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Floristic examination of diatom assemblage in the dim light-environment of water column and sea ice, Saroma Ko lagoon, Hokkaido, Japan

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Abstract: The species composition and abundance of diatoms were examined concurrently in both the sea ice and the water column of ice-covered Saroma Ko lagoon in early February 1996. Cell counts indicated that the ice algal assemblage collected from the bottom 10 cm of the sea ice was dominated by *Detonula confervacea, Thalassiosira* spp. and *Fragilariopsis cylindrus* in order of total cell volume. These three groups accounted for 66% of the total diatom abundance in the sea ice. The centric and pennate diatoms accounted for 52.3% and 47.7% of the abundance of the ice algal assemblage, respectively. The phytoplankton assemblage collected from the water column at the depth of 4 m was dominated by *Thalassiosira* spp., *T. nordenskioeldii* and *D. confervacea*. These three groups accounted for 92% of the total phytoplankton diatom abundance. The centric diatoms accounted for as much as 98.8% of the abundance of the phytoplankton assemblage whereas the pennate diatoms accounted for only 1.2%. Two of the three dominant phytoplankton groups were observed in both the ice algal and phytoplankton assemblages, but *T. nordenskioeldii* was present only in the latter. The groups observed only in the phytoplankton assemblage accounted for 20% of the total phytoplankton abundance. It was assumed that the phytoplankton assemblage included some species released from the sea ice and others living independently in the water column where light was severely limited. In response to the improvement of the light-environment, those cells surviving in the water column during winter can resume growth soon after the disappearance of the sea ice cover.

key words: diatom, winter phytoplankton, ice algae, light environment, ice edge

Introduction

In ice-covered seas, light energy penetrating into the water column is severely restricted by the presence of sea ice and snow during winter (Maykut and Grenfell, 1975; Kishino *et al.*, 1993). Ice algae proliferating within the ice layer further reduce the small amount of light energy (Meguro *et al.*, 1967; Kishino *et al.*, 1993). Thus, the formation of sea ice may drastically change the light environment for planktonic algae in the water column (Kudoh, 1993).

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During the ice coverage, the abundance of ice algae gradually increases due to the upward movement of nutrients through brine channels, whereas that of autotrophic phytoplankton is usually low due to light-limitation of growth (Horner and Schrader, 1982; Legendre *et al.*, 1992; Hegseth, 1992). After the ice breakup in spring, the phytoplankton bloom, mainly consisting of pennate and centric diatoms, immediately occurs in the surface low-salinity water which is derived from meltwater of sea ice (Taniguchi *et al.*, 1976; Smith and Nelson, 1985; Garrison *et al.*, 1987; Syvertsen, 1991; Hsiao, 1992). The phytoplankton bloom is dominated by algae released from the sea ice and also by pelagic species (Syvertsen, 1991; Hegseth, 1992). The sea ice supplies a habitat with adequate light to which the algae adhere, and may also play a role in increasing the inoculum for the early spring bloom (Schandelmeier and Alexander, 1981; Smith and Nelson, 1985; Garrison *et al.*, 1987; Syvertsen, 1991).

Taxonomic and ecological reviews are available for the ice algae (Horner, 1985; Medlin and Priddle, 1990). Relatively little information is available for the phytoplankton beneath the sea ice, although it is recognized as a possible seed population for the ice algae (Horner and Shrader, 1982; Syvertsen, 1991; Niimura *et al.*, 2000). It has been observed that pennate diatoms, which might be released from the sea ice, dominate the phytoplankton population in winter, but centric diatoms, such as *Thalassiosira* and *Chaetoceros*, occur at the surface of the water column early in the spring (Horner and Shrader, 1982). Such examination on a taxonomic basis should provide a clue to understanding the possible effect of sea ice on the phytoplankton assemblage during ice coverage as well as after ice melting.

This study was carried out in a semi-enclosed lagoon, Saroma Ko (44°N, 144°E) (near St. 1 by Kudoh *et al.*, 1997). The lagoon, which is connected to the Sea of Okhotsk via two channels, is located at the southernmost limit of seasonal sea ice in the Northern Hemisphere (*cf.* Fig. 1.1 in Medlin and Priddle, 1990). The mean depth of the lagoon is 14.5 m, and its surface is covered by sea ice for two to three months in winter (Taguchi and Takahashi, 1993, Shirasawa, 1993). Sea ice formation begins in January, the thickness increases to 20–30 cm, and ice covers the surface in February (Kudoh *et al.*, 1997). The abundance of Chl *a* in the ice ranges from a few tens to 100 mg m^{-2} (Kudoh *et al.*, 1997; Robineau *et al.*, 1997). Previous studies have demonstrated that the ice algal assemblage in Saroma Ko lagoon consists of centric diatoms, such as *Detonula confervacea* and *Melosira hyperborea* (*M. arctica*), and pennate diatoms, such as *Navicula* spp. and *Nitzschia* spp. (Takahashi, 1981; Kikuchi-Kawanobe and Kudoh, 1995). Immediately after the ice breakup, the phytoplankton bloom, mainly consisting of centric diatoms, is usually observed (Tada *et al.*, 1993; Kashino *et al.*, 1998).

This study aimed to investigate the species composition and the abundance of autotrophic diatoms in the sea ice as well as in the water column. The results are discussed, with attention to possible alteration of their seasonal occurrence by the sea ice.

Materials and methods

The field site was located 1 km offshore in the eastern Sakae-ura basin of Saroma Ko (44°07′N, 143°58′E). Water depth at the site was 6.5 m. The ice-core sample (diameter 7.5 cm, thickness 35 cm) was taken at 0930 on 7 February, 1996. The bottom 10 cm of the ice-core sample was collected for the ice algal sample and melted at $<5°$C. Unfortunately, some seawater might have drained from the brine channels during collection of the ice-core. At the same site, the vertical profile of temperature and salinity in the water column beneath the sea ice was measured with a CTD sensor (AST-200, ALEC Electronics Co.) at 1530 on 6 February and 1000 on 7 February. The light-intensities above the snow and at 30 cm beneath the bottom of the sea ice were measured with a 4π quantum sensor (SPQA, LI-COR) fixed to an L-shaped rod (50 cm long) together with a 2π quantum sensor (UWQ, LI-COR) in the air. The measurement was made after closing the ice hole through which the quantum sensor was lowered. Temperatures in the air, at the interface between the snow and the ice, in the ice at 10, 20 and 30 cm beneath the snow-ice interface, and in the seawater at 50 cm beneath the bottom of the ice were measured every 10 min with copper-constantan thermocouples. The measurements were initiated 12 hours after the fixation of the sensors.

A phytoplankton sample was collected from a depth of 4 m in the water column with a Kitahara-type water bottle. Glutaraldehyde solution was immediately added at 1% (final conc.) to the ice and water samples, which were covered with a sheet of aluminum foil and stored in the refrigerator until microscopic examination. Both ice and water samples were allowed to settle for three days and then reduced in volume from 50 to 25 m*l* for the ice and 150 to 2 m*l* for the water. Diatoms were identified and counted in 0.1 m*l* of each concentrated sample on a flat slide ruled by 1-mm squares (Rigo-sha & Co., Ltd.) with a light microscope (BX50, Olympus). In order to count those unamenable to sink by settlement (small *Chaetoceros* sp.), 2 m*l* for the ice and 10 m*l* for the water sample were filtered on a 0.2 μm Nucleopore filter and additional observation was also done with an epifluorescence microscope (EFD2, Nikon). The identification of species follows the literature (Poulin and Cardinal, 1982a, b, 1983; Medlin and Priddle, 1990; Hasle and Syvertsen, 1996). The approximate geometrical shape of each species or group was determined and cell volume was calculated based on measurements of one to 10 cells per group (Kovala and Larrace, 1966). The abundance of each species or group was evaluated from the cell density and the volume. The cell size is presented as the diameter of spherical volume equivalent to the cell volume (ESD).

Another five ice-core samples were collected and sliced every 5 cm thickness. Each section of the ice was crushed and melted at $<5°$C. A portion of the meltwater from each section was filtered through a glass fiber filter (GF/F, Whatman) to determine Chl *a* and phaeopigment concnetrations. Seawater samples were collected from depths of 0, 2, 4 and 6 m with a Kitahara-type water bottle and filtered through a GF/F filter. The filters were frozen in the dark until analysis. The concentration of Chl *a* was determined with a fluorometer (Model 10-AU, Turner Designs) after extraction in

N,*N*-dimethylformamide (Suzuki and Ishimaru, 1990). The fluorometer was calibrated with purified Chl *a* (Sigma).

Results

Sea ice formation at the study site in Saroma Ko lagoon started on 23 January, 1996. The thickness increased to 35 cm by 6 February. The snow thickness was 5–8 cm on 6 February. The sea ice continued to thicken to 50 cm on 6 March. The entire surface was covered by sea ice until early April. The vertical profiles of temperature, salinity, σ_t and Chl *a* in the water column on 6 and 7 February are shown in Fig. 1. Both temperature and salinity increased slightly with depth down to 2 m (Fig. 1A and C). Below 2.5 m, salinity continued to increase slightly whereas temperature was relatively homogeneous except near the bottom (6 m). The profile of σ_t shows a weak pycnocline at a depth of 2.5 m (Fig. 1B and D). The σ_t profile also indicates a pycnocline between the sea ice and the depth of 1.5 m. The former pycnocline was relatively stable, but the latter pycnocline varied due to the decrease in salinity beneath the sea ice on 7 February. The time measurement (Fig. 2) indicated that the temperature in the water column (50 cm beneath the bottom of the ice) ranged between -1.8°C and -1.4°C on 7 February, whereas at the interface between snow and sea ice it ranged between -5.6°C and -3.4°C. Thus, the water temperature was cooled at the interface between the water and sea ice. However, the snow temperature was higher than the ice temperature (down to 20 cm beneath the snow-ice interface) for two hours around mid-day. The ice temperature thereafter gradually increased whereas the snow temperature immediately decreased concomitantly with the decrease in the air temperature. Thus, the mean temperature between 1800 and 2000 at 10, 20 and 30 cm beneath the snow-ice interface was 0.3, 0.4 and 0.3°C higher than those between 0400 and 1300, respectively.

The light intensity beneath the sea ice on 7 February was 5μE $m^{-2}s^{-1}$, equivalent to 0.5% of the irradiance at the top sea ice surface. About 95% of the surface irradiance was reflected at the snow surface. The day length was 10.8 hours.

The concentration of Chl *a* in the water column decreased with depth, although the values in the upper low salinity layer fluctuated considerably during the two days (Table 1, Fig. 1B and D). Chl *a* was observed throughout the sea-ice layer; the highest concentration was in the bottom 5 cm layer. The value was an order of magnitude higher than the maximum value in the water column (at 0 m or 2 m). The concentration of Chl *a* at 4 m in the water column was 5% of the mean concentration in the bottom 10 cm sea-ice layer. The relative abundance of phaeopigments against Chl *a* plus phaeopigments in the water column was 10–20%, nearly the same as that in the sea ice.

Twenty-five taxonomic groups, though some groups were not identified to species level, were identified for the ice algal diatoms and the phytoplankton diatoms (Table 2). The groups consisted of 13 centric diatoms and 12 pennate diatoms. Six centric species, *Skeletonema costatum, Thalassiosira nordenskioeldii, Thalassiosira*. sp., *Chaetoceros debilis, Ch. socialis* and *Ch*. spp. and one pennate, a *Pseudo-nitzschia seriata* type, were observed only in the plankton sample. Four centric species, *Melosira arctica,*

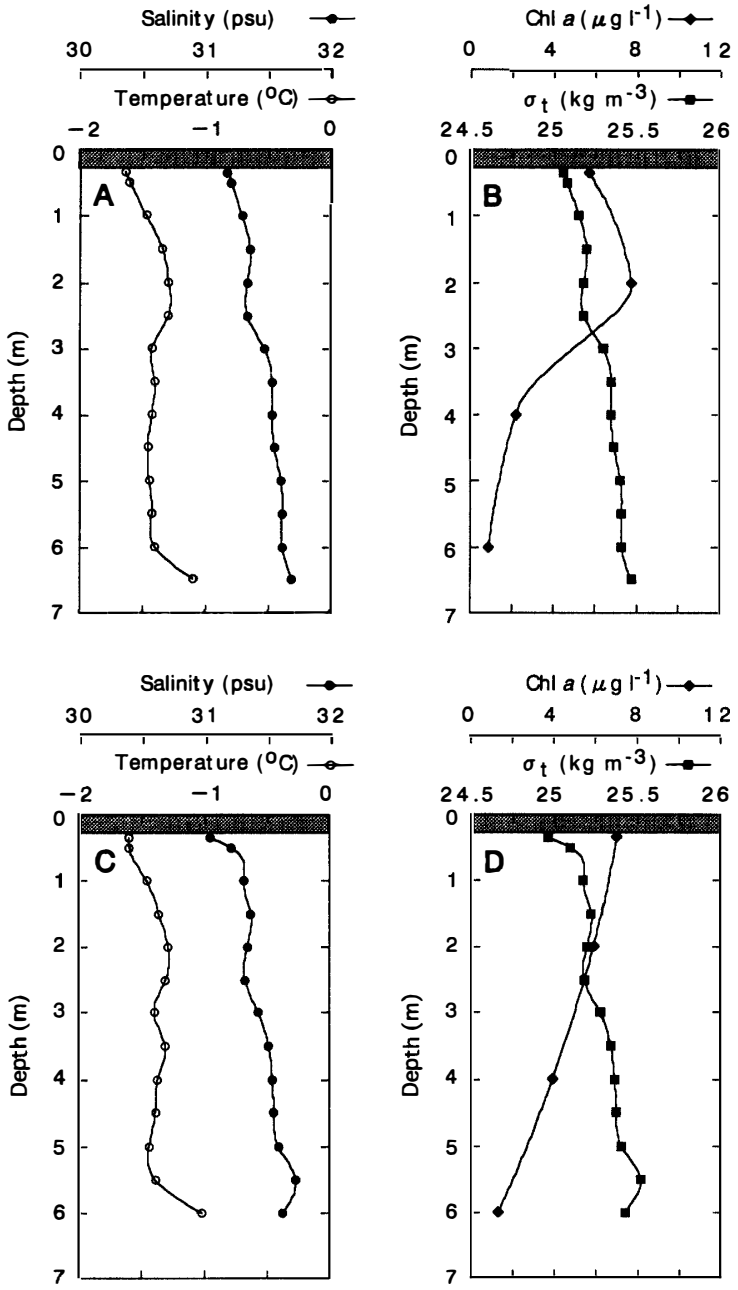

Fig. 1. Vertical profiles of salinity and temperature (A and C), and Chl *a* concentration and σ_t (B and D) in the water column below the sea ice on 6 (A and B) and 7 (C and D) February, 1996.

Ch. decipiens f. *singularis, Odontella aurita* and *O. longicruris* and seven pennate species, *Achnanthes taeniata, Entomoneis alata, Navicula pelagica, Nav.* sp., *Pinnularia quadratarea, Nitzschia arctica* type and *Nit. Frigida*, were observed only in the ice algae sample. Three centric species, *Detonula confervacea, Thalassiosira* spp. and *Ch.* sp. and four pennate species, *Nav. kariana* var. *detersa, Nav. kariana* var. *frigida, Nav. vanhoeffenii* and *Fragilariopsis cylindrus*, were commonly observed in both samples. It cannot not be concluded that the apparent preferential occurrence of the diatoms was

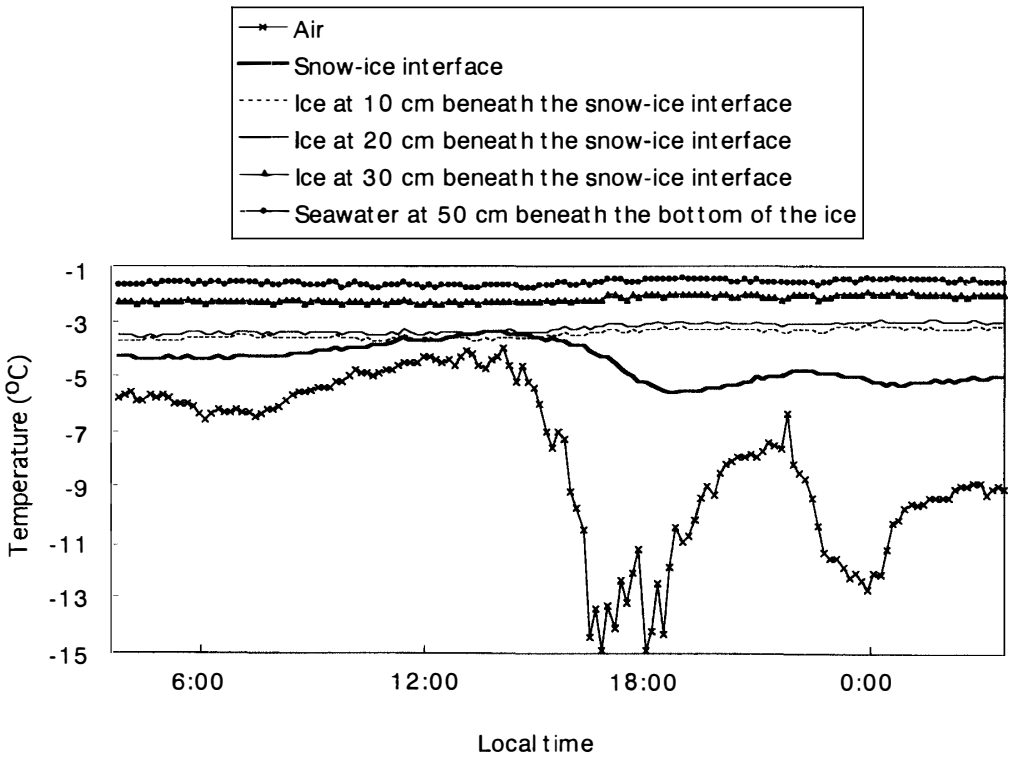

Fig. 2. Time variation of temperature in the air, the interface between the snow and the ice, the ice (at 10, 20, 30 cm below the snow) and the water at 50 cm below the bottom of the sea ice on 7 February, 1996.

Table 1. The concentration of Chl *a* and phaeopigments in and below the sea ice in Saroma Ko lagoon, Japan.

	6 February			7 February		
	Chl *a* ($\mu g\, l^{-1}$)	Phaeo. ($\mu g\, l^{-1}$)	Chl *a* (mg m^{-2})	Chl *a* ($\mu g\, l^{-1}$)	Phaeo. ($\mu g\, l^{-1}$)	Chl *a* (mg m^{-2})
In ice (from the top)			3.2			5.3
0 - 5 cm	2.9	1.0		4.5	1.3	
5 - 10 cm	1.7	0.5		4.3	1.0	
10 - 15 cm	2.0	0.5		3.3	0.8	
15 - 20 cm	2.2	0.3		3.8	0.5	
20 - 25 cm	4.8	0.9		6.4	0.9	
25 - 30 cm	4.5	0.8		18.5	4.6	
30 - 35 cm	93.1	9.5		136	14.9	
In seawater (below the ice)			26.3			28.1
0 m	5.7	0.9		7.0	1.2	
2 m	7.7	-0.7		5.9	1.0	
4 m	2.2	0.6		3.9	0.6	
6 m	0.9	0.2		1.3	0.4	

obligate for either assemblage or environment, since the data are based on a limited volume of samples. The counted cells in both the ice and plankton samples retained undistorted chloroplasts as well as clear chlorophyll fluorescence under the present microscopic observation.

In the ice algal assemblage, six groups occurred as more than 1000 cells ml^{-1} and

Table 2. Diatom species or groups observed in the bottom 10 cm of sea ice and in the water column at a depth of 4 m in Saroma Ko lagoon, Japan, on 7 February, 1996.

Order	Species or group	Ice algae			Phytoplankton			Ratio
		ESD* (μm)	Cell number [1] (Cells ml^{-1})	Cell volume (μm^3 ml^{-1})	ESD (μm)	Cell number [2] (Cells ml^{-1})	Cell volume (μm^3 ml^{-1})	[2] [1]$^{-1}$ (%)
Centrales	*Detonula confervacea*	16.4	3960	9220000	13	98.7	115000	2.5
	Skeletonema costatum	–	–	–	9.9	1.1	553	
	Thalassiosira nordenskioeldii	–	–	–	22.6	30.1	160000	
	Thalassiosira sp.	–	–	–	12.4	64.8	65000	
	Thalassiosira spp.	28.6	645	7900000	30	57.3	813000	8.9
	Melosira arctica	28.6	30	368000	–	–	–	
	Chaetoceros debilis	–	–	–	11.5	0.8	631	
	Chaetoceros decipiens f. *singularis*	13.6	90	118000	–	–	–	
	Chaetoceros socialis	–	–	–	10	24.5	12900	
	Chaetoceros sp.	3.7	1530	41800	3.7	24.8	631	1.6
	Chaetoceros spp.	–	–	–	10.9	5.6	3780	
	Odontella aurita	25.2	60	501000	–	–	–	
	Odontella longicruris	25.1	30	247000	–	–	–	
Pennales	*Achnanthes taeniata*	8.4	2910	891000	–	–	–	
	Entomoneis alata	31.6	45	742000	–	–	–	
	Navicula kariana var. *detersa*	21.2	690	3450000	19.3	0.3	1130	0.04
	Navicula kariana var. *frigida*	11.1	480	339000	11.3	2.7	2040	0.56
	Navicula pelagica	7.2	330	65000	–	–	–	
	Navicula vanhoeffenii	15.4	150	286000	13.8	4.3	5910	2.9
	Navicula sp.	5.1	15	1060	–	–	–	
	Pinnularia quadratarea var. *quadratarea*	36.2	75	1860000	–	–	–	
	Fragilariopsis cylindrus	6.3	45000	6010000	5.6	58.7	5290	0.13
	Pseudo-nitzschia seriata type	–	–	–	7.7	1.3	306	
	Nitzschia arctica type	12.0	2100	1890000	–	–	–	
	Nitzschia frigida	13.3	1010	1230000	–	–	–	
Total				35159860			1186171	

* : equivalent spherical diameter

– : not observed

five groups occurred as more than 100 cells ml^{-1}, these groups accounted for eleven groups within the eighteen groups found in the ice. However, caution must be paid to interpretation of the cell density figures. Some of the diatom cells in the brine channels were possibly lost, since the ice algal sample was obtained by melting the sea ice from which seawater might drain away during sampling of the ice-core. In addition, the cell density of ice algae proliferating mostly in the bottom few centimeters of the ice might be diluted by melting at the bottom of the ice. In the phytoplankton assemblages, all eleven of the dominant ice groups occurred as less than 100 cells ml^{-1}. The lower limit for detection in the present study was around 15 and 0.2 cells ml^{-1} for the ice algal assemblage and the phytoplankton assemblage, respectively. The ratios of occurrence of common groups were in the range between 0.04% and 8.9% and mostly less than 3%, when the cell densities in the phytoplankton assemblage were compared with those in the ice algal assemblage (Table 2). Most of the common groups occurred at high densities in the ice algal assemblage, although the cell density of *Nav. vanhoeffenii* was as low as 150 cells ml^{-1}. The cell densities of most of the groups observed only in the ice algal assemblage were less than 100 cells ml^{-1} whereas those of *A. taeniata, Nit. arctica* type and *Nit. frigida* were more than 1000 cells ml^{-1}.

The abundance of each group was evaluated from the cell volume. The abundant ice algae were *D. confervacea, Thalassiosira* spp. and *F. cylindrus*. These three groups accounted for 66% of the total abundance of the ice algal assemblage. These groups were observed in the phytoplankton sample as well. The centric diatoms and the pennate diatoms accounted for 52.3% and 47.7% of the abundance of the ice algal assemblage, respectively. The abundant plankton were *Thalassiosira* spp., *T. nordenskioeldii* and *D. confervacea*. These three groups accounted for 92% of the total plankton abundance. Two of the three dominant phytoplankton groups were commonly observed in both the ice algal and the phytoplankton assemblages, but *T. nordenskioeldii* was present only in the latter. The centric diatoms accounted for as much as 98.8% of the abundance of the phytoplankton assemblages whereas the pennate diatoms accounted for only 1.2%. The groups observed only in the phytoplankton assemblage accounted for 20% of the total abundance of the phytoplankton assemblage. The total abundance of the phytoplankton assemblage was 3.4% of that of the ice algal assemblage. The value was 0.7% if the groups observed observed only in the phytoplankton assemblage were considered.

The equivalent spherical diameter (ESD) of the ice algae ranged from 3.7 to 36.2 μm with a mean value of 17.2 μm; that of the plankton ranged from 3.7 to 30.0 μm with a mean value of 13.0 μm. The cells observed only in the plankton assemblage ranged from 3.7 to 22.6 μm with a mean value of 12.1 μm. If the values for Thalassiosira were excluded from the phytoplankton, the range of ESD tended to decrease further and ranged from 3.7 to 11.5 μm with a mean value of 10.0 μm.

Discussion

The examination of diatoms in the ice algal assemblage and in the phytoplankton assemblage beneath the sea ice showed distinct characteristics in species composition and the abundance of each assemblage, although the results were based on a single

limited volume of sample. The light energy penetrating into the water column was severely reduced due to reflection and attenuation by snow and sea ice. As much as 95% of the surface irradiance was reflected at the snow surface. The light intensity at the surface of the water column was 0.5% of the surface irradiance at the top of the sea ice. Thus, it is assumed that the light environment for the phytoplankton in the water column was unfavorable to sustain autotrophic growth by photosynthesis. The light intensity at a depth of 4 m where the sample for the phytoplankton assemblage was taken would be less than 0.1% if attenuation in the water column is considered. However, the profiles of hydrographic condition and Chl *a* concentration indicated that the water column below the ice was not always stable.

The concentration of Chl *a* in the lowermost section of the sea ice was at least an order of magnitude higher than that beneath the sea ice (Table 1). About 90% of the total Chl *a* abundance in the sea ice was found in the bottom 10 cm layer. The Chl *a* concentration at depth 4 m in the water column was about 3% of the Chl *a* concentration in the bottom 10 cm layer of the sea ice. However, the Chl *a* abundance of phytoplankton integrated throughout the water column was about 7 times as high as that of the ice algae. Due to the contribution of phytoplankton other than diatoms, the Chl *a* abundance should give an excessive estimate for the plankton diatoms (Robineau *et al.*, 1999). In addition, the abundance of ice algae might be underestimated due to possible loss of diatoms from brine channels in the ice core. Nevertheless, the Chl *a* abundance in the water column was large.

Several diatom groups, which were found in the ice algal assemblage at high cell density, were observed in the phytoplankton assemblage as well. The cell density in the phytoplankton assemblage accounted for from 0.04% to 8.9% of that in the ice algal assemblage when the latter value was estimated by melting the bottom 10 cm layer of sea ice (Table 2). It is possible that those species commonly observed in both the ice algal and the phytoplankton assemblages had been released from the sea ice into the water column. Floristic examination also showed that the species composition of the phytoplankton assemblage was not always similar to that of the ice algal assemblage. Thus, it was assumed that the phytoplankton assemblage included both species released from the sea ice and others independently living in the water column.

The concentration of Chl *a* beneath the sea ice on 7 February was the highest in the water column, 1.2 times higher than on the previous day (Table 1 and Fig. 1). It seemed likely that the temperature and salinity at the interface between the sea ice and the water column changed due to variations of the solar irradiance and air temperature. The process of sea ice formation provides dense high salinity water in brine channels and should result in vertical mixing in the upper layer of the water column and heat transport from the water column to the upper ice-layer. It also induces drainage of ice algae from brine channels (Ackley *et al.*, 1979). However, both snaps of vertical profiles of temperature and salinity and the time change of temperature in the sea ice showed that daily fluctuation occurred in the sea ice and the water column (Figs. 1 and 2). It is not probable that sea ice formation proceed without partial melting at the bottom of sea ice even in early February. The bottom sea ice transiently melts, which releases the ice algae. The release of the ice algae might increase the biomass of the phytoplankton assemblage in the water column where the light-energy is severely

limited. Nevertheless, the abundance of the groups observed only in the phytoplankton accounted for 20% of the total phytoplankton abundance (Table 2).

The groups observed only in the phytoplankton assemblage could tolerate the dim light in the water column. Using axenic cultures, Antia (1976) showed that many marine diatoms, mainly cold-water types, can tolerate darkness at 2°C for >5 months. Peters and Thomas (1996) further confirmed that several strains of polar phytoplankton survive as vegetative forms at 0°C for at least 3 and up to 9 months. The integrity of their photosynthetic apparatus lasted for 3 months and growth immediately recovered by returning to the light-conditions (Peters and Thomas, 1996). Such species could remain in the water column even in the dark and cold under sea ice. Otherwise, some of the phytoplankton might remain in the low salinity layer which developed beneath the sea ice and might increase the light absorption. Among the groups observed only in the phytoplankton assemblage, *T. nordenskioeldii* accounted for 66% of the abundance and was large in ESD whereas other diatoms had relatively smaller ESD. *T. nordenskioeldii* might not only continue to tolerate darkness but to grow actively in the low salinity layer. *T. nordenskioeldii* is one of the first diatoms to appear in the spring bloom; it grows well under low light intensity at low temperature (Jitts *et al.*, 1964). The daily temporal change in heat balance between the solar irradiance and the air temperature formed low-salinity water so as to create a temporal pycnocline beneath the sea ice (Figs. 1 and 2). The development of the low salinity layer due to the transient ice-melting at the bottom of sea ice might allow initial growth of such a species before the disappearance of the sea ice.

In Saroma Ko lagoon, sea ice cover usually disappears at the end of March or in early April (Taguchi and Takahashi, 1993; Shirasawa, 1993). Thereafter, the light environment in the water column suddenly becomes favorable due to direct solar-incidence into the water column; those species that survived in the vegetative form in the water column or in the low salinity water layer beneath the sea ice can resume growth soon after breakup of the sea ice.

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