

AN ABSTRACT OF THE THESIS OF

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Title: PRIMARY BIOMASS AND PRODUCTION PROCESSES IN THE COLUMBIA  
RIVER ESTUARY.

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Abstract approved: \_\_\_\_\_

Dr. Lawrence F. Small

The Columbia River Estuary appears to be a light-driven ecosystem, with solar radiation input, light attenuation in the water column, and the phytoplankton biomass itself the variables that mainly explain temporal changes in primary productivity. Freshwater nanoplankton dominated netplankton in terms of biomass and production, and riverine waters were substantially more productive than estuarine waters (121-140 vs. 68-84  $\text{gC m}^{-2} \text{yr}^{-1}$ ).

Upstream of the salt intrusion, homogeneous vertical distribution of suspended particles was observed in all seasons. Except for, chlorophyll a, all suspended particle properties showed homogeneous horizontal distribution. Chlorophyll a decreased markedly from the freshwater zone to the marine zone, with the greatest break in concentration occurring in the mixing zone. Cell disappearance from the water column by sinking to the bottom (due to salinity-induced cell damage to the freshwater phytoplankton) was probably the main process controlling chlorophyll distribution in the estuary; however, loss of chlorophyll without concomitant loss of cell biomass from the water column was also

a possibility. Entrapment of phytoplankton biomass in the estuarine mixing zone apparently creates a prime food zone for benthic and water column-grazers. In contrast to "classical" estuarine systems, however, the Columbia estuary was less productive than its two source waters (the ocean and the Columbia River). Grazing removal of phytoplankton biomass by zooplankton (from  $^{14}\text{C}$  labelling experiments) varied from  $0.06\% \text{ day}^{-1}$  (winter) to  $1.2\% \text{ day}^{-1}$  (spring-summer).

On a yearly basis, the water column budgets for the Columbia River 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, 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, probably by sinking, and 35% was exported to the adjacent coastal ocean. Losses via zooplankton grazing accounted for less than 1% of the live carbon.

PRIMARY BIOMASS AND PRODUCTION PROCESSES  
IN THE COLUMBIA RIVER ESTUARY

by

Jose Ruben Lara-Lara

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Typed by Joy Sharpe for Jose Ruben Lara-Lara

This thesis is dedicated to my  
lovely family.

Thanks for being my greatest source  
of encouragement, and for being so  
patient during all these years.

I love you and thank you.

My wife, my daughter and my son,  
XOCHITL, MARLENE, and ADRIAN LARA.

With love and infinite gratitude  
to my parents, JOSE and AUDELIA LARA,  
and my sister and brother, IRMA  
and OSCAR LARA.

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# PRIMARY BIOMASS AND PRODUCTION PROCESSES IN THE COLUMBIA RIVER ESTUARY

## INTRODUCTION

At the base of most aquatic food webs is phytoplankton, those small, free-floating algal cells or cell colonies which are found in the upper lighted zone of the waters covering about three-fourths of the earth's surface. Because of the wide range of physico-chemical attributes of the waters of the world, there is a great latitude in the adaptations of phytoplankton species to those attributes. There are species that characteristically live in fresh water, brackish water, and seawater, for example. Of all the aquatic ecosystems, estuarine systems perhaps are the ones exhibiting the widest and most frequent physico-chemical fluctuations, and the ones perhaps most difficult for phytoplankton (and other organisms) to adapt to. In estuarine systems, factors vary in response to tidal, diurnal, and seasonal cycles, as well as to sporadic changes caused by storms and mankind's intervention. For these reasons, understanding of the mechanisms controlling the estuarine abundance of phytoplankton, its production, and the species composition of populations, is most difficult. Yet estuaries are of primary importance both from an ecological and an economic view. In particular, the Columbia River Estuary, with the second largest volume of water discharge in the United States, is of prime importance.

My intent is to develop as fully as possible a budget for total suspended particulate matter in general, and for the living organic fraction (the phytoplankton) in particular, for the Columbia River Estuary. Evaluation of the standing stocks of particulate matter,

and the fluxes in and out of these standing stock "reservoirs", should aid in understanding the workings of the river-estuary-ocean continuum through time. Furthermore, I want to examine the primary biomass and production systems in a way that will be useful to other investigators studying other biological parts of the Columbia estuary, and in a way that will be useful to estuary management personnel.

### Conceptual Framework

Theoretically, an estuarine ecosystem can be conceptualized as a hierarchical system of biological processes, in the sense of Overton (1972, 1975) and McIntire and Colby (1978), with physical and chemical processes acting as driving functions and control variables (Fig. 1). In this scheme, any process can be partitioned into a system of coupled subprocesses (or considered as a component of some supra-processes) by identification of relevant coupling variables. For example, total estuarine biological processes might be partitioned into water-column processes, benthic processes, and emergent plant processes (Fig. 1). The water-column processes subsystem, which is of most interest herein, can be partitioned into primary food processes and consumer processes (Fig. 2). Primary food processes include the dynamics of variables associated with the accumulation and removal of the standing stock of small-sized particulate organic matter suspended in the water (the primary food supply). This suspended particulate biomass can be thought of as undifferentiated organic particles, or as separate living and detrital fractions. As a first approximation I have assumed that all suspended organic particles are potential food. It has been documented that small microcrustacean grazers feed

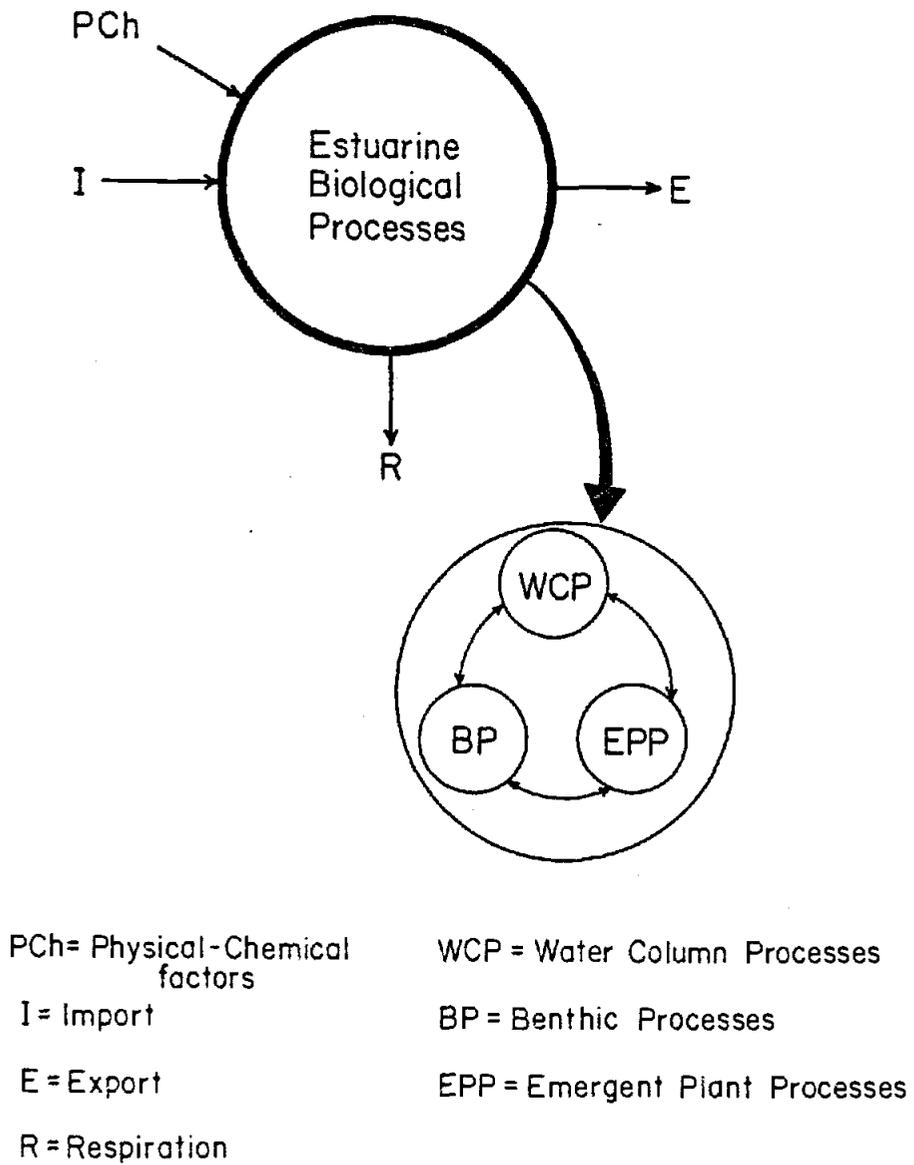
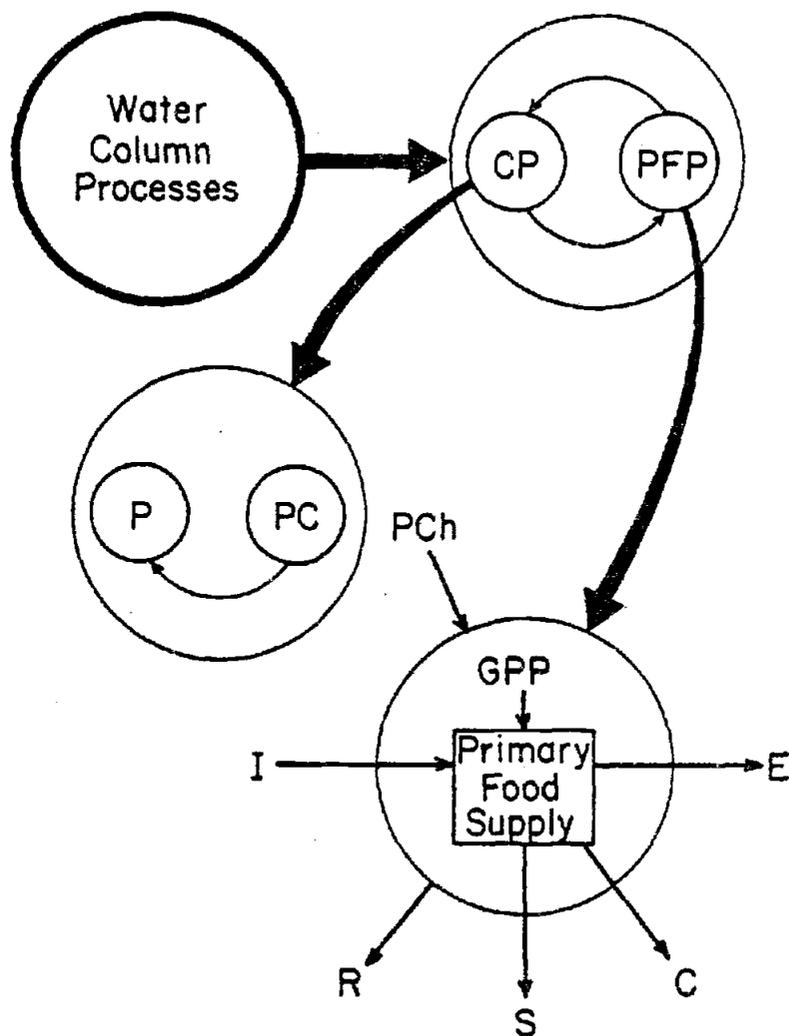


Figure 1. Conceptual model of estuarine biological processes.



PCh = Physical-Chemical factors

I = Import

E = Export

S = Sinking

C = Consumption

R = Respiration

PFP = Primary Food Processes

GPP = Gross Primary Production

CP = Consumer Processes

PC = Primary Consumption

P = Predation

Figure 2. Conceptual model of estuarine water column processes.

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). Then, the coupling between the primary food supply and consumer processes is a grazing term (C, in Fig. 2). During this study zooplankton grazing rates of natural populations were calculated from in situ experiments measuring the ingestion of prelabelled  $^{14}\text{C}$ -natural phytoplankton populations. I was interested in the removal of primary food by zooplankton consumption, not in the role of particles to supply an adequate ration for growth and metabolism of the zooplankton.

Other particle removal processes (besides grazing) are particle export from the system, and particle sinking (Fig. 2). Estimation of particle export was based on river flow data and particle concentrations, from which particle transport could be calculated. Because of extraordinary difficulty in measuring in situ phytoplankton sinking rates in such a high-energy environment as the Columbia River Estuary, direct measurements of sinking rates were not made. However, during the course of this investigation, downstream decreases in chlorophyll and freshwater phytoplankton species could have been due to sinking as the cells encountered slightly saline water in mid-estuary. Some of this presumed sinking may actually have been cell rupture due to osmotic stress, or loss of pigment from stressed cells, rather than sinking of intact cells to the estuary bottom; nevertheless, the loss could be quantified. Total particle removal is thus carried out by grazing activity, by horizontal export from the estuary, and by osmotic stress on the freshwater phytoplankton community.

The primary food supply is increased or maintained by primary production in the estuary as well as by particle import to the estuary (Fig. 2). Net primary production is the difference between photosynthetic production of organic matter by phytoplankton (gross primary production) and respiratory loss; hence, gross production is an input term and respiration a non-particulate output term in Fig. 2. Respiratory loss at night and from below the photic zone would also be included in the respiration term in Fig. 2.

Physical and chemical driving variables (Fig. 2) are the factors affecting all primary food processes in time and space. Major factors that affect primary food processes do so by advecting or dispersing particles (currents), by providing energy (light) and chemicals (nutrients,  $\text{CO}_2$ , and  $\text{O}_2$ ) as the "raw materials" for gross primary production, by regulating rates of reactions (temperature), and by creating different osmotic environments (salinity).

### Research Objectives

The main objectives of this study were to understand the mechanisms that control the water column phytoplankton biomass (primary food supply), and to relate these primary food processes to other biological processes in the Columbia River Estuary. The main objectives were accomplished by:

1. Studying the spatial and temporal distribution of phytoplankton biomass as well as the distribution of the physico-chemical driving variables in the estuary, throughout an annual cycle.
2. Determining the factors that control the distribution and abundance of phytoplankton biomass in the estuary.

3. Evaluating the rates of phytoplankton biomass increase (from production and import), and decrease (from grazing, export, and sinking).
4. Assessing the effects of each rate process on the phytoplankton biomass in the estuary through time and space, by employing a hierarchical model which also allows primary food processes to be coupled with other biological processes in the estuary.

#### Description of the Study Area

The Columbia River is 1210 miles long and drains an area of about 259,000 square miles (Lockett, 1963). It is the second largest river in the United States, after the Mississippi. The annual discharge of the Columbia is about 58% of the Mississippi, and constitutes about 1% of the total river input to the ocean worldwide. After flowing from its origin in British Columbia (Canada), the Columbia River is joined by several tributaries, the largest ones being the Snake (Washington) and the Willamette Rivers (Oregon).

The flow of the Columbia is highest in the period from May through July as winter snowfall melts in the mountains. A second, smaller peak occurs during the rainy season. The mean annual discharge at the mouth is  $7300 \text{ m}^3 \text{ sec}^{-1}$ , while monthly mean values range from 3000 to  $20,000 \text{ m}^3 \text{ sec}^{-1}$  (Neal, 1972).

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, as will be shown later.

The Columbia River Estuary is composed of two distinct geomorphic regions (Hubbell 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). Below Columbia River Mile 30 the river broadens and water flow becomes less channelized. Water spreads over the entire width of the estuary at high tide. 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.

The tides on the Columbia River Estuary are of the mixed, semi-diurnal type typical of the eastern North Pacific Coast. There are two high-water and two low-water periods daily, all of different tidal heights. At the mouth, mean and diurnal tide ranges are 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. 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 (in the sense of Burt and McAlister, 1959), is not possible, because the estuary may show one type at the mouth (i.e., vertically stratified) 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 River Mile 17 at lower low tide. During high river discharge (spring freshets), salinity intrusion occurs only in the lower first few miles of the estuary (Neal, 1965).

Lutz et al., (1975) 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) indicated that during flood tide most of the water is transported through the north channel, while during ebb tide the south channel 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.

The direction of net water transport in the estuary is also complicated by the complex bottom topography and the intrusion of the salt wedge (Lutz et al., 1975). Off Astoria, in general, at river discharges from 2000 to 8500 m<sup>3</sup> sec<sup>-1</sup>, net downstream flow through the complete water column is achieved. However, the lack of proper current data throughout the estuary is clearly evident.

With the objective of estimating budgets and fluxes of properties throughout the estuary, I divided the Columbia River Estuary into

eight zones or sub-areas (Fig. 3). These zones were defined in accordance with the CREST program sub-areas scheme (Thomas, 1981).

#### Zone 1: Marine Zone

This zone (Fig. 3) encompasses the mouth of the estuary, with an area of about  $41.8 \times 10^6 \text{ m}^2$  (15% of the total area studied), and a mean volume at MLLW of approximately  $287.7 \times 10^6 \text{ m}^3$  (21% of the total volume). More than 50% of the area has a mean depth equal to or greater than 10 m. This zone is characterized by two channels (north channel and south channel), with a shallow zone between them (Desdemona Sands). Currents in zone 1 are strongly influenced by the ocean as well as by the Columbia River. Water movement is typically upstream during flood flows and downstream during ebb (Jay, 1978). Salinity distribution here is very complex, varying in response to tidal cycles (flood-ebb) and river discharge intensity. Salinity stratification, with higher bottom salinities than on the surface, is apparent during much of the year in this zone. Water temperature is controlled by the riverine and marine entering waters. During summer, river water is warmer than ocean-derived water, while in winter, the river water is colder. During low river flow and flood tides, surface salinities up to 30‰ and 20‰ are characteristic at the west end and east end of this zone, respectively. Salinities are higher at depth. At high river flow and ebb tides, freshwater is found all along the surface, with 5‰ at 10 m depth at the west end.

For purposes of this work the marine zone represents the main area for exchanging properties with the adjacent oceanic ecosystem.

#### Zone 2: Mixing Zone

This subarea (Fig. 3) encompasses the main body of the estuary

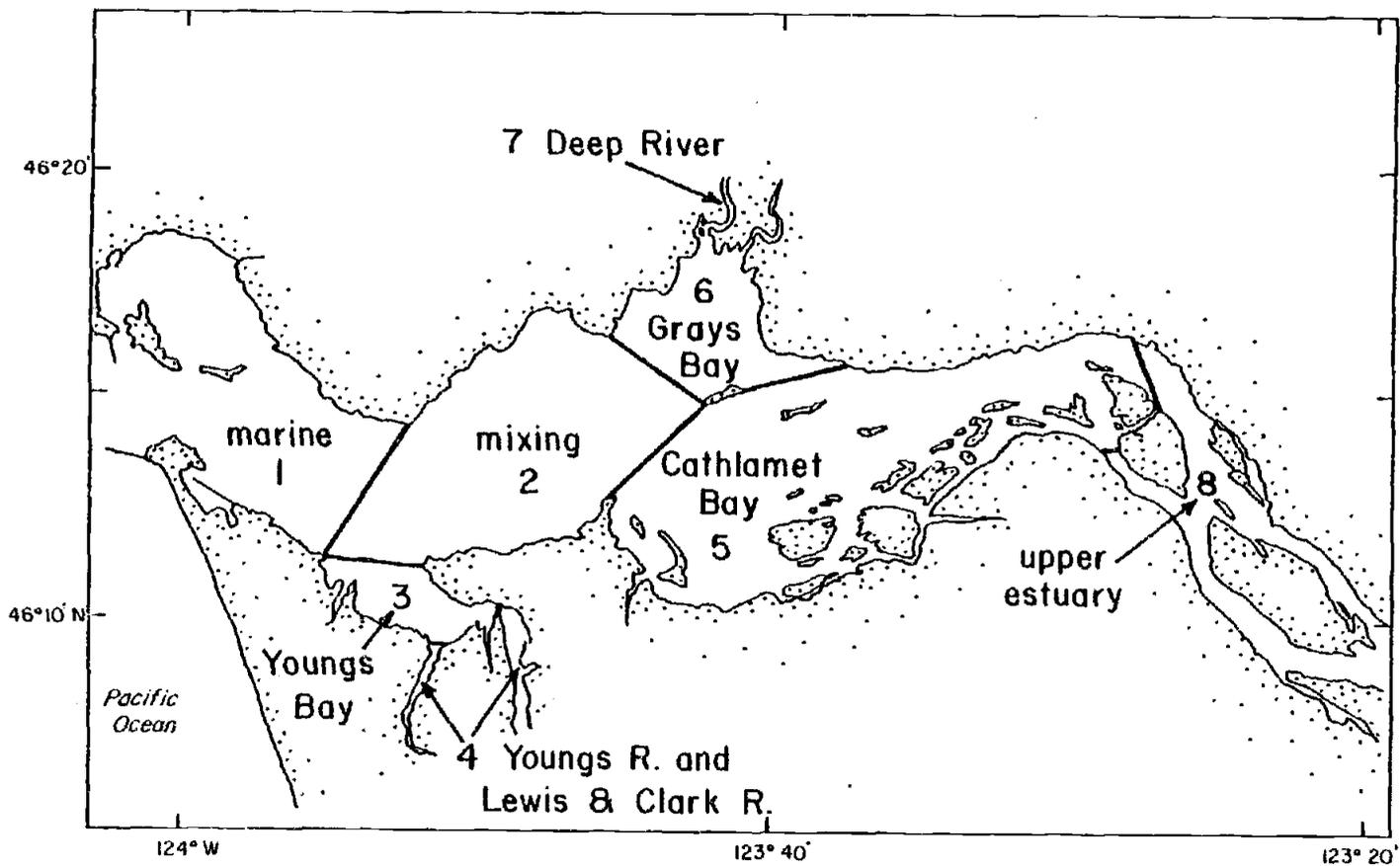


Figure 3. Columbia River Estuary zones.

from about River Mile 8 to River Mile 20, with an area of about  $86.1 \times 10^6 \text{ m}^2$  (31% of the total area studied), and a mean volume at MLLW approximately  $382.8 \times 10^6 \text{ m}^3$  (29% of the total volume). This zone presents a complex bottom topography, characterized by a network of deep channels interspersed by intertidal and shallow subtidal sand bars. Much of the vertical mixing between the upstream flow of marine water and the downstream freshwater flow occurs in this zone. Currents are strongly influenced by tide in this zone, as in zone 1. An upstream flow occurs during flood tide, while during ebb tide the flow is downstream, stronger on the surface than on the bottom (Jay, 1978). An entrapment, or null, zone occurs mainly within this sub-area, migrating longitudinally in response to river discharge rates and tides (Hubbell et al., 1971).

During low river discharge and flood tides, this zone is delimited by maximum surface salinities of 20‰ and <1‰ at its west and east end, respectively. At high river flow and ebb tides, the entire zone is freshwater. The fact that this subarea contains the boundary where freshwater phytoplankton begin to encounter saline water makes this a very interesting area (see later discussions).

### Zone 3: Youngs Bay

Youngs Bay is a shallow bay located on the south side of the estuary, into which drain two small rivers, the Youngs and Lewis and Clark Rivers (Fig. 3). The aquatic habitat of Youngs Bay (over 0.3 m depth) comes to about  $10.58 \times 10^6 \text{ m}^2$  (4% of the total area studied), with a mean volume at MLLW of approximately  $27.7 \times 10^6 \text{ m}^3$  (2% of the total volume). Nearly 60% of its area lies between 1.5 and 0.3 m depth. An extensive marsh area surrounds this bay.

Currents in Youngs Bay are influenced primarily by the Columbia River Estuary tidal currents and by those of the tributary rivers. Current velocities are high in the central bay and low on the mudflats. Flushing time of the bay has been estimated at 1-2 days (Boley et al., 1975); salinity ranges from 0‰ in June to 16‰ in October (Boley et al., 1975).

#### Zone 4: Youngs and Lewis and Clark Rivers

This zone encompasses the two most important rivers on the southern side of the study area (Fig. 3). Maximum discharges for these rivers occur during winter, and minimum discharges occur in summer. Discharges of 187 to 0.5 m<sup>3</sup> sec<sup>-1</sup> for Youngs River, and 85 to 0.2 m<sup>3</sup> sec<sup>-1</sup> for the Lewis and Clark River, have been reported (Boley et al., 1975). A 4 to 16 day water residence time has been estimated for these rivers (Boley et al., 1975).

#### Zone 5: Cathlamet Bay

This is the largest zone of the estuary, with an area of about 89.4 x 10<sup>6</sup> m<sup>2</sup> (32% of the area) and a mean volume at MLLW of 382.3 x 10<sup>6</sup> m<sup>3</sup> (29% of the total volume) (Fig. 3). This zone is characterized by the main channel flowing along the north, and many islands and shallows on the south side. Nearly 50% of its area lies between 3.0 and 0.3 m depth. Current patterns are determined by tides and river flow. Subsurface current reversals occur in the deep channels during flood tides (Jay, 1978). The dominant tidally averaged water flow is downstream (U.S. Army Corps of Engineers, 1960). Tidal currents in the channels separating the Cathlamet Bay islands are complex. Prairie Channel apparently drains the bay during ebb tides. The tributary streams contribute an insignificant amount of water to this zone

(Jay, 1978). During low river discharge and flood tides, surface salinities of about 1‰ and 5‰ are found at 10 m depth at the west end of this subarea. Otherwise, this is essentially a freshwater zone.

#### Zone 6: Grays Bay

Grays Bay is a shallow bay located on the north side of the estuary, into which drain two small rivers, Deep River and Grays River (Fig. 3). The aquatic area (over 0.3 m depth) is about  $18.5 \times 10^6 \text{ m}^2$  (6% of the area studied), and mean volume at MLLW is approximately  $36.8 \times 10^6 \text{ m}^3$  (3% of the total volume). Around 58% of the area lies between 1.5 and 0.3 m depth. Current patterns in this bay have not been measured. Water in this zone is generally fresh during most of the year.

#### Zone 7: Deep River and Grays River

A maximum discharge of  $252.0 \text{ m}^3 \text{ sec}^{-1}$  and a minimum of  $0.5 \text{ m}^3 \text{ sec}^{-1}$  have been reported for Grays River, the largest of the two main tributaries flowing into Grays Bay (Harstad Associates, 1970). Unfortunately, no discharge data are available for the smaller Deep River. Both rivers represent a relatively insignificant fraction of the total discharge of the Columbia River Estuary, however.

#### Zone 8: Upper Estuary

This zone is at the head of the area studied, with an approximate area of  $32.0 \times 10^6 \text{ m}^2$  (12% of the total area), and a mean volume at MLLW of about  $215.5 \times 10^6 \text{ m}^3$  (16% of the total volume) (Fig. 3). This subarea is characterized by two main channels surrounding a large island (Puget Island). Nearly 55% of the area of zone 8 has a mean depth equal to or greater than 10 m, with only 12% lying between 1.5 and 0.3 m depth. The small Elochoman River drains into this zone from

the north, with a maximum discharge of  $241 \text{ m}^3 \text{ sec}^{-1}$  and a minimum of  $0.3 \text{ m}^3 \text{ sec}^{-1}$  (Harstad Associates, 1970). Currents in this zone are predominantly downstream. Tidal effects decrease the velocities at flood tides and increase them at ebb (Jay, 1978). This subarea is completely freshwater.

For purposes of this work, the upstream boundary of zone 8 is considered as the main entrance for properties into the Columbia River Estuary ecosystem.

## METHODS

### General

Nine cruises were conducted on the Columbia River Estuary approximately every other month from April 1980 to 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 Fig. 4. 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. No stations were possible in Baker Bay because the bay was too shallow for the large boat and too dangerous to approach from the main channel in a small boat.

Samples were generally collected by submersible pump, although some surface samples were collected with a bucket. Properties measured for spatial and temporal variability were temperature, selected inorganic nutrients, chlorophyll a, phaeophytin a, in vivo fluorescence with and without DCMU treatment, total suspended particles, the organic and inorganic fractions of total suspended load, and particulate organic carbon and nitrogen.

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.

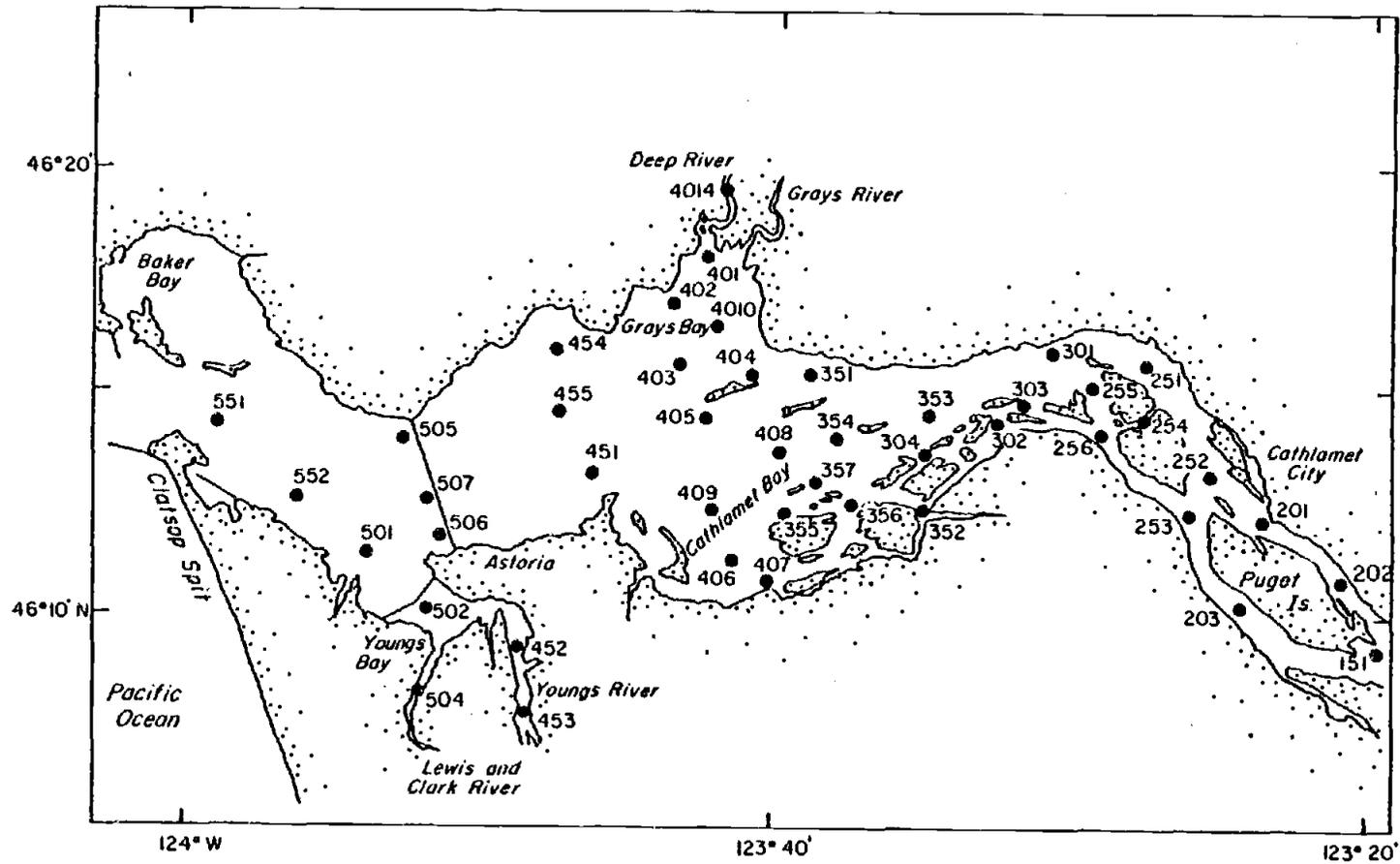


Figure 4. Columbia River Estuary sampling stations.

Samples for inorganic nutrient analyses were filtered through 0.4  $\mu\text{m}$  pore-size Nucleopore® 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®, 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). Phaeophytin a is one of the major degradative compounds from chlorophyll a. Pigment samples from the aphotic zone (Yentsch, 1965), sediments (Gorham, 1960), and samples from areas of high zooplankton grazing (Currie, 1962; Lorenzen, 1965) are particularly likely to contain inactive chlorophyll products such as phaeophytin a. 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  $\mu\text{m}$  pore-size Nucleopore® filter. Filters were placed in petrislides and frozen immediately. In the laboratory the filters were 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.

### 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. Station locations are shown in Fig. 5.

Primary productivity was assessed by the radiocarbon uptake method (Strickland and Parsons, 1972). Samples labelled with carbon-14 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, samples were gently filtered through 10  $\mu\text{m}$  and 33  $\mu\text{m}$  mesh screens prior to labelling with  $^{14}\text{C}$  in order to test the production attributable to different-sized phytoplankton fractions. Screening separation prior to labelling with  $^{14}\text{C}$  has been recommended in order to avoid losing  $^{14}\text{C}$  recently assimilated by cells (McCarthy *et al.*, 1974). At the end of all incubations, the  $^{14}\text{C}$ -labelled samples were immediately filtered through 0.8  $\mu\text{m}$  pore-size Millipore® filters, and the filters were

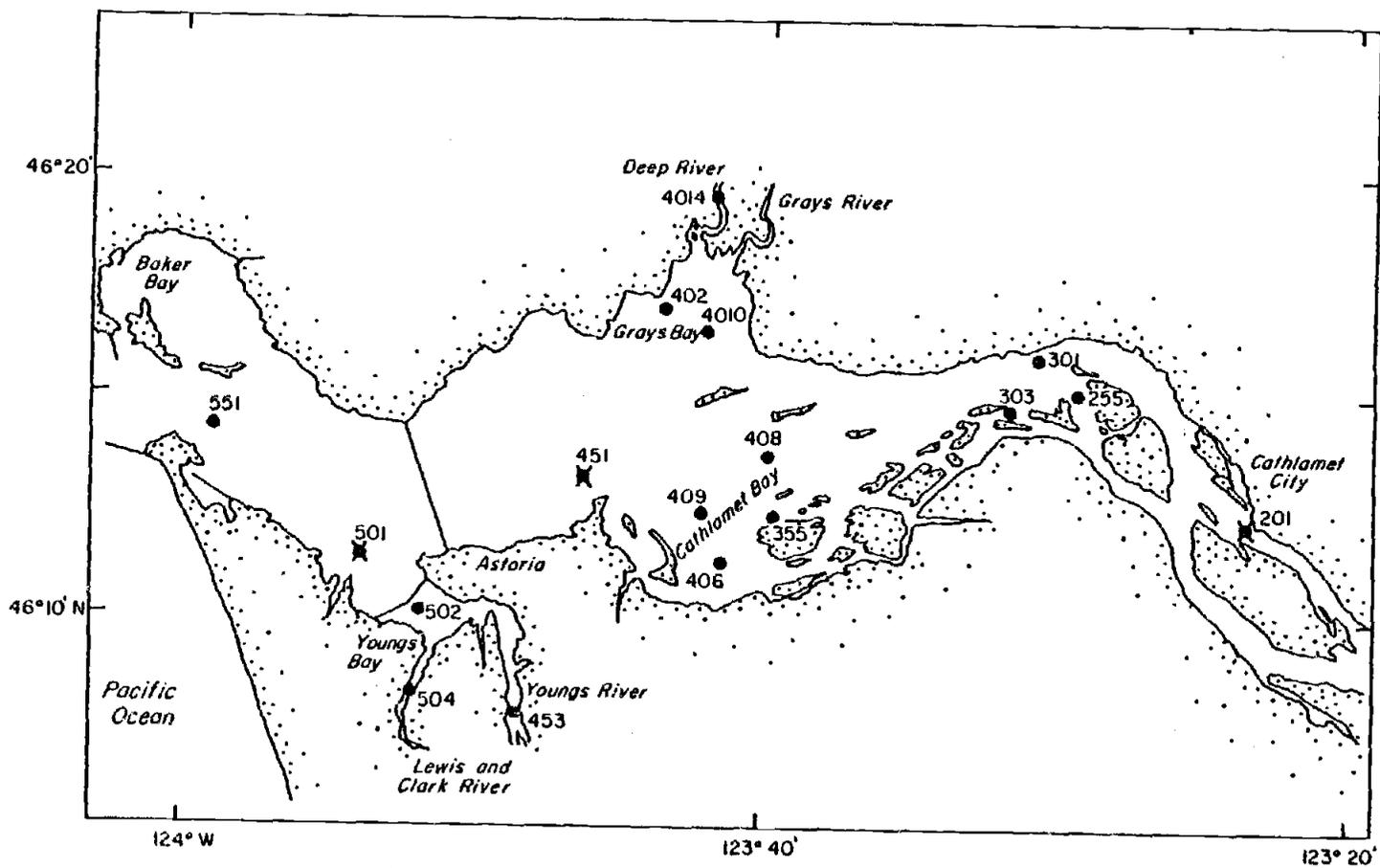


Figure 5. Columbia River Estuary sampling stations. (●,▲) phytoplankton productivity, (■) zooplankton grazing and phytoplankton size fractionation experiments.

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 ( $\text{mgC m}^{-3} \text{ hr}^{-1}$ ) using the equation in Strickland and Parsons (1972). Conversion to  $\text{mgC m}^{-2} \text{ day}^{-1}$  was done as needed, and the conversion technique is given later.

Incident light ( $I_0$ ) 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  $I_z = I_0 e^{-kz}$ , where  $I_0$  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 ( $\sim 295\text{-}695 \text{ nm}$ ) was measured by an Eppley Precision Spectral pyranometer in ( $\text{gcal cm}^{-2} \text{ day}^{-1}$ ) 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) (Fig. 6). Because of the small differences among the two records, and because the Corvallis data included the actual daily 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.

Carbonate alkalinity, required for conversion of  $^{14}\text{C}$  data to carbon-based productivity, was computed from alkalinity measurements

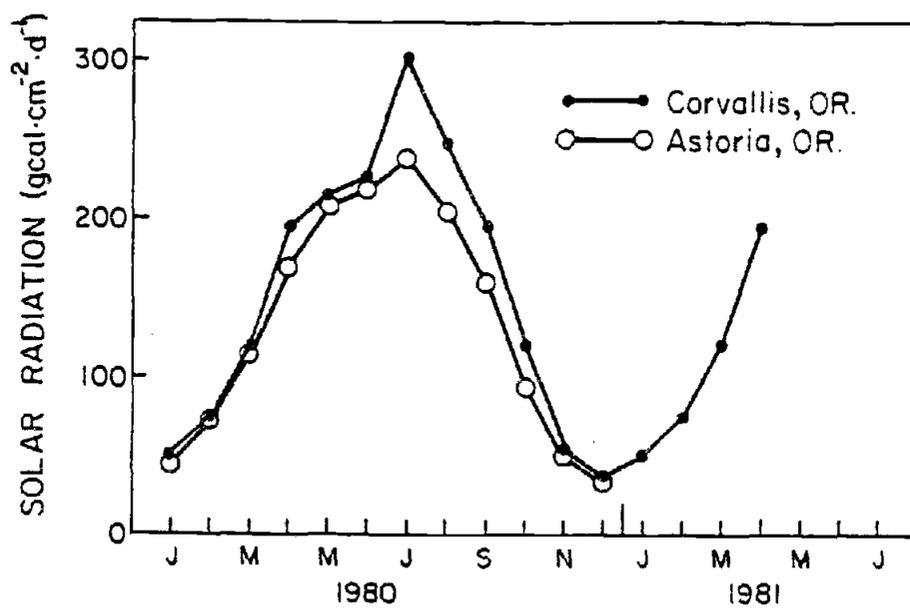


Figure 6. Monthly averages of daily solar radiation.

made by potentiometric titration with 0.2N  $H_2SO_4$ , 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. 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.

### Zooplankton Grazing

#### Field methods

During June and July 1981, six time-series zooplankton grazing experiments were conducted. Experiments were performed at Stations 501, 451 and 201 (Fig. 5), representing three major zones in the estuary.

For each experiment, two 9.5 liter Cubitainers® were filled with 8 liters of filtered (60  $\mu m$  mesh Nitex) surface water containing natural phytoplankton. One container was kept unlabelled for control experiments, while the other was inoculated with 500  $\mu Ci$  of  $NaH^{14}CO_3$  ( $\sim 60 \mu Ci l^{-1}$ ). Both containers were held in clear deck-tanks for approximately one day after inoculation, to allow  $^{14}C$  uptake by the phytoplankton.

Zooplankton were collected with a 250  $\mu m$  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 filtered through 30  $\mu\text{m}$  mesh. This 30  $\mu\text{m}$  filtration procedure was repeated several times before the zooplankton were added to the flask, to bring the chlorophyll fluorescence in 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, 1.5, 2, 3, 4, 6, 17, 19, 21, and 24 hours. After each experimental time period, zooplankton were retrieved from the bottles by filtering the contents of each bottle through 153  $\mu\text{m}$  Nitex filters in Gelman filter holders. These filter holders themselves were rigged above filter holders with 0.45  $\mu\text{m}$  pore-size AA Millipore filters. The Millipore filters collected the phytoplankton. The zooplankton on the Nitex 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  $\text{NaH}^{14}\text{CO}_3$  onto zooplankton surfaces. Approximately 50 ml of "zooplankton suspension" were added to 200 ml of 0.45  $\mu\text{m}$  Nuclepore-filtered estuarine water containing 16  $\mu\text{Ci}$  of  $\text{NaH}^{14}\text{CO}_3$ . The bottles were incubated in the deck-tank. The bottles were then removed at 1, 5, and 24 hours, and the zooplankton were removed on Nitex filters as above, for later  $^{14}\text{C}$  counting. A second control tested changes through time in  $^{14}\text{C}$  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, and the phytoplankton cells were filtered onto Millipore filters as above, and preserved in Aquasol for  $^{14}\text{C}$  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, a different grazing experiment was set up. Approximately 200 ml of unlabelled natural phytoplankton, 50 ml of zooplankton suspension (25-30 animals), and 20  $\mu\text{Ci}$  of  $\text{NaH}^{14}\text{CO}_3$  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.

#### Laboratory analyses

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  $^{14}\text{C}$  activity.

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

## RESULTS

### Spatial and Temporal Variability of Ecological Properties

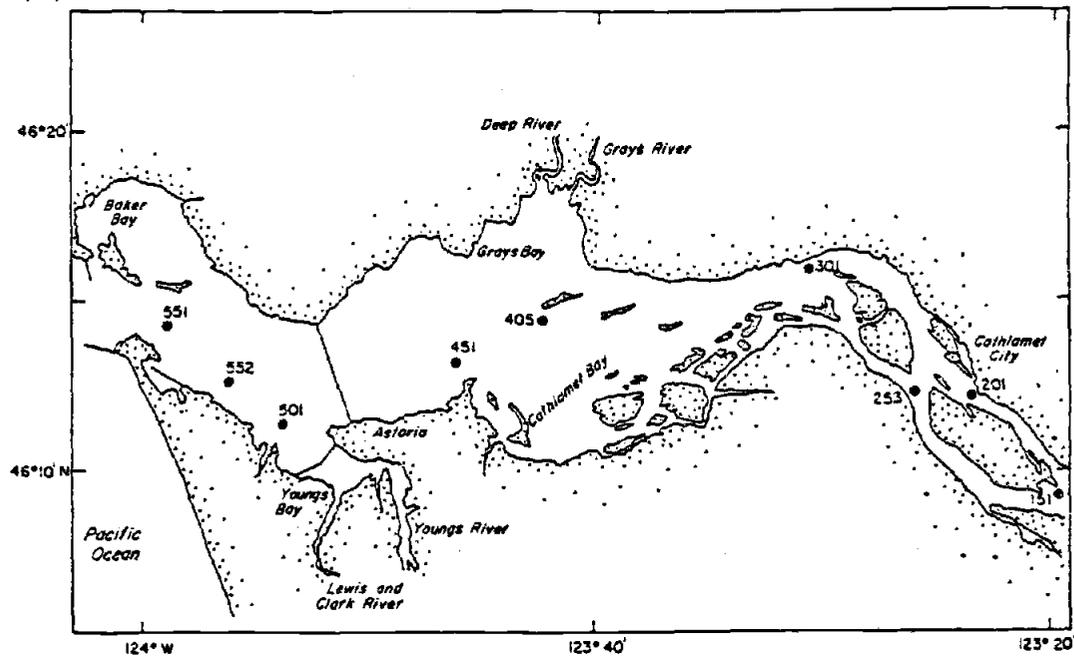
Certain stations were selected to represent: a) distributions of properties along the main channel of the estuary ( $\geq 10\text{m}$  depth), from the mouth (Sta. 551) through the uppermost station (Sta. 151) at the head of the study area (Fig. 7a); and b) distributions of properties in the major shallow bays (Youngs, Grays, and Cathlamet Bays) and rivers (Youngs, Lewis and Clark, and Deep Rivers) (Fig. 7b). 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. Vertical structure was examined only at the channel stations, because the shallow stations were all well mixed and only surface data were taken.

#### Channel stations

Surface temperature showed significant ( $p < 0.001$ ) temporal variation, but no significant spatial variation (Fig. 8a; Table 1). A seasonal trend matching the solar irradiation cycle (Fig. 6) was

(a)



(b)

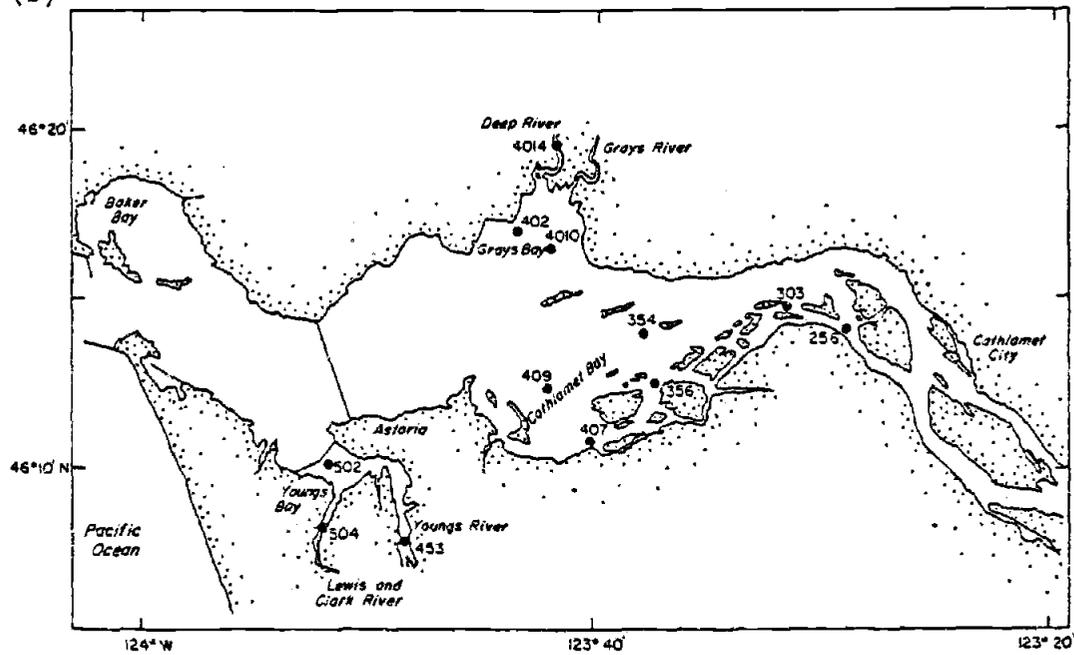


Figure 7. Columbia River Estuary sampling stations. (a) channel stations, (b) shallow stations.

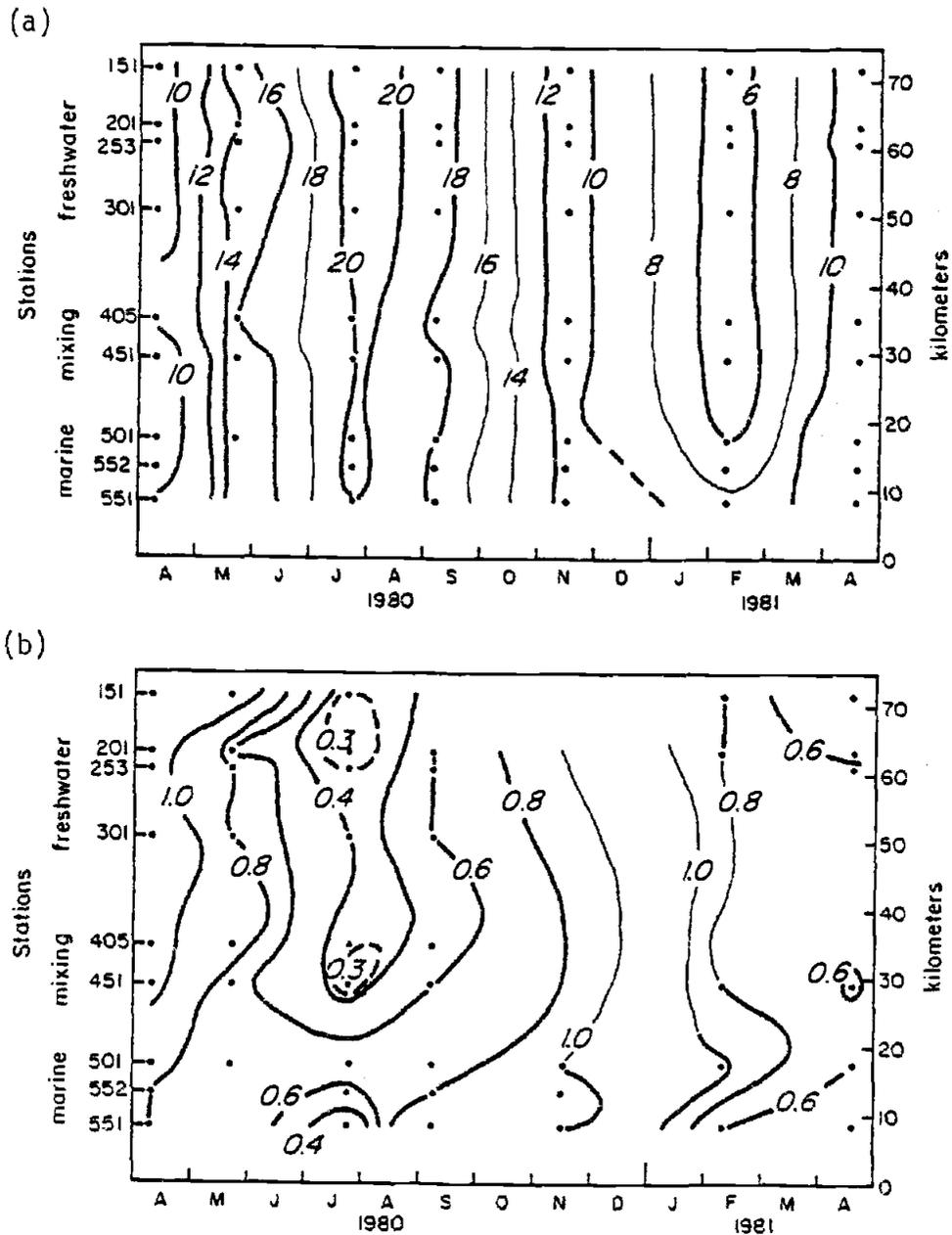


Figure 8. (a) Spatial-temporal distribution of temperature ( $^{\circ}\text{C}$ ).  
 (b) Spatial-temporal distribution of phosphate ( $\mu\text{M}$ ).  
 Thin lines through all the spatial-temporal figures, represent a lower confidence of contouring due to a reduced number of stations. Dashed lines represent different interval of contouring.

Table 1. Analyses of variance for properties in channel and shallow stations.

VARIABLE	FACTOR	CHANNEL		SHALLOW	
		F	P	F	P
Temperature	time	420.5	0.001	266.8	0.001
	space	1.1	n.s		
Phosphate	time	9.2	0.001	2.6	0.001
	space	0.3	n.s		
Nitrate-nitrite	time	95.3	0.001	11.9	0.001
	space	1.9	n.s		
Silicic acid	time	20.5	0.001	28.1	0.001
	space	1.5	n.s		
Chlorophyll <u>a</u>	time	39.0	0.001	8.0	0.001
	space	12.6	0.001		
Fluorescence	time	83.1	0.001	7.0	0.001
	space	19.4	0.001		
DCMU-Ratio	time	4.5	0.005	3.2	0.020
	space	4.0	0.005		
Phaeophytin <u>a</u>	time	20.6	0.001	2.3	0.100
	space	2.1	n.s		
Phaeophytin <u>a</u> : chlorophyll <u>a</u>	time	28.5	0.001	4.1	0.010
	space	6.5	0.001		
Total suspended particles	time	12.8	0.001	3.5	0.020
	space	1.6	n.s		
Inorganic suspended particles	time	13.6	0.001	3.7	0.020
	space	1.6	n.s		
Organic suspended particles	time	4.0	0.005	1.5	n.s
	space	2.1	n.s		
Particulate organic carbon	time	2.0	n.s	1.9	n.s
	space	1.9	n.s		
Particulate organic nitrogen	time	2.2	n.s	1.8	n.s
	space	2.0	n.s		

evident. Temperature 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 Fig. 8a has been reported for the Columbia River Estuary by Haertel (1970), and Park *et al.* (1972).

Salinity was always zero above Tongue Point (Sta. 451). Seaward of Tongue Point, vertical salinity structure was sometimes encountered, this depending mostly on tide and river flow characteristics. Because our sampling was not designed to study the salinity pattern in the estuary, our data do not reflect the tidal effects. However, earlier data show both tidal and river flow conditions (Table 2).

Dissolved phosphate was variable through the year (Fig. 8b; Table 1), being higher in winter and early spring (0.8-1.0  $\mu\text{M}$ ) than in summer and early fall (<0.3-0.8  $\mu\text{M}$ ). No statistically significant spatial variation was observed for phosphorus (Table 1); however, the marine zone showed a slight enrichment in summer due to Young's Bay influence and coastal upwelling (Fig. 8b). Phosphate did not show clear 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 (Fig. 9a; Table 1). Maximum values were in winter and early spring (over 20  $\mu\text{M}$ ), while minimum values during summer were less than 1.0  $\mu\text{M}$ . Unfortunately no other nitrogenous nutrients (ammonia, for example) besides nitrate

Table 2. Salinity (‰) distribution in the Columbia River Estuary<sup>1</sup>.  
Zones as in Fig. 3.

River flow	Tide condition	Depth (m)	Z O N E 1		Z O N E 2	
			west	east	west	east
Low	Flood	0	30	20	20	<1
"	"	4	>30	22	22	1
"	"	10	>30	25	25	5
Low	Ebb	0	5	3	3	0
"	"	4	10	4	4	0
"	"	10	15	10	10	1
High	Flood	0	15	1	1	0
"	"	4	22	12	12	0
"	"	10	>30	23	23	1
High	Ebb	0	0	0	0	0
"	"	4	1	0	0	0
"	"	10	5	0	0	0

1. After U.S. Army Corps of Engineers (1960)

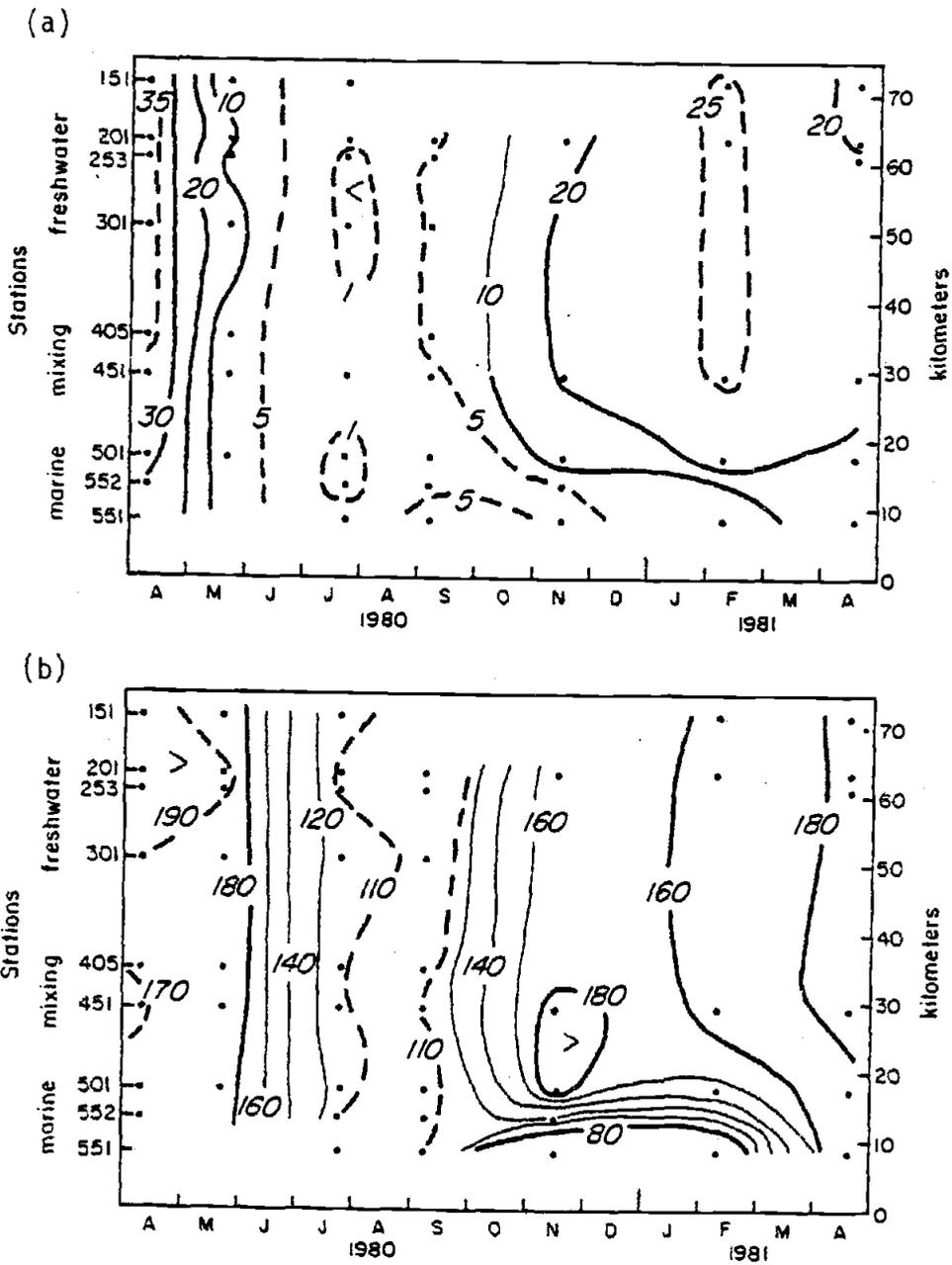


Figure 9. (a) Spatial-temporal distribution of nitrate plus nitrite ( $\mu\text{M}$ ).  
 (b) Spatial-temporal distribution of silicic acid ( $\mu\text{M}$ ).  
 Other comments as in Fig. 8.

plus nitrite have been studied in the Columbia River Estuary, so we cannot say for sure that nitrogen was absent or nearly absent during summer. During mid-autumn and winter, the marine zone averaged less than  $10 \mu\text{M NO}_3^- - \text{NO}_2^-$ , while the riverine waters averaged over  $20 \mu\text{M}$  (Fig. 9a).

Silicic acid (Fig. 9b; Table 1) showed a temporal pattern similar to nitrate plus nitrite in the channel, varying from high values ( $150\text{-}200 \mu\text{M}$ ) in winter and early spring to lower values (around  $100 \mu\text{M}$ ) 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 phytoplankton biomass level as determined by chlorophyll a concentration varied both spatially and temporally ( $p < 0.001$ ) (Fig. 10; 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  $8.0 \text{ mg m}^{-3}$  in the freshwater and mixing zones decreased to values of about  $4.0 \text{ mg m}^{-3}$  in the marine zone. During May 1980, when the highest chlorophyll a concentrations were reached, the freshwater and mixing zones averaged  $17.0 \text{ mg m}^{-3}$ , but concentrations decreased to  $11.2 \text{ mg m}^{-3}$  in the marine zone. Even though our May sampling was conducted three to six days after the Mt. Saint Helens' volcanic eruption, which caused increased levels of chlorophyll a from

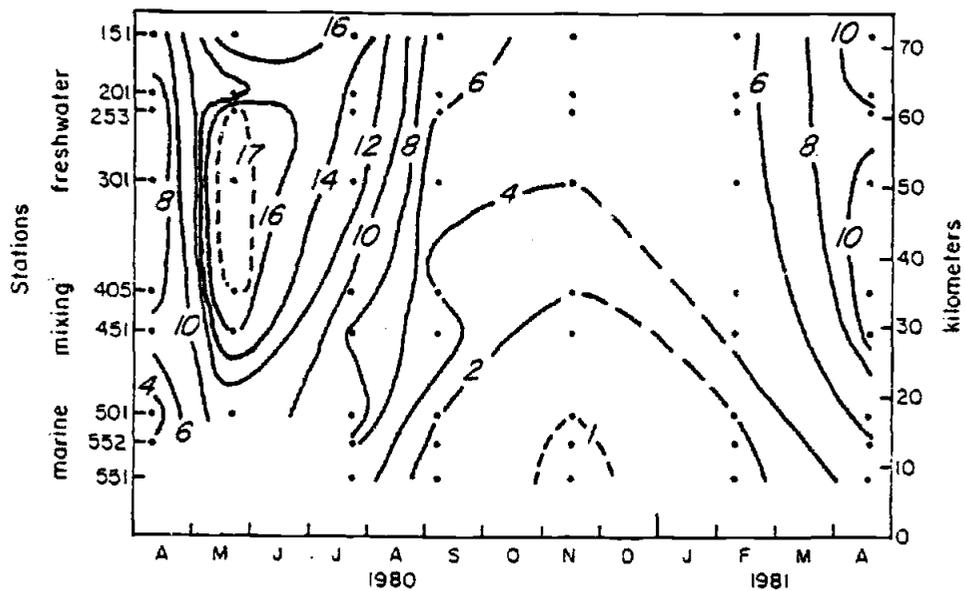


Figure 10. Spatial-temporal distribution of chlorophyll *a* ( $\text{mg m}^{-3}$ ). Other comments as in Fig. 8.

heavy particle loads, no effect was evident in the relative chlorophyll a distribution in the estuary. Photosynthetic rates, however, were greatly affected (see later).

During November we observed the minimum chlorophyll a concentration, and the gradient between freshwater and marine areas was less severe (Fig. 10). Concentrations below  $1 \text{ mg m}^{-3}$  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  $2.0 \text{ mg m}^{-3}$  in the marine zone, about  $5.0 \text{ mg m}^{-3}$  in the mixing zone, and somewhat greater than  $5.0 \text{ mg m}^{-3}$  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  $5.3 \text{ mg m}^{-3}$  in the marine zone, but averaged  $10.0 \text{ mg m}^{-3}$  in the mixing and freshwater zones.

In vivo fluorescence closely mirrored the chlorophyll a pattern, as expected (Fig. 11a; 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 some variability through the year (Fig. 11b; Table 1), being somewhat 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

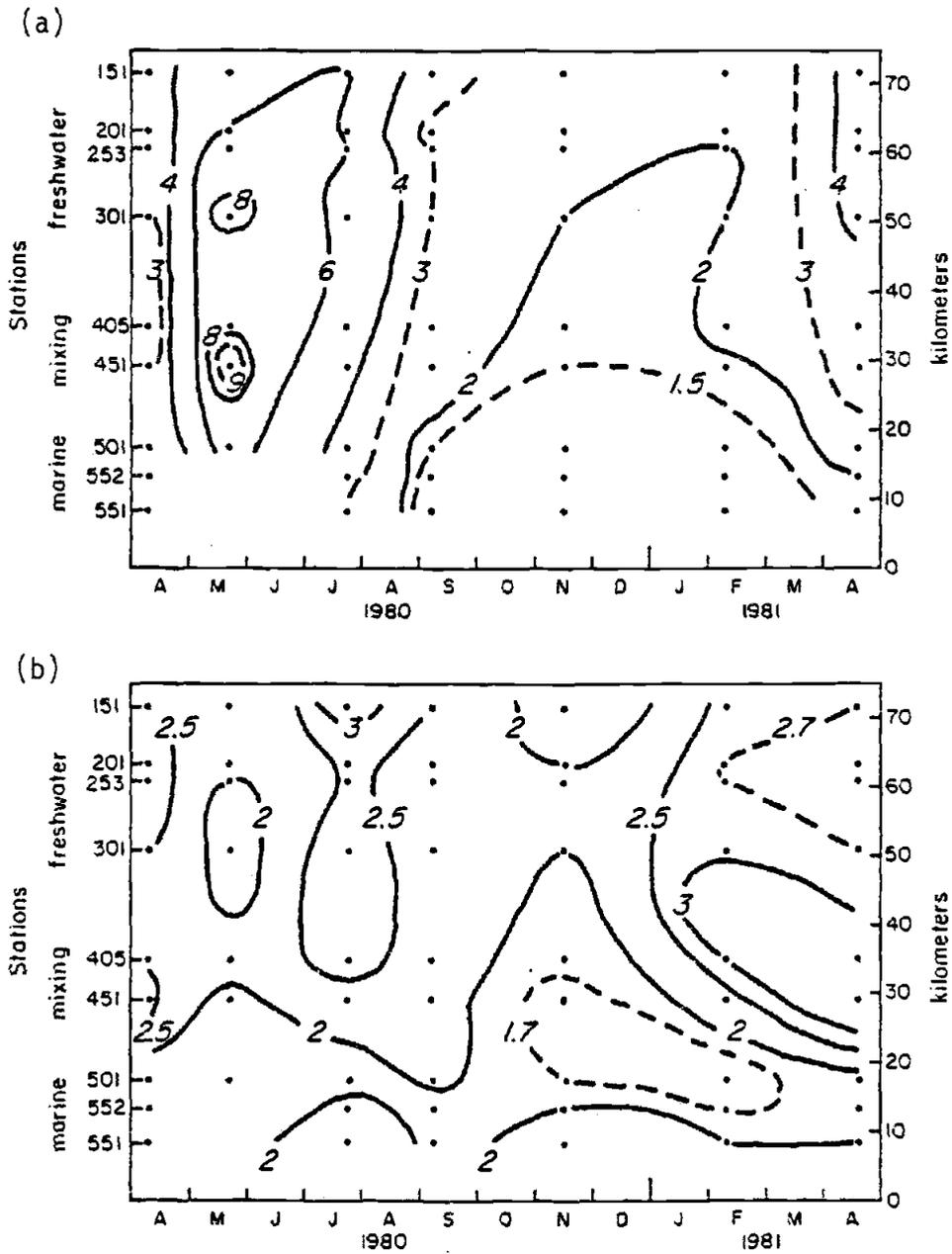


Figure 11. (a) Spatial-temporal distribution of *in vivo* fluorescence (relative units).  
 (b) Spatial-temporal distribution of DCMU:  
*in vivo* fluorescence ratio.  
 Other comments as in Fig. 8.

particle field. Possibly this was a response by in situ phytoplankton to the adverse, light-limited conditions in the estuary following the Mt. Saint Helen's 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 ( $p < 0.005$ ) spatial variability in the ratio (Table 1). In general the ratio decreased from freshwater to the marine zone.

Phaeophytin a showed only significant ( $p < 0.001$ ) temporal variability (Fig. 12a; Table 1). Maximum values were registered during later summer ( $2.0 - 3.5 \text{ mg m}^{-3}$ ), and minimum values during mid-winter and early spring ( $0.0 - 0.7 \text{ mg m}^{-3}$ ). Although no statistically significant spatial variation was observed, the marine zone usually had the lowest concentrations.

The ratio of phaeophytin a to chlorophyll a (as a percentage) varied significantly ( $p < 0.001$ ) both spatially and temporally (Fig. 12b; Table 1). The main spatial features 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 suspended particles (TSP), inorganic suspended particles (ISP), and organic suspended particles (OSP) were done without the May 1980 data, because of the extraordinarily high particulate concentrations during this period. Total suspended particles (TSP) showed significant ( $p < 0.001$ ) seasonal variation but no significant spatial variation (Fig. 13a; Table 1).

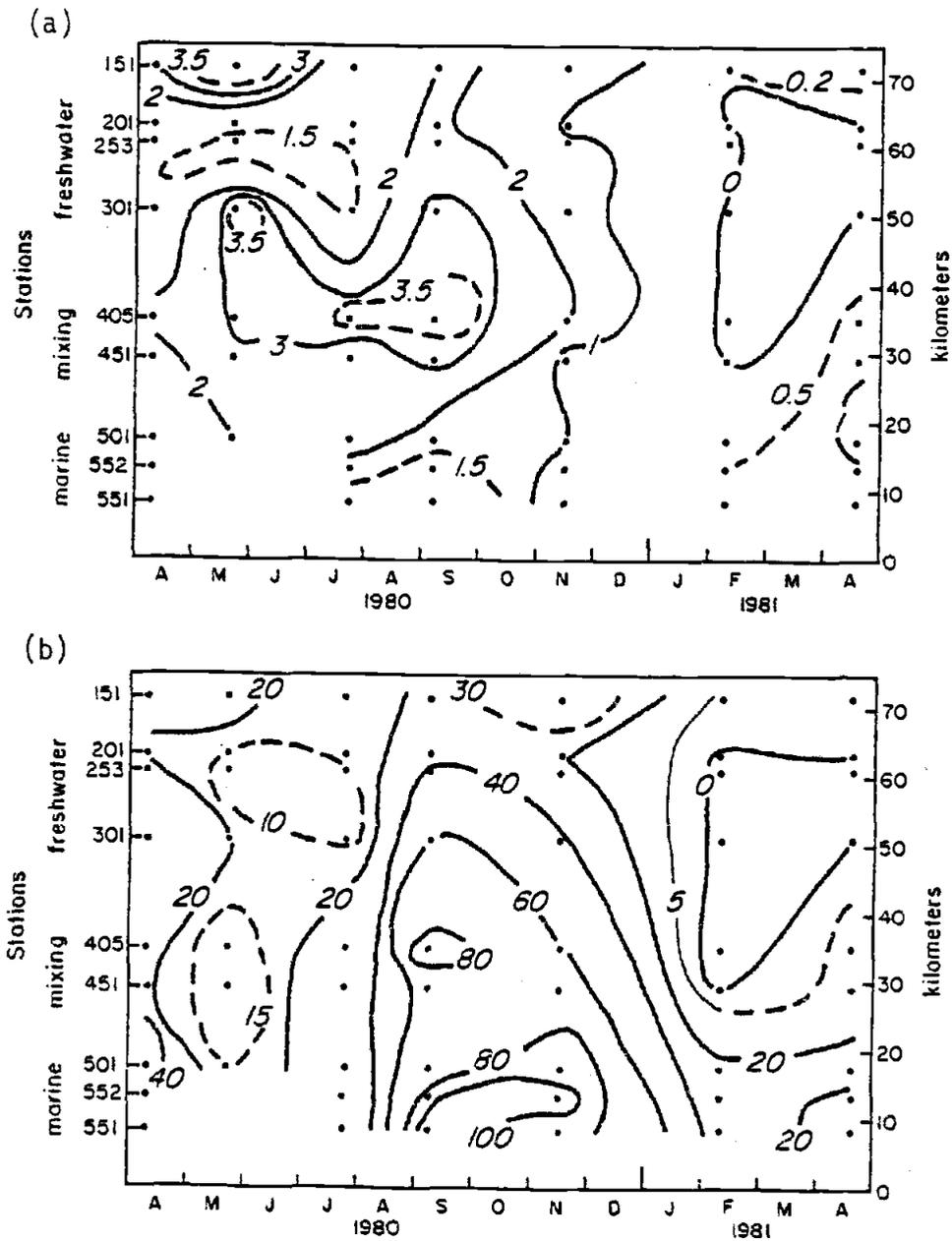


Figure 12. (a) Spatial-temporal distribution of phaeophytin  $\underline{a}$  ( $\text{mg m}^{-3}$ ).  
 (b) Spatial-temporal distribution of phaeophytin  $\underline{a}$ :  
 chlorophyll  $\underline{a}$  ratio (%).  
 Other comments as in Fig. 8.

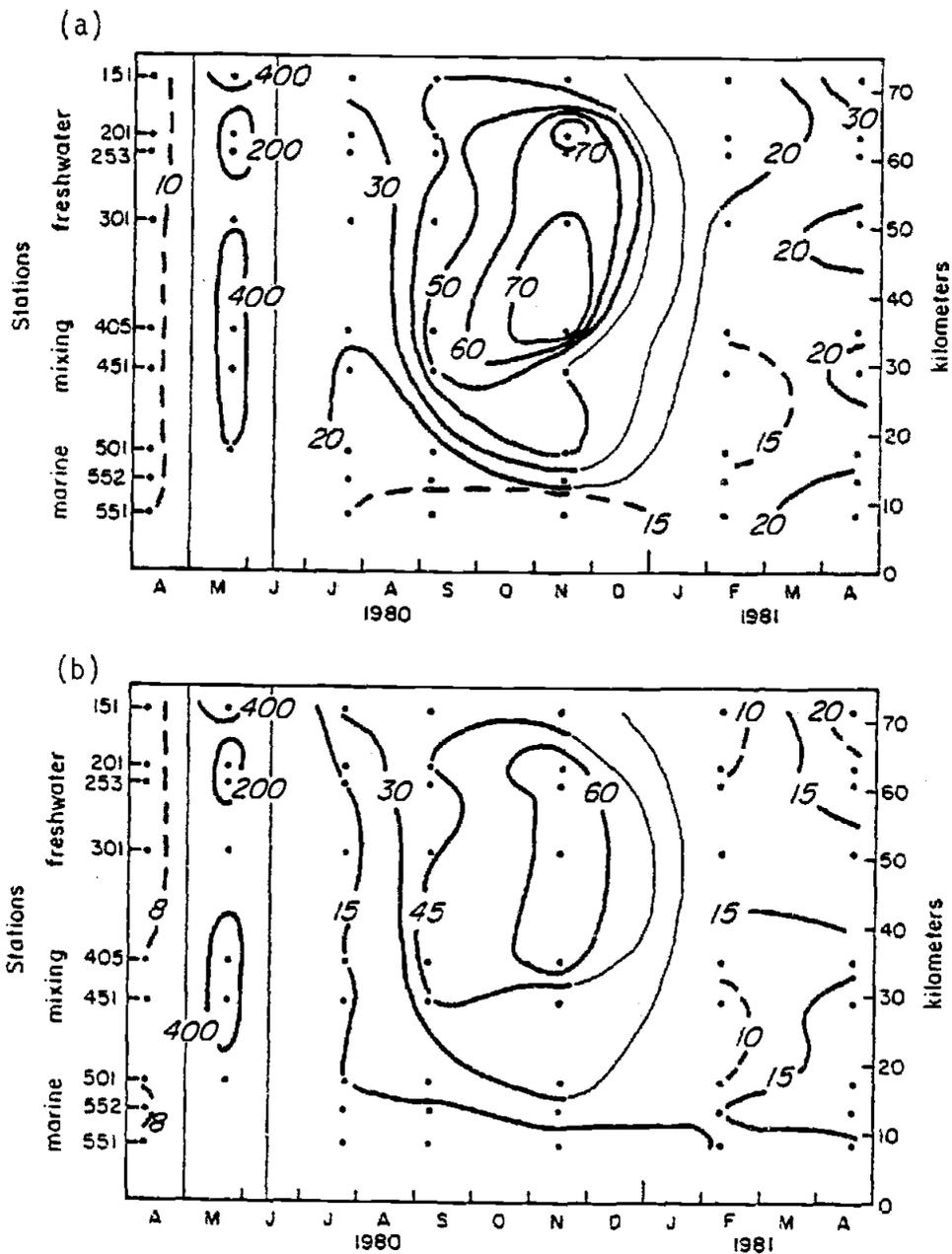


Figure 13. (a) Spatial-temporal distribution of total suspended particles ( $\text{mg l}^{-1}$ ).  
 (b) Spatial-temporal distribution of inorganic suspended particles ( $\text{mg l}^{-1}$ ).  
 The extraordinarily high concentrations in May 1980 were due to the Mt. Saint Helens' volcanic eruption. Other comments as in Fig. 8.

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. Saint 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 ( $50-70 \text{ mg l}^{-1}$ ), and minimum concentrations in mid-winter and early spring ( $8-20 \text{ mg l}^{-1}$ ).

The inorganic fraction of the total suspended particles (ISP) mirrored very closely the pattern of total suspended particles (Fig. 13b). There was significant ( $p < 0.001$ ) 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 ( $45-70 \text{ mg l}^{-1}$ ), and minimum concentrations in mid-winter and early spring ( $7-15 \text{ mg l}^{-1}$ ).

The organic fraction of total seston (OSP) also showed significant ( $p < 0.005$ ) seasonal variation but no significant spatial variation (Fig. 14a; Table 1). Ignoring the May 1980 data, highest concentrations occurred from summer to fall ( $4-8 \text{ mg l}^{-1}$ ), and lowest concentrations occurred during mid-winter and early spring ( $1-3 \text{ mg l}^{-1}$ ) (Fig. 14a).

The organic fraction as a percent of the total suspended particle load did not show spatial variability, but showed some seasonal variation (Fig. 14b). During spring and summer the organic fraction

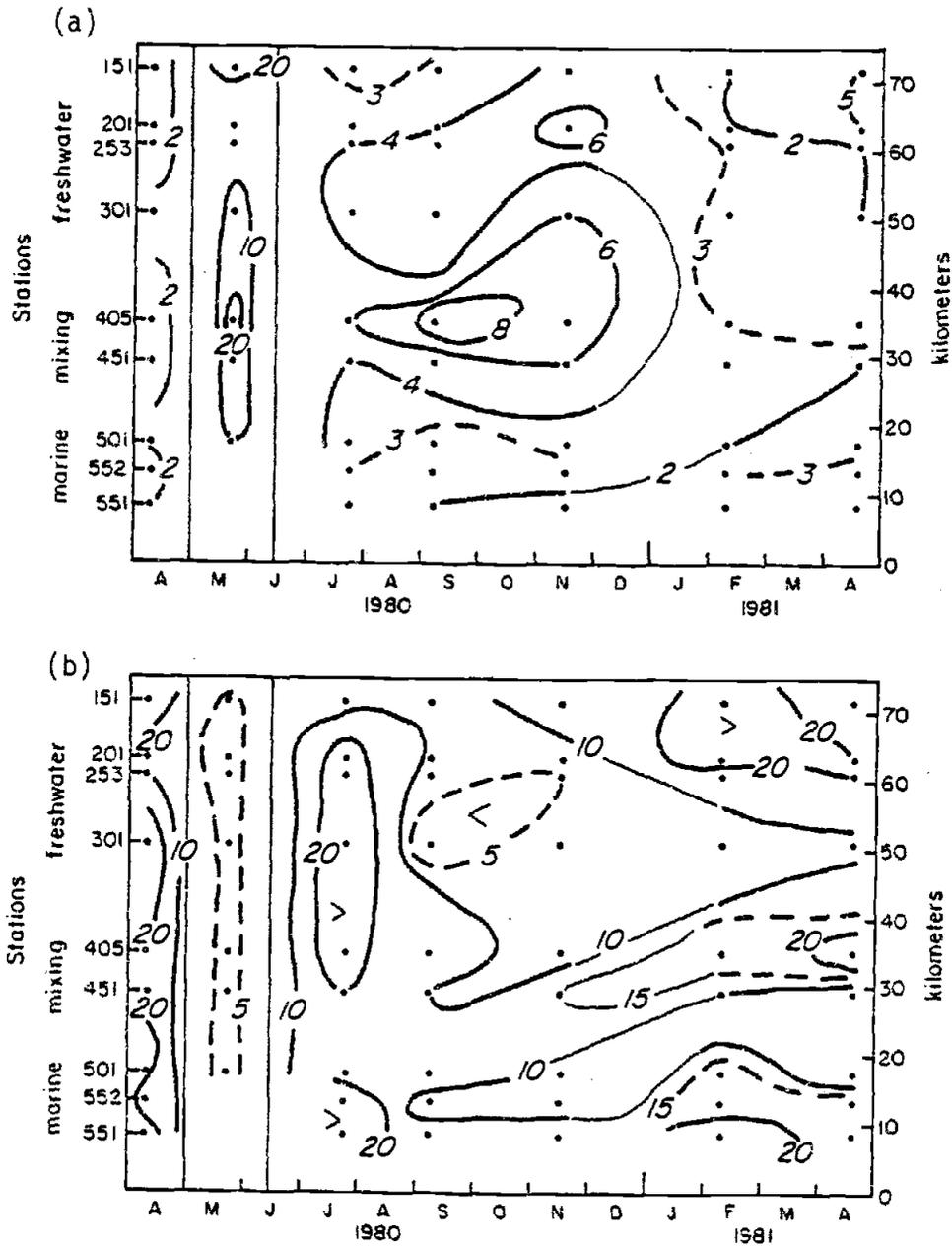


Figure 14. (a) Spatial-temporal distribution of organic suspended particles ( $\text{mg l}^{-1}$ ).  
 (b) Spatial-temporal distribution of organic suspended particles: total suspended particles ratio (%).

Other comments as in Fig. 8.

reached 25%, while minimum values of 10% or less were registered in September and November. The very low percentages in May (<5%, and usually 2-4%) were caused by the exceptionally high inorganic seston concentrations (Fig. 14b) derived from the volcanic eruption.

Particulate organic carbon (POC) (Fig. 15a) and particulate organic nitrogen (PON) (Fig. 15b) did not show spatial or temporal variations (Table 1). Typical concentrations were from 1.0 to 1.3 mg l<sup>-1</sup> for POC, and 0.1 to 0.3 mg l<sup>-1</sup> for PON. Although no statistically significant temporal variation was shown by PON, slightly higher values were registered during mid-winter and early spring.

The POC-to-PON ratio (C/N) (Fig. 16) varied greatly, but yielded no pronounced spatial or temporal trend. Although no clear temporal variation was evident, the rather consistently low C/N ratios during mid-winter and spring reflected the higher PON concentrations at this time.

#### Shallow 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 (Figs. 17 and 18) showed the same seasonal trends as the comparable properties in channel stations. However, the probability of obtaining statistical significance in the seasonal variations for phaeophytin, the phaeophytin-chlorophyll a ratio, the DCMU-in vivo fluorescence ratio, TSP, ISP, and OSP in the shallows was lower than for channel stations (Table 1). These lower probabilities suggest less pronounced seasonal effects in the shallow areas of the estuary.

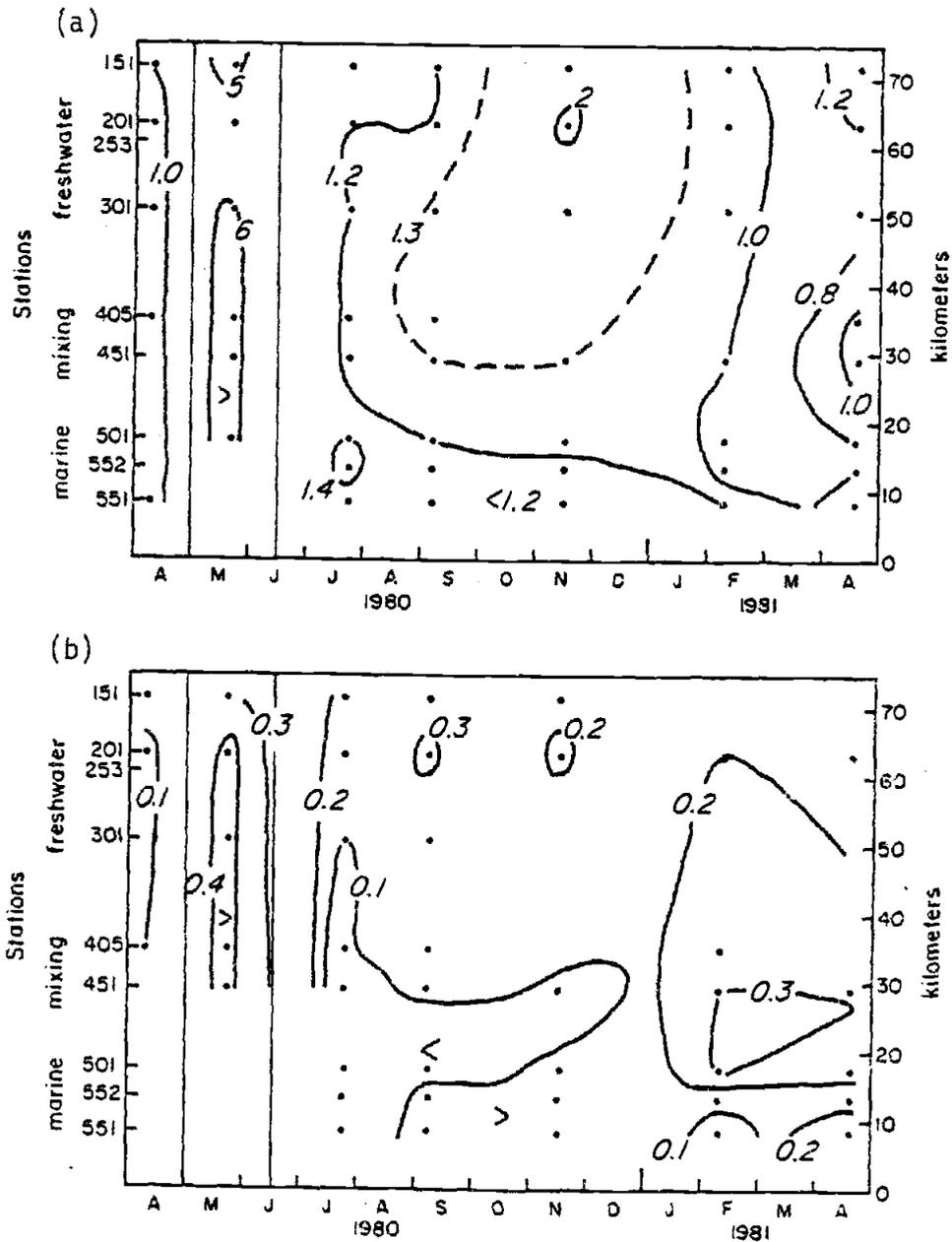


Figure 15. (a) Spatial-temporal distribution of particulate organic carbon ( $\text{mg l}^{-1}$ ).  
 (b) Spatial-temporal distribution of particulate organic nitrogen ( $\text{mg l}^{-1}$ ).  
 Other comments as in Fig. 8.

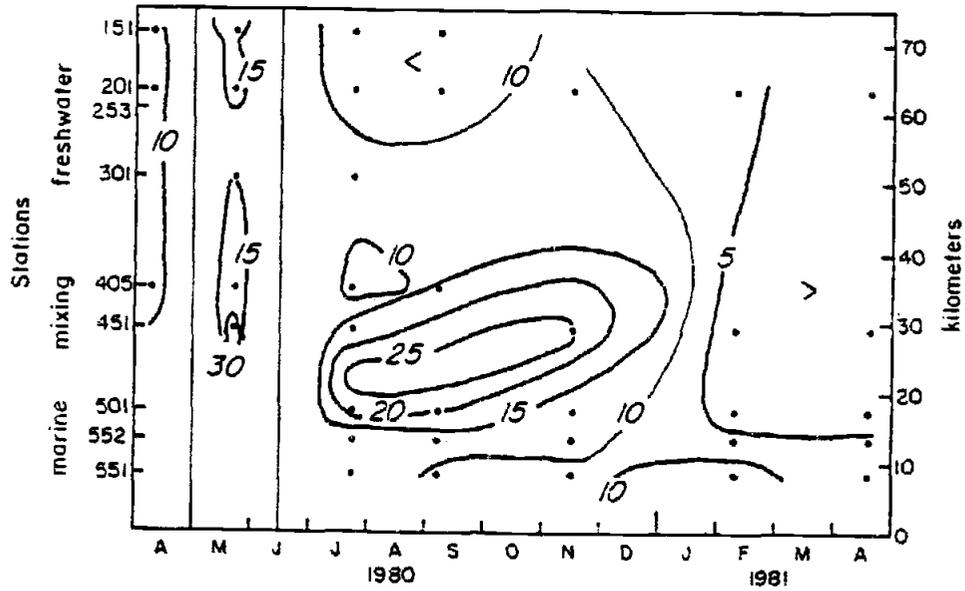


Figure 16. Spatial-temporal distribution of particulate organic carbon:particulate organic nitrogen ratio. Other comments as in Fig. 8.

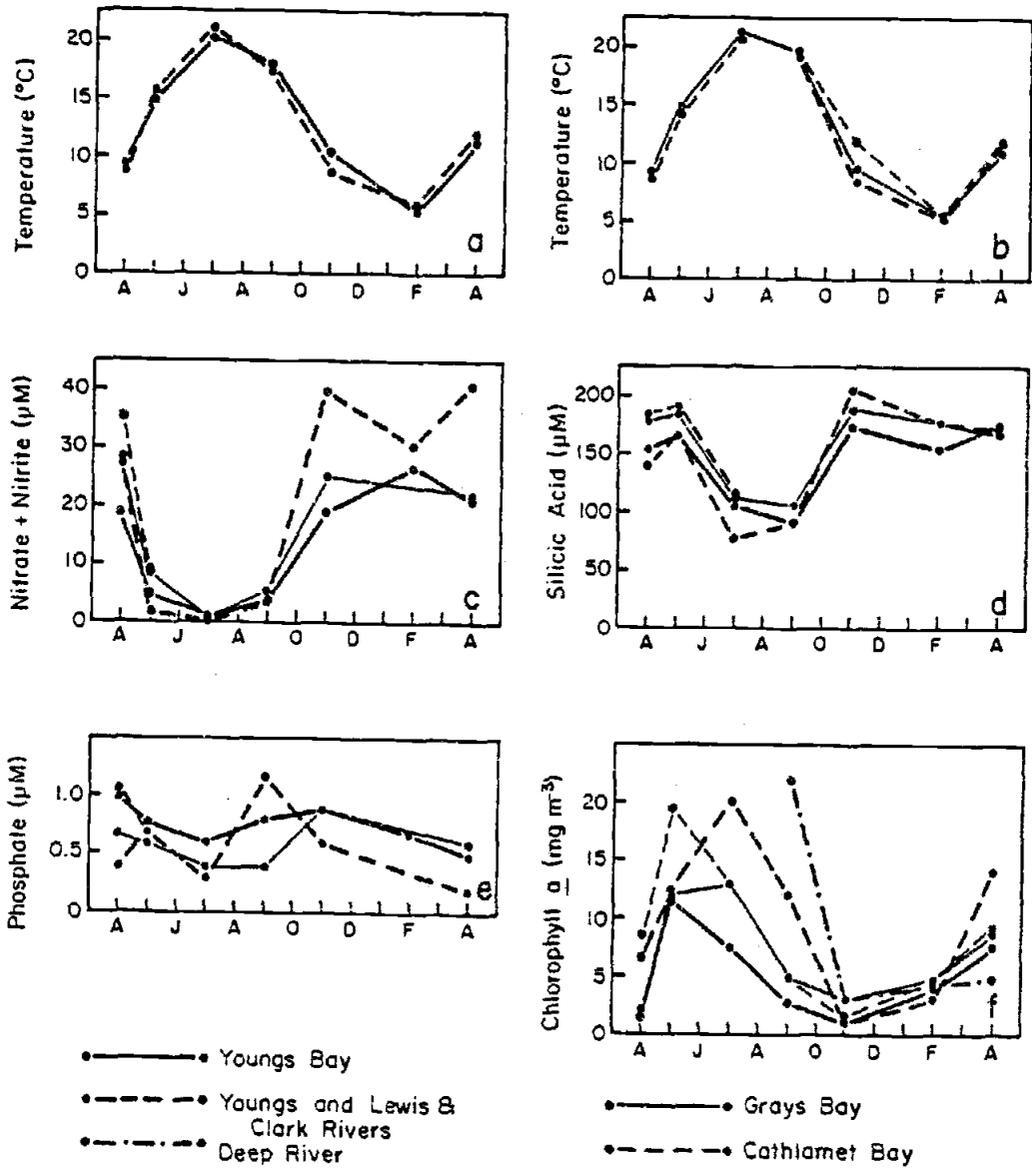


Figure 17. Temporal variability of properties in shallow areas. Notice that temperature is shown in two panels, a and b.

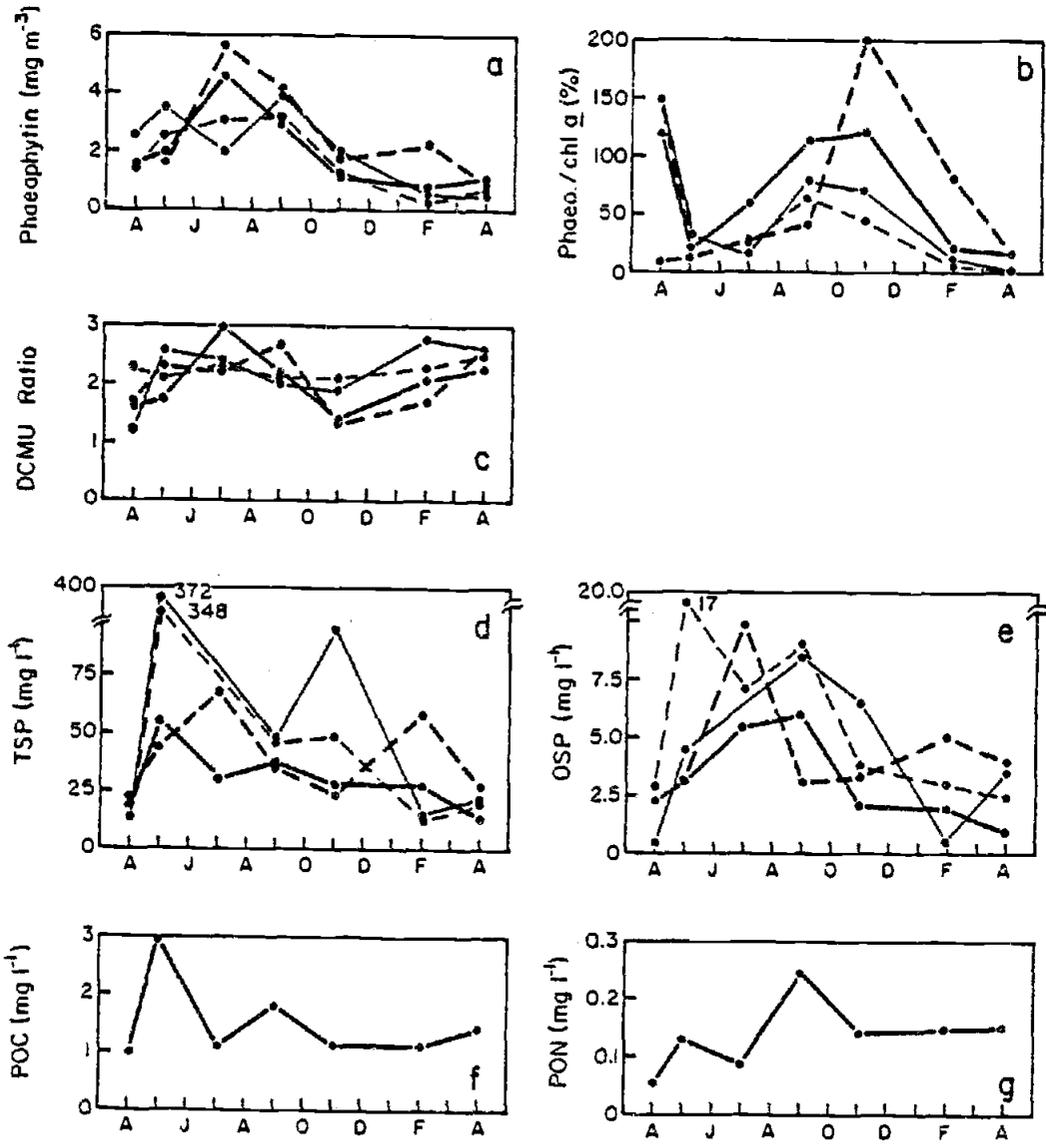


Figure 18. Temporal variability of properties in shallow areas. Traces as in Fig. 17.

### Comparison between channel and shallow stations

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 3). 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.

### Vertical distribution of properties

Vertical distributions of particles and their properties (chlorophyll a, OSP, TSP, POC, and PON) for three selected stations along the main channel of the estuary, are shown in Figs. 19 and 20. These profiles clearly show a homogenous water column in response to a very dynamic system along the main channel. The physical and chemical properties (not shown) yielded equally homogenous distributions in the freshwater and mixing zones.

The vertical distributions of physical and chemical properties, plus chlorophyll, in the mouth area (Figs. 21, 22, 23) are more complex. Here river flow and tidal conditions (flood-ebb), as well as seasonal cycles, will determine the depth 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 presented only for properties with significant differences in the riverine and marine waters. Due to the great variability presented by the other particulate properties, no significant differences were

Table 3. Comparisons of properties for channel and shallow stations. Means represent data from all cruises  $\pm$  one standard error. Z = calculated Z-value for testing mean differences; p = probability.

VARIABLE	MEANS $\pm$ s. e.		Z	p
	channel	shallow		
Temperature ( $^{\circ}$ c)	12.64 $\pm$ 0.73	12.72 $\pm$ 0.71	-0.07	n.s
Nitrate + nitrite ( $\mu$ M)	16.19 $\pm$ 1.64	15.95 $\pm$ 2.70	0.07	n.s
Silicic acid ( $\mu$ M)	145.78 $\pm$ 5.20	131.76 $\pm$ 7.47	0.53	n.s
Phosphate ( $\mu$ M)	0.72 $\pm$ 0.04	0.73 $\pm$ 0.15	-0.06	n.s
Chlorophyll <u>a</u> ( $\text{mg m}^{-3}$ )	6.27 $\pm$ 0.48	7.46 $\pm$ 0.70	-1.38	0.20
Fluorescence	2.69 $\pm$ 0.17	3.25 $\pm$ 0.29	-1.64	0.10
DCMU-ratio	2.29 $\pm$ 0.06	2.20 $\pm$ 0.06	1.00	n.s
Phaeophytin <u>a</u> ( $\text{mg m}^{-3}$ )	1.35 $\pm$ 0.12	2.11 $\pm$ 0.22	-2.92	0.001
Phaeophytin <u>a</u> : Chl <u>a</u>	0.32 $\pm$ 0.04	0.42 $\pm$ 0.05	-1.42	0.20
TSP ( $\text{mg l}^{-1}$ )	25.08 $\pm$ 2.65	33.66 $\pm$ 2.68	-2.27	0.05
ISP ( $\text{mg l}^{-1}$ )	21.68 $\pm$ 2.52	29.29 $\pm$ 2.43	-2.17	0.05
OSP ( $\text{mg l}^{-1}$ )	3.32 $\pm$ 0.25	4.38 $\pm$ 0.43	-2.12	0.05
POC ( $\text{mg l}^{-1}$ )	1.13 $\pm$ 0.07	1.30 $\pm$ 0.13	-1.13	0.26
PON ( $\text{mg l}^{-1}$ )	0.14 $\pm$ 0.02	0.16 $\pm$ 0.04	-0.40	n.s
C/N	10.90 $\pm$ 1.70	12.40 $\pm$ 2.20	-0.50	n.s

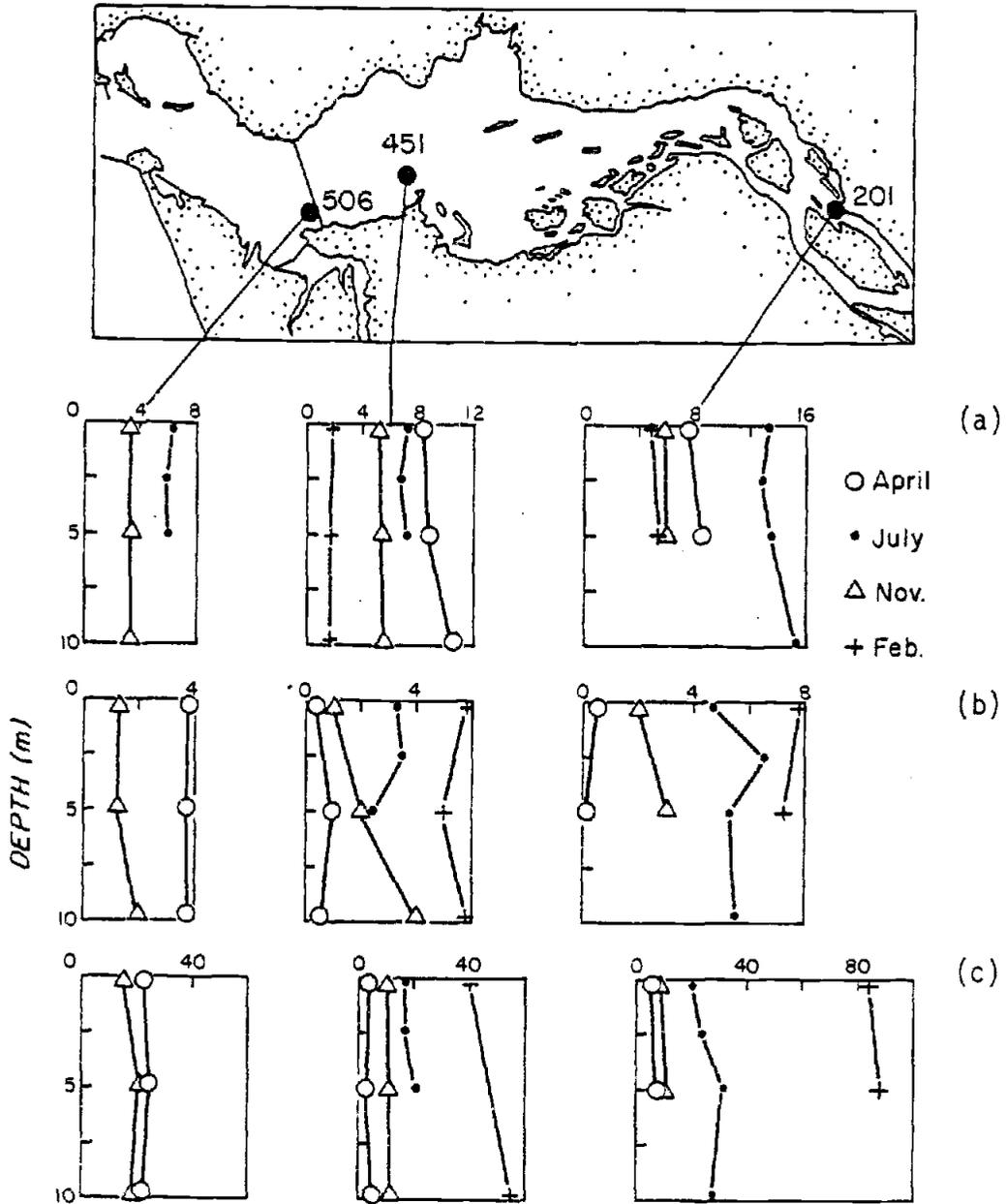


Figure 19. Vertical distributions of (a) chlorophyll a ( $\text{mg m}^{-3}$ ), (b) organic suspended particles ( $\text{mg l}^{-1}$ ), and (c) total suspended particles ( $\text{mg l}^{-1}$ ).

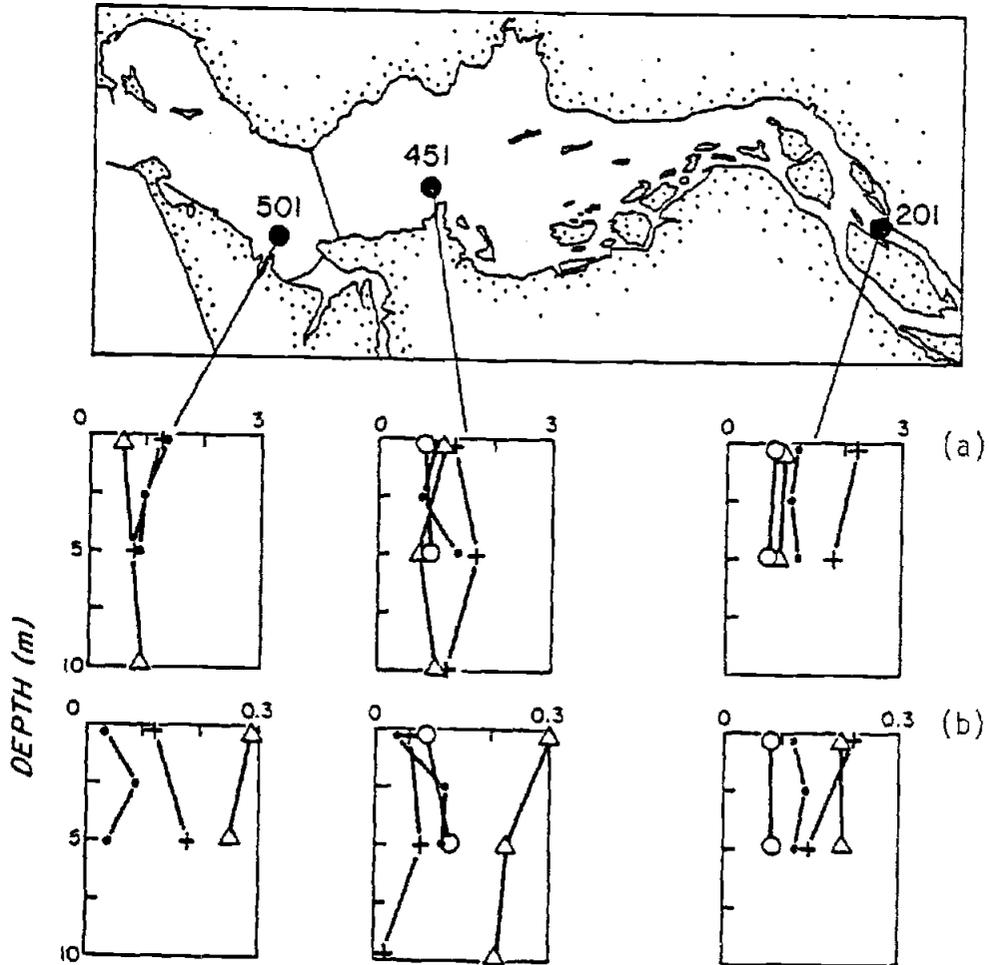


Figure 20. Vertical distributions of (a) particulate organic carbon ( $\text{mg l}^{-1}$ ), and (b) particulate organic nitrogen ( $\text{mg l}^{-1}$ ). Symbols as in Fig. 19.

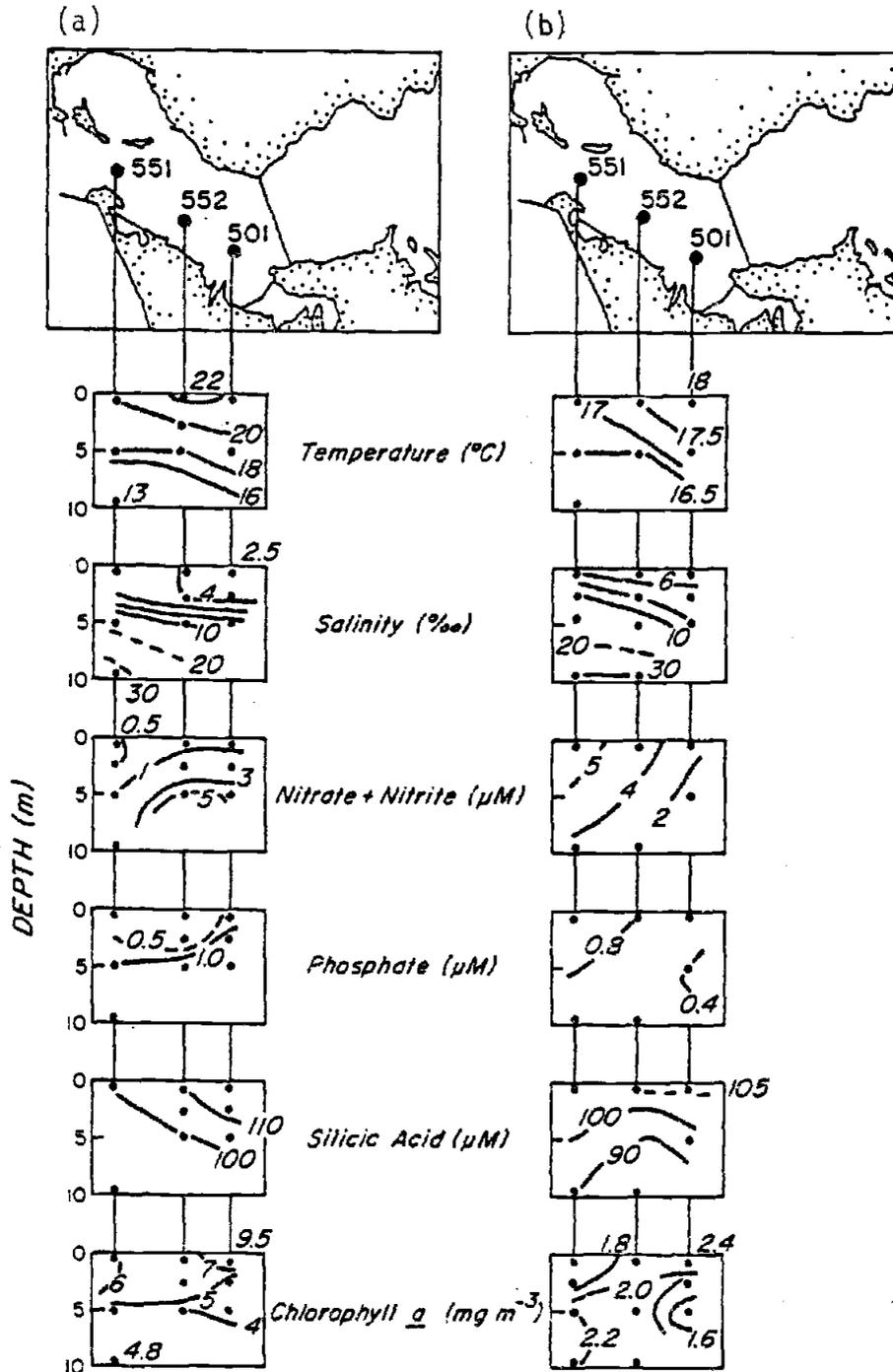


Figure 21. Vertical distributions of properties in the marine zone. (a) July, (b) September. The July data were taken on flood tide, while the September data were on ebb tide.

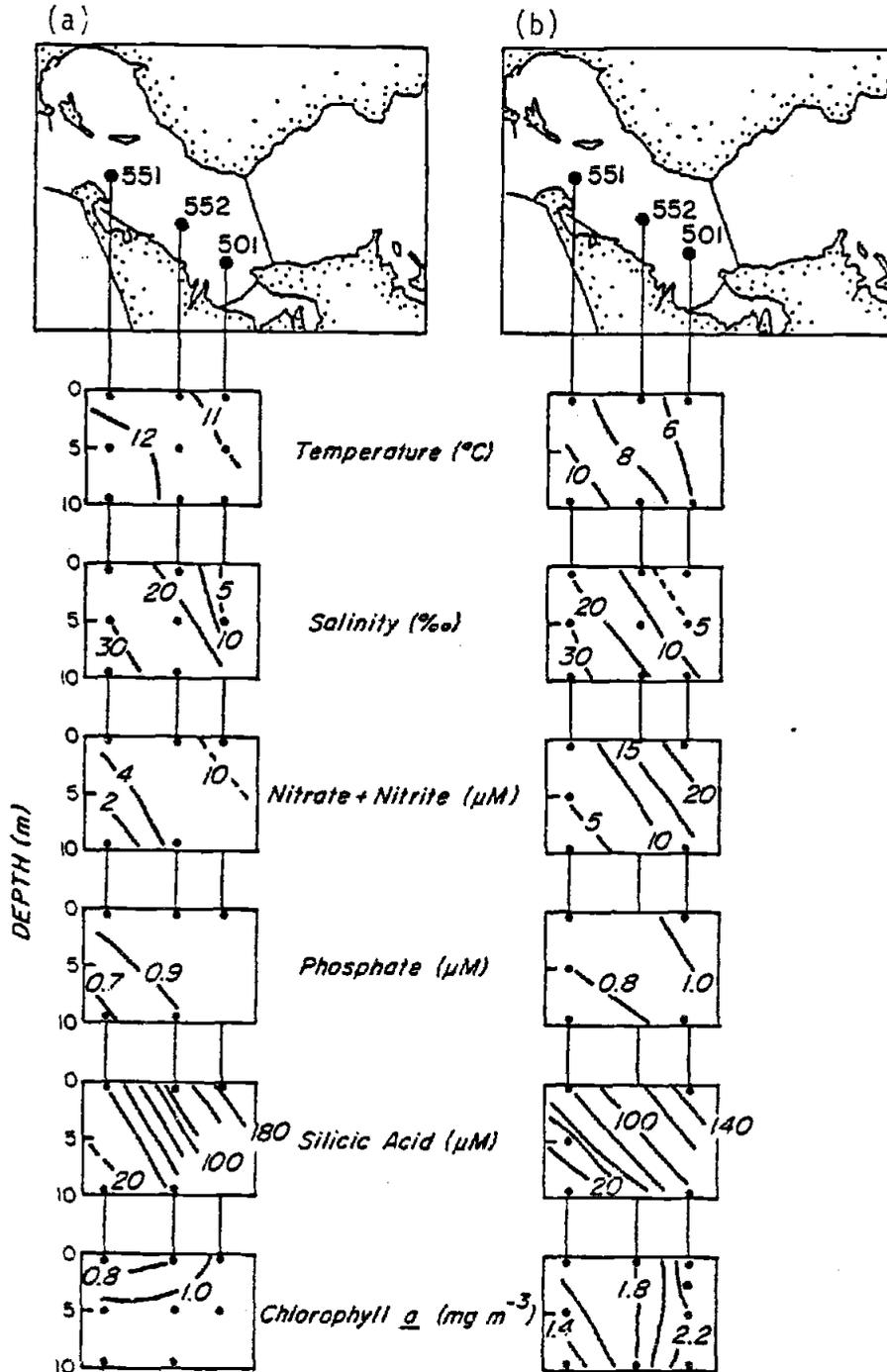


Figure 22. Vertical distributions of properties in the marine zone. (a) November, (b) February. All data were taken on flood tide.

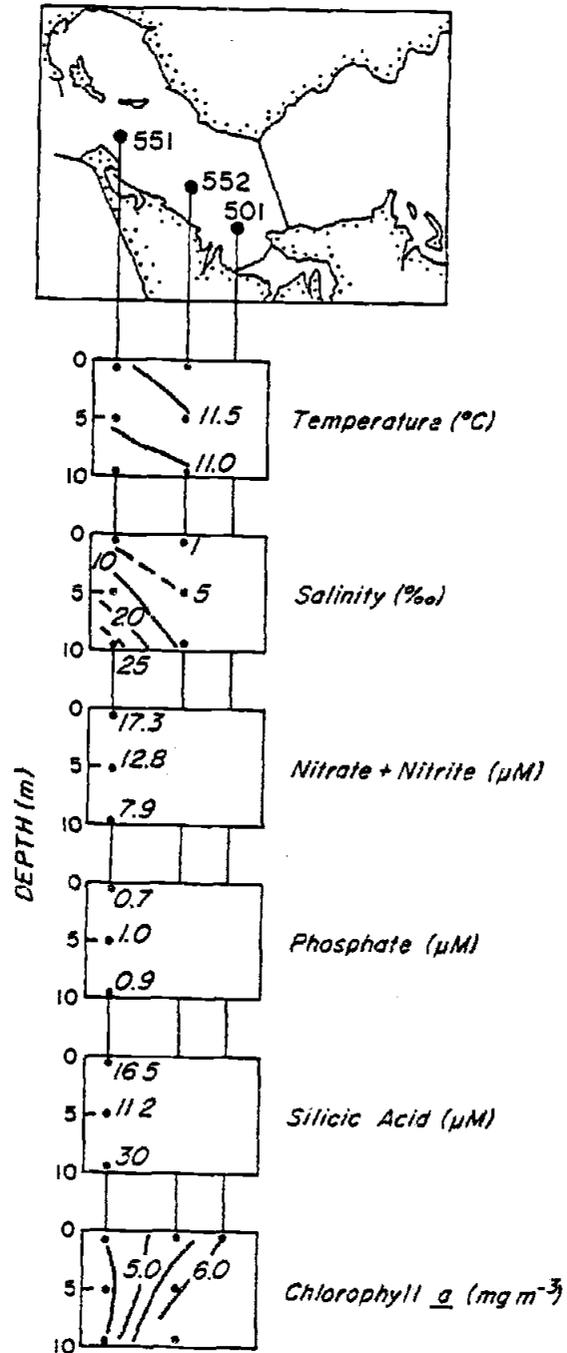


Figure 23. Vertical distributions of properties in the marine zone during April 1981. Data taken on flood tide.

observed in their concentrations in riverine and marine waters. Basically the physico-chemical properties change from vertical to horizontal structure as the marine zone is entered, but the particle distributions (except chlorophyll) do not.

During summer, near-surface, near-riverine waters showed the expected higher temperatures (18-22°C) and lower salinities (<6‰) than the entering near-marine waters (13-16°C and 20‰, respectively) (Fig. 21a). During late fall and winter opposite conditions were found (Fig. 22a,b), with river-dominated waters ranging from about 6 to 10°C and <5‰, and marine-dominated waters rising above 10°C and 15‰, approximately. Note that in November (Fig. 22a) there was almost no river influence, but by February (Fig. 22b) the condition began to reverse. By April (Fig. 23) enhanced river runoff brought slightly warmer temperatures and slightly reduced salinity structure to the water column.

During summer, marine coastal upwelled 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  $\text{NO}_3^- + \text{NO}_2^-$  and 0.5 μM  $\text{PO}_4^{3-}$ ) (Fig. 21). From late fall through early spring, riverine waters were highly enriched with respect to  $\text{NO}_3^- + \text{NO}_2^-$ , and to a modest amount with respect to phosphate (Figs. 22 and 23).

Silicic acid concentrations were always higher in river waters than in marine waters (Figs. 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  $\mu\text{M}$ ). During late fall and winter, river waters ranged from about 120 to greater than 180  $\mu\text{M}$ , while entering marine waters were generally below 40  $\mu\text{M}$ .

Chlorophyll a concentrations were almost always higher in the riverine waters, though distributions were often more variable than those of physical-chemical properties, and often more vertically uniform (Figs. 21, 22, 23). Maximum chlorophyll a concentrations in the entering marine waters were recorded during spring-summer (nearly 5.0  $\text{mg m}^{-3}$ ), dropping off to about 1.0  $\text{mg m}^{-3}$  by late fall.

### Water Column Primary Productivity

#### Seasonal vertical structure

The vertical distribution of net carbon fixed ( $\text{mgC m}^{-3} \text{hr}^{-1}$ ) by the phytoplankton community at three representative stations (501, 451, and 201) along the main channel of the Columbia River Estuary is shown in Fig. 24. A clear seasonal cycle is evident, with maximum summer values up to 35  $\text{mgC m}^{-3} \text{hr}^{-1}$  at 50% of surface light intensity ( $I_0$ ), and minimum values during November (2-5  $\text{mgC m}^{-3} \text{hr}^{-1}$ ). Euphotic zone depth (depth of 1%  $I_0$ ) varied from about 4 m in summer to around 1.4 m in late fall. No data are available for December or January, but these months may be expected to have production lower than or equal to November production, due to low solar radiation and short day lengths (Fig. 6). With few exceptions, from September to February light-saturated photosynthesis was not reached anywhere in the water column (Fig. 24). During the May cruise, suspended material resulting from the Mt. Saint Helens' eruption caused a marked reduction in the euphotic zone depth and in photosynthetic rates.

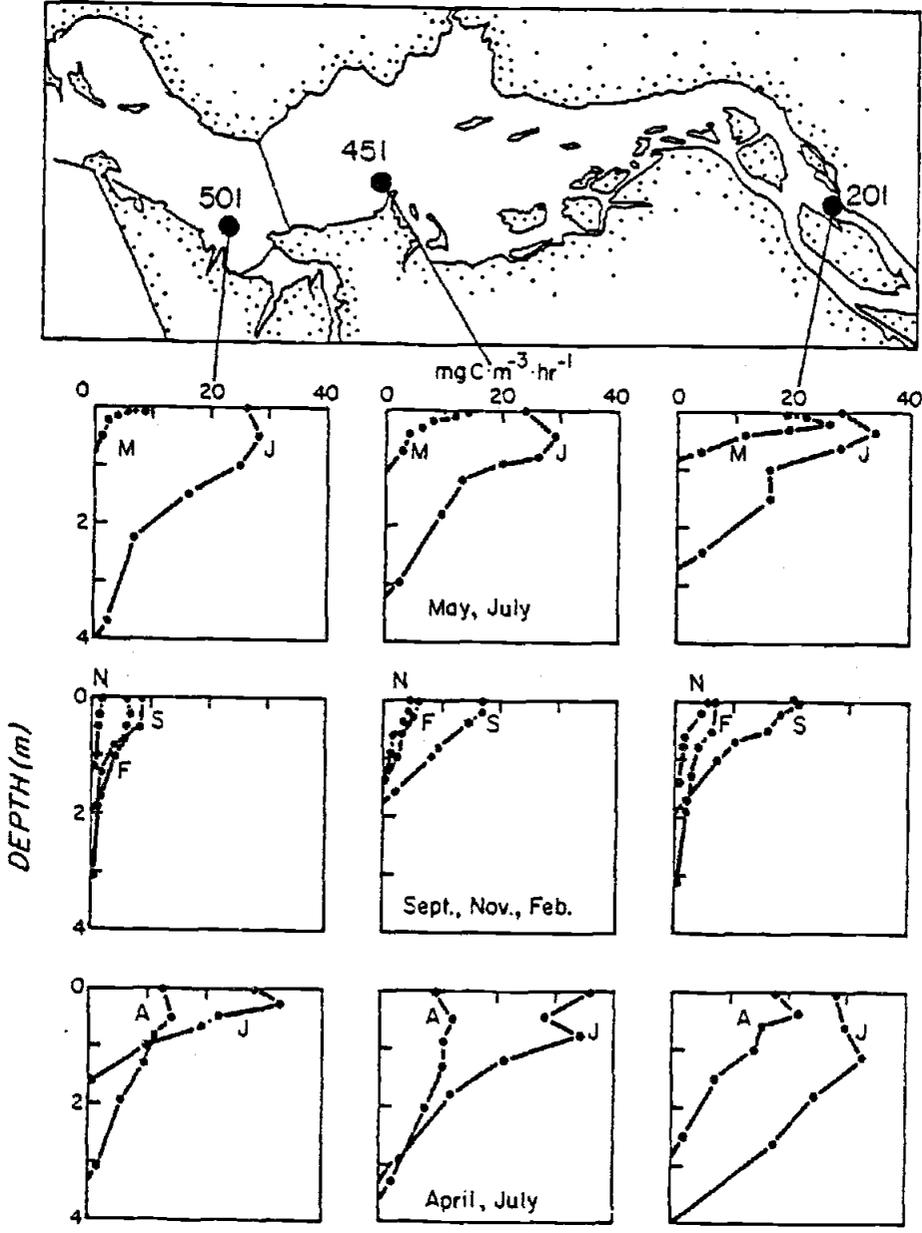


Figure 24. Vertical distribution of carbon uptake in the main channel.

Net carbon fixed by the phytoplankton community in shallow areas of the estuary (Fig. 25), presented a seasonal trend similar to the channel stations, with maximum values during summer ( $25-80 \text{ mgC m}^{-3} \text{ hr}^{-1}$ ) and minimum values during November ( $1.5 - 3.0 \text{ mgC m}^{-3} \text{ hr}^{-1}$ ). In the summer (July-September), Youngs River (Sta. 453) and Deep River (Sta. 4014) had much higher carbon fixation rates per  $\text{m}^3$ , but lower euphotic zone depth, than stations in the main channel.

#### Spatial and temporal variability

Primary productivity data in  $\text{mgC m}^{-3} \text{ hr}^{-1}$  were converted first to  $\text{mgC m}^{-2} \text{ hr}^{-1}$ , by plotting vertical profiles of  $\text{mgC m}^{-3} \text{ hr}^{-1}$  and integrating the area under the curves with a Model GP-6 Digitizer. Then, data in  $\text{mgC m}^{-2} \text{ hr}^{-1}$  were expanded to  $\text{mgC m}^{-2} \text{ day}^{-1}$ , by the following calculations. Total production during the incubation period was computed by multiplying  $\text{mgC m}^{-2} \text{ hr}^{-1}$  times the number of hours in the incubation period. This production was then divided by the light fraction (radiation in the incubation period/total daily radiation). This technique is probably not perfectly correct, because of changing production per unit of biomass at different times of the daylight day (Curl and Small, 1965; Fisher et al., in press), but it should serve reasonably well because incubation periods were selected for long enough periods during mid-day (so that the light fraction over which incubation took place was never exceedingly small).

Using data collected on eight of our cruises, a primary productivity regression model based on ecological properties was obtained in order to predict productivity values for zones lacking experimental data. Stations were separated into channel and shallow stations. Ten ecological properties acting as independent variables (daily

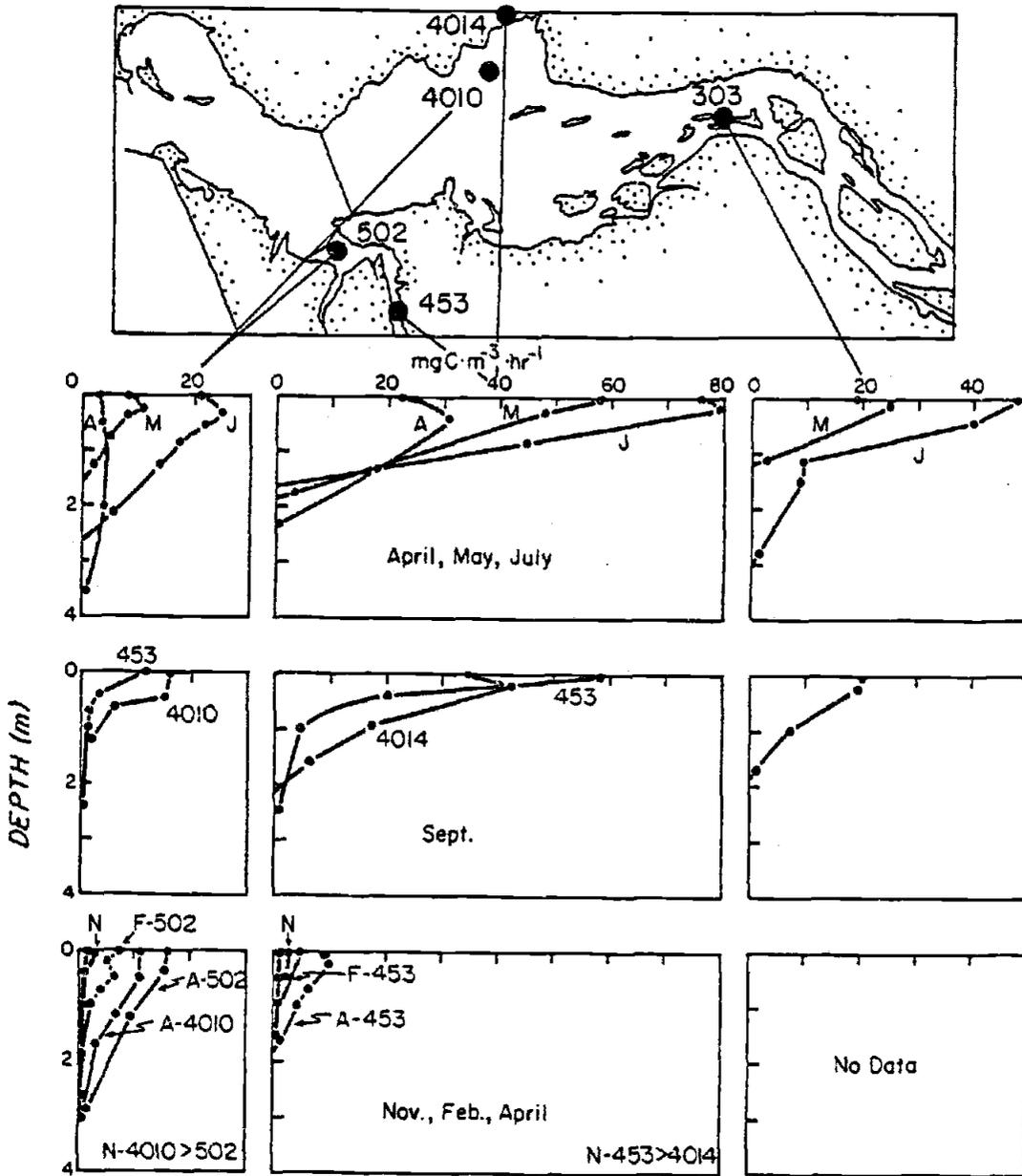


Figure 25. Vertical distribution of carbon uptake in shallow areas.

solar radiation, water temperature, chlorophyll a, phaeophytin a, diffuse light attenuation coefficient, nitrate plus nitrite, phosphate, silicate, total seston, and organic suspended particles) were regressed against primary productivity (dependent variable). 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 obtained are shown in Tables 4 and 5. In the model for channel stations, for example (Table 4), 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. Five factors accounted for 90% of the variability. In the regression model for shallow stations, three factors accounted for 85% of the variability in primary productivity (Table 5). 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 Tables 4 and 5), are shown for two stations in the channel and shallow areas (Fig. 26). The agreement seems acceptable, although high productivity values are always underestimated somewhat.

Phytoplankton productivity ( $\text{mgC m}^{-2} \text{ day}^{-1}$ ) for channel stations, using both measured and predicted values, showed strong seasonal variation (Fig. 27a). Maximum values during summer averaged  $795 \text{ mgC m}^{-2} \text{ day}^{-1}$  (range 467-1448) and minimum productivity in late fall (November), averaged  $64 \text{ mgC m}^{-2} \text{ day}^{-1}$  (range 19-102).

Table 4. Primary productivity regression model for channel stations (n = 29).  $R^2$  = coefficient of determination.

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

Table 5. Primary productivity regression model for shallow stations (n = 28).  $R^2$  = coefficient of determination.

VARIABLE	$R^2$	MODEL
R = Daily solar radiation (g cal cm <sup>-2</sup> day <sup>-1</sup> )	0.73	Log daily productivity = 1.605 + 0.003 R + 0.033 Chl <u>a</u> - 0.127 <u>k</u>
Chl <u>a</u> = Chlorophyll <u>a</u> (mg m <sup>-3</sup> )	0.78	
<u>k</u> = Light attenuation coefficient (m <sup>-1</sup> )	0.85	

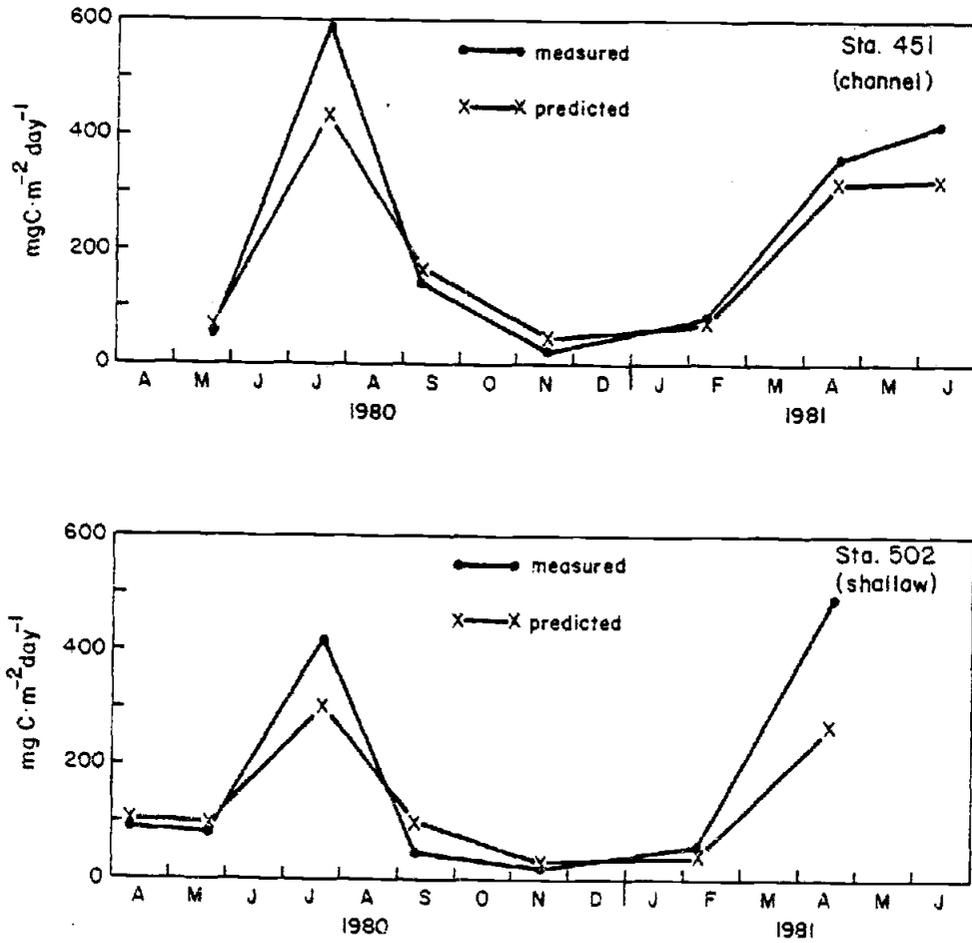


Figure 26. Temporal distribution of measured and predicted (by models) phytoplankton primary productivity.

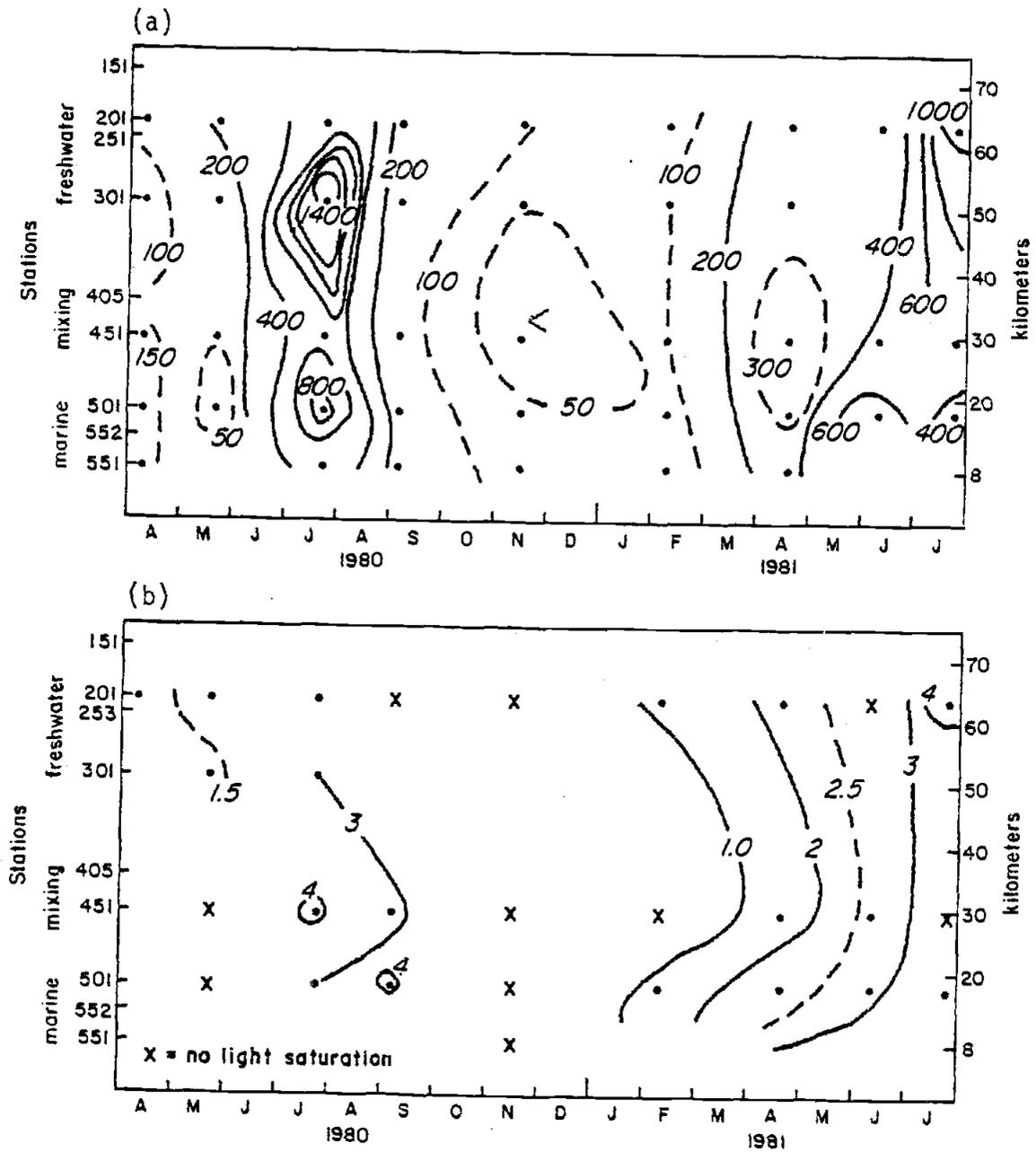


Figure 27. (a) Spatial-temporal distribution of phytoplankton production ( $\text{mgC m}^{-2} \text{ day}^{-1}$ ).  
 (b) Spatial-temporal distribution of assimilation number ( $\text{mgC mgChla}^{-1} \text{ hr}^{-1}$ ).  
 Other comments as in Fig. 8.

The assimilation number (Fig. 27b), expressed as  $\text{mgC (mg chlorophyll } a)^{-1} \text{ hr}^{-1}$  at light saturation, also showed seasonal variation, with maximum values (3-4.5) occurring during summer. Light saturation of photosynthesis in the water column was not observed in May 1980 at several stations because of the volcanic debris which limited light penetration. The assimilation number declined by late summer (September). In fall and winter, true assimilation numbers usually could not be calculated because light-saturated photosynthesis in the water column was almost never reached. By April 1981 light-saturated photosynthesis was again observed with regularity in the water column.

The diffuse light attenuation coefficient  $k$  ( $\text{m}^{-1}$ ) varied both spatially and temporally in the channel (Fig. 28). In general, the estuary can be divided into comparatively clear waters from station 501 to 551 (marine zone), with  $k$  values from 0.7 to 1.5, and more turbid waters from station 451 upstream (with  $k$  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 pattern for diffuse light attenuation coefficient closely mirrored the distribution of total suspended particles (Fig. 13a).

During May 1980, increased light attenuation in the water column resulted in a marked reduction in overall photosynthetic rates in the channel (Fig. 27a). A potential production for May, without the

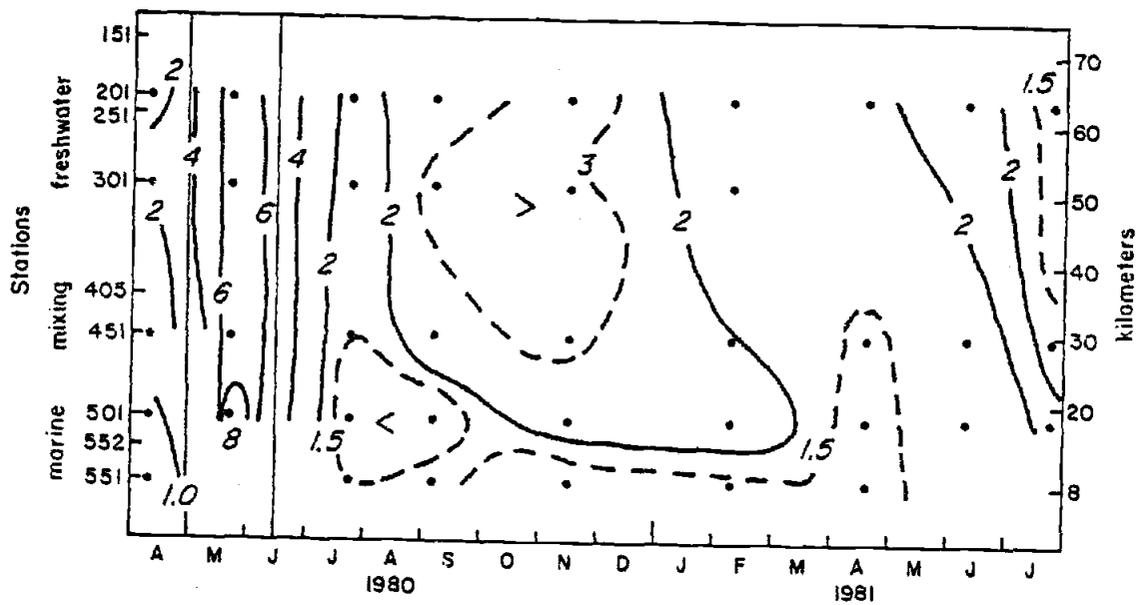


Figure 28. Spatial-temporal distribution of light attenuation coefficient,  $k$  ( $m^{-1}$ ). Other comments as in Fig. 8.

effects of the volcano, can be estimated by using the regression model in Table 4. Substituting  $k$  and total seston values obtained by averaging values from April and July (1.6 and 13.4, respectively), and using the actual chlorophyll  $a$ , temperature, and incident light values measured in May, a potential production rate of  $660 \text{ mgC m}^{-2} \text{ day}^{-1}$  is obtained from the model. Actual measured values of production in May averaged  $115 \text{ mgC m}^{-2} \text{ day}^{-1}$  (ranged 22-214). The difference between the average measured rate of carbon uptake and the calculated rate without the increased light attenuation and total seston load attributable to the eruption, represents a reduction in daily water column primary production of 82%.

For the shallow stations, no spatial variability in primary productivity was discerned. Temporal variability of phytoplankton productivity ( $\text{mgC m}^{-2} \text{ day}^{-1}$ ) and assimilation number in shallow areas (Fig. 29) showed the same seasonal trend as in channel stations, with maximum summer productivities averaging  $767 \text{ mgC m}^{-2} \text{ day}^{-1}$  (range 421-1026) and minimum late fall rates averaging  $28 \text{ mgC m}^{-2} \text{ day}^{-1}$  (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 6). Unlike its behavior in the channel stations, the diffuse light attenuation coefficient (Fig. 29) did not show seasonal variability. The  $k$  values were significantly ( $p < 0.10$ ) higher in the shallows than in the channel, however (Table 6).

#### Productivity of different phytoplankton size fractions

Phytoplankton productivity ( $\text{mgC m}^{-3} \text{ hr}^{-1}$ ) at 100%  $I_0$  for three

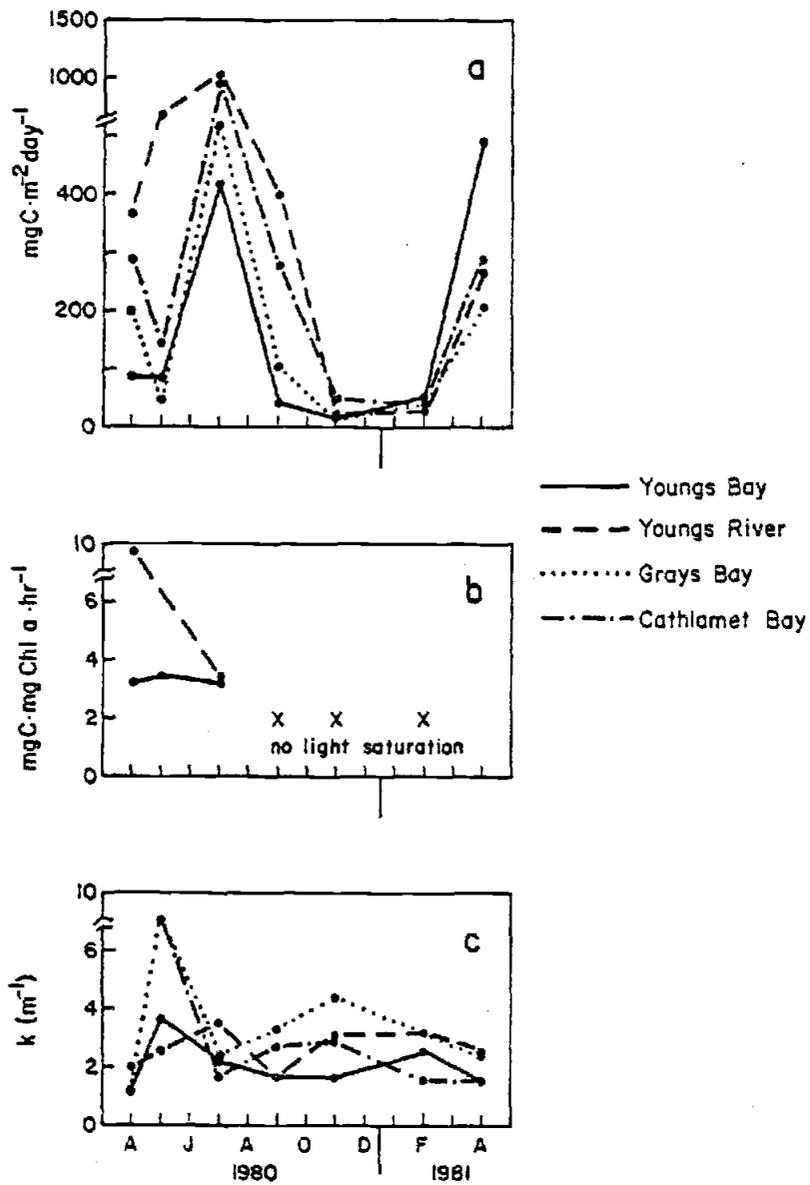


Figure 29. Temporal variability of properties in shallow areas.

Table 6. Comparisons of properties for channel and shallow stations. Means represent data from all cruises  $\pm$  one standard error.  $t$  = calculated  $t$ -value for testing mean differences;  $p$  = probability.

Variable	Channel Mean $\pm$ s.e.	Shallow Mean $\pm$ s.e.	$t$	$p$
Primary productivity (mgC m <sup>-2</sup> day <sup>-1</sup> )	348.5 ( $\pm$ 12.0)	379.8 ( $\pm$ 14.1)	-0.32	n.s.
Assimilation number (mgC mgChl <sub>a</sub> <sup>-1</sup> hr <sup>-1</sup> )	2.6 ( $\pm$ 0.2)	3.2 ( $\pm$ 0.5)	-1.05	n.s.
Light attenuation coefficient $k$ (m <sup>-1</sup> )	1.9 ( $\pm$ 0.1)	2.3 ( $\pm$ 0.1)	-1.77	0.10

size fractions ( $>33$ ,  $10-33$ , and  $<10$   $\mu\text{m}$ ) is shown in Fig. 30. Most production was done by cells either larger than  $33$   $\mu\text{m}$  or smaller than  $10$   $\mu\text{m}$  at all times of year. The  $<10$   $\mu\text{m}$  fraction was relatively the most prevalent fraction in winter (Fig. 30), and both fractions increased in spring and summer. During spring and summer (April through July) the  $>33$   $\mu\text{m}$  fraction contributed about 50% of the total production. The intermediate-sized fraction was significant only in spring and summer at Sta. 451.

Chlorophyll a ( $\text{mg m}^{-3}$ ) concentrations for these size fractions (Fig. 31) showed reasonably similar seasonal and spatial trends to the carbon assimilation rates.

#### Annual phytoplankton production

Eight zones in the area studied (Fig. 3) were used to examine daily phytoplankton primary productivity data generated from measured and predicted values (Fig. 32). Then, daily production values were expanded to monthly production estimates. For months not sampled (but with solar radiation data available), monthly production values were estimated based on a production: solar radiation ratio obtained from other data available. For example, during July the marine zone had a measured ratio of  $0.054$  ( $16.3 \text{ gC m}^{-2} \text{ month}^{-1} / \text{average } 303 \text{ gcal cm}^{-2} \text{ day}^{-1}$ ). In August this zone had a mean solar radiation value of  $248 \text{ gcal cm}^{-2} \text{ day}^{-1}$ , but no production rates were measured. The estimated monthly production for August became  $13.3 \text{ gC m}^{-2} \text{ month}^{-1}$  ( $0.054 \times 248$ ).

Values of monthly production were added to give annual production per zone (Table 7). A gradual decrease in annual production from the upper estuary zone to the marine zone is evident in the channel. In

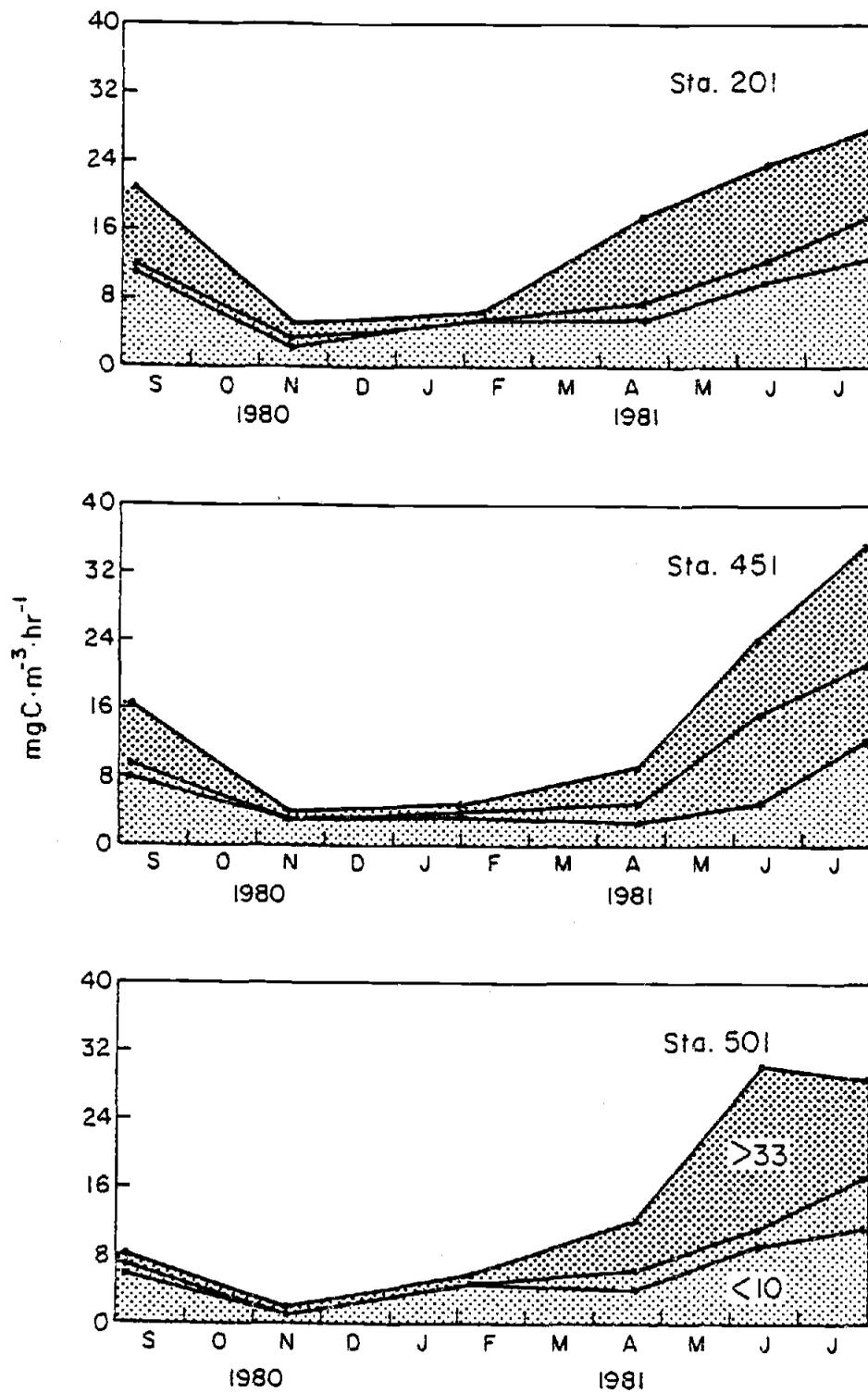


Figure 30. Cumulative graph of phytoplankton production by different size fractions, at three different stations along the main channel.

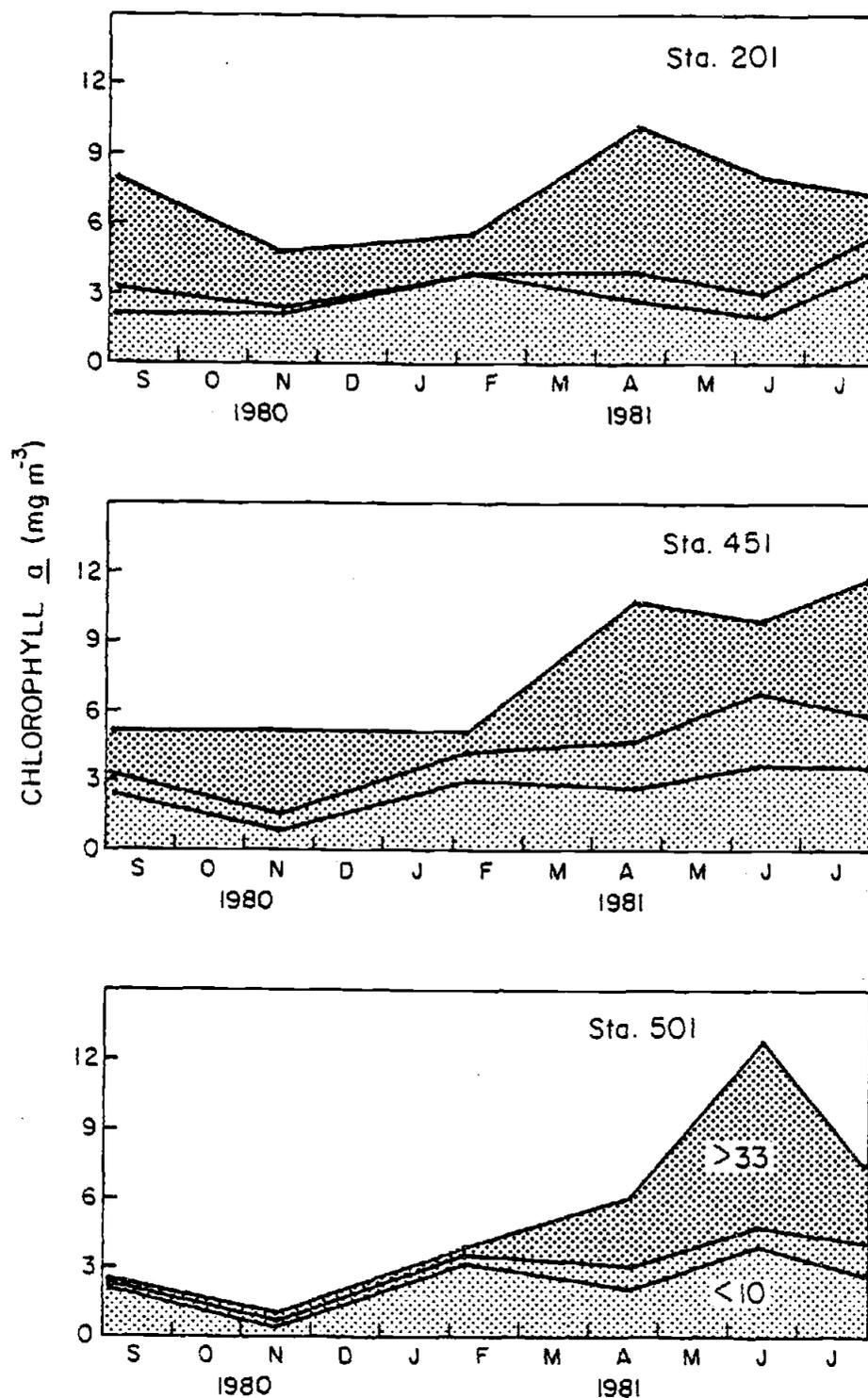


Figure 31. Cumulative graph of chlorophyll a content by different size fractions, at three different stations along the main channel.

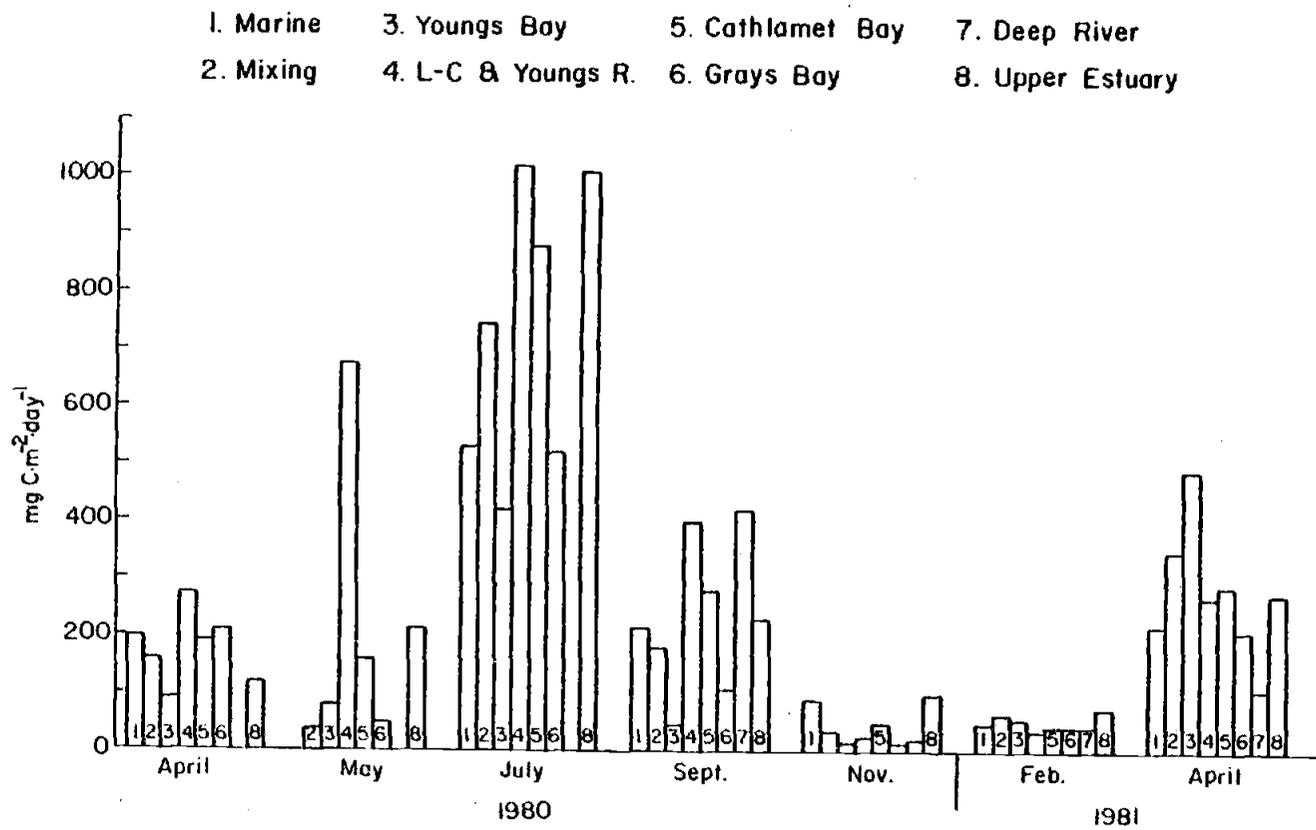


Figure 32. Temporal distribution of daily mean phytoplankton production by zones.

Table 7. Yearly phytoplankton primary production ( $\text{gC m}^{-2} \text{yr}^{-1}$ ) by zones. Numbers in parentheses refer to zones in Figure 3.

Channel		Shallow	
(8) upper estuary	121.0	(4) Youngs and L. and C. Rivers	140.0
(5) Cathlamet	104.7	(6) Grays Bay	66.3
(2) Mixing	84.9	(3) Youngs Bay	53.7
(1) Marine	69.3		

the bays and rivers, the maximum production was attained in the combined Youngs and Lewis and Clark Rivers, which may be a response to the relatively high residence time (4-16 days) of the water in these rivers (Boley et al., 1975). High residence time should enhance phytoplankton production before cells are washed out to Youngs Bay. Grays and Youngs Bay had lower production than other zones in the estuary. This may be an effect of their shallowness and turbidity, which produces a very shallow euphotic zone for photosynthesis. A weighted average, by the total area in each zone, gave an annual phytoplankton production for the entire estuary of about  $90 \text{ gC m}^{-2} \text{ yr}^{-1}$ .

#### Phytoplankton community composition

The readily identifiable estuarine phytoplankton is composed primarily of freshwater diatom species, which represent a downstream extension of the Columbia River flora. However, it is very clear from our phytoplankton size-fractionation experiments (Figs. 30 and 31) that the larger identifiable cells do not make up the total phytoplankton stock in the estuary. It has been reported that the technique of sample fixation also affects the resulting size composition of phytoplankton. Unpreserved samples contain a great number of smaller flagellates which are destroyed by fixation and missed in subsequent determination (Semina, 1978).

Diatom species collected during this study are shown in Table 8. The most abundant freshwater diatoms during this study were Asterionella formosa, Melosira islandica, M. italica, Fragilaria crotonensis, Cyclotella glomerata, and Stephanodiscus astraerea, all species which are common in eutrophic lakes (Hutchinson, 1967) and in other major

Table 8. Phytoplankton diatoms collected in the Columbia River Estuary.

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

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rivers; e.g., the Mississippi River (Baker and Baker, 1979) and the Saint Lawrence River (Cardinal and Therriault, 1976). Over 90% of the identifiable total cell abundance was composed of truly 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 identified diatom species were most abundant during July ( $12.5 \times 10^3$  cells  $\text{ml}^{-1}$ ), and decreased to  $8 \times 10^2$  cells  $\text{ml}^{-1}$  in November (Fig. 33a). Haertel et al. (1969) reported a maximum peak in May; however, May 1980 sampling was strongly affected by the volcanic eruption, which undoubtedly reduced densities of identifiable species. No samples were examined in June. The predominant species showed a seasonal trend, with maximum abundances during summer and minimum in late fall through winter (Fig. 33b).

### Zooplankton Grazing

#### Grazing rates (zooplankton ingestion in the dark)

The uptake of  $^{14}\text{C}$ -labelled natural phytoplankton in the dark by the three most abundant zooplankton taxa (mixed small copepods, Daphnia sp., and Bosmina longirostris) is shown in Fig. 34. Similar trends in the uptake curves were shown by all three taxa on a per animal basis.

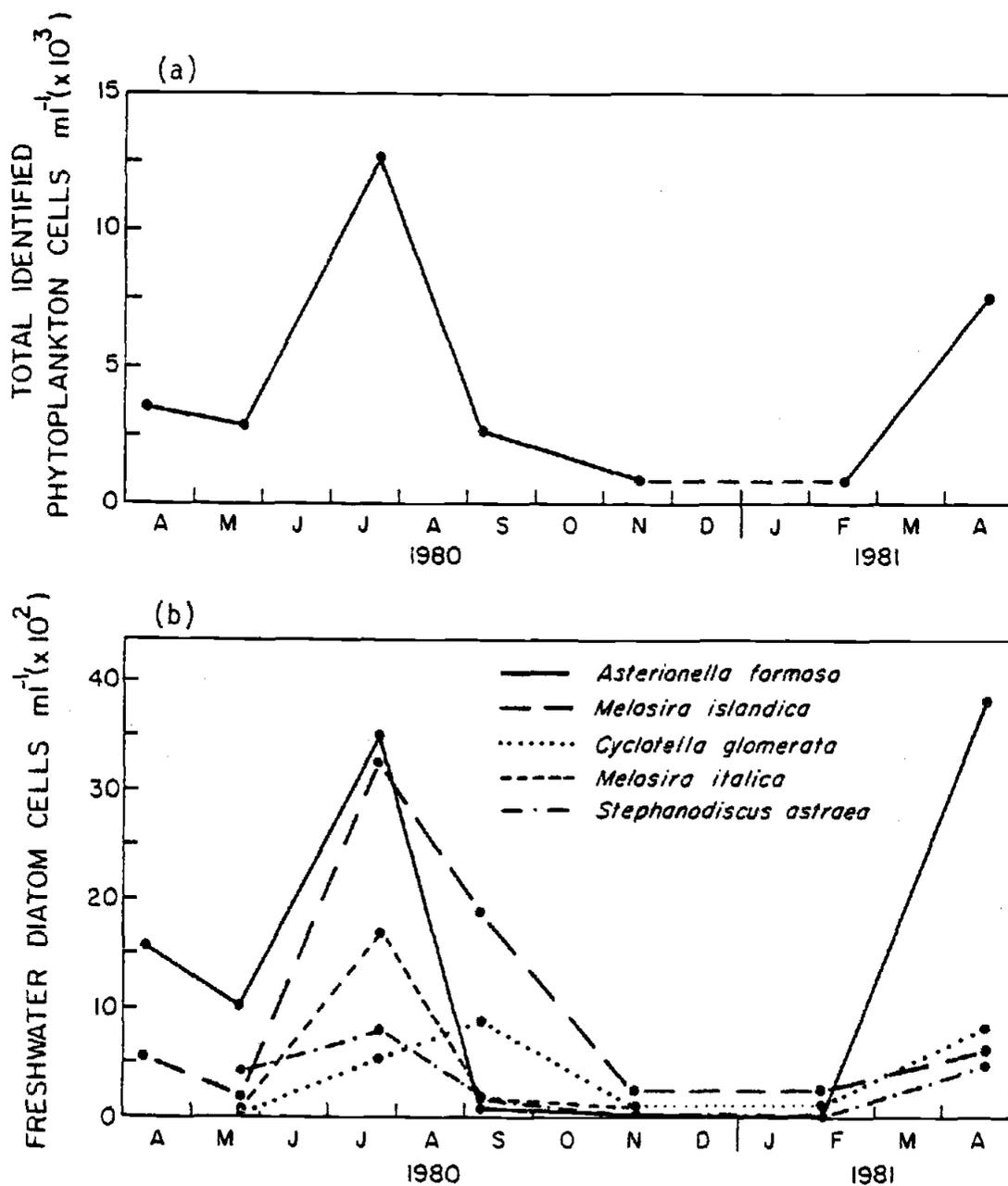


Figure 33. (a) Temporal distribution of total identified phytoplankton cells.  
 (b) Temporal distribution of the predominant freshwater diatom cells.

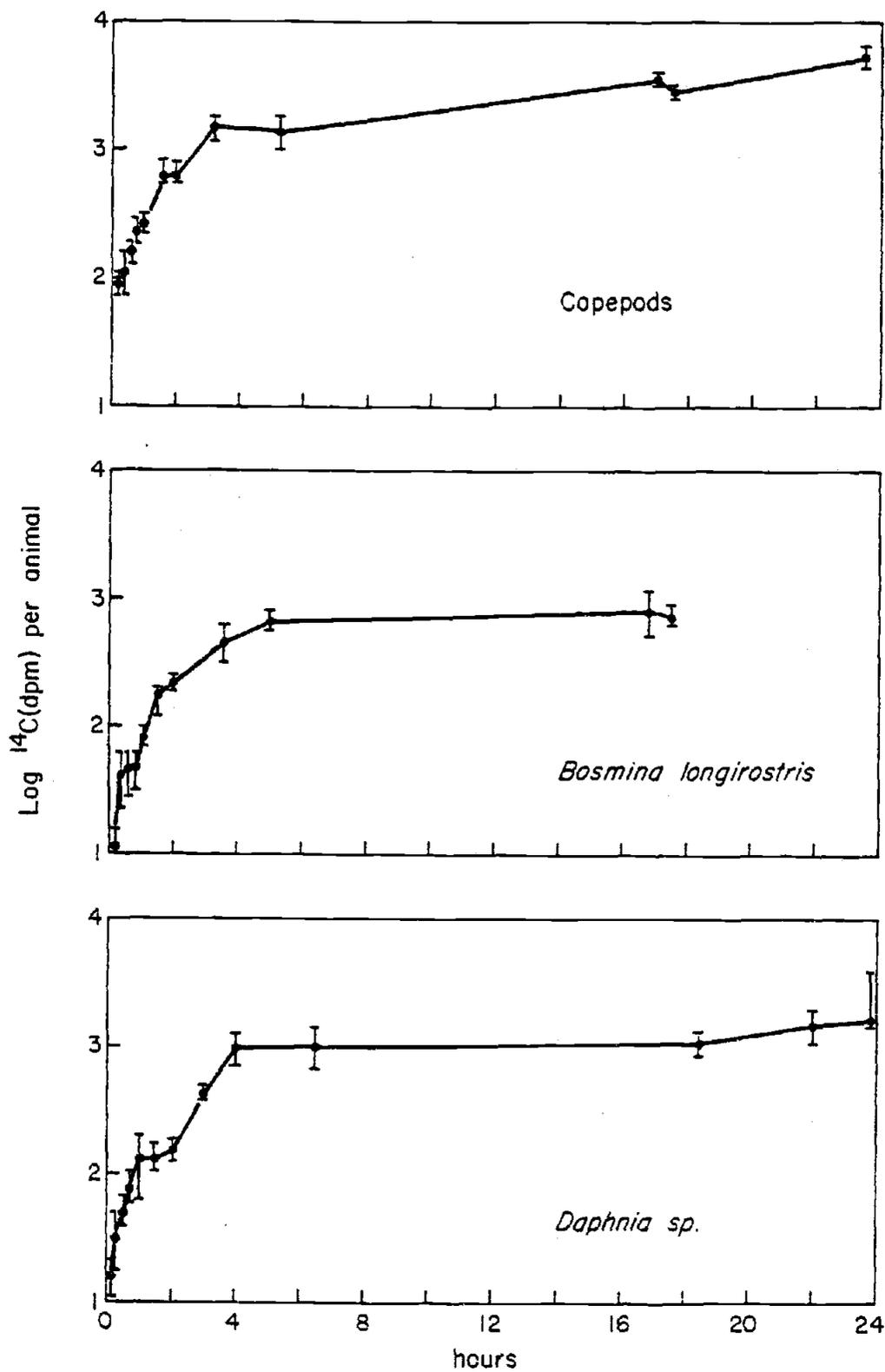


Figure 34. Time series of mean zooplankton uptake of  $^{14}\text{C}$ -prelabelled phytoplankton, by the 3 most common taxa in the estuary. Bars indicate  $\pm$  one standard error.

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  $^{14}\text{C}$  loss via fecal pellet production in the ingestion calculation. 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 assimilation and excretion processes.

Specific grazing rates (phytoplankton removed by zooplankton per phytoplankton available per unit of time) for the three most abundant zooplankton taxa were calculated separately according to the following formula:

$$g = \frac{a}{p \cdot h \cdot v} \quad (1)$$

where:  $g$  = specific grazing rate ( $\text{h}^{-1}$ )

$a$  = disintegrations per minute (dpm) per animal

$p$  = dpm per ml of phytoplankton suspension

$h$  = hours of feeding

$v$  = total volume of experimental flask (ml).

Specific grazing rates for the total community of zooplankton were computed by pooling the three taxa, and were calculated according to the formula:

$$G = \frac{z}{t \cdot h} \quad (2)$$

where:  $G$  = specific community grazing rate ( $\text{h}^{-1}$ )

$z$  = disintegrations per minute (dpm) per total zooplankton

$t$  = dpm per total phytoplankton

Daily rates can be obtained by multiplying  $g$  or  $G$  by 24, assuming zooplankton graze throughout the day. Filtering rates (volume of water swept clear per animal per day) were calculated for both copepods and cladocerans according to the formula:

$$f = \frac{a}{p \cdot h} \cdot \frac{24 \text{ h}}{\text{day}}$$

where:  $f$  = filtering rate ( $\text{ml animal}^{-1} \text{ day}^{-1}$ ).

Also notice that  $f = g \cdot v$ .

There were no significant differences between the grazing rates at the three stations within any given month, or between the two months (Tables 9 and 10); however, significant differences were observed between Bosmina longirostris and the other two taxa. Copepods had a mean specific grazing rate of  $48.0 \times 10^{-4} \text{ day}^{-1}$  (range  $37.2 \times 10^{-4}$  to  $64.8 \times 10^{-4}$ ), and Daphnia sp. had a similar mean specific grazing rate of  $48.7 \times 10^{-4} \text{ day}^{-1}$  (range  $47.0 \times 10^{-4}$  to  $50.4 \times 10^{-4}$ ), while Bosmina had a lower mean specific grazing rate of  $19.7 \times 10^{-4} \text{ day}^{-1}$  (range  $12.7 \times 10^{-4}$  to  $24.2 \times 10^{-4}$ ). Filtering rates ( $\text{ml animal}^{-1} \text{ day}^{-1}$ ) are shown in Table 11. Here also the only differences were between Bosmina longirostris and the two other taxa. Copepods and Daphnia sp. both had mean filtering rates of approximately  $1.2 \text{ ml animal}^{-1} \text{ day}^{-1}$  (ranges 0.93 to 1.62, and 1.19 to 1.26, respectively), while Bosmina longirostris had the lowest filtering rate,  $0.49 \text{ ml animal}^{-1} \text{ day}^{-1}$  (range 0.32 to 0.61).

Specific community grazing rates by the three taxa are shown in Table 12. During the July cruise the taxa with the highest specific grazing rates (copepods, Daphnia sp.) were predominant, resulting in significantly greater specific community grazing rates than in June,

Table 9. Mean specific grazing rates for copepods in the dark,  $\pm$  one standard error. n = six animals per station.

Month	Station	Species	$g(hr^{-1}) \times 10^{-4}$	$g(day^{-1}) \times 10^{-4}$
June	501	Copepods	$1.72 \pm 0.42$	$41.2 \pm 10.0$
"	451	"	$1.66 \pm 0.21$	$39.8 \pm 5.0$
"	201	"	$1.84 \pm 0.40$	$44.1 \pm 9.6$
		Mean	$1.74 \pm 0.34$	$41.7 \pm 8.2$
July	501	"	$2.70 \pm 0.42$	$64.8 \pm 10.0$
"	451	"	$1.55 \pm 0.67$	$37.2 \pm 16.0$
"	201	"	$2.55 \pm 0.52$	$61.2 \pm 12.4$
		Mean	$2.26 \pm 0.53$	$54.4 \pm 12.8$

Table 10. Mean specific grazing rates for cladocerans<sup>1</sup> in the dark,  $\pm$  one standard error. n = six animals per station.

Month	Station	Species	$g(hr^{-1}) \times 10^{-4}$	$g(day^{-1}) \times 10^{-4}$
June	501	<u>B. longirostris</u>	1.01 $\pm$ 0.41	24.2 $\pm$ 9.8
"	451	"	0.53 $\pm$ 0.05	12.7 $\pm$ 1.2
"	201	"	0.93 $\pm$ 0.33	22.3 $\pm$ 7.9
		Mean	0.82 $\pm$ 0.26	19.7 $\pm$ 6.3
July	501	<u>Daphnia</u> sp.	n.d	n.d
"	451	"	2.10 $\pm$ 0.53	50.4 $\pm$ 12.7
"	201	"	1.98 $\pm$ 0.37	47.0 $\pm$ 8.8
		Mean	2.04 $\pm$ 0.45	48.7 $\pm$ 10.7

<sup>1</sup>During June cruises only Bosmina species were collected, while in July Daphnia was the predominant taxon.

Table 11. Mean filtration rates for the 3 most abundant taxa in the estuary,  $\pm$  one standard error. n = six animals per station.

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

Table 12. Mean specific community grazing rates for zooplankton in the dark,  $\pm$  one standard error.

Month	Station	$G(\text{hr}^{-1}) \times 10^{-4}$	$G(\text{day}^{-1}) \times 10^{-4}$
June	501	$1.06 \pm 0.41$	$25.4 \pm 9.9$
"	451	$1.28 \pm 0.12$	$30.7 \pm 3.1$
"	201	$1.55 \pm 0.36$	$37.2 \pm 8.7$
	Mean	$1.29 \pm 0.29$	$31.1 \pm 7.2$
July	501	$2.70 \pm 0.41$	$64.8 \pm 10.0$
"	451	$1.90 \pm 0.59$	$45.6 \pm 14.3$
"	201	$2.45 \pm 0.44$	$58.8 \pm 10.6$
	Mean	$2.35 \pm 0.48$	$56.4 \pm 11.6$

when B. longirostris was predominant. There were no significant differences among the community grazing rates at the three stations studied.

#### Grazing rates (zooplankton ingestion in the light)

Specific zooplankton grazing rates for B. longirostris and mixed copepods, plus the community rates, are shown in Tables 13 and 14 for the light experiment performed in June at Station 201. Specific grazing rates appeared somewhat higher than comparable rates at Station 201 from the dark experiments, but were not significantly different.

#### Grazing rates by phytoplankton disappearance

During July 1981, changes in a grazed and ungrazed  $^{14}\text{C}$ -prelabelled natural phytoplankton community were followed during a 24-hour period (Fig. 35), as another approach to estimating grazing. Specific zooplankton community grazing rates were computed from the differences between the grazed and ungrazed phytoplankton populations, assuming that all phytoplankton loss was due to grazing. Specific community grazing rates calculated from these experiments (Table 15) were slightly higher than the community grazing rates calculated from the July zooplankton ingestion experiments (Table 12). However, the agreement is most satisfying when one considers the potential error in these types of experimental comparisons. Possibly the somewhat higher rates in Table 15 were due to the fact that not all phytoplankton loss was caused by grazing removal.

#### 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

Table 13. Mean specific grazing rates for taxa in the light,  $\pm$  one standard error. n = six animals per taxa.

Month	Station	Species	$g(\text{hr}^{-1}) \times 10^{-4}$	$g(\text{day}^{-1}) \times 10^{-4}$
June	201	Copepods	$2.5 \pm 0.3$	$60.0 \pm 7.2$
"	"	<u>B. longirostris</u>	$1.6 \pm 0.7$	$38.4 \pm 16.8$

Table 14. Mean community grazing rates for zooplankton in the light,  $\pm$  one standard error.

Month	Station	$G(\text{hr}^{-1}) \times 10^{-4}$	$G(\text{day}^{-1}) \times 10^{-4}$
June	201	$2.1 \pm 0.5$	$50.4 \pm 12.0$

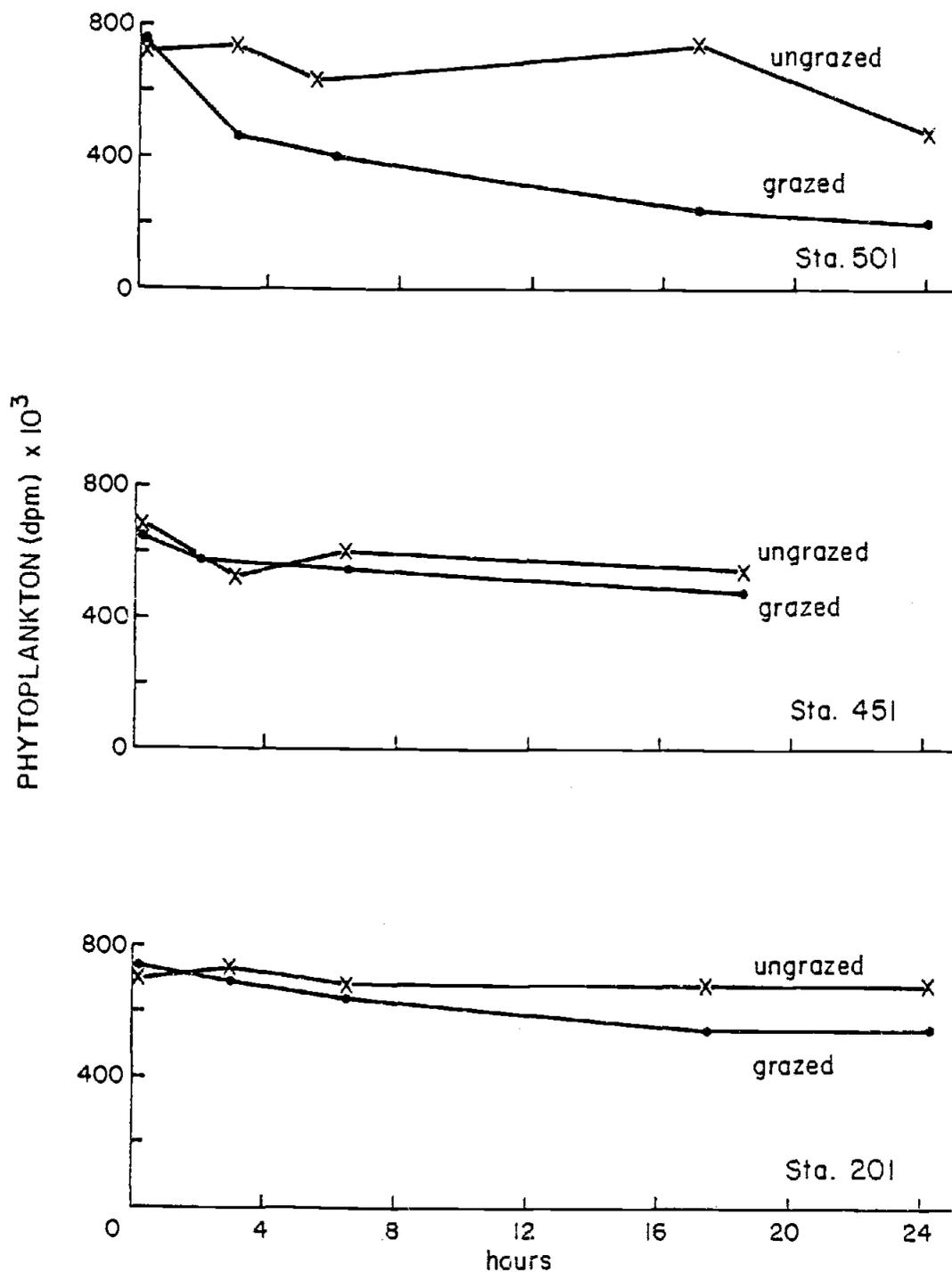


Figure 35. Time series of phytoplankton ( $\text{dpm} \cdot 10^3$ ) disappearance by community zooplankton grazing at three different stations along the main channel.

Table 15. Mean specific community grazing rates from phytoplankton disappearance experiments.

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

distributional studies exist. I have assumed that zooplankton concentrations previously reported in the literature during different seasons are representative of the entire estuary (Table 16). From these data I determined 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 under-estimation of grazing removal.

Daily phytoplankton removal by zooplankton grazing was estimated for each month of the year (Table 17) by using the representative seasonal value for total zooplankton concentration in the estuary (Table 16), an estimated monthly phytoplankton carbon biomass (Table 17), and an average filtration rate of  $1.2 \text{ ml animal}^{-1} \text{ day}^{-1}$  (Table 11). 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.

Maximum phytoplankton grazing removal (Table 17) was attained during later spring and summer (May through August), averaging  $4.6 \text{ mgC m}^{-3} \text{ day}^{-1}$  (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  $0.06 \text{ mgC m}^{-3} \text{ day}^{-1}$  (range 0.05 to 0.08), or about 0.06% of the phytoplankton carbon available.

Daily removal rates were expanded (multiplying by days month<sup>-1</sup>) to monthly removal estimates. Then values of monthly removal were

Table 16. Total zooplankton concentration for the dominant species in the Columbia River Estuary.

Dominant species	Habitat	Total zooplankton (animals m <sup>-3</sup> )			
		spring	summer	fall	winter
<u>Bosima</u> sp., <u>Cyclops vernalis</u> , <u>Daphnia longispina</u> .	freshwater <sup>1</sup>	<10 <sup>3</sup>	10 <sup>3</sup> -5X10 <sup>3</sup>	<10 <sup>3</sup>	<10 <sup>2</sup>
<u>Eurytemora affinis</u> , <u>Canuella canadensis</u> .	brackish <sup>1</sup>	10 <sup>3</sup> -4X10 <sup>4</sup>	10 <sup>3</sup> -10 <sup>4</sup>	10 <sup>3</sup>	<10 <sup>3</sup>
<u>Pseudocalanus minutus</u> , <u>Acartia clausi</u> , <u>A. longiremis</u> .	marine <sup>1</sup>	10 <sup>3</sup> -3X10 <sup>3</sup>	10 <sup>3</sup> -5X10 <sup>3</sup>	10 <sup>3</sup>	10 <sup>2</sup>
<u>Eurytemora hirundoides</u> , <u>Bosmina longirostris</u> , <u>Daphnia longispina</u> .	brackish <sup>2</sup> and freshwater	<10 <sup>3</sup>	10 <sup>3</sup> -2X10 <sup>3</sup>	10 <sup>3</sup>	10 <sup>3</sup>
<u>Eurytemora affinis</u> .	brackish <sup>3</sup>	<10 <sup>3</sup> -5X10 <sup>3</sup>	<10 <sup>3</sup> -10 <sup>3</sup>	n.d	n.d
Concentrations chosen for grazing removal estimations		10 <sup>4</sup>	10 <sup>4</sup>	10 <sup>3</sup>	0.5X10 <sup>3</sup>

<sup>1</sup>After Haertel (1970)

<sup>2</sup>After Misitano (1974)

<sup>3</sup>After English et al. (1980)

Table 17. Daily phytoplankton carbon removal by zooplankton grazing in the Columbia River Estuary, for each month of the sampling period.

Month	Zooplankton <sup>1</sup> 10 <sup>3</sup> (m <sup>-3</sup> )	Grazing rate <sup>2</sup> (% day <sup>-1</sup> )	Phytoplankton <sup>3</sup> biomass (mgC m <sup>-3</sup> )	Grazing removal (mgC m <sup>-3</sup> day <sup>-1</sup> )
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

<sup>1</sup>Concentrations from Table 16.

<sup>2</sup>Product of zooplankton concentration (No. m<sup>-3</sup>) times a mean filtration rate of 1.2 ml animal<sup>-1</sup> day<sup>-1</sup>, expressed as a percentage.

<sup>3</sup>Average chlorophyll a per estuary x 40, where C/chla = 40, (see discussions).

added to give a crude estimate of annual phytoplankton removal by grazing zooplankton. The annual phytoplankton grazing removal for the estuary was estimated at  $669 \text{ mgC m}^{-3} \text{ yr}^{-1}$ , 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.

### 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:  $T = \text{transport rate (g sec}^{-1}\text{)}$

$D = \text{river discharge (m}^3 \text{ sec}^{-1}\text{)}$

$C = \text{concentration (g m}^{-3}\text{)}$

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, and the cross-sectional areas at the two sites are similar. 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-to-1975 data record. This percent difference was then applied to the present river discharge at the mouth, in order to estimate present river discharge at Longview (and hence, by assumption, at the head of our study section at River Mile 47).

Columbia River flow is characterized by two peaks per year (Fig. 36). The spring peak, usually attaining a maximum in late 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  $14695 \text{ m}^3 \text{ sec}^{-1}$  in June, 1981, and  $2613 \text{ m}^3 \text{ sec}^{-1}$  in October, 1980. The similarity of the transports at the mouth and at River Mile 47 attest to the extreme dominance of the Columbia River over the small tributaries in the study area.

#### Chlorophyll a transport

For purposes of this analysis the area studied (up to River Mile 47) is considered as the Columbia River Estuary, which 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) (Fig. 3).

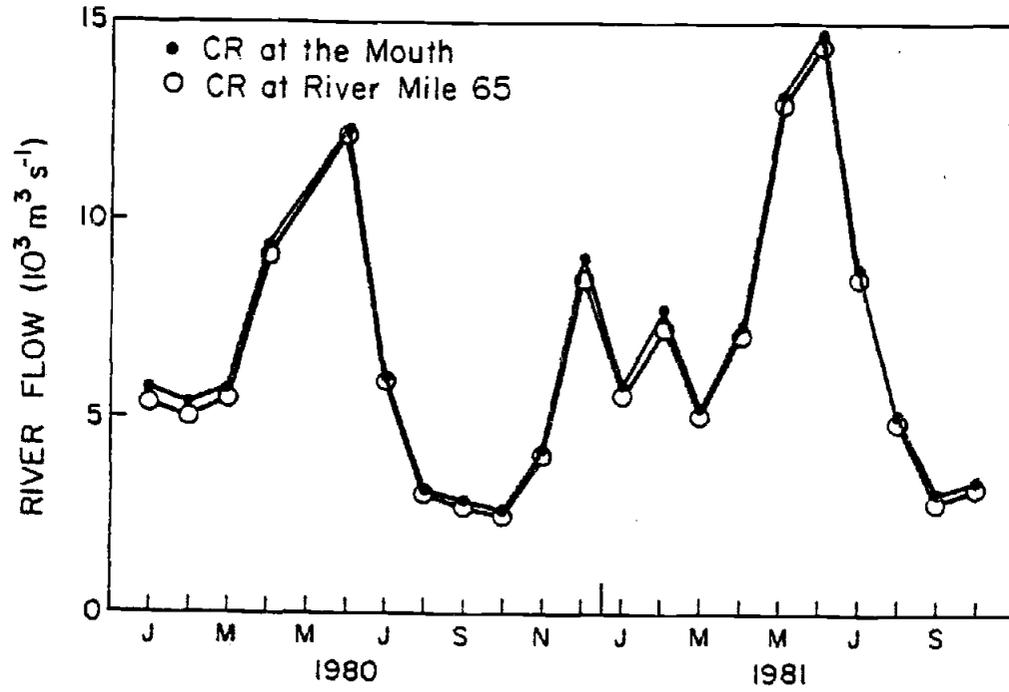


Figure 36. Monthly averages of Columbia River flow.

Of all the variables studied only chlorophyll a concentration presented significant ( $p < 0.001$ ) 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 (Fig. 37), and import-export was evaluated through zones 8, 5, 2, and 1 (Fig. 3). The transport of chlorophyll a (metric tons  $\text{day}^{-1}$ ) by zones and seasons is shown in Fig. 38. 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 zone 8 and zone 1 transport occurred in May. At this time the estuary imported up to 16 tons of chlorophyll a  $\text{day}^{-1}$ , while it only exported about 9 tons  $\text{day}^{-1}$  to the Pacific Ocean. Minimum transport rates occurred in November, with about 1.5 tons chlorophyll a  $\text{day}^{-1}$  imported and about 0.25 tons  $\text{day}^{-1}$  exported. The Columbia River Estuary thus acted as a sink for chlorophyll a throughout the whole year (Fig. 39), 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 (Fig. 39). The estuary received about  $1.9 \times 10^3$  tons of chlorophyll a during the year studied (over 50% during spring), but exported only around  $0.9 \times 10^3$  tons  $\text{year}^{-1}$  (over 50% in spring) to the Pacific Ocean (Table 18).

- 1. Marine            3. Youngs Bay            5. Cathlamet Bay            7. Deep River
- 2. Mixing            4. L-C & Youngs R.            6. Grays Bay            8. Upper Estuary

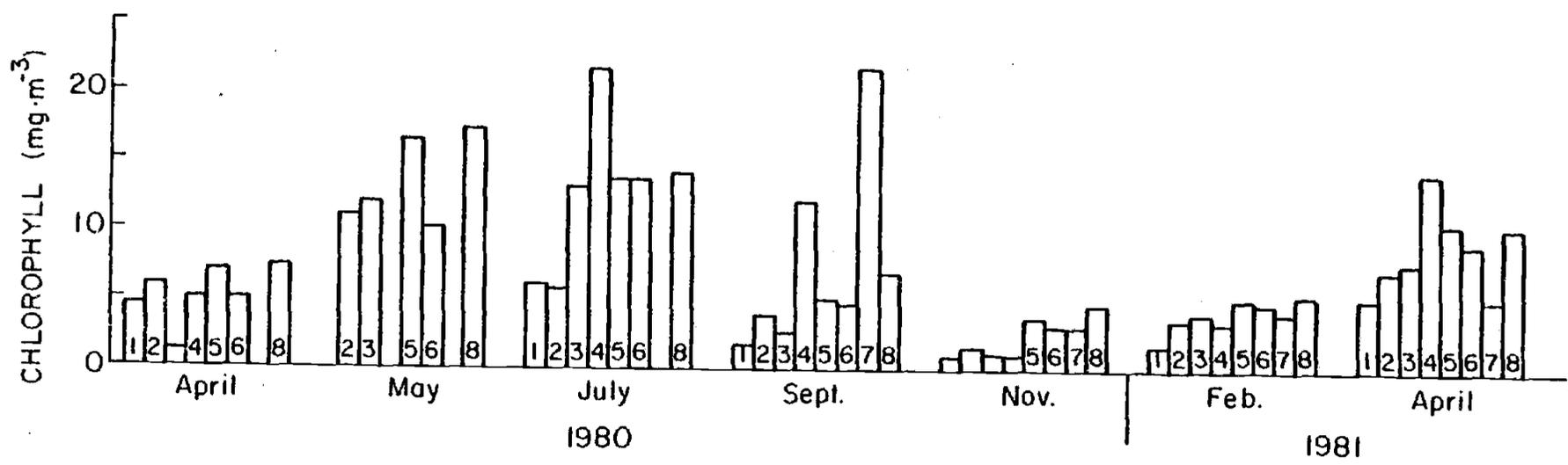


Figure 37. Temporal distribution of mean chlorophyll a concentration by zones.

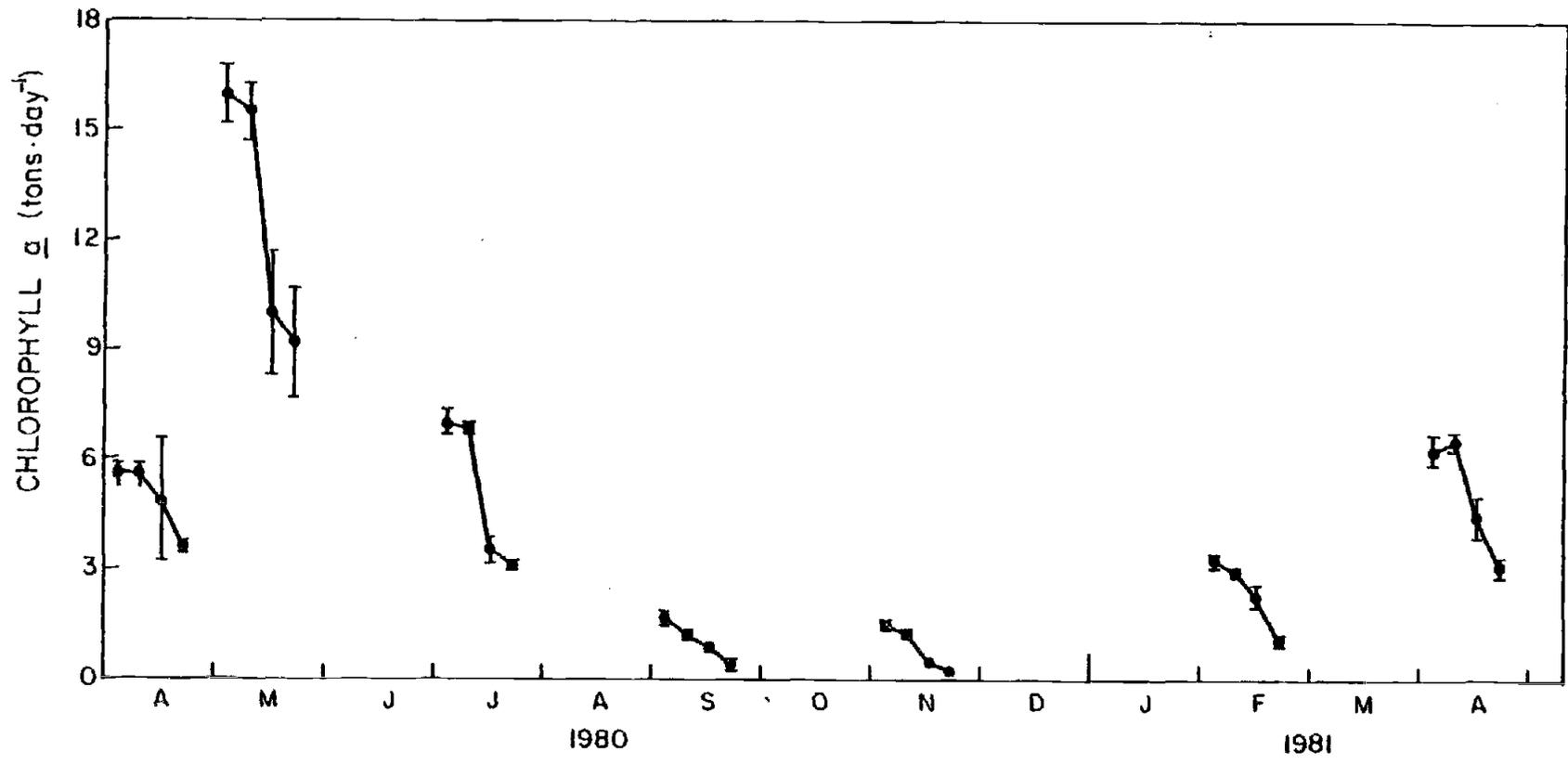


Figure 38. Daily mean transports of chlorophyll a by zones. Points represent from left to right, zones 8,5,2, and 1. Bars are  $\pm$  one standard error.

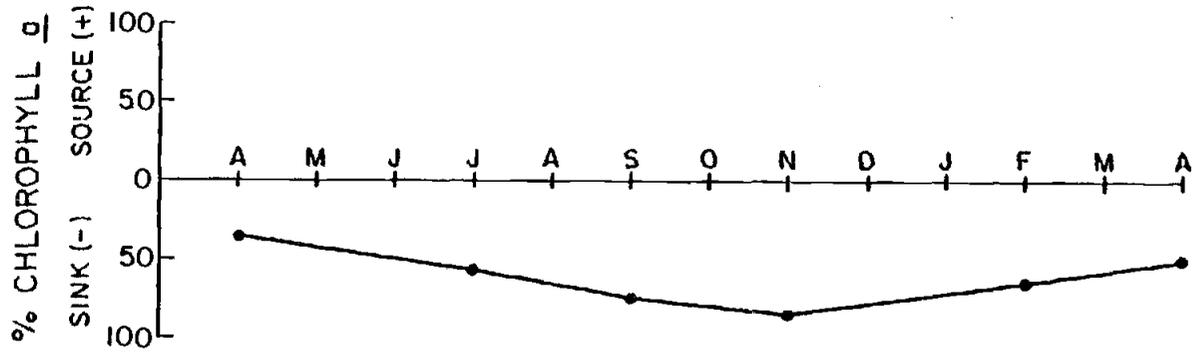


Figure 39. Chlorophyll a lost in the estuary as a percentage of chlorophyll a entering the estuary at River Mile 47.

Table 18. 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 <u>a</u> ** (tons)	108	287	253	96	32	12	8	7	17	19	31	46	916
Silicic Acid (10 <sup>6</sup> moles)	4395	5347	4725	1767	917	792	998	1920	4042	2498	2830	2325	32,556
Nitrate + Nitrite (10 <sup>6</sup> moles)	879	248	150	12	22	36	83	210	496	344	436	303	3,219
Phosphate (10 <sup>6</sup> moles)	26	22	15	5	3	4	5	9	20	12	14	9	144
POC (10 <sup>3</sup> tons)	21	159 (43) <sup>+</sup>	107 (63)	18	10	10	10	17	31	16	14	12	425 (265)
PON (10 <sup>3</sup> tons)	2	10 (7)	7 (6)	2	1	1	1	1	4	3	4	3	39 (35)
OSP (10 <sup>3</sup> tons)	47	360 (131)	285 (190)	86	47	42	34	44	80	40	33	34	1,132 (808)
ISP (10 <sup>3</sup> tons)	186	9993 (784)	5758 (1183)	218	211	271	272	446	755	336	219	204	18,869 (5,085)
TSP (10 <sup>3</sup> tons)	233	10353 (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

### Transport of nutrients and suspended particulate material

Transport rates for TSP, OSP, ISP, POC, PON, 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 40. 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 19). 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 18). During the 1980-1981 period,  $1.4 \times 10^8$  moles of phosphate,  $3.2 \times 10^9$  moles of nitrate plus nitrite, and  $3.2 \times 10^{10}$  moles of silicic acid were exported to the Pacific Ocean (Tables 18 and 19).

The daily outputs of POC and PON (Fig. 40) showed maximum values in May and June due to the Mt. Saint Helens' volcanic eruption. Apart from that, POC and PON both still tended toward highest concentrations in spring. The annual output to the Pacific Ocean (Table

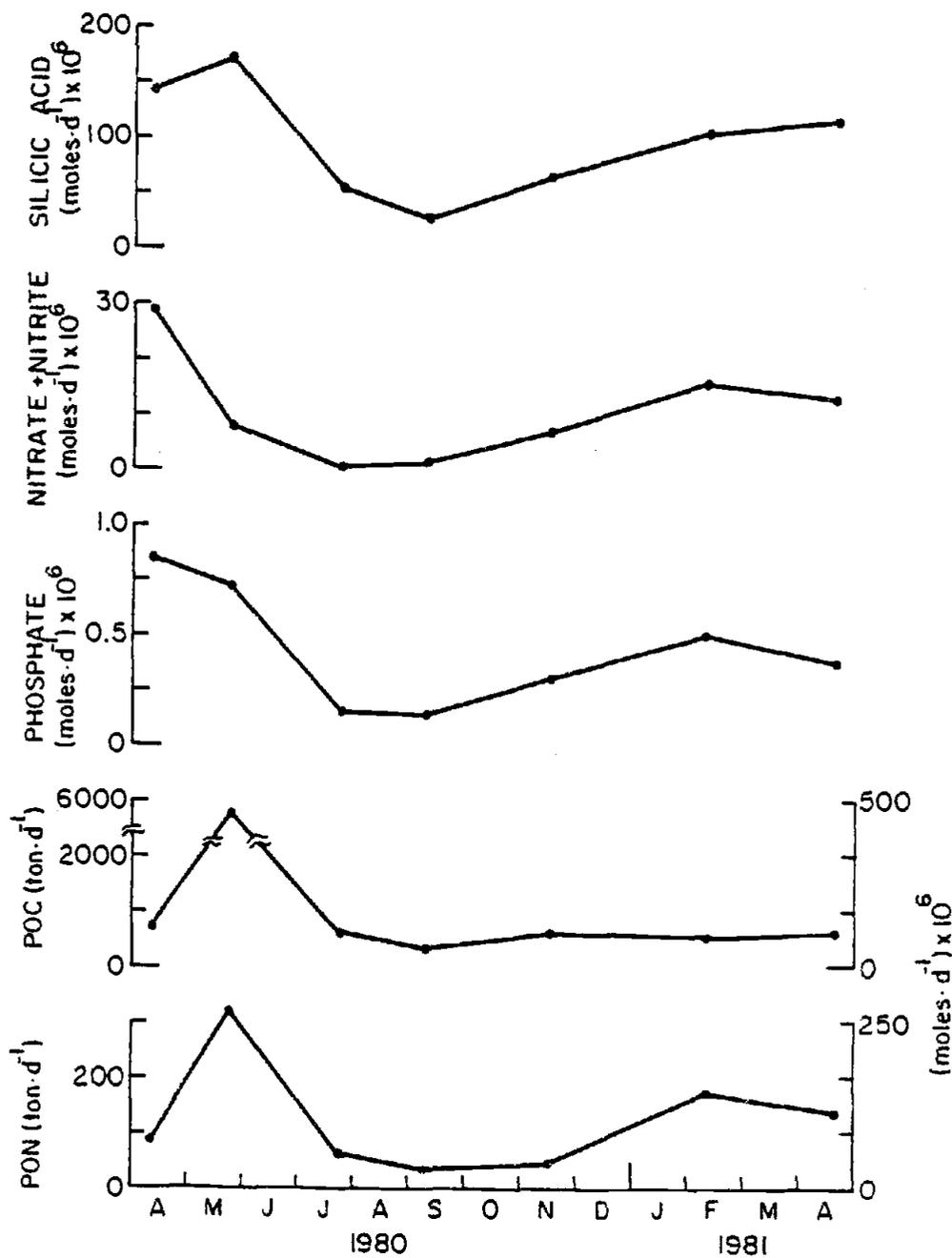


Figure 40. Daily mean transports of properties from the Columbia River to the Pacific Ocean.

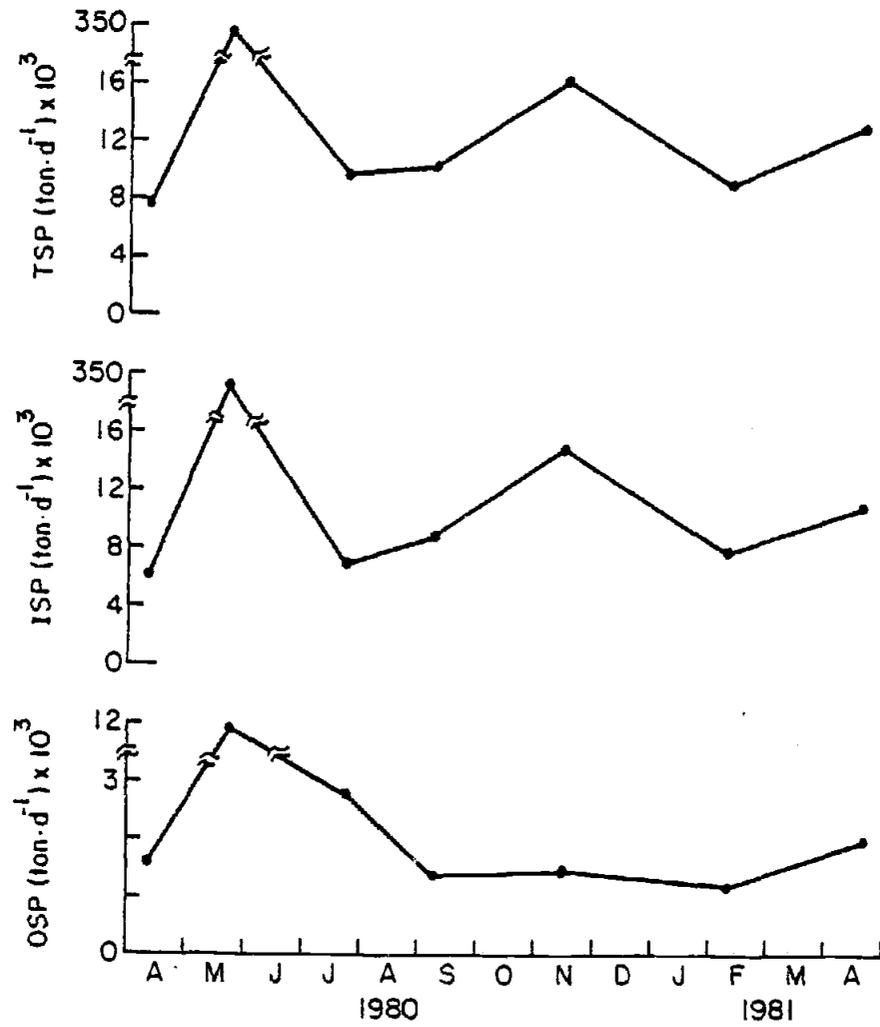


Figure 40. (continued)

Table 19. Annual chemical budgets for the Columbia River in 1966, 1967, 1974, and 1980-1981.

Variable	1966 <sup>1</sup>	1967 <sup>1</sup>	1974 <sup>2</sup>	1980-1981 <sup>3</sup>
Water (liters)	$2.0 \times 10^{14}$	$2.3 \times 10^{14}$	$2.5 \times 10^{14}$	$2.0 \times 10^{14}$
Phosphate (moles)	$1.2 \times 10^8$	$0.8 \times 10^8$	$2.8 \times 10^8$	$1.4 \times 10^8$
Nitrate + Nitrite (moles)	$2.5 \times 10^9$	$2.8 \times 10^9$	$3.5 \times 10^9$	$3.2 \times 10^9$
Silicic acid (moles)	$3.3 \times 10^{10}$	$3.5 \times 10^{10}$	$4.8 \times 10^{10}$	$3.2 \times 10^{10}$

<sup>1</sup>Park et al. (1972)

<sup>2</sup>Dahm (1980)

<sup>3</sup>This study

18) was about  $4.2 \times 10^5$  tons (over 60% from April to June) of POC and  $3.9 \times 10^4$  tons of PON. However, values without the volcanic input would have been much lower, about  $2.6 \times 10^5$  tons of POC and  $3.5 \times 10^4$  tons of PON.

The daily outputs of TSP, OSP, and ISP (Fig. 40) were greatly exaggerated 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 (Fig. 36). The annual exports to the Pacific Ocean (Table 18) were  $2.0 \times 10^7$  tons of TSP, about  $1.89 \times 10^7$  tons of ISP, and about  $1.1 \times 10^6$  tons of OSP. Again, transport rates without the volcanic input would have been much lower (Table 18), about  $5.8 \times 10^6$  tons of TSP,  $5 \times 10^6$  tons of ISP, and  $8 \times 10^5$  tons of OSP.

## DISCUSSION

Temporal Variability

The Columbia River Estuary clearly is a light-limited system, with daily solar radiation input, light attenuation in the water column, and the phytoplankton biomass itself (chlorophyll a) the variables that mainly explain temporal changes in primary productivity (Tables 4 and 5). The assimilation numbers as well showed light limitation throughout the seasons, reaching maximum values during summer (Fig. 27b). In fall and winter true assimilation numbers usually could not be calculated because light-saturated photosynthesis in the water column was almost never reached. Although the inorganic nutrient concentrations decreased during the maximum production season, nutrients apparently were sufficient during all seasons, and exercised no measurable control over phytoplankton productivity.

As expected in a light-limited system, both chlorophyll concentrations (Fig. 10) and carbon productivity (Fig. 27a) matched the solar irradiation cycle, with maximum values in late spring and early summer, and minimum values during late 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 (Takahashi et al., 1973), Chesapeake Bay (Patten et al., 1963; Flemer, 1970), and North Carolina estuaries (Thayer, 1971).

The significance of nanoplankton (cells  $<35 \mu\text{m}$ , and usually  $<20 \mu\text{m}$ ) over netplankton (cells  $>35 \mu\text{m}$ ) in terms of phytoplankton biomass and production 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 to 80% of the primary production in the Columbia River Estuary, and from 50-80% of the total phytoplankton standing stock, was due to the  $<33 \mu\text{m}$  fraction, and usually by the  $<10 \mu\text{m}$  fraction (Figs. 30 and 31). In the Columbia River plume waters off Oregon and Washington, about 80% of the production was due to cells less than  $35 \mu\text{m}$  in size (Anderson, 1965).

The chlorophyll a peak occurred in May. Haertel (1970) also reported the maximum chlorophyll a concentration during May 1967 and 1968 for the marine and mixing zones. This probably indicates that the chlorophyll peak that we observed in May 1980 was not enlarged during the Mt. Saint Helens' eruption. On the contrary, it may have been reduced. Photosynthetic rates were highly reduced during the volcanic eruption (Fig. 27a), mainly because of light limitation in the water (Figs. 24 and 28) caused by the abnormal concentrations of suspended particles. By using a primary production regression model (Table 4), the potential production of the estuary in May (without the volcano effects) was estimated to be much higher than that actually measured (Frey et al., in press); however, the calculated value was lower than the production measured in July. This indicates that the production peak probably lags the phytoplankton

biomass (chlorophyll) peak by a few weeks, probably in response to higher solar radiation intensities (and thus deeper light penetration into the water column) in summer.

Although inorganic nutrient supply apparently exerts little control on primary productivity in the estuary (Table 4), inorganic nutrient concentrations change with season (Figs. 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 in the entering marine waters up to 23  $\mu\text{M}$  during summer upwelling. During our summer sampling we indeed observed an enrichment of nitrates in the salt wedge below 5m depth (Fig. 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 + nitrite) was reduced the most during summer; however, because no other nitrogen nutrients (ammonia, for example) have been studied in the Columbia River Estuary, we can not conclude that nitrogen availability 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).

The abnormally increased suspended particle load during the Mt. Saint Helens' eruption, concomitant with the high river flow in May, masked the natural temporal variability patterns of all suspended particle properties. Temporal variability of properties in the shallow bays (Figs. 17 and 18) showed the same seasonal trend as in channel stations (Figs. 8 to 15); however, for some properties the seasonal pattern was even less significant in the shallow bays (Table 1).

### Spatial Variability and Comparison to Other Estuarine Systems

#### Primary Production

Significant spatial variation in phytoplankton production was found in the Columbia River Estuary system (Table 7). Riverine waters were substantially more productive ( $121-140 \text{ gC m}^{-2} \text{ yr}^{-1}$ ) than estuarine waters ( $69-84 \text{ gC m}^{-2} \text{ yr}^{-1}$ ). Also, Anderson (1972) has reported that production in the plume waters (off the Columbia River mouth) was about  $125 \text{ gC m}^{-2} \text{ yr}^{-1}$ , higher than in the estuary proper.

There is surprisingly little information on annual phytoplankton production in the major river-estuarine systems of the world, for comparison to the Columbia system. When compared to estuaries in which annual data are available, the Columbia River Estuary is the least productive on a per unit area basis (Table 20). This has to do with the distribution of primary biomass in the estuarine portions of the various river-estuary-ocean systems, and reasons for the disparity are addressed later, in the discussion on primary biomass variability.

On a per-unit-area basis, production due to benthic algae on the mudflats of the Columbia River Estuary is about the same as, or even higher than, water-column phytoplankton production in the estuary. Gross

Table 20. Phytoplankton primary production in some estuaries.

Area	gC m <sup>-2</sup> yr <sup>-1</sup>	References
Columbia River Estuary, OR.	69-84	This study
Fraser River Estuary, B.C.	120	Parsons <i>et al.</i> (1970)
Bedford Basin, N.S.	220	Platt (1975)
St. Margaret's Bay, N.S.	190	Platt (1971)
Narragansett Bay, RI.	310	Furnas <i>et al.</i> (1976)
Lower Hudson Estuary, NY.	690-925	O'Reilly <i>et al.</i> (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 <i>et al.</i> (In press)
South River Estuary, NC.	300-500	Fisher <i>et al.</i> (In press)

production due to benthic algae during the day has been estimated to range from about 100 to 250  $\text{gC m}^{-2} \text{yr}^{-1}$  (McIntire and Amspoker, 1980). Using a ratio of net to gross production of approximately 0.7 (McIntire, personal communication), net benthic production thus ranges from about 70 to 175  $\text{gC m}^{-2} \text{yr}^{-1}$  in the Columbia estuary. Annual production by emergent vegetation ringing the Columbia estuary is even higher, on a per unit area basis. Net production has been estimated to be 430  $\text{gC m}^{-2} \text{yr}^{-1}$  for marshes west of Tongue Point, and 348  $\text{gC m}^{-2} \text{yr}^{-1}$  for marshes east of Tongue Point (Wolf et al., 1980). None of these estimates have been corrected for night respiration.

One reason that primary production in the estuarine water column was lower than that on mud flats or in surrounding marshes might have to do with the fact that photosynthetic cells in the water column were more sparsely distributed with respect to the light field. The water column euphotic zone was only one to four meters deep, and optimum light for photosynthesis, when it was achieved at all, was restricted to a narrow band near the surface (Figs. 24 and 25). Sparsely distributed cells mixing through the complete water column would be in this band of optimal light only a fraction of each day. When out of the euphotic zone altogether, phytoplankton cells presumably would continue to respire carbon, but not replenish it through photosynthesis. Thus, real primary carbon production for the Columbia River Estuary might be even less than that reported in Tables 6 and 7, diminished by respiratory carbon loss below the euphotic zone. Of the processes that effect changes in natural phytoplankton populations, respiration has been one of the most difficult to evaluate (Vollenweider, 1973; Talling, 1975). During the present study several attempts

were made to evaluate the respiratory loss term by using the light-dark bottle oxygen method. However, because of the high variability observed in the experimental replications, and because of inconsistencies in the initial and final oxygen concentrations, no suitable respiration data could be generated for application to the time spent below the euphotic zone by phytoplankton cells.

Shallow areas of estuaries often are sites of rapid phytoplankton population increase; 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 (Table 6) averaged slightly higher than in the channel, but differences were not large. Primary productivity in the shallows apparently was limited by the very short surface-to-bottom distance, and possibly by increased suspended particle loads which may have retarded light penetration (Table 3). In the Columbia River Estuary the water residence time is only a few tidal cycles (2-10, according to Neal, 1965), while in the northern reach 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 time in the Columbia River Estuary might help explain the similarity of primary productivity in the shallows and channel.

#### Primary biomass and other properties

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

determined the depth distribution of certain properties (Figs. 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, (Figs. 10 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.

I have examined several hypotheses to explain the chlorophyll a pattern. First, because my sampling was not synoptic, diel chlorophyll a variability might have accounted for the spatial distribution observed, as has been reported by several investigators (Lorenzen, 1963; Wood and Corcoran, 1966; Glooschenko et al., 1972). To test this hypothesis, chlorophyll a concentrations from different seasons and stations along the estuary were plotted against the daily time of sampling (Fig. 41). 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 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

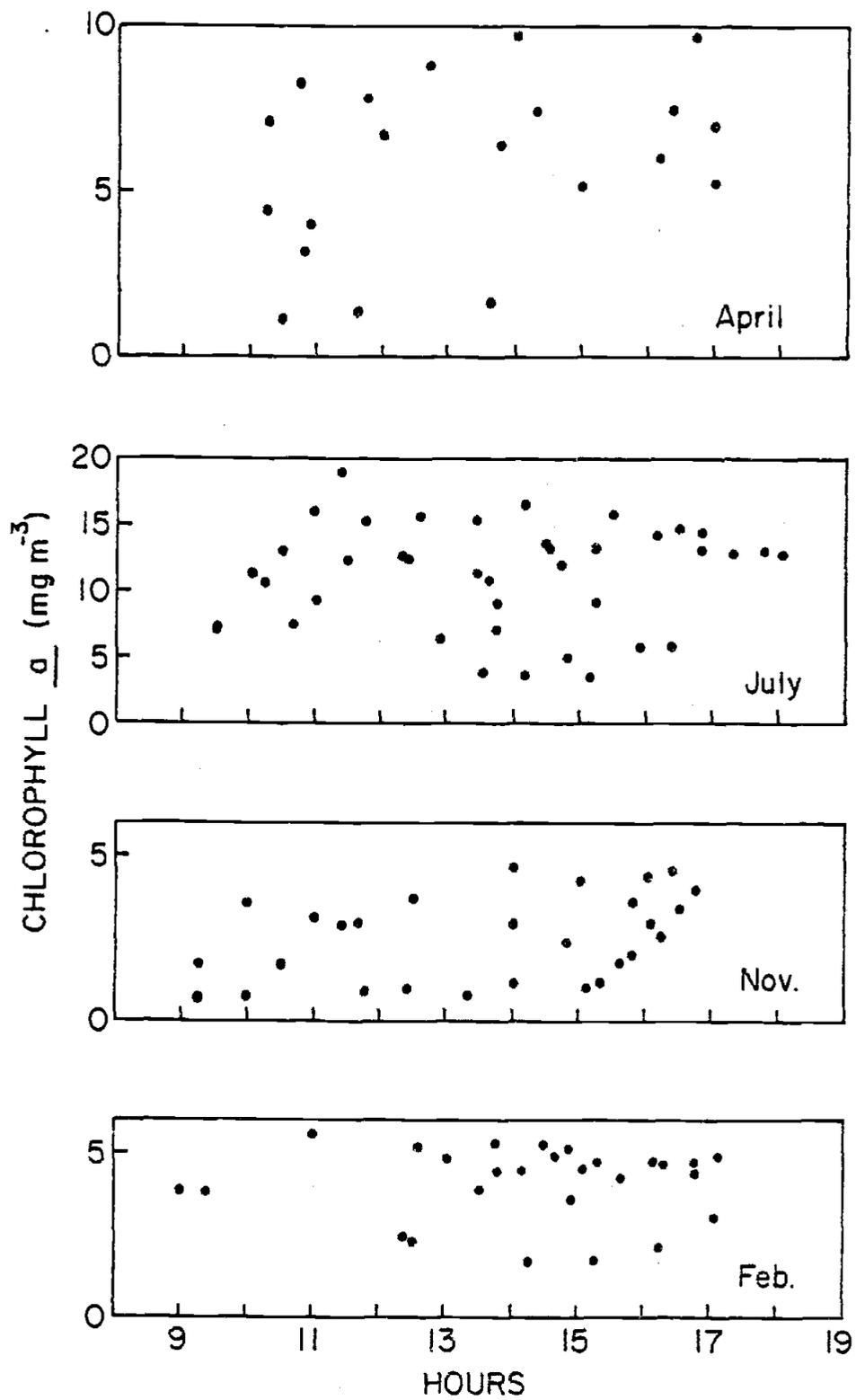


Figure 41. Daily chlorophyll a variability throughout the estuary.

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 (Fig. 42). 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  $15 \text{ mg m}^{-3}$  at the mouth up to  $40 \text{ mg m}^{-3}$  in the mixing zone, whereas at flood tide the range was from 5 to  $15 \text{ mg m}^{-3}$ , respectively.

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 or rupture, or rapid plasmolysis, 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 (Fig. 43), 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. Rapid decline in both freshwater species and chlorophyll concentrations at salinities of about 2 to 5‰ signals a rather definitive barrier between the fresh-water-dominated and marine-dominated sections of the estuary. The numbers of marine species in the estuary were so sparse that a definitive boundary for the marine flora could not be deduced.

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

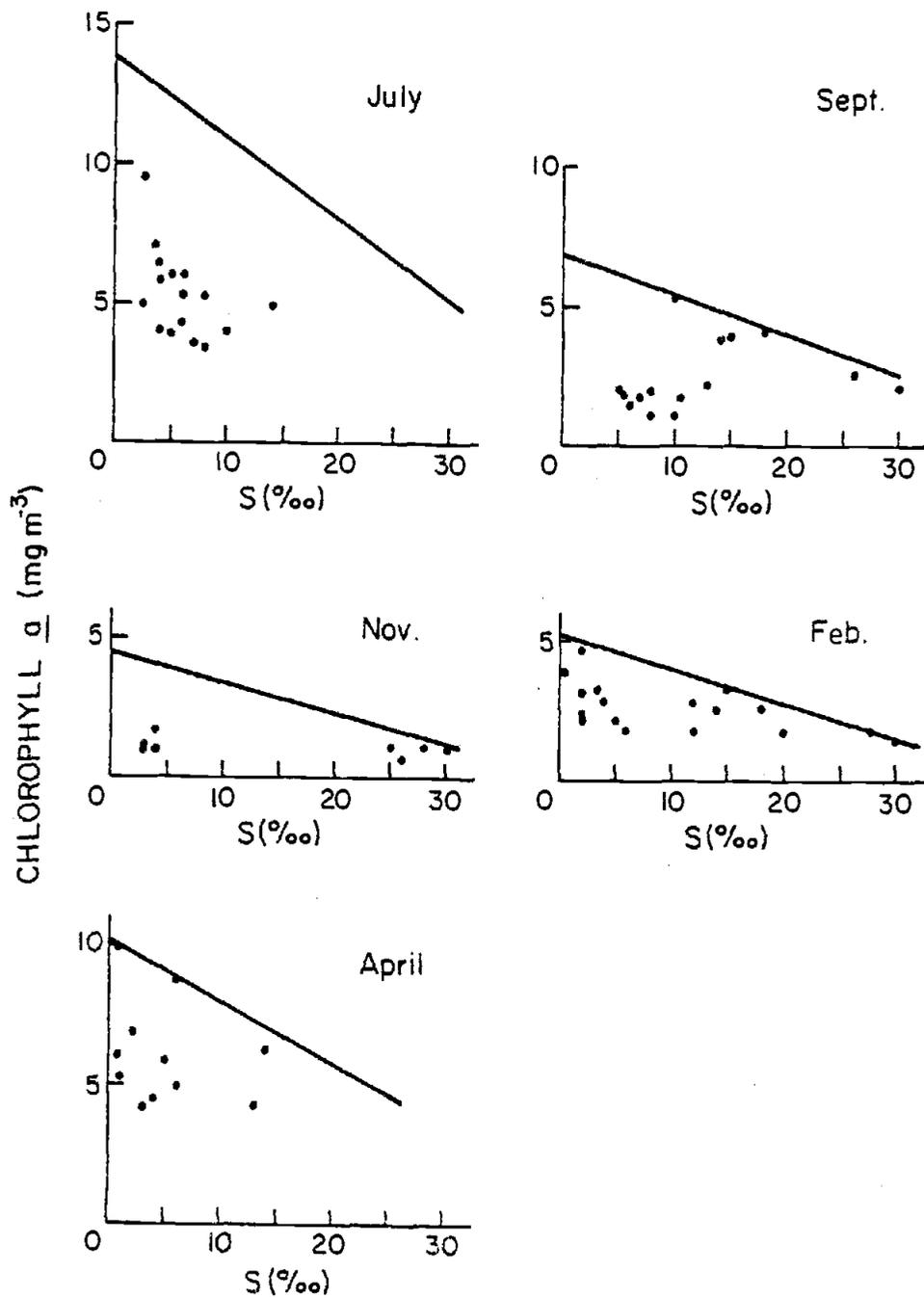


Figure 42. Chlorophyll a distribution against the salinity gradient. Straight lines represent riverine chlorophyll a decreasing by only dilution processes.

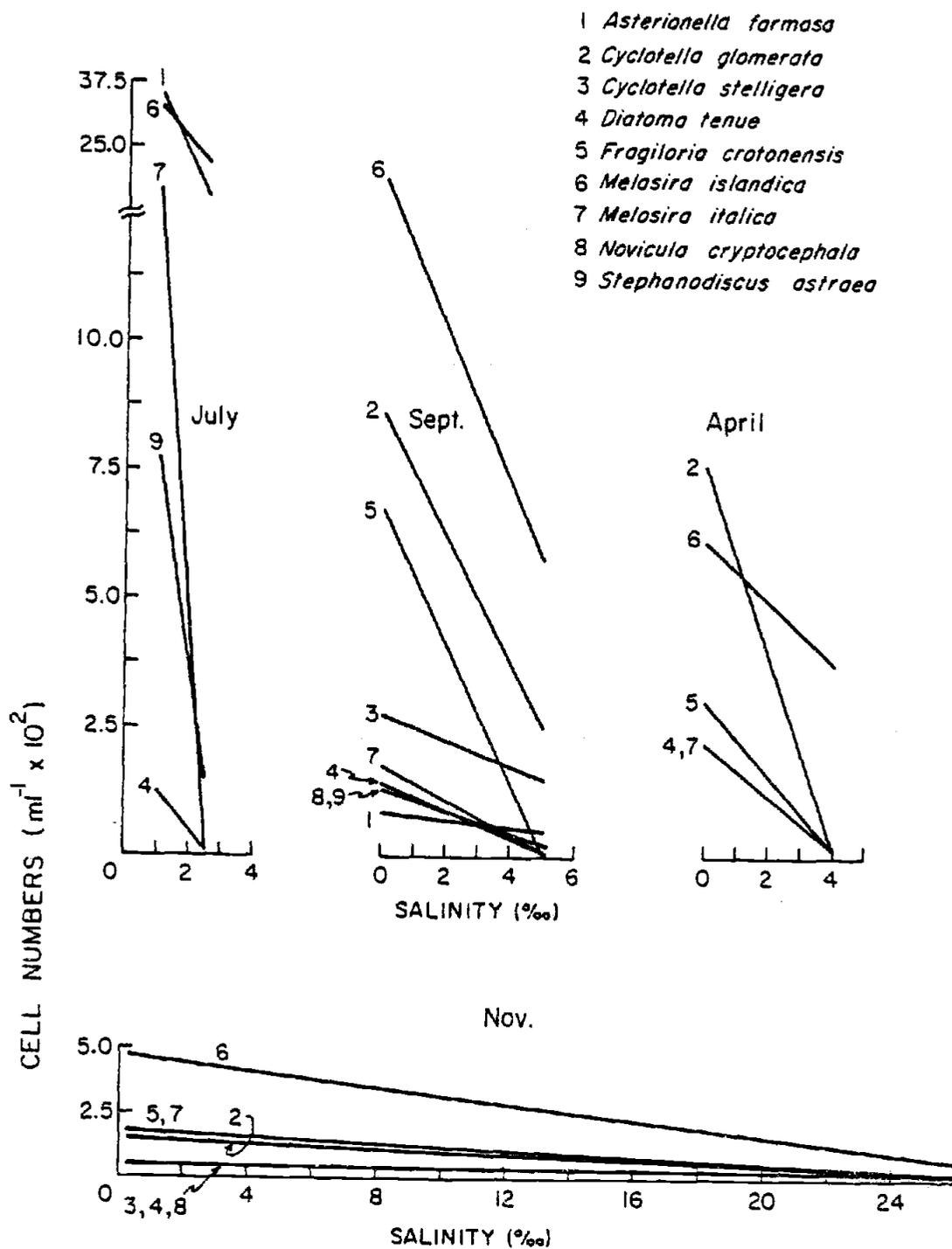


Figure 43. Freshwater diatom abundances distribution against the salinity gradient.

a, also reflected the break between fresh waters and marine waters. In general the DCMU-ratio decreased from fresh water to the marine zone (Fig. 11b), indicating a decrease in the phytoplankton growth rate capacity. Phaeophytin a per unit of chlorophyll a increased toward the marine zone (Fig. 12b), 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 (Table 7) 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 fresh water (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 (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 Scenedesmus obliquus. Photosynthesis of Chlamydomonas peaked at 30‰, but decreased rapidly only at salinities below 10‰. In contrast, Scenedesmus showed an optimum photosynthetic rate in fresh water, 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 dinoflagellate 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 species (Platymonas sp., Syracosphaera carterae, Monochrysis lutheri,

Olisthodiscus 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. Cadée (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<sup>-1</sup> at 0‰, and only 3 cells ml<sup>-1</sup> 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. Cadée suggested phytoplankton sedimentation. 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‰. (Cadée 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<sup>-2</sup> yr<sup>-1</sup> and the estuarine waters about 70 gC m<sup>-2</sup> yr<sup>-1</sup> (from my study), while Anderson (1972) reported about 125 gC m<sup>-2</sup> yr<sup>-1</sup> in the plume waters. Cadée'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 in both river and plume waters, separated by a 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 (Cadée and Hegeman, 1974). Blanc et al. (1969) reported that the mixing zone of the Rhône 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 Saint 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 Saint 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 production 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-Loutre (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 (Naragansett 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 autochthonous 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 (Cadée, 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 (Fig. 44): 1) estuaries with marine-dominated phytoplankton communities, which include the classical estuaries and external 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 least common type. A corollary distinction between these two estuarine types apparently is the average residence time of waters in the estuarine region 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

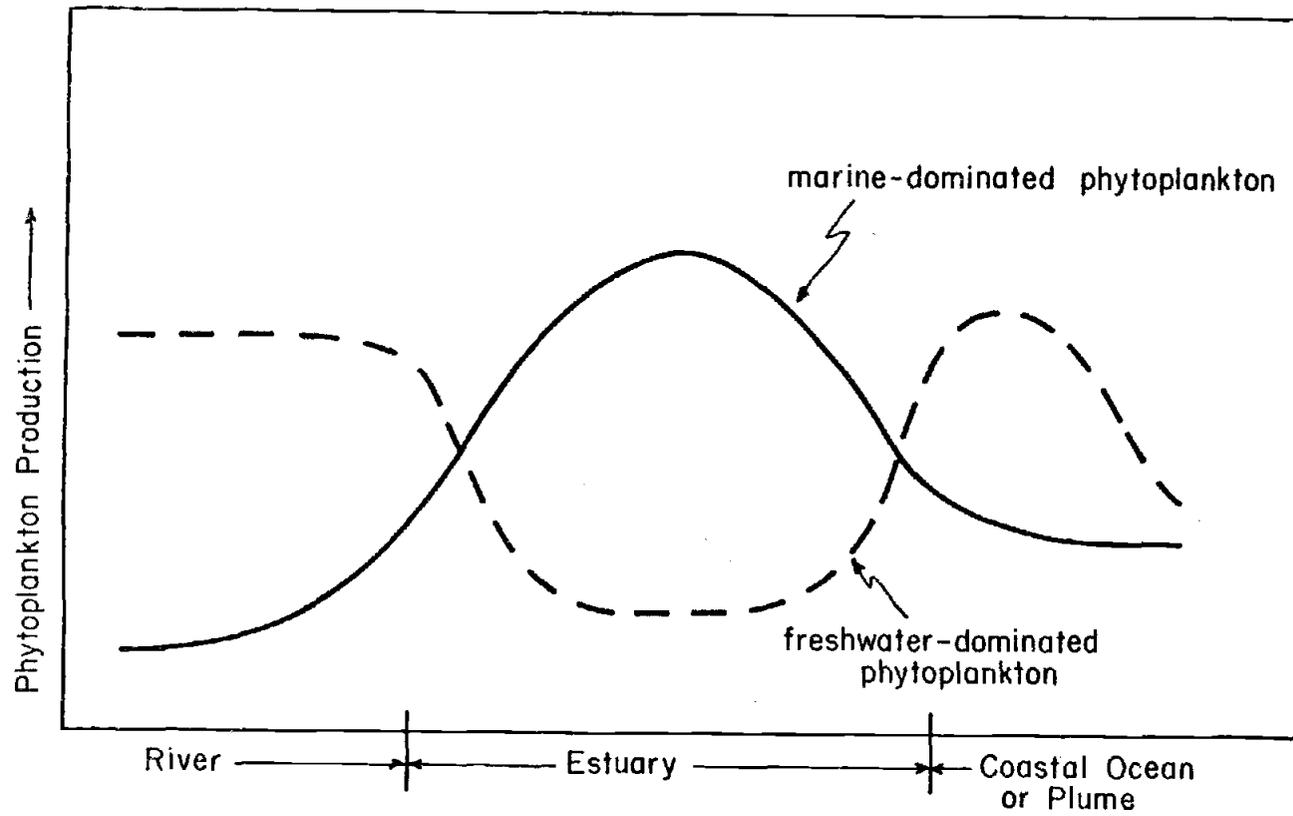


Figure 44. Estuarine system types.

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 water residence times on the order of a few tidal cycles. For example, the water residence time in the Columbia estuary is two to five days (Neal, 1965). In the Congo estuary the residence time is two or three days (Eisma and van Benekom, 1978).

The reason for the low annual primary production in the Columbia River Estuary, relative to other estuaries (Table 20), may be due partially to the fact that the Columbia estuary is a Type 2 estuary, but the others in Table 20 are either Type 1 or intermediate. Thus, the Columbia values in Table 20 are the lowest in the river-estuary-ocean continuum, but the values for the other estuaries may be the highest.

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 Figs. 45 and 46. In these models (one for low river discharge or flood tide, the other for high river discharge or ebb tide), a zone of lost or sinking phytoplankton cells and chlorophyll is located somewhere in the mixing zone of the estuary (Fig. 3). The most critical area in the mixing zone is that segment in which saline waters begin to mix with riverine waters (Figs. 38 and 43). The sedimentation of huge quantities of freshwater phytoplankton cells can act as a food source for benthic organisms (mainly epibenthic, because infauna requires more sediment-stable habitats), and for water-column grazers [the dominant copepod, Eurytemora affinis, has been

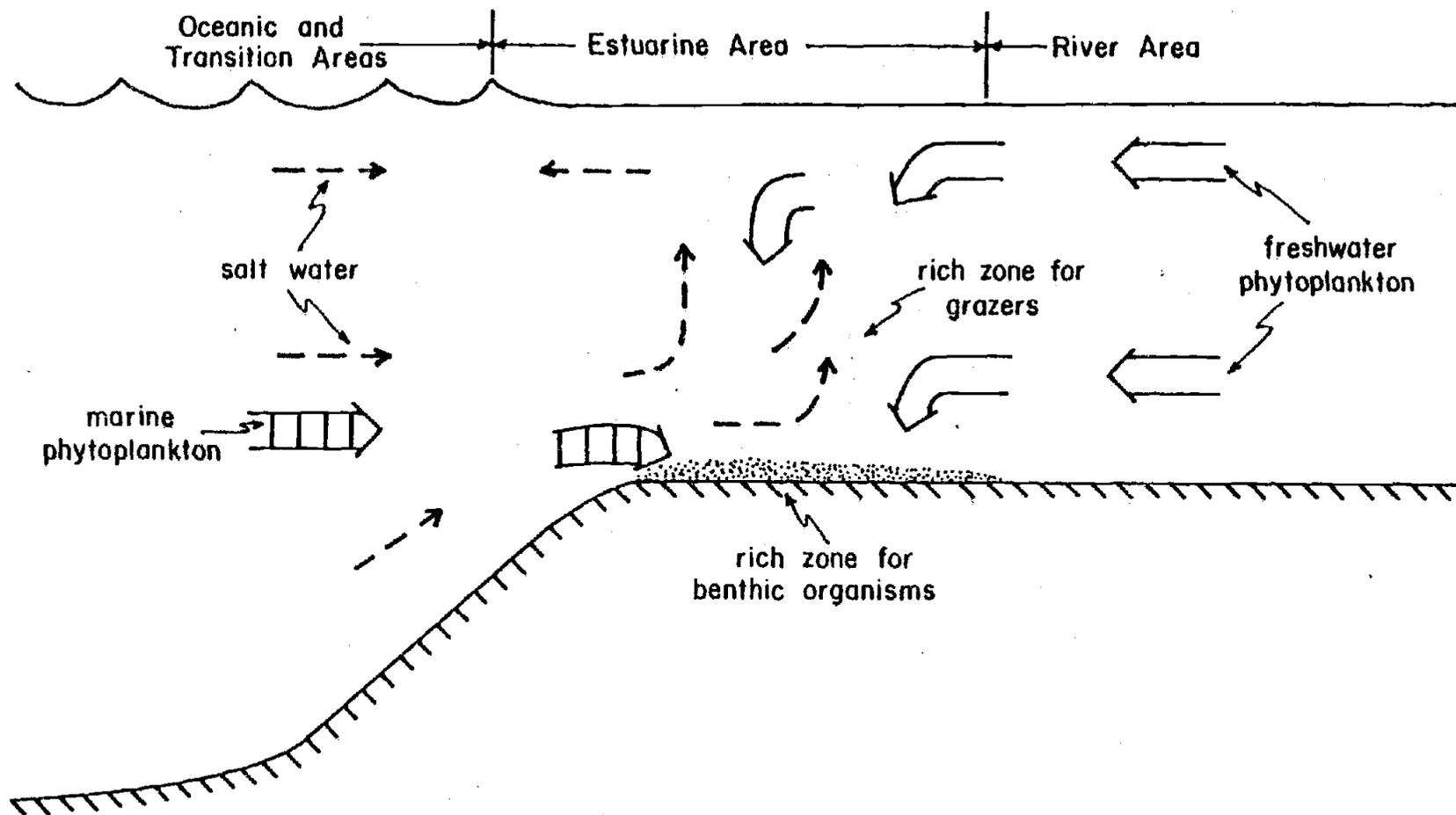


Figure 45. Freshwater phytoplankton-salinity encounter conceptual model during low river discharge or flood tide.

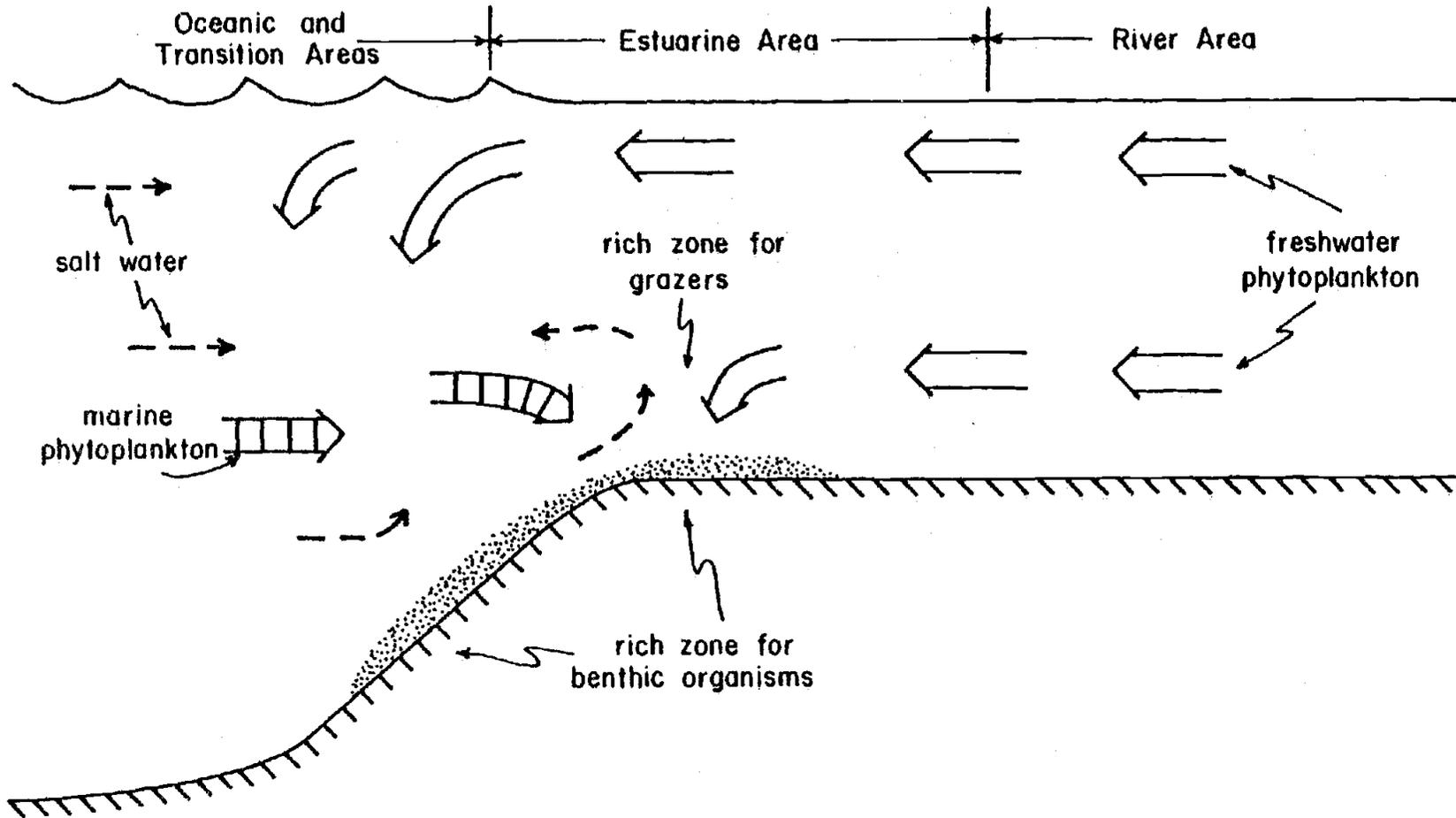


Figure 46. Freshwater phytoplankton-salinity encounter conceptual model during high river discharge or ebb tide.

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 (Figs. 45 and 46); 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 (Fig. 43). 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 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 can 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 allow retention in the zone of maximum food availability.

### 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 21).

Grazing removals from 0.06 (winter) to 1.2% day<sup>-1</sup> (spring-summer) of the available phytoplankton biomass were estimated for zooplankton in the Columbia River Estuary (Table 17). These removals were equivalent to approximately 1 (winter) to 5% day<sup>-1</sup> (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 to 7.4% day<sup>-1</sup> 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

Table 21. Reported filtering rates for representative zooplankton species in the Columbia River Estuary.

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

<sup>1</sup> dominant species were: Eurytemora affinis, Diaptomus (several species), and Canuella canadensis.

<sup>2</sup> cited in Jorgensen, 1966.

<sup>3</sup> dominant species were: Daphnia longispina, and D. pulex.

<sup>4</sup> cited in Burns and Rigler, 1967.

2 to 9% of the phytoplankton net productivity. Riley (1959) estimated that grazing removal accounted for only 4 to 6% day<sup>-1</sup> of the phytoplankton population available in Block Island Sound and Long Island Sound, and he invoked physical dispersal to the offshore water 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 of phytoplankton by 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 widely divergent 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; Rayment, 1980). Up to 90% particle removal via grazing is not uncommon.

#### 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 (Figs. 38 and 39). 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 (Fig. 43). 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 (see later); 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 reservoir, 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 of water in the estuary; 2) the lack of salinity (or other) effects on the mainly non-living particles; 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; and 4) continual resuspension of near-bottom particles in the channel, to help offset sinking losses in the shallows. 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  $25 \text{ g m}^{-3}$  for channel stations and  $33 \text{ g m}^{-3}$  for shallow stations was obtained for the Columbia. These concentrations are in line with previously reported TSP concentrations for the river; that is,  $30 \text{ g m}^{-3}$  (Weyl, 1970),  $8\text{-}40 \text{ g m}^{-3}$  (Conomos and Gross, 1972), and  $56 \text{ g m}^{-3}$  (Holland, 1978). In contrast, the Mississippi River averages  $510 \text{ g m}^{-3}$ , while the average TSP concentration for all U.S. rivers is about  $530 \text{ g m}^{-3}$  (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  $20 \times 10^6$  tons of TSP in 1980-81, or about  $5 \times 10^6$  tons without the volcanic input. Previously reported values were  $10 \times 10^6$  tons of TSP for 1952 (Judson and Ritter, 1964), and an average of  $10 \times 10^6 \text{ tons yr}^{-1}$  for the period 1963 to 1970 (Jay and Good, 1978).

The reason that the Columbia River, as the source of fresh water to the estuary, supports a relatively high phytoplankton biomass, remains unclear. The relatively low TSP concentrations, which would

allow light to penetrate deeper into the river water, may be one factor. 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 accelerates the settling of non-living suspended particles, thereby allowing greater light penetration for photosynthesis. Also, retardation of flow allows longer cell residence times in the euphotic zone (Wright, 1958; Hynes, 1970). The phytoplankton blooms in reservoirs behind dams thus can become the source for enhanced primary biomass levels in the estuaries downstream.

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 upper Columbia River, so no direct comparisons between the upper Columbia and the Columbia estuary can be made.

A Model: Sources and Fates of Particulate Organic Carbon

With all 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". I 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 about the mean was considered too great for practical use of the mean, however. The variation was caused by the large and variable amounts of non-phytoplanktonic carbon in the TPOC measurements. 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 Takahashi, 1973; Poulet, 1976; Chervin, 1978; Rayment, 1980). To have a reliable phytoplankton carbon-to-chlorophyll a ratio, then, a reasonable estimate of the PPOC fraction is required. I estimated the PPOC fraction in the Columbia estuary from the specific production relationship:

$$k = \frac{PP}{PPOC} \quad \text{or} \quad PPOC = \frac{PP}{k} ,$$

where:  $k$  = specific production rate or growth rate ( $\text{day}^{-1}$ ),

$PP$  = phytoplankton primary production ( $\text{mgC m}^{-3} \text{ day}^{-1}$ ),

$PPOC$  = phytoplanktonic particulate organic carbon ( $\text{mgC m}^{-3}$ ).

By using the measured phytoplankton production (from  $^{14}\text{C}$  studies) and a reasonable range of  $k$  values equivalent to  $<1$  to  $>1$  cell doubling per day, PPOC values were generated. However, when values equivalent to less than one doubling  $\text{day}^{-1}$  were used, generally the PPOC fraction dominated TPOC, which was unrealistic. Based on microscopic observation during cell counts, the detrital fraction (DPOC) was always the dominant fraction; therefore,  $k$  values equivalent to less than one doubling per day were not considered appropriate. On evaluating specific growth rate values from the literature for common phytoplankton species found in the Columbia River Estuary (Table 22), I decided that a specific growth rate value of  $k = 0.69$  (one doubling  $\text{day}^{-1}$ ) would be more representative for the estuary than values lower or greater than one doubling  $\text{day}^{-1}$ . The values in Table 22 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 (Fig. 27b); hence, a doubling rate somewhat less than the mean of the values in Table 22 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 yearly 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.

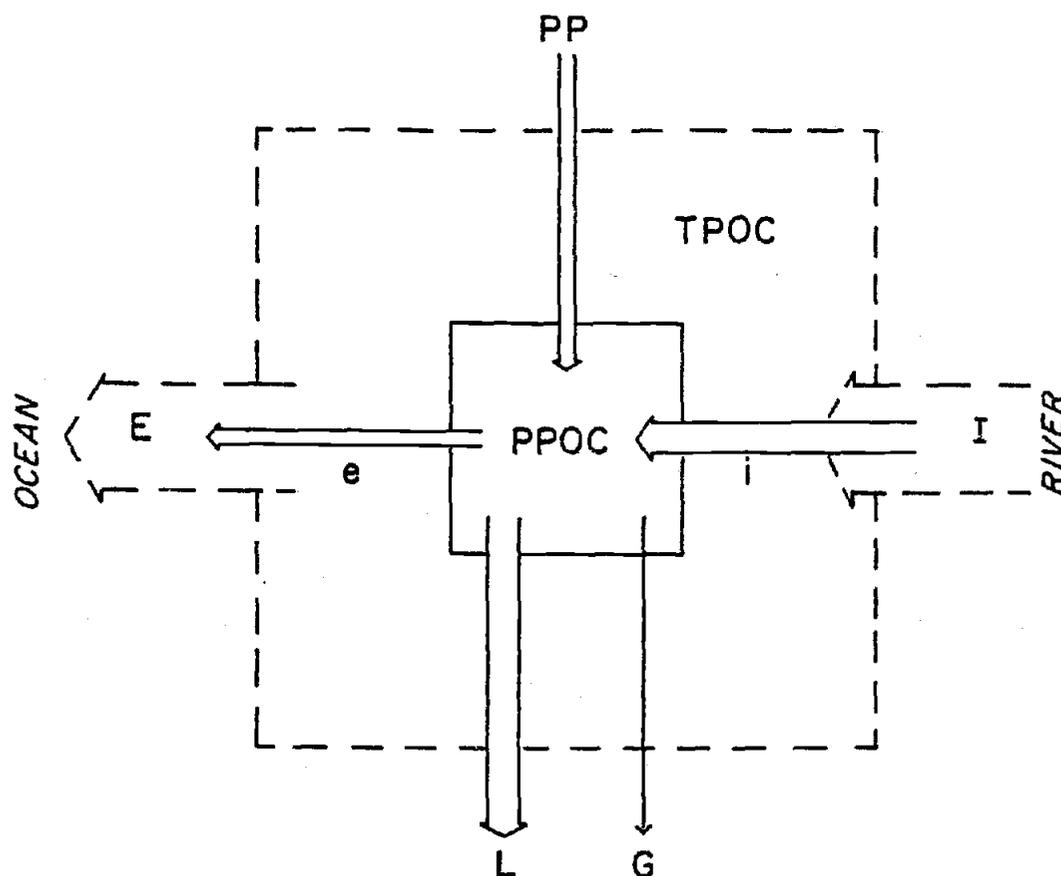
Table 22. Specific growth rates ( $k$  and doublings day<sup>-1</sup>) at light saturation for some freshwater species<sup>1</sup>.  $k = 0.69$  doublings day<sup>-1</sup>.

Species	doublings day <sup>-1</sup>	$k$	References
<u>Asterionella formosa</u>	1.9	1.3	Talling (1955)
<u>Stephanodiscus hantzschii</u>	1.7	1.2	Swale (1963)
<u>Cyclotella glomerata</u>	0.8 - 1.9	0.55 - 1.3	Peterson <u>et al.</u> (1974)
<u>Cyclotella compta</u>	0.1 - 0.8	0.07 - 0.55	"
<u>Scenedesmus</u> sp.	0.5 - 1.1	0.34 - 0.75	"
<u>Synedra</u> sp.	1.0 - 1.9	0.7 - 1.3	"

<sup>1</sup>All these species exist in the Columbia River Estuary. In some seasons A. formosa and S. hantzschii may be the dominant species.

Rough calculations of the detrital carbon fraction (DPOC), using the relationship  $DPOC = TPOC - PPOC$ , showed that 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 Fig. 47. 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, I 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. The sinking term then mainly represents the amount of phytoplankton carbon lost from the water column due to salinity effects previously discussed. Carbon losses due to phytoplankton respiration in the euphotic zone were not evaluated because it was assumed that phytoplankton 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 Fig. 47; thus, L might not solely represent sinking of phytoplanktonic carbon.



TPOC = total particulate organic carbon

I = import of TPOC

PPOC = phytoplankton particulate organic carbon

i = import of PPOC

PP = phytoplankton primary productivity

E = export of TPOC

G = zooplankton grazing

e = export of PPOC

L = sinking (and other) loss

Figure 47. 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.

A series of model evaluations were generated for each cruise (Figs. 48, 49 and 50), and finally a yearly particulate organic carbon budget for the total estuary was estimated (Fig. 51). 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 estuary is obviously 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 (Figs. 48, 49 and 50). 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 at night and below the euphotic zone). 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 not significant throughout the year (Figs. 48, 49 and 50). On the input side, import of PPOC always exceeded in situ primary production, although the two inputs were about equal in the summer months when river flow was low (Fig. 49).

On a yearly basis (Fig. 51) 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

Figure 48. Daily particulate organic carbon budgets for April and May. Bold-face numbers in the boxes are concentrations in metric tons of carbon. Concentrations in  $\text{mgC m}^{-3}$  are given in parentheses in the boxes. Arrows represent inputs-outputs in metric tons  $\text{day}^{-1}$  (bold-face numbers). In parentheses are given concentrations for transport rates in  $\text{mgC m}^{-3}$ ; phytoplankton production rates in  $\text{mgC m}^{-2} \text{day}^{-1}$ ; and zooplankton grazing rates in  $\text{mgC m}^{-3} \text{day}^{-1}$ . 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.

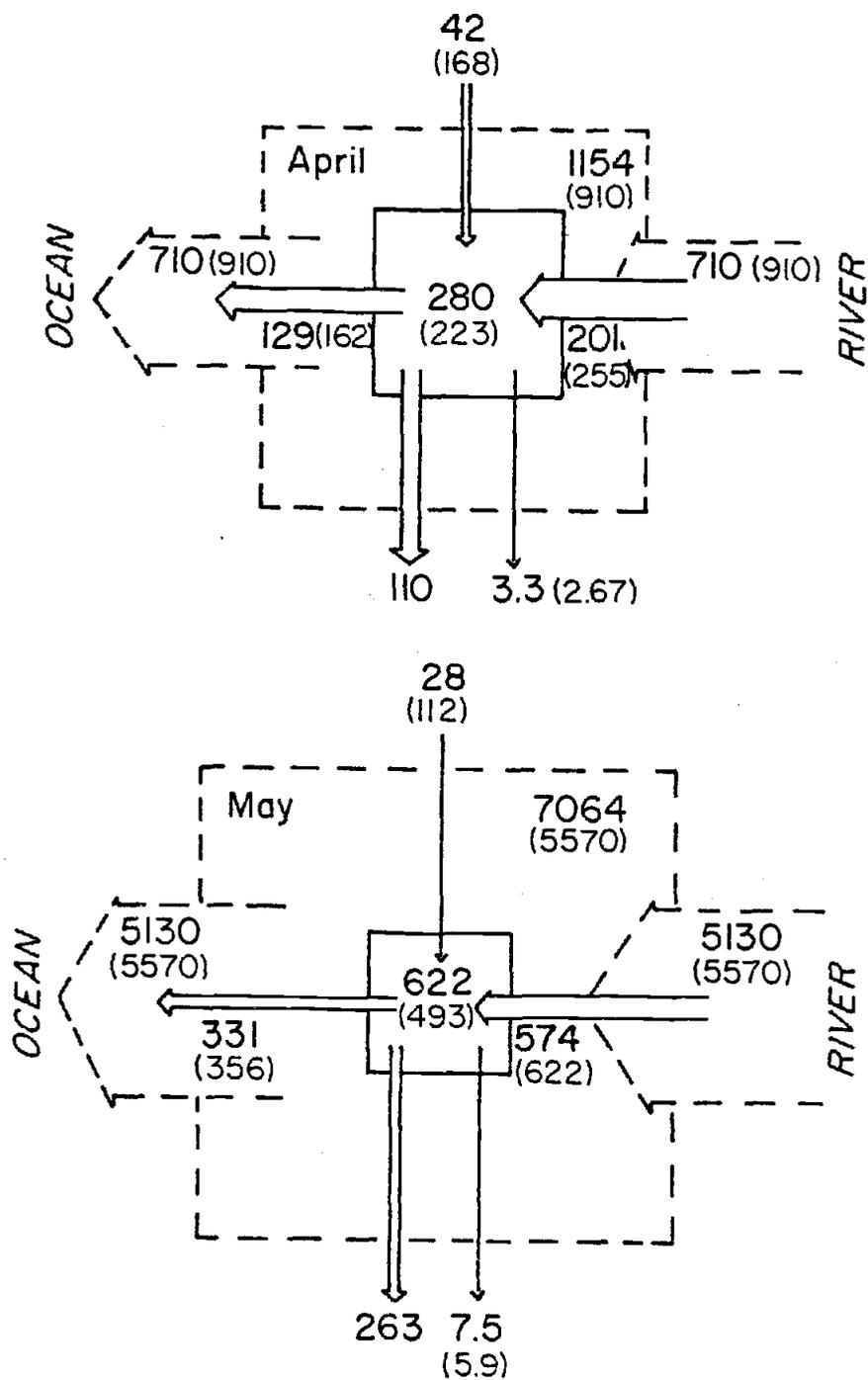


Figure 48

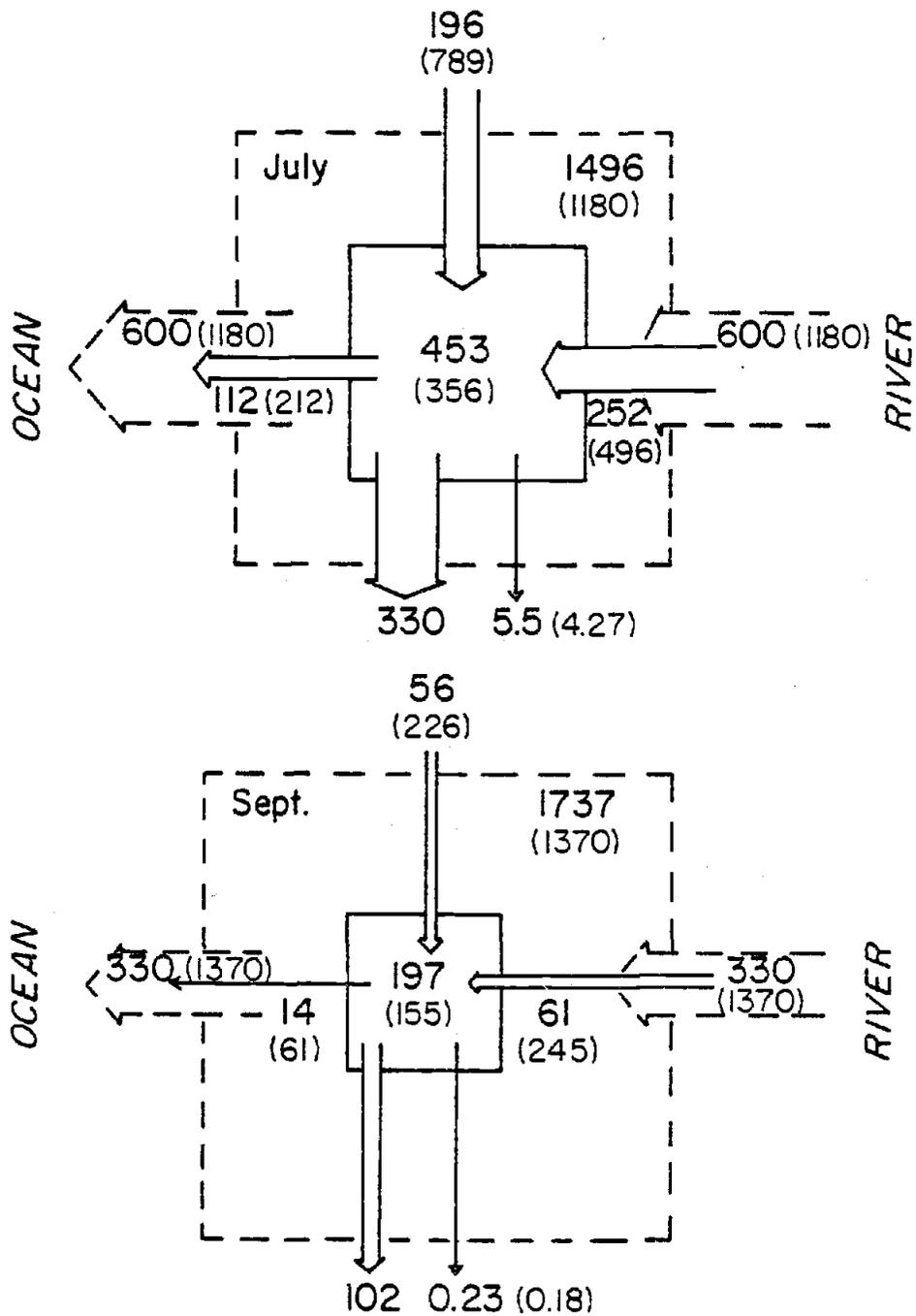


Figure 49. Daily particulate organic carbon budgets for July and September. For legend details see figures 47 and 48.

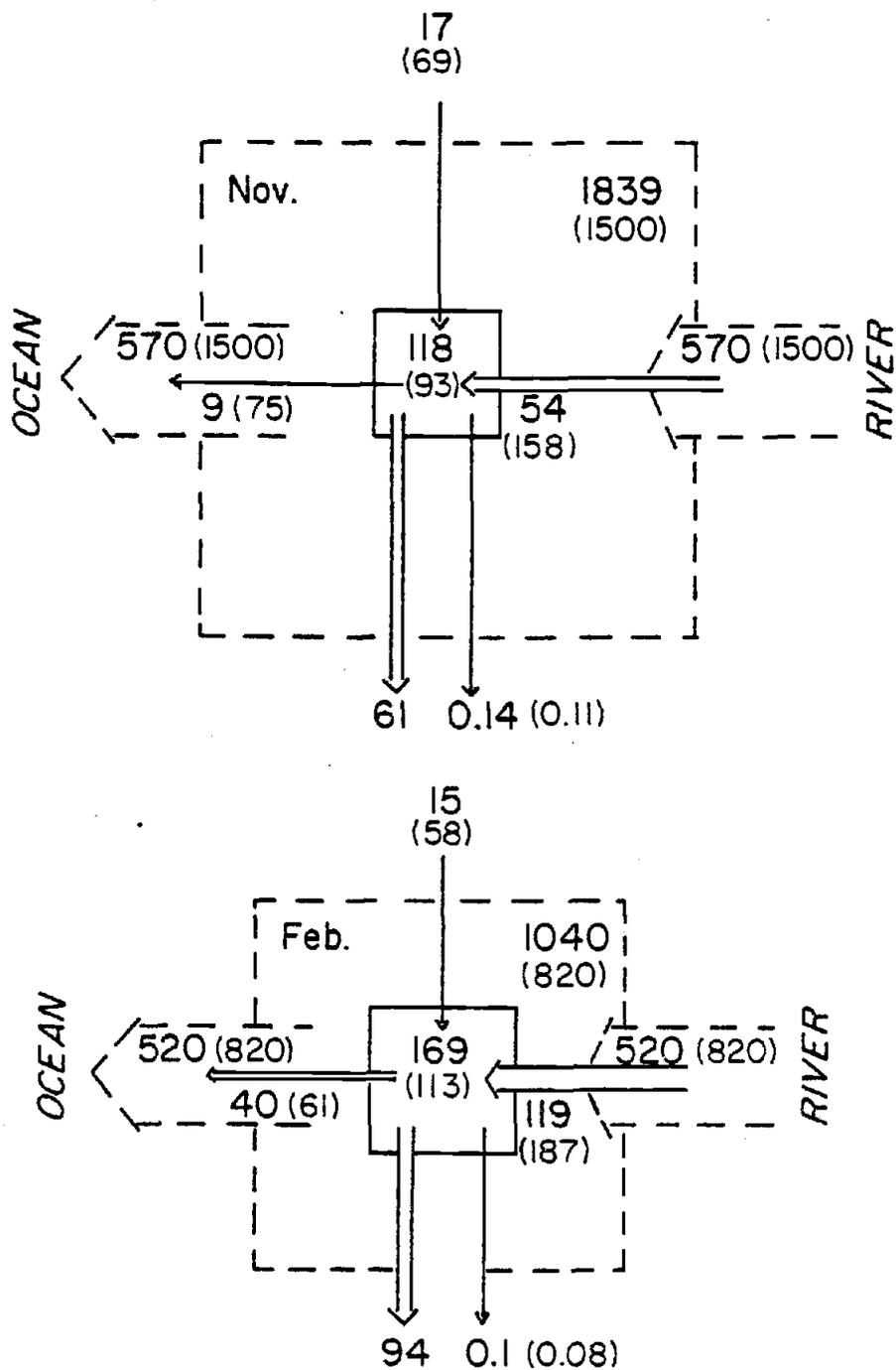


Figure 50. Daily particulate organic carbon budgets for November and February. For legend details see figures 47 and 48.

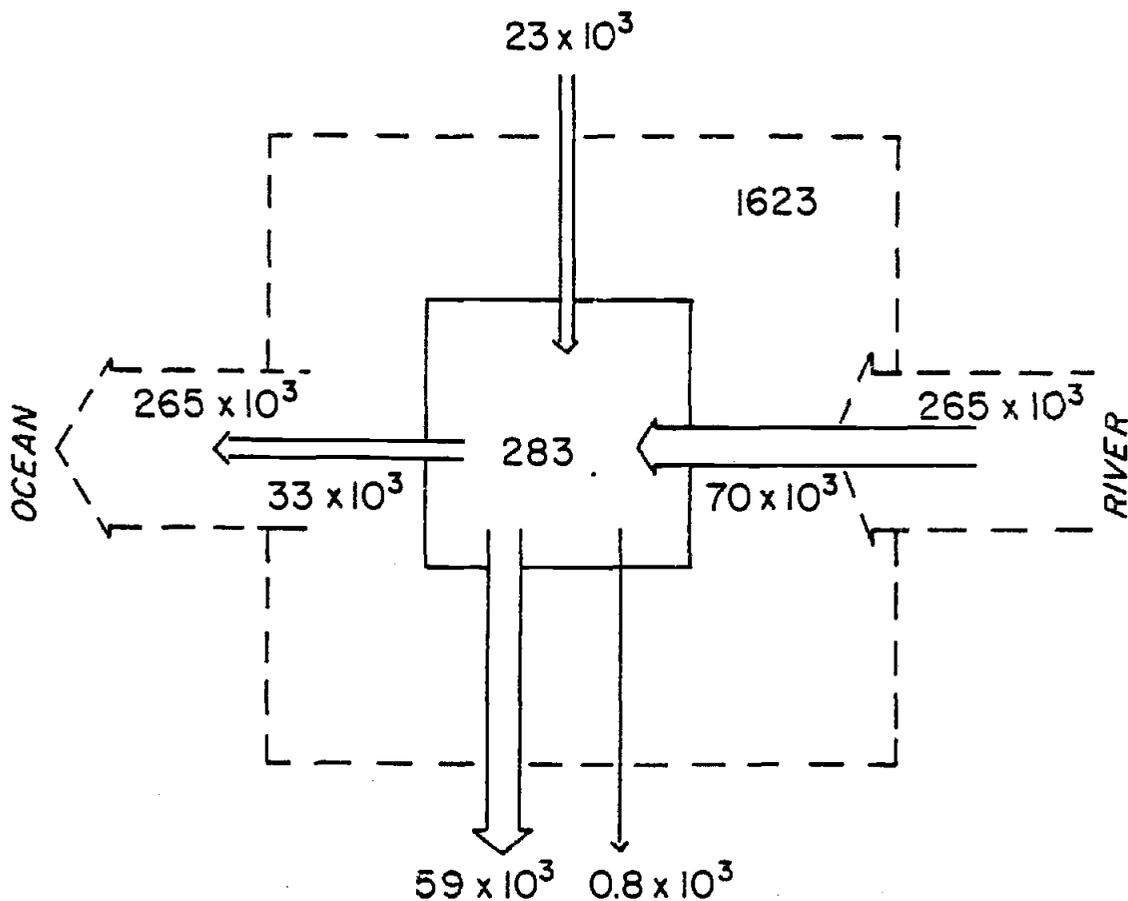


Figure 51. Yearly particulate organic carbon budgets for the Columbia River Estuary. Boxes represent the yearly average concentrations for total estuary in metric tons carbon. Arrows represent inputs-outputs in metric tons carbon  $\text{yr}^{-1}$ .

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.

## SUMMARY

The mechanisms that control the water column phytoplankton biomass were studied in the Columbia River Estuary throughout an annual cycle. Principle results and conclusions of the study are summarized below.

1. The Columbia River Estuary is a light-limited system, with daily solar radiation input, light attenuation in the water column, and the phytoplankton biomass itself (chlorophyll a) the variables that mainly explain temporal changes in primary productivity.

2. Inorganic 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; however, nutrient supply apparently exerts little control on water-column primary productivity in the estuary.

3. With the exception of the marine zone, there was homogeneous vertical distribution of all measured properties, throughout the seasons and along the estuary. In the marine zone, the physical and chemical properties, plus phytoplankton biomass-related parameters (chlorophyll a, fluorescence, etc.), were stratified horizontally as a result of ocean water intrusion at depth.

4. The concentrations of chlorophyll a and freshwater diatom species decreased from the freshwater zone to the marine zone, with the greatest rate of decrease usually occurring in the mixing zone. A "freshwater phytoplankton-salinity encounter hypothesis" explained the decrease best. As freshwater phytoplankton species encounter saline waters, the change in osmotic pressure causes cell disruption,

so that the cells disappear rapidly from the water column, probably by sinking to the bottom.

5. A conceptual model of the freshwater phytoplankton-salinity encounter process is presented for the Columbia River Estuary. The significance of this process is the creation of an area of sedimentation of huge quantities of fresh-water phytoplankton cells, which act as a food source for benthic organisms and water-column grazers. The Columbia River Estuary trapped about 63% of the yearly chlorophyll a received from the river and produced in situ. Spatial distributions and abundances of the main water-column grazers and epibenthic organisms in the estuary closely support the model.

6. It is also suggested that, depending on the water residence time and the capacity of the estuary to support phytoplankton, estuaries can be classified into two main types: 1) estuaries with marine-dominant phytoplankton communities, which include the classical estuaries; and 2) estuaries with freshwater-dominant phytoplankton communities. The latter type, which includes the Columbia River Estuary, apparently is the least common type. A characteristic of Type 2 estuaries is that the two source waters to the estuary (river and ocean) are more productive than the estuary itself. Phytoplankton production in the Columbia River was  $121-140 \text{ gC m}^{-2} \text{ yr}^{-1}$ , while in the estuary proper production was  $68-84 \text{ gC m}^{-2} \text{ yr}^{-1}$ . In classical estuarine systems (Type 1) the estuary generally supports higher phytoplankton biomass and production than the source waters. Classical estuaries were always more productive than the Columbia River Estuary.

7. Preserved phytoplankton species in the Columbia estuary were largely freshwater diatoms. Nanoplankton (cells  $<33 \mu\text{m}$ , and usually  $<10 \mu\text{m}$  cells) predominated over netplankton (cells  $>33 \mu\text{m}$ ) in the estuary.

8. Zooplankton grazing removal varied from  $0.06\% \text{ day}^{-1}$  (winter) to  $1.2\% \text{ day}^{-1}$  (spring-summer) of the phytoplankton biomass available, and approximately  $1\% \text{ day}^{-1}$  (winter) to  $5\% \text{ day}^{-1}$  (spring-summer) of the phytoplankton production. Grazing loss of this low magnitude was in agreement with previously reported zooplankton removal for other estuarine and shallow coastal waters.

9. 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. 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 oceans.

10. A process model was constructed and evaluated for the Columbia River Estuary. A main feature was 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 estuary was obviously the input from the main stem of the Columbia River. The sizes of the total particulate organic carbon (TPOC) standing stocks and fluxes overwhelmed those of phytoplanktonic particulate organic carbon (PPOC), indicating the large effect of non-living organic particles (detritus) on the TPOC budget. Outputs of living carbon via sinking (and/or

other loss routes) processes were very significant to the PPOC budget throughout the year. From July through February over 70% of the total loss of PPOC was accounted for by in situ sinking. 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 not significant throughout the year. On the input side, import of PPOC from upstream always exceeded in situ primary production, although the two inputs were about equal in the summer months when river flow was low.

11. On a yearly basis the water column budgets for the estuary were as follows. Of the total particulate organic carbon in the estuary, about 75% was detrital carbon and 25% was live carbon. Of the live fraction, 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.

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