AN ABSTRACT OF THE THESIS OF

LOIS STEBEN HAERTEL (Name) for the DOCTOR OF PHILOSOPHY (Degree)

in OCEANOGRAPHY (Major) presented on July 24, 1969 (Date)

Title: PLANKTON AND NUTRIENT ECOLOGY OF THE COLUMBIA RIVER ESTUARY

Abstract approved: Redacted for Privacy
Charles Osterberg

Monthly samples of nutrients, phytoplankton and zooplankton were taken in the Columbia River estuary over a period of 16 months in order to determine distribution with season and salinity, and interrelationships between plankton and nutrients.

Nitrate and phosphate levels in the river water entering the estuary are high in the winter and show depletion during the summer. Silicate levels are high in the river water at all seasons. Nitrate and phosphate levels are high in the entering ocean water during summer offshore upwelling. The nutrient levels in the estuary generally show a linear relationship with salinity, resulting from the levels of nutrients in the entering river and ocean water. Superimposed upon this linear relationship is a tendency for the nutrients to be enriched in the bottom waters of the central part of the estuary.

The estuary phytoplankton are primarily composed of freshwater forms, and probably represent a downstream extension of the

river flora. Regression analysis of phytoplankton levels vs. light, nutrients, and river flow indicates that light probably limits phytoplankton abundance on most dates.

The zooplankton of the estuary are composed of three groups, preferring fresh, oligohaline, and polyhaline waters respectively. Regression analysis indicates a strong correlation between abundance of the freshwater group and river temperature. The factors controlling the abundance of the oligohaline and polyhaline groups are less obvious. The oligohaline group, principally Eurytemora affinis, reaches the greatest population density (100,000/m^3 or more).

Regression analysis indicates a close correlation between Eurytemora abundance and phosphate levels. This indicates a strong potential for zooplankton regeneration of phosphate necessary for phytoplankton growth.

Plankton and Nutrient Ecology of the Columbia River Estuary

by

Lois Jean Steben Haertel

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

June 1970

APPROVED:

Redacted for Privacy

Professor of Oceanography
in charge of major

Redacted for Privacy

Chairman of the Department of Oceanography

Redacted for Privacy

Dean of Graduate School

Date thesis is presented July 24, 1969

Typed by Gwendolyn Hansen for Lois Steben Haertel

ACKNOWLEDGEMENTS

It is a pleasure to thank my major professor, Dr. Charles Osterberg for originally encouraging my interest in the plankton of the Columbia estuary, and for making this work possible. I am also grateful to Dr. William Renfro and Dr. William Forster for their assistance and advice in Dr. Osterberg's absence. I particularly wish to thank Dr. Herbert Curl who was an apparently inexhaustible source of ideas and help during this study.

To the above, and to Dr. Lawrence Small, go my thanks for reading the manuscript and offering constructive suggestions. To Dr. Kihlo Park go my thanks for advice and for making Columbia River chemical data available.

Mr. Norman Kujala and Dr. William Renfro provided extensive and valuable help in the field work. Mrs. Madeleine Catalfolmo and Mr. Lauren Larsen graciously assisted in sample processing.

Financial support from U. S. Department of the Interior Fellowship Number 5-F1-WP-31, 471-02 and U. S. Atomic Energy Commission Contract AT (45-1) 1750 is gratefully acknowledged.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

PLANKTON AND NUTRIENT ECOLOGY OF THE COLUMBIA RIVER ESTUARY

INTRODUCTION

The estuary, a unique environment where river water meets and mixes with sea water, is an area of rapid change and great extremes. The oscillations between fresh and salt water are often matched by oscillations in temperature, chemicals, and in the plant and animal communities present. The constant flux in environmental conditions requires difficult adjustments; as a result, estuaries frequently support fewer kinds of organisms than more stable environments. Nevertheless, those organisms which are present, are often present in great abundance.

The sources of estuarine flux, the seasonally increasing and decreasing volume of entering river water and the daily raising and lowering of the tide, are particularly great in the Columbia River estuary. The Columbia, the second largest river on the North American continent, experiences great differences in river flow. More than a ten-fold increase from low to high flow volumes was recorded during the course of this study, and larger differences are on record. This large and varying volume of entering fresh water, and the wide tidal range characteristic of the Pacific coast, combine to create an environment of rapid changes and swift currents that is extreme, even in comparison with other estuaries.

Although the Columbia drains a relatively sparsely populated portion of the American continent, it has been subjected to many man-made changes. Construction of many dams has modified the river flow and temperature regimes, and cities and industries along the river have contributed both thermal and chemical pollution. However, the diluting effect of the large volume of water has prevented the extreme pollution characteristic of the estuaries of smaller rivers.

The Columbia is regarded by some as a major untapped source of potable water and may well be subjected to major dimunition of flow in the future. Whether or not proposed water diversion projects are carried out, increased population and industrial growth in the drainage basin will likely cause major changes in water quality. An understanding of the interrelations between the physical, chemical, and biotic factors controlling the ecology is essential if future demands on the river are to be accurately evaluated and gross deterioration of the environment avoided.

Little work has been done on the Columbia estuary plankton and nutrient ecology. Haertel and Osterberg (1967) dealt with some aspects of hydrography and zooplankton ecology, but no previous publications exist on estuary phytoplankton or plankton-nutrient relations. Data taken by the U. S. Federal Water Pollution Control Federation Stream Survey (1957-1968) include chemical measurements and plankton counts forty miles upriver from the estuary, and studies by

Park, Osterberg, and Forster (1969) and Park, Catalfolmo, Webster and Reid (1969) discuss the river nutrients. Several studies provide information about the ocean at the mouth of the estuary (Barnes and Paquette, 1954; Park, Patullo and Wyatt, 1962; Stefansson and Richards, 1963; Anderson, 1965; and Duxbury and McGary, 1968).

The purposes of this study were as follows:

1. To conduct a preliminary floristic survey.
2. To determine the distribution in time and space of the nutrients and plankton. Specifically, this included distribution with season, salinity, depth, and location within the estuary.
3. To examine the relations between changes in the source waters (both river and ocean) and changes in the plankton and nutrient regimes within the estuary.
4. To examine the interrelations between plankton and nutrients.
5. To provide a basis for future studies on the radioecology of estuary plankton.

METHODS AND MATERIALS

Six stations (Figure 1) were selected to sample fresh water entering upstream, marine water entering downstream, and intermediate conditions in both channels of the estuary. All stations were sampled monthly, at both high and low tides, from 26 April 1967 through 20 September 1967. From 1 November 1967 through 7 June 1968, only the south channel stations (I, II, III, IV) were sampled, taking the downstream station at high tide. From 2 July 1968 through 26 August 1968 stations from both the north and south channels were again sampled.

Water samples for salinity, dissolved oxygen, nitrate, inorganic phosphate, silicate, chlorophyll a and phytoplankton cell counts were taken from the surface and 10m by means of bucket and Van Dorn Bottle. Temperature was measured with a bucket thermometer. Zooplankton were quantitatively measured at both surface and 10m by means of a closing type Clarke-Bumpus sampler with #6 mesh net (mesh diameter = .245mm). Phytoplankton samples for radioanalysis were collected by means of a #25 mesh net (mesh diameter = .064mm). Zooplankton samples for radioanalysis were collected by means of a #6 mesh net.

Previous samples for salinity, oxygen, temperature, and zooplankton abundance had been taken monthly by the author from

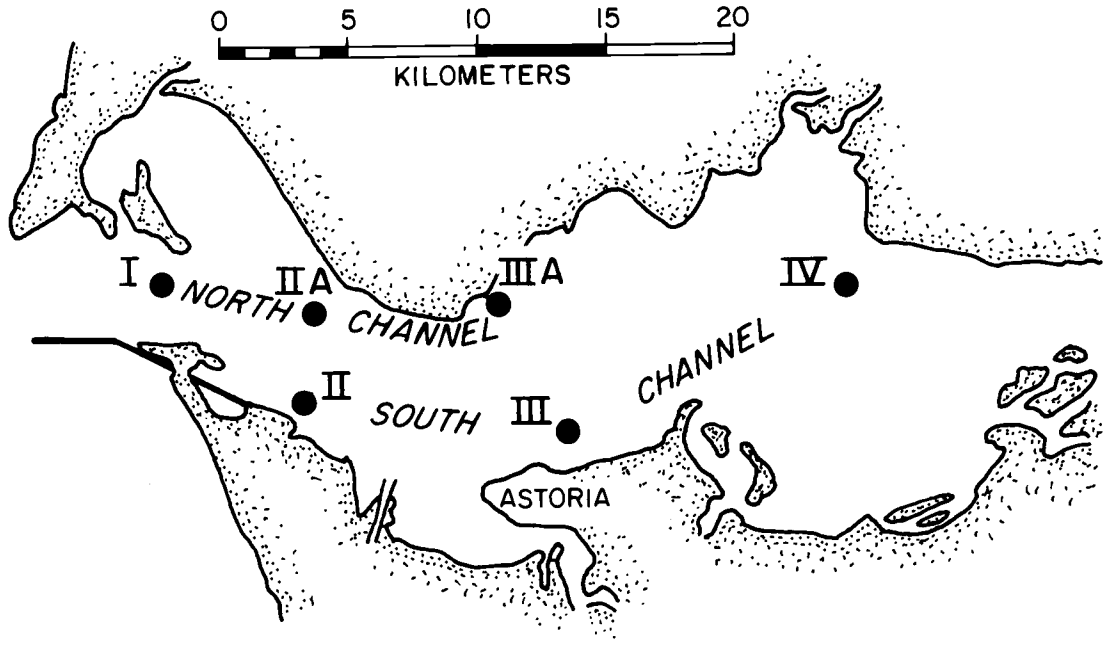


Figure 1. Location of sampling stations.

2 March 1964 through 8 August 1965 from stations IIA, III, and IV. Data on salinity, oxygen, inorganic phosphate, silicate, nitrate, temperature and zooplankton abundance were made available by Dr. Kilho Park and Mr. Norman Kujala for samples taken from 22 January 1966 through 24 March 1967 from stations I, IIA, III, and IV. All zooplankton sampling from 2 March 1964 through 24 March 1967 was done by means of oblique tows with a #6 mesh half meter net.

Laboratory analytical methods were: Inorganic phosphate--Murphy and Riley (1962); nitrate--Mullen and Riley (1955); silicate, dissolved oxygen and chlorophyll a--Strickland and Parsons (1965). The chlorophyll a method used differed slightly in that the pigment was extracted by placing the filter and 5 mls of acetone in a Servall Omnimixer and blending for 1-5 minutes.

Zooplankton samples were preserved in 10% formalin and counted as to species and abundance by the method given in Haertel and Osterberg (1967).

Samples for phytoplankton cell counts were preserved in Lugol's Solution and analyzed by placing 1 ml of sample in a Sedgewick-Rafter cell and recording the number of phytoplankton cells present in a measured portion of the counting cell until at least 100 cells of the most abundant species were recorded. It was occasionally necessary to condense the sample by centrifuging. Phytoplankton species

were further identified in some of the samples by making a permanent slide of part of the sample and examining under higher magnification than was possible in the Sedgewick-Rafter cell. It was necessary to use these slides to determine the relative abundance of the two major species of Melosira since they could not be differentiated in the Sedgewick-Rafter counts.

Phytoplankton samples for radioanalysis were immediately emptied into 4 liters of estuary water and returned to the laboratory as rapidly as possible with most of the phytoplankton presumably still alive. The samples were allowed to settle, and those phytoplankton still in suspension in the water were separated from floating and suspended detritus by passing the water through #0 and #6 mesh nets. In most cases, a sample that was 85-95% phytoplankton could be obtained in this manner. Purity of sample was estimated from microscopic examination. Samples were then preserved in 2-3% formalin, concentrated by evaporation or by trapping on a .80μ pore-size membrane filter, dried, and analyzed by gamma-ray spectrometry.

Zooplankton samples for radioanalysis were immediately emptied into 8 liters of estuary water and returned to the laboratory with most of the zooplankton still alive. Those plankton still in suspension were then poured through a #0 mesh net to remove large detritus, and a #6 mesh net to collect the zooplankton. If the sample

still appeared to be greatly contaminated with wood fibers and other detritus, it was placed into one half of a divided aquarium which was filled with estuary water which had been previously filtered through a #12 mesh net. The barrier between the two halves of the aquarium contained a window with large nylon screening which was closed off completely by a sliding plexiglass door. The half of the aquarium containing the zooplankton was darkened and the other half was brightly lit. The plexiglass door was removed, allowing the zooplankton to swim through the screen into the lighted side. After about 20 minutes, the plexiglass door was replaced and both halves of the aquarium were separately siphoned off, the light half filtered through a #6 mesh net to catch the zooplankton. The aquarium method made it possible to obtain a sample that was 95+% pure zooplankton; however, about one-third to two-thirds of the sample was lost as all the zooplankton did not swim to the lighted side, so an initially large quantity of zooplankton was required. This method worked well for samples composed primarily of Cyclops vernalis and Eurytemora affinis. It was not tried with other species. Zooplankton samples were examined for purity, preserved, condensed, dried, and radioanalyzed by the same methods as the phytoplankton samples.

HYDROGRAPHY

River Flow

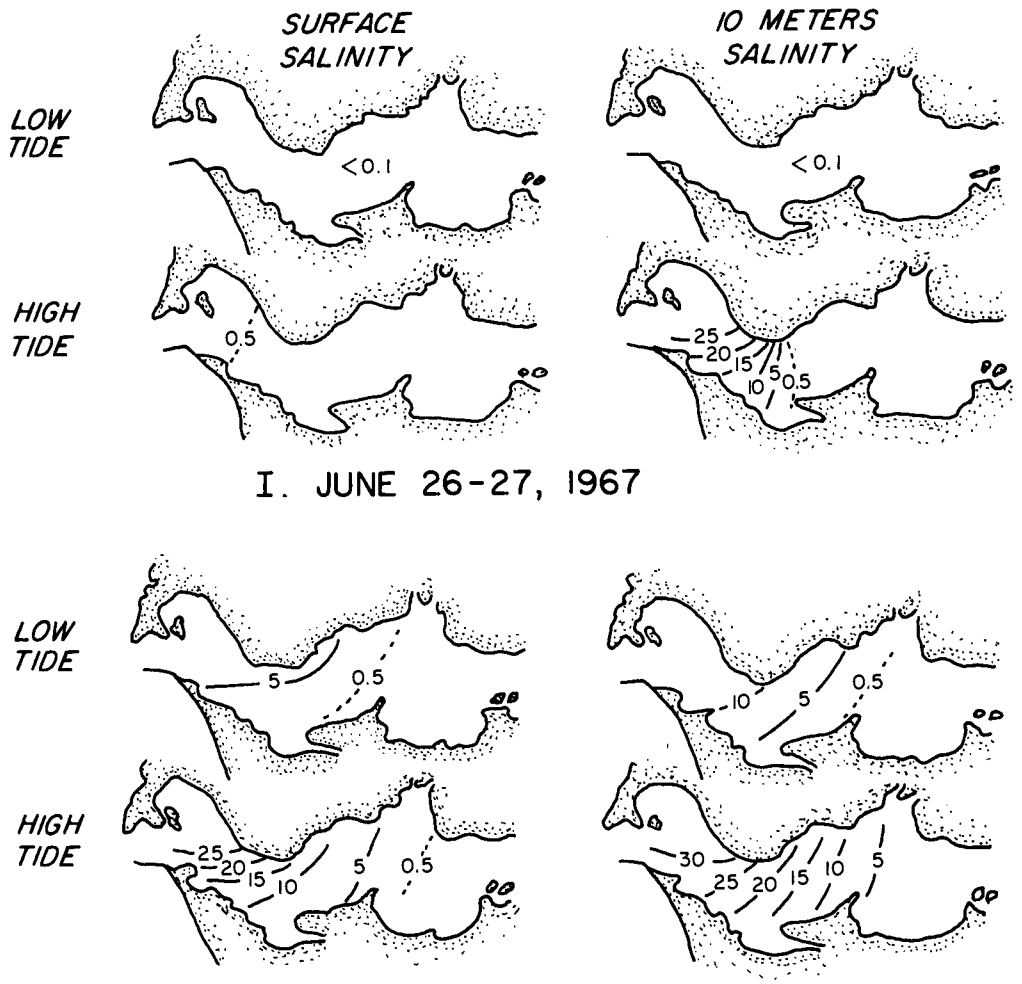
Daily river flow at the mouth (Figure 2) was determined by construction of a parallel hydrograph using daily values measured by the U. S. Geological Survey for the Columbia River at the Dalles and for the Willamette River at Salem, and monthly averages estimated by the U. S. Geological Survey for the Columbia River at the mouth.

Columbia River flow is characterized by two peaks per year. The spring peak, usually maximum in June, is due to snow melt in the mountainous parts 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 24, 300 m^3/sec on December 24, 1964, during unusual flooding, and 2300 m^3/sec on April 17, 1968, during the filling of an upstream reservoir.

The large river flow contributes to a rapid flushing time for the estuary. Neal (1966) has calculated flushing time to vary from about one day at high river flow to about five days at low river flow.

Salinity

Salinity of the Columbia estuary has been measured by the U. S. Corps of Engineers (1960), discussed by Neal (1966), and



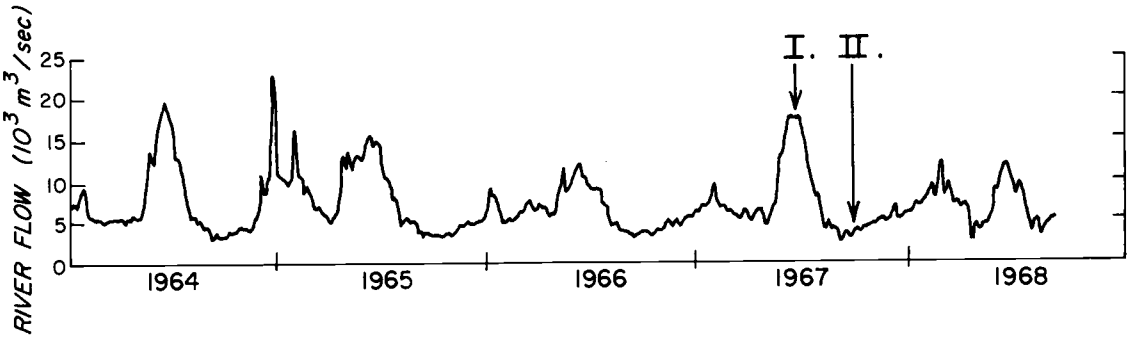


Figure 2. Columbia River flow, 1964-1968, and salinity distribution (‰) in the estuary at two dates representing high and low river flow.

measured and discussed by Haertel and Osterberg (1967). According to classifications of Pritchard (1955) and Burt and McAlister (1959), the estuary exhibits type B (partly mixed) circulation most of the time. At times of high river flow it approaches type A (two-layered) circulation, and at low river flow it approaches type D (well-mixed) circulation. The estuary exhibits lateral stratification; salinities are greater in the north channel than in the south (Figure 2). This is the opposite distribution to that which would be expected from the coriolus effect. Neal (1966) suggests that this is caused by the orientation and morphology of the two channels.

At low tide and high river flow, the salt wedge may be swept almost entirely from the estuary (Figure 2). At high tide and low river flow, slightly brackish water may penetrate more than 36 km upstream, and the central part of the estuary may be quite brackish (10-25 ‰).

Temperature

Regression analysis of temperature vs. salinity by the linear least squares method showed that a close correlation existed (Table 1). Because of the short flushing time of the Columbia estuary (one to five days), temperatures would not be likely to undergo much change while in the estuary. Therefore, a linear relationship is to be expected. Temperatures measured in entering river water ranged

Table 1. Results of linear regression analysis of temperature (°C), oxygen and AOU. (ml/l), and phosphate and nitrate (μM) vs. salinity (o/oo).

Date	N	Value when Salinity = 0*				Value when Salinity = 30				Slope (b)				Correl. Coefficient (r)			
		T	O_2	PO_4	NO_3	T	O_2	PO_4	NO_3	T	O_2	PO_4	NO_3	T	O_2	PO_4	NO_3
1/22/66	9	4.9	8.12	.95	27.2	11.5	6.11	.71	6.2	.22	-.07	-.008	-.70	.90	.97	.44	.67
3/ 2/66	9	5.6	8.54	1.25	24.2	7.4	6.11	.95	.1	.06	-.08	-.010	-.81	.92	.75	.27	.93
3/25/66	9	7.4	8.31	1.02	31.2	8.6	8.16	.96	.9	.04	-.01	-.002	-1.01	.85	.11	.08	.96
4/28/66	3	17.0	8.07	.49	3.0	10.7	5.07	1.54	3.3	-.21	-.10	.035	.01	.60	1.00	.69	.64
6/ 7/66	9	14.5	7.85	.26	.1	9.5	2.81	1.82	22.9	-.17	-.17	.052	.76	.99	1.00	.96	.94
7/ 7/66	9	16.5	7.94	.52	.1	7.9	1.55	1.72	8.8	-.29	-.21	.040	.29	.94	.83	.80	.96
8/ 4/66	9	20.2	6.81	.04	.0	12.5	2.46	.52	22.2	-.26	-.15	.016	.74	.88	.93	.98	1.00
9/12/66	12	18.9	5.98	.42	.8	10.9	4.71	1.32	13.7	-.27	-.03	.030	.43	.99	.61	.76	.90
10/13/66	12	16.1	5.99	.43	5.1	10.1	4.78	1.57	17.1	-.20	-.03	.038	.40	.99	.61	.93	.82
11/14/66	12	10.9	6.84	.87	13.8	10.4	6.36	1.05	5.4	-.02	-.02	.006	-.28	.80	.81	.29	.72
12/13/66	10	8.4	8.14	.37	30.7	10.5	6.79	.79	8.5	.07	-.05	.014	-.74	.83	.93	.65	.97
1/11/67	8	6.6	7.73	.71	24.9	9.5	6.75	.86	3.3	.10	-.04	.005	-.72	.97	.74	.22	.97
2/23/67	11	6.9	8.00	.76	31.7	9.0	6.50	.97	3.8	.07	-.05	.007	-.93	.96	.92	.30	.98
3/23/67	12	7.8	7.98	.58	21.9	9.1	6.51	.58	1.5	.04	-.05	.000	-.68	.92	.96	.01	.99
4/26/67	11	10.7	7.53	.47	2.1	9.9	5.70	2.18	2.7	-.03	-.06	.057	.02	.87	.77	.62	.02
5/24/67	24	15.0	7.27	.30	1.6	11.3	4.96	1.38	8.2	-.12	-.08	.036	.22	.73	.69	.90	.82
6/26/67	22	16.6	7.34	.30	3.8	11.3	3.56	2.04	8.9	-.18	-.13	.058	.17	.86	.96	.96	.87
7/24/67	24	20.0	6.07	.34	1.3	12.7	2.77	1.72	12.1	-.24	-.11	.043	.36	.98	.81	.78	.82
8/18/67	24	21.5	5.58	.08	1.1	12.6	3.96	1.70	16.7	-.30	-.05	.054	.52	.98	.66	.96	.96
9/19/67	24	20.2	5.84	.01	.1	14.1	3.26	.91	7.5	-.20	-.09	.030	.25	.97	.74	.90	.82
11/ 1/67	5	12.8	6.20	.98	12.9	13.9	6.05	.35	2.4	.03	-.01	-.021	-.35	.96	.26	.37	.97
12/12/67	8	7.2	7.93	.43	34.8	10.1	2.88	.91	6.9	.10	-.14	.016	-.93	.99	.88	.81	.98
1/27/68	3	4.6	5.47	.42	29.5	7.1	7.27	.87	8.8	.09	.06	.015	-.69	.99	.82	.87	1.00
2/23/68	8	7.7	8.26	.84	35.9	9.5	6.19	1.28	8.0	.06	-.07	.013	-.93	.85	.96	.87	.96
4/ 8/68	8	9.7	7.88	.78	18.2	9.6	4.16	.78	5.4	.00	-.12	.000	-.46	.08	.97	.00	.98
5/10/68	6	13.1	6.79	.87	1.5	10.6	4.72	.57	2.7	-.08	-.07	-.010	.04	.88	.89	.23	.41
6/ 7/68	6	15.4	7.03	.18	1.6	12.4	4.01	.76	2.5	-.10	-.07	.019	.03	.99	.91	.52	.42
7/ 2/68	6	18.1	7.68	.08	.3	10.9	3.30	1.78	21.8	-.24	-.15	.057	.72	.99	.99	.98	1.00
7/30/68	11	20.6	6.16	.18	.5	14.1	2.95	2.07	20.0	-.21	-.11	.063	.65	.91	.91	.97	.99
8/26/68	12	18.6	5.87	.22	1.6	15.5	3.32	.70	1.1	-.10	-.09	.016	-.02	.93	.78	.82	.38

* Y-intercept (a) $a = y + bx$

from 4.0 to 22.5°C. Temperature extremes were less in the salt wedge; extrapolation of regression lines to 30 ‰, often the highest salinity sampled, indicated a range of 7.1-15,5°C.

Dissolved Oxygen

Oxygen values in entering fresh water averaged 7-8 ml/l in winter and 5-6 ml/l in late summer. Oxygen values were lower in the salt wedge; values at 30 ‰ averaged 6-7 ml/l in winter and 2-3 ml/l during the summer offshore upwelling season. Oxygen-salinity regression analysis (Table 1) showed inverse correlation on most dates. Oxygen is non-conservative; it is affected by interactions with sediments, biota, and suspended organic matter, so deviations are not surprising. One specific source of deviations can be seen from a comparison of seasonal oxygen and salinity contours (Figure 3). Superimposed on the general inverse relation between oxygen and salinity is a tendency to oxygen depletion in the bottom waters at stations II and IIA, a phenomenon which is discussed in the section entitled "Phytoplankton-zooplankton-nutrient Relations."

Silicate

Silicate values in the entering freshwater were always high, ranging from about 240 μM in winter to about 60 μM in late summer. Silicate levels in the salt wedge were much lower, ranging from about

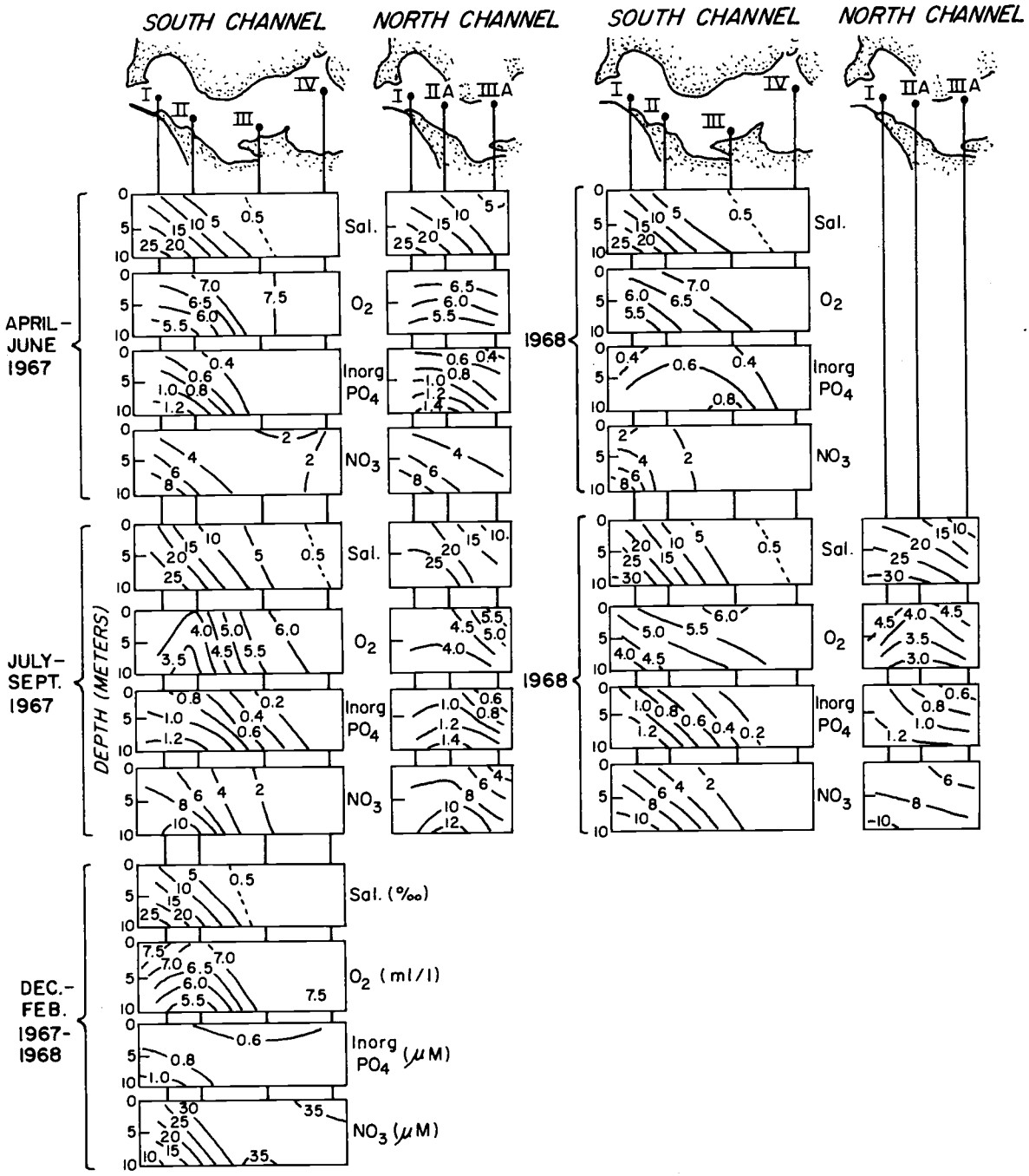


Figure 3. Seasonal distribution of salinity, oxygen, inorganic phosphate, and nitrate, 1967-1968.

10-50 μM. Any seasonal cycle which might have been present in the salt wedge was masked by the high freshwater values.

Inorganic Phosphate

During the winter, phosphate levels were approximately equal in both entering fresh and marine water, averaging slightly under 1 μM (Figure 4, Table 1). Phosphate was depleted to about 0.01 μM in late summer undoubtedly as a result of upstream phytoplankton growth and uptake. At the same time, phosphate was enriched in entering marine waters to as much as 2.2 μM, as a result of upwelling. Studies by Newcombe and Brust (1940), Rochford (1951), and Jeffries (1962) all indicated estuarine phosphate levels to be enriched following periods of flooding. Comparison of freshwater phosphate levels and river flow (Figure 4) showed little relation in the Columbia.

Phosphate-salinity regression analyses (Table 1) showed a significant correlation only during the upwelling season, when considerable slope was present. Phosphate is readily adsorbed and released by sediments (Hayes and Phillips, 1958; Jitts, 1959; Pomeroy et al., 1965), and is readily taken up and released by plankton (Harris, 1959; Pomeroy et al., 1963; Parker and Olson, 1966). Thus, local differences would be expected to eclipse the phosphate-salinity relationship when little slope is present. Comparison of seasonal phosphate and salinity contours (Figure 3) shows one of the

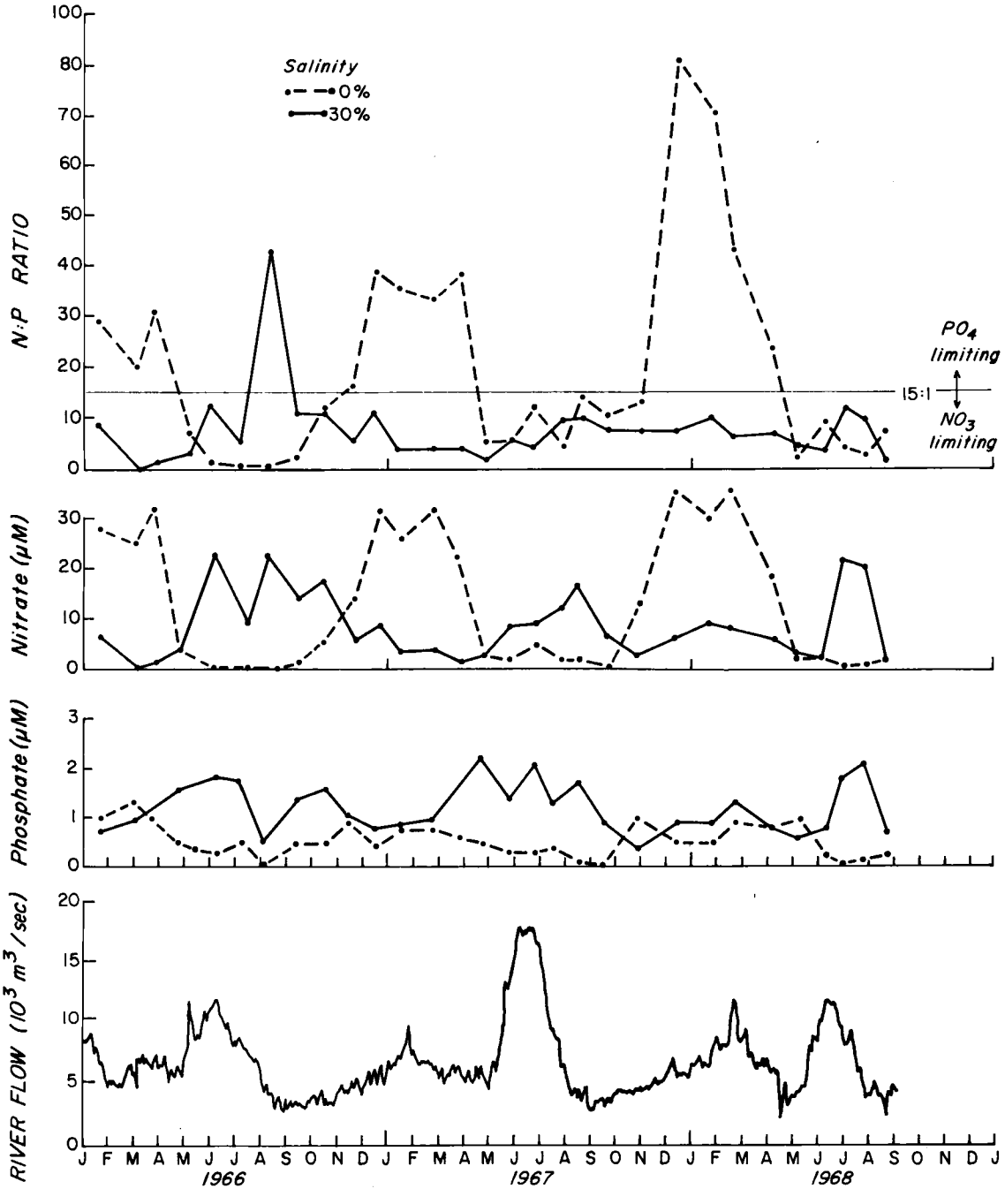


Figure 4. Changes in nitrate, phosphate, N:P ratio, and river flow with season, 1966-1968.

sources of deviations. Phosphate tends to be enriched in the bottom waters at stations II and IIA, the same locations (but not always the same seasons) at which oxygen is depleted.

Nitrate

Nitrate levels in entering fresh water varied from 0 in late summer to more than 30 μM during the winter (Figure 4, Table 1). Nitrate levels in entering marine waters behave in about the opposite manner to levels in freshwater; values are lower in the winter (2-9 μM) and higher during summer upwelling (10-23 μM). Nitrate-salinity regression analyses (Table 1) showed good correlation. Exceptions occurred during late April and early May of all three years, when values were low in both entering fresh and marine waters. Freshwater values were probably low as a result of upstream phytoplankton growth; marine values were low because upwelling had not yet begun. Nitrate showed less of a tendency to be enriched in the bottom waters at stations II and IIA than did phosphate.

Comparison of upstream nitrate determinations taken by Dr. Kilho Park during 1966 (Figure 5) shows that the Willamette River is a major source of Columbia River nitrate. Nitrate values are generally much higher in the Willamette River than in the Columbia upstream from the entrance of the Willamette; the estuary values tend to fall in between. As a result, estuary nitrate levels are high

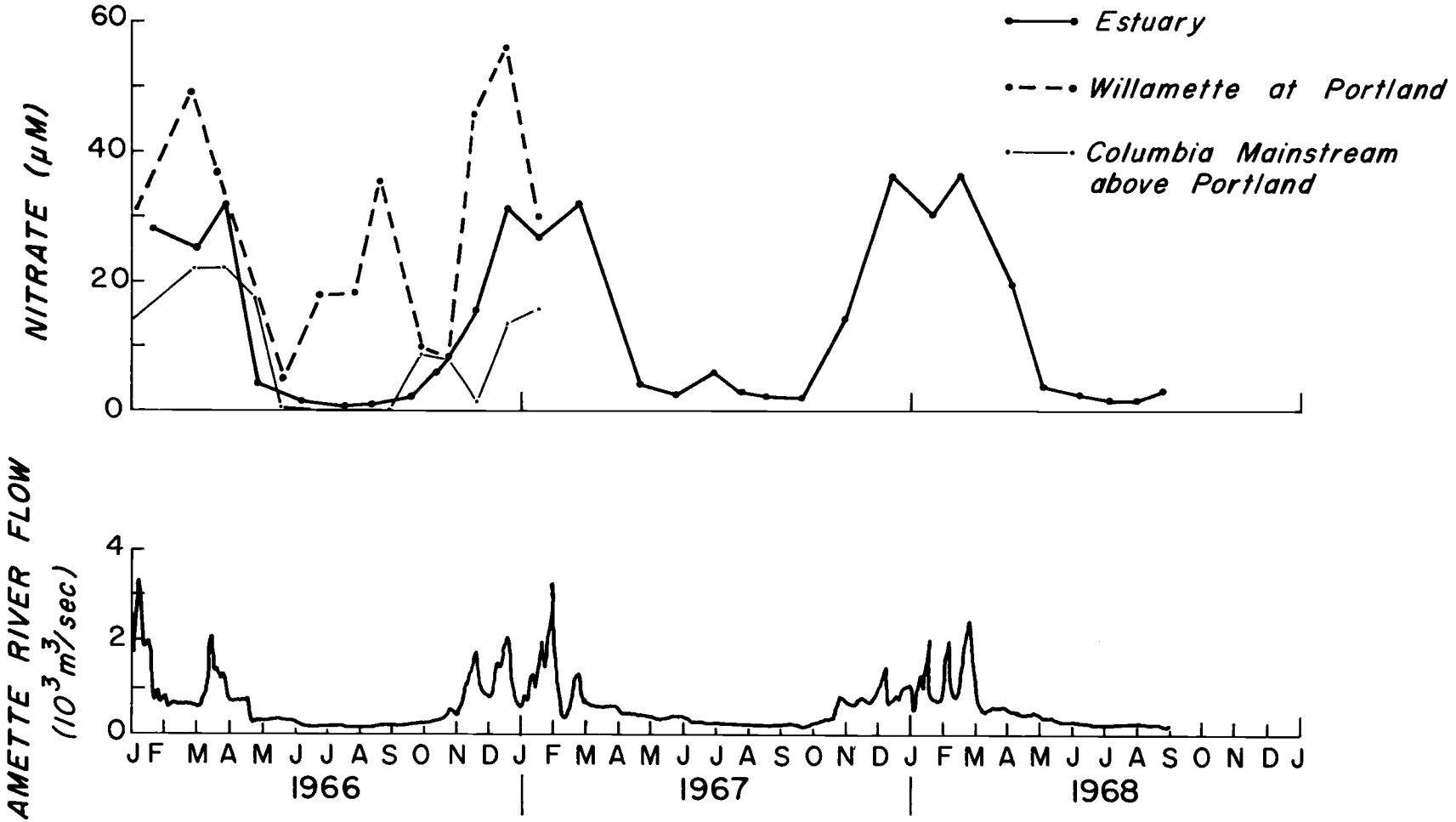


Figure 5. Estuary (freshwater) nitrate values compared with upstream nitrate values and Willamette River flow.

when Willamette River flow is high (Figure 5). During the summer, Willamette River flow is low, and even though Willamette nitrate values may be high, they have little effect on estuary values.

During the months that nitrate was depleted in entering river water, an anomalous nitrate distribution was present in the estuary at low tide. At this time, high nitrate levels were found in the surface waters of the most downstream station (I). Values were 3-8 μM higher than would have been predicted from the salinity present. Because the nitrate maximum was in the fresh surface waters and not the slightly more saline bottom waters, it probably did not originate with upwelled waters present in the salt wedge. Also, nitrate was not found to be enriched in either surface or bottom samples from any of the other stations at low tide. Enrichment of the surface waters at station I may also have occurred during the winter months; however, very high nitrate levels present in the entering fresh water at this time would mask its presence.

In order to determine the source of the enrichment, a grid of 5 stations was sampled at surface and 10m on June 17, 1968. The center of the grid was station I, and the 4 other stations were distributed 1 1/2 miles upstream in the direction of the north channel, 1 1/2 miles upstream in the direction of the south channel, and 2 stations 1 1/2 miles downstream, one on the north side, and one on the south side of the mouth of the estuary. Although nitrate levels

were low (0.2-1.3 μM), the distribution was consistent in that surface values at all 5 stations were higher than values at 10 m at the same station, and the 2 stations on the south side had the highest values of all. An additional 25 surface nitrate samples were taken in the south channel on July 31, 1968. The locations and results of these samples are shown on the top map of Figure 6. Although the values were somewhat inconsistent, they did tend to be minimum at some point in the center of the channel, and the mean values computed from the 5 samples taken across the channel at any one point were definitely higher downstream of Astoria and downstream of Hammond. Although inadequate knowledge of circulation patterns prohibited definite interpretation of the data, one possible contour diagram, shown in the lower map (Figure 6) would implicate Hammond and Astoria as sources of enrichment. Both communities have canneries which contribute raw sewage to the river, and Astoria also dumps untreated domestic sewage into the river. The relative contribution attributed to Hammond seems unrealistically large, considering the small size of the community, and some other source may be implicated. Although one would expect a much greater ammonia than nitrate enrichment from sewage, ammonia values were not measured. The possibility also exists that the nitrate enrichment was from the sediment depositional areas of Young's Bay and the small embayment into Clatsop spit. However, little is known of the

chemistry of the sediments in these areas. Chromium analysis by Jennings (1966) in Young's Bay indicated that the sediments in that area might be reduced, thus making them an unlikely source of oxidized nitrogen.

Nutrient-Upwelling Relations

Upwelling of subsurface waters is known to occur along the Oregon and Washington coasts during the summer months, and is associated with offshore transport of surface waters, caused by a wind from the north. Upwelled waters are characterized by high salinities and nutrients, and by low temperatures and dissolved oxygen (Park, Pattullo and Wyatt, 1962; Stefansson and Richards, 1963; Matson, 1964).

Bourke (1968) has devised a method by which upwelling can be determined from temperature measurements taken in the salt wedge in an estuary. He averaged the north component of the wind over a period prior to the day the water temperature was measured in the estuary, and performed linear regression analysis of the average wind velocity vs. the temperature. He was able to establish that the two were significantly related. He tried different time intervals and weighting schemes for determining the average wind velocity, but found the best correlation with a 4-day period, with the 3rd day prior to the temperature measurement doubly weighted.

The upwelling situation offshore from Yaquina Bay, the estuary studied by Bourke, should be somewhat less complicated than that offshore from the Columbia River. The tremendous quantity of water transported by the Columbia River forms a high temperature, low salinity surface plume, which in the summer months is transported west and south along the Oregon coast. When upwelling occurs offshore from Yaquina Bay, the warmer, fresher plume waters are displaced offshore and the difference is immediate and obvious. However, it is impossible for the plume to be displaced offshore at the mouth of the Columbia River, since the river is constantly supplying large quantities of new plume water. That upwelling does affect the salt wedge entering the Columbia River is clearly shown by the oxygen, phosphate and nitrate levels (Table 1). Levels of all three were greatly changed during the upwelling season. Nutrient levels were much higher and oxygen levels were much lower than those of either non-upwelled oceanic waters or Columbia River water. That the process is more complicated than that off Yaquina Bay is indicated by the temperatures, which were increased, rather than decreased, on most dates during the upwelling season. The increased temperatures might reflect mixing with the very warm river water. However, if the salt wedge were simply a mixture of Columbia River water and recently upwelled waters, extension of temperature regression lines to 33.8 ‰, a salinity characteristic of

upwelled waters, should give the lowered temperatures (9-10°C) associated with upwelling. It does not (Figure 7) indicate that this water has acquired heat from some other source. Possible sources of this heat could be either non-upwelled oceanic surface waters, or previously upwelled waters that have been at or near the surface for some time and thus affected by solar heating. The high nutrient levels present in the salt wedge would indicate that upwelled water is a likely source.

In order to determine if a correlation was present between wind and the nutrient and oxygen levels in the Columbia salt wedge, different periods of time were used to calculate the average north-wind component prior to a given sampling date. The periods tried were: 4-day, 15-day, 30-day, 30-day with the last 15 days double weighted, 45-day, 45-day with the last 15 days double weighted, 60-day, 60-day with the last 15 days doubly weighted, 60-day with the last 15 days triply weighted, and 75 day. None of the time periods tested showed a significant correlation with oxygen or phosphate, either when plotted vs. the value found at 30‰, or vs. the slopes of the oxygen or phosphate-saliniety regression lines. However, several of the time periods tested showed a correlation with both the nitrate values at 30‰ and the slopes of the nitrate-salinity regression lines. The best correlation coefficient (.81) was found plotting the nitrate-salinity slope vs. the 60-day wind component

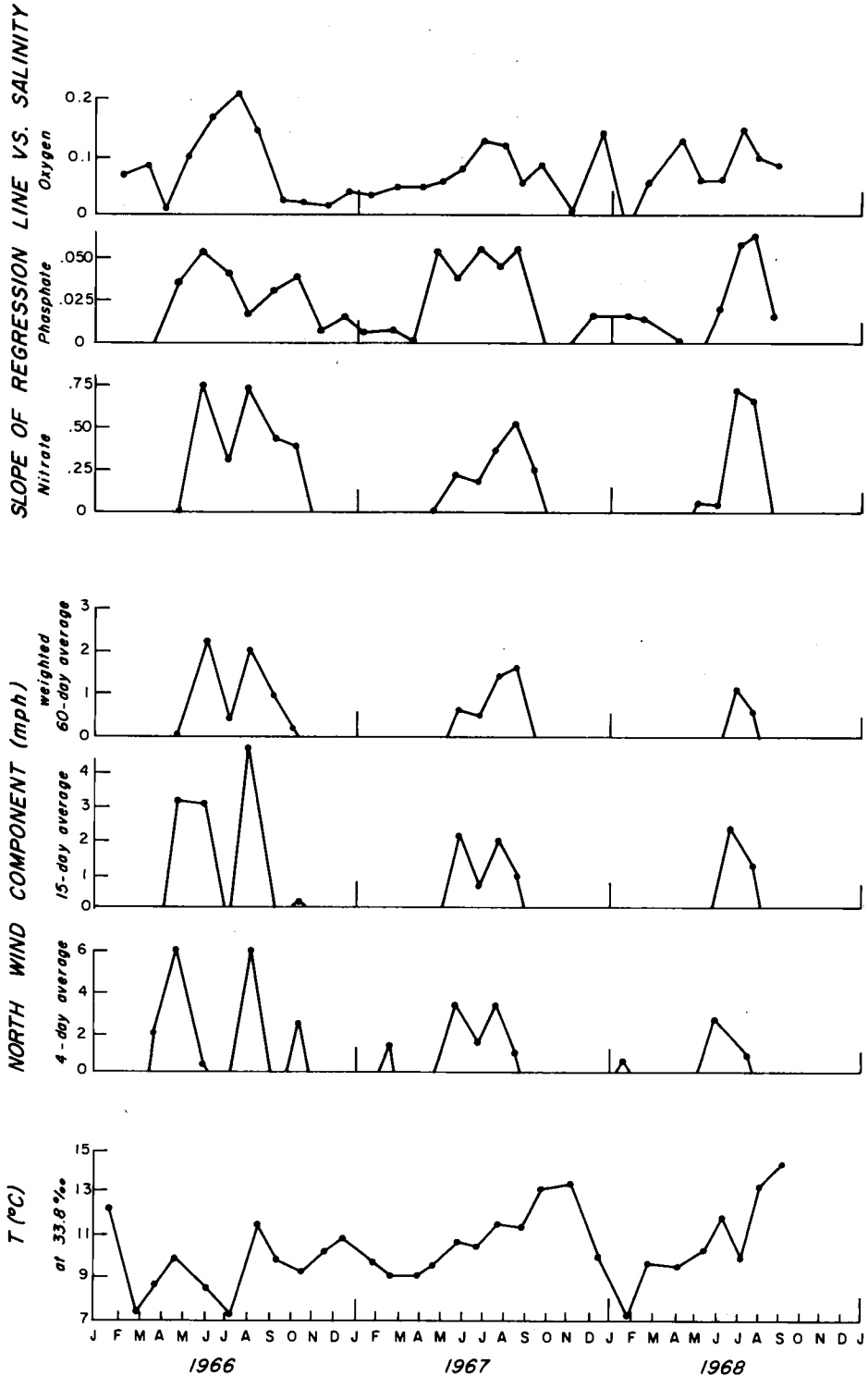


Figure 7. Oxygen and nutrients (slopes of regression lines vs. salinity) compared with various averages of the northwind component.

average with the last 15 days triply weighted. Figure 7, a comparison of oxygen and nutrient slopes with some representative wind averages, shows the excellent nitrate-wind correlation.

The extreme non-conservative nature of both oxygen and phosphate, discussed earlier, may explain their lack of correlation with any of the wind averages. The nitrate results are more difficult to interpret. The 60-day period seems unusually long, considering that nitrate is an essential phytoplankton nutrient; that nitrate is not depleted by the time these waters reach the salt wedge is a paradox. It is generally assumed that phytoplankton take up fifteen times as much nitrogen (by atoms) as phosphorus. However, the ratios of nitrate:phosphate in the salt wedge during the upwelling season (Figure 7) would indicate nitrate to be the limiting nutrient and thus liable to depletion by phytoplankton. A possible explanation might be that the phytoplankton were obtaining a major part of their nitrogen from ammonia or organic nitrogen and not depleting the nitrate. Another possibility might be that a substantial fraction of the upwelled water entering the Columbia salt wedge might have been below the surface, too deep to be noticeably depleted by phytoplankton, but sufficiently shallow to undergo some degree of solar heating.

The long (60-day) time period does provide a convenient explanation for the discrepancy between the low temperatures expected of upwelled waters, and the high temperatures found.

Presence of upwelled water at or near the surface for such a length of time in the summer would expose it to solar heating and certainly increase its temperature.

The predominant current direction of surface and near-surface offshore waters is from the north, with a southward velocity component of about 10 cm/sec (Stevenson, 1967), or approximately 8.6 km/day. This rate, together with the correlation shown between the nitrates and the 60-day wind average, would indicate that water found in the Columbia salt wedge could have its source in upwelled waters from as far as 516 km north of the river mouth. This would include the area offshore of the Washington Coast. Surface salinity and chlorophyll data (Anderson, 1963, 1964) indicates that upwelling probably does occur offshore of the Washington Coast.

PHYTOPLANKTON

Phytoplankton species are listed and described as to abundance and the frequency with which they were collected in Table 2. Although many marine species were encountered, they were present less frequently and in much smaller numbers than freshwater species, and their contribution to the estuary plankton was slight. The estuary phytoplankton was at all times dominated by Melosira spp., Fragilaria crotonensis, Asterionella formosa, Stephanodiscus astrea, and Synedra ulna, forms which are characteristic of eutrophic lakes (Hutchinson, 1967, p. 381). Freshwater populations sampled in the estuary bore a close floristic resemblance to those recorded by the U. S. Federal Water Pollution Control Administration at Clatskanie, Oregon, 30 miles upstream from the estuary (Table 2), indicating the estuary plankton to be a downstream extension of the river plankton.

Spatial Distribution

As would be expected of a plankton dominated by freshwater forms, populations were much higher in the entering freshwater, and both chlorophyll a and numbers of cells decreased downstream with increasing salinity. Chlorophyll a measurements tended to show less depletion than cell counts. In spite of the consistent depletions at high salinities, distributions tended to patchiness, and

Table 2. Phytoplankton collected in the Columbia River estuary.

Freshwater species	Range of[1] abundance	Sampling[2] frequency
Euglenophyta:		
*Unidentified	$10^{(-1)-1}$	x
Chlorophyta:		
Volvox sp.	-	-
Sphaerocystus sp.	10^{1-2}	x
*Dictyosphaerium sp.	$10^{(-1)-2}$	x
Hydrodictyon sp.	-	-
*Ankistrodesmus sp.	10^{0-1}	x
*Scenedesmus spp.	$10^{(-1)-3}$	xxx
Spirogyra spp.	-	-
Closterium sp.	$10^{(-1)-1}$	x
Staurastrum spp.	$10^{(-1)-2}$	x
Chrysophyta:		
*Melosira varians	$10^{(-1)-2}$	xxxx
*M. granulata	10^{1-4}	xxx
*M. italica	10^{2-5}	xxxxx
*Stephanodiscus astrea	10^{0-3}	xxxxx
Rhizoselenia sp.	$10^{(-1)-1}$	x
*Tabellaria fenestrata	$10^{(-1)-3}$	xxx
Meridion circulare	$10^{(-1)-1}$	xx
*Diatoma vulgare	$10^{(-1)-1}$	xxxx
*Fragilaria crotonensis	10^{1-4}	xxxxx
*F. construens	$10^{(-1)-3}$	xxx
*F. capucina	$10^{(-1)-2}$	x
*Synedra ulna	10^{0-3}	xxxxx
*Asterionella formosa	10^{1-4}	xxxxx
*Rhoicosphenia curvata	$10^{(-1)-0}$	x
*Cocconeis placentula	$10^{(-1)-0}$	x
*Navicula ludloviana	$10^{(-1)-0}$	x
*N. tripunctata	$10^{(-1)-0}$	x
Pinnularia sp.	$10^{(-1)-0}$	x
*Diploneis smithi	$10^{(-1)-1}$	xx
Gyrosigma sp.	$10^{(-1)-1}$	xx
*Cymbella spp.	$10^{(-1)-1}$	xxxx
C. turgida	$10^{(-1)-0}$	x
Amphora ovalis	$10^{(-1)-3}$	xx
*Nitzschia holsatica	$10^{(-1)-1}$	x
*N. dissipata	$10^{(-1)-1}$	x
N. amphibia	$10^{(-1)-2}$	xx
*Surirella spp.		
Pyrrophyta:		
Ceratium sp.	$10^{(-1)-1}$	x
Marine and brackish species		
Cyanophyta:		
*Anabaena sp.	10^{1-3}	x
*Aphanizomenon sp.	10^{1-3}	x
Spirulina sp.	$10^{(-1)-0}$	x
*Unidentified	10^{1-3}	x
Chrysophyta:		
Melosira sp.	10^{1-3}	x
Stephanopyxis palmeriana	$10^{(-1)-0}$	x
Skeletonema costatum	$10^{(-1)-3}$	xx
Thallassiosira spp.	$10^{(-1)-3}$	xx
T. decipiens		
T. nordenskioldii		
Coscinodiscus spp.	$10^{(-1)-2}$	xx
C. centralis		
C. excentricus		
Actinoptychus splendens	$10^{(-1)-0}$	x
Rhizoselenia sp.	$10^{(-1)-0}$	x
Bacteriastrum delicatulum	$10^{(-1)-3}$	xxx
Chaetoceras spp.	$10^{(-1)-3}$	xxx
C. didymus		
C. convolutus		
Ditylum sp.	$10^{(-1)-0}$	x
Biddulphia spp.	$10^{(-1)-2}$	xx
B. aurita		
B. longicruris		
Prorocentrum sp.	$10^{(-1)-0}$	x
Fragilaria oceanica	10^{0-3}	xxx
Grammatophora sp.	$10^{(-1)-0}$	x
Thallassionema nitzschiodes	10^{0-2}	xx
Asterionella japonica	10^{1-3}	xx
Nitzschia closterium	10^{0-3}	xx
Bacillaria paradoxa	$10^{(-1)-2}$	xx
Unid. Silicoflagellata	$10^{(-1)-0}$	x
Pyrrophyta:		
Ceratium sp.	$10^{(-1)-0}$	x
Peridinium sp.	$10^{(-1)-0}$	x
Unidentified	$10^{(-1)-2}$	xx

[1]Range of abundance (#/ml) calculated as average for entire estuary (freshwater species) and average for stations with > 15 o/oo salinity (marine and brackish species).

[2]Sampling frequency: x = 25%, xx = 25-49%, xxx = 50-74%, xxxx = 75-99%, xxxxx = 100%.

*Also identified at Clatskanie, Oregon by USDI FWPCA Stream Survey 1966-1967.

-Present in zooplankton tows, only.

least squares regression analysis failed to show consistently significant correlations for either chlorophyll a or numbers of cells vs. salinity. In addition, on any one date, or for any one season, spatial distribution of chlorophyll a was not consistently correlated with spatial distribution of numbers of cells, except when extremes were encountered (Figure 8).

An unusual phytoplankton distribution was present at low tide on August 18, 1967 and to a lesser extent on September 19, 1967. On both dates, phytoplankton were greatly increased in the bottom waters at station IIIA at low tide (Figure 8). The exact cause for this distribution is unknown. One possibility would be that the waters found at station IIIA during low tide are those which cover the large areas of shallows immediately upstream during the preceding high tide. The more rapid rate of photosynthesis per water column which would be possible in shallow areas might account for the increased population levels at station IIIA. A hint of the same phytoplankton distribution was present on July 30, 1968 (Figure 8). However, weather and boat operational difficulties prevented sampling station IIIA till several hours after low tide. On this date, the shallows upstream were sampled at high tide in two locations and at several depths, but no unusually high phytoplankton concentrations were found. Why the phytoplankton would be concentrated in the bottom waters remains unsolved. Munk and Riley (1952) have suggested that a diatom's

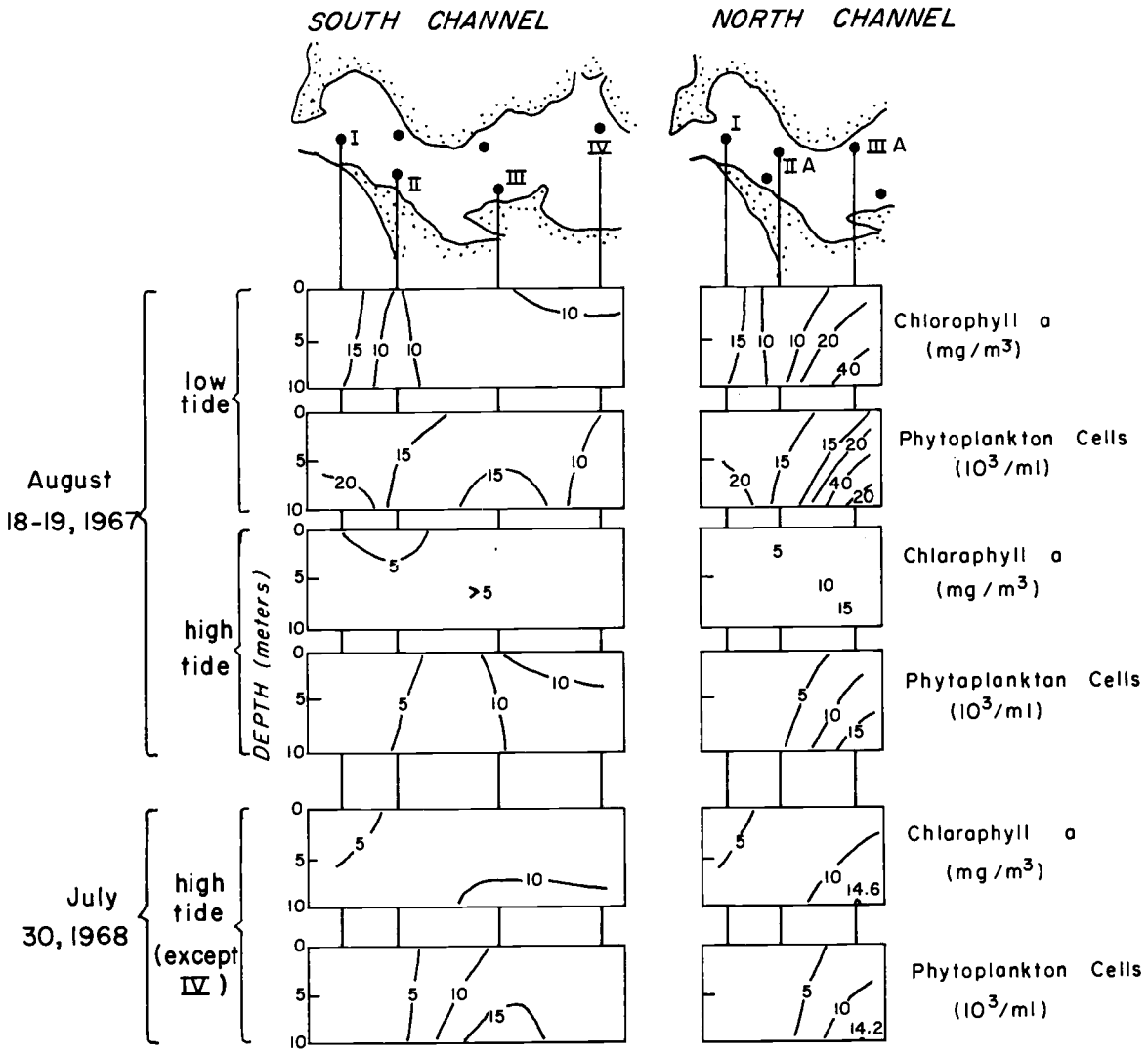


Figure 8. Comparisons of distribution of chlorophyll a and numbers of phytoplankton cells on August 18-19, 1967 and July 30, 1968.

sinking rate increases with nutrient depletion. Although nutrient levels were fairly low at this time (.1-.9 μM NO_3, .01-.2 μM PO_4) evidence is not available to show whether or not the cells were nutrient deficient. In addition, the amount of turbulence present shortly before the lower low tide when station IIIA was sampled would hinder sinking by any object as small as a planktonic diatom.

The amount of turbulence present might, however, suggest another cause for the increased population levels. Lund (1954, 1959) has shown that Melosira spp. undergo perennation; in the lakes he studied, Melosira italica sinks to the sediments when temperature stratification and decreased turbulence set in. The cells in the sediments remain alive and are returned to the water when turbulence resumes. At the sinking rates he calculated for Melosira, (2-8m/hr at 0°C) it should be possible for Melosira to sink in the Columbia estuary at those short periods of the tidal cycle between the ebb and the flood when the current velocity is essentially 0, especially considering the high water temperatures at this time (20-22°C). Resuspension due to turbulence during the subsequent ebb or flood might contribute to the high phytoplankton populations in the bottom waters.

Seasonal Distribution

Freshwater phytoplankton populations showed their greatest abundance between April and September, with the maximum peaks

(17,000 and 26,000 cells/ml) occurring in May of both years of this study. Populations were low to non-existant during the winter months (Figure 9). Marine populations were only found in the salt wedge. They were low to non-existant during the winter and reached maximums of 600 and 1600 cells/ml in late summer. An offshore bloom (primarily Chaetoceras spp.) probably caused the unusually high population level 7500 cells/ml, recorded in the salt wedge on May 10, 1968. Even on that date, however, the relative contribution of marine species (averaged over the entire estuary) to the estuary plankton was slight (Figure 9).

The major factors which might be expected to control phytoplankton population levels are light, nutrients, and river flow. Nutrient levels are high in the winter (Table 1) and would probably not be limiting in that season. River flow has both high and low periods in the winter with no apparent relation to phytoplankton abundance (Figure 9). However, the close correlations between the increases and decreases of phytoplankton populations and solar radiation in both spring and fall, together with the high year-round turbidity as indicated by the low secchi disc reading (Figure 9) would indicate that during the fall and winter, light is most certainly limiting. To partially determine which factors controlled phytoplankton populations during the summer (defined as late April to late August to avoid obvious low light levels), linear regression analysis was

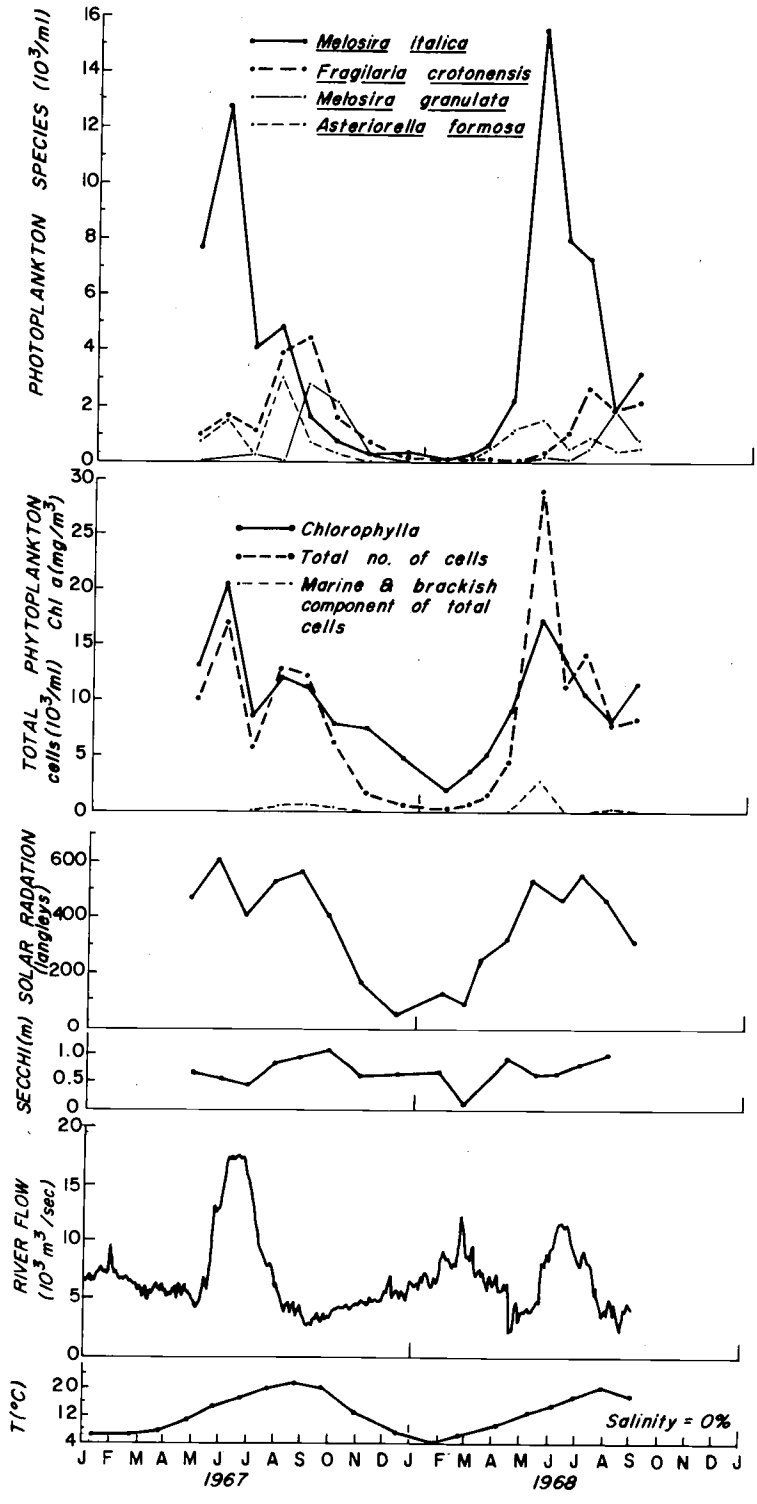


Figure 9. Chlorophyll a and phytoplankton cells (averaged by date from all stations sampled) compared with light, temperature, river flow, and secchi disc readings.

Table 3. Maximum abundance* and seasonal distribution of common freshwater phytoplankton species.

	Season of greatest abundance		
	Spring-Summer	Summer	Summer-Fall
Chlorophyta:			
Sphaerocystus sp.			10^{1-2}
Dictyosphaerium sp.			$10^{(-1)-3}$
Pediastrum spp.			10^{1-2}
Scenedesmus spp.			10^{1-3}
Closterium sp.			10^{0-1}
Staurastrum spp.			$10^{(-1)-2}$
Euglenophyta:			
Unidentified		10^{0-2}	
Chrysophyta:			
Stephanodiscus astrea	10^{2-3}		
Melosira italica	10^{4-5}		
M. granulata			10^{3-4}
M. varians			10^{1-2}
Synedra ulna		10^{2-3}	
Fragilaria crotonensis			10^{3-4}
F. construens	$10^{(1)-3}$		
Tabellaria fenestrata		10^{1-3}	
Asterionella formosa		10^{3-4}	
Nitzschia holsatica			10^{2-3}
Cyanophyta:			
Anabaena sp.			10^{2-3}
Aphanizomenon sp.			$10^{(-1)-2}$
Unidentified			$10^{(-1)-2}$

*Abundance given (no./ml) is the maximum average abundance present in the season of greatest abundance.

performed. Variables tested were: Solar radiation (using averages of 5, 7, and 10 days before sampling), Nitrate, Phosphate, River flow, and Temperature vs. Averages of Chlorophyll a, Freshwater cells, and Marine cells (the latter averaged only from those stations where the salinity was greater than 15‰). Silicate was not tested, since the lowest values measured in entering river water (50 μM) were probably too high to be limiting (Lund et al., 1963; Hutchinson, 1967, p. 447). Marine cells showed little correlation with any of the variables tested (Table 4). Chlorophyll a (primarily a measure of freshwater phytoplankton since the bulk of the phytoplankton was composed of freshwater forms) showed some correlation with both solar radiation and phosphate, and an interesting negative correlation with temperature. The strongest correlations shown were solar radiation (7-day average) and phosphate vs. freshwater cells. Phosphate shows the better correlation, however, plots of the values (Figure 10) show this to be misleading. The uniquely high phytoplankton bloom of May 10, 1968 was the main source of the correlation for the phosphate regression line, and the main source of the lack of correlation for the light regression line--dropping this point would give a much stronger light correlation and virtually no phosphate correlation. The high cell counts present on May 10, 1968 are particularly interesting since this date followed a period of about a week of greatly reduced river flows when an upstream reservoir was being filled.

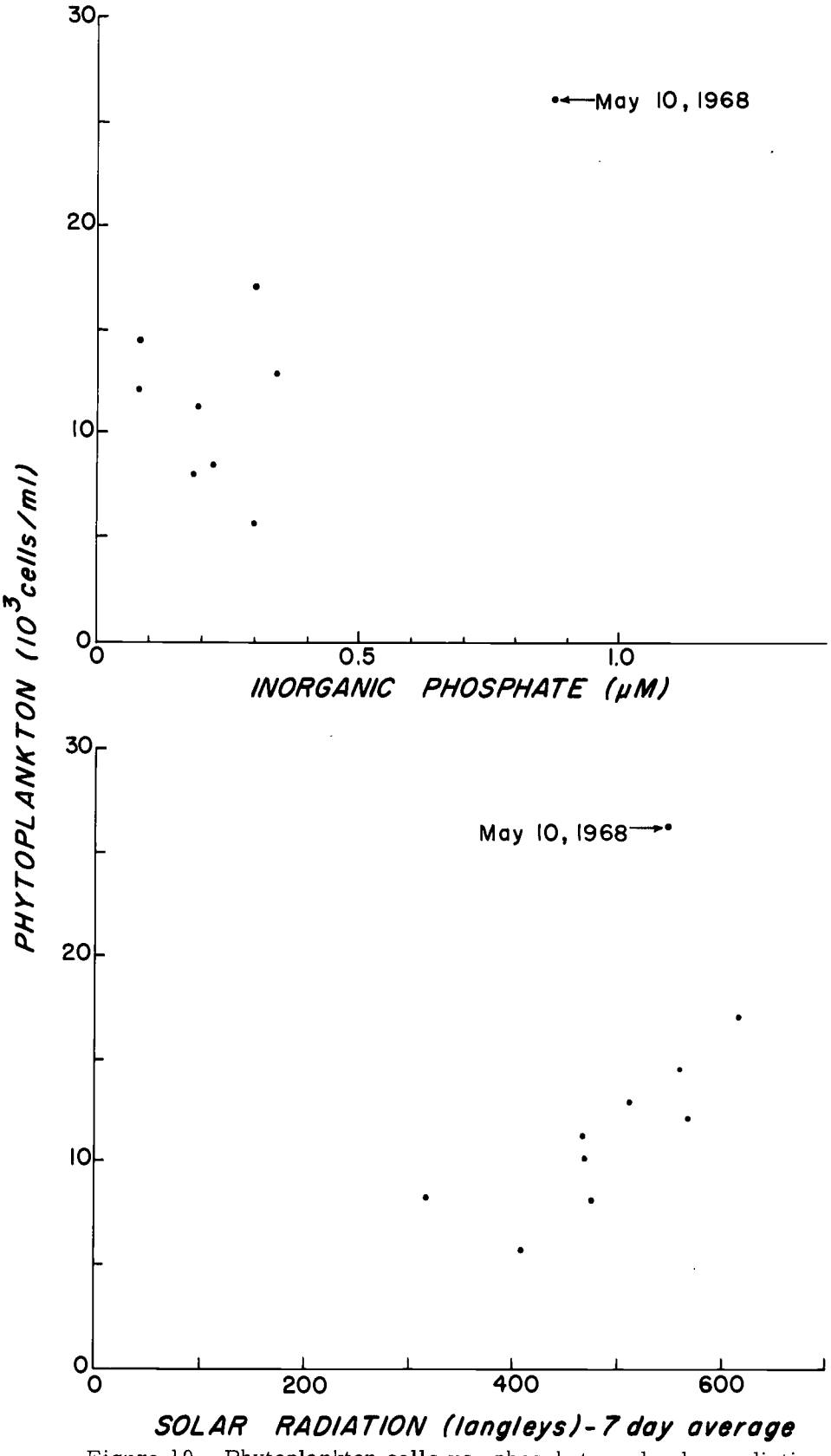


Figure 10. Phytoplankton cells vs. phosphate and solar radiation.

The decreased river flow may well have been accompanied by decreased turbidity making possible much greater photosynthetic activity during this period. Samples were not taken during the period of low river flow, but regression analysis of river flow vs. secchi disc readings showed a fairly strong correlation (-.65). Although Table 4 shows little direct correlation between either cells or chlorophyll a and river flow, this does not mean that river flow cannot limit phytoplankton populations either through dilution and more rapid downstream transport, or through the increased turbidity usually present with increased flow. High turbidity is probably at least partly responsible for the obvious light limitation.

Table 4. Correlation coefficients of linear regression analysis of phytoplankton abundance vs. environmental variables, late April-late August, 1967-1968.

	Chlorophyll a	Freshwater Cells	Marine and Brackish cells
Solar radiation:			
5 day average:	.44	.54	.16
7 day average:	.53	.64	.23
10 day average:	.46	.51	.13
River flow:	.07	-.29	-.34
Temperature:	-.55	-.35	-.24
Nitrate:	-.22	-.30	-.26
Phosphate:	.50	.67	-.53
N	10	10	10

Little correlation was found between phytoplankton and nitrate levels. Nitrate was at times sufficiently low to be limiting (0-.1 μM) and the possibility exists that the plankton were using some other nitrogen source, possibly ammonia, which was not measured in this study. The presence of high zooplankton populations which have been demonstrated to excrete significant amounts of ammonia (Corner and Newell, 1967) would indicate ammonia as a likely alternate nitrogen source.

The seasonal abundance of some of the more common freshwater species (Table 5) shows a typical eutrophic lake succession with diatoms abundant in spring and early summer, and greens and bluegreens becoming moderately abundant in early fall. The seasonal succession of the four major freshwater diatom species, Melosira italica, M. granulata, Fragilaria crotonensis, and Asterionella formosa (Figure 9) shows that M. italica is definitely a spring species, whereas F. crotonensis and M. granulata are more abundant in summer and late summer. A. formosa could apparently be abundant during both seasons. Regression analysis of some of the factors which might be expected to control this seasonal succession (Table 5) shows a significant negative correlation with temperature for M. italica and significant positive correlations with temperature for M. granulata and F. crotonensis, indicating temperature to be a major cause in the succession of these species.

Lund (1954, 1955) found M. italica to be limited by both high temperatures and high light intensities. The turbidity of Columbia River water in early summer may have prevented high light intensity from limiting M. italica populations at that time. The high correlation shown between M. italica and phosphate, like the high correlation shown between freshwater cells and phosphate, would not be present if the values from May 10, 1968 were dropped. The apparent negative correlations between F. crotonensis and M. granulata and nitrate, phosphate, and river flow may be coincidental, reflecting decreases in these variables in late summer when temperatures are high.

Table 5. Correlation coefficients of linear regression analysis of four phytoplankton species vs. environmental variables, late April-late August, 1967-1968.

	Melosira italica	Asterionella formosa	Fragilaria crotonensis	Melosira granulata
Solar radiation (7 day)	.48	.42	-.16	.06
River flow	.11	.06	-.16	-.61
Temperature	-.73	-.07	.74	.71
Nitrate	.04	-.23	-.35	-.48
Phosphate	.71	.33	-.51	-.53
N	10	10	11	9

ZOOPLANKTON

The same three major groups of zooplankton were found in this study as were reported in Haertel and Osterberg (1967); the freshwater group (dominated by Cyclops vernalis, Bosmina sp., and Daphnia longispina), the oligohaline group (most abundant in waters of 0.2-10‰ salinity, composed principally of Eurytemora affinis and Canuella canadensis), and the polyhaline group (most abundant in waters of 15‰ or more salinity dominated by Pseudocalanus minutus and Acartia clausi). Table 6 lists the species encountered, their range of abundance and sampling frequency. Those species designated with an asterisk are probably not planktonic, but are present in plankton tows as a result of greater velocity and scouring action at times of high river flow. Table 6 includes the species recorded since October 1965 and differs slightly from the records before that date (Haertel and Osterberg, 1967). Several additional species are listed. Acartia tonsa and Clausocalanus arcuicornis, not encountered since 1964, are not listed. Chydorus globosus, recorded in 1964 and 1965, was apparently replaced by Chydorus sphaericus in 1966.

Spatial Distribution

The freshwater group of zooplankton was abundant throughout the estuary at low tide, but showed obvious depletion at salinities

Table 6. Zooplankton collected in the Columbia River estuary.

Freshwater species	Range of[1] abundance	Sampling[2] frequency
Protozoa:		
Volvox sp.	$10^{(-1)-2}$	xx
Rotatoria:		
Brachionus plicatilis	10^{1-2}	x
B. calyciflorus	$10^{(-1)-3}$	xx
Asplanchna sp.	$10^{(-1)-3}$	xx
Keratella sp.	?	x
Arthropoda:		
Leptodora kindti	$10^{(-1)-0}$	x
Sida crystallina	$10^{(-1)-2}$	xx
Diaphanosoma brachyurum	$10^{(-1)-2}$	xx
Daphnia pulex	$10^{(-1)-1}$	x
D. longispina	$10^{(-1)-4}$	xxxx
Ceriodaphnia quadrangula	$10^{(-1)-3}$	xx
Moina sp.	10^{1-2}	x
Bosmina spp.	$10^{(-1)-4}$	xxxx
*Ilyocryptus sordidus	$10^{(-1)-2}$	x
Macothrix sp.	$10^{(-1)-0}$	x
*Eurycercus lamellatus	$10^{(-1)-1}$	x
*Monospilus dispar	$10^{(-1)-1}$	x
*Camptocercus rectirostris	$10^{(-1)-0}$	x
*Leydigia quadrangularis	$10^{(-1)-1}$	x
*L. acantherocoides	$10^{(-1)-2}$	x
Alona costata	$10^{(-1)-2}$	xx
A. quadrangula	$10^{(-1)-2}$	x
*A. affinis	10^{1-2}	x
*Pleuroxus striatus	10^{0-1}	x
*P. denticulatus	$10^{(-1)-0}$	x
Chydorus sphaericus	$10^{(-1)-2}$	xx
Diaptomus spp.	$10^{(-1)-3}$	xxx
D. ashlandi	$10^{(-1)-2}$	x
D. franciscanus	$10^{(-1)-1}$	x
*D. noviamexicanus	$10^{(-1)-1}$	x
*Paracyclops fimbriatus	$10^{(-1)-0}$	x
Cyclops vernalis	$10^{(-1)-4}$	xxxx
Bryocamptus hiemalis	$10^{(-1)-2}$	x

Oligohaline-brackish species	Range of[1] abundance	Sampling[2] frequency
Coelenterata:		
Cordylophora lacustris	$10^{(-1)-2}$	xx
Arthropoda:		
Eurytemora affinis	$10^{(-1)-5}$	xxxx
Canuella canadensis	$10^{(-1)-4}$	xxx
Corophium salmonis	$10^{(-1)-2}$	x
C. spinicorne	$10^{(-1)-0}$	x
Anisogammarus confervicolous	$10^{(-1)-0}$	x
Polyhaline-Marine species		
Coelenterata:		
Aequoria sp.	$10^{(-1)-0}$	x
Aurelia sp.	$10^{(-1)-1}$	x
Sarsia sp.	$10^{(-1)-0}$	x
Obelia sp.	$10^{(-1)-0}$	x
Ctenophora:		
Pleurobrachia	$10^{(-1)-0}$	x
Arthropoda:		
Evadne nordmanni	10^{0-3}	xx
Podon leuckarti	10^{0-3}	xx
Acartia clausi	10^{0-5}	xxxx
A. longiremus	$10^{(-1)-4}$	xxx
Pseudocalanus minutus	10^{0-4}	xxxx
Calanus finmarchicus	$10^{(-1)-4}$	xxx
Paracalanus parvus	10^{0-2}	x
Centropages mcmurrichi	10^{0-4}	xx
Epilabidocera amphitrites	10^{0-1}	x
Oithona similis	10^{0-4}	xxxx
O. spinirostris	$10^{(-1)-2}$	x
Corycaeus affinis	$10^{(-1)-2}$	xx
Cirripedia larvae	$10^{(-1)-3}$	xxx
Neomysis rayii	$10^{(-1)-0}$	x
N. kadiakensis	$10^{(-1)-0}$	x
Acanthomysis macropsis	$10^{(-1)-1}$	x
Archaeomysis grebnitzkii	$10^{(-1)-2}$	x
Gnorimosphaeroma oregonensis	10^{0-2}	x
Euphausiaceae larvae	10^{0-2}	x
Crangon larvae	10^{0-2}	x
Cancer larvae	$10^{(-1)-2}$	x
Chaetognatha:		
Sagitta elegans	$10^{(-1)-2}$	xx
Chordata:		
Oikopleura sp.	$10^{(-1)-3}$	xx

[1] Range of abundance (#/ml) calculated for freshwater species as average forstations with < 5 o/oo, for oligohaline species as average for stations with 0.2-25 o/oo salinity, for polyhaline species as average for stations with > 15 o/oo salinity.

[2] Sampling frequency: x = 25%, xx = 25-49%, xxx = 50-74%, xxxx = 75-99%.

*Present only at times of high river flow.

above 5‰ at high tide. No difference in abundance was noted between the two channels of the estuary. Distribution with depth was uniform for the population as a whole; however, Cyclops vernalis was definitely more abundant at 10m whereas Bosmina sp. was definitely more abundant at the surface.

The oligohaline zooplankton group was most abundant in the center of the estuary, in both channels, and showed obvious depletion both upstream and downstream. At low tide the center of abundance was found at stations II and IIA; at high tide it shifted upstream to stations III and IIIA. The salinity distribution of Eurytemora affinis, the major species (Figure 11), indicates that the center of abundance was found around .5-1.0‰ salinity. This group was definitely concentrated at depth. Both Eurytemora and Canuella tended to be an order of magnitude more abundant at 10m than at the surface of the same station, even though the salinity at the surface was apparently the more favorable. Considering the rapid flushing time of the estuary, the tendency of the population to be concentrated at depth, where the net circulation was usually upstream, was undoubtedly a significant factor in enabling the population to be maintained within the estuary.

The polyhaline group was associated with the salt wedge, and showed increasing abundance with increasing salinity in both channels. This group, too, was much more abundant at 10m than at the surface.

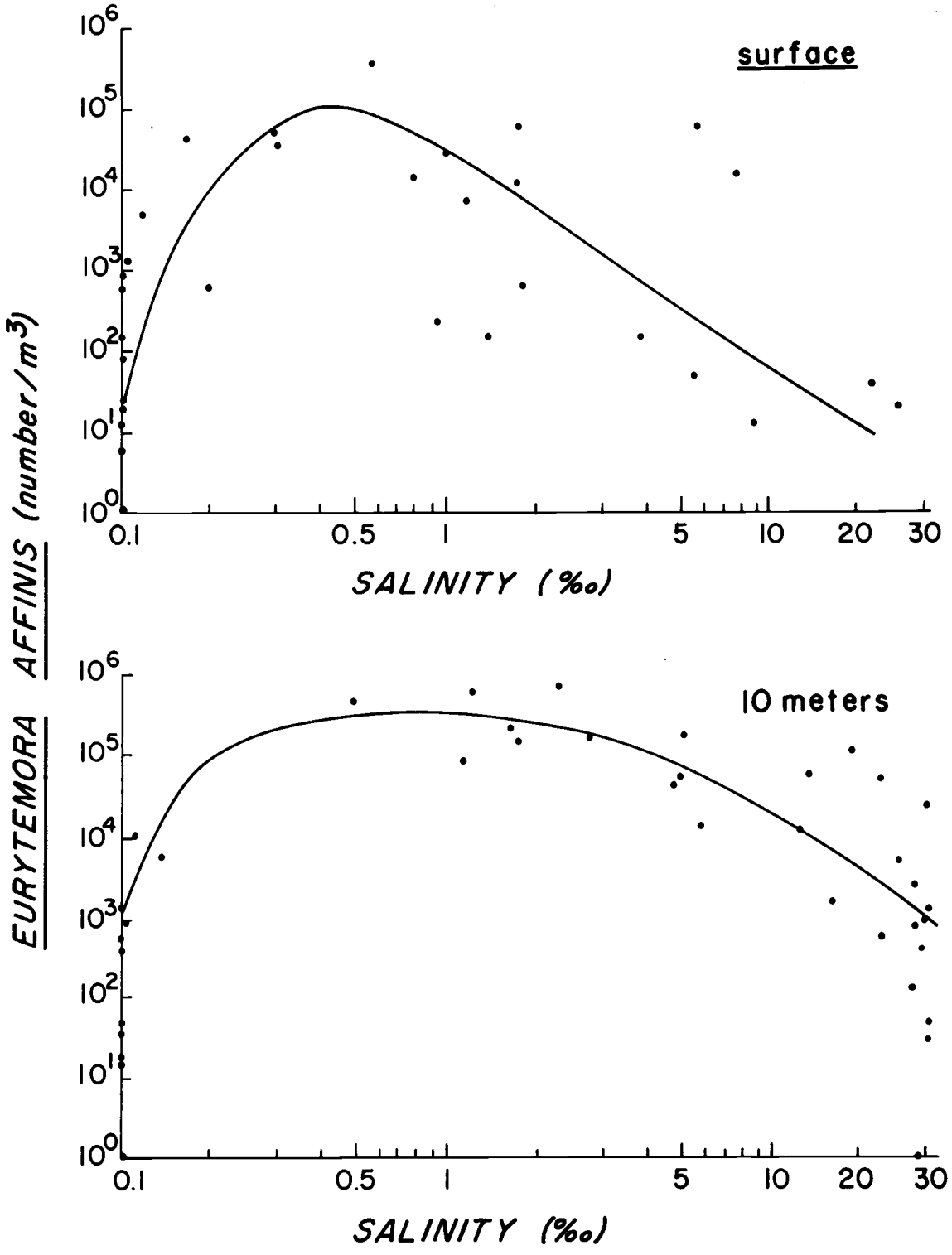


Figure 11. Salinity distribution of Eurytemora affinis on dates of peak population levels.

Although this was partly a reflection of the salinity distribution, samples taken at times of low river flow, when little salinity difference was present between 0 and 10m, still showed an order of magnitude more abundance at 10m. The tendency to be concentrated at depth probably also helped to maintain this group within the estuary.

Seasonal Distribution

Freshwater zooplankton populations (Figure 12) showed their greatest abundance in late summer (August-September) during all five years for which data are available, reaching highs of 2000-5000/m^3. A lesser spring peak was also present in three of the five years. The population decreased to 20-50/m^3 in winter, with the minimum usually occurring in February and March. Of the major species present, both Cyclops vernalis and Bosmina sp. showed a tendency to a dicyclic pattern, with a major peak in spring and again in late summer. The summer Bosmina peak always occurred before the summer Cyclops peak; throughout the year the oscillations of Cyclops and Bosmina peaks were suggestive of predator-prey interactions (Figure 12). Cyclops vernalis is known to be markedly carnivorous, eating oligochaetes, rotifers, cladocerans and other copepods (Fryer, 1957).

Linear regression analysis of the factors expected to affect

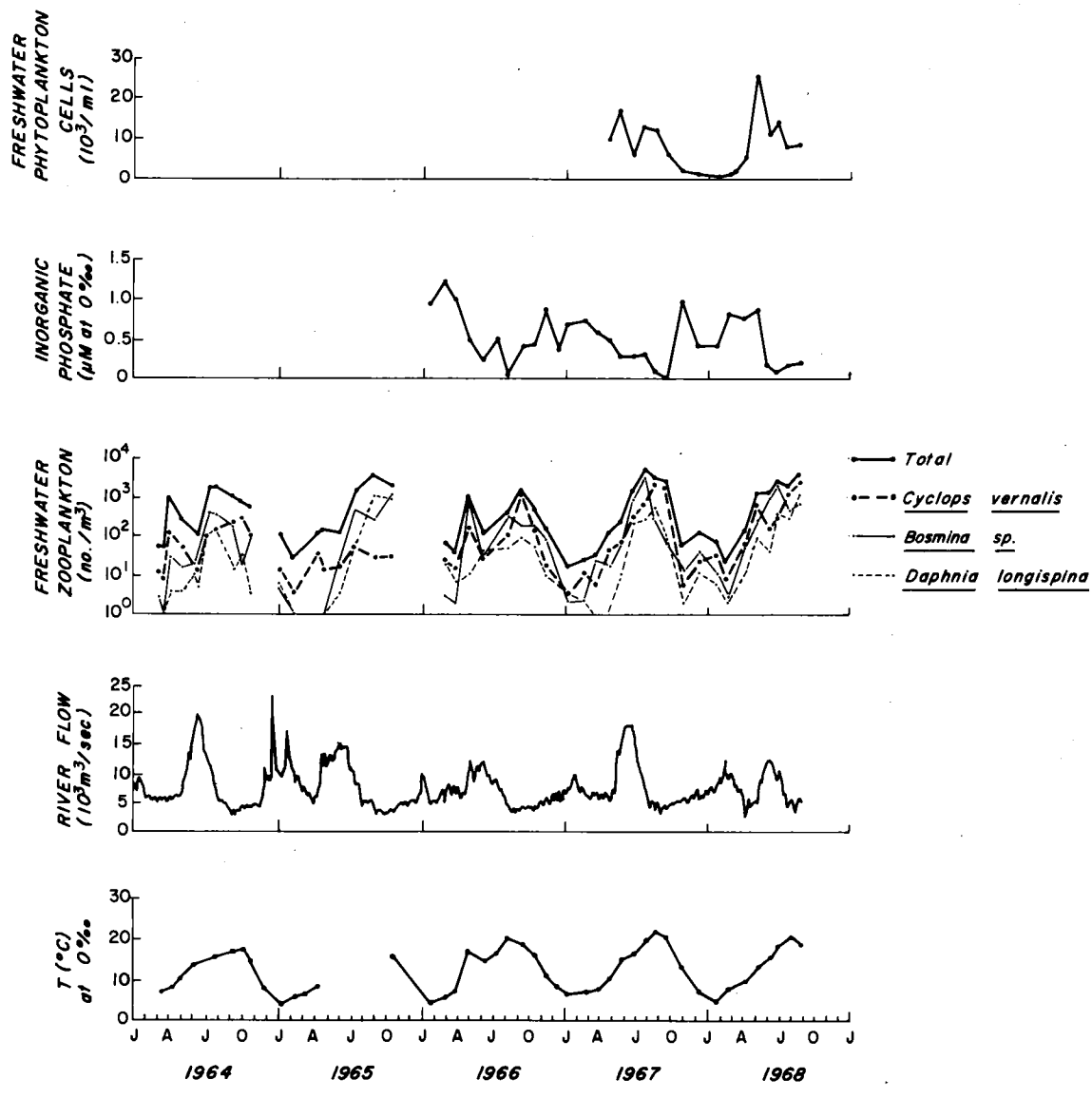


Figure 12. Freshwater zooplankton levels compared with phytoplankton, phosphate, river flow and temperature.

the zooplankton (Table 7) showed the best correlations to be those with temperature, both when analyzed for the entire year and for the summer only. The length of the life cycle and rate of reproduction of both Daphnia and Cyclops has been shown to be strongly dependent on temperature (Hall, 1962; Hutchinson, 1967, p. 581). Thus, in an environment such as the Columbia, where a large segment of the population is continually being lost to sea, the effect of temperature in controlling reproductive rate should be great. The tendency toward correlation with phytoplankton abundance on a yearly basis may be coincidental with the fact that phytoplankton, too, tend to be most abundant in summer, when light levels are highest. The lack of correlation between zooplankton and phytoplankton when analyzed for the summer only probably reflects the fact that phytoplankton are most abundant in early summer when light levels are highest, whereas freshwater zooplankton are most abundant in late summer when temperatures are highest. Although the zooplankton undoubtedly utilize phytoplankton for food, they also may extensively utilize organic debris of the right size; therefore phytoplankton need not limit the abundance of the zooplankton. The correlation between Cyclops and water transparency may reflect the fact that Cyclops is predatory and may well find food more easily with less debris in the water. It may also be coincidental with the fact that river flow is lowest and water transparency is highest at the same time that temperature is

highest, in late summer.

Table 7. Correlation coefficients for linear regression analysis of 1967-1968 freshwater zooplankton population levels vs. environmental variables and phytoplankton

	Temperature (at o/oo)		River flow (cfs)		Water transparency (secchi, m)		Freshwater phytopl. Cells(#/ml)	
	Entire Year	April-September	Entire Year	April-September	Entire Year	April-September	Entire Year	April-September
Daphnia longispina	.84	.80	.01	-.10	.53	.38	.41	-.12
Bosmina sp.	.78	.50	.17	-.29	.42	.01	.53	-.03
Cyclops vernalis	.86	.77	-.15	-.40	.68	.71	.51	-.15
Total Population	.92	.83	-.01	-.10	.58	.53	.52	-.19
N=	19	12	19	12	15	11	16	12

Oligohaline zooplankton populations were composed almost entirely of Eurytemora affinis, which was most abundant (10,000-100,000/m^3 or more) in late April and early May (Figure 13). Populations were decreased during the June period of high river flow and increased to a second, lesser peak in late July. Populations were again low in late August-early October, and reached a peak in late fall and early winter (November-January). Populations again decreased in February and March before the spring peak. Canuella canadensis was the only other species present in this area in any numbers, and had a seasonal distribution which varied greatly from year to year. Since Canuella, a harpacticoid copepod, is undoubtedly benthic, plankton tows may not accurately measure its abundance.

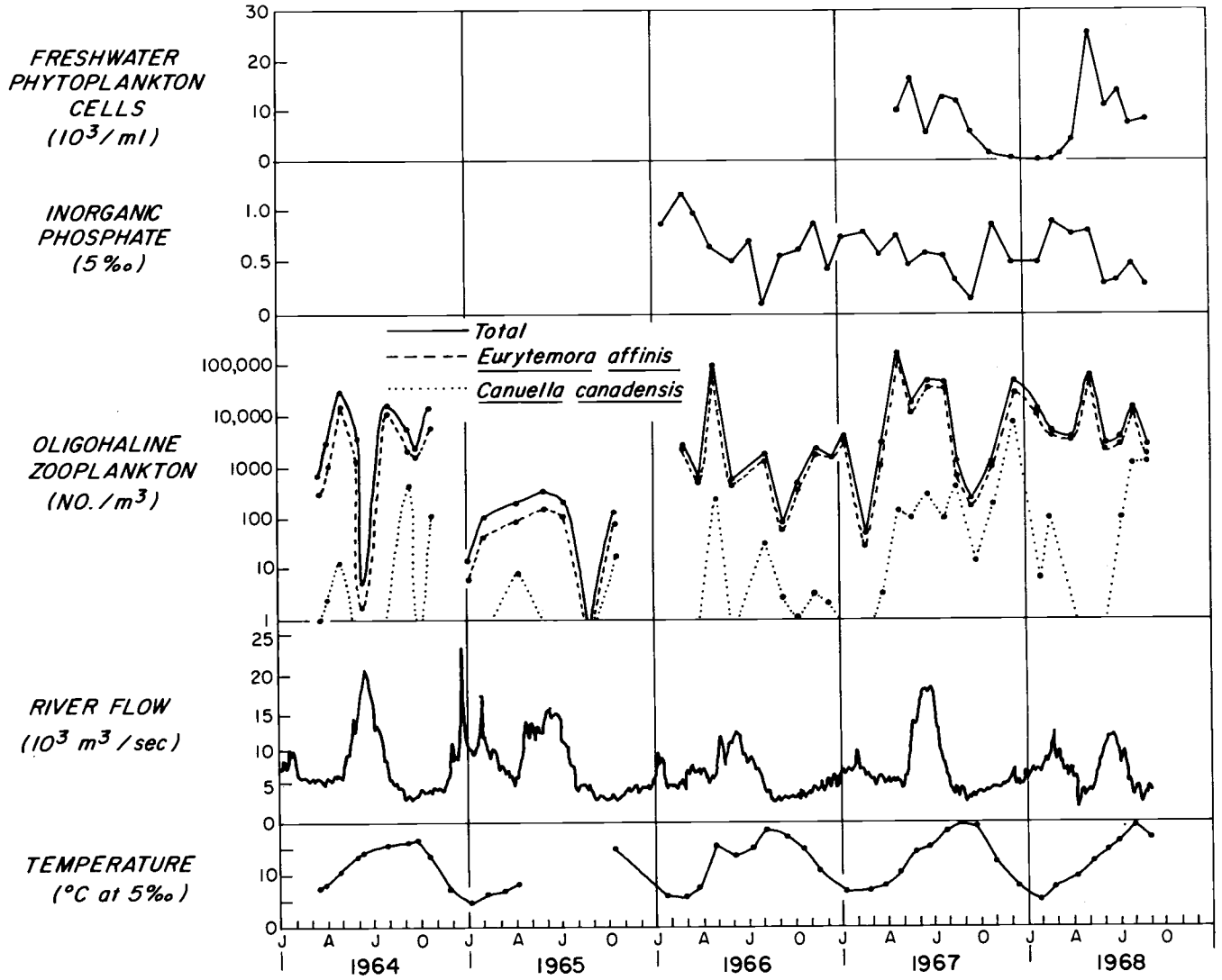


Figure 13. Oligohaline zooplankton levels compared with phytoplankton, phosphate, river flow and temperature.

The exact reasons for the sequence of peaks and depressions of the Eurytemora distribution are unknown. Eurytemora affinis is a filter feeder, and has been shown to feed on Melosira, the principle phytoplankter in the estuary (Burckhardt, 1935). However, examination of Figure 13 shows that during summer 1967, Eurytemora peaks preceded phytoplankton peaks (principally Melosira), the reverse of the relation expected if Eurytemora were dependent on Melosira for food. In addition, the Eurytemora winter peak occurred at a time when Melosira and other diatoms were absent from the water. It does seem feasible that the high spring Melosira population contributed to making the spring Eurytemora peak the highest of the three peaks.

Examination of Figure 13 shows a tendency of Eurytemora populations to be depressed during the June river flow maximum. However, the timing of the Eurytemora depression does not always correspond exactly to the time of high river flow (e.g. June, 1967). Sampling more frequently than once a month might show a more clear-cut relation. Also, the amount of depression varies greatly from year to year. Although it seems likely that high river flow and the resultant increased flushing time would have an effect on an estuarine population, a linear relationship probably does not apply (Table 8).

The late summer depression in Eurytemora populations occurs

at a time of very low river flow, high temperatures, and high water transparency. Any of these factors might conceivably limit Eurytemora populations. Results of decreased river flow include greater salt penetration and a tendency toward a well-mixed, vertically homogenous estuary (Figure 2). In a well-mixed estuary, the net direction of flow in the bottom waters is downstream (Pritchard, 1955). Considering the long generation time (several months) of most calanoid copepods, and the short flushing time of the Columbia, a decrease in the net upstream flow in the bottom waters could conceivably limit the population. It also seems likely that the greater salt penetration could be limiting, considering the apparent oligohaline preference of the population (Figure 11).

Table 8. Correlation coefficients for linear regression analysis of 1967-1968 Eurytemora affinis population levels vs. environmental variables and phytoplankton.

	Temperature (at 5o/oo)		River flow (cfs)		Water transp. (secchi m)		F. w. phytopl. cells (#/ml)		Melosira spp. (#/ml)	
	Entire Year	April-Sept.	Entire Year	April-Sept.	Entire Year	April-Sept.	Entire Year	April-Sept.	Entire Year	April-Sept.
Eurytemora affinis	-.19	-.50	.21	.26	-.33	-.58	.19	.35	.27	.44
N	19	12	19	12	15	11	16	12	16	12

Eurytemora is principally an arctic genus, and high temperatures might also be expected to limit the population. Regression analysis for the summer months only (Table 8) shows a tendency toward a negative correlation. Here again, the temperature maximum

and the Eurytemora minimum do not always occur on exactly the same date (Figure 13); however, once a month sampling is probably not frequent enough to accurately show the relation. The apparent negative correlation between Eurytemora and water transparency may be coincidental. Although Eurytemora is a filter feeder, and increased water transparency may reflect a decreased number of potential food particles, the method of measurement (secchi disc) only reflects the transparency of the surface waters, whereas the Eurytemora populations are concentrated at depth. Without direct measurement, it would be impossible to say whether the transparency of the bottom waters bears any relation to the transparency of the surface waters.

The cause for the late winter depression in Eurytemora numbers is even more obscure. Temperatures at this time are lower than those present in the spring and summer blooms, but higher than those present in the winter bloom. River flow also tends to be intermediate, as does water transparency. Phytoplankton are absent, but were also absent during the winter peak. This depression (and possibly the other peaks and depressions) may well be a function of breeding seasonality and/or the generation time of Eurytemora. Sampling of naupliar and copepodite stages would be necessary to determine if this were the case.

Polyhaline zooplankton populations (Figure 14) were less

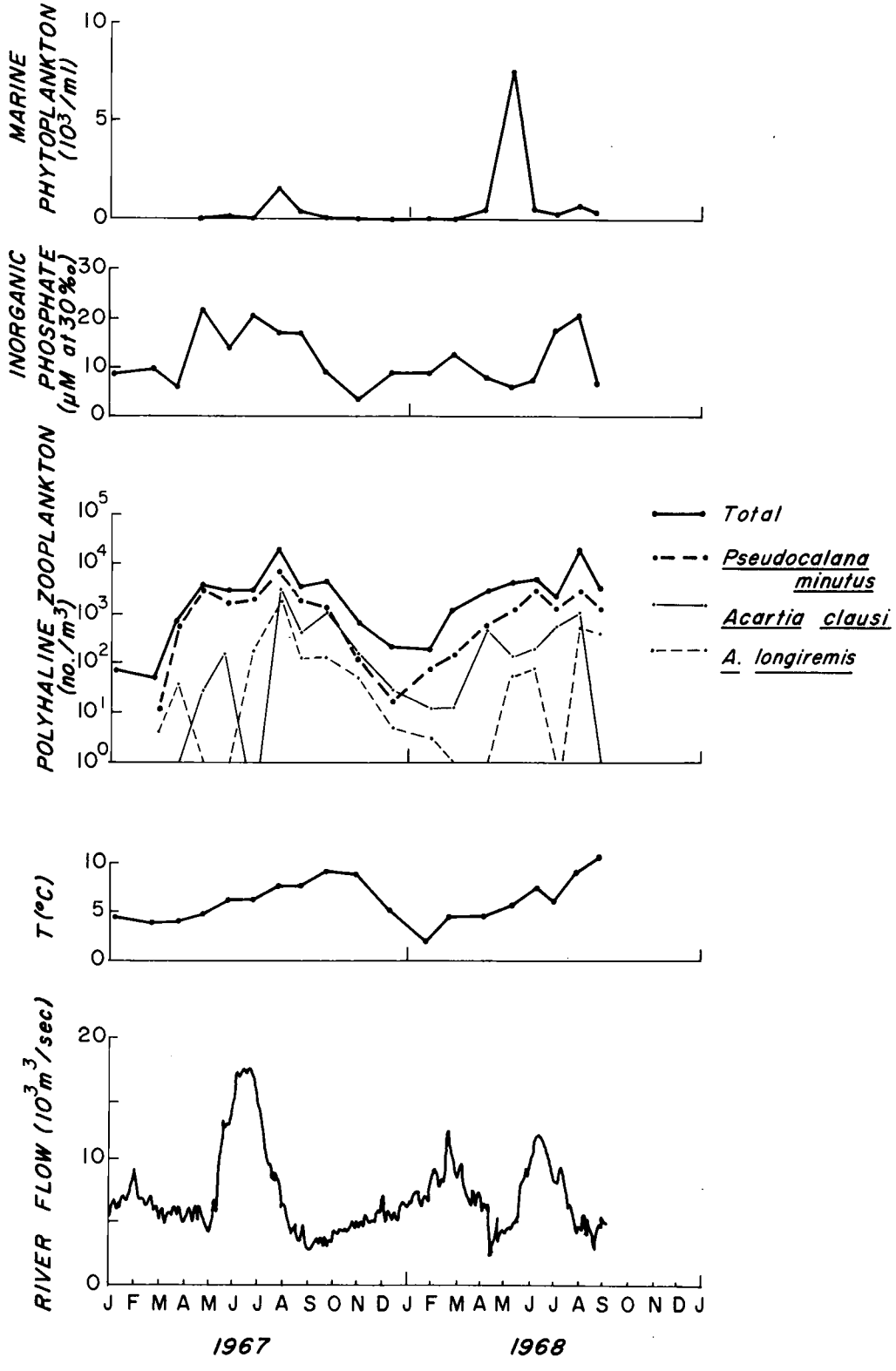


Figure 14. Polyhaline zooplankton levels compared with phytoplankton, phosphate, river flow, and temperature.

abundant than oligohaline populations, ranging from 1000-10,000/m^3 most of the year. They showed a definite peak in July of both years of this study, and were depleted to about 100/m^3 in winter (November-February). Pseudocalanus minutus was the most abundant species on most dates. Acartia clausi was the next most abundant species, but was not consistently present. Acartha longiremus, Calanus finmarchicus, and Oithona similis were also occasionally present in large numbers. The late July peak was in both years occasioned by simultaneous peak populations of P. minutus, A. clausi, and A. longiremus. The seasonal distributions of all species except P. minutus were not otherwise consistent between the two years of this study.

Linear regression analysis (Table 9) showed a high positive correlation with temperature for A. longiremus, and a high negative correlation with river flow for A. clausi. Regression analysis showed no correlation between marine phytoplankton and marine zooplankton, although Figure 14 indicates that the summer peak of marine cells occurred simultaneously with the summer peak of zooplankton. The lack of correlation was probably caused by the unusually high Spring 1968 phytoplankton bloom, which was not matched by a similar zooplankton peak.

Table 9. Correlation coefficients for linear regression analysis of 1967-1968 polyhaline zooplankton population levels vs. environmental variables and phytoplankton.

	Temperature °C (at 30 o/oo)		River flow (cfs)		Marine & brackish phytoplankton cells (#/ml)	
	Entire Year	April-September	Entire Year	April-September	Entire Year	April-September
Pseudocalanus minutus	.47	-.28	.15	.12	.16	-.22
Acartia clausi	.37	.00	-.42	-.69	.15	.11
Acartia longiremus	.70	.69	-.18	-.19	.22	.15
Calanus firmarchicus	.21	.04	.05	-.12	.39	.34
Oithona similis	.29	-.14	.24	.20	-.02	-.11
Total population	.65	.40	.02	-.02	.24	.08
N	19	12	19	12	16	12

RADIOANALYSIS OF PLANKTON

Since the mid 1940's, nuclear reactors at Hanford, Washing have released dilute concentrations of radionuclides into the Columbia River. These are formed by neutron-activation of corrosion products and of impurities in the river water which is used to cool the reactors. In addition, lesser amounts of radionuclides are present in the river water as a result of fallout from nuclear tests in the atmosphere. Many of these radionuclides are gamma-emitters and can be easily assayed by gamma-ray spectrometry. Presence of this radioactivity in the entering river water makes the Columbia estuary a natural laboratory for the study of interactions between radionuclides and the estuarine organisms.

Phytoplankton, zooplankton and detritus (principally wood fibers) radioanalyzed in this study showed a great variation in results. Technical difficulties in obtaining and preparing samples may have accounted for some of the inconsistencies. The major difficulties encountered were:

1. Separation of phytoplankton from detritus. When phytoplankton were present in peak levels, samples of 85-99% purity (by volume) were easily obtained by the methods previously described. On many dates however, it was necessary to repeatedly filter (through a #6 mesh net to

remove larger detritus and through a #25 mesh net to trap the phytoplankton), wash, resuspend, and let settle the sample. Inconsistencies in the numbers of washings and resuspensions may have resulted in inconsistent results by removing different amounts of surface radioactivity.

2. Small zooplankton sample size. Zooplankton could be successfully separated from wood fibers and other detritus by the aquarium method. However, when zooplankton were not present in peak levels, the size of the sample thus obtained was often less than 0.1g dry weight. Although this was partially corrected for by using a longer counting time in the gamma-ray spectrometer (800 minutes), highly inconsistent results were often obtained.

3. Small numbers of samples. On most dates only one to three of the stations yielded samples of either phytoplankton, zooplankton, or wood fibers that passed the arbitrarily set limits of greater than 0.1g dry weight and greater than 80% purity that were used to determine whether a sample would be included in the data. Results from dates when many acceptable samples were obtained indicated a wide range of values from sample to sample. For example, on 24 July 1967, when eight good Eurytemora samples were obtained, values for Zn^{65} ranged from 197-621 pCi/g dry

weight and for Cr^{51} from 266-1104 pCi/g dry weight. Ranges on other dates were equally large, with little of the variation consistent as to sampling locality. Any critical analysis on the basis of season was out of the question, since on most dates individual sample variation could greatly throw off the results.

In spite of the many possibilities for error, some consistencies were noted in the data. Averaging the results for those samples which met the arbitrarily set standards for sample size and purity (Table 10) showed that both wood fibers and freshwater phytoplankton showed much higher values of both Cr^{51} and Sc^{46} than did either freshwater or oligohaline zooplankton. This difference may result from the much greater surface area for adsorbtion present on phytoplankton and wood fibers than on zooplankton. The other artificial radionuclides for which the samples were tested included Ce^{144}, Cs^{137}, Mn^{54}, Co^{60}, and an unidentified β-emitter (probably P^{32}). Of those, Ce^{144} and Mn^{54} were sporadically present in low amounts, Mn^{54} especially in phytoplankton and wood fibers. The unidentified β-emitter could be present or absent in all types of samples. It was frequently present in levels greater than 10,000 pCi/g dry weight in zooplankton samples. Levels in phytoplankton and wood fibers were generally lower.

Table 10. Average values and ranges of values of Cr^{51}, Zn^{65}, and Sc^{46} (pCi/g dry weight) in Columbia estuary phytoplankton, zooplankton, and wood fiber samples.

	number of samples	Cr^{51}		Zn^{65}		Sc^{46}	
		mean	range	mean	range	mean	range
Freshwater phytoplankton	22	2293	0-6700	366	5-1052	192	0-769
Freshwater zooplankton	14	916	0-1954	279	99- 654	5	0- 73
Oligohaline zooplankton (principally Eurytemora)	28	513	0-1697	496	177- 997	6	0- 36
Wood fibers	33	1614	244-3875	539	98-1598	71	0-335

PHYTOPLANKTON-ZOOPLANKTON-NUTRIENT RELATIONS

Zooplankton Excretion of Phytoplankton Nutrients

The importance of zooplankton excretion of ammonia and phosphate to phytoplankton production has been discussed by many authors (Harris, 1959; Ketchum 1962; Pomeroy et al., 1963; Martin, 1965, 1968). Evidence that would suggest this to be important in the Columbia River estuary includes the following:

1. The zooplankton populations frequently reach great densities (10,000-100,000/m^3 or more), especially in the oligohaline area.
2. The excellent correlation between nitrate and wind-induced upwelling is not matched by a similar phosphate-upwelling correlation, although phosphate is known to be enriched in upwelled waters. Zooplankton is one of the likely sources of the phosphate anomalies.
3. Figure 13 shows a good correlation between the time sequence of increased oligohaline zooplankton, increased phosphate, and increased phytoplankton during the season of phytoplankton abundance, especially in 1967.

Unfortunately, data on ammonia are not available. However it was possible to indirectly test the zooplankton-phosphate relation

through regression analysis of freshwater, oligohaline, and polyhaline populations vs. the phosphate concentration at suitable salinities (Table 11). The negative correlation between phosphate and freshwater populations may be coincidental. The freshwater zooplankton maximum, probably as a result of high temperatures, occurs in late summer, and late summer is also the time of maximum river nutrient depletion. Freshwater and polyhaline zooplankton populations ranged from one to two orders of magnitude less abundant than oligohaline populations, and were possibly not abundant enough to noticeably affect phosphate levels. However, the striking positive correlation for the oligohaline population indicates that in this part of the estuary, zooplankton control of phosphate might have occurred. Should phosphate be a limiting element to phytoplankton growth in the estuary, the abundance of oligohaline zooplankton (principally Eurytemora) could affect phytoplankton abundance, providing that the freshwater phytoplankton species in question can reproduce at the slightly brackish salinities favored by Eurytemora.

Table 11. Correlation coefficients for regression analysis of zooplankton vs. phosphate during the season of phytoplankton abundance and nutrient depletion (April to September).

Freshwater Zooplankton vs. phosphate at salinity 0 o/oo (N = 11)	Oligohaline zooplankton vs. phosphate at salinity 5 o/oo (N = 11)	Polyhaline zooplankton vs. phosphate at salinities 15 o/oo, 20 o/oo, 25 o/oo, 30 o/oo (N = 12)	
-.41	.90	.10	.19
		.19	.24

The Columbia River Estuary as a Nutrient Trap

In estuaries where the physical forces predominate over the biological forces, the distribution of nutrients is likely to represent the distribution of the source waters (river and ocean) and thus the distribution of salinity. Where biological forces predominate, unique distributions are likely to occur. In the classic situation, surface phosphate concentrations are depleted in the central portion of the estuary whereas bottom phosphate concentrations are enriched in the center of the estuary. This is usually caused by a phytoplankton bloom in the center of the estuary depleting the surface nutrients. Following the death of the phytoplankton, the dead plankton and contained phosphate fall to the depths causing the increased phosphate concentration there. If a two-layer circulation is present, the nutrients will be recycled, causing continuous phytoplankton productivity. This mechanism was most clearly delineated by Hulburt (1957), but hinted at the Patuxent River (Newcombe and Brust, 1940), Long Island Sound (Riley and Conover, 1956) and Raritan Bay (Jeffries, 1962). The high tide nutrient distribution in the Columbia estuary (Figure 3) shows definite nutrient enrichment in the bottom waters at stations II and IIA, the area of greatest salinity change. The corresponding oxygen depletion would indicate that the nutrient enrichment might partially be a result of local regeneration.

An additional mechanism for entrapment of nutrients in the bottom waters of the central portion of an estuary was suggested by Rochford (1951), namely that phosphates adsorbed onto particulate matter settle out in the central part of the estuary where greatest salinity changes take place, as a result of both decreasing current velocities and electrolytic flocculation. Stations II and IIA are in the area of the greatest salinity gradient, and flocculation and/or sedimentation may well be a source of nutrient enrichment. Interactions with sediments could be a cause of phosphate anomalies, and zooplankton respiration and excretion could cause decreased oxygen and increased phosphate. However, the largest concentrations of zooplankton, the Eurytemora population, are found upstream from stations II and IIA at the stage of the tide when the anomalies occur (high tide).

SUMMARY AND CONCLUSIONS

The distribution of nutrients in the Columbia estuary results from the distribution in the source waters (river and ocean) with some tendency of both nitrate and phosphate to be enriched in the bottom waters in the central part of the estuary. Silicate concentrations are much higher in the river water than in the salt wedge, and are probably never low enough in the river water to limit phytoplankton growth. Phosphate concentrations are approximately equal in river and ocean water in the winter, but are greatly enriched in entering ocean water in the summer upwelling season. They are depleted in the river water in summer and may be low enough in late summer to limit phytoplankton growth. Nitrate concentrations are also enriched in entering ocean water during the summer upwelling season, and like phosphate, may be sufficiently depleted in the river water in late summer to limit phytoplankton growth. Nitrates are greatly enriched in the river water in winter.

The phytoplankton of the estuary is dominated by species characteristic of eutrophic lakes. Melosira italica is dominant in spring and early summer, with M. granulata and Fragilaria crotonensis becoming important in late summer. Regression analysis indicates that temperature may be an important factor in this succession. The phytoplankton are probably light-limited for

most of the year. Low nitrate and phosphate levels in late summer would suggest the possibility of nutrient limitation at this time. Nutrient enrichment studies might be undertaken to determine whether this were the case.

The principle zooplankter of the estuary is Eurytemora affinis, a species which reaches great abundance at low salinities. This species characteristically shows peaks of abundance in late April, late July, and late fall. The exact cause for this seasonal distribution is unknown; it may reflect the generation time of the species; however, data on copepodite and naupliar stages would be necessary to ascertain this. The amount of river flow and resultant estuarine circulation pattern probably influences the ability of the Eurytemora population to maintain itself within the estuary. The population shows a definite tendency to concentrate at depth, a behavioral mechanism which would help to maintain it within the estuary.

The freshwater zooplankton reach their greatest abundance in late summer, and regression analysis indicates a strong correlation between abundance and temperature. Unlike the Eurytemora population, members of this group show no tendency to concentrate at depth, and are constantly being lost to sea. The correlation of abundance with temperature probably results from the control which temperature exerts on rate of reproduction, and reflects the number of generations or offspring which can be produced upstream before

the population is lost to sea.

The polyhaline zooplankton show their greatest population density in late summer, apparently as a result of simultaneous peaks of the three most abundant species. Polyhaline populations show their greatest upstream extension in late summer and early fall. High river flow and resultant low salinities probably prevent this group from occupying much of the estuary during the rest of the year.

The large size of the Eurytemora population and the close correlation between Eurytemora abundance and phosphate levels indicates a strong potential for zooplankton regeneration of phosphate necessary for phytoplankton growth. This would also suggest that ammonia, which was not measured in this study, but which is also excreted by zooplankton, may be a major source of nitrogen for the phytoplankton in the Columbia.

BIBLIOGRAPHY

Anderson, G. C. 1963. Columbia River effluent in the northeast Pacific Ocean, 1961, 1962: Selected aspects of phytoplankton distribution and production. Seattle. 77 numb. leaves. (Washington. University. Department of Oceanography. Technical Report no. 96)

_____ 1964. The seasonal and geographic distribution of primary productivity off the Washington and Oregon coasts. Limnology and Oceanography 9:284-302.

Barnes, C. A. and R. G. Paquette. 1957. Circulation near the Washington coast. In: Proceedings of the Eighth Pacific Sciences Congress, Quezon City, Philippines, 1953. Vol. 3. Quezon City, National Research Council of the Philippines. p. 585-608.

Bourke, R. H. 1968. Monitoring coastal upwelling by measuring its effects within an estuary. Master's thesis. Corvallis, Oregon State University. 98 numb. leaves.

Burckhardt, A. 1935. Die Ernährungsgrundlagen der Copepodenschwärme der Niederelbe. International Revue der Gesamten Hydrobiologie Hydrographie 32:432-500.

Burt, W. V. and W. B. McAlister. 1959. Recent studies in the hydrography of Oregon estuaries. Oregon Fish Commission, Research Briefs 7(1):14-27.

Corner, E. D. W. and B. S. Newell. 1967. On the nutrition and metabolism of zooplankton. IV. The forms of nitrogen excreted by Calanus. Marine Biological Association of the United Kingdom, Journal 47:113-120.

Duxbury, A. C. and N. B. McGary. 1968. Local changes of salinity and nutrients off the mouth of the Columbia River. Limnology and Oceanography 13:626-636.

Fryer, G. 1957. The food of some freshwater cyclopoid copepods and its ecological significance. Journal of Animal Ecology 26: 263-286.

Haertel, L. and C. Osterberg. 1967. Ecology of zooplankton, benthos, and fishes in the Columbia River estuary. Ecology 43:459-472.

Hall, D. J. 1962. An experimental approach to the dynamics of a natural population of Daphnia galatae mendotae. Ecology 45: 92-112.

Harris, E. 1959. The nitrogen cycle in Long Island Sound. Bulletin of the Bingham Oceanographic Collection, Yale University 17(1):31-65.

Hayes, F. R. and J. E. Phillips. 1958. Lake water and sediment. IV. Radiophosphorus equilibrium with mud, plants and bacteria under oxidized and reduced conditions. Limnology and Oceanography 3:459-475.

Hulburt, E. M. 1956. Distribution of phosphorus in Great Pond, Massachusetts. Journal of Marine Research 15:181-192.

Hutchinson, G. E. 1967. A treatise on limnology. Vol. 2. Introduction to lake biology and the limnoplankton. New York, Wiley. 1115 p.

Jeffries, H. P. 1962. Environmental characteristics of Raritan Bay, a polluted estuary. Limnology and Oceanography 7:21-30.

Jennings, C. D. 1966. Radioactivity of sediments in the Columbia River estuary. Master's thesis. Corvallis, Oregon State University. 62 numb. leaves.

Jitts, H. R. 1959. The adsorbtion of phosphate by estuarine bottom deposits. Australian Journal of Marine and Freshwater Research 10:7-21.

Ketchum, B. H. 1962. Regeneration of nutrients by zooplankton. Conseil Permanent International pour l'Exploration de la Mer, Rapports 153:142-147.

Lund, J. W. G. 1954. The seasonal cycle of the plankton diatom Melosira italica subsp. subarctica O. Müll. Journal of Ecology 42:151-179.

_____ 1955. Further observations on the seasonal cycle of Melosira italica (Ehr.) Kutz subsp. subarctica O. Müll. Journal of Ecology 43:91-102.

Lund, J. W. G. 1959. Bouyancy in relation to the ecology of the freshwater phytoplankton. British Phycological Bulletin no. 7, p. 1-17.

Lund, J. W. G., F. J. H. Mackereth and C. H. Mortimer. 1963. Changes in depth and time of certain chemical and physical conditions and of the standing crop of Asterionella formosa Hass in the north basin of Windermere in 1947. Philosophical Transactions ser. B 246:255-290.

Martin, J. H. 1965. Phytoplankton-zooplankton relationships in Narragansett Bay. Limnology and Oceanography 10:185-191.

_____ 1968. Phytoplankton-zooplankton relationships in Narragansett Bay. III. Seasonal changes in zooplankton excretion rates in relation to phytoplankton abundance. Limnology and Oceanography 13:63-71.

Matson, A. L. 1964. Dissolved silicate in waters offshore Oregon and four adjacent rivers. Master's thesis. Corvallis, Oregon State University. 98 numb. leaves.

Mullin, J. and J. P. Riley. 1955. The spectophotometric determination of nitrate in natural waters with specific reference to sea waters. Analytica Chimica Acta 12:464-480.

Munk, W. H. and G. A. Riley. 1952. Absorbtion of nutrients by aquatic plants. Journal of Marine Research 11:215-240.

Murphy, J. and J. P. Riley. 1962. A modified single solution method for the determination of phosphate in natural waters. Analytica Chimica Acta 27:31-36.

Neal, V. T. 1967. Predicted flushing times and pollution distribution in the Columbia River estuary. In: Proceedings of the Tenth Conference on Coastal Engineering, Tokyo, 1966. Vol. 2. New York, American Society of Civil Engineers. p. 1463-1480.

Newcombe, C. L. and H. F. Brust. 1940. Variations in the phosphorus content of estuarine waters of the Chesapeake Bay near Solomon's Island, Maryland. Journal of Marine Research 3:76-88.

Park, K., J. G. Pattullo and B. Wyatt. 1962. Chemical properties as indicators of upwelling along the Oregon coast. Limnology and Oceanography 7:435-437.

Park, P. K., M. Catalfolmo, G. R. Webster and B. H. Reid. 1969. Nutrients and carbon dioxide in the Columbia River. Limnology and Oceanography (submitted for publication).

Park, P. K., C. L. Osterberg and W. O. Forster. 1969. Chemical budget of the Columbia River. In: Bioenvironmental studies of the Columbia River estuary and adjacent ocean region. (to be published by the Atomic Energy Commission).

Parker, R. A. and M. F. Olson. 1966. The uptake of inorganic phosphate by Daphnia schöderi Sars. Physiological Zoology 39:53-65.

Pomeroy, L. R., H. M. Mathews and H. S. Min. 1963. Excretion of phosphate and soluble organic phosphorus compounds by zooplankton. Limnology and Oceanography 8:50-55.

Pomeroy, L. R., E. E. Smith and C. M. Grant. 1965. The exchange of phosphate between estuarine water and sediments. Limnology and Oceanography 10:167-172.

Pritchard, D. W. 1955. Estuarine circulation patterns. American Society of Civil Engineers, Proceedings 81(717):1-11.

Riley, G. A. and S. M. Conover. 1956. Oceanography of Long Island Sound, 1952-1954. III. Chemical oceanography. Bulletin of the Bingham Oceanographic Collection, Yale University 15(1):47-61.

Rochford, D. J. 1951. Studies in estuarine hydrography. I. Introduction and comparative features. Australian Journal of Marine and Freshwater Research 2:1-116.

Stefánnson, U. and F. A. Richards. 1963. Processes contributing to the nutrient distribution off the Columbia River and Strait of Juan de Fuca. Limnology and Oceanography 8:394-410.

_____ 1964. Distribution of dissolved oxygen, density, and nutrients off the Washington and Oregon coasts. Deep Sea Research 11:355-380.

Stevenson, M. R. 1966. Subsurface currents off the Oregon coast. Ph. D. thesis. Corvallis, Oregon State University. 140 numb. leaves.

Strickland, J. D. H. and T. R. Parsons. 1965. A manual of sea water analysis. 2nd ed. Ottawa. 203 p. (Canada. Fisheries Research Board. Bulletin no. 125).

U. S. Corps of Engineers. 1960. Interim report on 1959 current measurement program Columbia River at mouth Oregon and Washington. Portland. 4 volumes.

U. S. Federal Water Pollution Control Administration. 1957-1968. Water Pollution Surveillance System data. (Annual Compilation of data published by the U. S. Dept. of Health, Education and Welfare 1957-1963. Since 1963, unpublished data available on request from the U. S. Federal Water Pollution Control Administration).

U. S. Geological Survey. Water Resources Division. 1964-1968. Water resources data for Oregon. Part 1. Surface Water Records. Portland.