Estimates of Primary Production by Ice Algae and Phytoplankton in the Coastal Ice-covered Area near Syowa Station, Antarctica

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昭和基地沿岸定着氷域におけるアイスアルジーおよび植物プランクトンの基礎生産量の見積もり

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要旨： 昭和基地周辺定着氷域において，1983年2月から翌年の1月にかけて水深12mの北の瀬戸で基礎生産量を試算した．計算には昭和基地で測定された天空日射量，日長時間，現場での積雪量，氷厚および海水による光の減衰率，クロロフィル*a*現存量および光合成量子収率を用いた．それぞれの値をもとにアイスアルジーと植物プランクトンの各月の平均日生産量を推定するモデル式を作り，年生産量を見積もった．氷上に対する海氷下の相対光強度は1年を通して6.5%以下であった．アイスアルジーの単位面積あたりの月平均生産力の最大は12月に34 mgC m^{-2} day^{-1}であり，植物プランクトンの生産力の最大は2月に450 mgC m^{-2} day^{-1}であった．植物プランクトンによる2月の生産量が極めて大きいため，年間の植物プランクトンの生産量はアイスアルジーによる3.5 gC m^{-2} $year^{-1}$を上回り，17 gC m^{-2} $year^{-1}$と見積もられた．

***Abstract*:** Annual primary production of ice algae and phytoplankton under fast ice near Syowa Station (69°00′S, 39°35′E), Antarctica, was estimated. Mean daily production in each month from February 1983 to January 1984 was calculated with a mathematical model based on measured parameters of solar radiation, day length, attenuation coefficients of snow, ice and water, chlorophyll *a* standing stock, quantum yield for photosynthesis etc. Solar radiation measured at Syowa Station ranged from 0 E m^{-2} h^{-1} in June to 13.3 E m^{-2} h^{-1} in December. Relative light intensity estimated at the bottom of sea ice during the year ranged from 0 to 6.5% of incident solar radiation, due to attenuation with snow and ice. Maximum daily production of ice algae (34 mgC m^{-2} day^{-1}) and phytoplankton (450 mgC m^{-2} day^{-1}) was reached in December and in February, respectively. The estimated annual production of ice algae and phytoplankton was 3.5 and 17 gC m^{-2}, respectively. These results indicate that summer phytoplankton production contributed remarkably to the primary production in the coastal ice-covered area near Syowa Station.

1. Introduction

In the past few decades a number of investigations on primary production have been carried out in the Southern Ocean (see EL-SAYED, 1970; HOLM-HANSEN *et al.*,

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1977; HEYWOOD and WHITAKER, 1984 for reviews). Most of these studies dealt mainly with phytoplankton production in the ice-free waters. However, because sea ice covers as much extent as 20×10^6 km^2 in the Southern Ocean (ZWALLY *et al.*, 1983), ice algae as well as phytoplankton, are the important primary producers in the Antarctic ecosystem. Unfortunately, relatively few studies have been made on primary production by ice algae and phytoplankton in ice covered waters (*e.g.* RIVKIN *et al.*, 1989; LIZOTTE and SULLIVAN, 1991).

In the coastal ice-covered area of Antarctica, the variation of water temperature and salinity during the year is very small, the nutrient concentrations are usually high (*e.g.*, DEACON, 1963; FUKUCHI *et al.*, 1985; SATOH *et al.*, 1986), and the grazing rate by herbivorous zooplankton is relatively low (*e.g.*, FUKUCHI and TANIMURA, 1981). There are, however, marked seasonal changes in incident solar radiation and underwater light intensity, particularly during the transition from winter to summer, and so it is generally believed that primary productivity is regulated mainly by the light regime (EL-SAYED, 1984).

We have calculated primary production in sea ice and the water column from measurements of light conditions, chlorophyll *a* concentrations and quantum yield of photosynthesis during the period from February 1983 to January 1984. From these calculations, we have estimated the contribution of ice algae and phytoplankton to total primary production in the seasonally ice-covered coastal area near Syowa Station.

2. Materials and Methods

A summary of data source used in our model is given in Table 1. Data on the solar radiation from February 1983 to January 1984 at Syowa Station (69°00′S, 39°35′E) was obtained from the JAPAN METEOROLOGICAL AGENCY (1985), and we assumed that the incident solar radiation on the fast ice at the Kita-no-seto Strait, about 800 m north of Syowa Station (Fig. 1), was the same as that at Syowa Station.

As an estimate of the light at the bottom of ice, solar radiation (MJ m^{-2} h^{-1}) was converted to photon flux density (μEinstein m^{-2} s^{-1}) using equations given by MOREL and SMITH (1974):

$$1\ \mathrm{W}=2.77\times10^{18}\ \text{quanta s}^{-1}\quad (1\ \mathrm{J}=1\ \mathrm{W\,s}^{-1}),$$
$$1\ \mu\mathrm{E\ m}^{-2}\,\mathrm{s}^{-1}=6.02\times10^{17}\ \text{quanta m}^{-2}\,\mathrm{s}^{-1},$$

Table 1. The data source of parameters used in the present study.

Parameters	References
Solar radiation	JAPAN METEOROLOGICAL AGENCY (1985)
Thickness ice and snow	WATANABE and SATOH (1987)
Phytoplankton chlorophyll *a*	SATOH *et al.* (1986)
Ice algal chlorophyll *a*	WATANABE and SATOH (1987)
Ice algal photosynthesis from January to March	SATOH and WATANABE (1988)
Ice algal photosynthesis from April to December	SATOH and WATANABE (1986)
Phytoplankton photosynthesis	SATOH and WATANABE (1988)

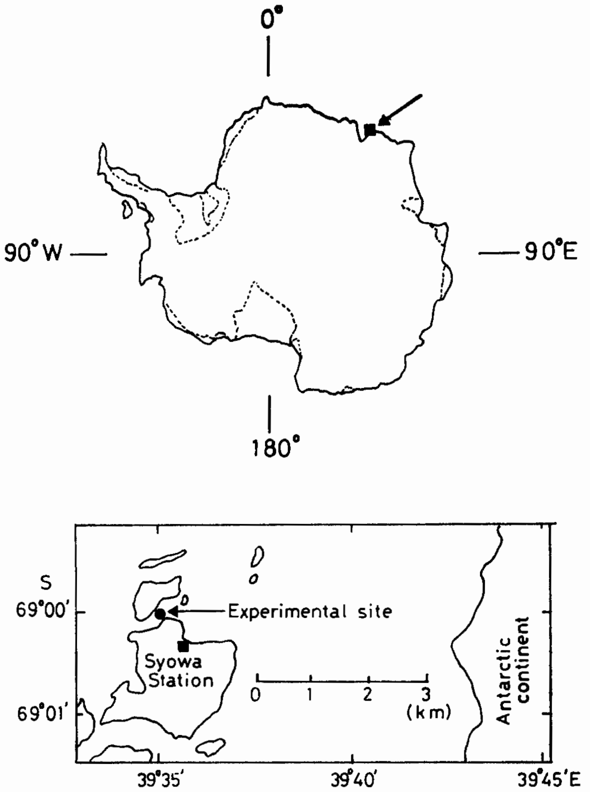

Fig. 1. Experimental site near Syowa Station (69°00'S, 39°35'E), in East Antarctica.

photon flux density ($E\,m^{-2}\,h^{-1}$) was obtained by multiplying the solar radiation (MJ $m^{-2}\,h^{-1}$) by 4.60.

As a sine curve was reasonably fitted to the mean values of actually observed solar radiation on monthly basis in August, October and December (Fig. 2), the photon flux density on the snow cover (I_0, $E\,m^{-2}\,h^{-1}$) at a given time t (hours after sunrise) of a given month was calculated by:

$$I_0 = I_{max} \cdot \sin^a(\pi t/L), \tag{1}$$

where I_{max} was the maximum I_0 during the daytime, L was the length of the dayhours (from sunrise to sunset) and "a" was the value obtained from sine curve in the month.

Underwater irradiance in the ice-covered area was determined from incident solar radiation and the thickness of snow and ice. The photon flux density at the bottom of ice (I_1) was estimated by the values of I_0 along with the thickness of snow and ice using the following equation (WATANABE and SATOH, 1987):

$$I_1 = 0.275\, I_0 \cdot \exp[-(0.134x_1 + 0.025x_2)], \tag{2}$$

where x_1 and x_2 were the thickness of snow and ice in centimeters, respectively (albedo $=0.725$). Underwater photon flux density (I_w) in the water column was estimated from the equation:

$$I_w = I_1 \cdot \exp(-kd), \tag{3}$$

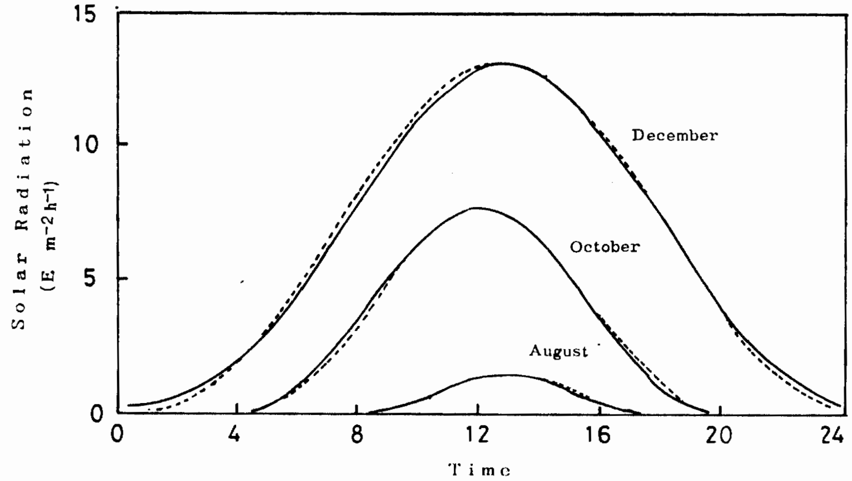

Fig. 2. *Diurnal changes in monthly average of photon flux density at the surface of ice in August, October and December 1983. The straight and broken lines show the curves from actual data and the sine curve fitted, respectively.* $I_0=1.52\sin^{1.0}(\pi t/6.9)$ *in August*; $I_0=7.27\sin^{2.1}(\pi t/15.4)$ *in October*; $I_0=13.3\sin^{2.3}(\pi t/24)$ *in Dcember.*

where the attenuation coefficient, k (m^{-1})$=0.052$, as calculated from data in WATANABE *et al.* (1986) and "d" as the depth in meters. The proportion of photon flux density under the sea ice (Z) to the density at the surface of the snow (I_0) was given by:

$$Z=I_i \quad (\text{or } I_w)/I_0. \tag{4}$$

The euphotic depth was estimated by the values of I_w and compensation point of photosynthesis as described later.

Measurements of the photosynthetic rates of ice algae were made by simulated *in situ* method based on the light-dark O_2 experiments (STRICKLAND and PARSONS, 1972) and the photosynthetic rates of phytoplankton were measured by *in situ* method based on the stable ^{13}C isotope method followed by infrared absorption spectrometry (SATOH *et al.*, 1985). The quantum yield attained for algal photosynthesis is a function of the light intensity and can be estimated by the photosynthetic rate divided by the incident irradiance (KIRK, 1983). The quantum yield for photosynthesis from April to December, when incident solar radiation is low, was estimated from initial slope of the photosynthesis-light curve in early November 1983 (SATOH and WATANABE, 1986), and the quantum yield from January to March, when the incident solar radiation is high, was obtained by *in situ* measurement in mid-January 1984 (SATOH and WATANABE, 1988). In our calculations, we assumed that the quantum yield remained constant throughout the day.

Chlorophyll *a* concentrations of ice algae and phytoplankton were measured by the fluorometric method of STRICKLAND and PARSONS (1972) as modified by ARUGA (1979). Ice thickness and overlying snow cover were measured. Bottom assemblages, which dominated ice algal standing stocks at Syowa (WATANABE and SATOH, 1987) were used in our calculations. The concentrations of chlorophyll *a* within the bottom 10 cm of ice sheet were used as an index of the biomass of ice algae.

The photosynthetic rate (P_t, mgC mgchl. a^{-1} h^{-1}) at a given time t hours after sunrise was given by:

$$P_t = q \cdot Z \cdot I_{max} \cdot \sin^a(\pi t/L). \tag{5}$$

Thus, the daily photosynthesis (Q_t, mgC mgchl. a^{-1} day^{-1}) was given by:

$$Q_t = \int_0^L [q \cdot Z \cdot I_{max} \cdot \sin^a(\pi t/L)]dt. \tag{6}$$

Estimated daily photosynthesis (mgC mgchl. a^{-1} day^{-1}) of ice algae and phytoplankton was multiplied by monthly-mean chlorophyll a standing stock (mg m^{-2}) to obtain the daily production (mgC m^{-2} day^{-1}), and monthly production was obtained by multiplying daily production by the number of days in each month. Annual production of both ice algae and phytoplankton was estimated by the sum of monthly values.

3. Results

The highest value of incident solar radiation was recorded in late December; radiation was reduced to undetectable level from late May until late July. The long daylight period at the peak of the summer (*i.e.* all day long) would result in a seasonal maximum of incident solar radiation and this should result in the highest value of primary production. The maximum photon flux density (I_i) at the bottom of ice was 0.389 E m^{-2} h^{-1} (*i.e.* 108 μE m^{-2} s^{-1}) in February, which corresponded to 4.8% of the incident radiation of 8.10 E m^{-2} h^{-1} (Table 2). The attenuation coefficients of snow and ice during the period from January to March were relatively high because of a decrease in the thickness of snow and ice. During the period from April to December the estimated photon flux density in the habitat of ice algae and phytoplankton was less than 0.050 E m^{-2} h^{-1}.

The quantum yields (q) of ice algae and phytoplankton during the period from April to December were estimated to be 7.6×10^{-5} and 1.2×10^{-4} mgC mgchl. a^{-1}

Table 2. *Average values of thickness of ice and snow, Z (photon flux density at the bottom of ice/density on the ice), I_{max} (maximum solar radiation), a (index number of sin function), L (length of dayhour), Q_t (daily photosynthetic rate) Chl. a (chlorophyll a standing stock) and P_t (daily production) of ice algae in each month of 1983/84.*

	Ice (cm)	Snow (cm)	Z	I_{max} (E m^{-2} h^{-1})	a	L (h)	Q_t*1	Chl. a (mg m^{-2})	P_t*2
February	70	0	0.048	8.10	1.7	17.3	1.2	0.01	0.01
March	58	0	0.065	4.83	1.4	12.9	7.8	0.63	4.9
April	80	0	0.037	2.30	1.1	8.6	2.7	1.1	2.9
May	61	0	0.061	0.32	0.8	3.7	0.36	2.5	0.90
June	71	1	—	—	—	—	—	1.2	—
July	90	3	0.019	0.09	0.8	1.5	—	1.3	—
August	115	3	0.010	1.52	1.0	6.9	0.41	1.6	0.64
September	118	5	0.007	3.68	1.3	11.2	1.0	4.7	4.9
October	120	7	0.005	7.27	2.1	15.4	1.6	19	30
November	122	18	0.001	10.7	2.2	21.0	0.43	63	27
December	122	16	0.002	13.3	2.3	24.0	1.3	25	34
January	119	0	0.014	12.3	2.3	22.9	6.4	1.8	12

*1 mgC mg chl. a^{-1} day^{-1}.
*2 mgC m^{-2} day^{-1}.

$(E\ m^{-2})^{-1}$, respectively. During the period from January to March the quantum yield of 3.3×10^{-5} for ice algae and 1.7×10^{-4} mgC mgchl. $a^{-1}(E\ m^{-2})^{-1}$ for phytoplankton was used.

The estimated daily photosynthesis and production (mgC m^{-2} day^{-1}) is shown in Tables 2 and 3; the annual production of ice algae and phytoplankton was 3.5 and 17 gC m^{-2} $year^{-1}$, respectively.

Table 3. Average values of E (depth of euphotic layer), Q_p (daily photosynthetic rate), Chl. a (chlorophyll a standing stock) and P_p (daily production of phytoplankton) in each month of 1983/84.

	E (m)	Q_p (mgC mgchl. a^{-1} day^{-1})	Chl. a (mg m^{-2})	P_p (mgC m^{-2} day^{-1})
February	>12	35	13	450
March	>12	22	2.4	53
April	>12	3.6	1.7	6.0
May	9.0	0.47	0.96	0.45
June	—	—	0.65	—
July	—	—	0.17	—
August	6.9	0.53	0.14	0.07
September	11.8	1.3	0.33	0.44
October	>12	1.6	0.75	1.2
November	1.7	0.53	0.53	0.28
December	>12	1.16	0.78	1.3
January	>12	20	3.8	74

4. Discussion

Photon flux under sea ice is determined largely by the thickness of ice and overlying snow and SULLIVAN *et al.* (1985) reported that primary production of ice algae is mainly controlled by the depth of the snow. The photosynthetic response of microalgae under low light conditions will provide a key to understanding the primary production under sea ice (SATOH *et al.*, 1989). In the report of IKUSHIMA (1970), "*a*" of the index number of eq. (1) was given by 2 (unit of klux). As modified by MAEGAWA *et al.* (1988), the index number of 1.3 (unit of photon flux density) could be used for middle-latitude region during the period from April to July, such as Honshu in Japan. At Syowa Station the index number varied from 0 to 2.3 because there is a marked diurnal changes in solar radiation during the transition from winter to summer (Fig. 2).

In our previous paper (SATOH and WATANABE, 1986), the compensation light intensity for ice algal photosynthesis was estimated to be 0.01 E m^{-2} h^{-1}. The photon flux density at the bottom of ice in July (0.002 E m^{-2} h^{-1}) was below the compensation light intensity, so the euphotic depth was determined by the thickness of snow and ice. The saturation intensity (0.09 E m^{-2} h^{-1}) in the present study was much lower than those of 0.38–0.78 E m^{-2} h^{-1} in the Antarctic ice-free waters (SAKSHAUG and HOLM-HANSEN, 1986). A depression of the photosynthetic rate of ice algae caused by photoinhibition occurred at 0.29 E m^{-2} h^{-1} (SATOH and WATANABE, 1986). We previously indicated (SATOH *et al.*, 1989) that microalgae grown under different light conditions have different photosynthetic characteristics; the photosynthetic capacity of the micro-algae exposed to higher light intensity have higher saturation point as compared with those exposed to lower light intensities. Although the quantum yield was given as daily average value in the present study, it is necessary to apply quantum yield as a function of time (hours after sunrise) (RIVKIN and PUTT, 1987) for better estimates. Thus, further investigations should be done in detail these points. However, the advantages of this simulation are effectiveness of the saving labor, in which logistic aspects on field works are difficult for the harsh environment, and usefulness of the solar radiation data obtained easily at Syowa Station.

The annual production (3.5 gC m^{-2} $year^{-1}$) of ice algae obtained from our calculations was almost the same as that of 3.3–3.4 gC m^{-2} $year^{-1}$ obtained by increase or maximum accumulation of chlorophyll *a* standing stock (WATANABE and SATOH, 1987). The contribution of ice algae to primary production was highest in the spring (from October to December) (Fig. 3). The primary production of ice algae in the autumn (from March to April) was less than 10% of that in the spring. Our estimate of high phytoplankton production (0.45 gC m^{-2} day^{-1}) in February was comparable with 0.47 gC m^{-2} day^{-1} reported by EL-SAYED and MANDELLI (1965) and with 0.41 gC m^{-2} day^{-1} in the Weddell Sea in summer (EL-SAYED and TAGUCHI, 1981). Our results indicate the annual production of phytoplankton in the water column (17 gC m^{-2} $year^{-1}$) was almost the same level as 16 gC m^{-2} $year^{-1}$ reported for phytoplankton production in the Antarctic open waters by EL-SAYED (1978), which is about 5 times larger than that of the ice algae.

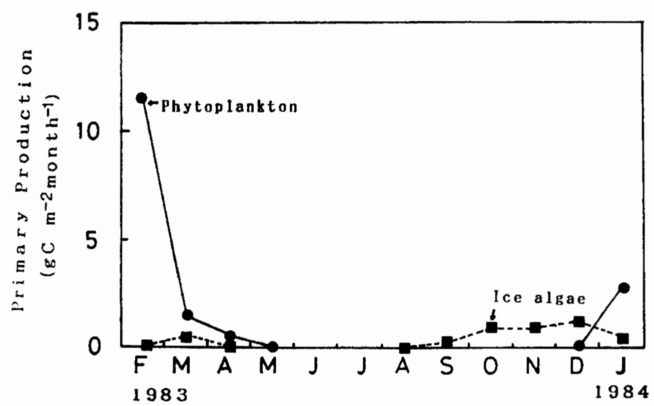

Fig. 3. Estimated primary production of ice algae and phytoplankton throughout the period from February 1983 to January 1984. Squares and circles indicate primary production of ice algae and phytoplankton, respectively.

Since standing stock of macrophytes near the experiment site was negligible (WATANABE *et al.*, 1982), the total primary production was estimated to be 20.5 gC m^{-2} $year^{-1}$ (the sum of phytoplankton and ice algae productions). The estimated contribution of ice algae to the annual primary production in the studied area (17%) is slightly higher than that of ice algae (12%) estimated by EL-SAYED (1978). This might be explained by the difference of euphotic depths (12 m for the present study).

The present study demonstrates that phytoplankton production concentrated in the short summer period contributed remarkably to the total annual primary production in the fast ice area near Syowa Station.

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