Lipid composition of phytoplankton from the Barents Sea and environmental influences on the distribution pattern of carbon among photosynthetic end products

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The colonial algae *Phaeocystis pouchetii* and *Dinobryon pellucidum* dominated the phytoplankton crop at three stations in the Polar Front area of the Barents Sea.

Lipid extracted from the seawater containing the phytoplankton was dominated by neutral lipid classes, particularly triacylglycerols, and phospholipids were more abundant than galactolipids at all stations. Polyunsaturated fatty acids comprised between 15 and 26% of fatty acids of total lipid.

Of the carbon assimilated into lipid over 24 hours, 40% was located in the neutral lipid fraction. Phospholipids contained a smaller proportion of fixed carbon than galactolipids.

No definte relationships were observed between the distribution of fixed carbon in photosynthetic end products and the temperature or irradiance at which the phytoplankton was incubated. At a constant irradiance of 8.5 μmol $m^{-2}s^{-1}$, the highest proportion of fixed carbon was recovered in protein at 4.5°C, but at −1.5°C most radioactivity was present in low molecular weight compounds. Regardless of incubation conditions, lipid always contained less than 30% of total assimilated carbon.

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Introduction

It is well known that irradiance and temperature are important variables in controlling phytoplankton primary production in polar and temperate regions (Harrison & Platt 1986; Mortain-Bertrand et al. 1988). Several quantitatively important phytoplankton species in Arctic/northerly waters, among them *Phaeocystis pouchetii*, adapt to low light by increasing their photosynthetic efficiency (Eilertsen et al. 1989a; Palmisano et al. 1986). Temperature is known to control the rate of light saturated photosynthesis, and an increase in the activity of ribulose-1,5-biphosphate carboxylase may occur in phytoplankton as an adaptation to growth at low temperature (Mortain-Bertrand et al. 1988).

Other adaptations to low environmental temperatures may also exist in Arctic phytoplankton. For example, temperature is known to influence the lipid composition of photosynthetic marine algae grown in batch cultures whereby a decrease in growth temperature corresponds with an increase in the degree of unsaturation of the component fatty acids (Ackman et al. 1968; Henderson & Mackinlay 1989; Mortenson et al. 1988). This is in keeping with the general phenomenon of homeoviscous adaptation which maintains the fluid state of biomembranes in poikilotherms as environmental temperature falls. Laboratory studies of the influence of temperature on fatty acid composition in algae have not employed temperatures as low as those encountered in Arctic waters. Although the lipid composition of phytoplankton sampled in temperate waters has been studied (Kattner et al. 1983; Claustre et al. 1990), little information is available for the lipid composition of natural populations of Arctic phytoplankton. It is not known whether the lipids of Arctic phytoplankton show any special adaptations to environment.

The incorporation of up to 80% of fixed carbon into lipid by field populations of Antarctic phytoplankton has been attributed to low environmental temperatures coupled with low ambient light intensities (Smith & Morris 1980a, b). In laboratory cultures of the cryptomonad *Chroomonas salina*, the proportion of carbon fixed into lipid is influenced more by growth temperature than by light (Henderson & Sargent,

1989). Extrapolation of this finding to natural phytoplankton populations would suggest that low temperature rather than low light enhances the assimilation of carbon into lipid in polar waters.

The present study had two aims: firstly to determine the lipid composition of phytoplankton taken from a Polar Front situation, and secondly to examine the influence of low temperature and light on the distribution pattern of fixed carbon within the various end products of photosynthesis, particularly lipids.

Materials and methods

Hydrography and phytoplankton

Studies were carried out on board R/V JOHAN RUUD. The hydrographic parameters of the stations at which phytoplankton were sampled in the present study have already been described in detail elsewhere (Hansen et al. 1989). The stations were located in the mixing zone between Atlantic and Arctic water masses at the edge of the drift ice.

Samples of seawater containing phytoplankton were collected by Niskin bottles. Irradiance was measured using a Lambda LI-185 quantum meter equipped with a spherical sensor. Chlorophyll *a* and phaeophytin determinations were carried out as described by Eilertsen et al. (1989a).

For analysis of lipid composition, phytoplankton was collected by filtering 5 to 7 l of seawater sampled from the layer of maximum chlorophyll *a* through glass fibre filters (type GF/C) which had previously been washed with chloroform : methanol (2 : 1, v/v). The filters containing phytoplankton were stored in glass vials filled with chloroform : methanol (2 : 1, v/v) and stored at −15°C until analysed further.

Carbon fixation incubations

Only samples taken from Stations 1 and 2 were used for the study of carbon fixation. Samples of seawater taken from the deep chlorophyll *a* maximum were placed in glass bottles and $NaH^{14}CO_3$ (56 mCi $mmol^{-1}$) added at a concentration of 250 μCi l^{-1}. For time course experiments, 2 l of seawater was incubated at 95 μmol $m^{-2}s^{-1}$ and 0.5°C. Aliquots of 200 ml were taken at each required time point. In experiments on the effects of variation in temperature and light, 100 ml of seawater was used in each incubation. Incubations were carried out for 12 hours in temperature-controlled incubators with artificial illumination supplied by fluorescent daylight tubes. Samples of seawater were subjected to different light intensities by surrounding the incubation bottles with nylon mesh of different mesh sizes. Light was measured inside the bottles using the probe of the quantum meter. Samples were equilibrated at the required temperature for 1 hour before the addition of $NaH^{14}CO_3$.

At the end of incubation time, 10% of total sample volume was filtered through a GF/C filter and a further 100 ml of previously-filtered seawater passed through the same filter. The filter was transferred to a scintillation vial and stored at −15°C for the later determination of total carbon fixation by scintillation counting after the addition of scintillant fluid. The remainder of each sample was collected onto another filter and stored in 7 ml chloroform : methanol (2 : 1, v/v) at −15°C for later analysis of the distribution of radioactivity in the end products of photosynthesis.

In the laboratory, cells retained on glass fibre filters were fractionated into chloroform soluble (lipid), methanol-water soluble (low molecular weight material), hot trichloroacetic acid soluble (polysaccharide) and hot trichloroacetic acid insoluble (protein) fractions according to the procedure of Rivkin (1985). Aliquots of the fractions were transferred to polythene scintillation vials, dried and resuspended in scintillation fluid prior to measurement of radioactivity content by liquid scintillation spectrophotometry.

Lipid analysis

For the analysis of lipid, filters stored in chloroform : methanol (2 : 1, v/v) were macerated in more of the same solvent system and filtered. The filtrate was shaken with one quarter its volume of 0.88% KCl. After centrifugation, the aqueous layer was discarded and the organic solvent evaporated to yield a lipid extract which was desiccated under vacuum and redissolved in chloroform : methanol (2 : 1, v/v).

The techniques employed for the separation and quantitation of lipid classes have been described elsewhere as have the procedures used for the analysis of fatty acid composition (Olsen & Henderson 1989; Henderson & Mackinlay 1989).

The distribution of fixed carbon in lipid fractions was measured by separating lipid classes by thin layer chromatography and measuring directly the radioactivity contained in bands of adsorbant by standard scintillation techniques.

Results

Characteristics of sampling stations

At the three stations examined, the chlorophyll *a* maximum occurred at a depth of 40 to 50 m and was located within a layer of cold water which occurred at all stations between 20 and 60 m. The highest chlorophyll *a* concentrations were observed at Station 3 (Table 1).

The colonial haptophyte *Phaeocystis pouchetii* and the colonial chrysophyte *Dinobryon pellucidum* always dominated the phytoplankton from the chlorophyll *a* deep maximum. Of the two species, *P. pouchetii* was the most abundant at all three stations but especially at Station 3 where it comprised some 70% of the total phytoplankton present in terms of cell numbers. Very small numbers of the diatoms *Thalassiosira nordenskioeldii* and *Chaetoceros compressus* were also observed in the samples from all three stations.

At Station 1 the irradiance at 40 m when the phytoplankton was sampled was 42 μmol $m^{-1}s^{-1}$, corresponding to 6.5% of the irradiance measured just beneath the surface of the water. The lowest temperature of water sampled occurred at Station 2.

Lipid composition of phytoplankton samples

The amounts of total lipid extracted from the phytoplankton samples were too small to be estimated gravimetrically. General similarities were notable between Stations 1 and 2 in the relative abundance of the lipid classes in lipid of phytoplankton (Table 2). Under the analytical conditions employed, lipid-soluble pigments were the most abundant component of the lipid extracted accounting for 38.9% and 29.4%, respectively, of the total lipid at Stations 1 and 2. Of the total lipid extracted from phytoplankton at Station 3, 17.7% was pigmented material and 19.5% was in the form of triacylglycerols, the major lipid class at this station. Excluding pigments, neutral lipids comprised a larger proportion than polar lipids of the total lipid from the phytoplankton at all three stations. Triacylglycerols were always the predominant lipid class. In addition to triacylglycerols, sterol esters were also a major neutral lipid and comprised approximately 10% of the lipid in phytoplankton from each station.

The proportion of monogalactosyldiacylglycerol in each lipid extract was more than twice that of the other two galactolipids present, digalactosyldiacylglycerol and sulphoquinovosyldiacylglycerol. The proportion of galactolipids was highest in phytoplankton from Station 3 (7.8% of total lipid) but at all stations the level of these lipids was lower than that of phospholipids which accounted for 14.9%, 18.2% and 23.8% of the total lipid in phytoplankton taken from Stations 1, 2, and 3. Phosphatidylcholine was the predominant phospholipid class in each case.

The fatty acid compositions of the total lipid from phytoplankton at all three stations were generally similar (Table 3). 16:0 was the most abundant fatty acid, accounting for 25 to 30% of the total fatty acids. In all samples the proportions of saturated fatty acids decreased in the order 16:0, 18:0, 14:0, 15:0, 17:0. Taken together, these fatty acids comprised around half the total fatty acids present in the lipid from the phytoplankton

Table 1. Characteristics of water sampling stations.

	Station 1	Station 2	Station 3
Location	75°46′N 34°48′E	75°58′N 28°24′E	76°04′N 33°18′E
Depth sampled (m)	40	50	40
Temperature (°C)	0.19	−0.82	−0.36
Chlorophyll *a* (μg l^{-1})	0.48	1.19	1.29
Phaeophytin (μg l^{-1})	0.78	1.49	0.98
Species composition (% Phaeocystis : % Dinobryon)	60 : 40	58 : 42	71 : 29

Table 2. Lipid composition (% total lipid) of phytoplankton from different stations.

Lipid class	Station 1	Station 2	Station 3
Hydrocarbons	6.6	8.2	5.8
Steryl esters	10.4	10.4	9.1
Triacylglycerols	12.8	11.3	19.5
Free fatty acids	6.0	8.6	9.2
Sterols/PAG	5.5	6.8	7.3
Pigment	38.9	29.4	17.7
MGDG	4.2	5.2	5.5
DGDG/SL	0.9	1.6	2.3
PE	4.7	4.6	5.3
PG/CL	2.6	4.2	5.5
PS/PI	2.7	3.3	5.1
PC	4.9	6.1	7.9

Abbreviations: PAG, partial acylglycerols; MGDG, monogalactosyldiacylglycerols; DGDG, digalactosyldiacylglycerols; SL, sulphoquinovosyldiacylglyercol; PE, phosphatidylethanolamine; PG, phosphatidylglycerol; CL, cardiolipin; PS, phosphatidylserine; PI, phosphatidyinositol; PC, phosphatidylcholine.

Table 3. Fauty acid composition (wt %) of total lipid.

Fatty acid	Station 1	Station 2	Station 3
14:0	5.8	6.7	5.5
15:0	3.3	4.0	3.2
16:0	25.4	29.6	30.2
16:1 (n-9/7)	8.4	9.9	7.9
16:2	0.3	0.4	0.3
16:3	—	1.2	0.9
16:4	—	—	0.3
17:0	2.1	2.6	2.0
18:0	7.6	10.3	7.6
18:1 (n-9)	13.2	13.3	13.9
18:1 (n-7)	2.6	2.7	1.9
18:2 (n-6)	3.0	2.1	3.2
18:3 (n-6)	0.4	0.5	0.7
18:3 (n-3)	1.2	1.6	1.7
18:4 (n-3)	3.2	2.0	3.1
18:5 (n-3)/20:0	2.9	3.3	3.5
20:1 (n-9)	0.3	0.5	0.6
20:4 (n-6)	—	0.7	0.6
20:4 (n-3)	0.3	0.2	1.1
20:5 (n-3)	10.4	2.4	3.9
22:1	0.7	0.4	0.8
22:5 (n-3)	—	—	—
22:6 (n-3)	7.4	4.3	6.2
24:1 (n-9)	—	—	0.3
Unknowns	1.4	1.4	0.9
Total sats.	47.0	56.3	52.0
Total monos.	25.1	26.8	25.1
Total PUFA	26.2	15.5	22.0

sats. = saturates; monos. = monounsaturates; PUFA = polyunsaturated fatty acids.

at each station. The levels of the monoenes (18:1(n-9) and 16:1(n-7) were very similar in all three lipid samples, accounting for some 13% and 9% of the fatty acids in each.

The lipid from Station 1 phytoplankton had a higher content of polyunsaturated fatty acids (PUFA) than that from the other two stations, due mainly to the fact that 20:5(n-3) accounted for 1.4% of the fatty acids in this lipid but only 2.4% and 3.9% in those from Stations 2 and 3. The level of 22:6(n-3) was also higher in the sample from Station 1 than from the other two stations. In all samples the level of 18:4(n-3) exceeded that of 18:3(n-3). Overall the (n-3) PUFA predominated over the (n-6) PUFA. 18:2(n-6) comprised less than 4%, and 20:4(n-6) less than 1%, of the total fatty acids in all samples. Lipid of phytoplankton from Station 2 contained the lowest proportion of PUFA, 15.5% of the total fatty acids.

Carbon fixation by phytoplankton

The rate of total carbon fixation was slightly higher at Station 1 than at Station 2 (Fig. 1). Differences were also observed in the incorporation pattern of fixed carbon into different cell fractions in relation to incubation time. At Station 1 polysaccharides were the most radioactively labelled components after 2 hours and contained 33% of the total fixed carbon. In contrast, this fraction contained only 19% of the total carbon fixed in the same time at Station 2. Low molecular weight (LMW) compounds showed the greatest labelling over 2 hours at Station 2. At Station 1 the incorporation rates of carbon into protein and lipid were similar. After 24 hours these fractions together contained two-thirds of the fixed carbon. At Station 2, the incorporation rates into protein and lipid were also linear and similar. The rates of carbon assimilation into LMW material and polysaccharides were less than those into protein and lipid by phytoplankton from both stations, although the differences were less pronounced at Station 2. Protein, lipid, LMW material, and polysaccharides contained 35.2%, 33.5%, 18.1%, and 13.2% of the total carbon assimilated by phytoplankton from Station 1 over 24 hours. The corresponding values for phytoplankton from Station 2 were 30.9%, 27.3%, 26.0%, and 15.8%.

Within the total lipid, phospholipids always contained less fixed carbon than neutral lipids or galactolipids at both stations (Fig. 2) and gen-

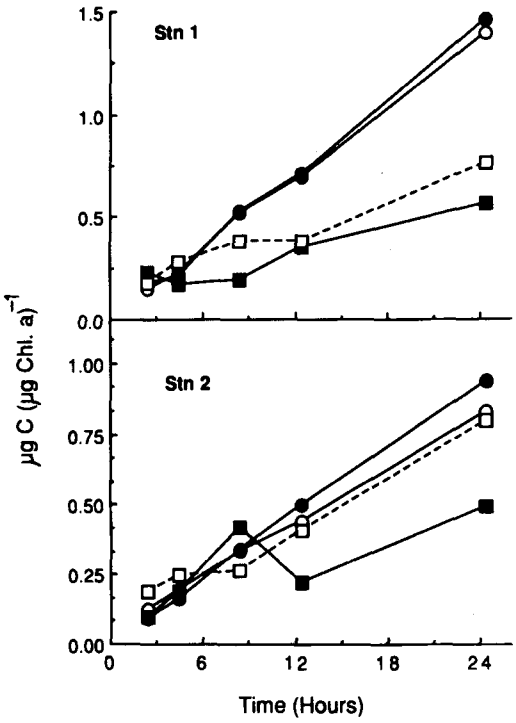

Fig. 1. Assimilation of carbon into end products of photosynthesis by water samples from layer of maximum chlorophyll *a* content. Note difference in scales used for Stations 1 and 2. Values are means of duplicate incubations: ○—○ = lipid; ●—● = protein; ■—■ = polysaccharides; □—□ = L.M.W. compounds.

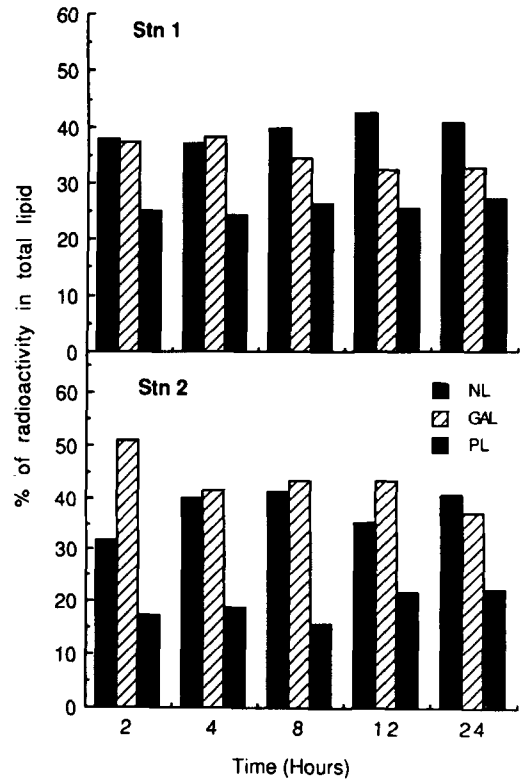

Fig. 2. Distribution of carbon fixed into total lipid within lipid fractions. Values are means of duplicate incubations.

erally accounted for 16 to 26% of the carbon assimilated into lipid. Differences were observed between the two stations in the relative distribution of fixed carbon between the neutral lipid and galactolipid fractions. With phytoplankton from both stations, however, the proportion of fixed carbon in galactolipids was least after 24 hours and neutral lipid contained the most fixed carbon after this time, accounting for 40% of the carbon fixed into lipid.

In general, no great differences were observed in the amount of carbon fixed in relation to light intensity or temperature over 12 h (Table 4). At Station 1, a slight trend was apparent whereby the amount of carbon fixed at 0.5 and 8.5 µmol $m^{-2} s^{-1}$ increased as temperature increased. This pattern was not apparent with phytoplankton from Station 2.

A high degree of variation was observed between replicate incubations in the distribution of assimilated carbon in cellular fractions (Figs. 3 and 4). At the lowest temperature examined (−1.5°C), LMW material contained the highest, and lipid the second highest, proportion of carbon assimilated at 0.5 and 8.5 µmol $m^{-2} s^{-1}$ by phytoplankton from both stations. At the same light and a temperature of 0.5°C, LMW material also

Table 4. Efects of temperature and light intensity on total carbon fixation.

Temp °C	Light intensity µmol $m^{-2} s^{-1}$	Station 1	Station 2
		µgC(µgChla)$^{-1}$ h^{-1}	
−1.5	0.5	0.16 ± 0.03	0.52 ± 0.02
	8.5	0.23 ± 0.04	0.64 ± 0.13
−0.5	0.5	N.D.	0.40 ± 0.17
	8.5	N.D.	0.66 ± 0.17
	95.2	N.D.	0.60 ± 0.09
0.5	0.5	0.27 ± 0.01	N.D.
	8.5	0.34 ± 0.13	N.D.
	95.2	2.57 ± 1.63	N.D.
4.5	8.5	0.48 ± 0.14	0.68 ± 0.01

N.D. = not determined. Values are means ± S.D. of three incubations.

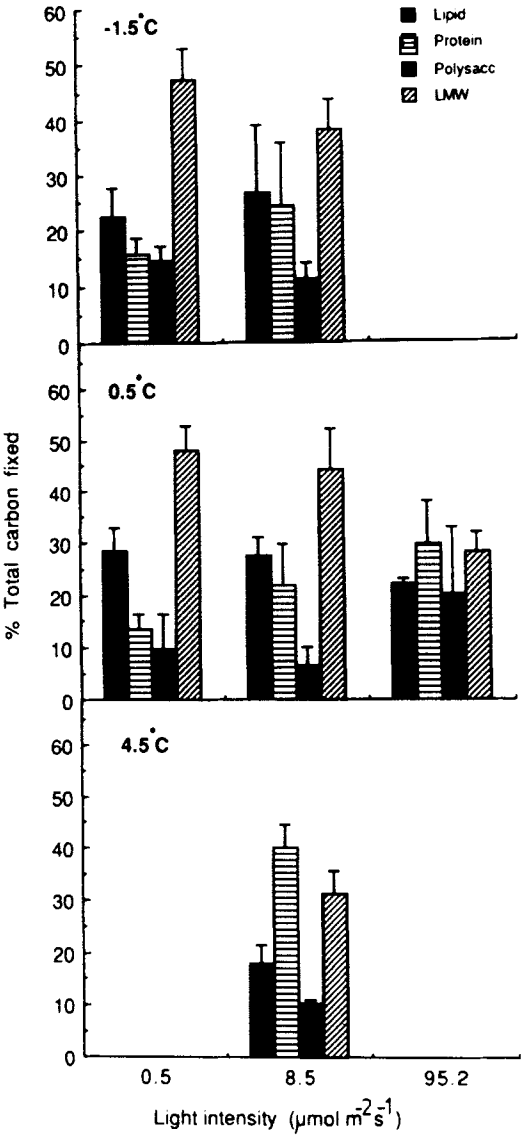

Fig. 3. Effects of light and temperature on the distribution of carbon assimilated by waters sampled at Station 1 into end products of photosynthesis. Values are means of 3 incubations. Vertical bars represent S.D.

contained most of the carbon fixed by phytoplankton from Station 1 and the distribution pattern was generally similar to that observed at −1.5°C. In contrast, the distribution pattern observed with phytoplankton from Station 2 at −0.5°C and 0.5 and 8.5 μmol $m^{-2}s^{-1}$ was not comparable with that seen with the same phytoplankton at −1.5°C.

In incubations with water from Stations 1 and 2 at 0.5 and −0.5°C, respectively, the distribution patterns observed at 95 μmol $m^{-2}s^{-1}$ were notably different from those of the same temperature but lower irradiance in that the LMW compounds contained less fixed carbon. Protein also contained more fixed carbon than polysaccharides at the higher light intensity. Although the percentage fixed into lipid decreased with increasing light intensity at 0.5°C at Station 1, the change

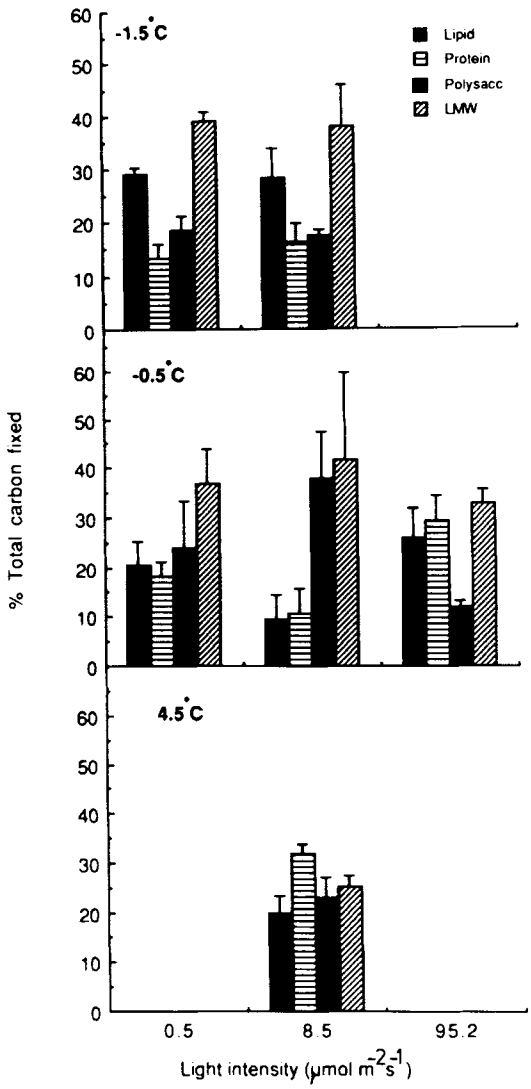

Fig. 4. Effects of light and temperature on the distribution of carbon assimilated by waters sampled at Station 2 into end products of photosynthesis. Values are means of 3 incubations and vertical bars represent S.D.

was not statistically significant and no such trend was observed in relation to light intensity at Station 2 at −0.5°C.

When the distribution patterns of fixed carbon at 8.5 μmol $m^{-2}s^{-1}$ were compared over three different temperatures, the most notable effect was that the proportion recovered in protein was highest at 4.5°C at both stations. Correspondingly, LMW material contained least assimilated carbon at this temperature. In contrast to the situation at 4.5°C, lipid accounted for a higher proportion of assimilated carbon than protein at −1.5°C.

Discussion

Phaeocystis pouchetii and *Dinobryon pellucidum*, particularly the former, are regular members of the phytoplankton community in the Atlantic and Arctic waters of the Barents Sea during spring and summer (Eilertsen 1989; Eilertsen et al. 1989a, b, c). Although the lipid composition of *P. pouchetii* has been examined in phytoplankton sampled from non-Arctic waters (Claustre et al. 1990; Sargent et al. 1985), it has not been examined in this species taken from the Barents Sea, and as far as we are aware no data are available on the lipids of *D. pellucidum*.

The lipid compositions reported here are those of the lipid extracted from the total assemblage of phytoplankton in the waters sampled. Although *P. pouchetii* dominated at all three stations in terms of cell numbers, it cannot be assumed that the overall lipid composition mainly reflects the lipid of this species since it is not known whether the two principal species have similar lipid contents. Neutral lipid classes predominated in the lipid of the phytoplankton examined. Such lipid classes have also been shown to be more abundant than phospholipids in the lipid of sea ice diatoms in the Antarctic (Nichols et al. 1986). It is known that the proportion of triacylglycerols, the major neutral lipid found here, increases in batch cultured algae during nutrient depletion and consequently the amount of saturated fatty acids present also increases (Piorreck et al. 1984; Mortensen et al. 1988). The lipid composition of natural populations is also likely to change with the growth stage. Consequently the pattern of dietary fatty acids available to herbivorous predators is not constant. Since *D. pellucidum* is capable of phagotrophy as well as photosynthesis (Bird & Kalff 1987), the overall lipid composition of this species may be less influenced by lipids associated with chloroplasts as that of purely photosynthetic species.

In comparison with phytoplankton material including *Phaeocystis* sp. sampled from temperate regions (Claustre et al. 1990; Kattner et al. 1983), the lipids from the Barents Sea phytoplankton which were analysed in this study contained higher levels of polyunsaturated fatty acids. This is particularly noticeable when it is considered that most of the lipid actually consisted of triacylglycerols, a situation which usually confers a low degree of unsaturation upon the total lipid (Piorreck et al. 1984). Although most fatty acids found in the total lipid in the present study also occurred in previous analyses of a surface slick of *P. pouchetii* from Arctic/boreal waters (Sargent et al. 1985) and in *Phaeocystis* sp. in the Irish Sea (Claustre et al. 1990), the overall fatty acid profile was not very similar to either. In particular only 4% of the total fatty acids in the *Phaeocystis* sp. from the Irish Sea were polyunsaturated (Claustre et al. 1990) in comparison with over 50% in that from northern Norwegian waters (Sargent et al. 1985) and around 20% in the phytoplankton analysed here. Apart from the fact that the fatty acids of *D. pellucidum* also contributed to the overall fatty acid composition in this study, differences in the stage of growth as well as environmental parameters are likely to influence the fatty acid composition of *Phaeocystis* species. Thus, no definite conclusions can be drawn from the present data about the fatty acid composition of phytoplankton adapted to the low temperatures of Arctic waters in comparison with the same species from more temperate waters. The detailed fatty acid composition of the lipid classes of phytoplankton from Arctic waters has not been examined, mainly due as in the present study to the collection of insufficient material. Further analyses of the lipid composition of Arctic phytoplankton may reveal specific adaptations to their habitat and also yield information on seasonal changes in their value as food for zooplankton.

The lowering of temperature in photosynthetic algae generally leads to an increase in the proportion of polyunsaturated fatty acids in the lipid (Ackman et al. 1968; Henderson & Mackinlay, 1989). However, it is to be noted that polyunsaturated fatty acids are not major components of any class of lipids on sea ice diatoms (Nichols et al. 1986). An increased content of polyun-

saturated fatty acids in comparison with phytoplankton from temperate waters may not be a general adaptation to low environmental temperature in polar phytoplankton.

The proportion of total fixed carbon incorporated into lipid never exceeded 30% under any of the conditions employed in this study. This is in agreement with the corresponding value reported for phytoplankton sampled from many locations, including the Arctic waters of eastern Canada (Li & Platt 1982), northern Norwegian fjords (Sargent et al. 1985), tropical waters (Morris et al. 1981), eutrophic Scandinavian lakes (Jensen 1985) and temperate waters (Harding et al. 1985).

The incorporation of 80% of fixed carbon into lipid by phytoplankton from the Antarctic Ocean (Smith & Morris 1980a, b) has been attributed to low temperature coupled with low irradiance. The present results imply that other factors must also be necessary for enhanced carbon assimilation into lipid by Arctic phytoplankton. It is well known that the Antarctic and Arctic waters differ in many respects, including post bloom nutrient levels (Sakshaug & Holm-Hansen 1984).

Previous studies on distribution of fixed carbon in photosynthesis end products have only considered total lipid. This study shows that within the lipids of the phytoplankton from the Barents Sea most of the assimilated carbon is located in neutral and galactolipids. The lipid contained insufficient radioactivity to permit the detailed analysis of the distribution of fixed carbon in specific lipid classes and component fatty acids. Galactolipids contained a higher proportion of the carbon than expected on the basis of mass. It can be expected that, as well as the fatty acid moieties, the glyceryl and galactosyl moieties of acylglycerols and galactolipids, respectively, contained fixed carbon. The distribution pattern of assimilated carbon between the moieties, and the effect of variations in temperature and irradiance on it, could not be determined in the present study due to the lack of sufficient incorporated radioactivity. Although no great differences were notable in the proportion fixed into lipid in response to different incubation temperatures and irradiances, unseen changes may have occurred in the distribution of carbon between the lipid classes and between the component portions of the actual lipid classes. Changes may also have occurred in the pattern of fatty acids synthesised. For example, the specific incorporation of radioactivity into PUFA increases as growth temperature decreases in at least one species of marine algae in batch culture (Henderson & Sargent 1989).

In the present study the phytoplankton were subjected to sudden changes in temperature and irradiance. Since adaptive mechanisms are dynamic processes (Mortain-Bertrand et al. 1988), longer incubation times than those employed here might be required before significant changes are observed in the assimilation of carbon into specific end products. Further studies are necessary to examine in detail lipid synthesis in Arctic phytoplankton in relation to the natural environmental parameters.

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