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PHOTOSYNTHETIC NATURE OF ICE-ALGAE UNDER FAST ICE NEAR SYOWA STATION, ANTARCTICA

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Abstract: The photosynthetic nature of the ice-associated microalgal assemblages (ice-algae) was investigated in the annual sea ice area near Syowa Station (69°00'S, 39°35'E), Antarctica. The maximum photosynthetic rate of 1.23 mgO₂/mg chl. *a*/h was obtained under the light intensity of $25 \,\mu\text{E/m}^2/\text{s}$. In a higher light condition above $80 \,\mu\text{E/m}^2/\text{s}$, a depression of the rate caused by photo-inhibition was observed. These results demonstrated the low-light-adaptation of Antarctic ice-algae under the exceedingly low light conditions. The light condition under the ice was largely controlled by the thickness of snow covering the fast ice as well as by the variation of solar radiation. The optimum temperature for photosynthesis of the ice-algae was about 8°C, while the rates of photosynthesis reduced at higher temperatures. In the present area, an average specific growth rate (μ) of the ice-algae was 0.25 div./day.

1. Introduction

Since the first report of HOOKER (1847) about the algal coloring of Antarctic icebergs, pack and fast ice, many investigations concerning the ice-associated microalgal assemblages (ice-algae) in the polar sea were performed (*e.g.* BUNT, 1964; HORNER and ALEXANDER, 1972; HOSHIAI, 1981). Most of them were related to the taxonomy and the standing crop, and their results indicated that the growth of ice-algae occurred mainly from spring to autumn within the lowermost layer of the sea ice. The maximum value reported on the chlorophyll *a* content was 2829.71 mg/m³ which had been observed in November 1982 near Syowa Station, Antarctica (HOSHIAI, 1985).

On the other hand, only a few works have been made on photosynthetic nature of ice-algae in the Antarctic Ocean (BUNT, 1964; PALMISANO and SULLIVAN, 1983). Clarification of the photosynthetic nature of the ice-algae is still needed for estimating their contribution to the annual total primary production in the ice-covered sea. In this paper we discuss mainly the state of physiological adaptation in photosynthesis of ice-algae to low-light and low-temperature conditions which was observed near Syowa Station (69°00'S, 39°35'E).

2. Materials and Methods

Field studies were carried out from early November to late December 1983 in the Kita-no-seto Strait, about 500 m north of Syowa Station (Fig. 1). To collect the algae, a hole was dug into the annual sea ice with a SIPRE ice-coring auger (7.6 cm in diameter).



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

The surface seawater containing both ice-algae detached from the undersurface of the ice by a disturbance due to coring and those which might be suspending in water just below the ice was collected and used in the experiments. Therefore, the microalgal population used here is the mixture of a sub-ice assemblage (HORNER *et al.* in prep.) and planktonic one in a strict sense. For determining plant pigments, aliquots of the seawater were immediately filtered through glass fiber filters (Whatman GF/C). The concentrations of chlorophyll a and phaeopigments were measured with a Hitachi model 650-40 fluorometer according to the procedure of ARUGA (1979) modified from the method described in STRICKLAND and PARSONS (1968).

Measurements of photosynthetic and respiration rates were made by a simulated *in situ* method with the oxygen light and dark bottle method, followed by the Winkler titration (STRICKLAND and PARSONS, 1968). The light intensity was regulated by changing the number of neutral vinyl sheets rolled around the bottles and then the bottles were placed in outdoor thermostated water baths (temperature range, -1.7° to $+16^{\circ}$ C) under the natural light condition. The measurements of the light intensity (400–700nm) on the baths were done with a LI-188B quantum meter and a LI-190SB quantum sensor (LI-COR, USA).

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Measurements of *in situ* photosynthetic rates and their diel variation were carried out on 8–9 November, 3–4 December and 22–23 December. The bottles were incubated in the surface layer just beneath the sea ice for every 4h throughout the day. All the experiments were made in duplicate. The total daily net-photosynthesis (mgC/m³/day) was estimated by planimetry of results obtained from 4-h incubations.

The light intensity at the surface of the ice (LI-190SB) and at 90cm depth within the ice (LI-193SB) was measured with quantum sensors connected to a printing integrator (LI-550B). The latter had been ice-bound, though originally suspended beneath the ice, during the preceding winter. The physico-chemical data of the seawater are published in SATOH *et al.* (1986). Relevant meteorological data could be referred to JAPAN METEOROLOGICAL AGENCY (1985).

3. Results

3.1. Environmental background

The mean air temperature in the summer of 1983 was -5.9° C in November-December, while it was about -11° C on annual base. The thickness of the sea ice



Fig. 2. Variation of solar radiation (cited from JAPAN METEOROLOGICAL AGENCY, 1985) and snow thickness from November to December 1983, and diel variation of light intensity on the surface of ice (solid line) and under the ice (dashed line) on November 8 and December 4, 1983. The light intensity under the ice at the depth of 90 cm from the ice-surface was measured with a LI-193SB sensor which had been set up by SCUBA divers in July 1983; its sensor was icebound in the experimental period.

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during this period was about 120cm. The thickness of the snow covering the ice was 10cm in early November, but in late December the snow cover disappeared (Fig. 2) and the puddles were formed. Water temperature and practical salinity at the depth of 0.8m below the undersurface of the ice ranged from -1.79° to -1.76° C and 34.10 to 34.06, respectively. The nutrient concentrations almost unchanged during the period and were more than 30 μ g-at/l for nitrate-N, 1.5μ g-at/l for phosphate-P and 60μ g-at/l for silicate-Si (SATOH *et al.*, 1986).



Fig. 3. Effect of light intensity on photosynthetic rates of ice-algae. Experimental water temperature was fixed at $-1.7^{\circ}C$.



Fig. 4. Effect of water temperature on rates of photosynthesis (solid circle) and respiration (solid square) of ice-algae under the light intensity, $34 \mu E/m^2/s$.

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3.2. Response of ice-algae to light intensity and water temperature

The photosynthesis vs. light curve of the ice-algae collected on November 1 showed the maximum photosynthetic rate (P_{max}) of $1.23 \text{ mgO}_2/\text{mg}$ chl. a/h at about $25 \mu \text{E/m}^2/\text{s}$ (Fig. 3). The depression of the rate under the higher light intensity over $80 \mu \text{E/m}^2/\text{s}$ was documented.

The dependence of photosynthetic and respiration rates of ice-algae on water temperature is shown in Fig. 4. The P-T (photosynthesis-temperature) curve on November 1 was obtained under the saturating light intensity of $34 \,\mu\text{E/m}^2/\text{s}$. The increase of temperature from ambient (-1.7°C) to 4° and 8°C resulted in a significant increase of the rates of photosynthesis and respiration, while at an exceedingly higher temperature (16°C) the rates reduced. The rates of respiration corresponded to 10-20% of the photosynthetic rate throughout the temperature range.

3.3. In situ photosynthesis of ice-algae

The variation of light intensity during the experimental period is shown in Fig. 2. The light intensity on and under the ice was 1492 and $123 \,\mu\text{E/m}^2/\text{s}$ for November 8, and 1803 and $283 \,\mu\text{E/m}^2/\text{s}$ for December 4 at local apparent noon, respectively. Although the light condition where the ice-algae had grown was lower than the value measured here, it was still higher than the light intensity of maximum photosynthetic rate. The duration of daytime at Syowa Station was 16.7h on November 8 and 19.8h on December 4. In order to compare our data with those reported previously, the present data on O₂ base were converted to carbon base by assuming that the photosynthetic quotient is unity (Table 1). The total daily photosynthesis estimated for November 8, December 4 and 22 was 893, 3833 and 2704 mgC/m³/day, respectively.

Date	Incubation time (local time)	Chl. <i>a</i> (mg/m ³)	Photosynthetic rate $(mgO_2/mg chl. a/h)$	Daily photosynthesis (mgC/m³/day)	Growth rate (day ⁻¹)
	1100-1500	101	0.62 (0.23)*		893 0. 24
Nov. 8-9	1600-2000	191	0.72 (0.28)*	893	
	2200-0200		N.D.		
Dec. 3-4	1600-2000	1110	0.48 (0.18)*		0. 18
	2200-0200		0.05 (0.02)*	3833	
	0400-0800		0.50 (0.19)*		
	1000-1400		0.52 (0.20)*		
Dec. 22-23	1100-1500		0.94 (0.35)*		
	1600-2000	407	1.00 (0.38)*	2704	0. 33
	2200-0200		0.08 (0.03)*		

Table 1. In situ photosynthetic rate, calculated daily photosynthesis and specific growth rate of ice-algae near Syowa Station in the summer of 1983.

* The available values converted to carbon base (mgC/mg chl. a/h).

4. Discussion

As shown in Fig. 2, while the light intensity on the surface of the ice increased 1.2 times from November 8 to December 3, the intensity under the ice increased 2.3 times

due to the decrease of the snow cover. This indicated that the light intensity under the ice is largely regulated by the thickness of the snow cover as well as by the level of solar radiation. Furthermore, the duration of daytime also increased 1.8 times in this period. These favorable changes doubtlessly contributed to the proliferation of ice-algae.

The shape of P-L (photosynthesis-light) curve (Fig. 3) shows the extreme shade adaptation of ice-algae. The maximum photosynthetic rate occurred at $15-35 \,\mu\text{E/m}^2/\text{s}$, which corresponded to only 1.5-2.0% of solar radiation, and the photo-inhibition was observed under the higher light intensity. According to HOLM-HANSEN and SAKSHAUG (cited by EL-SAYED, 1984), photo-chemical apparatus of the Antarctic phytoplankton distributed in the northern open area was saturated at about 100 and $180 \,\mu\text{E/m}^2/\text{s}$. The ice-algae are likely to adapt themselves to lower light intensity than the phytoplankton in the north. The value of P_{max} obtained in this area is almost at the same level as those of ice-algae in the McM urdo Sound reported by BUNT (1964) and PALMISANO and SULLIVAN (1985). The positive *in situ* photosynthesis was measured even at midnight when light intensity was below $3.0 \,\mu\text{E/m}^2/\text{s}$ (Table 1). All these mentioned above demonstrate that the ice-algae adapt themselves to low light condition under the Antarctic sea ice and can achieve a photosynthetic production under such a low light condition.

The P-T curve (Fig. 4) shows that the optimum temperature for photosynthesis of the ice-algae was about 8°C, under which the maximum rate corresponding to 1.5 times larger than that at ambient water temperature $(-1.7^{\circ}C)$ was observed. This optimum temperature is at almost the same level as for phytoplankton in the ice-free waters reported by NEORI and HOLM-HANSEN (1982) and YAMAGUCHI *et al.* (1985).

The reported values of photosynthetic rates of ice-algae and phytoplankton in the Antarctic waters are summarized in Table 2, together with the present result. The *in situ* rate in the present area is slightly lower than the values reported for ice-algae in the McMurdo Sound, and very much lower than those of phytoplankton in the ice-free waters. This lower rate might have resulted from the heavy snow cover (0-20 cm) in the present area compared with that (0-2 cm) in the McMurdo Sound (PALMISANO and SULLIVAN, 1983).

The daily growth rate (μ) of algae can be calculated from the following equation (PARSONS *et al.*, 1977):

Sample	Site	Photosynthetic rate (mgC/mg chl. a/h)	Method	Reference
Ice-algae	McMurdo Sound	0.4	¹⁴ C	Bunt (1964)
	McMurdo Sound	0.6	14C	PALMISANO and SULLIVAN (1985)
	Syowa Station	0.02-0.38	O_2	Present work
Phyto-	Weddell Sea	1.0 -2.3*	14 C	EL-SAYED and TAGUCHI (1981)
plankton	Indian Antarctic Ocean	0.5 -5.2	14C	Jacques (1983)
	Australian Antarctic Ocean	1.3 -1.5	¹³ C	Үамадисні <i>et al</i> . (1985)

 Table 2. Photosynthetic rate of ice-algae and phytoplankton in the ice-free waters of the Antarctic Ocean.

* Derived from day values.

$$\mu = \frac{1}{t} \times \log_2 \frac{C_0 + \Delta C}{C_0}$$

where C_0 is the initial algal biomass in carbon and ΔC is the increase of algal biomass during time t. In this study the C_0 was 'calculated using the carbon/chl. a ratio of 26.3 (from our unpublished data obtained in the present area), ΔC estimated by *in situ* daily photosynthesis, and t is one day. The mean growth rate of the present ice-algae was calculated to be 0.25 div./day. This value is coincident well with the rate of icealgae in the McMurdo Sound (BUNT and LEE, 1970; SULLIVAN *et al.*, 1985), and with the growth rate (0.05–0.33 div./day) of phytoplankton in the ice-free waters under subzero temperature (HOLM-HANSEN *et al.*, 1977).

As mentioned above, no apparent differences in dependence of photosynthetic rates on temperature were found between the present ice-algae and the planktonic algae reported by NEORI and HOLM-HANSEN (1982) and YAMAGUCHI *et al.* (1985). Habitable temperature of the phytoplankton of which growth rate was examined by the former authors (NEORI and HOLM-HANSEN, 1982) was equivalent to that in the present area. Therefore, the cause of differences in growth rate of ice-algae (Table 1) and phytoplankton (HOLM-HANSEN *et al.*, 1977) cannot be attributed to temperature conditions.

On the other hand, state of adaptation to light intensity was clearly different between ice-algae in the present area and phytoplankton reported by HOLM-HANSEN *et al.* (1977), as described above. The most important is the adaptation of the ice-algae to the extremely low light intensity (Fig. 3). Such an adaptation is doubtlessly advantageous when the ice is covered with snow, which is the prevailing condition in the permanently ice-covered sea areas. It is most likely, however, that the adaptation results in the brittleness of the ice-algae under the ice without snow cover during the short but bright summer. It can be evidently read in Fig. 2 that light intensity under the ice is largely exceeding supraoptimal light level on December 4.

Despite their lower growth rate, the standing crop of ice-algae is considerably large in most cases (*e.g.* HOSHIAI, 1985). While phytoplankton cells in the ice-free water are easily diffused out of the euphotic zone and/or consumed by zooplankton, the ice-algae grown on and beneath the ice are scarcely scattered and hardly consumed. Because the water motions such as current and wave are restrained by the ice cover (WAKATSUCHI, 1982), and only a small amount of zooplankton has been reported near Syowa Station (FUKUCHI and TANIMURA, 1981) except for *Paralabidocera antarctica* (Calanoida, Copepoda) which is abundant in winter (HOSHIAI and TANIMURA, 1986). These mean that, although intrinsic productivity of ice-algae is not large, the accumulated products play an important role in the ecosystem of the sea area permanently with covered ice, where the blooming season of phytoplankton under the ice is not long enough (FUKUCHI *et al.*, 1984; SATOH *et al.*, 1986).

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