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Spatial variability in lipid composition of calanoid copepods from Fram Strait, the Arctic

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Abstract

The calanoid copepods *Calanus hyperboreus* and *C. finmarchicus* were investigated in view of their lipid and wax ester content and their fatty acid and alcohol composition. Analyses were performed in females and copepodid stages V and IV from the Fram Strait region between Greenland and Spitsbergen in 1984. This region offers different food conditions like diatom blooms in the North East Water Polynya, food shortage in areas with very close ice cover, high phytoplankton biomass in the marginal ice zone and lower biomass in the open Atlantic water. Lipids contained generally more than 70% wax esters. Highest levels were found in *C. hyperboreus* with more than 90%. This percentage was not very variable, in spite of large differences in dry weight and lipid content. Copepods with particularly high weight and lipid content were found in the North East Water Polynya. The lightest individuals were found under the pack ice. Lipid proportions per unit dry weight were higher in *C. hyperboreus* than in *C. finmarchicus,* whose lowest values were found in the open Atlantic water. Spatial variability in fatty acid composition was much higher than in alcohol composition. The principle alcohols, 20:1 and 22:1, generally accounting for more than 80% of total alcohols. In the North East Water Polynya, the predominant monounsaturated fatty acid was 16:1, while under the ice 20:1 and 22:1 dominated. In the marginal ice zone and in the open water, the 18:4 acid reached percentages up to 30% of total fatty acids. These changes were related to the different food conditions. *C. hyperboreus* appears to be best adapted to the cold water and unfavourable conditions of polar regions because of its high lipid and wax ester store with long-chain wax esters of high calorific value.

Introduction

The life of herbivorous copepods in high latitudes is determined by the extreme seasonality of food availability. In the Greenland Sea in addition to seasonal gradients there are also sharp spatial gradients in food supply resulting from the hydrographic regime and ice cover. Thus, under the pack ice on the East Greenland Shelf, chlorophyll concentrations are very low during most of the year, while in polynyas phytoplankton blooms can develop much earlier. Highest chlorophyll concentrations were observed in the marginal ice zone of the Polar Front region where the Polar water meets Atlantic water (Smith et al. 1985, Smith et al. 1987, Spies 1987).

The life cycles of some calanoid copepod species are well adapted to this environment. They spend most of the year in a resting stage, metabolizing lipids stored in large oil sacs at a highly reduced rate (Hirche 1983). Lipids are also mobilised during gonadal maturation (Bamstedt 1979, Gatten et al. 1980) and are an essential component of copepod eggs (Sargent and Henderson 1986). Little is known on the lipid content of Arctic copepods. High concentrations were found, often consisting of a high proportion of wax esters (Lee 1974, 1975, Sargent et al. 1981, Tande and Henderson 1988; reviewed by Sargent et al. 1976, Clarke 1983, Sargent and Henderson 1986). The fatty acid component of wax esters is highly variable, reflecting the fatty acids of food organisms. Fatty alcohols are less variable, as are the principle alcohols, 20:1 and 22:1, which have to be synthesised de novo from precursors such as fatty acids, carbohydrates, and amino acids (Farkas et al. 1973, Sargent and McIntosh 1974).

During MIZEX (Marginal Ice Zone Experiment) 1984 in the Fram Strait region between East Greenland and Svalbard, samples were collected to study the lipid and wax ester content as well as the fatty acid and alcohol composition of the dominant calanoid copepods *Calanus finmarchicus* and *C. hyperboreus*. *C. hyperboreus* is at least a biennial (Harding 1966, Dawson 1978) Arctic species (Grainer 1963) while *C. finmarchicus* has one generation per year (Lie 1965) and is a boreal species inhabiting the North Atlantic (Marshall and Orr 1955). The distributions of the two species overlap in the Greenland Sea (Smith 1988). Reproduction in *C. finmar-*

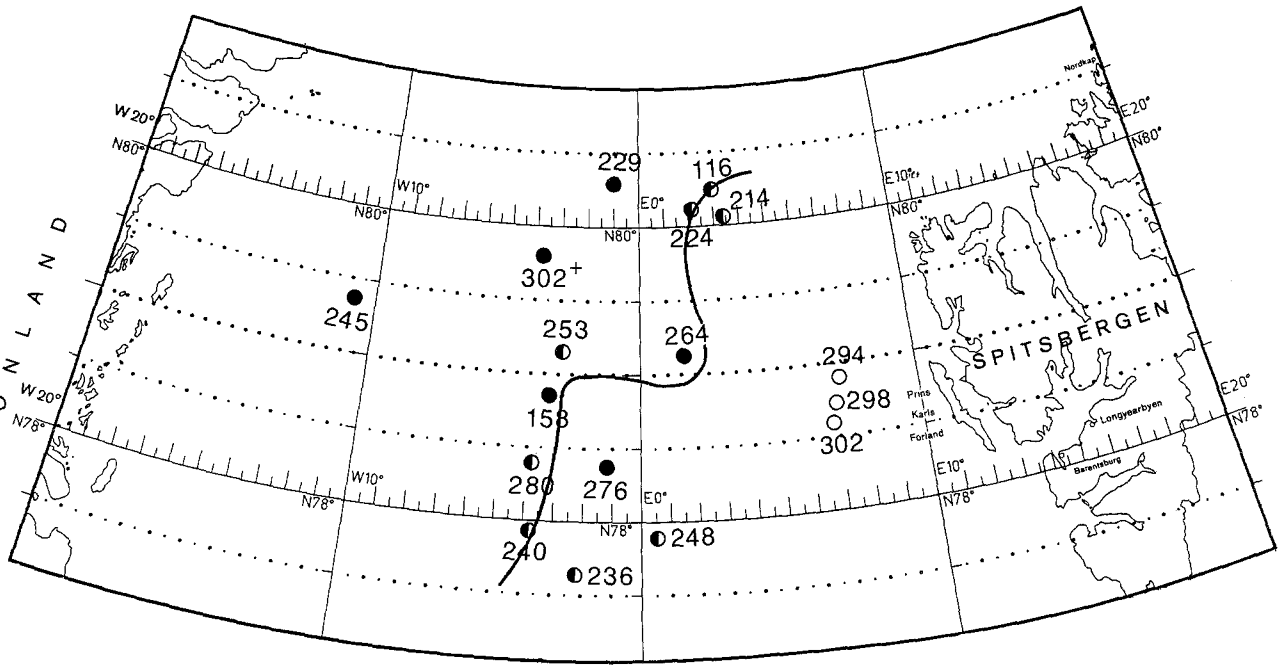

Fig. 1. Fram Strait between Greenland and Spitsbergen. Location of stations where calanoid copepods were collected. ●: *Calanus hyperboreus* only; ○: *C. finmarchicus* only: ◐: both species. Marginal ice zone indicated by 0 °C isotherm at 5 m depth (continuous line)

Table 1. *Calanus hyperboreus* and *C. finmarchicus*. Time and characterization from sampling locations of copepodid stages. Stations are grouped according to clusters (A to G). f: females; V and IV: copepodid stages; Cl: cluster; ×: sampled species

Station no.	Date (1984)	Position		*C. hyperboreus*				*C. finmarchicus*				Characterization
		Lat.	Long.	f	V	IV	Cl	f	V	IV	Cl	
245	30 June	79°23.6′N	10°43.2′W	×			A					North East Water Polynya
302⁺	14 July	79°46.8′N	03°56.6′W	×	×	×	B					Near the Polynya
253	01 July	79°18.0′N	02°55.5′W	×	×			×	×		C	Consolidated to close
229	27 June	80°20.2′N	01°00.4′W	×	×	×	C					pack ice
280	06 July	78°25.3′N	03°46.8′W	×	×	×			×		D	Marginal ice zone
158	16 June	78°53.4′N	03°20.1′W	×	×	×	D					
224	25 June	80°05.5′N	02°13.5′E	×	×	×	D	×	×		D	
116	24 June	80°14.7′N	02°59.5′E			×		×	×	×	D	
214	04 July	80°04.5′N	03°24.0′E		×	×		×	×	×	D	
264	02 July	79°06.3′N	01°46.5′E	×	×	×	E					Open water near
240	06 July	77°55.1′N	03°50.0′W	×	×	×		×	×		F	marginal ice zone
236	05 July	77°40.0′N	02°06.4′W	×	×		E	×	×	×	F	
276	05 July	78°25.1′N	01°15.5′W	×	×		F					
248	06 July	77°55.1′N	00°29.9′E	×	×	×	F	×	×	×	F	
302	12 July	78°40.3′N	06°44.2E					×	×	×	G	Open water near
298	12 July	78°47.8′N	06°59.3′E					×	×	×	G	Spitsbergen
294	10 July	78°55.6′N	07°08.9′E					×	×	×	G	

chicus is synchronised with the onset of phytoplankton blooms by the dependency of egg production on food uptake (Marshall and Orr 1955, Runge 1984). *C. hyperboreus*, on the other hand, is able to spawn in the absence of food, relying on fat reserves deposited the previous year (Conover 1962, 1967).

In this paper we compare, in these two species, possible effects of spatial and temporal patterns of environmental and feeding conditions upon fatty acid and alcohol composition.

Material and methods

Copepods were collected at 21 stations in Fram Strait between Greenland and Svalbard during the MIZEX cruises 1984 of RV "Polarstern" and RV "Valdivia" (Fig. 1). Table 1 presents data on species and stages collected at the various stations. Copepods from the upper 100 m were collected with a bongo net (330 and 500 μm mesh). Closed 2-l jars served as cod ends to avoid damage to individuals. Live copepods were sorted and identified immediately. Copepods for dry weight determination were stored at −60 °C and later dried at 65 °C for 14 to 16 h and weighed.

For each lipid analysis, ca 20 *Calanus hyperboreus* or 50 *C. finmarchicus* were transferred immediately into glass tubes containing chloroform:methanol (2:1, v:v) and stored at −20 °C. Copepods were later crushed in a mortar and extracted with chloroform:methanol (2:1). An aliquot of the supernatant was transesterified using 3% conc. sulfuric acid in methanol. After extraction with hexane, analysis was performed with a Hewlett Packard gas liquid chromatograph on a 50 m × 0.325 mm i.d. wall-coated open tubular (WCOT) glass capillary column coated with SILAR 10 C (Macherey and Nagel, Düren, FRG) using temperature programming. In a single chromatogram, fatty acid methyl esters and fatty alcohols were analysed simultaneously. The detailed method is described by Kattner and Fricke (1986). Twenty seven fatty acids and nine alcohols were determined. Fatty acids and alcohols were quantified using internal C_{17} or C_{19} fatty acid methyl ester standards which were added before extraction. Wax esters were calculated from the proportion of alcohols on a mole basis, assuming that copepods contain no free fatty alcohols. By this calculation, fatty acids were combined with alcohols to wax esters on a random basis. Total lipid was calculated as the sum of fatty acids and alcohols, which is a slight underestimation because sterols and the phosphobase of phospholipids were not taken into consideration.

At each station and for every copepodid stage, fatty acid and alcohol composition were expressed as a percentage of the total fatty acid or fatty alcohol content and compared with every other station using the percent similarity index (PSI, Whittaker 1952). This technique provides a dendrogram indicating groups of stations with similar fatty acid and alcohol composition using the method of weight-pair groups. Five fatty acids and two alcohols, which each constituted less than 0.5% of total fatty acids or alcohols, were not used for this analysis.

Results

Calanus hyperboreus was collected at 12 stations and *C. finmarchicus* at 11 stations in the various hydrographical regimes of Fram Strait (Fig. 1, Table 1). On the East Greenland Shelf, Stn 245 was located in a large polynya that regularly opens here starting in March – April. Stn 302^{+} was under the ice just beyond the edge of a smaller polynya. Stns 229 and 253 were under consolidated and close pack ice.

The position of the ice edge changed rapidly during the investigation period due to changes in winds and currents. In addition, various eddies shaped the appearance of the ice edge by their own drift and by advecting ice into the open water (Johannessen et al. 1987). In Fig. 1, we therefore show the position of the 0 °C surface isotherm rather than the ice edge as an indicator of the Polar Front which separates the East Greenland Current from the warmer more saline Atlantic water.

On the eastern side of Fram Strait, Stns 294, 298 and 302 were all located in the Atlantic Water of the West Spitsbergen Current. The boreal species *Calanus finmarchicus* clearly dominated samples. It was also found in lower numbers at all stations under the pack ice and on the East Greenland Shelf. There, it was probably transported with the Return Atlantic Current via deep throughs in the East Greenland Shelf. The Arctic species *C. hyperboreus* dominated in the East Greenland Current, and was also found in considerable numbers at all stations in the vicinity of the ice edge. However, it was absent from West Spitsbergen Current stations.

Dry weight

In *Calanus hyperboreus*, individual dry weight varied by a factor of four in females and copepodid stage V. Lowest values were found in the pack ice zone. In *C. finmarchicus*, dry weight variability was less pronounced. Individuals of lowest weight were found in the West Spitsbergen Current (Table 2).

Lipid

The lipid proportion of dry weight was, in *Calanus hyperboreus* females and copepodid stage IV, twice as high and one third higher in stage V than in the corresponding stages of *C. finmarchicus*. Average values were similar among *C. hyperboreus* stages, although there was considerable variability at the various stations. *C. finmarchicus* females exhibited the widest range in lipid content, with lowest values in the West Spitsbergen Current. On average, copepodid stage V had the highest lipid content (Table 2).

Wax ester

Wax esters were by far the most important lipid component. In *Calanus hyperboreus* they exhibited little variability and made up more than 90% of the total lipid in females. In this species, there was a clear decrease from females to copepodid stage IV at every station. In *C. finmarchicus* the proportion of wax ester was less, in all stages, than in *C. hyperboreus*, except at Stn 253 (under the pack ice), where the proportion of wax ester was in the range of *C. hyperboreus* females. Copepodid stage V had a much higher wax ester content than stage IV. In *C. finmarchicus* females and copepodid stage V, wax ester content was, in general, lower at West Spitsbergen Current stations than at closely neighbouring Stns 236, 240 and 248 at the southern tip of the study area (Table 2).

Fatty acid and alcohol composition

The same fatty acids and alcohols were found in both species, however, their relative importance varied according to species, stages and sampling locations. In *Calanus hyperboreus* the six most important fatty acids 16:1, 18:4, 20:1,

Table 2. *Calanus hyperboreus* and *C. finmarchicus*. Biochemical compositions of copepodid stages at different locations. Dry weight partly averaged from several determinations (mean ± SD), SD: standard deviation; –: no data available; Cl: Cluster. Cluster letters and dates from Table 1

Station	Cl	Dry weight			Lipid % dry weight			Wax ester % total lipid		
		Females	Stage V	Stage IV	f	V	IV	f	V	IV
Calanus hyperboreus										
245	A	4 980	2 110 ± 162	939	42	–	–	85	–	–
302[+]	B	1 740 ± 380	680 ± 25	–	29	25	–	95	88	71
253	C	–	653	–	–	41	–	93	91	–
229	C	1 330 ± 530	517	–	44	29	–	93	92	86
280		2 330 ± 140	–	420 ± 17	32	–	36	94	90	86
158	D	4 580 ± 610	3 250	336	32	31	36	95	91	88
224	D	–	–	–	–	–	–	95	91	89
116		–	–	441	–	–	37	–	–	88
214		4 785	1 490 ± 24	510 ± 80	–	33	32	–	90	89
264	E	3 070 ± 190	2 030 ± 110	660 ± 35	32	39	30	92	88	86
240		2 760 ± 580	1 500	457	24	40	33	91	89	85
236	E	4 920 ± 220	2 280 ± 160	520	25	32	–	96	89	–
276	F	3 550 ± 215	2 810 ± 480	–	32	29	–	95	91	–
248	F	3 910 ± 240	2 060 ± 190	540 ± 106	26	33	26	94	90	85
Mean					30.9	32.8	32.8	93.1	89.9	84.5
SD					5.7	4.7	3.8	3.0	1.4	5.9
Calanus finmarchicus										
253	C	–	163 ± 25	–	–	36	–	94	94	–
280	D	–	423 ± 41	–	–	23	–	–	88	–
224	D	450 ± 15	358 ± 16	–	15	34	–	83	90	–
116	D	–	281 ± 87	–	–	36	–	80	89	83
214	D	321	227 ± 16	74	29	27	15	87	85	74
240	F	390 ± 47	388 ± 50	–	13	17	–	70	87	–
236	F	–	–	116	–	–	18	76	83	77
248	F	397 ± 13	439 ± 31	85	15	19	–	77	86	–
302	G	328 ± 25	202 ± 15	–	9	14	–	75	76	69
298	G	290 ± 20	219 ± 24	83 ± 6	8	16	14	71	79	68
294	G	267 ± 19	186 ± 4	94 ± 2	7	18	16	61	84	69
Mean					13.7	24.0	15.8	77.4	85.5	73.3
SD					7.5	8.6	1.7	9.3	5.0	5.9

20:5, 22:1, and 22:6 represented, on average, 80% of total fatty acids and the three fatty alcohols 16:0, 20:1, and 22:1 accounted for about 94% of total fatty alcohols. In *C. finmarchicus*, the fatty acids 14:0 and 16:0 were also important and together with the six which dominated *C. hyperboreus*, represented 79% of total fatty acids. The three most important fatty alcohols were the same as in *C. hyperboreus* and formed 92% of total fatty alcohols.

To reduce the large data set of fatty acid and alcohol compositions, the different sampling locations were grouped using dendrograms of the percent similarity index (PSI) between fatty acid and alcohol compositions, as well as hydrographical and ice conditions.

Spatial variability in *Calanus hyperboreus*

The dendrograms show only a few relationships between sampling locations – consistent for all stages (Fig. 2), consequently, Table 3 contains only major fatty acid and alcohol data of similarity groups. These groups of stations are marked by cluster letters. The change in dominant fatty acids was not uniform for all stages and changed from cluster A to F (Table 4). On average, the major acids were the monounsaturated acids 20:1 and 22:1, which were highest under the close pack ice. In females and copepodid stage V levels of 22:1 acid were mostly higher than 20:1. For both acids a considerable amount for their isomers were detected, especially of the 22:1 (n-9) acid.

In females from the North East Water Polynya (A) and in copepodid stage V under the ice close to the Polynya (B), 16:1 dominated the fatty acid composition. It decreased towards the marginal ice zone and West Spitsbergen area. The spatial distribution of the 18:4 acid was the converse of the 16:1 acid, and accounted for more than 30% in the marginal ice zone (D). The lowest levels were found near the Polynya (A). The polyunsaturated acids 20:5 and 22:6 were

Table 3. *Calanus hyperboreus*. Compositions of major fatty acids and alcohols (in wt% of total fatty acids or alcohols). Monounsaturated fatty acids and alcohols include small amounts of their isomers [n−(x−2)]. PUFA = Polyunsaturated fatty acids. Letters refer to cluster, see Table 1

Lipid	Females						Stage V					Stage IV				
	A	B	C	D	E	F	B	C	D	E	F	B	C	D	E	F
Fatty acids																
14:0	2.5	4.2	4.2	2.6	3.3	2.9	5.6	7.8	2.6	2.9	2.4	4.4	8.7	3.0	3.1	4.0
16:0	3.2	4.0	4.4	2.4	3.3	3.7	5.3	5.4	2.3	2.7	2.9	7.6	8.3	3.0	2.9	4.0
16:1 (n-7)	25.4	16.3	9.1	2.7	3.5	4.9	21.6	6.8	2.0	2.8	3.6	16.2	9.3	2.3	3.0	2.4
16:PUFA	3.8	1.8	2.1	1.9	1.6	2.7	1.5	1.5	1.4	1.6	1.7	2.2	3.9	1.8	1.7	1.7
18:1 (n-9)	4.2	5.8	5.0	2.9	3.5	4.9	7.1	6.5	3.3	3.9	5.2	7.7	5.7	3.3	4.1	4.5
18:2 / 18:3	1.3	2.3	2.2	3.4	3.8	4.2	2.3	5.2	4.1	5.0	5.6	3.0	2.8	4.8	5.2	3.1
18:4 (n-3)	2.1	1.3	5.8	27.2	18.2	13.1	0.6	2.9	28.5	21.3	20.1	1.3	6.9	28.8	23.0	26.0
20:1 (n-9)	13.6	21.9	23.1	14.7	16.0	15.0	15.6	20.3	15.8	17.4	14.0	7.9	12.8	14.0	14.6	9.3
20:5 (n-3)	19.7	9.0	9.2	9.0	8.6	13.7	9.7	6.7	7.7	7.4	12.5	15.4	10.1	7.3	7.5	10.0
22:1 (n-11)	12.8	21.0	19.4	15.7	22.3	16.7	15.3	21.5	16.0	19.7	14.3	8.0	12.4	15.5	19.3	12.6
22:6 (n-3)	4.2	8.0	10.4	11.3	9.8	11.8	11.2	10.2	11.0	9.8	12.0	20.7	13.3	11.2	10.0	13.7
Fatty alcohols																
14:0	3.1	1.5	1.6	2.2	1.9	1.8	3.3	2.8	4.7	4.5	4.0	3.6	3.1	6.8	5.8	6.6
16:0	7.6	4.8	4.7	3.8	3.5	5.0	9.6	6.1	6.4	7.0	9.0	13.9	8.3	9.5	8.8	5.0
16:1 (n-7)	3.3	0.3	0.0	0.1	0.0	0.2	1.8	0.4	0.3	0.3	0.3	3.9	0.4	0.5	0.9	0.0
18 total	0.6	0.8	0.7	1.0	0.5	0.7	0.6	1.0	1.1	1.1	1.5	1.4	0.0	1.5	1.5	0.9
20:1 (n-9)	40.9	28.9	33.1	32.4	29.0	32.6	25.1	29.6	33.2	30.7	32.2	23.7	31.1	27.2	29.4	29.7
22:1 (n-11)	44.4	63.7	59.6	60.0	65.1	59.7	59.6	60.0	53.8	56.4	53.8	53.1	56.8	54.0	53.1	57.8

Table 4. *Calanus hyperboreus*. Dominant fatty acids of stages from different locations. In case of more than one acid, difference is below 2%. Letters refer to cluster, see Table 1

Stage	A	B	C	D	E	F
Females	16:1	20:1	20:1	18:4	22:1/18:4	4 acids
Stage V	–	16:1	20:1/22:1	18:4	22:1/18:4	18:4
Stage IV	–	22:6	20:1/22:6	18:4	18:4	18:4

more constant, with the exception of remarkable high levels of 20:5 acid (19.7%) found in females in the Polynya (A) and in copepodid stage IV near Polynya (B). In this stage we also found extremely high levels of 22:6 acid (20.7%), which was generally higher than 20:5 in all copepodid stages.

Except for the Polynya Stn (A), differences in the spatial distribution of fatty alcohols were small. Compositions were clearly dominated by the 22:1 alcohol (>50%). The levels of this alcohol decreased from females to copepodid stages IV and were compensated by 16:0 and 14:0 alcohols. There was a tendency in the ice covered area towards higher levels of the 22:1 alcohol. The ratio between 20:1 and 22:1 alcohols was mainly around 0.5, but was near unity at the Polynya station.

Spatial variability in *Calanus finmarchicus*

Cluster analysis groups fatty acid and alcohol compositions of females into at least four clusters (C, D, F, G). For classification of copepodid stages, female clusters were used (although they partly fell into different clusters, Fig. 3). Stn 253 (C), the only station under close pack ice, showed the most significant differences. The other clusters were formed by closely neighboured stations in the West Spitsbergen Current and locations along the marginal ice zone.

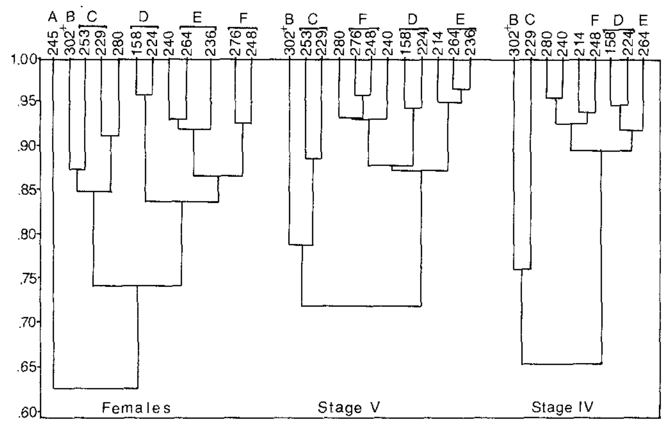

Fig. 2. *Calanus hyperboreus*. Dendrogram grouping of zooplankton samples according to percent similarity index (vertical axis). Stations are indicated across top. Subjective groups indicated by letters

Table 5 shows average fatty acid and alcohol compositions of *Calanus finmarchicus*. Under close pack ice (C) the 14:0 acid was the major acid in females and copepodid stage V. The 16:0 acid was uniform regardless of stage and sampling location. The monounsaturated acids 20:1 and 22:1 tended to decrease from the close pack ice (C) to near Spits-

Table 5. *Calanus finmarchicus*. Compositions of major fatty acids and alcohols. Further information refer to Table 3

Lipid	Females				Stage V				Stage IV		
	C	D	F	G	C	D	F	G	D	F	G
Fatty acids											
14:0	21.2	13.3	12.1	12.7	18.0	13.9	12.7	17.5	11.6	12.3	12.4
16:0	8.8	8.7	10.6	11.1	9.3	8.1	7.8	8.6	8.3	8.8	8.6
16:1 (n-7)	7.3	5.8	4.3	5.6	6.5	5.1	3.2	4.9	4.9	2.7	5.3
16 PUFA	1.2	2.1	1.7	1.4	2.3	1.8	2.6	2.5	1.6	1.3	2.6
18:1 (n-9)	5.7	5.1	5.2	5.5	5.3	4.7	4.1	4.5	4.3	3.4	5.2
18:2/18:3	2.8	4.1	4.4	3.5	3.9	4.1	4.7	4.1	3.7	4.6	3.5
18:4 (n-3)	1.6	11.5	10.3	5.2	9.3	16.8	18.2	13.6	17.7	20.5	11.8
20:1 (n-9)	13.4	11.2	7.6	6.0	9.6	9.0	8.8	5.1	5.8	5.2	4.5
20:5 (n-3)	7.4	10.6	13.8	19.3	9.8	9.7	11.8	17.1	13.6	12.7	22.2
22:1 (n-11)	15.7	10.5	7.9	6.2	12.0	10.9	10.7	6.1	7.6	7.8	4.8
22:6 (n-3)	9.8	10.1	15.0	16.4	7.7	9.0	9.2	10.0	13.8	13.2	12.1
Fatty alcohols											
14:0	0.4	1.4	1.2	0.9	1.1	1.9	1.6	2.1	2.5	3.0	3.5
16:0	3.0	6.8	7.3	8.5	6.6	9.3	7.6	9.5	12.5	12.7	11.9
16:1 (n-7)	0.7	1.8	1.4	1.0	1.8	2.4	0.9	1.6	3.3	1.3	2.8
18 total	1.9	3.1	3.1	3.9	4.0	4.2	3.0	5.2	4.5	5.1	6.1
20:1 (n-9)	39.8	43.1	41.9	36.9	41.0	42.8	42.9	40.6	40.1	35.1	39.3
22:1 (n-11)	54.3	43.3	44.9	48.8	45.2	39.0	43.9	41.2	36.5	42.1	36.5

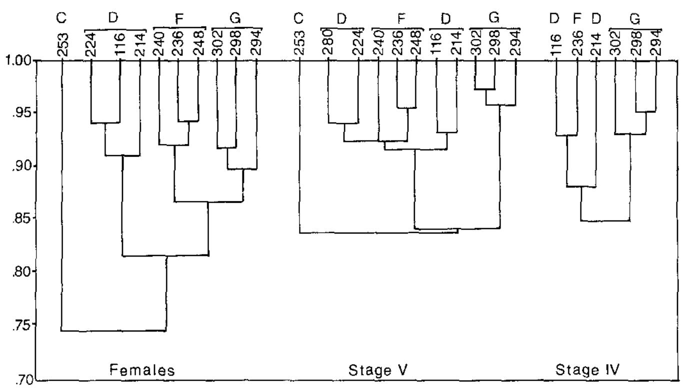

Fig. 3. *Calanus finmarchicus*. Dendrogram grouping of zooplankton samples according to percent similarity index (vertical axis). Stations are indicated across top. Subjective groups indicated by letters

bergen (G) and from females to copepodid stage IV. The 18:4 acid exhibited the most conspicuous variations, from 1.6% in females under the close pack ice (C) to 20.5% in copepodid stage IV in the marginal ice zone (F). The 20:5 acid exhibited a significant increase in all stages from the close pack ice and the marginal ice zone to the area near Spitsbergen. In females, the 22:6 acid showed a similar trend to the 20:5 acid although it remained unchanged in copepodid stages.

The major alcohols were 20:1 and 22:1 which together accounted for 76 to 94%. The saturated alcohol 16:0 varied between 3 and 12.5% with lowest levels in females and highest levels in copepodid stage IV. The 22:1 alcohol of females was distinctly higher under close ice cover. The ratio between 20:1 and 22:1 alcohol was mainly near unity.

Discussion

Lee and Hirota (1973) introduced the idea that marine animals rich in wax esters experienced short periods of food plenty followed by prolonged periods of food scarcity. Due to the relatively short period of sufficient light for phytoplankton growth in Polar regions, the zooplankters need special strategies to survive food-scarcity and to preserve energy for reproduction. The generally higher lipid and wax ester contents of *Calanus hyperboreus* in relation to *C. finmarchicus* thus reflect their habitat. Wax ester in Calanoids usually increases in the copepodid stages (Kattner and Krause 1987). Here it was already very high in the copepodid stage IV of both species, indicating their capability to overwinter. Indeed, overwintering populations of *C. finmarchicus* in the Subarctic (Balsfjord, northern Norway) consisted of stages IV and V (Tande 1982). In *C. hyperboreus* most of the copepodid stages are capable of overwintering (Ostvedt 1955).

Calanus hyperboreus females had, at all stations, the highest wax ester content. Similar values were only found in *C. finmarchicus* at Stn 253. Mobilisation of wax esters during the reproductive period is well documented (e.g. Gatten et al. 1980, Sargent and Henderson 1986). Large amounts of lipid are invested in the egg-spent females of *C. hyperboreus* had no wax esters left (Kattner and Hirche unpublished data). We therefore suggest that wax ester contents greater than 90% reflect a prespawning situation. In concurrent egg production experiments, no eggs were produced by *C. hyperboreus* and gonads were hardly visible (Hirche unpublished data). Spawning in *C. hyperboreus* occurred in January and February in north Norwegian Fjords and active egg laying was observed in late March in the Greenland Sea (Smith 1989).

In *Calanus finmarchicus*, wax ester content correlated with egg production. Under the close pack ice reproduction had not yet commenced or was negligible (Bohrer and Hirche 1989) and wax esters made up more than 90% of total lipid. In the marginal ice zone highest egg production was found, but also variability was greatest there. Wax esters of more than 80% of total lipid indicate that egg production is only at the start, while it was further advanced in the open water near the ice edge and still further in the West Spitsbergen Current.

In all stages of both species investigated the same fatty acids and alcohols were found. Differences in their relative frequency reflect feeding and physiological conditions. The similarity groups obtained by cluster analysis are in accordance with the hydrographical regime and ice cover – the major factors for primary production in Fram Strait.

In the North East Water Polynya (A) a diatom bloom in Polar water produced the highest primary production rates of the cruise (Baumann personal communication). Feeding rates of *Calanus hyperboreus* were highest at this station (Barthel 1988) and were associated with highest lipid content. Lipid composition of *C. hyperboreus* showed the most pronounced statistical differences to all other regions (Fig. 2). This is mainly due to the enormous proportion of the typical diatom fatty acids 16:1 and 20:5 (e.g. Kates and Volcani 1966, Ackman et al. 1968, Kattner et al. 1983).

The pack ice region (B) was described by low biomass and primary production (Smith et al. 1987, Spies 1987) and was dominated by flagellates (Baumann personal communication). Grazing rates were too low to be measured in *Calanus hyperboreus* and *C. finmarchicus* (Barthel 1988, Smith 1988). *Calanus finmarchicus* as a boreal species under the ice is expatriated (Hirche 1989, Smith 1989). Possible expatriation mechanisms are cross-frontal mixing, eddy advection or submergence with the Return Atlantic Current. In both species poor feeding condition was reflected in the low proportions of dietary fatty acids such as 18:4. Wax esters and 20:1 and 22:1 acid concentrations were highest here. The small body weight and relatively high lipid proportion were further indications of a starving condition.

The marginal ice zone (C, D, E) is an area of high phytoplankton (Smith et al. 1987) and zooplankton production (Bohrer and Hirche 1989). Due to frontal effects and eddies, variability of primary productivity is also high here. Phytoplankton species composition represents a summer population of dinoflagellates with partly large subsurface maxima of the prymnesiophyte *Phaeocystis pouchetii*. At some stations diatoms were also present in significant numbers (Smith et al. 1987, Gradinger and Baumann personal communication). This variability is reflected, in both species, in large variations in dry weight and lipid content, but less in fatty acid and alcohol composition. The three similarity groups in the marginal ice zone probably reflect different phytoplankton populations and therewith feeding conditions. Common to all clusters was the importance of 18:4, a major acid of *Phaeocystis pouchetii* (Sargent et al. 1985) and dinoflagellates (Harrington et al. 1970). This acid was the most abundant dietary acid in all species and stages examined, indicating the common consumption of *P. pouchetii*. This is confirmed by recent papers e.g. Huntley et al. 1987.

Calanus hyperboreus was absent from the West Spitsbergen Current. The fatty acid and alcohol compositions of *C. finmarchicus* were similar to those of other areas in the Northern Atlantic, like the North Sea (Kattner and Krause 1987, 1989) and Norwegian fjords (Volkmann et al. 1980, Falk-Petersen et al. 1987).

The differences in fatty acid compositions together with the more consistent alcohol compositions allow some general remarks about the biosynthesis of lipids and their metabolism in calanoid copepods. During active feeding, the majority of fatty acids are derived from phytoplankton lipid. Because of the high wax ester proportions in copepods nearly all fatty acids are combined to wax esters – including most of the polyunsaturated fatty acids. A significant difference between *Calanus hyperboreus* and *C. finmarchicus* is the amount of the saturated acids 14:0 and 16:0 present. Both acids accounted for more than 20% in *C. finmarchicus* but only traces were found in *C. hyperboreus*. If both species fed on the same diet, different pathways for the use of the fatty acids must be postulated. Beside carbohydrates and amino acids, the dietary saturated and monounsaturated acids may also serve as a basis for the de novo synthesis of the 20:1 and 22:1 components, since phytoplankton contain only traces (e.g. Kattner et al. 1983, Sargent et al. 1985). This pathway seems to be preferred by *C. hyperboreus* (and is already used if food is sufficient), in comparison to *C. finmarchicus*, as considerable amounts of saturated acids were never found for *C. hyperboreus*. Both acids serve as precursors for the corresponding alcohols, and are also main acid components in the wax esters.

The absence of typical phytoplankton fatty acids under unfavourable conditions, like close pack ice, leads to the assumption that dietary fatty acids are preferentially used up during starvation. This contradicts the theory that polyunsaturated, or at least short-chain fatty acids, are combined with long-chain monounsaturated alcohols to obtain low wax ester transition temperatures. *Calanus hyperboreus*, living in water with temperatures around freezing point contain up to 40% wax esters in the form of combinations of the 20:1 and 22:1 acids and alcohols. Adaption to low temperatures by polyunsaturated fatty acids is probably of great importance in retaining the fluiditiy of membranes.

Calanus hyperboreus seems to be best adapted, of the copepods from the northern oceans (including *C. glacialis* and *Metridia longa*, unpublished data), to life under the unfavourable conditions of cold regions. Adaptation may include (1) a high lipid proportion dry weight^{-1}, (2) large lipid stores of wax esters, (3) fast biosynthesis of wax esters using fatty acids as precursors in addition to de novo synthesis, (4) high proportions of long-chain fatty acids and alcohols and (5) the preferential consumption of fatty acids of less calorific value during unfavourable conditions.

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