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SEDIMENTATION OF MICROALGAE UNDER THE ANTARCTIC FAST ICE IN SUMMER

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Abstract: The development of ice algae and phytoplankton, and their sedimentation processes were studied in the Antarctic ice-covered sea near Syowa Station in the austral spring and summer 1982–83. The chlorophyll *a* concentration of ice algae at the bottom ice markedly increased from September to December, reaching the maximum of $>300\,mg\cdot m^{-3}$ in the ice algal bloom, and decreased abruptly in January. Phytoplankton chlorophyll *a* levels in the water column under the ice were low until December but increased in January ($>2\,mg\cdot m^{-3}$). Changes in sedimentation rates of sinking particles showed that large ice algal aggregates which were the major component during the ice algal bloom detached from the undersurface of the ice and sank down to the sea floor. On the contrary, during the phytoplankton bloom, solitary diatoms, chain-forming diatoms and small algal aggregates constituted a significant portion of sinking particles. Sedimentation fluxes of fecal pellets of herbivorous zooplankton including diatoms decreased during the ice algal bloom. The microalgae have a high probability of reaching the bottom during the summer growing season and become an important food for benthic organisms.

1. Introduction

Recent work indicates that microalgae associated with ice (ice algae) play an important role in primary production in the polar seas (*e.g.* BUNT, 1963; BUNT and LEE, 1970). Microalgae, usually pennate diatoms, form dense algal mats attached to undersurface of the ice. The ice algal biomass begin to increase in spring or early summer in response to increasing light (HOSHIAI, 1981a, b; SULLIVAN *et al.*, 1985). Suspending microalgae (phytoplankton) blooms in the shallow water column under the ice have also been observed to occur after the ice algal bloom (GRAINGER and HSIAO, 1982; HORNER and SCHRADER, 1982). LEGENDRE *et al.* (1981) suggested that one of the possible causes of phytoplankton blooms under the ice was the ice algae released from melting ice.

In the Antarctic ice-covered sea, a number of benthic animals have been observed by divers (GRUZOV, 1977) and by the use of an underwater television and camera system (HAMADA *et al.*, 1986). One of the major food sources for these benthic animals is derived from primary producers in the upper layers, particularly during spring and summer. It, therefore, is important to clarify the sedimentation processes of microalgae in order to understand the relationship between seasonal phytoplankton increase

and abundant benthic animals. Only a few workers observed the sedimentation rates of particles under the fast ice in Lützow-Holm Bay, Antarctica in February 1979 and suggested the primary importance of zooplankton fecal pellets in downward transportation with ice algae (FUKUCHI and SASAKI, 1981). However, the fate of detached ice algae, or the extent to which ice algae and phytoplankton are consumed by herbivores during sinking is not well known. Our objectives were to measure downward fluxes of organic particles in order to describe the sedimentation processes of microalgae in the Antarctic fast ice region during the spring and summer.

2. Materials and Methods

The observations were conducted at Stn. 1 (69°00′00″S, 39°35′00″E) in the Kita-no-seto Strait near Syowa Station, East Ongul Island, Antarctica, from September to December, 1982 (Fig. 1, Table 1). In January 1983, the sampling site was changed to Stn. 3 (68°59′57″S, 39°37′16″E), because Stn. 1 became inaccessible due to heavy ice melting. Depth of water at Stns. 1 and 3 was about 10 and 40 m, resepectively. The ice thickness at the stations was about 100 and 150 cm, respectively.

Particle interceptor traps used to measure the sedimentation rates were similar to those described by FUKUCHI and SASAKI (1981) and SASAKI and NISHIZAWA (1981). Traps were suspended through an ice hole (1 × 2 m) at the depths of 1.6 and 5.6 m under the ice bottom at Stn. 1, and 0.3, 10 and 30 m at Stn. 3. The trap at 0.3 m was separately suspended about 3 m away from the hole by a diver in order to collect directly ice algae released from the bottom ice. Suspension periods were three days at Stn. 1 and about eight days at Stn. 3. Plant pigments and particulate organic carbon (POC) were determined using an aliquot of each sample. The rest of the particles collected were counted according to their morphology, and were examined for their

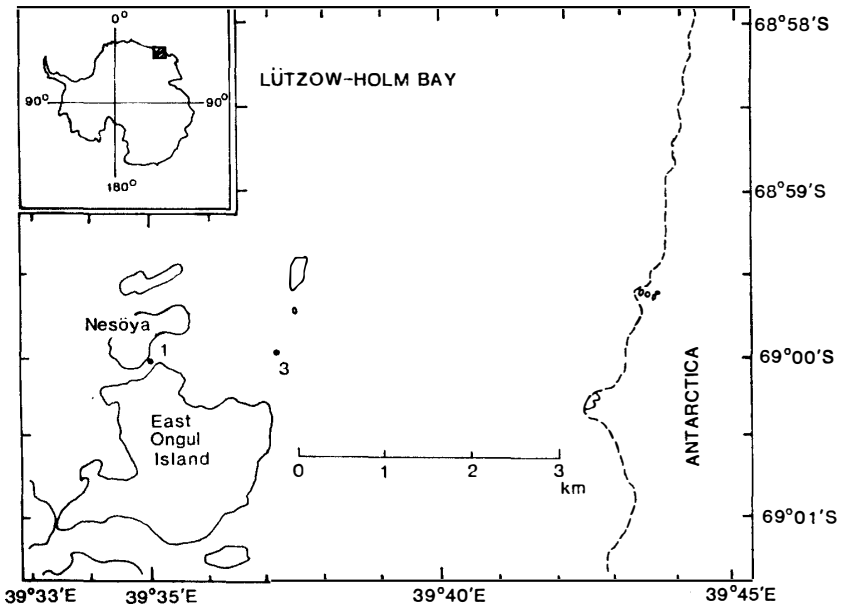

Fig. 1. Location of study sites of Stn. 1 (September–December 1982) and Stn. 3 (January 1983) near Syowa Station, Antarctica.

Table 1. Date of sampling of ice core, sea water and sinking particles.

	Ice core samplings	Sea water samplings	Trap deployments
September 15, 1982	×		
October 18	×		
November 5		×	
〃 5–7			×
〃 18	×		
〃 25		×	
〃 25–27			×
December 9		×	
〃 9–11			×
〃 17	×		
〃 23		×	
〃 23–25			×
January 14, 1983		×	
〃 19	×		
January 20–February 2			×

internal constituents. Collected particles were classified into three size fractions of small (50–200 μm), medium (200–1000 μm) and large (> 1 mm) particles in terms of the longest dimension.

Water samples (including phytoplankton) were taken with a Van Dorn bottle from the corresponding depths of suspended particle interceptor traps at Stn. 1. At Stn. 3, sampling depths were 1 and 5 m where the highest chlorophyll *a* concentrations were found in the whole water column. One liter of water from each sample was filtered through a Whatman GF/C glass fiber filter for fluorometric determination of plant pigments (SAIJO and NISHIZAWA, 1969). An aliquot of 2 *l* of water was filtered through a precombusted Whatman GF/C glass fiber filter for POC determination by a dry combustion method (STRICKLAND and PARSONS, 1972).

Ice core samples (including ice algae) were taken close to the hole with an ice corer (SIPRE ice-coring auger; 8 cm in diameter). The bottom 3–5 cm of cores were melted and used for the determinations of plant pigments. Date of samplings are summarized in Table 1.

3. Results

3.1. Ice algae

Concentrations of chlorophyll *a* in the bottom layers of the fast ice markedly increased from 15 September ($< 1\ mg \cdot m^{-3}$) to 17 December ($310\ mg \cdot m^{-3}$), indicating the ice algal bloom (Fig. 2). The concentration of ice algae, however, sharply decreased to less than $1\ mg \cdot m^{-3}$ by 19 January.

The maximum concentration of pheopigments in the botom ice was found on 18 November, about a month earlier than the time of chlorophyll *a* maximum (Fig. 2).

POC data of the ice were available only in January.

Preliminary microscopical observations of ice algae of 18 November and 17

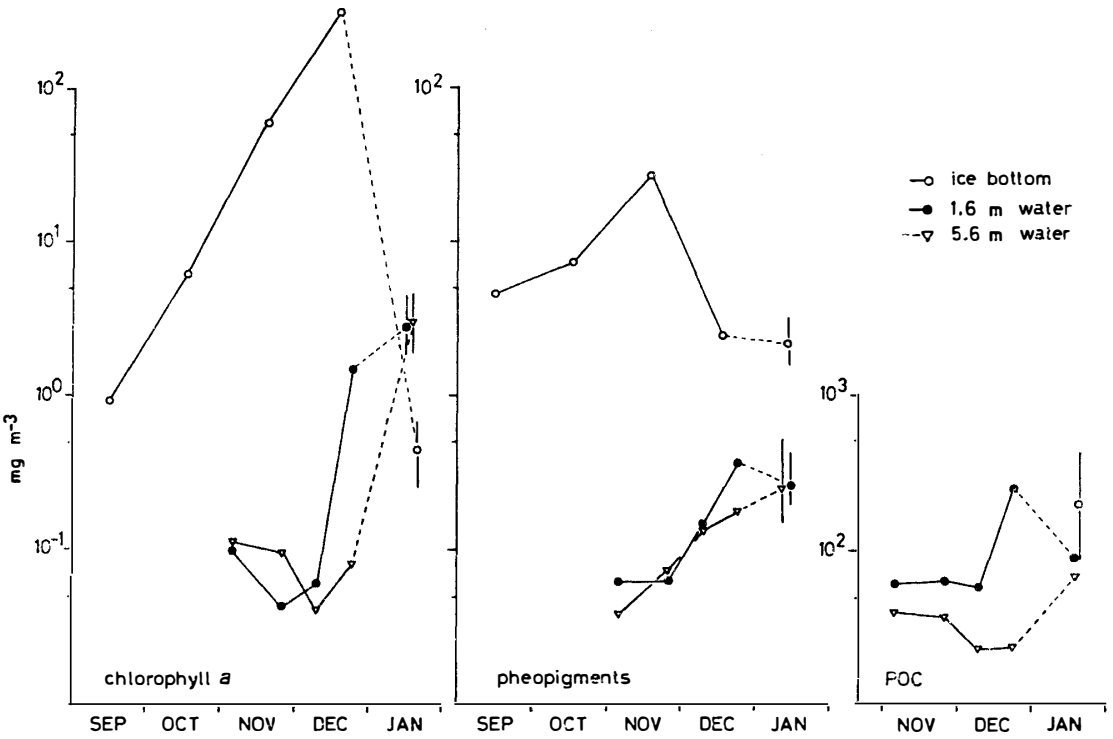

Fig. 2. Chlorophyll a, pheopigments and particulate organic carbon (POC) of the bottom of sea ice and water samples from 1.6 and 5.6 m depths at Stn. 1. Water samples in January were taken from 1 and 5 m depths at Stn. 3. Vertical bars indicate the ranges of observed data.

December, 1982 showed that ice algal communities were dominated by *Fragilariopsis* spp., *Navicula* spp. and *Nitzschia* spp.

3.2. Phytoplankton in the sea water

Chlorophyll *a* concentration of the water at 1.6 and 5.6 m depths under the fast ice maintained relatively low values of about 0.1 mg·m^{-3} or less from 5 November to 9 December (Fig. 2). On 23 December, just after the time of ice algal bloom, 1.6 m water contained a large amount of chlorophyll *a* (*ca.* 1.0 mg·m^{-3}), although the chlorophyll *a* at 5.6 m depth still remained low. The maximum value of chlorophyll *a* at both layers was observed on 14 January, which represented the phytoplankton bloom. The ice algal biomass had decreased by this time.

Pheopigment concentrations at 1.6 and 5.6 m depths gradually increased from November (*ca.* 0.05 mg·m^{-3}) to January (>0.2 mg·m^{-3}).

Changes of POC concentrations in the sea water within the observation period were similar to those of chlorophyll *a* in the water. The POC concentrations at 1.6 m depth were always higher than those at 5.6 m depth.

3.3. Changes in downward fluxes

Downward fluxes of chlorophyll *a* from 5 November to 9 December were 0.2 mg·m^{-2}·day^{-1} at 1.6 m and 0.2–0.3 mg·m^{-2}·day^{-1} at 5.6 m depth (Fig. 3). On 23 December, a marked flux increase was observed at both depths, and the 1.6 m flux was

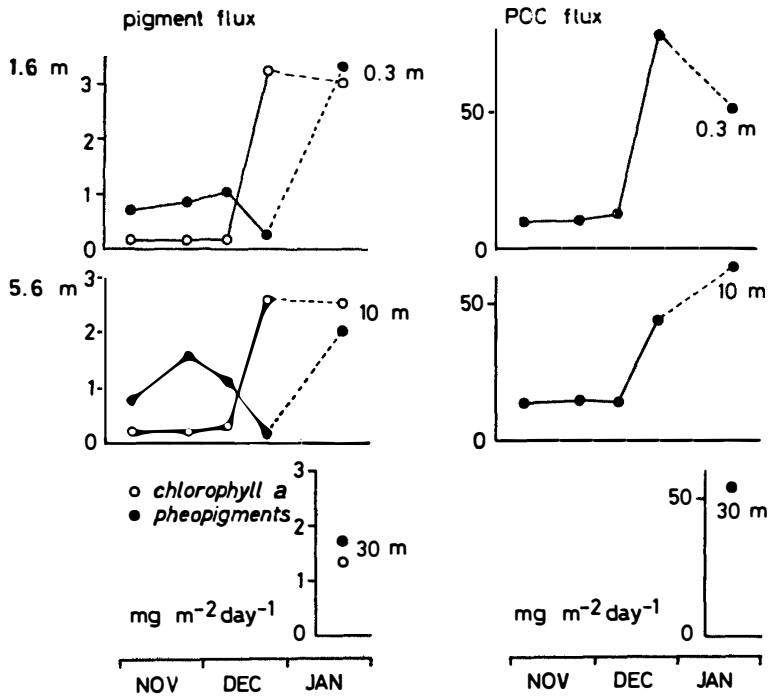

Fig. 3. Sedimentation fluxes of chlorophyll a, pheopigments and POC at the depths of 1.6 and 5.6 m. In January, the flux data were obtained from the depths of 0.3, 10 and 30 m.

slightly higher than the 5.6m flux. The higher flux level was maintained at both depths until 20 January.

The fluxes of pheopigments were much larger than those of chlorophyll *a* in the period before the ice algal bloom. The 5.6m fluxes exceeded the 1.6m fluxes. Unlike the chlorophyll *a* flux, the pheopigment flux on 23 December was lowest (<0.3 mg·m^{-2}·day^{-1}), but increased again on 20 January. The flux of pheopigments on 20 January gradually decreased with depth.

POC fluexes were also low between 5 November and 9 December, and the fluxes were considerably high at both depths on 23 December and 20 January (Fig. 3).

3.4. Changes in composition of sinking particles

Major identifiable components of sinking particles associated with microalgae under the light microscope were aggregates of algae, colonies of chain-forming diatoms, solitary diatom cells and fecal pellets (probably from crustaceans). Others were mainly small detritus ($<50\,\mu$m) which would be less important in sedimentation of microalgae. One of the most typical forms observed was the aggregate of algal cells. These aggregates ranging in diameter from several tens of microns to more than a centimeter contained numerous diatoms, usually mono-specific. While most of the large aggregates were somewhat flake-like particles, aggregates collected in January were very long and slender, and composed of many kinds of diatoms, flagellates and unidentifiable minute organisms.

Changes in downward flux differed for each component (Fig. 4). For example, marked increases were found on 25 November in the 200–1000 μm fraction of the

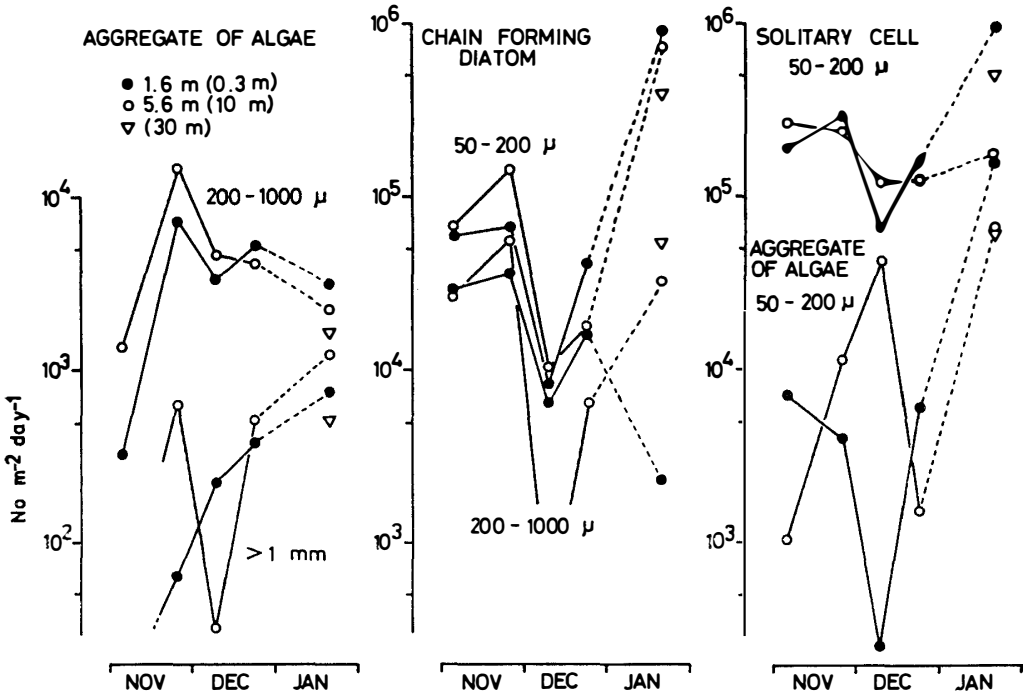

Fig. 4. Sedimentation fluxes of algal aggregates, chain-forming diatoms and solitary cells larger than 50 μm. In January, the flux data were obtained from the depths of 0.3, 10 and 30 m

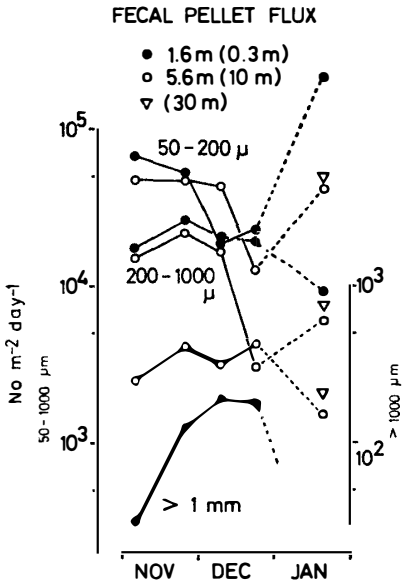

Fig. 5. Sedimentation fluxes of fecal pellets larger than 50 μm. In January, the flux data were obtained from the depths of 0.3, 10 and 30 m. A vertical scale at the right side is for >1 mm fraction.

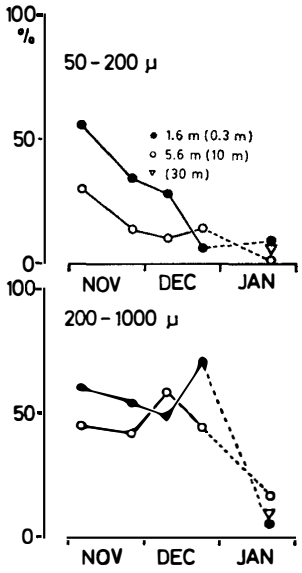

Fig. 6. Relative abundance of transparent fecal pellets in the size range of 50 to 1000 μm. In January, the data were obtained from the depths of 0.3, 10 and 30 m.

aggregate fluxes, and subsequently they decreased. On the contrary, from the end of November to January, >1 mm fraction of the aggregate flux at 1.6 m increased. On 23 December, the fluxes of the major component did not correspond to the high fluxes of plant pigments and POC, although extremely large aggregates of more than a centimeter occurred. Higher fluxes were obtained in January for almost all components, especially of 50–200 μm fraction of chain-forming diatoms, solitary cells and algal aggregates, suggesting the significant contributions to the total mass flux.

Fecal pellet, commonly cylindrical and elliptical forms, were abundant in the trap samples. Fluxes of small-(50–200 μm) and medium-(200–1000 μm) sized fecal pellets decreased in December at both 1.6 and 5.6 m depths (Fig. 5). The flux of large-sized fecal pellets (>1 mm), however, were slightly high between 25 November and 23 December.

Two distinct types of fecal pellets were collected. One of them was composed of small- and medium-sized transparent fecal pellets which were cylindrical and elliptical

Table 2. List of diatoms observed in the particle interceptor traps. Collected diatoms were settled freely or associated with fecal pellets or aggregates. Stars indicate diatoms commonly observed in the bottom ice (below the table).

	November 5	November 25	December 9	December 23	January 20
1.6 m					(0.3 m)
Fecal pellets					
Brown	s.c.d. Th	Fr	s.c.d. Fr	s.c.d. Nit	Fr
Transparent	Fr	Fr	Fr Nit		Fr
Aggregates					
Algae	s.c.d.	s.c.d. Fr Mel Nav Nit Pl	s.c.d. Fr Nav Nit	s.c.d. Fr Nav Nit	s.c.d. Co'ra Fr Nav Nit Pl Th
Diatoms					
Chain form	Fr Mel Th	Fr Mel Th	Fr	Fr Th	Co'ra Ch Fr Th
Solitary cell	s.c.d. Nav Nit Pl	s.c.d. Nav Nit Pl	s.c.d. Nav Nit Pl	s.c.d. Nav Nit Pl	s.c.d. Cocc Cosc Dip Nav Nit Pl
5.6 m					(10, 30 m)
Fecal pellets					
Brown	s.c.d. Fr Nav	s.c.d.	s.c.d. Fr Nit	s.c.d.	s.c.d.
Transparent	s.c.d. Fr	Fr	Fr	Fr	
Aggregates					
Algae	Fr Nit	s.c.d. Fr Mel Nav Nit Pl	s.c.d. Cocc Fr Nav Nit	Fr Nit Pl	s.c.d. Ch Co'ra Fr Nav Nit Pl Th
Diatoms					
Chain form	Fr Mel Th	Fr Mel Th	Fr Mel	Fr	Ch Co'ra Fr Th
Solitary cell	Nav Nit Pl	Nit Pl	Nit Pl	Nav Nit Pl	Dip Nav Nit Pl Rh

s.c.d.: small centric diatom*, Ch: *Chaetoceros*, Cocc: *Cocconeis*, Cosc: *Coscinodiscus*, Dip: *Diplonies**, Fr: *Fragilariopsis**, Mel: *Melosira*, Nav: *Navicula**, Nit: *Nitzschia**, Pl: *Pleurosigma**, Th: *Thalassiosira*, Bid: *Biddulphia*, Rh: *Rhizosolenia*.

in shape. Detailed microscopic observations revealed that these transparent fecal pellets were full of diatom frustules, and were usually monospecific, but contained no detrital particles. The other type of pellets was the brown fecal pellets, comprising cylindrical, elliptical and spherical forms, which contained several types of diatom remaines and a large percentage of unidentifiable detritus. Almost all of the large fecal pellets belonged to this type. In the small and medium size ranges, transparent fecal pellets decreased in relative abundance (percentage contribution of transparent fecal pellets to the total fecal pellets) from November to January and were rarely observed in January (Fig. 6). Conversely, the large sized brown fecal pellets increased from November to January.

3.5. Changes in internal constituents of sinking particles

Major diatom species associated with particles collected were preliminarily identified (Table 2). Small cells less than about 5 μm, flagellates and tintinnids, were not counted, although they were fairly abundant, especially in January. The number and diversity of constituents in the brown fecal pellets were probably underestimated due to the difficulty of detailed examination by their opaqueness. A few marked differences in composition of constituents were found between the particles collected at 1.6 m and those at 5.6 m. Small centric diatoms were always prevalent. While brown fecal pellets usually contained small centric diatoms, *Fragilariopsis* spp. was the dominant component of transparent fecal pellets. Algal aggregates collected from November to December were primarily composed of *Fragilariopsis*, *Navicula* and *Nitzschia*. Chain-forming diatoms were generally *Fragilariopsis* spp. Many solitary diatoms were observed, some of which were found in fecal pellets and aggregates. In January, the maximum number of diatom genera was found. The composition of diatom in aggregates was quite similar to that of the solitary cell population observed in the trap samples (Table 2).

4. Discussion

Due to heavy ice melting around Stn. 1, the final sampling was made at Stn. 3 instead of Stn. 1. Water temperature, salinity and chlorophyll *a* concentration for each depth were not significantly different between Stns. 3 and 1 (FUKUCHI *et al.*, 1984, 1985). Differences of ice algal concentrations between stations would depend on the depth of snow on the ice and the ice thickness (HOSHIAI, 1981a). The ice thickness was different between stations in this case. Although the seasonal change at Stn. 1 is not strictly comparable with that at Stn. 3, it can be assumed that the ice algal bloom preceded the phytoplankton bloom around the two stations.

It was directly observed that dense ice algal communities adhered to the undersurface of the fast ice in summer and that ice algal concentrations exceeded phytoplankton concentrations at that time (SASAKI and WATANABE, 1984). The last authors described that dense ice algae were easily detached from the undersurface of the ice by such a slight movement of water as diver's wake. There are three possible fates for ice algae once they leave the ice: (1) the ice algae sink through the water column and directly reach the bottom, (2) the ice algae are consumed by animals living in the water

column and their egested feces sink down to the bottom, and (3) the released ice algae become directly a component of the phytoplankton and possibly contributd to a phytoplankton bloom (LEGENDRE *et al.*, 1981). There is also a possibility that phytoplankton sink down to the bottom unless they are consumed by animals during their sinking. The processes described above other than (3) are discussed below.

From September to mid-December, the ice algal concentration increased, while both the concentration and flux of algae in the water column were relatively low (Figs. 2 and 3). In this period, the pheopigments: chlorophyll *a* ratios of the sinking particles ranged from 3.5 to 6.9. In January, this ratio was almost one. The observed values were lower than the values slightly less than ten observed in shallow pelagic waters of south of the Hawaiian islands (LORENZEN *et al.*, 1983). The last authors suggested that higher pheopigment fluxes indicate considerably large contributions of fecal pellets egested by herbivorous zooplankton to the total flux, whereas the present study implies that fecal pellets are less important in summer to the total flux under the fast ice system. The marked increases of chlorophyll *a* and POC fluxes at both depths (Fig. 3) and the low chlorophyll *a* concentration at the 5.6 m layer of water observed on 23 December (Fig. 2) strongly suggest that numerous ice algae detached from the ice and probably sank down directly to the sea bottom. The flux data also showed very low pheopigments: chlorophyll *a* ratio (<0.1) and low carbon: chlorophyll *a* ratio (*ca.* 30), representing actively living algal cells sinking downward without strong grazing pressure of animals in the water column.

As for the changes of major components of particles including microalgae (Fig. 4), no clear corresponding increase between algal aggregate flux and chlorophyll *a* flux was obtained. This contradictory situation would indicate that physiological conditions of algal cells in the aggregates were different from those collected in the other periods. It is possible that the chlorophyll *a* content per unit cell of ice algae might increase during the blooming season, resulting in the high chlorophyll *a* fluxes as observed on 23 December. The increase of chlorophyll *a* content of ice algae was observed by SULLIVAN *et al.* (1985) after mid-November at McMurdo Sound, possibly due to low light adaptation for self-shading. Another possible explanation is that exceptionally large (>1 cm) but rare aggregates would contribute to the increases of total mass flux. A few large algal aggregates were actually collected during December.

Dominant diatom genera associated with the sea ice were commonly found in all the trap samples. In particular, most of the sedimented microalgae taken on 23 December seemed to be derived from the sea ice algae (Table 2). In January, phytoplankton standing stock in the water column was highest. The major portion of collected particles in January was probably sinking phytoplankton, mainly composed of chain-forming diatoms, small algal aggregates and solitary cells. The ice algal sedimentation in January, however, occupied a smaller proportion within the total algal sedimentation than on 23 December, primarily because of a small amount of ice algal biomass remained in the sea ice. HORNER and SCHRADER (1982) presented a schematic representation showing that detachment and sinking of a number of ice algae would occur during the ice melt about a month earlier than phytoplankton bloom and its corresponding sinking in the Beaufort Sea. The present results are basically comparable with their scheme.

Figure 5 reveals that the fecal pellet fluxes of 50–200 μm fraction at 1.6 and 5.6 m depths and 200–1000 μm fraction at 5.6 m depth decreased on 23 December. This may be due to the inability of small animals to effectively feed on large ice algal aggregates in the water. If the relative abundance of the transparent fecal pellets represents the grazing impact of the ice algae feeders, it should be expected from the decline in relative abundance of small fecal pellets that small animals would reduce their feeding activities on ice algae. Medium-sized transparent fecal pellets, containing ice algal species, were about 50% of the total fecal pellets collected before January. Thus, medium pellet producing animals could have used ice algae as one of important food sources. No clear tendency was observed in the total fecal pellet flux change of the largest size fraction (>1 mm), mainly brown pellets, at the depth of 5.6 m. At the depth of 1.6 m, however, there was an apparent increase corresponding to the ice algal increase, probably indicating that large and brown pellet producers just beneath the ice may effectively catch ice algae in addition to other food items (phytoplankton, detritus or animals).

Judging from the transparent fecal pellet flux, contributions of small-sized fecal pellets to the ice algal sedimentation were relatively high among the three types of fecal pellets before the ice algal bloom, and medium-sized fecal pellets were also fairly important as ice algae carriers except in January. However, relative importance of fecal pellets to the total microalgae flux (ice algae and phytoplankton) would not be so high, particularly on 23 December, because of less abundance of total fecal pellets than the other components simultaneously collected, such as aggregates.

Although some questions remain to be answered, many of which concern the weak correspondence between the changes of carbon or pigment flux and major component flux, the gross pattern of the variation in sedimentation fluxes with the developments of the ice algal and phytoplankton blooms was drawn up. The relative contributions in the fluxes of ice algae, phytoplankton and fecal pellets are primarily documented. The present results show that a large amount of nutritive particles may settle at the sea floor and supply food for benthic animals during the ice algal and phytoplankton blooms. The major nutrient carrier is probably ice algal aggregates during the ice algal bloom without strong grazing and egestion processes, while a few types of carriers associated with microalgae comprise the sedimenting food particles during the phytoplankton bloom.

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