Seasonal variation in lipid class and fatty acid composition of two small copepods in Balsfjorden, northern Norway

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Abstract. Zooplankton were collected at Svartnes, northern Norway between 1985 and 1986. The lipid class and fatty acid composition of a subarctic population of *Pseudocalanus acuspes* (Giesbrecht, 1881) and *Acartia longiremis* Lilljeborg are described for four seasons of the year. The results are discussed in relation to the seasonal variation in abundance and dry weight of the predominant developmental stages. The lipid composition of these small copepod species resembles that of omnivorous or carnivorous species. *P. acuspes* and *A. longiremis* overwinter in a state of arrested development, but seem to feed actively throughout the year. This behaviour resembles that of the omnivore *Metridia longa* (Lubbock), but is in contrast to that of the herbivore *Calanus finmarchicus* (Gunnerus) from the same area, which spends the winter in diapause.

Introduction

Copepods in the zooplankton community of Balsfjorden, northern Norway (69°30'N; 19°20'E), exhibit various life-cycle strategies in their adaptation to the environment (Tande 1982, Tande and Grönvik 1983, Hopkins et al. 1984, Norrbin 1987). This subarctic fjord is characterized by large seasonal fluctuations in insolation and, therefore, in primary production. The spring bloom starts in mid-March or in the beginning of April, and primary production continues to the end of September (Eilertsen et al. 1981, Eilertsen and Taasen 1984). One of the basic problems confronting herbivorous and omnivorous copepods is to accommodate energy expenditure over the year with seasonal input. Species differences in lipid storage and utilization are, therefore, important clues to the different life history and reproductive strategies employed.

Wax esters have been shown to be important as long-term energy reserves in copepods, because they are both incorporated and utilized at a slower rate than triacylglycerols (Benson et al. 1972, Lee and Hirota 1973, Lee et al. 1974, Håkansson 1984, 1985). In north Norwegian fjords *Calanus finmarchicus* stores large amounts of wax esters and spends the winter in diapause, while *Metridia longa* (Lubbock) is primarily dependent on continuous feeding (Grönvik and Hopkins 1984, Falk-Petersen et al. 1987). This has great influence on their particular seasonal life cycles and on the timing of reproduction in spring (Hopkins et al. 1984, Båmstedt et al. 1985).

The small copepod *Pseudocalanus acuspes* (identified as the predominant *Pseudocalanus* species in this area; Frost 1989) stores appreciable amounts of lipid in an oil sac, whereas *Acartia longiremis* stores only moderate amounts. Does this biochemical distinction influence the life cycle and behaviour of small species in a similar way as for larger copepods? In this paper, which is part of a study on overwintering patterns of *Pseudocalanus* spp. and *Acartia longiremis* in a high-latitude environment, the seasonal composition of lipid classes and fatty acids in selected age groups is related to information on seasonal variation in copepod abundance and dry weight.

Materials and methods

Collection details

Zooplankton were collected monthly from October 1985 to October 1986 at Svartnes, the deepest basin in Balsfjorden, Norway. No samples were taken in July. A 200 μm WP-2 closing net was towed vertically through three depth intervals (40 to 0, 100 to 40 and 180 to 100 m). Towing speed was 0.5 m s^{-1}. Use of this large mesh-size will likely have resulted in an underestimate of the abundance of copepodid Stages CI to CIII of *Pseudocalanus acuspes* (Giesbrecht 1881) and *Acartia longiremis* Lilljeborg. Zooplankton were preserved in a solution of formaldehyde and propylene glycol (1.5 and 3.5%, respectively) for later quantification. Detailed data on abundances and stage composition are given elsewhere (Norrbin 1987). Copepods were taken from a separate sampling series (October 1985 to April 1986, August and October 1986) for the determination of dry mass. These specimens were rinsed with distilled water and dried in a desiccator. Two to six replicate samples were weighed for each of the copepodid Stages CIV and CV of *P. acuspes* and adult females of *A. longiremis*, which were the commonest developmental stages throughout the year.

Plankton were collected for lipid analyses on 25 November 1985, 17 February, 16 June and 23 September 1986 at Svartnes, Balsfjorden. A 200 μm WP-2-net was towed vertically from 180 m to the surface. Zooplankton were brought to the laboratory and kept in the dark at in situ temperature until they were sorted. The life history stages chosen for lipid analyses, CIV and CV of *Pseudocalanus acuspes* and adult females of *Acartia longiremis*, were common throughout the year. Copepods for lipid analyses derived from the overwintering generation in 1985 (G$_0$ in November and February), the first new generation in 1986 (G$_1$ in June) and the second and/or third generation in 1986, part of which formed the new overwintering generation (September, G$_2$ to G$_0$).

Copepods were narcotized with MS222 and sorted under a dissecting microscope. Sorted copepods were transferred to glass vials containing chloroform/methanol (1/1 by volume). Filled vials were than stored in a cryo-freezer at −65 °C until analysis in November 1986.

Fatty acid analyses

Lipids were extracted according to Folch et al. (1957) and lipid class analyses were done according to Olsen and Henderson (1989). Analyses of fatty acids and fatty alcohols were then performed according to Sargent and Falk-Petersen (1981)[1]. Due to loss of some of the lipid extract, total lipid could not be determined.

Some of the samples for analysis of wax ester fatty acids and alcohols contained small impurities (less than 1% of total). To avoid difficulties in interpretation of data, all peaks less than 0.5% were omitted from calculations. Consequently, no trace components are presented for fatty acids and alcohols of *Pseudocalanus acuspes* and for *Acartia longiremis* wax esters throughout the year (Tables 1 and 2).

Results

Abundance of copepods

The peak in *Pseudocalanus acuspes* abundance and biomass was reached in autumn (October to December; Fig. 1 A). After the beginning of September the molting rate of older copepodids (CIV to CV) abated, and an accumulation of these stages began. Adults and copepodids younger than CIII disappeared from the population during late autumn and winter and older juveniles formed the overwintering population. Approximately 10% of this population survived the winter and molted to adults in March and April. Actively reproducing *P. acuspes* females were present from April to August, as evidenced by the appearance of successive broods of young copepodids (Fig. 1 A).

Females dominated the *Acartia longiremis* population during most of the year (Fig. 1 B) and also constituted the overwintering population. Young stages and males were absent from December to May (Fig. 1 B). Note, Stages CI to CIII were incompletely captured (see Materials and methods). *A. longiremis* females were most likely inseminated before the overwintering season (Davis 1976, 1985,
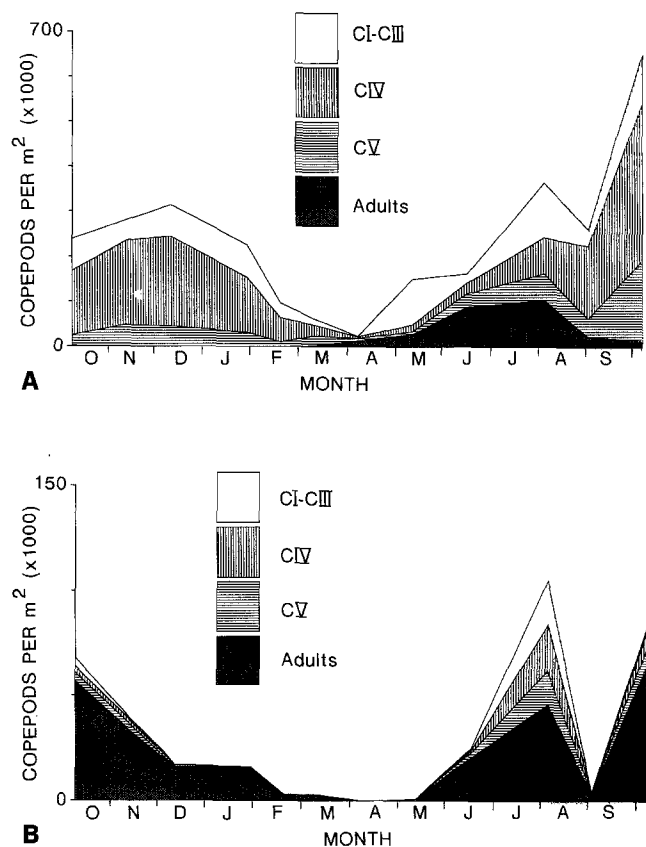

Fig. 1. *Pseudocalanus acuspes* (A) and *Acartia longiremis* (B). Abundances of copepodid populations at Svartnes, Balsfjorden (1985 to 1986). Depth at this site is ca 185 m

Norrbin 1987). After eggs were released in April, females were absent from the zooplankton until late May. The spring increase in *A. longiremis* abundance, therefore, occurred somewhat later than that of *Pseudocalanus acuspes* (Fig. 1 A, B). By June, however, the former species constituted a large proportion of the total small-zooplankton.

Dry mass

Pseudocalanus acuspes CV lost ca. 1/3 of their dry body mass between November and February, reaching a minimum of 6 g (Fig. 2 A). The 100% increase in mass between March and April can be explained by CIV molting to CV during a period with abundant food (the start of the vernal bloom). The CV appearing in April were also larger in size than those in March (Norrbin 1987). During the productive season, average dry mass was 11 to 14 g for *P. acuspes* CV (Fig. 2 A). A similar pattern was recorded for *P. acuspes* CIV. These weighed between 6 and 7.5 g during the productive season and reached a minimum of 4 g in February. Overwintering *Acartia longiremis* females decreased ca. 15% in dry mass between November and February (Fig. 2 B). Overwintering copepods again gained 40% in dry mass before April, when eggs were laid. The average dry weight of *A. longiremis* during the productive season was 8 g.

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[1] Fatty acids and alcohols are described using the denotation that 18:1(n-9) is a molecule with 18 carbon atoms and one double bond situated between the ninth and the tenth carbon atom from the methyl end of the molecule
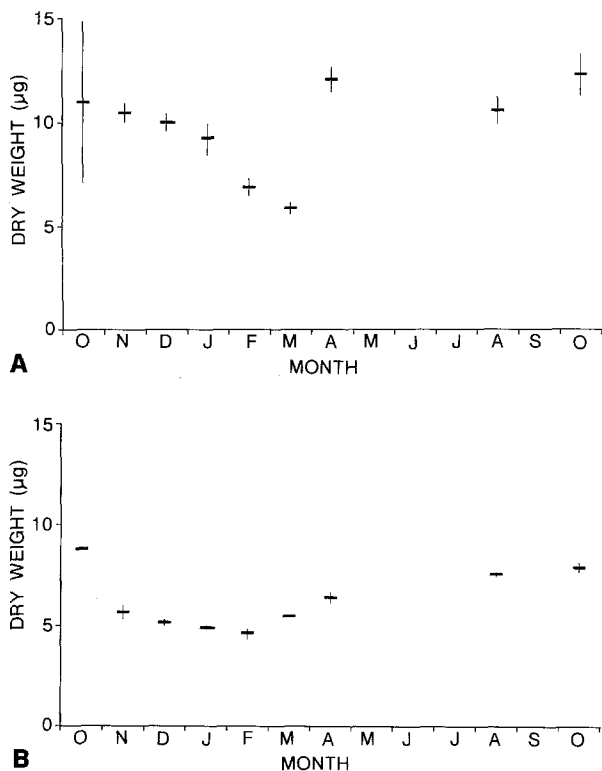
Fig. 2. *Pseudocalanus acuspes* CV (A) and *Acartia longiremis* females (B). Dry mass (1985 to 1986); vertical bars denote two SD. In March only one determination was made of *A. longiremis* dry weight

Fig. 3. *Pseudocalanus acuspes* (A) and *Acartia longiremis* (B). Proportion of wax esters (WE) and triacylglycerols (TAG) at different seasons relative to polar lipids (PL). The amount of polar lipid is set to 1

Lipid class composition

The composition of the main neutral lipid classes have been expressed relative to the polar lipid content (Fig. 3A, B). Polar lipids, forming the cell membranes, constitute a fairly constant biochemical property, usually comprising a few percent of the dry mass of copepods (Sargent and Whittle 1981, Håkanson 1984 Table 2, Båmstedt et al. 1990).

The dominating lipid class in *Pseudocalanus acuspes* was wax ester, comprising 55 to 72% of the total lipid. The high proportion of wax ester in *P. acuspes* in September 1986 (Fig. 3A) reflects the large oil sacs of copepodids "preparing" for overwintering. From November to June the proportion of wax ester in *P. acuspes* decreased by ca. 50%, compared with polar lipid (Fig. 3A). Triacylglycerol reserves in *P. acuspes* increased from February to September, reaching a maximum of 13.7% of the total lipid. These results agree with the lipid class composition in *Pseudocalanus* sp. from the west coast of Sweden (Båmstedt et al. 1990).

The ratio of neutral to polar lipids in *Acartia longiremis* was generally low, especially during the summer (Fig. 3B), also, the relative proportion of wax ester was low, between 4 and 12% of total lipids. There was a large seasonal variation in the proportion of triacylglycerol in *A. longiremis* lipids. The highest values were found in September (55%) and November (42%), i.e. at the beginning of the overwintering season. Between November and February, the proportion of triacylglycerol had been
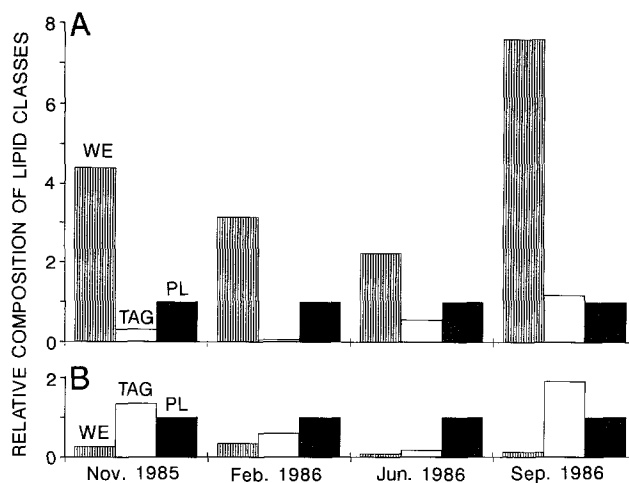
reduced by 50%. The lipid class composition of *A. longiremis* appears to be similar to that reported for *A. clausi* (Båmstedt et al. 1990).

Fatty acid composition

In the polar lipids of both species the dominating fatty acids were 16:0, 18:1(n-9), 20:5(n-3) and 22:6(n-3) (Tables 1 and 2). Polyunsaturated fatty acids (PUFA) comprised ca. 1/2 of fatty acids in *Pseudocalanus acuspes* and ca. 1/3 of those in *Acartia longiremis*.

In *Pseudocalanus acuspes* short chain fatty acids were the dominant components of wax esters and triacylglycerols, 16:0 and 18:1(n-9) being the most important throughout the year. In June 16:1(n-7) and 20:5(n-3) fatty acids were common among *P. acuspes* wax esters and triacylglycerols. The PUFA 18:4(n-3) occurred in wax esters of *P. acuspes* at all seasons. In *Acartia longiremis*, 16:0 and 18:1(n-9) dominated in the fatty acids of wax esters and triacylglycerols throughout (Table 2). In addition, PUFA such as 18:4(n-3), 20:5(n-3) and 22:6(n-3) occurred in triacylglycerols at all seasons. In June and November the most common fatty acid among *A. longiremis* triacylglycerols was 20:1(n-7).

The proportion of PUFA in the wax esters was 16 to 30% for *Pseudocalanus acuspes*, and 8 to 20% for *Acartia longiremis*. Triacylglycerols contained up to 45% PUFAs in *P. acuspes* and between 20 and 40% in *A. longiremis*.

In the fatty alcohols of wax esters 10:0 and 16:0 chains dominated in both species.

Discussion

Energy balance and seasonal variation in abundance

In some respects the seasonal cycle of *Pseudocalanus acuspes* resembles that of *Calanus finmarchicus* in Bals-

Table 1. *Pseudocalanus acuspes.* Fatty acid and fatty alcohol composition of major lipid classes in CIV to CV from November 1985 to September 1986. All data presented as percentage of total identified acids or alcohols. A plus sign denotes trace amounts (<0.5%). WE: wax esters; TAG: triacylglycerols; PL: polar lipids; Ac: fatty acid; Alc: fatty alcohol; PUFA: poly-unsaturated fatty acids; blanks: not detected. Traces not included in total sum

Fatty acids and fatty alcohols	November				February				June				September			
	WE		TAG	PL	WE		TAG	PL	WE		TAG	PL	WE		TAG	PL
	Ac	Alc			Ac	Alc			Ac	Alc			Ac	Alc		
14:0	2.9	30.4	3.7	0.9	3.5	29.4	3.2	2.0	2.5	39.0	3.6	2.2	2.6	35.6	2.1	0.7
15:0	1.8	1.4	1.2	+	+	1.8	1.3	2.0	+	1.0	0.6	1.4	0.8	0.9	+	+
16:0	2.2	59.2	21.9	14.0	4.6	57.5	16.5	17.1	3.6	51.4	16.5	19.7	2.9	56.1	21.5	22.2
16:1(n-9)								4.8			+	+				0.8
16:1(n-7)	11.3	+	6.3	1.5	13.4	+	2.5	1.7	23.3	+	13.8	1.0	9.5	0.8	6.8	0.7
16:2								1.2			4.6				+	+
16:3								+								
16:4			+				+									
17:0		+	1.5	0.7		+	1.0	1.0			0.6	0.6		+	1.1	1.6
18:0	2.0	1.7	3.2	3.7	4.2	1.8	4.9	2.6	1.1	1.4	2.3	2.3	1.4	1.5	2.1	7.3
18:1(n-9)	47.9	+	12.5	12.8	52.6	+	13.0	8.5	36.4	3.8	12.8	2.8	56.9	2.7	14.8	9.1
18:1(n-7)		3.5	3.2	2.6	2.9	4.5	2.3	1.9	1.5	1.4	3.3	2.2	1.7	1.6	2.0	3.1
18:2(n-6)	3.9		3.6	1.3	4.1		2.3	1.2	2.6		2.0	0.9	2.8		2.1	2.1
18:3(n-6)	4.3		1.1	6.1			1.8	6.0	+		+	2.3	1.1		+	4.1
18:3(n-3)	2.9		2.1	+	1.7		1.0	+	1.5		1.6	+	0.9		3.0	+
18:4(n-3)	2.7		7.0	0.8	+		2.2	0.6	3.0		4.8	1.0	0.8		12.5	0.7
20:0			+	1.0	+		1.7	+			0.8				+	0.9
20:1(n-9)		2.3	2.1	0.6	0.9	1.4	0.9			0.8	+	+	0.9	0.6	3.1	0.6
20:1(n-7)	3.4	+	11.4	3.3	+	+	23.9	3.9	+	+	1.0	2.3	0.9			3.0
20:4(n-6)			+	+	1.5			+	+		+	0.6	+		0.8	1.2
20:4(n-3)	2.9		2.0	1.1	1.7		+	1.0	1.0		1.1	+	1.2		3.0	0.6
20:5(n-3)	8.3		7.0	21.5	4.8		4.7	21.3	19.8		23.3	31.6	10.2		12.4	18.6
22:0						0.6					+					
22:1(n-11)			0.7	+				+			0.6				+	
22:1(n-9)			+	+			+	+								
22:4(n-6)				+								+				
22:5(n-3)			+					2.6			0.6	0.7			+	
22:6(n-3)	3.5		4.9	24.3	2.6		2.8	26.2	1.9		3.2	25.8	4.7		8.1	20.3
24:0						+										
24:1				1.8		0.8	2.8	1.2								1.1
Saturated	8.9	92.7	31.5	20.3	12.3	91.1	28.6	24.7	7.2	92.8	24.4	26.2	7.7	94.1	26.8	32.7
Monounsat	62.6	6.1	36.2	22.6	69.8	6.7	50.2	17.2	61.2	6.0	31.5	9.1	69.9	5.7	26.7	18.4
PUFA	28.5	0.0	27.7	55.1	16.4	0.0	18.6	56.3	29.8	0.0	41.2	62.9	21.7	0.0	41.9	47.6
Total	100.0	98.8	95.4	98.0	98.5	97.8	97.4	98.2	98.2	98.8	97.1	98.2	99.3	99.8	95.4	98.7

fjorden. Both species overwinter as juveniles that allocate energy to wax ester stores instead of to an energy-demanding maturation before winter (Figs. 1 A and 3 A; Hopkins et al. 1984, Norrbin 1987). However, *P. acuspes* does not enter true diapause (Davis 1976, 1985), but feeds omnivorously throughout the winter (Poulet 1974, 1976, Norrbin 1987). The seasonal cycle of *Acartia longiremis* can be said to mirror that of *Metridia longa*. Both species rely on omnivorous feeding instead of large energy reserves (Båmstedt et al. 1985, 1990). They also have a later start in spring reproduction than lipid-storing species (Fig. 1 B; Tande and Grönvik 1983, Norrbin 1987).

The small body size of the species under investigation here may also have constrained their adaptations to overwintering. The inverse relationship between basal metabolism and size causes small copepods to have a high metabolic rate per unit weight. Furthermore, there is limited room for lipid storage in small copepods. These stores will soon be depleted when food availability – and

quality – becomes low. During a long period of food shortage, as in northern Norwegian fjords, feeding must be a supplement to energy storage for smaller copepods. An alternative strategy to remaining in the plankton would be to overwinter as resting eggs. The fact that both *Pseudocalanus acuspes* and *Acartia longiremis* are present in the plankton during winter, and do not appear to produce resting eggs (Norrbin unpublished data), indicates that remaining in the water column is the most successful strategy for these species in this particular environment.

Storing wax ester may give *Pseudocalanus acuspes* an advantage in increased fecundity and/or egg quality in addition to an enhanced probability of individual survival. In spite of weight losses (Fig. 2 A), wax ester is still present in the maturing juveniles in February (Fig. 3 A). Gonad maturation in *P. acuspes* starts in January, i.e. during the starvation period (Norrbin 1987). In temperate waters, adult females contain considerably less lipid

Table 2. *Acartia longiremis.* Fatty acid and fatty alcohol composition of major lipid classes in females from November 1985 to September 1986. All data presented as a percentage of total identified acids or alcohols. A plus sign denotes trace amounts (<0.5%). WE: wax esters; TAG: triacylglycerols; PL: polar lipids; ac: fatty acid; alc: fatty alcohol; PUFA: poly-unsaturated fatty acids; blanks: not detected. Traces have not been included in total sum

Fatty acids and fatty alcohols	November WE		TAG	PL	February WE		TAG	PL	June WE		TAG	PL	September WE		TAG	PL
	Ac	Alc			Ac	Alc			Ac	Alc			Ac	Alc		
14:0	2.4	11.5	4.1	2.3	3.2	9.9	1.8	2.2	3.1	25.8	3.2	1.1	3.4	24.6	8.8	1.9
15:0	5.4	45.7	0.8	0.9	2.6	64.9	+	1.8	1.7	16.3	0.8	+	3.0	11.8	1.4	0.8
16:0	40.0	24.1	18.7	17.5	14.8	19.5	17.8	16.9	17.0	38.2	11.1	16.8	20.3	37.9	16.6	17.5
16:1(n-7)	8.9		3.9	2.5	14.3		4.6	1.9	14.2		4.2	1.9	13.4	+	7.0	1.6
16:2			+								0.7				4.1	
16:3			+													
16:4			+					0.8								
17:0		3.5	+	3.7			0.7	1.3			+	+		9.2	0.7	0.8
18:0	8.6	2.1	2.2	9.0	5.4	1.4	5.0	4.1	6.1	4.6	1.9	12.6	9.0	2.7	2.3	2.7
18:1(n-9)	29.5		6.8	18.6	49.0		17.3	9.9	29.0	2.4	6.2	20.4	29.4	1.6	3.8	2.6
18:1(n-7)		1.6	4.4	3.7	2.4	1.0	9.1	4.2		0.8	2.6	3.4	2.5	0.9	2.5	2.2
18:2(n-6)			5.8		3.1		6.3	2.0	2.4		3.7	0.7	2.4		3.4	1.9
18:3(n-6)	3.1		+				2.1	5.3			0.8	+	2.4		0.6	3.8
18:3(n-3)			3.3	2.6	1.5		2.2	+	1.1		2.1	0.6	0.9		2.9	1.4
18:4(n-3)			7.2	1.9			2.1	1.4	2.5		5.0	1.6			10.9	3.3
20:0		0.8	0.7	4.8				1.4		2.2	0.8	0.9		1.1	2.6	
20:1(n-9)		3.7	1.0	0.8			2.7	0.8		6.4	0.6	2.8		2.4	0.6	+
20:1(n-7)		+	22.3	0.9		1.6	6.6	4.2	1.4		37.5	0.6	1.5		1.8	2.9
20:4(n-6)			+	0.6			0.7	0.6			+				+	+
20:4(n-3)			1.1	0.6	0.9		1.9	1.1	1.0		+	+	1.0		+	+
20:5(n-3)			7.6	14.4	2.8		7.4	17.5	13.7		6.6	13.2	7.0		16.2	26.3
22:0		3.8				1.0				3.3				6.4		
22:1(n-11)	2.1		+				0.7	0.8	4.1		1.2		1.8		+	+
22:1(n-9)			0.7					+							0.9	
22:5(n-3)		0.7					1.3	1.1			+	+			0.7	0.8
22:6(n-3)			5.2	14.4			5.6	20.6	2.6		6.2	14.6	2.0		9.6	27.0
24:1		2.8		0.8			0.8	0.9			1.6	6.9		1.0	0.8	0.8
Saturated	56.4	91.5	26.5	38.2	26.0	96.7	25.3	27.7	27.9	90.4	17.8	31.4	35.7	93.7	32.4	23.7
Monounsat	40.5	8.1	39.1	27.3	65.7	3.3	41.9	21.9	48.7	9.6	53.9	36.0	48.6	5.9	17.4	10.1
PUFA	3.1	0.0	30.9	34.5	8.3	0.0	30.4	49.6	23.3	0.0	25.1	30.7	15.7	0.0	48.4	64.5
Total	100.0	99.6	96.5	100.0	100.0	100.0	97.6	99.2	99.9	100.0	96.8	98.1	100.0	99.6	98.2	98.3

than do Stage V copepodids (Norrbin unpublished data), which suggests that lipids are used for the final stages of gonad maturation. Wax ester stores are reported to be important for maturation and egg production in many calanoid copepods (Benson et al. 1972, Lee et al. 1972, Lee 1974, Båmstedt 1979, Gatten et al. 1980, Sargent et al. 1981).

Species of *Acartia*, in general, have a higher fecundity than *Pseudocalanus* species (see e.g. Corkett and Zillioux 1975), but are more dependent on a constant food supply (e.g. Dagg 1977). Weight losses (Fig. 2A) probably reduce the fecundity of overwintering *A. longiremis* females to some extent, but egg production is resumed in March to April (Norrbin 1987).

calanus acuspes nor in *Acartia longiremis*. The next generation of *P. acuspes* copepodids (which have, by September, been developing for more than 1 mo according to information in Corkett and McLaren 1978) have put most of their surplus energy into lipid stores and little into gonad development (Norrbin 1987). This lipid is probably used for maturation, beginning in January and proceeding until April (Norrbin 1987). In *A. longiremis*, there are some stores of triacylglycerols, but these are short term lipid stores, likely to be used as a buffer against starvation rather than for maturation. Full maturity and the production of eggs does not occur in this species until a good supply of phytoplankton is available in April (Norrbin 1987).

Lipid class composition

The proportion of polar lipid is highest and reserves of wax esters at their lowest in June (Fig. 3). This is the season of rapid growth and development, and little of the ingested energy is allocated to reserves, neither in *Pseudo-*

Fatty acid composition

The dominant fatty acids of the wax esters in these two small copepod species are notably different from those presented for *Calanus finmarchicus* from Balsfjorden, (collected in October, January, March and June 1982 to

1983; Falk-Petersen et al. 1987), and from *Calanus* spp. (in adjacent fjords and seas; Clarke et al. 1987, Falk-Petersen et al. 1987, Tande and Henderson 1988). The main difference is the dominance of shorter chain fatty acids in small copepods. In the fatty alcohols, the difference in chain length becomes even more striking; *Pseudocalanus acuspes* and *Acartia longiremis* have predominately 14 to 16 carbon chains, while *Calanus* spp. have high proportions of 20:1(n-9) and 22:1(n-11) (Clarke et al. 1987, Falk-Petersen et al. 1987, Tande and Henderson 1988). Polar lipids, however, seem to have a similar composition in all calanoids (Ackman et al. 1974, Lee 1974, Lee et al. 1974, Sargent and Whittle 1981, Clarke et al. 1987, Tande and Henderson 1988).

Lee et al. (1974) suggest that well nourished copepods incorporate dietary fatty acids without modifications. If this is true for the species in this study, then the best indications of dietary input would be found in June and September. During this time, 16:0, 16:1(n-7), 18:1(n-9) and 20:5(n − 3) fatty acids are common in wax esters and triacylglycerols of *Pseudocalanus acuspes* and *Acartia longiremis*.

The fatty acid composition in the two species in this study is most similar to that of the omnivore *Metridia longa* in Balsfjorden (Falk-Petersen et al. 1987) and the carnivore *Euchaeta japonica* in the Pacific (Lee et al. 1974). These display the same dominance of 16:0 and 18:1 (n-9) fatty acids in wax esters and triacylglycerols (only presented for *E. japonica*; Lee et al. 1974). They also have a dominance of 14:0 and 16:0 fatty alcohols.

From the above account we may conclude that insofar as fatty acids reflect dietary input (Sargent et al. 1981, 1985, Falk-Petersen et al. 1987), small copepods display a less strictly herbivorous feeding pattern than do *Calanus* species in high latitude environments.

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