

Chlorophyll *a* and primary production in the northwestern Pacific Ocean, July 1997

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Abstract : Chlorophyll *a* (Chl *a*) concentration and primary production were measured within the euphotic zone which was defined as from the surface to a depth corresponding to 1% of the surface light intensity (1% light depth), in the northwestern Pacific, July 1997. Stations were divided into the Western Subarctic Gyre (WSG) and the Transition Domain (TD). The Chl *a* concentrations ranged from 0.42 to 2.61 mg m⁻³ in the WSG (mean ± standard error: 1.86 ± 0.16 mg m⁻³, n=16) and from 0.33 to 0.57 mg m⁻³ in the TD (0.42 ± 0.01 mg m⁻³, n=24). The daily primary production integrated in the upper 1% light depth ranged from 910 to 2886 mgC m⁻² d⁻¹ in the WSG (1744 ± 459 mgC m⁻² d⁻¹, n=4), and from 738 to 1629 mgC m⁻² d⁻¹ in the TD (1094 ± 152 mgC m⁻² d⁻¹, n=6). The WSG in this study was on the relatively high side of Chl *a* concentrations compared to previous studies in the western subarctic North Pacific during summer season. Moreover, the relatively high Chl *a*-specific primary production (79.4 and 62.4 mgC (mgChl *a*)⁻¹ d⁻¹) was also observed compared with the values reported previously in the western subarctic North Pacific in summer (<55 mgC (mgChl *a*)⁻¹ d⁻¹). Therefore phytoplankton bloom may occur in the WSG in summer. It is possible that the rise in temperature in early summer is one of the factors for the occurrence of phytoplankton bloom in the summertime WSG. While in the TD, the Chl *a* standing stocks integrated in the upper 1% light depth were nearly equal between stations. However, the daily primary production tended to increase in the southward direction. This trend could be attributed to an increase of the phytoplankton growth rate due to the rise in temperature.

Keywords : chlorophyll *a*, primary production, Western Subarctic Gyre, summertime bloom

1. Introduction

The Alaskan Gyre (AG) is in the eastern subarctic North Pacific and the Western Subarctic Gyre (WSG) is in the west (e.g. FAVORITE *et al.*, 1976; Fig. 1). Many studies regarding chlorophyll *a* (Chl *a*) and primary production have been carried out in the AG, principally at or in the vicinity of station P (50° N and 145° W) (e.g. PARSONS and LALLI, 1988; WELSCHMEYER *et al.*, 1993; WONG

et al., 1995; BOYD and HARRISON, 1999). In contrast, there has been very little information regarding Chl *a* concentration and primary production in the WSG. Hence, SHIOMOTO *et al.* (1998) measured Chl *a* concentration and primary production in July 1993 and 1994. They observed summer phytoplankton bloom in 1993 (Chl *a* concentration: 6.95 mg m⁻³; primary production: 1050 mgC m⁻² d⁻¹) for the first time, but at only one station.

On the other hand, BANSE and ENGLISH (1994, 1999) showed that phytoplankton pigment levels are low during spring and summer, and that autumn blooms occur in the WSG, based on the Coastal Zone Color Scanner (CZCS) data during 1978 through 1986. In contrast, recently SASAOKA *et al.* (2002) observed an increase in Chl *a* concentration from summer in the WSG and maximum values in autumn, based on Sea-viewing Wide Field-of-

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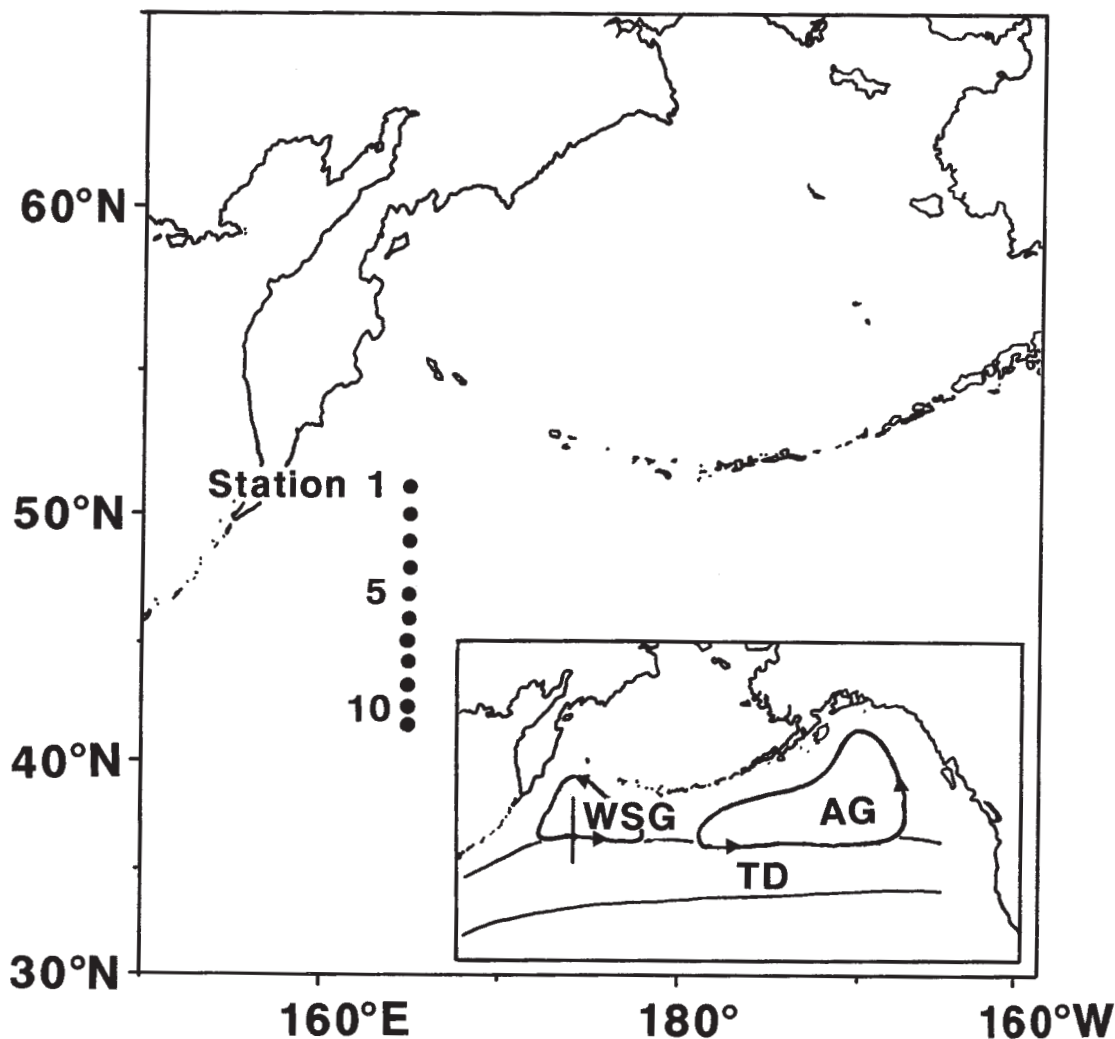


Fig. 1. Location of sampling stations in the northwestern subarctic Pacific in July 1997. Stations 1–4 and 5–11 were divided between the Western Subarctic Gyre and the Transition Domain, respectively. The vertical line in the superimposed figure indicates the observation line in the present study.

view Sensor (SeaWiFS) data. This implies that phytoplankton in the WSG set about blooming in early summer.

Hence, to ascertain whether or not phytoplankton bloom occurs in the summertime WSG, we measured Chl *a* concentration and primary production in July 1997 at the same stations as the observation stations of SHIOMOTO *et al.* (1998). In this paper, we suggest that phytoplankton in the WSG set to their bloom in summer. We, furthermore, refer to the characteristics of Chl *a* and primary

production in the Transition Domain (TD) located just south of the WSG (e.g. FAVORITE *et al.*, 1976; Fig. 1).

2. Materials and methods

This study was conducted during cruises of the R/V Hokko Maru belonging to the Hokkaido National Fisheries Institute in July 1997. Stations were located every 1° between 41° N and 51° N along 165° E (Fig. 1).

Seawater samples were collected at 2 a.m. from four depths corresponding to 100, 30, 10

and 1% of the surface light intensity (hereinafter e.g. 30% light depth) except 45° N (station 7), using acid-cleaned 30-l Niskin PVC samplers with Teflon-coated steel springs hung on a stainless-steel wire. Determination of the four light depths was done past noon the day before the collection of seawater samples with a 2π quantum sensor (LI-COR 192SA). The water samples were immediately sieved through a 200 μ m mesh plankton net to remove large-sized zooplankton, and transferred into acid-cleaned 1-l polycarbonate bottles. The seawater in the bottles was spiked with $\text{NaH}^{13}\text{CO}_3$ (Shoko Co., Ltd., Tokyo). The ^{13}C enrichment was about 10% of the total inorganic carbon in the ambient water. Two light bottles were used for each light depth. Dark bottle uptake is similar to the zero-time blank for the ^{13}C technique and thus dark uptake was not measured (SHIOMOTO *et al.*, 1998). Incubation experiments were begun within 1 hr of sample collection. Bottles with seawater samples inoculated with ^{13}C were held in a deck incubator during about 24-hr incubations in a range of irradiances corresponding to the depths at which the samples were taken, using black mesh screens. Constant temperature was maintained with continuous flowing surface seawater. The experiments were terminated by filtering the samples onto precombusted (450 °C for 4 hr) 47 mm Whatman GF/F filters. The filters were rinsed with prefiltered seawater and then immediately frozen at -20 °C and stored until isotope analysis later on land. After the filters were treated with HCl fumes for 4 hr to remove inorganic carbon, they were completely dried in a vacuum desiccator. The isotopic ratios of ^{13}C to ^{12}C and particulate organic carbon were determined using a mass spectrometer (ANCA SL, PDZ Europa). The total carbonate in the seawater was measured with a Shimadzu TOC 5000 infrared analyzer. Primary production was calculated according to the equation described by HAMA *et al.* (1983). The primary production values obtained in the two bottles were averaged.

We used on-deck incubations and neutral density filters (black mesh screen) to attenuate the light intensity. The discrepancy between the primary production obtained by the

simulated *in situ* method using the black mesh screen and that obtained by the *in situ* method at the 100, 30, 10 and 2% light depths was determined, by using samples collected in the springtime western subarctic North Pacific (SHIOMOTO *et al.*, 1998). The primary production obtained was multiplied by factors of 1.3 at the 30% light depth and 2.4 at the 10% light depth. The value at the 1% light depth was multiplied by a factor of 2.3 which was obtained at the 2% light depth. The primary production values given in the present study are therefore considered net daily primary production by the *in situ* method.

Daily primary production in the subarctic North Pacific was estimated by integrating from the surface to the 0.2–1.7% light depth (WELSCHMEYER *et al.*, 1993; WONG *et al.*, 1995; SHIOMOTO *et al.*, 1998). Hence, the daily primary production integrated from the surface to the 0.2% light depth was calculated by extrapolation, assuming that primary production decreases exponentially with depth (see SHIOMOTO *et al.*, 1998 for detail).

Chl *a* concentrations were measured by fluorometry (PARSONS *et al.*, 1984). Chl *a* was determined in samples (0.5 l) filtered through 47 mm Whatman GF/F filters. The filters were then stored frozen at -20 °C until analysis ashore. Pigments were extracted in 90% acetone and the fluorescence was measured with a Hitachi F-2000 fluorophotometer. Calibration of the fluorophotometer was performed with commercially prepared Chl *a* from Wako Pure Chemical Industries, Ltd. (Tokyo).

Nitrite + nitrate, silicate and phosphate concentrations were measured with a Bran and Luebbe Auto Analyzer Traacs 800 after storage at -20 °C. Surface temperature and salinity were measured with a thermometer and an Auto Lab salinometer, respectively. Subsurface temperature and salinity were measured with a Neil Brown Mark IIIB CTD.

3. Results

3.1 Physical and chemical description

The WSG is located just north of the TD in the northwestern Pacific Ocean (FAVORITE *et al.*, 1976). The southern and northern boundaries of the TD are bordered by the Subarctic

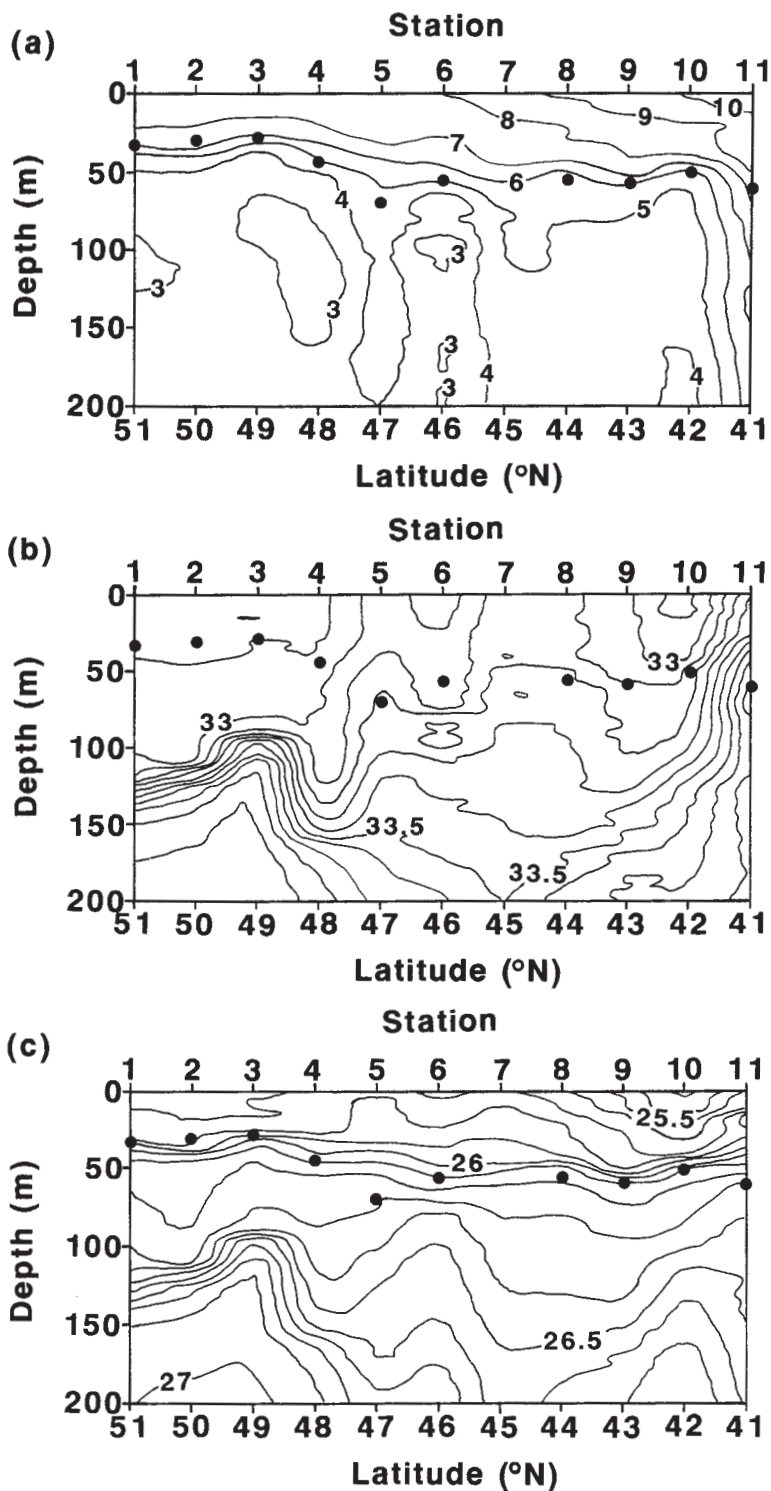


Fig. 2. Vertical sections of (a) temperature, (b) salinity and (c) sigma-t shallower than 200 m. Solid circles indicate the depths of the euphotic zone (1% light depth).

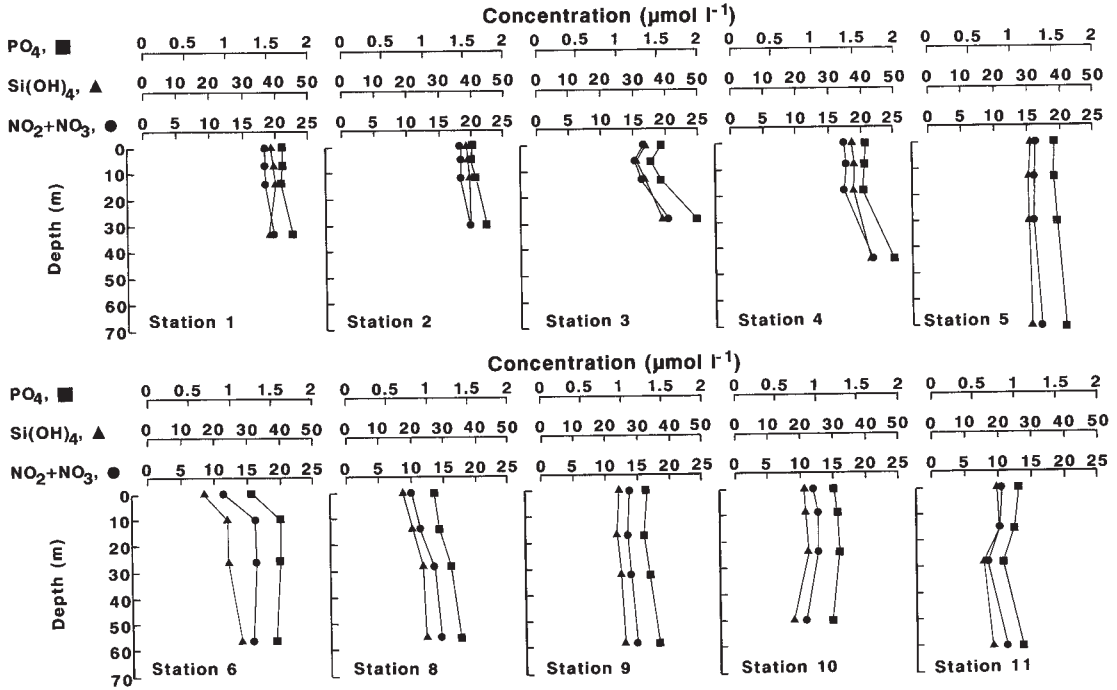


Fig. 3. Vertical profiles of nitrite + nitrate ($\text{NO}_2 + \text{NO}_3$), silicate (Si(OH)_4) and phosphate (PO_4) concentrations within the euphotic zone. Samples were collected at 100, 30, 10 and 1% light depths. Stations 1-4 and 5-11 were located in the Western Subarctic Gyre and the Transition Domain, respectively.

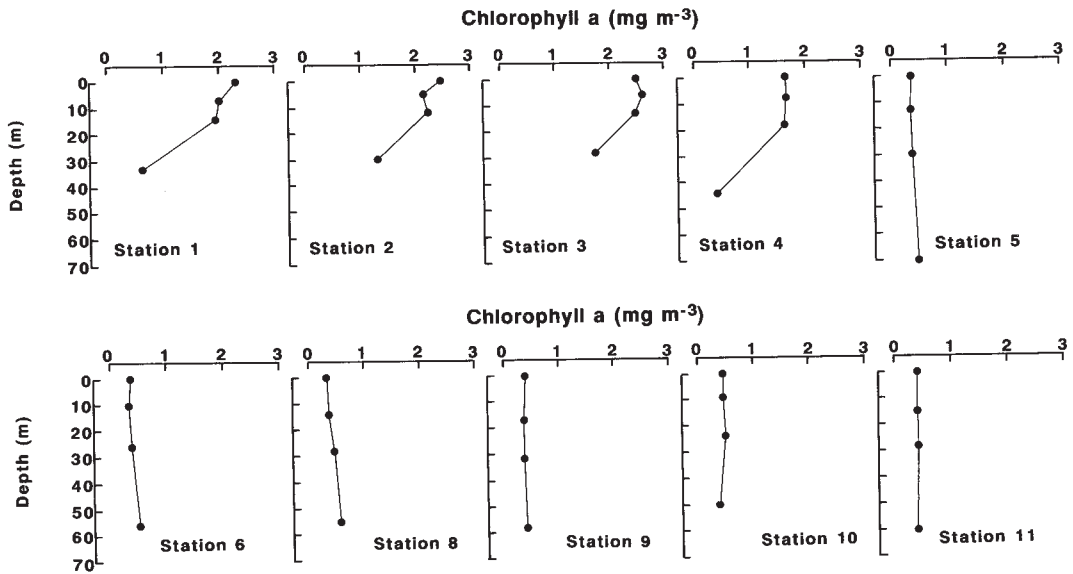


Fig. 4. Vertical profiles of chlorophyll *a* concentration within the euphotic zone. Samples were collected at 100, 30, 10 and 1% light depths. Stations 1-4 and 5-11 were located in the Western Subarctic Gyre and the Transition Domain, respectively.

Boundary, denoted as a vertical 34.0 psu isohaline in the upper layer, and by cold water of less than 4°C below 100 m, respectively (FAVORITE *et al.*, 1976). In this study, salinity of 34.0 psu was not observed in the upper 200 m (Fig. 2 (b)). The salinity in the upper layer increases southward and salinity of 34.0 psu is observed around 40° N (e.g. FAVORITE *et al.*, 1976). The latitude of station 11 was 41° N, and the salinity within the euphotic zone was 33.2–33.9 psu at the stations (Fig. 2 (b)). Salinity of 34.0 psu (the Subarctic Boundary) should have been to the south of station 11. Based on the vertical sections of temperature and salinity (Fig. 2 (a), (b)) and the definition for the WSG and TD, stations 1–4 and 5–11 were thus divided into the WSG and the TD, respectively. Cold water of <4°C at around 100 m was observed even at station 6 (Fig. 2 (a)). The TD is also characterized by a lower Chl *a* concentration compared with its northern and southern regions (SHIOMOTO *et al.*, 1999). The Chl *a* concentrations in the upper 1% light depth at station 6 were lower than most of the Chl *a* concentrations at stations 1–4, and almost equal to the Chl *a* concentrations at stations 5 and 8–11 (Fig. 4). Accordingly, stations 6 was divided into the TD.

The euphotic zone (1% light depth) was 30–45 m deep in the WSG and 50–70 m deep in the TD. The temperatures and salinity within the euphotic zone were mostly in the 6 to 7°C level and in the 32.8 psu level, respectively, at every station in the WSG (Fig. 2 (a), (b)). The temperature and salinity within the euphotic zone were nearly uniform throughout the WSG. The values of the temperature and salinity were within the range of those (temperature: 3–8°C; salinity 32.8–33.2 psu) in the upper layers of the summertime WSG reported by FAVORITE *et al.* (1976). In the TD, the temperatures within the euphotic zone increased southward rapidly at or near the surface, whereas the temperature increased slowly from stations 5 to 10 and rapidly at station 11 around the bottom of the euphotic zone. The salinity within the euphotic zone was nearly uniform at each station except station 11 where the salinity increased markedly with depth. The depths of the euphotic zone were nearly equal to the depths of the

pycnocline at all stations (Fig. 2 (c)).

Nutrient concentrations were mostly nearly uniform within the euphotic zone (Fig. 3). The concentrations were 15–20 $\mu\text{mol l}^{-1}$ for nitrite + nitrate, 30–43 $\mu\text{mol l}^{-1}$ for silicate and 1.5–2.0 $\mu\text{mol l}^{-1}$ for phosphate in the WSG, and 8–17 $\mu\text{mol l}^{-1}$ for nitrite + nitrate, 15–32 $\mu\text{mol l}^{-1}$ for silicate and 0.8–1.7 $\mu\text{mol l}^{-1}$ for phosphate in the TD. The result indicates that these nutrients were not limited for phytoplankton within the euphotic zone.

3.2 Chlorophyll *a*

Chl *a* concentrations in the upper 1% light depth ranged from 0.42 to 2.61 mg m^{-3} in the WSG and from 0.33 to 0.57 mg m^{-3} in the TD (Fig. 4). The Chl *a* concentrations were nearly equal in the upper 10% light depth and rapidly decreased at the 1% light depth at every station in the WSG. In contrast, the Chl *a* concentrations were nearly uniform within the euphotic zone at every station in the TD. The mean \pm standard error (SE) was $1.86 \pm 0.16 \text{ mg m}^{-3}$ ($n=16$) in the WSG and $0.42 \pm 0.01 \text{ mg m}^{-3}$ ($n=24$) in the TD. The mean value in the WSG was 4.4 times higher than that in the TD.

The Chl *a* standing stock, calculated by trapezoidal integration from the surface to the 1% light depth, was in the range of 54 and 65 mg m^{-2} in the WSG and in the range of 23 and 28 mg m^{-2} in the TD (Table 1). The mean \pm SE of Chl *a* standing stock was $58 \pm 3 \text{ mg m}^{-2}$ ($n=4$) in the WSG and $25 \pm 1 \text{ mg m}^{-2}$ ($n=6$) in the TD. The mean value in the WSG was 2.3 times higher than that in the TD.

3.3 Primary production

Primary production in the upper 1% light depth ranged from 0.3 to 155.6 $\text{mgC m}^{-3} \text{ d}^{-1}$ in the WSG and from 0.1 to 78.5 $\text{mgC m}^{-3} \text{ d}^{-1}$ in the TD (Fig. 5). In the WSG, the primary production was maximum at the 10% light depth at stations 1 and 2, and at the 30% light depth at station 3, whereas primary production was nearly equal in the upper 10% light depth and rapidly decreased at the 1% light depth at station 4. In the TD, primary production tended to decrease with depth, though the maximum value was observed at the 30% light depth at stations 5 and 6. In general, the vertical profiles

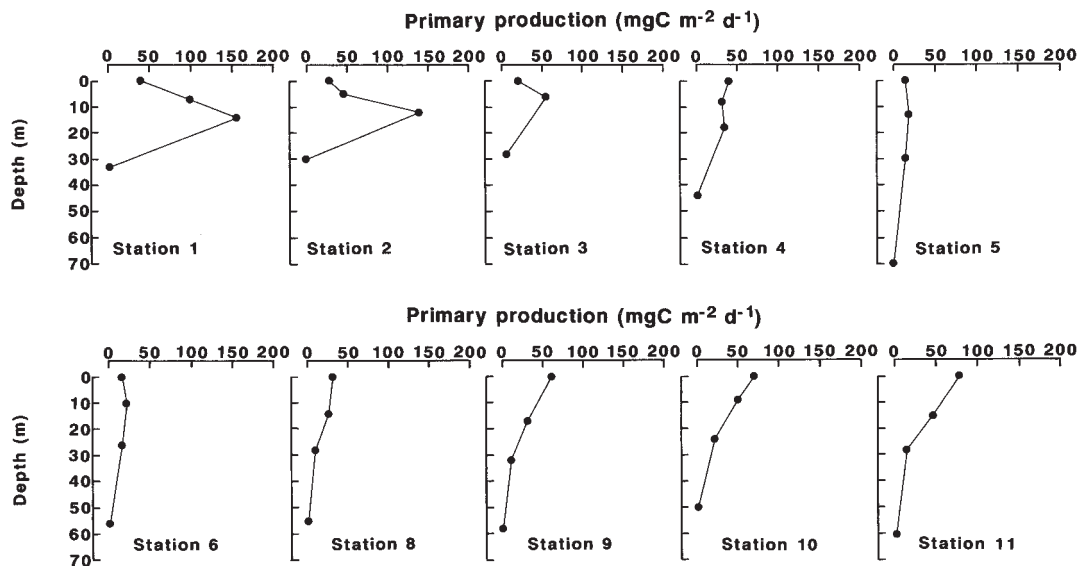


Fig. 5. Vertical profiles of primary production within the euphotic zone. Samples were collected at 100, 30, 10 and 1% light depths. The data at the 10% light depth at station 3 was missed. Stations 1-4 and 5-11 were located in the Western Subarctic Gyre and the Transition Domain, respectively.

of primary production were not the same as those of Chl *a* concentration. The mean \pm SE was 46.7 ± 12.4 mgC m⁻³ d⁻¹ (n=15) in the WSG and 23.3 ± 4.6 mgC m⁻³ d⁻¹ (n=24) in the TD. The mean value in the WSG was 2 times higher than that in the TD.

The daily primary production, calculated by trapezoidal integration from the surface to the 1% light depth, was in the range of 910 and 2886 mgC m⁻² d⁻¹ in the WSG and in the range of 738 and 1629 mgC m⁻² d⁻¹ in the TD (Table 1). The mean \pm SE of daily primary production was 1744 ± 459 mgC m⁻² d⁻¹ (n=4) in the WSG and 1094 ± 152 mgC m⁻² d⁻¹ (n=6) in the TD. The mean value in the WSG was 1.6 times higher than that in the TD. In addition, the daily primary production integrated in the upper 0.2% light depth was estimated. The values were in the range of 936 and 2901 mgC m⁻² d⁻¹ in the WSG and the range of 751 and 1689 mgC m⁻² d⁻¹ in the TD (Table 1). The mean \pm SE of daily primary production was 1759 ± 456 mgC m⁻² d⁻¹ in the WSG and 1111 ± 157 mgC m⁻² d⁻¹ in the TD.

3.4 Chl *a*-specific primary production

Chl *a*-specific primary production in the upper 1% light depth ranged from 0.3 to 79.4 mgC (mgChl *a*)⁻¹ d⁻¹ in the WSG and from 0.3 to 187.0 mgC (mgChl *a*)⁻¹ d⁻¹ in the TD (Fig. 6). The vertical profiles of Chl *a*-specific primary production were the same as those of primary production. The mean \pm SE was 23.2 ± 6.0 mgC (mgChl *a*)⁻¹ d⁻¹ (n=15) in the WSG and 57.9 ± 10.8 mgC (mgChl *a*)⁻¹ d⁻¹ (n=24) in the TD. The mean value in the WSG was 2.5 times lower than that in the TD.

4. Discussion

4.1 Bloom in the WSG

The Chl *a*-specific primary production at the 10% light depth of stations 1 and 2 (79.4 and 62.4 mgC (mgChl *a*)⁻¹ d⁻¹; Fig. 6) where relatively high daily primary production was observed was greater than the remaining values in the present study and the values reported in 1993 and 1994 in the WSG (less than 50 mgC (mgChl *a*)⁻¹ d⁻¹; SHIOMOTO *et al.*, 1998). Moreover, the relatively high Chl *a*-specific primary production in this study exceeded the summer values in the western subarctic North

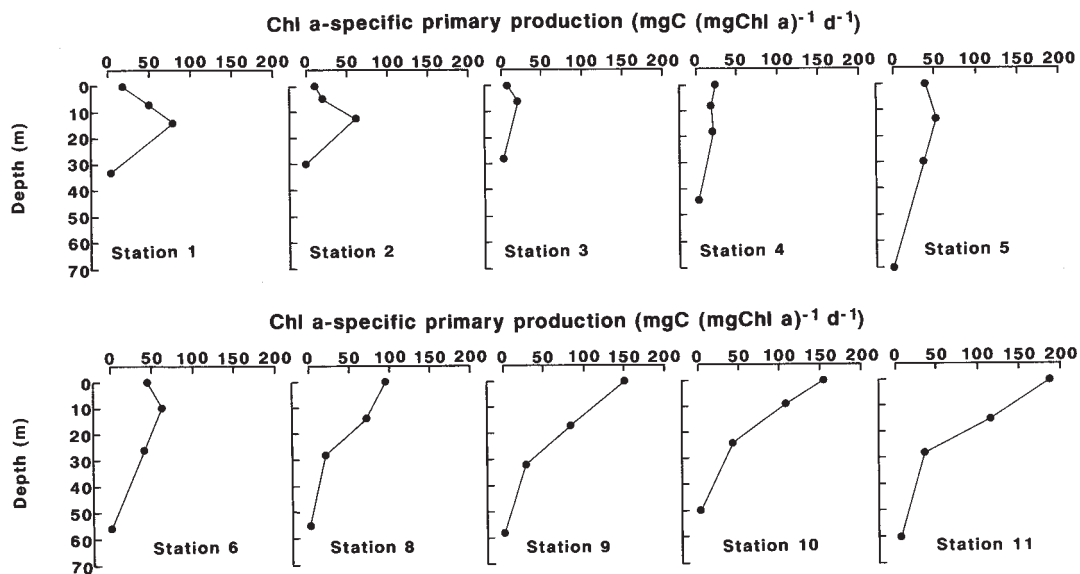


Fig. 6. Vertical profiles of Chl *a*-specific primary production within the euphotic zone. Samples were collected at 100, 30, 10 and 1% light depths. The data at the 10% light depth at station 3 was missed. Stations 1-4 and 5-11 were located in the Western Subarctic Gyre and the Transition Domain, respectively.

Pacific in other studies (maximum: $55 \text{ mgC (mgChl } a)^{-1} \text{ d}^{-1}$; TANIGUCHI and KAWAMURA, 1972; KASAI *et al.*, 1998; SHIOMOTO, 2000; IMAI *et al.*, 2002). Chl *a*-specific primary production is an index of the phytoplankton growth rate (e.g. LALLI and PARSONS, 1995). Thus, relatively high Chl *a*-specific primary production means an increase in the phytoplankton growth rate. On the other hand, the Chl *a* concentrations within the euphotic zone were mostly more than 1 mg m^{-3} in the WSG (Fig. 4). In the summer season, the Chl *a* concentrations more than 1 mg m^{-3} have been observed rarely in the oceanic region of western subarctic North Pacific on shipboard (ANDERSON and MUNSON, 1972; ODATE and FURUYA, 1995; ODATE, 1996; SHIOMOTO *et al.*, 1998; OBAYASHI *et al.*, 2001; IMAI *et al.*, 2002) and satellite observations (BANSE and ENGLISH, 1994, 1999; SASAOKA *et al.*, 2002). Thus, the Chl *a* concentrations in the WSG in this study are on the relatively high side of Chl *a* concentrations in the summertime western subarctic North Pacific. An increase in the phytoplankton growth rate precedes an increase in the phytoplankton biomass in the

process of phytoplankton proliferation (e.g. SPENCER, 1954). Accordingly, phytoplankton at the subsurface at stations 1 and 2 were considered to be in the early stage of bloom.

The relatively high Chl *a* concentration and an increase in Chl *a* concentration were observed in the summertime WSG (SHIOMOTO *et al.*, 1998; SASAOKA *et al.*, 2002). Based on the results in this study and the previous studies, phytoplankton bloom may occur in the WSG in summer.

SASAOKA *et al.* (2002) suggest that the rise in temperature is one in the factors causing an increase in Chl *a* concentration from summer and maximum values in autumn in the WSG, because, in the WSG, the sea surface temperature rises remarkably in early summer, reaching the maximum in late summer and autumn (DODIMEAD *et al.*, 1963; ANONYMOUS, 1993; SASAOKA *et al.*, 2002), and an increase of temperature causes an increase of the phytoplankton growth rate (e.g. EPPLEY, 1972). The relatively high Chl *a*-specific primary production obtained in this study supports their idea regarding the increase in phytoplankton from summer. It is possible

Table 1. Primary production (production) and chlorophyll *a* (chl *a*) integrated in the upper 1% light depth and 0.2% light depth in the Western Subarctic Gyre (WSG) and the Transition Domain (TD) in July 1997.

Region	Station	Integration	depth	Production		Chl <i>a</i>
		(%)	(m)	(mgCm ⁻² d ⁻¹)		(mg m ⁻²)
WSG	1	1	33	2886		54
		0.2	44	2901	(n=2)	
	2	1	30	2079		55
		0.2	41	2081	(n=2)	
	3	1	28	910 ^a		65
		0.2	33	936	(n=2) ^b	
4	1	44	1102		57	
	0.2	60	1117	(n=2)		
TD	5	1	70	782		28
		0.2	91	785	(r ² =0.95, n=3)	
	6	1	56	738		23
		0.2	81	751	(r ² =0.93, n=3)	
	8	1	55	801		25
		0.2	68	812	(r ² =0.95, n=4)	
	9	1	58	1239		23
		0.2	86	1253	(r ² =0.97, n=4)	
	10	1	50	1374		23
		0.2	73	1394	(r ² =0.97, n=4)	
	11	1	60	1629		25
		0.2	81	1669	(r ² =0.99, n=4)	

The values were estimated by trapezoidal integration. r^2 : the coefficient of determination when primary production (mgCm⁻³ d⁻¹) at the 100, 30, 10 and 1% light depths is applied to the exponential equation for estimation of the primary production at the 0.2% light depth. n : the number of data when the primary production in the upper 1% light depth is applied to the exponential equation. The exponential equation was adjusted by using the values at the 10 and 1% light depths in case of $n=2$, those at the 30, 10 and 1% light depths in case of $n=3$ and those at the 100, 30, 10 and 1% light depths in case of $n=4$. ^aPrimary production integrated in the upper 1% light depth was calculated by using the primary production at the 100, 30 and 1% light depths. ^bFitting of the exponential equation was done by using the primary production at the 30 and 1% light depths.

that the rise in temperature in early summer is one of the factors for the occurrence of phytoplankton bloom in the summertime WSG.

The temperatures in the upper layer were almost equal at stations 1–4 (Fig. 2 (a)). Accordingly, the relatively high Chl *a*-specific primary production should have also been observed at stations 3 and 4. However, relatively high values were not obtained at those stations. The Chl *a* concentrations at station 3 were nearly equal to those at stations 1 and 2, and the Chl *a* concentrations at station 4 were somewhat lower than those at stations 1 and 2 (Fig. 4). The nutrient concentrations in the upper 10% light depth, where relatively active primary production was observed (Fig. 5), were somewhat lower at stations 3 and 4 than at stations 1 and 2 (Fig. 3). These facts imply that the phytoplankton at stations 3 and 4 were in the late stage of bloom when the

growth rate of phytoplankton is considered to diminish.

Relatively high Chl *a*-specific primary production was observed at the subsurface at stations 1 and 2 (Fig. 6). In the subarctic North Pacific, solar radiation increases from spring and is maximum in summer (e.g. CAMPBELL and AARUP, 1989; WELSCHMEYER *et al.*, 1995). It is well known that the phytoplankton community suffers from photoinhibition at high light intensity (e.g. ARUGA and MONSI, 1962; PLATT *et al.*, 1980; WELSCHMEYER *et al.*, 1993). These imply a high frequency of photoinhibition in the surface waters during spring and summer. The relatively high Chl *a*-specific primary production at the subsurface can be thus attributed to photoinhibition at the surface. The phytoplankton bloom in the WSG possibly develops at the subsurface, because of avoidance of photoinhibition.

4.2 Characteristics in the TD

The daily primary production in the WSG was roughly equal to that in the TD in the summer season, whereas the Chl *a* concentration and standing stock tended to be higher in the WSG than in the TD (SHIOMOTO *et al.*, 1998). In this study, the daily primary production was higher at stations 1 and 2 in the WSG than in those in the TD, whereas the values at stations 3 and 4 were within the range of the values in the TD (Table 1). The Chl *a* concentration and standing stock were substantially higher in the WSG than in the TD (Fig. 5; Table 1). Stations 1 and 2 were considered to be in the early stage of bloom, and stations 3 and 4 in the late stage of it. Accordingly, primary production and phytoplankton biomass in the TD are possibly characterized by the following in the summer season. Ordinarily, there is no substantial difference between the daily primary production in the TD and in the WSG, whereas the value is lower in the TD than in the WSG in the early stage of the WSG bloom. In contrast, phytoplankton biomass always has a tendency to be lower in the TD than in the WSG. SHIOMOTO *et al.* (1999) suggested an intense grazing effect by zooplankton to explain the low Chl *a* concentration in the TD.

The Chl *a* standing stocks were nearly equal between stations in the TD, whereas the daily primary production tended to increase southward (Table 1). The southward increase of the daily primary production can thus be attributed to an increase of Chl *a*-specific primary production, i.e., the phytoplankton growth rate. Southward increasing trends can be also found for the daily primary production and Chl *a*-specific primary production in the previous shipboard observation in 1994 (SHIOMOTO *et al.*, 1998). According to EPPLEY (1972), the phytoplankton growth rate increases in proportion to temperature. Southward increase in the temperature in the upper mixed layer, i.e., within the euphotic zone, is evident in the TD in all seasons (DODIMEAD *et al.*, 1963; FAVORITE *et al.*, 1976). Accordingly, a southward increasing trend in the phytoplankton growth rate and hence daily primary production are necessarily expected throughout the

four seasons in the TD.

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