DISTRIBUTIONS OF FREE AMINO ACIDS IN SEA AND LAKE ICE CORES FROM ANTARCTICA WITH SPECIAL REFERENCE TO ICE BIOTA

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Abstract: Dissolved free amino acids (DFAA) of sea ice cores and lake ice cores collected from the vicinity of Davis Station, Antarctica were determined by HPLC. The results of DFAA analysis showed that concentrations of total DFAA in ice cores were higher compared to those in water and they varied from 8.0 μ M to 30.9 μ M and 14.0 μ M to 45.0 μ M in the sea and lake ice cores, respectively. The highest concentration of total DFAA in the sea ice core appeared in the bottom of 150 cm depth, while that in the lake ice core was found in the middle part of the 60-70 cm depth. The relative compositions of individual amino acids, such as serine, histidine and ornithine, which were present in higher concentrations, were similar in both types of ice cores. The variation in the total concentration of DFAA was related to the variation in microalgal cell numbers in the sea ice cores. These DFAA were probably derived from metabolism of the dominant organisms in the algal assemblage ice community. These amino acids are stored in the ice as a large portion of the dissolved organic matter (DOM). It is assumed that these amino acids might be a source of carbon and nitrogen for phytoplankton and/or other microorganisms which bloom during (the next) summer season in the water column.

1. Introduction

Sea ice in polar regions has a very complex microbial community structure. More and more results from recent investigations show that the sea ice cover, which separates sea water from the atmosphere, participates directly in the exchange of material and energy flux between sea and air (EICKEN, 1992; GOSSELIN *et al.*, 1985; WANG and DIECKMANN, 1993). Sea ice in Antarctica constitutes an important habitat for a variety of organisms and provides microhabitats for the growth of unique sea ice microbial communities (BUNT, 1968; HORNER, 1976). The concentrations of chlorophyll a in sea ice were up to 200 times higher than the concentrations measured in the water column (PALMISANO and SULLIVAN, 1983) because ice algae are physically concentrated during ice formation and adequately photosynthesize (GARRISON *et al.*, 1983, 1986). The sea ice biota is an important food resource for secondary and higher level consumers in the water column (JAMES *et al.*, 1988; DAVID *et al.*, 1986).

The countings of phytoplankton cells and measurements of chlorophyll a indicated that algae were abundant in the sea ice community of the area selected by

the present investigation (PERRIN et al., 1978; MCCONVILLE et al., 1985). Those living and decaying ice algal cells are able to fix extraordinarily high amounts of organic carbon and nitrogen in sea ice communities. Some experiments have shown that more than 30% of the organic carbon fixed by algae is released as dissolved organic material in the ice community (PALMISANO and SULLIVAN, 1985; PALMISANO et al., 1986). As a result of the metabolism of living organisms and posthumous decay of organisms, amino acids and peptides of various degrees of polymerization are released into the surrounding environment. Due to the high abundance of phytoplankton in the sea ice communities, the concentrations of DFAA in the ice core probably exceed by far those in the water.

The biological effects of DFAA that derived from metabolic processes and utilization by organisms (CRAWFORD, 1974; FERGUSON and SUNDA, 1984) mostly by growing algal cells was clear in sea water of the present study area (YANG, 1992; YANG *et al.*, 1990). However, it would be of interest to understand biochemical activities of the organisms and processes in the ice community. Whether DFAA from the ice biota acts as characteristic biochemical marker compounds and forms a large portion of the dissolved organic matter (DOM), and whether it is assumed that DFAA are a resource of carbon and nitrogen for phytoplankton or other microorganisms which bloom in (the next) summer season in the water column are important subject to analyse in ice cores. Also it is of interest to know how the DFAA composition in sea ice differs from that of lake ice. From these viewpoints, in this paper, the results of DFAA composition in sea ice cores and in Ace lake ice cores near Davis Station, Antarctica are compared.

2. Material and Methods

Two sea ice cores were taken with a 7 cm diameter SIPRE ice auger from a station 10 km north-west of Davis Station on November 14, 1988, and two lake ice cores were taken from the centre of Ace lake, Vestfold Hill, Antarctica (Fig. 1) on November 16, 1988. Ice cores were stored in freezing storage $(-20^{\circ}C)$ until analysis the next day. The salinity of Ace lake was *ca*. 15% at the surface and 30% at 10m depth. The ice cores were sliced into 10 cm sections which were allowed to melt at 4°C. Fifteen ml of melted water samples were filtered through Whatman GF/F glass filter (0.45μ) which was pre-combusted at 450°C.

A High Pressure Liquid Chromatography (HPLC) apparatus was used to determine amino acids. The system contained two Kortec ETP pumps, a Kortec mixing chamber, a Rainin microsorb 7125 injection valve with $500 \,\mu l$ loop, and a waters fluorescent detector (Model 420-E). The columns were Rainin microsorb C-18, 3 micron, $50 \times 4.6 \,\mathrm{mm}$ I.D. analytical columns with Rainin guard columns.

The amino acids derivatizing solution consisted of 50 mg o-phthalaldehyde (OPA) (Alltech company) dissolved in 1 ml methanol, added 750 μl 2-mercaptoethanol (Aldrich chemical company), and 150 μl Briji 35 (BDH 30% w/v solution in water) and mixed with 5 ml 0.4 M potassium borate (pH 10.4) in a 20 ml blank glass bottle over 24 hours.



Fig. 1. Sampling sites of sea ice core collected from 10 km north west of Davis Station and lake (Ace lake) ice core collected from Vestfold Hill.

Mobile phases were: (A) 0.1 M sodium acetate, 0.5% (v/v), tetrahydrofuran and 9.5% (v/v) methanol, adjusted to pH 6.8 with 0.1 M acetic acid; (B) methanol. The gradients elusion method was used beginning with 5% (B) to 65% (B) in 21 min, returning to initial conditions at a constant flow rate of 1 ml/min.

 $400 \,\mu l$ filtered samples were mixed with $100 \,\mu l$ 1.0 M sodium acetate buffer in the 1 ml vase, and $100 \,\mu l$ o-phthaladehyde derivatizing solution was added, with derivatizing time of 1 min before injection. The injected volume was $500 \,\mu l$. The peaks were identified by their characteristic retention time and quantification was done by linear comparison of the peaks area to standards.

Algal species in ice was examined and enumerated by setting 10 ml of preserved sample in a setting chamber and counted by an inverted microscope.

3. Results and Discussion

The results of DFAA measurement in the sea ice cores and Ace lake ice cores in Antarctica are summarized in Tables 1 and 2. The highest concentrations of DFAA in the sea ice core were found in the bottom part of ice core; the lowest concentrations appeared in the surface of the core which was near the infiltration layer under snow. The second peak of DFAA abundance was present in the 60–70 cm section of the core. The concentrations decreased in the 70 cm to 100 cm sections, and increased again from 100 cm until 160 cm (Fig. 2).

In the Ace lake ice core, the concentrations of DFAA were higher compared to those in the sea ice core from 70 to 120 cm sections of the core. The highest concentration of DFAA was 46 μ M in the 70 cm section of the core, while the lowest concentration appeared in the 50–60 cm (Fig. 2).

According to our measurement of DFAA in sea water samples during May 1988 to February 1989, the concentrations of those compounds in the sea ice core were much higher compared to those in the sea water. The concentration of total DFAA varied between 8 μ M and 30 μ M in sea ice core, while the highest concentration was only 0.30 μ M in sea water samples were collected from the sea water column in the same area during May 1988 to February 1989 (YANG *et al.*, 1990).

High concentrations of DFAA were related to abundance of algae in the sea ice community. The ice algae concentration was much higher in the sea ice community than that in sea water column, because ice physically concentrates the algae during frazil ice formation (GARRISON *et al.*, 1983, 1986). The ice communities were dominated by a few species of colonial pennate diatoms in our observation area, such as *Berkeleya*/*Amphiprora* (MCCONVILLE and WETHERBEE, 1983), *Entomoneis paludosa* var. *hyperborea* and *Nitzschia frigida* (MCCONVILLE *et al.*, 1985). *Nitzschia cylindrus*, *Navicula* sp., *Amphiprora kjellmanii* and *Synedra* sp. 1 (PERRIN *et al.*, 1978). *Nitzschia frigida*, *Navicula* sp. 1 and *Pleurasigma* sp. 1 were abundant.

The concentration of total DFAA in sea water varied during the transition from winter to summer. It increased from August to early December and then decreased from December which was the beginning of the *Phaeocystis pouchetii* bloom. The distributions of individual amino acids also varied in the water column. The vertical distributions of concentrations of these compounds also varied in the sea ice core. Within the ice and especially during sea ice formation, complex biological and chemical processes take place. Hence, it is assumed that most of the high concentrations of DFAA could be related to abundance and types of ice algal assemblages.

The ice algal assemblages can be divided into surface assemblages, interior assemblages and bottom assemblages in the Antarctic sea ice community. Most of the ice algae fall into those categories (HORNER, *et al.*, 1988). High concentrations of total DFAA, which were 27.3 μ M in sea ice core and 46.0 μ M in the Ace lake ice core, appeared in the 60–70 cm sections of both ice cores (Figs. 2 and 3). These sections contained part of the interior assemblages. Another high concentration of

No.	Depth (cm)		Amino acid* concentration (µM)															
		asp.	glu.	asn.	ser.	val.	his.	gly+thr.	orn.	arg.	ala.	tyr.+r-ABA	met.	trp.	phe.	iso.	leu.	lys.
1	0- 10	0.44	0.31	0.32	1.61	0.13	0.53	1.04	0.76	0.14	0.78	0.51	0.04	0.19	0.24	0.19	0.17	0.37
2	10-20	0.53	0.27	0.57	1.23	0.10	0.76	0.80	0.67	0.23	0.83	0.53	0.03	0.14	0.16	0.14	0.97	0.37
3	20- 30	1.45	0.68	1.58	4.05	0.43	2.64	2.74	2.21	0.83	2.59	1.02	0.09	0.29	0.23	0.87	1.61	0.95
4	30- 40	1.06	0.68	1.15	3.14	0.36	1.96	2.11	1.50	1.19	3.72	1.04	0.17	0.24	0.61	0.64	0.88	0.66
5	40- 50	1.60	0.75	1.80	4.40	0.52	3.04	2.92	2.40	1.04	1.84	1.41	0.10	0.35	1.56	1.01	1.27	0.77
6	50- 60	1.58	0.60	1.65	4.45	0.63	3.15	3.25	2.57	0.74	0.31	1.46	0.09	0.37	1.01	1.03	0.13	1.10
7	60- 70	1.81	0.60	1.84	4.67	0.65	3.25	3.13	2.88	1.00	0.75	1.45	0.08	0.42	1.05	1.05	1.30	0.97
8	70- 80	1.11	0.43	1.21	3.68	0.54	2.20	2.69	2.18	0.53	0.46	1.02	0.09	0.29	0.76	0.68	0.88	0.79
9	80-90	1.12	0.40	1.12	4.12	0.50	2.35	2.75	1.96	0.50	0.45	1.00	0.11	0.33	0.77	0.68	0.75	0.54
10	90-100	0.80	0.31	0.91	3.22	0.45	1.71	2.26	1.66	0.45	0.43	0.82	0.09	0.21	0.53	0.52	0.67	0.55
11	100-110	1.59	0.61	1.62	4.45	0.58	2.77	3.00	2.46	0.57	0.29	1.36	0.09	0.37	0.86	0.92	1.19	1.02
12	110-120	1.27	0.47	1.34	4.20	0.56	2.57	2.87	2.47	0.68	0.64	1.20	0.18	0.31	0.77	0.73	0.93	0.58
13	120-130	1.69	0.63	1.72	4.83	0.55	2.76	3.33	2.78	0.52	0.31	1.49	0.16	0.34	0.78	0.90	1.20	0.90
14	130-140	1.30	0.42	1.40	4.16	0.55	2.48	2.88	2.54	0.68	0.62	1.23	0.23	0.31	0.77	0.77	0.96	0.69
15	140-150	1.40	0.53	1.46	4.31	0.54	2.68	2.83	2.27	0.88	0.59	1.23	0.19	0.36	0.81	0.81	0.94	0.71
16	150-160	2.34	0.87	2.21	4.83	1.02	3.40	3.10	2.90	1.10	0.64	1.40	1.13	0.62	1.82	1.25	1.45	0.91
17	Sea water: tota	al conc	entratio	n of Dl	FAA is	302 nM	on No	ovember 23	1988									
Averag	e	1.32	0.54	1.37	3.83	0.51	2.39	2.61	2.14	0.69	0.95	1.14	0.18	0.32	0.80	0.76	0.96	0.74

Table 1. Concentrations of amino acids in the sea ice core.

* asp.—aspartic acid; glu.—glutamic acid; asn.—asparagine; ser.—serine; val.—valme; his.—histidine; gly.—glycine; thr.—threonine; orn.—L-ornithine; arg.—arginine; ala.—alanine; tyr.—tyrosine; met.—methionine; trp.—trytophane; phe.—phenylalanine; iso.—iso-leucine; leu.—leucine; lys.—lysine.

No.	Denth (cm)		Amino acid [*] concentration (μ M)															
	Deptil (cill)	asp.	glu.	asn.	ser.	val.	his.	gly+thr.	orn.	arg.	ala.	tyr.+r-ABA	met.	trp.	phe.	iso.	leu.	lys.
1	0- 10	1.65	0.51	1.82	3.96	0.45	2.26	2.62	1.74	0.28	0.15	3.20	0.38	0.34	0.73	0.47	0.61	0.29
2	10- 20	1.71	0.57	1.61	4.47	0.58	2.85	3.07	2.40	0.42	0.21	1.52	0.34	0.43	0.92	1.00	1.13	0.79
3	20- 30	1.39	0.51	1.59	4.12	0.51	2.38	2.95	2.14	0.41	0.17	1.28	0.33	0.36	0.85	0.89	1.10	0.88
4	30- 40	1.99	0.71	2.20	5.06	0.72	3.49	3.67	3.56	0.67	0.26	1.80	0.25	0.50	1.99	1.34	1.57	1.21
5	40- 50	1.71	0.65	1.71	4.88	0.56	3.10	3.64	3.51	0.51	0.38	1.71	0.21	0.41	0.95	1.01	1.25	1.02
6	50- 60	0.86	0.38	1.07	3,45	0.35	1.73	2.57	1.88	0.37	0.19	1.01	0.15	0.22	0.54	0.61	0.82	0.68
7	60- 7 0	3.37	1.00	3.49	6.06	1.43	5.78	4.51	5.19	0.96	0.53	2.24	1.89	0.99	2.80	1.99	2.26	1.51
8	70-80	2.18	0.81	2.25	5.06	0.75	3.44	3.64	3.30	0.69	0.31	1.96	0.41	0.54	1.19	1.34	1.57	1.18
9	80-90	1.67	0.62	1.72	4.50	0.56	2.74	3.14	2.51	0.54	0.20	1.53	0.28	0.42	0.89	1.10	1.27	0.97
10	90-100	1.86	0.74	2.13	5.06	0.69	3.55	3.73	3.65	0.63	0.34	1.80	0.16	0.42	1.85	1.18	1.41	1.07
11	100-110	2.53	0.84	2.39	5.05	1.04	3.56	3.46	3.19	0.69	0.34	1.66	1.90	0.73	1.88	1.47	1.60	0.92
12	110-120	1.97	0.67	2.02	4.89	0.95	3.18	3.40	3.00	0.67	0.31	1.45	1.33	0.59	1.68	1.21	1.38	0.90
13	120-130	1.02	0.44	1.12	3.72	0.39	1.88	2.61	1.73	0.42	0.20	1.02	0.37	0.26	0.89	0.66	0.83	0.70
14	130-140	1.15	0.47	1.41	3.83	0.35	1.98	2.50	1.70	0.49	0.14	1.01	0.21	0.26	1.12	0.71	0.88	0.61
15	140-150	1.03	0.35	1.14	3.54	0.45	1.60	2.53	1.69	0.29	0.21	0.81	0.59	0.47	0.37	0.60	0.76	0.60
Average	2	1.74	0.62	1.84	4.51	0.65	2.90	3.20	2.75	0.54	0.26	1.60	0.59	0.46	1.24	1.04	1.23	0.89

Table 2. Concentrations of amino acids in the Ace lake ice core.

* Same as Table 1.





Fig. 2. Concentration of total DFAA in sea and lake ice cores, and cell numbers in sea ice core.



Fig. 3. Composition of total DFAA in sea and lake ice cores.

total DFAA 30.9 μ M was found in the bottom assemblages in the sea ice core. The high concentration in the 110–140 cm sections (Fig. 2) may be derived from algal assemblages in the brine channels. The distribution of higher concentrations of total DFAA in the sea ice core is in parallel accordance with the phytoplankton cell numbers (Fig. 2) and, with respect to the high concentration within the 60–70 cm section. It is therefore concluded that the ice algal assemblages might be the source

of the DFAA.

The composition of the total DFAA in the sea ice core was shown in Table 1, Figs. 3 and 4. The highest portion was serine, which varied from 1.23–4.83 μ M, and the average was $3.83 \,\mu$ M. Serine represented 18.3% of the total DFAA. It was followed by histidine with an average concentration of which was $2.39 \,\mu$ M, which is 11.3% of the total DFAA. The concentrations of ornithine and glycine together with threonine were 2.14 μ M and 2.61 μ M, repectively, which are 10.3% and 11.6% of the total DFAA. These amino acids were dominant in the sea ice core, comprising 51.5% of the total concentration of DFAA. Methionine exhibited the lowest concentration with an average concentration of $0.18 \,\mu$ M and only 0.8% of total DFAA. Aspartic acid was the same as asparagine and their concentrations were in the middle level of the amino acid spectrum. Overall distributions of composition of individual DFAA were different when compared with intracellular composition of that in marine algal cell (TSEKOS et al., 1975). For example, the highest composition of dissolved free amino acid from Greek marine algae was glutamic acid, while this acid was present in lower concentration than other amino acids in the sea ice core in Antarctica. However, extracellular DFAA composition is quite distinct from that in the intracellular reserve. The results from marine diatoms (MYKLESTAD et al., 1989) have shown that serine is the main extracellular DFAA in culture (except glutamine which has not yet been measured in the ice core). The DFAA having the lowest concentration was methionine in the ice core



Fig. 4. Composition of total DFAA at the different sections in sea and lake ice cores.

as well as in extracellular and intracellular composition.

In the Ace lake ice core, the total concentration of amino acids was higher than that in the sea ice core. However, the composition of DFAA was similar to that in the sea ice core (Table. 2, Figs. 3 and 4). For example serine was the amino acid having the highest concentration in the ice core with an average concentration of $4.51 \,\mu$ M. It was 17.7% of the total concentration of DFAA. Histidine, ornithine and glycine plus threonine had average concentrations of $2.90 \,\mu$ M, $3.20 \,\mu$ M and $2.75 \,\mu$ M, representing 11.34%, 10.75% and 12.52% of the total DFAA, respectively. The only difference was between arginine and alanine. Their concentrations were lower than that in the sea ice core (Fig. 3). The similar compositions of the DFAA pool indicate that the source of the amino acids in the Ace lake ice core was probably the same as that in the sea ice core *i.e.* deriving from ice algal assemblages, because phytoplankton have revealed a distinict similarity in amino acid composition regardless of species composition (COWEY and CORNER, 1963; CHAU *et al.*, 1967; TSEKOS *et al.*, 1975; MYKLESTAD *et al.*, 1989).

Ace lake is a saline meromictic lake in the Vestfold Hills, Antarctica, located on a narrow section of Long Peninsula (Fig. 1). The lake has a surface area of 1.35 imes10⁵ m² and a maximun depth of 23.4 m (measured in November 1988). The lake provides no surface outflow or seepage. This lake had a marine origin (JOHNSTONE et al., 1973) and is currently 152 m from the sea at its nearest point. The salinity of the lake ranges from 80% of that of sea water in the top 10m to 30% greater than sea water at depth; thus, it provides an aquatic environment approximately same as marine systems. The biological community in Ace lake is relatively simple compared to that in sea water. One of the major organisms was calanoid copepod, Paralabidocera antarctica (BAYLY, 1978), which reaches a maximum density of about 3 organisms per liter in the water column. The major alga was a small green flagellate Pyramimonas gelidicola (Prasinophyceae). Smaller populations of a biflagellate alga, tentatively indentified as a Cryptomonas species, an unidentified biflagellate alga and a large unarmoured dinoflagellate related to Gymnodinium were also present. These algae showed discrete population distributions at different depths in the lake and migrate downward in summer. Some species, such as the microflagellates are adapted to live in the top of the water column (under ice) during winter time (BURCH, 1988). It is possible that these algae entered into the ice community and participated in metabolic processes, as in the sea ice community.

According to the physical processes which control the distribution of ice algae in different sections of the sea ice, those assemblages could sort out several more or less distinct microhabitats, called surface assemblages, interior assemblages, and bottom assemblages (HORNER *et al.*, 1988). The distributions and the proportions of individual amino acids were related to the percentages of total DFAA in each ice section. The variations of amino acid composition were mostly between 4% to 5%; some were only 1% and 2% in the sea ice core (Table 3 and Fig. 4). In the Ace lake ice core, variations of the amino acid were similar to those in the sea ice core (Table 3 and Fig. 4). The similarity of the amino acid compositions can be assumpted that they are directly derived from ice algal cells. High concentrations of amino acid

,		5	Sea ice co	ore (%)		Ace lake ice core (%)						
Amino acids	20-30	50-60	100-110	120-130	140-150 cm	20-30	30-40	50-60	80-90	130-140 cm		
Asp.	6.01	6.65	6.71	6.81	6.21	1.90	6.42	5.10	6.78	6.81		
Glu.	2.81	2.47	2.55	2.52	2.36	2.48	2.28	2.23	2.51	2.52		
Asn.	6.51	6.83	6.85	6.90	6.51	7.74	7.11	6.34	6.88	6.90		
Ser.	16.90	18.45	18.77	19.40	19.23	20.13	16.35	20.46	18.27	19.40		
Val.	1.78	2.59	2.44	2.20	2.38	2.48	2.32	2.06	2.28	2.20		
His.	10.88	13.07	11.68	11.08	11.94	11.62	11.28	10.23	11.80	11.08		
Gly. + Thr.	11.28	13.48	12.60	13.40	12.63	14.42	11.84	15.25	12.72	13.40		
Orn.	9.13	10.67	10.37	11.15	10.11	10.46	11.49	11.17	10.17	11.15		
Arg.	3.44	3.08	2.41	2.09	3.91	2.00	2.16	2.16	2.17	2.09		
Ala.	10.68	1.30	1.25	1.23	2.65	0.83	0.85	1.14	0.81	1.23		
Tyr.+r-ABA	4.21	6.05	5.72	5.99	5.50	6.25	5.81	5.97	6.20	5.99		
Trp.	1.15	1.55	1.55	1.38	1.60	1.77	1.62	1.30	1.71	1.38		
Phe.	0.97	4.17	3.65	3.12	3.59	2.36	6.41	3.21	3.64	3.12		
Lso.	3.66	4.25	3.88	3.60	3.62	4.37	4.31	3.62	4.47	3.60		
Lue.	6.61	0.52	4.92	4.83	3.76	5.31	5.08	4.88	5.14	4.83		
Lys.	3.93	4.56	4.31	3.63	3.19	4.23	3.90	4.02	3.93	3.63		
Met.	0.38	0.37	0.37	0.66	0.84	1.60	0.79	0.86	1.12	0.66		
Average	5.90	5.89	5.88	5.88	5.88	5.88	5.88	5.88	5.92	5.88		

Table 3. The percent composition of amino acids in sea and lake ice cores.

indicated that they are most likely not used by heterotroplic metabolism, *i.e.* uptake and recycling by the cells.

Ice bacteria are often present in the ice cores (DAVID et al., 1986). These bacteria may also be involved in the release of amino acids. This will be investigated further. We have also measured amino acids and volatile fatty acids in the water column of the same area from May 1988 to February 1989. The concentrations of DFAA in the area were higher than in other oceans. The concentrations of those compounds varied during winter time: they increased from August to the end of November and decreased from end of November, which was the beginning of the Phaeocystis sp. bloom (YANG et al., 1990). The distributions of individual amino acid were unstable in the water column. The concentrations of volatile fatty acids increased with increasing algal cell counts during the Phaeocystis sp. bloom (YANG, 1992). There was also a strong relationship between cell counts of Phaeocvstis sp. and acrylic acid and DMS (YANG, 1992). Those results indicate high activity of biochemical processes in the sea water column. DFAA are derived from metabolic processes and utilized by organisms (CRAWFORD, 1974; FERGUSON and SUNDA, 1984) mostly by growing algal cells. These amino acids are stored in the ice community as a large portion of the DOC during winter.

However, it is clear that DFAA were directly derived from ice algae and phytoplankton assemblage in the ice community. As the sea ice biota is an important food resource for secondary and higher level consumers, it is assumed that DFAA provide an important source of carbon and nitrogen for phytoplankton and other microorganisms which bloom during (the next) summer season in the water column.

Acknowlegments

I thank the Antarctic Division of the Australia Department of Science for logistic support. In particular I would like to express our cordial thanks to Dr. A. R. MCTAGGART and 1988 winter expeditioners at Davis Station for their assistances with field work and to Prof. G. O. KIRST (University of Bremen); Dr. G. DIECKMANN and Dr. D. THOMAS (Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany) for constructive criticism and revision of the manuscript.

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(Received January 10, 1994; Revised manuscript received October 28, 1994)