

# PRIMARY PRODUCTION IN THE MID-SUBARCTIC PACIFIC REGION, 1966-68

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## ABSTRACT

Primary productivity, chlorophyll *a*, net zooplankton, nutrients, and associated physical variables were measured on seven cruises in the mid-Subarctic Pacific Region in 1966-68. Most of the data were collected between lat 46° N and the central Aleutian Islands, although several measurements were made as far south as lat 40° N. Primary productivity and chlorophyll were higher in Aleutian coastal waters than in areas to the south, but no other major differences among upper zone domains were consistent seasonally. Production was low in winter, high in spring, and intermediate throughout the summer. Annual productivity was between 80 and 100 g C/m<sup>2</sup>. Chlorophyll *a* concentrations changed only slightly except in March when chlorophyll was high during the early part of the phytoplankton bloom.

Low light intensities limited primary production during the winter, and zooplankton grazing appeared to limit production in summer and part of spring. Nutrients and light were always sufficient to support high productivity during spring and summer except in late summer when some nutrients, particularly nitrate, were very low south of lat 44° N; however, the productivity did not appear severely limited. The main source of phosphate replenishment in the upper layers during spring and summer was probably in situ regeneration by zooplankton rather than upwelled deep water.

The pelagic biota of the Subarctic Pacific Region has long been recognized as distinct from that in the Subtropical Region, and the Subarctic is thought to be generally more productive. Until the introduction of the carbon-14 technique by Steemann Nielsen (1952), however, no adequate means existed for directly measuring primary productivity in the open ocean. Since that time thousands of measurements of primary production have been made throughout the Tropical and Subtropical North Pacific. Measurements in the Subarctic Pacific have been fewer and more localized.

Koblents-Mishke (1965), who summarized data from the Pacific Ocean, estimated that primary productivity in the mid-Subarctic Region averaged about 150 to 250 mg C/m<sup>2</sup> per day or 55 to 91 g C/m<sup>2</sup> per year. She estimated average production in the Gulf of Alaska and along the Washington and Oregon coasts to be between 250 and 650 mg C/m<sup>2</sup> per day (90-240 g C/m<sup>2</sup> per year) and in the transition area of the southern Subarctic to be 100 to 150 mg C/m<sup>2</sup>

per day (35-55 g C/m<sup>2</sup> per year). As discussed by Koblents-Mishke, these estimates are rather imprecise because productivity at most of the stations was measured only at the surface and not throughout the euphotic zone and because many of the measurements were made in artificial light of various intensities. Comprehensive analyses of annual cycles were seldom possible because surveys have been made during all seasons in only a few studies.

From detailed year-round surveys, Anderson (in press) estimated annual primary production in oceanic waters off Washington and Oregon to be 125 g C/m<sup>2</sup>. Mean annual primary production at Ocean Station "P" (lat 50° N, long 145° W) in the Gulf of Alaska was 48 g C/m<sup>2</sup> in 1960-66 (McAllister, 1969). Although primary productivity has been measured on several individual cruises through the region (McGary and Graham, 1960; Faculty of Fisheries, Hokkaido University, 1961; Doty, 1964; Koblents-Mishke, 1965), no previous time-series studies of productivity have been made in the central Subarctic Region west of Station "P."

Primary productivity, zooplankton abundance, and related physical and chemical oceanographic

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variables were measured on several cruises in 1966-68 within the Subarctic Region in conjunction with studies of abundance and distribution of Pacific salmon (genus *Oncorhynchus*). Productivity data are listed in Larrance (1971), zooplankton is discussed by Day (1970),<sup>2</sup> and physical data are listed in Ingraham and Fisk (1970). The objectives were to obtain an estimate of annual productivity and to detect what differences in levels of productivity, if any, occurred among several oceanographic areas identifiable by physical characteristics.

## METHODS

Primary productivity and related variables were measured on cruises of the RV *George B. Kelez* in March, June, and September 1966;

<sup>2</sup> Day, D. S. 1970. Distribution of zooplankton from the mid-Subarctic Region of the Pacific Ocean, 1966-67. Natl. Mar. Fish. Serv., Biol. Lab., Seattle, Wash. Unpubl. manuscr.

January-February, June-July, and August 1967; and May 1968; and on a cruise of the MV *Paragon* in June 1966 (Table 1). Measurements in 1966-67 were south of Adak Island (long 176°25' W) except in January-February 1967 when the cruise track was along long 162° W and in May 1968 when it was along long 165° W (Figure 1). Primary productivity was measured by the carbon-14 method introduced by Steemann Nielsen (1952) and modified by Strickland and Parsons (1965). Productivity stations were normally taken shortly before dawn and local apparent noon (LAN); incubation periods were for one-half the daylight period, i.e., from dawn to LAN and from LAN until about twilight. Seawater was sampled with 6-liter plastic water bottles at depths determined from the penetration of light below the sea surface. These "light depths" were 100, 61, 35, 18, and 3% of the surface intensity according to the fractions of light transmitted by neutral-light filters used in the productivity incubations. The depths

TABLE 1.—Summary of areas, dates, and stations on which primary productivity was measured, 1966-68<sup>1</sup>.

Cruise no.	Vessel	Dates	Number of stations	Area
1966				
K1-66	<i>Kelez</i>	March 18-28	Productivity - 6 Chlorophyll and nutrients - 9 Total - 9	Adak Is. to lat 41° N
P2-66	<i>Paragon</i>	June 10-21	Productivity - 8 Chlorophyll and nutrients - 10 Total - 10	Adak Is. to lat 41° N
K3-66	<i>Kelez</i>	Sept. 8-20	Productivity - 11 Chlorophyll and nutrients - 19 Surface productivity - 14 Total - 28	Adak Is. to lat 40° N
1967				
K1-67	<i>Kelez</i>	Jan. 30-Feb. 15	Productivity - 10 Total - 10	Along long 162° W between lat 54° and 46° N
K5-67	<i>Kelez</i>	June 24-July 3	Productivity - 10 Total - 10	Adak Is. to lat 46° N
<sup>2</sup> K6-67	<i>Kelez</i>	July 8-July 11	Productivity (1/2 day only) - 4	Alaskan Stream
K7-67	<i>Kelez</i>	Aug. 21-Aug. 28	Productivity - 7 Total - 7	Adak Is. to lat 46° N
1968				
K2-68	<i>Kelez</i>	May 9-15	Chlorophyll and nutrients - 5 Total - 5	Along long 164° W between lat 53° and 49° N

<sup>1</sup> Only portions of cruises discussed in this report are included in Table 1.

<sup>2</sup> Data from cruise 6-67 were averaged with data from station 5-67 for this report.

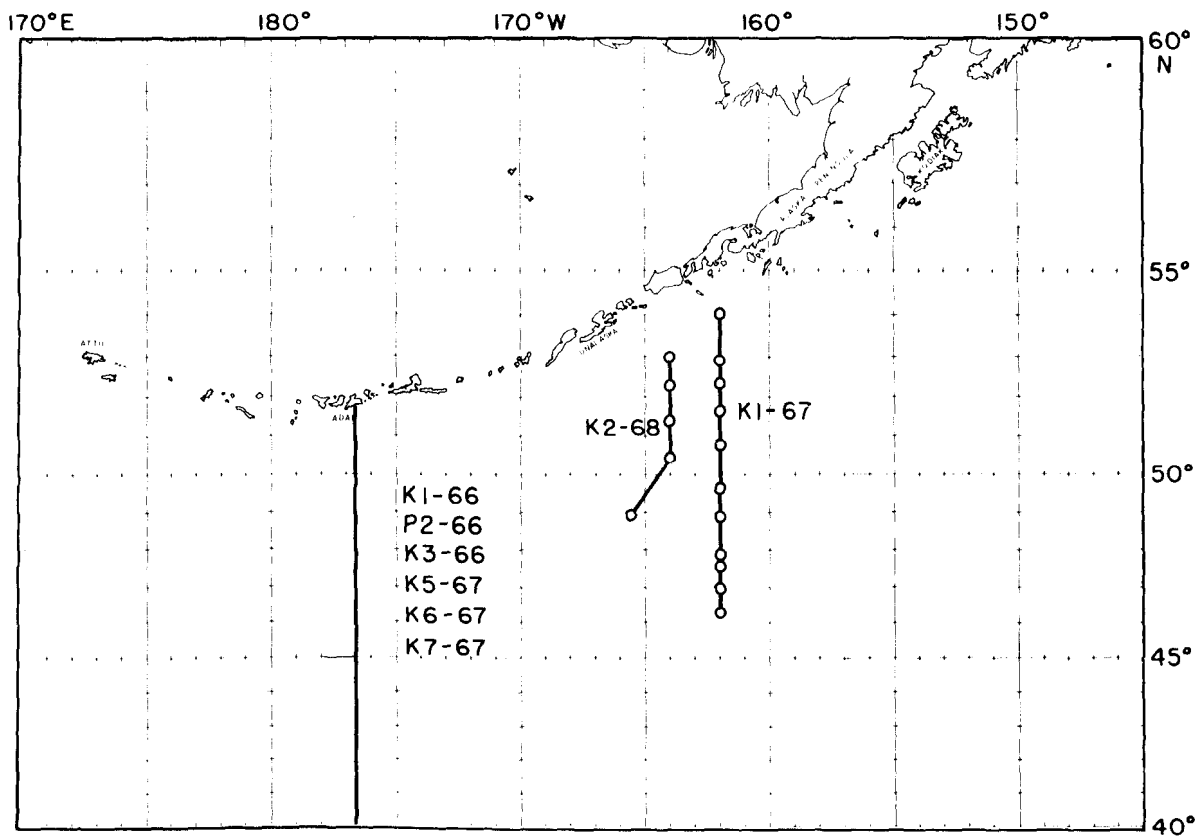


FIGURE 1.—Tracks of Bureau of Commercial Fisheries cruises in 1966-68 in the Subarctic Pacific Region during which primary productivity was measured.

were calculated from Secchi disk readings converted to extinction coefficients (Poole and Atkins, 1929). Sampling depths of the morning stations were computed from the preceding day's Secchi-disk readings. Duplicate light-bottle samples under the neutral-light filters were incubated on deck in daylight and cooled with running sea water. After incubation, samples were filtered through Millipore<sup>3</sup> filters, pore size  $0.45 \mu$ , for radioassay.

Stock solutions of  $\text{Na}_2^{14}\text{CO}_3$  were prepared according to Strickland and Parsons (1965) but were standardized by using liquid-scintillation techniques. A 1.00-ml portion from an ampoule

containing the stock carbonate solution was introduced in 10 ml of a suitable phosphor solution, and its count rate determined in a Packard Tri-Carb<sup>4</sup> scintillation spectrometer. One liter of phosphor solution contained 800 ml toluene, 200 ml Sterox<sup>5</sup> (a surfactant required to make the water miscible in toluene), 5.0 g PPO (2, 5-diphenyl-oxazole), and 0.3 g bis-MSB (p-bis-(o-methylstyryl)-benzene). Counts of an external radium standard were also recorded and the absolute activity (dpm) was determined from a quench correction curve relating efficiency to the count rate of the external standard (Wang and Willis, 1965). Although scintillation counting

<sup>3</sup> Millipore Corp., Ashby Rd., Bedford, Mass. 01730. References to trade names in this publication do not imply endorsement of commercial products by the National Marine Fisheries Service.

<sup>4</sup> Packard Instrument Co., Inc., 2200 Warrenville Rd., Downers Grove, Ill. 60515.

<sup>5</sup> Jefferson Chemical Co., P.O. Box 53300, Houston, Tex.

is more efficient than planchet counting, productivity samples were routinely counted on planchets in a gas-flow geiger detector for convenience. The efficiency of the geiger counter was determined by counting a standard source of known activity so that absolute activity of the samples could be related to those of the stock solution.

Samples for chlorophyll *a*, phosphate, silicate, and nitrate-nitrite were also drawn from the water bottles. Nutrient samples were frozen in plastic bottles and returned to Seattle for analysis. Phosphate and silicate concentrations were determined by methods given by Strickland and Parsons (1965), and nitrate-nitrite samples were analyzed by the method of Wood, Armstrong, and Richards (1967).

Four liters of water from each sampler were filtered through glass-fiber filters (Gelman, type A),\* stored in a dark desiccator at about 0° C, and returned to Seattle for chlorophyll *a* analyses. A layer of MgCO<sub>3</sub> was added to the filter prior to filtration. Chlorophyll *a* concentrations were determined by the method of Richards with Thompson (1952) but were computed with equations given by Parsons and Strickland (1963). Chlorophyll samples on the glass-fiber filters were ground in a tissue grinder as suggested by Yentsch and Menzel (1963). The resulting suspension was filtered through a very-fine-porosity (VF) fritted-glass disk under pressure, and the cake of residue remaining on the disk was stirred with a few ml of 90% acetone and refiltered. Absorbances at 750 m $\mu$ , which indicate turbidity, of the resulting effluents were seldom more than 0.010 per cm of light path and then only in the more highly colored samples. A series of 20 tests showed no more than traces of pigment remaining in the residue after the first wash. The above treatment for separating residue from samples was preferable to centrifugation because it resulted in generally lower turbidity and more complete recovery of extract.

Total incident solar and sky radiation (over the wavelength range 0.3 to 3  $\mu$ ) was continuously measured and graphically recorded by a

pyranometer. Although the photosynthetically active portion of the spectrum is roughly half the total radiation (Edmondson, 1956), total radiation values were used in productivity calculations. Salinity and temperature were measured and standard weather observations were recorded near the productivity stations (Larrance, 1971).

Measurements of productivity, chlorophyll *a*, and nutrients at various depths were integrated to the bottom of the euphotic zone (designated here as that depth where light intensity is 1% of the surface intensity), or other specified depth, and the integrated values expressed per square meter of sea surface. Mean values for several oceanographic domains were computed by weighting the values according to distances between stations. Details of the calculations were given in Larrance (1971).

## PHYSICAL OCEANOGRAPHY

The physical oceanography of the Pacific Subarctic Region has been described by Fleming (1955), Dodimead, Favorite, and Hirano (1963), and Tully (1964). On the basis of data from Ocean Station "P" (lat 50° N, long 145° W), Dodimead et al. (1963) divided the upper 1,000 m of the Subarctic Pacific Region into three permanent zones: an upper zone from 0 to about 100 m depth; a halocline from about 100 to 200 m through which the salinity increases downward by about 1‰; and a lower zone from about 200 to 1,000 m. During the spring and summer, warming of the surface layers causes a temporary thermocline in the upper zone which is subsequently destroyed by cooling in the autumn. Consequently the lower limit of the wind-mixed upper layer ranges from about 30 to 60 m in the spring and summer and extends to the top of the permanent halocline at 100 m during winter. The upper zone in the Subarctic Pacific has been divided by Dodimead et al. (1963) into Coastal, Alaskan Stream, Central Subarctic, Western Subarctic, and Transitional Domains (Figure 2).

The Coastal Domain south of the Aleutian Islands lies over the continental shelf and is strongly influenced by Bering Sea water mixed

\* Gelman Instrument Co., P.O. Box 1448, Ann Arbor, Mich. 48106.

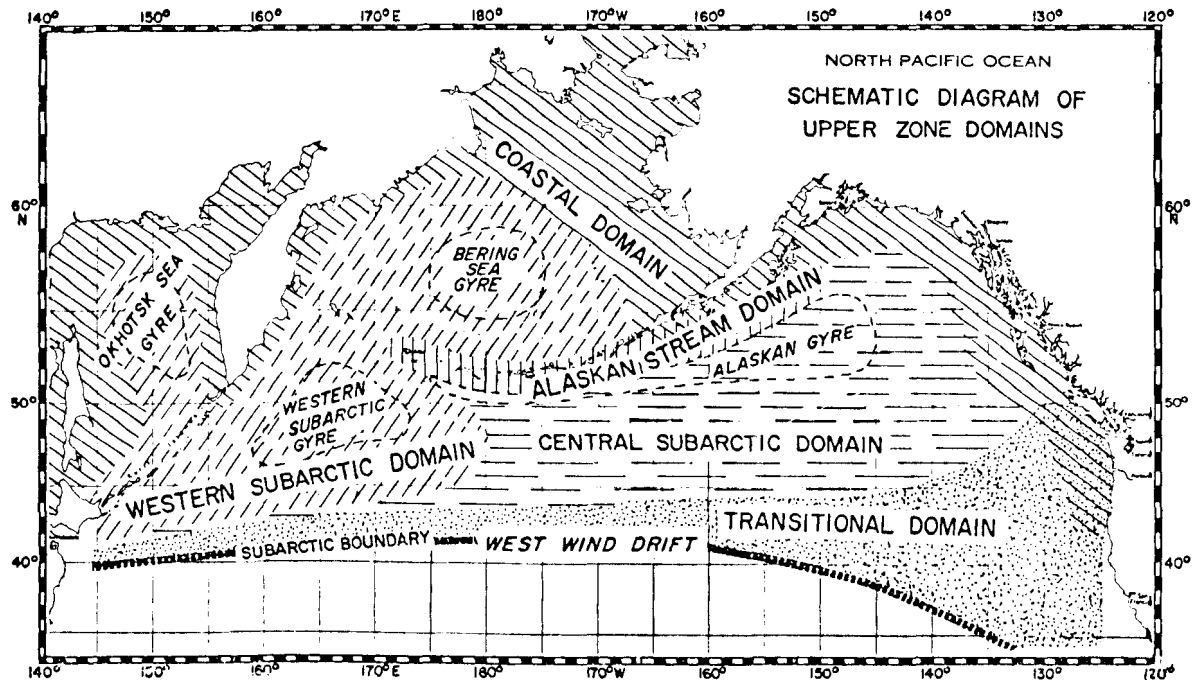


FIGURE 2.—Diagram of upper zone domains in the Subarctic Pacific Region (after Dodimead, Favorite, and Hirano, 1963).

through passes between the islands. To distinguish the Coastal from Alaskan Stream Domains, coastal water was arbitrarily defined by surface salinities greater than 32.9‰. The Alaskan Stream, described in detail by Favorite (1967), flows westward out of the Gulf of Alaska with velocities as high as 100 cm/sec. It is diluted by runoff from Alaska and can be detected by low salinity (less than 32.6‰) at the surface. The Central Subarctic Domain is an area of weak and variable currents bounded on the north by the Alaskan Stream and on the south by the Subarctic Current, which flows eastward at velocities between 5 and 20 cm/sec (McAlister et al., 1970). The Subarctic Current separates the Central Subarctic Domain from the Transitional Domain, which extends southward as far as the northern boundary of the Subtropical Region and is also an area of weak eastward flow. The nomenclature given by McAlister et al. (1970) was slightly different from that applied to the upper zone domains of Dodimead et al. (1963), but it was based in part on features

below the upper zone. For purposes of the present paper, the definitions of the upper zone domains as given in Dodimead et al. (1963) were used; the Subarctic Current, which originates in the Western Subarctic Domain, was thus included in the Central Subarctic Domain.

The Transitional Domain has been further divided into two areas (T-1 and T-2) on the basis of the salinity in the upper 50 m. The division between areas T-1 and T-2 was set in August 1967 at lat 47° N, where surface salinity was a maximum and decreased to the north and to the south at least as far as lat 46° N. The Transitional Domain was also divided in September 1966, when the northern area (T-1) extended from lat 47°05' N to a relatively sharp horizontal salinity gradient at lat 43°35' N. The southern area (T-2) extended to lat 40°45' N, where the boundary between transitional and subtropical waters was found. These divisions of the Transitional Domain are somewhat arbitrary but tend to be corroborated by biological and chemical characteristics.

## PRIMARY PRODUCTIVITY ESTIMATES ADJUSTED FOR DIFFERENCES OF LIGHT INTENSITY

Because productivity was measured in natural light which differed (by as much as fivefold) in total insolation from day to day, productivity values were adjusted by two methods to permit comparison of productivity estimates under similar light conditions for purposes of detecting possible differences in productivity among oceanographic areas. One method applied the relation given by Ryther (1956) and Ryther and Yentsch (1957) of relative daily productivity beneath a unit of sea surface to total daily surface radiation. The measured daily light intensities were averaged for each cruise and the corresponding values of  $R$  (photosynthetic rate relative to photosynthesis at light saturation), defined by Ryther and Yentsch (1957), were determined for the cruise mean of daily light and for the light observed on the particular day in question ( $R_{av}$  and  $R_m$ , respectively). Adjusted productivity was then computed by  $P_R = P_m \times R_{av}/R_m$  where  $P_R$  and  $P_m$  are the adjusted and observed productivities integrated through the euphotic zone and have the units of mg C/m<sup>2</sup> per day. This procedure amounts to using the shape of Ryther's (1956) curve but not his absolute values for estimating productivity.

Since Ryther derived his curve from photosynthesis measurements of phytoplankton from Woods Hole Harbor, that relationship is likely to differ from similar curves based on measurements from other areas. An attempt was made, therefore, to establish a simple empirical relation to estimate productivity in the mid-Subarctic Pacific Region from chlorophyll and light data obtained during the *Kelez* cruises. The regression of measured daily productivity ( $P_m$ ) per unit of chlorophyll  $a$  ( $C_a$ ) in the euphotic zone

$$\left(\text{where } P_m/C_a = \frac{\text{mg C assimilated/m}^2 \text{ per day}}{\text{mg chlorophyll } a/\text{m}^2}\right)$$

on daily light intensity measured on the ship's deck was computed (Figure 3). Only data from those stations where a full day's productivity and light were measured were used for the relation.

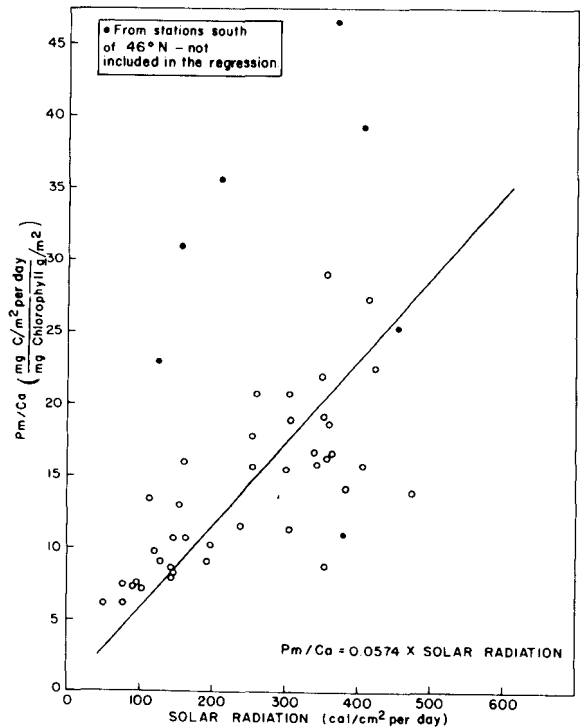


FIGURE 3.—Relation between the ratio of daily primary productivity to chlorophyll  $a$  ( $P_m/C_a$ ) in the euphotic zone and daily solar radiation above the sea surface in the Subarctic Pacific Region, 1966-67.

The intercept of the regression and the axes was not significantly different from the origin. The variability was generally large, as might be expected from data of this kind, and was especially high for stations in the southern portion of the study area (transitional and subtropical water). This variability suggests that productivity responses to the environment in the Transitional Domain and subtropical water were probably different from those north of about lat 46° N. Furthermore, relatively few measurements were taken south of lat 46° N—not enough for seasonal comparisons. For these reasons, the regression was computed for only those stations north of lat 46° N.

Productivities under average daily light intensities for each cruise ( $P_K$ ) were estimated by multiplying the chlorophyll  $a$  measured in the euphotic zone at a station by the estimate, from the regression, of  $P/C_a$  corresponding to the

average daily light intensity for the cruise. Although the relation was based on data taken north of lat 46° N, it was used to estimate productivity in June 1966 for stations as far south as lat 44° N (Figure 4).

These methods give rough approximations at best but probably indicate productivity responses to seasonal-average light conditions more accurately than those given by measured productivity values affected by large day-to-day fluctuations of light. The means of  $P_R$  for each cruise were higher than means of  $P_K$  except in September (Table 2, Figure 5). The higher  $P_R$  values may mean that the photosynthetic efficiency of the subarctic Pacific phytoplankton is lower than the average efficiency of populations represented in Ryther and Yentsch's (1957) analysis. Other possible explanations might involve differences between our experimental procedures and Ryther's (1956).

#### AREAL AND SEASONAL DISTRIBUTIONS OF PRIMARY PRODUCTIVITY AND CHLOROPHYLL *a*

Differences in productivity and chlorophyll *a* among the upper zone domains do not appear to be consistent from season to season except that mean values in the Coastal Domain and Adak Bay were higher than those farther from shore (Figure 4, Table 2). The Coastal and Alaskan Stream Domains can be compared only in June-July 1967 because both areas were not sampled on any other single cruise. Productivity and chlorophyll *a* were substantially higher in coastal water than in the Alaskan Stream. Unlike other times of the year, productivity and chlorophyll values were similar in nearshore and offshore areas in March 1966 and January-February 1967, probably because low light intensities in these months limited production to about similar levels throughout the northern Subarctic Region. This effect was especially pronounced at Adak Bay, where productivity estimates in March were between 350 and 460 mg C/m<sup>2</sup> per day but ranged between 840 and 2,400 mg C/m<sup>2</sup> per day in late spring and through the summer. The lowest productivity during each cruise was in the Central Subarctic Domain except in win-

ter, when productivity was uniformly low throughout the region. The mean productivity, however, was lower in the Central Subarctic Domain than in the other areas only in March 1966 and June 1967.

Daily carbon assimilation was normalized ( $P/C_a$ ) above to estimate productivity from chlorophyll and light measurements. The commonly used  $P/C_a$  ratio may also be considered as an index of the capacity of a population to photosynthesize under natural light and ambient nutrient and temperature conditions, and provides a basis for seasonal and areal comparisons. This ratio is similar to "turnover rate" (Cushing et al., 1958) and to the ratio discussed by Currie (1958), except that Currie used the concentration of the total complement of plant pigments instead of only chlorophyll *a*. Platt (1969) used an efficiency index (productivity/light energy) to normalize productivity measurements for comparison at designated chlorophyll concentrations by means of a regression of the efficiency index on chlorophyll. His method was similar to that used here except he could estimate productivity at individual depths. For analysis in this study, ratios of  $P/C_a$  were computed for measured productivities ( $P_m$ ) and productivities adjusted for differences in light ( $P_R$ ) by the curve of Ryther and Yentsch (1957).

Ratios of  $P_R/C_a$  were high at four of the nine stations at or south of lat 46° N (Figure 6). The southernmost stations in March and September 1966 were in subtropical water. In March,  $P_R$  (515 mg C/m<sup>2</sup> per day) and  $P_R/C_a$  (39) were high, suggesting conditions of a phytoplankton bloom, whereas in September,  $P_R/C_a$  was lowest (10) of any observed during summer (Table 2). At lat 44° N in June 1966 and at lat 42°50' N in September,  $P_R/C_a$  ratios were high (41 and 49), but  $P_R$  values were moderate (232 and 275 mg C/m<sup>2</sup> per day) and chlorophyll values were unusually low (5.6 mg/m<sup>2</sup> in each case). This combination of high  $P_R/C_a$  and low chlorophyll may be due to high carbon to chlorophyll ratios in the cells. At lat 46° N in August 1967, however,  $P_R$  and chlorophyll *a* were both relatively high (664 mg C/m<sup>2</sup> per day and 16.8 mg/m<sup>2</sup>); thus the high productivity and photosynthetic capacity ( $P_R/C_a = 40$ ) of the popu-

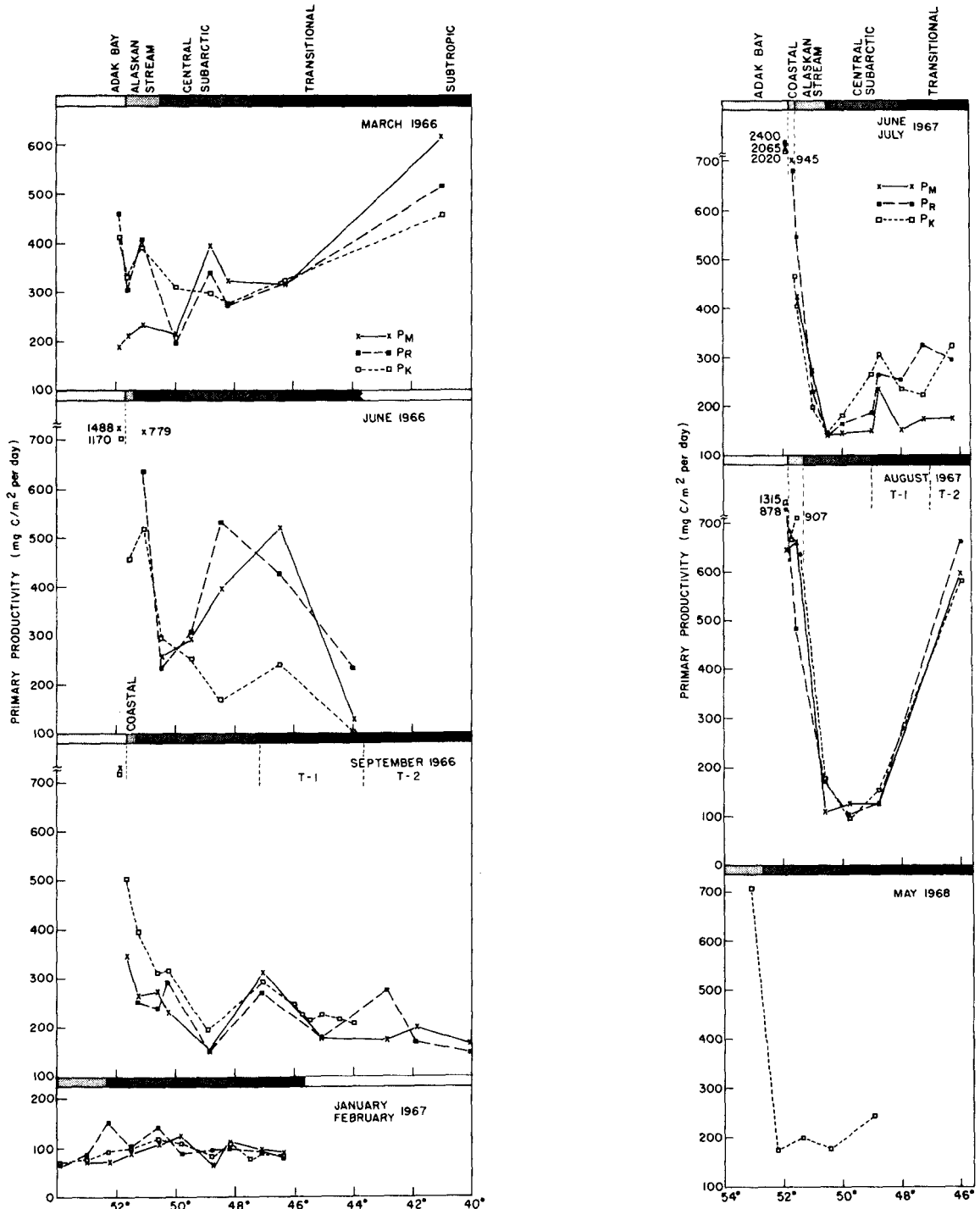


FIGURE 4.—Primary productivity in the mid-Subarctic Pacific Region, 1966-68.



## LARRANCE: PRIMARY PRODUCTION IN MID-SUBARCTIC REGION

TABLE 2.—Chlorophyll *a* in the euphotic zone, measured and estimated primary productivity values, and ratios of productivity to chlorophyll *a* in the mid-Subarctic Pacific Region (averaged within upper zone oceanographic domains) 1966-68.

Date and cruise no. and area	Chlorophyll <i>a</i> (mg/m <sup>2</sup> )	Primary productivity (mg C/m <sup>2</sup> per day)					
	<i>C<sub>a</sub></i>	<i>P<sub>m</sub></i>	<i>P<sub>R</sub></i>	<i>P<sub>K</sub></i>	<i>P<sub>m</sub>/C<sub>a</sub></i>	<i>P<sub>R</sub>/C<sub>a</sub></i>	<i>P<sub>K</sub>/C<sub>a</sub></i> <sup>1</sup>
March 1966 (K1-66)							
Adak Bay	24.9	187	460	351	7.5	18.5	
Alaskan Stream	23.2	229	392	327	9.9	16.9	
Central Subarctic	17.8	305	265	251	17.1	14.9	
Transitional	19.6	317	317	276	16.2	16.2	
Subtropic	13.2	612	515	--	46.4	39.0	
46°-51°40'	19.3	292	303	272	15.1	15.7	14.1
June 1966 (P2-66)							
Adak Bay	64.3	1485	1492	1061	23.1	23.2	
Alaskan Stream	25.0	--	--	412	--	--	
Central Subarctic	14.5	422	429	239	29.1	29.6	
Transitional	9.4	324	328	155	34.5	34.9	
46°-51°40'	14.4	431	426	238	29.9	29.6	16.5
September 1966 (K3-66)							
Adak Bay	42.4	914	--	827	21.6	--	
Coastal	23.8	345	--	464	14.5	--	
Central Subarctic	11.9	195	199	232	16.4	16.7	
Transitional 1	11.7	222	197	228	19.0	16.8	
Transitional 2	6.9	187	217	--	27.1	31.4	
Subtropic	15.0	165	150	--	11.0	10.0	
46°-51°40'	12.8	204	201	250	15.9	15.7	19.5
January-February 1967 (K1-67)							
Alaskan Stream	9.1	71	80	60	7.8	8.8	
Central Subarctic	12.4	93	108	82	7.5	8.7	
Transitional	10.1	94	82	67	9.3	8.1	
46°-53°53'	11.2	88	96	74	7.9	8.6	6.6
June-July 1967 (K5-67 and K6-67)							
Adak Bay	99.4	2068	2396	1889	20.8	24.1	
Coastal	22.8	945	680	433	41.5	29.8	
Alaskan Stream	14.0	290	265	266	20.7	18.9	
Central Subarctic	11.1	165	193	211	14.9	17.4	
Transitional	13.2	171	299	251	13.0	22.6	
46°-51°40'	12.7	202	248	241	15.9	19.5	19.0
August 1967 (K7-67)							
Adak Bay	60.6	648	878	867	10.7	14.5	
Coastal	41.8	661	483	598	15.8	11.6	
Central Subarctic	6.3	118	138	90	18.7	21.9	
Transitional 1	7.2	127	127	103	17.6	17.7	
Transitional 2	16.8	598	664	240	35.6	39.5	
46°-51°40'	10.7	238	247	153	22.2	23.1	14.3
May 1968 (K2-68)							
Alaskan Stream	41.3			710			
Central Subarctic	10.6			182			
Transitional	14.3			246			
48°50'-53°	14.3			246			

<sup>1</sup> Mean values for each cruise.

lation were undoubtedly real. From these results, productivity and photosynthetic capacity south of lat 46° N appear to be neither characteristically high nor low, except in spring during bloom conditions, but fluctuate over a wide range.

Because relatively few measurements were made south of lat 46° N and the  $P_R/C_a$  ratios varied rather widely, only the data between lat

46° N and the Aleutian Islands were compared to determine seasonal patterns of production. If all the data are treated as if taken in the same calendar year, a seasonal pattern of productivity can be approximated (Figure 5). Productivity in winter was uniformly low throughout the area ( $P_R = 96$  and  $P_K = 74$  mg C/m<sup>2</sup> per day). The mean chlorophyll *a* concentration (11.2 mg/m<sup>2</sup>), however, was similar to

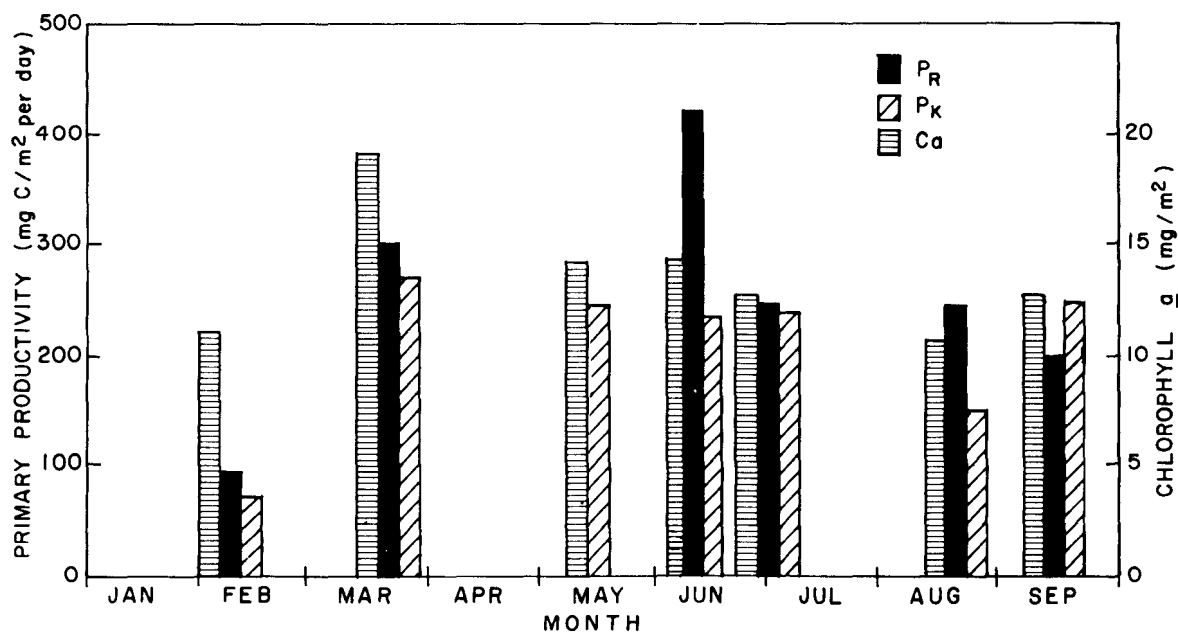


FIGURE 5.—Seasonal pattern of primary productivity and chlorophyll *a* in the mid-Subarctic Pacific Region between the Aleutian Islands and lat 46° N.

summer means. As might be expected, primary productivity was limited by low available light energy in the winter. The mean daily light intensity was low (116 cal/cm<sup>2</sup>), and the availability of light to the cells was further limited by their being distributed throughout the surface mixed layer, which reached well below the euphotic zone to the halocline at about 100 m.

In March, daily light intensities averaged 274 cal/cm<sup>2</sup> and thermal stratification had developed sufficiently to decrease the mixed-layer depth—thereby increasing exposure of the cells to light at shallower depths and consequently stimulating growth. The mean chlorophyll *a* concentration (19.3 mg/m<sup>2</sup>) was clearly higher than for any other season, and  $P_R$  and  $P_K$  (303 and 272 mg C/m<sup>2</sup> per day) were more than three times as high as in January and February (Figure 5, Table 2). The  $P_R/C_a$  and  $P_K/C_a$  ratios (16 and 14) were roughly twice those in midwinter, indicating that productivity was no longer limited by low light intensities. Although measurements in May 1968 were made at a considerable distance east of the Adak Line and may not be directly comparable, mean  $P_K$  values were re-

markably similar in June 1966 and 1967 and May 1968 (238, 241, and 246 mg C/m<sup>2</sup> per day, respectively) as were the mean chlorophyll values (14.4, 12.7, and 14.3 mg/m<sup>2</sup>, respectively).

In August, the mean  $P_K$  and  $P_R$  values differed significantly ( $P_K = 153$  and  $P_R = 247$  mg C/m<sup>2</sup> per day). A large part of this difference may be attributed to high productivity measured at lat 46° N in transition area T-2 ( $P_K = 240$  and  $P_R = 664$  mg C/m<sup>2</sup> per day). These estimates strongly influenced the means because the weights assigned to each in the averaging process were relatively large. The mean chlorophyll *a* concentration (10.6 mg/m<sup>2</sup>) was slightly less than in June, and the mean  $P_R/C_a$  (23) was higher than in June. In September, mean  $P_R$  and  $P_K$  were 201 and 250 mg C/m<sup>2</sup> per day, and the mean chlorophyll *a* was 13.0 mg/m<sup>2</sup>. These values were somewhat similar to the other summer values, as were the ratios  $P_R/C_a$  (16) and  $P_K/C_a$  (20).

The general time-distributional pattern of productivity and chlorophyll *a* between lat 46° and 51°40' N from January through September was drawn from the above results (Figure 5). Pro-

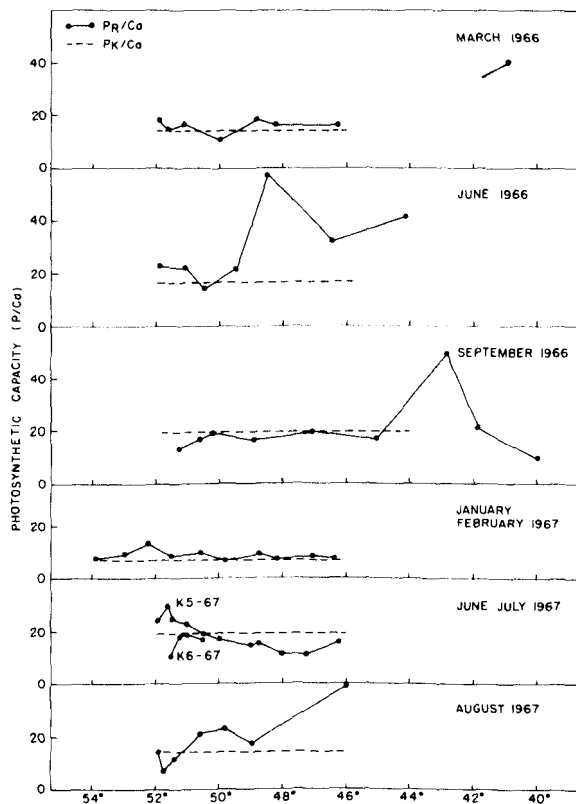


FIGURE 6.—Ratios of  $P_R/C_a$  and  $P_K/C_a$  in the Subarctic Region along long 175°-176° W, 1966-67.

duction was low in the winter, increased significantly in March, and was relatively steady at intermediate levels throughout the summer. Chlorophyll  $a$  also increased between February and late March as a consequence of high production but decreased significantly during the spring and decreased slightly throughout the summer. Some reasons for these changes can be inferred from the nutrient and zooplankton data and are discussed later.

Although primary production apparently continued at a high rate through the spring, chlorophyll  $a$  concentrations were significantly less in May and June than in March. Two probable reasons for this decrease are a decrease in cell chlorophyll content and an increased loss rate, primarily due to grazing. It is impossible to ascertain from the data which one of these causes was most important, but some trial cal-

culations can help explore the problem. The standing stock ( $S_t$ ) at  $t$  days (time between consecutive cruises) was predicted by the simple growth equation

$$S_t = S_0 e^{(a-b)t}$$

where  $S_0$  is the initial standing stock and  $a$  and  $b$  are growth and loss coefficients. Standing stock was expressed in mg chlorophyll  $a/m^2$ , and  $P/C_a$  ratios were multiplied by  $1/F$  (ratio of cell chlorophyll  $a$  to cell carbon) to give growth coefficients ( $a$ ) in units of  $day^{-1}$ .

The growth rate ( $a$ ) varied with time because  $P/C_a$  varied and  $1/F$  was assigned values according to those reported elsewhere (Strickland, 1960; Eppley, 1968; and Strickland et al., 1969). Populations in nutrient-rich water under suboptimum light intensities, conditions extant in February and March, contain larger amounts of chlorophyll per unit carbon than those in nutrient-poor water under brighter light. Eppley (1968) found  $F$  values of about 30 for deep nutrient-rich water and 90 for shallow water depleted of nutrients. Values of  $1/F$ , therefore, were assumed to be 0.04 in February and March and 0.01 in June. The June value is probably too low because the water still contained ample nutrients (although lower than in March) for vigorous growth, but was selected to maximize the decrement afforded to decreasing cell chlorophyll content and therefore minimize  $S_t$  in June.

Results of the calculations show (Table 3) that changes in cell chlorophyll content could account for only part of the decrease in chlorophyll concentration between March and June. The loss coefficient ( $b$ ) was computed for the period February to March and assumed to remain constant through June. The computed standing stock ( $S_t$ ) in June was 1096, about 80 times as high as the observed value. (For comparison, standing stocks were also computed for  $1/F = 0.04$  and  $1/F = 0.01$ , Table 3.) Since this (1096) is the minimum that could be expected from a loss of cell chlorophyll, grazing must have increased during the period to further decrease the chlorophyll concentration to its observed level. A concomitant increase in zooplankton corroborates this conclusion (discussed later).

TABLE 3.—Computed standing stock ( $S_t$ ), expressed in units of chlorophyll, for various cell chlorophyll to carbon ratios ( $1/F$ ) during spring 1966 in the mid-Subarctic Pacific Region.

Period	$S_0$	$t$	$1/F$	$P/C_a$	${}^1\bar{a}$	$b$	$S_t$
Feb.-Mar.	11.2	50	.04	7-15	0.433	20.422	19.3
Mar.-June	19.3	80	.04-.01	15-20	0.472	0.422	21096.
Mar.-June	19.3	80	.04	15-20	0.701	0.422	29.3 × 10 <sup>10</sup>
Mar.-June	19.3	80	.01	15-20	0.398	0.422	228.0

<sup>1</sup> $\bar{a}$  is the mean growth coefficient calculated by assuming that  $P/C_a$  varied linearly with time as did  $1/F$  in the second computation.

$$\bar{a} = a_0 + \frac{\Delta a}{t} \sum_{i=1}^{t-1} i$$

where  $\Delta a = \Delta P/C_a [(1/F)_0 + 1/t \cdot \Delta 1/F] + (P/C_a)_0 \cdot \Delta 1/F$  and  $\Delta$  is the difference between the initial and final values for the period.

<sup>2</sup> Computed values.

## AREAL AND SEASONAL DISTRIBUTION OF NUTRIENTS

Nutrient concentrations were always higher in Adak Bay and the Coastal Domain than in the other areas and generally decreased toward the south (Table 4, Figure 7). Average concentrations of nutrients in the Central Subarctic water exceeded those in the Alaskan Stream only in June 1967. In winter of 1967, the nutrients were relatively high and varied little throughout the cruise area. Low nutrient concentrations at a few stations to the south in September correspond to lower  $P_R/C_a$  ratios. The lowest average phosphate concentration in the upper 50 m, 10 mg-at/m<sup>2</sup>, was in subtropical water. Nitrate-nitrite was undetectable in the upper 10 m at one station in area T-2 (lat 43° N) and totaled only 12 mg-at/m<sup>2</sup> in the upper 50 m, whereas the minimum silicate observed was 187 mg-at/m<sup>2</sup> at the same station. Apart from the low nutrient values measured south of about lat 44° N in September and possibly in subtropical water in March, nutrients appeared to be in sufficient abundance to support vigorous phytoplankton growth. Even for these areas of low concentrations, productivity did not appear to be severely limited, as evidenced by the  $P_R/C_a$  ratios, but was probably somewhat suppressed.

To obtain a seasonal pattern of changes, the data on nutrients, like those on productivity, were treated as composite measurements from the same year. The changes of mean nutrient concentrations between lat 46° and 51°40' N from season to season were not large. In mid-

winter all nutrients were relatively abundant, as were phosphate and silicate in March. (Nitrate was not measured in March.) Phosphate decreased between March and June 1966 from 78 to 56 mg-at/m<sup>2</sup>, the largest fractional change measured during this study for any of the nutrients. In June 1967, nitrate and phosphate concentrations were nearly equal to those in winter, but concentrations of silicate were lower. The apparent difference in the phosphate fluctuations between the 2 years could be the result of a shift in timing of the periods of high primary productivity, differences in supply by circulation, or an overall net difference in the balance between phosphate assimilation and supply for the year. By August phosphate and silicate had increased to quantities considerably higher than those in winter, but in September phosphate was lower and silicate was only slightly higher than in winter.

The low nutrient concentrations to the south in the summer lend support to the proposal by Anderson (1969) that a trans-Pacific band of chlorophyll occurs between the seasonal and permanent pycnoclines in the summer. His measurements indicate that the algae are produced in situ at these depths (50 to 75 m) which receive less than 1% of the light energy at the sea surface. This band lies between lat 35° and 45° N and is coincident with and could explain the occurrence of a layer of maximum oxygen content (Reid, 1962). Anderson also found that nitrate in the surface mixed layer above the chlorophyll band was nearly absent, having been used up in the spring during high primary production. A nitrate gradient through the deep

TABLE 4.—Dissolved nitrate, phosphate, and silicate in upper 50 m of mid-Subarctic Pacific Region (averaged within upper zone oceanographic domains), 1966-68.

Cruise no. and area	Nitrate mg-at/m <sup>2</sup>	Phosphate mg-at/m <sup>2</sup>	Silicate mg-at/m <sup>2</sup>
<b>K1-66</b>			
Adak Bay	--	104.6	2,849
Alaskan Stream	--	88.8	1,990
Central Subarctic	--	81.2	1,903
Transitional	--	60.2	1,195
Subtropical	--	29.2	512
46°-51°40'	--	77.8	1,754
<b>P2-66</b>			
Adak Bay	--	94.9	2,871
Alaskan Stream	--	81.2	1,978
Central Subarctic	--	56.9	1,491
Transitional	--	49.6	1,155
46°-51°40'	--	56.0	1,480
<b>K3-66</b>			
Adak Bay	954	90.4	2,499
Coastal	--	88.7	2,331
Central Subarctic	583	75.4	1,692
Transitional I	492	56.7	1,143
Transitional II	64	16.8	280
Subtropical	76	10.0	335
46°-51°40'	579	72.0	1,597
<b>K1-67</b>			
Alaskan Stream	571	83.4	1,594
Central Subarctic	661	82.0	1,665
Transitional	599	69.0	1,314
46°-53°53'	627	79.0	1,561
<b>K5-67</b>			
Adak Bay	772	101.7	2,192
Coastal	1,160	117.4	2,806
Alaskan Stream	534	65.8	811
Central Subarctic	790	89.0	1,704
Transitional	248	42.2	588
46°-51°40'	579	78.6	1,247
<b>K6-67</b>			
Alaskan Stream	554	56.9	942
Central Subarctic	800	90.6	2,026
<b>K7-67</b>			
Adak Bay	1,111	113.6	3,012
Coastal	1,020	120.7	2,666
Central Subarctic	596	88.2	1,854
Transitional I	724	97.3	1,883
Transitional II	276	49.2	792
46°-51°40'	610	86.4	1,725
<b>K2-68</b>			
Alaskan Stream	--	60.0	868
Central Subarctic	--	63.1	1,022
Transitional	--	105.7	1,415

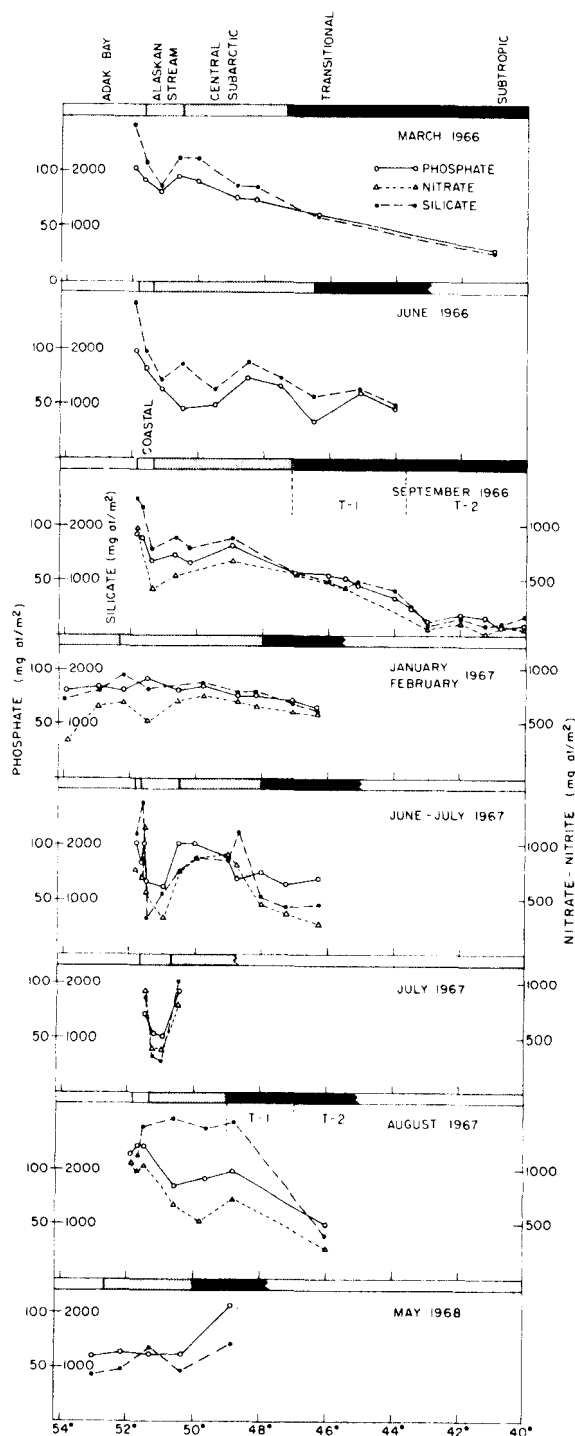


FIGURE 7.—Dissolved nitrate-nitrite, phosphate, and silicate in the upper 50 m of the mid-Subarctic Pacific Region, 1966-68.

chlorophyll maximum suggested that nitrate diffused toward the surface from deeper water was completely assimilated in the deep layer. During the present study, chlorophyll maxima were found at 50 m in June 1966 at lat 44° N and at 100 m in September at lat 43° N. Nitrate was not measured in June but it was undetectable in

the upper 10 m at lat 43° N in September. The deep chlorophyll layer at other stations could easily have been missed because sampling below the 1% light level was at standard depth.

## PHOSPHATE CHANGES AND THEIR RELATION TO PRIMARY PRODUCTION

An attempt was made to draw qualitative inferences from phosphate data about the relative levels of primary production between cruises to obtain a somewhat more detailed picture of the seasonal productivity pattern. The major factors generally affecting changes in dissolved phosphate concentration in the oceans are: (1) utilization by primary producers ( $P_u$ ), (2) regeneration by zooplankton and bacteria ( $P_r$ ), and (3) advective changes ( $P_a$ ). The relation among these factors is given by the formula:

$$P_0 = P_u + P_r + P_a,$$

where  $P_0$  is the net change of phosphate concentration with time,  $P_u$  is negative,  $P_r$  is positive, and  $P_a$  can be of either sign. Estimates of  $P_u$  between cruises were calculated by applying a ratio of carbon to phosphorus (C:P) to the carbon-14 data as discussed below,  $P_a$  was estimated from calculations of vertical velocities and phosphate concentrations measured at depth, and  $P_0$  was calculated from measurements of phosphate concentrations; however, no adequate estimate of  $P_r$  was possible. Two major assumptions were necessary to evaluate the above parameters:

1. The uptake ratio of C:P = 40 by weight (Strickland and Parsons, 1965). This value relates the C and P content of cells, but not the amounts assimilated. It is applied here, however, to carbon-assimilation rates measured by the carbon-14 method, which measures rates between net and gross production. The resulting estimate of phosphorus uptake, therefore, will be larger than the actual amount of phosphorus retained in new cell material.

2. Phosphate concentrations and their in situ changes were uniform within individual upper-zone domains. This assumption permits us to neglect the effect of horizontal advection.

Since nutrients were generally abundant in the Subarctic Region and changes were small during the year, circulation and regeneration must have supplied dissolved nutrients to the upper zone at rates sufficient to keep pace with their utilization, despite high assimilation rates by the algae during spring and summer. The amounts of phosphate supplied to the upper 50 m by upwelling were estimated from calculations of monthly mean vertical velocities (Wickett, 1966, 1968)<sup>7</sup> and observed phosphate concentrations at 50 m (Table 5). Wickett listed meridional components of Ekman and total transport for alternate points on a grid of 5-degree units of latitude and longitude. To obtain the phosphate estimates, the average of monthly mean vertical velocities for grid points at lat 45° N, long 175° W and at lat 50° N, long 180° W were used as single monthly estimates applicable to the Adak line of stations north of lat 45° N. To obtain the net amount of phosphate exchanged through the 50-m surface, the net vertical displacement of water during each month was multiplied by mean phosphate concentrations at 50 m. The computed vertical velocities refer to the bottom of the Ekman layer which extends to the halocline at 100 m in winter but is limited by the thermocline in summer to as shallow as 30 m. The error incurred, however, by applying the velocities to 50 m rather than any other level was probably within the range of precision of the estimated velocities.

Such estimates of vertical transport of phosphate must be considered minimal, because the turbulent flux of properties across a surface cannot be computed by using mean velocities. That is, mean vertical velocities indicate net upward flow, although water and its associated properties actually move up and down across horizontal surfaces. When phosphate concentration increases with depth (as it usually does), the shallower water loses less phosphate by downward flux than it gains by equivalent up-

<sup>7</sup> Wickett, W. P. 1966. Fofonoff transport computations for the North Pacific Ocean, 1966. Fish. Res. Board Can., Manusc. Rep. Ser. (Oceanogr. Limnol.) 229, 92 p. (Processed.)

1968. Transport computations for the North Pacific Ocean, 1967. Fish. Res. Board Can., Tech. Rep. 53, 92 p. (Processed.)

TABLE 5.—Changes of dissolved phosphate in upper 50 m of mid-Subarctic Pacific Region (attributable to vertical transport and assimilation by phytoplankton) and their relation to measured concentrations (shown in parentheses).

Period	$P_0$ mg P/m <sup>2</sup> per day (mg P/m <sup>2</sup> )	$P_a$ mg P/m <sup>2</sup> per day (mg P/m <sup>2</sup> )	$P_u$ mg P/m <sup>2</sup> per day (mg P/m <sup>2</sup> )	Residual change of $P^1$ mg P/m <sup>2</sup> per day (mg P/m <sup>2</sup> )
1966				
March-early June	-8.1 (-680)	1.0 (80)	-6.4 to -9.3 (-530 to -760)	-2.7 to 0 (-230 to 0)
Late June-Sept.	5.4 (500)	1.5 (140)	-5.5 to -8.4 (-500 to -770)	9.4 to 12.3 (860 to 1130)
1967				
Feb.-June	0 (0)	2.7 (310)	-4.0 to -4.3 (-570 to -620)	1.3 to 1.6 (260 to 430)
July-Aug.	4.3 (240)	-1.7 (-100)	-4.9 to -6.2 (-280 to -350)	10.9 to 12.2 (620 to 690)

<sup>1</sup> See text for definition.

ward motion; the net upward flux of phosphate, therefore, is underestimated when mean vertical velocities are applied.

Values of  $P_u$  for the periods between cruises were estimated from productivity data. The lesser values of the two productivity estimates ( $P_K$  or  $P_R$ ) from each of two succeeding cruises were averaged, as were the greater values. These averages represented the limits of the range of mean productivity during the period between cruises. For example, in the summer of 1966 (when in June,  $P_K = 238$  and  $P_R = 426$  mg C/m<sup>2</sup> per day, and in September,  $P_K = 250$  and  $P_R = 201$  mg C/m<sup>2</sup> per day), the range of mean productivity during the period was from 220 (the average of 238 and 201) to 338 (the average of 426 and 250) mg C/m<sup>2</sup> per day. The limits of the ranges were divided by the C:P ratio (40) to obtain the daily rate of phosphorus uptake in milligrams within a 1-m<sup>2</sup> cross-sectional column of the euphotic zone (Table 5). This rate was considered equivalent to the uptake in the upper 50 m. No error was incurred by this approximation when the euphotic zone was no deeper than 50 m. The "residual changes" of  $P$  were the changes unaccounted for by  $P_a$  and  $P_u$ ; thus they included regeneration, other changes not evaluated, and measurement errors:

$$\text{residual change} = P_0 - (P_a + P_u).$$

Although the accuracy of these estimates was low, the direction that  $P_a$  and  $P_u$  are likely to be in error is known and the direction of error of the

residual changes can be deduced. As the absolute values of  $P_a$  were minimal and those of  $P_u$  were too large (and  $P_a$  was either positive or negative and  $P_u$  was always negative), the sum  $P_a + P_u$  tended to be underestimated. The residual changes, therefore, tended to be overestimated.

The residual changes during similar seasons in the 2 years indicate similar trends (Table 5). Negative values during spring 1966 show that phosphorus assimilation, and hence primary productivity, must have averaged more than that calculated, even if no regeneration occurred. If phosphate regeneration is assumed to be zero, the productivity during spring 1966 could have been as much as 40% higher than that calculated to account for the changes in measured phosphate. Although regeneration rates were probably lower than in summer, some regeneration probably occurred, and therefore the residual change would have been greater and the productivity even higher. Clearly, spring phytoplankton production in 1966 must have been substantially greater than the measured productivities.

Larger residual changes in the summer indicate higher phosphate regeneration rates than in spring. Phosphate turnover times ranging from about one to several months have been reported (Ketchum, 1962). According to Ketchum, excretion by zooplankton accounts for large portions of regenerated phosphate as well as inorganic nitrogenous compounds. The residual changes were correlated with zooplankton

biomass in the Subarctic Region, which was roughly three times higher in summer than in February or March (Donald S. Day, unpublished data).<sup>\*</sup> If phosphate regeneration accounted for all the residual changes in summer, 45 to 50% of the phosphate in the water would be renewed by regeneration in 3 months. In contrast, the upwelled phosphate supplied only about 6% of the total concentration in summer of 1966 and phosphate was lost from the upper layers in 1967 by mean velocities downward. According to the computed values (Table 4), however, in the summer the residual change of phosphate was roughly twice that removed from the water by plants. If the residual change is assumed to be mostly due to regeneration, therefore, the zooplankton would have had to release twice as much phosphorus as was taken up by the algae during the same period. A more likely explanation is that more phosphate was supplied from below than is indicated by the  $P_a$  values and the consequent residual changes would be less. In either case, in situ regeneration by zooplankton appears to be a major source of nutrients supplied throughout the summer in the mid-Subarctic Pacific Region.

At Ocean Station "P" primary productivity accounted for the entire loss of phosphate between March and August (Parsons, 1965),<sup>o</sup> suggesting that regeneration was negligible. But, since zooplankton at Station "P" was sufficiently abundant to graze the phytoplankton to a stable level (McAllister, Parsons, and Strickland, 1960), it would seem that some phosphate regeneration should have occurred.

#### RELATION OF ZOOPLANKTON BIOMASS TO CHLOROPHYLL AND PRIMARY PRODUCTION

Data on zooplankton abundance and chlorophyll were compared to determine if these two

variables were correlated. The smaller zooplankters were sampled by raising a 1/2-m NOR-PAC net (mesh opening 0.33 mm) vertically from 150-m depth to the surface at about 1 m/sec. Displacement volumes of the catches weighted for distance between stations were averaged between lat 46° N and 51°40' N for each cruise. The mean volumes in February and March were about 0.070 ml/m<sup>3</sup> of water strained and ranged from about 0.250 to 0.280 ml/m<sup>3</sup> in summer, except in August 1967 when the mean volume was 0.550 ml/m<sup>3</sup> (Day, see footnote 8). Thus, the zooplankton standing stock increased to about four times its winter level sometime after the phytoplankton increase in March. Grazing by the zooplankton apparently occurred early enough to crop down the algae, thereby limiting primary productivity before it reached sufficiently high levels to deplete the nutrients from the upper layers. A relatively steady state of grazing pressure and phytoplankton standing stock seemed to hold during the summer (at least in summer 1966). These findings agree with the conclusion of McAllister et al. (1960) that zooplankton grazing limited primary production at Ocean Station "P" by maintaining the phytoplankton standing stock at relatively low concentrations.

The relation between zooplankton displacement volumes and chlorophyll *a* concentrations (Figure 8) shows a negative correlation, further corroborating the above conclusion. The regression of chlorophyll *a* on zooplankton includes only those stations north of lat 46° N, except in coastal water and Adak Bay, and excludes all winter data. As shown previously the nearshore and transition waters exhibit chemical and biological features, which indicate ecological areas somewhat distinct from the area between. The winter data were also excluded from the regression because productivity was limited by insufficient light. Chlorophyll *a* concentrations south of lat 46° N showed no apparent relation to the amount of zooplankton present. Chlorophyll in Adak Bay and coastal waters was always significantly higher than estimated from the regression, except in March in Adak Bay. All of the high chlorophyll values were near shore and associated with intermediate quantities of zooplankton.

<sup>\*</sup> Donald S. Day, Oceanographer, Natl. Mar. Fish. Serv. Biol. Lab., Seattle, Wash.

<sup>o</sup> Parsons, T. R. 1965. A general description of some factors governing primary production in the Strait of Georgia, Hecate Strait and Queen Charlotte Sound, and the N.E. Pacific Ocean. Fish. Res. Board Can., Manuscr. Rep. Ser. (Oceanogr. Limnol.) 193, 34 p. (Processed.)



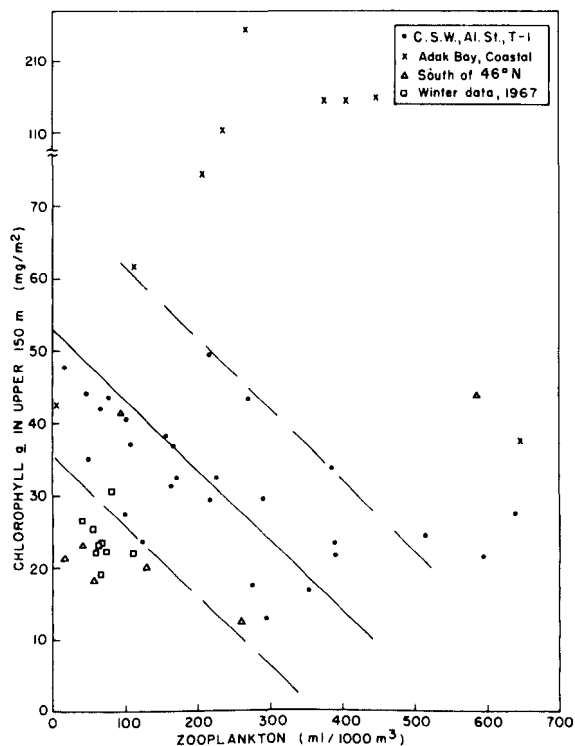


FIGURE 8.—Relation of chlorophyll *a* to net zooplankton in the upper 150 m of the Subarctic Pacific Region, 1966-68. Dashed lines represent 95% confidence limits.

The zooplankton value at the only nearshore station (Adak Bay) in March was the lowest observed. These data suggest that the zooplankton increase occurred later in the spring in coastal areas than farther offshore, a condition which could have permitted the phytoplankton bloom to reach much higher levels near shore before being controlled by grazing.

### ANNUAL PRIMARY PRODUCTION

The annual primary production between lat  $46^{\circ}$  and  $51^{\circ}40'$  N was estimated from values of  $P_K$ ,  $P_R$ , and  $P_M$ . The data from all cruises were combined into a single composite year for apportioning productivity to time periods. The lowest estimate was for  $P_K$  ( $72 \text{ g C/m}^2$  per year);  $P_m$  and  $P_R$  were somewhat higher ( $82$  and  $85 \text{ g C/m}^2$  per year). If the estimate of primary productivity from phosphate changes is correct,

annual productivity could be as high as  $100 \text{ g C/m}^2$ . These estimates are considerably higher than those reported by McAllister (1969), moderately higher than those of Koblents-Mishke (1965), and lower than those of Anderson (in press).

No reason is apparent from the quantitative data for the difference between annual productivity at station "P" ( $48 \text{ g C/m}^2$  per day; McAllister, 1969) and that in the mid-Subarctic Region. If zooplankton is the main factor limiting productivity, more zooplankton and less chlorophyll should be expected at station "P" than south of the Aleutians; however, zooplankton density was lower and chlorophyll *a* concentrations were about the same or slightly higher at station "P." More detailed seasonal observations from the mid-Subarctic, as well as a comparison of plankton communities in the two locations, will probably be necessary to explain the observed differences in annual productivity.

### CONCLUSION

The main conclusions drawn from the primary productivity and related data are listed below:

1. No significant differences in primary productivity were found consistently among the various oceanographic domains or other waters of the Subarctic Pacific Region except that Adak Bay and the Coastal Domain south of Adak Island were generally more productive than areas farther south.
2. The annual cycle of productivity is typical for temperate oceans: productivity is low in winter, increases in the spring until more or less of a bloom develops, and declines by summer to relatively steady intermediate levels. Productivity in autumn and early winter was not studied.
3. Light limits productivity during winter; less light penetrates the surface than during other seasons, and the greater thickness of the mixed layer in the upper zone further reduces the light available to the algae.
4. During spring and summer, nutrients and light are plentiful, but zooplankton appears to graze the standing stock of phytoplankton to relatively low levels—thereby limiting productivity of phytoplankton.

5. The main mechanisms of dissolved-phosphate supply in the upper 50 m of water during summer are in situ regeneration by zooplankton and upwelling. Regeneration supplies significant amounts of phosphate (perhaps more than is provided by upwelling) in the summer, but increased turbulence and upwelling in winter maintain high levels of nutrients throughout the upper 100 m of water.

6. The seasonal cycle and factors limiting productivity are similar to those at station "P" (lat 50° N, long 145° W), but some significant differences exist. Productivity in the study area is nearly twice that at station "P," and zooplankton biomass is also much greater. The change in measured phosphate concentrations at station "P" over the productive season can be accounted for by phosphate utilized by the algae and by phosphate supplied by upwelling. South of the Aleutian Islands, however, phosphate regenerated in situ must be invoked to balance the phosphate budget.

7. Annual primary production in the area studied is about 80 to 100 g C/m<sup>2</sup>.

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