Pacific Science (1990), vol. 44, no. 1: 17–37

Primary Production in the Columbia River Estuary I. Spatial and Temporal Variability of Properties[1]

J. Rubén Lara-Lara,[2] Bruce E. Frey,[3,4] and Lawrence F. Small[3]

ABSTRACT: Light, major nutrients, water temperature, turbidity and its organic and inorganic fractions, chlorophyll, phaeophytin, DCMU [3-(3,4-dichlorophenyl)-1, 1 dimethyl urea]-enhanced fluorescence (DCMU ratio), particulate organic carbon (POC), particulate organic nitrogen (PON), and primary production were measured from April 1980 through April 1981 in a 65-km stretch of the Columbia River estuary. Daily solar input, light attenuation in the water, and chlorophyll concentration accounted for 75% of the variability of daily primary production in the main estuarine axis and 85% in the shallows. The rapid appearance of a turbidity load created by the Mt. Saint Helens volcanic eruption in May 1980 and the subsequent clearing of the water as the load moved out of the estuary became a natural experiment to show that light availability was indeed the limiting factor to phytoplankton production in the estuary. Spatial variability in chlorophyll concentration was caused mainly by large summer reductions at the location where freshwater cells were lysed on contact with low-salinity intrusions. Mean values for properties in the main axis generally were not significantly different from those in the shallows, suggesting that the main axis and shallows experience similar, rapid flushing times. Total primary production for the estuary was almost 30,000 metric tons C yr^{-1}, but areal production was only 100 g C m^{-2} yr^{-1}, which puts the Columbia system at the low end of North American estuaries. The low areal production was likely a result of light limitation, chlorophyll reduction at the low-salinity boundary, and a short residence time of water and viable cells in the estuary.

Of all the aquatic ecosystems, estuarine systems are perhaps the ones exhibiting the widest and most frequent physicochemical fluctuations and the ones to which phytoplankton (and other organisms) find it most difficult to adapt. Factors vary in response to tidal, diel, 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. The lower Columbia River is a coastal plain estuary, or drowned river valley, separating the states of Washington and Oregon in northwestern USA. The estuary was 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 coastal plain estuaries in the world. The Columbia River is the second longest river in North America, with the second largest volume of discharge in

[1] This study was supported by a grant from the Pacific Northwest River Basins Commission and the U.S. Water Resources Council, administered through the Columbia River Estuary Data Development Program (CREDDP) and Columbia River Estuary Study Taskforce (CREST). J. R. Lara-Lara had a scholarship from the National Council of Science and Technology in México. Manuscript accepted 12 May 1989.

[2] Centro de Investigación Científica y Educación Superior de Ensenada, Ave. Espinoza no. 843, Ensenada, B. C., México 22830.

[3] College of Oceanography, Oregon State University, Corvallis, Oregon 97331.

[4] Present address: Oregon Health Sciences University, Portland, Oregon 97201.

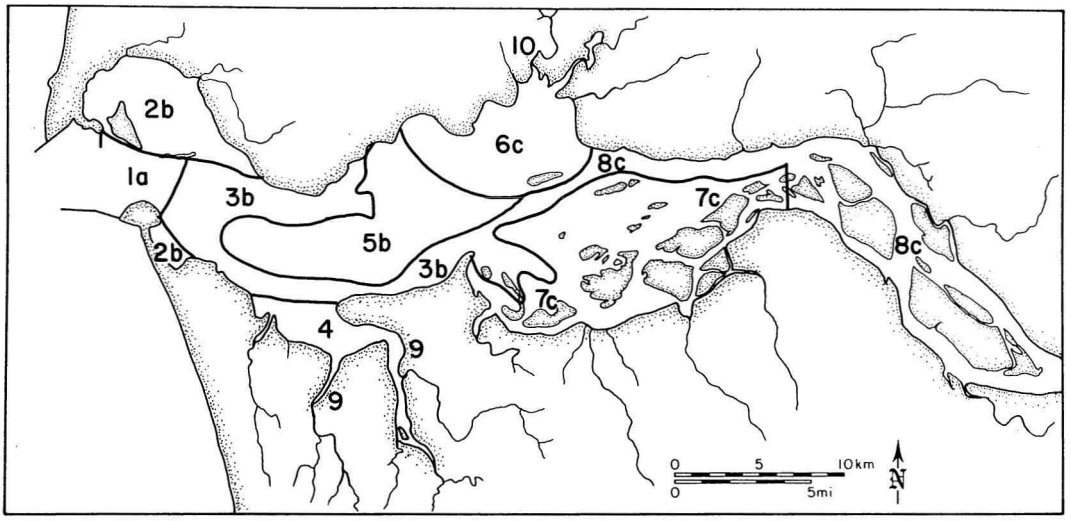

FIGURE 1. Map of the study area. Estuarine regions (numbers) are delineated by hydrographic and sedimentary properties. Zones (letters) are (a) marine zone, (b) estuarine mixing zone, and (c) freshwater, or tidal fluvial, zone.

the United States (annual discharge is about 2×10^{11} m^{-3}, or 58% that of the Mississippi River). The Columbia and its tributaries drain a region of ca. 660,500 m^2. River flow is now greatly regulated by dams, but still varies from about 3,000 to 12,000 m^3 sec^{-1}.

Williams and Scott (1962) and L. G. Williams (1964, 1972) reported the phytoplankton flora of the estuary. Haertel and Osterberg (1967) and Haertel et al. (1969) described some aspects of hydrography and plankton ecology for this system, and Park et al. (1969, 1972) discussed the estuarine nutrient budget. However, before our research there had been no reports on phytoplankton production for this ecosystem, and no attempts to understand the mechanisms that control the phytoplankton biomass in the estuary. Here we report the spatial and temporal distribution of phytoplankton biomass and primary production as well as the distributions of the physicochemical driving variables in the estuary throughout an annual cycle.

MATERIALS AND METHODS

The study area extended from the mouth of the estuary 56 km inland (Figure 1). Based mainly on river hydrology, circulatory processes, and sedimentary geology, Simenstad et al. (in press) sectioned the estuary into three principal zones and 10 different regions for purposes of analysis along the estuarine continuum and in the adjacent bays. For our phytoplankton studies, confined to the water column, we could not distinguish between regions 3 and 5 in the estuarine mixing zone, and therefore treated that area as combined region (3 + 5).

Nine cruises were conducted approximately every other month from April 1980 to July 1981. Stations in both shallows and main channels were sampled (Figure 2). With exception of the June and July 1981 cruises, when only three stations were sampled, the number of primary production experiments per cruise varied from 5 to 12. To study the spatial and temporal variability of temperature, selected inorganic nutrients, particulate chlorophyll *a* and phaeophytin *a*, particulate organic carbon and nitrogen, total suspended particle load, and the organic and inorganic fractions of the total suspended load, from 25 to 47 stations were sampled on each cruise. All stations were sampled at the surface, and at the deeper stations depths of 2.5, 5.0, and 10.0 m were sampled with Van Dorn bottles.

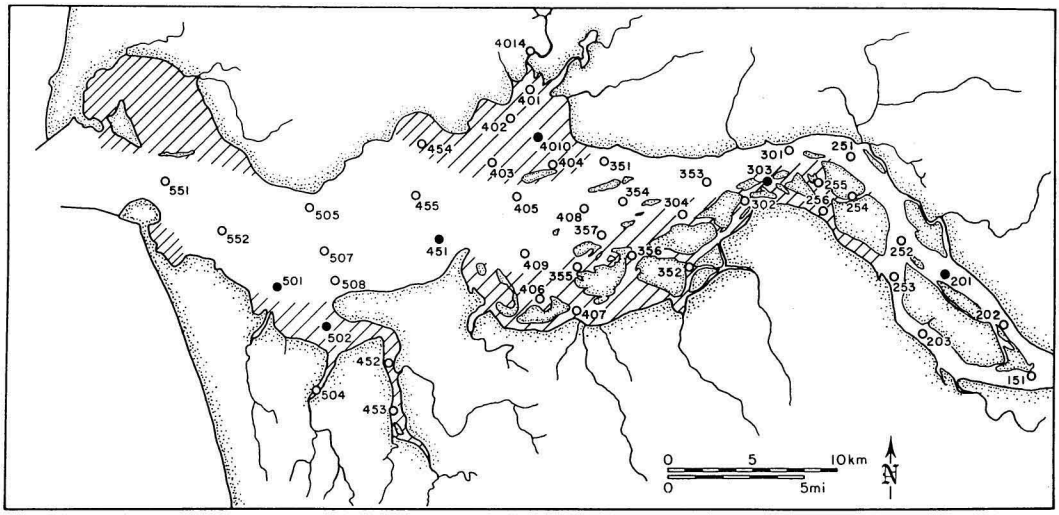

FIGURE 2. Sampling stations for the investigation of water column primary production. o = biomass measurements only; • = primary production and biomass measurements. The cross-hatched areas are those containing the shallow-water stations.

Primary production was assessed by the radiocarbon uptake method (Strickland and Parsons 1972). Because the shallow euphotic zone was always well mixed, samples were all collected from the surface. Once collected, the samples were labeled with carbon-14 and incubated in 80-ml clear polycarbonate bottles, with two replicates for each incubation. Incubations usually were done for 4 hr around local noon under natural sunlight in clear deck tanks. Surface water was circulated through the tanks to maintain temperature. Except for surface samples, light was attenuated with neutral screens to 50, 30, 15, 6, 1, and 0% of incident light. At the end of all incubations, the radiolabeled samples were immediately filtered through 0.8-μm-pore-size membrane filters, and the filters were preserved in Aquasol in individual liquid scintillation vials. No significant differences were found when we compared fumed (HCl) and unfumed carbon-14 samples. This was expected, because the estuarine phytoplankton was mainly diatoms and microflagellates (Amspoker and McIntire 1986). Radioactivity was analyzed in a Beckman Model 7500 liquid scintillation counter. Carbonate alkalinity, for conversion of radioactivity to carbon-based production, was computed from alkalinity measurements made by potentiometric titration with 0.1 N H_2SO_4, as described by Wetzel and Likens (1979).

Because phytoplankton was distributed homogeneously through the photic zone, and because the light intensity production rate relationship was unchanging over the experimental time (Lara-Lara 1982), conversion of primary production during the incubation period to daily integral production ($mg\,C\,m^{-2}\,d^{-1}$) was reasonably straightforward (Vollenweider 1971). Basically, a "surface rate curve" was determined from an equation describing the photosynthesis: depth curve (Vollenweider 1971) and a curve of daily photosynthetically active radiation (PAR). The ratio of the area under this surface rate curve to that fraction of the curve during which incubations were made was used to convert to $mg\,C\,m^{-2}\,d^{-1}$. Specification of the photosynthesis: depth curve and daily PAR curve required measurement of PAR at the estuary surface (I_0) and determination of the diffuse light extinction coefficient (k).

Daily PAR (295–695 nm) was measured by an Epply precision recording pyranometer mounted at a land-based location about 30 km up-estuary from the mouth. Light pen-

etration into the water column, for determination of k and the photic depth, was measured with a Licor submersible spherical quantum meter.

Chlorophyll *a* and phaeophytin *a* analyses, to determine the vertical distribution of autotrophic phytoplankton through the euphotic zone as well as spatial and seasonal distribution, were done by fluorometric measurement on acetone extracts of particles of 0.8-μm filters (Strickland and Parsons 1972). In addition, 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 between fluorescence after DCMU treatment and fluorescence before treatment was called the DCMU ratio, and this ratio was used as a rough measure of the photosynthetic capacity of the phytoplankton; that is, the greater the ratio, the greater the photosynthetic capacity (Samuelson and Oquist 1977, Vincent 1981). Samples were also taken for the determination of particulate organic carbon (POC) and nitrogen (PON) by Perkin-Elmer 240C elemental analyzer. Water temperatures were read from a thermometer submerged in a bucket filled with water from each collection depth. Salinities were measured to the nearest part per thousand with a Goldberg T/C refractometer. Detailed temperature and salinity data at selected times and locations were measured by Jay and Smith (in press), but seasonal patterns were only possible to elucidate with our own data. Inorganic nutrients (phosphate, silicate, and nitrate + nitrite) were analyzed using a Technicon Autoanalyzer, according to the techniques of Atlas et al. (1971). Total suspended particles (TSP), and the organic (OSP) and inorganic (ISP) fractions of the total, were determined by gravimetric analysis before and after peroxide oxidation (Peterson 1977).

RESULTS

Stations with water depths ≥ 10 m in regions 1, (3 + 5), 7, and 8, or with depths < 10 m but part of the main estuarine continuum from hydrographic and sedimentological data (Jay and Smith [in press]; Sherwood and Creager [in press]) were selected to represent distributions of properties along the main axis of the estuary, from near the mouth through the most riverine station at the head of the study area (Figure 2). Other stations were used to show distributions of properties in the major shallow bays (Youngs, Grays, and Cathlamet bays) and tributary rivers (Youngs, Lewis and Clark, and Deep rivers).

Properties along the Main Axis of the Estuary

Surface temperature (Figure 3, top) followed the solar irradiation cycle, as expected; thus, temperature increased from 9° to 15°C during spring (April–May), peaked in summer (at 22.5°C), decreased to 10°C by late fall, and reached its minimum in winter (5–6°C). Haertel et al. (1969) and Park et al. (1972) reported a similar cycle for the estuary. The extinction coefficient of light (k) in the estuary was a function of the turbidity of the water (Figure 3, bottom). On 18 May 1980 the volcanic eruption of Mt. Saint Helens caused the discharge of an exceptionally high load of sediment and detritus into the Columbia River above our estuarine study area. Extinction coefficients exceeded 6.0 m^{-1} on our sampling date a few days after the eruption and were still above 4.0 in mid-June (Figure 3, bottom). By July, however, k values were back into the range of pre-eruption values. Discounting the period affected by the volcano, k varied from ca. 0.8 to 3.5 throughout the year. Greatest light extinction occurred in the fluvial and mixing zones of the estuary in late summer and fall [regions 8, 7, and (3 + 5) in Figure 1], while greatest light penetration into the water column occurred generally in spring and near the estuary mouth. Extinction coefficients between 0.8 and 3.5 equate to photic depths (depths at which surface radiation is reduced to 1%) between 1.3 and 5.8 m. A large portion of the estuary had a photic depth of < 2.5 m over most of the year.

Dissolved phosphate (Figure 4, top) was generally higher in winter and early spring (0.8–1.0 μM) than in summer and early fall (0.3–0.8 μM). Nitrate plus nitrite (Figure 4, bottom) also registered maximum values in

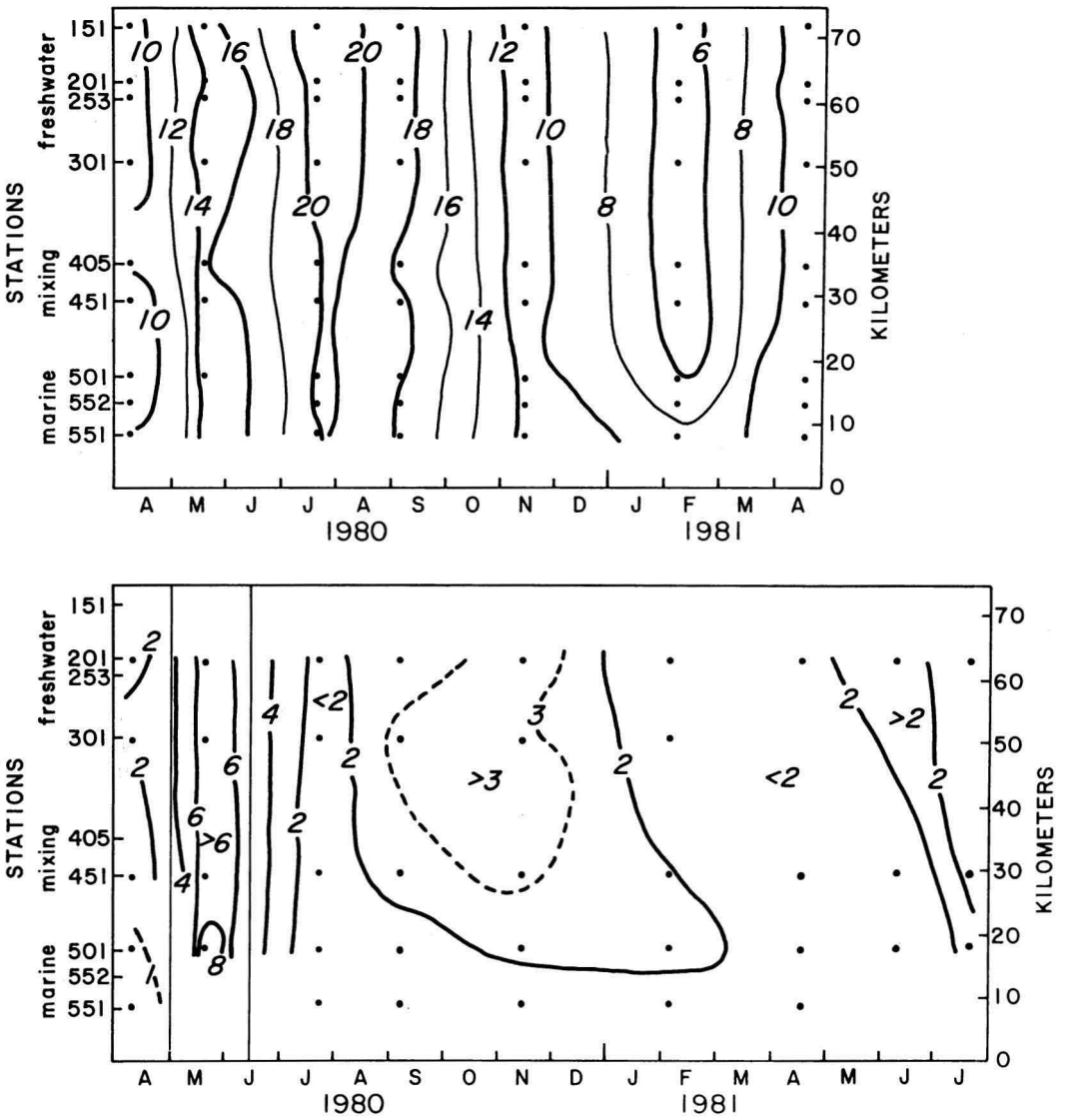

FIGURE 3. Spatial-temporal distributions of (top) surface temperature (°C), and (bottom) light extinction coefficient, k (m^{-1}). Dashed lines represent a change in contour interval, and thin lines represent a lower level of confidence in contouring due to a reduced number of stations. The vertical lines isolating May and part of June 1980 (bottom) delineate the time over which the volcanic eruption had significant effect.

winter and early spring (>20 μM), while minimum values during summer were <1.0 μM. No other nitrogenous nutrients besides nitrate and nitrite (ammonia, for example) were measured in the estuary, so we cannot say for sure that nitrogen was absent or nearly absent during summer. Silicic acid (Figure 5, top) varied from high values (160–200 μM) in winter and early spring to lower values (around 100 μM) in summer. Concentrations of silicic acid in fall and winter dropped abruptly near the estuary mouth because of intrusion of coastal oceanic waters, which contained much less silicic acid than river waters.

The distribution of total suspended particles (TSP) showed an abnormally high con-

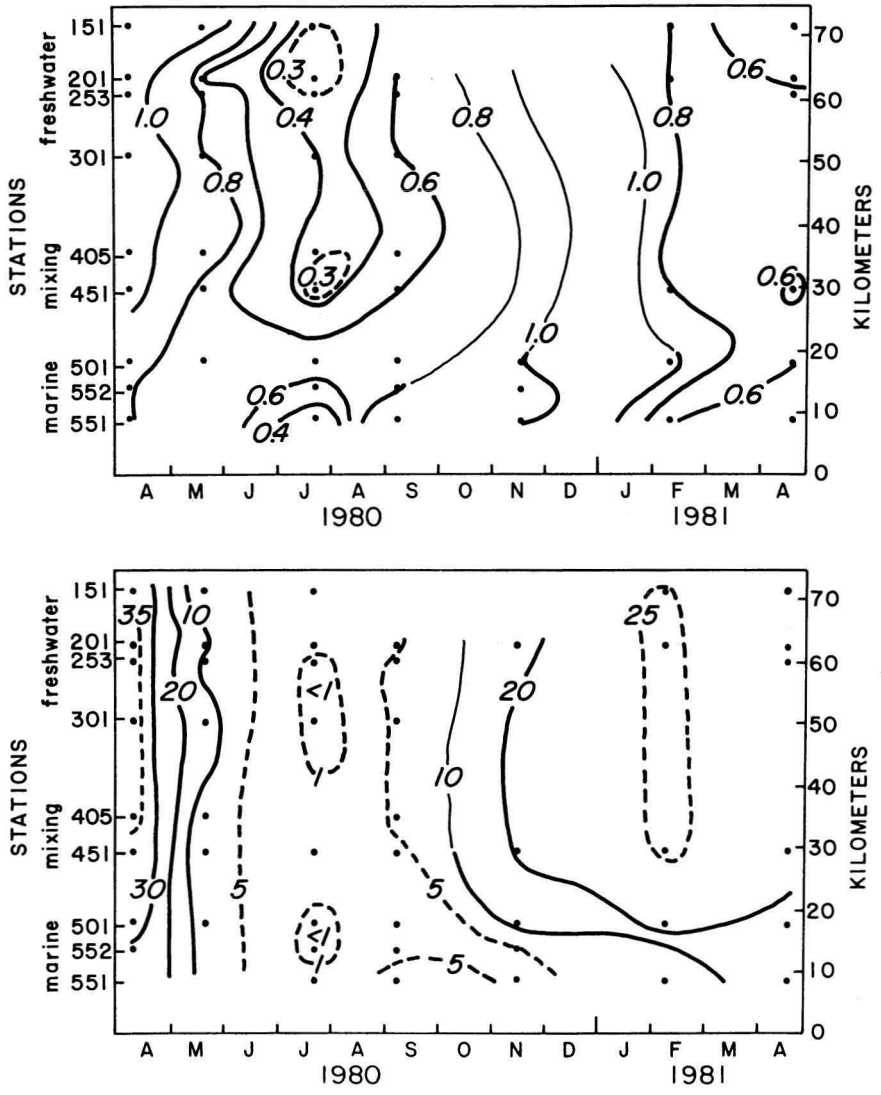

FIGURE 4. Spatial-temporal distributions of (top) surface-dissolved phosphate (μM), and (bottom) surface-dissolved nitrate (μM). Other comments as in Figure 3.

centration peak during May 1980 as a result of the Mt. Saint Helens eruption (Figure 5, bottom). Other than that, maximum loads were in late summer and fall (50–70 g m^{-3}), with minimum concentrations in midwinter and early spring (8–20 g m^{-3}). The inorganic (ISP) and organic (OSP) fractions of the TSP (not illustrated) mirrored very closely the pattern of total suspended particles. Maximum and minimum ranges for ISP were 45–70 and 7–15 g m^{-3}, respectively, while OSP maxima and minima were 4–8 and 1–3 g m^{-3}. Typical concentrations for particulate organic carbon and nitrogen were from 1.0 to 1.3 g m^{-3} for POC and from 0.1 to 0.2 g m^{-3} for PON (not illustrated). Slightly higher values were registered during midwinter and early spring.

The phytoplanktonic chlorophyll *a* concen-

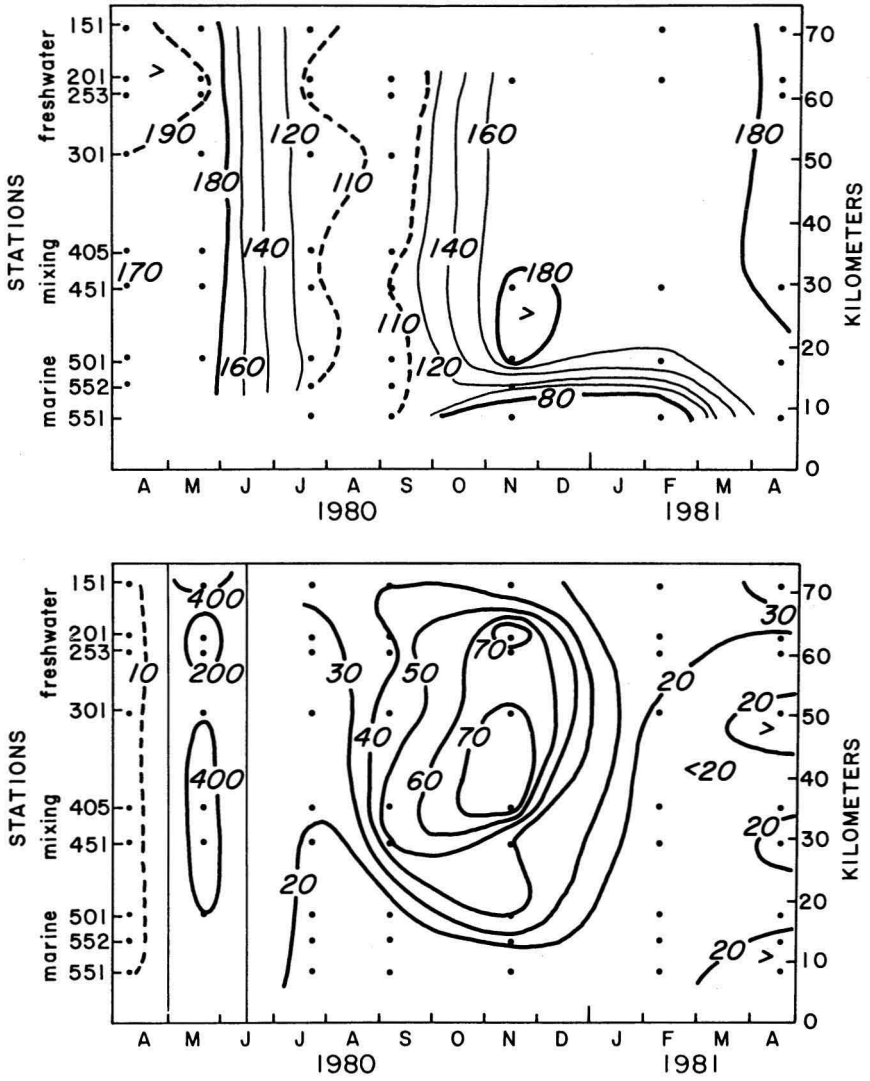

FIGURE 5. Spatial-temporal distributions of (top) surface silicic acid (μM), and (bottom) surface total suspended particles, TSP (g m^{-1}). Other comments as in Figure 3.

tration and the DCMU ratio varied both spatially and temporally (Figure 6, top and bottom). In a plot of mean chlorophyll *a* concentrations by sampling months and by regions for the main body of the estuary, the spatial and temporal variability became more evident (Figure 7). During fall and winter, for example, mean concentrations decreased rather uniformly from >5 mg m^{-3} in the fluvial stretch of the estuary to <2 mg m^{-3} in the entrance region. During spring and summer the mean concentrations usually showed a striking decrease at the interface between the tidal fluvial zone and the mixing zone. In July 1980, for example, concentrations fell from an average of 14.1 mg m^{-3} in the main-axis part of region 7 to 6.3 mg m^{-3} in the adjacent region (3 + 5) (Figure 7). Concentrations in

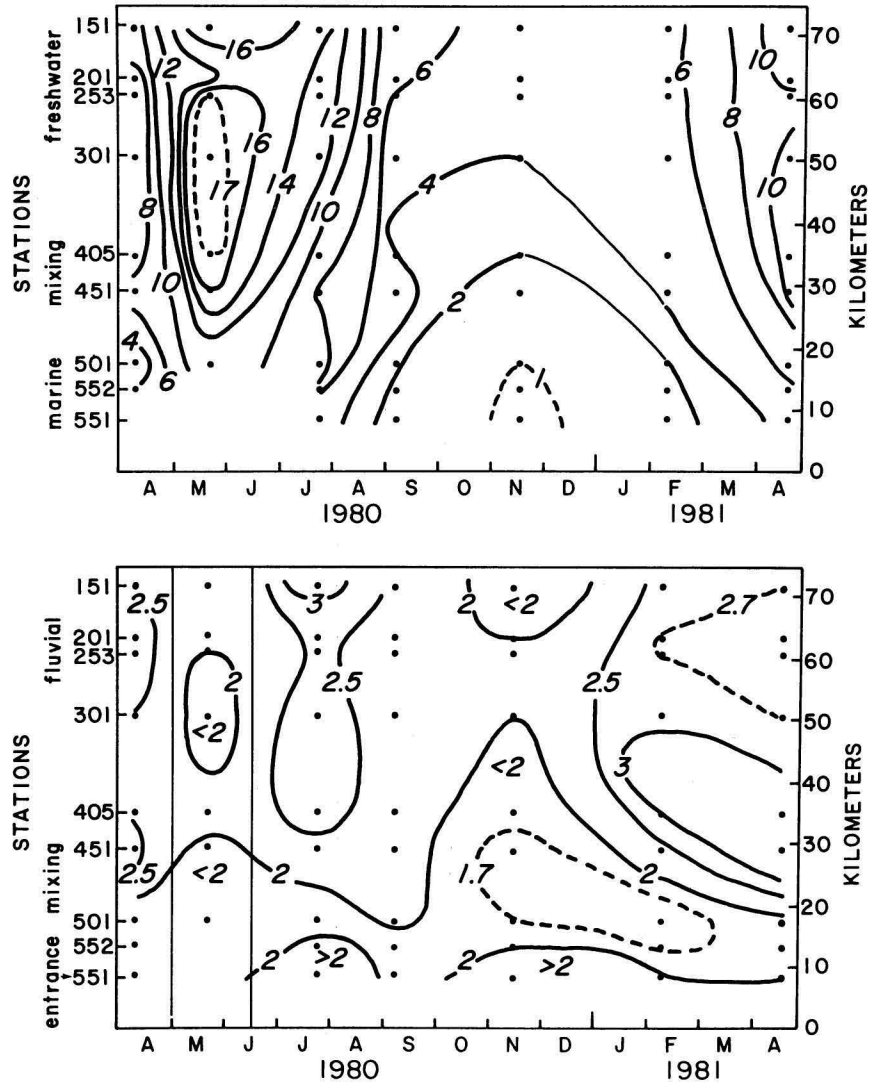

FIGURE 6. Spatial-temporal distributions of (top) surface chlorophyll *a* (mg m^{-3}), and (bottom) the ratio of DCMU-induced fluorescence to in vivo fluorescence. Other comments as in Figure 3.

region 8 always were similar to those in region 7 in spring and summer, while concentrations in region 1 were reasonably similar to those in region (3 + 5). Distributions in April 1980 were more winterlike, while distributions in April 1981 were closer to those found in summer, probably attesting to the spring months as being months of transition between winter and summer conditions. Likely the early fall months (September in Figure 7, for example) are also transition months. Even though the May 1980 chlorophyll *a* concentrations reflected the eruption of Mt. Saint Helens to some unknown extent, the distinct decline in chlorophyll *a* between regions 7 and (3 + 5) was still evident at this time. Phaeophytin *a* (not illustrated) showed maximum values in late summer (2.0–3.5 mg m^{-3}) and minimum concentrations during midwinter and early spring (0.0–0.7 mg m^{-3}).

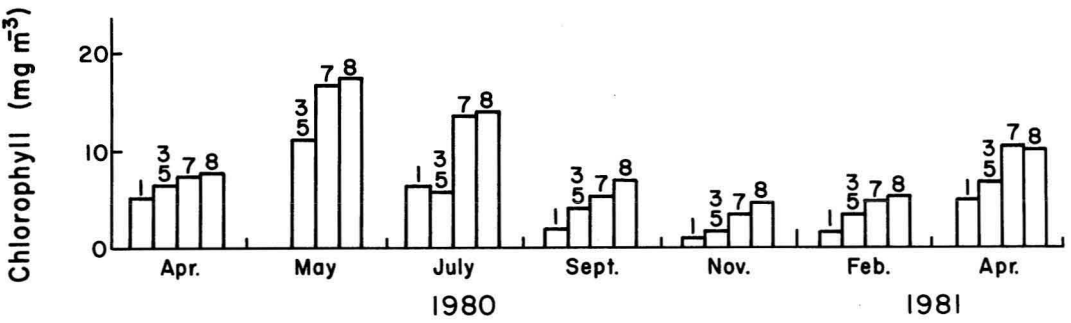

FIGURE 7. Mean chlorophyll *a* concentrations (mg m^{-3}) by sampling months and by regions (see Figure 1) along the main axis of the Columbia River estuary. May 1980 concentrations reflect the eruption of Mt. Saint Helens to some unknown extent. Regions 3 and 5 are combined because they were not differentiated during sampling for chlorophyll.

Like chlorophyll *a*, the DCMU ratio was significantly variable both temporally and spatially (Figure 6, bottom). With the exception of May 1980, when the volcanic eruption tended to decrease the DCMU ratio even in the fluvial regions of the estuary (Figure 6, bottom), the spring and summer months yielded enhanced ratios. In summer the highest ratios were in the fluvial stretch, while in spring the highest ratios often extended from the riverine areas through part of the mixing zone. The lowest ratios tended to occur in that part of the mixing zone adjacent to the entrance region, regardless of season. The entrance region itself often supported DCMU ratios >2.0 throughout the year.

Except for the entrance region and the western part of the mixing zone, vertical distributions of particles and most physicochemical properties along the main axis of the estuary were reasonably homogeneous. During periods of low river flow in the summer, temperature and salinity often showed distinct vertical inhomogeneity well into the tidal-fluvial zone (Jay and Smith [in press]). Vertical distributions of six properties to 10 m depth during flood tide in four different months are shown in Figure 8 for three stations in the entrance and south channel regions. The vertically stratified water column in July with respect to temperature and salinity is obvious, but in the other months the stratification is more nearly horizontal even at these near-ocean stations. During summer, marine coastal upwelled waters entered the estuary slightly enriched in nitrate plus nitrite (>3.0 μM) and phosphate (>1.0 μM) relative to riverine waters (which normally ranged below 1.0 μM of nitrate plus nitrite and 0.5 μM phosphate) (Figure 8). From late fall through early spring, riverine waters were highly enriched with respect to nitrate plus nitrite and to a modest amount with respect to phosphate. In contrast, silicic acid concentrations were always higher in the river waters than in marine waters (Figure 8). Marine waters showed maximum silicic acid concentrations during summer upwelling (close to 100 μM), when river waters showed their minimum (slightly greater than 100 μM). During fall and winter, river waters ranged from about 120 to >180 μM, while entering marine waters were generally <40 μM. Chlorophyll *a* concentrations were nearly always higher in river-derived waters than in marine waters in these regions of substantial mixing (Figure 8).

For purposes of estimating phytoplankton production over the entire estuary rather than just at the stations where carbon-14 measurements were made, empirical models based on the relationships between measured production rates and 10 ecological variables were developed separately for the shallow and deep stretches of the estuary. Step-wise multiple regression analysis (Rowe and Brenne 1981) was used to develop the relationships, with daily solar input, the light extinction coefficient, water temperature, chlorophyll *a*, phaeophytin *a*, nitrate plus nitrite, phosphate, silicate, total suspended seston load, and the

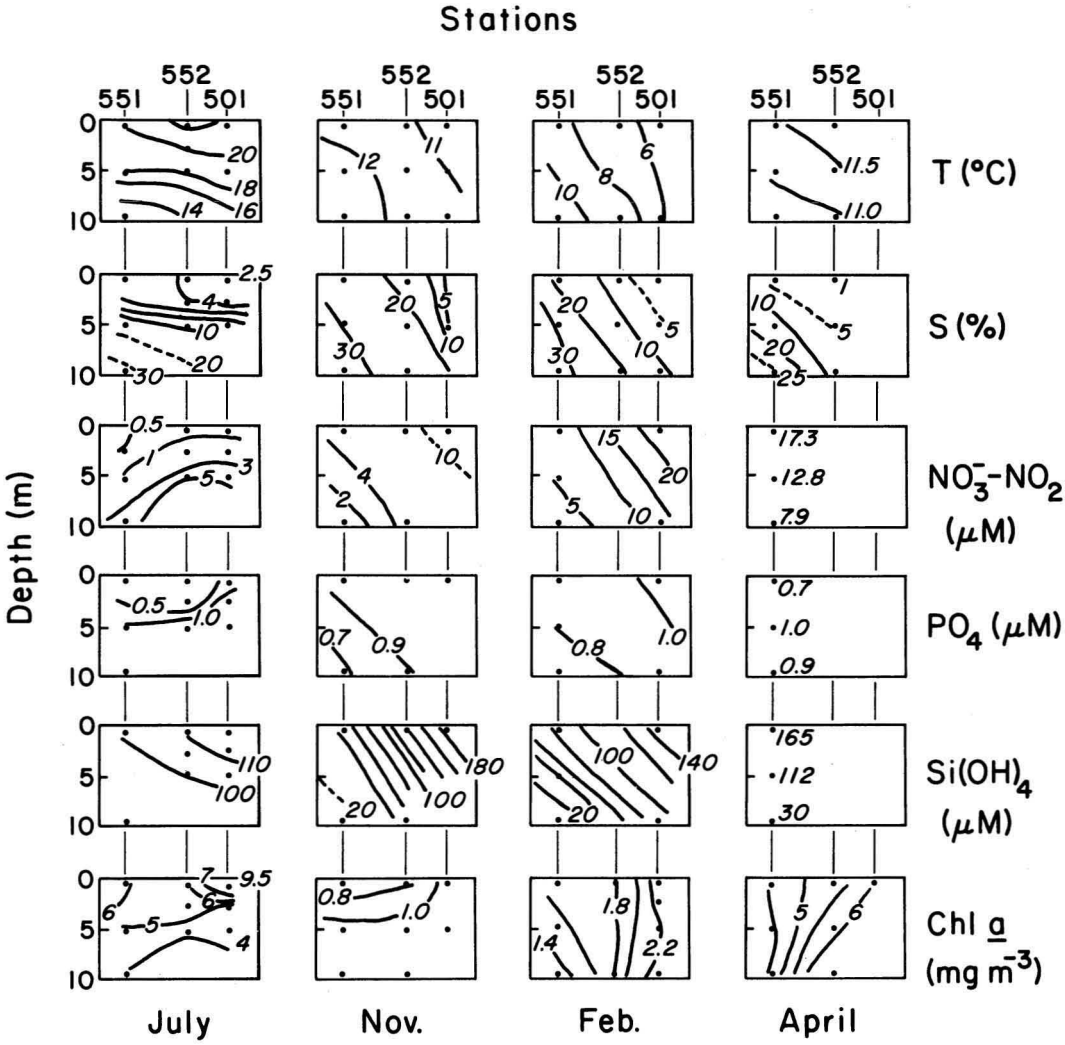

FIGURE 8. Vertical distributions of properties in the near ocean and lower estuarine mixing zones. All data were taken on flood tide.

organic portion of the total suspended seston being the variables examined. Five of the 10 variables cumulatively accounted for 90% of the variability in primary production in the main axis of the estuary (Table 1). Solar radiation input and the light extinction coefficient alone accounted for 75% of the variability. It must be emphasized that the model in Table 1 is specific to the Columbia River estuary and can predict primary production only within the ranges of the five key variables indicated in Table 1. The ranges are broad, however, and encompass the ranges characteristically found over the year in the estuary. More elegant theoretical models might extend the limits of prediction of primary production somewhat and will be examined in future work. Using both measured and calculated values, daily phytoplankton production showed strong seasonal variation (Figure 9), as expected from the annual patterns of solar radiation and chlorophyll (Figure 7). Unlike chlorophyll

TABLE 1

PRIMARY PRODUCTION REGRESSION MODEL FOR STATIONS IN THE MAIN AXIS OF THE COLUMBIA RIVER ESTUARY ($n = 29$)

ABBREV.	VARIABLE	CUMULATIVE R^2	MODEL
S	Daily solar radiation (g cal cm^{-2} day^{-1})	0.58	Log daily production = 1.548 + 0.001S − 0.103k + 0.56Chl$a$ + 0.28T − 0.001TSP
k	Light extinction coefficient (m^{-1})	0.75	
Chl$a$	Chlorophyll a (mg m^{-3})	0.84	
T	Temperature (°C)	0.87	
TSP	Total seston (g m^{-3})	0.90	

NOTE: Lower and upper ranges of values for the above variables:
S = 250–4,800
k = 1.06–9.29
Chl$a$ = 0.7–17.9
T = 5.1–21.3
TSP = 5.8–84.7

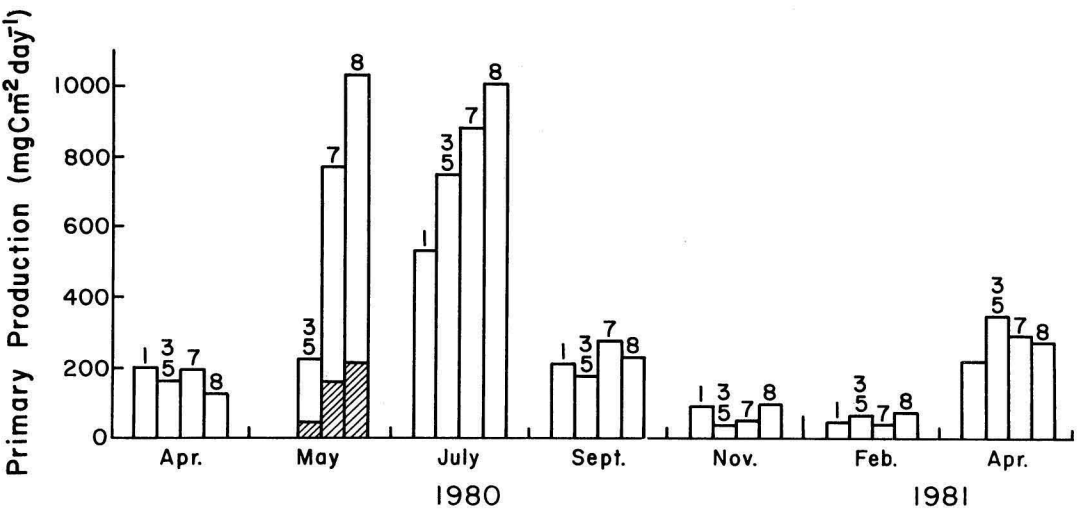

FIGURE 9. Mean daily phytoplankton production (mg C m^{-2} day^{-1}) by sampling months and by regions (see Figure 1) along the main axis of the Columbia River estuary. Actual rates in May 1980 (hatched bars) are reduced because of the Mt. Saint Helens eruption. Rates without the volcano effect (open plus hatched bars) have been computed and are also shown for May 1980. Numbers indicate the estuarine regions from Figure 1.

concentrations, however, primary production was greatly affected by the volcanic eruption. By reducing light penetration to a great extent in May 1980, volcanic debris in the estuary reduced primary production in all parts of the main estuarine axis by 75% (Frey et al. 1983). Correction of the measured May values was done by changing the light extinction coefficients in the model equation to values expected in the absence of the volcanic eruption. Recalculated estimates of May production rates were close to those for July in the riverine stretch of the estuary and more nearly representative of rates expected in spring (Figure 9). Large differences among the four regions along the estuary axis were observed only in May and July. The rather precipitous decreases in chlorophyll between regions 7 and (3 + 5)

during May and July (Figure 7) were in large part responsible for the decreases in production between the same two regions; however, close similarities in chlorophyll concentration between regions 8 and 7, and between regions (3 + 5) and 1 were not matched in the production data. Furthermore, no trends in the production data by region were noted in the other months (Figure 9). Such dissimilarities pointed up the fact that light mainly controlled production, with only moderate effect from chlorophyll concentration, on average (Table 1).

Selected vertical distributions of measured primary production for representative stations along the axis of the estuary are shown in Figure 10. The typical seasonal pattern was evident, with maximum hourly rates and deepest penetration of production in summer, to yield highest integral production at that time of year. Lowest integral production occurred in winter, the result of reduced solar input and a restricted euphotic zone, and reduced chlorophyll concentrations.

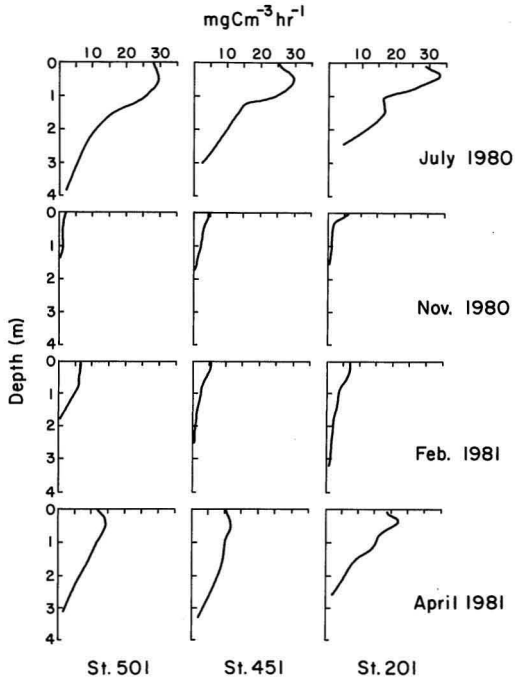

FIGURE 10. Typical primary productivity profiles near midday for three selected stations during four different seasons.

Properties in the Shallows and Bays

Temporal variability of properties in shallow areas showed the same seasonal trends as the comparable properties along the main axis (Figure 11).

Daily integral primary production in the shallows was adequately modeled using only daily radiation input, light extinction in the water column, and chlorophyll *a* concentration as variables (Table 2). The pattern of production developed from model-generated estimates plus measured rates, by region, showed strong seasonality as expected (Figure 12). What was not necessarily expected, however, was the lack of significant difference ($P > 0.05$) between mean daily production at the shallow stations and the main-axis stations (Table 3). The possibly longer residence times of cells in the shallower, more isolated reaches of the estuary, given sufficient nutrients and light throughout the shallow water columns, suggested that the shallows might have been more productive on an areal basis. Neither the mean chlorophyll *a* nor the light extinction coefficient by seasons were significantly different when stations in the main axis were compared with stations in the shallows (Table 3). The mean assimilation ratio was only significantly higher in the shallow regions during winter–spring 1980 (Table 3). The lack of significant differences between the means suggests that mean residence times of cells in the photic zones of both areas are similar.

Estuary-Wide Primary Production

The production data from Figures 9 and 12 (excluding the tributary rivers) can be integrated through one annual cycle after removing the effects of the volcanic eruption to yield annual areal production for each estuarine region (Table 4). The decrease in areal production from fluvial to entrance region down the main axis [regions 8, 7, (3 + 5), 1] is easily observed. The more isolated bays have the lowest areal production, although the lack of production data in the very shallow Baker and Trestle bays (region 2) makes the estimate there little more than speculation.

When the surface areas of each region in

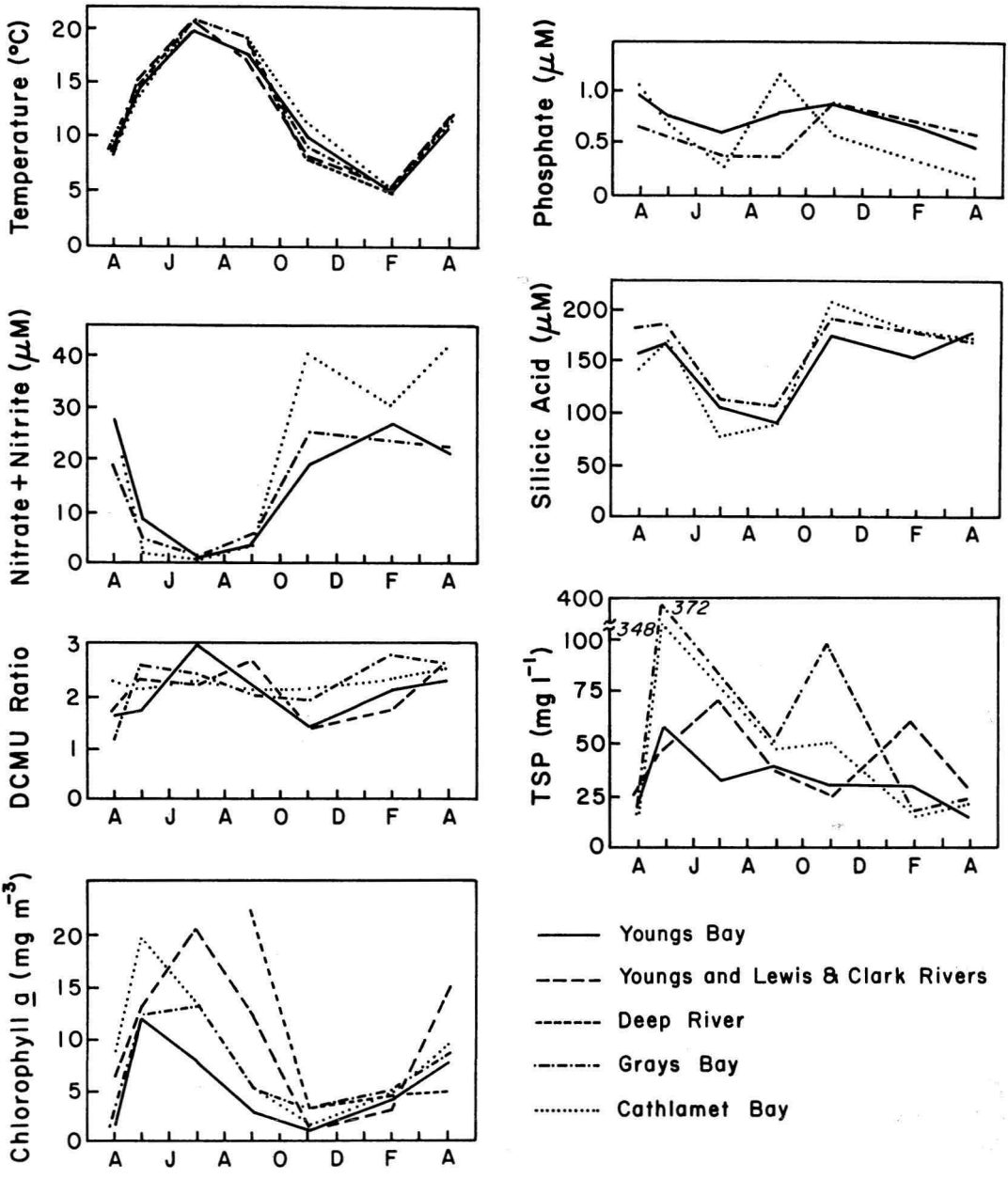

FIGURE 11. Temporal variability of properties in shallow areas (see Figure 2). Values are for surface samples, which reflect values through the shallow water columns in the different regions.

TABLE 2

PRIMARY PRODUCTION REGRESSION MODEL FOR SHALLOW STATIONS AND BAYS IN THE COLUMBIA RIVER ESTUARY (n = 28)

ABBREV.	VARIABLE	CUMULATIVE R^2	MODEL
S	Daily solar radiation (g cal cm^{-2} day^{-1})	0.73	Log daily production = 1.605 + 0.003S + 0.033Chl$a$ − 0.127k
k	Light extinction coefficient (m^{-1})	0.80	
Chl$a$	Chlorophyll a (mg m^{-3})	0.85	

NOTE: Lower and upper ranges of values for the above variables:
S = 250–4,800
k = 1.26–8.10
Chl$a$ = 0.8–24.0

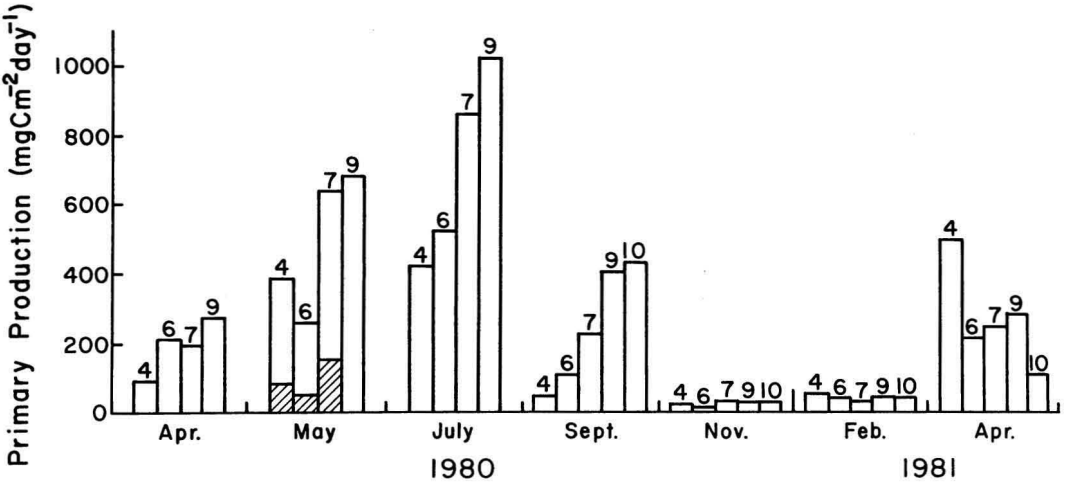

FIGURE 12. Mean daily phytoplankton production (mg C m^{-2} day^{-1}) by sampling months and regions in shallow-water bays and tributaries of the Columbia River estuary. Actual rates in May 1980 (hatched bars) are reduced in the bays because of the Mt. Saint Helens eruption, but the tributary rivers were not affected. Rates in the bays without the volcano effect (open plus hatched bars) have been computed and are also shown for May 1980. Numbers indicate the estuarine regions from Figure 1.

Figure 1 are computed and multiplied by the annual areal production rates for each region, estimates of total primary production are generated for each region (Table 4). We divided region 7 into a shallows area and a main-axis area (Figure 2) and computed surface areas and production rates separately for these two areas. Region (3 + 5), by virtue of its large area, had the greatest total annual phytoplankton production, approximately one-third of the total estuarine production of about 3 × 10^4 metric tons of carbon per year.

DISCUSSION

In general, light and the availability of nutrients are the environmental factors that regulate phytoplankton production in most marine and estuarine systems (Ryther and Dunstan 1971, MacIsaac and Dugdale 1972, R. B. Williams 1973, Ball and Arthur 1979, Sharp et al. 1982). Inorganic nutrient supply seems to exert little control on primary production in the Columbia River estuary, however. Although all measured nutrients de-

TABLE 3

COMPARISONS OF PROPERTIES FOR MAIN AXIS AND SHALLOW STATIONS IN THE COLUMBIA RIVER ESTUARY

VARIABLE	SEASON	MAIN AXIS MEAN ± SE	SHALLOWS MEAN ± SE	S ($P < 0.05$)
Primary productivity	Winter–spring 1980	216.8 (35.80)	257.7 (94.20)	ns
(mg C m^{-2} day^{-1})	Summer–fall 1980	396.4 (134.40)	472.3 (112.70)	ns
	Winter–spring 1981	200.3 (81.70)	212.0 (83.00)	ns
Chlorophyll *a*	Winter–spring 1980	10.3 (1.84)	8.0 (3.10)	ns
(mg m^{-3})	Summer–fall 1980	7.9 (1.40)	9.3 (1.70)	ns
	Winter–spring 1981	6.6 (1.00)	9.3 (3.70)	ns
Assimilation ratio	Winter–spring 1980	1.25 (0.17)	4.22 (1.18)	sig.
(mg C mg Chla^{-1} h^{-1})	Summer–fall 1980	3.40 (0.55)	2.78 (0.27)	ns
	Winter–spring 1981	1.71 (0.28)	1.40 (0.28)	ns
Light extinction	Winter–spring 1980	4.15 (1.31)	3.31 (1.01)	ns
coefficient *k*	Summer–fall 1980	2.08 (0.26)	2.46 (0.23)	ns
(m^{-1})	Winter–spring 1981	1.76 (0.17)	2.35 (0.33)	ns

NOTE: Means represent data from all cruises ± 1 SE.

TABLE 4

ANNUAL RATES OF NET AREAL AND TOTAL PHYTOPLANKTON PRODUCTION BY REGION

	REGION	AREAL PRODUCTION (g C m^{-2} yr^{-1})	TOTAL PRODUCTION (metric tons C yr^{-1})
1	Entrance region	80.3	2,493.3
2	Baker Bay and Trestle Bay	(72.1)	(1,192.6)
3 + 5	Estuarine channels and mid-estuary shoals	84.9	10,638.8
4	Youngs Bay	63.9	816.2
6	Grays Bay	66.3	2,323.5
7	Cathlamet Bay (shallows)	102.8	3,102.5
7	Cathlamet Bay (main axis)	146.2	4,412.3
8	Fluvial region	152.7	4,891.7
	Mean (including region 2)	96.2	
	Mean (excluding region 2)	99.6	
	Total (including region 2)		29,875.9
	Total (excluding region 2)		28,683.3

NOTE: The areal estimate for region 2, which was not sampled, was taken as a mean of the annual rates for regions 1 and 4.

creased in concentration in summer, at least partly because of greater phytoplankton demand, concentrations never became too low to measure, nor were they strongly correlated with primary production (Tables 1 and 2). Similar nutrient cycles have been reported earlier for the Columbia River estuary by Haertel et al. (1969) and Park et al. (1972). Part of the control on nutrient levels in the estuary is through offshore upwelling. Haertel et al. (1969) observed nitrate concentrations in the entering marine waters of up to 23 μM during summer upwelling, for example. During our summer sampling, we also observed an enrichment of nitrate (and phosphate) in waters of region 1 deeper than 5 m (Figure 8); however, at no time did we measure nitrate concentrations in the summer as high as those observed by Haertel et al. (1969). The intensity and extent of this summer enrichment must depend mainly on the timing and intensity of the coastal upwelling events. Halpern (1976), Walsh et al. (1977), and Small and Menzies (1981) indicated that the duration of

upwelling events in the eastern Pacific, including off the northwestern coast of the United States in summer, was anywhere from a few days to several weeks, interspersed with non-upwelling conditions of a few days' duration. Some events are intense, with nitrate levels of 30 μM surfacing near shore, and some are relatively weak with concentrations of 10 μM inshore (Small and Menzies 1981). Such sporadic inputs from the ocean, plus variable inputs from the riverine end of the estuary through the year, undoubtedly erode any reasonable correlation between point estimates of nutrient concentration and point estimates of primary production. In addition, not all nitrogenous nutrients were measured (ammonia, for example), further suggesting that nutrient supply did not exert major control on primary production.

Light is the main variable controlling phytoplankton production in the Columbia River estuary. Cumulative multiple regression analysis showed that daily solar radiation input and light extinction in the water column accounted for 75% of the variability in production along the main estuarine axis (Table 1) and 80% in the shallows (Table 2). In addition, the volcanic ash and mud from Mt. Saint Helens reduced primary production immediately by reducing the photic zone in the estuary (Figures 9 and 12; Frey et al. 1983). Nutrient concentrations either remained high (in the case of silicate) or at least did not approach unmeasurably low levels after the volcanic eruption (Figures 4, top and bottom and 5, top), and chlorophyll *a* concentrations remained high in May 1980 (Figure 7); hence, these variables were not responsible for the large decrease in primary production immediately after the eruption. Furthermore, two tributary rivers (region 9) draining into Youngs Bay from the south were not affected by the large turbid flows entering the Columbia River upstream of our study area, and so they retained their high combined areal production rate in May 1980 (Figure 12). Youngs Bay itself (region 4), however, did experience reduced primary production as a result of turbidity-induced decrease in the photic depth. Finally, primary production rebounded by July to rates more typical of summer rates, which coincided with the re-establishment of light extinction values typical of summer (Frey et al. 1983). The Mt. Saint Helens eruption thus performed a large-scale experiment in which light penetration into the estuary was rapidly and drastically reduced without concomitant reduction in nutrients or chlorophyll *a*. The reduction and subsequent recovery of primary production was directly caused by the reduction and subsequent re-establishment of the photic depth in the estuary. Sharp et al. (1982) postulated severe light limitation in the upper Delaware estuary, USA, as a result of high suspended sediment concentrations, and Pennock (1985) indicated that chlorophyll distributions in the Delaware estuary were light-limited.

Salinity exerted some control on primary production, and on chlorophyll biomass, in a specific way. Chlorophyll *a* and production along the main axis almost always decreased from the fluvial to the entrance regions (Figures 7 and 9), but dramatic reductions only occurred in spring and summer between regions 7 and (3 + 5). Haertel et al. (1969) also reported that cell numbers as well as chlorophyll *a* decreased downstream as the salinity increased, with the most striking changes occurring in the "mixing zone." We plotted the occurrence of numerically dominant freshwater diatoms against the salinity of the water in which they were collected during the course of our sampling in April, July, and September (Figure 13). All species declined from fresh to brackish water, some more dramatically than others. Most of the species disappeared from water with salinities >5‰ regardless of season, and in July three of the five species were drastically reduced at 2.5‰. Diatoms do not make up the complete phytoplankton assemblage in either fresh or brackish water, yet they undoubtedly demonstrate the general trend for many freshwater cells to rupture and lose their chlorophyll on encountering even very low salinities (Morris et al. 1978, 1982). The large decreases in both chlorophyll *a* and production between regions 7 and (3 + 5) are thus mainly the result of freshwater forms encountering the low-salinity tidal excursions that reach mid-estuary in summer. In winter, chlorophyll biomass and primary production

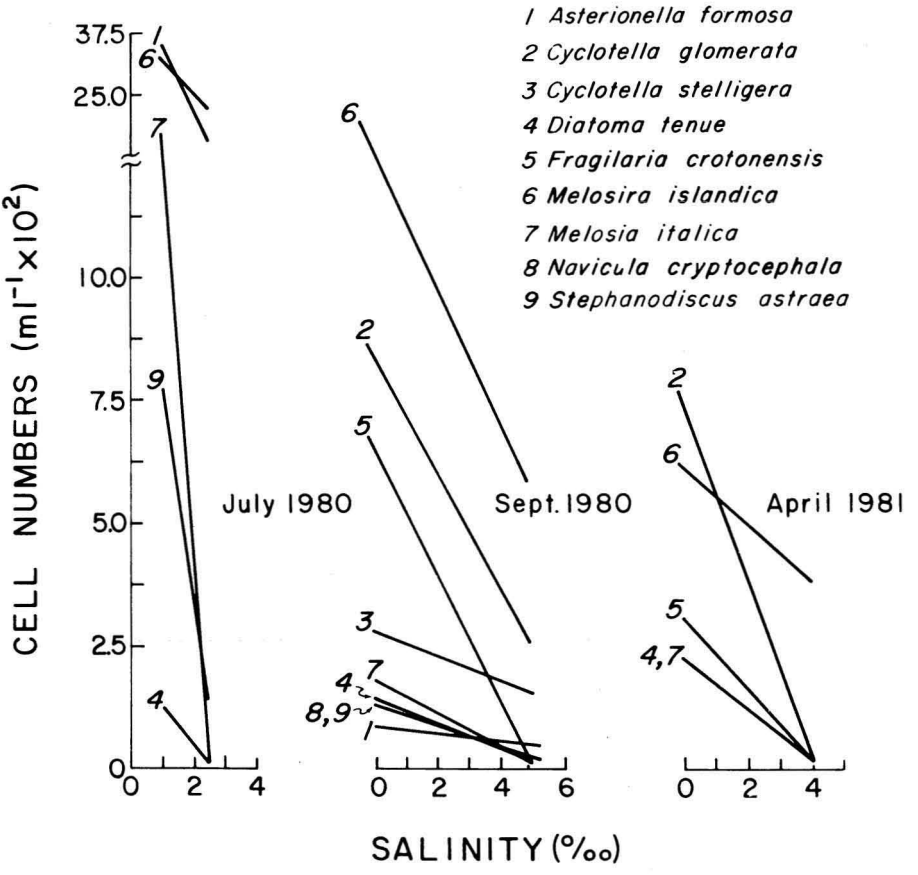

FIGURE 13. Abundances of freshwater diatom species as a function of salinity in the Columbia River estuary, at three different times of year.

are generally low as a result of reduced light intensity and day length, and river flow is higher than in late summer. These effects tend to damp biomass and production differences between contiguous regions along the estuarine axis (Figures 7 and 9). Filardo and Dunstan (1985) have observed these same effects in the James River estuary, Morris et al. (1978, 1982) in the Tamar estuary, and Cloern et al. (1983) in northern San Francisco Bay.

The pattern of high riverine production and biomass, followed by reduced production and biomass in the upper mixing zone at very low salinities, and terminating in slightly higher production and biomass at the estuary mouth in summer, has been observed in other estuarine systems. Cadee (1978), for example, reported maximum values of chlorophyll *a* and primary production in the Zaire River, decreasing values in the estuarine waters, and increasing values again in the plume waters at sea. Similar patterns have been reported in the Ems estuary in the Wadden Sea (Cadee and Hegeman 1974), in the Rhone River estuary (Blanc et al. 1969), in the upper part of the St. Lawrence estuary (Cardinal and Therriault 1976, Cote and Lacroix 1979), and in some branches of the Mississippi River (Riley 1937, Thomas and Simmons 1960). These patterns contrast with those of other estuaries, many from the eastern seaboard of the United States, in which the estuary proper supports higher phytoplankton biomass and production than either the major entering river(s) or the adjacent coastal ocean. Along the Pacific coast, the Fraser River estuary seems to be an exam-

TABLE 5

PHYTOPLANKTON PRIMARY PRODUCTION IN SOME NORTH AMERICAN ESTUARIES

ESTUARY	g C m^{-2} yr^{-1}	REFERENCES
Columbia River estuary, Oregon	100	This study
Fraser River estuary, British Columbia	120	Parsons et al. (1970)
Bedford Basin, Nova Scotia	220	Platt (1975)
St. Margaret's Bay, Nova Scotia	190	Platt and Conover (1971)
Narragansett Bay, Rhode Island	310	Furnas et al. (1976)
Chesapeake Bay (upper)	125–510	Biggs and Flemer (1972)
Chesapeake Bay (middle)	450–570	Stross and Stottlemeyer (1965)
Chesapeake Bay (lower)	385	Fournier (1966)
Neuse River estuary, North Carolina	300–500	Fisher et al. (1983)
South River estuary, North Carolina	300–500	Fisher et al. (1983)
Pamlico River estuary, North Carolina	200–500	Nixon et al. (1986)
North Inlet, South Carolina	260	Nixon et al. (1986)
Burrad Inlet, British Columbia	350	Nixon et al. (1986)

ple in which the estuarine water is more productive than its source waters (Parsons et al. 1970, Takahashi et al. 1973). The estuarine portion of San Francisco Bay may be an intermediate case, with phytoplankton biomass as abundant in the riverine sources as in the estuary, but decreasing sharply seaward of the estuary.

The biomass and production pattern exhibited by the Columbia River estuary likely results from the short residence time of water in the estuary. A residence time of 2 to 5 days (Neal 1965, Jay and Smith [in press]) suggests that freshwater phytoplankton species are rapidly carried into the low-salinity zone in mid-estuary, with little time for adjustment to mixing conditions. Even a tiny salinity change, when imposed abruptly on cells being transported rapidly through the system, apparently can effect immediate and dramatic changes to the phytoplankton community. It is perhaps important to note that the water residence time in the Zaire estuary is also 2 or 3 days (Eisma and van Bennekom 1978), while residence times in the Delaware estuary and in Narragansett Bay, for example, are respectively about 3 months (B. H. Ketchum, unpublished report on the distribution of salinity in the estuary of the Delaware River, Woods Hole Oceanographic Institution, Woods Hole, Mass., 1952) and 1 month (Kremer and Nixon 1978).

Rapid transport of cells through the Columbia estuary is also strongly suggested by the fact that primary production and chlorophyll *a* concentrations were only slightly higher in the shallows and bays than in the main axis, but not statistically significant. In some systems, for example in the northern reach of San Francisco Bay (Cloern 1979) and in the Potomac River estuary (DiToro et al. 1977), shallow regions are sites of rapid phytoplankton population increase. This simply does not occur in the shallower areas of the Columbia estuary, indicating the short residence times of cells in these areas as well as in the main axis.

A generally light-limited, short-residence-time system in which the phytoplankton community is also subject to salinity-induced depletions within the system should be a relatively nonproductive system. Indeed, when compared to a sampling of other North American estuaries, primary production in the Columbia estuary is the lowest (Table 5). The Columbia estuary is quite productive in terms of benthic infauna and other invertebrate life, however (Jones et al. [in press]). Autotrophic production within the estuary therefore is likely not the primary, direct supplier of food rations for small invertebrate organisms in the estuary. Rather it is more likely that secondary production is dependent upon large amounts of particulate organic matter imported into the estuary from upriver. Indeed, Bristow et al. (1985) determined from a laser fluorosensor

survey of surface chlorophyll along a 734-km segment of the lower Snake and Columbia rivers in late June 1982 that chlorophyll concentrations were highest (>20 mg m^{-3}) in a long stretch of river just upstream from our study area. Evaluation of particulate transport into and through the estuary is the subject of a second paper.

ACKNOWLEDGMENTS

Sandy Moore and Rae Deane Leatham provided invaluable assistance in parts of the field program and in some laboratory analyses.

LITERATURE CITED

AMSPOKER, M. C., and C. D. MCINTIRE. 1986. Effects of sedimentary processes and salinity on the diatom flora of the Columbia River estuary. Bot. Mar. 24:391–399.

ATLAS, E. L., S. W. HAGER, L. I. GORDON, and P. K. PARK. 1971. A practical manual for the use of the Technicon Autoanalyzer in seawater nutrient analysis: revised. Technical Report 215, School of Oceanography, Oregon State University, Corvallis.

BALL, M. D., and J. F. ARTHUR. 1979. Planktonic chlorophyll dynamics in the northern San Francisco Bay and delta. Pages 265–285 *in* T. J. Conomos, ed. San Francisco Bay: The urbanized estuary. Pacific Division, American Association for the Advancement of Science, San Francisco, California.

BIGGS, R. B., and D. A. FLEMER. 1972. The flux of particulate carbon in an estuary. Mar. Biol. 12:11–17.

BLANC, F., M. LEVEAU, and K. H. SZEKIELDA. 1969. Effects eutrophiques au débouche d'un grand fleuve (Grand Rhone). Mar. Biol. 3:233–242.

BRISTOW, M. P. F., D. H. BUNDY, C. M. EDMONDS, P. E. PONTO, B. E. FREY, and L. F. SMALL. 1985. Airborne laser fluorosensor survey of the Columbia and Snake rivers: Simultaneous measurements of chlorophyll, dissolved organics and optical attenuation. Int. J. Remote Sensing 6: 1707–1734.

CADEE, G. C. 1978. Primary production and chlorophyll in the Zaire River, estuary and plume. Neth. J. Sea Res. 3/4:368–381.

CADEE, G. C., and J. HEGEMAN. 1974. Primary production of phytoplankton in the Dutch Wadden Sea. Neth. J. Sea Res. 8:240–259.

CARDINAL, A., and L. B. THERRIAULT. 1976. Le phytoplancton de l'estuarie moyen de Saint-Laurent en amont de L'Ile-Aux-Coudres (Quebec). Int. Rev. Gesampten Hidrobiol. Hydrogr. 61:639–648.

CLOERN, J. E. 1979. Phytoplankton ecology of the San Francisco Bay system: The status of our current understanding. Pages 247–264 *in* T. J. Conomos, ed. San Francisco Bay: The urbanized estuary. Pacific Division, American Association for the Advancement of Science, San Francisco, California.

CLOERN, J. E., A. E. ALPINE, B. E. COLE, R. L. J. WONG, J. F. ARTHUR, and M. D. BALL. 1983. River discharge controls phytoplankton dynamics in the northern San Francisco Bay estuary. Estuarine Coastal Shelf Sci. 16:415–429.

COTE, R., and G. LACROIX. 1979. Influence de débits élevés et variables d'eau douce sur le régime saisonnier de production primaire d'un fjord subarctique. Oceanol. Acta 2: 299–306.

DITORO, D. M., R. V. THOMAN, D. J. O'CONNOR, and J. L. MANCINI. 1977. Estuarine phytoplankton biomass models. Verification analyses and preliminary applications. Pages 969–1020 *in* E. D. Goldberg, I. N. McCave, and J. H. Steele, eds. The sea. Vol. 6. John Wiley and Sons, New York.

EISMA, D., and A. J. VAN BENNEKOM. 1978. The Zaire river and estuary and the Zaire outflow in the Atlantic Ocean. Neth. J. Sea Res. 12:255–272.

FILARDO, M. J., and W. M. DUNSTAN. 1985. Hydrodynamic control of phytoplankton in low salinity waters of the James River estuary, Virginia, U.S.A. Estuarine Coastal Shelf Sci. 21:653–668.

FISHER, T. R., P. R. CARLSON, and R. T. BARBER. 1983. Carbon and nitrogen primary productivity in three North Carolina

estuaries. Estuarine Coastal Shelf Sci. 15: 621–644.

FOURNIER, R. O. 1966. Some implications of nutrient enrichment on different temporal stages of a phytoplankton community. Chesapeake Sci. 7:11–19.

FREY, B. E., J. R. LARA-LARA, and L. F. SMALL. 1983. Reduced rates of primary production in the Columbia River Estuary following the eruption of Mt. Saint Helens on 18 May 1980. Estuarine Coastal Shelf Sci. 17:213–218.

FURNAS, M. J., G. L. HITCHCOCK, and T. J. SMAYDA. 1976. Nutrient-phytoplankton relationships in Narragansett Bay during the 1974 summer bloom. Pages 118–133 *in* M. L. Wiley, ed. Estuarine processes: Uses, stresses and adaptation to the estuary. Vol. 1. Academic Press, New York.

HAERTEL, L. S., and C. L. OSTERBERG. 1967. Ecology of zooplankton, benthos, and fishes in the Columbia River Estuary. Ecology 48:459–472.

HAERTEL, L. S., C. OSTERBERG, H. CURL, and P. K. PARK. 1969. Nutrient and plankton ecology of the Columbia River Estuary. Ecology 50:962–978.

HALPERN, D. 1976. Structure of a coastal upwelling event observed off Oregon during July 1973. Deep-Sea Res. 23:495–508.

JAY, D. A., and J. D. SMITH. In press. Circulation, density distribution and neap-spring transitions in the Columbia River Estuary. Prog. Oceanogr.

JONES, K. K., O. A. SIMENSTAD, D. L. HIGLEY, and D. L. BOTTOM. In press. Community structure, distribution, and standing stock of benthos, epibenthos, and plankton in the Columbia River Estuary. Prog. Oceanogr.

KREMER, J. N., and S. W. NIXON. 1978. A coastal marine ecosystem. Simulation and analysis. Springer-Verlag, New York.

LARA-LARA, J. R. 1982. Primary biomass and production processes in the Columbia River estuary. Ph.D. dissertation, Oregon State University, Corvallis.

MACISAAC, J. J., and R. C. DUGDALE. 1972. Interactions of light and inorganic nitrogen in controlling nitrogen uptake in the sea. Deep-Sea Res. 19:209–232.

MORRIS, A. W., A. J. BALE, and R. J. M. HOWLAND. 1982. Chemical variability in the Tamar Estuary, Southwest England. Estuarine Coastal Shelf Sci. 14:649–661.

MORRIS, A. W., R. F. C. MANTURA, A. J. BALE, and R. J. M. HOWLAND. 1978. Very low salinity regions of estuaries; important sites for chemical and biological reactions. Nature (London) 274:678–680.

NEAL, V. T. 1965. A calculation of flushing times and pollution distribution for the Columbia River estuary. Ph.D. dissertation, Oregon State University, Corvallis.

NIXON, S. W., C. A. OVIATT, J. FRITHSEN, and B. SULLIVAN. 1986. Nutrients and the productivity of estuarine and coastal marine ecosystems. J. Limnol. Soc. S. Afr. 12:43–71.

PARK, P. K., M. CATALFOMO, G. R. WEBSTER, and B. H. REID. 1969. Nutrients and carbon dioxide in the Columbia River. Limnol. Oceangr. 14:559–567.

PARK, P. K., C. L. OSTERBERG, and W. O. FORSTER. 1972. Chemical budget of the Columbia River. Pages 123–134 *in* A. A. Pruter and D. L. Alverson, eds. The Columbia River estuary and adjacent ocean waters. University of Washington Press, Seattle.

PARSONS, T. R., R. J. LEBRASSEUR, and W. E. BARRACLOUGH. 1970. Levels of production in the pelagic environment of the Strait of Georgia, British Columbia: A review. J. Fish. Res. Board Can. 27:1251–1264.

PENNOCK, J. R. 1985. Chlorophyll distributions in the Delaware estuary: Regulation by light-limitation. Estuarine Coastal Shelf Sci. 21:711–726.

PETERSON, R. E. 1977. A study of suspended particulate matter: Arctic Ocean and northern Oregon continental shelf. Ph.D. dissertation, Oregon State University, Corvallis.

PLATT, T. 1975. Analysis of the importance of spatial and temporal heterogeneity in the estimation of the annual production by phytoplankton in a small, enriched, marine basin. J. Exp. Mar. Biol. Ecol. 18:99–109.

PLATT, T., and R. J. CONOVER. 1971. Variability and its effects on the chlorophyll budget of a small marine basin. Mar. Biol. 10:52–65.

RILEY, G. A. 1937. The significance of the Mississippi River drainage for biological conditions in the northern Gulf of Mexico. J. Mar. Res. 1:60–74.

ROWE, K., and R. BRENNE. 1981. Statistical interactive programming system (SIPS). Statistical Computing Report no. 7. Oregon State University, Corvallis.

RYTHER, J. H., and W. M. DUNSTAN. 1971. Nitrogen, phosphorus, and eutrophication in the coastal marine environment. Science 171:1008–1013.

SAMUELSON, G., and G. OQUIST. 1977. A method for studying photosynthetic capacities of unicellular algae based on *in vivo* chlorophyll fluorescence. Physiol. Plantarum 40:315–319.

SHARP, J. H., C. H. CULBERSON, and T. M. CHURCH. 1982. The chemistry of the Delaware estuary. General considerations. Limnol. Oceanogr. 27:1015–1028.

SHERWOOD, C. R., and J. S. CREAGER. In press. Sedimentary geology of the Columbia River Estuary. Prog. Oceanogr.

SIMENSTAD, C. A., L. F. SMALL, C. D. MCINTIRE, D. A. JAY, and C. R. SHERWOOD. In press. An introduction to the Columbia River Estuary: Brief history, prior studies, and the role of the CREDDP studies. Prog. Oceanogr.

SMALL, L. F., and D. W. MENZIES. 1981. Patterns of primary productivity and biomass in a coastal upwelling region. Deep-Sea Res. 28:123–149.

STRICKLAND, J. D. H., and T. R. PARSONS. 1972. A practical handbook of seawater analysis. J. Fish. Res. Board Can. Bull. 167.

STROSS, R. G., and J. R. STOTTLEMEYER. 1965. Primary production in the Patuxent River. Chesapeake Sci. 6:126–140.

TAKAHASHI, M., K. FUJII, and T. R. PARSONS. 1973. Simulation study of phytoplankton photosynthesis and growth in the Fraser River estuary. Mar. Biol. 19:102–116.

THOMAS, W. H., and E. G. SIMMONS. 1960. Phytoplankton production in the Mississippi delta. Pages 103–116 *in* F. P. Shepard, ed. Recent sediments, Northwest Gulf of Mexico. American Association of Petroleum Geologists, Tulsa, Oklahoma.

VINCENT, W. F. 1981. Photosynthetic capacity measured by DCMU induced chlorophyll fluorescence in an oligotrophic lake. Freshwater Biol. 11:61–78.

VOLLENWEIDER, R. A. 1971. A manual on methods for measuring primary production in aquatic environments. IBP Handbook no. 12, Blackwell Scientific Publications, Oxford.

WALSH, J. J., T. E. WHITLEDGE, J. C. KELLEY, S. A. HUNTSMAN, and R. D. PILLSBURY. 1977. Further transition states of the Baja California upwelling ecosystem. Limnol. Oceanogr. 22:264–280.

WETZEL, R. G., and G. E. LIKENS. 1979. Limnological analyses. W. B. Saunders, Philadelphia, Pennsylvania.

WILLIAMS, L. G. 1964. Possible relationships between plankton diatom species numbers and water-quality estimates. Ecology 45:809–823.

———. 1972. Plankton diatom species biomasses and the quality of American rivers and the Great Lakes. Ecology 53: 1038–1050.

WILLIAMS, L. G., and C. SCOTT. 1962. Principal diatoms of major waterways of the United States. Limnol. Oceanogr. 7:365–375.

WILLIAMS, R. B. 1973. Nutrient levels and phytoplankton productivity in the estuary. Pages 59–89 *in* R. H. Chabreck, ed. Proceedings of the Coastal Marsh and Estuary Management Symposium. Louisiana State University, Baton Rouge.