Photosynthetic characteristics of phytoplankton off Adélie Land, Antarctica, during the austral summer

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Abstract: The photosynthesis-irradiance characteristics (P-E curves) and quantum yields of natural phytoplankton were investigated in the Southern Ocean off Adélie Land, Antarctica, during the austral summer. Data were acquired at eight stations during a cruise of T/V Umitaka-Maru III. The photosynthetic P-E curves showed low light adaptation of phytoplankton. Mean value ($\pm$standard deviation) of the P-E curve parameters, α^*, and I_k, were 0.014 ($\pm$0.013) mgC (mg chl.a)$^{-1}$ h^{-1} (μmol photons m^{-2} s^{-1})$^{-1}$ and 76 ($\pm$55) μmol photons m^{-2} s^{-1}, respectively. Although phytoplankton were adapted to low irradiance, the phytoplankton in the SCM were not fully adapted to the low irradiance prevailing at those depths. P^*_{max} in the studied region was low (mean of 0.66 ($\pm$0.37) mgC (mg chl.a)$^{-1}$ h^{-1}) and generally lower than the previously reported values in waters near the Antarctic Peninsula. The maximum quantum yield varied widely, ranging from 0.001 to 0.038 mol C (mol photons absorbed)$^{-1}$ at the surface and from 0.007 to 0.092 mol C (mol photons absorbed)$^{-1}$ near the bottom of the euphotic zone. These values were within the range of published data. Comparison of photosynthetic parameters with historical data indicated that primary productivity from remotely sensed data for the whole of the Southern Ocean, based on these field estimates of photosynthetic parameters, has been overestimated.

key words: photosynthesis-irradiance curve, quantum yield, phytoplankton, Adélie Land, Antarctica

Introduction

The Southern Ocean covers 20% of the surface of the World Ocean and plays an important role as buffer for the atmospheric greenhouse gas CO_2. Atmospheric CO_2 is absorbed into seawater at the air-sea interface, and fixed as photosynthetic carbon by phytoplankton using light energy. Marine phytoplankton production has been estimated over several decades. Values in the Southern Ocean were once believed to be very high because of the high biomass of krill (Holm-Hansen and Mitchell, 1991). Measurements in the 1970's showed, however, that the rate of primary production in the Southern Ocean is not that high despite the generally high nutrient concentration (*e.g.* El-Sayed, 1970; Holm-Hansen *et al.*, 1977), and studies in the 1980's evidenced high spatial and temporal variability of primary production there (*e.g.* El-Sayed and Weber,

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1982; Gordon, 1988).

Several factors have been suggested that might control and reduce primary productivity in the Southern Ocean, *i.e.* temperature (Neori and Holm-Hansen, 1982), irradiance (Mitchell *et al.*, 1991), decrease of phytoplankton standing stocks by grazing of zooplankton (Smetacek *et al.*, 1990), iron (Martin *et al.*, 1990), vertical mixing of the water column (Mitchell and Holm-Hansen, 1991), and their interrelationships. Among these factors, the response of primary productivity to irradiance, characterized by the photosynthetic characteristics (photosynthesis-irradiance curve) and the quantum yield of phytoplankton, are critical to model and compute primary production from remotely sensed data.   Several primary production models (*e.g.* Longhurst *et al.*, 1995) are using the field estimates of photosynthetic parameters.   Thus, these parameters observed at sea directly affect the accuracy of the models.

Values for the photosynthetic characteristics have been reported for a limited region in the Southern Ocean, *i.e.* the Antarctic Peninsula region, showing low light saturation (*e.g.* Figueiras *et al.*, 1998).   To better parameterize and understand the process of primary production in the Southern Ocean, and use remotely sensed information, better knowledge of the photosynthetic characteristics are needed for this whole ocean, especially the Eastern Indian Ocean sector about which we know very little.

During the 1996 cruise of the Umitaka-Maru III, Tokyo University of Fisheries , we carried out a series of measurements to determine the photosynthetic characteristics of phytoplankton in the water off Adélie Land, Antarctica.   The general features of the horizontal distribution of primary productivity in the studied area have already been discussed in relation to the upper water mass structure (Chiba *et al.*, 1999).   The present paper focuses on the photosynthetic parameters and quantum yield during the austral summer.

Materials and methods

Field observation and water sampling

The study was conducted off Adélie Land, Antarctica, from 20 January to 3 February 1996, during a cruise of the T/V Umitaka-Maru III (Fig. 1).   Water temperature and salinity were measured with a CTD (ICTD, FSI): OCTOPUS system (OCTO-Parameter Underwater Sensor; Ishimaru *et al.*, 1984) at 27 stations.   The salinity sensor was calibrated with a salinometer.   Primary productivity of phytoplankton was determined at 8 stations.   The ice edge was defined as 15% ice concentration, based on SSM/I images (Cavalieri *et al.*, 1997).   Seawater samples for primary productivity were collected using Van Dorn bottles near the sea surface and near the bottom of the euphotic zone (irradiance=1–5% of that at sea surface). However the irradiance at 50 m at Stn. C05 was 21% of that at the sea surface. Additional water samples from several depths were collected using a Rosette multi water sampler equipped with an OCTOPUS system, for determination of chlorophyll *a* concentration.

Chlorophyll *a* concentration

Between 200 and 500 ml of water were filtered onto glass fiber filters (Whatman
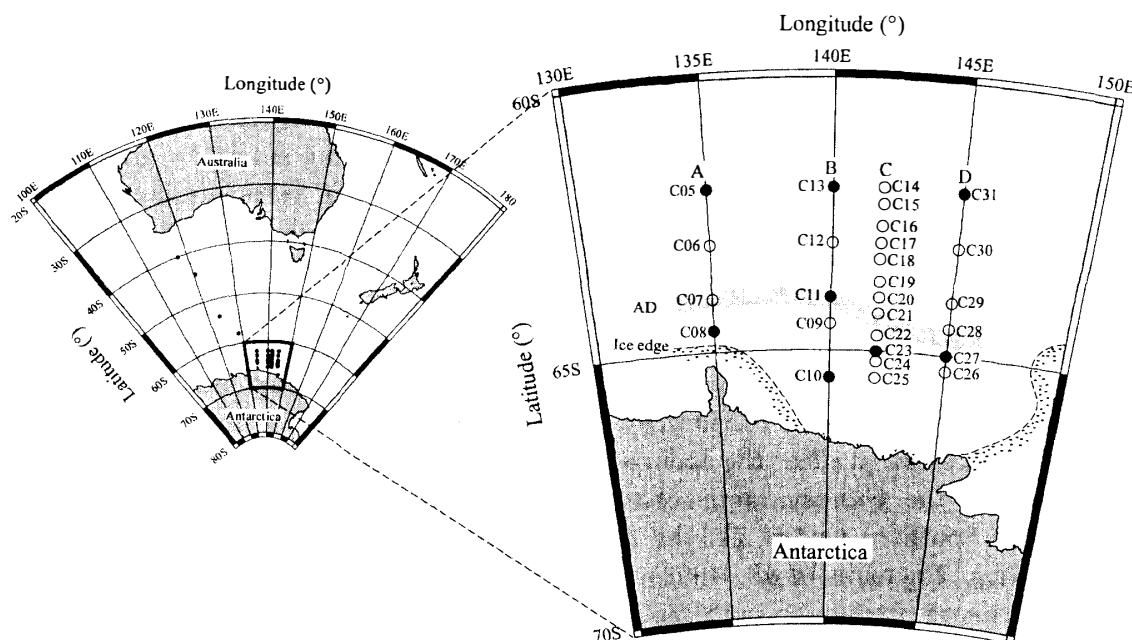
Fig. 1. Maps showing sampling stations. Solid circles: stations where the photosynthetic rate was
measured. Shaded band and dashed lines: Antarctic Divergence (AD) and ice edge, respectively.

GF/F, ϕ 25 mm) for determination of phytoplankton chlorophyll a (chl.a) and pheopigments.   The filters were immediately dropped in N, N-Dimethylformamide (DMF) and the pigments extracted in the dark (Suzuki and Ishimaru, 1990).   Concentrations of chl.a were determined fluorometrically with a Turner Designs 10-005R fluorometer within a few days of extraction (Parsons et al., 1984).   The fluorometer was calibrated against spectrophotometric values using pure chl.a (SIGMA) and the concentration of the standard solution was calculated using the value of chlorophyll a specific absorption coefficient in DMF (Porra et al., 1989).

Photosynthetically available radiation and euphotic zone

Photosynthetically available radiation (PAR) was measured with an LI-190SB air quantum sensor and an LI-192SB underwater quantum sensor (LI. COR Inc.), and recorded with an LI-1000 (LI. COR Inc.) quantum meter.   Underwater PAR was measured at depths between 1 m and 20 or 30 m.   The depth of the euphotic zone (Z_{eu}) was defined as the depth of 1% of sea surface PAR; it was calculated by extrapolating logarithmically the value of underwater PAR.

Photosynthetic activity

The photosynthetic activity of phytoplankton was determined using the stable ^{13}C isotope method (Hama et al., 1983).   Water samples were transferred into 1000 ml clear polycarbonate bottles.   After adding NaH^{13}CO$_3$ (approximately 10% of the total carbonate, ISOTEC Inc.), the samples from the two sampling depths were incubated during 4 hours in a water bath with controlled temperature corresponding to that at the sea surface, under natural light (full sunlight, 46, 21, 11, 6% and, dark).   After

incubation, the water samples were filtered through glass fiber filters (Whatman GF/F, ϕ 47 mm, precombusted at 450°C for 4 hours). The isotope ratios of ^{12}C and ^{13}C were determined by infrared absorption spectrometry (Satoh et al., 1985) with a ^{13}C analyzer (EX-130, JASCO). The photosynthetic activity was calculated using the equation of Hama et al. (1983), and the rate at each depth was calculated on the basis of the observed photosynthesis-irradiance (P-E) curve fit to the model of Eilers and Peeters (1988) with a nonlinear curve-fitting minimization method. The equation takes the form:

$$P^* = I/(aI^2 + bI + c),\qquad(1)$$

where P^* is photosynthetic rate, I is irradiance, and a, b, and c are the fitted parameters. Photosynthetic characteristics were calculated as follows: initial slope $(\alpha^*) = 1/c$, maximum photosynthetic rate $(P^*_{max}) = [b + 2(ac)^{0.5}]^{-1}$, and intensity of onset of light saturation $(I_k) = P^*_{max}/\alpha^*$. The irradiance, I, was the mean value to which the sample was exposed during the incubation period (Table 1).

Absorption coefficient

The absorption coefficient of particles was determined using the quantitative filter technique (Mitchell and Kiefer, 1984). The optical density, $OD(\lambda)$ between 400 and 750 nm was measured with a spectrophotometer (UV365, Shimadzu) equipped with an integrating sphere. The absorption coefficient was calculated from $OD(\lambda)$ as described by Mitchell (1990). The absorption coefficient of phytoplankton, $a_{ph}(\lambda)$, was determined by the methanol extraction method of Kishino et al. (1985). The chl.a specific absorption coefficient, $a^*_{ph}(\lambda)$, was derived by dividing $a_{ph}(\lambda)$ by the chl.a concentration; its units are m^2 (mg chl.$a)^{-1}$.

Maximum quantum yield

The maximum quantum yield, ϕ_m (mol C (mol photons)$^{-1}$), was computed as follows:

$$\phi_m = 0.02315 \frac{\alpha^*}{\bar{a}^*_{ph}},\qquad(2)$$

where the constant (0.02315) converts grams to moles and hours to seconds. $\bar{a}^*_{ph}$ is the spectrally averaged chl.a specific absorption coefficient (m^2 (mg chl.$a)^{-1}$):

$$\bar{a}^*_{ph} = \frac{\int_{400}^{700} a^*_{ph}(\lambda) \cdot I(\lambda) \cdot d\lambda}{\int_{400}^{700} I(\lambda) \cdot d\lambda},\qquad(3)$$

where $I(\lambda)$ is spectral irradiance at the sea surface measured with a spectroradiometer MER-2020A (Biospherical Instrument Inc.).

Results and discussion

Hydrographic structure, light penetration and chlorophyll a distribution

The vertical distributions of isotherms and isohalines in the 0–200 m layer along four transects (A, B, C and D in Fig. 1) are shown in Figs. 2 and 3, respectively. Although it is not clear in the upper water mass structure between 0 and 200 m, Chiba *et al.* (1999) showed in the structure between 0 and 4000 m that there was upwelling of warmer ($>1.0°C$) and higher salinity (>34.5 PSU) water at around 64.0–64.5°S, that formed the Antarctic Divergence (AD). The water column was well stratified between 30 and 125 m, where a mass of cold water (dichothermal layer) existed that vertically separated the water column. South of the AD, there was indication of a sinking water mass, which may be a major source of Antarctic Bottom Water (Chiba *et al.*, 1999).
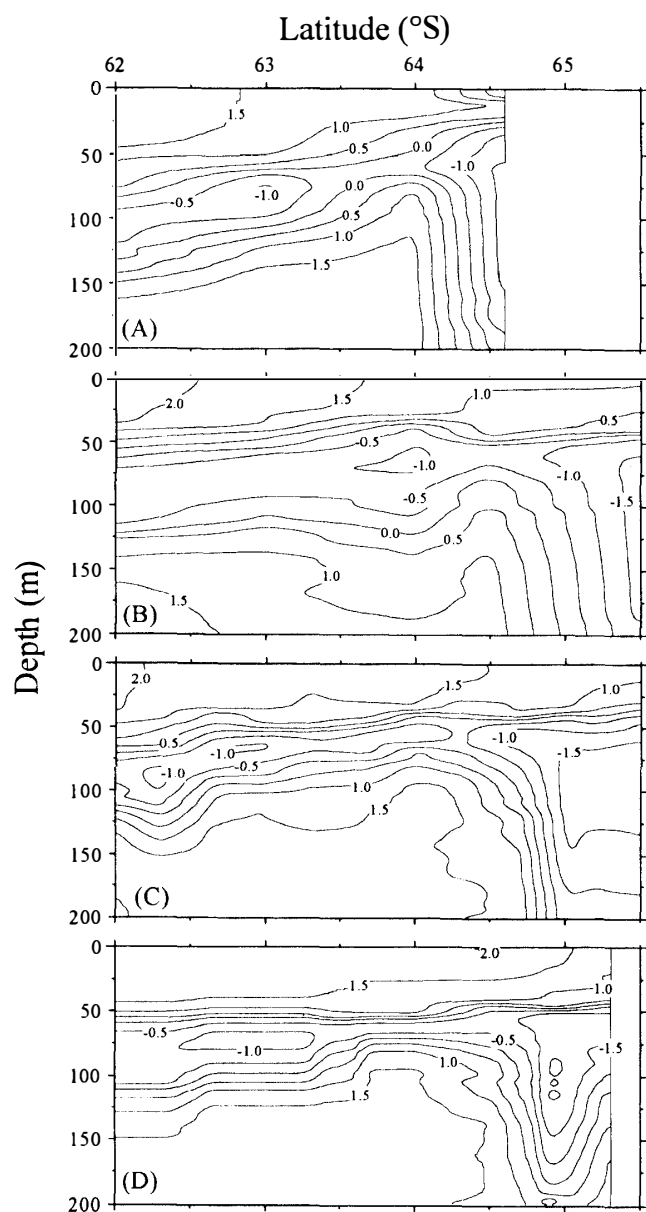

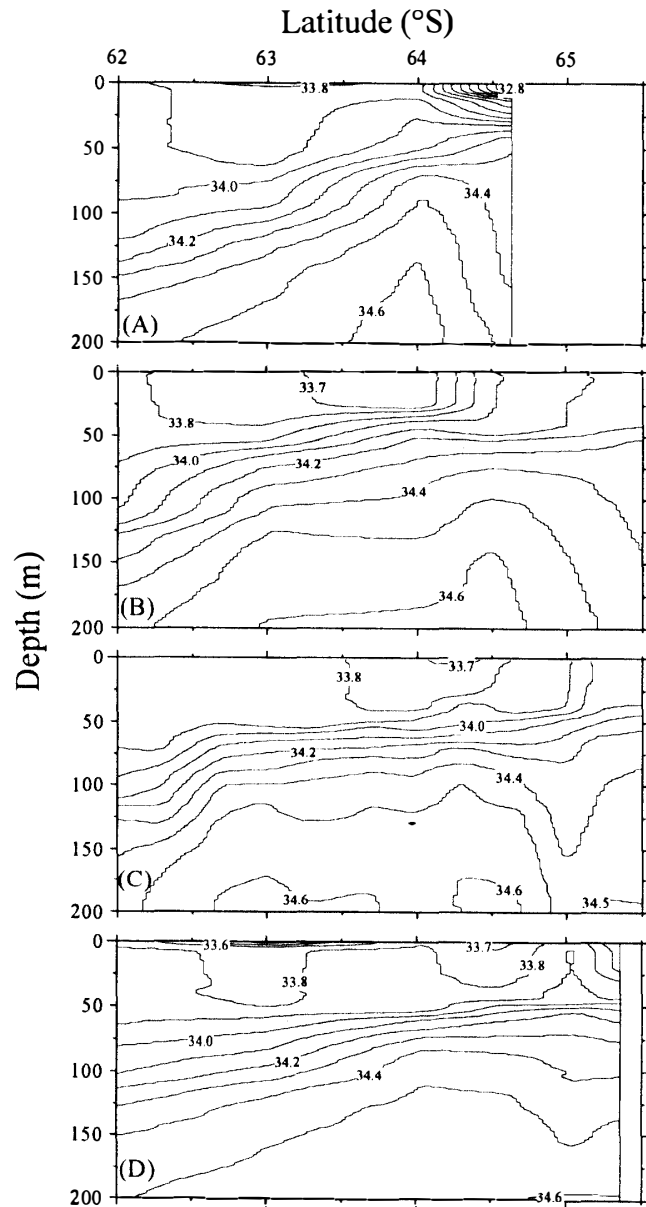Fig. 2. Vertical distribution of isotherms (°C) along transects A, B, C and D.

Fig. 3. Vertical distribution of isohalines (PSU) along transects A, B, C and D.

In the upper 50 m, warm ($> 1.5°C$) and relatively high salinity (> 33.8 PSU) water extended from the northeast to southwest of the studied region.

The vertical distribution of chlorophyll a isopleths is shown in Fig. 4. The concentrations varied from 0.03 to 1.92 mg m^{-3}. The highest concentrations in surface waters were observed close to the AD on each transect, and near the ice edge on transect A. There was a south-north gradient with the boundary at the AD, simultaneously with an east-west gradient corresponding to that of water masses (Chiba et al., 1999). The area was also characterized by a distinct subsurface chl.a maximum (SCM). The depth of the SCM, the mixed layer depth (MLD) and euphotic zone depth (Z_{eu}) are shown in Fig. 5. In the present study, the depth and the dispersion of the SCM were determined from the Gaussian Curve fit of Lewis et al. (1983) and Platt et al. (1988) as modified by Matsumura and Shiomoto (1993), and the MLD was defined as the upper
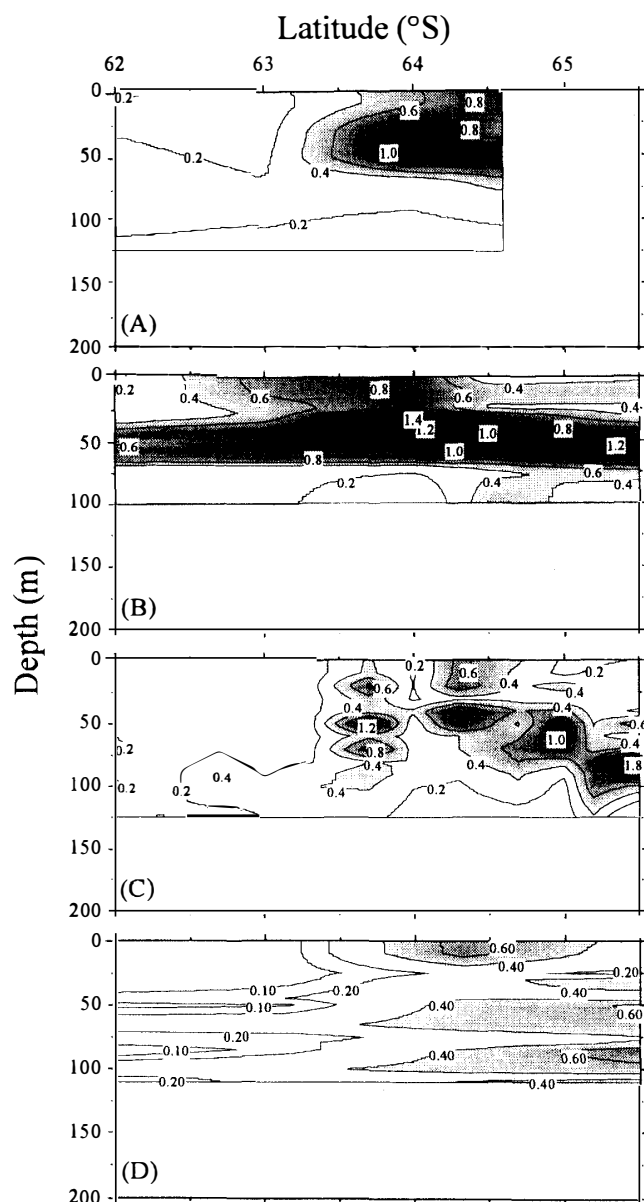
Latitude (°S)

Fig. 4.   Vertical distribution of chl.a con-
centration isopleths (mg m^{-3}) along
transects A, B, C and D. Concent-
rations > 0.4 mg m^{-3} are shaded.
The square shows the sampling
depth.

depth where the temperature is 1.0°C less than that at 10 m (Rao *et al.*, 1989).   The
peak depth of the SCM ranged from 35 to 127 m, except at Stn. 29 (5 m).   In most
cases, the depth of the SCM coincided with the depth of the dichothermal water, as
already reported by Yamaguchi *et al.* (1985).   Furthermore, the SCM corresponded to
low irradiance, as observed by El-Sayed (1988) and Holm-Hansen *et al.* (1994).
Although relatively high biomass of phytoplankton in the SCM may make efficient use
of input resources such as nutrients and iron from deep water, irradiance at the SCM
depth was only between 1 and 12% of the incident irradiance.   Therefore,
phytoplankton in the SCM could not take advantage of location in the deeper water
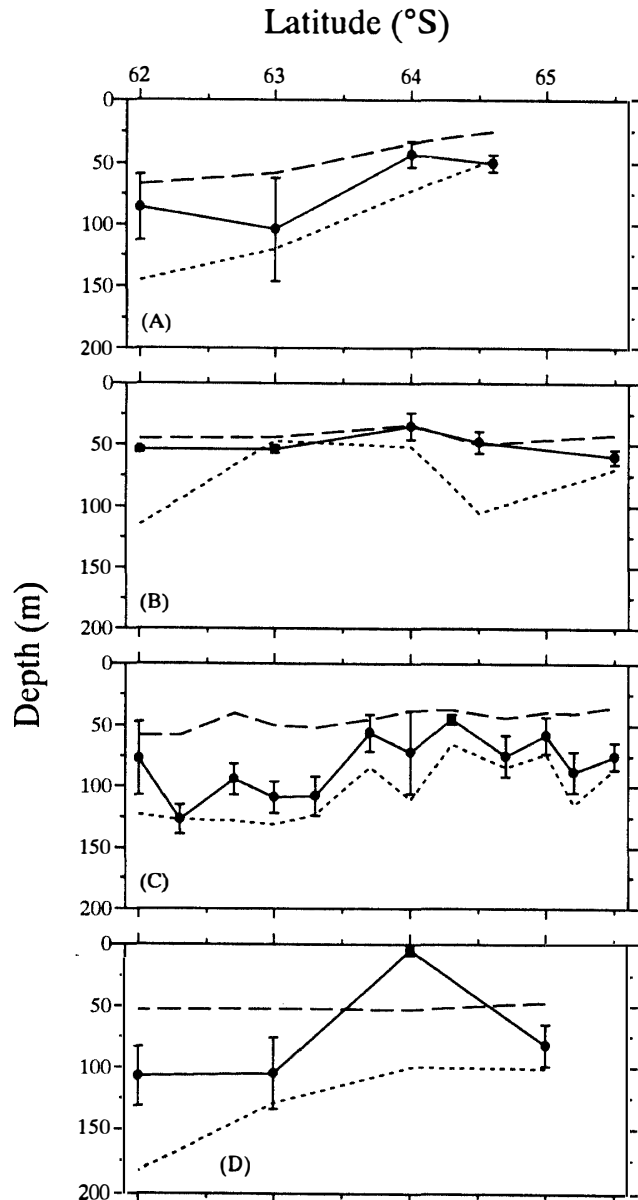without adaptation to the low irradiance.

Fig. 5. Positions of the peak depth of the subsurface chl.a maximum (SCM; solid circle), mixed layer depth (MLD; long dashed line) and euphotic zone depth (Z_{eu}; dashed line). The error bar on the SCM peak shows the dispersion of the SCM ($\pm$standard deviation).

Photosynthetic parameters

The photosynthesis–irradiance curves (P-E curves) at each station and their parameters are shown in Fig. 6 and Table 1, respectively. The initial slope (α^*) was generally high, whereas the maximum photosynthetic rate (P^*_{max}) and the onset of light saturation (I_k) were generally low, the mean values ($\pm$standard deviation) of α^*, P^*_{max} and I_k being 0.014 ($\pm$0.013) mg C (mg chl.a)$^{-1}$ h^{-1} (μmol photons m^{-2} s^{-1})$^{-1}$, 0.66 ($\pm$ 0.37) mgC (mg chl.a)$^{-1}$ h^{-1} and 76 ($\pm$55) μmol photons m^{-2} s^{-1}, respectively. The relatively high values of α^* and low values of I_k indicate that phytoplankton were adapted to low irradiance. The higher values of α^* (0.019 mgC (mg chl.a)$^{-1}$ h^{-1} (μmol photons m^{-2} s^{-1})$^{-1}$) and lower values of I_k at depth relative to the surface suggest that the phytoplankton in the SCM had high productivity. The irradiance intensity in
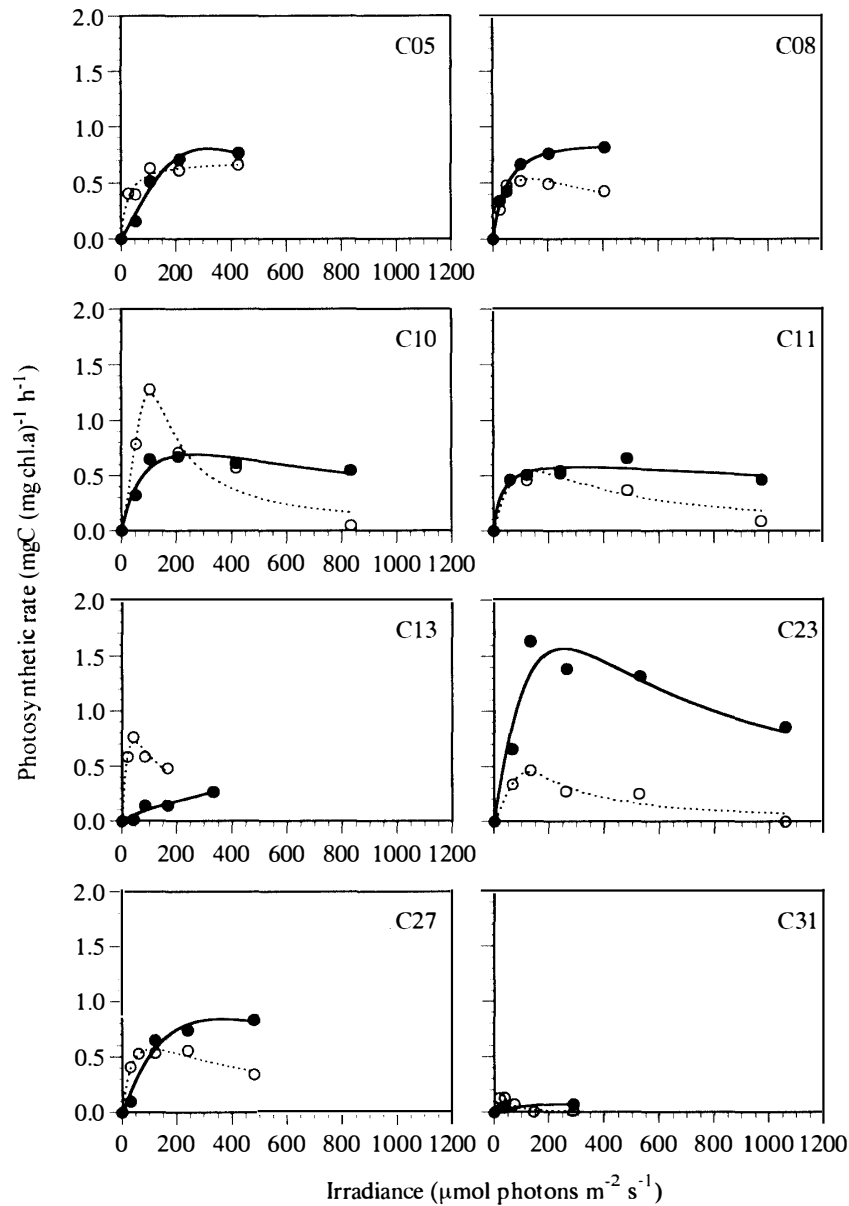
Fig. 6. P-E curves at each station. Solid circles and open circles show the data at the sea surface and near the bottom of the euphotic zone, respectively.

the SCM, computed using the average value of incident light during the cruise (332μmol photons m^{-2} s^{-1}) was, however, lower than I_k. Thus, the phytoplankton in the SCM were not fully adapted to the low irradiance prevailing at those depths.

The highest P^*_{max} values were observed at the sea surface of Stn. C23, near the AD (1.57 mgC (mg chl.a)$^{-1}$ h^{-1}), and at 65 m of Stn. C10, the southernmost station (1.24 mgC (mg chl.a)$^{-1}$ h^{-1}). The lowest P^*_{max} values were observed at Stn. C31, at the surface (0.07) and at 145 m (0.16 mgC (mg chl.a)$^{-1}$ h^{-1}). Comiso et al. (1990) showed enhanced phytoplankton standing stocks associated with ice retreat, from the CZCS (Coastal Zone Color Scanner) satellite imagery. We also observed the highest

Table 1. Photosynthetic characteristics of the P-E curves and maximum quantum yield.

Station	Depth (m)	I ($\pm$S.D.) [a]		α^* [b]	P^*_{max} [c]	I_k [d]	ϕ^m [e]
Sea surface							
C05	0	426.9	(176.5)	0.004	0.80	193	0.007
C08	0	406.3	(75.4)	0.017	0.82	47	0.031
C10	0	832.2	(162.9)	0.011	0.69	63	0.019
C11	0	974.9	(145.8)	0.020	0.58	29	0.038
C13	0	332.0	(72.5)	0.002	0.27	176	0.003
C23	0	1058.1	(138.0)	0.016	1.57	98	0.030
C27	0	478.5	(133.2)	0.007	0.84	125	0.012
C31	0	286.9	(54.8)	0.001	0.07	96	0.001
	Mean	599.5		0.010	0.71	103	0.018
	S.D.	306.2		0.007	0.45	59	0.014
Near the bottom of the euphotic zone (except C05)							
C05	50	426.9	(176.5)	0.029	0.68	23	0.043
C08	50	406.3	(75.4)	0.018	0.54	30	0.032
C10	65	832.2	(162.9)	0.011	1.24	110	0.016
C11	45	974.9	(145.8)	0.010	0.54	56	0.025
C13	75	332.0	(72.5)	0.053	0.72	14	0.092
C23	70	1058.1	(138.0)	0.005	0.45	93	0.009
C27	85	478.5	(133.2)	0.025	0.57	23	0.048
C31	145	286.9	(54.8)	0.004	0.16	41	0.007
	Mean	599.5		0.019	0.61	49	0.034
	S.D.	306.2		0.016	0.31	35	0.028
	Mean			0.014	0.66	76	0.026
	S.D.			0.013	0.37	55	0.023

[a] mean irradiance to which the sample was exposed during incubation period (μmol photons m^{-2} s^{-1})

[b] initial slope (mgC (mg chl.a)$^{-1}$ h^{-1} (μmol photons m^{-2} s^{-1})$^{-1}$)

[c] maximum photosynthetic rate (mgC (mg chl.a)$^{-1}$ h^{-1})

[d] intensity at the onset of light saturation (μmol photons m^{-2} s^{-1})

[e] maximum quantum yield (mol C (mol photons absorbed)$^{-1}$)

surface chl.a concentration near the ice edge (Stn. C08), together with evidence of reduced surface water salinities ($<$33.8) indicating sea-ice melting. However, the photosynthetic rate of phytoplankton was not high there.

Chiba et $al.$ (1999) showed an east-west gradient in the horizontal distributions of chl.a concentration and dominant phytoplankton taxa, that corresponded to a water mass gradient. The photosynthetic characteristics of phytoplankton are related not only to irradiance, temperature and nutrient conditions, but also to taxonomic factors (Platt et $al.$, 1983). In the present study, only α^* at the sea surface showed a significant difference ($p = 0.0093$, t-test) between north and south of the AD; α^* values were lower north than south of the AD. At the surface, warm ($>1.5°C$) and relatively high

Table 2. Historical photosynthesis-irradiance curve parameters in the Southern Ocean.

Source	Date	Area	α^*	P^*_{max}	I_k
Jacques (1983)	Mar. 1977/1980	Indian Ocean Sector (South of the Antarctic Convergence, West of Kerguélen Is.)	0.005-0.034	0.5-5.2	13.8-46.0
		Indian Ocean Sector (Continental shelf near Kerguélen Is.)	0.017-0.023	1.0-2.0	46.0-119.6
Yamaguchi et al. (1985)	Jan./Feb. 1984	Off Adélie Land	–	1.01, 0.73	–
Sakshaug and Holm-Hansen (1986)	Feb./Mar. 1981	Scotia/Weddell Seas	0.0094-0.049	0.75-4.4	38-190
Tilzer et al. (1986)	Oct./Nov. 1983	Scotia Sea and Bransfield Strait (South of PF)	0.0074	1.92	69
Holm-Hansen and Mitchell (1991)	Dec. 1986– Mar. 1987	Bransfield Strait	0.06	1.1	18
Cota et al. (1992)	Jun./Aug. 1988	Weddell-Scotia Sea (MIZ)	0.056	0.23	9.8
Figueiras et al. (1994)	Dec. 1988– Jan. 1989	Weddell, Elephant Is.– South Orkney Is.	0.058	1.94	35
Boyd et al. (1995)	Nov./Dec. 1992	Bellingshausen Sea	0.001-0.048	0.09-1.07	<20-90
Figueiras et al. (1998)	Jan. 1994	Bransfield-Bellingshausen	0.019	1.60	84
		Bransfield-Weddell	0.017	1.41	88
		Ice-Edge (Bransfield Strait)	0.022	1.63	82
		Weddell-Scotia Confluence	0.007	0.79	100
Moline et al. (1998)	Spring/Summer 1991-1994	Antarctic Peninsula shelf	0.043	2.99	78.44
This study	Jan./Feb. 1996	Off Adélie Land	0.014	0.66	76

salinity (>33.8 PSU) water extended from the northeast to southwest of the studied region (Figs. 2 and 3). Decline of photo-chemical response of phytoplankton in this water mass is suggested. However, there were no significant spatial differences in the photosynthetic parameters in the studied area. This may be due to a combination of several factors such as water mass structure, penetration of irradiance and dominant phytoplankton taxa among stations.

Historical photosynthetic parameters in the Southern Ocean are summarized in Table 2. Most of these data were collected from waters around the Antarctic Peninsula such as Bransfield Strait and the Weddell-Scotia Seas. Values of α^* and I_k in the present study are in the range of those previously published, but P^*_{max} is lower than values in waters around the Antarctic Peninsula during the austral summer that frequently exceed 1.5 mgC (mg chl.a)$^{-1}$ h^{-1}. Although high P^*_{max} was reported by Jacques (1983) in water near Kerguélen Island, P^*_{max} in the water off Adélie Land is generally lower than in water near the Antarctic Peninsula.

The duration of incubation in the present study (4 hours) is likely to be long. Because of the rapid and large changes in ambient light to which the samples are exposed, phytoplankton have a remarkable capability for photoacclimation (Dubinsky et al., 1995). The acclimation of the photosynthetic apparatus during incubation may cause P-E curve variability (Sakshaug et al., 1997). Moisan and Mitchell (1999) suggested that photophysiological acclimation may contribute to the ecological success

of a prymnesiophyte, *Pheochystis antarctica*, in polar regions. Since the results in this study cannot explain the photoacclimation during the incubation period, further studies of the acclimation of phytoplankton in polar regions with various durations of incubation are required to reveal the relationship between photosynthesis and the mixing rate of the water column.

Quantum yield

The values of maximum quantum yield, ϕ_m, are shown in Table 1. These varied widely, from 0.001 to 0.038 mol C (mol photons absorbed)$^{-1}$ for surface water and 0.007 to 0.092 mol C (mol photons absorbed)$^{-1}$ near the bottom of the euphotic zone. At the surface, values >0.03 mol C (mol photons absorbed)$^{-1}$ were observed at Stns. C 08, C11 and C23, near the AD. Near the bottom of the euphotic zone, values >0.04 mol C (mol photons absorbed)$^{-1}$ occurred at Stns. C05, C13 and C27, near the AD (or the northernmost stations).

Our ϕ_m, except for the lowest (<0.01), were in the range of values from previous field studies in temperate waters (*e.g.* Kishino *et al.*, 1986). Smith *et al.* (1996) computed ϕ_m values in the Antarctic Peninsula region from historical α^* data. Although the computation method was slightly different from that in the present study, our values are generally within the range of these values (0.002–0.094 mol C (mol photons absorbed)$^{-1}$).

Conclusions

Off Adélie Land, Antarctica, the maximum photosynthetic rate of phytoplankton was lower than values in the waters near the Antarctic Peninsula, but maximum quantum yield was in the same range as in waters near the Antarctic Peninsula. Therefore, the difference of photosynthetic rate between the two regions cannot be explained by the difference in the activity of the components of electron transfer. The present study was carried out in the declining period of the Antarctic phytoplankton (El-Sayed, 1984) as well as the period studied by Yamaguchi *et al.* (1985). Studies near the Antarctic Peninsula have generally focused on the period of phytoplankton bloom during December and January. It is suggested that the difference of the period was one of the factors in the difference of P^*_{max} between the two regions.

Some primary production models on the global/regional scale using satellite data have been developed recently (*e.g.* Platt and Sathyendranath, 1988; Morel, 1991; Platt *et al.*, 1991; Longhurst *et al.*, 1995; Antoine *et al.*, 1995; Behrenfeld and Falkowski, 1997; Arrigo *et al.*, 1998). Some of these models use the P-E parameters and quantum yield observed at sea. Such field data for the Southern Ocean have so far been concentrated in the region near the Antarctic Peninsula. Thus, primary productivity for the whole of the Southern Ocean based on these field estimates of photosynthetic parameters is likely overestimated.

Acknowledgments

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