availability of a limiting nutrient or nutrients, which at some point is accompanied by widespread changes in the entire ecological community, is termed eutrophication. At present, the major impact of eutrophication on eelgrass populations is negative because water clarity is reduced by increases in the phytoplankton, and eelgrass is further shaded by increases in epiphytes and seaweeds. In addition, pollution can directly decrease water clarity through increases in suspended particles.

The effects of pollution on eelgrass population characteristics in the Research Reserves are not obvious to the casual observer. Perhaps most important is the reduction in light transmission through the water (light extinction) as suspended load and algal competitors increase with greater nutrient loading. Light data collected during the same period at different sites within a Research Reserve can be compared since the sample times were coincident (i.e. incident light was the same at both sites). A coefficient to describe light extinction, k_T, was calculated using regional light levels for specific months, as defined in the Methods (above). Although light reduction by algal competitors and suspended load are combined and cannot be separated, their effects on eelgrass characteristics are similar (see Mesocosm Experiments) so that comparisons of sites within Reserves and years may be valuable. Three sites can be compared in Waquoit and Narragansett Bays, two sites can be compare in Great Bay, but no site comparisons are possible for North Carolina because only one site there was measured. Nevertheless, the rather high k_T values calculated for the water column in North Carolina suggest eelgrass distribution is limited to shallow intertidal areas by low light, due to poor water clarity (high turbidity and/or phytoplankton populations).

At Waquoit Bay, the central bay sustains healthy populations of eelgrass, while populations in Great River are declining dramatically and populations at the mouth of the Moonakis River appear to have been eliminated between 10 and 20 years ago (Fig. 9). In 1988, the k_T of the central bay was 0.90, while that at the mouth of the Moonakis was 1.5. In 1989, the k_T of the central bay was 1.0 and that of Great River was 1.1 (Table 4). The population of eelgrass at Great River was so reduced that no biomass samples were taken in 1989. Thus it appears that areas of historic eelgrass presence as well as areas exhibiting dramatic eelgrass decline show greater k_T values (poorer water clarity) than the central bay. Both these are upper estuary areas that are more susceptible to the effects of pollution on water clarity. In addition to the stress of low water clarity, mechanical disturbance from shellfishing impacts the area at the mouth of the Moonakis River.

In 1988, light attenuation by the water covering eelgrass beds in the central bay was compared with that of Hamblins Pond over a range of water depths from 0 to 1 m. Half of the surface light was removed by 0.5 m in Hamblins Pond, whereas only 30% was removed by 0.5 m of water in the central bay (Fig. 19). This was likely due to elevated phytoplankton levels, which appear to be causing eelgrass decline in Jehu Pond and in Great River, and may be impacting Hamblins Pond. These areas also support large populations of competing drift algae and epiphytes; drift algae is the most important eelgrass competitor in Hamblins Pond. Epiphytes pose the biggest threat to declining eelgrass populations in Eel Pond, which is part of the Waquoit estuarine system, but not within the Research Reserve boundaries. (Fig. 10d).

In Narragansett Bay in 1988, water clarity was greater in beds at South Prudence ($k_r = .48$) than at North Prudence ($k_r = .75$) which is further up the Bay and closer to pollution sources (Table 4). In turn, clarity was greater at North Prudence in 1989 ($k_r = .97$) than at the Potter's Cove site ($k_r = 1.1$) where eelgrass no longer exists. A comparison of the South and North Prudence eelgrass beds in 1988 reveals greater shoot density and plant biomass at South Prudence. Similar to the pattern at Waquoit Bay, up estuary areas show poorer water clarity in Narragansett Bay. In contrast to Waquoit Bay, the South Prudence eelgrass beds (lower estuary) had greater wasting disease infection than in the upper estuary, as expected. In addition, the overall health of the two sites in Narragansett Bay were similar, whereas the eelgrass beds in the lower estuary were healthier in Waquoit Bay.

The two sites that can be compared in Great Bay are close together (ca. 1 km), but the site that was impacted heavily by the wasting disease in 1988 (Seal Rock) exhibited lower water clarity than the Red Nun 6 eelgrass bed (Table 4). Although it is relatively near a large sewage outfall, Fishing Island at the mouth of the Great Bay Estuary has an extensive, healthy bed and water clarity was very good at this site.

Latitudinal Variation

Natural eelgrass populations occur in four of the five Reserves in this study. One of the goals of this work is to compare Reserves along the East Coast of the United States with respect to eelgrass habitats, including analyses of sediment, water column and plant population characteristics. For such comparisons, eelgrass biomass, plant size, density, and growth rate in analogous environments were measured at four Reserves.

Eelgrass characteristics versus latitude were plotted for each year. Eelgrass shoot density shows a general decrease with increasing latitude in 1988 and 1989, but not 1987 (Fig. 20). Densities were greatest in 1988, the year the samples were taken at the habitats with organic-poor sediment. Samples from habitats with organic-rich sediments were lower and similar in 1987 and 1989, with little variation among Reserves.

There was a strong gradient of increasing leaf length with latitude in 1987. The trend was evident in the following two years, but not as pronounced (Fig. 21). Much of this trend is due to availability of only intertidal populations with short-leaved plants in North Carolina coupled with deep,

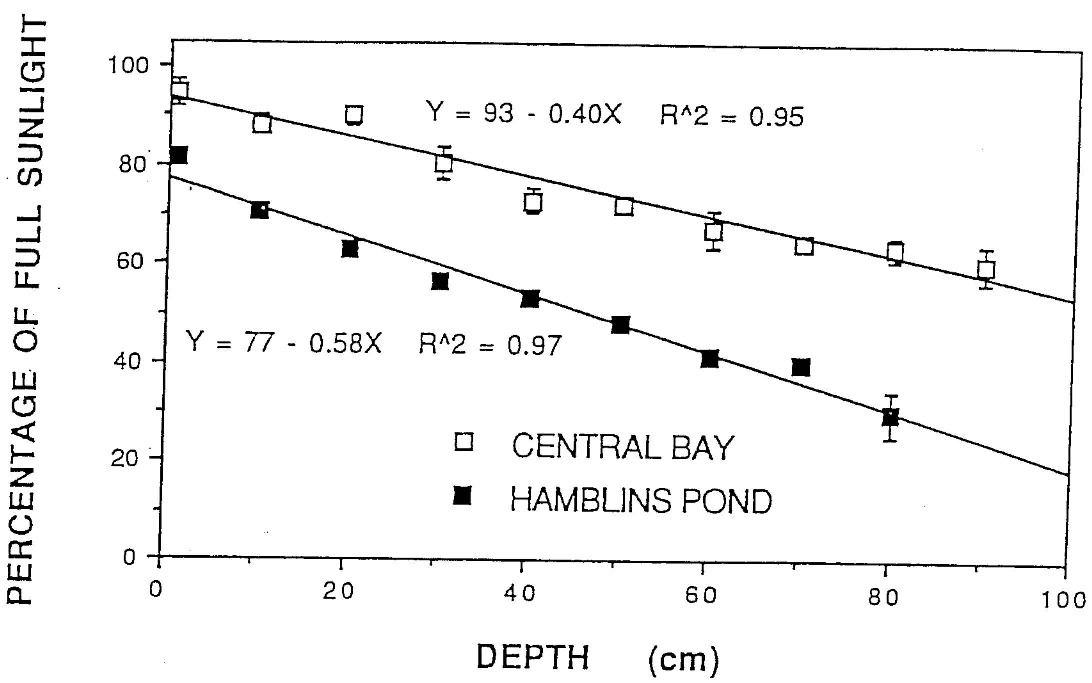


Figure 19. Light attenuation by the water overlying eelgrass habitats in the Central Bay and Hamblins Pond of the Waquoit Bay Reserve. Values are the means +/- standard error of two determinations.

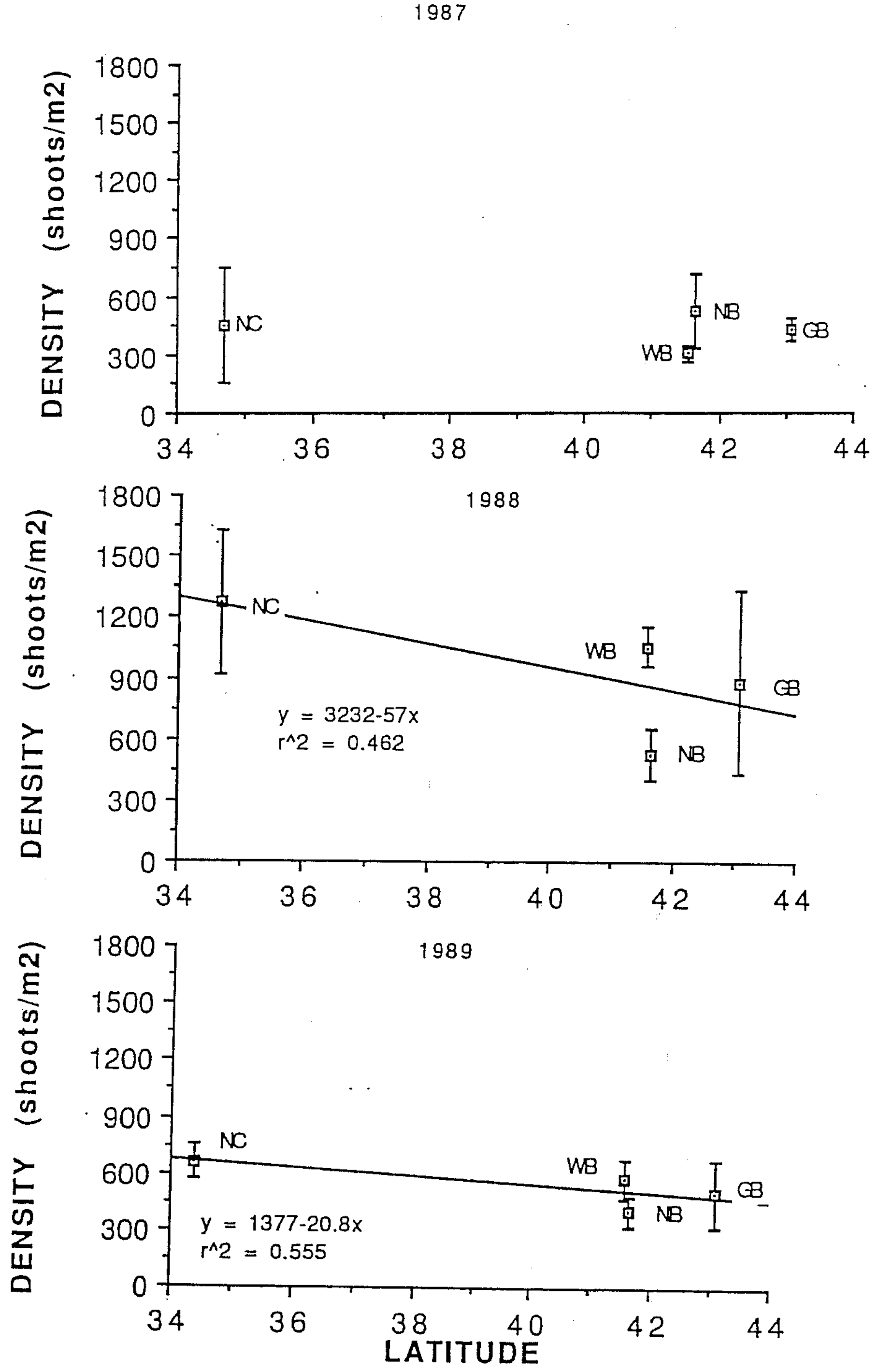


Figure 20. Latitudinal variation of eelgrass density in the Research Reserves from 1987 to 1989. Simple least squares regressions were not statistically significant for individual years, but a trend of greater density at lower latitudes was strongest in 1988, when the sampling locations were chosen to include sites with organic-poor sediments. Data from two 1989 organic poor sites (WB, NB) are not shown. Values are sample means +/- standard error (three per Reserve for 1987, and six for 1988 and 1989). The simple least squares regression in 1987 had a regression coefficient (r^2) of less than 0.35. Regressions with coefficients greater than 0.771 are significant at the 0.05 level (n=4).

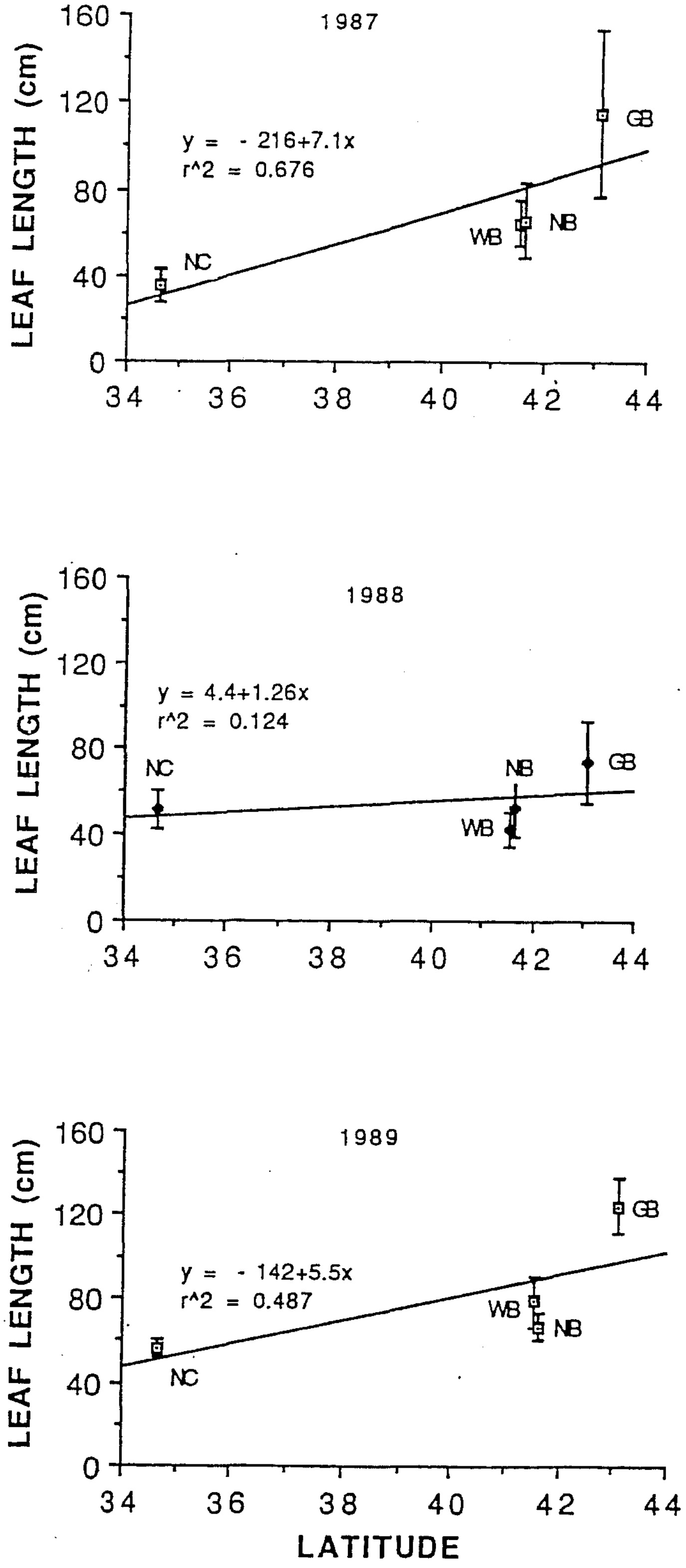


Figure 21. Latitudinal variation of longest leaf length of eelgrass in the Research Reserves from 1987 to 1989. Simple least squares regressions were not statistically significant for individual years, but showed a consistent trend of longer leaves at higher latitudes. Values are sample means +/- standard error (three per Reserve for 1987, and six for 1988 and 1989).

long-leaved plants sampled in Great Bay. In other words, the trend may be driven by the morphology of the estuaries characteristic of these latitudes, rather than by the capacities of eelgrass itself. In 1988, a population in very shallow water with sandy, phosphate-poor substrate was sampled from Fishing Island in the Great Bay Estuary, and this year the relationship between latitude and leaf length was poorest. In 1988 and 1989, Back Sound, NC had the greatest densities and the shortest leaf lengths, while Great Bay, NH had lower densities but greater leaf lengths (Figs. 20-21). Leaf widths and the number of leaves per shoot generally followed length measurements, but their latitudinal trends were not as strong, and showed no trends in 1988.

Leaf biomass was generally low in Back Sound, NC and Narragansett Bay, RI, and high in Great Bay, NH (Fig. 22). Leaf length and biomass generally tracked together (Figs. 21-22). In sediments with relatively greater organic matter content there appears to be a trend of increasing leaf biomass with latitude (1987 and 1989). Leaf biomass in Back Sound, NC was about half that of Great Bay, NH in those two years, but very similar in 1988. Low leaf biomass in Narragansett Bay, RI was generally due to small shoot length, but low density relative to the other Reserves in 1988 (Fig. 20) resulted in very low leaf biomass. Leaf biomass in Great Bay, NH was variable within sites (resulting in large error bars), but very consistent among years. This was not the case for Waquoit Bay, MA, where leaf biomass was similar in the first two years, then doubled in the last year (Fig. 22). Weak trends of increases at higher latitude were found for rhizome biomass and total rhizome length, but not for root biomass.

Leaf growth is presented as two different measures, the first as the growth per shoot, and the second as the growth on an areal basis. On a shoot basis, there were increases in growth with latitude in 1987 and 1989 (Fig. 23), which accompanies similar trends found for leaf lengths (Fig. 21). As g/m^2/day, eelgrass growth also increased with increasing latitude of Reserves (Fig. 24) and these trends were similar to trends seen for biomass (Fig. 22).

Trends observed in eelgrass populations along the East Coast were shown to have a strong latitudinal influence. These changes in plant morphology and habitat structure suggest that studies of eelgrass populations must take into consideration location when comparisons of results are made.

Mesocosm Experiments

Effects of Reduced Light

A series of mesocosm experiments were designed to examine the effects of reduced light intensity on the density, biomass, growth and morphology of eelgrass, *Zostera marina.* In 1988, six outdoor tanks (1.5 m^2) with a gradient of light intensity from 11% to 94% of surface light measured at 1 cm depth were planted with eelgrass seedlings in early June at a density of 133 m^{-2} and the plants were allowed to grow to maturity. Reduced light levels were achieved by covering the tanks above the

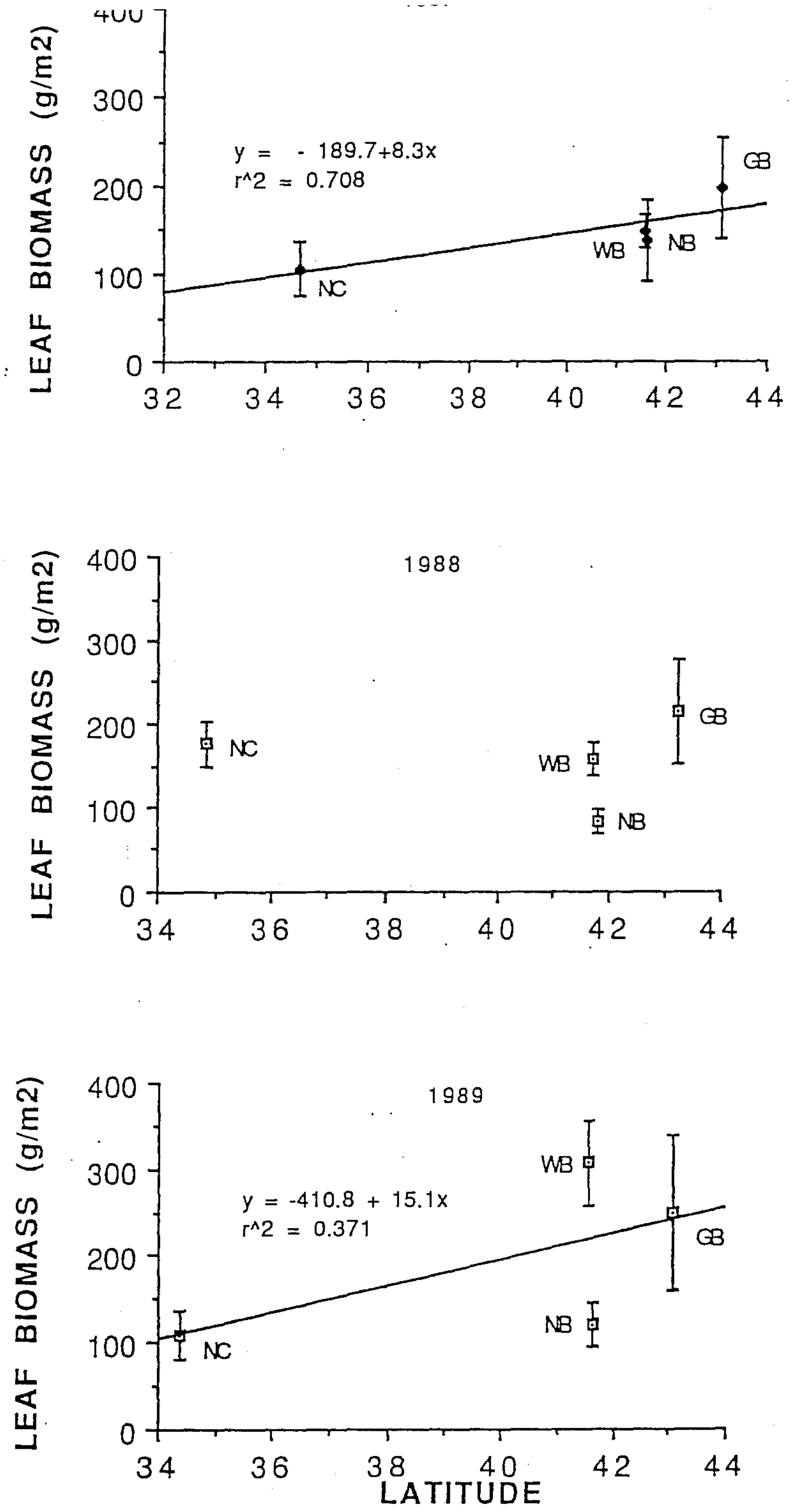


Figure 22. Latitudinal variation of eelgrass biomass in the Research Reserves from 1987 to 1989. Simple least squares regressions were not statistically significant for individual years, but showed a consistent trend of greater biomass at higher latitudes in years when sampling locations were chosen to include sites with organic-rich sediments (1987 and 1989). Values are sample means +/- standard error (three per Reserve for 1987, and six for 1988 and 1989). The simple least squares regression in 1988 had a regression coefficient (r^2) of less than 0.35. Regressions with coefficients greater than 0.771 are significant at the 0.05 level (n=4).

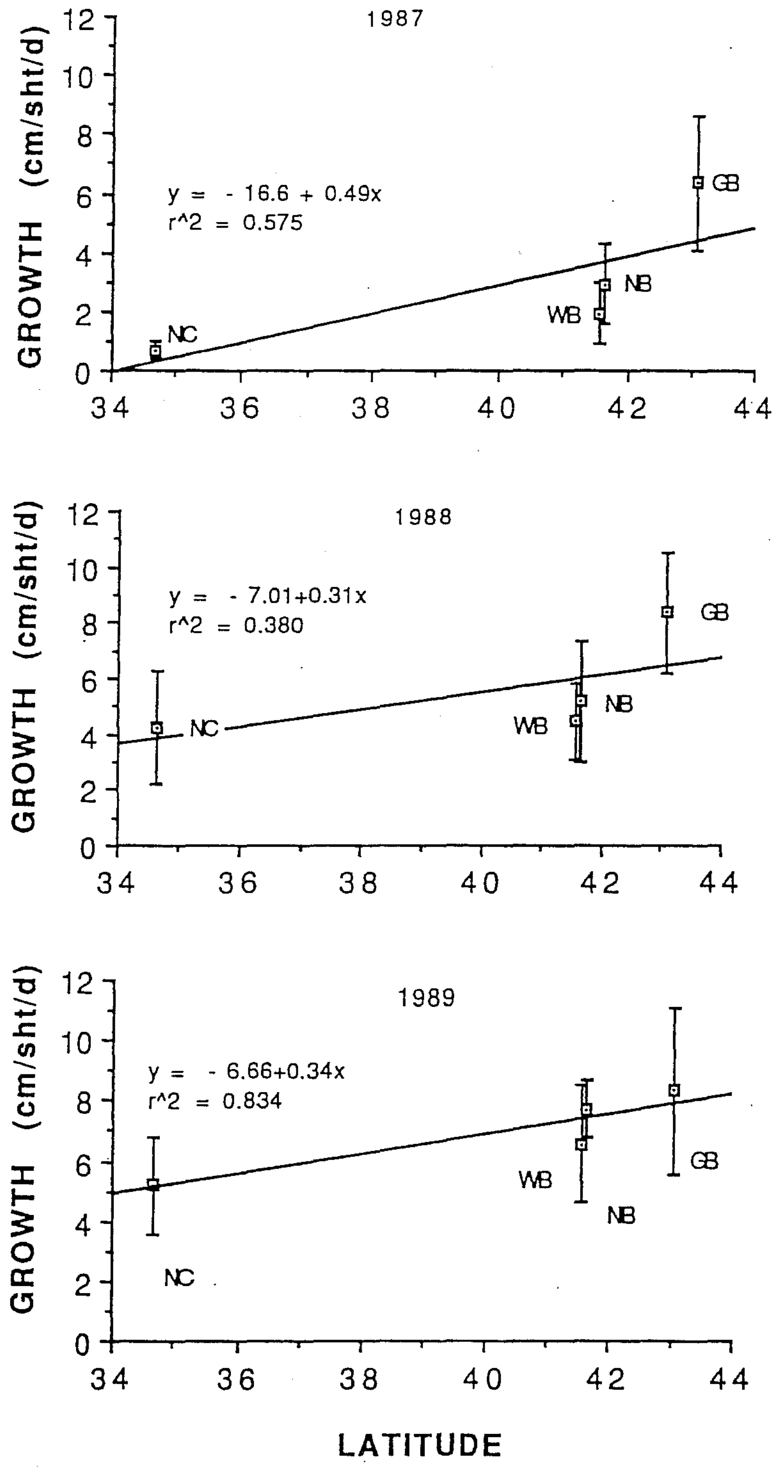


Figure 23. Latitudinal variation of eelgrass growth on a per shoot basis in the Research Reserves from 1987 to 1989. Simple least squares regressions were statistically significant for only 1989, but showed a consistent trend of faster growth at higher latitudes. Values are sample means +/- standard error (three per Reserve for 1987, and six for 1988 and 1989). Regressions with coefficients greater than 0.771 are significant at the 0.05 level (n=4).

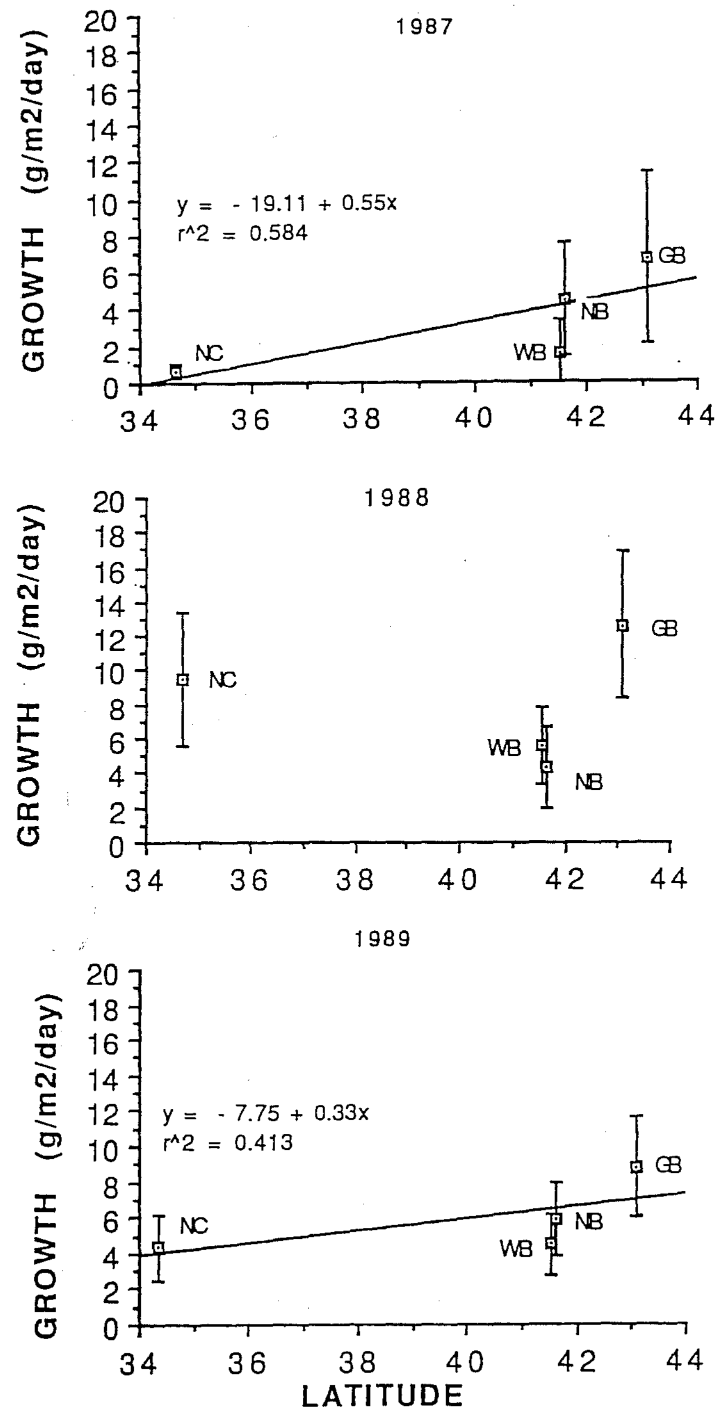


Figure 24. Latitudinal variation of eelgrass growth on an areal basis in the Research Reserves from 1987 to 1989. Simple least squares regressions were not statistically significant for individual years, but showed a consistent trend of greater growth at higher latitudes in years when habitats were chosen to include sites with organic-rich sediments (1987 and 1989). Values are sample means +/- standard error (three per Reserve for 1987, and six for 1988 and 1989). The simple least squares regression in 1988 had a regression coefficient (r^2) of less than 0.32. Regressions with coefficients greater than 0.771 are significant at the 0.05 level (n=4).

water level with neutral density screen which reduced incident irradiance to 61%, 41%, 20%, and 11% of the surface light conditions. It should be noted that the shading of these plants had no effect on the photoperiod, thus only the effect of reduced light intensity reaching the eelgrass leaves was examined. Reduction in light intensity by shading is analogous to decreased water clarity but not to changes in depth since the photoperiod for the plants remains unchanged (Dennison 1987). Throughout the mesocosm experiment, shoot density, morphology, and leaf growth were measured, while at the conclusion of the experiment, total biomass was also assessed.

A marked difference in shoot density was observed between treatments as the 1988 season progressed. Density at the lowest light level increased slightly then dropped to the initial planting density of 133 plants per square meter. Shoot density increased logarithmically with increased light to a maximum density of >400 shoots m^{-2} (Fig. 25); achieved at the end of the experiment under 'full' light conditions (94% of full sunlight at one cm depth). Differences in leaf size appeared to develop among the different treatments, with the plants in the most shaded tanks at the lowest light levels growing longer than the plants at the higher light levels, but the trend was not significant ($P>0.10$; Fig. 25). In all cases, leaf length exceeded the water depth and the plants grew with a portion of the leaves horizontal on the tank's water surface. The apparent increase in leaf size may be a morphological adaptation of the plants to reduced light intensity as the density of plants decreased, and this idea deserves further study. Standing leaf biomass was significantly higher at high light levels than at low light levels, reflecting the combined differences in plant size and density. The increased shoot density at high light conditions overwhelmed the effect of slightly larger plants at lower light levels and standing leaf biomass exhibited a logarithmic increase with light level (Fig. 25).

Leaf growth measured as leaf elongation on a per shoot basis showed a significant linear increase with increased light intensity (Fig. 26a). However, specific growth rate, that is growth in mg of new leaf per mg of shoot per day, showed little variation under the different light treatments (Fig. 26b). That is, the plants appear to have adapted to grow at a maximum specific production rate based on light availability. Utilizing density measurements to convert per shoot growth rates to per meter square growth rates, which combined the effects of increased density and increased growth, this measure showed a strong increase in production with light (Fig. 26c). Thus, it is clear that decreasing only light intensity, which is analogous to decreasing water clarity, has a major effect on eelgrass production, standing biomass, and morphology in experimental mesocosms. The plants responded to decreased light levels by lower shoot density and biomass production, but greater leaf size.

An unexpected result of this study is the evidence of plant adaptation to maximize specific growth rate at all light conditions by adjusting its morphology and shoot density. The specific growth rate varied the least of all parameters measured. However, growth per shoot varied substantially among the light treatments, primarily in response to the size differences. These studies show that under conditions where the plants are allowed to adapt to different light levels, eelgrass does not

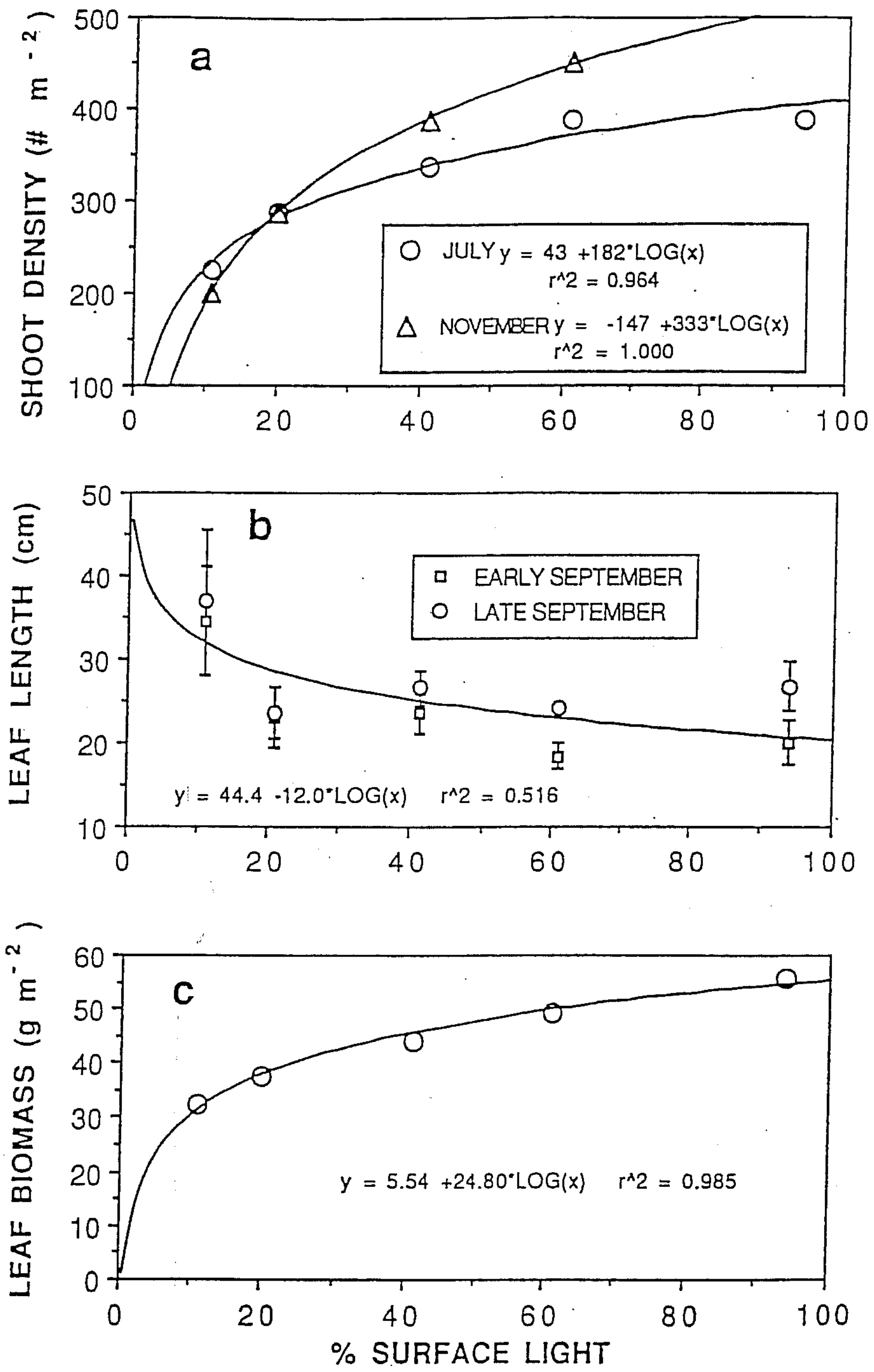


Figure 25. Eelgrass population characteristics developed under control and four reduced light level mesocosms in 1988. Simple linear regressions were performed on the logarithm of percentage of surface light at 1 cm depth. Regression coefficients indicate regressions are significant at the 0.01 level for density and biomass, and at the 0.10 level for longest leaf length. July shoot densities were an average of three 1/20 m^2 quadrats, and November shoots densities were determined for the entire tank. Shoot biomass was determined for the entire tank, and a subset of ten shoots was used to generate a mean for longest leaf length.

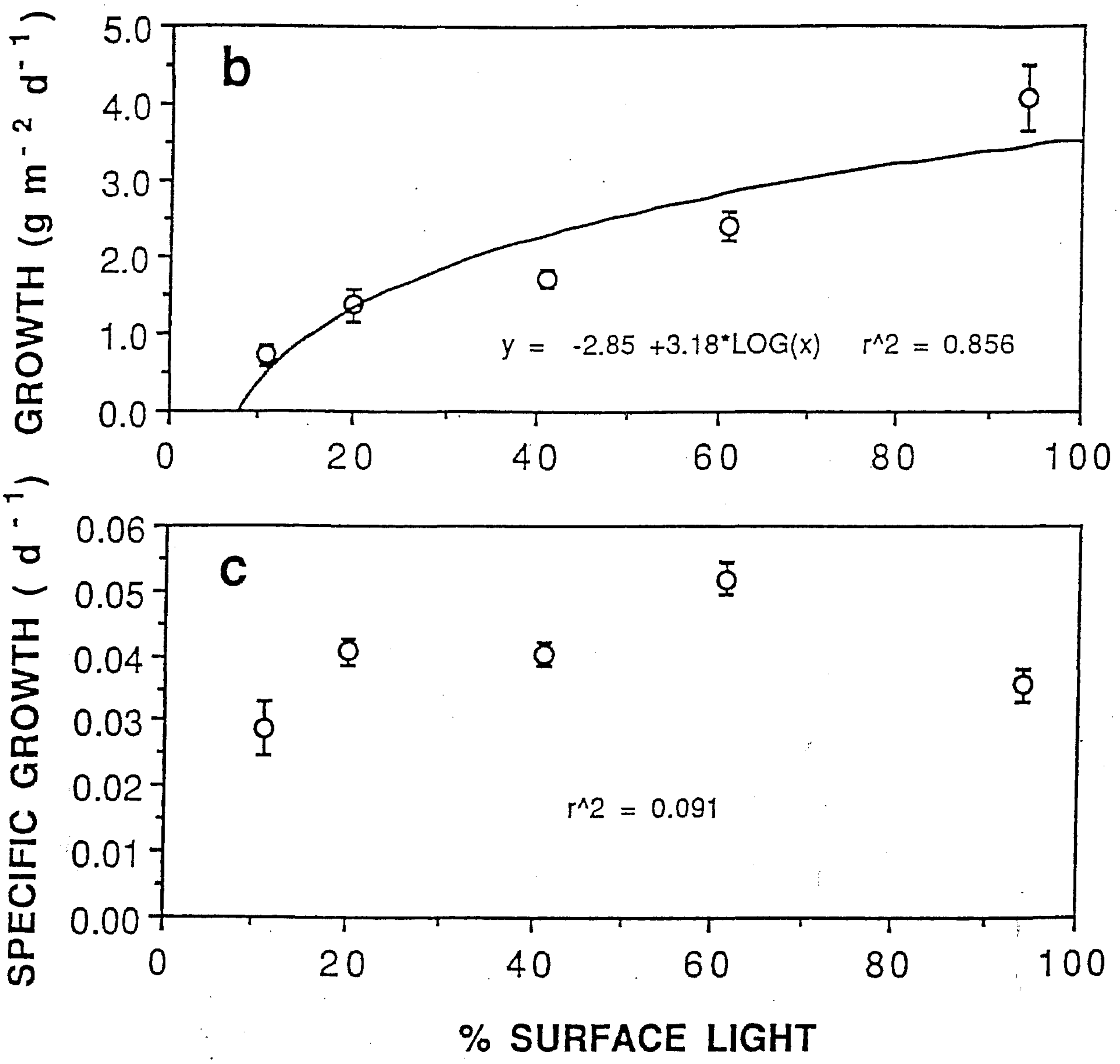


Figure 26. Eelgrass growth rates under control and four reduced light level mesocosms in 1988. Simple linear regressions were performed on the mean growth of ten shoots and the logarithm of percentage of surface light at 1 cm depth. For growth on an areal basis the regression coefficient was significant at the 0.05 level; trends in specific growth were not significant at the 0.10 level.

demonstrate light saturation in response to varying light, and in fact overall plant production increases linearly in response to increasing light intensity up to full sunlight.

Infection and spread rates of the wasting disease, *Labyrinthula zosterae*, were greater with decreased light, and light levels at 17% of full sunlight and below resulted in plant death (Fig. 27). Note that at several light levels (9, 33, 57, and 81%), the percentage of leaf area infected peaked on Day 27 following infection, then dropped off. This phenomenon is not a slowing of the disease; rather, it indicates the older leaves that have relatively greater infection are dehiscing (being cast off) from the plant. While this resulted in low wasting indices at the two highest light levels by the end of the experiment, plants at the two lowest light levels were nevertheless killed by the disease (Fig. 27).

Effects of Nutrient Loading

Experimental examination of the effects of nutrient loading on eelgrass growth and standing biomass was assessed in 1989 and again in 1990 in replicated enrichment studies using the mesocosms. The increased loading of estuaries with nitrogen and phosphorus has been suggested as a cause of eelgrass decline in many areas (see the Introduction in the Management Document).

As an estuary becomes eutrophic, the level of nutrient loading has a direct impact on the eelgrass community. The research reported here examines the effects of excess nutrient loading on eelgrass populations and the resulting changes in plant composition of the eelgrass community in both field and experimental mesocosm studies. The community dominated by eelgrass includes numerous species of both micro- and macroalgae which grow as epiphytes on the eelgrass blades, as well as unattached macroalgae. In addition to the plants, a host of animals is associated with the eelgrass community. This includes many invertebrates (worms, snails, and crustaceans) and numerous fish species, many of which can be important in influencing the effects of excess nutrient addition.

Excessive nutrient loading in an estuary can eliminate the eelgrass community by pushing the eelgrass system in one of three directions: toward a plankton dominated system, toward a macroalgal dominated ecosystem, or toward a system with excessive amounts of epiphytic algal growth (Fig. 28). All three possible outcomes of eutrophication have been observed in the field and have been directly associated with documented eelgrass declines. Although nutrient uptake at high concentrations by eelgrass leaves has been well documented (see review: Short 1987), there are severe indirect impacts of eutrophication on the eelgrass community. Nutrient loading can stimulate phytoplankton growth which shades eelgrass and can reduce its productivity and distribution. Benthic algal populations have been shown to overgrow eelgrass in situations of excessive nutrient loading (Harlin and Thorne-Miller 1981, Neckles 1990). Our observations of macroalgal, epiphytic algal, or phytoplankton inhibition of eelgrass communities along the East Coast have included Mumford Cove, Connecticut, Charlestown Pond, Rhode Island and Waquoit Bay, Massachusetts.

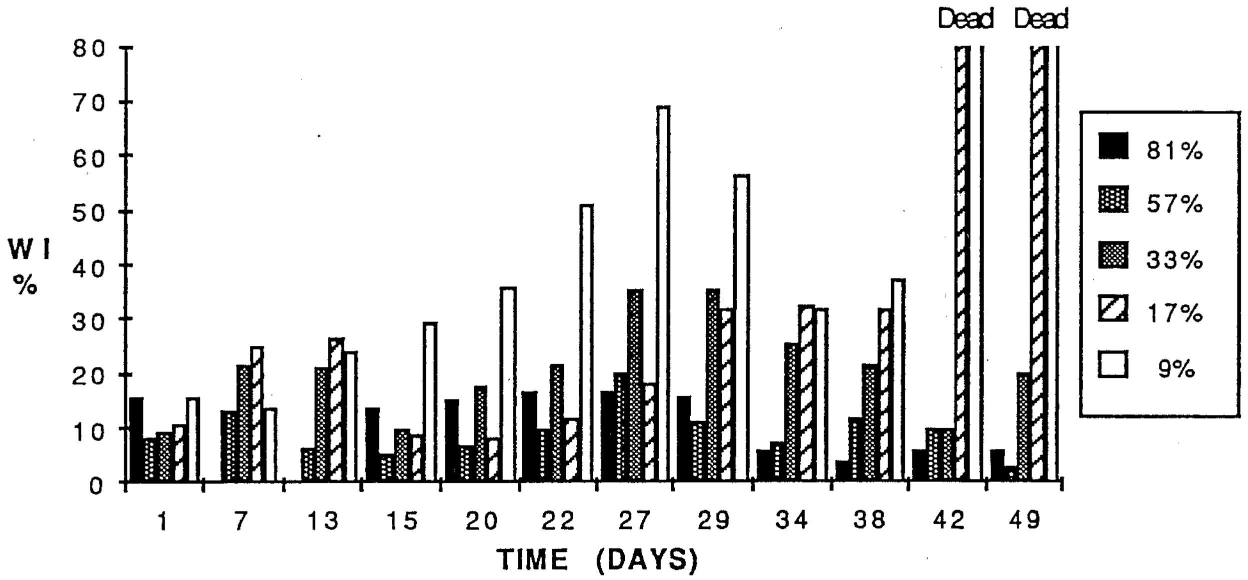


Figure 27. Progression of the wasting disease in the eelgrass mesocosms under control and four levels of reduced light. After six weeks, plants used for indexing in the two lowest light treatments (9 and 17%) had died (n=10 shoots per tank).

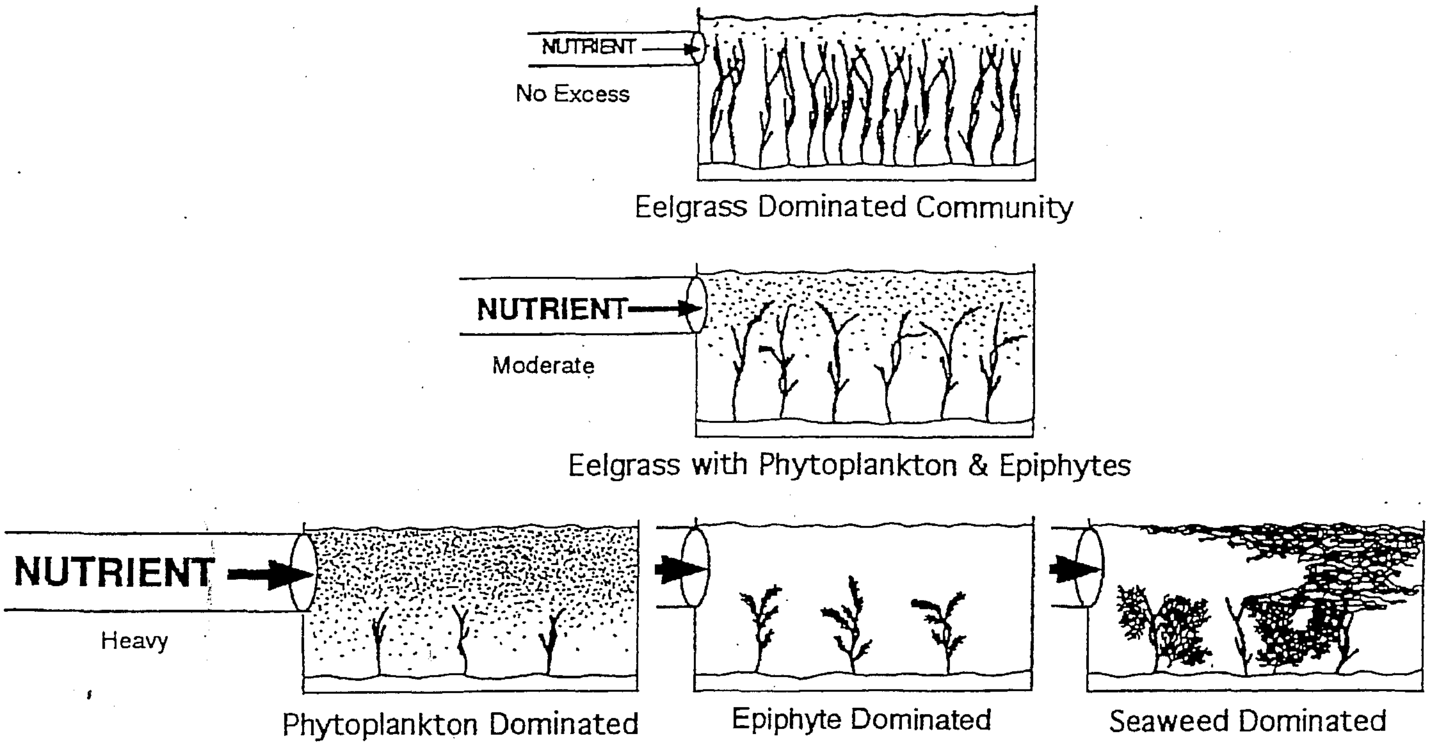


Figure 28. Schematic diagram showing the effects of eutrophication on the eelgrass community. Increased nutrient loading produces a shift in community dominance toward one of three nuisance algal groups.

Our experimental mesocosm studies have quantified the effects of specific nutrient loading levels on eelgrass communities (Short 1987). They have proven valuable in documenting the shift from an eelgrass-dominated community to communities dominated by various algal forms. In 1989, six mesocosms were planted with eelgrass and grown under the same conditions for two months, after which the tanks were paired according to eelgrass density and one of each pair was enriched with nitrogen and phosphorus at a level producing concentrations six times ambient nutrient concentrations. Although the tanks received a relatively constant loading rate, the concentration of nutrients in the tanks decreased over time as a result of increases in plant uptake rates and incorporation of nutrients into biomass (Fig. 29). Experiments were run for four months under continuous nutrient additions; plant characteristics, algal populations, and loading rates were monitored.

The overall effect of excessive nutrient loading on eelgrass populations was most evident in the reduction of shoot density and biomass observed in the enriched tanks versus the eelgrass density growing at ambient nutrient concentrations (Fig. 30a and b). Other responses to nutrient addition included a reduction in eelgrass areal growth rate (Fig. 31a), and a decrease in leaf length, by more than 20 cm in enriched eelgrass tanks as compared to controls (Fig. 30c). Although eelgrass responded by becoming shorter and less dense, the specific growth rate of the enriched treatments was slightly *greater* than that of the unenriched treatments (Fig. 31b). Stimulated specific growth rates coupled with reduced areal production, biomass and plant size may indicate stress in an eelgrass population.

Infection by *Labyrinthula*, introduced in the tanks immediately following an increase in salinity to ambient Great Bay levels, proceeded faster in the control tanks because the leaves were clean of epiphytes, promoting leaf-to-leaf contact. By the close of the experiment, however, the level of infection was greater in the enriched treatment tanks (Fig. 32). Mesocosm experiments currently underway suggest physical contact between plant leaves may be needed to spread the disease. The differences in disease infection between treatments suggest that the greater amount of epiphytes covering the leaves in the enriched treatment may afford eelgrass a small measure of the protection against the disease infection. Once infected, however, the added stress of light reduction caused by the epiphytes may increase the severity of the disease.

The reduction in eelgrass abundance and health in the enriched treatments appeared to result from light inhibition by various algal growth forms that were stimulated by the nutrient enrichment. Regular observations of the tanks provided qualitative results, while epiphytes were quantitatively sampled (Fig. 33). The response of the algal community to the enrichment treatment in 1989 reflected all three scenarios seen in field observations (Fig. 28). Of the three enriched tanks, one became dominated by phytoplankton, with an intensive phytoplankton bloom maintained throughout the experimental period and with some epiphytic growth on the plants and no macroalgal growth. The second "replicate" developed macroalgal mats floating at the surface which were dominated by the

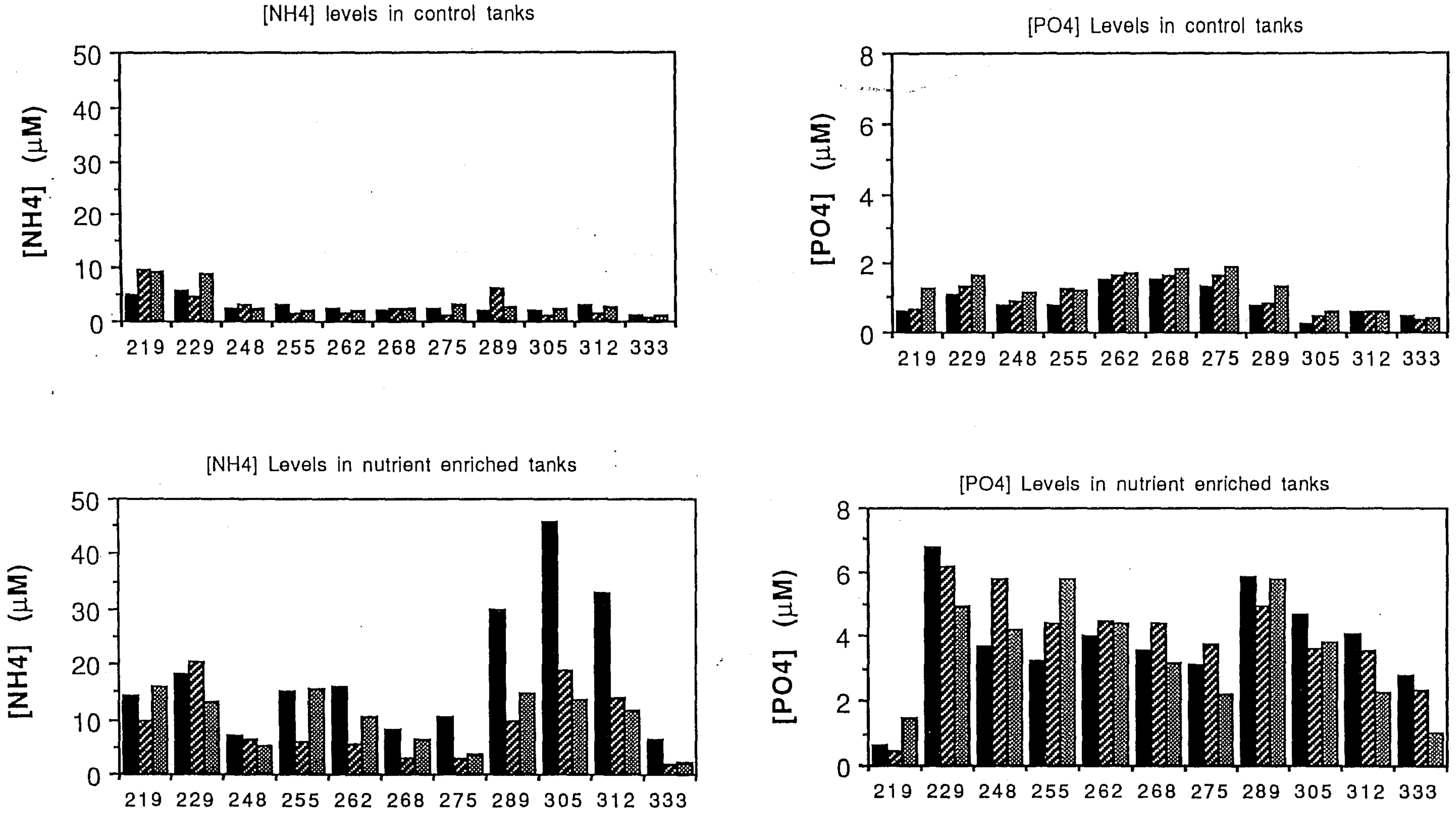


Figure 29. Ammonium and phosphate levels in the mesocosm tank water columns before (Julian day 219) and during (days 229-333) nutrient enrichment treatments, 1989. Mean values of two determinations from each of the three replicate tanks are shown.

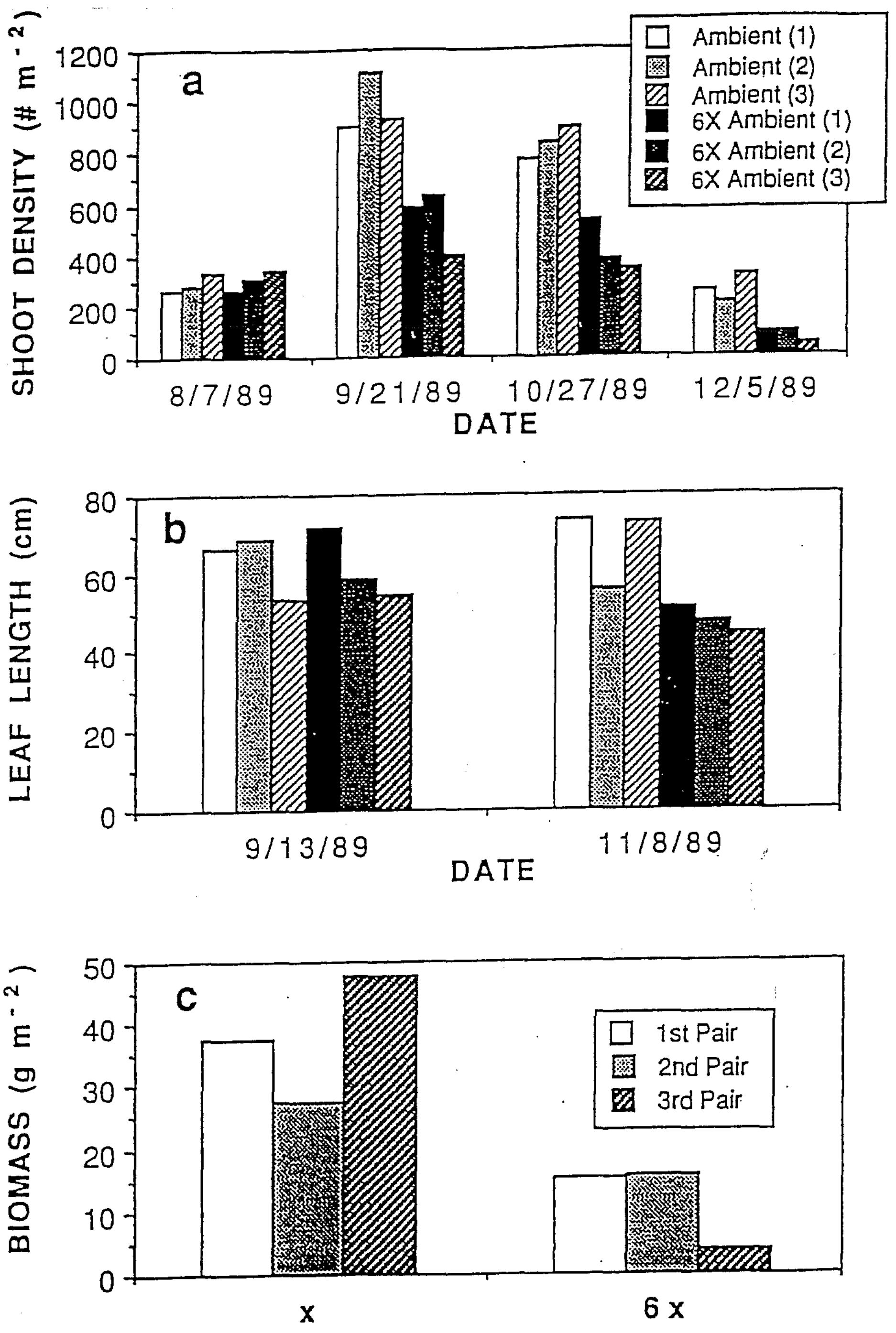


Figure 30. Population characteristics of eelgrass grown in mesocosms under ambient and enriched nutrient treatments that were started August 7, 1989. Values from each of the three replicates are shown. Densities were determined from 3 quadrats of $1/16m^2$ on Julian days 219 and 339. Leaf lengths were determined on ten terminal shoots for each tank on Julian day 256 and 312. Final biomass is live shoot biomass at the close of the experiment (Julian day 340), reported on a dry weight basis.

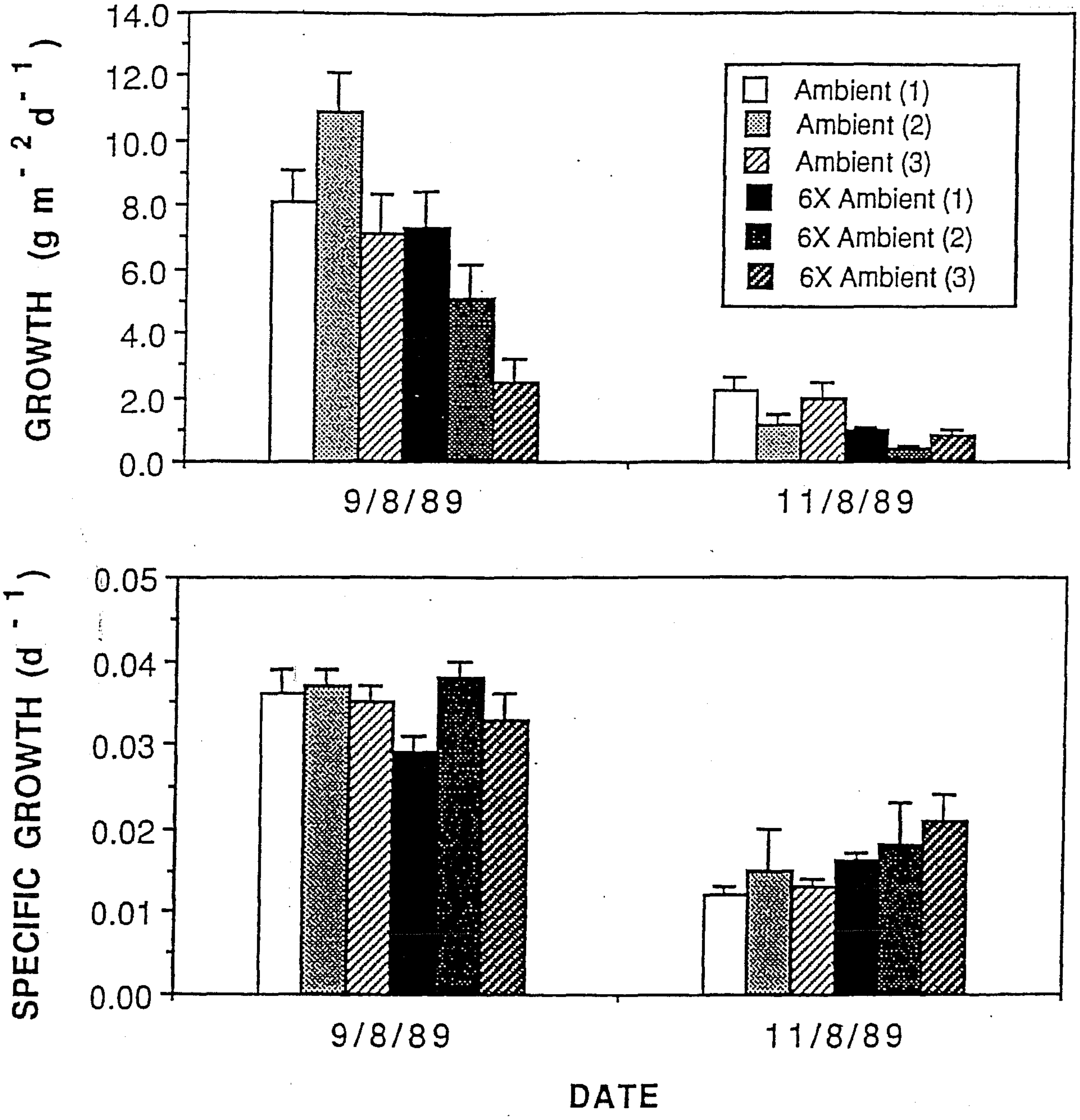


Figure 31. Eelgrass growth rates on an areal basis and as specific growth under ambient and enriched conditions in mesocosms, 1989. Values from each of the three replicates are means from ten terminal shoots.

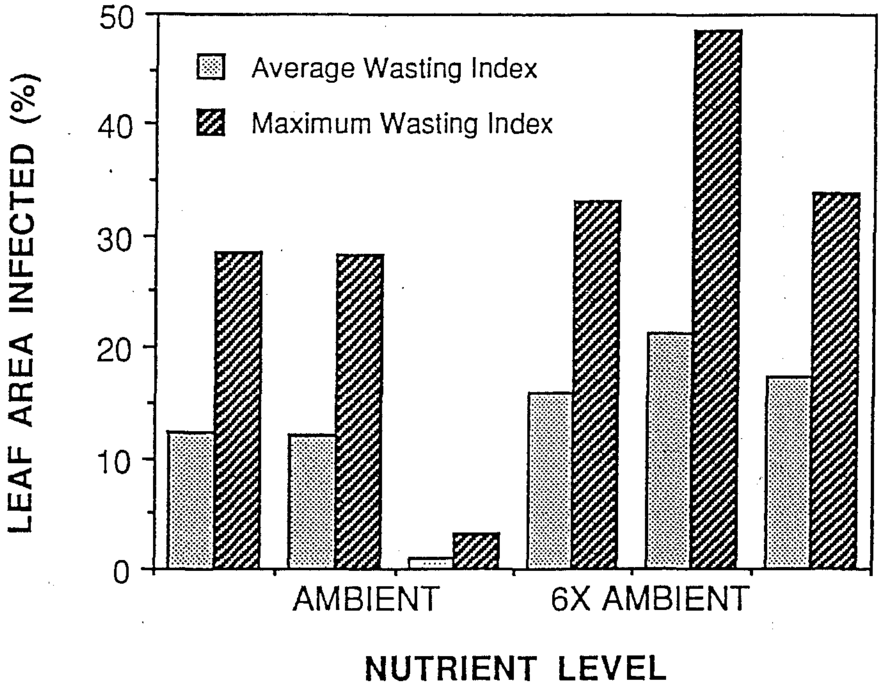


Figure 32. Wasting Indices at the close of the nutrient enrichment experiment, 1989, determined from ten shoots per tank. The Wasting Index is the percentage of leaf area blackened by the disease on the most infected leaf of the shoot. The Whole Shoot Wasting Index is the percentage of leaf area on the entire shoot blackened by the disease.

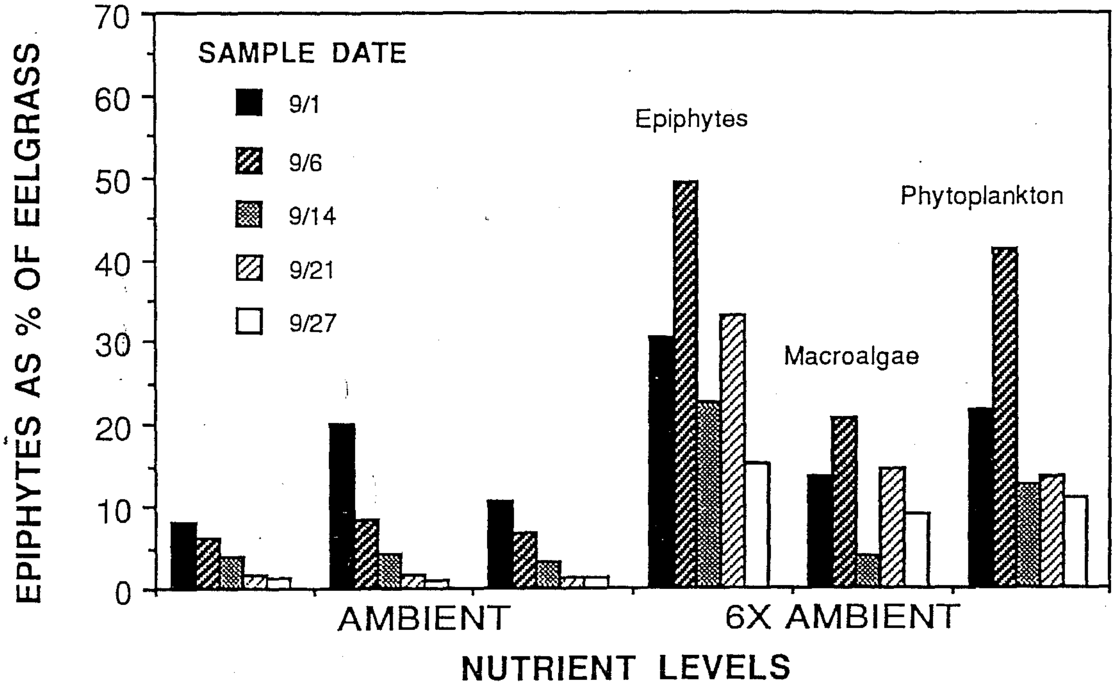


Figure 33. Epiphyte biomass, collected from ten shoots per tank, is reported as a percentage of the host eelgrass shoot biomass. Values of each of the three replicates are shown for five sample dates in September, 1989. At ambient nutrient levels, epiphyte biomass was less than 8% of the eelgrass biomass in the tanks. Under enriched conditions, each mesocosm tank appeared to favor a different competitor of eelgrass. Epiphyte biomass averaged over 30% of the eelgrass biomass in the tank co-dominated by epiphytes, over 20% in the tank that appeared to be co-dominated by phytoplankton, and over 10% in the tank co- dominated by macroalgae.

green alga *Enteromorpha*. In this treatment, extensive algal growth appeared to crowd out the eelgrass and block the amount of light reaching the plants. Some blades penetrated through the macroalgal mat while others died below the mat. Eelgrass in the third "replicate" became overgrown by epiphytic algae (Fig. 33). The epiphytic cover was composed primarily of diatoms and small macroalgal forms.

The reason for the variation in response to identical nutrient enrichment treatments is complex and as yet not completely understood. The first enrichment "replicate" became dominated by a phytoplankton community which appeared to inhibit the growth of other algae (Fig. 34). The second enriched tank initially showed a substantial increase in both epiphytic and macroalgal growth. However, the occurrence of an amphipod bloom within this treatment dramatically reduced the epiphyte population, allowing the macroalgae to dominate. The third enrichment "replicate" also began as a combination of epiphytic and macroalgal growth and had a population of amphipods develop. However, in this "replicate", the carnivorous fish that had been introduced to all tanks (primarily sticklebacks and pipefish), were able to keep the amphipod population under control. The fish prevented extensive amphipod grazing on the epiphytes. As a result, the third treatment ended up being dominated by epiphytic growth (Figs. 33-34), with the macroalgal component remaining small. This conceptual model was used and validated in our results for the following year, 1990. Judicious stocking of predatory fish (sticklebacks and pipefish) in the mesocosms controlled amphipods and resulted in a balanced plant community of eelgrass competitors in the high light, elevated nutrient treatment tanks (Fig. 35).

Thus, quite unexpectedly, eelgrass mesocosm enrichment studies have demonstrated the effectiveness of "top down control" of trophic levels for regulating macrophyte populations. Both the fish and herbivorous amphipods appeared to regulate the dominant form of primary producer within the experimental treatments. The factors determining the success of phytoplankton populations within experimental treatments of this kind are as yet unclear, and whether competition is important remains to be examined.

Interactive Effects of Reduced Light and Nutrient Loading

In 1990, 12 eelgrass community mesocosms were set up and subjected to three light (94, 41, and 11% of full surface sunlight at 1 cm depth) and two nutrient loading levels (ambient and six times ambient) in a factorial treatment arrangement that had two replicates for each treatment combination in a completely randomized design. Weekly shoot density estimates were averaged for each month (August to November) and analyzed using repeated measures ANOVA. Shoot densities were similar with respect to light and nutrients in August (Fig. 36a), and the overall mean was similar to the initial (June) planting density of $133/m^2$. Overall, shoot densities increased to a maximum in October, then began to decline. Significant month by light ($P<0.017$) and month by nutrient ($P<0.006$) interactions indicate that over time, decreased light and elevated nutrients both served to reduce eelgrass densities (Fig. 36).

PLANT DOMINANCE	CONTROL	NUTRIENTS	NUTRIENTS & AMPHIPODS	NUTRIENTS, AMPHIPODS & FISH
Eelgrass	X X X			
Plankton		X		
Macroalgae			X	
Epiphytes				X

Figure 34. Chart of the dominant factors that were likely to have controlled outcomes of the mesocosm nutrient enrichment experiment, 1989. At ambient nutrient levels (controls) eelgrass retained a strong competitive advantage. However, in each of the enriched treatment replicates, the dominant primary producer that was in competition with eelgrass was different. Domination of one alga over an other appeared to depend upon amphipod and predatory fish populations.

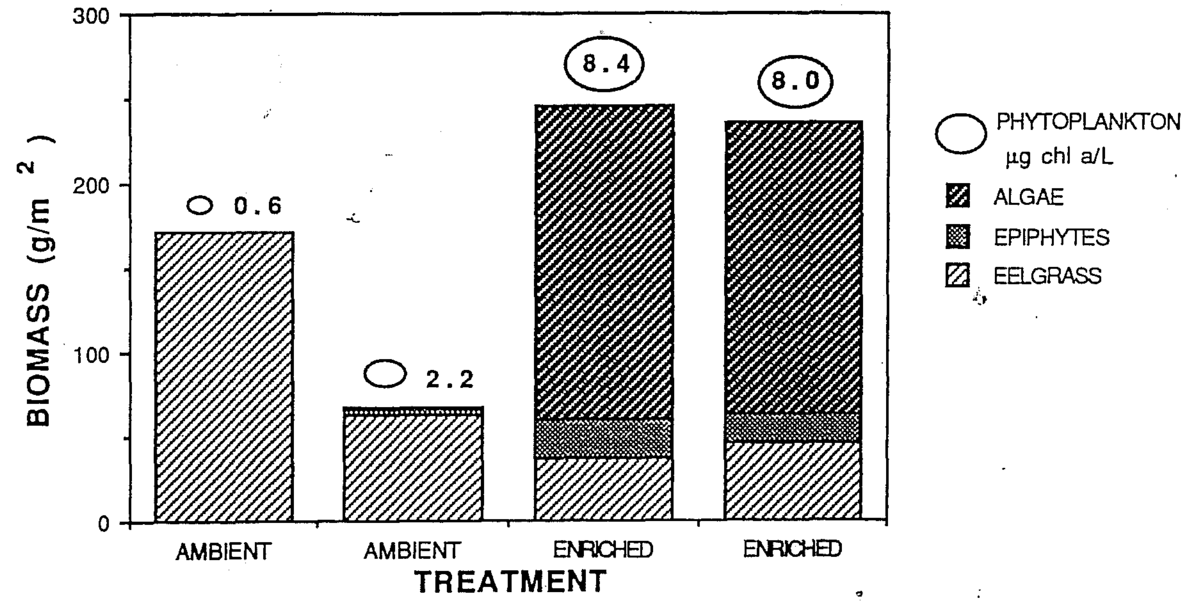


Figure 35. Community response of eelgrass mesocosms to nutrient enrichment at full sunlight, October 1990. Biomass values shown are on a dry weight basis from two replicates of each treatment. Eelgrass shoot biomass is based on the average weight of ten terminal shoots and tank densities when competitors were sampled (500 mls for phytoplankton, 10 shoots for epiphytes, and 1/16 m^2 quadrat for macroalgae).

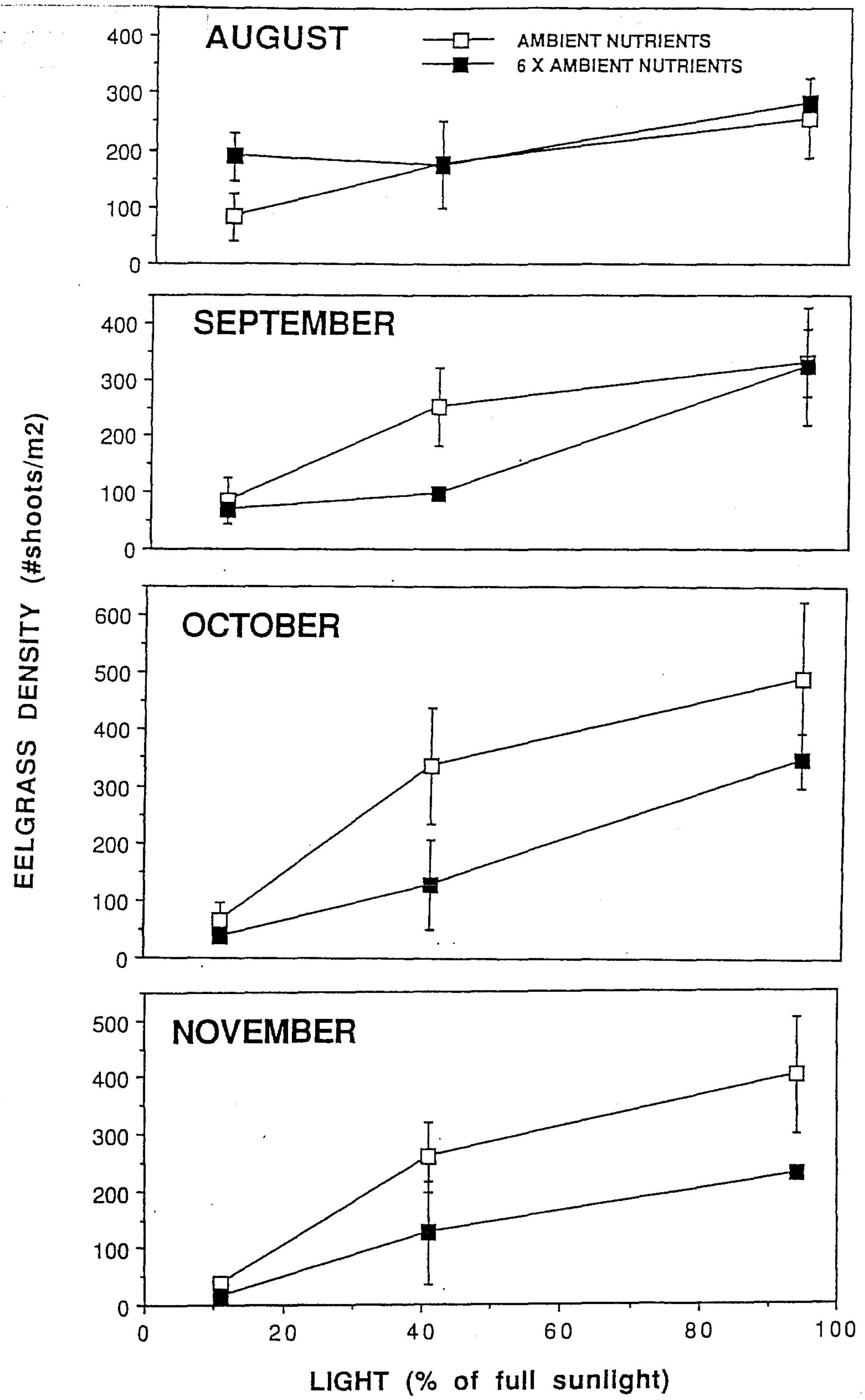


Figure 36. Monthly eelgrass shoot density in mesocosm tanks during the light by nutrient factorial experiment, 1990. Values are the means of shoot densities in three 1/20 m^2 quadrats per tank taken on each of three to five sampling dates per month for two replicate tanks (+/- standard error).

Aboveground biomass estimates for October and November were generated from shoot density estimates and shoot biomass of 10 plants harvested for the growth measurements. A final estimate was made at the close of the experiment in November when all shoots were dried and weighed. All three estimates of biomass were combined in a repeated measures ANOVA that indicated only light ($P<0.007$) and nutrient ($P<0.043$) effects were significant at the 0.05 level (Fig. 37). Nutrient loading at six fold of ambient levels reduced biomass by over 50%, and similar reductions were found for the intermediate light level of 41% (Fig. 37). At the lowest light level, biomass was reduced 27 fold compared to the highest light level. Although there still was a nutrient effect at the lowest light level, it is questionable whether eelgrass beds could sustain themselves at this light level in the field. Over all the treatment combinations, biomass declined almost 50% from October to the final estimate in November, and this seasonal decline was significant at the 0.10 level.

Growth was estimated for each tank in October and November using destructive harvesting, and the data were analyzed by blocking on month. On an areal basis, month, light, and nutrients all contributed to variation among estimates, but no interactions were present. Growth was six times greater in October than November, and decreased drastically with shading and nutrient loading (Fig. 38). Specific growth, the amount of new leaf tissue compared to the total shoot biomass, did not differ with light treatments, but declined five fold from October to November (Fig. 38). Since this measure removes the effects of shoot density and plant size from growth, it appears that the plants have adapted to grow at similar rates regardless of light intensity but have slightly elevated specific growth rates under nutrient additions. Differences in plant morphology are shown using the longest leaf length obtained during the growth measurements. Only the effect of nutrients was significant at the 0.05 level, showing smaller plants under the enriched treatment (Fig. 39). Reduction in leaf length due to nutrient enrichment also occurred in 1989 (Fig. 30c). Light reduction, which resulted in longer leaves in 1988 (Fig. 25) showed a nearly significant effect on leaf length in 1990.

Wasting disease was introduced to the 12 tanks in the fall of 1990, but the disease did not spread as it did in previous years. We have determined that the lack of disease resulted from the low natural salinity levels (<20 ppt) of Great Bay for that year. Although in laboratory culture we found that 14 ppt salinity supports rapid disease spread (Muehlstein et al. 1988), our analysis of disease progression in eelgrass mesocosms suggests that salinity greater than 24 ppt is necessary to ensure disease spread (Burdick et al. 1993).

The effects of light and nutrients on density, biomass, and growth were similar to light and nutrient effects for the previous two years of mesocosm experiments, and no light by nutrient interactions were found. The effects of reduced light and elevated nutrients both acted to reduce robustness of eelgrass populations, and one effect did not interfere with or change the other. Furthermore, it appears the primary negative effect of increased nutrients on eelgrass populations is the stimulation of phytoplankton, epiphytes, and macroalgal competitors that reduce the amount of light available to the eelgrass blades (Fig. 35).

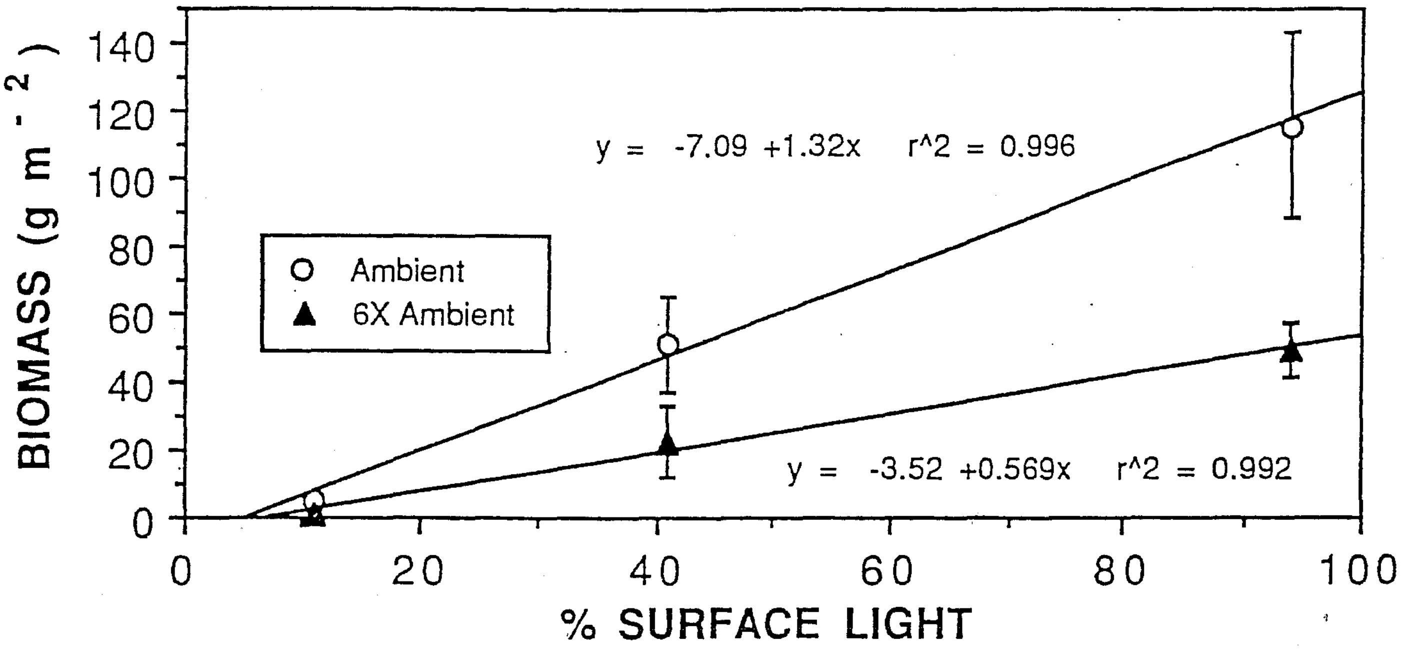


Figure 37. Average eelgrass shoot biomass on a dry weight basis from two estimates (based on average terminal shoot biomass and shoot density) and a biomass determination at the close of the light by nutrient factorial experiment, 1990. Values are means +/- standard error of two replicate tanks.

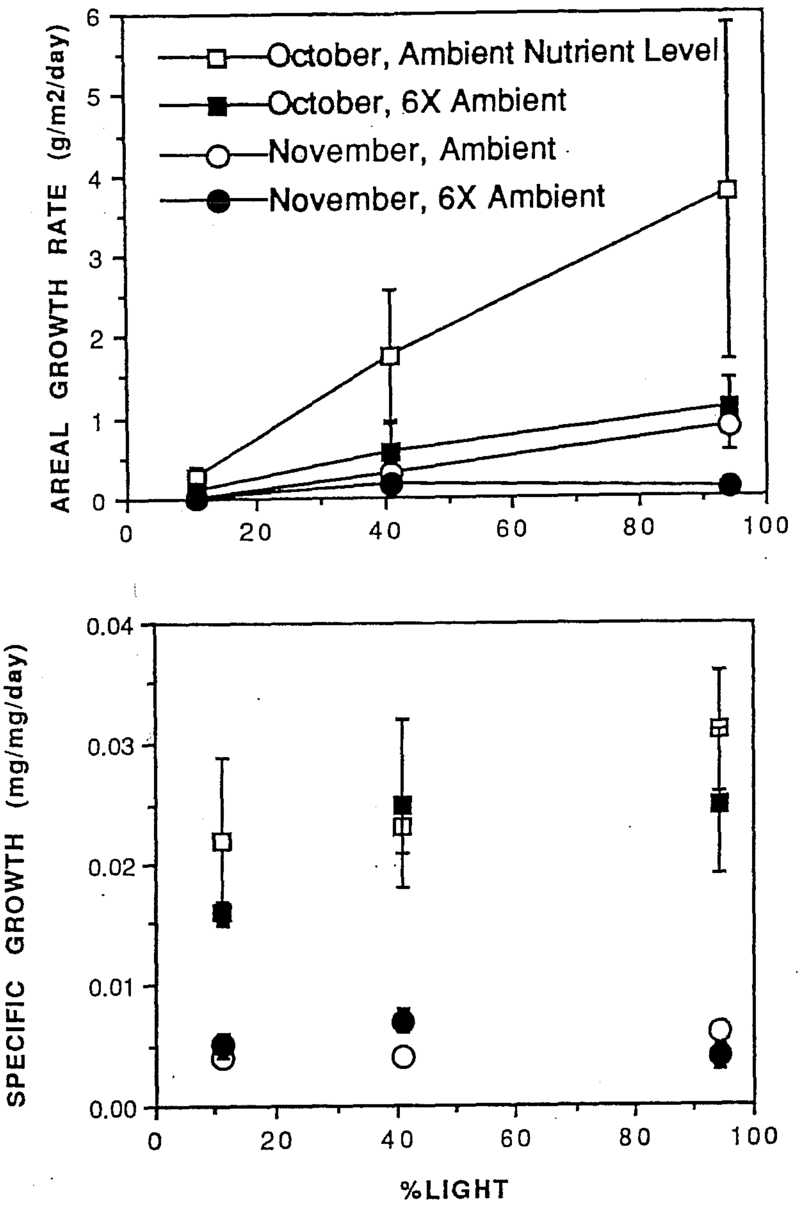


Figure 38. Eelgrass growth rates measured in October and November on an areal basis and specific growth basis for the light by nutrient factorial experiment, 1990. Values are means +/- standard error of two replicate tanks.

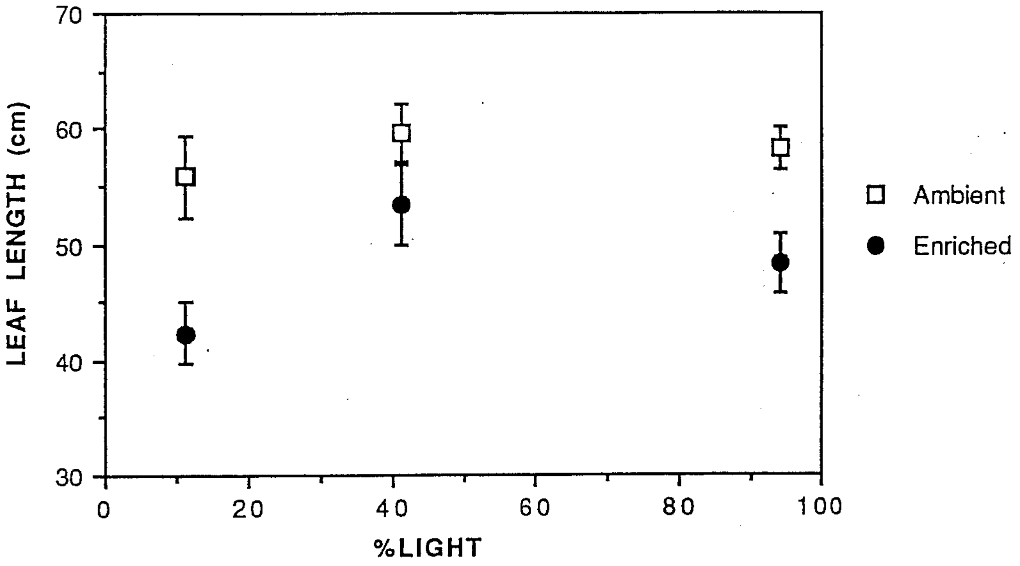


Figure 39. Longest leaf length of eelgrass in the light by nutrient factorial experiment. Values are the means of replicate tanks (ten shoots per tank) +/- standard error.

CONCLUSIONS

Within the mesocosms, the effects of our nutrient enrichments were an overall reduction in eelgrass health and biomass and a conversion to algal-dominated communities. Examples of these same types of community changes have been documented over the last five years in estuaries along the New England coast and include the decline and loss of eelgrass in Waquoit Bay, as a result of eutrophication. Within the Waquoit Bay System, epiphytic algal populations became dominant in Eel Pond, macroalgal blooms covered eelgrass beds in Hamblins Pond, and phytoplankton populations have eliminated eelgrass in parts of Great River and Jehu Pond. Similar evidence of eelgrass loss has been documented in New Hampshire, Rhode Island, Connecticut, and elsewhere in Massachusetts.

It is clear that eutrophication of coastal waters contributes to the demise of eelgrass populations. Eelgrass populations are also declining from other factors including wasting disease, mechanical disruption, and increased construction within estuarine areas. However, eutrophication is the major threat to the long term survival of eelgrass in coastal New England and elsewhere in the world.

Disease appears to be important in Great Bay, causing the loss of complete beds in the lower portions of Great Bay Estuary. Since 1981, disease has eliminated 15 of 17 beds in the Piscataqua River and Little Bay (about 99% of the original area has been lost), while two new beds have appeared (1991). In North Carolina, this study found only moderate disease levels (1987-1989), but in 1990 eelgrass die-offs were attributed to disease. Disease is present at high levels in Narragansett Bay and thins the beds, thereby reducing production. Although catastrophic decline from the disease has not been observed in Narragansett Bay, we believe it could be susceptible to such outbreaks. Since there are only two beds remaining off Prudence Island and both are subject to high salinities over long periods, a mass mortality event caused by disease could eliminate eelgrass from this Reserve. Waquoit Bay, with many scattered eelgrass beds separated by uplands, usually exhibits low infection by disease, even in the lower estuary, but pollution threatens upper estuarine eelgrass populations.

Decreased light appears to favor the spread of the disease in dense beds (Seal Rock, Great Bay, NH). At this point we have no evidence that decreased light and elevated nutrients interact to magnify or intensify the spread and destructiveness of the disease in estuaries. It appears the stress brought on by reduced light alone, whether it is from increased turbidity, phytoplankton, epiphytes, or drift seaweed, is sufficient to weaken the population and increase the susceptibility of the plants to lethal infection by *Labyrinthula.*

Our extensive work in the field and with mesocosms allows us to make some generalizations regarding the effects of pollution and disease on eelgrass decline and the resultant patterns of eelgrass distribution in the National Estuarine Research Reserves that we have examined. The change in eelgrass distribution over the last decades is generally one of decline. We hypothesize that reductions in eelgrass beds in upper estuaries are mainly due to pollution, specifically loss of water clarity and nutrient-induced competition with algae associated with the process of eutrophication. In the lower, more saline portions of estuaries, disease can be an important determinant of distribution patterns. The widespread decline of eelgrass habitats in upper estuaries is of great concern because disease can eliminate eelgrass beds in lower estuaries. A wasting disease epidemic could leave many estuarine systems without the seed source necessary for natural recolonization.

Future work should employ modelling to answer these questions: Considering flushing rates and estuarine hydrography, how much nutrient loading into each of the four Estuarine Reserves with eelgrass populations can occur before this pollution effect becomes significant? Which eelgrass beds in each Reserve would be significant seed sources if another wasting disease epidemic occurred? Estuarine managers would be directed to concentrate on preservation of these beds, so that seed sources would be available following wasting disease outbreaks. If management can control eutrophication to the point where these upper estuary beds maintain themselves, it is reasonable to assume that eelgrass beds in the lower estuary, where nutrient levels are generally lower, but salinities are higher, will flourish and be reseeded naturally if another disease epidemic occurs.

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