

# Size-Fractionated Primary Production Estimated by a Two-Phytoplankton Community Model Applicable to Ocean Color Remote Sensing

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**In order to estimate primary production from ocean color satellite data using the Vertical Generalized Production Model (VGPM; Behrenfeld and Falkowski, 1997), we propose a two-phytoplankton community model. This model is based on the two assumptions that changes in chlorophyll concentration result from changes of large-sized phytoplankton abundance, and chlorophyll specific productivity of phytoplankton tends to be inversely proportional to phytoplankton size. Based on the analysis of primary production data,  $P_{opt}^B$ , which was one parameter in the VGPM, was modeled as a function of sea surface temperature and sea surface chlorophyll concentration. The two-phytoplankton community model incorporated into the VGPM gave good estimates in a relatively high productive area. Size-fractionated primary production was estimated by the two-phytoplankton community model, and  $P_{opt}^B$  of small-sized phytoplankton was 4.5 times that of large-sized phytoplankton. This result fell into the ranges observed during field studies.**

Keywords:

- Primary production,
- remote sensing,
- phytoplankton size.

## 1. Introduction

Many studies of abundance and size composition of phytoplankton have been conducted. These revealed that low phytoplankton abundance is dominated by small-sized phytoplankton, while high phytoplankton abundance is dominated by large-sized phytoplankton (Raimbault *et al.*, 1988; Odate and Maita, 1988/1989; Odate, 1996). It is generally recognized that chlorophyll abundance is changed mainly by large-sized phytoplankton abundance (Chisholm, 1992). Since the size composition of phytoplankton communities affects primary production, the size-fractionated phytoplankton productivity has been measured. These results showed that the chlorophyll-specific productivity of small-sized phytoplankton tends to be higher than that of large-sized phytoplankton (Malone, 1980).

A series of datasets taken by ocean color sensors (e.g. Sea-viewing Wide Field-of view Sensor, SeaWiFS) is expected to be a useful aid in estimating the spatial distribution of primary production. Various primary productivity algorithms have been developed in order to estimate global distribution of primary production from sat-

ellite derived chlorophyll data (Platt and Sathyendranath, 1988; Morel, 1991; Behrenfeld and Falkowski, 1997). Among these algorithms, the Vertically Generalized Production Model (VGPM) proposed by Behrenfeld and Falkowski (1997) is the simplest and the most usable for primary production estimation, because it is possible to obtain all parameters used in the VGPM from satellite observation or mathematical computation. In the VGPM, the maximum chlorophyll-specific photosynthetic rate within a water column ( $P_{opt}^B$ ; mg C (mg Chl)<sup>-1</sup> h<sup>-1</sup>) is one of the key parameters. Behrenfeld and Falkowski (1997) defined  $P_{opt}^B$  as a function of temperature. However, results on the relationships between abundance, size and productivity of phytoplankton (Malone, 1980; Chisholm, 1992) allow us to hypothesize that  $P_{opt}^B$  is affected not only by temperature but also biotic factors. In the present study chlorophyll concentration was used to model  $P_{opt}^B$  as a biotic factor, because chlorophyll concentration is here regarded as an index of phytoplankton abundance and reflected size composition of phytoplankton.

The objective of this paper is to construct a two-phytoplankton community model of  $P_{opt}^B$  based on the difference in productivity between phytoplankton cell sizes. The relationship between chlorophyll concentration and  $P_{opt}^B$  was examined, and  $P_{opt}^B$  was modeled as a

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Table 1. Categories defined with sea surface temperature and chlorophyll concentration and number of data contained each categories.

Sea surface temperature category (°C)	Sea surface chlorophyll concentration category (mg m <sup>-3</sup> )						
	0–0.1	0.1–0.2	0.2–0.5	0.5–1.0	1.0–2.0	2.0–5.0	5.0–
–0	0	0	3	3	8	2	3
0–4	6	4	6	17	27	23	14
4–8	0	13	28	59	58	57	18
8–12	2	6	31	83	70	39	7
12–16	19	44	140	117	94	55	13
16–20	63	90	154	65	51	40	25
20–24	16	36	47	26	14	13	7
24–28	46	22	27	1	2	1	0
28–	20	18	12	1	0	0	0

function of temperature and chlorophyll concentration. This model was incorporated into the VGPM, and size-fractionated primary production was estimated.

## 2. Materials and Methods

### 2.1 Primary production database

A primary production database was constructed for this study. We extracted primary production measurements from two sources: one was the Behrenfeld and Falkowski dataset and the other was a Japanese dataset.

Behrenfeld and Falkowski (1997) assembled a dataset of primary production measured by the <sup>14</sup>C method (Steemann Nielsen, 1952). The dataset includes position, date, daily-integrated photosynthetically active radiation (PAR) above the sea surface, profiles of temperature and chlorophyll concentration, and euphotic depth. The dataset was extracted from the Website of Rutgers University (<http://marine.rutgers.edu/opp/>). Among the 2984 stations archived in the dataset, 1757 were used in the present study, the rest being rejected because they did not include temperature. These data were measured throughout the world's oceans from 80°N to 80°S. In addition, 109 profiles of primary production measured by the non-radioactive <sup>13</sup>C method (Hama *et al.*, 1983) in the western North Pacific was used (Shiomoto and Matsumura, 1992; Shiomoto *et al.*, 1994, 1996, 1998b, 1998c; Kasai *et al.*, 1998; Ishizaka and Ishida, unpublished data). We used these 1866 profiles for model development and testing.

All profiles were sorted into nine categories according to range of sea surface temperature (SST) and seven categories according to range of chlorophyll concentration at the sea surface (SSC). The number of data points included in each category is shown in Table 1. The criterion for defining these categories was that numbers of profiles included in each category must be for the analy-

sis described below, so categories containing fewer than five data points were excluded from subsequent analysis. Medians of SST, SSC and  $P_{opt}^B$  were calculated in each category, and relationships between SST or SSC and  $P_{opt}^B$  were examined.

### 2.2 Primary production algorithm

We used the VGPM (Behrenfeld and Falkowski, 1997) in order to estimate depth-integrated primary production ( $IPP$ : mg C m<sup>-2</sup> d<sup>-1</sup>). In the VGPM,  $IPP$  was calculated as follows:

$$IPP = 0.66125 \times P_{opt}^B \times \frac{E_0}{E_0 + 4.1} \times Z_{eu} \times Chl_{opt} \times D_{irr} \quad (1)$$

where  $E_0$  is daily PAR above the sea surface (mol quanta m<sup>-2</sup>),  $Z_{eu}$  is euphotic depth which is defined as physical depth at 1% of  $E_0$  (m),  $Chl_{opt}$  is chlorophyll concentration at  $P_{opt}^B$  (mg m<sup>-3</sup>) and  $D_{irr}$  is photoperiod (hr). Because it is impossible to estimate  $Chl_{opt}$  from satellite observation, Behrenfeld and Falkowski (1997) examined the relationship between  $Chl_{opt}$  and SSC. It showed a high correlation ( $r^2 = 0.94$ ) and Behrenfeld and Falkowski (1997) concluded that  $Chl_{opt}$  can be replaced by SSC in the VGPM.

In Behrenfeld and Falkowski (1997),  $P_{opt}^B$  was defined as a function of SST ( $T$ ; °C),

$$P_{opt}^B = -3.27 \times 10^{-8} \times T^7 + 3.4132 \times 10^{-6} \times T^6 - 1.348 \times 10^{-4} \times T^5 + 2.462 \times 10^{-3} \times T^4 - 0.0205 \times T^3 + 0.0617 \times T^2 + 0.2749 \times T + 1.2956. \quad (2)$$

In the present study  $P_{opt}^B$  turns out to be affected by SSC, and was parameterized from the relationship among  $P_{opt}^B$ , SST and SSC.

### 3. Two-Phytoplankton Community Model

#### 3.1 Relationships of $P_{opt}^B$ and environmental parameters

In the lower three SSC categories (ranges 0–0.1, 0.1–0.2 and 0.2–0.5  $\text{mg m}^{-3}$ ),  $P_{opt}^B$  tends to increase with increasing SST between 0° and 20°C (Fig. 1(a)). Above 20°C,  $P_{opt}^B$  decreases with increasing SST. The trend below 20°C is estimated from the increase in the photosynthesis rate of phytoplankton with the increase in temperature (Eppley, 1972), and the trend above 20°C may be caused by the depletion of nutrients within the upper mixed layer due to the stratification in the high SST area (Balch and Byrne, 1994). In the top four SSC categories, the ranges of 0.5–1.0, 1.0–2.0, 2.0–5.0 and 5.0– $\text{mg m}^{-3}$ ,  $P_{opt}^B$  also tends to increase monotonously with increasing in SST. The decrease in  $P_{opt}^B$  for the categories which SSC are  $>0.5 \text{ mg m}^{-3}$  is not recognized, because there are fewer than five data in high SST categories  $>24^\circ\text{C}$  (Table 1) and these were thus excluded from analysis.

$P_{opt}^B$  decreases with increasing in SSC except in the lower two SST categories (ranges  $<0^\circ\text{C}$  and  $0\text{--}4^\circ\text{C}$ ), and the higher two SST categories (ranges  $24^\circ\text{--}28^\circ\text{C}$  and  $>28^\circ\text{C}$ ) (Fig. 1(b)). These results show that  $P_{opt}^B$  tends to be inversely proportional to SSC. Studies regarding abundance and size composition of phytoplankton have shown that the change in chlorophyll concentration was mostly affected by large-sized phytoplankton (Malone, 1980; Raimbault *et al.*, 1988; Odate and Maita, 1988/1989; Chisholm, 1992; Odate, 1996).

In other words, small-sized phytoplankton dominates in low chlorophyll concentration and large-sized phytoplankton dominates in high chlorophyll concentration (Table 2). From the view of size-fractionated primary production, a summary of previous studies showed that phytoplankton productivity tended to be inversely proportional to phytoplankton size in warm and tropical waters (e.g. Malone, 1980; Table 3).

Thus, the decline in  $P_{opt}^B$  with the increase in SSC between  $4^\circ\text{--}24^\circ\text{C}$  in Fig. 1(b), was considered to be caused by the increase in the fraction of low-productive, large-sized phytoplankton. However, such trends were not generally observed in the higher two SST categories ( $24^\circ\text{--}28^\circ\text{C}$  and  $>28^\circ\text{C}$ ), because there are few  $P_{opt}^B$  data in each category (Fig. 1(b)). On the other hand, our analysis showed that  $P_{opt}^B$  of low SST categories ( $<0^\circ\text{C}$  and  $0\text{--}4^\circ\text{C}$ ) did not change for all SSC ranges.

In water colder than  $10^\circ\text{C}$ , the productivity of picoplankton ( $<2 \mu\text{m}$ ) was low due to the low temperature and equal to larger phytoplankton ( $>2 \mu\text{m}$ ) in the subarctic North Pacific and the Bering Sea (Shiomoto *et al.*, 1997) and the Antarctic Ocean (Shiomoto *et al.*, 1998a).

No difference of  $P_{opt}^B$  in the low SST category

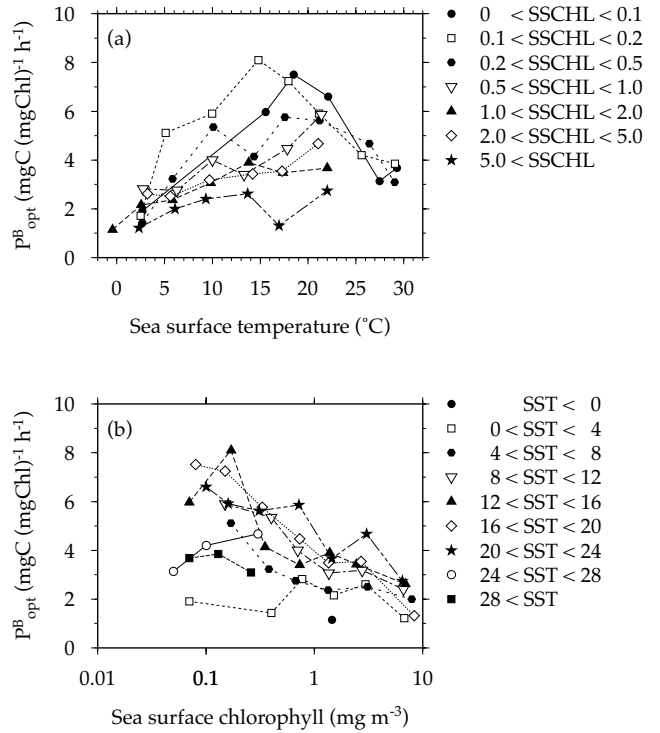


Fig. 1. Median value of maximum carbon fixation rate within a water column,  $P_{opt}^B$  (a) for 7 chlorophyll categories, (b) for 9 temperature categories.

( $<4^\circ\text{C}$ ) appeared since there is no difference of the productivity in each phytoplankton size group.

#### 3.2 Two-phytoplankton community model of $P_{opt}^B$

Our analysis of the database (Table 1) shows the increase of  $P_{opt}^B$  with increasing SST under  $20^\circ\text{C}$  and decrease of  $P_{opt}^B$  with increasing SST above  $20^\circ\text{C}$ , and inverse proportion of  $P_{opt}^B$  to SSC in the ranges of  $4^\circ\text{--}24^\circ\text{C}$  (Fig. 1). Thus it seems reasonable to express  $P_{opt}^B$  as a function of SST and SSC based on size dependency of primary productivity (Table 3). As the first step in modeling size dependency of productivity, we assumed that the phytoplankton community was composed of two groups; one was small-sized phytoplankton with high  $P_{opt}^B$  and the other was large-sized phytoplankton with low  $P_{opt}^B$ . Furthermore, fluctuation in the chlorophyll concentration is determined by the increase or decrease of large-sized phytoplankton. This two-phytoplankton community model is expressed by the following equations,

$$\text{Chl}_{total} = \text{Chl}_{small} + \text{Chl}_{large} \quad (3)$$

and

Table 2. Summary of percentage of chlorophyll concentration in 3 size fractions (mean  $\pm$  standard deviation).

Region	Chlorophyll concentration <1.0 (mg m <sup>-3</sup> )				Chlorophyll concentration >1.0 (mg m <sup>-3</sup> )				References
	pico	nano	micro	samples number	pico	nano	micro	samples number	
Arctic Ocean Foxe Basin	37 $\pm$ 20	63 $\pm$ 20		7	14 $\pm$ 4	86 $\pm$ 4		2	Smith <i>et al.</i> (1985) <sup>(1)</sup>
North Atlantic Ocean Georges Bank	69 $\pm$ 16	31 $\pm$ 16		14	24 $\pm$ 13	76 $\pm$ 13		11	Harrison and Wood (1988) <sup>(1)</sup>
North Pacific Ocean Subarctic	51 $\pm$ 11	24 $\pm$ 10	25 $\pm$ 17	14	29 $\pm$ 18	9 $\pm$ 11	61 $\pm$ 24	13	Odate and Maita (1988/1989) <sup>(2)</sup>
Transition	75 $\pm$ 10	17 $\pm$ 8	9 $\pm$ 6	17					
Subtropical	84 $\pm$ 5	7 $\pm$ 3	9 $\pm$ 4	20					
North Pacific Ocean and Bering Sea	59 $\pm$ 17	21 $\pm$ 9	20 $\pm$ 15	81	38 $\pm$ 20	16 $\pm$ 5	46 $\pm$ 20	20	Odate (1996) <sup>(2)</sup>
South Pacific Ocean Coral Sea	70 $\pm$ 9	13 $\pm$ 3	17 $\pm$ 8	7					Furnas and Mitchell (1988) <sup>(2)</sup>

<sup>(1)</sup>Picoplankton <1  $\mu$ m.<sup>(2)</sup>Picoplankton <2  $\mu$ m, nanoplankton 2–10  $\mu$ m, microplankton >10  $\mu$ m.

Table 3. Summary of size fractioned assimilation number (mean  $\pm$  standard deviation).

Region	Assimilation number (mg C [mg Chl] <sup>-1</sup> h <sup>-1</sup> )	Size fraction	Samples number	References
<b>Pacific Ocean</b>				
Subtropical off Oahu	8.09 $\pm$ 5.04	<3 $\mu$ m	4	Takahashi and Bienfang (1983)
	6.88 $\pm$ 6.34	3–20 $\mu$ m	3	
	2.11 $\pm$ 1.64	>20 $\mu$ m	4	
Coral Sea	6.30 $\pm$ 1.64	<2 $\mu$ m	3	Furnas and Mitchell (1988) <sup>(1)</sup>
	2.87 $\pm$ 0.76	>2 $\mu$ m	3	
<b>Atlantic Ocean</b>				
Mid Atlantic Ridge	0.68 $\pm$ 0.19	<1 $\mu$ m	11	Platt <i>et al.</i> (1983) <sup>(2)</sup>
	0.49 $\pm$ 0.19	>1 $\mu$ m	11	
Celtic Sea	4.436	<1 $\mu$ m		Joint (1986) <sup>(3)</sup>
	1.851	1–5 $\mu$ m		
	2.407	>5 $\mu$ m		
<b>Indian Ocean</b>				
Indian Ocean	1.7 $\pm$ 0.8	<0.8 $\mu$ m	7	Saijo and Takesue (1965) <sup>(4)</sup>
	2.0 $\pm$ 0.8	0.8–5.0 $\mu$ m	7	
	1.9 $\pm$ 1.0	5.0–90 $\mu$ m	7	
	0.8 $\pm$ 0.8	>90 $\mu$ m	7	

<sup>(1)</sup>Samples collected from near surface.

<sup>(2)</sup>The chlorophyll specific photosynthesis under the light-saturation condition.

<sup>(3)</sup>Samples collected from 10 m depth.

<sup>(4)</sup>Samples collected from surface.

$$P^B_{opt} = P^B_{opt-small} \times \frac{Chl_{small}}{Chl_{total}} + P^B_{opt-large} \times \frac{Chl_{large}}{Chl_{total}} \quad (4)$$

where  $Chl_{total}$  is total chlorophyll concentration at the sea surface (mg m<sup>-3</sup>) and subscripts “small” and “large” represent small-sized and large-sized phytoplankton, respectively.

$P^B_{opt}$  cannot be directly measured by remote sensing data, and it is necessary for  $P^B_{opt}$  to be related by environmental parameters (Behrenfeld and Falkowski, 1997). The physiological condition of phytoplankton is mainly affected by temperature (Eppley, 1972), and the productivity of phytoplankton has a temperature dependency. In addition, small- and large-sized phytoplankton show a different temperature-dependency (Shiomoto *et al.*, 1997). Thus, relationships of  $P^B_{opt}$  of both small-sized and large-sized phytoplankton were parameterized by sea surface temperature. Assuming that  $P^B_{opt-small}$  and  $P^B_{opt-large}$  were represented by equations in the third degree of SST,

$$P^B_{opt-small} = a_{small} + b_{small} \times T + c_{small} \times T^2 + d_{small} \times T^3 \quad (5)$$

and

$$P^B_{opt-large} = a_{large} + b_{large} \times T + c_{large} \times T^2 + d_{large} \times T^3. \quad (6)$$

Substituting Eq. (3) in  $Chl_{large}$  of Eq. (4) and substituting Eqs. (5) and (6) in  $P^B_{opt-small}$  and  $P^B_{opt-large}$  of Eq. (4) gives

$$P^B_{opt} = \left\{ (a_{small} - a_{large}) + (b_{small} - b_{large}) \times T + (c_{small} - c_{large}) \times T^2 + (d_{small} - d_{large}) \times T^3 \right\} \times \frac{Chl_{small}}{Chl_{total}} + (a_{large} + b_{large} \times T + c_{large} \times T^2 + d_{large} \times T^3). \quad (7)$$

Chisholm (1992) compiled size-fractionated chlorophyll *a* concentration data from all over the oceans, and found that the abundance of chlorophyll *a* smaller than 1  $\mu$ m shows an upper limit. Additionally, in the North Pacific, there is an envelope that shows the maximum fraction of the abundance of chlorophyll *a* smaller than 2  $\mu$ m (Fig. 2). Although the fraction of small-sized phytoplankton shows spatial and temporal variation, we then assumed that  $Chl_{small}$  is constant to simplify the equation. Hence Eq. (7) is modified to

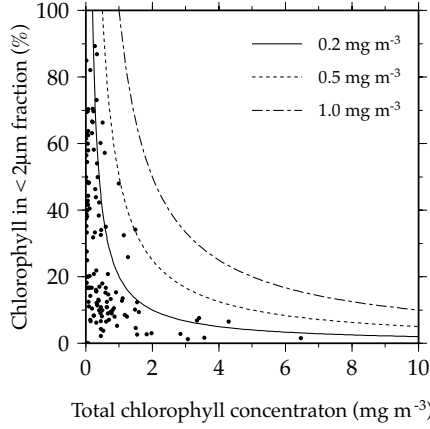


Fig. 2. Fraction of chlorophyll smaller than  $2 \mu\text{m}$  as a function of total chlorophyll concentration. The continuous line, the dashed line and the dotted line represent theoretical values where chlorophyll concentrations smaller than  $2 \mu\text{m}$  are 0.2, 0.5 and  $1.0 \text{ mg m}^{-3}$ , respectively. Data were extracted from Saito *et al.* (1998), Hashimoto and Shiomoto (2000) and Shiomoto and Hashimoto (2000).

$$P_{opt}^B = \frac{a_1 + b_1 \times T + c_1 \times T^2 + d_1 \times T^3}{Chl_{total}} + (a_2 + b_2 \times T + c_2 \times T^2 + d_2 \times T^3) \quad (8)$$

where,  $a_1 = (a_{small} - a_{large}) \times Chl_{small}$ ,  $b_1 = (b_{small} - b_{large}) \times Chl_{small}$ ,  $c_1 = (c_{small} - c_{large}) \times Chl_{small}$ ,  $d_1 = (d_{small} - d_{large}) \times Chl_{small}$ ,  $a_2 = a_{large}$ ,  $b_2 = b_{large}$ ,  $c_2 = c_{large}$  and  $d_2 = d_{large}$ .

Since the average of  $P_{opt}^B$  in the range of  $<0^\circ\text{C}$  contained in the database is 1.07 (standard deviation 0.36),  $P_{opt}^B$  was assumed to be  $1.0 \text{ mg C (mg Chl)}^{-1} \text{ h}^{-1}$  at  $0^\circ\text{C}$  regardless of chlorophyll concentration found when modeling  $P_{opt}^B$ . In order to estimate parameters of Eq. (8) from the relationship between SST, SSC and  $P_{opt}^B$  (Fig. 1), a nonlinear regression analysis was used, resulting in;

$$P_{opt}^B = \frac{0.071 \times T - 3.2 \times 10^{-3} \times T^2 + 3.0 \times 10^{-5} \times T^3}{Chl_{total}} + (1.0 + 0.17 \times T - 2.5 \times 10^{-3} \times T^2 + 8.0 \times 10^{-5} \times T^3). \quad (9)$$

This two-phytoplankton community model is valid for SST ranging from  $0^\circ$  to  $30^\circ\text{C}$  and for chlorophyll concentration above  $0.05 \text{ mg m}^{-3}$  (Fig. 3). In the two-phytoplankton community model, the trend of  $P_{opt}^B$  observed in Fig. 1 was well reproduced. That is,  $P_{opt}^B$

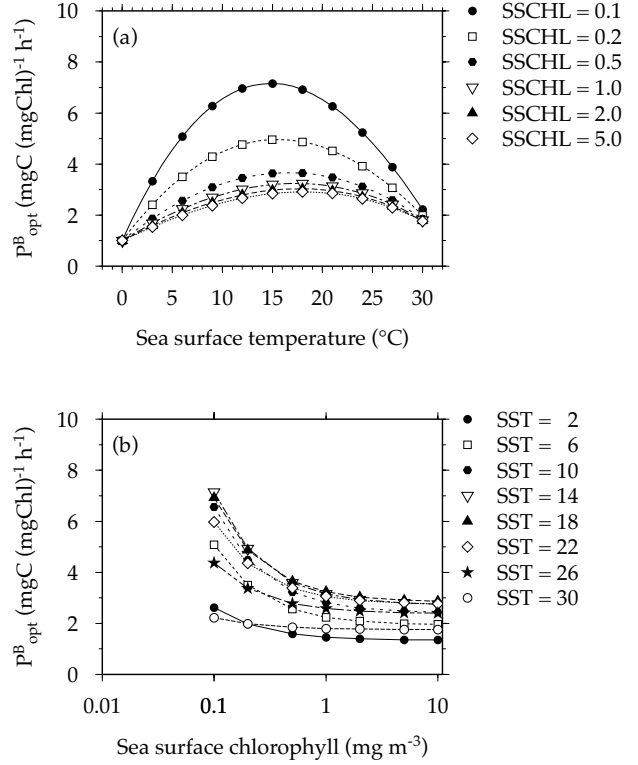


Fig. 3. Modeled values of  $P_{opt}^B$  as a function of temperature and chlorophyll concentration calculated from Eq. (9).

modeled with Eq. (9) increases below  $20^\circ\text{C}$  and decreases above  $20^\circ\text{C}$ , and is inversely proportional to chlorophyll concentration.

### 3.3 Comparison with the primary production database

The primary production database constructed in Subsection 2.1 was used for comparisons between measured and modeled primary production. Modeled primary production was calculated by the original VGPM (Eq. (1) with Eq. (2) for  $P_{opt}^B$ ) and the modified VGPM (Eq. (1) with Eq. (9) for  $P_{opt}^B$ ).

For each of the parameters  $E_0$ ,  $Z_{eu}$  and  $\text{SSC} (=Chl_{total})$  in Eq. (9) in Eq. (1) and  $T$  in Eq. (2) and Eq. (9), measured values in the primary production database assembled for this study were used.  $D_{irr}$  in Eq. (1) was calculated using the date and location of the station where each primary production profile was measured.

In order to quantify how well of the original VGPM and the modified VGPM matched measured primary production (Table 1), root mean square errors (RMSE) were calculated for each SSC category (Table 4). Additionally, estimation errors ( $\epsilon$ ) were calculated to evaluate over- or underestimation by the following equation,

Table 4. Summary of root mean squared error and estimation error.

(a) Root Mean Squared Error (RMSE)

Sea surface chlorophyll concentration category (mg m <sup>-3</sup> )	$P_{opt}^B$		$IPP$	
	Eq. (9)	Eq. (2)	Modified VGPM*	VGPM**
0–0.1	2.90	2.08	163	133
0.1–0.2	2.83	2.96	423	399
0.2–0.5	2.42	2.75	288	376
0.5–1.0	2.19	2.34	394	584
1.0–2.0	1.92	1.96	445	679
2.0–5.0	2.03	1.99	794	1210
5.0–	1.62	1.94	1334	2656
Total	2.21	2.31	548	892

(b) Estimation error ( $\epsilon$ )

Sea surface chlorophyll concentration category (mg m <sup>-3</sup> )	$P_{opt}^B$		$IPP$	
	Eq. (9)	Eq. (2)	Modified VGPM*	VGPM**
0–0.1	0.527	0.340	0.362	0.177
0.1–0.2	0.279	0.365	0.192	0.278
0.2–0.5	0.097	0.429	0.248	0.580
0.5–1.0	-0.045	0.357	0.232	0.633
1.0–2.0	-0.169	0.310	-0.003	0.476
2.0–5.0	-0.237	0.302	-0.020	0.520
5.0–	-0.088	0.458	0.186	0.731
Total	-0.035	0.356	0.141	0.532

\*Calculated with the two-phytoplankton community model for  $P_{opt}^B$ .

\*\*Calculated with the function of Behrenfeld and Falkowski (1997) for  $P_{opt}^B$ .

$$\epsilon = \frac{\sum_{i=1}^N (\log(E_i) - \log(R_i))}{N} \quad (10)$$

where  $R$  is the measured value,  $E$  is the estimated value and  $N$  is the number of data (Table 4).

For  $P_{opt}^B$  estimation, RMSE of  $P_{opt}^B$  estimated by the two-phytoplankton community model (Eq. (9)) shows a better match than that estimated by Eq. (2) except in two SSC categories (0–0.1 and 2.0–5.0 mg m<sup>-3</sup>), and  $\epsilon$  of  $P_{opt}^B$  by Eq. (9) shows a better match than that given by Eq. (2) except in the lowest SSC categories (0–0.1 mg m<sup>-3</sup>).

For  $IPP$  estimation, RMSE of  $IPP$  estimated by the modified VGPM shows a better match than that given by

the original VGPM except in the lower two SSC categories (0–0.1 and 0.1–0.2 mg m<sup>-3</sup>). Calculated  $\epsilon$  shows that  $IPP$  estimated by the original VGPM tends to overestimate. Overestimation in the high chlorophyll concentration of the original VGPM was improved considerably by the modified VGPM (Table 4).

#### 3.4 Estimation of size-fractionated $P_{opt}^B$ by the two-phytoplankton community model

On modeling  $P_{opt}^B$  in Subsection 3.2, we assumed that the phytoplankton community consists of small- and large-sized phytoplankton and each size class has different  $P_{opt}^B$ . From Eq. (9) and the relationship of coefficients between Eqs. (7) and (8), Eqs. (5) and (6) are modified to give the following equations,

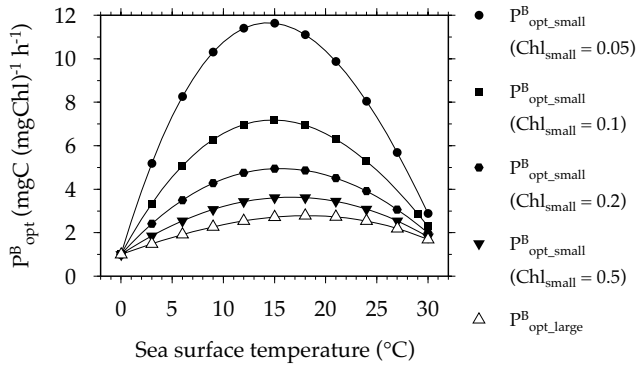


Fig. 4. Size-fractionated  $P^B_{opt}$ ,  $P^B_{opt-small}$  and  $P^B_{opt-large}$  were estimated by Eqs. (11) and (12), respectively.  $P^B_{opt-small}$  was calculated for four concentrations of  $Chl_{small}$ , which were 0.05, 0.1, 0.2 and 0.5  $\text{mg m}^{-3}$ .

$$P^B_{opt-small} = 1.0 + \left( 0.17 + \frac{0.071}{Chl_{small}} \right) \times T - \left( 2.5 \times 10^{-3} + \frac{3.2 \times 10^{-3}}{Chl_{small}} \right) \times T^2 + \left( -8.0 \times 10^{-5} + \frac{3.0 \times 10^{-5}}{Chl_{small}} \right) \times T^3 \quad (11)$$

and

$$P^B_{opt-large} = 1.0 + 0.17 \times T - 2.5 \times 10^{-3} \times T^2 - 8.0 \times 10^{-5} \times T^3. \quad (12)$$

In Eqs. (11) and (12), a variable which represents a criterion for dividing small- and large-sized phytoplankton was not contained explicitly. As an alternative to the criterion, it is necessary to give  $Chl_{small}$  in Eq. (11).

In order to determine  $Chl_{small}$ , we examined the fraction of small-sized phytoplankton to total phytoplankton from field study. Chisholm (1992) showed that the maximum biomass of phytoplankton less than  $1 \mu\text{m}$  had rarely exceeded  $0.50 \text{ mg m}^{-3}$  regardless of total chlorophyll concentration. Furthermore, there was an envelope which showed an upper limit of biomass of small-sized phytoplankton less than  $2 \mu\text{m}$  in the North Pacific Ocean (Fig. 2). Consequently, if the criterion of cell size between small- and large-sized phytoplankton was defined to be  $1 \mu\text{m}$ ,  $Chl_{small}$  should be regarded as the range from 0 to  $0.5 \text{ mg m}^{-3}$ .

For one example of the size-fractionated  $P^B_{opt}$ ,  $P^B_{opt-small}$  was calculated between  $0.05$  and  $0.50 \text{ mg m}^{-3}$  of  $Chl_{small}$  and was compared with  $P^B_{opt-large}$ . At  $10^\circ$ – $13^\circ\text{C}$

and at  $0.05 \text{ mg m}^{-3}$  of chlorophyll concentration,  $P^B_{opt-small}$  showed a value 4.5 times greater than  $P^B_{opt-large}$  (Fig. 4). As noted above, these values of  $Chl_{small}$  in the range  $0.05$ – $0.5 \text{ mg m}^{-3}$  correspond to the case when the cell size between small- and large-sized phytoplankton is  $1 \mu\text{m}$ . If a larger cell size was defined as the criterion between small- and large-sized phytoplankton, differences between  $P^B_{opt-small}$  and  $P^B_{opt-large}$  should become smaller.

#### 4. Discussion

Our study had three major results. First,  $P^B_{opt}$ , which was one parameter of the VGPM, was affected by both SST and SSC (Fig. 1). Second, we constructed the two-phytoplankton community model (Eq. (9); Fig. 3). Finally, the functions of size-fractionated  $P^B_{opt}$  were developed (Eqs. (11) and (12); Fig. 4).

In the present study,  $P^B_{opt}$  was parameterized by SST and SSC according to the result of analysis of the database. Estimated primary production by the modified VGPM was compared with measured primary production (Table 4). RMSE and  $\epsilon$  of the present study are smaller than that reported by Behrenfeld and Falkowski (1997) both for  $P^B_{opt}$  and  $IPP$  (in 5 of 7 categories in RMSE and in 6 of 7 categories in  $\epsilon$ ). In particular, our modification of the VGPM contributes to improving  $IPP$  estimation in relatively productive areas. Therefore, it seems reasonable to conclude that our attempt to construct a two-phytoplankton community model of  $P^B_{opt}$  has been successful.

There are some works that propose newly constructed  $P^B_{opt}$  models. Among them, Behrenfeld *et al.* (2002) modeled  $P^B_{opt}$  with a focus on the effect of photoacclimation and light limitation. Their approach will be valid in improving our two-phytoplankton community model.

In order to raise the performance of the model, it is necessary to gather more primary production data and to improve the primary production database. In the database, limited profiles were observed both at low temperature and low chlorophyll concentration and at high temperature and high chlorophyll concentration (Table 1). Thus, it is expected that the precision of model estimation would not be particularly good in such cases. Furthermore, stations and dates when primary production measurements were conducted are not distributed uniformly, so more effort must be done to collect in-situ observed data. This improved database should be useful to validate the model.

An introduction of the concept of the two-phytoplankton community model made it possible to estimate size fractionated primary production (Eqs. (11) and (12)).  $P^B_{opt-small}$  was 4.5 times more than  $P^B_{opt-large}$  at  $10^\circ$ – $13^\circ\text{C}$  and at  $0.05 \text{ mg m}^{-3}$  of chlorophyll concentration, and this value was the largest (Fig. 4). As for field studies, the productivity of nanoplankton ( $<20 \mu\text{m}$ ) was  $1.5$ –

13.5 times greater than that of netplankton in oceanic waters (Malone, 1980). The results of the two-phytoplankton community model fell into ranges reported from the results of field studies. Although our hypothesis of the two-phytoplankton community model was simple, size-fractionated primary production can be estimated by Eqs. (11) and (12). The number of trophic levels varies with locality and the length of the food chain is changed by the size of the dominant phytoplankton (Lalli and Parsons, 1997). Size-fractionated primary production estimated in this study contributes to an understanding of the energy flow in marine ecosystems.

We assumed that the phytoplankton community is composed of two groups, and estimated size-fractionated primary production by small-sized and large-sized phytoplankton. Of course, the community structure of phytoplankton is more complicated than we have assumed, and physiological characteristics and the rate of production of phytoplankton vary both spatially and temporally. Although it is difficult to estimate these factors from satellite observation, our model is a first step toward taking account of the differences in the phytoplankton community and/or physiological parameters of the primary production algorithm.

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