Proc. NIPR Symp. Polar Biol., 7, 17-31, 1994

ESTIMATION OF VERTICAL DISTRIBUTION OF CHLOROPHYLL *a* OFF EAST HOKKAIDO BY GAUSSIAN CURVE FITTING

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Abstract: Sea truth data on the concentration of chlorophyll pigments were used to determine the empirical relationship between surface chlorophyll a concentration and parameters derived from a Gaussian curve for a possible development of a local algorithm of primary production in the western subarctic North Pacific Ocean. Data were obtained from the line between 39°N, 146°45'E and $42^{\circ}50'$ N, $144^{\circ}50'$ E from April 1990 to July 1991. One optical depth (1/k)can be estimated from the concentration of chlorophyll a (B_c) at the surface depth. Surface B_c can be estimated from B_c+B_p (concentration of pheopigments) in one optical depth. The background concentration of chlorophyll a (B_{o}) , the depth of the subsurface chlorophyll maximum (z_{m}) , and the total biomass above the background (h) which control the Gaussian curve can be determined from the surface B_c . Therefore, once surface B_c is obtained, the vertical profile of B_c is determined. However relative variability in the estimated values from the surface B_c can be high when the standing stock of chlorophyll a is lower than 300 mg Chl. $a \text{ m}^{-2}$. This may suggest that the present model can be applied only to a relatively productive area. The standing crop of chlorophyll pigments in one optical depth, which can be estimated from the ocean color obtained from the satellite, would be useful to determine the standing crop of chlorophyll pigments in the euphotic layer.

1. Introduction

Oceanographic observation from space has been demonstrated as the most effective way to study global changes in not only physical oceanography but also biological oceanography with the Coastal Zone Color Scanner (*e.g.* PLATT *et al.*, 1991). Spectral radiance ratio algorithms have been developed to determine chlorophyll pigments in the ocean (CLARK *et al.*, 1980; GORDON *et al.*, 1983, 1988). The most widely accepted relationship used in satellite chlorophyll pigment retrieval applications takes the form:

$$\log_{10}[B_{\rm c} + B_{\rm p}] = a + b \ \log_{10}[Lu(r1)/Lu(r2)], \tag{1}$$

where B_c and B_p indicate concentrations of chlorophyll *a* and pheopigments, respectively. Lu(r1) and Lu(r2) represent radiances emitted from the water at two wavelengths. Depending on what wavelengths are employed, this relationship differs among ocean regions (MITCHEL, 1992). Information which the satellite can

provide from the space is not limited to the surface layer but also to some depths (GORDON and MCCLUNEY, 1975). The depth integrated information obtained from the satellite is associated with the quantity of particles in water and the extinction coefficient of water (SMITH, 1981). The left term in eq. (1) can be chosen to be either surface concentration or concentration at some depth.

When biomass of chlorophyll pigments at either the surface or in one optical depth is estimated, the vertical distribution of chlorophyll a is required to determine primary production in a water column. Primary production can be estimated from phytoplankton biomass and optical properties at a given depth. A linear relationship between primary production and chlorophyll a concentration is sometimes observed (HAYWARD *et al.*, 1982). Theoretical analyses, however, suggest that the relationship between primary production and chlorophyll a concentration should be nonlinear (BANNISTER, 1979; PLATT, 1986). This nonlinearity is presumably due to differences in optical properties of the waterbody, irradiance, species composition of the phytoplankton, temperature, and nutrient availability (EPPLEY *et al.*, 1985).

The present study aims to determine the spatial and temporal variability in the standing stock of chlorophyll pigments, to determine the association among four parameters which control the vertical distribution of chlorophyll pigments, and to establish an empirical relationship between those in the surface layer (not necessarily exactly at 0 m) which the satellite can determine from space and vertical profiles of chlorophyll a in the euphotic layer in the western subarctic North Pacific Ocean.

2. Materials and Methods

Oceanographic cruises were conducted along a line off east Hokkaido from April 1990 to July 1991 (Fig. 1). Dates of the eight cruises are given in Table 1. During each cruise the surface samples were collected with a bucket at all stations and samples for the vertical profile were taken with 1.7 *l* Niskin bottles at eight depths: 10, 20, 30, 50, 75, 100, 150, and 200 m at the selected stations; usually A2, A7, A11, and A17. Temperature and salinity were determined with either a Neal Brown Model Mark III CTD or Seabird Model Seacat 19 CTD to 1500 m at all stations. Secchi disc readings were taken at all day stations. The Secchi disc reading at stations occupied during the night was interpolated by the eight directional least fitting procedure (GOLDEN SOFTWARE, 1985). The extinction coefficient (*k* in m⁻¹) was calculated with the equation developed by PooL and ATKINSON (1929). Although the vertical profile of chlorophyll pigments is not uniform in the present study, the mean extinction coefficient below the Secchi disc reading is assumed to be similar to that above the Secchi disc reading.

Water samples for the analysis of chlorophyll a and pheopigments were filtered onto a glass fiber filter type GF/F. All filters were stored in a dark container at -20° C. Concentrations of chlorophyll a and phaeopigments were determined on a Turner Designs Model 10 fluorometer by the method described by HOLM-HANSEN *et al.* (1965).



Fig. 1. The Akkeshi oceanographic line off east Hokkaido.

Table 1.Summary of eight cruises conducted along a line off
the east Hokkaido from April 1990 to July 1991.

Cruise No.	Date	Research vessel	
1	April 16-21, 1990	Tankai Maru	
2	May 7–13, 1990	Tankai Maru	
3	June 4–8, 1990	Tankai Maru	
4	October 19-25, 1990	Tankai Maru	
5	January 19–21, 1991	Hokko Maru	
6	April 17–25, 1991	Tankai Maru	
7	May 7-13, 1991	Hokko Maru	
8	July 1–6, 1991	Tankai Maru	

The vertical profile of chlorophyll *a* concentration was fitted to the following equation provided by LEWIS *et al.* (1983):

$$B_z = B_o + \frac{h}{\sigma\sqrt{2\pi}} \exp\left[-\frac{(z-z_m)^2}{2\sigma^2}\right].$$
 (2)

The Gaussian curve is determined by four parameters. B_o is the background concentration of chlorophyll *a* in mg Chl. $a \text{ m}^{-3}$. z_m is the depth of subsurface chlorophyll maximum in meters. Sigma (σ) is the standard deviation in meters. Four sigmas were equal to the thickness of the subsurface chlorophyll *a* maximum at B_o concentration. *h* is the total biomass above the background in mg m⁻². The peak height of the subsurface chlorophyll *a* maximum above the background concentration is $h [\sigma \sqrt{2\pi}]^{-1}$. All four parameters derived from the fitting procedure were calculated at each station. Model II regression analysis (LAWS and ARCHIE, 1981) was used as significant variance in both the dependent and independent variables was present.

3. Results

3.1. Variability in standing crop of phytoplankton and relationship between surface biomass and standing crop of pigment in a water column

Spring bloom was identified in April and May in both years (Fig. 2). However, its areal extent showed a significant difference between years. The maximum concentrations of chlorophyll a in the surface water during the spring bloom were 10 mg Chl. $a m^{-3}$ in 1991 and 7.7 mg Chl. $a m^{-3}$ in 1990, respectively. Surface B_c decreased seaward during the spring bloom. Surface B_c was usually higher than 0.5 mg Chl. $a m^{-3}$ along the coast except in January.

Because phytoplankton tend to be logarithmically distributed in nature (SMITH and BAKER, 1982), variability of chlorophyll values was calculated both from the linear values and the log transformed chlorophyll values (Table 2). The



CHLOROPHYLL a (mg CHLa·m⁻³)

Fig. 2. Spatial and temporal distributions of surface chlorophyll a (B_c) (mg m⁻³) from April 1990 to July 1991.

Table 2. Variability in chlorophyll a biomass at 0 m, that from 0 m to one optical length (0m-1/k m), to the 1% surface irradiance depth (0m-1% m), and to the 0.1% irradiance depth (0m-0.1% m). SD and CV indicate one standard deviation and the percent coefficient of variation, respectively.

	Lin	ear value	es	Log-transformed values				
Depth or range	Mean	SD	CV	Mean	SD	CV	Number of obsevation	
0 m	1.7	2.5	147	1.1	0.98	92	37	
10 m	1.9	3.0	160	1.1	1.1	181	37	
20 m	1.9	2.6	139	1.2	0.96	161	37	
30 m	1.7	2.4	137	1.2	0.86	73	37	
50 m	1.1	1.6	156	0.75	0.69	93	37	
75 m	0.49	1.1	223	0.32	0.50	158	37	
100 m	0.18	0.37	208	0.14	0.23	164	37	
150 m	0.066	0.095	.143	0.062	0.085	137	36	
200 m	0.050	0.062	123	0.049	0.058	119	36	
0m–1/ <i>k</i> m	7.1	8.5	120	4.3	1.4	34	37	
0m–1% m	33.6	41.7	124	20.4	2.7	13	37	
0m–1% m	51.5	60.4	117	31.3	2.6	8.4	37	

mean calculated from log-transformed values was about 60 % of that calculated by linear values at the top three depths. The difference between them decreased with depth and was almost zero at 200 m depth. Coefficient variations, which indicate temporal and spatial variability, calculated with the log-transformed values were smaller than those based on the linear values except at 10 m and 20 m. Biomass of chlorophyll *a* integrated to the one optical depth, the 1%, and 0.1% surface irradiance layer showed that the variability based on the logtransformed values was smaller than those based on the linear values. The variability using the log transformed values in the integrated biomass of chlorophyll *a* decreased with the increase of depth of the water column. This is due to the addition of low variable values to the total integration, and to increase of the mean.

Estimated extinction coefficients are shown in Fig. 3A. They decreased generally seaward except in April. During the spring bloom of phytoplankton the extinction coefficient was generally higher than 0.2 m^{-1} . Low values were obtained in October and January. Radiance emitted from the water which the satellite can detect is thought to be a consequent product of one optical depth (SMITH and BAKER, 1978). The one optical depth ranged from 3m to 10m (Fig. 3B). It was usually deeper than 7 m in January.

Optical depths for 1% and 0.1% surface light were estimated with the estimated extinction coefficient at each station. Average 1% and 0.1% optical depths with one standard deviation were 26 ± 8.8 and 39 ± 13 m, respectively. The maximum 1% optical depth (46 m) was observed at St. A17 in January and July 1991. The minimum 1% optical depth (11 m) was found at St. A2 in May 1991.

The integrated values of chlorophyll a from 0 m to 1% optical depth ranged



Fig. 3. Spatial and temporal distributions of extinction coefficient (m^{-1}) (A) and one optical depth (m) (B) from April 1990 to July 1991.



Fig. 4. Spatial and temporal distributions of standing stock of chlorophyll a in the euphotic layer determined by the 1% light depth from April 1990 to July 1991.

from 5.5 mg m⁻² at St. A17 in October 1990 to 192 mg m⁻² at St. A4 in May 1991 (Fig. 4). Low standing stock of chlorophyll a was found in October and January. The highest standing stock was observed during the spring bloom in 1991.

The matrix of coefficient of regression among the surface chlorophyll pigments, the standing stock of chlorophyll pigments in one optical depth, 1%, and 0.1% surface irradiance layer are shown in Table 3. When the surface chlorophyll pigments were compared with those in three depth ranges, coefficient values for the one optical depth were highest. The percent contribution of

Table 3. Matrix of coefficients correlation between chlorophyll a concentrations at 0m, integrated biomass from 0m to one optical depth, from 0m to 1% optical depth, and from 0m to 0.1% optical depth. The upper right half of A shows the relation for chlorophyll a. The lower left half of A shows the relation for chlorophyll a plus pheopigments. The first row of B shows the relation for the biomass of chlorophyll a plus pheopigments at the surface and standing stock of chlorophyll a in the various depth ranges. The second row of B indicates the relation of chlorophyll a plus pheopigments in the optical depths to standing stock of chlorophyll a in the various depth ranges. All relations are significant at 0.001. n = 33.

	0m (mg m ⁻³)	0m-1/k m (mg m ⁻²)	0m-1% (mg m ⁻²)	0m-1% (mg m ⁻²)	
Α					
0m		0.968	0.920	0.913	
0m - 1/k	m 0.953		0.961	0.942	
0m-1%	0.885	0.948		0.991	
0m-0.1	% 0.879	0.925	0.989		
В					
0m	0.990	0.965	0.898	0.883	
0m-1/k	m 0.931	0.983	0.924	0.895	

pheopigments in total chlorophyll a plus pheopigment concentration ranged from 0 to 60% in the one optical depth. The average percent contribution of pheopigments to the total pigments with one standard deviation was $29\pm18\%$ in the present study. A more significant relationship was observed for the values of chlorophyll a plus pheopigments than for chlorophyll a alone. A significant relationship among the surface values of chlorophyll a plus pheopigments and the standing stock of chlorophyll a in a water column was obtained between the value in the one optical depth and the integrated value for the 1% light depth (Fig. 5).

3.2. Variability in the four parameters derived from a Gaussian curve fitting The Gaussian curve fitting was successfully performed in 30 profiles out of 37. Significant fit was not found in 7 profiles, which were not included in further analysis. No significant correlation was observed among four parameters derived from the Gaussian curve fitting. Although most values of B_0 ranged between 0.05 and 0, variability of B_0 was as high as 208% (Table 4). The next most highly variable parameter was h, of which the variability was 151%. Those high variabilities were caused by some extraordinary high values observed in May 1991 at St. A2 and A4 for B_0 and A2, A4, and A7 for h, respectively (Fig. 6A and B). However, the variabilities of sigma and z_m were 38% and 63%, respectively (Table 4). Sigma values larger than 35 m were observed in the southern half of



Fig. 5. Relationship between chlorophyll a plus pheopigment biomass in the 0m-1/k m layer and chlorophyll a integrated for the euphotic layer, which was determined by the 1% light depth. The regression fit was significant at 0.001.

Table 4. Mean, one standard deviation, and coefficient of variation of four parameters determined by the eq.
(2) obtained in the present study. The number of observation was 30.

	h	sigma	Z _m	B _o	
mean	163	32	23	0.048	
s.d.	245	14	15	0.10	
c.v. (%)	151	45	63	208	

the studied area in October, 1990. In January 1991 sigma values were larger than 35m (Fig. 6C). Values of z_m larger than 25 m were only observed at stations south of 40°N in July 1990 while higher values were observed in the southern half of the studied area from December to July 1991 (Fig. 6D).

Statistical analysis indicated that the variability in the parameters seemed to be not only independent within the parameters but also was not associated with .



Fig. 6. Spatial and temporal distributions of B_o (A), h (B), sigma (C), and z_m (D) from April 1990 to July 1991.

any environmental variables. The present analysis was performed on not only surface temperature and depth of the surface mixed layer, which can be estimated by satellite (YAN *et al.*, 1991), but also salinity and slope of the thermocline, which cannot be determined by satellite. Those mean values in Table 4 produce the average vertical distribution of chlorophyll *a* (Fig. 7) with a nonlinear fitting procedure. Surface B_c estimated from this procedure was 1.6 mg Chl. $a m^{-3}$, which was similar to the mean value of linear surface B_c but not to that of log-transformed values (Table 2). A curve fitted based on the mean four parameters (Table 4) showed the highest chlorophyll *a* values at the observed depths compared to the means based on the linear or log-transformed values (Table 2 and Fig. 7).



Fig. 7. Average profile of chlorophyll a based on the mean values of four parameters in Table 4.

3.3. Relationship between the four parameters and the surface concentration of pigments

Significant relationships were observed between all parameters but sigma and B_c at the surface or in the one optical depth (Table 5). Although a complete curve can be drawn with four parameters, the surface chlorophyll *a* value can be substituted for sigma once the other three parameters, *h*, z_m , and B_o , are estimated at a given station. Differences between the observed B_c and values estimated from the surface value, and values fitted by a Gaussian curve at each depth, were integrated for a given station by the following equations:

Table 5. Matrix of correlation coefficients between the four parameters and chlorophyll a concentration (B_c) at 0 m: $[B_c]_o$, and in one attenuation length : $[B_c]_{0-1/k}$. Y intercept and slope of the regression line are also included. * indicaties significant level higher than 0.05.

Chlorophyll <i>a</i> concentration	h	sigma	۲m	B _o
[<i>B</i> ,]o	0.9019*	0.0007	-0.4439*	0.7431*
Y-intercept	.11	-	28	-0.0030
Slope	90	-	-2.6	0.030
$[B_{\alpha}]_{\alpha,\mu}$	0.9132*	0.0167	-0.4361*	0.7081*
Y-intercept	-30	-	29	-0.013
Slope	28	-	-0.79	0.0087

$$D_{\rm e} = \sum_{i=1}^{n} \left(\frac{[B_{\rm c}]_{\rm est} - [B_{\rm c}]_{\rm obs}}{[B_{\rm c}]_{\rm obs}} \right)_{i}^{2}, \tag{3}$$

and

$$D_{\rm f} = \sum_{i=1}^{n} \left(\frac{[B_{\rm c}]_{\rm fit} - [B_{\rm c}]_{\rm obs}}{[B_{\rm c}]_{\rm obs}} \right)_{i}^{2}, \tag{4}$$

where $[B_c]_{est}$, $[B_c]_{fit}$, and $[B_c]_{obs}$ were chlorophyll *a* concentrations at the *i*th depth estimated from the surface chlorophyll *a* concentration, determined by the Gaussian curve fitting, and observed, respectively.

Ratio (R) was used to describe a relative difference:

$$R = D_{\rm e} \ [D_{\rm f}]^{-1}.$$
 (5)

Ratios (*R*) were plotted against either the surface concentration (Fig. 8A) or the integrated standing stock of chlorophyll *a* (Fig. 8B). The *R* values at chlorophyll *a* concentration lower than 2 mg m⁻³ were highly variable and indicated better fit by the procedure with surface values than by the Gaussian curve fitting at eight stations. The *R* values at chlorophyll *a* concentration higher than 2 mg m⁻³ indicated relatively good fit with the Gaussian curve. A similar distribution of the *R* values was obtained for the integrated standing stock of chlorophyll *a*. The distribution of the *R* values was skewed toward low standing stock of chlorophyll *a*. This may suggest that there is relatively less difference between the two fitting procedures at higher standing stock of chlorophyll *a* than 300 mg m⁻².

4. Discussion

It is imperative to understand the vertical distribution of chlorophyll a to estimate primary production in a water column (KIRK, 1983). Vertical profiles of chlorophyll a often have a subsurface maximum (CULLEN, 1982) even in the



Fig. 8. Relation between R values and surface chlorophyll a concentration (A) and the integrated chlorophyll a value from 0 m to 200 m (B). See the text for details.

western subarctic Pacific (TAGUCHI *et al.*, 1992). Such vertical profiles of chlorophyll *a* are well described by a Gaussian curve (PLATT *et al.*, 1988). More than 85% of variability in a vertical distribution of chlorophyll *a* are successfully expressed by a Gaussian curve in the present study. However, dependence of the parameters which control the Gaussian curve on the surface B_c has not been demonstrated.

Once B_c at the surface is observed, all parameters except sigma can be estimated in the western subarctic Pacific as indicated in the present study. Surface B_c with three parameters mentioned above (Table 5) can provide a vertical distribution of chlorophyll *a*. Comparison of vertical profiles of chlorophyll *a* based upon B_c at the surface depth and three parameters, *h*, z_m , and B_o , derived from each surface B_c indicates a limitation of the present procedure to an ocean area with higher standing stock of chlorophyll *a* than 300 mg Chl. *a* m^{-2} (Fig. 8B). The derived profiles are not wholly unrealistic. However, caution must be used when the standing stock of chlorophyll *a* is lower than 300 mg Chl. $a m^{-2}$ since the relative variability between values estimated from fitting a Gaussian curve to the observed data and estimated from the surface B_c with derived parameters of h, z_m and B_o can be 300%.

Satellites can detect pigment concentrations in one optical depth (SMITH and BAKER, 1978). When k is related to the surface B_c , the 1/k can be estimated from the surface B_c . A significant relationship has been obtained between them with the following form:

$$k=0.0245+0.163 \ [B_{\rm c}]_{0m}, \ r=0.69 \ n=33$$
 (6)

in the present study. The surface B_c can be calculated from the satellite signal when the chlorophyll information obtained by the satellite represents the standing stock of chlorophyll a plus pheopigments in one optical depth. If the satellite cannot distinguish chlorophyll a and pheopigments, it is necessary to establish a relation between B_c and B_c plus B_p . Recent evidence suggests that fluorometric determined pheopigments might be overestimated at some depth due to the occurrence of chlorophyll b based on high performance liquid chloromatography (GIESKES and KRAAY, 1986). Both chlorophyll a and pheopigments, however, are considered in the present study because of the lower effect of chlorophyll b on fluorometric pheopigment determination in the surface layer in the present study. Significant relationships are obtained between them at the surface or the one optical depth (Table 5). Significant relationships are also obtained between the concentrations of chlorophyll a and pheopigments at the surface or the one optical depth and the standing crop of chlorophyll a in a water column. Among those significant relationships, one between concentrations of chlorophyll a plus pheopigments in the one optical depth ($[B_c + B_p]_{1/k}$) and the standing stock of chlorophyll a $([B_c]_{0m-1\%})$ with the following form,

$$\log [B_{\rm c}]_{0m-1\%} = 0.574 + 0.986 \log [B_{\rm c} + B_{\rm p}]_{1/k}, \tag{7}$$

would be most useful to estimate standing crop of chlorophyll a in a water column from satellite information in the western subarctic Pacific.

5. Conclusions

Vertical distribution of chlorophyll a in the western subarctic Pacific can be estimated from B_c at the surface, which makes it possible to calculate the three parameters of the Gaussian curve. However, caution must be used when the standing stock of chlorophyll a is lower than 300 mg Chl. $a \text{ m}^{-2}$, in which case the relative variability in the estimated chlorophyll a profiles can be high. This may restrict the application of the present model to a relatively productive ocean. Another model should be developed for ocean areas with low biomass. Surface B_c is accurately estimated from the standing stock of chlorophyll a plus pheopigments in one optical depth. The latter is accurately provided by the satellite. In a stratified water column, the surface population of phytoplankton adapts to the light condition while the phytoplankton population in the deep layers adapts to the shade condition (FALKOWSKI and LAROCHE, 1991). This kind of situation may require a spectral model including different parameters of photosynthetic characteristics to estimate the primary production in a water column (SATHYENDRANATH *et al.*, 1989; MOREL, 1991). Knowledge of vertical distribution of chlorophyll amakes it possible to incorporate the physiological characteristics of phytoplankton photosynthesis into the calculation of primary production in a water column.

Acknowledgments

Laboratory assistance provided by T. KONUKI and E. HATANAKA was greatly appreciated. We acknowledge the captains and crews of RV TANKAI MARU and HOKKO MARU. Temperature and salinity data were kindly provided by T. KONO and Y. KAWASAKI. We are indebted to T. PLATT for fitting a Gaussian curve to the data. We are indebted to two unknown reviewers for constructive comments on an earlier version. This research was partially supported by various grants from the Fisheries Agency and the Science and Technology Agency. Contribution B-536 from the Hokkaido National Fisheries Research Institute.

References

- BANNISTER, T. T. (1979): Quantitative description of steady state, nutrient-saturated algal growth, including adaptation. Limnol. Oceanogr., 24, 79–96.
- CLARK, D. K., BAKER, E. T. and STRONG, A. E. (1980): Upwelled spectral radiance distribution in relation to particulate matter in sea water. Boundary-Layer Meteorol., 18, 287-291.
- CULLEN, J. J. (1982): The deep chlorophyll maximum: Comparing vertical profiles of chlorophyll a. Can. J. Fish. Aquat. Sci., 39, 791-803.
- EPPLEY, R. W., STEWART, E. M., ABOTT, M. R. and HEYMAN, H. (1985): Estimating ocean primary production from satellite chlorophyll: Introduction and regional statistics for the Southern California Bight. J. Plankt. Res., 7, 57-70.
- FALKOWSKI, P. G. and LAROCHE, J. (1991): Acclimation to spectral irradiance in algae. J. Phycol., 27, 8-15.
- GIESKES, W. W. and KRAAY, G. W. (1986): Floristic and physiological differences between the shallow and the deep nanophytoplankton community in the euphotic zone of the open tropical Atlantic revealed by HPLC analysis of pigments. Mar. Biol., 91, 567-576.
- GOLDEN SOFTWARE (1985): Surfer. Colorado, 291 p.
- GORDON, H. R. and MCCLUNEY, W. R. (1975): Estimation of the depth of sunlight penetration in the sea for remote sensing. Appl. Opt., 14, 413-416.
- GORDON, H. R., CLARK, D. K., BROWN, J. W., BROWN, O. B., EVANS, R. H. and BROENKOW, W. W. (1983): Phytoplankton pigment concentrations in the Middle Atlantic Bight: Comparison of ship determinations and CZCS estimates. Appl. Opt., 22, 20-36.
- GORDON, H. R., BROWN, O. B., EVANS, R. H., BROWN, J. W., SMITH, R. C., BAKER, K. S. and CLARK, D. K. (1988): A semianalytical radiance model of ocean color. J. Geophys. Res., 93, 10909-10924.
- HAYWARD, T. L. and VENRICK, E. L. (1982): Relation between surface chlorophyll, integrated chlorophyll and integrated primary production. Mar. Biol., 69, 247-252.
- HOLM-HANSEN, O., LORENZEN, C. J., HOLMES, R. N. and STRICKLAND, J. D. H. (1965): Fluorometric determination of chlorophyll. J. Cons. Perm. Int. Explor. Mer, 30, 3-15.
- KIRK, J. T. O. (1983): Light and photosynthesis in aquatic ecosystems. Cambridge, Cambridge University Press, 401 p.

- LAWS, E. A. and ARCHIE, J. W. (1981): Appropriate use of regression analysis in marine biology. Mar. Biol., 65, 13-16.
- LEWIS, M. R., CULLEN, J. J. and PLATT, T. (1983): Phytoplankton and thermal structure in the upper ocean: Consequences of nonuniformity in chlorophyll profile. J. Geophys. Res., 88, 2565-2570.
- MITCHEL, B. G. (1992): Predictive-bio-optical relationships for polar oceans and marginal ice zones. J. Mar. Syst., 3, 91-105.
- MOREL, A. (1991): Light and marine photosynthesis: A spectral model with geochemical and climatological implications. Prog. Oceanogr., 26, 263–276.
- 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.
- PLATT, T., CAVERHILL, C. and SATHYENDRANATH, S. (1991): Basin scale estimates of ocean primary production by remote sensing: The North Atlantic. J. Geophys. Res., 96, 15147–15159.
- PLATT, T., SATHYENDRANATH, S., CAVERHILL, C. M. and LEWIS, M. (1988): Ocean primary production and available light: Further algorithms for remote sensing. Deep-Sea Res., 35, 855–879.
- POOLE, H. H. and ATKINSON, W. R. G. (1929): Photoelectric measurements of submarine illumination through the year. J. Mar. Biol. Assoc. U. K., 16, 297-324.
- SATHYENDRANATH, S., PLATT, T., CAVERHILL, C. M., WARNOCK, R. E. and LEWIS, M. R. (1989): Remote sensing of oceanic primary production: Computations using a spectral model. Deep-Sea Res., 36, 431-453.
- SMITH, R. C. (1981): Remote sensing and depth distribution of ocean chlorophyll. Mar. Ecol. Prog. Ser., 5, 359–361.
- SMITH, R. C. and BAKER, K. S. (1978): The bio-optical state of ocean waters and remote sensing. Limnol. Oceanogr., 23, 247-259.
- SMITH, R. C. and BAKER, K. S. (1982): Oceanic chlorophyll concentrations as determined by satellite (Nimbus-7 coastal zone color scanner). Mar. Biol., 66, 269–279.
- TAGUCHI, S., SAITO, H., KASAI, H., KONO, T. and KAWASAKI, Y. (1992): Hydrography and spatial variability in the size distribution of phytoplankton along the Kurile Islands in the western subarctic Pacific Ocean. Fish. Oceanogr., 1, 227-237.
- YAN, X.-H., OKUBO, A., SCHUBEL, J. R. and PRITCHARD, D. W. (1991): An analytical model for remote sensing determination of the mixed layer depth. Deep-Sea Res., 38, 267-287.

(Received April 19, 1993; Revised manuscript received September 21, 1993)