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Lipids in Arctic benthos: does the fatty acid and alcohol composition reflect feeding and trophic interactions?

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Abstract Arctic benthic organisms of various taxa (Anthozoa, Polychaeta, Pantopoda, Crustacea, Echinodermata) were collected on the shelves off northeast Greenland, Spitsbergen and the western Barents Sea. Their fatty acid compositions were generally characterised by the predominance of the polyunsaturated fatty acids 20:5(n-3) and 22:6(n-3) together with the saturated fatty acid 16:0, which reflect the dominance of phospholipids. The fatty acid compositions of most benthic specimens were influenced by fatty acids of dietary origin. High amounts of the fatty acid 16:1(n-7), typical of diatoms, were found in different taxa from the northeast Greenland shelf. The 18:4(n-3) fatty acid, often typical of non-diatom input, was only dominant in *Ophiopholis aculeata* from the Spitsbergen shelf. In some taxa small amounts of wax esters were detected with alcohol moieties similar to those of the dominant Arctic copepods. The occurrence of intact wax esters, as well as the wax ester typical fatty acids 20:1(n-9) and 22:1(n-11), also suggested ingestion of large herbivorous copepods. An unusual fatty acid composition was found for most brittle stars, due to a ratio of the 18:1(n-9) and (n-7) fatty acid isomers below 1 with lowest ratios of 0.1. A similar low ratio was also detected in the polychaete *Onuphis conchylega.* The extremely low portions of the 18:1(n-9) fatty acid are striking, since carnivores are generally characterised by high levels of this fatty acid. A clear gradient from low 18:1(n-9) to (n-7) ratios in suspension feeders, via predatory decapods, to higher ratios in the scavenging amphipods was a major characteristic of the benthic species. Our investigations showed that lipid analyses can give important hints on trophic relationships of benthic species and may serve as means to establish the intensity of pelagic-benthic coupling.

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Introduction

Lipid investigations on benthic taxa from the Arctic are scarce (Graeve 1993) except for the deep-water prawn *Pandalus borealis.* Due to its commercial importance, extensive lipid investigations have been performed on *P. borealis* from the north Norwegian Balsfjord (Hopkins et al. 1993) and off the south coast of Nova Scotia (Ackman and Eaton 1967). Additionally, lipids of three sea star species from the Balsfjord were studied (Sargent et al. 1983), as well as fatty acids in species from a shallow-water hydrothermal habitat off the Kurile Islands (Kharlamenko et al. 1995). Generally, benthic species have relatively low lipid contents as compared to herbivorous zooplankton species (Clarke and Peck 1991).

The benthos inhabiting the shelves of northeast Greenland, Spitsbergen and the Barents Sea is locally rich in biomass. Very recent investigations on the structure of the zoobenthic communities have been carried out by several authors (Ambrose and Renaud 1995; Kendall 1996; Piepenburg and Schmid 1996a,b; Piepenburg et al. 1996). In addition, ecophysiological studies have been performed on the most common epibenthic species (Dorrien 1993; Schmid 1994). Little is known about the biochemical composition of these organisms and even less on the lipid and fatty acid compositions.

For many benthic species in the study area, little direct information is available on the feeding ecology and trophic niches. In both cases, allocation to a certain feeding type or food source has to be deduced from general biological knowledge of morphological features or knowledge about larger taxonomic units. The potential of fatty acids to reveal trophic relationships especially in herbivorous zooplankton has proven to be a useful tool for this kind of investigation.

In this study various species of Arctic benthic taxa have been investigated to obtain information on the spectrum and variety of their lipid compositions. Special emphasis was placed on detailed fatty acid and fatty alcohol compositions to elucidate similarities between taxa and reveal indications of feeding behaviour and food sources, discussed in the context of current knowledge of feeding biology.

Materials and methods

Benthic species were collected during three summer expeditions of RV "Polarstern" on the shelves of northeast Greenland, Spitsbergen and the Barents Sea (ARK VI/4, 29 June to 8 July 1989; ARK VII/2, 10 July to 15 August 1990; ARK VIII/2, 1 June to 30 July 1991). The species sampled are listed in Table 1. The animals were caught with an Agassiz trawl or a bottom trawl and sorted into species and sex on board (for details refer to Piepenburg et al. 1996). Due to a limited number of specimens of each catch, only one animal per station was sorted out. Afterwards, the specimens were transferred into seawater aquaria and kept at 4°C for about 1 day for defecation. Subsequently, they were deep frozen at −80°C in glass bottles until analysis at the institute.

The animals were homogenised and extracted in chloroform/methanol (2:1; v:v) according to Folch et al. (1957). The lipid class compositions were determined according to Fraser et al. (1985) by thin-layer chromatography-flame ionisation detection (TLC-FID) with an IATROSCAN Mark IV TH 10. Different standard mixtures were used for identification (Hagen 1988).

For the gas liquid chromatographic analysis of the fatty acid and fatty alcohol compositions, aliquots of the extracted samples were taken. Methyl esters of fatty acids and free fatty alcohols were prepared by transesterification with 3% concentrated sulphuric acid in methanol for 4 h at 80°C. After their extraction with hexane, the composition was analysed with a Chrompack gas liquid chromatograph (Chrompack 9000) on a capillary column (30 m × 0.25 mm; film thickness: 0.25 μm; liquid phase: DB-FFAP) using temperature programming according to the method of Kattner and Fricke (1986). Fatty acids and alcohols were identified with standard mixtures.

The data of the individual fatty acids are expressed as mass percentage of total fatty acids. The ratio between the two isomers 18:1(n-9) and 18:1(n-7) is presented at the end of the tables.

Results

Crustacea

The lipids of the decapods *Eualus gaimardi*, *Sabinea septemcarinata*, *Sclerocrangon ferox*, *Sclerocrangon boreas* and *Pandalus borealis* were dominated by phospholipids. Highest triacylglycerol levels were found in *Sclerocrangon ferox*; in contrast, triacylglycerols were hardly present in *E. gaimardi* (Table 2). The 16:0, 16:1(n-7), 18:1(n-9) and (n-7), 20:5(n-3) and 22:6(n-3) fatty acids were major lipid components of all female

Table 1 Sampling locations of the various benthic species

Taxa	Species	Date	Station	Latitude	Longitude	Region	Depth (m)
Actinaria							
	Anthosactis janmayeni	05/08/1990	222	81°48′ N	10°34′ W	NE Greenland	251
	A. janmayeni	05/08/1990	222	81°48′ N	10°34′ W	NE Greenland	251
	Actinaria, indet. spec.	22/07/1990	150	74°45′ N	16°00′ E	Barents Sea	200
Polychaeta							
	Onuphis conchylega	02/07/1989	161	76°22′ N	16°00′ E	Spitsbergen	50
Amphipoda							
	Anonyx nugax	25/06/1991	45	75°59′ N	34°49′ E	Barents Sea	250
	Stegocephalus inflatus	15/07/1990	101	75°02′ N	14°31′ W	NE Greenland	145
Isopoda							
	Arcturus baffini	22/06/1991	40	76°37′ N	34°51′ E	Barents Sea	200
	A. baffini	02/08/1990	205	80°10′ N	11°00′ W	NE Greenland	103
Decapoda							
	Eualus gaimardi	15/07/1990	101	75°02′ N	14°31′ W	NE Greenland	145
	Sabinea septemcarinata	15/07/1990	101	75°02′ N	14°31′ W	NE Greenland	145
	Sclerocrangon ferox	15/07/1990	101	75°02′ N	14°31′ W	NE Greenland	145
	Sclerocrangon boreas	02/07/1989	161	76°22′ N	16°00′ E	Spitsbergen	50
	Pandalus borealis	06/08/1990	225	81°09′ N	08°24′ W	NE Greenland	377
Pantopoda							
	Nymphon hirtipes	07/08/1990	228	80°36′ N	08°52′ W	NE Greenland	245
Ophiuroidea							
	Ophiopholis aculeata	02/07/1989	161	76°22′ N	16°00′ E	Spitsbergen	50
	O. aculeata	02/07/1989	161	76°22′ N	16°00′ E	Spitsbergen	50
	O. borealis	06/07/1991	84	80°23′ N	07°33′ E	Spitsbergen	700
	O. borealis	30/06/1989	158	77°12′ N	06°00′ W	NE Greenland	280
	Ophiacantha bidentata	02/07/1989	160	76°20′ N	15°24′ E	Spitsbergen	200
	Ophiura sarsi	07/07/1991	86	80°10′ N	09°51′ E	Spitsbergen	570
Crinoidea							
	Heliometra glacialis	15/07/1990	101	75°02′ N	14°31′ W	NE Greenland	145
	H. glacialis	07/08/1990	228	80°36′ W	08°52′ W	NE Greenland	245

Table 2 Lipid class composition of the vairous benthic species. Percentage distribution of phospholipids (*PL*), triacylgycerols (*TAG*) and wax esters (*WE*) of the sum of these main lipid classes (*tr* traces, – below limit of detection)

Species	Region	Station	Lipid classes		
			PL	TAG	WE
Anthosactis janmayeni	NE Greenland	222	47	53	–
A. janmayeni	NE Greenland	222	69	–	29
Actinaria indet. spec.	Barents Sea	150	58	11	tr
Onuphis conchylega	Spitsbergen	161	96	4	–
Anonyx nugax	Barents Sea	45	31	69	–
Stegocephalus inflatus	NE Greenland	101	41	59	–
Arcturus baffini	Barents Sea	40	99	–	–
A. baffini	NE Greenland	205	86	14	–
Eualus gaimardi	NE Greenland	101	99	–	–
E. gaimardi eggs	NE Greenland	101	97	3	–
Sabinea septemcarinata	NE Greenland	101	77	23	–
Sclerocrangon ferox	NE Greenland	101	65	35	–
S. ferox eggs	NE Greenland	101	67	32	–
Sclerocrangon boreas	Spitsbergen	161	87	13	–
Pandalus borealis	NE Greenland	225	92	8	–
P. borealis eggs	NE Greenland	225	58	41	–
Nymphon hirtipes	NE Greenland	228	80	20	–
Ophiopholis aculeata	Spitsbergen	161	99	–	–
O. aculeata	Spitsbergen	161	90	10	–
Ophiopleura borealis	Spitsbergen	84	99	1	–
O. borealis	NE Greenland	158	99	–	–
Ophiacantha bidentata	Spitsbergen	160	93	6	–
Ophiura sarsi	Spitsbergen	86	96	4	–
Heliometra glacialis	NE Greenland	101	91	9	tr
H. glacialis	NE Greenland	228	99	–	–

decapod species. Their proportions varied within a small range. The two 18:1 isomers, (n-9) and (n-7), occurred in equal portions (each up to 14%) (Table 3). The fatty acid compositions of male *E. gaimardi* and *P. borealis* were similar to those of the females.

The separately analysed eggs of three decapod species showed pronounced differences in their triacylglycerol contents. Eggs of *Sclerocrangon ferox* and *Pandalus borealis* were triacylglycerol-rich, whereas only trace amounts were found in the eggs of *E. gaimardi* (Table 2). However, the fatty acid compositions were similar. The most obvious difference, compared to the adults, was the high amount of the 16:1(n-7) fatty acid, with up to 23% (Table 3).

Both amphipod species (females), *Anonyx nugax* from the Barents Sea and *Stegocephalus inflatus* from the northeast Greenland Shelf, contained high amounts of triacylglycerols (Table 2) but their fatty acid compositions were clearly different. In *A. nugax*, the monounsaturated fatty acids 20:1(n-9), 22:1(n-11) and 18:1(n-9) were major components together with 16:0. In contrast, the polyunsaturated fatty acids 20:5(n-3) and 22:6(n-3) were dominant in *S. inflatus.* The 18:1(n-9) and 16:0 fatty acids were found in similar portions as in *A. nugax* (Table 4).

Specimens of the isopod *Arcturus baffini* from the Barents Sea contained little triacylglycerol, whereas the sample from the northeast Greenland shelf had 13% of this storage lipid. This difference is also reflected in the fatty acid compositions: in the individual from the Greenland shelf the 16:1(n-7) and 18:1(n-9) fatty acids composed 24% and 6%, respectively, while in the Barents Sea individual the 16:1(n-7) fatty acid accounted for only 5% and the 18:1(n-9) for 18%. The major fatty acid in both isopods was 20:5(n-3). Other important fatty acids were 16:0 and 22:6(n-3), occurring generally in similar portions (Table 4).

Echinodermata

The brittle stars (Ophiuroidea) were generally low in triacylglycerols (Table 2). The amounts of the major fatty acids were quite variable. *Ophiopholis aculeata*, *Ophiopleura borealis*, *Ophiacantha bidentata* and *Ophiura sarsi* had comparatively high levels of the 20:5(n-3) and very low levels of 22:6(n-3) fatty acids, except for *Ophiura sarsi*. The very low levels of the 18:1(n-9) fatty acid contrasted with those of its isomer 18:1(n-7), which were up to 10 times higher. This finding was most pronounced in *Ophiopholis aculeata* and *Ophiacantha bidentata.* The saturates 14:0, 16:0 and 18:0, as well as 16:1(n-7), occurred in moderate amounts (Table 5).

Two specimens of *Ophiopholis aculeata*, from the same station on the Spitsbergen shelf, exhibited distinct differences in their fatty acid compositions. One animal contained high amounts of the 18:4(n-3) fatty acid (24%), whereas this fatty acid was nearly absent in the other individual.

Another distinct intraspecific difference was detected in *Ophiopleura borealis* from the Spitsbergen shelf as

Table 3 Fatty acid composition (mass %) of decapods and decapod eggs (Total lipid extract of whole animal)

Species	*Eualus gaimardi*		*Sabinea septemcarinata*	*Sclerocrangon ferox*		*Sclerocrangon boreas*	*Pandalus borealis*	
	Total	Eggs	Total	Total	Eggs	Total	Total	Eggs
Region	NE Greenland		NE Greenland	NE Greenland		Spitsbergen	NE Greenland	
Station	101	101	101	101	101	161	225	225
Fatty acid								
14 : 0	1.5	3.3	0.5	2.0	2.3	1.4	2.6	2.4
16 : 0	15.5	12.1	14.4	13.2	12.3	15.0	13.6	11.5
16 : 1 (n-7)	7.5	22.5	5.6	7.9	18.3	4.6	8.7	19.0
18 : 0	3.5	0.9	3.9	3.5	1.0	3.7	2.1	1.5
18 : 1 (n-9)	12.0	14.7	9.4	13.6	18.0	12.7	11.3	12.7
18 : 1 (n-7)	11.0	8.4	12.1	13.7	10.7	9.1	9.6	12.0
18 : 2 (n-6)	1.4	1.6	0.8	0.9	1.6	1.4	1.0	1.0
18 : 3 (n-3)	–	0.5	–	–	0.4	–	–	–
18 : 4 (n-3)	–	0.8	–	–	0.4	–	–	–
20 : 1 (n-9)	–	–	0.9	3.7	1.5	1.5	4.7	2.4
20 : 1 (n-7)	–	–	0.3	2.0	0.8	1.4	0.5	1.5
20 : 4 (n-6)	4.4	4.3	5.8	3.6	2.3	4.6	2.0	2.1
20 : 5 (n-3)	27.2	23.4	25.9	20.2	17.4	26.1	20.5	22.6
22 : 1 (n-11)	–	–	0.6	2.4	0.6	0.7	5.1	1.6
22 : 1 (n-9)	–	–	0.4	0.9	0.3	0.6	0.6	0.3
22 : 5 (n-3)	0.9	0.5	1.8	1.6	1.6	–	0.5	1.2
22 : 6 (n-3)	15.3	6.4	16.5	10.0	10.0	17.2	16.9	7.9
Ratio								
18 : 1 (n-9) / (n-7)	1.09	1.75	0.77	0.99	1.68	1.39	1.17	1.05

Table 4 Fatty acid composition (mass %) of amphipods (*Anonyx nugax*, *Stegocephalus inflatus*) and an isopod (*Arcturus baffini*)

Species	*Anonyx nugax*	*Stegocephalus inflatus*	*Arcturus baffini*	
Region	Barents Sea	NE Greenland	Barents Sea	NE Greenland
Station	45	101	40	205
Fatty acids				
14 : 0	5.1	3.2	0.5	2.9
16 : 0	11.1	10.8	11.0	13.1
16 : 1 (n-7)	9.8	4.7	4.9	24.2
18 : 0	0.7	1.0	5.0	2.3
18 : 1 (n-9)	13.4	18.0	17.5	5.6
18 : 1 (n-7)	4.1	5.0	8.6	5.2
18 : 2 (n-6)	1.6	1.5	2.1	0.9
18 : 3 (n-3)	0.4	0.5	–	–
18 : 4 (n-3)	1.5	0.5	0.7	–
20 : 1 (n-9)	18.7	2.2	3.6	1.2
20 : 1 (n-7)	0.7	4.9	3.8	2.9
20 : 4 (n-6)	0.3	2.9	–	3.9
20 : 5 (n-3)	9.2	22.5	25.6	25.6
22 : 1 (n-11)	14.2	1.8	1.4	1.3
22 : 1 (n-9)	1.1	0.6	0.8	0.5
22 : 5 (n-3)	0.6	1.8	2.2	1.6
22 : 6 (n-3)	7.0	17.6	11.4	8.6
Ratio				
18 : 1 (n-9) / (n-7)	3.27	3.60	2.03	1.08

compared to the northeast Greenland shelf. The Spitsbergen animal had high portions of the 20:1(n-9) and smaller portions of the 22:1(n-11) fatty acids (22% and 7%, respectively). In the Greenland individual, these two fatty acids occurred only in low portions: its fatty acid composition was dominated by the 20:5(n-3) and 16:1(n-7) fatty acids (Table 5).

The fatty acid composition of the feather star (Crinoidea) *Heliometra glacialis* differed from that of the brittle stars with respect to the ratio of the 18:1 isomers and the low portion of the 14:0 fatty acid. One of the two individuals from different depths had small amounts of wax esters. The fatty alcohol moieties of these wax esters were 16:0, 20:1(n-9) and 22:1(n-11).

Table 5 Fatty acid composition (mass %) of brittle stars (*Ophiopholis aculeata*, *Ophiopleura borealis*, *Ophiacantha bidentata*, *Ophiura sarsi*) and a feather star (*Heliometra glacialis*)

Species	*Ophiopholis aculeata*		*Ophiopleura borealis*		*Ophiacantha bidentata*	*Ophiura sarsi*	*Heliometra glacialis*	
Region	Spitsbergen		Spitsbergen	NE Greenland	Spitsbergen	Spitsbergen	NE Greenland	
Station	161	161	84	158	160	86	101	228
Fatty acids								
14 : 0	9.3	13.7	7.2	6.6	7.2	11.4	2.3	1.7
16 : 0	7.6	10.0	8.2	10.7	9.5	11.5	9.9	10.3
16 : 1 (n-7)	4.5	5.7	7.3	12.7	10.1	5.8	8.4	10.2
18 : 0	7.6	9.1	4.7	6.3	7.6	6.7	4.7	6.1
18 : 1 (n-9)	0.7	1.2	7.2	5.2	1.1	6.5	6.4	4.2
18 : 1 (n-7)	6.5	8.8	6.3	9.2	11.1	4.5	4.1	2.8
18 : 2 (n-6)	1.6	2.4	0.5	0.7	1.3	1.2	0.5	0.5
18 : 3 (n-3)	1.2	1.3	–	0.3	0.6	1.1	0.3	–
18 : 4 (n-3)	24.4	3.7	0.6	0.3	4.5	2.8	1.0	1.2
20 : 1 (n-9)	5.1	–	22.3	2.2	2.2	1.8	5.4	0.7
20 : 1 (n-7)	2.0	2.4	1.3	2.2	2.6	0.9	3.2	1.5
20 : 4 (n-6)	1.2	1.5	–	3.3	4.8	–	3.6	5.2
20 : 5 (n-3)	22.1	30.5	15.6	27.4	32.8	23.7	27.3	37.7
22 : 1 (n-11)	1.4	0.3	6.6	4.0	1.5	9.7	3.8	5.0
22 : 1 (n-9)	0.2	0.3	6.5	4.0	0.5	1.4	6.9	0.9
22 : 5 (n-3)	–	–	0.3	0.3	–	1.0	2.0	1.3
22 : 6 (n-3)	2.7	5.3	4.9	4.5	2.0	8.5	9.0	9.5
Ratio								
18 : 1 (n-9) / (n-7)	0.11	0.14	1.14	0.57	0.10	1.44	1.56	1.50

The corresponding fatty acids were also present in slightly higher portions (Table 5).

Other taxa

Two individuals of the pantopod *Nymphon hirtipes* were collected at the same station off northeast Greenland. One individual was triacylglycerol-rich with a very high amount of the 16:1(n-7) fatty acid (42%). Other major fatty acids were 16:0 and 20:5(n-3). The other individual had less triacylglycerol, which was also reflected in its fatty acid composition. The percentage of the 16:1(n-7) fatty acid in this individual was only 8%. The polyunsaturates 20:5(n-3) with 32%, and 22:6(n-3) with 11%, together with the 16:0 (15%), were the dominant fatty acids in this individual (Tables 2 and 6).

One of the two samples of the actinarian species *Anthosactis janmayeni* from the northeast Greenland shelf contained wax esters (31%; Table 2). The major alcohol moieties were 16:0 and 20:1(n-9), as well as lower portions of 14:0 and 22:1(n-11). The fatty acid compositions of the two individuals were similar. The principal fatty acid was 20:5(n-3). The two isomers of the 20:1 and the 22:1 fatty acids occurred in similar proportions (4–7%). In contrast to all other species, enhanced levels of the 22:5(n-3) fatty acid were found (Table 6). The other anemone (species indet.) was collected on the Barents Sea shelf. This individual also contained wax esters with the alcohol moieties 16:0, 22:1(n-11), 14:0 and 20:1(n-9) (in descending sequence). Its fatty acid composition was slightly different from the Greenland shelf species: the percentages of the long-chain monounsaturated fatty acids, 20:1(n-9) and 22:1(n-11) (Table 6), especially, were much higher than those of their corresponding alcohol isomers.

The fatty acid compositions of the polychaete *Onuphis conchylega* showed similarities to that of the brittle stars. This is most obvious for the low ratio between the two 18:1 fatty acid isomers, the high proportion of the 20:5(n-3) and the small amounts of the 22:6(n-3) fatty acids (Table 6).

Discussion

The lipid and fatty acid/alcohol compositions of the investigated Arctic benthic organisms varied, not only among the different taxa, but also within the same species. Generally the reliance on lipid reserves was low. A few specimens with higher levels of depot lipids were found, but none reached levels of the lipid-rich Arctic zooplankton, such as the herbivorous copepods (Lee 1974, 1975; Conover and Huntley 1991; Kattner and Hagen 1995).

The fatty acid compositions of all analysed benthic animals were characterised by polyunsaturated fatty acids, mainly 20:5(n-3) but also 22:6(n-3) and the saturate 16:0. These three fatty acids are typical of marine organisms and they generally predominate the phospholipids (Sargent and Henderson 1986; Tande and Henderson 1988; Albers et al. in press), which are important membrane components. The dominance of membrane fatty acids also indicates the low dependence

Table 6 Fatty acid composition (mass %) of a pantopod (*Nymphon hirtipes*), two actinarians (*Anthosactis janmayeni*, indetectable species), and a polychaete (*Onuphis conchylega*)

Species	*Nymphon hirtipes*		*Anthosactis janmayeni*		*Actinaria* indet.	*Onuphis conchylega*
Region	NE Greenland		NE Greenland		Barents Sea	Spitsbergen
Station	228	228	222	222	150	161
Fatty acids						
14 : 0	5.4	1.3	1.6	0.9	0.5	2.4
16 : 0	12.0	15.0	9.6	8.4	7.1	18.0
16 : 1 (n-7)	41.7	7.9	7.3	6.5	6.6	6.1
18 : 0	0.6	4.2	3.5	3.4	3.1	7.5
18 : 1 (n-9)	5.5	4.3	5.1	6.7	10.2	2.6
18 : 1 (n-7)	3.3	7.4	5.1	4.2	3.7	10.8
18 : 2 (n-6)	1.1	–	0.6	0.6	0.9	1.2
18 : 3 (n-3)	–	–	–	0.4	0.7	0.5
18 : 4 (n-3)	1.1	–	–	0.7	0.6	0.7
20 : 1 (n-9)	3.7	3.0	7.1	4.6	8.1	1.9
20 : 1 (n-7)	0.7	1.1	5.1	6.6	1.4	1.1
20 : 4 (n-6)	0.7	7.1	3.4	3.2	1.0	5.8
20 : 5 (n-3)	15.6	32.3	19.9	25.3	15.1	35.3
22 : 1 (n-11)	2.4	0.9	7.3	3.8	11.6	1.1
22 : 1 (n-9)	0.4	–	7.2	7.0	3.1	0.3
22 : 5 (n-3)	–	4.1	7.4	8.7	8.7	–
22 : 6 (n-3)	4.3	11.2	10.5	8.5	15.6	4.3
Ratio						
18 : 1 (n-9) / (n-7)	1.67	0.58	1.00	1.60	2.76	0.24

on lipid reserves. In spite of this general uniformity, the occurrence and proportions of some fatty acids seem to be characteristic of individual taxa, but may be widely influenced by the diet as well.

The decapod specimens studied were characterised by a relatively uniform distribution of the (n-9) and (n-7) isomers of the 18:1 fatty acid. Usually, enhanced levels of the (n-7) isomer reflect herbivorous feeding (Sargent and Falk-Petersen 1981). The decapods, however, are known to be macrophagous predators, feeding on small organisms occurring on the seafloor or in the bottom-near water column (Feder and Jewett 1981). For an interpretation of their fatty acid composition, one has to consider that the decapods were collected on the Greenland shelf in the Northeast Water Polynya. In large parts of this area, the phytoplankton stock is dominated by diatoms throughout the productive season (Lara et al. 1994; Smith et al. 1995). The fatty acid compositions of diatoms are dominated by 16:1(n-7), as well as 20:5(n-3) fatty acids (e.g. Kates and Volcani 1966; Ackman et al. 1968; Graeve et al. 1994). Copepods from this region are also very rich in these fatty acids (Kattner et al. 1989; Graeve et al. 1994). The 16:1(n-7) fatty acid is the precursor of 18:1(n-7), synthesised by subsequent chain elongation (Sargent and Henderson 1986). Thus, the enhanced levels of 18:1(n-7) fatty acid in decapods suggest that it was of dietary origin rather than a species-specific marker fatty acid. This conclusion is also supported by the comparison with the fatty acid composition of *Pandalus borealis* from the north Norwegian Balsfjorden (Hopkins et al. 1993), in which only low levels of 18:1(n-7) were found. While the chain elongation of the 16:1(n-7) to 18:1(n-7) fatty acids seems to be an important process in the lipid biosynthesis of decapods, the production of eggs is obviously more directly fuelled by the incorporation of the 16:1(n-7) without further elongation. The enhanced levels of this dietary fatty acid suggest a dependence of egg production on sufficient food resources. Our finding points to an intense pelagic-benthic coupling in the Northeast Water Polynya and therefore supports the same conclusion made by Ambrose and Renaud (1995) based on correlations between benthic biomass and water column properties, as well as that made by Hobson et al. (1995) based on stable isotope analyses.

Brittle stars are generally known to be very opportunistic in their feeding mode and food source (Warner 1982). The lipids of the specimens investigated were clearly different from most other species because of the low ratio between the (n-9) and (n-7) isomers of the 18:1 fatty acid. Species that are known to act at least temporarily as suspension feeders, such as *Ophiopholis aculeata* and *Ophiacantha bidentata* (Warner 1982; Pearson and Gage 1984), yielded very low ratios of the two 18:1 fatty acid isomers, indicating either that they contain endosymbiotic sub-cuticular bacteria (McKenzie and Kelly 1994) or that they fed on fresh diatomous material from the water column before they were caught. The latter conclusion seems to be more probable since it is supported by evidence of the intense pelagic-benthic coupling in the area studied, as already discussed for the decapods. Similar to the decapods, the brittle stars also seem to elongate the diatom fatty acid 16:1(n-7) to 18:1(n-7). Other species of ophiuroids

(*Ophiopleura borealis*, *Ophiura sarsi*) were characterised by clearly higher ratios, pointing to a different trophic level and feeding behaviour. According to the, admittedly rather small, knowledge of their nutrition, ophiuroids exploit a very broad range of benthic food sources as predators, scavengers and surface deposit feeders (Warner 1982; H.M. Feder and S.C. Jewett personal communication). The relatively highest 18:1(n-9) to (n-7) ratio was found in *Ophiura sarsi*, a species that is reported to prefer predatory feeding (Warner 1982). The onuphoid *Onuphis conchylega* yielded a very low 18:1(n-9) to (n-7) ratio, similar to those of the suspension-feeding brittle stars. Onuphid polychaetes have been described as feeding primarily as predators or scavengers (Hartmann-Schröder 1971) but seem also capable of utilising a plankton-feeding mode (Fauchald and Jumars 1979). *Onuphis conchylega* was caught on the same shallow Spitsbergen shelf station (50 m) as the brittle stars. Thus, the fatty acids of the available food sources again dominated the fatty acid composition of the species, masking potential taxon-specific patterns and emphasising the intensity of the pelagic-benthic coupling in this area.

The unusual ratio of the two 18:1 isomers may be further influenced by the varying food supply. This is especially the case for *Ophiopholis aculeata* from the shallow Spitsbergen Shelf station where one individual was very rich in 18:4(n-3), while another individual had only small amounts of this fatty acid. The 18:4(n-3) fatty acid is typical for summer phytoplankton populations, such as flagellates (Harrington et al. 1970), and strongly indicates a non-diatom input (Graeve et al. 1994). This fatty acid was also found to be strongly enriched in calanoid copepods from this area (Kattner et al. 1989; Graeve et al. 1994; Kattner and Hagen 1995). This difference suggests a different nutrition of the two individuals within a very small area.

The isopod *Arcturus baffini* and the pantopod *Nymphon hirtipes* are other prime examples of the dietary influence on the fatty acid composition. The isopod belongs to a family of highly specialised, semi-sessile suspension feeders (Wägele 1987), whereas the pantopod is known to feed on sessile small-sized prey such as hydrozoans, alcyonarians, bryozoans etc. (Arnaud and Bamber 1987). Both specimens from the northeast Greenland shelf had extremely high levels of the 16:1(n-7) fatty acid, in contrast to moderate amounts in the individual from the Spitsbergen shelf. The enhanced level of the 16:1(n-7) fatty acid in most of the benthic organisms from the northeast Greenland shelf indicates that dietary fatty acids are important components in benthic animals. To what extent typical fatty acids are incorporated unmodified by benthic organisms is, of course, also dependant on the water depth in which they occur, since the lipid compositions of phytoplankton and detritus can be altered considerably during sedimentation due to catabolic processes (Peake et al. 1974; Wakeham et al. 1980; Kawamura & Ishiwatari 1981; Santos et al. 1994; Yunker et al. 1995). However, large diatom cells are known for their fast sedimentation to the seafloor, thus offering a nutritious diet to the benthic community (Yunker et al. 1995). Since phytoplankton marker fatty acids can be ingested by benthic specimens directly via phytoplankton and particles, as well as indirectly via zooplankton, the definite origin is uncertain. However, if for example, the 16:1(n-7) fatty acid originates from zooplankton, the wax ester typical fatty acids and alcohols have to be catabolised since neither intact wax esters nor their moieties were found in these species.

From the occurrence of specific lipid classes, such as wax esters, one can also conclude about diet and feeding behaviour. Wax esters can be synthesised by the benthic specimens themselves or originate from the diet. The first alternative cannot be excluded but the relatively low levels of wax esters suggest a dietary input. One important source of wax esters for benthic organisms are wax ester-rich copepods. Large herbivorous calanoid copepods especially accumulate high amounts of wax esters that are composed of fatty acids and alcohols not found in phytoplankton and other particulate matter, i.e. the long-chain monounsaturates 20:1(n-9) and 22:1(n-11) (Lee 1975; Sargent and Henderson 1986; Tande and Henderson 1988; Kattner et al. 1989). The alcohol moieties of the wax esters of omnivorous and carnivorous species are dominated by 14:0 and 16:0 alcohols (Falk-Petersen et al. 1987; Albers et al. in press). Among the benthos, wax esters were only found in three species, particularly in two actinarian species and, albeit only in trace amounts, in *Heliometra glacialis*. Their wax esters contained alcohols that occur in herbivorous, as well as in other, copepods. This finding can be explained by the feeding behaviour known for *Anthosactis janmayeni.* This is a sessile carnivore capturing small swimming animals with cnidocyte-laden tentacles (Brusca and Brusca 1990). The wax ester levels in *H. glacialis* were present in too small amounts to be indicative of its feeding mode.

The occurrence of fatty acids typical for animals rich in wax esters also provided some clues on the preferred food. The benthic species do not apparently synthesise wax esters, although in some species high amounts of the wax ester typical fatty acids, 20:1(n-9) and 22:1(n-11), were detected corresponding to the fatty alcohol moieties with the same structure. These fatty acids were found in considerable amounts in the amphipod *Anonyx nugax* and the unidentified anemone from the Barents Sea, which suggests that they had probably fed on copepods. *Anonyx nugax* is known as one of the most common scavengers in Arctic waters. However, it has also been reported to be a predatory species (Weslawski 1991) and this is corroborated by our results. Wax ester fatty acids were also detected in two brittle stars, *Ophiura sarsi* and *Ophiopleura borealis*, but in much lower amounts. This reflects a feeding behaviour that it is different from that of *Anonyx nugax*. The brittle stars are known to be very opportunistic, utilising a wide range of food sources. The incorporation of wax ester typical fatty acids might be caused by ingestion of copepods.

In conclusion, lipid analyses were shown to be useful for deducing the principal food sources of benthic species. The ratio of 18:1(n-9) to 18:1(n-7) especially reflects different feeding behaviours and, partially, the trophic levels. Clearly increasing ratios were found along a gradient from suspension feeders, exploiting freshly sedimented material, via predatory decapods to the scavenging amphipods. The incorporation of dietary fatty acids limits the use of fatty acids as taxon-specific markers. However, lipid determinations seem to be a promising tool to elucidate the adaptations to the seasonally pulsed food supply in polar regions. To further clarify the role and origin of the fatty acids with special regard to the diet, feeding experiments should be performed.

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