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# Lipid Content and fatty acid composition of algal communities in sea-ice and water from the Weddell Sea (Antarctica)

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**Abstract.** The lipid and fatty acid compositions of microalgae were investigated in sea-ice and water samples from six different habitats of the Weddell Sea (Antarctica). All sea-ice samples and ice-associated water contained high algal biomass dominated by centric and pennate diatoms. Cells partially filled with oil droplets and resting spores were found. In the cells from the ice platelet layer triacylglycerols formed the largest component of the lipids. The fatty acid composition of sea-ice microalgae was dominated by the 16:1(n-7), 16:0, 18:1(n-9) and 20:5 (n-3) fatty acids. Except 18:1, they are typical for diatom fatty acids. These fatty acids were most abundant in pieces of first year ice with a brown colouration ("brown-ice") and in the water column directly below sea-ice (sub-ice water). The small amounts of non-diatom acids, as 22:6 (n-3) and 18:4 (n-3), clearly showed that the sea-ice communities were not purely composed of diatoms. The most striking difference, in comparison to the general fatty acid composition of diatoms, was the high proportion of the 18:1 fatty acid in all samples, which might be caused by detrital material or lipid accumulation within cells and resting spores. In general, no clear adaptation of the fatty acid composition to the Antarctic and sea-ice environment was found. The fatty acid composition of the particulate matter from the water column was totally different from all other samples dominated by the saturated fatty acids 16:0 and 18:0.

The accumulation of lipids plays a major, and often crucial role in the survival strategies of organisms in polar regions. The importance of lipids has been better studied in higher trophic levels of the food web than in the primary producers. The lipid content of phytoplankton may vary widely due to the effect of changing biotic and abiotic factors. Lipid storage in phytoplankton is often related to unfavourable growth conditions, such as nutrient limitation, low temperature and low irradiance. Also the formation of diatom resting spores is coupled with an extensive accumulation of lipids (Doucette and Fryxell 1983; 1985 and references therein). Various studies have focused on biochemical pathways of carbon assimilation also with respect to lipid biosynthesis. However, the conditions responsible for lipid accumulation are not clear, especially regarding its relevance to phytoplankton and sea-ice microalgae (e.g., Smith and Morris 1980; Palmisano and Sullivan 1985; Rivkin and Voytek 1987; Palmisano et al. 1988; Nichols et al. 1988; 1989; Tillmann et al. 1989: Lizotte and Sullivan 1992: Thomas and Gleitz 1993). Apart from the determination of lipid classes (Palmisano et al. 1988) only very few fatty acid analyses from cultures of sea-ice diatoms have been performed (Gillan et al. 1981; Nichols et al. 1986), and even fewer data are available on the fatty acid compositions of natural sea-ice algal communities from various ice habitats (Whitaker and Richardson 1980).

In our study microalgal samples from various ice types and phytoplankton from adjacent water were collected during a summer phytoplankton bloom. Detailed lipid investigations including fatty acid compositions are discussed in conjunction with prevailing environmental conditions in order to obtain a better understanding of lipid accumulation in natural sea-ice assemblages. It should be clarified whether there is an adaptation of microalgae to the sea-ice environment in view of their lipid content and composition.

## Materials and methods

Samples were collected in the Weddell Sea (Antarctica) during the RV '*Polarstern*' expedition ANT IX/3 in January 1991 (Bathmann et al. 1992). The sampling took place in the area of 76°22′ to 76°28′ S and 30°07′ to 30° 48′E. Six different habitats were sampled: Samples in the water column were taken with Niskin bottles attached to a CTD probe. Water was drawn from two bottles between 0 and 40 m depth and combined. The water samples from the sub-ice water column were collected through ice holes with an L-shaped plastic tube connected to a vacuum pump (Smetacek et al. 1992). The ice

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platelet sample was taken with a plastic bucket from surface isolated ponds between rafted ice floes. The ice platelets were separated from the water by filtration through a sieve. The separated water is henceforth termed interstitial water. Pieces of first year ice with a brown colouration, "brown-ice", broken off between abutting ice floes, were also collected. One ice-core from first year ice was drilled with a 4 inch corer, and the total length of 56 cm was melted. Determination of chlorophyll *a* (chl *a*), nutrients and salinity is described by Bathmann et al. (1992).

All ice samples were melted at 0°C in the dark. We are aware that this method may result in a loss of intact flagellates and ciliates due to osmotic changes (Garrison and Buck 1986) but there is no evidence that this effects the lipid composition of the particulate matter. All samples were subsequently filtered through glass-fibre filters (Whatman GF/C, precombusted at 450°C). The particulate matter is called "microalgae" due to the high proportion of sea-ice algae. One set of samples was stored at −80°C for determination of dry weight and another in dichloromethane:methanol (2:1, by vol.) at −23°C until lipids were determined: Algal cells together with the filter were crushed with a teflon potter and extracted in the storage solution. An aliquot of the supernatant was used for the determination of lipid classes by thin layer chromatography with flame ionisation detection (TLC-FID) using an Iatroscan (Mark IV TH 10) analyser. The detailed method is described by Ackman (1981) and Fraser et al. (1985).

Triacylglycerols were separated from the total lipid extract by thin layer chromatography on glass plates coated with silica gel using hexane:diethyl ether:glacial acetic acid (90:10:1, by vol.) as the developing solvent. Methyl esters of fatty acids were prepared by transesterification with 3% concentrated sulphuric acid in methanol for four hours at 80°C. After their extraction with hexane the composition was analysed with a Carlo Erba gas liquid chromatograph (HRGC 5300) (column: 30 m * 0.25 mm; film thickness: 0.25 μm; liquid phase: DB-FFAP) using temperature programming according to Kattner and Fricke (1986). Fatty acids were identified with a standard mixture and for quantification an internal 19:0 fatty acid methyl ester standard was added to the samples before any analytical step.

## Results

The sea-ice and water samples of the different habitats were characterized by different salinities, nutrients and chl *a* concentrations (Table 1). In the water column high nutrient levels were measured. The sea-ice and the water closely associated with the ice (interstitial and sub-ice water) were depleted in nitrate and phosphate. The phosphate concentration in the "brown-ice" pieces collected between the floes was similar to that in the water column, however, nitrate was depleted. Silicate was not depleted, but was reduced compared to the water column sample, except in the ice core where silicate was highest. The salinity of the sub-ice water was lower than that of the open water.

Sea-ice samples and the water directly associated with the ice had a very high concentration of microalgae. Microscopic investigation showed that the main algal species in the interstitial water, separated from the ice platelets, were the centric diatoms *Thalassiosira antarctica*, *Thalassiosira* spp., *Porosira pseudodenticulata* and pennate *Nitzschia* spp.. One half to two thirds of the *Thalassiosira* cells contained large lipid droplets (Scharek, pers. comm.). The same species also dominated the other samples but in different abundances.

There was a strong gradient from very high chl *a* values and algal dry weights in the sea-ice samples to lower levels in the ice-associated water and lowest values in the open water. The highest values were measured in the "brown-ice" (158 μg chl *a* /L and 24 mg/L dry weight). The ice platelets also contained high concentrations of microalgae and particulate material (81 μg chl *a* /L and 25 mg/L dry weight). Highest levels of fatty acids reached nearly 4 mg/L in the ice platelets and interstitial water, where the fatty acids made up ca. 14% of the dry weight. In the "brown-ice" the proportion was lower, decreasing further in the ice core and in the water column, where the fatty acid fraction was less than 1% of dry weight (Table 1).

The fatty acid compositions of the various samples are presented in Table 2. The same fatty acids generally occurred in all samples but in different quantities. The microalgae of the interstitial water were rich in short chain saturates (31%), especially 14:0 and 16:0 and monounsaturated fatty acids (45%), mainly 16:1 and 18:1. Polyunsaturated fatty acids (18:2, 18:4, 20:5, 22:6) altogether comprised 22%. The fatty acid composition of the ice platelet microalgae was very similar to that of the interstitial water but with a shift to a higher proportion of 16:1, at the expense of the 18:1 fatty acid. The same shift was found between the 20:5 and the 22:6 fatty acids, with a higher proportion of 20:5. One major difference in both samples was the high proportion of triacylglycerols in the ice platelet microalgae representing ca. 40% of total lipid compared to ca. 5% in the interstitial water. For this reason the fatty acid composition of the triacylglycerols

**Table 1.** Environmental conditions of the different habitats. Chlorophyll *a* (Chl *a*), salinity (psu: practical salinity units), nutrient concentrations, dry weight (DW), total concentration of fatty acid (FA) and total fatty acid in %DW. Dash means no data

| | "Brown-ice" | Ice core | Ice platelets | Interstitial water | Sub-ice water | Water column |
|---|---|---|---|---|---|---|
| Nitrate (μM) | 0.00 | 0.26 | 0.02 | 0.01 | 0.05 | 28.11 |
| Nitrite (μM) | 0.12 | 0.11 | 0.03 | 0.09 | 0.02 | 0.84 |
| Silicate (μM) | 45.7 | 80.2 | 29.3 | 33.1 | 17.6 | 57.8 |
| Phosphate (μM) | 1.40 | 0.76 | 0.07 | 0.01 | 0.30 | 1.89 |
| Chl *a* (μg/L) | 158 | – | 81.7 | 42.2 | 6.0 | 0.21 |
| Salinity (psu) | – | – | – | – | 27.72 | 34.18 |
| DW (mg/L) | 24 | 11 | 25 | 27 | 10 | 7 |
| Total FA (mg/L) | 5.2 | 0.7 | 3.4 | 3.9 | 0.4 | 0.02 |
| Total FA (%DW) | 9.7 | 6.3 | 13.5 | 14.1 | 3.4 | 0.2 |

**Table 2.** Fatty acid composition (weight%) of phytoplankton from the different habitats. Dash indicates not detected or trace amounts (<0, 1%). Total sats.: Total saturated, Total monos.: Total monounsaturated, Total PUFA: polyunsaturated fatty acids

| Fatty acid | "Brown-ice" | Ice core | Ice platelets | Interstitial water | Sub-ice water | Water column |
|---|---|---|---|---|---|---|
| 14:0 | 7.1 | 11.9 | 9.8 | 14.5 | 5.8 | 7.1 |
| 15:0 | 0.7 | – | 0.4 | 0.5 | 0.8 | – |
| 16:0 | 18.0 | 19.3 | 16.9 | 15.5 | 19.4 | 33.6 |
| 16:1(n-7) | 31.9 | 21.1 | 26.4 | 16.1 | 34.2 | 4.9 |
| 16:2(n-6) | 1.4 | 0.7 | 1.4 | 0.8 | 1.5 | – |
| 16:3(n-3) | 0.9 | – | 0.8 | 0.5 | 0.8 | – |
| 16:4(n-?) | 4.2 | 2.2 | 5.3 | 2.6 | 4.3 | – |
| 18:0 | 0.9 | 1.6 | – | 0.5 | 1.1 | 25.2 |
| 18:1(n-9) | 11.6 | 19.7 | 14.8 | 23.7 | 9.9 | 12.4 |
| 18:1(n-7) | 1.2 | 1.2 | 0.4 | 1.0 | 1.2 | 1.4 |
| 18:2(n-6) | 3.6 | 3.0 | 4.9 | 4.4 | 4.3 | – |
| 18:3(n-3) | 0.3 | 0.6 | 0.7 | 0.8 | 0.5 | – |
| 18:4(n-3) | 3.8 | 3.7 | 4.2 | 3.8 | 3.8 | 12.5 |
| 20:1(n-9) | 0.6 | 1.9 | 1.6 | 3.6 | 0.3 | – |
| 20:5(n-3) | 11.2 | 8.2 | 9.4 | 5.8 | 10.3 | 1.5 |
| 22:6(n-3) | 2.5 | 2.7 | 3.1 | 5.8 | 1.9 | – |
| Total sats. | 26.7 | 32.8 | 27.1 | 31.0 | 27.1 | 65.9 |
| Total monos. | 45.0 | 43.9 | 43.4 | 44.4 | 45.6 | 18.7 |
| Total PUFA | 27.9 | 21.1 | 25.3 | 21.9 | 27.4 | 14.0 |

**Table 3.** Fatty acid composition (wt%) of the triacylglycerols. For further information see Table 2

| Fatty acids | Ice platelets | Interstitial water |
|---|---|---|
| 14:0 | 13.1 | 8.2 |
| 15:0 | 3.8 | 0.5 |
| 16:0 | 14.8 | 14.7 |
| 16:1(n-7) | 16.8 | 26.8 |
| 16:2(n-6) | 0.7 | 1.5 |
| 16:3(n-3) | – | – |
| 16:4(n-?) | 1.2 | 4.9 |
| 18:0 | 0.4 | 0.3 |
| 18:1(n-9) | 28.4 | 17.1 |
| 18:1(n-7) | – | – |
| 18:2(n-6) | 5.0 | 5.8 |
| 18:3(n-3) | 0.9 | 0.8 |
| 18:4(n-3) | 3.4 | 4.6 |
| 20:1(n-9) | 2.1 | 1.7 |
| 20:5(n-3) | 4.8 | 10.2 |
| 22:6(n-3) | 4.5 | 2.8 |
| Total sats. | 32.0 | 23.6 |
| Total monos. | 47.6 | 45.6 |
| Total PUFA | 20.5 | 30.7 |

from both samples were analyzed separately (Table 3). Major differences again occurred in the mono- and polyunsaturated fatty acids. The triacylglycerols of the interstitial water contained higher levels of the 16:1 and lower levels of the 18:1 fatty acid than the ice platelet microalgae.

In the "brown-ice" the proportion of the 16:1 fatty acid was higher than in the ice platelet sample. The same was true for the 20:5. This was mainly compensated by lower proportions of the 18:1 and 22:6 fatty acids. The fatty acid composition of the ice core material was very similar to that of the interstitial water. In the sub-ice water microalgae the trend to higher values of the 16:1 acid continued up to a maximum of 34%. However, the compositions were very similar to those in "brown-ice".

The fatty acid composition of the particulate matter from the water column was totally different from all other samples. It was rich in saturated fatty acids (66%) with the main compounds 16:0 and 18:0. Moderate amounts of mono- and polyunsaturated fatty acids were present mainly as 18:1 and 18:4. The very small amount of fatty acids (0.2% of dry weight) consisted of 97% polar lipids.

## Discussion

Several studies on lipids of sea-ice microalgae have been performed in McMurdo Sound, Ross Sea, in which the fatty acid compositions were not considered (e.g., Palmisano and Sullivan 1985; Palmisano et al. 1988; Nichols et al. 1989; Priscu et al. 1988, 1990). In our study, samples of sea-ice and ice-associated water originated from an extremely dense phytoplankton bloom causing brown colouration of water and ice. Such a bloom in this area in the ice platelet layer had already been observed by Smetacek et al. (1992) in spring 1986, before the seasonal melting of the sea-ice. It was composed of the same centric diatoms as found in our study. The nitrate and phosphate limitation in the different habitats resulted from uptake by microalgae and dilution by nutrient-poor melt water. However, it is not possible to reconstruct the developmental history of the microalgal bloom prior to sampling. Due to the nitrate and phosphate limitation it can be assumed that at least some microalgal species were in a late growth phase or already senescent. The microalgae below and within the ice may be released into the water column upon melting which may result in further growth due to better light and nutrient conditions. The low level of particulate matter in the water column confirmed that the microalgae accumulation was restricted to the sea-ice and ice-associated water.

The species composition of the microalgal communities in austral summer in the Weddell Sea was different to that of other Antarctic areas in spring, from which lipid investigations have previously been reported (see references on McMurdo Sound). The main difference was the dominance of the large centric *Thalassiosira* spp. in our study. The high lipid content in the sea-ice algae was already evident on microscopic examination because of the large oil droplets. This lipid content is higher than reported for phytoplankton species cultured in the laboratory or in the open sea (e.g., Parsons et al. 1961; Ackman et al. 1968; Platt and Irwin 1973; Tillmann 1987).

Enhanced assimilation of carbon into carbohydrates and lipids is thought to be indicative of nutrient-limited algal populations in the Antarctic (Lizotte and Sullivan 1992; and references therein). On the other hand, investigations by Smith and Morris (1980) showed no influence of nutrient depletion on lipid accumulation. They suggested that low light intensity and low temperature stimulate lipid synthesis. Tillmann et al. (1989), however, found that lipid synthesis in *Thalassiosira antarctica* does not increase at temperatures ranging between $-2$ and $+3\,^{\circ}C$ and low irradiances. This is in accordance with results of Palmisano and Sullivan (1985), Rivkin and Voytek (1987) and Palmisano et al. (1988) in natural sea-ice algal communities. Doucette and Fryxell (1983; 1985) found that in *T. antarctica* the formation of resting spores is coupled to an extensive accumulation of lipids.

Palmisano et al. (1988) described an enhanced assimilation of $^{14}C$ into the neutral lipids dominated by triacylglycerols during certain growth phases. Further information can be obtained by fatty acid analysis of the lipids, although to our knowledge there have been only two fatty acid analyses for sea-ice diatom cultures (Gillan et al. 1981; Nichols et al. 1986). Only one study has investigated the fatty acid compositions of a natural sea-ice population which was purely composed of the diatom *Navicula glaciei* (Whitaker and Richardson 1980).

It is well established that phytoplankton groups contain similar principle fatty acids. Thus, the fatty acid composition of cultured diatom species is dominated by the 16:1 and 20:5 fatty acids (e.g., Kates and Volcani 1966; Orcutt and Patterson 1975; Pohl and Zurheide 1979; Kattner and Brockmann 1990). The same result has been found for sea-ice diatoms (Whitaker and Richardson 1980; Gillan et al. 1981; Nichols et al. 1986) and natural phytoplankton blooms dominated by diatoms (Kattner et al. 1983; Mayzaud et al. 1989). On the other hand, Nichols et al. (1986) found very low relative levels of polyunsaturated fatty acids in a culture of the sea-ice diatom *Nitzschia cylindrus*. In the discussion about fatty acid compositions of natural phytoplankton assemblages, it has to be considered that assemblages consist of a mixture of detritus and a variety of different species. Our sea-ice and ice-associated water samples (with the exception of the water column) were mainly dominated by diatoms, especially *Thalassiosira* and *Nitzschia* spp.. A steady increase in the two principal diatom fatty acids 16:1 and 20:5 from interstitial water, ice platelet to the "brown-ice" and sub-ice water samples indicates an increasing proportion of diatom species in the total particulate material. Compared to the fatty acid composition of a natural population of *Navicula glaciei* (Whitaker and Richardson 1980) and a *Thalassiosira antarctica* culture grown at about 0 °C (Hirche, pers. comm.), the proportion of the 20:5 fatty acid was much lower in the sea-ice and the water samples. The culture contained 29% of the 20:5 acid whereas the highest value of 20:5 (ca. 11%) in our samples was found in the "brown-ice". This confirms the assumption that the proportion of polyunsaturated fatty acids seems to be higher in phytoplankton cultures than in natural communities (Kattner and Brockmann 1990). The small amounts of non-diatom fatty acids, as 22:6 and 18:4, show clearly that the sea-ice communities were not purely composed of diatoms.

The unusually high proportion of the 18:1 fatty acid (compared to culture-grown diatoms) was found in all samples, but especially in the interstitial water. Even higher proportions of the 18:1 fatty acid were found in the particulate matter during spring in the North Sea, and the proportion decreased only during the exponential growth phase of a diatom bloom (Kattner et al. 1983). We therefore speculate that the high proportion of the 18:1 acid in our samples may be due to detrital matter. However, it is known that *Thalassiosira antarctica* forms resting spores under unfavourable conditions with a change in the chemical composition, and spores contain noticeably more lipid reserves than vegetative cells (Doucette and Fryxell 1983, 1985). Unfortunately these workers did not determine the fatty acid composition of the resting spores but it might be possible that they are rich in the 18:1 acid, too.

Particulate matter in waters of low productivity is deficient in polyunsaturated fatty acids. It contains high levels of saturates and fatty acids with 18 carbon atoms (Goutx and Saliot 1980; Mayzaud et al. 1989; Henderson et al. 1991; Graeve 1992). The same was true for the open water column sample which probably only contained a mixture of detritus and green algae.

In summary, lipids play an important role in the physiology of sea-ice algal communities. However, the reasons for the initiation of enhanced lipid biosynthesis are not clear, although it is probably prerequisite that a multitude of factors interact together to induce lipid accumulation. One of the major factors may be nutrient limitation. The synthesis of storage products increases the chances to survive long periods of unfavourable conditions such as freezing into the ice. Thus, algae which have survived the winter may be released into the water column during next spring to inoculate the nutrient rich waters. Resting stages contain considerable amounts of lipid, but the cells themselves may also be rich in lipids as shown by the oil droplets comprising most of the cell volume. The fatty acid composition of the sea-ice algae showed due to the large variability, no clear adaptation to the conditions in the Antarctic and to the sea-ice environment was observed. The most striking difference to the fatty acid composition of the sea-ice algal community to that of diatoms is the high proportion of the 18:1 fatty acid.

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## References

Ackman RG (1981) Flame ionization detection applied to thin-layer chromatography on coated quartz rods. Methods in Enzymology 72:205–252

Ackman RG, Tocher CS, McLachlan J (1968) Marine phytoplankter fatty acids. J Fish Res Board Can 25:1603–1620

Bathmann U, Schulz-Baldes M, Fahrbach E, Smetacek V, Hubberten H-W (1992) The expeditions ANTARKTIS IX/1-4 of the Research Vessel '*Polarstern*' in 1990/91. Ber Polarforsch 100, pp 403

Doucette GJ, Fryxell GA (1983) *Thalassiosira antarctica*: vegetative and resting stage chemical composition of an ice-related marine diatom. Mar Biol 78:1–6

Doucette GJ, Fryxell GA (1985) *Thalassiosira antarctica* (Bacillariophyceae): vegetative and resting stage ultrastructure of an ice-related marine diatom. Polar Biol 4:107–112

Fraser FG, Tocher DR, Sargent JR (1985) Thin-layer chromatography – Flame ionization detection and the quantification of marine neutral lipids and phospholipids. J Exp Mar Biol Ecol 88:91–100

Garrison DL, Buck KR (1986) Organism losses during ice melting: A serious bias in sea ice community studies. Polar Biol 6:237–239

Gillan FT, McFadden GI, Wetherbee R, Johns RB (1981) Sterols and fatty acids of an Antarctic sea-ice diatom *Stauroneis amphioxys*. Phytochemistry 20:1935–1937

Goutx M, Saliot A (1980) Relationship between dissolved and particulate fatty acids and hydrocarbons, chlorophyll *a* und zooplankton biomass in Villefranche Bay, Mediterranean Sea. Mar Chem 8:299–318

Graeve M (1992) Umsatz und Verteilung von Lipiden in arktischen marinen Organismen unter besonderer Berücksichtigung unterer trophischer Stufen. PhD thesis, Universität, Bremen, pp 145

Henderson RJ, Olsen RE, Eilertsen HC (1991) Lipid composition of phytoplankton from the Barents Sea and environmental influences on the distribution pattern of carbon among the photosynthetic end products. Polar Res 10:229–237

Kates K, Volcani BE (1966) Lipid components of diatoms. Biochem Biophys Acta 116:2264–278

Kattner G, Brockmann UH (1990) Particulate and dissolved fatty acids in an enclosure containing a unialgal *Skeletonema costatum* (Greve.) Cleve culture. J Exp Mar Biol Ecol 114:1–13

Kattner G, Fricke HSG (1986) Simple gas-liquid chromatographic method for the simultaneous determination of fatty acids and alcohols in wax esters of marine organisms. J Chromatogr 361:263–286

Kattner G, Gercken G, Eberlein K (1983) Development of lipids during a spring phytoplankton bloom in the northern North Sea. I. Particulate fatty acids. Mar Chem 14:149–162

Lizotte MP, Sullivan CW (1992) Biochemical composition and photosynthate distribution in the sea ice microalgae of McMurdo Sound, Antarctica: evidence for nutrient stress during the spring bloom. Antarctic Sci 4:23–30

Mayzaud P, Chanut JP, Ackman RG (1989) Seasonal changes of the biochemical composition of marine particulate matter with special reference to fatty acids and sterols. Mar Ecol Prog Ser 56:189–204

Nichols PD, Palmisano AC, Smith GA, White DC (1986) Lipids of the Antarctic sea-ice diatom *Nitzschia cylindrus*. Phytochem 25:1649–1653

Nichols PD, Volkman JK, Palmisano AC, Smith GA, White DC (1988) Occurrence of an isoprenoid $C_{25}$ diunsaturated alkene and high neutral lipid content in Antarctic sea-ice diatom communities. J Phycol 24:90–96

Nichols PD, Palmisano AC, Rayner MS, Smith GA, White DC (1989) Change in the lipid composition of Antarctic sea-ice diatom communities during a spring bloom: an indication of community physiological status. Antaractic Sci 1:133–140

Orcutt DM, Patterson GW (1975) Sterol, fatty acid and elemental composition of diatoms grow in chemical defined media. Comp Biochem Physiol 50B:579–583

Palmisano AC, Sullivan CW (1985) Pathways of photosynthetic carbon assimilation in sea-ice microalgae from McMurdo Sound, Antarctica. Limnol Oceanogr 30:674–678

Palmisano AC, Lizotte MP, Smith GA, Nichols PD, White DC, Sullivan CW (1988) Changes in photosynthetic carbon assimilation in Antarctic sea-ice diatoms during spring bloom: Variation in synthesis of lipid classes. J Exp Mar Biol Ecol 116:1–13

Parsons TR, Stephens K, Strickland JDH (1961) On the chemical composition of eleven species of marine phytoplankton. J Fish Res Bd Can 18:1001–1016

Platt T, Irwin B (1973) Coloric content of phytoplankton. Limnol Oceanogr 18:306–310

Pohl P, Zurheide F (1979) Fatty acids and lipids of marine algae and their control of biosynthesis by environmental factors. In: Hoppe HA et al. (eds) Marine algae in pharmaceutical science. Walter de Gruyter, Berlin, pp 473–523

Priscu JC, Priscu LR, Howard-Williams C, Vincent WF (1988) Diel patterns of photosynthate biosynthesis by phytoplankton in permanently ice-covered Antarctic lakes under continuous sunlight. J Plankton Res 10:333–340

Priscu JC, Priscu LR, Palmisano AC, Sullivan CW (1990) Estimation of neutral lipid levels in Antarctic sea-ice microalgae by nile red fluorescence. Antarctic Sci 2:149–155

Rivkin RB, Voytek MA (1987) Photoadaptation of photosynthesis and carbon metabolism by phytoplankton from McMurdo Sound, Antarctica. I. Species-specific and community response to reduced irradiance. Limnol Oceanogr 32:249–259

Smetacek V, Scharek R, Gordon LI, Eicken H, Fahrbach E, Rohardt G, Moore S (1992) Early spring phytoplankton blooms in the ice platelet layers of the southern Weddell Sea, Antarctica. Deep-Sea Res 39:153–168

Smith AE, Morris I (1980) Synthesis of lipid during photosynthesis by phytoplankton of the Southern Ocean. Science 207:197–199

Thomas DN, Gleitz M (1993) Allocation of photoassimilated carbon into major algal metabolite fractions: Interspecific differentiation between diatoms isolated from the Weddell Sea (Antarctica). Polar Biol

Tillmann U (1987) Versuche zur Abhängigkeit des Fett- und Proteingehaltes arktischer Diatomeen von Temperatur und Licht in statischen Kulturen. Diplomarbeit, RWTH Aachen, pp 100

Tillmann U, Baumann MEM, Aletsee L (1989) Distribution of carbon among photosynthetic end products in the bloom-forming Arctic diatom *Thalassiosira antarctica* COMBER. Polar Biol 10:231–238

Whitaker TM, Richardson MG (1980) Morphology and chemical composition of a natural population of an ice-associated Antarctic diatom *Navicula glaciei*. J Phycol 16:250–257