Lipids of North Atlantic krill

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Abstract The seasonal variations in the total lipid content, lipid class composition, fatty acid composition, and fatty alcohol composition of *Meganyctiphanes norvegica* (M. Sars), *Thysanoessa inermis* (Krøyer), and *T. raschii* (M. Sars) have been examined. The total lipid content was highest in the autumn and early winter months and lowest in the spring. In *M. norvegica*, triacylglycerols served as the only depot lipids, whereas in *T. inermis* and *T. raschii* triacylglycerols, wax esters, and glycerophospholipids varied in proportion to the total lipid content. This suggests that glycerophospholipids, as well as wax esters and triacylglycerols, constitute depot lipids in these species. Wax esters and glycerophospholipids were the dominating depot lipids in *T. inermis*, whereas triacylglycerols and glycerophospholipids were most important in *T. raschii*. Results suggest that non-depot glycerophospholipids may constitute 3.5–4.5% of the dry weight of the three species of krill examined. *T. inermis* and *T. raschii*, from the same catches, had very similar fatty acid compositions for each of the major lipid classes, with the exception of a few minor fatty acids. The major lipid classes in all three species showed complex seasonal variations in the content of the fatty acids that typically reflect the diet, particularly in the case of the triacylglycerols. The results suggest that all the species examined are more herbivorous during the summer than during the autumn and winter. *M. norvegica* seemed to be significantly more carnivorous than the two *Thysanoessa* species. The degree of incorporation of individual fatty acids from the diet is probably specific for each lipid class in each krill species. The proportion of polyenoic fatty acids in the glycerophospholipids and the proportion of monoenoic fatty acids in the wax esters may be of importance for the temperature adaptation of *T. inermis* and *T. raschii*. —**Saether, O., T. E. Ellingsen, and V. Mohr.** Lipids of North Atlantic krill. *J. Lipid Res.* 1986. **27:** 274–285.

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The deposition of large amounts of lipids as an energy reserve is frequently encountered in aquatic animals, including marine mammals (1, 2), fishes (2, 3), and crustaceans (2, 4–8). The storage lipids occurring most commonly in such systems are triacylglycerols, although high levels of wax esters are occasionally found in certain species, particularly in pelagic crustaceans such as copepods (2, 4–8).

Ellingsen and co-workers (7–9) have recently established that glycerophospholipids and triacylglycerols, either alone or together with wax esters, occur as depot lipids in two different species of Antarctic krill. Antarctic krill may accumulate large amounts of glycerophospholipids. Ellingsen (8) has reported that these lipids represent up to 12% of the dry weight of the animal in periods of abundant food during the antarctic summer. The lipid reserves seem to be depleted during the antarctic winter. The reason why glycerophospholipids serve as storage lipids in Antarctic krill is not understood, but may be associated with the need for rapid mobilization of lipid and the particular demands placed on the physical properties of the lipid reserves of these crustaceans living at exceptionally low water temperatures (7, 8).

The role of glycerophospholipids as depot lipids in Antarctic krill is the first example of this class of lipids having functions other than being an essential non-depot lipid in biological membranes and mediating transport of fatty acids in animal organisms. As a consequence, the function of glycerophospholipids as storage lipids in Antarctic krill is of considerable biological interest.

The fatty acid composition of the lipids of different species of North Atlantic and Antarctic krill has already been published (6, 8, 10, 11). However, the seasonal variations in the fatty acid and fatty alcohol composition of the main classes of lipid have not as yet been studied in detail. The present study was undertaken to provide a better understanding of the lipid deposition, lipid metabolism, and fatty acid and fatty alcohol composition of the main classes of lipid in three common species of North Atlantic krill, *Meganyctiphanes norvegica, Thysanoessa inermis* and *T. raschii*.

We wish to report that the role of glycerophospholipids as an energy reserve is not limited to Antarctic krill; a similar situation exists also in certain species of North Atlantic krill. Further, we provide evidence that special fatty acid markers, in the different lipid classes, reflect herbivorous or carnivorous feeding habits, and that the unsaturation of glycerophospholipids and wax esters may also be influenced by the environmental temperature.

Abbreviation: GLC, gas-liquid chromatography.

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MATERIALS AND METHODS

Specimens

The studies were carried out on samples of *M. norvegica, T. inermis,* and *T. raschii* caught in the Trondheim Fjord in the central part of Norway (63°26'N, 10°46'E and 63°47'N, 11°25'E) and the Bals Fjord (69°21'N, 19°06'E) and the Ulls Fjord (69°40'N, 19°47'E) in northern Norway. In the Trondheim Fjord, *M. norvegica* was caught using an Isaacs-Kidd midwater trawl with a plankton net (opening 1 × 1 m, mesh size 5–6 mm, trawl speed 4 knots, trawl time 0.5–1 hr). The krill were detected by a 60 kHz sonar.

In the Bals Fjord and the Ulls Fjord, *M. norvegica, T. inermis* and *T. raschii* were caught using a capelin trawl with a plankton net (opening 3 × 3 m, mesh size 5–6 mm, trawl speed 4–5 knots, trawl time 1 hr). Krill swarms were detected by a 60 kHz and a 120 kHz sonar. Data on the krill catches are given in **Table 1**.

The krill were drained for 2–3 min and frozen within 5–15 min after catching. Freezing was carried out in a specially designed CO_2-ice plate freezer where polythene bags containing krill were placed between aluminum boxes filled with CO_2-ice in the manner described by Ellingsen (8). It has been shown that the temperature in the middle of the krill block dropped from 0 to −3°C within 1 min, and to −60°C within 5–7 min (8). The krill blocks were stored at −80°C for no longer than 1 year before being used experimentally.

Extraction and separation of lipid

Frozen blocks containing unsorted *T. inermis* and *T. raschii* were placed at room temperature, and when the temperature reached −5 to −2°C the samples were subjected to total lipid extraction with chloroform–methanol–water in accordance with Hardy and Keay (12). In separate studies the two types of *Thysanoessa* were sorted after being thawed. Frozen blocks of krill were placed at room temperature until the temperature reached −5 to 0°C. The krill were then transferred to polythene bags in an ice-water bath where individual krill were separated. Each animal was subsequently refrozen on a block of CO_2-ice. Krill belonging to the same species and haul were pooled, homogenized in the frozen state using an Ultra-Turrax TP 18-10 (Janke and Kunkel KG), and subsequently subjected to total lipid extraction. Individual specimens of *M. norvegica* and *Thysanoessa* species were also dissected on a block of CO_2-ice into fractions comprising the abdomen and thorax, respectively. Corresponding tissue fractions from about 20 specimens of *M. norvegica* and about 50 specimens of *Thysanoessa* were pooled for the extraction of total lipid.

TABLE 1. Data on the krill catches

Haul No.	Date	Locality	Krill Species	Female krill (%)	Male krill (%)	Total Lipid (% of the dry weight)
2	18.05.81	Hommelvik, Trondheim Fjord	*M. norvegica*	100	0	13.2
2	18.05.81	Hommelvik, Trondheim Fjord	Thorax of *M. norvegica*			15.8
2	18.05.81	Hommelvik, Trondheim Fjord	Abdomen of *M. norvegica*			9.1
7	15.09.81	Verdal, Trondheim Fjord	*M. norvegica*	45	55	24.0
10	16.09.81	Verdal, Trondheim Fjord	*M. norvegica*	50	50	22.5
15	09.12.81	Hommelvik, Trondheim Fjord	*M. norvegica*	45	55	33.7
16	09.12.81	Hommelvik, Trondheim Fjord	*M. norvegica*	30	70	24.2
21	23.02.82	Svartnes, Bals Fjord	*T. inermis*			35.3
21	23.02.82	Svartnes, Bals Fjord	*T. raschii*			27.6
21	23.02.82	Svartnes, Bals Fjord	Unsorted *Thysanoessa*[a]			33.1
21	23.02.82	Svartnes, Bals Fjord	Thorax of unsorted *Thysanoessa*[a]			45.1
21	23.02.82	Svartnes, Bals Fjord	Abdomen of unsorted *Thysanoessa*[a]			15.8
22	24.02.82	Svartnes, Bals Fjord	*M. norvegica*	30	70	28.7
23	22.03.82	Ulls Fjord	*M. norvegica*			26.0
24	23.03.82	Svartnes, Bals Fjord	*T. inermis*			28.3
24	23.03.82	Svartnes, Bals Fjord	*T. raschii*			19.9
24	23.03.82	Svartnes, Bals Fjord	Unsorted *Thysanoessa*[b]			25.5
27	20.04.82	Ulls Fjord	*M. norvegica*			22.7
28	21.04.82	Svartnes, Bals Fjord	*T. inermis*			14.9
28	21.04.82	Svartnes, Bals Fjord	*T. raschii*			11.7
28	21.04.82	Svartnes, Bals Fjord	Unsorted *Thysanoessa*[b]			13.9
28	21.04.82	Svartnes, Bals Fjord	Abdomen of unsorted *Thysanoessa*[b]			8.9
30	29.07.83	Svartnes, Bals Fjord	*T. inermis*			36.2
30	29.07.83	Svartnes, Bals Fjord	*T. raschii*			33.8
31	02.11.83	Ulls Fjord	*T. inermis*			50.0
31	02.11.83	Ulls Fjord	*T. raschii*			43.9

[a] Mixture of 70% *T. inermis* and 30% *T. raschii*.
[b] Mixture of 80% *T. inermis* and 20% *T. raschii*.

The main classes of lipid were separated by thin-layer chromatography in accordance with Ellingsen (8), as described by Saether, Ellingsen, and Mohr (9). Dry weights were determined by drying 1–2 g of homogenate for 24 hr at 105°C.

Determination of fatty acids in the main classes of lipid

Saponification, acetylation, and methylation were carried out as described by Ellingsen (8). The triacylglycerol and glycerophospholipid fractions were saponified in 0.5 M NaOH in methanol, and subsequently methylated using 12% BF_3 in methanol. The free fatty acid fraction was methylated without prior saponification. After methylation, a saturated solution of NaCl was added to the fractions, and the fatty acid methyl esters were extracted with *n*-hexane. The cholesteryl ester and wax ester fractions were saponified in 0.5 M NaOH in methanol. The reaction mixture was subsequently extracted with *n*-hexane, and the extracts were acetylated with acetic anhydride dissolved in pyridine. The acetylated fatty alcohols were extracted with *n*-hexane. The residues, after *n*-hexane extraction of the saponified wax ester and cholesterol/diacylglycerol fractions, were acidified with 6 M HCl and extracted with diethyl ether. The diethyl ether extract was evaporated to dryness and methylated using 12% BF_3 in methanol. The fatty acid methyl esters were finally extracted with *n*-hexane.

The fatty acid methyl esters and fatty alcohol acetates were determined both by packed column and capillary gas–liquid chromatography. The packed column GLC analyses were done using a Perkin Elmer Sigma 1 gas chromatograph equipped with a flame ionization detector. The 6-ft long stainless steel column was packed with 10% SP-2330 on 100–120 mesh Chromosorb W AW (Supelco), and nitrogen was used as carrier gas. The analytical conditions were as follows: carrier gas flow, 30 ml/min; column temperature, 170–210°C; temperature gradient, 3°C/min; injector temperature, 230°C; detector temperature, 230°C; hydrogen pressure, 1.1 kg/cm^2; and air pressure, 2.1 kg/cm^2. The concentration of the components was calculated automatically by the Perkin Elmer Sigma 1 computer. The capillary GLC analyses were carried out using a Carlo Erba Fractovap 2900 gas chromatograph equipped with a CP-sil 88 glass capillary column (Chrompack), on-column injection, and flame ionization detector. The analyses were done with helium as carrier gas under the following conditions: column temperature, 60–160°C (gradient 25°C/min) and 160–200°C (gradient 1°C/min); detector temperature, 230°C; carrier gas pressure, 1.1 kg/cm^2; hydrogen pressure, 0.5 kg/cm^2; air pressure, 1 kg/cm^2. The concentrations were calculated by a Shimadzu Chromatopack C-R3A computing integrator. Standards were supplied by Nu-Chek-Prep.

RESULTS

Biological data and total lipid content

The biological data on the three species of North Atlantic krill examined, *M. norvegica*, *T. inermis*, and *T. raschii*, are given in Table 1, **Table 2**, and **Table 3**. Based on the relationship between length and sexual maturity of krill, as discussed Mauchline and Fisher (13) and Falk-Petersen and Hopkins (14), it appeared that a majority of the krill examined in the present study were sexually mature.

The proportion of males and females in catches of *M. norvegica* was determined. The results showed that males and females occurred in about equal proportions during the autumn and winter, whereas females possibly dominated in the spring (Table 1). The catches of *Thysanoessa* species were not examined with respect to sex distribution.

In all three krill species examined, the total lipid content was highest in the autumn and early winter months and lowest in the spring. The total lipid content of *T. inermis* was 15 to 50% on a dry weight basis; in *T. raschii* it constituted 12 to 44%, and in *M. norvegica* 13 to 34% of the dry weight (**Fig. 1**).

Variations in lipid class composition

The relationship between the content of the main classes of lipid and the total lipid content of the krill was examined. In *M. norvegica*, triacylglycerols, glycerophospholipids, and sterols (most probably cholesterol, c.f., Discussion) were the major lipids, but only the triacylglycerol content varied in proportion to the total lipid content (**Fig. 2**). The glycerophospholipids, cholesterol, free fatty acids, and wax ester contents constituted 4.6, 1.2, 0.6, and 0.6% of the dry weight, respectively (Fig. 2). Regression curves and correlation coefficients for the content of the main classes of lipid as a function of total lipid content in *M. norvegica* are presented in **Table 4**.

In *T. inermis* and *T. raschii*, glycerophospholipids, triacylglycerols, wax esters, and sterols (most probably cholesterol) were the predominate lipids. The glycerophospholipid, triacylglycerol, and wax ester contents varied in proportion to the total lipid content, whereas the content of cholesterol and free fatty acids was fairly constant,

TABLE 2. Length frequency distributions of *M. norvegica*

Species	Haul No.	Number of Specimens Measured	Length Groups (mm)				
			<20	21–25	26–30	31–35	>36
			%				
M. norvegica	2	8	0	38	38	25	0
M. norvegica	23	36	22	31	22	22	3
M. norvegica	27	24	0	8	4	63	25

TABLE 3. Length frequency distributions of *T. inermis* and *T. raschii*

Krill Species	Haul No.	Number of Specimens Measured	Length Groups (mm)		
			<14	15–18	>19
				%	
T. inermis	21	58	2	79	19
T. inermis	24	61	21	79	0
T. inermis	28	63	30	70	0
T. inermis	31	56	25	52	23
T. raschii	21	22	0	68	32
T. raschii	24	16	25	69	6
T. raschii	28	17	29	71	0
T. raschii	31	47	15	57	28

1.5 and 0.6% of the dry weight, respectively (**Fig. 3, Fig. 4**, and **Fig. 5**). Regression curves and correlation coefficients are presented in Table 4. The correlations describing the content of individual lipid classes of unsorted *Thysanoessa* species and *M. norvegica* also include the data referring to different body fractions (Figs. 2 and 3).

Fatty acid and fatty alcohol composition

The fatty acid and fatty alcohol compositions of the lipids of different species of North Atlantic krill were analyzed by packed column GLC. Most of the samples were also analyzed by capillary GLC. Both methods gave similar results, with the exception of the fatty acids 18:3, 18:4, 20:1, 20:4, and 22:1, which were difficult to compute in the packed column GLC analysis due to poor resolution. Isomers of the different fatty acids were not separated in the packed column GLC analysis. For the samples analyzed by both capillary GLC and packed column GLC, only the data obtained by capillary GLC are presented. The fatty acid isomers identified in the present work are in accordance with the major fatty acids presented by Ackman et al. (4). The methylation yields of the different samples were 62% ± 2% for glycerophospholipids, 97% ± 4% for triacylglycerols, and about 50% for wax esters. Acetylation of the cholesterol/diacylglycerol fraction gave a yield of 103% ± 25%. The free fatty acid fractions were too small to measure methylation yields.

The fatty acid compositions of the total lipids of *T. inermis* and *T. raschii* from the same haul were very similar, as can be calculated from the data in Table 4 and **Table 5**. In both *Thysanoessa* species, the proportion of the fatty acids 16:1 (n-7), 18:1 (n-7), 20:1 (n-9), 22:1 (n-11), and 22:6 (n-3) showed seasonal variations. The lipids of *M. norvegica* contained a considerably higher proportion of 20:1 (n-9) and 22:1 (n-11) and a much lower proportion of 20:5 (n-3) and 18:1 (n-7) + (n-9) than the lipids of the *Thysanoessa* species. The fatty acid composition of the total lipid was similar in both catches of *M. norvegica*.

The fatty acid composition of the different main classes of lipid was examined in detail (Table 5). The principal saturated fatty acid was 16:0 in all major lipid classes of the different species of krill. In *T. inermis* and *T. raschii* it was most abundant in the triacylglycerol and glycerophospholipid fractions, in which it accounted for 10–30% of the fatty acids. The wax esters contained less than 10% of 16:0. In *M. norvegica*, 16:0 made up 10–15% of the fatty acids of the triacylglycerol and glycerophospholipid fractions. Also 14:0 was found in significant amounts in the triacylglycerols of all three krill species, but it was almost absent in the other lipid classes.

The monounsaturated fatty acids 16:1 (n-7), 18:1 (n-7), and 18:1 (n-9) were very abundant in all krill species, and in all major lipid classes. The content of 18:1 (n-9) was especially high in the wax esters of *T. inermis* and *T. raschii*, accounting for 40–60% of the fatty acids of the wax ester fraction. In *M. norvegica* the fatty acids 20:1 (n-9) and 22:1 (n-11) were the dominating monounsaturated fatty acids in the triacylglycerol fraction, and the content of 18:1 (n-7) was low compared to that in *T. inermis* and *T. raschii*. In both species of *Thysanoessa* the contents of 20:1 (n-9) and 22:1 (n-11) were rather low in all major lipid classes.

In general, the glycerophospholipid fraction contained a much higher proportion of unsaturated fatty acids than the other major lipid fractions. The polyunsaturated fatty acids 20:5 (n-3) and 22:6 (n-3) constituted 40–55% of the fatty acids in the glycerophospholipid fraction. These polyunsaturated fatty acids accounted for less than 10% of the triacylglycerol fatty acids in all three species examined, and less than 12% of the fatty acids in the wax ester fractions of *T. inermis* and *T. raschii*.

The lipid compositions of *M. norvegica* and of unsorted *Thysanoessa* species are probably very close to that of living krill, because these specimens were not subjected to thawing and refreezing before analyses, as was the case with

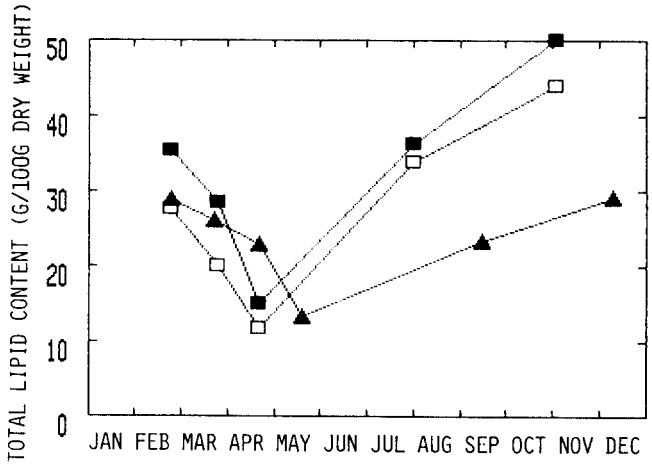

Fig. 1. Seasonal variation in the total lipid content of *T. inermis* (■), *T. raschii* (□), and *M. norvegica* (▲). The data refer to *T. inermis* and *T. raschii* from the Bals Fjord (catch Nos. 21, 24, 30, and 31) and *M. norvegica* from the Bals Fjord (catch No. 22), from the Ulls Fjord (No. 23 and 27) and from the Trondheim Fjord (No. 2, mean values of No. 7 and 10 and No. 15 and 16) (Table 1).

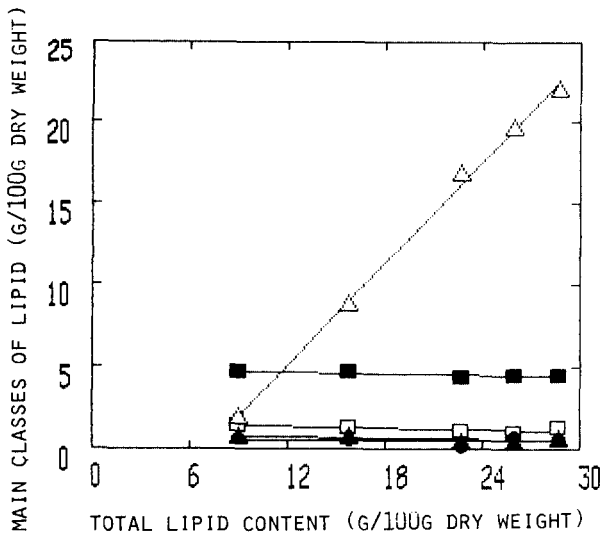

Fig. 2. Relationship between total lipid content and content of main classes of lipid in whole krill and body fractions of *M. norvegica*. The data refer to whole krill (catch Nos. 22, 23 and 27) as well as thorax and abdomen of krill (catch No. 2) (c.f., Table 1). Wax esters, (●); triacylglycerols, (△); free fatty acids, (▲); cholesterol + diacylglycerols, (□); glycerophospholipids, (■).

the sorted *T. inermis* and *T. raschii*. The percentage of 20:1 + 18:4 in the free fatty acid fraction of unsorted *Thysanoessa* species was considerably higher than in any of the depot lipids, but the other free fatty acids represented a composition somewhat intermediate to those of the wax esters, triacylglycerols, and glycerophospholipids (**Table 6**). In *M. norvegica*, the free fatty acid composition represented an intermediate of the composition of the glycerophospholipid and the triacylglycerol fraction, with 16:0, 18:1 (n-9), 20:1 (n-9), 20:5 (n-3), and 22:6 (n-3) as the major fatty acids (Table 5).

Analyses of the fatty alcohols of the wax ester fractions of *T. inermis* and *T. raschii*, caught in April and July, revealed that the major fatty alcohols were 14:0, 16:0, and 18:0, which accounted for 56–93% of the wax alcohols (**Table 7**). In November, however, *T. raschii* contained a considerably lower proportion of 18:0, and a higher proportion of 20:1 and 22:1.

DISCUSSION

The catches of *M. norvegica* examined in the present work were obtained from fjords at widely different latitudes, and included samples that reflected seasonal variations. In the case of *T. inermis* and *T. raschii*, the material was obtained at different times of the year from fjords at nearly the same latitude (Table 1). Thus, there was considerable span in the material examined. Results revealed that the catches of *M. norvegica* obtained in the Trondheim Fjord contained about equal proportions of males and females, except in May, when females seemed to dominate. The dominance of females during spring could be related to breeding mortality of males as discussed by Mauchline and Fisher (13). The *Thysanoessa* species were not examined with respect to the sex ratio, but Falk-Petersen and Hopkins (14) have reported a dominance of female *T. inermis* and *T. raschii* during summer and about equal proportions of males and females during the rest of the year.

Studies of both Antarctic (8) and North Atlantic krill (15) have shown that there is an extremely rapid and extensive production of free fatty acids post mortem. Thus, the level of free fatty acids may provide an effective measure of the state of the material analyzed. In the present study, special precautions were taken to avoid post mortem

TABLE 4. Regression curves and correlation coefficients for the relationship between the content of the main classes of lipid and total lipid content (TL)

Krill Species		Lipid Class Content (g/100 g dry weight)	Correlation Coefficient r^2
M. norvegica	Wax esters	= 0.50 − 0.000 × TL	−0.01
	Triacylglycerols	= −7.49 + 1.040 × TL	1.00
	Free fatty acids	= 0.80 − 0.012 × TL	−0.64
	Cholesterol	= 1.47 − 0.016 × TL	−0.67
	Glycerophospholipids	= 4.71 − 0.012 × TL	−0.75
T. inermis	Wax esters	= −2.49 + 0.410 × TL	1.00
	Triacylglycerols	= −0.80 + 0.222 × TL	0.99
	Free fatty acids	= 0.60 + 0.015 × TL	0.58
	Cholesterol	= 2.43 − 0.022 × TL	−0.39
	Glycerophospholipids	= 0.28 + 0.373 × TL	0.97
T. raschii	Wax esters	= −1.29 + 0.248 × TL	0.95
	Triacylglycerols	= −2.29 + 0.404 × TL	0.98
	Free fatty acids	= 1.18 + 0.002 × TL	−0.06
	Cholesterol	= 1.46 − 0.031 × TL	0.80
	Glycerophospholipids	= 1.04 + 0.315 × TL	0.99

The data were derived from Fig. 2 (*M. norvegica*), Fig. 4 (*T. inermis*), and Fig. 5 (*T. raschii*).

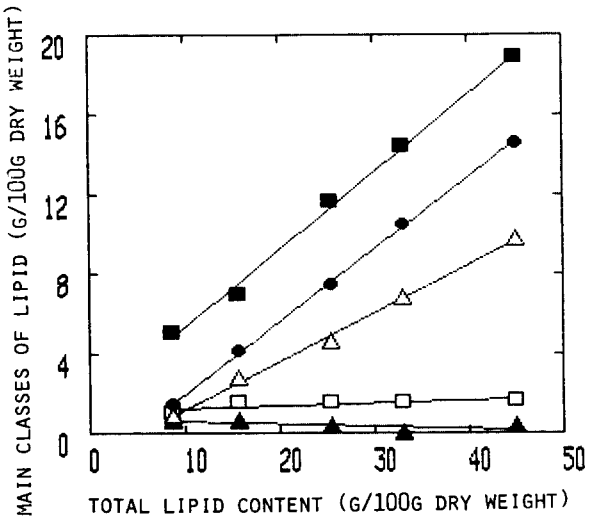

Fig. 3. Relationship between total lipid content and content of main classes of lipid in whole krill and body fractions of the *Thysanoessa* species. The catches contained about 70–80% *T. inermis* and 20–30% *T. raschii*. The data refer to whole krill (catch Nos. 21 and 24), abdomen of krill (catch Nos. 21 and 28) and thorax of krill (catch No. 21) (c.f., Table 1). Wax esters, (●); triacylglycerols, (△); free fatty acids, (▲); cholesterol + diacylglycerols, (□); glycerophospholipids (■).

lipolysis in the krill (c.f., Methods), and analysis of the best preserved samples of *M. norvegica* and the *Thysanoessa* species suggest a free fatty acid content of 0.6% of the dry weight or less in living krill. An increase in the content of freey fatty acids of about 0.6% of the dry weight in sorted *T. inermis* and *T. raschii*, as compared to unsorted samples, is most likely due to post mortem lipolysis during sorting.

The low free fatty acid contents found in the different species of North Atlantic krill examined in the present work contrast with the results of Ackman et al. (4) and Sargent and Falk-Petersen (6), who reported values in the range of 2–8% of the dry weight.

Seasonal variations in total lipid content

The total lipid content of krill may be influenced by several factors including food supply, sex, maturity, spawning, season, and locality (7, 8). All three species of krill examined in the present work accumulated lipid during the summer, autumn, and early winter when food is abundant and depleted their lipid reserves during the late winter and spring when food is scarce. As a consequence, the food supply may be of major importance for the variations in the total lipid content of krill examined in the present study. These seasonal changes in total lipid content are in accordance with the results presented by Falk-Petersen (16).

T. inermis and *T. raschii* are held to be mainly herbivorous, whereas *M. norvegica* is probably more omnivorous or carnivorous (16). The *Thysanoessa* species may therefore starve for periods during late winter due to lack of phytoplankton. As a result, it may be advantageous for the *Thysanoessa* species to deposit large amounts of lipids during periods of an abundance of food, which is consistent with the observation that *T. inermis* and *T. raschii* have a higher lipid content than *M. norvegica* during the autumn and early winter.

Depot lipids

The deposition of triacylglycerols, and the lack of wax esters as depot lipids in *M. norvegica* may reflect carnivorous feeding habits (6, 17). By extrapolating the experimental data in Fig. 2, it can be shown that the triacylglycerol content reaches zero at a total lipid content of about 7.2% of the dry weight, which probably represents the lowest possible total lipid content of *M. norvegica*. The glycerophospholipids did not show any significant variation with total lipid content and constituted about 4.6% of the dry weight. The content of wax esters was very low (Fig. 2), which is in accordance with the data reported by Sargent and Falk-Petersen (6), who suggested that the traces of wax esters in *M. norvegica* might stem directly from undigested calanoids.

In both of the *Thysanoessa* species examined, the triacylglycerol, wax ester, and glycerophospholipid contents all varied in proportion to the total lipid content (Figs. 4 and 5 and Table 4). As a result these three lipid classes should all be regarded as depot lipids in the *Thysanoessa* species. In the case of glycerophospholipids, the content of this class of lipids attained levels that are far in excess of those normally associated with glycerophospholipids in structural membranes in animals. The results presented in Figs. 4 and 5 show that wax esters and glycerophospho-

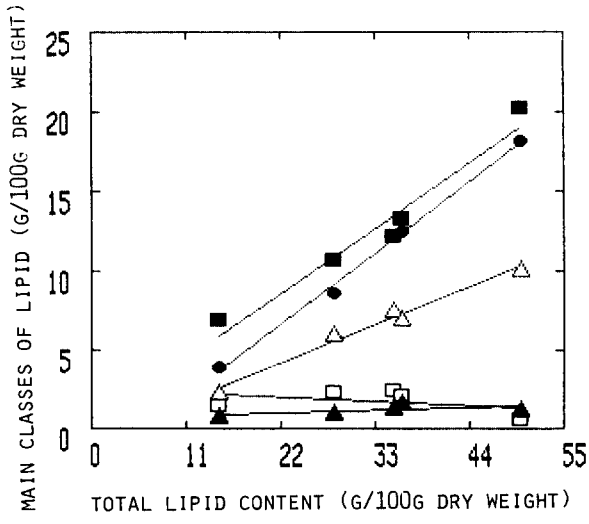

Fig. 4. Relationship between total lipid content and content of main classes of lipid in *T. inermis*. The data refer to catch Nos. 21, 24, 28, 30, and 31 (c.f., Table 1). Wax esters, (●); triacylglycerols, (△); free fatty acids, (▲); cholesterol + diacylglycerols, (□); glycerophospholipids, (■).

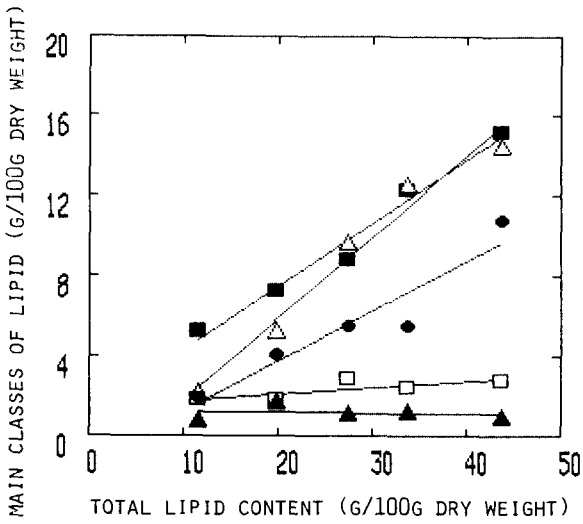

Fig. 5. Relationship between total lipid content and content of main classes of lipid in *T. raschii*. The data refer to catch Nos. 21, 24, 28, 30, and 31 (c.f., Table 1). Wax esters, (●); triacylglycerols, (△); free fatty acids, (▲); cholesterol + diacylglycerols, (□); glycerophospholipids, (■).

lipids are more important as depot lipids than triacylglycerols in *T. inermis*, whereas triacylglycerols and glycerophospholipids are the two most important in *T. raschii*. The finding that wax esters in *T. inermis* and triacylglycerols in *T. raschii* are the most important depot lipids corresponds to data presented by Falk-Petersen et al. (17) and Sargent and Falk-Petersen (6). It has been suggested that the deposition of wax esters indicates a herbivorous nature for the two *Thysanoessa* species (6).

When extrapolating the experimental data in Figs. 3–5, it can be shown that both triacylglycerol and wax ester concentrations reach zero at about the same total lipid content (5.5% of the dry weight) for both *T. inermis* and *T. raschii*. Consequently, this value probably represents the lower limit for the total lipid content of the two *Thysanoessa* species. The same lower limit for total lipid content has been reported for the Antarctic krill *Euphausia superba* (7, 8). From the present data it may be concluded that *T. inermis* and *T. raschii* start depositing triacylglycerols, wax esters, and glycerophospholipids at the minimum total lipid content, but that each of these lipid components is laid down and utilized at a different rate. It can be shown by extrapolation that the amount of glycerophospholipid corresponding to zero content of triacylglycerols and wax esters, which probably represents non-depot glycerophospholipids, is about 3.5% of the dry weight in unsorted samples of the *Thysanoessa* species. This is the same content as in the Antarctic krill *E. superba* (7, 8), but somewhat lower than in *M. norvegica*, which contained 4.6% glycerophospholipid. Examination of sorted *T. inermis* and *T. raschii* indicated the same level of non-depot glycerophospholipid in both species. The somewhat lower content of glycerophospholipids of sorted, compared to unsorted *Thysanoessa* species, may be explained by a minor hydrolysis of these lipids in the sorted material. The decrease in the content of glycerophospholipids during sorting corresponds with the increase in the content of free fatty acids. A glycerophospholipid content of 3.5–4.6% of the dry weight is consistent with the level of these lipids in membranes reported for fish muscle (3).

A linear increase in the amount of depot lipids with increasing total lipid content, as shown by Figs. 4 and 5, has not as yet been reported for North Atlantic krill. However, Ellingsen and Mohr (7) and Ellingsen (8) have established such relationships for the Antarctic krill *E. superba*, and they concluded on this basis that both triacylglycerols and glycerophospholipids constitute depot lipids in this species.

The correlations relating the content of the main classes of lipid to the total lipid content seem to apply to krill irrespective of sex, season, and geographic origin of the catch. Analyses of different body fractions of the *Thysanoessa* species and *M. norvegica* show that the correlations are also valid for different body fractions of the krill (Figs. 2 and 3). A similar situation has already been reported for the Antarctic krill *E. superba* (9). The present correlations imply that triacylglycerols, glycerophospholipids, and wax esters are laid down and are utilized, respectively, when the *Thysanoessa* species build up or deplete their lipid reserves; whereas in *M. norvegica*, only the triacylglycerol content varies in proportion with the total lipid content.

The suggestion has been made that marine crustacea use wax esters more slowly than other storage lipids during periods of starvation (11, 18, 19). If this is correct, one would expect to find a relative increase in the proportion of wax esters in the two species of *Thysanoessa* during starvation in the late winter months. However, this situation would be incompatible with the proportional variation in the content of wax esters, triacylglycerols, and glycerophospholipids with the total lipid content, which has been clearly established in this work. Consequently, the proposals made in the literature regarding the utilization of wax esters in *T. inermis* and *T. raschii* during starvation do not find support in the results of the present work.

An examination of the methylation and acetylation yields obtained for the different main classes of lipid suggest that sterols are the dominant components in the cholesterol + diacylglycerol fraction, and that the glycerophospholipid fraction contains only minor amounts of other lipid classes. The dominance of sterols in the cholesterol + diacylglycerol fraction of the *Thysanoessa* species (haul 24) was confirmed by 400 MHz H-NMR analysis, which indicated the presence of less than 10% diacylglycerols in this fraction and suggested that cholesterol most probably was the dominant sterol (unpublished work). The methylation and acetylation yields for the wax ester fraction of *T. raschii* and *T. inermis* suggest a negligible hydrocarbon content. An examination of the wax ester

TABLE 5. Fatty acid composition of the main classes of lipid of *M. norvegica*, *T. inermis*, and *T. raschii*

Haul No.	Krill Species	Lipid Class	Fatty Acids (% of total) 14:0	16:0	18:0	16:1 n-7	18:1 n-9	18:1 n-7	20:1 n-9	22:1 n-11	22:1 n-9	18:2	18:3	18:4	20:4 n-3	20:5 n-3	22:6	Sum
21	*T. raschii*	TG	8.6	30.2	8.8	8.1	14.4	8.0	0	1.7	0	2.3	0.7	2.9	0.7	4.5	1.0	91.9
28	*T. inermis*	TG	3.4	28.5	4.5	8.1	9.7	10.8	0.9	0.9	0	2.5	1.2	10.8	0.9	6.4	1.9	89.0
28	*T. raschii*	TG	2.9	23.4	4.3	6.3	16.2	10.1	2.6	2.1	0.1	2.7	1.3	8.6	0.8	7.5	2.5	90.0
30	*T. inermis*	TG	4.1	30.3	4.9	15.7	8.1	13.1	0.7	0.6	0.1	1.5	0.6	4.6	0.3	5.6	1.1	90.7
30	*T. raschii*	TG	4.9	29.6	4.0	13.5	16.2	11.7	0.9	0.7	0	1.4	0.6	2.7	0.2	5.3	1.1	92.5
31	*T. inermis*	TG	4.2	28.6	2.5	9.7	9.0	11.8	3.8	4.9	0.2	1.5	1.3	4.8	0.3	6.1	1.6	89.6
31	*T. raschii*	TG	8.0	28.8	2.2	10.2	12.9	9.6	3.1	3.8	0.2	1.2	1.0	2.7	0.2	5.6	1.4	88.2
21	*T. raschii*	PG	0.9	23.2	3.2	2.1	8.5	6.3	0	0	0	1.8	1.1	3.5	0.4	29.6	15.3	95.9
28	*T. inermis*	PG	0.4	16.7	2.3	1.2	9.3	5.4	0.7	0.8	0	1.9	1.1	4.0	0.2	26.8	23.1	93.5
28	*T. raschii*	PG	0.1	10.9	2.1	0.7	7.8	6.4	0.8	0.8	0	2.0	0.9	2.2	0.2	25.8	32.2	92.4
30	*T. inermis*	PG	0.4	17.5	2.9	2.8	5.8	7.4	0.5	0.7	0	1.2	0.8	2.9	0.1	34.4	16.8	94.1
30	*T. raschii*	PG	0.2	13.1	2.9	2.1	6.5	8.0	0.9	1.3	0	1.4	1.0	2.3	0.1	38.1	18.0	95.2
31	*T. inermis*	PG	1.0	22.7	2.7	2.3	6.7	5.9	2.2	2.3	0	1.6	2.1	4.1	0.1	28.8	13.1	95.2
31	*T. raschii*	PG	0.9	19.5	2.4	2.3	6.3	5.9	2.2	2.3	0.2	1.5	1.8	3.2	0.1	30.6	14.4	92.0
28	*T. inermis*	WE	1.2	4.3	1.5	4.2	58.7	10.1	1.7	1.0	0	2.2	0.6	1.6	0.3	8.2	0.7	95.0
28	*T. raschii*	WE	0.7	7.6	2.8	2.7	46.3	11.2	2.2	1.6	0.3	2.4	1.2	2.6	0.5	10.3	1.2	91.5
30	*T. inermis*	WE	1.3	4.5	1.8	8.3	50.9	16.0	0.8	0.9	0	1.2	0.2	0.5	0.1	10.3	0.3	96.1
30	*T. raschii*	WE	1.7	10.2	2.7	7.7	38.5	15.1	0.6	1.1	0	1.3	0.4	0.7	0.1	11.2	0.6	91.7
31	*T. inermis*	WE	1.2	3.7	1.2	4.5	50.5	9.8	9.7	6.9	0.4	1.3	0.5	0.7	0.1	5.9	0.3	96.1
31	*T. raschii*	WE	1.4	5.8	1.4	4.2	41.0	9.5	12.1	11.7	0.6	1.2	0.5	0.6	0.4	6.4	0.4	96.7
21	*T. raschii*	FFA	0.0	13.6	10.5	2.5	14.9	5.3	0	0	0	3.3	1.4	9.5	0	23.5	5.8	90.3
28	*T. inermis*	FFA	0.1	9.2	2.0	0.8	9.8	6.6	0.6	0.7	0	1.5	0.8	5.5	0	37.2	17.3	91.6
28	*T. raschii*	FFA	0.1	2.5	3.7	0.0	6.1	6.1	1.8	1.5	0	1.3	0.5	1.8	0	43.6	25.7	93.9
30	*T. inermis*	FFA	0.0	8.8	3.0	1.5	8.3	8.5	0.6	0.7	0	1.0	0.7	1.6	0	42.9	16.8	93.9
30	*T. raschii*	FFA	0.0	6.7	3.1	1.1	6.8	8.5	0.6	0.3	0	1.2	0.6	1.4	0	45.4	19.7	95.1
31	*T. inermis*	FFA	0.0	10.3	2.6	2.6	10.4	8.1	4.5	7.2	0.5	1.4	1.4	5.6	0	28.5	11.6	94.7
31	*T. raschii*	FFA	1.9	11.6	2.8	4.1	6.9	5.5	3.2	4.5	0.4	1.1	1.3	5.5	0	22.2	6.1	74.3
23	*M. norvegica*	TG	7.6	9.4	0.9	3.6	8.8	2.6	21.9	26.6	1.1	1.0	1.2	0.8	0	2.6	4.0	92.1
27	*M. norvegica*	TG	6.9	10.3	1.0	3.7	10.2	3.3	20.9	26.1	1.0	1.0	1.1	0.9	0	3.2	4.3	93.9
23	*M. norvegica*	PG	1.5	13.7	1.0	1.6	10.5	3.4	6.0	4.5	0.3	2.5	1.7	0.4	0	16.9	29.1	93.1
27	*M. norvegica*	PG	1.4	15.1	1.1	1.7	12.6	4.0	5.6	4.0	0.3	2.4	1.5	0.4	0	16.0	27.1	93.2
23	*M. norvegica*	FFA	8.4	11.6	1.3	4.1	9.6	3.4	13.7	15.6	1.0	1.5	2.1	2.6	0	7.5	8.0	90.4
27	*M. norvegica*	FFA	8.4	16.8	1.5	4.0	10.8	5.5	8.9	7.6	0.6	1.7	1.9	2.1	0	11.7	11.0	92.5

The fatty acids were analyzed by capillary GLC, and the data are given as % (w/w) of the total fatty acid content of each fraction. WE, wax esters; TG, triacylglycerols; FFA, free fatty acids; PG, glycerophospholipids.

fraction by 400 MHz C-NMR analysis gave a positive indication of aliphatic wax esters in *Thysanoessa* species (haul 24), but cholesteryl esters were not detected (unpublished work). Steroid esters have been found in appreciable amounts in the Antarctic krill *E. crystallorophias* (11).

Fatty acid and fatty alcohol indicators of herbivorous and carnivorous diets

Since it is generally accepted that the fatty acid composition of storage lipids reflects the composition of the

TABLE 6. Fatty acid composition of the main classes of lipid in unsorted *Thysanoessa* species

Haul No.	Krill Species	Lipid Class	Fatty Acids (% of total) 14:0	16:0	18:0	16:1	18:1	18:4 + 20:1	20:4 + 22:1	18:2	18:3	20:5	22:6	Sum
21	*Thysanoessa*	TG	8.4	29.5	4.0	11.4	19.7	6.8	1.3	2.4	1.2	5.6	1.4	91.7
24	*Thysanoessa*	TG	3.6	28.2	4.5	9.9	24.9	5.9	2.6	2.7	3.2	6.0	1.4	92.9
21	*Thysanoessa*	PG	1.2	22.2	2.6	2.7	13.6	5.1	1.5	1.9	0.6	27.8	15.2	94.4
24	*Thysanoessa*	PG	1.0	21.6	2.5	2.3	14.8	4.0	1.6	1.8	0.6	27.8	17.1	95.1
21	*Thysanoessa*	FFA	1.6	13.7	5.9	3.7	18.4	10.8	3.8	1.9	1.5	19.8	5.2	86.3
24	*Thysanoessa*	FFA	2.4	16.4	3.0	7.2	16.6	15.0	1.8	2.4	2.5	14.1	2.6	84.0
21	*Thysanoessa*	WE	2.4	6.2	5.0	8.9	53.3	3.2	1.0	3.1	1.2	11.3	0.4	96.0
24	*Thysanoessa*	WE	0.2	3.3	1.9	4.3	66.2	1.8	0.9	2.7	0.3	13.9	0.5	96.0

The catches contained 70–80% *T. inermis* and 20–30% *T. raschii* (Table 1). The fatty acids were analyzed by packed column GLC. The fatty acid contents are given as % (w/w) of the total fatty acid content of each fraction. WE, wax esters; TG, triacylglycerols; FFA, free fatty acids; PG, glycerophospholipids.

TABLE 7. Fatty alcohol composition of the total lipid of *T. inermis* and *T. raschii*

Haul No.	Krill Species	Fatty Alcohol (% of total)							
		14:0	16:0	18:0	16:1	18:1	20:1	22:1	Sum
28	*T. inermis*	12.3	50.7	23.1	3.7	0	1.2	2.5	93.5
28	*T. raschii*	4.8	30.3	51.9	2.1	0	1.3	2.6	93.0
30	*T. inermis*	16.0	53.3	18.5	7.1	0	0.3	1.3	96.5
30	*T. raschii*	2.1	27.2	64.2	3.2	0	0	0	96.7
31	*T. raschii*	7.5	28.9	19.8	3.0	0.5	10.3	24.4	94.4

The fatty alcohols were analyzed by capillary GLC and the fatty alcohol contents are given as % (w/w) of the total fatty alcohol content of each fraction.

food (10), the observed seasonal variations may reflect the variations in the fatty acid composition of the diet of the krill. In the spring, the phytoplankton bloom in the Bals Fjord starts in late March and reaches a peak in late April or early May. The phytoplankton concentration reaches a second maximum in early September and decreases rapidly towards the end of September (14). The biomass of copepods also increases during the spring, and it is much higher during the summer and autumn than during the winter. The biomass of copepods in relation to phytoplankton is considerably higher during the winter than during the rest of the year.

The fatty acid composition of different North Atlantic phytoplankton has been reported by Ackman et al. (4, 20). The mean composition of 12 different phytoplankton species showed a comparatively high content of 16:1 (n-7) (16% of the total fatty acids), which is referred to as a marker of phytoplankton diets. The two fatty acids 20:1 (n-9) and 22:1 (n-11), which are considered to be markers of carnivorous diets, were found only in traces. North Atlantic copepods may contain similar proportions of the fatty acid 16:1, but, in contrast to the phytoplankton, copepods contain very high proportions of the fatty acids and fatty alcohols 20:1 and 22:1 (21–25). Detailed studies have revealed that the 20:1 (n-9) and 22:1 (n-11) isomers dominated in copepods (24, 25). Since the copepods contain a high proportion of 16:1 (n-7), it may be concluded that a high content of 16:1 (n-7) in krill is not, in itself, indicative of a herbivorous diet. However, if the content of the fatty acids 20:1 (n-9) and 22:1 (n-11) is low at the same time, this may be a true indication of a herbivorous diet. The fatty acids 18:1 (n-7) and 18:1 (n-9) and the C18 polyunsaturates are present in variable proportions in both phytoplankton and zooplankton, whereas the C16 polyunsaturates seem to be absent or present in very low proportions (4, 20, 21). These fatty acids, therefore, seem to be less suitable as markers of the feeding habits of krill than 16:1 (n-7), 20:1 (n-9), and 22:1 (n-11). This conclusion differs from the view held by Sargent and Falk-Petersen (6), who proposed that the fatty acids 16:1 (n-7) and 18:1 (n-7) and the C16 and C18 polyunsaturates reflected a phytoplankton diet, whereas a carnivorous diet was reflected by the fatty acids 20:1 (n-9), 22:1 (n-11), and 18:1 (n-9) and the fatty alcohols 20:1 (n-9) and 22:1 (n-11).

Fatty acid and fatty alcohol composition of the major lipid classes of krill in relation to their herbivorous and carnivorous nature

In *M. norvegica* a low content of 16:1 (n-7) and a high content of 20:1 (n-9) and 22:1 (n-11) in the triacylglycerols may reflect a carnivorous or omnivorous diet with cope-

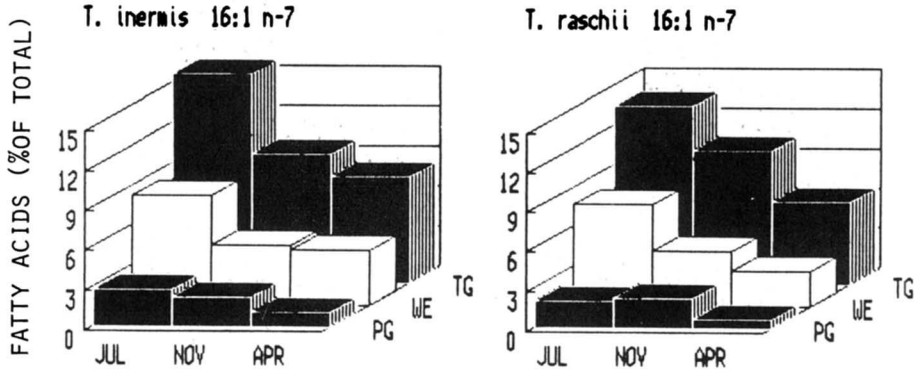

Fig. 6. Seasonal variation in the content of selected fatty acids in the depot lipids of *T. inermis* and *T. raschii*. The fatty acids selected represent those which are believed to reflect a herbivorous diet. The data refer to catch Nos. 28, 30, and 31 (c.f., Tables 1 and 3). TG, triacylglycerols; WE, wax esters; PG, glycerophospholipids.

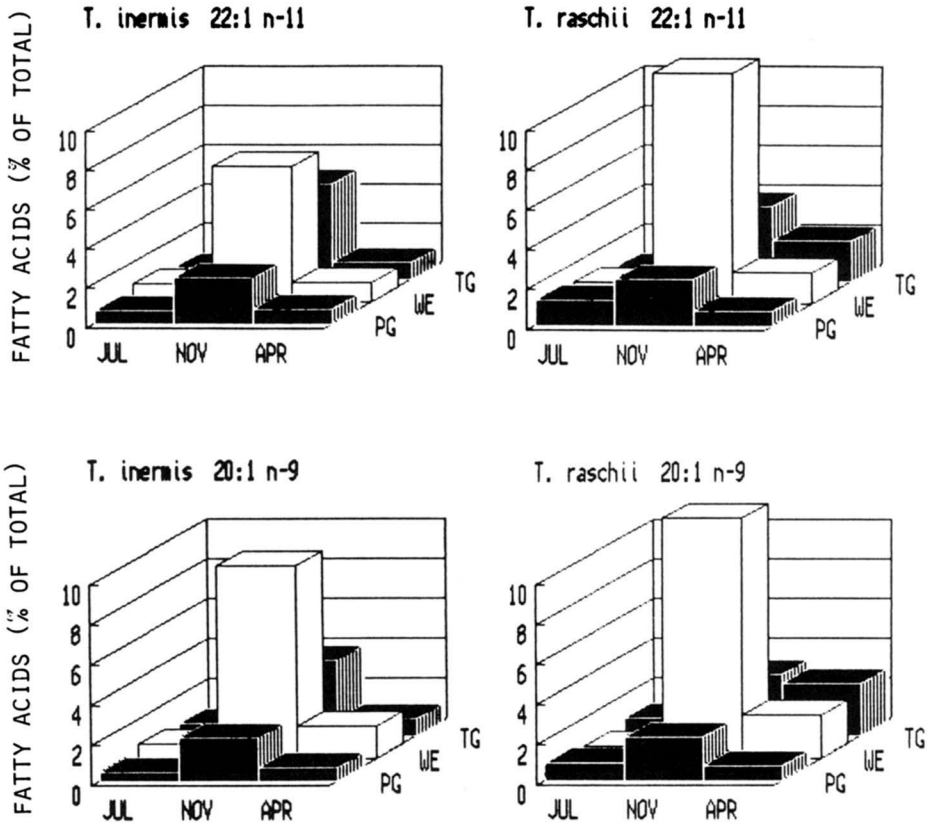

Fig. 7. Seasonal variation in the content of selected fatty acids in the depot lipids of *T. inermis* and *T. raschii*. The fatty acids selected represent those which are believed to reflect a carnivorous diet. The data refer to catch Nos. 28, 30, and 31 (c.f., Tables 1 and 3). TG, triacylglycerols; WE, wax esters; PG, glycerophospholipids.

pods as the major food. On the other hand, the two species of *Thysanoessa* had a very low content of 20:1 (n-9) and 22:1 (n-11) and at the same time a high content of 16:1 (n-7) in the triacylglycerols, which suggests that *T. inermis* and *T. raschii* are of a more herbivorous nature than *M. norvegica*.

The fatty acid composition of the corresponding major lipid classes of *T. inermis* and *T. raschii*, obtained in the same hauls, was very similar with the exception of a few fatty acids (Table 5). The great similarities in the relative proportions of the fatty acids that typically reflect the diet in the corresponding lipid classes of *T. inermis* and *T. raschii* suggests a similarity in the feeding habits of the two species. This contrasts with Sargent and Falk-Petersen (6), who concluded, on the basis of the fatty acid and fatty alcohol composition, that *T. raschii* was more carnivorous than *T. inermis*. The systematic differences in the fatty alcohol compositions of the two *Thysanoessa* species, where *T. inermis* has a considerably higher proportion of 16:0, and a considerably lower proportion of 18:0 than *T. raschii*, may not be the result of different feeding habits, because none of these fatty alcohols is considered to be indicative of different diets.

The free fatty acid composition of *M. norvegica* and the unsorted *Thysanoessa* species is probably representative of living krill and may be a reflection of the diet and/or result from a selective catabolism or anabolism of fatty acids in the krill. The differences observed in the free fatty acid composition of sorted *T. inermis* and *T. raschii* and unsorted *Thysanoessa* species are probably due mainly to hydrolysis of glycerophospholipids.

Seasonal variations in the fatty acid and fatty alcohol composition

The seasonal variations in the fatty acids that typically reflect the diet are worth a detailed consideration. In the triacylglycerols of both *T. inermis* and *T. raschii*, the proportion of 16:1 (n-7) reached a maximum in July when the proportion of 20:1 (n-9) and 22:1 (n-11) was lowest, whereas a maximum proportion of 20:1 (n-9) and 22:1 (n-11) was observed in November (**Fig. 6** and **Fig. 7**). This suggests a more carnivorous diet for both species during the autumn and winter than during summer.

The fatty acid composition of the wax esters from *E. crystallorophias* has been examined by Bottino (10), who found that they do not reflect the diet in the same way as the triacylglycerols. This is partly supported by the present

studies of *T. inermis* and *T. raschii*, which reveal a considerably higher content of 18:1 (n-9) and a much lower content of 16:1 (n-7) in the wax esters compared with the triacylglycerols. However, the relative proportion of the fatty acids 16:1 (n-7), 20:1 (n-9), and 22:1 (n-11) followed the same pattern of seasonal variation as in the triacylglycerols (Figs. 6 and 7). This applied to both *T. inermis* and *T. raschii*, and indicates that the food regulates the fatty acid composition of the wax esters in the same manner as the triacylglycerols, but the degree of incorporation of fatty acids into the wax esters and triacylglycerols seems to be different.

In both *Thysanoessa* species the fatty alcohols 14:0, 16:0 and 18:0 dominated, and 20:1 and 22:1 were almost absent during spring and summer. However, in November, the content of the alcohols 20:1 and 22:1 was significant (Table 7). These observations support the contention that the krill have a more carnivorous diet during the autumn than during the summer. It has been maintained that the major alcohols of several marine crustacea, are 16:0, 20:1 and 22:1 (21–23, 26). However, Sargent and Falk-Petersen (6) claim that the wax esters and *T. raschii* essentially contain phytol as the fatty alcohol, whereas the major fatty alcohols of *T. inermis* were 14:0 and 16:0. The Antarctic krill *E. crystallorophias* contained the same major fatty alcohols as those found during spring and summer in the two *Thysanoessa* species in the present study (8, 11).

The glycerophospholipids seemed to be the least affected by food of all lipid classes in all the three species of krill. The glycerophospholipids of *T. inermis* and *T. raschii* showed a slight variation in the content of 16:1 (n-7), 20:1 (n-9), and 22:1 (n-11), which corresponded to the pattern of seasonal variations of these fatty acids in the wax esters and triacylglycerols. (Figs. 6 and 7).

Effects of temperature on the fatty acid composition

According to present hypotheses, biological membranes are thought to contain lipids in a highly fluid, dynamic state interacting with proteins (27). Highly unsaturated lipids are required to ensure sufficient membrane fluidity at low temperatures (28), thus ensuring an acceptable rate of transport across the membranes (29). Studies on crustacea (30) and fish (29, 31) have revealed that the unsaturation of glycerophospholipids is closely related to the temperature, showing an increased desaturation with decreasing temperature. In addition to unsaturation of glycerophospholipids, the monoenoic wax esters of *E. crystallorophias* may have a role in the adaptation of these animals to the extremely low sea temperatures (11). Because of this, it is possible that the high content of monoenoic wax esters of *E. crystallorophias* may compensate for the rather low content of polyunsaturated fatty acids in its glycerophospholipids compared to *E. superba* which lacks wax esters (8, 11).

The present study suggests that the wax esters of the *Thysanoessa* species play a role in the temperature adaptation similar to those of *E. crystallorophias*. The two *Thysanoessa* species, caught in the same hauls, were evidently exposed to the same temperature prior to catching. Nevertheless, the proportion of polyunsaturated fatty acids in the glycerophospholipids of *T. raschii* was systematically higher than that of *T. inermis*, whereas *T. inermis* had both the highest relative content of wax esters and the highest proportion of monounsaturated fatty acids in the wax esters.

The observation that the proportions of polyunsaturated fatty acids of the glycerophospholipids and monounsaturated fatty acids of the wax esters were similar in April and July in both of the *Thysanoessa* species may suggest that this unsaturation is determined by the relatively constant minimum temperature (2–4°C) of the water throughout the year. The temperature profile and minimum temperature have been established by Falk-Petersen and Hopkins (14). The proportion of monounsaturated fatty acids in the wax esters was also the same in November as in April and July, but the proportion of polyunsaturated fatty acids in the glycerophospholipids was lower in November than in April and July. If monounsaturated fatty alcohols have the same significance in adaptation to cold environments as monounsaturated fatty acids seem to have, the lower unsaturation of the glycerophospholipids of *T. raschii* in November may be related to the increased proportion of monounsaturated fatty alcohols in its wax esters. In contrast, studies on the Antarctic krill *E. superba*, which lacks wax esters, have revealed a very constant fatty acid composition of glycerophospholipids during the antarctic summer when the sea temperature is constant (8).

The unsaturation of glycerophospholipids of *M. norvegica*, caught in the Ulls Fjord in March and April, seemed to be about the same as that of *T. inermis* caught in the Bals Fjord in April. Since *M. norvegica* has no wax esters, this may indicate a poor adaptation to very cold environments compared to the *Thysanoessa* species. This is further supported by the observation that *M. norvegica* does not spawn in fjords that are as cold as the Bals Fjord, whereas *T. inermis* and *T. raschii* both spawn in these fjords (14).

From the present work and the studies of Ellingsen and Mohr (7) and Ellingsen (8), it may be concluded that there are distinctly different patterns of lipid deposition within both North Atlantic and Antarctic krill. Depending on the species, glycerophospholipids, triacylglycerols, and wax esters serve as depot lipids, either singly or in a combination of two or three. It may further be concluded that the fatty acid compositions of the main classes of lipid of common species of North Atlantic krill seem to be influenced by seasonal variations in diet. The unsaturation of the glycerophospholipids and wax esters may also be influenced by variations in temperature.

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