AN ABSTRACT OF THE THESIS OF

Michael William Davis for the degree of Doctor of Philosophy in Botany and Plant Pathology presented on October 6, 1981

Title: Production dynamics of sediment-associated algae in two Oregon estuaries

Abstract approved by: Signature redacted for privacy.

Dr. C. David McIntire

Sediment-associated gross primary production, oxygen uptake, microalgal biomass expressed as chlorophyll *a* concentration, macroalgal biomass and total organic matter concentration expressed as ash-free dry weight were measured monthly at medium sand, fine sand and coarse silt sites between 0.5 m and 2.0 m above MLLW during an entire year at Netarts Bay, Oregon. Maximum biomass of microalgae occurred during the spring in medium and fine sand and during the fall and winter in coarse silt. Maximum biomass of macroalgae, primarily *Enteromorpha* and *Ulva*, was found during the summer in medium and fine sand. Factors controlling microalgal production dynamics were: daylength, temperature, water currents, sediment moisture and stability, animals and macrophyte cover. Apparently nutrients did not limit microalgal growth. Daylength and temperature appeared to control the initiation and cessation of macroalgal growth. Macroalgae were excluded from silt sites, probably because of relatively high turbidity which caused low available light intensity.

In Netarts Bay estimated annual net primary production of

microalgae was 13 g $C \cdot m^{-2}$ in medium sand, 17 g $C \cdot m^{-2}$ in fine sand and 5 g $C \cdot m^{-2}$ in coarse silt; Enteromorpha contributed 2700 g $C \cdot m^{-2}$ in medium and fine sand even though its growing season was only 60 days, during the summer. The concentration of organic matter and the rate of community oxygen uptake were maximum during the summer.

Laboratory studies of intact sediment communities, isolated epipelic diatoms and macroalgae from Yaquina Bay, Oregon indicated that photosynthesis was light-saturated at 200 to 400 $\mu E \cdot m^{-2} \cdot sec^{-1}$. Gross primary production per unit chlorophyll a (mg C·mg chl $a^{-1} \cdot h^{-1}$) was lowest for intact sediment communities (0.1 to 1.7), followed by isolated epipelic diatoms (2.3 to 6.9) and macroalgae (4.4 to 9.4). Mean algal respiration per hour for isolated epipelic diatoms and macroalgae was 34% and 15%, respectively, of hourly gross primary production. Microalgal biomass expressed as ash-free dry weight, was estimated from chlorophyll a concentration (mg chl $a \cdot m^{-2}$) with an expression determined in the laboratory using isolated epipelic diatoms (microalgal biomass = 167 x chlorophyll a concentration). Field and laboratory studies indicated that removal of infauna, primarily tanaids, allowed the increase of sediment-associated microalgal biomass and production. Grazing of microalgae appeared to be a mechanism for limitation of microalgal growth.

Production Dynamics of Sediment-Associated Algae in Two Oregon Estuaries

by

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

PRODUCTION DYNAMICS OF SEDIMENT-ASSOCIATED ALGAE IN TWO OREGON ESTUARIES

I. INTRODUCTION

An estuary is a coastal body of water connecting the ocean to freshwater sources from land and within which seawater is measureably diluted by freshwater (Pritchard, 1967). Estuaries are physical, chemical and biological mixing zones. Organisms from marine and freshwater sources interact in estuarine habitats while tidal action and, in some cases, freshwater discharge, provide the physical mixing energy.

Estuaries are typically surrounded by intertidal sediment flats and wave benches (banks) formed by marsh or swamp wetlands coincident with high-water levels. A great diversity of fish and invertibrate animals use the unique substrates available in estuaries for breeding. Moreover, estuaries are a concentration zone of nutrients and a refuge where juvenile animals can mature. For these reasons estuaries are studied and modelled in an effort to evaluate the effects of destroying estuarine habitats and to suggest actions toward mitigating effects of human activity. The relative importance of specific habitats and processes must be determined and incorporated into a holistic perspective of estuarine ecosystems.

Estuarine ecosystems, like all other ecosystems, are organized and maintained by food webs. To understand changes in these webs, we must define the food web components and their relationships. In estuarine sediment habitats, food for macroconsumers is derived both from allochthonous detritus and *in situ* primary and secondary production. Forms of estuarine sediment-associated algae include diatoms as non-motile attached forms (epipsammon) and motile free-living forms (epipelon), other microscopic taxa such as flagellates and blue-green algae, and macroalgae (e.g., species of *Enteromorpha*, *Gracilaria* and *Ulva*). Sediment-associated algal primary production may be an important component of estuarine food webs. Vascular plants such as seagrasses, emergent marsh plants and swamp trees also can contribute organic matter to benthic food webs. Detrital inputs are derived from estuarine, terrestrial and oceanic sources of dead organic matter and its associated bacteria and fungi.

The general objective of this research was to determine mechanisms that control production dynamics of estuarine sediment-associated algae. Two Oregon estuaries, Netarts Bay and Yaquina Bay, were chosen as field sites for intensive study. Previous research on the physical and chemical characteristics of Netarts Bay (EPA, 1979) and Yaquina Bay (see Morgan and Holton, 1977) provided background information about the dynamics of the physical environment. Therefore, the investigation of biological processes was made within the context of known physical patterns in the bays. Ranges of physical, chemical and biological conditions were investigated intensively during an entire year in the field and in the laboratory using intact sediment cores and samples of macroalgae. The results of this research are presented within the framework of a conceptual process model of Oregon estuaries, the structure of which is consistent with FLEX, a general ecosystem model paradigm developed by W.S. Overton (1972, 1975) and based on the general systems theory of Klir (1969).

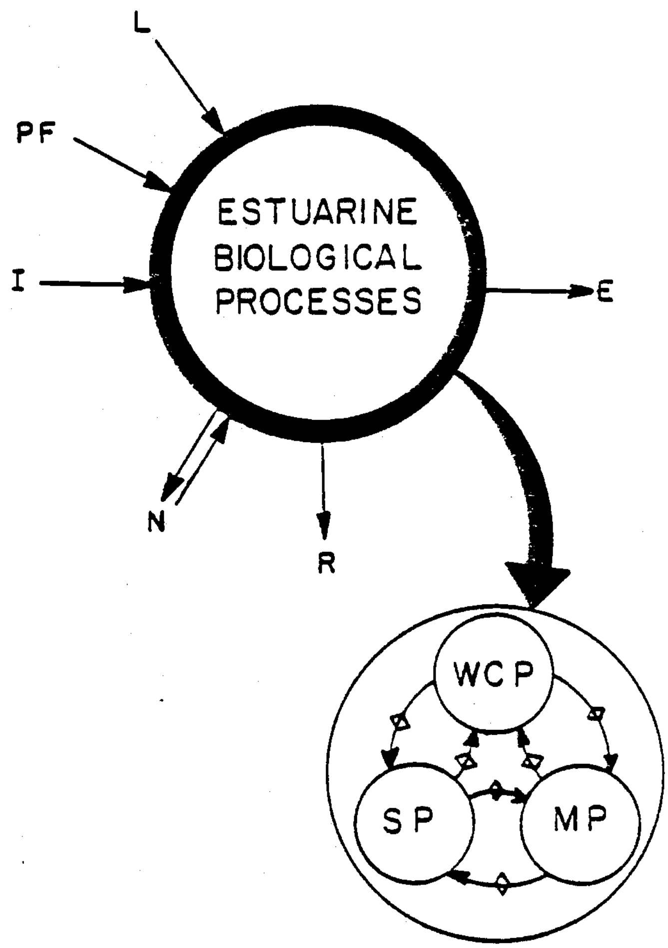
Conceptual Framework

An ecosystem can be conceptualized as a hierarchical system of biological processes, while physical processes are considered as driving functions and control variables. McIntire and Colby (1978) defined a process as a series of actions relevant to the dynamics of a system as it is conceptualized. Any process can be partitioned into coupled subprocesses by identification of relevant coupling variables. At each level of resolution, the details of the process in question may be elaborated as variables, interaction functions and parameters. In this manner a target system may be identified for intensive study within the coupling structure of the whole ecosystem of which it is a part.

McIntire and Colby (1978), Colby and McIntire (1978) and McIntire (in press) have presented a formal development of the process concept in ecosystem research. The process convention ignores taxonomic position and uses energy flow criteria. The process concept is related to the functional group approach of Cummins (1974) and McIntire *et al.* (1975) in which the functional activities are defined in terms of groups of similar acting species. Process dynamics can be examined relative to the capacity to process. Capacity has quantitative (biomass) and qualitative (taxonomic) aspects which are a function of biomass and other properties of the ecosystem that change with community composition.

A conceptual process model of Oregon estuaries is shown in Figures 1 and 2. This framework was used to isolate the target subsystem relevant to the general research goal, i.e. the investigation of mechanisms that control production dynamics of estuarine sediment-associated algae. Such a structure identifies levels of resolution appropriate to the goal and allows the goal-oriented research to be integrated into an emerging holistic view of the entire estuarine ecosystem.

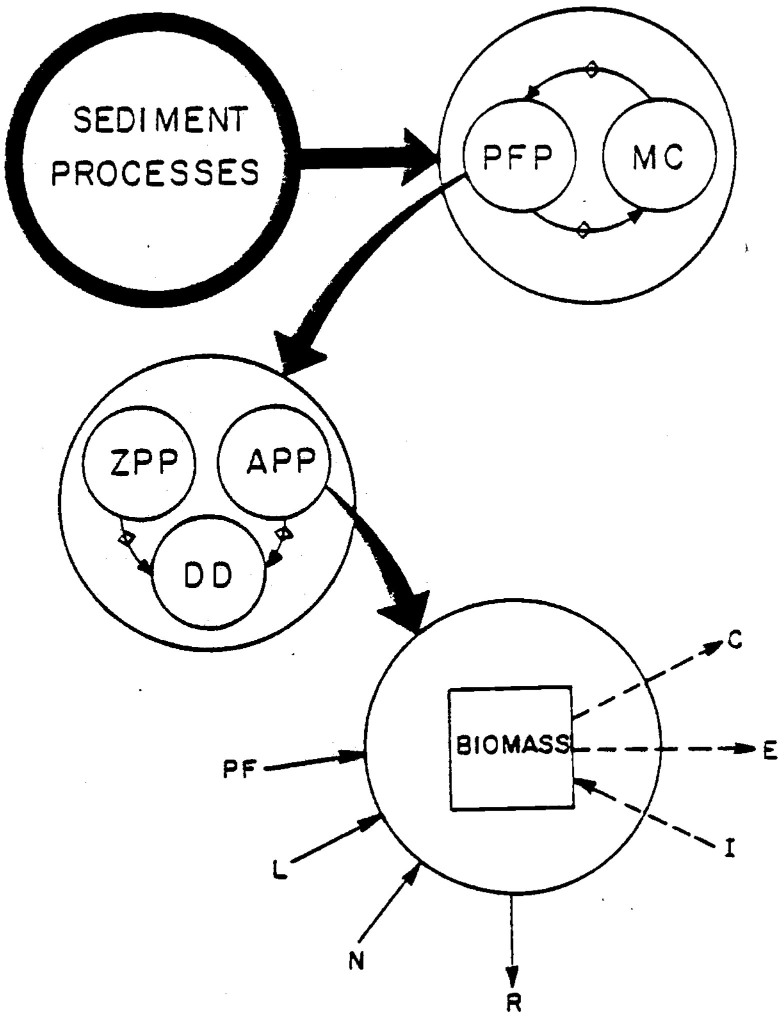
Estuarine Biological Processes can be considered holistically in terms of inputs and outputs relative to the entire ecosystem (Figure 1). Or alternatively, the ecosystem can be conceptualized mechanistically as a system of three coupled subsystems which can be uncoupled and each investigated holistically and mechanistically. Estuarine Biological Processes can be partitioned into Water Column Processes (WCP), Marsh Processes (MP) and Sediment Processes (SP). SP and MP exchange organic matter with WCP and with each other. This set of estuarine biological processes is compatible with Netarts Bay and Yaquina Bay, the intensive study areas for this research. Examples of other habitats and processes are estuaries in tropical parts of the world which have large areas of mangrove habitat, and fjords which have extensive rock surfaces.



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.



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

PFP = PRIMARY FOOD PROCESSES
MC = MACROCONSUMPTION
DD = DETRITAL DECOMPOSITION
ZPP = ZOSTERA PRIMARY PRODUCTION
APP = ALGAL PRIMARY PRODUCTION

Figure 2. Conceptual model of estuarine sediment biological processes.

Sediment Processes (Figure 2) can be partitioned into two coupled subsystems: Primary Food Processes (PFP) and Macroconsumer Processes (MC). PFP and MC can be considered holistically in terms of inputs and outputs relative to these subsystems. MC includes all secondary production processes by animals, i.e. suspension feeding, deposit feeding and predation. PFP is further partitioned into three coupled subsystems: Zostera Primary Production (ZPP), Algal Primary Production (APP) and Detrital Decomposition (DD). ZPP includes both host and epiphyte production dynamics. DD includes organic matter and associated bacteria and fungi. The target subsystem of this study is designated as APP, Algal Primary Production. For the purpose of research, APP can be examined relative to the algal biomass, a state variable, and some of its associated variables: light, nutrients, other physical factors and respiration. Import, export and animal consumption affect biomass and taxonomic composition of APP directly, and are indicated in Figure 2 by dotted lines connected to the state variable.

Elaboration of the details of APP defined the priorities of this research. Seasonal and yearly patterns of algal biomass and gross primary production were monitored at the intensive study sites, while the regulation of APP by physical and chemical factors were examined under controlled conditions in the laboratory. In particular the laboratory work investigated the relationship between light intensity and the rate of primary production, the rates of algal respiration, the relationship between the concentration of chlorophyll _a_ concentration and algal biomass and some effects of animal activity on the APP subsystem. This information, along with estimates of imports and exports, provided a scientific basis for understanding state variable and process dynamics observed at the field sites.

This research was organized into three sections. Chapter 2 presents the results of intensive monitoring in Netarts Bay of monthly patterns of sediment-associated algal biomass, gross primary production, community organic matter concentration, community oxygen uptake and associated physical variables. Chapter 3 presents the results of laboratory investigations of intact sediment communities, isolated epipelic diatoms and macroalgae. Chapter 4 presents the results of studies in the field and laboratory which were designed to investigate possible effects of animals on sediment-associated microalgal biomass and primary production.

Relevant Literature

Literature related to estuarine research is voluminous. This short review is restricted to representative references directly relevant to the research goal of defining mechanisms that control the production dynamics of sediment-associated algae.

Research in Oregon estuaries of general interest is listed in "A Bibliography of Estuarine Research in Oregon" (Morgan and Holton, 1977). The research is indexed geographically, giving information on specific estuaries. Other sources of information on Oregon estuaries are found in general references by Percy et al., (1974), Stout (1976) and Kreag (1979).

The microphytobenthos of intertidal estuarine sediments consists predominately of benthic diatoms. Round (1971) and more recently McIntire and Moore (1977) have reviewed literature on various aspects of benthic diatom ecology and physiology, reflecting recent interest in the relations of these organisms with their biotic and abiotic environment. Annual rates of primary production by microalgae in estuarine sediment flats generally range between 20 and 200 g $C \cdot m^{-2} \cdot y^{-1}$ (Steele and Baird, 1968; Grontved, 1960; Pomeroy, 1959; Cadée and Hegeman, 1974; Pamatmat, 1968). Pigments have been found to be concentrated in the upper few millimeters of sediment, but living cells are often found to a depth of 10 cm or more (Taylor and Gebelein, 1966; Riznyk and Phinney, 1972). Vertical distribution of microalgae is related to the degree of sediment mixing by scouring and animal activity and the vertical movements of epipelic diatoms (Harper, 1977). Taylor (1964) and Haardt and Nielsen (1980) have shown that penetration of photosynthetically active radiation in sediments is dependent on type of sediment and wavelength of light. Depths of 1% of surface light intensity for sand and silt ranged from 2.40 to 0.38 mm, respectively. Admiraal (1977a) found that net photosynthesis of cultured benthic diatoms was optimal at 16° to 25°C and a light intensity of 2.5 to 5.0 $E \cdot m^{-2} \cdot day^{-1}$.

Admiraal and Peletier (1979a) found that several species of benthic diatoms were tolerant of chemical ion concentrations typical of anoxic sediments, and concluded that benthic diatom species have differing tolerances to sulphide. Benthic diatoms also have capacity for heterotrophic growth and survival in prolonged darkness and anaerobiosis (Admiraal and Peletier, 1979b; Hellebust and Lewin, 1977). Furthermore, occurrence of benthic diatoms in reduced sediments was strongly related to their tolerance of these conditions in culture. Admiraal (1977b) also found wide tolerance by benthic diatoms of high concentrations of ammonia, nitrite, nitrate and orthophosphate, all of which are periodically present in estuarine sediments in large amounts.

The importance of control of benthic microalgae by nutrients is variable. Experiments have shown that nutrient additions to intact estuarine sediments may or may not create increased microalgal biomass and/or production. For example, studies done in northwestern Atlantic saltmarshes indicated that edaphic algae are nutrient-limited at certain times of the year (Darley _et al._, 1981; Van Raalte _et al._, 1976; Sullivan and Daiber, 1975). However, saltmarsh angiosperms probably strongly affect the availability of nutrients and light in these habitats (Estrada _et al._, 1974). A recent study in Yaquina Bay, Oregon indicated that edaphic algae apparently were not nutrient-limited (Cardon, 1981). Mudflats which do not have large populations of angiosperms probably have sufficient nutrients for benthic algal growth (Welsh, 1980).

Studies of the effect of herbivores on estuarine microphytobenthos are almost completely lacking, although herbivores are known to affect many other types of aquatic plant assemblages (Brook, 1955; Castenholz, 1961; McIntire and Phinney, 1965; Hargrave, 1969; Paine, 1971; Lubchenco, 1978). Gut contents of infauna in a northwestern Atlantic estuarine mudflat showed that relatively small species ate microalgae and ciliates, while large species ate smaller animals and associated food particles (Sanders _et al_., 1962). The occurrence of the mud snail _Nassarius_ on a northwestern Atlantic mudflat caused a decrease in abundance of other sediment-associated animals, probably the result of competition for algal food and space (Mills, 1967). Pace _et al_. (1979) quantified the effect of _Nassarius_ upon the microphytobenthos, indicating that natural densities of _Nassarius_ reduced microalgal biomass and production. Similar studies with _Bembicium_, a tropical estuarine mud snail, demonstrated the same results (Branch and Branch, 1980). Therefore, grazing by herbivores in or on estuarine sediments probably has a significant limiting effect on microalgal biomass and production dynamics.

Various studies have determined that large changes in salinity are tolerated by benthic diatoms in culture. This tolerance was affected only slightly by the salinity of preculture medium and by prolonged cultivation under controlled conditions of constant salinity (Williams, 1964; Admiraal, 1977c). Estuarine diatoms are probably of limited value as indicators of salinity (Drum and Webber, 1966). In the Yaquina River estuary, Oregon, dominant species of benthic diatoms exhibited overlapping distributions along a salinity gradient with an abrupt change in species composition at a salinity of 5 °/oo (Amspoker and McIntire, 1978).

In Oregon estuaries, species of Enteromorpha, Ulva, Lola, Gracilaria, Vaucheria and Polysiphonia are the dominant macroalgae associated with the sediment flats. Macroalgae typically have a high biomass (50 to 500 g $C \cdot m^{-2}$) and rate of net primary production (500 to 3000 g $C \cdot m^{-2} \cdot y^{-1}$) on sediment flats (Conover, 1958; Fitzgerald, 1978; Zedler, 1980). These algae also form part of the drift community which often exists in the estuarine water column (Cowper, 1978). Drift algae absorb nutrients which are exported from high marshes and redistribute these nutrients to sediment flats and other marsh areas (Welsh, 1980).

Physical factors strongly influence the primary production and biomass of sediment-associated macroalgae, and substrate type influences colonization patterns (Conover, 1958; Edwards and Kapraun, 1973). Macroalgal distribution in estuaries of the northeastern Atlantic was related to stability of sediments and was negatively correlated with silt content of the sediments (Nienhuis, 1970). In the Fraser River estuary, interaction between substrate stability and salinity controlled patterns of macroalgal biomass and production (Pomeroy and Stockner, 1976). A more stable environment with lower sedimentation and higher salinity resulted in greater algal species diversity, biomass and primary production.

Nutrient concentration also influences macroalgal growth, suggesting that pollution sources of enrichment enhance total primary production and biomass. This type of link between organic pollution and _Ulva_ growth was found by Sawyer (1966) in Boston harbor. As in the case of microalgae, sediments probably supply adequate nutrients for the growth of macroalgae (Cadée and Hegeman, 1974). Therefore, exclusion of macroalgae from estuarine sediment habitats by nutrient limitation is not probable (DeBoer _et al._, 1978).

The impact of grazing on sediment-associated macroalgae is not known, and grazing is not readily observed in these populations. However, birds have been shown to consume algae and seagrasses as a large proportion of their diet (Wolff _et al._, 1976; Charman, 1979). Woodin (1977) observed the capture and consumption of _Ulva_ and _Enteromorpha_ by nereid polychaetes, suggesting that this activity increased available food supply and regulated salinity and temperature stress in the sediment by shading the area where the algae were held. The growth response of _Ulva_ to organic pollution suggests that algae like _Ulva_ and _Enteromorpha_ can escape herbivore-induced control of biomass and primary production by growing larger than their potential consumers. Macroalgae associated with sediments are probably not controlled by herbivores except in early sporeling stages of development when they are part of the microphytobenthos.

II. PRODUCTION DYNAMICS OF SEDIMENT-ASSOCIATED ALGAE IN NETARTS BAY, OREGON

Introduction

Studies of algal production dynamics in Oregon estuaries have been limited, but some early studies included production measurements made in the laboratory using intertidal sediment (Riznyk and Phinney, 1972), artificial substrates (McIntire and Wulff, 1969) or macroalgae (Kjeldsen and Phinney, 1971). Results reported here, together with a recent study in the Columbia River estuary (McIntire and Amspoker, in preparation), are the first measurements of algal production associated with intact sediment communities in Oregon estuaries.

The purpose of this research was to describe seasonal patterns of algal production dynamics and associated physical and biological variables in Netarts Bay. This research, in addition to laboratory studies (Chapters 3, 4), was used to generate hypotheses concerning the quantitative importance of sediment-associated algal production and mechanisms which control this production in Oregon estuaries. Because this research examines processes that occur in many estuaries, the understanding of these processes in Netarts Bay is relevant to problems that extend beyond the geographical limits of this particular estuary.

Study Site

Netarts Bay (45°25'N; 123°55'W) is Oregon's sixth largest estuary with a surface area of 941 hectares of which 612 hectares is tide land (Figure 3). The subtidal area is 329 hectares, restricted to a narrow central channel that connects to the Pacific Ocean. Erosion of soft sedimentary rock (Astoria Formation) between basaltic headlands of Cape Meares and Cape Lookout during the late Tertiary Period formed the basin for Netarts Bay. Only 36.3 km^2 of watershed drains into Netarts Bay. The basin of the bay is characterized by mudflats which grade into sandy, wave-exposed beaches at the mouth. The sandspit separating the bay from the Pacific Ocean is a remnant of dunes eroded by an increase in sea-level after the last period of glaciation.

The bay is subjected to mixed, semi-diurnal tides, and maximum tidal range is 3.0 m. Mean low water (MLW) and mean high water (MHW) are 0.5 m and 2.0 m above mean lower low water (MLLW), respectively. Freshwater input occurs primarily in the winter from three small creeks. Salinity in the estuary remains high, usually greater than 25 °/oo. Dye studies by the Environmental Protection Agency (EPA, 1979) indicated that limited mixing occurs between ocean water and bay water during each tidal cycle. At low tide, water retained in the channel (bay water) is the same water that was over the sediment flats at high tide. Flooding ocean water displaces the bay water onto the sediment flats, and mixing occurs primarily in the channel.

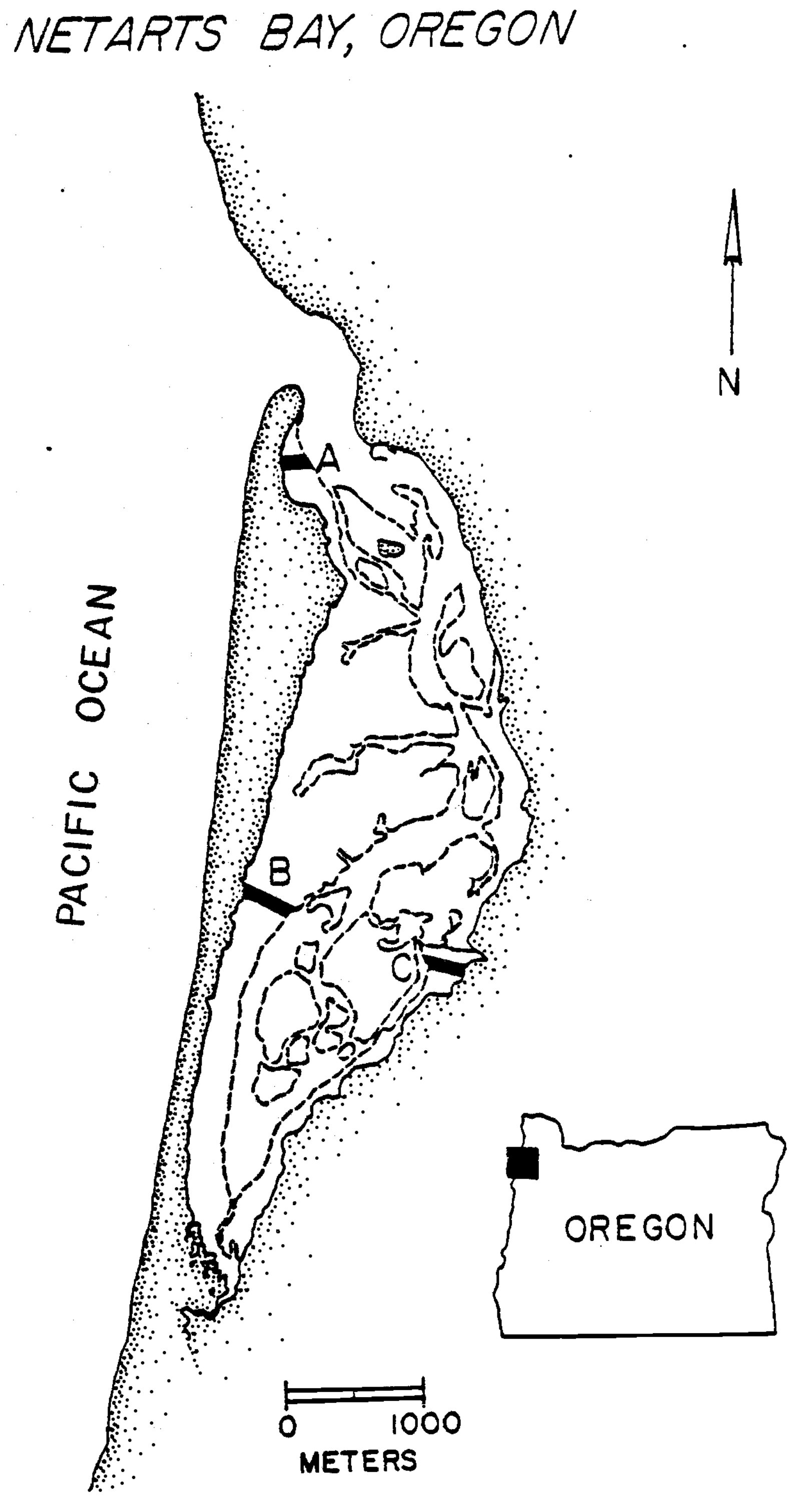


Figure 3. Map of Netarts Bay, showing intensive sampling sites: SAND site (A), FINE SAND site (B) and SILT site (C).

During the period of an entire year, water temperature over the sediment flats usually ranges from 4°C to 25°C, and the air temperature over exposed sediment flats ranges from 0°C to 30°C. Daylight hours of active photosynthesis vary from 12.2 h in June to 6 h in December.

Sampling Strategy

Research priorities of this study were defined according to a conceptual process model of Oregon estuaries (see Chapter 1, Figures 1 and 2). This model identified the process of sediment-associated algal production within the coupling structure of the entire estuary.

The field aspect of this research involved the investigation of seasonal changes in algal biomass and patterns in primary production in Netarts Bay. Relevant biological variables included microalgal biomass expressed as the chlorophyll *a* concentration in the sediment, the concentration of organic matter in the sediment expressed as ash-free dry weight, and the rates of gross primary production and community oxygen uptake as measured in light and dark chambers. The sampling strategy was consistent with the known dynamics of physical and chemical processes in Netarts Bay (EPA, 1979). This information provided a unique opportunity to design a sampling strategy compatible with known physical patterns in the bay prior to the investigation of biological variables.

A suitable sampling strategy was chosen from two alternatives: (1) a broad survey involving the collection of non-replicated samples from as many locations as possible over the entire year; or (2) frequent replicated sampling at relatively few intensive study sites. The first approach provides insight about the largest possible spatial area but not about local variation in space and time. If the intensive study sites are representative of large areas of the estuary, the second approach can provide more insight into process mechanisms than the first approach, particularly if concurrent measurements of physical variables are obtained together with the biological data. Data obtained during this study were generated from a sampling program based on the second approach. Replicated samples were obtained at monthly intervals from three intensive study sites. Since the objective of this research was to describe seasonal patterns of algal production dynamics, sampling at intensive study sites was considered appropriate.

Netarts Bay was surveyed to identify potential sites for intensive study which were representative of large areas of the bay. Three sites were identified on the basis of sediment type and location in the bay (Figure 3). The site at the mouth of the bay was characterized by medium sand (SAND site), the site along the western shore of the bay had fine sand (FINE SAND site) and the site along the eastern shore had coarse silt (SILT site). All sites were exposed to moderate wave action. Macroalgae were absent from the SILT site, and blue-green algae occurred at the MHW level at the FINE SAND and SILT sites.

At each intensive study site, 50-m horizontal transects were marked with wooden stakes. The transects were located at 0.5, 1.0, 1.5, and 2.0 m above MLLW at each site. The sampling strategy at each site involved the monthly collection of sediment cores for the measurement of primary production and the analysis of chlorophyll _a_ and organic matter concentrations. Cores were obtained randomly along each transect between March, 1980 and March, 1981: three for measurement of primary production, six for analysis of chlorophyll _a_ concentration and three for analysis of organic matter concentration. Cores for the measurement of primary production were incubated _in situ_ and subsampled after incubation for the measurement of chlorophyll _a_ concentration in the top cm of sediment. Cores for the measurement of chlorophyll _a_ concentration and organic matter content were subsampled in the laboratory to obtain estimates of concentrations in the top cm of sediment and at a depth of 4.0 to 5.0 cm from the surface.

Monthly measurements of physical variables also were made at the transects of all three intensive study sites. These variables included temperature, salinity, light intensity of photosynthetically active radiation and change in sediment height.

Methods

1. Primary Production

Gross primary production and community oxygen uptake were estimated in the field from oxygen measurements in stirred, light and dark chambers designed to hold intact cores of sediment. Between

May and September, *in situ* measurements were made in plexiglas chambers which were 92 cm in height, had an internal diameter of 12.8 cm and enclosed a sediment surface area of 128.61 cm^2 (Figure 4). Two light chambers and one dark chamber were used to estimate primary production. Each chamber was carefully inserted 30 cm into the sediment, filled with 5.7 l of seawater from the bay and sealed. Water in the chamber was circulated by a magnetic stirrer with a motor speed of 27 rpm. Rates of oxygen evolution and uptake were based on measurement periods of 4.0 to 7.5 hours between initial and final readings. Measurements of dissolved oxygen were made polarographically with an Orbisphere® salinity-corrected dissolved oxygen system, by inserting the oxygen probe into a port at the side of the chamber.

Between October and March, estimates of primary production were made in plexiglas chambers which were 14.2 cm in height, had an internal diameter of 6.8 cm and enclosed a sediment surface area of 36.32 cm^2 (Figure 5). Three replicate chambers were carefully inserted 5 cm into the sediment, withdrawn with intact sediment cores and plugged with rubber bungs. Each chamber was filled with 300 ml of seawater from the bay, sealed and placed in a water bath. Water in the chambers was circulated by a magnetic stirrer with a motor speed of 300 rpm. Rates of oxygen evolution and uptake were based on measurement periods of 0.5 to 1.0 hour between initial and final readings. Readings were made by replacing the stirrer on top of the chamber with an oxygen probe. Rates of net community production or oxygen uptake were measured when the chambers were exposed to full

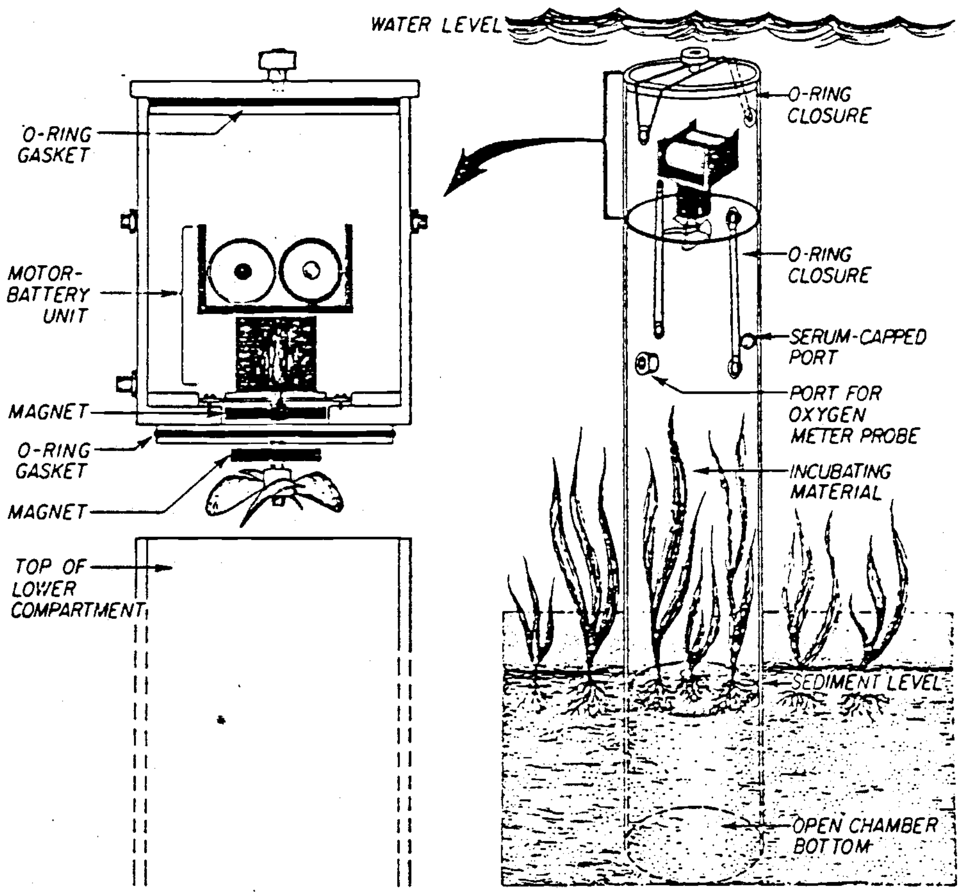


Figure 4. Diagram of a plexiglas chamber for measuring oxygen metabolism of intact sediment cores, <u>in situ</u>. See text for dimensions.

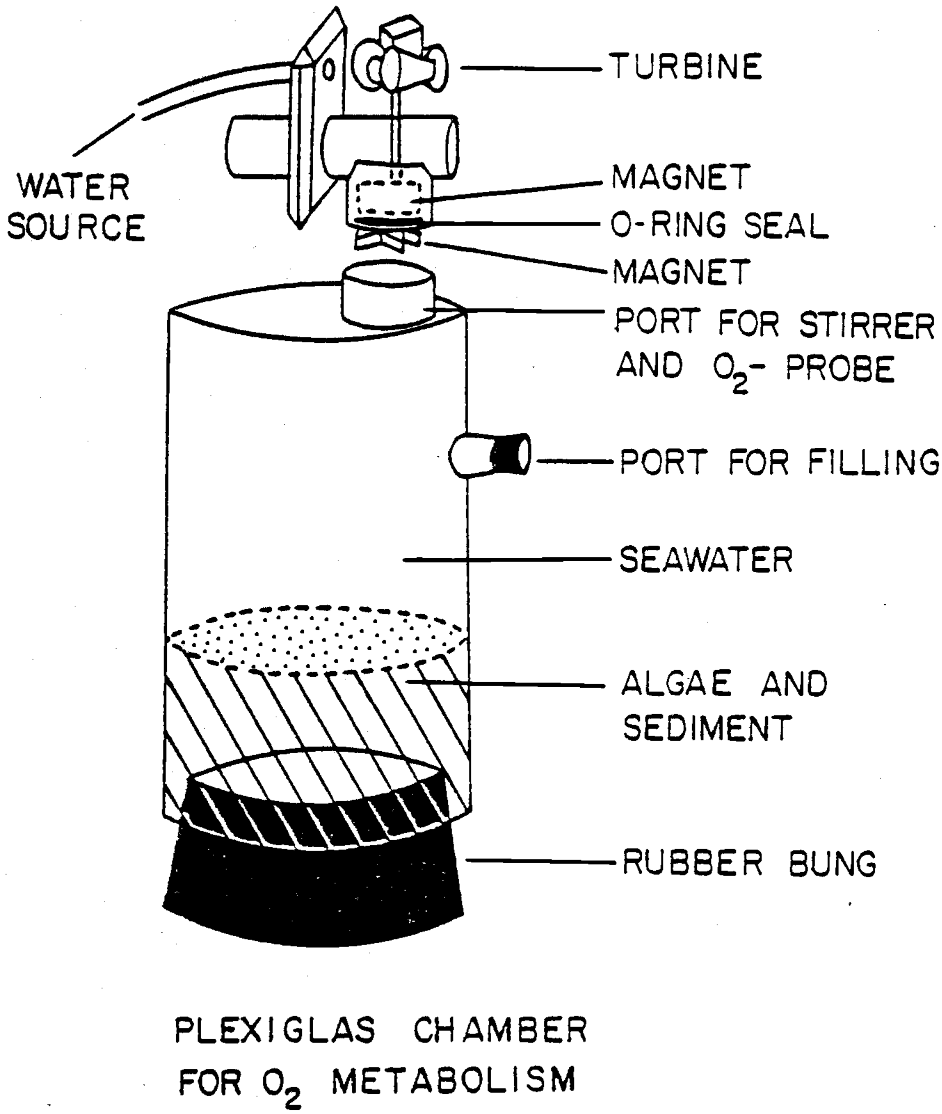


Figure 5. Diagram of a plexiglas chamber for measuring oxygen metabolism of intact sediment cores. See text for dimensions.

sunlight or darkened by covering the water bath with black plastic, respectively.

Simultanious incubations of intact sediment in both types of chambers indicated that chamber type had no significant effect on the rate of primary production. All production rates were corrected for seawater-associated oxygen production in the light and oxygen uptake in the dark using the light and dark BOD bottle method for measuring plankton metabolism (Strickland and Parsons, 1972). Plankton metabolism was negligible except during August.

Gross primary production was estimated by adding the rate of community oxygen uptake in the dark to the rate of net community production in the light for an equivalent period of time. Estimated rates of gross primary production expressed as mg $O_2 \cdot m^{-2} \cdot h^{-1}$ were converted to mg $C \cdot m^{-2} \cdot h^{-1}$ while assuming a photosynthetic quotient of 1.2 (i.e., mg C = 0.312 x mg O_2). Estimated rates of community oxygen uptake expressed as mg $O_2 \cdot m^{-2} \cdot h^{-1}$ were converted to mg $C \cdot m^{-2} \cdot h^{-1}$ while assuming a respiratory quotient of 1.0 (i.e., mg C = 0.375 x mg O_2)(Westlake, 1965).

2. Biomass

Samples for chlorophyll a analysis were collected using a 12-cm long plastic corer of 2.3 cm diameter. The corers were gently pressed about 10 cm into the sediment and carefully removed. The corers were capped, frozen and transported back to the laboratory.

In the laboratory the frozen sediment was extruded from the corers and sections from the top cm and 4 to 5 cm from the surface were excised with a knife. A core section was placed in a mortar with 0.5 ml of saturated magnesium carbonate solution and 10 ml of 90% acetone (v/v). The slurry was ground with a pestle for one minute, poured into a screw-capped test tube and kept in the dark at 4°C for 24 hours. The extract was centrifuged, and chlorophyll a concentration was measured using the method of Strickland and Parsons (1972). The Lorenzen equation (corrected for pheopigments) was used to calculate mg chlorophyll $a \cdot m^{-2}$. These values are uncorrected for chlorophyllide (Whitney and Darley, 1979).

Macroalgal biomass was sampled by harvesting six replicate 0.25 m^2 quadrats randomly along a 50-m transect. Samples were rinsed in freshwater, weighed, dried at 70°C for 48 hours and reweighed. Dried samples were ashed at 450°C for 24 hours and reweighed to determine weight of organic matter. Chlorophyll a concentration in the macroalgae was determined as described above, using approximately 1.0 g wet weight of algae per sample.

3. Sediment Properties

Sediment was sampled for organic matter content using the same coring devise described above for the chlorophyll a samples. Samples were collected, frozen and transported back to the laboratory. In the laboratory the frozen sediment was extruded from the corers and sections from the top cm and 4 to 5 cm from the surface were excised with a knife. Core sections were dried at 70°C for 48 hours and weighed. These sections were then ashed at 450°C for 24 hours and reweighed. A correction for loss of sediment water of hydration after ashing was determined by adding distilled water to the ashed sediment, and drying at 90°C for 24 hours and reweighing.

Bimonthly samples of sediment from the top cm of sediment were taken for grain size analysis (Buchanan and Kain, 1971). Sediment was wet-sieved with a 63 μm mesh sieve. The coarse fraction was dried at 70°C for 24 hours and then sieved through a set of graded sieves to determine fraction weights above 63 μm. Fractions below 63 μm were determined using a pipette analysis. Values were expressed in phi-units where $\Phi = \log_2$ grain size in mm. Sediment statistics included mean grain size, sorting coefficient and skewness (Inman, 1952). The sorting coefficient expresses the uniformity of grain size, i.e., the better sorted sediments exhibit the less uniform distribution of size classes. Skewness measures the degree of symmetry in the grain size distribution, with positive values indicating skewness to the smaller grain size and negative values indicating skewness to the larger grain size.

4. Physical and Chemical Variables

Light intensity was measured in $\mu E \cdot m^{-2} \cdot sec^{-1}$ photosynthetically active radiation with a Licor® quantum meter. Bimetal or thermistor probes were used to measure temperature. Salinity was measured using a temperature-compensated AO Goldberg® refractometer. Samples for analysis of nitrite-nitrate (NO_2-NO_3), ammonia (NH_4), orthophosphate (PO_4) and molybdate-reactive silica (SiO_3) were taken July, August and September from water in the metabolic chambers, before and after incubation *in situ*. Nutrient samples were analyzed by methods for autoanalysis of nutrients (Strickland and Parsons, 1972).

5. Data Analysis

A three-way analysis of variance (ANOVA) was performed with sediment type, tidal height and time as main effects; the three-way interaction mean square was used as the error term in calculating F-values. All statistical analyses were performed with a Control Data Corporation Cyber 70 computer at the Oregon State University Computing Center using the SPSS system (Nie *et al.*, 1975) and the REGRESS subsystem of SIPS (Rowe and Brenne, 1981).

Results

1. Physical Properties

Sediment characteristics were determined for the intensive study sites (SAND, FINE SAND and SILT; see Figure 3), from March, 1980 to March, 1981 in Netarts Bay. Mean grain sizes in phi-units (Φ) were

2.28 at the SAND site, 2.66 at the FINE SAND site and 3.79 at the SILT site (Table 1). Mean values for the sorting coefficient were 0.34 (well-sorted) at the SAND site, 0.64 at the FINE SAND site and 1.13 (poorly-sorted) at the SILT site; while mean skewness was 0.25 at the SAND site, 0.10 at the FINE SAND site and -0.04 at the SILT site (Table 1). In summary, the sediment at the SAND site was medium to fine sand, well-sorted, with the most positive skew; the sediment at the FINE SAND site was fine to very fine sand, with medium sorting and a positive skew; and the sediment at the SILT site was very fine sand to coarse silt, poorly sorted and the least positive skew.

Monthly change in sediment height was measured at the three intensive study sites from April to October (Figure 6). There was little net change in sediment height, except at the SAND site at 1.0 m above MLLW and at the FINE SAND site at 2.0 m and 0.5 m above MLLW. Monthly changes in sediment level usually ranged from 0 cm to 3 cm and could easily explain burial of surface chlorophyll a and organic matter. The SILT site appeared to be the most stable site with respect to change in sediment level.

Temperatures of the air, exposed sediment and water were usually greater than 10°C (Figure 7). Air, exposed sediment and water temperature ranges were from 0°C to 24°C, from 2°C to 19°C and from 8°C to 18°C, respectively.

Photosynthetically active radiation ranged from 0.5 to 60 $E \cdot m^{-2} \cdot day^{-1}$ and was chiefly influenced by daylength and cloud cover (Figure 8). Extinction coefficients were calculated from light intensity

Table 1. Results of sediment grain size analysis for samples obtained every two months from March, 1980 to March, 1981 at intensive study sites. Tidal level is above MLLW: 0.5 m (1), 1.0 m (2), 1.5 m (3) and 2.0 m (4). Mean grain size (Mean) is in phi-units, sorting (Sort) and skewness (Skew) are dimensionless. Statistics were calculated according to Inman (1953). Values are annual means of n replicates ± one standard error.

Site	Level	n	Mean	Sort	Skew
SAND	All	23	2.28±0.03	0.34±0.03	0.25±0.43
	1	5	2.28±0.10	0.31±0.10	1.25±1.25
	2	6	2.27±0.03	0.36±0.04	0.47±1.20
	3	6	2.22±0.05	0.33±0.03	-0.54±0.50
	4	6	2.34±0.03	0.35±0.02	0.00±0.01
FINE SAND	All	21	2.66±0.10	0.64±0.06	0.10±0.65
	1	3	3.04±0.35	0.70±0.25	-0.05±0.22
	2	6	2.64±0.14	0.61±0.17	0.15±0.11
	3	6	2.52±0.25	0.64±0.14	0.06±0.07
	4	6	2.64±0.13	0.65±0.11	0.17±0.08
SILT	All	23	3.79 ±0.11	1.13±0.06	-0.04±0.17
	1	5	4.03±0.09	1.24±0.08	0.10±0.03
	2	6	3.95±0.13	1.00±0.11	-0.54±0.61
	3	6	3.78±0.34	1.08±0.16	0.01±0.08
	4	6	3.44±0.19	1.20±0.12	0.29±0.07

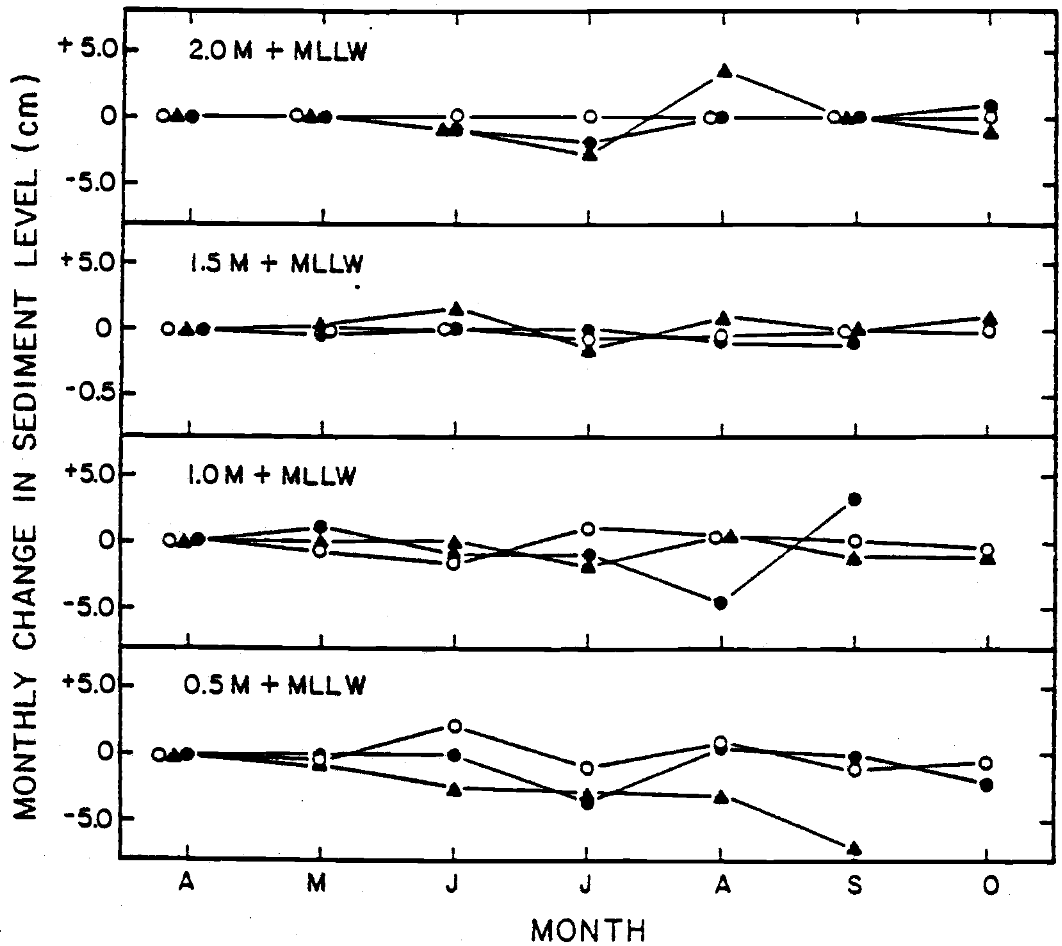


Figure 6. Monthly changes in sediment height at the intensive study sites in Netarts Bay. Sites include SAND (●), FINE SAND (▲) and SILT (○).

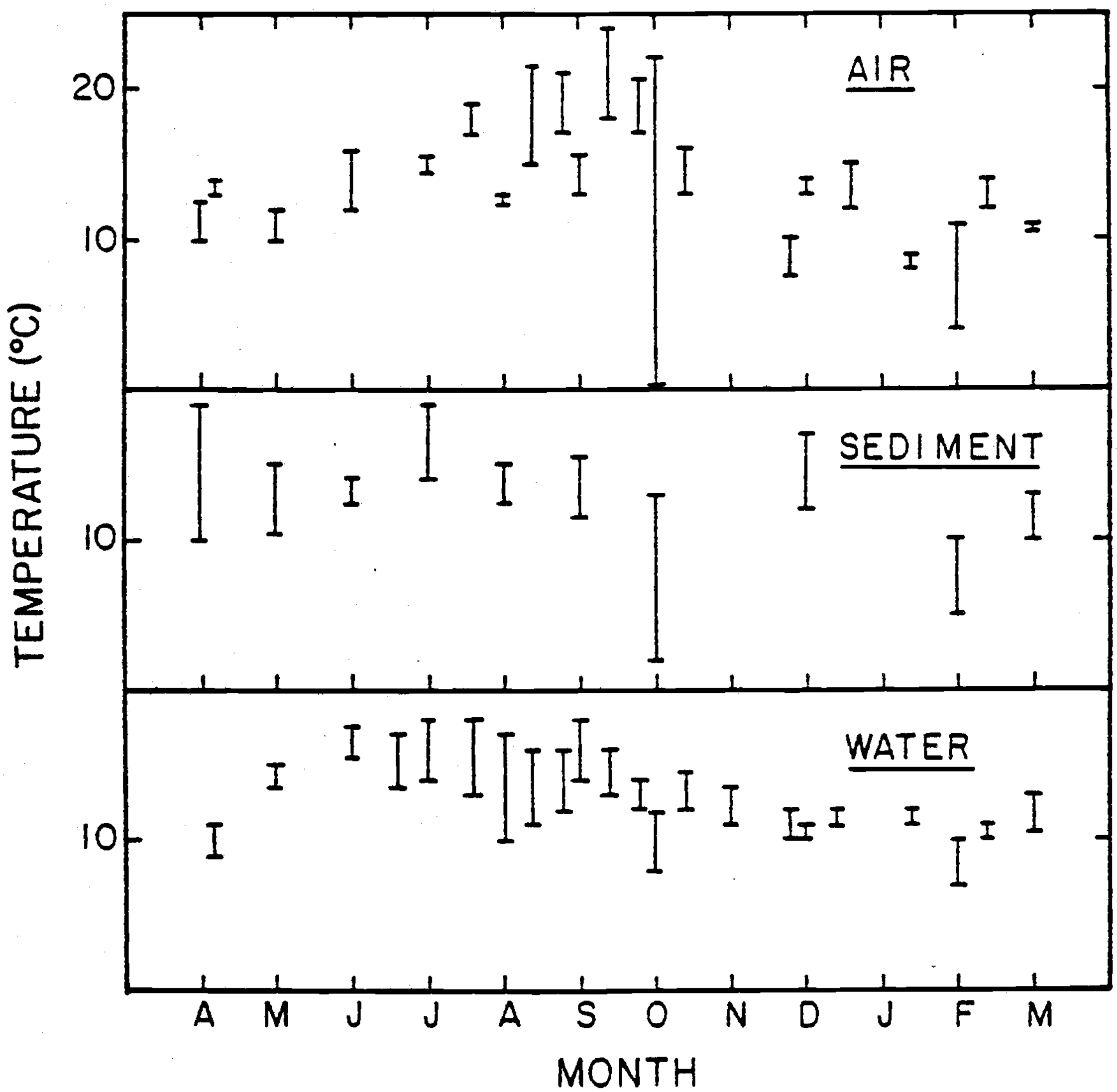


Figure 7. Temperature of air, sediment and water during the period from April, 1980 to March, 1981 in Netarts Bay. Bars indicate daily range of temperature at all intensive study sites on the days sampled.

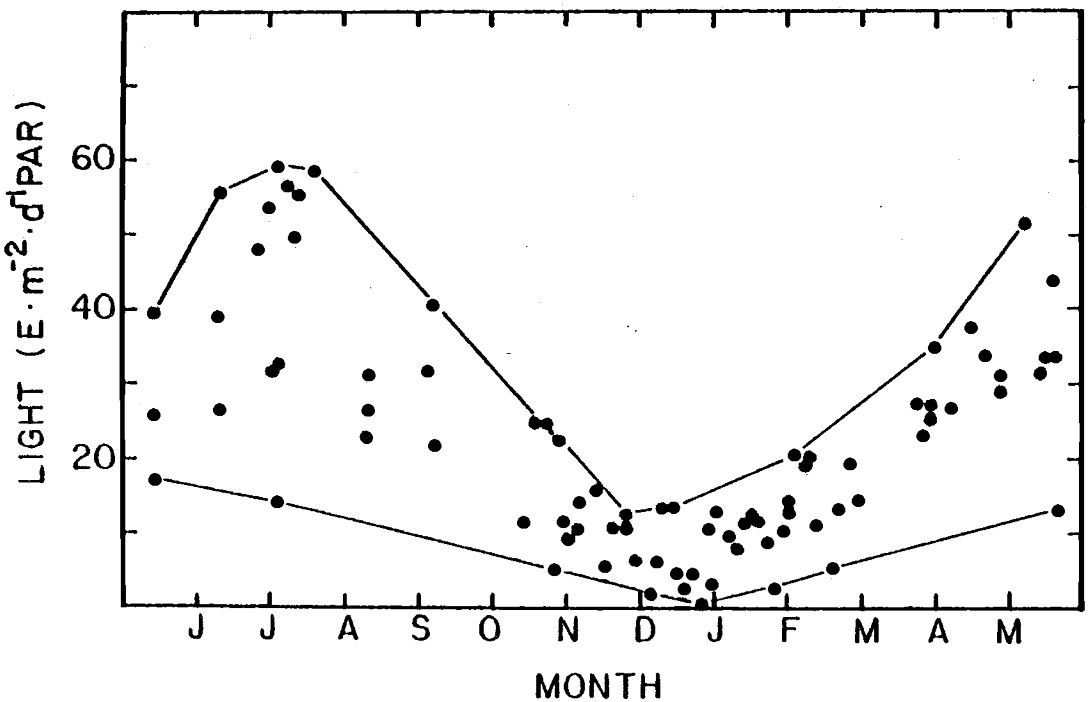


Figure 8. Photosynthetically active radiation ($E \cdot m^{-2} \cdot d^{-1}$) for the period from May, 1980 to May, 1981 at Netarts Bay.

measurements taken at high tide at all three intensive study sites (Table 2). These coefficients ranged from 0.400 to 0.870 and were generally lower at the SAND and FINE SAND sites as compared to the SILT site.

The effect of water depth on light available at the sediment surface is shown in Figure 9. <u>In situ</u> measurements were made of surface light intensity, water depth and extinction coefficients in Netarts Bay for a day in July and a day in September. The light intensity at the sediment surface was calculated for each hour between 8:00 and 4:00 PST, at three tidal elevations, by substituting the appropriate light intensity, water depth and extinction coefficients into the expression: $I_z = I_0/e^{-\eta z}$; where I_z is the light intensity at depth z, I_0 is the light intensity at the surface and η is the extinction coefficient. A clear, sunny day occurred in July, while in September, the sun only appeared between 11:00 and 12:30 PST. Light intensity was adequate for photosynthesis during the entire day in July, but during September the light intensity often fell below light-saturation of photosynthesis which is approximately 1 $E \cdot m^{-2} \cdot h^{-1}$.

Light transmission through the sediment at all three of the intensive study sites was determined by measuring light transmission through 1 mm thicknesses of sediment in a petri dish (Haardt and Nielsen, 1980). Reduction of photosynthetically active radiation to 1.0% of surface light intensity was reached at 2.55 mm at the SAND site, 2.00 mm at the FINE SAND site and 1.30 mm at the SILT site.

Table 2. Extinction coefficients $(\eta)^a$, measured at high tide at the SAND, FINE SAND and SILT intensive study sites. Light intensity at the surface and 1.0 m depth is photosynthetically active radiation ($\mu E \cdot m^{-2} \cdot s^{-1}$). High tide was between 11:00 and 13:00 PST.

Site	Date	Light Intensity Surface	Light Intensity 1.0 m Depth	η
SAND	13 May	1375	737	0.624
	11 June	1250	670	0.624
	11 July	1350	804	0.518
	10 August	1000	509	0.675
	7 Sept.	1500	804	0.624
FINE SAND	12 May	570	281	0.707
	10 June	2100	1206	0.555
	10 July	1800	1206	0.400
	9 August	820	496	0.503
	6 Sept.	1500	804	0.624
SILT	11 May	615	295	0.735
	9 June	800	335	0.870
	9 July	460	241	0.646
	8 August	870	375	0.842
	5 Sept.	680	375	0.595

a) $\eta_z = \ln I_o - \ln I_z$; where I_o = surface light intensity and I_z = light intensity at 1.0 m depth

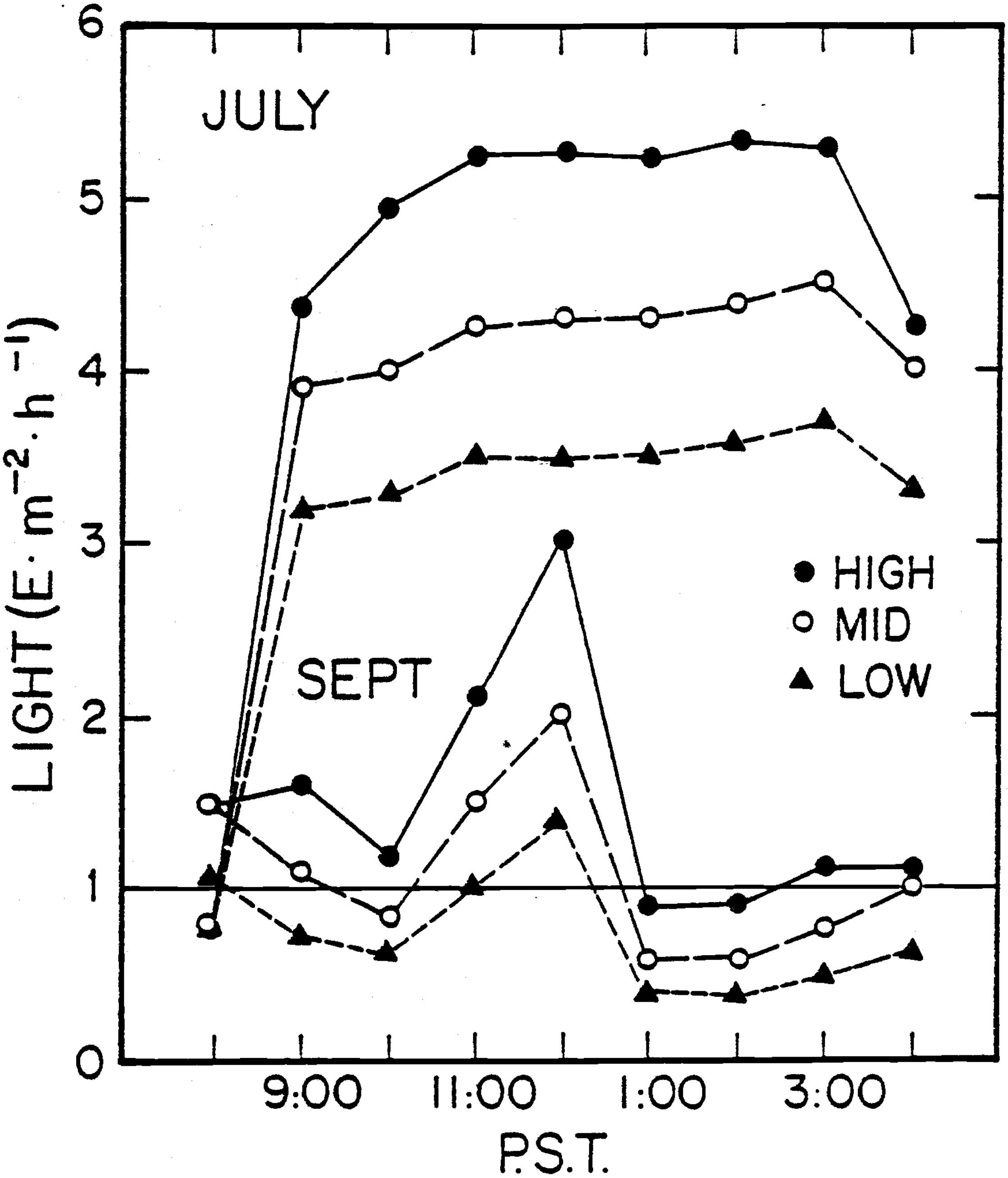


Figure 9. The effect of water depth on light available to sediment-associated algae in Netarts Bay for a day in July and a day in September at intertidal heights: HIGH (1.5 m above MLLW), MID (1.0 m above MLLW) and LOW (0.5 m above MLLW). High tide was at noon (2.0 m above MLLW). Values were calculated using measured water levels, extinction coefficients and *in situ* surface light intensities. The line at 1.0 E·m^{-2}·h^{-1} approximates light saturation by algal photosynthesis.

Salinity in the water column of Netarts Bay ranged from 28 to 34 °/oo. Values for interstitial water usually varied between 25 and 35 °/oo. However, interstitial water at 2.0 m above MLLW in all sediment types reached values as low as 5 °/oo during rainstorms or periods of terrestrial runoff from groundwater seepage.

During July, August and September, nutrients (NO_2-NO_3, NH_4, PO_4 and SiO_3) were sampled from water in the metabolic chambers before and after in situ incubation (Table 3). The only changes in nutrient concentrations in the light and dark chambers were noted when Enteromorpha prolifera (Setch.) S.&G. was present in the chambers. These were changes in NO_2-NO_3 during July and August at the SAND site. Concentrations fell from 3.23 to 1.05 μM N during six hours of incubation in August.

2. Organic Matter

There was a significant positive correlation ($n = 34$, $r^2 = 0.67$; $p < .01$) between sediment mean grain size in phi-units (Φ) and the organic matter concentration (AFDW) in the top cm of sediment. AFDW $= -89.54 + 109.21\ \Phi$. An analysis of variance indicated that there were significant differences ($p < .01$) in organic matter concentration in the top cm of sediment associated with differences in sediment type. The SILT site had the highest mean organic matter concentration followed by the FINE SAND site and the SAND site, respectively (Table 4). There also were significant differences ($p < .01$) in the concen-

Table 3. Initial nutrient concentrations (μM) in metabolic chambers at the SAND, FINE SAND and SILT intensive study sites during sampling in July, August and September.

	July	August	September
NO_2-NO_3			
SAND	3.23	3.23	0.81
FINE SAND	0.16	0.32	0.16
SILT	0.48	0.24	0.16
NH_4			
SAND	0.56	1.11	2.78
FINE SAND	0.56	2.22	2.22
SILT	1.11	1.67	2.22
PO_4			
SAND	0.48	0.48	0.34
FINE SAND	0.39	0.39	0.39
SILT	0.39	0.39	0.39
SiO_3			
SAND	14.46	14.46	10.51
FINE SAND	11.83	11.17	17.09
SILT	13.14	12.49	15.77

Table 4. Concentration of organic matter ($g \cdot m^{-2}$) in the top cm of sediment, expressed as ash-free dry weight at the intensive study sites. Values represent mean concentrations of n replicates $\pm$ one standard error for a period from March, 1980 to March, 1981.

Site	n	$\bar{x} \pm SE$
SILT	43	377.76 $\pm$ 13.93
FINE SAND	38	203.88 $\pm$ 33.07
SAND	43	134.05 $\pm$ 8.56

tration of organic matter associated with the effects of tidal height, time and a two-way interaction between sediment type and tidal height (Figures 10 and 11). Organic matter concentration was highest during the summer. At the SILT and FINE SAND sites, the transects at 2.0 m above MLLW had the highest concentration of organic matter; while at the SAND site, the highest concentrations of organic matter were at 0.5 m above MLLW.

The ratio of organic matter in the top cm of sediment to that at the 4 to 5 cm depth was calculated and used as an index of mixing of organic matter in the sediment. No significant differences related to the effects of sediment type, tidal height, or time were found in the bay sediments relative to this ratio. The mean value of the ratio for all sediment types was 1.50, indicating that in any single sample, organic matter was present at both depths in similar concentrations.

Sediment-associated total organic matter was separated into its component fractions (Table 5). The total represents monthly measurements of organic matter concentration in the top cm of sediment. Microalgal biomass was calculated using a conversion factor between chlorophyll a and organic matter determined in the laboratory throughout the year with epipelic diatoms isolated from the sediment (see Chapter 3). For these calculations, microalgal organic matter concentration = 166.98 x chlorophyll a concentration. Animal organic matter was determined by harvesting in April. The concentration of detritus was calculated by the subtraction of microalgal and animal organic matter from the total. The results of these calculations indicated that

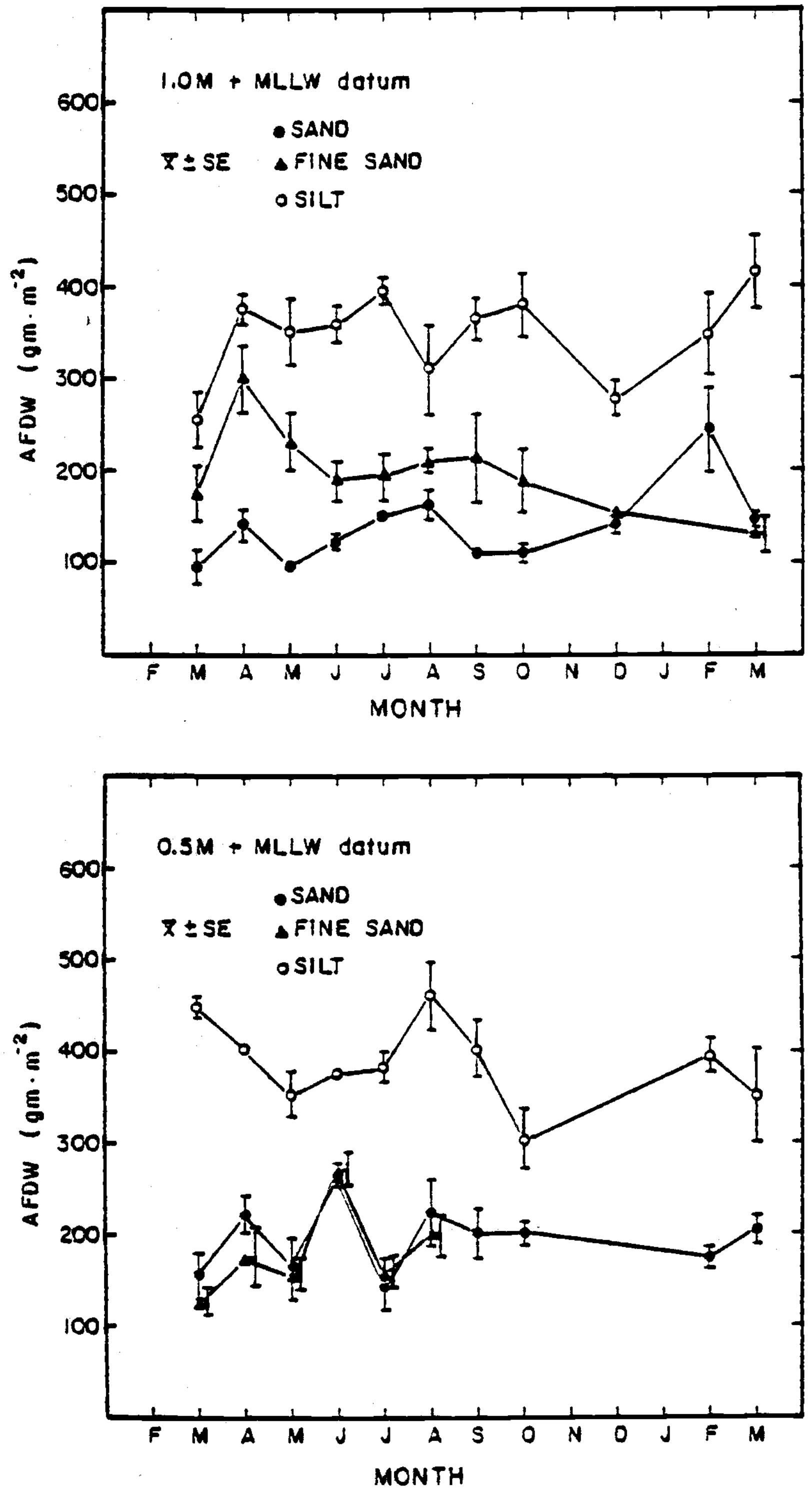


Figure 10. Concentration of organic matter in the top cm of sediment expressed as ash-free dry weight (AFDW) at intensive study sites from March, 1980 to March, 1981. Sites were SAND (●), FINE SAND (▲) and SILT (○) at tidal heights 1.0 m and 0.5 m above MLLW. Values are means of three replicates ± one standard error.

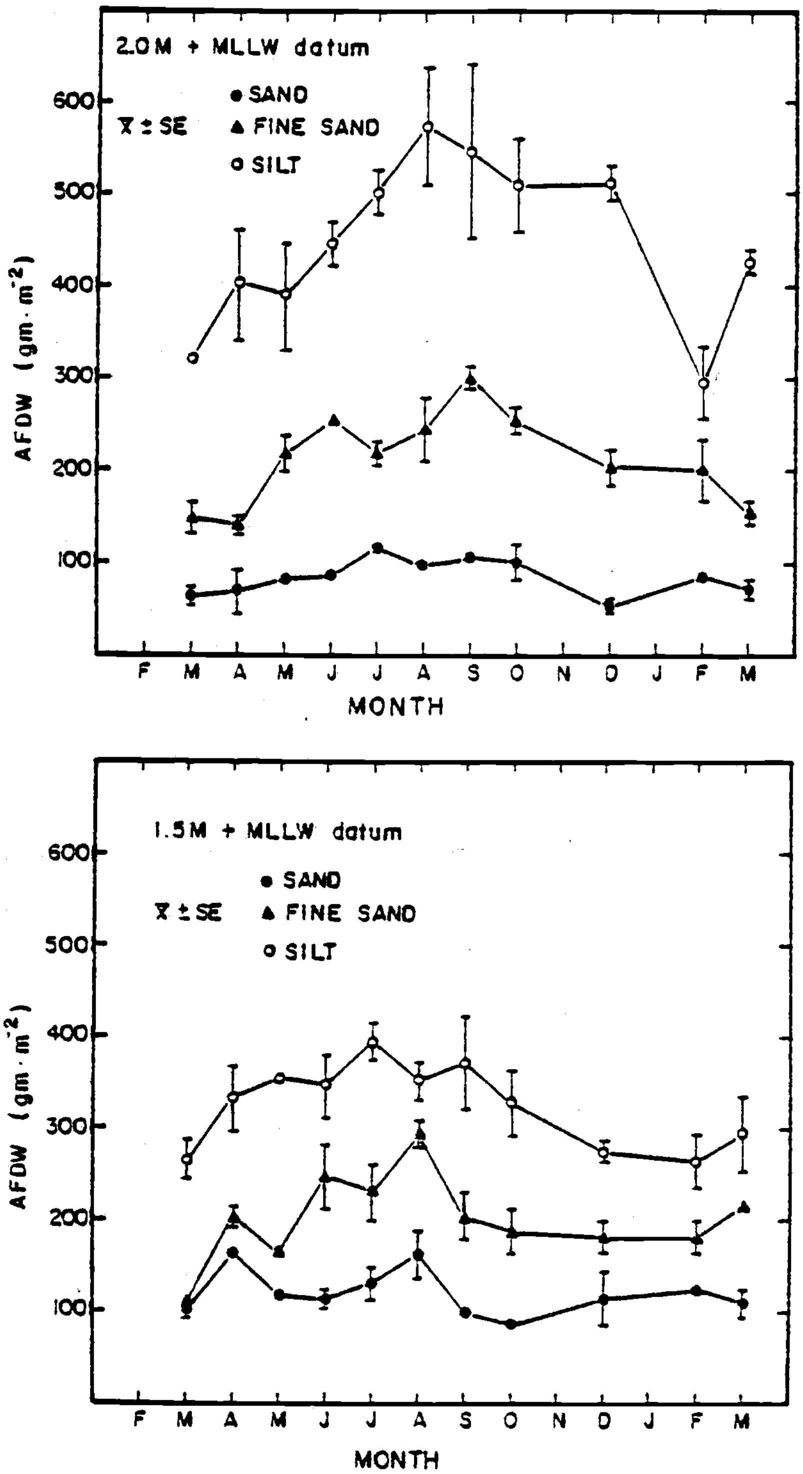


Figure 11. Concentration of organic matter in the top cm of sediment expressed as ash-free dry weight (AFDW) at intensive study sites from March, 1980 to March, 1981. Sites were SAND (●), FINE SAND (▲) and SILT (○) at tidal heights 2.0 m and 1.5 m above MLLW. Values are means of three replicates ± one standard error.

Table 5. Ranges of component fractions of organic matter ($g \cdot m^{-2}$) in the top cm of sediment, expressed as ash-free dry weight at the intensive study sites. Total organic matter and animal organic matter were measured by direct sampling. Microalgal organic matter was calculated from chlorophyll a concentrations[a]. Detrital organic matter was calculated by the subtraction of microalgal and animal organic matter from the total organic matter.

Fraction	Intensive Study Site		
	SAND	FINE SAND	SILT
Total	69.8-268.4	128.0-303.2	256.5-575.0
Microalgae	1.6-23.2	4.3-31.8	4.3-48.0
Animals	1.3-11.8	3.9-8.2	1.1-5.5
Detritus	(66.9-233.4)	(119.8-263.2)	(251.1-521.5)

a) Microalgal organic matter concentration = chlorophyll a concentration x 166.98 (see Chapter 3).

detritus was the major source of organic matter in these sediments.

3. Chlorophyll a Concentrations

An analysis of variance indicated that there were significant differences ($p < .01$) in the chlorophyll a concentration in the top cm of sediment associated with the effect of sediment type. The SILT site had the highest mean chlorophyll a concentration, followed by the FINE SAND site and the SAND site, respectively (Table 6). There were also significant differences ($p < .01$) in chlorophyll a concentration associated with the effects of tidal height, time and a two-way interaction between sediment type and tidal height (Figures 12 and 13). Chlorophyll a concentration were highest during the spring at the SAND and FINE SAND sites, while chlorophyll a concentration was highest during the fall or winter at the SILT site. At the SILT and FINE SAND sites, the 2.0 m transects had the highest concentration of organic matter; while at the SAND site, the highest concentrations of chlorophyll a were found for the transect at 1.0 m above MLLW.

The ratio of chlorophyll a concentration in the top cm of sediment to that at the 4 to 5 cm depth was calculated as an index of mixing of chlorophyll a in the sediment. There were significant differences ($p < .01$) in the chlorophyll a ratios associated with the effects of sediment type, tidal height and a two-way interaction between sediment type and time. The SAND site had the highest mean chlorophyll a ratio followed by the SILT and the FINE SAND sites (Table 7). At all sites

Table 6. Concentration of chlorophyll a ($mg \cdot m^{-2}$) in the top cm of sediment at the intensive study sites. Values represent mean concentrations of n replicates $\pm$ one standard error for a period from March, 1980 to March, 1981.

Site	n	$\bar{x} \pm SE$
SILT	46	93.70 $\pm$ 11.07
FINE SAND	42	74.72 $\pm$ 7.37
SAND	45	46.18 $\pm$ 6.02

Table 7. Ratios of the chlorophyll a concentration in the top cm of sediment to the concentration at 4 to 5 cm depth at the intensive study sites. Values represent mean ratios of n replicates $\pm$ one standard error for a period from March, 1980 to March, 1981.

Site	n	$\bar{x} \pm SE$
SAND	45	41.73 $\pm$ 13.49
SILT	46	11.50 $\pm$ 17.35
FINE SAND	42	9.31 $\pm$ 13.86

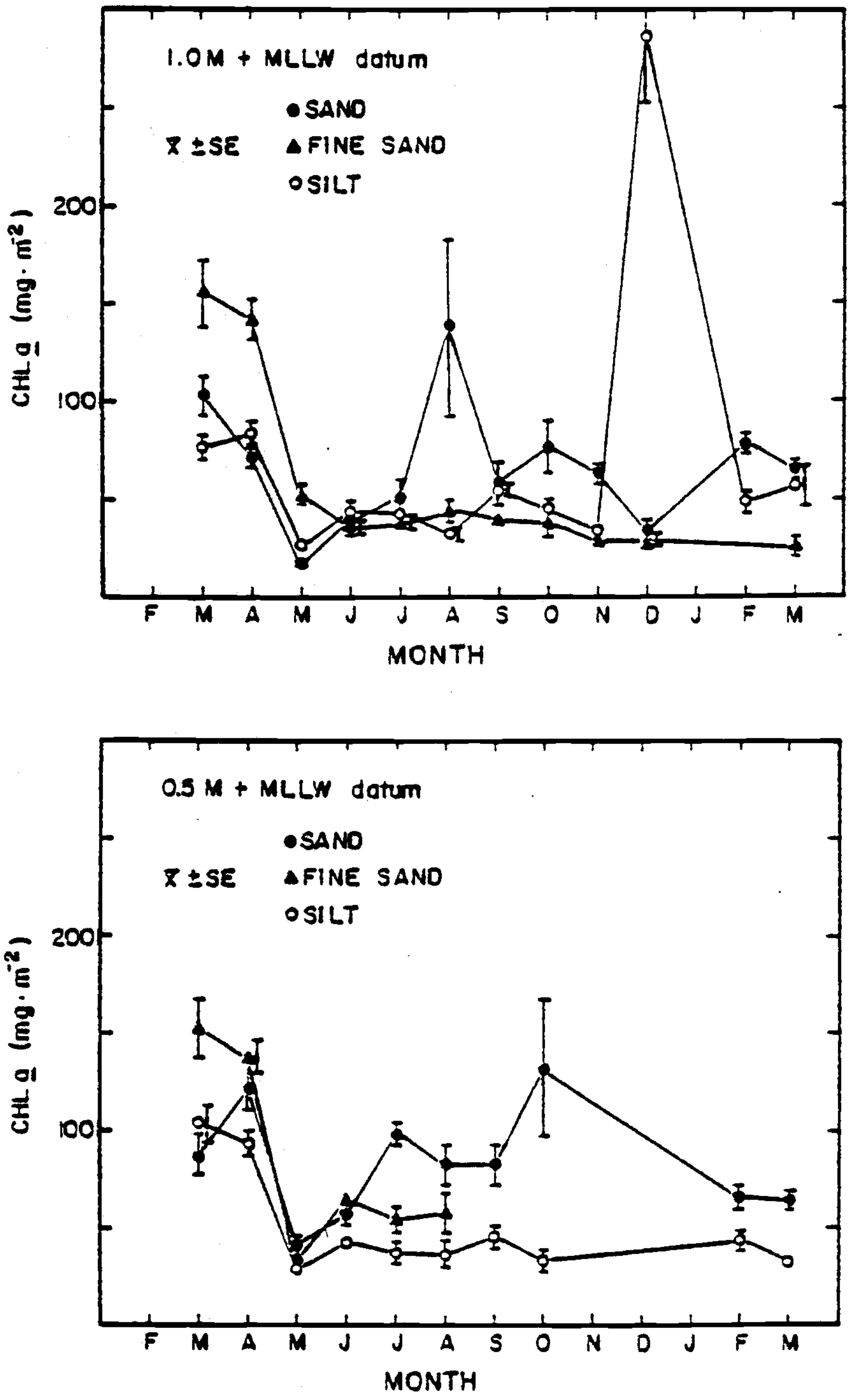


Figure 12. Concentration of chlorophyll a in the top cm of sediment (CHL a) at intensive study sites from March, 1980 to March, 1981. Sites were SAND (●), FINE SAND (▲) and SILT (○) at tidal heights 1.0 m and 0.5 m above MLLW. Values are means of six replicates ± one standard error.

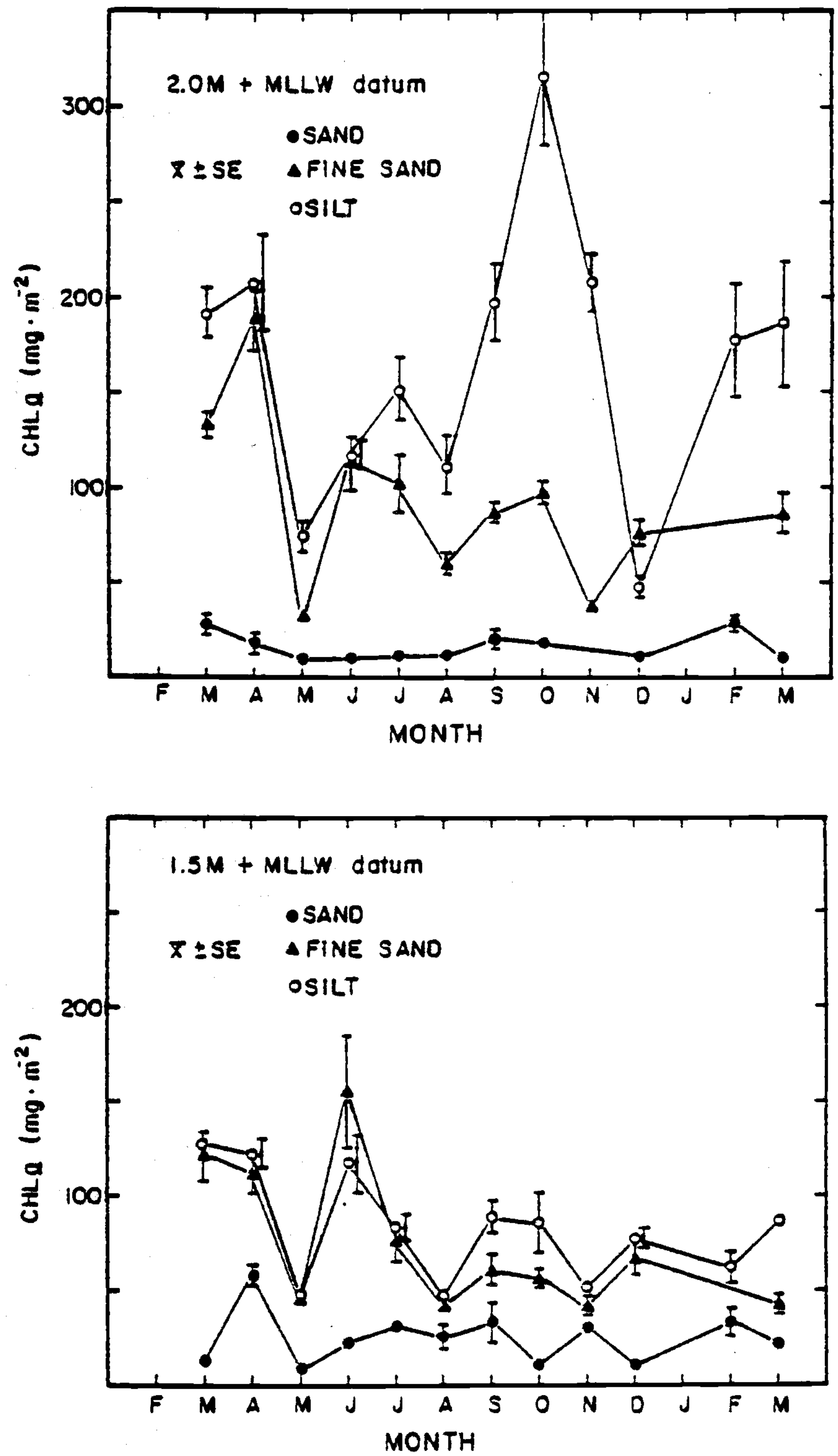


Figure 13. Concentration of chlorophyll a in the top cm of sediment (CHL a) at intensive study sites from March, 1980 to March, 1981. Sites were SAND (●), FINE SAND (▲) and SILT (○) at tidal heights 2.0 m and 1.5 m above MLLW. Values are means of six replicates ± one standard error.

the mean ratio was higher at the 2.0 m above MLLW transects than at the other intertidal transects. At 2.0 m above MLLW the SAND, FINE SAND and SILT sites had mean ratios of 102.53, 27.27 and 38.77 respectively. Lower tidal heights at all sites had mean chlorophyll a ratios of approximately 2 to 3. High chlorophyll a ratios indicated a paucity of chlorophyll a in the 4 to 5 cm depth sediment, while relatively low values showed that chlorophyll a was mixed to the 4 to 5 cm depth.

4. Primary Production

An analysis of variance indicated that there were significant differences ($p < .05$) in gross primary production associated with the effect of time. Maximum gross primary production occurred in the summer when Enteromorpha prolifera was abundant in the sediment community (Figures 14 and 15). The contribution of Enteromorpha to the mean rate of gross primary production during the study is shown in Table 8. When Enteromorpha production was included in the calculations, the FINE SAND site had the highest mean rate of gross primary production followed by the SAND site and the SILT site. Without Enteromorpha all sediment types had similar mean rates of gross primary production. Enteromorpha was never present at the SILT site.

There were significant differences ($p < .01$) in community oxygen uptake associated with the effect of sediment type. The FINE SAND site had the highest mean rate of community oxygen uptake followed by the

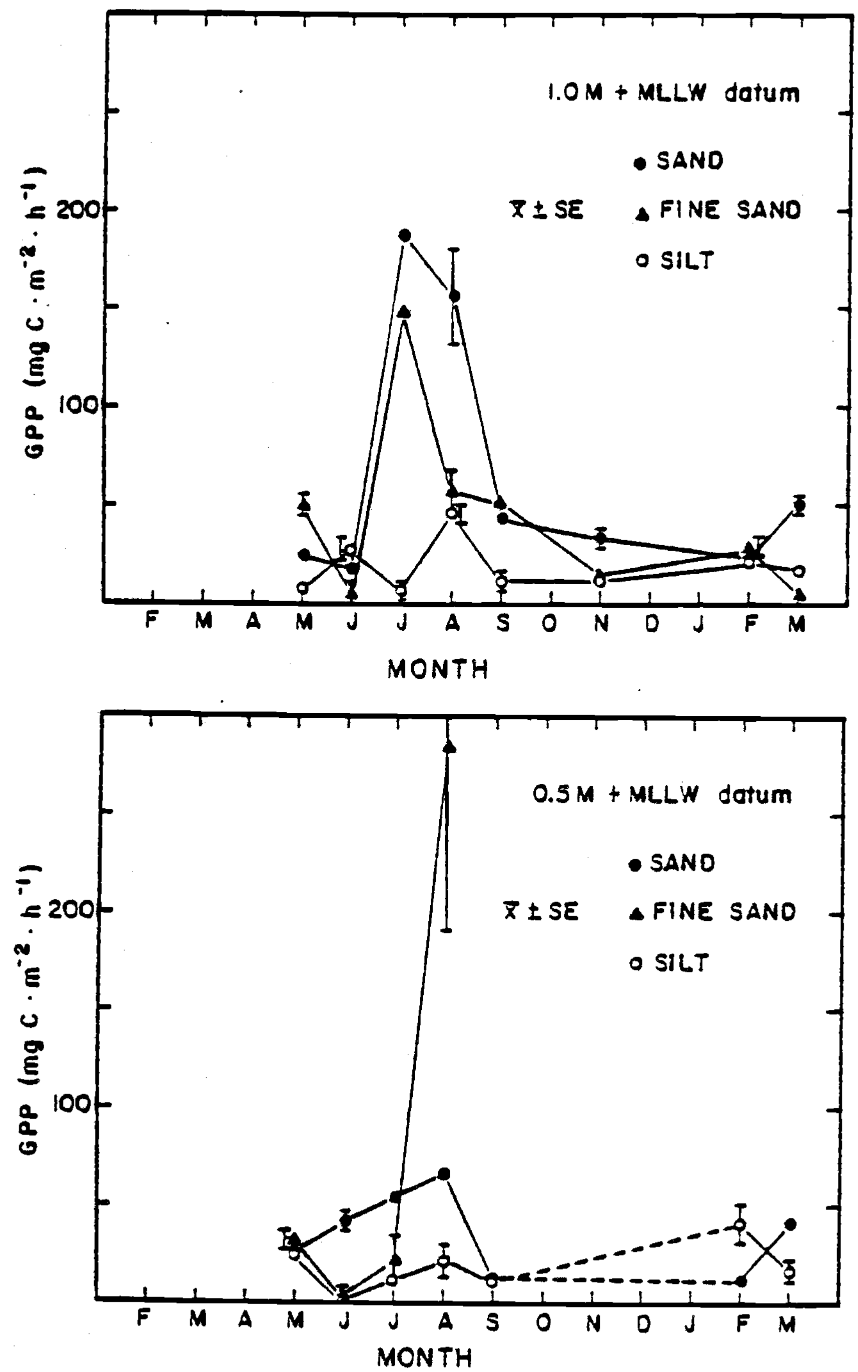


Figure 14. Gross primary production (GPP) at intensive study sites from May, 1980 to March, 1981. Sites were SAND (●), FINE SAND (▲) and SILT (○) at tidal heights 1.0 m and 0.5 m above MLLW. Values are means of two replicates from May to September and three replicates from October to March ± one standard error.

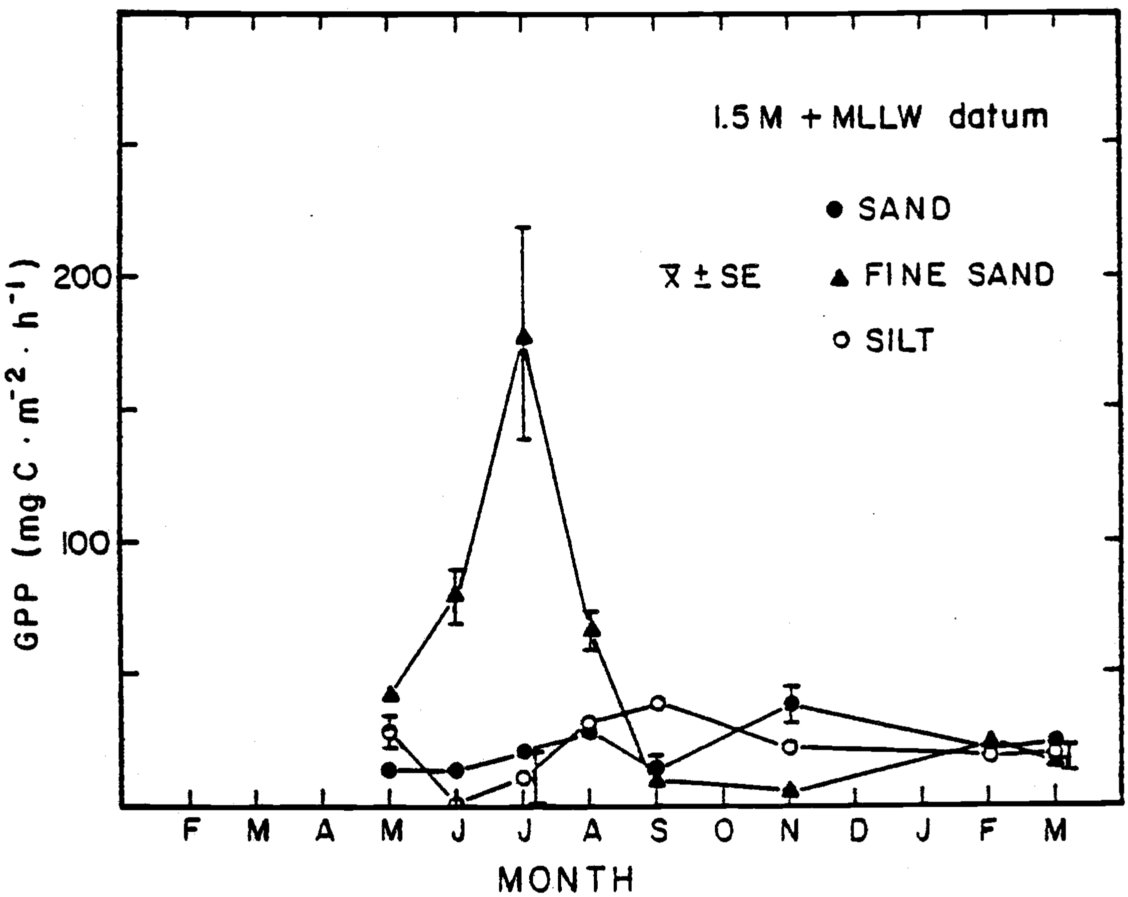


Figure 15. Gross primary production (GPP) at intensive study sites from May, 1980 to March, 1981. Sites were SAND (●), FINE SAND (▲) and SILT (○) at tidal height 1.5 m above MLLW. Values are means of two replicates from May to September and three replicates from October to March $\pm$ one standard error.

Table 8. Intertidal gross primary production (mg $C \cdot m^{-2} \cdot h^{-1}$) at the intensive study sites. Values represent means of n replicates $\pm$ one standard error for a period from May, 1980 to March, 1981 and are: a) including *Enteromorpha* and b) excluding *Enteromorpha*.

Site	n	$\bar{x} \pm$ SE
a)		
FINE SAND	22	47.15 $\pm$ 13.84
SAND	25	37.43 $\pm$ 7.94
SILT	26	25.06 $\pm$ 3.97
b)		
FINE SAND	20	28.05 $\pm$ 5.12
SAND	23	27.82 $\pm$ 3.25
SILT	26	25.06 $\pm$ 3.97

Table 9. Intertidal community oxygen uptake (mg $C \cdot m^{-2} \cdot h^{-1}$) at the intensive study sites. Values represent means of n replicates $\pm$ one standard error for a period from May, 1980 to March, 1981.

Site	n	$\bar{x} \pm$ SE
FINE SAND	22	27.16 $\pm$ 3.87
SILT	26	18.34 $\pm$ 2.37
SAND	25	11.49 $\pm$ 1.86

SILT site and the SAND site (Table 9). There were also significant differences ($p < .05$) in community oxygen uptake associated with the effects of time and a two-way interaction between sediment type and tidal height (Figure 16). Maximum community oxygen uptake in all sediment types was detected in the summer when temperature was relatively high.

The ratio of daily gross primary production to daily community oxygen uptake was calculated using data from the primary production estimates of this study. Daylength ranged from 6 h in December to 12.2 h in June. This ratio is an index of autotrophic activity in the sediment community, higher values indicating relatively greater gross primary production. There were significant differences ($p < .05$) in the mean ratios associated with the effect of sediment type. The SAND site had the highest mean ratio followed by the FINE SAND site and the SILT site (Table 10). There were no significant differences in the mean values of this ratio associated with effects of either tidal height or time.

The ratio of gross primary production to chlorophyll a concentration in the top cm of sediment was calculated to give a measure of production per unit of microalgal chlorophyll a. No significant differences associated with the effects of sediment type, tidal height or time were observed. Regression analysis relating sediment-associated gross primary production to chlorophyll a concentration in the top cm of sediment was performed using measurements made without *Enteromorpha* present. Equations derived for all sediment types in-

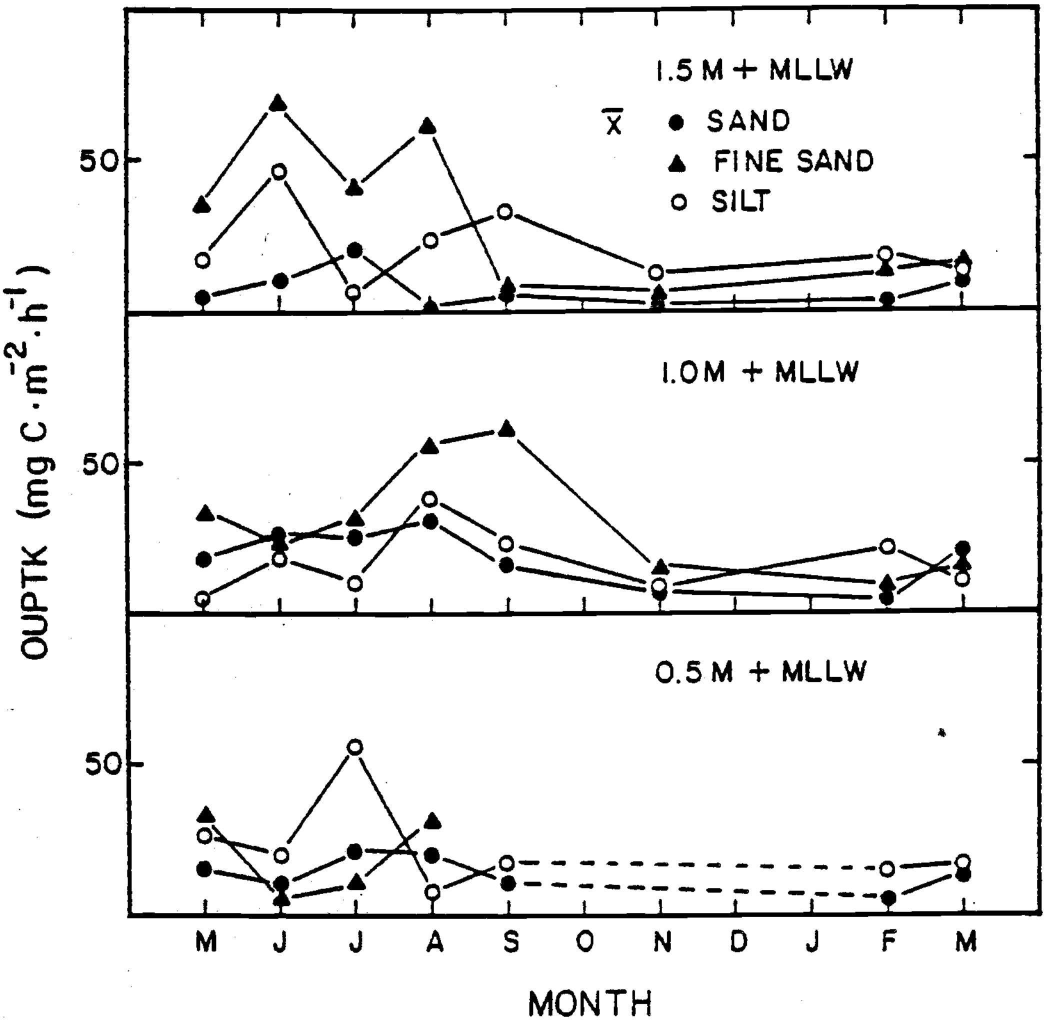


Figure 16. Community oxygen uptake (OUPTK) at intensive study sites from May, 1980 to March, 1981. Sites were SAND (●), FINE SAND (▲) and SILT (○) at tidal heights 1.5 m, 1.0 m, and 0.5 m above MLLW. Values are single observations from May, 1980 to September, 1980 and means of three replicates from Oct., 1980 to March, 1981.

Table 10. Ratios of daily gross primary production to daily community oxygen uptake at the intensive study sites. Values represent mean ratios of n replicates ± one standard error for a period from May, 1980 to March, 1981. Daylength ranged from 6 h (Dec.) to 12.2 h (June).

Site	n	$\bar{x} \pm$ SE
SAND	25	3.19 ± 1.69
FINE SAND	22	0.77 ± 0.20
SILT	26	0.75 ± 0.21

dicated that only 37 to 55% of the variation in gross primary production could be associated with chlorophyll a concentration in a linear model (Table 11).

5. Relationships Between Variables

Pearson coefficients of correlation (r) were calculated to show associations between physical and biological variables under the conditions measured during the study (Table 12). In general, correlations were low (less than 0.50). Exceptions to this were correlations between chlorophyll a concentration in the top cm of sediment and chlorophyll a concentration in the top cm of sediment contained in the metabolic chambers (0.81), between mean sediment grain size in phi-units and organic matter concentration in the top cm of sediment (0.70), between gross primary production and chlorophyll a concentration in the top cm of sediment (0.63) and between daylength and temperature (0.74).

Linear regression analysis was performed using selected physical and biological variables measured during the study (Table 13). Here, the independent variables were gross primary production, community oxygen uptake, organic matter concentration in the top cm of sediment and water temperature. This regression analysis only applied to the sites and conditions where measurements were made. The resulting models are not intended to be used for general prediction purposes, but instead for showing associations between relevant variables. The independent variables were selected by two criteria: (1) the model

Table 11. Linear regression analysis of sediment-associated gross primary production (GPP) as predicted by chlorophyll _a_ concentration (CHLR) in the top cm of sediment. Models correspond to the SAND, FINE SAND and SILT sites and to pooled data for the three sites.

Model	n	Significance	R^2
Pooled Data			
$\widehat{GPP} = 9.57 + 0.35$ CHLR	69	$p < .01$	0.40
SAND			
$\widehat{GPP} = 10.47 + 0.41$ CHLR	23	$p < .01$	0.50
FINE SAND			
$\widehat{GPP} = -3.56 + 0.65$ CHLR	20	$p < .01$	0.37
SILT			
$\widehat{GPP} = 7.60 + 0.30$ CHLR	26	$p < .01$	0.55

Table 12. A matrix of Pearson product moment coefficients of correlation (r) relating chlorophyll *a* concentration in the top cm of sediment (CHLS), organic matter concentration in the top cm of sediment (AFDW), chlorophyll *a* concentration in the top cm of sediment in production samples (CHLR), gross primary production (GPP), community oxygen uptake (OUPTK), sediment mean grain size (SEDMEAN), daylength (DAYL) and water temperature (TEMP) in Netarts Bay.

	CHLS	AFDW	CHLR	GPP	OUPTK	SEDMEAN	DAYL	TEMP
CHLS	-	0.40	0.81	0.46	0.08	0.29	-0.07	-0.07
AFDW		-	0.18	-0.05	0.13	0.70	0.12	0.15
CHLR			-	0.63	0.08	-0.10	-0.31	-0.26
GPP				-	0.42	-0.24	0.01	-0.01
OUPTK					-	0.15	0.38	0.45
SEDMEAN						-	0.11	0.07
DAYL							-	0.74
TEMP								-

Table 13. Linear regression models relating physical and biological variables. Variables include gross primary production (GPP), chlorophyll a concentration in the top cm of sediment (CHLR), community oxygen uptake (OUPTK), organic matter concentration in the top cm of sediment (AFDW), sediment mean grain size in phi-units (SEDMEAN), water temperature (TEMP) and daylength (DAYL). Data are from the intensive study sites in Netarts Bay. The slopes of all models were significantly different from zero, at the 1% level.

Model	n	R^2
$\widehat{GPP} = 9.57 + 0.35\ CHLR$	69	0.40
$\widehat{GPP} = 1.62 + 0.34\ CHLR + 0.46\ OUPTK$	69	0.53
$\widehat{OUPTK} = 7.60 + 0.48\ GPP$	69	0.30
$\widehat{OUPTK} = -17.68 + 0.35\ GPP + 2.01\ TEMP$	69	0.38
$\widehat{AFDW} = -89.54 + 109.21\ SEDMEAN$	34	0.67
$\widehat{AFDW} = -123.50 + 104.41\ SEDMEAN + 0.92\ CHLR$	34	0.73
$\widehat{TEMP} = -1.62 + 1.30\ DAYL$	128	0.56

with one independent variable was chosen which had the highest r^2; and (2) the model with two independent variables was chosen which had the highest r^2. Using this approach, the best predictors of gross primary production were chlorophyll a concentration in the top cm of sediment and community oxygen uptake, while the best predictors of community oxygen uptake included gross primary production and water temperature. The corresponding predictors of organic matter in the top cm of sediment included mean grain size in phi-units and chlorophyll a concentration in the top cm of sediment, and water temperature was most closely associated with variation in daylength. Except for organic matter concentration in the top cm of sediment, the linear relationships were relatively weak with r^2 values ranging between 0.30 and 0.56.

Discussion

Sediment characteristics of Netarts Bay remained relatively constant at any single intensive study site during the study period. This would be expected for a bay which does not receive large seasonal inputs of terrestrial runoff and associated silt. Sediment type ranged from medium sand to coarse silt and corresponded to sources of material to the bay. Marine sand originated from the eastern shore of the bay. Previous research in Yaquina Bay, Oregon showed that sediments of estuarine environments reflected hydrographic conditions within and adjacent to the estuary (Kulm and Byrne, 1966). The extent, magnitude and rate of sedimentation in Yaquina Bay was influenced by whether the estuary was fully or partially mixed, the amount of river runoff, the direction of littoral drift and the wind direction. All four factors were related to seasonal changes in meteorological conditions (Kulm and Byrne, 1966).

Changes in sediment height in Netarts Bay during the spring and summer corresponded to areas with wave action and strong water currents. Most of these areas were on the western side of the bay. Frostick and McCave (1979) found an association between algal growth and sediment accretion, with subsequent erosion of sediment when the algae died. Wave action also strongly influenced the amount of erosion. No simple association between algal growth and sediment accretion was found in Netarts Bay, although it was observed that Enteromorpha did trap large amounts of sediment. Mucus secreted by diatoms, blue-green algae and flagellates also helps to bind sediment (Coles, 1979; Frostick and McCave, 1979).

Organic matter concentration in the top cm of sediment was related to mean grain size. Seasonal changes in organic matter corresponded to changes in plant, animal and detrital biomass. Similar seasonal changes were observed in other estuaries (e.g., Edwards, 1978; Cadée and Hegeman, 1977). In Netarts Bay, there were no large differences between organic matter concentration in the top cm of sediment and that at the 4 to 5 cm depth. However, differences in the chemical composition of organic matter may vary with depth as sediment is disturbed by benthic animals (Johnson, 1977).

In Netarts Bay, large amounts of *Enteromorpha* and *Zostera* were transported to the strand line at 2.0 m above MLLW during the summer and the fall. This accumulation occurred primarily on the shores furthest away from the mouth of the bay. The material was fragmented and incorporated as organic matter into the intertidal sediments rapidly during these seasons. Josselyn and Mathison (1980) also observed large biomasses of macrophyte litter at the strand line in Great Bay, New Hampshire, reporting that seaweeds composed 35 to 85% of the material throughout the year.

In general, chlorophyll *a* concentration in the top cm of sediment was higher at the SILT site than at the SAND site. A similar pattern was found for other estuaries (Cadée and Hegeman, 1977; Coles, 1979; Colijn and Dijkema, 1981). In Netarts Bay, there was a relatively high concentration of chlorophyll *a* in the top cm of sediment at 2.0 m above MLLW, a pattern apparently related to abundant soil moisture and the lack of benthic animals. Blue-green algae also were common at this location. At lower tidal heights at the SILT site ($\leq$ 1.5 m above MLLW), the chlorophyll *a* concentration in the top cm of sediment was the same or lower than that at the FINE SAND and SAND sites. At these tidal heights the flora was dominated by epipelic and epipsammic diatoms. Chlorophyll *a* concentration in the top cm of sediment at the FINE SAND site at 2.0 m above MLLW was maximum during the summer, a pattern that was associated with abundant moisture and blue-green algae, and the lack of benthic animals. The SAND site had low chlorophyll *a* concentration, a pattern associated with a wave-exposed beach which lacked moisture during exposure to the air.

Animal holes in the sediment, made primarily by *Callianassa*, were abundant at all study sites at the tidal height of 1.5 m above MLLW. These disturbances resulted in a decrease in chlorophyll *a* concentration in the top cm of sediment expressed on an areal basis. Animal holes were more abundant at the SILT site than at the FINE SAND and SAND sites at tidal heights less than 1.5 m above MLLW. However, at these tidal heights, benthic animals were abundant at all sites. Information concerning the relative disturbance created by different species of animals would be useful in evaluating their effect on algal primary production.

Other factors limiting microalgal biomass at the study sites were scouring and turbidity associated with water current, and interactions with *Enteromorpha* and *Zostera*. Both *Enteromorpha* and *Zostera* can shade the sediment-associated microalgal populations and also compete for space. Large "ropes" of *Enteromorpha* can also become entangled in *Zostera* beds and trap large amounts of sediment which inhibits the growth of microalgae. Similar factors apparently limited microalgae in long-term studies in salt marshes (Gallagher and Daiber, 1974; Van Raalte, *et al.*, 1976).

Ratios of chlorophyll *a* concentration in the top cm of sediment to the concentration at the 4 to 5 cm depth were highest at 2.0 m above MLLW at all three intensive study sites. The 2.0 m above MLLW transect at the SAND site was a relatively barren beach strand line, while the 2.0 m above MLLW transects at the FINE SAND and SILT sites had compacted subsurface sediments. At these sites, high ratios apparently were associated with the relative stability of these sediments and the poor survival of subsurface populations of microalgae once they have been buried in compacted subsurface sediment. At transects lower than 2.0 m above MLLW, animal activity and scouring disturbed the sediment and lowered the chlorophyll *a* ratio.

The complicated pattern of chlorophyll *a* distribution apparently was controlled by sediment moisture, animal holes, animals, macrophyte cover, water currents and wave action. Maximum chlorophyll *a* concentrations were observed in the spring during a period of relative high microalgal growth and inactivity of benthic animals, and again in the fall during fair weather and a decrease in animal activity (Pamatmat, 1968). Experiments in the field and in the laboratory indicated that benthic animals inhibited microalgal biomass accumulation significantly (see Chapter 4; Admiraal, 1977d; Coles, 1979). In other estuaries, chlorophyll *a* concentration near the sediment surface also was related negatively to wave action, water currents and storm activity (Pamatmat, 1968; Gallagher and Daiber, 1974; Colijn and Dijkema, 1981).

Maximum gross primary production occurred during the summer at all three intensive study sites. Although large plants of *Enteromorpha* were excluded from production measurements, sporelings were present in the sediment at the SAND and FINE SAND sites and presumably contributed significantly to sediment-associated gross primary production in the summer. When *Enteromorpha* was excluded, the mean hourly rate of gross primary production was relatively constant at all intensive study sites. This is in contrast to the mean chlorophyll a concentration in the top cm of sediment which was higher at the SILT site. The presence of blue-green algae at 2.0 m above MLLW contributed large biomasses but did not appreciably alter the hourly rate of gross primary production at the SILT site.

Light intensity at the intertidal sites was usually 10 to 20% of full sunlight, an intensity that was above the level necessary for light saturation of photosynthesis (Admiraal, 1977a; Colijn and van Buurt, 1975). Exceptions to this included days of heavy cloud cover and fog, and periods of wind-induced wave activity which stirred up the sediments in certain areas. Apparently, photosynthesis was controlled by daylength which was determined by cloud cover, turbidity, water depth and sunrise-sunset times. Similar control by daylength of sediment-associated photosynthesis was observed in other estuaries (Cadée and Hegeman, 1974; Admiraal and Peletier, 1980; Pamatmat, 1968).

Maximum community oxygen uptake occurred during the summer, corresponding to increases in temperature, organic matter concentration and metabolic activity (Pamatmat, 1968; Duff and Teal, 1965). The FINE SAND site apparently had the most favorable conditions for the growth of animals and plants. Although the organic matter concentration was higher at the SILT site, apparently community oxygen uptake was not limited by substrate concentration. Some earlier work indicated that community oxygen uptake may be correlated with organic matter concentration (Pamatmat, 1975; Edwards, 1978). Much of the organic matter at the SILT site was refractory (e.g., twigs and leaves) and derived from terrestrial sources. This material was probably relatively unavailable to the detrital food web. Further research is necessary to partition the various organic components in estuaries into available and unavailable fractions (Johnson, 1977).

The highest ratios of daily gross primary production to daily community oxygen uptake occurred at the SAND site when sporelings and young plants of *Enteromorpha* were dominant. The communities at the SILT and the FINE SAND sites had ratios below unity, and were therefore supported in part by detrital inputs. Odum (1956) discussed the convergence of the ratio of daily primary production to daily community oxygen uptake (P/R) towards unity, which occurs during the course of community development. Disturbed areas are often dominated by autotrophic organisms which shift the P/R ratio away from unity. Stable habitats have relatively more consumer processes which mediate community development and are associated with P/R values approaching unity. Apparently the FINE SAND and SILT sites were more stable habitats with a greater organic matter concentration and more consumer activity than the SAND site (Stout, 1976).

The ratio of gross primary production to chlorophyll *a* concentration in the top cm of sediment was relatively constant throughout the year at all three intensive study sites. A possible source of variation in the relationship between gross primary production and chlorophyll *a* is that values obtained from the chlorophyll *a* analysis include chlorophyllides which are not photosynthetically active pigments (Whitney and Darley, 1979). Moreover, chlorophyll a sampled from the top cm of sediment includes microalgal biomass which is below the level of 1% of the surface light intensity (1.3 to 2.6 mm depth), an intensity at which photosynthesis is equal to or below respiratory losses. Also, diurnal rhythms of microalgal migration and photosynthetic activity control the proportion of biomass able to photosynthesize in the surface sediments (Pamatmat, 1968; Taylor, 1964), and seasonal variations in the ratio of carbon to chlorophyll a may account for fluctuations in the ratio of gross primary production to chlorophyll a (Jonge, 1980). Jonge (1980) found a negative correlation between microalgal growth rate and the ratio of carbon to chlorophyll a in estuarine sediment for a period of one year.

Linear multiple regression analysis of the production and biomass variables discussed above showed that there were no simple relationships explaining a large proportion of the variance in the data. This complexity is the result of many interactions and nonlinear relationships between primary production and the effects of light intensity, temperature, chlorophyll a concentration and organic matter concentration. Previous studies had detected a diurnal rhythm of sediment-associated algal primary production (Pamatmat, 1968; Gallagher and Daiber, 1974). However, no such rhythms were found during the daylight hours in Netarts Bay. Other factors which were not measured in Netarts Bay, but could possibly explain variation in primary production include microalgal migration in the sediment, sediment stability, grazing pressure and import-export of microalgal biomass

(Cadée and Hegeman, 1974; Pamatmat, 1968).

A carbon budget for three sediment types in Netarts Bay was calculated to show seasonal patterns of production and to suggest possible mechanisms which control these patterns. Table 14 gives the mean seasonal and annual microalgal biomass and total seasonal and annual primary production for the sediment types in Netarts Bay. There were obvious seasonal differences in mean biomass and primary production, and these differences corresponded to seasonal variances in light, temperature and biotic interactions. Net primary production was low at all three intensive study sites. Also, negative net primary production was observed during the winter at all sites, although maximum mean biomass occurred at the SILT site during the winter. This pattern suggested that heterotrophic growth of microalgal populations was occurring during the winter at the SILT site. The calculated microalgal respiration rates may have been too high, however this would not change the fact that maximum biomass was occurring during the time of minimum net production at the SILT site, regardless of the magnitude of net primary production.

The idea of heterotrophic growth of sediment-associated microalgae is not new (Admiraal and Peletier, 1979b; Jorgensen _et al_., 1980; McLean _et al_., 1981; Hellebust and Lewin, 1977). Microalgal populations probably were growing actively during periods of low storm-related export during the winter in sediment which contained high concentrations of organic matter. Conditions of low light intensity (below 0.5 $E \cdot m^{-2} \cdot d^{-1}$) stimulate photoheterotrophy in epipelic

Table 14. Seasonal sediment-associated biomass and production in Netarts Bay (g C·m^{-2}) at the SAND, FINE SAND and SILT sites (0.5 m to 2.0 m above MLLW). Variables include: mean seasonal and annual biomass of microalgae (BIOMASS), and the seasonal (90 days) or annual (360 days) rates of gross primary production (GPP), microalgal respiration (RESP), net primary production (NPP), community oxygen uptake (OUPTK) and non-algal community oxygen uptake (NON-ALGAL OUPTK). Values were calculated from monthly values, see Appendix Table 3. Monthly daylength ranged from 6 h (Dec.) to 12.2 h (June). Microalgal respiration was 34% of gross primary production on an hourly basis (see Chapter 3). Non-algal OUPTK was calculated by subtraction of RESP from OUPTK.

	BIOMASS	GPP	RESP	NPP	OUPTK	NON-ALGAL OUPTK
SAND						
SPRING	4.85	27.57	22.43	5.14	30.82	8.39
SUMMER	4.37	37.99	26.80	11.19	40.92	14.12
FALL	4.62	21.11	21.82	-0.71	26.04	4.22
WINTER	3.43	14.40	17.55	-3.15	23.13	5.58
ANNUAL	4.32	101.07	88.60	12.47	120.91	32.31
FINE SAND						
SPRING	8.84	29.12	22.38	6.74	61.25	38.87
SUMMER	5.01	39.45	28.10	11.35	81.58	53.48
FALL	3.69	15.71	14.90	0.81	47.81	32.91
WINTER	4.03	13.11	15.23	-2.12	26.45	11.22
ANNUAL	5.39	97.39	80.61	16.78	217.09	136.48
SILT						
SPRING	6.57	18.79	14.87	3.92	33.12	18.25
SUMMER	4.45	17.83	12.75	5.08	56.34	43.59
FALL	4.44	14.60	14.55	0.05	36.64	22.09
WINTER	7.80	17.90	21.53	-3.63	36.65	15.12
ANNUAL	5.82	69.12	63.70	5.42	162.75	99.05

diatoms (Admiraal and Peletier, 1979b). The possibility of heterotrophic growth further complicates the problem of interpreting patterns of chlorophyll _a_ concentration in the top cm of sediment and associated gross primary production. Survival of subsurface diatoms has also been observed (Riznyk and Phinney, 1972; Pamatmat, 1968) and could be enhanced by heterotrophic nutrition or by decreased metabolic rate during burial (McIntyre _et al_., 1970).

Sources of carbon to non-algal community oxygen uptake probably included both algal and non-algal organic matter. At the SAND, FINE SAND and SILT sites, 39%, 12% and 5%, respectively, of the carbon for metabolism could have been derived from microalgae which were available during the entire year. The remaining carbon was probably supplied by detrital sources from other areas. Other studies have found that detritus is a major source of carbon to estuarine secondary production (Pomeroy _et al_., 1977; Tenore, 1977). Sources of detrital carbon to Netarts Bay included _Enteromorpha_, _Zostera_, bacteria, fungi, animals and microalgae. There did not appear to be major contributions of carbon from the high marsh because of the limited export of particulate matter from the area. However, studies have shown that some of this high marsh production may be exported as energy to the intertidal habitats in the form of dissolved reduced inorganic sulfur compounds and used chemotrophically by anaerobic organisms while their carbon source is carbon dioxide (Howarth and Teal, 1979).

Table 15 summarizes the maximum biomass and annual rates of gross

Table 15. Maximum biomass (BIOMASS), and annual rates of gross primary production (GPP), respiration (RESP) and net primary production (NPP) of *Enteromorpha prolifera* at the SAND and FINE SAND sites in Netarts Bay.

	SAND	FINE SAND
BIOMASS ($g\ C{\cdot}m^{-2}$)	149	162
GPP ($g\ C{\cdot}m^{-2}{\cdot}y^{-1}$)	3691	3880
RESP ($g\ C{\cdot}m^{-2}{\cdot}y^{-1}$)	907	994
NPP ($g\ C{\cdot}m^{-2}{\cdot}y^{-1}$)	2712	2886

primary production, respiration and net primary production of Enteromorpha (see Chapter 3). This alga grows from June to August at the SAND and FINE SAND sites. Growth of Enteromorpha appears to be related to seasonal increases in temperature and daylength in the bay. Enteromorpha was excluded from the SILT site, probably because of relatively high turbidity causing low available light intensity. Similar patterns of Enteromorpha growth were observed in other estuaries (Conover, 1958; Nienhuis, 1970).

The net primary production of Enteromorpha (2800 g $C \cdot m^{-2} \cdot y^{-1}$) is a large seasonal input of organic matter into the bay, especially during the summer and fall. This is a source of organic matter which has been ignored in studies of estuarine food webs and deserves further research into its sources and fates in estuarine ecosystems. By comparison, microalgae supplied a much smaller proportion of organic matter to the total net primary production of algae in the bay (5 to 18 g $C \cdot m^{-2} \cdot y^{-1}$). However, this microalgal contribution is also important and represents a significant source of food which is available throughout the year for benthic organisms (Baillie and Welsh, 1980; Ribelin and Collier, 1980).

In conclusion, it was evident that microalgal production and biomass in Netarts Bay was controlled by daylength, temperature, water currents, sediment moisture and stability, animals and macrophyte cover. The effects of some of these factors on production dynamics were interrelated and this was evident in the effects of sediment type and tidal height on algal biomass and production.

Nutrients did not appear to limit microalgal growth, apparently because of the abundance of nutrients in the intertidal sediments (Admiraal, 1977b, d; Cardon, 1981). The possibility of heterotrophic growth in microalgae was suggested by maximum biomass of microalgae during periods of low net primary production during the winter in sediment with high concentrations of organic matter. The sediment community derived most of its carbon from detrital sources rather than *in situ* microalgal net primary production. However, *Enteromorpha* and/or *Zostera* production represented more than adequate supplies of carbon for sediment community metabolism during the summer and fall.

III. RELATIONSHIPS BETWEEN BIOMASS AND PRIMARY PRODUCTION FOR INTACT ESTUARINE SEDIMENT COMMUNITIES AND THEIR COMPONENT EPIPELIC DIATOMS AND MACROALGAE

Introduction

Studies of sediment-associated microalgal production dynamics have included general surveys of annual production (Pomeroy, 1959; Pamatmat, 1968), as well as laboratory studies (Admiraal, 1977a, d; Admiraal and Peletier, 1980) and field studies of mechanisms controlling microalgal production (Sullivan, 1976; Van Raalte et al., 1976). Mechanisms controlling the growth of sediment-associated macroalgae also have been studied in the field (Conover, 1958) and in the laboratory (Edwards, 1969). As part of a research program designed to investigate production dynamics of sediment-associated algae in Oregon estuaries, laboratory studies were conducted to investigate the relationships between component populations of sediment-associated algae and physical factors affecting their growth.

Research on estuarine benthic primary production has been focused on saltmarsh systems which are dominated by seed plants such as *Spartina* (Pomeroy et al., 1978). Marsh seed plants are very competitive with algae for nutrients and light, and therefore there is strong biotic control of algal growth in saltmarshes (Van Raalte *et al*., 1976). Estuaries in Oregon and adjacent to the North Sea have extensive sediment flats and a limited area of saltmarsh (Cadée and Hegeman, 1974; 1977). The absence of competition by seed plants for nutrients and light where *Zostera* and other seagrasses are not present makes sediment flats a favorable habitat for algal growth. However, colonization by *Zostera* and other seagrasses may reduce sediment-associated algal production, while increasing growth of epiphytic algae and drift macroalgae. Oregon estuaries typically have large seasonal populations of macroalgae (e.g., *Enteromorpha* and *Ulva*) which along with microalgae, probably represent a major seasonal source of food for estuarine organisms, either in the form of fresh material or detritus.

The research objectives of this study were identified within the context of a conceptual framework of sediment-associated algal primary production (see Chapter 1, Figure 2). Prediction of algal primary production requires knowledge of the effects of physical factors, light energy input, nutrient input, respiratory losses and algal biomass. Prediction of algal biomass requires knowledge of algal primary production, respiratory losses, animal consumption and import-export of algal biomass.

The purpose of this research was to define relationships between biomass and primary production for intact estuarine sediment communities and their component epipelic diatom and macroalgal populations. Specific objectives of this research included: a) determination of the relationship between light intensity and gross photosynthesis in intact sediment communities; b) determination of the relationship between temperature and metabolism of intact sediment communities; c) isolation and physiological characterization of component populations of epipelic diatoms and macroalgae from sediment communities; and d) comparison of relationships between biomass and primary production for intact sediment communities and their component algal populations. From these results, hypotheses can be generated concerning the quantitative importance of sediment-associated algal production as a basis for estuarine food webs and mechanisms which control this primary production.

Study Site

Yaquina Estuary (44°35' N; 124°04' W) drains 656 km^2 of the Coast Range (Figure 17) and is Oregon's fifth largest estuary, with a surface area of 1583 hectares, of which 548 hectares is tideland and 1035 hectares is subtidal. Experiments were done at field sites in Yaquina Bay and at the Oregon State University Marine Science Center which is located at the mouth of the Yaquina River near Newport, Oregon.

The estuary is subjected to mixed semi-duirnal tides and is classified as a partly-mixed system in the winter and spring and a well-mixed system during the summer and fall. Maximum tidal range is 3.0 m. Mean low water (MLW) and mean high water (MHW) are 0.5 m and 2.0 m above the mean lower low water datum (MLLW), respectively.

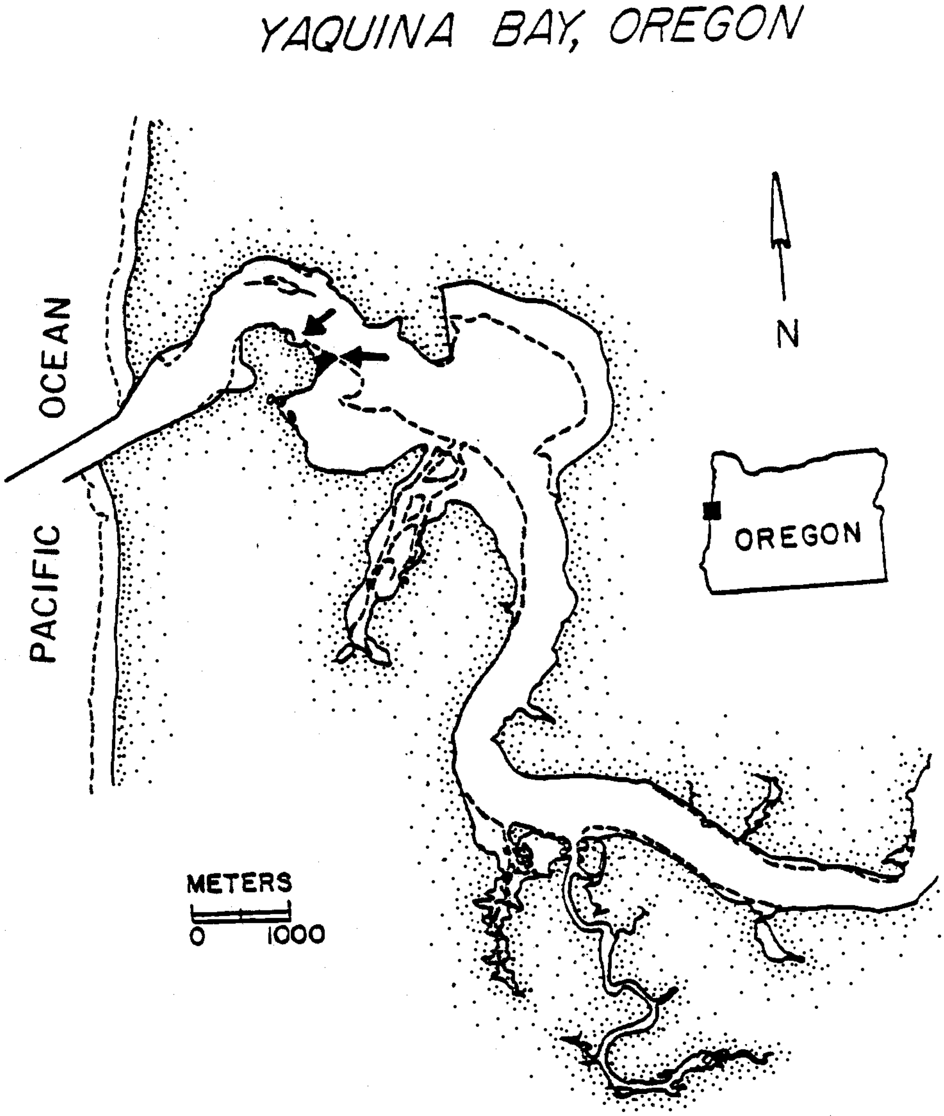


Figure 17. Map of Yaquina Bay with arrows showing intensive study sites.

Daylight hours in Newport vary from 12.2 per day in June to 6.0 per day in December. The salinity pattern in the estuary is complex. In the summer, upwelled bottom water from off the Oregon coast combines with insignificant fluviatile input to account for a relatively high salinity (33 to 35 °/oo) in Yaquina Bay. In the winter, high freshwater discharge is responsible for salinities as low as 8 °/oo at the Marine Science Center during low tide. During a complete tidal cycle, 70% of the water in the bay is exchanged with ocean water (Goodwin et al., 1970). During an entire year, water temperature over the sediment flats usually ranges from 6°C to 20°C, and the air temperature over exposed sediment flats ranges from 0°C to 30°C.

Methods

1. Primary Production

Gross primary production and community oxygen uptake were estimated in the laboratory from oxygen measurements in stirred, light and dark chambers designed to hold intact cores of sediment. Between March and September, measurements were made in plexiglas chambers which were 32.5 cm long and had an internal diameter of 14.5 cm (Figure 18). Each chamber held three intact sediment cores, and these cores were 5 cm deep and included a total sediment surface area of 136.08 cm^2. The chambers were filled with 5.7 l of filtered seawater, sealed and placed into a water bath. Water in each chamber was circulated through

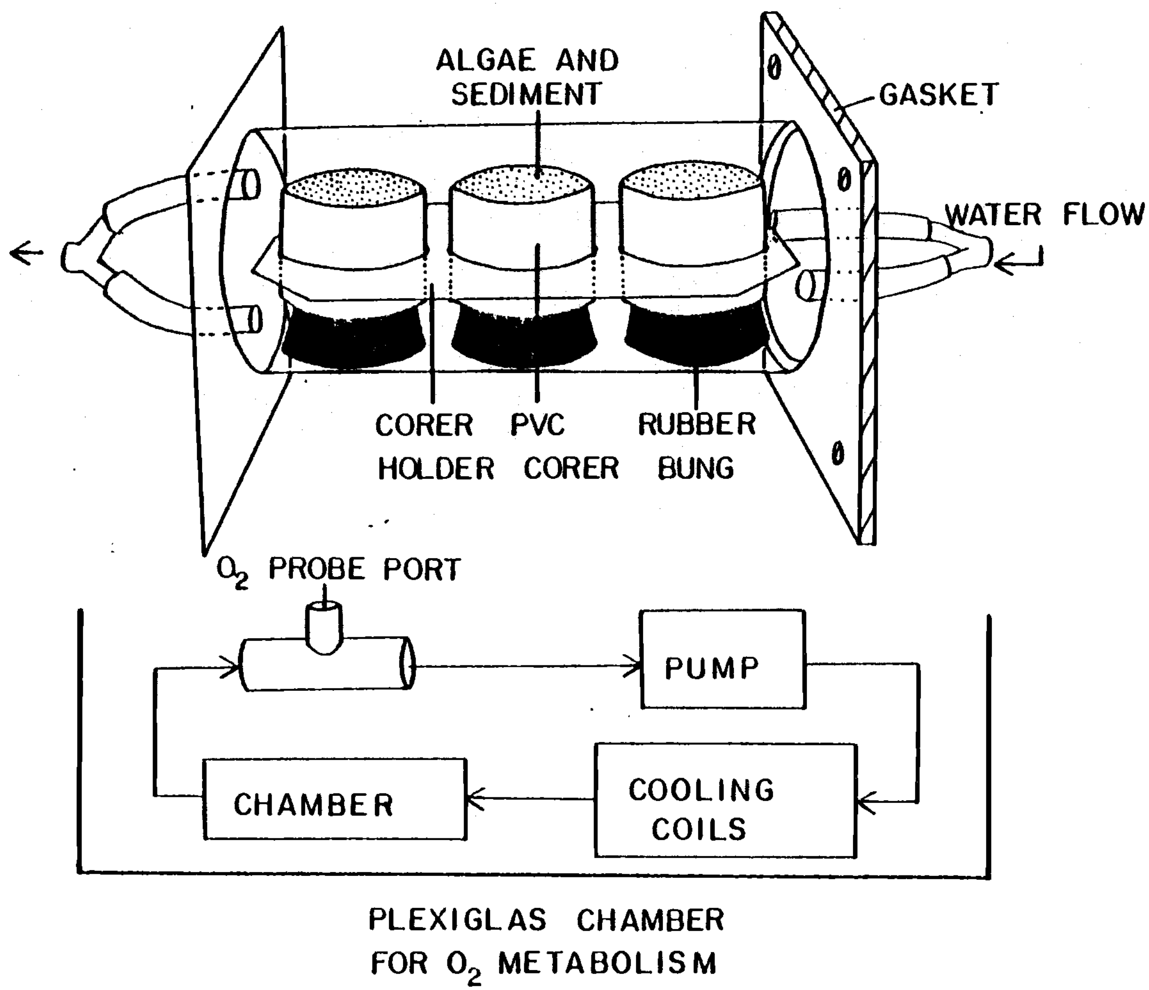


Figure 18. Diagram of a plexiglas chamber for measuring oxygen metabolism of intact sediment cores or macroalgae. See text for dimensions.

tygon tubing by a pump. Rates of oxygen evolution were based on measurement periods of 0.5 to 1.0 hour between initial and final readings. Measurements of dissolved oxygen were made polarographically with an Orbisphere® salinity-corrected dissolved oxygen system by inserting the oxygen probe into a port connected to the water circulation line.

Between October and May, estimates of primary production were made in plexiglas chambers which were 14.2 cm tall, had an internal diameter of 6.8 cm and enclosed sediment surface area of 36.32 cm^2 (Figure 19). Three replicate chambers were carefully inserted 5 cm into the sediment, withdrawn and plugged with rubber bungs. Each chamber was filled with 300 ml of filtered seawater, sealed and placed in a waterbath. Water in the chamber was circulated by a magnetic stirrer with a motor speed of 300 rpm. Rates of oxygen evolution and uptake were based on measurement periods of 0.5 to 1.0 hour between initial and final readings. Readings were made by replacing the stirrer in a port on the top of the chamber with an oxygen probe.

Rates of net community production or oxygen uptake were measured when either type of chamber was exposed to light or darkened by covering with a sheet of black plastic, respectively. All chambers were preincubated in the dark for 1.0 hour. Incubations were done under sunlight or cool-white flourescent and incandescent lamps, and fiberglas screening was used as a neutral density filter to reduce light intensity. Simultaneous incubations of intact sediment cores in both types of chamber indicated that there were no significant differences in primary production attributable to chamber type.

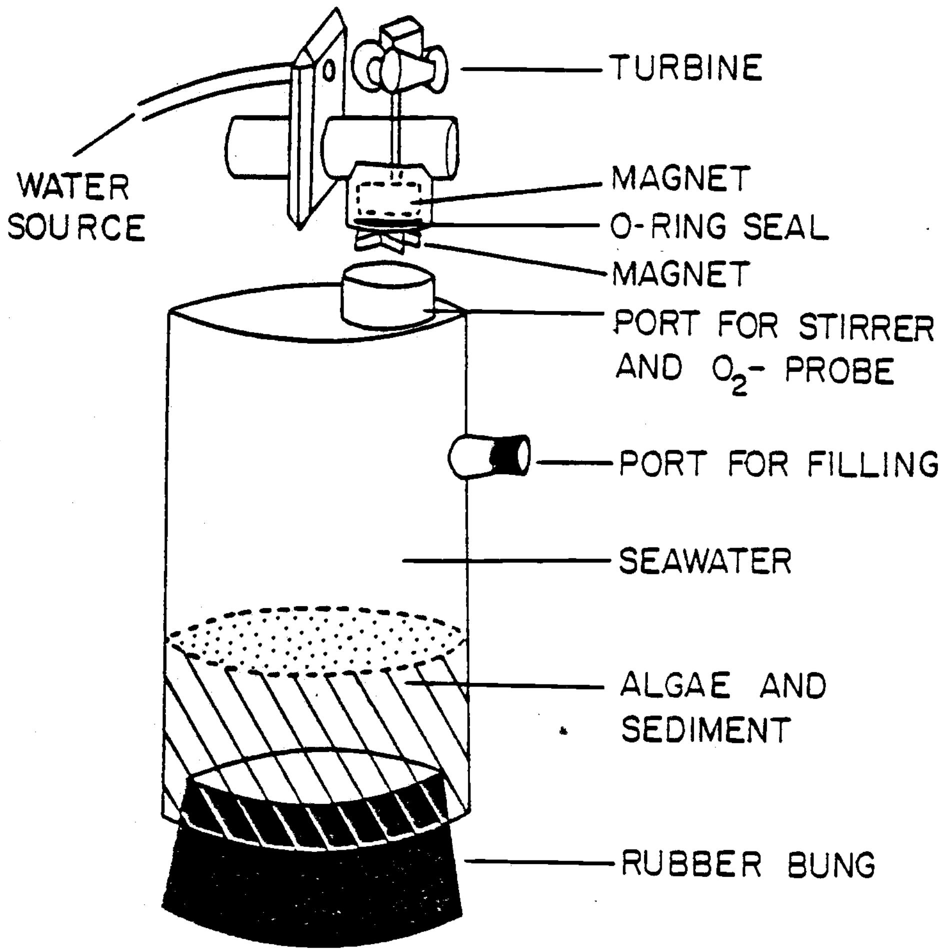


Figure 19. Diagram of a plexiglas chamber for measuring oxygen metabolism of intact sediment cores. See text for dimensions.

Gross primary production was estimated by adding the rate of community oxygen uptake to the rate of net community production for an equivalent period of time. Estimated rates of gross primary production in mg $O_2 \cdot m^{-2} \cdot h^{-1}$ were converted to mg $C \cdot m^{-2} \cdot h^{-1}$ while assuming a photosynthetic quotient of 1.2 (i.e., mg C = 0.312 x mg O_2). Estimated rates of community oxygen uptake in mg $O_2 \cdot m^{-2} \cdot h^{-1}$ were converted to mg $C \cdot m^{-2} \cdot h^{-1}$ while assuming a respiratory quotient of 1.0 (i.e., mg C = 0.375 x mg O_2)(Westlake, 1965).

2. Biomass

Samples for chlorophyll a analysis were collected using a 12 cm long plastic corer of 2.3 cm diameter. The corers were gently pressed 3 cm into the larger sediment cores from which estimates of primary production had been made. The corers were carefully removed, capped and frozen. The frozen sediment was extruded from the corers and the top cm was excised with a knife. A core section was placed in a mortar with 0.5 ml of saturated magnesium carbonate solution and 10 ml of 90% acetone (v/v). The slurry was ground with a pestle for one minute, poured into a screw-cap test tube and kept in the dark at 4°C for 24 hours. The extract was centrifuged and chlorophyll a concentration was measured using the method of Strickland and Parsons (1972). The Lorenzen equation (corrected for pheopigments) was used to calculate mg chlorophyll $a \cdot m^{-2}$. These values are uncorrected for chlorophyllide (Whitney and Darley, 1979).

Macroalgal biomass samples were rinsed in freshwater, weighed, dried at 70°C for 48 hours and reweighed. Dried samples were ashed at 450°C for 24 hours and reweighed to determine weight of organic matter. The chlorophyll a concentration in macroalgae was determined as described above using approximately 1.0 g wet weight of algae per sample. Carbon content was estimated by multiplying the weight of organic matter by 0.5 (Vollenweider, 1974).

3. Isolation of Diatom Assemblages

Motile, epipelic diatoms were isolated from sediment samples obtained each season during an entire year at the intensive study sites in Yaquina Bay using the method of Jonge (1980). Approximately 1000 cm^3 of the top cm of sediment was taken from the field and transported to the laboratory. This sediment was mixed with 100 ml of sand-filtered, UV-treated seawater (30 to 33 °/oo salinity) and spread out in a shallow tray, 40 by 50 cm. Clean white quartz sand (125 to 250 μm particle diameter) was spread over the sediment in a 1 mm layer, and three layers of lens tissue were placed over the sand and the sediment. The entire tray was covered with clear plastic and incubated for 36 hours at 15°C and a light intensity of 150 $\mu E \cdot m^{-2} \cdot sec^{-1}$.

After the incubation period, the lens tissue was lifted carefully off the sediment and combined with 500 ml of sand-filtered and UV-treated seawater to make a slurry mixture. The mixture was filtered through four layers of 2.5 mm thick foam plastic and then through a 55 μm Nitex® mesh net. The foam plastic filtered out lens tissue fibers, and the mesh filtered out smaller animals. Microscopic inspection confirmed that the light brown-colored suspension contained primarily diatoms and few bacteria or flagellates.

The diatom suspension obtained from the isolation procedure was used to establish relationships between primary production and chlorophyll a, organic matter and chlorophyll a and for measurements of respiration. Four replicate 50 ml screw-cap test tubes with a diatom sample were incubated for 0.5 hour at a light intensity of 210 $\mu E \cdot m^{-2} \cdot sec^{-1}$, a temperature of 14°C, and a salinity of 30 to 33 °/oo. Measurement of oxygen and calculation of production was performed as described above. After these measurements, 50 ml replicates of diatom suspensions were filtered on pre-ashed glass fiber filters, and chlorophyll a was extracted from four filters in acetone using methods described above. Also, four filters were dried at 70°C for 24 hours and reweighed to determine dry weight. Then the filters were ashed at 450°C for 24 hours and reweighed to determine weight of organic matter. Carbon content was estimated by multiplying the weight of organic matter by 0.5 (Vollenweider, 1974).

5. Physical Variables

Light intensity was measured in $\mu E \cdot m^{-2} \cdot sec^{-1}$ photosynthetically active radiation using a Licor® quantum meter. Temperature was measured using bimetal or thermistor probes. A temperature-compensated AO Goldberg® refractometer was used to measure salinity.

Results

The relationship between light intensity and gross primary production of intact sediment cores was determined seasonally from March, 1980 to May, 1981. Sediment communities were sampled to include a wide range of microalgal biomass (23.9 to 226.0 mg chl $\underline{a}\cdot m^{-2}$). Figure 20 illustrates the results of three representative experiments. Light saturation of gross primary production ranged from 200 to 400 $\mu E\cdot m^{-2}\cdot sec^{-1}$. No inhibition of gross primary production was observed at 950 $\mu E\cdot m^{-2}\cdot sec^{-1}$. Full sunlight ranged from 1500 to 2000 $\mu E\cdot m^{-2}\cdot sec^{-1}$.

Production values for microalgae exposed to light saturating conditions were analyzed using linear regression analysis to predict gross primary production with chlorophyll a concentration in the top cm of sediment as an independent variable (Table 16). This relationship was established for two tidal heights and for the pooled data. The slopes for these equations were significantly different from zero ($p < .01$), and between 46 and 65% of the annual variation in gross primary production could be associated with variation in chlorophyll a concentration in the top cm of sediment.

Effects of temperature on community oxygen uptake and gross primary production are summarized in Table 17. Q_{10} is a multiplier

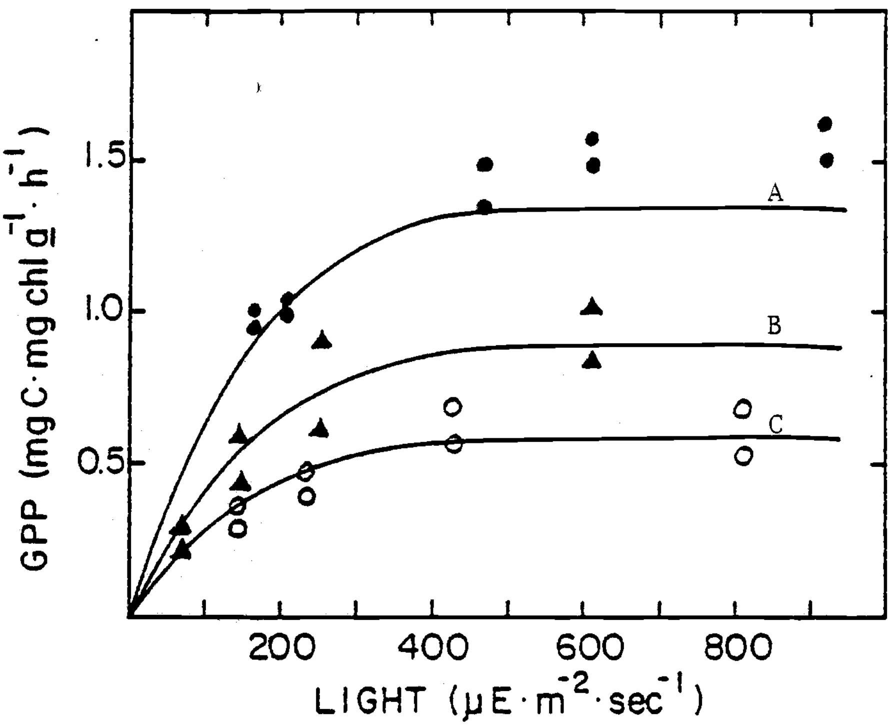


Figure 20. Relationship between gross primary production (GPP) per unit chlorophyll a of sediment-associated microalgae and photosynthetically active light intensity (LIGHT). Models for three representative experiments are: A ($\widehat{GPP}$ = -1.42 + 0.46 ln LIGHT, n = 10, r^2 = 0.81); B ($\widehat{GPP}$ = -1.09 + 0.33 ln LIGHT, n = 8, r^2 = 0.74); C ($\widehat{GPP}$ = -0.50 + 0.18 ln LIGHT, n = 10, r^2 = 0.71). Points show individual measurements. The slopes of all models were significantly different from zero at the 1% level.

Table 16. Linear regression models relating gross primary production (GPP) of sediment-associated microalgae to the chlorophyll a concentration in the top cm of sediment (CHLR) at intensive study sites in Yaquina Bay. Equations correspond to data for 1.9 m above MLLW (High), 1.0 m above MLLW (Mid) and pooled data. The slopes of all models were significantly different from zero at the 1% level.

High	$\widehat{GPP} = 11.43 + 0.49\ CHLR$	$n = 33$	$r^2 = 0.65$
Mid	$\widehat{GPP} = -26.51 + 1.12\ CHLR$	$n = 60$	$r^2 = 0.58$
Pooled Data	$\widehat{GPP} = 2.46 + 0.66\ CHLR$	$n = 93$	$r^2 = 0.46$

Table 17. Q_{10}[a] for community oxyen uptake (OUPTK) and gross primary production (GPP) in intact intertidal sediment from Yaquina Bay. Temperature range was from 7°C to 17°C, salinity was 30 °/oo and light intensity was 600 $\mu E \cdot m^{-2} \cdot sec^{-1}$. Data correspond to samples from 1.9 m above MLLW (High) and 1.0 m above MLLW (Mid). Values are expressed as means of n replicates ± one standard error and ranges.

	Level	n	$\bar{x} \pm$ SE	range
OUPTK Q_{10}	High	6	3.32 ± 0.70	1.15 - 5.32
	Mid	6	2.08 ± 0.16	1.71 - 2.64
GPP Q_{10}	High	6	2.23 ± 0.17	1.59 - 2.69
	Mid	6	1.86 ± 0.23	1.42 - 2.83

a) $Q_{10} = (v_1/v_2)(10/t_1-t_2)$; where v_1 and v_2 are the reaction rates at temperatures t_1 and t_2, respectively.

for calculating the change in reaction rate associated with a 10°C change in temperature. Apparently, temperature change affected community oxygen uptake to a greater extent than gross primary production. The mean Q_{10} values for community oxygen uptake were 3.32 and 2.08 for sediment at 1.9 m and 1.0 m above MLLW, respectively. The mean Q_{10} values for gross primary production were 2.23 and 1.86 for sediment at 1.9 m and 1.0 m above MLLW, respectively. The sediment cores in these experiments were held for 1.0 hour at the temperature at which measurements of primary production and community oxygen uptake were to be made. During the coarse of a typical day during the spring, summer and fall, the intertidal sediment was exposed to a temperature range similar to that used in these experiments (7° to 17° C). Therefore these experiments were appropriate for the determination of the effect of changing temperature on sediment-associated primary production and community oxygen uptake in Yaquina Bay.

Results of the experiments with isolated epipelic diatoms in suspension are summarized in Table 18. Mean gross primary production per unit chlorophyll a was considerably higher for isolated epipelic diatoms than for intact diatom communities in the sediment, i.e., 3.75 as compared to 0.66 mg C·mg chl $a \cdot h^{-1}$. Mean hourly net primary production was 66% of hourly gross primary production, and mean hourly respiration was 34% of hourly gross primary production. The mean ratio of carbon to chlorophyll a was 83.49.

Rates of primary production and biomass of sediment-associated

Table 18. Conversion factors for primary production and biomass of epipelic diatoms isolated from intertidal sediment samples using lens tissue. Variables include: gross primary production (GPP); net primary production (NPP); chlorophyll a concentration (CHLR); organic matter concentration (AFDW); and carbon (C) calculated as AFDW x 0.5. Values are expressed as means of n replicates $\pm$ one standard error and ranges.

Factor	n	$\bar{x} \pm$ SE	range
GPP/CHLR ($mg \cdot mg^{-1} \cdot h^{-1}$)	4	3.75$\pm$0.76	2.32-6.91
Daylight NPP/GPP	4	0.66$\pm$0.10	0.30-0.87
AFDW/CHLR ($mg \cdot mg^{-1}$)	5	166.98$\pm$16.40	124.50-171.60
C/CHLR ($mg \cdot mg^{-1}$)	5	83.49$\pm$8.20	62.25-85.80

macroalgae are summarized in Table 19. Three species of algae were studied: Enteromorpha prolifera (Mull.) J.Ag.; Ulva expansa (Setch.) S.&G.; and Gracilaria verrucosa (Huds.) Papenf. Rates of respiration per gram dry weight were similar for all three species, while gross and net primary production were higher for Enteromorpha and Ulva than for Gracilaria. Maximum biomass at the intensive study sites and chlorophyll *a* concentration per gram dry weight were much higher for the green algae. However, gross primary production per mg chlorophyll *a* was higher for Gracilaria than for Ulva and Enteromorpha. Mean net primary production for Enteromorpha, Ulva and Gracilaria was 4.7, 4.2 and 0.2 g $C \cdot m^{-2} \cdot h^{-1}$, respectively. Light saturation of macroalgal photosynthesis was similar to that for microalgae (200 to 400 $\mu E \cdot m^{-2} \cdot sec^{-1}$). No inhibition of photosynthesis was noted at full sunlight (1500 to 2000 $\mu E \cdot m^{-2} \cdot sec^{-1}$), although bleaching of thalli was observed in the field if macroalgae were exposed to full sunlight while in a dried condition.

Discussion

Gross primary production of sediment-associated microalgae (predominantly diatoms) was light-saturated at relatively low light intensity (10 to 20% full sunlight). Similar results were shown by Admiraal (1977a) and Colijn and van Buurt (1975). Therefore, photosynthesis on intertidal sediment flats would not be expected to be limited by light intensity except during periods of high turbidity

Table 19. Primary production rates and biomass of sediment-associated macroalgae in Yaquina Bay. Species include: Enteromorpha prolifera; Ulva expansa; and Gracilaria verrucosa. Measurements were made at 13° to 15°C, salinity of 30 °/oo and a light intensity of 600 $\mu E \cdot m^{-2} \cdot sec^{-1}$. Variables include: respiration (RESP), net primary production (NPP), gross primary production (GPP), dry weight (DW), organic content (AFDW), carbon (C) calculated as AFDW x 0.5 and chlorophyll a concentration (CHLR). Values are expressed as means of 6 replicates ± one standard error. Biomass values are from the period of maximum standing crop which was from June to Aug. for Enteromorpha, July to September for Ulva and March to May for Gracilaria.

	Enteromorpha	Ulva	Gracilaria
RESP (mg $C \cdot g\ DW^{-1} \cdot h^{-1}$)	1.4±0.3	1.4±0.4	1.0±0.2
NPP (mg $C \cdot g\ DW^{-1} \cdot h^{-1}$)	9.5±1.2	10.3±0.4	7.6±1.2
GPP (mg $C \cdot g\ DW^{-1} \cdot h^{-1}$)	10.9±0.9	11.7±0.8	8.5±1.1
DW ($g \cdot m^{-2}$)	497.8±69.6	411.9±65.9	19.5±2.2
AFDW ($g \cdot m^{-2}$)	323.6±48.5	267.7±25.2	13.1±2.2
C ($g \cdot m^{-2}$)	161.8±24.3	133.9±8.03	6.5±1.1
CHLR/DW ($mg \cdot g^{-1}$)	2.5±0.0	1.9±0.0	0.9±0.1
GPP/CHLR ($mg \cdot mg^{-1} \cdot h^{-1}$)	4.4±0.4	6.2±0.5	9.4±0.9
Daylight NPP/GPP	0.87±0.04	0.88±0.02	0.88±0.03
NPP (g $C \cdot m^{-2} \cdot h^{-1}$)	4.7	4.2	0.2

or cloudly weather. No inhibition of gross primary production was observed at high light intensity, which was similar to observations reported by Colijn and van Buurt (1975). Sediment probably provides a favorable habitat for microalgae, especially motile forms such as epipelic diatoms which can move to favorable conditions when necessary (Taylor, 1964). Phytoplankton are often not able to move actively, and hence cannot avoid light intensities to which they are not adapted (Ryther, 1956; Parsons _et al_., 1977). Daylength is a limiting factor for sediment-associated microalgae because it determines the total flux of energy available for gross primary production (Admiraal, 1977a).

The mean specific rate of gross primary production associated with intact sediment at light saturation, 0.66 mg C·mg chl _a_·h^{-1} (Pmax), was very similar to that found in other studies of sediment-associated microalgae (Colijn and van Buurt, 1975; Admiraal, 1977a), although a wider range of values (0.15 to 1.70) was observed for intact populations from Yaquina Bay. Studies in the Columbia River estuary showed that the mean Pmax for sediment-associated microalgae was approximately 0.30 (McIntire and Amspoker, in preparation). This apparent difference in mean Pmax between estuaries in close proximity indicates that prediction of gross primary production from chlorophyll _a_ concentration must be made using equations based on data from the specific estuary in question. This variation in Pmax apparently was not attributable to tidal height, species composition or season and suggested that these populations of microalgae underwent periodic alternation of growth and senescence. Further experimentation is needed to determine possible mechanisms which control Pmax in sediment-associated microalgae. Other possible controlling factors include migration patterns, physiological condition of microalgae and the ratio of chlorophyll _a_ to chlorophyllides.

Possible effects of low light intensity on sediment-associated microalgae are an inducement of photoheterotrophy and heterotrophy (Admiraal and Peletier, 1979b; McLean _et al_., 1981; Jorgensen _et al_., 1980; Hellebust and Lewin, 1977). Low light intensity (less than 1% full sunlight), such as exists during winter or turbid conditions, can stimulate heterotrophic uptake of organic compounds essential for growth. Therefore, healthy microalgal populations can grow under seemingly light-limited conditions. Survival of sub-surface populations of microalgae may also be associated with heterotrophic nutrition or decreased metabolic rate (Riznyk and Phinney, 1972; Pamatmat, 1968; McIntyre _et al_., 1970).

Linear regression analysis indicated that the concentration of chlorophyll _a_ in the top cm of sediment was a relatively good predictor of gross primary production. However, there were sources of error associated with this relationship which need further investigation. The relationship between microalgal migration and Pmax is still unclear (Harper, 1977), and the relationship between the depth of light penetration and sediment type needs to be examined in more detail (Haardt and Nielsen, 1980). Studies of the seasonal changes in the ratio of chlorophyll _a_ to chlorophyllides (i.e., active and inactive chlorophyll) are also needed to understand the relationship between gross primary production and chlorophyll _a_ concentration (Whitney and Darley, 1979).

In general, an increase in temperature stimulated community oxygen uptake more than gross primary production. Similar results were observed for a variety of estuarine sediment flats (Duff and Teal, 1965; Pamatmat, 1968; Davies, 1975). Therefore, as temperature increases in the sediment, net primary production and the ratio of gross primary production to community oxygen uptake usually decrease.

Gross primary production of diatom assemblages isolated from the sediment was very similar to the gross primary production reported for phytoplankton assemblages (Steeman Nielsen and Hansen, 1959), indicating physiological similarities in photosynthesis between benthic and pelagic diatoms. Similar values have been obtained for benthic diatoms grown in liquid pure culture (Admiraal, 1977a). Hourly net primary production averaged 66% of hourly gross primary production for isolated diatoms. Colijn and van Buurt (1975) measured net primary production of isolated diatoms, but their measurements did not include an estimate of algal respiration. Such information is useful in field studies when it is desirable to partition algal respiration from community oxygen uptake, and to calculate net primary production from gross primary production estimates. Community oxygen uptake includes microbial, plant and animal respiration, as well as chemical oxygen uptake.

Pomeroy (1959) calculated microalgal respiration by subtraction and found net primary production to be not less than 90% of gross primary production, a value considerably higher than that found in this study by direct measurement. These respiration values obtained by direct measurement may have been too high. Although bacteria were not observed in the suspensions of isolated epipelic diatoms, they may have been present and contributed to the measured respiration. However, for macroalgae, rates of respiration per hour were 15% of rates for gross primary production per hour. Therefore sediment-associated microalgal respiration is expected to be between 15 and 34% of hourly gross primary production associated with the sediment. Further research is necessary to evaluate the potential contribution of bacteria to the measurement of microalgal respiration.

The ratio of chlorophyll *a* concentration to organic matter concentration was determined experimentally from isolated assemblages of epipelic diatoms. These results were similar to values reported by Jonge (1980). However, Jonge cautioned that chlorophyll *a* concentration was insufficient to describe fluctuations in sediment-associated microalgal biomass over a period of time because of the change in the ratio of chlorophyll *a* concentration to organic matter with time. This ratio was similar between different sites at any one time and therefore made chlorophyll *a* concentration a useful measure of microalgal biomass for comparison of sites at any single time (Jonge, 1980). Information concerning seasonal changes in the ratio of chlorophyll *a* concentration to organic matter concentration is necessary to eliminate potential error in the estimation of microalgal biomass from measurements of chlorophyll _a_ concentration. Jonge (1980) found a negative correlation between specific growth rate of microalgae and this ratio.

Primary production and biomass of sediment-associated macroalgae were measured separately. Ratios of gross primary production to chlorophyll _a_ concentration were the same order of magnitude as those measured for isolated diatom assemblages, but an order of magnitude higher than those for microalgae in intact sediment. Macroalgae were found to be very productive. Although their photosynthetic rates were similar to rates reported previously on a gram dry weight basis, mean biomass and the mean hourly rate of net primary production were much higher for _Enteromorpha_ and _Ulva_ in Oregon estuaries than had been previously reported for other estuaries (Littler _et al_., 1979; King and Schramm, 1976; Buesa, 1977; Conover, 1958). The biomass and mean hourly rate of net primary production for _Gracilaria_ were similar to values reported in previous investigations (Lapointe _et al_., 1976; Dawes _et al_., 1978). Light saturation of macroalgal photosynthesis was similar to that for microalgal photosynthesis and agreed well with previously measured values (King and Schramm, 1976; Dawes _et al_., 1978; Ramus and Rosenberg, 1980). Ramus and Rosenberg (1980) found distinct diurnal variation in photosynthesis of macroalgae. However, this pattern was not observed for macroalgae collected from Yaquina Bay. Perhaps the lack of diurnal variation was the results of the relatively low incubation temperature used in this study (mean value of 14°C). No inhibition of photosynthesis at full sunlight was observed.

The net daily primary production of sediment-associated algae was estimated to compare the productive potential of green algae, red algae and sediment-associated microalgae (Table 20). Estimates for macroalgae were made assuming a daylength present during the period of maximum growth and biomass as measured at the intensive study sites. Microalgal biomass was estimated from chlorophyll *a* concentrations at the intensive study sites during maximum growth. Net primary production and respiration rates of macroalgae per hour were taken from Table 19. Net primary production and respiration rates per hour were estimated from measurements of gross primary production during maximum growth using the conversion factors given in Table 18. Daily net primary production was estimated by summing net primary production during daylight hours and subtracting respiration during the remaining dark hours of the day.

Macroalgae were highly productive (20 to 27% growth per day), especially *Enteromorpha* and *Ulva*, which represent large seasonal inputs of organic matter into Oregon estuaries. Other studies of growth of *Gracilaria* showed a similar percentage growth per day (DeBoer *et al.*, 1978; Lapointe *et al.*, 1976). Mean sediment-associated microalgal production in the summer was much less than that of macroalgae (3.09% growth per day). Admiraal and Peletier (1980) found similar growth rates in intact sediment-associated diatom populations. Macroalgae are probably able to grow at a much greater rate than sediment-associated microalgae because of their ability to live on

Table 20. Daily net primary production of sediment-associated algae in Yaquina Bay. Algae are: *Enteromorpha prolifera*, *Ulva expansa*, *Gracilaria verrucosa* and sediment-associated microalgae (predominately diatoms). Data are from Tables 18 and 19, and field observations. Daylength is expressed as mean hours during the growing season, and biomass as mean values during the growing season. The growing season for *Enteromorpha* and *Ulva* was between June and August; for *Gracilaria* was between March and May; and for microalgae was between April and September.

	Enteromorpha and *Ulva*	*Gracilaria*	Microalgae
DAYLENGTH (hours)	12	9	12
BIOMASS ($g\ C \cdot m^{-2}$)	148.5	6.5	8.3
NET PRODUCTION ($g\ C \cdot m^{-2} \cdot h^{-1}$)	4.50	0.20	0.045
RESPIRATION ($g\ C \cdot m^{-2} \cdot h^{-1}$)	0.63	0.02	0.023
DAILY NET PRODUCTION ($g\ C \cdot m^{-2} \cdot d^{-1}$)	46.44	1.50	0.26
% GROWTH/DAY[a]	27.21	20.76	3.09

a) % Growth/Day = $100(\ln(N_t/N_0))/t$; where N_0 is the biomass at time sero, N_t is the biomass at time t and t is in days.

the sediment and in the water column, and their greater rate of photosynthesis per unit chlorophyll a. The macroalgae can absorb nutrients from the sediment at low tide and maximize light capture by becoming suspended in the water column during periods of inundation (Welsh, 1980). Sediment-associated microalgae can also become suspended during inundation, but their growth is probably limited by turbidity created by sediment particles associated with the microalgae and their mucus (Baillie and Welsh, 1980).

IV. EFFECTS OF ESTUARINE INFAUNA ON SEDIMENT-ASSOCIATED MICROALGAE

Introduction

Estuarine sand and mud habitats harbor diverse assemblages of pennate diatoms, blue-green algae and flagellates (Fenchel, 1969). These microalgae can be highly productive (Pomeroy, 1959; Cadée and Hegeman, 1974). Physical factors such as light, temperature, and sediment type play an important role in regulating the distribution and abundance of sediment-associated microalgae (Pomeroy, 1959; Cadée and Hegeman, 1974). However, nutrients usually do not limit algal production (Admiraal, 1977d) because of relatively high concentrations in estuaries and the release of nutrients from sediments (Montgomery *et al.*, 1979; Welsh, 1980).

The importance of biotic factors in regulating sediment-associated microalgae is poorly understood. Many epifaunal and infaunal deposit-feeders ingest and assimilate microalgae (Sanders *et al.*, 1962; Levinton, 1980). Experimental manipulations of the estuarine gastropods *Hydrobia* spp. (Fenchel and Kofoed, 1976), *Nassarius obsoletus* (Say)(Pace *et al.*, 1979) and *Bembicium auratum* (Quoy and Gainard) (Branch and Branch, 1980) demonstrated that epifaunal deposit-feeders can regulate microalgal biomass. A freshwater epibenthic amphipod, *Hyalella azteca* (Sauggure), either stimulated or depressed microalgal production depending on amphipod density (Hargrave, 1970). Experimental studies of infaunal regulation of microalgae include the investigation by White _et al._ (1980) who found that the sand dollar, _Mellita quinquiesperforata_ (Leske), had no significant effect on chlorophyll _a_ concentration in sediment and the study by Coles (1979), who gave qualitative data for regulation of microalgae by infauna.

Defaunated sediment in Yaquina Bay developed a golden brown "diatom" layer within a few days of transplantation during the spring and summer (Lee, H. and Lee, J., unpublished). This suggested the hypotheses that microalgal colonization was rapid and that infauna limited microalgal production. To test these hypotheses, microalgal colonization of defaunated sediment in the field and the laboratory was examined. Results of these experiments and discussion of the role of infauna in the control of sediment-associated microalgae are presented here.

Methods

1. Study Site

Experiments were performed on an intertidal sand flat in Yaquina Bay, Oregon (44°35' N; 124°04' W) adjacent to the Oregon State University Marine Science Center and in a laboratory at the Marine Science Center. The field study site was 1.0 to 1.1 m above Mean Lower Low water (MLLW) and was exposed twice daily to the air for an average period of six hours per day. The maximum tidal amplitude was 3.0 m, and the sediment mean grain size was 2.64 phi, a fine sand. The microalgal community was composed primarily of a diverse assemblage of pennate diatoms (Amspoker and McIntire, 1978). During the summer, the macroalgae Enteromorpha prolifera (Müll) J.Ag. and Ulva expansa (Setch.) S.&G. covered a large portion of the study site. Seasonal rates of gross primary production by sediment-associated microalgae ranged from 20 to 150 mg $C \cdot m^{-2} \cdot h^{-1}$ (see Chapter 3).

2. Experimental Design

The effect of infauna on microalgae was evaluated by comparing the microalgal biomass and production on undisturbed sediment with that associated with defaunated sediment. Defaunated sediment was sediment collected at the field site, sieved through a 1.0 mm mesh screen and frozen for approximately one month. In the field experiment, defaunated sediment was placed in cylinders of fiberglass screening (1.5 mm mesh). The cylinders enclosed 411.9 cm^2 of surface area, were 10 cm deep and were completely embedded within the sediment. Eight defaunated sediment cylinders and eight control cylinders of unmanipulated sediment were randomly assigned to 57 x 57 cm plots within a 285 x 285 cm block, and the experiment was initiated in June, 1980. Macroalgae were periodically removed from the study site. Defaunated and control cylinders were sampled 1, 10 and 40 days after transplanting the defauntated sediment into the field. At each sampling date, two defaunated and two control cylinders were sampled by taking three cores (45.6 cm^2 surface area and 4 cm deep) within each cylinder. These cores were brought into the laboratory and used for measurements of primary production, community oxygen uptake, chlorophyll a concentration and macrofaunal abundance.

In the laboratory experiment, cores (36.3 cm^2 surface area and 4 cm deep) were taken in the field or made with defaunated sediment. Both types of cores were maintained in flowing seawater. The seawater was sand-filtered and UV-treated and had a temperature of 11.0 ± 1.0°C and a salinity of 30 °/oo. Light was supplied by cool-white flourescent and incandescent lamps at 150 $\mu E \cdot m^{-2} \cdot sec^{-1}$ photosynthetically active radiation with a 12-hour light and 12-hour dark photoperiod. Light was measured with a Licor® quantum meter and salinity with a AO Goldberg® temperature-compensanted refractometer. The laboratory experiment was initiated in January, 1981. The rate of primary production and community oxygen uptake, chlorophyll a concentration and macrofaunal abundance were determined 1, 10 and 40 days after initiation of the experiment. Three cores of each treatment were sampled on each of the three dates. On day 39, three cores were sampled from the field site where the control cores were obtained. The rate of primary production and community oxygen uptake, chlorophyll a concentration and macrofaunal abundance associated with these cores were compared with those associated with the control cores at day 40 to determine the effects of maintaining cores in the laboratory.

3. Primary Production

Gross primary production and community oxygen uptake were estimated in the laboratory from oxygen measurements in stirred, light and dark plexiglas chambers designed to hold intact cores of sediment (see Chapter 3; Figures 18 and 19). Rates of oxygen evolution and uptake were based on measurement periods of 0.5 to 1.0 hour between initial and final readings. Measurements of dissolved oxygen were made polargraphically, with an Orbisphere® salinity-corrected dissolved oxygen system. Chambers were incubated at 13° to 14°C, a light intensity of 210 $\mu E \cdot m^{-2} \cdot sec^{-1}$ and a salinity of 30 °/oo. All chambers were preincubated in the dark for 1.0 hour. In the field experiment, three cores from a defaunated or control cylinder were incubated in a plexiglas chamber, and two replicate chambers were used for estimates of primary production. In the laboratory experiment, three replicate chambers were used, each holding one intact core.

Gross primary production was estimated by adding the rate of community oxygen uptake in the dark to the rate of net community production in the light for an equivalent period of time. Estimated rates of gross primary production in mg $O_2 \cdot m^{-2} \cdot h^{-1}$ were converted to mg $C \cdot m^{-2} \cdot h^{-1}$ while assuming a photosynthetic quotient of 1.2 (i.e., mg C = 0.312 x mg O_2). Estimated rates of community oxygen uptake in mg $O_2 \cdot m^{-2} \cdot h^{-1}$ were converted to mg $C \cdot m^{-2} \cdot h^{-1}$ while assuming a respiratory quotient of 1.0 (i.e., mg C = 0.375 x mg O_2)(Westlake, 1965).

4. Chlorophyll *a* Analysis

Samples for chlorophyll *a* analysis were collected using a 12-cm long plastic corer of 2.3 cm diameter. The corers were gently pressed 3 cm into the sediment from which estimates of primary production had been made. The cores were frozen intact and the top cm was excised with a knife. A core section was placed in a mortar with 0.5 ml of saturated magnesium carbonate solution and 10 ml of 90% acetone (v/v), and ground with a pestle for one minute. The extract was centrifuged after storage at 4°C in the dark for 24 hours. Chlorophyll *a* concentration was measured using the method of Strickland and Parsons (1972). The Lorenzen equation (corrected for phaeopigments) was used to calculate mg chlorophyll $a \cdot m^{-2}$. These values are uncorrected for chlorophyllide, but are useful for comparing the effect of grazing on adjacent plots (Whitney and Darley, 1979; Pace *et al*., 1979).

5. Macrofaunal Abundance

After removing the subcores for chlorophyll *a* analysis, the remaining sediment in each field core (surface area of 40.05 cm^2) or laboratory core (32.15 cm^2) was sieved through a 1.0 mm mesh screen. The residue was preserved in buffered 10% seawater formalin which was dyed with rose bengal stain. Later the residue was sorted under 12x magnification and the animals identified.

6. Statistical Analysis

Effects of time and defaunation on microalgal biomass, gross primary production, community oxygen uptake and animal abundance was examined by an analysis of variance (ANOVA) using the SPSS programs (Nie et al., 1975). A one-way ANOVA was performed to analyze the effect of time on microalgal processes in the control and defaunation replicates separately. The effects of time and defaunation were investigated in all samples using a two-way ANOVA. The small-sample t-test was used to test the hypothesis that means were equal for specific dates.

Before data analysis, infaunal abundance values were transformed by the expression $y = \log_{10}(x + 1)$, where x was the number of organisms per m^2 of sediment surface area. Data expressing chlorophyll *a* concentration, and rates of primary production and community oxygen uptake were not transformed before analysis. In the field experiment, data for the three cores from each defaunated or control cylinder were averaged, resulting in two replicates for each of the two treatments at each sampling date. In the laboratory experiment, each core was analyzed independently, resulting in three replicates for each treatment at each sampling date.

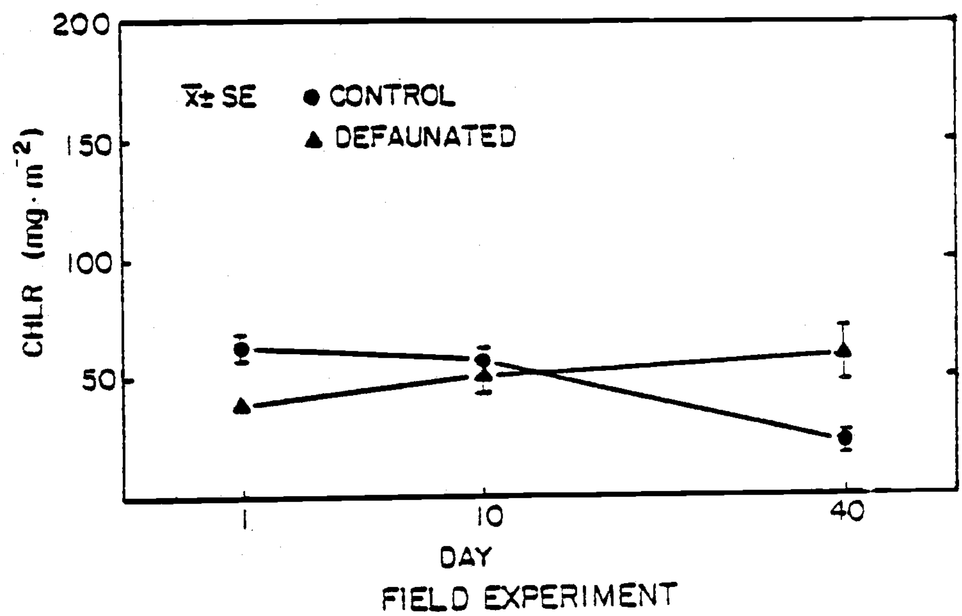
Results

1. Field Defaunation Experiment

Chlorophyll _a_ concentration in control sediment decreased significantly ($p < .05$) during the 40 day experiment, whereas chlorophyll _a_ in defaunated sediment increased significantly ($p < .01$) during this period (Figure 21). Colonization of defaunated sediment by microalgae was evident as golden-brown patches where defaunated sediment had been transplanted. This pattern resulted in a significant ($p < .01$) two-way interaction between time and defaunation relative to chlorophyll concentration. However, neither gross primary production (Figure 21) nor community oxygen uptake (Figure 22) varied significantly over time or between control and defaunated sediment. Also, total infauna abundance in control sediment did not vary significantly over time, while animals in defaunated sediment increased significantly ($p < .05$) to control values by day 40 (Figure 22). The tanaid, _Leptochelia dubia_ (Kroyer), constituted greater than 63% of the individuals in defaunated and control sediment, while other abundant infaunal taxa were spionids, capitellids, amphipods and the venerid bivalve _Transennella tantilla_ (Gould); epifaunal species were not abundant at the study site.

2. Laboratory Defaunation Experiment

To better evaluate the influence of the infauna on biomass and



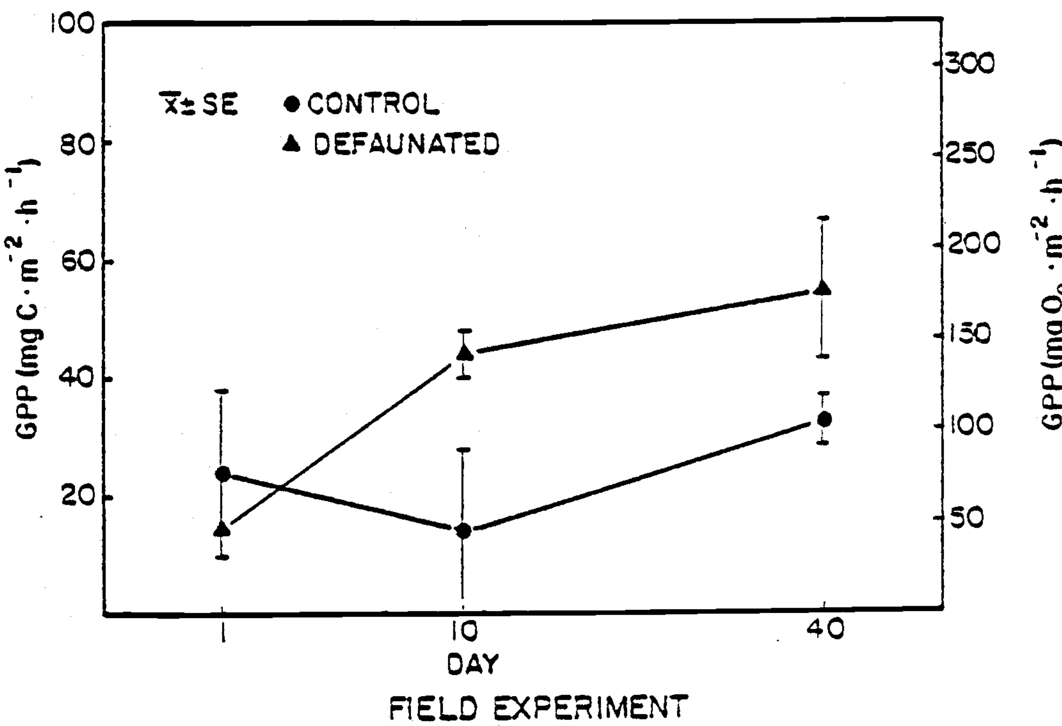


Figure 21. Concentration of chlorophyll a and rate of gross primary production during the field defaunation experiment in June, 1980. Values are means of two replicates ± one standard error.

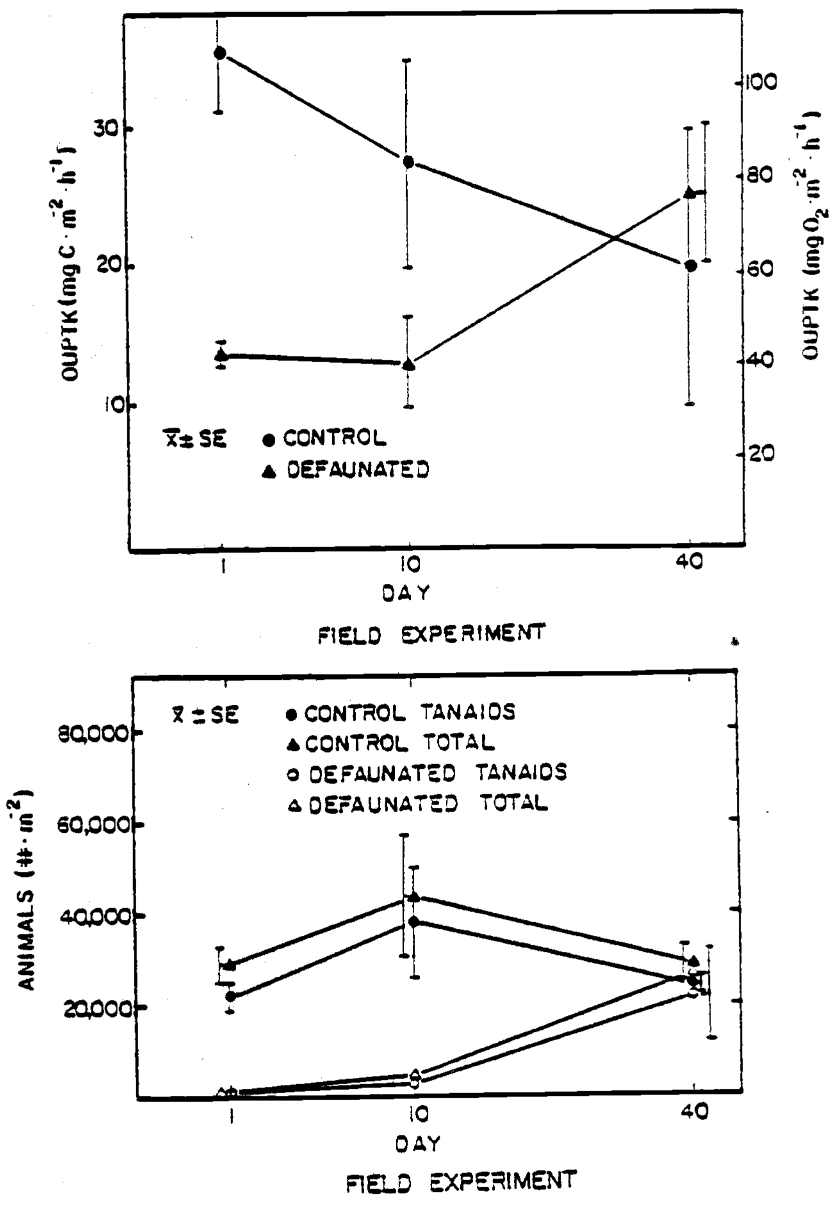


Figure 22. Rate of community oxygen uptake and abundance of animals during the field defaunation experiment in June, 1980. Values are means of two replicates ± one standard error.

production of microalgae, a laboratory experiment was performed which eliminated the confounding effects of import-export of microalgae and infaunal colonization. Similarity of levels of chlorophyll *a*, gross primary production, community oxygen uptake and infaunal abundance between control cores held in the laboratory for 40 days and the natural field community suggested that maintenance of cores did not affect community structure or function. Therefore, the laboratory experiment was an appropriate method to determine effects of infauna on sediment-associated microalgae.

The chlorophyll *a* concentration in control sediment did not vary significantly over time (Figure 23). A two-way ANOVA indicated that there were significant time ($p < .05$) and defaunation ($p < .01$) effects on chlorophyll *a* concentration. By day 40, chlorophyll *a* concentration was approximately four times greater in defaunated sediment than in control sediment (t-test significant at $p < .05$). Gross primary production in control sediment did not vary significantly over 40 days, but increased significantly ($p < .01$) with time in defaunated sediment (Figure 23). A two-way ANOVA indicated significant effects ($p < .01$) of time and a two-way interaction between time and defaunation relative to gross primary production. Both effects resulted from gross primary production associated with defaunated sediment starting at zero and reaching high values by day 10. By day 40 gross primary production was approximately 2 times greater in defaunated sediment than in control sediment (t-test significant at $p < .05$). Community oxygen uptake in control sediment did not vary

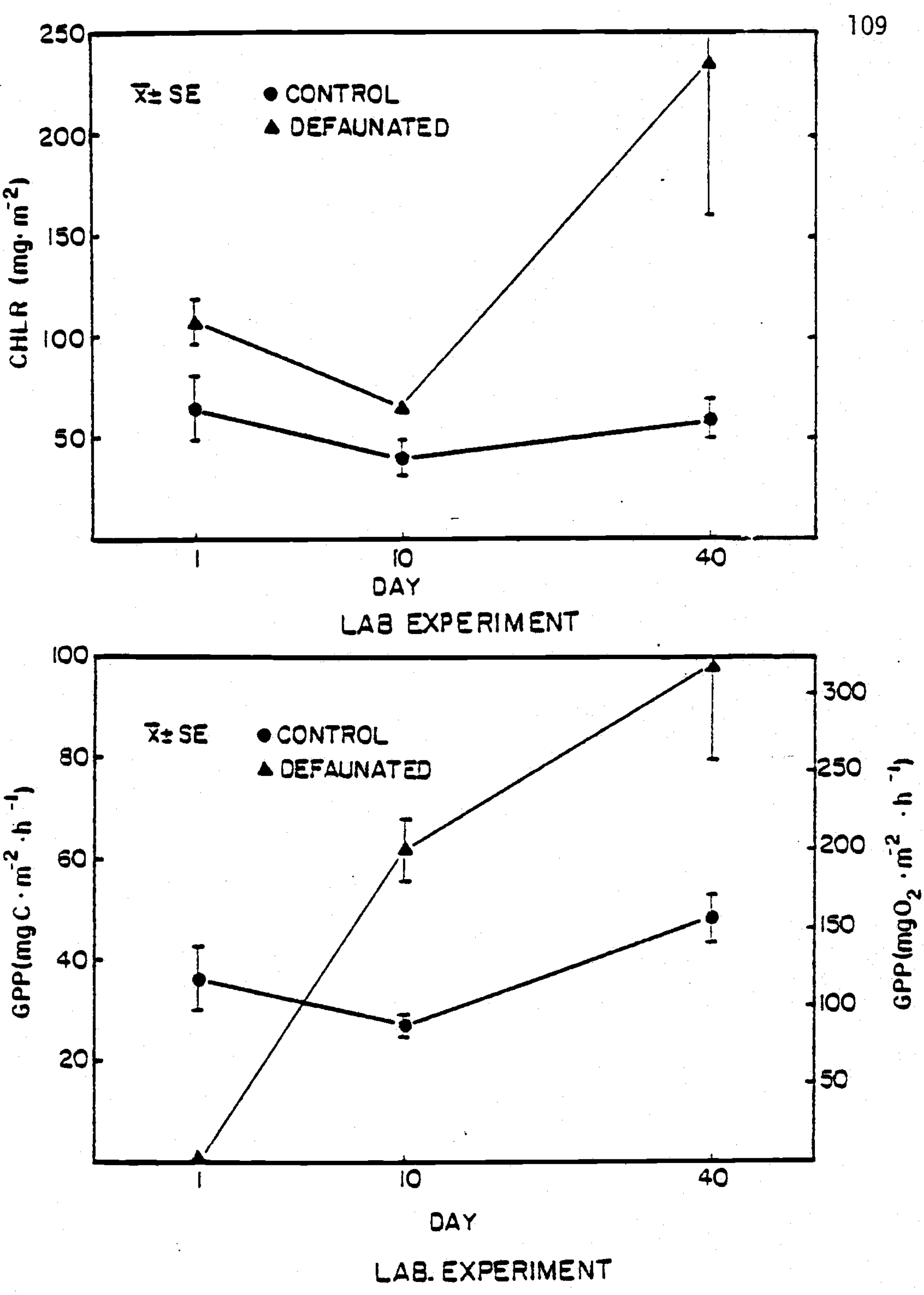


Figure 23. Concentration of chlorophyll a and rate of gross primary production during the laboratory defaunation experiment in January, 1981. Values are means of three replicates ± one standard error.

significantly during the experiment (Figure 24). A two-way ANOVA indicated significant effects ($p < .05$) of defaunation and a two-way interaction between time and defaunation relative to community oxygen uptake.

Total infaunal abundance in control sediment did not vary significantly during the experiment, whereas infaunal abundance in defaunated sediment was zero on days 1 and 10 and then increased to 311 tanaids$\cdot m^{-2}$ on day 40 (Figure 24). _Leptochelia dubia_ constituted greater than 75% of the individuals in control sediment, while other abundant taxa in control sediment included spionids, capitellids and amphipods.

Discussion

Microalgal colonization of defaunated sediment in the field as measured by gross primary production was rapid. Chlorophyll _a_ appeared to increase rapidly although it was not possible to separate the effects of chlorophyllides initially in the defaunated sediment from the import of microalgae. Placement of defaunated sediment in the field simulated localized natural disturbances such as those caused by epibenthic fishes and invertibrates or bioturbation (Lee and Swartz, 1980). The rapid colonization of microalgal production and possibly biomass after animal removal indicated that microalgal assemblages were responsive to small scale disturbances. This response was probably facilitated both by rapid growth of microalgae (Admiraal

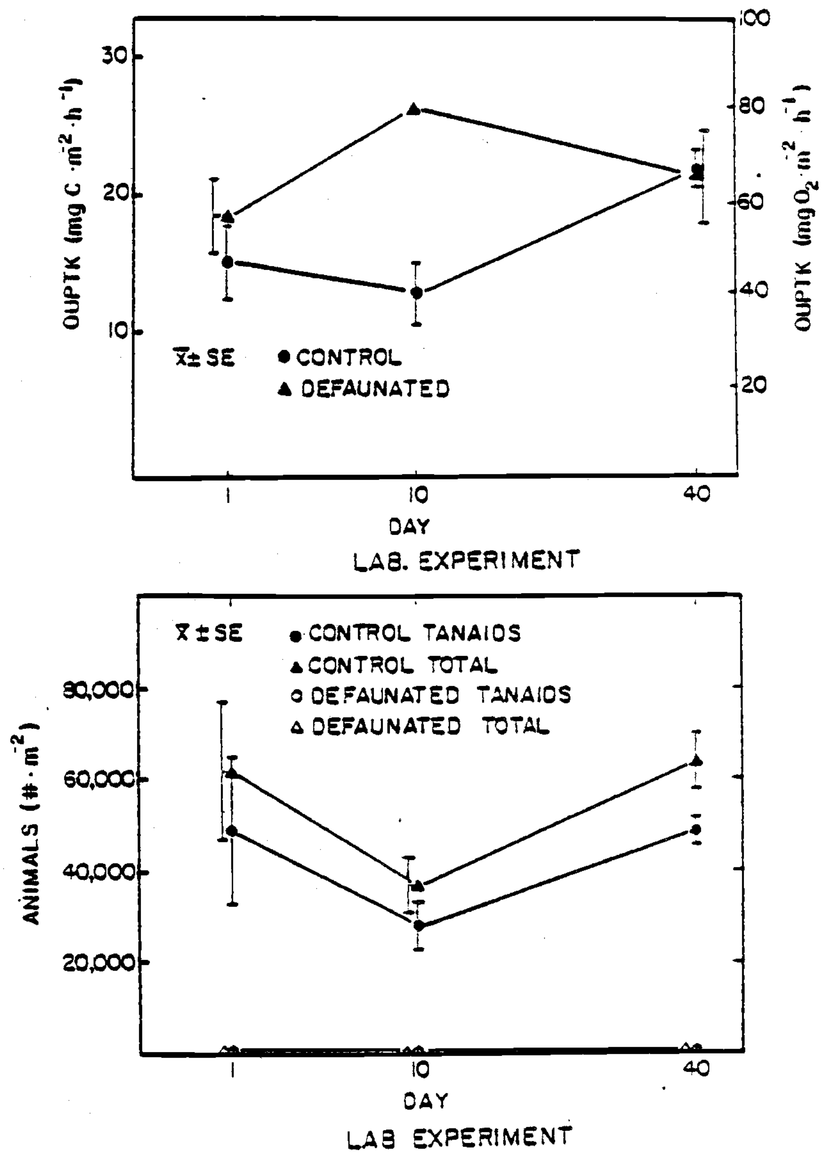


Figure 24. Rate of community oxygen uptake and abundance of animals during the laboratory defaunation experiment in January, 1981. Values are means of three replicates $\pm$ one standard error.

and Peletire, 1980) and by transport of microalgae into disturbed areas (e.g. Tenore, 1977; Baillie and Welsh, 1980). Rapid colonization on a localized scale does not imply that microalgae are resistant to a generalized stress (e.g. pollution) or overlapping localized disturbances created by the burrowing activities of larger animals. It was hypothesized that removal of infauna would increase microalgal production and biomass in the field, but this result was not observed. The possible import of microalgae into defaunated sediment during initial stages of colonization, export during later stages of colonization and initial presence of chlorophyllides in defaunated sediment would tend to minimize differences in chlorophyll _a_ concentration and gross primary production between control and defaunated sites. Recolonization of defaunated sites by infauna could also minimize differences between treatments.

In the laboratory, removal of infauna caused a significant increase in microalgal biomass and production. The relatively high concentration of chlorophyll _a_ in defaunated sediment by day 1 was not functional, as indicated by the zero rate of gross primary production. Growth of microalgae was indicated by an increase in gross primary production by day 10, although chlorophyll _a_ concentration remained constant, and by the higher concentration of chlorophyll _a_ and gross primary production relative to control values on day 40. These results indicate that natural densities of infauna limit both microalgal biomass and production. Similar results have been found for several estuarine gastropods (Fenchel and Kofoed, 1976; Pace et al., 1979; Branch and Branch, 1980). Natural infaunal densities at the study site exceeded the level at which microalgal and microbial populations are stimulated by consumption of senescent cells or nutrient additions (Hargrave, 1970, 1976; Cooper, 1973; Pace et al., 1979; Porter, 1976).

Grazing is the most likely mechanism by which infauna limited microalgal biomass and production in this study. The most abundant species at the study site, Leptochelia dubia, contained both broken and whole diatom frustules in its gut, an observation that indicates herbivory. Kneib, et al. (1980) reported that another tanaid, Leptochelia rapax (Harger), consumes microalgae. Burial of cells by sediment turnover is another mechanism by which infauna can limit microalgae. However, Leptochelia does not appear to turn over large quantities of sediment (Meyers, 1977), and large sediment reworkers such as Callianassa and Upogebia were not abundant at the study site. The process of defaunation may increase nutrients which are released from dead animals, plants and bacteria which were killed by freezing. These nutrients could in turn stimulate microalgal growth. However, field and laboratory nutrient-addition experiments at the study site showed that sediment-associated microalgae apparently were not nutrient-limited (Cardon, 1981).

Patterns of community oxygen uptake were difficult to interpret. In the field, community oxygen uptake in defaunated sediment recovered to control values between days 10 and 40. In the laboratory, community oxygen uptake of defaunated sediment was initially identical to control sediment, increased between day 1 and 10 and decreased to control values between day 10 and 40. Causes for the different patterns in the field and laboratory experiments were not apparent. The low macrofaunal density (0 to 311 animals$\cdot m^{-2}$) and diversity (0 to 1 species) in the defaunated sediment in the laboratory would normally constitute strong evidence for a highly degraded benthic community. Yet community oxygen uptake at day 40 was the same for control and defaunated sediment. This similarity of community metabolism between these radically different benthic communities indicates that there is no simple relationship between community oxygen uptake and community structure.

Experimental evidence has been presented for a limiting effect of infaunal animals on estuarine sediment-associated microalgae. As suggested by Pace et al., (1979), herbivory is one of the factors regulating microalgal biomass and production although its relative importance, compared to other factors, is unknown. Differences in infaunal abundance and activity may be one of the factors influencing both spatial and temporal patterns of microalgae (e.g. Cadée and Hegeman, 1974; Coles, 1979). The influence of animals on plant communities is a widespread phenomenon and should not be ignored when assessing controlling factors of plant growth (Brook, 1955, 1975).

V. CONCLUSIONS

The primary goal of this study was to investigate the production dynamics of sediment-associated algae in two Oregon estuaries. The process of sediment-associated algal primary production was conceptualized as a set of variables, interaction functions and parameters which are associated with algal primary production and biomass (see Chapter 1, Figure 2). These variables were investigated in the field and in the laboratory in order to observe seasonal patterns of primary production and associated variables, and to examine hypotheses concerning the mechanisms that control algal primary production.

The process of sediment-associated algal primary production is a subprocess of primary food processes and is viewed as being linked with other processes on the same or higher levels of organization of biological processes in an estuary (see Chapter 1, Figures 1 and 2). In Netarts Bay, carbon from microalgal net primary production could account for 39, 12 and 5% of the non-algal community oxygen uptake at the SAND, FINE SAND and SILT sites, respectively. Net primary production by Enteromorpha was an order of magnitude greater than non-algal community oxygen uptake. This primary production was exported seasonally from the Sediment Processes to the Water Column Processes and Marsh Processes.

Primary production by sediment-associated macroalgae and by the seagrass Zostera can be exported into Detritus Decomposition

Processes and ultimately into Consumer Processes in the water column, sediment and high marsh. Few studies have included macroalgal primary production as an important contribution to the estuarine detrital food web, and further research into the sources and fates of this production is recommended (Josselyn and Mathieson, 1980). Other studies have shown that resuspended benthic microalgae also can contribute organic matter throughout the year to Consumer processes in the water column, sediment and high marsh (e.g., Baillie and Welsh, 1980; Tenore, 1977).

The pattern of values for variables associated with estuarine biological sediment processes was controlled by season, sediment type and tidal height. These variables included primary production, community oxygen uptake and the concentration of chlorophyll a and organic matter. Sediment-associated primary production and community oxygen uptake were highest during the summer, a pattern associated with a relatively long daylength and high temperature. Organic matter concentration also was highest during the summer during a period of relatively high production and the concurrent incorporation of organic matter into the sediment. Chlorophyll a concentration was highest during the spring and fall, associated with low animal activity and fair weather. Mean annual chlorophyll a and organic matter concentrations were highest at the SILT site, followed by the FINE SAND and SAND sites. Primary production and community oxygen uptake were highest at the FINE SAND site, while the SILT site had the lowest primary production and the SAND site had the lowest community oxygen uptake.

The effect of tidal height was complex and different at each intensive study site. At the SAND site, chlorophyll a concentration was highest at the lower tidal heights. The opposite pattern was apparent at the FINE SAND and SILT sites, where blue-green algae produced large biomasses during the spring and fall at mean high water. Organic matter concentration followed the same pattern as chlorophyll a concentration with respect to tidal height. Large rafts of Enteromorpha and Zostera were periodically transported to the strand line at mean high water where they decomposed and entered the detritus pool of sediment, water column and high marsh.

A conceptual model of sediment-associated algal primary production was developed to organize the mechanistic knowledge of algal primary production in Oregon estuaries. This model is useful for the conceptualization of processes related to algal primary production and biomass associated with estuarine sediment. Moreover, the model helps in the establishement of research priorities and hypotheses which can be tested under controlled conditions in the laboratory and in the field. Some of these hypotheses are:

1) Sediment-associated primary production is limited by daylength and scouring of the sediment which is caused by water currents and biotic interactions of macroalgae and animals.
2) Microalgal biomass is closely related to consumer and resuspension processes.

3) The relationship between algal biomass and primary production is controlled by migration patterns and the periodic growth and senescence of algal populations.

4) Microalgae are a useful food resource for estuarine benthic consumers.

5) Production by macroalgae is rapidly decomposed and incorporated into the sediment, water column and high marsh.

6) Macroalgal production creates habitats and food for estuarine detrital food webs.

7) Although microalgae are apparently not nutrient-limited in Oregon estuaries, growth of macroalgae is probably related to nutrient concentrations and could control these concentrations in the estuarine water column during the summer growing season.

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APPENDICES

Appendix Table 1. Annual means of sediment-associated biological variables in Netarts Bay at SAND, FINE SAND and SILT sites. Intertidal levels are above MLLW: 0.5 m (1), 1.0 m (2), 1.5 m (3) and 2.0 m (4). Values are expressed as means of n replicates ± one standard error.

		n	$\bar{x}$	SE
Chlorophyll a concentration at the 0 to 1 cm depth ($mg \cdot m^{-2}$)				
SAND				
	Level 1	10	79.71	11.59
	2	12	66.09	13.24
	3	12	25.12	4.83
	4	11	16.94	2.81
FINE SAND				
	1	6	83.12	20.16
	2	12	54.73	13.26
	3	12	73.90	12.41
	4	12	91.34	3.89
SILT				
	1	10	49.50	8.87
	2	12	69.16	20.89
	3	12	82.86	9.61
	4	12	165.91	24.45
Organic matter concentration at the 0 to 1 cm depth ($g \cdot m^{-2}$)				
SAND				
	Level 1	10	196.95	15.71
	2	11	138.88	14.72
	3	11	119.73	9.93
	4	11	86.36	7.41
FINE SAND				
	1	6	182.11	23.20
	2	10	201.53	20.30
	3	11	205.38	16.82
	4	11	216.38	17.02
SILT				
	1	10	385.99	19.09
	2	11	350.07	20.18
	3	11	325.61	19.42
	4	11	450.11	33.59

Appendix Table 1. (continued)

		n	$\bar{x}$	SE
Ratio of chlorophyll *a* concentration at the 0 to 1 cm depth to the concentration at the 4 to 5 cm depth				
SAND				
	Level 1	10	2.25	0.38
	2	11	2.40	0.49
	3	11	56.13	39.80
	4	11	102.53	26.94
FINE SAND				
	1	6	1.21	0.21
	2	10	3.25	1.81
	3	11	1.27	0.22
	4	11	27.27	50.23
SILT				
	1	10	1.53	0.22
	2	11	3.29	4.19
	3	11	1.51	0.24
	4	11	38.77	69.74
Ratio of organic matter concentration at the 0 to 1 cm depth to the concentration at the 4 to 5 cm depth				
SAND				
	Level 1	10	1.49	0.15
	2	11	1.18	0.09
	3	11	1.05	0.10
	4	11	5.20	5.88
FINE SAND				
	1	6	0.93	0.11
	2	10	1.24	0.22
	3	11	0.96	0.09
	4	11	1.32	0.14
SILT				
	1	10	1.06	0.09
	2	11	0.99	0.08
	3	11	0.99	0.08
	4	11	1.33	0.13

Appendix Table 1. (continued)

		n	$\bar{x}$	SE
Chlorophyll *a* concentration at the 0 to 1 cm depth associated with the cores used in measurements of primary production ($mg \cdot m^{-2}$)				
SAND				
	Level 1	7	65.11	7.23
	2	8	81.84	31.44
	3	8	22.50	3.61
	4	2	20.55	9.41
FINE SAND				
	1	4	37.56	3.98
	2	8	44.75	9.33
	3	8	54.26	7.88
	4	2	61.83	17.54
SILT				
	1	7	39.21	9.84
	2	8	37.12	4.53
	3	8	48.31	6.04
	4	3	163.33	34.44
Gross primary production ($mg\ C \cdot m^{-2} \cdot h^{-1}$) assuming a photosynthetic quotient of 1.2				
SAND				
	Level 1	7	35.80	7.26
	2	8	62.16	21.28
	3	8	23.04	3.38
	4	2	8.98	2.34
FINE SAND				
	1	4	84.88	65.75
	2	8	40.78	15.53
	3	8	47.13	19.11
	4	2	27.10	14.56
SILT				
	1	7	20.07	5.75
	2	8	19.34	4.46
	3	8	21.42	4.25
	4	3	53.70	22.12

Appendix Table 1. (continued)

	n	$\bar{x}$	SE
Community oxygen uptake (mg $C \cdot m^{-2} \cdot h^{-1}$) assuming a respiratory quotient of 1.0			
SAND			
Level 1	7	13.81	2.31
2	8	17.72	3.57
3	8	6.57	2.33
4	2	1.20	1.20
FINE SAND			
1	4	21.18	6.50
2	8	28.98	6.49
3	8	29.05	8.12
4	2	24.63	5.76
SILT			
1	7	22.74	5.56
2	8	17.23	3.48
3	8	20.67	4.22
4	3	7.93	2.33
Ratio of daily gross primary production to daily community oxygen uptake			
SAND			
Level 1	7	1.13	0.17
2	8	1.56	0.40
3	8	7.24	5.19
4	2	0.71	0.33
FINE SAND			
1	4	1.42	0.86
2	8	0.65	0.26
3	8	0.69	0.21
4	2	0.27	0.21
SILT			
1	7	0.44	0.14
2	8	0.48	0.07
3	8	0.51	0.09
4	3	2.86	1.47

Appendix Table 1. (continued)

	n	$\bar{x}$	SE
Ratio of gross primary production to chlorophyll *a* concentration (mg C·mg chlorophyll $\underline{a}^{-1}\cdot h^{-1}$)			
SAND			
Level 1	7	0.55	0.10
2	8	1.16	0.41
3	8	1.17	0.17
4	2	0.67	0.36
FINE SAND			
1	4	2.13	1.62
2	8	1.13	0.62
3	8	1.30	0.83
4	2	0.41	0.23
SILT			
1	7	0.57	0.12
2	8	0.54	0.15
3	8	0.54	0.16
4	3	0.31	0.08

Appendix Table 2. Monthly mean sediment-associated microalgal biomass (g $C \cdot m^{-2}$) and production (g $C \cdot m^{-2} \cdot mo^{-1}$) at Netarts Bay at SAND, FINE SAND and SILT sites (0.5 m to 2.0 m above MLLW). Variables include: daylength (DAYL), biomass of microalgae (BIOMASS), gross primary production (GPP), microalgal respiration (RESP), net primary production (NPP), community oxygen uptake (OUPTK) and non-algal community oxygen uptake (NON-ALGAL OUPTK). Grams oxygen per hour were converted to grams carbon per hour assuming a PQ = 1.2 and RQ = 1.0.

	DAYL	BIOMASS	GPP	RESP	NPP	OUPTK	NON-ALGAL OUPTK
SAND							
DECEMBER	6.0	1.88	4.86	6.61	-1.75	8.64	2.03
JANUARY	6.5	3.43	4.80	5.85	-1.05	7.71	1.86
FEBRUARY	7.6	4.97	4.74	5.09	-0.35	6.78	1.69
MARCH	8.9	5.73	10.68	9.79	0.89	10.80	1.01
APRIL	10.4	6.98	9.36	7.34	2.02	10.80	3.46
MAY	11.6	1.83	7.53	5.30	2.23	9.22	3.92
JUNE	12.2	3.32	8.81	5.89	2.92	11.79	5.90
JULY	12.0	5.38	13.55	9.21	4.34	16.70	7.49
AUGUST	10.9	4.42	15.63	11.70	3.93	12.43	0.73
SEPTEMBER	9.5	4.89	6.63	5.75	0.88	7.85	2.10
OCTOBER	8.0	5.10	7.20	7.34	-0.14	7.92	0.58
NOVEMBER	6.8	3.88	7.28	8.73	-1.45	10.26	1.53
FINE SAND							
DECEMBER	6.0	3.95	2.70	3.67	-0.97	8.64	4.97
JANUARY	6.5	4.03	4.37	5.08	-0.71	8.82	3.74
FEBRUARY	7.6	4.11	6.04	6.48	-0.44	8.99	2.51
MARCH	8.9	11.93	5.34	4.90	0.44	14.40	9.50
APRIL	10.4	10.96	9.36	7.34	2.02	21.60	14.26
MAY	11.6	3.63	14.42	10.14	4.28	25.25	15.11
JUNE	12.2	7.06	10.95	7.32	3.63	24.53	17.21
JULY	12.0	4.51	8.15	5.54	2.61	20.71	15.17
AUGUST	10.9	3.45	20.35	15.24	5.11	36.34	21.10
SEPTEMBER	9.5	4.20	9.08	7.80	1.28	25.24	17.44
OCTOBER	8.0	3.91	4.80	4.90	-0.10	14.40	9.50
NOVEMBER	6.8	2.96	1.83	2.20	-0.37	8.17	5.97

Appendix Table 2. (continued)

	DAYL	BIOMASS	GPP	RESP	NPP	OUPTK	NON-ALGAL OUPTK
SILT							
DECEMBER	6.0	15.10	5.40	7.34	-1.94	10.80	3.46
JANUARY	6.5	4.00	5.97	7.18	-1.21	12.22	5.04
FEBRUARY	7.6	4.30	6.53	7.01	-0.48	13.63	6.62
MARCH	8.9	8.65	5.34	4.90	0.44	10.80	5.90
APRIL	10.4	8.22	6.24	4.90	1.34	10.80	5.90
MAY	11.6	2.84	7.21	5.07	2.14	11.52	6.45
JUNE	12.2	5.65	3.47	2.32	1.15	21.10	18.78
JULY	12.0	4.48	3.65	2.48	1.17	17.98	15.50
AUGUST	10.9	3.22	10.62	7.95	2.67	17.26	9.31
SEPTEMBER	9.5	5.26	6.18	5.31	0.87	17.88	12.57
OCTOBER	8.0	4.48	4.80	4.90	-0.10	10.80	5.90
NOVEMBER	6.8	3.59	3.62	4.34	-0.72	7.96	3.62