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Carbon assimilation and lipid production in phytoplankton in northern Norwegian fjords

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Abstract

Carbon assimilation and lipid production were studied in phytoplankton in Balsfjorden and Ullsfjorden, northern Norway, during the exponential growth phase of the spring bloom in 1983 (6–7 April). In Balsfjorden, phytoplankton biomass was constant with depth and equivalent to 1.5 μg chlorophyll a l^{-1}. Phytoplankton biomass in Ullsfjorden varied with depth, with a maximum of ca. 7 μg chlorophyll a l^{-1} occurring at 5 to 10 m. Particulate carbon-14 assimilation was about 18 mg C per m^{-2} h^{-1} in Balsfjorden and about 39 mg C per m^{-2} h^{-1} in Ullsfjorden over the depth range 4 to 8 m. In Balsfjorden, the percentage of total fixed carbon recovered as total lipid was 14.7 and 20.4% at 4 and 8 m depth, respectively. In Ullsfjorden, the corresponding values were 8.8 and 28.1% at 4 and 8 m, respectively. The percentages of total fixed carbon present as fatty acids were 1.1 and 1.6% at 4 and 8 m, respectively, in Balsfjorden, and 0.8 and 6.4% at 4 and 8 m in Ullsfjorden. The majority of the radioactivity in lipid at both locations and at both depths was present as polar lipid, with small percentages present in triacylglycerols and very small percentages present in free fatty acids. On average, about 18% of the total carbon-14 incorporated into phytoplankton over a 6 to 7 h mid-day period was recovered as total lipid and its percentage tended to increase with depth. The relatively low percentage of incorporated carbon-14 present as fatty acids in total lipid implies that most of the radioactivity is present in glyceryl and/or glucosyl moieties and that measurement of total radioactivity in total lipid does not necessarily give an accurate estimation of lipogenesis in phytoplankton. Fatty acid analyses of total phytoplankton in Balsfjorden and Ullsfjorden in 1983 and of a surface slick at the end of a bloom of *Phaeocystis pouchetii* in Balsfjorden in May 1980 showed an abundance (more than 40% of the total) of (*n*-3) polyunsaturates in all cases. C-18 polyunsaturates, especially 18:4 and 18:5, were very abundant (about 30% of the total) in the *P. pouchetii* surface slick in Balsfjorden in 1980. Both *P. pouchetii* biomass and C-18 polyunsaturates were more abundant in Ullsfjorden than in Balsfjorden (1983). Lipids from the *P. pouchetii* surface slick were deficient in C-16 polyunsaturates and relatively deficient in C-20 polyunsaturates, but both these classes of fatty acids were abundant in Balsfjorden and Ullsfjorden in 1983. The phytoplankton in both locations in 1983 was dominated by *P. pouchetii* and diatoms; *Chaetoceros socialis* was especially abundant in Balsfjorden. The results are discussed in terms of the fatty acids present in herbivorous zooplankton in northern Norwegian fjords.

Introduction

Balsfjorden (Fig. 1) is a single-basin, cold-water fjord with a maximum depth of ca. 195 m, a temperature range from ca. 1° to 7 °C, and a salinity range from 32.80 to 34.00‰ during most of the year. Details of topography, physical environment and hydrography have been given by Eilertsen *et al.* (1981a). Ullsfjorden (Fig. 1) has a rather wide and open outer section, with a maximum depth of about 280 m at the entrance. From this depth, the bottom rises to a threshold about 170 m deep at its connection with the offshore coastal waters. The temperature range is from ca. 2° to 10 °C, and the salinity range from ca. 32.50 to 34.50‰ for most of the year in the main basin (Sælen, 1950; Heimdal, 1974).

The spring bloom in Balsfjorden and Ullsfjorden usually starts at the end of March and culminates at the end of April/beginning of May. At the culmination, nitrate and phosphate were measured as ca. 0.5 μg-at l^{-1}, and silicate decreased to minimum values of ca. 1.5 μg-at l^{-1} before rapidly increasing again (Eilertsen and Taasen, in press). In areas further south, growth is known to proceed at much lower nutrient values. The spring bloom in Balsfjorden and Ullsfjorden probably culminates as an effect of lowered light intensities combined with a rela-

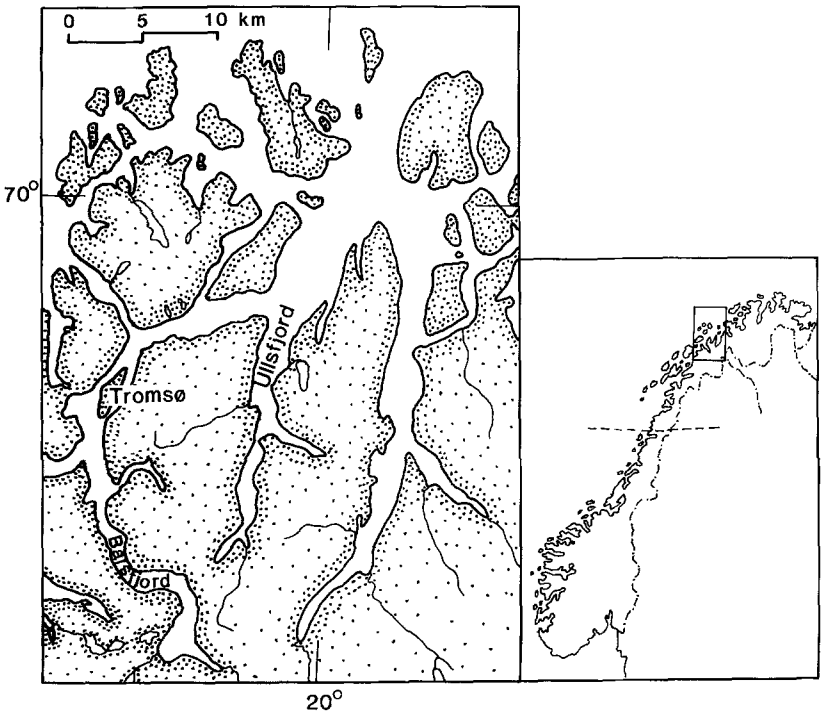

Fig. 1. Map of Balsfjorden and Ullsfjorden, northern Norway

Table 1. Species succession during spring bloom in Balsfjorden and Ullsfjorden, northern Norway (after Eilertsen *et al.*, 1981 b)

Balsfjorden	Ullsfjorden
Phaeocystis pouchetii	*Phaeocystis pouchetii*
Chaetoceros socialis	*Chaetoceros socialis*
Nitzschia grunowii	*Nitzschia grunowii*
Chaetoceros furcellatus	*Chaetoceros compressus*
Chaetoceros compressus	*Skeletonema costatum*

tively mixed water column, and probably also because of grazing pressure. The bulk of phytoplankton present during spring are colony-forming diatoms such as *Chaetoceros socialis* Laud and *Nitzschia grunowii* Hasle together with *Phaeocystis pouchetii* (see Table 1 and Gaarder, 1938; Heimdal, 1974; Eilertsen *et al.*, 1981 b; Bech, 1982).

Marine animals from high latitudes are generally very rich in lipid content (see Sargent et al., 1976; Sargent and Whittle, 1981). However, the extent to which marine animal lipid originates from phytoplankton is not known, partly due to a lack of knowledge of the production rate of phytoplanktonic lipid and its detailed composition. Recent work suggests that rates of lipid production can vary widely in phytoplankton in high latitudes. Smith and Morris (1980) reported that Antarctic phytoplankton at low light intensities and temperatures of −0.2° to −1.8 °C incorporated up to 80% of their total fixed carbon into total lipid. In contrast, phytoplankton from eastern Canadian Arctic waters incorporated only about 18% of their total fixed carbon into total lipid (Li and Platt, 1982). The differences in lipid production between these two findings probably reflects different environmental conditions rather than species differences (Colloyer and Fogg, 1955).

The present study was undertaken to determine rates of lipogenesis in the phytoplankton in Balsfjorden and Ullsfjorden during the spring bloom and to determine the fatty acid composition of the phytoplanktonic lipids. Balsfjorden has been the subject of numerous ecological studies, and the lipids of its major herbivores have already been investigated (Sargent and Falk-Petersen, 1981; Falk-Petersen *et al.*, 1981; Hopkins *et al.*, in press; Falk-Petersen and Sargent, unpublished data).

Materials and methods

Sampling

Sampling was carried out at Svartnes in Balsfjorden on 6 April 1983 and at Oldervik in Ullsfjorden on 7 April 1983. Sea-water samples were collected from fixed depths of 0, 1, 2, 4, 8, 16, 32 and 50 m for measurement of radioactive-carbon assimilation *in situ*. *In situ* fluorescence profiles of chlorophyll *a* were also taken down to 32 m, using a Turner Fluorometer. Sea water was sampled with a non-toxic, non-transparent Niskin water sampler.

Light measurements

Incident radiation and sub-surface light extinction were measured *in situ* during the experiments in $\mu E\ m^{-2}\ s^{-1}$ in the 400 to 700 nm waveband (1 μE being equivalent to 6.02×10^{17} Quanta). Sub-surface light extinction was measured with a Lambda Instruments LI-185 Quantumeter and Underwater Quantum Sensor LI-192S. Fluctuations in irradiance were continually monitored with a LI-190S surface Quantum Sensor for correction of sub-surface values.

In situ carbon-assimilation experiments

The method for measuring ^{14}C uptake followed procedures outlined by Strickland and Parsons (1972). Bottles containing 100 ml of sea water were each inoculated with 0.5 ml containing 5 μCi of sodium ^{14}C-bicarbonate (0.1 mCi mmol^{-1}), and exposed to natural light for 6 to 7 h. After incubation, the phytoplankton was collected by filtration onto Millipore HA 47 mm filters at a maximum pressure of 0.3 kg cm^{-1}, and washed briefly with non-radioactive sea water. The filters were transferred to scintillation vials, which were stored at −15 °C until return to the laboratory. Duplicate filters from 4 and 8 m depths were transferred to scintillation vials which were then filled with chloroform-methanol (2:1 by vol) containing 0.05% butylated hydroxytoluene as antioxidant. These were sealed under nitrogen and stored at −15 °C.

For measurement of the incorporation of carbon-14 into total material, vials containing filters were exposed to fumes of HCl for 10 min in a desiccator. Slight vacuum was then applied to the desiccator for 5 min using a pump. Ten ml of "Instagel" were added to each vial, and radioactivity was determined in a Packard Tricarb Model 3385 scintillation spectrometer. The counting efficiency under these conditions was 75%.

For measurement of incorporation of carbon-14 into total lipid, the contents of the vials containing chloroform-methanol were filtered through Whatman phase-separating (PS) papers and the filtrate extracted with 0.25 vol of water. After phase separation the organic phase was taken to dryness under a stream of nitrogen at room temperature. The dried material was redissolved in chloroform-methanol (2:1 by vol), re-extracted with 0.25 vol of water, and the organic phase dried under nitrogen. The resulting material represents total lipid extracted from total phytoplankton by the method of Folch *et al.* (1957). Total lipid was dissolved in chloroform-methanol (2:1 by vol) for the following analyses:

(1) Determination of total radioactivity. Aliquots were transferred to scintillation vials, dried under a stream of nitrogen, and assayed for radioactivity as above after adding 10 ml of Instagel.

(2) Determination of radioactivity in lipid classes. Aliquots were subjected to thin-layer chromatography on layers of silicic acid (250 μm) using hexane-diethyl ether-acetic acid (90:10:1 by vol) as solvent. Radioactive zones were detected by exposing the dried plates to X-ray film for 7 d. The resulting radioautographs were used to locate the positions on the original plates of radioactive zones which were scraped off and radioassayed after addition of Instagel.

(3) Determination of radioactivity in fatty acids. Aliquots were submitted to acid-catalysed transmethylation in methanol-sulphuric acid (Christie, 1973) for 16 h at 50 °C. Reaction media were diluted with water, and fatty acid methyl esters were extracted into hexane-diethyl ether (1:1 by vol). The organic phases were washed thoroughly with water before being dried under nitrogen and assayed for radioactivity as above.

Fatty acid analyses of total phytoplankton lipid

Bulk samples of phytoplankton were collected from the stations in Balsfjorden and Ullsfjorden in 1983 by filtering approx 25 litres of sea water from 4 to 8 m depth through Millipore glass-fibre discs. The latter were rapidly transferred to scintillation vials, which were then filled with chloroform-methanol (2:1) containing 0.05% butylated hydroxytoluene as antioxidant and stored at −15 °C under nitrogen. Total material had similarly been collected from a surface slick consisting of nearly pure gelatinous colonies of *Phaeocystis pouchetii* towards the end of a bloom of this species in Balsfjorden in May 1980. In the laboratory, total lipid was isolated from these samples using the procedure of Folch *et al.* (1957) as above. The resulting total lipid was subjected to acid-catalysed transmethylation, and the fatty acid methyl esters formed were extracted as previously and finally purified by thin-layer chromatography on silicic acid using hexane-diethyl ether (70:30:1 by vol) as solvent. Fatty-acid methyl-ester zones were eluted from the plates with hexane-ether (1:1 by vol) and analysed by gas-liquid chromatography using a 50 m × 0.32 mm column of CP Wax 51 and a Packard Model 429 gas liquid chromatogram. Full details of the methods have already been given by Sargent *et al.* (1983).

Results

The hydrographic conditions at both stations in the present study were characterised by low temperature combined with relatively high salinities, S (Balsfjorden: T = 2.3° to 2.80 °C, S = 33.10 to 33.30‰; Ullsfjorden: T = 3.6° to 5.2 °C, S = 33.80 to 34.40‰, respectively), resulting in high mixing coefficients approaching infinity. Sampling in both Balsfjorden and Ullsfjorden was performed in early April, when the light regime gradually changes towards the midnight-sun period. The length of daylight was approximately 14 h. In Balsfjorden, the depth of 1% of the surface incident radiation was measured at 29 m, and in Ullsfjorden at 21 m, reflecting higher phytoplankton densities in Ullsfjorden than in Balsfjorden. The experimental bottles at 0 and 1 m probably underwent light-saturated photosynthesis, receiving 40 to 80 μE m^{-2} s^{-1} (Eilertsen and Taasen, 1981).

In situ fluorescence profiles in Ullsfjorden indicated higher phytoplankton densities than in Balsfjorden. The highest fluorescence values in Balsfjorden and Ullsfjorden corresponded to approximately 1.5 and 7.0 μg chlorophyll *a* l^{-1}, respectively (Fig. 2). In Balsfjorden and Ullsfjorden, phytoplankton standing stock was dominated by *Phaeocystis pouchetii* followed by *Chaetoceros socialis* and

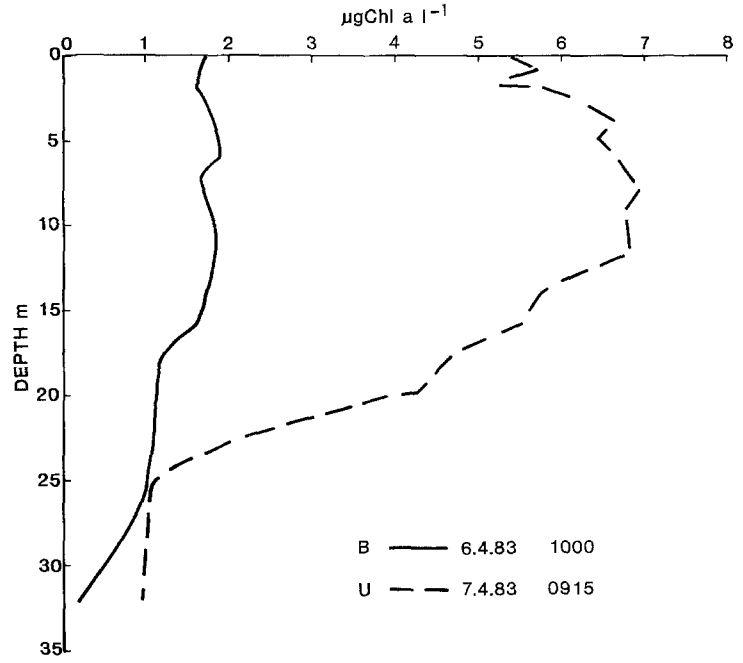

Fig. 2. Variation of relative fluorescence intensity (μg chlorophyll a l^{-1}) with depth in Balsfjorden (B), 6 April 1983, and Ullsfjorden (U), 7 April 1983, at 10.00 and 09.15 hrs, respectively

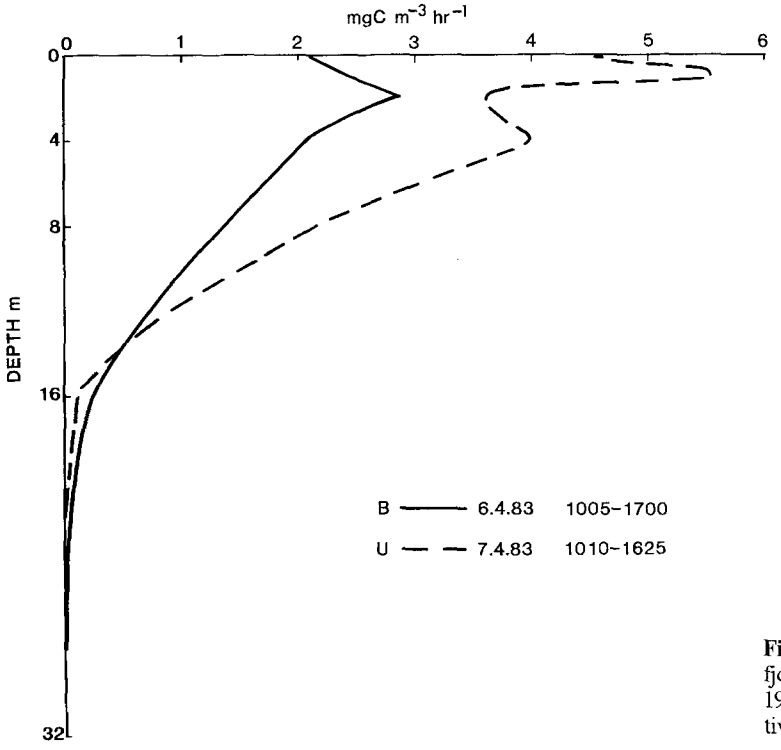

Fig. 3. Variation of carbon assimilation with depth in Balsfjorden (B), 6 April 1983, and Ullsfjorden (U), 7 April 1983, from 10.05–17.00 hrs and 10.10–16.25 hrs, respectively)

Nitzschia grunowii (Table 1). In Ullsfjorden, the phytoplankton standing stock contained a larger proportion of *P. pouchetii* than in Balsfjorden.

Carbon assimilation variations with depth in Balsfjorden are shown in Fig. 3. Relatively low values were recorded, with a maximum at 2 m corresponding to approximately 2.8 mg C m^{-2} h^{-1}. Production rates were higher in Ullsfjorden, corresponding to the higher standing stock at that location, with a maximum equivalent to about 5.6 mg C m^{-2} h^{-1} at 1 m (Fig. 3). Production rates declined after the maximum in both locations to near negligible values at 16 m depth.

The percentage of the total carbon assimilated that was present as total lipid at 4 and 8 m at each location is shown in Table 2. At 4 m in Balsforden, a greater fraction of total production was present as lipid than at the same depth in Ullsfjorden. A higher percentage of total production was also present as lipid at 8 m than at 4 m at both stations.

Table 2 shows additionally that, with the exception of Ullsfjorden at 8 m, very little of the total radioactivity present in total lipid was recovered as fatty acid methyl esters after transmethylating total lipid. This implies that the bulk of radioactivity in total lipid was present in the

Table 2. Carbon assimilation in phytoplankton from Balsfjorden and Ullsfjorden, presented as total carbon production, carbon production in total lipid, and carbon production in fatty acids

	Balsfjorden, April 6, 10.05–17.00 hrs		Ullsfjorden, April 7, 10.10–16.25 hrs	
	4 m	8 m	4 m	8 m
Total C (mg C m^{-3})	1.95	1.50	3.95	2.10
Total lipid (mg C m^{-3})	0.29	0.31	0.35	0.59
Fatty acids (mg C m^{-3})	0.02	0.02	0.03	0.13
% of total C as lipid	14.7	20.4	8.8	28.1
% of lipid as fatty acids	7.7	7.7	8.6	22.7
% of total C as fatty acids	1.1	1.6	0.8	6.4

Table 3. Percentage distribution of radioactivity in phytoplanktonic lipid classes

Sampling area	Polar lipid	Triacylglycerols	Free fatty acids
Balsfjorden, April 6 (10.05–17.00 hrs)			
4 m	63.1	27.4	9.5
8 m	77.0	15.8	7.2
Ullsfjorden, April 7 (10.10–16.25 hrs)			
4 m	77.8	17.1	5.2
8 m	85.6	9.1	5.3

water-soluble components of the lipid generated by transmethylation, i.e., in the glyceryl and glycosyl moieties of the mainly polar glycolipid extracted from the phytoplankton. The highest percentage recovery of radioactivity in fatty acid methyl esters occurred in Ullsfjorden at 8 m, where the total productivity present as lipid was greatest. The data in Table 2 are also presented as the percentage of total carbon-14 assimilated present as fatty acids. Apart from Ullsfjorden at 8 m, there was relatively little production of fatty acids, a situation in contrast to the apparent production of total lipid.

Table 3 establishes that the radioactivity present in total lipid at both depths at each location was located mainly in the polar lipid fraction, with small amounts being present in triacylglycerols and very small amounts in free fatty acids. Treating thin-layer plates similar to those used to generate the data in Table 3 with a charring reagent to detect lipid mass revealed that all the lipid samples were composed almost entirely of polar lipid with traces of triacylglycerols; free fatty acids were not significant components. There was a tendency, revealed by Table 3, for a greater percentage of radioactivity in total lipid to be located in polar lipid with increasing depth, the converse being true for triacylglycerols. We inferred earlier that the bulk of the radioactivity in the total lipid is present in glyceryl or glycosyl moieties of the predominantly polar glycolipid. This is supported by the presence of most of the radioactivity in the polar lipid (Table 3).

Fatty acid analyses of the total lipid recovered from phytoplankton taken in Balsfjorden and Ullsfjorden in 1983 are presented in Table 4. Similar data for material taken from Balsfjorden in 1980 from a surface slick of *Phaeocystis pouchetii* are also presented. Since the total lipid in all these samples was dominated (> 90%) by polar lipid, the results may be taken to approximate fatty acid analyses of polar lipid, presumably derived mainly from the chloroplasts of the organisms. Fatty acids from lipid extracted from the *P. pouchettii* in 1980 were characterised by high percentages of (*n*-3) polyunsaturates, especially 18:4, 18:5, 20:5 and 22:6. The abundance of the former two fatty acids is particularly notable. The phytoplankton in Ullsfjorden in 1983 contained much *P. pouchettii*, but diatoms were also abundant. Total lipid in this case was also rich in (*n*-3) polyunsaturates. Substantial amounts of 18:4 and 18:5 were present, and C-16 polyunsaturates were prominent, especially 16:4, as was 20:5. Balsfjorden in 1983 contained less *P. pouchettii* than Ullsfjorden in 1983, but more diatoms, especially *Chaetoceros socialis*, were present. Balsfjorden in 1983 contained less 18:4 and 18:5 but more C-16 polyunsaturates, especially 16:4, as well as 20:5 than Ullsfjorden. The long-chain polyun-

Table 4. Percentage fatty acid composition of total lipid recovered from phytoplankton taken in Balsfjorden and Ullsfjorden in 1983. Similar data for surface slick of *Phaeocystis pouchettii* in Balsfjorden, 1980 are also shown. PUFA: polyunsaturated fatty acids

Fatty acid	Balsfjorden (1983)	Ullsfjorden (1983)	Balsfjorden (1980)
14:0	6.9	13.4	10.2
16:0	14.9	16.1	20.0
16:1 (*n*–7)	12.3	13.2	10.7
16:1 (*n*–5)	1.6	1.6	–
16:2 (*n*–3)	1.4	1.9	–
16:3 (*n*–3)	3.1	1.9	–
16:4 (*n*–3)	9.7	6.8	–
18:0	2.0	2.1	1.1
18:1 (*n*–9)	8.4	6.3	1.2
18:1 (*n*–7)	3.7	0.7	–
18:2 (*n*–6)	1.2	2.6	0.8
18:3 (*n*–3)	0.5	1.3	1.0
18:4 (*n*–3)	5.1	6.7	21.4
18:5 (*n*–3)	0.6	5.2	7.2
20:1 (*n*–9)	1.2	0.7	–
20:5 (*n*–3)	16.0	12.6	6.5
22:5 (*n*–3)	0.5	–	4.1
22:6 (*n*–3)	7.5	3.8	13.2
Total saturated	24.2	32.1	31.3
Total monounsaturated	25.6	21.21	11.9
Total (*n*–6) PUFA	1.2	2.8	0.8
Total (*n*–3) PUFA	45.3	40.9	53.4

saturate 22:6 (*n*-3) was more abundant in the total lipid of Balsfjorden in 1983 than of Ullsfjorden in 1983, but less abundant than in the total lipid of the *P. pouchettii* bloom of 1980.

Discussion

The results of this study show that the conditions recorded in Ullsfjorden and Balsfjorden were typical of an early-stage spring bloom in northern Norway. The spring bloom in Ullsfjorden had reached a later stage than in Balsfjorden. Differences in timing of the blooms probably reflects different hydrographic conditions combined with different starting populations. Incident radiation during spring at the two locations was similar, and growth was not nutrient-limited (Eilertsen and Taasen, in press).

As expected, maximum carbon assimilation rates were measured near the surface (1 to 2 m depth). The mixing coefficients were high at both stations, and the species compositions were probably similar at all the sampled depths. The spring bloom in northern Norway normally takes place in a mixed water-column (Eilertsen and Taasen, 1981). Carbon assimilation rates were 18 mg C m^{-2} h^{-1} in Balsfjorden and 39 mg C m^{-2} h^{-1} in Ullsfjorden.

Percentages of total production present as lipid were determined in this study at depths where standing stock rather than production rate was maximal. It has been reported that Antarctic phytoplankton incorporate up to 80% of their total fixed carbon into total lipid at low temperatures (less than 0 °C) and relatively low light intensities (Smith and Morris, 1980). In contrast, phytoplankton from the eastern Canadian Arctic incorporated on average 18% of their total fixed carbon into total lipid (Li and Platt, 1982). Total lipid did not exceed 30% of the total fixed carbon within the temperature range −1 ° to 6.0 °C and the light range 1 to 700 W m^{-2} (Li and Platt, 1982). The results of the present study, though variable, are similar to the results of Li and Platt in that, on average, 18% of the total fixed carbon was recovered as total lipid (Table 2). At 4 m in Balsfjorden, a higher percentage of total assimilation was present as total lipid than at the same depth in Ullsfjorden. Integrated *in situ* sub-surface light measurements showed that the phytoplankton in Balsfjorden received less light than in Ullsfjorden at the same depths (Table 5). Moreover, a higher part of the total production was present as lipid at 8 m than at 4 m at both stations (Table 2). It seems, therefore, that there is a general trend for the amount of lipid formed to be inversely related to light intensity. It should also be noted that the water was colder in Balsfjorden than in Ullsfjorden.

Table 5. Incident radiation (E m^{-2} h^{-1}) during incubation experiments in Balsfjorden and Ullsfjorden

Area	Depth	
	4 m	8 m
Balsfjorden	80	50
Ullsfjorden	95	65

An important aspect of the present study is that the foregoing, conventional interpretation of the data in terms of rates of lipid formation by phytoplankton is oversimplistic. Thus, of the radioactivity incorporated into total lipid over the 6 to 7 h study period, only a small percentage was recovered in fatty acids. A similar situation occurs during the first hour at least of fixation of $^{14}CO_2$ into the lipids of green leaves of terrestrial plants (Heinz and Harwood, 1977), and probably reflects metabolic turnover of the glycosyl moieties of chloroplast polar lipid in the absence of a net synthesis of new lipid. Chloroplast formation does not occur uniformly in phytoplankton over the diurnal period (Stross, 1975) and most phytoplankton in northern Norwegian fjords probably divides during the early morning when there is little light present. There is also diurnal variation in the photosynthetic capacity of phytoplankton (Sournia, 1974). Clearly, chloroplast lipid and membrane formation also shows diurnal variation, and a study of the time course of incorporation of $^{14}CO_2$ into chloroplast lipids in phytoplankton is a major priority of future work. The studies of Smith and Morris (1980) and Li and Platt (1982) referred to earlier involved a 24 h period of incorporation of $^{14}CO_2$ into total lipid, by which time it is presumed that labelling of the fatty acid moieties of phytoplankton lipid is extensive if not maximal. Nonetheless, the present study is salutary in that application of a routine method that is widely applied to measure "productivity" in phytoplankton essentially failed to detect significant production of fatty acids that are major chemical components of phytoplankton. The consequences of failing to allow for metabolic turnover in isotope experiments designed to measure net biosynthesis are self-evident.

The lipids of all the phytoplankton analysed in the present study were rich in (*n*-3) polyunsaturated fatty acids, which are concentrated in the lipids of chloroplast membranes (Erwin, 1973). This is consistent with the total lipid here being predominantly polar, membrane lipid with little triacylglycerols or free fatty acids. Laboratory-grown diatoms are rich in C-16 and C-20 polyunsaturates (Ackman *et al.*, 1968; Wood, 1974). Both C-16 and C-20 polyunsaturates were relatively abundant in phytoplanktonic lipid in Balsfjorden and Ullsfjorden in 1983, when diatoms were abundant in the phytoplankton. The surface slick of *Phaeocystis pouchettii* from Balsfjorden in 1980 was deficient in C-16 polyunsaturates, relatively deficient in C-20 polyunsaturates, but rich in C-18 polyunsaturates, especially 18:4. Ullsfjorden phytoplankton contained a higher proportion of *P. pouchettii* and a higher proportion of C-18 polyunsaturates in its total lipid than Balsfjorden 1983 phytoplankton. Thus, the general conclusion derived from laboratory-grown cultures (Ackman *et al.*, 1968; Wood, 1974), that algal lipid is predominantly rich in (*n*-3) polyunsaturates, applies to all the phytoplankton samples

examined in the present study and the laboratory results obtained with diatoms can help account for the observed differences in the phytoplankton samples.

The foregoing results differ from recent findings of Morris (1984) that a diatom-dominated population developing in a sea-water enclosure had total lipid relatively deficient in polyunsaturated fatty acids. Likewise, Kattner *et al.* (1983) have recently observed that the fatty acids of diatom-dominated phytoplankton during a North Sea bloom are relatively deficient in (*n*-3) polyunsaturates. It is well known that the amount of neutral lipid rises markedly in algal cultures as a consequence of ageing or nitrogen limitation (Lewin, 1962), and this condition could well generate fatty acids relatively deficient in (*n*-3) polyunsaturates. The phytoplankton analysed by Morris (1984), and probably also by Kattner *et al.* (1983), certainly experienced nutrient limitation towards the end of the bloom (Morris *et al.*, 1983). However, the phytoplankton analysed by both these authors was relatively deficient in (*n*-3) polyunsaturates both early in the bloom, when nutrient limitation is unlikely to occur, and later in the bloom. As discussed earlier, the available evidence suggests that phytoplankton blooms in the locations studied here are not nutrient-limited.

The fatty acid analyses reported here for phytoplanktonic lipid can reasonably account for the abundance of (*n*-3) polyunsaturated fatty acids, especially 18:4 (*n*-3) and 20:5 (*n*-3) in the neutral lipids (wax esters and triacylglycerols) of major zooplanktonic herbivores such as *Calanus finmarchicus, Thysanoessa inermis* and *T. raschi* in northern Norwegian fjords (Volkman *et al.*, 1980; Sargent and Falk-Petersen, 1981; Sargent and Falk-Petersen, unpublished data). The abundance of 18:4 (*n*-3) in the lipids of these herbivorous zooplankton and of *Phaeocystis pouchettii*, at first sight supports the proposition that this species is a major dietary component of the zooplankton. This proposition has recently been confirmed for zooplankton in the German Wadden Sea (Weiße, 1983). However, in terms of the fatty acid data here, we caution that the appearance of 18:4 (*n*-3) in an animal's lipid can equally be accounted for by its ingesting 16:4 (*n*-3), e.g. from diatoms, followed by chain-elongation of the latter to 18:4 (*n*-3). Irrespective, the present study is in accord with the supposition that the abundance of (*n*-3) polyunsaturated fatty acids in the large amounts of neutral lipids in herbivorous zooplankton in arctic-boreal waters is a direct consequence of the abundance of (*n*-3) polyunsaturates in the biomembrane lipid of the phytoplankton in these waters.

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