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Light conditions and photosynthetic productivity of ice algal assemblages in Lake Saroma, Hokkaido

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Photosynthetic productivity of ice algal assemblages was investigated in Lake Saroma on the Okhotsk Sea coast of Hokkaido in early March of 1987 and 1988. Relative light intensity at the bottom of ice was about 1.0% of incident solar radiation in 1987, whereas it was about 4.4% in 1988. In photosynthesis-light curves, the photosynthetic rate was saturated at 27.5 μE m^{-2} s^{-1} in 1987, the saturated rate being 0.42 mgC mgchl.a^{-1} h^{-1}, while it was not saturated even at 162 μE m^{-2} s^{-1} in 1988, the maximum rate being 0.43 mgC mgchl.a^{-1} h^{-1}. The compensation light level of ice algae was 0.04–0.05% of the incident light intensity. The daily production of ice algae in 1987 (14.3 mgC m^{-2} day^{-1}) was 6.2 times greater than that in 1988 (2.3 mgC m^{-2} day^{-1}). The specific growth rate (μ) of ice algae was 0.12 and 0.027 div. day^{-1} in 1987 and 1988, respectively. The present study demonstrates that the growth of ice algae is strongly controlled by light conditions at the bottom of ice in the ice-covered season.

Key Index Words: compensation point—growth rate—ice algae—Lake Saroma—photosynthesis.

Ice algae (ice algal assemblages) are present in all areas where sea ice is a regular feature of the environment (HORNER 1985). The role of ice algae is doubtlessly important in such ecosystems of ice-covered seas (MCROY *et al.* 1972, HORNER 1977, DUNBAR 1979, PLATT *et al.* 1982, PALMISANO and SULLIVAN 1983, WATANABE 1988, SATOH and WATANABE 1988). In the previous paper (SATOH *et al.* 1989), the present authors reported the photosynthetic production of ice algae under extremely low light conditions in Lake Saroma, which is known as the southernmost area of seasonal sea ice extension in the northern hemisphere, and suggested that their contribution to primary production in the lake was considerablely large. The obtained values of primary production of ice algae were comparable to those reported in the polar regions (BUNT 1964, BURKHOLDER and MANDELLI 1965, ALEXANDER 1979, SATOH and WATANABE 1986).

In Lake Saroma, ice algae were found in the bottom layer of ice core and grew most extensively between mid-February and early March (HOSHIAI and FUKUCHI 1981). The light intensity at the bottom layer of ice was very low (SATOH *et al.* 1989) because of light extinction by ice and snow. Thus, it is important to know the photosynthetic rate accurately at light regimes near the compensation point for estimating primary production in the ice-covered season.

In this paper, the authors describe the under-ice light conditions with reference to the photosynthetic nature of ice algae in Lake Saroma. The results obtained in the ice-covered season of 1988 are compared with those in the preceding year (SATOH *et al.* 1989).

Material and methods

Field studies were carried out on 7–9

March in both 1987 and 1988 at the same site (44°10′N, 143°46′E) in Lake Saroma, Hokkaido, which is a lagoon of seawater flowing in through the two channels from the Sea of Okhotsk. For collection of ice algal samples, ice was cut in a mass of about 1 m^2 surface with a chain saw. The colored part within a few cm from the bottom of ice was scraped off into filtered seawater, and maintained at temperatures below 0°C for experiments. Three ice cores were collected with a SIPRE coring auger, and average concentrations of chlorophyll *a* within 4 cm from the bottom of ice cores were used as an index of biomass of ice algae. For this purpose, after the ice cores were melted at room temperatures, the samples were immediately filtered through glass fiber filters (Whatman GF/C). Pigments of ice algae retained on the filters were extracted with 90% acetone. Chlorophyll *a* and pheopigment concentrations were determined by the fluorometric method of STRICKLAND and PARSONS (1972) modified by ARUGA (1979) with a Hitachi 650-40 fluorometer or a Turner Designs 10-005R fluorometer.

Estimations of daily primary production of ice algae were done with two different methods; the *in situ* method and the chlorophyll method based on photosynthesis-light curve. All measurements of photosynthetic activity of ice algae were made by the stable ^{13}C isotope method (SATOH *et al.* 1985).

To obtain the photosynthesis-light curves, $Na^{13}CO_3$ (Prochem) was added to algal samples in 100 m*l* DO bottles with 9.9% of the final atom percent of ^{13}C. The samples were exposed to different light intensities from 0 to 162 $\mu E\ m^{-2}\ s^{-1}$ by using a projector lamp (Kondo 100V-150W) as the light source. Light intensities were regulated with neutral density filters (Toshiba TND-50, 20, 10, 5, 1, 0.5, 0.2). Measurements of light intensity (400–700 nm) were done with an LI-188B quantum meter equipped with an LI-190SB quantum sensor (LI-COR). After the incubation for 3 hours, the samples were filtered through glass fiber filters (Whatman GF/C) precombusted at 450°C for 4 hours. Isotope ratios of ^{12}C and ^{13}C in the samples were determined by infrared absorption spectrometry with a JASCO ^{13}C analyzer EX-130. Calculation of photosynthetic activity was made using the equation of HAMA *et al.* (1983). Daily production (mgC m^{-2} day^{-1}) was calculated on the basis of the daily photosynthetic rate (mgC mgchl.a^{-1} day^{-1}) multiplied by the chlorophyll *a* concentration (mg m^{-2}) of ice core, because the ice algal samples were diluted with filtered lake water for measurements of photosynthetic activity.

In situ primary production of ice algae was also measured. The samples were incubated at the layer immediately beneath the ice during the period from noon to sunset on a clear day. The obtained value was multiplied by a factor of 2 to obtained the *in situ* daily production (mgC m^{-2} day^{-1}). Incident and under-ice photosynthetically active radiations (PAR, 400–700 nm) were measured with an LI-1000 integrating quantum meter equipped with an LI-190SB quantum sensor on snow cover and an LI-192SB underwater quantum sensor.

Results and Discussion

Environmental conditions of the study area

Lake Saroma is iced over usually from January to April. Comparing the environmental conditions in early March of 1987 with those in 1988, the thickness of ice in

Table 1. Environmental parameters, chlorophyll *a*, POC, chl.*a*/(chl.*a*+pheopigments), and POC/chl.*a* of ice algae in early March of 1987 and 1988. The light conditions were measured at local noon.

	1987	1988
Solar radiation ($\mu E\ m^{-2}\ s^{-1}$)	1325	1395
Thickness of ice (cm)	38	19
Overlying snow (cm)	8	8
PAR beneath ice ($\mu E\ m^{-2}\ s^{-1}$)	14	62
Water temperature (°C)	−1.4	−1.4
Salinity	32.4	31.6
Chl.*a* (mg m^{-2})	5.68	1.68
POC (mgC m^{-2})	160.2	120.0
Chl.*a*/(chl.*a*+pheopigments)	0.99	0.86
POC/chl.*a*	28.2	71.4

1988 was as half that in 1987 and snow covering the ice attained 8 cm in both years (Table 1). Differences in water temperature and salinity were very small between the two years. The relative light levels at the bottom of ice were 1.0% and 4.4% of the incident solar radiation at around local noon on a clear day in 1987 and 1988, respectively. Although the level of solar radiation in the ice-covered period of 1988 was almost the same as that in 1987, the light intensity at the bottom of ice was more than 4 times greater in 1988 than in 1987. In considering these facts, it can be said that the under-ice light conditions were controlled by the thickness of ice and snow cover (WATANABE and SATOH 1987).

The standing stock of ice algae was concentrated within the bottom 4 cm layer of ice in Lake Saroma (SATOH *et al.* 1989), the situation being quite similar to that in the Antarctic ice algae (WATANABE and SATOH 1987). The standing stock of ice algae was 5.68 and 1.68 mg chl.a m^{-2} in 1987 and 1988, respectively. The dominant species of ice algae were pennate diatoms *Nitzschia* spp. in both years.

Photosynthesis-light curves

Photosynthesis-light curves of ice algae obtained in 1987 and 1988 are shown in Fig. 1. In the curve in 1987 the photosynthetic rate was 0.42 mgC mgchl.a^{-1} h^{-1} at the saturated point of about 27.5 μE m^{-2} s^{-1}. Contrarily, the photosyntheis-light curve in 1988 did not show the light saturation. The maximum photosynthetic rate was 0.43 mgC mgchl.a^{-1} h^{-1} at 162 μE m^{-2} s^{-1}. The steep initial slope and low saturating light intensity obtained in 1987 indicate the shade adaptation of ice algae (PLATT *et al.* 1982, PALMISANO and SULLIVAN 1985, SATOH and WATANABE 1986). On the other hand, the gentle initial slope with expected higher saturating light intensity obtained in 1988 suggests that the ice algae in that season had adapted to higher light intensities. The variations in such parameters as the saturated rate and the initial slope of photosynthesis-light curves of ice algae might be caused by the light conditions at the bottom of ice.

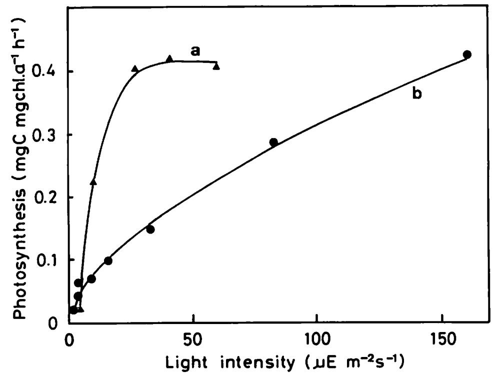

Fig. 1. Photosynthesis-light curves at 0°C of ice algae obtained in 1987 (a) and 1988 (b). The available values in oxygen were converted to those in carbon in the curve of 1987 (Satoh *et al.* 1988).

The compensation light intensity of ice algae both in 1987 and 1988 was about 0.5 μE m^{-2} s^{-1}, which corresponds to 0.04–0.05% of the down-welling irradiance in early March in the area. The compensation point was almost the same as those of ice algae obtained in the Antarctic region (PALMISANO and SULLIVAN 1983, SATOH and WATANABE 1986). The light intensity in the habitat of ice algae was remarkablely low as compared with that of phytoplankton obtained in the ice-free waters of the Antarctic (JACQUES 1983, SAKSHAUG and HOLM-HANSEN 1986). Thus, it is concluded that photosynthetic production of ice algae proceeds usually under extremely low light conditions.

Daily production and growth rate of ice algae in 1987 and 1988

The standing stock of ice algae in 1987 (5.68 mgchl.a m^{-2}) was 3.4 times greater than that in 1988 (1.68 mgchl.a m^{-2}). The *in situ* photosynthetic rate was 2.52 and 1.34 mgC mgchl.a^{-1} day^{-1} in 1987 and 1988, respectively. Based on these values, the daily production of ice algae was estimated to be 14.3 and 2.3 mgC m^{-2} day^{-1} in 1987 and 1988, respectively. It was 6.2 times greater in 1987 than in 1988.

The daily production was also estimated indirectly by the chlorophyll method (ICHIMURA *et al.* 1962) and compared with that obtained by *in situ* measurements. On the basis of the diurnal change of incident light instensity, relative light intensity at the bottom of ice, photosynthesis-light curve and chlorophyll *a* concentration of ice algae, the daily photosynthetic rate is calculated as 1.82 mgC mgchl.a^{-1} day^{-1} in 1987 and 1.38 mgC mgchl.a^{-1} day^{-1} in 1988 (Table 2). The daily photosynthetic rates and production thus estimated agreed well with those obtained by *in situ* measurements (Table 2).

Based on the *in situ* daily production of ice algae, the growth rates (μ) were calculated by the following equation (PARSONS and TAKAHASHI 1973):

$$\mu=\frac{1}{t}\times\log_2\frac{C_o+\Delta C}{C_o},$$

where C_0 is the initial algal biomass in carbon calculated from the POC/Chl.*a* ratio, and ΔC is the increase of algal biomass during time t estimated directly by the photosynthetic production. The calculated growth rates were 0.12 and 0.027 div. day^{-1} in 1987 and 1988, respectively. The growth rate in 1987 was coincident well with those estimated for Antarctic ice algae in the spring seasons (SULLIVAN *et al.* 1985, SATOH and WATANABE 1986). The growth rate in 1988 was remarkablely low as compared with that in 1987. The high POC/chl.*a* ratio and low chl.*a*/(chl.*a* and pheopigments) ratio were the main causes for low growth rate of ice algae in the season of 1988.

In conclusion, the photosynthetic nature and growth rate of ice algae were strongly influenced by the light conditions at the bottom of ice which were controlled by thickness of ice and snow cover, if any, as well as by solar radiation.

Table 2. Daily photosynthetic rate and prodcution obtained by *in situ* measurements or estimated from photosynthesis-light curves, and grwoth rate calculated on the basis of *in situ* production of ice algae in early March of 1987 and 1988.

	1987	1988
In situ measurments:		
Photosynthetic rate (mgC mgchl.a^{-1} day^{-1})	2.52	1.34
Production (mgC m^{-2} day^{-1})	14.3	2.3
Estimation from P-L curves:		
Photosynthetic rate (mgC mgchl.a^{-1} day^{-1})	1.82	1.38
Production (mgC m^{-2} day^{-1})	10.3	2.3
Growth rate (div. day^{-1})	0.12	0.027

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佐藤博雄*・山口征矢**・渡辺研太郎***・有賀祐勝*：サロマ湖における ice algae の光合成生産力

1987年および1988年の3月上旬，サロマ湖の結氷期に ice algae（氷に付着する微細藻類）の生産力を調査した。氷直下の相対光強度は，1987年（氷厚，38 cm）には氷上の日射量の1.0%，1988年（氷厚，19 cm）には4.4%であった。1987年の光合成–光曲線で，光合成速度は 27.5 μE m^{-2} s^{-1} で光飽和に達し 0.42 mgC mg.chla^{-1} h^{-1} であったが，1988年には 162 μE m^{-2} s^{-1} のもとでも光飽和に達しなかった（最高値は 0.43 mgC mg.chla^{-1} h^{-1}）。ice algae の推定光補償点は著しく低く，相対光強度として0.04–0.05%であった。現場法によって得られた ice algae の生産量は，1987年に 14.3 mgC m^{-2} day^{-1}，1988年には 2.3 mgC m^{-2} day^{-1} であった。生産量から求めた ice algae の増殖速度は，1987年は 0.12 div. day^{-1}，1988年は 0.027 div. day^{-1} であり，ice algae の増殖は氷下の光条件によって大きく支配されていることが推察された。（*108 東京都港区港南4–5–7　東京水産大学，**338 埼玉県浦和市下大久保255　埼玉大学教養部，***173 東京都板橋区加賀1–9–10　国立極地研究所）