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Lipids and trophic interactions of ice fauna and pelagic zooplankton in the marginal ice zone of the Barents Sea

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Abstract *Gammarus wilkitzkii*, *Apherusa glacialis*, *Onismus nanseni*, *Onismus glacialis*, *Boreogadus saida*, *Parathemisto libellula* and *Calanus hyperboreus*, collected in late June in the Barents Sea marginal ice zone, contained substantial levels (28–51% of the dry mass) of total lipid, the highest levels (51% and 41% respectively) being in *A. glacialis* and *C. hyperboreus*. Neutral lipids were present in greater amounts than polar lipids in all species. Triacylglycerols were major neutral lipids in *A. glacialis*, *G. wilkitzkii* and *O. nanseni*; triacylglycerols and wax esters were present in similar amounts in *O. glacialis*; higher levels of wax esters than triacylglycerols occurred in *P. libellula*; wax esters greatly exceeded triacylglycerols in *C. hyperboreus*, the opposite being true for *B. saida*. Diatom fatty acid markers were prominent in the triacylglycerols of *G. wilkitzkii*, *O. nanseni*, *O. glacialis* and, particularly, of *A. glacialis*; 20:1(n-9) and 22:1(n-11) moieties were abundant in wax esters of *G. wilkitzkii*, *O. nanseni*, *O. glacialis*, *P. libellula* and *C. hyperboreus*, and in triacylglycerols of *B. saida*. We deduce that *A. glacialis* feeds mainly on ice algae and phytodetritus, *G. wilkitzkii* and the *Onismus* spp. feed on calanoid copepods as well as ice algae, whereas *P. libellula* and especially *B. saida* feed extensively on calanoid copepods.

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Introduction

Rapidly growing and dividing phytoplankton contain ca. 10–20% of their dry mass as lipid consisting mainly of polar lipid that is rich in n-3 polyunsaturated fatty acids (PUFA) (Sargent et al. 1985). The main PUFA of diatoms are 20:5(n-3) and a range of C16 PUFA, especially 16:4(n-1), whereas the main PUFA of flagellates including dinoflagellates and haptophytes are 18:4(n-3) and 22:6(n-3) (Sargent et al. 1987; Graeve et al. 1994a). Ice algae from the Marginal Ice Zone (MIZ) consist mainly of diatoms dominated by assemblages of *Melosira arctica* and *Nitzschia frigida*, and the total lipid of both species is rich in C16 PUFA, especially 16:4(n-1), and 20:5(n-3) (Falk-Petersen et al. in press). Open water phytoplankton from the MIZ is richer in flagellates than the ice algae and contains proportionally less C16 PUFA and 20:5(n-3), and proportionately more C18 PUFA and 22:6(n-3) (Falk-Petersen et al. in press).

Pelagic herbivorous zooplankton retains ingested phytoplanktonic fatty acids, i.e. mainly 14:0, 16:0, 16:1(n-7), C16 PUFA, C18 PUFA, 20:5(n-3) and 22:6 (n-3), and augments its dietary fatty acids by internal *de novo* biosyntheses of saturated and monounsaturated fatty acids and/or fatty alcohols. Such fatty acids and/or fatty alcohols are accumulated as large stores of triacylglycerols or wax esters, particularly in high-latitude species (Lee et al. 1971; Sargent and Henderson 1986; Sargent and Falk-Petersen 1988; Falk-Petersen et al. 1990; Hagen and Schnack-Schiel 1996). The fatty acids and fatty alcohols biosynthesised by zooplankton can be characteristic of the species elaborating them, for example, the 20:1(n-9) and 22:1(n-11) fatty acids and fatty alcohols that are major components of the calanoid wax esters (Sargent and Henderson 1986; Sargent and Falk-Petersen 1988; Falk-Petersen et al. 1990).

Thus, an organism's position in a food web can be illuminated by determining its body lipid composition and identifying particular "trophic marker fatty acids" (Sargent and Whittle 1981; Sargent and Henderson

1986; Sargent et al. 1987; Falk-Petersen et al. 1987; Hopkins et al. 1989; Graeve et al. 1994a,b). We use this approach here to illuminate trophic links in ice fauna and pelagic zooplankton associated with the MIZ in the Barents Sea.

Materials and methods

The ice fauna and zooplankton species analysed were sampled between 17 and 26 June, 1995, at latitude 77.1° to 78.2°N (Fig. 1). Detailed information about the cruise is given in Falk-Petersen and Hop (1996). The samples were taken from three locations: either dense 1st year pack ice with ice concentrations of 8/10–9/10 (ICE 1, Fig. 1), or a vast ice floe of 5 km^2 of thick 1st year hummock ice with ice concentrations of 7/10 (ICE 2, Fig. 1), or small 1st year ice floes with a size of approximately 20–30 m^2 with ice concentrations of 6/10 close to open water (ICE 3, Fig 1). The ship was anchored to the ice floe at the ice stations and the main engine turned off. Under-ice fauna was collected using scuba equipment from the edge of ice floes, with either a rectangular-mouth hand net (Gulliksen 1984) or an electric suction sampler (Lønne 1988). Pelagic zooplankton was collected at each station with a WP-3 net (120 cm opening diameter, 1000 μm mesh size) towed vertically from a depth of 100 m to the surface. Live animals for lipid analyses were immediately identified to species level and then either carefully packed in single layers in plastic bags and stored at −20°C, or dropped into chloroform:methanol (2:1, v/v) contained in Teflon-capped glass vials and stored at −20°C. Other animals were frozen at −20°C, weighed and then dried at 60°C for 12 h to determine the % of wet mass as dry mass.

Total lipid was extracted from known wet masses of identified samples of zooplankton and ice fauna by the method of Folch et al. (1957) and the lipid class composition measured by quantitative thin-layer chromatography (TLC)-densitometry (Olsen and Henderson 1989). Triacylglycerols and wax esters were separated on TLC silica gel plates using hexane:diethyl ether:acetic acid (90:10:1, v/v/v). The resultant lipid classes, as well as total lipid from each sample, were supplemented with a known amount of the fatty acid 21:0 as internal standard and transmethylated in methanol containing 1% sulphuric acid with toluene for 16 h at 50°C. The reaction products were extracted into ether, dried under nitrogen and subjected to TLC in hexane:diethyl ether:acetic acid (70:30:1, v/v/v) to separate fatty acid methyl esters and free fatty alcohols. These were recovered from the plates and the fatty alcohols converted to acetate derivatives by reacting with acetic anhydride in pyridine (Farquhar 1962). Fatty acid methyl esters and fatty alcohol acetates were identified and quantified by gas-liquid chromatography, by comparison with the internal standard and a well-characterised marine fish oil (Tande and Henderson 1988).

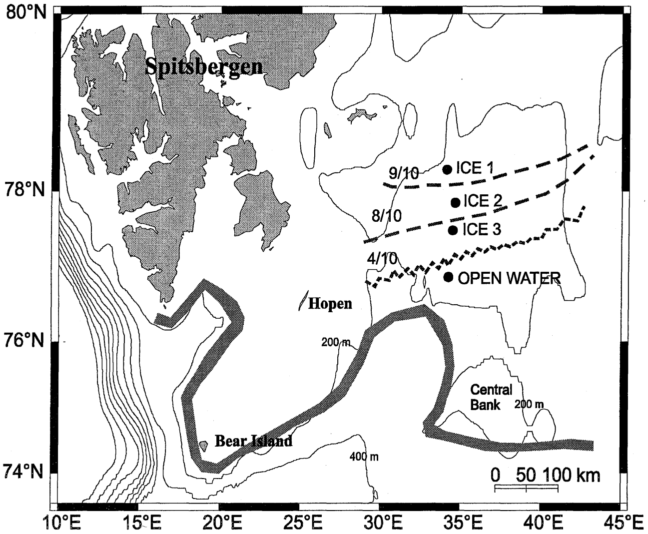

Fig. 1 Position of Ice Stations in the Barents Sea. Ice Station 1 was situated in dense first year ice with concentrations of 8/10 to 9/10. Ice Station 2 was situated in thick first year hummock ice with ice concentrations of 7/10. Ice Station 3 was located in an area with small first year ice floes with a ice concentration of 6/10

Results

The lipid class analyses revealed, for any given species, only small differences between the three ice stations. Therefore, the data are presented for each species as mean values for the three ice stations combined. The mean percentages of total lipid in the dry mass of the ice faunal and pelagic species analysed ranged from a modest 28% in *Gammarus wilkitzkii* to a substantial 51% in *Apherusa glacialis* (Table 1).

All species had very significant levels of free fatty acids in their total lipid (Table 1). This could be indicative of active ingestion and digestion of dietary lipid by the animals immediately prior to their capture. Alternatively, significant hydrolyses of total lipid may have occurred post-sampling, in which case the percentages of polar lipid and neutral lipids in total lipid in Table 1 will be underestimated and overestimated respectively. However, this does not materially alter a major conclusion from Table 1 that all the ice faunal species, *Gammarus wilkitzkii*, *Apherusa glacialis*, *Onismus nanseni* and *Onismus glacialis*, contain substantially more neutral lipid than polar lipid and, for the first three species, the neutral lipid is predominantly triacylglycerols. Only in *O. glacialis* does the level of wax esters approach that of triacylglycerols. *Parathemisto libellula* differs from the other species analysed by having a substantially higher level of polar lipid. It also has a higher level of wax esters than triacylglycerols in its relatively low level of neutral lipid. *Calanus hyperboreus* has wax esters as its major lipid whereas polar cod (*Boreogadus saida*) has triacylglycerols as its major lipid.

Fatty acid analytical data also varied much less between the three ice stations for a given species sampled than between different species at the same ice station and are consequently presented as means for a given species at the three ice stations. The results (Table 2) show that *A. glacialis* has the highest percentages of 16:1(n-7), C16 PUFA especially 16:4(n-1), and 20:5(n-3) in its triacylglycerols of all the species analysed. The amphipod *Gammarus wilkitzkii* differs from *A. glacialis* in having substantially lower percentages of 16:1(n-7) and C16 PUFA in its triacylglycerols, this being offset by higher percentages of 18:1(n-9), 20:1(n-9) and 22:1(n-11), the latter two fatty acids being negligible in *A. glacialis*. The trends of decreasing 16:1(n-7) and 20:5(n-3), and increasing 20:1(n-9) and 22:1(n-11) in the triacylglycerols

Table 1 Lipid class composition of ice fauna and pelagic zooplankton from the Barents Sea MIZ. Data are mean values ± SD from analyses of individual specimens of the species collected from the three ice stations (Abbreviations: *DM* dry mass; *TL* total lipid; *PL* polar lipid; *NL* neutral lipid; *Chol* cholesterol; *FFA* free fatty acids; *TAG* triacylglycerols; *WE* wax esters; *nd* not determined)

Species	Length (mm)	TL (%DM)	PL (%TL)	NL (%TL)	Chol (%TL)	FFA (%TL)	TAG (%TL)	WE (%TL)
Apherusa	10.9	50.9	8.1	78.0	8.2	21.6	43.7	4.5
glacialis (*n* = 10)	± 1.1	± 6.2	± 3.0	± 7.0	± 2.8	± 5.9	± 9.4	± 3.0
Gammarus	23.3	27.6	14.5	80.9	5.5	13.2	43.5	18.6
wilkitzkii (*n* = 30)	± 5.3	± 5.4	± 5.1	± 9.5	± 2.8	± 4.9	± 10.8	± 6.2
Onismus	17.4	35.4	8.1	89.3	3.8	7.0	58.4	20.1
nanseni (*n* = 10)	± 2.1	± 4.9	± 2.7	± 8.6	± 0.8	± 1.1	± 5.8	± 10.1
Onisimus	10.1	38.6	11.9	83.8	4.6	17.2	32.0	30.0
glacialis (*n* = 10)	± 3.2	± 10.9	± 8.0	± 8.1	± 2.4	± 4.5	± 8.2	± 13.1
Parathemisto	9.2	38.9	39.9	48.8	5.3	15.3	10.5	17.7
libellula (*n* = 8)	± 5.3	± 7.9	± 26.4	± 21.0	± 2.7	± 7.9	± 2.1	± 1.6
Calanus	nd	40.9	15.0	76.7	1.1	12.6	9.7	53.4
hyperboreus (*n* = 9)		± 8.2	± 4.7	± 6.5	± 1.4	± 3.3	± 7.1	± 8.0
Boreogadus	85.8	35.8	18.2	81.3	7.7	10.9	58.4	4.4
saida (*n* = 10)	± 8.8	± 4.9	± 2.1	± 6.5	± 1.5	± 2.8	± 6.3	± 1.0

of *G. wilkitzkii* are more marked in the triacylglycerols of both *O. nanseni* and *O. glacialis*, where 20:1(n-9) is especially prominent and 22:1(n-11) is also notable. However, the percentages of 18:1(n-9) in the triacylglycerols of the two *Onismus* spp. are not notably lower than in *G. wilkitzkii*. In contrast, 18:1(n-9) is notably decreased in the triacylglycerols of *P. libellula*, which are again rich in 20:1(n-9) and 22:1(n-11). The triacylglycerols of the polar cod contain the highest levels of 20:1(n-9) and 22:1(n-11) of all the species analysed in this study. The PUFA 20:5(n-3) and 22:6(n-3) are significant constituents of the triacylglycerols of all the species analysed and, except for *C. hyperboreus*, 20:5(n-3) is consistently present at a higher percentage than 22:6(n-3).

The compositions of the fatty acids and fatty alcohols of the wax esters present in the species analysed are shown in Tables 3 and 4. *A. glacialis* has very low levels of wax esters (Table 1), which are notable in having very low levels of 20:1(n-9) and 22:1(n-11) fatty acids (Table 3) and zero levels of 20:1(n-9) and 22:1(n-11) fatty alcohols (Table 4). This is in marked contrast to all the other species where 20:1(n-9) and 22:1(n-11) are very prominent fatty acids in the wax esters (Table 3) and 20:1(n-9) and 22:1(n-11) are dominant fatty alcohols (Table 4). The abundance of 20:1 and 22:1 fatty acids and fatty alcohols in the wax esters of *C. hyperboreus*, shown in Tables 3 and 4, is typical of wax ester-rich, high-latitude calanoids. Strictly limited amounts of fatty alcohols were available for analyses from *A. glacialis* so

Table 2 Fatty acid composition (mass %) of triacylglycerols in ice fauna and pelagic zooplankton from the Barents Sea MIZ. The data are mean values for triacylglycerols isolated from the samples of total lipid from the individual specimens in Table 1. SD are omitted for clarity (*tr* < 0.5%; 0.0 not detected)

Fatty acid	*Apherusa glacialis*	*Gammarus wilkitzkii*	*Onismus nanseni*	*Onismus glacialis*	*Parathemisto libellula*	*Calanus hyperboreus*	*Boreogadus saida*
14:0	5.5	5.5	2.8	3.2	8.2	2.0	5.2
16:0	16.7	11.4	8.5	11.8	11.4	8.6	8.1
16:1n-7	39.8	21.4	16.8	18.0	9.3	7.9	13.3
16:2	1.8	0.9	0.5	0.6	2.4	0.0	0.6
16:3	0.8	0.8	tr	0.0	0.5	0.0	0.0
16:4n-1	2.9	0.8	tr	0.0	1.1	0.0	0.0
18:0	0.9	0.7	tr	0.6	tr	2.4	1.2
18:1n-9	4.9	22.2	14.1	19.7	4.1	11.8	8.0
18:1n-7	1.9	4.3	3.0	3.3	1.4	2.2	2.6
18:2n-6	0.7	1.2	1.1	0.9	0.6	1.3	1.2
18:3n-6	0.8	tr	0.0	tr	tr	0.0	0.0
18:3n-3	tr	tr	tr	tr	tr	1.0	0.5
18:4n-3	2.7	1.8	0.9	tr	2.4	2.1	1.0
20:1n-9	0.8	6.9	23.9	27.9	21.8	15.2	27.8
20:1n-7	tr	0.7	3.0	0.0	0.6	2.6	0.0
20:4n-6	tr	tr	tr	tr	tr	tr	tr
20:4n-3	0.5	0.5	tr	tr	0.5	0.0	tr
20:5n-3	16.0	11.4	5.6	2.3	12.7	4.3	3.5
22:1n-11	tr	3.6	6.7	8.0	12.0	22.0	21.1
22:5n-3	tr	tr	tr	tr	0.6	0.5	tr
22:6n-3	1.5	2.9	2.7	1.5	7.7	10.6	4.7
C16 PUFA	5.5	2.4	0.5	0.6	4.0	0.0	0.6
(n-6) PUFA	1.7	1.7	1.4	1.3	1.2	1.5	1.2
(n-3) PUFA	21.1	17.2	10.0	4.3	24.3	18.5	10.2

Table 3 Fatty acid composition (mass %) of wax esters in ice fauna and pelagic zooplankton from the Barents Sea MIZ. The data are mean values for wax esters isolated from samples of total lipid from the individual specimens in Table 1. SD are omitted for clarity (*tr* < 0.5%; 0.0 not detected)

Fatty acid	*Apherusa glacialis*	*Gammarus wilkitzkii*	*Onismus nanseni*	*Onismus glacialis*	*Parathemisto libellula*	*Calanus hyperboreus*	*Boreogadus saida*
14:0	0.5	2.0	1.2	1.7	2.5	1.6	3.7
16:0	23.5	2.3	1.5	3.4	2.3	1.6	7.5
16:1n-7	38.8	10.5	17.6	14.6	14.4	27.4	11.5
16:2	1.3	tr	tr	0.5	0.5	1.3	0.6
16:3	0.0	tr	tr	0.6	0.5	0.8	0.6
16:4n-1	0.0	tr	0.0	0.7	1.0	0.9	0.7
18:0	0.0	0.5	tr	0.5	tr	tr	1.7
18:1n-9	12.9	17.8	15.1	10.8	11.8	13.4	7.0
18:1n-7	0.0	3.0	2.0	1.8	2.7	1.1	2.1
18:2n-6	0.6	0.6	0.9	0.8	2.3	1.9	1.5
18:3n-6	0.0	tr	0.0	0.0	tr	tr	tr
18:3n-3	0.0	tr	0.0	0.0	0.8	0.9	0.5
18:4n-3	2.8	tr	0.0	1.4	4.2	3.7	2.9
20:1n-9	6.8	21.4	37.8	35.1	37.5	16.6	19.9
20:1n-7	0.0	2.6	3.7	3.7	0.7	1.2	0.0
20:4n-6	0.0	tr	0.0	0.0	tr	tr	tr
20:4n-3	0.0	tr	0.0	tr	tr	0.7	0.6
20:5n-3	6.2	4.1	0.0	8.8	1.6	7.5	17.0
22:1n-11	2.0	29.9	15.7	11.3	9.6	10.8	10.0
22:5n-3	0.0	tr	0.0	tr	tr	0.5	0.6
22:6n-3	1.4	2.4	1.1	1.6	4.5	5.5	10.7
C16 PUFA	1.3	0.0	0.0	1.8	2.0	3.0	1.9
(n-6) PUFA	0.6	0.8	0.9	0.8	4.1	2.5	1.9
(n-3) PUFA	10.5	7.3	1.1	12.2	11.6	18.7	32.3

that the atypical abundance of 18:0 and especially 24:1(n-9) should be regarded as a preliminary finding until validated by further analyses.

Discussion

According to the terminology of Lønne and Gulliksen (1991), ice fauna is sympagic, i.e. it encompasses all animals living temporarily or permanently in physical contact with the submerged parts of sea ice. Autochthonous sympagic species are species derived from ice sites and they dependent on permanent ice cover throughout their life-cycle. Allochthonous sympagic species are temporarily associated with ice, originate from outside the ice sites and are relatively rare. The true macro ice-fauna (Gulliksen and Lønne 1991) uses the lower layer of the sea ice as substratum and consists of four amphipods: *A. glacialis*, *G. wilkitzkii*, *O. nanseni* and *O. glacialis*. *A. glacialis* is regarded as one of the most numerous and prominent species of the true ice-fauna in the Arctic (Lønne and Gulliksen 1991). *G. wilkitzkii* is also quantitatively important and is often more abundant in the multi-year ice (Melnikov and Kulikov 1980). Polar cod (*B. saida*) is also regarded as a member of the true ice-fauna, with mostly juvenile cod (ages 1–2 years) present in cavities in the ice. The macro zooplankton associated with the open water between the floes and the pelagic zone under the ice is dominated by

Table 4 Fatty alcohol compositions (mass %) of wax esters in ice fauna and pelagic zooplankton from the Barents Sea MIZ. The data are mean values for wax esters isolated from samples of total lipid from the individual specimens in Table 1. SD are omitted for clarity (*tr* < 0.5%; 0.0 not detected)

Fatty alcohol	*Apherusa glacialis*	*Gammarus wilkitzkii*	*Onismus nanseni*	*Onismus glacialis*	*Parathemisto libellula*	*Calanus hyperboreus*	*Boreogadus saida*
14:0	4.3	1.5	1.8	3.0	2.1	13.7	2.8
16:0	9.3	7.1	7.4	11.9	6.7	11.3	13.6
16:1n-7	0.0	0.0	0.0	0.0	0.0	3.4	6.9
18:0	10.8	0.3	1.4	2.8	0.4	0.4	3.0
18:1n-9	0.0	0.6	0.5	1.3	1.2	1.0	1.2
phytol	0.0	0.6	0.0	0.0	1.2	0.6	0.0
18:1n-7	0.0	0.9	0.5	0.0	1.4	2.2	0.6
20:1n-9	0.0	33.9	20.7	40.3	42.6	28.8	36.9
20:1n-7	0.0	1.7	tr	0.0	0.0	0.0	0.0
22:1n-11	0.0	52.7	59.0	31.2	45.1	27.0	34.2
22:1n-9	0.0	0.5	3.7	0.0	0.0	10.9	0.0
24:1	42.2	0.6	2.6	9.6	0.5	0.6	0.8

calanoid copepods, the amphipod *P. libellula* and occasionally krill, mainly *Thysanoessa inermis* although *T. raschi* is also present (Gulliksen 1984; Lønne 1992).

Ice algae, i.e. algae found in or attached to sea ice, are composed principally of diatoms, whereas in open waters between ice floes both diatoms and flagellates are common. In a recent study ice algae from the MIZ in the Barents Sea could be separated into two categories, one dominated by assemblages of *Melosira arctica*, and the other dominated by assemblages of *Nitszchia frigida* and associated diatoms (Falk-Petersen et al. in press). Total lipid from both of these assemblages is rich in the typical diatom fatty acid markers 16:1(n-7), C16 PUFA especially 16:4(n-1) and 20:5(n-3) (Falk-Petersen et al. in press). The fatty acid composition of the triacylglycerols of the amphipod *A. glacialis* analysed here strongly indicates herbivorous feeding, since 16:1(n-7) and 20:5(n-3) contribute more than 50% of the fatty acids present. Moreover, only trace amounts of 20:1(n-9) and 22:1(n-11) are present indicating a negligible consumption of calanoid copepods. Furthermore, the fatty acids identified in the triacylglycerols of *A. glacialis* show substantial amounts of C16 PUFA and the highest level of 16:4(n-1) of all the other ice fauna and pelagic species analysed here. This is consistent with *A. glacialis* feeding directly on the assemblages of *M. arctica* and *N. frigida*, not excluding diatom detritus associated with its ice floe habitat. The unusual fatty alcohol composition of the wax esters of *A. glacialis* may be consistent with the presence of detrital material in its diet.

The two *Onismus* species and *G. wilkitzkii* show a different fatty acid composition from *A. glacialis*, especially with respect to their high levels of 20:1(n-9) and 22:1(n-11). There is, as yet, no evidence that marine organisms other than calanoid copepods synthesise 20:1(n-9) and 22:1(n-11) in significant amounts *de novo* (Sargent and Henderson 1986; Sargent and Falk-Petersen 1988; Falk-Petersen et al. 1990). Therefore, the results here point to *G. wilkitzkii* and both of the *Onismus* species consuming calanoid copepods. Furthermore, there are significant amounts of the diatom-derived fatty acids 16:1(n-7) and 20:5(n-3) in the lipids of *G. wilkitzkii* and the two *Onismus* species. Therefore *G. wilkitzkii* and the *Onismus* spp. can be considered omnivorous. However, the relative levels of herbivore-specific fatty acids are higher in *G. wilkitzkii* than in the *Onismus* spp., whereas 18:1(n-9) is more abundant in the *Onismus* spp. This is consistent with the former species consuming greater quantities of ice algae, i.e. being more herbivorous, than the latter.

High energy, long-chain monounsaturated fatty acids and alcohols synthesised as 20:1(n-9) and 22:1(n-11) moieties of wax esters are abundant in herbivorous copepods such as the Antarctic *Calanus acutus* and the Arctic *C. hyperboreus*, *C. finmarchicus* and *C. glacialis* (Lee 1974, 1975; Falk-Petersen et al. 1987; Tande and Henderson 1988; Kattner et al. 1989; Hagen et al. 1993). Wax esters are thought to be more energetically valuable as storage lipids compared to triacylglycerols (Hagen et al. 1993) and longer chain fatty acids and fatty alcohols have a higher calorific value than their shorter chain counterparts (Kattner and Hagen, 1995). Accumulation of large amounts of wax esters is indicative of a markedly seasonal feeding pattern exemplified by the wax ester-rich Antarctic *C. acutus*. In contrast, its congener *C. propinquus* stores large amounts of triacylglycerols and probably feeds year-round (Schnack-Schiel et al. 1991; Hagen et al. 1993; Hagen and Schnack-Schiel 1996), as does the triacylglycerol-rich *Euphausia superba* (Clarke 1980; Knox 1994; Hagen et al. 1996). *A. glacialis* is the most lipid-rich of all the species analysed here and triacylglycerols are its sole neutral lipid. Given the year-round availability of ice algae, it is probable that *A. glacialis* feeds throughout the year. However, the availability and also the nutritional quality of ice algae are likely to decrease throughout the long winter season in parallel with a relative increase of ice algal-derived phytodetritus.

G. wilkitzkii and the two *Onismus* species have lesser amounts of triacylglycerols than *A. glacialis* and this supports our conclusion, based on the fatty acid analyses, that these species are omnivorous members of the ice fauna. Bradstreet and Cross (1982) found crustacean parts in the guts of *G. wilkitzkii* and *P. libellula*. Members of the genus *Onismus* are considered to be phytophagous by Horner (1989) and Bradstreet and Cross (1982), and are also thought to be highly adapted necrophages (Sainte-Marie 1984; M. Poltermann, personal communication) with an omnivorous scavenger mode throughout winter (Percy 1979).

P. libellula in the MIZ has no obviously dominant neutral lipid class, with wax esters accounting for less than 20% of its total lipid and triacylglycerols about 10%. Falk-Petersen et al. (1987) consider *P. libellula* to be mainly carnivorous whereas Bradstreet and Cross (1982) believe the species to be omnivorous. The fatty acid analysis of its wax esters points to an omnivorous diet in that both diatom and dinoflagellate markers are present as well as copepod markers. In the pelagic species *P. libellula* and *C. hyperboreus*, dinoflagellate markers 18:4(n-3) and 22:6(n-3) are relatively high compared with the ice fauna and the diatom marker 16:4(n-1), linked with the ice algae, is notably absent. This illustrates the differences in phytoplankton species and fatty acid compositions between the ice habitat and the pelagic habitat.

Polar cod (*B. saida*) has triacylglycerols with fatty acid compositions typical of a carnivore consuming large amounts of copepods rich in 20:1(n-9) and 22:1(n-11) entities. Polar cod are allochthonous sympagic members of the ice fauna with only the juveniles living within the ice. All the cod sampled here were less than 11 cm in length, i.e. 1 year old or less (Gjøsæter and Ajiad 1994). Juvenile polar cod feed predominantly on calanoid copepods, with the diets of older fish including also amphipods, mysids, ostracods and chaetognaths (Bradstreet and Cross 1982; H. Hop, personal communication).

Finally, the analyses here were performed on specimens collected at one time of the year only and at three sites only. The similarity in lipid contents and compositions for given species between the three sites suggests, perhaps surprisingly, that the ice fauna is uniform over the wide area of the MIZ sampled. However, this may well reflect the temperature and light regimes being essentially invariant over the area. Continuing studies over additional sites and over a yearly cycle are required to evaluate fully spatial and temporal variability in the ice fauna. Irrespective of the outcome, this study is consistent with ice algae and ice fauna playing a substantial role in polar ecosystems, not least as potentially important food sources for over-wintering marine animals.

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