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).

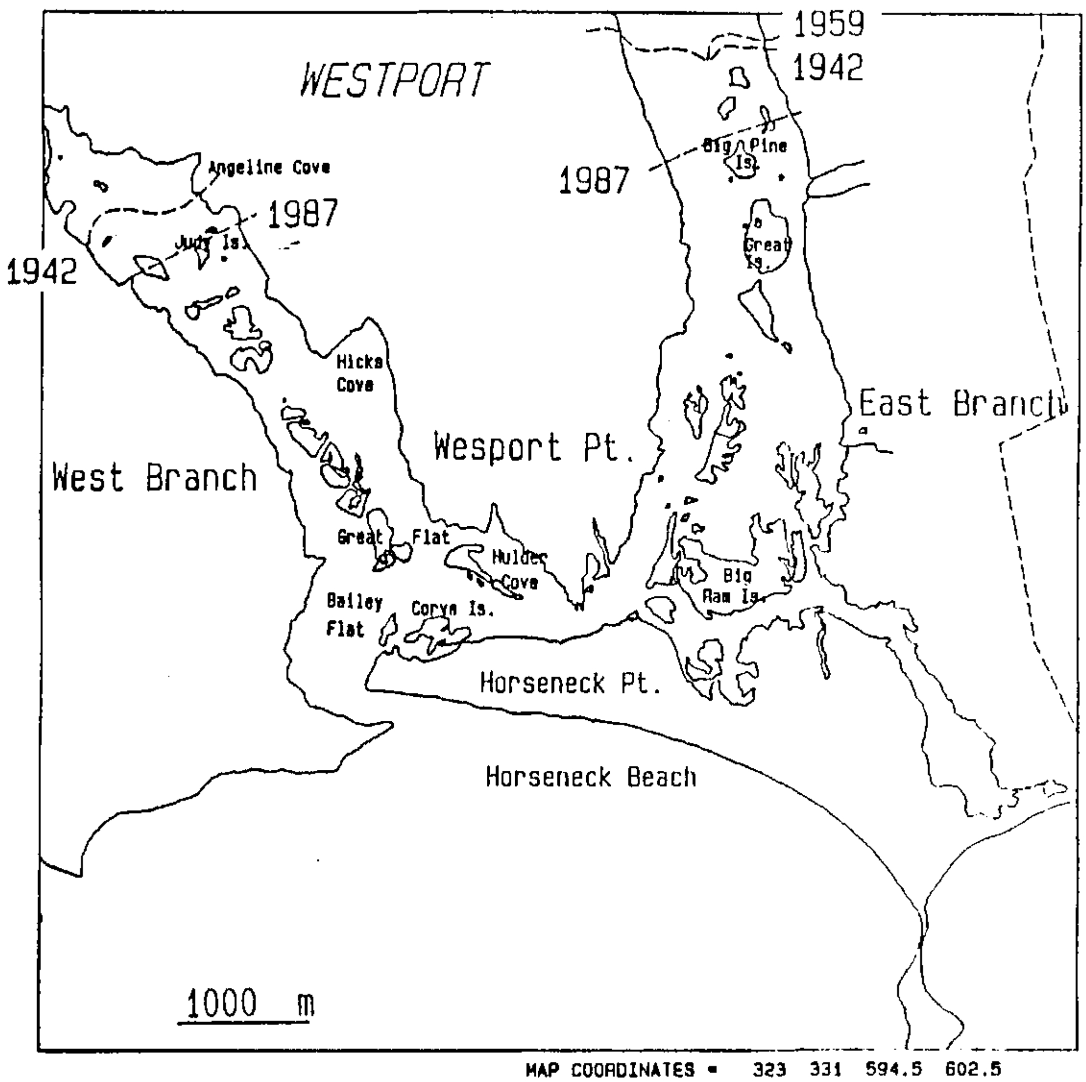
Most fresh water enters through the East Branch of the Westport River (Fig. 1). Riverine inputs into this Branch declined during the early 1960s because of construction of the Calamut dam and Intestate Highway 195. The mouth of the estuary is moderately well flushed and experiences a 0.9 m tidal range, 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.



1959
1942
WESTPORT
Angeline Cove
1987
Judy Is.
1942
Big Pine Is.
1987
Great Is.
Hicks Cove
East Branch
Wesport Pt.
West Branch
Great Flat
Hulder 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.

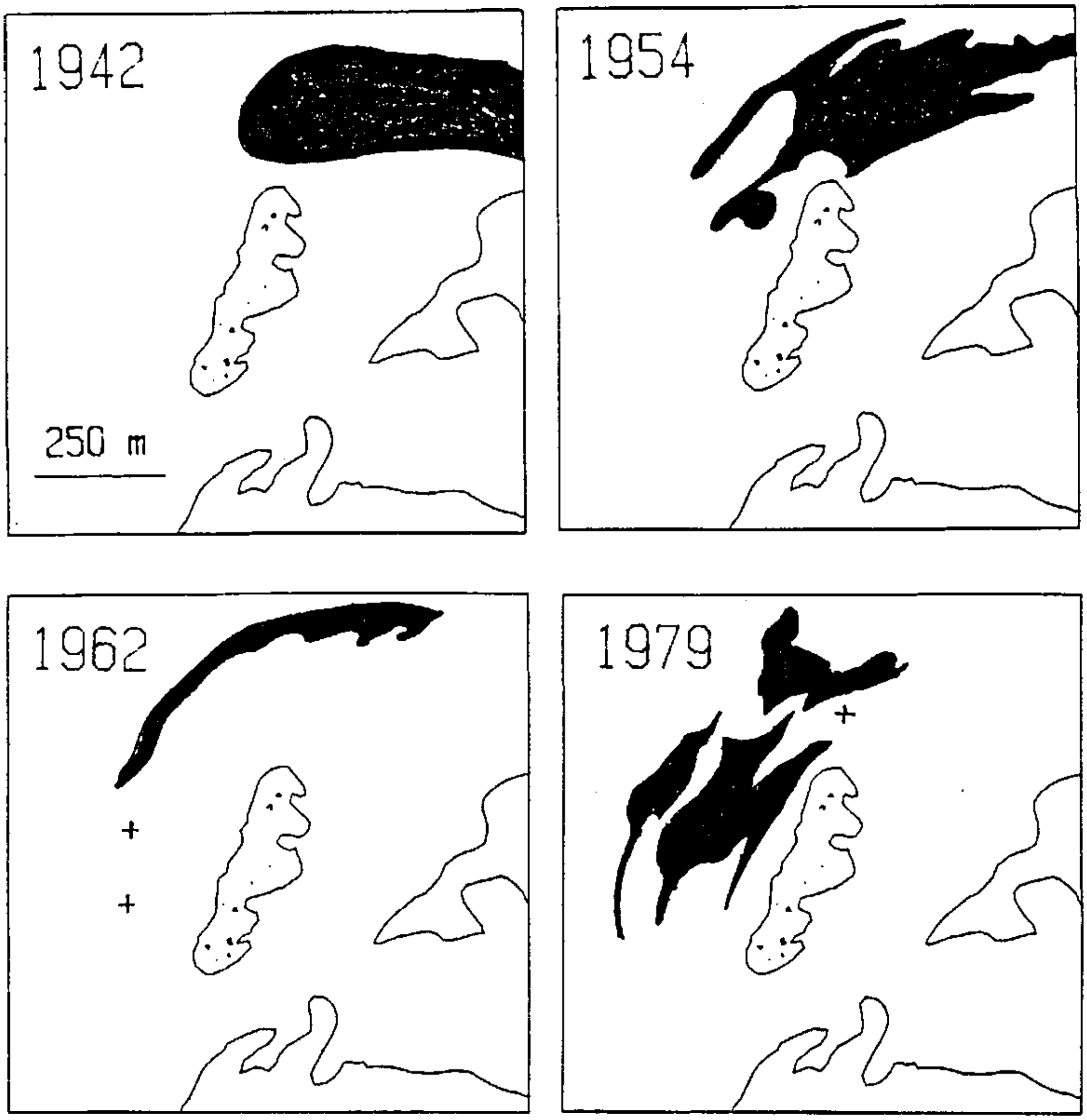
A September 1969 image has too much cloud cover to observe fine detail, but eelgrass is abundant north of Bailey Flat and appears to extend in the West Branch to Judy Island and in the East of Great Island. In November 1979, eelgrass distribution is abundant in the main channel at the bottom of the east 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.

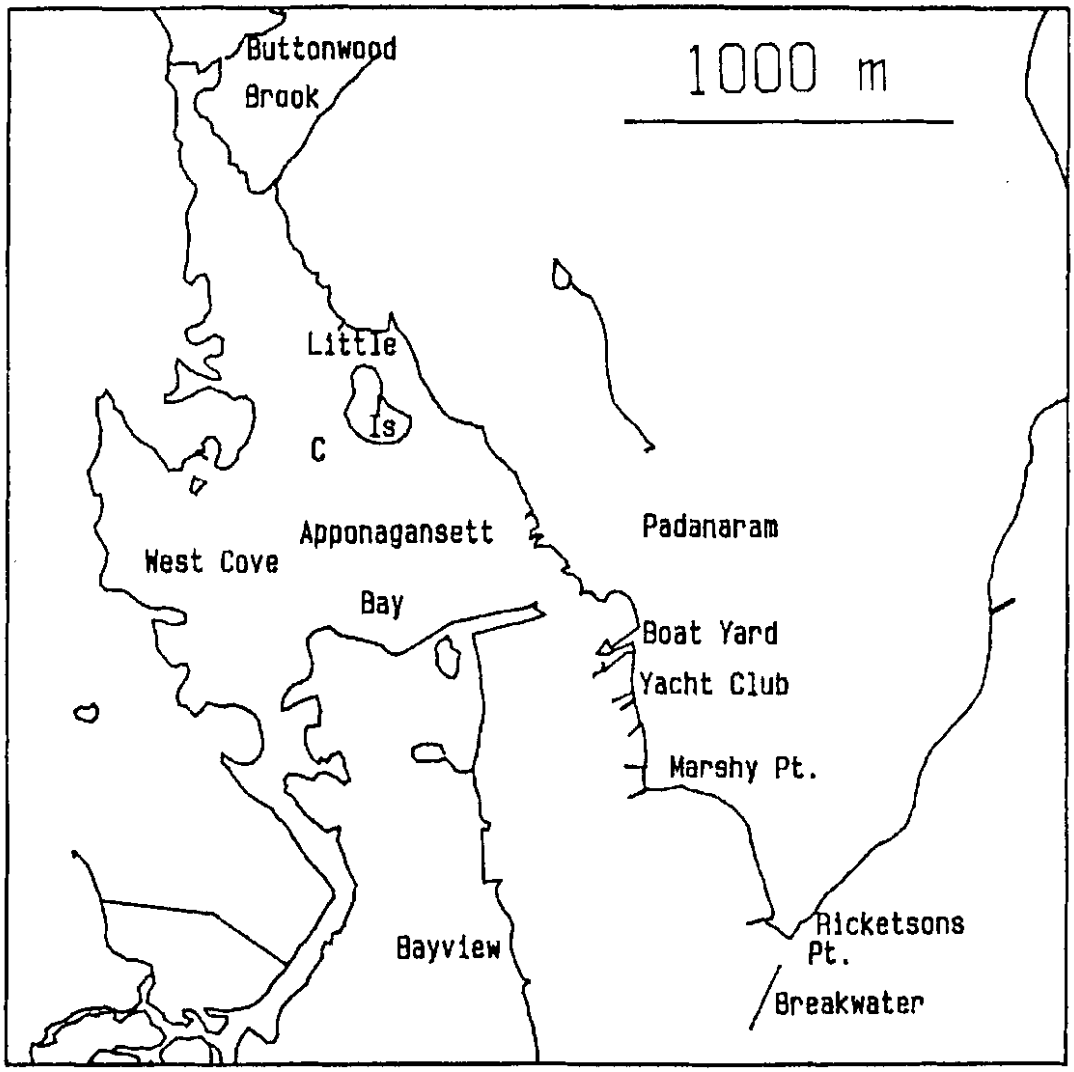
Given the importance of this estuary, a more comprehensive understanding of the changing eelgrass abundance there is desirable. Periodic photographic surveys should be taken under favorable conditions during several growing seasons, and damage from storms and ice scouring should be monitored. Historical 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'.



Buttonwood
Brook
1000 m
Little
Is
C
Apponagansett
West Cove
Bay
Padanaram
Boat Yard
Yacht Club
Marshy Pt.
Ricketsons
Pt.
Bayview
Breakwater

eastern shore is densely developed, and residences are serviced by septic tanks.

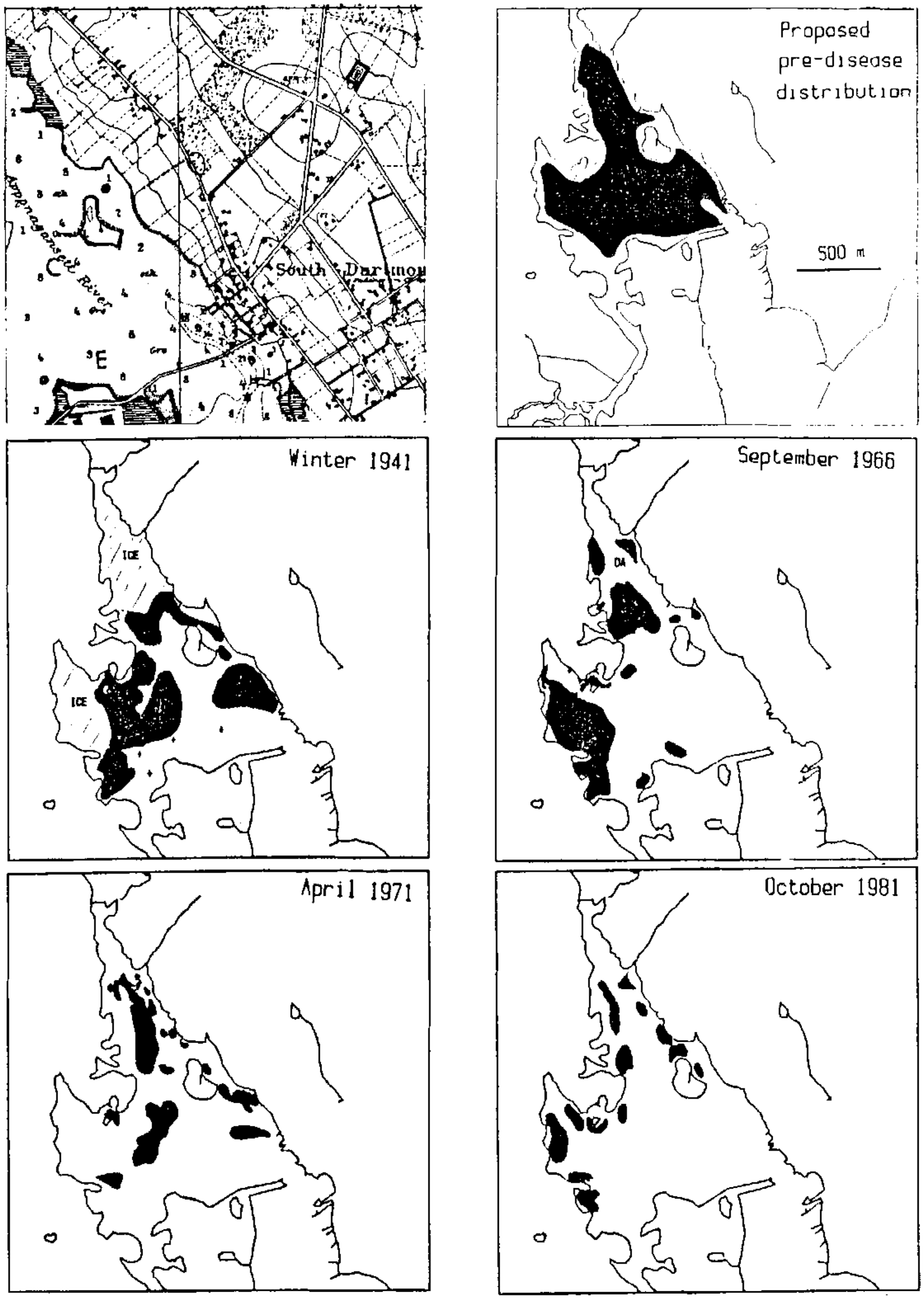
A sediment core taken 150 m west of Little Island (see chapter 3) and other historical documentation was suggest that eelgrass was abundant in the inner Bay for many years prior to the decline of the wasting disease. Afterwards. eelgrass began to recover with some major fluctuation during 1940-1960, 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.



South Dartmou
Apponagansett River
C
E
Proposed pre-disease distribution
500 m
Winter 1941
ICE
ICE
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.

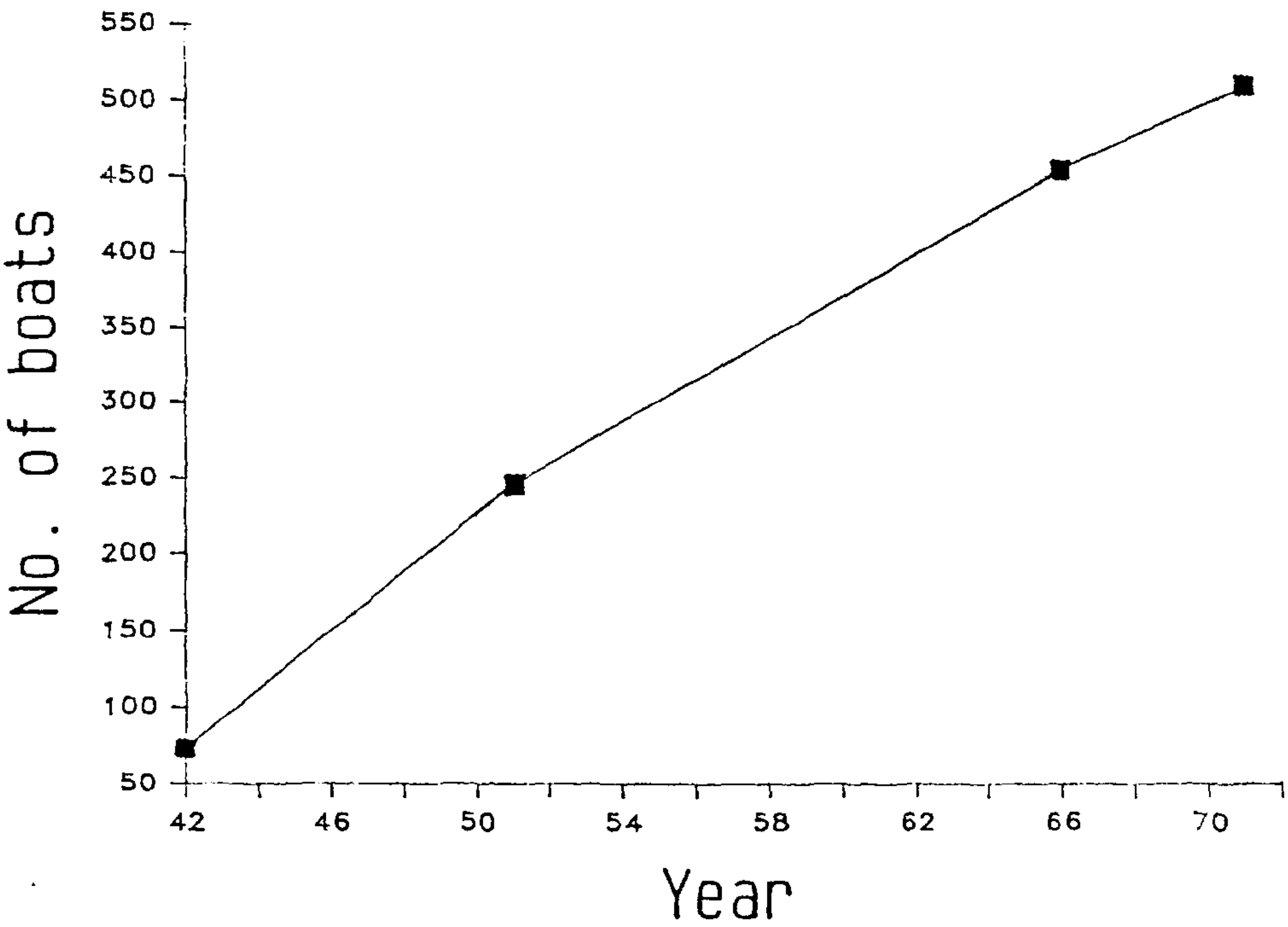
Boat traffic may also be contributing to decreased light availability to eelgrass because boat use has increased substantially in this bay in recent decades (Fig. 5). The inner bay has a shallow, muddy bottom, and power boats leave conspicuous plumes (pers. observ). This activity not only resuspends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


No. of boats
550
500
450
400
350
300
250
200
150
100
50
42
46
50
54
58
62
66
70
Year

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.

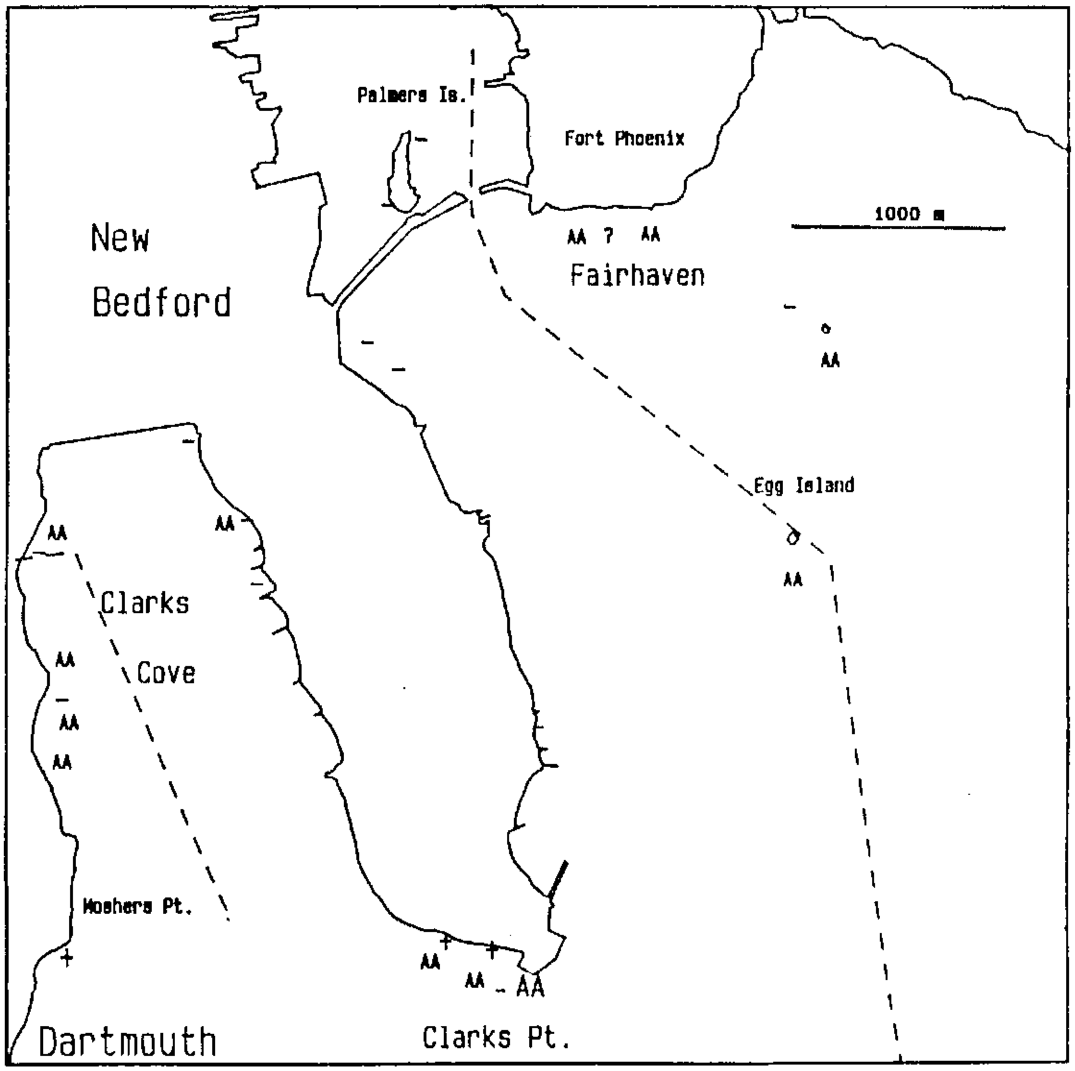
Even with these limitations, there are some areas where eelgrass is visible on aerial photographs during the 1950's or 60's, but no longer present today (Fig 6). Only in two areas (tip of Clarks Point, So of Moshers Point) did eelgrass abundance increase after 1966 (Fig. 6).

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.


Palmers Is.
Fort Phoenix
1000 m
New Bedford
AA ? AA
Fairhaven
AA
Egg Island
AA
AA
Clarks
Cove
AA
AA
AA
Moshers Pt.
AA
AA AA
Dartmouth
Clarks Pt.

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.

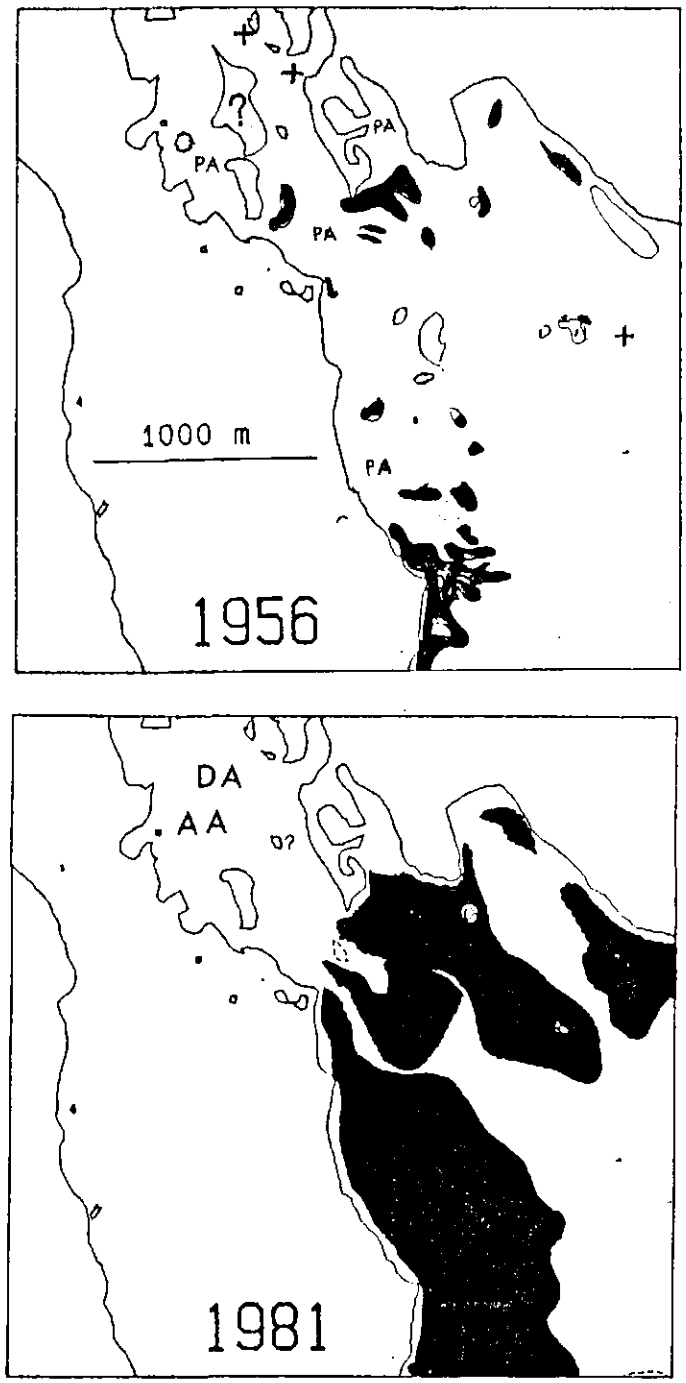
The earliest photographs (1951 and 1956) show that many populations of eelgrass are scattered around Nasketucket and Little Bays (Fig. 7). Some populations occurred up to 2 km offshore suggesting that refuge populations in deeper water survived the disease. The loss of eelgrass in Little Bay may be due 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.


?
PA
PA
PA
PA
1000 m
1956
DA
AA
D?
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.

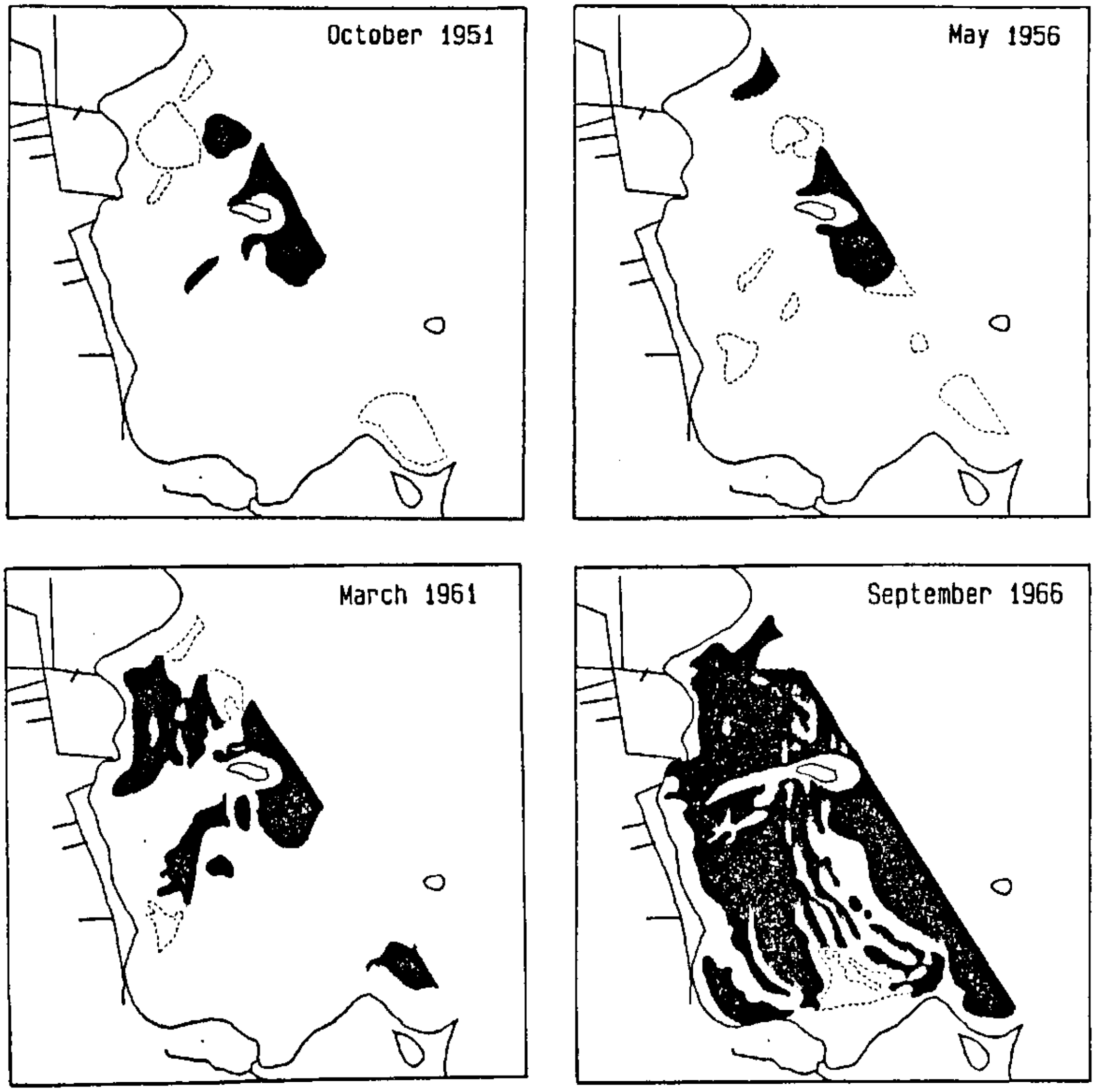
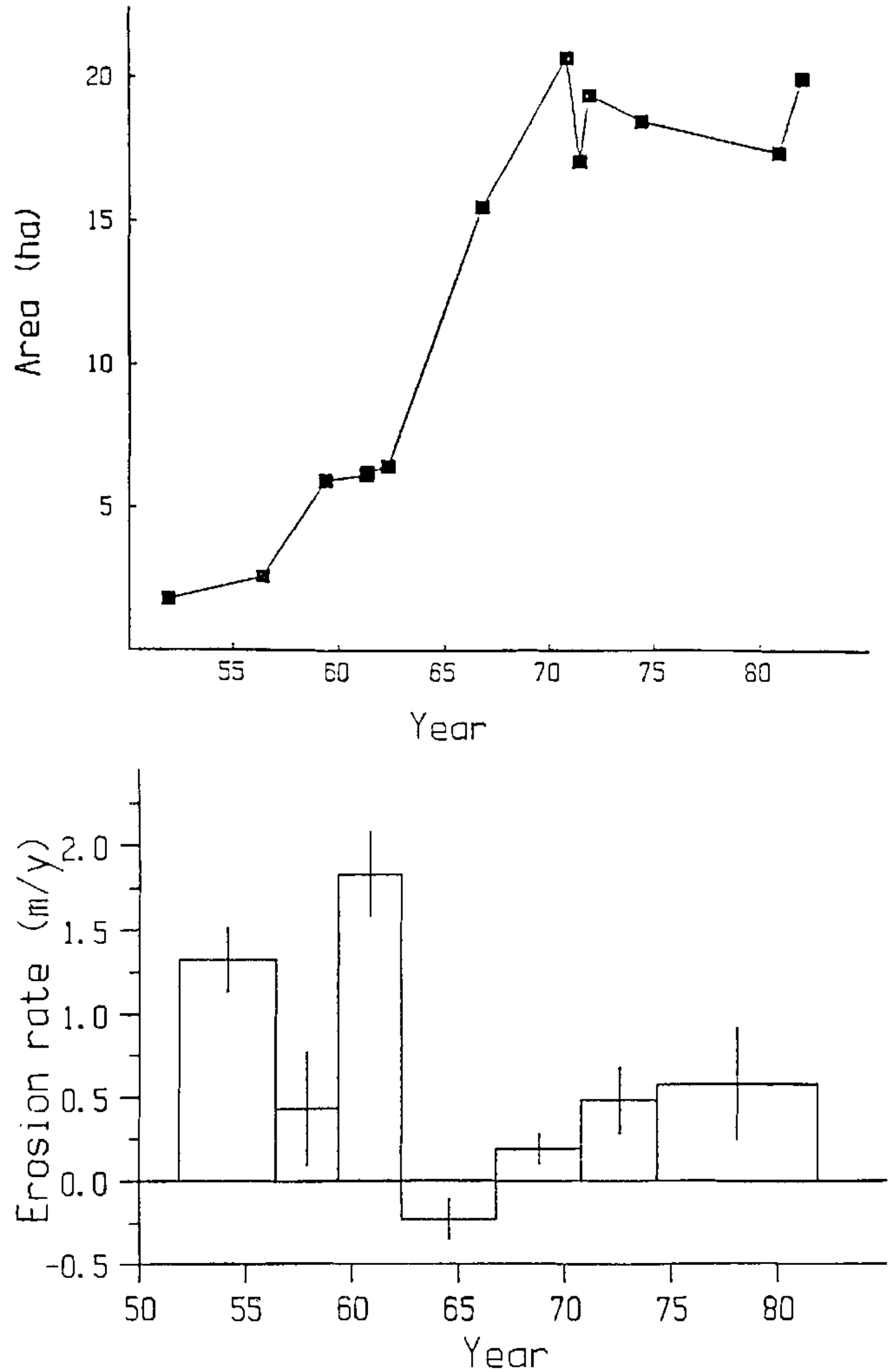

October 1951
May 1956
March 1961
September 1966

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.


Area (ha)
20
15
10
5
55
60
65
70
75
80
Year
Erosion rate (m/y)
2.0
1.5
1.0
0.5
0.0
-0.5
50
55
60
65
70
75
80
Year

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.

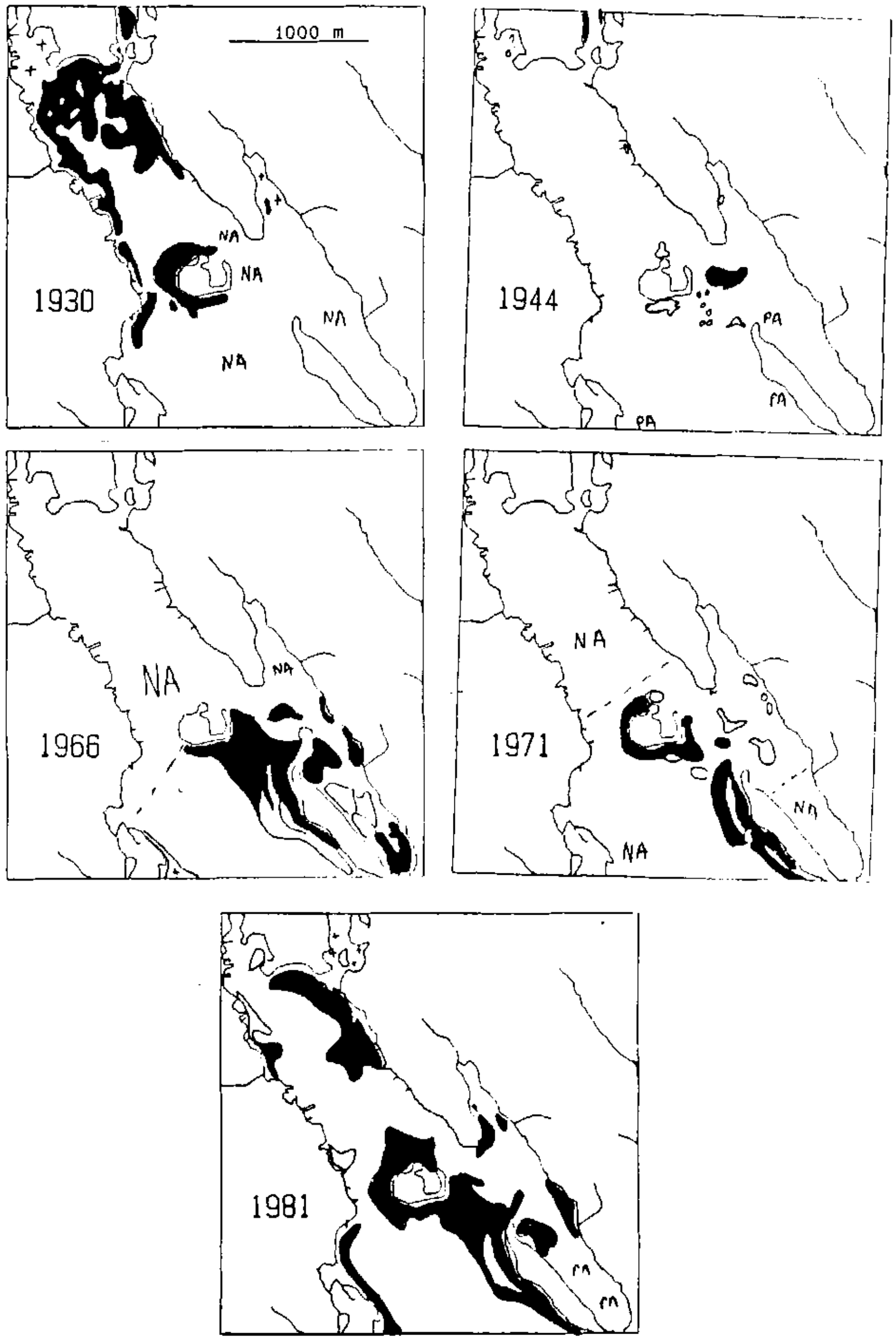
Sippican Harbor, Marion

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.


1000 m
1930
NA
NA
NA
NA
1944
PA
PA
PA
1966
NA
NA
1971
NA
NA
NA
1981

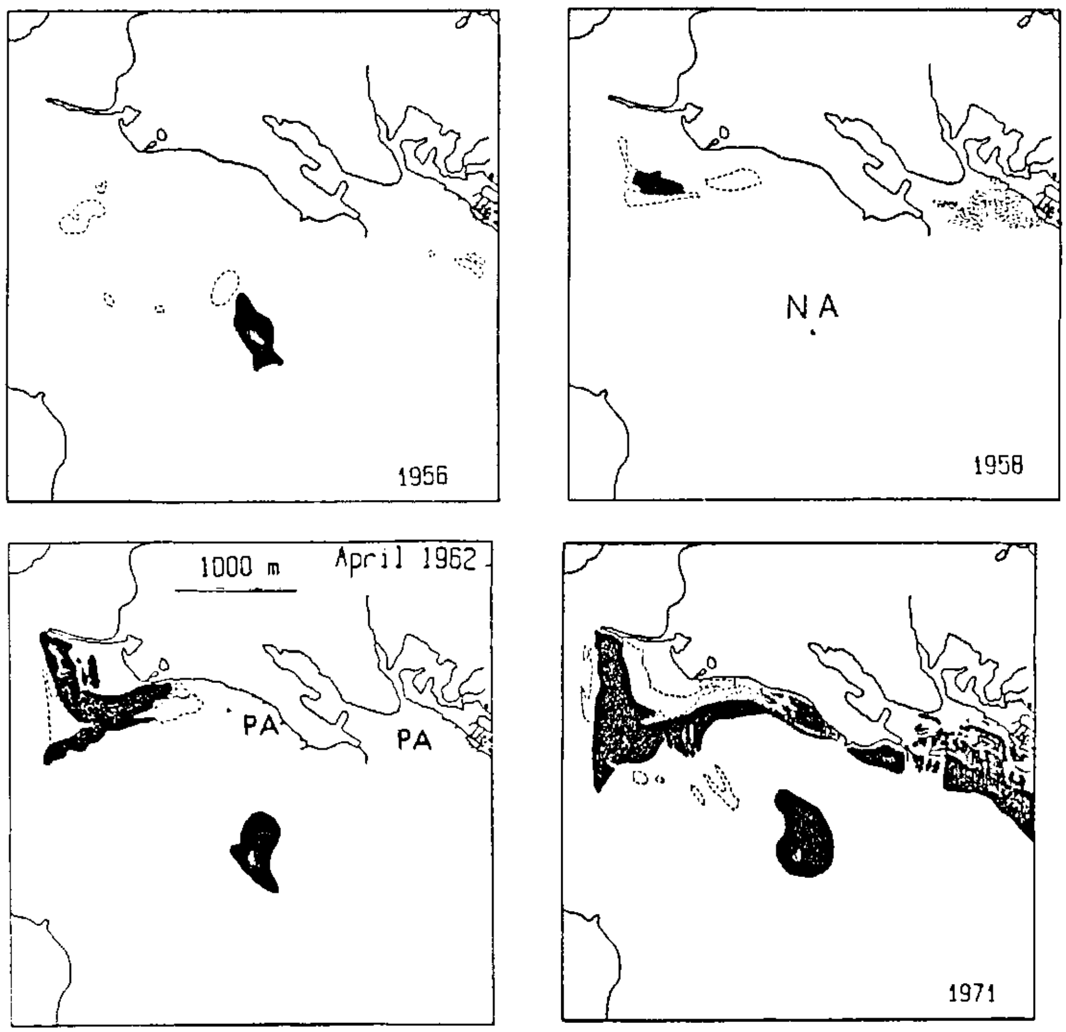
parts of the Harbor also suggest water quality problems. The large decline of eelgrass by Ram Island between 1966 and 1971 is more enigmatic because the central part of the Harbor is better flushed. This too may be the result of decreased light availability because of nutrient loading in the watershed. 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
N A
1958
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

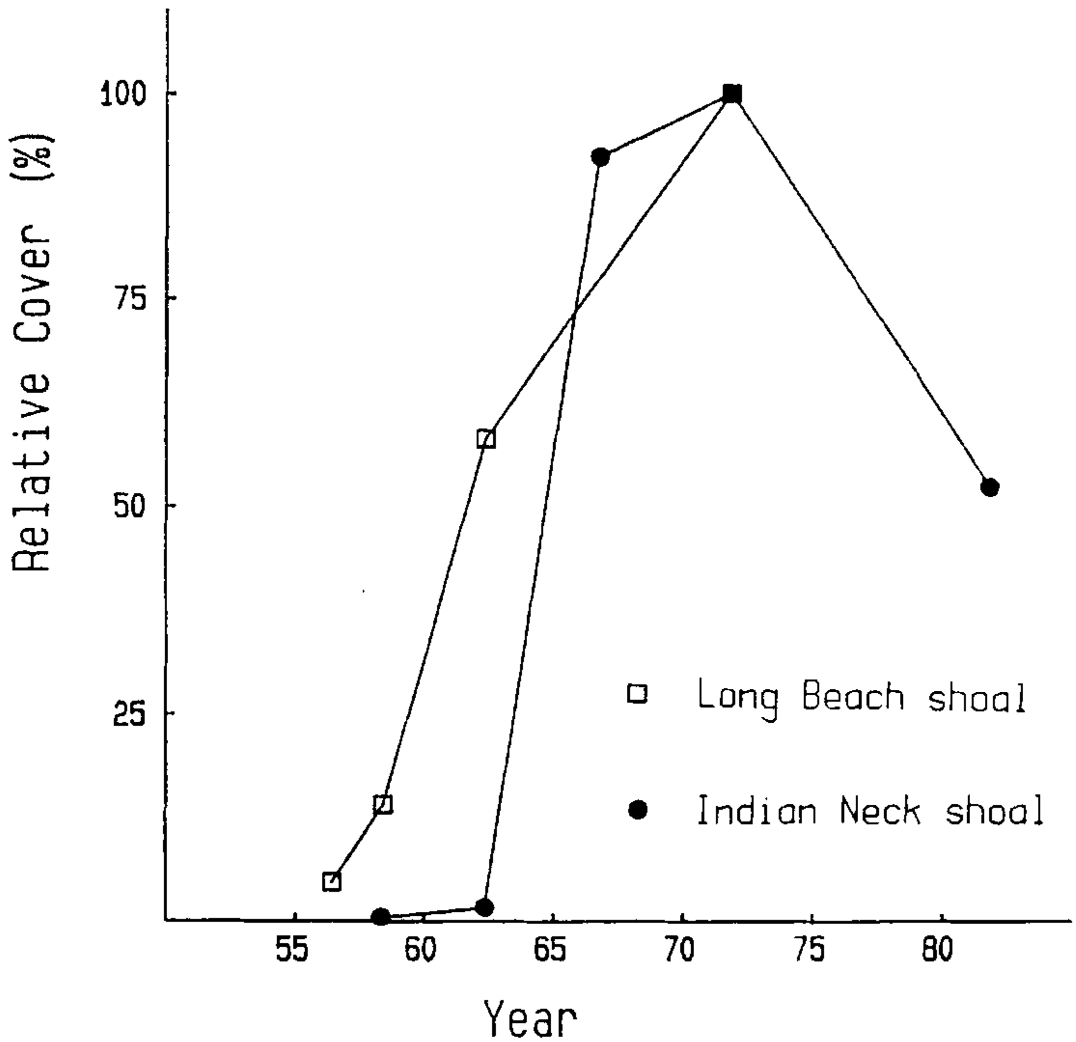
Buttermilk Bay is a protected embayment at the north end of Buzzards Bay, with an area of 200 ha, and a 1 m MLW mean depth. In recent years, Buttermilk Bay has become polluted from development in the surrounding watershed, and the Bay is now closed to shellfishing each summer. Nutrient loading in the 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.



Relative Cover (%)
100
75
50
25
55
60
65
70
75
80
Year
Long Beach shoal
Indian Neck shoal

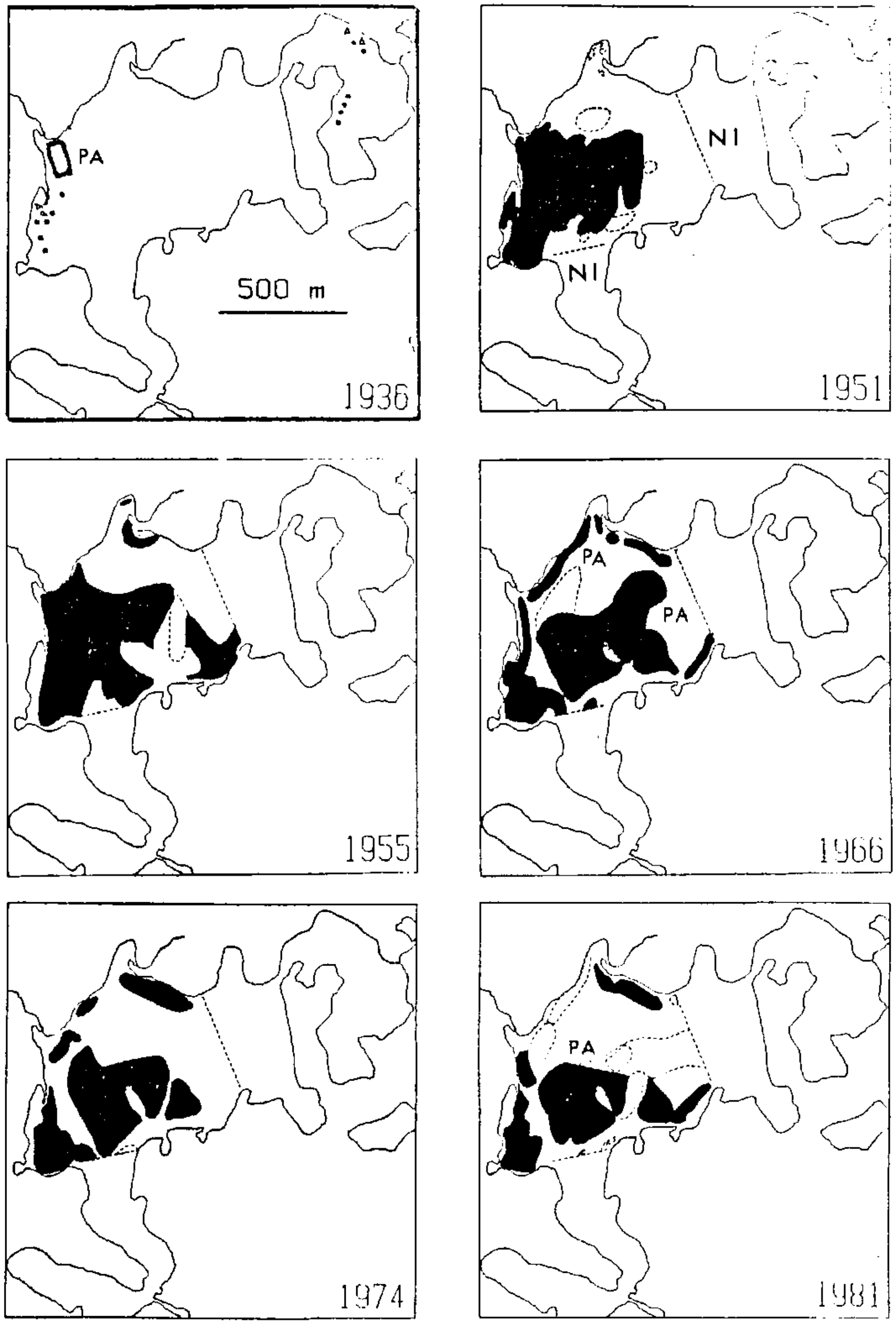
beds near fresh water inputs were refuge populations from the disease. He also noted that eelgrass first appeared in Little Buttermilk Bay along its most northern shore where no streams entered. It is apparent now that this area has large groundwater inputs (pers. obser., Moog, 1987), further supporting 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.


PA
500 m
1936
NI
NI
1951
1955
PA
PA
1966
1974
PA
1981

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.

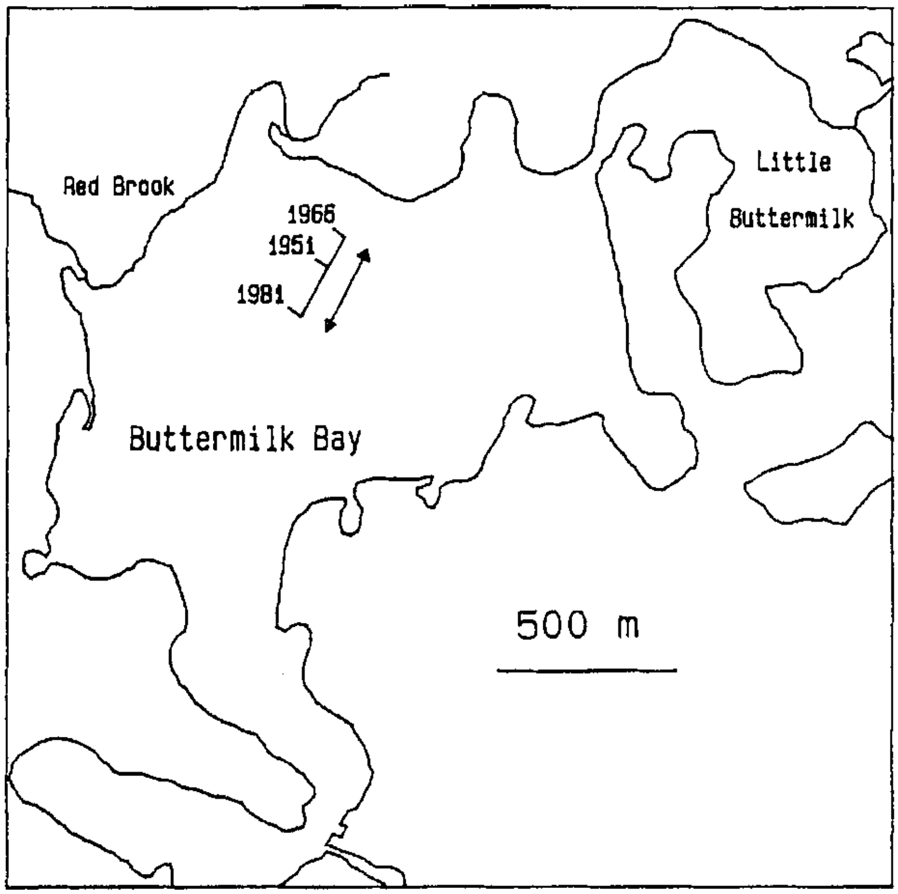
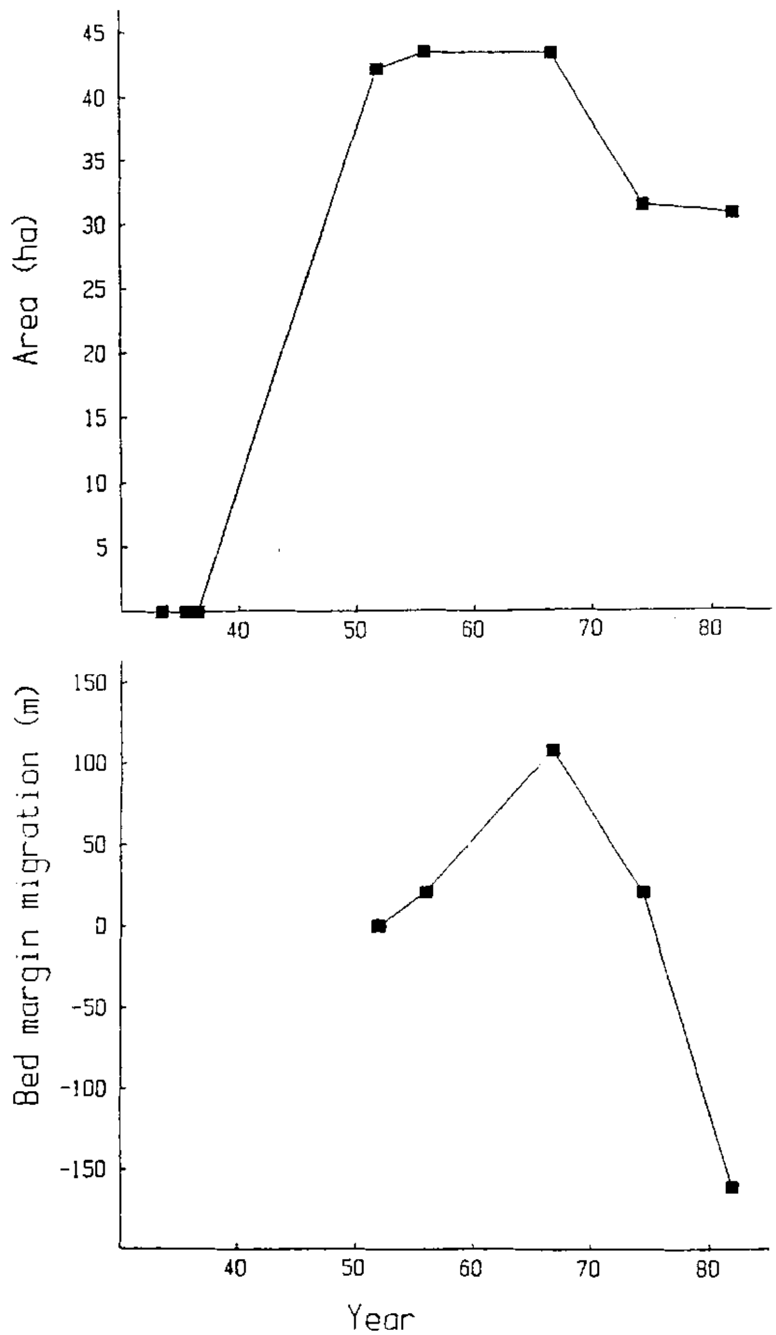

Red Brook
1966
1951
1981
Little
Buttermilk
Buttermilk Bay
500 m

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



Area (ha)
45
40
35
30
25
20
15
10
5
40
50
60
70
80
Bed margin migration (m)
150
100
50
0
-50
-100
-150
40
50
60
70
80
Year

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.

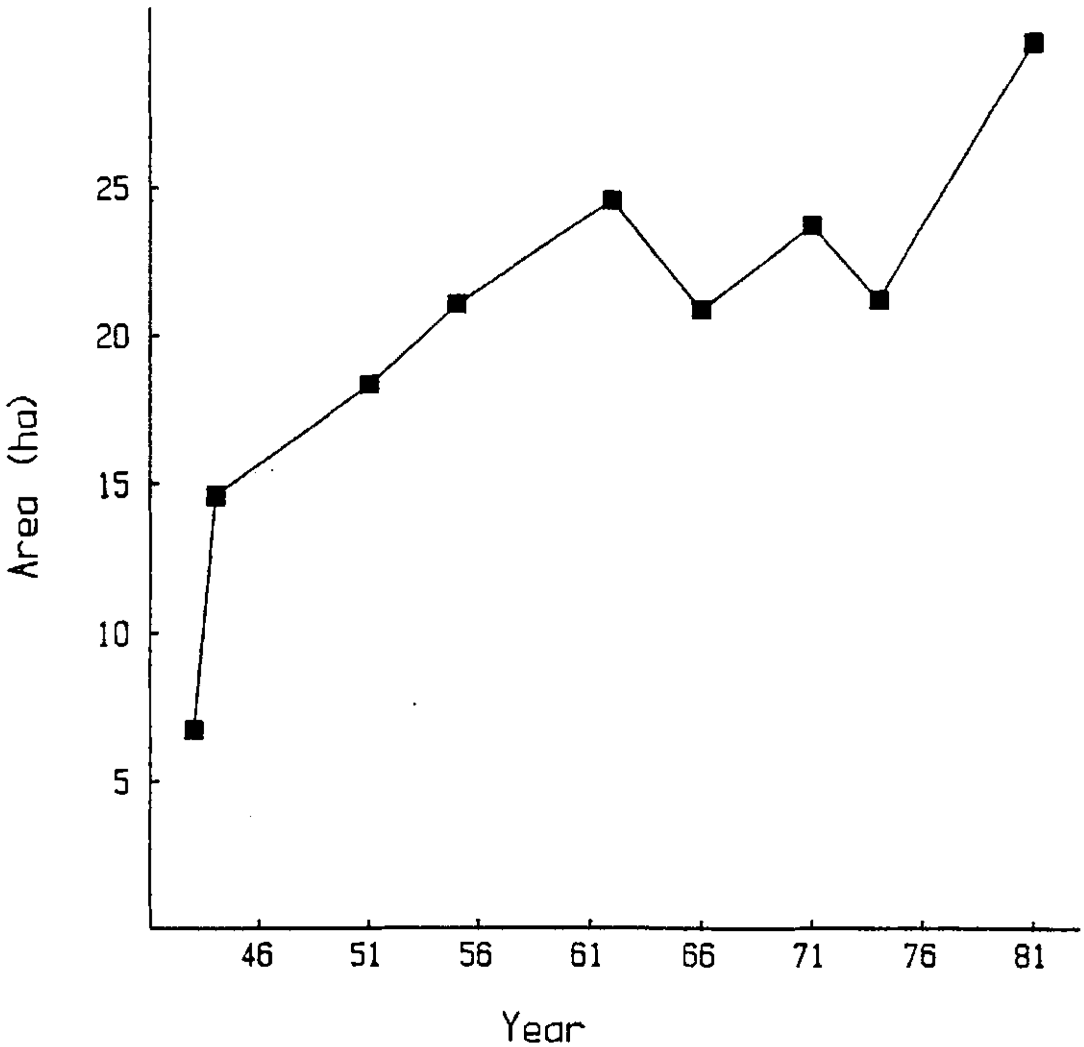
Megansett Harbor, Bourne and Falmouth

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.


25
20
15
10
5
Area (ha)
46
51
56
61
66
71
76
81
Year

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.

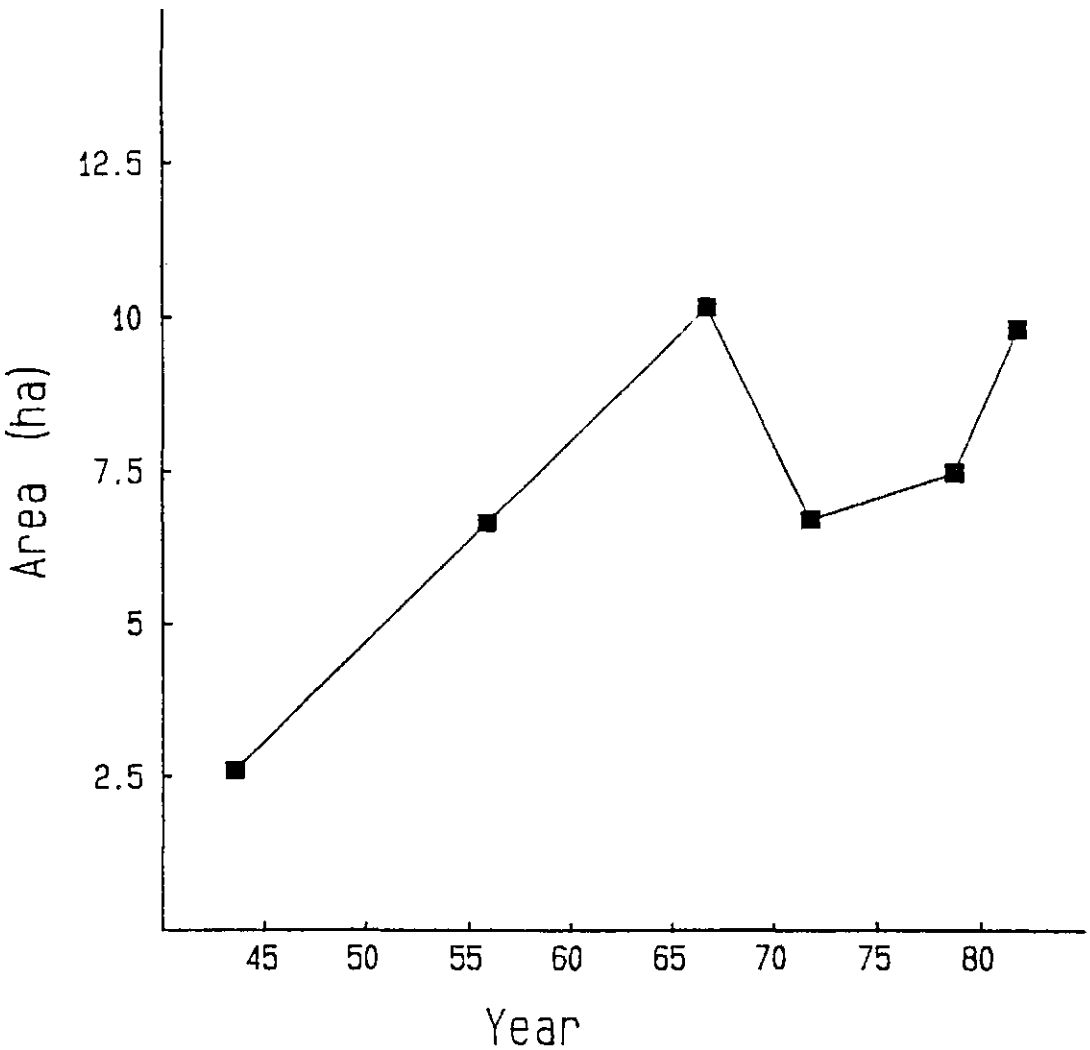

12.5
10
7.5
5
2.5
Area (ha)
45
50
55
60
65
70
75
80
Year

Figure 18. Eelgrass cover on the eastern shore of Waquoit Bay during four periods

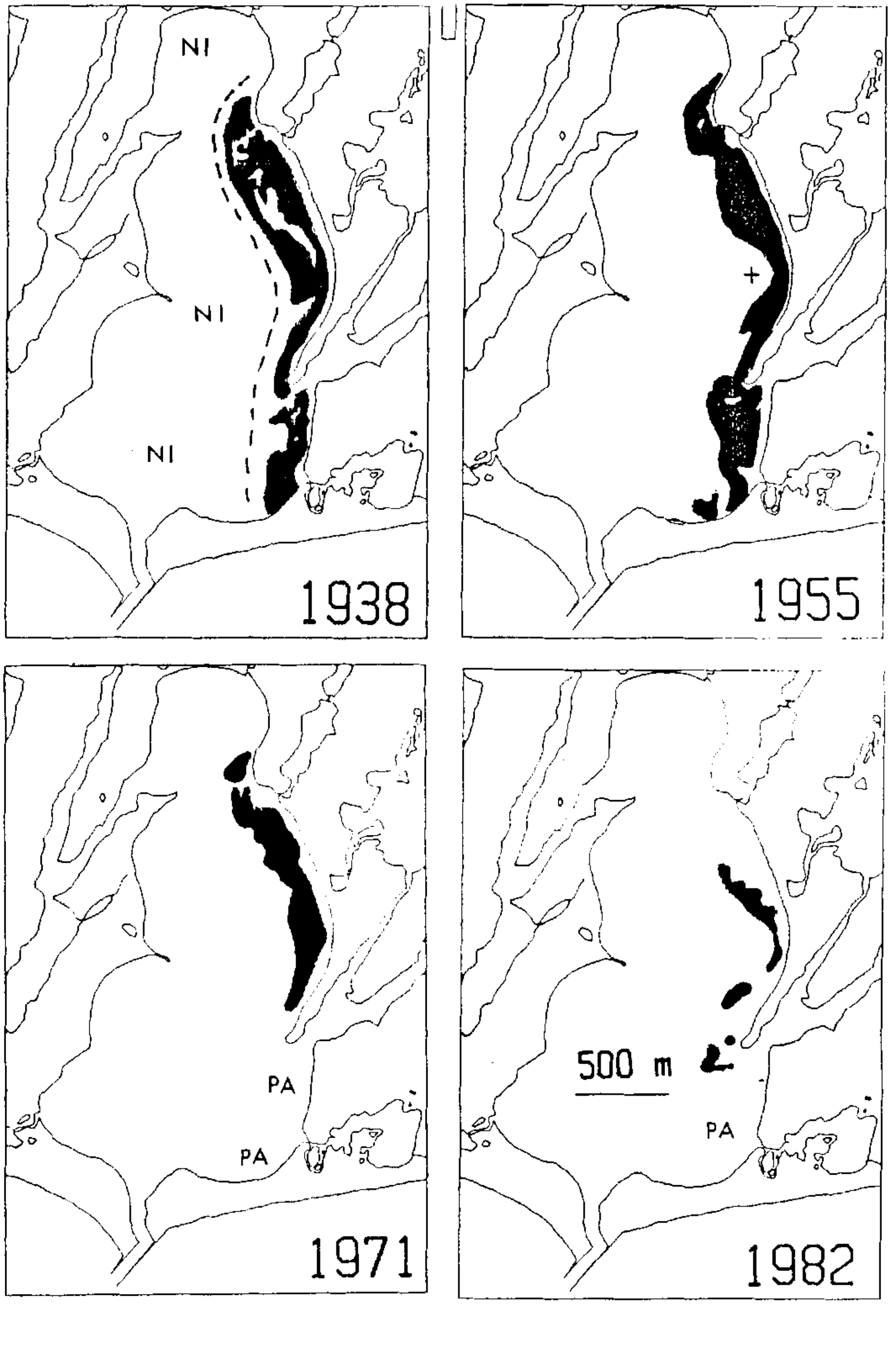
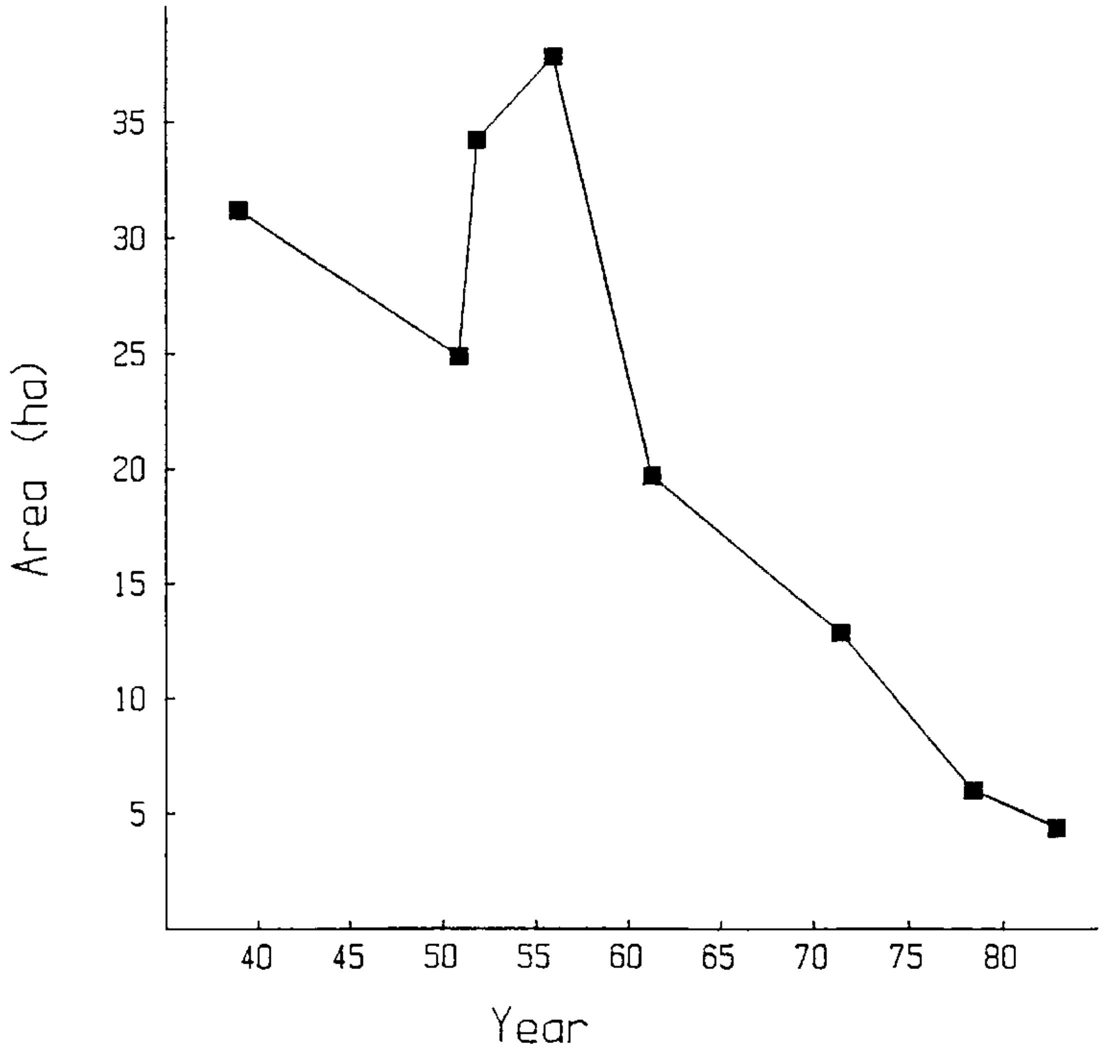

NI
NI
NI
1938
+
1955
PA
PA
1971
500 m
PA
1982

Figure 19. Eelgrass bed area in Waquoit Bay (adjusted for % cover) between 1938 and 1981.


Area (ha)
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
Year

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 ($r2= 0.62$, $\alpha > 0.05$). 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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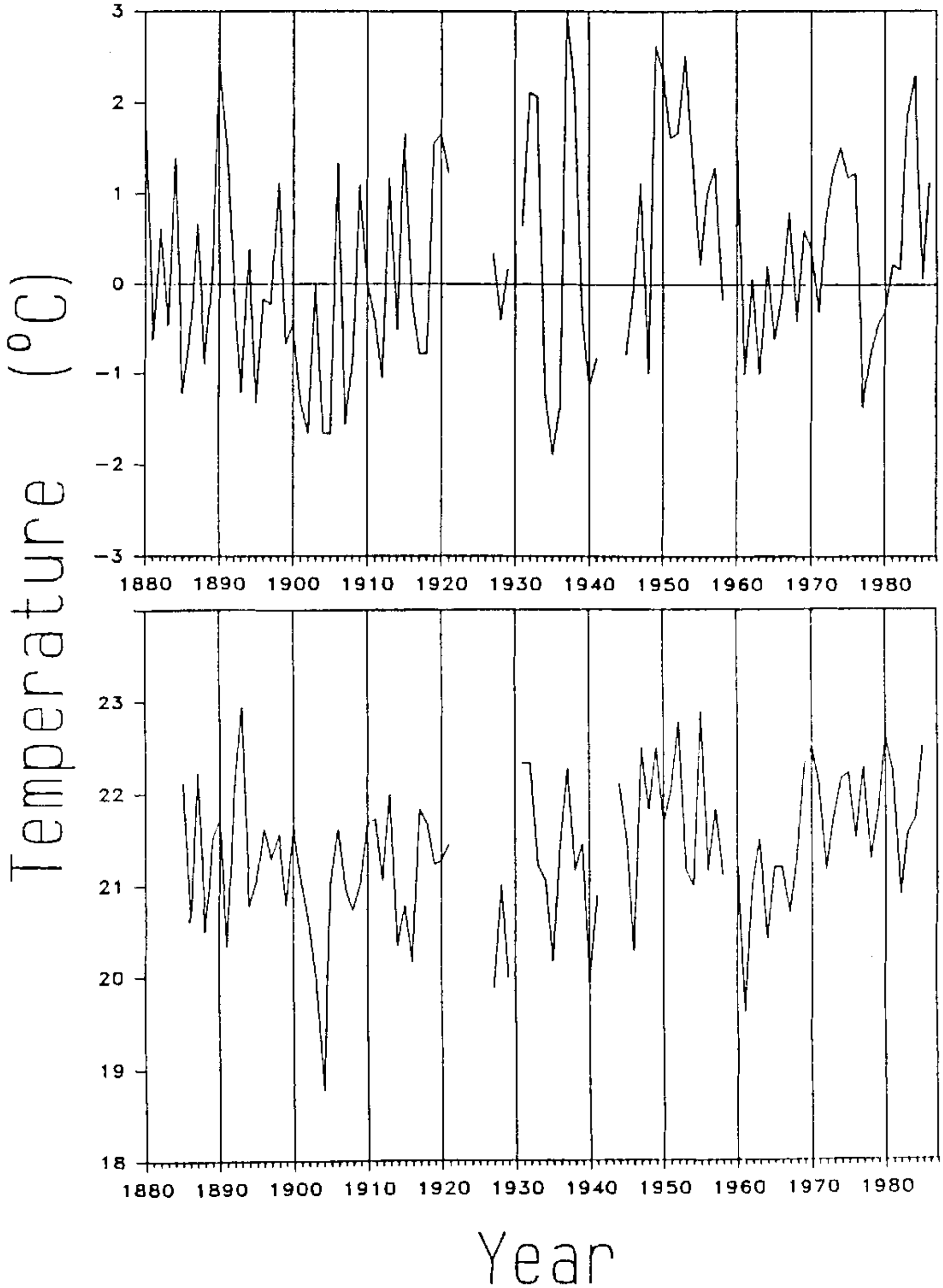
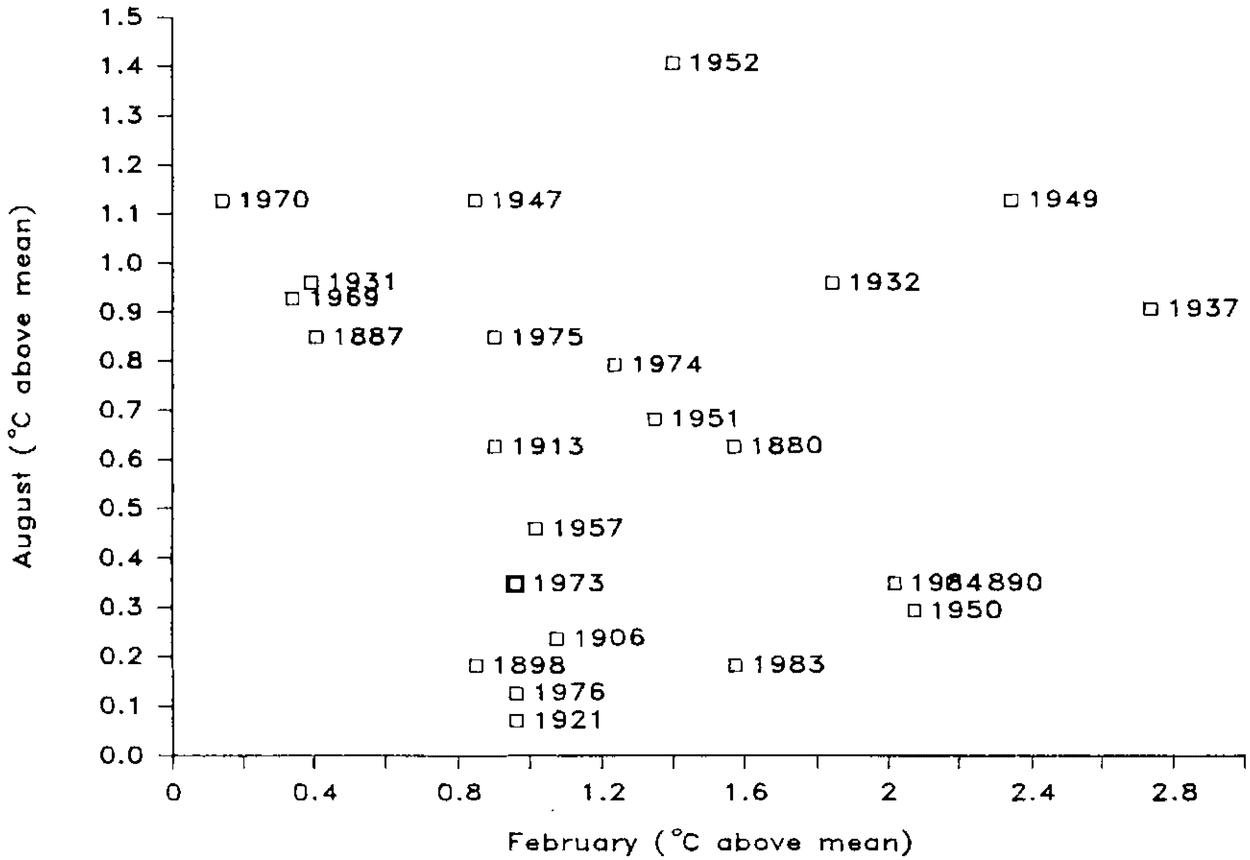
Top: Mean February temperature in Woods Hole: 1880-1986. Bottom: Mean August water temperatures in Woods Hole for the same period. Data 1931 was estimated (see text).



Temperature (°C)
3
2
1
0
-1
-2
-3
1880 1890 1900 1910 1920 1930 1940 1950 1960 1970 1980
23
22
21
20
19
18
1880 1890 1900 1910 1920 1930 1940 1950 1960 1970 1980
Year

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.


August (°C above mean)
February (°C above mean)
1.5
1.4
1.3
1.2
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
0
0.4
0.8
1.2
1.6
2
2.4
2.8
1952
1970
1947
1949
1931
1969
1932
1937
1887
1975
1974
1951
1913
1880
1957
1973
1984890
1950
1906
1898
1983
1976
1921

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.

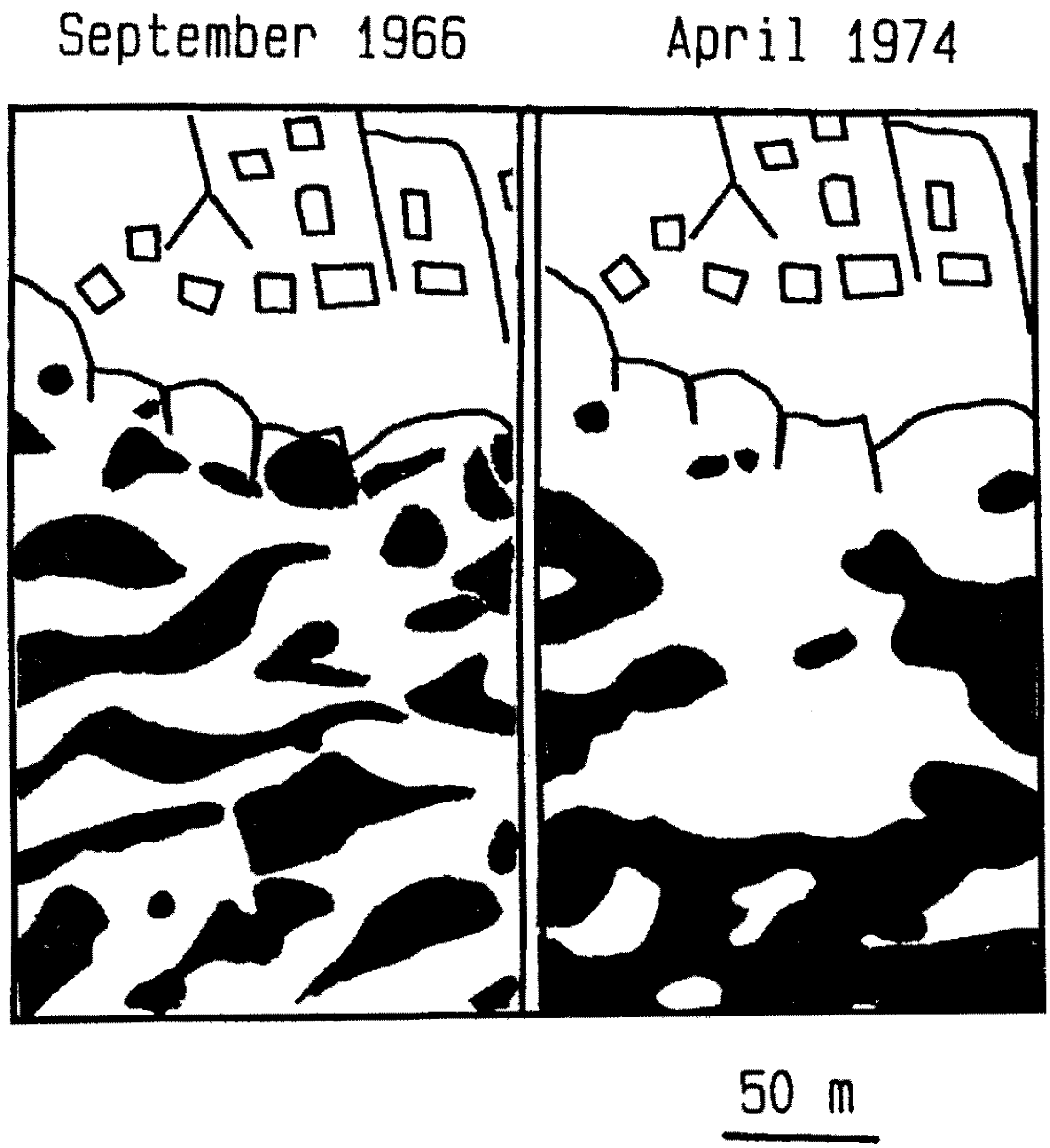
Around Buzzards Bay, once eelgrass began to colonize an area, the time to reach peak abundance varied markedly. On a small scale (below 10 ha) growth is typically logistic, and habitat is saturated in 8 to 15 years (Costa, 1988 and in prep.). In some locations, such as on the shallow shoal south of Little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