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Dissertation

DISTRIBUTION, PRODUCTION, AND HISTORICAL CHANGES IN ABUNDANCE OF

EELGRASS (*ZOSTERA MARINA* L.) IN SOUTHEASTERN MASSACHUSETTS

by

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Acknowledgements

EELGRASS (*ZOSTERA MARINA* L.) IN BUZZARDS BAY:

DISTRIBUTION, PRODUCTION, AND HISTORICAL CHANGES IN ABUNDANCE

(Order No.   )

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Abstract

The past and present-day distribution of eelgrass (*Zostera marina* L.) was documented using aerial photographs, field surveys, nautical charts, sediment cores, and first-hand accounts. Eelgrass growth correlates with local temperature and insolation, and annual production is ≈ 350 g C m^{-2} yr^{-1}. In Buzzards Bay, eelgrass beds cover 41 km^2 of substrate and account for 12% of primary production; in shallow bays, eelgrass equals 40% of production.

Prior to the "wasting disease" of 1931-32, eelgrass populations equaled or exceeded present-day abundance. Six to 10 years after the disease, eelgrass covered less than 10% of the present-day habitat area. The process of recolonization was similar in many areas: new beds initially appeared on bare substrates, beds expanded, new beds appeared, and some beds were removed by disturbance. A computer simulation modeled these events, and showed that rapid recolonization of eelgrass

populations is highly dependant on new bed recruitment, which in nature depends on seed dispersal. High disturbance rates slow eelgrass recolonization and lower peak cover.

Local changes in eelgrass abundance are driven by anthropogenic and natural disturbances which are superimposed on the regional pattern of catastrophic decline and gradual recovery. Hurricanes, ice scour, and freezing periodically destroyed eelgrass beds in some areas. Eelgrass populations in poorly flushed, developed bays, with declining water quality, never recovered from the wasting disease or showed new declines in recent years.

The distribution of eelgrass is light limited, and eelgrass beds may disappear in enriched areas because of increases in algal epiphytes and phytoplankton. To identify what levels of nutrient loading cause these changes, concentrations and inputs of dissolved inorganic nitrogen (DIN) in Buttermilk Bay were measured. Periphyton on eelgrass leaves and plastic screen strips on floats correlated well to mean DIN. Experimental floats released nutrients and demonstrated that small increases in DIN significantly increase periphyton abundance. The depth of eelgrass growth in Buttermilk Bay decreased by 9 cm for every 1 µM increase in DIN. Periphyton abundance is more important than phytoplankton concentrations in limiting eelgrass growth in Buttermilk Bay, because water in this bay has a short residence time, and phytoplankton gradients are less prominent.

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Overview

Introduction

Eelgrass (*Zostera marina* L.) is a subtidal marine angiosperm common in temperate waters in the Northern Hemisphere. It is one of more than 60 species of seagrasses that grow in the worlds oceans. In Buzzards Bay and Cape Cod, eelgrass beds are abundant, often forming extensive underwater meadows. The areal cover of eelgrass habitat is twice that of salt marshes in this region, but because these beds are subtidal, they are unnoticed, except by boaters, shellfisherman and divers.

Eelgrass beds are often inconspicuous from the surface, but they are productive and valuable resources. Eelgrass beds are ecologically important in coastal waters because they serve as nurseries, refuge, and feeding grounds for fish, waterfowl and invertebrates. Eelgrass meadows also bind, stabilize, and change the chemistry of sediments.

In Chapter 1, I describe in detail the present day distribution of eelgrass in Buzzards Bay, and in Chapter 2, I estimate the contribution of eelgrass growth to productivity in Buzzards Bay.

The wasting disease of 1931-32 destroyed virtually all eelgrass in the region, and most areas did not recover for many decades. In Chapter 3, I document this and other declines due to disease by analyzing eelgrass seed deposition in sediment cores. I also reanalyze the causes of the disease and the slow recolonization process in Chapter 4.

Superimposed on the collapse of eelgrass populations during this century are local patterns of decline and recolonization driven by both natural and anthropogenic disturbances, including storms, ice scour and freezing, and pollution. In Chapter 4, I also document 12 "case histories" of changing eelgrass abundance that involve these processes.

Because eelgrass beds are ecologically important, and are increasingly affected by anthropogenic perturbations, there is interest in resource management initiatives to protect these communities. In addition, the widespread distribution of eelgrass and its sensitivity to pollution make it a potential indicator species for changes in water quality. I address both these management concerns in Chapter 5.

There are some excellent reviews of eelgrass biology and ecology available (e.g. Thayer et al., 1984) and certain topics are covered in detail elsewhere in this report, therefore I will outline only the more salient features of eelgrass biology below.

General biology and ecology of eelgrass.

Eelgrass is a vascular plant composed of 3-7 strap-like leaves, bound together in a sheath attached to an underground rhizome (Fig. 1). In this region, the leaves are less than 1 cm wide, and range 20 - 160 cm long. The leaves are adapted to the marine environment in several ways. The leaf cuticle is thin and multiperforate and allows the uptake of nitrogen, phosphorus, and inorganic carbon through the leaf surface (McRoy and Barsdate, 1970; Penhale and Thayer, 1980; Thursby and Harlin, 1982). Air compartments (lacunae) extend throughout the leaves and keep them buoyed in the water. Most chloroplasts are located in epidermal

Figure 1. General morphology of *Zostera marina*.

Eelgrass leaves are bound together in a sheath attached to an underground rhizome with clusters of roots on each rhizome node. Lateral vegetative or reproductive shoots may originate from within the sheath of the main shoot. The inflorescence on the lateral reproductive shoot contains both male and female flowers. Reproductive shoots may also originate from new seedlings or the main vegetative shoot may develop into a flowering shoot.

Flower primordia

Algal epiphytes

Unfertilized flower

Main shoot

Inflorescence with mature seeds

Ligule

Sheath

Lateral flowering shoot

10 cm

Rhizome

Lateral shoot

Root cluster on rhizome node
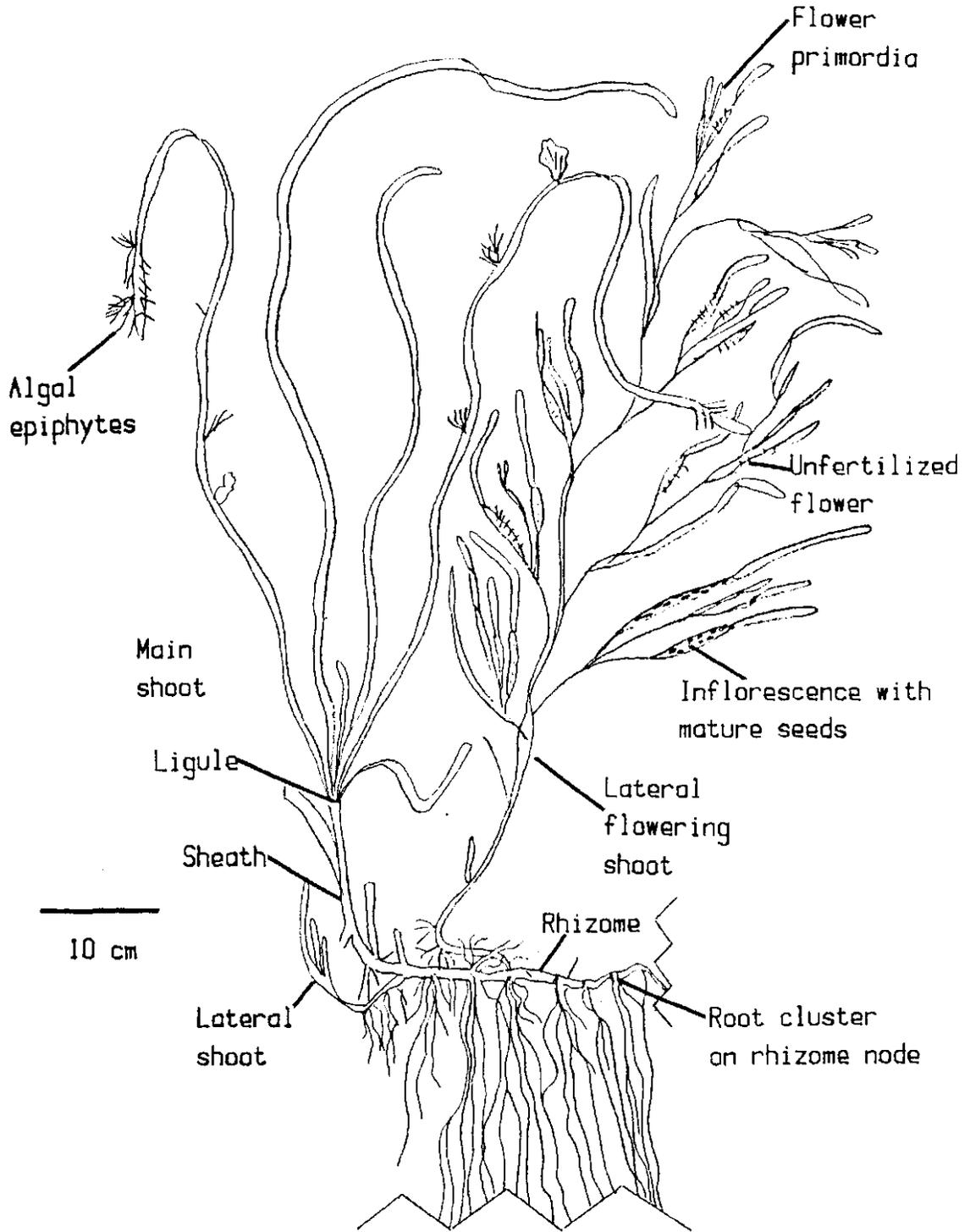
cells of eelgrass, for efficient light absorption (Tomlinson, 1980; Dennison and Alberte, 1982).

A basal meristem, enclosed within the leaf sheath, produces new leaves, rhizome segments, and lateral shoots. Clusters of roots on each rhizome node, penetrate the sediment 30 cm or more. The roots function both in anchoring the plant and are the primary site of N and P uptake (Penhale and Thayer, 1980). As eelgrass grows, the base of the shoot pushes through the sediment.

Eelgrass is found in diverse habitats in temperate waters. Locally, the upper limit of growth is set by physical factors such as wave action, ice scour, and desiccation. The lower limit of eelgrass growth is set by the period of light intensity above photosynthetic saturation and compensation (Dennison and Alberte, 1985, 1986; Dennison, 1987). Thus in turbid bays without appreciable wave energy, eelgrass ranges from low intertidal to 2.0 m MLW or less; in wave-swept coasts with clear water, eelgrass begins at 1-2 m MLW and may grow as deep as 12-45 m (Sand-Jensen and Borum, 1983; Lee and Olsen, 1985, Cottam and Munroe, 1954). Mean secchi disk depth is a good predictor of maximum depth of eelgrass growth (Dennison, 1987).

All stages of the eelgrass life cycle occur underwater, including flowering, pollination, and seed germination (Ackerman, 1983; den Hartog, 1977, Taylor, 1957a+b). There is latitudinal variation in phenology, and in New England, peak flowering occurs in April and May (Silberhorn et al., 1983), but there is often variation among habitats.

Eelgrass is a perennial, and grows during winter, but plants in shallow water (<1 m MLW) are functional annuals because they are killed

by ice scouring, freezing, or other stresses (Phillips et al. 1983; Robertson and Mann, 1984). Plants exposed to these conditions typically have a high incidence of flowering. There have been reports of genetically determined annual populations (Keddy and Patriquin, 1978; Keddy, 1987), but evidence for this hypothesis is not conclusive (Gagnon et al., 1980; Phillips et al., 1983).

Eelgrass grows in diverse habitats ranging from anoxic muds in poorly flushed areas to sand and gravel bottoms with current velocities up to 1.2-1.5 m s^{-1} (2.3-2.9 kt; Fonseca et. al. 1982a, 1983; Pregnall et al., 1984). The morphology of eelgrass shows considerable plasticity in growth in response to physical energy of the environment and nutrient content of sediments (Kenworthy and Fonseca, 1977; Phillips et al, 1983; Short, 1983; Thayer et al., 1984). For example, plants growing in shallow, wave-swept bottoms tend to have short narrow leaves, grow in high densities (>1000 shoots m^{-2}), and produce dense root and rhizome clusters; whereas plants growing in deeper water have longer broader leaves, grow in lower densities (<200 m^{-2}), and produce less root and rhizome material.

Eelgrass beds are maintained and expand by vegetative lateral shoots and by recruitment of new seedlings. Because most shoots in a bed may be derived from vegetative growth of a few plants, it is often stated that eelgrass beds are large clonal populations. Bare areas not adjacent to existing eelgrass beds are colonized almost completely by new seedlings because uprooted plants float and tend to be cast ashore or washed out to sea.

Eelgrass aboveground production typically ranges 200-500 g C m^{-2} y^{-1} (Jacobs, 1979; Kentula and McIntire, 1986; Robertson and Mann, 1984; Thayer et. al, 1984; McRoy and McMillan, 1977) and may locally exceed production by phytoplankton and macroalgae in shallow bays (Sand-Jensen and Borum, 1983). Epiphytic algae often contribute sizably to the productivity of these communities (Penhale, 1977; Penhale and Smith, 1977; Mazella and Alberte, 1986). Most eelgrass production enters a detritus based food web (Harrison and Mann, 1975; Kenworthy and Thayer, 1984; Mann, 1972; Thayer et al., 1975), but direct consumption by herbivores such as waterfowl and isopod crustaceans may be locally significant (Nienhuis and Van Ireland, 1978; Nienhuis and Groenendijk, 1986).

Carbon fixation is just one role of eelgrass beds in coastal waters. Eelgrass meadows act as a nursery, feeding ground, and refuge for numerous animals (Adams, 1976; Heck and Orth, 1980a+b; Kickuchi, 1980; Lewis, 1931; Thayer and Stuart, 1974; Thayer et al., 1984;). When eelgrass colonizes an area, it changes the physical, chemical, and biotic properties of sediments (Kenworthy et al., 1982; Marshall and Lukas, 1970). As eelgrass biomass increases, so does organic matter, fine sediment fractions, and infaunal invertebrate diversity (Orth, 1973, 1977).

Eelgrass beds, like other seagrasses, bind, baffle, and stabilize sediments and may also influence coastal erosion (Burrell and Schubel, 1977; Churchill et al., 1978; Fonseca et al., 1982a, 1983; Fonseca and Kenworthy, 1987; Schubel, 1973). Eelgrass leaves reduce shear stress of water motion on sediments because current velocity at the top of an

eelgrass canopy may exceed 1 m s^{-1}, whereas velocity at the base of the shoots is nil (Thayer et al., 1984; Fonseca et al., 1982a). When the wasting disease destroyed eelgrass beds in the 1930's, the physical characteristics of adjacent beaches often changed appreciably (Rasmussen, 1977).

Anthropogenic and natural disturbances play a significant role in regulating the abundance and distribution of eelgrass and other seagrasses. Certainly the most profound natural disturbance affecting eelgrass abundance during this century was the wasting disease of 1931-33 that eliminated at least 90% of the eelgrass in the North Atlantic, including Massachusetts (Cottam, 1933, 1934; den Hartog, 1987; Rasmussen, 1977). Many areas were not recolonized for decades, and in some locales, eelgrass is still expanding today (den Hartog, 1987). There is evidence that eelgrass populations periodically collapse (Cottam, 1934), and recent outbreaks of the wasting disease have been reported (Short et al., 1986). Other natural disturbances remove eelgrass including catastrophic storms, periodic storms, sediment transport, ice damage, and biological removal (Harlin et al., 1982; Jacobs et al., 1981; Nienhuis and van Ireland, 1978; Orth, 1975; Robertson and Mann, 1984).

Anthropogenic disturbances include physical removal, toxic pollution, and degradation of water quality (Borum, 1985; Cambridge, 1979; Cambridge and McComb, 1984; Fonseca et al., 1985; Kemp et. al., 1983; Larkum and West, 1982; Nienhuis, 1983; Orth and Moore, 1983b; Thayer, et al., 1975). While any of these human perturbations may be locally important, declining water quality has often resulted in the

largest areal losses of eelgrass and other seagrasses (Cambridge, 1979;
Cambridge and McComb, 1984; Lee and Olsen, 1985; Orth and Moore, 1983b;
Nienhuis, 1983).

Chapter 1

The distribution of eelgrass (*Zostera marina* L.) in Buzzards Bay

Introduction

Coastal regulators and biologists need accurate inventories of seagrass distribution to understand the biological role of these communities and to manage them. In Buzzards Bay, eelgrass (*Zostera marina* L.) is a major component of shallow waters, and an important habitat and nursery for many species, but knowledge of eelgrass distribution has been lacking. This report is intended to fill this void.

Elsewhere, seagrass distribution has been mapped over large geographic areas using aerial photographs together with field verification (Orth and Moore, 1983a). Under favorable conditions, such as good water clarity, low winds, and low tides, eelgrass beds can be seen easily on vertical aerial photographs. As with any remote sensing methods, photographs must be interpreted carefully; for example, annual beds in very shallow waters may be absent between December and early March. Nonetheless, photographs can provide a reliable and accurate record of eelgrass abundance, especially when several recent surveys are available for comparison.

Methods

Eelgrass was mapped in Buzzards Bay using vertical aerial photographs and field validation. The region was subdivided into 12 subareas (Fig. 1), each of which are mapped and described in detail (Appendix II). The Elizabeth Islands were not mapped, but eelgrass abundance there was estimated from substrate area on maps (Appendix II).

Figure 1. Map of Southeastern Massachusetts.

The location of the 12 subareas individually mapped and described
in Appendix II.
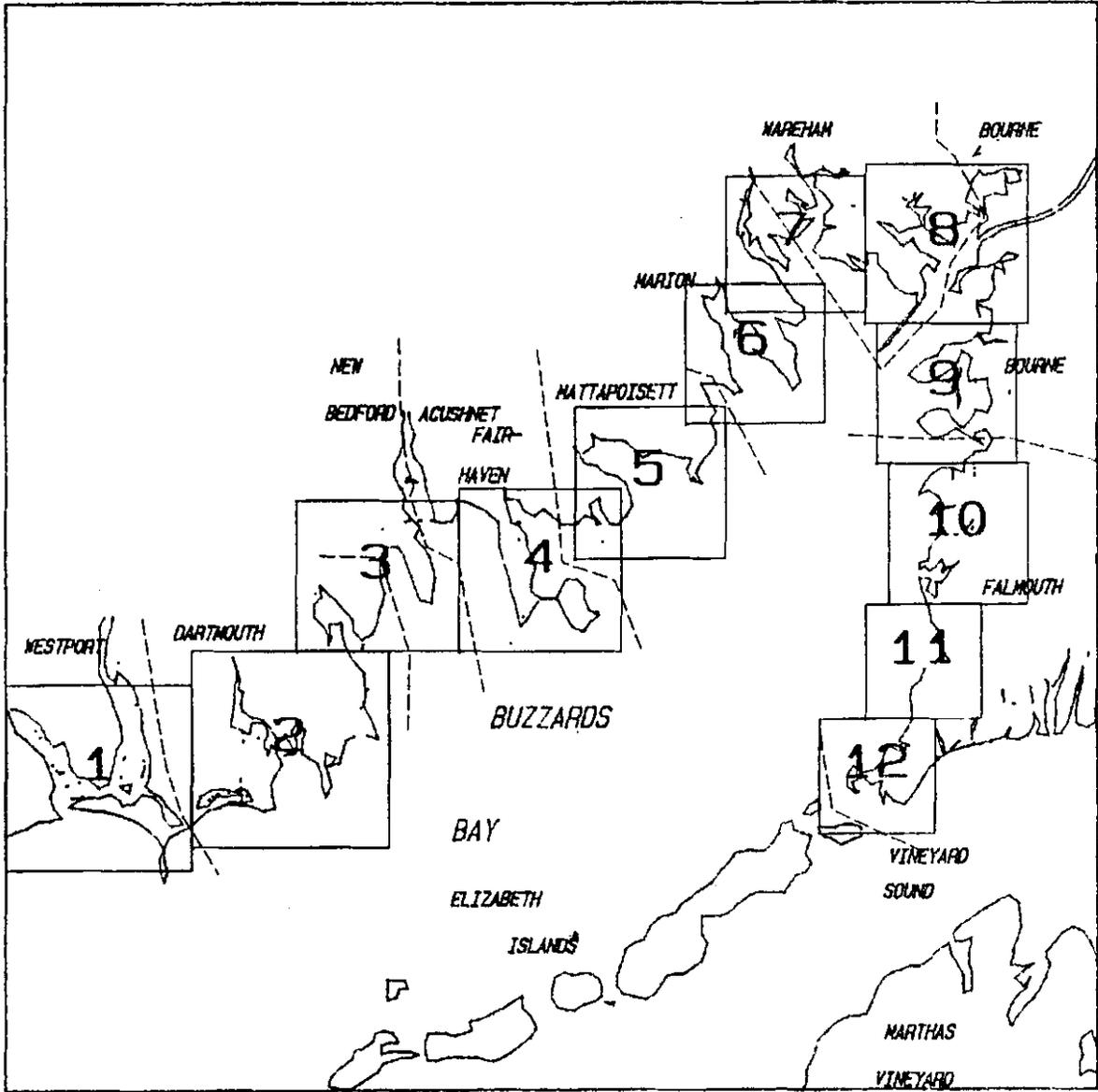
MAP COORDINATES = 323 370 585 632

Photograph interpretation

The maps of the present-day distribution of eelgrass were based on existing black and white or color vertical aerial photographs taken by private and governmental agencies (Appendix I). Most of the photographs used were taken between Spring and Fall, during 1974 - 1981. Maps of eelgrass based on photographs taken during the 1970's are often representative of present-day eelgrass distribution because eelgrass had saturated available habitat in most areas by that time (refer to chapter 4). Because older photographs may lead to underestimates of new eelgrass losses or other recent changes, the dates of aerial surveys used to make each map are listed in Appendix II.

Field verification of photographs was accomplished either by skin- or SCUBA diving, or surface observations from boats in 1984-1986. In some embayments, interpretation of photographs was aided by information from shellfish wardens, other researchers, or local residents.

Older photographs and winter surveys were used to interpret recent photographs. For example, a submerged feature unchanging in area over several decades is either a rock field or peat reef, whereas a patch of dense vegetation that shows gradual expansion is eelgrass because only eelgrass beds change in this way. Submerged features in basins that show radical movement within one or two growing seasons are probably drift material. Vegetation present only on summer imagery is likely to be an annual eelgrass bed.

The lower boundaries of eelgrass beds could not be identified in some instances on any photographs and were estimated from bathymetry and

typical depth of eelgrass growth for that area. These beds are listed in the results.

Eelgrass beds are rarely continuous patches of vegetation; instead there are bare areas within these beds of varying size. Some of these bare areas are apparent on photographs to the unaided eye, some become apparent when a photograph image is magnified, others are below the limit of resolution of a photograph and can only be measured in the field or on small scale aerial surveys. Alternatively, eelgrass may occur as numerous discrete patches too small and numerous to digitize. In all these cases, a perimeter was drawn around eelgrass beds or clusters of eelgrass beds on photographs, and the percent cover of this outlined "bed" --as viewed on a photograph with the unaided eye-- was estimated using a percent cover scale chart (Fig. 2, c.f. Orth and Moore, 1983a).

The accuracy of visually estimating percent cover was tested by placing a photograph under a dissecting scope with cross-hairs, and randomly moving the photograph between 50 and 100 times. The actual percent cover was calculated by dividing the number of times the cross-hair landed on eelgrass by the total number of observations. In general, visual estimates of large scale percent cover were accurate within 15% of this random count method.

Mapping techniques

To map eelgrass beds, aerial prints were overlaid with a sheet of acetate, eelgrass beds were outlined, and other notes were recorded. The photographs and overlays were subsequently photographed with B&W

Figure 2. Percent cover scale.

This scale was used to visually estimate eelgrass cover of eelgrass beds outlined on photographs. The two 20% cover boxes showing different degree of clumping illustrate how patchiness may vary with the same degree of cover.

PERCENT COVER SCALE

10 %
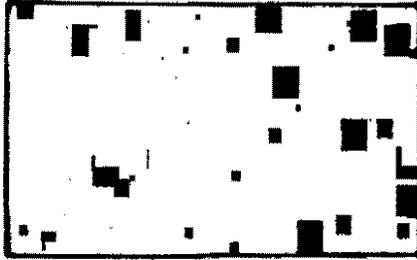
60 %

20 %

70 %

20 % (less clumped)
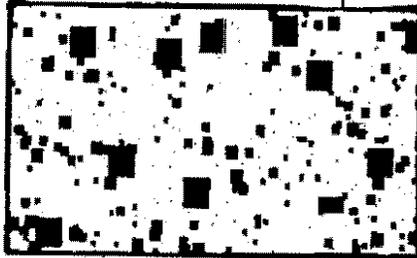
80 %

45 %

90 %
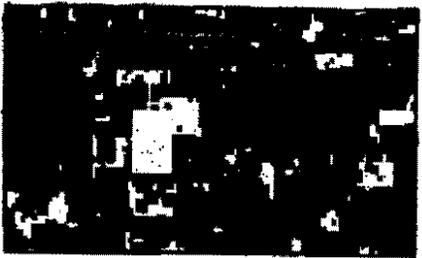
slide film, and this image was projected onto a map of 1:25,000 scale or smaller. The eelgrass beds were then redrawn by hand and distortions in the image were compensated for by eye or manipulating the image on a film enlarger. These bed outlines were re-traced using a digitizing pad connected to a microcomputer. Digitizing and mapping programs for a microcomputer were used for data storage, area analysis, and plotting at different scales.

The maps produced here have ≈25 m resolution. The process of projection, tracing, and digitizing, however, introduced random errors in bed position. These errors were small, and the position of eelgrass beds on the maps in this report were generally accurate within 40 m for beds adjacent to the shore, 60 m for beds within 0.5 km of shore, and within 80 m for eelgrass beds more than 0.5 km from any shoreline when compared to bed positions measured directly from the source photographs.

Each subarea is shown with political boundaries and site names and again with eelgrass beds drawn. In the latter, eelgrass beds are drawn with dashed lines and coastlines as solid lines. Bed areas were computed from the stored coordinates and reported as hectares [1 ha = 2.47 acres].

Not all areas were mapped because of inadequate aerial coverage. Areas where eelgrass is present, but its exact boundaries are unclear, are labeled "+". Areas where eelgrass is present, but has a patchy distribution covering less than 5% of the bottom over large areas, are labeled "SP". Areas where vegetation is present, but its identity is unclear, are labeled "?". These and other symbols used on the maps are

summarized in Table 1. All maps are oriented with true north at the top.

Results

General features

The central portion of Buzzards Bay is too deep for eelgrass growth, however eelgrass meadows typically dominate shallow areas (refer to Appendix II for a detailed description of eelgrass in the Bay). On high energy coasts and well flushed areas, eelgrass typically grows on sand or sandy-mud to 3-6 m MLW; in protected embayments, eelgrass most often grows on mud bottoms to 1-2 m. In fact, eelgrass beds are a dominant feature in nearly all shallow areas in the region--often forming a continuous belt of vegetation for thousands of meters--except around New Bedford, and the heads of certain bays and estuaries (e.g. Apponagansett Bay, East Branch of the Westport River, the upper Wareham River, and coastal ponds in Falmouth).

Several features are apparent on aerial photographs that deserve discussion because they affect estimates of eelgrass cover. On the outer coast, eelgrass beds appear as dark patches on a light background (sand). In some exposed areas, algae covered rock and cobble dominate the bottom, as well. Algal diversity is high in this region, but *Fucus* and *Ascophyllum* are most common in the intertidal, and *Chondrus*, *Ceramium*, *Codium* and *Sargassum* in the subtidal. In addition, kelps are abundant in some deep, rocky areas with clear water, such as around the Elizabeth Islands and off Westport and Dartmouth. Most of these algae-

Table 1. Key to the symbols used on the maps.

On all maps in this report, the north-south meridian is parallel to the sides of the maps, and true north is at the top.

       Coastline (solid line)

       Eelgrass bed (dashed lines or darkened area)

+   Eelgrass present, bed dimensions unclear

±   Eelgrass distribution variable on recent photographs

?   Submerged vegetation, possibly eelgrass

PA   Patches of eelgrass present

NA   Photograph coverage not available for area

NI   Area not included in survey

AA   Attached algae, usually on rock or cobble

DA   Drift algae may be present on some photographs

B   Location of shoot counts or biomass harvesting

PE   Salt marsh peat reef offshore

BOPH5 Eelgrass bed ID #. The first two letters indicate town, the second two indicate local, then the number of the bed. In this case bed 5 in Phinneys Harbor in the town of Bourne. The town letters are omitted on the maps, but are included in Appendix III.

covered rock and cobble fields can be distinguished from eelgrass beds by their characteristic "texture".

In protected areas with mud bottoms, contrast between eelgrass and its background is reduced, but eelgrass can usually be discerned as a dark patch on a slightly lighter bottom. In some bays, benthic drift algae form large mats which can be mistaken for eelgrass beds, but eelgrass growing in these areas appear as slightly lighter patches on a dark background.

In moderate energy environments, with shell and gravel bottoms, the green alga *Codium* may be abundant within eelgrass beds. *Codium* can also dominate the bottom below depths of eelgrass growth, making it difficult to estimate eelgrass bed dimensions and percent cover of eelgrass in some areas. Even though *Codium* is common, it rarely covers the bottom in as large an area, or as densely as eelgrass beds.

Salt marsh peat reefs, remnants of salt marshes covered by migrating barrier beaches then re-exposed after sea-level rises, are common in some areas, usually near existing marshes. These reefs have a similar appearance to eelgrass beds, but usually can be identified on photographs, because, unlike eelgrass beds, they frequently appear in the surf zone.

Questionable areas that were not field validated are identified in Appendix II.

Region wide summary

Eelgrass coverage was broken down by town, including the estimate for the Elizabeth Islands (Table 2). On the mainland portion of the

Table 2. Eelgrass cover by town around Buzzards Bay.

All areas in ha, including eelgrass habitat area, area corrected for

percent cover, and additional estimated area in unmapped regions,

including the Elizabeth Islands.

Town	Total habitat area	Eelgrass beds (adj % cov.)	Additional bed area (est.)	Total (adj % cov.)
Bourne	656	447	30	477
Dartmouth	>107	74	30	104
Fairhaven	450	346	-	346
Falmouth (Bay shore)	559	397	-	397
Marion	331	189	-	189
Mattapoisett	446	317	-	317
New Bedford	0.7	0.2	-	0.2
Wareham	918	564	-	564
Westport	>180	125	140	265
Elizabeth Islands (est)	540	270	-	270
TOTALS:	4188	2729	200	2929

bay, there are 3600 hectares of eelgrass habitat. An additional 540 ha were added for production measurements as to account for eelgrass along the Elizabeth Islands (Appendix II). When these bed areas are corrected for percent cover, they amount to a total of 2670 ha of eelgrass bed cover in Buzzards Bay.

Several comparisons can be made between eelgrass habitat area and other substrate types. For example, in Buzzards Bay, eelgrass beds cover twice the area salt marshes (Table 3). To a large degree, the amount of eelgrass within a towns boundary depends on the area of suitable substrate. Bathymetric contours are drawn on nautical charts at 1.8, 3.6, and 5.4 m (6, 12, and 18 ft). Most (but not all), eelgrass grows in less than 3.6 m of water in Buzzards Bay, therefor this is the most meaningful reference contour.

The ratio of eelgrass habitat area to substrate area less than 3.6 m varies markedly in each town (Table 3), and this pattern of distribution can be explained by differences in hydrography, water quality, and disturbance levels in each part of the Bay. Three towns (New Bedford, Dartmouth, Westport) have substrate-eelgrass area ratios higher than other towns in Buzzards Bay which range 1.5-2.5. These higher ratios (e.g. 350 for New Bedford) can be explained in part by the loss of eelgrass bed area that I report in Chapter 4. If the substrate-eelgrass habitat area throughout Buzzards Bay equaled the mean ratio for the less polluted towns (2.1), then there would be 10% more eelgrass along the mainland portion of Buzzards Bay. This suggests that chronic pollution in Buzzards Bay has already eliminated 10% of potential eelgrass habitat.

Table 3. Eelgrass habitat area in Buzzards Bay compared to salt marsh area, and substrate less than 3.6 m MLW.

Eelgrass habitat areas in Dartmouth, Westport, and Bourne were adjusted for missing coverage. Salt marsh areas from (Hankin et al., 1985). The Elizabeth Islands are not included in totals. The mean substrate-eelgrass habitat area ratio was 2.1 (excluding New Bedford, Dartmouth, and Westport).

Town	Eelgrass habitat area	Substrate < 3.6 m area	Substrate -eelgrass ratio	Salt marsh area
Bourne	700	1130	1.6	121
Dartmouth	151	823	5.5	463
Fairhaven	450	1190	2.6	246
Falmouth (Bay side)	559	1397	2.5	106
Marion	331	870	2.6	124
Mattapoisett	446	630	1.4	142
New Bedford	0.7	240	343	0
Wareham	914	1480	1.6	364
Westport	389	1420	3.7	427
TOTALS:	3940	9180		1993

Discussion

In Buzzards Bay today there are ≈4500 hectares of benthic habitat where eelgrass is a conspicuous biological component. When corrections are made for percent cover of this habitat as apparent on aerial photographs, as well as adjustments for unmapped area, there are approximately 2900 hectares of eelgrass bed cover.

In one sense, this is an underestimate, because this total does not take into account the eelgrass indicated with a "+" on the maps or other questionable areas. On the other hand, the eelgrass bed dimensions reported here were largely based on photographs between 1974 and 1981, and documentation in Chapter 4 suggests that eelgrass cover has declined in some areas and expanded in others in recent years. Nonetheless, given these errors and omissions, as well as including mistakenly identified submerged vegetation, this estimate of total eelgrass cover for Buzzards Bay is probably accurate within 300 hectares.

For mapping and data management purposes, this eelgrass coverage was subdivided approximately 400 "beds" as listed in Appendix III. Because eelgrass may grow continuously along several kilometers of shore with different levels of density, and sometimes span several photographs, the borders of the beds that I have drawn often reflect the scale of the imagery, extent of photograph coverage, and idiosyncrasies of the mapping process. Thus, it is not meaningful to say that town A has more eelgrass beds than town B; instead it is more appropriate to discuss the total eelgrass bed area in each town.

Less than one third of the eelgrass in Buzzards Bay occurs in shallow, protected bays and estuaries with restricted water flows; the remainder occurs in higher energy, better flushed offshore waters. Because water transparency is not good in shallow, poorly flushed embayments, particularly where there is considerable human development, eelgrass grows only to 0.6 - 1.8 m. In cleaner, offshore, well flushed waters, eelgrass grows to 3.0 to greater than 6.0 m (Fig. 3). This distinction is relevant because each of these areas are host to different communities of animals.

In shallow, quiescent lagoons, eelgrass grows as high as the low water mark, and annual plants may even occur on intertidal flats. Plants in shallow areas are available to, and important food sources for waterfowl, particularly Canada geese. These beds are also important habitats and nursery grounds for estuarine fish and invertebrates. In contrast, eelgrass growing along exposed beaches may begin 1.0 m MLW or deeper because of wave action, and leaves are generally not available to waterfowl. Furthermore, while there is considerable overlap of invertebrate species, larger fish such as striped bass, bluefish, tautog, flounder, and cownosed rays forage much more frequently in offshore eelgrass beds than beds in shallow embayments. Thus, the ecological consequences of loss of eelgrass habitat will greatly depend on the location of the bed.

The depth that eelgrass grows depends on light availability. Light availability is largely controlled by phytoplankton abundance and algal epiphyte cover (mostly determined by nutrient loading and flushing) and sediment resuspension (Dennison, 1987; Kemp et al., 1983;

Figure 3. Maximum depth (m MLW) of eelgrass in different parts of Buzzards Bay.

In general, water transparency is greater in the southern region of the Bay than northern parts, and better outside of small embayments than within.

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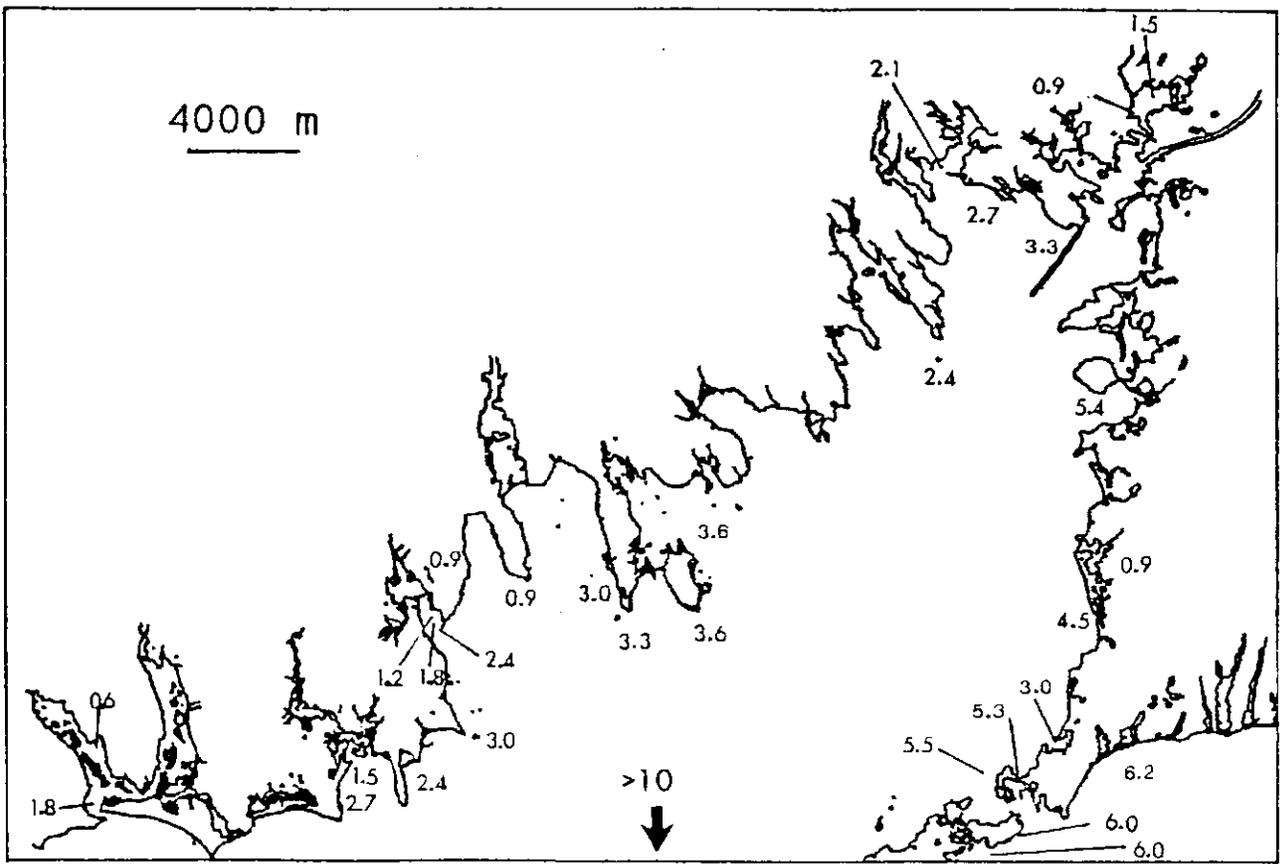
Lee and Olsen, 1985; Orth and Moore, 1983b; Sand-Jensen and Borum, 1983). Figure 3 shows that light is less available to eelgrass in poorly flushed embayments than on more exposed shorelines, and water transparency is best near the southern and eastern shores of Buzzards Bay, than the northwestern end which is not as well flushed, and has moderate riverine and larger anthropogenic inputs.

The absence of eelgrass in the north ends of embayments such as New Bedford Harbor, Little Bay, Fairhaven, and Apponagansett Bay, Dartmouth does not correspond to physiological limits of eelgrass growth due to the low salinities or damage due to natural disturbances. Because eelgrass grew in these areas in the past (Chapter 4), alternate explanations must account for the absence of eelgrass, such as toxic pollution, sediment resuspension, or nutrient enrichment.

Chapter 2

Eelgrass (*Zostera marina* L.) production in Buzzards Bay

Introduction

The contribution of *Zostera marina* L. (eelgrass) to primary production in Buzzards Bay has not been estimated. Elsewhere, *Zostera* beds contribute sizably to coastal primary production, especially in shallow embayments, where they may account for 50% of all primary production including benthic algae and phytoplankton (Sand-Jensen and Borum, 1983; Nienhuis and Van Ireland, 1978).

Because eelgrass grows subtidally, it is difficult to measure primary production in the field. Often production is estimated by multiplying peak summer biomass by a factor of 2 (McRoy and Phillips, 1977), or multiplying growth rate during a summer period by the length of a "growing season". Both of these approaches has limitations because growth rate changes during the year and many beds grow in winter.

Dennison (1985) measured carbon fixation and respiration by eelgrass in the laboratory under different light and temperatures, and estimated seasonal changes in production rates of eelgrass in Woods Hole, MA from local radiant energy and temperature data. This approach suggested that eelgrass production should be higher in late spring rather than late summer when water temperatures were warmer because a shorter photoperiod and higher respiration rates in late summer resulted lower net photosynthesis. These results are corroborated by eelgrass growth data in Woods Hole and elsewhere in similar climates (e.g Jacobs, 1979).

Dennison (1985) did not integrate this production data to estimate annual production, but I reanalyzed of his published data and estimated net production as 3225 mg C g^{-1} leaf tissue y^{-1}. Dennison (1985)

provided a regression between carbon fixation and biomass production, and this carbon fixation value translates to 6000 mg dry g^{-1} leaf y^{-1}. Because mean leaf biomass in Woods Hole is $\approx$100-200 g dry wt m^{-2} (see below), this suggests local production equals 600-1200 g dry wt m^{-2}.

There are several difficulties extrapolating Dennisons' data in this way. His conversion from net photosynthesis to biomass production was based on only 4 data points, and though the fit is good, the confidence interval of this relationship is necessarily large. Second, the temperature and light measurements were made on leaf tissue collected in July, acclimatized to experimental light and temperature for only hours before changes in oxygen output were measured. Summer collected *Zostera* may not respond to winter conditions in the same way as acclimatized plant tissue collected during the winter. Even with this limitations, this data is valuable because it is the best estimate of annual eelgrass growth and production in this region to date.

In this paper I relate field data on eelgrass growth to local light and insolation to generate a production curve for eelgrass in the region. I use this unit area production data, and eelgrass bed cover in Buzzards Bay that I have reported elsewhere (Costa, 1987), to estimate the total contribution of eelgrass in Buzzards Bay compared to estimates of other primary producers. The growth of eelgrass has been described elsewhere, and in some cases correlated to light or temperature. Because this paper relates to these other studies, a brief description of eelgrass growth and results of other studies are warranted.
Measuring eelgrass production

The most widely accepted and reliable method for estimating seagrass production in the field are direct leaf marking techniques (Zieman and Wetzel, 1980). There are several variations of this method, but all are based on marking a leaf (punching a small hole, attaching a staple) in the field, and returning after 1 to 4 weeks to measure production of new leaf biomass (usually after harvesting).

Eelgrass leaves have basal growth, and new leaves are produced in the center of the leaf cluster, and each time a leaf is produced by a shoot, a new rhizome node and root cluster is also produced on the rhizome (Fig. 1). This one-to-one correspondence of leaf parts simplifies production calculations, and the weight of a mature leaf, mature rhizome internode, and root cluster are usually termed plastochrone units (Tomlinson, 1974, Jacobs, 1979). Each time a new leaf appears, the equivalent of one new plastochrone unit (PU) is produced, and the duration between leaf production is termed the plastochrone interval (PI). Because leaf growth occurs simultaneously on several younger leaves, rhizomes, and root internodes, and because the oldest leaf does not always drop off when a new leaf appears, and leaf lifespan is roughly 5 times the PI, the term PI is preferable to "leaf turnover" time, and its use is retained in this paper.

PI during the year and typically ranges 7 - 20 days during spring and summer, but may exceed 40 days during winter (Jacobs, 1979; Robertson and Mann, 1984). Jacobs (1979) reported that PI in Denmark eelgrass beds correlated well with daily insolation, and production peaked in June, whereas Robertson and Mann (1984) reported that PI in Nova Scotia was a function of temperature and production peaked in May.

Figure 1. A typical vegetative eelgrass shoot (ramet) showing major
anatomical features and marking technique. Leaf 'a' is the youngest,
'f' the oldest. Each node is associated with the production of one
leaf, fragments of which often remain attached. The leaf hole in the
meristem (Ho) is the original pinhole punched approximately one leaf
width below the sheath ligule at the top of the meristem. Outgrowth
scars on older leaves show typical 2 week summer growth. PI in this
study equals third leaf area / new leaf tissue $(\Sigma[(ah-Ho) + (bh-Ho)+ (ch-Ho)+ \ldots]$ x marking days.
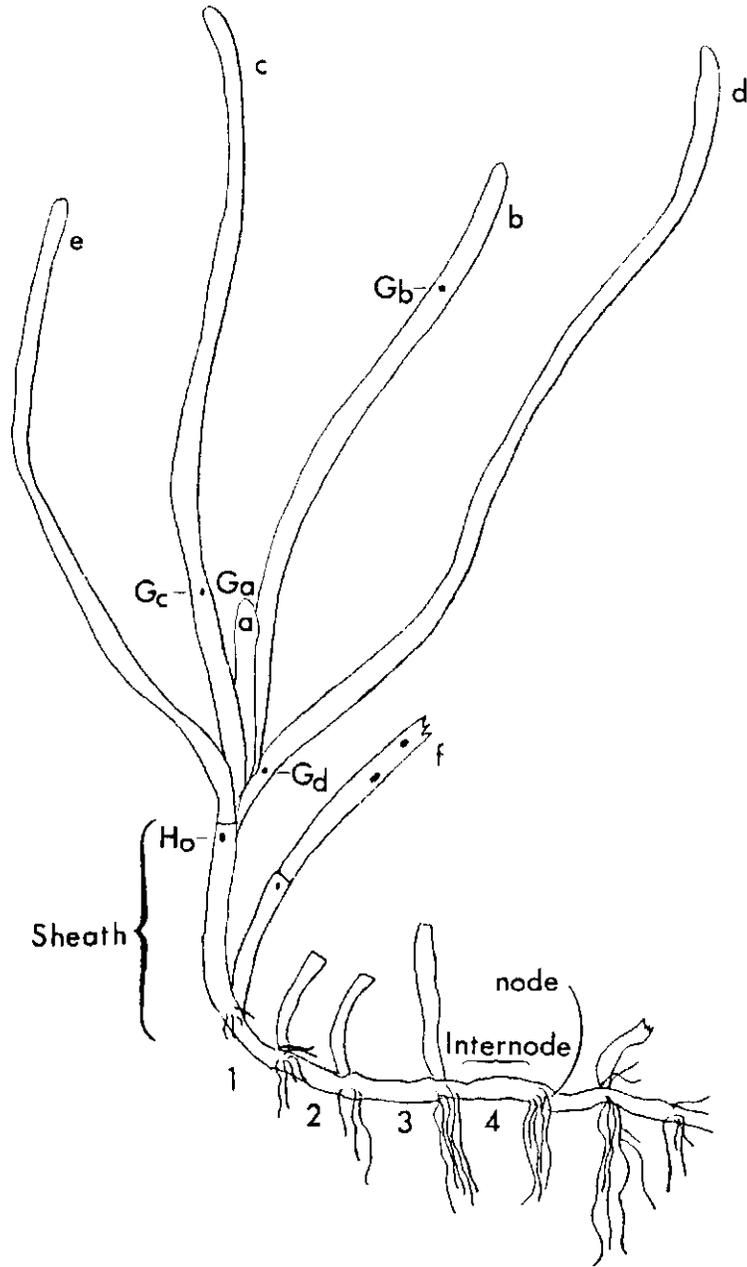
Plant growth is a function of both light and temperature the discrepancy between these interpretations can be explained by climatic differences because in both areas, eelgrass grew faster in May and June than in late Summer. In the Northern Hemisphere at the latitude of these sites there is considerably more light in May and June the late summer, however in Denmark water temperatures are higher in July and August, whereas in Nova Scotia, water temperatures are higher in May and June. I reanalyzed Jacobs data and found that PI correlates better with both light and temperature [r^2= 0.89; PI= 14.5 - 0.734 x (light as 10^{-3} J m^{-2} d^{-1})-1.14 x ($C°$)], than with light alone (r^2= 0.67). These coefficients, however, do not result in a reasonable PI curve when used with Woods Hole temperature and insolation data (data not shown), and may only apply to beds in Denmark.

The objective of this study was to estimate annual production of eelgrass in Woods Hole by correlating changes in plastochrone interval with local light and temperature data. Based on the relationship between these parameters, an annual PI curve can be modeled and integrated to obtain the total number of PUs produced each year.

Methods

Total annual net production of eelgrass in Buzzards Bay was estimated by multiplying eelgrass bed production area by the mean number of plastochrone units produced each year times the mean plastochrone unit weight per area.

Elsewhere I have calculated the total eelgrass bed area in Buzzards Bay (2920 ha; Costa, 1988). This estimate was calculated from

photographs of ≈1:25,000 scale photographs, and adjusted for percent cover as perceived on that scale imagery. This process ignores bare patches within eelgrass beds that are too small to be seen on those photographs, and which are only visible underwater or with small scale imagery. It is impossible to quantify small scale patchiness in every bed in this region, so a correction factor was estimated based on field experience and microscopic study of photographs was factored into the estimate of bed area.

Vegetative and flowering shoot densities, were measured at 92 1/16 m^2 quadrats taken randomly or along transects at 16 sites in Buzzards Bay and Cape Cod (Fig. 2) spanning a wide range of habitat diversity. Most observations and biomass collections were made in the center of the depth distribution of each eelgrass bed, rather than at bed margins. To determine mean plastochrone biomass, above and below ground biomass was collected in 64 of these quadrats. Vegetative biomass was separated into third leaves, other leaves, meristems, and mature rhizome internodes (generally the 4th internode). Reproductive shoots were treated separately, and seed and flower counts were noted. The dimensions of the biomass clippings were recorded, then leaves were cleaned, first by removing large epiphytes by hand or razor, then by soaking in 10% phosphoric acid for several minutes to remove encrusting and smaller epiphytes (Jacobs, 1979). Leaves were rinsed in tap water, blotted dry, damp weight taken, then dried at 50 °C for at least 36 hr. Total aboveground plastochrone unit weight for each quadrat was calculated as total 3rd leaf weight + (total sheath weight/mean leaf no.).

Figure 2. Map of southeastern Massachusetts showing where biomass samples were harvested (B) and sites for measurement of production rates (P).

8000 m

CAPE COD

Woods Hole
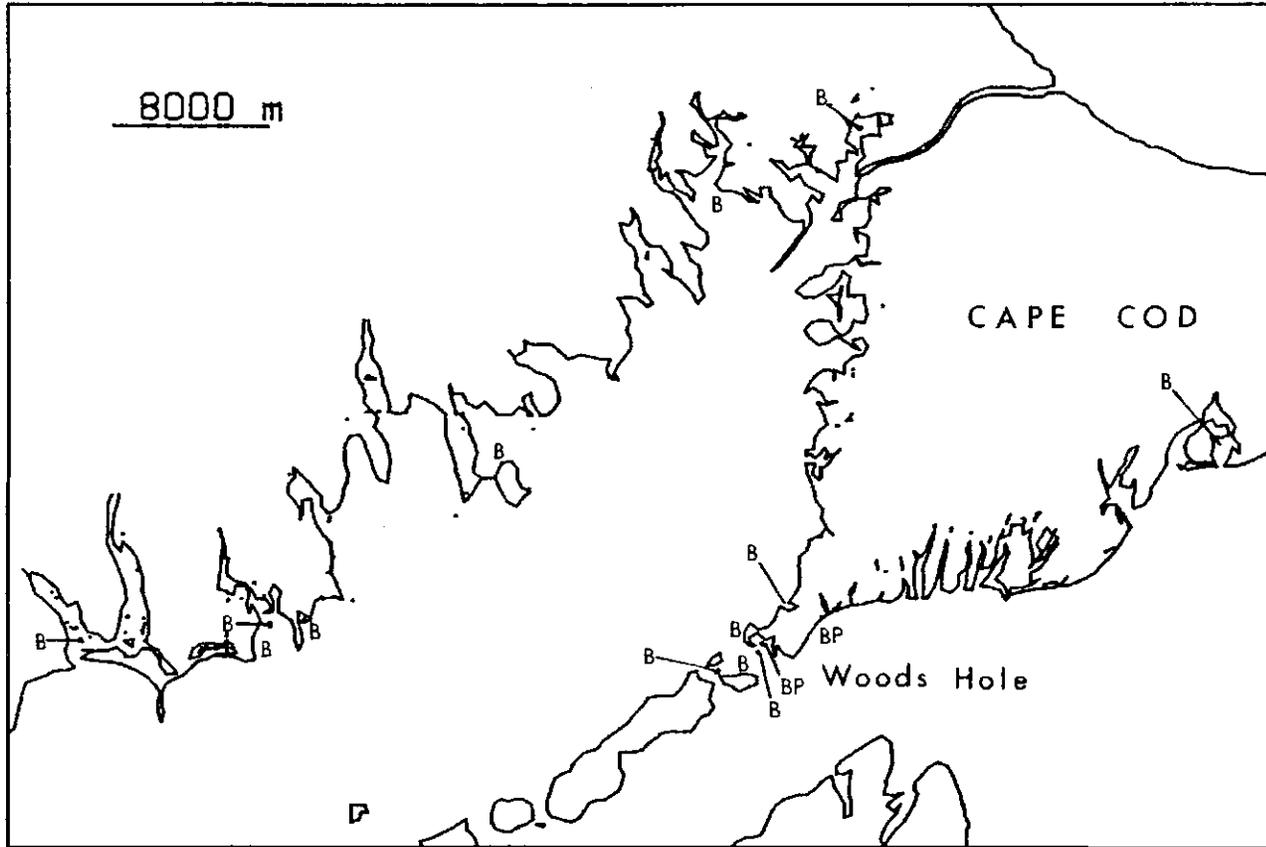
In some samples, adequate rhizome material was not collected for every shoot. In these cases, total rhizome plastochrone unit weight was calculated as shoot no. per quadrat x mean collected mature rhizome weight. Roots were not harvested, but assumed to be equal to 50% of rhizome biomass (Jacobs, 1979).

PI on various dates between May 1984 and March 1985 was measured off Quisset Beach, and Garbage Beach in Woods Hole (Fig. 2). To measure plastochrone interval, quadrats ($1/16$ m^2) were set at different stations in the bed. A hole was punched one leaf width below the top of the leaf sheath of most shoots in the quadrat using a fine pin (Fig. 1). After two to three weeks, all the plants in the quadrat were harvested, and plant tissue was processed as described above.

PI was calculated for each punched shoot in the quadrat by measuring the distance each leaf hole grew from the residual scar on the sheath. If a young leaf had no scar, it was completely new growth. PI was calculated as follows:

$$PI\ days = \frac{(marking\ period\ days) \times (area\ of\ a\ mature\ leaf)}{(total\ new\ leaf\ area\ produced)}$$

Leaf area was used to calculate PI because older leaves have a higher weight per unit area than younger leaves (Jacobs, 1979; Pregnall, unpub.) because of encrusting algae and dissolved salts, which leads to underestimates of PI. Leaf area of oldest mature older shoots was not always suitable, especially in spring, because winter leaf lengths are

somewhat shorter than summer leaf lengths, and this would lead to overestimates of production. The area of the third leaf, or sometimes the average of third and fourth leaves if there was considerable variability among mature leaves, was used as mature leaf area.

To obtain temperature and light coefficients of growth, PI was correlated with local insolation and water temperature (Woods Hole Oceanographic Institution) during the leaf marking interval. The coefficients were applied to the year long record of light and temperature to model eelgrass growth for 1985. To obtain the total number of PU's produced that year, the inverse of the PI curve was integrated. This number was multiplied times the mean vegetative PU weight at the 16 sites to determine annual vegetative production per unit area. Reproductive shoot production was calculated as 2 x summer biomass and added to vegetative production to obtain total annual aboveground production (Robertson and Mann, 1984).

Results

PI was shortest in May 1986 (8.9 days) and longest in February 1986 (51 days for mid and deep beds, and ≈80 in shallow beds; Fig 3). PI correlates well with water temperature, insolation, and [r^2= 0.75; PI= 77.9 - 0.160 x (light as 10-3 J m^{-2} d^1) - 20.3 x Ln(C^o+2), Fig. 3]. The adjustment of temperature in this equation was necessary because water temperature in Woods Hole may reach -2 °C in winter. Using °K (e.g. Robertson and Mann, 1984) does not result in a good correlation (r^2= 0.55), because as temperature approaches freezing, eelgrass growth slows dramatically.

Figure 3. Water temperature, surface insolation, plastochrone interval
(PI) data and PI curve for Woods Hole, 1985-1986.

The PI curve was based on a multiple correlation between, PI,
light, and water temperature from eight dates.
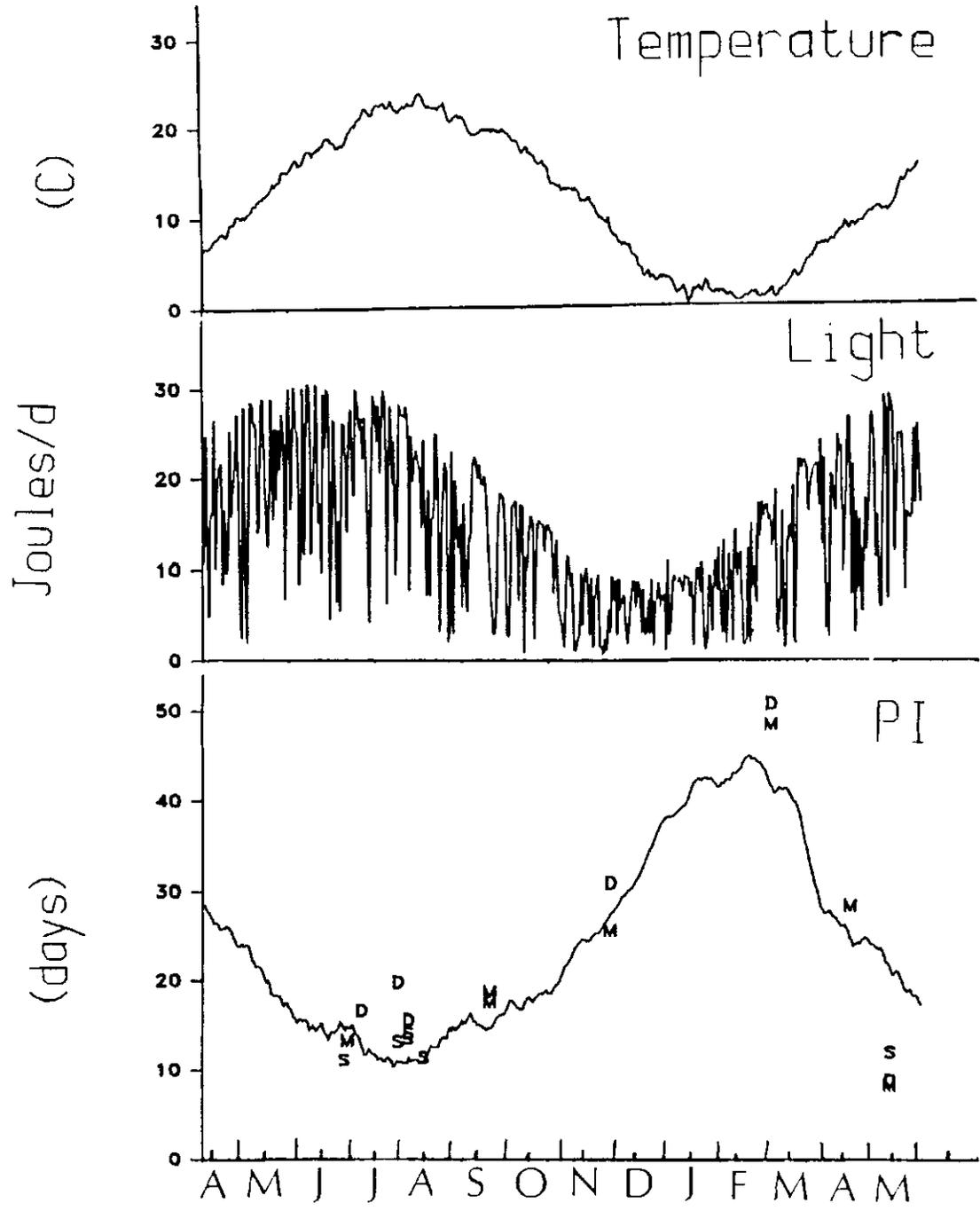
Integration of the inverse PI curve yielded 19 PUs, that is, each plant produces 19 leaves, rhizome segments and root clusters during the year. Alternate methods of generating a PI curve based on this data, such as by a forth order polynomial, or integration of a hand drawn curve, changed this estimate by less than 15%.

The mean aboveground vegetative plastochrone unit weight for the harvested quadrats 38 g dry wt m^{-2} (SE=3.1). If regional annual production is 19 PUs, then mean annual production is 722 g m^2 yr^{-1}. When corrected for reproductive shoot production, total above-ground production is 892 g m^{-2} yr^{-1}. If the mean below ground production is included, and root biomass estimated as 50% of rhizome production (Jacobs, 1979), then mean total above and belowground production equals 1008 g dry m^2 yr^1. Carbon composition measured from eelgrass tissue collected in Woods Hole during Spring 1981 was 39%, thus above ground production is 347 g C m^{-2} yr^{-1} and above + below ground production is 393 g C m^{-2} yr^{-1}.

There are several differences between beds at the upper limits of growth and the deep edges of beds. Except in winter, shallow stations have shorter PIs than deeper stations (Fig. 3), but insufficient data was collected from shallow stations to generate a separate curve. The quicker summer growth rates of shallow beds do not result in higher production than mid-depth beds, because above-ground plastochrone unit weight is somewhat less at shallow sites (Table 1). The differences between production in shallow and mid-depth bed may be less than indicated because shallow beds devote more production to roots than do mid-depth beds (Thayer et. al., 1984). Both mid-depth and shallow beds,

Table 1. Measures of biomass (means±SE) in shallow, mid-depth and deep beds off Quisset beach.

To calculation total PU weight, root weight was assumed to equal 50% of rhizome weight.

Parameter	Shallow (1-2 m MLW)		Mid (≈3 m MLW)		Deep (≈5 m MLW)	
density:	704	±97	445	±52	141	±17
aboveground biomass: (g dry m^{-2}):	128	±30	162	±27	85	±12
mean shoot dry wt: (mg)	187	±44	427	±122	611	±68
aboveground PU wt: (g m^{-2}):	34.3	±11.7	37.6	±8.0	14.9	±3.9
rhizome PU weight: (g m^{-2}):	9.9	±2.2	8.8	±1.3	3.6	±1.2
Total PU wt (g m^{-2})	48.7		49.8		20.8	

Figure 4. Regional frequencies of various measures of eelgrass biomass.

Top: Aboveground biomass (mean = 149 g dry wt m^{-2}, SE= 8.7, n=67),

Middle: Shoot density, and Bottom: Aboveground annual production.
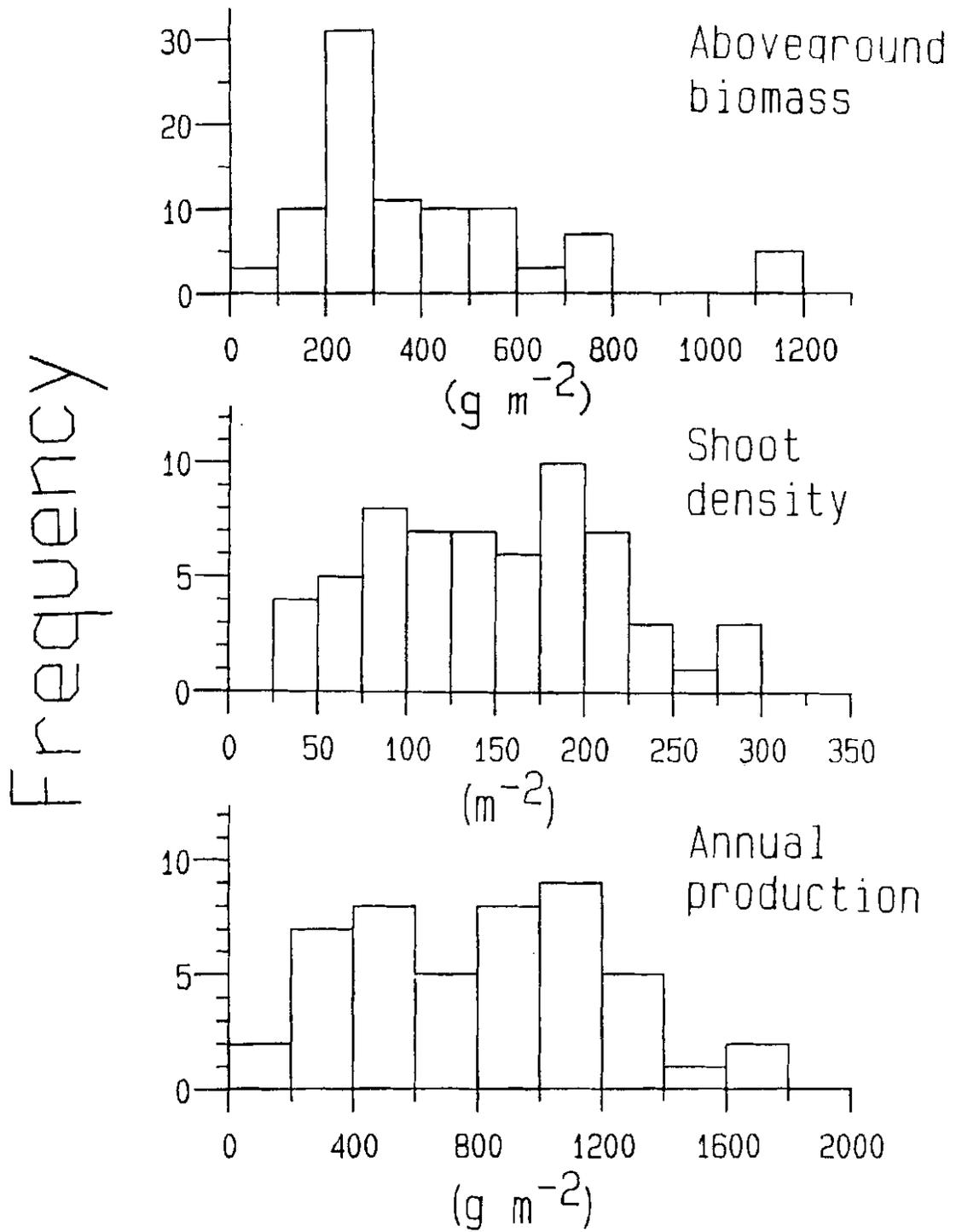
Figure 5. Log-Log plot of mean shoot weight vs shoot density. Slope = -0.78.
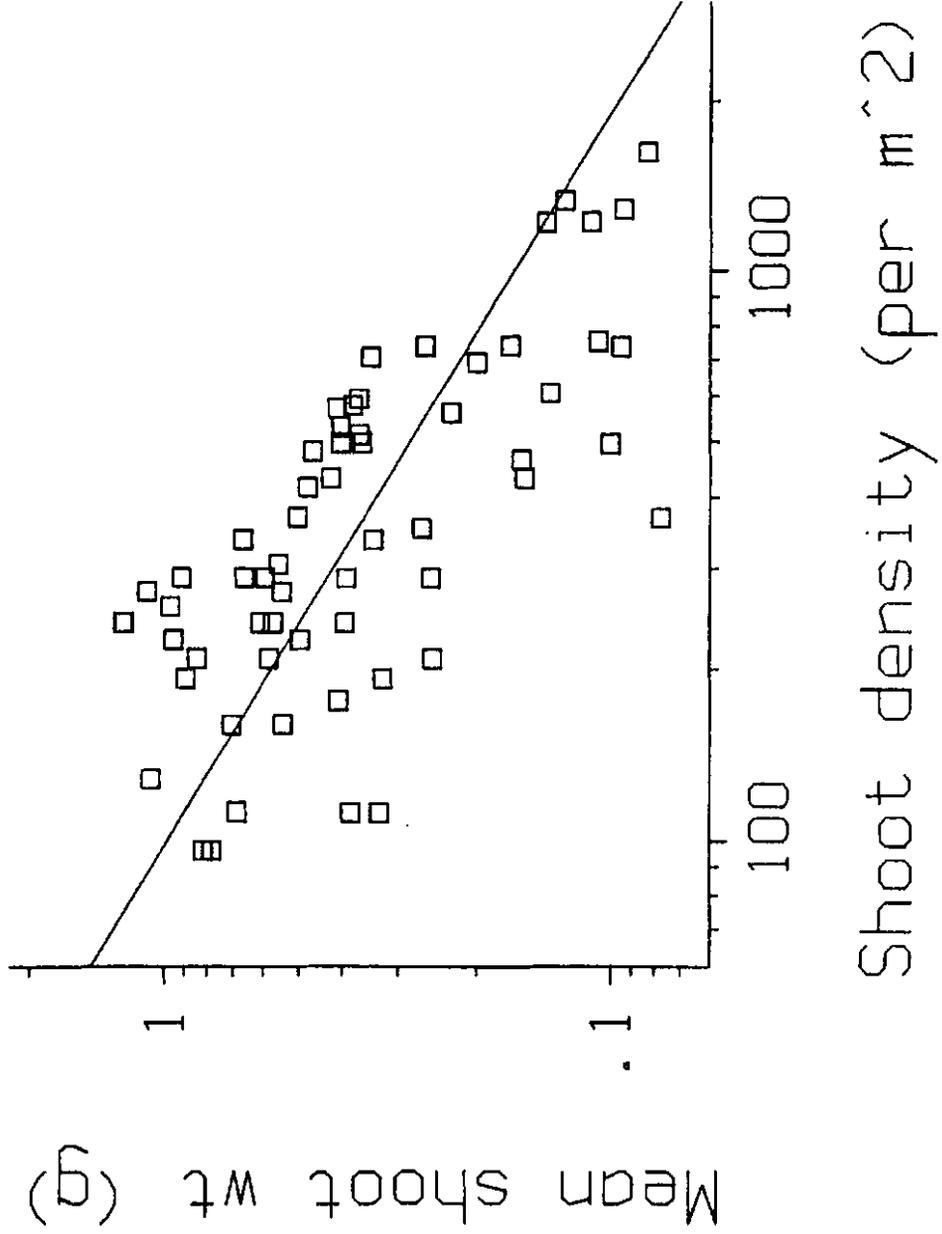
however, have higher production than deep beds which have both less above and below-ground plastochrone unit weight and grow more slowly.

Eelgrass beds in Buzzards Bay are remarkably varied in terms of aboveground biomass, shoot density, and total annual production (Fig. 4); but certain biomass relationships are consistent throughout the region. Shoot densities are higher in shallow and high energy environments, but shoots size is smaller (Table 1.). Consequently, aboveground biomass does not change appreciably with changing shoot densities. A log-log plot of these two variables results in a linear relationship with a slope of -0.78 (Fig. 5).

Eelgrass bed area in Buzzards Bay (corrected for large scale percent cover) is 2920 ha (Costa, 1988). Based on transects in the field and detailed analysis of low scale photographs (unpublished observations), 0.85 was used as a correction factor to account for small bare areas (<2 m^2) that exist in eelgrass beds, but are not resolved in large scale aerial photographs. Thus "production area" of eelgrass beds in Buzzards Bay is 2482 ha. If mean annual proction is 393 g C m^{-2} yr^{-1}, total annual production in this region is 2.4 x 10^{10} g dry, or 9.2 x 10^9 g C. Aboveground annual production alone is 2.1 x 10^{10} g dry or 8.1 x 10^9 g C.

Discussion

Production of organic matter is just one contribution of *Zostera* beds to coastal ecosystems. Eelgrass beds also act as a refuge, habitat, and nursery for a diverse assemblage of algae, plants, and animals and important in binding and stabilizing sediments. Knowledge

of rates of production by *Zostera* and other primary producers, however, is fundamental for understanding carbon flow in coastal ecosystems.

The estimate of production of eelgrass in Buzzards Bays bay depends upon three assumptions: the area of eelgrass is accurate, the concept of a regional PI curve is valid, and the mean weight of plastochrone units used in the calculations are representative of the diverse habitats of the region. Clearly there are difficulties with each of these premises, but a realistic range can be ascribed to the estimate of regional production.

Biomass of plastochrone unit area weight is variable both within and between beds, and only further sampling of beds in this area can shed light on whether these biomass samples represent a regional average for eelgrass biomass. The range of biomass (Fig 4, 42-298 g m^{-2}) and production (210 -1540 g m^{-2} yr^{-1}) reported here is well within the range of values reported elsewhere (Kentula, 1985; Robertson and Mann, 1982).

The largest uncertainty in estimating production is the calculation of total plastochrone events per year, and the assumption that one curve is characteristic for the whole region. The plastochrone curve was based on data collected from well flushed somewhat exposed beds, typical of most eelgrass bed cover in Buzzards Bay. But PI even within these beds changes with depth, and shallow beds appear to grow quicker in summer and slower in winter.

The cause of these differences in growth rate may be due to both light and temperature effects. In summer, water overlying the shallow beds is often 1 or 3 °C warmer in the summer than deeper beds even in well flushed areas as along surf drive and although not measured,

shallow areas may exhibit more cooling in winter. Moreover, shallow beds receive a longer duration of light above saturation (longer "Hsat"), and this affects growth rate as well (Dennison and Alberte, 1985). Of course, other factors such as physical damage and nutrient availability may play a role in explaining these growth rate differences.

Differences in summer production between shallow and mid-depth beds are small because total plastochrone unit size in shallow areas is slightly less than mid-depth beds (Table 1). Root production was not measured, and if root production in shallow beds is double mid-depth root production, then total plastochrone unit weight may be equal in the two areas, however. This may be the case because beds in shallow wave swept areas have considerably more biomass in below ground production than deeper beds in undisturbed areas (Thayer, et al. 1984; pers. obser.). Shallow and mid-depth beds have higher growth rates and plastochrone units than deep beds where annual production is considerably less.

The relationship between shoot weight and density has been extensively studied in terrestrial systems, and virtually all agricultural and forestry studies show that the slope of a log-log plot is near -1.5, and this has become known as the "-3/2 power law" (White and Harper, 1970). That is, shoot weight = $cp^{-3/2}$, where p=density, and c is a species specific constant. It is remarkable that eelgrass does not conform to this relationship, and instead shows a -0.78 power relationship. This is not because eelgrass is a clonal species, because this relationship applies to terrestrial clonal grasses as well (Kays

and Harper, 1973). Kays and Harper, however, found that terrestrial grass exposed to 30% ambient sunlight showed a depression of the curve to $\approx$ -1 slope. This also results in biomass to be constant, independent of density. These authors concluded that low light intensity induces density dependant growth and mortality because of mutual self-shading, and this may also explain the unusual shoot density relationship in eelgrass as well.

Locally, eelgrass production is approximately 6.5 x aboveground biomass (Fig. 6). Thus the extrapolation of Dennisons data (1985) showing yearly production to be 6x active leaf weight seems reasonable.

Comparison of eelgrass and other primary producers in Buzzards Bay
Phytoplankton

Carbon fixation in Buzzards Bay is approximately 10^7 g C m^{-2} y^{-1} (Roman and Tenore, 1978). Because the area of Buzzards Bay and its adjoining bays and estuaries is 5.5 x 10^8 m^{-2} (Signell, 1987), phytoplankton annual production in Buzzards Bay is $\approx$ 5.9 x 10^{10} g C.

Macroalgae

Many macroalgae grow deeper than eelgrass, and drift algae often accumulate on the bottoms of quiescent bays. Nonetheless, macroalgal cover, like eelgrass, is not appreciable in Buzzards Bay because most of the Bay is greater than 10 m deep, and light penetration is insufficient at that depth to support a large biomass of benthic algae. Furthermore, in the open bay, most algae are restricted to solid substrate, and rocky areas are only extensive around the Elizabeth Islands, offshore of

Figure 6. Regression between total aboveground biomass and above and belowground annual production (r^2= 0.82, m= 6.5).
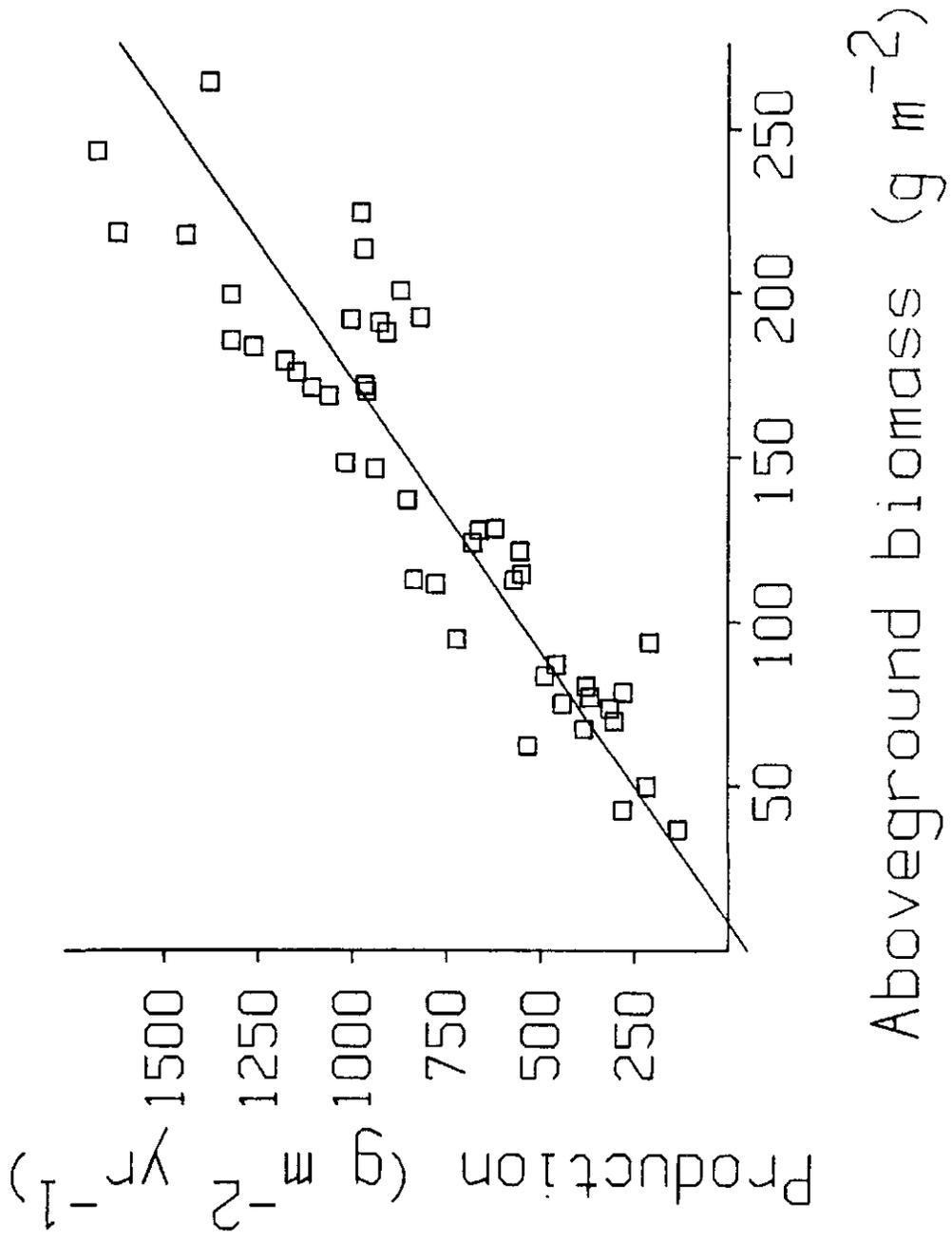
Westport and Dartmouth, and in shallow areas, especially within 100 m of shore. The vast majority of the shallow margins of the Bay bottom is mud and sand, and is suitable only for eelgrass colonization. Based on aerial photographs, it appears that algae cover less than 10% of the habitat area of eelgrass, or about 400 ha.

Production estimates for attached algae in temperate waters are quite variable and generally range from 100 - 1000 g C m^{-2} y^{-1} (Ferguson et al., 1980; Josselyn and Mathieson, 1978; Mann, 1972; Wassman and Rasmuss, 1973). Estimates of drift algae production are infrequent. Thorne-Miller et al (1983) found summer biomass of unattached benthic algae in Rhode Island Coastal lagoons to be 14 - 125 g dry m^2 but did not estimate annual production. Sand-Jensen and Borum (1983) estimated macroalgal production in coastal waters with eelgrass beds 200-500 g C m^{-2} y^{-1}. In this paper, 500 g C m^{-2} y^{-1} was conservatively estimated for both drift and attached macroalgae, where they are dense. Thus macroalgal production in Buzzards Bay is $\approx$ 20 x 10^8.

Epiphytic algae

Numerous species of algae are epiphytic on eelgrass (Harlin, 1980), and production estimates range from 1 to 100% of eelgrass production, although 20 - 40% are most frequently reported (Borum and Wium-Anderson, 1980; Mazella and Alberte, 1986, Penhale, 1977; Sand-Jensen and Borum, 1983). In Buzzards Bay, dense accumulations of epiphytic algae are usually found in poorly flushed areas, especially near sources of nutrient inputs. Offshore eelgrass beds typically have much lower accumulations of algal epiphytes, and because these beds make

up approximately 70% of eelgrass cover in Buzzards Bay, total overall epiphytic algal production was conservatively estimated to be 20% of eelgrass production.

Periphyton

Periphyton production on the surface of sediments and solid surfaces range from 4 to 200 g C m^{-2} y^{-1} and are most abundant on muddy sediments in shallow waters without macrophytes, and are less productive in sand (Hickman and Round, 1970; Marshall et. al., 1971; Ferguson, et al., 1980, Revsbeck et al., 1981; Sand-Jensen and Borum, 1983). Sand-Jensen and Borum (1983) found in Danish waters that microbenthic algal production peaked at 120 g C m^{-2} y^{-1} at 0.5 m MLW, dropped to 35 g C m^{-2} y^{-1} at 2 m MLW, and decline to negligible values below 5 m..

The production rate of periphyton declines more rapidly than macrophytes. Thus, the total shallow (photic) substrate area in Buzzards Bay (10,380 ha, Chapter 1) overestimates the areal extent of periphyton production area, because more than 80% of this substrate is covered with eelgrass beds, rock fields, or sand flats without appreciable periphyton densities. If the remaining area has a mean production rate of 45 g C m^{-2} y^{-1}, then periphyton contribute 9 x 10^8 g C y^{-1} in Buzzards Bay.

Salt marshes

Salt marshes cover 1900 ha in Buzzards Bay (Hankin et al, 1985). These communities are productive, but they do not export appreciable amounts of organic matter (Nixon, 1980). One well studied salt marsh in

Buzzards Bay has a mean annual production of 160 g C m^{-2} y^{-1} (Valiela et al., 1975), however, only 20% of its production is released into Buzzards Bay (Valiela and Teal, 1979). If this marsh is typical for the region, then the contribution of salt marshes to Buzzards Bay is 6.0 x 10^8 g C m^{-2} y^{-1}.

Relative contribution of eelgrass production in Buzzards Bay and adjoining shallow embayments

Most of Buzzards Bay is too deep to support eelgrass growth, hence eelgrass and epiphytic algae contribute only 15% of the total production in Buzzards Bay (Table 2). In contrast, eelgrass communities may account for a larger portion of total production in shallow embayments.

For example, Buttermilk Bay is a 210 ha lagoon at the north end of Buzzards Bay with a mean depth of 1.0 m (Costa, 1988; Valiela and Costa, in press), and 47 ha of eelgrass production area (Appendix III). Assuming eelgrass production rates described above, then *Zostera* production in Buttermilk Bay equals 1.8 x 10^8 g C y^{-1}.

Other producers can also be estimated as before. Algal epiphytes are very abundant in parts of Buttermilk Bay, and if they equal 40% of *Zostera* production (Penhale, 1977), they account for an additional 0.7 x 10^8 g C y^{-1}. In a shallow, enriched Rhode Island lagoon, Nowicki and Nixon (1985) estimated phytoplankton production to 120 g C m^{-2} y^{-1}. If Buttermilk Bay has similar rates of production, then phytoplankton produce 2.5 x 10^8 g C y^{-1}.

Drift algae are abundant in some areas of Buttermilk Bay, (Costa, 1988). Algal biomass in 1985 was 77 g dry wt m^{-2} (n=8, SE=22) in a

Table 2. Eelgrass production in Buzzards Bay compared to estimates of
other producers.

Salt marsh production for Falmouth and the Elizabeth Islands was
based on the area salt marsh adjoining Buzzards Bay (from Hankin et al.,
1985).

Component	Production $(g \ C \ y^{-1} \ x \ 10^8)$	Percent of Total
Phytoplankton	588	80
Eelgrass	92	13
Eelgrass epiphytes	18	2.5
Other periphyton	9.0	1.2
Macroalgae	20	2.7
Salt marshes	6.1	0.8
TOTAL	733	

transect from mid-bay to Red Brook. If annual production is 6x summer biomass then annual production is ≈500 g C m^{-2} y^{-1}. This transect was centered near a major source of nutrients, and probably overestimates algal abundance in the Bay. In Buttermilk Bay, drift algae occur mostly in quiescent areas, depressions, or tangled within eelgrass shoots, especially near nutrient sources. Total drift algae area was conservatively estimated to be 20% of eelgrass cover, and therefore contributes 0.5 x 10^8 g m^{-2} y^{-1} to Buttermilk Bay.

Attached algal production in Buttermilk Bay is negligible, because rock and cobble are common in only a few areas. Altogether there is less than 6.5 ha of attached algae habitat in this Bay, or 0.3 g C x 10^8 y^{-1}. Epipelic periphyton are more important in Buttermilk Bay because there are $\approx$ 50 ha of unvegetated mud bottom where periphytic algae may be abundant. Assuming production rates of 100 g C m^{-2} y^{-1}, then this component may equal 0.5 x 10^8 g C y^{-1}.

Based on these estimates, eelgrass beds and their epiphytes account for 40% of all production in Buttermilk Bay (Table 3).

Table 3. Eelgrass production in Buttermilk Bay compared to estimates of
other producers.

No estimates of salt marsh production were made.

Production Component	Percent of $(g\ C\ y^{-1}\ x\ 10^8)$	Total
Phytoplankton	2.4	39
Eelgrass	1.8	29
Eelgrass epiphytes	0.7	11
Drift algae	0.5	8.1
Macroalgae	0.3	4.8
Other periphyton	0.5	8.1
TOTAL	6.2	

Chapter 3

Evidence for long-term cycles in eelgrass (*Zostera marina* L.) abundance

in Massachusetts using sediment cores

Introduction

Analysis of core sections from coastal depositional environments shows great promise for assessing the impact of anthropogenic and natural disturbances that have taken place during recent centuries. For example, in Chesapeake Bay, sediment cores were used to document increases in algal biomass, nutrient loading, and sediment deposition, and decreases in submerged aquatic vegetation as a result of human development (Brush, 1984; Brush and Davis, 1984; Davis, 1985; Orth and Moore, 1983b). In this paper I document past cycles in eelgrass (*Zostera marina* L.) abundance with cores from bays on Cape Cod and Buzzards Bay, Massachusetts.

Eelgrass populations undergo major fluctuations in abundance due to disease, storms, ice scour, and pollution (Harlin and Thorn-Miler, 1981; Orth and Moore, 1983b; Robertson and Mann, 1984, den Hartog, 1987). For example, the wasting disease destroyed at least 90% of all eelgrass in the Western Atlantic during 1931-32 (Rasmussen, 1977; den Hartog, 1987) and less dramatic declines of eelgrass were reported along the eastern seaboard of the US in 1894, in New England in 1908, and in Popponesset Bay (adjacent to Waquoit Bay) during 1915 (Cottam, 1934). In recent decades, nutrient loading has been implicated in local eelgrass declines. Added nutrients elevate the biomass of epiphytes on eelgrass and phytoplankton, both of which decrease light availability, and thereby cause the death of eelgrass beds (Orth and Moore, 1983b; Sand-Jensen and Borum, 1983).

Most macrophyte seeds in marine and estuarine environments sink. Davis (1985) examined the morphology, density, and settling velocities of seeds produced by aquatic vegetation and concluded that most seeds are deposited in or near the beds that produced them, even in moderate currents. Because eelgrass seed coats are resistant to decay and remain in the sediment even if a seed germinates, they are good indicators of eelgrass abundance and distribution over many decades or centuries. Eelgrass leaf and rhizome fragments are also present at considerable depths in cores, but are less quantitative indicators of eelgrass abundance.

Cores can be dated by pollen profiles, radioisotopes, or by remnants of human activity such as coal particles or other refuse (Brush, 1984; Brush and Davis, 1984, Redfield, 1972). Changes in diatom community, invertebrate abundance, and chemical composition can also be used to date core sections if some information is already available on historical changes in the environment. Generally cores are meaningful only when taken in depositional environments, remote from high current velocities, wave action, dredging, or construction (Davis, 1984). When cores are not dated independently, a realistic range for sedimentation rates for depositional environments can be approximated from the depth of the wasting disease event, plant community changes, sea level rise, and cores taken elsewhere. For example, tidal records indicate that sea level is rising relative to the land in the northeast U.S. at a rate of 2-3 mm y^{-1} during the last 2 centuries (Emery, 1980). Because depths of local undredged, quiescent areas have changed little on maps during the last 100 years, sedimentation in many areas, are probably within a

factor or two of the sea level rise rate. Some cores show community transitions from recent *Zostera* beds to *Ruppia* beds to the salt marsh grass *Spartina* with increasing depth (pers. obser.), indicating that overall, sediment deposition rates were less than sea level rise rates.

In Chesapeake Bay, recent sedimentation rates for cores taken in quiescent areas ranged from 2 to 10 mm y^{-1}, with higher rates occurring near rivers (Brush, 1984; Davis, 1985). In Boston Harbor, sedimentation rates near a sewage outfall were as high as 30 mm y^{-1} (M. Bothner, pers. comm.). Lower rates may be typical for undisturbed areas in bays on Cape Cod because river discharges are small. For example, if local sediment deposition is 2-10 mm year, declines in seed abundance due to the wasting disease can be expected to occur between 10 and 40 cm in cores. Of course channels, deeper basins, sites near barrier beaches, dredged areas, or streams may experience considerably higher rates of deposition or even sediment removal.

Methods

To determine regional fluctuations in eelgrass abundance, nine cores were taken in 4 bays around Cape Cod (Fig. 1). One core was taken in the north central region of Apponagansett Bay, So. Dartmouth (core AB) at 1.4 m MLW where no eelgrass grows today. Another was taken along Goats Neck, Naushon Is. (GN) at 0.7 m MLW with a shallow eelgrass bed. Three cores taken in Buttermilk Bay, Wareham either within or adjacent to eelgrass beds: one (BB1) on the north side of the flood delta at 1.2 m MLW, one (BB2) 20 m from a marsh at 0.8 m MLW, near the north end of the bay, 60 m east of Red Brook, a small stream there, and the third

Figure 1. Location of sediment cores taken in Buzzards Bay and around Cape Cod.

The four bays examined were Apponagansett Bay (AB), Naushon Is. (NI), Buttermilk Bay (BB1-3), and Waquoit Bay (WB1-4).

8000 m

BB1-3

AB

WB4

WB1-3

NI
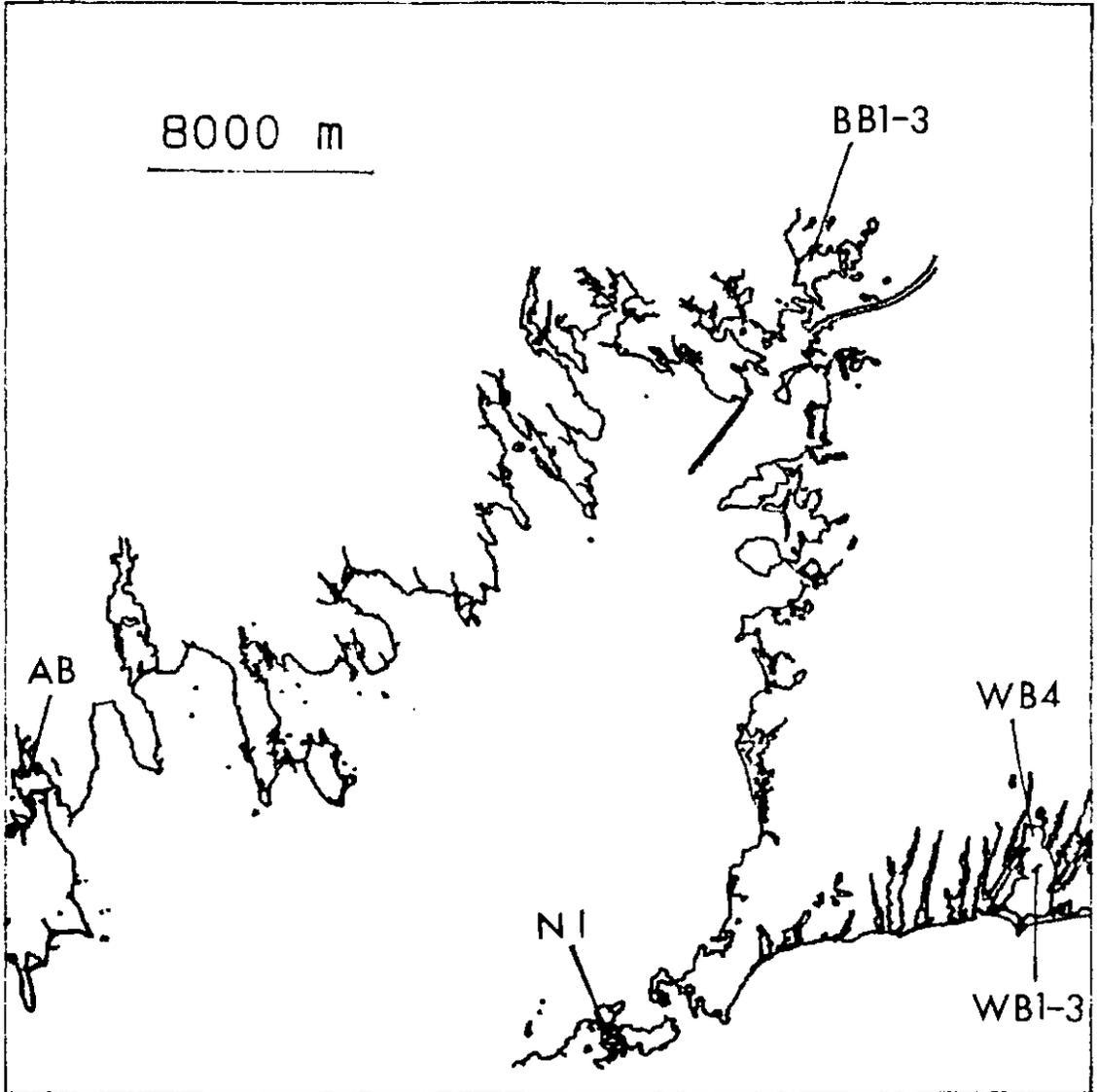
(BB3) in the same area but 50 m from shore at 1.1 m MLW. Four cores
were taken in Waquoit Bay, at the border of Falmouth and Mashpee. Three
of the cores formed a transect from the deep east central part of the
bay at 2.1 m MLW (WB1), toward the east within 0.5 km of both the
eastern shore and the mouth of the Quashnet river, a large stream
entering the Bay. Cores WB2 and WB3 were taken at 1.9 and 1.8 m MLW
respectively, and each core was at least 200 m from the nearest core. A
fourth core (WB4) was 60 m south of the northern shore of the Bay at 1.1
m.

The cores were taken underwater by pushing a 10 cm diameter PVC
pipe into the sediment 40 to 80 cm, plugged, brought to the laboratory,
and sectioned in 1.5 or 3 cm intervals. Sections were wet sieved into
three fractions: 1-2 mm, 2-10 mm, and >10 mm, to determine the abundance
of eelgrass fragments and seed coats, as well as invertebrate remains.

In Waquoit Bay today, sizable beds of eelgrass grows only near the
mouth of the Bay, 1.5 km from the nearest any core and is found today.
To determine if these beds contribute any seeds to the area where the
core was taken, 24 10 cm shallow cores were taken around this bed to
determine the distribution of seed dispersion. Four cores were taken
near the center of the bed at 0.9 m, 4 were taken at the deep edge of
the bed at 1.4 m, and 4 cores each at were taken 5, 20, 50, and 100 m
from the edge of the bed at depths between 1.4 and 1.6 m.

Recent changes in eelgrass abundance were determined from aerial
photographs, oral and published reports, and nautical charts. *Ruppia
maritima* L. (widgeon grass) sometimes co-occurs with eelgrass in this
region, but is more abundant in shallow quiescent or estuarine

environments where eelgrass is less common. Its seeds are also found in the sediment and are good indicators of a shallow or estuarine habitat.

Results

In all the cores, eelgrass seed coats and eelgrass detritus were well preserved in anoxic mud. Whenever eelgrass rhizome fragments were present within core sections, eelgrass seed coats were present as well. Eelgrass seeds may occur without rhizome fragments within a core section, but other eelgrass detritus is usually present. Living eelgrass seeds were found only in cores (near the surface) taken near existing eelgrass beds (Naushon Is. and Buttermilk Bay cores), and not in the other cores.

The annual mean seed deposition rate and propagation distance were calculated from living seed densities measured in surface cores taken from within the bed, and at distances of 1.5-6 m, 12-30 m, and >1500 m (the profile cores), and plotted against distance from the existing bed at the mouth of Waquoit Bay (Fig. 2). The greatest number of seeds were found with the beds (mean annual rate $\approx$1000 seeds m^{-2}, high = 2700 seeds), compared to no seeds found at the core profile stations. Because there were no intermediate stations 30 and 1500 m, it is unclear how far seeds can travel, but these results suggest that most seeds land near the beds that produced them. Thus the contribution of seeds by the existing beds in Waquoit Bay are negligible where the seed profile cores were taken, and instead reflect eelgrass cover in the center of the Bay. These results are also consistent with exponential declines in seed

Figure 2. Seed densities distribution in Waquoit Bay.

Distance values were transformed Log(x+1). Samples were taken north of eelgrass on the flood delta at the mouth of the Bay; 0 = within the bed.
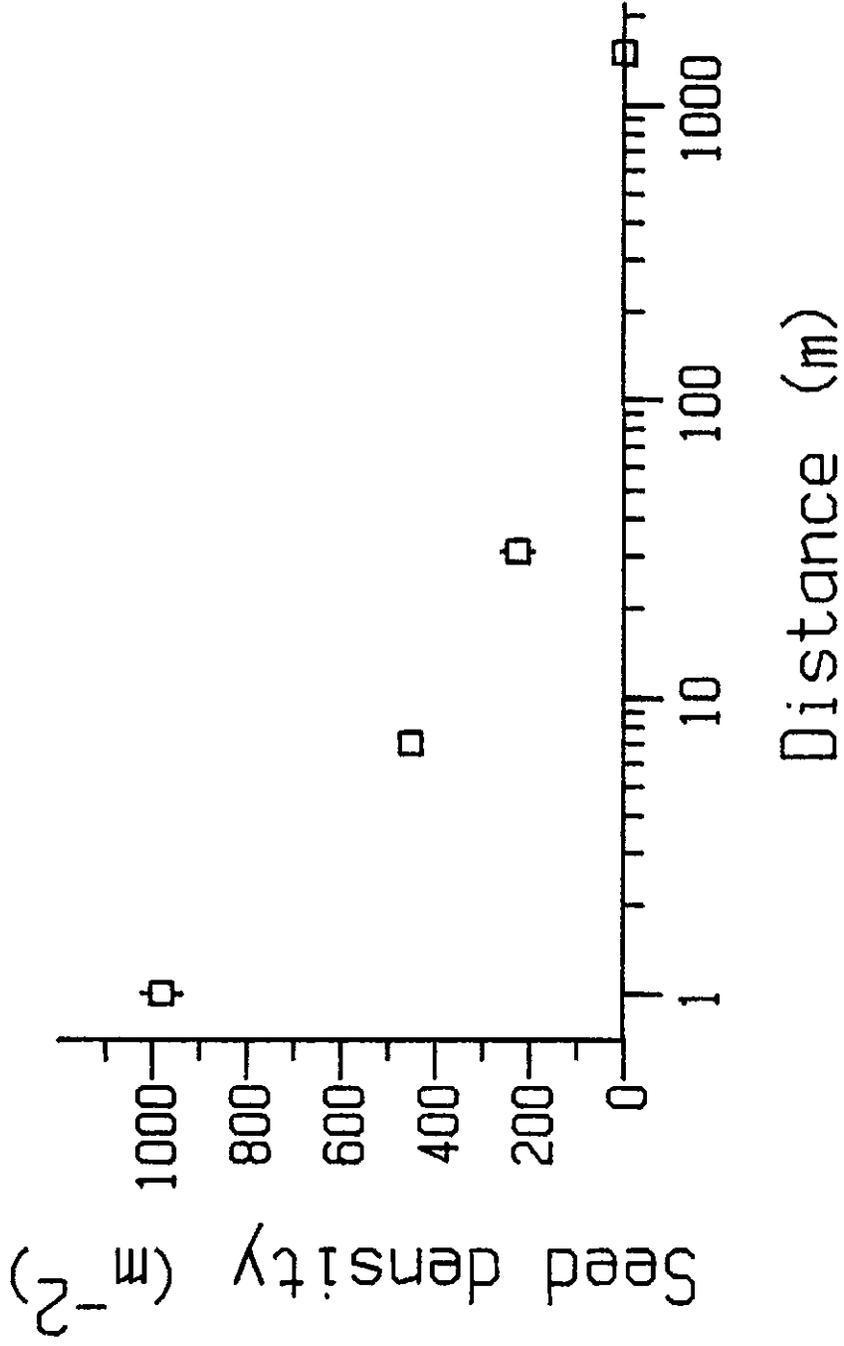
densities observed in wind dispersed seeds from trees (Sharpe and Fields, 1982).

All the cores documented major fluctuations in eelgrass abundance in the past reflecting local fluctuations in abundance (Fig. 3). Because the cores taken in Waquoit Bay were all taken from stable environments, analyzed in more detail, and had more replicates, they will be discussed first.

Waquoit Bay

The cores from the Waquoit Bay transect (WB1-WB3) each showed three major peaks (B-D) in eelgrass abundance, separated by periods when eelgrass was absent (Fig. 3, WB2 not shown). The depth of each these peaks was progressively deeper along the transect toward the Quashnet River and eastern shore, indicating higher rates of sediment deposition from either of these sources. Biogenic depositional markers demonstrate that these three peaks are identical. Three major mortalities of bay scallop *Argopectin* juveniles between peaks B and C occur in the three cores (S's in Fig. 3). For example, in the 31.5-33.0 cm section in core WB2 (117 cm^3), 42 valves *of Argopectin* juveniles were found that lacked signs of predation. Furthermore the snail *Bittium alternatum* is abundant on the bottom of Peak B and top of Peak C on all three cores, with densities exceeding 3 *Bittium* per cm^3 in some sections. A large population of the mud snail *Nassarius* sp. appear in eelgrass peak D of cores WB2 and WB3 as well, which were sampled to greater depths than core WB1.

Figure 3. Sediment core eelgrass seed profiles in 4 Bays.

Apponagansett Bay (AB), Naushon Is. (NI), Buttermilk Bay (BB) and

Waquoit Bay (WB). Symbols indicate peaks *Nassarius* (N) and *Argopectin*

juvenile mortality (S). A-D indicate *Zostera* peaks described in text.

Bittium peaks are not shown.

Depth (cm)
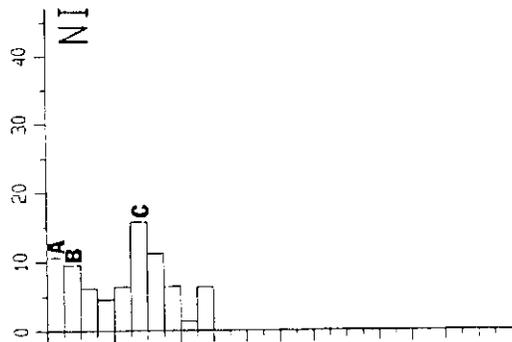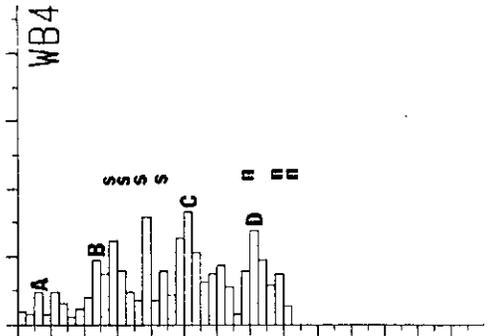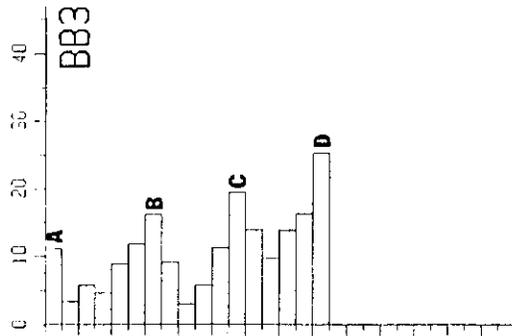
The seed profile in the core taken along the northern shore of Waquoit Bay (WB4, Fig 3) appears dissimilar from the mid-bay cores, nonetheless, the *Argopectin* mortality, *and Bittium* and *Nassarius* peaks indicate that the three lower, less distinct peaks in this core correspond to peaks B-D in cores WB1-3. In addition, photographs show that eelgrass grew later here (peak A), in this shallow, nearshore area than the deep cores.

The dates of these changes in eelgrass abundance can be deduced from the recent history of eelgrass changes in Waquoit Bay. Today no eelgrass grows near any of the cores, and is largely restricted to the flood delta in the south end of the Bay. The wasting disease of 1931-32 destroyed eelgrass throughout the region, but the cores demonstrate that eelgrass grew even in the deepest parts of the Bay in the past. The photographic record (1938-present) indicates that in 1938 eelgrass was absent throughout the deep areas of the Bay, but grew abundantly nearshore, especially along the eastern margin of the bay, as well as near core 4. In the 1940's eelgrass began to recolonized the central portion of the Bay, and was very abundant there by the late 1950's. After 1965, eelgrass began to disappear in the deepest parts of the bay, and by the mid-1970's had disappeared from the along the Bay margins as well, including near core 4.

This most recent eelgrass decline appears to be to decreased light availability because of increased epiphyte growth and phytoplankton from nutrient loading (Valiela and Costa, in press), and in recent decades, dense layers of drift algae (primarily *Cladophora*, *Gracillaria*, and *Agarhdiella*, up to 70 cm thick) have been accumulating. This dense

layer of algae precludes future recolonization of eelgrass because seedlings cannot survive under dense layers of unconsolidated algae.

From these observations, it appears that the decline of peak C was due to the wasting disease. Peak B documents the recovery of eelgrass in the bay during the 1950's then subsequent decline, and Peak A is present only when eelgrass persisted in recent years as was the case in the vicinity of core WB4. Based on this chronology, the scallop mortalities appear to coincide with the three major hurricanes to impact this region during this century: 1938, 1944, and 1954. Scallop populations have been historically high in Waquoit Bay, accounting for 80% of the fishery in all of Falmouth (Alber, 1987). The bay is large and shallow, which may contribute to the burial of spat during storms.

Within each core, the depositional markers are consistent, but differences exist at each station. The depth of peak B and the most recent *Argopectin* mortality in this core suggests that the recent depositional rate in the north end of the bay (WB4) is similar to the mid-Bay cores (5.5 mm y^{-1}), but slower between 1932 and 1954 (4.8 mm y^{-1}) than comparable periods in the mid-Bay (5.5 mm y^{-1}). During earlier periods at this station the depositional rate here was even lower because peak D is nearer the surface than elsewhere. The more recent increases in sedimentation rate at core WB4 may be due to the enlargement of the flood delta of a small lagoon nearby (Quahog Pond). On recent photographs, this delta is more prominent because of loss of eelgrass cover, and may have expanded during the last 40 years. Boat activity in the Bay has increased appreciably in recent decades and the

resulting sediment resuspension may have contributed to increases in sedimentation there.

The loss of resolution in the seed peaks in core WB4 may be due to the slower deposition rates, increased disturbance from wave action nearshore, or greater contribution from shallow annual beds that persisted between declines.

The highest rates of sedimentation occurred at the station nearest to the Quashnet River (WB3) during the period 1932-1954 (8.8 mm y^{-1}) which was higher than stations further offshore (5.5) during the same period, and higher than observed later at the same station (1954-1987, 6.4 cm y^{-1}). The higher rates may have been associated with cranberry bog construction and use along the Quashnet River during the earlier period. It is unlikely that the higher rates of deposition were due to storms because deposition in all mid-bay cores would be similarly affected.

Using the biogenic markers and rates of sedimentation, the date of recent and earlier declines can be calculated. If the most recent scallop mortality is used as a marker, the date of the decline in peak B can be calculated for each core. At the deepest mid-Bay station (WB1), eelgrass disappeared first ≈1961, then at the shallow mid-bay stations in ≈1971 (core WB2), ≈1973 (WB3, Fig. 4). In the north end of the Bay, eelgrass disappeared ≈1965. The loss of eelgrass in deeper and upper bay stations first, supports the hypothesis that these declines were associated with declining light availability, because this pattern has been observed elsewhere nutrient loading has increased (Orth and Moore, 1983b).

Figure 4. Depth of depositional markers in core WB4.
The date of the most recent decline was estimated from its depth and deposition rates.
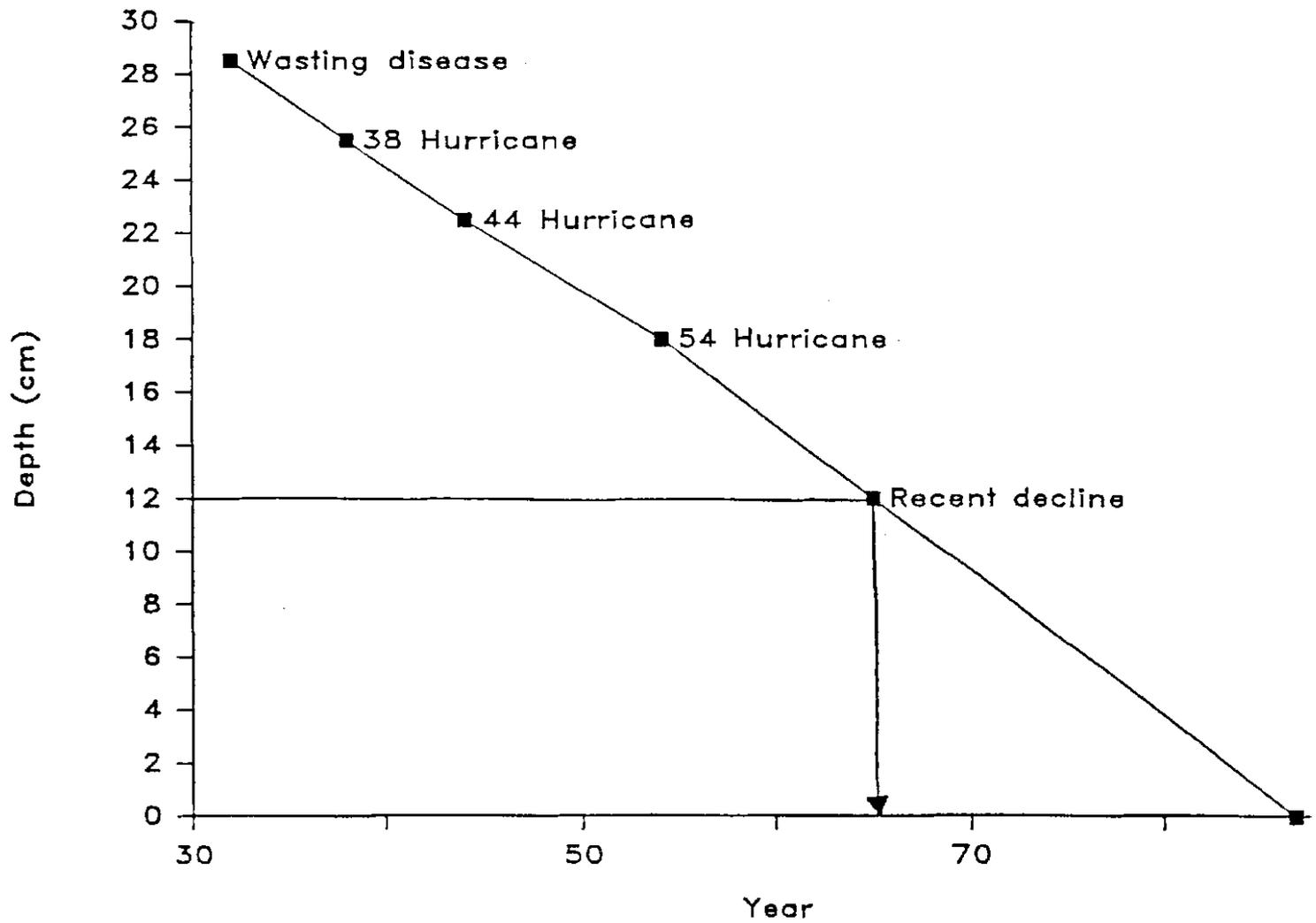
If deposition rates prior to the wasting disease are equal to post-disease rates, then the date of the first pre-wasting disease decline appeared circa 1902-1906 for all four Waquoit Bay cores. In addition, the two cores (WB3 and WB4) with the earliest depositional records indicate an even earlier decline circa 1870-1890.

The cause of the 1902-1906 has several plausible explanations. Some shallow coastal lagoons on Cape Cod close periodically, and a closure of Waquoit Bay would reduce mouth would reduce salinity in the Bay and possibly change water transparency. It is unlikely that Waquoit Bay had become fresh during the last 100 y because all nautical charts to 1865 Waquoit Bay with a prominent channel at the mouth, and marine species persist throughout the core including when eelgrass is absent.

Another possibility is that some other factor caused water transparency to decline, and eelgrass disappeared from the deep areas where the cores were taken. This seems unlikely, because prior to 1931, there was little development around the Bay. Farms were common, but levels of fertilization were far less prior to the use of manufactured fertilizer. Cape Cod has undergone considerable deforestation and conversion to farmland in the past, and topsoil runoff on nutrient release from soils could have been a contributing factor, but this too seems unlikely because river flow into the bay is nominal.

Instead the most plausible explanation is that these declines coincide with the eelgrass population collapses due to disease reported by Cottam in 1908 or 1894.

Other areas

Buttermilk Bay core WB1 (taken on the north end of the flood delta) proved undesirable because 2 dense layers of sand occurred within the core indicating this environment was disturbed or altered in the past. A dense layer of sand at 15 appeared to coincide with dredging nearby that occurred between 1943 and 1951 photographs. A layer of sand at 40 cm may coincide with completion of the Cape Cod Canal nearby around 1916 which caused a change in the hydrography of the bay (Stevens, 1935). Core 2 was taken too close to shore, and rapidly graded into *Ruppia* community, then salt marsh peat. The tops of these cores, nonetheless, showed similar patterns of abundance as BB3 which showed eelgrass declines at 12, 27 and 42 cm.

In Buttermilk Bay, eelgrass was widespread prior to the wasting disease (Stevens, 1935, 1936), and photographs show a broad recovery during the 1940's and 1950's. Eelgrass was somewhat less abundant near this core during the early 1960's, but has expanded since then. Given these observations, and assuming rates of deposition are similar to Waquoit Bay, it appears that the wasting disease began at 27 cm. If sedimentation rates were similar prior to the wasting disease, the earlier decline occurred ≈1903.

The core at Naushon Island was insufficiently deep for comparison to the other cores. This core was taken in a quiescent area 20 m from an undisturbed, protected shore, with no local riverine inputs, therefore sediment deposition rates may be very low here, and the wasting disease may account for the decline in seed abundance at 18 cm. This is supported by the observation that eelgrass declines at the

bottom of the core coincide with large increases in *Ruppia* seeds, which exceed 1 seed per cm^3. This suggests that either the environment was shallow or more estuarine during deposition. Alternately, *Ruppia* replaced eelgrass when the latter disappeared, because both species occupy the habitat today, and *Ruppia* is a relatively minor component. This seems unlikely, however, because *Ruppia* did not become abundant during the most recent decline. If rates of deposition prior to the wasting disease were similar to post disease rates, then the earlier decline at 27 cm occurred ≈1906.

The Apponagansett Bay core is least typical. Eelgrass seems to be persistent in the bay with minor declines at 60 and 33 cm, until a major decline at 21 cm. Subsequently eelgrass recovered, then again declined. This pattern agrees with other evidence: eelgrass is abundant in the bay on nautical charts from the 19th century, eelgrass was destroyed in 1931-32, then showed recovery on aerial photographs during the 1950's and 60's, then disappeared again. In 1985, no eelgrass was found in the inner Bay. The most recent loss of eelgrass appears due to declining water quality from nutrient loading or increased turbidity form sediment resuspension by boats (Costa, 1988).

If the wasting disease occurred 21 cm here, and sedimentation rates are constant, then the minor declines at 33 and 60 cm would coincide with 1902 and 1834.

Discussion

Based on the estimated sedimentation rates and seed densities, seed deposition rates were as high as 2000-6000 m^{-2} y^{-1} in Waquoit Bay,

which is somewhat higher than the mean deposition of new seeds measured at the mouth of that Bay ($\approx$1000 seeds m^{-2} y^{-1}). This difference may not be significant because there considerable variability in the density of recently produced seeds in surface cores within beds. Similarly, cores from the other bays suggest that the seed deposition rates generally peak between 1500-2500 seeds m^{-2} y^{-1}. These rates of seed deposition are consistent with seed production rates measured elsewhere (Thayer et al., 1984), and with rates that I have measured locally (up to 15,000 seeds m^{-2} y^{-1}).

Other factors may contribute to different seed deposition rates in eelgrass beds. Environmental conditions have a strong effect on the expression of flower abundance in eelgrass, and therefore seed production (Phillips et al., 1983). Some eelgrass beds produce mostly reproductive shoots and others produce mostly vegetative shoots, and there is a high degree of consistency for beds in a particular habitat (Phillips et al.,1983; Keddy, 1987). For example, Allee (1923b) noted that eelgrass beds in the Northwest gutter of Uncatena Island in the Elizabeth Islands always have high flower densities. These beds continue to have high flower densities today (pers. obser).

Thus, eelgrass seed coat abundance is a good indicator of local, relative eelgrass abundance, but not necessarily an absolute indicator of biomass or production. Undoubtedly there are yearly differences in seed production, but because these core sections equal 2.5 - 8 years of deposition, this variation should be diminished. Processes that bioturbate the sediment, such as sediment ingestion and excretion by worms, blur the stratigraphic record of some sediment markers such as

radioactive isotopes or pollen profiles. These processes are relatively unimportant in altering the eelgrass record because eelgrass seeds are too large to be ingested by most deposit feeders.

The rates of seed deposition, sedimentation rates, depths of deposition markers, and photograph documentation are all consistent with the interpretations given here, but additional dating methods should be employed to verify actual dates. Nonetheless, these results demonstrate eelgrass populations in each bay have shown sizable fluctuations in the past, and that some of the trends are regional. Some of these fluctuations like the wasting disease of 1931-32 appear clearly in depositional record. Furthermore, reports of declines prior to the wasting disease are substantiated because all the cores show a decline around the turn of the century. If sedimentation rates were similar prior to the wasting disease, as after, then the declines in each bay most closely match the 1908 eelgrass decline in New England reported by Cottam (1934). It is plausible that sedimentation rates prior to the disease were lower, because the frequency of intense storms increased after 1930 (Aubrey and Speer, 1984; Zeeb, 1985), which could have also increased sedimentation rates. If so, then these declines coincide with the 1894 decline reported by Cottam (1934).

The two bays with evidence of nutrient loading effects (Waquoit and Apponagansett Bays) show eelgrass declines that are well documented in the photographic and sedimentary record. Therefor, the use of sediment cores show promise in assessing the impact of anthropogenic disturbance in coastal depositional environments.

Chapter 4

Historical Changes in eelgrass (*Zostera marina* L.) abundance in Buzzards

Bay: Long term patterns and twelve case histories

Introduction

During the 1930's, the "wasting disease" destroyed virtually all
eelgrass (*Zostera marina* L.) along the coasts of eastern North America
and Europe (Rasmussen, 1977). Recovery by eelgrass populations from
this catastrophic disturbance was slow and took 30 or more years in most
areas (den Hartog, 1987). Superimposed on this long term cycle of
collapse and recovery are more recent, local, short and long-term losses
of eelgrass due to declining water quality, storms, dredging,
shellfishing, and other sources (Orth and Moore, 1983b, Kemp et al.,
1983; Thayer et al., 1975). Too often, documentation of declines and
recolonization of eelgrass have been qualitative and this has hindered
an understanding of the mechanisms or relative importance of different
disturbances on eelgrass distribution and abundance. To understand or
predict the impact of these disturbances, it is necessary to have data
of present-day eelgrass cover, historical changes, or data from
comparable areas.

The main objective of this paper is to document long-term changes
in eelgrass abundance in areas of Buzzards Bay that have had different
histories of anthropogenic and natural disturbances. From this
information, inferences can be made on the relative impact and return
time of eelgrass populations impacted by disturbances of different scale
and intensity. Because the effects of the wasting disease were so
longlasting, and because new outbreaks of the disease have been
reported, I also reassess the causes and impact of the wasting disease
in Buzzards Bay. In particular I examine the relevance of the

temperature hypothesis to this and earlier declines in eelgrass populations.

I have documented changes in eelgrass abundance from aerial photographs, written reports, old charts, observations of local residents, and in a few cases, sediment cores. This approach has been used elsewhere, most notably in Chesapeake Bay, where the loss of eelgrass and other submerged macrophytes in recent years has been documented (Brush and Davis, 1984; Davis, 1985, Orth and Moore, 1983b). I have based my interpretation of the historical record on factors that limit eelgrass distribution and on the local history of natural and human disturbances.

Factors limiting eelgrass distribution

Eelgrass may be absent from an area because of factors that prevent growth or colonization, or because eelgrass has not yet recovered from disease or other disturbance. The most important factor limiting the geographic distribution of eelgrass is light (Dennison, 1987; Wetzel and Penhale, 1983; Sand-Jensen and Borum, 1983). In clear temperate waters, eelgrass grows to 11 m MLW or more, but to less then 1 m MLW in some turbid or enriched bays (Sand-Jensen and Borum, 1983). The deepest reported growth of eelgrass was reported by divers at 45 m in Southern California (Cottam and Munroe, 1954). When there is sufficient light available, the next most important factors limiting eelgrass distribution are physical energy, salinity, and temperature.

Eelgrass is euryhaline, but is usually not found where salinities persist below 5 ppt (Sand-Jensen and Borum, 1983; Bieble and McRoy,

1971). In Buzzards Bay and on Cape Cod, there are few sizable inputs of freshwater, and eelgrass distribution is limited by salinity in only a few areas.

Physical energy also controls eelgrass distribution, but eelgrass can has the ability to grow in diverse habitats. For example, eelgrass beds can grow at sustained current velocities up to 150 cm sec^{-1}, and may tolerate brief exposure to higher velocities (Fonseca et at., 1982a, 1983). Eelgrass beds can tolerate considerable wave exposure as well, but are generally not found in the surf zone. Thus, on exposed coasts eelgrass may not grow above 2 m MLW, whereas in protected areas, eelgrass may be found in the intertidal. There are exceptions: clumps of eelgrass can be nestled between boulders or in intertidal pools in high energy areas (pers obs).

Eelgrass is eurythermal, and can survive between the freezing point of seawater and 40° or more, therefore temperature is important only in shallow stagnant waters such as salt ponds and salt marsh pans which are exposed to wide temperature fluctuations or appreciable icing (e.g. Keddy, 1987). In these and other shallow areas, freezing and ice scour may remove beds (Robertson and Mann, 1984), and annual populations of eelgrass are most common in these types of habitats.

The wasting disease

The "wasting disease" of 1931-32 greatly depleted eelgrass (*Zostera marina* L.) populations in the North Atlantic, and most populations did not recover for many decades (den Hartog, 1987). Other declines were reported in 1890 in the Eastern U.S., and in 1906 in New

England (Cottam, 1934). The loss of eelgrass in the 1930's resulted in declines in many animal populations, as well as increased erosion on some beaches (Thayer et al., 1984; Rasmussen, 1977). Because effects of this decline were so profound and longlasting, and because new outbreaks of the disease have been reported (Short et al., 1986), there has been concern about new collapses of eelgrass populations.

The wasting disease was documented by numerous observers, and its causes and effects have been periodically reassessed (Stevens, 1939; Milne and Milne, 1951; Rasmussen, 1977; den Hartog, 1987). Before the wasting disease, eelgrass populations were generally described as dense and widespread in temperate waters (den Hartog, 1987). In the western Atlantic in the summer of 1931, black and brown spots appeared on eelgrass leaves, spread to other leaves and shoots; leaves became necrotic and plants died. The outbreak of the disease continued the following year, and by the end of 1932, the vast majority of eelgrass populations on the east coast of North America disappeared. Events were similar in Europe, but the declines in eelgrass abundance began in 1932, and continued in 1933 (Rasmussen, 1977). Neither eelgrass populations in the Pacific, nor other *Zostera* spp. endemic in Europe were affected by the disease.

Assessment of loss of eelgrass were generally qualitative because most eelgrass populations were not previously mapped, and descriptions were limited to areas where shellfish wardens or researchers had been familiar. Observers described how eelgrass had formerly covered the bottom of certain bays before the disease, whereas after the disease, eelgrass was no longer present. It is generally believed that the

disease destroyed at least 90% of all existing eelgrass beds throughout Atlantic coasts, and in many areas destruction was complete (den Hartog, 1987). Observations in Denmark substantiate this view, because eelgrass beds were studied and mapped during the early in the 20th century. Eelgrass populations around Cape Ann Massachusetts disappeared (Cottam 1933, 1934). In Buzzards Bay, eelgrass virtually disappeared from Buttermilk Bay, Bourne (Stevens, 1935, 1936), Sconticut Neck, Fairhaven, and West Falmouth (Lewis and Taylor, 1933), and around Woods Hole (Stauffers, 1937). Stevens et al. (1950) estimated that less than 0.1 % of pre-existing eelgrass bed cover in upper Buzzards Bay survived the disease.

Since the wasting disease, eelgrass populations slowly recovered on both sides of the Atlantic, and greatest rates of expansion occurred during the 1950's and 1960's (den Hartog, 1987; Rasmussen, 1979), but some areas are still expanding today (den Hartog, 1987).

Considerable controversy has arisen as to the cause of the wasting disease. In the 1930's, the cellular slime mold, Labarynthula, was associated with the wasting disease, however, it was unclear at the time whether the slime mold was the cause of the disease or merely a symptom of a disease caused by pollution, abnormally warm or dry weather, or some other physical factor or biological agent (Cottam, 1934; Milne and Milne, 1951). Recently, Short (pers. comm.) has demonstrated that Labarynthula was the biological cause of the wasting disease, but what triggered the catastrophic decline in 1931-32 remains unclear.

Rasmussen (1977) presented an analysis of the wasting disease that has been widely accepted. He rejected all previous hypotheses

concerning the disease except the effect abnormally warm temperatures
which were elevated during the early 1930's. Water temperatures were
not exceptionally warm in all areas during that period, but came after a
prolonged cool period. This warm period resulted in the elevation of
mean water temperatures by several °C that stressed eelgrass, making it
more susceptible to a pathogen. He explained the occurrence of the
disease one year later in Europe was because the warming period occurred
one year later there as well.

Rasmussen acknowledged that *Zostera* can tolerate wide temperature
ranges throughout its geographical range, but suggested that eelgrass
populations are adapted to local temperature conditions and were
sensitive to these changes. He suggested that the survival of eelgrass
populations near streams and other sources of freshwater may have been
due to higher rates of germination in annual populations near these
sources or that the disease organism was stenohaline.

The temperature hypothesis cause of the decline of 1931-32 has
been criticized for several reasons, and these are discussed below.
Past declines of eelgrass have also been reported, such as in 1894 in
the eastern U.S., around 1908 in New England, and in 1916 in Poponesset
Bay, Cape Cod (Cottam, 1934). These events, perhaps due to disease,
were not as catastrophic as the 1931-32 decline, and were not well
documented.

Anthropogenic and natural disturbances

Light, wave and current energy, salinity, and temperature limit
eelgrass distribution, but many natural and anthropogenic disturbances

of varying scale and frequency destroy eelgrass beds. Certainly the most important natural disturbance during this century was the wasting disease, but other natural disturbances such catastrophic storms, periodic storms, sediment transport, ice damage, and grazing play an important role in controlling eelgrass abundance (Harlin et al., 1982; Jacobs et al., 1981; Kirkman, 1978; Orth, 1977; Rasmussen, 1977; Robertson and Mann, 1984).

Anthropogenic disturbances that may destroy seagrass beds include physical disturbances (dredging, groin construction, shellfishing, propeller damage), toxic pollution, and degradation of water transparency from nutrient enrichment, topsoil runoff, and activities that resuspend sediments (Cambridge, 1979; Kemp et al., 1983; Orth and Moore, 1983b; Orth and Heck, 1980; Sand-Jensen and Borum, 1983; Thayer, et al., 1975).

The cause of a particular loss of eelgrass can often be inferred from the pattern and rate of loss, the rate or lack of recovery, and the local history of an area. Of all the anthropogenic an natural disturbances affecting eelgrass populations, severe climatological events and declining water quality have had the greatest impact on eelgrass abundance in southeastern Massachusetts, and are discussed in greater detail below.

Storm damage and ice scour

Natural physical disturbances such as storms, ice scour, and sediment erosion affect large scale patterns of seagrass distribution (Harlin et al., 1982; Kirkman, 1978; Robertson and Mann, 1984). Aubrey

and Speer (1984) and Zeeb (1985) documented that hurricanes in 1938 and September, 1944 had the greatest impact on Cape Cod during this century, and these and other major storms affect this region are listed in Table 1.

Ice scouring, can have a great impact on eelgrass abundance in shallow water, but because it does not greatly impact human activity locally, it has not been well documented. Periodically, Buzzards Bay accumulates considerable ice cover that may extend several miles offshore in places, and ice thickness may exceed 30 cm in some poorly flushed areas where icing is more frequent (pers. obs. and press reports). Years in which ice scour was appreciable can be determined from winter water temperature data because water temperature correlates well with reported ice accumulation (Wheeler, 1986, and other sources). In general, years in which mean February water temperatures (c.f. fig 16) is below -0.5 °C in Woods Hole, ice accumulation in Buzzards Bay is appreciable. These years are summarized in Table 1.

Based on Table 1, the years 1938, 1944-1945, 1954, 1960-1961, and 1977-1978 had the greatest storm intensity or combination of disturbances that could have impacted eelgrass abundance. Undoubtedly, wind direction, orientation of the shore, path of storm, and local hydrography had a great effect on the local impact of these events, and smaller storms and wave scour define some smaller patterns of eelgrass colonization and patchiness observed as well.

Declining water quality

Water quality declines result from pollution by toxic compounds, enrichment by nutrients, and increased suspended sediment loads.

Table 1. Major meteorological disturbances in Southeastern
Massachusetts since 1938. The storms are roughly ranked in terms of
severity (from Zeeb, 1985; Aubrey and Speer, 1984, and other accounts)
Ice accumulation was based on mean February temperature (Bumpus, 1957;
NOAA, 1973) and other documentation.

Date		Event	Severity
26 September	1938	Hurricane	extreme
Winter	1940	Ice accumulation	severe
Winter	1941	Ice accumulation	moderate
Winter	1944	Ice accumulation	moderate
Winter	1944	2 storms	strong
September	1944	Hurricane	extreme
Winter	1945	6 storms	strong
Winter	1945	Ice accumulation	moderate
Winter	1948	Ice accumulation	moderate
September	1954	Hurricane	severe
Winter - Spring	1958	>12 storms	moderate-strong
September	1960	Hurricane	strong
January	1961	Blizzard	moderate
Winter	1961	Ice accumulation	moderate
Winter	1963	Ice accumulation	moderate
February	1976	Storm	moderate
Winter	1977	Ice accumulation	severe
February	1978	Blizzard	moderate
Winter	1978	Ice accumulation	moderate
Winter	1981	Ice accumulation	moderate
Winter	1984	Ice accumulation	moderate

Nutrient loading is typically most important over large regions (e.g. Orth and Moore, 1983b), and is caused by human and livestock waste disposal, and fertilizer applications. Increased suspended sediment loading may result from dredging, topsoil runoff, shellfishing, and boating. Pollution by toxic compounds is generally localized.

Nutrient loading and sediment resuspension can have profound effects on eelgrass abundance. The lower limit of eelgrass growth is determined by the duration of light intensity above compensation (Dennison, 1987; Dennison and Alberte, 1985,1986). Hence, in a fundamental way, the distribution of eelgrass is determined by factors that affect water transparency and epiphyte densities (Sand-Jensen and Borum, 1983). Nutrient loading increases phytoplankton and algal epiphyte abundance, which in turn shade eelgrass, causing lower growth and recruitment, or death (Borum, 1985; Bulthuis and Woerkerling, 1983; Kemp et al., 1983; Sand-Jensen and Borum, 1983). Eelgrass beds often first disappear in upper estuaries where nutrient loading is highest, and at the deep edges of beds where light limits growth (Orth and Moore, 1983b).

Along a nutrient gradient in a Danish estuary, biomass of eelgrass algal epiphytes increased 50-100 fold, and phytoplankton abundance increased 5 - 10 fold (Borum, 1985). Light attenuation by epiphytes on eelgrass shoots was 90% on older leaves in these enriched areas (Sand-Jensen and Borum, 1983). Besides shading, algal epiphytes slow photosynthesis by forming a barrier to carbon uptake (Sand-Jensen, 1977). In Buttermilk Bay, the depth of eelgrass growth decreased by 9

cm for every 1 μM increase in dissolved inorganic nitrogen in the water column (Costa, 1988).

The loss of eelgrass in enriched environments is not unique and has been reported for other submerged macrophytes in freshwater lakes and ponds (Moss, 1976; Sand-Jensen and Sondergaard, 1981; Phillips, et. al, 1978), artificial freshwater ponds (Mulligan et al., 1976), tidal estuaries (Haramis and Carter, 1983), artificial estuarine ponds (Twilley, et. al., 1985), and marine embayments (Brush and Davis, 1984; Cambridge, 1979, Cambridge and McComb, 1984; Kautsky et al., 1986; Kindig and Littler, 1980; Orth and Moore,1983b). Experiments on marine ponds containing eelgrass are now in progress in Rhode Island (S. Nixon, pers. comm.).

Alternate explanations have been offered for some eelgrass declines. For example, Nienhuis (1983) suggested that the recent disappearance of eelgrass in a Danish coastal pond was not due to epiphyte abundance, but "toxification" of the sediments from decomposing drift algae that accumulated because of nutrient loading. Sediment suspension from topsoil runoff or boat propeller often contribute to water transparency decline and loss of eelgrass (Brush and Davis, 1984; Orth and Moore, 1983b). Even where sediment turbidity is high, however, such as parts of Chesapeake Bay, attenuation of PAR by inorganic particles is generally less than the combined effects of PAR absorption by algal epiphytes and phytoplankton (Kemp et al., 1983). Nonetheless, sediment resuspension from dredging and motor boat activity is prominent in some local bays (pers. obser.), and may significantly decrease water

transparency. This phenomenon has not been quantified, but may be locally important in affecting eelgrass distribution.

In southern New England, eelgrass grows as deep as 6-12 m MLW in clear offshore waters, but only to 1-2 meters in shallow bays with poor water transparency (Costa, 1988 and below). Thus, small changes in light availability to eelgrass populations, for whatever reason, may result in larges losses of eelgrass cover.

Drift algae

Drift algae typically show conspicuous increases where nutrient loading is high, and often accumulate in poor flushed bays in layers exceeding 40 cm (Lee and Olsen, 1985; pers obs.) This accumulation may smother shellfish (Lee and Olsen, 1985) and eelgrass (pers. obser.). Locally, red algae such as *Gracillaria*, *Agahrdiella*, and *Ceramium* are most abundant, often mixed with green filamentous algae such as *Cladophora*. Many of these algae are specialized morphological varieties of their species (Taylor, 1957) which grow and reproduce on the bottoms of bays. In more enriched areas, particularly near polluted streams or near enriched groundwater inputs, green algae such as *Ulva* and *Enteromorpha* replace the red algae that dominate less enriched areas (Lee and Olsen, 1985; Pregnall, 1983; pers. obser.). This difference in species composition can be explained by the fact red algae are effective in storing "pulses" of nutrients, whereas these green algae grow quicker under more continuous exposure to high nutrients (Fujita, 1985).

Drift material may also consist of shed eelgrass leaves and detached *Codium*. Algae that are abundant on eelgrass such as the red alga *Polysiphonia*, are abundant in drift material in these areas.

Recolonization and interpreting historical changes

Eelgrass may decline in some areas due to disturbance, but will recolonize any devegetated area, as well as newly created habitat, if conditions are conducive to lateral growth of vegetative shoots or germination and survival of seedlings. Colonization rates have been documented in transplant studies. For example, Fonseca et al. (1979, 1982b) state that full coverage can be obtained in one year by transplanting 20 shoots on a 1 m grid. Similarly high rates of expansion have been noted in other studies (Araski, 1980; Goforth and Peeling, 1979).

In related work (in prep.), I have studied the colonization of bare substrate by eelgrass using sequences of aerial photographs. From these photographs, vegetative growth rate, recruitment rate, disturbance size and frequency (= bed mortality) can be measured and these four parameters, were incorporated in a computer simulation. The results of this model demonstrated that the colonization of bare areas by eelgrass greatly depends on colonization by new seedlings. To a lesser degree, rates of colonization depend on vegetative growth rates and levels of disturbance. Disturbance intensity, however, does affect the % cover of an eelgrass bed at peak abundance. Hence, an eelgrass bed in a high energy, wave swept shore, may never cover more than 50% of the available substrate due to winter storms and wave scour.

Methods

Photograph analysis

In Massachusetts, parts of the coastline have been repeatedly photographed since 1938, and these photographs were obtained from various private and governmental agencies (Appendix I). Most of these photographs were taken between late spring and fall when eelgrass is densest, but photographs taken during other periods were are also informative, particularly when mapping perennial eelgrass populations. Only one set of photographs taken prior to the wasting disease was found (Sippican Harbor, Marion, taken June of 1930).

Photographs were analyzed and interpreted as described in chapter 1. As described earlier, there are four types of vegetation that resemble eelgrass beds, but can usually be distinguished on photographs: drift algae, salt marsh peat reefs, algal covered rock fields, and shell and gravel areas where the green alga *Codium* may be abundant. *Codium*, however, is a recent introduction and was not abundant in Buzzards Bay prior to the late 1960's (Carlton and Scanlon, 1985). Similarly, drift algae is increasing in some bays, but is absent from nearly all areas on early photographs.

Nautical charts

The presence of eelgrass on old nautical charts (especially US Coastal and Geological Survey charts), is sometimes denoted by "Grs", "Grass" or "Eelgrass". Only rarely were boundaries of eelgrass beds mapped. This documentation apparently depended greatly on the whim of

the field observer or mapmaker, and indications of eelgrass appear on some maps or map editions and not on others. Furthermore, because observations were made from boats, only beds that were conspicuous from the surface (general less than 3.0 m) are recorded. Even then, to prevent map clutter, "Grs" may be written once within a bay. Thus the denotation of eelgrass on a nautical charts affirms that eelgrass was present, but the lack of denotation does not imply eelgrass was absent.

Study sites

Changes in eelgrass abundance was studied at 12 sites around Buzzards Bay: The Westport Rivers; Apponaganset Bay, Dartmouth; Clarks Cove, South Dartmouth; New Bedford inner and outer harbor; Nasketucket Bay, Fairhaven; East Bay, West Island, Fairhaven; Sippican Harbor, Marion; Great Neck, Wareham and the Wareham River Estuary; Buttermilk Bay, Bourne and Wareham; Megansett Harbor, Bourne and Falmouth; Wild Harbor, Falmouth; and West Falmouth Harbor. In addition, data from another site on Cape Cod (Waquoit Bay) was included because this bay has had prominent declines in eelgrass. These sites had different histories of anthropogenic and natural disturbances which are detailed in the results section along with their description.

Results

Westport Rivers

The East and West Branch of the Westport Rivers form the largest estuary in Buzzards Bay and historically have provided a substantial coastal fishery (Fiske et al. 1968, Alber, 1987). The land around the

Westport Rivers is rural with considerable agricultural development. This agricultural land is used for both crops and livestock and residential sewage disposal consists of septic tanks. The northern end of the East Branch of the Westport River has been closed to shellfishing due to fecal contamination (Alber, 1987).

Most fresh water enters through the East Branch of the Westport River (Fig. 1). Riverine inputs into this Branch declined during the early 1960s because of construction of the Calamut dam and Intestate Highway 195. The mouth of the estuary is moderately well flushed and experiences a 0.9 m tidal range, but residence times for different sections of the estuary have not been calculated. Photographs and observations of residents indicate there has been considerable meandering of the channels and migration of sand flats within the bay, especially near the mouth.

No early documentation on eelgrass abundance was discovered, but some residents recall that eelgrass was far more abundant in the past than its present-day maximum, and eelgrass was virtually eliminated by 1932. Since then, eelgrass has slowly recovered and during the 1980's has shown dramatic increases in abundance.

The recovery of eelgrass in the Westport rivers has not been steady, and like several other shallow embayments in Buzzards Bay, there have been great fluctuations in eelgrass abundance during the last 50 years. Because of insufficient spatial and temporal coverage of aerial photographs, poor image quality, or water transparency, changes in eelgrass abundance could not be quantified for the entire estuary.

Figure 1. Site names around the Westport Rivers.

Dashed lines indicate upper extent of eelgrass in the northern part of the estuary on different dates. The position of eelgrass beds north of detail of the Westport Rivers showing site names, and changes in the upper estuary limits of eelgrass growth.

WESTPORT

1959
1942

Big Pine Is.

1987

Great Is.

Angeline Cove

1987

East Branch

1942

Judy Is.

Hicks Cove

Wesport Pt.

West Branch

Great Flat

Mulder Cove

Big Ram Is.

Bailey Flat

Corys Is.

Horseneck Pt.

Horseneck Beach

1000 m
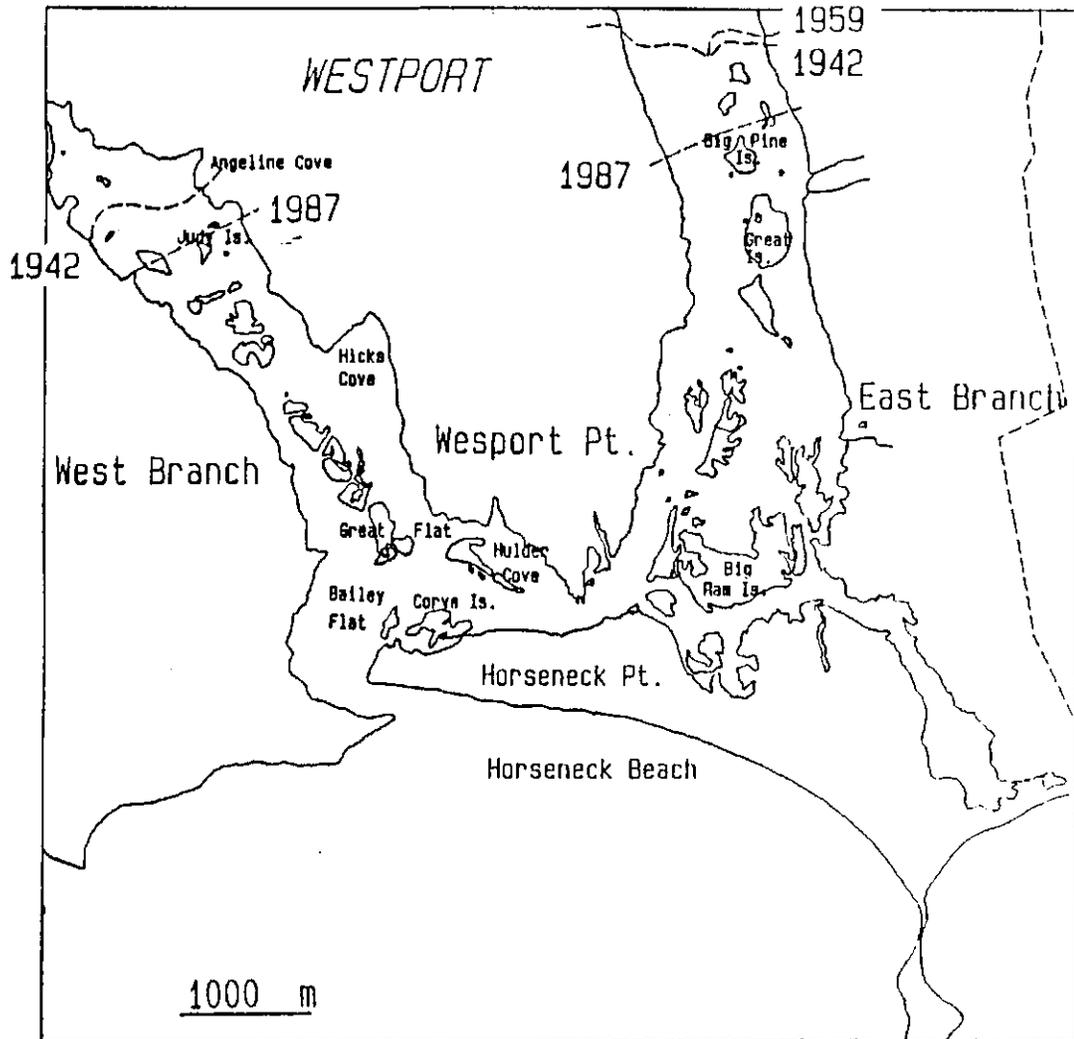
MAP COORDINATES = 323 331 594.5 602.5

Nonetheless, a brief description of available photographs demonstrate some features of changing eelgrass abundance in this estuary.

The earliest photograph (13 December 1938) has poor image quality, high water turbidity, and taken near high tide. There is virtually no eelgrass apparent on this photograph, and it is unclear if the absence of eelgrass is an artifact of poor imagery, or due to the September 26 hurricane. A few shoals near the mouth are visible, however, and do not have eelgrass beds that appear on later photographs.

A June 1942 photograph sequence shows eelgrass widely dispersed in the bay, but the beds are small. In the East Branch, numerous circular patches 5 - 30 m in diameter are aggregated on submerged sand bars, with more continuous beds stretching along channels. Eelgrass was considerably less abundant in the West Branch during this period, and the most prominent beds grew in the north end of the bay, around Great Island, and near the mouth of the estuary, particularly north of Bailey Flat. The upper estuarine limit of eelgrass in the East Branch was 200 m north of Upper Spectacle Island, and 100 m north of Great Island in the West Branch.

Because more freshwater enters the East Branch, the higher densities of eelgrass there are consistent with higher bed survival near streams observed elsewhere after the wasting disease Rasmussen (1977). This does not explain bed abundance near the mouth, although it is possible that these beds were recruited after the disease.

No photographs were obtained showing changes in eelgrass abundance due to the 1944 hurricane. During the 1950's, three sets of imagery are available: 22 April 1954, 1 May 56, and 22 September 1959, but none of

these surveys had complete coverage of submerged features. The 1954
survey of the West Branch shows eelgrass is absent from the north end of
that river, but abundant near the mouth of the estuary. The absence of
eelgrass near in the upper part of the River is due to the fact that
even today, many of these beds in shallow water are annual, and do not
appear until after June.

Like the 1954 imagery, 1956 photographs show eelgrass nearly
absent in the upper West Branch, but eelgrass is diminished near the
mouth as well. In particular, beds around Whites Flat and Bailey Flat
are substantially reduced, even though this photograph series was taken
later in the growing season. The cause of this decline appears to be do
to the September 1954 hurricane, and there are several changes in
bathymetry near the mouth such as shoal movement around Bailey Flat, and
enlargement of a channel across Whites Flat.

The September 1959 survey included only the upper East Branch, but
eelgrass is more abundant than summer 1942, and occurs as large
continuous beds. The northern limit of growth has extended 100 m
further north, and a 9.5 ha bed grows across the channel north of Little
Spectacle Island.

A 10 April 1962 series of photographs are remarkable in that
eelgrass is nearly absent from all parts of the bay, including the deep
perennial beds that are visible on the early spring 1954 and 1956
photographs. The only perennial vegetation near the mouth are beds
along the deepest parts of the main channel walls. Some small patches
occur in shallow water around the bay, and the largest of these were
several <0.5 ha beds around Great Island in the West Branch. The likely

cause of this decline was the September 1960 hurricane, and ice scouring and a blizzard in 1961. These storms also caused shoal movement near the mouth, and further enlarged the channel across Whites Flat.

A September 1969 image has too much cloud cover to observe fine detail, but eelgrass is abundant north of Bailey Flat and appears to extend in the West Branch to Judy Island and in the East of Great Island. In November 1979, eelgrass distribution is abundant in the main channel at the bottom of the east branch, and some patches extend north at least to Sanford Flat in the West branch and Great Island in the East Branch. Vegetation is sparse in both Branches, but this could be due to severe ice scour in 1977, and a blizzard with exceptional tides and winds in 1978. A June 1982 photograph of the West Branch shows that eelgrass remains sparse throughout the upper limits of the estuary, even though there was no recent disturbance. Since 1985, eelgrass has expanded greatly in the lower end of each Branch of the Westport River, but has not extended further north into the estuary.

Overall, the Westport River has the most complex history of changing eelgrass abundance of any site studied in Buzzards Bay. The shallow bathymetry in this estuary make eelgrass populations susceptible to storms and ice scour, and likely accounts for the wide fluctuations in eelgrass cover observed. This pattern is markedly different from bed recolonization on the outer coast which typically show continuous expansion over decades.

Changes in bed cover around some areas like Bailey Flat (Fig. 2) can be explained by migrating shoals, storms and ice scouring. Other changes, like the migrating upper estuarine limit of eelgrass growth

Figure 2. Changes in eelgrass bed position and flat migration
north of Bailey Flat, Westport.

Darkened areas indicate where eelgrass is present.

1942

250 m

1954

1962

1979
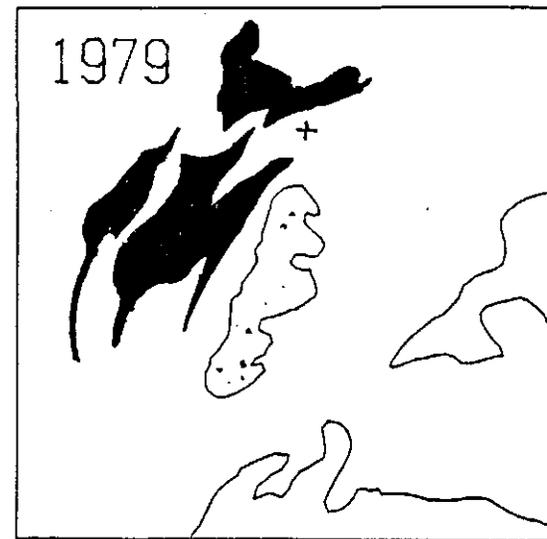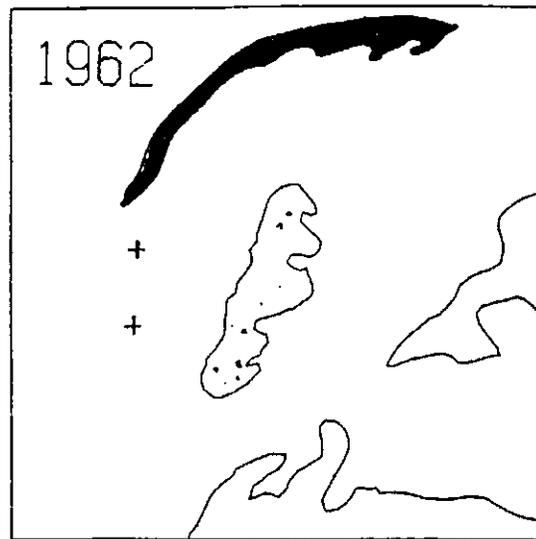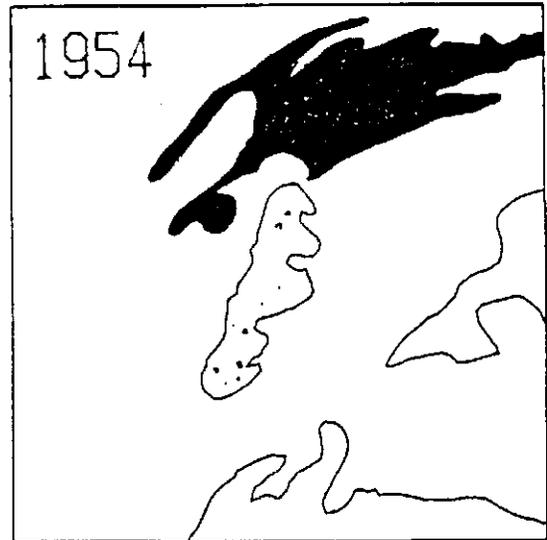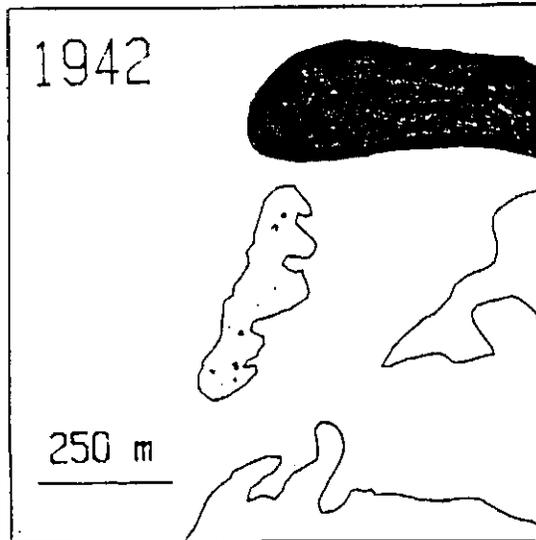
(Fig. 1), and the general decline in eelgrass abundance in the upper part of the estuary since the 1940's and 1950's are likely due to other causes such as nutrient loading. For example, benthic algae and eelgrass algal epiphytes become more conspicuous as one moves northward into the West Branch. Near the mouth, the depth of eelgrass growth is 2.5 m whereas east of Sanford Flat, eelgrass grows to less than 0.5 meters. Shellfish beds in the north end of the East Branch have been closed due to high fecal coliform counts, and elsewhere bacterial inputs are usually associated with nutrient inputs. Together, these facts suggest that nutrient loading is becoming problematic in the Westport Rivers, and needs further study.

Given the importance of this estuary, a more comprehensive understanding of the changing eelgrass abundance there is desirable. Periodic photographic surveys should be taken under favorable conditions during several growing seasons, and damage from storms and ice scouring should be monitored. Historical changes in distribution and abundance can be accurately documented from sediment cores taken at suitable locations around the bay.

Apponaganset Bay, Dartmouth

Like the Westport Rivers, Apponagansett Bay, in South Dartmouth is a shallow embayment with abundant shellfish beds. There is considerably less freshwater input here than in the Westport Rivers, and the main surface input is from Buttonwood Brook (Fig.3), which includes animal waste from the New Bedford Zoo. The salinity of virtually all of the bay is above 20 ppt (J. Freitas, pers. communication). Padanaram on the

Figure 3. Map showing site names around Apponagansett Bay, So.
Dartmouth.

The location of a sediment core is labeled 'C'.
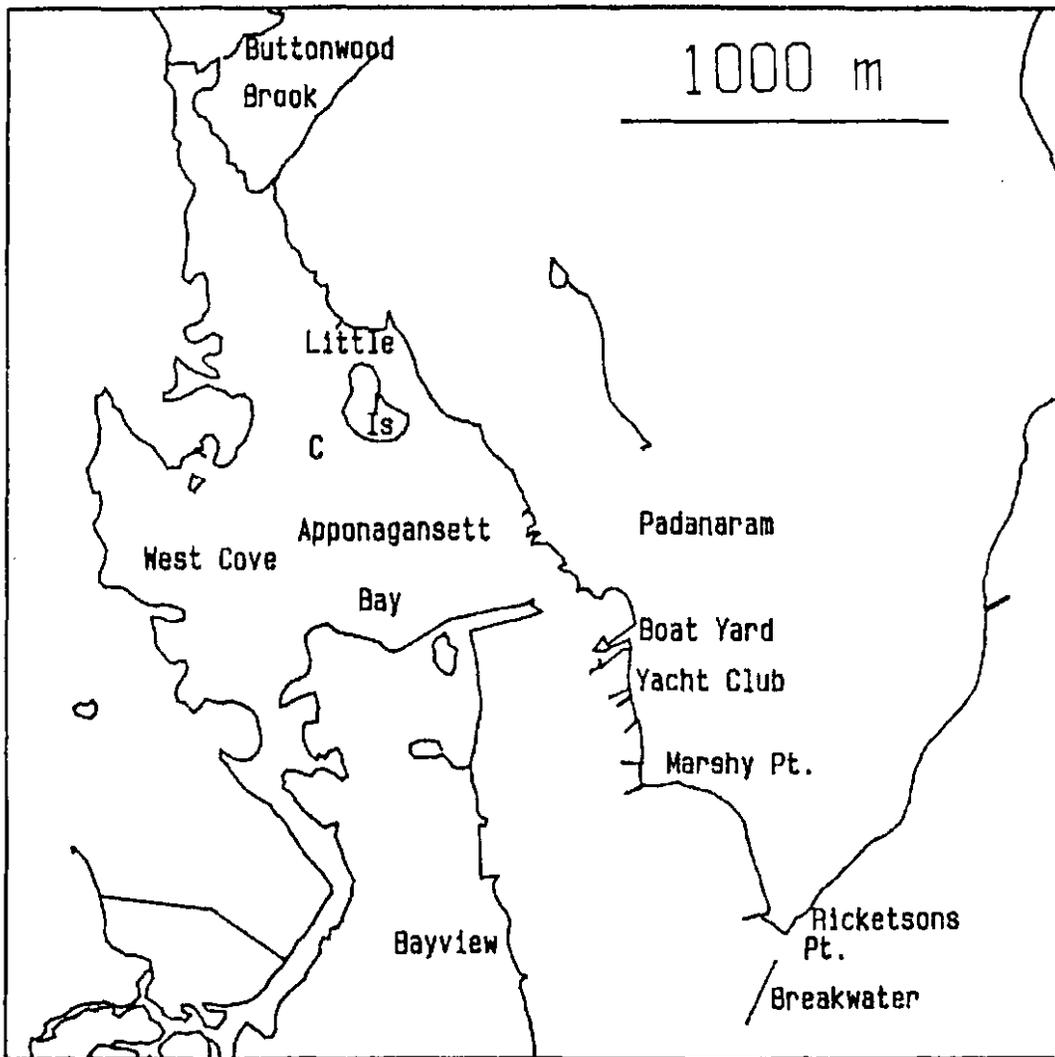
eastern shore is densely developed, and residences are serviced by septic tanks.

A sediment core taken 150 m west of Little Island (see chapter 3) and other historical documentation was suggest that eelgrass was abundant in the inner Bay for many years prior to the decline of the wasting disease. Afterwards. eelgrass began to recover with some major fluctuation during 1940-1960, but declined again in the last 15 years. In contrast, eelgrass in the outer Bay continuously expanded after onset of colonization in the 1940's.

The cause of these changes can be inferred from the long-term patterns of eelgrass distribution in this Bay, and the time when changes occurred. For example, coastal charts of Apponagansett Bay from the turn of the century shows that eelgrass is abundant in the deeper part of the inner harbor (0.9-1.8 m MLW; Fig. 4). Typical of these charts, eelgrass is occasionally noted where it is abundant, but to avoid clutter eelgrass is not identified in all areas where it grows. This fact is demonstrated by the core data, because eelgrass was continuously abundant west of Great Island prior to the wasting disease, but is not indicated there on these early charts. If recent photographs can be used as a guide to determine the nearshore and northern limits of growth, it would appear that all but the deepest parts of the Bay was filled with eelgrass early in this century (Fig. 4).

A 12 December 1938 is difficult to interpret because of unsuitable field conditions and poor imagery, and virtually no eelgrass is visible. No eelgrass grew around Marshy Pt. or south to Ricketsons Pt. The

Figure 4. Eelgrass in Apponagansett Bay, So. Dartmouth during 6 periods.

Top left, a USCGS nautical chart ca. 1890 indicating the presence of eelgrass (arrows). Also indicated are denotation of eelgrass on another nautical chart (E), and location of sediment core (C) showing long-term presence of eelgrass. Top right, likely pre-wasting disease distribution, based on charts, core data, and anecdotes. Other maps from photographs, solid areas indicate eelgrass beds of any % cover. No eelgrass was found during a field survey in 1985.

Proposed pre-disease distribution

500 m

Winter 1941

September 1966

April 1971

October 1981
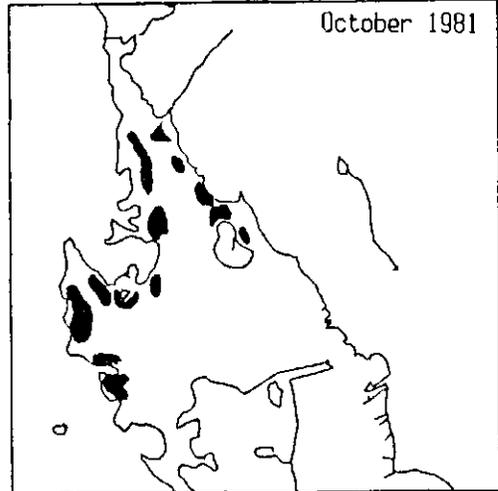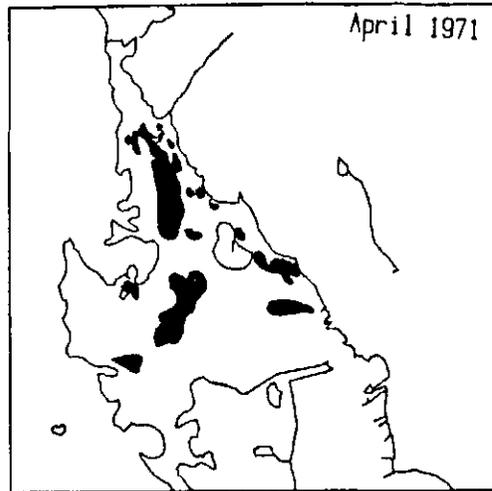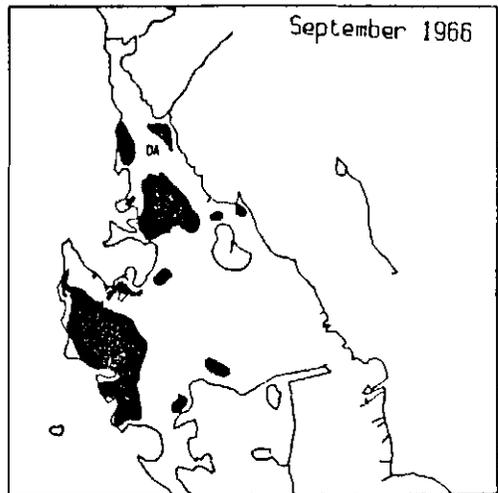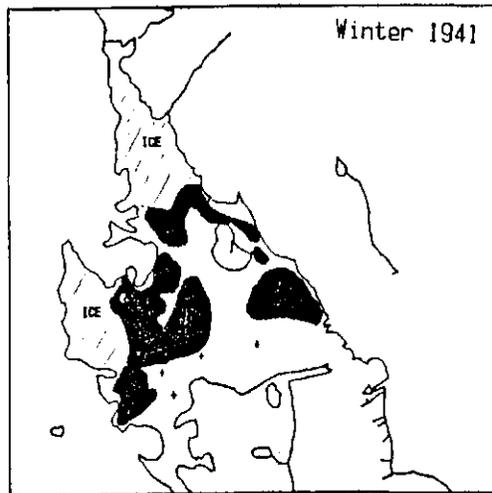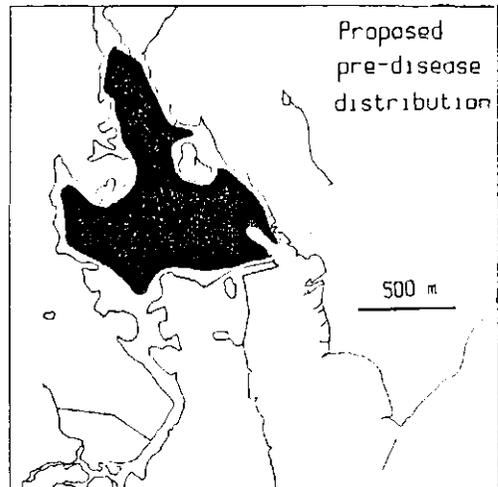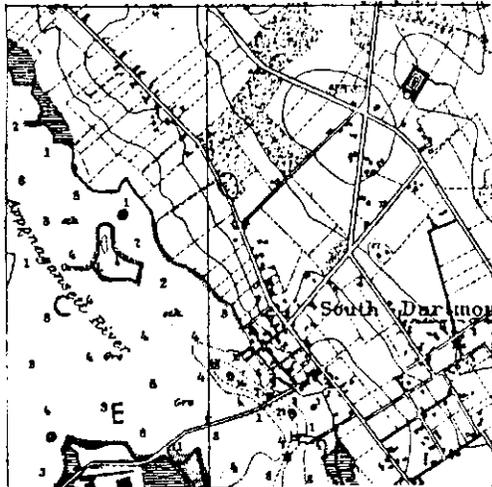
bottom of the inner harbor appears uniform and free of eelgrass which could be the result of the September 1938 hurricane, or image quality.

In contrast, a winter 1941 photograph shows eelgrass abundant throughout the bay (Fig.4). This photograph is remarkable because eelgrass is dense and continuous, even though much of the western and northern ends of the Bay are iced over, and obscures the full extent of eelgrass cover. At this time eelgrass began to colonize near Giffords Boat Yard and between Marshy Point and Ricketsons Point, as well as among the boulder field east of Ricketsons Pt. A photograph taken June, 1942 has too much water turbidity for interpretation, but parts of some 1941 beds are visible.

A September 1951 image shows that eelgrass is widespread, but is largely confined to the margins of the harbor, and no patches occur in water great than 1.0 m MLW (Fig. 4). Outside the bay, however, eelgrass is expanding and becoming more dense around Marshy Point and south to Ricketsons Point. Some patches are present on the west side of the outer bay as well. Because there were no major disturbances for several years prior to this photograph, these trends suggest declining water transparency in the inner bay was the likely cause for the absence of eelgrass there, rather than disease or ice scour.

A summer 1959 image of the northern fifth of the bay shows a large diffuse patch of eelgrass north of Little Island. An April 1962 photograph shows eelgrass widespread throughout the bay (Fig. 4), but the beds are sparse, possibly because the photo was taken early in the growing season, or like the Westport River, these beds were greatly affected by storms and ice scour during 1960 and 1961. Nonetheless,

eelgrass is more widespread, and shows a greater depth of growth than present on the 1951 imagery. Beds on the eastern shore of the outer bay appear denser as well.

Eelgrass was even more abundant in September 1966, and beds proliferated especially in the western lobe of the inner bay. The positions of many beds, but positions were again different from the 1962 distribution. Beds on the eastern shore of the outer Bay were the more extensive than any time since 1938.

A October 1971 photograph lacks detail, but eelgrass appears abundant south of Great Island. In 1975, dense vegetation is present in several patches around the bay, but by October 1981, most eelgrass is absent from the inner bay. Some vegetation appears along the banks at the head of the Bay in the 1981 photograph, but it was assumed to be largely composed of drift algae or Ruppia.

The greatest post-disease cover in the inner Bay occurred during the mid 1960's, but eelgrass never returned to its pre-wasting disease abundance. This contrasts with the outer Bay, which showed continuous expansion of eelgrass cover for decades. These observations, and the loss of eelgrass in inner Bay during the 1980's suggest there have been declines in water quality in the inner Bay. For example, the eastern shore of the inner bay has also been closed to shellfishing for several years due to high loads of fecal coliform. Sources of these coliform may include failing septic tanks, waste discharges in Buttonwood Brook, or feces from several thousand Canada geese that often feed on local agricultural land and roost along shore. Each of these sources is associated with nutrient inputs.

Nutrient loading is implicated as the cause of the recent decline because drift algae have been increasing conspicuously, and the odor of decaying algae has become a public nuisance in some areas (press reports). Large sheets of *Ulva* or clumps of *Gracillaria* cover the bottom of parts of the Bay. Some parts of the inner harbor is covered with a rich gelatinous ooze of mud and decaying algae that has been observed in other enriched embayments (e.g., Brush, 1984). The maximum depth of growth of eelgrass declines from 2.4 m MLW near the mouth to 1.2 m MLW by the marina, then disappears altogether in then inner Bay.

Boat traffic may also be contributing to decreased light availability to eelgrass because boat use has increased substantially in this bay in recent decades (Fig. 5). The inner bay has a shallow, muddy bottom, and power boats leave conspicuous plumes (pers. observ). This activity not only resuspends sediments, but releases nutrients from pore water.

The history of pollution in Apponagansett Bay needs further study because eelgrass was less abundant in the Bay in 1951 than in the 1940's or 1960's. This loss does not appear to be do to disease because eelgrass disappeared from the deeper parts of the Bay, but persisted in shallow water. This Bay has been disturbed for many decades, and this observation suggests that water transparency decreased at that time.

Clarks Cove and New Bedford Harbor

The Clarks Cove-New Bedford Harbor-Acushnet River estuary system has undergone major physical and chemical perturbations from industrial and urban activity for more than a century. The history of discharges

Figure 5. Boats moored or in transit in inner and outer of
Apponagansett Bay on four dates during comparable times in the
recreational season.
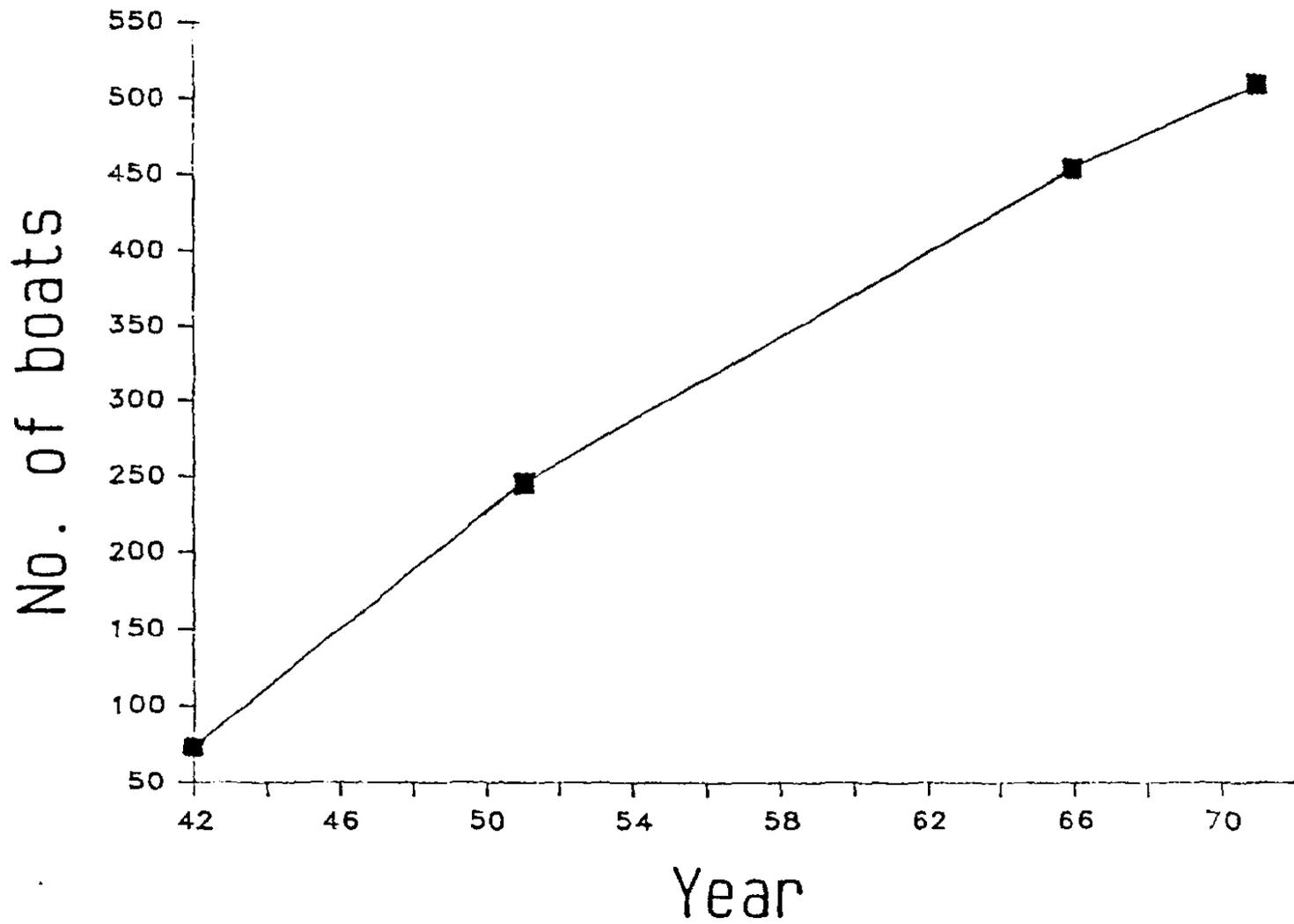
in this area is complex and includes sewage, dyes, PCBs, and heavy metals during different periods. Three towns (Dartmouth, New Bedford, and Fairhaven) adjoin these waters, but the largest and most toxic inputs have originated from New Bedford. In addition, a hurricane barrier was constructed during 1962-64 in New Bedford, along the northeast and northern shores of Clarks Cove, and along the eastern shore of Clarks Point to the inner harbor of New Bedford.

Most of New Bedford's sewage discharges at the tip of Clarks Point today. This may be an important factor affecting local water transparency because the resulting plume offshore is conspicuous on all aerial surveys obtained, and the 100-200 m wide plume is visible often stretching 1000's of m into the waters of the neighboring town. In the past, more than 170 pipes discharged along shore as well (New Bedford Town Hall Report). Prior to 1970 many of these outfalls were in use and received both industrial waste and street runoff. Others were tied in to the sewer-street drain system, and during periods of high rains, sewage was discharged diverted to them as well.

Today, no eelgrass grows in New Bedford Harbor-Acushnet River or Clarks Cove, except for a bed at the tip of Clarks Point and south of Moshers Point (Appendix I). The absence of eelgrass is not due to salinity limitations because fresh water discharge by the Acushnet River is not large. Furthermore, eelgrass grew elsewhere along the coast prior to the construction of the hurricane barriers, including around Palmers Island in the inner harbor, and around cotton mill discharge pipes at the northeast shore of Clarks Cove (B. Burke, New Bedford shellfish warden and James Costa, pers comm.). The construction of the

barriers may have contributed to the loss of some eelgrass and potential eelgrass habitat because several km of beach and shallow shoals were eliminated, and tidal flushing was reduced in the inner harbor.

Ten different aerial surveys since 1944 were obtained that included this area, but it was difficult to document changes in eelgrass abundance on these photographs for several reasons. This area was urbanized prior to the wasting disease, and on the earliest photographs, large portions of shore had been replaced by piers, revetments, and warehouses. Beach slopes are steep, and the zone where eelgrass grows is often too narrow to be interpreted from photographs. Water transparency is poor on most available photographs, especially in the inner harbor. Algae covered rock and cobble are abundant in some areas, making it difficult to delimit eelgrass bed boundaries. Finally, eelgrass never became abundant in this area after the wasting disease.

Even with these limitations, there are some areas where eelgrass is visible on aerial photographs during the 1950's or 60's, but no longer present today (Fig 6). Only in two areas (tip of Clarks Point, So of Moshers Point) did eelgrass abundance increase after 1966 (Fig. 6).

Other changes in vegetation are also visible on the photographs. For example, *Codium* is now abundant between Fort Phoenix, Little Egg Island, and Sconticut Neck, and probably accounts for the vegetation to increase in this area between 1966 and 1981 photographs. In some areas (such as south of Fort Phoenix), it is difficult to identify vegetation.

These observations are fragmentary, but eelgrass colonized few areas in this area after the wasting disease, and the few existing beds

Figure 6. Dates and locations of former eelgrass populations around New Bedford based on reports and photographs.

Areas where eelgrass has declined during 1944-1981 are marked by (-); areas of increase after 1966 are marked by (+). The (?) indicates increasing vegetation of questionable identity.
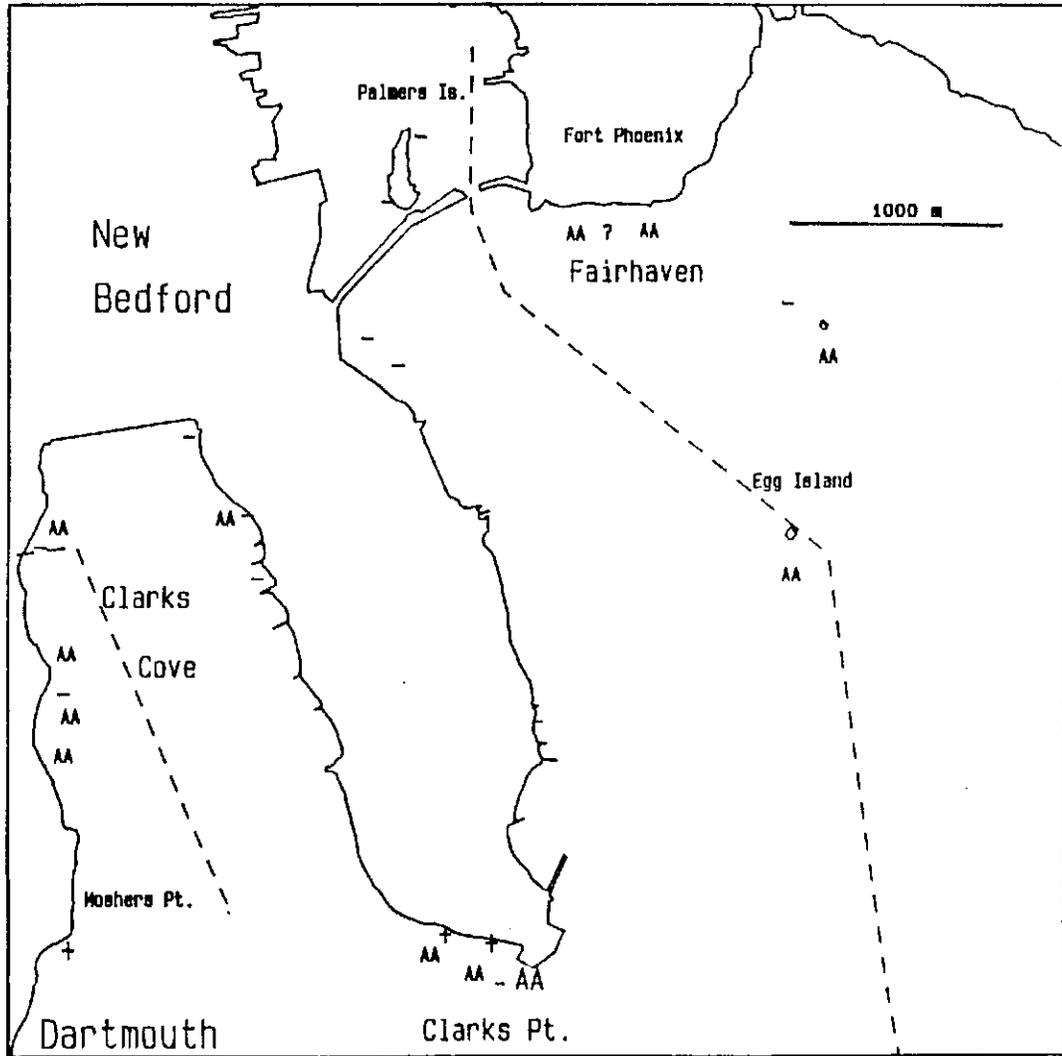
were destroyed by the late 1960's. Whether the lack of recovery and new
losses were the result of burial, changing hydrography, declining water
quality, or buildup of toxic substances in the sediments is unclear.
The absence of eelgrass over such a large area, is unique in Buzzards
Bay and suggests that there have been large scale effects of human
perturbations.

Nasketucket Bay, Fairhaven

Nasketucket Bay is an enclosed area on the eastern side of
Sconticut Neck. This bay is relatively protected from storms, has had
little housing development along shore, and has been a productive
shellfish habitat (Durso et al., 1979). The only appreciable surface
flow of freshwater entering the Bay is through a network of creeks and
streams entering Little Bay. This input is noteworthy because these
streams drain hundreds of ha of farmland, pastures, and developed land,
and Little Bay is the only area where eelgrass is absent today.

Lewis and Taylor (1933), listed areas of eelgrass decline on the
east coast as a result of the wasting disease, and noted the "well-known
meadows about ... Sconticut Neck in Buzzards Bay ... [which] were
nearly or quite depopulated." The recolonization of eelgrass after the
disease was documented with 8 aerial surveys taken between 1951 and
1981. A town shellfish report (Durso et al., 1979) and field
observations in 1985 were used to document recent distribution.

The changes in eelgrass abundance here are typical of deeper, well
flushed embayments in Buzzards Bay: slow and nearly steady
recolonization over 30 years, without the wide swings in abundance seen

in shallow estuaries like the Westport Rivers. Most expansion occurred during the late 1950's to early 1960's.

The earliest photographs (1951 and 1956) show that many populations of eelgrass are scattered around Nasketucket and Little Bays (Fig. 7). Some populations occurred up to 2 km offshore suggesting that refuge populations in deeper water survived the disease. The loss of eelgrass in Little Bay may be due to enrichment because drift algae and periphyton are very abundant there today. Photographs of Little Bay from the 1950's and early 1960's shows a light colored, sandy mud bottom, later photographs show a darker bottom suggesting an increase of organic matter or silt.

East Bay, West Island, Fairhaven

Like Nasketucket Bay, East Bay is a good example of an isolated, relatively undisturbed, well flushed coastal area. Unlike the former, it is very shallow, and exposed to moderate wave scour. This bay, like other undisturbed areas on the outer coast show continuous expansion for decades after the wasting disease. Because of local hydrography, wave scour, and longshore sand transport, eelgrass beds growing here have a "banded" or granular appearance.

Early records or descriptions of eelgrass abundance are not available for East Cove. Lewis and Taylor (1933) state that eelgrass was abundant on Sconticut Neck prior to the wasting disease. It is likely eelgrass also grew along West Island because eelgrass is equally abundant in both areas today.

Figure 7. Eelgrass distribution in Nasketucket Bay during 1956 and 1981. Solid beds have greater than 50% cover.

1956

1981
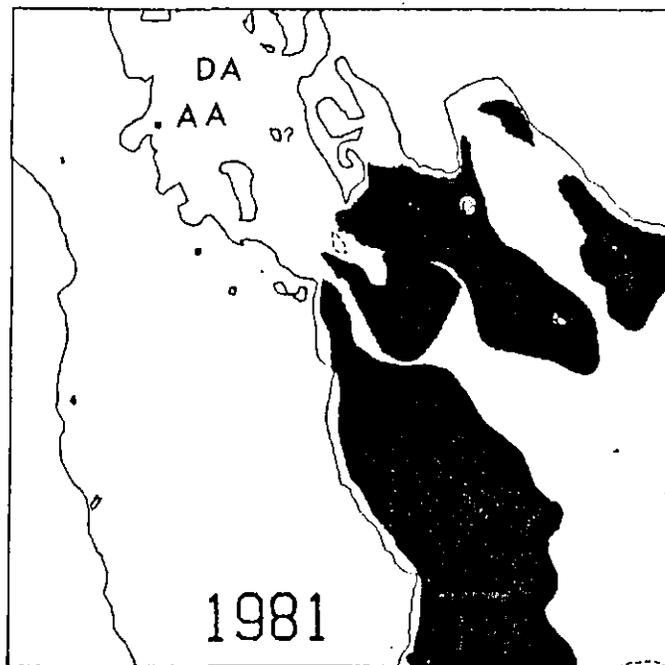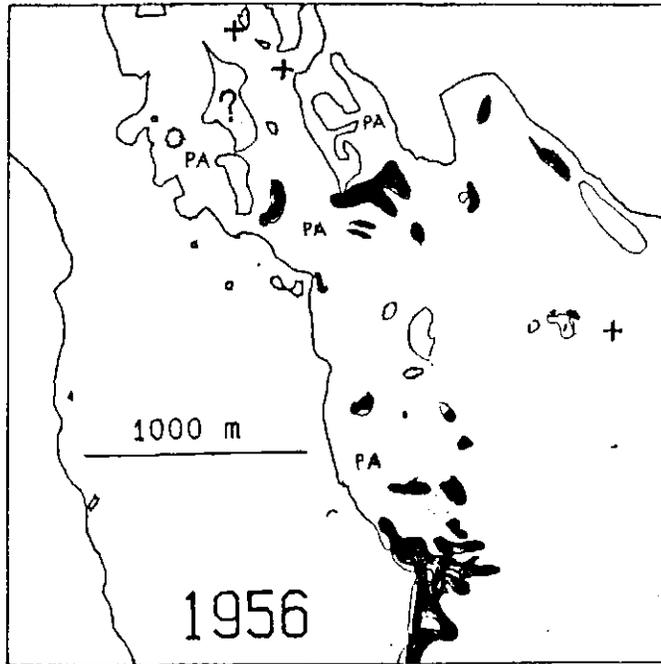
The beds that colonized the shallow areas of East Bay were derived from deep beds offshore the rocky island mid-bay (Fig. 8). The process of colonization here was similar to other moderate to high energy coasts: new, discrete patches of vegetation appeared on bare areas during the 1950's and 1960' and available habitat was saturated by a combination of vegetative growth and recruitment of new beds. The hurricane in 1954 destroyed some shallow beds that were established by 1951 (Fig. 8). This disturbance resulted in slower eelgrass expansion, rather than decline, when total eelgrass cover is examined (Fig. 9, top), because eelgrass cover expanded in deeper areas during the photograph sequence that included this storm.

By 1971, most of East Bay was colonized with eelgrass, including very shallow stations nearshore (Fig. 8 and 9, top). The decline in early 1971 (Fig. 9) is an artifact because this datum is based on a photograph taken in early spring, while the data surrounding it are from Fall surveys. Because the beds in the shallowest parts of the cove are mostly annual populations, they are not always apparent in early spring photographs. The decline in 1981, however, is based on Fall imagery, and probably due to storms and ice scouring in the late 1970's. Declines during this period occurred elsewhere in Buzzards Bay as well (see Great Neck, Wareham description below).

The west shore of East Bay has been conspicuously eroding, and the width of vegetated land between the beach and a salt marsh drainage channel was measured on eight positions on different dates. Erosion rate was higher prior to eelgrass colonization than after (Fig. 9). This may not be due to solely to the damping or baffling effects of

Figure 8. Eelgrass distribution in East Cove of West Island,
Fairhaven during four different periods.

The lines cutting into the western shore are a network of salt
marsh drainage ditches that were used as reference points to measure
beach erosion. Beds covering more than 50% of the bottom are solid,
open beds have less than 50% cover. Total eelgrass cover for these and
other date are shown in Fig. 9.

October 1951

May 1956

March 1961

September 1966
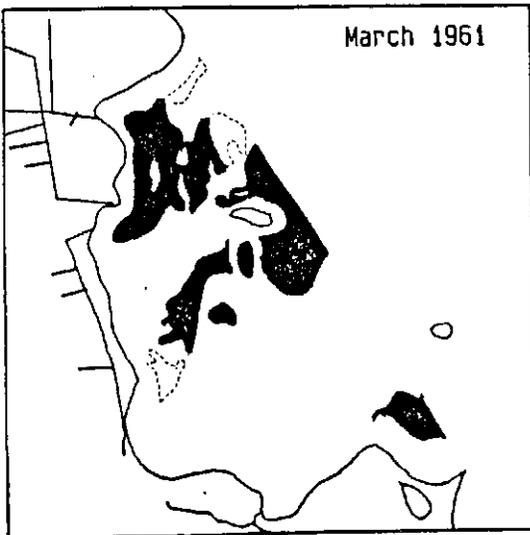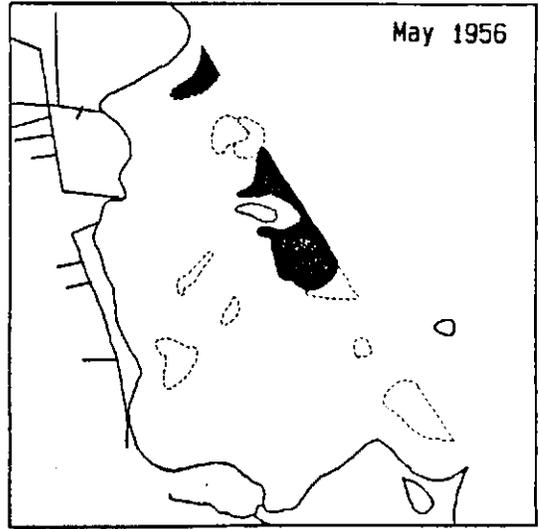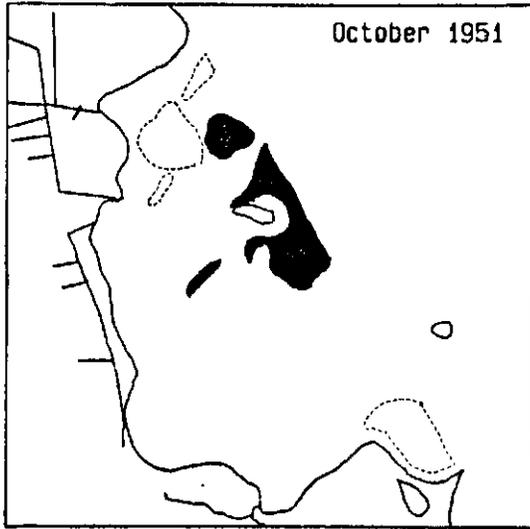
Figure 9. Recent changes in eelgrass cover and beach erosion on West Island.

Top: eelgrass area (corrected for percent cover) in East Bay 1951-1981. Bottom: Mean erosion rates at eight stations along shore (± SE), during the same period.
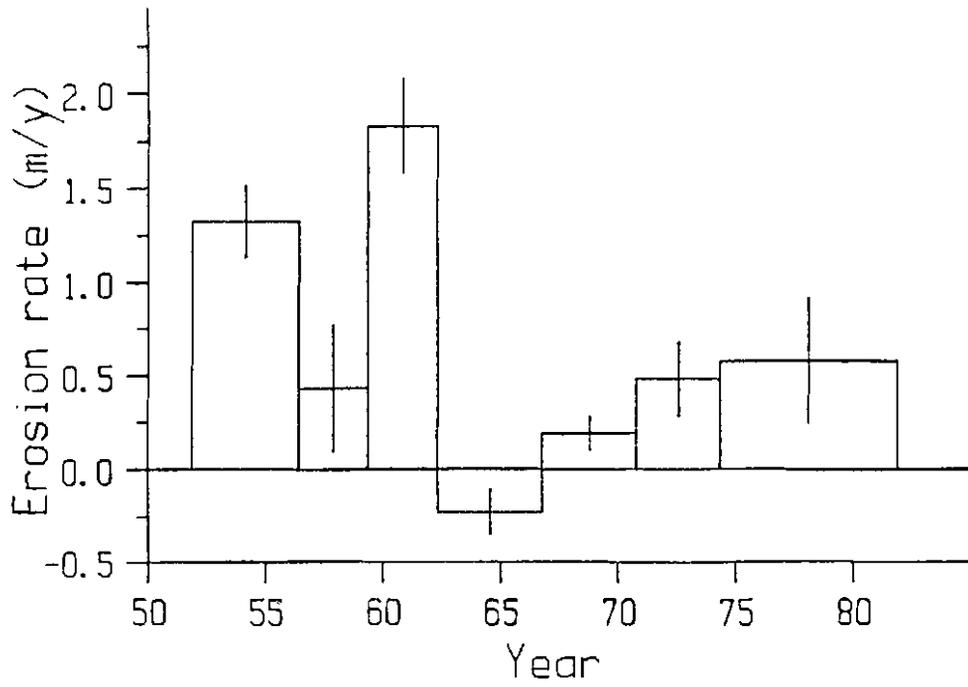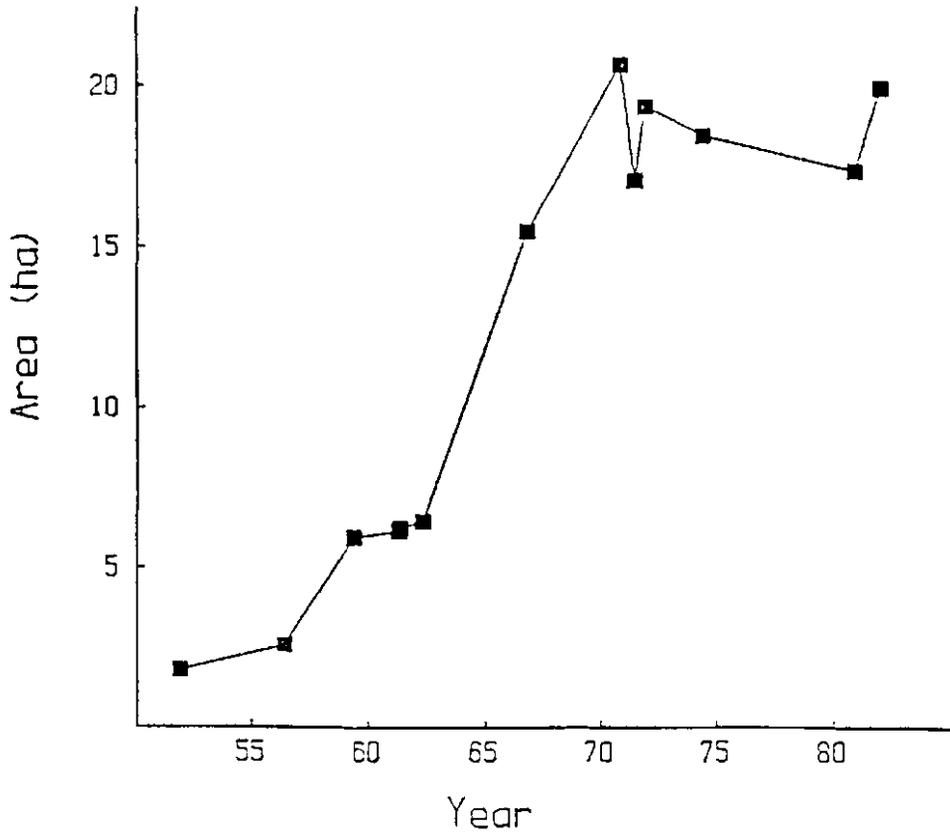
eelgrass offshore since hurricanes in 1954 and 1960 probably account for the higher rates observed during those periods. Eelgrass must play a role, however, since the Blizzard of 1978, a powerful northeaster that eroded other areas (Aubrey and Speer, 1984; Zeeb, 1985), did not result in appreciably higher erosion rates here.

Sippican Harbor, Marion

Sippican Harbor is surrounded by rural and suburban house densities and some agricultural land. Many shellfish beds exist here, and oyster reefs were denoted at the mouth of Briggs Cove on nautical charts prior to the 1930.

Photographs dated June 1930 of upper Sippican Harbor (Marion Town Hall vault) were the only photographs taken prior to the wasting disease discovered for any part of Buzzards Bay. These photographs are oblique, but eelgrass could be mapped (Fig. 10). Remarkably, the present day distribution of eelgrass in 1981 is almost identical to the 1930 distribution. The one exception is that eelgrass is less abundant today in the innermost parts of the harbor. These photographs suggest that peak eelgrass abundance and distribution today (except in disturbed areas) is indicative of patterns prior to the disease.

Eelgrass showed the greatest rates of expansion during the 1950's and 1960's (Fig. 10). Declines in upper Sippican Harbor, Briggs Cove, and Planting Island Cove, appear related to declining water quality from development or boat traffic. For example, the shellfish warden (G. Taft, pers. comm.) noted that periphyton and drift algae has become abundant Planting Island Cove, and the latter has caused a loss of shellfish habitat. Shellfish bed closures during recent decades in

Figure 10. Historical changes in eelgrass cover in Sippican Harbor, Marion during 5 periods: June 1930, September 1944, September 1966, September 1971, and October 1981.
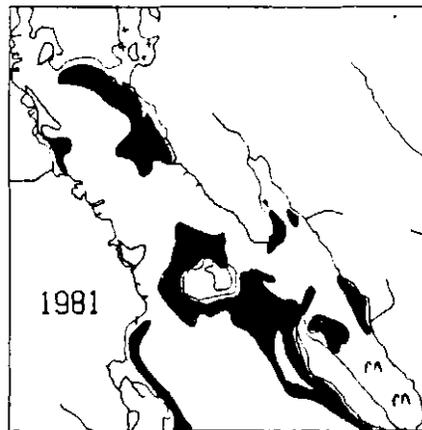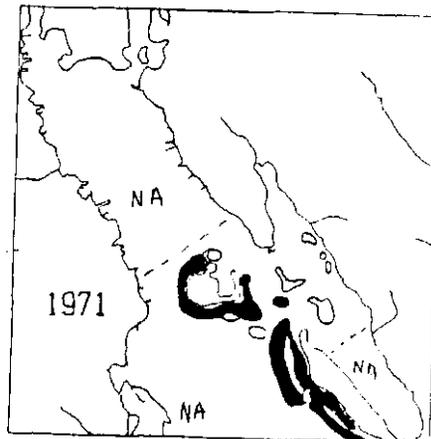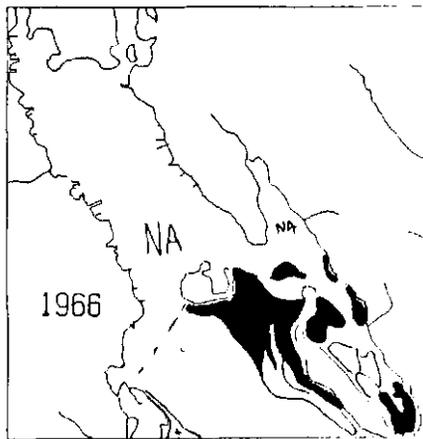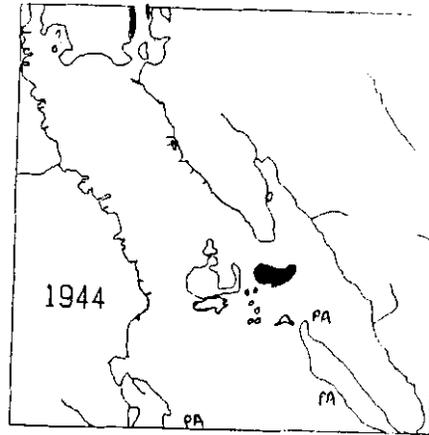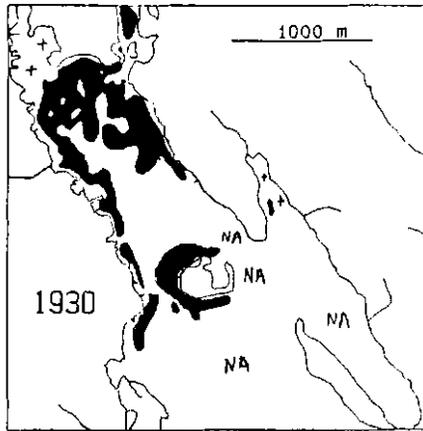
parts of the Harbor also suggest water quality problems. The large decline of eelgrass by Ram Island between 1966 and 1971 is more enigmatic because the central part of the Harbor is better flushed. This too may be the result of decreased light availability because of nutrient loading in the watershed. In the early 1970's, most residences were tied to a new sewer system that emptied into a neighboring bay. This may have led to water quality improvements, and new expansion of eelgrass by 1981. This explanation seems more plausible that declines due to disease, because most of the losses occurred at the deeper margins of beds, which suggests declining light availability, and because beds closer to the mouth of the Bay expanded or remained static during the same period.

Great Neck, Wareham and the Wareham River Estuary

The waters off Great Neck are moderately well flushed, in part due to water exchange in the Cape Cod Canal, and the shoreline somewhat exposed. A shallow shelf less than 4 m MLW covers more than 800 ha offshore. Today eelgrass is extensive on these shallows.

The earliest photographs obtained (a 1956 aerial survey and fragmentary coverage from 1944 and 1951) show that eelgrass was absent from most areas, except for a large and conspicuous bed around Little Bird Island (Fig. 11). Because this bed is isolated, and little eelgrass is present onshore at this time, this population may have survived the wasting disease. These beds colonized the western lobe of Great Neck during the early fifties, then migrated eastward along Great Neck between 1955 and 1960 (Fig. 11).

Figure 11. The pattern of eelgrass recolonization along Great Neck during four decades. Solid beds have greater than 50% cover.

1956

1958

N A

1000 m   April 1962

PA   PA

1971
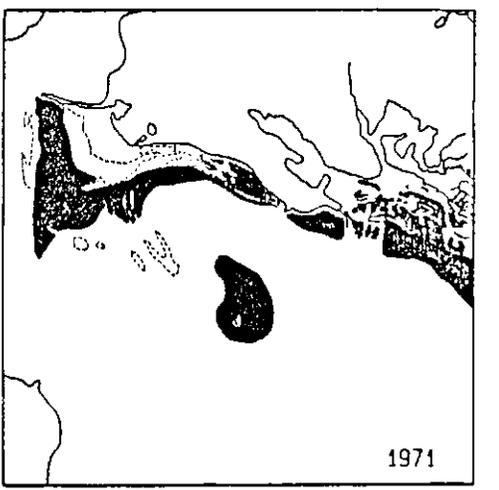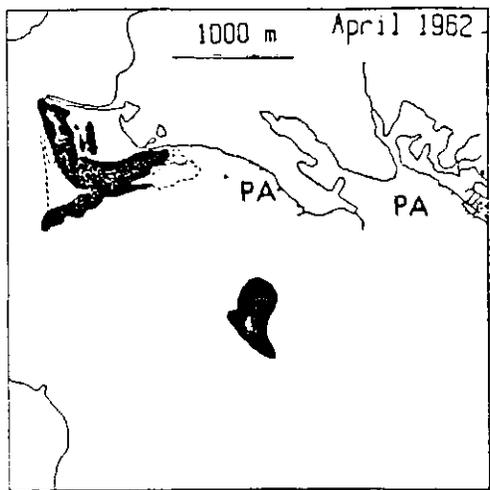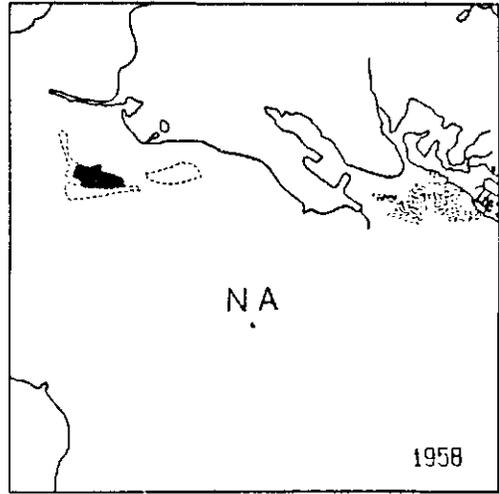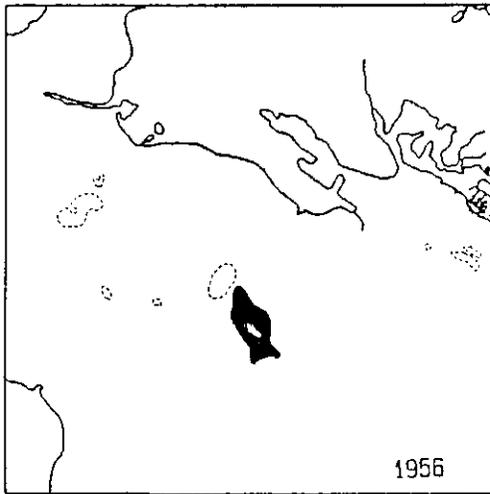
The onset of colonization south of Long Beach occurred at least 10 years earlier than colonization on the shoal south of Indian Neck, 1.5 km to the east, where the first beds appeared in 1958 (Fig. 12). These beds expanded greatly, and by 1966, the population had nearly reached peak cover.

Buttermilk Bay, Bourne and Wareham

Buttermilk Bay is a protected embayment at the north end of Buzzards Bay, with an area of 200 ha, and a 1 m MLW mean depth. In recent years, Buttermilk Bay has become polluted from development in the surrounding watershed, and the Bay is now closed to shellfishing each summer. Nutrient loading in the bay is high (Valiela and Costa, in press), but effects are localized because the tidal range is 1 m, and 50% of the water is flushed with each tide (Costa, 1988). The Cape Cod Canal (built ≈1910) discharges less enriched water from Cape Cod Bay into Buzzards Bay, 1 km from the mouth of Buttermilk Bay. This additional flushing may be keeping pollution levels in Buttermilk Bay from being worse than they are.

Buttermilk Bay is the only site in Buzzards Bay where colonization of eelgrass was mapped after the wasting disease (Stevens 1935, 1936, Stevens et al., 1950). Recently, Buttermilk Bay has been studied to measure hydrography, nutrient loading, eelgrass abundance, and groundwater movement (Valiela and Costa, in press; Fish, in prep; Moog, 1987) that shed light on Stevens observations.

Stevens noted that eelgrass survived or first appeared near Red Brook, and his observations were one of many that demonstrated eelgrass

Figure 12. Recolonization of eelgrass on two areas on Great Neck, Wareham.

Data are bed cover (corrected for % cover) for the area south of Long Point Beach ( ), and the shoal south of Indian Neck ( ). Relative cover 100 =   ha for Long Point Beach and ha for Indian Neck.
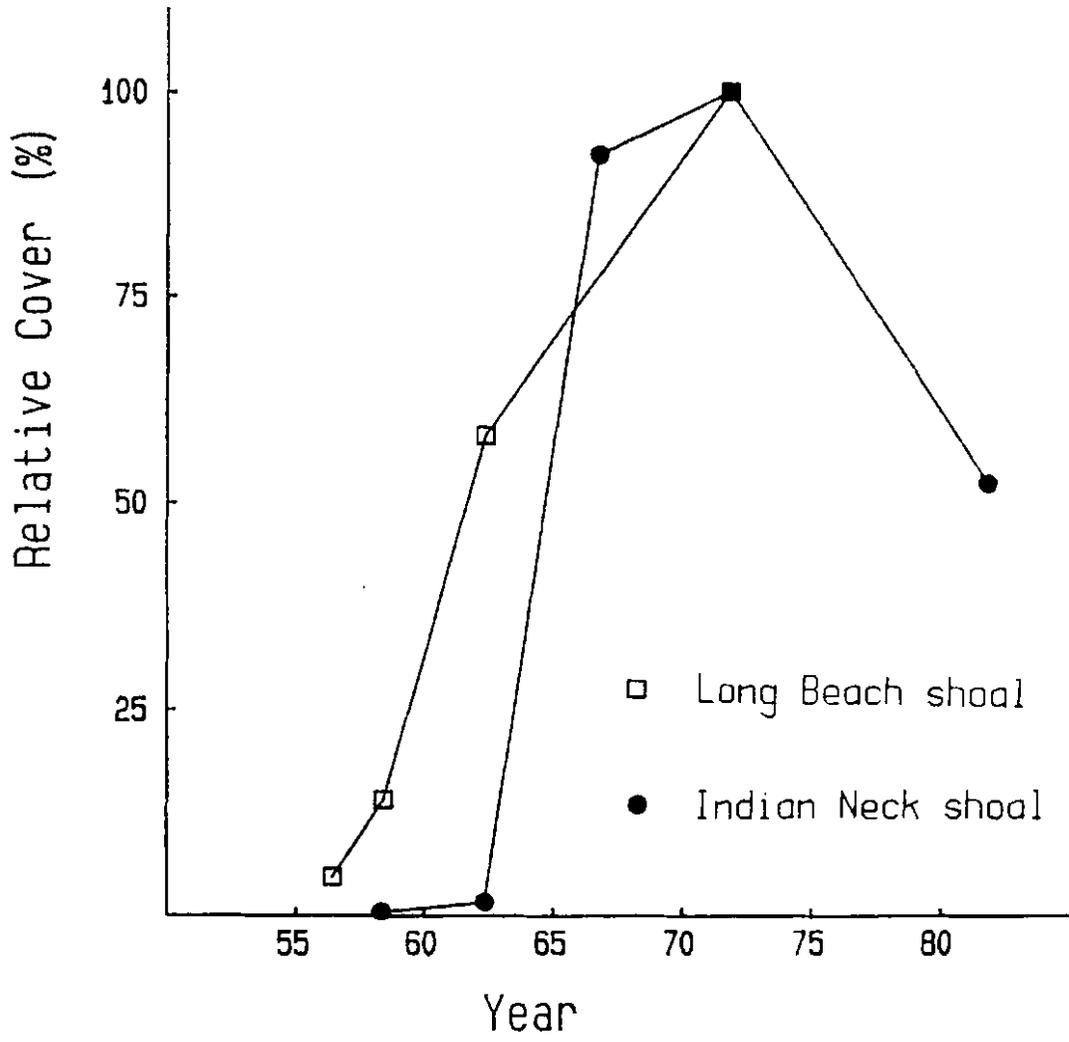
beds near fresh water inputs were refuge populations from the disease. He also noted that eelgrass first appeared in Little Buttermilk Bay along its most northern shore where no streams entered. It is apparent now that this area has large groundwater inputs (pers. obser., Moog, 1987), further supporting the premise that plants near freshwater inputs better survived the disease or were the first to recover.

Analysis of eelgrass bed survival and recovery near streams after the wasting disease focused on salinity (e.g. Rasmussen, 1977). Water temperature is cooler by several degrees near Red Brook, where Stevens observed the first beds. Furthermore, groundwater springs near some areas recolonized in Little Buttermilk, locally cool seawater and sediments (pers. obs). The possible role of cooler temperature as providing a refuge from the disease is addressed in the discussion.

Stevens did not map abundance prior to the wasting disease, but he described eelgrass cover in Buttermilk and Little Buttermilk Bays as "notably abundant for many years and was almost completely destroyed between September, 1931 and September, 1932." Stevens descriptions, a 1916 Eldridge nautical chart, and sediment cores taken 60 m east of Red Brook, all suggest that eelgrass was abundant in Buttermilk Bay prior the wasting disease. The earliest photographs (June 1943) are of poor quality for vegetation analysis, but eelgrass is not as abundant in the Bay as today.

Eelgrass greatly expanded in the Bay during the 1940's, and this expansion may have been facilitated by seed production from beds outside the Bay (Stevens et al., 1950). By 1951, eelgrass had virtually filled the central portion of Buttermilk Bay (Fig. 13) , but grew only in a few

Figure 13.   Eelgrass in Buttermilk Bay during various periods.
Only areas included within dashed lines were analyzed for changes in
area, a description of other areas is in the text.   The 1935 map was
based on the maps of Stevens (1936); the rectangular area denotes a
region containing several beds.   The "M"-shaped feature and new channels
were dredged after 1955.   Solid beds have greater than 50% cover.
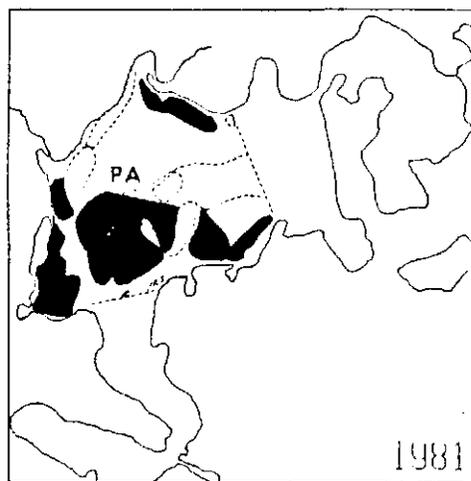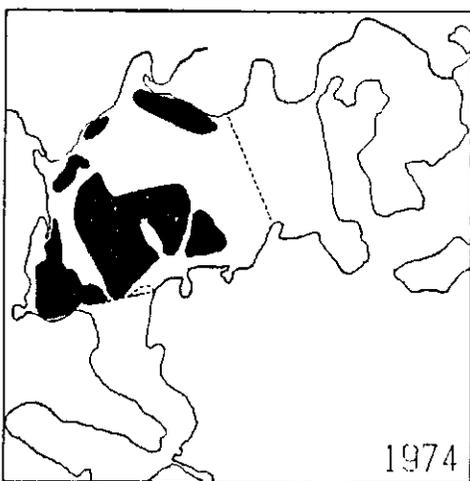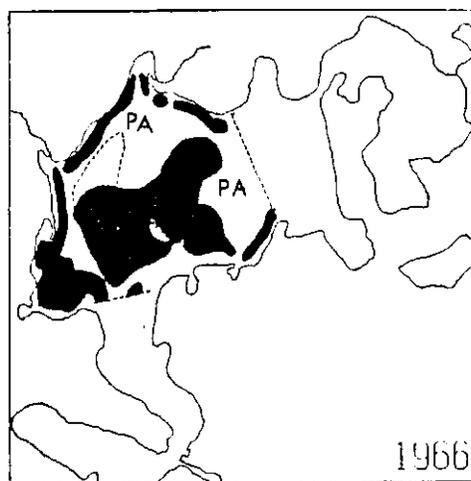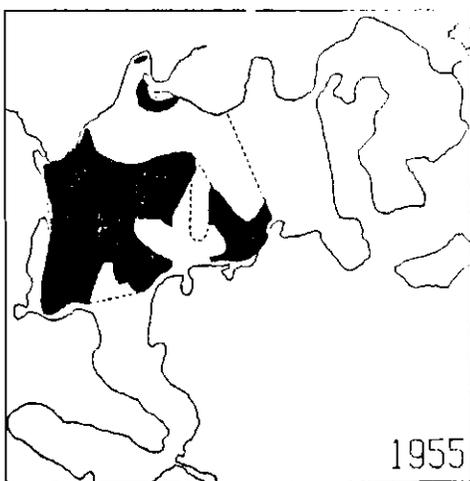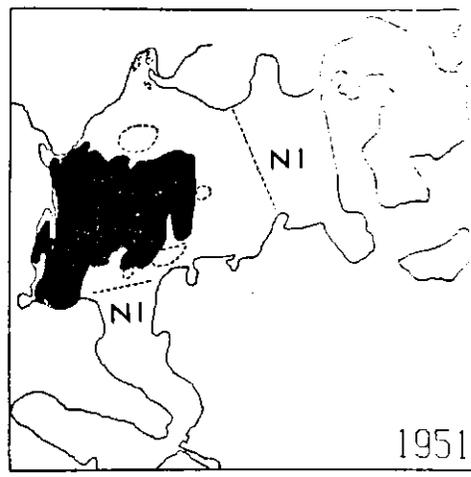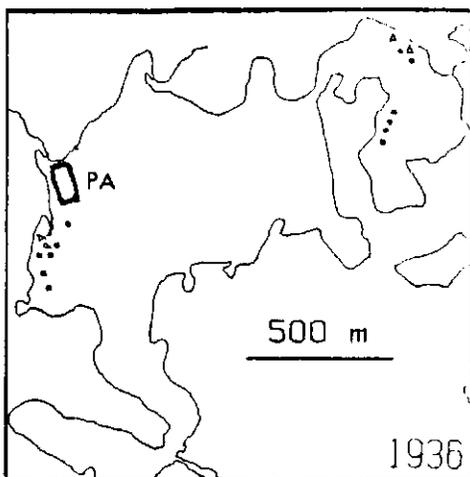
areas of Little Buttermilk Bay. During the 1960's, eelgrass began to extensively colonize Little Buttermilk Bay, and grew deeper in Buttermilk Bay than during any other recent period (Fig. 14, 15 bottom). Total eelgrass cover in the central part of Buttermilk Bay in 1966 was unchanged from the 1950's (Fig. 15 top) because of losses due to dredging and new declines in poorly flushed coves. For example, eelgrass was present in Hideaway Village Cove during the 1950's, but largely disappeared by 1966. Today no eelgrass grows along the inner shore of this cove. Eelgrass continued to decline in the deepest parts of the Bay during the 1970's and 1980's (Fig 15, bottom) but greatly expanded in Little Buttermilk Bay and other shallow areas.

The losses of eelgrass in the deep portions of the Bay and in some poorly flushed coves appear related to nutrient loading or increased turbidity. Today, eelgrass is absent from areas with the highest nutrients concentrations, depth of growth in Buttermilk Bay correlates with dissolved inorganic nitrogen content of seawater (Costa, 1988).

Overall, Buttermilk Bay has not experienced the large declines observed in other highly developed bays. This is probably due to the high flushing rate, and because the Bay is so shallow, most beds are not at the lower depth limit of growth. The loss of some vegetation since the 1960's, however, suggests that Buttermilk Bay may be affected by future increases in nutrient loading and sediment resuspension.

South of Buttermilk Bay, a 1 km wide tidal delta has been formed at the entrance of the Cape Cod Canal. This delta has been migrating southward at rates as high as 9 to 18 m y^{-1}. This feature is interesting because a large eelgrass bed grows on the south edge of the

Figure 14.   Relative migration ($\updownarrow$) of a bed boundary in central Buttermilk Bay.

The central part of the Buttermilk Bay is very shallow, therefore progression of the bed to the northeast (north at top) indicates growth in deeper water.   Compare to Fig. 15, bottom.

Red Brook

Little Buttermilk

1966
1951
1981

Buttermilk Bay

500 m
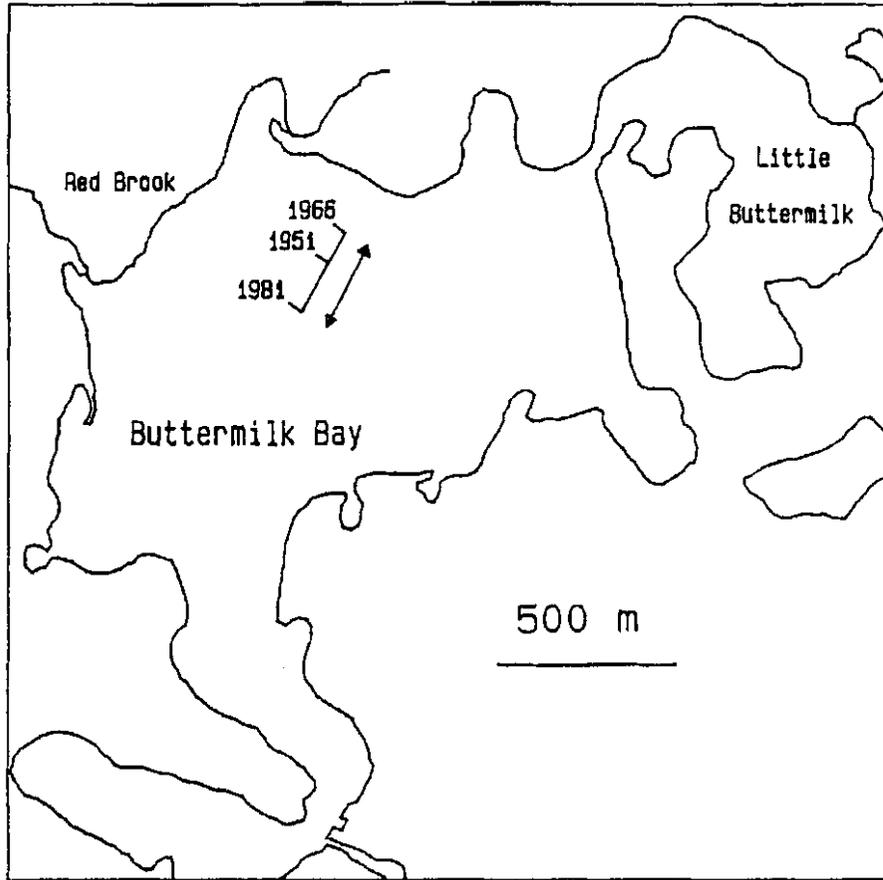
Figure 15. Eelgrass bed area (corrected for percent cover) in Buttermilk Bay (top) and position of central bed margin (bottom).

Positive bed positions represent growth in deeper water relative to 1951, negative values represent growth in shallow water. The net depth difference between the extreme positions (based on nautical charts) is between 0.3 and 0.6 m
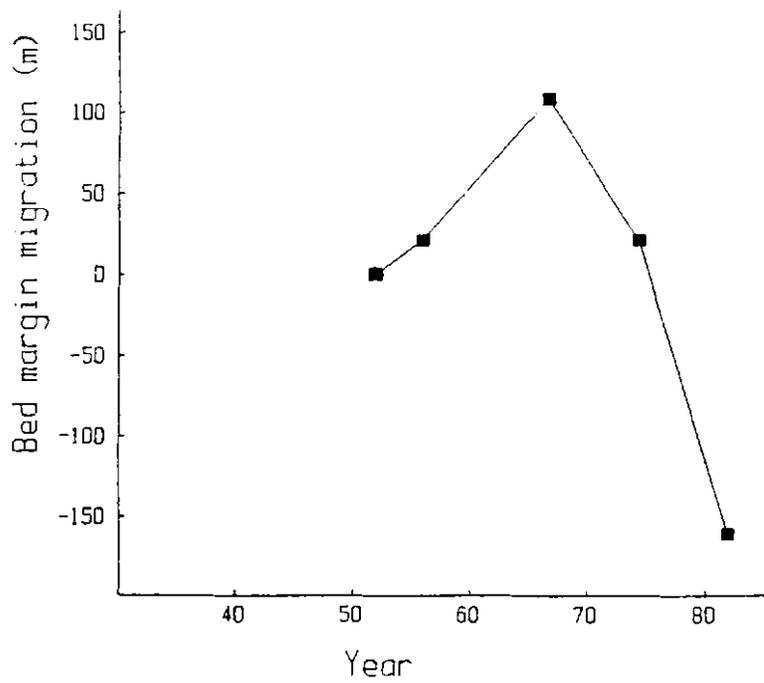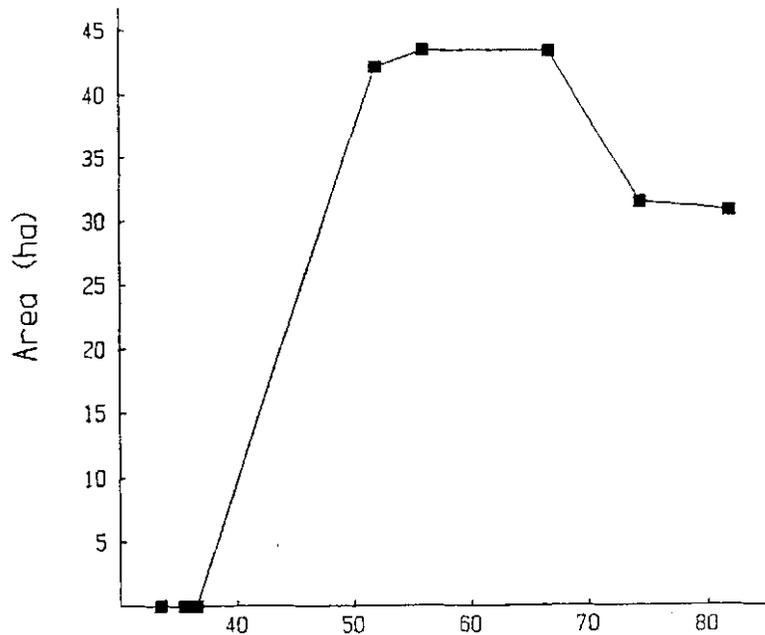
delta. In effect, eelgrass is constantly being covered on the advancing edge of the delta. Virtually no eelgrass grew on the north side of this delta until the 1970's. Since then, eelgrass has colonized there and begun to migrate southward at rates as high as 36 to 72 m y^{-1}, and has met the eelgrass bed on the south side in places.

Megansett Harbor, Bourne and Falmouth

Megansett Harbor is a moderate to high energy, well-flushed environment with a sandy bottom covered with sand waves. Most of the bay is less than 4.5 m, and today eelgrass is abundant throughout. Many beds here have a banded appearance because they grow in the troughs of sand waves or have large bare areas within them because of wave scour and storm action.

Prior to the wasting disease, eelgrass was probably equally abundant in Maganset Harbor as today, because there are numerous denotations of eelgrass alongshore on nautical charts from the 1800's. Colonization began first in the north end of the bay where a large bed on the southeast corner of Scraggy Island may have survived the disease. This bed expanded greatly and new areas were vegetated during the 1940's and 50's (Fig. 16). Bed cover remained constant in this area for 2 decades, but increased in the 1980's because of eelgrass colonization in some of the deepest parts of the Harbor.

Eelgrass colonization in the south side of Meganset Harbor lagged behind the north side, and the most rapid expansion occurred there during the 1950's.

Figure 16. Eelgrass bed area (corrected for % cover) of the North side of Megansett Harbor from 1943 to 1981.
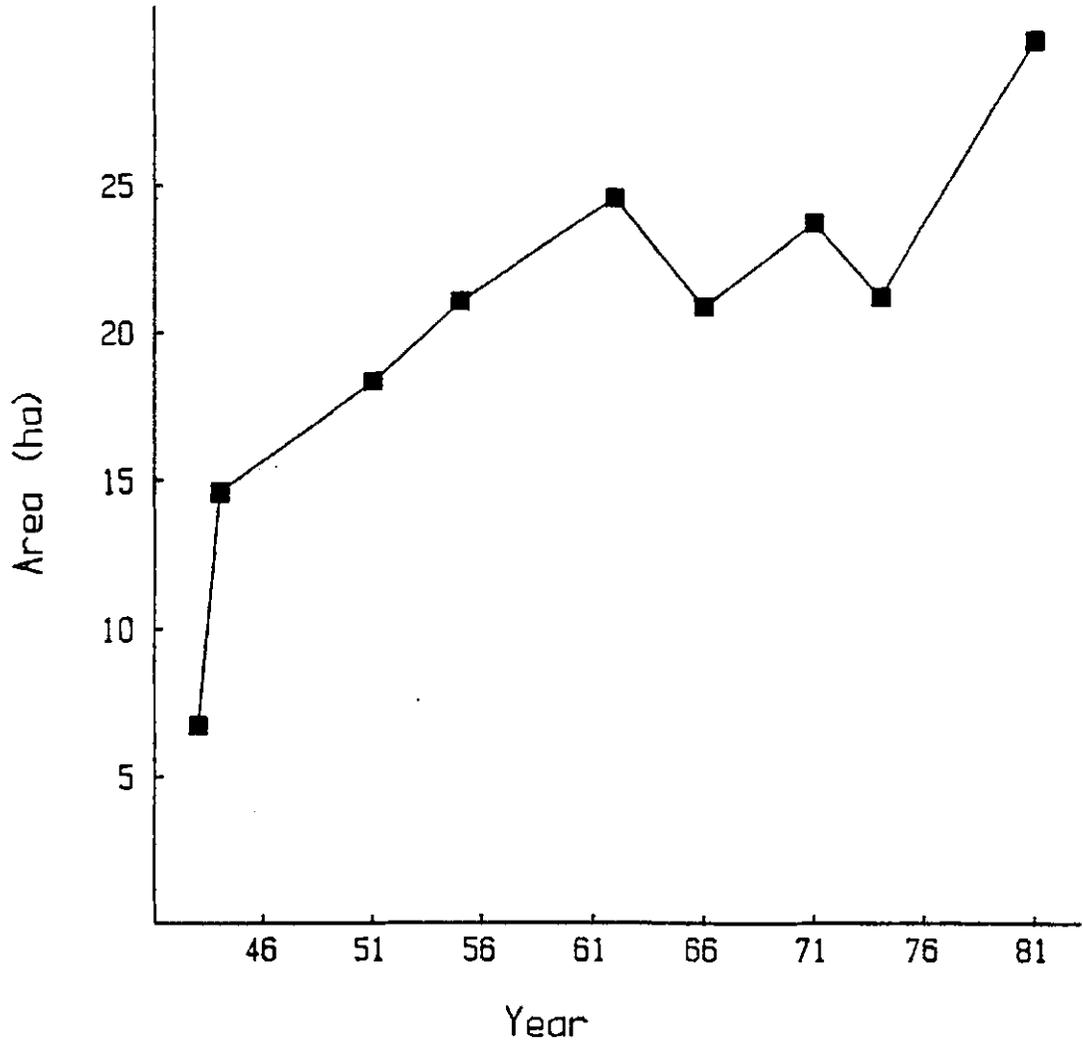
Wild Harbor, Falmouth

Wild Harbor, is an exposed well-flushed southwest facing harbor fringed with marshes, and covered with a sandy bottom. The surrounding watershed has a moderate density of homes with on-site sewage disposal. Little eelgrass grows here because the inner Harbor has appreciable wave scour, and the outer harbor to drops rapidly to 6.0 m MLW. Nonetheless this site is interesting because it was the focal point of a large spill of No. 2 fuel oil on 16 September 1969 (Sanders et. al., 1980).

Because this is a high energy environment, the beds positions are somewhat variable between surveys. Nonetheless, beds on each side of the entrance of Silver Beach Harbor are present on most photographs, but show changes in boundaries. These beds are dense and persistent on all photographs including within one year of storms and ice scour. Nonetheless, the beds here are noticeably less dense and cover less area in April 1971 than prior to the oil spill. In 1974, eelgrass cover remains somewhat depressed, but by 1975 and 1981, these beds seem to have largely recovered. There is evidence that the concentration of fuel oil in the sediments was high enough to account for these changes (Costa, 1982).

West Falmouth Harbor

West Falmouth Harbor is a protected embayment with freshwater stream input primarily from . The watershed surrounding this bay is developed and there is evidence of water quality declines such as algal blooms and shellfish bed closures. This area was also impacted by a small oil spill in November 1970 (Sanders et al., 1980).

No early documentation of eelgrass abundance was discovered. Eelgrass was abundant outside West Falmouth Harbor and just within the bay in 1943 (Fig. 17). Eelgrass expanded considerably during the 1950's and 1960's, but a November 1971 photograph shows that some beds had disappeared or had less cover than in 1966, particularly in the deeper parts of the bay, such as at the channel by the mouth of the bay. Like Wild Harbor, this decline could have been related to the oil spill because most other parts of Buzzards Bay do not a decline at this time, suggesting local conditions were the cause.

Waquoit Bay, Falmouth

A 100 to 500 m shoal is present on the eastern shore of Waquoit Bay, south of the Quashnet River. After the wasting disease, and prior to the mid-1970's, eelgrass was abundant on that shoal (Figs. 18 and 19). There is some question about the composition of vegetation along this shore in the 1938 photograph because a longtime shellfisherman (O. Kelly, pers. comm) claimed that Ruppia was the sole species on this shoal during a visit in 1937. If so, Ruppia was replaced by eelgrass in subsequent decades. By early 1970's eelgrass began to decline in this area, beginning first along the deeper bed margins and the innermost parts of the Bay. Virtually all eelgrass disappeared between the Quashnet and Little Rivers by the early 1980's, and no beds and few shoots were observed in 1985 and 1987 field observations.

In addition to these events on the eastern shoal, drift algae became more prominent in the deep central part of the Bay after 1960. Today Cladophora and other drift species accumulate to depths of 70 cm

Figure 17. Eelgrass bed area (corrected for % cover) in West Falmouth Harbor (near entrance) between 1943 and 1981.
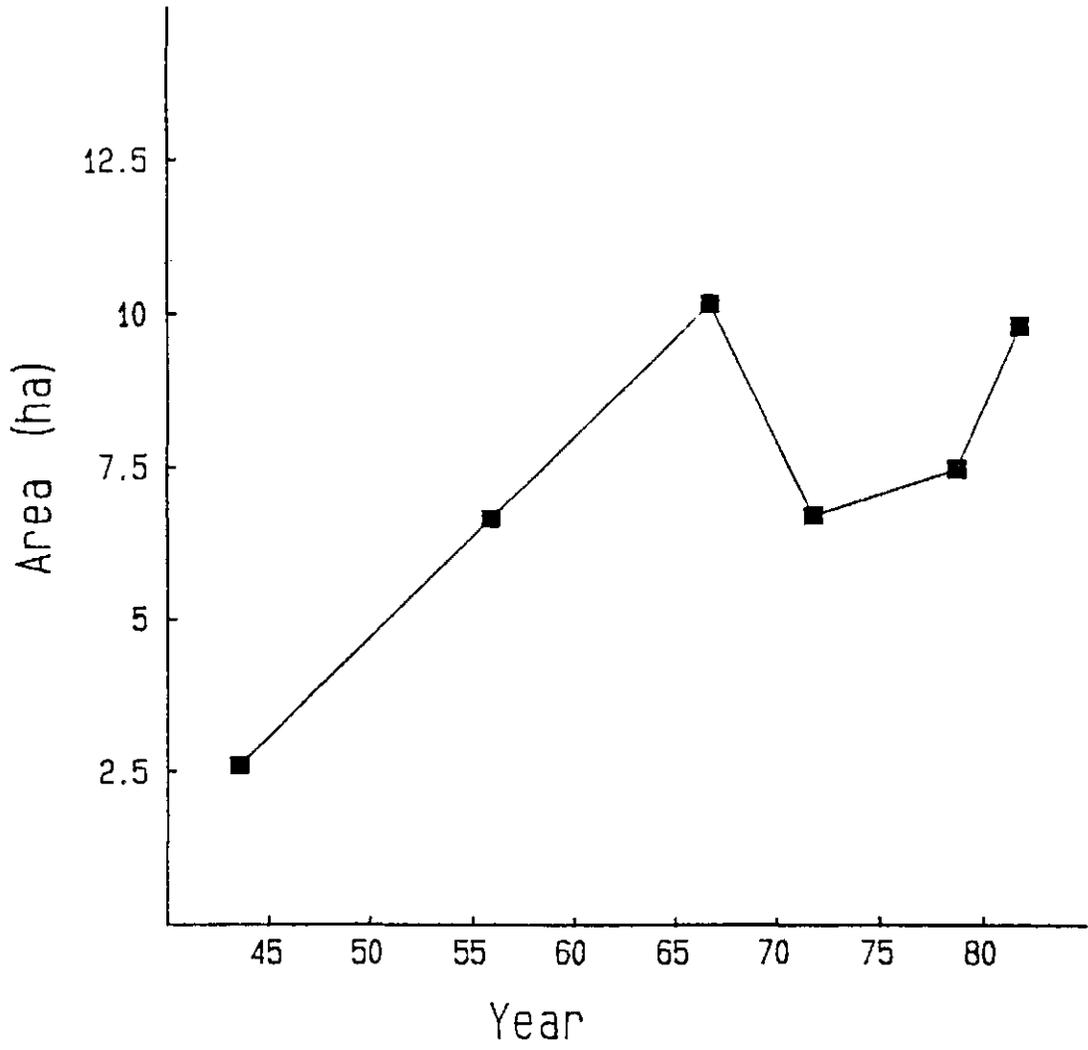
Figure 18. Eelgrass cover on the eastern shore of Waquoit Bay during four periods
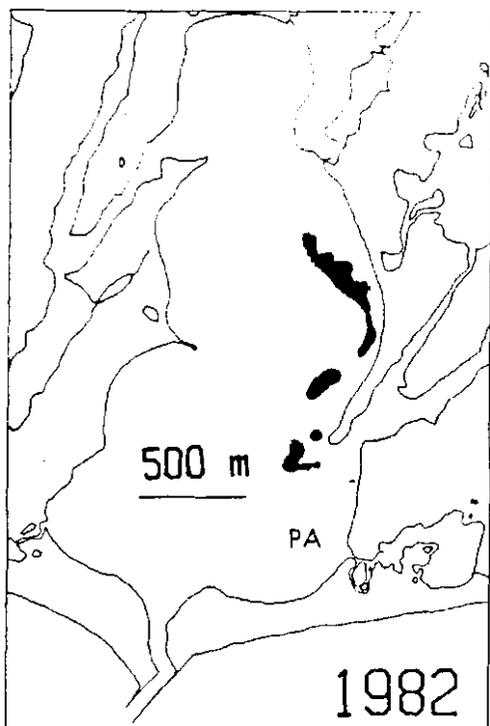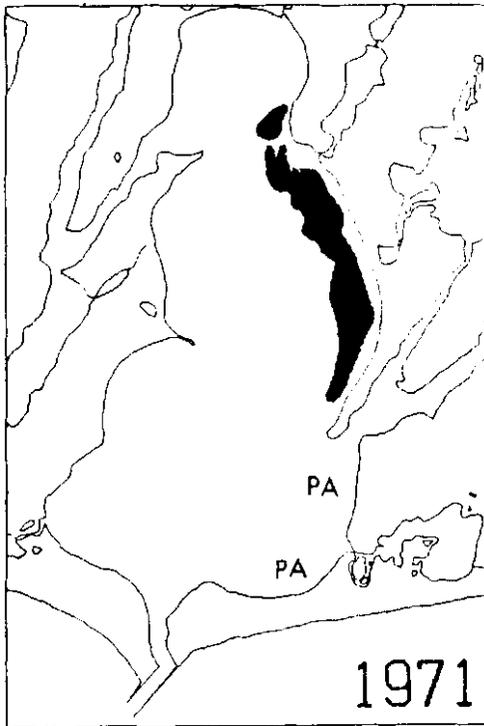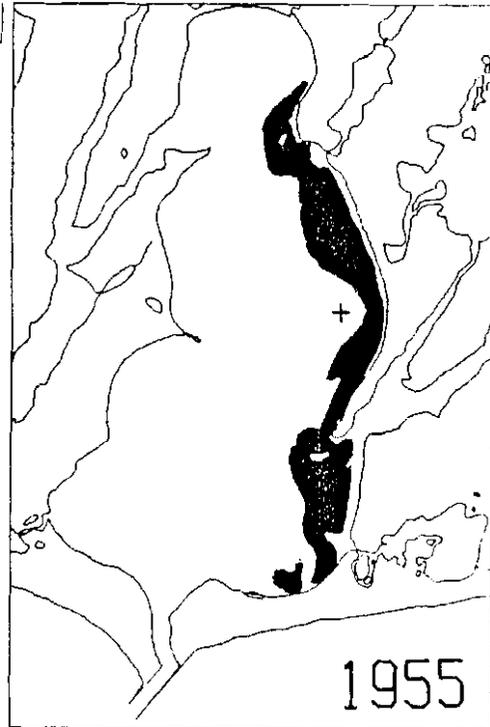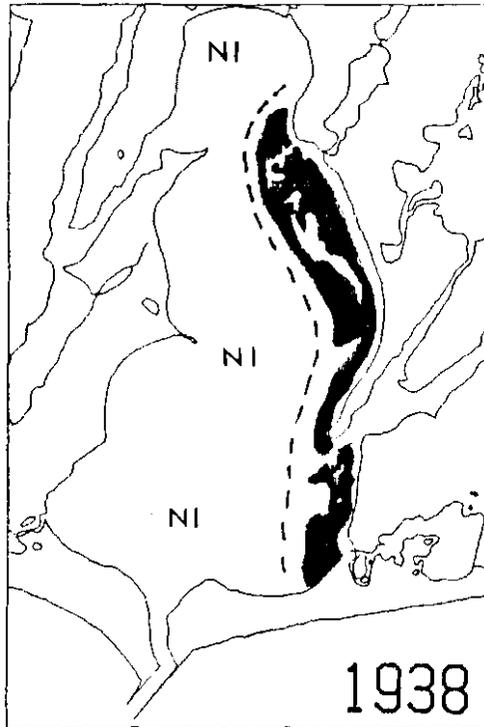
Figure 19. Eelgrass bed area in Waquoit Bay (adjusted for %
cover) between 1938 and 1981.
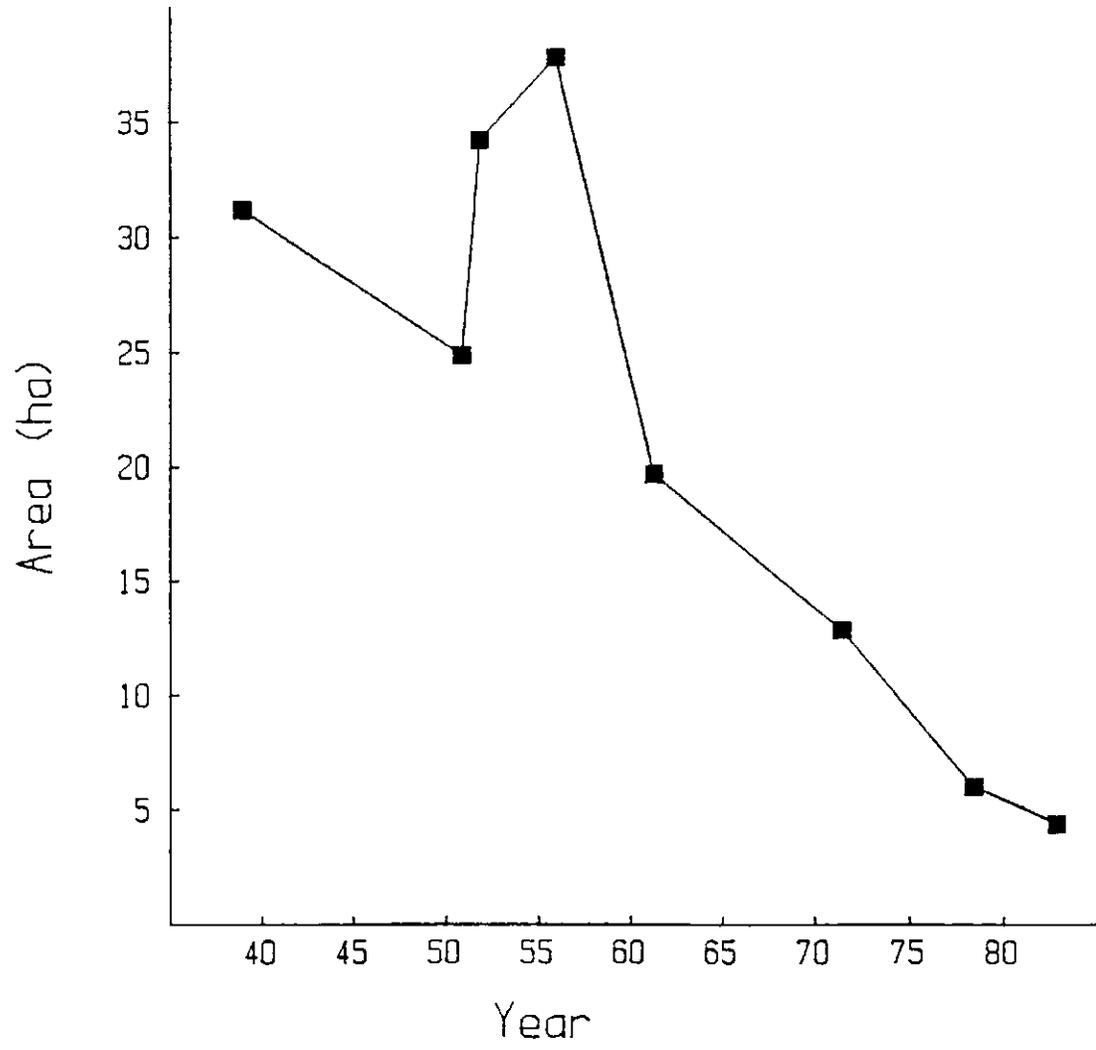
in places (Valiela and Costa, in prep). Sediment cores show that
eelgrass was abundant in the central Bay prior to the wasting disease.
Photographs and core data show that eelgrass returned there by the
1950's, but disappeared again between 1965 and 1973 (Chapter 3).

The increased growth of algae and the pattern of eelgrass decline
in Waquoit Bay suggest that these events were related to nutrient
loading.

Discussion

Impact of the wasting disease in Buzzards Bay

Documentation of eelgrass prior to the wasting disease is
fragmentary, but all evidence suggests that eelgrass cover in Buzzards
Bay equaled or exceeded present day abundance: Aerial photographs of
Sippican Harbor, Marion taken before the wasting disease show that
eelgrass was as abundant near the mouth of the bay in 1930 as in 1981,
and even more abundant at the head of the bay during 1930. Sediment
cores show that eelgrass was more abundant in several areas prior the
disease (and in some cases 20 years later) than today. This is
corroborated by photographs that show that eelgrass populations in some
bays had greater coverage during the 1940-1960's than today.
Fragmentary documentation of eelgrass distribution on old nautical
charts demonstrate that eelgrass grew in the same areas prior to the
disease as recolonized after. Residents have noted that eelgrass has
not returned to some areas. Available published descriptions of
eelgrass distribution around Cape Cod prior to the wasting disease also
match or exceed the present abundance. For example, Allee (1919) in his

survey of invertebrates described eelgrass in Quisset Harbor, Falmouth, as growing within 5 m of shore, and "continuous throughout" the bay. Today eelgrass grows primarily near the mouth and only to 2 m, and is absent from the less flushed and deeper parts of the bay. Davis (1913a+b) dredged eelgrass from greater depths in Buzzards Bay and Cape Cod than observed today.

In light of these observations, the assessment by Stevens et al., (1950) that eelgrass cover in upper Buzzards Bay equaled less than 0.1% of prior cover seems realistic, especially because the earliest photographs (6 to 10 years after the epidemic) generally show that surviving eelgrass beds in Buzzards Bay equaled 10% or less of the peak eelgrass cover observed today. In most areas, eelgrass did not begin to recolonize until the 1950's.

As reported elsewhere, the earliest photographs from Buzzards Bay show that eelgrass populations beds near streams and rivers survived or recovered soonest after the disease. Not noted earlier, were that some beds on the outer coast or in deeper waters survived as well. For example, eelgrass beds are abundant around Little Bird Island, Wareham, a shallow shoal 1 km off Great Neck where eelgrass is absent virtually absent. This occurrence can only be explained if this offshore population survived the disease. This bed is not unique, other beds on exposed coasts, often 100's of m from freshwater sources survived as well. The absence of records of surviving offshore or deep beds in Buzzards Bay is not surprising because documentation in most areas was poor, and observations during the wasting disease were made from the surface, nearshore. Local observers noted at the time that living

shoots occasionally washed from offshore areas (e.g. Lewis and Taylor, 1933). Little significance was attached to these observations, but in Buzzards Bay, these offshore beds were equally important in facilitating the recovery of eelgrass populations after the disease. In general, the onset of colonization of bare substrate was dependant on the distance from these refuge populations.

Cause of the wasting disease and the temperature hypothesis

Labarynthula causes all symptoms of the wasting disease (Short, pers. comm), but it is always present in eelgrass populations; diseased plants are common, but normally do not reach epidemic proportions. Therefore, what conditions in 1931-1932 led to the outbreak of the wasting disease? One possibility is that more virulent strains of *Labarynthula* may arise (Short, pers. comm). The transmission of a virulent agent, as Rasmussen (1977) points out, cannot explain the near instantaneous appearance of the disease throughout North America.

As stated earlier, the most popular hypothesis concerning the onset of the wasting disease is that abnormally high summer water temperatures and mild winter temperatures somehow made eelgrass more susceptible to a parasite (Rasmussen, 1977). Bulthuis (1987) rejected the supposition that temperature stresses eelgrass, because recent research has shown that eelgrass is so eurythermal, and an elevation of several degrees is insignificant. Also, water temperatures were not elevated in all areas in Europe where eelgrass declined because of local climactic variations (Bulthius, 1987). The recent losses to disease in Great South Bay, New Hampshire during the 1980's (Short, 1985) were not

associated with elevated temperatures, and again suggests that
temperature elevation cannot be the sole explanation for disease
outbreaks.

The observation that some beds offshore in Buzzards Bay survived
the wasting disease does support the temperature hypothesis because beds
in deeper water are insulated from the extreme temperature that occur in
some shallow embayments. For example, in summer, shallow areas may be
as much as 10 °C higher than temperatures recorded in well flushed areas
(pers. obser., Allee, 1923a). This phenomenon may not be the sole
reason for bed survival because some shallow beds along shore, not near
freshwater sources, survived or quickly recolonized as well.

Temperature and climactic conditions in Massachusetts during the
early 1930's have not been critically analyzed. Were water temperatures
in Buzzards Bay high during the early 1930s as observed elsewhere?
Water temperature in shallow coastal waters correlates with air
temperature. In eastern North America, mean winter temperatures cycle
every twenty years (Mock and Hibler, 1976). This short-term oscillation
is superimposed on a one hundred cycle of winter temperature
oscillation, and the coincidence of peaks and nadirs of these cycles
resulted in the warmest winter ever recorded in the east north central
US during 1931-32 (October - March mean = 3.7 °C), and the coldest in
1977-78 (October - March mean = -1.4 °C; Diaz and Quayle, 1978). Air
temperature data for Boston show that both that the summers of 1931 and
1932 had three times the number of days above 32 °C (90 °F) than did the
average for all other summers between 1900-1935 (Chief of the Weather
Bureau Reports). Localized differences in this trend exist, and in New

England, the winter of 1932-33 was warmer than the previous winter. Furthermore, New England had a warmer winter in 1889-90, and one nearly as warm 1912-13.

February water temperature in Woods Hole is generally the coldest month of the year, and August the warmest. Water temperature data for Woods Hole is not available for 1931, but is available for a station in Nantucket sound, 30 km to the East, and a station in Rhode Island, 50 km to the west for this and other years. At these neighboring stations, mean February and August temperatures were warmer in 1932 than 1931 (Bumpus, 1957), which also coincides with air temperature trends described above for New England. In Figures 20 + 21, February 1931 temperature data was estimated from a multiple linear correlation from these stations (r2= 0.62, α > 0.05). August temperatures in Woods Hole do not correlate well with the other stations and was conservatively estimated as equal to the 1932 data.

Like winter air temperatures over the Northeast U.S., water temperature in February 1932 was the warmest since 1890, but February 1913 was only slightly warmer than usual (Fig. 20, top). Furthermore, many subsequent years had February water temperatures nearly as warm or warmer. August water temperature in Woods Hole (Fig. 20, bottom) show less distinct cycling, and is out of phase with the winter climate cycle. Hence, August water temperature 1932 was also the warmest in 40 years, but warmer events occurred often in subsequent decades.

These data substantiate Rasmussens' view that 1931 and 1932 were the first consecutive 2 year period of warm summers and winters in decades. Nonetheless, subsequent two year periods (1949-1952, 1969-

Figure 20.   One hundred year record of water temperatures in Woods Hole.

Top: Mean February temperature in Woods Hole: 1880-1986.   Bottom:

Mean August water temperatures in Woods Hole for the same period.   Data

1931 was estimated (see text).

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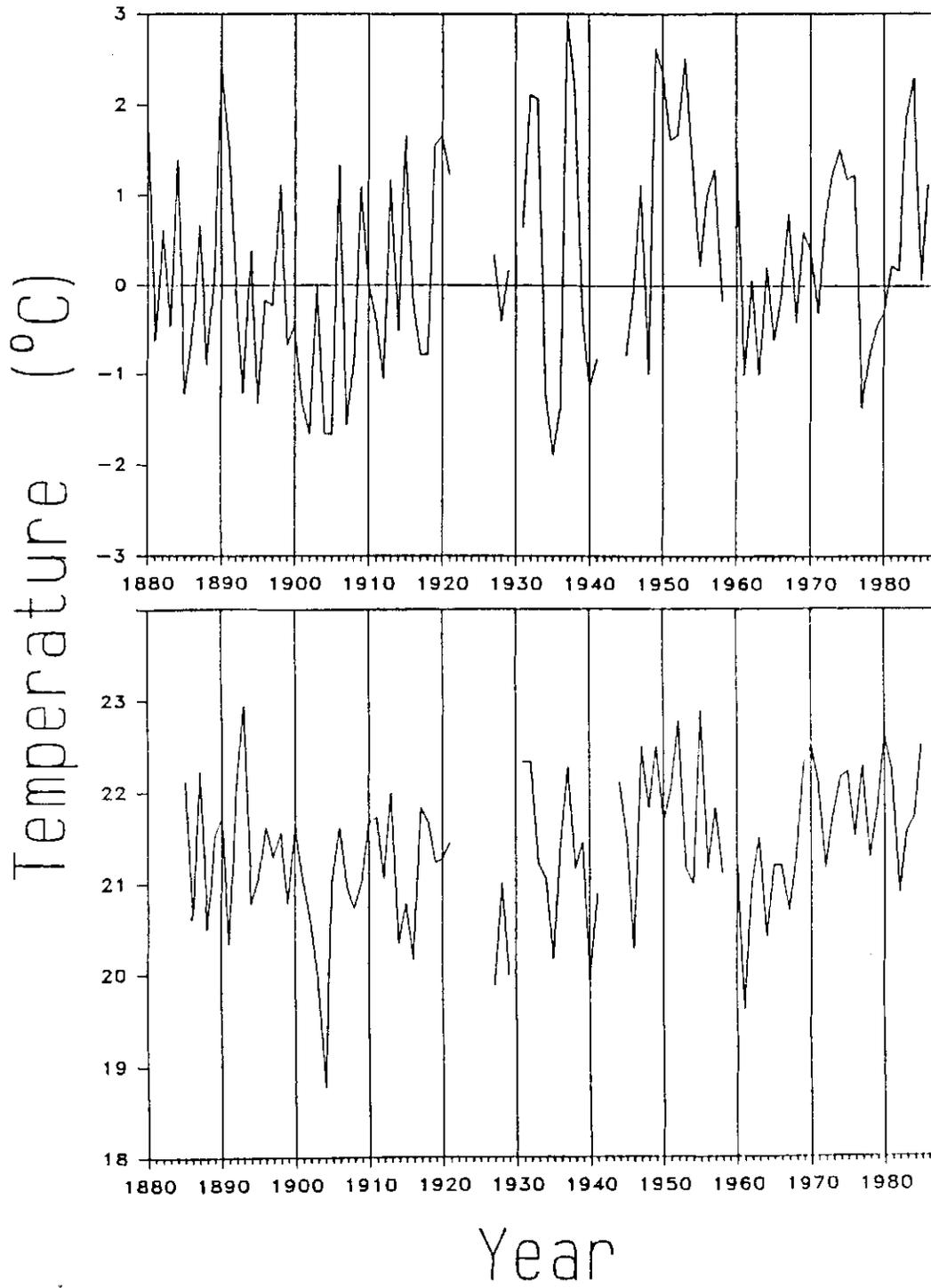
Figure 21.   Temperature deviation above the long-term mean for August

and February in Woods Hole for 96 years of data between 1880 and 1987.

Years with temperatures below the mean for either month are below

the lower limits of the graph and not shown.

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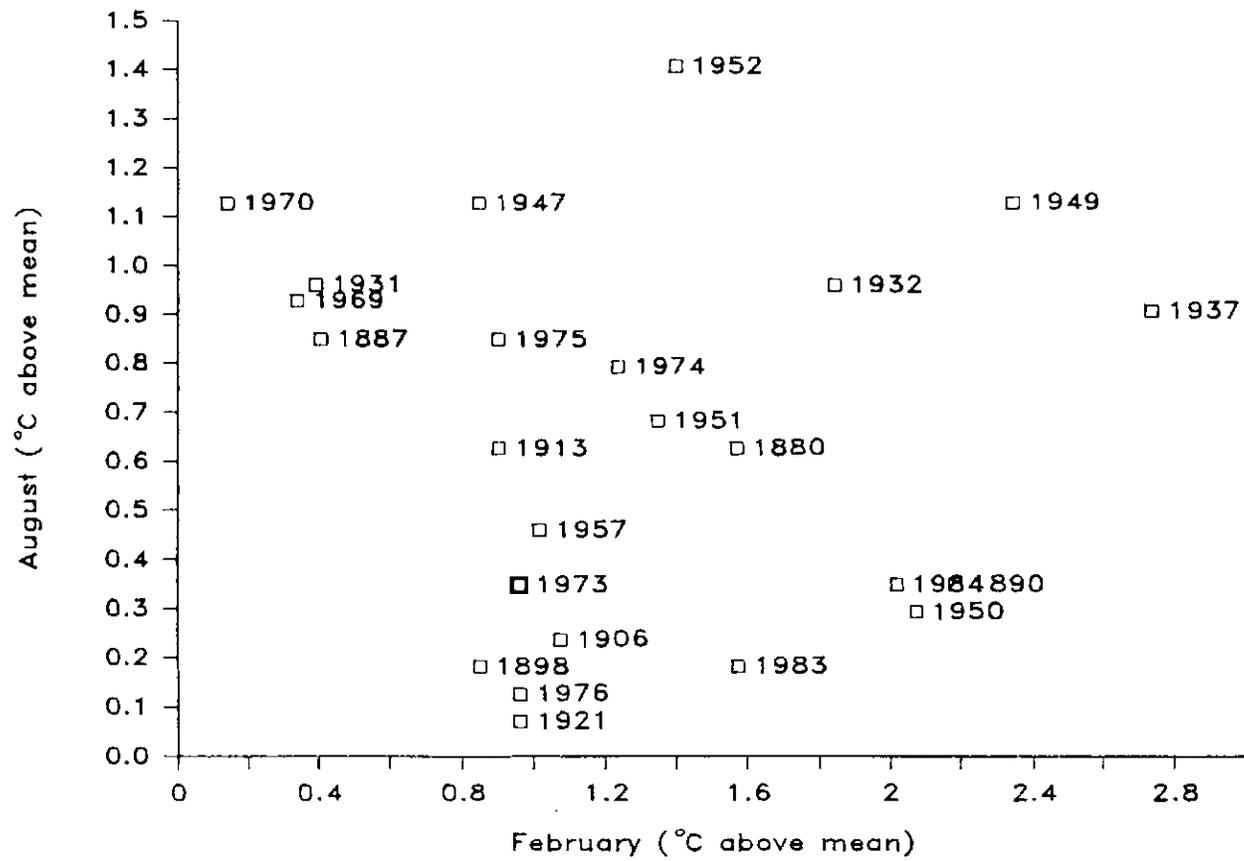
1970, 1974-1975) had winter and summer water temperatures that were as warm or warmer than the 1931-32 event (Fig. 21), but no general declines in eelgrass were reported in New England, or apparent on photographs of Buzzards Bay. A decline between 1949 and 1952 could have gone unnoticed, because eelgrass populations had only partly recovered in most areas. A decline during the late 1960's or mid-1970's, however, would have been much more apparent because eelgrass had recovered considerably by that time and there had been no recent major storms or ice accumulation that could cause a decline that could be mistaken for disease-caused declines.

One additional line of evidence contradicts the temperature hypothesis. Past declines of eelgrass in New England (1894, and 1908) reported by Cottam (1934) do not coincide with the warm summer and winter pattern. In 1894, the winter was cool, and the decline came 4 years after a record breaking warm winter. The 1908 event was not characterized by unusual weather.

These observations do not rule out the possibility that warm temperatures played a role in the 1931-32 decline, but suggest that temperature cannot be the sole factor in causing regional collapses in eelgrass populations. Instead, other unknown factors must be involved.

General patterns of recolonization

Regionally, recovery was slow, and the greatest increases in abundance occurred during between 1955 and 1970. By the 1980's, eelgrass had saturated much of the available substrate, but eelgrass populations continue to expand in some areas today, and residents claim

that eelgrass has not fully recovered to its former abundance in some bays.

The onset of recolonization began in most areas during the 1940's and early 1950's. In some areas, recolonization did not begin until the 1960's or later because they were remote from refuge populations, and propagation of eelgrass over 1000's of meters is slow. This pattern explains why some populations in this region and elsewhere (e.g., den Hartog, 1987) are still recovering 50 years after the decline.

The colonization of bare areas by eelgrass beds in offshore or euryhaline environments around West Island, Great Neck, and Megansett Harbor is inconsistent with general opinion today that eelgrass populations in estuaries or near fresh water sources were the main surviving populations that later recolonized the area. In fact, while many shallow bays with freshwater input had refuge eelgrass populations, they were generally unimportant in the colonization of offshore and exposed coasts.

Around Buzzards Bay, once eelgrass began to colonize an area, the time to reach peak abundance varied markedly. On a small scale (below 10 ha) growth is typically logistic, and habitat is saturated in 8 to 15 years (Costa, 1988 and in prep.). In some locations, such as on the shallow shoal south of Little Harbor on Great Neck, Wareham, peak abundance occurred in as little as 6 years after the first patches of eelgrass appeared.

The percent cover of eelgrass beds at peak abundance also varied among sites. In high energy environments like Megansett Harbor, Falmouth, wave scour and storms frequently remove patches of eelgrass of

various size so some beds never exceed 50% cover, even over decades. In shallow areas like this, eelgrass beds survive and recolonize in the troughs of migrating sand waves (Fig. 22). In contrast, beds in quiescent areas eventually nearly cover all of the bottom.

Differences in both colonization rate and peak cover can be explained by differences in disturbance size, disturbance frequency, vegetative growth rate, and seedling recruitment rate that can be measured from photographs. These variables were included in a computer simulation that accurately predicted changes observed on sequences of photographs (Costa, 1988 and in prep.). Results of this simulation suggest that physical removal of patches of eelgrass less than 10 m^2 have little effect on rate of colonization or peak cover, even when 25% of the bed is removed each year. Other disturbances, such as declining water quality or catastrophic storms may lead to sizeable and longlasting losses.

The pattern of eelgrass colonization on a larger scale (100's to 1000's of ha) is distinct from the small scale pattern of colonization. On large parcels of coast, such as around Great Neck (above) or high energy areas like Wianno Beach on Cape Cod (in prep.) eelgrass took 20 to 30 years to reach peak abundance after onset of colonization. Growth on a large scale is not logistic, rather staggered or linear because of stepwise colonization, hydrographic and geographic isolation, and heterogeneity of the substrate (above and Costa, 1988).

Figure 22. Eelgrass beds growing between sand waves (near Little
Harbor Beach, Great Neck Wareham). Eelgrass cover on this habitat did
not change appreciably between the two years shown. This demonstrated
that colonization and growth kept up with losses from sand wave
migration. Most of these beds, however, were destroyed by ice scour and
winter storms during the late 1970's.

September 1966   April 1974
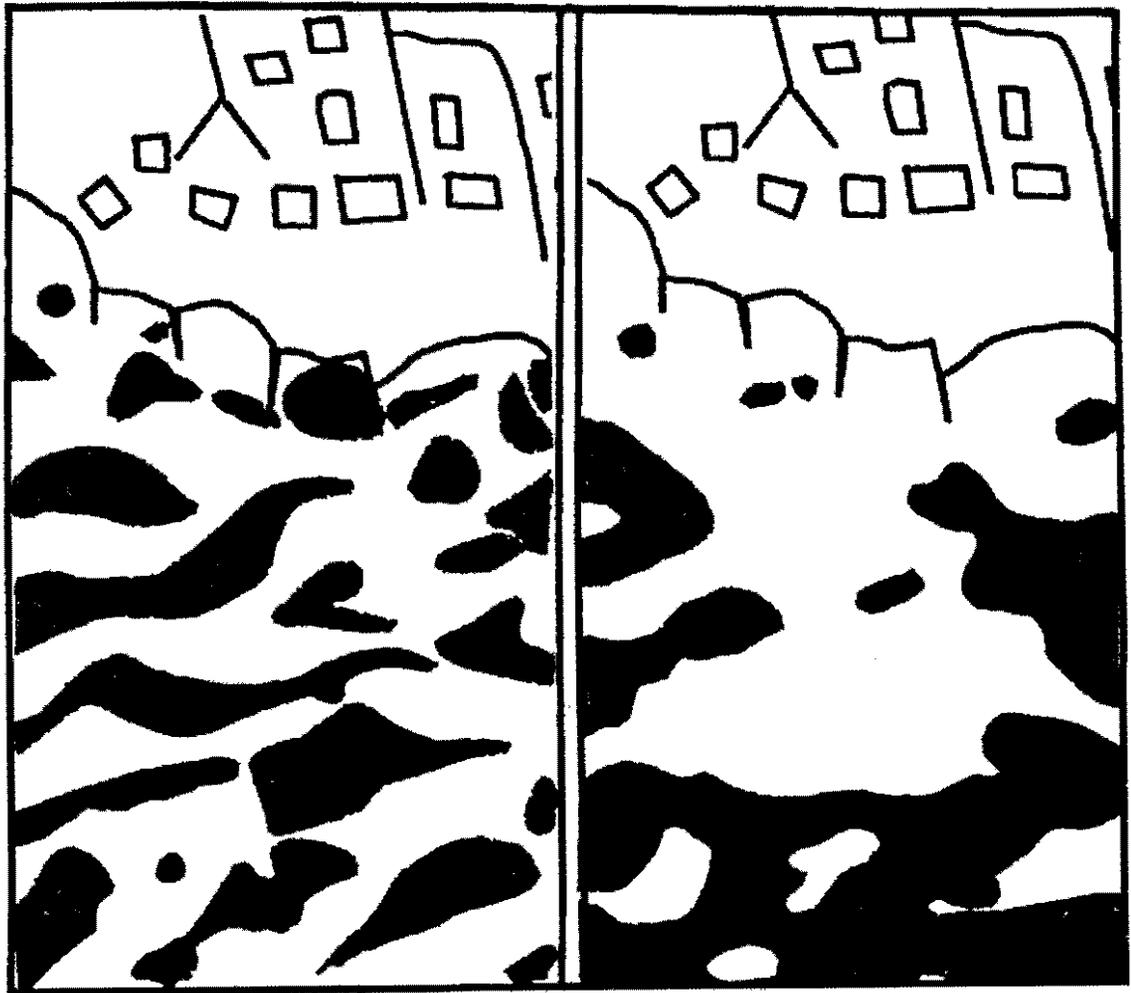
50 m

Causes of recent declines

Superimposed on the long-term pattern of gradual recovery and continued expansion after the disease are local declines that were the result of other natural or anthropogenic disturbances. Eelgrass populations generally recovered from natural disturbances within ten years. For example, severe storms in 1938, 1944, and 1954 destroyed eelgrass in some exposed or shallow areas in Buzzards Bay and Cape Cod (above and Costa, 1988). In less exposed areas, eelgrass recolonization was only slowed by these disturbances. Ice scour often removes eelgrass in shallow areas, as was evident along the shallow margins of beds in East Bay, Fairhaven and along Great Neck, Wareham during severe winters in 1977-1979. In shallow Bays like Apponagansett Bay, So. Dartmouth and the Westport River basin, ice accumulation coincide with major fluctuations in eelgrass abundance.

New losses due to human perturbation have been longer lasting. The disappearance of eelgrass in the north end of the Westport Rivers, Apponagansett Bay, Dartmouth; Little Bay, Fairhaven; Wareham River, parts of Sippican Harbor, Marion; Clarks Cove, Dartmouth; Waquoit Bay, Falmouth (on Vineyard Sound), and other coastal lagoons on Cape Cod (in prep.) appears to be due to decline in water transparency from nutrient loading because these areas have conspicuous macroalgal growth, poor water transparency, abundant periphyton, prominent gradients of maximum eelgrass growth and related declines in water quality such as shellfish and beach closures. Resuspension of sediments by propeller wash and subsequent decline of light availability to eelgrass beds may be a contributing factor for declines in some shallow bays.

Dense accumulations of drift algae that often result from nutrient loading contribute to eelgrass loss because drift material can smothers young eelgrass seedlings an adult shoots (pers. obs.) and increases in abundance of drift algae have been related to eelgrass losses elsewhere (Nienhuis, 1983). Drift algae were not quantified in this study but it is apparent from aerial photographs that this material has been increasing in many bays during recent decades. Such changes in bottom flora can be verified by analysis of core sections for changing chlorophyll degradative products (Brush, 1984) and stable isotope ratios (Fry et al., 1987), and should be studied.

The loss of eelgrass from New Bedford Harbor could be due to any number of causes including declining water quality, toxic pollutant accumulation in the sediments (PCBs and heavy metals among others), or changes in hydrography resulting from the construction of hurricane barriers there. No study of the effects of PCBs on eelgrass have been undertaken, and no studies on long term changes of water quality have been made in this area, therefore no conclusion can be made on the exact causes of declines in New Bedford until further studies are conducted.

There is no evidence for recent large scale declines of eelgrass populations due to new outbreaks of the wasting disease as has been reported elsewhere (Short et al., 1986). In two photograph sequences (such as in Sippican Harbor during the early 1970's, Apponagansett Bay during the early 1950's), isolated declines in eelgrass do not coincide with ice accumulation or storms. These declines are enigmatic, but are probably linked with pollution events, because both areas have been

developed for many decades, and have had variable water quality in the past.

Most recent declines in eelgrass abundance in Buzzards Bay that are not related to physical removal have occurred in areas where there are large anthropogenic inputs in relation to local flushing rates. There are unanswered questions concerning human impact on eelgrass abundance, but it is clear from this and other studies that eelgrass is sensitive to water quality decline. Therefore, in light of increasing rate of development and discharges along the shores of the Buzzards Bay, it is likely that new declines in eelgrass cover will occur.

Chapter 5

Mechanism of eelgrass (*Zostera marina* L.) colonization: Patch dynamics

and effect of disturbance

Abstract

The process of re-colonization of bare substrate by eelgrass
(*Zostera marina*) was documented using a forty year record of historical
photographs of two regions in Massachusetts (West Island, Fairhaven;
Wianno Beach, Osterville). The pattern of colonization were similar at
subsites within each region: discrete circular patches of eelgrass first
appeared on bare areas (via seed dispersal) and grew laterally, and
additional new patches appeared each year. On a scale of 1000's of m,
eelgrass took 25 and 40 yr respectively to reach peak cover after
initial colonization subsequent to the wasting disease. On a smaller
scale (100's of m) eelgrass expanded to peak cover 15 yr after at
subsites in each area.

On the smaller scale, rates of colonization, and peak eelgrass
cover at these and other areas appeared to vary primarily due to
differences in lateral bed growth, new bed recruitment, disturbance
size, and percent of the substrate disturbed each year by non-
catastrophic disturbances. These phenomena could be measured by
analyzing photograph sequences, and were incorporated in a computer
simulation. Lateral growth rate, bed recruitment rate, percent of the
area disturbed, and disturbance size were set in the simulation and
validated with values documented in the photograph record.

The simulation agreed well with observed small-scale colonization
rates and percent cover at peak abundance at validation sites in each
area. Changes in recruitment rate within the model demonstrated that

new bed recruitment was fundamental for rapid colonization. Higher lateral growth rates also shortened the time for eelgrass to reach peak cover, but not to the same degree as recruitment rate. In contrast, both disturbance size and percent area disturbed had much less effect on the time for eelgrass to reach peak abundance. The percent of the habitat disturbed each year primarily affects the percent of the habitat covered by eelgrass at peak abundance. High levels of disturbance explain why eelgrass cover in some areas never exceeds 50% of the available habitat. Disturbance sizes less 10 m^2 had little effect on colonization rates or percent cover at peak abundance, even when 20% or more of the eelgrass cover was removed each year. Changes in disturbance size when disturbances are greater than 100 m^2, also have little effect on peak cover or time to reach peak cover. Disturbance sizes in the range 10-100 m^2 can greatly affect the time to reach peak cover, especially when more than 10% of the eelgrass habitat is disturbed each year.

The slower colonization on a large scale (1000's of m) can be explained by stepwise colonization from refuge populations. That is, numerous small subareas showing logistic growth will result in linear expansion on larger scales. The slow large scale dispersion of eelgrass populations, together with catastrophic storms, and in some areas, human disturbance, explain why eelgrass populations took many decades to recover from the wasting disease, and why some areas are still recovering today.

Introduction

Disturbance, patch formation, succession, recruitment, and growth
are fundamental processes affecting the abundance in sessile organisms
(Picket and White, 1987; Paine and Levin, 1981). In addition to these
factors, analysis of succession and patch dynamics are generally altered
or defined by competition and predation among species. Thus,
interspecific interactions make it more difficult to study the effects
of patch formation and disturbance on the colonization and abundance of
a sessile species, especially on a large scale.

Eelgrass (*Zostera marina* L.) meadows are one community where the
relation between population growth and disturbance can be studied
without complicating effects of predation and competition. This
community is ideal for a number of reasons. For most of its range, and
in most habitats, eelgrass does not compete for space with other species
(Thayer et al., 1984). That is, eelgrass beds exhibit the simplest form
of succession: bare substrate $\xrightarrow{colonization}$ eelgrass meadow
$\xrightarrow{disturbance}$ bare substrate. Less than 10% of eelgrass primary
production is directly consumed, and eelgrass beds are rarely denuded by
herbivores (Jacobs et al., 1979; Nienhuis and Groenendijk, 1986).
Consequently, the role of herbivory in eelgrass colonization can be
ignored for most sites. Virtually all eelgrass beds were destroyed by a
"Wasting Disease" in the early 1930's (Rasmussen, 1977); thus a large-
scale natural "experiment" has occurred. Finally, eelgrass beds often
show up clearly on aerial photographs, and many areas have been repeated

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surveyed since the late 1930's, hence a large data base exists for analysis. In this paper, I document and model the process of eelgrass colonization at two sites in southeastern Massachusetts (USA), and determine how population growth is affected by different levels of disturbance and rates of population expansion.

Eelgrass life history

Eelgrass is a marine angiosperm that grows subtidally in Northern temperate waters, often forming extensive meadows. All stages in the life cycle of eelgrass including pollination and germination occur underwater. Expansion of existing beds occurs by production of new shoots and recruitment of new seedlings, whereas the colonization of bare areas not adjacent to existing beds almost completely depends on propagation and germination of seeds because uprooted plants float and are usually lost to sea or get cast on shore. Seed production often exceeds many thousands of seeds per square meter (Thayer et al., 1984). Eelgrass seeds are negatively buoyant, and most fall near the beds that produced them (Robertson and Mann, 1984; c.f. Davis, 1985); but some may also be carried by currents or uprooted flowering shoots (Churchill et al., 1978).

Disturbances

Like most regions, nearly all eelgrass populations in Massachusetts were destroyed (Cottam, 1933, 1934; Stevens, 1935; Stevens et al., 1950; Costa, 1987, 1988). One of the most remarkable aspects of the wasting disease was that eelgrass populations took many decades to

recover, and are still expanding in some areas today (Costa, 1987; den Hartog, 1987). Superimposed on this gradual recovery were smaller or localized impacts from natural or human disturbances of various scale. These chronic or periodic disturbances slowed or sometimes "reinitialized" colonization. Human disturbances affecting eelgrass and other seagrass populations include physical removal, toxic pollution, and degradation of water transparency (Cambridge, 1979; Cambridge and McComb, 1984; Orth and Moore, 1983b; Orth et al, 1980; Phillips, 1972; Thayer, et al., 1975). Natural disturbances affecting eelgrass and other seagrasses (besides disease) include catastrophic storms, periodic non-catastrophic storms, sediment transport, ice damage, and grazing pressures (Harlin et al., 1982; Jacobs et al., 1981; Kirkman, 1978; Orth, 1975; Rasmussen, 1977; Robertson and Mann, 1984). On Cape Cod and Buzzards Bay, MA, storms and ice scouring are the principal disturbances affecting the two areas studied here (storm dates and severity are summarized in Costa, 1987).

This study documents recolonization after the wasting disease and analyzes the mechanisms and patterns of colonization based on growth and natural disturbances. In general, there has been little effort to model large-scale seagrass bed growth and recruitment. Many of the techniques used here, such as mapping of seagrass beds using aerial photographs is now routine (e.g. Kirkman, 1977; Harlin and Thorne-Miller, 1982). In addition, small scale (10's of m) patterns of colonization have been studied in transplanted eelgrass (e.g. Fonseca et al. 1979; Kenworthy et al., 1982). What is lacking is a quantification of eelgrass colonization rates at larger scales, especially how they are affected by

disturbances that remove eelgrass, recruitment rate of new beds, and bed lateral growth.

Abundance or the percent of surfaces covered over time typically follows a logistic curve. A species may not completely cover a habitat either because of competition, disturbance, or suitability of habitat. In this study, the asymptotic portion of the curve is termed percent cover at peak abundance, and the time to reach the asymptotic phase was termed years to peak abundance (Fig. 1).

After the wasting disease, surviving eelgrass populations took 30 to 50 years to recolonize parts of Buzzards Bay and Cape Cod Massachusetts (Costa, 1987). These long colonization periods are due to the fact that initial re-colonization in some areas did not begin until 20 or 30 years after the disease because they were remote from refuge populations. In small areas (less than 20 ha), once colonization began, peak cover would nearly always be reached in less than 20 years, and in some cases, in as few as 5 years.

On high energy coasts, discrete circular beds of eelgrass first appeared, which expanded laterally. Each year new beds were recruited nearby, and they too expanded, and this process continued until peak cover was achieved. There was considerable variation in this colonization process: not only did the time to reach peak cover vary, but some areas had nearly continuous eelgrass cover at peak abundance whereas others had less than 50% of the available substrate covered, even after decades. This variability in colonization patterns appeared to be due to differences in bed recruitment rates, bed lateral growth, disturbance size, and the percent of the habitat disturbed each year.

Figure 1. Hypothetical colonization of an area by vegetation as percent of the area covered over time. In this paper, the asymptotic part of the curve is termed percent cover at peak abundance. The time to reach the asymptote is termed years to peak abundance.
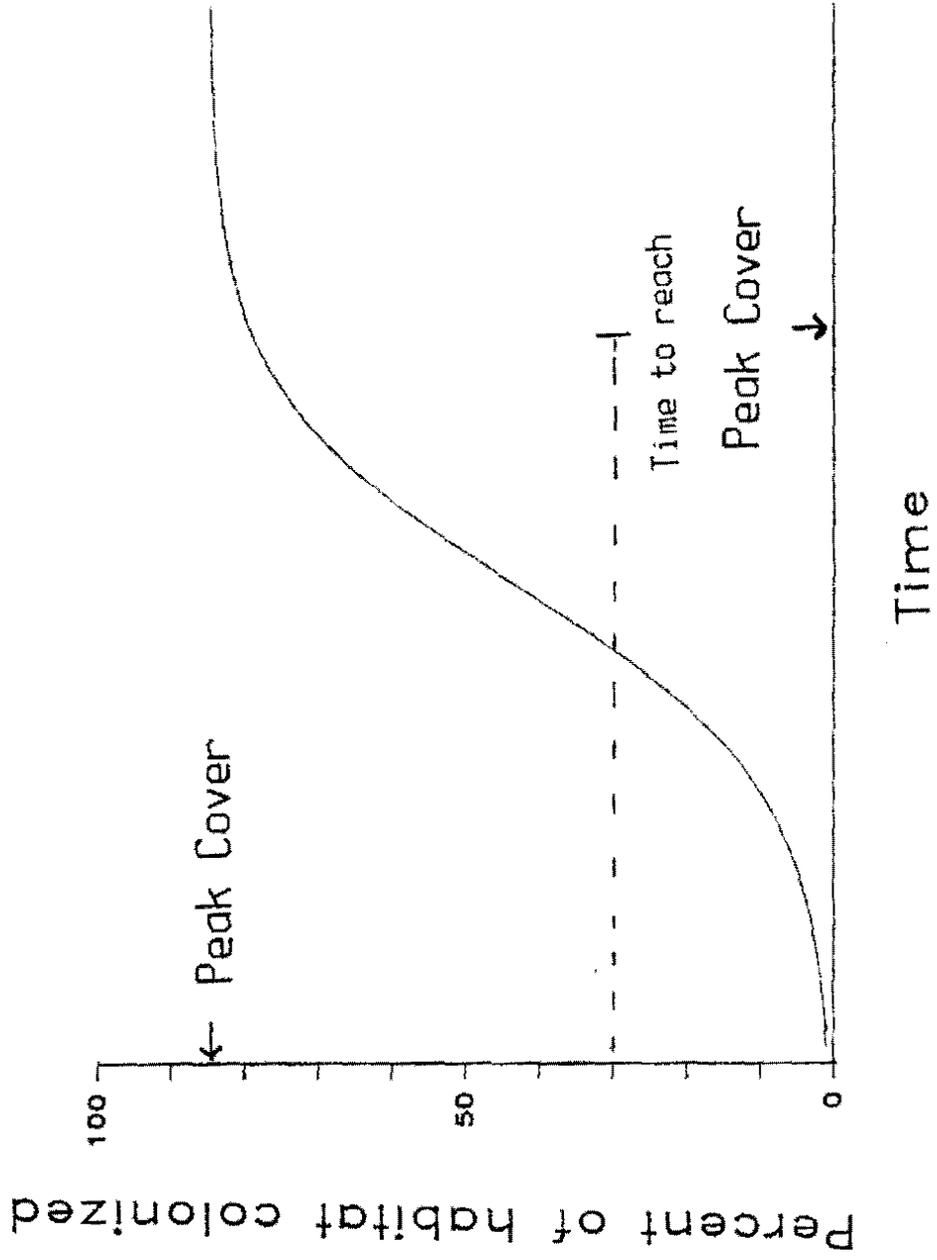
To test how changes in colonization rates depended upon differences in bed lateral growth rate, bed recruitment, and disturbance size and frequency, a graphical simulation (a two-dimensional cellular automata) was developed that incorporated these parameters. Cellular automata are mathematical systems that simulate complex spatial or temporal patterns using lattice matrices of cells whose value or contents are determined by the contents of adjoining cells, based on a set of rules (Cocho et al., 1987; Wolfram, 1984). This type of model is necessary where spatial relationships exist that cannot be evaluated algebraically or through differential calculus. In this case, eelgrass mortality cannot be modeled using classical growth equations because a 10% annual mortality rate results in very different patterns of colonization if the mortality consists of numerous small disturbances or large infrequent ones. Similarly, eelgrass cover expands both by vegetative growth of existing shoots and recruitment of new seedlings, but the relative importance of each phenomenon cannot be distinguished by an analysis of intrinsic growth rates.

Materials and methods
Site description

Two regions typical of moderate to high energy coastlines were studied: 50 ha in East Bay off West Island, Fairhaven, MA, and 150 ha off Wianno Beach, Osterville, MA (Fig. 2). These regions were chosen because aerial surveys were available and eelgrass grows on broad sandy coastal shelves, and patterns of eelgrass distribution are distinct. The Wianno beach site is a more exposed south facing shore and

Figure 2. The site locations in Massachusetts. The areal extant
of beds is marked by the dashed line which encloses 50 ha at West Island
and 1500 ha at Wianno Beach. The outlined area within each site denotes
the subsite (6.5 and 6.2 ha, respectively) in which detailed changes in
percent coverage were mapped and for which rates of lateral expansion,
disturbance, and recruitment were measured.

WEST ISLAND

SUBSITE

STUDY AREA

500 m

CAPE COD

WI   WB

WIANNO BEACH

500 m

SUBSITE

STUDY AREA
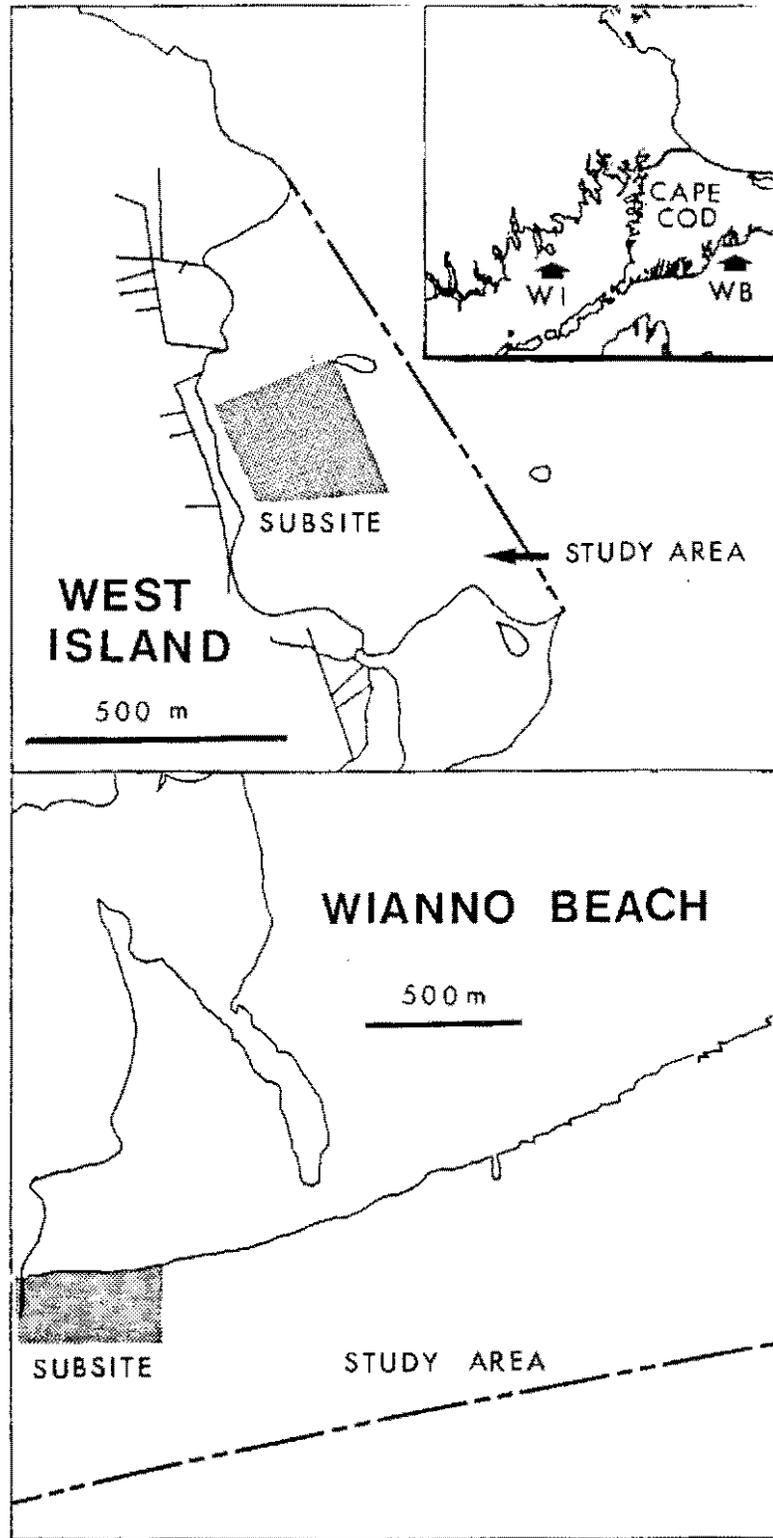
experiences more wave and storm action than the West Island site. Ice scouring is more important in East Bay, West Island because it is shallower, and ice accumulation is more prominent in that area.

Both areas have experienced little human activity. The Wianno Beach had extensive groin construction during the 1940's and 1950's, but the eelgrass beds there grow away from shore, and were probably not influenced by changes in sand transport caused by the groins.

Photograph analysis

Data on changing eelgrass abundance was obtained from analyzing sequences of aerial photographs at each site (Costa, 1987; Orth and Moore, 1983b). Photographic coverage was obtained for West Island beginning 1951, and Wianno Beach beginning 1940, with a 1 to 5 year spacing between photographs.

Eelgrass beds are rarely continuous patches of vegetation; instead there are bare areas within beds of varying size. Some of these bare areas are apparent on the photograph, others are below the limit of resolution on the photograph and are measurable only by field observations. Alternatively, eelgrass may occur as numerous discrete patches too small and numerous to digitize. In all these cases, a border was drawn around eelgrass beds or clusters of eelgrass beds on photographs, and the area of each "bed" was measured by digitizing. These bed areas were corrected percent cover by comparing them to a cover scale chart (Costa, 1987).

To map bed positions and calculate areas, a sheet of acetate was placed on the photograph, and the borders of eelgrass beds and notes on

percent cover were recorded. The photograph and overlay were photographed with slide film, and this slide was projected onto coastline maps. The edge of the eelgrass beds were traced onto the maps from the slide image. The eelgrass beds were digitized using mapping software, and stored for later analysis and plotting.

Each of these coastal regions have complex habitat heterogeneities such as sand waves and long-shore currents. No attempt was made to include these features in the model. Photographs showed that the larger coastal regions exhibited asynchronous colonization along different parts of shore, but small parcels of substrate showed relatively uniform and synchronous colonization. Consequently a small subsites in each study area (Fig. 2, West Island subsite = 6.2 ha , Wianno Beach subsite = 6.5 ha) was analyzed for differences growth, recruitment, and disturbance and used to validate the computer model.

Lateral growth of eelgrass was measured by changes in bed area of new discrete eelgrass beds between two consecutive photographs. The beds were treated as circles to calculate radius, and the change in radius between two time periods was divided by the number of growing seasons to obtain bed lateral growth rate (Gr). Only during early stages of eelgrass colonization were individual eelgrass beds sufficiently circular and recognizable for this calculation.

Disturbances may remove pieces of, or entire eelgrass beds. These disturbances occur during all stages of eelgrass colonization, but is easiest to measure during early stages of eelgrass colonization when there are many small discrete beds covering the bottom and the identity and survivorship of individual beds can be followed over time. If there

was only one year between photographs, yearly bed mortality rate (M_y) was calculated as:

$$(M_y) = 1-(N_s - N_0)/N_0,$$

where N_s equals the number of surviving beds, and N_0 is the original number of beds (new beds are ignored). If there is more than one year between photograph pairs, My was calculated from the exponential decay equation:

$$M_y = 1-(N_s/N_0)^{(1/yr)}$$

It was assumed that both disturbances and beds are randomly distributed and independent. Therefore, the percent of the habitat disturbed each year (PHD) also equals My.

Similarly, the yearly recruitment rate of eelgrass (b) can calculated by counting the number of new beds formed between photograph pairs during early stages of colonization. Because the model required an estimate of bed formation rate produced by existing eelgrass bed area, b was calculated as multiplicative percent increase in bed number each year (rather than from the calculating intrinsic rate of growth of bed number, r) as:

$$b = (N_0+N_n)/N_0-1$$

If more then one year occurred between photographs then:

$$b = ((N_0+N_n)/N_0)^{(1/yr)}-1.$$

Because this estimate of b ignores mortality of newly recruited beds that may have occurred during the interval, the equation was revised as:

$$b' = b - b \times M_y.$$

Because eelgrass populations do not exist as discrete units in late stages of colonization in the field or model, bed recruitment for

the model (R_b) was defined as the number of new beds produced per 1000 m^2 of initial bed area, or:

$$R_b = (b' * N_0)/(1000's \text{ of } m^2 \text{ of } N_0).$$

This method may slightly overestimate bed recruitment because it ignores increased eelgrass bed area during the intervals during photograph sequences separated by more than one year. Nonetheless, as shown in the results, this estimate is sufficiently accurate for the operation of the model.

In nature, recruitment is a function of the available seed pool which ultimately is a function of local eelgrass abundance, because eelgrass seeds fall near the beds that produced them (Davis, 1985; Robertson and Mann, 1983; Costa, 1987). In this model the effects of current velocity and direction were ignored, and seeds were randomly dispersed throughout the model area.

Disturbance size was calculated from the mean size of bare areas within eelgrass beds that were at peak abundance. This clearly underestimates disturbance size because existing bare areas are of different age and lateral expansion of bed margins could have taken place. This estimate of disturbance size is a first approximation, and the implications of disturbance size on colonization are discussed below.

Model configuration

Lateral expansion rate, recruitment rate, disturbance size, and percent of the habitat disturbed were incorporated in a two-dimensional graphical simulation written in TURBO Pascal[TM] for a microcomputer. The

model was composed of a spatial lattice of 310 x 190 square cells which represented the habitat on which eelgrass grew. Each cell could be empty or contain eelgrass. To eliminate edge effects in the lattice, the habitat was defined as a "wraparound" universe; that is, an expanding bed or disturbance propagating at the edge of this spatial lattice appeared on the other side of the habitat lattice.

The model was initialized (year = 0) with 2% of the model habitat area randomly covered with eelgrass, composed of both 9 cell (3x3 cells) and 1 cell beds. This initial cover was similar to the cover observed at the validation sites after initial colonization. The model ran simulating 30 years of growth and disturbance. During each year in the model: 1) existing beds would expand laterally, 2) disturbances would randomly remove some existing eelgrass, and 3) new beds were recruited (Fig. 3). To validate the model, the four parameters (lateral expansion rate, bed recruitment, disturbance size, and percent area disturbed) were set with values measured from the validation sites, and the resulting colonization curve was compared to actual colonization curve for each site. To test the relative importance of each parameter, on colonization, the simulation was repeated with each of the parameters changed over a wide range of possible values. Since the model includes stochastic events, each 30 year run of the model was repeated four times to obtain a mean and standard error of the percent cover at peak abundance, and the time to reach peak cover.

Lateral expansion of beds in the model was accomplished by cells containing eelgrass "growing into" the adjacent eight cells (Fig 3). If eelgrass grew into a cell that already contained eelgrass, that cell was

Figure 3. A small portion of the habitat lattice in the model.
The model underwent 3 phases each year. 'a' shows eelgrass coverage at
time t. The model first randomly disturbed areas (b), cross hatched
area), removing all eelgrass within the disturbance. Next, new eelgrass
beds are recruited (b, new bed). This was followed by vegetative
lateral expansion (c) which is now at time t+1. The size of each cell
varied depending on what lateral expansion rate was desired (refer to
text).
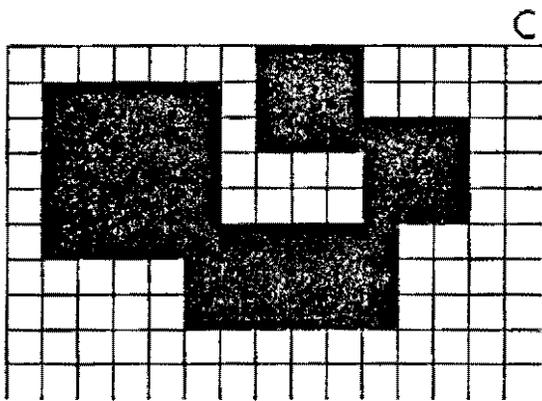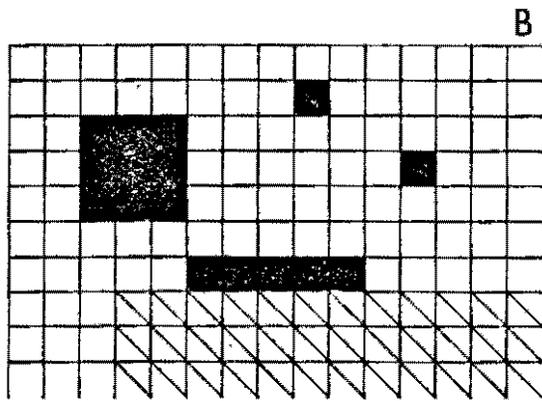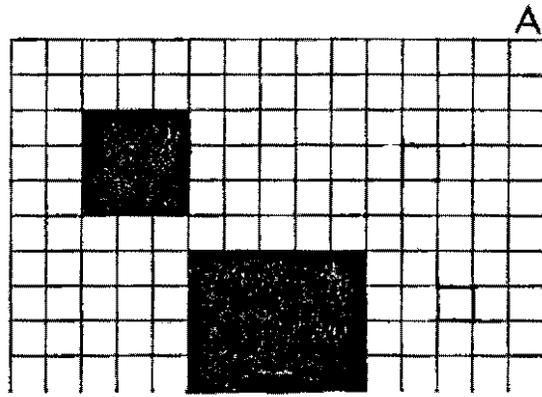
not affected. Thus an isolated, undisturbed cell could in subsequent years grow into beds composed of 9, 25, 36, 49, etc. cells. The mean lateral expansion rate of this process can be calculated if each square bed is assumed to be circular with initial radius (r_i) and area = 9, 25, 36, etc. The change in radius between any two years ($r_{(i+1)} - r_i$) equals $2 \times (area/pi)^{0.5}$. Because the square root of the area of a square equals the length of a side, then lateral expansion rate = length of square x 1.13. Because of computer memory limitations, lateral expansion rate in the model was adjusted by changing the size of each cell. This changed the absolute size of simulation lattice, but did not affect recruitment rates, percent of the habitat disturbed, or disturbance size, because each of these parameters was determined by cell size.

In nature, many more seeds are produced than either germinate or survive to form new beds. In the model and photograph analysis, new bed recruitment is conceptually equal to a seed being dispersed, germinating, and growing into a new bed. For clarity, I will call this process "new bed dispersal".

New beds were randomly dispersed throughout the area of the model. Like lateral growth, if a new bed "landed" in an empty cell, that cell became filled with eelgrass; if the cell already had eelgrass, it was unaffected. Recruitment would continue until a specific number of "beds" were dispersed (based on the area of existing eelgrass bed area as described above), regardless of whether they landed empty or full cells.

The mean size of large disturbances was measured from photographs with beds near peak eelgrass abundance, and was varied in the model. Disturbances of greatly differing sizes occur naturally, but small patch removal is probably more common. In the model, disturbance size was randomly generated, nearly conforming to a Poisson distribution centered around the mean disturbance size selected, and bounded by 0.2 x and 2.0 x mean disturbance area. This distribution was similar to the size distribution of bare areas at Wianno site. These limits in disturbance size were arbitrarily set to simplify the model, and the robustness of the model with respect to disturbance size are discussed.

The disturbances were randomly placed without respect to previous disturbances. Thus it was possible to have an area disturbed more than once during one year of the model. Disturbances would continue in the habitat lattice of the model until the total area disturbed in that year equaled the disturbance area selected when the model was initialized.

Percent eelgrass cover in the model area was calculated by dividing the number of cells containing eelgrass by the total number of cells times 100. The size of the model lattice habitat area was approximately the same size as the validation sites. At this scale, the distance effects on new bed recruitment colonization were assumed to be unimportant, and were not part of the model. Because of scale effects and because the larger regions have too much habitat heterogenity, only data from the validation sites could be compared to the model in a meaningful way.

Results

Like other areas in Massachusetts, eelgrass populations took forty years to fully recover in East Cove of West Island, and 45 years to recolonize Wianno Beach (Fig. 4; see also Costa, 1987). Over these regions, periods of areal expansion were nearly linear reaching an asymptotic peak cover. Colonization in both locals was asynchronous and occurred stepwise along each coastline: from east to west at Wianno Beach, and from northern deep parts of East Cove to shallow flats at the south end (data not shown). In particular, East Cove, West Island was characterized by two major phases of expansion: extension of deep beds at the north end of the Cove during 1956-1960, and colonization of shallow areas in the south part of the cove during 1962-1966 (Fig 4, top). Colonization may have been slowed during the mid-1950's in part due to a hurricane. Eelgrass expanded into the shallow nearshore of West Island during the 1960's and 1970's, but large portions of these beds were destroyed during the late 1970's due to severe ice scour and winter storms.

At Wianno Beach, eelgrass showed major expansion between 1948 and 1954, and between 1966 and 1973 (Fig. 4, bottom), and appears to be still expanding today, but at slower rates. This coast is more exposed, and catastrophic storms (hurricanes in 1954, and a hurricane and severe blizzard in 60-61) resulted in the loss 60% of existing eelgrass cover. Eelgrass beds on deeper habitat than at West Island, and ice does not accumulate along Wianno Beach to the same degree. Consequently, losses of eelgrass along Wianno Beach during the late 1970's were nominal.

Figure 4. Historical changes in eelgrass abundance at East
Cove,West Island, 1951-1983 (top) and Wianno Beach, 1940-1981 (bottom).
Slow eelgrass growth (East Bay) or declines (Wianno Beach) resulted from
hurricanes in 1954 and a hurricane-blizzard combination in 1960-61.
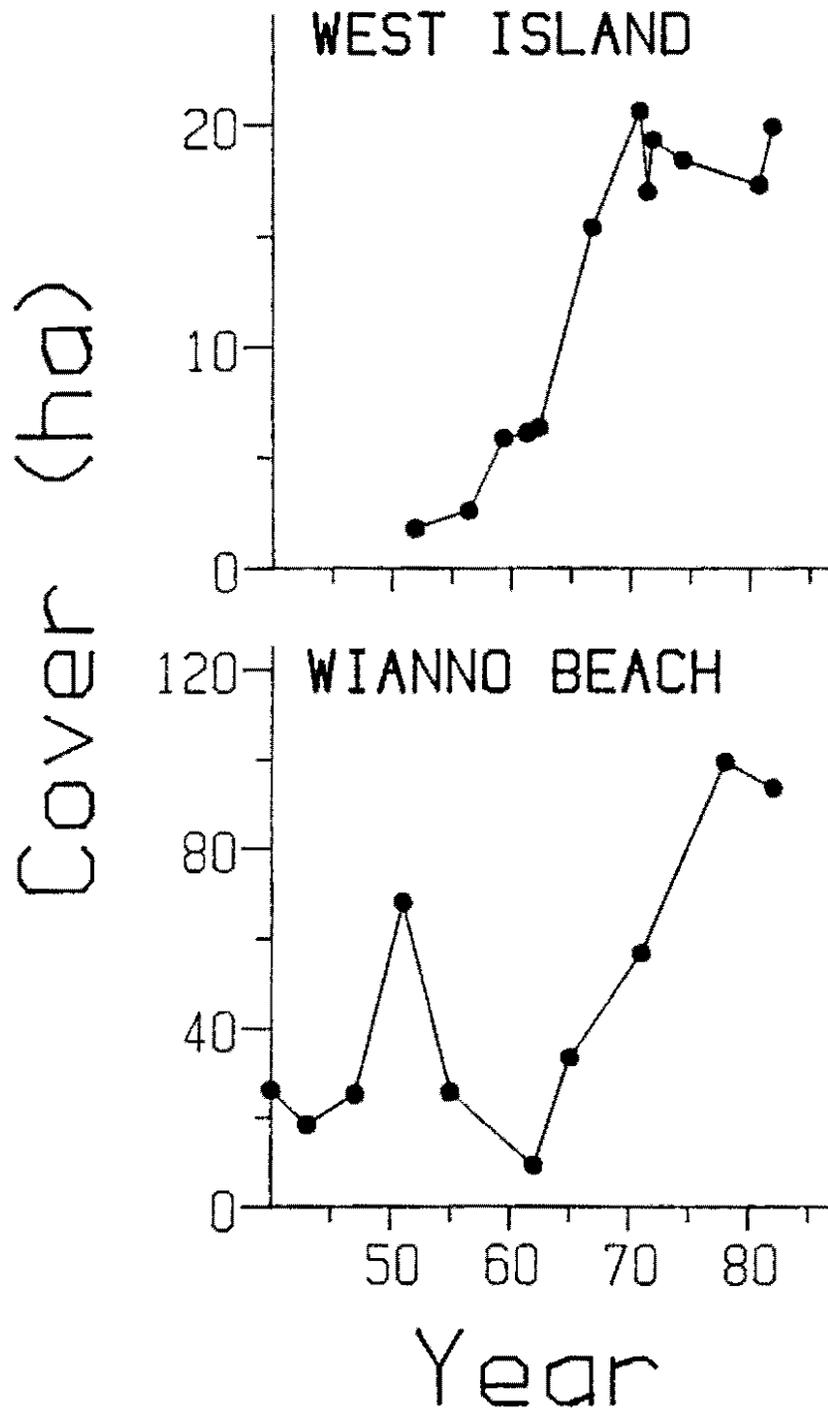
Colonization of the validation subsites (Fig. 5) was more rapid than the larger study area (Fig. 4), and at both sites, eelgrass achieved peak abundance 13-15 years after initial colonization. The process of colonization at the two subsites differed in several respects. Eelgrass at the West Island site reached 90% peak cover whereas the Wianno Beach site reached only 77% peak cover. The two validation sites had different rates of lateral expansion, bed recruitment, and size and frequency of non-catastrophic disturbances (Table 1).

When values of each of the parameters modeled were initialized in the model, the simulation results compared well with actual colonization (Fig 5). Also, the spatial pattern of eelgrass cover in the model had a similar appearance as on photographs (Fig. 6). Because the model matched the photographic record well, the model was run through 100's of iterations to determine how changes in lateral bed expansion rate, bed recruitment rate, disturbance size, and percent of the habitat disturbed affected the process of colonization.

For example, recruitment rate was changed, but lateral expansion rate, disturbance size, and percent of the habitat disturbed were kept constant, with values appx. equal to the Wianno Beach validation site. Results from the model (Fig. 7) suggest that at low recruitment rates, it would have taken more 30 years for colonization to reach peak abundance at the Wianno subsite, instead of the 13 years observed. At higher recruitment rates, changes in rate had less effect on years to peak abundance than low recruitment rates, but still reduced the time to reach peak abundance, <8 years for very high rates. The curve is not

TABLE 1. Bed lateral expansion, survivorship, and recruitment at early stages of succession for the two validation sites. Bed numbers for the West Island site during the 61-62 sequence were too merged for bed count calculations, but this was unnecessary because of there was only 1 growing season between photographs and R_b could be calculated directly as number of beds produced per existing bed area. For validation purposes, the model was tested with the 1951-56 data for West Island.

	Wianno Beach	West Island	
Photograph pair sequence:	4/62-10/65	10/51-5/56	4/61-4/62
Growing seasons in sequence:	4	4	1
Initial # of beds (N_0):	128	42	nd
initial bed area (A_i):	1400	75	776
Bed survivorship (N_s):	100	36	nd
New beds recruited (N_n):	113	9	47
Final bed area (A_f):	5850	179	nd
Parameters used in model:			
Bed recruitment/1000 m^2 of N_0 ($=R_b$):	36	49	61
Percent of habitat disturbed per yr (PHD):	6.0	3.2	nd
Mean disturbance size (m^2):	78	≤10	nd
Bed lateral expansion rate (m/yr):	0.45	0.29	0.45

Figure 5. Top: Colonization by eelgrass at the West Island subsite (see fig. 2) beginning 1956 (closed squares) compared and results of the 4 runs (mean +/- sd) of the simulation set with the four parameters set as in Table 1. Bottom: Colonization by eelgrass at the Wianno Beach subsite beginning 1962 (closed squares) compared and results of the 4 runs (mean +/- sd) of the simulation set with the four parameters set as in Table 1.
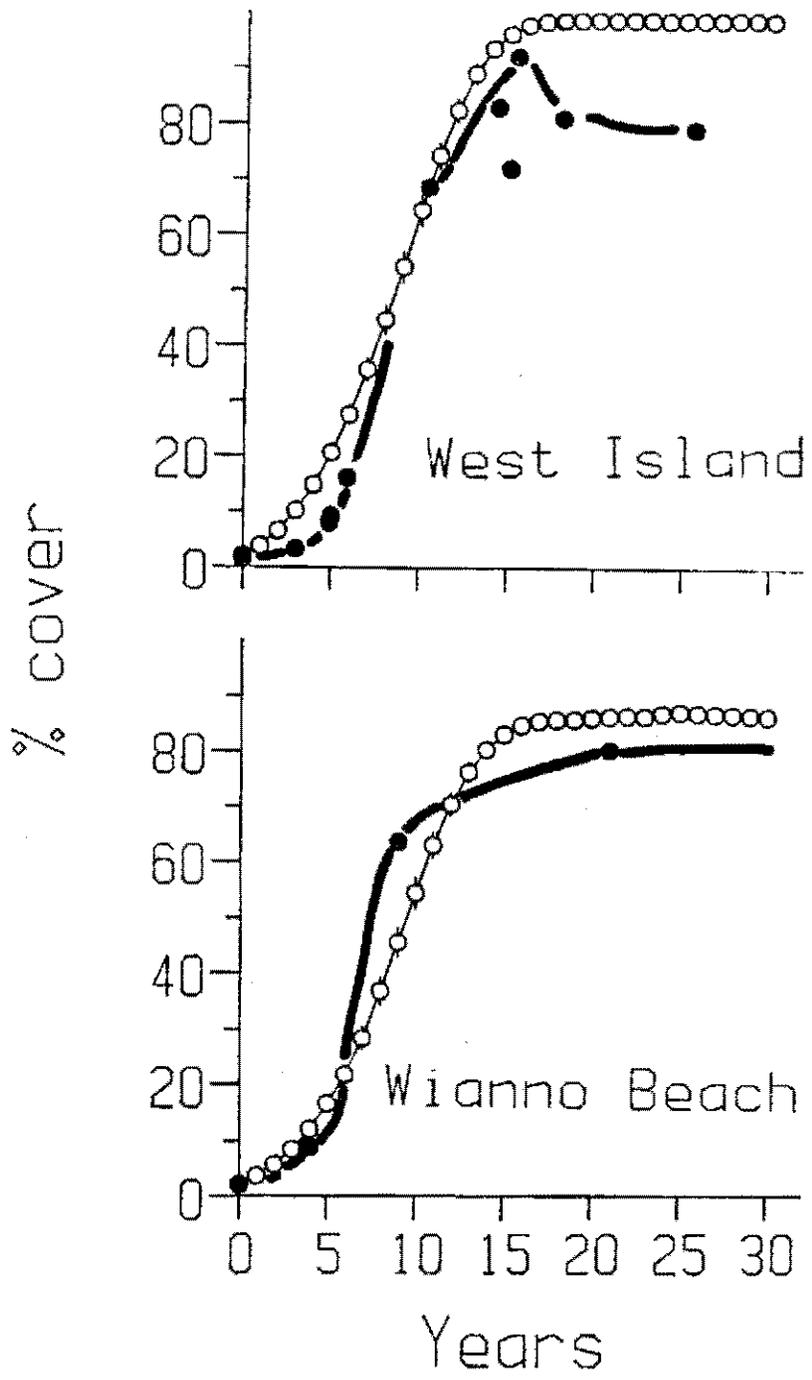
Figure 6. A comparison between a 1.3 ha portion of the model (bottom), and photograph area of equal size (top) at Wianno Beach, on which this model run was based. Both are at 19 years after colonization.

2 5 m

Figure 7. The effect of recruitment rate (# of beds produced per 1000 m^{-2} of existing eelgrass) on years to peak abundance (top) and percent cover at peak abundance (bottom). For these runs, percent of the habitat disturbed = 5.0, mean disturbance size = 76.5 m^2, and lateral expansion rate = 0.45 m yr^{-1}
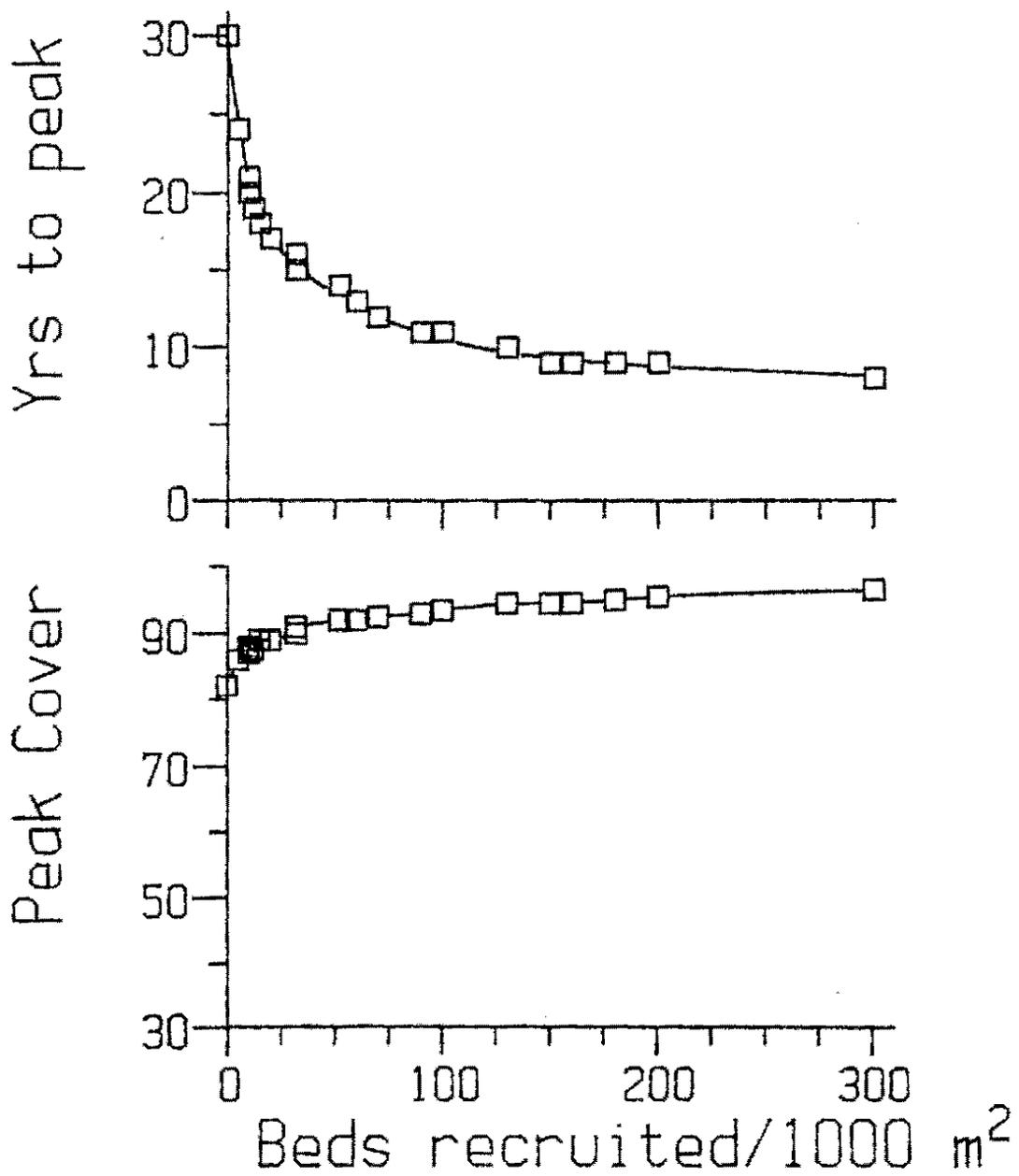
asymptotic but instead becomes linear with a shallow slope suggesting that if higher recruitment rates are possible, colonization may occur in periods less than 8 years. Increased recruitment rates increased slightly percent cover at peak abundance (from 85 to 93%). The impact of changes in recruitment rate were much less than the effect of changes in disturbance size or percent area disturbed.

Increased lateral expansion, like increased bed recruitment, reduces both peak cover and the number of years to reach peak abundance (Fig. 8). Changes in lateral expansion rate between 0.1 and 0.5 m year resulted in the greatest changes on peak cover and years to peak abundance. Over this interval, colonization time decreased from thirty years to less than fifteen years, and increased percent cover from 73% to more than 90%. Nonetheless, increases in lateral expansion rate had less effect on reducing colonization time than increases in bed recruitment rate.

The percent of the habitat area disturbed each year had a strong effect on peak abundance, but had only a moderate effect on years to reach peak abundance (Fig. 9). The slope of the percent cover curve was linear (Fig. 9, bottom) with a slope of -2.1. Thus, if 10% of an eelgrass habitat is disturbed each year, under the specified rates of bed lateral expansion and bed recruitment, eelgrass cover will never exceed 80% of the bottom. The effect of percent habitat disturbed on years to reach peak cover was less than the effect of changes bed recruitment rates or bed lateral expansion. If 30% of the habitat is disturbed each year, eelgrass will take 30 years to colonize an area

Figure 8. The effect of changes in lateral expansion rate on years to peak abundance (top) and percent cover at peak abundance (bottom). For these runs, recruitment rate = 35 beds/1000 m^2, disturbance size = 77 m^2, and percent of habitat disturbed 5%.
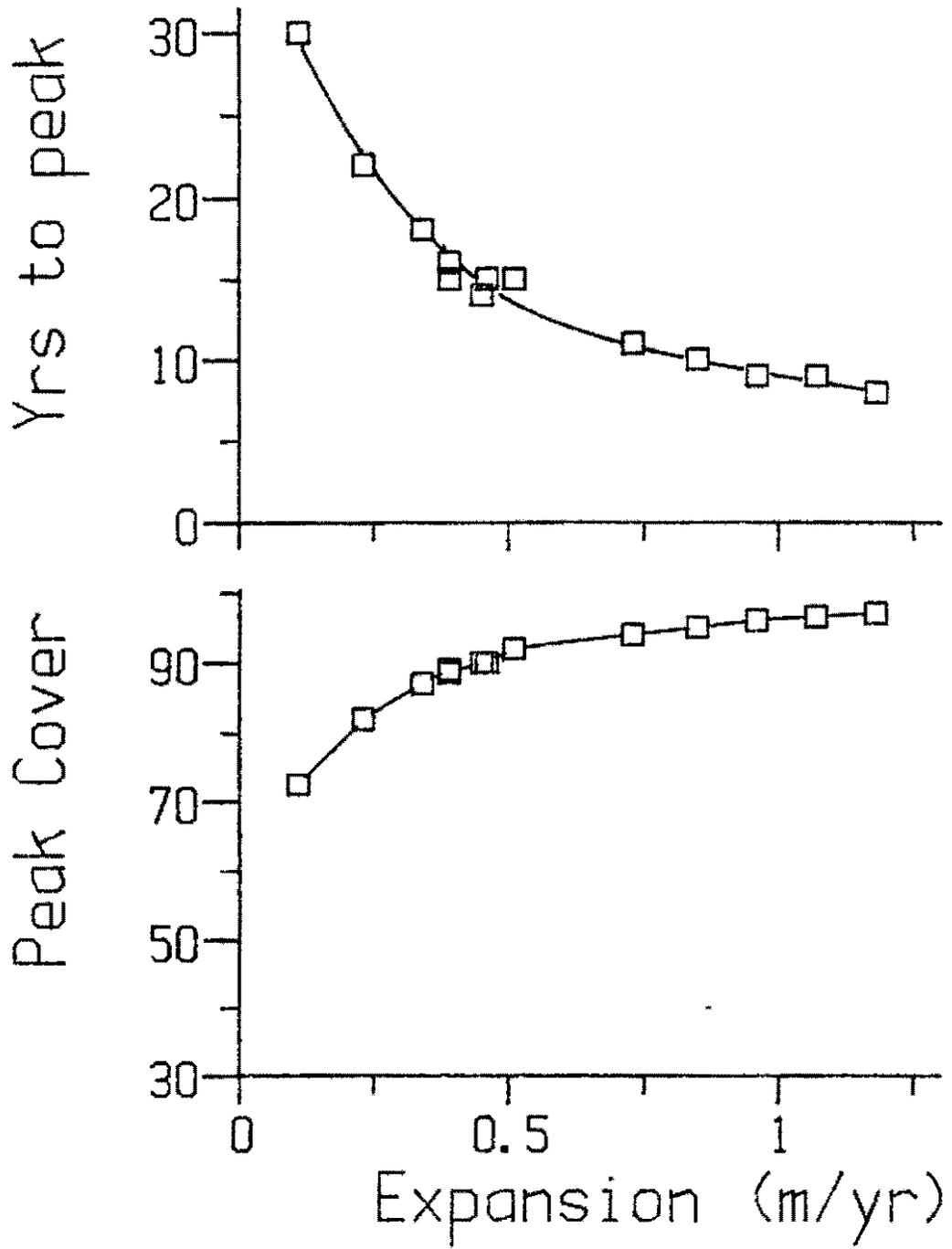
Figure 9. The effect of percent of the habitat area disturbed each year on years to peak abundance (top) and peak abundance (bottom). For these runs, recruitment rate = 35 beds/1000 m^2, mean disturbance size = 76.5 m^2, and lateral expansion rate = 0.45 m yr^{-1}
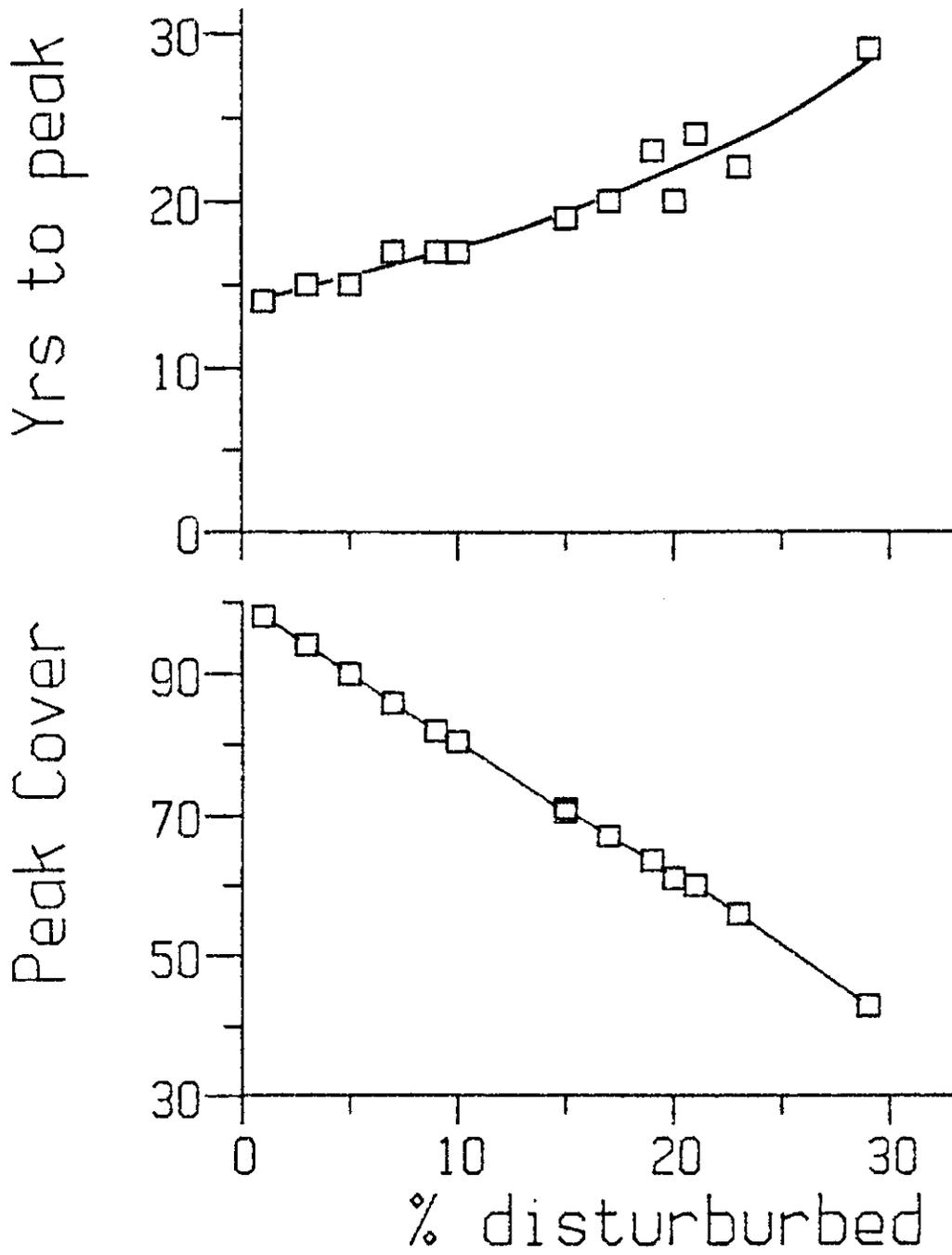
instead of the 14 years required when none of the habitat is disturbed under this set of conditions.

Disturbance size did not affect the time to reach peak abundance at all (Fig. 10), but was an important factor regulating peak cover. The impact of disturbances of 10-100 m^2 on peak cover depended greatly on the percent of the habitat disturbed (Fig. 10). For example, if mean disturbance size is 80 m^2 but only 5% of the bottom is disturbed each year, 90 percent of the bottom will be cover by eelgrass when the population reaches peak abundance. In contrast, 80 m^2 disturbances totalling 20% of the habitat each year will result in eelgrass habitat area that never exceeds 40% cover.

Changes in the size of disturbances for disturbances greater than 100 m^2, however, had less effect on peak cover, irrespective of percent of the habitat disturbed. Disturbance less than 5 m^2, had virtually no effect on peak abundance, even if 20% of the habitat was disturbed each year (Fig. 10).

Discussion and conclusions

Overall the model closely fit observed patterns of colonization at each validation subsite. Differences between the model and data from the subsites can be explained in part by uncertainty in the calculated parameters since small changes in some of the parameters. For example, in the model, a 9 % yearly disturbance level and recruitment rate of 80 beds per 1000 m^2 would give a nearly perfect fit to the Wianno Beach data. Alternatively, some the parameters in the model such as lateral expansion and recruitment rates may change during different periods as

Figure 10. The effect of disturbance size on years to peak

abundance (top) and peak cover (bottom). For these runs, recruitment

rate = 35 beds (1000 m^2)$^{-1}$, and lateral expansion rate = 0.45 m yr^{-1}.

The model was reiterated in both cases for 5%, 10%, 15%, and 20% percent

of the habitat area disturbed.
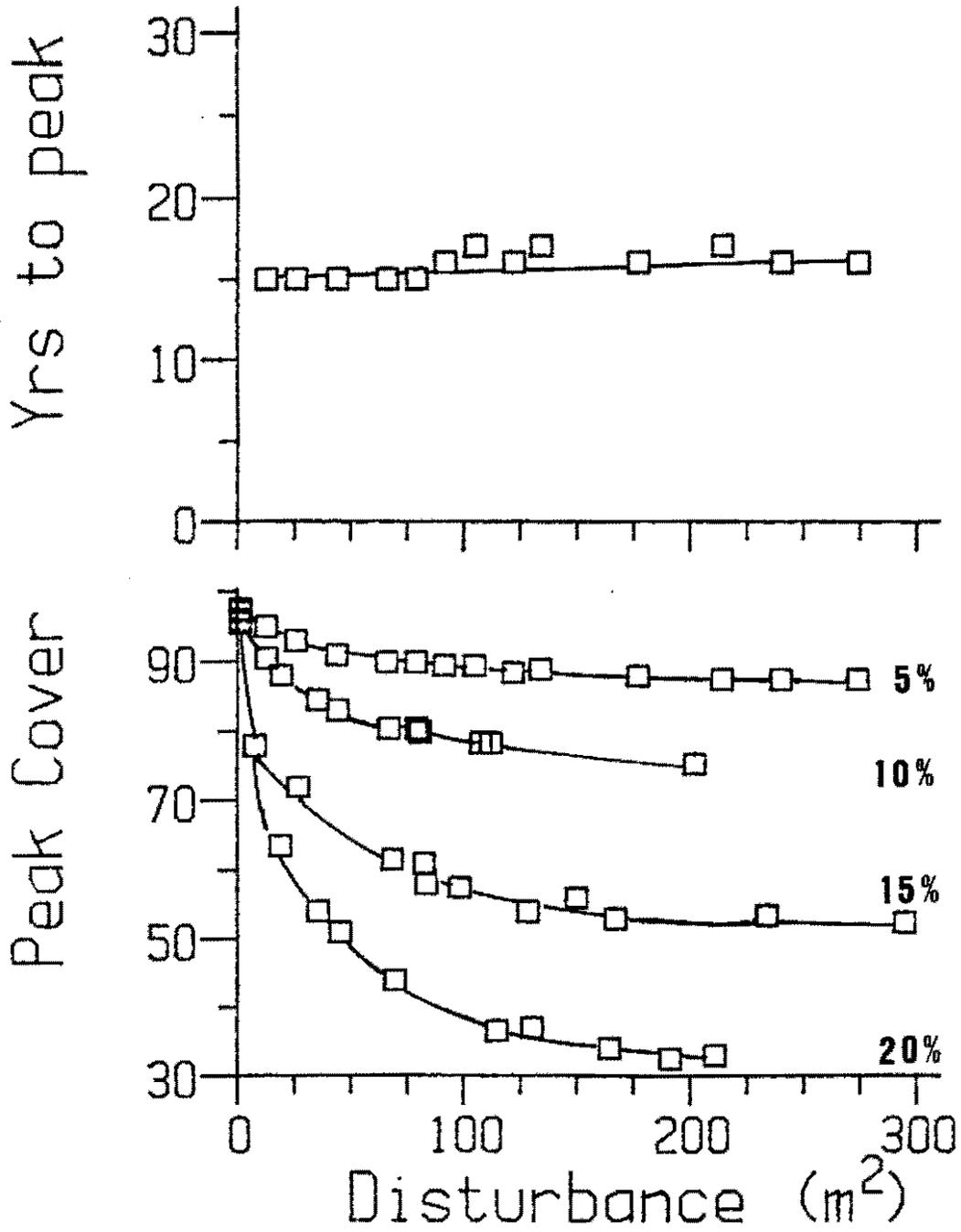
illustrated in Table 1. These differences could be due to changing

habitat conditions ("good" and "bad" years, effects of catastrophic

storms), or alteration of habitat and facilitation of growth. Because

neither lateral expansion or bed recruitment can be easily from

photographs during late stages of colonization, field studies over long

periods are necessary to answer these questions.

To simplify the model, several assumptions were made which are not

necessarily true, but these assumptions probably do not affect the

results. For example, bed recruitment rate may not be proportional to

bed area in later stages of colonization, but this unimportant because

vegetative growth is more important in expanding bed cover at that time.

I assumed random dispersion of eelgrass propagules throughout the

colonized area of the model, but observations on eelgrass and other

passively dispersed seeds show that most seeds fall near their source,

and decline exponentially with increasing distance (Sharpe and Fields,

1982; Costa, 1988). This may not be a serious conflict, however,

because beyond a certain distance, the 'tail' of an exponential decay

curve at great distances may not be statistically significant from a

random or uniform distribution of low frequency (Poisson). The

distribution of disturbance size probably has little bearing on the

model results because disturbance size does not affect peak cover at

all, and for many class sizes, has only marginal effects on peak cover.

Bed margin lateral expansion rates used in the model are realistic

based on reports in the literature for actively growing beds (Araski,

1980; Fonseca et al., 1979). The highest rates observed in photographs

could also be an artifact due to new seedlings that may recruit near the

edge of existing beds; a phenomenon that cannot be resolved from photographs. Functionally, however, this mechanism does not affect the model, because all that was considered is the net expansion of existing beds.

The graphical simulation approach used here is heuristic in many ways. The model used here was based on three well documented phenomena: eelgrass beds expand vegetatively, new beds may recruit from seeds, and eelgrass may be removed by disturbances of various size and frequency. Because this model was based on these concepts, it can operate without any a priori knowledge of the values of any of these parameters. In this case, when values of each parameter (derived from photographic observations) were used the model, they matched well with the real world.

The results of the model suggest that many patterns of colonization observed in the field can be explained by differences in bed lateral expansion rates, new bed recruitment, disturbance size, and per cent of the habitat disturbed each year. For example, a high energy site near Wianno Beach never has never exceed 40-55% cover, even after many decades. Assuming similar rates of bed recruitment and lateral expansion as the Wianno Beach site, the model results suggest that approximately 20% of the eelgrass habitat is removed each year at this site by large disturbances. At a site in Buzzards Bay (Great Neck, Wareham), peak cover was reached in less than 8 years after initial colonization (Costa, 1987). This phenomenon can only occur if the rates of new bed recruitment were 3 to 4 times higher than observed at Wianno Beach. Thus this model is both heuristic and predictive, and these

hypotheses are testable. This model could also be used to predict eelgrass growth in transplanted areas with known rates of vegetative expansion, recruitment, and disturbance.

The photographic record and model results show that recruitment of new beds greatly enhances the rate of colonization of the area. In the simulation, bed recruitment generally accounted for less than three percent of the cells filled in each year, yet this dispersal could at least halve the time it took to reach peak abundance by vegetative growth alone. Bed recruitment showed its greatest contribution to colonization during midpoint of the colonization when both propagule production and open space are high (Fig.11). The importance of seed dispersal has broad implications because seedlings and seed germination is often the most sensitive stage in a plants life history, and is fundamental for colonizing new habitat. Any disturbance preferentially affecting seedling survival, such as toxic pollutants, or shading effects from enrichment induced algal growth can greatly slow recovery in an area.

The results from the simulation suggest that small disturbances (<5 m^2) have little effect on colonization, even when the percent of the habitat disturbed per year is very large (Fig. 8). This suggests that eelgrass beds can accommodate frequent small disturbance such as may occur from animal foraging or shellfishing. This does not mean however that shellfisherman do not have any impact because sizable areas of eelgrass may be removed from heavily fished areas (pers. obser.). Furthermore, shellfishing generates much suspended sediment and releases

Figure 11. Relative contribution of recruitment to colonization during the model run for R_b=56, PHD =5.6%, Gr= 0.45 and DS=74.
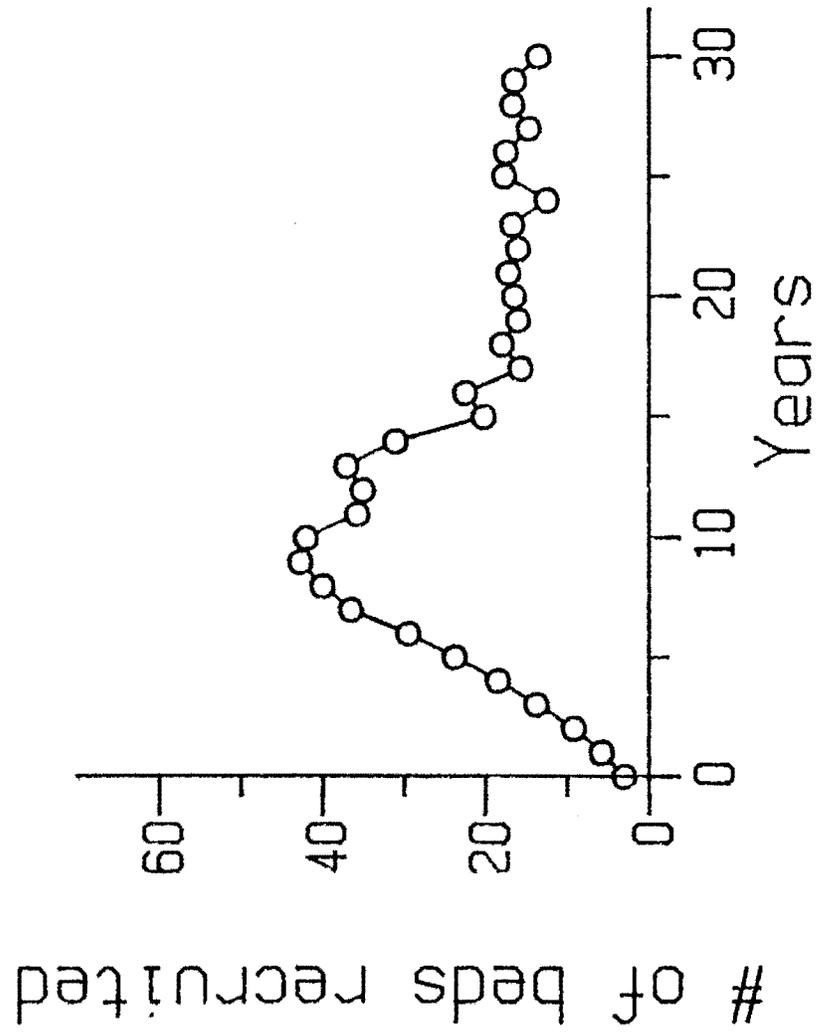
nutrients, both of which will result ultimately decrease light availability, which can lead to loss of eelgrass (see also Costa, 1987).

This model and photograph analysis elucidate the mechanism of colonization, but other patterns of eelgrass colonization such as bed morphology, onset of colonization, and distribution are set by other factors such as large scale disturbances, wave scour, long shore sand transport, sand wave migration, and habitat heterogeneities. Also, the pattern of colonization described here (expanding, recruiting, and merging of distinct beds) is prominent only in more exposed environments, whereas in sheltered shallow bays, eelgrass abundance may show rapid colonization or wide fluctuations in abundance (Costa, 1987). The rapid colonization seen in these shallow protected bays can only be simulated in the model with very high recruitment rates. This may be realistic, however, because beds in these areas are often annuals and show high rates of seed production. In deeper offshore areas, seed production is lower, and seedling survival is also lower because the substrate is unstable. New beds, once established, have higher rates of survival than individual shoots, and this leads to the discrete pattern of colonization observed in exposed areas.

The patterns of colonization modeled here reflect only small scale phenomenon. Colonization of eelgrass over 1000's m is often linear, or shows temporal and spatial stepwise expansion, often set back by catastrophic disturbances (here and Costa, 1987). These results can be explained by the results of another model shown in Fig. 12. In a one "cell" model (a single subsite), a species could show logistic expansion in cover. In an adjoining subsite became colonized only after the first

Figure 12. Comparison of colonization curves of a species with logistic growth in a single cell system (top), in a two cell system (middle) where logistic growth begins in second cell only after 50% cover is achieved in the first cell. The four cell model used the same stepwise colonization process as the two cell module. Increasing designed Relative contribution of recruitment to colonization during the model run for R_b=56, PHD =5.6%, Gr= 0.45 and DS=74.
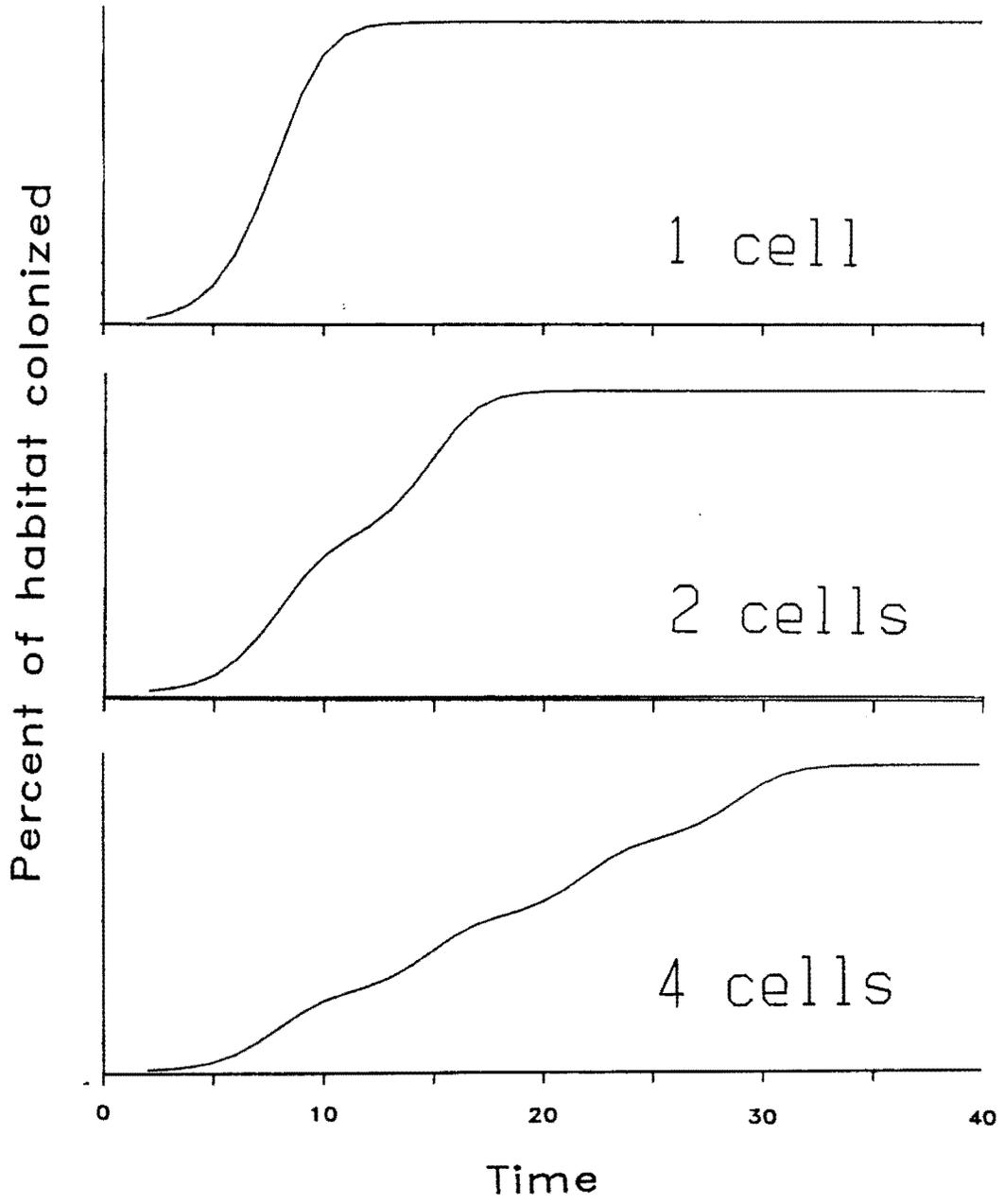
site reached 50% cover, then in a 2 step colonization would occur (2 cell model, Fig 12). By adding more cells, the colonization curve became both increasingly linear, and of longer duration. The onset of colonization depended on the distance of each portion of shore from existing beds (and refuge beds that survived the wasting disease. This phenomenon is visible on many sequences of photographs and explains why eelgrass populations took so many decades to recover from the wasting disease, and why some populations are still expanding today.

Acknowledgments

Chapter 6

Nitrogen loading in Buttermilk Bay (MA, USA): Correlations with

phytoplankton density, periphyton abundance, and eelgrass (*Zostera*

marina L.) distribution

Introduction

The addition of nutrients, particularly nitrogen, has become a serious problem in coastal embayments throughout the world (Nixon ,1983; Nixon, et al., 1987). The sources of added nutrients usually include rainwater, wastewater disposal, fertilizer use, livestock, and street runoff. Nutrient additions may increase planktonic, periphytic, and benthic algae which in turn can cause important changes in coastal ecosystems (Lee and Olsen, 1985). One of the consequences of nutrient loading and increased algal growth is the disappearance of eelgrass (*Zostera marina* L.) meadows, and large scale declines of this and other species of seagrasses due to declining water quality have been reported in Chesapeake Bay and elsewhere (Cambridge and McComb, 1984; Orth and Moore, 1983, Sand-Jensen and Borum, 1985; Nienhuis, 1983).

Elsewhere I reported on the nutrient concentrations and nutrient loading in Buttermilk Bay, a Cape Cod, MA (USA) coastal embayment (Valiela and Costa, in press). In this paper, I examine how dissolved nitrogen concentrations, and patterns of nitrogen loading correlate to phytoplankton density, periphyton abundance, and eelgrass distribution and growth. This work is part of an ongoing study to quantify the impact of nutrient loading on eelgrass distribution.

Nutrient-algae-eelgrass relationships

Increased growth of algae is a common symptom of nitrogen loading in coastal embayments (Valiela, 1984). In coastal waters and estuaries, phytoplankton can increase conspicuously in response to added nitrogen,

and often correlate with nitrogen concentrations (Ryther and Dunstan, 1971; Jarworski, 1981; Monbet et al., 1981). In shallow bays where sufficient light reaches the bottom, benthic algae, especially morphological varieties of unattached "drift" algae may accumulate to a large degree (Lee and Olsen, 1983). Periphyton (microalgae on surfaces) are also more abundant in enriched environments (Sand-Jensen and Borum, 1983), and the accumulation of periphyton on artificial substrates has been used to assess the degree of eutrophication in freshwater systems (Marcus, 1980; Fairchild et al., 1985).

Increased nitrogen loading does not benefit benthic angiosperms such as eelgrass. Part of the reason for this is that in most environments, eelgrass takes up most of its nitrogen through its roots (Dennison et al., 1987; Short, 1983; McRoy and Goering, 1974; Thursby and Harlin, 1982). More importantly, increased growth of epiphytic, planktonic, and drift algae shade eelgrass populations. The lower limit of eelgrass growth is determined by the duration of light intensity above compensation (Dennison, 1987). Hence, in a fundamental way, the distribution of eelgrass is determined by factors that affect water transparency and epiphyte densities (Sand-Jensen and Borum, 1983). In southern New England, eelgrass grows only to 1-2 meters or less in shallow bays with poor water transparency, but grow as deep as 12 m MLW in clear offshore waters (Costa, 1987).

As a result of declining light availability from nutrient loading, eelgrass may show slower growth, recruitment, or death (Sand-Jensen and Borum, 1983; Borum, 1985; Kemp et al., 1983). Eelgrass beds often first

disappear in upper estuaries where nutrient loading is highest, and at the deep edges of beds where light limits growth (Orth and Moore, 1983).

Other factors may contribute to seagrass declines, and need to be considered. Sediment suspension from topsoil runoff or boat propeller wash may also contribute to water transparency decline and loss of eelgrass (Brush and Davis, 1984; Orth and Moore, 1983). This component of water quality decline may be very localized or seasonal. For example, attenuation of PAR was locally important in parts of Chesapeake Bay, but for most parts of Chesapeake Bay, results from artificial estuarine ponds and a computer simulation suggest that nutrient loading effects, rather than suspended sediments, account for most PAR attenuation (Kemp et al., 1983).

In southeastern Massachusetts, eelgrass has been declining in several bays where water quality has declined (Costa, 1987). For example, in Waquoit Bay, a Cape Cod lagoon that has been extensively developed during the last 40 years, eelgrass populations have been declining in most of the Bay since the mid-1960's (Costa, 1988). At that time, eelgrass began to disappear first from the deep central portion of the bay (2-2.4 m), then in shallower areas, especially in the inner half of the Bay. Today eelgrass is limited to the flood delta at the mouth of Waquoit Bay, and covers less than 10% of its peak abundance during the 1950's and 60's.

The loss of eelgrass in enriched environments is not unique and has been reported for other submerged macrophytes in freshwater lakes and ponds (Sondergaard and Sand-Jensen, 1981; Phillips, et. al, 1978), artificial freshwater ponds (Mulligan et al., 1976), tidal estuaries

(Haramis and Carter, 1983), artificial estuarine ponds (Twilley, et. al., 1985), and other species in marine embayments (Brush and Davis, 1984; Cambridge and McComb 1984; Littler and Murray, 1975; Orth and Moore,1983; Kautsky et al. 1986).

It is not always clear if periphyton or phytoplankton are more important in causing macrophyte loss. For example, in enriched artificial estuarine ponds, submerged angiosperms were nearly eliminated at the high loadings because epiphytes attenuated 80% of incident photosynthetically active radiation (PAR) at leaf surfaces (Twilley et al., 1985). Nonetheless, nutrient loading would not have caused the observed loss without co-occurring increases in phytoplankton (Twilley et al., 1985).

Along a nutrient gradient in a Danish estuary, biomass of eelgrass algal epiphytes increased 50-100 fold, whereas phytoplankton abundance increased only 5 - 10 fold (Borum, 1985). Light attenuation by epiphytes on eelgrass shoots was 90% on older leaves in these enriched areas (Borum, 1985). Besides shading, algal epiphytes can slow photosynthesis by forming a barrier to carbon uptake (Sand-Jensen, 1977). These observations suggest that epiphytic algae are more important in limiting eelgrass growth, but the problem is complex.

Epiphyte biomass is highest on old, slow growing plant material which contribute less to production (Borum, 1985; Sand-Jensen and Borum, 1983). Furthermore, eelgrass declines also often occur where both phytoplankton and epiphytes increase (Sand-Jensen and Borum, 1983). In less enriched habitats, epiphyte abundance is less important than water transparency in affecting eelgrass growth and photosynthesis (Mazella

and Alberte, 1986). Accumulation of epiphytes in general may only slow macrophyte growth during periods of light intensity near compensation (Sand-Jensen and Revsbach, 1987).

Alternate explanations have been offered for some eelgrass declines. For example, Nienhuis (1983) suggested that the recent disappearance of eelgrass in a Danish coastal pond was not due to epiphyte abundance, but "toxification" of the sediments from decomposing drift algae that accumulated because of nutrient loading. This mechanism has not been well studied, but decomposing drift material can change appreciably pore water chemistry in seagrass beds (Zimmerman and Montgomery, 1984).

Identifying the impact of nutrient loading is complicated because eelgrass populations here and elsewhere in the Atlantic have been recovering for decades from massive declines induced by disease during the early 1930's (den Hartog, 1987; Costa, 1987). Consequently, in some polluted, poorly flushed bays in Southeastern Massachusetts, eelgrass populations never recovered from the wasting disease or showed new declines in subsequent decades (Costa, 1987, 1988).

Buttermilk Bay has been studied to determine stream and groundwater flow (Moog, 1987), water circulation (Fish, 1987), and fecal coliform pollution (Heufelder, 1987). Elsewhere I examined nutrient concentrations and inputs in Buttermilk Bay and its surrounding watershed (Valiela and Costa, in press). We reported that nitrogen concentrations were highest along shore, especially near groundwater and streams inputs carrying high DIN loads (generally from human inputs). Concentrations of DIN were variable in different parts of the Bay;

concentrations were highest in Hideaway Village Cove, Millers Cove, and near Red Brook, intermediate in Queen Sewell Cove, Skunk Cove, and Little Buttermilk, and lowest in the central portions of the Bay (see Fig. 1). In effect, a large scale natural "experiment" on nitrogen loading is underway in Buttermilk Bay.

The impact of the added nitrogen in Buttermilk Bay is not fully apparent, but there have been modest declines in eelgrass cover in the deepest parts of the Bay during the last 15 years (Costa, 1987). In this paper I present data on the relationships between nitrogen concentrations and abundance of phytoplankton, periphyton, and eelgrass depth distribution, and discuss how these data corroborate other studies of nitrogen loading in marine ecosystems.

Methods

Water sampling methods and sites

Water samples (250 ml) were taken from bay, stream, and groundwater stations located in and around Buttermilk Bay (Fig 1). The water sampling methods and nitrogen analysis protocols are described elsewhere (Valiela and Costa, in press). The bay water samples were taken during ebbing, at least two hours after high tide and at least 2 days after any major storm.

The impact of nitrogen loading was assessed by examining depth of eelgrass growth, phytoplankton, and periphyton abundance. The depth of eelgrass growth at 9 stations was compared to mean DIN observed during the most active growing period for eelgrass (March- November; 5 to 15 sample dates per station). The accumulation of periphyton on eelgrass

Figure 1. Map of Buttermilk Bay showing site names and stations sample for nutrients and phytoplankton chl_a (●), similar stations but with settlement substrate floats set out (▣), transplant stations (T_c= control, T_e= enriched stations), and position of enrichment floats (EF). For purposes of clarity, not all stations measured for nutrients and phytoplankton chl_a are shown.

Hideaway
Village
Cove

Skunk
Cove

LITTLE
BUTTERM.

Red
Brook

EF

Tc

Queen
Sewell
Cove

Te

Millers
Cove

500 m

CAPE
COD
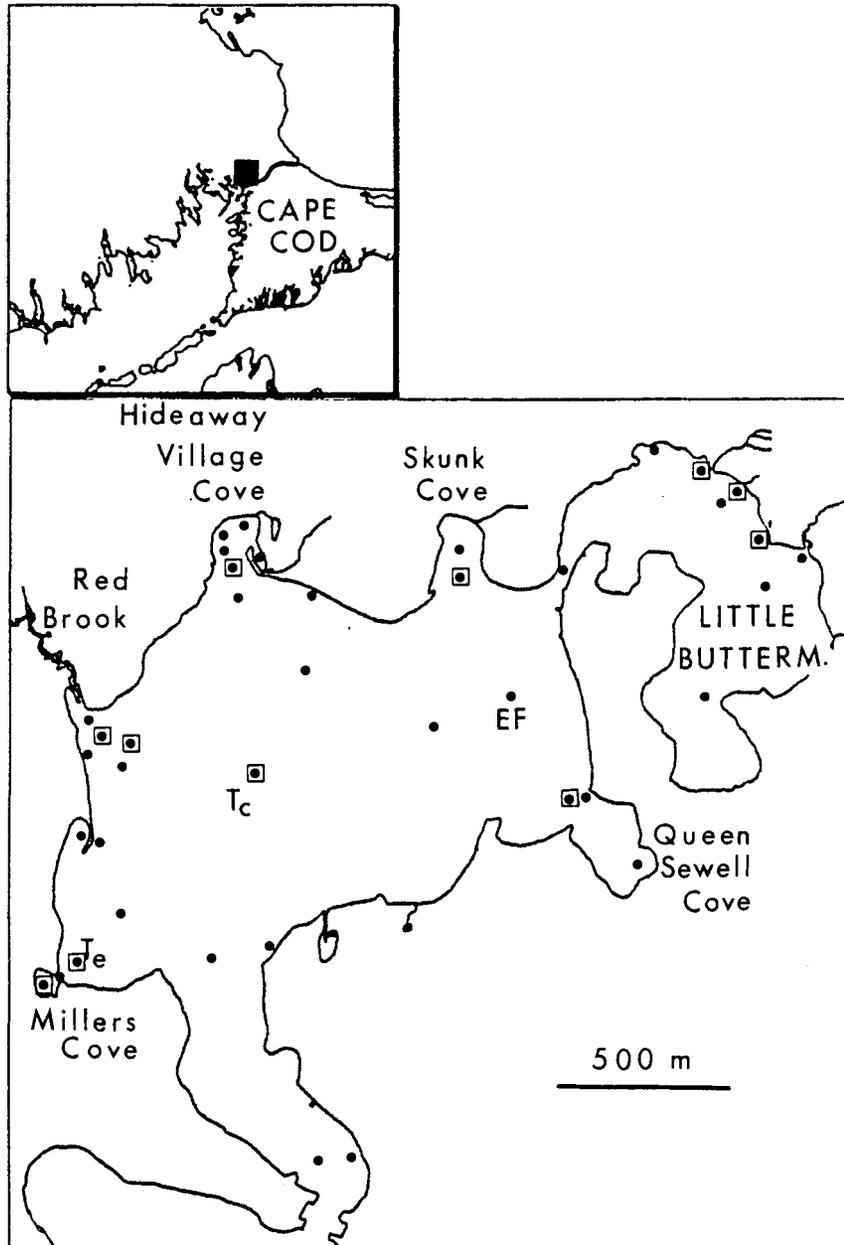
(11 stations) and artificial substrate (15 stations) was compared to mean DIN observed within one month of sampling (1-8 water samples dates per station).

To measure chlorophyll content, Bay water samples were filtered (Whatman GF/C), and the filter extracted in 90% acetone, placed in the dark at -15°C until analyzed, generally within 48 hr. The extract was then sonicated, centrifuged, and the absorbance read at 480, 630, 645, 650, and 750, and converted to chl_a, chl_b, and chl_c, by the trichromatic method (Strickland and Parsons, 1972).

Periphyton sampling

Periphyton attached to eelgrass was sampled by collecting 3 randomly selected shoots at 9 water sampling stations where eelgrass grew. Each shoot was placed in a bag, then later placed in a tray of filtered seawater and epiphytes were removed with a razor blade. The suspension of epiphytes was filtered and extracted as described above. The abundance of periphyton was calculated as μg chl_a cm^{-2} of eelgrass leaf surface.

Periphyton on eelgrass leaves may not be a reliable indicator of nitrogen exposure because of eelgrass depth of growth (thus variable light), herbivore grazing, and differences in leaf age. Consequently, periphyton was also measured on artificial settlement strips (3 strips, 1 cm x 10 cm) attached to floats and placed in different parts of the Bay. Pilot experiments on float design showed that settlement surfaces that were textured or made of screen minimized the effects of local differences in wave and current action on the colonization of epiphytes,

and in the experiments reported here, polyester screening (100 μm) was used. These floats were left out for 1 - 2 weeks so that the periphyton consisted primarily of benthic diatoms. A preliminary study showed that the diatoms on the artificial substrate were the same species that settled on eelgrass. Longer duration exposure of the strips resulted a larger algal taxa whose composition varied among the different habitats. Hence, the short settlement strip exposure minimized variability in the chl composition (see results). When the strips were harvested, they were immediately placed into centrifuge tubes containing buffered 90% acetone, and stored in the dark on ice until analysis.

To test whether small increases in nitrogen loading can cause an elevation in periphyton abundance comparable to enriched parts of Buttermilk Bay, chambers that released nutrients were attached to other floats that held settlement strips. The nutrient chamber consisted of a corked PVC pipe with perforated with holes. A slow-release fertilizer "tree spike" (Jobes, 16:8:8, N as ammonium) was added to the chamber. To slow the dissolution of the fertilizer stick and lower nutrient concentrations that the strips were exposed to, the sticks were wrapped in dialysis membrane. The strips were attached to a current vane on the float to keep them downstream of the nutrient chamber. Eight floats (4 control, 4 experimental), each with 3 settlement strips, were placed in the east central portion of Buttermilk Bay, an area of low nutrient concentrations (see Valiela and Costa, in press). Two trials were performed: one for 6 days and one for 14 days. In the longer experiment, the fertilizer sticks were replaced on the 6th day. In both experiments, nutrient concentration in the water near the strips was

measured 3 days after fertilizer sticks were added and at the end of the experiment.

Eelgrass growth and transplantation

To determine if nutrient loading slows growth of endemic populations, the growth of shoots in 3, 625 cm^{-2} quadrats were measured in two areas: an enriched and a less enriched part of the Bay, both at 30-40 cm MLW. The less enriched site was located on the north lobe of an eelgrass bed in center of the bay (Fig. 1) which generally had the lowest nitrogen concentrations of any station during summer months. The enriched site was located in Millers Cove, which typically had high concentrations of DIN (Valiela and Costa, in press).

To measure eelgrass growth, randomly selected shoots within each quadrat were marked by inserting an insect pin through the top of the leaf sheath (c.f. Jacobs, 1979). After 9 days, the outgrowth of hole scars were measured to calculate the Plastochrone Interval (PI; the number of days between successive new leaves).

To rule out growth differences between the endemic populations due to sediment quality or population differences, clumps of eelgrass where collected from another locale (Ram Island in Great Harbor, Woods Hole, MA), and transplanted to these two sites in Buttermilk Bay. These shoots were collected with sediment, potted in peat fiber pots (10 cm diameter), and transplanted adjacent to the quadrats described above after an equal area of plants were removed to accommodate them. After the plants were acclimatized for two weeks, the growth of these plants were measured as described above.

The growth of the endemic populations were measured in mid-September, and the growth of the transplants were measured in Mid-October. Since the observations were not concurrent, only relative growth rates between endemic and transplanted eelgrass were considered.

Results

Chl_a correlated well with chl_c in periphyton from artificial substrates, eelgrass leaves, and water samples (Fig. 2). Because chl_c estimation is unreliable using the trichromatic method under some conditions, (Strickland and Parsons, 1972), all comparisons were made using chl_a. The closer correlation between chl_a and chl_c of periphyton on the artificial substrate (Fig. 2) was due to a similar taxa composition (primarily diatoms) after colonization and growth.

Chl_a concentration in the water column during June, July, and August did not correlate with surrounding water nitrate + nitrite, ammonia, total dissolved inorganic nitrogen (DIN), phosphate, or N/P ratio (DIN shown only, Fig. 3). This is because nitrogen gradients do not remain established long enough for phytoplankton abundance to build up (Valiela and Costa, in press). The absence of nitrogen gradients in Buttermilk Bay is due both to uptake by phytoplankton and benthic macrophytes and microphytes, and because the Bay is well flushed (50% of the water is exchanged with each tide (Valiela and Costa, in press). Uptake of nitrogen by benthic producers may be appreciable because this component account for 60% of the production in the Bay (Costa, 1987).

In contrast to phytoplankton, both periphyton (as chl_a) on eelgrass and periphyton on settlement strips correlated with DIN at each

Figure 2. Chl_c vs chl_a on settlement strips, eelgrass leaves, and seawater.   The slopes were not statistically different ($p<0.05$).
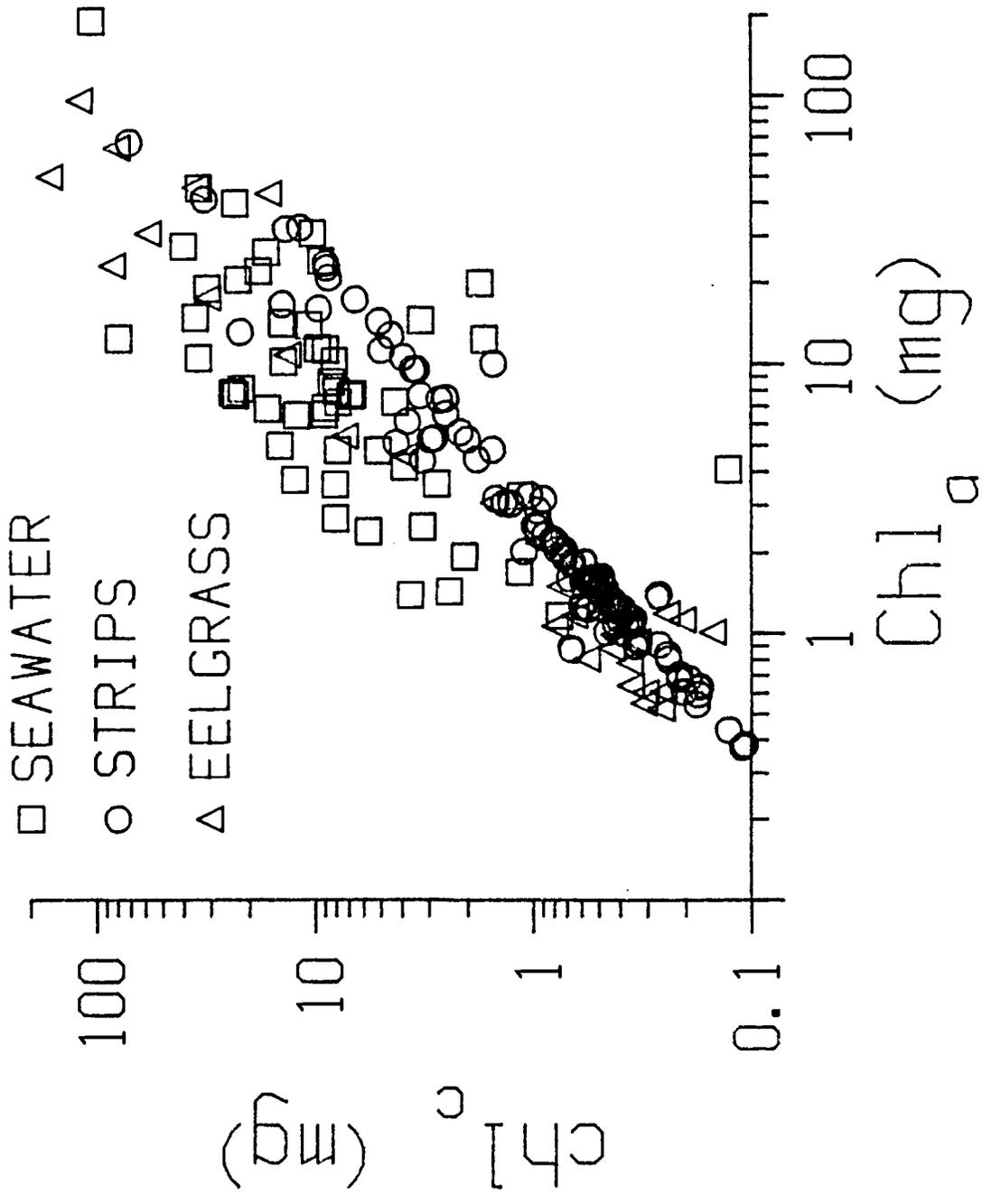
Figure 3. Chl$_a$ in the water column vs DIN on each date. There was no significant correlation.
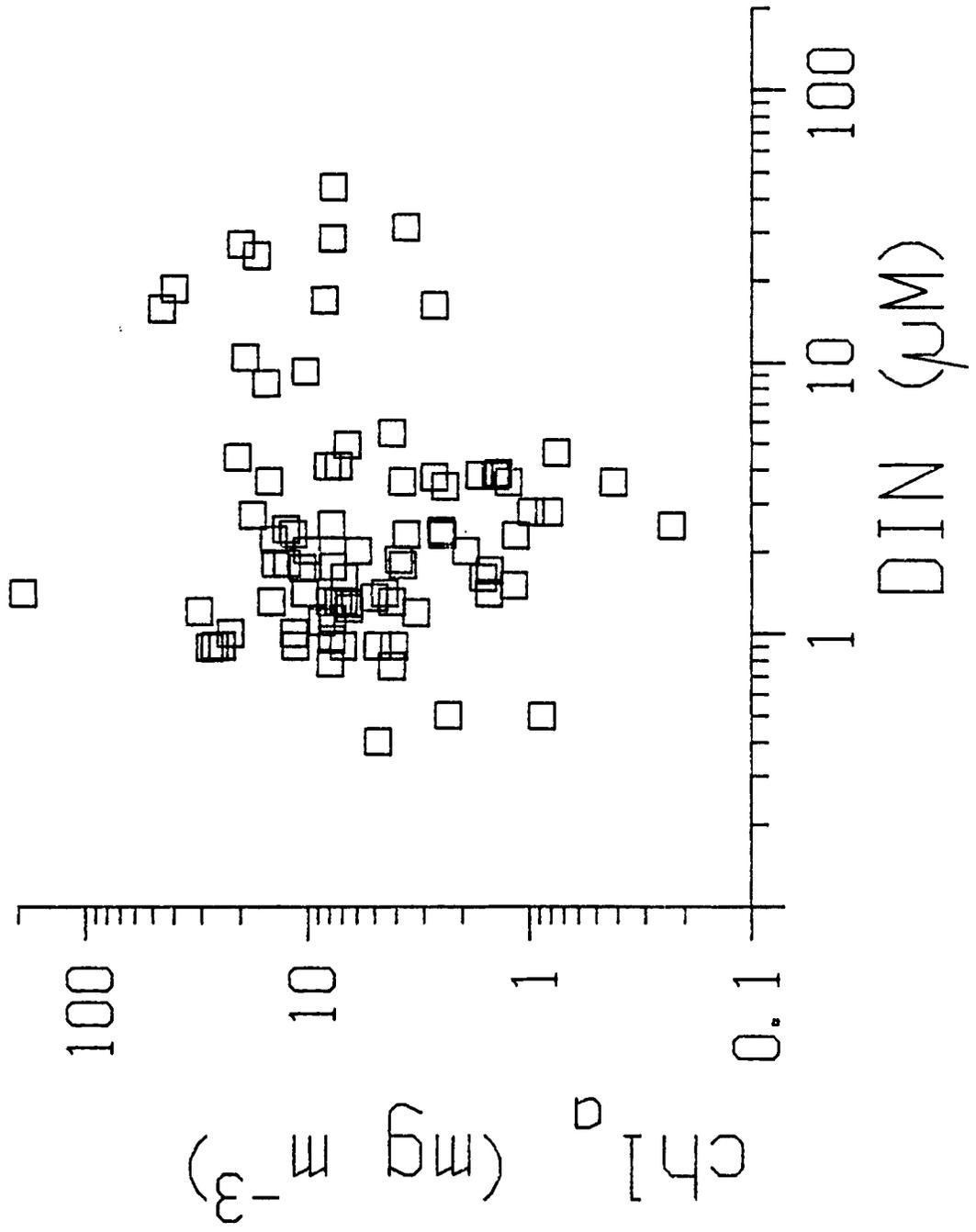
station ($r^2 = 0.62$, $p > 0.05$, $r^2 = 0.44$, $p > 0.05$ respectively, Fig. 4). In both instances, periphyton correlated better with DIN than with ammonia or nitrate + nitrite alone (not shown).

The floats containing slow release fertilizer elevated DIN concentrations ≈ 1.0 µM DIN over background concentrations (mean = 2.5 µM DIN), but increases in phosphate were not measurable. These added nutrients enhanced the growth of periphyton on strips attached to these floats at levels comparable to enriched parts of the Bay (Fig. 4).

The eelgrass shoots transplanted in pots had poor survival, and one pot in each treatment disappeared. Of the surviving marked plants, the growth rate of eelgrass transplanted to the enriched area was slightly slower (higher PI) than observed in the unenriched area , but this difference was not significant. Similarly, endemic populations of eelgrass grew slightly slower in Millers Cove, but these results also were not significant (Table 1). These results also indicate that larger scale, or longer running growth experiments are necessary to resolve whether high nutrient concentrations can lower eelgrass growth.

Depth of eelgrass growth significantly correlated with mean DIN concentration at each station (Fig. 5). The few data points is due to the limited number of deep sites in Buttermilk Bay near sampling stations. Some stations showed more variability in nitrogen concentrations than others.

Discussion

Assessing nitrogen loading impacts

Table 1. Growth rate (as PI ±SE) of endemic and transplanted eelgrass at an enriched (Millers Cove) and less enriched (mid-Bay) areas. Growth rate of endemic and transplanted eelgrass was not measured concurrently (see text).

	PI (days)	
	Endemic	Transplanted
Mid-Bay:	17.7 ± 1.04 n = 8	33.6 ± 3.0 n = 17
Millers Cove:	$18.7. \pm 3.7$ n = 14	36.3 ± 5.1 n = 26

In order to quantify the levels and impacts of nitrogen loading, and to regulate pollution in coastal embayments, environmental managers must have a way of objectively determining to what degree a bay is polluted by nutrients. Frequently chl_a and nutrients in the water column concentrations are used to assess the effects of enrichment. Valiela and Costa (in press) showed that nitrogen concentrations in the water column of a shallow, well-mixed coastal embayment like Buttermilk Bay, are not always a good indicator of nutrient loading because of tidal flushing and nitrogen uptake by plants and algae. In particular, nutrient data collected on a single date was often unrepresentative of long term patterns at many stations. In this study, it is also clear that chl_a in water of a well-mixed and flushed Bay, do not always correlate with nitrogen concentrations. Thus, low nitrogen concentrations or phytoplankton abundance in the water column, particularly on single sampling dates, do not necessarily imply low nutrient exposure.

In this study, stationary biological indicators correlated well with long-term nitrogen exposure. I should also note that benthic drift algae accumulated in enriched parts of Buttermilk Bay, but were not studied because patterns of abundance seemed equally affected by the topography and hydrography of the Bay.

Depth of eelgrass growth correlated well with DIN, but depth of eelgrass growth is often influenced by other factors such as water turbidity, thus other data are necessary to estimate nitrogen impact. Periphyton growth on artificial substrates and eelgrass show similar degrees of correlation with DIN. Periphyton growth on artificial

Figure 4. Chl$_a$ on settlement strips (top) and eelgrass (bottom) vs. DIN during the experimental period. Standard errors of the mean are shown for three replicate strips for chl$_a$, and a variable number of nutrient samples for an extended period at each station (see text).

Eelgrass periphyton

Strip periphyton

Chl a (µg/cm^2)

DIN (µM)
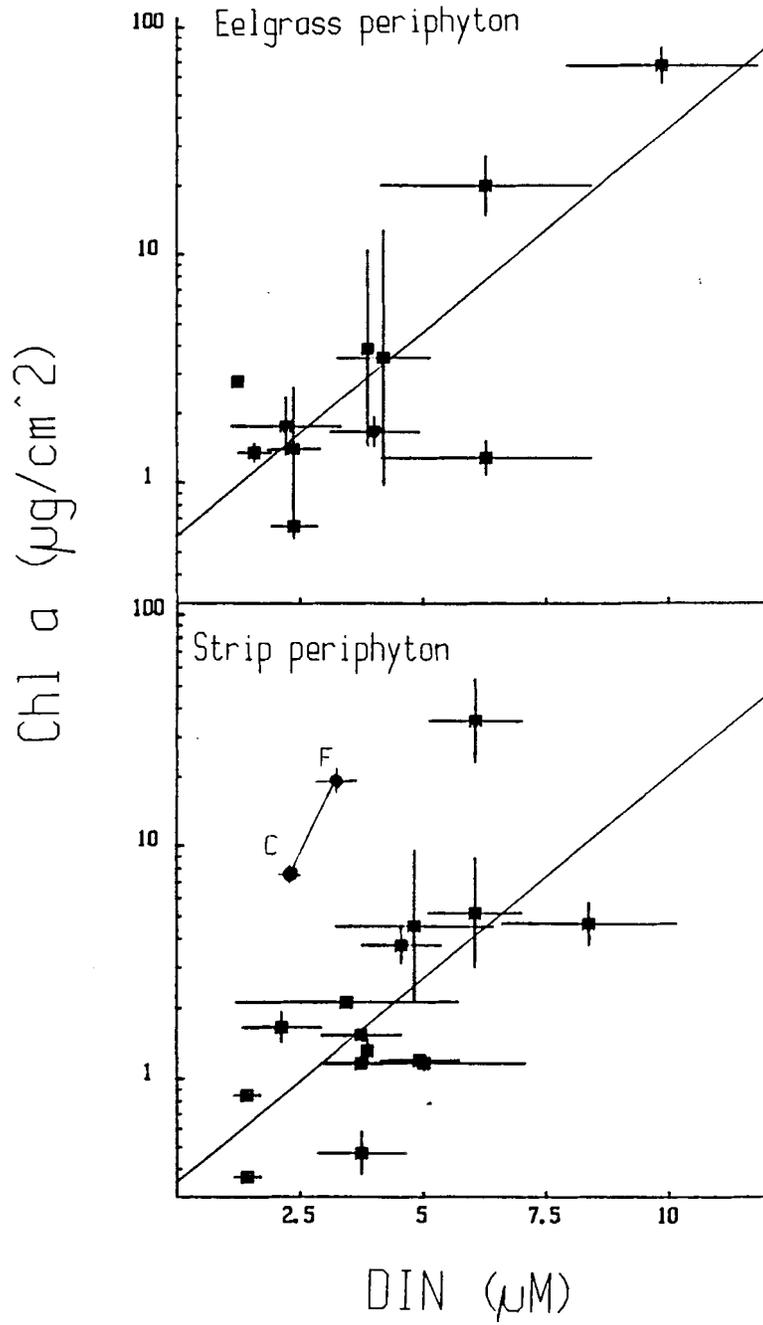
Figure 5. Depth of eelgrass growth vs DIN (±SE).
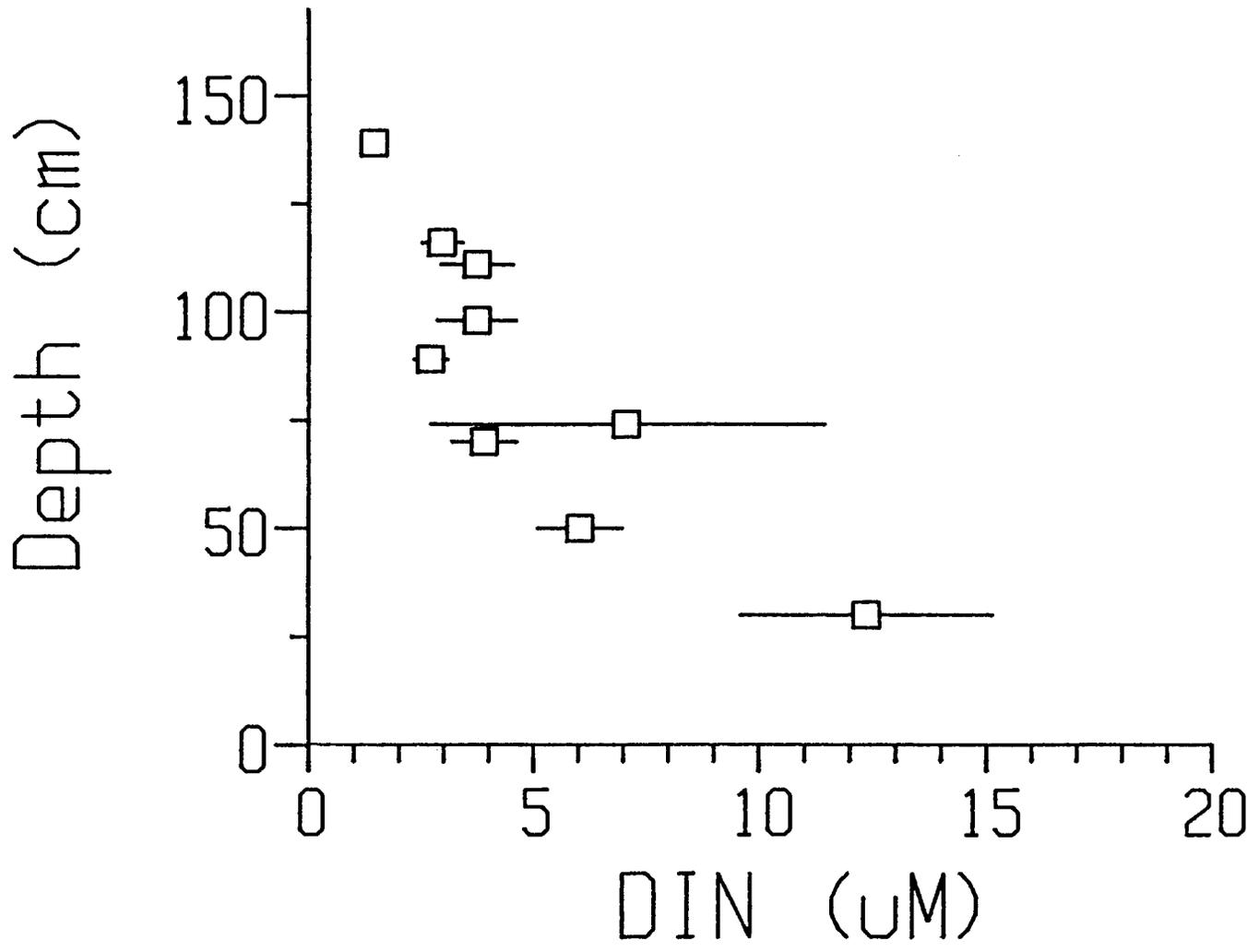
substrates as an assay offers advantages over eelgrass periphytes because eelgrass does not grow in all areas, and differences in periphyton abundance on eelgrass may be due to other factors controlling epiphyte abundance, such as invertebrate grazing, leaf age, and plant depth. Periphyton growth on settlement strips is a relative index of nitrogen exposure because growth rates of periphyton vary with light and temperature as well as nutrients (Sand-Jensen and Borum, 1983). Consequently interpretation of periphyton growth requires the simultaneous deployment of many floats with settlement strips.

The results of the growth experiment are inconclusive because of the large variability among shoots in relation to differences among between the two sites. Elsewhere I have seen that loss of eelgrass is gradual, and often occurs over 5 to 15 years. If the loss of eelgrass beds in an enriched bay results from lower vegetative growth or recruitment so that maintainence of populations cannot keep up with attrition from physical disturbance and death, then annual differences in eelgrass growth between enriched and unenriched areas may be small, and larger sample populations may be needed to resolve growth differences.

Other factors may explain the lack of distinct growth rates between the two sites data. The bed and transplants in Miller Cove were not at the limit of eelgrass depth distribution there (which was 50 cm deeper). This small difference may be critical in terms of observing reduced growth in enriched areas. Also, declines of eelgrass populations may involve some seasonal declines or slightly higher rates

of shoot death that can only be measured with large numbers of plants over long periods.

Even though the results of the growth experiments are unclear, eelgrass distribution in Buttermilk Bay shows that eelgrass grows to lesser depths in enriched areas (Fig 5). Since periphyton is more abundant in these areas, I concur with Sand-Jensen and Borum (1983) and others that the distribution of eelgrass beds may be controlled by nitrogen inputs and concentrations.

In the deeper parts of the Bay where the slope of the bottom is small, eelgrass has receded by ≈200 m during the last 20 years (Costa, 1987). While the areal declines of eelgrass in Buttermilk Bay have been small, theses losses indicate this Bay will be sensitive to additional loading. The mean depth of a bay is a critical component in estimating the impacts of nitrogen inputs. For example, Waquoit Bay, which has similar levels of development (in prep), but has a mean depth greater than 1.5 m, has lost 90% of its eelgrass population (Costa, 1987). It is likely that if the mean depth of Buttermilk Bay were 0.5 m deeper, the impacts of nitrogen loading would have been greater.

The depth of Buttermilk Bay may only partly explain why eelgrass has not declined appreciably. The nutrient concentration data from Buttermilk Bay (Valiela and Costa, in press) and phytoplankton chl data (here) illustrate the importance of tidal mixing when assessing the effects of nutrient loading. At any level of nutrient loading, the effects of that nutrient loading will be more pronounced if only 10% of bay water is exchanged with each tide than if 50% is exchanged. To assess the impact of nitrogen loading on eelgrass distribution, the

residence period of water in the bay must be considered. In Table 2 I ranked nitrogen loading of some well studied bays and coastal lagoons based on volume, area, and tidal flushing (data from Nixon, 1983; Giblin et al., 1983; Gaines, 1985, Valiela and Costa, in press). On a volume basis, Buttermilk Bay is one of the most polluted bays shown. In contrast, when nitrogen additions are considered on a volume basis during the residence time of water in each bay (Table 2, 4th column), Buttermilk Bay is one of the least enriched systems. This may explain both the absence of large declines in eelgrass, or large accumulations of drift algae in Buttermilk Bay as has occurred elsewhere in the region (Costa, 1987, 1988).

The results reported here, in Valiela and Costa (in press), and in other studies, suggest that many parameters need to be examined or monitored together to assess the impact of nitrogen additions. The most practical assays with the best correlations to nitrogen concentrations in Buttermilk Bay were depth distribution of eelgrass, and growth of periphyton on artificial substrates. These types of observations, together with long-term sampling of nitrogen concentrations in the water column and measurement of tidal flushing should be a fruitful approach for studying the impact of added nutrients in shallow coastal lagoons.

Table 2. Nutrient loading (per m^3, per m^2, and turnover-weighted) for various estuaries and embayments. Data taken from Nixon (1983), Nixon and Pilson (1983), Lee and Olsen (1985), and Gaines (1985). Method of calculation of turnover times indicated as "a" are described in Valiela and Costa (in press); other values as reported in literature by various methods.

| | Loading | | Turnover | Turnover-weighted loading |
	$m\ mol\ N\ m^{-3}yr^{-1}$	$m\ mol\ N\ m^{-2}yr^{-1}$	times (d)	$(m\ mol\ N\ m^{-3}r^{-1})$
Long Island Sound	30	400	27	2.2
Kaneohe Bay	40	230		
Lagoon Pond	57	261	21.5	3.4
Chesapeake Bay	80	510	166	36.4
Narraganset Bay	100	950	25	6.8
Town Cove	100	860	26	7.1
Patuxent Estuary	110	600	51	15.4
Delaware Bay	140	1350	97	37.2
Potomac Estuary	140	810	45	17.3
Apalachicola Bay	213	315	10[a]	5.9
Point Judith Pond	240	560	6	3.9
Pamlico Estuary	250	430	12.5[a]	17.1
Ninigret Pond	280	340	24.5[a]	37.6
Barataria Bay	290	570		
North San Francisco Bay	290	2010		
South San Francisco Bay	310	1600	320	271.8
Raritan Bay	330	1460		
Buttermilk Bay	390	543	5.0	5.6
Mobile Bay	400	1280		
Green Pond	500	1144	20[a]	27.4
Green Hill Pond	780	620	56.5[a]	121
Potter Pond	1050	710	25[a]	72
New York Bay	4550	31930	3	37.4

Chapter 7

Stress ethylene production in four marine macrophytes

ABSTRACT

To determine if stress ethylene production could be used to screen pollutants for sublethal toxicity on marine plants, four marine macrophytes (*Spartina alterniflora* Loisel, *Zostera marina* L., *Ulva lactucum* L., and *Ceramium* sp.) were exposed to phytotoxicants (Cu^{2+}, No. 2 fuel oil, 2,4-D, and naphthalene; $\approx 10^{-7}$ to 10^{-3} M or v/v). The response of each species to chemical stress varied greatly, but in all cases, Cu^{2+} induced the highest rates of stress ethylene production, and showed effects at lower concentrations than the other compounds tested. *Ulva* and *Zostera* significantly increased ethylene production when exposed to the highest concentrations of Fuel oil, but *Spartina* showed no response. Similarly, 2,4-D was a weak inducer of ethylene in *Ulva* and *Spartina*, and did not induce a response in *Zostera*, even at 10^{-4} M. None of the species produced ethylene in response to naphthalene exposure.

Ethane production was also produced by the plants in response to the phytotoxicants. Because significant increases in ethane production often co-occurred with increases in ethylene, the production of some of the ethylene observed may be from a peroxidation pathway, and indication of severe toxicity. These results suggest that this assay is not sensitive enough for assaying sublethal toxicity of pollutants in marine plants. Because Cu^{2+} induced an ethylene response in *Ulva* at 10^{-7} M, this assay may have limited use in assessing the relative toxicity of different algal species to Cu^{2+}. This is the first observation of

stress ethylene production in macroalgae, but other studies suggest ethylene production is widespread among phototrophs.

INTRODUCTION

Ethylene is a metabolite that controls fruit ripening, leaf senescence, and other physiological processes in higher plants (1,13). Photosynthetic aquatic organisms also produce ethylene, including submerged freshwater angiosperms during senescence and in response to IAA and kenetin (8), a green macroalga (*Ulva*) in response to IAA, a phytoplankter (*Scenedesmus*) in response to Cu^{2+} (12), and as a natural product in blue-green algae (7). It is unclear how ethylene production affects algal metabolism, or if production is ubiquitous among all algal groups.

In the 1970's it became apparent that ethylene can be induced in plants by a variety of mechanisms including physical injury, waterlogging and waterdeficit, freezing, or exposure to ozone, SO_2, NaCl, or soluble toxic compounds (4,5,6,9,11,15,17). The production of ethylene as a response to plant injury has become known as "wound ethylene" or "stress ethylene" and its production has been clearly identified as the degradation product of ACC which is derived from a methionine based precursor (6,9,17).

Tingey (15) and Rhodecap and Tingey (11) were the first to outline a rapid assay for testing the toxicity of phytotoxicants using stress ethylene production. With this assay, they were able to rank the relative toxicity of both organic and inorganic compounds applied to the rhizosphere of *Phaseolus*.

Ethane is often measured concurrently with ethylene and can also be used as a measure of stress. Its production, however, is dependant upon a different pathway--the peroxidation of fatty acids in membranes

(10)--thus it is considered an indicator of severe stress or cell death and less sensitive than ethylene production (9). Sometimes the production of ethylene is attributed to this pathway (10,11), but it is generally assumed that ACC metabolism is the primary pathway of ethylene production in higher plants. The induction of stress ethylene in marine macrophytes by toxic compounds has not been previously examined.

To assess the impact of pollutants in the marine environment, bioassays are needed which are fast, simple, and sensitive. The purpose of this study was to test if stress ethylene is produced in several taxonomically diverse macrophytes, and if so, to determine if it meets these criteria.

MATERIALS AND METHODS

An emergent marine angiosperm (*Spartina alterniflora* Loisel), a submerged angiosperm (*Zostera marina* L.), a green algae (*Ulva lactuca* L.), and a red alga (*Ceramium* sp.) were exposed to two or more of the following compounds: $CuSO_4$, naphthalene, 2,4-D, and the water soluble fraction (WSF) of No. 2 fuel oil (Bayton, Texas Exxon oil refinery)[2]. Test solutions were prepared using glass fiber (Whatman C) filtered seawater. Concentrations are given as molarity, except for No. 2 fuel oil solutions, which was reported as the concentration of the water soluble fraction (WSF) as v/v. The WSF test solutions were made from a 1 ppt WSF stock solution. The 1 ppt WSF was prepared by mixing 1 ml of No. 2 fuel oil and 1 l of GFC filtered seawater. This mixture was stirred vigorously in a flask with a stir bar for 2 hr, then allowed to

separate in a separatory funnel overnight. The WSF stock solution consisted of the aqueous phase.

Plants were collected in the field and acclimatized to laboratory conditions for at least 24 h. Plant segments of approximately equal size (0.1 to 0.4 g depending upon species) and were cut with a razor blade. These samples were inserted in 15 x 85 mm test tubes containing 4 ml of test solution, and sealed with a serum stopper. Conditions were altered for some experiments, but unless specified, the samples were incubated in a recirculating seawater aquarium at 18-20° C, with a 16:8 light:dark cycle under a light bank of incandescent and fluorescent light yielding ca. 180 µE m-2 sec-1 (PAR, measured with a Li-Cor Inc. calibrated light meter). Incubation time varied between experiments and typically ranged from 24 to 96 h. Within any one experiment, however, all samples were treated identically and generally consisted of 3 to 5 replicates at 4 or 5 concentrations plus controls and blanks. The *Ulva* time-course experiment consisted of 25 samples, 5 of which were sampled approximately every 24 h. The *Zostera* and *Spartina* samples consisted of healthy tissue with epiphytes removed, and unless specified otherwise, consisted of mid-leaf segments.

To measure ethylene and ethane concentrations, 1 ml gas samples (collected in gas tight syringes), were injected into a Varian 1400 gas chromatograph equipped with a flame ionization detector and supporting a 1800 x 6-mm Porapak N column (column temp. 65° C, N2 carrier 40 ml min-1). Standard curves were made from dilutions of 100 ppm ethylene and pure ethane (Suppleco Inc. Houston, TX). Background concentrations were 10 ppb, near the level of detectability. Blanks (test solutions

incubated without plant tissue) were indistinguishable from normal background levels except in the highest test concentration of No. 2 fuel oil, but even then it was not high enough to alter the interpretation of the results. Ethylene production was corrected for sample volume, pressure reduction, gas solubility, and plant weight which was measured at the end of each experiment and is presented as total nl accumulated per g wet wt. Concentrations were not adjusted for length of the incubation because most ethylene accumulates during the first 24 h and long incubation times do not result in proportionally large accumulations (see RESULTS). Ethylene production was log-transformed to normalize variance (11) and all treatments were compared using one-way anovas. If the phytoxicant demonstrated a significant in the anova test, the first treatment concentration illiciting a ethylene response higher than the control was identified using a GT2 paired mean test (14). Both tests were assessed at $\alpha = 0.05\%$.

RESULTS

All the macrophytes showed stress ethylene production, but response varied among species and test compounds. A time course experiment for $Ulva$ exposed to 10^{-4} M Cu^{2+} is shown in Fig. 1. Ethylene production was most rapid in the first 24 h (80% of total accumulation) and stopped after 48 h. The decrease in ethylene after 48 h was probably due to diffusion out of the tubes, whereas the increases in ethane probably resulted from continual peroxidation of cell membranes.

These results are similar to observations of ethylene production in higher plants, which terminate ethylene production between 6 and 60

Fig. 1. Ethylene (●) and ethane (O) production in *Ulva* exposed to 10^{-4} M Cu. Production is shown as total accumulation over time. The mean ± SE of 5 samples at each time are shown for 25 different samples.
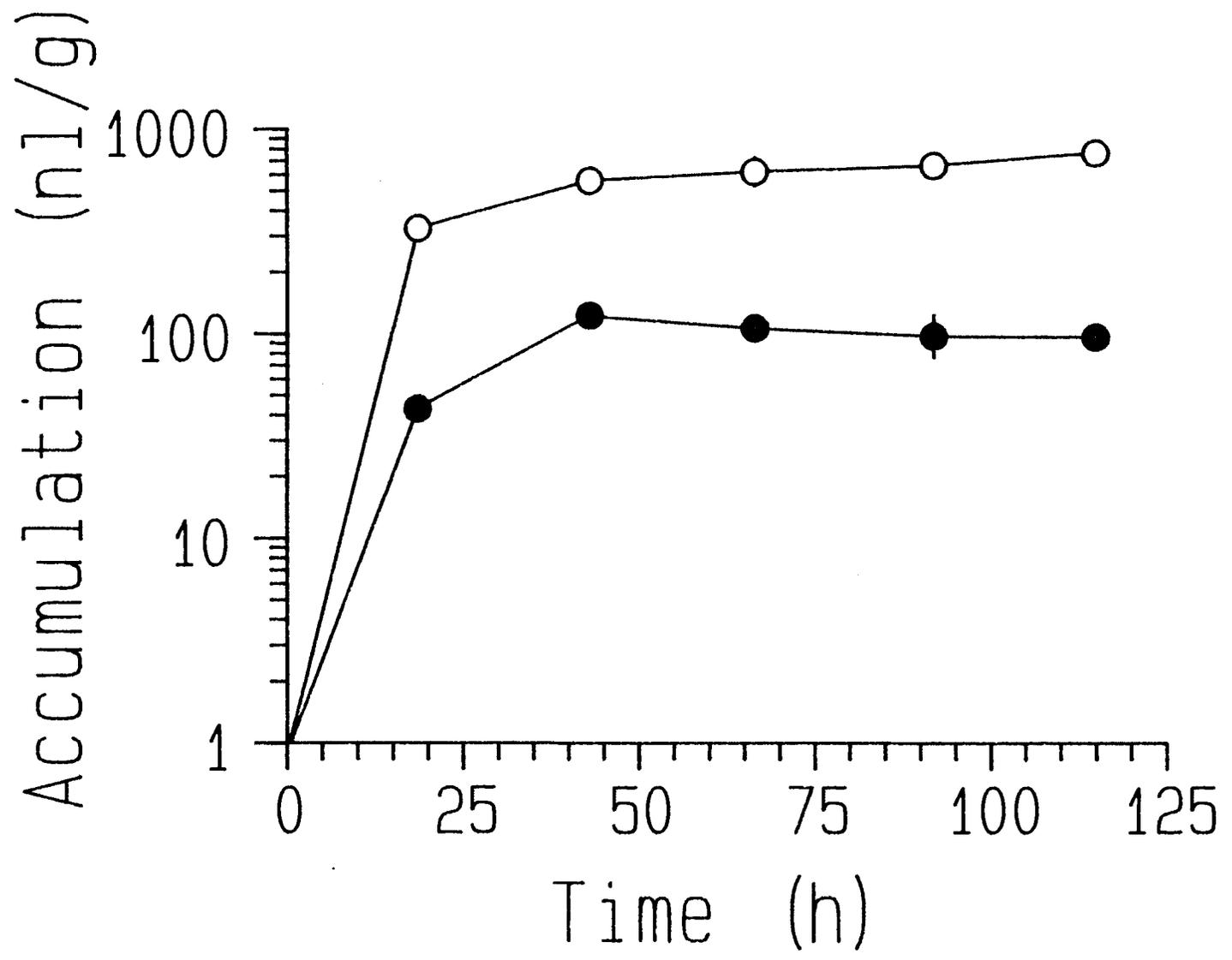
hr depending upon conditions (6,15). Consequently, even though the incubations were of somewhat different length in each of the experiments, comparisons of maximum rates of ethylene production among species are valid because most experiments continued for more than 20 h, and also because the ethylene production response among species often differed by an order of magnitude or more.

Stress ethylene was induced by Cu^{2+} in each species (Fig 2). At 10^{-3} M Cu^{2+} ethylene production was highest in *Ulva* (250 nl g^{-1}) and lowest in *Spartina* (11 nl g^{-1}). *Ulva* showed a significant increase in ethylene production at 10^{-6}. *Ceramium* showed a slight increase 10^{-6}, and a significant increase in ethylene production at 10^{-5}. The angiosperms were less sensitive to Cu^{2+}, both of which showed significant increases in ethylene production only at 10^{-3} M. For all species, the samples became chlorotic or necrotic at 10^{-3} M, and except for *Spartina*, which showed some discoloration at 10^{-4} M Cu^{2+}.

Neither *Ulva* nor *Zostera* responded to naphthalene, even at 1.6 x 10^{-3} M (data not shown). These plants also did not become chlorotic. The responses of *Ceramium* and *Spartina* to naphthalene were not tested.

The WSF of No. 2 fuel oil induced a slight but statistically significant increase in ethylene production in *Zostera* leaves at 1 ppt , but no measurable effects on *Zostera* root and rhizome samples at that concentration (Fig. 3). *Ulva* showed an ethylene response at 100 ppm WSF (Fig. 3), but *Spartina* did not show increased ethylene production (not shown). The maximal rate of ethylene production in *Ulva* in response to fuel oil (32.6 nl/g, Fig. 3) was far less than observed with exposure to Cu^{2+}. *Ceramium* was not tested with fuel oil.

Fig. 2. Ethylene and ethane production after Cu^{2+} exposure. *Ulva*: duration 65.5 h, mean and standard deviation of 5 replicates at each concentration; *Ceramium*: 61.5 h, 5 replicates each; *Zostera*: 123 h, 3 replicates each; *Spartina*: leaf base, 48 h., 2 replicates each except for the control (4 replicates) and 10^{-7} M (3 replicates). Asterisk indicates statistically significant difference from the control (C) (see text).
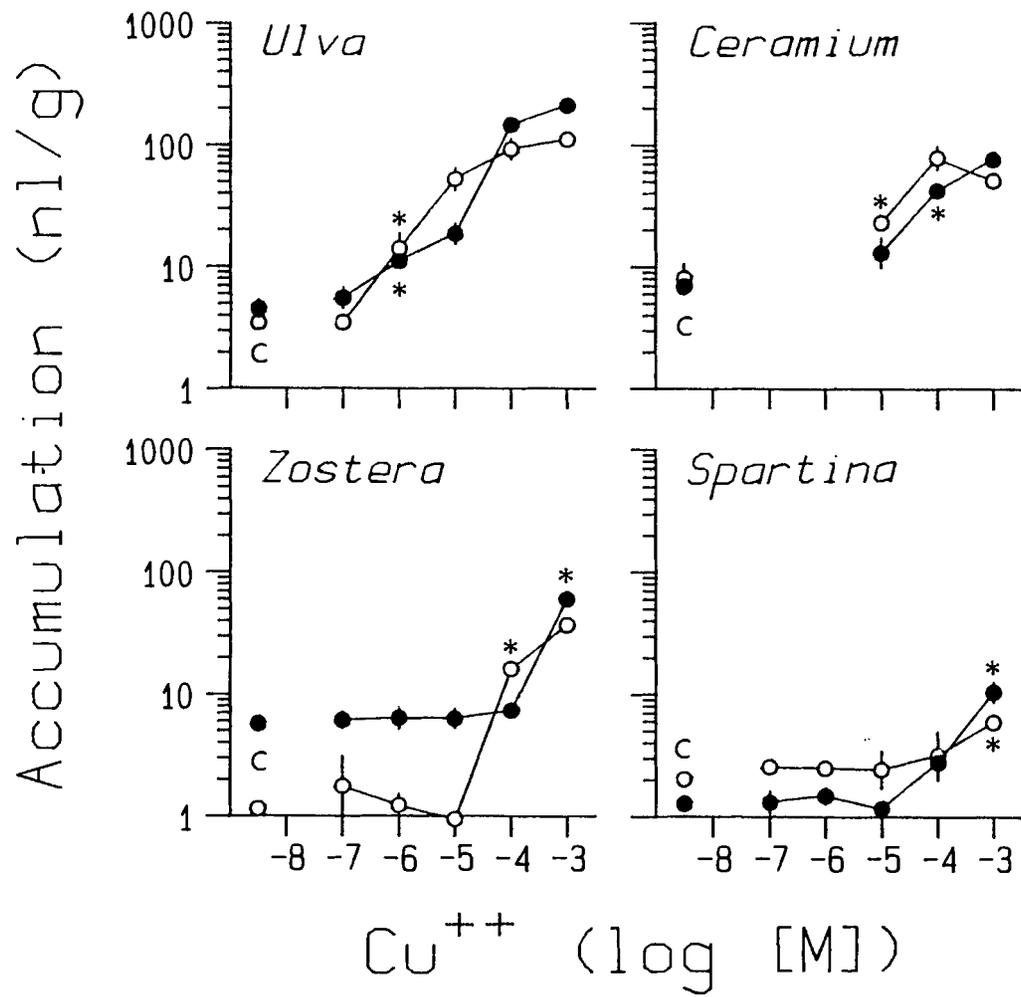
Fig. 3. Ethylene and ethane production induced by the water-soluble fraction of No. 2 fuel oil. *Ulva*: 13 h, in sunlight at 31°, 5 replicates at each concentration; *Zostera* 13 h in sunlight at 31°, 3 replicates at each concentration.
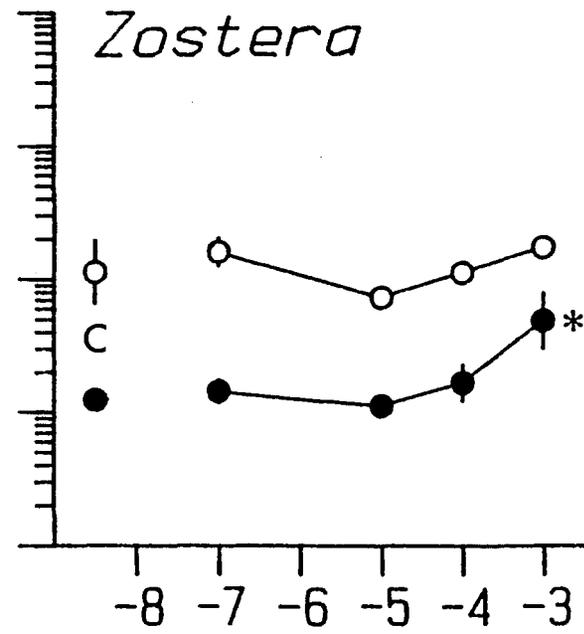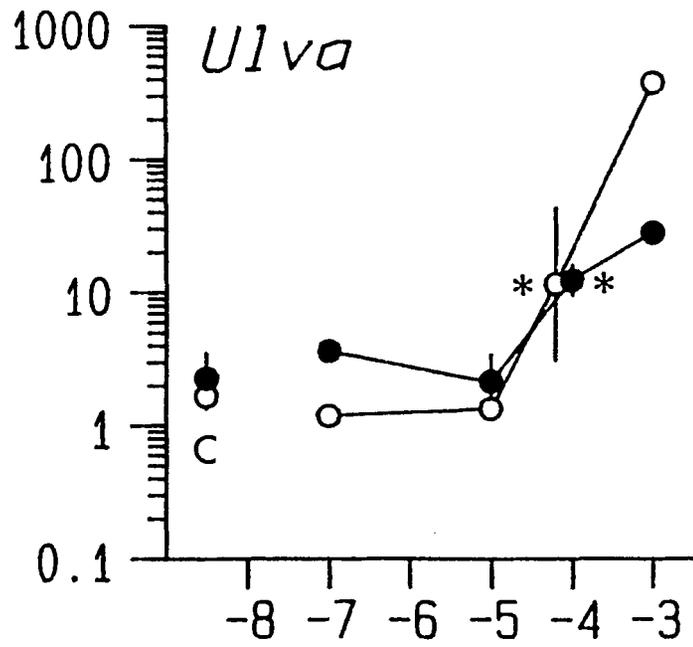
Fig. 4. Ethylene and ethane production after 2,4-D exposure.
Ulva: 13 h incubation with sunlight, 31° C, 3 replicates at each
concentration except control (4 repl.) and 10^{-5} and 10^{-3} M (2 each);
Spartina: leaves 48 h sunlight/dark incubation, 31° C, 3 replicates at
each concentration.

270
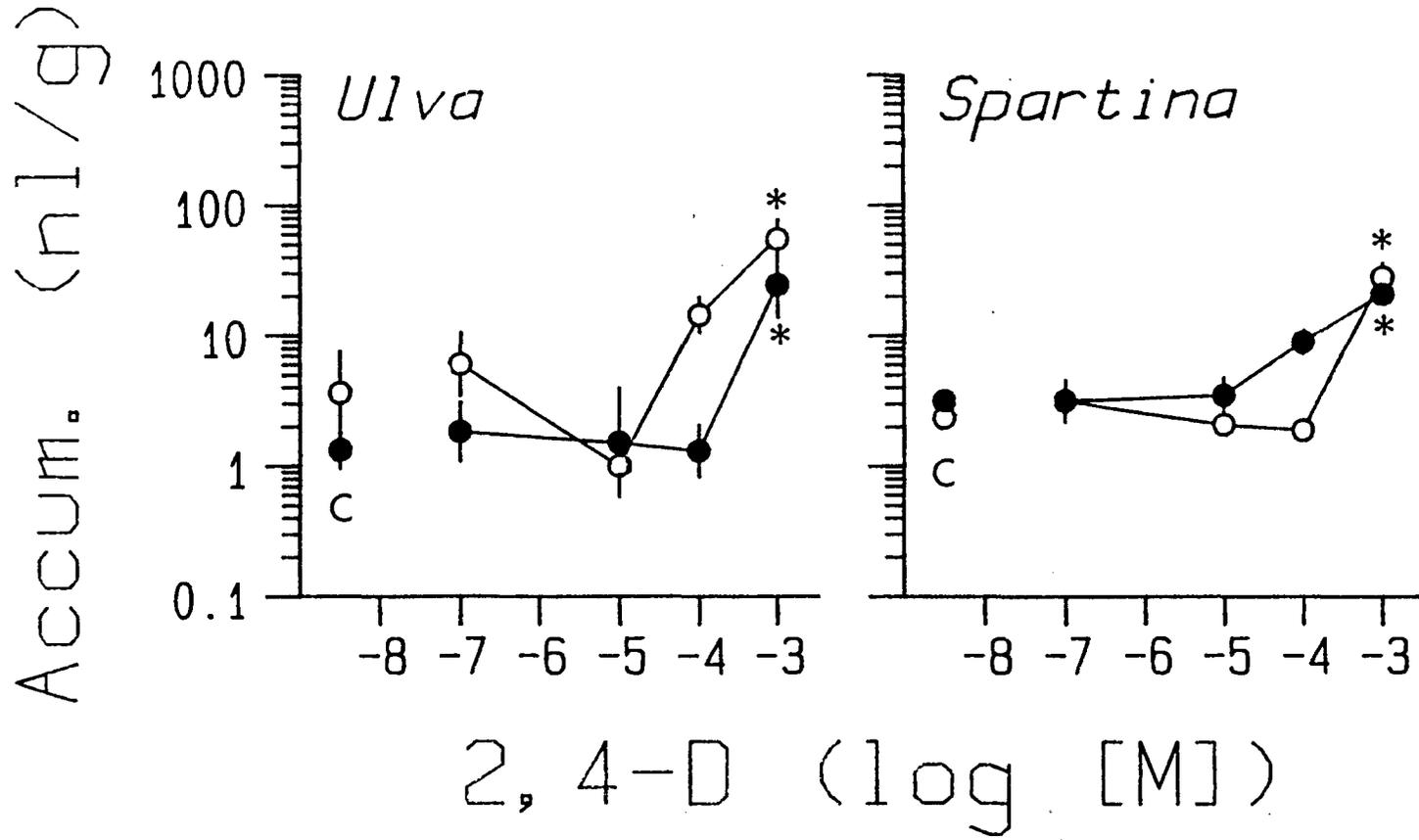
Ulva and *Spartina* showed a significant increase in ethylene production when exposed to 10^{-3} M 2,4-D (Fig 4). Both species became necrotic at the two highest concentrations, thus ethylene production coincide with cell death. Only the areas near cut leaf margins became chlorotic in *Spartina*, illustrating that 2,4-D did not pass through the epidermis, but instead diffused through the vascular tissue. *Spartina* meristems were also tested (not shown), and they showed a slight increase throughout the range of treatments, down to 10^{-8} M (not shown). This observation may be due to higher sensitivity of dividing cells to 2,4-D. 2,4-D toxic effects are known to be most acute in dicots, and monocots do not generally show lethal effects at low concentrations. . *Zostera* showed no ethylene production at the highest concentration that it was exposed to (1.6×10^{-4} M, not shown), and it did not become necrotic or chlorotic. These results were surprising because 2,4-D had been described as effective in destroying eelgrass beds with water-bourne applications (3). *Ceramium* did not show increased ethylene production at the highest concentration to which it was exposed (10^{-5} M 2,4-D).

DISCUSSION

These experiments illustrate that stress ethylene production in aquatic producers is not a sensitive enough assay to assess sublethal effects of phytotoxicants on aquatic plants because the species tested only responded to acutely toxic concentrations, if at all. This results show, however, that the mechanism of stress ethylene production can be

studied in aquatic plants and algae in ways that may be difficult in terrestrial studies.

Two trends are apparent from the responses of the four plants to Cu^{2+}. First, these algae were more sensitive to Cu^{2+} than the angiosperms. For example, *Zostera* became necrotic at both 10^{-3} M and 10^{-4} M--the same concentrations at which both ethane and ethylene were induced--therefore ethylene was produced only at acute concentrations. The second trend is that the absolute rate of ethylene production per plant weight positively correlates with surface:volume ratios of the four plants. *Ulva* is a sheetlike bilayered algae and all cells come in contact with the test solution, and its ethylene production peaked at 250 nl g^{-1}. The next highest rates occurred in *Ceramium*, a pseudoparenchemous filamentous algae that has fewer cells in contact with the test solution. *Zostera* has parenchymous, strap-like parenchymous leaves with a thin, multiperforate cuticle had lower rates than the algae, *and Spartina*, which has thicker leaves covered with a waxy cuticle, and had the lowest rates of ethylene production. Thus, the per unit weight ethylene production rate is probably a function of the degree of contact between the test solution and the plant cells.

In higher plants, Cu^{2+} and Cd^{2+} are strong inducers of stress ethylene production in other plants (4,10), and here, Cu^{2+} induced stress ethylene production in algae nearest to sublethal concentrations. Therefore this assay may have limited use in assessing the relative sensitivity of different algal species to certain metals.

In some trial experiments, the samples were exposed to elevated temperatures (27-30° C) and direct sunlight. This elevated the response

of the plants, but too few trials were made to determine if this also increased the sensitivity of the assay. Light plays an important role in ethylene production (7), and this explains why eelgrass leaves and not roots showed increased ethylene production when exposed to fuel oil.

This is the first account of stress ethylene production in macroalgae. In a pilot experiment I observed ethylene production in *Fucus vesiculosus* L. (not shown), and elsewhere non-stress ethylene production has been observed in green microalgae (12), a blue green algae (7) and in the green macro-alga *Codium* (16). Thus it appears that ethylene production may be ubiquitous in diverse groups of algae. The significance of this is not clear, however, since ethylene is not recognized as a hormone in algae. It is not known if the production of stress ethylene in algae is involved with in tissue senescence or some another similar role that ethylene performs in higher plants, and this area needs further study.

It is also unclear by which pathway algae produce ethylene. Sandmann and Boeger (12) assumed that ethylene production in *Scenedesmus* is derived from the peroxidation of lipids as is ethane. In this paper, increased ethane production often occurred at the same concentration of phytotoxicant that induced increased ethylene production. That is, ethylene was produced only at acutely toxic concentrations. One possibility that could explain this result is that a large fraction of the ethylene produced by the algae is, in fact, derived (like ethane) from peroxidation of membranes. Alternatively, both pathways may be triggered by similar concentrations of phytotoxicants. There is evidence that the ACC pathway exists in algae because blue-green algae

have been shown to metabolize ACC to ethylene (7), and I have also observed high rates of ethylene production in *Ulva* when exposed to ACC (not shown).

One additional ramification of these results, is that the production of stress ethylene by algae may affect laboratory measurement of N-fixation in sediments. This is because N-fixation is usually measured by the reduction of acetylene to ethylene. Thus the presence of microalgae could lead to artificially high estimates of N-fixation if plant cells have been chemically or physically stressed during sample processing.

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Chapter 8

Management considerations of eelgrass (*Zostera marina* L.) populations in

Massachusetts

Resource assessment

It is generally agreed that eelgrass beds are important to the ecology of the coastal zone, but there is no consensus on how to manage this resource. The newly realized ecological, economic, and aesthetic value of eelgrass beds and the biological community they support has brought them under some local, state, and federal coastal resource regulations. Because there is no consistent management policy concerning eelgrass beds, it is worth considering how governmental agencies in Massachusetts manage these communities.

In general, the effects of eelgrass bed removal on coastal production and ecology are rarely considered. To date, most decisions in Massachusetts relating to eelgrass beds have centered on physical removal or damage from dredging projects, or pier construction. Rarely are changes in water quality induced by these or other projects considered, but potential changes in water quality may be weighed when the overall "health" of a bay is considered. Often the decision to dredge through an eelgrass bed is ultimately based on whether these beds also coincide with shellfish beds.

Federal, state, and local laws

The coast of Massachusetts is regulated principally by town conservation commissions, local planning boards, the State Department of Environmental Quality Engineering (DEQE), Army Corps of Engineers, Massachusetts Environmental Protection Agency (MEPA), and the State Coastal Zone Management (CZM). Most state regulations concerning

coastal impacts are included in the state Wetland Regulations, (310 CMR 10.00).

In these regulations, eelgrass beds may enjoy protection under the law as "land under salt ponds" (10.33) where no project may affect "productivity of plants, and water quality". In "land containing shellfish" (10.34), and "land under the ocean" (10.25), there are broad guidelines protecting "water circulation", "water quality", and "marine productivity". Section 10.26 specifically states: "projects shall be designed and constructed, using best available measures so as to minimize adverse effects on marine fisheries caused by .... b) destruction of eelgrass (*Zostera marina*) beds". Thus, while destroying eelgrass beds is not prohibited, damage should be minimized.

In practice, coastal projects often do not go beyond the local conservation commissions. If they do, most decisions are managed by DEQE at the state level, but other state agencies (e.g. MEPA) may also be involved. In addition, CZM provides an advisory role at all levels of the decision making process and checks for consistency in local and federal regulations. Curiously, CZM policy guidelines (301 CMR 20.00) do not specifically include eelgrass beds as valuable underwater habitat, but in practice, this organization is interested in protecting eelgrass communities.

Large construction projects frequently must be approved by the US Army Corps of Engineers which considers eelgrass beds in there decisions. In recent years, the Corps has sponsored eelgrass transplant studies as a form of mitigation to disturbances (e.g. Fonseca et al., 1979, 1985; Goforth and Peeling, 1979).

Towns often have bylaws which may broadly cover coastal impacts, but no towns in Buzzards Bay have any bylaws specifically protecting eelgrass. Some local bylaws (e.g. Title V Amendments) extend the distance of septic tanks from shore (the "setback"), to further reduce the risk bacterial and viral contamination of shellfish. These laws indirectly benefit eelgrass beds because increased distance of septic tanks from shore reduces nutrient loading of bays (Valiela and Costa, in press).

Town conservation commissions may have broad powers to consider aesthetic and ecological impact of a project. While their decisions are based on both local and state laws, their decision is independent of state decisions, and technically they may prohibit a project even if approved by the state, although in practice, this is infrequent.

Most direct management of eelgrass beds, if any, is conducted by the town shellfish warden. In some towns, the shellfish warden may view existing eelgrass beds as valuable habitat, as is the case in Fairhaven, and harvesting shellfish in eelgrass beds may be discouraged. In other towns the shellfish warden may view eelgrass beds as a nuisance weed that reduce the quantity or quality of shellfish harvested, and the removal of eelgrass has been considered. Methods of eelgrass removal in the past were more extreme, and the application of the herbicide 2,4-D was attempted in Fairhaven in the 1960's (Fiske et al., 1968).

If there is an active policy by environmental managers today, it is usually toward conservation of eelgrass. In Westport, a large parcel of tidal flat, with extensive eelgrass coverage, is set aside as a shellfish refuge. On Nantucket, a multimillion dollar scallop industry

is based within extensive eelgrass beds within a coastal lagoon. To reduce physical damage to the eelgrass beds by the scallop dredges, the shellfish warden has persuaded local fisherman to remove some weight from their scallop dredges so that they skim the surface, cropping eelgrass leaves, but leaving behind roots and rhizomes to regenerate.

At all levels of management, lack of knowledge about the importance of eelgrass, eelgrass bed locations, and the effects human impacts, has limited proper management of this resource.

Implications of changing eelgrass abundance

This study raises several questions relating to the management of eelgrass beds and interpretation of their changing abundance. It is apparent that most eelgrass disappeared in Buzzards Bay as a result of the wasting disease, then gradually recovered over many decades. Superimposed on this trend are complex patterns of destruction and recolonization driven by catastrophic storms, ice scour, and anthropogenic disturbance.

One consistent trend observed was the continual expansion of eelgrass on the outer coast and well flushed areas. Here, occasionally moderate declines in eelgrass abundance result from ice scouring and catastrophic storms, but these beds typically recover after several years. In contrast, many poorly flushed bays did not recover appreciably after the wasting disease, or showed major new declines with no subsequent recovery. These areas had known histories of anthropogenic disturbances such as fecal pollution, sediment resuspension, and wastewater loading through either direct discharges or

via contaminated groundwater or stream flows. This trend is alarming because, unlike natural disturbances, eelgrass will not recover where human perturbation persists. Furthermore, many of these estuarine areas supported refuge eelgrass populations that facilitated eelgrass recovery after the wasting disease. Because beds in many of these areas have now disappeared, a recurrence of a wasting disease will have a longer lasting impact on the coastline.

This study adds to the growing literature showing seagrasses may disappear because of water quality decline, and that the disappearance of eelgrass may be a early warning sign that important changes are occurring in a coastal ecosystem.

Future monitoring

Throughout much of this report, eelgrass abundance was documented using fragments of information from many sources. A more thorough understanding of eelgrass dynamics can be achieved through continuous monitoring and by analyzing sediment cores.

The easiest way to monitor changes in eelgrass abundance is through periodic aerial surveys together with some field verification. This is a highly desirable approach because other aspects of coastal ecosystems, such as erosion rates, harbor usage, salt marsh bed loss, and drift algae accumulation will be documented as well.

One difficulty of using previous aerial surveys in this study was that the imagery was not taken with submerged features in mind, and field conditions were often unconducive to analysis. It is advisable that any town or agency conducting an aerial survey of the coastal zone,

do so using the guidelines in Table 1. Routine vertical aerial surveys should be conducted at least once every 3 years, especially in valuable resource areas or embayments undergoing rapid development.

Sediment core analysis is the most accurate way of assessing past local fluctuations in eelgrass abundance during this and previous centuries. Furthermore, the physical and chemical characteristics of core sections, along with the remains of plants and animals, can document long term changes in nutrient levels, shellfish abundance, sediment depositional rates, rates pollutant inputs, nutrient loading, and macroalgal and periphyton abundance (Brush and Davis, 1984; Fry et al., 1987, unpub. data). Sites for coring should be chosen carefully, and best results are achieved in quiescent, depositional areas, away from erosion and dredging influences (Davis, 1985). Together with aerial surveys and other documentation, sediment core analysis is a powerful tool for understanding the recent ecological history of coastal waters.

One intriguing possibility that needs study is that the depth of eelgrass growth throughout the Bay may have declined slightly. If prior to urban and industrial inputs in Buzzards Bay, eelgrass grew 0.5 m deeper in each habitat throughout the region and was present in coves in which it is absent today, then total eelgrass area may have been 50 % greater than todays cover. This hypothesis is testable because changes in eelgrass depth distribution and relative contribution of eelgrass to primary production can be assessed by analyzing sediment cores.

Table 1. Guideline for taking aerial photographs to maximize interpretation of submerged features.

The guidelines and months are listed in approximate order of desirability.

-during October, September, August, July, June, November, and May

-within 2 hours of low tide

-low sun angle, preferably early morning

-low wind velocity (< 5 kts)

-at least 2 days after any severe storm or rain event

-color photography preferable to black & white, IR is undesirable

-overexposure by 1/2 to 1 f-stop

-polarized filter

Eelgrass can sequester heavy metals in its leaf tissue, and it has been suggested that eelgrass be used as an indicator organism for this type of pollution (Brix et al., 1983).

Mitigation efforts

In recent years there has been considerable effort to mitigate eelgrass habitat loss by transplanting eelgrass into areas where it was removed, or if that proves unfeasible, transplant it to other suitable habitat (Boorman et al., 1978; Churchill et al., 1978; Fonseca et al., 1985; Goforth and Peeling, 1979; Kenworthy et al., 1980; Phillips, 1974, Robilliard and Porter, 1976). There are several problems inherent in mitigation efforts in general. First it may take many years for an eelgrass community to fully recover after initial colonization or transplantation.

Often, coastal dredging increases depths to such an extant that habitat area is permanently lost. In these cases, bare areas nearby may be chosen as the site of transplantation. Because there may be hydrological or physiological reasons for the absence of eelgrass in these areas, transplant efforts to these areas often fail (Ranwell et al., 1978).

Nonetheless, sufficient number of projects have succeeded in reestablishing eelgrass where it has been removed. This approach, while experimental, has a role in coastal management. For example, transplantation may facilitate a more rapid recovery of eelgrass populations where there have been large losses due to storms, disease,

or pollution. Transplanting as a form of mitigation, however, should
not be used to rationalize incremental permanent loss of habitat.

Future management

Eelgrass beds are not well protected under current Massachusetts
regulations, and a coherent management policy regarding eelgrass beds
should be formulated, especially because eelgrass is declining in some
Bays. Because salt marshes are rigorously protected in Massachusetts,
as maps of eelgrass abundance become available, the question will arise:
should eelgrass beds be regulated as carefully as salt marshes? To
answer this question, comparisons between the two communities can
highlight potential management strategies.

Eelgrass beds are more abundant and productive than salt marshes,
and are a dominant feature of nearshore waters in Buzzards Bay. These
two ecosystems are host to different communities of organisms, and each
serves a different ecological role. Salt marshes build dense layers of
peat over decades and centuries which become an intrinsic part of the
stability and biology of those communities. Eelgrass beds do not form
peat mats, and although they change the chemistry and biological
components of the sediments (Orth, 1973, 1977), the time to create an
eelgrass habitat after initial colonization is shorter than the time to
create a mature salt marsh community. Furthermore, the range of
habitats that eelgrass can colonize is more diverse and expansive than

the habitats available to salt marshes. Some eelgrass beds are seasonal or may appear on marginal habitat only intermittently.

Given these characteristics of eelgrass beds, the main priority in regulating physical disturbances should be to prevent alterations to the environment that permanently eliminates eelgrass habitat. Dredging and construction in shallow, poorly flushed bays is especially critical because water transparency in these areas is usually poor, and channels dredged for boats are often so deep and so disturbed that eelgrass can never grow there, and habitat area is lost. Construction of a single private boat channel may result in the removal of only 5% or less of existing eelgrass cover in a bay, but permitting channels to be dredged to every private dock may result in intolerably large losses.

Small physical disturbances like eelgrass removal during shellfish harvesting with rakes or tongs are probably unimportant for bed survival under low intensity (Costa, 1988, and in prep.), but high intensity shellfishing efforts, or continued dredging from boats can remove large areas of eelgrass beds, as well as increase sediment resuspension and decrease water transparency.

Past declines of eelgrass due to physical removal, however, have been less important in Buzzards Bay as a whole, than losses due to general declines in water quality. This is understandable because eelgrass beds are subtidal, and their distribution is light limited. In contrast, protecting salt marshes from nutrient loading is rarely an

issue, because salt marsh production is enhanced by added nutrients (Valiela et al., 1975).

Because water quality declines are often due to many sources, and often difficult to quantify or assess, some managers view protection of eelgrass beds from water quality declines as uneconomical or unworthy. This view is short sighted, because eelgrass beds are closely linked to the ecology of coastal waters. Many other species besides eelgrass are also affected by water quality declines or disappearance of eelgrass. Beaches and shellfish beds may be closed due to fecal coliform contamination. Shellfish habitat may disappear because dense growths of drift algae form an impenetrable layer preventing oxygenated water from reaching the bottom (Lee and Olsen, 1985), smothering bivalves and other infauna. This dense growth may create such a high oxygen demand during quiescent summer periods that anoxic events may occur resulting in fish kills. Excessive algal growth sometimes release displeasing odors or cover beaches, making them unaesthetic. Other synergistic effects are now being realized. Algal growth, decreased water transparency, and nutrient loading facilitates fecal coliform survival or even promotes growth (Heufelder, 1985).

Thus, eelgrass beds are merely one component of coastal waters that are sensitive to declining water quality. In many areas, the loss of eelgrass could have been used as an early warning for more damaging changes that were to occur; that is, eelgrass bed declines may be used as a tool for diagnosing the "health" of a bay. Protecting water quality should be a primary goal of coastal managers, not only because

eelgrass beds are protected, but because other valuable resources are protected as well.

Water quality protection

Declines in water quality are due to many sources, some of which are difficult to control. For example, resuspension of sediments caused by boat motor use in shallow bays can only be reduced if either there is less boat traffic, enforced speed limits, or exclusion zones. Dredging projects not only eliminate eelgrass habitat, but generate high sediment loads. Some operations such as "jet-clamming",--the harvest shellfish by resuspending large volumes of sediment--could potentially have strong impacts on water quality because this process creates large sediment plumes and releases nutrients from sediment pore water. Serious questions must be answered before this technique becomes widespread.

Land based sewage disposal nearshore and sewage discharge offshore are two of the most serious problems affecting Buzzards Bay. New Bedford now discharges secondarily treated sewage offshore. The turbid plume from this outfall is conspicuous from air, and the several hundred meter wide plume often stretches 1000's into waters of neighboring towns.

Smaller outfalls from street run-off are common throughout the region. In some bays, nutrient inputs through these is small compared to other sources (Valiela and Costa, in press), but they may be important sources of pathogens and other pollutants (Heufelder, 1985).

A more widespread problem in the region is the siting of septic tanks nearshore. One of the difficulties with coastal management in

Massachusetts is that nutrients are not considered pollutants. Septic tanks and leaching systems are designed to reduce contamination of bacterial pathogens into groundwater; even a properly constructed septic tanks release large volumes of nutrients into the groundwater. When the State considers an application for a septic tank nearshore, it considers only the impact of a single proposed project on public health, rather than the effects of similar projects on water quality and nutrient loading. Because it is difficult to demonstrate that nutrients from a single septic will have a deleterious impact on a bay, such projects are usually approved, even if serious water quality declines would occur if every parcel of land along shore were similarly developed.

Presently, Massachusetts guidelines specify that these systems may not be placed within 15 m (50 ft) of wetlands or bodies of water (the "setback"). Many towns have set their own stringent setback bylaws, because the state regulations are viewed by many as inadequate to protect the publics interest in the coastal system. This is a positive step, but what is needed is town planning boards to set maximum nutrient loading limits for watersheds, and State managers to accept nutrient loading as a form of pollution, and hence regulate it.

Appendix I--Repositories of aerial photographs and nautical charts used in study.

Aero Service Division

Western Geophysical Company

8100 Westpark Dr.

Houston, TX   77063

(713) 784-5800

Col-East, Inc.

Harriman Airport

North Adams, MA 01830

(413) 664-6769

Lockwood, Kesseler & Bartlett, Inc.

1 Aerial Way

Syosset, NY 11791

(516) 938-0600

Lockwood Mapping Inc.

1 Aerial Way

Syosset, NY 14623

WHOI Woods Hole Oceanographic Institution

Woods Hole, MA 02543

(617) 548-1400

James W. Sewall Co.

147 Center St.

Old Town, ME   04468

(207) 827-4456

Town offices in Falmouth, Bourne, Wareham, Dartmouth, New Bedford, Fairhaven, Mattapoisett, and Marion

New Bedford Whaling Museum

New Bedford, MA 02740

Woods Hole Oceanographic Institution

Document Archives

Woods Hole, MA   02543

(617) 548-3705

Agricultural Stabilization and Conservation Service

Aerial Photography Field Office

US Department of Agriculture

2222 W. 2300 South

PO Box 30010

Appendix I--Repositories of aerial photographs and nautical charts used
in study.

Salt Lake City, UT 84125

(801) 524-5856

EROS Data Center

U.S. Geologic Survey

Sioux Falls, SD 57198

(605) 594-6511 x151

National Cartographic Information

Center

U.S. Geological Survey

507 National Center

Reston, VA 22090

(703) 860-6336

National Ocean Survey

Coastal Mapping Division, 03415

NOAA

Rockville, MD 20852

Massachusetts Geodetic Survey

Boston, MA

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Boston, MA

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Vita

Joseph Edward Costa was born in New Bedford, MA on 29 June 1958.
He grew up one block from shore, and one block from what he would later
realize was a major PCB polluter in Buzzards Bay. In part because of
his many exploratory hikes along the shores of New Bedford, and
especially because of his attendance at the New Bedford Oceanography
School, Sea Lab, during summers between the 6th and 9th grades, he
decided at a early age to become a marine biologist. After graduating
from New Bedford High School in 1976, he went off to college in
California to pursue his dream, and have a little fun.

He spent his freshman year at the University of Southern
California, decided this move was a great mistake, and transferred to
the University of California, Berkeley. There he thrived and grew in an
environment of innovation, brilliant thinkers, and diverse ideas and
values. After he graduated in 1980, he returned to Massachusetts and
the glamor of Woods Hole as part of the BUMP program. After a few false
starts, he finally settled on a thesis that satisfied his needs (and go
back to his roots?) to accomplish both basic and applied research. He
finished his degree after 7 1/2 years of hard work and mostly
independent funding and research.

Today Joe Costa is happily married to Maureen. They have a
wonderful dog named Skee, and they look forward to their future life,
many fishing trips, and family additions.