

## NOTES

### Efficiency of water-column light utilization in the subarctic northwestern Pacific

**Abstract**—Efficiency of water-column light utilization in the upper 2% light depth ( $\psi$ ) tended to be high during spring and summer (means: 0.75 and 0.96 g C g Chl  $a^{-1}$  mol quanta $^{-1}$  m $^2$ ) and low during autumn and winter (means: 0.33 and 0.53 g C g Chl  $a^{-1}$  mol quanta $^{-1}$  m $^2$ ). Higher  $\psi$  values were probably due to an increase in the phytoplankton growth rate in the blooms. With the exception of bloom conditions, the  $\psi$  tended to increase with a decrease of the daily photosynthetically active radiation (PAR), and variations in the  $\psi$  in relation to the daily PAR were within the range of those summarized by Falkowski and Raven (1997). The water-column light utilization efficiency in the subarctic northwestern Pacific at the bloom times was noticed to be by far the highest in the world oceans.

Falkowski (1981) related photosynthetically active radiation (PAR: 400–700 nm) at the sea surface to depth-integrated primary productivity and chlorophyll *a* (Chl *a*) to obtain a total water-column light utilization index ( $\psi$ ). This index provides information on phytoplankton physiology which is useful in interpreting the distribution of phytoplankton standing stock. The relative constancy of  $\psi$  was proposed by Platt (1986) and Platt et al. (1988), who reviewed various studies and averaged about 0.4 g C g Chl  $a^{-1}$  mol quanta $^{-1}$  m $^2$ , across all possible environments in the ocean. In contrast, Falkowski and Raven (1997) revealed that  $\psi$  was not constant but increased as the daily PAR decreased. Moreover, Falkowski and Raven (1997) stated that the index was lower in low-nutrient regions of the open ocean.

The subarctic northwestern Pacific is classified as a region of high primary productivity and Chl *a* standing stock (e.g., Falkowski and Raven 1997). It is useful to estimate  $\psi$  in elucidating characteristics of the region. However, little is known about  $\psi$  in the subarctic northwestern Pacific. The purpose of this study is to elucidate the seasonal variation of  $\psi$  in the region and compare these with values reported previously from other regions.

This study was conducted on cruises of the RV *Shunyo Maru* (National Research Institute of Far Seas Fisheries) in the northwestern Pacific in 1993 and 1994, on a cruise of the RV *Tankai Maru* (Hokkaido National Fisheries Research Institute) in 1995, and on a cruise of the RV *Kaiyo Maru* (Fisheries Agency of Japan) in 1996. Observations were carried out in mid May and early June (spring) of 1993, 1994, and 1995; in mid July (summer) of 1993; in mid September (autumn) of 1994; and in mid January (winter) of 1996. The subarctic region in the North Pacific is located north of the Subarctic Boundary, denoted as the vertical 34.0 psu isohaline in surface layers (Dodimead et al. 1963). Accordingly, stations with a surface layer salinity of less than 34 psu were selected (Fig. 1).

Seawater samples were collected between 0500 and 0600

h in the spring, summer, and autumn observations in 1993–95 and between 0800 and 1000 h in the winter observation in 1996. Samples were taken from four depths corresponding to 100, 30, 10, and 2% light depths, using acid-cleaned 30-liter Go-Flo samplers hung on a stainless-steel wire. The four depths were determined 30 min before sampling with a cosine response quantum sensor (LI-COR 192SA). The water samples were immediately sieved through a 200  $\mu$ m mesh plankton net to remove large zooplankton, and transferred into acid-cleaned 1-liter polycarbonate bottles. The seawater in the bottles was spiked with NaH $^{13}$ 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 started within about 1 h of sample collection.

In 1993, incubation experiments were carried out over approximately 21 h using a simulated in situ method: Bottles with seawater inoculated with  $^{13}$ C were held in a deck incubator at the irradiances corresponding to the 100, 30, 10, and 2% light depths using black mesh screens at constant temperature attained by continuous flowing surface seawater. Similarly, the incubation experiments in winter 1996 were carried out over approximately 6 h using the simulated in situ method. The incubation experiments in 1994 and 1995 were carried out over approximately 9 and 21 h, respectively, by the in situ method. After incubation the samples were filtered onto precombusted (450°C for 4 h) 47 mm Whatman GF/F filters. The filters were rinsed with prefiltered seawater and then immediately frozen at  $-20^{\circ}$ C and stored for isotope analysis later on land. The filters were subsequently treated with HCl fumes for 4 h to remove inorganic carbon and then 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-R SL, PDZ Europa). The total carbonate in the seawater was measured with a Shimadzu TOC-5000 infrared analyzer. Primary productivity was calculated according to the equation described by Hama et al. (1983).

Black mesh screen was used to attenuate the light intensity in 1993 and 1996 experiments. Using simultaneously collected samples at Sta. 2 (Fig. 1) in 1995, the difference in primary productivity obtained by the simulated in situ method (using the screen) and that obtained by the in situ method was estimated at the four light depths. Accordingly, the primary productivity obtained by the simulated in situ method was multiplied by factors of 1.3 at the 30% light depth, 2.4 at the 10% light depth, and 2.3 at the 2% light depth, to make them identical to the primary productivity obtained by the in situ method.

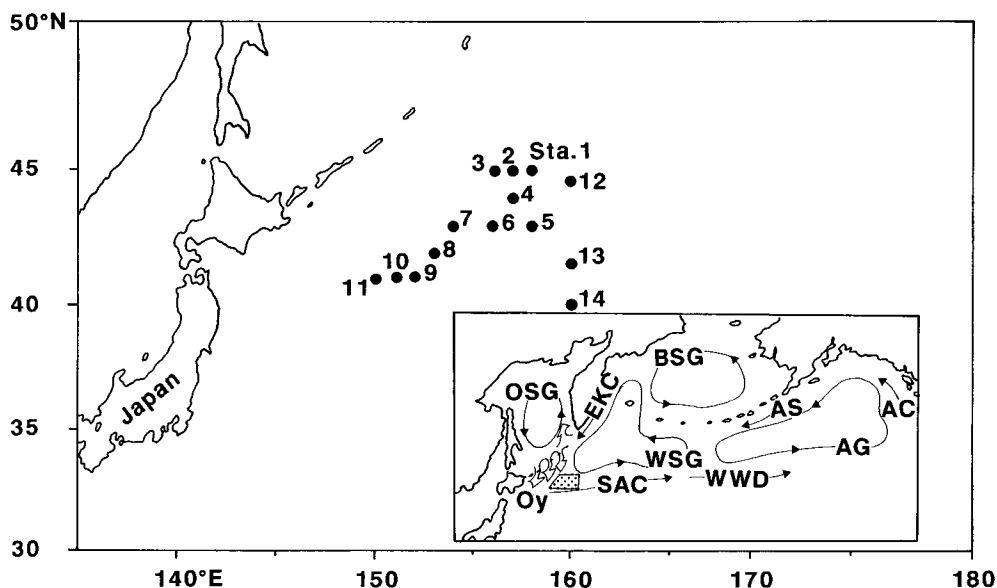


Fig. 1. Location of sampling stations in the subarctic northwestern Pacific. The superimposed illustration shows a schematic circulation of the subarctic North Pacific (modified from Ohtani 1991). Shaded area shows study area. EKC, Eastern Kamchatka Current; Oy, Oyashio water; WSG, Western Subarctic Gyre; SAC, Subarctic Current; WWD, West Wind Drift; AG, Alaska Current; AS, Alaskan Stream; BSG, Bering Sea Gyre; OSG, Okhotsk Sea Gyre.

Bottles were incubated during the day and night (about 21 h) in 1993 and 1995, but only during the day in 1994 (about 9 h) and 1996 (about 6 h). The discrepancy between the primary productivity ( $\approx$  net productivity) obtained from the day and night (21 h) incubation and that ( $\approx$  gross productivity) obtained by the day (9 h) incubation was estimated at the four light depths, using simultaneously collected samples at Sta. 11 (Fig. 1) in 1995. The net productivity obtained by a 21 h incubation was almost equal to the gross productivity obtained by a 9 h incubation at the 100% and 30% light depths, whereas the net productivity was 73% of the gross productivity at the 10% light depth, and 84% at the 2% light depth. The primary productivity in 1994 and 1996 was thus converted to net productivity by multiplying by factors of 0.73 at the 10% light depth and 0.84 at the 2% light depth. In addition, to correct the difference between the daily integrated PAR and the PAR integrated by the incubation periods, the primary productivity was multiplied by the ratio of the former PAR to the latter PAR.

Therefore the primary productivity values given in this study are considered net productivity by the in situ method. However, the values in 1993 and 1995 are probably somewhat underestimated, because the primary productivity including respiration loss due to the day and night incubation was multiplied by the ratio of the daily integrated PAR to the PAR integrated by the incubation periods.

Seawater samples (1 liter) were filtered through a 47 mm Whatman GF/F filter to determine Chl *a* concentration. For the 1993–95 samples, the filters were stored frozen at  $-20^{\circ}\text{C}$  for analysis later on land. Chl *a* concentration was measured with a Hitachi F-2000 fluorophotometer according to Parsons et al. (1984) for samples extracted with 90% acetone. Calibration of the fluorophotometer was performed with

commercially prepared Chl *a* standard from Wako Pure Chemical Industries (Tokyo). For 1996 samples, Chl *a* measurements were carried out on board, immediately after filtration according to Parsons et al. (1984), with a Shimadzu RF-5000 fluorophotometer calibrated with a commercially prepared Chl *a* standard from Sigma Chemical (St. Louis).

Surface temperature and salinity were measured using a thermometer and an Auto Lab salinometer, respectively. Subsurface temperature and salinity were measured with a Neil Brown Mark II CTD. During 1993–95, incident solar radiation (PAR) was recorded at an interval of 10 min using a cosine response quantum sensor (LI-COR 192SA) installed on the ship. In 1996, the radiation was monitored at 10-min intervals in lux units with an Automatic Meteorological Observation System (SCS-9810ED; Nippon Electric Instrument) mounted aboard the ship. The lux units were converted to  $\mu\text{mol quanta m}^{-2}\text{ s}^{-1}$  using the relationship,  $1\text{ Klux} = 16.5\ \mu\text{mol quanta m}^{-2}\text{ s}^{-1}$  (Richardson et al. 1983). Nitrogenous nutrient ( $\text{NO}_2 + \text{NO}_3$ ) concentrations were measured on board, immediately after sampling according to Parsons et al. (1984) in 1993 and 1994, and with a Bran and Luebbe Auto Analyzer II in 1996. In 1995, the concentrations were measured with a Bran and Luebbe Auto Analyzer TRAACS 800 after storage at  $-20^{\circ}\text{C}$ .

Temperatures above the 2% light depth were not substantially different in spring between the three years and were generally less than  $10^{\circ}\text{C}$  (Fig. 2a). Temperatures were  $3\text{--}17^{\circ}\text{C}$  in summer,  $15\text{--}18^{\circ}\text{C}$  in autumn, and  $6\text{--}9^{\circ}\text{C}$  in winter. Salinities above the 2% light depth were generally between 33.0 psu and 33.7 psu in all seasons, with values occasionally observed, less than 33.0 psu (Fig. 2b). Mean  $\text{NO}_2 + \text{NO}_3$  concentrations above the 2% light depth were generally between 5 and 20

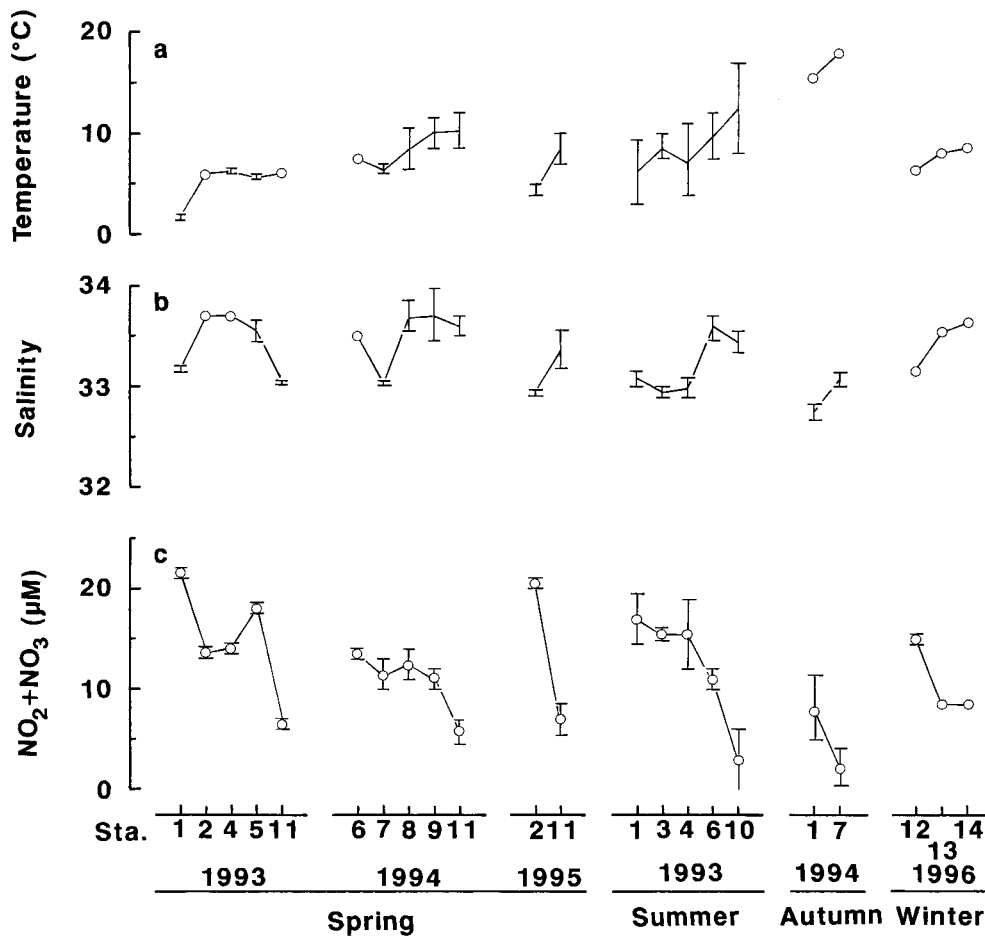


Fig. 2. Variations in maximum and minimum (upper and lower horizontal bars, respectively) temperature (a) and salinity (b) in the upper 2% light depth, and variations in mean  $\pm$  standard deviation of nitrogenous nutrient ( $\text{NO}_2 + \text{NO}_3$ ) concentration (c) in the upper 2% light depth. In Fig. 2a, b, open circles indicate that maximum and minimum values are almost equal. In Fig. 2c, open circles and bars indicate mean values and standard deviations, respectively.

$\mu\text{M}$  in all seasons, although the concentrations less than  $5 \mu\text{M}$  were observed in summer and autumn (Fig. 2c).

The primary productivity and Chl *a* standing stock, calculated by trapezoidal integration from the surface to the 2% light depth, were at a maximum at Sta. 11 in 1993 (Table 1). The primary productivity ( $1,695 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) and Chl *a* concentration ( $6\text{--}7 \text{ mg m}^{-3}$ ) in the upper 2% light depth were well within the range of primary productivity ( $1,000\text{--}2,000 \text{ mg C m}^{-2} \text{ d}^{-1}$ ) and Chl *a* concentration ( $5\text{--}20 \text{ mg m}^{-3}$ ) previously reported in the subarctic northwestern Pacific for the spring (Kawarada and Sano 1972; Taniguchi and Kawamura 1972; Nishihama and Kawamata 1979; Maita and Yanada 1985; Odate and Maita 1988/89; Ogishima 1991; Kasai et al. 1997; Obayashi et al. 1997) and summer blooms (Shiomoto et al. 1998), indicating that the phytoplankton community at the station was in bloom condition. The Chl *a*-specific primary productivity, an index of growth rate (e.g., Lalli and Parsons 1991), was also at a maximum at Sta. 11 in 1993, implying that the growth rate of the phytoplankton community increases due to occurrence of bloom.

Excluding the primary productivity and Chl *a* standing

stock at Sta. 11 in 1993, there were not much differences between the three years in spring, nor between the four seasons (Table 1). In contrast, Chl *a*-specific primary productivity often exceeded  $20 \text{ mg C mg Chl } a^{-1} \text{ d}^{-1}$  in the spring and summer, but not in autumn nor winter. All values were less than  $11 \text{ mg C mg Chl } a^{-1} \text{ d}^{-1}$  in autumn and winter. Chl *a*-specific primary productivity seemed to be higher in spring and summer than in autumn and winter.

The light-utilization efficiency of a water column ( $\text{g C g Chl } a^{-1} \text{ mol quanta}^{-1} \text{ m}^2$ ),  $\psi$  (notation of Falkowski 1981), is defined as:

$$\Psi = \frac{\int_{t_0}^{t_d} \int_{z_{100\%}}^{z_{2\%}} P(t, z) dz dt}{\int_{z_{100\%}}^{z_{2\%}} B(z) dz \cdot \int_{t_0}^{t_d} I_0(t) dt} \quad (1)$$

where  $\int_{t_0}^{t_d} \int_{z_{100\%}}^{z_{2\%}} P(t, z) dz dt$  is the primary productivity integrated from the 100% light depth (surface) to the 2% light depth over a day,  $\int_{z_{100\%}}^{z_{2\%}} B(z) dz$  is the Chl *a* standing stock

Table 1. Summary of primary productivity (Productivity), chlorophyll *a* standing stock (Chl *a*), Chl *a*-specific primary productivity (Productivity/Chl *a*), daily photosynthetically active radiation (PAR), and the total water-column light utilization index ( $\psi$ ) in the upper 2% light depth in the subarctic northwestern Pacific.

Season	Year	Station	Productivity (mg C m <sup>-2</sup> d <sup>-1</sup> )	Chl <i>a</i> (mg m <sup>-2</sup> )	Productivity/ Chl <i>a</i> (mg C mg Chl a <sup>-1</sup> d <sup>-1</sup> )	PAR (mol quanta m <sup>-2</sup> d <sup>-1</sup> )	$\psi$ (g C g Chl a <sup>-1</sup> mol quanta <sup>-1</sup> m <sup>2</sup> )
Spring	1993	1	103	13	7.92	11.2	0.71
		2	631	31	20.35	38.1	0.53
		4	551	22	25.05	26.2	0.96
		5	504	28	18.00	23.0	0.78
		11	1,695	43	39.42	32.6	1.21
	1994	6	94	4	23.50	29.3	0.80
		7	414	20	20.70	18.7	1.11
		8	75	15	5.00	5.4	0.93
		9	250	22	11.36	19.8	0.57
		11	351	12	29.25	49.3	0.59
	1995	2	327	40	8.18	23.0	0.36
11		652	29	22.48	45.3	0.50	
Summer	1993	1	133	14	9.50	14.9	0.64
		3	509	21	24.24	21.1	1.15
		4	208	16	13.00	16.0	0.81
		6	128	20	6.40	6.6	0.97
		10	144	19	7.58	6.2	1.22
Autumn	1994	1	196	22	8.91	33.1	0.27
		7	186	17	10.94	27.7	0.39
Winter	1996	12	109	30	3.63	11.6	0.31
		13	77	21	3.67	6.6	0.56
		14	37	18	2.06	2.8	0.74

integrated from the surface to the 2% light depth, and  $\int_{10}^{\text{sd}} I_0(t) dt$  is the PAR incident on the surface integrated over a day.

The  $\psi$  values in spring ranged from 0.53 to 1.21 g C g Chl a<sup>-1</sup> mol quanta<sup>-1</sup> m<sup>2</sup> in 1993, from 0.57 to 1.11 g C g Chl a<sup>-1</sup> mol quanta<sup>-1</sup> m<sup>2</sup> in 1994, and were 0.36 and 0.50 g C g Chl a<sup>-1</sup> mol quanta<sup>-1</sup> m<sup>2</sup> in 1995 (Table 1). Mean  $\psi \pm$  standard deviation was  $0.84 \pm 0.26$  g C g Chl a<sup>-1</sup> mol quanta<sup>-1</sup> m<sup>2</sup> ( $n = 5$ ) in 1993,  $0.80 \pm 0.23$  g C g Chl a<sup>-1</sup> mol quanta<sup>-1</sup> m<sup>2</sup> ( $n = 5$ ) in 1994, and  $0.43$  g C g Chl a<sup>-1</sup> mol quanta<sup>-1</sup> m<sup>2</sup> ( $n = 2$ ) in 1995. The means in 1993 and 1994 were approximately double the 1995 value. Mean  $\pm$  standard deviation of combined spring data was  $0.75 \pm 0.26$  g C g Chl a<sup>-1</sup> mol quanta<sup>-1</sup> m<sup>2</sup> ( $n = 12$ ).

The  $\psi$  values in summer ranged from 0.64 to 1.22 g C g Chl a<sup>-1</sup> mol quanta<sup>-1</sup> m<sup>2</sup>, and mean  $\psi \pm$  standard deviation was  $0.96 \pm 0.24$  g C g Chl a<sup>-1</sup> mol quanta<sup>-1</sup> m<sup>2</sup> ( $n = 5$ ). The  $\psi$  values were 0.27 and 0.39 g C g Chl a<sup>-1</sup> mol quanta<sup>-1</sup> m<sup>2</sup> in autumn and mean was  $0.33$  g C g Chl a<sup>-1</sup> mol quanta<sup>-1</sup> m<sup>2</sup>. The winter  $\psi$  values ranged from 0.31 to 0.74 g C g Chl a<sup>-1</sup> mol quanta<sup>-1</sup> m<sup>2</sup>, with a mean  $\pm$  standard deviation of  $0.54 \pm 0.22$  g C g Chl a<sup>-1</sup> mol quanta<sup>-1</sup> m<sup>2</sup> ( $n = 3$ ). There was a significant difference in the  $\psi$  between the four seasons (Kruskal–Wallis test,  $P < 0.05$ ), with higher values in spring and summer than in autumn and winter.

Morel (1991) showed that  $\psi$  tends to decrease from the winter to the summer at a given latitude in the northern hemisphere and the seasonal variation is more striking at high latitudes. This trend is consistent with the inverse re-

lationship between daily PAR and  $\psi$  (Falkowski and Raven 1997). The seasonal trend of  $\psi$  observed in this study seems to be inconsistent with the previous findings (Morel 1991; Falkowski and Raven 1997). Probable factors leading to the high  $\psi$  in spring and summer are discussed below.

In spring,  $\psi$  values exceeding 0.9 g C g Chl a<sup>-1</sup> mol quanta<sup>-1</sup> m<sup>2</sup> were found at Sta. 4 and 11 in 1993, and Sta. 7 and 8 in 1994 (Table 1). Values exceeding 0.9 g C g Chl a<sup>-1</sup> mol quanta<sup>-1</sup> m<sup>2</sup> were not observed in autumn or winter. Both the Chl *a*-specific primary productivity and the daily PAR were comparatively low at Sta. 8 in 1994 (Table 1), indicating that the high  $\psi$  value was due to low daily PAR. This is consistent with the previous findings (Morel 1991; Falkowski and Raven 1997). In contrast, the two parameters were comparatively high at Sta. 4 and 11 in 1993 and Sta. 7 in 1994, indicating that high  $\psi$  values were due to a high growth rate. Spring is bloom season for the phytoplankton community in the subarctic northwestern Pacific (Kawarada and Sano 1972; Taniguchi and Kawamura 1972; Nishihama and Kawamata 1979; Maita and Yanada 1985; Odate and Maita 1988/89; Ogishima 1991; Kasai et al. 1997; Obayashi et al. 1997). High values of  $\psi$  can be attributed to the high growth rates due to bloom, observed frequently in the subarctic northwestern Pacific in spring.

In summer,  $\psi$  values exceeding 0.9 g C g Chl a<sup>-1</sup> mol quanta<sup>-1</sup> m<sup>2</sup> were found at Sta. 3, 6, and 10 (Table 1). Both the Chl *a*-specific primary productivity and the daily PAR were comparatively low at Sta. 6 and 10, indicating that the

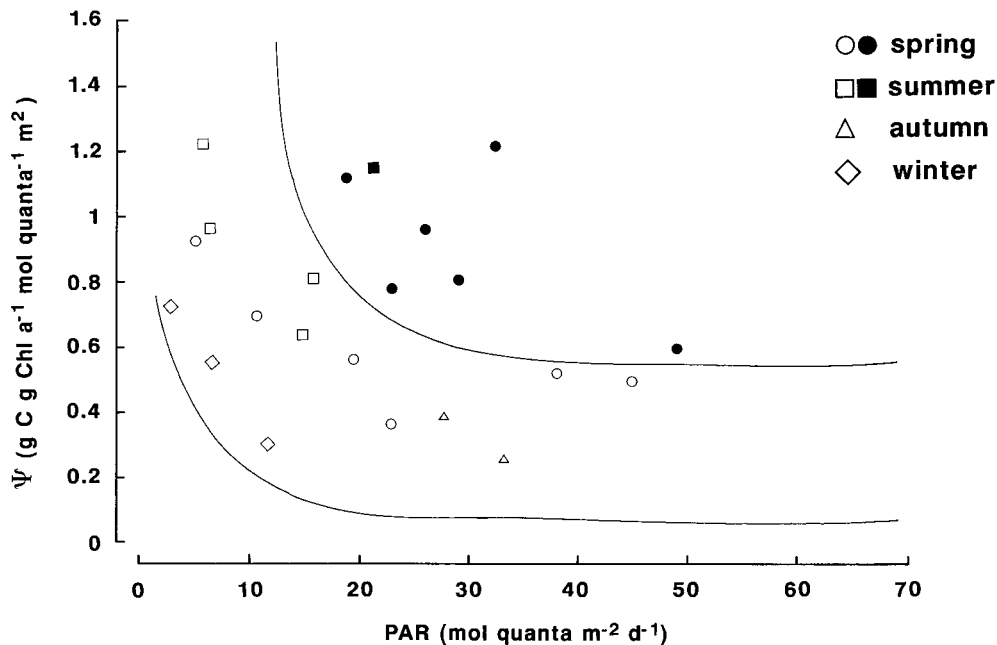


Fig. 3. Variations in the total water-column light utilization index,  $\psi$ , in relation to total daily incident PAR. The solid curves indicate the upper and lower limits of the data given by Falkowski and Raven (1997). Solid symbols indicate the data exceeded the upper limit.

high  $\psi$  values were due to low daily PAR. This observation is also consistent with previous findings (Morel 1991; Falkowski and Raven 1997). Unclear weather conditions that prevailed during the summer observation resulted in low daily PAR and hence probably high  $\psi$  values in the summer. In contrast, both parameters were comparatively high at Sta. 3, indicating that the high  $\psi$  value was due to high growth rate. These summer observations were carried out in mid July, around the same time that a phytoplankton bloom had been reported in the northwestern Pacific (Shiomoto et al. 1998). Thus higher growth rate can be attributed to the summer bloom condition in the study area.

Falkowski and Raven (1997) plotted  $\psi$  values against daily PAR by using a data set compiled from hundreds of stations worldwide, and stated that  $\psi$  was not constant but increased as the daily PAR decreased (cf. Falkowski and Raven's figure 9.9). The data set from this study was added to Falkowski and Raven's (1997) figure (Fig. 3). With the exception of the six spring values and one summer value (solid symbols in Fig. 3), the variations in  $\psi$  in the relation to the daily PAR were within the range of those shown by Falkowski and Raven (1997). Moreover, in agreement with Falkowski and Raven (1997), the remaining  $\psi$  has a tendency to increase with a decrease in daily PAR.

No significant difference was found for the daily PAR between the seven stations where  $\psi$  exceeded the upper limit of the data given by Falkowski and Raven (1997) (solid symbols in Fig. 3), and the remaining stations (open symbols) (Mann-Whitney  $U$ -test,  $P > 0.05$ , two-tailed test). On the contrary, a significant difference was found for Chl  $a$ -specific primary productivity between both ( $U$ -test,  $P < 0.001$ ). Mean  $\pm$  standard deviation of Chl  $a$ -specific primary productivity was  $25.74 \pm 6.98$  mg C mg Chl  $a^{-1} d^{-1}$  ( $n =$

7) at the seven stations and  $9.40 \pm 5.77$  mg C mg Chl  $a^{-1} d^{-1}$  ( $n = 15$ ) at the others. These results indicate that growth rates of phytoplankton communities at the seven stations were higher than those at the others, resulting in higher  $\psi$ . An increase of growth rate was probably due to occurrence of bloom. During the bloom times in the subarctic northwestern Pacific,  $\psi$  is likely to be frequently beyond the range given by Falkowski and Raven (1997).

Primary productivity has been reported to be seriously underestimated by using nonclean sampling techniques (Fitzwater et al. 1982; Williams and Robertson 1989; Welschmeyer et al. 1993) and on-deck incubations with neutral density filters (Laws et al. 1990; Shiomoto et al. 1998), or both. There is a possibility that the primary productivity data used for computing  $\psi$  in Falkowski and Raven (1997), were subjected to such methods. It has been found out from Falkowski (pers. comm.) that the data source of primary productivity in the figure 9.9 of Falkowski and Raven (1997) is summarized in the table 1 of Behrenfeld and Falkowski (1997). The data sets used in the figure 9.9 of Falkowski and Raven (1997) included a number of primary productivity measurements using clean technique and in situ incubation, specifically in U.S. Joint Global Ocean Flux (JGOFS) research programs in the subtropical and tropical regions (Lohrenz et al. 1992; Karl et al. 1996; Barber et al. 1996). The seven  $\psi$  values in this study, exceeding the range given by Falkowski and Raven (1997), were noticed with more than about  $20$  mol quanta  $m^{-2} d^{-1}$  of the daily PAR (Fig. 3). The daily PARs in the JGOFS study areas are generally more than  $20$  mol quanta  $m^{-2} d^{-1}$  throughout the year (Karl et al. 1996). Moreover, Falkowski and Raven (1997) stated that the  $\psi$  was influenced by nutrient condition. The data sets in the JGOFS study areas used in the figure 9.9 of Falkowski

and Raven (1997) included data from the upwelling area in the equatorial Pacific, where surface  $\text{NO}_2 + \text{NO}_3$  concentrations were between 2 and 6  $\mu\text{M}$  (Murray et al. 1995). The comparable nutrient condition to that in this study was observed in the JGOFS study areas. Accordingly, comparison of  $\psi$  values from this study was made against the values reported in Falkowski and Raven (1997). Taking the above facts into account, water-column light utilization efficiency in the subarctic northwestern Pacific at the bloom times was noticed to be by far the highest in the world oceans.

Akihiro Shiimoto<sup>1</sup>

National Research Institute of Far Seas Fisheries  
7-1 Orido 5 Chome, Shimizu  
Shizuoka, 424-8633 Japan

### References

- BARBER, R. T., M. P. SANDERSON, S. T. LINDLEY, F. CHAI, J. NEWTON, C. TREES, D. G. FOLEY, AND F. P. CHAVEZ. 1996. Primary productivity and its regulation in the equatorial Pacific during and following the 1991–1992 El Niño. *Deep-Sea Res. II* **43**: 933–969.
- BEHRENFELD, M. J., AND P. G. FALKOWSKI. 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnol. Oceanogr.* **42**: 1–20.
- DODIMEAD, A. J., F. FAVORITE, AND T. HIRANO. 1963. Review of oceanography of the subarctic region. *Int. North Pacific Fish. Comm. Bull.* **13**: 1–195.
- FALKOWSKI, P. G. 1981. Light-shade adaptation and assimilation numbers. *J. Plankton Res.* **3**: 203–216.
- , AND J. A. RAVEN. 1997. Aquatic photosynthesis. Blackwell.
- FITZWATER, S. E., G. A. KNAUER, AND J. H. MARTIN. 1982. Metal contamination and its effects on primary production measurements. *Limnol. Oceanogr.* **27**: 544–551.
- HAMA, T., T. MIYAZAKI, Y. OGAWA, T. IWAKUMA, M. TAKAHASHI, A. OTSUKI, AND S. ICHIMURA. 1983. Measurement of photosynthetic production of a marine phytoplankton population using a stable  $^{13}\text{C}$  isotope. *Mar. Biol.* **73**: 31–36.
- KARL, D. M., J. R. CHRISTIAN, J. E. DORE, D. V. HEBEL, R. M. LETELIER, L. M. TUPAS, AND C. D. WINN. 1996. Seasonal and interannual variability in primary production and particle flux at Station ALOHA. *Deep-Sea Res. II* **43**: 539–568.
- KASAI, H., H. SAITO, A. YOSHIMORI, AND S. TAGUCHI. 1997. Variability in timing and magnitude of spring bloom in the Oyashio region, the western subarctic Pacific off Hokkaido, Japan. *Fish. Oceanogr.* **6**: 118–129.
- KAWARADA, Y., AND A. SANO. 1972. Distribution of chlorophyll *a* and phaeopigments in the northwestern North Pacific in relation to the hydrographic conditions, p. 125–138. *In* A. Y. Takenouti et al. [eds.], *Biological oceanography of the northern North Pacific Ocean*. Idemitsu Shoten.
- LALLI, C. M., AND T. R. PARSONS. 1991. *Biological oceanography: An introduction*. Butterworth-Heinemann.
- LAWS, E. A., G. R. DITULLIO, K. L. CARDER, P. R. BETZER, AND S. HAWES. 1990. Primary production in the deep blue sea. *Deep-Sea Res.* **37**: 715–730.
- LOHRENZ, S. E., G. A. KNAUER, V. L. ASPER, M. TUEL, A. F. MICHAELS, AND A. H. KNAP. 1992. Seasonal variability in primary production and particle flux in the northwestern Sargasso Sea: U.S. JGOFS Bermuda Atlantic Time-series Study. *Deep-Sea Res.* **39**: 1373–1391.
- MAITA, Y., AND M. YANADA. 1985. Chemistry in Funka Bay, p. 113–125. *In* Coastal Oceanography Research Committee, the Oceanographical Society of Japan [ed.], *Coastal oceanography of Japanese Islands*. Tokai Univ. Press. In Japanese.
- MOREL, A. 1991. Light and marine photosynthesis: A spectral model with geochemical and climatological implications. *Prog. Oceanogr.* **26**: 263–306.
- MURRAY, J. W., E. JOHNSON, AND C. GARSIDE. 1995. A U.S. JGOFS Process Study in the equatorial Pacific (EqPac): Introduction. *Deep-Sea Res. II* **42**: 275–293.
- NISHIHAMA, Y., AND K. KAWAMATA. 1979. Primary production in Funka Bay, Hokkaido. *Bull. Jpn. Soc. Fish. Oceanogr.* **34**: 71–74. In Japanese.
- OBAYASHI, Y., K. SUZUKI, N. HANDA, Y. NOJIRI, AND C. S. WONG. 1997. Distribution of phytoplankton pigments in the northern North Pacific by ship-of-opportunity sampling between Canada and Japan, p. 197–204. *In* S. Tsunogai [ed.], *Biogeochemical processes in the North Pacific*. Japan Marine Science Foundation.
- ODATE, T., AND Y. MAITA. 1988/89. Regional variation in the size composition of phytoplankton communities in the western North Pacific Ocean, spring 1985. *Biol. Oceanogr.* **6**: 65–77.
- OGISHIMA, T. 1991. Distribution of chlorophyll *a* as a phytoplanktonic food for Japanese sardine in the sea area off southeast Hokkaido. *Bull. Hokkaido Natl. Fish. Res. Inst.* **55**: 173–184. In Japanese with English abstract.
- OHTANI, K. 1991. To confirm again the characteristics of the Oyashio. *Bull. Hokkaido Natl. Fish. Res. Inst.* **55**: 1–24. In Japanese with English abstract.
- PARSONS, T. R., Y. MAITA, AND C. M. LALLI. 1984. *A manual of chemical and biological methods for seawater analysis*. Pergamon Press.
- PLATT, T. 1986. Primary production of the ocean water column as a function of surface light intensity: Algorithms for remote sensing. *Deep-Sea Res.* **33**: 149–163.
- , S. SATHYENDRANATH, C. M. CAVERHILL, AND M. R., LEWIS. 1988. Ocean primary production and available light: Further algorithms for remote sensing. *Deep-Sea Res.* **35**: 855–879.
- RICHARDSON, K., J. BEARDALL, AND J. A. RAVEN. 1983. Adaptation of unicellular algae to irradiance: An analysis of strategies. *New Phytol.* **93**: 157–191.
- SHIIMOTO, A., Y. ISHIDA, M. TAMAKI, AND Y. YAMANAKA. 1998. Primary production and chlorophyll *a* in the northwestern Pacific Ocean in summer. *J. Geophys. Res.* **103**: 24,651–24,661.
- TANIGUCHI, A., AND T. KAWAMURA. 1972. Primary production in the Oyashio region with special reference to the subsurface chlorophyll maximum layer and phytoplankton-zooplankton relationship, p. 231–243. *In* A. Y. Takenouti et al. [eds.], *Biological oceanography of the northern North Pacific Ocean*. Idemitsu Shoten.
- WELSCHMEYER, N. A., S. STROM, R. GOERICKE, G. DITULLIO, M. BELVIN, AND W. PETERSEN. 1993. Primary production in the subarctic Pacific Ocean: Project SUPER. *Prog. Oceanogr.* **32**: 101–135.
- WILLIAMS, P. J. LEB, AND J. I. ROBERTSON. 1989. A serious inhibition problem from a Niskin sampler during plankton productivity studies. *Limnol. Oceanogr.* **34**: 1300–1305.

<sup>1</sup> Corresponding author (shiimoto@enyo.affrc.go.jp).

### Acknowledgments

I am extremely grateful to the captains and crews of the RV *Shunyo Maru* of the National Research Institute of Far Seas Fisheries, *Tankai Maru* of the Hokkaido National Fisheries Research Institute, and *Kaiyo Maru* of the Fisheries Agency of Japan, for their kind cooperation during the collection of samples. I express my gratitude to K. Mahapatra, Tokai University, for correcting the manuscript and his helpful comments.

Received: 18 October 1999

Accepted: 23 February 2000

Amended: 3 March 2000