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GEOGRAPHICAL VARIATION OF PRIMARY PRODUCTION IN THE WESTERN PACIFIC OCEAN AND ADJACENT SEAS WITH REFERENCE TO THE INTER-RELATIONS BETWEEN VARIOUS PARAMETERS OF PRIMARY PRODUCTION

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I. Introduction

Since Steemann Nielsen and Aabye Jensen (1957) introduced during the Galathea Expedition the ^{14}C method in assessing primary production in the oceans, many data of primary production as obtained by using essentially the same method (Steemann Nielsen, 1952) have been accumulated in various sea areas of the world oceans. As for the Pacific Ocean, the following works, excluding numerous isolated observations within limited regions, are particularly important to review the general geographical variation in primary production in the entire area: Holmes *et al.* (1957), Holmes (1958), Forsbergh and Joseph (1964), Blackburn (1966), McAllister *et al.* (1960) and Owen and Zeitzschel (1970) in the eastern Pacific Ocean; Saijo and Ichimura (1960), Jitts (1965), Motoda *et al.* (1970a, b), Saijo *et al.* (1969), Taniguchi and Kawamura (1970), Nishizawa *et al.* (1971) and

Taniguchi and Nishizawa (1971) in the western Pacific Ocean; Kawamura (1963) and Taniguchi (1969) in the northern North Pacific Ocean. In addition, an excellent summary of the world wide geographical distribution of primary production was given by Koblentz-Mishke (1959). It is noticed that, looking over these new information, the schema of relative primary production in the oceans presented by Sverdrup (1955) does remain still valid (Fig. 1). The production map of Sverdrup (1955) was derived fundamentally from the consideration of the relative intensity of nutrient supply into the euphotic layer from underlying water by the physical mechanisms of water movements such as vertical convection, upwelling and turbulent diffusion of sea waters.

The major factors limiting the primary production in open oceans are nutrient and light (Ryther, 1963). However, the incident light intensity will not be taken directly into consideration, because the effect of light may be reduced to some extent in nature by the adaptation of phytoplankton to different light intensities (Steemann Nielsen and Hansen, 1959; Steemann Nielsen and Park, 1964; Jørgensen, 1964). Furthermore, since the geographical variation in solar radiation is in a relatively narrow range over a major part of the northern or southern hemisphere except polar regions at least during warm seasons, the effect of light intensity is rather insignificant in the geographical variation in primary production during the period from spring to autumn in both hemispheres (Ryther, 1963; Riley, 1965).

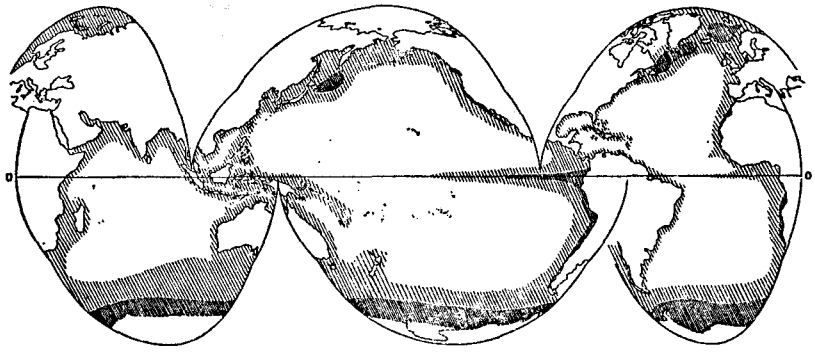

Fig. 1. Schematic representation of the probable relative productivity of ocean areas. Heavy shading indicates very productive area, light shading moderately productive regions (after Sverdrup, 1955).

Thus, it is suggested that the concentration of available nutrient in the euphotic layer is the factor that is most important in limiting the primary production in open oceans. The supply of nutrient into the euphotic layer is generally effected by the physical conditions of sea waters such as vertical mixing and upwelling of waters (*cf.* Sverdrup, 1955; Ryther, 1963; Raymont, 1963). Furthermore, the

vertical distribution of phytoplankton in a water column is also primarily controlled by the physical conditions of sea waters. There are many instances that a shallow thermocline located above the critical depth in a nutrient rich water mass induces comparatively high primary production, because the density discontinuity of the water makes a barrier against sinking loss of phytoplankton from the favourable euphotic layer down to the disphotic and aphotic layers (Riley, 1942; Sverdrup, 1953; Semina, 1960; Parsons and LeBrasseur, 1968; Taniguchi, 1969; Anderson, 1969; Taniguchi and Kawamura, MS; etc.). The vertical structure of hydrographic characteristics within the photic layer of water masses generally varies with main current systems (*cf.* Sverdrup *et al.*, 1942).

Conclusively, it is generally recognized that the geographical variation in primary production as well as in biological production of higher levels is closely related to the surface current systems. This is virtually sustained by many investigations in the Pacific Ocean (*e.g.*, Graham, 1941; Sverdup *et al.*, 1942; Sette, 1955; Barnes, 1957; Holmes *et al.*, 1957; King and Hida, 1957; King *et al.*, 1957; Brandhost, 1958; Holmes, 1958; Saijo and Ichimura, 1960; Reid, 1962; Raymont, 1963; Forsbergh and Joseph, 1964; Jitts, 1965; Blackburn, 1968; Kawarada and Sano, 1969; Blackburn *et al.*, 1970; Motoda *et al.*, 1970a, b; Taniguchi and Kawamura, 1970; Nishizawa *et al.*, 1971; Taniguchi and Nishizawa, 1971). Bogorov (1958) suggested that in dealing with general biogeography in the sea, one should take into consideration areal differences in primary production that are essentially conditioned by the differences in current systems (*cf.* Ekman, 1953).

This paper deals with the geographical variation of primary production over the major current systems in the western Pacific Ocean and adjacent seas in relation to physical conditions of waters, and is based on the data collected on 14 cruises during the years from 1959 to 1969. The direct measurement of *in situ* primary production is time consuming, and was often impossible due to the shortage of available time or rough sea. So, the correlations between the observed daily *in situ* primary production in the euphotic layer and each of more easily measurable parameter such as surface chlorophyll *a* and zooplankton biomass in the upper 150 m water column, were examined.

II. Methods and Materials

1. Cruises and stations

The fourteen sea trips during which the present data were obtained include 3 cruises of the T.S. *Oshoro Maru II* of the Faculty of Fisheries, Hokkaido University, during 1959 to 1963, 10 cruises of her successor the T.S. *Oshoro Maru III* from 1965 to 1969 and one cruise of the R.V. *Kaiyo Maru* of the Japan Fisheries Agency in 1968. Details of all the data collected on the cruises of the *Oshoro*

Table 1. Sources of data on primary production used which were collected and adjacent seas, and references in which details of these data are

Vessel, cruise number and area		Number of station	Period
Oshoro Maru II			
45	East China Sea	5	Nov.-Dec. 1959
	off Boso Peninsula	1	Nov. 1959
	south of Kyushu	7	Nov. 1959
46	Bering Sea	29	June-July 1960
	Alaskan Stream	6	July 1960
	Subarctic Current	2	June 1960
	Oyashio Current	15	June & Aug. 1960
	North Pacific Current	9	Aug. 1960
	Kuroshio Extension	4	Aug. 1960
49	Okhotsk Sea	7	Aug. 1963
Oshoro Maru III			
13	Oyashio Current	3	May 1965
16	south of Kyushu	1	Nov. 1965
	east of Philippines	3	Dec. 1965
	Great Australian Bight	3	Dec. 1965
	Equatorial Counter Current	1	Jan. 1966
	North Equatorial Current	7	Jan. 1966
	Kuroshio Counter Current	2	Jan. 1966
	off Boso Peninsula	1	Jan. 1966
18	Oyashio Current	2	April 1966
21	North Equatorial Current	4	Jan. 1967
	Kuroshio Counter Current	3	Jan. 1967
23	Oyashio Current	2	April 1967
24	Subarctic Current	1	June 1967
	Bering Sea	22	June-Aug. 1967
	Alaskan Stream	1	July 1967
26	Kuroshio Counter Current	3	Jan. 1968
	North Equatorial Current	6	Jan. 1968
	Equatorial Counter Current	2	Jan. 1968
29	Okhotsk Sea	1	Sept. 1968
30	east of Philippines	6	Nov. 1968
	South Equatorial Current	2	Jan. 1969
	Equatorial Counter Current	3	Jan. 1969
	North Equatorial Current	3	Jan. 1969
	Gulf of Carpentaria	24	Dec. 1968
33	Oyashio Current	2	Sept. 1969
Kaiyo Maru			
KY 68-1	North Equatorial Current	12	Aug. 1968
	Equatorial Counter Current	5	Aug. 1968
	South Equatorial Current	8	Aug. 1968
	North of Fiji Islands	15	Aug. 1968
	East of New Zealand	11	June-July 1968

* C^{14} isotope solution used had been contaminated with bacteria

on board the *Oshoro Maru* and *Kaiyo Maru* in the western Pacific Ocean published

Item of investigations	Reference
cell, tank	Data Rec. 5
cell, tank	Data Rec. 5
cell, tank	Data Rec. 5
cell, chl. *a*, tank	Data Rec. 5
cell, tank	Data Rec. 5
cell, chl. *a*, tank	Data Rec. 5
cell, chl. *a*, tank	Data Rec. 5
chl. *a*, tank	Data Rec. 5
chl. *a*, tank	Data Rec. 5
cell, chl. a, tank, *in situ*	Nil
cell, chl. *a*, tank, *in situ*, simulated *in situ*	Data Rec. 10
cell, chl. *a*, tank, simulated *in situ*	Data Rec. 10
cell, chl. *a*, tank, simulated *in situ*	Data Rec. 10
cell, chl. *a*, tank	Data Rec. 10
cell, chl. *a*, tank, simulated *in situ*	Data Rec. 10
cell, chl. *a*, tank, *in situ*, simulated *in situ*	Data Rec. 10
cell, chl. *a*, tank, *in situ*, simulated *in situ*	Data Rec. 10
cell, chl. *a*, tank	Data Rec. 10
cell, chl. *a*, tank, *in situ*, simulated *in situ*, Ass. cruve	Data Rec. 11
cell, chl. *a*, tank, *in situ*	Data Rec. 12
cell, chl. *a*, tank, *in situ*	Data Rec. 12
cell, chl. *a*, tank, *in situ*, simulated *in situ*, Ass. curve	Data Rec. 12
cell, chl. *a*, tank, *in situ*, simulated *in situ*	Data Rec. 12 & 13
cell, chl. *a*, tank, *in situ*, simulated *in situ*, Ass. curve	Data Rec. 12 & 13
chl. *a*	Data Rec. 12 & 13
cell, chl. *a*, tank,* *in situ**	Data Rec. 13
cell, chl. *a*, tank,* *in situ**	Data Rec. 13
cell, chl. *a*, tank,* *in situ**	Data Rec. 13
chl. *a*, Ass. curve	Data Rec. 13
chl. *a*, tank	Data Rec. 14
cell, chl. *a*, tank, *in situ*	Data Rec. 14
chl. *a*, tank	Data Rec. 14
chl. *a*, tank, Ass. curve	Data Rec. 14
cell. chl. *a*, tank	Data Rec. 14
cell, chl. *a*, tank, *in situ*, Ass. cruve	Data Rec. 14
chl. *a*, *in situ*, Ass. curve	Nil
chl. *a*, Ass. curve	Nil
chl. *a*, *in situ*, Ass. curve	Nil
chl. *a*, Ass. curve	Nil
chl. *a*, tank, *in situ*, Ass. curve	Nil

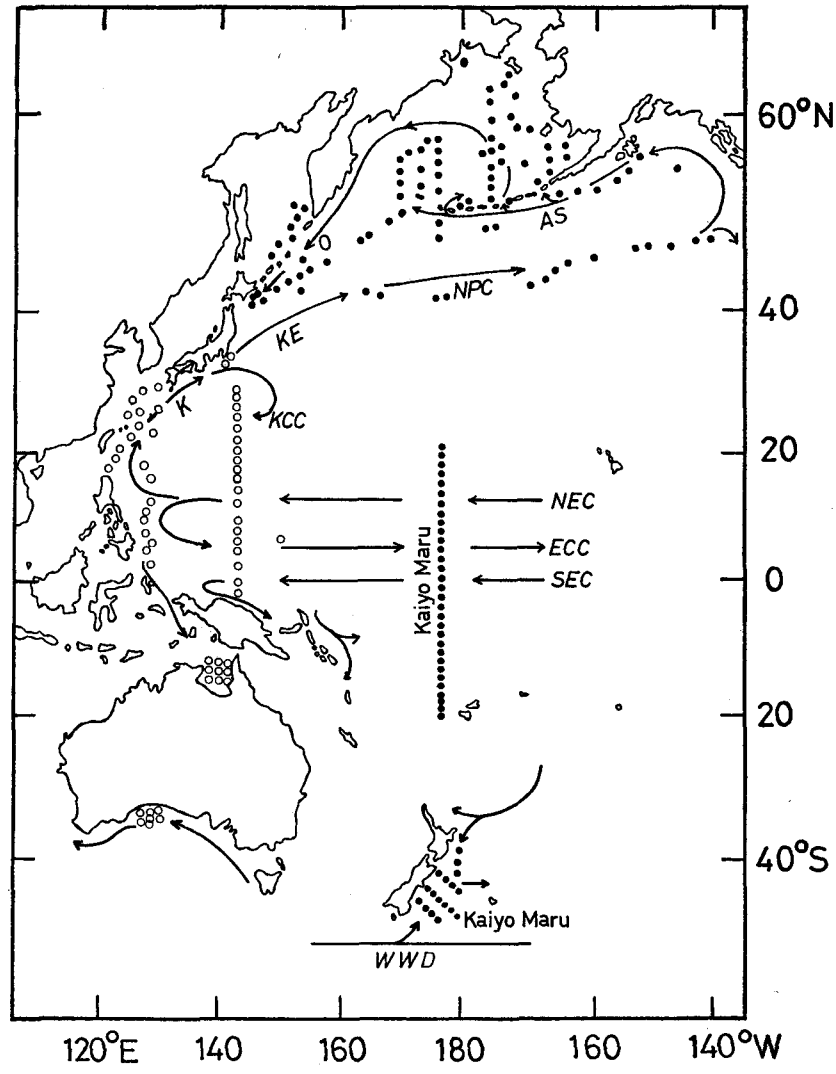

Fig. 2. Schematic diagram of major currents in the western Pacific Ocean and adjacent seas and approximate location of stations where data used in this study were collected on board the *Oshoro Maru* and *Kaiyo Maru* (●: northern summer station, ○: northern winter station)

Maru II and *III* have been published in "Data Record of Oceanographic Observations and Exploratory Fishing", Nos. 5 and 10–14 (Faculty of Fisheries, Hokkaido University, 1961 and 1967–1971) (Table 1) except the data on Cruise 49 of the *Oshoro Maru II* to the Okhotsk Sea in the summer of 1963. The data obtained on the latter cruise and on Cruise KY 68–1 of the *Kaiyo Maru* are filed in the Plankton Laboratory of the Faculty of Fisheries, Hokkaido University.

A total of 244 stations occupied on these 14 cruises distributed over almost

all the major currents in the western Pacific Ocean (Fig. 2). Of these, 127 stations in the northern hemisphere and 30 stations in the southern hemisphere, were occupied in northern summer from April to September, and the remaining 87 stations in northern winter from November to February. The winter stations, however, were concentrated in the tropical and subtropical Pacific Ocean where the seasonal variation in primary production is minor.

The results obtained at each station are not described individually, but each representative case in the 7 major currents are described here. The station number is expressed by an array of six figures headed by two letters indicating the name of the vessel used; for example, Os 672301 should be read as the first station occupied on Cruise 23 of the *Oshoro Maru* in 1967.

2. Phytoplankton standing crop

Phytoplankton standing crop was measured in terms of chlorophyll *a* (mg/m^3) and of cell number (cells/m^3). Major species of phytoplankton were identified and counted under the microscope. Chlorophyll *a* concentration was determined by the colorimetric method (Richards with Thompson, 1952; and SCOR-UNESCO Working Group 17, 1964) for the samples collected before 1966 and for the samples collected thereafter by the fluorometric method (Yentsch and Menzel, 1965; Saijo and Nishizawa, 1969).

3. Primary production

The primary production was measured by the following two methods. The first is the direct *in situ* ^{14}C experiment and the second is the simulated *in situ* ^{14}C experiment. For these two experiments, water samples were collected with paired Van Dorn Water Samplers (Motoda, 1967) from the sea surface (*ca* 0.5 m) and from 4 depths where underwater light intensities were 50%, 30%, 10% and 1%, respectively, of that just below the sea surface. In the *in situ* experiment, each water sample in light and dark bottles was suspended back to the respective sampling depth after the inoculation of a $NaH^{14}CO_3$ solution and incubated for half a day, generally from noon to sunset. The simulated *in situ* conditions were made in a tank on deck under natural light; each bottle was wrapped up in a number of white vinyle sheets, so as to receive nearly the same light intensity as at each sampling depth. Primary production (gC/m^2/day) was calculated by simply doubling the observed half day production in the 5 layers by the above-mentioned two methods and integrating through the euphotic layer. No corrections of respiration loss were made.

To measure the primary productivity (mgC/m^3/hr), all water samples were incubated for 1–4 hrs in a tank under a constant fluorescent light of 8–16 Klux (tank experiment). Assimilation number (mgC/mgChl. *a*/hr) was calculated

from the productivity and the concentration of chlorophyll *a* measured on the same water sample. The primary productivity as well as the assimilation number gives a measure of potential photosynthetic activity and is a useful index for regional comparison.

4. Zooplankton biomass

Zooplankton was collected by the vertical haul with Norpac nets (Motoda, 1957; Morioka, 1965) through the upper 150 m water column. The mesh size of bolting cloth used was 0.33–0.35 mm. In the seas shallower than 150 m such as the Great Australian Bight, Gulf of Carpentaria and the continental shelf water in the Bering Sea, the net was hauled from the sea bottom to the surface. The volume of water filtered by net was registered by a flow-meter mounted at the center of the mouth ring. The wet sample of zooplankton caught was weighed, and the biomass was expressed in a standard unit of g wet-wt/1000 m^3.

5. Inorganic nutrients

Data on nitrate-nitrogen and phosphate-phosphorus referred to in this paper were cited from "Data Record", Nos. 5, 10–14 (Fac. Fish., Hokkaido Univ., 1961, 1967–1971). These were determined by the staffs of the Division of Oceanography of the Research Institute of North Pacific Fisheries, the Laboratory of Analytical

Table 2. Average values of parameters of primary production in 17 sea

Area	Pigments (mg/m^3)		
	Chl. *a* (Fluor.)	Pheop. (Fluor.)	Chl. *a* (Color.)
Bering Sea	0.69	0.80	0.93
Alaskan Stream	0.20	0.26	0.31
Subarctic Current	0.19	0.28	0.24
Oyashio Current	0.33	0.46	3.42
North Pacific Current	—	—	0.45
Okhotsk Sea	—	—	0.11
Kuroshio Extension	—	—	0.36
Kuroshio Current			
off Boso Peninsula	—	—	0.61
south of Kyushu	—	—	0.16
east of Philippines	0.06	0.01	0.06
East China Sea	—	—	—
Kuroshio Counter Current	0.05	0.10	0.12
North Equatorial Current	0.03	0.10	0.06
Equatorial Counter Current	0.08	0.20	0.25
South Equatorial Current	0.22	0.28	0.37*
north of Fiji Islands	0.09	0.13	0.15*
east of New Zealand	0.37	0.79	0.63*
Gulf of Carpentaria	0.20	0.33	0.34*
Great Australian Bight	—	—	0.13

* calculated values (see p. 14)

Chemistry, and the Laboratory of Marine Chemistry of the Faculty of Fisheries, Hokkaido University.

III. Results and Discussion

The entire sea area investigated was divided into 17 areas with 3 subareas according to geographical locations combined with dominating current systems (Sverdrup *et al.*, 1952; Dodimead *et al.*, 1963) (Table 2). Among the 17 areas, the Bering Sea, Oyashio Current, Okhotsk Sea, East China Sea, eastern sea of New Zealand, Gulf of Carpentaria and Great Australian Bight are obviously isolated from other water masses, and the Alaskan Stream, Subarctic Current, Kuroshio Counter Current, North Equatorial Current, Equatorial Counter Current, South Equatorial Current and north of Fiji Islands were separately characterized on the basis of obtained hydrographical data (*cf.* Motoda *et al.*, 1970a, b; Nishizawa *et al.*, 1971).

Table 2 shows average concentrations of pigments, phytoplankton cell number and nutrients in the surface water (*ca* 0.5 m) together with primary production and zooplankton biomass as defined above in each of these 17 sea areas.

1. Inter-relations between various parameters of primary production

The regional distribution of each of the items given in Table 2, excluding

areas with 3 sub-areas of the western Pacific Ocean and adjacent seas

Phytoplankton cell number (cells/m³)	Nutrients		Primary production		Zooplankton (g/1000 m³)
	PO_4-P (μg-at/l)	NO_3-N (μg-at/l)	tank (mgC/m³/hr)	*In situ* (gC/m²/day)	
1.1×10^8	0.66	15.95	1.22	0.49	449
—	0.73	—	1.23	—	280
2.5×10^6	1.10	11.59	0.52	0.16	158
4.6×10^8	1.26	7.80	9.47	1.08	368
—	—	—	0.82	—	—
1.3×10^7	0.48	6.63	1.31	0.08	66
—	—	—	2.18	—	—
4.8×10^7	0.33	3.80	1.52	—	21
4.9×10^5	0.27	0.40	0.68	0.06	13
—	0.21	1.13	0.38	0.14	19
1.4×10^7	—	—	2.51	—	—
3.0×10^5	0.02	0.50	0.44	0.16	19
3.7×10^5	0.12	0.41	0.13	0.09	9
3.6×10^5	0.19	1.30	0.45	0.19	32
—	0.07	0.26	0.95	0.29	76
—	—	—	0.19	—	18
—	—	—	1.70	0.29	25
4.5×10^7	0.14	0.18	1.73	—	339
3.3×10^4	0.09	0.40	0.40	—	10

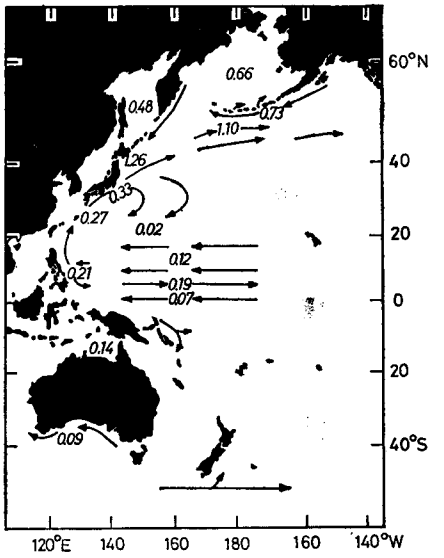

Fig. 3. Geographical distribution of the surface phosphate-phosphorus (μg-at P/l) in the western Pacific Ocean and adjacent seas

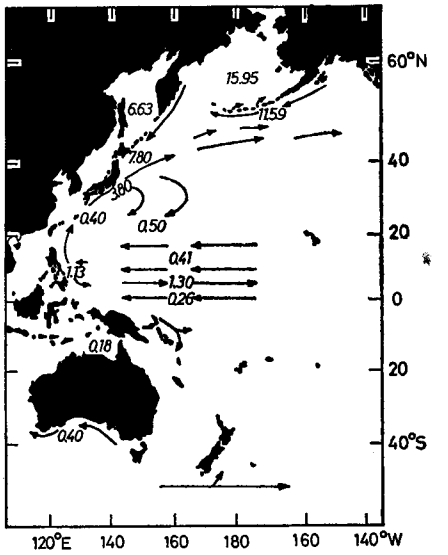

Fig. 4. Geographical distribution of the surface nitrate-nitrogen (μg-at N/l) in the western Pacific Ocean and adjacent seas

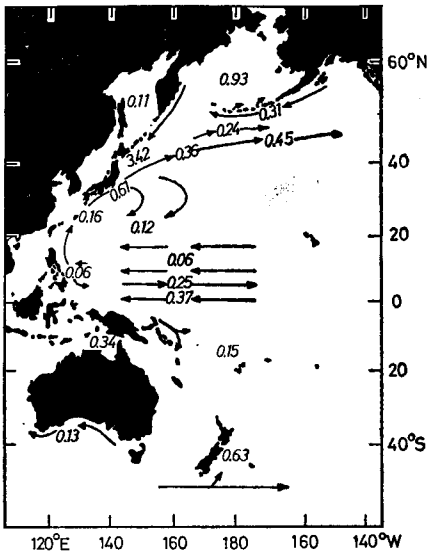

Fig. 5. Geographical distribution of the surface chlorophyll *a* determined colorimetrically (mg/m^3) in the western Pacific Ocean and adjacent seas

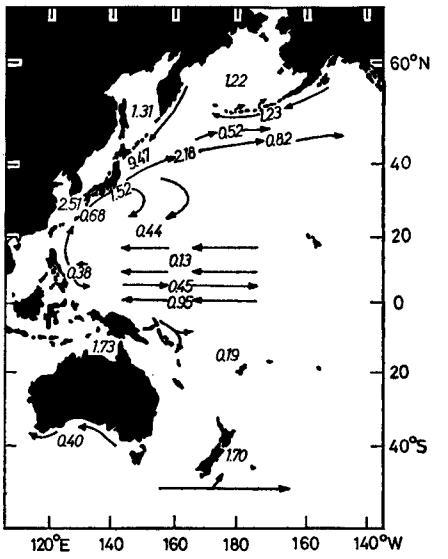

Fig. 6. Geographical distribution of the surface primary productivity under the constant light intensity (mgC/m^3/hr) in the western Pacific Ocean and adjacent seas

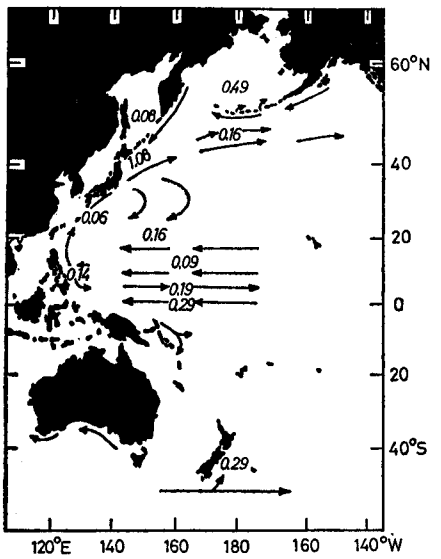

Fig. 7. Geographical distribution of the daily primary production integrated through the euphotic layer (gC/m²/day) in the western Pacific Ocean and adjacent seas

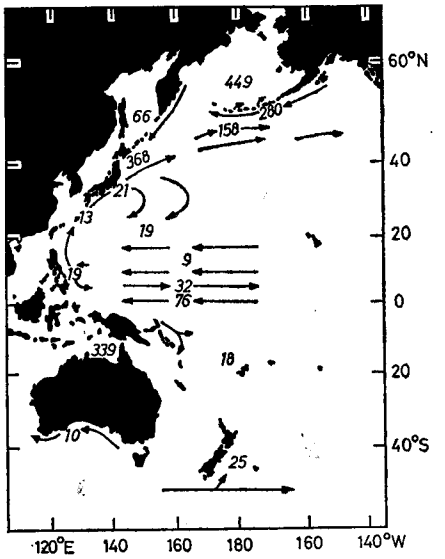

Fig. 8. Geographical distribution of the zooplankton biomass in the upper 150 m (g wet-wt/1000 m³) in the western Pacific Ocean and adjacent seas

surface phytoplankton cell number, is separately illustrated on the sketch map of the major surface currents in the western Pacific Ocean and adjacent seas (Figs. 3–8). Surface values of nutrient concentration (Figs. 3, 4), chlorophyll *a* concentration (Fig. 5), and primary productivity (Fig. 6) are exceedingly high in the Bering Sea and Oyashio Current, and lowest in the Great Australian Bight and North Equatorial Current. The highest value of *in situ* primary production (Fig. 7) and zooplankton biomass (Fig. 8) occur in the Bering Sea and Oyashio Current, and the lowest values in the North Equatorial Current. The primary production in the Okhotsk Sea was unexpectedly low either in direct or simulated *in situ* estimate, but the small number of observations available for the sea area permits no further generalization.

It is evident that high primary productions occurred in the sea areas where nutrient concentrations, phytoplankton standing crops and primary productivity in the surface water were also high. Surface chlorophyll *a* and zooplankton biomass in the upper 150 m water column were regularly measured on all the cruises, so that these two parameters will be of particular use if they are proved to be in a good correlation to the primary production. However, there are a number of variables which are interrelated with each other and eventually correlated with the primary production. So, the present analyses begin with a statistical assay of interdependence within several biologically important variables.

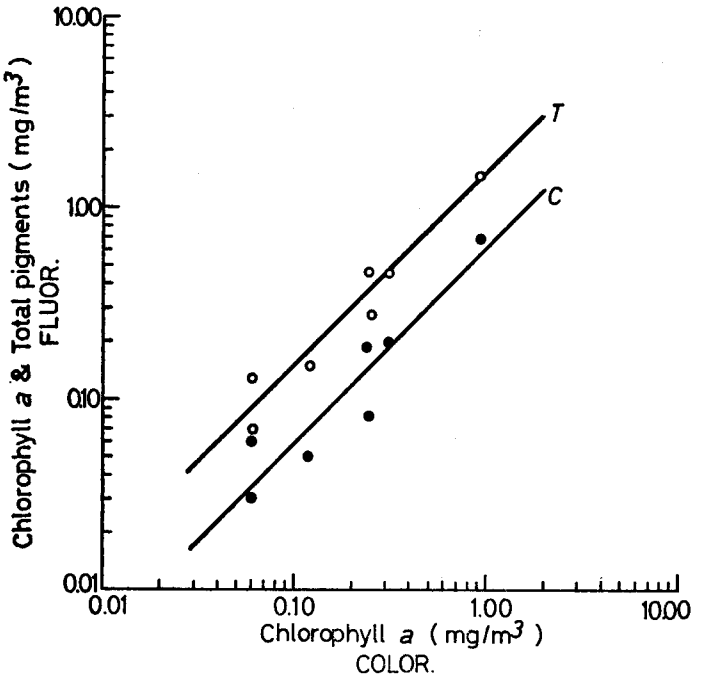

Fig. 9. Relationships between log surface chlorophyll *a* (● and C) and total pigments (○ and T) determined fluorometrically and log surface chlorophyll *a* determined colorimetrically for the average values in 7 areas shown in Table 2

Ratio of active chlorophyll a *to total pigments in surface phytoplankton* (Fig. 9)

Two regressions of chlorophyll *a* and total pigments (chlorophyll *a*+pheopigments) observed by the fluorometric method on chlorophyll *a* determined by the colorimetric method for 7 areas where both methods were used are given in equations (1) and (2) and graphically in Fig. 9. In these calculations, the mean values given in Table 2 were subjected to logarithmic transformation and used. The data from the Oyashio Current were excluded because the latter method was employed only in eutrophic spring observations, while the fluorometric method was adopted mainly in oligotrophic summer observations.

$$Y=-0.222+1.009\ X\ \ (r=0.928) \qquad (1),$$

and

$$Y'=0.178+1.005\ X\ \ (r=0.968) \qquad (2),$$

where X : Log surface chlorophyll *a* determined colorimetrically (mg/m³),
Y : Log surface chlorophyll *a* determined fluorometrically (mg/m³),
and Y′: Log surface total pigments (chlorophyll *a*+pheopigments) determined fluorometrically (mg/m³).

The two regression coefficients (slope) obtained are almost identical and very close to 1.0. The equation (1) suggests that the ratio of chlorophyll *a* determined fluorometrically to that determined colorimetrically is nearly 60% in the surface phytoplankton populations. Further, the practical identity of slope of the two regression lines indicates that the ratio of photosynthetically active chlorophyll *a* to total pigments (chlorophyll *a*+pheopigments) is constant at about 40% for the surface waters over the large part of the Pacific Ocean, although the ratio considerably varied with depth through the water column (Lorenzen, 1967;

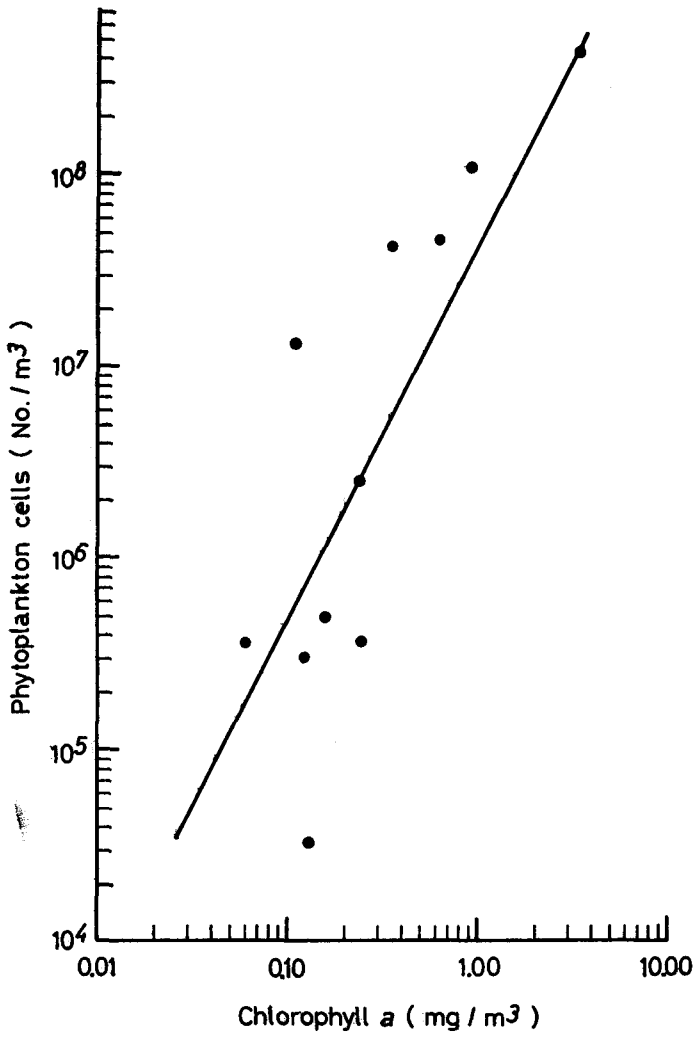

Fig. 10. Relationship between log surface cell number and log chlorophyll *a* for the average values in 11 areas shown in Table 2

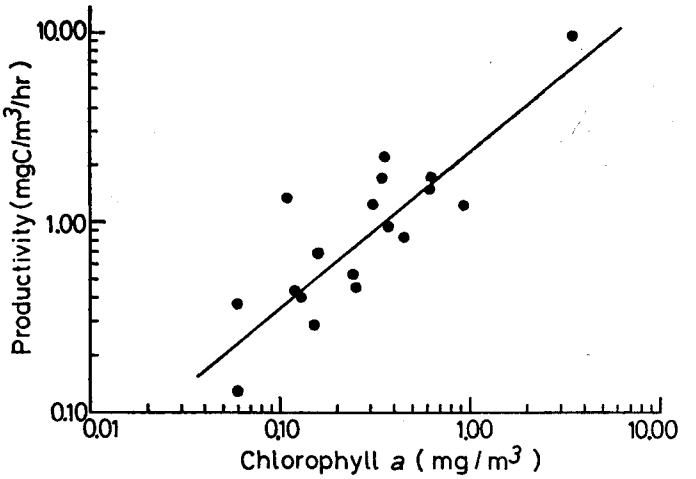

Fig. 11. Relationship between log surface primary productivity and log surface chlorophyll *a* determined colorimetrically for the average values in 18 areas shown in Table 2

Nakajima, 1969; Saijo *et al.*, 1969; Nishizawa *et al.*, 1971).

To obtain a complete set of data on the surface chlorophyll *a* throughout the entire area observed in the western Pacific Ocean and adjacent seas, the fluorometric chlorophyll *a* obtained in 4 southern sea areas were converted to colorimetric chlorophyll *a* using equation (1) and are tabulated in Table 2.

Correlation between cell number and chlorophyll a *in surface phytoplankton* (Fig. 10)

Regression of cell number on chlorophyll *a* in the surface water was calculated and no linear correlation between these two parameters was found. The equation obtained is:

$$Y=7.776+2.129\ X\ (r=0.820) \qquad (3),$$

where X: Log surface chlorophyll *a* determined colorimetrically (mg/m^3),
and Y: Log surface phytoplankton cell number (cells/m^3).

The equation (3) shows that a simple count of the phytoplankton cell number is inadequate as a parameter of standing crop of primary producer as well as basic food for herbivores as discussed previously (Paache, 1960; Smayda, 1965; Mullin *et al.*, 1966). However, the species composition is sometimes an important key to understand the characteristic behavior of the photosynthetic activity of a natural population (*cf.* Steele, 1962; Eppley *et al.*, 1969; and Thomas and Owen, 1971), and is also important in considering food consumptions by herbivores, because most of the herbivores feed selectively on certain phytoplankters or can

graze phytoplankton of a limited size range (Anraku, 1963; Parsons *et al.*, 1967; Hargreves and Geen, 1970).

Correlation between primary productivity under a constant light and chlorophyll a *in surface waters*
(Fig. 11)

Regression of photosynthetic activity on chlorophyll *a* concentration for the surface waters of the 18 sea areas is shown in Fig. 11. The regression equation obtained is:

$$Y=0.383+0.819\ X\ (r=0.830) \qquad (4),$$

where X: Log surface chlorophyll *a* determined colorimetrically (mg/m^3),
and Y: Log surface primary productivity (mgC/m^3/hr).

The regression coefficient was 0.819 and significantly less than 1.0. This suggests that there is no linear relationship between productivity and chlorophyll *a* in the surface water over the vast areas of the western Pacific Ocean in northern summer, and that the assimilation number (mgC/mgChl.*a*/hr) gradually decreases with increasing chlorophyll *a* concentration. For example, the surface

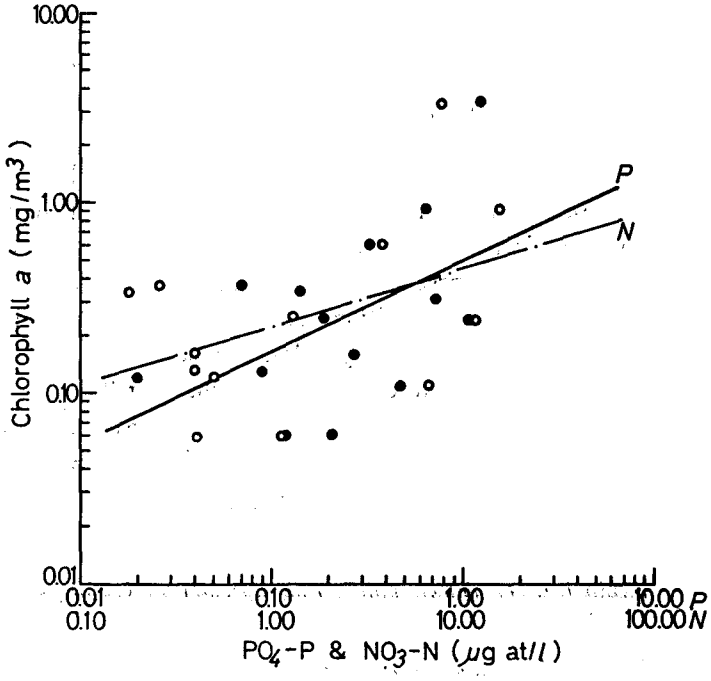

Fig. 12. Relationships between log surface chlorophyll *a* and log surface nutrients (●: PO_4-P, ○: NO_3-N) for the average values in 14 areas shown in Table 2

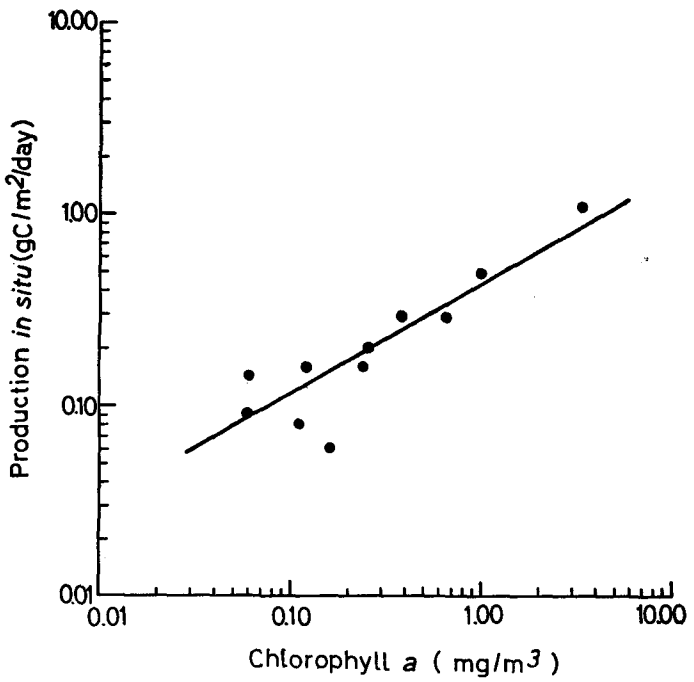

Fig. 13. Relationship between log daily primary production *in situ* and log surface chlorophyll *a* for the average values in 11 areas shown in Table 2

productivity per unit chlorophyll *a*, assimilation number, expected from equation (4) are 5.56, 3.66 and 2.42 mgC/mgChl.*a*/hr, respectively, when the chlorophyll *a* concentrations are 0.01, 0.1 and 1.0 mg/m^3. However, Anderson (1964) found that the linear relationships between productivity and chlorophyll always existed in the offshore waters of Washington and Oregon, eastern North Pacific, although a remarkable seasonal variation of the assimilation number was observed.

The present result may suggest that there occurs "self shading" (Myers, 1953 cited from Fogg, 1965) or "autoinhibition" (Harder, 1917 cited from Fogg, 1965) under the condition of over-crowded phytoplankton population. The result may also be partly due to an increased dominancy of dinoflagellates in the tropical and subtropical water masses where the total chlorophyll concentration was usually low: there is evidence that dinoflagellates usually have a higher photosynthetic activity per unit chlorophyll *a* than diatoms (Kawamura, 1963; Taniguchi, 1969; also *cf.* Steele, 1962).

Correlation between chlorophyll a *and nutrient in surface waters* (Fig. 12)

No significantly consistent relationships between chlorophyll *a* and standing stocks of phosphate-phosphorus and nitrate-nitrogen were found for the data

given in Table 2, and the regression equations obtained are:

$$Y=-0.654+0.343\ X\ (r=0.473) \quad (5),$$

and

$$Y=-0.300+0.473\ X'\ (r=0.499) \quad (6),$$

where Y : Log surface chlorophyll *a* (mg/m^3),
X : Log surface nitrate-nitrogen (μg-at/l),
and X′: Log surface phosphate-phosphorus (μg-at/l).

The correlation coefficients are lower than 0.5 in both cases. However, the chlorophyll *a* concentration was exceptionally high in the sea areas of high nutrient concentration.

Correlation between in situ *primary production and surface chlorophyll* a
(Fig. 13)

Regression of daily primary production *in situ* integrated through the euphotic layer on surface chlorophyll *a* concentration proved that:

$$Y=-0.357+0.611\ X\ (r=0.893) \quad (7),$$

where X: Log surface chlorophyll *a* (mg/m^3),
and Y: Log daily primary production *in situ* (gC/m^2/day).

The correlation coefficient is sufficiently high, but the regression coefficient is markedly lower (0.611) than that of productivity on surface chlorophyll *a* (equation (4)). This means that the daily primary production *in situ* does not increase linearly with the increase in surface productivity as well as with the increase surface chlorophyll *a*. This can be explained again by the "self shading" due to crowded phytoplankton population near the sea surface. Under this condition, the depth of the productive euphotic layer will be reduced. Such a "shading effect" could be further intensified by the existence of detritus suspending in the uppermost layer; the concentration of the detritus is generally high in phytoplankton rich waters (*cf.* Nishizawa, 1966).

Correlations between zooplankton biomass (0–150 m) and surface chlorophyll a, *and between zooplankton biomass and* in situ *primary production in the euphotic layer*
(Figs. 14–15)

Holmes *et al.* (1957) and Holmes (1958) observed that the surface concentration of chlorophyll *a* is a good indicator of the amount of zooplankton biomass living in the upper 300 m water column in the eastern Pacific Ocean. It has been generally recognized that both phytoplankton and zooplankton are usually rich in nutrient rich waters (see p. 3), although there is a phase lag in the mode of development between phytoplankton and zooplankton in high latitudes (Heinrich, 1962).

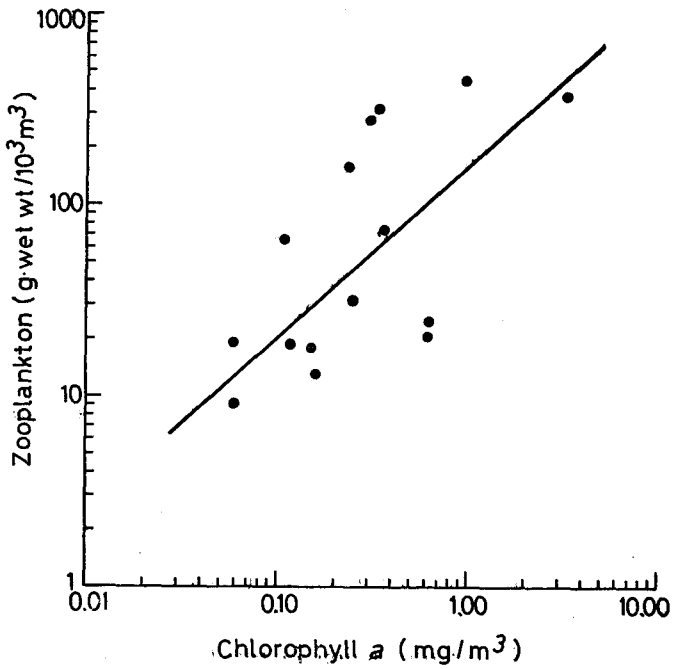

Fig. 14. Relationship between log zooplankton biomass in upper the 150 m water column and log surface chlorophyll *a* for the average values in 15 areas shown in Table 2

Regressions of zooplankton biomass as expressed in wet weight inclusive of both herbivores and carnivores in the upper 150 m on surface chlorophyll *a* and on *in situ* primary production integrated through the euphotic layer are as follows:

$$Y=2.200+0.854\ X\ (r=0.650) \quad (8),$$

and

$$Y=2.537+1.174\ X'\ (r=0.742) \quad (9),$$

where X : Log surface chlorophyll *a* (mg/m^3),
X′: Log daily primary production *in situ* ($gC/m^2/day$),
and Y : Log zooplankton biomass in the upper 150 m (g wet-wt/1000 m^3).

The low regression coefficient of equation (8) less than 1.0 indicates that the increases of zooplankton biomass progressively lags behind the increase of the surface chlorophyll *a*. The coefficient would be further reduced if the amount of chlorophyll is integrated through the euphotic layer (*cf.* Fig. 5 in Blackburn, 1966).

Zooplankton generally ascend to the shallow layer at night (Vinogradov, 1968; Morioka, 1970; Minoda, 1971; *etc.*). On the other hand, a major part of primary production takes place in the upper half of the euphotic layer (Steemann Nielsen and Aabye Jensen, 1957) especially in eutrophic high latitudes (Semina,

1960; Taniguchi, 1969; Taniguchi and Kawamura, MS). In other words, zooplankton are concentrated in the shallow layer of the euphotic layer at night and obtain ample food which had been produced in daytime. This situation would favour zooplankton to utilize efficiently concentrated food stuff and to grow rapidly. This is probably reflected in the regression coefficient higher than 1.0 of equation (9).

Considering exceptionally favourable condition in northern eutrophic areas, the regression coefficient in equation (9) would tend to reduce under usual conditions of the average ocean and approach close to unity. A similar regression analysis with existing amount of phytoplankton crop yields a coefficient that is significantly lower than unity (*cf.* Riley, 1956; Taniguchi and Kawamura, MS).

The ratio of herbivores to total zooplankton in biomass is higher in eutrophic high latitudes than in oligotrophic low latitudes (Timonin, 1971). This may also be responsible for the higher regression coefficient of the equation (9) than unity, because the present zooplankton biomass includes both herbiovres and carnivores and the ratio of the latter to the total zooplankton biomass is higher, or the grazing pressure on phytoplankton may be lower, in the oligotrophic low latitudes.

The ratio of zooplankton biomass to phytoplankton standing crop varies with the season in high latitudes (Heinrich, 1962) but the phytoplankton-zooplankton relationship cannot be realized merely on the basis of phytoplankton standing crop (Taniguchi and Kawamura, MS). It is supposed that an extremely high primary production in spring can temporarily excess over the combined loss by zooplankton and sinking.*

2. Geographical variation in primary production in relation to physical conditions of water

In this chapter, characteristics of primary production in various sea areas of the western Pacific Ocean and adjacent seas are discussed in relation to the physical condition of the surface layer of each sea area. The areas described are the Bering Sea, Oyashio Current, Kuroshio Counter Current, North Equatorial Current, Equatorial Counter Current, South Equatorial Current and the eastern sea

**Note*: Recently, Thomas (1971) emphasized that the ratio of released DOM (dissolved organic matter) to primary production in natural phytoplankton population is increasing seawards or high in the oligotrophic oceanic waters and suggested that, in some oligotrophic oceanic sea areas, ^{14}C experiments have largely underestimated the primary production by at most 50% of real production, and the experiments can only measure the "primary particulate organic production". Consequently, the present data on primary production would be underestimated to various extends with sea areas of different trophic environments. No adequate methods of correction for this underestimation has so far been available. These data, however, may be still valid as index to basic food production for herbivour zooplankton, since the latter could probably utilize only the "particulate organic matter" in nature. (Thomas, J.P., 1971. Release of dissolved organic matter from natural populations of marine phytoplankton. MS submitted to *Marine Biology*).

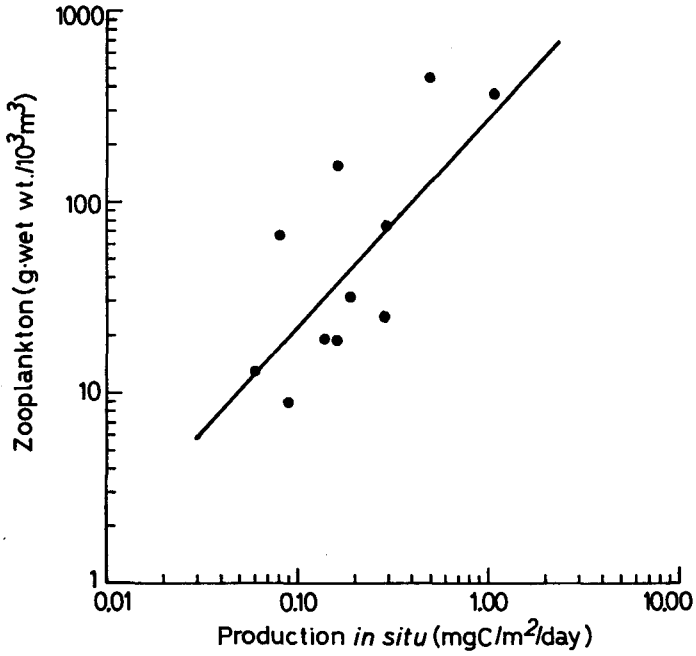

Fig. 15. Relationship between log zooplankton biomass in the upper 150 m water column and log daily primary production *in situ* for the average values in 11 areas shown in Table 2

of New Zealand. Although some features of primary production in the 7 sea areas were already described separately in published papers (Kawamura, 1963; Taniguchi, 1969; Taniguchi and Kawamura, 1970, MS; Nishizawa *et al.*, 1971; Taniguchi and Nishizawa, 1971), they will be synoptically discussed here on a consistent basis of hydrographical conditions in regulation nutrient supply to the euphotic layer and vertical distribution of phytoplankton population.

Bering Sea and Oyashio Current
(Figs. 16–17)

An exceedingly high primary production occurring in these sea areas was reported by many authors (Bogorov, 1958; Semina, 1960; Saijo and Ichimura, 1960; Kawamura, 1963; Taniguchi, 1969; Taniguchi and Kawamura, MS). The high production is principally caused by abundant supplies of nutrients to the euphotic layer during the winter mixing period (Anderson, 1969) and also by the occurrence of subsurface chlorophyll maximum layer that is usually shallower than the bottom of the euphotic layer (Taniguchi and Kawamura, MS).

In high latitudes, a large scale vertical convection takes place in winter and the summer thermocline is normally developed at a depth shallower than or near

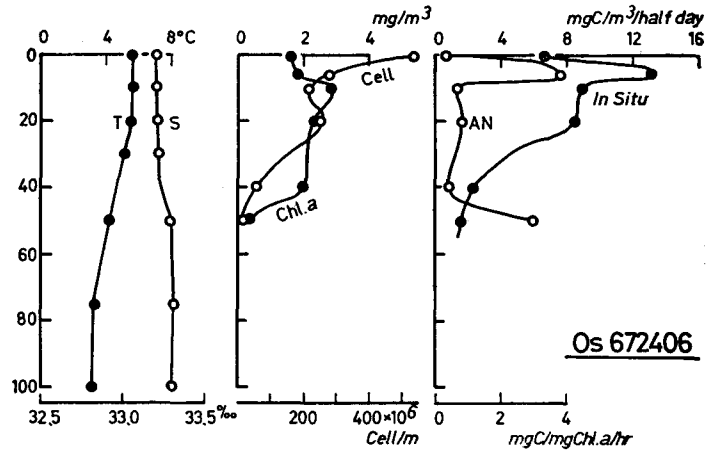

Fig. 16. Vertical profiles of chlorophyll *a* (Chl. *a*), phytoplankton cells (Cell), assimilation number (AN) and primary production *in situ* (*In Situ*) with those of temperature (T) and salinity (S) in the Bering Sea in summer 1967

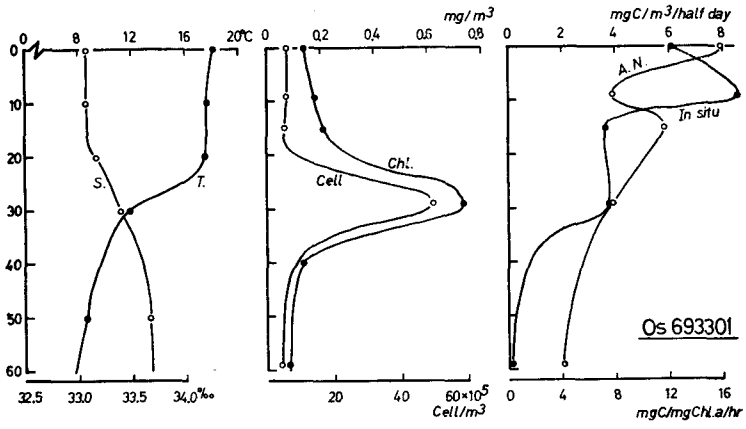

Fig. 17. Vertical profiles of chlorophyll *a* (Chl. *a*), phytoplankton cells (Cell), assimilation number (AN) and primary production *in situ* (*In Situ*) with those of temperature (T) and salinity (S) in the Oyashio Current in summer 1969

the bottom of the euphotic layer. Such a thermocline induces high primary production, and at the same time plays a role of barrier against the sinking loss of phytoplankton (*cf.* Riley, 1942; Sverdrup, 1953; Semina, 1960). Thus, the situation leads to the establishment of a subsurface chlorophyll maximum layer within the euphotic layer (Taniguchi and Kawamura, MS).

Subtropical and tropical areas
(Figs. 18–20)

In a vast area of the tropical and subtropical sea, the euphotic layer is general-

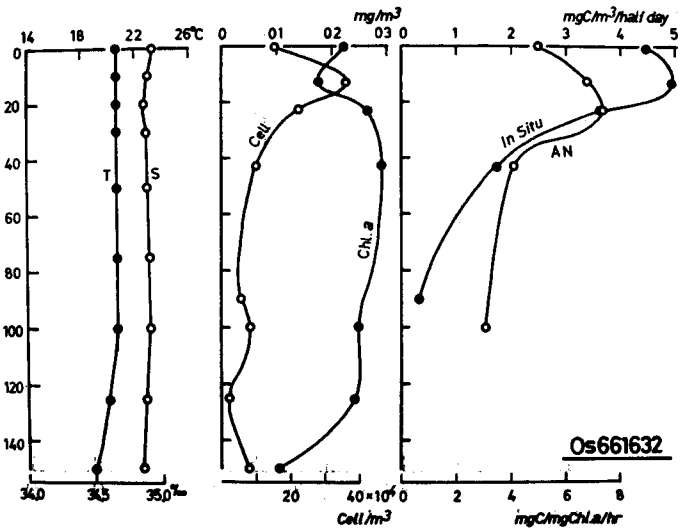

Fig. 18. Vertical profiles of chlorophyll *a* (Chl. *a*), phytoplankton cells (Cell), assimilation number (AN) and primary production *in situ* (*In Situ*) with those of temperature (T) and salinity (S) in the Kuroshio Counter Current in winter 1966

Table 3. Average values of phytoplankton pigments and primary productivity in surface waters and primary production *in situ* in 5 areas of the tropical and subtropical Pacific Ocean in summer and winter

Area	Primary production *in situ* ($gC/m^2/day$)	Surface productivity ($mgC/m^3/hr$)	Pigments (mg/m^3)			Season
			Chl. *a**	Chl. *a***	Pheop.**	
Kuroshio Counter Current	0.16	0.44	0.12	0.05	0.10	Winter
North Equatorial Current	0.09	0.28	0.06	0.03	0.11	Winter
	0.08	0.07	—	0.03	0.07	Summer
Equatorial Counter Current	0.19	0.58	0.25	0.07	0.10	Winter
	—	0.32	—	0.08	0.29	Summer
South Equatorial Current	0.27	1.30	0.07	0.26	0.27	Winter
	0.31	0.61	—	0.17	0.29	Summer
north of Fiji Islands	—	0.19	—	0.09	0.13	Summer

* determined colorimetrically
** determined fluorometrically

ly poor in nutrients throughout a year mainly due to the existence of a permanent deep thermocline. Because, the thermocline is deeper than the bottom of the euphotic layer, the nutrient supply to the euphotic layer from below is only minimal. A major source of nutrient supply for the phytoplankton in the euphotic layer is attributed to decomposition and mineralization in the euphotic layer. However, the contribution of the regenerated nutrients in the euphotic layer to

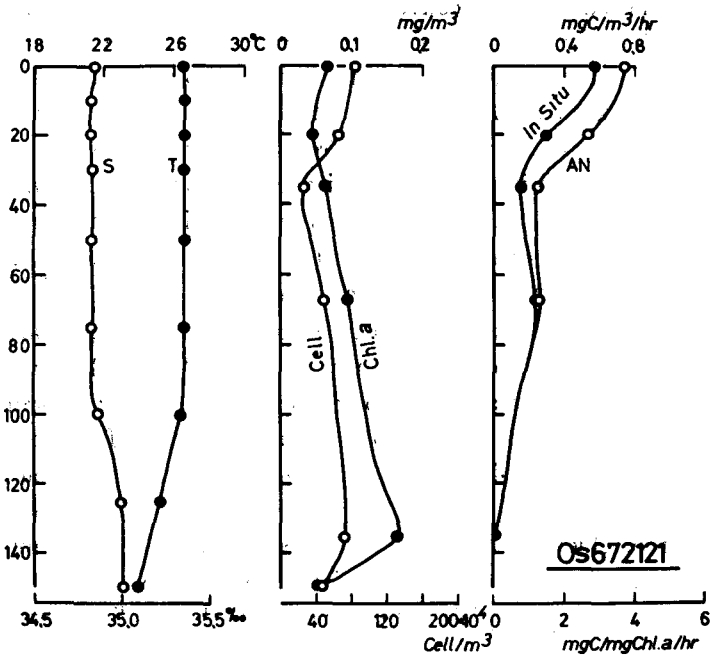

Fig. 19. Vertical profiles of chlorophyll *a* (Chl. *a*), phytoplankton cells (Cell), assimilation number (AN) and primary production *in situ* (*In Situ*) with those of temperature (T) and salinity (S) in the North Equatorial Current in winter 1967

the total phytoplankton requirements is as low as 18–25% in the open seas (*cf.* Ketchum *et al.*, 1958). Consequently, the euphotic layer in permanently stable tropical and subtropical sea areas is everlastingly nutrient depleted. Only in some limited areas where an intensive upwelling of water occurs or an occasional strong wind stirs the stratification an enhanced primary production can occur (Holmes *et al.*, 1957; Menzel and Ryther, 1961; Forsbergh and Joseph, 1964; Blackburn, 1966; Taniguchi and Kawamura, 1970; *etc.*).

KUROSHIO COUNTER CURRENT (Fig. 18): Because of a considerable seasonal variation of sea temperature, the vertical stratification of water in this area is less developed than in other areas within the tropical and subtropical Pacific Ocean (*cf.* Motoda *et al.*, 1970b; and Knauss, 1963). This can allow a vertical mixing of water extending to a considerable depth particularly in the seasons of typhoon (late summer) and winter monsoon. Actually the primary productivity of the surface water and the primary production *in situ* in this area in winter were about double as those in the stable North Equatorial Current (Table 3) (Taniguchi and Kawamura, 1970).

NORTH EQUATORIAL CURRENT (Fig. 19): The North Equatorial Current is

bordered by the subtropical convergence on the north and separated from the Equatorial Counter Current by the divergence on the south. The vertical stability of water in a large part of this current is high because a well defined thermocline generally exists in a layer deeper than the euphotic layer. This steep thermocline obstructs the nutrient supply from underlying layers to the euphotic layer. So, the average primary productivity in this current is low, but within the area, a relatively higher productivity was observed in the southern half of the current touching the divergent zone (0.13–0.15 gC/m²/day) than in the northern half (0.03–0.05 gC/m²/day) (Taniguchi and Kawamura, 1970).

Phytoplankton chlorophyll *a* slightly increased with depth attaining the maximum layer at a depth of the thermocline in the North Equatorial Current. Generally, the maximum layer of chlorophyll in the tropical and subtropical waters is formed near the bottom of the euphotic layer as a result of the phytoplankton adaptation tending to avoid photo-oxidation that can occur in the well illuminated surface water (Saijo *et al.*, 1969). Vinogradov *et al.* (1970) argued that the maximum layer of chlorophyll spontaneously occurs in a limited depth range in which both the illumination and the nutrient concentration are favourable; the layer above are nutrients-depleted and the layers below light-depleted.

Photosynthetic activity per unit of chlorophyll *a*, assimilation number, of the phytoplankton population at the bottom of the euphotic layer, however, was not so high and the contribution of the production in the maximum layer to the total primary production *in situ* integrated through the euphotic layer was nearly negligible (Fig. 19).

Equatorial Counter Current and South Equatorial Current (Figs. 20–21): The biological production along the equator, central zone of the South Equatorial Current, and the northern boundary of the Equatorial Counter Current, is remarkably high within the tropical and subtropical Pacific Ocean principally due to the prevailing upwelling of the surface water. Circumstantially, Desrosieres (1969) showed that there is a marked east-west gradient in enrichment intensity due to the upwelling along the equator and the intensity gradually decreases westwards accompanied by a westward decline of phytoplankton standing crop as well as of available nutrient stock.

The upwelling at the northern edge of the Equatorial Counter Current, of course, enriches both the surface waters in this current and in the North Equatorial Current. The surface waters over almost all the narrow belt of the Equatorial Counter Current are continuously enriched by this upwelling (Taniguchi and Kawamura, 1970), but the enrichment effect is extending northwards only to the southern part of the North Equatorial Current. The average primary production of the surface waters of Counter Current was 0.19 gC/m²/day and the average

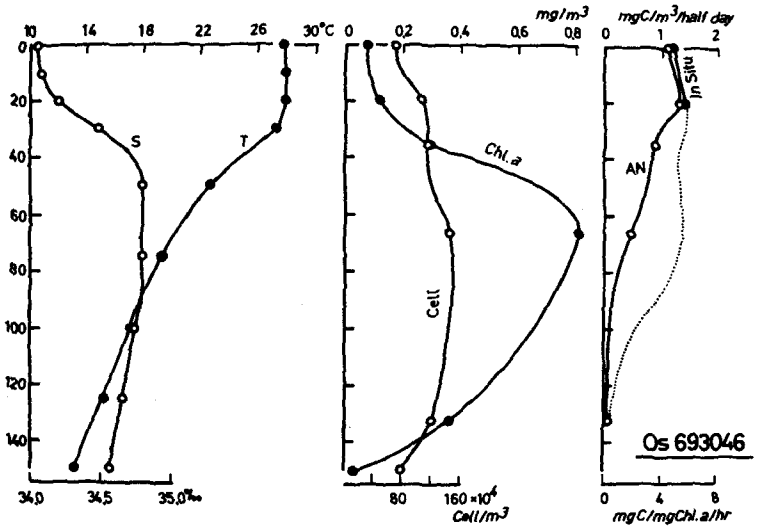

Fig. 20. Vertical profiles of chlorophyll *a* (Chl. *a*), phytoplankton cells (Cell), assimilation number (AN) and primary production *in situ* (*In Situ*) with those of temperature (T) and salinity (S) in the Equatorial Counter Current in winter 1969. Broken line was drawn in regards to vertical changes of chlorophyll *a* and assimilation number with underwater light.

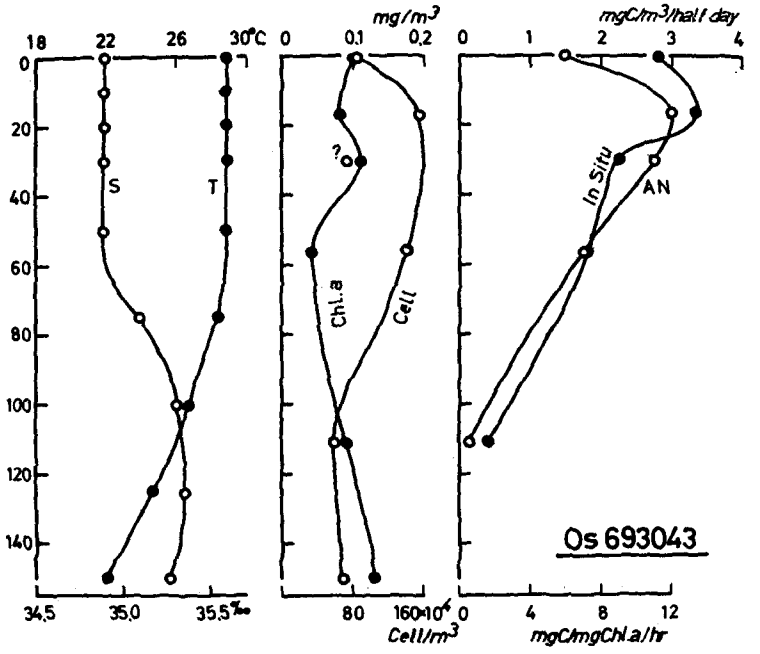

Fig. 21. Vertical profiles of chlorophyll *a* (Chl. *a*), phytoplankton cells (Cell), assimilation number (AN) and primary production *in situ* (*In Situ*) with those of temperature (T) and salinity (S) in the South Equatorial Current in 1969

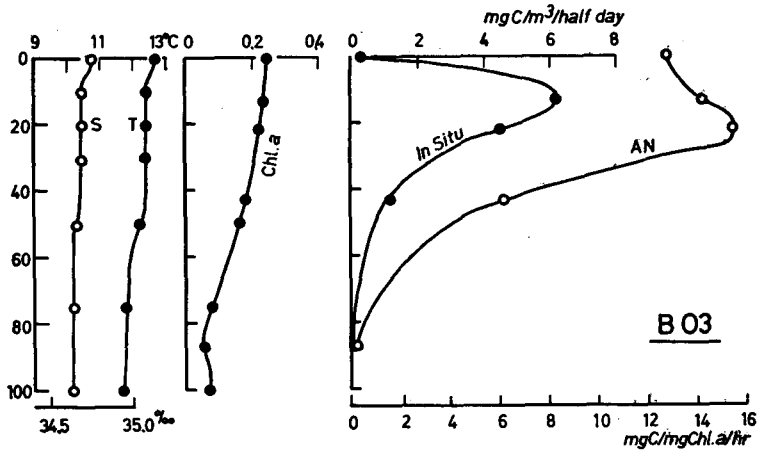

Fig. 22. Vertical profiles of chlorophyll *a* (Chl. *a*), assimilation number (AN) and primary production *in situ* (*In Situ*) with those of temperature (T) and salinity (S) in the subtropical water region east of New Zealand in winter (northern summer) 1968

production over the entire North Equatorial Current was 0.08–0.09 gC/m²/day (Table 3). However, the average production in the southern part of the North Equatorial Current was 0.13–0.15 gC/m²/day.

Among the western subtropical and tropical Pacific Ocean, the South Equatorial Current is continuously enriched by the equatorial upwelling and is undoubtedly the most productive sea area in which the production is nearly one order of magnitude higher than in the northern part of the North Equatorial Current (Table 3).

In the Equatorial Counter Current and the South Equatorial Current, the subsurface maximum layer of chlorophyll *a* is formed in a layer shallower than the bottom of the euphotic layer probably due to the ascending water movement, and this may be also responsible for the high production.

Taniguchi and Kawamura (1970) suggested that the newly upwelled nutrients of the surface Equatorial Counter Current off the eastern coast of the Philippines are gradually exhausted during the eastward flow of the Current.

Eastern sea of New Zealand
(Fig. 22)

The waters in the sea area east of New Zealand can be divided by the subtropical convergence into two major water regions, *i.e.*, subtropical and subantarctic water regions. The hydrographical features of these two water regions are essentially identical to those of the Kuroshio Counter Current and the Oyashio Current, respectively. Accordingly, the characteristics of primary production in

the subtropical water region and in the subantarctic water region are also nearly the same as those of the Kuroshio Counter Current and the Oyashio Current, respectively (Taniguchi and Nishizawa, 1971). In the subtropical water region, primary production may be accerelated by the vertical mixing of water which easily occurs under the low stability of water in southern winter. On the other hand, in the nutrient rich subantarctic water region (Jitts, 1965), the subsurface maximum layer of chlorophyll within the euphotic layer is formed near the discontinuity layer, and may contribute to the high primary production during southern summer (Taniguchi and Nishizawa, 1971; also *cf.* Jitts, 1965).

Kuroshio Current

An examination of the regional variation in surface primary productivity along the pathway of the Kuroshio Current reveals that a series of enrichment either by the mixing with coastal waters or by the upwelling of deep waters takes place at various locations along the continental slope (Table 4) (Taniguchi and Kawamura, 1970). This suggests that the horizontal as well as vertical mixing that occur when the current hits a landmass are responsible for the progressively enhanced primary production along the flow.

Table 4. Changes in chlorophyll *a* concentration determined colorimetrically and in primary productivity in the surface water of the Kuroshio Current with pathway of the Current

Area	Chlorophyll *a* (mg/m³)	Productivity (mgC/m³/hr)	Season
Kuroshio Current			
east of Philippines	0.06	0.38	Winter, 1965 & 1968
south of Kyushu	0.16	0.68	Winter, 1959 & 1966
off Boso Peninsula	0.61	1.52	Winter, 1959 & 1966
Kuroshio Extension	0.36	2.18	Summer, 1960
North Pacific Current	0.45	0.82	Summer, 1960

3. Annual primary productions in 7 main sea areas

The primary production in the sea is fundamentally controlled by the physical conditions of water and the geographical variation in the latter generally coincides with the geography of surface current systems.

The sea areas where intensive vertical mixing of the surface water occurs in cold seasons are well fertilized and are characterized by high levels of primary production. In these areas the high production is usually maintained for a period from spring to fall when the surface water is well stratified with the shallow seasonal thermocline. Such areas are the Bering Sea, Oyashio Current and the subantarctic water region east of New Zealand. The shallow summer thermo-

cline within the euphotic layer of these waters serves to enhance the production by developing a well defined subsurface maximum layer of photosynthetically active chlorophyll *a* within the euphotic layer.

In the Kuroshio Counter Current and the subtropical water region east of New Zealand, the vertical mixing of surface water induced by occasional winter winds temporarily enriches the surface water.

The upwelling of underlying nutrient rich waters in the divergence zones in the South Equatorial Current and Equatorial Counter Current continuously supplies nutrient to the surface layers resulting in relatively high primary productions throughout a year.

In large parts of the North Equatorial Current, the permanent thermocline develops below the bottom of the euphotic layer, so that the nutrient supply is minimal throughout a year resulting in permanently poor productions.

The annual primary production of the 7 main sea areas of the western Pacific Ocean and adjacent sea was tentatively estimated (Table 5). The assumptions for the estimation are as follows: (1) in the Bering Sea winter primary production from October to April is negligible, (2) winter primary production in the Oyashio Current from October to March and those in the subantarctic water region east of New Zealand from March to August are of the same magnitude, (3) summer primary production in the Kuroshio Counter Current under the stabilized condition of water from April to August is equal to those in the North Equatorial Current, and finally (4) seasonal variation of primary production in the subantarctic water region east of New Zealand is identical with that in the Oyashio Current.

Table 5. Calculated annual primary production in 7 main sea areas of the western Pacific Ocean and adjacent sea

Area	Average daily production ($gC/m^2/day$)	Calculated annual production ($gC/m^2/year$)	Depth of euphotic layer (m)	Depth of thermocline (m)
Bering Sea	0.49(May-Sept.) 0.0 (Oct.-April)*	89	40-70	20-50
Oyashio Current	1.70(April) 0.45(May-Sept.) 0.20(Oct.-March)*	156	20-60	20-50
Kuroshio Counter Current	0.16(Sept.-March) 0.09(April-Aug.)*	48	90-100	weak
North Equatorial Current	0.09(Jan.-Dec.)	33	110-150	150-300
Equatorial Counter Current	0.19(〃)	69	100-140	40-150
South Equatorial Current	0.29(〃)	106	100-120	60-200
East of New Zealand	1.70(Sept.)* 0.45(Oct.-Feb.)* 0.20(March-Aug.)	156	50-100	40-75

* not observed values (see text)

IV. Summary

1. This paper described the geographical variations in primary production and related biological variables in the western Pacific Ocean and adjacent seas based on the data collected on the occasions of 14 cruises during the period of 1959–1969.

2. The ratio of photosynthetically active chlorophyll *a* to total pigments (chlorophyll *a*+pheopigments) for the surface waters was nearly constant at about 40% over the western Pacific Ocean in northern summer, even though the data were collected from both eutrophic sea areas such as the Bering Sea and oligotrophic sea areas such as the North Equatorial Current.

3. The assimilation number (mgC/mgChl.*a*/hr) in the surface waters varied regionally and tended to decrease with increasing chlorophyll *a*. This was considered to be mostly due to the "self shading" that occurred under the crowded condition of phytoplankton population. The daily *in situ* primary production integrated through the euphotic layer did not increase linearly with the surface chlorophyll *a* concentration, although the correlation between these two parameters, if log transformed, was significantly high ($r=0.893$). This might also be largely due to the "self shading".

4. Zooplankton biomass in the upper 150 m was well correlated with daily *in situ* primary production in the euphotic layer ($r=0.742$). This evidently showed that the zooplankton biomass was primarily controlled by the level of the primary production over the ocean areas.

5. The geographical variation in primary production was closely matched by the map of the large-scale current systems in the area, and could be explained in terms of the characteristic physical condition that controlled the nutrient supply to the euphotic layer from the underlying layer in respective current systems. On this basis, the existing data on primary production obtained in limited seasons from various areas were extrapolated to calculate the annual primary productions in the 7 main sea areas in the western Pacific Ocean and adjacent sea. The range obtained was from 33 gC/m²/year to 156 gC/m²/year; the highest production was obtained in the Oyashio Current and the lowest one in the North Equatorial Current.

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