# ON THE BIOLOGY OF EELGRASS IN ALASKA

APPROVED:

Robert J. Barsdate

Donald W. Hood

Mary Belle Allen

Laurence Irving

John J. Goering
Chairman

D B Hawkins

APPROVED: ______________________ Date: ______________
Vice President for Research and Advanced Study

# ON THE BIOLOGY OF EELGRASS IN ALASKA

A

DISSERTATION

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C. Peter McRoy, B.S., M.S.

College, Alaska

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## Abstract

# ON THE BIOLOGY OF EELGRASS IN ALASKA

C. Peter McRoy, Ph.D.
Institute of Marine Science
University of Alaska, 1970

Supervisor: Dr. John J. Goering

A collection of essays is presented that are a contribution toward a biology of eelgrass (Zostera marina L.) in Alaska. Eelgrass is the most abundant seagrass on the coast of Alaska. The distribution of the plant in Alaska is disjunct and extends from Kotzebue Sound to the southern border of the state. The present circumboreal distribution is thought to be the result of dispersal from a west Pacific origin around the Pacific rim and through the Arctic into the Atlantic. Ten widely scattered eelgrass populations in Alaska have been sampled for quantitative comparison. The highest standing stocks (1510 g dry wt/m$^2$) were found in Kinzarof and Izembek lagoons on the Alaska Peninsula. The caloric content, chlorophyll a concentration, turion density, and leaf size varied greatly among the populations. The eelgrass in Safety Lagoon survives the arctic winter under one meter of sea ice in conditions of extremely low light intensity and anoxic water.

In chemical composition, eelgrass is similar to other angiosperms, but it also reflects adaptation to the marine environment. Trace elements are accumulated in the plant in proportion to their concentration in the sea. The roots as well as the leaves function as the sites for the uptake of phosphate. Using radioactive phosphate it was shown that phosphate was absorbed greatest in the light and transported throughout the plant; a portion of the phosphate removed from solution by the roots was lost across the leaves.

The metabolism of eelgrass in the dark is extremely dependent on temperature. Physiological differences exist between shallow water and deep water plants and between summer and winter plants. A depressed rate of respiration in winter is an adaptation enhancing survival in high latitudes.

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## Chapter 1.

# REVIEW OF ECOLOGICAL RESEARCH ON EELGRASS

## Introduction

There are no cornfields in the sea; the great monospecific terrestrial crops have no parallel in the marine environment. The one group of marine macrophytes most resembling a terrestrial crop is the seagrasses. The seagrasses are a taxon of submerged, flowering vascular plants that consists of some 45 species, many forming expansive meadows in shallow marine waters. The most important of the three species of seagrasses occurring in Alaska is *Zostera marina*, eelgrass. Eelgrass is a primary food item for many species of waterfowl and marine organisms and has been the basis of certain industries in Europe and Canada.

Eelgrass communities occupy shallow coastal embayments and estuaries of the Northern Hemisphere from the north coast of the Mediterranean Sea to Arctic Alaska. In spite of this widespread distribution and accessibility, eelgrass and the other species of marine flowering plants in the world have been largely ignored by ecologists. One of the more studied seagrasses, in terms of modern ecological methods, is the turtle grass (*Thalassia testudinum*) community off the coasts of Florida and Texas (Odum, 1967).

## Past Research on Eelgrass and Related Species

Eelgrass has long been known in Europe and America as a food for several waterfowl species, especially brant (Butcher, 1941; Yocom, 1951). In early investigations at the Danish Biological Station, eelgrass in coastal waters was found to be the principal contributor of organic matter to the food webs of commercial fishery species (Boysen-Jensen, 1914). On the coast of British Columbia, eelgrass leaves are a substrate for the attachment of herring spawn (Outram, 1961). In addition, dried eelgrass has been the basis of mattress and furniture stuffing and housing insulation industries in Great Britain, France, Holland, and Canada (Scagel, 1961).

Most of the industries based on eelgrass ended during the wasting disease period of 1931-32 when the species nearly disappeared from the Atlantic coast of North America and Europe (Cottam, 1933). This destruction caused severe declines in numerous other species, including waterfowl, fish, and shellfish (Cottam, 1934; Dexter, 1944; Wood, 1965).

The disappearance of eelgrass was attributed to many forms of pollution (Butcher, 1941), but the cause of the wasting disease was considered by most to be the myxomycete Labyrinthula sp. (Renn, 1936). The question, however, remains disputed and Johnson and Sparrow (1961) stated that the evidence is not unequivocal that Labyrinthula sp. was the culprit. There have been two recent reports of similar eelgrass depletions, from New Zealand (Armiger, 1964) and the White Sea (Zenkevitch, 1963).

The shallow, protected bays, lagoons, and estuaries required for eelgrass growth are the regions of the coast destined to receive the most pollution (Føyn, 1965). In addition, parts of the California coast are experiencing a conflict between eelgrass and recreation in shallow bays (Waddell, 1964). Studies have shown that eelgrass and benthic algae effectively concentrate radioactive isotopes to hazardous levels (Williams et al., 1965; Gutnecht, 1965). In Alaska, some eelgrass populations in shallow water in Prince William Sound were destroyed by the earthquake of March 1964 (Johansen, 1965).

Most of the studies of eelgrass communities have been limited to surveys of standing stock (Grøntved, 1958; Keller, 1963; Moeller, 1964; Vozzhinskaya, 1964); only in a few cases has ecological information been sought. The literature has been compiled by Phillips (1964) and McRoy and Phillips (1968). Conover (1958) noted the influence of benthic plants, including eelgrass, on nitrogen and phosphorus concentrations. In another study, Conover (1961) related the dissolved oxygen concentration to the attached vegetation in coastal ponds; Broekhuysen (1935) found that eelgrass meadows could become anoxic during summer nights. Indirect information was provided by the fertilization experiments of Marshall and Orr (1948), who found that fertilizing a sea loch did not increase the phytoplankton but that eelgrass flourished. Also Walsh (1965) measured high concentrations of dissolved carbohydrates in lagoons with dense eelgrass populations.

A recent study of a salt marsh environment showed considerable diurnal and seasonal variations in pH, oxygen, water temperature, and salinity that were in part directly attributable to plant metabolism; oxygen saturation ranged from 0 to 275 per cent and pH from 6.7 to 8.5 (Phleger and Bradshaw, 1966). Other studies of benthic marine communities in shallow water have reiterated the fact that these are highly dynamic systems that exhibit large diurnal and seasonal fluctuations in metabolism and in cycles of organic matter and nutrients (Bruce and Hood, 1959; Odum and Wilson, 1962; Putnam, 1966; Pamatmat, 1966).

After examining eelgrass from the Atlantic and Pacific coasts of Europe and North America, Setchell (1929) found that growth and morphology were directly related to temperature. Arasaki (1950) concurred for his studies in Japan. In Alaska, investigation has also suggested that temperature is of prime importance to the growth and morphology of eelgrass and may even offer an explanation of the wasting disease (McRoy, 1966).

Recent research in the region of the western Alaska Peninsula indicates that the eelgrass communities can contribute a substantial amount of organic material to food webs of species such as king crab, halibut, sea otter, and harbor seals found in the area (McRoy, 1966). The evidence is increasing that a substantial amount of the organic matter available to off-shore benthic communities results from advective processes rather than from production in the euphotic zone (Menzel and Goering, 1966; Sorokin, 1966).

## Studies of Eelgrass in Izembek Lagoon

A study of the ecology of eelgrass, *Zostera marina*, was initiated in 1963 in Izembek Lagoon, Alaska by the Aleutian Islands National Wildlife Refuge, Bureau of Sport Fisheries and Wildlife, U. S. Fish and Wildlife Service. This study was principally concerned with the quantitative estimation and distribution of the standing stock and the ecology of the plant (McRoy, 1966). Izembek Lagoon was selected as the study site because of its large eelgrass population near laboratory facilities in Cold Bay and because it is the principal migratory feeding area in western Alaska for many species of waterfowl (Einarsen, 1965).

Izembek Lagoon is a shallow embayment of the Bering Sea on the Alaska Peninsula that contains a well-developed system of tide channels and flats. A large portion of the tide flats supports eelgrass meadows that become large pools during slack tide. Hydrographically the lagoon can be classed as marine. Dilution is slight and limited to areas near streams. The mean tidal range is 1 m; the volume of the tidal prism is estimated to be 67% of the total. Ocean water entering the lagoon is altered principally with respect to temperature and oxygen saturation.

The total crop of eelgrass in the lagoon is on the order of $2.3 \times 10^6$ metric tons fresh weight, the largest reported single stand of eelgrass. The statistical analysis of the standing stock for characters of biomass, plant size, density, chlorophyll _a_ concentration, and productivity indicated three types of eelgrass beds--subtidal, deep tide pools, and shallow tide pools. The stratification of the eelgrass beds is related to water temperatures.

The average net production of eelgrass in Izembek Lagoon is estimated to be 8 to 9 g dry wt/$m^2$-day; this rate results in an annual yield of about 10 metric tons fresh weight per hectare, a quantity that compares favorably with many terrestrial crops.

A large amount of detached eelgrass leaves is transported out of the lagoon each autumn and deposited offshore. This organic matter could be important to numerous benthic species. The numbers of benthic-feeding organisms, such as king crab, halibut, and sea otter, that congregate in the ocean surrounding the lagoon support this.

## Current Research

Research on eelgrass since the termination of the original Izembek study has proceeded along several lines. Work has expanded from Izembek Lagoon to a survey of the eelgrass populations on the coast of Alaska. Initially this was a detailed examination of the distribution in Alaska (Chapter 4). Subsequently it was possible to visit several geographically divergent parts of Alaska to quantitatively examine the eelgrass populations and associated ecological conditions (Chapters 5 and 6).

The original study at Izembek suggested that temperature played a leading role in the ecology of eelgrass. This initiated a detailed investigation of temperature in the environment and its role in the physiological ecology of the plant (Chapter 8). Another question concerning physiological ecology that arose in studies of nutrient cycling in Izembek Lagoon was whether eelgrass absorbed nutrients through the leaves from ambient water or through the roots from the sediment. The results of this study are presented in Chapter 7.

Additional chapters are compilations of the chemical composition of eelgrass from a variety of sources (Chapter 3) and a summary of the life history with a detailed description of Alaskan eelgrass (Chapter 2). The final chapter synthesizes these studies into the general picture of eelgrass ecology.

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# Chapter 2.

# CHARACTERISTICS OF EELGRASS TAXONOMY AND GROWTH

## Phylogenetic Affinities

*Zostera marina*, eelgrass, is one of the commonest seagrasses in coastal waters and is one of some 45 species of seagrasses (Dawson, 1966). The seagrasses, a group of marine spermatophytes, constitute two closely related families of aquatic plants, the Hydrocharitaceae and the Potamogetonaceae. The Hydrocharitaceae includes the seagrass genera *Thalassia*, *Halophila*, and *Enhalus*. The Potamogetonaceae includes the seagrass genera *Zostera*, *Phyllospadix*, *Ruppia*, *Posidonia*, *Halodule* (*Diplanthera*), *Cymodocea*, *Syringodium*, and *Amphibolis*. The Potamogetonaceae also includes a large number of the species of freshwater aquatic plants. These families are the monocotyledonous plants, the large subdivision of angiosperms that includes the grasses, sedges, lillies, and many others.

Most of the seagrasses are confined to the tropics. Centers of distribution of seagrass species are the Indo-West Pacific and the Caribbean Sea (Dawson, 1966). About 75% of the species grow only on the coasts of Eur-Asia and northern Africa. Few seagrasses have colonized the western coasts of Africa and South America.

Seven genera of seagrasses are represented in the coastal waters of North America (Table 1). In these genera are 13 species, 9 of which are tropical. The genus *Zostera* consists of 11 species: 6 occurring in the northern hemisphere and 5 in the southern hemisphere (Setchell, 1933). In North America there is but one species, *Zostera marina*. This extremely widespread species is found from Hudson Bay to Cape Hatteras on the Atlantic coast (Cottam, 1935) and from Kotzebue

Table 1. Seagrass genera in North America (from Dawson, 1966).

| Genus | Number of Species in North America | Distribution |
|---|---|---|
| Thalassia | 1 | Tropical Atlantic |
| Halophila | 3 | Tropical Atlantic and Pacific |
| Halodule | 4 | Tropical Atlantic and Pacific |
| Syringodium | 1 | Tropical Atlantic |
| Phyllospadix | 2 | Temperate Pacific |
| Ruppia | 1 | Temperate Atlantic and Pacific |
| Zostera | 1 | Temperate Atlantic and Pacific |

Sound to the Gulf of California on the Pacific coast (McRoy, 1968). In world distribution, eelgrass is circumboreal and grows on both sides of the North Pacific Ocean, the north shore of the Mediterranean, the Black Sea coast, both sides of the North Atlantic Ocean, and in isolated bays in the marginal seas of the Arctic Ocean (Setchell, 1935; Zenkevitch, 1963).

## Morphology

*Zostera marina* as a flowering vascular plant has all of the structures typical of flowering plants (Fig. 1). In most cases these structures have been modified as a result of the marine habitat of the plant. Eelgrass has two types of stems, a perennial, vegetative stem that is a prostrate, rooting rhizome and an annual reproductive or flowering stem that is an erect branch of a prostrate rhizome.

The leaves of eelgrass are long and thin. In Alaska, eelgrass leaves are typically 2 to 5 mm wide and up to 1 meter long. Farther south on the coast of Washington, Oregon, and California the leaves can be 8 to 12 mm wide and 1 to 2 meters long. The leaves of the eelgrass of the Atlantic coast resemble the narrow-leaved plants of Alaska rather than the wide-leaved forms. This difference has been the basis for taxonomically subdividing the species (Setchell, 1929). Recent studies (Phillips and Grant, 1965; McRoy, 1966) have shown that leaf size varies with environmental conditions and should not be the basis for taxonomic classification.

Figure 1. Eelgrass (Zostera marina L.) from Izembek Lagoon, Alaska, showing vegetative and flowering turions (drawn by G. B. Threlkeld).

The leaves have 3 to 9 primary veins. These veins are the external manifestation of the vascular bundles in the leaf (Fig. 2). The leaf also has large air spaces, lacunae, that can function in the storage and recycling of the gases used in metabolism. As many as 6 to 7 leaves may grow in a single clump from a prostrate stem (constituting a turion).

The flowering stem develops from the terrestrial turion of the prostrate vegetative stem. The flowers are unisexual and are borne on a leaf in a spadix covered by a spathe. Male and female flowers alternate in two rows (Fig. 3). Twelve pairs are in a single spadix. The male flowers have a single stamen. The pollen in the male flowers is filamentous and is distributed by water circulation. The female flower consists of a single ovary with a style that is split into two stigmas. Flowering and fertilization occur in mid-summer.

After fertilization the ovary develops into a fruit attached in the spadix by a short stipe and covered by a sheath, the pericarp, which has a long spike on the upper tip (Fig. 3). The mature seeds are about 2 to 3 mm long and are longitudinally ribbed.

The prostrate stem or rhizome is branched to form several turions. The rhizome has clumps of roots growing in nodes separated by smooth internodes (Fig. 4). The roots penetrate several centimeters into the sediment and are covered with numerous fine root hairs.

## Development

The growth of eelgrass from seed to mature plant has been described in detail by Setchell (1929). He divided this growth into successive

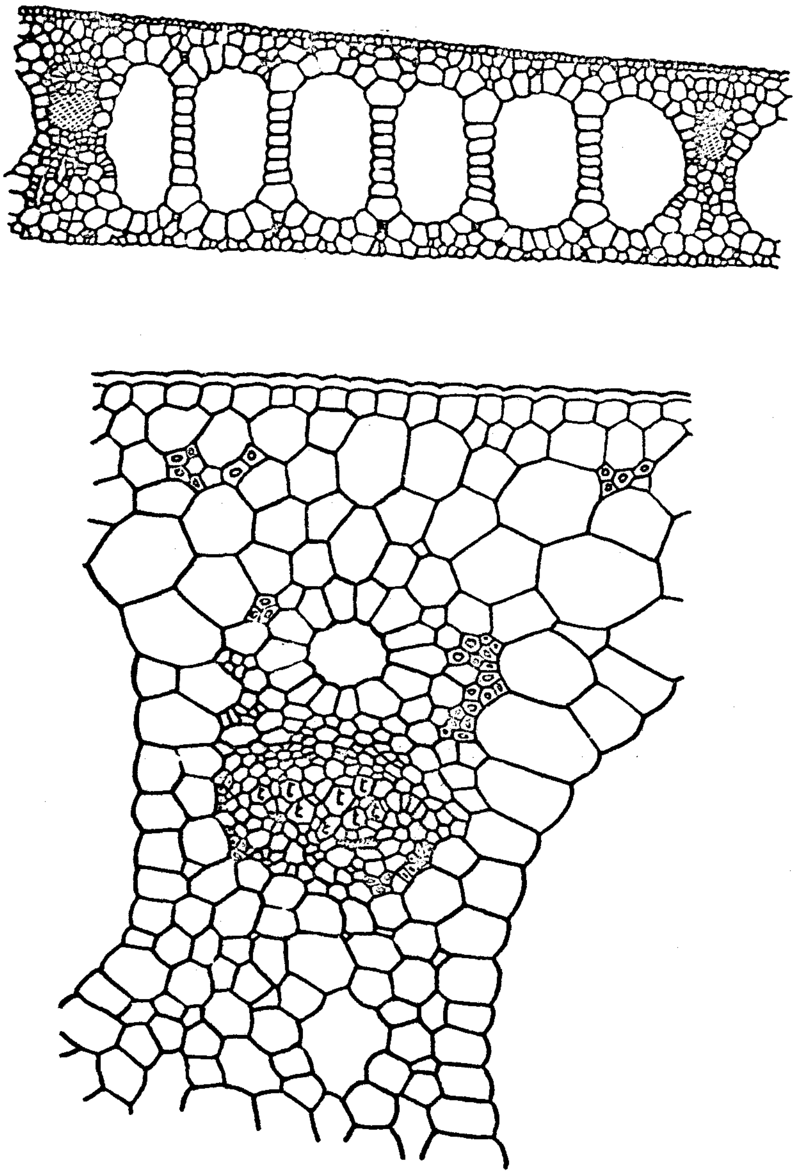

Figure 2. Cross sections of eelgrass leaves (from Sauvageau, 1891). Upper: section between median and lateral vascular bundles; phloem indicated by shading. Large ovals are spaces (lacunae) in leaves. Lower: enlarged section of median vascular bundle; sieve tubes are marked by t's.

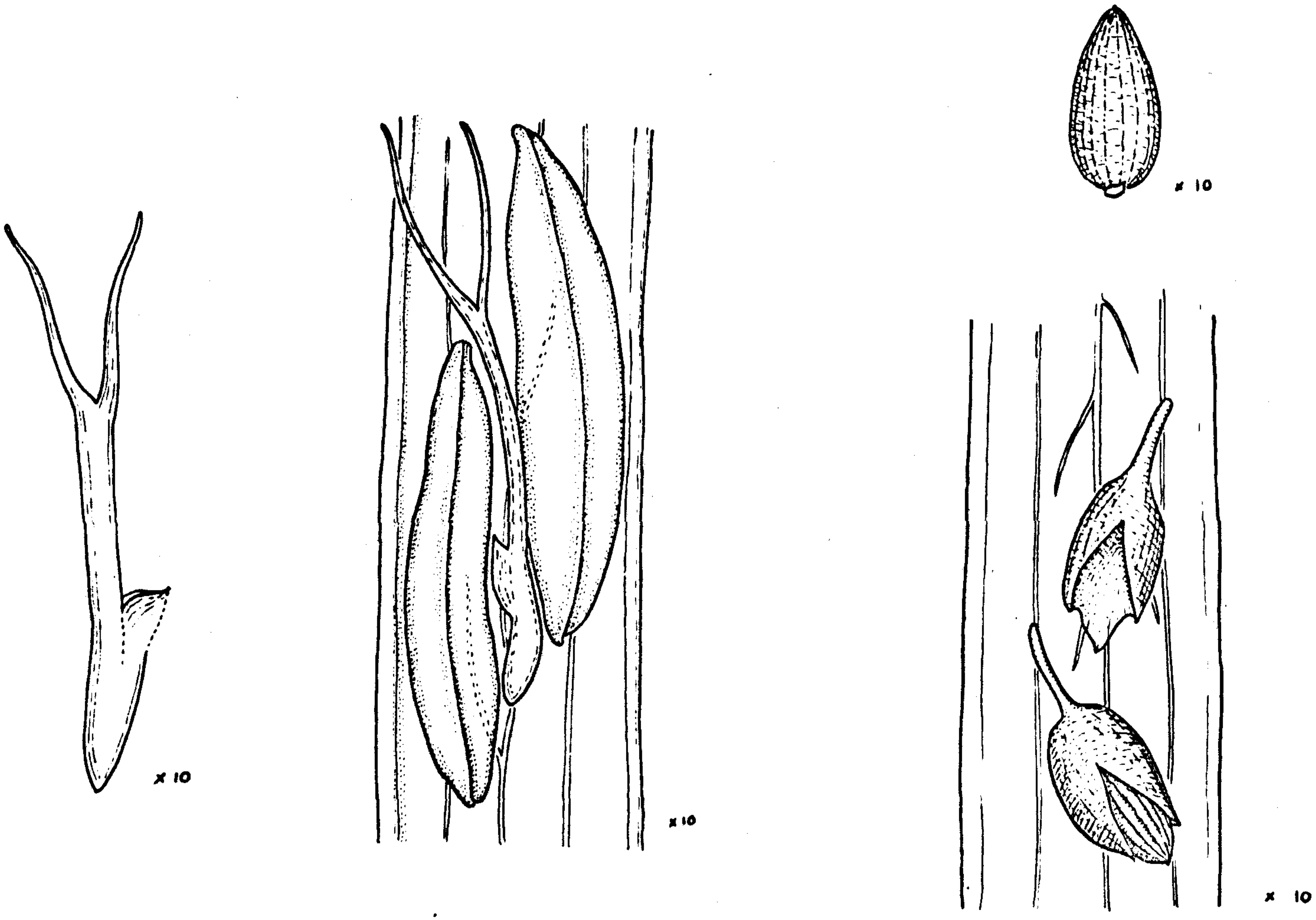

Figure 3. Flowers and fruits of eelgrass (drawn by G. B. Threlkeld). Left: female flower dissected from spathe, showing divided stigma. Center: female flower flanked by male flowers. All are attached in spathe but the covering sheath has been removed. Right: ripening fruits attached in spathe (below) and mature seed removed from spathe (above).

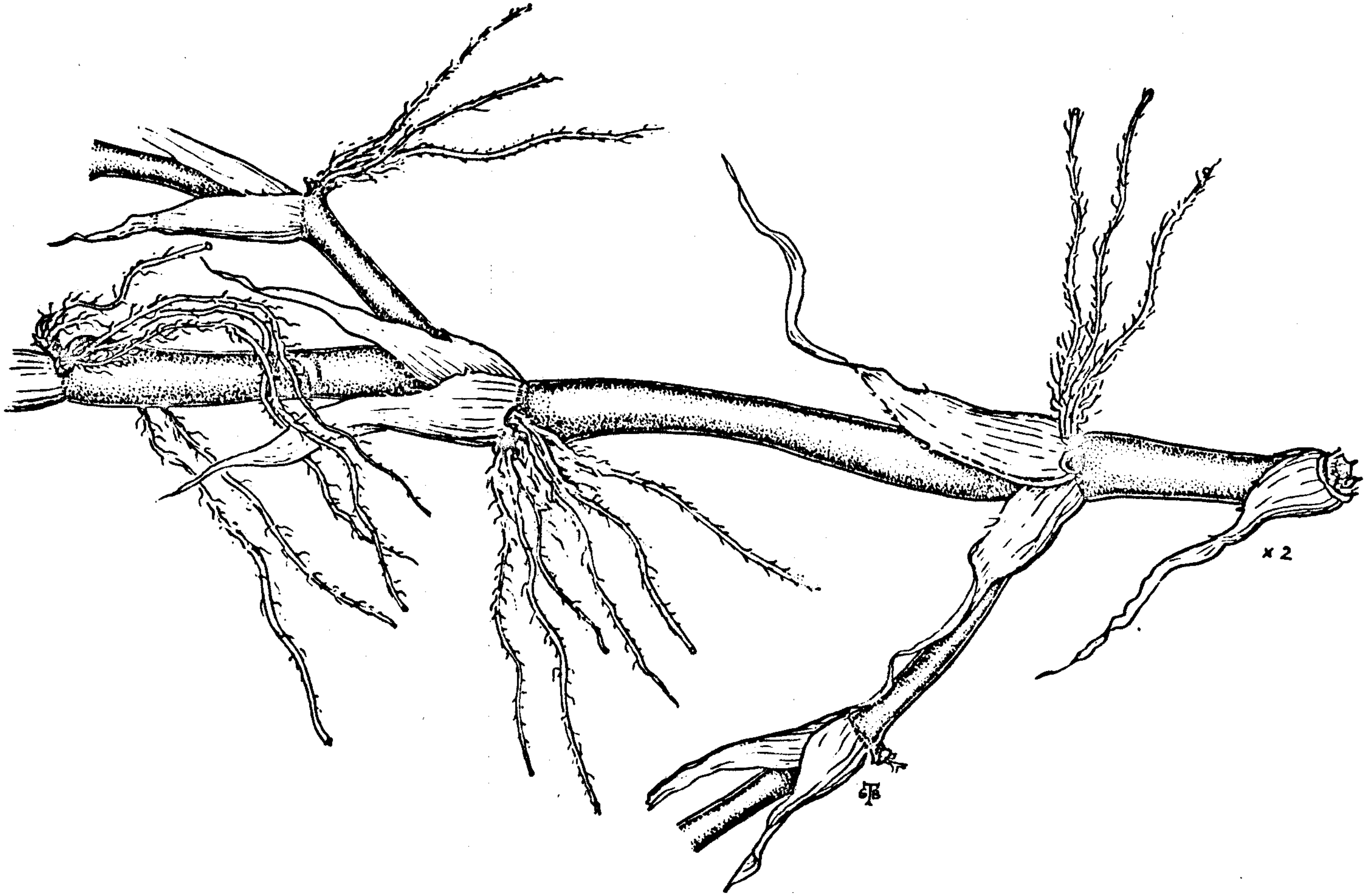

Figure 4. Rhizome and roots of eelgrass (drawn by G. B. Threlkeld). Rhizome branches and roots grow from nodes separated by smooth internodes. Root hairs cover the surface of the roots.

stages of development. In the first stage the seed germinates and develops into a turion with up to 6 or 7 leaves. Seeds germinate in spring in cold waters and in late fall in warmer waters. The second stage of development immediately follows the first in the lower latitudes of the range of eelgrass; in higher latitudes the turion overwinters in a stage of dormancy. In the latter case, which applies to eelgrass in Alaska, the turion will lose some of its oldest leaves at the end of the first growing period.

During the second growth stage the internodes of the rhizome elongate and several turions are produced. The plant after this growth period covers an area of about 30 $cm^2$ (Arasaki, 1950). In the end of the second growth stage the oldest leaves and rhizomes die and break off of the younger plant. The second stage of growth is followed by a quiescent winter period.

The third phase of development is a period of prolific vegetative growth. The rhizomes continue to elongate and branch and more turions are formed. The multiplication of turions proceeds in a geometric scale by doubling each season. In addition the terminal turion elongates to form an erect stem that bears the flowering spathes. Antithesis of the flowers is dependent on water temperature and usually occurs from late spring to mid-summer. The flowers are fertilized by the water-carried, filamentous pollen grains; the fruits ripen and seeds are formed by late summer. The flowering stem is an annual and is sloughed off at the end of the growing season along with the oldest leaves. These parts of the plant often form large, dense mats that drift on the sea surface for long distances before sinking.

After the third growth period the plant covers about 90 $cm^2$ of the sea bed. The third and successive growth periods are followed by winter quiesence during which the old rhizomes die and break off the plant. The pattern of development in subsequent growth seasons follows that described for the third period.

Once eelgrass plants are established, vegetative growth becomes the quantitatively most important means of adding new plant material. Seeds are produced each year but they only colonize a small area. In established eelgrass beds, such as in Izembek Lagoon, Alaska, seeds annually germinate in the intertidal zone on the upper fringes of the beds. These plants do not persist over the winter but each year new seeds develop in this zone (McRoy, 1966). In the mature eelgrass beds few, if any, germinating seeds are found. All new growth is through the process of vegetative production.

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# Chapter 3.

# THE CHEMICAL CONSTITUENTS OF EELGRASS

## Introduction

The chemical composition of eelgrass (Zostera marina) shows which elements it abstracts from sea water and gives a first approximation of the role of the plant in biogeochemical cycles. In addition, the chemistry of the plant can provide much of the evidence needed to decide how far adaptation to life in the sea has proceeded from the plant's terrestrial ancestors. Furthermore, to understand the ecology of eelgrass some insight is necessary into the status of eelgrass as either a terrestrial angiosperm with only slight modifications for the marine environment or a highly modified plant more similar to a marine macrophytic alga.

Investigations into the chemical composition of eelgrass began long ago with the studies of iodine concentration (Cassola, 1822; Balard, 1825). Forchhammer (1844) a short time later detected boron, cobalt, and barium and measured the zinc content of the ash. Vinogradov (1953) has concisely presented more than 30 chemical studies of compounds and elements in eelgrass.

In the early 20th century, C. G. J. Peterson, director of the Danish Biological Station, initiated some of the first quantitative studies of eelgrass ecology and urged P. Boysen-Jensen (1914) to examine the carbon, nitrogen, and organic matter content of the plant. The conclusions of these studies were that eelgrass in Danish waters was the main source of organic matter to the sea bed and to food webs involving benthic invertebrates and several species of commercial fishes.

## Elemental Composition

The elemental composition of an organism reflects its physiological requirements and the character of its environment. The incorporation of an element into the plant from sea water may be directly or indirectly tied to metabolism or it may be a physical absorption-exchange process. The accumulation of an element in the plant is a balance between uptake and loss. Accumulation and loss depend on many physiological factors (growth rate, age, type of tissue, etc.) as well as the conditions of the environment (temperature, pH, salinity, and light).

Sutcliffe (1959, 1962) reviewed the mechanisms of salt accumulation in plants. Plant cells are surrounded by a semipermeable membrane that permits accumulation or exclusion against a concentration gradient. Many elements are linked to the metabolic activity of the plant. The rates of uptake of carbon, oxygen, and nitrogen have been used as direct measurements of the rate of metabolism in a variety of organisms. The uptake of phosphorus, on the other hand, is dependent on metabolic activity but is not a direct indication of metabolic rate.

The concentrations of 27 elements have been quantitatively determined in eelgrass (Table 1). More trace elements could be added to the list but their concentrations have not been measured. The list is divided into 3 categories on the basis of function and concentration in the plant. The first group consists of the major elements carbon, oxygen, hydrogen, phosphorus, and nitrogen, the building blocks of organic matter. The second group is composed of the minor elements that occur in eelgrass in an abundance greater than 100 ppm. Zinc (56 ppm) is an exception to this group and occurs in a concentration that is intermediate between the minor elements and the trace elements. The last group, the trace elements, includes the elements that are found in eelgrass in less than 10 ppm. All the elements listed except beryllium, rubidium, bromine, and fluorine are known to be required in the biochemical processes of spermatophytes (Altman and Dittmer, 1964). The elemental composition of eelgrass shows that the plant is an effective concentrator of numerous elements that occur only sparingly in the sea.

## Eelgrass Compared to the Ocean

The chemical composition of eelgrass is presented (in Table 1) along with comparative concentrations of the elements in the ocean. A concentration factor, the ratio of the element in the plant to that in the ocean, has been calculated on the basis of live weight. The live weight of eelgrass includes 80% water (McRoy, 1966). The concentration factors assume that eelgrass absorbs elements across the leaves. The plant also absorbs elements from the interstitial water through the roots (see Chapter 7). Concentration factors calculated relative to interstitial water might be very different from those for the open sea. Unfortunately the data on the chemistry of the sediments are too sparse to make valid computations.

There are few principles to rely on when comparing the abundance of an element in an organism with that in the ocean. Polikarpov (1966) states that the concentration of a trace element in an organism is generally proportional to its concentration in sea water up to $10^{-6}$ to $10^{-4}$ moles/l. Also Goldberg (1957) finds that the concentration factors

Table 1. Elemental composition of eelgrass compared to the ocean.

| | | Eelgrass[1] (ppm dry wt) | Ocean[2] (ppm) | Concentration Factor[3] (live wt) |
|---|---|---|---|---|
| I. | Major Elements | | | |
| | Oxygen | 390,000 | 857,000 | 0.091 |
| | Hydrogen | 59,500 | 108,000 | 0.110 |
| | Carbon | 385,000 | 28 | 275 |
| | Phosphorus | 2,860 | 0.07 | 8,170 |
| | Nitrogen | 30,450 | 0.5 | 12,200 |
| II. | Minor Elements | | | |
| | Sodium | 19,590 | 10,500 | 0.37 |
| | Chlorine | 45,680 | 19,000 | 0.46 |
| | Magnesium | 7,380 | 1,350 | 1.09 |
| | Potassium | 22,640 | 380 | 1.14 |
| | Sulfur | 7,300 | 885 | 1.65 |
| | Calcium | 20,010 | 400 | 10.0 |
| | Boron | 310 | 4.6 | 13.5 |
| | Silicon | 840 | 3.0 | 56 |
| | Iodine | 203 | 0.06 | 680 |
| | Zinc | 56 | 0.01 | 1,120 |
| | Iron | 245 | 0.01 | 4,900 |
| | Aluminum | 500 | 0.01 | 10,000 |
| | Manganese | 1,825 | 0.002 | 182,500 |
| III. | Trace Elements | | | |
| | Bromine | 9.59 | 65 | 0.03 |
| | Rubidium | 0.14 | 0.12 | 0.24 |
| | Fluorine | 3.61 | 1.3 | 0.55 |
| | Nickel | 0.4 | 0.002 | 40 |
| | Barium | 7.2 | 0.03 | 48 |
| | Molybdenum | 3.12 | 0.01 | 62 |
| | Cadmium | 0.23 | 0.00011 | 420 |
| | Copper | 7.50 | 0.003 | 500 |
| | Cobalt | 0.3 | 0.001 | 600 |
| | Beryllium | 0.12 | $6 \times 10^{-7}$ | 40,000 |

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[1] Data from Candussio, 1960; Vinogradov 1953; Meehan and Smythe, 1967; Hutchinson and Wollack, 1943.

[2] Data from Goldberg, 1965.

[3] Converted by the dry to wet weight ratio of 1:5.

of trace metals in an organism generally parallel the order of stability of the metal ions with organic ligands.

In eelgrass the concentration factors range from 0.03 for bromine to $1.8 \times 10^5$ for manganese. Calcium, magnesium, and potassium occur in about the same amounts in eelgrass and sea water. The concentration factors are, of course, subject to a range of variations and may be very different for eelgrass and sea water in a specific location.

The concentration factors in the plant are proportional to the abundance of an element in the ocean (Fig. 1). The minor elements and the trace elements have a different but parallel relationship to the abundance of elements in the ocean. For the same oceanic abundance a minor element will be 1000 times more concentrated in the plant than a trace element. I can find no comparable example of this empirical relationship in the literature; the principle is not evident.

The atomic ratios of C:N:P in eelgrass are 354:23:1. These ratios are very different from the model for the average ocean and plankton (106:16:1) proposed by Redfield _et al_. (1963). The high values in eelgrass indicate a lower requirement or a deficiency of phosphorus. The changes due to eelgrass in nutrient concentrations in sea water as a result of these high ratios will be quite different from those due to a plankton community.

## Eelgrass Compared to Other Plants

The quantity of some of the minor elements required for growth by all plants can be compared in eelgrass and other marine, freshwater,

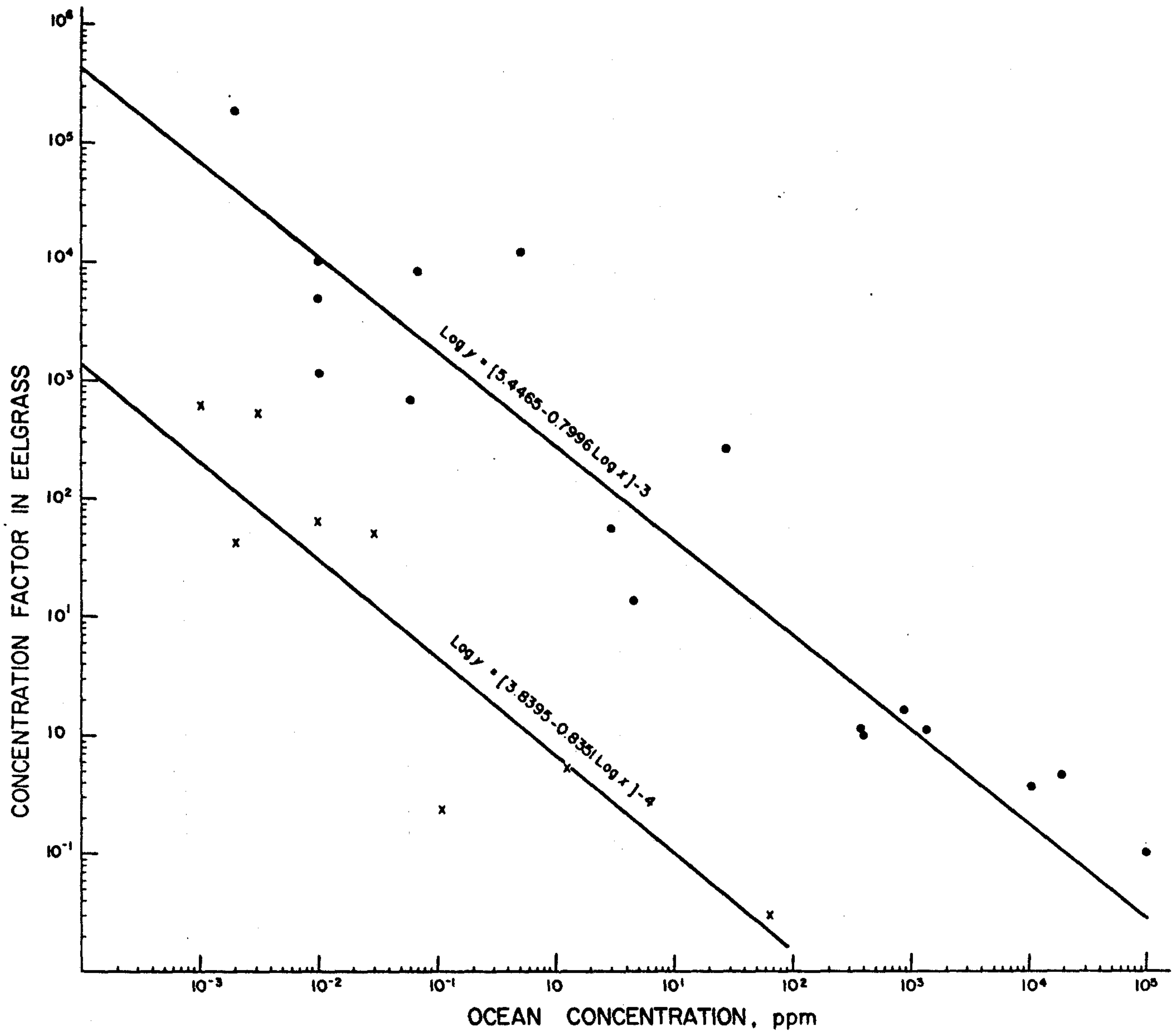

Figure 1. Concentration factors (ratio of abundance in plant to that in ocean) of elements in eelgrass as a function of the concentration of the elements in the ocean (data from Table 1). Upper regression equation applies to minor elements; lower regression equation applies to trace elements.

and terrestrial plants (Table 2). There is a good deal of similarity among these plants despite their diverse habitats. In general, rice shows the lowest quantity of all elements and Elodea and kelp the highest. Eelgrass is most similar to red clover for everything but sulfur. The marine and freshwater plants are characterized by a high sulfur concentration. Kelp contains a large amount of potassium (this was once the basis of an industry).

In another comparison the concentration factors for three trace metals in eelgrass are listed with those in six seaweeds (Table 3). Although some uniformity in these factors exists amongst the seaweeds, eelgrass is very different. It concentrates less nickel and much more molybdenum and zinc than do the seaweeds. Some of the increased concentrations in eelgrass may be due to the storage and support tissues characteristic of vascular plants but lacking in seaweeds.

## Radionuclides in Eelgrass

In addition to accumulating metal and other ions to 100 or 1000 times the natural concentration, eelgrass also concentrates many radioactive isotopes (Table 4). These concentration factors, mostly determined in experimental conditions, range from 2 to 3 for $^{90}$Sr and $^{137}$Cs to 1100 for $^{95}$Zr and $^{95}$Nb. The values in eelgrass are compared to those in brown algae. The factors are similar for the two types of marine plants, with the exception of $^{95}$Zn, which becomes more concentrated in eelgrass and, of $^{137}$Cs, which is higher in the brown algae. The concentration of radioactive isotopes by plants can be a mechanism

Table 2. Minor elements in eelgrass compared to marine, freshwater, and terrestrial plants (from Candussio, 1960; Vinogradov, 1953; Morrison, 1936; Altman and Dittmer, 1964).

| | | Concentration (ppt dry wt) | | | | |
|---|---|---|---|---|---|---|
| Plant Species | Habitat | K | P | Ca | Mg | S |
| Eelgrass (*Zostera marina*) | marine | 22.6 | 2.9 | 20.0 | 7.4 | 7.3 |
| Kelp (*Laminaria digitata*) | marine | 36.7 | 3.3 | -- | 11.2 | 13.8 |
| Canada Waterweed (*Elodea canadensis*) | freshwater | 14.8-30.1 | 2.8-7.4 | 29.1- 8.3 | 4.7-11.7 | 1.5-9.7 |
| Rice (*Oryza satira*) | freshwater | 9.3-16.4 | 0.7-1.3 | 1.9- 3.0 | 0.6- 1.1 | 1.0-1.4 |
| Red Clover (*Trifolium pratense*) | terrestrial | 18.5-19.7 | 2.3-3.4 | 20.3-27.6 | 4.7- 7.1 | 0.4-0.5 |
| Alfalfa (*Medicago sativa*) | terrestrial | 7.0-40.3 | 1.5-7.1 | 3.5- 5.5 | 0.6-10.2 | 1.9-4.0 |

Table 3. Concentration factors (live weight basis) in eelgrass and seaweeds for some trace metals (from Candussio, 1960; Black and Mitchell, 1952).

| Plant Species | Ni | Mo | Zn |
|---|---|---|---|
| Eelgrass (*Zostera marina*) | 200 | 312 | 5,600 |
| Kelp (*Ascophyllum nodosum*) | 600 | 14 | 1,400 |
| Kelp (*Laminaria digitata*) | 200-400 | 2-3 | 400-1,000 |
| Brown Alga (*Fucus spiralis*) | 1,000 | 15 | - - - |
| Brown Alga (*Fucus vesiculosis*) | 900 | 4 | 1,100 |
| Brown Alga (*Fucus serratus*) | 600 | 3 | 600 |
| Brown Alga (*Pelvetia cunaliculata*) | 700 | 8 | 1,000 |

Table 4. Concentration factors (live weight basis) of radioactive isotopes in eelgrass and brown algae (Polikarpov, 1966).

| Isotope | Eelgrass | Brown Algae |
|---|---|---|
| $^{90}Sr$ | 3 | 6.5-40 |
| $^{38}Sr$ | 5 | 16-60 |
| $^{137}Cs$ | 2 | 2-30 |
| $^{65}Zn$ | 336 | 190 |
| $^{90}Y$ | 210 | 220 |
| $^{144}Ce$ | 130 | 200-350 |
| $^{95}Zr$ | 1,120 | 170 |
| $^{71}Ge$ | 197 | 66 |
| $^{95}Nb$ | 1,094 | 2,000 |
| $^{32}P$ | 51 | 30 |
| $^{51}Cr$ | 40 | 60 |
| $^{131}I$ | 30 | 140-300 |
| $^{54}Fe$ | 435 | 1,100 |
| $^{106}Ru$ | 181 | 170-366 |

for transferring and accumulating these isotopes to high levels in the ecosystem.

Eelgrass, a primary producer, will transfer its chemical constituents to other organisms through the food web, where they may become additionally concentrated. The principal grazers on eelgrass in Alaska are waterfowl. These birds are in many cases the only intermediate link between man and the plant. Other higher elements of the food web include invertebrates and fishes.

Polikarpov (1966) calculated the percentage of extraction of an isotope by an aquatic organism from data on biomass and concentration factors. For plankton the biomass in the ocean is low, about 10 $g/m^2$, and the percentage of an element that they can extract from the water is small, generally less than 1%. Eelgrass, on the other hand, attains a biomass of 2 to 3 $kg/m^2$ and could extract up to 90% of the quantity of an element in sea water. In shallow water the eelgrass beds play an important role in biochemical cycles.

## Nutritive Value

Eelgrass is food for many organisms. It is the principal diet item of the Atlantic and Pacific brant geese. It is also a food item in the diets of the following birds (from Martin et al., 1951):

Baldpate
Black Duck
American Goldeneye
Mallard
Pintail
Greater and Lesser Scaup
American, Surf, and White-winged Scoter

Canada Goose
Emperor Goose
American Knot

Many other marine animals utilize eelgrass once it becomes detritus.

The nutritive value of fresh eelgrass as a food is indicated by a proximate analysis (Table 5). The data are from Candussio (1960), who analyzed eelgrass from the Adriatic Sea. The content of protein from his determination is relatively high when compared to the few other analyses that are available. Einarsen (1965) reported that protein ranged from 7 to 15% dry weight in eelgrass collected from Alaska, Washington, and Oregon. The lowest values were for the Alaska samples and he suggested that a marked geographic variation in protein occurs. Other analyses of eelgrass from Alaska indicate that protein varies from 13 to 18% dry weight (McRoy, unpublished). Burkholder and Doheny (1968) also measured the protein in eelgrass; they report values of 6 to 11% dry weight for plants from Long Island Sound. These analyses indicate that the variability in protein content may be more a result of local and seasonal differences in plants and differences in experimental technique than a geographic variation.

The proximate analysis of eelgrass is also compared to that of other plants, another seagrass and two terrestrial fodder plants (alfalfa and red clover). Protein is highest in eelgrass. Lipids are higher in the fodder plants, but Parker (1967) reports a higher value (1.3 to 6.4%) for seagrasses than the one given in Table 5. The fiber content of the seagrasses is about 50% lower than for the terrestrial plants. This is likely to be a result of adaptation to the marine environment where

Table 5. Proximate analysis of eelgrass compared to marine and terrestrial plants (in % dry wt).

| Plant Species | Protein | Lipids | Fiber | Ash | Other Carbohydrate |
|---|---|---|---|---|---|
| Eelgrass (*Zostera marina*)[1] | 19.03 | 1.60 | 16.60 | 18.15 | 44.62 |
| Turtlegrass (*Thalassia testudinum*)[2] | 13.1 | 0.5 | 16.4 | 24.8 | 35.6 |
| Red Clover (*Trifolium pratense*[3] | 13.4 | 2.9 | 30.9 | 7.3 | 45.5 |
| Alfalfa (*Medicago sativa*)[3] | 16.2 | 2.2 | 32.0 | 8.3 | 40.1 |

[1] From Candussio, 1960

[2] From Burkholder *et al.*, 1959

[3] From Morrison, 1936

supporting tissue is not essential. The ash content is highest in the marine plants. The amount of carbohydrates is lowest in turtlegrass but similar in the other 3 species.

In addition to the protein, lipids, and other materials contained in eelgrass, there are vitamins that will be transferred to other organisms in the food web (Table 6). In eelgrass biotin, thiamine, and $B_{12}$ concentrations are low whereas niacin and pantothenate are high.

Eelgrass has a fairly good nutritional value. Its quality compares favorably with the terrestrial fodder plants alfalfa and red clover. Eelgrass should satisfy the requirements of most herbivores. In the past it has been used as a food supplement for domestic livestock (Scagel, 1961).

The proximate analysis of eelgrass and turtlegrass reflects some of the consequences of the marine environment to which the plants have adapted.

## Other Constituents

A few other studies have reported chemical components of eelgrass. Maeda et al. (1966) examined the constituents of the cell walls of eelgrass. Using eelgrass from the waters surrounding Japan they found in the aqueous extracts rhamnose, xylose, and galactose derived from hemicellulose, and glucose and fructose derived from sucrose. The insoluble fraction was cellulose. D-galacturonic acid was the principal constituent of the pectin fraction. The sugars of the pectin fraction were similar to those in terrestrial plants. The methoxyl content of

Table 6. Amounts of B vitamins in eelgrass (from Burkholder and Doheny, 1968).

| Vitamin | Concentration (ppm dry wt) |
|---|---|
| Biotin | 0.04 |
| Thiamine | 0.38 |
| Niacin | 11.13 |
| Pantothenate | 16.34 |
| $B_{12}$ | 0.022 |

the pectin was 2.03% of which 12.4% was esterified. This content is much less than that in cell walls of land plants and the authors suggest that the pectic substance has a role in ion absorption. Additionally the pectin contained 9% of an ester sulfate that was suggested to be involved in ion absorption. The cell wall constituents are another adaptation to the marine environment. The absorption of ions across the leaves in eelgrass, suggested by Maeda _et al_. (1966), is documented in Chapter 7.

## Conclusions

1. The accumulation of elements in eelgrass is proportional to the abundance of an element in the ocean.
2. Eelgrass is more similar in composition to seagrasses and terrestrial plants than it is to seaweeds. The chemical constituents of eelgrass reflect several adaptations to the marine environment.
3. Eelgrass is a good quality food for other organisms.

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# Chapter 4.

# THE DISTRIBUTION AND BIOGEOGRAPHY OF _ZOSTERA_ _MARINA_ (EELGRASS) IN ALASKA

(published in PACIFIC SCIENCE)

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# The Distribution and Biogeography of *Zostera marina* (Eelgrass) in Alaska[1]

C. PETER MCROY[2]

ALTHOUGH INNUMERABLE BOTANISTS have visited Alaska to record and study its flora, most accounts terminate at the high-tide line. Consequently, the marine vegetation, especially that of the most northern coasts of Alaska, has received little attention and the distributions of many species are sketchily known. *Zostera marina* Linnaeus, the common eelgrass, has probably received more interest than most, because of its importance as a waterfowl food. In spite of this, the distribution outlined by Hultén (1941:95, 1960:69, 1964:256) and other published sources (Anderson, 1959:48; Porsild, 1932:90–94; Polunin, 1940:40–41; Setchell, 1920:563–579, 1935:560–577; Murie and Scheffer, 1959:396) is very incomplete in the light of recent surveys of the coast. By compiling the results of personal efforts and communications over the past few years, I can now document in detail the distribution of this species in Alaska.

An additional result of searching and studying the distribution of *Zostera* in Alaska has been a review of the mechanisms of dispersion that have established and maintained this distribution. These aspects of the study of *Zostera* have in turn led to considerations of the biogeography of the species which can be reconstructed from distribution records and dispersion mechanisms.

## *Distribution Survey*

The genus *Zostera* contains 11 species of shallow-water, soft-bottom marine plants (Setchell, 1935). The most widespread species of the genus, *Zostera marina*, occurs discontinuously throughout the boreal Northern Hemisphere from the seas of Okhotsk and Japan to the Baltic and Mediterranean (Setchell, 1935: 571). On the Pacific coast of North America *Z. marina* extends from Port Clarence, 65° N (Porsild, 1932:90) to Agiabampo Lagoon, 26° N, in the Gulf of California (Steinbeck and Ricketts, 1941:254).

In Alaska, *Zostera* forms a distinct subtidal zone in protected bays, inlets, and lagoons along the coast from Bering Strait south (Hultén, 1941:95). During 1967 I was able to survey many miles of the Alaska coast to locate and examine the *Zostera* beds. These surveys included Southeast Alaska, Prince William Sound, the Cold Bay region of the Alaska Peninsula, parts of the Seward Peninsula near Nome and Teller, the coast of the Chukchi Sea between Kivalina and Cape Thompson, and the vicinity of Point Barrow. The observations from these field trips have been combined with the published records and personal observations of several people to present a detailed listing of the locations of *Zostera* beds on the coast of Alaska (Fig. 1 and Table 1).

In Southeast Alaska, the Alexander Archipelago, *Zostera* is found in most of the bays and inlets of the outer coast, but it is absent from many of these on the inside waters (Fig. 1 and Table 1). This is apparently due to the turbid effluent of glaciers. No plants were found in any of the areas receiving large amounts of glacial runoff although other environmental conditions appeared quite suitable for their growth. For example, in Doty Cove and Limestone Inlet in Stephens Passage (near Juneau) the absence of *Zostera* is enigmatic in winter months when ambient waters are clear; but in summer the problem is solved by the presence of very turbid water from nearby Taku Inlet. In bays and inlets receiving quantities of the turbid glacial water the subtidal zone of soft bottoms usually occupied by *Zostera* is devoid of all macrophytes.

The coast from Cross Sound to Prince William Sound is rugged and exposed to the open sea; most of the existing bays harbor glaciers or glacial streams. *Zostera* has been reported only in Yakutat Bay (Setchell, 1920:567; Fig.

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[2] Institute of Marine Science, University of Alaska, College, Alaska 99701.

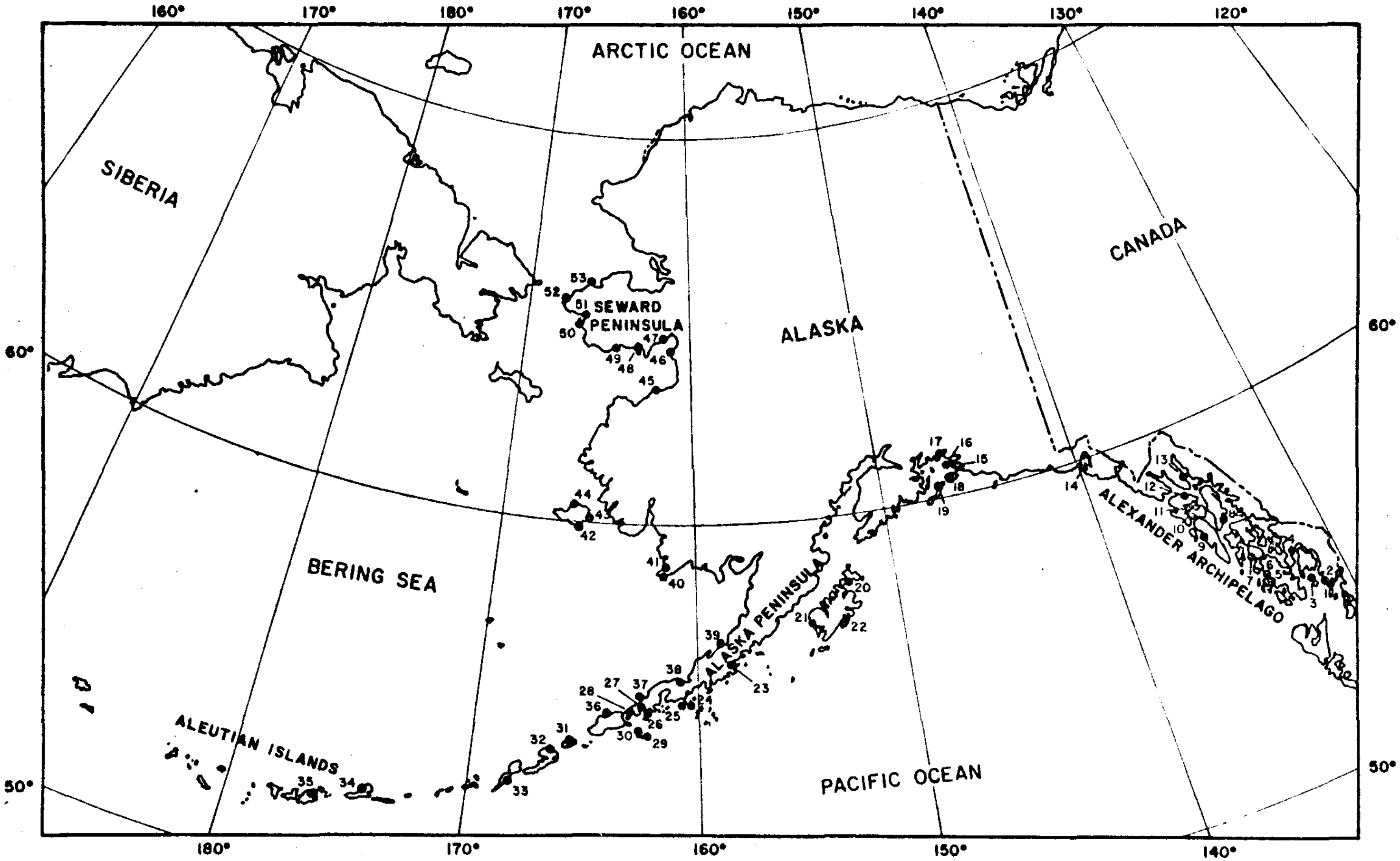

FIG. 1. Chart of Alaska showing the location of records of *Zostera marina* on the coast. Numbers refer to locations given in Table 1.

TABLE 1

Records of *Zostera marina* in Alaska

| CHART NUMBER* | LOCATION | SOURCE |
|---|---|---|
| Alexander Archipelago | | |
| 1 | Foggy Bay | Hultén, 1941 |
| 2 | Cape Fox | Hultén, 1941 |
| 3 | Gravina Lake | Hultén, 1941 |
| 4 | Yes Bay | Hultén, 1941 |
| 5 | Craig | Hultén, 1941 |
| 6 | Klawak | McRoy, this study |
| 7 | Calder Bay | McRoy, this study |
| 8 | Pybus Bay | McRoy, this study |
| 9 | Sitka | Hultén, 1941 |
| 10 | Hoonah Sound | McRoy, this study |
| 11 | Tenakee Inlet | McRoy, this study |
| 12 | Port Frederick | McRoy, this study |
| 13 | St. James Bay | Palmer, 1941 |
| Cross Sound to Prince William Sound | | |
| 14 | Yakutat Bay | Setchell, 1920 |
| Prince William Sound | | |
| 15 | Olsen Bay | Johansen, 1965 |
| 16 | Redhead Lagoon | McRoy, this study |
| 17 | Sawmill Bay | McRoy, this study |
| 18 | Port Etches, Hinchinbrook Island | Johansen, 1965 |
| 19 | Stockdale Harbor, Montague Island | Johansen, 1965 |
| Kodiak Island, Alaska Peninsula and Aleutian Islands | | |
| 20 | Afognak Island | Beals, 1941 |
| 21 | Sturgeon River | Hultén, 1941 |
| 22 | Port Hobron, Kodiak Island | Hultén, 1941 |
| 23 | Chignik Bay | Hultén, 1941 |
| 24 | Popof Island | Hultén, 1941 |
| 25 | Unga Island | Hultén, 1941 |
| 26 | King Cove | Hultén, 1941 |
| 27 | Cold Bay | McRoy, this study |
| 28 | Morshovi Bay | McRoy, this study |
| 29 | Caton Island | Beals, 1941 |
| 30 | Sanak Island | Beals, 1941 |
| 31 | Akun and Akutan islands | Beals, 1941 |
| 32 | Dutch Harbor | Beals, 1941 |
| 33 | Vsevidof Island | Murie and Scheffer, 1959 |
| 34 | Atka Island | Jones, 1965 |
| 35 | Adak Island | Jones, 1965 |
| 36 | Unimak Island | Hultén, 1941 |
| Bering Sea | | |
| 37 | Izembek Lagoon | McRoy, 1966 |
| 38 | Herendeen Bay | McRoy, 1966 |
| 39 | Port Heiden | McRoy, 1966 |
| 40 | Nanvak Bay | King, 1963 |
| 41 | Chagvan Bay | King, 1963 |
| 42 | Ingrimiut, Nunivak Island | King, 1963 |
| 43 | Ikongimuit, Nunivak Island | King, 1963 |
| 44 | Mekoryuk, Nunivak Island | King, 1963 |
| 45 | St. Michaels | Porsild, 1932 |
| 46 | Malikfik Bay, Norton Sound | Porsild, 1932 |
| 47 | Kwiniuk Inlet, Norton Sound | Porsild, 1932 |
| 48 | Golovin Bay | Porsild, 1932 |
| 49 | Safety Lagoon | Burns, 1967 |
| 50 | Port Clarence | Kjellman, 1883 |
| 51 | Grantly Harbor | McRoy, this study |
| Bering Straits | | |
| 52 | Lopp Lagoon | Burns, 1967 |
| 53 | Ikpek Lagoon | Burns, 1967 |

* Numbers refer to the geographical locations shown in Figure 1.

1 and Table 1). Isolated populations in other more inaccessible areas are of course possible. Prince William Sound contains many *Zostera* beds (Fig. 1 and Table 1), but their distribution was altered by the earthquake of March 1964. Johansen (1965:93–94) lists nine localities where he found dead *Zostera* attributable to the seismic uplift of the region. In June 1967 I revisited many of Johansen's stations. In several of these, the most striking being the vicinity of Cordova, no new *Zostera* was seen; in other places, such as Redhead Lagoon, reduced populations were evident.

The outer coast of the Kenai Peninsula is a glaciated region where no *Zostera* has been reported, nor has any been found in Cook Inlet, which might be expected from the turbidity and currents in the Inlet. There are, however, unconfirmed reports of *Zostera* in Kachemak Bay.

Several bays on Kodiak and Afognak islands, on the Alaska Peninsula, and in the Aleutian Islands contain *Zostera* beds (Hultén, 1941:95; Beals, 1941; Fig. 1 and Table 1). The western limit of the species in North America was Vsevidof Island (Murie and Scheffer, 1959: 369). This limit can now be extended to Atka and Adak islands (Jones, personal communication, 1965). The plants on Adak are evidently a result of transplantation experiments by the

U.S. Fish and Wildlife Service. No plants are known to occur in the western Aleutian Islands, probably due to the lack of protected bays. Plants are known from Kamchatka Peninsula and Bering Island on the Asian side of the Bering Sea (Hultén, 1926:75, 1960:69).

In the Bering Sea *Zostera* forms extensive meadows in the numerous coastal lagoons of the Alaska Peninsula (Fig. 1 and Table 1). The meadows in Izembek Lagoon on the Peninsula are the largest known single stand of the species (McRoy, 1966:103). Farther north, *Zostera* occurs in Nanvak and Chagvan bays and in many of the lagoons at the mouths of rivers on Nunivak Island (King, personal communication, 1963). No other *Zostera* beds have been found between King Salmon and St. Michael.

Porsild (1932:90–94) recorded the northern distribution of *Zostera* from St. Michael to Port Clarence (Fig. 1 and Table 1). Kjellman (1883:53) first observed *Zostera* in Port Clarence, the accepted northern limit in Alaska. Recently, *Zostera* has been seen beyond Bering Strait in the lagoons (Lopp and Ikpek) of the north coast of the Seward Peninsula (Burns, personal communication, 1967). I have also extended surveys to portions of the coast between Kotzebue and Barrow, but have not uncovered any other *Zostera* producing areas.

### *Mechanisms of Dispersion*

The distribution of *Zostera* in Alaska and elsewhere in the Northern Hemisphere is the result of dispersion by several mechanisms. Oceanic currents appear to be the most effective means of long range dispersion, although there is some disagreement on this. Löve (1963:195) observes that saltwater plants are adapted to dispersal in sea water and cites as an example the seeds of *Zostera* with their corky appendages and bouyant vegetative parts. Sculthorpe (1967:358), on the other hand, considers Löve's view of dispersal an "unfortunate generalization," since the seeds of *Zostera* and other marine angiosperms either float for only a short time or sink immediately. The seeds of *Zostera* have a specific gravity of 1.17 (Arasaki, 1950:70–76), a value somewhat greater than the 1.025 average of the ocean (Von Arx, 1962:118) and so would be expected to sink. In fact, however, the seeds are released attached to a reproductive stem which has several leaves and is capable of floating for long distances. Mats of *Zostera* and other marine angiosperms have been seen at sea several hundred miles from the coast (Menzies, Zaneveld, and Pratt, 1967:112). There can be no doubt that dispersion on a large scale is accomplished through the seed-producing and perhaps vegetative plants that annually detach and drift with oceanic surface circulation.

The several species of waterfowl that feed on *Zostera* are another vehicle for dispersion. Löve and Sculthorpe concur. Arasaki (1950:70–76) demonstrated that ducks do not destroy the viability of all seeds they ingest. The coast of Alaska is a flyway for numerous species of waterfowl that annually transport seeds over at least short distances and probably farther. This is a mechanism for dispersion in a direction opposite to that of the coastal oceanic currents.

In a local area *Zostera* extends its cover principally by vegetative growth from rhizomes, a process quantitatively more important than the growth of new seed plants. Again, Arasaki (1950:70–76) has shown that a single plant will cover 30 cm$^2$ the first year, 1 m$^2$ the second, and 2 m$^2$ the third. At this rate, it would not take long for a population to develop in a new area once a plant has been introduced.

### *Biogeographical Considerations*

The global distribution of this species is discontinuous circumboreal. The other species of the seagrasses, with few exceptions, are tropical or subtropical and are considered to have originated in the Indian Ocean (Setchell, 1935:564–572). The genus *Zostera*, however, has no tropical representatives and apparently arose in the western Pacific Ocean, dispersing into the Northern and Southern hemispheres at a time when the tropics were less tropical. This history is supported by the present distribution of the 11 species of *Zostera* (Setchell, 1935:572) and the locations of fossils of *Zostera* ancestors in Japan (Koriba and Miki, 1930:165–204; Miki, 1932:774–778).

If the origin of *Zostera marina* was the western Pacific, then migration could have taken either of two routes. In the first case, dispersion could have moved in two directions from the origin, populating both sides of the Pacific Ocean in one direction and through the Indian Ocean and the Mediterranean Sea to both sides of the Atlantic Ocean in the other. Setchell (1935:572) suggested that a route of this sort could have occurred at a time, probably in the early Tertiary, when the Tethys Sea covered much of the Northern Hemisphere. The other possibility for dispersion is a one-way movement. This is really an argument for a one-way dispersion route through the Pacific Ocean rather than through the Indian Ocean. This path would result logically in the present distribution of the species. The theory demands that the Atlantic and its adjacent seas were populated by migration through the Arctic during a prehistoric milder climate, which should be entirely possible, for, as the distribution in Alaska illustrates, *Zostera marina* is a cold-tolerant species. If continuity through the Arctic once existed, relict populations would be expected along the Arctic coast. These do exist in the White Sea, the Barents Sea, the Kara Sea, and Hudson Bay (Zenkevitch, 1963:195–198; Blinova, 1962:150; Setchell, 1920:567; Porsild, 1932:91). Ekman (1953:160–164) describes similar patterns for many species of marine invertebrates and vertebrates that have discontinuous distributions in the Pacific and Atlantic oceans. Additionally, Durham and MacNeil (1967:343) report that a large number of species, more than 125, of marine invertebrates have dispersed from one ocean to the other mostly in one direction—into the Arctic-Atlantic; they consider these migrations to have occurred during the late Cenozoic.

The evidence available indicates that *Z. marina* originated in the western Pacific and dispersed to the north along the coast of Asia and then around to North America. Its tolerance to low temperatures permitted it not only to cross the subarctic Pacific to North America, but also to populate the Arctic and move eventually to both shores of the Atlantic. Perhaps in times of cooler climates migration continued into the north coast of the Mediterranean Sea and its adjacent seas. No other species of *Zostera* has this widespread distribution, nor is there another one tolerant to low temperatures. The single closely related species that has a similar, but more restrictive, temperature tolerance is *Phyllospadix scouleri* Hook which is endemic to the temperate Pacific Ocean. This species provides an example of the limited distribution of a less cold-tolerant species originating in the same area; it never reached the Atlantic. The opposite situation is illustrated by the distribution of *Zostera nana* Roth, a species less tolerant to cold water but more so to warm water; it is limited to the western Pacific, but has also been able to move through the Indian Ocean to populate parts of Africa, the Mediterranean (both north and south) and parts of the southern Atlantic coast of Europe.

## SUMMARY AND CONCLUSIONS

*Zostera marina*, eelgrass, is a common inhabitant of the Alaska coast, occurring from the lagoons on the north coast of the Seward Peninsula to the southern limit of Alaska and beyond. New records of *Zostera* in Alaska are from Adak and Atka in the Aleutian Islands, Chagvan and Nanvak bays and Nunivak Island, and Lopp and Ikpek lagoons on the Seward Peninsula. In Prince William Sound the distribution of *Zostera* was markedly altered by uplift associated with the earthquake of March 1964.

*Zostera* grows in the soft sediments of shallow, protected marine bays, inlets, and lagoons. It is excluded from large river deltas, glacial fjords, and arctic environments. The distribution in Alaska is disjunct, a result of environmental restrictions rather than a lack of dispersion mechanisms. Global dispersion is a result of oceanic circulation and waterfowl migrations. Vegetative growth is the most important means of extending coverage of a restricted area. In view of the present distribution of the species and the geological structure of the Alaska coast, no extensions of the range of *Zostera* are expected. Populations may exist, of course, in remote places along the coast.

Alterations in the present distribution are possible only with major geological or climatic changes. Seismic uplift or depression of the south coast of Alaska could eliminate a large portion of the present populations. On the other hand, amelioration of conditions in arctic waters by a change in ice conditions could permit further extension of the present range.

The circumboreal distribution of *Z. marina* is considered to be a result of dispersion from a western Pacific origin around the Pacific and through the Arctic into the Atlantic and its adjacent seas. That this was the path of migration is supported by the present distribution of the species, the location of its fossil ancestors, and similar dispersal patterns for marine invertebrates.

The migration and present distribution of *Z. marina* have resulted from the eurythermality of the plant. This feature probably also permitted survival during oscillating Pleistocene climates.

The *Zostera* communities on the Alaska coast are important contributors to all levels of production in the food web and provide refuges to innumerable species of organisms. Research is in progress on the ecology of these interesting communities.

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# Additional Records of Zostera marina (Eelgrass) in Alaska[1]

C. Peter McRoy[2]

Until every bay and inlet of the coast has been examined, no list of the locations containing eelgrass (Zostera marina L.) can be complete. After compiling a detailed list for the coast of Alaska (McRoy, 1969) I have come across several records that should be included in this list (Fig. I and Table 1).

Bousfield and McAllister (1962) surveyed the coast of Alaska to collect marine invertebrates and fishes. In their detailed list of collecting stations they kept notes on the environment and noted eelgrass whenever it was seen. In addition to providing many new locations their records confirm my observation that eelgrass is excluded from part of the inside waters of Southeastern Alaska (the Alexander Archipelago), apparently as a consequence of the influence of glaciers.

The records from Resurrection Bay and Kachemak Bay are the first confirmed reports for the Kenai Peninsula and Cook Inlet. The sparsity of records for the outer coast of the Kenai Peninsula seems to be due to its remoteness rather than lack of eelgrass.

The eelgrass records from Shishmaref and Cape Espenberg are the northernmost findings for North America. Other populations may exist in Kotzebue Sound. The northern limit of eelgrass in Alaska has not yet been found and the plant may not be excluded from the Arctic seas. I now believe that eelgrass populations can occur in places protected from grounding sea ice in the Chukchi and Beaufort Seas.

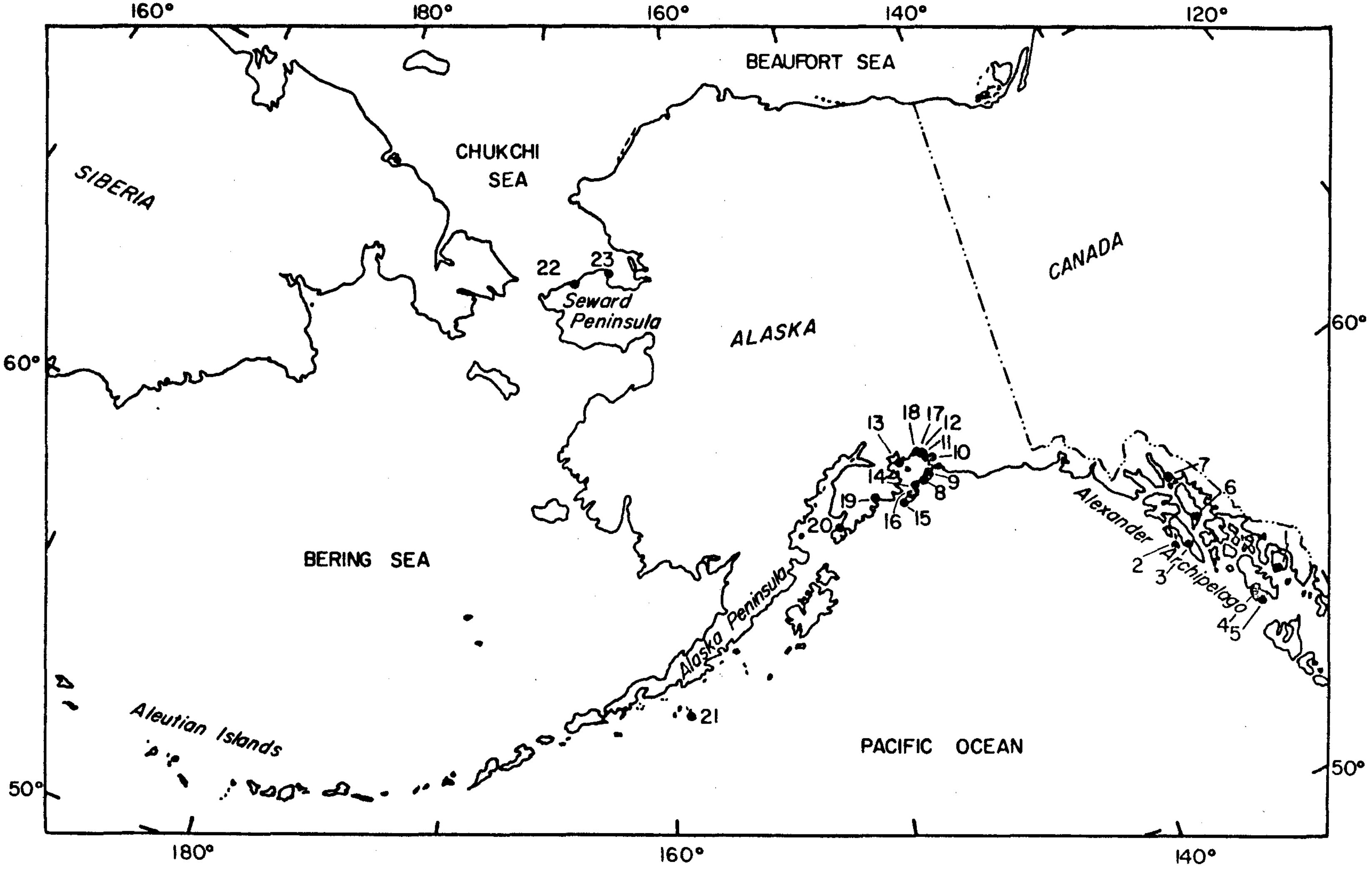

Figure 1. Chart of Alaska showing additional records of <u>Zostera marina</u> on the coast. Numbers refer to locations given in Table 1.

Table 1. Additional records of Zostera marina in Alaska.

| CHART NUMBER* | LOCATION | SOURCE |
|---|---|---|
| Alexander Archipelago | | |
| 1 | Bostwick Bay, Gravina Island | Bousfield and McAllister, 1962 |
| 2 | Tava Island | " " " " |
| 3 | Sitka, Baranof Island | " " " " |
| 4 | Point Cuerbo, San Fernando Island | " " " " |
| 5 | Point Eugenia, San Juan Batista Island | " " " " |
| 6 | Gambier Bay, Admiralty Island | D. Wallen, personal communicatio |
| 7 | Auke Bay | J. Quast, personal communication |
| Prince William Sound | | |
| 8 | Constantine Harbor, Hinchinbrook Island | Bousfield and McAllister, 1962 |
| 9 | Johnstone Point, Hinchinbrook Island | " " " " |
| 10 | Sheep Bay | " " " " |
| 11 | Parshas Bay, Port Gravina | " " " " |
| 12 | Two Moon Bay | " " " " |
| 13 | Esther Island | " " " " |
| 14 | Little Bay, Knight Island | " " " " |
| 15 | MacLeod Harbor, Montague Island | " " " " |
| 16 | Port Chalmers, Montague Island | " " " " |
| 17 | Jack Bay, Valdez Arm | McRoy, personal observation |
| 18 | Port Valdez | " " " " |
| Kenai Peninsula | | |
| 19 | Thumb Bay, Resurrection Bay | Bousfield and McAllister, 1962 |
| 20 | Kachemak Bay, Cook Inlet | McRoy, personal observation |
| Kodiak Island, Alaska Peninsula and Aleutian Islands | | |
| 21 | Simeonof Island | Troyer, 1969 |
| Bering Strait and Chukchi Sea | | |
| 22 | Shishmaref | McRoy, personal observation |
| 23 | Cape Espenberg | " " " " |

*Numbers refer to the geographical locations shown in Figure 1.

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## FOOTNOTES

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[2] Institute of Marine Science, University of Alaska, College, Alaska, 99701.

# Chapter 5.

# STANDING STOCKS AND OTHER FEATURES OF EELGRASS POPULATIONS ON THE COAST OF ALASKA

## Introduction

Non-algal marine plants inhabit lagoons and shallow bays from the equator to the polar circles. Seagrasses as a result of being vascular plants with roots have colonized an environment that is unavailable to nearly all macroscopic marine algae. In Alaska occur two species of seagrasses--Zostera marina L. and Phyllospadix scoulteri Hooke. Of the two only Zostera marina, eelgrass, is widespread and abundant (McRoy. 1968). It constitutes a major food crop for millions of migratory birds on the Pacific flyways.

Eelgrass is a well known organism, largely because of a period in the early 1930's when thousands of acres of it vanished from the shores of the North Atlantic Ocean (Cottam, 1933; Cotton, 1933; Petersen, 1933). The "wasting disease" of eelgrass instigated many studies but few quantitative ones. The literature concerned with this species has been compiled in two bibliographies (Phillips, 1964; McRoy and Phillips, 1968).

The quantitative study of eelgrass populations began with the work of Petersen and Boysen-Jensen (1911), who related the abundance of eelgrass in Danish waters to the amount of organic material in the sediment. They concluded that eelgrass in Danish waters was the main contributor of organic detritus to the sea bed. Boysen-Jensen (1914) also estimated the annual production of eelgrass in Danish waters. These studies are the only quantitative ones that precede the wasting disease. Since the wasting disease period Grøntved (1957, 1958) has again measured the standing stocks of eelgrass in Danish waters. Other studies include several made by the Soviets, who have determined the standing stocks of macrophytes, including eelgrass, in their coastal seas (Zenkevitch, 1963; Vozzhinskaya, 1964; Kireeva, 1965); and in the British Isles Burton (1961, 1962) estimated eelgrass crops as food resources for brent geese. Also Kita and Harada (1962) reported observations of eelgrass biomass in coastal waters of Japan.

For North America there exists a handful of quantitative studies of eelgrass standing stocks. Regrettably, no quantitative data are available for the period preceding the wasting disease. The first report of the biomass of eelgrass in American waters was published by Conover (1958) who studied benthic plant ecology in Great Pond, Massachusetts. There have been two additional reports of standing stocks from the American Atlantic coast (Moeller, 1964; Burkholder and Dohney, 1968). These studies and other descriptive reports (Cottam and Munro, 1954; Stevens _et al_., 1950) indicate that eelgrass has attained a biomass equal to that of the pre- wasting disease period.

The eelgrass beds of the Pacific coast of North America were not affected by the wasting disease of the 1930's (Cottam and Munro, 1954). There have been three quantitative studies of Pacific coast eelgrass populations. In Humboldt Bay, California, Keller (1963) and Keller and Harris (1966) examined the depth distribution of eelgrass biomass and Waddell (1964) studied the effects of dredging for oysters on eelgrass standing stocks. In Alaska, McRoy (1966) studied the standing stock and ecology of eelgrass in Izembek Lagoon. This lagoon, at the end of the Alaska Peninsula in the Bering Sea, may well contain the largest single stand of eelgrass in the northern hemisphere.

In this study several features of the eelgrass populations on the coast of Alaska from the temperate bays of Southeast Alaska to the arctic lagoons of the Bering Straits are compared (Fig. 1). The observations on eelgrass include measurements of the standing stock, caloric content, chlorophyll _a_ concentration, turion density, and leaf size. (A turion consists of an individual stem and group of leaves growing from a prostrate rhizome. An individual plant may consist of many turions.)

## Methods

A sampler modified from Grøntved (1957) was used to quantitatively collect samples of eelgrass. The sampler took an area of 0.042 $m^2$. Processing the eelgrass samples consisted of washing to remove sediments, sorting into leaves and roots and rhizomes, counting, and weighing for fresh weight (biomass). After drying for 24 hr at 90°C, the samples were cooled in a dessicator and weighed again to determine dry weight. The dried samples were stored in plastic bags for further analyses. The fresh and dry weights of algae in the samples were also measured.

The caloric contents of the eelgrass samples were determined with a Parr oxygen bomb calorimeter. Samples were prepared by being ground to a fine powder, dried overnight at 60°C, and cooled in a dessicator. A subsample of the material was weighed and combusted. The ash weight of the sample was taken to be the residual weight after combustion.

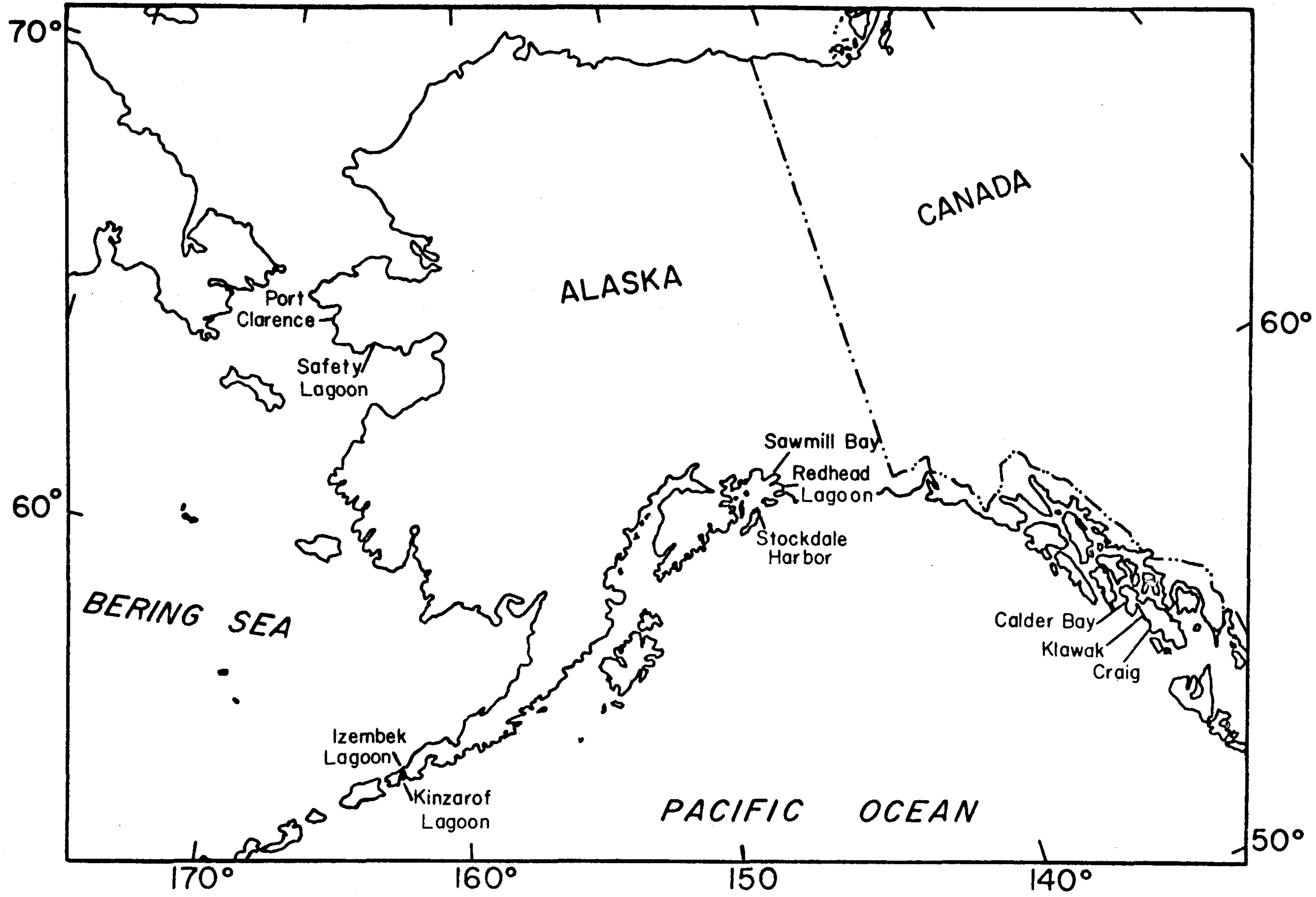

Figure 1. Chart of Alaska showing the locations of the ten eelgrass populations selected for quantitative sampling.

Chlorophyll a was measured in fresh eelgrass leaves using a procedure for macrophytes outlined by Odum et al. (1958). The concentrations were calculated with the Richards with Thompson (1952) equations.

Turion density was estimated by counting the vegetative and reproductive (flowering) turions in the standing stock samples.

Leaf size observations involved measurements of length and width of fresh leaves from several turions. Leaf length was taken to be the distance from the leaf base to tip; width was measured midway between base and tip.

The experimental design consisted of collecting replicate samples from ten bays and lagoons on the coast of Alaska (Table 1). In most cases it was possible to collect at least ten replicate samples from an area; four replicates was a minimum requirement (McRoy, 1966). The samples were collected in the spring and summer of 1967. Not all determinations were made in each area.

The sampling areas included Klawak, Craig, and Calder Bay in Southeast Alaska; Redhead Lagoon, Sawmill Bay, and Stockdale Harbor in Prince William Sound; Izembek and Kinzarof Lagoons on the Alaska Peninsula; and Safety Lagoon and Port Clarence on the Seward Peninsula (Fig. 1).

## Statistical Procedures

The observations on the eelgrass populations were examined using analysis of variance techniques (Snedecor, 1956). Where the standard

Table 1. Sampling program for ten eelgrass populations on the Alaska coast.

| | | Number of Observations | | | | | |
|---|---|---|---|---|---|---|---|
| Location | Survey Date | Standing Stock | Leaf Length | Leaf Width | Turion Density | Caloric Content | Chlorophyll *a* Content |
| Klawak | Apr 1967 | 4 | 12 | 12 | --- | 5 | --- |
| Craig | Apr 1967 | 16 | 64 | 64 | --- | 5 | --- |
| Calder Bay | Apr 1967 | 9 | 36 | 36 | --- | 5 | --- |
| Redhead Lagoon | June 1967 | 18 | 93 | 25 | 18 | 4 | 6 |
| Sawmill Bay | June 1967 | 12 | --- | --- | 12 | 4 | 6 |
| Stockdale Harbor | June 1967 | 11 | 139 | 29 | 11 | 5 | 4 |
| Kinzarof Lagoon | July 1967 | 4 | --- | --- | 4 | 10 | --- |
| Izembek Lagoon | July 1967 | 38 | 185 | 63 | 38 | 8 | 10 |
| Safety Lagoon | Sept 1967 | 10 | --- | 40 | 10 | 5 | 5 |
| Port Clarence | Sept 1967 | 10 | --- | 11 | 10 | 4 | 5 |
| Total | | 132 | 529 | 229 | 103 | 55 | 36 |

deviation of the replicate observations was proportional to the mean, a logarithmic transformation of the data was used to conform the data to the assumptions implicit in analysis of variance. To avoid difficulty with zero observations, one was added to each datum before transformation.

## Results

The one-way analysis of variance showed statistically significant differences in the means for nine of the eleven types of observations made on the eelgrass populations from the ten locations on the coast of Alaska (Table 2). The differences were found to be significant at the 0.01 probability level.

### 1. Standing Stock

The observations of standing stock of eelgrass were collected from all ten of the sampling locations. The standing stock varied considerably along the coast (Fig. 2). It attained maximum values in the lagoons on the Pacific Ocean and Bering Sea sides of the Alaska Peninsula and decreased in both directions away from the Peninsula. The analysis of the data indicated statistically significant differences in the means. A high standing stock in Kinzarof and Izembek Lagoons averaged 1510 g dry wt/m$^2$; an intermediate level of standing stock in Safety Lagoon and Sawmill Bay averaged 415 g dry wt/m$^2$; and a low level in the six other areas averaged 113 g dry wt/m$^2$.

Table 2. Results of statistical tests of one-way analysis of variance for ten eelgrass populations on the Alaska coast.

| Type of Observation | F Ratio | Degrees of Freedom | Probability | Result |
|---|---|---|---|---|
| Total eelgrass standing stock | 30.3 | 9/122 | < 0.01 | Significant |
| Leaf standing stock | 30.0 | 9/122 | < 0.01 | " |
| Root and rhizome standing stock | 17.8 | 9/122 | < 0.01 | " |
| Algae standing stock | 6.38 | 9/122 | < 0.01 | " |
| Caloric content of leaves | 7.55 | 9/17 | > 0.05 | Not Significant |
| Caloric content of roots and rhizomes | 3.86 | 9/19 | > 0.05 | " |
| Chlorophyll _a_ content | 13.54 | 6/40 | < 0.01 | Significant |
| Total turion density | 54.1 | 6/96 | < 0.01 | " |
| Reproductive turion density | 8.92 | 6/96 | < 0.01 | " |
| Leaf length | 90.7 | 6/96 | < 0.01 | " |
| Leaf width | 62.2 | 7/272 | < 0.01 | " |

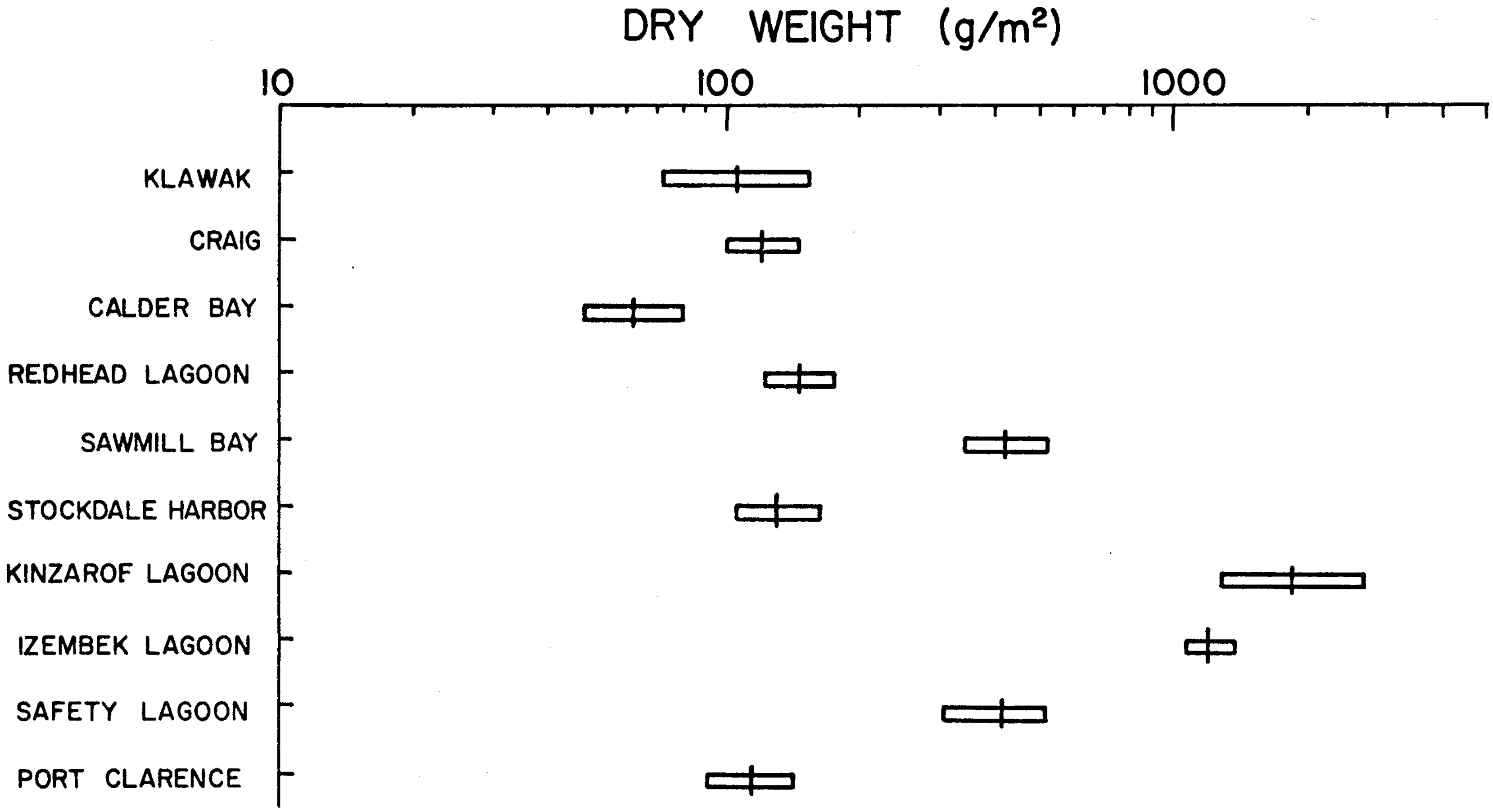

Figure 2. Standing stock of eelgrass in ten locations on the coast of Alaska. Mean and standard error about the mean for replicate observations.

The standing stock measurements can be combined with an estimate of the area of eelgrass coverage in each of the ten locations to provide an approximation of the total crop for each place (Table 3). The estimates of coverage are based on field observations applied to large scale charts. For Izembek Lagoon detailed aerial photographs permitted a more accurate estimate (McRoy, 1966). The total crops varied from 44 metric tons in Klawak to $2.3 \times 10^6$ metric tons in Izembek Lagoon. These estimates are based on fresh weights. The ratio of fresh weight to dry weight for eelgrass samples is 9 to 1.

The eelgrass standing stock can be divided into the components of leaf standing stock and root and rhizome standing stock (Fig. 3). The means of these components for the ten areas resembled the picture for the total standing stock but the root and rhizome standing stock showed less geographical variation.

The geometric analysis of variance indicated that significant differences existed in the means of root and rhizome standing stock from the ten locations. Three levels of root and rhizome standing stock were apparent: a low level averaged 11 g dry wt/$m^2$ at Craig; a high level averaged 382 g dry wt/$m^2$ at Kinzarof and Izembek Lagoons; and an intermediate level averaged 65 g dry wt/$m^2$ in all remaining areas. For all areas, the roots and rhizomes averaged 35% of the total eelgrass standing stock.

Three levels of leaf standing stock are also evident. A high level averaged 1047 g dry wt/$m^2$ in Izembek and Kinzarof Lagoons; an

Table 3. Estimates of total crops of eelgrass in ten locations on the Alaska coast

| Location | Total Area $m^2 \times 10^4$ | Eelgrass Area $m^2 \times 10^4$ | Total Crop Fresh wt, mt |
|---|---|---|---|
| Klawak | 6.2 | 4.3 | 44 |
| Craig | 32 | 26 | 300 |
| Calder Bay | 86 | 51 | 320 |
| Redhead Lagoon | 89 | 45 | 890 |
| Sawmill Bay | 122 | 97 | 5,700 |
| Stockdale Harbor | 150 | 45 | 570 |
| Kinzarof Lagoon | 1,452 | 871 | 153,000 |
| Izembek Lagoon | 21,800 | 17,000 | 2,300,000 |
| Safety Lagoon | 4,542 | 910 | 47,000 |
| Port Clarence | 4,232 | 420 | 5,000 |

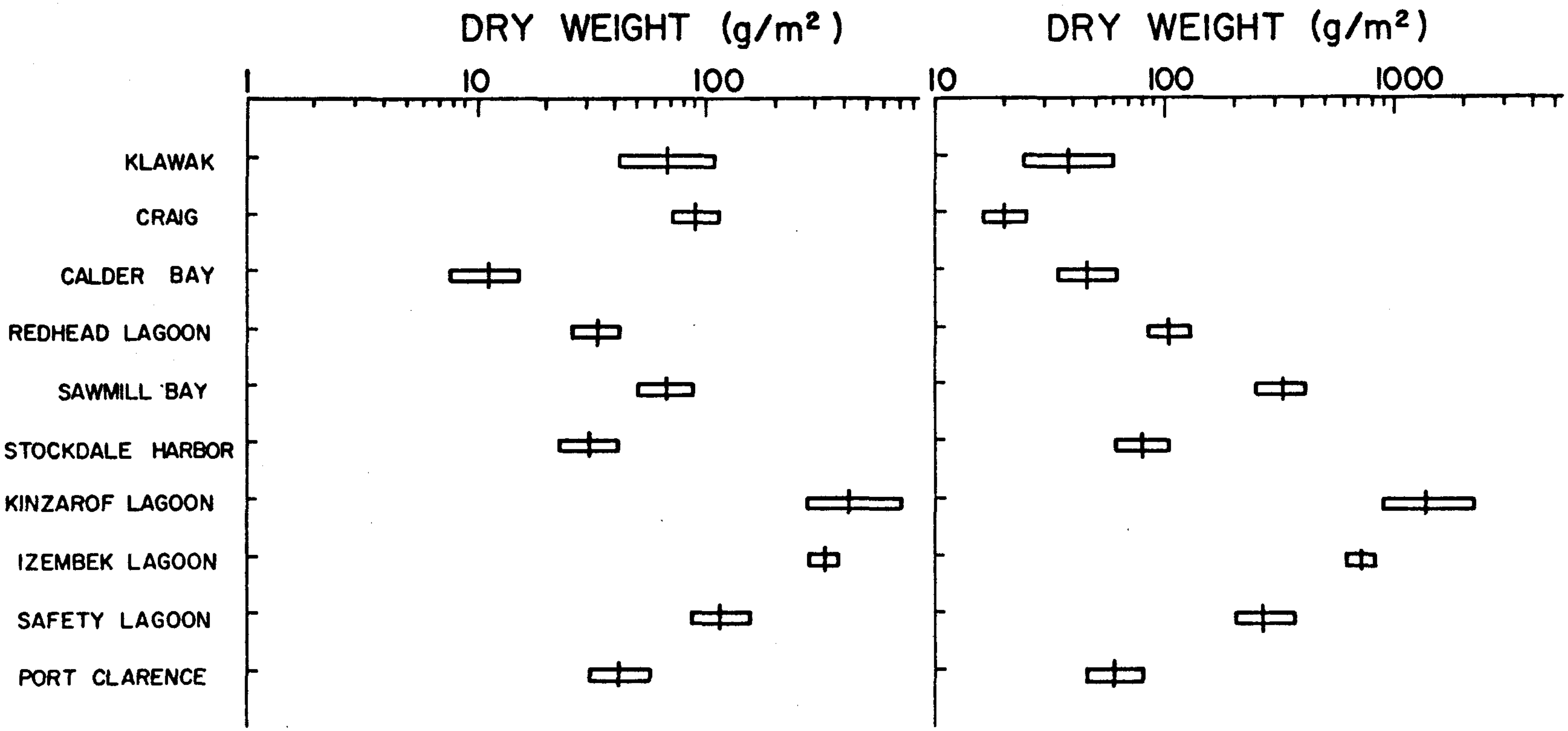

Figure 3. Standing stock of eelgrass roots and rhizomes (left) and leaves (right) in ten locations on the coast of Alaska. Mean and standard error about the mean for replicate observations.

intermediate level averaged 296 g dry wt/m$^2$ in Safety Lagoon and Sawmill Bay; and a low level averaged 57 g dry wt/m$^2$ for the other areas. These levels correspond to the results of the analysis of the total eelgrass standing stock. The standing stock of leaves was directly proportional to that of rhizomes in the ratio of 1.5 to 1.

The standing stock of algae in the eelgrass beds showed somewhat different variations than did the means of eelgrass standing stock in the ten areas (Fig. 4). The statistical analysis of means of algal biomass indicated three levels: a low level with a mean of 2.39 g dry wt/m$^2$ for Craig, Redhead Lagoon, Sawmill Bay, Izembek Lagoon, and Safety Lagoon; an intermediate level with a mean of 28.5 g dry wt/m$^2$ for Klawak, Stockdale Harbor, Port Clarence, and Calder Bay; and a high level with a mean of 393 g dry wt/m$^2$ for Kinzarof Lagoon. Algae composed 0.3% to 72% of the total macrophyte standing stock in the eelgrass beds. These levels of algal biomass reflect the species composition of the algae in the samples. The low level was due almost entirely to the filamentous green algae _Chaetomorpha_ sp. The higher biomass levels included several species of the larger seaweeds (_Fucus_ sp., _Ulva_ sp., and others).

## 2. Caloric Content

Caloric contents were determined for leaves and roots and rhizomes of eelgrass from the ten locations (Fig. 5). The mean caloric content of eelgrass leaves ranged from 3950 to 4382 cal/ash-free g. The differences between means were not statistically significant. The mean

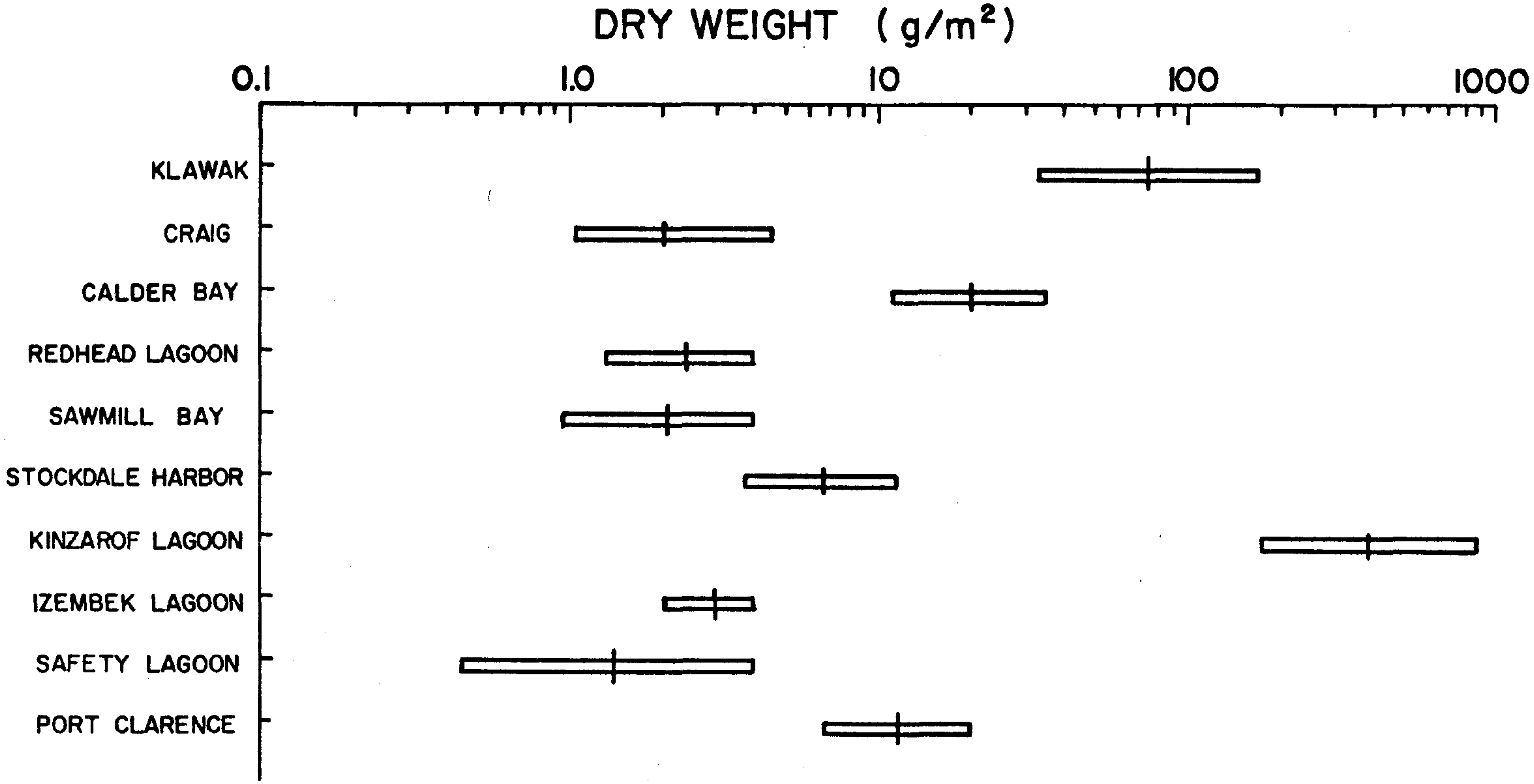

Figure 4. Standing stock of algae in eelgrass beds in ten locations on the coast of Alaska. Mean and standard error about the mean for replicate observations.

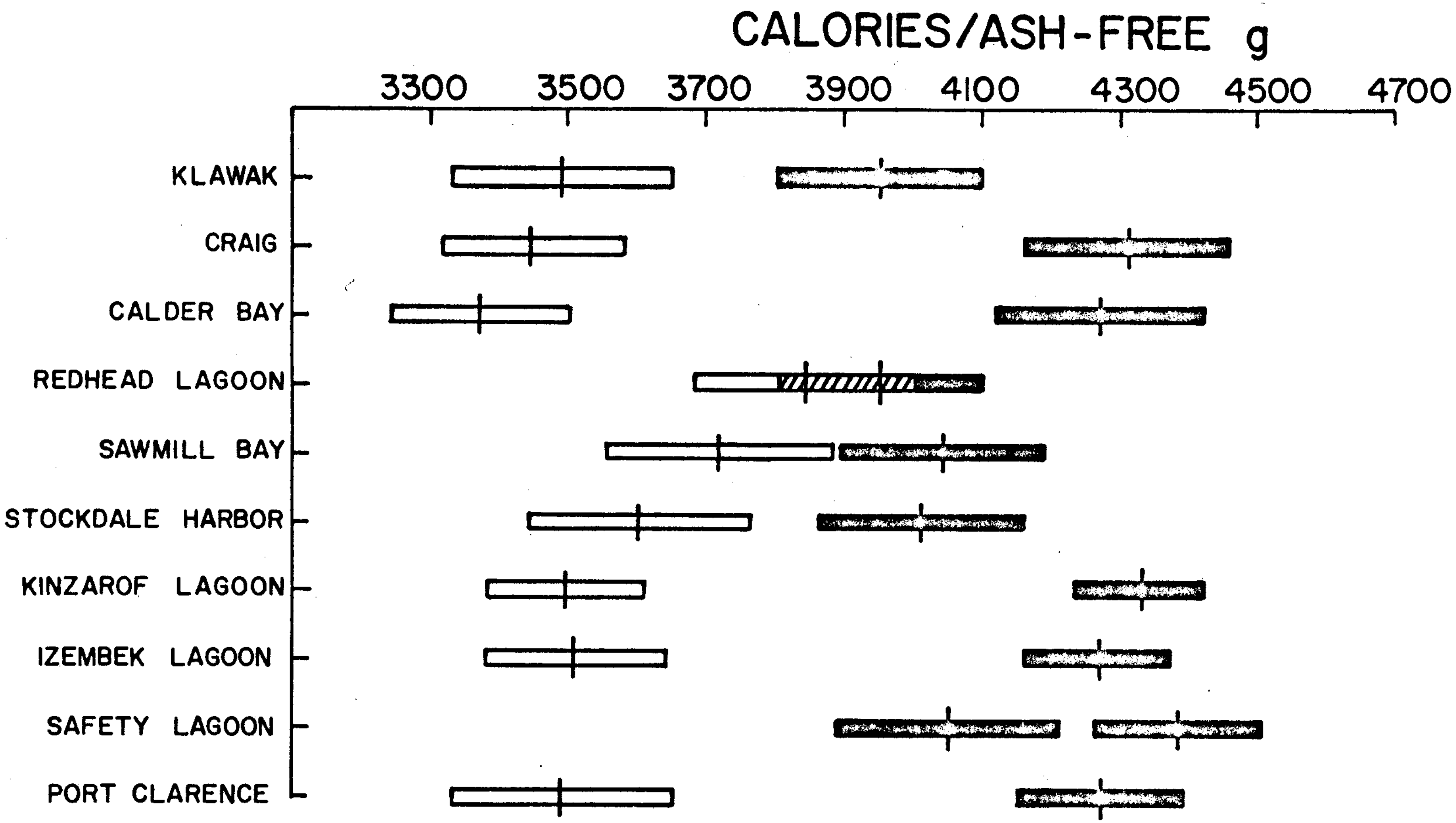

Figure 5. Caloric content of eelgrass leaves (solid) and roots and rhizomes (open) in ten locations on the coast of Alaska. Mean and standard error about the mean for replicate observations.

of all areas for the leaves was 4211 cal/ash-free g.

The caloric content of the roots and rhizomes exhibited more variation than the leaves. The analysis of variance result was not significant at the 0.05 probability level. The mean caloric content of the roots and rhizomes ranged from 3368 to 4047 cal/ash-free g. The average for all areas was 3571 cal/ash-free g.

The average ash content of the 55 samples used in the caloric determinations was 20% of the dry weight.

### 3. Chlorophyll _a_ Concentration

The amount of chlorophyll _a_ in the fresh leaves of eelgrass was measured at six locations on the coast (Fig. 6). The geometric analysis of variance yielded statistically significant differences between the means. Two levels of chlorophyll _a_ concentration in leaves are evident. A high concentration of 1.20 mg/g fresh wt occurred in leaves from Stockdale Harbor. A low concentration with a mean of 0.513 mg/g fresh wt was found in the five other places.

The average chlorophyll _a_ content of the leaves can be combined with the mean leaf biomass converted to fresh weight to provide an estimate of the quantity of chlorophyll _a_ in a unit area of the eelgrass beds. These calculations indicate that chlorophyll _a_ ranges from 0.3 to 1.7 g/m$^2$ in eelgrass beds.

### 4. Turion Density

The number of turions in a square meter is a measure of population

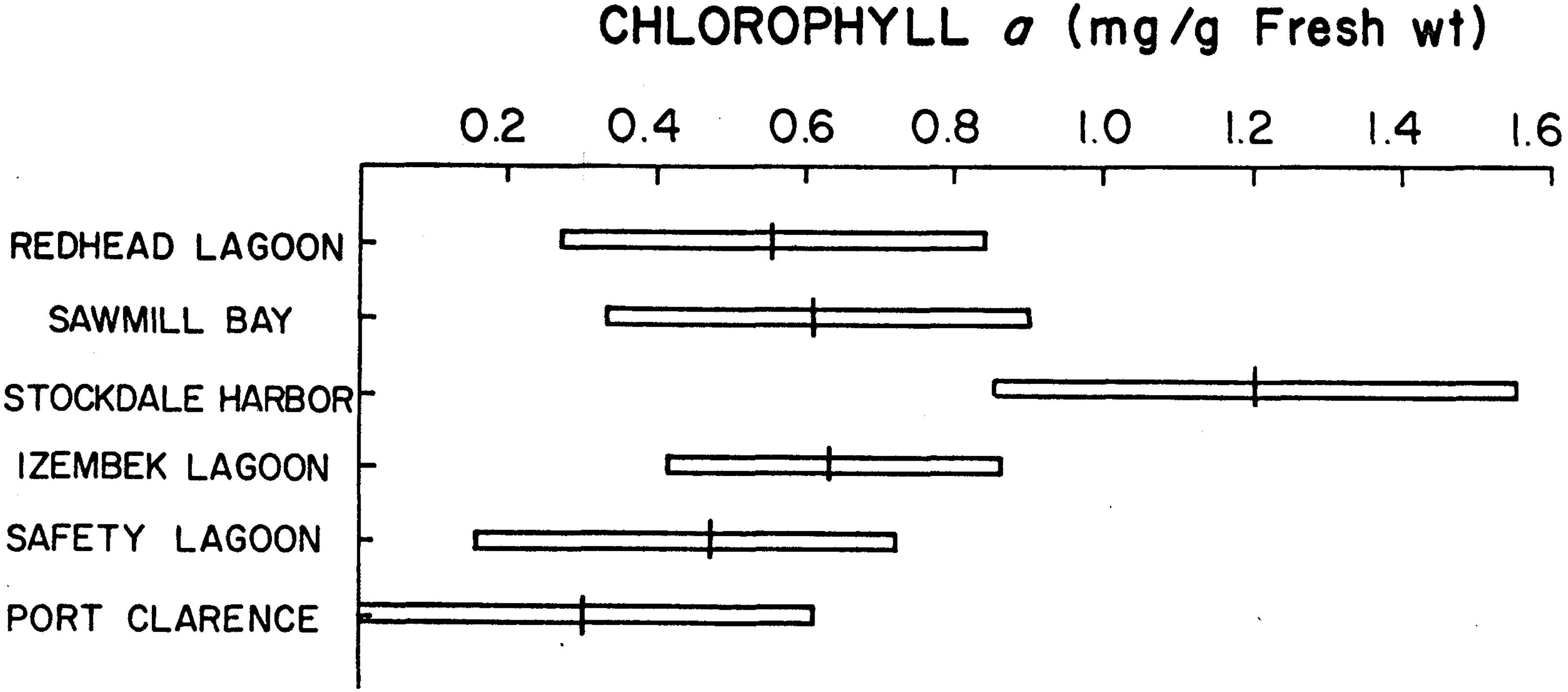

Figure 6. Chlorophyll a concentration in eelgrass leaves in six locations on the coast of Alaska. Mean and standard error about the mean for replicate observations.

density. Two morphologically distinct types of turions exist--vegetative and reproductive or flowering turions. Turion density was measured in seven locations on the coast of Alaska (Fig. 7).

A geometric analysis of variance of the means of total (vegetative plus reproductive) turion density indicated that significant differences existed. Two levels of total turion density appeared. The lower level with an average of 599 turions/$m^2$ included Redhead Lagoon, Sawmill Bay, Stockdale Harbor, Safety Lagoon, and Port Clarence. The high level of density occurred in Kinzarof and Izembek Lagoons; the average was 4576 turions/$m^2$.

The reproductive turion density also resulted in significant differences between the means (Fig. 7). Redhead Lagoon, Sawmill Bay, and Stockdale Harbor with an average of 20 reproductive turions/$m^2$ formed a low density group and Izembek, Kinzarof, and Safety Lagoons, and Port Clarence, with a mean of 192 reproductive turions/$m^2$, constituted a high density group. The flowering turions varied from 3.3% to 4.4% of the total turions.

## 5. Leaf Size

Leaf width was measured in eight locations on the coast (Fig. 8). The geometric analysis of variance showed statistically significant differences existed in the means. The leaves can be placed into three groups on the basis of width. The narrow leaves were found in Craig and in Izembek Lagoon and averaged 2.38 mm. The intermediate width

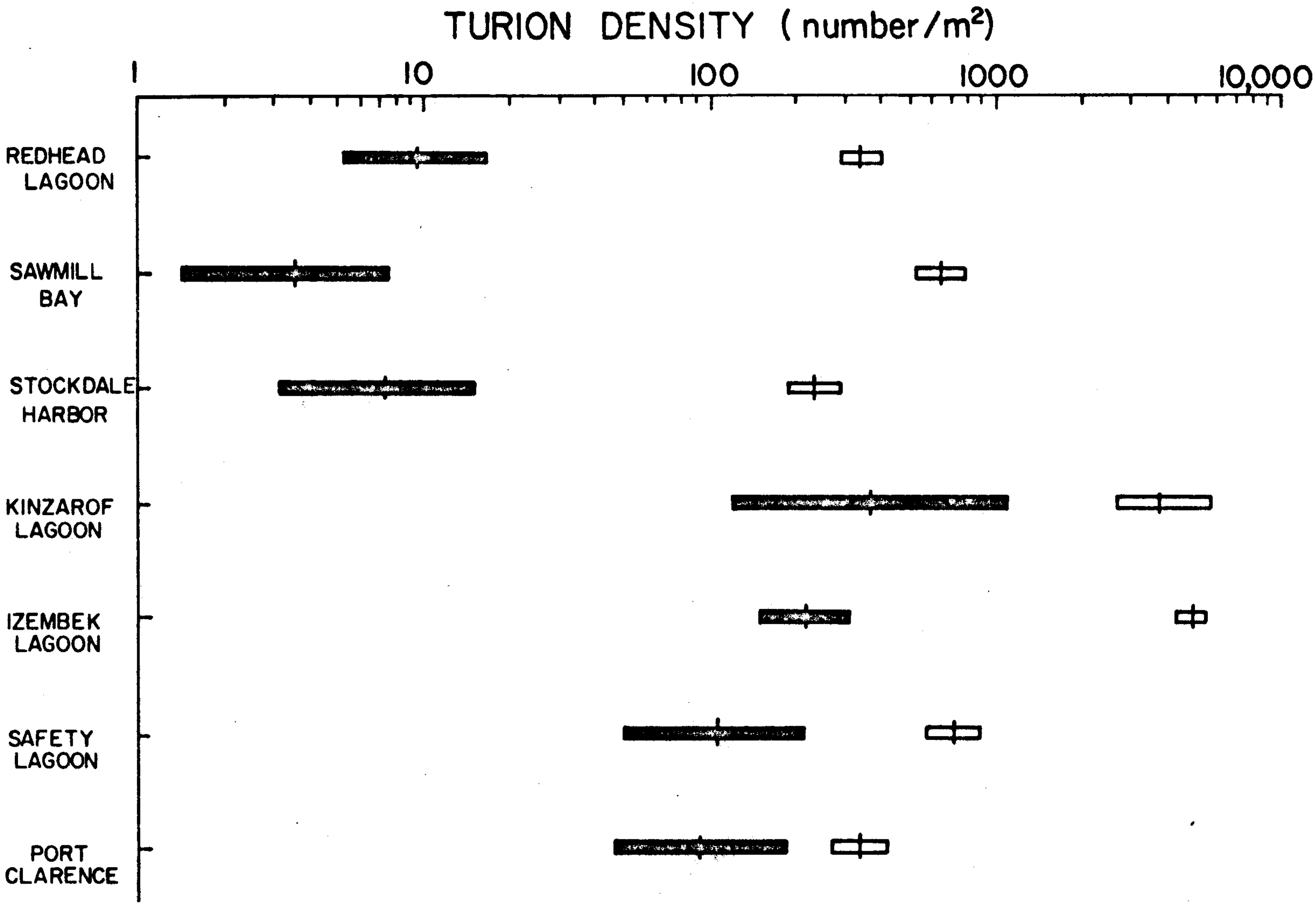

Figure 7. Total turion density (open) and flowering turion density (solid) in seven locations on the coast of Alaska. Mean and standard error about the mean for replicate observations.

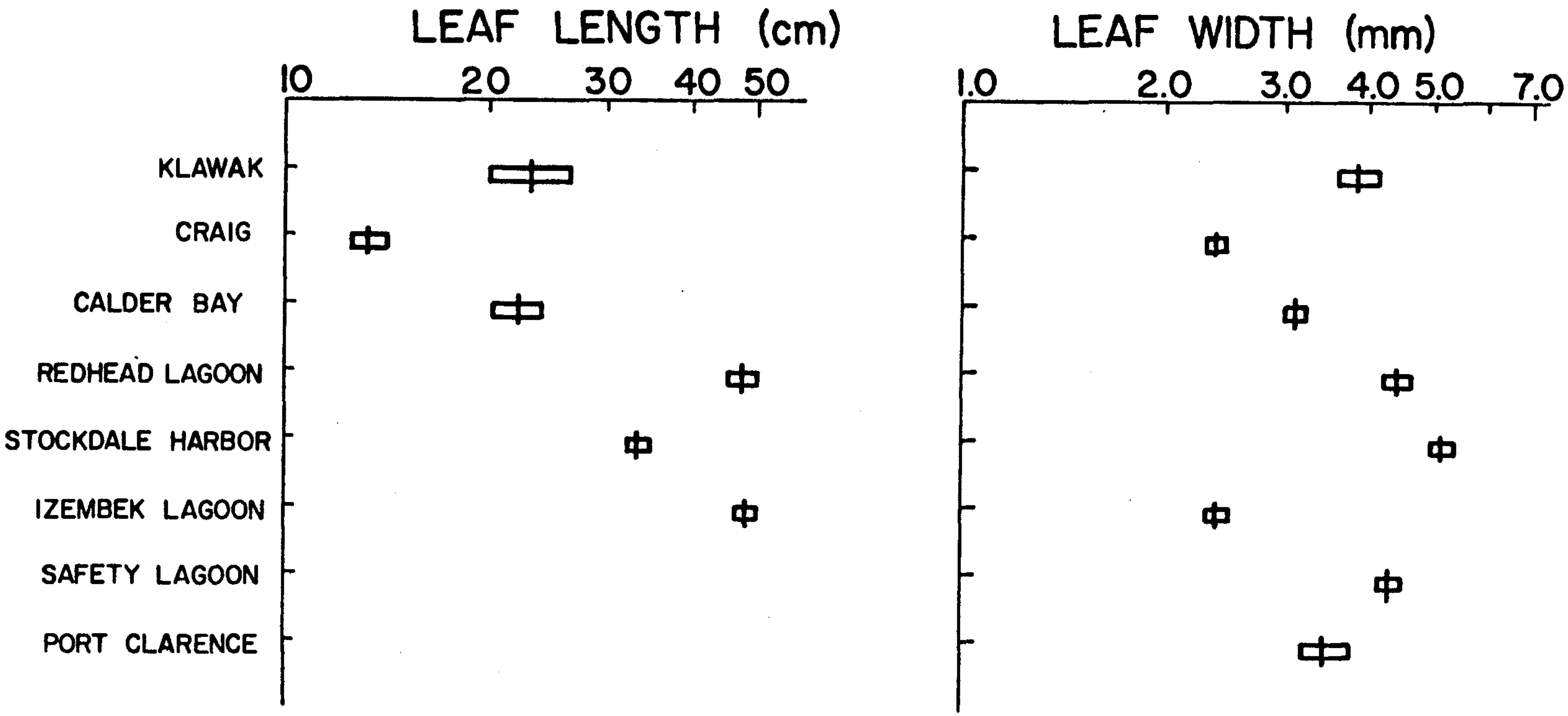

Figure 8. Length and width of eelgrass leaves in eight locations on the coast of Alaska. Mean and standard error about the mean for replicate observations.

leaves were found in Klawak, Calder Bay, Redhead Lagoon, Safety Lagoon, and Port Clarence; these averaged 3.80 mm. The widest leaves were found in Stockdale Harbor and averaged 5.11 mm.

Leaf lengths were measured in six locations (Fig. 8). The geometric analysis of variance indicated that significant differences also existed in the means. Mean leaf lengths increased from 13 cm in Craig to 48 cm in Izembek Lagoon. Similarities occurred between leaves from Izembek Lagoon and Redhead Lagoon and between leaves of Klawak and Calder Bay.

## Discussion

### 1. Comparisons of the Standing Stock

The quantity of eelgrass in an area is the result of the rate of growth and the rate of loss. Similar standing stocks can be the result of low losses, a high growth rate, or some combination of these two. In the ten locations on the coast of Alaska the mean standing stock ranged from 62 to 1840 g dry wt/m$^2$, a 30-fold variation. Part of these differences can be attributed to the different times of sampling, although this is compensated to some extent by the changes in latitude. The difference in standing stock in the ten areas does not indicate a relationship between standing stock and latitude (the increasingly arctic environment in going from southeast Alaska to the Seward Peninsula) but that the standing stock quantitatively and qualitatively depends on the conditions of the local environment.

In this study the maximum standing stocks were all found in shallow lagoons. Apparently the lagoon environment results in a combination of light, temperature, sediments, and nutrients that enhance the growth of eelgrass. Ecological studies of eelgrass have documented the variation in turion density, leaf size, and biomass with gradients in the environment (Setchell, 1929; Phillips and Grant, 1965; Keller and Harris, 1966; Arasaki, 1950; McRoy, 1966).

The biomass of algae in the eelgrass beds in Alaska varied mostly with species of algae and bottom type. In all locations the *Chaetomorpha* sp. occurred entangled in the eelgrass. Where the sediments in the eelgrass bed were not well sorted, larger seaweeds were found attached to stones. In well sorted sediments where few stones occur the algal biomass was restricted to *Chaetomorpha* sp.

Caloric values for eelgrass have not previously been reported. In this study the caloric contents showed no relationship to latitude and the increasingly more arctic conditions. A seasonal cycle in the caloic content is expected.

The chlorophyll *a* measurements are also new for eelgrass. In all cases but one the concentration of chlorophyll *a* in eelgrass leaves was similar. No effects of the varying environment were evident. The one high mean from the leaves of plants from Stockdale Harbor appears to be anomalous. These similar concentrations of chlorophyll *a* in eelgrass leaves from different environments indicate that eelgrass does not adapt to varying light intensities by changing the amount of chlorophyll in the leaf. That is, there do not appear to be sun-adapted and shade-adapted eelgrass plants in Alaska. The plant could be adapted to light by varying leaf size; larger leaves have more chlorophyll a than smaller ones. Chlorophyll a, like the caloric content, would be expected to vary with the season.

The standing stock of eelgrass in Alaska can be compared to that in other areas of the temperate northern hemisphere (Table 4). Reported extremes of eelgrass standing stock are from 5 g dry wt/m$^2$ in Great Pond, Massachusetts to 2445 g dry wt/m$^2$ in Long Island Sound, New York; most reports range from 100 to 1000 g dry wt/m$^2$. The range of mean standing stock in Alaska is comparable to that in other areas. The high value from New York is not likely to be statistically different from the high values found in Alaska. The variation in standing stock in Alaska and throughout the distribution of the species indicates that in most regions the environmental conditions (including grazing) prevent accumulation of the maximum attainable standing stock.

### 2. Indices of Standing Stock

A comparison of the several features of eelgrass standing stock suggests interrelationships between types of measurements that can be used as indices. One of these is the close relationship between total standing stock and total turion density (Fig. 9). These two features of the eelgrass populations are highly correlated (correlation coefficient = 0.82). A regression equation can be used to predict standing stock from density. The regression equation for these data has a

Table 4. Comparison of standing stocks of eelgrass in the Northern Hemisphere

| Location | Standing Stock (dry weight, $g/m^2$) | Source |
|---|---|---|
| Denmark | 272-960 | Petersen, 1914 |
| Denmark | 210-487 | Grøntved, 1957 |
| England | 120 | Burton, 1961 |
| White Sea | 550 | Kireeva, 1965 |
| Black Sea | 166-550 | Zenkevitch, 1963 |
| Sakhalin Island (Bering Sea, USSR) | 31-895 | Vozzhinskaya, 1964 |
| Japan | 70-235 | Kita and Harada, 1962 |
| California | 32-421 | Keller and Harris, 1966 |
| Massachusetts | 5-29 | Conover, 1958 |
| New Jersey | 110-426 | Moeller, 1964 |
| New York | 133-2445 | Burkholder and Dohney, 1968 |
| Alaska | 62-1840 | This study |

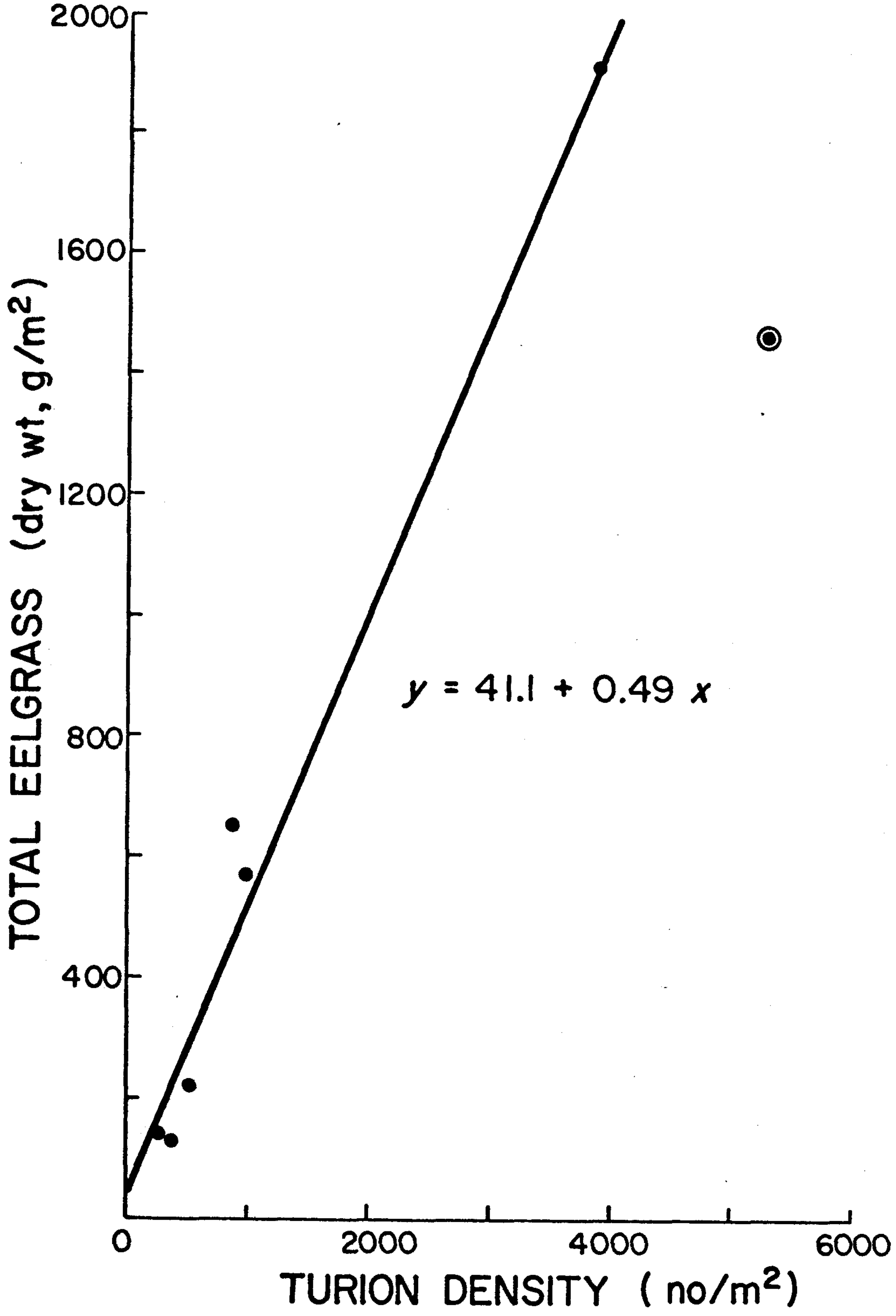

Figure 9. Linear regression of means of total eelgrass standing stock (leaves plus roots and rhizomes) to total turion density (vegetative plus flowering) for seven eelgrass populations on the coast of Alaska.

negative Y intercept that is likely to be a result of the new seed plants that are counted as turions but have a negligible biomass.

Conceivably, direct relationships could exist between turion density and leaf size but the results do not suggest this. However, a direct proportion does exist between leaf dry weight and leaf length (Fig. 10). The correlation coefficient for this relationship is 0.88. A linear equation can be used to estimate leaf standing stock from measurements of leaf length. In this regression the Y intercept is positive as a result of the weight of stems that are included in leaf weight but not measured in determining leaf lengths.

These relationships of the standing stock would permit a rapid survey of eelgrass stocks in a new area. That is, the standing stock of eelgrass in a bay or inlet on the coast of Alaska could be estimated from only measuring the length of the leaves. The regression equations need further substantiation, especially for seasonal differences, to evaluate their general application.

### 3. Production of the Standing Stock

Individual standing stock measurements of eelgrass do not provide an estimate of productivity or production capacity. Eelgrass in shallow water shows a more pronounced seasonal cycle of standing stock than that in deeper water (McRoy, 1966). In shallow water the annual loss of leaves generally occurs in autumn at the end of the growing season; in this case production could be estimated from short term

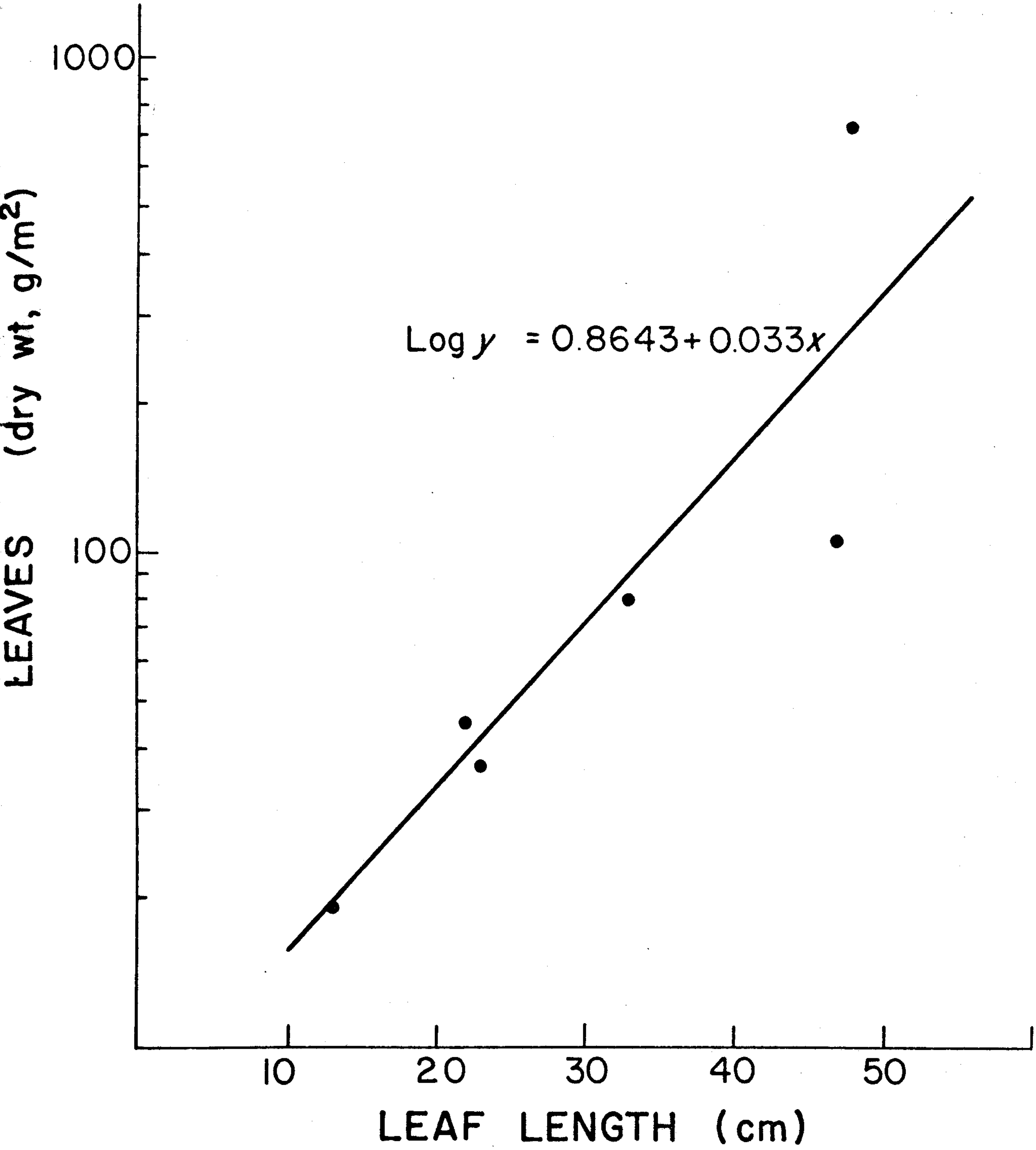

Figure 10. Linear regression of leaf weight to leaf length for six eelgrass populations on the coast of Alaska.

changes in standing stock if measured before the summer maximum. In deep water the oldest leaves are lost at irregular intervals during the year and even short term measurements of the standing stock do not yield accurate estimates of production. Production is best measured from metabolic rates.

McRoy (1966) measured the productivity of eelgrass in Izembek Lagoon using changes in dissolved oxygen in light and dark bottles. These measurements when applied to the standing stock in Izembek Lagoon yield rates of net productivity of 1.46 g $O_2/m^2$ per hour or 0.55 g $C/m^2$ per hour. In a 15-hour day the net production of eelgrass would be 8 g $C/m^2$ or 27 g dry $wt/m^2$. Turnover of the standing stock in Izembek Lagoon based on this rate would be about 2% per day. This estimate is consistent with the early estimate of Petersen (1914) who doubled the standing stock to approximate the annual production of eelgrass in Danish coastal waters.

The estimate of production of eelgrass in Izembek Lagoon is also consistent with the classification of Westlake (1963) of plant communities on the basis of their average annual net production. He ranked tropical marine submerged macrophytes higher than temperate submerged marine macrophytes and both of these were considered to have higher annual productions than the tropical and temperate terrestrial macrophytes. Westlake also reported that temperate submerged marine macrophyte communities are 10 times as productive as coastal phytoplankton communities.

## 4. Utilization of the Standing Stock

The existence of an eelgrass bed in an area means a significant increase in the productivity and standing stock of that area compared to surrounding waters. The diversity of organisms in an eelgrass bed is large. The leaves have large populations of epiphytic algae and invertebrates. Also numerous fishes and invertebrates seek shelter and food in the eelgrass beds. In southeast Alaska and British Columbia eelgrass is an important substrate for herring spawn (Outram, 1961). Eelgrass on the coast of Alaska is also an important food for several species of waterfowl, especially black brant, Canada geese, and emperor geese. The eelgrass lagoons of the Bering Sea coast are heavily utilized by these waterfowl.

Besides the large herbivore populations many predators are attracted by the eelgrass beds. In Alaska, eagles, hawks, falcons, owls, foxes, bears, and many other terrestrial species are closely associated with the eelgrass communities.

The utilization of eelgrass standing stock by black brant can be estimated from known feeding rates. Sincock (1965) determined that the daily consumption of eelgrass by American brant, the closely related Atlantic subspecies, was 180 g dry wt/bird. Assuming the black brant, a bird similar in size and habits, has the same requirement and eats mainly leaves, a black brant would graze in one day about 5.5 $m^2$ in southeast Alaska, about 1 $m^2$ in Prince William Sound and on the Seward Peninsula, and 0.2 $m^2$ on the Alaska Peninsula.

In Izembek Lagoon, the major feeding area on the Pacific flyway, the some 300,000 black brant remove an estimated 3800 metric tons dry weight of eelgrass each autumn. This is about 2% of the total crop or 3.5% of the leaf crop.

A portion of the standing stock of eelgrass is lost each year as detritus. In the lagoons on the Bering Sea coast where eelgrass meadows stretch for miles, a large quantity of organic material is annually washed out to sea. This organic material must be a sizable contribution to the food webs of the coastal waters.

Up to recent times eelgrass has been the raw material for a small insulation industry on the Atlantic coast (Scagel, 1961). No commercial use has been made of eelgrass on the Pacific coast of North America but the standing stocks in Alaska are high enough to support this type of utilization.

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## Chapter 6.

# EELGRASS UNDER ARCTIC WINTER ICE

(to be published in NATURE)

# ABSTRACT

Eelgrass (Zostera marina) was found living in anoxic water under 1 meter of sea ice covered by 0.5 meters of snow in Safety Lagoon near Nome, Alaska. This is the first report of a non-algal marine plant surviving these conditions.

Eelgrass, Zostera marina L., a marine angiosperm that grows on the Pacific coast of North America from the Gulf of California to the Chukchi Sea (1), was found living under the winter sea ice in Safety Lagoon, an embayment of the Bering Sea near Nome, Alaska (Fig. 1). A submarine television system showed the plants to be existing in good vegetative condition in the 20 to 30 cm of water between the sediment and the undersurface of the ice. The unpleasant odor of hydrogen sulfide and subsequent tests with an oxygen probe proved this water to be anoxic.

Observations on the eelgrass beds under the ice, made in March 1969, included quantitative measurements of the standing stock of eelgrass and some measurements of the physical environment as well as the production of a video tape of the in situ conditions. The quantitative samples of the bottom were collected using techniques previously developed for eelgrass (2). The submarine television system and video tape recorder were leased from the Dillingham Corporation; the system performed without failure in spite of wind, low temperature, and operation from a dog sled (pulled by a snow machine in the modern Arctic). Salinity, temperature, and pH were measured in situ using a portable salinometer and pH meter. Dissolved oxygen was also monitored in situ with a polarographic probe. The conditions in March are here compared with those in September 1968 during the ice-free season (Table 1).

The television system, used with a mercury vapor lamp, clearly showed eelgrass living freely in the shallow space between the sediment and ice. The zone of ice growth at the water-ice interface was evident. Intermediate in the ice was seen a layer of pieces of old eelgrass leaves. These were the mature leaves of the previous growth season that had been trapped in the ice shortly after the lagoon froze in the autumn.

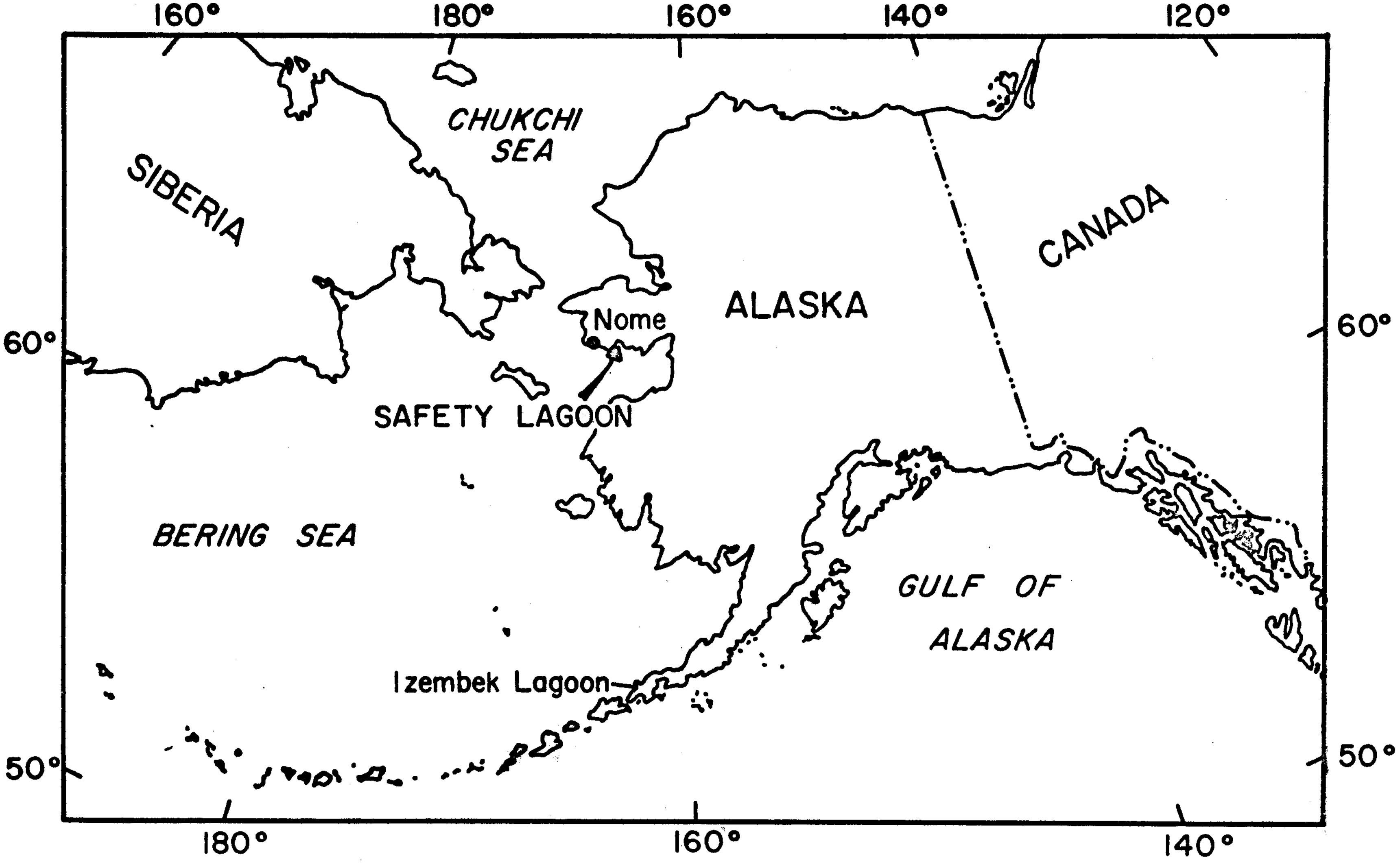

Figure 1. Map of Alaska showing the location of Safety Lagoon.

Examination of plants retrieved from under the ice indicated that some new roots, rhizomes, and leaves had grown since the previous September. These tissues are morphologically distinct from the older ones and their production is usually associated with the onset of spring. Their presence suggests that the plants were not dormant but actively metabolizing.

The water surrounding the plants under the ice was saline and very near its freezing point. No oxygen could be detected in this water at any time. The pH of 7.09 is very low for a marine environment and reflects the anoxic conditions (3).

In this region, September marks the end of summer when the Bering Sea is ice free. Ice covers the lagoon from October through May. March is the period when the ice is thickest and most widespread. Ice on Safety Lagoon in 1969 was 100 cm thick and covered by 50 cm of snow. The anoxic water under the ice indicates that continuity of the lagoon with the Bering Sea was interrupted by the ice. In summer the lagoon circulates freely with the ocean and water entering the lagoon retains its oceanic properties. Oxygen must be present there until midwinter since the lagoon is a favorite fishing place in early winter for the Eskimos of Nome.

The quantitative samples of eelgrass indicate a reduction in biomass and density of the standing stock from September to March (Table 1). This reduction is an annual event in the cycle of the plant and represents the sloughing off of the flowering plants and of the oldest leaves and rhizomes (4). The annual cycle of standing stock of eelgrass in Safety Lagoon is comparable to that in Izembek Lagoon 650 miles to the south on the Bering Sea coast (Fig. 1; 2).

Table 1. Comparison of some seasonal differences in the eelgrass beds in Safety Lagoon.

| | Environment | | | | | | Eelgrass | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Sampling Date | Temperature °C | Salinity o/oo | pH | Oxygen % | Ice Thickness cm | Snow Cover cm | Dry Wt g/m$^2$ | Standard Error | Plant Density no/m$^2$ | Standard Error |
| 11 Sept 68 | 8.5 to 10.3 | -- | -- | Saturated | 0 | 0 | 357 | ± 43 | 770 | ± 62 |
| 12 Mar 69 | -1.8 | 30.82<br>31.35 | 7.09 | 0 | 100 | 50 | 134 | ± 42 | 619 | ± 390 |

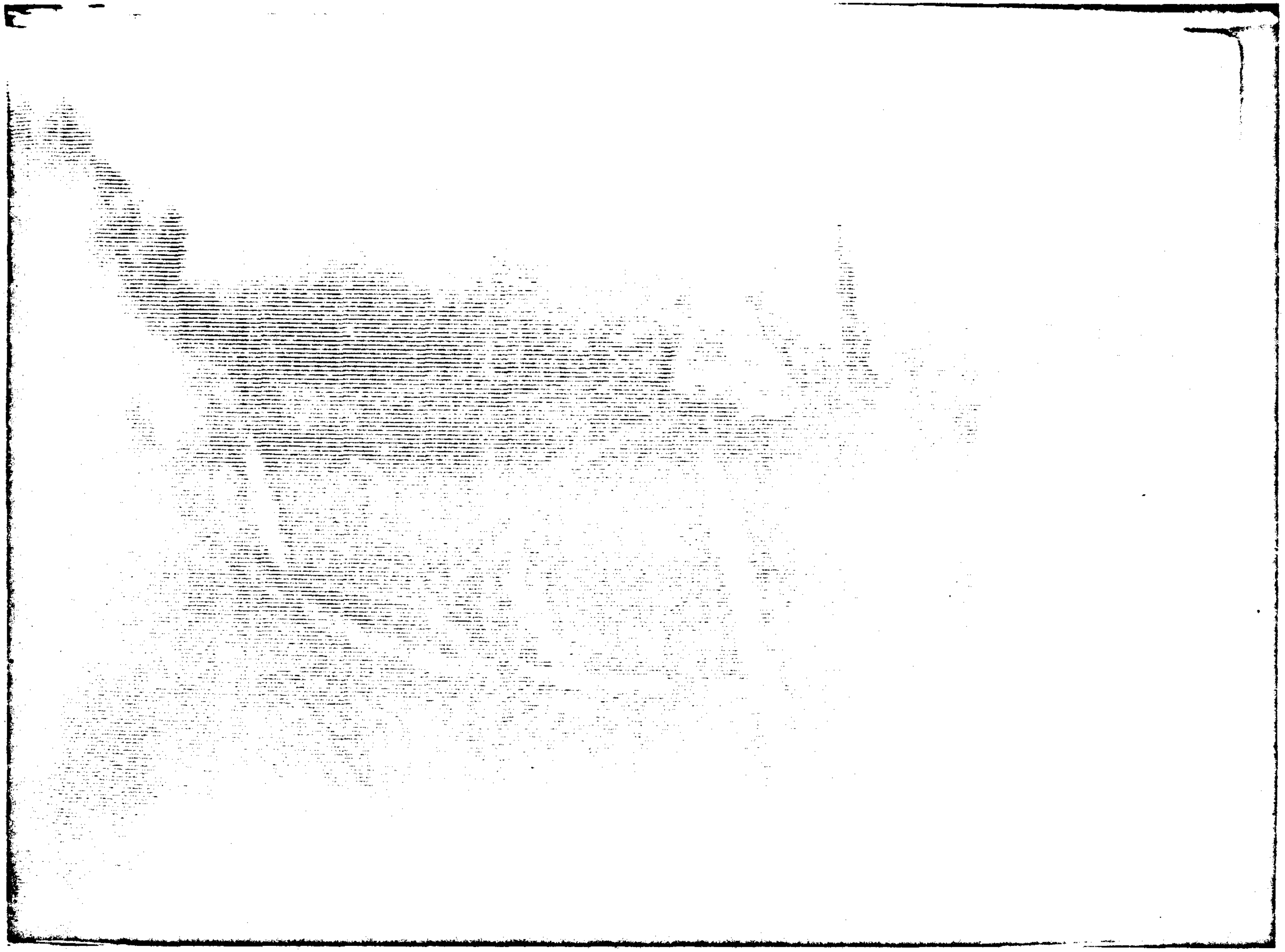

Figure 2. Photograph of video tape from submarine television system showing eelgrass (lower) under the sea ice (upper) in Safety Lagoon.

The bottom samples also included a gastropod, a bivalve, a polychaete, and a filamentous alga all living in the anoxic environment with the eelgrass.

The survival of organisms under ice in the arctic winter has long intrigued biologists. Macroscopic and microscopic marine algae living under winter sea ice have been reported (5). This is the first report of a non-algal marine plant surviving these conditions. The anoxic environment adds another dimension to the problems of survival in the polar night.

Eelgrass in Safety Lagoon must endure the winter with a low intensity and quantity of light. Consequently photosynthesis can proceed only at a very low rate and the source of nutrition becomes the basic problem of survival. Wilce (5) has proposed that benthic algae in the high Arctic subjected to complete darkness for a portion of the winter are capable of facultative heterotrophic nutrition. Many algae, especially microscopic forms, are known to have some capacity for utilizing organic compounds as a carbon source. Angiosperms, however, are thought to rely exclusively on the process of photosynthesis for nutrition. The survival and growth of eelgrass under the ice probably does not involve heterotrophy but may result from different rates of photosynthesis and respiration with varying temperature and light.

The rate of respiration in plants is depressed by cold. Kanwisher (6) demonstrated that the seaweed Laminaria sp. under the ice in Labrador seasonally shifted its metabolism to respire at lower rates in winter than in summer at the same temperature. In addition to the depressed respiration-temperature curve he confirmed Kneip's (7) finding that metabolism in arctic seaweeds decreased as winter progressed. A depressed metabolic rate permits stored food compounds to last longer and thus helps prevent starvation.

Since at low light intensities the temperature coefficient ($Q_{10}$) of photosynthesis is approximately unity (8) the small amount of photosynthesis that does occur can still result in a net grain in organic matter formed over that utilized by depressed respiration. As winter progresses toward spring the increasing day length (but not necessarily light intensity) and decreasing respiration are a positive feedback mechanism enhancing survival and growth. Breakup of the sea ice should result in a spurt of rapid growth.

Preliminary experiments have shown that eelgrass has a depressed respiration temperature curve in winter (10) permitting maximum benefit from what little light is available. The new root, rhizome, and leaf tissues observed in the eelgrass collected in March add support to the mechanism outlined above.

The anoxic conditions present another problem for the survival of eelgrass in Safety Lagoon. Anaerobic metabolism can occur commonly in aquatic plants. Broekhuysen (9) reported that an eelgrass meadow in the Netherlands became anoxic nightly without apparent harm to the plants. McRoy (2) showed that the pathway of anaerobic metabolism is readily invoked in eelgrass tissues. Eelgrass in Safety Lagoon may need to tolerate an anoxic environment for weeks or months.

A possible relief from anaerobiosis is the oxygen produced during photosynthesis. Eelgrass, like its freshwater relatives, undoubtedly stores this oxygen in the lacunar system of the leaves (11). The oxygen can then be recycled in respiration, providing a respite in anaerobiosis.

In most freshwater plants the product of anaerobic metabolism is ethyl alcohol (12) and this may well be true for eelgrass.

C. Peter McRoy
Institute of Marine Science
University of Alaska
College, Alaska 99701

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# Chapter 7.

## PHOSPHATE ABSORPTION IN EELGRASS

(to be published in LIMNOLOGY AND OCEANOGRAPHY)

# PHOSPHATE ABSORPTION IN EELGRASS[1]

C. Peter McRoy and Robert J. Barsdate

Institute of Marine Science
University of Alaska
College, Alaska 99701

Running title: Phosphate Absorption in Eelgrass

# ABSTRACT

The absorption of phosphate in eelgrass (Zostera marina) was studied using $^{32}P$ in a partitioned container where leaves were separated from roots and rhizomes. Absorption, which was greatest in the light, occurred through both the leaves and roots, and the absorbed phosphorus was transported rapidly to all parts of the plant. It therefore appears that eelgrass can utilize phosphate from sediments and water. Phosphate removed from solution by the roots and rhizomes was returned in part to the surrounding water through the leaves, suggesting that in nature seagrass may act either as a sink or a source for dissolved phosphorus in estuarine waters.

Shallow, protected bays and lagoons frequently harbor dense populations of seagrasses. In temperate and higher latitudes of the coast of North America eelgrass, Zostera marina, is the dominant seagrass. The seagrasses are spermatophytes, monocotyledonous angiosperms; they have all the structures typical of vascular flowering plants--roots, rhizomes, leaves, flowers, seeds, and a vascular system with a xylem and a phloem. These structures distinguish the seagrasses from the macrophytic marine algae (seaweeds).

Eelgrass and the associated community is important in the biogeochemical cycle of nutrients in the ocean. Eelgrass communities have standing stocks and productivities that greatly exceed those of the surrounding ocean. In Alaska, eelgrass is the principal food of hundreds of thousands of migratory waterfowl. In addition fresh or detrital eelgrass is the sustenance of numerous species of invertebrates and fishes, many of which are commercially harvested.

In this study we examined the sites of uptake and subsequent transport of phosphate in eelgrass using radioactive phosphorus as a tracer. The sites of nutrient uptake have been investigated rather intensively in freshwater plants but no studies exist for marine plants.

We are grateful to Mr. Robert D. Jones, Jr., Refuge Manager of the Aleutian Islands National Wildlife Refuge, Bureau of Sport Fisheries and Wildlife, for assistance and for the use of the facilities of the Izembek Marine Station. The advice and criticisms of Drs.

Donald W. Hood and John J. Goering are most appreciated.

## Background Studies

The root and vascular systems in aquatic plants are reduced in comparison to those of terrestrial plants. These reductions plus the small amount of cuticle on epidermal cell walls led to the generalization that nutrients were absorbed primarily through the leaves of submerged plants and that the roots only functioned for attachment (Arber, 1920). Sutcliffe (1959, 1962) reviewed the absorption of mineral salts in plants and stated that in the aquatic plants this occurs mainly through the leaves. Foliar absorption has been demonstrated in _Elodea_ sp., _Vallisneria_ sp., and other freshwater vascular plants (Olsen, 1953; Arisz, 1953). Evidence for the absorption of nutrients by roots is principally from studies relating the abundance and distribution of aquatic plants in lakes to the chemistry of the sediments (Rickett, 1921, 1924; Veatch, 1933; Wilson, 1939, 1941; Moyle, 1945). Evidence has been presented supporting both the view that leaf absorption dominates and the view that root absorption dominates (Sculthorpe, 1967).

The phosphorus cycle has been investigated in considerable detail for the open sea (Armstrong, 1965). Pomeroy (1963) has studied the cycle of phosphorus in coastal waters. Only a few reports relate the phosphorus variations in shallow waters to standing stocks of seagrasses. Conover (1958) measured the quantities of phosphate and benthic plants, including eelgrass, in Great Pond, Massachusetts and found the highest concentration of phosphate in the regions of the estuary containing the highest biomass of seagrasses. In another study, Rochford (1951) determined that high concentrations of phosphate in interstitial waters resulted in high standing stocks of eelgrass. Other evidence on the role of seagrasses in the cycling of phosphorus is available from studies of the experimental fertilization of marine bays. Raymont (1947) found, to his distress, that adding sodium nitrate and superphosphate fertilizer to a sea loch on the coast of Scotland resulted in prolific growths of eelgrass. In a bay of the Adriatic Sea, Buljan (1957) added a phosphate fertilizer that produced large crops of benthic algae, phytoplankton, and seagrasses. These studies indicate that phosphate in the water as well as in the sediment is important to growth of the seagrasses.

Radioactive phosphorus, $^{32}P$, has been used as a tracer in numerous studies of phosphate movement in marine and freshwater organisms. Pomeroy (1963) measured rapid turnover rates, ranging from 1 to 70 hrs, of phosphate in coastal waters using $^{32}P$. Odum _et al_. (1958) studied $^{32}P$ uptake in some of the larger marine algae and concluded that the rate was not directly related to metabolism but that both were related to the surface to volume ratio of the algae. The authors were surprised to find similar uptake rates in the light and dark in a given tissue. Kuenzler (1961) used $^{32}P$ to determine the phosphorus budget of a mussel population. Ball and Hooper (1963) used it to study a trout stream ecosystem. All of these studies show that phosphate is a highly mobile compound in the ecosystem and that $^{32}P$ is an effective tracer of phosphate movements in organisms.

The general path and uptake of phosphorus in plants (mainly terrestrial) has been determined using $^{32}P$ (Stumpf, 1952). Phosphate in the soil is absorbed by the roots of an actively transpiring plant and enters the xylem where it is rapidly transported to the extremities of the plant. Lateral exchange from the xylem into the phloem also occurs and phosphate is transported in both directions. Experiments by Brewer and Bramley (1940) demonstrated that phosphate accumulates in the portions of the plant undergoing most rapid growth. Phosphate is transported from an accumulation site to any region of the plant that develops intense metabolic activity.

## Methods

### 1. Laboratory Studies

The experimental procedure used a technique similar to that of Frank and Hodgson (1964) and involved placing individual eelgrass plants, cleaned of epiphytes, in 250 ml polyethylene containers partitioned by a layer of paraffin (Fig. 1). The water surrounding the roots and rhizomes of the turions (a clump of leaves attached to a rhizome) was isolated from that around the leaves and stem by the layer of paraffin sealed by a fat with a low melting temperature. The upper and lower compartments were then filled with a standard sea water (S=31 °/₀₀) that had been passed through an 0.45 μ filter. The phosphate concentration of this water was 25 μgP/liter as determined by the single solution method of Murphy and Riley (1962). Septum stoppers in the 250 ml polyethylene containers permitted addition of isotope to either compartment.

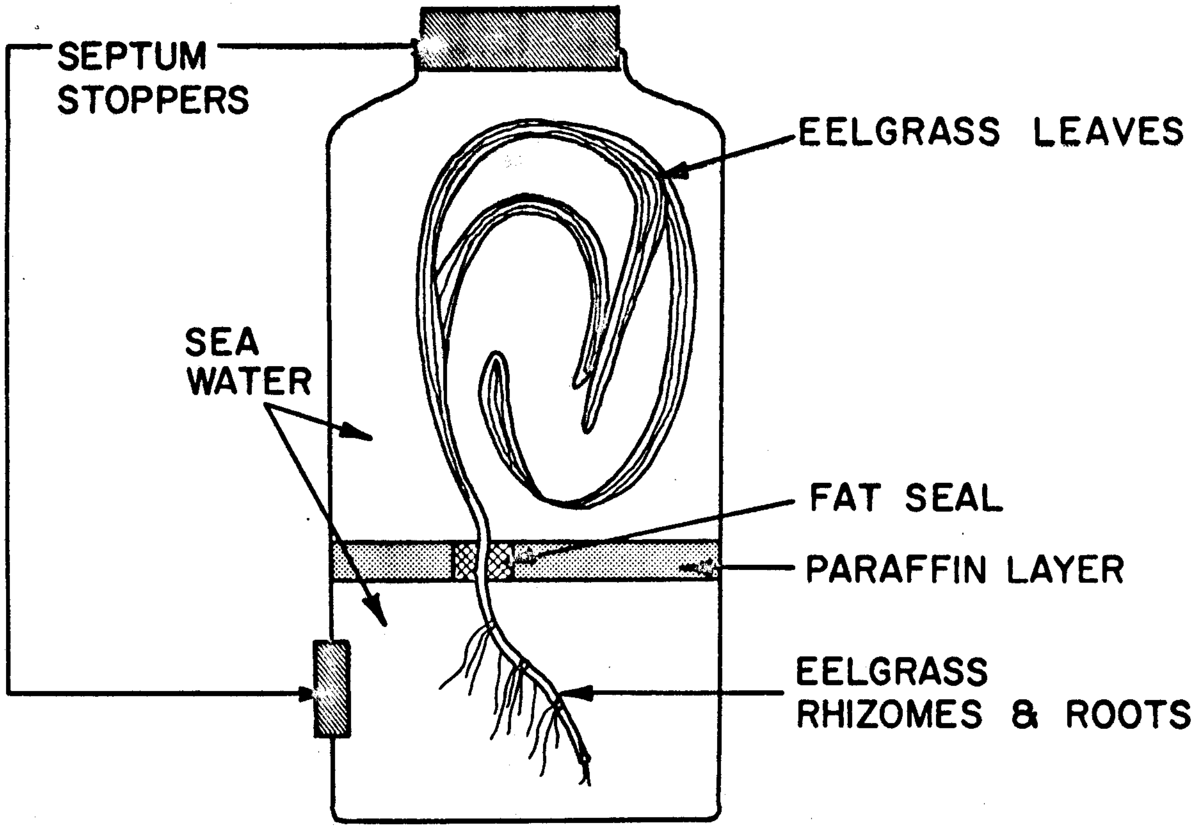

Figure 1. Experimental arrangement in 250 cc polyethylene container for measuring the uptake of $^{32}P$ by eelgrass.

In these experiments 5 or 10 μc of carrier-free radioactive phosphorus, $^{32}P$, as phosphate were added to a compartment. On termination of an experiment a water sample was removed from each compartment, the compartments drained, and the eelgrass turion removed. The turion was immediately bisected at the base of the stem and the two pieces were rinsed with distilled water. The plant material was further dissected into roots, rhizome, stem, leaf base, leaf middle, and leaf tip and all pieces were then dried separately at 90°C. Division of the tissue prevented movement of tracer during drying. Dried plant and water samples were counted on metal planchets with a Picker Model 600010 scaler equipped with a thinwindow gas flow Geiger-Müller detector.

The experimental design consisted of four time series: (1) tracer added to upper compartment (containing leaves and stem), container incubated in the light; (2) as before, container incubated in the dark; (3) tracer added to lower compartment (containing roots and rhizome), incubated in the light; (4) as before, incubated in the dark. The light source was four gro-lux fluorescent bulbs placed about 5 cm in front of a glass water bath holding the experimental containers. The water bath was kept at 15°C in all experiments. This work was done in the field station at Izembek Lagoon, Alaska where fresh eelgrass was readily available.

The phosphorus content of eelgrass from Izembek Lagoon was determined by the single solution method referenced above after chloric acid digestion and neutralization with sodium carbonate.

2. Field Studies

To supplement the laboratory experiments we performed a study of the uptake of $^{32}P$ by eelgrass in the natural, undisturbed environment. In this experiment 1.5 μc of carrier-free $^{32}PO_4$ added to 1 ml of filtered sea water was injected at a depth 7 cm below the sediment surface in an eelgrass bed in the lower intertidal. The syringe was left in place during the experiment, a period of 24 hrs covering 2 tide cycles, to prevent loss of tracer through a channel of disturbed sediment and to determine precise location of the injection site. After 24 hrs, samples of eelgrass and sediment were collected 2 cm and 6 cm away from the site of injection. After drying to constant weight the radioactivity of the samples was measured.

## Uptake in Partitioned Containers

The uptake of $^{32}P$ was studied using a series of individual experiments to examine the variation in rate and amount of light and dark uptake. The uptake of $^{32}P$ followed a similar pattern in all conditions (Fig. 2). A portion of the activity also was transferred via the plant from the upper water to the lower water, or the lower water to the upper water; however, the site of maximum $^{32}P$ accumulation and the relative activity of the various tissues were influenced by the experimental conditions. Some of the variability apparent in Fig. 2 is the result of plant-to-plant differences, as individual plants were used for each time interval under each set of conditions. Initial uptake was extremely rapid, but after 125 min the rates slowed and continued to

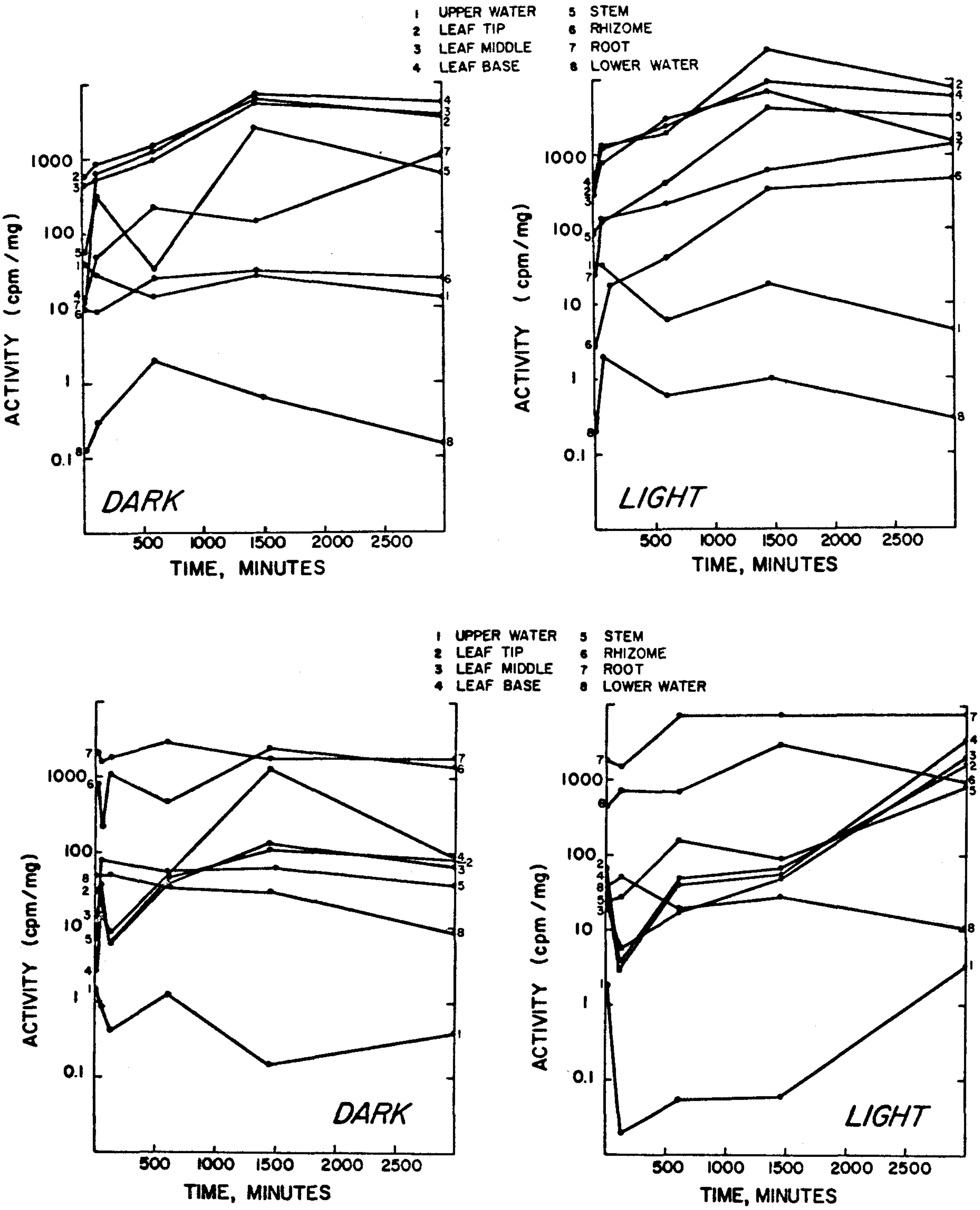

Figure 2. Light and dark absorption of $^{32}P$ by eelgrass as a function of time. Upper: tracer added to leaves compartment. Lower: tracer added to roots and rhizomes compartment.

approach an equilibrium during the longer experiments. The longest experiments lasted for 3000 min. In each experiment $^{32}P$ was absorbed by the leaves or roots in light or dark and transported throughout the plant.

The concentration factor is the ratio of the activity in the plant to that in the surrounding water and indicates the sites of accumulation of phosphate in the plant (Fig. 3). When $^{32}P$ was added to the roots and rhizomes the concentration factors after 3000 min were lowest in rhizome (87) and highest in the leaf base (1011) and root (743) in the light; in the dark these values ranged from lowest in the stem (96) to highest in the leaf base (215) and leaf tip (213).

The second series of experiments involved adding the $^{32}P$ to the upper compartment (Fig. 4). After 3000 min the concentration factors were lowest in the leaf middle (382) and highest in the roots (4823) and leaf tip (1806) in the light. In the dark after 3000 min the stem was lowest (47), and the roots (695) and leaf base (455) highest. In most cases maximum accumulation was in the roots or in the leaf base. Accumulation varied considerably between the light and dark. Concentration factors in the light were always higher than in the dark.

The determination of phosphorus in the tissues of eelgrass yielded the following distribution: leaves 7 µg/g dry wt, stem 17 µg/g dry wt, roots and rhizome 5 µg/g dry wt. Using the concentration of phosphate in the water (25 µgP/liter) and the distribution of activity after 3000 min, we made some quantitative estimates of phosphate transport and distribution in the system (Table 1).

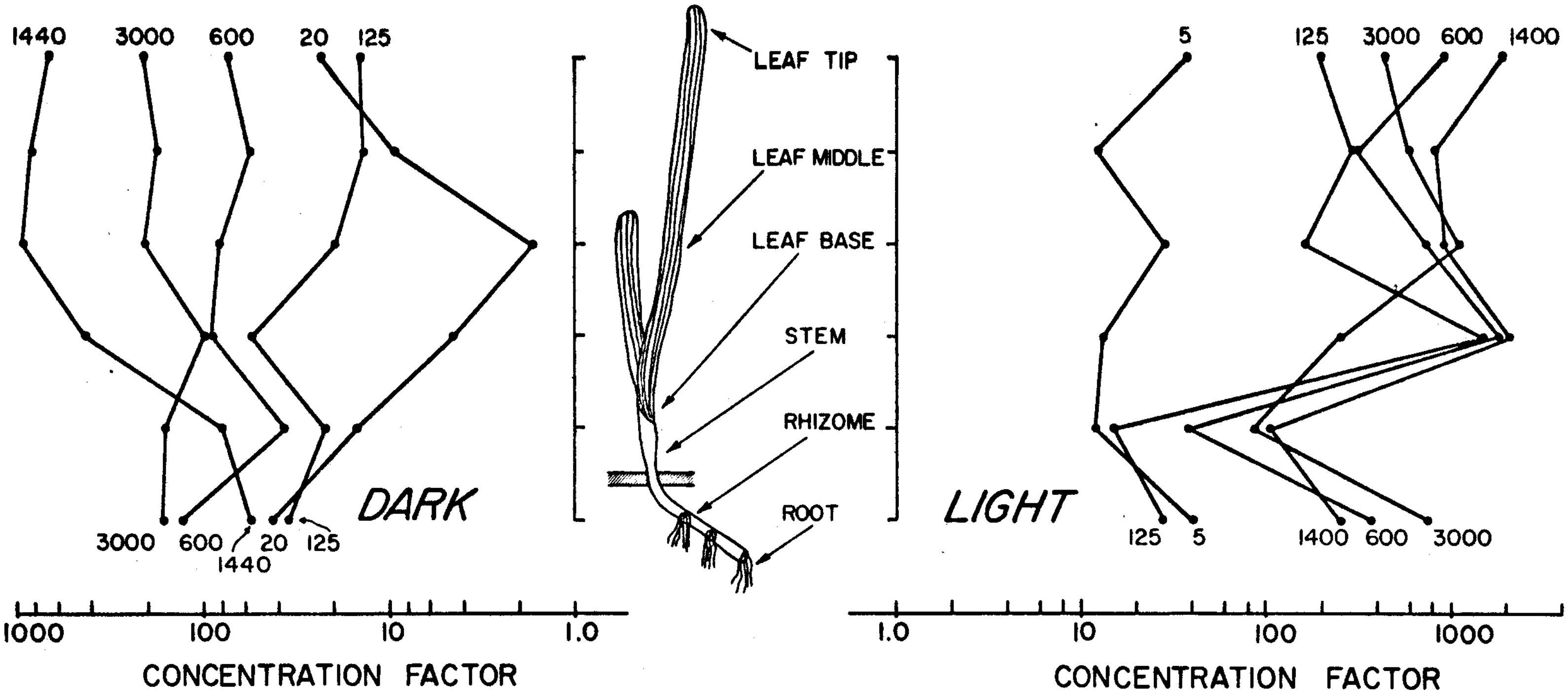

Figure 3. Concentration factors (ratio of $^{32}P$ activity of 1 g tissue to 1 cc water) for eelgrass. Numbers with each line of data points indicate incubation time in minutes. Tracer added to roots and rhizome compartment.

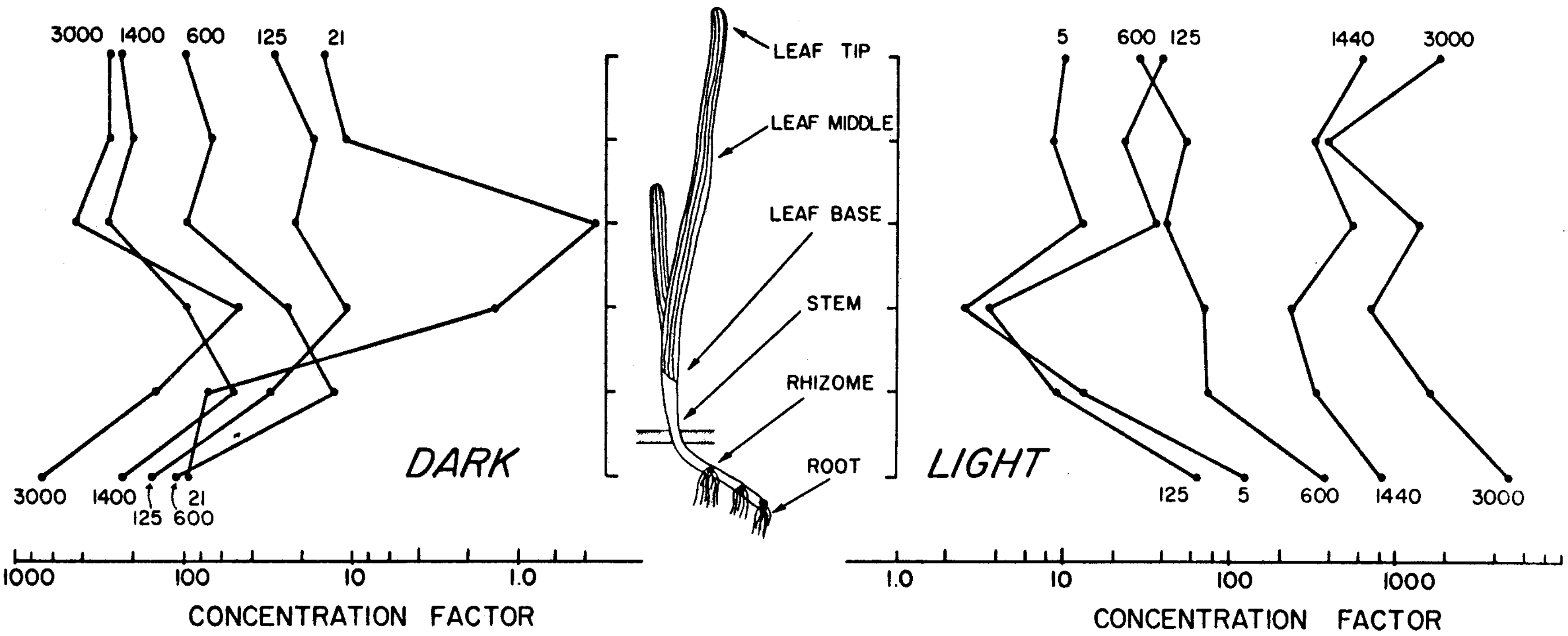

Figure 4. Concentration factors (ratio of $^{32}P$ activity of 1 g tissue to 1 cc water) for eelgrass. Numbers with each line of data points indicate incubation times in minutes. Tracer added to leaves compartment.

Table 1. Distribution of phosphorus (in initial conditions) and of $^{32}P$ tracer after 3000 min in experimental containers that consisted of a system with 160 cc seawater in upper compartment, a plant and 80 cc seawater in lower compartment.

| | | Initial Conditions | | | $^{32}P$ Tracer |
|---|---|---|---|---|---|
| Compartment or Tissue | | Mass g | Phosphorus µg | % | % Total activity after 3000 min |
| I. $^{32}P$ Added to Lower Compartment | | | | | |
| Upper water | Light | 160 | 4 | 0.4 | 33 |
| " " | Dark | 160 | 4 | 0.6 | 8 |
| Leaves and stem | Light | 0.084 | 660 | 65.6 | 9 |
| " " " | Dark | 0.046 | 587 | 81.8 | 0.5 |
| Roots and rhizome | Light | 0.038 | 340 | 33.8 | 8 |
| " " " | Dark | 0.034 | 124 | 17.2 | 4.4 |
| Lower water | Light | 80 | 2 | 0.2 | 51 |
| " " | Dark | 80 | 2 | 0.3 | 87 |
| II. $^{32}P$ Added to Upper Compartment | | | | | |
| Upper water | Light | 160 | 4 | 0.4 | 66 |
| " " | Dark | 160 | 4 | 0.6 | 95 |
| Leaves and stem | Light | 0.071 | 780 | 79.9 | 22 |
| " " " | Dark | 0.063 | 460 | 72.3 | 2.9 |
| Roots and rhizome | Light | 0.068 | 190 | 19.5 | 2.1 |
| " " " | Dark | 0.025 | 170 | 26.7 | 2.5 |
| Lower water | Light | 80 | 2 | 0.2 | 2.2 |
| " " | Dark | 80 | 2 | 0.3 | 0.04 |

Each experimental situation was similar: the eelgrass contained more than 99% of the phosphorus in the system. The leaves, because of their higher biomass, contained 2 to 3 times the phosphorus in the roots and rhizomes. The distribution of activity after 3000 min reveals a picture very different from the one the activity or the concentration factors portray. When the tracer was added to the lower compartment in the light, 33% of the tracer was transported through the plant and released in the upper water, 51% remained in the lower water, and 17% was absorbed by the plant. The distribution of tracer in the dark experiment revealed that 87% stayed in the lower water, 8% was released in the upper water, and 5.2% was absorbed by the plant.

The distribution of tracer added to the upper water after 3000 min was equally interesting. In the light, 66% remained in the upper water, 2.2% was released to the lower water, and 24.1% stayed in the plant. In the dark, 94% of the activity remained in the upper water, 5.4% was absorbed by the plant, and 0.04% appeared in the lower water.

From these data it is possible to compute some estimates of phosphorus transport rates. These calculations are minimal estimates of the actual rates since they assume that the specific activity of the tracer remains constant throughout the experiments. Particularly in the case of movement of radiophosporus from plant to the untagged water compartment, mixing of non-radioactive phosphorus (in the case from the plant) with the $^{32}P$ tracer would result in underestimation of the rate of phosphorus movement. Also the calculations are made only for the final experiments that had been incubated for 3000 min; the uptake curve

(Fig. 2) shows that much higher rates could be obtained if calculations were made on some of the shorter experiments.

Transport is highest in the light; the most active movement occurs from the upper water into the leaves (Table 2). Net movement of phosphorus is from the water into the plant. Very little transport of phosphorus occurred in the opposite direction especially in the dark. Leaves and stems absorbed more phosphorus in the light or dark than did the roots and rhizomes.

## Uptake in the Natural Environment

Activity in the sediment of the $^{32}P$ decreased in all directions from the injection point (Table 3). The decrease was between 100- and 1000-fold in 5 cm above and to the side of the injection point. Very little $^{32}P$ was transported upwards in the sediment by water movements. In a turion located 2 cm from the injection point the tracer accumulated primarily in the rhizome and roots (Table 4). In a turion 6 cm from the injection point more tracer accumulated in the leaves and stem but the major portion was still in the rhizome and roots. In both turions the $^{32}P$ was taken up through the roots and transported to all parts of the plant.

## Discussion

Eelgrass absorbs phosphate through roots and through leaves. The roots have a dense covering of root hairs that must be the active sites of root absorption. Root hairs are known to be the major participants

Table 2. Transport rate of phosphorus by eelgrass in a closed system during a 3000 min experiment.

| Pathway | Transport Rate µgP/plant | |
|---|---|---|
| | Light | Dark |
| Lower water → Upper water | 0.66 | 0.16 |
| Upper water → Lower water | 0.088 | 0.0016 |
| Upper water → Leaves and stems | 0.88 | 0.116 |
| Lower water → Roots and rhizomes | 0.16 | 0.088 |
| Upper water → Plant | 0.964 | 0.216 |
| Lower water → Plant | 0.34 | 0.098 |
| **Net Overall Transport** | | |
| Lower water → Plant | 0.912 | 0.256 |
| Upper water → Plant | 0.392 | 0.057 |

Table 3. Activity of $^{32}P$ in sediment after 24 hrs.

| Location | Depth (cm) | Activity (cpm/g dry wt) |
|---|---|---|
| Injection site | 0 | < 1 |
| " " | 0.5 | 52 |
| " " | 1.0 | 960 |
| " " | 2.0 | 370 |
| " " | 6.0 | 210,000 |
| 6 cm from injection site | 2.0 | 500 |
| " " " " " | 6.0 | 770 |

Table 4. *In situ* uptake of $^{32}P$ by eelgrass after 24 hr. Turion A was 2 cm from site of isotope injection; turion B was 6 cm from the site.

| Tissue | Approximate Biomass (% dry wt.) | Isotope Tracer (% total activity) Turion A | Turion B |
|---|---|---|---|
| Upper leaf | 40 | 3.4 | 4.6 |
| Leaf base | 5 | 0.2 | 11.7 |
| Stem | 5 | 1.1 | 14.5 |
| Rhizome and roots | 50 | 95.3 | 69.2 |

in nutrient absorption in all plants (Sutcliffe, 1962). Eelgrass leaves also participate in phosphate absorption. The leaves have only a thin cuticle that would facilitate absorption. In addition, the chemical constituents of the cell walls show that eelgrass leaves are different from terrestrial plants and that the leaves function in ion absorption (Maeda et al., 1966).

In this study the absorption of phosphate in the leaves exceeded that in the roots. The controversy over the site of nutrient absorption in submerged freshwater and marine vascular plants (Sculthorpe, 1967) apparently has persisted because both sites, leaves and roots, are active in absorption. This could account both for observations of direct uptake in leaves and for those relating plant distribution to chemistry of the sediments.

Phosphate absorption in eelgrass proceeded most rapidly in the light; dark uptake also occurred. This evidence and the high concentration factors (Fig. 3 and 4) indicate that absorption of phosphate depends on metabolism as well as a physical process of absorption-exchange. Absorption is initially a physical process; subsequent uptake is coupled to the metabolic activity of the plant (Sutcliffe, 1959).

After entering the plant, the phosphate in eelgrass was translocated to all portions of the plant. This translocation in both directions must occur in the xylem and phloem of the vascular system, even though these are considerably reduced in eelgrass. In several of the experiments there was a tendency for phosphate accumulation in the roots and the leaf base or stem. Since these are the locations of the most active cell division and growth they would be expected to accumulate phosphate (Stumpf, 1952).

A portion of the phosphate absorbed by the roots was subsequently released into the water surrounding the leaves. The reverse process also occurred but the intensity of the former process was much greater. Lowenhaupt (1956) showed that a mechanism exists in aquatic plants for absorption, transport, and subsequent release of calcium from the leaves of aquatic plants. This mechanism may also apply to phosphate and other ions.

Eelgrass in nature can utilize phosphate from the sediment or the water. The results of our field study show that eelgrass in Izembek Lagoon absorbs phosphate from the interstitial water of the sediment. The studies of Raymont (1947) and Buljan (1957) of the experimental fertilization of marine bays with phosphate resulted in increased standing stocks of eelgrass and the other seagrasses; these results showed that eelgrass in nature can also absorb nutrients through the leaves. The principal source of phosphate in nature for eelgrass may depend on the relative concentrations of phosphate in the water and the sediment.

This study indicates that the cycle of phosphorus in the eelgrass beds can be extremely complex. In addition to the usual pathways of phosphorus in shallow water marine ecosystems (Bruce and Hood, 1959) we found evidence that eelgrass can pump phosphate from the sediments through the plant and release it into the ambient water. Transport can also occur in the opposite direction but (with solutions of similar phosphate concentrations) the net effect is from sediments into the water. The observations of Conover (1958) that in Great Pond, Massachusetts the highest phosphate concentrations continually occurred in the eelgrass beds may be evidence that phosphate is pumped from the sediments into the water in nature. This process would return to the water phosphorus that is released in the sediments by decomposition and might otherwise be lost to the ecosystem. This is a positive feedback mechanism that enhances the production of the eelgrass community.

Movement of phosphorus probably occurs continuously between eelgrass roots and interstitial water and between the leaves and the water surrounding them. The net direction and intensity of this transport no doubt depends upon a number of chemical and physical, as well as biological, parameters.

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Footnotes:

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## Chapter 8.

# ENVIRONMENTAL TEMPERATURE AND EELGRASS ECOLOGY IN IZEMBEK LAGOON, ALASKA

## Introduction

The role of temperature in the life cycle of eelgrass (*Zostera marina* L.) was expounded some forty years ago by W. A. Setchell (1929). On the basis of extensive collections of eelgrass specimens that ranged from the shores of the Mediterranean to the Greenland coast he outlined the annual cycle of eelgrass growth and reproduction in relation to the temperature of the environment. He also used temperature gradients to explain the reports of varying plant size and geographical distribution. Subsequent studies of eelgrass phenology have supported Setchell's hypothesis of temperature control (Cottam, 1935; Arasaki, 1950a, 1950b; McRoy, 1966).

I have studied the ecology of eelgrass in Izembek Lagoon for the past seven years. An early study indicated that the eelgrass beds in the lagoon could be stratified into subtidal and tidepool beds on the basis of standing stock and morphology (McRoy, 1966). Further, this response of the plants appeared to be principally a result of the temperature gradient of the environment. This conclusion nicely supported the work of Setchell.

In this early study in Izembek Lagoon detailed temperature observations were not collected but the temperature regime of the subtidal and tidepool waters was predicted from an empirical model based on tides, air temperature, and solar radiation. This model predicted temperatures above 25 C in the tidepools, a prediction important to the ecology of eelgrass and one that needed to be confirmed by observation. The conclusions of Setchell and others on the role of temperature were also based on empirical observations. The temperature hypothesis needed to have a physiological basis.

In the present study detailed measurements of temperature in Izembek Lagoon are combined with studies of the effect of temperature on the metabolism of the plant to evaluate the role of temperature on eelgrass ecology.

This work was supported by the Arctic Institute of North America under contractual agreements with the Office of Naval Research and by the Federal Water Pollution Control Administration. The U.S. Bureau of Sport Fisheries and Wildlife provided the logistic support that made the field work possible.

## Description of Izembek Lagoon

Izembek Lagoon contains the largest and most important eelgrass meadows on the coast of Alaska. This lagoon, an embayment of the Bering Sea at the tip of the Alaska Peninsula (Fig. 1), is a major feeding area for millions of migratory birds of the Pacific Flyway and has been reserved as a national wildlife range. The eelgrass community in the lagoon attracts many species of marine and terrestrial organisms that seek food and shelter, and as a result the productivity of the lagoon greatly exceeds that of the adjacent sea.

The lagoon is a shallow marine basin separated from the Bering Sea by barrier islands and spits. The lagoon is 41 km long and from 3 to 12 km wide. An estimated 78% of the surface area is tide flats; the remaining 22% is tide channels (Fig. 2). The tide channels form a tributary-distributary system which converges in three places to form

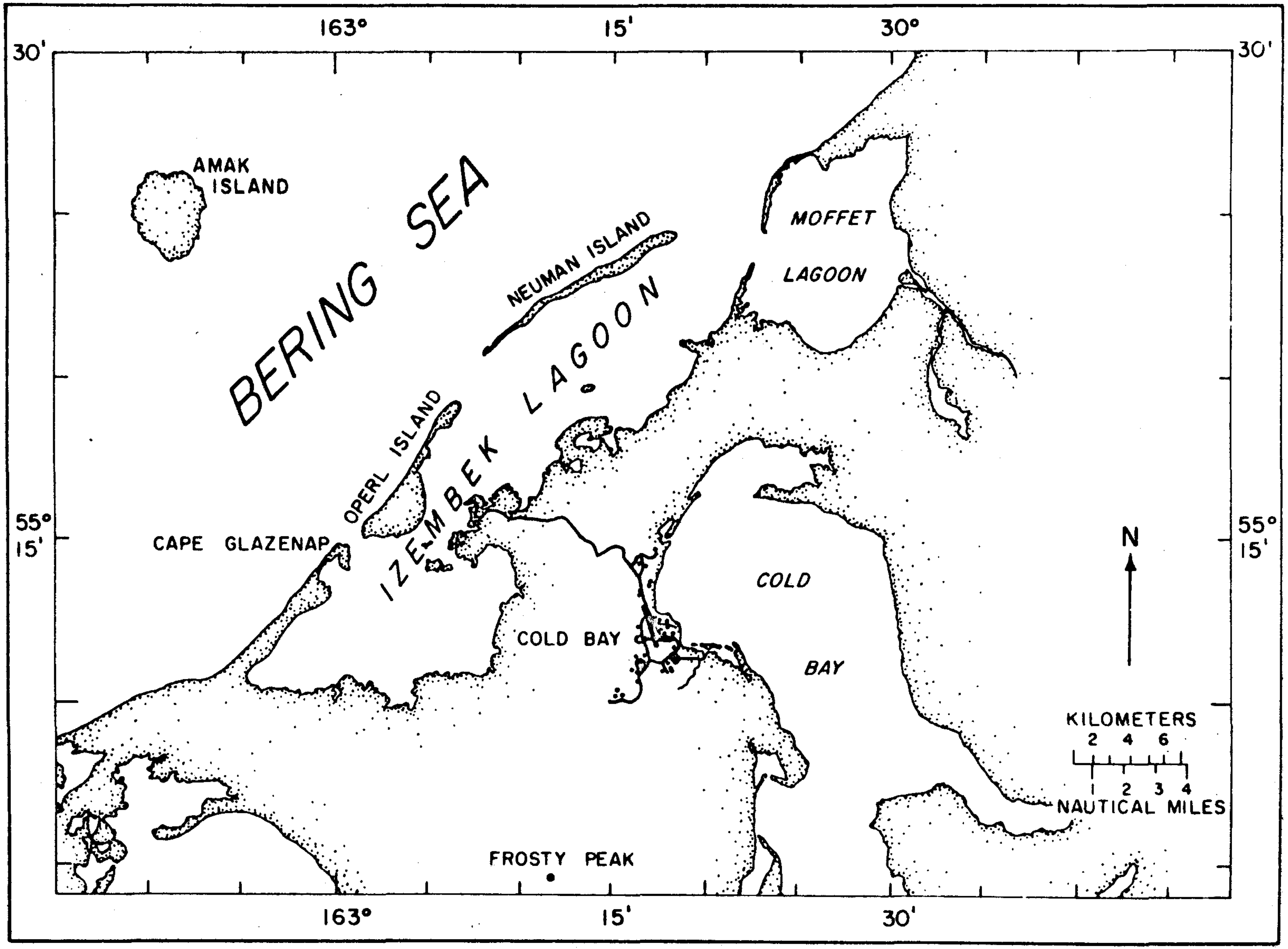

Figure 1. Chart of the Izembek Lagoon region of the Alaska Peninsula (from McRoy, 1966).

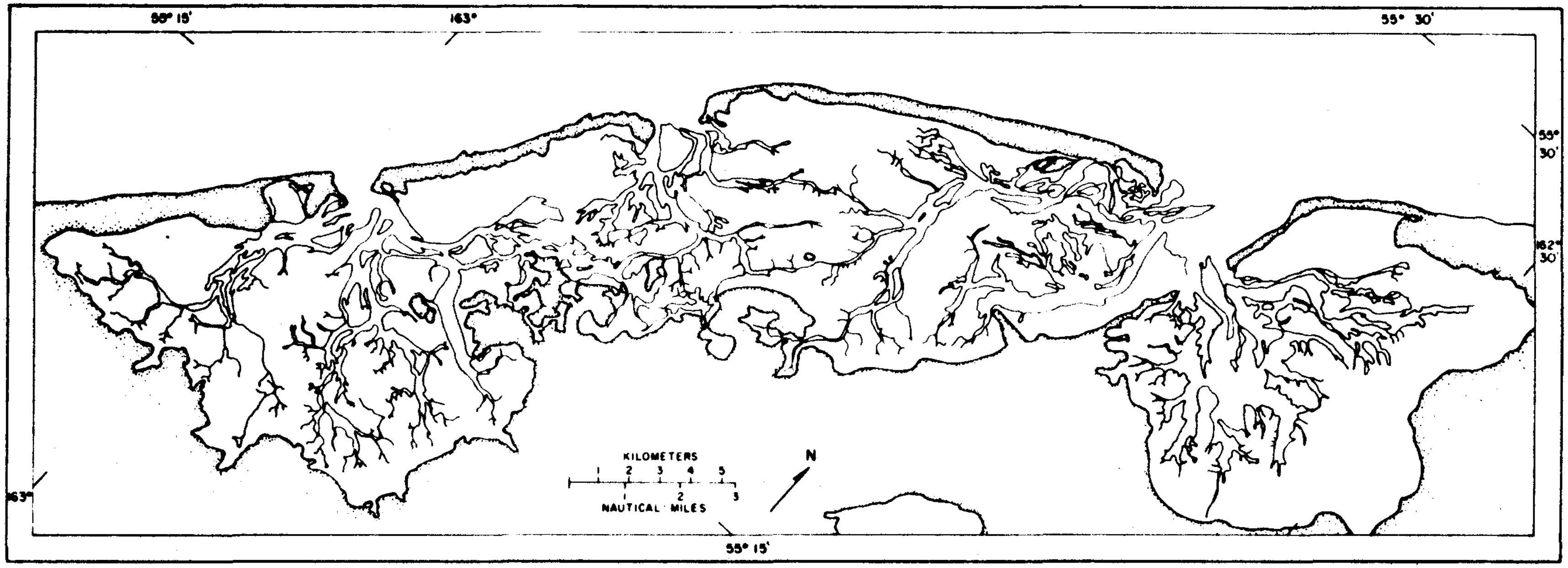

Figure 2. Chart of Izembek Lagoon showing the distribution of tidal flats and channels (from McRoy, 1966).

large passes between the barrier islands and spits. Some 60 to 70% of the tide flats is covered with eelgrass beds. The eelgrass flats are large shallow pans or tidepools that hold water during all levels of the tide.

Dilution in the lagoon is slight and limited to areas near streams. Salinity is primarily that of the adjacent sea (Fig. 3). Residence time of water in the lagoon is short; the tidal prism is estimated to be 67% of the total volume at mean high water. The tides have a mixed period characterized by a diurnal inequality that results in a vanishing tide. There is also a seasonal aspect of the tidal period that results in low tides during daylight hours in spring and summer and during night in fall and winter.

Ocean water entering the lagoon is subjected to rapid temperature changes (Fig. 3). The highest temperatures occur in the tidepools during summer days. In winter, water entering the lagoon cools. Freezing of the lagoon occurs intermittently during winter; rarely does ice completely cover the lagoon.

The climate of the region is dominated by frequent cyclonic storms that cross the North Pacific and Bering Sea bringing persistent clouds, high winds, and precipitation. In winter, when ice covers much of the Bering Sea, the climate has a more continental character.

The eelgrass beds in Izembek Lagoon have been stratified into subtidal and tidepool beds (McRoy, 1966). The subtidal eelgrass beds have a character and biomass distinct from the tidepool eelgrass beds. The subtidal beds show little seasonal cycle and are rarely exposed during low tides. The tidepool eelgrass beds show a marked seasonal

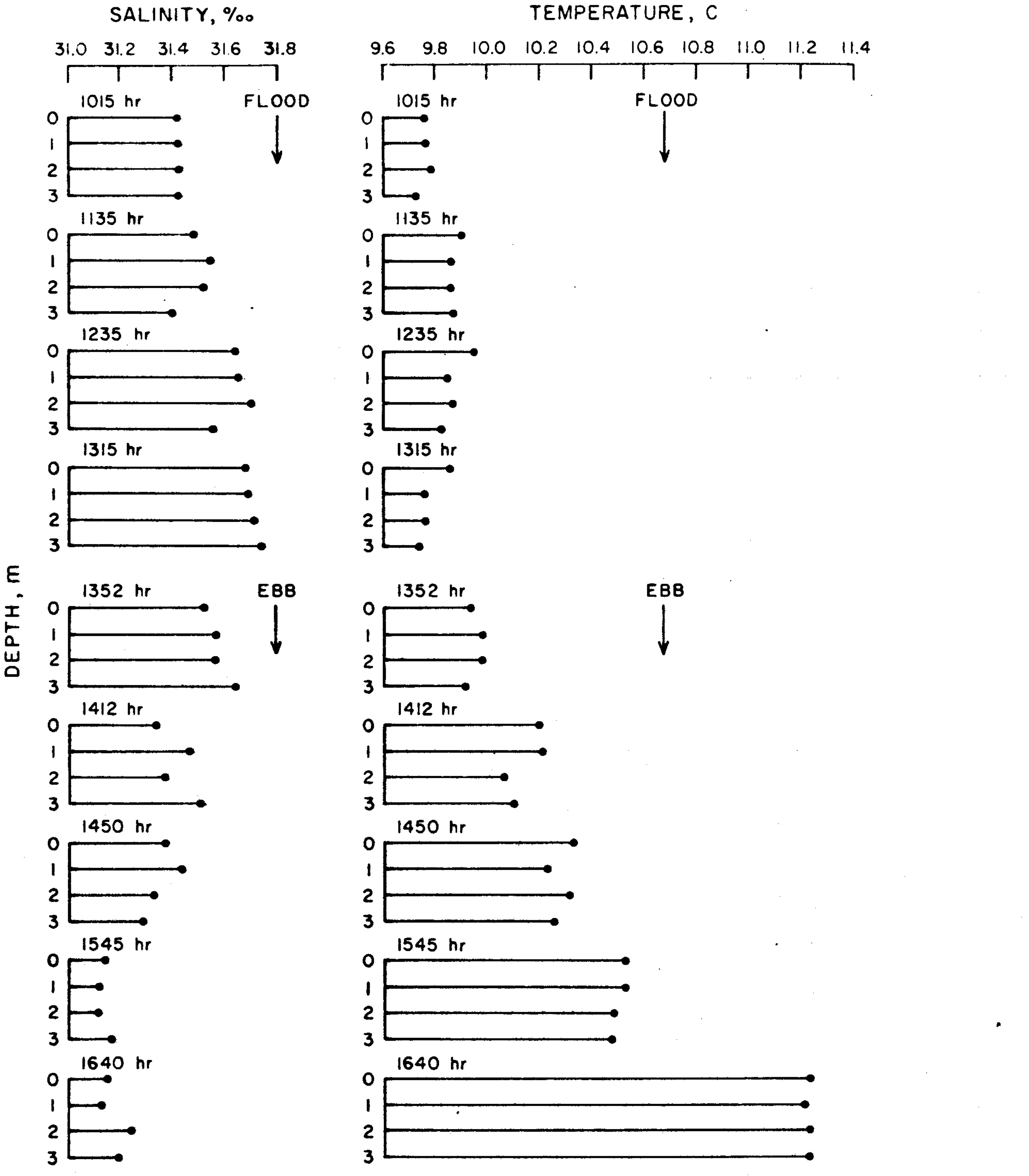

Figure 3. Depth distribution of salinity and temperature during a tidal cycle in an ocean pass of Izembek Lagoon on 13 August 1964 (from McRoy, 1966).

cycle and are daily isolated from the ambient lagoon waters during low tides. The differences in the two types of eelgrass beds have been attributed principally to a temperature gradient in the two environments.

## Methods

### 1. Environment Temperatures

Two types of instruments were used to measure water temperatures: (1) an alcohol thermometer with a range of -5 to 30 C, and (2) a Ryan thermograph with a range of -5 to 25 C and a 45 day clock drive. The thermometer was used for measurements of surface temperature at a given place and time. A thermograph was anchored on the bottom in a subtidal eelgrass bed and in a shallow tidepool eelgrass bed. Continuous temperatures were recorded from April through October, 1967 with additional observations at irregular intervals during the winter months.

### 2. Determination of Metabolic Rates

The influence of temperature on the rate of metabolism of eelgrass was determined by measuring changes in the dissolved oxygen concentration due to plant respiration. Eelgrass leaves (about 0.2 to 0.6 g fresh wt.) were placed in 60 cc glass bottles filled with filtered sea water (S= 31 °/₀₀). Septum stoppers sealed the bottles and permitted withdrawl by a syringe of any entrapped air bubbles. The bottles were wrapped in aluminum foil and placed on a shaking apparatus in a constant temperature water bath. Dissolved oxygen was determined using the Winkler technique (Strickland and Parsons, 1966) in the bottles after an incubation of 1 to 2 hrs. Reagents were added to the bottles with syringes without removing the stoppers. After acidifying the samples the leaves were removed.

The experimental design consisted of using six bottles for each rate determination at a given temperature. Two of these contained only sea water and were used to determine an initial oxygen concentration for the series. The remaining four bottles contained eelgrass leaves and were treated as replicates. The rates of oxygen consumption in the dark were determined for leaves from eelgrass in shallow tide pools and for leaves from subtidal eelgrass. Shallow water plants were examined in summer and winter; deep water plants in summer only.

## Results

### 1. Environment Temperatures

Continuous records of water temperature in the shallow and deep eelgrass beds collected during summer, 1967, showed that there was a marked difference in these two environments. Beginning in May and ending in September the shallow eelgrass bed could daily attain temperatures from 5 to 10 C above the deep eelgrass bed (Fig. 4). This temperature rise occurred during low tide when the shallow eelgrass bed formed a large tidepool that was only about 30 cm deep. During this low tide period the deep eelgrass bed was covered by one meter or more of water.

The daily maximum temperatures attained by the shallow eelgrass bed were recorded during 10 months of 1967 (Fig. 5). Continuous records

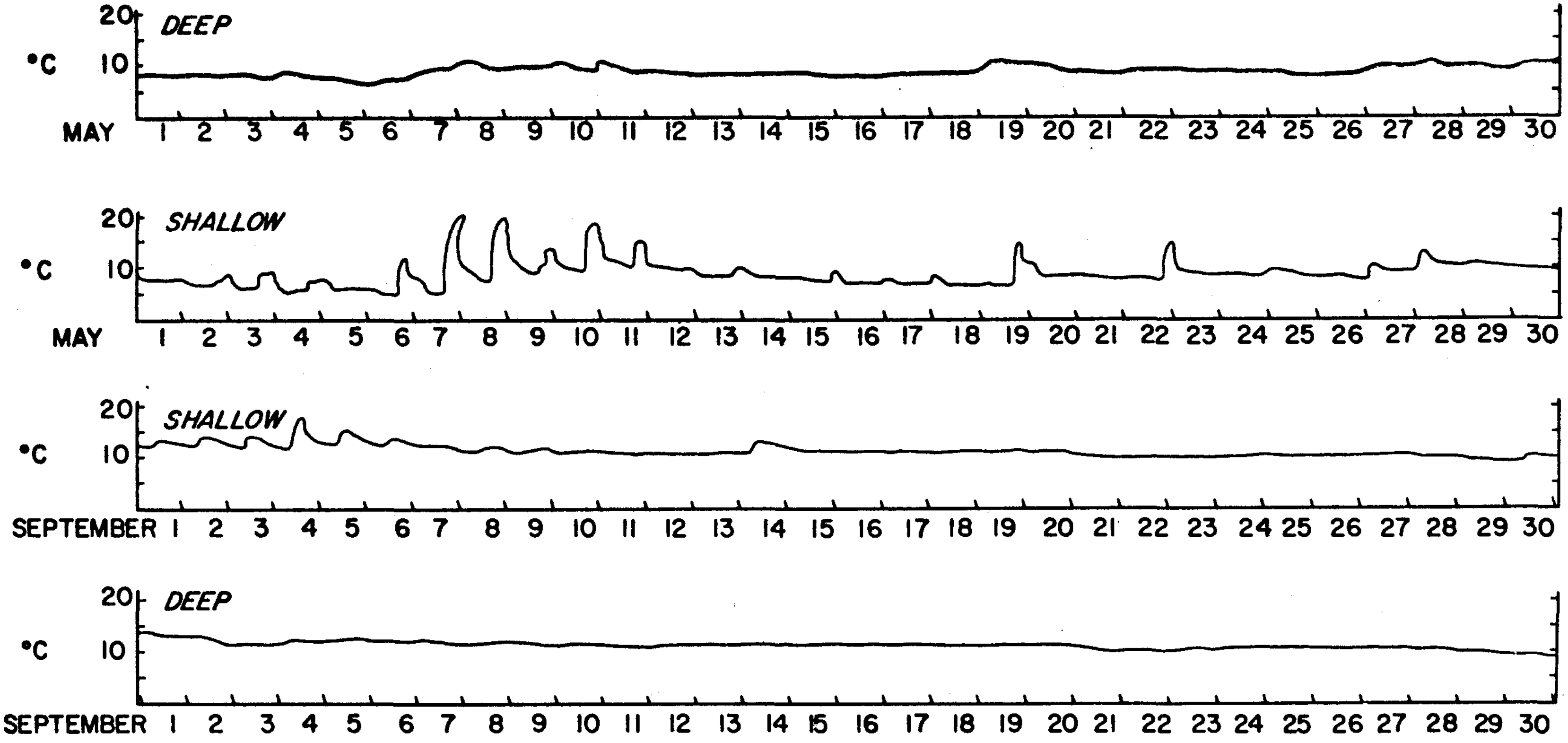

Figure 4. Continuous temperature records in deep (subtidal) and shallow (tidepool) eelgrass beds in Izembek Lagoon during May and September, 1967.

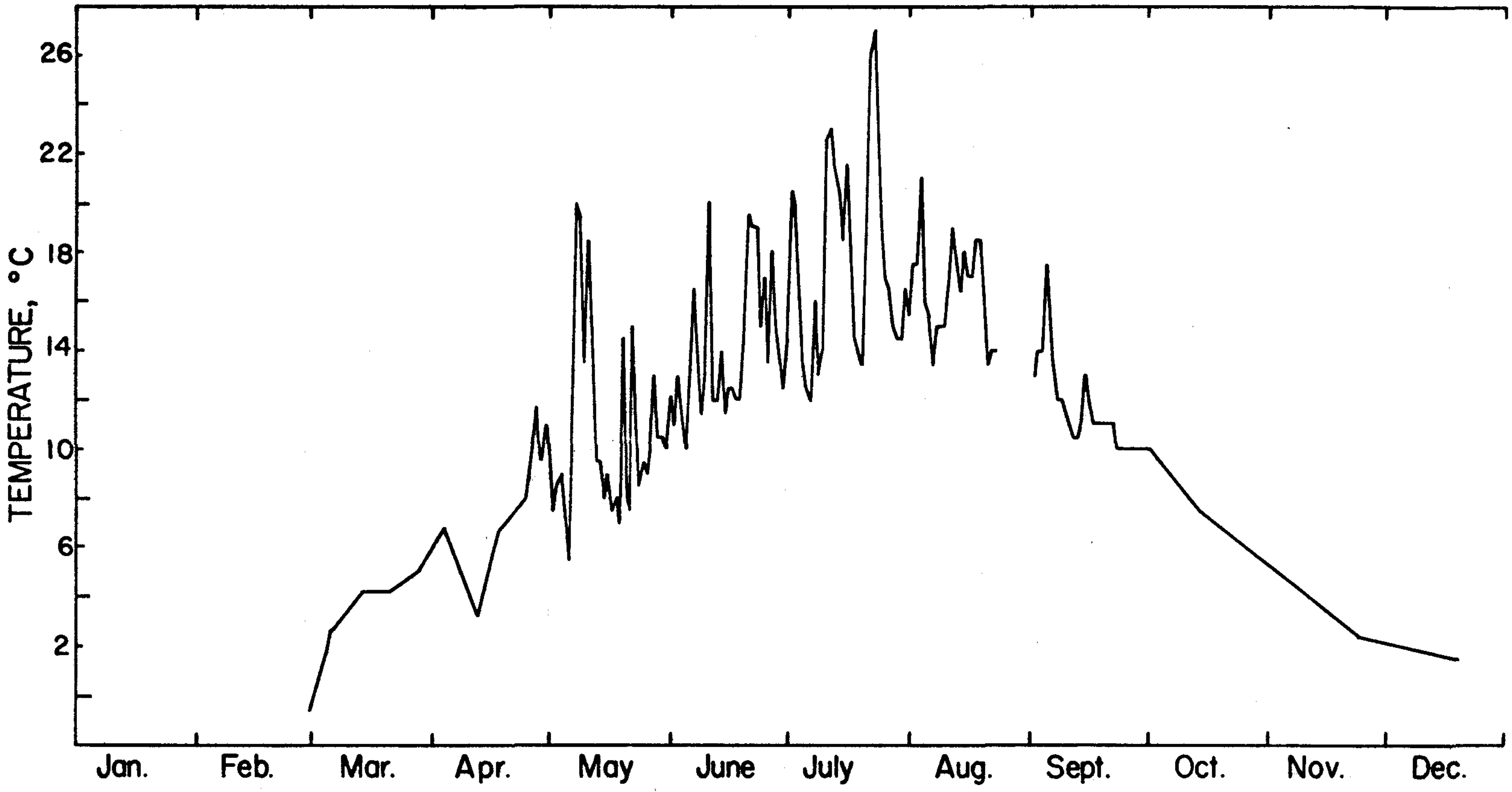

Figure 5. Daily maximum temperatures in a tidepool eelgrass bed in Izembek Lagoon during 1967.

were obtained from 27 April through 30 September. These observations were supplemented by individual measurements in the preceding and following months. The individual measurements were taken during the warmest part of the day and are thought to be a good approximation of the daily maximum temperature.

The shallow eelgrass bed could attain temperatures above 10 C from the last week of April until the first week of October. Temperatures above 15 C were reached between the first week of May and the first week of September. Water in this eelgrass bed rose to 20 C and above on 12 occasions in 1967. The highest temperature observed was 27 C.

## 2. Metabolic Rates

The rate of respiration was measured over the range of 0 C to 40 C in eelgrass leaves from shallow and deep environments. The rate in eelgrass from shallow water was measured in summer and winter; that in deep water only in summer. The severity of winter conditions prevented the possibility of obtaining eelgrass from deep water during the time available.

During summer in eelgrass from a tidepool, oxygen consumption was proportional to temperature over the range of 0 to 15 C (Fig. 6). Above 15 C the rate showed no correlation to the increasing temperature. A linear regression of the data in the range 0 to 15 C had a correlation coefficient of 0.89. The regression equation is:

$$\text{Log } Y = 0.274 + 0.033X$$

where $Y$ = respiration rate in mg $0^2 (\text{g dry wt})^{-1} \text{ hr}^{-1}$
$X$ = temperature in degrees C

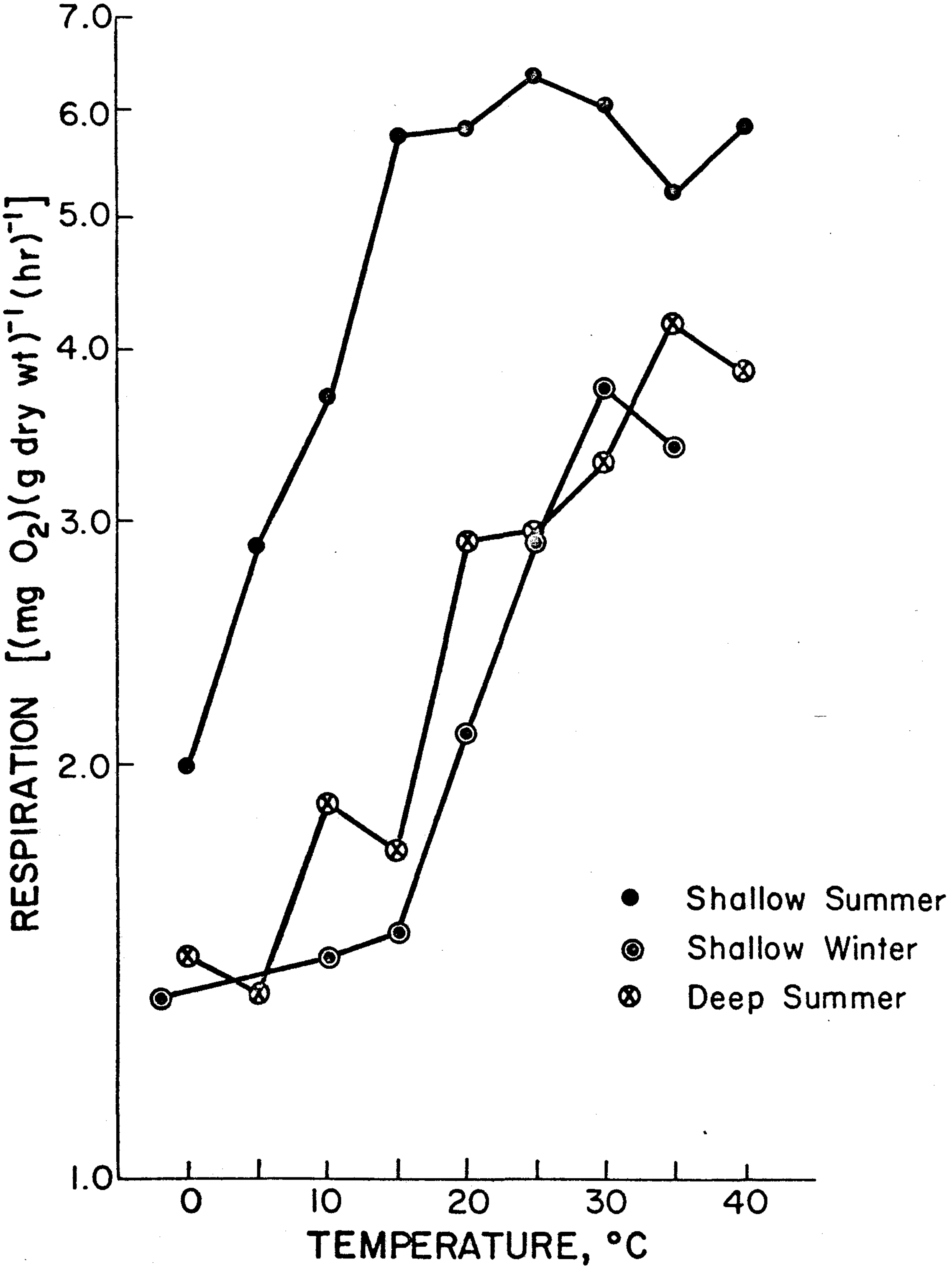

Figure 6. Relationship between respiration (log) and temperature in a shallow (tidepool) eelgrass bed in summer and winter and in a deep (subtidal) eelgrass bed in summer. Means of four replicate observations.

Eelgrass from deep water (subtidal) in summer showed a very different relationship to temperature. In these plants oxygen consumption was proportional to temperature in a range of 0 to 35 C. Only above 35 C did the rate decrease with the increasing temperature. In addition, at any temperature the rate was considerably lower in plants from deep water than in those in shallow water. The data were subject to linear regression analysis yielding a correlation coefficient of 0.90 and the equation:

$$\log Y = 0.086 + 0.015X$$

In the other series of experiments the respiration rate of eelgrass from shallow water in winter contrasted with the summer values for shallow water plants. This rate was proportional to temperature over the range 0 to 30 C and decreased with the temperature increase above 30 C. The rate in winter plants was much lower than the rate in summer plants at the same temperature. The winter rate in plants from the tidepool approximated the summer rate in plants from the subtidal bed. A linear regression in the range of 0 to 30 C had a correlation coefficient of 0.78 and the equation:

$$\log Y = 0.012 + 0.016X$$

The regression was statistically significant at the 99% probability level.

The regression equations of the relationship between respiration and temperature under the three conditions can be examined using statistical techniques (Snedecor, 1956). Using the 95% confidence level the slope for the tidepool plants in summer is significantly different from the other two slopes. However, the slope of the tidepool plants in winter is not significantly different from that of the subtidal plants in summer.

The temperature coefficient ($Q_{10}$) for the tidepool plants in summer is 2.1 in the 0 to 15 C range. In winter and in the subtidal plants the $Q_{10}$ is 1.4 over the 0 to 30 C range.

## Discussion

These studies of temperature gradients in Izembek Lagoon show that eelgrass growing in the shallow tidepools experiences very different conditions from that growing in the subtidal, even though the two habitats occur in close proximity to one another. Previous detailed studies of eelgrass in Izembek Lagoon suggested that this environmental temperature gradient was a primary factor controlling the ecology and productivity (McRoy, 1966). The eelgrass beds in the lagoon were stratified into subtidal and tidepool beds. The subtidal eelgrass beds were characterized by a high root and rhizome biomass, a low turion (a clump of leaves and its prostrate, rooted rhizome) density, few or no flowering turions, and long, wide leaves. The eelgrass from the tidepools was identified by a low root and rhizome biomass, a high turion density with a large number of flowering turions, and short, narrow leaves. The tidepool beds showed a marked seasonal cycle of biomass and were the areas most accessible to waterfowl feeding; the subtidal beds showed little seasonal differences and were beyond the reach of most waterfowl. In the 1966 study I attributed the differences in the eelgrass to the physiological response of the plants to temperature.

Setchell (1929) outlined five stages of the annual cycle of eelgrass growth and reproduction in relation to temperature (Fig. 7). Below 10 C a condition of quiescence or cold rigor existed; between 10 and 15 C active vegetative growth occurred; between 15 and 20 vegetative growth was reduced but reproductive activity and flowering occurred; above 20 C a condition of heat rigor prevailed; and, finally, above 30 C the plants expired. The reduced activity following the seasonal temperature maximum was designated "recrudescent rigor."

Setchell showed that eelgrass in deep water usually has a long vegetative period and seldom experiences heat rigor. He also used the temperature of the environment to explain reports of varying plant size and geographic distributions. He proposed that eelgrass growing in Arctic regions could only flower if it occurred in tidepools where the water could rise above 15 C during low tides.

The environmental conditions in Izembek Lagoon support the findings of Setchell. The eelgrass in shallow water produces numerous flowering turions yet the vegetative biomass is proportionately low. The subtidal eelgrass produces few if any flowering turions and is characterized by vegetative growth. As predicted, only the plants in the tidepools experience temperatures above 15 C; the subtidal plants pass the summer in water temperatures that range from 10 to 15 C.

The warming of the tidepools occurs during low tide on summer days when the water in these eelgrass beds becomes isolated. The subtidal beds may be covered by less than a meter of water on low tide but this water is in constant motion and is not isolated from the ambient sea; as

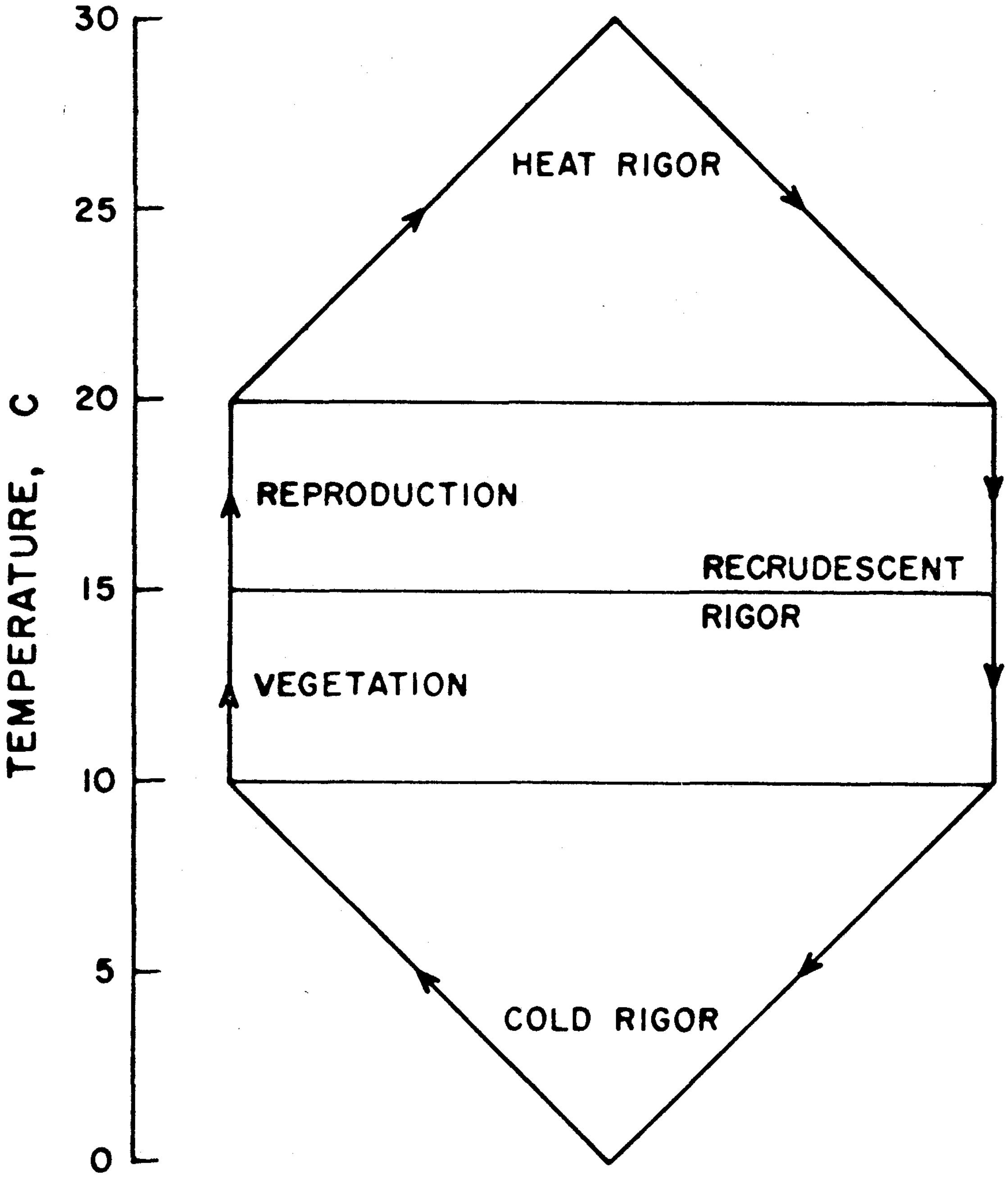

Figure 7. Idealized polygon representing the annual cycle of growth and reproduction of eelgrass as dependent on environmental temperature (from Setchell, 1929). A particular habitat may experience only a part of the cycle and have a differently shaped polygon.

a result the subtidal areas do not reach the high temperatures that are seen in the tidepools. The tides are most important in this temperature structure. There is a seasonal aspect of the tidal period such that the low tides coincide with daylight hours in summer and with night in winter.

The physiological experiments clearly demonstrate the dependence of the rate of respiration on temperature. The results probably reflect the true trend of the relationship although the actual quantities involved may be different. The technique used assumes that there was no storage of oxygen in the lacunae of the leaves, that the leaf was not affected by the experiment, and that the dry weight of the leaf did not change during the experiment. Wetzel (1965) cautions about the effects of oxygen storage on the determination of metabolic rates in aquatic plants. This complication, however, is mostly applicable to the oxygen produced by the plants in the light, which is apparently not released into the water but stored in the lacunae of the leaves. In the present study the utilization of oxygen by the tissues in the dark appeared to be reflected in the changes in dissolved oxygen concentration of the ambient water.

The results of the respiration studies suggest that the eelgrass growing in the subtidal and that in the tidepools are distinct physiological races. The plants from the tidepools shifted their entire temperature-respiration relationship toward the consumption of more oxygen in summer for any given temperature. The subtidal eelgrass was measured only in the summer but its respiration-temperature curve coincided with that of the winter values for the tidepool plants. It is possible that this coincidence occurred by chance and that the subtidal plants also shift their respiration-temperature curve with the season. It is more probable that the subtidal plants do not shift this relationship but maintain the lower rates throughout the year. In either case this is good evidence that physiological races of eelgrass exist. Further experiments are needed to establish whether these differences are controlled genetically or are environmentally induced.

A seasonal shift in the respiration-temperature curve has been observed in one arctic seaweed. Kanwisher (1966) concluded that the decreased metabolism in winter of Laminaria sp. from northern Labrador was an adaptation to the darkness of the high latitude winter. The decreased metabolism was a partial protection from starvation. In Izembek Lagoon this adaptation would benefit the over-wintering eelgrass population in a similar way. In addition the increased summer metabolism of these plants evidently permits the formation of flowering turions which are not found in the subtidal plants.

The respiration-temperature relationships lend little support to the empirical scheme of Setchell (1929). Only in the tidepool plants was there a change in the slope of the curve above 15 C. In addition, in not one of the experimental series did the plants show effects of enzyme denaturation at 30 C. There is no basis here to suggest that 30 C is lethal as Setchell suggested. Dr. Richard Biebl (personal communication) has found that eelgrass in Izembek Lagoon can tolerate temperatures of 40 C and slightly higher for at least 12 hr periods.

In view of these results, Setchell's scheme of the annual cycle of eelgrass on the basis of environmental temperature is more likely a scheme that integrates the effects of light and temperature. As in Izembek Lagoon the temperature structure of the environment is closely related to the light and radiation budget. The shallow tidepool eelgrass beds warm during low tides on summer days; at this time they also receive a maximum of solar radiation. Waters around the subtidal eelgrass are not only colder but also receive less radiation. The combined effects of these two most important environmental variables could produce the type of cycle that Setchell has observed.

Future studies of the physiological ecology of eelgrass should be directed toward the combined effects of light and temperature. This should involve more intensive field research as well as laboratory experiments. The meaning of winter must also be examined in detail.

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## Chapter 9

## SUMMARY

This dissertation is a collection of studies on the biology of eelgrass, Zostera marina L. It is not a biology of eelgrass but rather a compilation of research and literature that is a contribution toward a comprehensive biology.

Eelgrass is one of the forty-five species of monocotyledonous angiosperms that grow only in shallow coastal marine waters. This group of plants, the seagrasses, consists mostly of tropical species. In the temperate and boreal regions of the Northern Hemisphere, the common eelgrass, Z. marina, is the single most abundant and widespread seagrass (Chapter 2). Eelgrass is the only species of seagrass occurring in all oceans of the Northern Hemisphere and is the only species of the genus on the coasts of North America. It is quantitatively the most important seagrass in Alaska.

The principal site for field studies in Alaska has been Izembek Lagoon, an embayment of the Bering Sea on the Alaska Peninsula. This lagoon is a major feeding area for migratory waterfowl and has been reserved as a National Wildlife Range. Past studies have involved the standing stock and ecology of eelgrass in the lagoon. Current work has extended the original study to other areas of the coast and has examined in greater detail certain aspects of eelgrass ecology in the lagoon (Chapter 1).

Eelgrass is a flowering plant; it has all the structures characteristic of vascular flowering plants. It grows rooted in soft sediments and totally submerged in salt water. Flowers develop in spathes on stems that are distinctly different from the vegetative stems.

Pollen is waterborne. Seeds are produced annually, but reproduction by vegetative growth is quantitatively more important (Chapter 2).

The chemical composition of eelgrass has been the subject of numerous studies and is presented largely from the literature (Chapter 3). Available studies span a 155-year period and include concentrations of some 28 elements in addition to the proximate analysis of the plant.

In eelgrass the abundance of an element, especially a trace element, is proportional to the abundance of that element in the sea. The amounts of carbohydrate, protein, lipid, and fiber in eelgrass are similar to those in other seagrasses and some closely related terrestrial plants. The plant does reflect adaptation to the sea with respect to certain constituents of the cell wall of the leaves. This adaptation is thought to enhance the absorption of ions across the leaf surfaces; absorption of ions across the leaf surface is proven by experiment in Chapter 7.

With a radioactive isotope it was shown that eelgrass is capable of absorbing phosphate either from the sediments through the roots or from the water through the leaves (Chapter 7). Absorption was greatest in the light. Phosphate once absorbed was rapidly transported throughout the plant. A portion of the phosphate absorbed from solution by the roots was returned to solution across the leaves. These results suggest that eelgrass in nature can function either as a sink or source of phosphate.

The distribution and biogeography of eelgrass in the waters of Alaska has been studied in detail (Chapter 4). This plant occurs from

Kotzebue Sound, in the Chukchi Sea, to the southern limit of Alaska and beyond. New records in this study extend to the west and north previous limits of the species in Alaska. This distribution in Alaska is disjunct, a result of environmental restrictions rather than a lack of dispersion mechanisms. The circumboreal distribution of the plant in the Northern Hemisphere is considered to be the result of dispersion from a western Pacific origin around the Pacific and through the Arctic into the Atlantic and its adjacent seas. This is supported by the present distribution of the species, the locations of its fossil ancestors, and similar dispersal patterns for marine invertebrates.

Ten eelgrass populations ranging from Southeast Alaska to Bering Strait were sampled for quantitative comparison (Chapter 5). Standing stocks were highest in Kinzarof and Izembek lagoons (1510 g dry wt/m$^2$) on the Alaska Peninsula and lowest in Calder Bay in Southeast Alaska (65 g dry wt/m$^2$). Other quantitative observations included caloric content, chlorophyll a concentration, turion density, and leaf size. Statistical analyses indicated that with the exception of caloric content these features varied greatly among the ten populations. This variation appeared to be related to differences in the local environment rather than a larger geographical gradient. Comparison of standing stocks in Alaska with other regions in the Northern Hemisphere also suggests this conclusion.

In one of the ten areas, Safety Lagoon on the Seward Peninsula, eelgrass was found surviving the arctic winter under heavy sea ice covered by snow in anoxic water (Chapter 6). This is the first report of a non-algal marine plant surviving these conditions.

A partial explanation of the survival of eelgrass during the arctic winter is the observation that the rate of respiration in the plant is depressed as the winter progresses (Chapter 8). This was demonstrated in a series of experiments on eelgrass from Izembek Lagoon. The rate of respiration in eelgrass is extremely dependent on temperature. In summer in Izembek Lagoon large temperature gradients exist between the subtidal and tidepool habitats containing eelgrass. The metabolic studies showed that physiological differences exist in the plants from these two habitats.