AN ABSTRACT OF THE THESIS OF

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Title: Production Dynamics of a Zostera marina L. Bed in Netarts Bay, Oregon

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C. David McIntire

This research examined the production dynamics and the mechanisms that accounted for such dynamics in a Zostera marina L. bed in Netarts Bay, Oregon. Specific objectives included a description of the autecology of Zostera in Netarts Bay, an investigation of macrophyte-epiphyte relationships and the monitoring of the primary production of Zostera and its epiphytes. Monthly changes in biomass, growth form, and primary production were monitored along transects at three tidal heights.

Shoot density was independent of mean leaf area per unit substrate ($m^2 m^{-2}$) until a threshold leaf area (7.5 to 11.0 $m^2 m^{-2}$) was reached, above which leaf area was negatively correlated with density. Zostera biomass was maximum along all transects immediately following the maximum rate of production, which occurred in late June and early July in 1980, and in May in 1981. Maximum values of Zostera biomass ranged from 143 g dry weight m^{-2} (high

intertidal) to 463 g dry weight m^{-2} (low intertidal). Maximum values of epiphyte biomass ranged from 2.6 g ash-free dry weight m^{-2} (high intertidal) to 27.5 g ash-free dry weight m^{-2} (low intertidal). Sharp decreases in epiphyte biomass were related to the sloughing of particular groups of Zostera leaves. Maximum values of leaf production ranged from 4.7 g dry weight m^{-2} day^{-1} (high intertidal) to 13.6 g dry weight m^{-2} day^{-1} (low intertidal). Factors having the most influence on Zostera production were light and the physical damage to the shoots associated with an annual bloom of Enteromorpha in the bay. Mean turnover time for Zostera biomass from April through October ranged from 25.1 days (high intertidal) to 26.8 days (low intertidal). Biomass loss as sloughed leaves accounted for 35 to 100% of the net primary production of aboveground Zostera each month. Mean turnover time for epiphyte biomass was 33.9 days (high intertidal) and 49.9 days (low intertidal). The annual net production of the Zostera, including aboveground and belowground parts, was 3.1 kg dry weight m^{-2} yr^{-1} or 1.2 kg C m^{-2} yr^{-1}. The annual net production of the epiphyte assemblage was 284 g dry weight m^{-2} yr^{-1} or 34.1 g C m^{-2} yr^{-1}.

Production Dynamics of a *Zostera marina* L. Bed in Netarts Bay, Oregon

by

Mary E. Kentula

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PRODUCTION DYNAMICS OF A ZOSTERA MARINA L. BED IN NETARTS BAY, OREGON

I. INTRODUCTION

Seagrasses are aquatic angiosperms adapted to life in the marine environment. They are derived from terrestrial vascular plants that invaded the water in relatively recent times (Pettitt et al., 1981). Unlike the other plants of the sea, i.e., the algae, seagrasses produce flowers, fruit, seeds, true roots, stems and leaves. Their root systems use the sediments to anchor the plant. In addition, seagrass can obtain nutrients from both the water column and the sediments. McRoy and Barsdate (1970) found that Zostera marina L. absorbs phosphate through both its roots and leaves. Later, McRoy and Goering (1974) demonstrated that the plant at times will pump phosphate and nitrogen from the sediments into the water column. In contrast, many sessile macroalgae treat their substrate as a planar surface for attachment and must depend solely on the water column for their nutrients (Dayton, 1971, 1975).

Unlike their freshwater counterparts, the seagrasses show a high degree of uniformity in their vegetative appearance. They typically have a well-developed system or rhizomes and linear on strap-shaped leaves (den Hartog, 1977). The leaves exhibit morphological adaptations to the aquatic environment, particularly to conditions of relatively low light intensity and nutrient availability. The leaves are thin, only one to three cell layers

thick, and there is little cuticular development. The chloroplasts are located mainly in the epidermis, while the mesophyll is reduced in thickness. As is typical in other aquatic spermatophytes, massive intercellular spaces, the lacunae make up over 70% of the volume of the plant (Zieman and Wetzel, 1980).

Although seagrasses are a prominent feature of nearshore marine and estuarine systems, their importance in the maintenance of the productivity and stability of these regions has only been recognized in the past 20 years (Zieman and Wetzel, 1980). Wood et al. (1969) have summarized the contributions of seagrasses to these systems:

(1) Seagrasses are major primary producers. Production values of 500-1000 g C m^{-2} yr^{-1} or 2.2-10 g leaf dry weight m^{-2} day^{-1} are typical.

(2) The leaves support a large biomass of epiphytes.

(3) Few animals graze directly on seagrass leaves. The bulk of the material is consumed as detritus.

(4) Detrital seagrass aids in the maintenance of an active sulfur cycle.

(5) The leaves act to dampen currents, thereby increasing sedimentation. Increased sedimentation along the margins of the bed, may lead to a distinct raising of the outermost part, with the bulk of the plants growing in a depression (den Hartog, 1971).

(6) The extensive root-rhizome system binds the sediments. In conjunction with the damping effect of the leaves, they also inhibit erosion.

In addition to these contributions, Thayer et al. (1975) added the nutrient transfer properties of seagrasses demonstrated by McRoy and Barsdate (1970) and McRoy and Goering (1974). Recently, den Hartog (1977) included the function of seagrasses as a food source for waterfowl, and as a nursery and shelter for juvenile fish populations.

This research examined the production dynamics and the mechanisms that accounted for such dynamics in a Zostera marina L. bed in Netarts Bay, Tillamook County, Oregon. Specific objectives included: (1) a description of the autecology of Zostera in Netarts Bay; (2) an investigation of macrophyte-epiphyte relationships, and (3) the monitoring of the primary production of Zostera and its epiphytes in the intertidal region over a growing season.

Background

Zostera marina L., is the most common and abundant seagrass in north temperate Atlantic and Pacific coastal waters (McRoy and Lloyd, 1981), including those of Oregon. Other Oregon seagrasses are Zostera nana Roth, Phyllospadix scouleri Hooker, Phyllospadix serrulatus Ruprecht ex Aschers., and Phyllospadix torreyi Watson (Phillips, 1979).

Studies of the growth of Zostera marina L. on the Pacific coast of North America are limited. Exclusive of Oregon, this species has been examined in Alaska (McRoy, 1966, 1970a,b), Puget Sound, Washington (Phillips, 1972), Humboldt Bay, California

(Keller, 1963; Waddell, 1964; Keller and Harris, 1966; Harding and Butler, 1979) and a southern California lagoon (Backman and Barilotti, 1976). Studies of Zostera in Oregon include the work of Stout (1976) and Bayer (1979). Most recently, the Environmental Protection Agency (EPA) supported a holistic study of estuarine nutrient processes in Netarts Bay, near Tillamook, Oregon.

EPA Study

In August, 1978, and January, 1979 scientists associated with the EPA, Corvallis Environmental Research Laboratory, conducted field studies to examine nutrient fluxes in Netarts Bay. Rhodamine dye was introduced into the water at the south end of the estuary at low tide, and the distribution and concentration of the dye was monitored at stations throughout the bay over a period of two weeks. Analysis of the patterns of circulation and horizontal mixing in the estuary revealed that there were two distinct water masses in the estuary -- the bay water and the ocean water. The bay water was defined as the water that remained in the channel during low tide, whereas ocean water was defined as the water that left the bay with the outgoing tide. With an incoming tide, ocean water displaced the bay water, pushing it toward the edge of the bay over the mudflats and seagrass beds. Relatively little mixing occurred between bay water and ocean water during a single tidal cycle. One-half of the rhodamine introduced into the bay water was flushed out

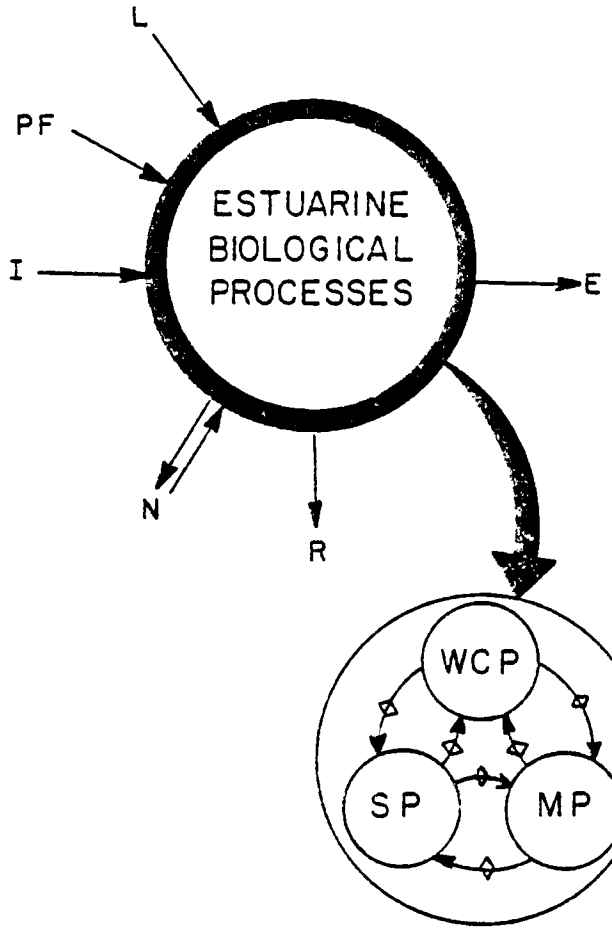
with the tide in two days. However, rhodamine was still detected in the bay water 14 days after the initiation of the study. During the summer the two water masses could easily be distinguished by temperature differences. The temperature of the warmer bay water ranged from 16° to 24°C, while the ocean water varied between 11° and 13°C.

Nutrient fluxes were examined by comparing selected nutrient concentrations with the rhodamine concentration in water samples taken at particular times and positions in the bay. Processes of interest included the transport of nutrients by advection, nutrient fluxes within the water column and fluxes between the water column and the seagrass and mudflat subsystems. The results of the August study indicated that the seagrass subsystem accounted in part for the distributional patterns of silica, nitrite and nitrate, and dissolved organic carbon during the summer months. The January study established that nutrient fluxes in the winter were controlled primarily by physical processes rather than biological processes.

While the EPA studies have examined the total flux of selected nutrients in and out of the entire system and have generated hypotheses about seasonal controls, an investigation at a finer level of resolution was needed to help explain mechanisms that accounted for the observed nutrient patterns. The research reported in this thesis was designed to provide biological explanations for such patterns, and the sampling strategy was based in part on a concurrent EPA study of nutrient gradients in the water column.

Conceptual Model

The EPA studies provided an opportunity to investigate biological processes within the context of the behavior of the entire estuarine system. Although Netarts Bay was the estuary of interest, a process perspective provides the basis for the extension of the results to estuarine systems in general. The estuarine ecosystem can be conceptualized as a hierarchy of biological processes that are driven and controlled by their relation to each other and to the physical processes (Figure 1). A process is defined as a systematic series of actions relevant to the dynamics of the system as it is conceptualized or modeled. An ecosystem has a characteristic capacity to process inputs. Process capacity has quantitative (biomass) and qualitative (taxonomic, genetic and physiological state) components. Changes in process capacity are exemplified by changes in the ecosystem, i.e., changes in biomass and other properties that occur with changes in community composition. This conceptual framework ignores taxonomic position and uses energy flow criteria in its evaluations. Therefore, the process approach is related to the functional group approach of Cummins (1974) and McIntire, et al. (1975) where functional groups are defined as groups of taxonomic entities that are engaged in similar activities. This conceptual structure is consistent with FLEX, a general ecosystem modeling paradigm developed by W. S. Overton (1972, 1975) and is based on the general systems theory of Klir (1969). The process concept in ecosystem research is



PF = PHYSICAL FACTORS
L = LIGHT
N = NUTRIENTS
R = RESPIRATION
I = IMPORT
E = EXPORT

WCP = WATER COLUMN PROCESSES
SP = SEDIMENT PROCESSES
MP = MARSH PROCESSES

Figure 1. Conceptual model of estuarine biological processes.

presented by McIntire and Colby (1978), Colby and McIntire (1978) and McIntire (in press).

Estuarine biological processes can be considered holistically in terms of inputs and outputs relative to the entire ecosystem, or mechanistically in terms of a system of coupled subsystems. These subsystems may be uncoupled and investigated separately after the coupling variables have been identified and taken into account. Such a structure defines levels of resolution in the context of the holistic view of the ecosystem. Therefore, specific, goal-oriented research directed at a target subsystem is approached within the coupling structure of the entire ecosystem.

A conceptual model of an estuary was developed initially and was continually refined during the course of this study (Figure 1). The Estuarine Biological Processes system was partitioned into three coupled subsystems -- Water Column Processes, Sediment Processes and Marsh Processes. The work reported in this thesis was concerned with the Sediment Processes subsystem. Sediment Processes was further partitioned into Primary Food Processes and Macroconsumption (Figure 2). The target subsystem for this work was the Primary Food Processes subsystem. Primary Food Processes included the dynamics of variables associated with the accumulation and degradation of detritus and autochthonous plant material, e.g., detrital and living plant biomass. To obtain a finer level of resolution, the Primary Food Processes subsystem can be decomposed into the coupled subsystems of Algal Primary Production, Zostera Primary Production and Detrital Decomposition.

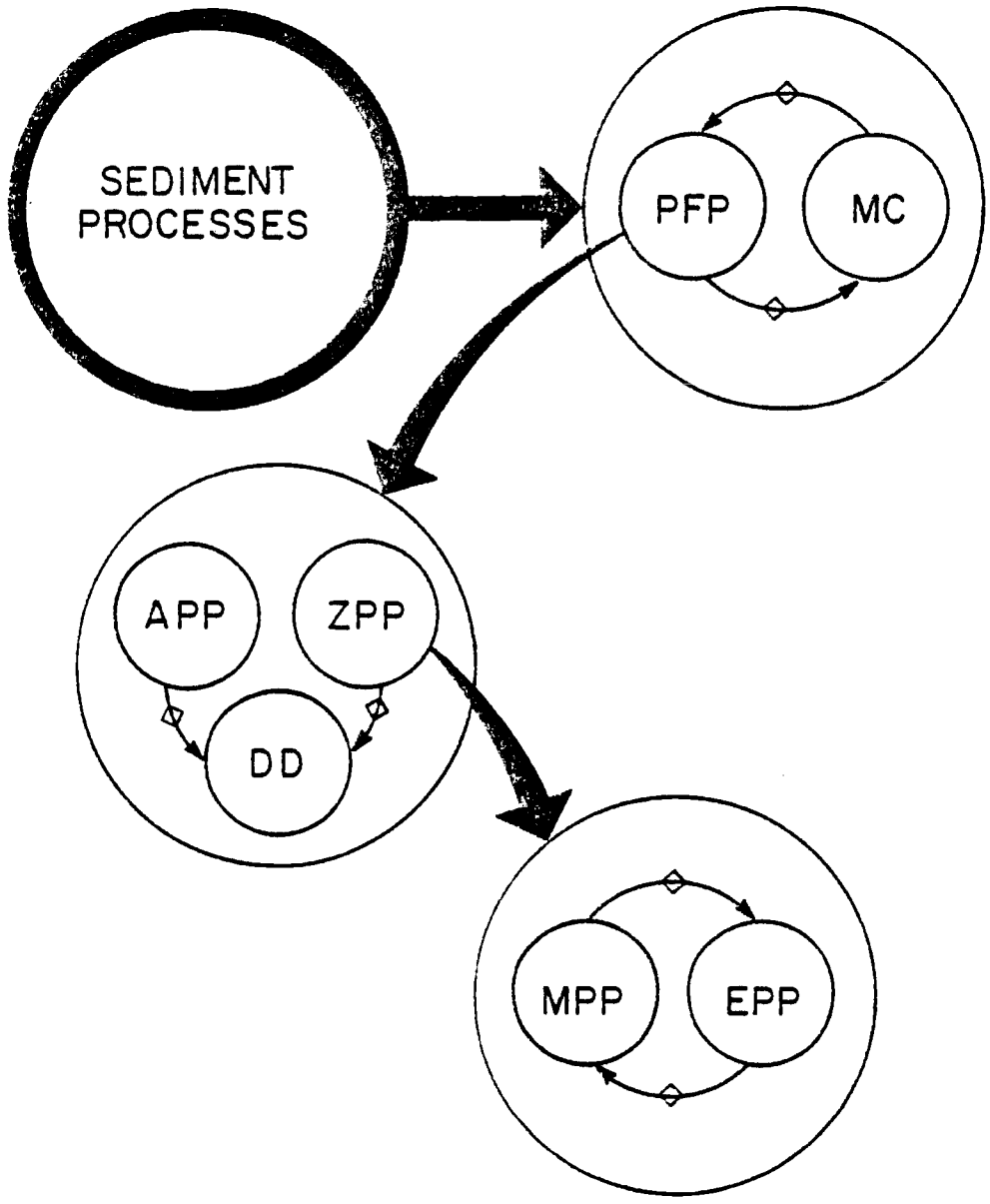


Figure 2. Schematic representation of the hierarchical structure of Sediment Processes indicating the subsystems of Zostera Primary Production.

In this way, the primary food supply associated with the sediments, i.e., the energy source originating with plants, was represented.

In summary, this study examined the autotrophic processes associated with the Sediment Processes subsystem relative to the EPA conclusion that benthic autotrophy has a dominant influence on the nutrient patterns in the water column of Netarts Bay during the summer months. Two levels of resolution consistent with the conceptual model were considered (Figure 2). At the finest level of resolution the biology of Zostera and its associated epiphytes were considered relative to their process capacity. At a higher level of organization, the bioenergetics of the Zostera Primary Production subsystem were described.

Literature Review

Historical Aspects of Seagrass Research.

The first work on the ecology of Zostera marina L. (eelgrass) was done by researchers from the Danish Biological Station, Copenhagen. The earliest of these studies was that of Petersen (1891), which related the abundance of fish in Danish waters to the presence of Zostera. Additional ecological studies were conducted by Ostenfeld (1905, 1908). Eelgrass growth, plankton densities, and deposition of organic matter were described by Petersen and Boysen-Jensen (1911). Petersen (1913) estimated the standing stock of Zostera in Danish waters, while Blegvad (1914, 1916) studied the food of invertebrates and fish. In

a series of two papers, Petersen (1915, 1918) synthesized the work that had been done, constructed food chains and pyramids for the system, and concluded that Zostera detritus formed the base of the food chain.

In 1913 the "wasting disease" of eelgrass appeared on the Atlantic Coast of North America and quickly spread to the Northern European Coast. By 1933 90% of the standing stock along the Atlantic Coast of North America was destroyed (Milne and Milne, 1951). From 1931 to the 1950's the bulk of the research on Zostera centered around elucidating the cause of the disease and describing the impact that the loss of the eelgrass beds had on coastal marine systems.

In the 1950's the emphasis of research again concerned the ecology of Zostera. This change was marked by the work of Arasaki (1950a, 1950b) in Japan. Conover (1958) presented the first quantitative data on American Zostera beds with a study of the factors relating to the seasonal growth of benthic macrophytes. Other early studies in America included: Williams (1959) in Virginia; McRoy (1966, 1970a, 1970b) in Alaska; Keller (1963), Waddell (1964), and Keller and Harris (1966) in Humboldt Bay, California; and Burkholder and Doheny (1968) on Long Island, New York.

Indicative of the increasing interest in seagrass ecosystems, an International Seagrass Workshop was held in 1973 in Leiden, Netherlands. Committees of scientists discussed the progress of seagrass research (productivity and physiology, systematic

ecology, decomposition, consumer ecology, and oceanography) and made recommendations for future work (McRoy, 1973). This meeting resulted in the establishment of the International Seagrass Ecosystem Study Program in 1974. The program was designed to encourage international cooperative seagrass ecosystems investigations, to bring diverse expertise to bear on the study of seagrass ecosystems, and to establish a centralized bibliographic source for seagrass literature (McRoy, 1973).

In the past twenty years there has been significant progress in seagrass research. As a result, seagrass ecosystems have become recognized as one of the most productive types of ecosystems (Zieman and Wetzel, 1980).

Several general articles review the role of seagrasses in the coastal marine environment, particularly that of Zostera and Thalassia. The role of seagrasses in coastal lagoons was described by Wood et al. (1969). Thayer et al. (1975) briefly evaluated the value of seagrass communities and man's impact on them. A broad perspective of seagrasses, the coastal marine environment and associated managerial concerns was presented by Phillips (1978).

In an effort to present the status of the knowledge of the seagrass ecosystem, den Hartog (1971, 1977) presented a survey of the structural and functional features of seagrass communities, as well as an attempt at their classification. Aspects discussed included growth forms, zonation, establishment, succession and community structure. McRoy and Lloyd (1981) approached the

functional aspects of seagrass communities in terms of processes that maintain the stability of marine macrophyte-based systems. They presented arguments to support two conceptual models--an algal-based, or marine model, and a seagrass-based, or terrestrial model.

In conjunction with the outcomes of the International Seagrass Ecosystem Study Program two volumes of review articles on various aspects of seagrass research have been published (McRoy and Hefferich, 1977 and Phillips and McRoy, 1980). The article by McRoy and McMillan (1977) discussed the production ecology and physiology of seagrasses, while the methods for determining production in seagrasses were reviewed by Zieman and Wetzel (1980).

Natural History of *Zostera marina* L.

The vegetative shoot of *Zostera marina* L. comprises an extensive rhizome system that bears erect, leafy shoots. The linear leaves with basal sheaths are 3-12 mm broad and up to 12 dm long (Hitchcock and Cronquist, 1973). The rhizome has a meristem associated with each leaf that is positioned immediately below the node (Tomlinson, 1974). At each node two bundles of roots are formed. Since *Zostera* persists in natural habitats primarily through vegetative reproduction, a continually active meristem is necessary to maintain the populations. This requirement is termed meristem dependence (Tomlinson, 1974). The shoot apical meristem produces leaves dichotomously, giving the shoot a laterally, flattened appearance. An internode remains small

until the leaf associated with one of the nodes becomes the next to the oldest leaf on the plant. At this time the internode elongates, and the roots are produced at the node. Consequently, the shoot is pushed ahead through the sediment by the growth of the youngest internodes along the rhizome. The life of an internode is about 90 days during the growing season in North Carolina (Kenworthy, personal communication). New shoots are produced by the development of axillary buds in the nodes of the oldest leaves. With the loss of the leaf whose node produced it, and with the branching of the rhizome, these shoots become independent from the parent shoot.

Studies on the Production and Ecology of *Zostera marina* L.

McRoy (1966) distinguished between *Zostera* growing subtidally as compared to that growing intertidally on the basis of plant morphology and physiology. Phillips (1972) established that these were not separate races of plants, but an example of the great phenotypic plasticity that can be found in natural populations. When plants from the subtidal were transplanted into the intertidal they took on the characteristics of the plants in that region, and vice versa. McMillan and Phillips (1979) further concluded that seagrass populations reflect the selective influence of the local habitat conditions in the morphological and physiological characteristics of the plants. Percentage cover, shoot size and biomass all increase with a decrease in elevation in Humboldt Bay, California (Keller and Harris, 1966). Bayer (1979) reported a

difference in the way beds of Zostera were perpetuated in intertidal region of Yaquina Bay, Oregon. The upper intertidal zone (above MLW) was characterized by annual growth from seeds, while the low intertidal zone (below MLW) was characterized by vegetative growth from rhizomes.

In attempts to explain these differences several factors have been considered. In particular, studies have concentrated upon the responses of seagrasses to salinity, temperature and insolation (McRoy and McMillan, 1977). Setchell (1929) proposed five stages in the annual cycle of eelgrass growth and reproduction in relation to temperature. This scheme was modified for Alaska by McRoy (1966). While McRoy (1966) and Arasaki (1950b) supported Setchell's model, Burkholder and Doheny (1968) did not. Most recently, the temperature responses of Zostera were studied by Biebl and McRoy (1971) in Alaska. They noted that the intertidal form was tolerant of temperatures up to 35°C while temperatures above 30°C were detrimental to the subtidal form. McRoy (1969) reported that plants were in good vegetative condition under arctic ice in water at -1.8°C.

Biebl and McRoy (1971) also studied the salinity tolerance of Zostera from Alaska. They found plasmatic resistance in a range from distilled water up to 3X seawater. Leaves were dead within 24 hr after exposure to salinities 4X seawater. Ogata and Matsui (1965) investigated the effects of salinity, drying, and pH on the photosynthesis was depressed in concentrated seawater, but the effect was less severe with an ample supply of

carbon dioxide. Keller and Harris (1966) attributed the patterns of Zostera marina zonation in Humboldt Bay primarily to desiccation related to exposure during low tides.

Of the physical factors controlling the distribution of Zostera along an elevational gradient, light is most often named as the controlling factor (Burkholder and Doheny, 1968; Sand-Jensen, 1975; Jacobs, 1979; and Mukai et al., 1980). Backman and Barilotti (1976) and Dennison (1979) investigated the mechanisms by which Zostera adjusts to a reduction in light. Backman and Barilotti (1976) described a corresponding decrease in shoot density and suppression of flowering. In a series of experiments Dennison (1979) tested four possible adaptations of Zostera to reduced light levels. He concluded that change in leaf area is the major adaptive mechanism of Zostera to changing light regimes, while other physiological adaptive mechanisms, i.e., changes in photosynthetic pigment ratios, and concentrations, are less important.

The factors controlling the limits of Zostera in the upper intertidal (above MLW) also involve uprooting by wave action and grazing by waterfowl (Keller, 1963; McRoy, 1966, 1970a). Bayer (1979) observed the foraging habits of herbivorous waterfowl on the mudflats of Yaquina Bay, Oregon. Eelgrass in the upper intertidal was available to uprooting by waterfowl longer than eelgrass in the lower zones. In addition, Bayer (1979, 1980) described the ingestion and uprooting of eelgrass covered with herring eggs by non-herbivorous birds.

Another aspect of seagrass research is concerned with the primary production of Zostera. These studies range from measures of aboveground standing stock to attempts at estimating the production of the various components of the seagrass ecosystem. Studies that were concerned with the measurement of standing stock and, in some cases, estimation of production from these measurements, include: Burkholder and Doheny (1968) in New York; Thayer, et al. (1975) in North Carolina; Phillips (1972) in Puget Sound; Keller (1963), Waddell (1964) and Harding and Butler (1979) in Humboldt Bay, California; Stout (1976) in Netarts Bay, Oregon; McRoy (1966, 1970a, 1970b) in Alaska; Harrison (1982) in Boundary Bay, Canada; Nienhuis and De Bree (1977) in The Netherlands; and Mukai, et al. (1980) and Aioi (1980) in Japan.

Production has been measured using a variety of methods. Changes in the dissolved oxygen content of the water surrounding the plants was used by McRoy (1966) and Stout (1976). On a community level, the midsummer metabolism in eelgrass beds in a pond and river in Rhode Island was measured by Nixon and Oviatt (1972) using the diurnal oxygen curve method. The use of the oxygen method in production measurements of aquatic macrophytes has been criticized. It assumes that the oxygen produced by the submersed macrophyte is released from the plant into the surrounding water at a rate that is proportional to the rate of photosynthesis. Such a relationship does not clearly exist for angiosperms like Zostera that have extensive lacunar systems (Hartman and Brown, 1967). The ^{14}C method of measuring the

production of Zostera has been used by Dillon (1971), McRoy (1974) and Penhale (1976, 1977). The ^{14}C method, also, is receiving close scrutiny, particularly with respect to the internal recycling of carbon dioxide (Sondergaard, 1979; Zieman and Wetzel, 1980).

The best accepted method for measuring Zostera production is the leaf marking method first developed by Zieman (1974) for Thalassia. This method has been modified in a variety of ways. Patriquin (1973) modified the leaf marking method to include the production of the belowground parts of Thalassia. Sand-Jensen (1975), Jacobs (1979), Mukai, et al. (1979), Nienhuis (1980), Nienhuis and De Bree (1980) and Aioi, et al. (1981) have all used a marking method to estimate the aboveground and belowground production of Zostera.

The use of leaf marking also has led to descriptions of the growth of an individual leaf. Sand-Jensen (1975) determined that elongation was confined to the basal portion of the leaf. Jacobs (1979) demonstrated that the growth rate of a leaf decreases with age. Similar experiments measuring leaf production and defoliation rates, and mean lifetime of leaves were done by Mukai, et al. (1979) and Aioi, et al. (1981).

Epiphytic Assemblages.

An epiphyte is any organism that lives upon a plant. Bacteria, fungi, algae and a variety of invertebrates make up the community of organisms that live on the leaves of Zostera. Much of the attention given this community has focused on the plants. More

recently, the fungi and bacteria have been studied, e.g. Hossell and Baker (1979) and Newell (1981).

The bulk of the literature on the algal epiphytes of seagrasses describes the floristics. In a recent review, Harlin (1980) compiled 27 previously published species lists. Floristic works published since that time include: Hall and Eiseman (1981) for the Indian River, Florida; Sullivan (1979) for the Mississippi Sound; Jacobs and Noten (1980) for Roscoff, France; and Whiting (in progress) for Netarts Bay, Oregon.

Epiphyte biomass can equal that of the leaves (McRoy and McMillan, 1977). Moul and Mason (1957) established that the amount of epiphytes increased toward the tip of the blade.

Other investigators have been interested in the distribution of the epiphytes on the leaf of the macrophyte. Van de Ende and Haage (1963) reported that macroalgae growing on Zostera preferred the edge of the leaf in plants growing in sheltered areas, while those growing on plants in strong currents preferred the leaf surface. This pattern was also seen on Zostera marina and Phyllospadix scouleri in Puget Sound and the San Juan Archipelago (Harlin, 1971). Sieburth and Thomas (1973) used scanning electron microscopy to examine the fouling community of eelgrass at a finer level of resolution.

Harlin (1975) listed a series of factors that influenced the coexistence between host and epiphyte. Obviously, leaves of seagrasses increase the area on which algae can settle. Certain species, e.g., Smithora naiadum, have become specialized

to the point that the only environment in which they are found is on the leaves of seagrasses. Epiphytes located on a seagrass blade have access to the photic zone and nutrients in the surrounding water. McRoy and Goering (1974) speculated that epiphyte loads on seagrasses were inversely related to the availability of nutrients in the water column, but transfer of nutrients from the macrophyte to the epiphytes does occur. The phosphate that is leaked from the leaves of seagrasses is first available to epiphytes (McRoy and Barsdate, 1970; Harlin, 1971, 1973; McRoy et al., 1972; Penhale and Thayer, 1980). Goering and Parker (1972) reported that nitrogen fixed by blue-green algae epiphytic on Thalassia finds its way into the seagrass host. Therefore, nutrients are exchanged between epiphyte and macrophyte in both directions. There is also evidence for the transfer of organic carbon from Phyllospadix and Zostera to epiphytic algae and vice versa (Harlin, 1971, 1973; Penhale and Thayer, 1980).

In contrast, epiphytes were also shown to have an adverse affect on the photosynthesis of eelgrass. Sand-Jensen (1977) demonstrated that epiphytes reduced the photosynthetic rate of the leaves both by acting as a barrier to carbon uptake and by reducing light intensity. He suggested that the macrophyte is able to reduce the epiphytic biomass by constantly producing new photosynthetic tissues and by excreting algal antibiotics. Zapata and McMillan (1979) and McMillan, et al. (1980) have identified phenolic acids and sulfated phenolic compounds in seagrasses. These compounds have been cited in the literature

of allelopathy in land plants as major water-borne inhibitors, and may play a role in the adjustment to the seawater habitat as well as in the allelochemical relations of seagrasses, e.g., as a chemical barrier to microbial invasion.

Despite these complex interactions between macrophyte and epiphytes, the epiphytic algae do not form an unique group of organisms. Brown (1962) and Main and McIntire (1974) found similar assemblages on seagrass blades, rocks, macroalgae, and the sediments, and in the water column. Main and McIntire (1974) further stated that an epiphyte and a macrophyte are often associated when their responses to environmental parameters coincide. Therefore, there seem to be few epiphytes that form obligate associations with seagrasses.

There have been only a few studies on the production of epiphytes. Jones (1968) estimated production of epiphytes on dead or dying Thalassia leaves. Hickman (1971) scraped the epiphytes off Equisitum in a freshwater pond and incubated them in light and dark bottles with ^{14}C. Wetzel and Allen (1972) measured ^{14}C uptake of epiphytes that colonized glass slides in a Michigan Lake. The only study that considered the production of the macrophyte and epiphyte in situ is that of Penhale (1977). Using the ^{14}C method, she incubated the intact Zostera with its associated epiphytes in plexiglass chambers. The epiphytes and macrophyte were physically separated, and the ^{12}C assimilation rate determined.

II. MATERIALS AND METHODS

Description of Netarts Bay

Netarts Bay, Oregon's sixth largest estuary, is located on the northwestern coast of the state, approximately sixty miles south of the mouth of the Columbia River (Figure 3). The bay was created during the late Tertiary Period when wave action eroded the soft, sedimentary rock of the Astoria Formation which is located between the basalt headlands forming Cape Lookout and Cape Meares in Tillamook County, Oregon. The western boundary of the bay is currently formed by a sand spit which represents the remains of the three sand dunes that were eroded with the rise in sea level during recent geologic time.

Netarts Bay receives fresh water from twelve small creeks that drain the surrounding watershed. Freshwater input is mainly restricted to the winter, and salinity is high, usually greater than 25 $^{o}/oo$. Water temperature varies annually from 4° to 25°C, while the air temperature ranges from 0° to 30°C.

The bay is influenced by mixed, semi-diurnal tides characteristic of the North Pacific Ocean. The maximum tidal range is 3 m, and mean low water (MLW) and mean high water (MHW) are 0.5 m and 2.0 m above mean lower low water (MLLW), respectively. The volume of the tidal prism between MLW and MHW is 9.4×10^{6} m^{3}, while the volume of the bay at MLW is 3.2×10^{6} m^{3}. The surface area of the estuary is 941 ha, of which 612 ha are tideland and 329 ha are permanently submerged. This submerged area is restricted primarily to the narrow channel.

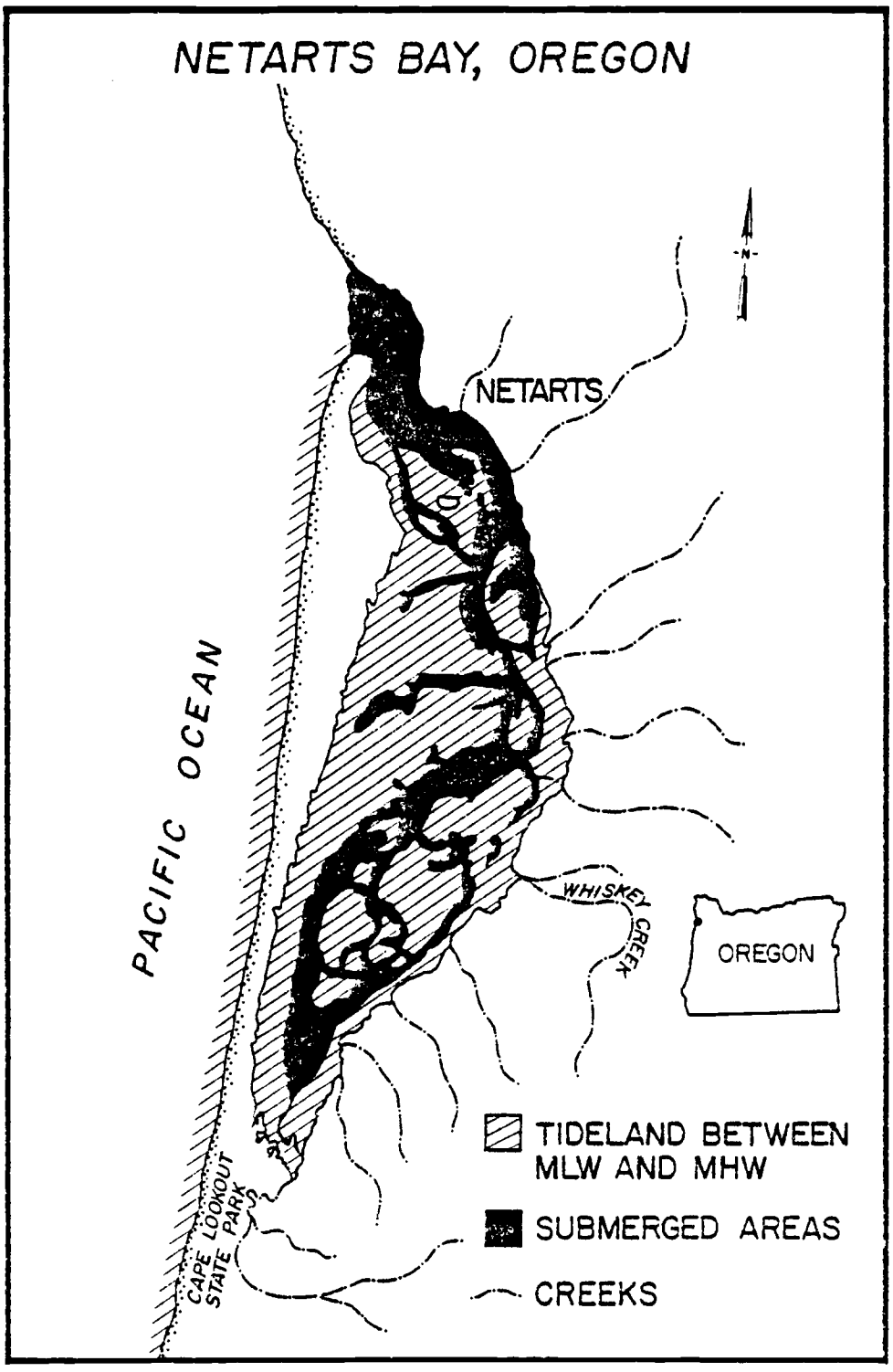


Figure 3. Map of Netarts Bay.

Description of Intensive Study Area

The EPA studies were used to generate hypotheses for further investigations at a finer level of resolution. A detailed study of the vertical and horizontal nutrient profiles of the water column over a transect from the channel through the seagrass beds to the open mudflat was proposed by EPA. Related biological aspects were examined by the research reported in this thesis. Interpretation of the results of the nutrient profile study in relation to the biological processes study required that both aspects be conducted during the same time period at the same location. A site appropriate for both projects was selected on the basis of the results of a field study of the circulation pattern of water over the seagrass beds. Criteria used in the selection included: (1) the presence of a large expanse of Zostera marina L. that was representative of the Zostera beds in the estuary; (2) evidence of a straight line flow of water over the Zostera beds during an incoming tide; and (3) accessibility for sampling.

The intensive study area included approximately 37,500 m^2 located within the shellfish reserve and research area managed by the Oregon State Department of Fisheries and Wildlife (Township 2S, Range 10W, in the vicinity of Whiskey Creek). This region lies near the north end of the large intertidal Zostera bed that occupies the southern and western regions of Netarts Bay (Figure 4).

Three transects over a range of tidal heights were chosen within the intensive study area. These were labelled transects 1 through 3 (Figures 5 and 6).

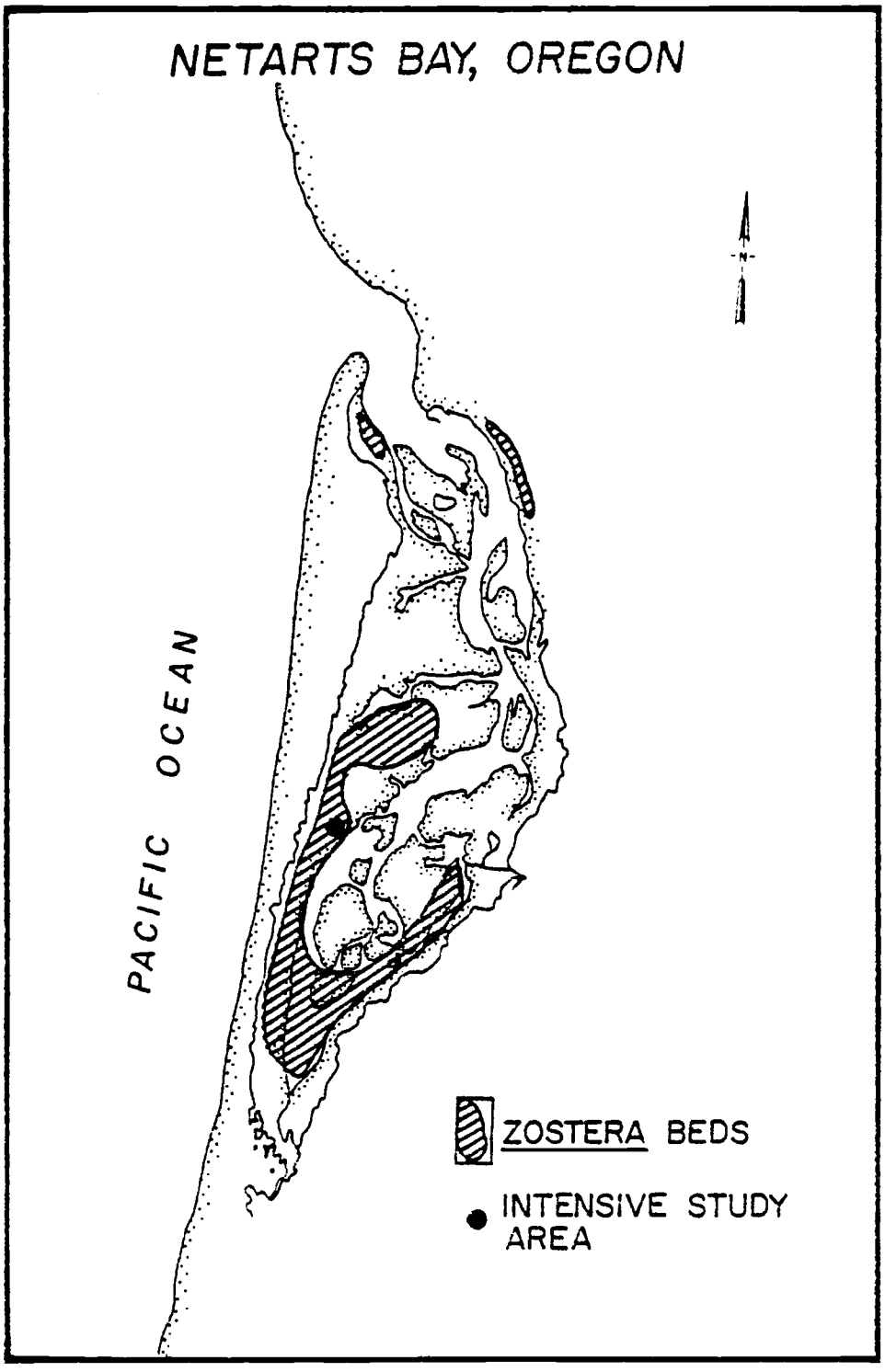


Figure 4. Location of Zostera beds and the intensive study area in Netarts Bay.

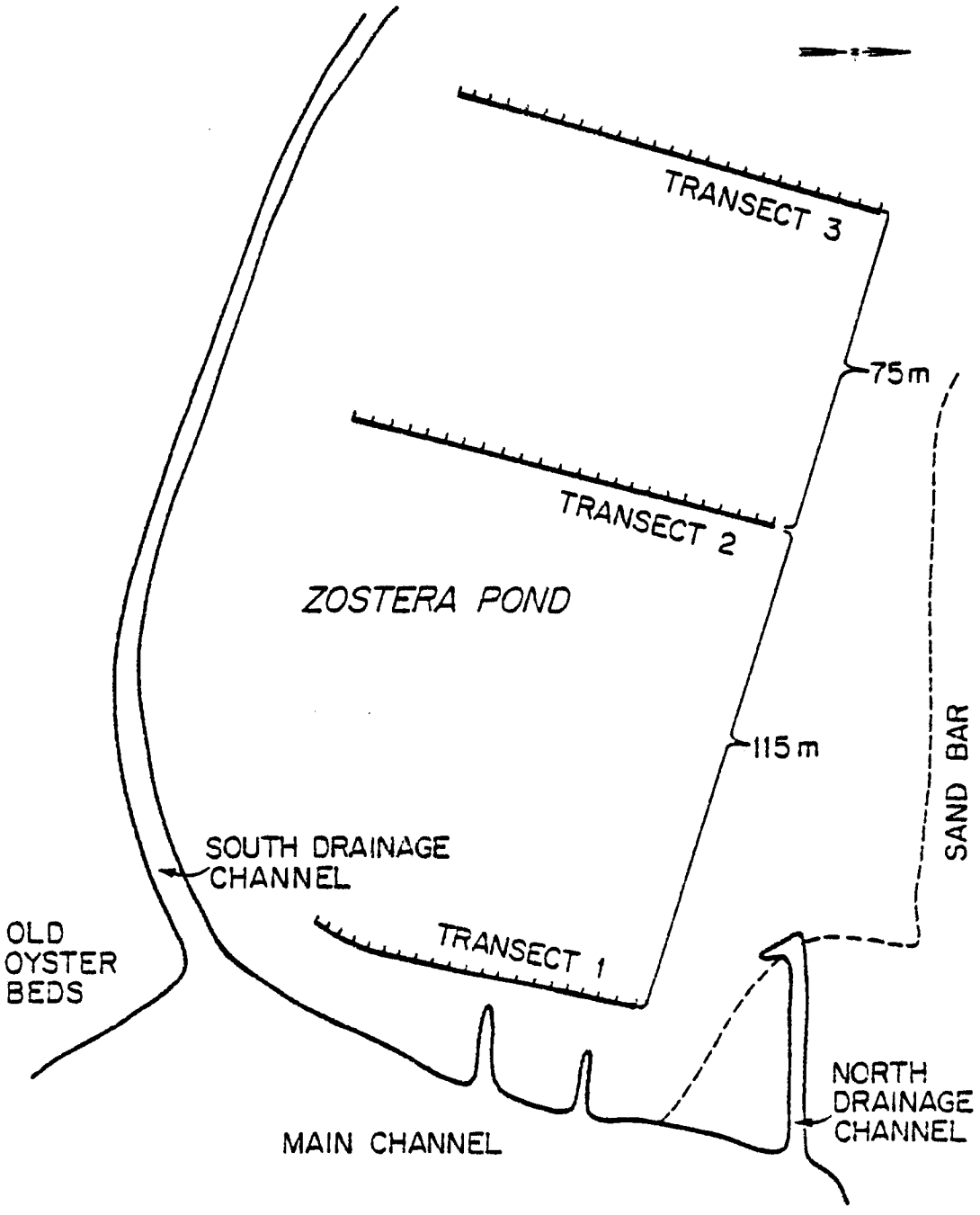


Figure 5. Map of the area of intensive study, indicating the location of the sampling transects relative to the main channel.

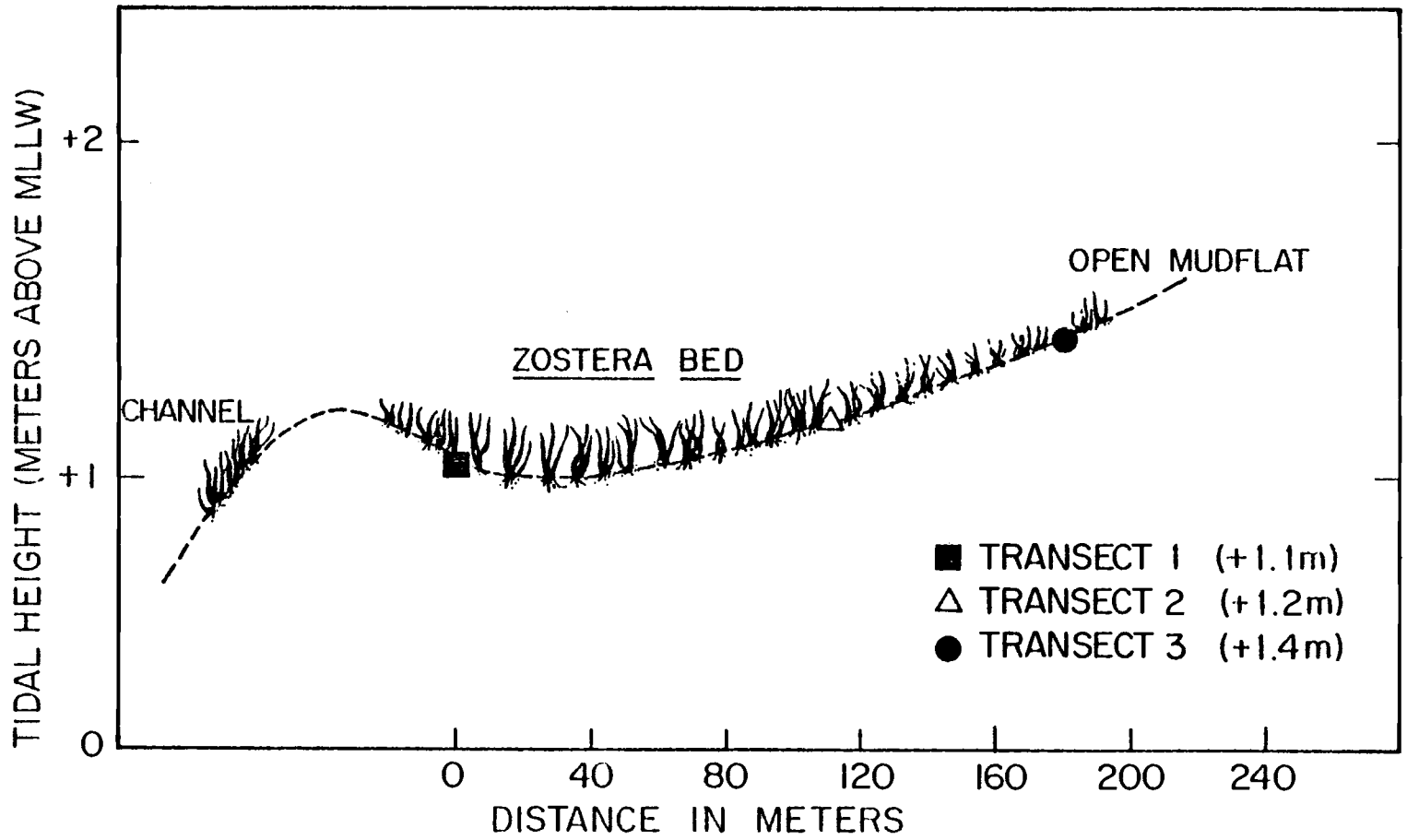


Figure 6. Cross section of the area of intensive study indicating the location and height of the sampling transects.

Transect 1 was 1.1 m above MLLW and was located within the Zostera bed away from the region of obvious influence from the channel. The other transects were located during an incoming tide by placing a stake in the sediment at the water's leading edge when the water at the next lower transect was 15 cm deep. This procedure located transect 2 at 1.2 m above MLLW, and transect 3 at 1.4 m above MLLW. Transects 1 and 3 represented the upper and lower limits of the Zostera bed within the intertidal region; transect 2 represented a region of transition. Moreover, transect 2 was at the edge of a large pool of water that was created at low tide by the damming effect of the larger Zostera shoots in the area. Therefore, this transect was located between an area that was regularly exposed at low tide, and one that did not drain completely at low tide.

The transects were established by positioning stakes with an Abney level and measuring tape at 5 m intervals at the appropriate elevation. Transects 1, 2, and 3 were 75 m, 100 m, and 100 m in length, respectively. The ends of the transects were located away from any obvious influence of the drainage channels that bordered the study area. The elevation at each transect was checked relative to prediced values for the height of the high tide for Tillamook County beaches. Stakes marked at 1 cm intervals along their length were placed in the channel at the intensive study area and at each of the transects. The difference in the depth of the water in the channel at slack low tide and at the following slack high tide was determined, and the depth of the water at each

transect was measured. The ratio between the predicted height of the high tide and the measured height was used to calculate the elevation of each transect relative to MLLW.

A series of 0.5 X 0.5 m sample sites were designated along each transect. Transect 1 had 150 sample sites and transects 2 and 3 each had 200 sample sites. The sites to be sampled along each transect on a particular date were chosen from a random number table without replacement. Individual random number tables of the proper size for each transect were generated by a computer using a random iterative process.

Selection of Quadrat and Sample Size

Choice of quadrat size and sample size for biomass determinations was based on data collected during the 1979 growing season. Quadrats larger than 400 cm^2 were considered unsuitable because the large biomass from such a quadrat limited the number of replicates that could be processed before the material deteriorated. Quadrat sizes from 100 to 400 cm^2 were tested. Counts of shoot density along each transect were used as an indicator of the variance among biomass samples. These counts were taken at the beginning and end of the growing season, i.e., in June and September. In general, variance at all transects decreased with an increase in quadrat size from 100 to 400 cm^2 (Table 1); 400 cm^2 (20 X 20 cm) quadrats were used for all subsequent samples. The harvest of a 400 cm^2 quadrat did no obvious, lasting damage to the system. During the subsequent growing season harvested areas were being recolonized vegetatively by shoots from neighboring regions.

Table 1. Sample statistics from shoot density data used to determine quadrat size (n = 7).

TRANSECT	1				2				3			
QUADRAT SIZE (cm^2)	100	200	300	400	100	200	300	400	100	200	300	400
JUNE, 1979												
MEAN	957	1186	1238	1236	529	443	410	518	1171	879	919	1007
STANDARD ERROR	104	138	130	117	170	109	90	99	333	224	208	193
STANDARD ERROR = X% OF MEAN	11	12	10	10	32	25	22	19	28	25	23	19
SEPTEMBER, 1979												
MEAN	657	686	710	721	847	900	762	954	1286	1143	1052	1025
STANDARD ERROR	92	81	44	24	182	112	140	108	310	265	206	188
STANDARD ERROR = X% OF MEAN	14	12	6	3	21	12	18	11	24	23	20	18

The shoot density data from June and September, 1979 was also used to select a suitable sample size. Factors considered in choosing the number of quadrats per sample for each transect included the level of precision of the estimate of the mean of the biomass, and the cost in time and materials of processing the samples. For the intensive study area, it was determined that a sample size of seven 400 cm^2 quadrats had a standard error that was less than 20% of the mean (Table 1). Also, seven quadrats per transect could be harvested by one person during the low tide in two or three consecutive days. In 14 days or less the plant material from seven 400 cm^2 quadrats per transect could be processed to the point where it could be stored indefinitely without deterioration until all necessary measurements could be made. This was an important consideration in choosing a sample size, because fresh samples of Zostera could be refrigerated longer than 14 days without significant deterioration. Therefore, the standard sample size selected for this study was seven quadrats per transect. However, depending on weather conditions, time and help available for field work, and the biomass of the Zostera, as few as five quadrats at a transect were sampled at certain times.

Measurement of Biomass

The intensive study site was visited monthly from May, 1979 through June, 1981. Monthly biomass samples were taken from April 1 to September 8, 1980, on February 12, 1981 and from April 6 to May 31, 1981.

Individual sample sites were located by extending a 5-m rope marked at 0.5 m intervals between two of the stakes along a transect (Figure 7). A 20 X 20 cm quadrat frame made of polyvinyl chloride (PVC) welding rod was positioned on the right hand side of the site, approximately 10 cm back from the rope (Figure 7,B). Shoots inside the quadrat were moved away from the edges, and the sediment and rhizome mat along the outer edge of the quadrat were cut through with a trowel. Zostera and associated sediment were then placed in a 1.00 mm mesh sieve, and the sediment washed from the roots with water. Therefore, coarse particulate organic matter (CPOM) was retained since CPOM is defined as particles larger than 1 mm in diameter. Plants with associated epiphytes were put in labelled, plastic bags with a minimum of water, while the litter was retained in the sieve. The remaining sediment in the quadrat was dug out to a depth of about 20 cm below the rhizosphere and was added to the sieve. The sand was washed from the sieve and the remaining litter material was placed in a labelled, plastic bag. All material was kept on ice until it could be refrigerated after returning to the laboratory.

During the time each sample was taken, selected physical properties of the bay and ocean water was measured. Surface water temperature was measured with a hand-held thermometer. A temperature compensated AO Goldberg refractometer was used to determine salinity. Light intensity at the water's surface and at a depth of 0.25 m were measured with a LICOR Underwater Photometric Sensor and Quantum Radiometer Photometer. These values were used to calculate extinction coefficients.

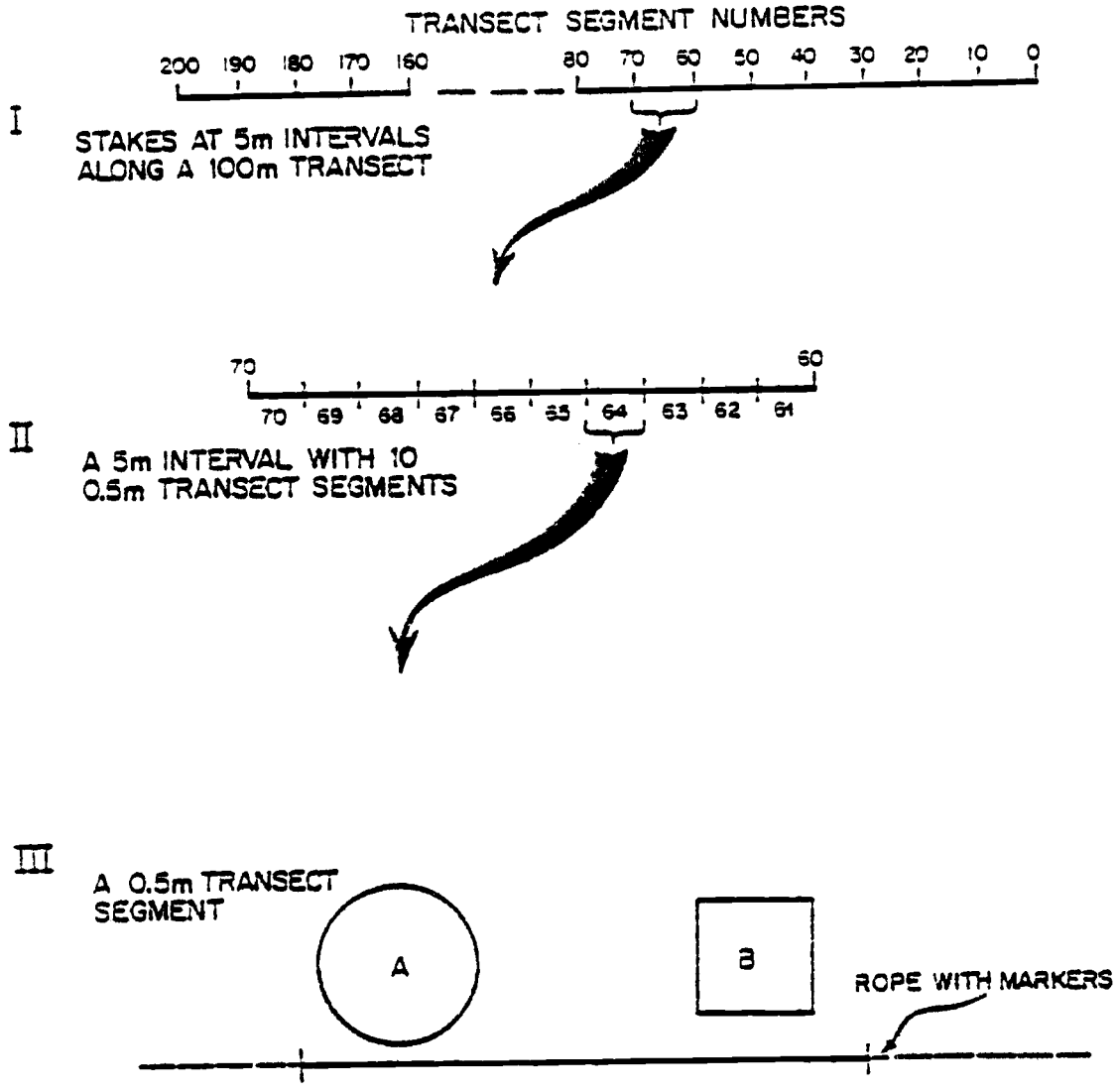


Figure 7. A 100-m sampling transect at three levels of spatial resolution: I. 200 0.5-m transect segments; II. 5-m segment of transect with 10 0.5-m transect segments; and III. The details of one sampling site at a transect segment.

Zostera biomass from each sample quadrat was divided into a series of subsamples to reduce the biomass of the material to be handled at one time and minimized exposure to room temperature. Each subsample was placed in a 1 mm mesh sieve, and individual shoots were cut from the rhizome at the nodes. This material was transferred to a second 1 mm mesh sieve along with any loose leaves, shoots and seedlings.

The sieve containing the leaves, shoots and seedlings, i.e. the aboveground material, was carefully dipped several times into a basin of distilled water to rinse away salt and any remaining sand. The shoots were sorted and the following information was recorded: the number of vegetative shoots, reproductive shoots, and seedlings; the number of leaves per vegetative shoot; and the number of leaves and flowers per reproductive shoot. Leaves were cut from their sheaths, and the sheaths placed into labelled 55 X 15 mm aluminum weighing dishes that had been brought to constant weight at 70°C. These containers had been bent to fit inside a 60 X 20 mm plastic petri plate. To minimize handling errors, a weighing dish was kept inside a petri plate unless a weight was being determined. The leaves were laid out on a labelled 20 X 20 cm glass plate until an area of approximately 16 X 20 cm was covered. The length and width of the area covered were measured to the nearest 0.5 cm and recorded. The glass plates were covered with leaves, and then were coated with distilled water, placed in wooden racks and transferred to a freezer. When the water was frozen, the plates were wrapped in alumninum foil and stored in

a freezer. Reproductive shoots were processed in the same manner. Stems and flowers were combined with the sheaths from the vegetative shoots.

The sieve with the belowground material, i.e., roots, rhizomes and litter, was thoroughly washed in a basin of tap water to remove any remaining sand, and then was dipped several times in distilled water to complete rinsing away the salt. Material from this sieve was sorted by inspection into living and dead roots and rhizomes, and each fraction was placed into labelled containers that had been brought to constant weight at 70°C. Other detritus in the sieve was combined with dead rhizome material, along with unsprouted Zostera seeds. Notes were taken on the quality of the litter.

All sorted material was kept frozen and stored until it was lyophilized. The process of lyophilization was of particular importance because it facilitated the removal of epiphytes from the leaves (Penhale, 1977). After lyophilizing, epiphytes were removed from the leaves and glass plate with a scraper made from a plastic cover slip glued between two glass microscope slides with 3-4 mm of its edge protruding. Epiphytes and leaves were each placed in containers that had been brought to constant weight at 70°C. Finally, all sorted, lyophilized material was brought to constant weight at 70°C and its dry weight determined.

To determine the ash-free dry weight of the leaves, sheaths, roots and rhizomes, and epiphytes, all the material of one kind from the sample quadrats at a transect was combined and ground to a powder in a Waring blender. This homogenized material was

subsampled to fill a maximum of three porcelain crucibles (COORS, size 0) which had been brought to constant weight at 70°C. The material in the crucibles was weighed, ashed for 48 hours at 500°C in a muffle furnace, and reweighed to determine the weight of the ash. To determine the time necessary to completely ash the material, crucibles with organic matter were repeatedly ashed until they came to constant weight. The difference between the dry weight of the material before ashing and the weight of the ash was recorded as ash-free dry weight.

Measurement of Primary Production

Shoot Marking Method.

Net primary production of *Zostera* shoots was measured by a modified shoot marking technique (Zieman, 1974). Bieweekly samples of 14 ot 15 shoots per transect were taken, with two or three shoots marked at each sample site (Figure 7,A). Individual shoots typical of the area were selected. A 0.5 m stake of white PVC welding rod bent into a ring at one end was inserted into the sediment, and the base of a shoot was encircled with the ring. Another PVC stake extending 15 cm above the sediment was placed in the area of the marked shoots to make the region easy to locate, since the PVC rings at the sediment surface were not readily visible (Figure 8,A). Each shoot was marked by inserting a 22 gauge hypodermic needle above the level of the youngest sheath through all the leaves at the same time. The distance between the PVC ring at the base of the shoot and the needle was

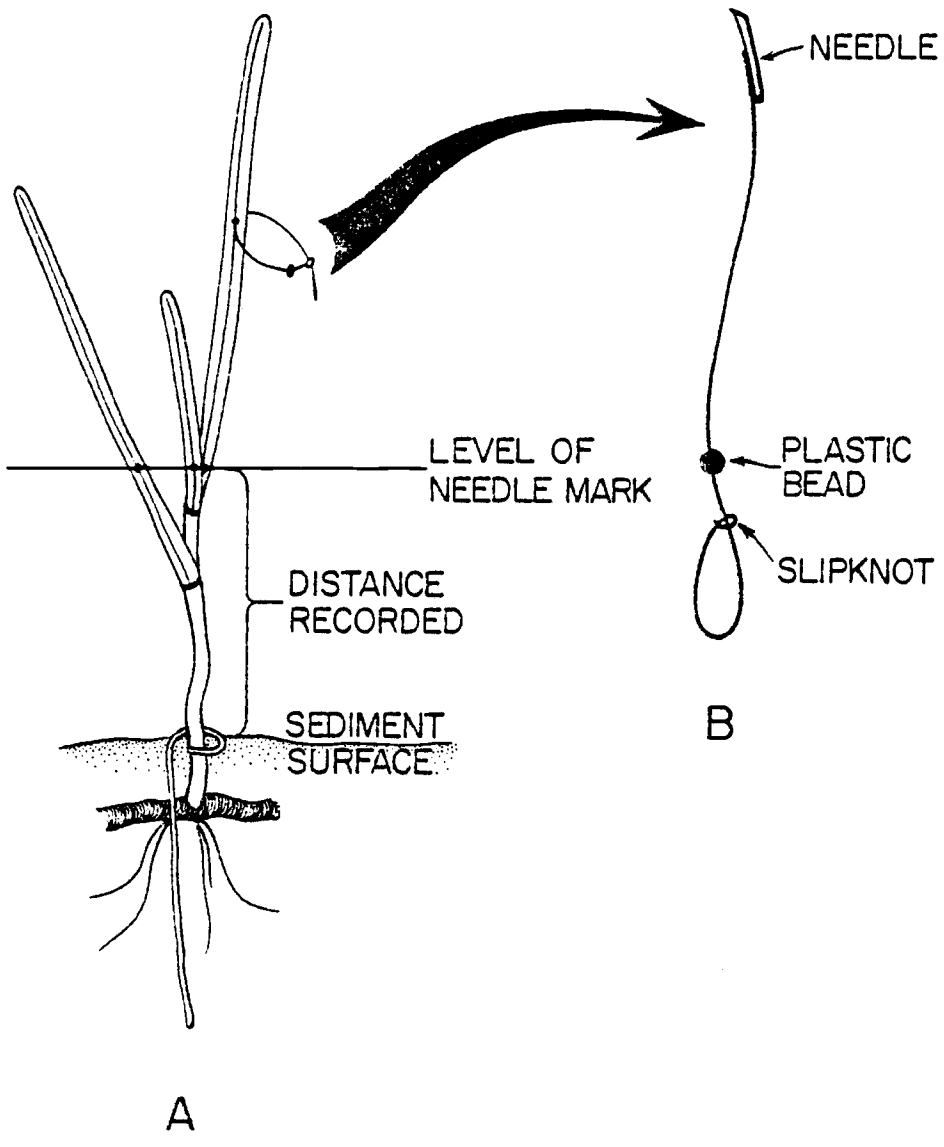


Figure 8. Shoot marking technique. A. Zostera shoot with next to youngest leaf marked with monofilament line. B. The monofilament leaf marker with plastic bead.

measured to the nearest 0.5 cm and recorded. The needle was removed and the number of leaves and lateral shoots were counted and recorded. A marker was placed midway along the length of the next to youngest leaf (Figure 8,B). This marker, made from a 20-cm length of one pound test nylon monofilament had a loop formed by a slipknot at one end; a 1 cm length of 15-pound test monofilament was glued to the other end to serve as a needle. To make the marker more visible, a plastic colored bead was threaded onto the line and glued in place below the slip-knot. The needle end of the marker was passed through the leaf and through the loop at the other end. The loop then was pulled closed, securing the marker in place around the leaf. After twelve to sixteen days, the shoots were harvested at the level of the PVC ring, and placed in individual, labelled plastic bags until they could be refrigerated at the laboratory. At the same time, new shoots were marked for the next two-week period.

In the laboratory individual shoots were rinsed in distilled water to remove sand and salt. The leaf with the plastic marker was located; and the number of leaves present, the number of new leaves, the number of leaves lost, and the number of lateral shoots were determined and recorded (Figure 9). The length and width of each leaf above its sheath was measured and recorded relative to its position on the shoot. Then the distance from the base of the shoot to the original location of the needle mark was measured, and the leaves were cut free at this point. If the PVC ring obviously had moved during the incubation time, the level of the needle mark in the oldest leaf was used as the reference point,

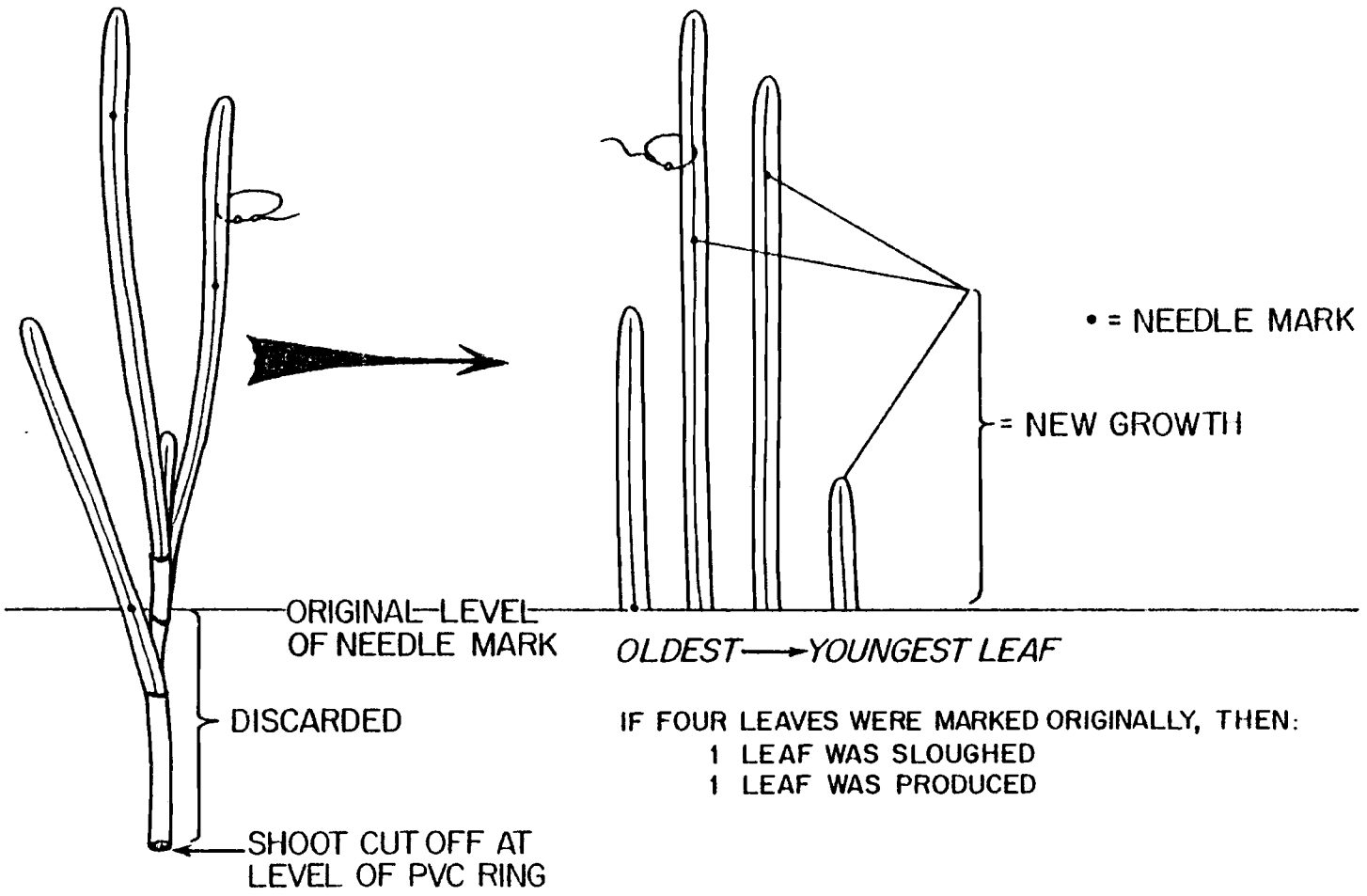


Figure 9. Shoot marking technique indicating the above-ground net primary production (new growth) and leaf export.

as this leaf usually did not grow during the measurement period. Leaves were laid out in the order of their age, and their needle marks were located. The distance between the original level of the mark (i.e., the cut end of the leaf) and its new position was the net primary production of the leaf. This new growth was removed from the leaf and placed on a 20 X 20 cm labelled glass plate. The length and width of this tissue were measured and recorded relative to the position of the leaf on the shoot. Glass plates with this material were treated in the same manner as those processed with Zostera leaves for the biomass determination. Epiphytes removed from the leaves were discarded and the dry weight of the new growth per shoot was determined.

Radioactive Carbon (^{14}C) Method.

The relative net primary production of Zostera and the epiphytes was based on in situ ^{14}C incorporation measurements (Wetzel, 1974). The Bittaker and Iverson (1976) design for an incubation chamber was adapted for use with this method (Figure 10). The cylindrical, Plexiglas chambers were composed of two units. The upper section, stirring unit, housed a magnetically coupled stirring device which operated at 26 rpm. The magnetic drive eliminated the problems of water leakage associated with a shaft that penetrates the chamber wall. This problem was pointed out by Iverson (personal communication). The lower section of the chamber served as the incubation unit. Light and dark chambers were used for the field measurements. Light chambers were constructed of transparent,

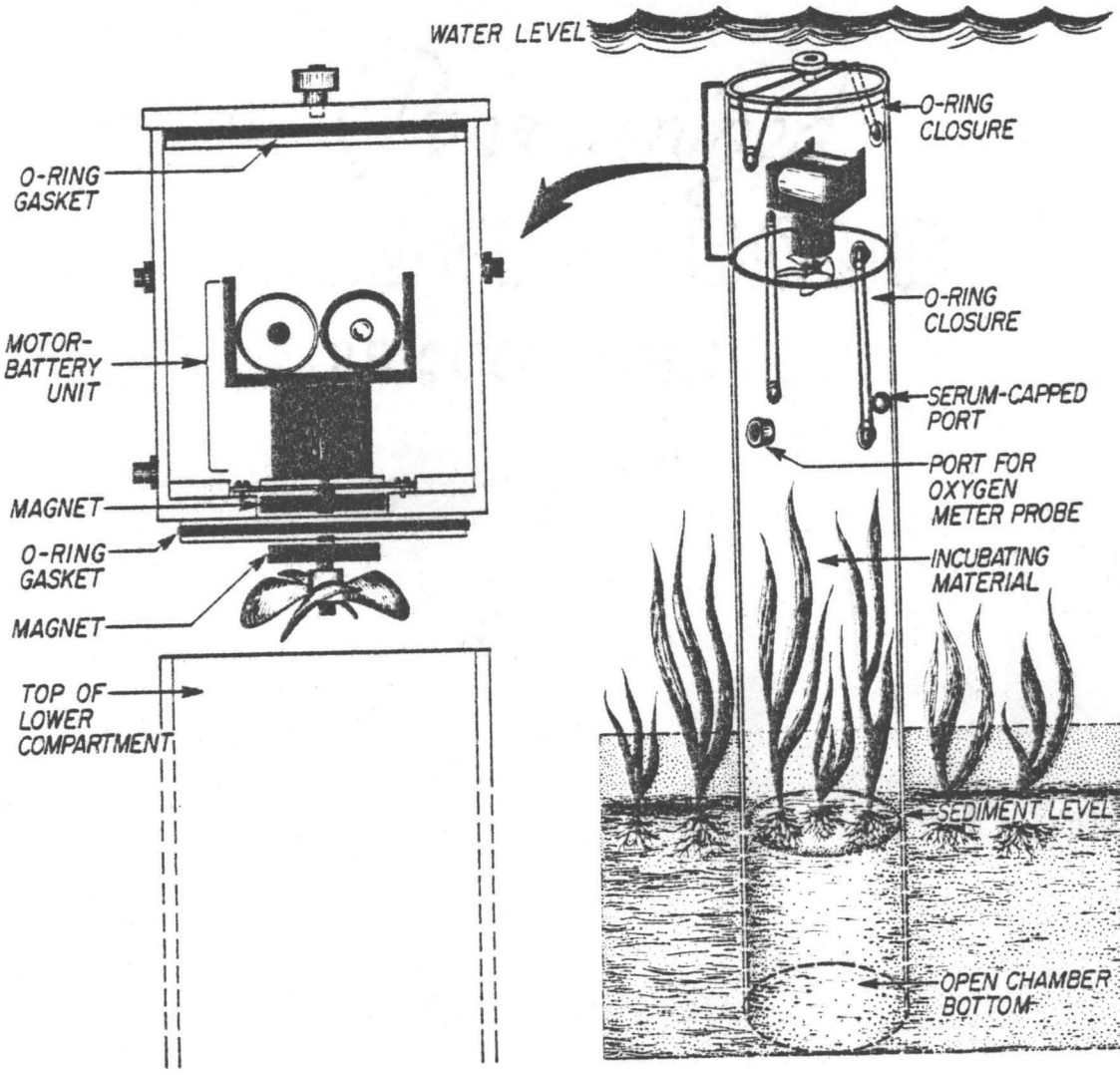


Figure 10. Incubation chambers for measuring net primary production of Zostera and its epiphytes by the ^{14}C method. The entire Plexiglas chamber was 92 cm high, i.d. = 12.8 cm. The incubation unit enclosed a volume of 5.8 l when inserted 30 cm into the sediment.

tubular Plexiglas, while dark chambers were constructed of white, tubular Plexiglas. The exterior of each dark chamber was painted silver and wrapped with silver duct tape to insure no leakage of light.

The ^{14}C-sodium bicarbonate ($NaH^{14}CO_3$) used was obtained from New England Nuclear Corporation as a powder with a specific activity of 7.5 mCi/mmol. The powder was dissolved in sterile, distilled water in a stoppered volumetric flask, was stored in at ca. 5°C until use. The solution was standardized in April, 1982.

At each transect measurements were obtained from two light chambers and one dark chamber. Monthly measurements were made from June 29 to August 24, 1980 and on May 31, 1981. At each sample site a clump of Zostera was selected. A 30-cm length of PVC pipe (i.d. = 10.5 cm, o.d. = 11.5 cm) was placed around the clump and was inserted into the sediment until about 2 cm remained above the surface. To contain the leaves of the Zostera shoots, a bag made of nylon net was fastened around the top of the pipe with a rubber band. When the water from the incoming tide was approximately 50 cm deep at the sample site, the incubation unit of the chamber was positioned around the net and the PVC pipe. Next, the net was removed, and the incubation unit was inserted 30 cm into the sediment. When the incubation unit filled with water, the stirring unit was attached, thereby sealing the chamber. Then 7.3 µCi of a standardized solution of $NaH^{14}CO_3$ solution was injected into the incubation unit and the time was recorded.

An external water sample was taken, fixed with mercuric chloride and later the total available inorganic carbon in the sample was determined by the EPA Water Testing Laboratory using a split beam infrared spectrometer.

During the incubation period, light intensity ($\mu E \cdot m^{-2} \cdot s^{-1}$) was measured continuously using a LICOR Spherical Quantum Sensor and Printing Integrator. In addition, salinity, surface water and air temperatures, and light intensity at the water's surface and at a depth of 25 cm were measured hourly over the Zostera bed.

After a period of 4 to 7.5 hours, the stirring unit was removed, and the time was recorded. The incubation unit was then pulled from the sediment, and the PVC pipe containing the incubated core of Zostera was removed. The Zostera core was transferred to a 1 mm sieve, and the associated sediment was washed away from the roots and rhizomes. The Zostera was then rinsed in distilled water to remove the salt, wrapped in foil, placed in a labelled plastic bag and quick frozen on dry ice.

Samples were stored in a freezer until they were lyophilized. Dried Zostera was sorted into roots and rhizomes, leaves, and epiphytes. The dry weight of each fraction was determined. Samples were then exposed to concentrated HCl fumes to remove residual labelled inorganic carbon (Allen, 1971). Samples obtained on June 29 thawed because of a power failure at the laboratory. Because of cell rupture and expected leakage of incorporated ^{14}C during the freezing and thawing, these samples

were not sorted into their components. They were otherwise treated the same as the other samples. Material from each sample was ground to a powder in a Waring blender and subsamples of 0.1 to 0.2 g were placed in filter paper cones, compressed into pellets and brought to constant weight at 70°C. The pellets were combusted in a Packard TRI-CARB Oxidizer (Model 306) where evolved CO_2 was chemically trapped in 4 ml of Packard CARBOSORB. This was transferred into a scintillation vial with 12 ml of Packard PERMAFLUOR V. The vials were counted in a Packard TRI-CARB Liquid Scintillation Spectrometer System (Model 2425). Counts were corrected for recovery from the oxidizer (92% for Zostera, 91% for epiphytes), counting efficiency (59% for aboveground Zostera, 56% for belowground Zostera, 54% for epiphytes), and background. Assimilation of ^{12}C was calculated according to an equation of Penhale (1977), but disintegrations per minute (dpm) were substituted for counts per minute (cpm).

Data Analysis

Morphometric and biomass data were analyzed by multiple regression analysis (Snedecor and Cochran, 1967) and principal components analysis (Cooley and Lohnes, 1971). Data analyses were performed on a Control Data Corporation CYBER 170 (Model 720) computer at the Oregon State University Computer Center. The computer programs used were part of the REGRESS and MULTIVARIATE subsystems of the Systems Interactive Programming System (SIPS).

III. RESULTS AND INTERPRETATION

Morphometrics and Autecology of *Zostera marina* L. in Netarts Bay

Sexual Reproduction.

Events in the life of *Zostera marina* L. occurred with seasonal regularity in Netarts Bay. Seeds were found in the sediments throughout the year, but germination was restricted to spring (Figure 11, Table 2), starting between mid-February and early April, and concluding by the end of June. Seedlings were not found in the sample taken on February 12, 1981, but were present at all transects in the samples taken in early April 1980 and 1981. They disappeared from the samples at all transects by the end of June. Moreover, seedling data indicated that sexual reproduction did not play a major part in the growth and maintenance of the *Zostera* bed in Netarts Bay. This is compatable with the conclusion of McRoy (1966) and Phillips (1972). However, although the majority of the new shoots are produced by vegetative reproduction, the seedlings are probably important to the maintenance of the genetic diversity within the population. At no time did seedlings represent more than 7% of the shoot population at all transects (Table 3). The mean percentage of the total shoot density that was represented by seedlings when they were present was 2.7% (S.E. = 0.4%).

In samples obtained during 1980 and 1981, the presence of reproductive shoots was variable (Figure 12, Table 4). In 1980,

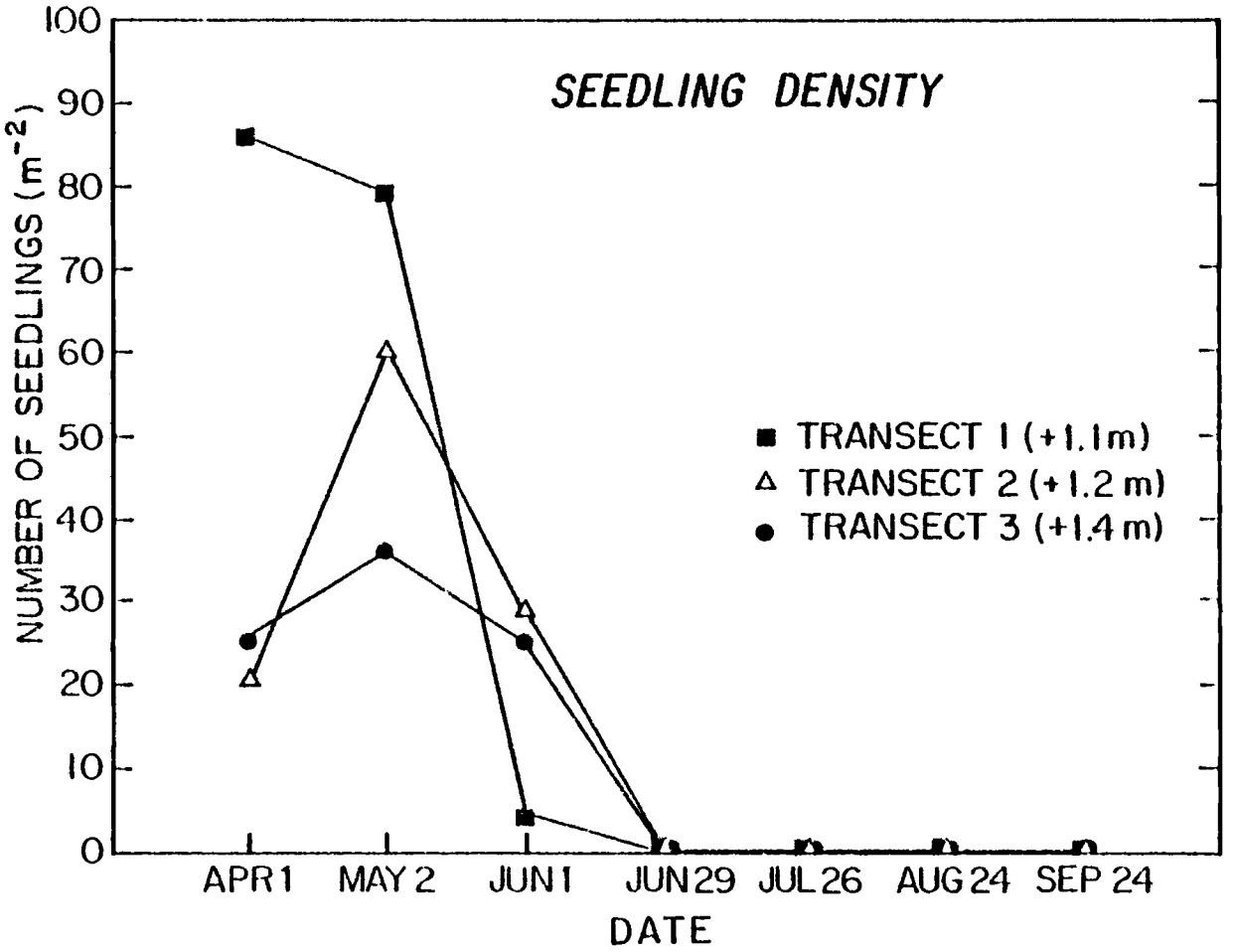


Figure 11. Density of seedings along the three transects during the 1980 sampling period. Each point represents the mean of 5 to 7 observations.

Table 2. Mean number of seedlings per square meter during the period from April 1980 through May 1981. Values in parentheses represent the standard error of the mean of 5 to 7 observations.*

TRANSECT	1980							1981			
	APR 1	MAY 2	JUN 1	JUN 29	JUL 26	AUG 24	SEP 24	FEB 12	APR 6	MAY 3	MAY 30
1	86 (22)	79 (26)	4 (4)	0	0	0	0	0	70 (24)	85 (19)	25 (25)
2	21 (9)	60 (15)	29 (8)	0	0	0	0	-	-	-	-
3	25 (14.4)	36 (13)	25 (11)	0	0	0	0	0	25 (14)	5 (5)	21 (10)

*Dashes indicate no data available.

Table 3. Percentage of the total shoot density represented by seedlings during the period from April 1980 through May 1981. *The percentages were calculated from the ratio of the means of 5 to 7 observations.

	1980							1981			
TRANSECT	APR 1	MAY 2	JUN 1	JUN 29	JUL 26	AUG 24	SEP 24	FEB 12	APR 6	MAY 3	MAY 30
1	3.0	3.7	0.2	0	0	0	0	0	1.8	2.5	0.7
2	2.7	5.1	3.1	0	0	0	0	-	-	-	-
3	3.2	6.7	3.1	0	0	0	0	0	2.2	0.5	1.8

*Dashes indicate no data available.

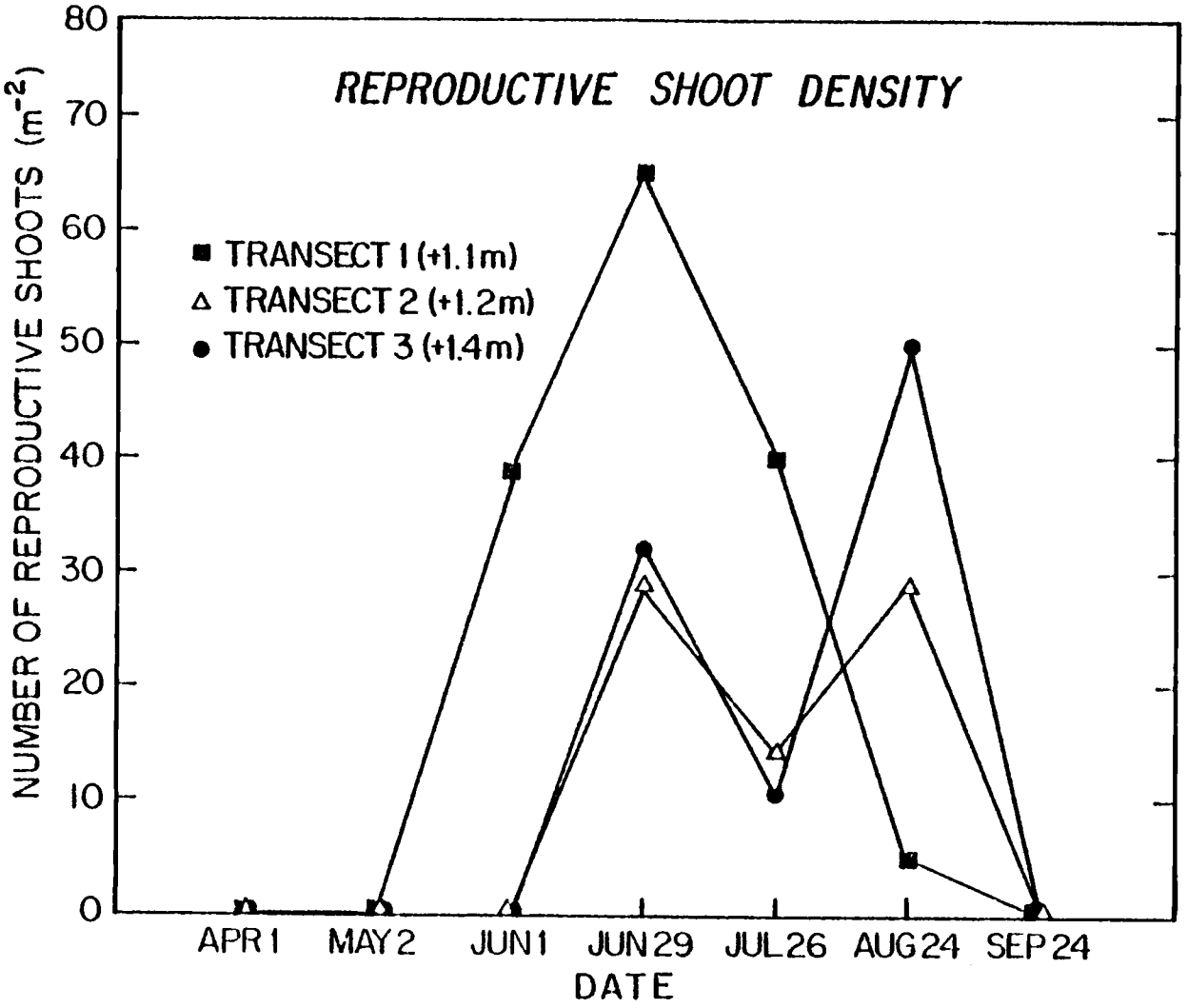


Figure 12. Density of reproductive shoots along the three transects during the 1980 sampling period. Each point represents the mean of 5 to 7 observations.

Table 4. Mean number of reproductive shoots per square meter during the period from April 1980 through May 1981. Values in parentheses represent the standard error of the mean of 5 to 7 observations. *

TRANSECT	1980							1981			
	APR 1	MAY 2	JUN 1	JUN 29	JUL 26	AUG 24	SEP 24	FEB 12	APR 6	MAY 3	MAY 30
1	0	0	39 (7)	65 (20)	40 (13)	5 (5)	0	0	0	0	40 (19)
2	0	0	0	29 (41)	14 (7)	25 (17)	0	-	-	-	-
3	0	0	0	32 (50)	11 (7)	50 (21)	0	0	0	0	100 (28)

*Dashes indicate no data available.

flowering shoots were present from April to September. In the low intertidal region reproductive shoots were first seen in April, extending up to the mean tidal height of the winter higher low tide. Flowers were seen throughout the bed in May, and they first appeared in the samples on June 1 at transect 1 and on June 29 at transects 2 and 3. Flowers were absent in the samples taken from all transects on September 24. In 1981 reproductive shoots observed during February in pools at the higher intertidal region (+1.4 m above MLLW), did not become numerous enough to appear in the samples until May 30. Data related to reproductive shoot densities also suggested that sexual reproduction did not play a major role in the growth and maintenance of the Zostera bed in Netarts Bay. When present, reproductive shoots represented no more than 6% of the total shoot density at all transects (Table 5). The mean percentage of the total shoot density that was represented by flowering shoots when they were present was 2.6% (S.E. = 0.5%).

Vegetative Growth.

Because the majority of the shoots in the bed at any time were vegetative, the results of this study relates primarily to the biology of the vegetative shoots of Zostera marina in Netarts Bay.

Short, narrow leaves were produced by each shoot in the autumn, and in this form, the plant survived the winter. In Netarts Bay the change to the winter morphology began in

Table 5. Percentage of the total shoot density represented by reproductive shoots during the period from April 1980 through May 1981. The percentages were calculated from the ratio of the means of 5 to 7 observations.*

TRANSECT	1980							1981			
	APR 1	MAY 2	JUN 1	JUN 29	JUL 26	AUG 24	SEP 24	FEB 12	APR 6	MAY 3	MAY 30
1	0	0	1.9	3.4	2.8	0.5	0	0	0	0	1.1
2	0	0	0	3.0	1.0	2.8	0	-	-	-	-
3	0	0	0	3.0	0.8	5.3	0	0	0	0	5.7

*Dashes indicate no data available.

September and was complete at the upper intertidal transects (2 and 3) by the end of November and at transect 1 by the end of December. Growth in the leafy portions of the plant resumed sometime in late February or March when the transition from the narrow-bladed form to the broader-bladed form occurred. The winter leaves were systematically sloughed off as the summer leaves were produced. The leaves produced during the period of transition were usually 1-2 mm wider at the base than at the tip, while the summer leaves had a uniform width along their entire length from May until the change to the winter morphology began in September.

There was a regular pattern in the production and sloughing of leaves from vegetative shoots in Netarts Bay. The time interval between the initiation of two successive leaves on one shoot was termed the plastochrone interval (PI). The PI for the period between samples was calculated from the expression proposed by Jacobs (1979):

$$PI = \frac{\text{number of shoots marked X observation period in days}}{\text{number of new leaves on marked shoots}}.$$

The time interval between the sloughing of two successive leaves on one shoot was termed the export interval (EI). The average EI for a sample period was calculated from the expression:

$$EI = \frac{\text{number of shoots marked X observation period in days}}{\text{number of leaves sloughed from marked shoots}}.$$

Trends for the entire growing season were examined by using data from transects 1 and 3 from June through October 1980 and from April through June 1981 (Table 6). The value of the PI ranged from 7.0 to 25.6 days, while the value of the EI ranged from 7.1 to 23.3 days. In general, the PI was shorter than or equal to the EI during April and May. This resulted in an increase in number of leaves per shoot during that period, because leaves were being produced faster than they were being shed. From June through October the trend reversed, and the EI was shorter than the PI. The net result of this pattern was a reduction in the number of leaves per shoot, since during that period leaves were lost faster than they were produced. A plot of the average number of leaves per shoot against time illustrated the effect of these patterns for the entire growing season in 1980 and for the time measured in 1981 (Figure 13). The relatively low number of leaves per shoot determined for June 29, 1980 was probably due to experimental error, as inexperienced new workers were involved in the laboratory work at that time. There was little correlation between number of leaves per shoot and other variables associated with Zostera and its epiphytes (Table 7). Therefore, the number of leaves per shoot was not a linear function of these other variables, but instead, was more closely related to changes in the PI and EI.

The PI measured the average length of time a leaf spent in each position on a shoot. Therefore, the PI multiplied by the mean number of leaves per shoot equalled the average lifetime of a leaf on a shoot. To examine the changes in the length of

Table 6. Mean plastochrone interval (PI) and mean export interval (EI) expressed as days for the period from June 1980 through June 1981. *Values listed are the means of 14 or 15 observations.*

	TRANSECT 1		TRANSECT 2		TRANSECT 3	
	PI	EI	PI	EI	PI	EI
1980						
JUN 14-29	15.0	10.0	8.3	13.6	9.0	7.9
JUN 29-JUL 13	21.0	8.8	12.9	10.0	13.3	10.7
JUL 13-26	18.0	12.0	14.4	14.4	13.0	11.4
JUL 26-AUG 12	25.0	16.0	20.0	12.8	14.2	9.1
AUG 12-24	16.5	19.0	14.7	11.0	21.7	10.8
AUG 24-SEP 8	17.0	19.0	16.0	13.1	11.7	16.0
SEP 8-24	25.6	16.0	19.6	11.0	-	-
SEP 24-OCT 7	22.0	15.0	19.6	12.3	10.5	7.6
OCT 7-23	19.0	15.0	12.4	11.4	18.0	18.0
1981						
APR 6-18	9.0	15.0	-	-	10.0	14.0
APR 18-MAY 3	9.5	9.4	-	-	7.0	18.7
MAY 3-16	12.2	11.8	-	-	8.0	7.8
MAY 16-30	10.0	11.7	-	-	7.0	23.3
MAY 30-JUN 17	13.0	8.5	-	-	9.4	7.1
JUN 17-JUL 1	18.0	11.6	-	-	10.5	8.4

*Dashes indicate no data available.

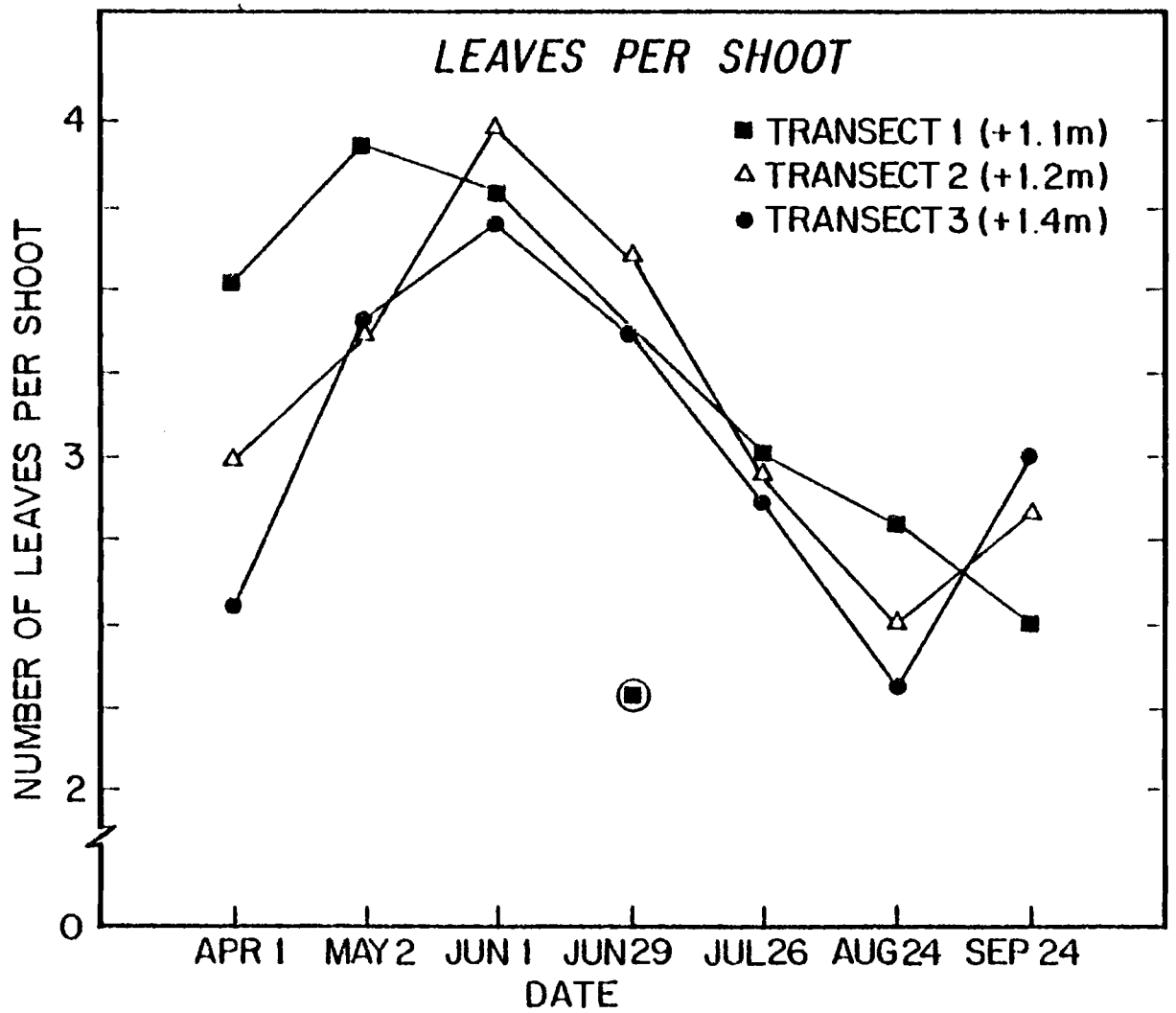


Figure 13. Average number of leaves per vegetative shoot at the three transects during the period from April through September, 1980. Each point represents the mean of 5 to 7 observations.

Table 7. Correlation coefficients (r) relating the number of leaves per shoot to selected variables. Values greater than 0.2 are significantly different than zero where $P < 0.01$.

Variables	r
Total shoot density (shoots m^{-2})	0.166
Average area of a vegetative leaf (cm^2)	-0.253
Aboveground biomass (g dry wt. m^{-2})	0.075
Belowground biomass (g dry wt. m^{-2})	0.005
Total *Zostera* biomass (g dry wt. m^{-2})	0.045
Epiphyte biomass (g ash-free dry wt. m^{-2})	0.010
Epiphyte leaf (g dry wt. epiphyte/g dry wt. leaf)	0.072

the lifetime of a leaf, the sampling period was divided into growth phases according to changes in the ratio between the PI and the EI (Table 8). Plants along transect 1 exhibited three phases. In April, the PI (9 days) was shorter than the EI (15 days), in May the PI and the EI were equal (each 12 days), and from June through October the PI (20 days) was longer than the EI (15 days). Transect 3 had two phases. In April and May the PI (9 days) was shorter than the EI (13 days), and from June through October the PI (14 days) was longer than the EI (11 days). Transect 2 was only measured from June through October when the PI (15 days) was longer than the EI (12 days). The average lifetime of a leaf was calculated for each phase for each transect (Table 9). Comparison of the lifetime of a leaf for each transect revealed that from June through October, leaves remained on the shoots in the lower intertidal region (transect 1) longer than they did on shoots in the upper intertidal region (transects 2 and 3). In general, the time a leaf remained on a shoot increased from April to September.

Growth of a leaf in relation to its age or position on the shoot also was analyzed. Data were standardized by expressing the amount of growth of each leaf as a proportion of the total growth of the shoot. Since the absolute age of each leaf measured was not known, relative ages were used. The youngest leaf on a shoot was designated as number one, and each successive leaf was numbered in order from the youngest to the oldest. This avoided problems when comparing shoots with different

Table 8. Mean plastochrone interval (PI), mean export interval (EI), and mean number of leaves per shoot (LVS) for periods from April to June, 1981 and from June to October, 1980. PI and EI are expressed as days. The values in parentheses represent the standard error of the mean for 9 to 26 observations.*

	1981 APRIL TO JUNE			1980 JUNE TO OCTOBER		
TRANSECT	PI	EI	LVS	PI	EI	LVS
1	12.0 (1.4)	11.4 (0.9)	3.7 (0.1)	19.9 (1.3)	14.5 (1.2)	2.8 (0.1)
2	- -	- -	- -	15.3 (1.3)	12.3 (0.5)	2.7 (0.4)
3	8.7 (0.6)	13.2 (2.7)	4.0 (0.1)	13.9 (1.5)	11.4 (1.3)	2.9 (0.1)
TOTAL BED	10.3 (0.9)	12.3 (1.4)	3.9 (0.1)	16.5 (0.9)	12.8 (0.8)	2.9 (0.1)

*Dashes indicate no data available.

Table 9. Mean lifetime of a leaf (days) for each transect during the growing season. PI = mean plastochrone interval; EI = mean export interval; LVS = mean number of leaves per shoot.*

	PI<EI	PI=EI	PI>EI
TRANSECT 1			
Period	April	May	June-October
PI	9.2	11.1	19.9
LVS	3.7	3.6	2.8
Lifetime	34.0	40.0	55.7
TRANSECT 2			
Period	-	-	June-October
PI	-	-	15.3
LVS	-	-	2.7
Lifetime	-	-	41.3
TRANSECT 3			
Period	April-May		June-October
PI	8.7		13.9
LVS	4.0		2.9
Lifetime	34.8		40.7

*Dashes indicate no data available.

numbers of leaves, because any group of leaves in the same position relative to the youngest leaf on their respective shoot were approximately the same age. At all transects throughout the study the greatest proportion of growth occurred while a leaf was in position 2 (Table 10). During the first phase of growth (April and May) the youngest and next to youngest leaf accounted for 48 to 65% of the total growth of the shoot. During the last phase of growth (June to October) these leaves accounted for 75 to 95% of the growth of the shoot. As the growing season progressed, the number of leaves per shoot decreased, the PI became longer, the average lifetime of a leaf became longer, and an average leaf spent more time in each position. Therefore, as fall approached, more of the growth occurred at positions 1 and 2 and less occurred at position 3, and more than half of the total growth of a shoot was due to the growth of leaves two PI or less old.

Production Dynamics of *Zostera*

Biomass.

The general pattern for the accumulation of the total biomass of *Zostera*, i.e., the summation of aboveground and belowground biomasses, was similar at transects 1 and 3 (Figure 14). In 1980 total biomass increased along both transects through the spring to a maximum in July, and then declined (Table 11). The maximum total biomass at transect 1 was 463.1

Table 10. Percentage of total shoot growth distributed among leaves of different relative ages, where 1 = youngest leaf on shoot. Values in parentheses represent the standard error of the mean of 14 or 15 observations.*

	APRIL-MAY	JUNE	JULY-OCTOBER
TRANSECT 1			
% 1	21.0	33.7	41.5
	(1.4)	(3.8)	(1.9)
% 2	41.3	46.3	50.0
	(2.6)	(2.6)	(1.7)
% 3	28.5	19.0	8.5
	(1.3)	(1.5)	(1.3)
% 1 + 2	64.8	80.0	91.5
	(0.5)	(2.1)	(1.3)
% 1 + 2 + 3	93.3	99.0	99.9
	(1.3)	(0.6)	(0.1)
TRANSECT 2			
% 1	-	-	35.9
			(2.2)
% 2	-	-	48.4
			(2.0)
% 3	-	-	13.6
			(2.3)
% 1 + 2	-	-	84.3
			(3.6)
% 1 + 2 + 3	-	-	97.9
			(1.3)
TRANSECT 3			
% 1	14.3	25.7	27.1
	(2.8)	(4.3)	(3.8)
% 2	34.3	43.7	48.1
	(2.0)	(3.2)	(1.2)
% 3	32.5	24.3	22.1
	(1.9)	(4.3)	(3.0)
% 1 + 2	48.5	72.7	75.3
	(4.0)	(2.0)	(3.7)
% 1 + 2 + 3	81.0	96.7	97.4
	(3.5)	(2.0)	(0.9)

*Dashes indicate no data available.

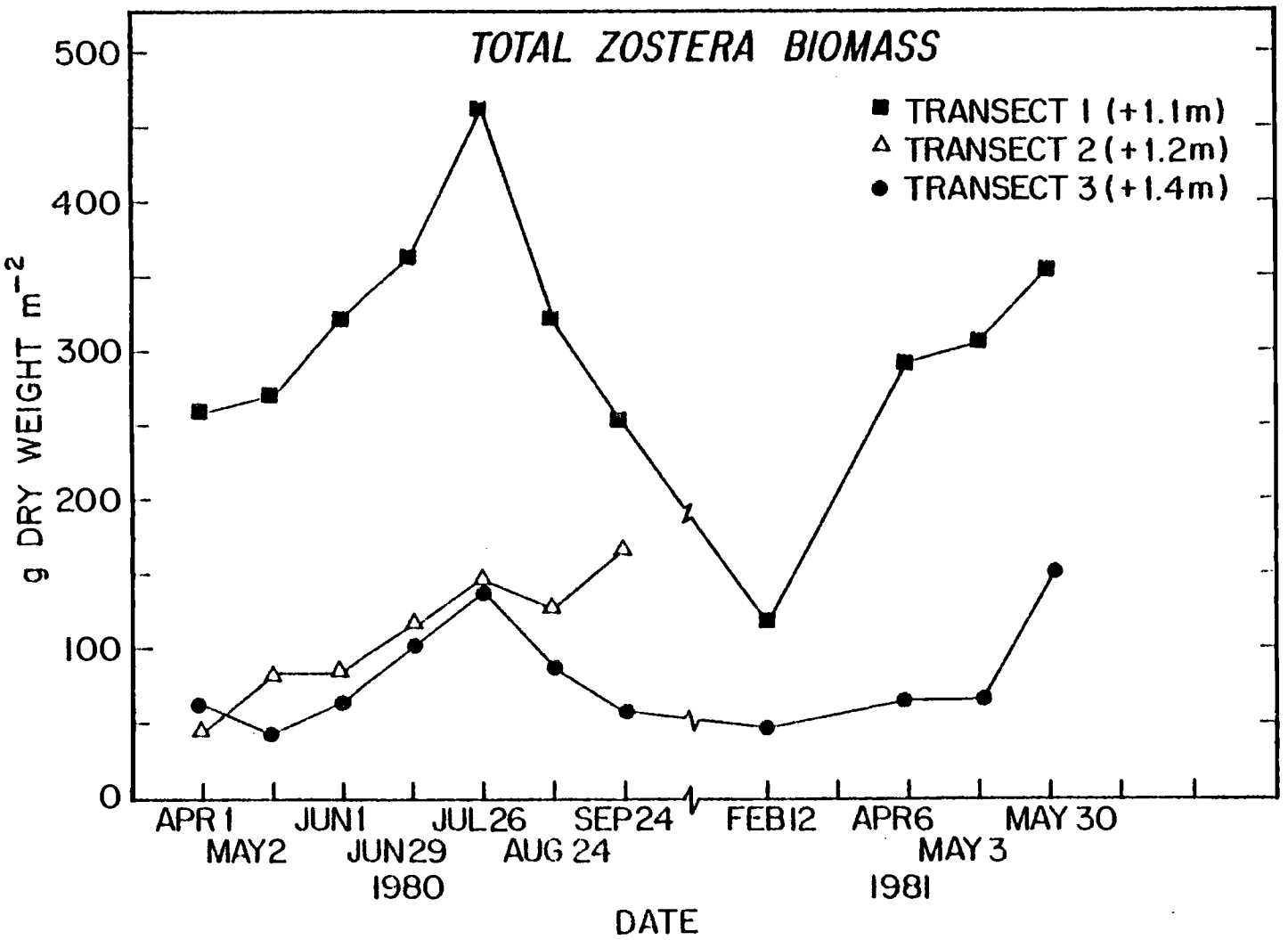


Figure 14. Total Zostera biomass at three transects in Netarts Bay during the period from April 1, 1980 to May 30, 1981. Each point represents the mean of 5 to 7 observations.

Table 11. Mean total Zostera biomass expressed as g dry weight m^{-2} at the three transects during the period from April 1, 1980 to May 30, 1981. The values are the means of 5 to 7 observations. The standard error of the mean is in parentheses.*

	1980							1981			
TRANSECT	APR 1	MAY 2	JUN 1	JUN 29	JUL 26	AUG 24	SEP 24	FEB 12	APR 6	MAY 3	MAY 30
1	259.5 (25.8)	269.9 (12.4)	321.8 (31.4)	362.5 (54.2)	463.1 (23.1)	321.2 (11.5)	252.0 (22.5)	119.6 (15.9)	292.6 (38.1)	305.4 (12.4)	353.9 (25.1)
2	45.6 (9.9)	84.0 (12.4)	82.0 (21.4)	113.9 (34.3)	147.3 (23.4)	128.0 (24.3)	166.9 (14.4)	-	-	-	-
3	64.5 (13.9)	45.4 (12.0)	65.4 (5.0)	103.6 (38.2)	142.8 (26.8)	88.7 (19.3)	57.5 (22.0)	47.1 (15.7)	62.7 (17.5)	63.8 (29.2)	147.5 (39.4)

*Dashes indicate no data available.

g dry weight m^{-2}, while that at transect 3 was 142.8 g dry weight m^{-2}. In the spring of 1981 the rate of increase of total biomass at transects 1 and 3 was higher than the rate of increase in the spring of 1980 (Table 11). Total biomass at transect 1 on May 30, 1981 was equivalent to that on June 29, 1980. Total biomass at transect 3 on May 30, 1981 was equivalent to that on July 26, 1980. In contrast, total biomass of transect 2 increased throughout the summer of 1980. The pattern for the increase of total biomass at transect 2 during 1980 closely followed that for transect 3 until July 26. Subsequently, total biomass at transect 3 decreased, while that for transect 2 continued to increase (Figure 14). Field notes taken during April and May described a sparse, patchy distribution of shoots at transects 2 and 3; evidence of erosion and burial of shoots also were noted. An impoundment of water in the low intertidal region was formed by the large, dense Zostera shoots growing in a basin created by sand deposition along the edges of the bed. This area was termed the Zostera pond (Figure 5). Its boundaries were made obvious during the lowest tides by the presence of about 15 cm of water, and during high tides by calm water in the region, caused by the dampening effects of the leaves. As the summer progressed and the shoots increased in size throughout the bed, the boundaries of the Zostera pond increased to include transect 2, and that transect began to look more like transect 1. Furthermore, at transect 3 plants growing in areas where pools formed were in better condition than plants growing in areas completely exposed at low tide.

When total biomass was compartmentalized into aboveground and belowground biomass, some new patterns emerged. Aboveground and belowground biomass at transect 2 and aboveground biomass at transects 1 and 3 reflected the pattern described for total biomass, while the pattern for belowground biomass at transects 1 and 3 was different (Tables 11, 12, and 13). In 1980 at transect 1 belowground biomass changed relatively little from April 1 to June 29 (Table 13). A maximum belowground biomass of 206.9 g dry weight m^{-2} was recorded a month later on July 26. Belowground biomass decreased during late summer and fall, and increased again between February 12 and April 6, 1981. In contrast to the rapid accumulation of total and aboveground biomass observed at transect 1 in the spring of 1981, belowground biomass did not reach a level comparable to that of spring 1980 until May 3, 1981. At transect 3 there was a small peak in belowground biomass in April during both 1980 and 1981, followed by a larger peak that occurred with the maximum aboveground biomass (Tables 12 and 13). In 1980 belowground biomass declined during late summer, fall and winter. Therefore, an increase in belowground biomass during April 1981 preceeded the increase in aboveground biomass at transect 3.

There was a striking difference between aboveground biomass at transects 1 and 3 during 1980 and 1981 (Table 12). At transect 1 the aboveground biomass for May 30, 1981 was 25% higher than that recorded on June 1, 1980. At transect 3 the aboveground biomass on May 30, 1981 was 48% higher than the maximum aboveground biomass reached in 1980.

Table 12. Mean aboveground Zostera biomass expressed as g dry weight m^{-2} at the three transects during the period from April 1, 1980 to May 30, 1981. The values are the means of 5 to 7 observations. The standard error of the mean is in parentheses.*

	1980							1981			
TRANSECT	APR 1	MAY 2	JUN 1	JUN 29	JUL 26	AUG 24	SEP 24	FEB 12	APR 6	MAY 3	MAY 30
1	98.7 (10.9)	114.8 (5.4)	162.1 (21.4)	197.8 (37.0)	256.2 (21.1)	173.9 (7.6)	119.4 (13.0)	57.6 (7.9)	166.5 (21.6)	181.0 (5.1)	202.4 (16.6)
2	11.3 (2.7)	26.6 (3.1)	37.8 (9.3)	60.8 (19.9)	71.0 (10.0)	53.5 (10.8)	70.4 (7.8)	-	-	-	-
3	7.2 (1.0)	8.1 (2.6)	30.3 (4.1)	49.5 (21.6)	57.1 (8.7)	34.9 (7.3)	22.0 (8.3)	22.3 (7.7)	21.6 (8.4)	32.4 (14.1)	84.4 (23.5)

*Dashes indicate no data available.

Table 13. Mean belowground *Zostera* biomass expressed as g dry weight m^{-2} at the three transects during the period from April 1, 1980 to May 30, 1981. The values are the means of 5 to 7 observations. The standard error of the mean is in parentheses.*

	1980							1981			
TRANSECT	APR 1	MAY 2	JUN 1	JUN 29	JUL 26	AUG 24	SEP 24	FEB 12	APR 6	MAY 3	MAY 30
1	160.8 (15.2)	154.1 (14.5)	151.7 (14.1)	164.4 (18.9)	206.9 (11.7)	147.2 (5.0)	132.5 (14.6)	62.0 (8.2)	126.1 (18.5)	124.4 (7.8)	151.6 (12.1)
2	34.3 (7.4)	58.5 (1.0)	44.2 (12.6)	53.1 (16.0)	76.3 (15.5)	74.5 (14.3)	96.6 (8.1)	-	-	-	-
3	71.7 (10.4)	37.3 (9.8)	35.1 (5.2)	54.1 (17.6)	85.6 (22.3)	53.7 (12.5)	35.5 (14.3)	24.8 (8.3)	41.1 (12.1)	31.4 (15.3)	63.2 (16.6)

*Dashes indicate no data available.

In general, at all three transects belowground biomass was a more conservative factor than aboveground biomass. The percentage increase of aboveground biomass was compared to that for the belowground biomass for the period from April 1 to September 24, 1980 (Table 14). The percentage increase of aboveground biomass ranged from 161% at transect 1 to 714% at transect 3. The percentage increase of belowground biomass ranged from 55% at transect 1 to 185% at transect 2. Therefore, the percentage increase of aboveground biomass was much higher than the percentage increase of belowground biomass at all transects.

Comparing aboveground and belowground biomass as a proportion of total biomass gave additional insights into seasonal trends. At all transects belowground biomass comprised the greater proportion of the total biomass at the beginning and end of the sampling period in 1980 (Table 15). At transect 1 both aboveground and belowground biomass accounted for between 40 and 60% of the total biomass over the entire sampling period, each fraction averaging approximately 50%. In contrast, belowground biomass at transects 2 and 3 always comprised more than 50% of the total biomass in 1980, and in April 1980, it represented 90% of the total biomass at transect 3 (Table 15).

Changes in total biomass were the result of changes in shoot density, and leaf or plant size along the transects. Leaf size was monitored as the change in the average area of a leaf from a vegetative shoot. Mean plant size was calculated by dividing

Table 14. Percentage increase of aboveground and belowground biomass along transects 1, 2, and 3 during the period from April 1 to September 24, 1980. Biomass was expressed as g dry weight m^{-2}. The percentages were calculated from the ratio of the means of 5 to 7 observations.

Transect	Aboveground Biomass			Belowground Biomass		
	Range	Difference	% Increase	Range	Difference	% Increase
1	98-256	158	161	133-206	73	55
2	11-71	60	546	34-97	63	185
3	7-57	50	714	35-85	50	143

Table 15. Percentage of total biomass corresponding to aboveground and belowground material at the three transects for the period from April 1, 1980 to May 30, 1981. The percentages were calculated from the ratio of the means of 5 to 7 observations.*

	1980							1981			
	APR 1	MAY 2	JUN 1	JUN 29	JUL 26	AUG 24	SEP 24	FEB 12	APR 6	MAY 3	MAY 30
TRANSECT 1											
Aboveground	37.9	43.5	49.6	53.3	55.1	54.1	47.3	48.2	56.9	59.3	57.2
Belowground	62.1	56.5	50.4	46.3	44.9	45.9	52.7	51.8	43.1	40.7	42.8
TRANSECT 2											
Aboveground	26.1	31.7	49.6	49.7	50.1	40.9	42.0	-	-	-	-
Belowground	73.9	68.3	50.4	50.4	49.9	57.7	58.0	-	-	-	-
TRANSECT 3											
Aboveground	9.9	21.6	46.8	41.9	44.1	41.7	37.5	47.2	34.4	50.8	57.2
Belowground	90.1	78.4	53.2	58.1	55.9	58.3	62.6	52.5	65.6	49.2	42.8

*Dashes indicate no data available.

total Zostera biomass by mean shoot density. Multiple regression analysis of the relationship between total biomass and plant size and density, and between total biomass, and leaf size and density indicated that there was a linear relationship between the dependent and independent variables (Table 16). Plant size and density were better predictors of total biomass than were leaf size and density. This was understandable because plant size included both aboveground and belowground portions of the plant, while leaf size represented only the aboveground parts. These relationships can be used to obtain an estimate of total biomass through a combination of field counts of density and an estimate of leaf or plant size rather than by harvesting and sorting material from quadrats.

Average leaf size expressed as cm^2 increased from April 1 to August 24, 1980 at all transects (Figure 15, Table 17). The relatively small leaf size measured on September 24, 1980 reflected the completion of the sloughing of the large leaves produced during the sampling period in 1980 and the beginning of the change to the small, narrow leaves typical in the winter. In the spring of 1981, at transect 1 leaf size increased at a lower rate than it did in the spring of 1980. Mean leaf size on May 30, 1981 was similar to that for May 2, 1980 (Table 17). In contrast, at transect 3 mean leaf size increased at a higher rate in the spring of 1981 than it did in the spring of 1980. Mean leaf size on May 30, 1981 was similar to that for June 29, 1980 (Table 17).

The changes in plant size were similar in pattern to changes in total biomass at all transects during the sampling period in

Table 16. Multiple regression of mean total Zostera biomass (TZOS) against mean leaf size (AREA), mean plant size (SIZE), and mean shoot density (TSHD) for each transect. R^2 is the coefficient of determination.

TRANSECT	R^2	MODEL
1	0.66	$\hat{TZOS} = 18.54 + 6.73$ AREA $+ 0.07$ TSHD
	0.80	$\hat{TZOS} = -101.41 - 1.29$ SIZE $+ 1.22$ TSHD
2	0.86	$\hat{TZOS} = 69.74 + 7.36$ AREA $- 0.03$ TSHD
	0.98	$\hat{TZOS} = 78.04 + 1.08$ SIZE $+ 0.07$ TSHD
3	0.84	$\hat{TZOS} = -27.37 + 0.53$ AREA $+ 5.00$ TSHD
	0.98	$\hat{TZOS} = -97.63 + 0.01$ SIZE $+ 1.05$ TSHD

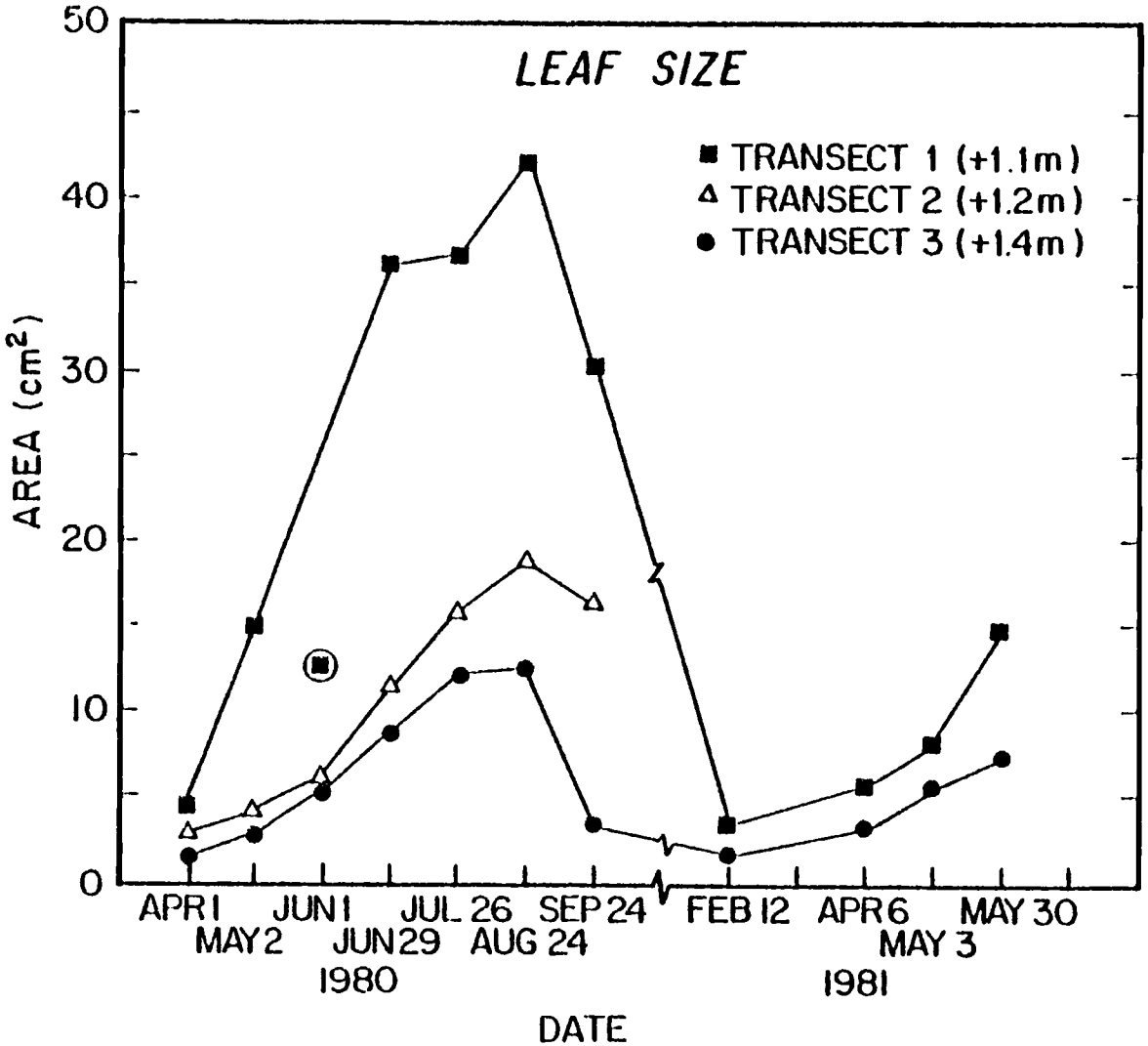


Figure 15. Mean leaf size as expressed by the average area of a leaf from a vegetative shoot, considering both sides, along the three transects in Netarts Bay. Each point represents the mean of 5 to 7 observations.

Table 17. Mean leaf size measured as the average area of a leaf from a vegetative shoot and expressed as cm^2 for the three transects for the period from April 1, 1980 to May 30, 1981. The values represent the means of 5 to 7 observations. The standard error of the mean is in parentheses.*

	1980							1981			
TRANSECT	APR 1	MAY 2	JUN 1	JUN 29	JUL 26	AUG 24	SEP 24	FEB 12	APR 6	MAY 3	MAY 30
1	4.8 (0.4)	15.0 (1.8)	12.3 (1.7)	36.7 (4.6)	37.2 (1.6)	42.1 (4.0)	30.3 (2.4)	3.0 (0.11)	5.5 (0.5)	8.0 (0.6)	14.5 (1.8)
2	2.5 (0.2)	4.6 (0.2)	6.0 (0.6)	12.0 (1.8)	15.1 (1.7)	18.6 (2.0)	16.4 (3.8)	-	-	-	-
3	1.8 (0.3)	2.5 (0.3)	5.8 (0.4)	7.6 (1.3)	12.0 (1.3)	12.1 (2.9)	10.6 (2.1)	2.3 (0.3)	3.3 (0.6)	5.7 (0.2)	7.2 (0.7)

*Dahses indicate no data available.

1980 (Figures 14 and 16). In the spring of 1981 at transects 1 and 3 plant size increased at a lower rate than in the spring of 1980. At transect 1 the mean plant size on May 3, 1981 was similar to that measured on April 1, 1980, and at transect 3 the mean plant size for April through June 1, 1980 was not reached until May 30, 1981 (Table 18).

Differences between the leaf and plant sizes measured in 1980 and those measured in 1981 can be explained in conjunction with the changes in shoot density. At transects 2 and 3 during the sampling period in 1980, shoot density, plant size, leaf size and total biomass follow the same general patterns of change (Figures 14, 15, 16, and 17). At transect 1 during the same period shoot density decreased as plant size and leaf size increased. Total biomass was greater at transect 1 than at transects 2 and 3 in April 1980 because the shoot density at transect 1 was 3 times greater than that at transects 2 and 3 (Figures 14 and 17) when plant size was similar at all three transects (Figure 16). Although shoot density decreased from April through September at transect 1, total biomass continued to increase in response to the increase in leaf and plant size until July 26 (Figures 14, 15, 16, and 17). Therefore, the data indicated that shoot density was independent of plant size until some threshold was reached, above which plant size has a negative effect on density.

Mean leaf area per unit area of substrate expressed as $m^2\ m^{-2}$ measured the combined effects of shoot density and plant size.

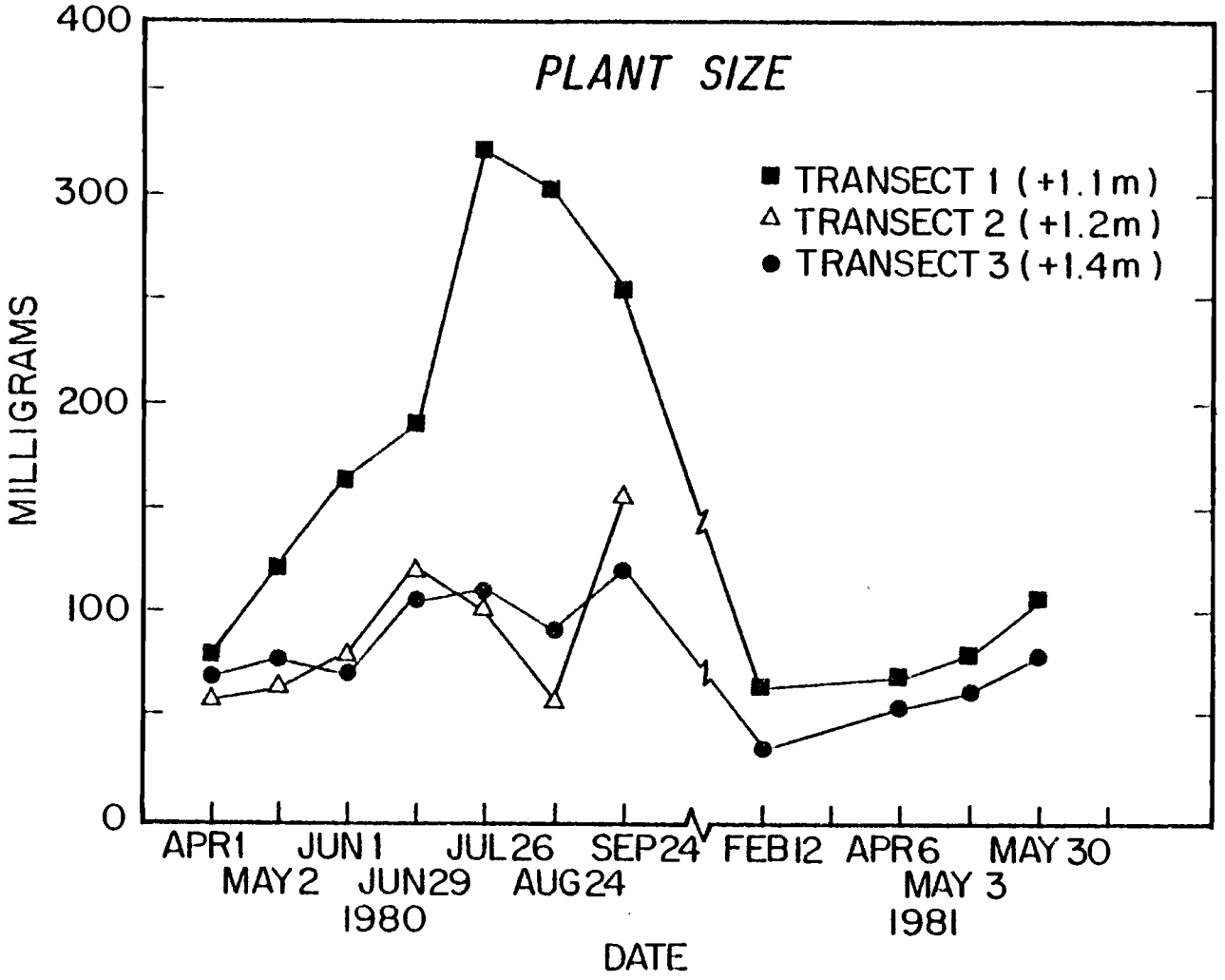


Figure 16. Mean size (mg) of a vegetative plant along the three transects in Netarts Bay during the period from April 1, 1980 to May 30, 1981. Each point represents the mean of 5 to 7 observations.

Table 18. Mean size of a vegetative plant expressed as milligrams at the three transects for the period from April 1, 1980 to May 30, 1981. The percentages were calculated from the ratio of the means of 5 to 7 observations.*

	1980							1981			
TRANSECT	APR 1	MAY 2	JUN 1	JUN 29	JUL 26	AUG 24	SEP 24	FEB 12	APR 6	MAY 3	MAY 30
1	88.7	127.0	160.9	194.9	330.8	313.4	253.3	66.8	76.1	88.7	104.2
2	58.7	70.7	88.2	119.4	105.2	68.8	152.4	-	-	-	-
3	81.7	84.7	81.4	101.1	104.4	90.0	115.0	42.0	54.5	70.1	88.8

*Dashes indicate no data available.

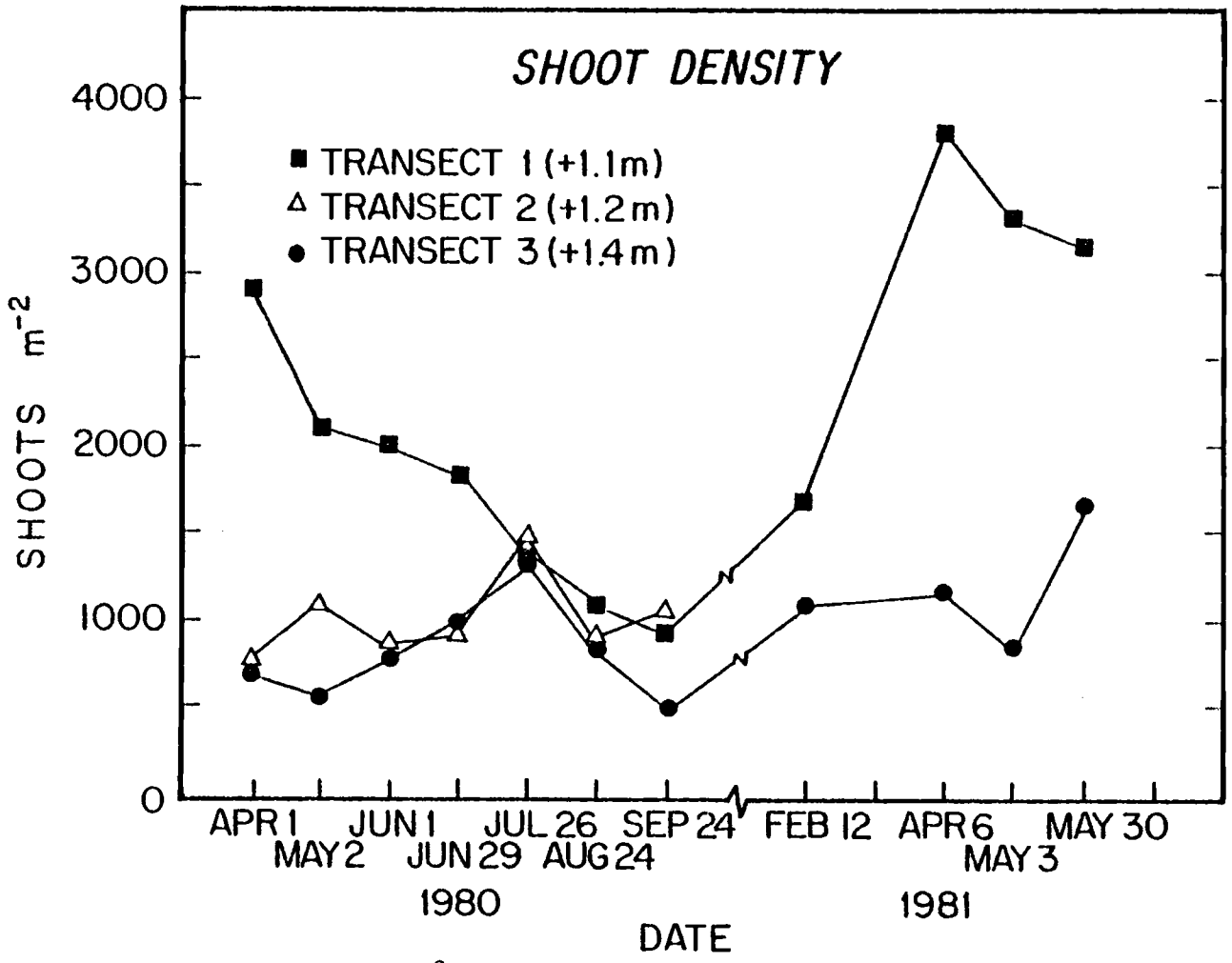


Figure 17. Mean shoot density (shoots m^{-2}) along the three transects in Netarts Bay during the period from April 1, 1980 to May 30, 1981. Each point represents the mean of 5 to 7 observations.

Both sides of the leaf were considered in this measurement. When plant size and density combined to produce a mean leaf area per unit of substrate of between 7.5 and 11 m^2 m^{-2}, shoot density began to decrease at transect 1 (Tables 19 and 20). Transects 2 and 3 never reached this mean leaf area per unit area of substrate. This response was probably the result of self-shading within the Zostera bed in the region of transect 1. In addition, plant sizes were relatively large in the samples taken on June 29 and July 26, 1980 at transect 1. This suggested that there had been a selective loss of small shoots prior to that time, possibly due to shading from the large shoots.

Data from all transects for 1980 and 1981 were pooled to examine the properties of the entire Zostera bed. Sample statistics for the variables of interest were listed in Table 21. Relationships that existed for each transect were still evident when the data were pooled (Table 22). Aboveground and belowground biomass were highly correlated with each other and with total biomass. Total shoot density and the average area of a vegetative leaf were less highly correlated with total biomass. However, since they represented components of biomass, i.e. number of shoots and size of aboveground parts, when they were combined in a multiple regression against total Zostera biomass they accounted for a large proportion of the variance in total biomass (Table 23). Again, this supported the idea presented earlier that measurement of shoot density and the

Table 19. Mean shoot density expressed as shoots m^{-2} at the three transects during the period from April 1, 1980 to May 30, 1981. Values represent the means of 5 to 7 observations. Standard error of the mean is in parentheses.*

	1980							1981			
TRANSECT	APR 1	MAY 2	JUN 1	JUN 29	Jul 26	AUG 24	SEP 24	FEB 12	APR 6	MAY 3	MAY 30
1	2925	2125	2000	1860	1400	1025	995	1790	3845	3445	3395
	(293)	(176)	(97)	(253)	(156)	(160)	(87)	(136)	(387)	(143)	(359)
2	789	1188	929	954	1400	886	1095	-	-	-	-
	(148)	(134)	(212)	(236)	(295)	(162)	(120)				
3	782	536	804	1025	1368	896	500	1135	1150	910	1761
	(148)	(140)	(111)	(308)	(140)	(228)	(185)	(359)	(436)	(428)	(387)

*Dashes indicate no data available.

Table 20. Mean leaf area per unit area of substrate expressed as $m^2\ m^{-2}$ at the three transects during the period from April 1, 1980 to May 30, 1981. Values represent the means of 5 to 7 observations. Standard error of the mean is in parentheses.*

	1980							1981			
TRANSECT	APR 1	MAY 2	JUN 1	JUN 29	JUL 26	AUG 24	SEP 24	FEB 12	APR 6	MAY 3	MAY 30
1	4.9 (0.6)	11.9 (1.4)	9.1 (1.1)	14.4 (2.4)	15.7 (1.9)	11.1 (0.9)	7.5 (0.8)	1.8 (0.1)	7.5 (1.3)	11.0 (0.4)	15.9 (1.2)
2	0.6 (0.1)	1.8 (0.3)	2.4 (0.6)	4.1 (1.1)	5.4 (0.9)	4.1 (0.8)	4.6 (0.6)	-	-	-	-
3	0.3 (0.1)	0.5 (0.2)	1.7 (0.2)	3.0 (1.3)	4.6 (0.6)	2.3 (0.1)	1.5 (0.6)	0.9 (0.3)	1.4 (0.5)	2.4 (0.9)	6.0 (1.5)

*Dashes indicate no data available.

Table 21. Sample statistics for Zostera biomass and selected morphometric data corresponding to the entire Zostera bed over the whole sampling period from April 1 to September 24, 1980 and from February 12 to May 30, 1981 (n = 175).

	Mean	Standard Error	Range
Total Biomass (g dry wt. m^{-2})	165.3	9.5	0-554
Aboveground Biomass (g dry wt. m^{-2})	79.2	5.5	0-326
Belowground Biomass (g dry wt. m^{-2})	86.0	4.4	0-240
Shoot Density (shoots m^{-2})	1454.1	75.9	0-4950
Average Area of Vegetative Leaf* (cm^2)	11.5	0.8	0-57

*Both sides considered.

Table 22. A matrix of correlation coefficients relating *Zostera* biomass and selected morphometric variables for the pooled data set, i.e., all samples from the three transects. TZOS = total *Zostera* biomass; ABGB = aboveground biomass; BLGB = belowground biomass; TSHD = total shoot density; AREA = average area of a vegetative leaf, both sides considered. Values greater than 0.2 are significantly different than zero where $P < 0.01$.

	TZOS	ABGB	BLGB	TSHD	AREA
TZOS	1.00	0.97	0.95	0.67	0.64
ABGB		1.00	0.84	0.65	0.65
BLGB			1.00	0.63	0.56
TSHD				1.00	0.03
AREA					1.00

Table 23. Multiple regression of total Zostera biomass (TZOS) against total shoot density (TSHD) and the average area of a vegetative leaf (AREA) for the entire Zostera bed. R^2 is the coefficient of determination.

R^2	MODEL
0.40	$\hat{TZOS} = 43.2 + 0.08\ TSHD$
0.40	$\hat{TZOS} = 81.8 + 7.3\ AREA$
0.83	$\hat{TZOS} = -36.0 + 0.06\ TSHD + 4.2\ AREA$

average area of a vegetative leaf can be used to obtain an estimate of total Zostera biomass.

Primary Production.

The pattern of shoot net primary production (g dry weight m^{-2} sample $period^{-1}$) as measured by the leaf marking method had a similar pattern at all transects throughout the study (Figure 18, Table 24). During the period from June 14 to October 23, 1980 there were two peaks in net primary production of the shoot. The first occurred between June 29 and July 26, and was reflected by peaks in total biomass at transects 1 and 3 (Figure 14). A second and smaller peak in net primary production of the shoot occurred between August 24 and September 24. This maximum was not reflected in the measurements of total biomass at transect 1 and 3 for the same period because of a decrease in shoot density and plant size that occurred at the same time (Figures 16 and 17). Total biomass at transect 2 increased throughout the sampling period in 1980. The decrease in net primary production of the shoot at all transects between July 13 and August 24 was concurrent with a bloom of Enteromorpha prolifera in the area (See Davis, 1982). As the Enteromorpha drifted through the Zostera bed with the incoming or outgoing tide, the long leaves of the seagrass became tangled in the ropes of the alga, and the Zostera was uprooted as it was dragged along. In areas where Enteromorpha had become caught in the sediment or on some object, the Zostera in the vicinity became buried from an increase in the

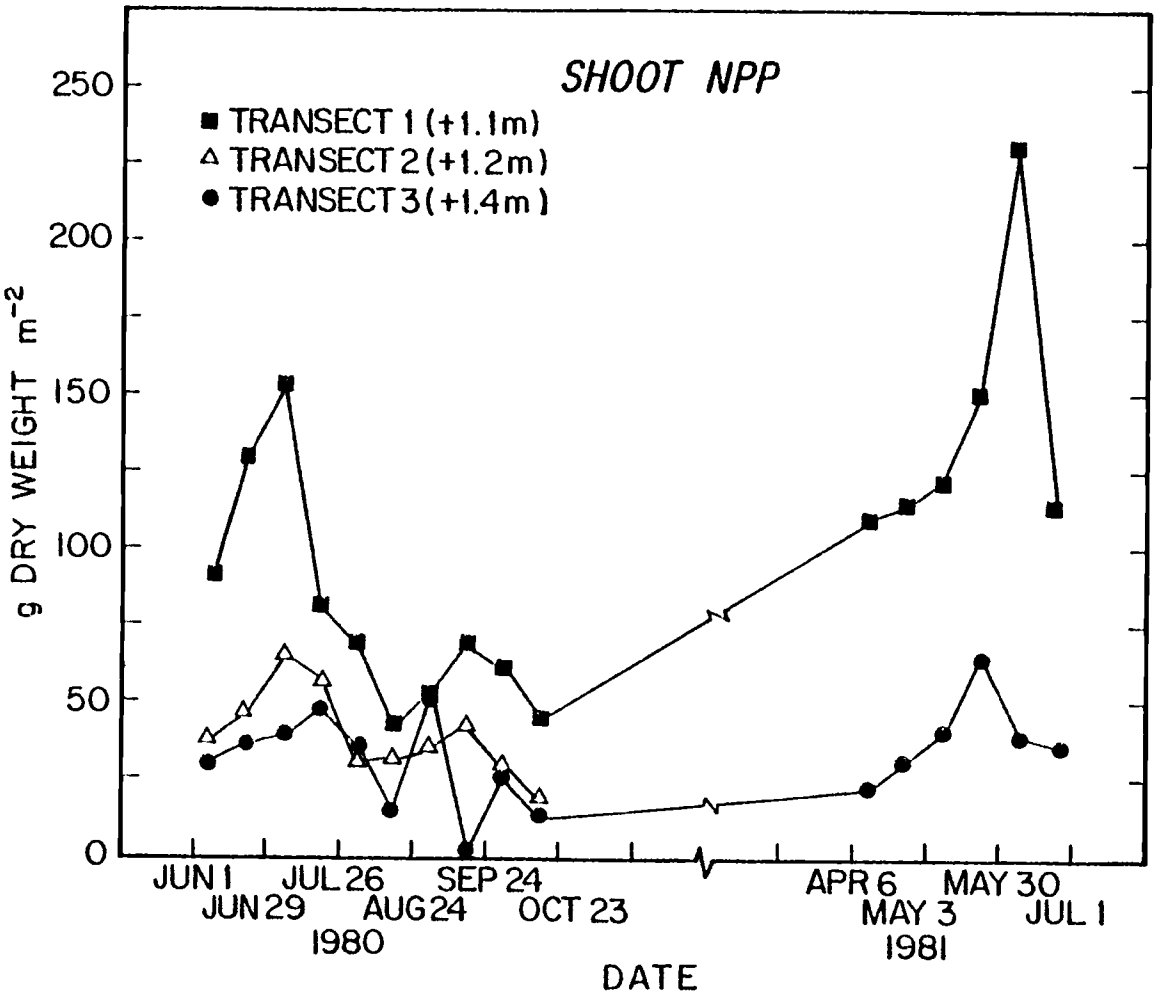


Figure 18. Shoot net primary production expressed as g dry weight m^{-2} along three transects for the period from June 1980 to July 1981. Each point represents the mean of 14 or 15 observations.

Table 24. Shoot net primary production along the three transects during the period from June 14, 1980 to July 1, 1981. NPP-PER = shoot net primary production expressed as g dry weight m^{-2} sample $period^{-1}$; NPP-DAY = shoot net primary production expressed as g dry weight m^{-2} day^{-1}. The values represent the means of 14 or 15 observations.

Sampling Period 1980		JUN 14-JUN 29	JUN 29-JUL 13	JUL 13-JUL 26	JUL 26-AUG 12	AUG 12-AUG 24	AUG 24-SEP 8	SEP 8-SEP 24	SEP 24-OCT 7	OCT 7-OCT 23
Transect 1	NPP-PER	129.1	153.4	81.1	69.3	41.7	53.8	68.7	61.4	44.4
	NPP-DAY	8.6	10.2	6.2	4.3	3.5	3.4	4.3	4.4	2.8
Transect 2	NPP-PER	47.6	66.0	57.1	32.0	31.7	35.3	43.4	31.0	20.2
	NPP-DAY	3.2	4.4	4.8	2.0	2.6	2.2	2.7	2.2	1.3
Transect 3	NPP-PER	36.0	39.5	48.7	36.3	13.5	54.0	1.9*	27.1	14.8
	NPP-DAY	2.6	2.5	3.7	2.3	1.0	3.4	0.1*	1.9	0.9

Sampling Period 1981		APR 6-APR 18	APR 18-MAY 3	MAY 3-MAY 16	MAY 16-MAY 30	MAY 30-JUN 17	JUN 17 JUL 1
Transect 1	NPP-PER	108.9	113.8	122.2	150.0	230.5	114.2
	NPP-DAY	9.1	7.6	9.4	10.7	13.6	8.2
Transect 3	NPP-PER	22.5	30.0	39.6	65.1	42.1	37.2
	NPP-DAY	1.6	2.1	2.8	4.7	2.5	2.7

*Based on data from two shoots.

sedimentation caused by the slowing of the water by the tangled mass of the Enteromorpha. Eventually, even the Enteromorpha was buried, and an oozing, sulfurous mound of sediment marked the place where there had been a patch of Zostera. The disappearance of Enteromorpha from the Zostera bed in early August was followed by an increase in net primary production of the Zostera shoots (Figure 18).

The rate of shoot net primary production was increased in 1981 as compared to 1980 (Figure 18). The maximum rate of shoot net primary production was reached in early June in 1981 as compared to early July in 1980. At transect 1 the maximum rate of shoot net primary production in 1981 was 50% higher than that for 1980, while that for transect 3 was 21% higher (Table 24).

At transect 1 the accumulation of total biomass was divided into five phases. Between February 12 and April 6, 1981 there was a large increase in total Zostera biomass that was primarily due to a large increase in shoot density (Figures 14 and 17). During the same period of time mean leaf size increased slightly from 3.0 cm^2 to 5.5 cm^2. Mean plant size also increased slightly from 66.8 mg to 76.1 mg. A similar pattern was noted in 1980. Presample data from February 23, 1980 gave a mean density of 1387.5 shoots m^{-2} with a standard error of 143.9 shoots m^{-2}. Subsequently, density increased to 2925 shoots m^{-2} by April 1, 1980 (Table 19). Therefore, primary production in the early spring at transect 1 was first channeled into the production of new shoots. Then, the change in leaf morphology from small,

narrow leaves typical in the winter to long, wide leaves typical in the summer occurred during April and May 1981. It was only after this change was completed that the sharp increase in shoot net primary production was initiated during the month of May 1981, thereby marking a shift in growth strategy to the production of aboveground parts. The sharp decrease in net primary production of shoots observed at transects 1 and 3 during June 1981, coincided with a bloom of Enteromorpha, just as the decrease in net primary production of shoots during July and August 1980 coincided with a similar bloom. Therefore, the same pattern of growth was followed during both 1980 and 1981. The stages involved in this general pattern are summarized in Figure 19.

Conditions for the growth of Zostera were better at transect 1 than at transects 2 and 3. Maximum mean total biomass, mean shoot density, mean leaf size, mean plant size and mean shoot net primary production at transect 1 were always greater than at transects 2 and 3 (Table 25). During the summer low tides Zostera growing in the region of transect 1 was never exposed. Even during the lowest tides, 10 to 15 cm of water remained in the Zostera pond. This layer of water protected the plants from exposure to the air. This conclusion was further supported by the relatively high shoot density and relatively large shoots observed in areas with pooled water during low tide at transect 3. In the winter there was a noticeable difference in the density and condition of plants located above and below the level of the higher low tide. Transect 1 was located below

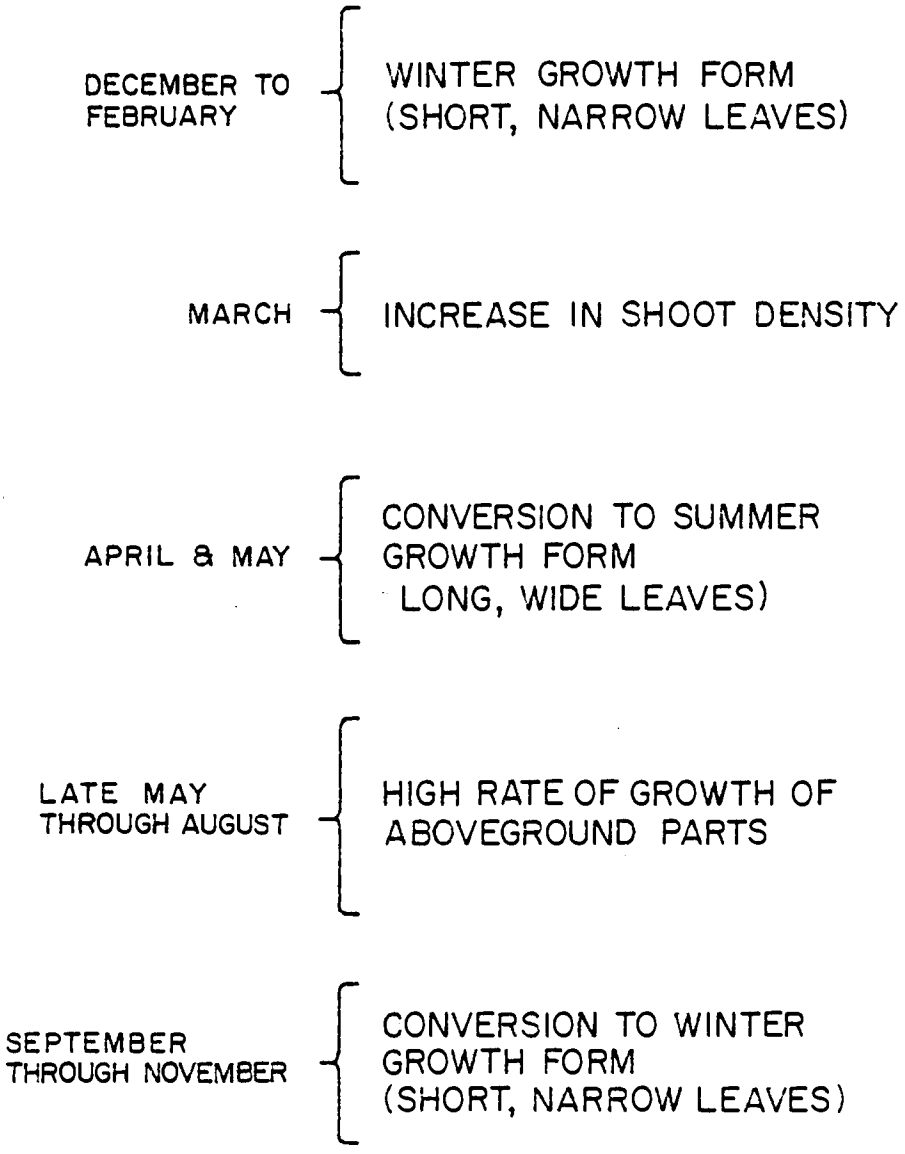


Figure 19. The annual phases of growth exhibited by Zostera marina L. growing along transect 1 in Netarts Bay, Oregon.

Table 25. Maximum mean values of total biomass, leaf size, shoot size, and shoot density along the transects in 1980 and 1981.

	Total Biomass (g dry wt. m^{-2})	Leaf Size (cm^2)	Shoot Size (mg)	Shoot Density (shoots m^{-2})
1980				
Transect 1	463	42.1	313.4	2925
Transect 2	186	18.6	152.4	1400
Transect 3	143	12.1	115.0	1368
1981				
Transect 1	354	14.5	104.2	3845
Transect 3	148	7.2	88.8	1661

this elevation, while transects 2 and 3 were located above it. Shoots in the region below the average height of the winter higher low tide appeared to be protected. These shoots were exposed to the air during low tide no more than once a day during the winter, while the rest of the Zostera bed was exposed twice each day. The edges of the bed showed evidence of erosion, and plants in this area often had their rhizomes exposed as the sand around them was washed away. During the entire year there was evidence of sand deposition in the high intertidal region, especially along transect 3. Neither erosion nor sedimentation was as evident in the region of the bed where transect 1 was located. Therefore, a combination of factors apparently contributed to the differences between plants that grew in the region of transect 1 and those located in the region of transects 2 and 3.

Relationship Between Zostera and Epiphytic Assemblages

Description of Epiphytic Assemblages.

Epiphytic assemblages on Zostera in Netarts Bay were primarily composed of diatoms. Epiphyte biomass expressed as ash-free dry weight m^{-2} from pooled data representing the entire Zostera bed had a high correlation with biomass expressed as dry weight. The mean ratio of ash-free dry weight to dry weight was 0.24% which is a typical value when the flora consists of diatoms (McIntire and Phinney, 1965). The ratio of ash-free dry weight to dry weight for each transect also indicated a diatom flora,

except for the samples in 1980 taken on June 1 and 29 (Figure 20). By inspection under a microscope it was noted that during this time of the year Smithora naiadum (Anderson) Hollenb. and Ectocarpus sp., or non-diatom algae were prominent components of the epiphyte community. The addition of these taxa increased the organic matter content of the epiphytic assemblage, as the percentage ash-free dry weight for most algae other than diatoms is usually greater than 60% (e.g., see Davis, 1982). The percentage ash-free dry weight for samples obtained in February and April, 1981 also was high. During this period, the combination of a small biomass of epiphytes and unusually brittle Zostera leaves created a problem of contamination of the epiphytic samples with particles of Zostera leaves.

The taxonomic structure of the diatom assemblages epiphytic on Zostera marina L. in Netarts Bay was described by Whiting (in progress). From November through July, the flora was dominated by species of Cocconeis, Synedra, Navicula, Nitzschia, Gomphonema, and Rhoicosphenia. From August through October, Cocconeis, Gomphonema and Rhoicosphenia virtually disappeared from the samples, and different species of Navicula and Nitzschia became the dominant taxa. The Shannon-Weaver diversity index revealed that the epiphytic flora was generally low in species richness and high in dominance.

Scanning electron microscopy was used to examine the arrangement of the epiphytes on the Zostera leaf. Leaves pictured in this section were collected in May and June 1979. On areas of

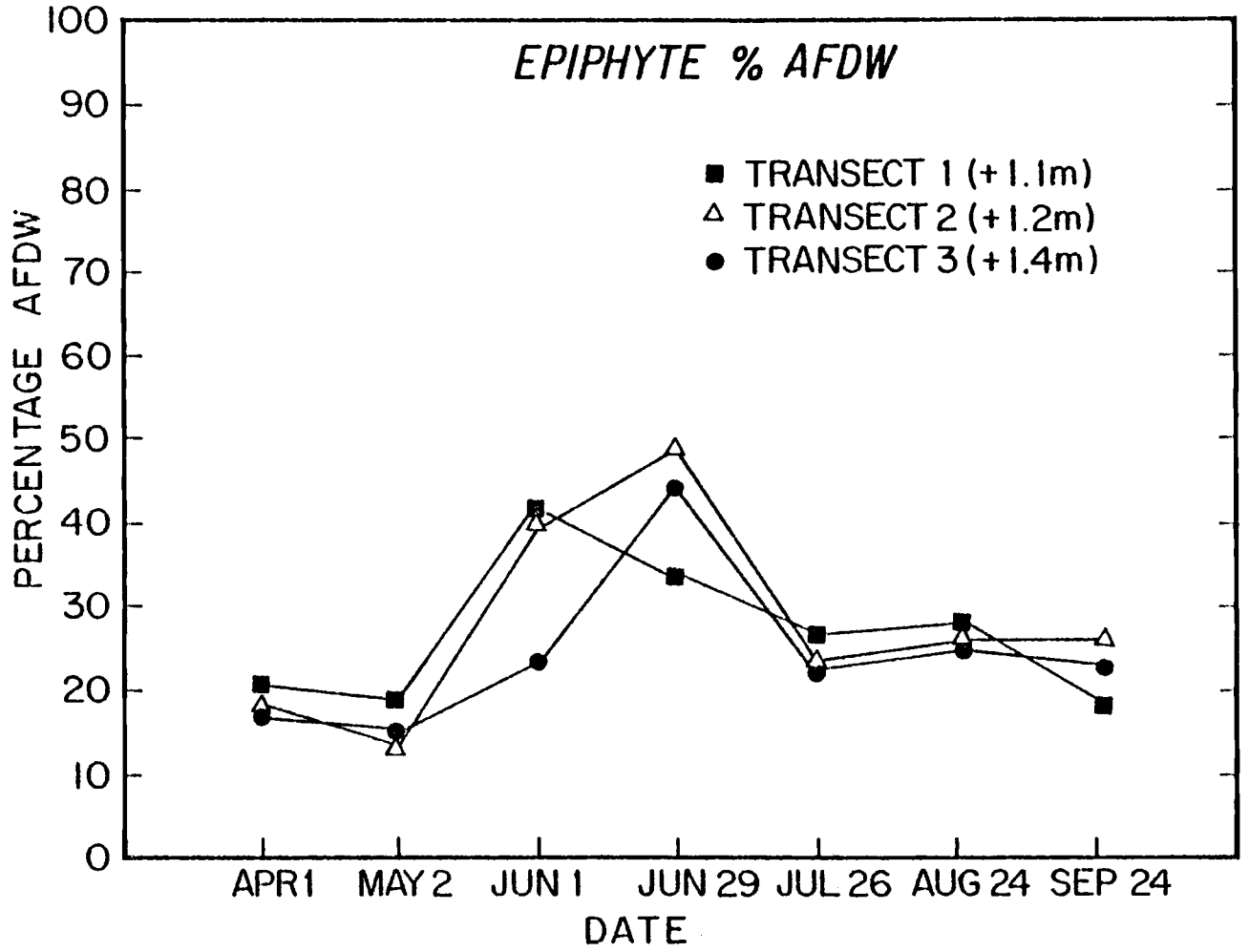


Figure 20. Percentage ash-free dry weight associated with the biomass of epiphytes at the three transects during the period from April through September 1980. Each point represents the mean of 3 subsamples.

a leaf with a well developed epiphytic assemblage, a distinct layering of the diatoms was evident. Cocconeis scutellum covered the surface of the leaf, while other genera of diatoms and assorted debris composed an overstory layer (Figures 21, 22, and 23). A section from the lower portion of a leaf revealed that during early stages of colonization the epiphytic community developed mainly over the surface of the leaf, while the narrow edge of the blade remained relatively uncolonized (Figure 24). As the community developed the edge of the leaf also became epiphytized. In particular, Smithora and Ectocarpus occupied the edge of the leaves during June and July (Figure 25).

Biomass.

The interpretation of changes in epiphyte loads was related to the units that were used to express biomass. Epiphyte biomass expressed as g dry weight m^{-2} also included inorganic material, e.g., debris and dead diatom frustules. Therefore, dry weight expressed the actual load of material that was distributed over the leaves. Biomass expressed as ash-free dry weight m^{-2} was considered an indicator of the organic matter present.

Epiphytes were prominent on the Zostera leaves from April through October. During the winters of 1979 and 1980, field notes indicated that the Zostera leaves were essentially free from epiphytes. This conclusion was supported by biomass measurements taken on February 12, 1980, when epiphyte biomass for transects 1 and 3 were 0.4 and 0.7 g dry weight m^{-2}, respectively.

Figure 21. Scanning electron micrograph of epiphytic diatoms on a Zostera leaf. Cocconeis scutellum is seen on the surface of the leaf. Synedra fasciculata and assorted debris form the overstory (Magnification = 300X).


FIG 21

Figure 22. Surface view of a well-developed assemblage of diatoms on a Zostera leaf (Magnificiation = 120X).

Figure 23. Close-up view of the surface of the epiphytic assemblage pictured in Figure 22. The stalked diatom, Rhoicosphenia and assorted debris are predominant (Magnification = 480X).

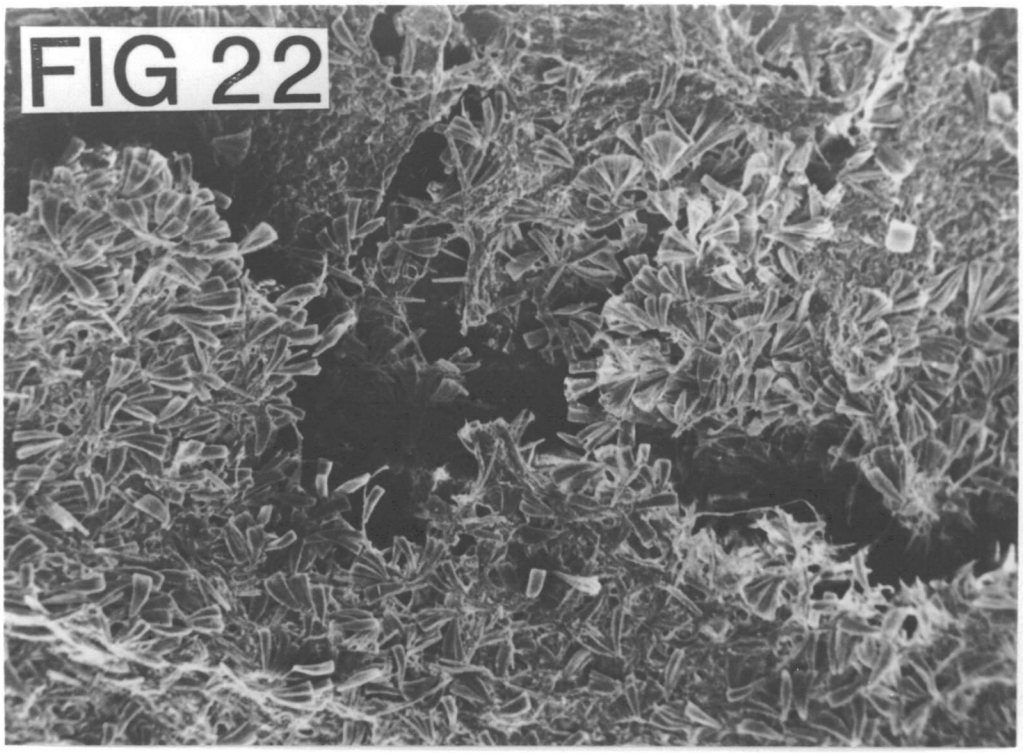


FIG 22

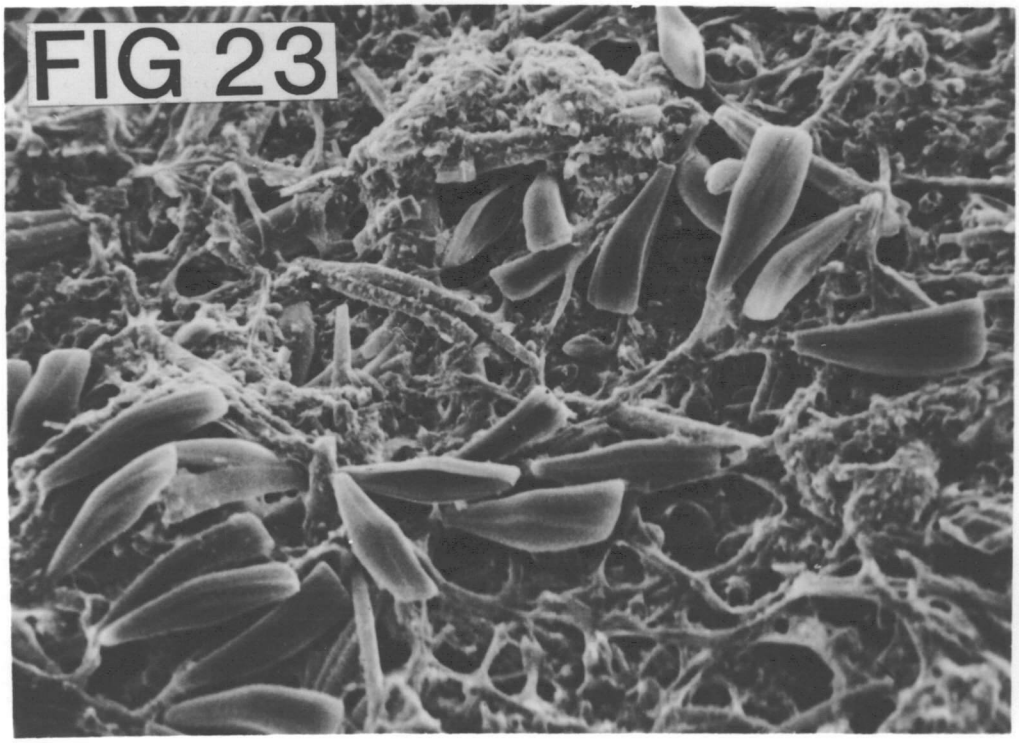


FIG 23

Figure 24. Scanning electron micrograph of an early epiphytic community on the lower portion of a leaf. Cocconeis scutellum is the dominant taxon. Note the absence of epiphytes from the edge of the leaf in the foreground (Magnification = 480X).

Figure 25. Smithora attached to the edge of a leaf of Zostera and epiphytized by Rhoicosphenia and Licmophora (Magnification = 240X).

FIG 24

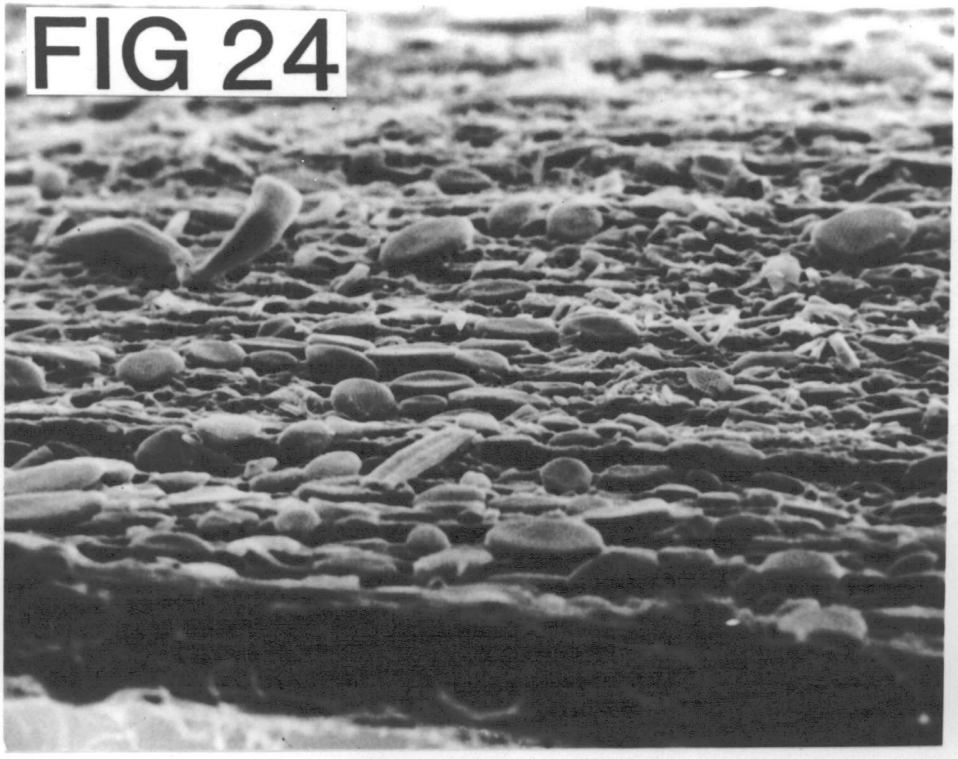
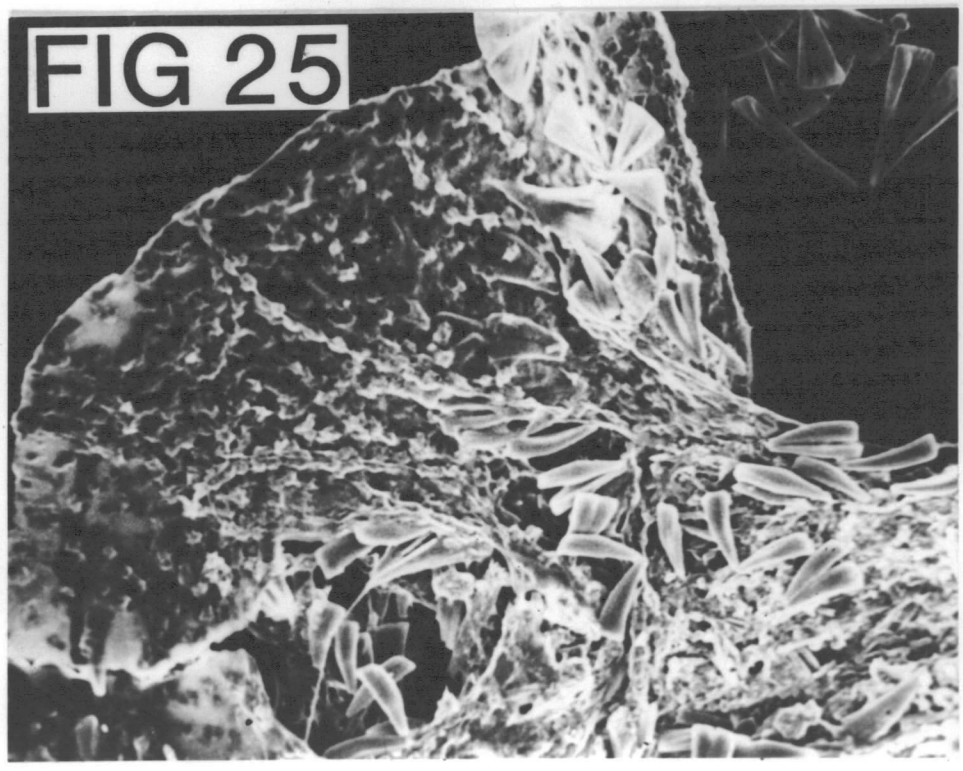


FIG 25



During the sampling period from April through September 1980, epiphyte biomass expressed as dry weight was the greatest at transect 1. There was little net increase or decrease in epiphyte biomass at the transects from May through September 1980 (Figure 26, Table 26).

The principal difference between the pattern in epiphyte biomass expressed as g dry weight m^{-2} and that expressed as g ash-free dry weight m^{-2} was an obvious increase in organic matter relative to dry weight biomass at transect 1 in June and July 1980 (Figure 27, Table 27). This was the result of the increase in percentage ash-free dry weight that occurred when the flora changed from exclusively diatoms to an assemblage that included Smithora and Ectocarpus. Therefore, biomass as ash-free dry weight reflected shifts in the composition of the flora that were not evident from biomass data expressed as dry weight.

Epiphyte biomass was significantly correlated ($r > 0.6$, $P < 0.01$) with Zostera aboveground, belowground and total biomass, and with the average area of a vegetative leaf and shoot density (Table 28). However, epiphyte biomass was not correlated with number of leaves per shoot ($P > 0.01$). Changes in number of leaves per shoot occurred indpendent of changes in Zostera biomass, and of changes in leaf area and shoot density which were closely related to changes in the growth rate of the host plant. Therefore, the data indicated that the pattern in the epiphyte biomass was closely related to the accumulation of Zostera biomass.

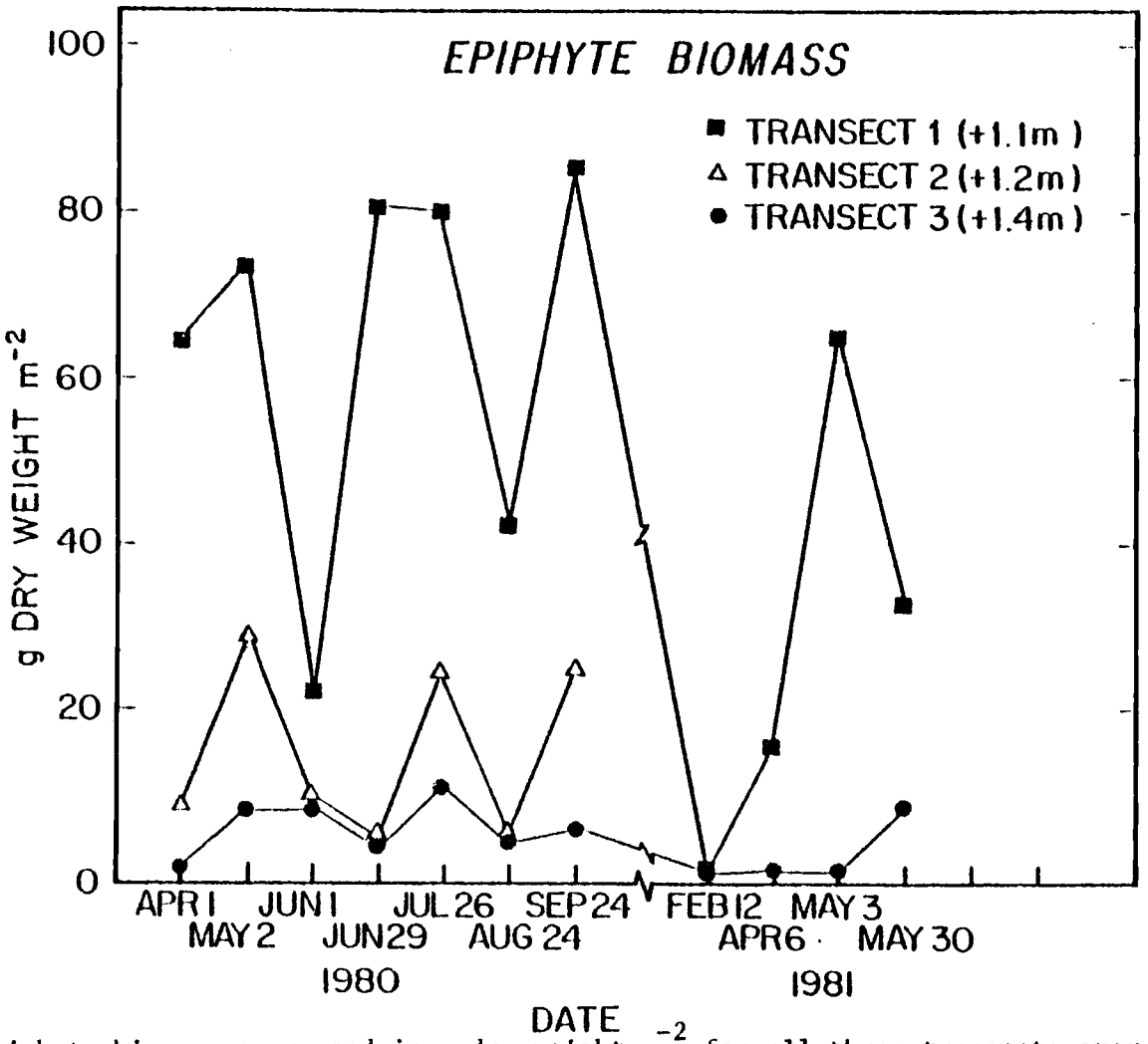


Figure 26. Epiphyte biomass expressed in g dry weight m^{-2} for all three transects over the period from April 1980 through May 1981. Each point represents the mean of 5 to 7 observations.

Table 26. Mean epiphyte biomass (g dry wt. m^{-2}). Values are the means of 5 to 7 observations. Standard error of the mean is in parentheses.*

TRANSECT	1980							1981			
	APR 1	MAY 2	JUN 1	JUN 29	JUL 26	AUG 24	SEP 24	FEB 12	APR 6	MAY 3	MAY 30
1	66.1 (7.1)	72.1 (11.0)	23.4 (5.7)	81.4 (25.2)	80.7 (22.3)	44.1 (11.4)	87.0 (12.6)	0.4 (0.1)	16.0 (3.0)	65.0 (9.2)	34.3 (6.5)
2	8.4 (3.3)	29.3 (9.0)	10.1 (2.3)	5.5 (2.4)	24.7 (6.1)	8.8 (2.7)	24.1 (3.7)	-	-	-	-
3	1.5 (0.5)	8.0 (3.6)	10.0 (4.6)	5.1 (3.3)	11.0 (3.9)	5.1 (1.4)	6.7 (2.9)	0.7 (0.2)	0.7 (0.3)	1.8 (0.9)	8.6 (2.1)

*Dashes indicate no data available.

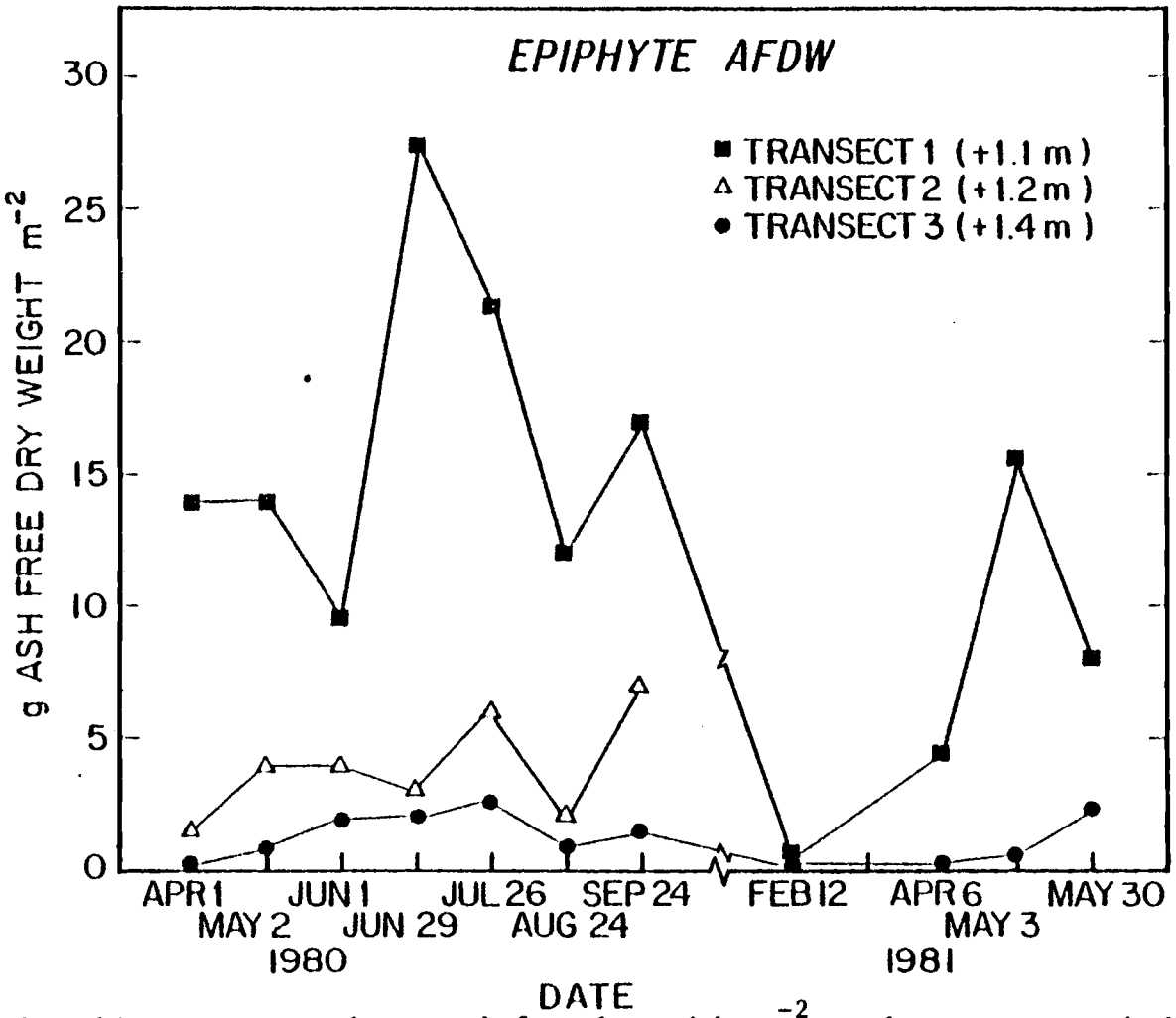


Figure 27. Epiphyte biomass expressed as g ash-free dry weight m^{-2} at three transects in Netarts Bay during the period from April 1980 to May 30, 1981. Each point represents the mean of 5 to 7 observations.

Table 27. Mean epiphyte biomass expressed in g ash-free dry wt. m^{-2}. Values are the means of 5 to 7 observations. Standard error of the mean is in parentheses.*

	1980							1981			
TRANSECT	APR 1	MAY 2	JUN 1	JUN 29	JUL 26	AUG 24	SEP 24	FEB 12	APR 6	MAY 3	MAY 30
1	13.8 (1.5)	13.6 (2.0)	9.6 (2.4)	27.5 (8.5)	21.5 (5.9)	12.4 (3.2)	17.3 (2.5)	0.2 (0.0)	5.0 (0.9)	15.5 (2.2)	8.0 (1.5)
2	1.5 (0.6)	4.0 (1.2)	4.0 (0.9)	2.7 (1.2)	5.7 (1.4)	2.3 (0.7)	6.6 (1.0)	-	-	-	-
3	0.3 (0.1)	1.2 (0.5)	2.4 (1.1)	2.3 (1.5)	2.6 (0.9)	1.3 (0.4)	1.6 (0.7)	0.4 (0.1)	0.3 (0.1)	0.6 (0.3)	2.3 (0.6)

*Dashes indicate no data available.

Table 28. Correlation between epiphyte biomass and total shoot density (TSHD), average number of leaves per shoot (LVES), average area of a vegetative leaf (AREA), aboveground biomass (ABGB), belowground biomass (BLGB), and total Zostera biomass (TZOS). Epiphyte biomass is expressed as dry weight (EPDW) and ash-free dry weight (EPAF). Values greater than 0.2 are significantly different than zero where $P < 0.01$.

VARIABLE	EPDW	EPAF
TSHD	0.39	0.38
LVES	0.01	-0.01
AREA	0.57	0.63
ABGB	0.67	0.74
BLGB	0.70	0.72
TZOS	0.71	0.76

Epiphyte load was examined by expressing epiphyte biomass as g dry weight per g dry weight of Zostera leaf. Epiphyte loads were highest in April and May 1980; a maximum value of 2.3 g epiphytes/g leaf was measured at transect 2 in May (Figure 28). From June 1 through September 1980 the loads averaged 0.4 g epiphytes per g leaf with a standard error of 0.06 g epiphytes per g leaf. Therefore, during the period of time when Zostera biomass was highest, the epiphyte loads were the lowest, apparently because of an increase in Zostera biomass during a time when there was no net increase in epiphyte biomass.

Epiphyte biomass was influenced by the regular loss of that portion of the standing crop which had colonized the oldest Zostera leaf on a shoot. At certain times during the study the loss of a particular group of leaves had more impact on the epiphyte biomass than the loss of leaves at other times. The low epiphyte biomasses at transects 1 and 2 on June 1 and August 24, 1980 and at transect 1 on May 30, 1981 were probably related to the loss of Zostera leaves that carried a larger proportion of the epiphyte biomass than was usually associated with the leaves that were sloughed. The highest loads of epiphytes in the study were recorded for the sample taken on May 2, 1980 (Figure 28). One can predict the time when the leaves present in the Zostera bed at the time of the sample were sloughed by considering the mean lifetime of a leaf (34 days), the mean PI (9 days) and the mean number of leaves per shoot (4) during the time period under consideration

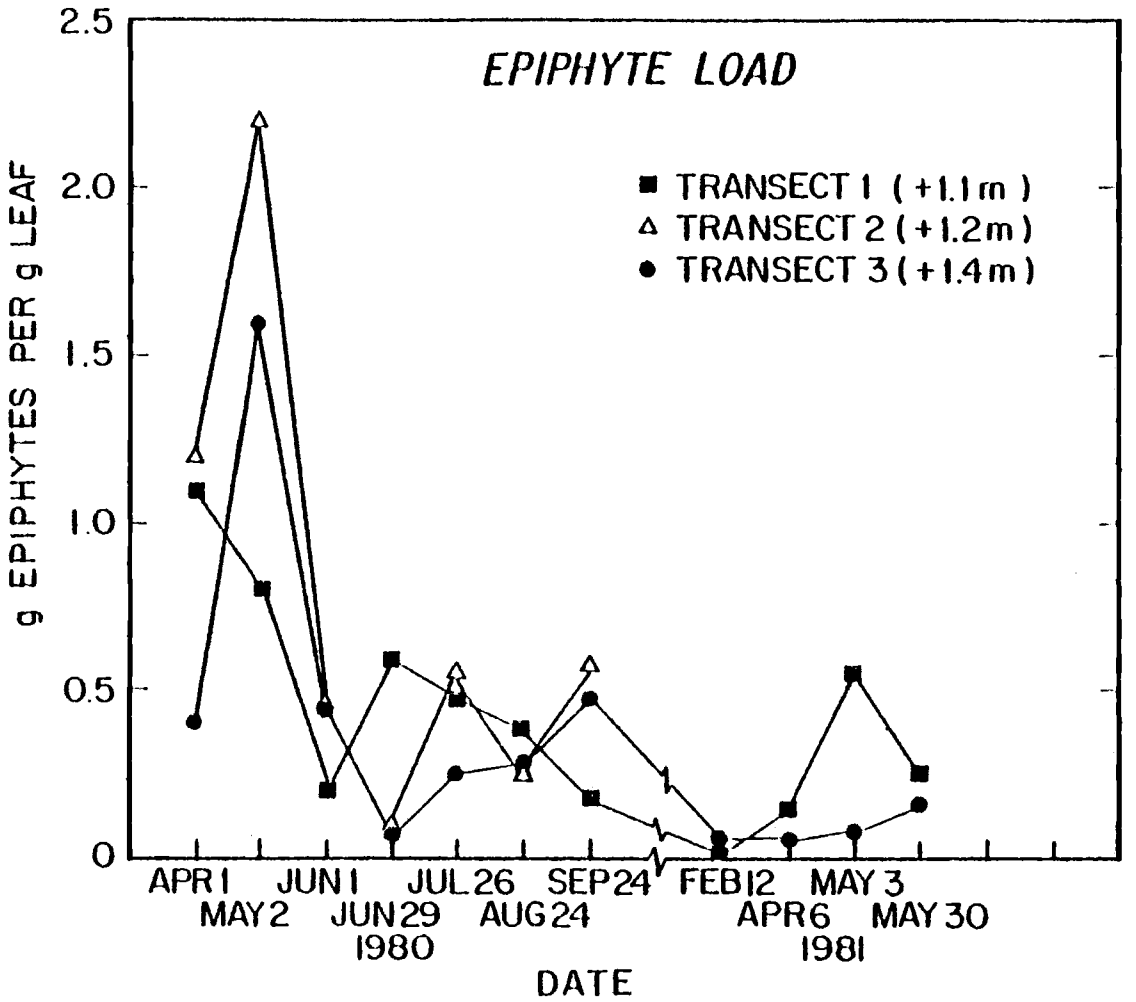


Figure 28. Epiphyte load expressed as g dry weight of epiphytes per g dry weight of Zostera leaf along three transects for the period from April 1980 through May 1981. Each point represents the mean of 5 to 7 observations.

(Figure 29A). A leaf initiated by a shoot with four leaves on April 28 would be sloughed 34 days later on May 31. The oldest leaf on such a shoot would have initiated growth three PI earlier on April 2 and would have been sloughed 34 days later on May 6. Therefore, most of the leaves present in the Zostera bed on May 2 were probably sloughed together with their heavy epiphyte load before June 1, thereby accounting for the decrease in epiphyte biomass measured at that time. The loss of epiphyte biomass that occurred between July 26 and August 24, 1980 was explained using the same reasoning. The leaves that would have been sloughed during that period were in positions 1 and 2 on the shoot during the time of maximum shoot production (Figure 29B). Leaves in positions 1 and 2 on a shoot together accounted for 75 to 92% of the shoot's growth from July to October (Table 11). Therefore, the leaves that were sloughed between July 26 and August 24, 1980 were among the largest leaves produced that year. Since they were also the oldest leaves on the shoot, they probably carried a large portion of the epiphyte biomass. In addition, notes made while sorting the sample taken in August indicated that many amphipods were present, and that the Zostera leaves showed signs of herbivory. Perhaps, the process of grazing also accounted for at least some of the decrease in epiphyte biomass in August 1980.

Production.

Measurements of epiphyte primary production using the ^{14}C method were made monthly from June to September, when the summer

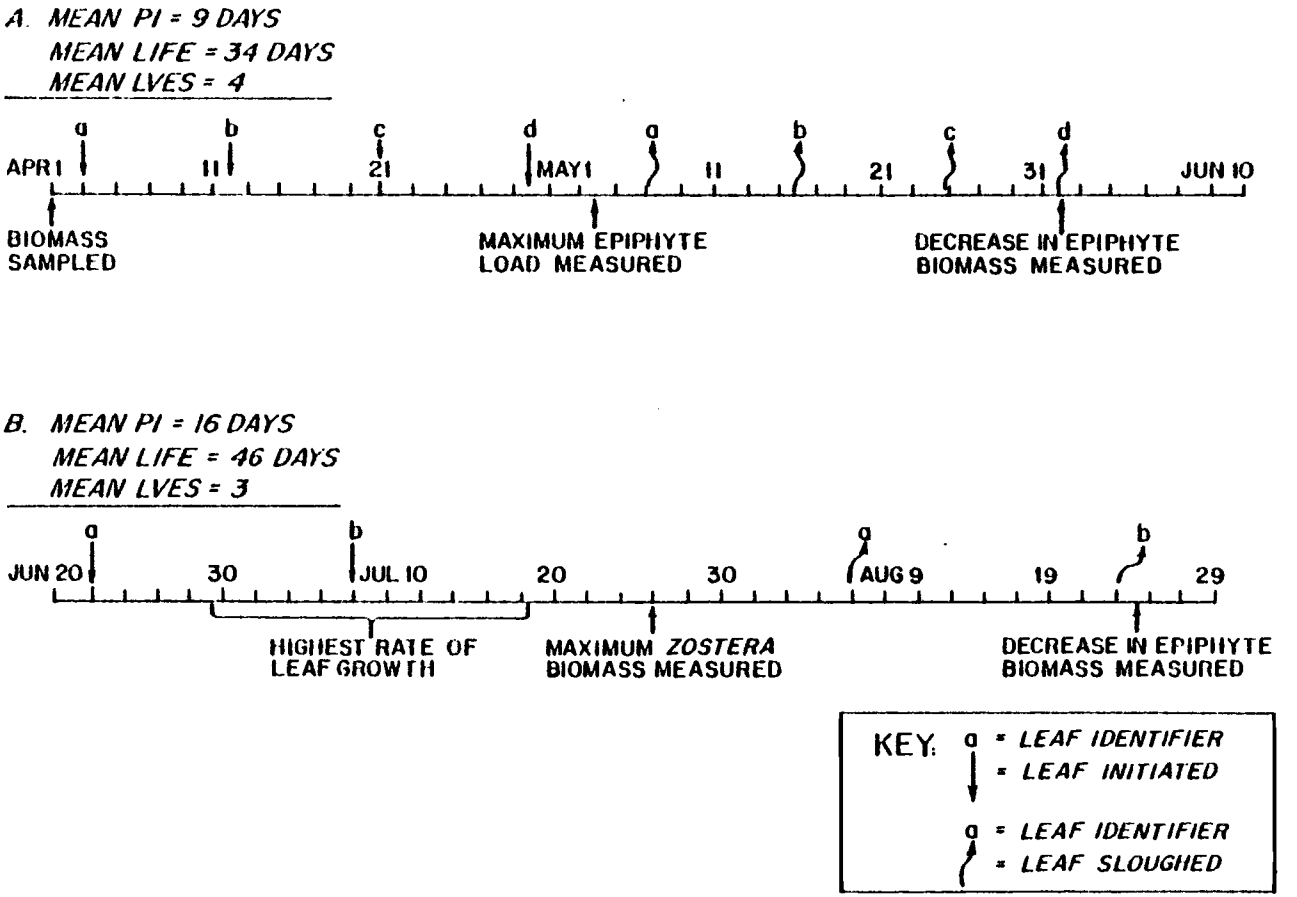


Figure 29. Time line of leaf initiation and sloughing explaining the sharp decreases in epiphyte biomass observed on June 1 and August 24, 1980. A. The decrease in epiphyte biomass on June 1, 1980 is due to the prior sloughing of the majority of the leaves that carried the highest epiphyte load of the study. B. The decrease in epiphyte biomass on August 24, 1980 is due to the loss of some of the largest leaves produced during the study. Factors considered included the plastochrone interval (PI), lifetime of a leaf (LIFE), and number of leaves per shoot (LVES).

lower low tides were early in the day. The results from the ^{14}C measurements were used to establish a ratio between the rates of ^{12}C assimilation for the Zostera and the epiphytic assemblage rather than as a direct estimate of epiphyte production. It was assumed that Zostera and epiphyte respiratory losses per unit biomass were the same. The rates of ^{12}C accumulation for Zostera and epiphytes and their ratios are presented in Table 29. The mean ratio of the rates of ^{12}C assimilated expressed as mg ^{12}C assimilated (g dry weight)$^{-1}$ h^{-1} for the epiphytic assemblage and Zostera was 0.60 with a standard error of 0.08.

This ratio was used to estimate the net primary production of the epiphytes from the net primary production of Zostera obtained with the shoot marking period. The net primary production for the epiphytic assemblage was calculated for each time interval during which the net primary production of Zostera was measured. First, the specific growth rate for Zostera was calculated by dividing the net primary production of the aboveground portions of Zostera by the mean aboveground biomass for the period of time under consideration. Then the specific growth rate of the epiphytes was calculated by multiplying the specific growth rate of Zostera by the mean ratio of the rates of ^{12}C assimilation for Zostera and the epiphyte assemblage (0.60). Finally, net primary production of the epiphytes was calculated by multiplying the mean biomass of the epiphytes by the specific growth rate of the epiphytes. These values are listed in Table 30.

Table 29. Net primary production of *Zostera* and the epiphyte assemblage measured using the ^{14}C method along three transects on July 26 and August 24, 1980 and May 31, 1981. Production is expressed as mg ^{12}C assimilated (g dry weight)$^{-1}$ h^{-1} (DRY WT) and as mg ^{12}C assimilated (g ash-free dry weight)$^{-1}$ h^{-1} (AFDW). Values listed are the means of 2 or 3 replicate samples.*

	Epiphyte Production		*Zostera* Production		Epiphyte Production: *Zostera* Production	
	DRY WT	AFDW	DRY WT	AFDW	DRY WT	AFDW
July 26, 1980						
Transect						
1	0.6	2.2	1.9	2.6	0.46	0.85
2	0.4	1.7	2.4	3.4	0.20	0.50
3	18.5	80.4	59.3	84.2	0.45	0.96
August 24, 1980						
Transect						
1	71.1	253.9	153.4	207.0	0.86	1.23
2	19.0	73.1	43.8	60.3	0.77	1.21
3	22.9	91.6	56.9	79.7	0.67	1.15
May 31, 1981						
Transect						
1	161.9	702.6	434.3	577.1	0.59	1.22
2	-	-	-	-	-	-
3	85.6	329.2	196.6	260.2	0.77	1.26

*Dashes indicate no data available.

Table 30. Net primary production of the epiphyte assemblage measured along the three transects from June 1, 1980 to May 30, 1981. Production is expressed as g dry weight m^{-2} (DRY WT) and g ash-free dry weight m^{-2} (AFDW) for each period of time.*

	TRANSECT					
	1		2		3	
	DRY WT	AFDW	DRY WT	AFDW	DRY WT	AFDW
1980						
JUN 1-JUN 29	36.7	98.3	7.8	17.5	6.8	20.0
JUN 29-JUL 26	40.5	134.1	16.6	46.0	8.1	23.9
JUL 26-AUG 24	18.7	68.5	10.0	40.4	5.6	21.2
AUG 24-SEP 24	29.5	123.2	13.6	51.4	7.0	28.7
1981						
APR 6-MAY 3	28.4	103.3	-	-	1.1	3.0
MAY 3-MAY 30	39.7	168.2	-	-	2.6	8.7

*Dashes indicate no data available.

The net primary production of the epiphyte assemblage at transect 1 ranged from 68.5 to 168.2 g ash-free dry weight m^{-2} $month^{-1}$ (18.7 to 40.5 g dry weight m^{-2} $month^{-1}$) during the period from June 1980 through June 1981, while that for transect 3 ranged from 3.0 to 28.7 g ash-free dry weight m^{-2} $month^{-1}$ (1.1 to 8.1 g dry weight m^{-2} $month^{-1}$).

Components of Variance

To gain added insight into the relationships among the morphometric and biomass variables, principal components analysis (PCA) was performed on a pooled data set for the three transects. Variables in the data matrix included shoot density (shoots m^{-2}), number of leaves per vegetative shoot, mean area of a vegetative leaf (cm^2), aboveground and belowground Zostera biomass (g dry weight m^{-2}), epiphyte biomass (g ash-free dry weight m^{-2}), and epiphyte load (g dry weight per m^2 leaf surface). Only the first three components, with eigenvalues greater than or equal to one, were interpretable.

The first three principal components accounted for 82.9% of the variation in the seven variables (Table 31). Factor loadings indicated that principal component 1 (PC1) primarily expresses shoot density, average area of a vegetative leaf, aboveground and belowground Zostera biomass and epiphyte biomass. These variables all were expressions of the biomass associated with the Zostera Primary Production subsystem (Figure 2). Total biomass for the Zostera Primary Production subsystem expressed

Table 31. Factor loadings corresponding to the first three principal components (PC1, PC2, PC3) of the morphometric and biomass variables, the corresponding eigenvalue and accumulated percentage of the variance. The analyses was based on 175 observations.

Variables	PC1	PC2	PC3
Shoot density (shoots m^{-2})	0.644	0.557	-0.162
Number of leaves per vegetative shoot	-0.002	0.804	0.120
Average area of a vegetative leaf (cm^2)	0.704	-0.570	-0.017
Aboveground biomass (g dry wt. m^{-2})	0.953	0.081	-0.132
Belowground biomass (g dry wt. m^{-2})	0.922	0.070	0.008
Epiphyte biomass (g ash-free dry wt. m^{-2})	0.856	0.116	0.285
Epiphyte load (g dry wt. m^{-2} leaf area)	0.009	0.027	0.976
Eigen value	3.403	1.305	1.093
Accumulated % of variance	48.6	67.3	82.9

in g ash-free dry weight m^{-2} (ZPP) was regressed against PC1, generating an R^2 value of 0.97; the regression model was $\hat{ZPP}$ = 125.87 + 53.03 PC1. Factor loadings also indicated that the second principal component (PC2) was an expression of the inverse relationship between the average area of a vegetative leaf on the one hand and the shoot density and number of leaves per vegetative shoot on the other hand, i.e., the morphometrics of a vegetative shoot. The third principal component (PC3) was highly correlated with epiphyte load (r = 0.98). When correlation coefficients were calculated for this group of variables, epiphyte load was not correlated with any of the other variables. In summary, this set of data generated three independent (orthogonal) components of variance: autotrophic biomass, leaf-shoot density and morphometrics, and epiphyte load.

Bioenergetics of the *Zostera* Primary Production Subsystem

In the introduction to this work, a conceptual model of the Sediment Processes subsystem was presented as a hierarchy of coupled subsystems (Figure 2). This model was used to organize the examination of the bioenergetics of the seagrass ecosystem in Netarts Bay. The following analysis considers several levels of resolution. At the finest level of resolution, the Macrophyte Primary Production Subsystem is decomposed into aboveground and belowground *Zostera*. The gains and losses of biomass for each of

these components are partitioned and are presented as an energy budget. The Macrophyte Primary Production subsystem then is integrated with the Epiphyte Primary Production subsystem to form the Zostera Primary Production subsystem. The gain of biomass from the primary production of this subsystem is expressed as annual net production.

Information accumulated on the growth of Zostera marina L. was synthesized with respect to the bioenergetics of the Macrophyte Primary Production subsystem. The changes in its state variable, the macrophyte biomass, were examined in terms of the inputs and outputs that affected its value. These inputs and outputs were related to the dynamics of the Macrophyte Primary Production subsystem, as primary production of Zostera was related to the physiological activities of the plant. The inputs and outputs that affect Zostera biomass also represented the couplings between the Macrophyte Primary Production subsystem and the rest of the subsystems in the conceptual model. Consequently, the perspective gained by such an approach contributed to the understanding of the role that Zostera marina played in the estuary.

Changes in aboveground biomass were caused by inputs from shoot net primary production and outputs as lost shoots, sloughed leaves and grazing. Biomass accumulation due to shoot net primary production and losses due to sloughed leaves were measured directly and were partitioned separately in the energy budget. Shoot net primary production for each sampling period was calculated

according to the following expression:

Shoot net primary production (g dry wt. m^{-2})	=	Rate of net primary production per shoot (g dry wt. per shoot)	X	Mean shoot density (shoots m^{-2})

Monthly shoot net primary production, estimated as g dry weight m^{-2}, was calculated by summing the values for the constituent sampling periods. Losses due to sloughing of leaves expressed as g dry weight m^{-2} for the time period under consideration was calculated according to the following expression:

Mean leaf loss per m^2	=	Number of leaves lost per shoot	X	Mean number of shoots per m^2	X	Mean dry weight per leaf lost

The mean dry weight per leaf of the leaves lost was estimated as the mean weight of the largest leaf on a shoot at the beginning of the sampling period.

The energy budgets for aboveground Zostera are presented in Tables 32, 33, and 34. The column labelled "difference" represents biomass losses not accounted for directly in this study, and includes biomass lost as entire shoots and to grazing.

At all transects during each time interval considered, biomass losses accounted for at least 50% of the shoot net primary production. From July through October 1980, the biomass losses were equal to or higher than the shoot net primary production. This indicated the great capacity of the Zostera to turnover its aboveground biomass. The lifetime of a leaf ranged from

Table 32. Energy budget accounting for the gains and losses of aboveground biomass along transect 1 between April 1, 1980 and July 1, 1981. Values are expressed as g dry weight m^{-2} for the period of time under consideration.*

DATE	BIOMASS	ΔBIOMASS	NET PRIMARY PRODUCTION	BIOMASS LOSS	LOSS AS LEAVES	DIFFERENCE
APR 1, 1980	98.7					
		+16.1	-	-	-	-
MAY 2, 1980	114.8					
		+47.3	-	-	-	-
JUN 1, 1980	162.1					
		+35.7	220.8**	185.1	98.0	87.1
JUN 29, 1980	197.9					
		+58.3	234.5	176.2	170.3	5.3
JUL 26, 1980	256.2					
		-82.3	111.0	193.3	98.0	95.3
AUG 24, 1980	173.9					
		-54.5	122.5	177.0	106.3	70.7
SEP 24, 1980	119.4					
		-49.2	105.8	155.0	80.6	74.4
OCT 23, 1980	70.2**					
		-12.7	-	-	-	-
FEB 12, 1981	57.6					
		+108.9	-	-	-	-
APR 6, 1981	166.5					
		+14.5	222.7	208.2	89.6	118.6
MAY 3, 1981	181.0					
		+21.3	272.2	250.9	88.9	162.0
MAY 30, 1981	202.4					
		+23.6	344.7	321.1	127.2	193.9
JUL 1, 1981	226.0**					

*Dashes indicate no data available.

**Extrapolated.

Table 33. Energy budget accounting for the gains and losses of aboveground biomass along transect 2 between April 1 and October 23, 1980. Values are expressed as g dry weight m^{-2} for the period of time under consideration.*

DATE	BIOMASS	ΔBIOMASS	NET PRIMARY PRODUCTION	BIOMASS LOSS	LOSS AS LEAVES	DIFFERENCE
APR 1, 1980	11.3					
		+15.3	-	-	-	-
MAY 2, 1980	26.6					
		+11.2	-	-	-	-
JUN 1, 1980	37.8					
		+23.0	85.3	62.3	17.9	44.4
JUN 29, 1980	60.8					
		+10.2	123.1	112.9	30.8	82.1
JUL 26, 1980	71.0					
		-17.5	63.7	81.2	43.3	37.9
AUG 24, 1980	53.5					
		+16.9	78.8	61.9	49.8	12.1
SEP 24, 1980	70.4					
		-10.4	51.2	61.6	53.1	8.5
OCT 23, 1980	60.0**					

*Dashes indicate no data available.

**Extrapolated.

Table 34. Energy budget accounting for the gains and losses of aboveground biomass along transect 3 between April 1, 1980 and July 1, 1981. Values are expressed as g dry weight m^{-2} for the period of time under consideration.*

DATE	BIOMASS	ABIOMASS	NET PRIMARY PRODUCTION	BIOMASS LOSS	LOSS AS LEAVES	DIFFERENCE
APR 1, 1980	7.3					
		+ 0.8	-	-	-	-
MAY 2, 1980	8.1					
		+22.2	-	-	-	-
JUN 1, 1980	30.3					
		+19.2	66.5**	47.3	25.2**	22.1
JUN 29, 1980	49.5					
		+ 7.6	88.2	80.6	27.4	53.2
JUL 26, 1980	57.1					
		-22.1	49.8	71.9	41.5	30.4
AUG 24, 1980	35.0					
		-13.0	55.9	68.9	17.4	51.5
SEP 24, 1980	22.0					
		0	41.8	41.8	14.9	27.2
OCT 23, 1980	22.0**					
		+ 0.3	-	-	-	-
FEB 12, 1981	22.3					
		- 0.7	-	-	-	-
APR 6, 1981	21.6					
		+10.8	52.5	41.7	10.6	31.1
MAY 3, 1981	32.4					
		+52.0	104.7	52.7	19.7	33.0
MAY 30, 1981	84.4					
		-24.4	79.3	103.7	59.4	44.3
JUL 1, 1981	60.0**					

*Dashes indicate no data available.

**Extrapolated.

34 to 55 days during the course of this study. Therefore, every 34 to 55 days each shoot had an entire set of new leaves. With this in mind, it was not surprising that 35 to 100% of the biomass loss was due to sloughed leaves. The biomass loss from leaf export occurred in response to the changes in leaf size. In April and May the small leaves of the winter growth form were shed, and leaves exported during this period represented a smaller proportion of biomass loss than when the larger summer leaves were lost from June to October.

An energy budget also was constructed for belowground Zostera biomass. The net primary production of belowground Zostera was measured between April 6 and May 16, 1981, according to the method of Jacobs (1979) and Kenworthy (personal communication). The net production of the belowground Zostera during this period of time was 219.8 g dry weight m^{-2} at transect 1 and 45.3 g dry weight m^{-2} at transect 3. Since a direct measurement of belowground net primary production was made for only a short time period during this study, an alternative method of estimating belowground net primary production was adopted. For the development of an energy budget shoot net primary production was used to estimate belowground net primary production. Since both variables were measured concurrently from April 6 to May 16, 1981, these data were used to establish the relationship between the net production of aboveground and belowground Zostera. The specific growth rate for the net production of aboveground and belowground Zostera was calculated by dividing the net production (g dry weight m^{-2}) by the mean

biomass (g dry weight m^{-2}) for the period of time under consideration. The ratio between specific growth rate for aboveground Zostera and the specific growth rate for belowground Zostera was calculated for that period of time. For transect 1 this ratio was 0.90, while for transect 3 it was 0.46. It was assumed that the ratio between the specific growth rates of aboveground and belowground Zostera remained constant throughout the study. The specific growth rate for shoots was calculated for each sample period and the corresponding specific growth rate for belowground Zostera was estimated using the appropriate ratio. The estimate of the specific growth rate for belowground Zostera then was multiplied by the mean belowground biomass for the corresponding period of time to obtain the net production of belowground Zostera. The energy budgets based on these estimates are presented in Tables 35 and 36.

At transect 1 throughout the study period the biomass loss of belowground Zostera was greater than or nearly equal to the net primary production. At transect 3 the biomass loss was generally between 25 and over 100% of the net primary production for belowground Zostera. Therefore, as was the case for aboveground Zostera, belowground Zostera biomass was regularly being turned over.

The large biomass loss from the Macrophyte Primary Production subsystem represented the coupling of this subsystem with the Detrital Decomosition subsystem, as well as the Consumer Processes

Table 35. Energy budget accounting for the gains and losses of belowground biomass along transect 1 between April 1, 1980 and July 1, 1981. Values are expressed as g dry weight m^{-2} for the period of time under consideration.

DATE	BIOMASS	ΔBIOMASS	NET PRIMARY PRODUCTION	BIOMASS LOSS
APR 1, 1980	160.8			
		- 6.7	-	-
MAY 2, 1980	154.1			
		- 2.4	-	-
JUN 1, 1980	151.7			
		+12.7	174.5	161.8
JUN 29, 1980	164.4			
		+42.5	167.1	124.8
JUL 26, 1980	206.9			
		-59.7	79.7	139.4
AUG 24, 1980	147.2			
		-14.7	105.1	119.8
SEP 24, 1980	132.5			
		-15.0	125.0	140.0
OCT 23, 1980	117.5**			
		-55.5	-	-
FEB 12, 1981	62.0			
		+64.1	-	-
APR 6, 1981	126.1			
		- 1.7	150.3	152.0
MAY 3, 1981	124.4			
		+27.2	179.4	152.2
MAY 30, 1981	151.6			
		-21.6	197.1	218.7
JUL 1, 1981	130.0			

*Dashes indicates no data available.

**Extrapolated.

Table 36. Energy budget accounting for the gains and losses of belowground biomass along transect 3 between April 1, 1980 and July 1, 1981. Values are expressed as g dry weight m^{-2} for the period of time under consideration.

DATE	BIOMASS	ΔBIOMASS	NET PRIMARY PRODUCTION	BIOMASS LOSS
APR 1, 1980	71.7			
		-34.4	-	-
MAY 2, 1980	37.3			
		- 2.2	-	-
JUN 1, 1980	35.1			
		+19.0	31.2	12.2
JUN 29, 1980	54.1			
		+31.5	55.9	24.4
JUL 26, 1980	85.6			
		-31.9	34.8	66.7
AUG 24, 1980	53.7			
		-18.2	40.1	58.3
SEP 24, 1980	35.5			
		- 5.5	29.5	35.0
OCT 23, 1980	30.0**			
		- 5.2	-	-
FEB 12, 1981	24.8			
		+16.2	-	-
APR 6, 1981	41.0			
		- 9.6	25.3	34.9
MAY 3, 1981	31.4			
		+31.8	18.9	-12.9
MAY 30, 1981	63.2			
		-13.2	39.6	52.8
JUL 1, 1981	50.0*			

* Dashes indicate no data available.

** Extrapolated.

subsystem (Figure 2). Losses of belowground biomass were primarily retained within the Zostera bed, while the losses of aboveground biomass not retained within the Zostera bed were transported to other regions within the estuary, to the salt marsh and to the ocean. It was through this export of primarily aboveground biomass that Zostera had an impact as an input of organic matter on regions distant from its source.

At a higher level of resolution processes associated with the Zostera Primary Production Subsystem were described. The growing season for Zostera in Netarts Bay was defined in April through October, which is typical of temperate seagrass beds (Phillips, 1972; Sand-Jensen, 1975; Stout, 1976). Since production data for months representing an entire growing season were available only for transects 1 and 3, data from those regions were used as a basis for the following estimates.

The total net primary production of aboveground and belowground Zostera and epiphytes for the entire growing season was obtained from the production values measured for the period from April through October during the course of the study. Production expressed as g dry weight m^{-2} day^{-1} was calculated by dividing by 214 days, or the length of the growing season. The dimensions of the Zostera bed were measured and the bed was stratified into regions representative of transect 1 and transect 3. The total area of the study site was 17,562 m^2. Of this total, an area of 10,062 m^2 was designated as equivalent to transect 1 and an area

of 7500 m^2 was designated as equivalent to transect 3. The net primary production for each region was then estimated by multiplying its area by the production m^{-2}.

The turnover time was calculated from the following expression:

$$\text{Turnover time (days)} = \frac{\text{Mean biomass during the period from } t_1 - t_o \text{ (g } m^{-2})}{\text{Net production during the period from } t_1 - t_o \text{ (g } m^{-2} \text{ day}^{-1})}$$

where t_o = the beginning of the measurement period and t_1 = the end of the measurement period.

Measurements of Zostera biomass expressed in g dry weight were converted to g C by multiplying by 0.38, the proportion of the dry weight that is carbon (Westlake, 1963). Measurements of epiphyte biomass expressed as g dry weight were converted to g C using the expression proposed by Davis (1982):

$$\text{g carbon} = \text{g dry weight} \times \text{proportion ash-free dry weight} \times 0.50,$$

where 0.50 is the proportion of the ash-free dry weight that is carbon.

The region represented by transect 1 accounted for 80% of the primary production of the Zostera Primary Production subsystem (Table 37). Although the mean biomasses for aboveground and belowground Zostera were nearly equivalent in this region, aboveground biomass accounted for 58% of the net primary production of the

Table 37. Annual net primary production for the region of the Zostera bed represented by transect 1. A growing season from April to October was assumed. $NPPd^{-1}$ = net primary production expressed as g dry weight m^{-2} day^{-1}; $NPPm^{-2}$ = annual net primary production expressed as g dry weight m^{-2}; NPP/AREA = annual net primary production for the entire area (10,062.5 m^2) expressed as kg dry weight; $\overline{X}BIO$ = mean biomass expressed as g dry weight m^{-2}; X-OVER = the number of times biomass turned over; d-OVER = the number of days for the biomass to turnover during the growing season. The values in parentheses are the corresponding measurements expressed as grams carbon.

	$NPPd^{-1}$	$NPPm^{-2}$	NPP/AREA	$\overline{X}BIO$	X-OVER	d-OVER
Aboveground Zostera	6.6 (2.5)	1413.4 (537.1)	14,000 (5300)	153.9 (58.5)	9.2	23.3
Belowground Zostera	4.7 (1.8)	1003.1 (381.2)	10,000 (3800)	148.8 (56.5)	6.7	31.7
Macrophyte Primary Production Subsystem	11.3 (4.3)	2416.5 (918.3)	24,000 (9100)	302.7 (115.0)	8.0	26.8
Epiphyte Primary Production Subsystem	0.9 (0.1)	247.4 (29.7)	2,500 (300)	57.7 (6.9)	4.3	49.9
Zostera Primary Production Subsystem	12.12 (4.4)	2713.8 (948.0)	26,500 (9400)	360.4 (121.9)	7.5	28.4

macrophyte, and was turned over about three more times during the season than the belowground material. In contrast, the region similar to transect 3 maintained a mean belowground biomass that was 30% higher than the mean aboveground biomass (Table 38). The aboveground biomass turned over almost 3 times as fast as the belowground biomass, and its rate of production was almost double that of the belowground biomass. Therefore, the plants in two regions of the bed had different growth strategies.

The net primary production by the Epiphyte Primary Production subsystem only accounted for 8% of the net primary production associated with the Zostera Primary Production subsystem during the growing season (Table 39). The mean turnover time for epiphyte assemblages was more than twice that of the aboveground Zostera.

Stout (1976) reported that 161 ha in Netarts Bay were occupied by shallow eelgrass beds. Her description of a shallow eelgrass bed was similar to that for transect 3. She also reported that 176 ha were occupied by deep eelgrass beds, i.e., equivalent to transect 1. To calculate the production of the entire bay associated with each region, the net primary production values expressed in g dry weight m^{-2} for each region was multiplied by 10,000 times the area of the region. Therefore, an estimate of total annual net primary production for the eelgrass beds in Netarts Bay was 6.0 X 10^6 kg.

Table 38. Annual net primary production for the region of the Zostera bed represented by transect 3. A growing season from April to October was assumed. $NPPd^{-1}$ = net primary production expressed as g dry weight m^{-2} day^{-1}; $NPPm^{-2}$ = annual net primary production expressed as g dry weight m^{-2}; NPP/AREA = annual net primary production for the entire area (7500 m^2) expressed as kg dry weight; $\overline{X}BIO$ = mean biomass expressed as g dry weight m^{-2}; X-OVER = the number of times biomass turned over; d-OVER = the number of days for the biomass to turnover during the growing season. The values in parentheses are the corresponding measurements expressed as grams carbon.

	$NPPd^{-1}$	$NPPm^{-2}$	NPP/AREA	$\overline{X}BIO$	X-OVER	d-OVER
Aboveground Zostera	2.2 (0.8)	461.3 (175.3)	35,000 (1300)	33.6 (12.8)	13.7	15.6
Belowground Zostera	1.1 (0.4)	244.1 (92.8)	18,000 (700)	49.0 (18.6)	5.0	42.9
Macrophyte Primary Production Subsystem	3.3 (1.3)	705.4 (268.1)	5,300 (2000)	82.6 (31.4)	8.5	25.1
Epiphyte Primary Production Subsystem	0.1 (0.01)	36.9 (4.4)	280 (30)	5.8 (0.7)	6.3	33.9
Zostera Primary Production Subsystem	3.4 (1.3)	742.3 (272.5)	5,600 (2030)	88.4 (32.1)	8.5	25.2

Table 39. Annual net primary production for the entire Zostera bed. A growing season from April to October was assumed. $NPPd^{-1}$ = net primary production expressed as g dry weight m^{-2} day^{-1}; $NPPm^{-2}$ = net primary production expressed as g dry weight m^{-2}; NPP/AREA = net primary production for the entire area (17,562.5 m^{-2}) expressed as kg dry weight; $\overline{XBIO}$ = mean biomass expressed as g dry weight m^{-2}; X-OVER = the number of times biomass turned over; d-OVER = the number of days for the biomass to turnover during the growing season. The values in parentheses are the corresponding measurements expressed as grams carbon.

	$NPPd^{-1}$	$NPPm^{-2}$	NPP/AREA	$\overline{XBIO}$	X-OVER	d-OVER
Aboveground Zostera	8.8 (3.3)	1874.7 (712.4)	17,500 (6600)	187.5 (71.3)	10.0	21.4
Belowground Zostera	5.8 (2.2)	1247.2 (474.0)	11,800 (4500)	197.8 (75.1)	6.3	33.9
Macrophyte Primary Production Subsystem	14.6 (5.6)	3121.9 (1186.4)	29,300 (11,100)	385.3 (146.4)	8.1	26.4
Epiphyte Primary Production Subsystem	1.0 (0.1)	284.3 (34.1)	2,800 (300)	63.5 (7.6)	4.5	47.8
Zostera Primary Production Subsystem	15.6 (5.7)	3406.2 (1220.5)	32,100 (11,400)	448.8 (154.0)	7.6	28.2

IV. DISCUSSION AND SYNTHESIS

The pattern of growth of Zostera marina L. in Netarts Bay, Oregon is typical of Zostera growing in temperate regions. However, the results of this study also support the conclusion of McMillan and Phillips (1979) that seagrass populations reflect the selective influence of local habitat conditions. In Netarts Bay, the initiation of growth in the spring is marked by shoot proliferation, change to the summer morphology and rapid growth of the leaves as Tutin (1942), Phillips (1972), Sand-Jensen (1975), Jacobs (1979), and Harrison (1982) also found. Flowering begins during the spring and early summer. Maximum vegetative growth occurs after the maximum density of reproductive shoots is reached (Phillips, 1972). In the late summer and into fall there is a gradual decline in density and biomass. Despite agreement on this general pattern of events, reports differ as to the timing and magnitude.

Sexual reproduction does not play a major role in the maintenance of Zostera beds. Reproductive shoots comprise on the average from 2.6% (this study) to 15% of the total shoots in an area (Phillips, 1972; Sand-Jensen, 1975; Aioi, 1980; Harrison, 1982). The timing of events associated with the sexual reproduction of Zostera in Netarts Bay is very similar to that in Puget Sound (Phillips, 1972). Flowers appear in the bed from March to May and disappear between August and October. Although Phillips (1972) found seeds germinating throughout the year, the time of

peak seed germination in Puget Sound (April to July) coincides with the time that seedlings were found in Netarts Bay.

The leaf marking technique permits the analysis of the growth of individual leaves on a vegetative shoot. This study agrees with previous investigations that most of the growth of a leaf occurs when it is the youngest and next to the youngest leaf on the shoot (Sand-Jensen, 1975; Mukai, et al., 1979; Jacobs, 1979). Differences in the time it takes for a leaf to reach its maximum growth reflect local differences in the PI and number of leaves per shoot, i.e., lifetime of a leaf (Table 40). The life of a leaf on a vegetative shoot in Netarts Bay is most similar to that reported for Roscoff, France (Jacobs, 1979). He reported a change in the number of leaves per shoot and the PI during the course of his study. As in this study, he noted an increase in the number of leaves per shoot in the spring, and a decrease during the summer and into the fall. Moreover, he found a negative correlation between the PI and insolation. This is not the case for Netarts Bay, where the PI was longest June through August, 1980, when photosynthetically active radiation was maximum (Figure 30). Instead, changes in the lifespan of a leaf in Netarts Bay were related to the regularly occurring annual changes in the plant between the winter and summer shoot morphology.

Biomass and density of Zostera in Netarts Bay, Oregon is comparable to that for Zostera in other temperate regions (Table 41). The highest densities and biomasses were measured along transect 1 and are similar to the highest densities and biomasses reported in the literature.

Table 40. Plastochrone interval (PI), mean number of leaves per vegetative shoot (LVES) and mean lifetime of a leaf (LIFE) from data for various localities. PI and LIFE are expressed in days.

LOCATION	PI	LVES	LIFE	REFERENCE
Japan	8	5.5	44	Mukai, et al. (1979)
Denmark	14	3.9-4.5	56	Sand-Jensen (1975)
France	13-19	2.1-4.4	40-57*	Jacobs (1979)
Oregon	9-20	2.7-4.0	34-56	This Study

*Calculated from data.

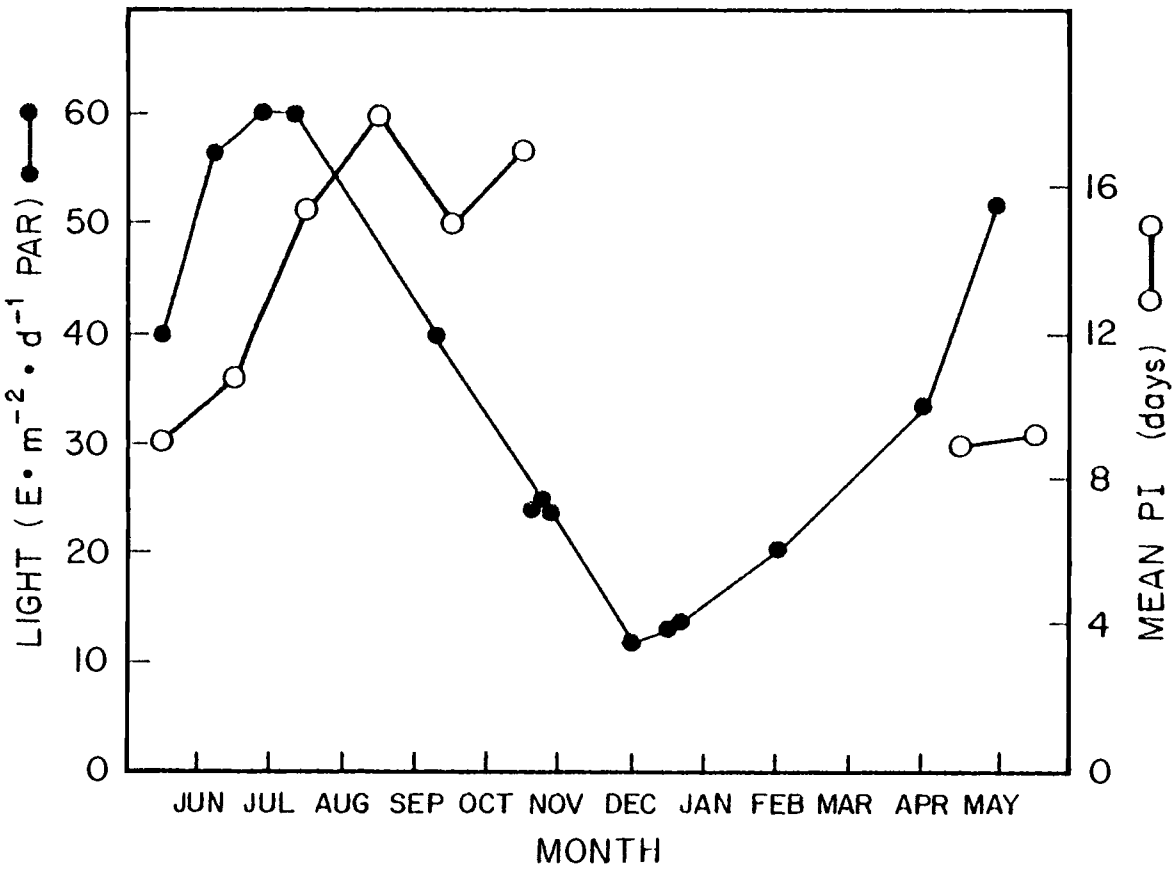


Figure 30. Maximum photosynthetically active radiation (PAR) and mean plastochrone interval (PI) of the three transects from June 1980 to May 1981. PAR is expressed as $E \cdot m^{-2} \cdot d^{-1}$; PI is expressed as days. PAR values were adapted from Davis (1982).

Table 41. Reported biomass and density values measured for Zostera marina L. Biomass is expressed in g dry weight m^{-2}; density is expressed as numbers of shoots m^{-2}.

LOCALITY	BIOMASS	DENSITY	REFERENCE
Denmark	272-960*	-	Petersen, 1913
	157-443	1200-1800	Sand-Jensen, 1975
The Netherlands	1-116	0-3600	Nienhuis and DeBree, 1980
France	200-470	580-700	Jacobs, 1979
Canada	5-15	50-160	Harrison, 1982
New York	247-2062	-	Burkholder and Doheny, 1968
North Carolina	175-545	-	Dillon, 1971
	50-185*	-	Penhale, 1977
California	12-421*	-	Keller, 1963
	6-192*	-	Waddell, 1964
	30-730	-	Harding and Butler, 1979
Washington	116-231	151-893	Phillips, 1972
Alaska	186-324	710-2101	McRoy, 1966
	62-1840	599-4576	McRoy, 1970a, 1970b
Oregon	288-467	671-1056	Stout, 1976
			This Study
	120-463	995-3845	Transect 1
	46-167	789-1414	Transect 2
	47-148	500-1761	Transect 3

*Only aboveground Zostera considered.

Reported values for production were converted to carbon following the recommendations of Westlake (1963). Values from the literature for aboveground Zostera production range from 0.5 to 8 g C m^{-2} day^{-1}. The results of this study are within these ranges with 0.6 to 4.2 g C m^{-2} day^{-1} for aboveground Zostera production and 1.0 to 6.6 g c m^{-2} day^{-1} for total Zostera production (Table 42).

As in this study, relationships among changes in shoot density, total Zostera biomass and aboveground production are reported in the literature. One such relationship is that described for transects 2 and 3 where changes in shoot density, total Zostera biomass and aboveground production followed a similar pattern (Phillips, 1972; Neinhuis and De Bree, 1980; Aioi, 1980; Harrison, 1982). Another is the pattern described for transect 1 in this study where shoot density is highest in the spring and decreases during the summer as total Zostera biomass and aboveground production increase (Sand-Jensen, 1975; Jacobs, 1979).

Sand-Jensen (1975) attributed the decrease in shoot density that he observed to the loss of reproductive shoots during the summer. However, he reported that shoot density decreased from 1800 shoots m^{-2} to about 1200 shoots m^{-2}, and that reproductive shoots accounted for no more than 4% of the total density or about 72 shoots m^{-2}. Therefore, loss of reproductive shoots can not totally account for the change in density that he observed. Jacobs (1979) did not attempt to explain the pattern.

Table 42. Net production values reported for the shoots of Zostera marina L. and for the whole plant (aboveground plus belowground material). Net production is expressed in g C m^{-2} day^{-1}.

LOCALITY	PRODUCTION	METHOD	REFERENCE
Denmark	2-7.3	Biomass	Petersen, 1913
	1.4-3.7*	Marking	Sand-Jensen, 1975
The Netherlands	0.0-3.5*	Marking	Nienhuis and DeBree, 1980
France	0.6-3.3*	Marking	Jacobs, 1979
North Carolina	0.5-1.7	^{14}C Method	Dillon, 1971
	0.6-1.2	^{14}C Method	Penhale, 1977
Washington	0.7-4.0	Biomass	Phillips, 1972
Alaska	8.0	O_2 Method	McRoy, 1966
	3.3-3.8	O_2 Method	McRoy, 1970a, 1970b
Oregon		Marking	This Study
	1.4-4.1		Transect 1
	0.7-1.7		Transect 2
	0.5-1.4		Transect 3
		Marking	This Study
	2.5-6.6*		Transect 1
	0.9-1.9*		Transect 3

*Summation of aboveground and belowground production.

These patterns are explained by the hypothesis presented in this study that there is a threshold leaf area per unit area of substrate. Results of this study indicate that this threshold value is between 7.5 and 11.0 m^2 leaf m^{-2} area of substrate. When the leaf area per unit area of substrate is below the threshold value, shoot density, total Zostera biomass and aboveground production are positively correlated. When the leaf area per unit area substrate is above the threshold value, shoot density is negatively correlated with total Zostera biomass and aboveground production. For example, the leaf areas reported by Phillips (1972) range from 2 to 8 m^2 leaf m^{-2} are of substrate. Therefore, the leaf area at Puget Sound during the time of his study was below the threshold value suggested by this study, and as the hypothesis predicts the shoot density and biomass values that he measured increased and decreased together. Considering the conclusion of Dennison (1979) that Zostera adjusts to a decrease in light levels of decreasing leaf area, this threshold leaf area must represent a critical reduction of light in the Zostera bed due to self-shading.

Light is considered an important factor in the determination of the distribution and production of Zostera marina (Burkholder and Doheny, 1968; Sand-Jensen, 1975; Jacobs, 1979; and Mukai, et al., 1980). Sand-Jensen (1975) clearly illustrated that the pattern of leaf production was closely related to that of insolation but not that of temperature. The correlation between insolation and leaf production is also supported by this study

(Figure 31). This relationship explains the earlier and higher shoot production reported for 1981 as compared to 1980. Rates of leaf production for May 1981 were comparable to those for July 1980, and photosynthetically active radiation for May 1981 was comparable to that for July 1980.

The curves for photosynthetically active radiation and mean shoot production had a similar shape except during August 1980, when there was a relatively sharp decrease in shoot production. This decrease was attributed to the bloom of Enteromorpha prolifera in Netarts Bay. No other study has reported such an interaction between the seagrass community and the drift algae.

There are few determinations of the biomass and productivity of the epiphytes of seagrasses. The most complete study of the production of Zostera and its epiphytes is that of Penhale (1977). Using the ^{14}C method she established that the ratio between the mean rates of the production for epiphytes and Zostera was 0.74, i.e. 0.65 mg C (g dry weight)$^{-1}$ h^{-1} for the epiphytes divided by 0.88 mg C (g dry weight)$^{-1}$ h^{-1} for Zostera. The corresponding value for this ratio determined in this study was 0.60.

Production values for Zostera and epiphytic assemblages determined through the coupling of the ^{14}C method and the leaf marking method are comparable to those reported for by other investigators using only the ^{14}C method (Table 43). The only production values for the epiphytic assemblages are those reported by Penhale (1977) and this study. Mean primary production

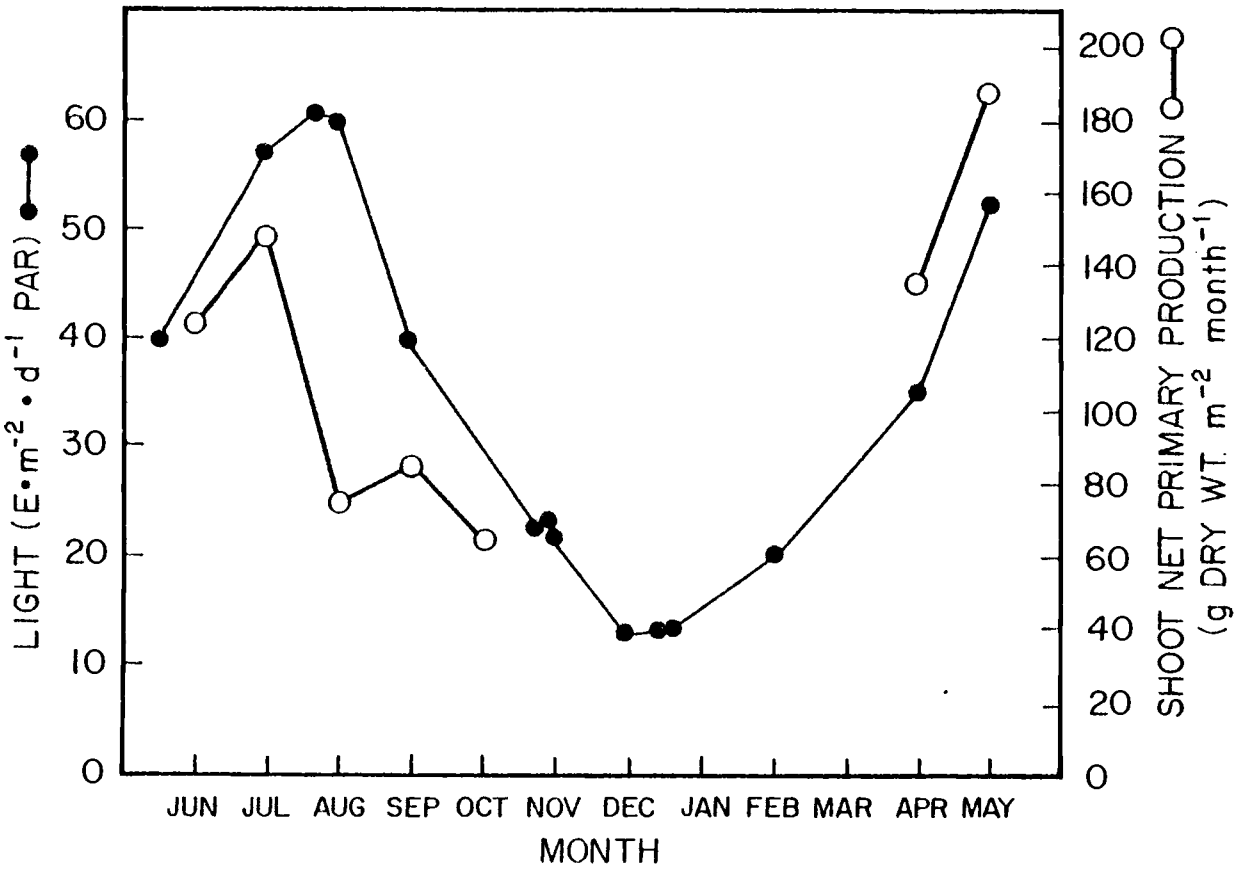


Figure 31. Maximum photosynthetically active radiation (PAR) and mean shoot net primary production for the three transects from June 1980 to May 1981. PAR is expressed as $E \cdot m^{-2} \cdot d^{-1}$. Shoot net primary production is expressed as g dry weight m^{-2} $month^{-1}$. PAR values were adapted from Davis (1982).

Table 43. Comparisons of estimates of the primary production of *Zostera* and associated epiphytic assemblages obtained by the ^{14}C method. Production is expressed as g C m^{-2} day^{-1}.

COMPONENT	LOCALITY	PRODUCTION	REFERENCE
Zostera	North Carolina	1.7	Dillon, 1971
		0.9	Penhale, 1977
	Alaska	11.0	McRoy, 1974
	Oregon	1.0-6.6	This Study
Epiphytes	North Carolina	0.2	Penhale, 1977
	Oregon	0.3-4.9	This Study

of epiphytes in North Carolina is at the lower end of the range reported in this study. The mean biomass of aboveground Zostera and epiphytes reported by Penhale (1977) was 105 g dry weight m^{-2}, while the mean biomass of aboveground Zostera and epiphytes found in this study was 251 g dry weight m^{-2}. In both studies 25% of the biomass was epiphytes. Therefore, the production values reported in this study are higher than those reported by Penhale (1977) because of the greater biomass in Netarts Bay.

It has been postulated that the constant replacement of the leaf biomass on a shoot of seagrass is a control on the development of stands of epiphytes (Sand-Jensen, 1977; Ott, 1980). Until this work, no study of seagrasses has monitored the biomass of the epiphytic assemblage and related it to the pattern of the loss of leaves from the macrophyte. The ceiling on epiphyte biomass observed along each transect can be explained in terms of the regular loss of a portion of the epiphyte biomass coupled with the sloughing of the epiphyte community from the surface of the leaves as the water flows past. Sharp decreases in epiphyte biomass measured on June 1 and August 24, 1980 were related to the sloughing of particular groups of leaves. When a transition in the growth pattern of Zostera occurred there was a greater loss of leaf biomass than usual and a decrease in epiphyte biomass was noted. Since new leaves are continually being produced on a shoot, the epiphyte biomass that is lost is also continuously replaced as the new tissue is colonized.

Phillips (1972) demonstrated that individual shoots of Zostera grown in culture without epiphytes had a regular pattern of initiation and loss of leaves. Therefore, he hypothesized that the timing of the loss of leaves is inherent to the Zostera plant and is not tied to any critical load of epiphytes. Results of the PCA done in conjunction with this study supported this hypothesis. Epiphyte load was highly correlated with one of the principal components while the other variables considered were correlated with the two other principal components. These principal components represented orthogonal axes. Therefore, epiphyte load may be independent of these variables or may be associated by complex non-linear relationships.

There are few studies in the literature that attempted to partition the changes in the biomass of Zostera as was done in this study. This is primarily because the techniques for measuring belowground production were not developed until recently. Sand-Jensen (1975) and Jacobs (1979) reported annual production of the Zostera beds in their localities partitioned into aboveground, belowground and total Zostera (Table 44). The values for Netarts Bay are higher, although the Zostera biomass for all three areas are similar.

This study has described the biological processes relative to a Zostera marina bed in Netarts Bay at several levels of resolution. These levels of resolution correspond to the hierarchy of subsystems presented in the conceptual model of

Table 44. Mean values of annual net primary production values partioned into aboveground and belowground Zostera.

	PRODUCTION (g dry wt. m^{-2})	PRODUCTION (g C m^{-2})	DURATION OF EXPERIMENT	REFERENCE
Aboveground	1116	389	12 months	Jacobs, 1979
Belowground	492	183		
Total	1608	572		
Aboveground	856	328	Apr.-Oct.	Sand-Jensen, 1975
Belowground	241	87		
Total	1097	415		
Aboveground	1874.7	712.4	Apr.-Oct.	This Study
Belowground	1247.2	474.0		
Total	3121.9	1186.4		

the Sediment Processes subsystem (Figure 2). The autecology and production dynamics of Zostera form a principal part of this thesis. Coupled with information on the Epiphyte Primary Production subsystem, changes in biomass at a higher level of resolution were described -- the Zostera Primary Production subsystem. Mechanisms affecting these changes, in particular, the effects of light and desiccation were suggested.

This study was designed to augment the ongoing work of the EPA relative to physical processes in the estuary. The coupling of these studies was designed to test the hypothesis that nutrient dynamics in Netarts Bay during the growing season (April through October) are closely related to the biological processes associated with the Zostera Primary Production subsystem. The future application of the results of this study will involve the development of a holistic conceptualization of the estuary. Data concerned with detrital and benthic microflora biomass data also were gathered in the course of this study. This information will be integrated with data from the algal net primary production work done by Davis (1982) and the Zostera decomposition work done by EPA (unpublished data), and used to describe the changes in biomass associated with the Algal Primary Production and the Detrital Decomposition subsystems. These two subsystems, can be then coupled with the Zostera Primary Production subsystem described in this work to examine Primary Food Processes, a subsystem at a coarser level of resolution.

In addition to describing the changes in biomass associated with each of these subsystems and their couplings, an understanding

of the dynamics of the physical processes under investigation by the EPA will provide a knowledge of the driving variables that affect these subsystems. This synthesis of biological and physical processes will contribute to the understanding of the fundamental mechanisms regulating processes common to many estuaries.

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