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Lipids and fatty acids in ice algae and phytoplankton from the Marginal Ice Zone in the Barents Sea

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Abstract Samples of ice algae from the Marginal Ice Zone in the Barents Sea could be divided into two categories: one dominated by assemblages of *Melosira arctica*, and the other dominated by *Nitzschia frigida* and associated diatoms. Total lipid from the *Melosira* assemblages consisted of approximately equal amounts of polar lipids and triacylglycerols. Total lipid from the *Nitzschia* assemblages contained more triacylglycerols than polar lipids. Total lipid from the *Melosira* assemblages had higher percentages of C16 PUFA, especially 16:4(n-1) and 20:5(n-3), than that from the *Nitzschia* assemblages, this reflecting the higher percentages of both C16 PUFA and 20:5(n-3) in polar lipids than in triacylglycerols. Phytoplankton from the pelagic zone were richer in flagellates and contained less C16 PUFA and 20:5(n-3) but more C18 PUFA and 22:6(n-3). The dominance of diatoms in the ice-algae assemblages in the Marginal Ice Zone and their high nutritional value as a source of 20:5(n-3) for higher trophic levels are emphasised.

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Introduction

The Marginal Ice Zone (MIZ) of the northern Barents Sea is a variable biological environment where the phytoplankton and ice algae are subject to extreme oscillations of abiotic factors stemming from strong interannual and seasonal fluctuations in light, insulation, ice cover, fresh water inflow, surface salinity and sedimentation, occurring at an overall low temperature. The physiological and biochemical states of the algae are affected by these abiotic factors and are also influenced by other factors such as grazing pressure, nutrient depletion and deep vertical mixing.

The MIZs of the Barents Sea and Arctic fjords of Svalbard are some of the most productive marine areas in the northern hemisphere with short, but very intense, algal blooms (Eilertsen et al. 1989; Falk-Petersen et al. 1990). The blooms follow the receding ice edge during the summer melt period and intense production can occur in open leads in the MIZ (Zenkevitch 1963; Sakshaug and Skjoldal 1989). One basic adaptation characteristic of polar marine systems is the accumulation of large lipid or oil reserves by herbivorous zooplankton and ice fauna during the highly productive spring-summer algal bloom. Such reserves allow the animals to survive through the following winter and subsequently reproduce.

Lipids in herbivores originate from both lipoidal and non-lipoidal precursors formed by, and assimilated from, relative low-lipid primary producers (Sargent and Henderson 1986; Sargent and Falk-Petersen 1988). Actively growing and dividing algae, including those from polar regions, contain 10–20% of their dry weight as total lipid, which are mainly polar glycolipids located in the cells' thylakoid membranes, these glycolipids being rich in (n-3) polyunsaturated fatty acids (PUFA) (Barashkov 1963; Sargent et al. 1985; Nichols et al. 1989). Algae may have variable amounts of neutral lipids, mainly triacylglycerols (TAG), present as membrane-bound oil droplets in their cytoplasm, with nutrient

limitation generally favouring neutral lipid storage (Shifrin and Chisholm 1981; Reitan et al. 1994). For example, diatoms deprived of silica are unable to divide but continue to produce organic material which is stored as lipid (Taguchi et al. 1987). Resting stages of diatoms can also contain considerable amounts of lipid (Doucette and Fryxell 1983).

Low temperatures and low light intensity have been reported to favour lipid production; for example, Smith and Morris (1980) found that 80% of the carbon assimilated by algae was incorporated into the lipid fraction under such conditions. Smith et al. (1989) also reported higher levels of lipids in ice algae than in phytoplankton from the Canadian Arctic. In general, rates of lipid synthesis in phytoplankton can be expected to be high early in the season when the cells are actively growing and dividing, and their lipids are predominantly polar lipids in biomembranes. Later in the season, when nutrient depletion develops and cell division slows or ceases, accumulation of neutral storage lipids such as triacylglycerols will be predominant. This was shown in the study by Nichols et al. (1989, 1993) of an Antarctic spring bloom sea-ice diatom community in McMurdo Sound where the lipids were rich in 16:1(n-7) and C16 PUFA, especially 16:4(n-1) and 20:5(n-3). Similar results had been reported earlier by Fahl and Kattner (1993) for a sea-ice algal community from the Weddell Sea, except that in this area the algal lipids were less rich in 20:5(n-3) and C16 PUFA and richer in 18:1(n-9) than those in McMurdo Sound.

Due to the importance of the MIZ for the production of northern seas, the Norwegian Polar Institute initiated an international, multidisciplinary research programme, ICE-BAR, on the ecological and physical processes in the MIZ of the northern Barents Sea. During the melting period in June–August 1995 and 1996, research cruises with the R/V "Lance" were conducted in the northern Barents Sea. The ICE-BAR cruises included studies of, inter alia, hydrography, primary and secondary production, and trophic relationships. As a part of the ICE-BAR programme, lipid compositions of phytoplankton, ice algae, zooplankton and ice fauna were determined to gain information on the role of lipids and trophic relationships in the Arctic ecosystem. We here present results of lipid and fatty acid analyses of ice algae and phytoplankton in relation to environmental data collected during the 1995 cruise.

Materials and methods

Phytoplankton and ice algae were sampled from ice stations during the ICE-BAR 95 cruise, between 17 and 26 June 1995 at latitudes 77.1–78.2°N (Fig. 1). At ice stations the ship was anchored to an ice floe with the main engine turned off. All pelagic samples were taken from the ship, either with water bottles or phytoplankton nets, and ice-algae samples were collected by scuba divers from the underside of ice floes. Ice-algae samples were taken by either a rectangular mouth hand net (Gulliksen 1984), or by an electric suction sampler (Lønne 1988). The ice algae were found mainly as dense mats or looser aggregations that could easily be sampled in large quantities.

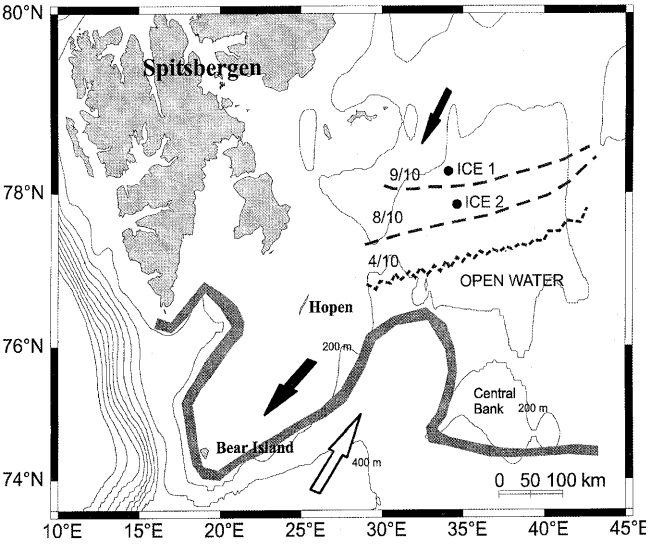

Fig. 1 Topography, ice cover and main features of current systems in the Barents Sea. Average position of the Polar Front is indicated with *thick grey line*. The *broken lines* indicate the ice density; *numbers* indicate an average ice concentration (10/10 is solid pack ice). Sampling stations are shown on the map

Taxonomic classification of the dominant algal species was performed on board R/V "Lance". Live samples were investigated directly under the microscope. The samples were then fixed in Lugol solution with acetic acid (0.4% final solution), or formaldehyde (1–2%) with hexamethylene tetramine for later examinations under an inverted microscope.

Samples of phytoplankton, as well as most of the ice-algae samples, were filtered onto glass fibre filters (GF/C) and immediately placed in chloroform:methanol (2:1 v/v) containing 0.5% w/v butylated hydroxytoluene as antioxidant and stored at −20°C before analyses, Parallel ice-algae samples were placed directly in large plastic flasks and stored at −20°C without adding chloroform : methanol. Samples stored by the two methods yielded the same result when subjected to lipid class analyses with, in particular, the % of free fatty acids in total lipid being the same for the two methods. Total lipid was extracted from each sample by the method of Folch et al. (1957) and lipid class composition was measured by quantitative thin-layer chromatography densitometry as described by Olsen and Henderson (1989). Individual lipid classes were isolated on thin layers of silicic acid (250 mm thick) using hexane:dimethyl:ether:acetic acid (90:10:1, v/v/v) as solvent. Total lipid, glycolipids, triacylglycerols and free fatty acids (FFA) were transmethylated in methanol containing 2% v/v sulphuric acid for 16 h at 50°C to generate fatty acid methyl esters (FAME) which were extracted with hexane and purified by thin-layer chromatography. Wax esters were saponified using potassium t-butoxide (Lee et al. 1971), and the resulting free fatty acids and free fatty alcohols were isolated by thin-layer chromatography using hexane: diethyl ether:acetic acid (70:30:1 v/v/v) as eluting solvent. Fatty alcohols recovered form the plates were converted to acetate esters by reaction with acetic anhydride in pyridine (Farquhar 1962). Fatty acid methyl esters and fatty alcohol acetates were analysed by gas liquid chromatography as detailed by Tande and Henderson (1988).

Results

Environmental factors

The large-scale water masses and currents in the northern Barents Sea (Fig. 1) are related to a branch of the Norwegian Atlantic Current entering the Barents Sea and flowing eastward along the southern edge of the Bear Island Trough into the Hopen Trench, where it partly submerges under the less dense Arctic water. Arctic water flows southwards into the Barents Sea between Spitsbergen and Franz Josefs Land (Loeng 1991). The Polar Front is identified as the transition zone between the Atlantic and Arctic water masses, roughly following the 250-m isobath along the Hopen Trench. The warm Atlantic water is characterised by salinities above 35 psu, while the intermediate Arctic water, found between 20 and 150 m has temperatures close to the freezing point (below −1.5°C) and salinities between 34.4 and 34.6 psu. A striking feature of the hydrography in the MIZ in spring early summer, also seen in this investigation, is a 20-m-thick layer of melt water due to melting of the first-year ice (Orvik and Kuznetzov 1996). All samples analysed in the present study were from the melting zone. The ice conditions varied from dense first-year pack ice, with ice concentrations of 8/10–9/10 at a large ice floe of 5 km^2 at ice station 1, to small first-year ice floes with a size of approximately 20–50 m and ice concentration 6/10–8/10 at ice station 2 (Fig. 1).

Ice algae and phytoplankton communities

Ice algae were found either as *Nitzschia frigida* (diatom) assemblages (Syvertsen 1991) loosely attached as lumps under the ice, or as long strands of densely matted *Melosira arctica* (Melnikov 1997). *Melosira* assemblages were up to 2 m length in sheltered locations such as inside cavities and tunnels in multi-year ice, but were also observed as smaller tufts attached to first-year ice.

At ice station 1, strands of ice algae of 50 cm length were found under some first-year ice floes. These strands were formed by the dominant diatom *Melosira arctica* and three epiphytic diatom species on the *Melosira* strands: *Attheya septentrionalis*, *Pseudogomphonema arcticum* and *Synedropsis hyperborea*. Some chains of *Melosira* had no epiphytes, but on others the number of epiphytic species exceeded that of *Melosira* by a factor of 5.

At ice station 2, the dominant and subdominant ice algae were *Nitzschia frigida*, *N. promare*, *Fossula arctica*, *S. hyperborea* and *A. septentrionalis*. More than 30 species of algae were present in some of the lumps, and much slime with bacteria, protozoans and many empty frustules of diatoms were observed. In a tunnel in multi-year ice floe, *Melosira arctica* forming long strands up to 2 m was found. Phytoplankton was also sampled at ice station 2. The populations were dominated by a mixture of the diatom *Fragilariopsis oceanica*, a dinoflagellate of the genus *Gymnodinium* and small, unidentified flagellates. Low biomass and the presence of *Fragilariopsis oceanica* indicated a pre-bloom or very early bloom phase (Hegseth et al. 1995).

Lipids

At ice station 1, the total lipid from the three *Melosira arctica* samples analysed contained modest levels (25–30%) of polar membrane lipids, comprising mainly glycolipids and phospholipids, and higher levels (40–50%) of neutral lipids comprising mainly triacylglycerols and free fatty acids and smaller amounts of wax esters (Table 1). Fatty acid analyses of the total lipids from these samples revealed a dominance of 20:5(n-3), 16:1(n-7) and C16 PUFA, especially 16:4(n-1)

Table 1 Lipid class composition (%) of *Melosira arctica* association samples taken at ice station 1 (*FFA* free fatty acids; *TAG* triacylglycerols; *WE* wax esters)

Lipid class	Ice st. 1-3	Ice st. 1-4	Ice st. 1-6
Polar lipids	23.2	31.0	28.6
Sterols, pigments and other alcohols	9.8	18.1	13.0
FFA	10.2	24.1	11.1
TAG	27.4	20.2	20.1
WE	10.8	6.3	2.3
Unknown	18.9	0.1	24.3
Total neutral lipids	77.1	68.8	70.8
Polar lipids	23.2	31.0	28.6

Table 2 Fatty acid composition (wt. %) of total lipid from samples of the *Melosira arctica* association taken at ice station 1 (*sats* saturated; *monos* monounsaturated; *tr* trace)

Fatty acid	Ice st. 1-3	Ice st. 1-4	Ice st. 1-6
14:0	7.2	16.5	8.6
16:0	8.9	11.8	9.4
16:1(n-7/9)[a]	15.4	22.2	16.4
16:2	1.8	2.8	2.0
17:0	–	–	–
16:3	4.0	3.0	4.5
16:4(n-1)	8.1	6.3	9.3
18:0	1.1	0.9	1.0
18:1(n-9)	5.7	1.6	0.9
18:2(n-6)	0.8	1.0	0.6
18:4(n-3)	1.4	1.3	1.5
20:1(n-9)	4.5	–	–
20:5(n-3)	28.8	20.1	35.0
22:1(n-11)	1.3	–	–
22:1(n-9)	0.5	0.5	tr
22:6(n-3)	2.5	1.5	2.5
Total sats	18.2	30.7	20.3
Total monos	29.9	26.2	19.0
Total PUFA	49.0	37.5	57.4
Unidentified	2.9	5.6	3.2
Sum (n-3)	33.4	23.4	39.8
Sum (n-6)	1.7	1.9	1.8

[a] Predominantly 16:1(n-7)

(Table 2). Substantial amounts of 14:0 and 16:0 were also present with more variable amounts of 18:1(n-9) and 20:1(n-9), small amounts of 22:6(n-3) and smaller amounts of C18 PUFA, mainly 18:4(n-3). The triacylglycerols in the *Melosira* samples (Table 3) contained higher levels of 16:1(n-7), much lower levels of C16 PUFA and lower levels of 20:5(n-3) than the corresponding total lipid samples (Table 2). Conversely, the polar lipids in the *Melosira* samples were much enriched in C16 PUFA, especially 16:4(n-1), compared to the total lipids (Table 3). The small amounts of wax esters present in the total lipid extracts of the *Melosira* samples from ice station 1 showed an abundance of 22:1(n-11) and 20:1(n-9) fatty alcohols, and 22:1(n-11), 20:1(n-9), 18:1(n-9) and 16:1(n-7) fatty acids (Table 3).

At ice station 2, the samples analysed were variable in composition but fell into two main categories: one dominated by *Melosira arctica* and the other dominated by mixed diatoms such as the *Nitzschia frigida* assemblage. The *Melosira* samples in general contained higher levels of polar lipid and correspondingly lower levels of neutral lipid than the *Nitzschia* mixed diatom samples (Tables 1, 4). The higher levels of neutral lipid in the mixed diatom samples were mainly due to triacylglycerols, although in one case substantial levels of wax esters were also present (Table 4). Both categories of samples also contained high levels of free fatty acids, the highest levels being recorded in the *Melosira* samples (Table 4). Fatty acid analyses revealed that the total lipids from the *Melosira* samples contained higher levels of 20:5(n-3) and C16 PUFA, especially 16:4(n-1), than the total lipids from the mixed diatom samples, i.e. the *Nitzschia frigida* assemblage (Table 5). Conversely, the total lipids from the mixed diatom samples contained higher levels of 16:0 and especially 16:1(n-7) than those from the *Melosira* samples (Table 5).

These differences reflect the abundances of 16:4(n-1) in the polar lipids and 16:1(n-7) in the triacylglycerols, which occur in the polar lipids and triacylglycerols of the *Melosira*-rich samples from both ice stations 1 and 2 (Tables 3, 6). The substantial quantities of wax esters in the *Nitzschia frigida* assemblage from ice station 2 consisted principally of 22:1(n-11) and 20:1(n-9) fatty alcohols and 20:5(n-3), 20:1(n-9) and 16:1(n-7) fatty acids (Table 6).

The total lipid isolated from the sample of mixed phytoplankton from ice station 2 (Table 5) had a high level (28%) of 16:0 and a moderate level (9%) of 18:0. Monounsaturates, chiefly 16:1(n-7) (7%) and 18:1(n-9) (10%), were also recorded at moderate levels, together with the PUFA 20:5(n-3) (5%), 22:6(n-3) (6%), 18:2(n-6) (4%) and 18:4(n-3) (4%) (Table 5).

Discussion

The sub-ice algal assemblages studied in this investigation consisted of two distinct communities: the diatom *Melosira arctica*, forming strands up to 2 m long, and its associated epiphytic diatom species, such as *Attheya septentrionalis*, *Pseudogomphonema arcticum* and

Table 3 Fatty acid composition (wt. %) of triacylglycerols and total polar lipid, and fatty acid and alcohol composition of wax esters from *Melosira arctica* association samples taken at ice station 1 (*sats* saturated; *monos* monounsaturated; *tr* trace)

Fatty acid	Triacylglycerols		Total polar lipids		Wax esters	
	Ice st. 1-3	Ice st. 1-6	Ice st. 1-3	Ice st. 1-6	Ice st. 1-3	
					Fatty acid	Alcohol
14:0	8.4	11.5	3.6	4.9	2.3	0.7
16:0	14.0	16.5	10.1	13.1	9.3	9.1
16:1(n-9/7)[a]	30.2	41.6	12.7	16.3	11.3	1.6
16:2	1.4	1.7	2.8	2.8	tr	–
16:3	0.6	0.6	6.2	5.7	–	–
16:4(n-1)	tr	tr	18.4	15.6		
18:0	1.3	1.9	0.6	0.9	2.1	0.6
18:1(n-9)	12.4	2.1	3.4	1.2	15.6	0.6
18:4(n-3)	1.2	1.2	2.1	2.5	tr	–
20:1(n-11)	0.9	–			3.0	tr
20:1(n-9)	7.5	–	1.0	tr	27.5	31.5
20:5(n-3)	12.2	17.0	18.6	12.7	0.6	–
22:1(n-11)	1.5	tr	tr	–	15.7	44.1
22:1(n-9)	tr	–	tr	tr	3.6	5.8
22:6(n-3)	1.1	0.9	9.2	9.5	tr	–
Total sats	24.1	30.2	15.3	19.9	14.8	10.8
Total monos	55.4	44.6	21.3	23.7	81.9	89.0
Total PUFA	20.0	24.8	59.6	51.6	2.8	–
Unidentified	0.5	0.4	3.8	4.8	0.5	1.6
Sum (n-3)	15.4	20.0	30.7	25.4	1.7	–
Sum (n-6)	2.1	2.2	1.5	2.0	1.5	–

[a] Predominantly 16:1(n-7)

Table 4 Lipid class composition of ice algae samples taken at ice station 2 (*FFA* free fatty acids; *TAG* triacylglycerols; *WE* wax esters)

Lipid class	*Nitzschia frigida* association		*Melosira arctica* association	
	Ice st. 2-17	Ice st. 2-18	Ice st. 2-22	Ice st. 2-25
Polar lipids	22.2	21.8	15.0	38.0
Sterols, pigments and other alcohols	8.2	13.2	11.0	19.1
FFA	6.0	16.0	10.8	22.9
TAG	32.1	40.4	44.1	14.6
WE	28.0	6.6	2.2	3.8
Unknown	2.1	2.0	16.4	0.0
Total neutral lipids	76.4	78.2	84.3	60.4
Polar lipids	22.2	21.8	15.0	38.0

Table 5 Fatty acid composition (wt. %) of total lipid from ice alge and phytoplankton samples taken at ice station 2 (*sats* saturated; *monos* monounsaturated)

Fatty acid	*Nitzschia frigida* association		*Melosira arctica* association		Phytoplankton
	Ice-st. 2-17	Ice-st. 2-18	Ice st. 2-22	Ice st. 2-25	Ice st.2
14:0	6.2	9.0	8.5	11.8	6.1
16:0	14.6	18.8	13.7	13.6	27.9
16:1(n-7/9)[a]	33.2	46.1	26.6	23.1	6.7
16:2	0.8	1.2	1.7	2.7	tr
16:3	0.6	0.8	2.6	2.9	tr
16:4(n-1)	1.2	1.2	6.0	5.7	0.6
18:0	1.9	0.7	1.5	1.2	8.9
18:2(n-6)	–	–	–	–	3.9
18:1(n-9)	2.8	1.3	1.6	2.0	9.8
18:3(n-6)	1.4	1.4	0.6	0.5	–
18:3(n-3)	tr	tr	tr	tr	1.8
18:4(n-3)	1.7	2.1	1.6	1.1	4.4
20:1(n-9)	8.6	tr	–	–	4.5
20:4(n-6)	tr	tr	0.5	tr	–
20:5(n-3)	9.5	12.2	26.8	20.6	4.7
22:1(n-11)	6.4	–	–	tr	2.2
22:1(n-9)	2.7	–	–	tr	0.5
22:6(n-3)	1.0	0.8	1.9	1.4	5.7
Total sats	23.5	29.1	24.6	28.7	44.7
Total monos	57.2	48.3	29.8	28.6	31.0
Total PUFA	18.6	21.5	43.3	36.9	22.6
Unidentified	0.7	1.0	2.3	5.8	1.7
Sum (n-3)	12.8	15.9	31.0	23.9	17.4
Sum (n-6)	3.5	2.4	1.9	1.9	3.9

[a] Predominantly 16:1(n-7)

Synedopis hyperborea, and mats or balls of *Nitzschia frigida* forming arborescent assemblages in association with other subdominant diatoms such as *N. promare* and *Fossula arctica*. The diatom *N. frigida* and its associated species are the most common ice-algal assemblages in the Barents Sea (Syvertsen 1991; Hegseth 1992), whereas *Melosira* has thus far been found mainly in the central polar basin (Melnikov and Bondarchuk 1987; Melnikov 1997). We recorded the species for the first time from first-year ice in the MIZ of the Barents Sea.

The two ice-algae assemblages analysed here both had substantial levels of neutral lipids (40–60%) with TAG and FFA acids being the major classes, i.e. polar lipids in the algae were collectively relatively minor. The assemblages also contained significant levels of wax esters (in one case the level was substantial) but fatty alcohol and fatty acid analyses of these esters provide strong evidence that they are derived from calanoid copepods since it is known that calanoid copepods present at the MIZ stations studied are rich in wax esters whose composition closely resembles those shown in Tables 3 and 6 (S. Falk-Petersen, J.R. Sargent, J. Henderson, E.N. Hegseth, H. Hop, Y.B. Okolodkov, unpublished data). However, microscopic examination of the algal samples analysed here (when determining cell counts) failed to reveal copepods or even fragments of copepods. Therefore, we believe the calanoid copepod wax esters in the algal samples are probably derived from copepod oil released from dead animals and entrapped in the extensive mucilage associated with the ice algae. The preponderance of neutral lipids in the present ice-algal samples is consistent with a pre-bloom/over-

Table 6 Fatty acid composition (wt. %) of triacylglycerols and total polar lipid, and fatty acid and alcohol composition of wax esters Nitzschia frigida and Melosiva Cartica association samples at ice station 2 (*sats* saturated; *monos* monounsaturated *tr* trace)

Fatty acid	Triacylglycerols		Total polar lipids		Wax esters	
	Nitzschia Ice st. 2-17	*Melosira* Ice st. 2-22	*Nitzschia* Ice st. 2-17	*Melosira* Ice st. 2-22	*Nitzschia* Ice st. 2-17	
					Fatty acid	Alcohol
14:0	5.9	11.1	4.1	3.4	2.5	1.7
16:0	21.5	20.6	12.2	6.1	5.9	5.1
16:1(n-9/7)[a]	50.5	42.8	11.4	12.8	13.5	1.2
16:2	0.8	1.4	1.8	2.8	tr	–
16:3	tr	0.5	2.6	6.8	tr	–
16:4(n-1)	tr	tr.	8.2	18.3		
18:0	0.8	2.2	3.3	0.5	1.9	0.7
18:1(n-9)	2.2	2.4	2.4	tr	4.8	tr
18:4(n-3)	2.2	1.4	2.6	2.4	–	–
20:1(n-9)	tr	–	1.8	–	30.8	32.4
20:4(n-3)		0.7	0.5	–	tr	–
20:5(n-3)	9.0	12.3	28.6	23.8	tr	
22:1(n-11)	tr	tr	1.3	–	22.8	46.3
22:1(n-9)	–	–	–	–	8.6	8.2
22:6(n-3)	tr	0.6	6.6	7.9	–	–
Total sats	28.6	34.3	20.9	11.6	11.2	8.4
Total monos	53.5	46.0	20.7	17.1	86.9	91.2
Total PUFA	17.6	19.1	55.6	64.9	1.7	–
Unidentified	0.3	6.0	2.7	6.4	tr	–
Sum (n-3)	12.4	15.1	39.2	35.0	tr	–
Sum (n-6)	3.8	1.8	3.9	1.9	1.8	

[a] Predominantly 16:1(n-7)

wintering phase and is also in agreement with analyses of ice algae sampled in the Barents Sea in 1988 (Henderson et al. in press). Conversely, the samples analysed by Nichols et al. (1989) for the Antarctic sea-ice diatom community in McMurdo Sound were taken during the spring bloom and, consequently, their lipid was dominated by polar lipid with a ratio of triacylglycerols:polar lipid of 1.0–2.5.

The *Melosira* strands were rich in 16:1(n-7), 20-5(n-3) and the C16 PUFA typical of diatoms. This generates a total PUFA level (37–57%) in the upper range of the data reported for ice algae sampled from Antarctica (26–52% PUFA) (Nichols et al. 1993), and also for temperate species (12–53% PUFA; Volkman et al. 1989). Our values are very similar to the levels found in phytoplankton from an Arctic Norwegian fjord (41–53% PUFA) (Sargent et al. 1985). The very high levels of C16 PUFA and 20:5(n-3) in the polar lipid in the *Melosira* assemblage are noteworthy. The *Nitzschia frigida* assemblage, which is also mainly diatoms, likewise had a high level of 16:1(n-7) but only moderate amounts of 20:5(n-3) and small amounts of C16 PUFA.

Total lipid from the mixed phytoplankton samples taken from ice station 2 differed substantially from those of both the *Melosira* and *Nitzschia* assemblages in being much richer in saturated fatty acids. Both total PUFA and (n-3) PUFA in the mixed phytoplankton sample were similar to those in the *Nitzschia* assemblage, but differed from it in detail in containing less C16 PUFA and 20:5(n-3), and more 18:2(n-6), 18:4(n-3) and especially 22:6(n-3). The phytoplankton populations were dominated by dinoflagellates and other small flagellates, and only about 30% of the cell numbers were diatoms.

Diatoms tend to be rich in 20:5(n-3) and 16:1(n-7) and relatively deficient in C18 PUFA and 22:6(n-3). In addition, they can have very appreciable amounts of C16 PUFA, especially 16:4(n-1) (Chuecas and Riley 1969). Dinoflagellates tend to be rich in 22:6(n-3) and C18 PUFA and relatively deficient in 16:1(n-7) and 20:5(n-3) (Ackman et al. 1968; Chuecas and Riley 1969; Sargent and Whittle 1981; Dunstan et al. 1994; Servel et al. 1994), which is in accordance with the fatty acid composition of phytoplankton sampled here. It can be deduced from the data here that, should the *Nitzschia* assemblages in the ice be derived from open-water phytoplankton, then the process involved must be rather specific, selecting only species rich in C16 PUFA and 20:5(n-3), i.e. mainly chain-forming diatoms, and not species rich in C18 PUFA and 22:6(n-3), i.e. mainly motile flagellates. The main conclusion from this study is that the ice algae are dominated by diatoms and represent a rich source of C16 PUFA and especially 20:5(n-3), whereas the mixed phytoplankton from open waters is relatively richer in flagellates containing substantial amounts of C18 PUFA and 22:6(n-3), which are of importance to higher trophic levels.

We also wish to note that several of the samples of mixed phytoplankton from the water column analysed in the present investigation had very low levels of total

lipid that was unusually rich in saturated fatty acids, especially 16:0 and 18:0 (data not shown, since the very limited amounts of lipid available precluded detailed analyses). The source of the relatively high levels of 16:0 and 18:0 in these samples is not known. However, high levels of 16:0 and 18:0 (34 and 25% respectively) have been previously recorded in water column samples from the Weddell Sea (Fahl and Kattner 1993). Our impression is that phytoplanktonic material collected on at least some occasions from the MIZ may contain substantial amounts of decaying or decomposed organic matter. This raises the question of how fast the products of primary production decay and decompose in regions covered by ice for prolonged periods; this is a question to be addressed in future work in the MIZ.

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