

PHOTOSYNTHETIC NATURE OF ICE ALGAE AND THEIR
CONTRIBUTION TO THE PRIMARY PRODUCTION
IN LAGOON SAROMA KO, HOKKAIDO, JAPAN

Hiroo SATOH¹, Yukuya YAMAGUCHI², Kentaro WATANABE³,
Atsushi TANIMURA³, Mitsuo FUKUCHI³
and Yusho ARUGA¹

¹Tokyo University of Fisheries, 5-7, Konan 4-chome, Minato-ku, Tokyo 108

²Laboratory of Biology, College of Liberal Arts, Saitama University,
255, Shimo-Ookubo, Urawa 338

³National Institute of Polar Research, 9-10, Kaga 1-chome, Itabashi-ku, Tokyo 173

Abstract: Photosynthetic activity of ice algae and phytoplankton was investigated under sea ice at two stations (ca. 44°10'N, 143°46'E) in lagoon Saroma Ko, Hokkaido, Japan, in early March 1987. Water temperature and salinity ranged from -1.1 to -1.4°C and from 32.4 to 33.5, respectively. The maximum chlorophyll *a* concentrations of ice algae within 4 cm from the bottom of sea ice and phytoplankton in water column were 385 and 0.77 mg m⁻³, respectively. The maximum photosynthetic rate (1.12 mgO₂ mgchl. a⁻¹ h⁻¹) of ice algae was obtained under 37.5 μE m⁻² s⁻¹, which corresponds to only 3% of incident solar radiation. These results demonstrate the low-light adaptation of ice algae grown under low light conditions. The optimum temperature for photosynthesis of ice algae was around 8°C. *In situ* measurements on a clear day gave the primary production of 1.59 mgC m⁻² h⁻¹ by ice algae and that of 1.92 mgC m⁻² h⁻¹ by phytoplankton. It was concluded that the ice algae contribute to a considerable extent to the production of organic carbon in the ice-covered area of Saroma Ko during winter.

1. Introduction

The role of ice algae as well as phytoplankton is doubtlessly important in the polar marine ecosystems (e.g., HEYWOOD and WHITAKER, 1984; HORNER, 1985). Relatively few works have been made on ice algae in areas other than the polar seas, such as in the Bering Sea (MCROY *et al.*, 1972; MCROY and GOERING, 1974), the Baltic Sea (HORNER, 1977) and the Gulf of St. Lawrence (DUNBER, 1979).

In Japan, SAJO and SAKAMOTO (1964) and MAEDA and ICHIMURA (1973) investigated the primary productivity by phytoplankton in ice-covered freshwater lakes, but they did not refer to the ice algal assemblages proliferated under ice. Although the coloration of ice by microalgae was reported in lagoon Saroma Ko when covered by sea ice (HOSHIAI and FUKUCHI, 1981), information about the photosynthetic nature of ice algae and their contribution to the primary production is still scarce.

During the ice-covered period in 1986/87, we conducted a series of investigations focussed on the photosynthetic characteristics of ice algal assemblages harvested from the sea ice as well as phytoplankton under the sea ice in Saroma Ko. In this paper,

we discuss the contribution of ice-algal production to the total primary production during the ice-covered period in Saroma Ko.

2. Materials and Methods

Field studies were carried out in early March 1987 in Saroma Ko, Hokkaido, which is a lagoon of seawater flowed in through the two channels from the Sea of Okhotsk (Fig. 1). The depth of water was 7.3 m at Stn. A and 11 m at Stn. B. The sea ice was cut out in a mass of 1 m² surface with a chain saw for the survey, and samplings of water were made through this hole. Temperature and salinity of the lagoon water were measured with a mercury thermometer and an Auto-Lab Model 601 Mk III salinometer, respectively. Water samples were taken from the layer just below the undersurface of sea ice to the bottom layer with a Van Dorn sampler made of plastic.

To collect the ice algal samples, a few centimeters of colored undersurface of ice was scraped with a knife, and the obtained ice algal samples were immediately suspended in filtered lagoon water which was kept below 0°C. Thus, the ice algae used in the present study were "a bottom assemblage" as reviewed by HORNER (1985).

Chlorophyll *a* was measured as an index of standing stock of ice algae and phytoplankton. A suitable volume of sample was filtered through a glass fiber filter (Whatman GF/C). After filtration the filters were kept frozen in a deep freezer until analyses. Pigments in the samples were extracted in 90% acetone and the concentrations of chlorophyll *a* and phaeopigments were determined by the fluorometric method of STRICKLAND and PARSONS (1972) modified by ARUGA (1979) using a Hitachi model 650-40 fluorometer.

Incident and underwater photosynthetically active radiations (PAR, 400–700 nm) were measured with an LI-COR model LI-188 integrating quantum/radiometer/photometer equipped with an LI-192SB underwater quantum sensor and an LI-190SB quantum sensor on snow cover.

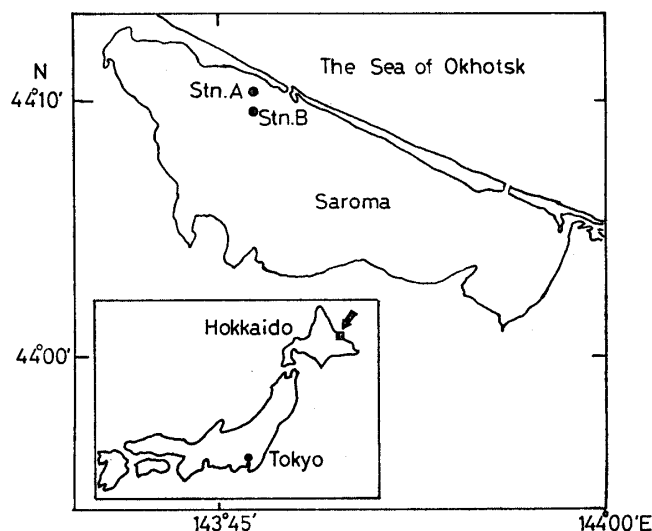


Fig. 1. Location of sampling stations in lagoon Saroma Ko, Hokkaido.

Measurements of photosynthetic activity of ice algae and phytoplankton were made with the following procedures.

Ice algae: Measurements of photosynthetic activity of ice algae were made by a tank method with the ordinary light-dark bottles, followed by the Winkler titration for dissolved oxygen (STRICKLAND and PARSONS, 1972). The light intensity was attenuated by neutral vinyl sheets rolled around the bottles. The incubations were made in temperature-controlled incubators (temperature range from 0 to 20°C) under an incandescent lamp (National, RF 110V 500W).

Phytoplankton: Measurements of photosynthetic activity of phytoplankton were made by the stable ^{13}C isotope method (SATO *et al.*, 1985). Water samples collected from the surface to 6 m depth were transferred into 1000 ml polycarbonate bottles. After adding $\text{NaH}^{13}\text{CO}_3$ (16.5% of the final atom percent of ^{13}C , Prochem), the samples were incubated at their respective original depths from noon to sunset. Immediately after the incubation, the samples were filtered through glass fiber filters (Whatman GF/C) precombusted at 450°C for 4 h. The filters were washed with the filtered seawater for removing inorganic carbon, dried completely, and stored until analyses. The concentrations of organic carbon in the samples and the isotopic ratios of ^{13}C and ^{12}C were determined by infrared absorption spectrometry (SATO *et al.*, 1985) with a JASCO ^{13}C analyzer EX-130 (Japan Spectroscopic Co., Ltd.). The calculation of photosynthetic activity was made according to the equation of HAMA *et al.* (1983).

3. Results and Discussion

3.1. Environmental conditions of the study area

Saroma Ko is iced over usually from January to April. In 1987, the ice began to grow in early January, and grew up to about 40 cm thick by early March. In late April, the ice melted and flowed away from the lagoon. The thickness of snow covering the ice attained to 8 cm at Stn. A and 5 cm at Stn. B in early March when the present study was performed. Water temperature and salinity ranged from -1.1 to

Table 1. Some environmental conditions and standing stock of phytoplankton and ice algae in lagoon Saroma Ko. For comparison, the data obtained at Syowa Station during the autumn season are included.

	Saroma Ko		Syowa Station
	Stn. A	Stn. B	
Thickness of ice (cm)	38	41	40-60*
Overlying snow (cm)	8	5	0-11*
Water temp. (°C)	-1.1 to -1.4	-1.1 to -1.4	-0.79 to -1.79*
Practical salinity	32.5-32.6	32.4-33.5	32.4-34.0*
Solar radiation ($\text{cal cm}^{-2} \text{ day}^{-1}$)	185.1-369.8**		150-250**
Maximum chl. <i>a</i> of phytoplankton (mg m^{-3})	0.63	0.77	0.59*
Maximum chl. <i>a</i> of ice algae (mg m^{-3})	142	385	237*

* The available data during the period from March to April 1983 from SATO *et al.* (1986) and WATANABE and SATO (1987).

** The available values from HOSHIAI (1981).

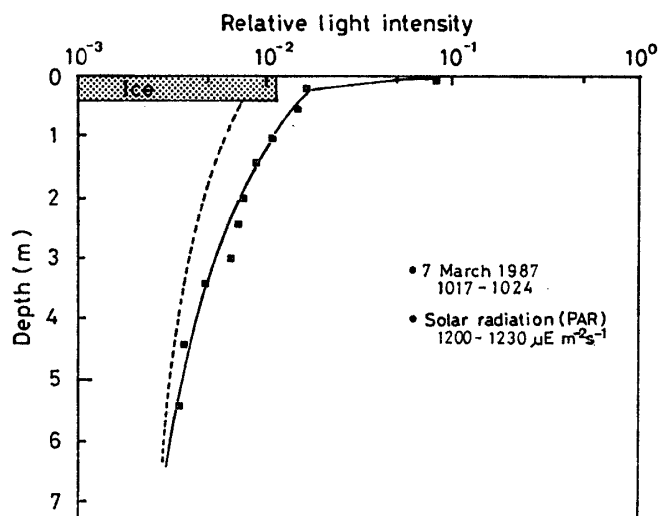


Fig. 2. Vertical profile of relative light intensity at Stn. A. The solid line represents the actual values obtained from ice hole. The dashed line indicates the values indirectly estimated in consideration of the light extinction by ice. See text for details.

—1.4°C and from 32.4 to 33.5, respectively (Table 1). Thus, the ice in Saroma Ko can be said to be sea ice as described by HOSHIAI and FUKUCHI (1981).

Incident and underwater light intensity obtained at Stn. A is shown in Fig. 2. The measured underwater light intensity in the ice-covered area might have been overestimated due to the light penetrating through the ice hole. Therefore, the approximate values extrapolated from the intensity just beneath the sea ice were estimated according to the method of WATANABE and SATOH (1987). These results indicate that the light condition at the bottom of ice was less than 1% of the incident solar radiation (Fig. 2).

Comparing the environmental conditions in winter of Saroma Ko with those in autumn of Syowa Station (HOSHIAI, 1981; SATOH *et al.*, 1986), the differences in water temperature and salinity are very small. As shown in Table 1, the thickness of ice, overlying snow and the level of solar radiation in the present site were almost the same as those in the ice-covered area near Syowa Station in autumn. Thus, the level of PAR under sea ice is considered to be almost the same at both study sites. Accordingly, it is considered that the environmental conditions in winter of Saroma Ko are similar to those in autumn in ice-covered water near Syowa Station, and that under such conditions the ice algae can favorably proliferate at the bottom of sea ice.

3.2. Standing stock of ice algae and phytoplankton

The coloration of sea ice by ice algae in Saroma Ko began from late January, and reached its maximum in early March 1987 (FUKUCHI *et al.*, 1989). More than 90% of chlorophyll *a* of ice algae was concentrated within the bottom 4 cm layer of sea ice, and the maximum value of chlorophyll *a* at Stn. B was 385 mg m^{-3} . The dominant species was *Nitzschia frigida* (WATANABE *et al.*, in prep.). The maximum concentration is almost at the same level as that obtained in autumn near Syowa Station, but it is remarkably low as compared with the values obtained in spring at

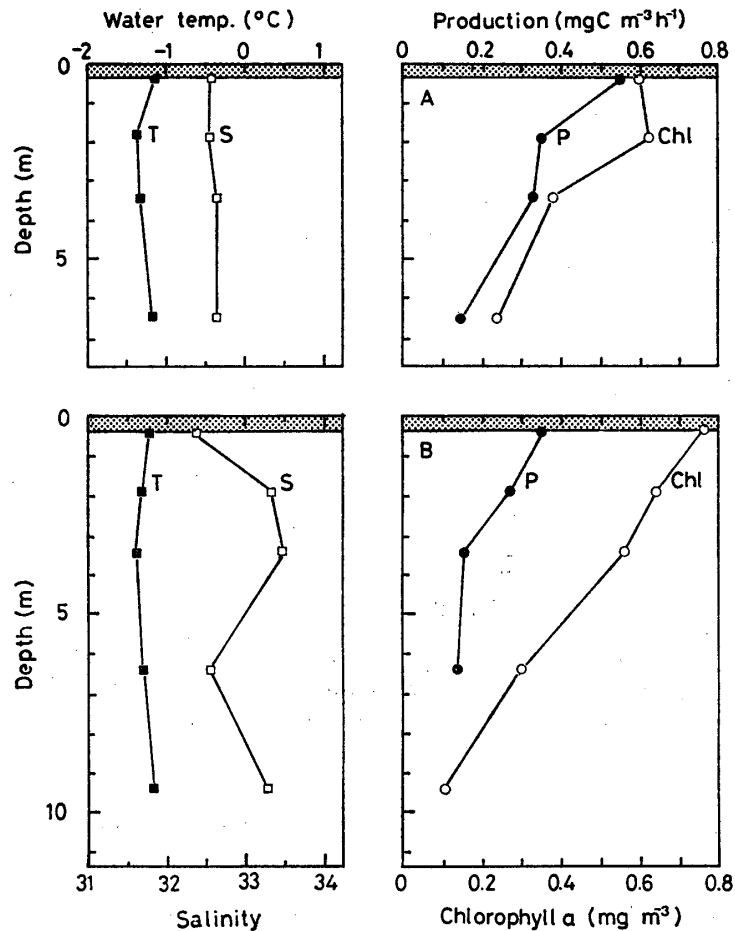


Fig. 3. Vertical distributions of temperature (T), salinity (S), chlorophyll *a* (Chl) and in situ primary production (P) at Stns. A and B.

Syowa Station (WATANABE and SATOH, 1987).

The maximum phytoplankton chlorophyll *a* concentration of 0.77 mg m^{-3} was recorded in the 0.5 m layer at Stn. B (Fig. 3). The chlorophyll *a* concentration decreased with depth at both Stns. A and B. The integrated chlorophyll *a* standing stock in the water column was 2.60 mg m^{-2} at Stn. A (0.5–6.5 m) and 3.87 mg m^{-2} at Stn. B (0.5–9.5 m). *Thalassiosira* sp. and *Nitzschia frigida* were dominant throughout the water column (WATANABE *et al.*, in prep.). The standing stock values are almost at the same level as those obtained in autumn in the coastal area near Syowa Station (SATOH and WATANABE, 1986), but they are fairly lower than those reported in Japanese freshwater lakes under ice-covered conditions (SAIJO and SAKAMOTO, 1964; MAEDA and ICHIMURA, 1973).

3.3. Photosynthetic response of ice algae to different light intensity and temperature

The photosynthesis vs. light curves of ice algae collected at Stn. A showed the maximum rate (P_{max}) of $1.12 \text{ mgO}_2 \text{ mgchl. a}^{-1} \text{ h}^{-1}$ under $37.5 \mu\text{E m}^{-2} \text{ s}^{-1}$ (Fig. 4a). The photosynthetic rate was nearly saturated at $26 \mu\text{E m}^{-2} \text{ s}^{-1}$. The saturated light intensity corresponded to 2–3% of the full sunlight at the ice surface. Thus, the ice

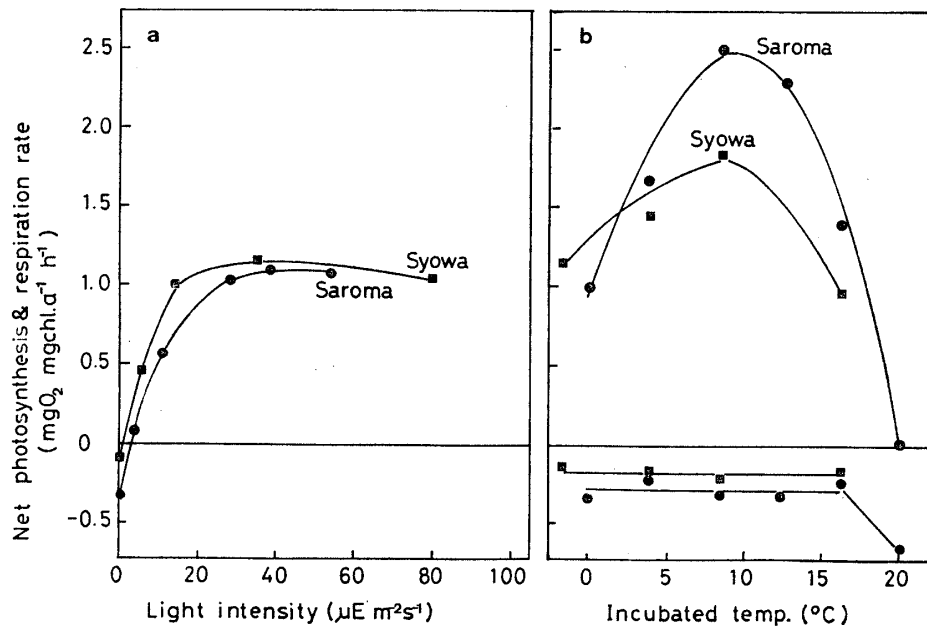


Fig. 4. A photosynthesis vs. light curve at 0°C (a), a photosynthesis vs. temperature curve under $57 \mu E m^{-2} s^{-1}$, and a dark respiration vs. temperature curve (b) of ice algae in lagoon Saroma Ko. The curves at Syowa Station are from SATOH and WATANABE (1986).

algae in Saroma Ko are said to adapt themselves to the low-light condition. The P_{max} values and the saturated light intensity for photosynthesis of ice algae in Saroma Ko were almost the same as those obtained in spring near Syowa Station (SATOH and WATANABE, 1986).

The photosynthetic rates of ice algae in Saroma Ko are shown in Fig. 4b as a function of water temperature. The photosynthetic activity was accelerated with the increase of water temperature from 0 to 8°C and the maximum rate was observed at around 8°C. Above 8°C, the photosynthetic rates declined rapidly with increasing temperature to become almost zero at 20°C. The optimum temperature for photosynthesis was almost the same as that of ice algae obtained in the Antarctic ice-covered area (SATOH and WATANABE, 1986; KOTTMEIER and SULLIVAN, 1988) and phytoplankton in the ice-free water of the Antarctic (NEORI and HOLM-HANSEN, 1982; YAMAGUCHI *et al.*, 1985). It is most likely that the optimum temperature for photosynthetic activity of ice algae in Saroma Ko as well as those of microalgae in the polar regions is around 8°C.

The rates of respiration corresponded to 10–20% of the photosynthetic rates at temperatures from 0 to 16°C, while the rate remarkably increased at 20°C (Fig. 4b).

3.4. *In situ* primary production in water column

The profiles of *in situ* primary production at Stns. A and B are shown in Fig. 3. The maximum production of $0.55 \text{ mgC m}^{-3} \text{ h}^{-1}$ was measured at 0.5 m depth at Stn. A, where the light intensity corresponded to 0.8% of the solar radiation. The *in situ* production decreased sharply with depth, and was $0.16 \text{ mgC m}^{-3} \text{ h}^{-1}$ at a 6.5 m layer. The integrated primary production in the water column was $1.92 \text{ mgC m}^{-2} \text{ h}^{-1}$ at Stn. A and $1.13 \text{ mgC m}^{-2} \text{ h}^{-1}$ at Stn. B. The difference of primary production between Stns.

A and B might, in part, be due to the difference of PAR. When the *in situ* primary production was measured, the solar radiation at around noon was about $1200 \mu\text{E m}^{-2} \text{s}^{-1}$ (clear day) at Stn. A and $700 \mu\text{E m}^{-2} \text{s}^{-1}$ (cloudy day) at Stn. B. The assimilation number, $0.27\text{--}0.90 \text{ mgC mgchl. } a^{-1} \text{ h}^{-1}$, of phytoplankton in Saroma Ko was fairly lower than that of phytoplankton in summer in fast ice area near Syowa Station ($1.14 \text{ mgC mgchl. } a^{-1} \text{ h}^{-1}$; SATOH and WATANABE, 1988) and in the ice-free water in the Antarctic (SMITH and MORRIS, 1980; JACQUES, 1983; YAMAGUCHI *et al.*, 1985; SAKSHAUG and HOLM-HANSEN, 1986), but it was almost the same as that of phytoplankton in the ice-covered season in freshwater Lake Haruna (MAEDA and ICHIMURA, 1973).

3.5. Contribution of ice algae to primary production

In the present measurements the ice algal samples were diluted with filtered lagoon water. Therefore, in the calculation the assimilation number ($\text{mgC mgchl. } a^{-1} \text{ h}^{-1}$) was multiplied by the chlorophyll *a* concentration (mg m^{-3}) to obtain the primary production. Based on the *in situ* measurements of assimilation number ($0.28 \text{ mgC mgchl. } a^{-1} \text{ h}^{-1}$) and chlorophyll *a* concentration in ice (142 mg m^{-3}), the primary production of ice algae at Stn. A was calculated for a clear day. As a result, the production by ice algae was $1.59 \text{ mgC m}^{-2} \text{ h}^{-1}$. The production by phytoplankton at Stn. A was $1.92 \text{ mgC m}^{-2} \text{ h}^{-1}$ as described above. Thus, the total primary production at Stn. A, the sum of production by ice algae and that by phytoplankton, was to be $3.51 \text{ mgC m}^{-2} \text{ h}^{-1}$. The primary production by ice algae during the ice-covered season was as much as that by phytoplankton in the water column. The contribution of ice algae to primary production in Saroma Ko was lower than that in spring near Syowa Station but higher than that in summer near Syowa Station (SATOH and WATANABE, 1988).

In conclusion, the field study demonstrated that in Saroma Ko the ice algae as well as phytoplankton play an important role as primary producers in the ice-covered season. The primary production by ice algae can provide a source of organic carbon for benthic communities, particularly for the shellfish such as scallops and oysters, which are widely maricultured in Saroma Ko.

Acknowledgments

The authors express their sincere gratitude to Prof. T. HOSHIAI (NIPR) for his helpful advice during the present study, and also to Messrs. M. OOTOMO, S. MIURA (Yubetsu Fisheries Cooperative) and H. NUMANAMI (Tokyo Univ. Fish.) for their cooperation in the field study. This study was supported in part by a Grant-in-Aid for Scientific Research from the Ministry of Education, Science and Culture, Japan (61760170).

References

- ARUGA, Y. (1979): *Sôri seiri-seitai kenkyû-hô* (Physiological and ecological methods). *Sôri Kenkyû-hô* (Methods in Phycological Studies), ed. by K. NISIZAWA and M. CHIHARA. Tokyo, Kyôritsu Shuppan, 387–412.
- DUNBAR, M. J. (1979): Biological production in the Gulf of St. Lawrence. *Marine Production Mechanisms*, ed. by M. J. DUNBAR. Cambridge, Cambridge Univ. Press, 115–171.
- FUKUCHI, M., WATANABE, K., TANIMURA, A., HOSHIAI, T., SASAKI, H., SATOH, H. and YAMAGUCHI, Y. (1989): A phytoplankton bloom under sea ice recorded with a moored system in lagoon Saroma Ko, Hokkaido, Japan. *Proc. NIPR Symp. Polar Biol.*, 2, 9–15.

- HAMA, T., MIYAZAKI, T., OGAWA, Y., IWAKUMA, T., TAKAHASHI, M., OTSUKI, A. and ICHIMURA, S. (1983): Measurement of photosynthetic production of marine phytoplankton population using a stable ^{13}C isotope. *Mar. Biol.*, **73**, 31–36.
- HEYWOOD, R. B. and WHITAKER, T. M. (1984): The Antarctic marine flora. *Antarctic Ecology*, ed. by R. M. LAWS. London, Academic Press, 373–419.
- HORNER, R. A. (1977): History and recent advances in the study of ice biota. *Polar Oceans*, ed. by M. J. DUNBAR. Calgary, Arct. Inst. North Am., 307–317.
- HORNER, R. A. (1985): Ecology of sea ice microalgae. *Sea Ice Biota*, ed. by R. A. HORNER. Boca Raton, CRC Press, 83–103.
- HOSHIAI, T. (1981): Solar radiation and stability of the undersurface of sea ice governing ice algal proliferation. *Nankyoku Shiryô (Antarct. Rec.)*, **73**, 23–29.
- HOSHIAI, T. and FUKUCHI, M. (1981): Sea ice colored by ice algae in a lagoon, Lake Saroma, Hokkaido, Japan. *Nankyoku Shiryô (Antarct. Rec.)*, **71**, 114–120.
- JACQUES, G. (1983): Some ecophysiological aspects of the Antarctic phytoplankton. *Polar Biol.*, **2**, 27–33.
- KOTTMEIER, S. T. and SULLIVAN, C. W. (1988): Sea ice microbial communities (SIMCO) 9. Effects of temperature and salinity on rates of metabolism and growth of autotrophs and heterotrophs. *Polar Biol.*, **8**, 293–304.
- MAEDA, O. and ICHIMURA, S. (1973): On the high density of a phytoplankton population found in a lake under ice. *Int. Rev. ges. Hydrobiol.*, **58**, 673–685.
- MCROY, C. P. and GOERING, J. J. (1974): The influence of ice on the primary productivity of the Bering Sea. *Oceanography of the Bering Sea*, ed. by D. W. WOOD and E. J. KELLEY. Fairbanks, Univ. Alaska, 403–421.
- MCROY, C. P., GOERING, J. J. and SHIELS, W. E. (1972): Studies of primary production in the eastern Bering Sea. *Biological Oceanography of the Northern North Pacific Ocean*, ed. by A. Y. TAKENOUTI *et al.* Tokyo, Idemitsu Shoten, 199–216.
- NEORI, A. and HOLM-HANSEN, O. (1982): Effect of temperature on the rate of photosynthesis in Antarctic phytoplankton. *Polar Biol.*, **1**, 33–38.
- SAKSHAUG, E. and HOLM-HANSEN, O. (1986): Photoadaptation in Antarctic phytoplankton; Variations in growth rate, chemical composition and *P* versus *I* curves. *J. Plankton Res.*, **8**, 459–473.
- SAIJO, Y. and SAKAMOTO, M. (1964): Photosynthetic production of phytoplankton in some ice covered lakes in the central Japan. *Recent Researches in the Fields of Hydrosphere, Atmosphere and Nuclear Geochemistry*, ed. by Y. MIYAKE and T. KOYAMA. Tokyo, Maruzen, 289–303.
- SATO, H. and WATANABE, K. (1986): Photosynthetic nature of ice-algae under fast ice near Syowa Station, Antarctica. *Mem. Natl Inst. Polar Res., Spec. Issue*, **44**, 34–42.
- SATO, H. and WATANABE, K. (1988): Primary productivity in the fast ice area near Syowa Station, Antarctica, during spring and summer 1983/84. *J. Oceanogr. Soc. Jpn.*, **44**, 287–292.
- SATO, H., YAMAGUCHI, Y., KOKUBUN, N. and ARUGA, Y. (1985): Application of infrared absorption spectrometry for measuring the photosynthetic production of phytoplankton by the stable ^{13}C isotope method. *La Mer*, **23**, 171–176.
- SATO, H., WATANABE, K., KANDA, H. and TAKAHASHI, E. (1986): Seasonal changes of chlorophyll *a* standing stocks and oceanographic conditions under fast ice near Syowa Station, Antarctica. *Nankyoku Shiryô (Antarct. Rec.)*, **30**, 19–32.
- SMITH, A. E. and MORRIS, I. (1980): Pathways of carbon in phytoplankton from the Antarctic Ocean. *Limnol. Oceanogr.*, **25**, 865–872.
- STRICKLAND, J. D. H. and PARSONS, T. R. (1972): A practical handbook of seawater analysis. *Bull. Fish. Res. Bd. Can.*, **167**, 1–310.
- WATANABE, K. and SATO, H. (1987): Seasonal variations of ice algal standing crop near Syowa Station, East Antarctica, in 1983/84. *Bull. Plankton Soc. Jpn.*, **34**, 131–150.
- WATANABE, K., SATO, H., FUKUCHI, M., TANIMURA, A. and YAMAGUCHI, Y. (in prep.): Seasonal variations in standing crop and species composition of ice algae and phytoplankton in lagoon Saroma Ko in the 1986/87 season.
- YAMAGUCHI, Y., KOSAKI, S. and ARUGA, Y. (1985): Primary productivity in the Antarctic Ocean during the austral summer of 1983/84. *Trans. Tokyo Univ. Fish.*, **6**, 67–84.

(Received April 5, 1988; Revised manuscript received September 22, 1988).