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REGIONAL VARIATIONS OF SURFACE PRIMARY PRODUCTION IN THE BERING SEA IN SUMMER AND THE VERTICAL STABILITY OF WATER AFFECTING THE PRODUCTION*

Akira TANIGUCHI**

Introduction

There have been several works on the primary production in the Subarctic Pacific Ocean (Bogorov, 1958; Holmes, 1958; Saijo & Ichimura, 1960; McAllister *et al.*, 1960; Semina, 1960), indicating that the area is highly productive in general. The data from Cruises 46 and 49 of the *Oshoro Maru II* (1960, 1961) and Cruise 24 of the *Oshoro Maru III* (1967) of Hokkaido University in summer show that the average photosynthetic activity of phytoplankton per cubic meter of surface water under the almost optimum illumination (8 Klux and 15 Klux) is 3.06 mgC/m^3/hr in the Bering Sea, 1.23 mgC/m^3/hr in the northern part of the Gulf of Alaska, 5.10 mgC/m^3/hr in the Oyashio region and 1.27 mgC/m^3/hr in the southeastern part of the Sea of Okhotsk (Taniguchi, Motoda & Kawamura, unpublished). Primary production of the surface water in the Bering Sea was studied on Cruise 46 of the *Oshoro Maru II* in the summer of 1960 with the results of that optimal light intensity of surface phytoplankton in the Bering Sea is rather low (about 8 Klux) and its photosynthetic activity per unit volume of water is as high as given above (Anonymous, 1961; Kawamura, 1963; Motoda & Kawamura, 1963). The daily production *in situ* in summer (June-August) in the Bering Sea is 0.34–0.63 gC/m^2/day which is also high compared with that in the Tropical and the Subtropical Pacific (0.08–0.31 gC/m^2/day) (unpublished data) and with that at station "P" (0.2 gC/m^2/day) (McAllister *et al.*, 1960).

Kawamura (1963) found regional variations in the primary production of the surface water in the Bering Sea on Cruise 46 of the *Oshoro Maru II.*

The author had an oppotunity to measure the primary production on Cruise 24 of the *Oshoro Maru III* to the Bering Sea in the summer of 1967. He observed similar regional variations of the surface primary production in the Bering Sea in a previous report (Kawamura, 1963) and found characteristic features of primary production when a distinct thermocline was present or absent.

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Methods and Materials

The experiments were undertaken during the period from June 10 to August 17, 1967 on Cruise 24 of the *Oshoro Maru III*, sailing to the west coast of Canada through the Bering Sea. Location of stations at which the experiments were made is given in Fig. 1. At 5 stations, Os 2, Os 6, Os 8, Os 10 and Os 96, ^{14}C tank experiments on the samples collected from 6–7 depths were made under the constant

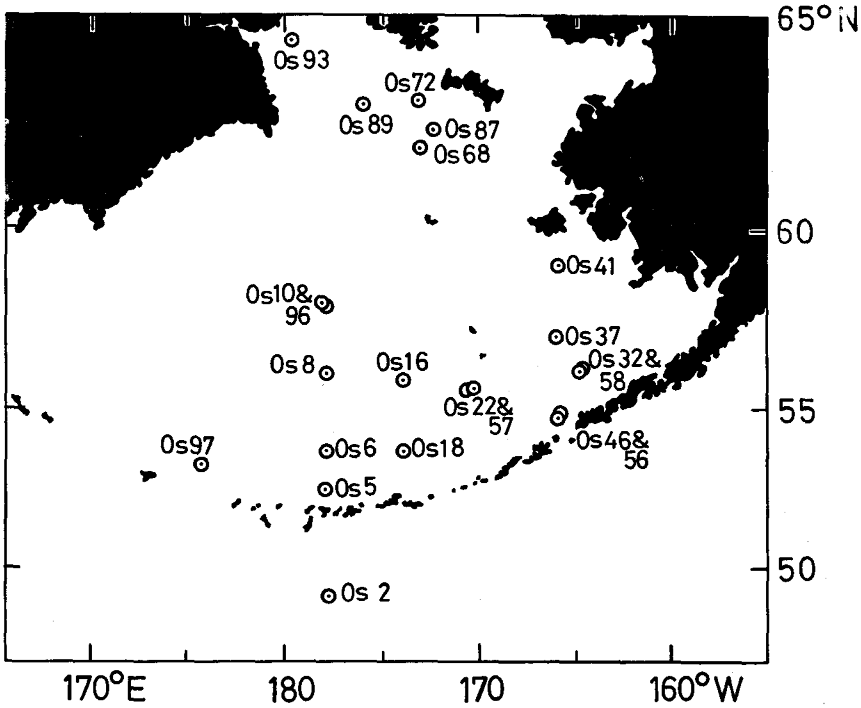


Fig. 1. Location of stations occupied on Cruise 24 of the *Oshoro Maru III* in the summer of 1967

illumination of 15 Klux; at other stations, Os 16, Os 22, Os 37, Os 41, Os 87 and Os 89, the light-photosynthesis experiments were made on the samples collected from several depths, exposing them under several grades of light intensities, 200–8000 lux, in a tank; and at 4 stations, Os 2, Os 6, Os 8, and Os 10, *in situ* primary production was measured by suspending the experimental bottles in the sea for a half day. Sampling time varied from 2130 to 0135 throughout all the stations above, except 3 stations, Os 2, Os 10 and Os 96 where sampling was made before noon, 0920–1100.

In all the samples collected at all the stations (Fig. 1), except 3 stations Os 5, Os 46 and Os 56, the phytoplankton cell count was made on a fraction of the samples concentrated from 500 ml of water.

The samples collected at 22 stations were presented to Mr. Kohki Nakajima for pigment determination by a fluorometric method using a fluorometer incorporated with the Hitachi 139 Spectrophotometer. Data on hydrography, cell count, pigment concentrations and primary production measurement on this cruise (Cruise 24) were published in Anonymous 1968 and 1969 (in press).

Surface Phytoplankton Standing Crops and Primary Production

The Bering Sea is divided into 6 areas according to the characteristics of water masses as follows (Dodimead *et al.*, 1963): these 6 areas were covered in this study.

1) Gulf of Anadyr
2) Bristol Bay
3) Central Part of Coastal Domain between the former two areas
4) Bering Sea Gyre
5) West of Bowers Bank
6) East of Bowers Bank

Outside the Bering Sea, 7) Central Subarctic Domain (Dodimead *et al.*, 1963) is also included in the present study (Fig. 2).

Chlorophyll *a* contents, cell numbers and photosynthetic activity under the constant illumination of surface phytoplankton population, an average in each area referred to above, are given in Table 1. The maximum value of both chlorophyll *a* and cell numbers appeared in the Gulf of Anadyr. No experiment on the primary production was made in this area. On the other hand, the minimum chlorophyll *a* appeared in the Bering Sea Gyre, while the minimum cell numbers appeared in the Central Subarctic Domain. The highest primary production was found in the East of Bowers Bank among all areas, though there was no available data from the Gulf of Anadyr and the West of Bowers Bank. The largest cell numbers were in the East of Bowers Bank among all areas except the two areas mentioned above. The cell numbers in the Gulf of Anadyr were extremely large.

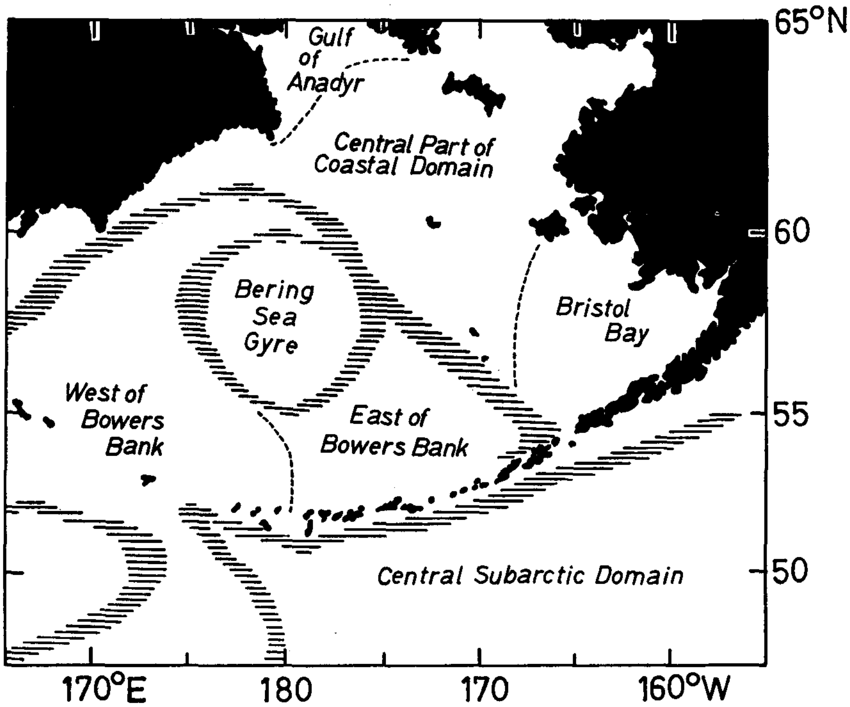


Fig. 2. Seven areas of surface water in the Northern North Pacific (Dodimead *et al.*, 1963, slightly modified the parts of Coastal and Western Subarctic Domains)

Table 1. Chlorophyll *a* and pheopigments, phytoplankton cell numbers and photosynthetic activity of the surface water in 7 areas of the Bering Sea in the summer of 1967 (Average values of all stations)

Area	Chlorophyll *a* (mg/m^3)	Pheopigments (mg/m^3)	Phytoplankton ($10^6 cells/m^3$)	Photosynthesis ($mgC/m^3/hr$)
Gulf of Anadyr	5.56	1.71	742.2	—
Central Part	0.23	0.43	29.6	1.71
Bristol Bay	0.57	1.82	9.5	1.46
Bering Sea Gyre	0.15	0.31	42.0	1.59
East of Bowers Bank	0.64	0.94	133.3	5.04
West of Bowers Bank	0.81	0.94	17.1	—
Central Subarctic Domain	0.28	0.19	2.9	0.48

The area of the large cell numbers was not always a high productive one. Generally speaking, at a station where dinoflagellates were predominant, the primary productivity per unit cell number and per unit weight of chlorophyll *a* was high, while at a station largely occupied by the diatom, *Chaetoceros*, the productivity was considerably low. A moderate productivity was seen at a station where a diatom, *Nitzschia closterium*, was a major component (Table 2). Such a phenomenon had already been noted by Kawamura (1963) in the Bering Sea.

The data on phytoplankton cell numbers, chlorophyll *a* and photosynthetic activity at the surface of the Bering Sea on Cruise 46 of the *Oshoro Maru II* in the summer of 1960 are available (Anonymous, 1961). Gathering those data together with the present data (Cruise 24) (Table 3), the regional variations are discussed. Pigment concentrations were determined spectrophotometrically in 1960 and chlorophyll *a* was not distinguished from pheopigments. In 1967 the pigments were determined by the fluorometric method distinguishing chlorophyll *a* from pheopigments. However, for the sake of convenience of treatment of the data on both cruises altogether, chlorophyll *a* plus pheopigments were used.

General features of phytoplankton standing crops and photosynthetic activity

Table 2. Photosynthetic activity of dominant species in natural phytoplankton communities at the surface in the Bering Sea in the summer of 1967

Station	Dominant species	Phytoplankton (10^6cells/m^3)	Chlorophyll *a* (mg/m^3)	Photosynthetic activity	
				mgC/mgChl.*a*/hr	mgC/10^6cells/hr
Os 10	*Chaetoceros debilis*(62%) (*Chaetoceros* spp.(83%))	34.6	0.16	0.29	0.001
Os 32	Dinoflagellates (86%)	11.6	0.04	16.50	0.06
Os 96	*Nitzschia closterium* (86%)	26.4	0.29	2.69	0.03

Table 3. Chlorophyll concentrations, phytoplankton cell numbers and photosynthetic activity of the surface water in 7 areas of the Bering Sea in the summers of 1960 and 1967 (Average values of all stations)

Area	Year	Number of stations	Chlorophyll (mg/m^3)*	Phytoplankton (10^6cells/m^3)	Photosynthesis (mgC/m^3/hr)	Daily production (mgC/m^2/day)
Gulf of Anadyr	1960	0	—	—	—	—
	1967	1	7.27	742.2	—	—
Central Part	1960	9	0.27	2.2	0.65	—
	1967	4	0.66	29.6	1.71	—
Bristol Bay	1960	5	2.00	543.0	2.42	—
	1967	6	1.75	9.5	1.46	—
Bering Sea Gyre	1960	1	0.78	3.2	0.65	—
	1967	3	0.46	42.0	1.59	340
East of Bowers Bank	1960	6	0.44	28.1	1.46	—
	1967	6	1.58	133.3	5.04	630
West of Bowers Bank	1960	7	0.50	2.6	0.75	—
	1967	1	1.75	17.1	—	—
Central Subarctic Domain	1960	9	0.41	2.0	0.72	—
	1967	1	0.47	2.9	0.48	160

* Chlorophyll *a* plus pheopigments

at the surface are as follows: high values of standing crops and photosynthetic activity are seen in the East of Bowers Bank and the Bristol Bay, and low values of both elements are seen in the Bering Sea Gyre and the Central Subarctic Domain.

However, a large year-to-year difference in the same region is observed. Such a large variation in the standing crops in an area with the years is seemingly due to the intermittent production of phytoplankton at short intervals in the warm seasons in the Bering Sea (Karohji, personal communications). Four stations were occupied twice on Cruise 24 (1967), Os 10 and Os 96, Os 22 and Os 57, Os 46 and Os 56, Os 32 and Os 58 (Fig. 1), advantaging the comparison of standing crops at an interval of about one month at the same station. It was shown that there was a great variation in phytoplankton standing crops accompanied by a variation of phytoplankton communities in the same geographical locality within one month (Table 4).

In situ primary production measurements also indicated a great variation in the Bering Sea according to the localities. The daily primary production under

Table 4. Variations in pigments and cells of the surface phytoplankton within about one month at the four locations in the Bering Sea in the summer of 1967

Station	Date	Chlorophyll *a* (mg/m^3)	Pheopigments (mg/m^3)	Phytoplankton (10^6cells/m^3)	Dominant species
Os 10	June 15	0.17	0.49	34.6	*Chaetoceros debilis*
Os 96	August 17	0.29	0.35	26.4	*Nitzschia closterium*
Os 22	June 20	0.12	0.34	36.8	*Denticula seminae*
Os 57	July 29	0.94	1.34	382.8	*Rhizosolenia hebetata* f. *semispina*
Os 46	July 1	1.12	0.64	—	—
Os 56	July 28	1.01	3.75	—	—
Os 32	June 25	0.04	0.22	11.6	Dinoflagellates
Os 58	July 30	0.29	0.51	5.1	Dinoflagellates

Table 5. Vertical differences of photosynthetic activity at stations Os 37 and Os 96 where distinct thermocline was observed at a depth 10–20 m and 20–40 m respectively in the summer of 1967

	Photosynthetic activity			
	Os 37		Os 96	
	mgC/mgChl.*a*/hr	mgC/10^6cells/hr	mgC/mgChl.*a*/hr	mgC/10^6cells/hr
Surface	—	0.14	2.74	0.03
Above thermocline	10.44	0.08	6.46	0.02
Thermocline	15.96	0.11	7.55	0.01
Below thermocilne	1.04	0.05	37.70*	0.24*

* sampled from 55m depth within the Intermediate Cold Water (Fig. 3g)

1 m^2 of the surface was high in the East of Bowers Bank, and low in the Bering Sea Gyre and the Central Subarctic Domain. This regional variation in primary production *in situ* coincided with the regional variation in phytoplankton standing crops and also photosynthetic activity of the surface water (Table 3). The Gulf of Anadyr is the area of the largest standing crops in the present observations, as reported by Semina (1960). Although the primary production was not measured this time, it should be very high in the Gulf of Anadyr.

Vertical Stability of Water inducing High Primary Production
(Fig. 3a-g)

Phytoplankton cell numbers decreased rapidly below the euphotic zone at all stations, except at station Os 2 which is located in the Central Subarctic Domain outside the Bering Sea. At this station cell numbers and primary productivity were very low through water column from the surface to the lower limit of the euphotic zone despite the high concentrations of nutrients (0.86–1.31 μg-atP/l, 11.59–19.73 μg-atN/l) (Fig. 3a).

The thermocline was well developed at two stations, Os 37 and Os 96, and it was indistinct or entirely absent at other 5 stations. At the stations where a thermocline was distinctly developed (Os 37, Os 96), the maximum cell numbers and the maximum photosynthetic activity (mgC/m^3/hr) were the largest at the depth of the thermocline or thereabout. Vertical distribution of phosphate was rather constant from the surface to the thermocline at Os 96 (1.02–1.68 μg-atP/l) and sharply increased with depth at Os 37, from 0.11 μg-atP/l to 1.40 μg-atP/l. Photosynthetic activity per unit phytoplankton standing crops (mgC/mgChl. *a*/hr, mgC/10^6 cells/hr) at the thermocline was comparable to those at the surface (Fig. 3f-g, Table 5). This indicates that the phytoplankton distributed at the depth of the thermocline was similarly active to those distributed at the surface under suitable conditions of illumination and nutrients in the Bering Sea.

At the stations where the thermocline was indistinct, vertical profiles of phytoplankton standing crops and photosynthetic activity showed three different types. In type I (Os 10) there was generally poor phytoplankton standing crops throughout the vertical range of the euphotic zone, and photosynthetic activity was considerably low at every depth, although concentrations of nutrients were high (1.03–1.70 μg-atP/l, 19.23–26.24 μg-atN/l) (Fig. 3d). In type II (Os 6, Os 8) the maximum standing crops and photosynthetic activity were seen near or at the surface and concentration of phosphate in the euphotic zone was high (1.31–1.81 μg-atP/l) except at the surface at Os 6 (0.0 μg-atP/l) (Fig. 3b-c). In type III (Os 16) both standing crops and photosynthetic activity were high through the layer from the surface to the upper limit of the thermocline and concentration of phosphate was increased with depth (0.60–0.96 μg-atP/l) (Fig. 3e). These pheno-

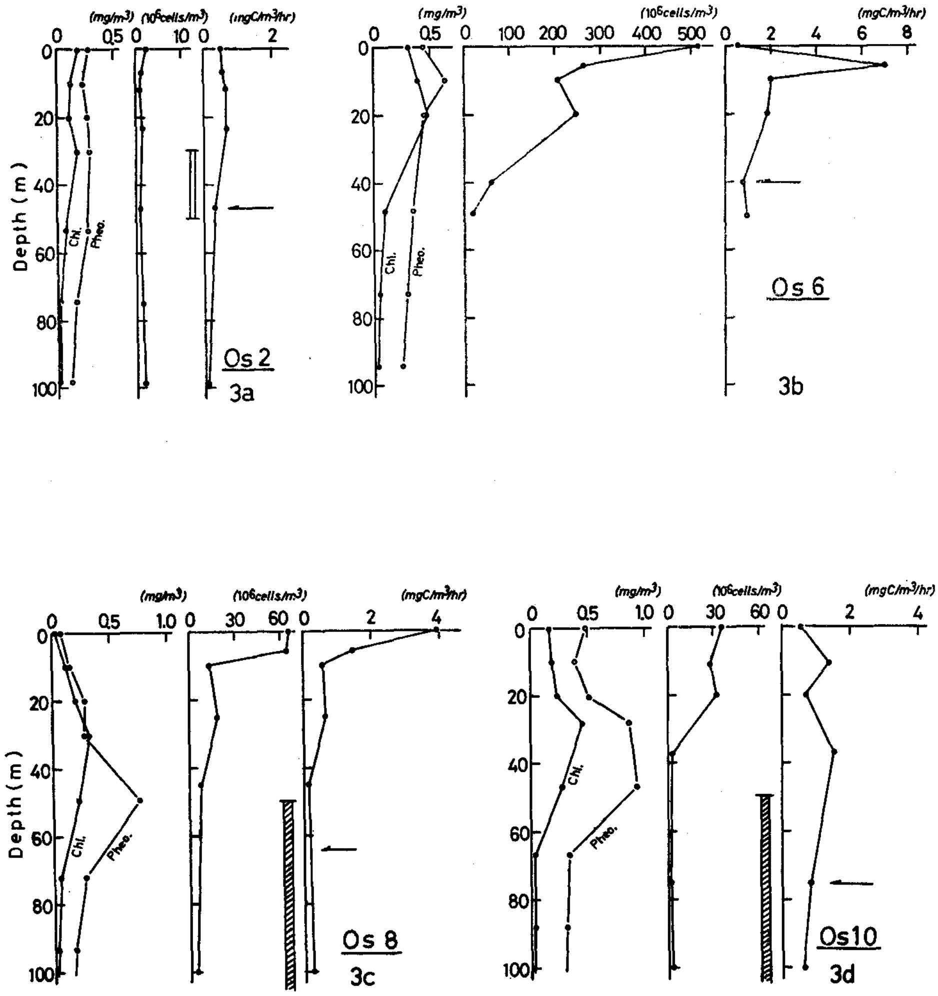
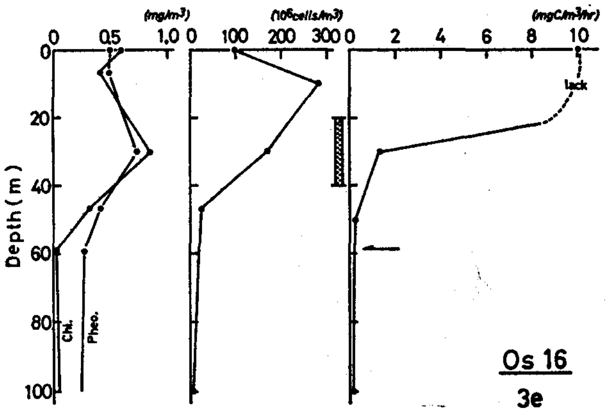
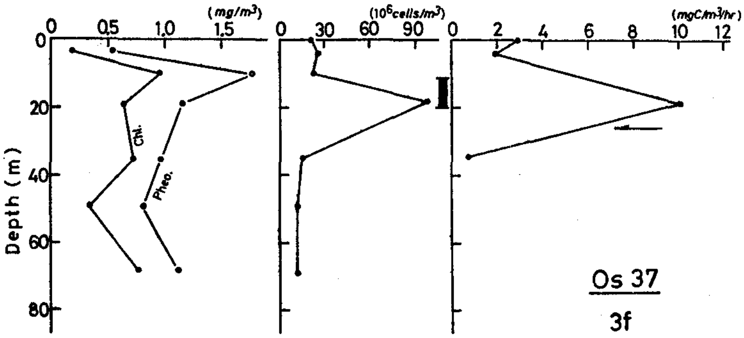


Fig. 3 a-g. Vertical distributions of chlorophyll *a*, pheopigments, phytoplankton cells and photosynthetic activity at 7 stations. Horizontal arrow (←—) indicates the lower limit of the euphotic zone. Vertical column indicates a thermocline (opened column: indistinct thermocline; doted column: moderately developed thermocline; solid column: well developed thermocline) and the Intermediate Cold Water (shaded column)





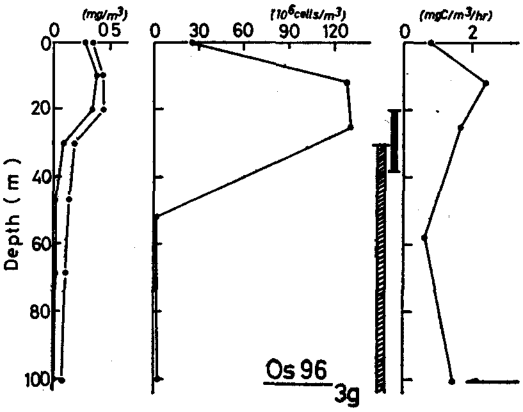


Fig. 3a-g. Continued

mena are related to the difference in the degree of stability of sea water and the time course of phytoplankton blooming. Generally speaking, a mixing of water is confined to a layer shallower than the critical depth in high latitudes in warm seasons, that so phytoplankton cummunities placed under favourable light conditions are able to grow (Riley, 1942 ; Sverdrup, 1953; Hasle, 1956; Marshall, 1958; Semina, 1960; Cushing, 1962; Parsons *et al.*, 1966). The growth rate of phytoplankton is limited by the deficiency of one nutrient: for instance, the productive rate of *Nitzschia closterium* decreases at low concentration of phosphate below 0.55 mg-atP/m^3 (Ketchum, *cf.* Riely *et al.*, 1949) and the growth rate of *Skeletonema costatum* also decreases when concentrations of phosphate and nitrate are less than 0.03 μg-atP/1 and 0.5 μg-atN/1 respectively (McAllister *et al.*, 1964). During the present observation, average concentrations of phosphate and nitrate in upper 10 m in the Bering Sea varied from 0.14–1.40 μg-atP/1 and 7.73–19.87 μg-atN/1 respectively (Anonymous, 1968), so that inhibition of growth due to nutrients deficiency sometimes occurred in the surface layer but it would not be severe in the Bering Sea in summer.

The blooming of the phytoplankton generally begins at the surface when conditions are suitable, and with progressive time the productive layer spreads downwards. When the conditions for growth near the surface become temporarily unfavourable, phytoplankton communities sink and accumulate around the thermocline. When the sea is rough, distribution of phytoplankton as well as nutrients will become homogeneous through mixing layer (*cf.* Menzel & Ryther, 1960). Table 4 indicates that the high primary production at the surface occurred intermittently in the same locality. It is suggested that the phytoplankton blooming occurs several times during a season from spring to summer as a result of the repetition of stable and unstable conditions of the water above the thermocline. This may cause accumulated high primary production in the Bering Sea throughout summer.

Summary

(1) Results of experiments on the primary productivity carried out on Cruise 24 of the *Oshoro Maru III* in the summer of 1967 to the west coast of Canada *via* the Bering Sea are reported.

(2) There are regional variations in primary productivity in the Bering Sea in summer, and, at the same time, large year-to-year variations in the productivity in the same locality and season.

(3) A thermocline develops in the depths (10–30 m) shallower than the lower limit of the euphotic zone (26–100 m) in the Bering Sea from spring to summer. The depth of the thermocline is still favourable for the growth of phytoplankton owing to light condition and nutrients.

(4) During spring and summer, phytoplankton seems to grow intermittently several times, as a result of the repetition of stable and unstable conditions of the water in the upper 10–30 meters caused by the alternation of calm and rough weather.

(5) Such a repeated production will causes a high total primary production in the Bering Sea in summer.

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