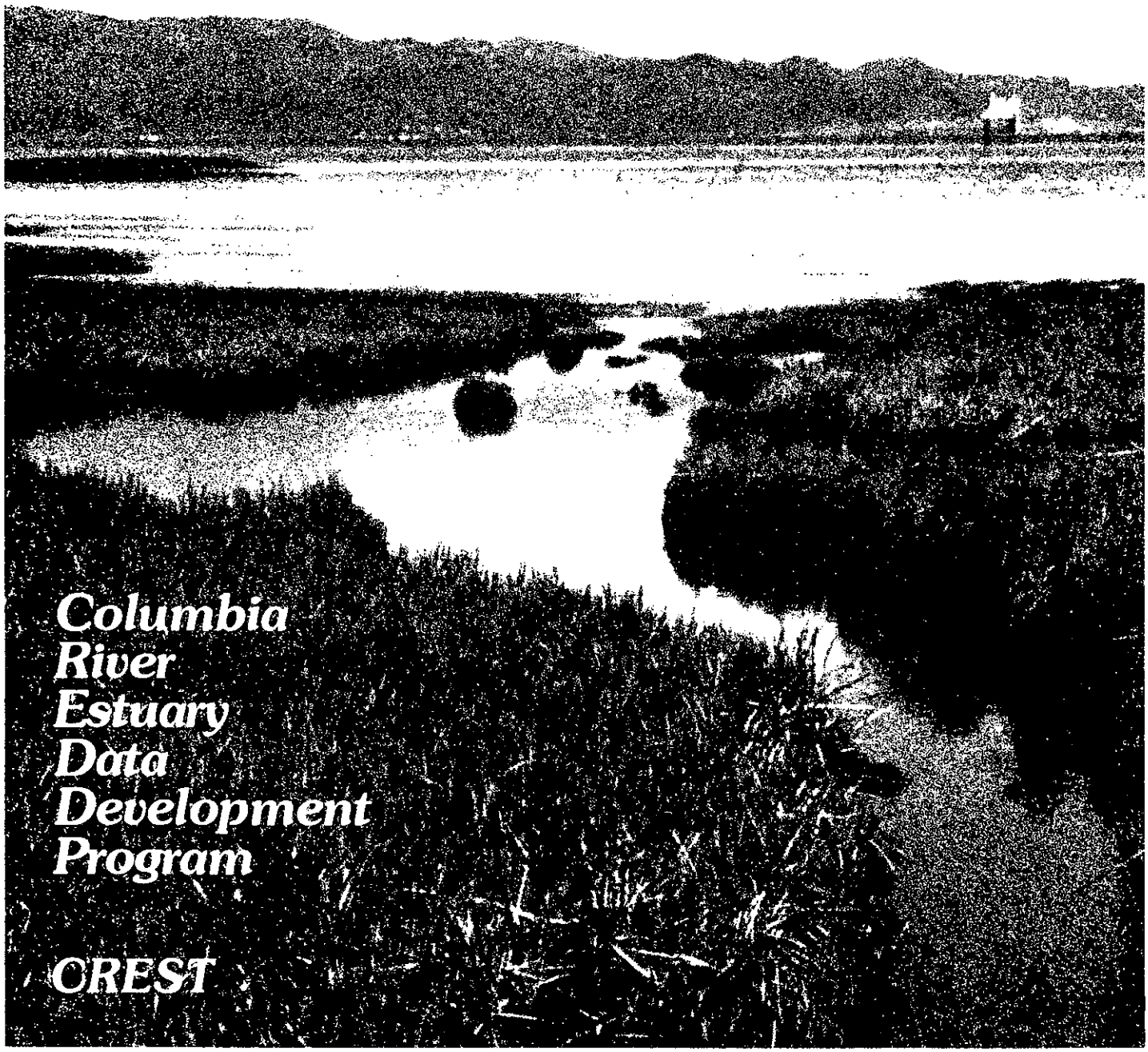
WATER COLUMN PRIMARY PRODUCTION IN THE COLUMBIA RIVER ESTUARY



Final Report on the Water Column Primary Production Work Unit of

the Columbia River Estuary Data Development Program

WATER COLUMN PRIMARY PRODUCTION

IN THE COLUMBIA RIVER ESTUARY

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February 1984

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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

This report on water column primary production in the Columbia River Estuary was prepared for the Columbia River Data Development Program by Drs. Bruce E. Frey and Lawrence F. Small of the College of Oceanography, Oregon State University, Corvallis, Oregon, and Dr. Ruben Lara-Lara, of the Centro de Investigacion Cientifica y Educacion Superior de Ensenada, Ensenada, Mexico. Also participating in this project were Ms. RaeDeane Leatham and Mr. Stanley Moore.

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EXECUTIVE SUMMARY

This program was designed to study the water column primary production of the Columbia River Estuary, and the factors affecting primary production. Primary production, or photosynthesis, is carried out in the water column chiefly by small, free-floating algal cells which constitute the phytoplankton. Obtaining energy from sunlight, and using inorganic raw materials, the phytoplankton produce organic compounds to increase their own cell numbers. The phytoplankton become food for planktonic animals (the zooplankton) which in turn become food for larger animals. Thus the phytoplankton constitute the base of most marine and aquatic food webs. In the Columbia River Estuary, detritus (non-living organic particles) may also be a significant food source for zooplankton.

Prior to our CREDDP study there had been very little research on primary production and the base of the food web in either the Columbia River Estuary or the Columbia River itself. This is remarkable considering the importance of the Columbia River as the second largest river in the United States. Our overall objectives were to describe the yearly cycle of abundance and distribution of the primary food supply (particularly phytoplankton) in the waters of the Columbia River Estuary, and to assess the physical, chemical, and biological factors affecting the primary food supply.

During an eighteen-month period, ten cruises were conducted in the CREDDP study area on the Columbia River Estuary, using the research vessels Sacajawea, Cathlamet Bay, and Tenasillahe. Samples were collected from up to 52 stations per cruise, using a submersible pump system to deliver samples from depth. Some determinations were made aboard at the time of collection, while others were conducted later in our Corvallis laboratories. In addition to obtaining information on the normal cycles of events relating to phytoplankton in the estuary, interesting data were collected concerning the effects of the May 1980 eruption of nearby Mt. Saint Helens on the estuarine ecosystem.

It was determined that light is the most important factor limiting primary production in the Columbia River Estuary. Both the intensity of incident light reaching the water surface, and the attenuation of light within the water column are critical in determining the rates of primary production per unit of plant biomass. Of the major plant nutrients (nitrogen, phosphorus, and silica), only nitrogen appears to ever become depleted to the point where it might limit phytoplankton growth. This occurs in late spring and summer.

Import from the upstream Columbia River, as opposed to <u>in situ</u> production, is the most important factor in determining the abundance of phytoplankton in the waters of the estuary. On a yearly basis, we estimate that 75% of the phytoplankton in the estuary is supplied by the Columbia River, while only 25% is produced <u>in situ</u>. The

phytoplankton species in the estuary are dominated by freshwater diatoms. Smaller nanoplankton dominated over larger netplankton.

The concentrations of both chlorophyll a and freshwater diatoms decreased from the freshwater zone to the marine zone. Apparently as freshwater phytoplankton mix rapidly with saline water the increased osmotic pressure destroys the cells. For properties other than phytoplankton concentrations, the estuary acts as a conduit for export from the Columbia River to the Pacific Ocean, with little change occurring within the estuary itself. This is doubtless due to the low residence time of water in the estuary (one to five days), and the high turbulence of the system, which allows little sinking to occur. All measured properties were vertically homogeneous in the freshwater portions of the estuary. Where the salt wedge was encountered, properties were stratified as a result of the marine-source water intrusion at depth.

Of the total particulate organic carbon in the estuarine water column, about 75% is detrital and 25% is live phytoplankton. About 63% of the phytoplankton is lost within the estuary, and the remainder is exported to the Pacific Ocean. Zooplankton grazing removal of phytoplankton amounts to only about 1% per day of the available phytoplankton biomass.

The eruption of Mt. Saint Helens on May 18, 1980 added large amounts of particulate material to the waters of the Columbia River Estuary. This in turn greatly reduced the amount of primary production by reducing light penetration in the water. During the five-week period in which the estuary was unusually turbid, we estimate primary production to have been reduced by about 75%. We observed no effect on levels of phytoplankton biomass in the water attributable to this reduction in productivity. This is evidently because phytoplankton biomass levels are affected mostly by import from the Columbia River above the mouth of the Cowlitz River at Longview, Washington, where the St. Helens sediment entered the Columbia River.

1. INTRODUCTION

1.1 GENERAL INTRODUCTION

The Columbia River Estuary is dominated by the Columbia River, the second largest river in North America. The river has an annual discharge of about 2×10^{11} m^3, about 58% that of the Mississippi, and drains a region of 670,000 km^2. River flow varies from about 3,000 to 20,000 $m^3 sec^{-1}$. This results in estuarine flushing times which are estimated to be from 0.5 to 5 days (Neal 1972). The high freshwater flow and rapid flushing times are of major importance in determining the distribution of physical, chemical, and biological properties in the estuary, and in determining the characteristics of primary production (the formation of organic "food" material from inorganic raw materials).

Phytoplankton, microscopic single-celled plants that float freely in the water, are the principal primary producers of most aquatic ecosystems. Also important at the base of aquatic food webs are benthic algae, vascular plants, and detritus. The objectives of our project have been to describe the spatial and temporal variations of phytoplankton suspended in the waters of the Columbia River Estuary, and to evaluate the environmental factors affecting their growth and distribution. Specifically, our research was designed to achieve the following objectives:

1. Describe the spatial and temporal distribution of phytoplankton biomass and other suspended particulate material.

2. Describe the spatial and temporal distributions of the physical and chemical variables which may affect phytoplankton productivity.

3. Determine which environmental factors are important in controlling the distribution and abundance of phytoplankton in the estuary.

4. Evaluate the relative importance of environmental factors causing phytoplankton biomass increase and decrease.

A convenient way to look at an ecosystem is as a multi-tiered complex of producers and consumers through which move various essential commodities. These commodities serve as building blocks and energy sources that enable the individuals comprising the communities within the ecosystem to survive, grow, and reproduce. The ecosystem is made up of plants, animals, bacteria, organic debris, nutrients, and the physical environment in which they all interact in some self-regulating manner. At the base of most ecosystems are the photosynthetic primary producers. The primary energy source which powers practically all ecosystems is solar radiation. However, the only fraction of solar energy which actually becomes available as a commodity in the ecosystem (apart from the physical effects

of solar radiation on temperature and stratification) is the relatively small fraction which is stored by photosynthetic primary producers in forms available to other organisms.

An estuarine ecosystem can be conceptualized as a hierarchical system of biological processes (Overton 1972, 1975; McIntire and Colby 1978), with physical and chemical processes acting as driving functions and control variables (Figures 1 and 2). In this scheme, any process can be partitioned into a system of coupled subprocesses (or considered as a component of some supraprocesses) by identification of relevant coupling variables. Primary food processes include the dynamics of variables associated with the accumulation and removal of particulate organic matter suspended in the water (the primary food supply). This suspended particulate biomass includes both living and detrital fractions. It has been documented that small microcrustacean grazers feed on detritus as well as on phytoplankton cells (Paffenhofer and Strickland 1970; Poulet 1976; Heinle et al. 1977; Chervin 1978), and there is evidence that some water-column suspension feeders consume organic muds (Small et al. 1979). The coupling between the primary food supply and consumer processes (Figure 1) is grazing. During our study, grazing rates of natural zooplankton populations were calculated from field experiments measuring the ingestion of carbon-14-pre-labelled natural phytoplankton populations.

The primary food supply is increased or maintained by primary production in the estaury as well as by particle import to the estuary (Figure 2). Net primary production is the difference between photosynthetic production of organic matter by phytoplankton (gross primary production) and respiratory loss. Respiratory loss at night and from below the photic zone would also be included in the respiration term in Figure 2.

Light and nutrients (Figure 2) are essential inputs for photosynthesis, or primary production, and one or more of these frequently limits or controls growth. Physical processes may affect primary production and the primary food supply by advecting or dispersing particles (currents), by regulating rates of reactions through temperature, or by changing osmotic pressure (salinity), as a few examples.

It has been our hope that a reasonably detailed and coherent picture of the flow of some essential commodities through the ecosystem of the Columbia River Estuary, and the factors regulating the rates of flow, would emerge from CREDDP. There are many different commodities which can be followed along their pathways through the ecosystem. Carbon is universally involved in biological reactions, and its distribution and rates of flux are relatively easy to measure. For these reasons, we feel that carbon is the commodity of choice to follow and, whenever possible, we have tied rates and biomass to units of carbon.

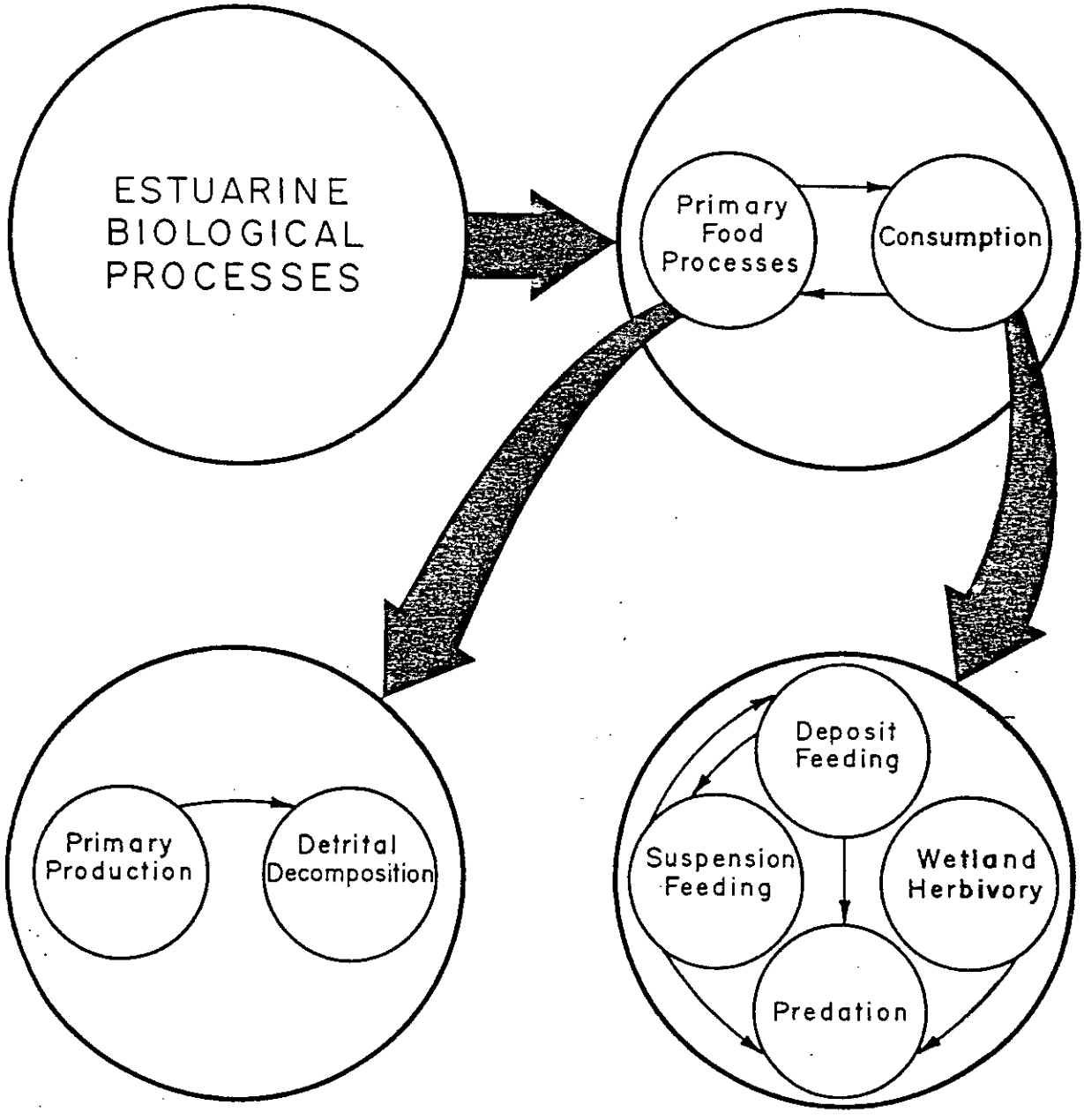


Figure 1. Conceptual framework of estuarine biological processes.

PRIMARY PRODUCTION

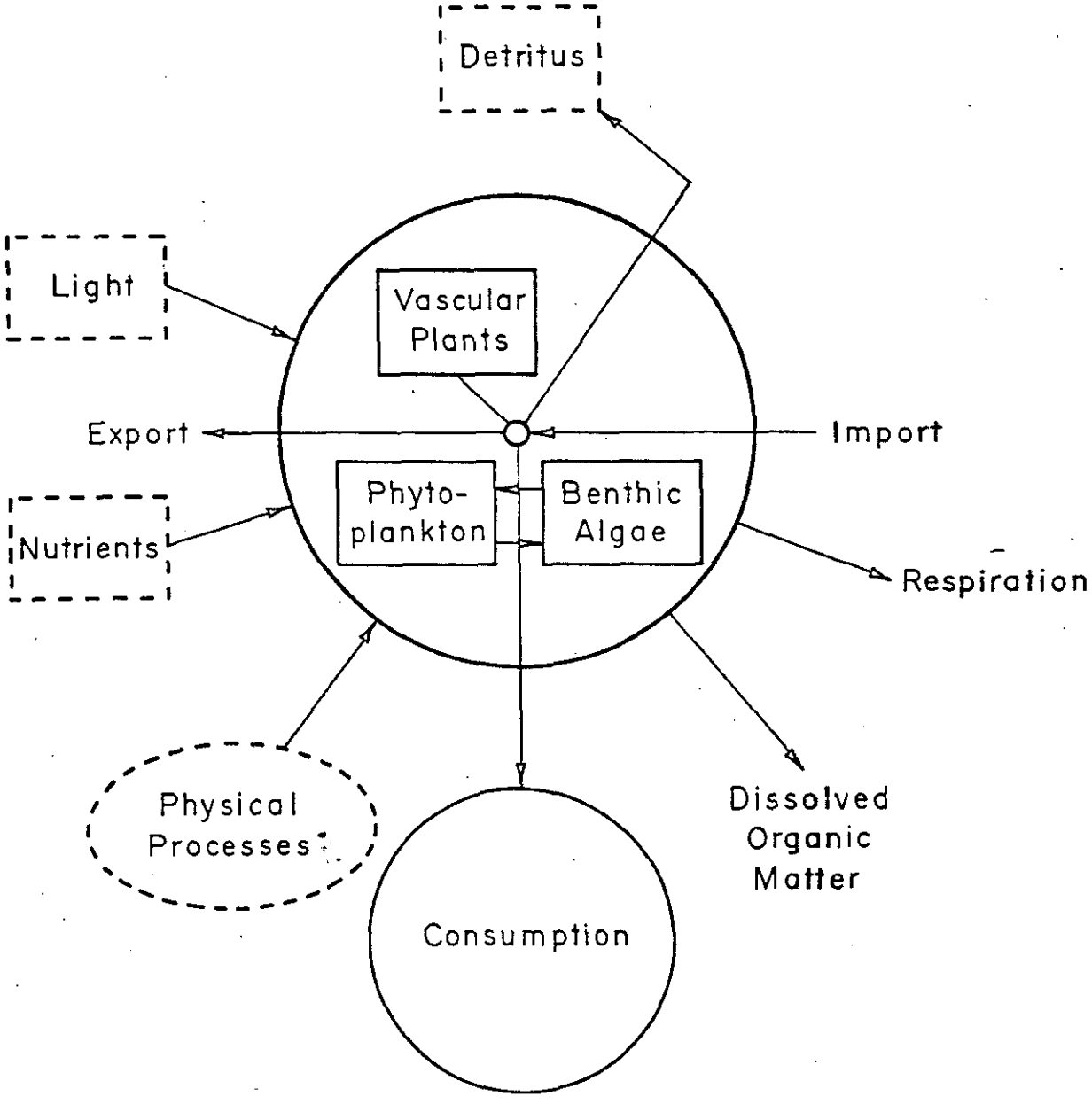


Figure 2. Conceptual framework of estuarine primary production.

Our general approach was to measure in detail the distribution of phytoplankton biomass, rates of photosynthesis, and physical-chemical environmental factors, about every other month through a 16-month period. Samples were collected from several standard depths at selected stations covering main channels, bays, shallows, and side rivers. From these data the horizontal and vertical distribution of phytoplankton in the estuary, the changes exhibited by the phytoplankton on a seasonal basis, the rates of photosynthesis or primary production in the water column, and the environmental factors controlling the distribution and production of phytoplankton were determined. The rate of loss of phytoplankton to zooplankton grazers was also evaluated.

1.2 Brief Description of the Study Area

The Lower Columbia River is a coastal plain estuary, or drowned river valley, formed as the sea level rose to its present position after the last glaciation. However, the Columbia River Estuary is much more river-dominated than most other classical coastal plain estuaries.

The Columbia River Estuary is composed of two distinct geomorphic regions (Hubbel and Glenn 1973). Above Columbia River Mile 30, the river runs in a main channel 1 to 2 km wide. Islands surrounded by small channels and sloughs are characteristic. The river bottom is composed predominantly of sand deposits (Whetten et al. 1969, Sherwood et al. 1984). Below Columbia River Mile 30 the river broadens and water flow becomes less channelized. The central region of the estuary is composed of vast shallow flats and shoals, which are exposed at low tide. Four large, shallow embayments (Cathlamet Bay, Grays Bay, Youngs Bay, and Baker Bay) drain adjacent highlands through small rivers. About 19% of the estuary has depths exceeding 30 feet and about 18% has depths less than 3 feet (Figure 3).

The tidal circulation of the Columbia River Estuary occurs at diurnal and semi-diurnal frequencies, typical of the eastern North Pacific Coast (Jay 1984). There are two high-water and two low-water periods daily, all of different tidal heights. At the mouth, mean and dirunal tide ranges are approximately 1.7 m and 2.3 m, respectively. The extreme tidal range, however, may exceed 4 m (Neal 1972).

Because of the large river discharge and strong tidal currents, the estuary is characterized by a very dynamic hydrological regime (Jay 1984). Flushing times in the estuary have been estimated to be one to five days, depending on tidal and river flow conditions (Neal 1972). These are rather rapid flushing times compared to those calculated for other estuaries (Ketchum 1952; Kremer and Nixon 1978; Conomos 1979).

Classification of the Columbia River Estuary based on salinity gradients (Burt and McAlister 1959) is not possible, because the estuary may show one type at the mouth (i.e., vertically stratified)

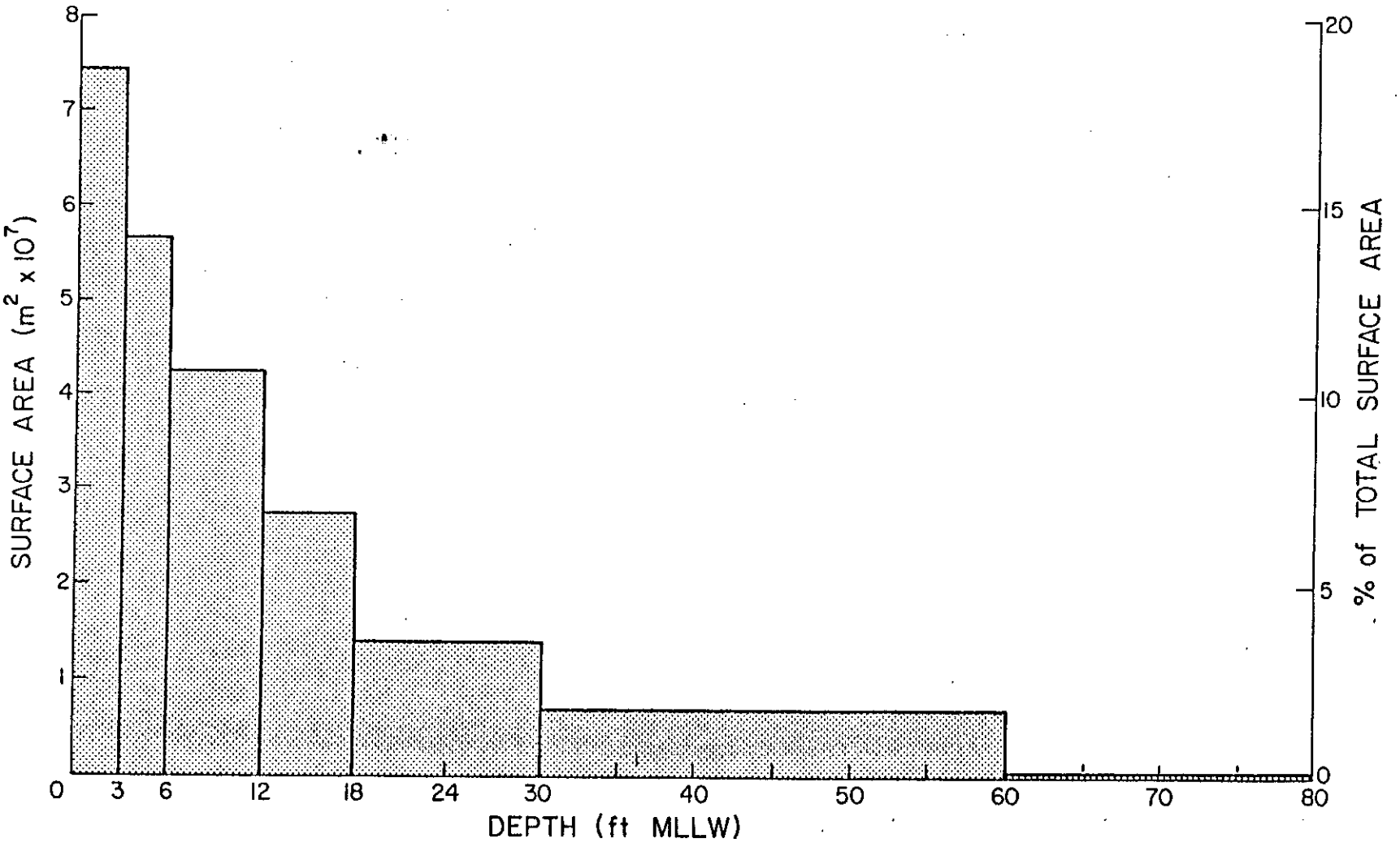


Figure 3. Histogram of depths within the Columbia River Estuary.

but at the same time show a different type upstream (vertically homogeneous). During most of the year, however, the estuary can be classified as being partially mixed (Neal 1965). During low river discharge (midsummer to fall) the salinity intrusion may extend up to Harrington Point (River Mile 23) during maximum flood tide, and to about River Mile 17 at lower low tide (Jay 1984). During high river discharge (spring freshets), salinity intrusion occurs only in the lower few miles of the estuary (Neal 1965; Jay 1984). Salinity intrusion into the shallow bays, and particularly into Cathlamet Bay which is at the upstream limits of salinity intrusion, is likely to be strongly variable (Jay 1984).

Lutz et al. (1975) and Jay (1984) reported that, due to the lateral exchange between the north and south channels, the circulation pattern in the lower estuary is extremely complicated. Neal (1965) and Jay (1984) indicated that during flood tide most of the water is transported through the north channel, while during ebb tide the south channel apparently is the main path. This circulation, contrary to that expected from Coriolis effect, has been explained in terms of geomorphology (Neal 1965). It is thought that the north channel offers an easier and more direct route upstream for water derived from the coastal zone, and that the south channel conveys downstream flow more efficiently because of its continuous deep path through the lower estuary. This phenomenon results in a generally clockwise circulation in the estuary.

With the objective of estimating budgets and fluxes of properties throughout the estuary, we divided the Columbia River Estuary into eight zones or subareas (Figure 4). These zones are similar to those adopted by Thomas (1983).

The explosive eruption of Mt. Saint Helens on May 18, 1980, generated a plume of sand, ash, and debris which entered the Columbia River Estuary at the mouth of the Cowlitz River, near Longview, Washington (Figure 5). Within three days turbid water filled the entire estuary. It took about five weeks for the water to return to relatively normal levels of turbidity. Since we sampled before, during and after this event, it served as a vast nautral experiment to test the effects of greatly diminished light penetration in the water column on primary production and the overall ecosystem in the Columbia River Estuary. We examined the effects of post-eruption turbidity on phytoplankton primary production by comparing measured and estimated rates of carbon assimilation with and without the post-eruption turbidity.

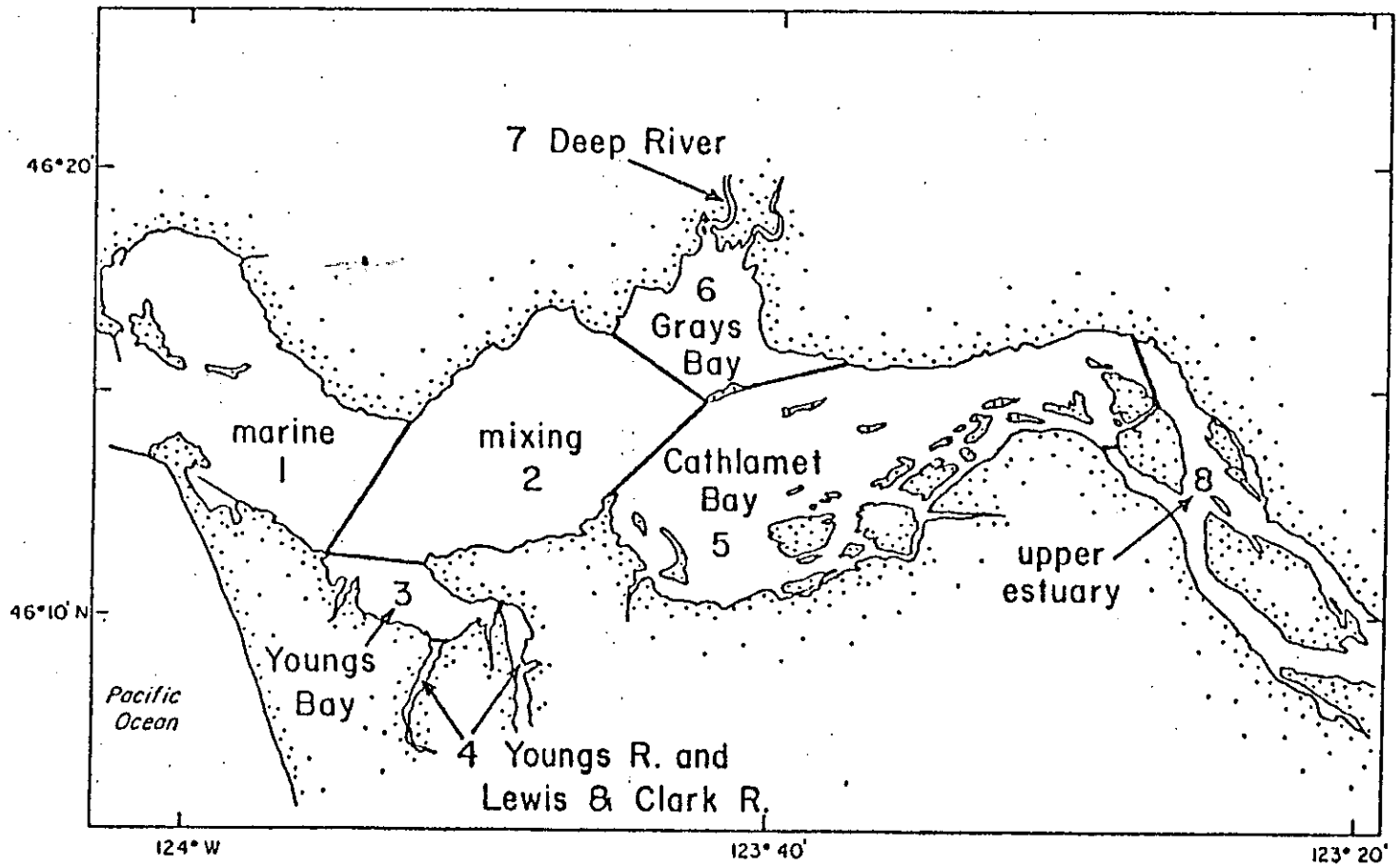


Figure 4. Columbia River Estuary zones.

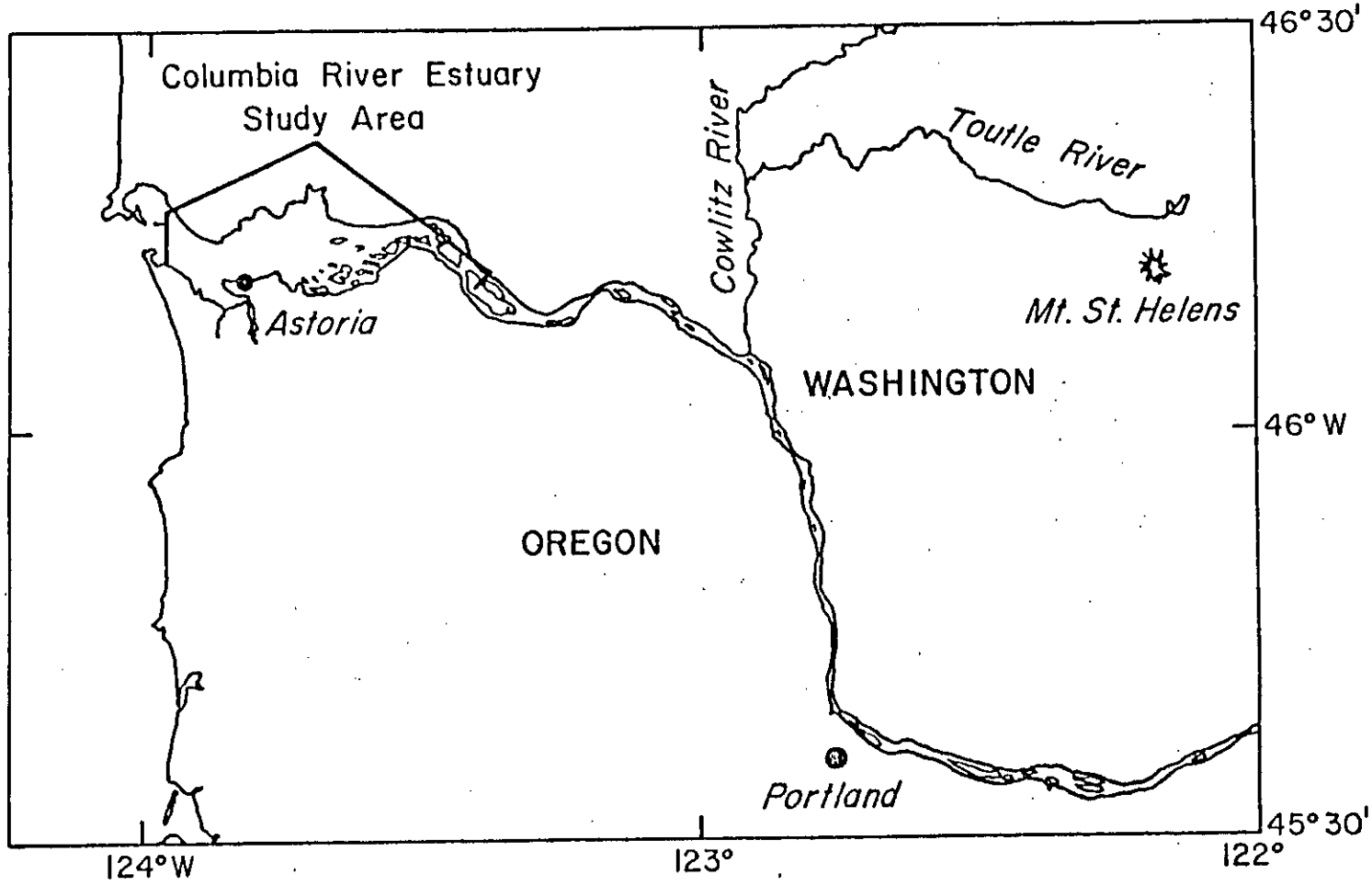


Figure 5. The study area and its relationship to Mt. Saint Helens.

2. METHODS

2.1 GENERAL

Nine cruises were conducted on the Columbia River Estuary approximately every other month from April 1980 through July 1981. Stations in both shallows and main channels were sampled in the area extending from Clatsop Spit at the mouth of the Columbia River Estuary (River Mile 5), to the east end of Puget Island (River Mile 47). Station locations are shown in Figure 6. With the exception of the June and July 1981 cruises, when only 3 stations were sampled, the number of stations sampled per cruise varied from 25 to 47 throughout this study. All stations were sampled at the surface, and at some stations 2.5, 5.0, and 10.0 meter depths were sampled.

Samples from depth were collected by submersible pump, and surface samples were collected with a bucket. Properties measured for spatial and temporal variability were temperature, selected inorganic nutrients (nitrate plus nitrite, phosphate, silicic acid), chlorophyll a, phaeophytin a, in vivo fluorescence with and without DCMU treatment, total suspended particles (organic and inorganic fractions), particulate organic carbon and nitrogen, light attenuation, and primary production. At selected locations we also measured salinity, alkalinity, zooplankton grazing rates, and phytoplankton species composition.

Temperatures were read from a thermometer submerged in a bucket either filled by hand at the surface, or filled by pump from depth. Salinity was measured with a Goldberg T/C refractometer.

Samples for inorganic nutrient analyses were filtered through 0.4 µm pore-size Nucleopore^{R} filters, and then divided into two 75 ml polyethylene bottles. One bottle was frozen in dry ice for analyses of reactive phosphate and nitrate plus nitrite, and the other was kept cold (but above freezing) for silicic acid analysis. Samples were analyzed in the laboratory using a Technicon Autoanalyzer^{R}, according to the techniques of Atlas et al. (1971).

Chlorophyll a and phaeophytin a analyses were done by the fluorometric measurement of an acetone extract as described by Yentsch and Menzel (1963). In addition to extracted chlorophyll measurements, in vivo fluorescence measurements were made both with and without the electron-transport block DCMU (3-(3,4-dichlorophenyl)-1, 1 dimethyl urea), at all stations and depths sampled. The ratio of in vivo fluorescence with DCMU to in vivo fluorescence without DCMU, has been considered as an indicator of the stage of growth of the phytoplankton community (Samuelson and Oquist 1977; Frey 1981).

Total suspended particles (seston), and the organic and inorganic fractions of the total, were determined by gravimetric analysis. Each water sample (50 to 150 ml) was filtered through a pre-weighed 0.45 µm pore-size Nucleopore^{R} filter. Filters were placed in petrislides and frozen immediately. In the laboratory the filters were

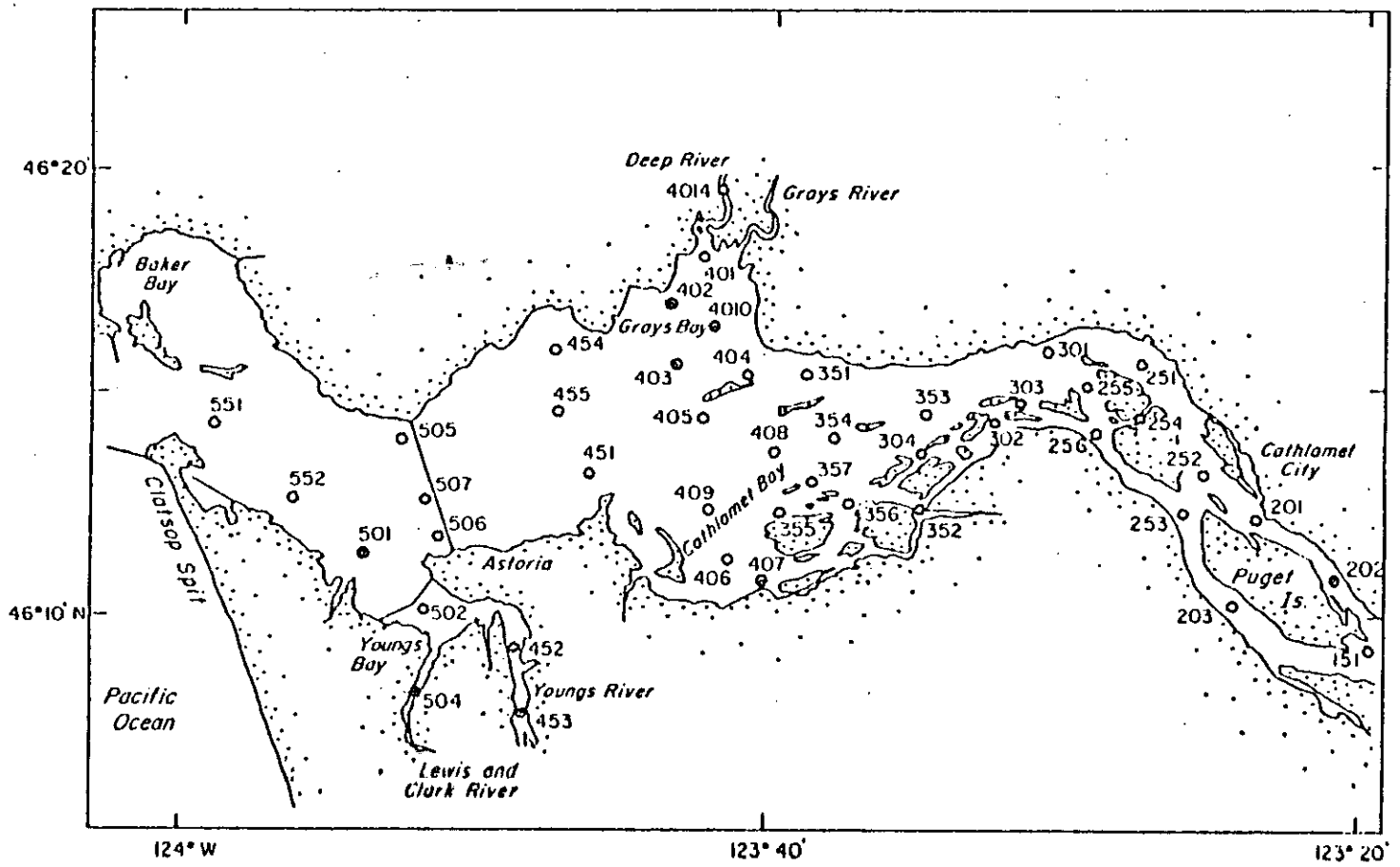


Figure 6. Columbia River Estuary sampling stations.

dried and weighed again, then digested for 30 minutes with hydrogen peroxide and reweighed, to give the weight of total, organic, and inorganic suspended particles. Details of this technique are described by Peterson (1977). Particulate organic carbon and nitrogen were analyzed with a Perkin-Elmer elemental analyzer model 240C ®.

2.2 WATER COLUMN PRIMARY PRODUCTIVITY

Phytoplankton primary productivity experiments were performed at 5 to 12 stations per cruise from April 1980 to April 1981, and at 3 stations in June and July 1981. Primary productivity was assessed by the radiocarbon uptake method (Strickland and Parsons 1972). Samples labelled with carbon-14 (^{14}C) were incubated in 80 ml polycarbonate bottles, with two replicates for each treatment. Incubations usually were done for about 4 hours, under natural sunlight in clear deck-tanks. Surface water was circulated through the tanks to maintain temperatures. Except for surface samples, light was attenuated with neutral screens to 50, 30, 15, 6, 1, and 0% of incident light. From September 1980 to July 1981, at stations 501, 451, and 201, additional samples were gently filtered through 10 μm and 33 μm mesh screens prior to labelling with ^{14}C in order to test the production attributable to different-sized phytoplankton fractions. Screening separation prior to labelling and incubation has been recommended in order to avoid losing ^{14}C recently assimilated by cells (McCarthy et al. 1974). At the end of all incubations, the ^{14}C-labelled samples were immediately filtered through 0.8 μm pore-size Millipore ® filters, and the filters were preserved in Aquasol ® in individual liquid scintillation vials. Radioactivity was analyzed in a Beckman Model 7500 ® liquid scintillation counter, and these measurements were converted to carbon productivity (mgC $m^{-3}hr^{-1}$) using the equation of Strickland and Parsons (1972). Conversion to mgC in $m^{-2}day^{-1}$ was done as needed, and the conversion technique is given later.

Incident light (I_o) and light penetration in the water column was measured with a Licor ® submersible spherical quantum meter. The diffuse light attenuation coefficient and theoretical depth of each of the incubation light levels were calculated from the well-known equation

$$I_z = I_o e^{-kz},$$

where I_o is the light intensity at the surface, I_z is the light intensity at depth z, and k is the diffuse light attenuation coefficient.

Photosynthetically active solar radiation (295-695 nm) was measured by an Eppley Precision Spectral pyranometer ® in (gcal $cm^{-2}day^{-1}$) at the Field Observing Facility in Corvallis, Oregon (this facility is part of the Oregon State University Solar Energy Meteorological Research and Training Site program [Rao et al. 1981]).

Monthly averages of daily solar radiation for Corvallis (1980-1981) were compared with monthly averages of daily solar radiation for Astoria, Oregon (based on a 1941-1970 record)(Figure 7). Because of the small differences between the two records, and because the Corvallis data included the actual hourly solar radiation record during the period needed for our daily productivity prediction model, the Corvallis data were used. Solar radiation data for Astoria were discontinued by U.S. Governmental agencies after 1970, and were not resumed by CREDDP until the end of the field program.

Carbonate alkalinity, required for conversion of ^{14}C data to carbon-based productivity, was computed from alkalinity measurements made by potentiometric titration with 0.1N H_2SO_4, as described by Wetzel and Likens (1979).

Samples for taxonomic identification were collected at most of our productivity stations, and were preserved in glass bottles containing Lugol's solution. Due to limitations of time and resources, only selected samples were analyzed. During analysis, samples were cleared of salt and concentrated by repeated settling in distilled water and decanting. Permanent slides were prepared with Cumar resin. Cells were counted using a Zeiss compound microscope, under oil at 1000X. A Whipple ocular micrometer was used to record the area enumerated.

2.3 ZOOPLANKTON GRAZING

During June and July 1981, six time-series zooplankton grazing experiments were conducted. Experiments were performed at Stations 501, 451 and 201 (Figure 6), representing three major zones in the estuary. For descriptions of similar techniques for measuring zooplankton grazing rates, see Honey (1973) and Daro (1978).

For each experiment, two 9.5 liter Cubitainers^{R} were filled with 8 liters of filtered (60 µm mesh Nitex) surface water containing natural phytoplankton. One container was kept unlabelled for control experiments, while the other was inoculated with 500 µCi of $NaH^{14}CO_3$ (60 µCi l^{-1}). Both containers were held in clear deck-tanks for approximately one day after inoculation, to allow ^{14}C uptake by the phytoplankton. This pre-labelled phytoplankton was fed to zooplankton in order to measure by radioactive count the amount of phytoplankton consumed.

Zooplankton were collected with a 250 µm mesh net towed at low speed for 10 minutes. The full sample was put into a battery jar to let heavy material settle out, and then the swimming zooplankton were decanted into a shallow plastic tray. A water bath was used through all these procedures to avoid exposing zooplankton to temperature changes. The tray was darkened except for one end, to effect light sorting. Zooplankton were transferred with a turkey baster syringe into a holding flask containing estuarine water

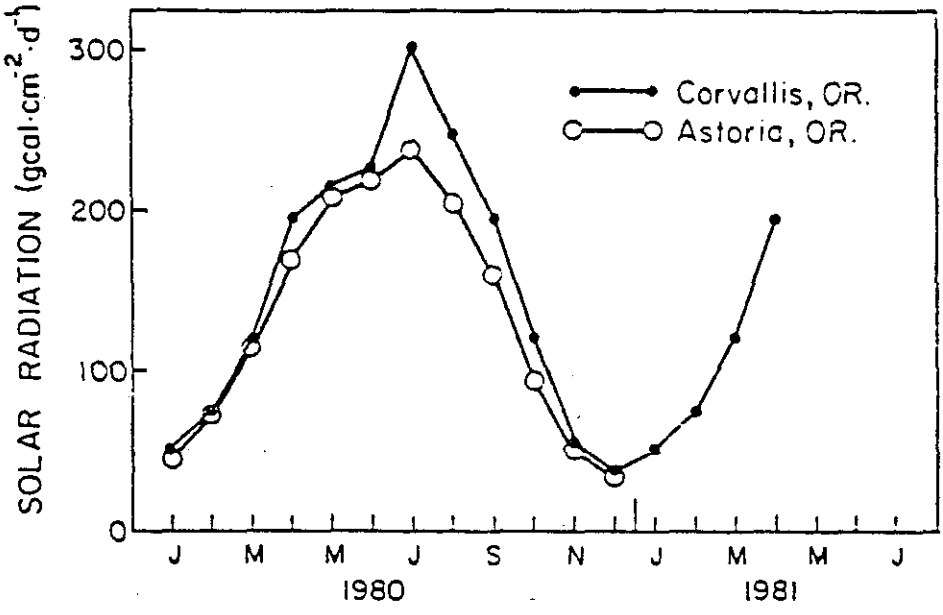


Figure 7. Monthly averages of daily solar radiation.

filtered through 30 μm mesh. This 30 μm filtration procedure was repeated several times before the zooplankton were added to the flask, to bring phytoplankton concentrations (as measured by chlorophyll fluorescence) into line with natural levels in the estuary.

Approximately 200 ml of prelabelled phytoplankton and 50 ml of zooplankton (25-30 animals) were added to each experimental bottle (250 ml). Bottles were covered at once with aluminum foil to keep samples in the dark, and incubated in deck-tanks filled with water circulating from the estuary surface to maintain temperature. Bottles were harvested at 0, 0.25, 0.5, 0.75, 1, 1.45, 2, 3, 4, 6, 17, 19, 21, and 24 hours to get a time-series of accumulation of ^{14}C in the zooplankton. After each experimental time period, zooplankton were retrieved from the bottles by filtering the contents of each bottle through 153 μm Nitex® filters in Gelman filter holders (collecting zooplankton, but not phytoplankton). These filter holders themselves were rigged above filter holders with 0.45 μm pore-size AA Millipore® filters which collected the phytoplankton. The Millipore® filters were thoroughly but gently washed with filtered estuarine water, after which the filters with zooplankton were placed into empty scintillation vials. The vials were then frozen. Millipore® filters with phytoplankton were placed into scintillation vials containing Aquasol®. All were taken back to the laboratory for analysis.

Several controls were run. One control tested adsorption of $NaH^{14}CO_3$ onto zooplankton surfaces. Approximately 50 ml of "zooplankton suspension" were added to 200 ml of 0.45 μm Nucleopore®-filtered estuarine water containing 16 μCi of $NaH^{14}CO_3$. The bottles were covered with foil for darkness and were incubated in the deck-tank. The bottles were removed at 1, 5, and 24 hours, and the zooplankton were filtered onto Nitex filters as above, for later ^{14}C counting. A second control tested changes through time in ^{14}C activity of the phytoplankton, without zooplankton present. Approximately 250 ml of prelabelled phytoplankton were incubated under the same experimental conditions as before. Bottles were harvested at 0, 3, 5, 17, and 24 hours, the phytoplankton cells were filtered onto Millipore® filters as above, and preserved in Aquasol® for ^{14}C counting in the laboratory.

Chlorophyll *a*, carbon, and nitrogen contents of the phytoplankton community during grazing periods were followed by incubating 200 ml of unlabelled phytoplankton plus 50 ml of zooplankton. Bottles were filtered after 0, 3, 5, 17, and 24 hours.

During June 1981, at station 201, an additional grazing experiment was set up. Approximately 200 ml of unlabelled natural phytoplankton, 50 ml of zooplankton suspension (25-30 animals), and 20 μCi of $NaH^{14}CO_3$ were added simultaneously to each experimental bottle (250 ml). Bottles were incubated at ambient light (not in the dark as before) in deck-tanks, and harvested at 1, 2, 4, and 8 hours. Phytoplankton and zooplankton were retrieved as described above.

From each Nitex® filter containing zooplankton that had grazed, six individuals of each of the two dominant groups (copepods and cladocerans) were selected under a binocular microscope and placed in individual 20 ml scintillation vials. Two drops of Amersham NCS® tissue solubilizer were added to each vial. Samples were digested for 24 hours prior to adding Aquasol®. They were analyzed in a Beckman Model 7500® liquid scintillation counter for ^{14}C activity.

Phytoplankton on Millipore® filters, already immersed in Aquasol® in scintillation vials, were also analyzed for ^{14}C in the liquid scintillation counter.

2.4 QUALITY CONTROL PROCEDURES

2.4.1 Selection of Sampling Sites and Frequency of Sampling

In selecting sampling sites (stations) we attempted to cover in some detail the various regions and environments of the Columbia River Estuary. This included stations which could characterize such subareas as the main channels, the various bays, small side rivers, shallow back waters among the islands, the riverine environment, and the marine environment. At the same time, stations had to be reasonably accessible by the research boats, without undue risk to personnel and equipment, or excessive expenditure of time.

Decisions on station locations were aided by use at the start of the project of a continuous flow, recording fluorometer to measure spatial variation of chlorophyll a in great detail. This was helpful in deciding on the density of stations needed to characterize the zone, as well as appropriate locations.

Samples were collected about every other month through the study period. In spring and summer sampling was somewhat more closely spaced since this is the most active time of phytoplankton growth, and in winter sampling was more spread out. We felt this made the best use of our resources.

2.4.2 Standard Environmental Measurements

A. Temperature and salinity

1) Refractometer and thermometer were checked before each cruise.

2) Data sheets were checked for accurate entry of dates, stations, depths, and times of day, as well as for accurate entry of temperature, refractive index and salinity.

B. pH

1) Calibration of the pH meter was checked before each cruise.

2) pH meter was standardized before use.

3) Standard was rerun every few hours during operation.

4) Data sheets were checked for accurate entry of water temperature, pH values of samples and standard, as well as station, depth, date and time of day.

C. Carbonate alkalinity

1) pH meter was calibrated and standardized as above.

2) A log of temperature and pH of the sample, as well as station, depth, date and time of day was maintained.

3) Calculations for total and carbonate alkalinity were checked for one or two samples per cruise.

D. Light penetration

1) Battery of Licor light meter was checked before each cruise using test function on meter.

2) Data sheets were checked for accurate entry of date, station, depth, time of day, and light level.

E. Nutrients

1) Field data sheets were checked for correct completion.

2) Duplicate nutrient analyses were performed routinely

(a) Frozen samples (2) for nitrate-nitrite and phosphate.
(b) Unfrozen samples (2) for silicate.

3) Standards and blanks were analysed for each group of 15 samples. Both distilled and artificial seawater blanks were analyzed. Duplicate standards prepared both in distilled and artificial seawater were also analyzed with each group ("run") of samples.

4) For each survey, a standard series was prepared in seawater of high to low salinity to give a calibration function. This allowed the effect of salinity on nutrient concentration determination to be accounted for.

5) A continuous record of sensitivity (mm/chart unit) was kept to insure the satisfactory determination of nutrient concentration.

6) Records were kept, noting chemical, pump-tubing, calibration and other changes that might affect autoanalyzer operation.

7) Chemical linearity as a function of concentration (calibration function) was checked quarterly. A number of replicates was determined for each concentration checked, and an estimate of variance was determined. From this analysis, appropriate detection limits were calculated.

8) As an external check of standards, we obtained appropriate working standards from another autoanalyzer operation within the College of Oceanography.

2.4.3 Biomass Estimates

A. Particulate carbon and nitrogen

1) Field Procedures

a) Before each cruise field equipment was checked.

b) Vacuum pressure was checked every few samples and maintained at or less than 5 lbs in^{-2}.

c) Data sheets were checked for accurate entry of volume filtered and vial number, as well as date, station, depth, and time of day.

2) Laboratory Procedures

a) For each set of samples run on the CHN analyzer, a record of weight of standard chemical used and peak heights of the standard was maintained. Calibration curves were checked with standard C and N peak heights to insure adequate function of analyzer before processing samples.

b) A log of number sets run and dates was maintained. Date of replacement and number of sets between replacement) of chemicals in both the combustion column and reduction tube of the analyzer were recorded.

c) Data recorded were checked for proper entry of sample number (vial number), boat number, attenuation values, carbon and nitrogen peak heights.

d) Data entered into computer were checked with original data.

e) One computer entry was rerun on a hand calculator.

f) Labelled recorder scrolls with annotations were retained.

g) Based on data from paired sample analysis of Oregon coastal waters our accuracy is ±.5 µg N/ℓ^{-1} and ±1.0 µg C ℓ^{-1}.

B. Seston - organic and inorganic

1) All Nucleopore^{R} filters were weighed using an alpha emitting device to eliminate static charges from the filter surface. Filters were stored in labelled plastic Milipore Petri-slides^{R}. Record of filter weights and date weighed were kept.

2) For each sample, a log of volume filtered, station, depth, time of day and sample number was kept.

3) Field data sheets were checked for accurate completion.

4) Blanks were run with samples from every new box of filters used. This generated a correction factor due to filter weight change during the peroxide leaching.

5) A log of correction factor, filter weight before and after peroxide leaching, and calculations for total suspended matter, organic fraction and inorganic fraction was maintained.

6) Calculations for one or two samples per cruise were checked.

7) Accuracy of method = ±0.03 mg ℓ^{-1}.

C. In vitro chlorophyll a by fluorometric methods

1) Field equipment was checked before each cruise.

2) For each sample, a log of volume filtered, date, station, depth, time of day, and sample number was kept.

3) Label information between log and sample was checked to assure agreement.

4) Turner Designs^{R} fluorometer was calibrated and standardized before each set of samples.

5) Phaeophytin was measured by adding 1 ml of HCl to cuvette after initial chlorophyll a fluorescence reading.

6) A log of sample number, fluorescence readings (before and after HCl addition), and calculated values for chlorophyll a (and phaeophytin) was maintained.

7) Calculations for mg m^{-3} of chlorophyll a were checked on one or two samples from each cruise.

8) At the 5 µg level the correct value lies in the range: mean of n determinations $\pm 0.26/n^{1/2}$ h chlorophyll a.

D. In vivo chlorophyll a fluorescence

1) Fluorometer was checked before each cruise.

2) Fluorometer was standardized at least every 4 hours during use.

3) For each sample, a log of fluorescence, fluorescence with DCMU added (Frey 1981), date, station, time, and sample number was maintained.

4) Recorded information was checked.

2.4.4 Species Enumeration

A. Information on data and sheets and labeled was checked for accurate and complete entry.

B. Log was kept of volume settled, number of grids counted, number of cells per species and total number of cells counted (100 cells is minimum number for statistical purposes). Record of species identified was maintained.

C. Number of cells/ml was recalculated for selected stations.

2.4.5 Carbon Uptake Rate Estimates

A. ^{14}C-uptake by deck incubation.

1) A data log was kept noting station, depths of surface light penetration, light screens used, Nitex^{R} filters used, date, time of day and vial labels. Accurate completion of data was checked.

2) In every experiment a 1 ml sample of the ^{14}C solution was taken for standardization. A log of the date, time, and µCi ml^{-1} of ^{14}C used was maintained.

3) A log of background Aquasol^{R} solution (blanks), sample activity and activity of ^{14}C solution(s) used was maintained.

4) One or two calculations of net carbon productivity per data set (i.e., cruise) were checked.

2.4.6 Computing

A. Key-punched data was verified by double-punching all data.

B. Results were verified by hand-calculating a few samples of each parameter calculated during a run.

3. RESULTS

3.1 VARIABILITY OF ENVIRONMENTAL FACTORS AND PRIMARY BIOMASS

Stations were selected according to location and depth to represent: a) distributions of properties along the main channel of the estuary (≥10 m depth), from the mouth (Station 551) through the uppermost station (Station 151) at the head of the study area; and b) distributions of properties in the major shallow bays (Youngs, Grays, and Cathlamet Bays) and rivers (Youngs, Lewis and Clark, and Deep Rivers). Because the bays and rivers were in semi-enclosed areas (not part of the main estuarine continuum), they were not particularly suitable for analysis of spatial variability relative to a common mean; therefore, only temporal variation was considered in these areas. Stations intermediate or transitional between channel and shallow stations were not used in these analyses.

Two approaches were followed for the channel station: first, spatial-temporal contours were graphed; and second, a two-way analysis of variance model was applied to the data sets in order to test the statistical significance of the variations in each property over time and horizontal space. For the shallow stations, temporal variability was investigated by a one-way analysis of variance model.

Surface temperature showed a significant ($p < .001$) temporal variation, but no significant spatial variation (Figure 8a; Table 1). A seasonal trend matching the solar irradiation cycle (Figure 7) was evident. Temperatures ranged from 9°C to 16°C during spring (April-May, and peaked in summer (to 22.5°C). Temperature decreased to 10°C by late fall and reached its minimum in winter (5-6°C). During this study no data were available for December or January; however Park et al. (1972) reported average temperatures of 4.8°C for the Columbia River Estuary during January. A temperature cycle similar to that in Figure 8a has been reported for the Columbia River Estuary by Haertel (1970), and Park et al. (1972).

We encountered measurable salinities only up to river mile 30. Usually saline waters were only found much further seaward (Jay 1984). It was only where saline waters were enountered that substantial vertical gradients of water column properties were observed.

Dissolved phosphate was variable through the year (Figure 8b; Table 1), being higher in winter and early spring (0.8-1.0 μM) than in summer and early fall (0.3-0.8 μM). No statistically significant spatial variation was observed for phosphorus (Table 1); however, the marine zone showed a slight enrichment in summer due to Youngs Bay influence and coastal upwelling (Figure 8b). Phosphate did not show signs of being biologically limiting at any time of the year.

Nitrate plus nitrite in the channel showed clear seasonal variation, but no significant spatial variation (Figure 9a; Table 1).

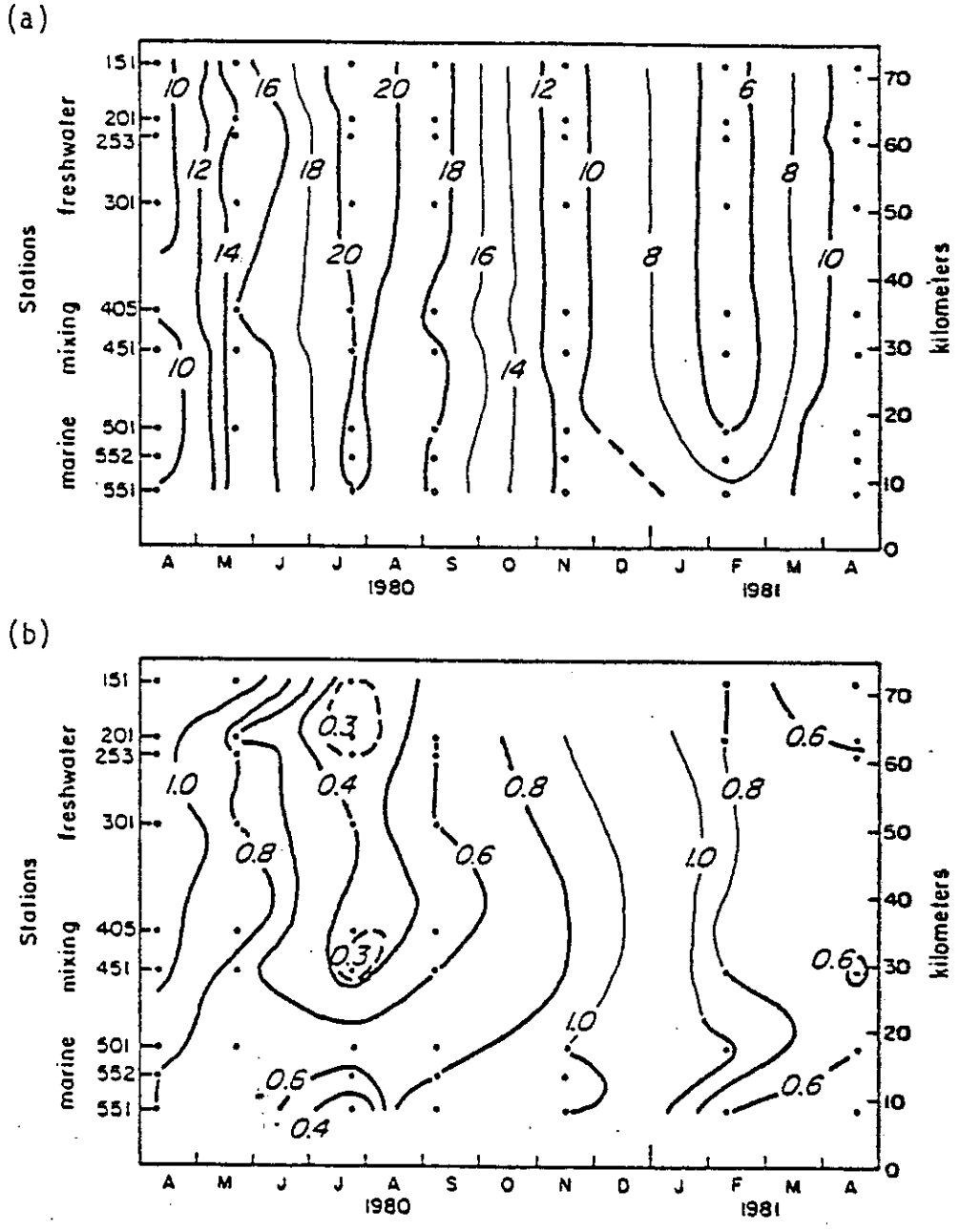


Figure 8. (a) Spatial-temporal distribution of temperature (°C) in the Columbia River Estuary.
(b) Spatial-temporal distribution of phosphate (μM). Thin lines through all the spatial-temporal figures, represent a lower confidence of contouring due to a reduced number of stations. Dashed lines represent different interval of contouring. Values are for surface samples.

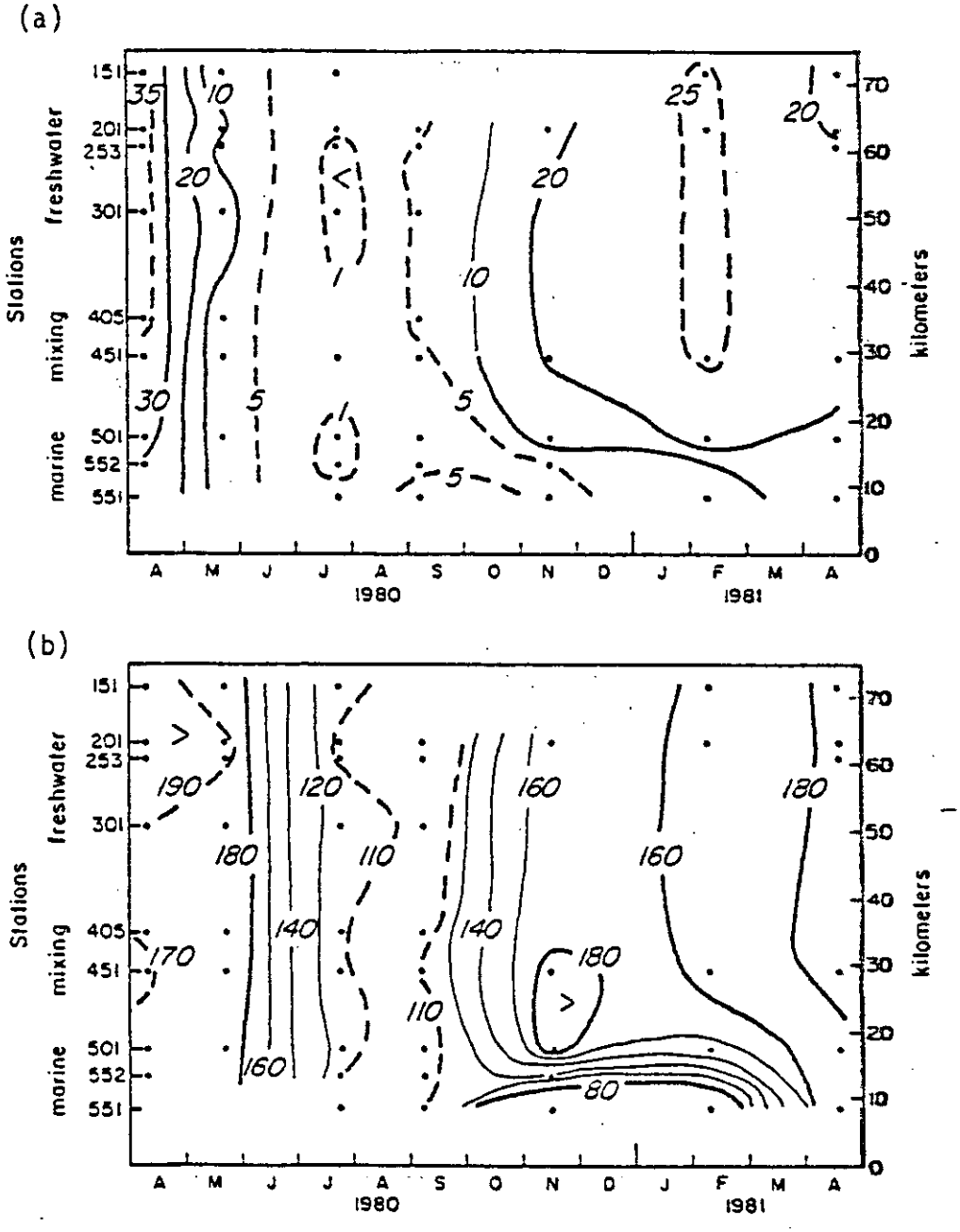


Figure 9. (a) Spatial-temporal distributions of nitrate plus nitrite (μM) in the Columbia River Estuary.
(b) Spatial-temporal distribution of silicic acid (μM).
Other comments as in Figure 8.

Table 1. Analyses of variance for properties in channel and shallow stations of the Columbia River Estuary. Significance level: p = .005

VARIABLE	FACTOR	P CHANNEL	P SHALLOW
Temperature	time	sig.	sig.
	space	n.s.	
Phosphate	time	sig.	sig.
	space	n.s.	
Nitrate-nitrite	time	sig.	sig.
	space	n.s.	
Silicic acid	time	sig.	sig.
	space	n.s.	
Chlorophyll *a*	time	sig.	sig.
	space	sig.	
Fluorescence	time	sig.	sig.
	space	sig.	
DCMU-Ratio	time	sig.	sig.
	space	sig.	
Phaeophytin *a*	time	sig.	sig.
	space	n.s.	
Phaeophytin *a*: chlorophyll *a*	time	sig.	sig.
	space	sig.	
Total suspended particles	time	sig.	sig.
	space	n.s.	
Inorganic suspended particles	time	sig.	sig.
	space	n.s.	
Organic suspended particles	time	sig.	n.s.
	space	n.s.	
Particulate organic carbon	time	n.s.	n.s.
	space	n.s.	

Maximum values were in winter and early spring (over 20 μM), while minimum values during summer were less than 1.0 μM. Unfortunately no other nitrogenous nutrients (ammonia, for example) besides nitrate plus nitrite have been studied in the Columbia River Estuary, so we cannot say for sure that nitrogen was absent during summer; however, the rapid rate of decrease in concentration, and the low levels observed, strongly suggest nitrogen limitation of phytoplankton at certain times in summer. During mid-autumn and winter, the marine zone averaged less than 10 μM nitrate plus nitrite, while the riverine waters averaged over 20 μm (Figure 9a).

Silicic acid (Figure 9b; Table 1) showed a temporal pattern similar to nitrate plus nitrite in the channel, varying from high values (150-200 μM) in winter and early spring to lower values (around 100 μM) in summer. Although no statistically significant spatial variability was observed (Table 1), concentrations in fall and winter dropped abruptly in the marine zone due to intrusion of coastal oceanic waters which contained much less silicic acid than riverine waters. However, concentrations of silicic acid limiting to phytoplankton growth were never approached.

The diffuse light attenuation coefficient $\underline{k}$ (m^{-1}) varied both spatially and temporally in the channel (Figure 10). In general, the estuary can be divided into comparatively clear waters from station 501 to 551 (marine zone), with $\underline{k}$ values from 0.7 to 1.5, and more turbid waters from station 451 upstream (with $\underline{k}$ values from 1.0 to 3.0 and usually greater than 2.0). A seasonal cycle is evident, with higher values (1.5-3.0) during September and November, and minimum values in spring and summer (1.0-2.0). The exceptionally high values during May are due to the high turbidity caused by the volcanic eruption.

The phytoplankton biomass level as indicated by chlorophyll *a* concentration varied both spatially and temporally ($p < .001$)(Figure 11; Table 1). An evident spatial feature was the fairly rapid decrease in chlorophyll *a* concentrations from the freshwater region to the marine zone in the spring. During April 1980, for example, chlorophyll *a* concentrations of around 8.0 mg m^{-3} in the freshwater and mixing zones decreased to values of about 4.0 mg m^{-3} in the marine zone. During May 1980, when the highest chlorophyll *a* concentrations were reached, the freshwater and mixing zones averaged 17.0 mg m^{-3}, but concentrations decreased to 11.2 mg m^{-3} in the marine zone. Even though our May sampling was conducted three to six days after the Mt. St. Helens volcanic eruption, which caused increased levels of chlorophyll *a* from heavy particle loads, no effect was evident in the relative chlorophyll *a* distribution in the estuary. Photosynthetic rates, however, were greatly affected (see Section 4.3).

During November we observed the minimum chlorophyll *a* concentration, and the gradient between freshwater and marine areas was less

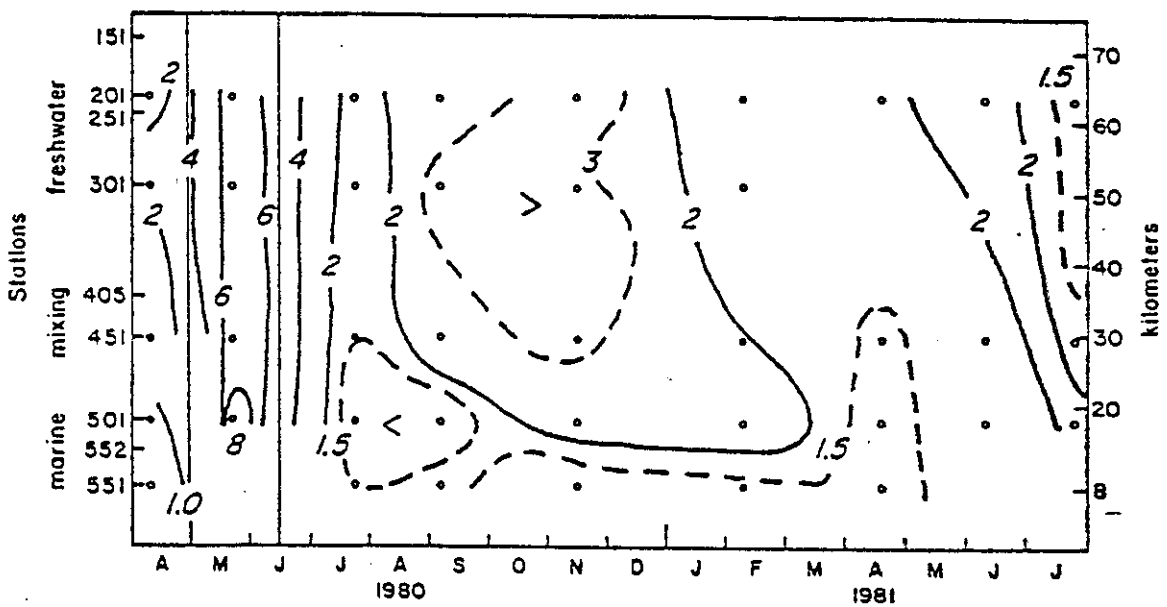


Figure 10. Spatial-temporal distribution of light attenuation coefficient, $\underline{k}(m^{-1})$ in the Columbia River Estuary. Other comments as in Figure 8.

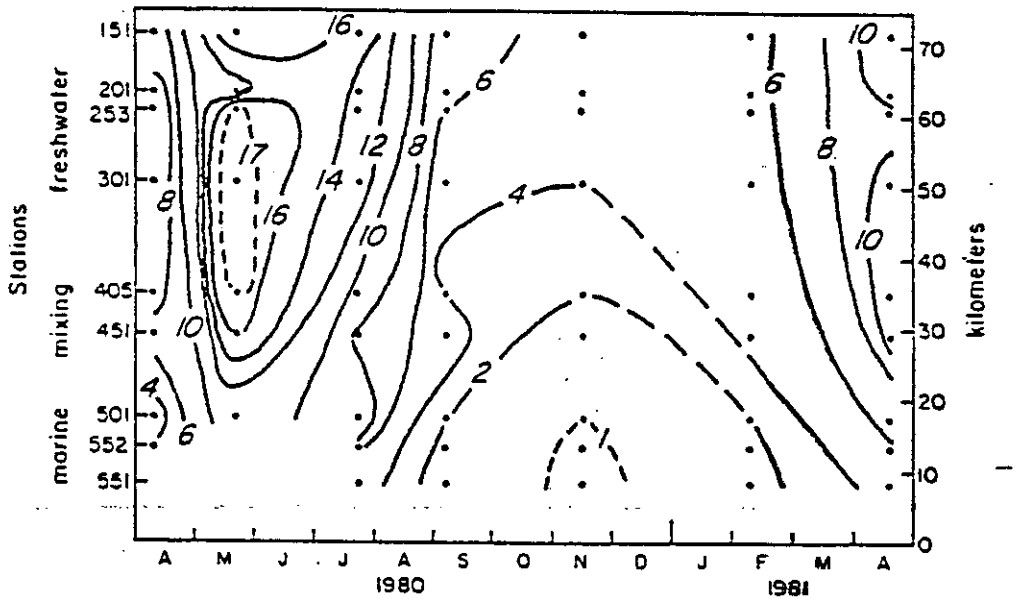


Figure 11. Spatial-temporal distribution of chlorophyll a (mg m^{-3}) in the Columbia River Estuary.
Other comments as in Figure 8.

severe (Figure 11). Concentrations below 1 mg m^{-3} were recorded in the marine zone in November. No data are available for December or January , but these months may be expected to have the lowest phytoplankton biomass, due to the lowest annual solar radiation intensity and shortest day lengths. Apparently by February 1981 a new cycle started to build, with chlorophyll a values averaging 2.0 mg m^{-3} in the marine zone, about 5.0 mg m^{-3} in the mixing zone, and somewhat greater than 5.0 mg m^{-3} in the freshwater area. Spring conditions during 1981 (April 1981) yielded somewhat higher chlorophyll a concentrations than those in April 1980, but the rather abrupt gradient between freshwater and marine zones was re-established. April 1981 chlorophyll a values averaged 5.3 mg m^{-3} in the marine zone, but averaged 10.0 mg m^{-3} in the mixing and freshwater zones.

In vivo fluorescence closely mirrored the chlorophyll a pattern, as expected (Figure 12; Table 1). A ratio of chlorophyll a to in vivo fluorescence of about 2 to 3 was representative for the whole estuary throughout the year (not illustrated).

The ratio DCMU to in vivo fluorescence showed seasonal variability (Figure 12; Table 1), being higher in summer (2-3) than in fall and winter (1.7-2.0). In May the ratio declined, indicating poorer photosynthetic capability of the total suspended particle field. Possibly this was a response by in situ phytoplankton to the adverse, light-limited conditions in the estuary following the Mt. St. Helens eruption. Possibly the low ratio indicated heavy loads of poorly photosynthesizing plant fragments brought into the estuary by post-eruption runoff. There is no way to distinguish. There was significant (p .005) spatial variability in the ratio (Table 1). In general the ratio decreased from freshwater to the marine zone.

Phaeophytin a showed significant (p .001) temporal variability (Figure 13; Table 1). Maximum values were registered during late summer (2.0-3.5 mg m^{-3}), and minimum values during mid-winter and early spring (0.0-0.7 mg m^{-3}). Although no statistically significant spatial variation was observed, the marine zone usually had the lowest concentrations.

The ratio of phaeophytin a to chlorophyll a varied significantly (p .001) both spatially and temporally (Figure 13; Table 1). The main spatial feature was a gradual increase from the freshwater to the marine zone at most times of the year. A seasonal trend was clearly shown, with highest ratios during late summer and fall (30-100), and lowest ratios in winter and early spring (0-20).

The analyses of variance for total seston (suspended particles), inorganic seston, and organic seston were done without the May 1980 data, because of the extraordinarily high particulate concentrations

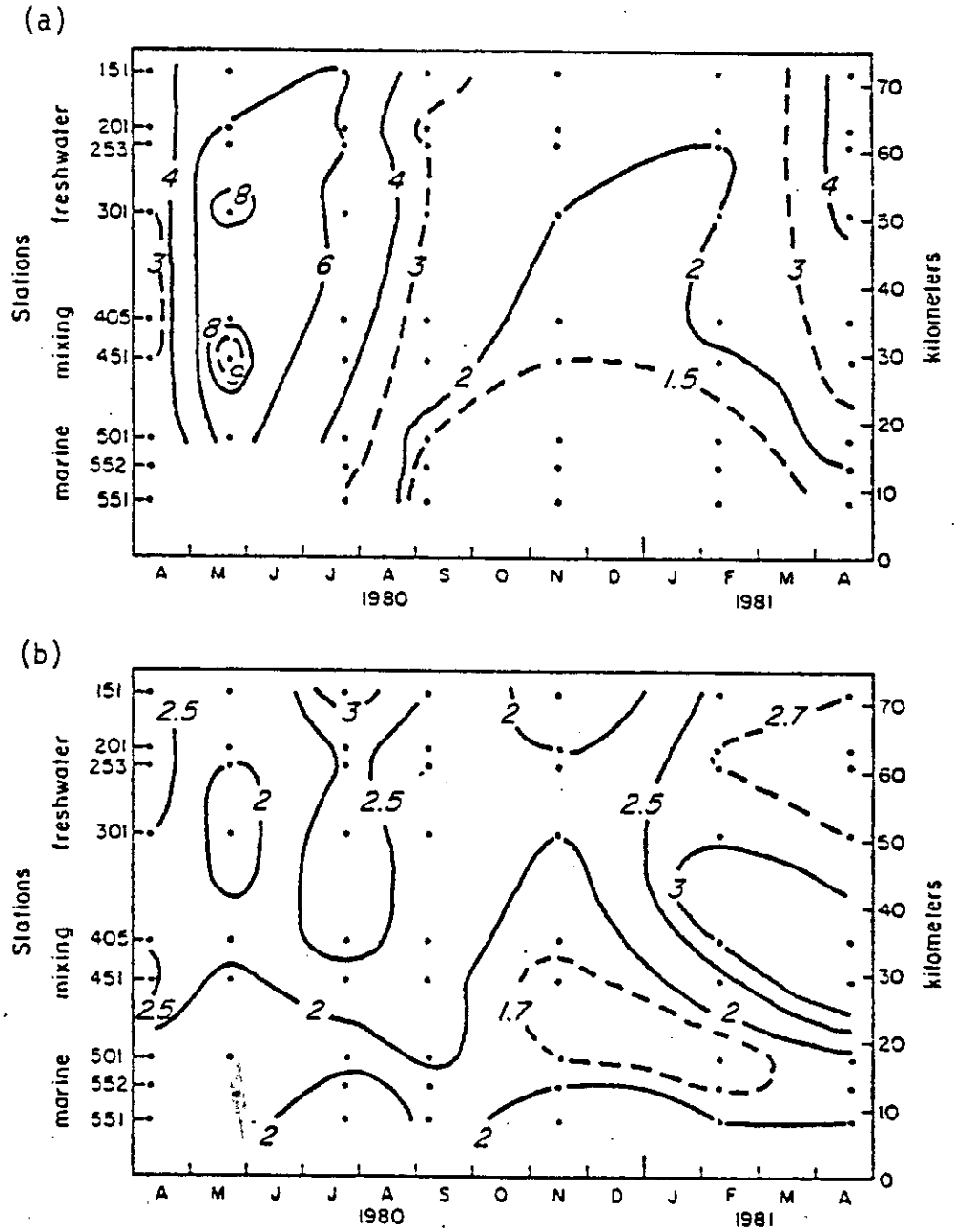


Figure 12. (a) Spatial-temporal distribution of in vivo fluorescence (relative units) in the Columbia River Estuary.
(b) Spatial-temporal distribution of DCMU: in vivo fluorescence ratio.
Other comments as in Figure 8.

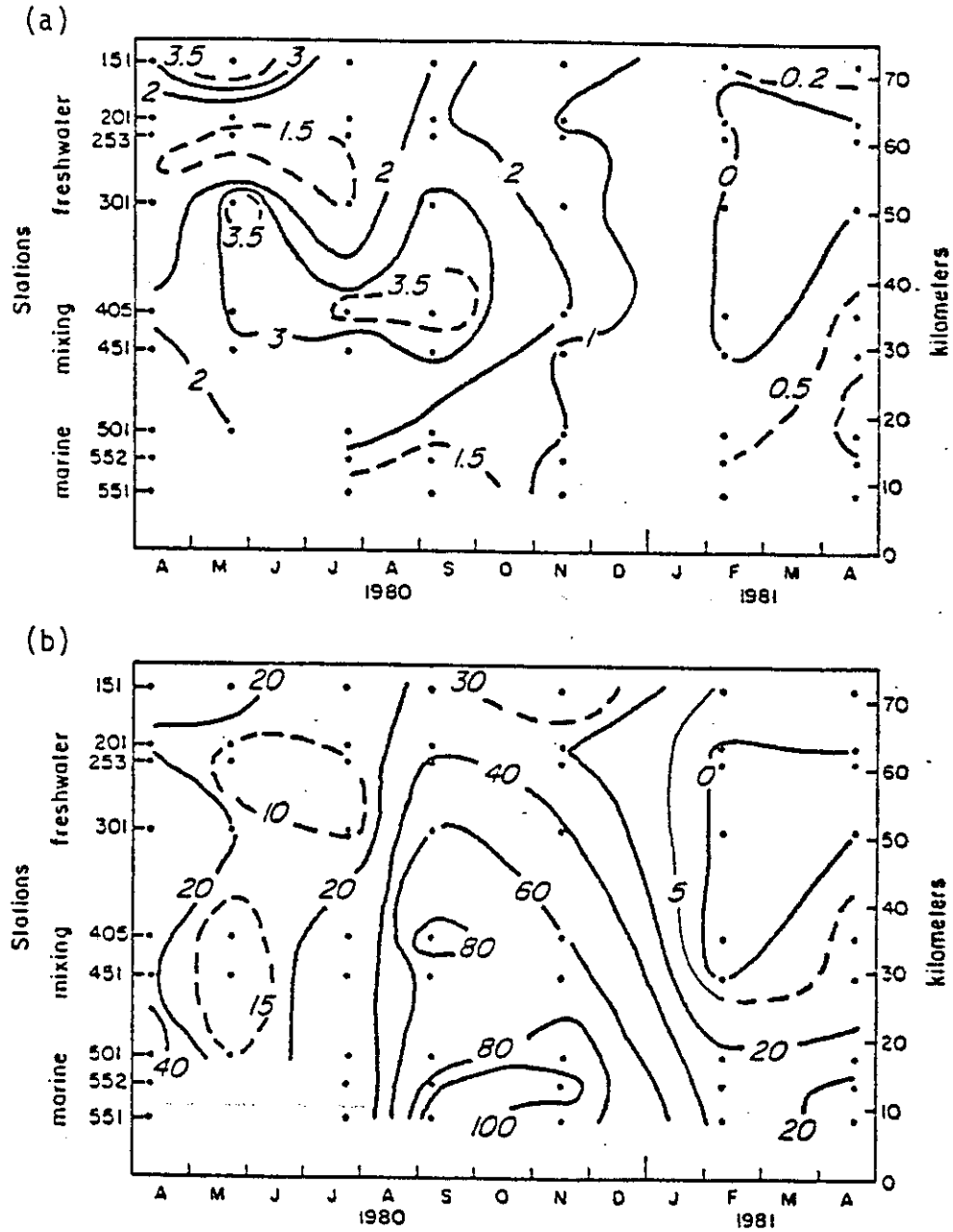


Figure 13. (a) Spatial-temporal distribution of phaeophytin a (mg m^{-3}) in the Columbia River Estuary.
(b) Spatial-temporal distribution of phaeophytin a: chlorophyll a ratio (%).
Other comments as in Figure 8.

during this period. Total seston showed significant (p .001) seasonal variation but no significant spatial variation (Figure 14; Table 1). Although no statistically significant spatial variation was observed, the marine zone had the lowest concentrations in autumn and early winter. The abnormal peak during May, up to six times the maximum concentration that normally occurred, was a result of the Mt. St. Helens eruption, which caused exceptionally high loads of sediment and detritus to be discharged into the Pacific Ocean via the Columbia River Estuary. Other than that, maximum values were in late summer and fall (50-70 mg l^{-1}), and minimum concentrations in mid-winter and early spring (8-20 mg l^{-1}).

The inorganic fraction of the total seston mirrored very closely the pattern of total seston (Figure 14). There was significant (p .001) seasonal variation but no significant spatial variation. Again, the marine zone usually registered the lowest concentrations in fall and early winter. The abnormal peak during May is again obvious. Other than in May, maximum values were in late summer and fall (45-70 mg l^{-1}), and minimum concentrations in mid-winter and early spring (7-15 mg l^{-1}).

The organic fraction of total seston (OSP) also showed significant (p .005) seasonal variation but no significant spatial variation (Figure 14a; Table 1). Ignoring the May 1980 data, highest concentrations occurred from summer to fall (4-8 mg l^{-1}), and lowest concentrations occurred during mid-winter and early spring (1-3 mg l^{-1}) (Figure 15).

The organic fraction as a percent of the total seston load did not show spatial variability, but showed some seasonal variation (Figure 15). During spring and summer the organic fraction reached 25%, while minimum values of 10% or less were registered in September and November. The very low percentages in May <5%) were caused by the exceptionally high inorganic seston concentrations (Figure 15) derived from the volcanic eruption.

Particulate organic carbon (POC)(Figure 16) showed neither significant spatial or temporal variations (Table 1). Typical concentrations were from 1.0 to 1.3 mg l^{-1}.

3.2 SHALLOW STATIONS AND COMPARISON TO DEEP STATIONS

Temporal variability of properties in shallow areas (Youngs, Grays, and Cathlamet Bays; and Youngs, Lewis and Clark, and Deep Rivers) of the Columbia River Estuary (Figures 17 and 18) showed the same seasonal trends as the comparable properties in channel stations (see below). However, the statistical significance in the seasonal variations for phaephytin, the phaeophytin-chlorophyll a ratio, the DCMU to in vivo fluorescence ratio, TSP, ISP, and OSP in the shallows was lower than for channel stations (Table 1). These

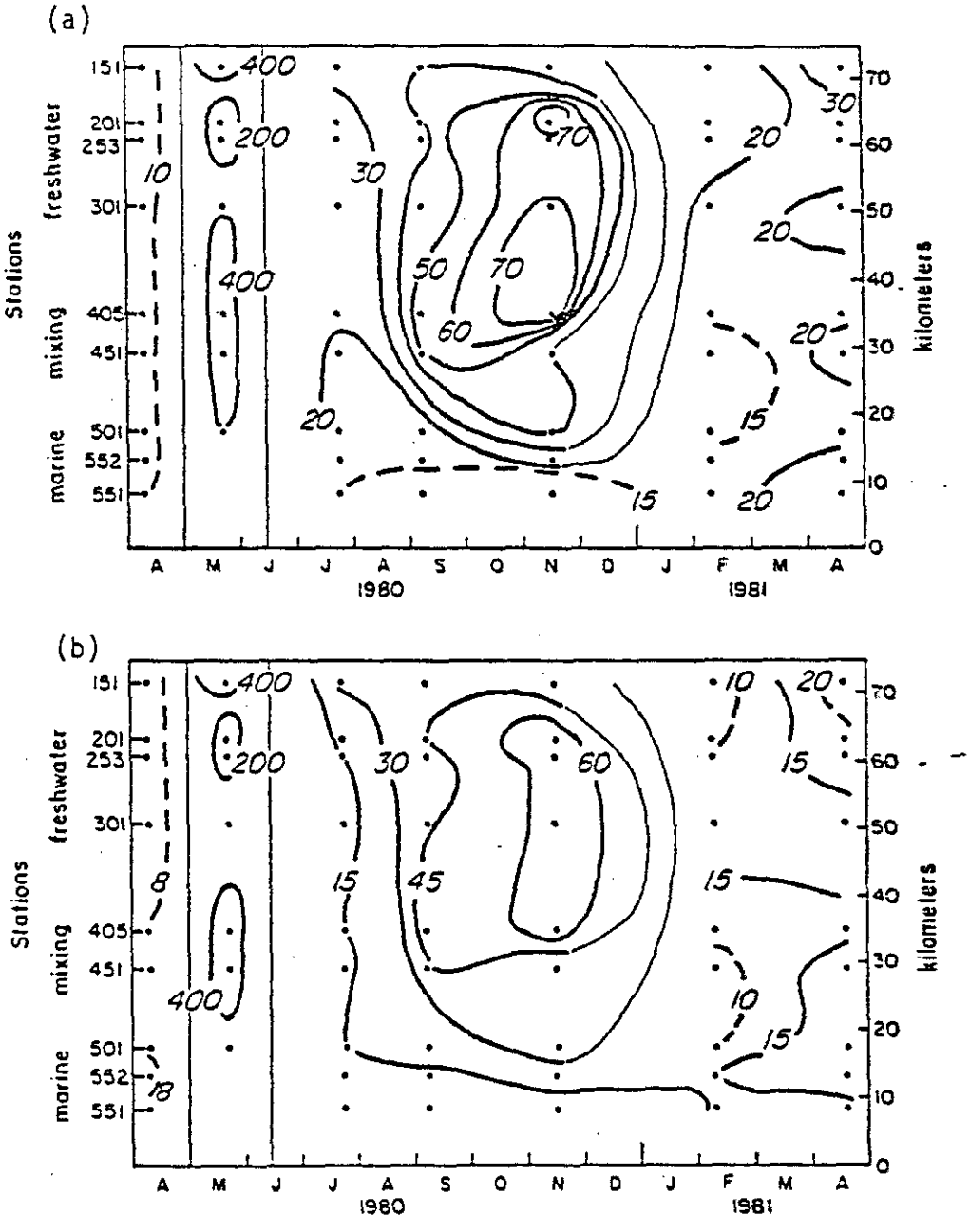


Figure 14. (a) Spatial-temporal distribution of total seston (mg l^{-1}) in the Columbia River Estuary.
(b) Spatial-temporal distribution of inorganic seston (mg l^{-1}).
The extraordinarily high concentrations in May 1980 were due to the Mt. St. Helens Volcanic eruption. Other comments as in Figure 8.

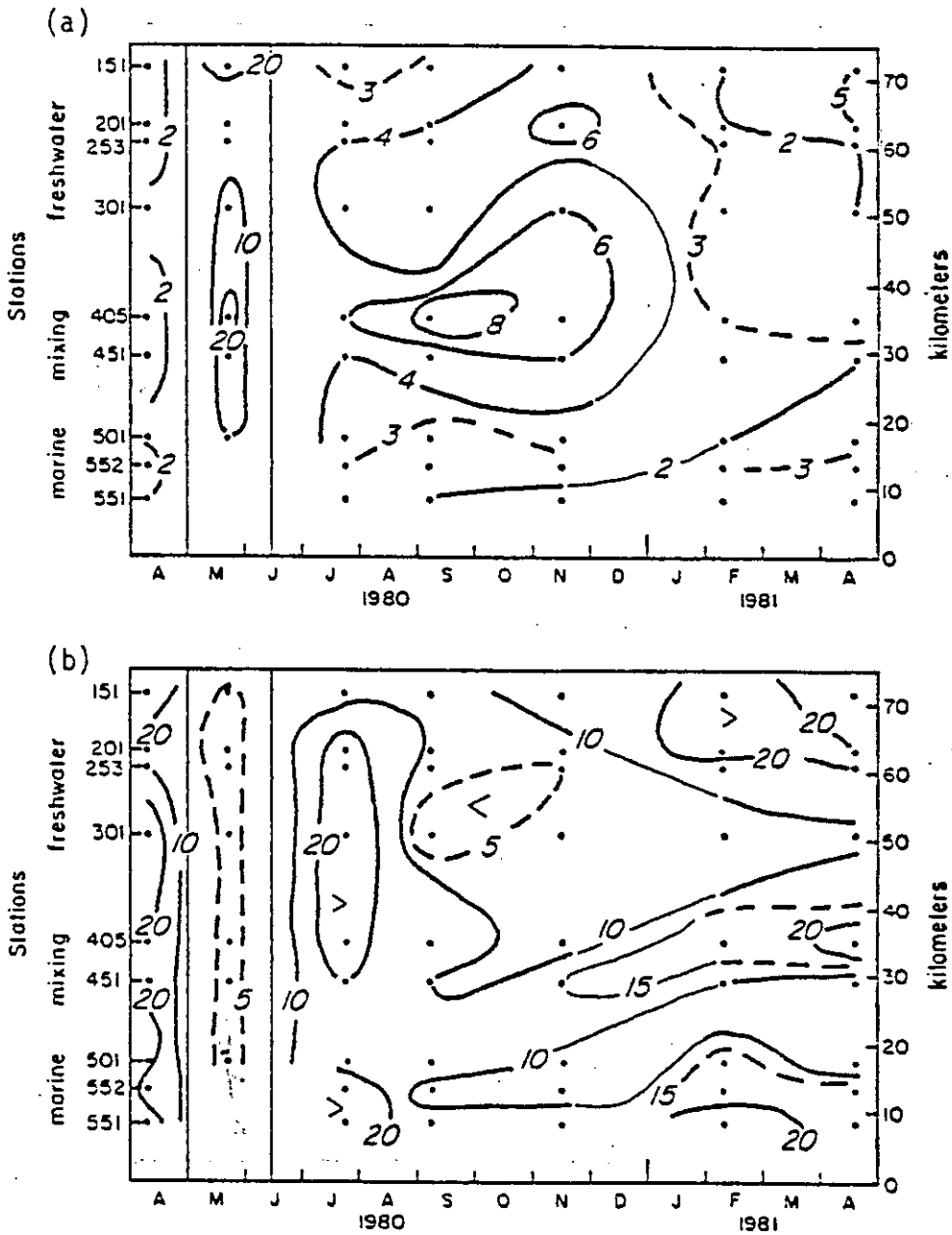


Figure 15. (a) Spatial-temporal distribution of organic seston (mg l^{-1}) in the Columbia River Estuary.
(b) Spatial-temporal distribution of organic seston: total seston ratio (%).
Other comments as in Figure 8.

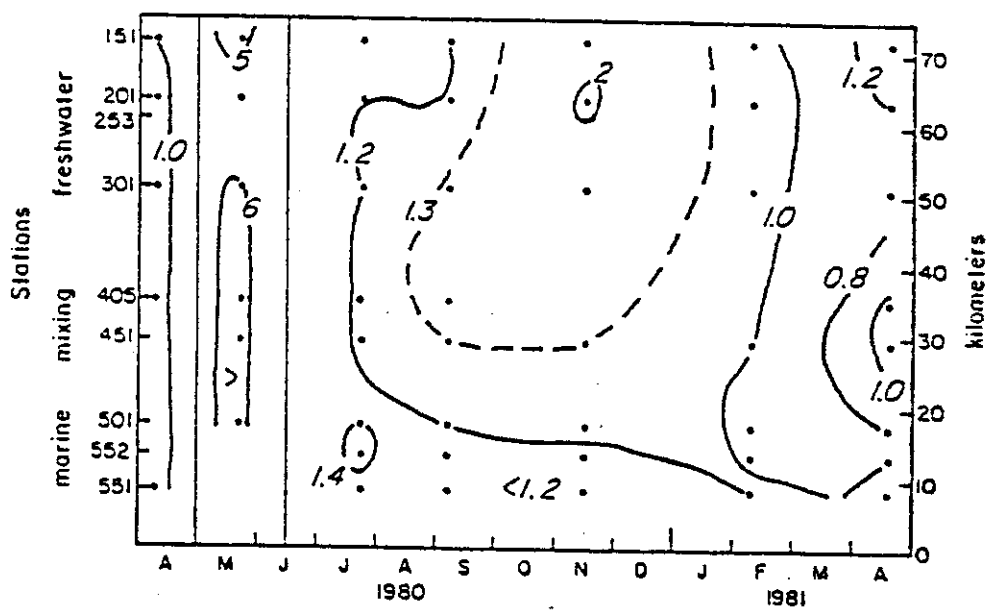


Figure 16. Spatial-temporal distributions of particulate organic carbon (mg l^{-1}) in the Columbia River Estuary. Other comments as in Figure 8.

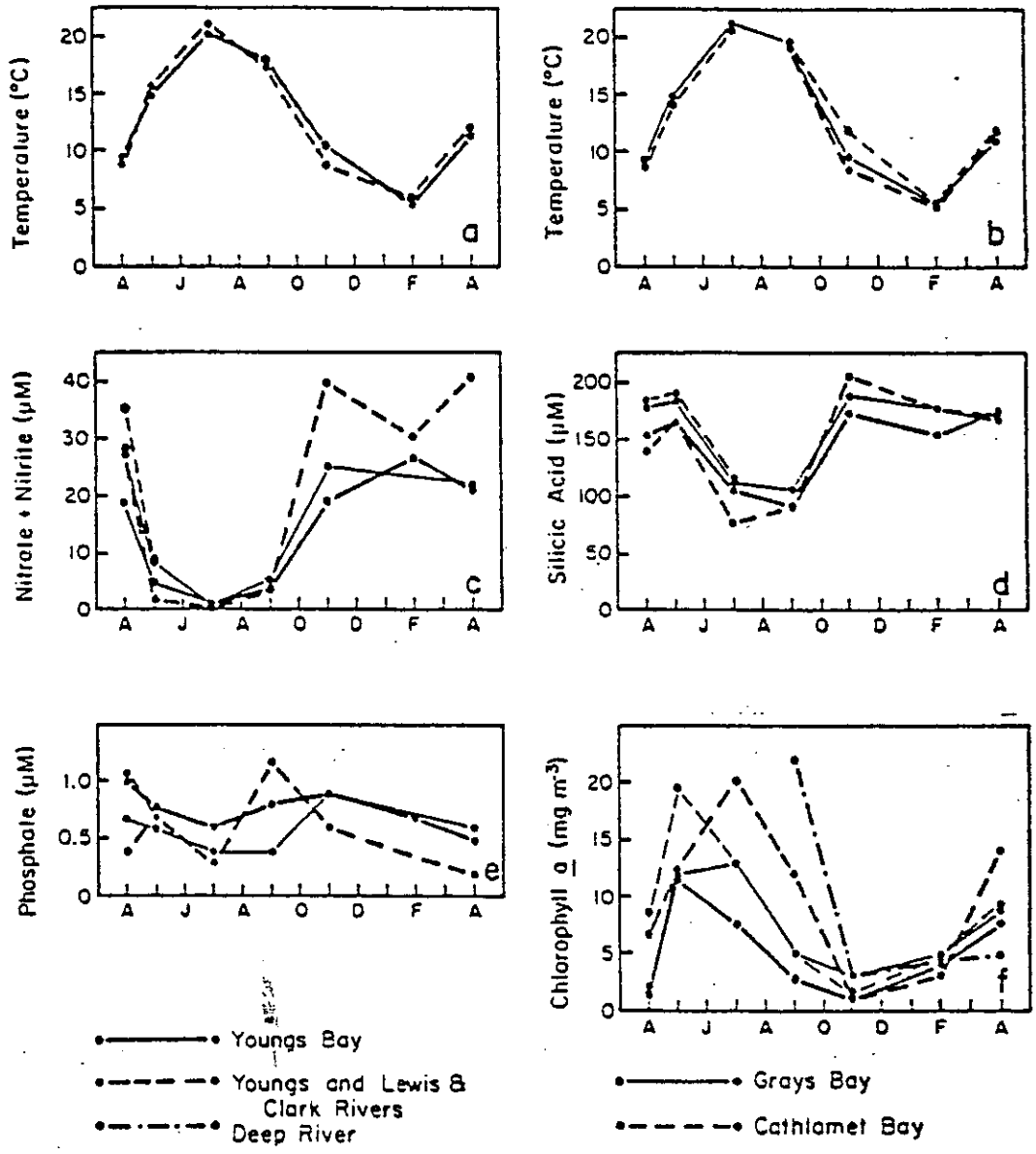


Figure 17. Temporal variability of proeperties in shallow areas of the Columbia River Estuary. Notice that temperature is shown in two panels, a and b. Values are for surface samples.

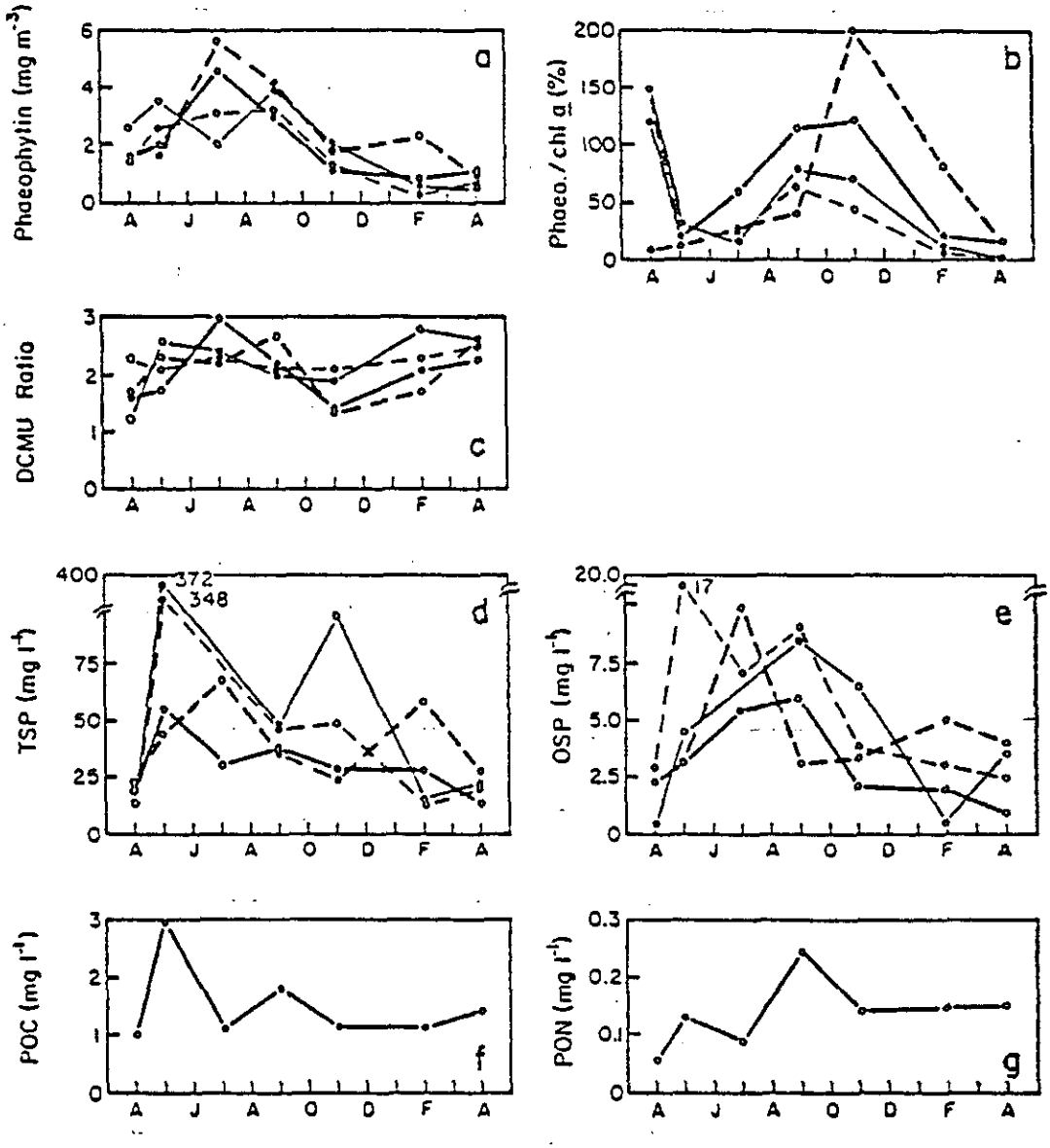


Figure 18. Temporal variability of properties in shallow areas of the Columbia River Estuary. Traces as in Figure 17.

lower probabilities suggest less pronounced seasonal effects in the shallow areas of the estuary.

Means of properties for channel stations were compared with means of properties in the shallow zones. Significantly higher mean values were obtained in the shallow areas for chlorophyll a, fluorescence, phaeophytin a, the phaeophytin a-chlorophyll a ratio, TSP, ISP, OSP, and POC (Table 2). All these variables can be strongly influenced by sediment resuspension, as well as higher residence time of the water in shallow areas; therefore, enrichment relative to channel stations is expected.

3.3 VERTICAL DISTRIBUTION OF PROPERTIES

Vertical distributions of particles and their properties (chlorophyll a, OSP, TSP, and POC) for three selected stations along the main channel of the estuary, are shown in Figures 19 and 20. These profiles clearly show a homogeneous water column in response to a very dynamic system along the main channel. The physical and chemical properties, plus chlorophyll, are more complex. Here river flow and tidal conditions will determine the vertical distribution of properties. With the exception of the September cruise, near-mouth stations 501, 551, and 552 were sampled during flood tide when the maximum differences in marine-riverine concentrations were expected. Vertical structure is observed only for properties with significant differences between riverine and marine waters.

During summer, near-surface, near-riverine waters showed higher temperatures (18-22°C) than the entering near-marine waters (23-16°C) (Figure 21a). During late fall and winter opposite conditions were found (Figure 22a,b), with river-dominated waters ranging from about 6 to 10°C, and marine-dominated waters rising above 10°C. Note that in November (Figure 22a) there was little river influence, but by February (Figure 22b) the condition began to change. By April (Figure 23) enhanced river runoff brought slightly warmer temperatures and slightly reduced salinity structure to the eater column.

During summer, marine coastal waters entered the estuary slightly enriched in nitrate plus nitrite (3.0 µM) and phosphate (0.8 µM), relative to riverine waters which normally ranged below 1.0 µM and 0.5 µM, respectively (Figure 21). From late fall through early spring, riverine waters were highly enriched with respect to nitrate plus nitrite, and to a modest extent with respect to phosphate (Figures 22 and 23).

Silicic acid concentrations were always higher in river waters than in marine waters (Figures 21, 22, 23). Marine waters showed maximum silicic acid concentrations during summer upwelling (close to 100 µM), when river waters showed their minimum (slightly greater than 100 µM). During late fall and winter, river waters ranged from

Table 2. Comparisons of properties for channel and shallow stations in the Columbia River Estuary. Means represent data from all cruises + one standard error. Z = calculated Z-value for testing mean differences; p = probability. Level of significance: p = .05

VARIABLE	MEAN + s.e. channel	shallow	Z	p
Temperature (°C)	12.64 ± 0.73	12.72 ± 0.71	-0.07	n.s.
Nitrate + nitrite (μM)	16.19 ± 1.64	15.95 ± 2.70	0.07	n.s.
Silicic acid (μM)	145.78 ± 5.20	131.76 ± 7.47	0.53	n.s.
Phosphate (μM)	0.72 ± 0.04	0.73 ± 0.15	-0.06	n.s.
Chlorophyll *a* (mg m^{-3})	6.27 ± 0.48	7.46 ± 0.70	-1.38	sig.
Fluorescence	2.69 ± 0.17	3.25 ± 0.29	-1.64	sig.
DCMU-ratio	2.29 ± 0.06	2.20 ± 0.06	1.00	n.s.
Phaeophyptin *a* (mg m^{-3})	1.35 ± 0.12	2.11 ± 0.22	-2.92	sig.
Phaeophytin *a*: Chla *a*	0.32 ± 0.04	0.42 ± 0.05	-1.42	sig.
TSP (mg l^{-1})	25.08 ± 2.65	33.66 ± 2.68	-2.27	sig.
ISP (mg l^{-1})	21.68 ± 2.52	29.29 ± 2.43	-2.17	sig.
OSP (mg l^{-1})	3.32 ± 0.25	4.38 ± 0.43	-2.12	sig.
POC (mg l^{-1})	1.13 ± 0.07	1.30 ± 0.13	-1.13	sig.
PON (mg l^{-1})	0.14 ± 0.02	0.16 ± 0.04	-0.40	n.s.
C/N	10.90 ± 1.70	12.40 ± 2.20	-0.50	n.s.

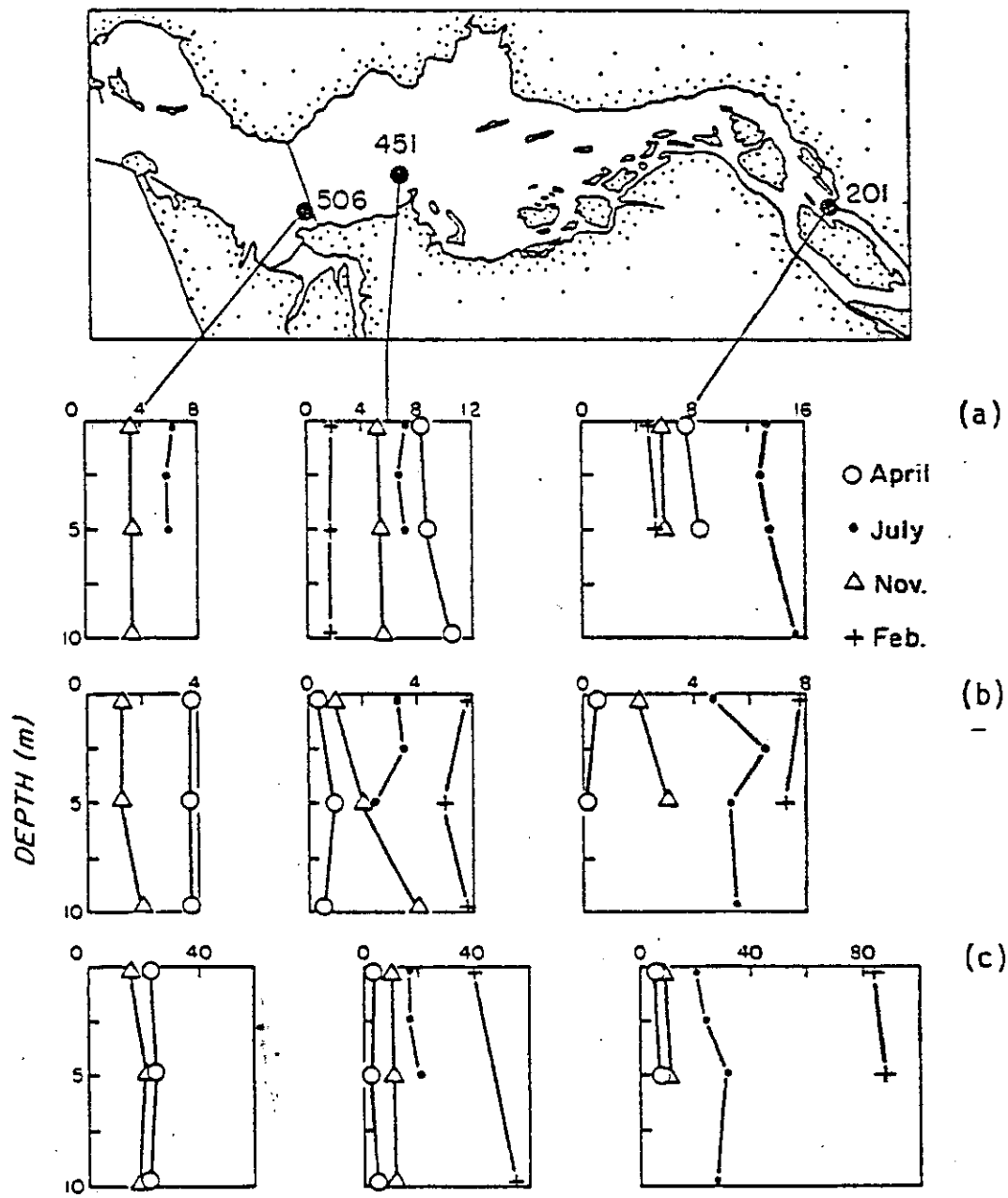


Figure 19. Vertical distributions of (a) chlorophyll a (mg m^{-3}), (b) organic suspended particles (mg mg l^{-1}), and (c) total suspended particles (mg l^{-1}) in the Columbia River Estuary.

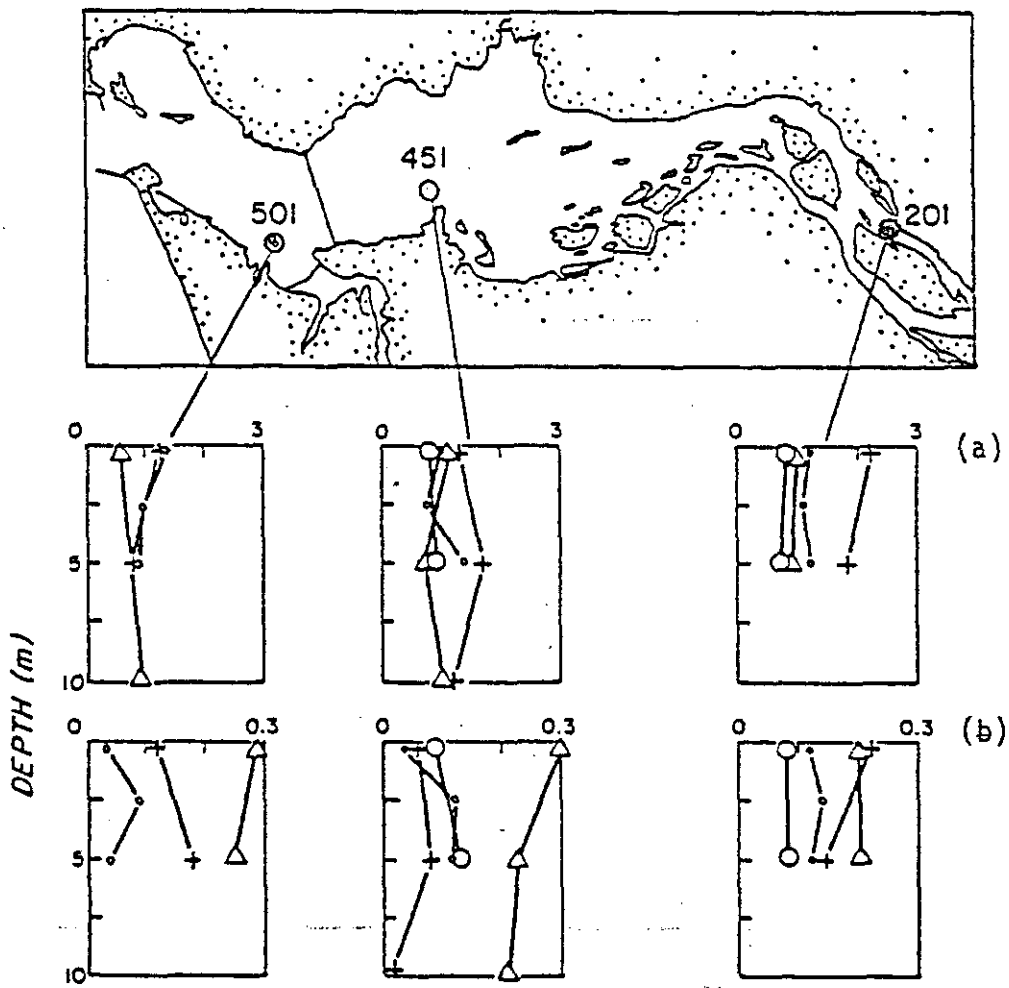


Figure 20. Vertical distributions of (a) particulate organic carbon (mg l^{-1}), and (b) particulate organic nitrogen (mg l^{-1}) in the Columbia River Estuary. Symbols as in Figure 19.

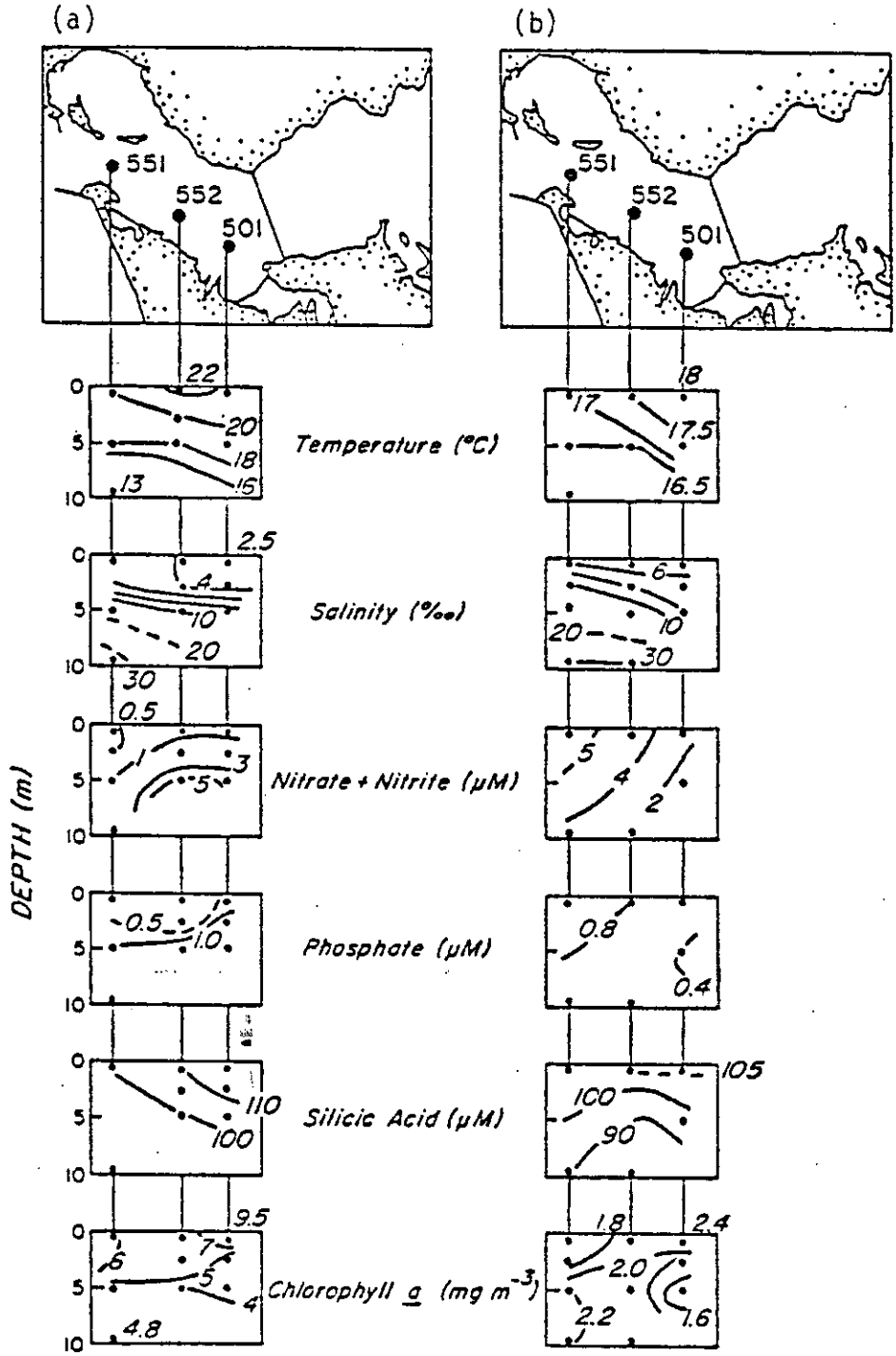


Figure 21. Vertical Distributions of properties in the marine zone of the Columbia River Estuary. (a) July, (b) September. The July data were taken on flood tide, while the September data were on the ebb tide.

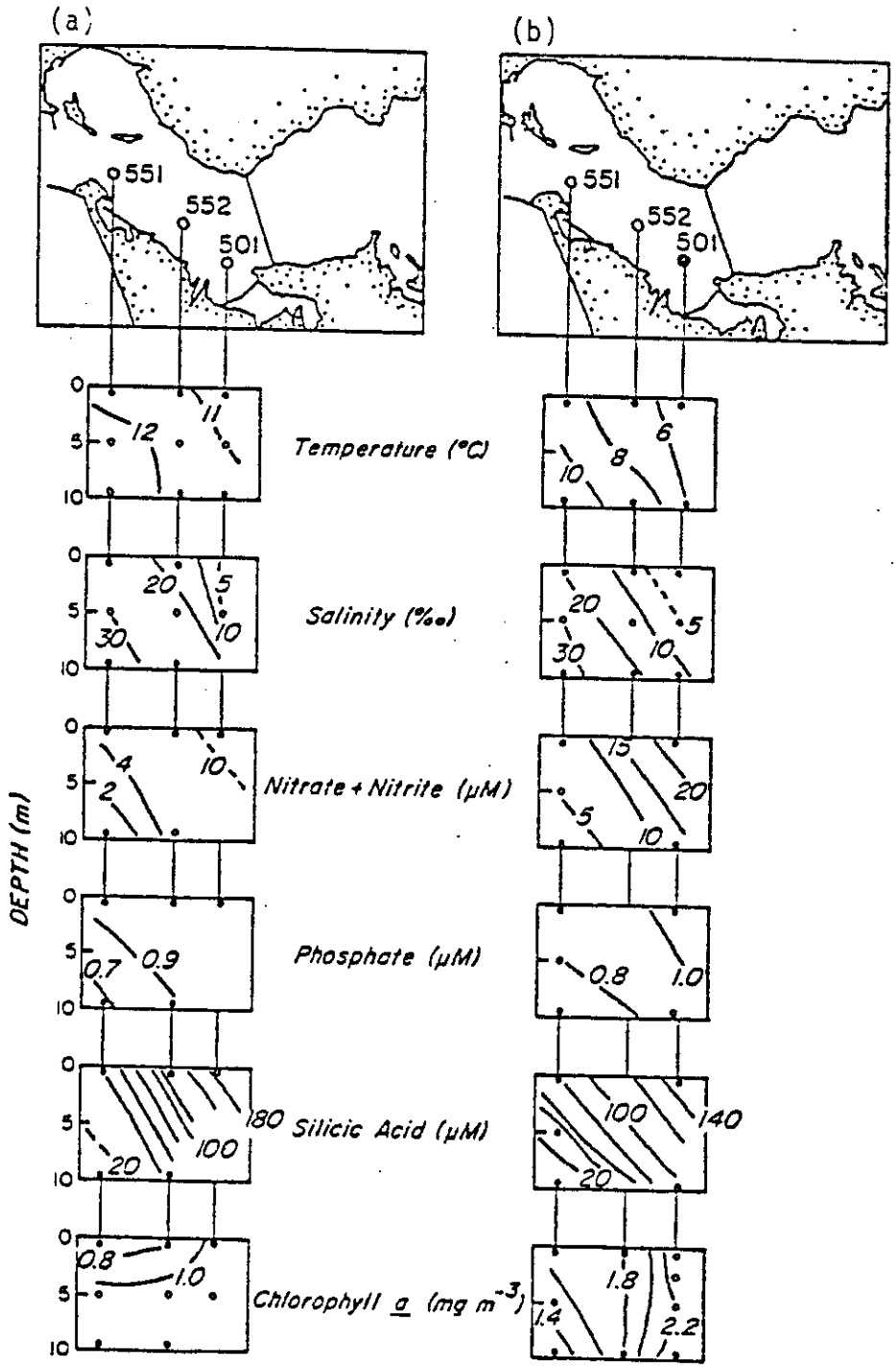


Figure 22. Vertical distributions of properties in the marine zone of the Columbia River Estuary. (a) November, (b) February. All data were taken on flood tide.

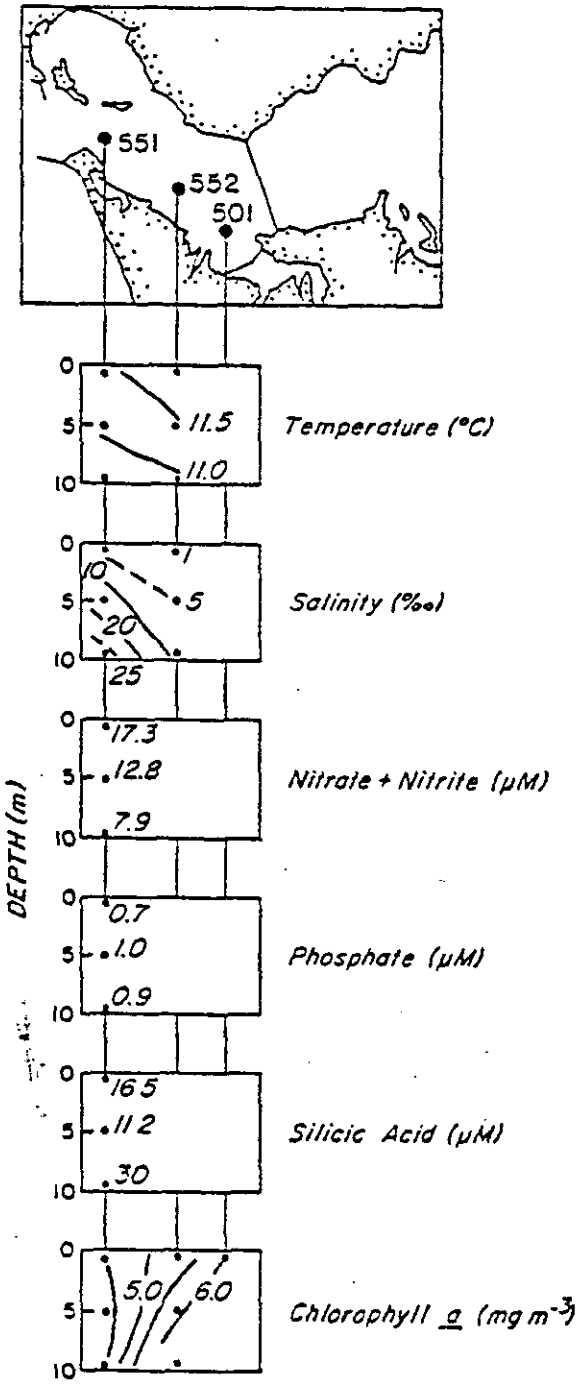


Figure 23. Vertical distributions of properties in the marine zone of the Columbia River Estuary during April 1981. Data taken on flood tide.

about 120 to greater than 180 μM, while entering marine waters were generally below 40 μM.

Chlorophyll a concentrations were almost always higher in the riverine waters. Maximum chlorophyll a concentrations in the entering marine waters occurred during spring-summer (nearly 5.0 mg m^{-3}), dropping off to about 1.0 mg m^{-3} by late fall.

3.4 PRIMARY PRODUCTION

A clear seasonal pattern of primary production was observed (Figure 24). Fall and winter samples throughout the estuary displayed low levels of photosynthetic carbon uptake/m^2, with values in November and February averaging 99 $mgCm^{-2}d^{-1}$ (range 14-103). Carbon uptake rates showed a general increase in spring 1981, and reached high values in July, averaging 759 $mgCm^{-2}d^{-1}$ (range 442-1449) for the three stations. Rates in May 1980 might have been depressed somewhat by the volcanic eruption. The productivity pattern closely paralleled the annual patten of phytoplankton biomass, as indicated by chlorophyll a concentrations (Figure 25), except in May 1980. In this month, chlorophyll a concentrations were higher than expected whle turbidity from the eruption reduced productivity.

Carbon uptake per unit chlorophyll a (assimilation number) was calculated using carbon uptake m^{-3} at the level of natural light which gave the maximum rate of uptake during incubation. This was usually the 50% light level, but in fall and winter the values were somewhat higher at 100% light than at 50%. Lowest production per unit chlorophyll was in winter, and highest was in summer (Figure 26). In May 1980 anomalously low production to chlorophyll a ratios resulted from the post-eruption high chlorophyll concentration coupled with relatively lwo primary production.

Our size fractionation experiments showed that throughout the year most production in the study area was attributable to the fractions of cells either larger than 33 μm, or less than 10 μm (Figure 27). A similar pattern was seen with chlorophyll a concentrations (Figure 28). During winter the 10 μm fraction predominated, while the ≥33 μm forms became proportionately more important in spring.

Predictive models of primary production in the study area were generated based on measured production rates (dependent variable), and ten ecological properties acting as independent variables (daily solar radiation, water temperature, chlorophyll a, pheophytin a, diffuse light attenuation coefficient, nitrate plus nitrite, phosphate, silicate, total seston, and organic suspended particles). Multiple regression analysis was done by a "forward stepwise" selection procedure (Rowe and Brenne 1981). At each step, the independent variable added to the model is that one which makes the greatest contribution to the reduction of the residual variability. The best models

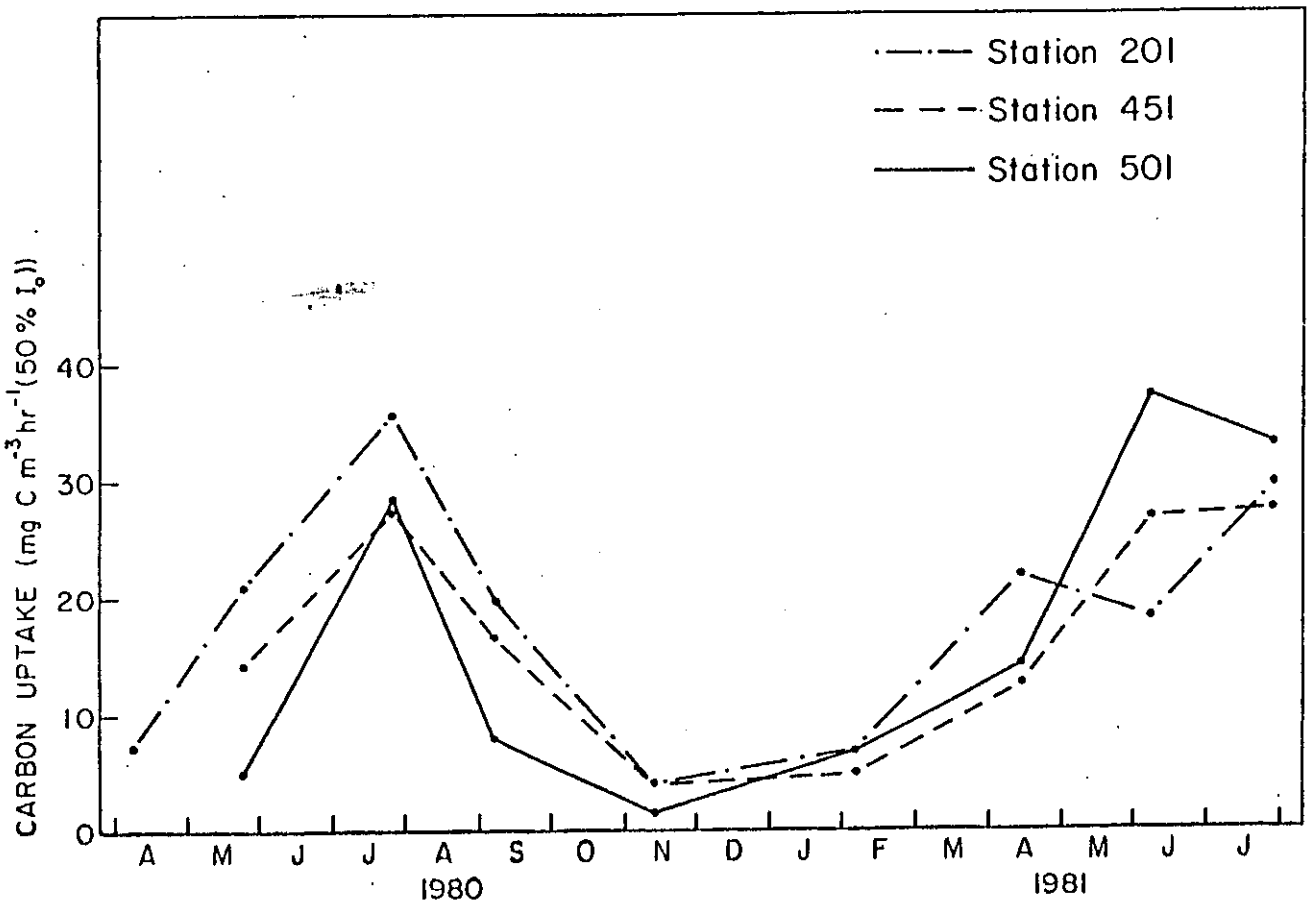


Figure 24. Temporal variation of carbon uptake rate at three representative stations.

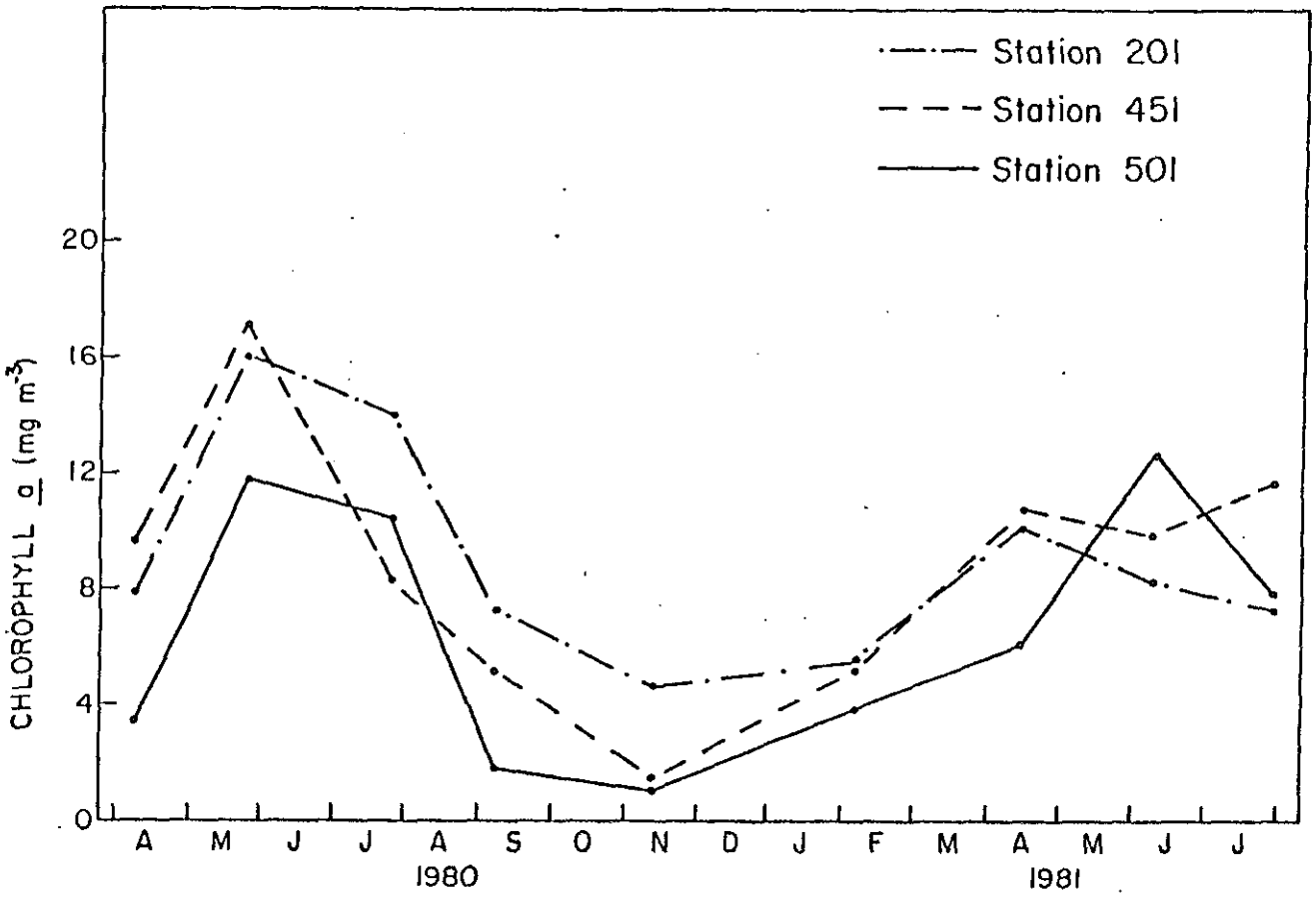


Figure 25. Temporal variation of Chlorophyll a concentrations at three representative stations.

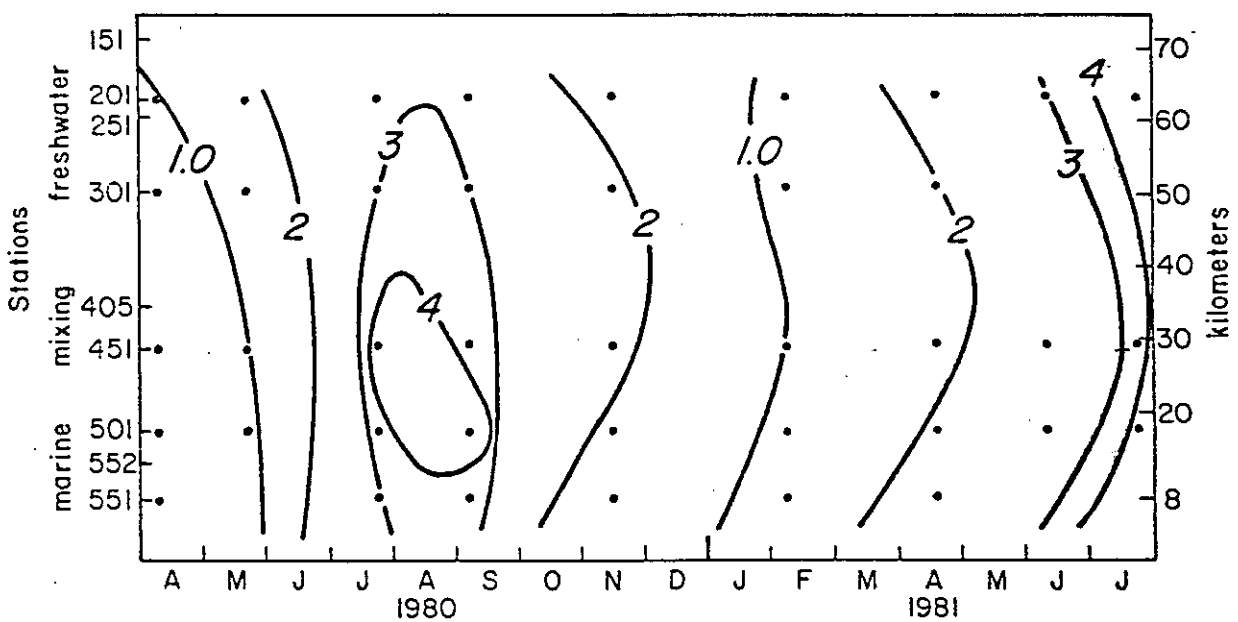


Figure 26. Spatial-temporal distribution of assimilation number in the Columbia River Estuary (mg C mg Chl $\underline{a}^{-1}hr^{-1}$).

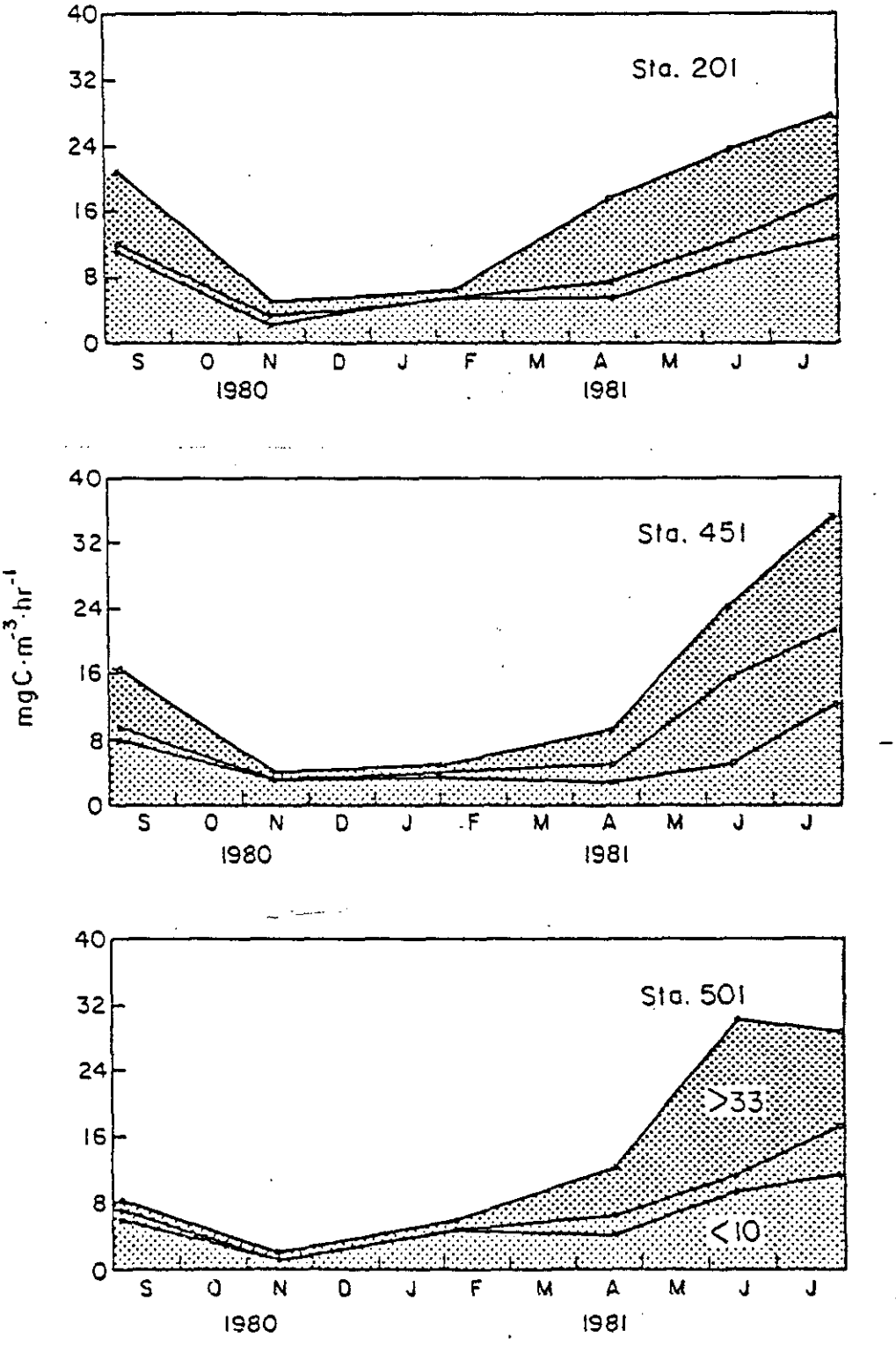


Figure 27. Cumulative graph of phytoplankton production by different size fractions, at three different stations along the main channel of the Columbia River Estuary.

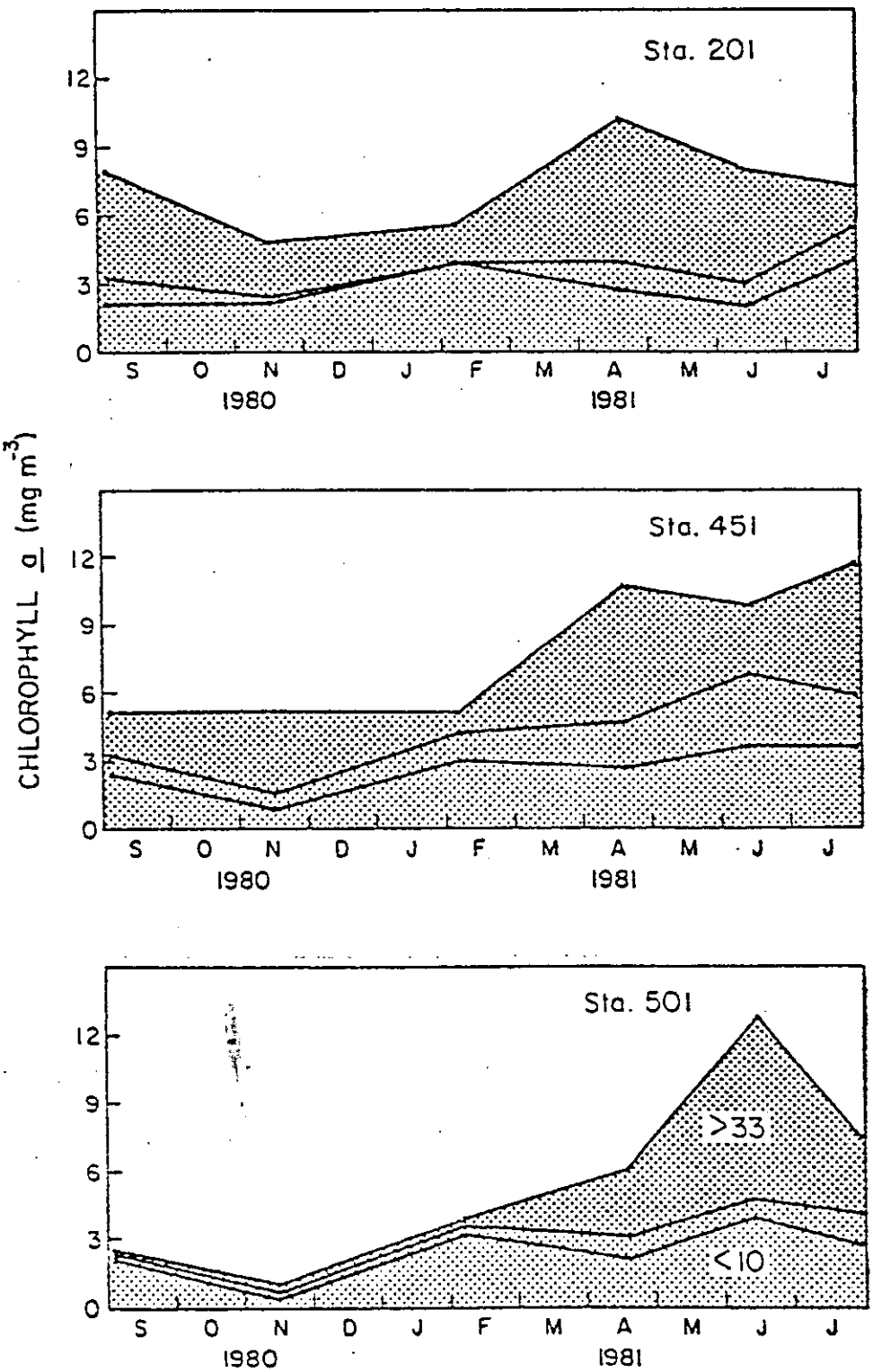


Figure 28. Cumulative graph of chlorophyll a content by different size fractions, at three different stations along the main channel of the Columbia River Estuary.

obtained are shown in Table 3. In the model for channel stations, for example, the daily solar radiation accounted for 58% of the variability in primary productivity. The light attenuation coefficient accounted for an additional 17% of the variability, so that the combined effect of daily solar radiation and light attenuation coefficient accounted for 75% of the variability. Daily solar radiation, light attenuation, chlorophyll a, temperature, and total seston accounted for 90% of the variability. In the regression model for shallow stations, three factors (daily solar radiation, light attenuation, and chlorophyll a) accounted for 85% of the variability in primary productivity. The remaining factors did not contribute significantly to the models. A time series of measured and predicted primary productivity values (predicted by the models in Table 3), are shown for two stations in the channel and shallow areas (Figure 29). The agreement seems acceptable, although high productivity values are always underestimated somewhat.

Phytoplankton productivity (mgC $m^{-2}day^{-1}$) for channel stations, using both measured and predicted values, showed strong seasonal variation (Figure 30). Maximum values during summer averaged 795 mgC $m^{-2}day^{-1}$ (range 467-1448) and minimum productivity in late fall (November), averaged 64 mgC $m^{-2}day^{-1}$ (range 19-102). Temporal variability of phytoplankton productivity (mgC $m^{-2}day^{-1}$) at the shallow stations (Figure 31) showed the same seasonal trend as in channel stations, with maximum summer productivities averaging 767 mgC $m^{-2}day^{-1}$ (range 421-1026) and minimum late fall rates averaging 28 mgC $m^{-2}day^{-1}$ (range 17-50). Although the shallow stations had slightly higher mean values for phytoplankton productivity and assimilation number than channel stations, no statistically significant differences were obtained (Table 4). The light attenuation coefficient (k) was significantly (p 0.10) higher in the shallows than in the channel (Table 4).

For purposes of estimating phytoplankton production over the entire estuary, the study area was divided into seven representative zones. Both measured and model-predicted primary production data were used to assign an average monthly production for each zone. For months not sampled, monthly production values were estimated using solar radiation data for that month and the ratio of monthly production:monthly solar radiation for adjacent months which had been sampled. Annual production m^{-2} in each zone was obtained by summing monthly production estimates. A gradual decrease from the upper estuary to the marine zone is evident (Figure 32). Highest production was measured in the Youngs River and the Lewis and Clark River (Figure 33); however, their total area is relatively small. A weighted average, based on the surface area of each zone, gave an annual phytoplankton production rate for the entire estuary of 90 gC $m^{-2}yr^{-1}$.

Table 3. Primary productivity regression model for channel stations in the Columbia River Estuary (n = 29). R^2 = coefficient of determination.

VARIABLE	R^2	MODEL
S = Daily solar radiation (g cal $cm^{-2}day^{-1}$)	0.58	Log daily productivity = 1.548 + 0.0015 S -0.103 k + 0.056 chla + 0.028 T -0.001 TSP
k = Light attenuation coefficient (m^{-1})	0.75	
Chla = Chlorophyll a (mg m^{-3})	0.84	
T = Temperature (°C)	0.87	
TSP = Total seston (mg l^{-1})	0.90	

Primary productivity regression model for shallow stations in the Columbia River Estuary (n = 28).

VARIABLE	R^2	MODEL
S = Daily solar radiation (g cal $cm^{-2}day^{-1}$)	0.73	Log daily productivity = 1.065 + 0.0035 S + 0.003 Chla -0.127 k
k = Light attenuation coefficient (m^{-1})	0.85	
Chla = Chlorophyll a (mg m^{-3}	0.78	

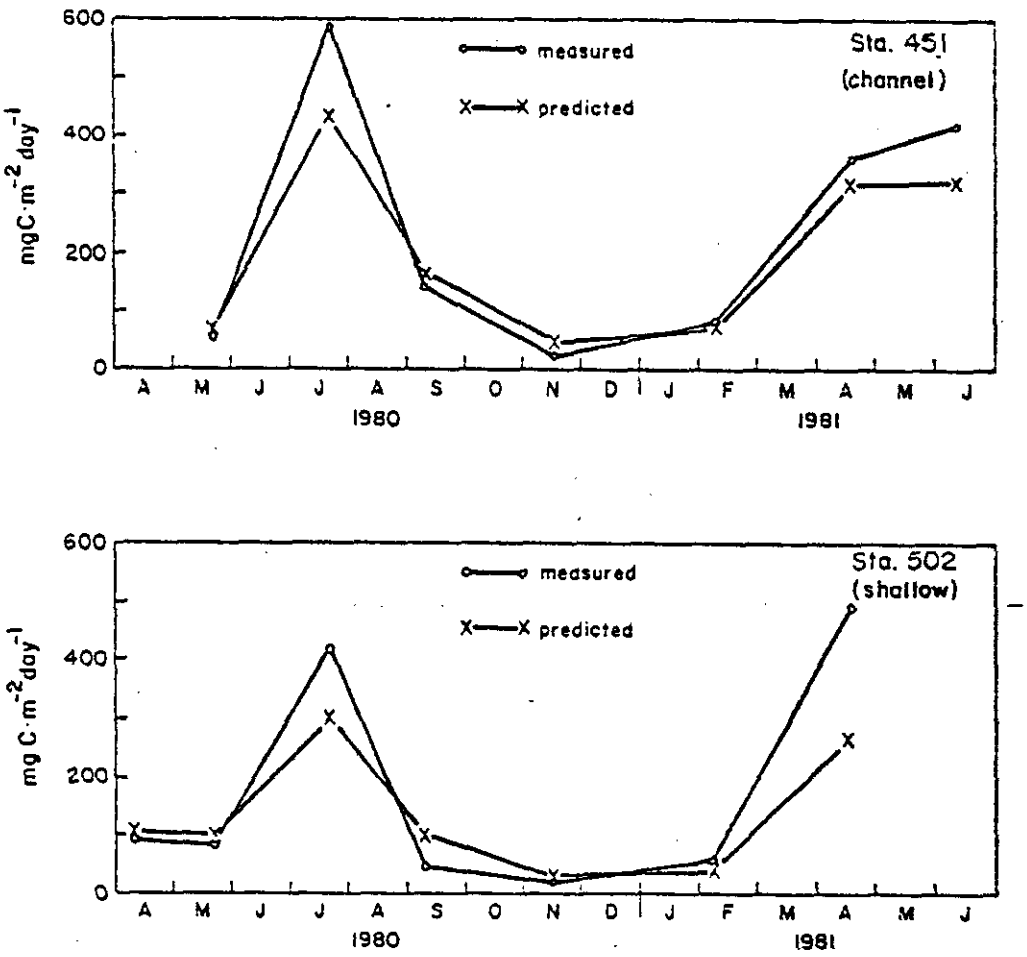


Figure 29. Temporal distribution of measured and predicted (by models) phytoplankton primary productivity in the Columbia River Estuary.

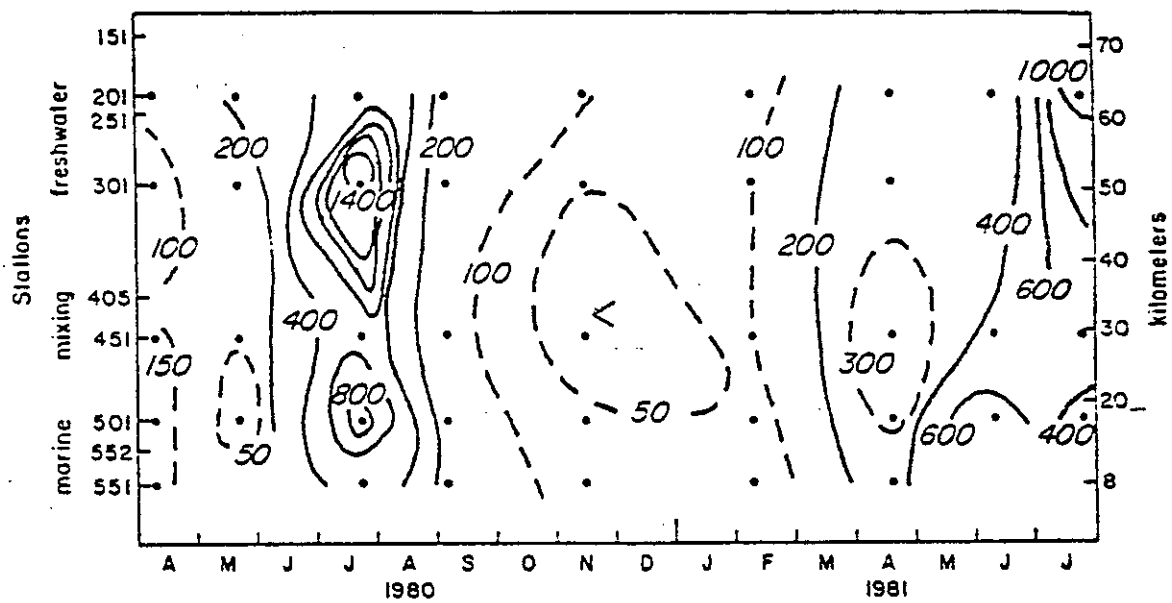


Figure 30. Spatial-temporal distribution of phytoplankton production in the Columbia River Estuary (mgC $m^{-2}day^{-1}$). Other comments as in Figure 8.

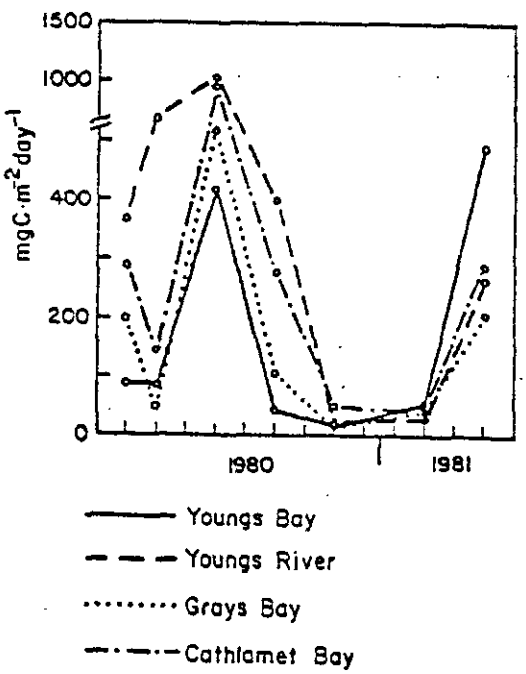


Figure 31. Temporal variability of primary production in shallow areas of the Columbia River Estuary.

Table 4. Comparisons of properties for channel and shallow stations. in the Columbia River Estuary. Means represent data from all cruises ± one standard error. t = calculated t-values for testing mean differences; p = probability.

Variable	Channel Mean ± s.e.	Shallow Mean ± s.e.	t	p
Primary productivity ($mgC\ m^{-2}day^{-1}$)	348.5 (± 12.0)	379.8 (±4.1)	-0.32	n.s.
Assimilation number ($mgC\ mgChla^{-1}hr^{-1}$)	2.6 (± 0.2)	3.2 (±0.5)	-1.05	n.s.
Light attenuation coefficient k (m^{-1})	1.9 (±0.1)	2.3 (±0.1)	-1.77	0.10

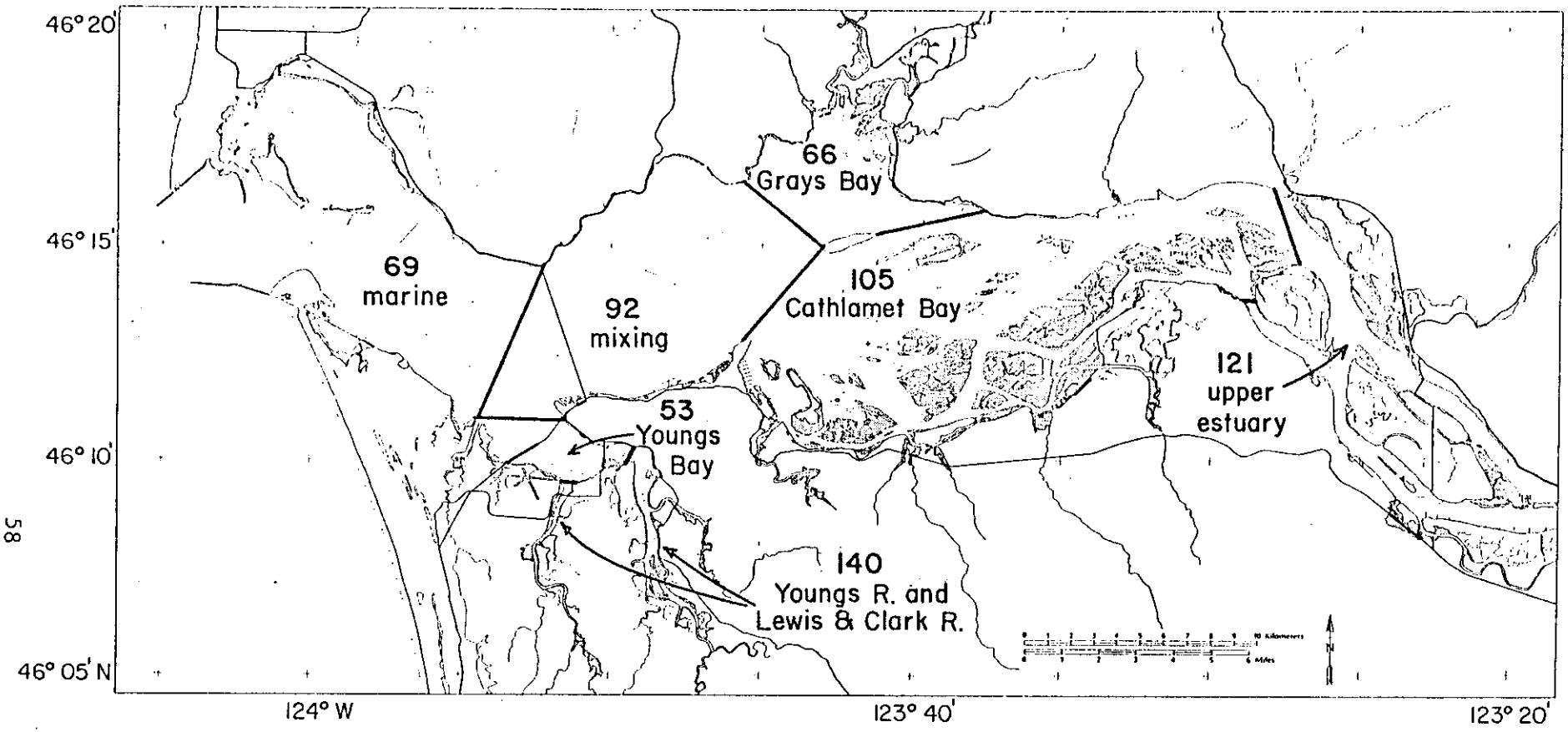


Figure 32. Annual primary production by zones in the Columbia River Estuary (gm C $m^{-2}yr^{-1}$).

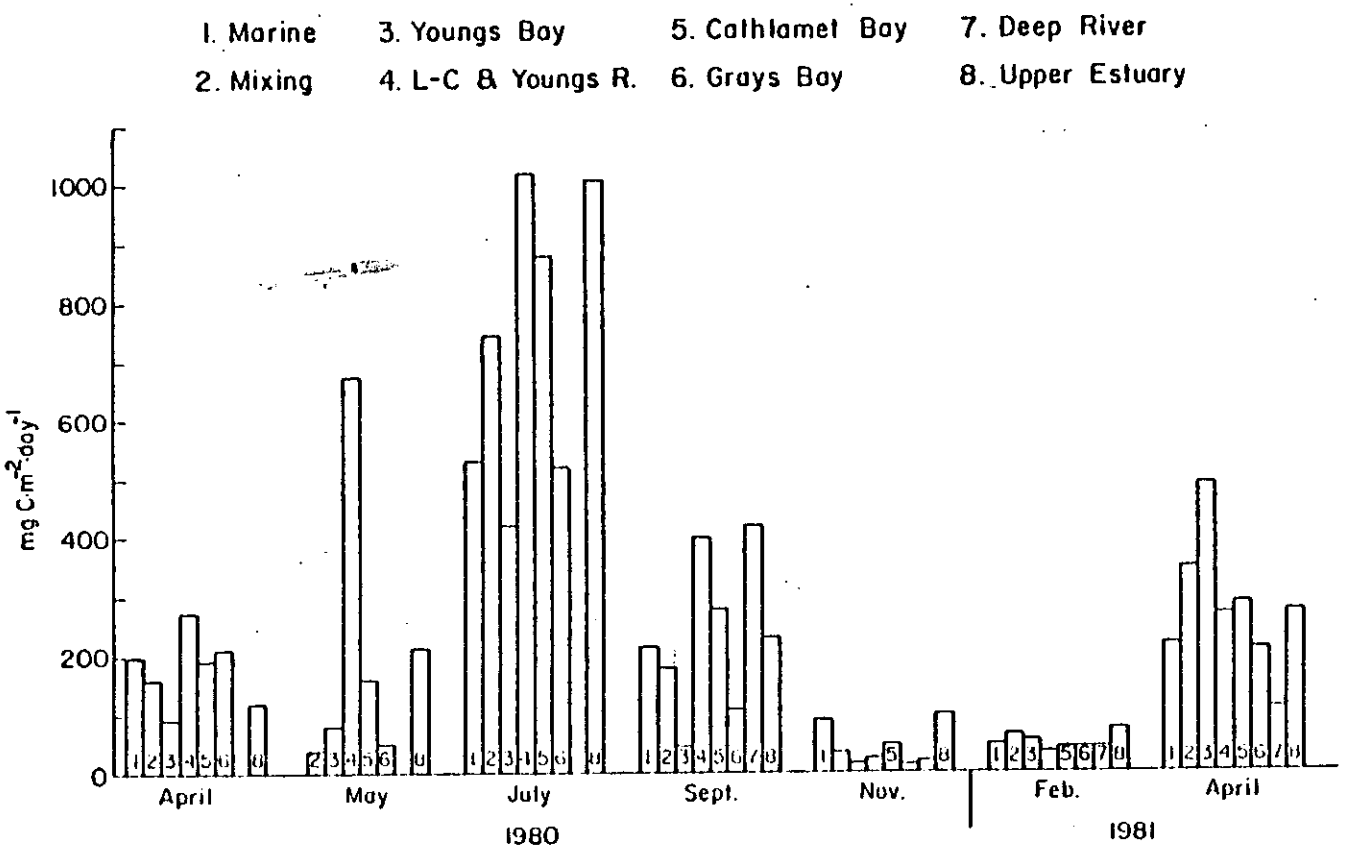


Figure 33. Temporal distribution of daily mean phytoplankton production in the Columbia River Estuary by zones.

3.5 ESTIMATED IMPACT OF THE MAY 18 1980 ERUPTION OF MT. ST. HELENS ON PRIMARY PRODUCTION

The explosive eruption of Mt. St. Helens on May 18, 1980, generated a plume of sand, ash, and debris which entered the Columbia River Estuary at the mouth of the Cowlitz River, near Longview, Washington (see Figure 5). Within three days turbid water filled the entire estuary. Analysis of data from our study shows that light attenuation in the water column is one of the most important factors in determining the amount of primary production taking place in the water column. The effects of post-eruption turbidity on phytoplankton primary production in the Columbia River Estuary were examined by comparing measured and estimated rates of carbon assimilation with and without the post-eruption turbidity.

Results comparing various physical and biological characteristics of the estuary one month before the initial eruption, several days after, and two months after the eruption are shown in Table 5. The diffuse light attenuation coefficient ($\underline{k}$) was greatly increased in May, and the depth of the 1% light level was, therefore, diminished. The concentrations of all particulate materials we measured were higher in May, but inorganic seston was most markedly increased. Riley (1959) related chlorophyll *a* concentration and light attenuation coefficient with the equation:

$$\underline{k} = 0.04 + 0.0088\ Chl + 0.054\ Chl^{2/3},$$

where $\underline{k}$ is the attenuation coefficient in m^{-1} and Chl is the particulate chlorophyll *a* concentrations in mg m^{-3}. Small and Curl (1972) showed the general applicability of this equation to coastal ocean water and estuarine discharge off Oregon, including the Columbia River Estuary. According to the equation, chlorophyll *a* in May should account for an attenuation coefficient of 0.4 m^{-1}, or about 5% of the diffuse attenuation coefficient. The remaining 95% of the diffuse attenuation coefficient after the eruption is attributable to the high non-chlorophyll *a*-associated seston load in the water.

Using $\underline{k}$ obtained by averaging values from April and July (1.6 m^{-1}), and actual values for chlorophyll *a* and incident light in May, a potential production rate of 585 mgC $m^{-2}day^{-1}$ is calculated for May from our channel productivity model. Production measured during our May cruises averaged 115 mgC $m^{-2}day^{-1}$. The difference between the actual measured rates and the calculated value without the increased light attenuation attributable to the eruption amounted to 470 mgC $m^{-2}day^{-1}$, or 1.3×10^8 gC day^{-1} in the entire 75 km length of the estuary. This is a reduction in daily water column primary production of 80% (Table 6).

By the time of our July cruise, the water had cleared to normal turbidity levels. Secchi disk data collected every two weeks (English

Table 5. Physical and biological surface characteristics of the Columbia River Estuary before, shortly after, and 2 months after the initial eruption of Mt. St. Helens.

	April 9-11 1980		May 22 1980		July 22-24 1980	
	mean	range	mean	range	mean	range
Light attenuation coef. ($\underline{k}$) (m^{-1})	1.5	(1.2-2.3)	8.7	(6.4-11.0)	1.7	(1.3-2.6)
1% light depth (m)	3.1	(2.0-3.8)	0.5	(0.4-.7)	2.7	(1.8-3.5)
Chlorophyll $\underline{a}$ (mg m^{-3})	6.3	(1.7-9.7)	12.55	(5.2-21.2)	11.8	(3.6-16.6)
Total seston (g m^{-3})	10.6	(3.5-24.2)	353.0	(130.0-638.0)	28.3	(13.3-37.3)
Inorganic seston (g m^{-3})	8.8	(2.5-22.2)	343.5	(125.7-618.8)	23.6	(13.3-28.6)
Organic seston (g m^{-3})	1.8	(0.0-4.3)	9.5	(2.5-28.0)	4.7	(0.0-9.3)
Particulate carbon (g m^{-3})	0.92	(0.87-1.05)	7.03	(3.47-13.04)	1.22	(0.81-2.72)
Particulate nitrogen (g m^{-3})	0.11	(0.09-0.15)	0.42	(0.06-0.74)	0.10	(0.03-0.17)

Table 6. Rates of primary production in the Columbia River Estuary following the eruption of Mt. St. Helens.

	May 22 1980		Total primary production integrated during the period May 20-June 25 1980	
	$mgC\ m^{-2}d^{-1}$	$gC\ d^{-1}$ in whole estuary	$gC\ m^{-2}$	gC in whole estuary
A. Mean measured production	115	0.3×10^8		
B. Calculated production with actual $\underline{k}$			5.7	1.6×10^9
C. Calculated potential production with $\underline{k} = 1.6\ m^{-1}$	585	1.6×10^8	23.2	6.5×10^9
D. Production lost by increased $\underline{k}$ (C-A for May 22; C-B for May 20 to June 25)	470	1.3×10^8	17.5	4.9×10^9
E. % Reduction	80	80	75	75

and Kisker, unpublished data) allowed us to estimate the rate of recovery of transparency in the water column. Secchi depths from stations in the freshwater portion of the estuary were averaged, and these mean Secchi depths were converted to k, based on our less-frequent submarine photometer readings, in order to estimate k through the recovery period. Water transparency stabilized at relatively normal values by the last week of June 1980.

Using the equation relating production rate to light attenuation, incident light, and chlorophyll a (Table 3), we estimated the difference between production with normal light attenuation values (averaging April and July), and with actual light attenuation values during the 5 weeks it took for the water to clear to normal levels. We estimate that during this period total water column primary production was reduced by 17.5 gC m^{-2}, or 14.9×10^9 gC throughout the estuary (Table 6). This constitutes a 75% reduction of the primary production expected with normal levels of turbidity over the 5-week period.

3.6 PHYTOPLANKTON COMMUNITY COMPOSITION

The readily identifiable estuarine phytoplankton consists primarily of freshwater diatoms. However, it is clear from our phytoplankton size-fractionation experiments (Figures 27, 28) that small cells were abundant, and it is possible that smaller flagellates were destroyed by fixation and missed in subsequent determination (Semina 1978).

Diatom species collected during this study are shown in Table 7. The most abundant freshwater diatoms during this study were Asterionella formosa, Melosira islandica, M. italica, Fragilaria crotonensis, Cylotella glomerata, and Stephanodiscus astraea. All these species are common in eutrophic lakes (Hutchinson 1967) and in other major rivers; e.g., the Mississippi River (Baker and Baker 1979) and th St. Lawrence River (Cardinal and Therriault 1976). Over 90% of the identifiable total cells were planktonic species, with very few benthic forms observed. Very few marine species were encountered during the course of this study, and their numerical abundance was low; however, samples from the salt wedge were not collected. Similar phytoplankton assemblages were reported by Williams and Scott (1962) and Williams (1964, 1972), and by Haertel et al. (1969) in a more detailed taxonomic examination of the phytoplankton flora of the Columbia River Estuary.

Total numbers of diatoms in the mixing zone were greatest during July (12.5×10^3 cells ml^{-1}), and decreased to 8×10^2 cells ml^{-1} in November (Figure 34a). The predominant species showed a seasonal trend, with maximum abundances during summer and minimum in late fall through winter (Figure 34b).

Table 7. Phytoplankton diatoms collected in the Columbia River Estuary.

Achnanthes hauckiana	Navicula cryptocephala
A. minutissima	N. gregaria
A. lanceolata	N. mutica
Amphora ovalis	N. pupula
Asterionella formosa	N. viridula
Cocconeis pediculus	Nitzschia dissipata
C. placentula	N. frustulum
Cyclotella compta	N. kutzingiana
C. glomerata	N. recta
C. kutzingiana	Opephora martyi
C. stelligera	Plagiogramma vanheurkii
Cymbella prostrata	Rhoicosphenia curvata
Diatoma tenue	Scenedesmus quadricauda
Fragilaria capucina	S. obliquus
F. construens	Stephanodiscus astraea
F. crotonensis	S. alpinus
F. pinnata	S. hantzschii
F. vaucheriae	Surirella angustata
Gloeocystis sp.	Synedra delicatissima
Gomphonema intricatum	S. fasciculata
G. olivaceum	S. filiformis
Hannea arcus	S. parasitica
Melosira distans	S. ulna
M. granulata	Tabellaria fenestrata
M. islandica	Thalassiorsira sp.
M. italica	
M. sulcata	
M. varians	

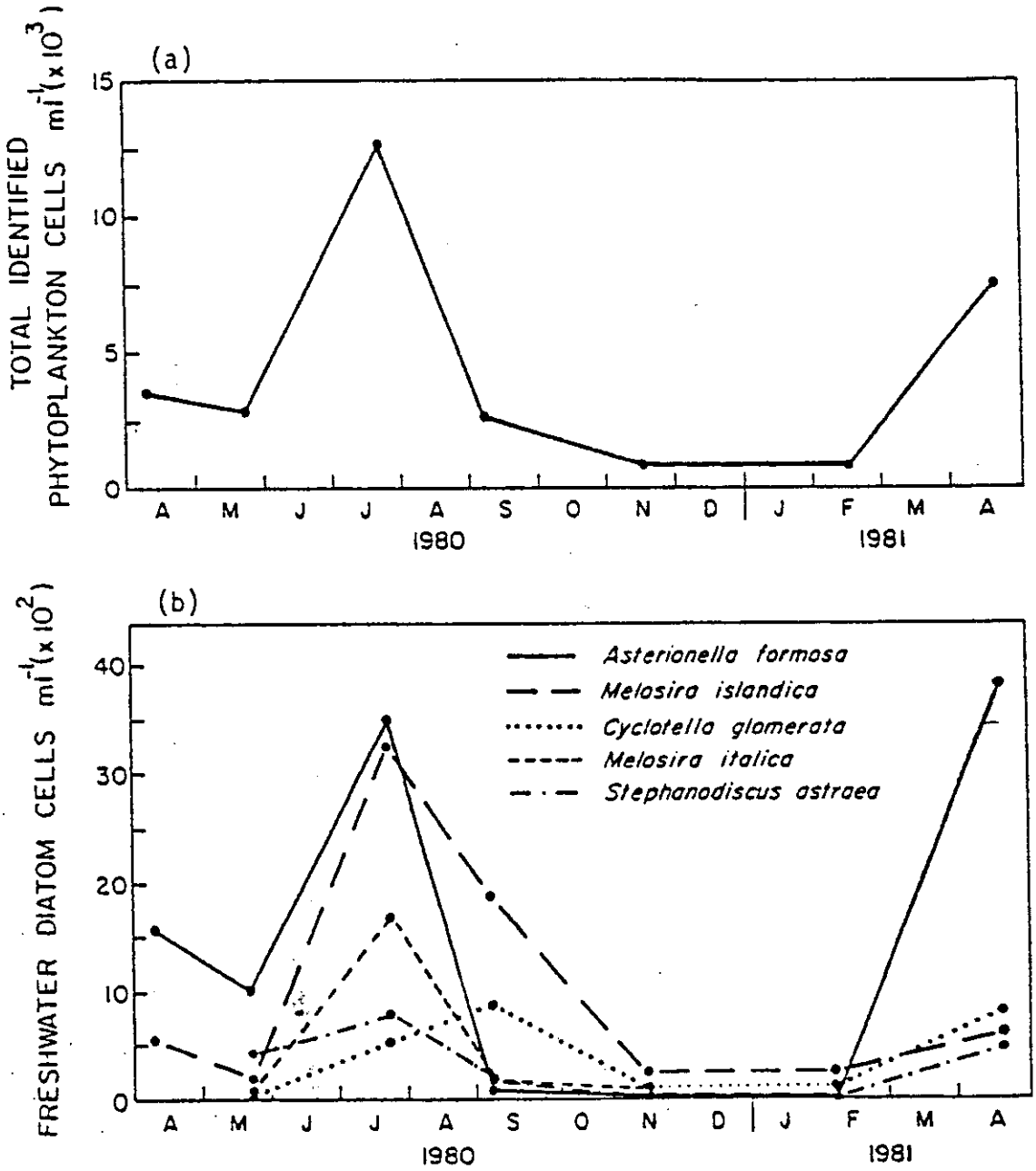


Figure 34. (a) Temporal distribution of total identified phytoplankton cells in the mixing zone of the Columbia River Estuary.
(b) Temporal distribution of the predominant freshwater diatom cells.

3.7 ZOOPLANKTON GRAZING

3.7.1 Zooplankton Ingestion in the Dark

The accumulation of ^{14}C from pre-labelled natural phytoplankton in the dark by the three most abundant zooplankton groups (small copepods, Daphnia sp., and Bosmina longirostris) is shown in Figure 35. Similar trends in the uptake curves were shown by all three groups on a per animal basis.

The first two hours of uptake could be fit by straight lines, so this early portion of the curve might be considered representative of ingestion processes. However, grazing rates were calculated using only the uptake values for the first hour in order to reduce the probability of including ^{14}C loss via fecal pellet production in the ingestion calculation. Reported gut passage time measurements for mixed species of copepods have ranged from one to three hours (Dagg and Grill 1980; Hayward 1980). After two hours, the curve was considered to be affected by ingestion, assimilation, and excretion processes.

Filtering rates (volume of water swept clear per animal per day) were calculated for both copepods and cladocerans according to the formula:

$$f = \frac{a}{p} \times \frac{24\ hr}{h} \times \frac{}{day}$$

where: f = filtering rate (ml animal^{-1}day^{-1})
a = disintegrations per minute (dpm) per animal
p = dpm per ml of phytoplankton suspension
h = hours of feeding

There were no significant differences between the filtering rates at the three stations within any given month, or between the two months (Table 8); however, significant differences were observed between Bosmina longirostris and the other two groups. Copepods and Daphnia sp. both had mean filtering rates of approximately 1.2 ml animal^{-1}day^{-1} (ranges 0.93 to 1.62, and 1.19 to 1.26, respectively), while Bosmina longirostris had the lowest filtering rate, 0.49 ml animal^{-1}day^{-1} (range 0.32 to 0.61).

3.72 Zooplankton Ingestion in the Light

Zooplankton filtering rates for B. longirostris and mixed copepods are shown in Table 9 for the light experiment performed in June at Station 201. Rates were somewhat higher than comparable rates at Station 201 from the dark experiments, but were not significantly different.

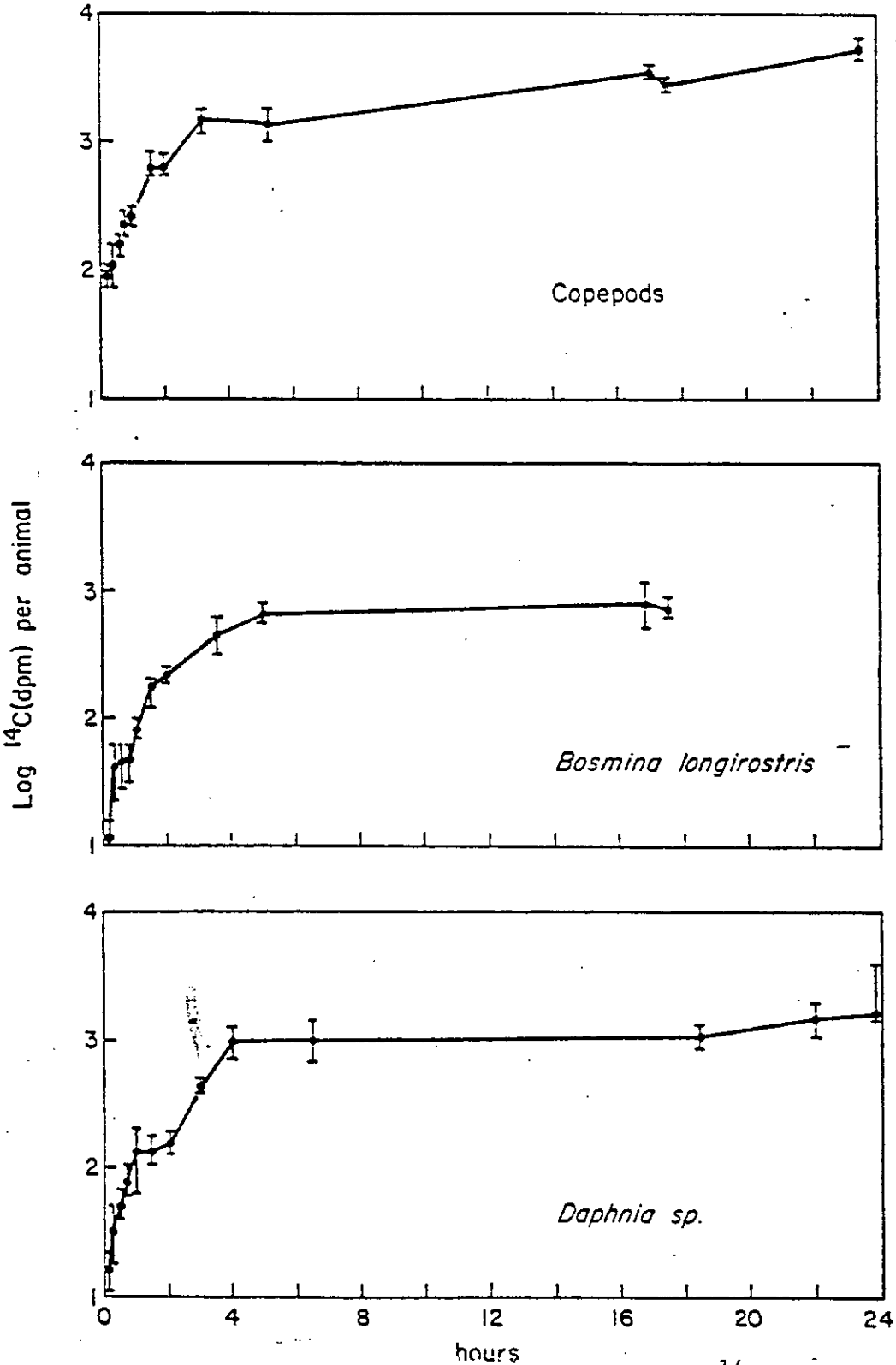


Figure 35. Time series of mean zooplankton accumulation of ^{14}C from pre-labelled phytoplankton, by the 3 most common taxa in the Columbia River Estuary. Bars indicate ± one standard error.

Table 8. Mean filtration rates for the three most abundant taxa in the Columbia River Estuary ± one standard error. n = six animals per station.

Group	Station	f (ml animal^{-1} day^{-1}) June	f (ml animal^{-1} day^{-1}) July
Copepods	501	1.03 ± 0.25	1.62 ± 0.25
"	451	1.00 ± 0.13	0.93 ± 0.40
"	201	1.10 ± 0.24	1.53 ± 0.31
	Mean	1.04 ± 0.20	1.36 ± 0.32
B. longirostris	501	0.61 ± 0.24	
"	451	0.32 ± 0.03	
"	201	0.55 ± 0.19	
	Mean	0.49 ± 0.15	
Daphnia sp.	451		1.26 ± 0.32
"	201		1.19 ± 0.22
			Mean 1.22 ± 0.27

Table 9. Mean filtration rates for zooplankton taxa in the light, ± one standard error. n = six animals per taxa.

Month	Station	Species	ml (day^{-1}) x 10^{-4}
June	201	Copepods	1.5 ± 0.2
June	201	*B. longirostris*	0.9 ± 0.4

3.73 Grazing Rates by Phytoplankton Disappearance

During July 1981, changes in the grazed and ungrazed ^{14}C-prelabelled natural phytoplankton community were followed during a 24-hour period (Figure 36), as another approach to estimating grazing. Specific zooplankton community grazing rates were computed from the differences between the grazed and ungrazed phytoplankton populations. Specific community grazing rates calculated from these experiments (Table 10a) were slightly higher than the community grazing rates calculated from the July zooplankton ingestion experiments (Table 10b). The latter specific grazing rates for the total community of zooplankton were computed by pooling the three groups, and were calculated according to the formula:

$$G = \frac{z}{t\,h} \qquad (2)$$

where G = specific community grazing rate (h^{-1})
z = disintegrations per minute (dpm) per total zooplankton
t = dpm per total phytoplankton
h = hours of feeding

The agreement between the results from these two methods is good considering the potential error in these types of experimental comparisons.

Total Estuarine Phytoplankton Removal by Grazing

For purposes of this analysis it is necessary to have estimates of the concentrations of zooplankton in the estuary. No detailed distributional studies exist. We have assumed that zooplankton concentrations previously reported in the literature during different seasons are representative of the entire estuary (Table 11). From these data we estimated seasonal values of total zooplankton concentration that best represent the available data. Where there is a large concentration range for a given season, values toward the maximum concentration have been selected, in order to avoid underestimation of grazing removal.

Daily phytoplankton removal by zooplankton grazing was estimated for each month of the year (Table 12) by using the representative seasonal value for total zooplankton concentration in the estuary (Table 11), an estimated monthly phytoplankton carbon biomass (Table 12), and an average filtration rate of 1.2 ml $animal^{-1}day^{-1}$ (Table 8). It was assumed that the filtration rate per animal was constant throughout the year only because there were few grazing data available during the year (none available in winter). Likely the use of one filtration rate based only on spring and summer rates will yield some overestimate of true annual grazing pressure.

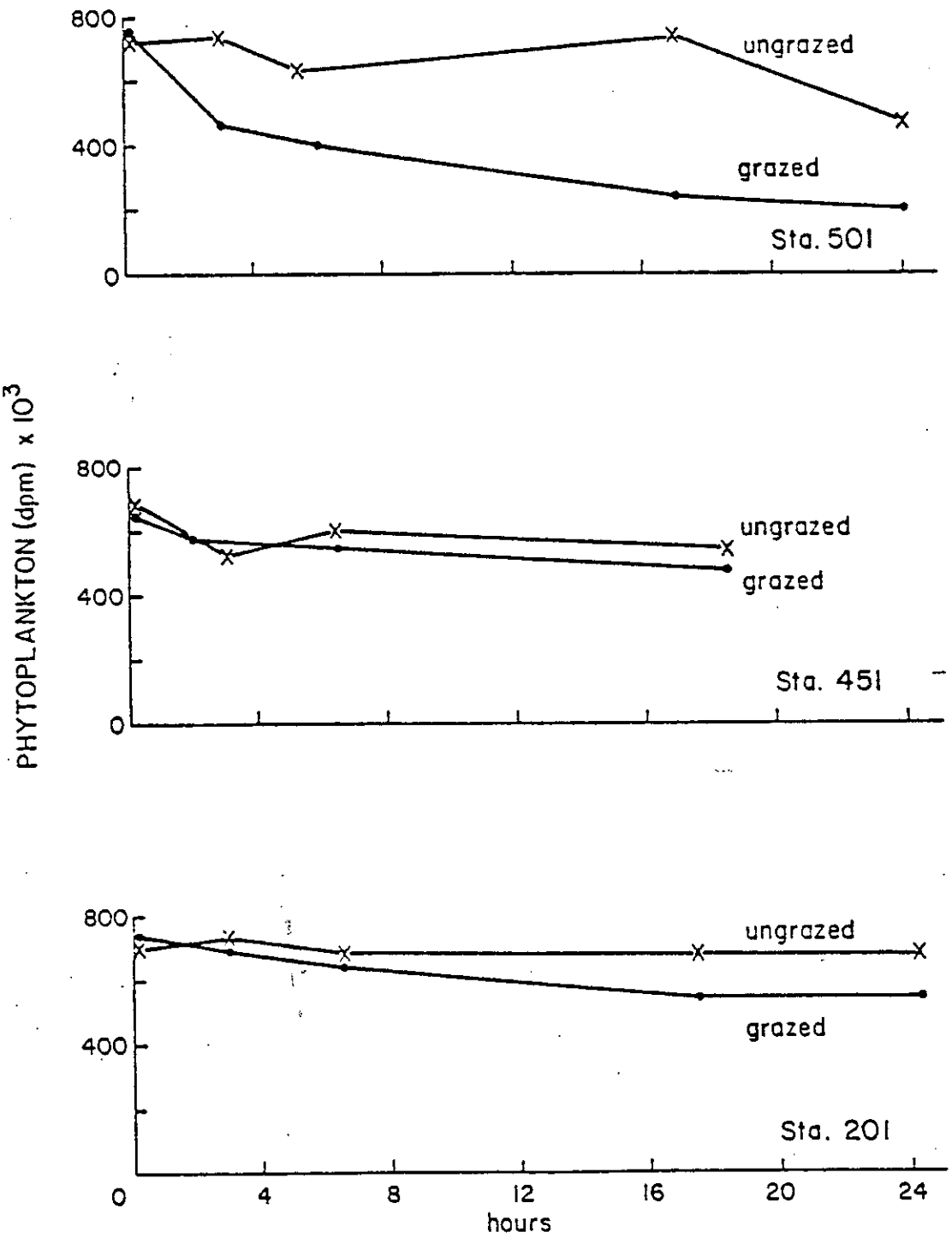


Figure 36. Time series of phytoplankton (dpm·10^3) disappearance by community zooplankton grazing at three different stations along the main channel of the Columbia River Estuary.

Table 10a. Mean specific community grazing rates from phytoplankton disappearance experiments.

Month	Station	$G(hr^{-1}) \times 10^{-4}$	$G(day^{-1}) \times 10^{-4}$
July	501	3.54	85.1
July	451	2.69	64.7
July	201	3.12	75.0
	Mean	3.11	74.9

Table 10b. Mean specific community grazing rates for zooplankton in the dark, $\pm$ one standard error.

Month	Station	$G(hr^{-1}) \times 10^{-4}$	$G(day^{-1}) \times 10^{-4}$
July	501	2.70 ± 0.41	64.8 ± 10.0
July	451	1.90 ± 0.59	45.6 ± 14.3
July	201	2.45 ± 0.44	58.8 ± 10.6
	Mean	2.35 ± 0.48	56.4 ± 11.6

Table 11. Total zooplankton concentration of the dominant species in the Columbia River Estuary.

Dominant species	Habitat	Total zooplankton (animals m^{-3}) spring	summer	fall	winter
Bosmina sp., Cyclops vernalis, Daphnia longispina	freshwater[1]	10^3	10^3-$5x10^3$	10^3	10^2
Eurytemora affinis, Canuella canadensis	brackish[1]	10^3-$4x10^4$	10^3-10^4	10^3	10^3
Pseudocalanus minutus, Acartia clausi, A. longiremis	marine[1]	10^3-$3x10^3$	10^3-$5x10^3$	10^3	10^2
Eurytemora hirundoides (affinis) Bosmina longirostris, Daphnia longispina	brackish[2] and freshwater	10^3	10^3-$2x10^3$	10^3	10^3
Eurytemora affinis	brackish[3]	10^3-$5x10^3$	10^3-10^3	n.d.	n.d.
Concentrations chosen for grazing removal estimations		10^4	10^4	10^3	$0.5x10^3$

[1]After Haertel (1970)

[2]After Misitano (1974)

[3]This study

Table 12. Daily phytoplankton carbon removal by zooplankton grazing in the Columbia River Estuary, for each month of the sampling period.

Month	Zooplankton[1] 10^3 (m^{-3})	Grazing rate[2] (% day^{-1})	Phytoplankton[3] biomass (mgC m^{-3})	Grazing removal (mgC m^{-3} day^{-1})
A	10	1.2	223	2.67
M	10	1.2	493	5.91
J	10	1.2	424	5.08
J	10	1.2	356	4.27
A	10	1.2	255	3.06
S	1	0.12	155	0.18
O	1	0.12	124	0.15
N	1	0.12	93	0.11
D	0.5	0.06	93	0.05
J	0.5	0.06	113	0.06
F	0.5	0.06	133	0.08
M	1	0.12	214	0.25

[1]Concentrations from Table 16.

[2]Product of zooplankton concentration ($No.m^{-3}$) times a mean filtration rate of 1.2 ml $animal^{-1}day^{-1}$, expressed as a percentage.

[3]Average chlorophyll *a* m^{-3} x 40, where C/chl*a* = 40 (see discussion).

Maximum phytoplankton grazing removal (Table 12) was attained during later spring and summer (May through August), averaging 4.6 mgC $m^{-3}day^{-1}$ (range 3.06 to 5.91), or about 1.2% of the phytoplankton carbon available. Minimum rates were obtained during winter (December through February), averaging 0.06 mgC $m^{-3}day^{-1}$ (range 0.05 to 0.08), or about 0.06% of the phytoplankton carbon available.

Daily removal rates were expanded (multiplying by days $month^{-1}$) to monthly removal estimates. Then values of monthly removal were added to give a crude estimate of annual phytoplankton removal by grazing zooplankton. The annual phytoplankton grazing removal for the estuary was estimated at 669 mgC $m^{-3}yr^{-1}$, which is probably in the right order of magnitude. It should be noted that phytoplankton removal by phytophagous fishes, etc. was not assessed, but the effort to err on the side of overestimation in the case of zooplankton grazing perhaps offset the lack of data on phytoplankton removal by biota other than zooplankton.

3.8 TRANSPORT RATES OF ECOLOGICAL PROPERTIES

Transport rates of chlorophyll a, inorganic nutrients (nitrate plus nitrite, phosphate and silicic acid), particulate organic carbon (POC), particulate organic nitrogen (PON), total suspended particles (TSP), organic suspended particles (OSP), and inorganic suspended particles (ISP), were calculated with the following formula:

$$T = D \cdot C$$

where T = transport rate (g sec^{-1})
D = river discharge (m^3 sec^{-1})
C = concentration (g m^{-3})

River discharge data for the mouth of the Columbia River Estuary were taken from the U.S. Geological Survey (1980, 1981) for the period studied. In order to estimate the amount of materials imported to the area studied from the main stem of the Columbia River, river discharge data were estimated for the upper-most station (River Mile 47) by calculating the river discharge at Longview, Washington (River Mile 65, where data are available), and assuming that river discharge at mile 65 was the same as at mile 47. The assumption of discharge similarity at River Miles 47 and 65 was considered a good one, because there are no other rivers flowing into the main stem of the Columbia River along this section. Present river discharge at River Mile 65 was estimated by calculating the percent difference between the river discharge at the river mouth and at Longview, based on a 1961-1975 data record. This percent difference was then applied to estimate the river discharge at Longview (and hence, by assumption, at the head of our study section at River Mile 47) during our study.

Columbia River flow is characterized by two peaks per year (Figure 37). The spring peak, usually reaching a maximum in late

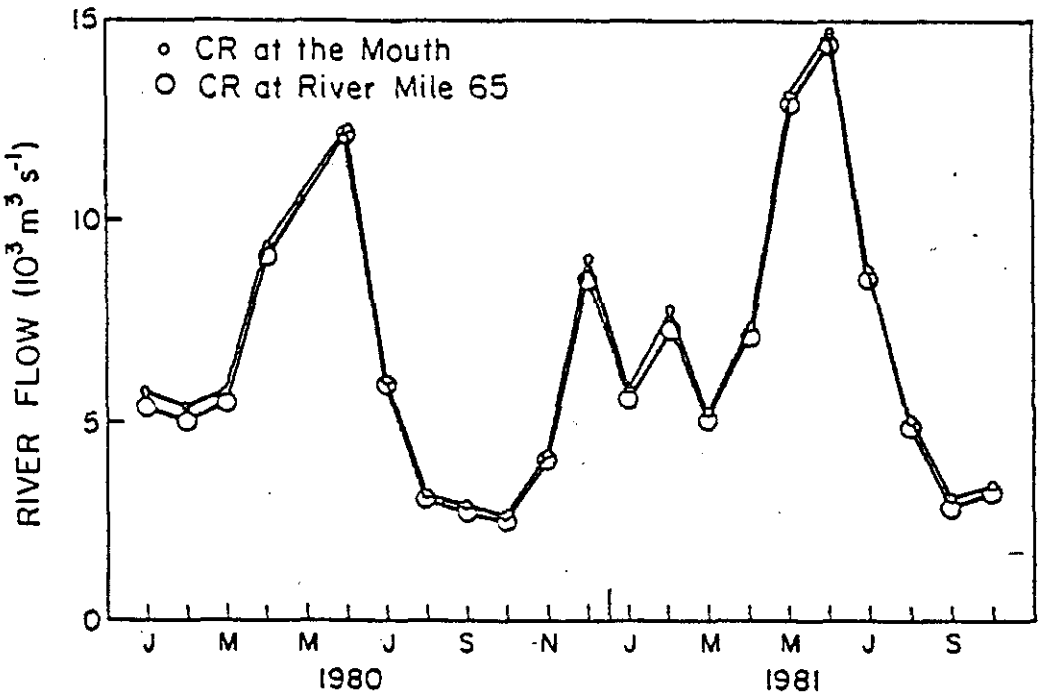


Figure 37. Monthly averages of Columbia River flow.

May or June, is caused by snow melt in the mountains of the drainage basin. The winter peak can occur from December through March, and is primarily caused by precipitation and flooding in the tributaries west of the Cascade Range. Extremes encountered during the course of this study were 14695 m^3sec^{-1} in June 1981 and 2613 m^3sec^{-1} in October 1980. The similarity of the transports at the mouth and at River Mile 47 result from the extreme dominance of the Columbia River over the small rivers in the study area.

Estimation of the mass flux of constituents at an estuary mouth is often a very difficult problem in which river flow, tidal flow and mixing, wind-driven circulation, and horizontal dispersive transport all can be factors. Moreover, the significance of these factors can change in time. For the Columbia River Estuary, river flow exerted an overwhelming effect on transport most of the time, mainly because of the volume of water transported by the Columbia River and the relatively simple, straight morphometry of the estuary basin. Tidal excursions during flood flow had most effect during lowest river flow in late summer and early fall, but this effect was still relatively small when evaluated in two-dimensional box models in which both net circulation and tidal exchange across vertical boundaries between boxes were considered. Horizontal dispersive transport was not evaluated in this study because of lack of enough data on particle concentrations and current flow. Wind-mixing was minor in the Columbia River Estuary. Even though a more finely-tuned analysis of mass flux of materials is warranted in the future, estimates of transport using the product of river flow and material concentration seemed acceptable within the limits of the CREDDP data base.

Chlorophyll a transport

For purposes of this analysis the area studied (up to River Mile 47) is considered as the Columbia River Estuary. The Estuary imports materials from the main stem of the Columbia River through zone 8 (upper-estuary), and exports materials to the northeastern Pacific Ocean via zone 1 (marine)(Figure 4).

Of all the variables studied, only chlorophyll a concentration presented significant ($p < 0.01$) spatial variability in the estuary, with concentrations decreasing from upriver to the marine zone. In order to assess the transport rates of chlorophyll a within the estuary, chlorophyll a concentration was averaged by zones and selected months (Figure 38), and import-export was evaluated through zones 8, 5, 2, and 1 (Figure 4). The transport of chlorophyll a (metric tons day^{-1}) by zones and seasons is shown in Figure 39. The most evident feature is the consistent decrease in chlorophyll a transport from the upper-estuary zone (8) through the marine zone (1). Often there is a sharp break between the freshwater zone (5) and the mixing zone (2), where freshwater phytoplankton encounter saline waters. The maximum transport rates of chlorophyll a were registered during May, and also the maximum difference between

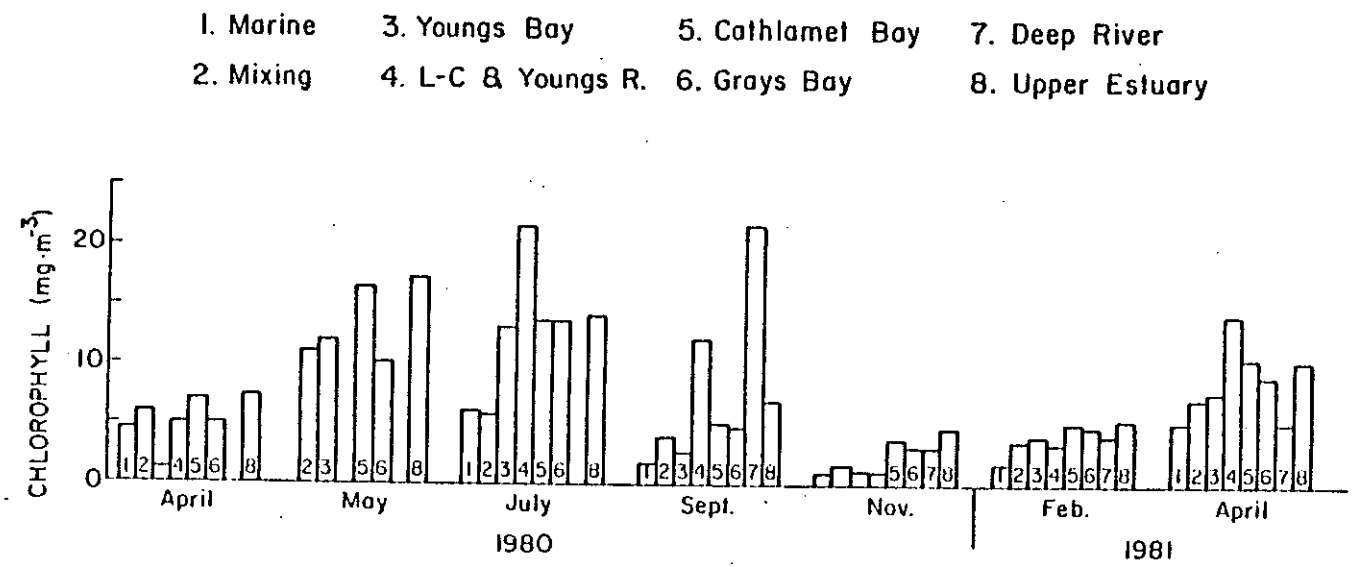


Figure 38. Temporal distribution of mean chlorophyll a concentration by zones.

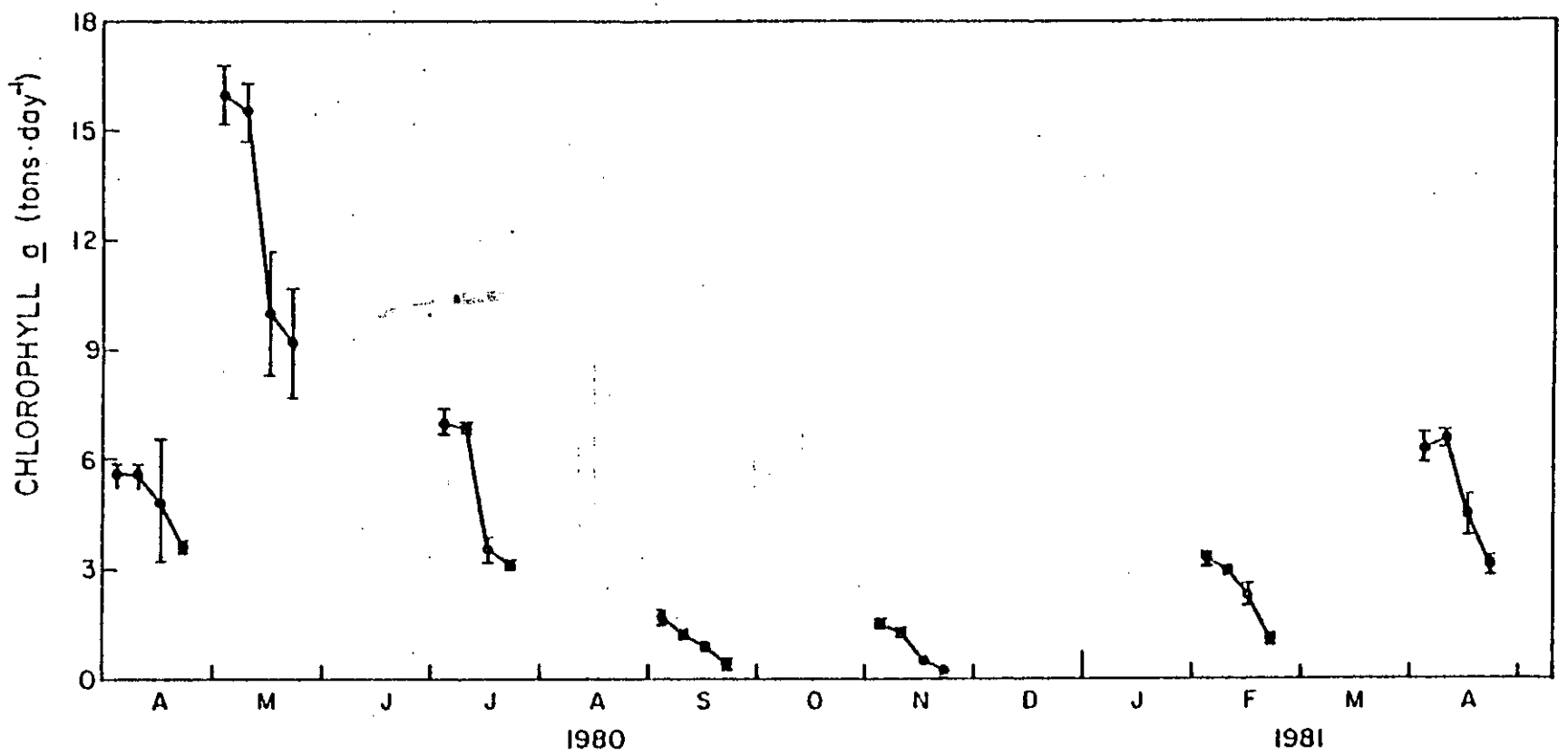


Figure 39. Daily mean transports of chlorophyll a by zones. Points represent from left to right, zones 8, 5, 2, and 1. Bars are ± one standard error.

zone 8 and zone 1 transport occurred in May. At this time the estuary imported up to 16 tons of chlorophyll *a* day^{-1}, while it only exported about 9 tons day^{-1} to the Pacific Ocean. Minimum transport rates occurred in November, with about 1.5 tons chlorophyll *a* day^{-1} imported and about 0.25 tons day^{-1} exported. The Columbia River Estuary thus acted as a sink for chlorophyll *a* throughout the year (Figure 41), with the most active region for removal usually being the mixing zone. During November, up to 80% of the chlorophyll *a* imported from the river was lost in the estuary (Figure 40). The estuary received about 1.9×10^3 tons of chlorophyll *a* during the year studied (over 50% during spring), but exported only around 0.9×10^3 tons $year^{-1}$ (over 50% in spring) to the Pacific Ocean (Table 13).

Transport of Nutrients and Suspended Particulate Material

Transport rates for TSP, OSP,ISP, POC, and inorganic nutrients were calculated by averaging concentrations from stations in zones 8, 5, and 2. Because there was no significant variation in concentrations among the three zones, transport rates represent both the quantity of materials that the estuary imports from the Columbia River, and the quantity of materials that the river exports to the ocean.

The daily contributions from the Columbia River to the northeastern Pacific Ocean are shown in Figure 41. Inorganic nutrients were transported at maximum rates during winter and spring, and at minimum rates in summer. Annual output during this study can be compared to that in 1966 and 1967 (Park et al. 1972), and to that in 1974 (Dahm 1980)(Table 14). Results from the present study are consistent with results from the earlier studies. The annual outputs of nutrients in 1980-1981 were calculated from actual transport calculations in months in which ample nutrient data were available, plus interpolated estimates (averaging adjacent months) in months in which no nutrient data were on hand (Table 13). During the 1980-1981 period, 1.4×10^8 moles of phosphate, 3.2×10^9 moles of nitrate plus nitrite, and 3.2×10^{10} moles of silicic acid were exported to the Pacific Ocean (Tables 13 and 14). The daily output of POC (Figure 41) showed maximum values in May and June coincident with the Mt. St. Helens volcanic eruption. Apart from that, POC still tended toward highest concentrations in spring. The annual output to the Pacific Ocean (Table 13) was about 4.2×10^5 tons (over 60% from April to June) of POC. However, values without the volcanic input would have been about 2.6×10^5 tons of POC, using values interpolated from adjacent months in place of the actual post-eruption values.

The daily outputs of TSP, OSP, and ISP (Figure 41) were greatly increased during May following the volcanic eruption. With May data not considered, maximum transport rates for TSP, ISP, and OSP occurred in June when maximum river flow occurred (Figure 37). The annual exports to the Pacific Ocean (Table 13) were 2.0×10^7 tons of TSP, about 1.89×10^7 tons of ISP, and about 0.22×10^7 tons of OSP.

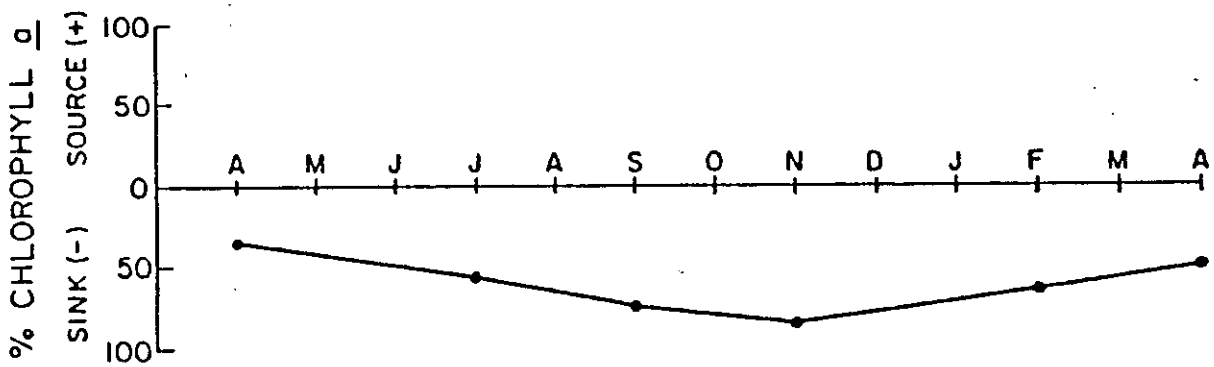


Figure 40. Chlorophyll a lost in the estuary as a percentage of chlorophyll a entering the estuary at River Mile 47.

Table 13. Monthly nutrient and suspended particulate export from the Columbia River into the Pacific Ocean during 1980-1981.

	Apr.	May	June*	July	Aug*	Sept	Oct*	Nov.	Dec*	Jan*	Feb.	Mar*	Annual Export
Chlorophyll a** (tons)	108	287	253	96	32	12	8	7	17	19	31	46	916
Silicic Acid (10^6 moles)	4395	5347	4725	1767	917	792	998	1920	4042	2498	2830	2325	32,556
Nitrate + Nitrite (10^6 moles)	879	248	150	12	22	36	83	210	496	344	436	303	3,219
Phosphate (10^6 moles)	26	22	15	5	3	4	5	9	20	12	14	9	144
POC (10^3 tons)	21	159 (43)+	107 (63)	18	10	10	10	17	31	16	14	12	425
OSP (10^3 tons)	47	360 (131)	285 (190)	86	47	42	34	44	80	40	33	34	1,132 (808)
ISP (10^3 tons)	186	9,993	5758	218	211	271	272	446	755	336	219	204	18,869
TSP (10^3 tons)	233	10,353 (915)	6043 (1373)	304	258	313	306	490	835	376	252	238	20,001 (5,893)

* interpolated
**represents marine zone only
+concentrations from 1981 in parentheses

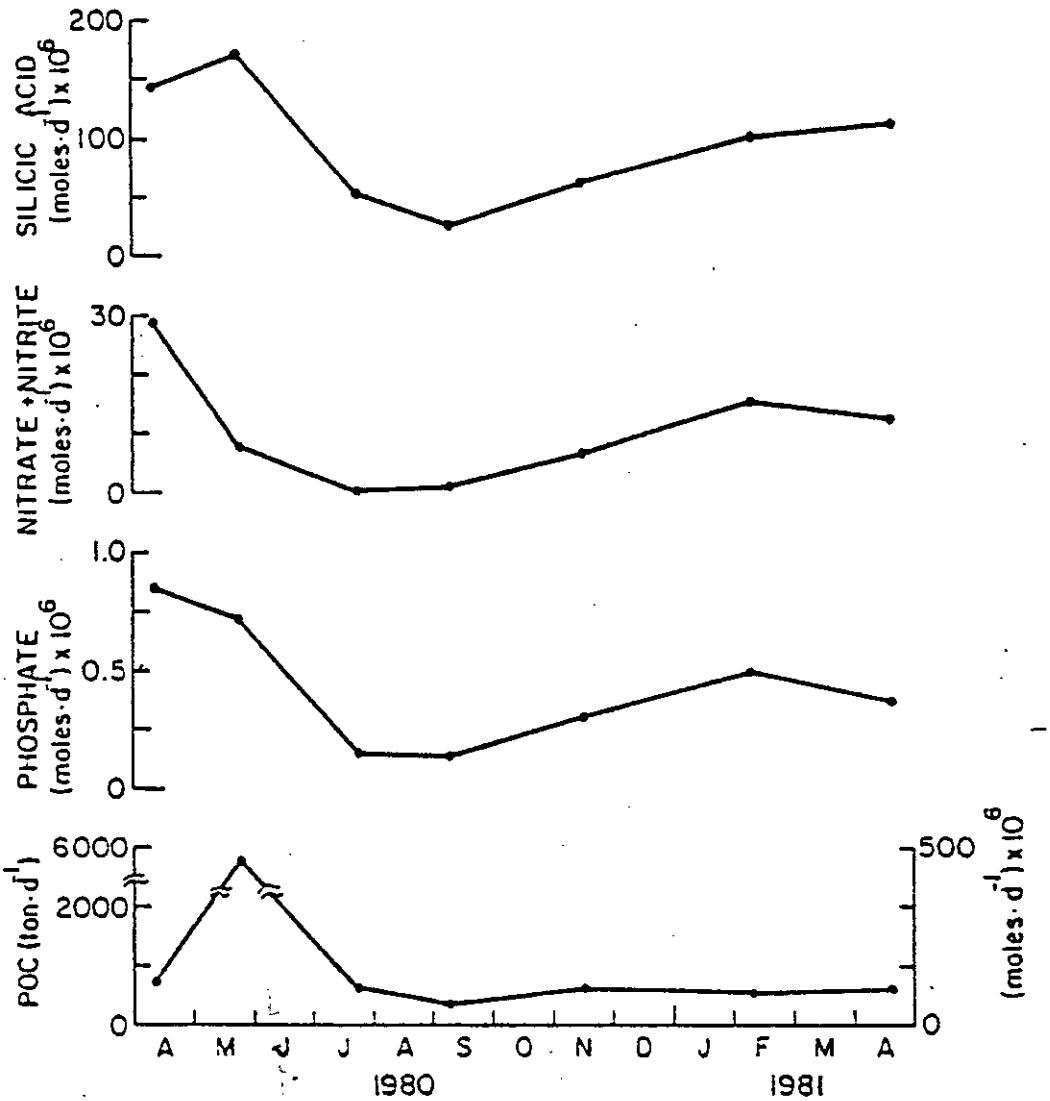


Figure 41. Daily mean transports of properties from the Columbia River to the Pacific Ocean.

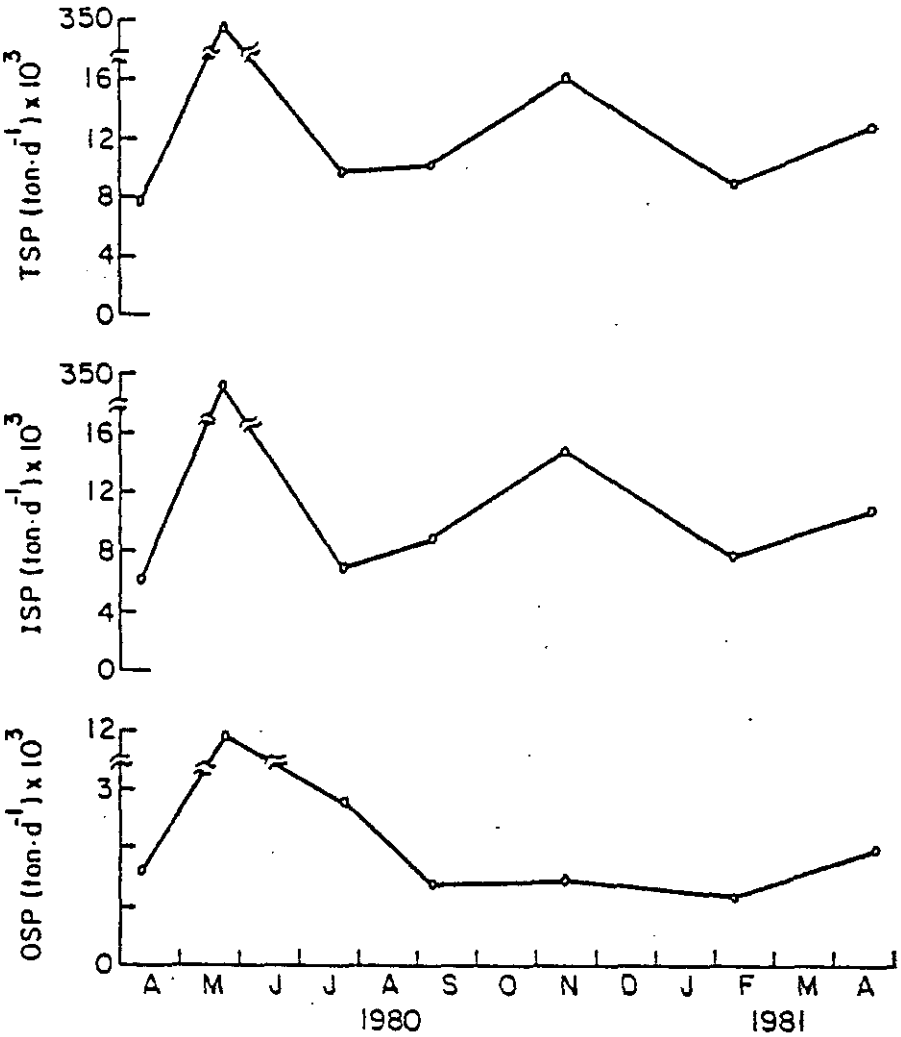


Figure 41. (continued)

Table 14. Annual chemical budgets for the Columbia River in 1966, 1967, 1974, and 1980-1981.

Variable	1966[1]	1967[1]	1974[2]	1980-1981[3]
Water (liters)	2.0×10^{14}	2.3×10^{14}	2.5×10^{14}	2.0×10^{14}
Phosphate (moles)	1.2×10^{8}	0.8×10^{8}	2.8×10^{8}	1.4×10^{8}
Nitrate + Nitrite (moles)	2.5×10^{9}	2.8×10^{9}	3.5×10^{9}	3.2×10^{9}
Silicic acid (moles)	3.3×10^{10}	3.5×10^{10}	4.8×10^{10}	3.2×10^{10}

[1] Park et al. (1972)

[2] Dahm (1980)

[3] This study

Again, transport rates without the volcanic input would have been much lower (Table 13): about 5.8×10^6 tons of TSP, 5×10^6 tons of ISP, and 0.8×10^6 tons of OSP.

4. DISCUSSION

4.1 ANNUAL PRIMARY PRODUCTION

When compared to other ecosystems of the world, the Columbia River Estuary, with an annual estimated water column primary production rate of 90 gC $m^{-2}yr^{-1}$, is surprisingly impoverished. It is roughly equivalent to semi-desert on the land, and the mid-ocean gyres in the sea (National Academy of Sciences 1975). When compared to estuaries for which annual data are available, the Columbia River Estuary is the least productive of them all (Table 15). This low productivity seems surprising because the region seems quite productive in other terms, most notably as a major fishery. Benthic primary production rates on the shallows and mud flats on the estuary appear to be quite similar to those of the water column (McIntire and Amspoker 1980).

We have shown that primary production is limited by light in the Columbia River Estuary. The water is highly turbid due to large amounts of suspended particulate material kept suspended by the fast-moving, turbulent waters of the Columbia River. Moreover, the skies are overcast or foggy over the estuary a good deal of the time. The well-mixed water column keeps the phytoplankton uniformly suspended at all depths, and this means even more time is spent at low light by the average cell than if they were not mixed below the upper, better-lit waters. Since in deep, turbid, well-mixed waters phytoplankton respiration through the water column could exceed gross photosynthesis (which would occur only near the surface), net production can be negative. While nutrients are generally in great abundance in the estuary, they are of little use to cells exposed to insufficient light.

The higher trophic levels of the estuary can be productive despite the low primary production rates, for the same reason that phytoplankton biomass was not adversely affected by the greatly increased light attenuation caused by the eruption of Mt. St. Helens: The phytoplankton biomass in the Columbia River Estuary is for the most part dependent on import from the Columbia River, rather than *in situ* production. The primary production in the main Columbia River and tributaries above the estuary has not been studied to date, but, using an airborne remote-sensing system, we found that the chlorophyll *a* concentration gradually increased in value from the Snake River down to the upper part of our study area, and then decreased towards the ocean (Bristow et al. in prep.). Thus it appears that the biological richness of the Columbia River Estuary is due not so much to primary production in the estuary itself, but rather to primary production in the Columbia River.

As expected in a light-limited system, both chlorophyll concentrations (Figure 11) and carbon productivity (Figure 24) matched

Table 15. Phytoplankton primary production in some estuaries.

Area	gC $m^{-2}yr^{-1}$	References
Columbia River Estuary, OR	90	This study
Fraser River Estuary, B.C.	120	Parsons et al. (1970)
Bedford Basin, N.S.	220	Platt (1975)
St. Margaret's Bay, N.S.	190	Plat and Conover (1971)
Narragansett Bay, RI	310	Furnas et al. (1976)
Lower Hudson Estuary, NY	690-	O'Reilly et al. (1976)
Chesapeake Bay (upper)	125-510	Biggs and Flemer (1972)
Chesapeake Bay (middle)	450-570	Stross and Stottlemeyer (1965)
Chesapeake Bay (lower)	385	Fournier (1966)
Neuse River Estuary, NC	300-500	Fisher et al. (in press)
South River Estuary, NC	300-500	Fisher et al. (in press)

the solar irradiation cycle (Figure 7), with maximum values in late spring and early summer, and minimum values during fall and winter. Similar phytoplankton biomass and productivity seasonal cycles have been reported for many other inshore and estuarine regions, including the plume waters off the Columbia River mouth (Anderson 1964), the northern reach of San Francisco Bay (Ball and Arthur 1979), the Fraser River Estuary (Takahaski et al. 1973), Chesapeake Bay (Patten et al. 1963; Flemer 1970), and North Carolina estuaries (Thayer 1971). The chlorophyll a peak we observed occurred in May. Haertel (1970) also reported the maximum chlorophyll a concentration during May 1967 and 1968 for the marine and mixing zones.

The predominance of nanoplankton (cells $\leq$33 µm, and usually $\leq$10 µm) over netplankton (cells $\geq$ 33 µm) in terms of phytoplankton biomass and reproduction in estuarine systems, has been documented by several investigators (Smayda 1973; McCarthy et al. 1974; Durbin et al. 1975; Malone 1977; Malone and Neale 1981). Although variable through the seasons, from 50-80% of the total phytoplankton standing stock was attributable to the $\leq$33 µm fraction, and usually to the $\leq$10 m fraction (Figures 27 and 28). In the Columbia River plume waters off Oregon and Washington, about 80% of the production was due to cells $\leq$35 µm in size (Anderson 1965).

Although the inorganic nutrient supply apparently exerts little control on primary productivity in the estuary (Table 3), inorganic nutrient concentrations do change with season (Figures 8b and 9a,b). Nutrients are in ample supply during winter when light limitation on phytoplankton growth occurs, and they decrease in concentration in summer due to the greater phytoplankton demand. Similar nutrient cycles have been reported earlier for the Columbia River Estuary by Haertel (1970) and Park et al. (1972). Haertel (1970) observed nitrate concentrations up to 23 µM in the entering marine waters during summer upwelling. During our summer sampling we observed an enrichment of nitrates in the salt wedge below 5 m depth (Figure 21a); however at no time did we measure nitrate levels in the summer as high as those observed by Haertel. The intensity and extent of this summer enrichment must depend mainly on the timing and intensity of the coastal upwelling events. Nitrogen (nitrate plus nitrite) concentrations reached very low levels during summer; however, because no other nitrogen nutrients (ammonia, for example) have been studied in the Columbia River Estuary, we cannot conclude that nitrogen availabilility limited phytoplankton growth during summer. Generally it has been shown that light and the availability of nitrogen compounds are the external factors which regulate productivity of the plankton community in most marine and estuarine systems (Ryther and Dunstan 1971; MacIsaac and Dugdale 1972; Williams 1973; Ball and Arthur 1979).

4.2 SPATIAL VARIABILITY

A consistent pattern of variation in phytoplankton production was found in the Columbia River Estuary system (Figures 30 and 31).

Riverine waters were substantially more productive (121-140 gC $m^{-2}yr^{-1}$) than estuarine waters (69-84 gC $m^{-2}yr^{-1}$). Also, Anderson (1972) has reported that production in the plume waters (off the Columbia River mouth) was about 125 gC $m^{-2}yr^{-1}$, higher than in the estuary proper.

Shallow areas of estuaries often are sites of rapid phytoplankton population increase; this occurs, for example, in the northern reach of San Francisco Bay (Cloern 1979) and in the Potomac River Estuary (DiToro et al. 1977). In the shallow areas of the Columbia River Estuary, primary productivity averaged slightly higher than in the channel, but differences were not significant (Table 4). In the Columbia River Estuary the water residence time is only a few tidal cycles (2-10 cycles [Neal 1964]), while in the northern reaches of San Francisco Bay water residence times have been calculated to be two to three weeks during winter and on the order of two months in summer (Conomos 1979). The relatively short residence times in the Columbia River Estuary probably explain the similarity of primary productivity in the shallows and channel, since times would not be long enough for local differences to develop.

As expected in a system as dynamic as the Columbia River Estuary, homogenous vertical distribution of suspended particles, including phytoplankton biomass, was clearly shown (Figures 19 and 20). The exception was the marine zone, where tidal and river flow conditions determined the depth distribution of certain properties (Figures 21, 22, 23).

The horizontal distribution of chlorophyll *a* presented a very characteristic feature, decreasing from the freshwater zone to the marine zone, with the greatest rate of decrease usually occurring in the mixing zone (Figures 11 and 38). Haertel (1970) also reported that both chlorophyll *a* and cell numbers decreased downstream with increasing salinity. She further stated that chlorophyll *a* concentration tended to show less depletion than cell counts (we also observed this phenomenon). However, Haertel made no attempt to explain the species or chlorophyll *a* patterns. We observed from a remote-sensing aircraft that chlorophyll *a* values dropped as water moved seaward, before it would be expected to from purely mixing processes (Frey et al. in prep.).

We have examined several hypotheses to explain the chlorophyll *a* pattern. First, because our sampling was not synoptic, diel chlorophyll *a* variability reported by several investigators (Lorenzen 1963; Wood and Corcoran 1966; Glooschenko et al. 1972) might have accounted for the spatial distribution observed. To test this hypothesis, chlorophyll *a* concentrations from different seasons and stations along the estuary were plotted against the daily time of sampling (Figure 42). No diel pattern could be discerned during any season; thus, diel variability was not an explanation for the distinct concentration break in the mixing zone. the second hypothesis was

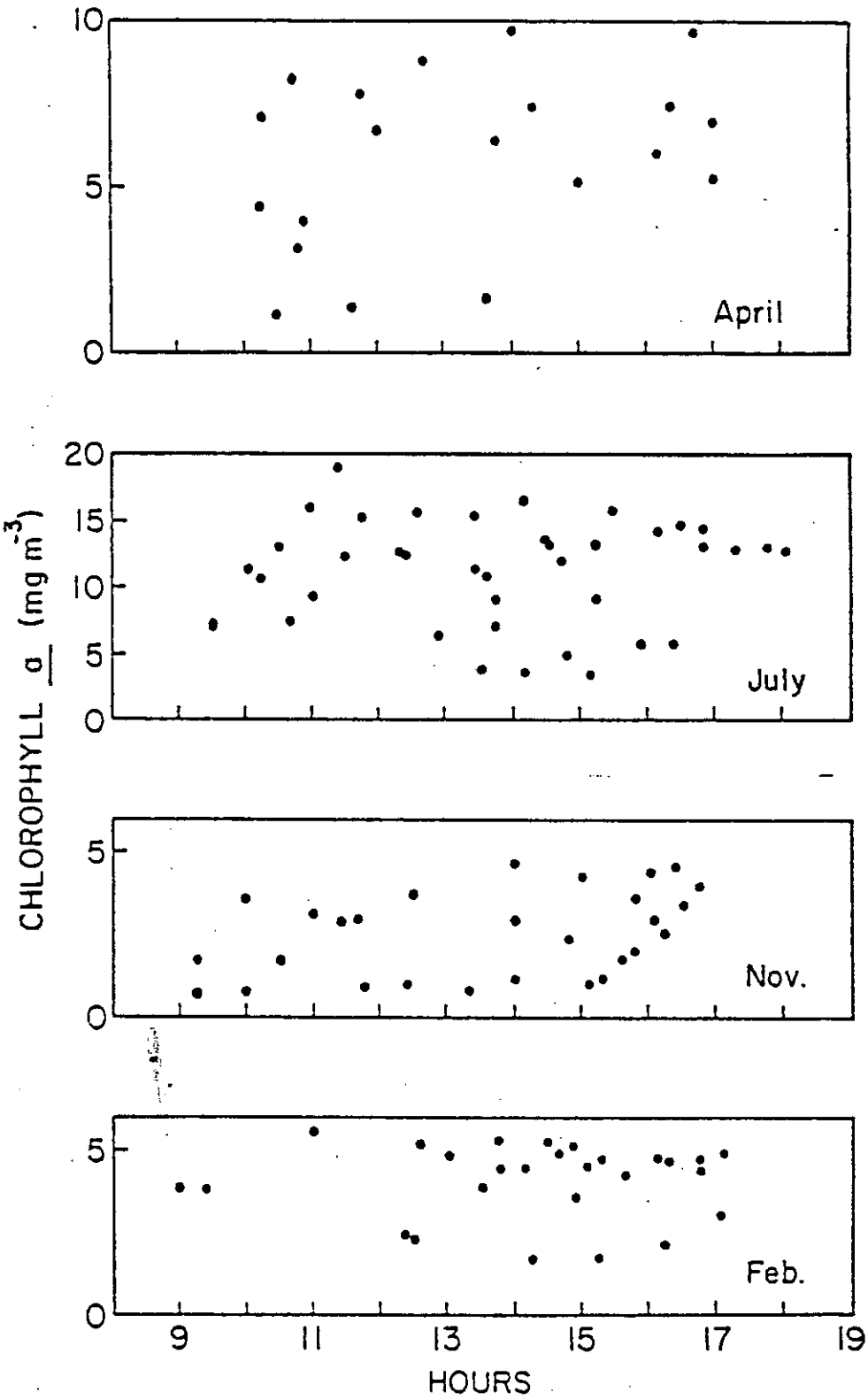


Figure 42. Daily chlorophyll a variability throughout the Columbia River Estuary.

that chlorophyll a decreased toward the marine zone because riverine waters with high chlorophyll concentrations mixed with marine-derived waters containing less chlorophyll a, to yield a dilution in the mixing and marine zones. If chlorophyll a was behaving as a conservative property affected only by dilution processes, we should expect to see a more or less linear decrease in chlorophyll a content in a plot of chlorophyll a vs. salinity. Such was not the case (Figure 43). The chlorophyll a decrease was much more rapid than predicted by a dilution model. Rapid change in chlorophyll a concentration in the mixing zone is also supported by data from Haertel (1970). She reported that during ebb tide chlorophyll a concentrations ranged from 15 mg m^{-3} at the mouth up to 40 mg m^{-3} in the mixing zone, whereas at flood tide the range was from 5 to 15 mg m^{-3}, respectively. That the chlorophyll a decrease is not purely a mixing process is supported by our remote-sensing data.

A third hypothesis was formulated, a "freshwater phytoplankton-salinity encounter hypothesis." As freshwater phytoplankton species encounter saline waters the osmotic pressure changes cause cell distortion and destruction, so that the cells disappear rapidly from the water column by sinking or disintegrating. A plot of the occurrence of the nine dominant freshwater phytoplankton species in the estuary against the salinity gradient (Figure 44), supports the hypothesis, particularly during spring and summer. All the species showed a sharp break in cell numbers at salinities as low as 2.5‰. Some species such as Diatoma tenue, Fragilaria crotonensis, and Melosira italica were never found at salinities greater than 5.0‰ in spring and summer.

Parameters associated with the physiological state of the phytoplankton community, such as the ratio of DCMU-enhanced fluorescence to in vivo fluorescence and the ratio of phaeophytin a to chlorophyll a, also reflected the break between fresh waters and marine waters. In general the DCMU-ratio decreased from freshwater to the marine zone (Figure 12b), indicating a decrease in the phytoplankton growth capacity. Phaeophytin a per unit of chlorophyll a increased toward the marine zone (Figure 13b), indicating that chlorophyll a degradative products were increasing as freshwater phytoplankton cells encountered more saline waters. The decline in primary productivity between freshwater and marine zones (Figures 30 and 31) has already been noted.

Salinity has been considered an important ecological variable in the marine environment, particularly in inshore areas. Variation in the total salt content of water, ranging from freshwater (lakes and rivers) through the brackish water of estuaries to the high salinities of the open sea, presents barriers to the spatial distribution of phytoplankton organisms (Braarud 1951; Provasoli 1958; Smayda 1958). However, surprisingly little research has been conducted on the physiological effects induced by the inflow of salt water into areas of fresh water, and vice versa. Lewin and Guillard

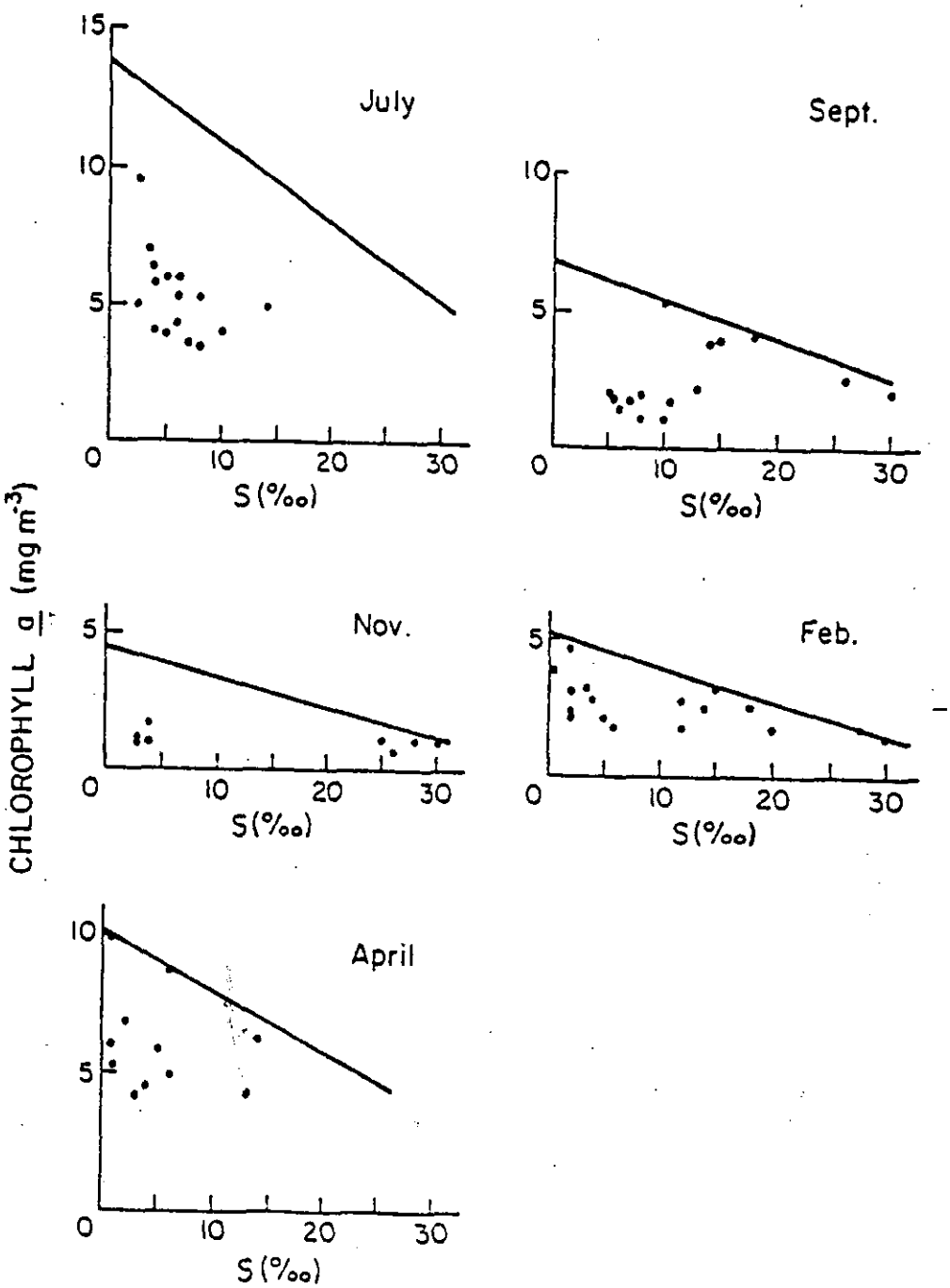


Figure 43. Chlorophyll a distribution against the salinity gradient in the Columbia River Estuary. Straight lines represent riverine chlorophyll a decreasing by only dilution processes.

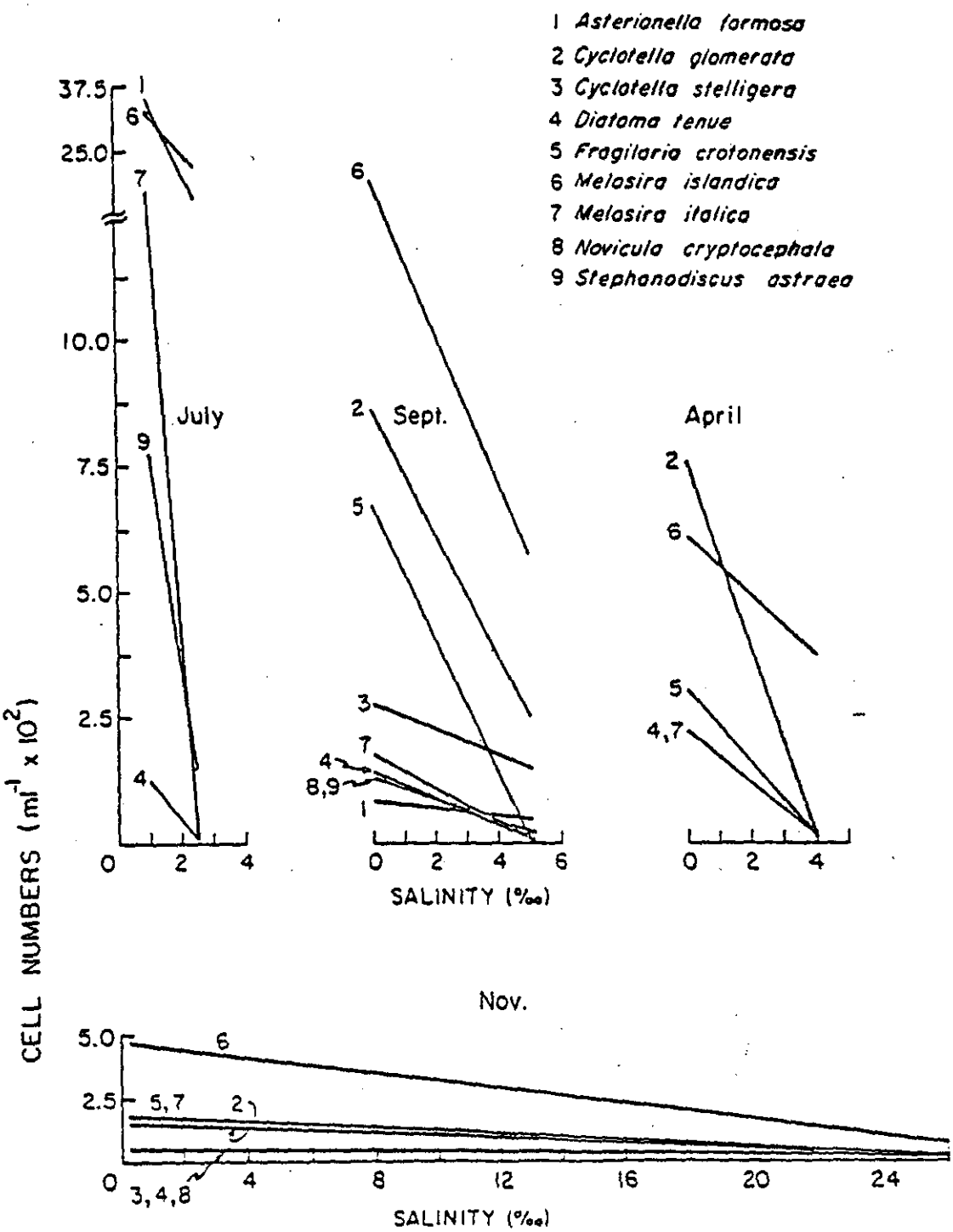


Figure 44. Freshwater diatom abundances distribution against the salinity gradient in the Columbia River Estuary.

(1963), in a detailed literature review, stated that "there are no experimental studies comparing salinity tolerances of diatoms characteristic of different types of freshwaters though this is important ecologically." However, the few references available support the idea that true freshwater species are less tolerant to salinity changes than coastal marine species. Coastal species perhaps have had the opportunity to evolve into true estuarine species, able to withstand greater salinity excursions than their counterparts in lakes and rivers. Chu (1942) showed that certain strictly freshwater species will divide only at salinities less than 2‰. Vosjan and Siezen (1968) determined salinity effects on the photosynthetic rates of the marine alga Chlamydomonas uva-maris and the freshwater alga Scenedesums obliquus. Photosynthesis of Chlamydomonas peaked at 30‰, but decreased rapidly only at salinities below 10‰. In contrast, Scenedesmus showed an optimum photosynthetic rate in freshwater, with about 50% reduction in the rate at about 8‰. These salinity effects were obtained in dilutions of natural seawater as well as by addition of NaCl to distilled water; therefore, the authors suggested that the measured decrease in photosynthesis was caused by osmotic stress.

Most of the experimental studies concerning salinity effects have been done with marine, coastal or estuarine species. The main conclusion has been that salinity changes affect cell division rates, although there are species differences (Rice and Ferguson 1975). For instance, Guillard and Ryther (1962) reported that the nearshore diatom Thalassiosira pseudonana is unaffected by salinities between 0.5 to 35‰, while the division rate of Isochrysis galbana is unaffected by salinities between 15 to 40‰ but is reduced by 25% at a salinity of 10‰ (Kain and Fogg 1958b). Asterionella japonica cells divide at a maximum rate between 30 and 35‰, and cease dividing only when the salinity decreases to 15‰ (Kain and Fogg 1958a). The division rate of the dinoflagellte Prorocentrum micans is maximum at a salinity of 25‰, decreases at 20‰ and ceases at 15‰ (Kain and Fogg 1960). McLachlan (1961) reported that for several marine species (Platymonas sp., Syracosphaera carterae, Monochrysis lutheri, Ollisthodiscus sp., Thalassiosira decipiens, Cyclotella sp., Cryptomonas sp., Amphydinium carteri, and Porphyridium sp.) a sharp decrease or cessation of growth rate, and a decrease in chlorophyll a content, generally occurred at about 10-15‰.

In the field, phytoplankton biomass and productivity data have been collected over the full salinity range from zero to completely marine in only a few cases. Cadee (1978) reported primary production, chlorophyll a distribution, and phytoplankton species in the Congo (Zaire) River, its estuary, and the plume at sea. The diatom Melosira granulata was the dominant species identified (625 cells ml^{-1} at 0‰, and only 3 cells ml^{-1} at 19.6‰). As in the Columbia River Estuary, the number of freshwater cells at 19.6‰ was much lower than the number anticipated via dilution only. Cadee suggested

phytoplankton sedimentation as the loss mechanism. The marine phytoplankton were important only at salinities greater than 15‰ in the Congo system.

Chlorophyll *a* and primary production in the Congo system decreased almost linearly with salinity between 0 and 20‰ and increased again between 25 and 30‰ (Cadee 1978). The peaks at 0 and 25-30‰ were of the same magnitude. A similar production pattern exists in the Columbia system, as noted earlier; that is, the river averaged 120 gC $m^{-2}yr^{-1}$ and the estuarine waters about 70 gC $m^{-2}yr^{-1}$ (from our study), while Anderson (1972) reported about 125 gC $m^{-2}yr^{-1}$ in the plume waters. Cadee's (1978) explanation of the distribution of chlorophyll *a* and primary production in the Congo system was as follows:

> ". . . freshwater phytoplankton rapidly dies and disappears when the Congo River water enters the ocean. the river water flows rapidly as a thin surface layer into the ocean and covers the distance between 0 and 30‰. . . . in about 3 days (Eisma and van Bennekom, 1978). A bloom of marine phytoplankton occurs in the plume but it takes some time to build up such a population (and a peak of phytoplankton biomass is only found when a salinity above 20‰ is surpassed). However, as the water is still very turbid in this part of the plume *in situ* production remains low."

The Congo River Estuary system thus apparently behaves in the same manner as the Columbia River Estuary system, with higher phytoplankton biomass and production depression in the estuarine region. This pattern of a productivity depression at intermediate salinities has also been observed during summer in the Ems Estuary (Wadden Sea), an estuary protected from the North Sea by a barrier of islands which may reduce the effects of the inflow of marine waters (Cadee and Hegeman 1974). Blanc et al. (1969) reported that the mixing zone of the Rhone River Estuary (France) contains great abundances of freshwater phytoplankton, but the cells are dead or almost dead; low chlorophyll *a* concentrations were also associated with this zone. Similarly the upper part of the St. Lawrence Estuary has been described as a system dominated by freshwater phytoplankton species (Lafleur et al. 1979). Dominance shifts from freshwater to marine species at 15‰ salinity in the St. Lawrence Estuary (Cardinal and Therriault 1976). Low phytoplankton production rates and biomass in Saguenay Fjord (part of the St. Lawrence Estuary) were interpreted as the result of low residence time of the plankton cells, due to persistent net flushing toward more saline lower parts of the fjord (Cote and Lacroix 1979). These latter investigators also suggested that the freshwater species either were eliminated along the increasing salinity gradient, or were too rapidly carried into waters of unsuitable salinity to be highly productive.

The Mississippi River has been credited with input of large quantities of inorganic nutrients into the Gulf of Mexico (Riley 1937; Ho and Barret 1977), which in turn (via phytoplankton photosynthesis) supports one of the largest fisheries in the United States. However, no single, extensive study of phytoplankton biomass and production in the river-estuary-plume continuum is available. Riley (1937), studying an area (South Pass) at the mouth of the Mississippi River, noted that no freshwater phytoplankton occurred at 5‰ salinity or above. A depression in chlorophyll a concentration along the salinity gradient from 5 to 20‰ was observed. Riley hypothesized that the causes were:

> ". . . increase in turbidity in this area or probably salinity itself, which in the brackish water zone, has an inhibiting effect on both marine and freshwater plankton."

Thomas and Simmons (1960) did some seaward transects from a freshwater portion of the Mississippi River (North Pass) to the Gulf waters. They also observed that the phytoplankton producton dropped sharply at a boundary between turbid freshwater and relatively clean saline water. They reasoned, in the sense of Riley (1937), that the decrease was due to turbidity or an inhibitory effect of the saline water on the freshwater phytoplankton production. The phytoplankton species distribution for the same area was reported later by Simmons and Thomas (1962). A river and a gulf community were reported. None of the species of the river community were significantly associated with species of the gulf community. Simmons and Thomas again postulated that the freshwater species were destroyed by the increased salinity. Sediments taken just off the mouth of Pass-a-Lourtre (one of the Mississippi River mouths) contained many cells of these freshwater species (Simmons and Thomas 1962).

All the estuarine systems above, including the Columbia system, seem to fit a category in which the two source waters to the estuary are more productive than the estuary itself. These systems contrast with the "classical" estuarine systems in which the estuary proper generally supports higher phytoplankton biomass and production than either the major entering river(s) or the adjacent coastal ocean. Most of the estuaries along the east coast of the United States (Narragansett Bay, Chesapeake Bay, Newport River Estuary, etc.) fit the "classical" category. However, the Hudson River Estuary may be an intermediate case. This estuary apparently acts as a sink for phytoplankton biomass derived from the coastal ocean in winter and spring, but acts as a source to the ocean during the summer due to *in situ* growth in the estuary (Malone et al. 1980). The Hudson River phytoplankton populations were not evaluated, unfortunately. Along the Pacific coast, the Fraser River Estuary (British Columbia, Canada) is a typical example in which the estuarine water is more productive than its source waters (Parsons et al. 1970; Takahashi et al. 1973). In San Francisco Bay, only the northern arm (Suisun Bay and San Pablo Bay) possesses estuarine conditions, due to the influx of the two main tributaries, the Sacramento and San Joaquin Rivers (Conomos et al. 1979). San Pablo Bay (8-25‰) is dominated

by marine-derived phytoplankton species, while Suisun Bay (1-10‰) yields a mixture of marine and freshwater species. The two main tributaries (mainly the San Joaquin River) support extensive freshwater populations, with chlorophyll a concentrations equal to or higher than the estuarine concentrations (Ball and Arthur 1979). The estuarine portion of San Francisco Bay thus seems to be another intermediate case, with phytoplankton biomass as abundant in the river source as in the estuary, but decreasing sharply seaward of the estuary.

The estuarine regions of other major rivers that have been studied behave as classical estuaries. For example, the Amazon (the largest river in the world) is known to support a poor authochthonous phytoplankton community due to its high turbidity and high acidity (low pH)(Sioli 1964; Gessner and Simonsen 1967; Sioli 1975). Gibbs (1970) reported that because of the large river discharge, there is no salt water penetration into the river mouth either during low or high river flow periods. Consequently, the Amazon Estuary is an external estuary, in which the estuarine waters actually occur in the coastal zone of the ocean. Thus, the Amazon River is an exporter of inorganic nutrients, which in turn support large blooms of marine diatoms in the estuarine and plume waters (Milliman and Boyle 1975; Milliman et al. 1975). The great majority of the phytoplankton species in the estuarine waters of the Amazon are marine (Wood 1966). Primary production is an order of magnitude higher in these waters than in the adjacent ocean (Cadee 1975).

Rzoska (1974) and Talling and Rzoska (1967) have stated that all the rivers in the White-Blue Nile system have very high turbidity and are mostly dark in color, so that phytoplankton photosynthesis in the rivers is limited by light penetration. Halim (1960) showed that the Nile River discharge into the Mediterranean Sea produces a fertilizing effect due to the flow of nutrient-rich waters into an otherwise impoverished sea. Exceptionally dense marine phytoplankton crops have been reported in this external estuary, following the discharges of the Nile (Halim 1960; and others cited therein). Thus the Nile, like the Amazon, supports only low quantities of freshwater phytoplankton, but its nutrient-laden discharge enhances the production of marine phytoplankton in the estuarine water off the mouth.

The above evidence indicates that, on the basis of phytoplankton biomass and production, estuaries can be classified into two main types (Figure 45): 1) estuaries with marine-dominated phytoplankton communities, which include the classical estuaries such as the Amazon and Nile; and 2) estuaries with freshwater-dominated phytoplankton communities. The latter type, which includes the Columbia River Estuary, apparently is the less common type. A corollary distinction between these two estuarine types apparently is the average residence time of waters in the estuarine region

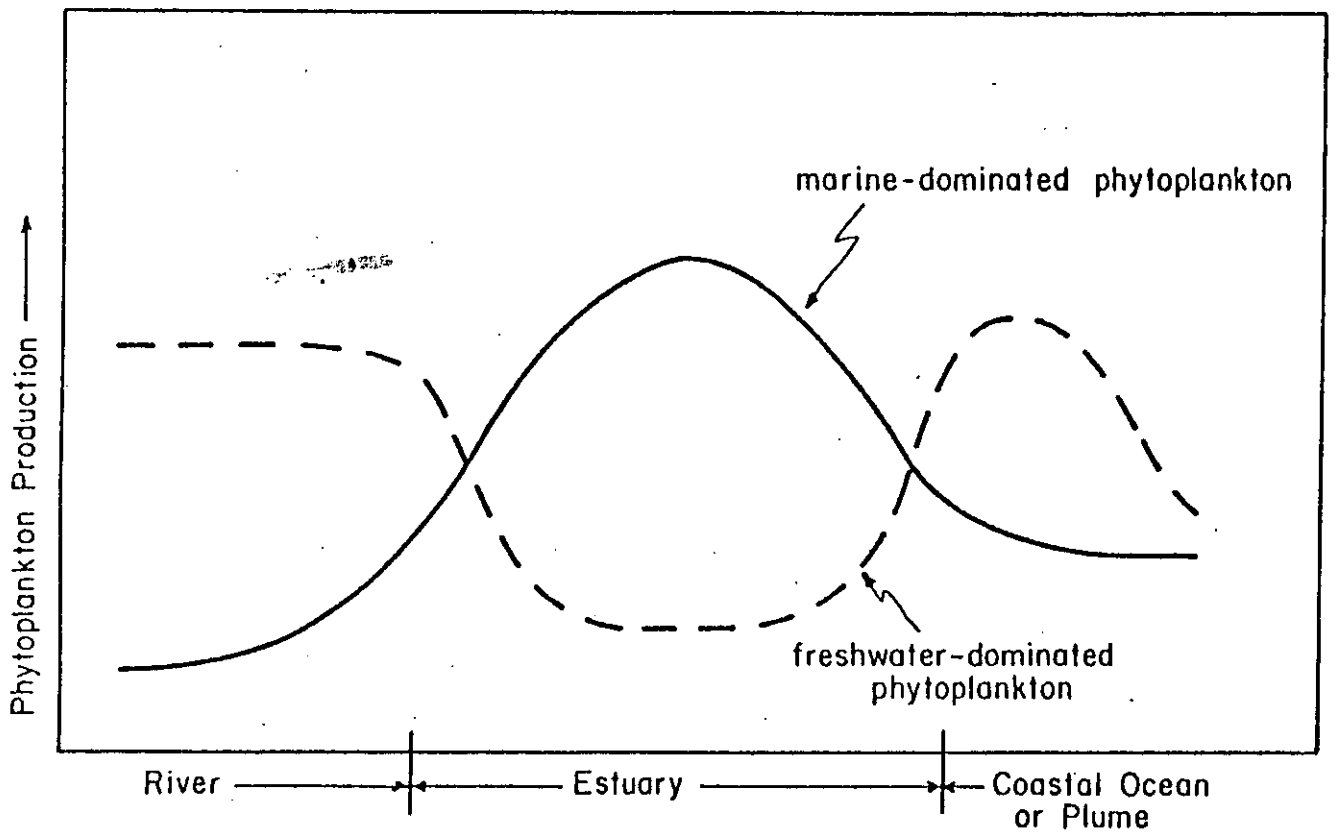


Figure 45. Estuarine system types.

proper. In the Type 1 ("classical") estuary, water residence times are usually long. For example, water residence time is about three months in the Delaware Estuary (Ketchum 1952), one month in Narragansett Bay (Kremer and Nixon 1978), and about two months in San Francisco Bay (Conomos 1979). Long water residence times allow for phytoplankton species compositions to adjust and for blooms to develop in response to nutrient inputs from river and/or ocean sources. Type 2 estuaries (dominated by freshwater phytoplankton) have short residence times on the order of a few tidal cycles. For example, the water residence time in the Columbia Estuary is one to five days (Neal 1965). In the Congo Estuary the residence time is two or three days (Eisma and van Benekom 1978).

Based on the spatial chlorophyll a distribution in the Columbia River Estuary and supportive evidence on Type 2 estuaries from the literature, conceptual models of freshwater phytoplankton-salinity encounter processes are shown in Figures 46 and 47. In these models (one for low river discharge or flood tide, the other for high river discharge or ebb tide), a zone of lost phytoplankton cells and chlorophyll is located somewhere in the mixing zone of the estuary. The most critical area in the mixing zone is that segment in which saline waters begin to mix with riverine waters (Figures 39 and 44). The sedimentation of huge quantities of freshwater phytoplankton cells can act as a food source for benthic organisms and for water-column grazers (the dominant copepod, Eurytemora affinis, has been reported to be most abundant at depth, close to the bottom, and in the mixing zone [Haertel 1970; Houghton et al. 1980]). This area of heavy sedimentation likely migrates in response to tidal cycles and river discharge (Figures 46 and 47); thus, during ebb tide and high river discharge, the zone might extend near the mouth of the estuary, but during flood tide and low river discharge the zone is well upriver where salinities less than 2‰ initiate rapid sinking of some species in summer (Figure 44). The upper edge of the mixing zone can extend to the Tongue Point-Rice Island area in the Columbia River Estuary.

It is interesting to note that a seasonal shift in spatial distribution from the marine zone (mouth area) in spring and early summer (during highest river flow) to the upper mixing zone (Tongue Point-Rice Island area) in summer-fall (during lowest river flow), has been documented for the most abundant zooplankton species (the copepod Eurytemora affinis, the mysid Neomysis mercedis [English et al. 1980], and juveniles of the shrimp Crangon franciscorum [Houghton et al. 1980]). In addition, Houghton et al. (1980) reported that epibenthic detrital and plankton feeders reached highest densities and greatest species diversity in the mixing zone. Haertel and Osterberg (1967) reported that despite the fact that the Columbia River Estuary is a very dynamic system, it supports a rather diverse benthic crustacean fauna relative to other estuaries. The benthic infauna, however, is not as abundant in the mixing zone as in the shallow bays. The mixing zone is a very high

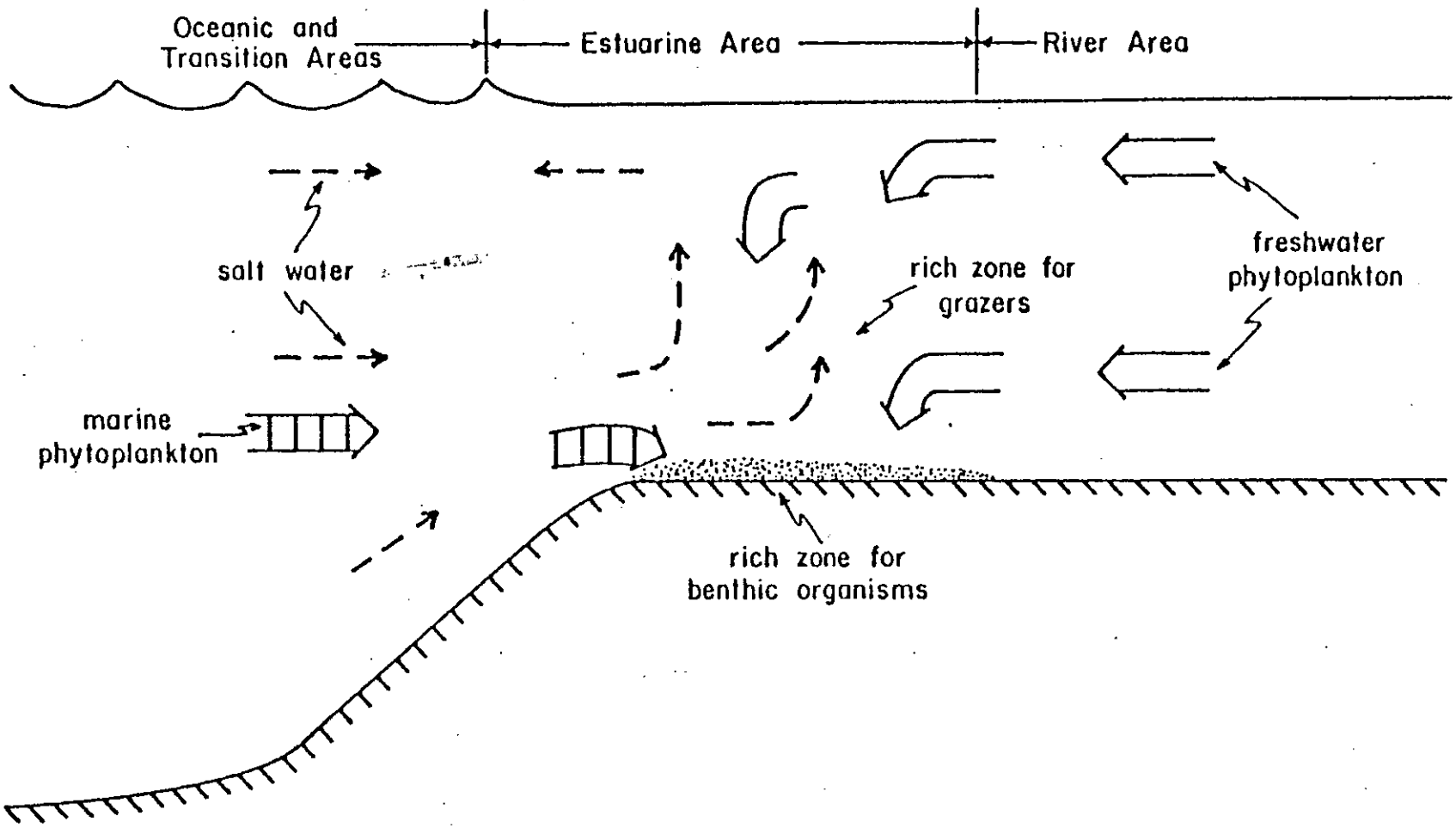


Figure 46. Freshwater phytoplankton-salinity encounter conceptual model during low river discharge or flood tide.

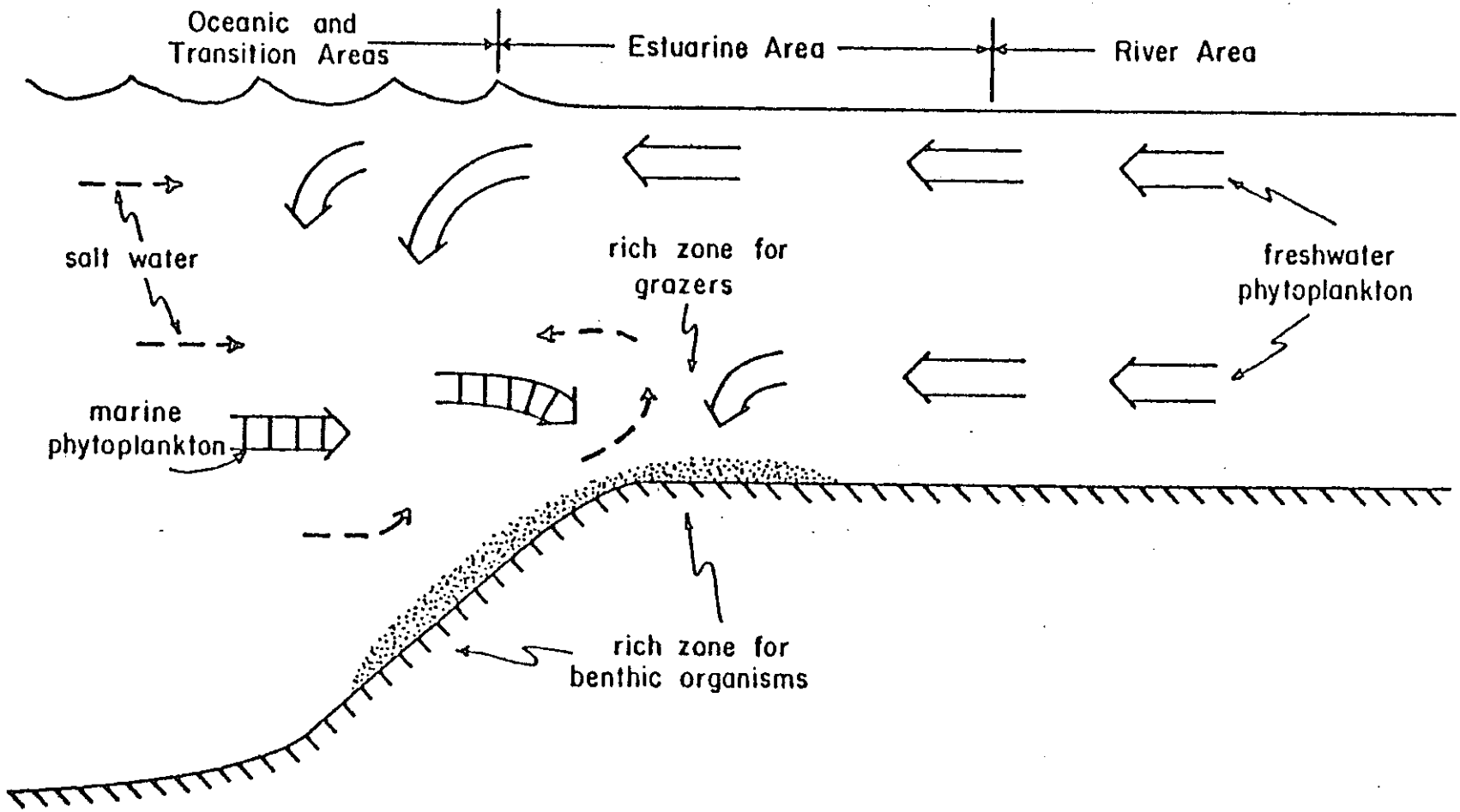


Figure 47. Freshwater phytoplankton-salinity encounter conceptual model during high river discharge or ebb tide.

energy environment with low sediment stability, unsuitable for many infaunal species (Higley et al. 1976; Holton et al. 1980).

The seasonal shift in spatial distribution for the most abundant zooplankters has been linked to the need for these organisms to maintain themselves in the estuary. They apparently can follow the leading edge of the salt intrusion during its seasonal excursions. The seasonal shift might also be explained in terms of food availability. Thus, the seasonal migration patterns of zooplankton and epibenthos not only allow retention of the organisms in the estuary, but may allow retention in the zone of maximum food availability.

4.3 EFFECTS OF THE ERUPTION OF MT. ST. HELENS

The effect of the reduced rate of estuarine primary production following the eruption of Mt. St. Helens on the overall estuarine and coastal ecosystem is dependent on a number of factors, including residence time of the water in the estuary, total primary food concentrations available to herbivores and detritovores, and quality of primary food supply in the estuary. The suspended particulate material from the eruption entered the Columbia River at the mouth of the Cowlitz River at river mile 68 (Figure 5), while tidal reversal of river flow extends only to about river mile 53 (Neal 1972), so the suspended material from the Cowlitz River should have a purely downstream influence. Columbia River flows during the period of increased light attenuation ranged from 10.8×10^3 to 12.3×10^3 $m^3 sec^{-1}$ (U.S. Geological Survey 1980). At these river flows, the residence time of water in the estuary is from 1-4 tidal cycles, or 0.5-2 days, depending on the method of computation (Neal 1972).

During both the May cruise, at the height of increased turbidity, and the July cruise, after the estuary water had cleared, chlorophyll *a* concentrations throughout the estuary were relatively high compared to concentrations seen at other times during our 16-month study, including the May-July period in 1981. That chlorophyll *a* concentrations were not depressed in May-July 1980 is a result of the large biomass present in the water imported from the Columbia River and the relatively short residence time of phytoplankton in the estuary. That there was not a phytoplankton population crash induced by high levels of turbidity below river mile 68, is evidence that phytoplankton biomass concentrations in the Columbia River Estuary are mostly a function of import from the Columbia River, rather than a function of *in situ* production.

It would seem likely that a 75% reduction in primary production extending over a 5-week period would have important consequences for higher trophic levels in the estuarine ecosystem. However, the ample particulate biomass indicated by high chlorophyll *a*, particulate carbon, and particulate nitrogen values suggests that primary food supplies were not markedly reduced. While primary production in the estuary was lowered by 1.3×10^8 gC d^{-1} in May, just after

the eruption, the amount of particulate carbon in the estuary at this time was 9.4×10^9 gC, and the flux of particulate carbon through the estuary was 6.3×10^9 gC d^{-1}. Thus the amount of carbon production lost per day was only about 2% of the total particulate carbon flux per day, at the time of maximum turbidity. Concentrations of organic seston, particulate carbon, and particulate nitrogen were all higher just after the eruption than during cruises 1 month earlier and 2 months later (Table 5). This indicates that suspended sediment added to the estuary as a result of the eruption contained substantial quantities of organic material. The food value of this material to estuarine organisms is unknown. While it appears that the particulate carbon in the Columbia River Estuary was not much affected by the great loss of primary production, this is not to say that the high suspended particle load in the water may not have affected higher trophic levels and food-chain transfers in other ways.

Material deposited by the volcanic eruption which was vulnerable to erosion during rainy periods must have added to the suspended sediment load of the water at times later in the year, particularly in the fall of 1980, when heavy rains began. Lack of multi-year data with which to compare data from 1980-81 makes the importance of rainy-period runoff difficult to assess. In our own fall and winter data we observed no dramatic increase in turbidity like that seen shortly after the eruption.

4.4 ZOOPLANKTON GRAZING

Zooplankton filtration rate estimates vary widely depending upon the technique used for estimation (Taguchi and Fukuchi 1975). Filtering rates depend on animal body weight, concentration and quality of food, size of the food, physiological state of the animals, environmental variables, etc. (Adams and Steele 1966; Paffenhofer 1971; Rigler 1971). Despite all these effects, filtering rates of natural zooplankton populations in the Columbia River Estuary were in line with values previously reported in the literature (Table 16).

Grazing removals from 0.06 (winter) to 1.2% day^{-1} (spring-summer) of the available phytoplankton biomass were estimated for zooplankton in the Columbia River Estuary (Table 12). These removals were equivalent to approximately 1 (winter) to 5% day^{-1} (summer) of the phytoplankton primary production. Grazing removals of these low magnitudes seem to be characteristic of shallow estuarine and coastal waters. For example, Heinle (1974) estimated that the large populations of Acartia tonsa grazed only between 2.5 and 7.4% day^{-1} of the total algal biomass in the Patuxent River Estuary. Williams et al. (1968) found daily zooplankton grazing in the estuarine system at Beaufort, North Carolina to be only 2 to 9% of the phytoplankton net productivity. Riley (1959) estimated that grazing removal accounted for only 4 to 6% day^{-1} of the phytoplankton population available in Block Island Sound, and he invoked physical dispersal to the offshore water

Table 16. Reported filtering rates for representative zooplankton species in the Columbia River Estuary.

Group	Algal Food	ml animal^{-1}day^{-1}	References
Marine copepods			
Acartia clausi	>10 µm diatoms	2.7	Marshall and Orr (1962)
Pseudocalanus minutus	natural phytoplankton	0.4-6.1	Taguchi and Fukuchi (1975)
Acartia longiremis	natural phytoplankton	0.4-6.1	Taguchi and Fukuchi (1975)
Oithona similis	>10 µm flagellates	0.02	Marshall and Orr (1962)
Freshwater copepods			
mixed copepods	natural phytoplankton	0.9-1.6	This study[1]
Diaptomus graciloides	natural phytoplankton	1.0-3.0	Nauwerck (1959)[2]
Diaptomus oregonensis	natural phytoplankton	1.9-12.9	McQueen (1970)
Freshwater cladocerans			
Daphnia sp.	natural phytoplankton	1.2	This study[3]
Daphnia longispina	natural phytoplankton	0.5-4.6	Nauwerck (1963)[4]
Daphnia pulex	*Chlamydomonas*	0.9-5.1	Richman (1958)
Bosmina longirostris	natural phytoplankton	0.3-0.6	This study
Bosmina longirostris	yeast, bacteria, algae	0.2-0.9	Haney (1973)

[1]Dominant species were: *Eurytemora affinis*, *Diaptomus* (several species), and *Canuella canadensis*.

[2]Cited in Jorgensen, 1966.

[3]Dominant species were: *Daphnia longispina* and *D. pulex*.

[4]Cited in Burns and Rigler, 1967.

as the main factor controlling the phytoplankton populations. Deason (1975) and Johnson (1981) concluded that grazing was not significant to the phytoplankton populations in Yaquina Bay, Oregon, and Taguchi and Fukuchi (1975) reported that the loss to phytoplankton grazing was exceedingly low in shallow Akkeshi Bay, Japan. Similarly, Bakker and de Pauw (1975) reported that grazing by zooplankton was not a major factor in controlling the algal crop in estuarine waters of the Netherlands.

The great amounts of organic detritus suspended in estuarine waters (about 75% of the total organic carbon in the Columbia River Estuary was detrital carbon, as will be shown later) might be available to zooplankton as food. Several investigators have recently found that large fractions of the diets of estuarine and coastal zooplankton are composed of detrital particles. For example, Gerber and Marshall (1974) reported that about 34% of the food ration of Acartia tonsa in Narragansett Bay was detritus. Heinle and Flemer (1975) suggested that Eurytemora affinis could use detritus as a food source during seasons when phytoplankton was not abundant. Similarly, Heinle et al. (1977) reported growth and egg production by Eurytemora on a detrital diet. The average percentages of living and non-living particulate carbon in Bedford Basin, Nova Scotia, over the year were 21% and 79%, respectively, while the percentages in the food of Pseudocalanus minutus averaged 29% and 71% (Poulet 1976). Based on zooplankton body size increases and egg production, Poulet suggested that detritus was truly assimilated. Chervin (1978) reported that detritus formed between 26 and 44% of the grazers' diet in the Hudson River Estuary, and from 31 to 81% in the apex of the New York Bight. However, based on net growth efficiencies, Chervin concluded that detritus was inferior to phytoplankton as a food source. The evidence thus supports the idea that the great amounts of detrital carbon in estuarine systems are potential food sources for grazers. The use of detrital particles might tend to increase the grazing rates obtained by zooplankton in the Columbia system, as these rates were based only on phytoplankton biomass changes. Even if the grazing rates were doubled, however, particle removal via grazing would still be minor relative to particle losses via export to the ocean, and probably to losses via sinking as well (see later).

It should be noted that the effect of grazing in estuaries is very different from the general effect in the open ocean. Grazing has been considered one of the main factors, if not the main factor, regulating phytoplankton populations in the open ocean (Steele 1974; Raymont 1980). Up to 90% particle removal via grazing is not uncommon.

4.5 PARTICLE TRANSPORT

Only about 50% of the chlorophyll a received from the river was exported to the ocean, the remainder being lost upon contact

with the salinity barrier in the mixing zone (Figures 39 and 40). Whether this loss of chlorophyll is due to pigmented cells sinking to the bottom in the mixing zone, or due to loss of pigment from ruptured cells (with the non-pigmented cell fragments continuing downstream in the water column) is not known. There is some evidence for both processes occurring. It was shown before, for example, that the numbers of freshwater diatoms often decreased sharply upon contact with saline waters (Figure 44). This sharp decrease indicated that whole cells were disappearing from the water column, and, by inference, were sinking to the bottom in the mixing zone. On the other hand, it was also found that the loss of phytoplanktonic carbon (converted from a carbon/chlorophyll ratio - see later) was not reflected in the total particulate organic carbon budget; i.e., there was no measurable change in total particulate organic carbon concentration throughout the study area. Such a result suggests that the chlorophyll content was lost from the cells, but the non-pigmented cells and cell fragments were still part of the suspended organic load. It will be shown later, however, that phytoplanktonic carbon made up only a small fraction of the total particulate organic carbon reservoirs, so that losses of phytoplanktonic carbon could have been masked by the large suspended carbon pool and by detrital carbon gains from the marshes and benthic systems between the mixing zone and estuary mouth.

With the exception of chlorophyll a, the Columbia River Estuary apparently acts mainly as a conduit for the export of suspended particles from the river to the ocean. This condition results from the fact that no differences in concentrations of TSP, OSP, ISP, etc. can be measured along the length of the estuary as indicated above. These uniform distributions are perhaps due to several things: 1) the low residence time of water in the estuary; 2) the lack of salinity (or other) effects on the mainly non-living particles; and 3) contributions of particles from the mud flats and marsh systems bordering much of the estuary, which help to balance particle losses due to settling in the estuary. The low water residence time (1-5 days) in the estuary points to the ability of this high-energy system to keep particles in suspension and keep them flushing out into the ocean.

The total suspended particle concentration (TSP) of the Columbia River is remarkably low in comparison with other major rivers (Holeman 1968). An average TSP of 25 g m^{-3} for channel stations and 33 g m^{-3} for shallow stations was obtained for the Columbia. These concentrations are in line with previously reported TSP concentrations for the river; that is, 30 g m^{-3} (Weyl 1970), 8-40 g m^{-3} (Conomos and Gross, 1972), and 56 g m^{-3} (Holland 1978). In contrast, the Mississippi River averages 510 g m^{-3}, while the average TSP concentration for all U.S. rivers is about 530 g m^{-3} (Holland 1978). Thus, although the Columbia River ranks second in the U.S. in river discharge, the low TSP concentrations make for a relatively low transport of TSP. The annual export to the Pacific Ocean was 20 x 10^6

tons of TSP in 1980-81, or about 5 x 10^6 tons without the volcanic input. Previously reported values were 10 x 10^6 tons of TSP for 1952 (Judson and Ritter 1964), and an average of 10 x 10^6 tons yr^{-1} for the period 1963 to 1970 (Jay and Good 1978).

The reason that the Columbia River supports a relatively high phytoplankton biomass remains unclear. There is indirect evidence that the series of dams along the upper Columbia River and its tributaries may be responsible for much of the high phytoplankton biomass observed in the river. Impoundment of water behind dams changes riverine conditions to lake-like conditions, which enhances phytoplankton development (Talling and Rzoska 1967; Taylor 1971; Greene et al. 1975; Baker and Baker 1981). The main effect of impoundment is to greatly retard water flow. This in turn greatly increases residence times of water in the river, thus allowing more time for *in situ* growth. Also, water may stratify behind dams, allowing cells to remain in the euphotic zone. Phytoplankton blooms in reservoirs behind dams may become the source for enhanced primary biomass levels in the estuaries downstream. Our remote-sensing study indicated a significant chlorophyll *a* change occurring consistently within each reservoir (Bristow et al. in prep.).

Phytoplankton growth in the upper Nile River system has been enhanced by dam building (Talling and Rzoska 1967), and phytoplankton biomass in the upper Mississippi River (Minnesota) has increased as much as 40-fold in the past half-century, due both to dam construction and increased fertilization from urban sewage and farmland runoff (Baker and Baker 1981). Thick blooms of algae in the Snake River Basin (the largest tributary to the Columbia River) have been related to the high concentrations of basic nutrients and the effects of dams (Greene et al. 1975). However, no lengthy series of phytoplankton data, suitable for calculation of transport, are available for the Columbia River, so no direct comparisons between the Columbia and the Columbia Estuary can be made.

4.6 A MODEL: SOURCES AND FATES OF PARTICULATE ORGANIC CARBON

With major increases and decreases in phytoplankton biomass estimated through time for the Columbia River Estuary, a process model can be constructed and evaluated. For purposes of the model, all phytoplankton processes must be in the same "currency." We chose to convert all measurements to a carbon base. Biomass had to be converted from chlorophyll *a* to carbon. Ratios of total particulate organic carbon (TPOC) to chlorophyll *a* were first computed, and a mean of 300 (range 150-1000) was obtained. The variation was caused by the large and variable amounts of non-phytoplanktonic carbon in the TPOC measurements, and was considered too great for practical use of the mean. In general, TPOC can be divided into live carbon (here considered solely as phytoplanktonic particulate organic carbon, PPOC), and non-living carbon (the detrital carbon, DPOC). In estuarine systems DPOC has been reported to be the dominant fraction (Parsons

and Takahaski 1973; Poulet 1976; Chervin 1978; Raymont 1980). To have a reliable phytoplankton carbon-to-chlorophyll a ratio, then, a reasonable estimate of the PPOC fraction is required. We estimated the PPOC fraction in the Columbia Estuary from the specific production relationship:

$$q = \frac{PP}{PPOC} \text{ or } PPOC = \frac{PP}{q},$$

where: q = specific production rate or growth rate (day^{-1}),
PP = phytoplankton primary production ($mgC\ m^{-3} day^{-1}$,
$PPOC$ = phytoplanktonic particulate organic carbon ($mgC\ m^{-3}$).

On evaluating specific growth rate values from the literature for common phytoplankton species found in the Columbia River Estuary (Table 17), we decided that a specific growth rate value of $q = 0.69$ (one doubling day^{-1}) would be more representative for the estuary than values lower or greater than one doubling day^{-1}. The values in Table 17 are computed at light saturation of photosynthesis, a condition that does not exist in the Columbia River estuary for a considerable part of the year; hence, a doubling rate somewhat less than the mean of the values in Table 17 was considered appropriate.

Using PPOC values estimated by the method described above, a carbon-to-chlorophyll a ratio was calculated for each cruise. The variability in the ratio was low, with a mean of 40 (range 20-50). This ratio agrees well with previously reported values; for example, Strickland (1960) suggested a ratio of 30, Heinle and Flemer (1975) obtained a ratio of 50 for the Patuxent River Estuary, Kremer and Nixon (1978) found a ratio of 30 for Narragansett Bay, and Chervin (1978) obtained a range of ratios ranging from 46 to 72 for the lower Hudson River Estuary.

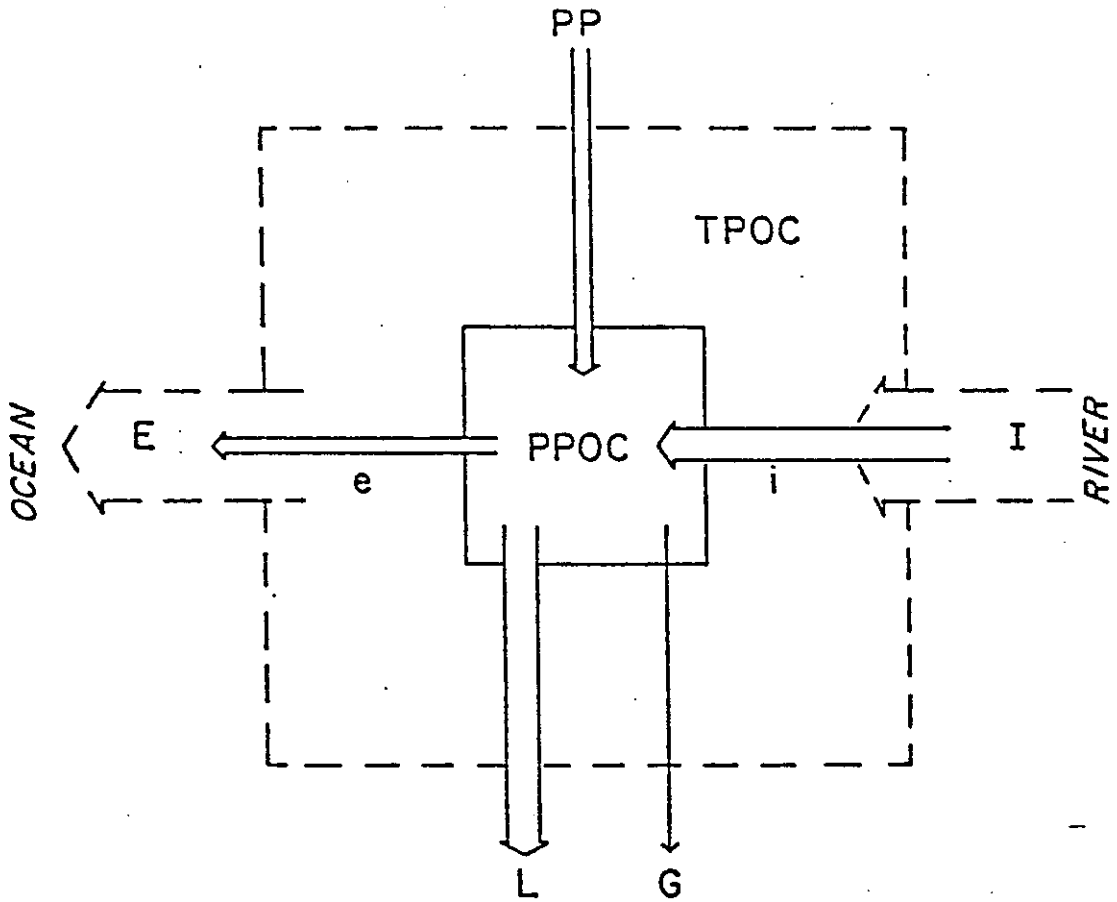
Rough calculations of the detrital carbon fraction (DPOC), using the relationship DPOC = TPOC-PPOC, showed tht DPOC made up about 75% of the total particulate organic carbon throughout the year. Similar fractionation of TPOC has been reported for the Bedford Basin (Poulet 1976); i.e., 79% of TPOC over the year corresponded to detrital carbon and 21% to live carbon.

The model constructed for water-column particulate organic carbon in the Columbia River Estuary is shown in Figure 48. The contribution of each process is evaluated as previously described, except the in situ "sinking" term (L) is estimated by difference (the standing stock values minus the algebraic sum of all other input/output processes). In order for this difference term to truly represent sinking, we had to assume that the losses in chlorophyll a represented losses of phytoplankton carbon (via the chlorophyll/carbon ratio); i.e., carbon loss was due to sinking of pigmented cells. Carbon losses due to phytoplankton respiration in the euphotic zone were not evaluated because it was assumed that phytoplankton

Table 17. Specific growth rates (q and doublings day^{-1}) at light saturation for some freshwater species[1]. q = 0.69 doublings day^{-1}.

Species	Doublings day^{-1}	q	References
Asterionella formosa	1.9	1.3	Talling (1955)
Stephanodisucs hantzschii	1.7	1.2	Swale (1963)
Cyclotella glomerata	0.8-1.9	0.55-1.3	Peterson et al. (1974)
Cyclotella compta	0.1-0.8	0.7-0.55	"
Scenedesmus sp.	0.5-1.1	0.34-0.75	"
Synedra sp.	1.0-1.9	0.7-1.3	"

[1]All these species exist in the Columbia River Estuary. In some seasons *A. formosa* and *S. hantzschii* may be the dominant species.



TPOC = total particulate organic carbon

PPOC = phytoplankton particulate organic carbon

PP = phytoplankton primary productivity

G = zooplankton grazing

L = sinking (and other) loss

I = import of TPOC

i = import of PPOC

E = export of TPOC

e = export of PPOC

Figure 48. Input-output model of water column particulate organic carbon, sources and fates. The sizes of the boxes denote the relative sizes of the standing stocks of TPOC (dashed-line boxes) and PPOC (solid-line boxes) in the whole estuary. The thickness of the arrows denote the relative magnitudes of the rates of input and output to and from the standing stocks.

production measured by the ^{14}C technique yielded values close to net production, as suggested by Bunt (1965), Ryther and Menzel (1965), Eppley and Sloan (1965) and Strickland and Parsons (1972); i.e., the ^{14}C measurements have already accounted for the respiratory losses of carbon in the euphotic zone, so they do not need to be evaluated separately. There is no loss term for respired carbon at night and below the euphotic zone, as mentioned before. Any respiratory loss at night and below the euphotic zone would have to be a part of the difference term (L) in Figure 48; thus, L might not solely represent sinking of phytoplankton carbon.

A series of model evaluations were generated for each season (Figures 49, 50, and 51), and finally a yearly particulate organic carbon budget for the total estuary was estimated (Figure 52). A main feature is the great predominance throughout the year of the transport processes through the estuary relative to in situ processes. The main source of particulate organic carbon (total and living) to the the estuary is clearly the input from the main stem of the Columbia River. A second major feature is the fact that the import of TPOC to the estuary balanced the export from the estuary, while there was no import-export balance for PPOC. This feature was noted and discussed earlier.

Outputs of living carbon via "sinking" processes were very significant to the PPOC budget throughout the year (Figures 49, 50 and 51). From July through February over 70% of the total loss of PPOC was accounted for by in situ sinking (or by other loss such as respiration). Only during high flow periods (April and May) did export of PPOC to the ocean exceed sinking of PPOC in the estuary. Loss of phytoplankton carbon via zooplankton grazing was insignificant throughout the year (Figures 49, 50 and 51). On the input side, import of PPOC always exceed in situ primary production, although the two inputs were about equal to the summer months when river flow was low (Figure 50).

On a yearly basis (Figure 52) the water column budgets for the estuary were as follows. Of the total particulate organic carbon that the estuary received, about 75% was detrital carbon and 25% was live carbon. Of the live fraction (PPOC), 75% was supplied by the main stem of the Columbia River, while only 25% was produced in situ by the phytoplankton. About 63% of the live carbon was lost in the estuary by sinking (or other loss routes), and 35% was exported to the adjacent coastal ocean. Losses via zooplankton grazing accounted for less than 1% of the live carbon.

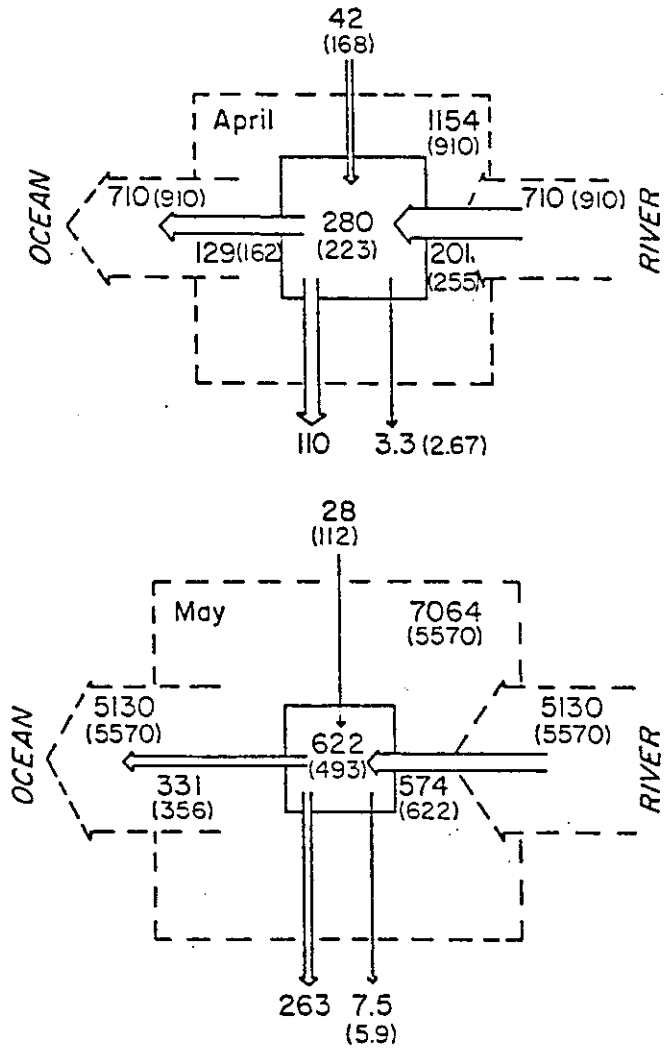


Figure 49. Daily particulate organic carbon budgets for April and May. Bold-face numbers in the boxes are concentrations in metric tons of carbon. Concentrations in mgC m^{-3} are given in parentheses in the boxes. Arrows represent inputs-outputs in metric tons day^{-1} (bold-face numbers). In parentheses are given concentrations for transport rates in mgC m^{-3}; phytoplankton production rates in mgC m^{-2} day^{-1}; and zooplankton grazing rates in mgC m^{-3} day^{-1}. The size of the May figure has been reduced four times in comparison with the rest of the figures. The huge concentrations and transports in May are the result of the Mt. Saint Helens' volcanic eruption.

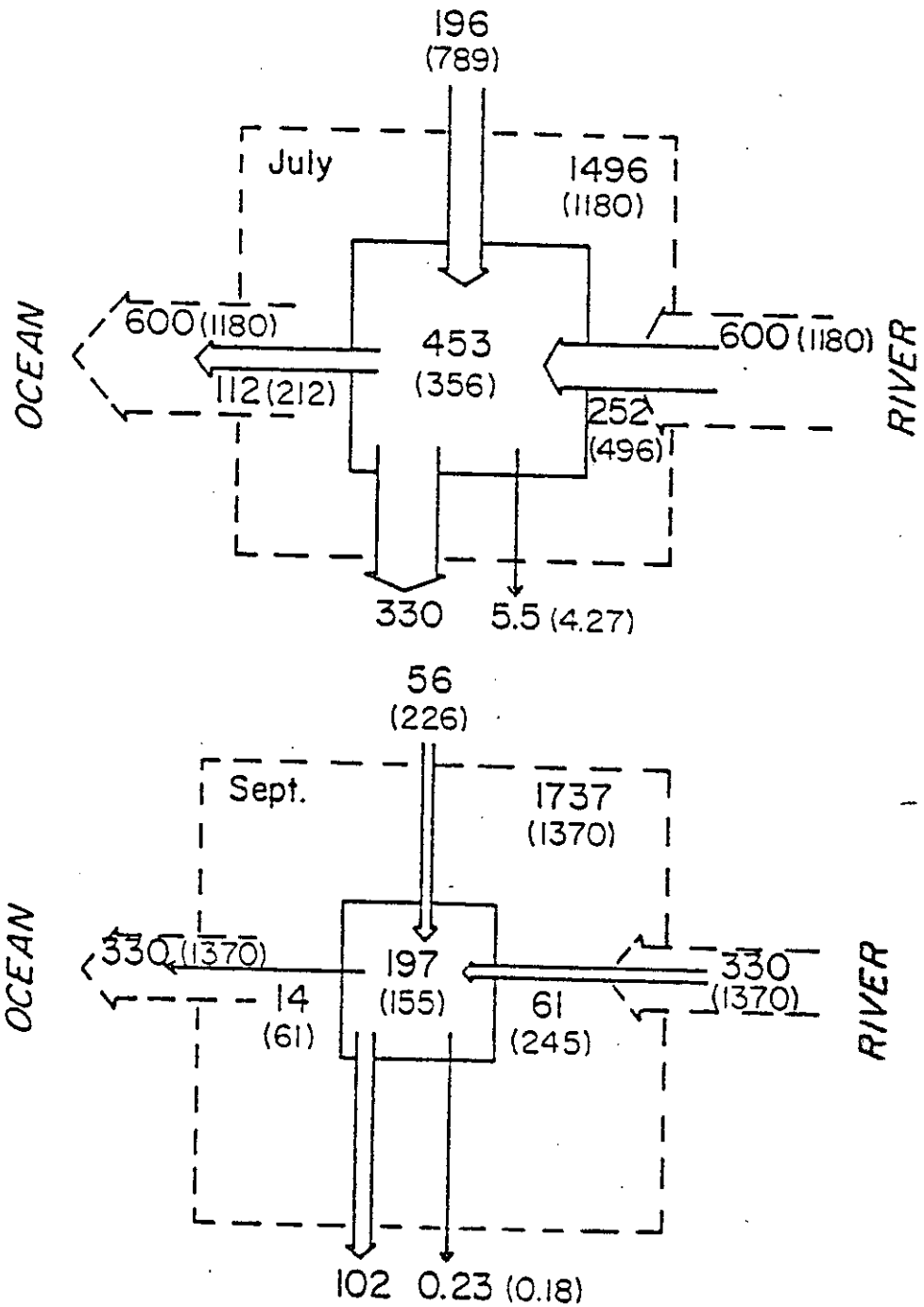


Figure 50. Daily particulate organic carbon budgets for the Columbia River Estuary; July and September. For legend details see Figures 47 and 48.

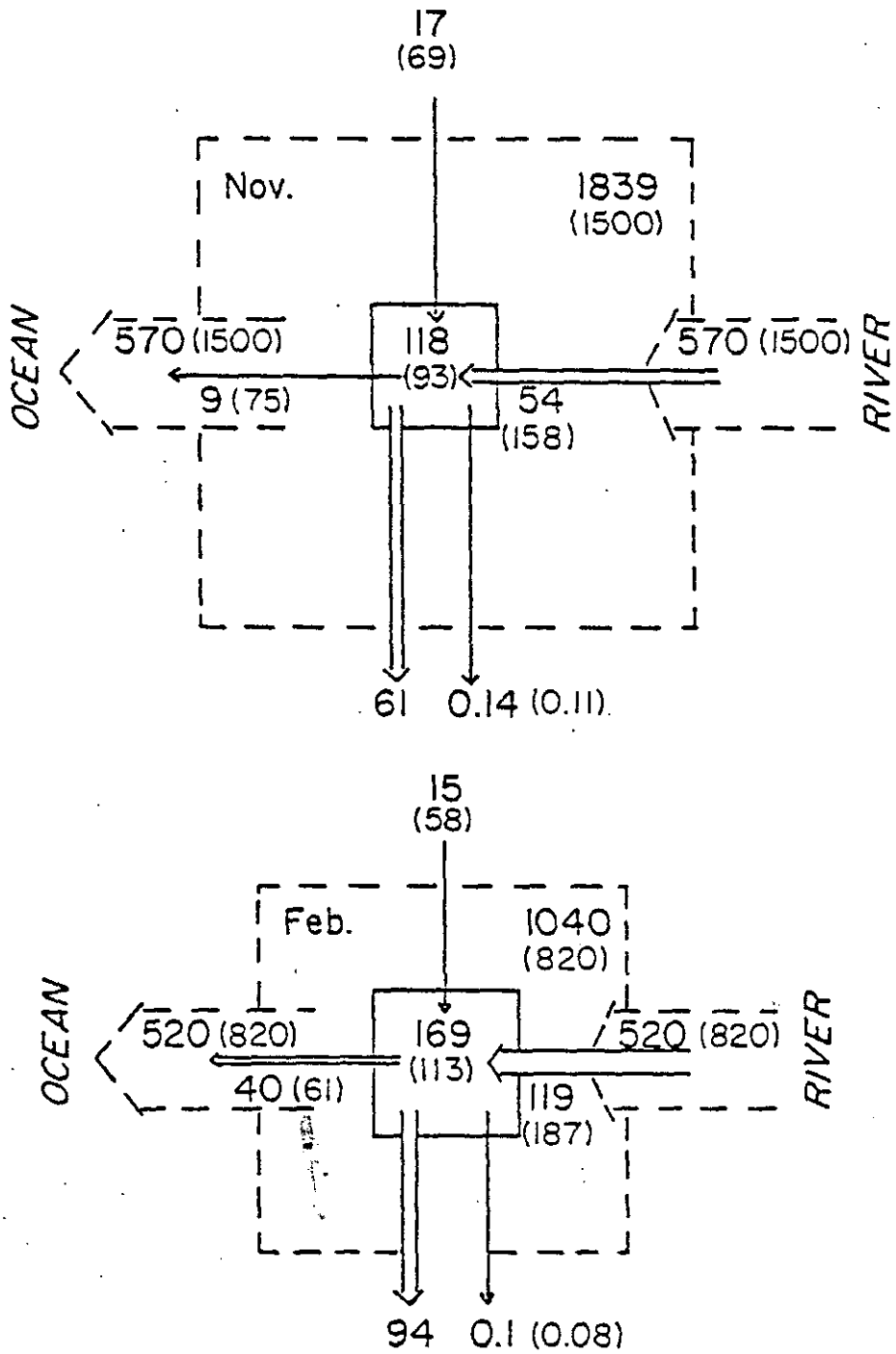


Figure 51. Daily particulate organic carbon budgets for the Columbia River Estuary; November and February. For legend details see Figures 47 and 48.

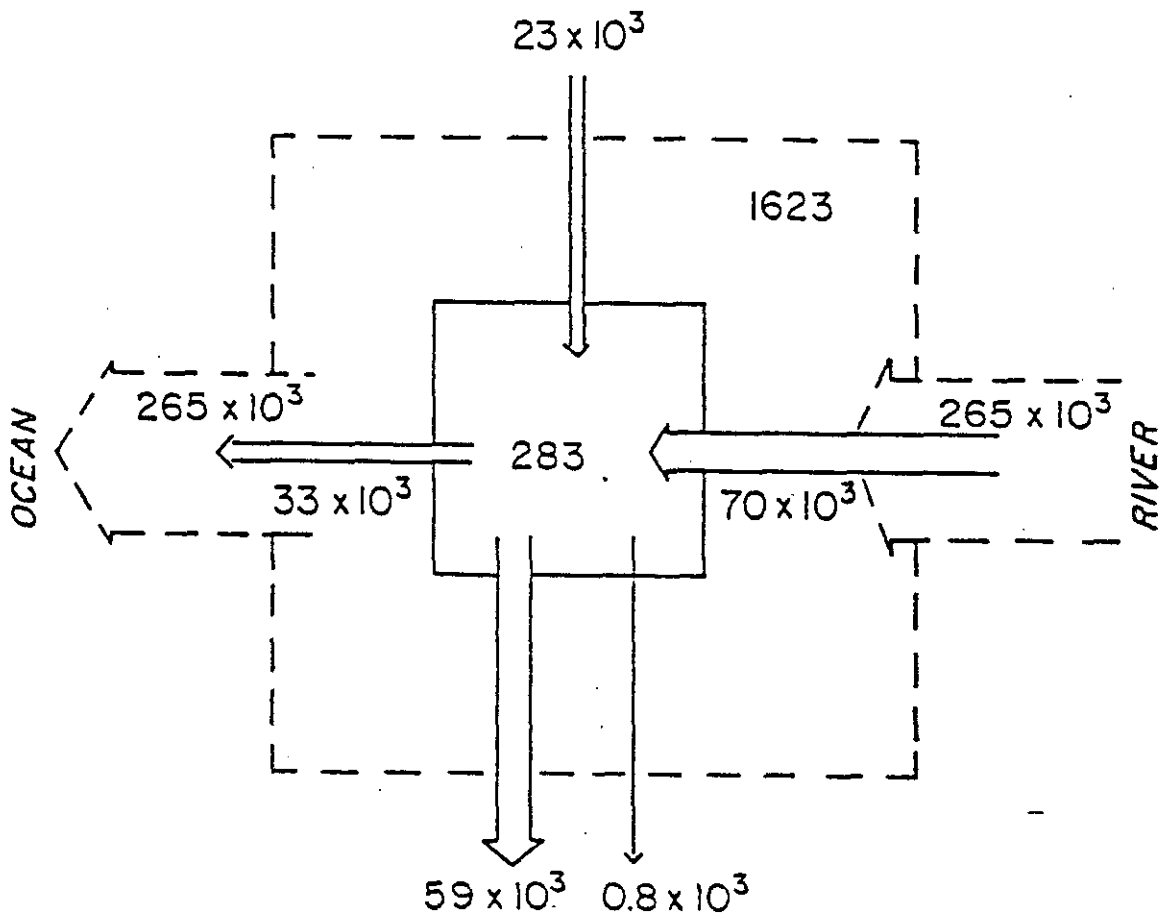


Figure 52. Yearly particulate organic carbon budgets for the Columbia River Estuary. Boxes represent the yearly average concentrations for total estuary in metric tons carbon. Arrows represent inputs-outputs in metric tons carbon yr^{-1}.

5. CONCLUSIONS AND RECOMMENDATIONS

Over an eighteen-month period of field sampling, the spatial and temporal distribution of phytoplankton and other suspended particulate materials in the Columbia River Estuary was determined. The relative importance of the factors which affect the distribution and abundance of phytoplankton in the estuary through the annual cycle was also determined. The impact of the eruption of Mt. St. Helens was estimated. Major conclusions and recommendations are summarized below.

5.1 CONCLUSIONS

(1) Light is the major factor limiting phytoplankton primary production in the Columbia River Estuary. Both the intensity of incident solar radiation, and the attenuation of light within the water column are critical variables in determining the rates of primary production per unit of plant biomass or chlorophyll a.

(2) Import from the upstream Columbia River, as opposed to in situ production, is the most important factor in determining the concentration of phytoplankton in the water of the estuary. On a yearly basis, 75% was supplied by the Columbia River, while only 25% was produced in situ.

(3) Of the major inorganic nutrients necessary for phytoplankton growth (nitrogen, phosphorus, and silica), only nitrogen appears to become depleted to the point of limiting phytoplankton growth. All three nutrients are in ample supply in utilizable forms most of the time, but in late spring and summer nitrogen-nutrients appeared to approach limiting concentrations; however, not all nitrogen forms were measured.

(4) In the freshwater portions of the estuary, all measured properties (except light) were vertically homogeneous through the water column. Where the salt wedge was encountered, properties were stratified as a result of the marine-source water intrusion at depth.

(5) Phytoplankton species in the estuary are dominated by freshwater diatoms. Nanoplankton cells $<33\ \mu m$, and generally $<10\ \mu m$) predominated over netplankton (cells $>33\ \mu m$) in the estuary.

(6) The concentrations of chlorophyll a and freshwater diatom species decreased from the freshwater zone to the marine zone, with the greatest decrease occurring in the mixing zone. Apparently as freshwater phytoplankton mix rapidly with saline waters, the change in osmotic pressure destroys the cells.

(7) For properties other than chlorophyll a, the estuary acts as a conduit for export from the Columbia River to the Pacific Ocean. Little change appears to take place within the estuary itself. This is doubtless due to the low residence times of water in the estuary (one to five days), and the high turbulence of the system which keeps the estuary well mixed.

(8) Zooplankton grazing removal of phytoplankton amounted to only about 1% per day of the available phytoplankton biomass.

(9) The eruption of Mt. St. Helens on May 18, 1980, added large amounts of particulate material to the water column in the estuary. This in turn greatly reduced the amount of primary production in the water by reducing light penetration in the water. During the 5-week period in which the estuary was unusually turbid, we estimate primary production to have been reduced by about 75%. We observed no effect on levels of phytoplankton biomass in the water attributable to this reduction in productivity.

(10) Of the total particulate organic carbon in the estuary, about 75% was detrital and 25% was live phytoplankton. About 63% of the phytoplankton was lost in the estuary, and the remainder was exported to the Pacific Ocean.

5.2 RECOMMENDATIONS

(1) Because the basic water-column fertility of the Columbia River Estuary is mainly a function of particulate organic material imported into the estuary from the main stem of the river, the formation and distribution of particulate organic matter must be studied in the river itself, particularly above and below the dams. This up-river productivity and biomass largely controls the estuarine concentrations.

(2) Because light is the major controlling factor in water-column primary production in the estuary, a detailed study of the seasonal and regional differences in the functional relationship between light and primary production is needed for the Columbia River Estuary. Included in this recommendation is a corollary recommendation for the estimation

of phytoplankton respiratory losses below the photic zone and at night, for the purpose of estimating 24-hr net phytoplankton production.

(3) Nitrogen, as nitrate, appears to be the only nutrient possibly limiting phytoplankton production in the summer in the Columbia River Estuary. However, concentrations of reduced nitrogen forms such as nitrite and ammonia were not measured, nor were the uptake rates of all nitrogen forms by the estuarine phytoplankton. These concentrations and rates must be assessed before nutrient limitation, or the lack of it, can be determined.

(4) Finer-resolution studies are needed to pinpoint the seasonal and regional shifts of the 1-5‰ salinity intrusions upriver, to better pinpoint the areas where freshwater phytoplankton meet this slight salinity gradient and presumably die. Corollary to the need for these salinity intrusion studies is the need for more detailed studies of the phytoplankton species, their pigment contents, and their productivities on either side of the "salinity boundary."

(5) Much better estimation of grazing removal of phytoplankton can be accomplished with more spatial-temporal data on distributions of major herbivorous suspension feeders in the estuary. In addition, grazing rates for more herbivores, including larval fish, are needed.

(6) Better estimation of the rates of conversion of living phytoplankton to detrital particles, and of conversion of marsh and tidal flat vegetation to detritus, is needed in order to assess the relative roles of *in situ* production and detrital production.

(7) Better estimation of mass transport of dissolved and suspended materials can be done if box models are employed to account for tidal mixing and horizontal dispersive transport across the estuary; therefore, more detailed spatio-temporal estimates of current speeds and directions, and of concentrations of materials, are needed.

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