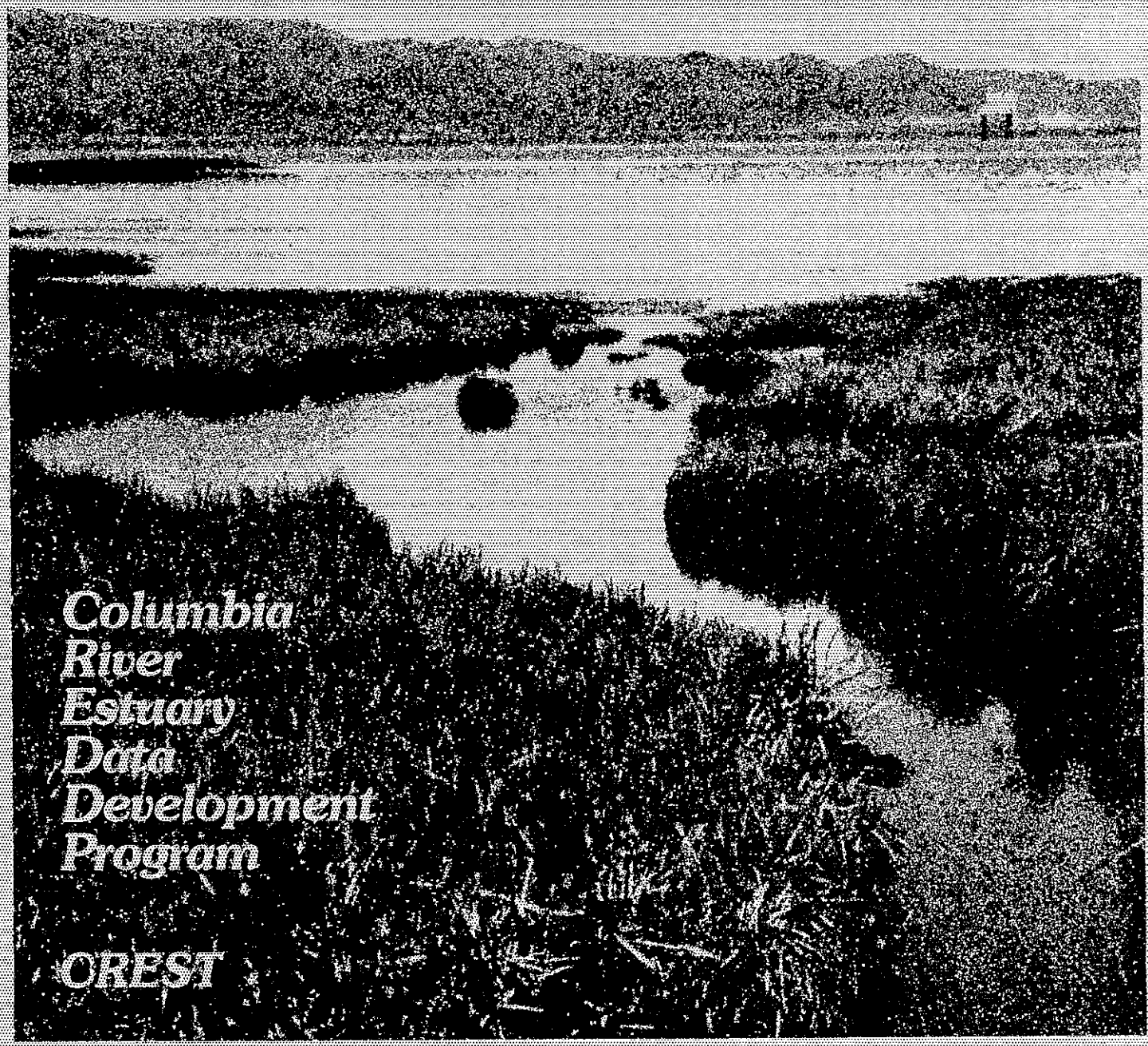
BENTHIC PRIMARY PRODUCTION IN THE COLUMBIA RIVER ESTUARY



Final Report on the Benthic Primary Production Work Unit

of the Columbia River Estuary Data Development Program

BENTHIC PRIMARY PRODUCTION IN THE COLUMBIA RIVER ESTUARY

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PREFACE

The Columbia River Estuary Data Development Program

This document is one of a set of publications and other materials produced by the Columbia River Estuary Data Development Program (CREDDP). CREDDP has two purposes: to increase understanding of the ecology of the Columbia River Estuary and to provide information useful in making land and water use decisions. The program was initiated by local governments and citizens who saw a need for a better information base for use in managing natural resources and in planning for development. In response to these concerns, the Governors of the states of Oregon and Washington requested in 1974 that the Pacific Northwest River Basins Commission (PNRBC) undertake an interdisciplinary ecological study of the estuary. At approximately the same time, local governments and port districts formed the Columbia River Estuary Study Taskforce (CREST) to develop a regional management plan for the estuary.

PNRBC produced a Plan of Study for a six-year, $6.2 million program which was authorized by the U.S. Congress in October 1978. For the next three years PNRBC administered CREDDP and $3.3 million was appropriated for the program. However, PNRBC was abolished as of October 1981, leaving CREDDP in abeyance. At that point, much of the field work had been carried out, but most of the data were not yet analyzed and few of the planned publications had been completed. To avoid wasting the effort that had already been expended, in December 1981 Congress included $1.5 million in the U.S. Water Resources Council (WRC) budget for the orderly completion of CREDDP. The WRC contracted with CREST to evaluate the status of the program and prepare a revised Plan of Study, which was submitted to the WRC in July 1982. In September, after a hiatus of almost one year, CREDDP work was resumed when a cooperative agreement was signed by CREST and the WRC to administer the restructured program and oversee its completion by June 1984. With the dissolution of the WRC in October 1982, the National Oceanic and Atmospheric Administration (NOAA) assumed the role of the WRC as the federal representative in this cooperative agreement.

CREDDP was designed to meet the needs of those groups who were expected to be the principal users of the information being developed. One such group consists of local government officials, planning commissions, CREST, state and federal agencies, permit applicants, and others involved in planning and permitting activities. The other major anticipated user group includes research scientists and educational institutions. For planning purposes, an understanding of the ecology of the estuary is particularly important, and CREDDP has been designed with this in mind. Ecological research focuses on the linkages among different elements in the food web and the influence on the food web of such physical processes as currents, sediment transport and salinity intrusion. Such an ecosystem view of the estuary is necessary to

predict the effects of estuarine alterations on natural resources.

Research was divided into thirteen projects, called work units. Three work units, Emergent Plant Primary Production, Benthic Primary Production, and Water Column Primary Production, dealt with the plant life which, through photosynthesis and uptake of chemical nutrients, forms the base of the estuarine food web. The goals of these work units were to describe and map the productivity and biomass patterns of the estuary's primary producers and to describe the relationship of physical factors to primary producers and their productivity levels.

The higher trophic levels in the estuarine food web were the focus of seven CREDDP work units: Zooplankton and Larval Fish, Benthic Infauna, Epibenthic Organisms, Fish, Avifauna, Wildlife, and Marine Mammals. The goals of these work units were to describe and map the abundance patterns of the invertebrate and vertebrate species and to describe these species' relationships to relevant physical factors.

The other three work units, Sedimentation and Shoaling, Currents, and Simulation, dealt with physical processes. The work unit goals were to characterize and map bottom sediment distribution, to characterize sediment transport, to determine the causes of bathymetric change, and to determine and model circulation patterns, vertical mixing and salinity patterns.

Final reports on all of these thirteen work units have been published. In addition, these results are integrated in a comprehensive synthesis entitled The Dynamics of the Columbia River Estuarine Ecosystem, the purpose of which is to develop a description of the estuary at the ecosystem level of organization. In this document, the physical setting and processes of the estuary are described first. Next, a conceptual model of biological processes is presented, with particular attention to the connections among the components represented by the work unit categories. This model provides the basis for a discussion of relationships between physical and biological processes and among the functional groups of organisms in the estuary. Finally, the estuary is divided into regions according to physical criteria, and selected biological and physical characteristics of the habitat types within each region are described. Historical changes in physical processes are also discussed, as are the ecological consequences of such changes.

Much of the raw data developed by the work unit researchers is collected in a magnetic tape archive established by CREDDP at the U.S. Army Corps of Engineers North Pacific Division Data Processing Center in Portland, Oregon. These data files, which are structured for convenient user access, are described in an Index to CREDDP Data. The index also describes and locates several data sets which were not adaptable to computer storage.

The work unit reports, the synthesis, and the data archive are intended primarily for scientists and for resource managers with a scientific background. However, to fulfill its purposes, CREDDP has developed a set of related materials designed to be useful to a wide

range of people.

Guide to the Use of CREDDP Information highlights the principal findings of the program and demonstrates how this information can be used to assess the consequences of alterations in the estuary. It is intended for citizens, local government officials, and those planners and other professionals whose training is in fields other than the estuary-related sciences. Its purpose is to help nonspecialists use CREDDP information in the planning and permitting processes.

A detailed portrait of the estuary, but one still oriented toward a general readership, is presented in The Columbia River Estuary: Atlas of Physical and Biological Characteristics, about half of which consists of text and illustrations. The other half contains color maps of the estuary interpreting the results of the work units and the ecological synthesis. A separate Bathymetric Atlas of the Columbia River Estuary contains color bathymetric contour maps of three surveys dating from 1935 to 1982 and includes differencing maps illustrating the changes between surveys. CREDDP has also produced unbound maps of the estuary designed to be useful to resource managers, planners and citizens. These black-and-white maps illustrate the most recent (1982) bathymetric data as contours and show intertidal vegetation types as well as important cultural features. They are available in two segments at a scale of 1:50,000 and in nine segments at 1:12,000.

Two historical analyses have been produced. Changes in Columbia River Estuary Habitat Types over the Past Century compares information on the extent and distribution of swamps, marshes, flats, and various water depth regimes a hundred years ago with corresponding recent information and discusses the causes and significance of the changes measured. Columbia's Gateway is a two-volume set of which the first volume is a cultural history of the estuary to 1920 in narrative form with accompanying photographs. The second volume is an unbound, boxed set of maps including 39 reproductions of maps originally published between 1792 and 1915 and six original maps illustrating aspects of the estuary's cultural history.

A two-volume Literature Survey of the Columbia River Estuary (1980) is also available. Organized according to the same categories as the work units, Volume I provides a summary overview of the literature available before CREDDP while Volume II is a complete annotated bibliography.

All of these materials are described more completely in Abstracts of Major CREDDP Publications. This document serves as a quick reference for determining whether and where any particular kind of information can be located among the program's publications and archives. In addition to the abstracts, it includes an annotated bibliography of all annual and interim CREDDP reports, certain CREST documents and maps, and other related materials.

To order any of the above documents or to obtain further information about CREDDP, its publications or its archives, write to CREST, P.O. Box 175, Astoria, Oregon 97103, or call (503) 325-0435.

FOREWORD

Research presented in this report was initiated in September 1979, and continued until 30 September 1981, when the PNRBC was abolished by the federal government. During this period the Benthic Primary Production work Unit of CREDDP designed a sampling program compatible with the contract work tasks, developed field methods and procedures, conducted research at intensive study sites, and initiated sampling at a series of validation and survey sites. After the program resumed again under the administration of CREST in November 1982, the principal activities of the work unit included data organization, data anlysis, preparation of maps of selected variables, and report preparation. Additional financial support for the research was obtained in August 1982 from the U.S. Army Corps of Engineers. This support was provided for an analysis of the taxonomic structure of benthic diatom assemblages in relation to salinity patterns in the Columbia River Estuary.

The authors of this report gratefully acknowledge contributions from other scientists involved with the Columbia River Estuary Data Development Program. Specifically, Chris Sherwood and Ed Roy analyzed the sediment samples collected from the intensive study sites, the results of which are summarized in Tables 6, 7, 9, 10 and 11; and Larry Small and Bruce Frey kindly supplied estimates of light attenuation in the water column during the study. Thanks also are due Kevin Kirk for his help with the sampling in the field and for performing chlorophyll analyses in the laboratory. Finally, we greatly appreciate the able administrative assistance of Jack Damron and David Fox during the last year of CREDDP, and the help from Anne Saari and other concerned citizens of the Astoria area during the difficult period following the temporary termination of the program in October 1981.

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EXECUTIVE SUMMARY

The general objective of the research associated with the Benthic Primary Production Work Unit of CREDDP was to determine mechanisms that control the production dynamics and species composition of benthic plant assemblages in the Columbia River Estuary. In particular, the work was concerned with effects of selected physical variables on structural and functional attributes of micro- and macro- vegetation, and on the productivity and biomass of benthic autotrophs on the tidal flats of the estuary.

The sampling program during the study was organized into two phases: (1) monthly replicated sampling at five intensive study sites from April 1980 through April 1981; and (2) a broad survey involving the collection of samples at 31 other locations in the estuary during a period from May through September 1981. Research at the intensive study sites examined relationships between autotrophic processes and relevant physical variables, relationships that provided the basis for the prediction of benthic primay production and related variables in other areas of the estuary. Data from the survey represented information about benthic autotrophy for a large spatial area, and therefore provided the basis for the development of distributional maps of plant biomass and production rates. The intensive study sites were: (1) a sandy beach on Clatsop Spit, (2) a mudflat near the Ilwaco Airfield in Baker Bay, (3) a mudflat on the west side of Youngs Bay, near Highway 101, (4) a mudflat on the east side of Grays Bay, and (5) a sandflat on the eastern tip of Quinns Island. At these sites, samples were collected for the determination of sediment grain size distribution; species composition of the flora; concentrations of chlorophyll a, phaeo-pigments, and organic matter in the sediment; and rates of benthic primary production and community oxygen uptake. Sampling at the survey sites was primarily concerned with the measurement of plant biomass expressed as the concentration of chlorophyll a.

The microalgae, which consist almost entirely of diatoms, are the most abundant group of plants on the tidal flats of the Columbia River Estuary. Along with the diatoms, blue-green algae are frequently found growing beneath emergent vascular plants in the low marsh in late summer. Submergent vascular plants and macroalgae are not conspicuous on the tidal flats of the estuary. Zostera marina has a patchy distribution in Baker Bay, but does not develop dense beds characteristic of other Oregon estuaries. A sparse growth of Potamogeton richardsonii and P. pectinatus occurs on the tidal flats of Grays Bay during spring and summer, while Ceratophyllum demersum and Elodea canadensis are often abundant in marsh pools of the bay. Enteromorpha intestinalis is often abundant in sediment samples from the low marsh in Youngs Bay during the spring months.

A quantitative analysis of the benthic diatom flora of the estuary indicated that the species compositions associated with the tidal flats of Cathlamet Bay, Grays Bay, and the freshwater region upriver from Russian Island are similar. Moreover, the flora in Youngs Bay is more similar to the freshwater floras of Cathlamet Bay, Grays Bay, and the Upper Estuary than to the flora of Baker Bay, a pattern apparently

related to freshwater input into Youngs Bay from the Lewis and Clark River, the Youngs River, and the main channel of the Columbia River. Assuming that the species composition of the diatom flora is a satisfactory indicator of salinity in the estuary, the analysis indicates that the intertidal regions of Cathlamet Bay, Grays Bay, and the Upper Estuary are freshwater areas, while the corresponding zone in Baker Bay is under the influence of brackish water. Youngs Bay is affected to some degree by slightly brackish water, although intermittent periods of high freshwater discharge are responsible for the presence of a large number of freshwater planktonic and benthic taxa in the sediment associated flora.

Mean hourly rates of gross primary production for the daylight hours at the intensive study sites in Youngs Bay, Baker Bay, Grays Bay, and on Clatsop Spit and Quinns Island for the entire period were 84, 43, 33, 5, and 30 mg C m^{-2} hr^{-1}, respectively. In general, rates were lower during late fall and winter than at other times of the year, and the transects in the low marsh and upper intertidal zone were more productive than the transects in the lower intertidal zone nearer the main channel. A regression analysis indicated that there was a linear relationship between the concentration of chlorophyll a in the top cm of sediment (CHLOR) and the rate of gross primary production (GPP). The best predictive equation derived from CREDDP data is GPP = 0.63 + 0.28 CHLOR, where GPP and CHLOR are expressed as mg C m^{-2} hr^{-1}, and mg m^{-2}, respectively. Correlation coefficients examining the covariance for gross primary production and selected sediment properties were 0.44 (mean sediment diameter), 0.42 (sorting coefficient), and 0.68 (an index to sediment mixing).

Regional maps of benthic primary production in the Columbia River Estuary were developed from data collected at the intensive study sites and survey sites. Such maps indicated that in Baker Bay and Youngs Bay there are tidal flats that support relatively high mean rates of benthic primary production, in the range of 60 to 80 mg C m^{-2} hr^{-1}. In Grays Bay and Cathlamet Bay mean rates usually varied between 20 to 40 mg C m^{-2} hr^{-1}, although some of the sandy regions with a high degree of sediment mixing had mean rates less than 20 mg C m^{-2} hr^{-1}. Moreover, the sandy intertidal areas of the many islands in the upper estuary exhibited relatively low mean rates of primary production, usually between 10 and 20 mg C m^{-2} hr^{-1}. Annual rates of benthic gross primary production in Baker Bay, Youngs Bay, Grays Bay, Cathlamet Bay, and on the islands in the upper estuary are estimated to be about 97, 71, 26, 23, and 38 g C m^{-2} yr^{-1}, respectively. Productive capacity of the various intertidal regions of the estuary is probably determined primarily by the properties and stability of the sediment, position in intertidal zone relative to the mean lower low water level, and seasonal changes in daylength and the optical properties of the water column.

A rough estimate of the total annual benthic gross primary production for the intertidal region of the entire estuary (the CREDDP study area), excluding areas occupied by emergent macrophytes, is 2.175×10^6 kg, or 2.175 metric tons of carbon. This value corresponds to about 4,350 metric tons of organic matter per year. In comparison to the inputs of fine particulate organic carbon from upriver, the contri

bution of organic carbon to the estuary by resident benthic autotrophs is relatively small.

Dredging and filling operations in the Columbia River Estuary may affect benthic communities in two ways: (1) a change in species composition in response to changes in the chemical and physical environment; and (2) a reduction in productive capacity of the system brought about by a physical disruption or complete habitat destruction as material is removed or redistributed. The taxonomic structure of the benthic diatom flora may provide a useful index to the potential of an impact to bring about changes in species composition, while the distribution of chlorophyll in the sediment can serve as an indication of productive capacity.

The Columbia River Estuary

Columbia River Estuary

Scale 1:160,000

0 1 2 3 4 5 6 7 8 9 10 Kilometers

0 1 2 3 4 5 6 Miles

Map produced in 1983 by Northwest Cartography, Inc.
for the Columbia River Estuary Data Development Program

- Shoreline (limit of non-aquatic vegetation)
- Intertidal vegetation
- Shoals and flats
- Lakes, rivers, other non-tidal water features
- Major highways
- Megler — Cities, towns
- Railroads
- Other cultural features

1. INTRODUCTION

This report is concerned with the production dynamics of benthic (bottom-dwelling) plants in the Columbia River Estuary. The information is structured primarily for a reader with professional training in the fields of biology and aquatic ecology. For additional information concerning the relationships between benthic plants and other components of the Columbia River Estuary ecosystem, the reader may refer to the CREDDP integration report entitled The Dynamics of the Columbia River Estuarine Ecosystem (CREDDP 1984).

1.1 PROJECT OBJECTIVES

The general objective of this research was to determine mechanisms that control the production dynamics of benthic plants relative to physical and biological processes in the Columbia River Estuary. In particular, the work was concerned with effects of physical gradients on structural and functional attributes of micro- and macro-vegetation and on the productivity and biomass of benthic autotrophs associated with the tidal flats of the estuary. These studies were conceived within the coupling structure of the entire ecosystem, an approach that helped to maximize relevance to other aspects of the Columbia River Estuary Data Development Program.

Two levels of work were required to achieve the general objective of the project: (1) a descriptive study of the production dynamics of benthic plants on the tidal flats of the Columbia River Estuary, and (2) an investigation of mechanisms accounting for the observed dynamics in the field. From April 1980 through April 1981, a descriptive study was conducted at five intensive study sites, and the results of laboratory studies at the Oregon State University Marine Science Center at Newport were used to help interpret system dynamics in the field. Also, work at the intensive study sites allowed the establishment of relationships between primary production and the concentration of chlorophyll a in the sediment. Such relationships provided the basis for the prediction of primary production at survey and validation sites from which chlorophyll samples were obtained between May and September 1981. To generate hypotheses relative to process mechanisms, selected physical variables also were monitored, and these data were related to selected biological variables of interest.

1.2 CONCEPTUAL FRAMEWORK OF THE RESEARCH

This research on benthic plant processes was conducted in relation to the coupling structure of a conceptual process model of the entire Columbia River Estuary ecosystem (Figure 1). This approach provided the theoretical basis for uncoupling the Primary Production subsystem (Figure 2) for research in a manner that preserved its relevance to other subsystems, i.e., the other work units described in the CREDDP Plan of Study (CREST 1982). In large ecosystem programs some integrating structure is essential to optimize the relatedness of the component projects within the framework of total program goals. The conceptual structure illustrated in Figure 1 and 2 and in the CREDDP integration report was consistent with FLEX, a general ecosystem

modeling paradigm developed by W. S. Overton (1972, 1975) and based on the general systems theory of Klir (1969). Within CREDDP, the conceptual framework was compatible with both the process-oriented projects and projects emphasizing species distributions.

A hierarchical model of an estuarine ecosystem from a biological perspective is illustrated in Figure 1. Estuarine Biological Processes can be investigated as a system with two coupled subsystems: Primary Food Processes and Consumption. The Primary Food Processes subsystem represents the dynamics of variables associated with the accumulation and degradation of plant biomass and detritus, while the consumption subsystem is concerned with the dynamics of macrofauna as they function as consumers of living plant biomass and detritus. The subsystems within Primary Food Processes are Primary Production, which represents the production dynamics of autotrophic organisms, and Detrital Decomposition, a process that is concerned with the breakdown of dead organic material. The process of Consumption is partitioned mechanistically into four coupled subsystems: Deposit Feeding, Suspension Feeding, Wetland Herbivory, and Predation. Structural details of these subsystems are described in The Dynamics of the Columbia River Estuarine Ecosystem (CREDDP 1984).

The target subsystem for the research presented in this report was Primary Production (Figure 2). The process of primary production generates inputs of light energy and nutrients and outputs of dissolved organic matter and respiratory products, variables represented by arrows to or from the perimeter of the circle. In addition, the process is also influenced by physical variables and processes (e.g., sediment properties, temperature and hydrologic factors) which are indicated collectively by the dotted ellipse. The Primary Production subsystem has three state variables, the biomasses of benthic algae, phytoplankton, and vascular plants. Inputs and outputs acting directly on the state variables include consumption by macroconsumers, transfer to a detrital state variable after natural mortality, and imports and exports into and out of the spatial area under consideration. In the benthos of the Columbia River Estuary the microalgae were the dominant functional group of autotrophs, while the benthic macroalgae and submergent vascular hydrophytes were relatively rare with a patchy distribution. The work presented in subsequent sections of this report was concerned with autotrophic processes associated with the benthic vegetation, whereas research concerning the dynamics of phytoplankton and emergent vascular hydrophytes was the responsibility of the Water Column Primary Production and Emergent Plant Primary Production work unit researchers, respectively.

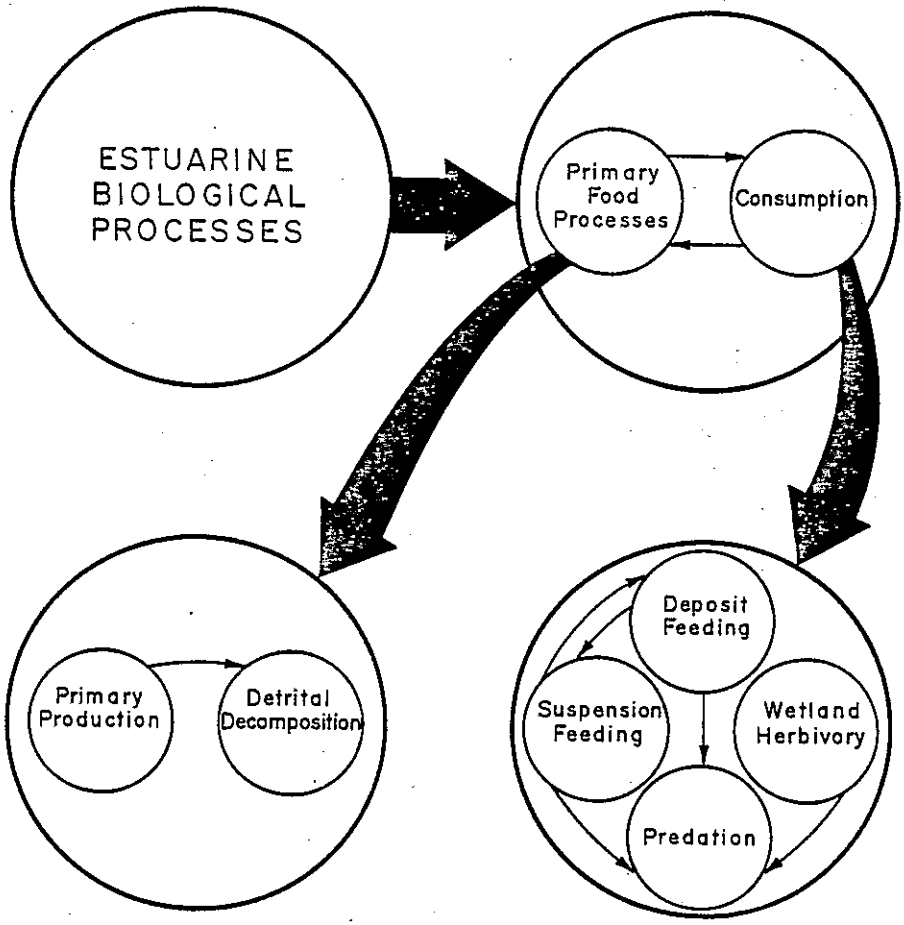

Figure 1. Systems diagram of Estuarine Biological Processes and associated subsystems.

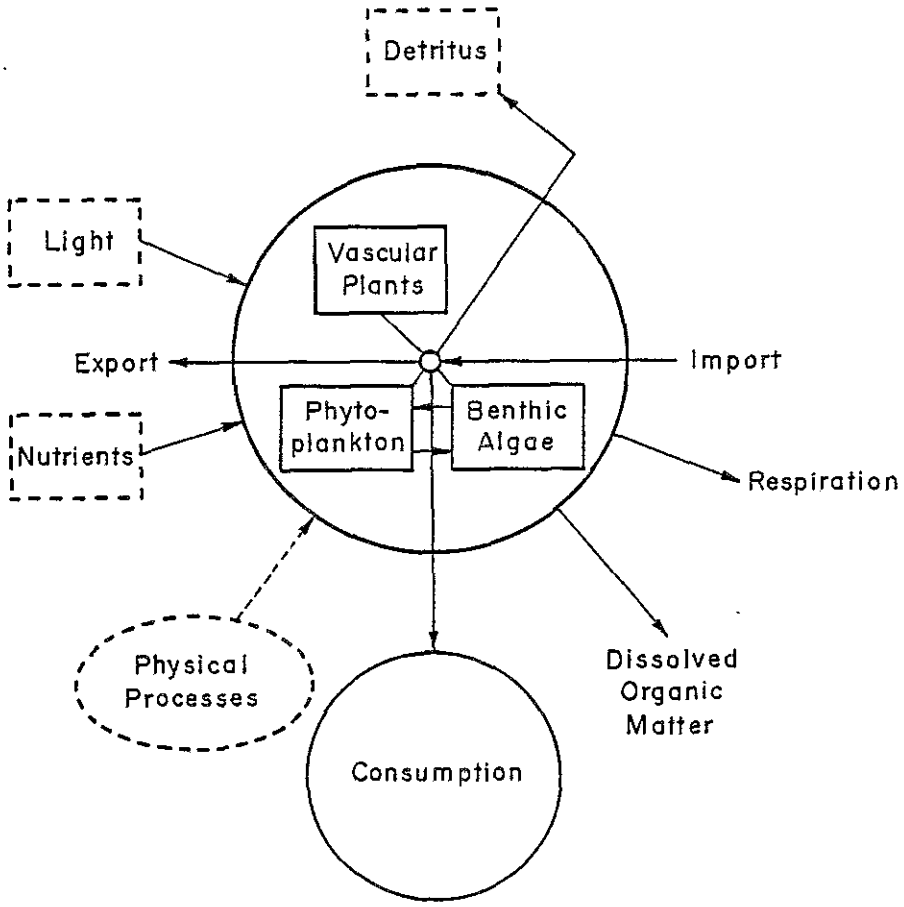

Figure 2. Systems diagram illustrating the Primary Production subsystem and associated state variables with relevant inputs and outputs.

2. MATERIALS AND METHODS

2.1 SAMPLING STRATEGY

Because of the enormous size of the area under investigation by the Columbia River Estuary Data Development Program (ca. 150 square miles), the selection of a suitable sampling strategy for measurement of benthic primary production and related variables was a difficult problem. Essentially two approaches were adopted for the project: (1) monthly replicated sampling at five intensive study sites, and (2) a broad survey involving the collection of samples from as many locations as possible over the entire study area. The first approach allowed the calculation of a variance structure for each site and provided information about temporal variation. Also, research at the intensive study sites examined relationships between autotrophic processes and relevant physical variables, relationships that provided the basis for the prediction of benthic primary production and related variables in other areas of the estuary. The second approach provided information about benthic autotrophy for a large spatial area and generated the data necessary for the development of distributional maps. Unfortunately, CREDDP was terminated before the study of the survey and validation sites was completed, and the mapping of selected variables was based on less information than originally anticipated by work unit personnel.

2.1.1 Intensive Study Sites

Prior to the beginning of the field sampling program in April 1980, the estuary was surveyed to identify potential sites for intensive study. Five sites were selected on the basis of their relative positions along the salinity gradient, their sediment type, and whether or not they were representative of large, common habitat types in the estuary. The intensive study sites with corresponding CREDDP coordinates were Clatsop Spit (3-59-13), Youngs Bay (3-53-10), Baker Bay (4-0-18), Grays Bay (3-40-17), and Quinns Island (3-29-14), and the general location of each site is indicated in Figure 3. The sites at Clatsop Spit and Baker Bay were under marine influence, and surface salinities ranged from 32 °/oo at high tide during low freshwater discharge to 0 °/oo at low tide during high discharge (Hansen 1965). The Clatsop Spit site is located on the northern side of Clatsop Spit, approximately 1 km west of Parking Lot D. This site was characterized by fine sand and relatively high current velocities. The Baker Bay site was located on the northern side of Baker Bay, near the Ilwaco Airfield. The sediment is primarily coarse silt to very fine sand. The site at Youngs Bay was on the western side of the bay, approximately 1 km south of the mouth of the Skipanon River. Here, surface salinities varied from 0 to 10 °/oo during the study, and grain size of the sediments ranged from medium silt to fine sand. Sites in Grays Bay and on Quinns Island were under strong freshwater influence, with surface salinities always near 0 °/oo. The Grays Bay site was located on the eastern side of the bay, approximately 1 km south of the mouth of the Grays River. The sediments were composed primarily of very fine sand. The site at Quinns Island was located on the eastern tip of the island. Because it was more exposed to river currents than the Grays Bay site, the sediments were coarser, ranging in grain size from very fine sand to medium sand.

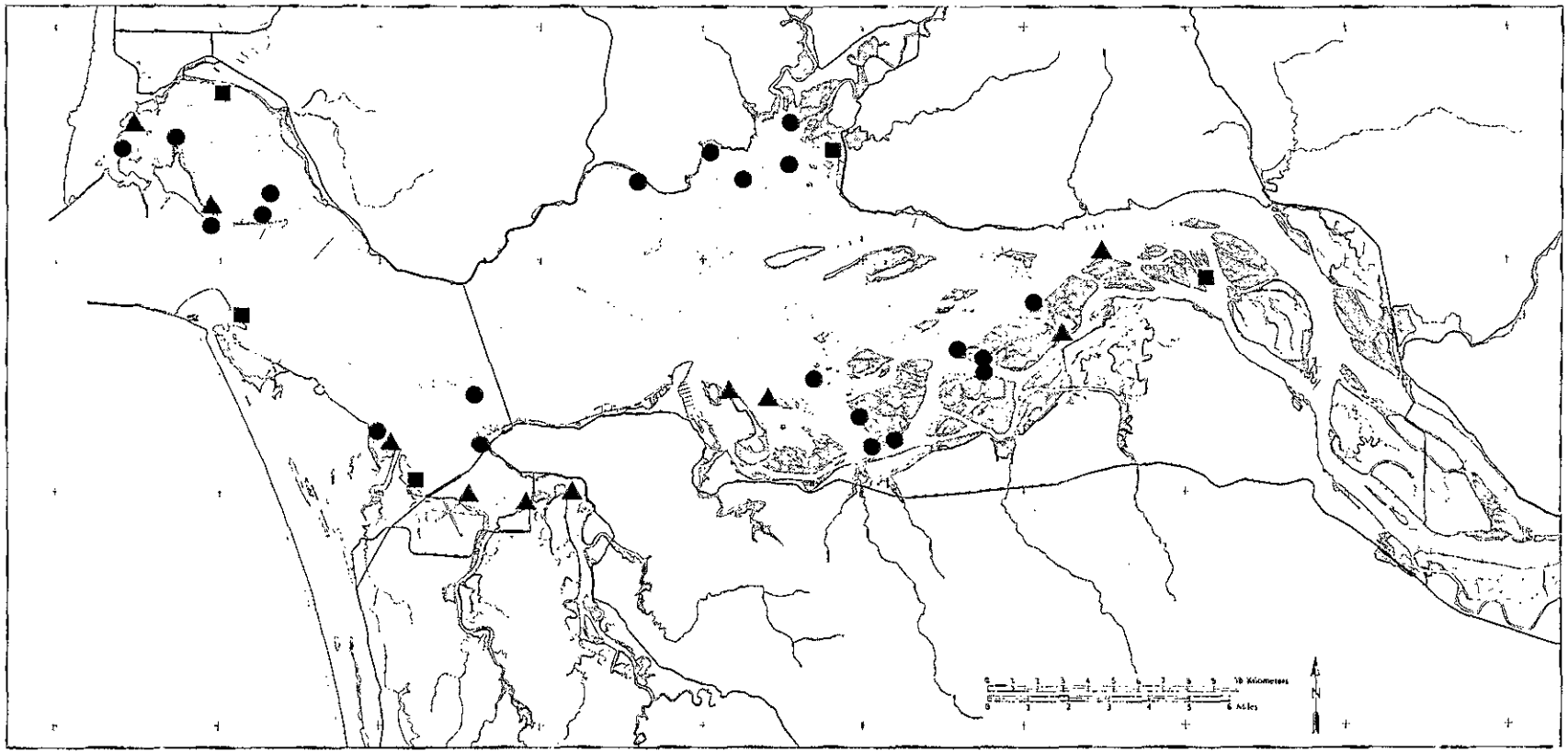

Figure 3. Sampling sites for the investigation of benthic primary production in the Columbia River Estuary.

At each intensive study site, 25 m horizontal transects were identified and marked with wooden stakes. The transects were located in the high, mid and low intertidal zones at each station and in the low marsh at all stations except Clatsop Spit, where no marsh exists. The distance between the upper transect in the low marsh and the lowest intertidal transect varied from station to station depending on the slope of the tidal flat (Table 1). The transects in the marsh and in the high, mid and low intertidal regions were approximately 0.9 m, 0.7 m, 0.5 m and 0.3 m above mean lower low water, respectively.

Table 1. Height of sampling transects above mean lower low water and the distance between the lowest transect and the other transects at each intensive study site. Values are expressed in meters. CS, YB, BB, GB and QI refer to Clatsop Spit, Youngs Bay, Baker Bay, Grays Bay and Quinns Island, respectively.

Tidal Height	CS	YB	BB	GB	QI
Marsh	-	0.9	0.9	0.9	0.9
Upper	0.7	0.7	0.7	0.7	0.7
Mid	0.5	0.5	0.5	0.5	0.5
Lower	0.3	0.3	0.3	0.3	0.3
Distance from Lowest Transect:					
Mid	23	75	180	235	116
Upper	46	150	340	501	168
Marsh	-	245	420	659	190

The sampling strategy at each intensive study site involved the collection of sediment cores for the analysis of chlorophyll *a* concentration and for measurements of primary production in a respirometer chamber. Chlorophyll *a* concentration in the top cm of sediment is a state variable closely associated with the capacity of the system for benthic autotrophy. The measurement of this variable provided an indirect estimate of plant biomass in complex assemblages of microorganisms and detritus. Primary production is a dynamic process, one of the few ecosystem processes that can be monitored directly in the field.

Six sediment cores were obtained at 5 m intervals along each transect, and each of these was subsampled in the laboratory to obtain estimates of the chlorophyll *a* concentration in the upper cm, between 4.5 and 5.5 cm from the surface, and between 9 and 10 cm from the surface. Concurrently, two sediment cores were obtained from each of the transects in the marsh and in the upper and lower intertidal regions for measurements of primary production and oxygen consumption. The cores were subsampled after these measurements for estimates of chlorophyll *a* concentration and organic matter in the upper cm of sediment.

In summary, 24 core samples for chlorophyll analysis and six core samples for primary production measurements were obtained on each sampling date from Youngs Bay, Baker Bay, Grays Bay and Quinns Island; at Clatsop Spit the marsh was not present and the corresponding core numbers were 18 and 4. At the intensive study sites a set of samples was obtained once each month in April, May, June, July, August, September, October, November of 1980, and in January, February, March and April of 1981. Because of the lack of a low tide series during the daylight hours in November and January, the data sets are incomplete for these months (Appendix A).

2.1.2 Validation and Survey Sites

In the spring of 1981, 10 sampling sites were selected to validate predictions of primary production which were based on relationships established during the investigation of the intensive study sites. Regression equations derived from data collected from the intensive study sites were used to predict rates of primary production from measurements of chlorophyll concentration at the validation sites, and the predicted values were checked against field measurements of primary production at those sites. An early termination of support for the CREDDP field research limited work at the validation sites to visits in August and September 1981.

A list of the validation sites with the corresponding CREDDP coordinates is presented in Table 2, and the locations of these sites are illustrated in Figure 3. At these sites sampling transects were established in the low marsh (0.9 m above MLLW), and on the tidal flats at 0.7 m above MLLW and 0.3 m above MLLW. These depth levels correspond to the depths labeled marsh, upper, and lower in Table 1. Sampling along these transects followed the same procedures outlined above for the intensive study sites. Variables measured at the validation sites included gross primary production, oxygen consumption, and the concentration of chlorophyll a, phaeopigments, and organic matter. The number of observations obtained for each site at each transect on each date is reported in Appendix B.

Survey sites were established in the estuary during the spring 1981 to provide a basis for estimating primary production at various locations throughout the entire estuary. At these sites the concentrations of chlorophyll a and phaeopigments were measured, and the chlorophyll data were used to predict rates of primary production from the regression equations obtained from the analysis of data from the intensive study sites. The 21 survey sites are listed with corresponding CREDDP coordinates in Table 2, and their approximate locations are indicated in Figure 3. Transect locations and sampling procedures for pigment analyses were the same as those described above for the intensive study sites. The early termination of support for the CREDDP field research reduced the period of sampling at the survey sites from one year to a four-month period between May 1, 1981 to September 1, 1981. The number of observations obtained for each site at each transect on each visit is presented in Appendix B.

Table 2. List of validation and survey sites and corresponding CREDDP coordinates. Gross primary production, oxygen uptake and concentrations of chlorophyll a, phaeopigments and organic matter were measured at the validation sites in August and September 1981. Chlorophyll a and phaeopigment concentrations were measured at the survey sites at various times from May to September 1981.

Site	CREDDP Coordinates
Validation Sites:	
Clatsop Airport	3-51-10
Daggett Point	3-49-9
Horseshoe Island	3-33-13
Ilwaco	4-2-17
Lois Island	3-44-11
Old Bridge	3-50-9
Skipanon Channel	3-54-11
West Sand Island	4-0-16
Woody Island	3-32-14
Cathlamet Bay	3-43-11
Survey Sites:	
Bay between Rocky Point and Portugese Point	3-44-17
Bay west of Grays Point	3-46-16
Brush Island	3-34-14
Desdemona Sands	3-52-12
East Sand Island - North Side	3-58-15
East Sand Island - Bar North of Island	3-58-16
Marsh Island - Bar South of Island	3-36-12
Marsh Island - South Flat	3-36-12
Marsh Island - Western Tip	3-37-12
McGregor Island	3-41-12
Millers Point	3-41-18
Russian Island - South Side	3-39-11
Russian Island - SSW Corner	3-40-11
Russian Island - WSW Corner	3-40-12
Grays Bay - Front Sand Bar	3-43-16
Grays Bay - Middle Sand Bar	3-42-17
Smith Point	3-51-11
Tansy Point	3-55-11
West Sand Island - New Boat Ramp	4-2-17
West Sand Island - North Tip	4-1-17
West Sand Island - South Tip	4-0-15

2.2 TAXONOMIC ANALYSIS OF THE DIATOM FLORA

Samples for taxonomic analysis of the diatom flora were collected concurrently with the chlorophyll samples at all sampling sites using an 8 cm long plastic tube of 1.6 cm diameter. The tube was pushed about 3 cm into the sediment and carefully removed with the intact sediment. The tubes were capped, frozen, and transported back to the laboratory. In the laboratory, the frozen sediment cores were removed from the tubes and the top 1.0 cm was removed with a razor blade. The top 1.0 cm with its associated diatom flora was placed in a modified Kjeldahl apparatus and boiled in nitric acid for 15-30 minutes. This procedure destroyed most of the organic matter in the sample and left the empty diatom frustules with the associated sediment. After neutralizing the samples by repeated washings with distilled water, permanent mounts were prepared by placing a few drops of the diatom-sediment slurry on a cover glass, allowing it to dry, and mounting the cover glass on a microscope slide in Cumar R-9 (Holmes et al. 1981).

Diatom taxa were identified to species or varieties of species while examining each slide at 1250x magnification under a Zeiss RA research microscope. When a taxon could not be identified with available literature, it was given a unique code number so it could be specified when found in other samples. The relative abundances of the taxa in each sample were based on counts of 300 valves. The mechanical stage on the microscope was moved, and the valves encountered in horizontal rows were identified and counted until this total was reached. Earlier work (McIntire and Overton 1971) indicated that a sample size of 300 is sufficient for estimation of the community composition parameters presented in this report.

2.3 BIOMASS AND PRIMARY PRODUCTION

Samples for chlorophyll *a* analysis were collected using 15 cm long plastic tubes of 1.6 cm diameter. The tubes were pressed about 12 cm into the sediment and were removed so as not to disturb the sediment. The tubes with sediment were capped, frozen and transported back to the laboratory. In the laboratory, the frozen sediment cores were extracted from the tubes, and sections from 0-1 cm, 4.5-5.5 cm and 9-10 cm were excised with a razor blade. A core section was placed in a mortar with 1 ml of magnesium carbonate solution and approximately 5 ml of 90% acetone. The slurry was ground with a pestle for 2 minutes, poured into a stoppered centrifuge tube, and placed in a dark refrigerator for 24 hr. The pigments were clarified by centrifugation and analyzed following the method of Strickland and Parsons (1972). The Lorenzen equation, which corrected for phaeopigments, was used to calculate the concentration of chlorophyll *a* (Lorenzen 1967). This method provides a measure of the total quantity of chlorophyll *a* and phaeophytin *a* plus phaeophorbide *a*, but not of chlorophyllide *a* or the phaeophytins and phaeophorbides of other chlorophylls.

Samples for measurement of primary production were collected in 5.7 cm long plastic cores of 7.4 cm diameter. The plastic cores were pressed into the subtrate to minimize disturbance to the flora. The cores and sediments were removed, capped and transported to a nearby

floating dock. Two sediment cores from each transect were transferred to 1.5 liter field respirometers (Figure 4). The respirometers were placed in a water bath, filled with water, and sealed. Water was circulated through each chamber with a 12V battery-powered submersible centrifugal pump. Rates of oxygen evolution and uptake were based on measurement periods of approximately 1 hr between initial and final readings. Measurements of dissolved oxygen were made with an Orbisphere salinity corrected dissolved oxygen system. Dissolved oxygen readings were obtained by disconnecting the pump and placing the oxygen probe in a screw-topped sample bottle which was built into the water flow system of each chamber. Rates of net community production or oxygen consumption were measured when the respirometers were exposed to full sunlight or darkened, respectively. Rates of gross primary production were estimated by adding the rate of oxygen consumption in the dark to the rate of net community production in the light for an equivalent period of time. Measurements of light intensity above the water and below the water at the sediment surface were made with a Li-Cor quantum meter (Model LI-185A). Curves relating primary production to light intensity determined experimentally by Davis and McIntire (1983) indicated that the benthic flora was not light limited during the field measurements, and that maximum photosynthetic rates were recorded. Salinity of the water in the respirometers was measured with a temperature-compensated AO Goldberg® refractometer. Temperature of the water bath was monitored with a hand-held thermometer.

Upon completion of production measurements, the cores were removed from the respirometers. Each core was subsampled with four smaller 3 cm long plastic tubes of 1.6 cm diameter. Each smaller core was frozen and transported to the laboratory. The top 1 cm of two of the smaller cores was analyzed for chlorophyll *a* as outlined above. The top 1 cm of the other two cores was removed with a razor blade, dried at 70°C, and analyzed for ash-free dry weight as an estimate of organic matter (A.P.H.A. 1971). Consequently, four measurements of chlorophyll *a* and four estimates of ash-free dry weight were made for the cores from each respirometer.

2.4 DATA PROCESSING

2.4.1 Data Structure

Data obtained by the Benthic Primary Production research unit were organized for analysis into seven data files: CHLORP, GPROD, ENVIRO, SURCHL, VALPRO, VALEN and COE. The data in these files are accessible through the U.S. Army Corps of Engineers, North Pacific Division Computer Services facility in Portland, Oregon.

The file CHLORP contained the chlorophyll and phaeopigment data derived from measurements at the intensive study sites, whereas GPROD contained values for gross primary production, oxygen consumption and corresponding values for the concentrations of chlorophyll *a*, phaeopigments and organic matter from measurements at the intensive study sites. Values for selected physical variables that corresponded to biological variables in GPROD made up the file entitled ENVIRO. The variables of ENVIRO included salinity, the ratio of the chlorophyll *a*

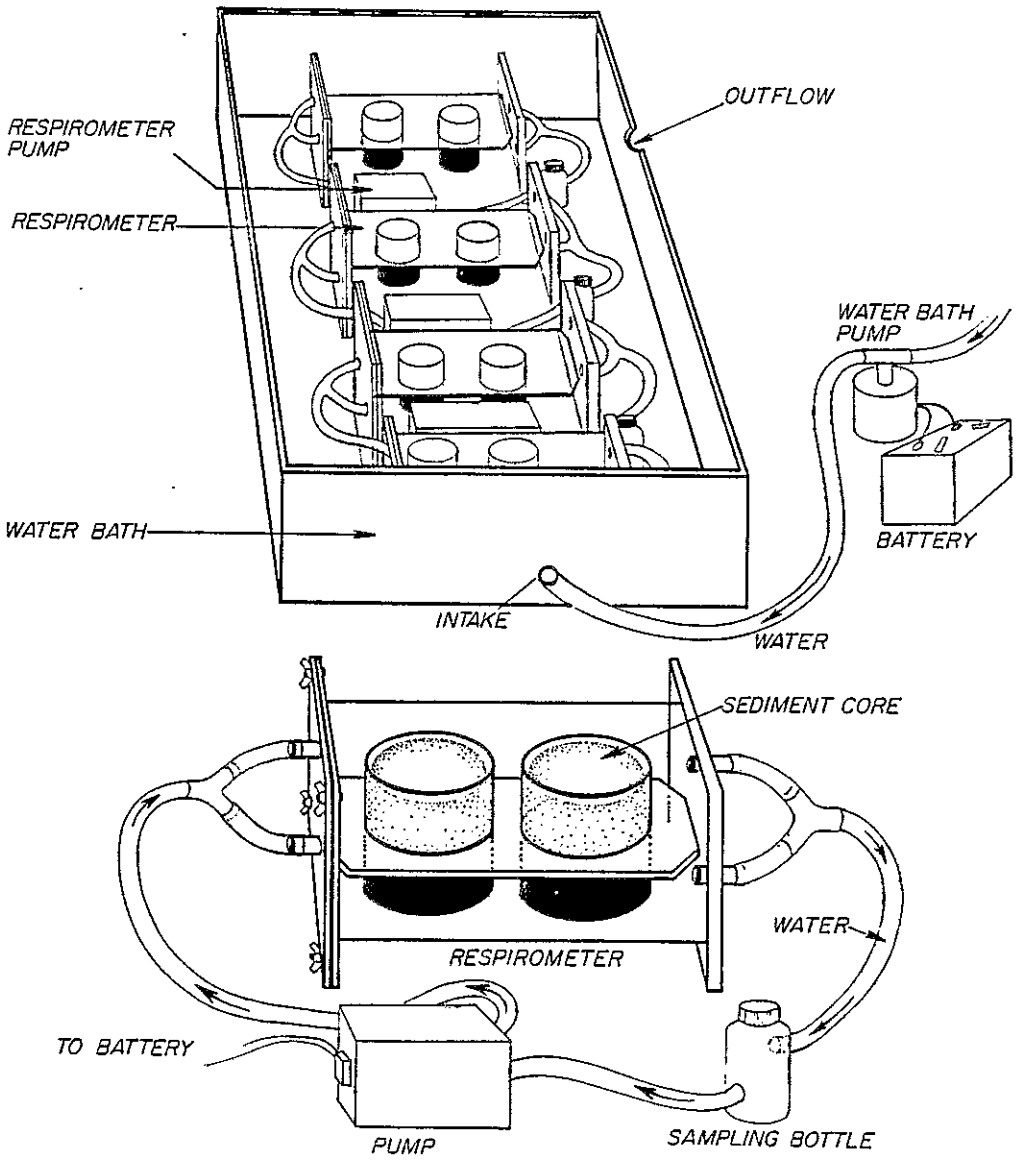

Figure 4. Diagram of the apparatus used to measure benthic primary production in the Columbia River Estuary.

concentration in the top cm of sediment to that at the 4-5 cm depth and the 9-10 cm depth, and four sediment properties, namely mean grain size, the sorting coefficient, the skewness coefficient, and a coefficient of kurtosis. Data relating to the chlorophyll a and phaeopigment concentrations at the survey and validation sites were contained in the file SURCHL, while VALPRO consisted of values for gross primary production and oxygen consumption obtained from the validation sites. Values for light intensity, temperature and selected sediment properties that corresponded to the biological observations in VALPRO were in the file VALEN. Data relating to the distribution of diatom species in the Columbia River Estuary were organized in the file COE, a file representing research supported in part by the U.S. Army Corps of Engineers.

2.4.2 Data Analysis

Taxonomic Structure

The information measure of species diversity was used to express the taxonomic structure of the diatom assemblages in each sample:

$$H' = -\sum_{i=1}^{s} \frac{n_i}{N} \ln \frac{n_i}{N} ,$$

where n_i is the number of individuals in the i-th taxon, N is the number of individuals in the sample, and S is the number of taxa in the samples. This index is a biased, but consistent estimator of the parameter

$$-\sum_{j \in p} \pi_j \ln \pi_j ,$$

where π_j is the population proportion for taxon j. Past experience with diatom assemblages indicates that bias is negligible at the sample size used in this work, i.e., at N equal to approximately 300 individuals (McIntire and Overton 1971). H' increases as the number of taxa in the sample increases and as the number of individuals become more evenly distributed among the taxa.

Since H' expresses both species richness and dominance, it is desirable to partition these components of diversity into separate numerical expressions. Here, the number of species in the sample (S) is reported as an expression of species richness, while dominance is expressed by R, a well-known redundancy index. The mathematical expression for redundancy is:

$$R = \frac{H'_{max|s} - H'_{obs}}{H'_{max|s} - H'_{min|s}} ,$$

where

$$H'_{max|s} = \ln S,$$

and

$$H'_{min|s} = -\left[\frac{S-1}{N}\log_e\frac{1}{N} + \frac{N-S+1}{N}\ln\frac{N-S+1}{N}\right]$$

$H'_{max|s}$ and $H'_{min|s}$ are the conditional maximum and minimum possible values of H', given a sample size of N with a species richness of S. R can range from zero, when the taxa in a sample are equally common, to one, when maximum dominance occurs, i.e., all but the dominant taxon is represented by just one individual.

Comparative studies of diatom samples require an objective measure of similarity between assemblages. Similarity in this study was expressed by

$$SIMI\ (1,2) = \sum_{i=1}^{s} p_{1i}\ p_{2i} \Big/ \sum^{s}\left[p_{1i}^{2} \sum^{s} p_{2i}^{2}\right]^{1/2}$$

SIMI is the degree of similarity between samples 1 and 2; p_{1i} and p_{2i} are the proportions of individuals represented by the i-th taxon in samples 1 and 2, respectively; and S is the total number of taxa in each sample. This measure of similarity varies from zero, when the samples have no taxa in common, to one, when both samples have the same species composition and relative abundance.

Computations relating to the taxonomic structure of diatom assemblages were performed with a CYBER 170/720 computer (Control Data Corporation) at the Oregon State University Computer Center. Two computer programs were used for the analysis: AIDONE and AIDN. AIDONE calculated diversity and redundancy indices for each individual sample, while AIDN generated similarity indices for a variety of community comparisons.

Primary Production and Biomass

The relatively large sets of observational data relating to biomass and primary production at the intensive study sites and at the survey and validation sites required a descriptive approach to analysis, the results of which allowed the generation of hypotheses concerned with mechanisms that control benthic autotrophy in the Columbia River Estuary. The approach to analysis of data in the CHLORP, GPROD, ENVIRO, SURCHL, VALPRO and VALEN files involved (1) the calculation of means and variances for variables of interest, with the observations pooled by site, time of sampling, tidal level, and sediment depth; (2) generation of computer plots that illustrated temporal variation of selected variables and relationships between selected pairs of variables; (3) a correlation analysis that indicated the covariance of selected pairs of biological and physical variables; and (4) a regression analysis that generated predictive equations for variables of special interest. The calculation of means and the plotting of variables provided a description of the patterns of benthic autotrophy in the estuary, while the correlation analysis provided a basis for generating hypotheses related to mechanisms controlling production dynamics; equations derived from

the regression analysis gave the predictions that were necessary for mapping spatial patterns of primary production.

Computations relating to the analysis of the primary production and biomass data also were performed with a CYBER 170/720 computer at the Oregon State University Computer Center. For these analyses, the BREAKDOWN subprogram of SPSS (Nie et al. 1975), the program EZPLOT, and the REGRESS subsystem of the Statistical Interactive Programming System (Rowe et al. 1982) were used to generate the desired output.

2.5 QUALITY ASSURANCE PROCEDURES

Quality assurance procedures for sampling and sample processing were developed in the early part of 1980, near the beginning of CREDDP. Preliminary sampling in the field allowed the determination of the sample sizes required to obtain adequate estimates of benthic algal biomass and primary production at the intensive study sites. The variance of such estimates was monitored during the sampling program to check for seasonal changes in spatial heterogeneity. This procedure indicated that the sampling strategy was satisfactory during the work at the intensive sites, and that no major adjustments in sample size or field procedures were necessary. In the laboratory, laboratory technicians were continuously supervised by the program manager, and all raw data were checked and synthesized by either the program manager or principal investigator. Data analysis involved the transfer of raw data to computer cards, the retrieval of a listing of the corresponding data file, and a check on every data entry against the raw data sheets. Once the data files were validated by this procedure, a listing was obtained, and this listing was compared with a new listing whenever the files were transferred to a different system.

3. RESULTS AND INTERPRETATION

Results of research by the Benthic Primary Production Work Unit are organized into two major subsections: (1) Taxonomic Structure, and (2) Production Dynamics. In the first subsection the species composition of the benthic macro- and micro-flora of the Columbia River Estuary is described in general, and the taxonomic structure of the diatom flora, the dominant functional group of benthic plants, is analyzed statistically and discussed in detail. The second subsection presents patterns of benthic primary production and related variables at the intensive study sites and at the validation and survey sites. This subsection also is concerned with the interpretation of autotrophic patterns and the generation of hypotheses relating to mechanisms that control the process of benthic autotrophy in the estuary.

3.1 TAXONOMIC STRUCTURE

3.1.1 Species Composition of the Benthic Flora

The conceptual model of the Primary Production subsystem (Figure 2) represents the plants of the Columbia River Estuary as three functional groups: benthic algae, vascular plants, and phytoplankton. In this report the vegetation associated with the tidal flats of the estuary is of primary concern; the vegetation of the water column and the emergent vascular plant vegetation of the estuarine marshes and swamps are discussed in reports by the Water Column Primary Production and Emergent Plant Primary Production research units.

By far the most abundant group of plants associated with the tidal flats of the Columbia River Estuary was the microalgae, which consisted almost entirely of diatoms. Although many diatom species were found on each tidal flat under investigation, the species composition varied greatly among tidal flats. Because of the dominance of this group of plants in the benthos, and because of their potential as indicators of environmental changes in the estuary, the taxonomic structure of benthic diatom assemblages was analyzed quantitatively by statistical procedures. The details of this analysis are presented in the next section of this report. The only other conspicuous group of microalgae was the blue-green algae which were found frequently growing on the sediment beneath the emergent marsh plants in late summer at the intensive study sites.

Macroalgae and submergent vascular plants exhibited a patchy distribution and were relatively rare on the tidal flats of the estuary. *Zostera marina* L. (eelgrass) and another species of *Zostera* (probably *Z. japonica* Aschers. and Braebn.) had a sparse distribution in Baker Bay, the only sampling location where this genus was observed. In the shallow regions of the bay east of the town of Ilwaco, Washington, individual shoots, spaced approximately 1-3 m from one another, were often conspicuous between MLLW and 0.7 m above MLLW. Apparently the habitat in this region was marginal for the growth and survival of *Zostera* species, as the plants did not develop dense beds similar to populations in some of the other estuaries of Oregon (e.g., Netarts Bay, Yaquina Bay and Coos Bay). Possible factors limiting the growth of

Zostera in the Columbia River Estuary include low salinity, turbidity, and the properties and stability of the sediment. However, it is doubtful that low salinity was a limiting factor in Baker Bay, as a relatively dense growth of Z. marina occurred along a segment of the boat channel near Ilwaco. Other submergent vascular plants were found in fresh water at the intensive study site in Grays Bay. At this location a sparse growth of Potamogeton richardsonii (Benn.) Rydb. (pond weed) and P. foliosus Raf. was observed on the tidal flats during spring and summer, while Ceratophyllum demersum L. (horn wort) and Elodea canadensis Michx. (water weed) were often abundant in the small pools of the lower marsh. Enteromorpha intestinalis var. maxima J. Ag., a filamentous green alga, was the only conspicuous taxon of macroalgae observed at the sampling sites. This taxon was abundant in samples from the low marsh in April and May at sites in Youngs Bay and Baker Bay. Considering the total estuarine area under investigation by CREDDP, the contribution of submergent vascular plants and macroalgae to benthic primary production in the study area was insignificant in comparison to the productivity of the benthic microalgae.

3.1.2 Taxonomic Structure of the Benthic Diatom Flora

Research presented in this section was supported in part by the U.S. Army Corps of Engineers (COE). This support was related to the potential of the diatom flora as an indicator of salinity change in the Columbia River Estuary. In particular, the COE was interested in identifying projects that were relevant to the impact assessment of a proposed dredging project. The collection of samples for the taxonomic analysis of the benthic diatom flora was supported by CREDDP, while support for the microscopic analysis of a subset of these samples was obtained from the COE. Sample sorting and data analysis were performed during August and September 1982.

Sampling

All benthic diatom samples were obtained concurrently with the productivity studies by the Benthic Primary Production research unit of CREDDP during a period extending from April 1980 to October 1981. To examine transport processes and to evaluate the contamination of benthic samples by planktonic diatoms, samples of phytoplankton also were collected from fresh water, brackish water and a mixing zone near Tongue Point. Because of time and financial constraints, it was necessary to select a subset of samples for analysis from the total number generated by the Benthic Primary Production research unit. Fifty-six samples were included in the data set. The final selection included samples from four of the five intensive study sites at six different times during 1980 and 1981, a subset of samples from sites surveyed between May and October 1981, and seven samples of planktonic diatoms. Four of the phytoplankton samples were obtained from the Water Column Primary Production research unit, while the other three samples were obtained by M. Amspoker during a cruise in October 1979. For analysis each sample was numbered and classified according to: (1) site location; (2) regional location; and (3) month that the sample was obtained (Table 3).

Table 3. List of 56 diatom samples coded by number, site, region, and month. Regions are Baker Bay (BB), Youngs Bay (YB), Cathlamet Bay (CB), Grays Bay (GB), Upper Estuary (UE), and locations of plankton samples: near Clatsop Spit (CSP), Tongue Point (TPP), Puget Island (PIP), and in the Youngs River (YRP). Samples 1-24 were obtained from four intensive study sites.

Number	Site	Region	Time
1	Baker Bay - Airport Road	BB	April 1980
2	Baker Bay - Airport Road	BB	June 1980
3	Baker Bay - Airport Road	BB	August 1980
4	Baker Bay - Airport Road	BB	October 1980
5	Baker Bay - Airport Road	BB	January 1981
6	Baker Bay - Airport Road	BB	March 1981
7	Youngs Bay - West Flat	YB	April 1980
8	Youngs Bay - West Flat	YB	June 1980
9	Youngs Bay - West Flat	YB	August 1980
10	Youngs Bay - West Flat	YB	October 1980
11	Youngs Bay - West Flat	YB	January 1981
12	Youngs Bay - West Flat	YB	March 1981
13	Grays Bay - East Flat	GB	April 1980
14	Grays Bay - East Flat	GB	June 1980
15	Grays Bay - East Flat	GB	August 1980
16	Grays Bay - East Flat	GB	October 1980
17	Grays Bay - East Flat	GB	January 1981
18	Grays Bay - East Flat	GB	March 1981
19	Quinns Island - East Flat	UE	April 1980
20	Quinns Island - East Flat	UE	June 1980
21	Quinns Island - East Flat	UE	August 1980
22	Quinns Island - East Flat	UE	October 1980
23	Quinns Island - East Flat	UE	January 1981
24	Quinns Island - East Flat	UE	March 1981
25	Lois Island - West Tip	CB	May 1981
26	Lois Island - West Tip	CB	June 1981
27	Lois Island - West Tip	CB	August 1981
28	Lois Island - West Tip	CB	September 1981
29	Grassy Island	CB	May 1981

Table 3 (continued)

30	Grassy Island	CB	June 1981
31	Grassy Island	CB	August 1981
32	Grassy Island	CB	September 1981
33	McGregor Island	CB	May 1981
34	Russian Island - WSW	CB	May 1981
35	Russian Island - UN	CB	May 1981
36	Russian Island - SSW	CB	May 1981
37	Grays Bay - Millers Point	GB	June 1981
38	Grays Bay - Middle Sand Bar	GB	June 1981
39	Grays Bay - Front Sand Bar	GB	June 1981
40	Grays Bay - Rock & Portugese Point	GB	June 1981
41	Grays Bay - West of Grays Point	GB	June 1981
42	Marsh Island - West Tip	UE	May 1981
43	Marsh Island - Sand Bar	UE	May 1981
44	Marsh Island - South Flat	UE	May 1981
45	Horseshoe Island - SW Flat	UE	May 1981
46	Horseshoe Island - SW Flat	UE	July 1981
47	Horseshoe Island - SW Flat	UE	August 1981
48	Horseshoe Island - SW Flat	UE	September 1981
49	Brush Island	UE	May 1981
50	Plankton - Puget Island	PIP	October 1979
51	Plankton - Tongue Point	TPP	October 1979
52	Plankton - Near Clatsop Spit	CSP	October 1979
53	Plankton - Tongue Point	TPP	April 1980
54	Plankton - Near Clatsop Spit	CSP	April 1980
55	Plankton - Youngs River	YRP	November 1980
56	Plankton - Youngs River	YRP	April 1980

Species Composition and Diversity

The analysis of the 56 samples involved the counting and identification of 17,057 diatom valves, approximately 300 per sample. Exactly 150 diatom taxa (species and varieties of species) were found in these samples, of which only 23 were represented by 1 percent or more of the total number of valves. For the purposes of discussion and interpretation, it was convenient to partition the samples on the basis of regional area and whether or not the sample was from the sediment or water column. The regional areas under consideration were Baker Bay, Youngs Bay, Cathlamet Bay, Grays Bay and the Upper Estuary. Baker Bay included one site near the airport road, and Youngs Bay was represented by one site on the west side of the bay near the Youngs Bay bridge. Cathlamet Bay included sites on Lois Island, Grassy Island, McGregor Island and Russian Island; while Grays Bay was represented by sites on the east side, at Millers Point, on sand bars in the middle of the bay, on the west side, and between Rocky Point and Portugese Point. All sites on Marsh Island, Horseshoe Island, Brush Island and Quinns Island were classified as Upper Estuary. Plankton samples were obtained from the water column near Clatsop Spit, Puget Island, Tongue Point, and in the Youngs River. Distributional patterns exhibited by the diatom flora are discussed for each region individually and summarized in a master species list (Appendix C) which indicates regional relative abundance for each taxon.

Baker Bay (Sediment Samples)

Samples from Baker Bay represented material obtained from one site in April, June, August, October, January and March. Therefore, these samples provided some indication of seasonal changes in this area of the estuary.

The dominant diatom taxa (greater than 5% of total valves counted) in the sediment samples from Baker Bay were Navicula diserta, Achnanthes hauckiana, Achnanthes lemmermanni, Navicula salinicola, and Navicula cf. arvensis. Of these, Navicula diserta and N. salinicola are well known brackishwater taxa, while Achnanthes hauckiana and A. lemmermanni are euryhaline taxa tolerant of a wide range of salinity. These taxa, along with the occurrence of such species as Navicula gregaria, Amphora micrometra, Amphora sabyii, Opephora schulzi, Bacillaria paxillifer, and Berkeleya rutilans clearly indicated that this site in Baker Bay was under the influence of brackish water. In comparison with the other regions the diatom flora indicated that the Baker Bay site was subjected to a higher salinity than any of the other sites under consideration.

The flora at the Baker Bay site also contained a few freshwater taxa that were present in very small numbers. The most notable of the benthic freshwater taxa included Fragilaria pinnata, Fragilaria construens, Diatoma tenue v. elongatum, Navicula submuralis, Amphora ovalis v. pediculus, Navicula decussis, Achnanthes lanceolata, and Fragilaria vaucheriae; while the freshwater planktonic taxa were Asterionella formosa and Fragilaria crotonensis. None of these freshwater taxa had a relative abundance value greater than 1 percent of the total number of valves counted for the site in Baker Bay. Two alterna-

tive hypotheses are proposed to account for the presence of freshwater taxa at this site: (1) dead cells from upriver deposited at the site by downstream movements of fresh water; or (2) the cells were remnants of a freshwater flora that developed during a brief period when freshwater discharge was high. More information on salinity distribution in the estuary will provide a better basis for evaluating these hypotheses. At this time, hypothesis (1) appears more reasonable, as Baker Bay is usually considered to be a brackishwater region.

The diatom flora at the Baker Bay site exhibited very little seasonal change. The mean value for the SIMI index of similarity for the 15 possible comparisons of the six samples was 0.894, with a standard error equal to 0.024. In other words, the six samples taken at different times during the year were almost identical in relation to the relative abundances of the dominant taxa. The sample obtained in October was least similar to the other samples, a difference that was related to the abundance of Navicula salinicola at that time of year. However, the SIMI value for comparisons between this sample and the samples taken at other times was still relatively high (0.789).

Mean species diversity expressed by the information measure (H') for the samples from Baker Bay was 2.349, with a standard error of 0.094. Species richness ranged from 22 to 30 taxa in a count of 300 individuals, and the mean dominance expressed by R was 0.309. Considering the possible ranges and maximum values for the H' and R indices, the species diversity was relatively high and the dominance was relatively low in the samples from Baker Bay. However, the input of allochthonous frustules from upriver undoubtedly contributed to an increase in species richness and a decrease in the degree of dominance in the assemblages.

Youngs Bay (Sediment Samples)

The samples from Youngs Bay were obtained from the one site on the west side of the bay at approximately the same times that the site in Baker Bay was sampled, i.e., in April, June, August, October, January and March. The dominant species (over 5 percent of the total valves counted) in the samples from Youngs Bay were Achnanthes hauckiana, Asterionella formosa, Melosira italica, Navicula cryptocephala, Nitzschia hungarica, Nitzschia cf. palea, and Stephanodiscus no. 2. In contrast to the samples from Baker Bay, two of the dominant taxa were typical freshwater planktonic diatoms (A. formosa and M. italica), indicating that the water column in this area is fresh water much of the time. Youngs Bay also receives freshwater input from the Lewis and Clark River and the Youngs River, an input that apprarently provides the the necessary conditions for the development of phytoplankton assemblages that have a species composition characteristic of fresh water. However, the brackish water influence also is apparent in the benthic samples, as A. hauckiana, N. cryptocephala, N. hungarica, and probably N. cf. palea are euryhaline taxa tolerant of a wide range of salinity. In addition, the presence of Bacillaria paradoxa, Gyrosigma fasciola, Melosira nummuloides, Navicula gregaria, Navicula salinarum, Nitzschia sigma v. sigmatella and Nitzschia subhybrida was indicative of the brackishwater influence, whereas the occurrence of such benthic taxa as

Achnanthes lanceolata, Achnanthes minutissima, Amphora ovalis, Diatoma tenue v. elongatum, Fragilaria pinnata, and Synedra ulna was suggestive of fresh water. Therefore, it appeared that the site in Youngs Bay was exposed to intermittent periods of fresh water with enough influence from brackish water to generate a benthic diatom flora that was dominated by a few euryhaline species. In comparison to Baker Bay, the Youngs Bay site apparently is exposed to a lower mean salinity, and the diatom flora on the sediment is more closely related to allochthonous inputs from fresh water. However, the freshwater input into Youngs Bay is not continuous enough to allow the dominance of typical stenohaline, freshwater benthic taxa.

Seasonal changes in the diatom flora at the site in Youngs Bay were relatively small and primarily related to the relative abundances of the freshwater planktonic taxa. The mean SIMI value for 15 possible comparisons among the six samples was 0.811, with a standard error of 0.016. This SIMI value is less than the corresponding mean for the samples from Baker Bay, but still relatively high on this scale of similarity. The differences among the Youngs Bay samples were primarily related to seasonal changes in the relative abundances of Asterionella formosa and Melosira italica. A. formosa was 2 to 3 times more abundant in the June samples than in the other samples, while M. italica reached its maximum abundance during late summer and early fall. The dominant euryhaline benthic taxa exhibited no discernible seasonal trends.

Mean species diversity (H') for the six samples from Youngs Bay was 2.890, with a standard error of 0.067. In this case, species diversity is relatively high and the samples from this site contained between 33 and 42 taxa in contrast to the corresponding range from 22 to 30 found for the site in Baker Bay. Dominance (R) was also less in the Youngs Bay samples than in samples from Baker Bay; the mean R value for the former set of samples was 0.253, with a standard error of 0.013. The relatively high H' values and low R values for the Youngs Bay samples are probably related to relatively high deposition rates of freshwater taxa settling from the water column.

Grays Bay (Sediment Samples)

The samples from the Grays Bay region included six samples from a tidal flat on the east side of the bay taken from the same site at approximately the same time as the samples from Baker Bay and Youngs Bay (April, June, August, October, January and March), and five samples obtained in June from sites near Millers Point, between Rocky Point and Portugese Point, on two sand bars in the bay, and from a site in a small bay west of Grays Point. Dominant benthic taxa (greater than 3 percent of the total valves counted for the entire region) were Achnanthes hauckiana, Achnanthes lanceolata, Cocconeis no. 1, Navicula gregaria, Navicula submuralis, and Nitzschia cf. palea. The presence of A. lanceolata and N. submuralis among the dominant taxa is indicative of a freshwater environment, as the former species is a well known stenohaline freshwater taxon. Also, the occurrence of other typical freshwater taxa in the samples, namely Achnanthes clevei, Achnanthes deflexa, Achnanthes minutissima, varieties of Amphora ovalis, Cymbella minuta, Diatoma tenue v. elongatum, Fragilaria pinnata, Fragilaria

vaucheriae, Comphonema parvulum, Melosira varians, varieties of Navicula capitata, Navicula minima, Nitzschia linearis, and Synedra ulna was further evidence of the lack of a saltwater influence in the region.

Seasonal changes in the Grays Bay region were examined by comparing the six samples obtained at different times of the year from the tidal flat on the east side of the bay. The mean SIMI value for the 15 possible comparisons was 0.675, with a standard error of 0.066, indicating that there was more seasonal variation in the diatom flora at this site than at the sites in Baker Bay and Youngs Bay. Seasonal differences as indicated by SIMI were primarily related to the samples collected in March, as the mean SIMI value with this sample deleted (i.e., 5 samples and 10 values) was 0.827, with a standard error of 0.031. Therefore, the latter mean is relatively high and roughly equivalent to the mean obtained for the six samples from Youngs Bay. Navicula gregaria and Navicula submuralis were largely responsible for seasonal variations exhibited by the SIMI index. N. gregaria reached its maximum relative abundance in March and April, while N. submuralis reached maxima in June and January.

A pattern of variation among the six sites within the Grays Bay region also was obvious from the examination of the relevant SIMI values. The flora from the intensive study site on the east side of the bay was similar to that from the sand bar in the middle of the bay and that from a location between Rocky and Portugese Points. Excluding the dissimilar March sample from the east flat, the mean SIMI value for comparisons between five east flat samples and the samples from the middle sand bar and between Rocky Point and Portugese Point was 0.674, with a standard error of 0.033, while the corresponding values for comparisons between the east flat and sites at Millers Point, in a bay west of Grays Point, and on a sand bar near the channel were only 0.251 and 0.040, respectively. Similarity among the sites at Millers Point, the middle sand bar, the sand bar near the channel, between Rocky Point and Portugese Point, and west of Grays Point was relatively low; the mean SIMI value for these comparisons was 0.149, with a standard error of 0.041. Variation in the diatom flora among these stations was primarily associated with relative abundances of Navicula submuralis, Navicula cf. palea, Stephanodiscus no. 1, and a freshwater planktonic taxon, Asterionella formosa. N. submuralis was abundant in samples from the middle sand bar and from the site between Rocky Point and Portugese Point, a pattern that accounted in part for the similarity between these samples and samples from the east flat. Contamination of benthic samples by freshwater planktonic taxa (e.g., Asterionella formosa) was more pronounced at Millers Point, the sand bar near the channel, the bay west of Grays Point, and between Rocky Point and Portugese Point than at the sites on the east flat and sand bar in the middle of the bay. Moreover, the relative abundance of well-known freshwater planktonic diatoms in the combined samples for the Grays Bay region was 19.6 percent as compared to 31.2 percent and 0.6 percent for the samples from Youngs Bay and Baker Bay, respectively. In this respect the principal difference between the Grays Bay and Youngs Bay regions was the relatively high abundance of Melosira italica (14.8%) in the samples from the latter location, as contamination by Asterionella formosa was about the same for both regions.

Mean species diversity in the Grays Bay region, as expressed by H', was 2.324 with a standard error of 0.153. Therefore, the species diversity in this region was similar to that found for Baker Bay. However, variability in the H' value among samples from the Grays Bay region was greater than the corresponding variation from the Baker Bay samples, an observation undoubtedly related to the number of sites sampled within each region. The number of taxa found in the 11 samples from the Grays Bay region also was variable, ranging from 14 to 39, with a mean of 28.8; mean dominance for these samples expressed by R was 0.372, with a standard error of 0.036.

Cathlamet Bay (Sediment Samples)

The Cathlamet Bay region includes the samples obtained from Lois Island, Grassy Island, McGregor Island, and three locations on Russian Island. Since all samples from this region were obtained during a period from May to early September, a detailed seasonal analysis was not possible. Dominant benthic taxa (greater than 2 percent of total values counted) in the Cathlamet Bay region were Navicula submuralis, Navicula gregaria, Fragilaria pinnata, Achnanthes lanceolata, Amphora ovalis v. pediculus, Nitzschia cf. palea, and unidentified species of Cocconeis. Among the identified taxa, Navicula gregaria is euryhaline and the rest are typical freshwater, stenohaline taxa. Dominant planktonic taxa in the combined samples from Cathlamet Bay were Asterionella formosa (16.6%), Melosira italica (2.6%), and Fragilaria crotonensis (1.5%), a pattern that was similar to that found for the Grays Bay region.

Variation among the 12 samples from the Cathlamet Bay region appeared to be related primarily to time, as SIMI values for comparisons among the Lois Island samples and the Grassy Island samples were lower in mean value than the corresponding mean for samples from Russian Island (including McGregor Island). All samples from Russian Island and McGregor Island were obtained in May, whereas samples from the Lois Island and Grassy Island sites were obtained in May, June, August and September. The mean SIMI values for within site comparisons of samples from Lois Island, Grassy Island and Russian Island (including McGregor Island) were 0.475, 0.350 and 0.732, with standard errors of 0.076, 0.053 and 0.076, respectively. Also there was high similarity (SIMI greater than 0.89) between samples from Lois Island and Grassy Island taken in May and between samples from the same sites obtained in August, indicating uniformity in the samples from different sites obtained at approximately the same time of year. The mean SIMI value for all possible comparisons among the 12 samples from the Cathlamet Bay region (99 values) was 0.464, with a standard error of 0.027. This value reflects both spatial and temporal heterogenity and is similar to a corresponding mean of 0.520 (with a standard error of 0.039) found for the 11 samples from the Grays Bay region.

Temporal changes in the diatom flora during late spring and summer at Lois Island and Grassy Island were closely related to changes in the relative abundance of Asterionella formosa, a freshwater planktonic taxon. A. formosa was very abundant in May at both sites, but decreased in the samples during the summer months. Navicula bacillum, Navicula tenuipunctata and Navicula placentula also varied in relative abundance

between May and September at Lois Island, while Navicula submuralis and Amphora ovalis accounted for temporal changes on Grassy Island. These five species are freshwater, benthic taxa, presumably intolerant of brackish water.

Mean species diversity for the 12 samples from the Cathlamet Bay region expressed at H' was 2.757, with a standard error of 0.090. Therefore, mean diversity for this region was similar to that found for Youngs Bay and slightly higher than values calculated for the Baker Bay and Grays Bay regions. The number of species found in the 12 samples from the Cathlamet Bay region ranged from 30 to 45, and the mean dominance expressed by R was 0.296, with a standard error of 0.021.

Upper Estuary (Sediment Samples)

The Upper Estuary region included samples from three sites on Marsh Island and one site on Horseshoe Island, Brush Island and Quinns Island. Quinns Island was an intensive study site and was sampled in April, June, August, October, January and March, at approximately the same time that samples were obtained at the other intensive study sites in Baker Bay, Youngs Bay and Grays Bay (east flat). Samples from the site on Marsh Island and Brush Island were obtained in May, while the site on Horseshoe Island was sampled in May, June, August and early September. The total number of samples obtained from the Upper Estuary region was 14.

The sites included in the Upper Estuary region are undoubtedly exposed to freshwater conditions throughout the year. Consequently, this region provides a convenient basis for comparing the diatom floras from the other regions with floras that are responding to a freshwater environment characteristic of the lower Columbia River. Dominant benthic diatoms in the samples (greater than 1 percent of total valves counted) from the Upper Estuary region included Amphora ovalis, Amphora ovalis v. pediculus, Achnanthes lanceolata, Achnanthes hauckiana, Navicula arenaria, Navicula capitata, Navicula gregaria, Navicula protracta, Navicula submuralis, Navicula tenuipunctata and Diatoma tenue v. elongatum. Of these, A. hauckiana and N. gregaria are euryhaline and the rest are freshwater stenohaline taxa. Moreover, some of these taxa also were among the dominants at sites in the Cathlamet Bay and Grays Bay regions. The most prominent species of planktonic diatoms found in benthic samples from the Upper Estuary region were Asterionella formosa, Melosira italica and Fragilaria crotonensis. This pattern also was observed in samples from the Cathlamet Bay and Grays Bay regions.

Seasonal changes in the Upper Estuary region were examined by looking at SIMI values for comparisons among samples from Quinns Island. In this case, the April and June samples were very similar to each other (SIMI = 0.935) but dissimilar to samples obtained in August, October, January and March (mean SIMI = 0.343). The mean SIMI value for comparisons among samples obtained from August through March was 0.823, and the mean for all comparisons of the six samples from Quinns Island (15 values) was 0.574, with a standard error of 0.072. The latter mean indicated that temporal variation at Quinns Island was greater than that at the other intensive study sites in Baker Bay, Youngs Bay and Grays

Bay. Seasonal changes at the Quinns Island site were primarily related to temporal patterns in unidentified species of Cocconeis and Stephanodiscus and fluctuations in the relative abundances of Achnanthes clevei, Fragilaria pinnata and Nitzschia cf. palea. However, many benthic taxa were present in the samples from this site throughout the year.

Samples from one site on Horseshoe Island obtained in May, July, August and early September indicated that the flora was similar in May and July and in August and September. The mean SIMI value for the six possible comparisons for this site was 0.635.

The mean SIMI value for all possible comparisons of the 14 samples (91 values) from the Upper Estuary region was 0.436, with a standard error of 0.026. Within this group of samples the most pronounced dissimilarities were between the April and June samples from Quinns Island as compared to the May samples at Marsh Island, Horseshoe Island and Brush Island, and the July, August and September samples at Horseshoe Island. These differences were primarily related to the lack of plankton contamination by Asterionella formosa in the April and June samples from Quinns Island. In other words, the benthic forms had little to do with the larger differences among the samples from the Upper Estuary region.

Mean species diversity for samples from the Upper Estuary region expressed by H' was 2.626, with a standard error of 0.107. The number of taxa in these samples ranged from 28 to 43, and the mean R value was 0.316, with a standard error of 0.030. The highest degree of dominance (R between 0.47 and 0.49) was related to the abundance of Asterionella formosa, a planktonic taxon, in four of the 14 samples from this region.

Plankton Samples

The plankton sample obtained near Puget Island at the upper end of the estuary in October consisted of 99% freshwater planktonic taxa and 1% freshwater benthic taxa. The dominant species in this sample were Melosira italica (44.9%), Fragilaria crotonensis (40.0%), M. granulata (10.2%), and Asterionella formosa (2.6%). These species are more heavily silicified than many of the relatively fragile, marine planktonic diatoms. Consequently, freshwater planktonic diatom frustules were deposited and preserved in the sediments and occurred in many benthic samples from the Youngs Bay, Cathlamet Bay, Grays Bay and Upper Estuary regions.

Similarity between the October and April plankton samples collected near Tongue Point was relatively low (SIMI = 0.207). The October collection was composed of 98% freshwater taxa, 0.7% marine planktonic taxa, 0.3% freshwater benthic taxa, and about 1% euryhaline benthic taxa. The most prominent freshwater planktonic species were Melosira italica (16.7%) and Asterionella formosa (1%). The only marine planktonic taxon present in this sample was Coscinodiscus perforatus v. cellulosa, which had a relative abundance of only 0.7%. The April collection from the same location contained 90% freshwater planktonic taxa and 10% freshwater benthic taxa. A. formosa (60.6%), M. italica

(12.7%), two unidentified species of Stephanodiscus (8.1% and 6.8%), and Nitzschia cf. palea (2.6%) were the most prominent taxa. The low SIMI value between the October and April collections reflects a seasonal shift in the relative abundances of the dominant freshwater phytoplankton.

The plankton sample collected off Clatsop Spit in October contained 75.1% marine planktonic taxa, 19.4% freshwater planktonic taxa and 5.5% benthic forms. The fragile nature of many marine planktonic species accounted for the lack of contamination of the Baker Bay sediment samples by these taxa. The April collection off Clatsop Spit was very dissimilar to the corresponding October sample (SIMI = 0.084). The April flora was dominated by typical freshwater forms: Asterionella formosa (45.8%), two unidentified species of Stephanodiscus (12.9% and 11.6%), and Melosira italica (8.1%). The only marine planktonic species present in this sample were Chaetoceros decipiens (2.6%) and Skeletonema costatum (1.6%). Relatively few benthic taxa were present. The October and April collections contrast periods of low and high freshwater discharge, respectively. Spring freshet creates a plume of freshwater carrying freshwater species which extends to near the mouth of the estuary. The paucity of freshwater planktonic taxa and the dominance of euryhaline and brackishwater diatoms on the sediments of Baker Bay throughout the year suggest that relatively little upstream water circulates through Baker Bay, and that even during spring freshet Baker Bay is a brackishwater region.

In contrast to phytoplankton collections from the Columbia River, planktonic assemblages in the Youngs River in November and April contained high percentages of freshwater benthic diatoms. The April collection was dominated by Nitzschia cf. palea (52.8%), Surirella ovata (8.5%), Asterionella formosa (6.8%), and an unidentified Stephanodiscus (6.5%). Dominant taxa in the November sample were Melosira italica (15.2%), an unidentified Cyclotella (11.7%), A. formosa (7.1%), and an unidentified Stephanodiscus (8.7%). Few living cells were observed in the November collection, and the presence of marine and brackishwater taxa in this sample (e.g., Opephora schulzi, Campylosira cymbelliformis and Chaetoceros subtile) was evidence of particle transport from the lower estuary to the Youngs River. The seasonal nature of the planktonic assemblage in the Youngs River was indicated by a relatively low SIMI value (0.422) between the April and November collections. It is also evident that the Youngs River, and probably the Lewis and Clark River, contributes freshwater benthic diatom valves to the sediments of Youngs Bay.

Interregional Comparisons of Community Structure

The AIDN program allowed the calculation of the SIMI index of similarity for samples pooled by region and season. In this section, matrices of SIMI values are presented comparing the five regions under consideration to each other and to each of the plankton samples. Also, samples from the four intensive study sites in Baker Bay, Youngs Bay, Grays Bay and Quinns Island taken at the same time of year in April, June, August, October, January and March are pooled and compared by season. Although most of the relevant details of community difference

were discussed in the previous section, the AIDN analysis of the data pooled in this way provided a convenient, information-rich approach to the summarization of the results of this study.

Similarity Among Regional Diatom Floras

Appendix C provides a master list of diatom taxa identified in the 56 samples and indicates the relative abundance of each taxon in each region and in the plankton samples. In addition, the relative abundance of each taxon in the entire set of samples pooled as one assemblage is designated in the column entitled Pooled Samples.

Of the 150 taxa found in the 56 samples, 73 were classified as freshwater benthic taxa, 26 as brackishwater benthic taxa, 12 as euryhaline benthic taxa, 6 as freshwater plankton, 16 as marine plankton, and the rest as unknown. These evaluations were based on 14 years of field observations in Oregon estuaries and on autecological information reported in the literature. Although the freshwater planktonic and euryhaline categories were represented by relatively few taxa, they accounted for 23.3% and 19.5% of the total valves counted, respectively. The corresponding relative abundances for the freshwater benthic, brackishwater benthic, and marine planktonic categories were 33.7%, 4.7% and 1.8%. Therefore, the diatom flora in the Columbia River Estuary clearly reflects the influence of a system characterized by high freshwater discharge. This is in sharp contrast to many other Oregon estuaries (e.g., Yaquina Bay and Netarts Bay) where the abundance of brackishwater benthic taxa is much more evident, particularly during the summer months when freshwater discharge is low.

Table 4 represents all possible comparisons among pooled samples from the five regions, and comparisons between these samples and the plankton samples. The triangular matrix is partitioned into three parts: interregional comparisons (triangle to the left), comparisons among plankton samples (lower right triangle), and comparisons between regional samples and plankton samples (lower left rectangle). The conclusions from this analysis are:

1. The diatom floras from the Cathlamet Bay, Grays Bay and Upper Estuary regions were similar. The corresponding mean SIMI value for the three possible comparisons at this level of resolution was 0.830.

2. The Youngs Bay flora was more similar to the flora from the freshwater regions (i.e., Grays Bay, Cathlamet Bay and Upper Estuary) than to the flora from Baker Bay, a pattern apparently related to freshwater input into Youngs Bay from the Lewis and Clark River and Youngs River. The mean SIMI values for comparisons of Youngs Bay and Baker Bay with the three freshwater regions was 0.517 and 0.171, respectively.

Table 4. A matrix of SIMI values indicating similarity of samples pooled by region and similarity between pooled samples from each region and the pooled samples from locations where phytoplankton collections were obtained. The regions are Baker Bay (BB), Youngs Bay (YB), Cathlamet Bay (CB), Grays Bay (GB) and Upper Estuary (UE). Plankton samples are from the water column near Clatsop Spit (CSP), Tongue Point (TPP), Puget Island (PIP) and in the Youngs River (YRP).

	BB	YB	CB	GB	UE	CSP	TPP	PIP	YRP
YB	0.367								
CB	0.201	0.472							
GB	0.083	0.402	0.854						
UE	0.230	0.677	0.845	0.790					
CSP	0.028	0.519	0.371	0.430	0.581				
TPP	0.015	0.731	0.349	0.410	0.578	0.669			
PIP	0.006	0.523	0.147	0.114	0.255	0.299	0.717		
YRP	0.134	0.544	0.286	0.313	0.513	0.309	0.394	0.225	

3. Similarity between the benthic flora from the three freshwater regions and the three plankton samples from the freshwater regions was relatively low. The corresponding mean SIMI value for the nine possible comparisons was 0.329.

4. The benthic flora from Youngs Bay was more similar to the flora in the plankton sample from Puget Island, Tongue Point and Youngs River than any of the benthic samples from the other regions, a pattern related to the high relative abundance of Melosira italica and Asterionella formosa in the Youngs Bay and plankton samples. The mean SIMI value for the three possible comparisons was 0.599.

5. The benthic flora from Baker Bay was dissimilar to the flora in the four plankton samples. The mean SIMI value for the corresponding comparisons was 0.046.

6. The planktonic floras off Puget Island and Tongue Point were similar to each other (SIMI = 0.717). This similarity value undoubtedly would have been greater if a plankton sample had been obtained off Puget Island in spring when Asterionella formosa was more abundant. These floras were relatively dissimilar to the planktonic flora near Clatsop Spit (mean SIMI = 0.484).

7. The Youngs River plankton was dissimilar to the Clatsop Spit, Tongue Point and Puget Island plankton (SIMI = 0.309, 0.394 and 0.255, respectively). This dissimilarity was related to the presence of many benthic taxa in the plankton from the Youngs River, which did not appear in the Columbia River planktonic assemblages.

In summary, the analysis of the pooled samples indicated that the intertidal zones of the Cathlamet Bay, Grays Bay and Upper Estuary regions are freshwater areas, while the corresponding zone in Baker Bay is under the influence of brackish water. The Youngs Bay region apparently is influenced to some degree by slightly brackish water, although intermittent periods of high freshwater discharge are responsible for the presence of a large number of freshwater planktonic and benthic taxa in the sediment associated flora. The degree to which the presence of stenohaline, freshwater benthic taxa in the sediments of Youngs Bay is related to allochthonous inputs from fluviatile processes is unknown.

Seasonal Variations at Intensive Study Sites

Since the diatom flora at the four intensive study sites was sampled at the same time throughout the year, it was possible to examine seasonal changes for samples from these sites pooled by month. In this case, there were six pooled samples representing the months of April, June, August, October, January and March; and there were 15 possible comparisons (Table 5). The results of this analysis indicated that there was relatively little seasonal change in the diatom flora at the intensive study sites. Corresponding to this conclusion, the mean SIMI value for

Table 5. A matrix of SIMI values indicating the similarity of samples from four intensive study sites (Baker Bay, Youngs Bay, Grays Bay and Quinns Island) pooled by month.

	Apr	Jun	Aug	Oct	Jan	Mar
Apr						
Jun	0.859					
Aug	0.801	0.861				
Oct	0.636	0.745	0.905			
Jan	0.835	0.949	0.824	0.747		
Mar	0.737	0.668	0.843	0.830	0.666	

the 15 comparisons was 0.794. In other words, when repeated sampling occurred at the same locations throughout the year, seasonal changes in benthic species composition was minimal. However, some seasonal variation was apparent in regions where more than one site was sampled, a temporal heterogeneity probably related, in part, to variations in the physical properties of the sediment within a region. The absence of marked seasonal shifts in the community structure of sediment-associated diatom floras has also been observed in other Oregon estuaries (Amspoker and McIntire 1978; Whiting 1983). In contrast to benthic assemblages, the phytoplankton exhibited pronounced seasonal shifts in species composition. Furthermore, the relatively small degree of seasonality which was observed in benthic assemblages could be explained in large part by seasonal inputs of planktonic diatoms from the water column.

3.2 PRODUCTION DYNAMICS

Results of the investigation of the production dynamics of benthic plants in the Columbia River Estuary are presented in three subsections: Intensive Study Sites, Validation and Survey Sites, and Regional Patterns of Benthic Primary Production. In the first subsection, details of seasonal patterns in autotrophic biomass and benthic primary production are reported for the intensive study sites, and relationships among biological variables and between biological and physical variables are explored. Additional data on primary production and biomass are discussed in the subsection about the validation sites, and observed values for primary production at these sites are compared with values predicted from regression equations derived from studies at the intensive study sites. This subsection also reports the patterns of sediment chorophyll at the survey sites and corresponding rates of

primary production predicted from the chlorophyll data. In the last subsection, patterns of autotrophic biomass and primary production are summarized in maps for selected regions of the estuary, and annual rates of benthic primary production are estimated for these regions and more specifically for the intensive study sites.

3.2.1 Intensive Study Sites

Sediment Properties

The properties and stability of the sediment are closely related to species composition and production dynamics of benthic plant assemblages in the Columbia River Estuary. At the intensive study sites, sediment samples were collected for grain size analysis by the Benthic Primary Production research unit, and the laboratory analyses were performed by the Sedimentation and Shoaling research unit. As an index of sediment stability, the ratios of chlorophyll a concentration in the top cm of sediment to the concentrations at the 4.5-5.5 cm depth and the 9-10 cm depth were determined from replicated measurements along each transect. At best, these ratios are only a crude indication of sediment mixing. However, benthic diatoms remain in the upper few mm of sediment if the system is undisturbed, but can survive relatively long periods of burial when the sediments are mixed. Therefore, sediment disturbance can be investigated by measurements of the chlorophyll concentration in these organisms at various depths in the sediment. Sediment properties and chlorophyll ratios for the intensive study sites are presented in Tables 6-11; these data also were used in the correlation and regression analyses reported in a later section.

The sediments along the sampling transects at Clatsop Spit were well sorted and consisted of fine sand (Table 6). Mean grain sizes for the upper and lower transects where samples for measurements of primary production were obtained were 2.47 and 2.36 phi (0.181 and 0.195 mm), respectively. The percentage of sand in the samples from this site varied from 99.2% to 100% throughout the study, and seasonal variation in sediment properties was very small. Because of the loose, sandy nature of these sediments, it was not possible to remove the cores from the tubes without disturbing the sediments below the top cm. Therefore, the chlorophyll a concentration was measured for the top cm of sediment only, and the chlorophyll ratios were not determined for the transects on Clatsop Spit. However, it was obvious from field observations that the sediments at this site shifted around in response to river flow and tidal movement, and in general were an unstable substrate for the growth of aquatic plants.

At the Youngs Bay site the sediments were relatively fine, particularly in the lower marsh and along the upper transect of the intertidal region (Table 7). Mean grain sizes along the marsh, upper and lower transects where samples for primary production measurements were obtained were 6.03, 5.84 and 4.34 phi (0.015, 0.017 and 0.049 mm), respectively. In comparison with samples from Clatsop Spit, these sediments were poorly sorted. Also, the lower transect had a larger percentage of sand in the samples (mean of 56.2%) than either the upper or marsh transects (11.3% and 9.2%), a pattern that was apparently

Table 6. Results of the sediment grain size analysis for the intensive study site at Clatsop Spit. The transects are the same as those indicated in Table 1. The mean grain size is expressed in phi units, while measures of sorting and skewness are dimensionless (Inman 1952).

Transect and Date	SAND %	SILT %	CLAY %	MEAN	SORT	SKEW
Upper:						
May 1980	99.4	0.6	0.0	2.37	0.32	0.23
July 1980	99.9	0.1	0.0	2.46	0.23	0.01
August 1980	99.7	0.4	0.0	2.47	0.23	0.01
Sept. 1980	99.5	0.4	0.2	2.49	0.23	0.03
Oct. 1980	99.8	0.2	0.0	2.48	0.23	-0.02
Feb. 1981	99.6	0.0	0.4	2.47	0.28	0.02
March 1981	99.7	0.3	0.0	2.56	0.24	0.02
April 1981	99.8	0.2	0.0	2.43	0.25	0.00
Mean	99.7	0.3	0.1	2.47	0.25	0.04
Mid:						
May 1980	99.4	0.6	0.0	2.37	0.32	0.23
Lower:						
May 1980	99.2	0.8	0.0	2.56	0.55	-0.41
July 1980	99.7	0.3	0.0	2.40	0.23	-0.03
August 1980	99.3	0.7	0.0	2.27	0.28	-0.02
Sept. 1980	99.4	0.1	0.5	2.33	0.25	-0.06
Oct. 1980	100.0	0.0	0.0	2.31	0.25	0.01
Feb. 1981	99.5	0.5	0.0	2.37	0.28	-0.03
March 1981	99.6	0.3	0.1	2.37	0.27	-0.03
April 1981	99.7	0.3	0.0	2.29	0.31	-0.01
Mean	99.6	0.4	0.1	2.36	0.30	-0.07

Table 7. Results of sediment grain size analyses for the intensive study site at Youngs Bay. Transects and units are the same as indicated in Tables 1 and 6, respectively.

Transect and Date	SAND %	SILT %	CLAY %	MEAN	SORT	SKEW
Marsh:						
May 1980	11.4	73.6	15.0	6.05	1.75	0.56
August 1980	14.3	82.6	3.1	5.67	1.54	-0.11
Sept. 1980	12.0	71.2	16.8	6.13	1.98	0.17
Oct. 1980	7.4	70.6	22.1	6.68	2.29	0.19
Feb. 1981	14.1	74.4	11.5	5.75	1.60	0.40
March 1981	14.9	72.2	12.7	5.81	1.71	0.20
April 1981	5.0	80.5	14.5	6.12	1.67	0.11
Mean	11.3	75.0	13.7	6.03	1.79	0.22
Upper:						
May 1980	8.3	73.2	18.5	6.46	2.29	0.58
July 1980	11.0	75.0	14.0	5.95	1.80	0.17
August 1980	8.6	80.9	10.5	5.66	1.49	0.57
Sept. 1980	9.5	77.9	12.6	5.85	1.62	0.36
Oct. 1980	7.1	78.5	14.4	5.98	1.80	0.24
Feb. 1981	13.4	78.4	8.1	5.37	1.26	0.54
March 1981	8.8	81.6	9.6	5.63	1.44	0.29
April 1981	7.0	81.1	11.9	5.84	1.52	0.06
Mean	9.2	78.3	12.5	5.84	1.65	0.35
Mid:						
May 1980	27.1	63.1	9.8	4.70	1.76	0.19
Lower:						
May 1980	85.1	11.5	3.4	3.02	0.85	0.67
July 1980	54.5	39.5	5.9	4.64	2.38	0.67
August 1980	60.4	32.7	6.9	4.30	2.08	0.78
Sept. 1980	52.0	38.6	9.4	4.60	2.34	0.40
Oct. 1980	28.8	60.1	11.1	5.01	2.50	-0.07
Feb. 1981	66.4	28.6	5.0	4.05	1.86	0.80
March 1981	59.2	33.3	7.5	4.40	2.20	0.78
April 1981	43.5	47.1	9.4	4.66	2.40	0.08
Mean	56.2	36.4	7.3	4.34	2.08	0.51

related to turbulence and the velocity of water movements in the area. Seasonal patterns in sediment properties at the Youngs Bay site were not apparent from the data in Table 8. Chlorophyll ratios indicated that the sediments were relatively undisturbed, however, as the concentrations near the surface were from four to seven times greater than concentrations at the other depths under consideration (Table 8).

Sediments along the transects in Baker Bay were also relatively fine. Mean grain sizes corresponding to the marsh, upper and lower transects at this site were 6.02, 4.61 and 5.69 phi (0.015, 0.041 and 0.019 mm), respectively (Table 9). In contrast to the Youngs Bay site, the lower transect had finer sediment than the upper transect, although mean grain sizes in the lower marsh transects were almost identical for the two sites. Moreover, seasonal trends were not particularly conspicuous at the Baker Bay transects, with the exception that the sediment appeared to be slightly finer during the fall than during the winter and spring months, a pattern undoubtedly related to seasonal changes in freshwater discharge.

In general, sediments from the marsh and upper transects had a larger percentage of sand than sediments from the corresponding transects in Youngs Bay. The mean chlorophyll ratios for the Baker Bay site were very similar to those calculated for the Youngs Bay site, indicating a relatively stable substrate suitable for the growth of microalgae. However, apparently the area is marginal for the growth of seagrass and macroalgae as noted earlier.

At the intensive study site in Grays Bay, sediments were composed of sandy silt (Table 10). Mean grain sizes for samples collected along the marsh, upper and lower transects were 4.72, 4.29 and 4.69 phi (0.038, 0.051 and 0.039 mm), respectively. The percentage of sand in the samples from these transects varied from 19.5% (marsh transect) to 89.4% (upper transect) and fluctuated around a mean value of 56.1%. At the Grays Bay site, sediment properties were less variable among the transects than at the sites in Youngs Bay and Baker Bay, and on an average the sediments in the lower marsh were just as coarse as sediments in the intertidal region. Sediments in the lower marsh were coarser in the winter and spring than during the summer and fall, but seasonal patterns were not obvious in samples from the intertidal transects. However, sediment from all transects exhibited a relatively high percentage of sand (64.8 to 89.4%) in May 1980. Chlorophyll ratios for the Grays Bay site were relatively low, indicating considerable sediment disturbance and mixing. In this case, the chlorophyll concentration was almost uniform to a depth of 5 cm, and the microhabitat apparently was less suitable for the development of microalgal assemblages than the areas in Youngs Bay and Baker Bay.

The intertidal region at the intensive study site on Quinns Island was a sandy area with relatively little silt and clay (Table 11). Mean grain sizes for sediments from the upper and lower transects were 2.21 and 2.78 phi (0.216 and 0.146 mm), respectively; sediments along the marsh transect were much finer, with a mean grain size of 4.94 phi (0.33 mm). Apparently, the intertidal area at this site is strongly affected by water movements, particularly during periods of high freshwater discharge. The most interesting seasonal change in sediment

Table 8. Ratios of the concentration of chlorophyll a in the top cm of sediment to the concentrations at the 4.5-5.5 cm depth (C1:C2) and the 9-10 cm depth (C1:C3) at four intensive study sites. Data are mean values for n observations at the same transects described in Table 1.

Site	Transect	n	C1:C2	C1:C3
Youngs Bay:				
	Upper	72	4.00	10.06
	Mid	66	3.61	5.96
	Lower	66	4.48	5.11
	Mean	204	4.03	7.13
Baker Bay:				
	Upper	72	3.64	11.00
	Mid	66	3.30	10.21
	Lower	66	3.69	5.42
	Mean	204	3.55	9.05
Grays Bay:				
	Upper	66	0.91	1.47
	Mid	66	0.86	1.50
	Lower	60	1.02	2.54
	Mean	192	0.93	1.81
Quinns Island:				
	Upper	72	2.59	2.93
	Mid	66	1.68	2.72
	Lower	60	2.42	3.06
	Mean	198	2.26	2.91

Table 9. Results of sediment grain size analysis for the intensive study site at Baker Bay. Transects and units are the same as indicated in Tables 1 and 6, respectively.

Transect and Date	SAND %	SILT %	CLAY %	MEAN	SORT	SKEW
Marsh:						
May 1980	56.7	31.3	12.0	4.78	1.97	0.56
July 1980	17.3	50.8	31.9	6.88	3.22	-0.04
August 1980	25.2	48.9	25.8	6.48	3.18	0.04
Sept. 1980	19.0	51.1	29.8	6.96	3.44	0.06
Oct. 1980	2.5	64.7	32.8	7.78	2.36	0.43
Feb. 1981	63.9	26.3	9.8	4.59	1.79	0.61
March 1981	51.5	35.3	13.2	5.19	2.32	0.57
April 1981	51.1	33.6	15.4	5.46	2.44	0.64
Mean	35.9	42.8	21.3	6.02	2.59	0.36
Upper:						
May 1980	74.2	19.7	6.1	4.12	0.93	0.67
July 1980	19.4	54.0	26.6	6.62	3.10	-0.01
August 1980	80.4	13.8	5.8	2.62	2.56	0.95
Sept. 1980	39.7	43.5	16.7	5.64	2.52	0.19
Oct. 1980	34.0	56.5	9.4	5.03	1.74	0.47
Feb. 1981	66.8	25.2	8.0	4.60	1.72	0.61
March 1981	78.3	17.2	4.8	3.60	0.75	0.17
April 1981	66.8	25.0	8.2	4.63	1.77	0.63
Mean	57.5	31.9	10.7	4.61	1.89	0.46
Mid:						
May 1980	72.3	21.2	6.4	3.73	0.62	0.30
Lower:						
May 1980	43.1	45.3	11.7	5.13	1.74	0.60
July 1980	35.2	50.4	14.4	5.56	2.17	0.51
August 1980	13.9	66.7	19.4	6.66	2.56	0.19
Sept. 1980	15.5	63.1	21.4	6.55	2.50	0.10
Oct. 1980	22.9	63.6	13.4	5.64	2.01	-0.03
Feb. 1981	34.4	51.9	13.7	5.49	2.05	0.55
March 1981	41.6	48.8	9.7	5.05	1.71	0.54
April 1981	37.0	50.0	13.0	5.43	2.06	0.59
Mean	30.5	55.0	14.6	5.69	2.10	0.38

Table 10. Results of sediment grain size analysis for the intensive study site at Grays Bay. Transects and units are the same as indicated in Tables 1 and 6, respectively.

Transect and Date	SAND %	SILT %	CLAY %	MEAN	SORT	SKEW
Upper:						
May 1980	86.1	10.4	3.5	3.35	0.59	-0.12
July 1980	19.5	64.7	15.8	5.80	2.18	-0.36
August 1980	47.6	40.8	11.6	5.24	2.07	0.53
Sept. 1980	41.2	45.6	13.1	5.46	2.22	-0.15
Oct. 1980	31.4	52.9	15.7	5.67	2.30	-0.25
Feb. 1981	81.3	16.0	2.7	3.83	0.83	0.59
March 1981	89.3	8.9	1.8	3.29	0.30	-0.11
April 1981	50.5	41.4	8.1	5.13	1.94	0.65
Mean	55.9	35.1	9.0	4.72	1.55	0.10
Upper:						
May 1980	89.4	8.3	2.3	3.30	0.48	0.07
July 1980	61.5	34.3	4.2	4.54	1.71	0.69
August 1980	60.0	34.1	5.9	4.74	1.65	0.75
Sept. 1980	75.6	21.5	2.9	4.21	1.19	0.67
Oct. 1980	53.2	42.2	4.7	4.72	1.59	0.63
Feb. 1981	60.3	34.4	5.3	4.73	1.69	0.69
March 1981	76.9	20.1	3.0	4.07	1.12	0.66
April 1981	78.0	19.3	2.7	3.99	1.01	0.63
Mean	69.4	26.8	3.9	4.29	1.31	0.60
Mid:						
May 1980	86.4	10.6	3.0	3.26	0.74	-0.04
Lower:						
May 1980	64.8	30.0	5.2	3.84	0.56	0.33
July 1980	51.7	43.6	4.7	4.39	0.99	0.45
August 1980	42.7	51.4	5.9	4.78	1.33	0.51
Sept. 1980	42.4	53.6	4.1	4.70	1.25	0.47
Oct. 1980	43.4	52.5	4.2	4.74	1.27	0.53
Feb. 1981	39.6	54.3	6.1	4.96	1.52	0.42
March 1981	19.6	72.8	7.6	5.25	1.62	-0.14
April 1981	40.0	55.0	5.1	4.84	1.42	0.35
Mean	43.0	51.7	5.4	4.69	1.25	0.37

Table 11. Results of sediment grain size analysis for the intensive study site at Quinns Island. Transects and units are the same as indicated in Tables 1 and 6, respectively.

Transect and Date	SAND %	SILT %	CLAY %	MEAN	SORT	SKEW
Marsh:						
May 1980	57.3	33.5	9.1	4.38	1.72	0.43
July 1980	27.8	60.4	11.8	5.08	2.50	-0.12
August 1980	11.3	71.8	16.9	6.23	1.90	-0.04
Sept. 1980	32.2	52.7	15.1	5.37	2.51	-0.04
Oct. 1980	81.5	18.5	0.0	2.89	1.51	0.51
Feb. 1981	3.7	91.7	4.7	5.15	0.77	0.46
March 1981	8.8	87.1	4.1	5.08	0.88	0.46
April 1981	5.1	89.3	5.6	5.34	1.00	0.40
Mean	28.5	63.1	8.4	4.94	1.60	0.26
Upper:						
May 1980	97.2	2.9	0.0	2.05	0.85	-0.03
July 1980	98.9	1.1	0.0	1.74	0.71	0.25
August 1980	98.9	1.2	0.0	1.81	0.73	0.30
Sept. 1980	91.3	6.9	1.8	1.85	0.83	0.32
Oct. 1980	68.2	25.8	6.0	3.81	2.63	0.66
Feb. 1981	93.7	6.0	0.4	2.25	1.22	0.49
March 1981	95.9	3.4	0.8	2.16	0.98	0.39
April 1981	95.7	3.7	0.6	2.04	0.93	0.28
Mean	92.5	6.4	1.2	2.21	1.11	0.33
Mid:						
May 1980	97.2	2.8	0.0	1.63		
Lower:						
May 1980	99.0	1.0	0.0	1.71	0.49	0.73
July 1980	98.2	1.6	0.3	1.92	0.65	0.49
August 1980	97.9	2.1	0.0	1.89	0.64	0.55
Sept. 1980	88.1	10.3	1.7	2.12	0.90	1.63
Oct. 1980	12.8	66.8	20.4	6.54	1.90	1.14
Feb. 1981	76.7	21.7	1.6	2.92	1.43	0.77
March 1981	92.9	6.6	0.5	2.33	0.97	0.56
April 1981	84.0	14.9	1.0	2.78	1.21	0.61
Mean	81.2	15.6	3.2	2.78	1.02	0.81

properties at the Quinns Island site took place between September and October 1980, when the mean grain size decreased to 3.81 phi at the upper transect and to 6.54 phi at the lower transect. These changes corresponded to sharp increases in rates of primary production, suggesting that the finer grain sizes in October were indicative of a temporary increase in sediment stability during a period of low freshwater discharge. Mean chlorophyll ratios were 2.26 and 2.91 for the near surface to 4.5-5.5 cm and the near surface to 9-10 cm values, respectively. These values were relatively low in comparison with the sites in Youngs Bay and Baker Bay, but slightly higher than values found for the site in Grays Bay.

Autotrophic Biomass

In benthic communities that consist of complex mixtures of microalgae, detritus, and associated animals and heterotrophic microorganisms, the concentration of chlorophyll *a* in the top cm of sediment provides a good index to the biomass of the autotrophic organisms. In the Columbia River Estuary there is a relatively good correlation between the concentration of chlorophyll *a* and rates of benthic primary production, a relationship that is valuable for predicting primary production when direct measurements are not possible. Moreover, recent research by Davis and McIntire (1983) has established a ratio between chlorophyll *a* concentration in benthic diatoms and the biomass of these organisms, thereby providing a basis for converting chlorophyll data to estimates of autotrophic biomass. Such conversions are useful for the development of energy budgets.

Table 12 represents a summary of the mean concentrations of chlorophyll *a* in the top cm of sediment at the five intensive study sites. Mean values were calculated from data pooled relative to time of sampling (month), intensive study site, and tidal level (transect). Also included in the table are the means for all samples taken at the three different depths in the sediment. A more detailed breakdown of the same data is presented in Appendix A.

The mean concentration of chlorophyll *a* in the top cm of sediment for all five intensive study sites exhibited relatively little seasonal change, varying from a minimum value of 11.83 $\mu g\ cm^{-3}$ in March 1981 to a maximum of 19.18 $\mu g\ cm^{-3}$ in November 1980; the mean value of all observations obtained from the top cm of sediment was 15.21 $\mu g\ cm^{-3}$ (Table 12). These values can be converted to units of $mg\ m^{-2}$ in the top cm layer by multiplying by a factor of 10. Mean values for observations pooled by intensive study site ranged from 1.38 $\mu g\ cm^{-3}$ for the Clatsop Spit site to 26.44 $\mu g\ cm^{-3}$ for the Youngs Bay site. If it is assumed that chlorophyll concentration in the top cm of sediment is a reliable

Table 12. Mean concentrations of chlorophyll a ($\mu g\ cm^{-3}$), sample sizes, and standard error of the means for five intensive study sites in the Columbia River Estuary. Data pooled by sampling time (month), site, and tidal level (transect) represents means of measurements in the top cm of sediment. Data pooled by sediment depth represent means of all observations for the top cm of sediment and at depths 4.5-5.5 cm and 9-10 cm below the surface.

Variable	Sample Size	Mean	Standard Error
Time:			
April	90	17.63	1.47
May	114	17.81	1.14
June	114	18.95	1.36
July	114	13.68	0.93
August	114	14.31	1.01
September	114	17.45	1.73
October	114	15.15	1.23
November	48	19.18	1.94
January	96	13.08	1.29
February	114	13.80	1.30
March	114	11.83	0.95
April	114	12.17	0.99
Site:			
Clatsop Spit	204	1.38	0.12
Youngs Bay	270	26.44	0.78
Baker Bay	270	25.06	0.67
Grays Bay	252	10.33	0.35
Quinns Island	264	9.02	0.50
Tidal Level:			
Marsh	258	21.02	0.71
Upper	354	16.10	0.83
Mid	336	14.04	0.71
Lower	312	10.67	0.51
Sediment Depth:			
Top cm	1260	15.21	0.37
4.5-5.5 cm	798	8.10	0.17
9-10 cm	798	5.18	0.15

index to the capacity for benthic autotrophy, these data indicated that the most productive sites were Youngs Bay and Baker Bay, while the sites at Grays Bay and Quinns Island had a productive capacity of about 40% of the capacities at Youngs Bay and Baker Bay. The productive capacity at the Clatsop Spit site was extremely low, a pattern apparently related to the stability and properties of the sediment in that area. On an average, sediments near the surface had the highest concentration of chlorophyll a along the marsh transect, followed by the upper, mid and lower transects, in that order. In general, the lower transects at the sites were more exposed to physical disruption from water movements than the transects nearer the low marsh.

Although the means tabulated in Table 12 are indicative of general patterns at the intensive study sites, there were strong interactions among the effects of season, site location, tidal transect, and sediment depth. These interactions are illustrated by plots of the temporal patterns of chlorophyll a concentration for each site relative to transect and sediment depth (Figures 5-9). These graphs show the differences between chlorophyll a concentrations in the top cm of sediment and concentrations at the lower depths in the sediment cores. The data indicated that the sites at Youngs Bay and Baker Bay had large differences, while sites at Grays Bay and Quinns Island exhibited small differences. Seasonal departures from this pattern occurred at the Quinns Island site in the fall of 1980 at the upper transect and in April of 1980 at the lower transect. The sites with large differences between near-surface chlorophyll a concentrations and concentrations at the lower depth of the sediment cores (Youngs Bay and Baker Bay) usually had higher rates of benthic primary production than the sites where the concentration was more uniform with increasing depth (Grays Bay and Quinns Island), a pattern that was probably related to sediment stability as noted above in the Sediment Properties section of this report.

Primary Production and Related Variables

At the intensive study sites, rates of primary production were determined for core samples collected from the marsh, upper and lower transects, with the exception of Clatsop Spit where just the Upper and Lower transects were sampled. In addition, measurements of oxygen consumption and the concentrations of organic matter and chlorophyll a in the top cm of sediment were obtained for the same cores that were used for measurements of primary production. Therefore, this data set, which is summarized in Appendix D, provided a basis for exploring relationships among selected biological rate and state variables by correlation and regression analysis.

Mean rates of gross primary production for all intensive study sites ranged from 11.11 mg C m^{-2} hr^{-1} in February 1981, to 75.72 mg C m^{-2} hr^{-1} in May 1980 (Table 13). In general, rates were lower in the late fall and winter than at other times of the year. Youngs Bay was the most productive site with a mean value of 84.22 mg C m^{-2} hr^{-1}, while Clatsop Spit was the least productive (5.22 mg C m^{-2} hr^{-1}); mean rates for Grays Bay and Quinns Island were similar, 33.01 and 29.56 mg C m^{-2}

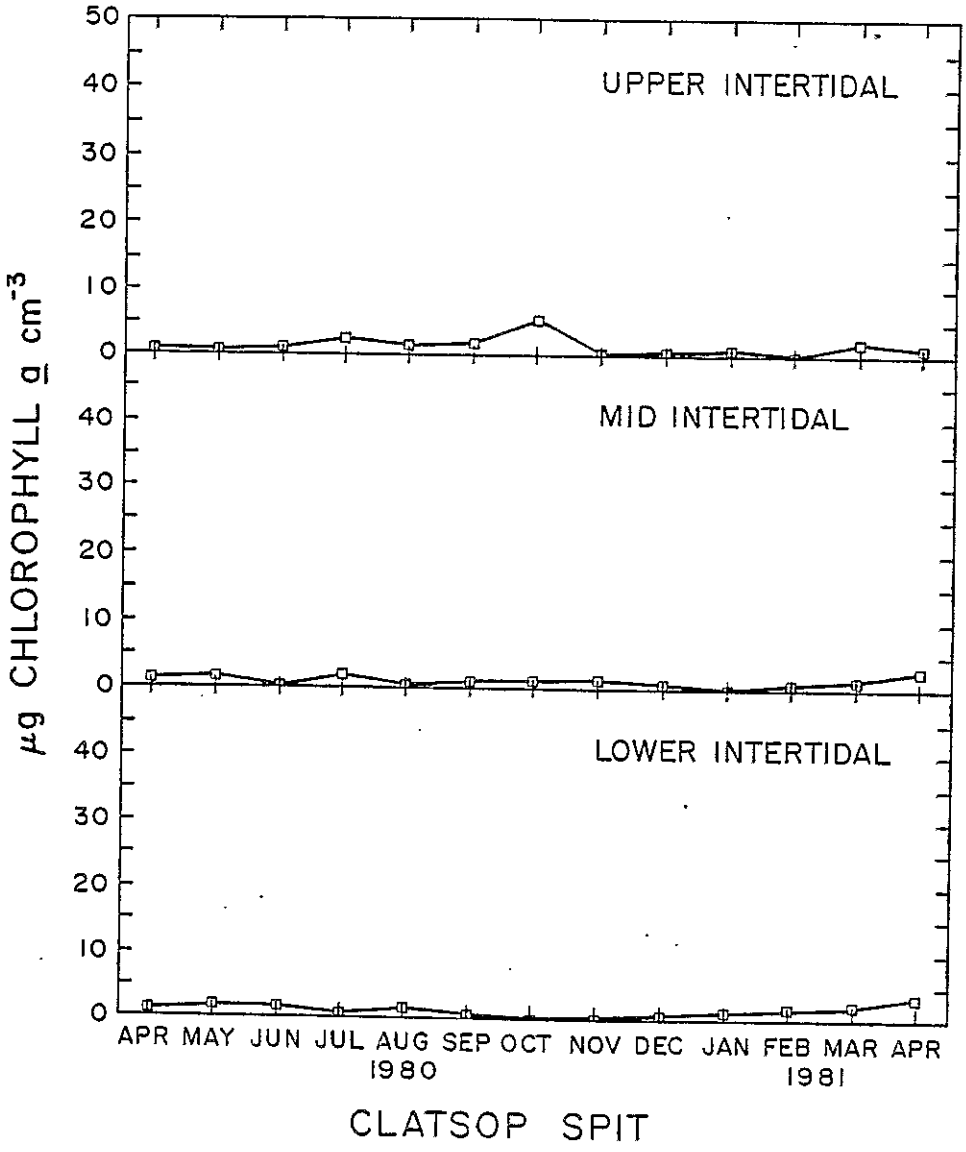

Figure 5. Chlorophyll a concentrations in the top cm of sediment along the Upper, Mid and Lower transects at the Clatsop Spit site. Each point represents a mean of six observations.

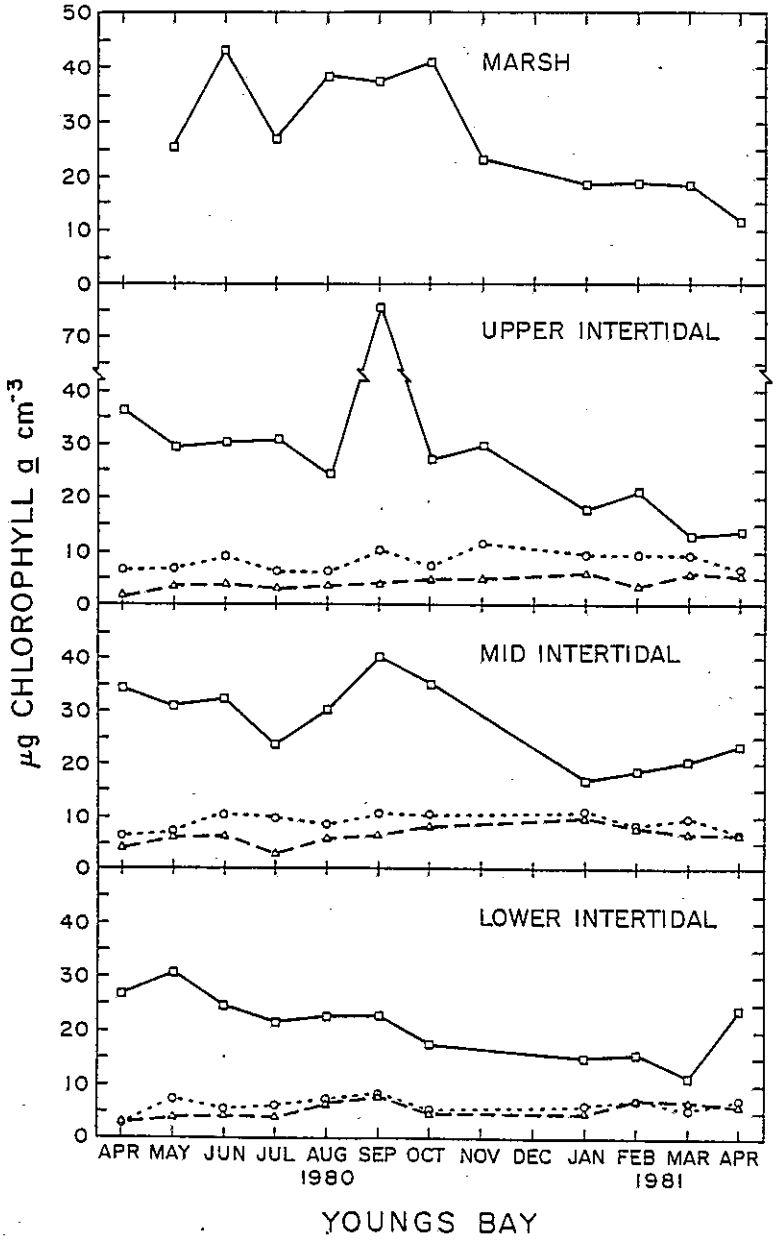

Figure 6. Chlorophyll a concentrations in the top cm of sediment (squares) and at sediment depths of 4.5-5.5 cm (circles) and 9-10 cm (triangles) along the Marsh, Upper, Mid and Lower transects at the Youngs Bay site. Each point represents a mean of six observations.

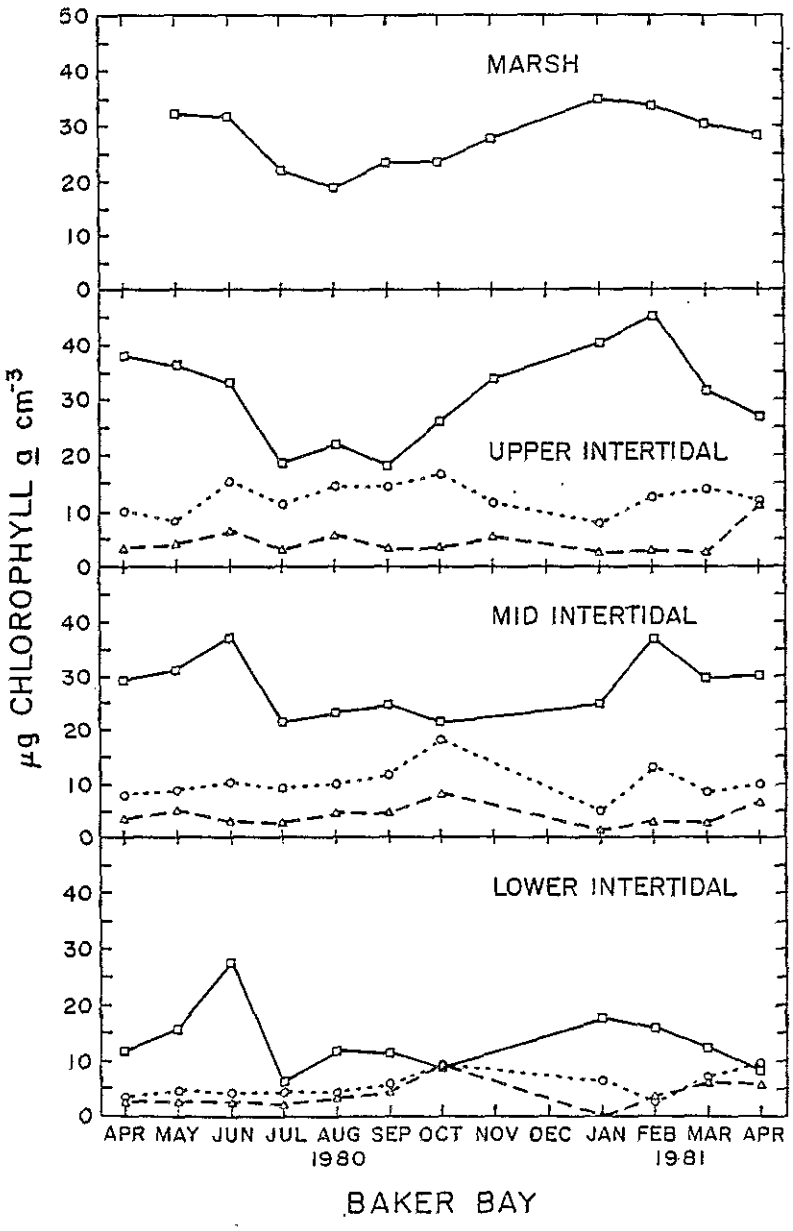

Figure 7. Chlorophyll a concentrations in the top cm of sediment (squares) and at sediment depths of 4.5-5.5 cm (circles) and 9-10 cm (triangles) along the Marsh, Upper, Mid and Lower transects at the Baker Bay site. Each point represents a mean of six observations.

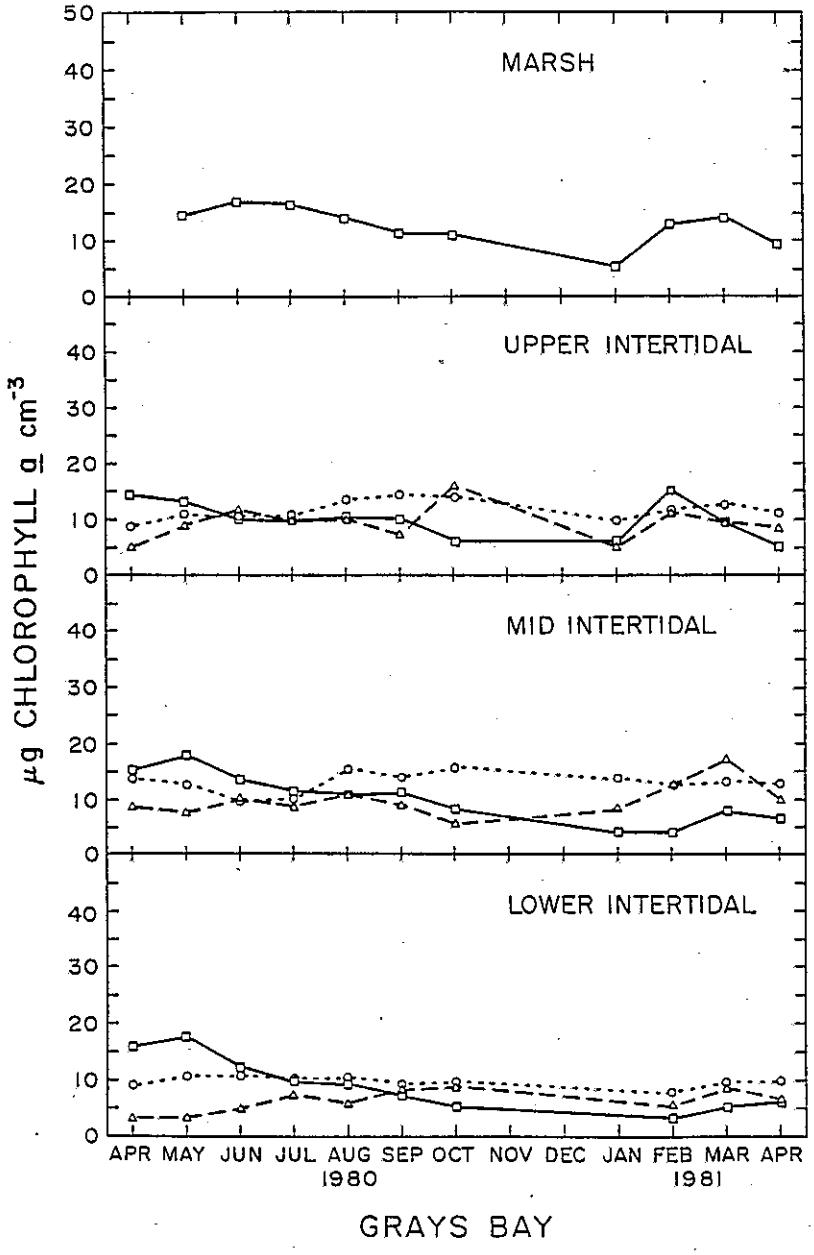

Figure 8. Chlorophyll a concentrations in the top cm of sediment (squares) and at sediment depths of 4.5-5.5 cm (circles) and 9-10 cm (triangles) along the Marsh, Upper, Mid and Lower transects at the Grays Bay site. Each point represents a mean of six observations.

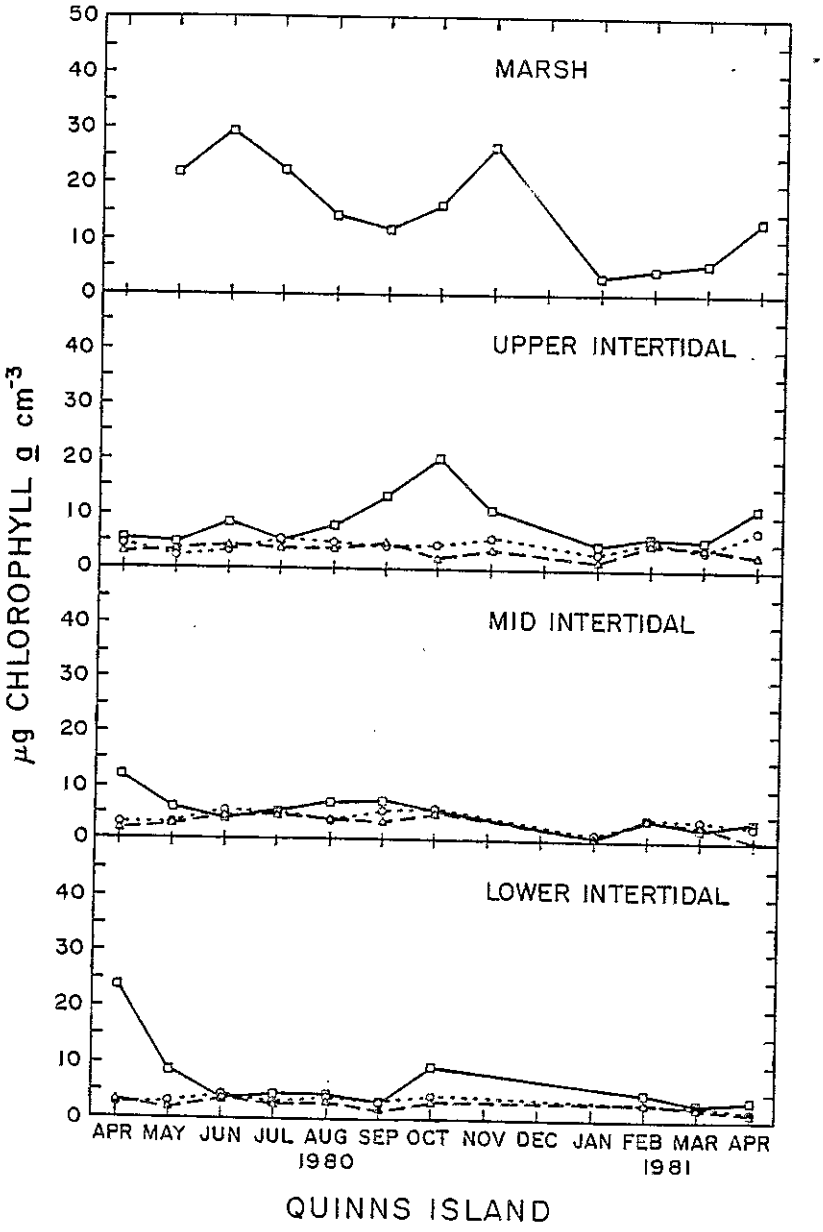

Figure 9. Chlorophyll a concentrations in the top cm of sediment (squares) and at sediment depths of 4.5-5.5 cm (circles) and 9-10 cm (triangles) along the Marsh, Upper, Mid and Lower transects at the Quinns Island site. Each point represents a mean of six observations.

Table 13. Mean rates of gross primary production (mg C m^{-2} hr^{-1}), sample sizes, and standard error of means for five intensive study sites in the Columbia River Estuary. Data are pooled by sampling time (month), site and tidal level (transect).

Variable	Sampling Size	Mean	Standard Error
Time:			
May	14	75.72	28.71
June	14	39.07	9.32
July	12	51.62	10.75
August	14	37.54	6.40
September	14	48.12	13.37
October	14	53.35	12.80
November	7	28.38	8.07
February	14	11.11	4.39
March	14	38.92	7.50
April	14	31.45	7.40
Site:			
Clatsop Spit	17	5.22	1.85
Youngs Bay	29	84.22	14.37
Baker Bay	29	42.50	5.18
Grays Bay	29	33.01	4.85
Quinns Island	29	29.56	5.56
Tidal Level:			
Marsh	39	54.98	10.91
Upper	48	43.21	5.99
Lower	44	29.40	4.72

hr^{-1}, respectively. The mean rate of gross primary production for the Baker Bay site was about one-half that for the Youngs Bay site, but higher than the rates found for the Grays Bay and Quinns Island site. Consequently, patterns of the mean benthic primary production at the intensive study sites were similar to patterns of the mean chlorophyll _a_ distribution at those sites (Table 12) with the exception that mean primary production at Baker Bay was lower than would be expected from its mean concentration of chlorophyll _a_. The mean rate of gross primary production was higher for cores obtained from the marsh and upper transects than for cores sampled from the lower transects, a pattern similar to the corresponding pattern of chlorophyll _a_ (Table 12).

The temporal patterns of gross primary production at the intensive study site are illustrated in Figures 10 and 11. These graphs show decreases in rates during the fall and winter months. The decrease in rates along the marsh transect during early summer at Baker Bay, Youngs Bay and Quinns Island was associated with the growth of emergent vascular hydrophytes which shaded the sediment below during this time of year. This pattern was not evident in Grays Bay, as the aquatic macrophytes had a more patchy distribution in the vicinity of the marsh

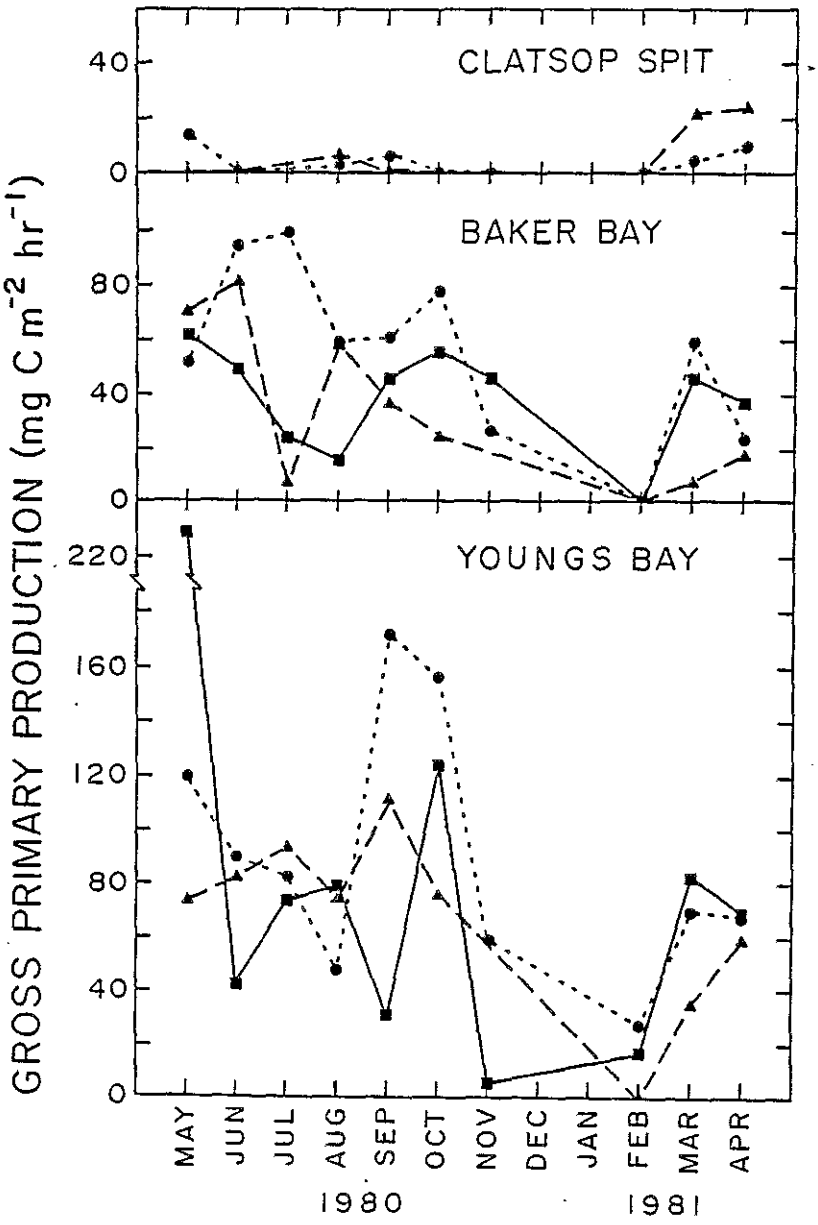

Figure 10. Rates of gross primary production for the Marsh (squares), Upper (circles) and Lower (triangles) transects at the Clatsop Spit, Baker Bay and Youngs Bay sites.

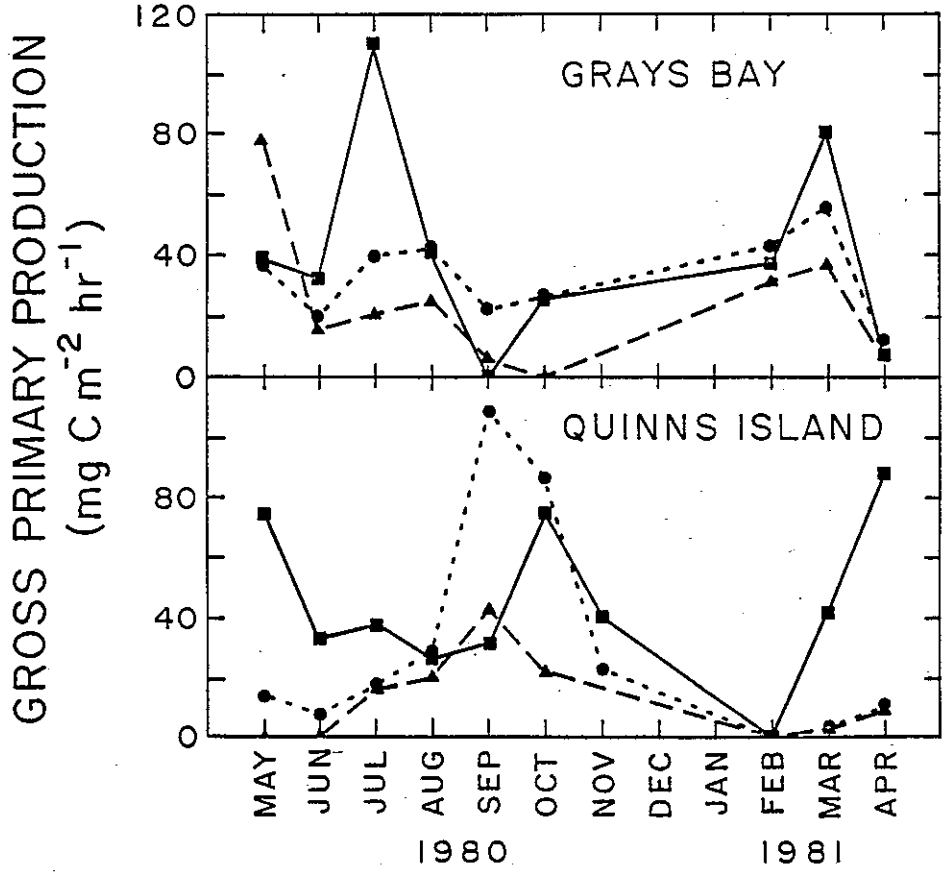

Figure 11. Rates of gross primary production for the Marsh (squares), Upper (circles) and Lower (triangles) transects at the Grays Bay and Quinns Island sites.

transect at this site. The relatively high value for the marsh transect in May 1980 at the Youngs Bay site occurred during a brief period when Enteromorpha was present in the low marsh (Figure 10). Rates at the upper transects at Baker Bay, Youngs Bay, Grays Bay and Quinns Island were higher than rates at the lower transects during most of the study.

Oxygen consumption in benthic communities results from respiratory activities of both autotrophic and heterotrophic organisms and from the chemical oxidation of reduced compounds in the sediment. Rates of oxygen uptake by estuarine sediments and associated organisms are often used by ecologists as a measure of total community metabolism (Jorgensen 1977). Even in sediment where anerobic respiration is responsible for a large proportion of this metabolism, the sulfide produced from sulfate reduction by microorganisms is reoxidized by oxygen at the surface of the sediment, and this oxygen uptake is usually roughly equivalent to the corresponding anaerobic respiration. In the work presented here, oxygen consumption was measured as part of the procedure for the estimation of gross primary production and as a rough index of total community metabolism.

Mean rates of oxygen consumption and the temporal patterns of this variable are summarized in Table 14 and Figures 12 and 13. Mean values for all sites varied from 24.08 mg O_2 m^{-2} hr^{-1} in February 1981 to 66.27 mg O_2 m^{-2} hr^{-1} in May 1980, and the highest mean rate was obtained for the site at Youngs Bay (66.55 mg O_2 m^{-2} hr^{-1}). The mean value for the marsh transect was higher than the means for the intertidal transects, a pattern related to inputs of detrital material from vascular hydrophytes of the low marsh. Rates of oxygen consumption at the Baker Bay and Youngs Bay sites were greater during the spring and summer months than in the fall and winter (Fig. 12), whereas rates at the Grays Bay and Quinns Island sites exhibited less variation with season (Fig. 13).

Mean concentrations of chlorophyll a and organic matter expressed as ash-free dry weight in the top cm of the cores used in the respirometers are summarized in Tables 15 and 16. The patterns of chlorophyll a distribution in these cores were very similar to patterns obtained from the replicated sampling along each transect (Tables 12 and 15). In contrast, the mean concentration of organic matter was highest for the cores from Baker Bay, and concentrations for Youngs Bay and Grays Bay were almost equal in mean value (Table 16). Differences between patterns of chlorophyll a and organic matter distribution in these cores are probably related to differences in detrital inputs at the intensive study sites. Apparently the retention of detrital material in the low marsh at Baker Bay, where Scirpus americanus Pers. (three-square) is the dominant plant, is relatively high (Fig. 14). At the Youngs Bay, Grays Bay and Quinns Island sites, the organic matter concentrations along the marsh transect were high early in the summer, but decreased to a lower level by late summer (Figs. 14 and 15). Concentrations on the tidal flats exhibited less seasonal variation than those in the adjacent low marsh.

Table 14. Mean rates of oxygen consumption (mg O_2 m^{-2} hr^{-1}), sample size, and standard error of the means for five intensive study sites in the Columbia River Estuary. Data are pooled by sampling time (month), site and tidal level (transect).

Variable	Sample Size	Mean	Standard Error
Time:			
May	14	66.27	12.75
June	14	50.68	10.51
July	12	58.06	9.22
August	14	55.88	6.65
September	14	58.62	12.06
October	14	41.39	6.59
November	7	47.88	14.15
February	14	24.08	6.59
March	14	48.66	4.77
April	14	37.45	5.30
Site:			
Clatsop Spit	17	18.05	5.30
Youngs Bay	29	66.55	7.22
Baker Bay	29	60.37	5.45
Grays Bay	27	44.83	4.99
Quinns Island	29	41.25	5.52
Tidal Level:			
Marsh	39	61.94	5.13
Upper	48	46.80	5.32
Lower	44	39.37	4.22

Table 15. Mean concentrations of chlorophyll *a* in the top cm of sediment (mg m^{-2}) of the cores used for measurement of primary production at the intensive study sites in the Columbia River Estuary. Data are pooled by sampling time (month), site and tidal level (transect).

Variable	Sample Size	Mean	Standard Error
Time:			
May	14	182.52	33.26
June	14	161.33	30.36
July	12	147.46	21.63
August	14	151.80	25.40
September	14	166.29	43.86
October	14	171.06	29.06
November	7	190.03	45.83
February	14	137.26	28.12
March	14	129.12	26.94
April	14	154.71	31.83
Site:			
Clatsop Spit	17	13.27	2.89
Youngs Bay	29	262.92	19.22
Baker Bay	29	223.16	15.28
Grays Bay	27	123.28	10.05
Quinns Island	29	103.66	14.04
Tidal Level:			
Marsh	39	203.48	14.33
Upper	48	163.89	19.26
Lower	44	110.33	12.92

Table 16. Mean concentrations of organic matter in the top cm of sediment (g m^{-2}) of the cores used for measurement of primary production at the intensive study sites in the Columbia River Estuary. Data are pooled by sampling time (month), site and tidal level (transect).

Variable	Sample Size	Mean	Standard Error
Time:			
May	14	235.33	31.94
June	14	256.12	33.31
July	12	197.21	19.51
August	14	162.86	18.07
September	14	164.58	15.33
October	14	210.97	23.09
November	7	190.93	35.00
February	14	145.24	18.84
March	14	134.79	14.71
April	14	108.69	10.98
Site:			
Clatsop Spit	17	61.73	3.47
Youngs Bay	29	196.31	13.59
Baker Bay	29	247.05	12.96
Grays Bay	27	195.62	13.76
Quinns Island	29	150.84	17.57
Tidal Level:			
Marsh	39	247.49	14.33
Upper	48	148.74	11.45
Lower	44	153.90	10.92

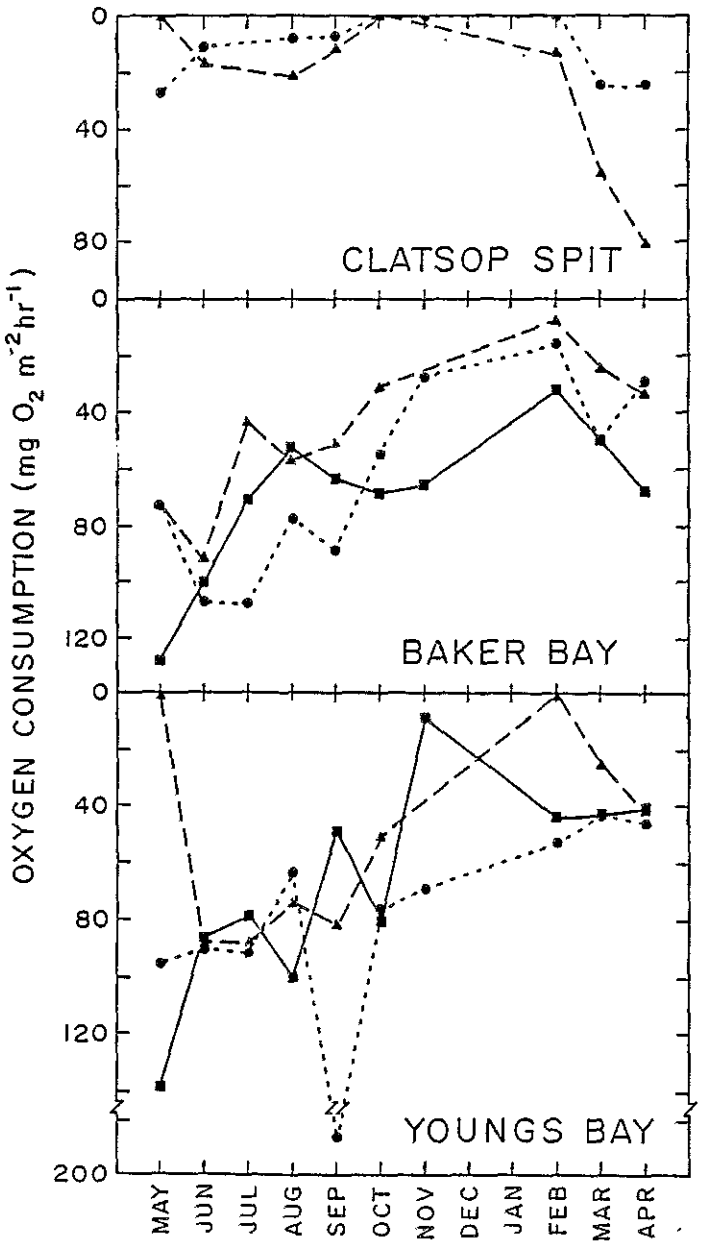

Figure 12. Rates of oxygen consumption for the Marsh (squares), Upper (circles) and Lower (triangles) transects at the Clatsop Spit, Baker Bay and Youngs Bay sites.

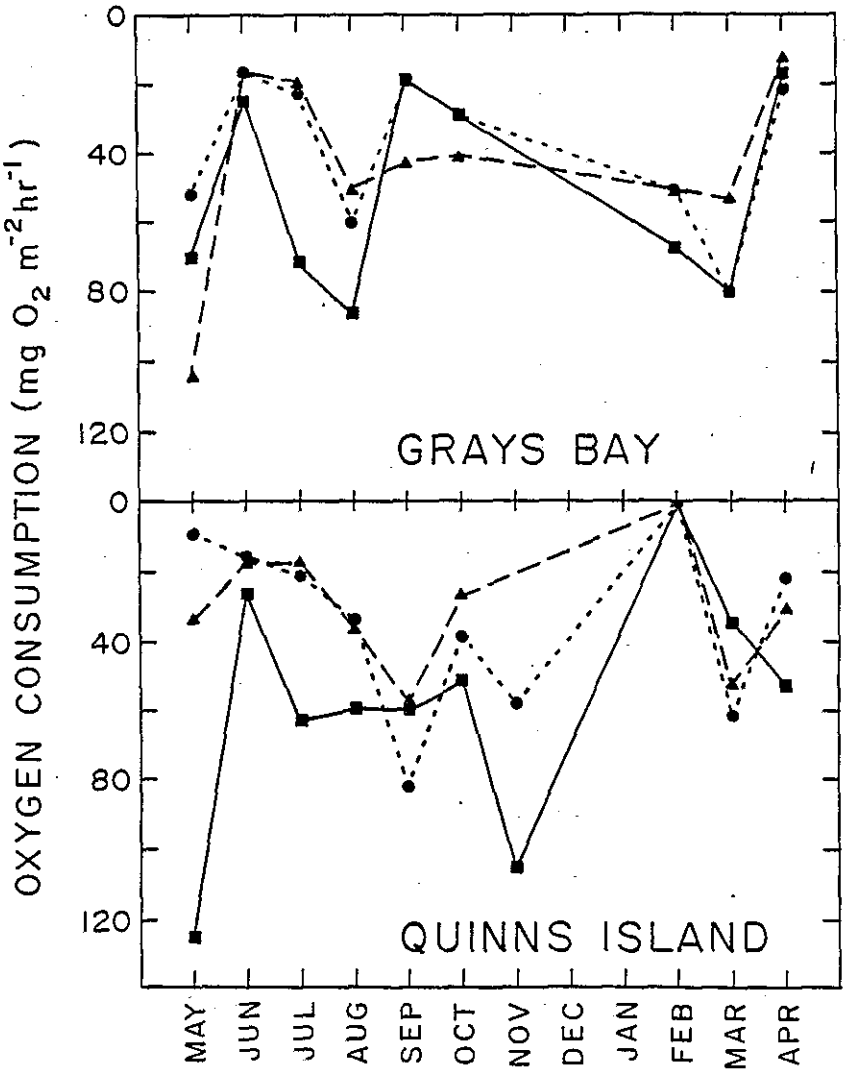

Figure 13. Rates of oxygen consumption for the Marsh (squares), Upper (circles) and Lower (triangles) transects at the Grays Bay and Quinns Island sites.

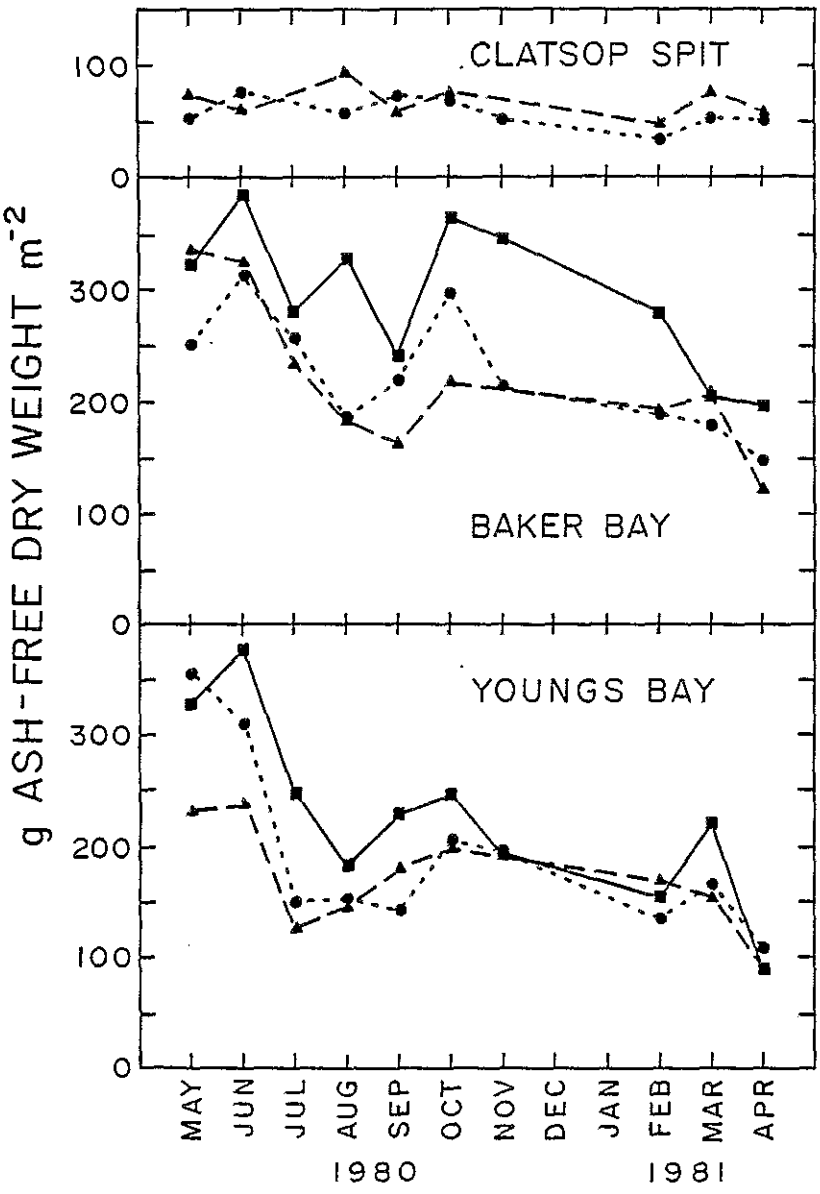

Figure 14. Concentrations of organic matter (expressed as ash-free dry weight) for the Marsh (squares), Upper (circles) and Lower (triangles) transects at the Clatsop Spit, Baker Bay and Youngs Bay sites.

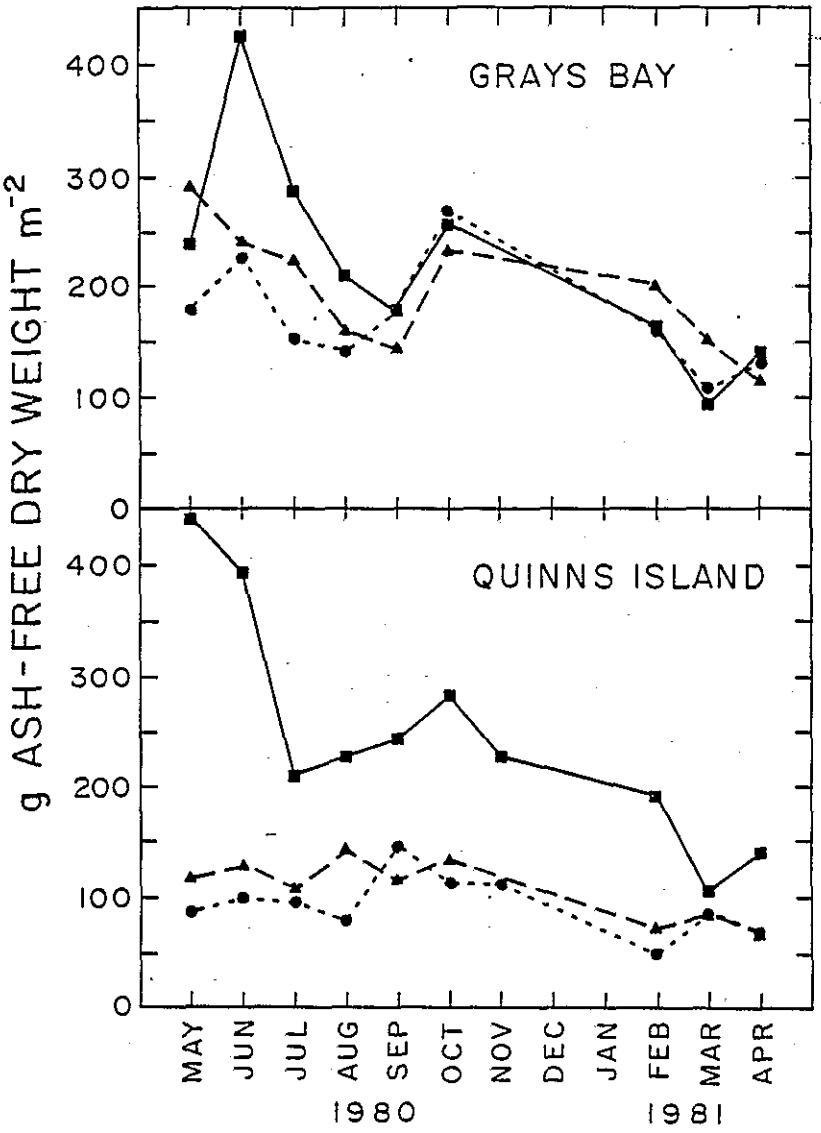

Figure 15. Concentrations of organic matter (expressed as ash-free dry weight) for the Marsh (squares), Upper (circles) and Lower (triangles) transects at the Grays Bay and Quinns Island sites.

Relationships Among Variables

Concurrent measurements of biological and physical variables at the intensive study sites allowed the examination of relevant relationships by correlation and regression analysis. In this section the covariance of selected pairs of variables are presented in matrices of Pearson product-moment coefficients of correlation (r), and alternative regression equations for the prediction of primary production at the survey sites are evaluated. In addition, the results of relevant research conducted by Davis and McIntire (1983) at the Oregon State University Marine Science Center are reviewed briefly. This experimental work, which was supported by the Environmental Protection Agency, provided a basis for the interpretation of some of the patterns of benthic autotrophy observed in the field.

Correlation Analysis

Correlations among the variables measured at the intensive study sites are presented in three ways: (1) among biological variables (Tables 17 and 18); (2) between biological and physical variables (Table 19); and (3) among physical variables related to sediment properties (Table 20). Correlations among the biological variables monitored along the marsh transects were relatively weak, presumably because of interactions with emergent vascular hydrophytes. Consequently, correlations for the marsh transects are presented in a single table (Table 17), and the analysis of data for transects on the tidal flats are emphasized in three separate tables (Tables 18, 19 and 20). While correlations are often unrelated to causation, they do provide a useful insight into the structure of the data that can aid in the interpretation of other analyses. Although the tables indicate coefficients that are significantly different from zero at the 5% level, such tests provide little useful ecological information. Here, we adopt the view that the coefficients are simply an indication of the degree to which variables covary, and make a note of some of the higher values for future reference.

Interactions between benthic microalgae and emergent vascular hydrophytes apparently accounted for the relatively low correlations among the biological variables in the marsh transects (Table 17). At these transects, detrital inputs from the vascular plants were high during the summer and fall, and the aboveground biomass shaded the sediment below during the growing season (ca., May through September). The correlation between microalgal primary production and oxygen uptake by the sediment was relatively high (0.57), but not as high as that found for transects on the tidal flats (Table 18). In the marsh some of the oxygen uptake was related to the decomposition of the vascular plants and the respiratory metabolism of the belowground parts of these plants, and unrelated to rates of microalgal production. The relatively low correlation between microalgal primary production and the concentration of chlorophyll _a_ in the top cm of sediment may have been related to seasonal changes in light intensity which corresponded to the shading of the sediment surface by the vascular plants. The significant but relatively weak correlations between the concentration of phaeo-pigments in the top cm of sediment and the concentrations of chlorophyll _a_ and

Table 17. A matrix of Pearson product-moment coefficients of correlation (r) for selected pairs of biological variables monitored along the transects in the lower marsh at the intensive study sites from May 1980 to April 1981. The variables are gross primary production (GPP), community oxygen uptake (OCON), chlorophyll a concentration in the top cm of sediment in the respirometer cores (CHLOR), concentration of phaeo-pigments in the respirometer cores (PHAEO), and the concentration of organic matter in the top cm of the cores (AFDW). Each r value is based on 39 pairs of observations.

Variable	GPP	OCON	CHLOR	PHAEO	AFDW
GPP	-	0.57*	0.27	-0.07	0.15
OCON		-	0.27	0.30	0.34*
CHLOR			-	0.37*	0.28
PHAEO				-	0.48*
AFDW					-

*r significantly different from zero at $P < 0.05$

Table 18. A matrix of Pearson product-moment coefficients of correlation (r) for selected pairs of biological variables monitored along transects on the tidal flats at the intensive study sites from May 1980 to April 1981. Variables are the same as in Table 17. Each r value is based on 90 pairs of observations.

Variable	GPP	OCON	CHLOR	PHAEO	AFDW
GPP	-	0.81*	0.81*	0.74*	0.54*
OCON		-	0.72*	0.63*	0.49*
CHLOR			-	0.75*	0.62*
PHAEO				-	0.73*
AFDW					-

*r significantly different from zero at $P < 0.05$

Table 19. A matrix of Pearson product-moment coefficients of correlation (r) relating biological variables with selected physical variables monitored along transects on the tidal flats at the intensive study sites from May 1980 to April 1981. Variables related to sediment properties are mean grain size (MEAN), the sorting coefficient (SORT), the skewness coefficient (SKEW), and the chlorophyll ratios (C1C2 and C1C3); other physical variables are light intensity (LITE), temperature (TEMP), and salinity (SALT) during the respirometer measurements. Biological variables are the the same as in Table 17. Each r value relating biological variables to the sediment properties is based on 72 or 77 pairs of observations; other values are based on 92 pairs of observations.

	Sediment Properties							
Variable	C1C2	C1C3	MEAN	SORT	SKEW	LITE	TEMP	SALT
GPP	0.56*	0.68*	0.44*	0.42*	-0.02	-0.15	0.30*	0.11
OCON	0.36*	0.60*	0.37*	0.27*	-0.04	-0.17	0.24*	0.09
CHLOR	0.55*	0.69*	0.36*	0.29*	0.13	-0.24*	0.05	0.19
PHAEO	0.29*	0.53*	0.55*	0.42*	-0.05	-0.13	0.25*	0.12
AFDW	0.05	0.35*	0.45*	0.22	0.15	-0.07	0.25*	0.19

*r significantly different from zero at $P < 0.05$

Table 20. A matrix of Pearson product-moment coefficients of correlation (r) for selected pairs of variables related to sediment properties monitored along transects on the tidal flats at the intensive study sites from May 1980 to April 1981. Variables are the same as in Table 19. Each r value is based on 80 pairs of observations.

Variable	C1C2	C1C3	MEAN	SORT	SKEW
C1C2	-	0.77*	0.18	0.30*	-0.04
C1C3		-	0.27*	0.17	-0.03
MEAN			-	0.62*	-0.15
SORT				-	0.00
SKEW					-

*r significantly different from zero at $P < 0.05$

organic matter probably reflected the degradation of chlorophyll a and the concurrent accumulation of detrital materials. However, low correlations between oxygen uptake and the concentrations of chlorophyll a, phaeo-pigments and organic matter indicated that community metabolism in the sediments of the low marsh involved both autotrophic and detrital decomposition processes and that some of the detrital materials were refractory.

Correlation coefficients among the biological variables monitored along transects on the tidal flats were relatively high (Table 18). In particular, high values ($r = 0.81$) for gross primary production and chlorophyll a and for gross primary production and oxygen uptake indicated that such relationships could be used for the prediction of benthic autotrophy in regions where direct measurements of primary production were not available. Regression equations that correspond to the most useful of these relationships are presented in the next section. Although the concentration of organic matter in the top cm of sediments on the tidal flats was more highly correlated with metabolic rates and pigment concentrations than in the low marsh sediments, this variable was less closely related to the rate of oxygen uptake than were concentrations of chlorophyll a and phaeo-pigments. Therefore, these data indicated that community metabolism on the tidal flats of the estuary was more closely associated with autochthonous production by the microalgae than with allochthonous inputs of detritus. In other words, detrital inputs to the tidal flats in many regions of the Columbia River Estuary are not high enough to obscure the effects of benthic autotrophy on total community metabolism.

On the tidal flats of the estuary, biological variables were more highly correlated with sediment properties than with light intensity, temperature and salinity (Table 19). The low correlations with light intensity are not surprising, however, as the diatom flora reaches its maximum photosynthetic rate at relatively low intensities (see experimental work in a later section of this report). While salinity affects the species composition of the diatom flora, this variable has no apparent effect on rates of primary production. The species composition of the microalgal flora simply changes in response to local variations in salinity, without a related effect on the productive capacity. Correlations between gross primary production and the chlorophyll ratios were higher than between gross primary production and the other sediment properties, suggesting that the degree of sediment mixing may be more closely related to productive capacity than distribution of grain size. Moreover, the correlation was higher with the ratio of the chlorophyll concentration in the top cm of sediment to that at the 9-10 cm depth than with the ratio indicating mixing in the upper 5 cm of sediment. Of the biological variables, the concentration of phaeo-pigments was the most closely related to mean phi size ($r = 0.55$). In general, the highest concentrations of plant pigments and organic matter and the highest rates of primary production were associated with sediments with a relatively small mean grain size. However, a number of exceptions to this generalization were obvious from a close examination of the data. Among the sediment properties, the skewness coefficient had the lowest correlations with the biological variables.

Correlations among variables representing sediment properties were relatively low, with the exception of r values for the two pigment ratios, and for the relationship between mean phi size and the sorting coefficient. The two pigment ratios were indicative of how deep sediment mixing extends and the departure from an r value of unity ($r = 0.77$) suggested that mixing depth is variable throughout the estuary. The relative high value for mean phi size and the sorting coefficient indicated that sediments with the smaller grain sizes tended to be more poorly sorted than sediments with larger grain sizes.

Regression Analysis

Some useful regression equations for the prediction of selected biological variables associated with the tidal flats of the estuary are summarized in Table 21. Although a large number of models were examined, in most cases simple linear relationships were satisfactory for estimation of values in locations where direct measurements were not available. The use of such models was essential for mapping the distributional patterns of primary production and community oxygen uptake. All models in Table 21 were based on data from transects on the tidal flats. Predictive equations for the marsh transects were not satisfactory.

The relationship between the rate of gross primary production and the concentration of chlorophyll a in the top cm of sediment provided a valuable approach for the expansion of estimates of benthic primary production from the intensive study sites to the survey sites, where concentrations of chlorophyll a and phaeo-pigments were the only available data. The corresponding linear equation derived from respirometer and chlorophyll data obtained at the intensive study sites is:

$$GPP = 0.63 + 0.28\ CHLOR,$$

where GPP is the rate of gross primary production (mg C m^{-2} hr^{-1}) and CHLOR is the concentration of chlorophyll a (mg m^{-2}). In this case, R^2 is 0.66, and the equation is based on 90 pairs of observations representing a period from May 1980 through April 1981. The R^2 value was not increased by adding a quadratic term:

$$GPP = -0.10 + 0.29\ CHLOR - 0.00003(CHLOR)^2$$

If the curve is forced through the origin, the expression is:

$$GPP = 0.28\ CHLOR,$$

which suggests a GPP - CHLOR ratio of about 0.28. All predictions of primary production at the survey and validation sites that follow were based on equation 1 of Table 21, i.e., the linear equation, not forced through the origin.

Table 21. Linear regression equations expressing gross primary production (GPP), oxygen uptake (OCON), and the concentration of organic matter in the top cm of sediment (AFDW) as a function of selected biological and physical variables. Other variables are the chlorophyll ratios (C1:C2 and C1:C3 of Table 8), mean grain size in phi units (MEAN), and concentrations of chlorophyll *a* (CHLOR) and phaeo-pigments (PHAEO) in the top cm of sediment. Units for GPP and OCON are mg C m^{-2} hr^{-1} and mg O_2 m^{-2} hr^{-1}, respectively; units for AFDW, CHLOR, and PHAEO are mg m^{-2}.

Model	Sample Size	R^2
1. GPP = 0.63 + 0.28 CHLOR	90	0.66
2. GPP = -1.38 + 0.20 CHLOR + 0.14 PHAEO	90	0.70
3. GPP = 13.00 + 11.99 C1:C2	72	0.32
4. GPP = 14.68 + 6.67 C1:C3	72	0.44
5. GPP = -16.46 + 13.10 MEAN	77	0.27
6. GPP = -13.17 + 7.60 MEAN + 13.99 SORT + 0.26 SKEW	77	0.31
7. OCON = 9.93 + 0.21 AFDW	89	0.30
8. OCON = 17.05 + 0.72 GPP	90	0.66
9. AFDW = 90.86 + 0.70 PHAEO	90	0.53

Graphic representations of the relationship between gross primary production and chlorophyll *a* are illustrated in Figure 16 and 17. Figure 16 represents the plot of gross primary production against the concentration of chlorophyll *a* in the top cm of sediment contained in the cores that were used in the respirometers for the production measurements. Equation 1 of Table 21 was derived from these data. Figure 17 is a plot of gross primary production against the mean of six replicated samples of chlorophyll obtained along the transects that correspond to the cores used in the respirometers. Therefore, this relationship is indicative of how well a location estimate of primary production corresponded to a transect mean concentration of chlorophyll *a*. Also, the curve and equation illustrated in Figure 16 is included in Figure 17 for comparative purposes. Differences between the two equations and their respective R^2 values are related to the spatial heterogeneity in benthic autotrophy along the sampling transects.

Linear relationships between gross primary production and sediment properties (equations 3, 4 and 5 of Table 21) are illustrated in Figures 18, 19 and 20. The relationship with mean grain size expressed in phi units was relatively weak, with an R^2 value of 0.27 (Fig. 18). The

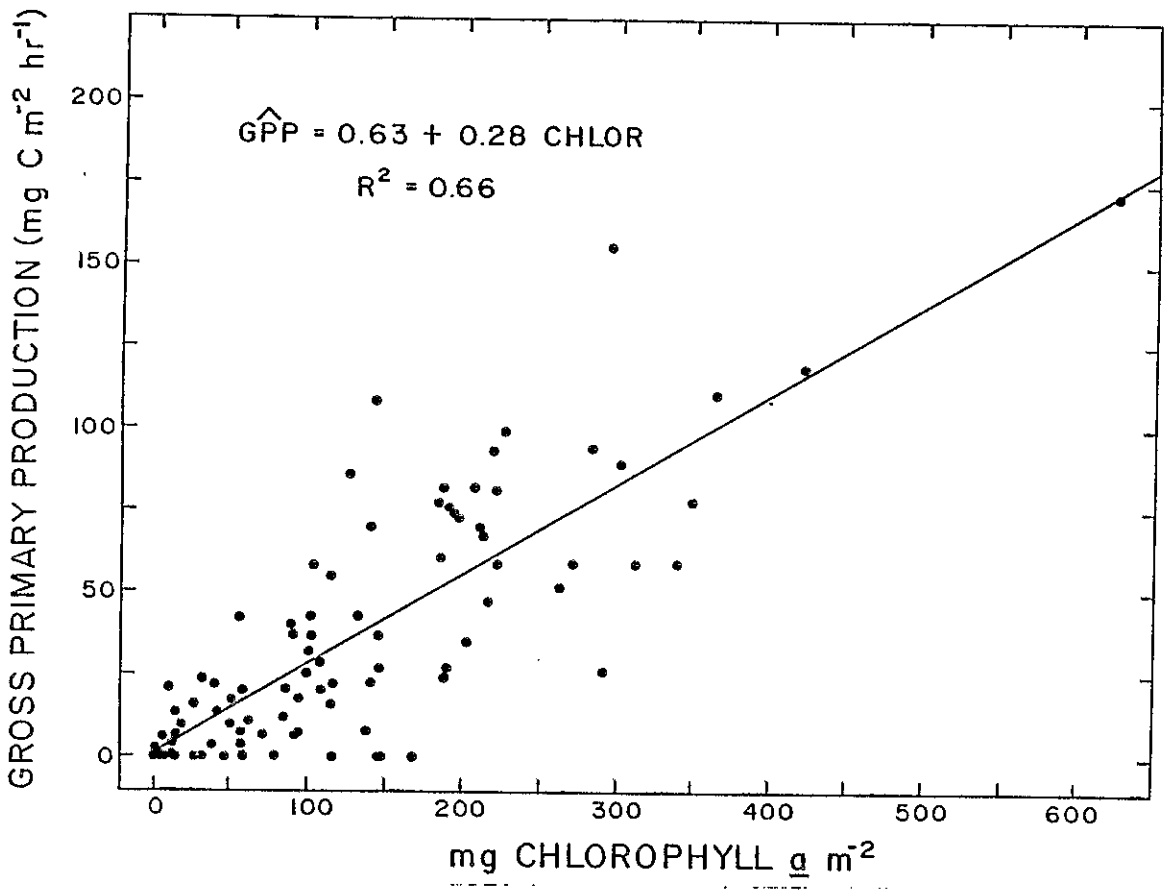

Figure 16. Relationship between the rate of gross primary production (GPP) and the concentration of chlorophyll a in the top cm of sediment (CHLOR) from the cores used in the respirometer chambers. Data relate to measurements at the Upper and Lower intertidal transects at the intensive study sites.

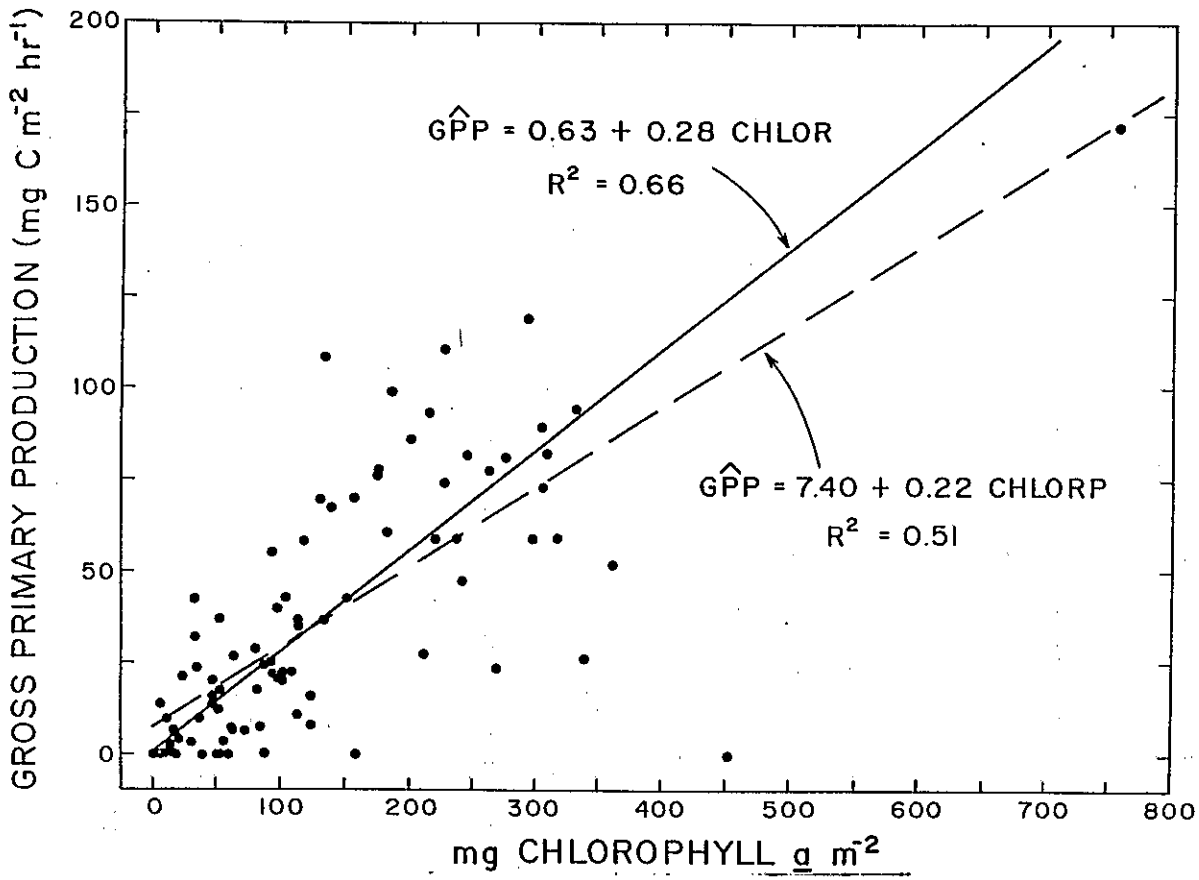

Figure 17. Relationship between the rate of gross primary production (GPP) and the mean concentration of chlorophyll a (CHLORP) in the top cm of sediment from six cores obtained along the Upper and Lower transects at the intensive study sites. The curve for the respirometer cores from Figure 16 is also given for comparison.

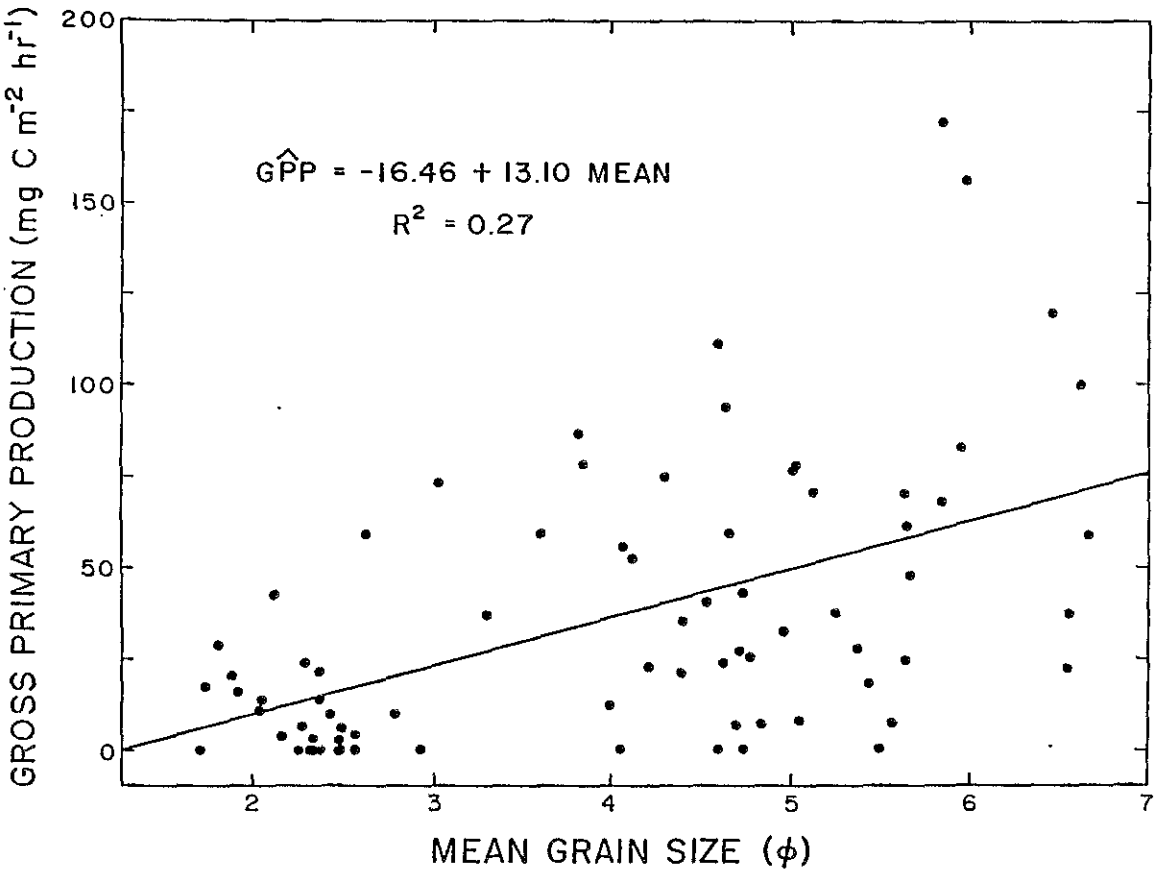

Figure 18. Relationship between the rate of gross primary production (GPP) and mean sediment grain size expressed in phi units (MEAN). Data relate to measurements at the Upper and Lower intertidal transects at the intensive study sites.

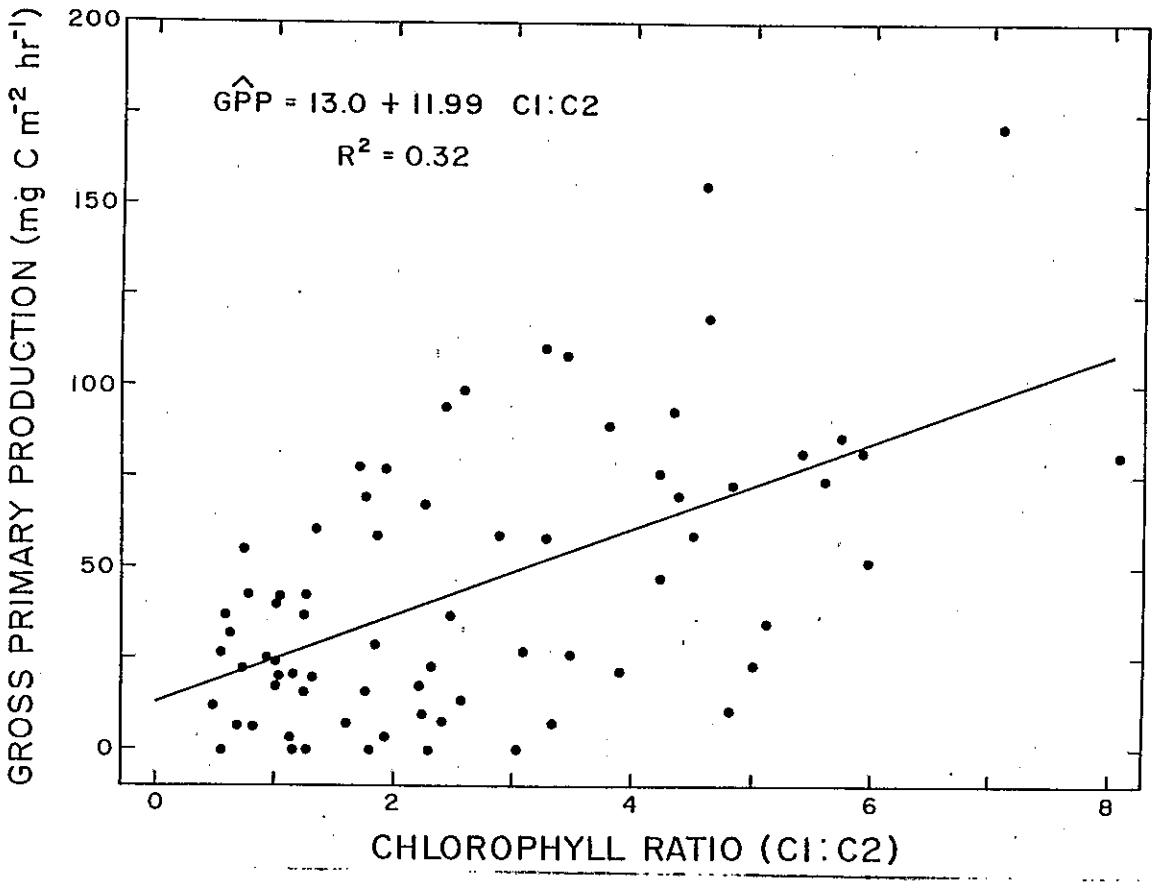

Figure 19. Relationship between the rate of gross primary production (GPP) and the ratio of the concentration of chlorophyll a in the top cm of sediment to that at the 4.5-5.5 cm depth (C1:C2). Data relate to measurements at the Upper and Lower intertidal transects at the intensive study sites.

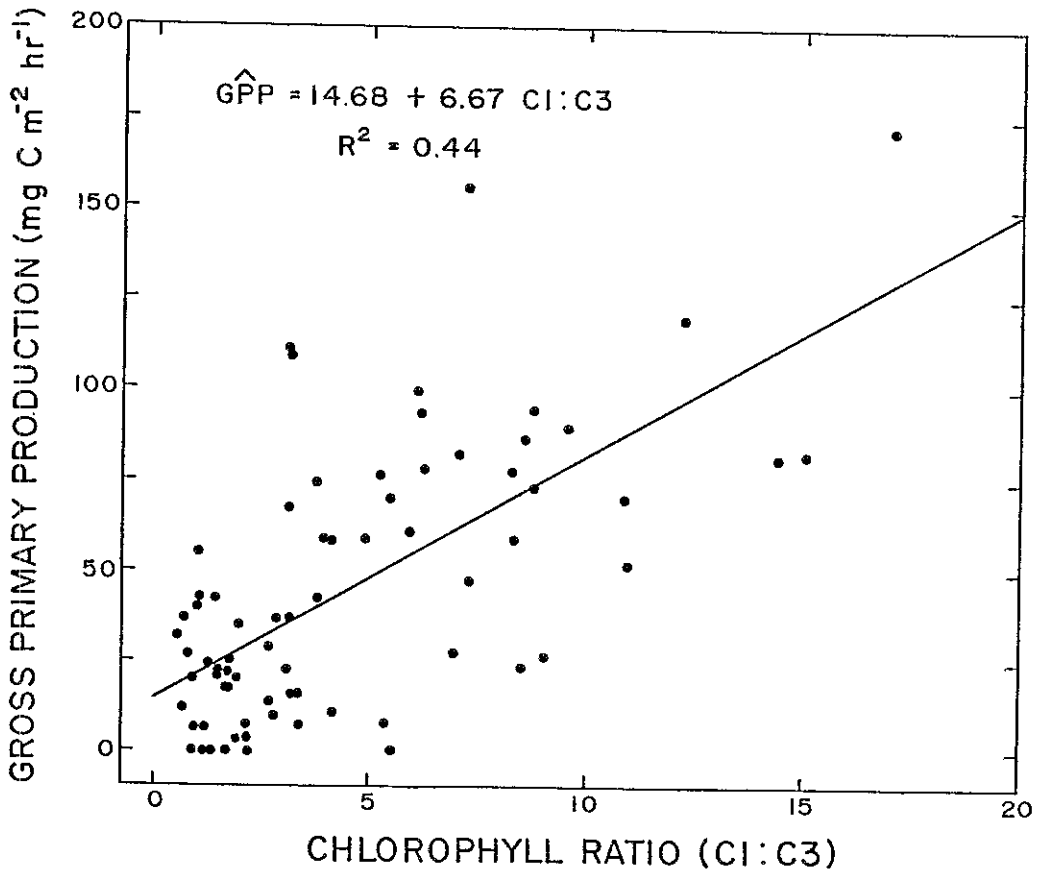

Figure 20. Relationship between the rate of gross primary production (GPP) and the ratio of the concentration of chlorophyll a in the top cm of sediment to that at the 9-10 cm depth ($C1:\overline{C3}$). Data relate to measurements at the Upper and Lower intertidal transects at the intensive study sites.

addition of the sorting and skewness coefficients to the regression model only increased R^2 to 0.31 (equation 6 of Table 21). Moreover, variability around the regression line becomes greater with decreasing grain size (increasing phi value), indicating that sites with fine sediment were both productive and unproductive, depending on location and season. One of the primary causes of the variation illustrated in Figure 18 was related to spatial and seasonal differences in the degree of sediment disturbance among the sampling transects. Figures 19 and 20 are plots of gross primary production against the chlorophyll ratios discussed in an earlier section. In this case, the correspondence between primary production and the ratio of chlorophyll a concentration in the top cm to that at the 9-10 cm depth is closer than the relationship with the ratio expressing a more shallow disturbance (4-5 cm in depth). While the graphs indicate that the C1:C3 ratio is a better predictor of gross primary production than the C1:C2 ratio or mean grain size, this ratio is not as good for predicting primary production as the chlorophyll a concentration near the sediment surface.

The best predictor of the organic matter concentration in the top cm of sediment was the concentration of phaeo-pigments (Fig. 21 and equation 9 of Table 21). Phaeo-pigments are degradation products of chlorophyll which at times may constitute a significant fraction of the total green pigments in the sediment. In the case of the intensive study site, it was not always clear whether the phaeo-pigments represented accumulations from the autochthonous production of microalgae or instead were derived from allochthonous inputs of detrital material from the low marsh. However, close examination of the sediments along the intertidal transects indicated that the retention of detritus from emergent vascular plants was minimal, and that detrital vascular plants were either processed locally in the marsh or were exported as rafted or particulate material in the water column.

The linear relationship between community oxygen uptake and gross primary production is presented in Figure 22. This relationship was established to provide estimates of oxygen consumption for the survey sites from indirect estimates of gross primary production. The relatively high R^2 value also indicates that detrital inputs to the intertidal sediments from the adjacent marshlands are minimal and that most of the community metabolism can be associated with biological activities of the resident microalgae. The weak relationship between oxygen uptake and the concentration of organic matter in the top cm of the sediment (equation 7 of Table 21) is suggestive of the presence of refractory organic material and the relative importance of the living microalgae.

Experimental Studies

During the investigation of benthic primary production in the Columbia River Estuary, concurrent experimental studies of the benthic microalgae were conducted at the Oregon State University Marine Science Center (Davis 1981; Davis and McIntire 1983). In particular, these experiments were concerned with the relationship between microalgal primary production and light intensity; also, the ratio of chlorophyll a to algal biomass was investigated in isolated diatom assemblages. The

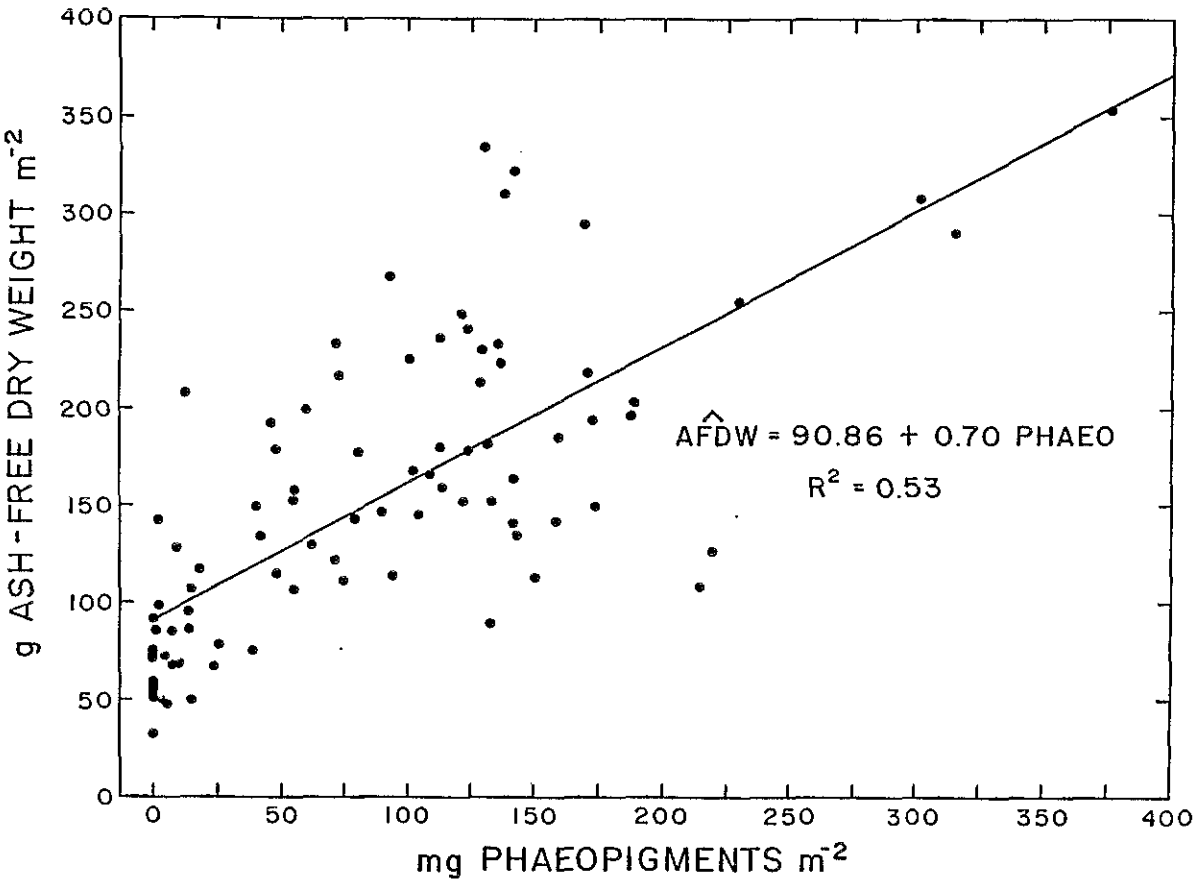

Figure 21. Relationship between the concentration of organic matter (AFDW) and the concentration of phaeo-pigments (PHAEO) in the top cm of sediment from the cores used in the respirometer chambers. Data relate to measurements at the Upper and Lower intertidal transects at the intensive study sites.

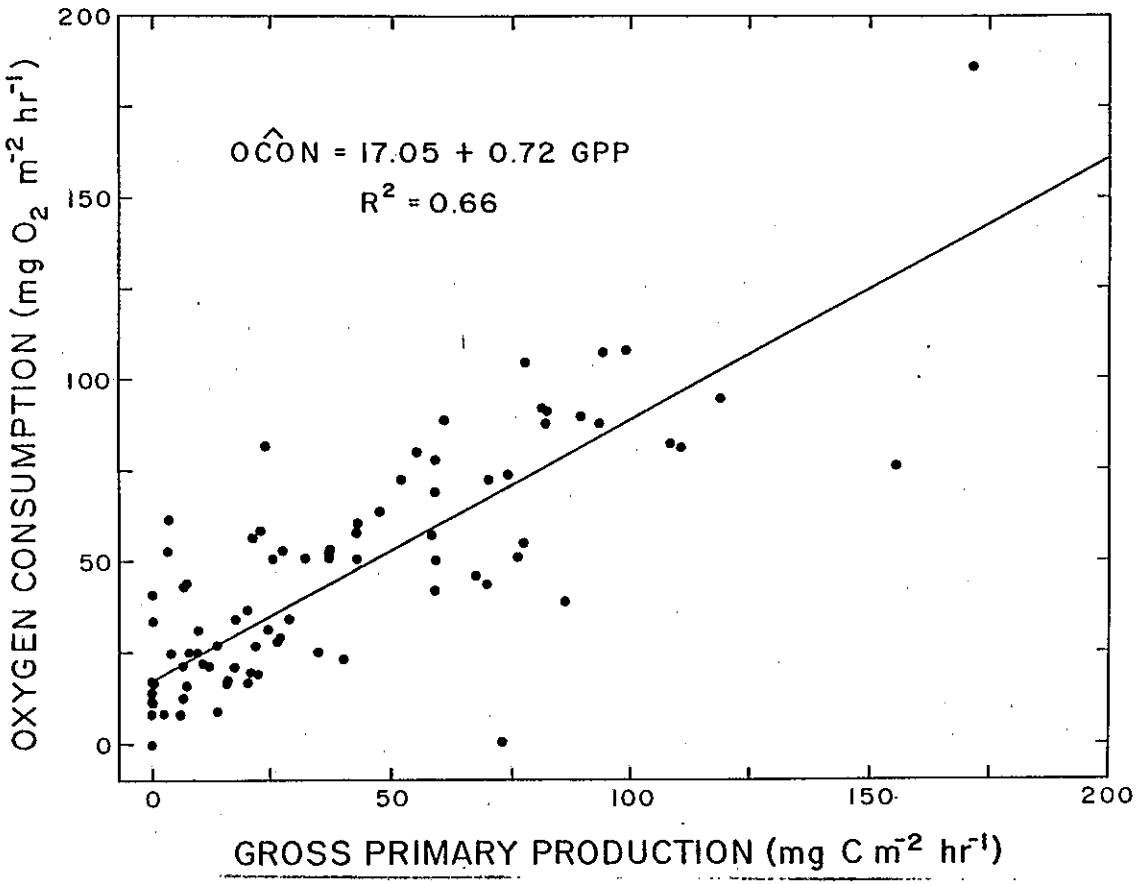

Figure 22. Relationship between the rate of oxygen consumption (OCON) and the rate of gross primary production (GPP) for the sediment cores used in the respirometer chambers. Data relate to measurements at the Upper and Lower intertidal transects at the intensive study sites.

results of these experiments are highly relevant to the interpretation of patterns of benthic autotrophy in the Columbia River Estuary and for the generation of carbon budgets that are presented in an integration report entitled The Dynamics of the Columbia River Estuarine Ecosystem (CREDDP 1984).

Experiments with Intact Sediment Cores. The relationship between light intensity and gross primary production of intact sediment cores was investigated in March, August and September 1980 (Fig. 23). Experiments A, B and C were conducted outdoors under natural sunlight and fiberglass screens, while experiment F was performed in the laboratory under a fluorescent-incandescent lamp fixture and fiberglass screens. Mean microalgal biomasses, expressed as mg chlorophyll a m^{-2} in the top cm of sediment, for two replications (i.e., two respirometers with intact sediment cores) during experiments A, B, C and F were 134, 199, 213 and 115, respectively.

Data from the experiments suggested that the relationship between light intensity and gross primary production was approximately linear at intensities between zero and 250 $\mu E\ m^{-2}\ sec^{-1}$, except in experiment C, where the linear segment was between zero and about 150 $\mu E\ m^{-2}\ sec^{-1}$. The equation for a linear segment from zero to 248 $\mu E\ m^{-2}\ sec^{-1}$ estimated from data pooled for all four experiments is

$$GPP = 0.59\ I,$$

where GPP is the rate of gross primary production expressed as mg C m^{-2} hr^{-1} and I is the light intensity. To estimate the asymptotic maxmimum rate (P_{max}) and the shape of the curves above 248 $\mu E\ m^{-2}\ sec^{-1}$, several functions were examined for experiments A, B and C. The rectangular hyperbola, a function commonly used as a model of photosynthesis-light relationships (Lederman and Tett 1981), generated P_{max} estimates of 248 (A), 269 (B) and 172 (C) g C m^{-2} hr^{-1}, values that were inconsistent with the distribution of the data points. This model forced the curve through the origin and, in this case, provided relatively high estimates of P_{max}. A more satisfactory estimate was obtained by the exponential model:

$$GPP = \beta_o - \beta_2 e^{-\beta_3 I},$$

where β_o is equal to P_{max}. Curves generated by this function for experiments A, B and C are plotted in Figure 22. The curves for experiments A and B intersect the linear segment at 267 and 260 $\mu E\ m^{-2}$ sec^{-1}, while the curve for experiment C does not intersect the linear segment; the latter curve is terminated at an intensity of 157 $\mu E\ m^{-2}$ sec^{-1}. Estimates of P_{max} for experiments A, B and C from the exponential model are 233, 181 and 136 mg C m^{-2} hr^{-1}, respectively.

Data in Figure 22 indicate that the onset of light saturation of photosynthesis occurs between 200 and 400 $\mu E\ m^{-2}\ sec^{-1}$. The results of these experiments are similar to the results of other studies with isolated assemblages of benthic diatoms (Admiraal 1977; Rasmussen et al 1983). Here, the onset of light saturation (I_k) is defined as the light intensity at which extrapolations of the linear segment and the light-

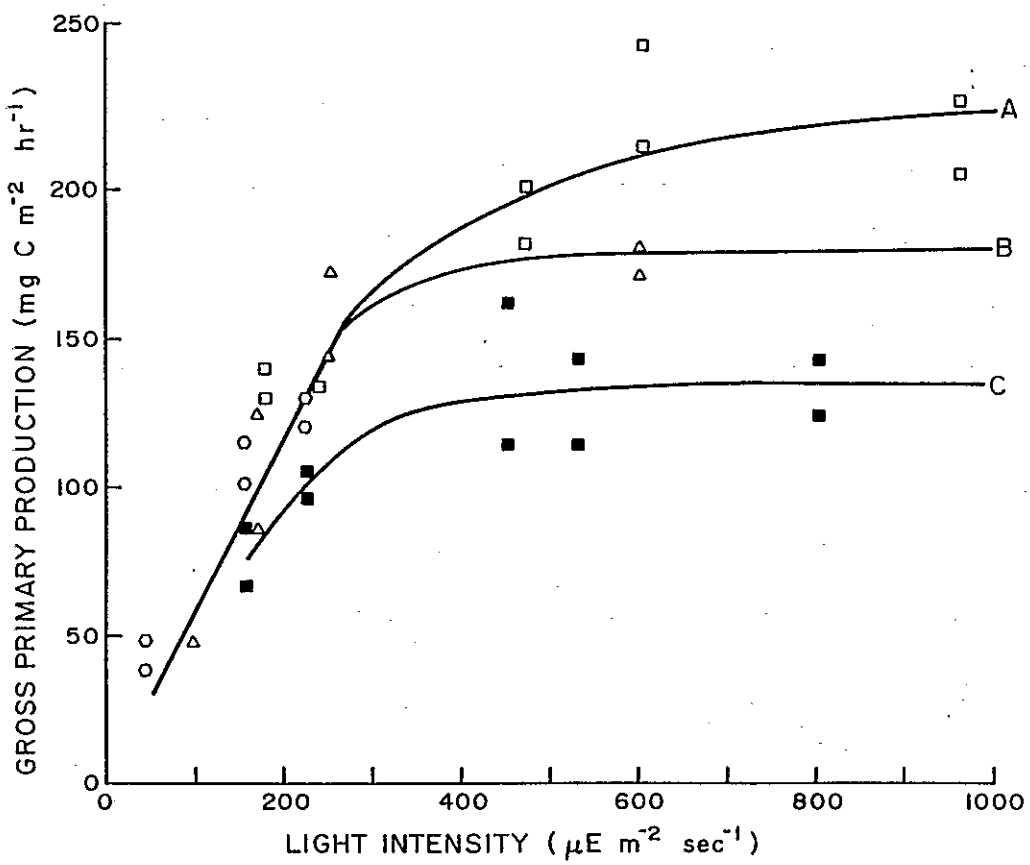

Figure 23. Relationship between the rate of gross primary production and light intensity obtained in four experiments by Davis and McIntire (1983). Chlorophyll a concentrations in the top cm of sediment during experiments A (open squares), B (triangles), and C (solid squares) were 134, 199 and 213 mg m^{-2} respectively. Temperature and salinity during the experiments ranged from 12° to 14°C, and from 30 to 33 °/oo, respectively.

saturated region of the GPP-intensity curve intersect (Talling, 1957). For our purposes, $I_k = P_{max}/0.59$, where P_{max} is estimated by the exponential model and 0.59 is the slope of the linear segment. Therefore, I_k values for experiments A, B and C are 395, 307 and 231 $\mu E\ m^{-2}\ sec^{-1}$, respectively.

The effect of temperature on rates of gross primary production and oxygen uptake in assemblages of sediment-associated microalgae was investigated in May 1981 (Tables 22 and 23). Each experiment consisted of three replications, i.e., three respirometers with intact sediment cores; and sediment cores for each replication were collected from two intertidal levels in Yaquina Bay, Oregon: 1.9 m and 1.0 m above MLLW. The mean chlorophyll a concentration in the top cm of the sediment cores was 151 mg m^{-2}, and the corresponding standard deviation was 21.7 mg m^{-2}. Water temperature in Yaquina Bay during April and May varied between 11° and 14°C. The temperature range under investigation was from 7°C to 17°C, a range between the maximum and minimum annual values recorded for the bay. The light intensity during the primary production measurements was 600 $\mu E\ m^{-2}\ sec^{-1}$, an intensity well above the I_k values determined during the experiments illustrated in Figure 22. Data are reported as hourly rates and Q_{10} values, where

$$Q_{10} = [r_2/r_1]^{10/(t_2-t_1)}.$$

The temperature coefficient (Q_{10}) is a multiplier that predicts the rate for a 10°C change in temperature, t_2 and t_1 are the upper and lower temperatures of the range under consideration, and r_2 and r_1 are metabolic rates corresponding to t_2 and t_1, respectively.

Rates of gross primary production varied between 24.68 and 252.30 mg C $m^{-2}\ hr^{-1}$, depending on temperature, experiment number and replication (Table 22). Therefore, estimates of Q_{10} at light saturation were based on a set of samples representing a wide range of photosynthetic capacities. The mean Q_{10} value for three replications of each of four experiments (n = 12) was 2.05 with a standard error of 0.15. There was no significant correlation between the mean rate of gross primary production for a particular replication and its corresponding Q_{10} value ($r = -0.08$ with 10 d.f.). However, the mean Q_{10} value was significantly higher for samples obtained at 1.9 m above MLLW than for samples obtained at 1.0 m above MLLW ($t = 22.27$ with 10 d.f.); the corresponding means were 2.23 and 1.87, respectively.

Temperature coefficients for rates of oxygen uptake in the dark were more variable than values associated with changes in the rate of gross primary production (Table 23). The mean Q_{10} value for measurements of oxygen uptake (n = 12) was 2.70, with a standard error of 0.39. There was a significant negative correlation between the mean uptake rate for a replication and the corresponding Q_{10} value ($r = -0.72$ with 10 d.f.). Also, the mean Q_{10} value for samples from 1.9 m above MLLW was significantly higher than the mean for samples from 1.0 above MLLW ($t = 10.04$ with 10 d.f.); these means were 3.32 and 2.08, respectively.

Table 22. The rate of gross primary production (mg C m^{-2} hr^{-1}) at different water temperatures and corresponding Q_{10} values for intact sediment cores from Yaquina Bay. Mean biomass for three replications at each temperature is expressed as mg chlorophyll a m^{-2}. Temperature range was from 7°C to 17°C; salinity was 30 °/oo, and light intensity was 600 μE m^{-2} sec^{-1}. Data corresponds to samples from 1.9 m and 1.0 m above MLLW.

Experiment	Tidal Level	Mean Biomass	Temperature	Replication 1 GPP	1 Q_{10}	2 GPP	2 Q_{10}	3 GPP	3 Q_{10}	Mean GPP	Mean Q_{10}
1	+1.1	137.51	8.0	76.54		107.72		113.39		99.22	
					1.46		1.42		1.51		1.46
		152.52	17.0	107.72		147.41		164.42		139.85	
2	+1.1	154.02	7.0	119.06		141.74		175.76		145.52	
					2.83		2.24		1.68		2.25
		181.65	14.0	246.63		249.47		252.30		249.47	
3	+1.9	127.00	7.0	36.85		48.19		51.03		45.36	
					2.53		2.30		2.43		2.45
		151.92	16.0	85.04		102.05		113.39		100.16	
4	+1.9	144.12	8.0	24.68		33.93		40.10		32.90	
					2.69		1.86		1.59		2.04
		162.13	15.0	49.35		52.43		55.52		52.43	

Table 23. The rate of oxygen uptake (OUPTK) expressed as carbon equivalent (mg C m^{-2} hr^{-1}) at different water temperatures and corresponding Q_{10} values for intact sediment cores from Yaquina Bay. Mean biomass for three replications at each temperature is expressed as mg chlorophyll *a* m^{-2}. Temperature range was from 7°C to 17°C; salinity was 30 °/oo. Data corresponds to samples from 1.9 m and 1.0 m above MLLW.

Experiment	Tidal Level	Mean Biomass	Temperature	Replication 1 OUPTK	1 Q_{10}	Replication 2 OUPTK	2 Q_{10}	Replication 3 OUPTK	3 Q_{10}	Mean OUPTK	Mean Q_{10}
1	+1.1	137.51	8.0	17.04		20.44		37.48		24.99	
					2.64		2.36		1.73		2.24
		152.52	17.0	40.88		44.29		61.33		48.84	
2	+1.1	154.02	7.0	30.67		37.48		40.89		36.35	
					2.27		1.71		1.78		1.92
		181.65	14.0	54.52		54.52		61.33		56.79	
3	+1.9	127.00	7.0	6.81		6.81		6.81		6.81	
					4.03		4.67		5.32		4.67
		151.92	16.0	23.85		27.26		30.67		27.26	
4	+1.9	144.12	8.0	11.12		22.24		29.66		21.01	
					3.36		1.15		1.38		1.96
		162.13	15.0	25.95		29.66		37.07		30.89	

Experiments with Isolated Epipelic Diatoms. Motile, epipelic diatoms were isolated from sediment samples obtained each season during an entire year at study sites in Yaquina Bay using the method of Jonge (1980). Approximately 1000 cm^3 of the top cm of sediment were 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 $\mu E\ m^{-2}\ sec^{-1}$.

After the incubation period the lens tissue was lifted off the sediment and mixed with 500 ml of sand-filtered, UV-treated seawater. 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 outlens tissue fibers, and the net filtered out small animals. Microscopic inspection confirmed that the light brown-colored suspension contained primarily diatoms and few bacteria or flagellates.

The procedure for isolating living epipelic diatoms from sediment samples provided the opportunity to estimate some useful ratios for sediment-associated microalgal assemblages. The ratios of interest were (1) biomass as ash-free dry weight to chlorophyll a (AFDW/CHLOR); (2) gross primary production to chlorophyll a (GPP/CHLOR); and (3) net primary production to gross primary production in the light (NPP/GPP). The ratio AFDW/CHLOR provided a basis for estimating autotrophic biomass in sediment-associated microalgal assemblages when such assemblages consist primarily of diatoms, while NPP/GPP provided corresponding estimates of respiratory losses.

Results of experiments with isolated epipelic diatoms are presented in Tables 24-26. AFDW/CHLOR values varied from 107.55 to 254.98, with a mean for all experiments of 166.98 and a standard error of 8.20 (Table 24). The lowest mean value for a particular experiment was obtained during January, and the most variation among replications occurred in an experiment conducted in February. Estimates of GPP for the calculation of GPP/CHLOR and NPP/GPP were based on the assumption that respiration in the dark was equal to respiration in the light. Four replicate 50 ml screw-cap test tubes with a diatom sample were incubated for 0.5 hr at a light intensity of 210 $\mu E\ m^{-2}\ sec^{-1}$, a temperature of 14°C, and a salinity of 30 to 33 °/oo. Samples also were incubated in the dark for 0.5 hr under similar conditions. Measurements of oxygen concentration and calculation of production were performed as described above for the respirometer chambers. GPP/CHLOR values were considerably higher than values obtained for intact sediment cores (Table 25) and were more similar to values reported for algal cultures and natural populations of phytoplankton (see Table 17 in Parsons et al. 1977). The mean value for seven experiments (28 replications) was 5.12, and the associated standard error was 0.40. The mean ratio of net primary production to gross primary production for seven experiments was 0.71 (Table 26), indicating that respiration was approximately 29% of GPP for an equivalent period of time.

Table 24. Ratio of biomass expressed as ash-free dry weight to chlorophyll a concentration in assemblages of epipelic diatoms isolated by the lens paper method from intertidal sediment samples from Yaquina Bay. Data include the ratio for each replication and the mean ratio and standard error for each experiment.

Date of Experiment	Replication 1	2	3	4	$\bar{x}$	S.E.
10/1/80	209.96	192.85	177.42	177.25	189.37	7.78
10/28/80	176.22	189.86	186.16	189.11	185.34	3.14
1/21/80	107.55	132.44	135.25	122.76	124.50	6.25
2/26/80	113.51	254.98	161.70	126.22	164.10	31.96
4/2/80	108.20	190.17	143.23	168.84	171.62	10.51
Pooled					166.98	8.20

Table 25. Ratio of gross primary production (mg C hr^{-1}) to chlorophyll a (mg) in assemblages of epipelic diatoms isolated by the lens paper method from intertidal sediment samples from Yaquina Bay. The light intensity, temperature, and salinity during the experiments were 210 $\mu E\ m^{-2}\ sec^{-1}$, 14°C, and from 30 to 33 °/oo, respectively. Data include the ratio for each replication and the mean ratio and standard error for each experiment.

Date of Experiment	Replication 1	2	3	4	$\bar{x}$	S.E.
2/26/81	5.58	5.47	6.91	6.48	6.11	0.35
3/14/81	2.29	2.43	2.43	3.54	2.67	0.29
4/2/81	3.07	3.49	2.86	3.18	3.15	0.13
5/9/81	3.13	2.23	2.78	4.17	3.08	0.41
10/30/81	10.49	7.37	6.44	7.01	7.83	0.91
11/9/81	6.91	6.40	6.43	6.92	6.67	0.14
12/11/81	6.27	5.57	6.10	7.46	6.35	0.40
Pooled					5.12	0.40

Table 26. Ratio of net primary production to gross primary production in assemblages of epipelic diatoms isolated by the lens paper method from intertidal sediment samples from Yaquina Bay. The light intensity, temperature, and salinity during the experiments were 210 μE m^{-2} sec^{-1}, 14°C, and from 30-33 °/oo, respectively. Data include the ratio for each replication and the mean ratio and standard error for each experiment.

Date of Experiment	Replication 1	2	3	4	$\bar{x}$	S.E.
2/26/81	0.86	0.86	0.87	0.86	0.86	0.00
3/14/81	0.41	0.50	0.50	0.69	0.53	0.06
4/2/81	0.88	0.87	0.88	0.86	0.87	0.00
5/9/81	0.30	0.40	0.55	0.30	0.39	0.06
10/30/81	0.80	0.73	0.81	0.82	0.79	0.02
11/9/81	0.81	0.76	0.71	0.74	0.76	0.02
12/11/81	0.82	0.76	0.79	0.74	0.78	0.02
Pooled					0.71	0.03

3.2.2 Validation and Survey Sites

Sampling at the validation sites (Table 2 and Figure 3) provided an opportunity to compare rates of gross primary production estimated by equation 1 of Table 21 to direct field measurements at those sites. Unfortunately, the early termination of CREDDP field work greatly limited the size of the data set. Also, funds were not available to finish the analysis of chlorophyll samples obtained in September 1981 from six of the validation sites. Consequently, the results presented here represent only a preliminary evaluation of the use of chlorophyll a concentration in the top cm of sediment as a predictor of benthic primary production at sites where direct measurements are not available. Measurements of chlorophyll a and primary production at the validation sites also contributed descriptive information that, along with chlorophyll measurements at the survey sites, provided a basis for the distributional maps presented in this report and in The Columbia River Estuary: Atlas of Physical and Biological Characteristics (CREDDP 1984). A summary of the sample sizes and mean values for the chlorophyll concentrations at the validation sites is presented in Appendix B.

A comparison of the observed and predicted values for the rate of gross primary production at four validation sites is presented in Table 27. This analysis indicated that predictions were close to observed values for the samples from Horseshoe Island, West Sand Island, and two transects in the Skipanon Channel; while predictions were less satisfactory for samples from Lois Island and the Lower transect in the Skipanon Channel. However, correspondence between the mean observed value and the mean predicted value for the 12 samples is remarkably close. Therefore, the analysis of this very small data set indicates that equation 1 of Table 21 at least may provide reasonable predictions of mean rates of primary production for large regions when a representative set of chlorophyll data are available.

Mean chlorophyll concentrations and rates of gross primary production predicted from equation 1 of Table 21 for the survey sites are presented in Appendix B. The early termination of CREDDP field work limited the number of survey sites to 21 and restricted sampling to a period from May through August 1981. In spite of these constraints, 126 chlorophyll samples were obtained at the survey sites, all of which were analyzed by the laboratory procedure.

The validation and survey sites listed in Appendix B were classified into five regions: Baker Bay, Youngs Bay, Grays Bay, Cathlamet Bay, and Upper Estuary. These regions correspond to the same regional areas described earlier in the section concerned with taxonomic structure (Table 3). Moreover, the regions also correspond to four of the regions described in Chapter 8 of The Dynamics of the Columbia River Estuarine Ecosystem (CREDDP 1984), with the exception that the Cathlamet Bay region of the integration report is treated here as two regions, Cathlamet Bay which extends to the east side of Russian Island, and Upper Estuary which extends from east of Russian Island to the east side of Quinns Island. Data from the validation and survey sites then were summarized as regional means of the chlorophyll concentrations and the predicted rates of gross primary production (Table 28). Each mean value

Table 27. Chlorophyll concentrations in the top cm of sediment expressed as mg m^{-2} (CHLOR), observed rates of gross primary production as mg C m^{-2} hr^{-1} (OGPP), and rates of gross primary production predicted from equation 1 of Table 21 (PGPP) for four validation sites in the Columbia River Estuary. Tidal levels correspond to depths presented in Table 1. All samples were obtained in August 1981.

Site	Tidal Level	CHLOR	OGPP	PGPP
Horseshoe Island	Marsh	110.50	35.53	31.04
Horseshoe Island	Upper	108.70	35.36	30.55
Horseshoe Island	Lower	99.50	35.24	28.02
Lois Island	Marsh	108.60	10.75	30.52
Lois Island	Upper	55.80	32.02	15.99
Lois Island	Lower	36.10	29.85	10.57
Skipanon Channel	Marsh	910.40	209.43	251.19
Skipanon Channel	Upper	188.10	57.12	52.40
Skipanon Channel	Lower	298.70	38.20	82.84
West Sand Island	Marsh	173.90	31.54	48.49
West Sand Island	Upper	191.00	69.08	53.20
West Sand Island	Lower	99.60	35.06	28.04
Mean		198.41	51.60	55.24
Standard Error		67.86	14.93	18.68

Table 28. Mean concentration of chlorophyll a in the top cm of sediment expressed as μg cm^{-3} (CHLOR) and mean predicted gross primary production expressed as mg C m^{-2} hr^{-1} (GPP) for five regions in the Columbia River Estuary. The values represent unweighted means for the survey and validation sites located in each region; data from the intensive study sites were not included in the calculations. GPP values were based on values predicted from equation 1 of Table 21.

Region	Sample Size	CHLOR	GPP
Baker Bay	108	18.22	50.77
Youngs Bay	96	18.59	51.80
Grays Bay	30	5.88	16.83
Cathlamet Bay	108	6.15	16.97
Upper Estuary	114	8.26	23.06

is an unweighted average of the means for the sites located in a particular region. This simple analysis of information from the validation and survey sites clearly indicated the difference in productive capacity between the two bays in the lower estuary (Baker Bay and Youngs Bay) and regions upriver from these brackishwater areas. This difference was also evident from the detailed information obtained at the intensive study sites in Baker Bay, Youngs Bay, Grays Bay, and on Quinns Island.

3.2.3 Regional Patterns of Benthic Primary Production

Spatial Distribution and Annual Rates

Because benthic primary production is largely confined to the shallow regions of the Columbia River Estuary, most of the interesting patterns occur in the four large bays: Baker Bay, Youngs Bay, Cathlamet Bay, and Grays Bay. In Baker Bay and Youngs Bay there are tidal flats that exhibit relatively high mean rates of benthic primary production, in the range of 60 to 80 mg C m^{-2} hr^{-1} (Figures 24 and 25). The highest rate (430 mg C m^{-2} hr^{-1}) was recorded for the low marsh at the intensive study site in Youngs Bay during May 1980 when Enteromorpha was abundant on the sediment surface. This value was atypical of the other observations when microalgae were the only benthic plants. In the intertidal regions, high rates of benthic primary production were found in Youngs Bay in September 1980 (172 mg C m^{-2} hr^{-1}) and October 1980 (156 mg C m^{-2} hr^{-1}), and on a tidal flat near the town of Ilwaco, Washington, in July 1981 (106 mg C m^{-2} hr^{-1}). The tidal flats in Grays Bay and Cathlamet Bay were less productive than such regions in Baker Bay and Youngs Bay. In Grays Bay and Cathlamet Bay mean rates of gross primary production usually varied between 20 and 40 mg C m^{-2} hr^{-1}, although some of the sandy regions had mean rates less than 20 mg C m^{-2} hr^{-1} (Figures 26 and 27). In general, the sandy intertidal areas of the many islands in the study area exhibited relatively low mean rates of benthic primary production, usually between 10 and 20 mg C m^{-2} hr^{-1}. However, data from the intertidal region in Quinns Island indicated that sandy sites can be productive if sediment disturbance is minimal. In this case, the rate of benthic primary production on the sandy sediments along the upper transect varied from 7 mg C m^{-2} hr^{-1} in June when freshwater discharge was high, to 189 mg C m^{-2} hr^{-1} in September when the substrate was relatively undisturbed by water movements.

For the tidal flats the data indicated the relationship between total benthic oxygen uptake (OCON) and gross primary production (GPP) was approximately linear. From the regression analysis (equation 8 of Table 21) the predictive equation with an R^2 of 0.66 is

$$OCON = 17.05 + 0.72\ GPP,$$

where OCON and GPP are expressed as mg O_2 m^{-2} hr^{-1} and g C m^{-2} hr^{-1}, respectively. This equation can be used to determine the approximate distribution of benthic oxygen uptake from the maps in Figures 24-27. A linear equation relating OCON and GPP for transects in the low marsh was unsatisfactory for predictive purposes (R^2 = 0.33), a difficulty apparently related to the high input of vascular plant detritus in these areas.

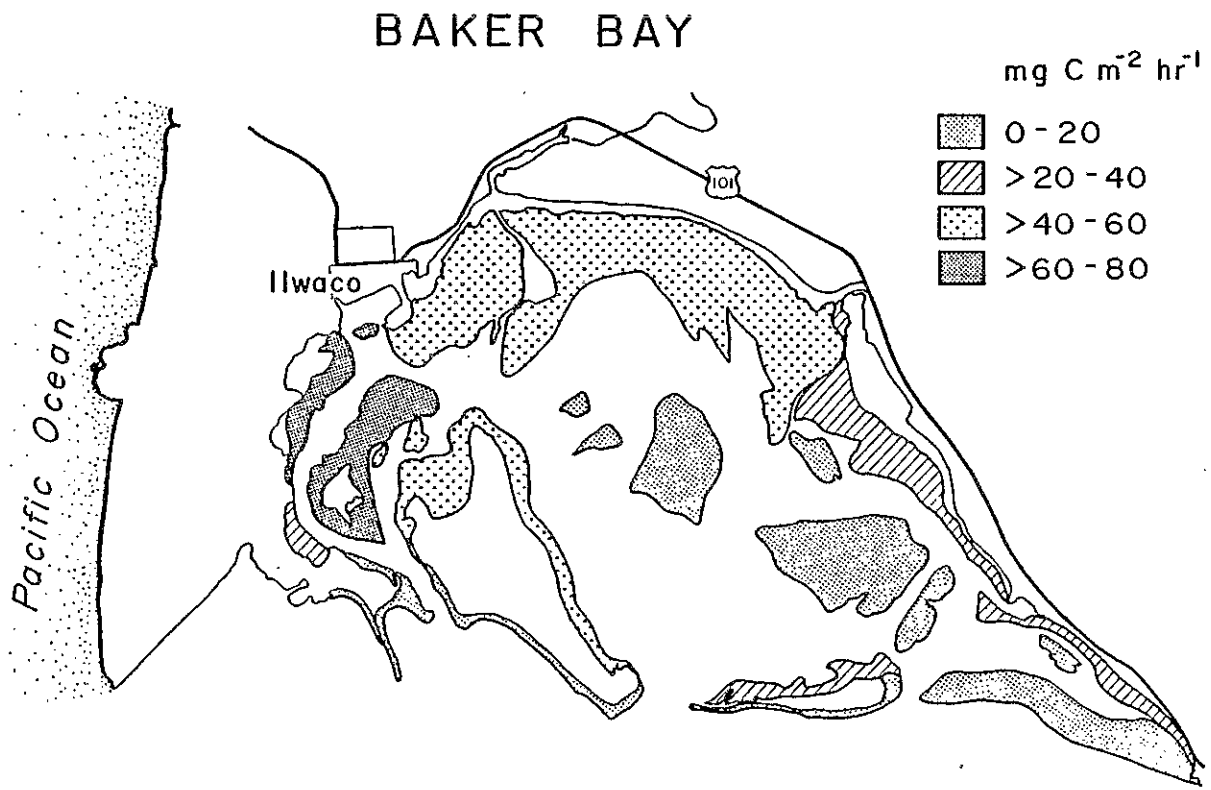

Figure 24. Pattern of gross primary production in Baker Bay. The distribution categories represent ranges for the mean hourly rate at light saturation during the study period from May 1980 through April 1981.

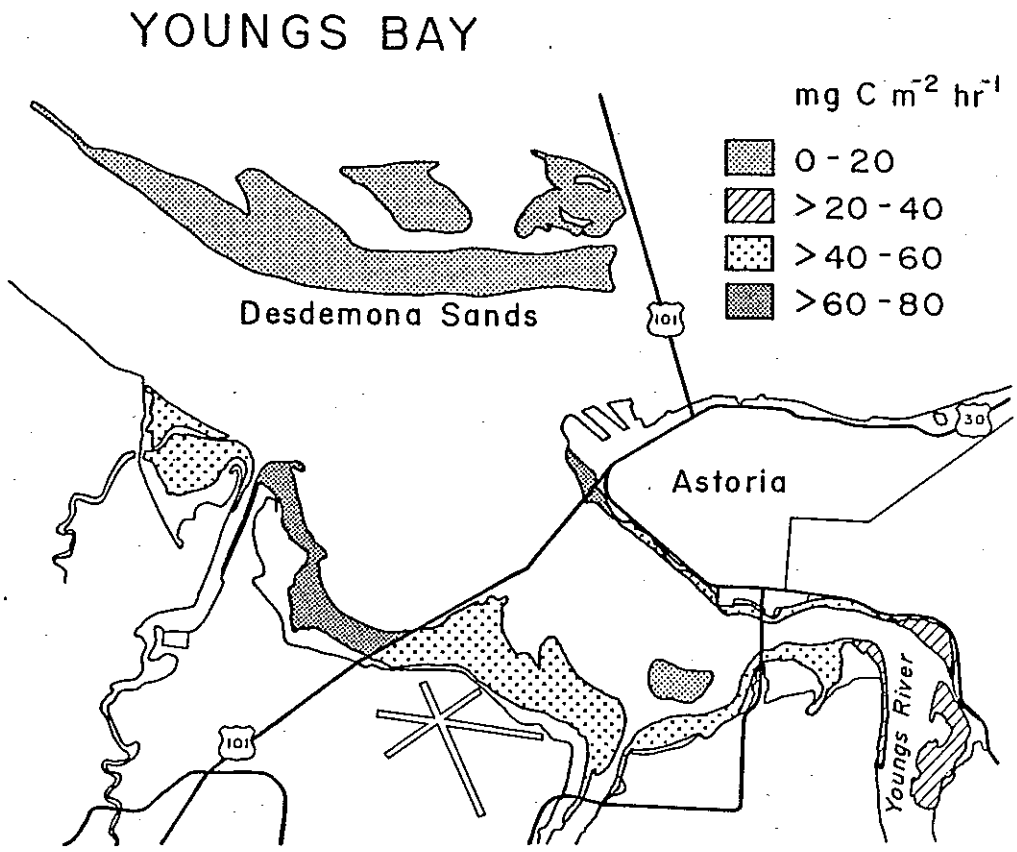

Figure 25. Pattern of gross primary production in Youngs Bay. The distribution categories represent ranges for the mean hourly rate at light saturation during the study period from May 1980 through April 1981.

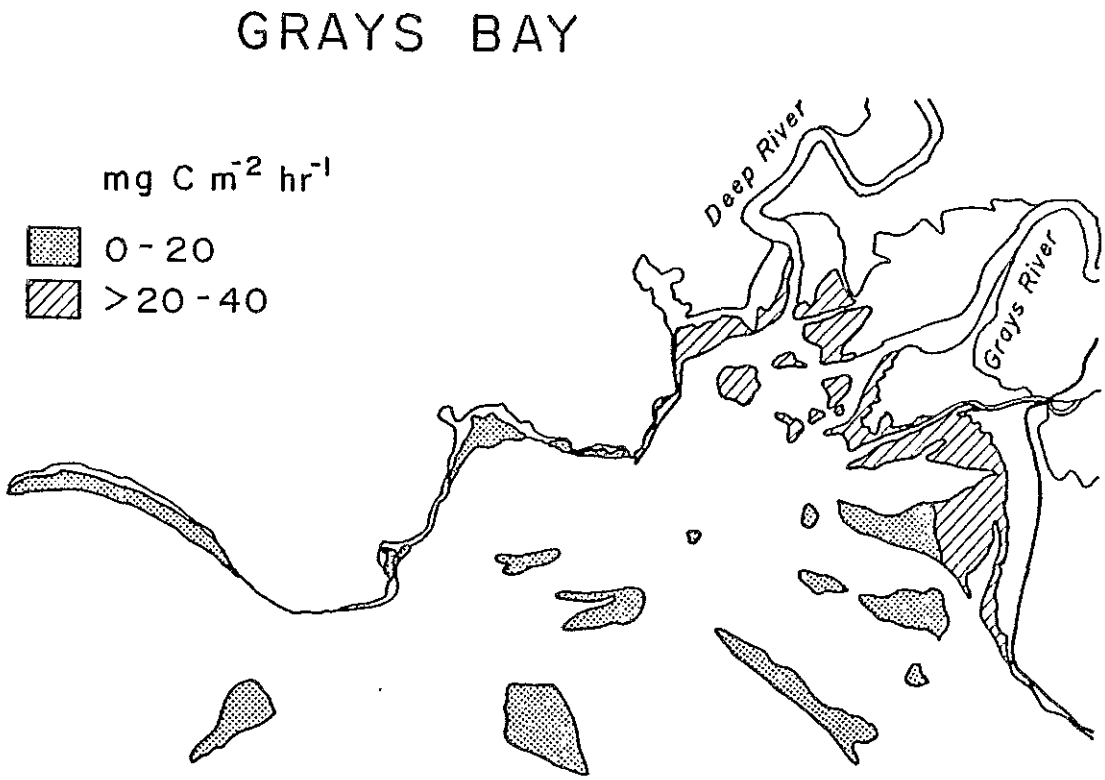

Figure 26. Pattern of gross primary production in Grays Bay. The distribution categories represent ranges for the mean hourly rate at light saturation during the study period from May 1980 through April 1981.

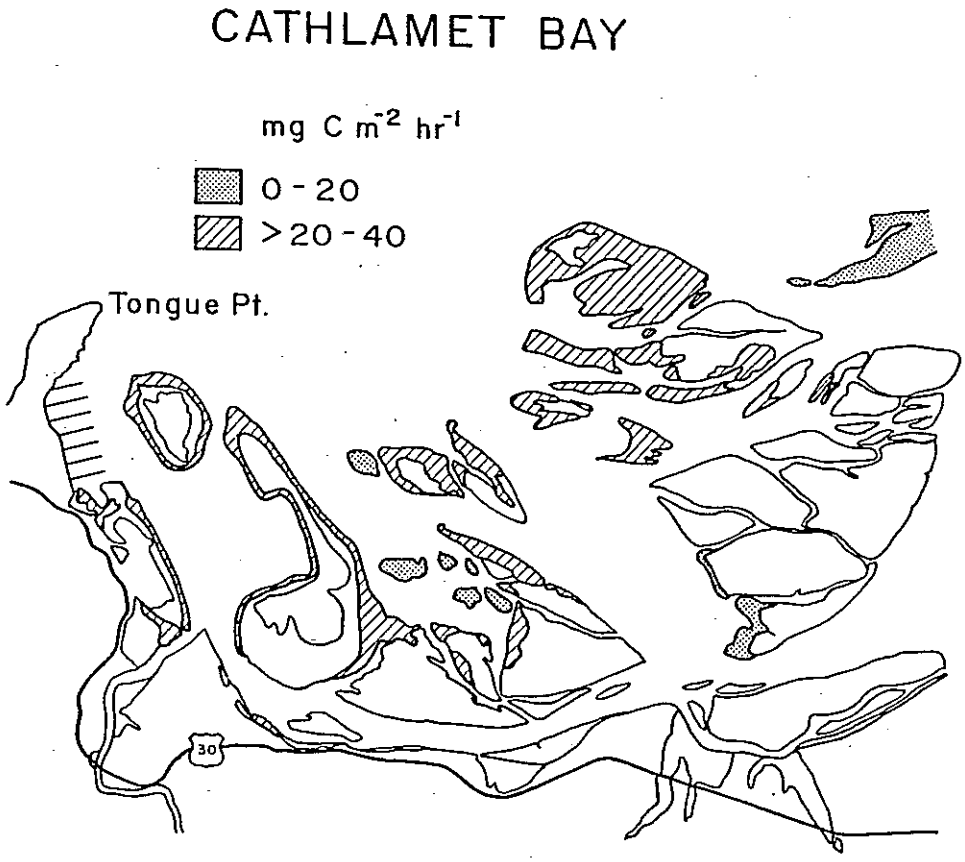

Figure 27. Pattern of gross primary production in Cathlamet Bay. The distribution categories represent ranges for the mean hourly rate at light saturation during the study period from May 1980 through April 1981.

Rates of benthic primary production given in earlier sections of this report, and in Figures 24-27, correspond to the time scale, hourly in this case, at which the measurements were actually made in the respirometer chambers. To extrapolate these data to estimates of annual rates is a difficult problem that requires explicit assumptions relating to light intensity at the water surface, light attenuation in the water column, and tidal inundation time. The approach taken here applies to the tidal flats, i.e., the region from MLLW to the edge of the low marsh. Annual rates were not estimated for the subtidal region or for the low and high marshes.

The assumptions for the conversion of hourly rates to annual rates were:

1. The annual mean value for the light attenuation coefficient $\underline{k}$ during the study was 2.75;

2. P_{max} was attained at a light intensity of 400 $\mu E\ m^{-2}\ sec^{-1}$;

3. The mean light intensity at the water surface during daylight for the period of the study was 1,428 $\mu E\ m^{-2}\ sec^{-1}$.

Assumption 1 was based on data from the Water Column Primary Production Work Unit (Frey et al. 1984), while assumption 3 was derived from measurements of light intensity during the respirometer studies of benthic primary production. The experimental work reported in Figure 23 was the basis for assumption 2.

If the mean light intensity at the water surface is 1,420 $\mu E\ m^{-2}\ sec^{-1}$, the mean maximum depth (Z_{max}) at which photosynthesis can occur at its light-saturated rate (P_{max}) is calculated from the well-known equation for light attenuation in the water column:

$$I_z = I_o e^{-\underline{k}z},$$

where I_z is the intensity at depth z, I_o is the intensity at the surface, and $\underline{k}$ is the extinction coefficient. Therefore, from assumption 2 above, $Z_{max} = \ln(400/1{,}428) \div -2.75 = 0.46$ m. The sampling transects at the intensive study sites on the tidal flats were at 0.3 m (lower), 0.5 m (mid), and 0.7 m (upper) above MLLW. Therefore, maximum photosynthetic rates by benthic plants can still occur along these transects when the water level is approximately 0.5 m higher than the transect levels or less (i.e., at water levels of $\leq$ 0.8 m, $\leq$ 1.0 m, and $\leq$ 1.2 m above MLLW, respectively). From tidal inundation data for seven locations in the estuary (Jay 1983), the 0.8 m, 1.0 m, and 1.2 m levels are exposed to the air for annual mean periods of 6.45, 8.43, and 10.43 hours per day. Assuming a mean value for the three transects is a reasonable time estimate for the entire tidal flat, the annual mean number of hours per day at which the water level is at a height that can allow maximum photosynthesis is 8.44 hours per day. With a mean daylength for the entire year of approximately 12 hours, or one-half the length of a day, a reasonable estimate of the mean number of hours per day during the year that benthic plants are exposed to enough light to support the light-saturated rate of photosynthesis is only one-half of

8.44, or 4.22. Since benthic microalgal assemblages reach P_{max} very rapidly with increasing light intensity and all mean hourly rates measured for the study sites are light-saturated rates, a rough estimate of the mean annual rate for a particular tidal flat expressed as g C m^{-2} yr^{-1} is obtained from:

Mean hourly rate as mg C m^{-2} hr^{-1} X 4.22 hr day^{-1} X 365 days yr^{-1} ÷ 1,000

Estimates of annual rates of benthic gross primary production are given in Table 29. These estimates correspond to the intensive study sites, where direct measurements of hourly rates were obtained, and to the survey sites grouped by region, where hourly rates were estimated from measurements of chlorophyll a and equation 1 of Table 21. Mean rates for the regions ranged from about 20 to 100 g C m^{-2} yr^{-1}, although values were as high as 250 g C m^{-2} yr^{-1} or more at specific site locations. These mean rates and ranges are very similar to values reported by other investigators for various geographical locations (Tables 29 and 30). If the five regions listed in Table 29 are given equal weight, the mean for the intertidal region of the entire estuary is about 50 g C m^{-2} yr^{-1}. The total intertidal area from MLLW to the lower boundary of the emergent vegetation in the Columbia River Estuary, as defined by the CREDDP study area, is 10,750 acres (43.5 x 10^6 m^2). Therefore, a rough estimate of the total annual benthic gross primary production for the intertidal region of the entire estuary is about 2.175 x 10^6 Kg or 2,175 metric tons of carbon. Since organic matter is about 50% carbon, this value corresponds to 4,350 metric tons of organic matter per year. This value is not a very large number considering the acreage involved. In comparison, 835 acres of a well-developed eelgrass bed in Netarts Bay yielded about 6,000 metric tons of organic matter as net primary production (Kentula 1983), indicating that such systems are at least 20 times more productive than the tidal flats in the Columbia River Estuary.

Carbon Budgets for Intensive Study Sites

Experimental work with isolated assemblages of epipelic diatoms (Davis and McIntire 1983) indicated that the mean ratio of net primary production to gross primary production for liquid suspensions of these organisms was 0.71. This value was derived from 28 experiments conducted from February through December 1981 at the Oregon State University Marine Science Center (Table 26). Results of this research give an estimate of mean respiratory losses for sediment associated diatoms and provide a basis for the calculation of simple carbon budgets. Examples of such budgets for four intensive study sites are presented in Table 31. Assumptions associated with these calculations are:

1. During daylight hours respiratory losses by autotrophic organisms are 29% of gross photosynthesis;

2. The hourly rate of plant respiration in the dark is equal to the hourly rate in the light;

Table 29. Annual rates of benthic gross primary production expressed as g C m^{-2} yr^{-1} for the intensive study sites and the validation and survey sites grouped by region. Values are based on direct measurements of hourly rates (intensive study sites) and hourly rates predicted from the concentration of chlorophyll *a* in the top cm of sediment (validation and survey sites). Hourly rates were converted to annual rates by the procedure described in the text.

Location	Mean	Range
Intensive Study Sites:		
Clatsop Spit	8.04	0.00 - 36.54
Youngs Bay	120.94	0.00 - 264.28
Baker Bay	69.25	0.00 - 152.72
Grays Bay	44.56	0.00 - 119.99
Quinns Island	33.46	0.00 - 167.17
Validation and Survey Sites:		
Baker Bay Region	97.24	8.58 - 156.31
Youngs Bay Region	71.19	30.34 - 101.55
Grays Bay Region	25.92	16.50 - 37.18
Cathlamet Bay Region	22.63	15.57 - 33.61
Upper Estuary	38.28	15.74 - 63.91

Table 30. Some annual rates of benthic gross primary production (G) and net primary production (N) determined by different investigators for various geographical locations.

Study	Location	Rate ($g\ C\ m^{-2}\ yr^{-1}$)
1. Steele & Baird (1968)	Scotland, exposed beach	4-9 (N)
2. Pomeroy (1959)	Georgia salt marsh	200 (G)
3. Grøntved (1960)	Danish Fjords	116 (N)
4. Cadee & Hegeman (1977)	Western Wadden Sea	29 - 188 (N)
5. Pamatmat (1968)	False Bay, San Juan Island	143 - 226 (G)
6. Gallagher & Daiber (1974)	Delaware Salt Marsh	38 - 99 (G)
7. Marshall et al (1971)	Southern New England estuarine shoals	100 (G)
8. Leach (1970)	Northern Scotland mudflat	31 (N)
9. Riznyk & Phinney (1972)	Yaquina Estuary, Oregon:	
	sandy silt	275 - 325 (G)
	fine silt	0 - 125
10. Davis & McIntire (1983)	Netarts Bay, Oregon:	
	sand	129 (G)
	sandy silt	153
	silt	72

Table 31. Community metabolism at four intensive study sites partitioned by gross primary production (GPP), respiration by autotrophic organisms (AR), net primary production (NPP), and carbon equivalents of total benthic oxygen consumption (OCON) and oxygen uptake not associated with metabolism of autotrophs (HR). The sites are Youngs Bay (YB), Baker Bay (BB), Grays Bay (GB), and Quinns Island (QI). All rates are expressed as g C m^{-2} day^{-1}; calculations are based on data in Tables 13 and 14, and on the assumptions given in the text.

Rates	YB	BB	GB	QI
GPP	1.011	0.510	0.396	0.355
AR	0.586	0.295	0.230	0.206
NPP	0.425	0.215	0.166	0.149
OCON	0.599	0.543	0.403	0.371
HR	0.013	0.248	0.173	0.165

3. The light and dark periods during the day are both 12 hours in length.

The values in Table 31 are representative of the middle of the growing season, as the number of daylight hours per day are assumed to be 12 instead of the estimated annual mean of 4.22. Moreover, the values in the table are based on the mean rates of gross primary production and oxygen consumption presented in Tables 13 and 14 for the intensive study sites at Youngs Bay, Baker Bay, Grays Bay, and Quinns Island. For example, the mean rate of gross primary production for the Youngs Bay site is 84.22 mg C m^{-2} hr^{-1}, which is equivalent to 1.011 g C m^{-2} for a 12 hour day. From the experimental work and assumption 1, the mean rate of respiration by autotrophic organisms is 0.29 x 84.22 mg C m^{-2} hr^{-1} or 24.42 mg C m^{-2} hr^{-1}; the daily rate is therefore 24.42 x 24 or 0.586 g C m^{-2} day^{-1}. The mean rate of net primary production at the Youngs Bay site is 1.011 - 0.586 or 0.425 g C m^{-2} day^{-1}. From Table 14 the mean rate of oxygen consumption at this site is 66.55 mg O_2 m^{-2} hr^{-1} which, assuming a respiratory quotient of one, is equivalent to 0.375 x 66.55 equals 24.96 mg C m^{-2} hr^{-1} or 0.599 g C m^{-2} day^{-1}. Therefore, the carbon loss not associated with autotrophs is the difference between the latter value and the estimate of autotrophic respiration: 0.599 - 0.586 = 0.013 g C m^{-2} day^{-1}. The latter value is simply the carbon equivalent of the oxygen consumption that is not attributable to metabolic activities of autotrophic organisms. This fraction results from the respiratory activities of heterotrophic organisms, and from the chemical oxidation of reduced compounds, a process that may be indirectly coupled to the metabolic activities of anaerobic microorganisms (Jorgensen 1977).

The values in Table 31 indicate that the sites at Baker Bay, Grays Bay, and Quinns Island may be close to a steady state dynamics, as total losses (OCON) are only slightly greater than gross primary production (GPP). At these sites, values for the ratio GPP/OCON are 0.939, 0.983, and 0.957, respectively, values that are all near unity. Detrital imports could account for the slight heterotrophic tendency. At the Youngs Bay site, GPP/OCON is 1.688, and the system is more autotrophic. These data suggest that benthic plant biomass may be exported from this site, at least during certain times of the year. In particular, some of the biomass of Enteromorpha which is abundant on the sediment in the low marsh during the spring may be transported out of the marsh by water movement.

4. SUMMARY AND CONCLUSIONS

1. The microalgae were by the far the most abundant group of plants associated with the tidal flats of the Columbia River Estuary. Assemblages of microalgae on the tidal flats of the estuary consisted almost entirely of diatoms, while blue-green algae were found occasionally growing on the sediment beneath emergent vascular plants in the low marsh.

2. Submergent vascular plants exhibited a patchy distribution and were relatively rare on the tidal flats of the estuary. Zostera marina had a sparse distribution in Baker Bay and was collected in Trestle Bay, but the estuary apparently lacks the habitat necessary to support the large, dense beds of Zostera that are found in other Oregon estuaries. Possible factors limiting the growth of Zostera in the Columbia River Estuary include low salinity, turbidity, and the properties and stability of the sediment. Other submergent vascular plants were found at freshwater sites in Grays Bay. At this location, a sparse growth of Potamogeton richardsonii and P. pectinatus occurred on the tidal flats during spring and summer, while Ceratophyllum demersum and Elodea canadensis were often abundant in small pools near the low marsh.

3. Enteromorpha intestinalis was the only species of macroalgae observed at the sampling sites during the study. This filamentous green alga was abundant in sediment samples from the low marsh in April and May at a site in Youngs Bay; it also occurred in association with individual shoots of Zostera marina on a tidal flat in Baker Bay.

4. A detailed quantitative analysis of the taxonomic structure of the diatom flora of the estuary indicated that the benthic floras in the Cathlamet Bay, Grays Bay, and in the Upper Estuary region above Cathlamet Bay were similar. The Youngs Bay benthic diatom flora was more similar to the floras in Grays Bay, Cathlamet Bay, and Upper Estuary than to the flora in Baker Bay, a pattern apparently related to freshwater input into Youngs Bay from the Lewis and Clark River, the Youngs River, and the main channel of the Columbia River. Using the species composition of the diatom flora as a salinity indicator, the statistical analysis indicated that Cathlamet Bay, Grays Bay, and the Upper Estuary region were freshwater regions in the intertidal zone, while the tidal flats in Baker Bay were under the influence of brackish water. Youngs Bay apparently is influenced to some degree by slightly brackish water, although intermittent periods of high freshwater discharge were responsible for the presence of a large number of freshwater planktonic and benthic taxa in the sediment-associated flora.

5. The properties and stability of the sediment were closely related to the production dynamics of benthic plant assemblages on the tidal flats of the Columbia River Estuary. Sediment properties were investigated in detail at five intensive study sites and related to rates of benthic primary production and the biomass of microalgae expressed as the concentration of chlorophyll *a* in the sediment. Sediments at the intensive study site at Clatsop Spit were well sorted and consisted of fine sand. At this site the sand shifted around in response to river flow and tidal movement, and such sediments were an unstable substrate for the growth of aquatic plants. At the intensive study sites in Youngs Bay and Baker Bay, the sediments were relatively fine, poorly sorted, and relatively undisturbed by water movements. These conditions corresponded to high rates of benthic primary production. Sediments at the intensive study site in Grays Bay were composed of sandy silt, and ratios of the chlorophyll concentration near the sediment surface to that at lower depths indicated considerable sediment disturbance and mixing. The microhabitat at this site apparently was less suitable for the development of microalgal assemblages than at the intensive study sites in Youngs Bay and Baker Bay. The intertidal region at the intensive study site on Quinns Island was a sandy area with relatively little silt and clay. Rates of primary production at this site were usually similar to rates found for the site in Grays Bay.

6. Mean biomasses of microalgae at the intensive study sites during the entire study expressed as μg chlorophyll *a* cm^{-3} were 1.38 (Clatsop Spit), 26.44 (Youngs Bay), 25.06 (Baker Bay), 10.33 (Grays Bay), and 9.02 (Quinns Island). In general, there was relatively little seasonal change in the microalgal biomass at these sites, and the biomass was usually highest along the transect in the low marsh and lowest along the intertidal transect nearest the main channel.

7. Mean rates of gross primary production at the intensive study sites during the entire study expressed as mg C m^{-2} hr^{-1} were 5.22 (Clatsop Spit), 84.22 (Youngs Bay), 42.50 (Baker Bay), 33.01 (Grays Bay), and 29.56 (Quinns Island). Mean rates of benthic primary production were highest during the period from March through October, and lowest during the winter months. Moreover, rates were higher in the low marshes and upper intertidal regions than in the lower intertidal regions of the estuary.

8. There was a strong linear relationship between the rate of gross primary production (GPP) and the concentration of chlorophyll *a* in the top cm of sediment (CHLOR), suggesting that the chlorophyll concentration in the sediment could be used to predict rates of benthic primary production in regions where direct measurements cannot be made. The best predictive equation from CREDDP data is: GPP = 0.63 + 0.28CHLOR, where GPP is expressed as mg C m^{-2} hr^{-1}, and CHLOR is expressed as mg m^{-2}.

9. Experimental work by Davis and McIntire (1983) is relevant to the interpretation of the patterns of benthic primary production in the Columbia River Estuary. These studies indicated that sediment-

associated assemblages of benthic microalgae usually reach their maximum light-saturated rate of photosynthesis at light intensities between 200 and 400 μE m^{-2} sec^{-1}, i.e., between 10% and 20% of the intensity of full sunlight. In a series of experiments relating temperature to rates of primary production, it was determined that the mean Q_{10} value was 2.05, which means that the rate is doubled if the temperature is increased 10°C. In another series of experiments, it was found that the mean ratio of organic matter to chlorophyll a in assemblages of epipelic diatoms was 167. Also, the mean hourly rate of respiration in such assemblages was approximately 29% of the hourly rate of gross primary production. The experimental estimates of the organic matter-chlorophyll ratio and respiratory rate were used to calculate annual rates of primary production and carbon budgets for the Columbia River Estuary.

10. Direct measurements of benthic primary production at the intensive study sites and validation sites, along with values predicted from chlorophyll measurements at the survey sites, provided the data necessary to map the pattern of this variable for the CREDDP study area. A corresponding regional analysis indicated that mean rates of benthic gross primary production for the regions designated as Baker Bay, Youngs Bay, Grays Bay, Cathlamet Bay, and Upper Estuary, were approximately 51, 52, 17, 17, and 23 mg C m^{-2} hr^{-1}, respectively. In other words, Baker Bay and Youngs Bay were more productive in general than the freshwater regions upriver from Tongue Point.

11. Estimates of annual rates of benthic gross primary production for the intensive study sites at Clatsop Spit, Youngs Bay, Baker Bay, Grays Bay, and Quinns Island, were 8.04, 120.94, 69.25, 44.56, and 33.46 g C m^{-2} yr^{-1}, respectively. From these data and the annual rates calculated for the validation and survey sites, it is estimated that the total annual benthic gross primary production for the intertidal region of the entire estuary is about 2,175 metric tons of carbon. While the rates per square meter are similar to values reported for other estuaries of the world, the contribution of carbon to the estuary by the benthic primary producers is still relatively small in comparison to contributions by the emergent vegetation and by the fine particulate organic particles transported into the estuary from upriver (Frey et al. 1984).

12. Benthic primary production on the tidal flats of the Columbia River Estuary is probably controlled primarily by the properties and stability of the sediment. Also, the optical properties of the water column (turbidity) and daylength undoubtedly have significant seasonal effects on autotrophic processes. The extent to which deposit feeding by burrowing animals or direct grazing on benthic microalgae affect the process of primary production in the estuary is unknown. However, effects of animal activities are not as conspicuous in the Columbia River Estuary as in the brackishwater regions of other Oregon estuaries where animal holes in the sediment are relatively large and numerous.

13. Dredging and filling activities in the Columbia River Estuary may affect benthic communities in two ways: (1) a change in species composition in response to changes in the chemical and physical environment; and (2) a reduction in the productive capacity of the system brought about by a physical disruption or complete habitat destruction as material is removed or redistributed. The taxonomic structure of the sediment-associated diatom flora may provide a useful index to the potential of an impact to bring about changes in species composition, while the distribution and abundance of chlorophyll in the sediment can serve as an indication of the productive capacity.

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APPENDIX A

Number of samples (n), means (μg chl *a* cm^{-3}) and standard errors (S.E.) for chlorophyll *a* samples collected from the top cm of sediment at the intensive study sites, and ratios of chlorophyll *a* from the top cm of sediment to chlorophyll *a* from 4.5-5.5 cm in the sediment (C1:C2) and to chlorophyll *a* from 9-10 cm in the sediment (C1:C3).

Site	n	µg chl *a* cm^{-3}	S.E.	C1:C2	C1:C3
Clatsop Spit	204	1.38	0.12	–	–
Upper	72	1.47	0.23	–	–
April	6	0.68	0.28	–	–
May	6	0.58	0.31	–	–
June	6	1.00	0.38	–	–
July	6	2.45	0.61	–	–
August	6	1.38	0.52	–	–
September	6	1.77	0.62	–	–
October	6	5.25	1.53	–	–
November	6	0.35	0.30	–	–
January	6	0.92	0.44	–	–
February	6	0.15	0.16	–	–
March	6	2.06	0.73	–	–
April	6	1.09	0.44	–	–
Mid	72	1.17	0.18	–	–
April	6	1.16	0.33	–	–
May	6	1.60	0.89	–	–
June	6	0.28	0.28	–	–
July	6	1.89	0.70	–	–
August	6	0.54	0.54	–	–
September	6	1.05	0.52	–	–
October	6	1.18	0.67	–	–
November	6	1.41	0.65	–	–
January	6	0.00	0.00	–	–
February	6	0.82	0.53	–	–
March	6	1.42	0.48	–	–
April	6	2.68	0.83	–	–
Lower	60	1.51	0.22	–	–
April	6	1.20	0.48	–	–
May	6	1.70	0.53	–	–
June	6	1.58	0.61	–	–
July	6	0.70	0.49	–	–
August	6	1.65	0.73	–	–
September	6	0.66	0.46	–	–
October	6	0.00	0.00	–	–
November	6	–	–	–	–
January	6	–	–	–	–
February	6	1.82	0.58	–	–
March	6	2.34	0.55	–	–
April	6	3.47	1.21	–	–
Youngs Bay	270	26.44	0.78	4.03	7.13
Marsh	66	27.69	1.42	–	–
April	–	–	–	–	–
May	6	25.63	1.25	–	–

Site	n	µg chl a cm^{-3}	S.E.	C1:C2	C1:C3
June	6	43.26	3.44	–	–
July	6	27.19	1.07	–	–
August	6	38.59	2.46	–	–
September	6	37.55	1.47	–	–
October	6	41.30	4.86	–	–
November	6	23.28	1.40	–	–
January	6	18.56	1.35	–	–
February	6	18.96	0.38	–	–
March	6	18.51	1.19	–	–
April	6	11.73	1.69	–	–
Upper	72	29.09	2.10	4.00	10.06
April	6	36.20	3.41	5.91	23.69
May	6	29.27	3.21	4.60	12.24
June	6	30.34	1.45	3.78	9.56
July	6	30.75	2.54	5.91	15.06
August	6	24.19	2.40	4.22	7.29
September	6	75.70	6.29	7.07	17.06
October	6	27.08	7.48	4.57	7.22
November	6	29.69	1.72	2.87	8.31
January	6	17.84	1.91	2.55	5.97
February	6	21.15	3.54	3.09	6.94
March	6	13.01	1.07	1.74	5.45
April	6	13.84	3.30	2.24	3.12
Mid	66	27.68	1.28	3.61	5.96
April	6	34.34	3.92	6.28	9.51
May	6	30.92	2.69	4.90	6.69
June	6	32.09	3.99	3.52	6.30
July	6	23.53	0.38	2.76	9.09
August	6	30.22	2.75	4.04	6.02
September	6	40.14	6.45	4.17	7.27
October	6	34.88	3.53	3.80	7.85
November	–	–	–	–	–
January	6	16.62	1.03	1.59	1.79
February	6	18.42	0.96	2.47	2.47
March	6	20.13	2.42	2.24	4.54
April	6	23.15	2.53	3.73	3.77
Lower	66	21.05	0.90	4.48	5.11
April	6	26.56	3.76	7.34	10.95
May	6	30.50	1.02	4.82	8.77
June	6	24.48	2.25	5.39	7.05
July	6	21.50	1.70	4.32	6.15
August	6	22.65	1.49	5.58	3.74
September	6	22.67	1.01	3.25	3.08
October	6	17.42	1.86	4.21	5.22
November	–	–	–	–	–
January	6	14.99	1.02	2.96	3.15
February	6	15.74	1.44	2.28	2.19
March	6	11.34	2.97	5.11	1.96
April	6	23.70	3.33	4.49	4.88

Site	n	µg chl a cm^{-3}	S.E.	C1:C2	C1:C3
Bakers Bay	270	25.06	0.67	3.55	9.05
Marsh	66	27.78	0.92	-	-
April	-	-	-	-	-
May	6	32.10	1.60	-	-
June	6	31.59	2.64	-	-
July	6	21.88	2.84	-	-
August	6	18.76	2.61	-	
September	6	23.42	1.27	-	-
October	6	23.43	3.91	-	-
November	6	27.56	2.93	-	-
January	6	34.73	1.48	-	-
February	6	33.59	2.03	-	-
March	6	30.19	1.52	-	-
April	6	28.31	2.73	-	-
Upper	72	30.85	1.34	3.64	11.00
April	6	38.05	2.66	4.56	12.19
May	6	36.13	2.62	5.96	10.96
June	6	33.11	2.85	2.41	8.76
July	6	18.52	2.45	2.56	6.08
August	6	21.98	2.08	1.83	3.91
September	6	18.19	2.79	1.31	5.91
October	6	26.24	4.01	1.91	8.27
November	6	33.85	2.37	3.47	9.03
January	6	40.34	3.56	5.52	20.48
February	6	45.24	6.98	5.89	18.12
March	6	31.65	1.34	3.20	21.50
April	6	26.87	3.96	5.00	8.50
Mid	66	27.77	0.96	3.30	10.21
April	6	28.95	3.62	4.01	10.10
May	6	30.77	0.85	3.94	8.54
June	6	36.78	2.16	3.98	19.59
July	6	21.11	1.48	2.59	9.12
August	6	22.92	1.85	2.52	5.75
September	6	24.21	1.25	2.36	6.38
October	6	21.05	2.58	1.42	5.33
November	-	-	-	-	-
January	6	24.53	2.83	6.50	4.94
February	6	36.46	3.25	3.94	15.72
March	6	29.12	1.78	3.92	17.65
April	6	29.55	4.03	4.02	6.97
Lower	66	13.31	0.91	3.69	5.42
April	6	11.57	1.22	3.54	5.54
May	6	15.61	2.69	4.36	10.86
June	6	27.54	4.02	8.06	14.41
July	6	6.15	0.42	1.59	3.35
August	6	11.74	0.70	3.27	4.10
September	6	11.30	1.23	2.46	3.15
October	6	8.67	0.82	0.99	1.24
November	-	-	-	-	-

Site	n	µg chl a cm^{-3}	S.E.	C1:C2	C1:C3
January	6	17.50	3.68	-	-
February	6	15.78	2.39	7.46	4.74
March	6	12.35	1.27	2.40	5.35
April	6	8.16	0.87	2.20	1.65
Grays Bay	252	10.33	0.35	0.93	1.81
Marsh	60	12.49	0.67	-	-
April	-	-	-	-	-
May	6	14.40	1.20	-	-
June	6	17.04	1.51	-	-
July	6	16.36	1.64	-	-
August	6	13.92	2.08	-	-
September	6	11.16	2.23	-	-
October	6	10.97	2.28	-	-
November	6	-	-	-	-
January	6	5.28	0.98	-	-
February	6	12.69	2.64	-	-
March	6	13.88	1.03	-	-
April	6	9.24	0.93	-	-
Upper	66	10.01	0.66	0.91	1.47
April	6	14.40	1.95	1.74	3.99
May	6	13.31	0.87	1.22	2.83
June	6	10.10	1.60	1.01	0.88
July	6	9.74	0.93	0.99	1.00
August	6	10.36	1.15	0.76	1.05
September	6	10.14	1.49	0.72	1.48
October	6	6.33	1.54	0.53	0.78
November	-	-	-	-	-
January	6	6.18	0.66	0.59	1.01
February	6	15.09	4.79	1.24	1.40
March	6	9.28	1.73	0.72	1.01
April	6	5.14	1.09	0.47	0.66
Mid	66	9.75	0.68	0.86	1.50
April	6	14.84	3.87	1.00	2.77
May	6	17.52	2.30	1.42	3.63
June	6	13.32	0.73	1.47	1.59
July	6	11.09	0.68	1.23	1.44
August	6	10.38	1.23	0.68	1.38
September	6	10.75	1.02	1.26	1.63
October	6	7.91	0.64	0.61	1.78
November	6	-	-	-	-
January	6	3.81	1.07	0.29	0.56
February	6	3.82	1.20	0.37	0.63
March	6	7.63	0.76	0.60	0.45
April	6	6.20	0.48	0.52	0.68
Lower	60	9.18	0.69	1.02	2.54
April	6	15.67	1.13	1.85	7.78
May	6	17.52	1.77	1.68	6.23
June	6	12.34	1.85	1.23	3.19
July	6	9.76	0.63	1.14	1.48

Site	n	µg chl a cm^{-3}	S.E.	C1:C2	C1:C3
August	6	9.21	1.66	0.92	1.75
September	6	7.22	0.86	0.81	0.94
October	6	5.32	0.63	0.54	0.89
November	-	-	-	-	-
January	-	-	-	-	-
February	6	3.30	1.65	0.61	0.52
March	6	5.22	0.33	0.57	0.70
April	6	6.25	1.07	0.67	1.19
Quinns Island	264	9.02	0.50	2.26	2.91
Marsh	66	15.34	1.25	-	-
April	-	-	-	-	-
May	6	21.84	1.80	-	-
June	6	29.34	4.20	-	-
July	6	22.42	3.30	-	-
August	6	14.29	2.46	-	-
September	6	11.88	1.38	-	-
October	6	16.15	1.76	-	-
November	6	26.55	4.40	-	-
January	6	3.06	0.44	-	-
February	6	4.36	0.47	-	-
March	6	5.62	0.93	-	-
April	6	13.28	1.16	-	-
Upper	72	8.60	0.71	2.59	2.93
April	6	5.39	1.22	1.55	1.98
May	6	4.70	0.53	2.56	2.68
June	6	8.42	0.89	3.33	2.13
July	6	5.22	0.34	0.99	1.73
August	6	8.01	0.53	1.83	2.66
September	6	13.40	1.56	3.43	3.15
October	6	20.07	3.45	5.72	8.56
November	6	10.79	1.32	2.30	3.07
January	6	4.48	0.30	1.66	2.17
February	6	5.99	0.40	1.26	1.34
March	6	5.54	0.93	1.91	2.17
April	6	11.24	4.28	4.81	4.15
Mid	66	4.99	0.42	1.68	2.72
April	6	11.54	2.01	4.50	9.97
May	6	5.54	1.31	2.09	3.36
June	6	3.61	0.69	0.70	1.15
July	6	4.92	0.73	1.06	1.38
August	6	6.55	0.61	2.36	2.25
September	6	7.05	0.83	1.42	2.61
October	6	5.20	0.84	1.14	1.67
November	-	-	-	-	-
January	6	0.46	0.46	-	-
February	6	3.82	0.35	1.00	1.08
March	6	2.48	0.28	0.81	1.00
April	6	3.77	0.58	-	-

Site	n	µg chl *a* cm^{-3}	S.E.	C1:C2	C1:C3
Lower	60	7.01	0.93	2.42	3.06
April	6	23.84	4.25	7.88	7.36
May	6	8.73	0.65	3.04	5.51
June	6	3.89	0.43	1.14	1.16
July	6	4.69	0.40	1.75	3.34
August	6	4.65	0.60	1.29	1.91
September	6	3.23	0.81	1.02	3.78
October	6	9.40	3.26	3.89	1.71
November	-	-	-	-	-
January	-	-	-	-	-
February	6	5.01	0.72	1.78	1.68
March	6	3.07	0.40	1.11	1.91
April	6	3.66	0.63	2.23	2.79

APPENDIX B

Number of samples (n), means (µg chl *a* cm^{-3}) and standard errors (S.E.) for chlorophyll *a* samples from survey and validation sites, and predicted values of gross primary production (GPP). Predictions were generated from equation 1 of Table 21.

Site	n	μg chl *a* cm^{-3}	S.E.	GPP mg C m^{-2} hr^{-1}
Rocky Point**	6	8.54	1.16	24.14
Grays Point**	6	5.83	0.46	16.69
Brush Island+	12	9.47	1.05	26.70
Upper	6	12.59	0.99	35.27
Lower	6	6.36	0.17	18.13
Clatsop Airport	18	15.57	3.37	43.49
Upper**	6	31.69	5.70	87.85
Lower	12	7.51	1.15	21.31
July	6	6.47	2.07	18.43
August	6	8.56	0.92	24.19
Daggett Point	12	6.93	0.64	19.70
Lower	12	6.93	0.64	19.70
July	6	7.70	0.74	21.82
August	6	6.16	1.00	17.57
Desdemona Sands**	6	13.21	2.00	36.99
E. Sand Isl. North**	6	7.23	0.89	20.53
E. Sand Isl. Bar**	6	5.82	0.24	16.65
Horseshoe Island	42	14.31	1.29	40.00
Marsh	12	11.67	2.14	32.76
July	6	16.26	2.94	45.37
August	6	7.09	1.76	20.14
Upper	18	17.41	2.35	48.54
May	6	25.60	4.23	71.10
July	6	19.77	0.67	55.04
August	6	6.85	1.06	19.49

* = Upper, May

** = Upper, June

\+ = May

Site	n	µg chl a cm^{-3}	S.E.	GPP mg C m^{-2} hr^{-1}
Lower	12	12.28	1.46	34.44
July	6	15.70	1.73	43.84
August	6	8.87	1.32	25.03
Ilwaco	36	34.70	1.76	96.13
Marsh	12	39.05	3.65	108.12
July	6	32.97	6.27	91.36
August	6	45.14	2.08	124.87
Upper	12	34.75	2.29	96.27
July	6	38.15	3.85	105.63
August	6	31.35	1.89	86.91
Lower	12	30.29	2.74	83.99
July	6	38.02	2.47	105.27
August	6	22.56	1.76	62.71
Lois Island	42	6.82	0.63	19.39
Marsh	12	7.09	1.33	20.14
July	6	7.76	2.54	22.00
August	6	6.41	1.06	18.28
Upper	18	7.79	1.09	22.06
May	6	11.32	2.53	31.79
July	6	5.72	0.59	16.38
August	6	6.32	1.25	18.02
Lower	12	5.09	0.58	14.64
July	6	4.89	0.21	14.09
August	6	5.29	1.19	15.20
Marsh Island-Bar*	6	6.12	1.08	17.49
Marsh Island-Flat*	6	7.98	0.51	22.60

* = Upper, May

** = Upper, June

+ = May

Site	n	µg chl a cm^{-3}	S.E.	GPP mg C m^{-2} hr^{-1}
Marsh Island-West*	6	8.38	0.80	23.70
McGregor Island*	6	7.70	0.94	21.82
Millers Point**	6	4.53	2.02	13.10
Old Bridge	18	14.20	3.36	39.72
Upper**	6	31.24	5.08	86.61
Lower	12	5.68	0.98	16.27
July	6	7.04	0.93	20.01
August	6	4.32	0.73	12.53
Russian Island-SSW*	6	4.82	0.44	13.91
Russian Island-WSW*	6	6.11	0.95	17.45
Grays Bay Bar-Front**	6	3.66	0.91	10.71
Grays Bay Bar-Mid**	6	6.86	1.51	19.50
Skipanon	36	29.16	3.85	80.89
Marsh	12	43.26	10.22	119.69
July	6	19.49	5.09	54.26
August	6	67.04	14.39	185.12
Upper	12	18.99	2.10	52.90
July	6	16.17	3.68	45.14
August	6	21.81	1.65	60.65
Lower	12	25.23	1.89	70.08
July	6	20.11	1.98	55.97
August	6	30.36	1.15	84.18
Smith Point**	6	23.73	2.68	65.93
Tansy Point**	6	21.97	1.20	61.08

* = Upper, May

** = Upper, June

+ = May

Site	n	μg chl *a* cm^{-3}	S.E.	GPP mg C m^{-2} hr^{-1}
W. Sand Isl.-East	42	18.52	1.53	51.61
Marsh	12	26.96	3.35	74.82
July	6	36.05	3.45	99.85
August	6	17.86	2.11	49.80
Upper	18	18.59	1.56	51.80
June	6	23.04	2.78	64.04
July	6	12.03	1.62	33.73
August	6	20.71	1.04	57.62
Lower	12	9.99	0.76	28.12
July	6	10.21	1.14	28.73
August	6	9.76	1.12	27.50
W. Sand Isl.-West**	6	36.64	1.71	101.48
W. Sand Isl.-North**	6	22.81	1.59	63.42
W. Sand Isl.-South**	6	1.80	0.19	5.57
Woody Island	42	3.30	0.57	9.73
Marsh	12	2.03	0.37	6.22
July	6	1.80	0.24	5.58
August	6	2.26	0.73	6.86
Upper	18	5.13	1.18	14.76
May	6	11.23	1.20	31.54
July	6	0.96	0.11	3.27
August	6	3.21	1.04	9.46
Lower	12	1.84	0.31	5.68
July	6	1.50	0.24	4.77
August	6	2.17	0.57	6.60

* = Upper, May

** = Upper, June

\+ = May

APPENDIX C

Relative abundance of diatom taxa encountered in 56 samples from the Columbia River Estuary. Relative abundance is expressed as a percentage of the total number of valves counted for each region and for all samples pooled and treated as one collection. The number of samples pooled in each region is indicated in parentheses below the regional acronym. The regions are Baker Bay (BB), Youngs Bay (YB), Cathlamet Bay (CB), Grays Bay (GB), Upper Estuary (UE), Clatsop Spit Phytoplankton (CSP), Tongue Point Phytoplankton (TPP), Puget Island Phytoplankton (PIP) and Youngs River Phytoplankton (YRP). The letters a and r indicate that a taxon was absent or rare, respectively, in the set of samples under consideration.

Taxon	Sediment Samples					Plankton				Pooled Samples
	BB (6)	YB (6)	CB (12)	GB (11)	UE (14)	CSP (2)	TPP (2)	PIP (1)	YRP (2)	(56)
Achnanthes clevei Grun.	a	a	0.6	0.8	1.1	a	a	a	a	0.6
A. deflexa Reim.	a	0.1	0.7	0.4	0.7	a	0.3	a	2.9	0.5
A. hauckiana Grun.	28.7	9.6	4.3	1.4	4.6	0.3	a	a	0.5	6.5
A. hauckiana v. rostrata Schulz	a	0.1	0.2	0.2	1.5	a	a	a	a	0.5
A. lanceolata Grun.	0.1	0.3	1.7	2.2	3.3	0.5	a	a	0.8	1.7
A. lemmermanni Hust.	16.4	a	0.7	0.5	0.5	a	a	a	a	2.1
A. minutissima Kutz.	a	0.3	0.9	0.5	0.9	a	a	a	1.1	0.6
Actinocyclus ehrenbergi Ralfs	a	a	a	a	a	0.7	a	a	a	r
Actinoptychus undulatus (Bail.) Ralfs	a	a	a	a	a	0.3	a	a	a	r
Amphora angustata Greg.	a	a	a	a	a	0.5	a	a	a	r
A. coffeiformis (Ag.) Kutz.	a	0.2	r	a	a	a	a	a	a	r
A. micrometra Giff.	1.7	a	a	a	a	a	a	a	a	0.2
A. ovalis (Kutz) Kutz.	a	0.2	6.4	0.2	0.2	a	a	a	a	1.5
A. ovalis v. pediculus (Kutz) V.H. ex D.T.	0.1	0.1	1.2	2.1	0.7	0.2	a	a	0.5	0.9

Taxon	Sediment Samples					Plankton				Pooled Samples
	BB (6)	YB (6)	CB (12)	GB (11)	UE (14)	CSP (2)	TPP (2)	PIP (1)	YRP (2)	(56)
A. sabyii Salah	1.1	a	a	a	a	a	a	a	a	0.1
A. tenerrima Al. & Hust.	0.2	a	a	a	a	a	a	a	a	r
Asterionella formosa Hass.	0.3	10.6	7.9	16.6	13.9	23.1	30.8	2.6	8.0	11.8
Asteromphalus heptactis (Breb.) Ralfs	a	a	a	a	a	0.2	a	a	a	r
Bacillaria paxillifer (O.F. Mull.) Hend.	0.2	0.6	r	a	0.2	0.2	a	a	0.2	0.2
Bacteriastrum delicatulum Cl.	a	a	a	a	a	0.8	a	a	a	r
Berkeleya rutilans (Trent.) Grun.	0.3	a	a	a	a	a	a	a	a	r
Biddulphia longicruris Grev.	a	a	a	a	a	0.2	a	a	a	r
Campylosira cymbelliformis (A. Sch.) Grun. ex V.H.	a	a	a	a	a	a	a	a	0.3	r
Chaetoceros decipiens Cl.	a	a	a	a	a	9.8	a	a	a	0.4
C. radicans Schutt	a	a	a	a	a	0.5	a	a	a	r
C. subtile Cl.	a	a	a	a	a	a	a	a	0.5	r

Taxon	Sediment Samples					Plankton				Pooled Samples
	BB (6)	YB (6)	CB (12)	GB (11)	UE (14)	CSP (2)	TPP (2)	PIP (1)	YRP (2)	(56)
Cocconeis placentula v. euglypta (Ehr.) Cl.	a	a	0.2	a	a	0.2	a	a	0.7	0.1
C. no. 1	a	1.3	3.4	2.1	3.9	a	a	a	0.2	2.3
C. no. 2	0.9	0.4	0.3	1.7	2.3	a	a	a	a	1.1
C. no. 3	0.1	0.1	1.3	2.4	0.1	a	a	a	a	0.8
Coscinodiscus apicutulus Ehr.	a	a	a	a	a	0.2	a	a	a	r
C. curvatulus Grun.	a	a	a	a		1.0	a	a	a	r
C. perforatus v. cellulosa Grun.	a	a	a	a	a	16.7	0.3	a	a	0.6
Cyclotella no. 1	0.2	0.3	1.4	0.8	1.0	0.5	0.7	a	8.3	1.1
C. no. 2	a	0.1	0.1	r	0.1	a	a	a	4.2	0.2
Cylindrotheca closterium (Ehr.) Reim. & Lewin	a	a	a	a	a	a	a	a	0.3	r
C. gracilus (Breb.) Grun.	0.1	0.1	a	0.6	0.8	0.2	a	a	a	0.3
Cymbella cuspidata Kutz.	a	a	a	r	a	a	a	a	a	r
C. minuta Hilse ex Rabh.	a	0.1	0.1	0.1	0.1	a	a	0.3	0.2	0.1
C. sinuata Greg.	a	0.1	a	0.1	r	a	a	a	0.3	r

Taxon	Sediment Samples					Plankton				Pooled Samples
	BB (6)	YB (6)	CB (12)	GB (11)	UE (14)	CSP (2)	TPP (2)	PIP (1)	YRP (2)	(56)
Cymbellonitzschia diluviana Hust.	a	a	a	r	r	a	a	a	a	r
Diatoma hiemale v. mesodon (Ehr.) Grun.	a	a	a	a	0.1	a	a	a	a	r
D. tenue As.	a	0.1	a	a	a	a	a	a	a	r
D. tenue v. elongatum Lyngb.	0.2	1.6	1.2	1.3	1.7	1.0	0.7	a	0.5	1.2
D. vulgare v. breve Grun.	a	a	a	0.1	0.1	a	a	a	a	r
Diploneis subovalis Cl.	a	a	r	a	r	a	a	a	a	r
Dityum brightwellii (West) Grun.	a	a	a	a	a	0.5	a	a	a	r
Eucampia zoodiacus Ehr.	a	a	a	a	a	0.2	a	a	a	r
Eunotia pectinalis (O.F. Mull.) Rabh.	a	a	a	r	a	a	a	a	0.2	r
E. perpusilla Grun.	a	a	a	a	a	a	a	a	0.2	r
Fragilaria brevistriata Grun.	a	0.1	0.5	0.2	1.3	a	a	a	a	0.5
F. construens (Ehr.) Grun.	0.3	a	0.1	0.2	0.1	a	a	a	a	0.1

Taxon	Sediment Samples					Plankton				Pooled Samples
	BB (6)	YB (6)	CB (12)	GB (11)	UE (14)	CSP (2)	TPP (2)	PIP (1)	YRP (2)	(56)
F. crotonensis Kitton	0.2	3.4	1.7	1.5	3.2	3.9	9.0	40.0	0.8	3.1
F. leptostauron (Ehr.) Hust.	a	a	0.1	a	r	a	a	a	a	r
F. pinnata Ehr.	1.0	4.2	2.5	3.0	2.0	0.2	a	a	1.6	2.2
F. vaucheriae (Kutz.) Peters	0.1	0.1	0.7	0.1	0.4	0.5	0.2	a	0.3	0.3
Frustulia rhomboides (Ehr.) D.T.	a	a	a	r	a	a	a	a	a	r
Gomphonema grovei M. Sch.	a	a	a	a	r	a	a	a	a	r
G. parvulum (Kutz.) Grun.	a	0.1	0.1	0.3	0.2	a	a	a	0.8	0.2
Gyrosigma fasciola (Ehr.) Giff. & Henfr.	a	2.2	a	a	a	a	a	a	0.2	0.3
G. hummii Hust.	a	0.2	a	a	a	a	a	a	a	r
G. wormleyi (Sullv.) Boyer	a	a	a	a	0.2	a	a	a	a	r
G. no. 1	0.1	a	r	a	0.2	a	a	a	a	0.1
Hannaea arcus (Ehr.) Patr.	a	a	a	a	a	a	a	a	0.2	r
Hantzschia distincte-punctata Hust.	a	a	1.0	a	r	a	a	a	a	0.2
H. cf. marina (Donk.) Grun.	a	a	0.3	a	a	a	a	a	a	0.1

Taxon	Sediment Samples					Plankton				Pooled Samples
	BB (6)	YB (6)	CB (12)	GB (11)	UE (14)	CSP (2)	TPP (2)	PIP (1)	YRP (2)	(56)
Melosira granulata (Ehr.) Ralfs	a	1.0	1.0	0.7	2.3	1.1	8.7	10.2	0.8	1.6
M. italica (Ehr.) Kutz.	0.1	14.8	2.5	2.6	4.3	8.6	36.8	44.9	9.2	6.5
M. nummuloides (Dillw.) C.A. Ag.	a	0.4	a	a	a	a	a	a	a	0.1
M. varians C.A. Ag.	a	a	0.2	0.1	0.4	0.2	a	a	a	0.2
Meridion circulare (Grev.) Ag.	a	a	0.1	r	0.1	a	a	a	a	r
Navicula arenaria Donk.	a	a	1.3	a	0.6	a	a	a	a	0.4
N cf. arvensis Hust.	5.1	a	a	a	a	0.2	a	a	a	0.6
N. aurora Sov.	a	a	0.3	0.1	r	a	a	a	a	0.1
N. bacillum Ehr.	a	a	0.2	a	a	a	a	a	a	r
N. capitata Ehr.	a	0.2	1.3	0.6	0.4	a	a	a	a	0.5
N. capitata v. hungarica (Grun.) Ross	a	0.3	3.9	2.1	1.1	a	a	a	1.5	1.6
N. cryptocephala Kutz.	2.7	7.0	r	a	r	0.2	a	a	1.9	1.1
N. cryptocephala v. veneta (Kutz.) Rabh.	a	a	a	0.1	a	a	a	a	a	r

Taxon	Sediment Samples					Plankton				Pooled Samples
	BB (6)	YB (6)	CB (12)	CB (11)	UE (14)	CSP (2)	TPP (2)	PIP (1)	YRP (2)	(56)
N. decussis Ostr.	0.1	0.1	0.9	a	0.2	a	a	a	a	0.3
N. diserta Hust.	9.3	0.4	a	a	a	a	a	a	a	0.1
N. dissipata Hust.	1.1	a	a	a	a	a	a	a	a	0.1
N. gastrum (Ehr.) Kutz.	a	a	0.5	0.2	0.1	a	a	a	a	0.2
N. gregaria Donk.	0.6	1.4	9.4	2.6	7.5	0.3	0.3	a	1.9	6.7
N. lanceolata (Ag.) Kutz.	a	a	a	a	a	a	0.3	a	0.3	r
N. minima Grun.	a	a	0.2	1.5	0.4	a	a	a	a	0.5
N. mutica Kutz.	a	0.4	0.4	a	0.4	0.2	a	a	0.7	0.3
N. placentula (Ehr.) Kutz.	a	a	1.3	a	a	a	a	a	a	0.3
N. protracta Grun.	a	a	0.1	r	a	a	a	a	a	r
Navicula arenaria Donk.										
N. pupula Kutz.	a	a	0.2	a	a	a	a		0.2	r
N. pygmaea Kutz.	3.8	0.4	a	a	r	a	a	a	a	0.5
N. radiosa Kutz.	a	a	0.1	0.4	0.1	a	a	a	a	0.1
N. reinhardtii v. elliptica Herib.	a	a	0.2	0.4	0.1	a	a	a	a	0.1

Taxon	Sediment Samples					Plankton				Pooled Samples
	BB (6)	YB (6)	CB (12)	GB (11)	UE (14)	CSP (2)	TPP (2)	PIP (1)	YRP (2)	(56)
N. salinarum Grun.	a	1.0	a	a	a	a	a	a	0.2	0.1
N. salinicola Hust.	10.6	a	a	a	a	a	a	a	a	1.1
N. schonfeldii Hust.	a	a	a	0.1	a	a	a	a	a	r
N. scutelloides W. Sm. ex Greg.	a	a	a	r	a	a	a	a	a	r
N. submuralis Hust.	0.1	0.1	13.6	25.1	7.2	a	0.2	a	a	9.7
N. tenuipunctata Hust.	a	a	2.6	0.3	0.1	a	a	a	a	0.7
N. viridula v. avenacea (Breb. ex Grun.) V.H.	a	a	a	a	r	a	a	a	a	r
N. viridula v. rostellata (Kutz.) Cl.	a	a	a	r	a	a	a	a	a	r
N. no. 2	0.1	0.1	0.3	0.4	1.4	0.2	a	a	0.5	0.5
N. no. 3	2.6	a	a	a	a	a	a	a	a	0.3
N. no. 4	0.4	0.2	0.3	0.5	1.0	a	a	a	a	0.5
Neidium iridis (Ehr.) Cl.	a	a	a	a	r	a	a	a	a	r
Nitzschia acuminata (W. Sm.) Grun.	0.1	a	a	a	a	a	a	a	a	r

Taxon	Sediment Samples					Plankton				Pooled Samples
	BB (6)	YB (6)	CB (12)	GB (11)	UE (14)	CSP (2)	TPP (2)	PIP (1)	YRP (2)	(56)
N. amphibia Grun.	0.1	a	0.1	a	0.1	0.2	0.2	a	0.2	0.1
N. angustata (W. Sm.) Grun.	a	0.3	a	0.6	r	a	a	a	a	0.2
N. apiculata (W. Sm.) Grun.	a	0.1	0.1	0.1	0.1	a	a	a	a	0.1
N. dissipata (Kutz.) Grun.	0.4	0.9	0.5	0.6	0.7	0.3	0.3	a	0.2	0.6
N. frustulum v. perpusilla (Rabh.) Grun.	2.6	1.4	2.8	1.5	2.4	0.8	0.5	0.3	0.5	2.0
N. hungarica Grun.	a	7.8	a	a	a	a	a	a	0.3	0.8
N. linearis W. Sm.	a	a	a	a	0.2	a	a	a	a	r
N. longissima (Breb.) Ralfs	a	a	a	a	a	a	a	a	0.2	r
N. cf. palea (Kutz.) W. Sm.	4.8	6.9	2.0	4.4	6.7	1.0	1.5	a	29.5	5.3
N. parvula Lewis	a	0.3	0.1	0.1	0.1	a	a	a	a	0.1
N. recta Hantz.	a	0.1	0.1	a	0.4	a	a	a	a	0.1
N. seriata Cl.	a	a	a	a	a	0.7	a	a	a	r
N. sigma (Kutz.) W. Sm.	a	0.2	0.1	0.3	0.5	0.2	a	a	0.2	0.2
N. sigma v. sigmatella Grun.	0.1	2.1	a	a	a	a	a	a	a	0.2

Taxon	Sediment Samples					Plankton				Pooled Samples
	BB (6)	YB (6)	CB (12)	GB (11)	UE (14)	CSP (2)	TPP (2)	PIP (1)	YRP (2)	(56)
N. subhybrida Hust.	0.1	0.7	a	a	a	a	a	a	0.7	0.1
cf. sublinearis Hust.	0.1	0.7	0.1	a	0.1	a	a	a	a	0.1
Nitzschia acuminata										
N. tryblionella v. subsalina Grun.	a	a	a	a	a	a	a	a	0.5	r
N. tryblionella v. victoriae Grun.	a	1.0	0.1	0.2	0.1	a	a	a	a	0.2
N. no. 1	a	0.3	0.1	a	a	a	a	a	a	r
Opephora martyi Herib.	0.9	0.2	0.3	1.1	0.3	a	a	a	a	0.5
O. schulzi (Brock.) Simon.	0.8	1.5	a	a	a	a	a	a	0.2	0.3
Rhaphoneis amphiceros Ehr.	a	a	a	a	a	0.9	a	a	a	r
R. psammicola Riz.	a	a	a	a	a	0.2	a	a	a	r
Rhoicosphenia curvata (Kutz.) Grun. ex Rabh.	a	0.2	0.3	a	0.2	0.2	0.2	a	0.3	0.1
Skeletonema costatum (Grev.) Cl.	a	0.1	a	a	a	7.8	a	a	a	0.3
Stauroneis spicula Hick.	a	1.2	a	a	a	a	a	a	a	0.1

Taxon	Sediment Samples					Plankton				Pooled Samples
	BB (6)	YB (6)	CB (12)	GB (11)	UE (14)	CSP (2)	TPP (2)	PIP (1)	YRP (2)	(56)
Stephanodiscus astraea (Ehr.) Grun.	a	a	0.2	a	0.1	0.7	0.7	0.7	1.3	0.2
S. no. 1	0.1	2.0	1.9	2.6	2.2	5.8	3.4	0.3	7.6	2.3
S. no. 2	1.3	7.0	10.2	6.0	11.7	6.8	4.2	a	2.6	7.6
Stephanopyxis palmeriana (Grev.) Grun.	a	a	a	a	a	0.2	a	a	a	r
Surirella angustata Kutz.	a	a	0.1	r	0.1	a	a	a	a	r
S. gemma Ehr.	0.1	a	a	a	a	a	a	a	a	r
Surirella angustata Kutz.										
S. linearis W. Sm.	a	a	a	a	0.1	a	a	a	a	r
S. ovata Kutz	a	0.1	0.6	0.5	0.3	a	a	a	4.7	0.5
S. cf. robusta Ehr.	a	0.2	a	a	0.1	a	a	a	a	0.1
S. suecica Grun.	a	0.1	r	a	0.3	a	a	a	a.	0.1
Synedra acus Kutz.	a	a	a	r	a	a	a	a	a	r
S. berolinensis Lemm.	a	0.1	a	a	0.1	1.3	0.2	a	0.5	0.1

Taxon	Sediment Samples					Plankton				Pooled Samples
	BB (6)	YB (6)	CB (12)	GB (11)	UE (14)	CSP (2)	TPP (2)	PIP (1)	YRP (2)	(56)
S. capitata Ehr.	a	a	a	a	r	a	a	a	a	r
S. fasciculata v. truncata (Grev.) Patr.	a	a	0.1	a	a	a	a	a	a	r
S. rumpens v. meneghiniana Grun.	a	0.2	0.2	a	0.1	a	a	a	a	0.1
S. ulna (Nitz.) Ehr.	a	0.3	0.2	0.1	0.6	0.5	0.2	0.3	0.2	0.3
Tabellaria fenestrata (Lyngb.) Kutz.	a	0.2	0.1	r	0.1	a	0.3	0.3	a	0.1

APPENDIX D

Means of gross primary production, chlorophyll *a* concentration, oxygen consumption and ash-free dry weight for respirometer cores obtained at the intensive study sites.

Site	Gross Primary Production mg C m^{-2} hr^{-1}	mg chl *a* m^{-2}	Oxygen Consumption mg O_2 m^{-2} hr^{-1}	g ash-free dry wt m^{-2}
Clatsop Spit	5.22	13.27	18.05	61.73
Upper	4.07	10.27	11.65	56.56
May	13.71	14.00	27.00	51.14
June	0.35	3.80	11.29	75.00
July	-	-	-	-
August	2.67	1.40	8.51	55.69
September	6.14	5.60	7.92	71.96
October	0.00	26.40	0.00	68.12
November	0.00	6.80	0.00	51.72
February	0.00	4.40	0.00	32.98
March	4.16	11.97	24.98	52.38
April	9.64	18.03	25.16	50.08
Lower	6.50	16.66	25.24	67.54
May	0.00	6.90	3.00	72.48
June	0.46	10.70	16.65	59.52
July	-	-	-	-
August	6.64	14.10	21.30	92.20
September	0.00	0.00	11.76	58.99
October	0.04	46.30	0.00	75.79
November	-	-	-	-
February	0.00	14.20	14.05	48.01
March	21.15	9.48	56.42	75.79
April	23.72	31.57	81.76	57.50
Youngs Bay	84.22	262.92	66.55	196.31
Marsh	95.11	272.19	66.84	225.37
May	429.67	278.60	138.23	326.72
June	41.66	373.00	86.23	375.26
July	73.15	242.00	78.36	245.77
August	79.30	296.70	99.80	181.08
September	30.64	288.40	48.96	226.99
October	123.37	426.40	80.30	243.65
November	5.38	298.53	8.62	191.93
February	16.49	142.70	43.96	153.57
March	82.58	143.08	43.06	218.65
April	68.82	232.50	40.83	90.08
Upper	88.82	298.56	81.26	191.24
May	119.08	420.80	94.85	353.57
June	89.44	301.00	89.75	308.73
July	82.15	206.20	91.36	149.73
August	47.39	215.80	63.57	152.25
September	171.58	623.50	185.78	142.06
October	155.55	294.70	76.20	203.04
November	58.83	311.65	68.93	194.05
February	27.21	189.60	52.75	134.74
March	69.61	210.07	43.40	166.14
April	67.39	212.30	46.01	108.07
Lower	67.00	213.01	49.88	169.66
May	72.91	196.40	0.30	230.29

Site	Gross Primary Production mg C m^{-2} hr^{-1}	mg chl *a* m^{-2}	Oxygen Consumption mg O_2 m^{-2} hr^{-1}	g ash-free dry wt m^{-2}
June	81.97	186.60	87.72	236.50
July	93.37	218.50	87.78	126.59
August	74.17	193.30	73.71	146.43
September	110.78	363.40	81.30	179.89
October	76.08	189.90	51.00	196.56
November	-	-	-	-
February	0.00	145.30	0.00	168.06
March	34.85	201.98	25.25	153.31
April	58.85	221.75	41.83	89.29
Baker Bay	42.50	223.16	60.37	247.05
Marsh	37.83	240.76	70.14	294.22
May	61.27	261.80	127.76	321.69
June	49.05	207.70	100.04	384.13
July	23.32	208.50	70.93	279.50
August	14.93	285.00	52.66	327.51
September	45.64	148.30	63.81	239.81
October	55.72	209.20	68.80	363.62
November	45.80	214.28	65.79	345.50
February	0.00	302.20	32.82	278.57
March	45.67	293.50	50.18	205.55
April	36.87	277.13	68.58	196.29
Upper	55.11	281.62	63.38	224.43
May	51.88	262.30	72.46	249.07
June	94.29	282.60	107.29	311.38
July	99.15	226.10	107.96	254.76
August	58.84	270.50	77.69	185.18
September	60.73	184.80	88.90	218.12
October	77.43	183.50	54.91	295.50
November	26.27	290.53	28.06	213.62
February	0.00	388.70	16.41	189.28
March	59.09	339.15	50.18	179.10
April	23.38	388.03	29.90	148.28
Lower	33.69	138.65	46.19	219.78
May	70.07	140.00	72.30	334.92
June	81.19	220.50	92.12	323.28
July	7.23	94.20	43.82	233.46
August	58.22	103.20	57.22	182.14
September	36.77	102.50	51.10	163.89
October	24.31	187.70	31.59	217.06
November	-	-	-	-
February	0.00	167.90	8.21	192.86
March	7.83	137.80	25.09	208.33
April	17.59	94.03	34.29	122.09
Grays Bay	33.01	123.28	44.83	195.62
Marsh	41.17	130.06	51.79	221.01
May	38.78	148.70	70.53	239.02
June	32.58	151.70	25.08	424.34
July	109.62	169.60	72.00	286.77

Site	Gross Primary Production mg C m^{-2} hr^{-1}	mg chl *a* m^{-2}	Oxygen Consumption mg O_2 m^{-2} hr^{-1}	g ash-free dry wt m^{-2}
August	40.93	172.30	86.40	208.99
September	0.00	93.50	18.93	177.25
October	25.35	131.20	29.16	257.50
November	-	-	-	-
February	37.22	104.60	67.58	162.30
March	79.37	100.50	79.94	93.12
April	6.65	98.48	16.48	139.81
Upper	33.20	115.45	39.16	170.94
May	36.75	145.30	52.22	178.57
June	20.14	108.40	16.71	225.53
July	40.00	89.80	23.09	152.51
August	42.71	132.10	60.24	140.87
September	22.38	116.70	19.14	177.65
October	26.82	145.90	29.16	268.12
November	-	-	-	-
February	42.69	101.90	50.68	158.20
March	55.22	114.53	79.94	107.01
April	12.09	84.38	21.25	130.03
Lower	24.66	124.34	43.55	194.91
May	77.90	348.30	104.65	290.61
June	15.84	115.00	16.59	240.87
July	20.83	86.20	19.60	223.81
August	25.22	99.70	50.76	159.39
September	6.57	91.70	42.94	143.12
October	0.00	116.20	41.00	233.33
November	-	-	-	-
February	31.94	100.30	50.68	199.60
March	36.97	90.80	53.30	149.87
April	6.66	70.85	12.45	113.62
Quinns Island	29.56	103.66	41.25	150.84
Marsh	44.44	163.55	57.99	246.70
May	74.08	211.70	124.69	442.50
June	32.53	208.60	26.72	393.39
July	37.24	151.10	63.44	210.32
August	25.75	175.40	59.58	227.05
September	31.39	111.30	60.30	243.78
October	74.26	271.20	51.70	283.47
November	39.78	67.80	105.36	228.04
February	0.00	54.00	0.00	192.06
March	41.44	59.78	35.17	106.22
April	87.97	324.65	52.89	140.21
Upper	29.91	93.34	34.29	93.51
May	13.74	41.70	8.87	86.51
June	7.46	57.20	15.93	99.12
July	17.40	51.10	21.16	95.63
August	28.70	107.80	34.20	78.57
September	108.53	142.50	82.20	145.37
October	86.24	126.40	38.77	113.23
November	22.61	140.65	58.43	111.64

Site	Gross Primary Production mg C m^{-2} hr^{-1}	mg chl *a* m^{-2}	Oxygen Consumption mg O_2 m^{-2} hr^{-1}	g ash-free dry wt m^{-2}
February	0.00	147.40	0.00	50.40
March	3.58	56.80	61.54	85.98
April	10.84	61.83	21.82	68.65
Lower	12.63	48.59	30.40	108.02
May	0.21	78.80	33.86	117.46
June	0.00	31.80	17.44	128.57
July	15.97	26.20	17.18	107.65
August	20.12	57.90	36.72	142.72
September	42.46	55.80	57.70	115.21
October	21.77	39.80	26.85	134.65
November	-	-	-	-
February	0.00	58.40	0.00	72.75
March	3.32	38.18	52.75	85.58
April	9.79	50.40	31.08	67.59