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Food utilization of two pelagic crustaceans in the Greenland Sea: *Meganyctiphanes norvegica* (Euphausiacea) and *Hymenodora glacialis* (Decapoda, Caridea)

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ABSTRACT: Large pelagic crustaceans from Greenland Sea waters, the northern krill *Meganyctiphanes norvegica* (Euphausiacea) and the decapod shrimp *Hymenodora glacialis* (Caridea), were captured in depths down to 1500 m and studied with respect to their physiological food utilization abilities. Both species showed distinct differences in the amount of total lipids (TLs), lipid class and fatty acid (FA) compositions as well as proteolytic enzyme activities. In *M. norvegica*, the overall amount of TLs and storage lipids was much lower than in *H. glacialis*, and triacylglycerols formed the major lipid fraction with a mean of 48% TLs. Major FAs comprised the trophic markers 20:1(n-9) and 22:1(n-11), indicating the ingestion of calanid copepods. Additionally, the FAs 22:6(n-3), 18:1(n-9) and 16:0 prevailed. In *H. glacialis*, TLs (mean = 44% dry mass) were about twice as high as in krill, with wax esters comprising up to 89% TLs. *H. glacialis* seems to accumulate these lipids as energy reserves to survive periods of food limitation. Moreover, high lipid levels, particularly wax esters, also help to maintain neutral buoyancy. The major FA in *H. glacialis* was 18:1(n-9); other dominant FAs were 20:1(n-9) and 22:1(n-11), typical of calanid copepods, as well as the diatom trophic marker 16:1(n-7). Both species showed omnivorous feeding behaviour with a strong tendency towards carnivory. Total proteolytic activities in midgut gland tissue were higher in *M. norvegica* than in *H. glacialis*. In *M. norvegica*, proteinases were dominated by serine proteinases, whereas cysteine proteinases formed the major group in *H. glacialis*. High proteolytic activity in *M. norvegica* indicates a high digestive potential for proteins and efficient utilization of prey. The presence of different proteinase classes in both species may be due to different group-specific enzyme expression patterns between euphausiids and caridean decapods. Both species follow highly deviating life strategies, as reflected by their specific lipid and enzymatic characteristics.

KEY WORDS: Life strategies · Feeding · Lipids · Fatty acids · Trophic markers · Proteinases

INTRODUCTION

Marine pelagic invertebrates show a variety of ecological and physiological strategies to cope with abiotic and biotic environmental factors such as currents, temperature or food availability. Particularly, high-latitude regions provide challenging conditions for zooplankton species. Productivity of polar and sub-polar regions is restricted to the short summer season. During polar winter, however, phytoplankton production is primarily limited by low light intensity (Codispoti et al. 1991).

Northern krill *Meganyctiphanes norvegica* (Euphausiacea) appear frequently in the northern and northeastern parts of the Atlantic Ocean. *M. norvegica* covers a wide distributional area from the Mediterranean to sub-polar waters but is not an explicit Arctic species (Mauchline & Fischer 1969, Mauchline 1980). Northern krill is able to perform extended diel vertical

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migrations of more than 800 m as shown in the Mediterranean by Tarling et al. (2001). At night the animals enter the productive surface layers, where they feed on phytoplankton and small zooplankton (Sameoto 1976, 1980, Lass et al. 2001), while they descend to deeper layers during daytime.

Hymenodora glacialis (Oplophoridae) is a genuine deep-water decapod inhabiting Arctic waters (Ritterhoff & Zauke 1997, Auel & Hagen 2002) and Northeast Atlantic deep-sea basins (Domanski 1986). Its vertical distribution ranges between 200 and 4100 m. It was classified as truly bathypelagic (Mauchline 1988) and may dominate macrozooplankton biomass in the Arctic deep water (Auel & Hagen 2002).

Both species co-occur in the Greenland Sea, a region with highly variable seasonal food availability. Strategies to successfully cope with food limitation during the winter may comprise elevated protein catabolism, shrinking of body mass, decrease of metabolic rates or diapausing (Ikeda & Dixon 1982, Quetin & Ross 1991, Torres et al. 1994). The efficiency of prey utilization and the ability to accumulate large energy reserves represent other physiological key adaptations to survive unfavourable polar conditions.

We performed a comparative niche-overlapping study between the euphausiid *Meganyctiphanes norvegica* and the decapod *Hymenodora glacialis* to investigate their physiological capabilities with regard to lipid storage and alimentary protein utilization. A huge body of literature exists on the biology and life history of *M. norvegica*. In contrast, very little is known about the biology and ecophysiology of *H. glacialis*, since this species is much less abundant and therefore not easy to sample. This comparative study aims at elucidating the life strategies and ecophysiological adaptations of *M. norvegica* and *H. glacialis*.

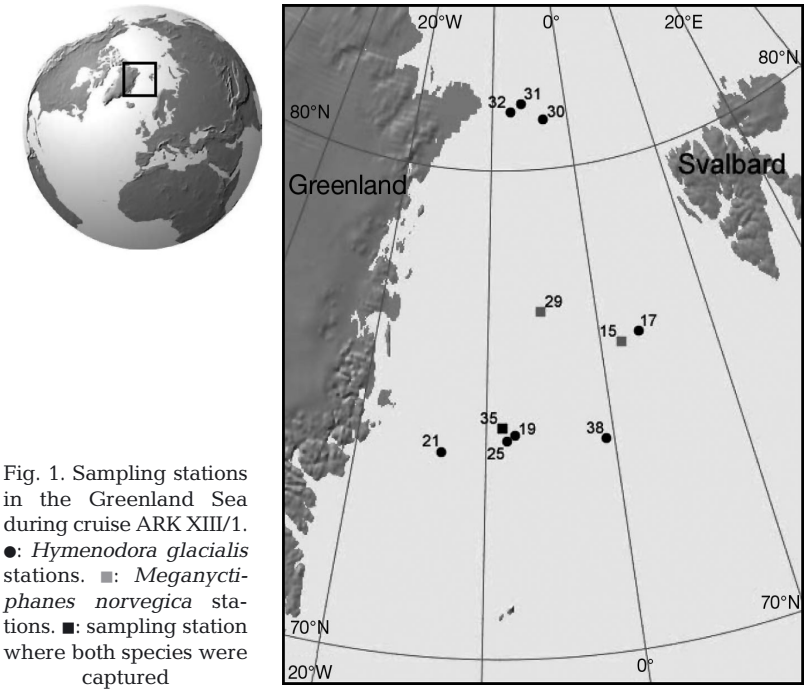

Fig. 1. Sampling stations in the Greenland Sea during cruise ARK XIII/1. ●: *Hymenodora glacialis* stations. ■: *Meganyctiphanes norvegica* stations. ■: sampling station where both species were captured

MATERIALS AND METHODS

Origin of animals. *Meganyctiphanes norvegica* and *Hymenodora glacialis* were caught in May–June 1997 during the ARK XIII/1 cruise of RV 'Polarstern' to the Greenland Sea (74° 41′ N to 80° 58′ N, 13° 08′ W to 04° 39′ E; Fig. 1). Sampling was performed with a rectangular midwater trawl, a bongo net or a multinet (Spindler et al. 1998). Sampling depth ranged from 1500 m to the surface. Net hauls lasted for ≤60 min. Immediately after capture, specimens were briefly rinsed with distilled water, gently blotted dry on filter paper, shock-frozen, and shipped at −80°C to the home laboratories. The biochemical analyses were carried out only on adult individuals with a length of >30 mm in the case of *H. glacialis* (Mauchline 1988) and 25 mm in the case of *M. norvegica*, measured from the eyes to the telson tip (Einarsson 1945, Boysen & Buchholz 1984). The individuals were in the intermoult stage and ovigerous females were among the samples.

Analysis of total lipid, lipid classes, fatty acids and fatty alcohols. Frozen whole animals were weighed in evacuated glass vials for wet mass determination. Dry mass (DM) was measured after 48 h of lyophilisation (Leybold-Heraeus, LYOVAC GT2). Lipids were extracted with dichloromethane:methanol (2:1 v/v). The lipid content was determined gravimetrically (Hagen 2000). In order to prevent alterations in lipid composition, lipid extracts were stored at −80°C. Lipid classes were separated and analysed after Fraser et al. (1985) by thin-layer chromatography flame ionisation detection (TLC-FID) with an IATROSCAN (Iatron Laboratories, MK-5 TLC/FID Analyser). Fatty acids (FAs) and fatty alcohols were extracted after Kattner & Fricke (1986) and analysed by gas chromatography (Hewlett Packard, HP 6890 Series) on a wall coated DB-FFAP column (30 m × 0.25 mm i.d., film thickness 0.25 µm) using a temperature programme (start 165°C, 4°C min^{-1}, end 240°C for 15 min).

Extracts for enzyme assays. Midgut gland tissue (up to 50 mg) was dissected from frozen animals, transferred into

cooled 1.5 ml reaction tubes and weighed. The samples were homogenized in 1 ml of ice-cold demineralised water (aqua dem.). Homogenization was performed with an ultrasonic cell disruptor (Branson, Sonifier Cell Disruptor B15) for 3 × 5 s at 30% of maximum energy, while keeping the samples chilled in an ice-water bath. The homogenates were centrifuged at 15 000 × *g* (4°C) for 15 min. The supernatants (extracts) were transferred into new reaction tubes, kept on ice and used for subsequent protein and enzyme analyses.

Soluble protein content was quantified after Bradford (1976) using a commercial protein assay (BioRad, 500-0006) and BSA (BioRad, 500-0007) as a standard. The assays were carried out in microplates. Samples were applied in triplicate and standards (0 to 5 µg well^{-1}) in duplicate. The optical density of the plates was read after 5 to 15 min of incubation at room temperature with a microplate reader at 600 nm (OD_{600}).

Total proteinase and trypsin activities. Total proteolytic activity was measured with the substrate azocasein. Assays containing 200 µl of buffer (0.1 mol l^{-1} Tris/HCl, supplemented with 10 mmol l^{-1} $CaCl_2$, adjusted to pH 6.0) and 20 µl of sample were first incubated for 5 min at 30°C. Fifty µl azocasein (Fluka 11615, 1% in aqua dem.) were added and incubated for another 30 min at 30°C. The reactions were stopped with 500 µl trichloroacetic acid (8% in aqua dem.) and cooling on ice. Controls received 20 µl of supernatant after the enzymatic reactions were stopped. The reaction cups were centrifuged at 15 000 × *g* (4°C) for 15 min. The supernatants of samples and controls were measured photometrically at 366 nm.

Tryptic activity was measured with N_α-Benzoyl-L-arginine-4-nitroanalide-hydrochloride (L-BAPNA) as substrate. Twenty µl of sample were added to 960 µl of buffer (0.1 mol l^{-1} Tris/HCl, supplemented with 10 mmol l^{-1} $CaCl_2$, pH 8.0) and incubated for 5 min at 30°C. The trypsin assay was started with 20 µl of the substrate L-BAPNA (Fluka, 12915, 50 mmol l^{-1}). The reaction was monitored continuously for 180 s at 405 nm and 30°C. The activity was expressed as U per g fresh mass (g_{FM}^{-1}) (= µmol min^{-1} g_{FM}^{-1}).

Inhibitor studies. Inhibitor assays were carried out as reported by Teschke & Saborowski (2005). Serine proteinase (EC 3.4.21) were inhibited with AEBSF (4-[2-Aminoethyl] benzenesulfonyl fluoride hydrochloride; Merck, Pefabloc® SC) and cysteine proteinase (EC 3.4.22) with E-64 (*trans*-Epoxysuccinyl-L-leucylamido[4-guanidino]butane; Sigma, E 3132). Midgut gland extracts (20 µl) were incubated at 25°C with 20 µl of aqueous solutions of inhibitors (1 mmol l^{-1}). After 60 min, 180 µl of Tris-HCl buffer (0.1 mol l^{-1}, 10 mmol l^{-1} $CaCl_2$, pH 6.0) were added and incubation was continued as described above for the assay of total proteinase. The remaining activity was calculated in relation to a control, which received water but no inhibitors.

Statistics. Statistical analyses were performed with the computer programme SigmaStat (SPSS, Version 2.03). Normal distributions and homogeneity of variances were determined with the Kolmogorov-Smirnov and Levine median tests, respectively. Data sets were compared with a *t*-test, a 1-way ANOVA (data normally distributed) or a Whitney-Mann rank sum test (data not normally distributed). Post-hoc tests consisted of Dunn's or Tukey's tests, respectively. The α-value was set at 0.05. Data in figures and tables are means ± SD.

Similarity analysis of FA data sets was performed with Primer 5 (Primer-E, Version 5.2.9). The data sets consisted of the relative amounts (%) of the FAs in relation to total lipids. Only major fatty acids (≥1% of total fatty acids, TFAs) were considered. The data were arcsin square root-transformed and subjected to a Bray-Curtis similarity analysis. The result of the similarity analysis is presented as a dendrogram using the complete-linkage procedure.

RESULTS

Morphometric data

Adult specimens of *Meganyctiphanes norvegica* which were selected for biochemical analysis ranged in size from 25 to 44 mm. *Hymenodora glacialis* specimens ranged from 30 to 82 mm. The details of morphometric data are listed in (Table 1).

Total lipids and lipid classes

The total lipid concentration was significantly lower in *Meganyctiphanes norvegica* than in *Hymenodora glacialis* (Table 2). In *M. norvegica*, triacylglycerols formed the major portion of total lipids. Conversely, wax esters were the dominant storage lipids in *H. glacialis*, while the concentration of triacylglycerols was low. Free fatty acids appeared in low amounts in both species, indicating a low degree of autolysis of the samples. The amounts of sterols as well as phospholipids were significantly higher in *M. norvegica* than in *H. glacialis*.

In *Meganyctiphanes norvegica* the triacylglycerol content was positively correlated with total lipid content (Fig. 2a). Conversely, in *Hymenodora glacialis* the amount of wax esters was positively correlated with the overall amount of lipids, while no correlation was found between triacylglycerols and total lipids (Fig. 2b). In both species, phospholipids (% DM) re-

Table 1. *Meganyctiphanes norvegica* and *Hymenodora glacialis*. Morphometric details of analysed specimens. M: male; F: female; Lip: lipid analysis; Enz: enzyme assay; nd: not determined

Species and ID	Sampling station	Total length (mm)	Fresh mass (mg)	Dry mass (mg)	Sex	Analysis
Meganyctiphanes norvegica						
Mn-15/1	15	32	nd	16.87	M	Lip
Mn-15/2	15	35	nd	24.45	F	Lip
Mn-29/1	29	37	nd	22.36	F	Lip
Mn-29/2	29	37	nd	27.57	F	Lip
Mn-15/3	15	38	nd	40.01	M	Lip
Mn-15/4	15	40	nd	49.62	F	Lip
Mn-29/3	29	42	nd	26.98	F	Lip
Mn-29/4	29	42	nd	33.11	F	Lip
Mn-15/5	15	42	nd	39.27	M	Lip
Mn-29/5	29	44	nd	22.75	M	Lip
Mn-32/1	32	37	nd	nd	F	Enz
Mn-32/2	35	39	nd	nd	M	Enz
Mn-32/3	35	27	nd	nd	W	Enz
Mn-29/6	29	38	nd	nd	M	Enz
Mn-29/7	29	39	nd	nd	F	Enz
Mn-29/8	29	25	nd	nd	M	Enz
Mn-29/9	29	33	nd	nd	M	Enz
Mn-29/10	29	40	nd	nd	F	Enz
Mn-29/11	29	36	nd	nd	M	Enz
Mean ± SD		37.0 ± 4.96	nd	30.3 ± 10.1		
Range (min.–max.)		25–44	nd	16.87–49.62		
N		19	nd	10		
Hymenodora glacialis						
Hg-17/1	17	35	355.5	57.2	nd	Lip
Hg-31/1	31	35	946.1	177.1	nd	Lip
Hg-32/1	32	35	412.9	77.3	nd	Lip
Hg-25/1	25	37	511.9	141.7	nd	Lip
Hg-38/1	38	37	437.9	93.8	nd	Lip
Hg-25/2	25	39	687.9	165.4	nd	Lip
Hg-21/1	21	40	544	148.7	nd	Lip
Hg-35/1	35	40	1251.2	264.9	nd	Lip
Hg-30/1	30	45	826.7	169.1	nd	Lip
Hg-38/2	38	45	1518.7	369.2	nd	Lip
Hg-32/2	32	47	918.6	100.3	nd	Lip
Hg-25/3	25	49	1142.1	208.9	nd	Lip
Hg-38/3	38	50	1491.7	485.6	nd	Lip
Hg-25/4	25	50	994.4	162.4	nd	Lip
Hg-19/1	19	52	1218.2	248.3	nd	Lip
Hg-32/3	32	52	1176.9	242.8	nd	Lip
Hg-25/5	25	70	3317.4	896.1	nd	Lip
Hg-21/2	21	82	4445.2	1056.6	nd	Lip
Hg-31/2	31	34	nd	nd	nd	Enz
Hg-32/4	32	36	nd	nd	nd	Enz
Hg-32/5	32	37	nd	nd	nd	Enz
Hg-32/6	32	38	nd	nd	nd	Enz
Hg-32/7	32	39	nd	nd	nd	Enz
Hg-32/8	32	40	nd	nd	nd	Enz
Hg-25/6	25	41	nd	nd	nd	Enz
Hg-32/9	32	44	nd	nd	nd	Enz
Hg-25/7	25	46	nd	nd	nd	Enz
Hg-32/10	32	46	nd	nd	nd	Enz
Hg-32/11	32	47	nd	nd	nd	Enz
Hg-32/12	32	47	nd	nd	nd	Enz
Hg-32/13	32	48	nd	nd	nd	Enz
Hg-32/14	32	48	nd	nd	nd	Enz
Hg-35/2	35	49	nd	nd	nd	Enz
Hg-25/8	25	53	nd	nd	nd	Enz
Hg-25/9	25	57	nd	nd	nd	Enz
Hg-25/10	25	57	nd	nd	nd	Enz
Hg-19/2	19	59	nd	nd	nd	Enz
Hg-35/3	35	62	nd	nd	nd	Enz
Hg-38/4	38	70	nd	nd	nd	Enz
Mean ± SD		47.1 ± 10.8	1233 ± 1046	281.4 ± 274.9		
Range (min.–max.)		34–82	355.5–4445.2	57.2–1056.6		
N		39	18	18		

mained at constant levels irrespective of the amount of total lipids.

Fatty acids and fatty alcohols

Only the major FAs (>1% of TFAs) were considered for the interspecific comparison (Fig. 3). The share of the saturated fatty acids (SFAs) 14:0 and 16:0 differed significantly between *Meganyctiphanes norvegica* and *Hymenodora glacialis*, while 18:0 showed no differences. The amount of the monounsaturated fatty acids (MUFAs) 16:1(n-7), 18:1(n-9) and 22:1(n-9) were lower in *M. norvegica* than in *H. glacialis*. In contrast, the MUFA 18:1(n-7) did not differ significantly between species (~3.6% TFAs), nor did the long-chain FA 22:1(n-11) (~12% TFAs). Three polyunsaturated fatty acids (PUFAs), 18:4(n-3), 20:5(n-3) and 22:6(n-3), were identified (Fig. 3). Each of these PUFAs showed significant differences between species.

No fatty alcohols were identified in *Meganyctiphanes norvegica*, while various fatty alcohols were present in *Hymenodora glacialis* (Table 3). The major fatty alcohol was 22:1(n-11), which accounted for >40% of total fatty alcohols. The monounsaturated fatty alcohol 18:1(n-9) showed values of ~25.0%, but with the highest variability. The major saturated fatty alcohol was 16:0.

Data sets of the relative FA composition of individuals of both species were subjected to a similarity analysis. The resulting dendrogram displays distinct species-specific clusters, clearly separating *Meganyctiphanes norvegica* from *Hymenodora glacialis* at a similarity level of 62% (Fig. 4).

Enzyme activities

In *Meganyctiphanes norvegica*, the average total proteolytic activity amounted to 57.4 ± 27.1 ΔE_{366} (photometric extinction at 366 nm) min^{-1} g_{FM}^{-1} (Fig. 5a). In *Hymenodora glacialis*, total proteolytic activities were <5% of that in *M. norvegica*, at 2.4 ± 2.3 ΔE_{366} min^{-1} g_{FM}^{-1} (Fig. 5a). Trypsin activity was highest in

Table 2. *Meganyctiphanes norvegica* and *Hymenodora glacialis*. Total lipid content (mg, mean ± SD, range in parentheses) and composition of lipid classes (% dry mass [DM], % total lipids [TL]) of *M. norvegica* (n = 10) and *H. glacialis* (n = 18). Significance levels were calculated with a Mann-Whitney rank sum test[a] or a *t*-test[b]. nd: not determined; ns: not significant; *p < 0.05; **p < 0.01; ***p < 0.001

Lipid content/composition	Units	*M. norvegica*	*H. glacialis*	Significance
Total lipids	mg	15.1 ± 5.0 (8.4–24.8)	83.6 ± 127.8 (2.0–474.7)	***[a]
	% DM	27.6 ± 5.2	43.9 ± 14.2	***[a]
Neutral lipids				
Wax esters	% DM	1.6 ± 0.6	38.8 ± 13.6	***[b]
	% TL	6.0 ± 3.1	88.6 ± 10.2	**[a]
Triacylglycerols	% DM	17.5 ± 5.3	3.1 ± 4.9	***[b]
	% TL	62.2 ± 9.6	6.8 ± 9.9	***[b]
Free fatty acids	% DM	0.04 ± 0.1	0.02 ± 0.07	ns
	% TL	0.1 ± 0.3	0.02 ± 0.11	ns
Sterols	% DM	0.4 ± 0.2	0.2 ± 0.2	***[b]
	% TL	1.6 ± 0.8	0.5 ± 0.3	***[b]
Membrane lipids				
Phospholipids	% DM	7.7 ± 1.2	1.7 ± 1.3	***[b]
	% TL	29.1 ± 7.6	4.1 ± 2.5	***[b]
Unknown lipids	% DM	0.3 ± 0.4	nd	
	% TL	1.1 ± 1.1	nd	

M. norvegica as well, reaching 7.3 ± 2.6 U g_{FM}^{-1} (Fig. 5b). *H. glacialis* showed much lower trypsin activities (0.32 ± 0.16 U g_{FM}^{-1}) than *M. norvegica*.

Inhibition assays

In *Meganyctiphanes norvegica*, the cysteine proteinase inhibitor E-64 lowered proteolytic activity to 76.1% of initial values (Fig. 6). The specific serine proteinase inhibitor AEBSF caused a significantly higher degree of inhibition to 44.9% of the initial value (p = 0.006). In *Hymenodora glacialis*, a significantly higher inhibition of proteinase activity was obtained with E-64 than with AEBSF (p < 0.001). The residual proteolytic activity amounted to 12.0% of the uninhibited values after E-64 treatment. In contrast, residual activity remained at 93.8% after applying AEBSF.

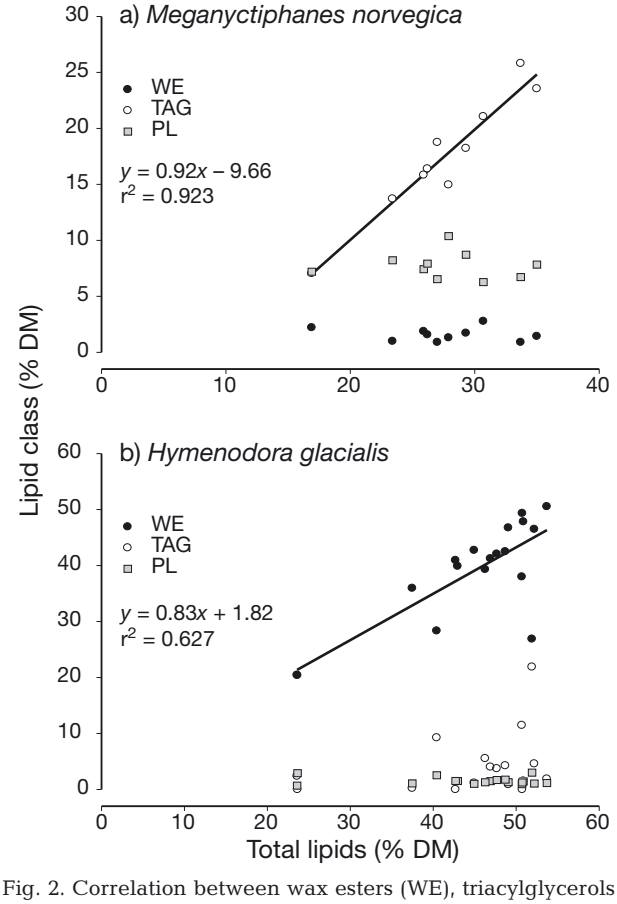

Fig. 2. Correlation between wax esters (WE), triacylglycerols (TAG), phospholipids (PL) and the amount of total lipid in % dry mass (DM) for (a) *Meganyctiphanes norvegica* (n = 10) and (b) *Hymenodora glacialis* (n = 18). Note different scaling

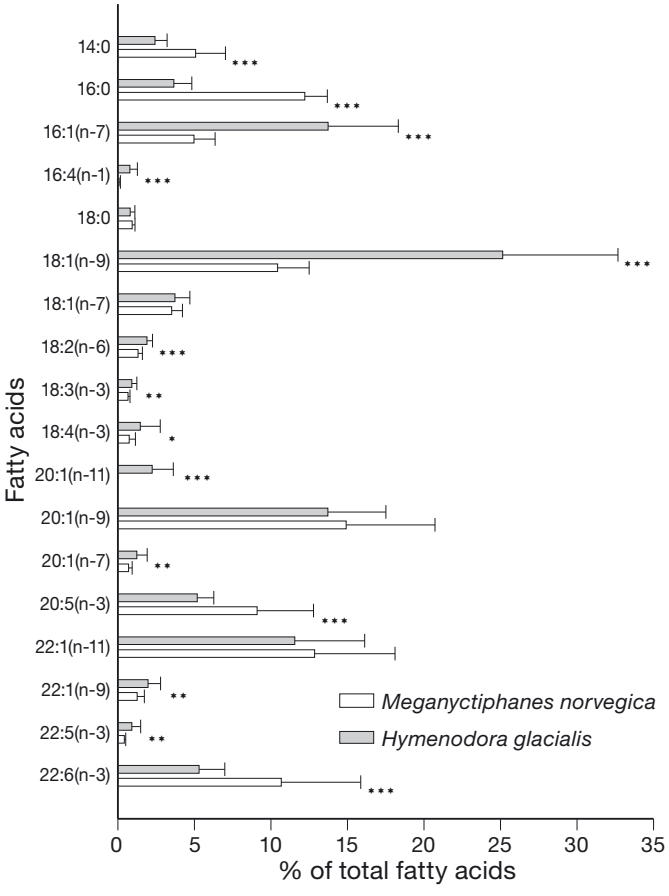

Fig. 3. Selected fatty acids (>1% of total fatty acids, means ± SD), of *Meganyctiphanes norvegica* (n = 10) and *Hymenodora glacialis* (n = 18). *p < 0.05; **p < 0.01; ***p < 0.001

Table 3. *Hymenodora glacialis*. Major fatty alcohols in % of total fatty alcohols (mean ± SD, n = 18)

Fatty alcohol	% of total alcohols
14:0	3.1 ± 1.8
16:0	9.6 ± 3.3
18:0	1.1 ± 0.4
18:1(n-7)	2.2 ± 1.5
18:1(n-9)	10.6 ± 11.7
20:1(n-7)	0.9 ± 1.3
20:1(n-9)	25 ± 2.4
22:1(n-9)	5.2 ± 3.2
22:1(n-11)	42.2 ± 13.5

DISCUSSION

Meganyctiphanes norvegica and *Hymenodora glacialis* showed distinct differences in the quantity and quality of storage lipids, FA composition, proteolytic enzyme activity and expression of proteinase classes. These results clearly indicate that, at least during the sampling period, both crustacean species followed very different physiological traits of food utilization and energy storage.

Feeding ecology

A huge body of literature exists on the feeding ecology of *Meganyctiphanes norvegica*. Different zooplankton and phytoplankton species have been identified as major food items (e.g. Mauchline 1980, Sameoto 1980, McClatchie 1985, Lass et al. 2001). Although prey preference varies strongly with season and location (Lass et al. 2001), the feeding mode of northern krill has been classified as opportunistic and non-selective (Mauchline 1980, Buchholz et al. 1995, Lass et al. 2001). However, Kaartvedt et al. (2002) suggested that carnivorous feeding is performed selectively by visually hunting zooplankton, e.g. various copepod species. Northern krill perform extended and energy-demanding diurnal vertical migrations which are associated with feeding activities at the surface during darkness, whereas during the daytime krill stay at depth and feed on zooplankton such as copepods (Sameoto 1980, Tarling et al. 1999, Kaartvedt et al. 2002).

In contrast, information about the vertical distribution and feeding preferences of *Hymenodora glacialis* is limited. Mauchline (1988) categorized these decapods as bathypelagic non-migrators. *H. glacialis* specimens were mostly caught below 1000 m (Domanski 1986, Ritterhoff & Zauke 1997, Auel & Hagen 2002), while they were rarely observed in epipelagic waters (Wishner 1980, Mauchline 1988). In Arctic deep waters, *Calanus hyperboreus* represents one of the dominant copepod species. Depending on the season, adults as well as juvenile stages occur frequently between the surface and 3000 m depth (Head & Conover 1983, Hirche 1989, 1997, Richter 1995, Hirche & Niehoff 1996). Thus *C. hyperboreus* may provide a major food source for *H. glacialis*, especially in winter, when *Calanus* species descend to deeper waters. Stomach content analyses of *H. glacialis* by Domanski (1986) revealed parts of small crustaceans, chaetognaths and undefined gelatinous matter, which also support the notion of carnivorous feeding preferences. In contrast, there is no indication of herbivory for *H. glacialis* from the literature.

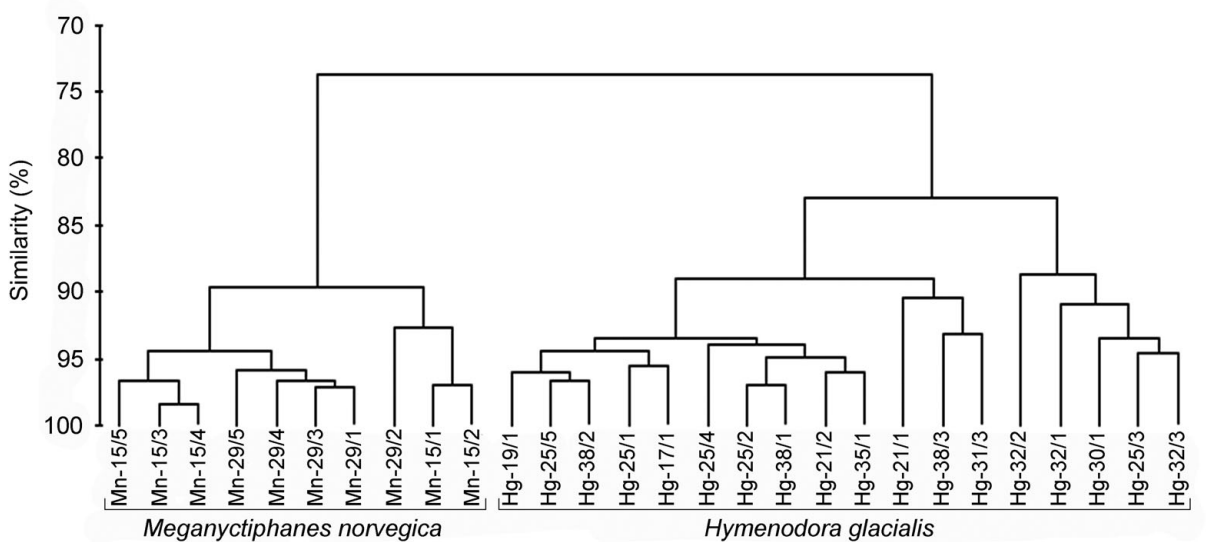

Fig. 4. Dendrogram of Bray-Curtis similarities between the fatty acid patterns of individual *Meganyctiphanes norvegica* and *Hymenodora glacialis*

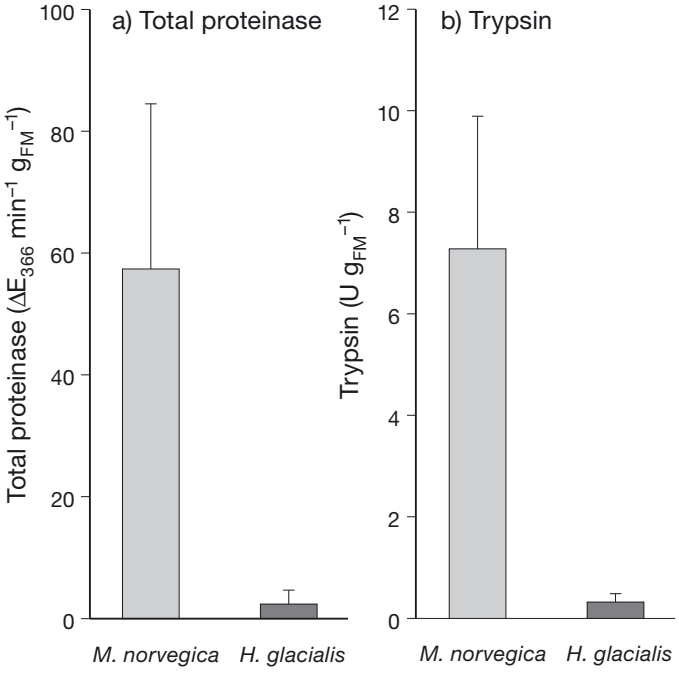

Fig. 5. Activities of (a) total proteinase and (b) trypsin in the midgut glands of *Meganyctiphanes norvegica* and *Hymenodora glacialis* at optimum pH (means ± SD, n = 4 to 21). Both activities were significantly higher in *M. norvegica* than in *H. glacialis* ($p = 0.001$). ΔE_{366}: photometric extinction at 366 nm; g_{FM}: g fresh mass

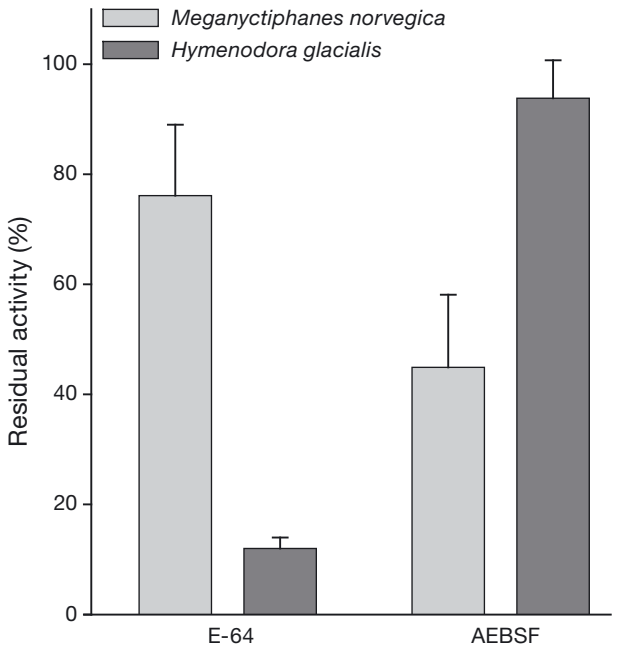

Fig. 6. Residual activities (relative values) after inhibition of total proteinase with the cysteine proteinase inhibitor E-64 and the serine proteinase inhibitor AEBSF in midgut gland extracts of *Meganyctiphanes norvegica* and *Hymenodora glacialis* (n = 3 to 5). Inhibition with E-64 was significantly stronger in *H. glacialis* than in *M. norvegica* ($p < 0.001$)

Lipids

Both species are strongly influenced by the pronounced seasonal changes of productivity in sub-arctic waters. However, the amount of total lipids in relation to dry mass was twice as high in *Hymenodora glacialis* as compared to *Meganyctiphanes norvegica*.

The total lipid content in *Meganyctiphanes norvegica* may range from <25% DM in late spring and early summer to >50% DM in winter (Sargent & Falk-Petersen 1981, Saether et al. 1986, Falk-Petersen et al. 2000, W. Hagen unpubl. data). In our samples from May–June, lipid contents averaged 22.1 ± 9.4% DM, which indicates that krill were passing through the period of low lipid levels. According to Falk-Petersen et al. (2000), *M. norvegica* mobilizes storage lipids during winter and spring resulting in lipid levels of <20% DM during summer. Lipid accumulation takes place mainly during the following autumn. Reproduction does not seem to influence lipid dynamics, since *M. norvegica* does not spawn in Arctic waters (Einarsson 1945). Triacylglycerols formed the major fraction of neutral lipids in *M. norvegica*, while the amount of wax esters was rather low. Triacylglycerols are known as short-term depot lipids which are used to meet metabolic energy requirements (Mayzaud et al. 1998, Lee et al. 2006). Their function as a major energy store in *M. norvegica* may be related to a rapid lipid turnover, possibly due to an active mode of life year-round, which thus may entail a more or less continuous food uptake throughout all seasons (Sargent et al. 1981). The traces of wax esters in the samples originate most likely from freshly ingested and thus incompletely digested prey rich in wax esters, e.g. calanid copepods (*Calanus* spp.).

The lipid content of *Hymenodora glacialis* averaged 44% DM. Unfortunately, limited data were available on the seasonal lipid dynamics of this species. However, in catches from other seasons the average lipid content amounted to 46% DM in April (ARK IX) and 35 to 40% DM in August (ARK VII) (W. Hagen unpubl. data). In other pelagic crustaceans this level may represent the seasonal lipid maximum (Falk-Petersen et al. 2000). Accordingly, *H. glacialis* seems less affected by seasonal fluctuations of internal lipid stores than *Meganyctiphanes norvegica*. In contrast to northern krill, *H. glacialis* predominantly accumulated wax esters, which reached almost 90% of total lipids. Wax esters are major storage products in many high-latitude zooplankton species (Lee et al. 2006). They are suggested to be more suitable for rapid accumulation of large lipid stores (Sargent et al. 1974) and they can

be deposited in the body for extended periods, e.g. for up to 8 mo in adult *Acanthephyra pelagica* (Oliphoridae) (Clarke & Holmes 1986). As suggested by Hagen et al. (1993) from studies on 2 sympatric primarily herbivorous copepod species from Antarctic waters, the deposition of wax esters may be related to discontinuous seasonal feeding, while triacylglycerol accumulation may reflect continuous seasonal food uptake. The carnivorous wax ester-rich *H. glacialis*, however, appears to exhibit continuous feeding throughout the year, since no pronounced fluctuations of the lipid depots were obvious from the existing data, characteristics similar to the carnivorous Antarctic copepod *Paraeuchaeta antarctica*, which also stores wax esters (Hagen et al. 1995). The accumulation of wax esters reflects the chemical composition of preferred prey species, among them C. *hyperboreus*, which are rich in wax esters with long-chain MUFAs and fatty alcohols (Kattner & Hagen 1995). However, it remains to be investigated whether or not *H. glacialis* are capable of synthesising wax esters themselves. Wax esters may also play an important role in reproductive processes (Hagen & Kattner 1998) and they prevail in the large lipid-rich eggs of *H. glacialis* (W. Hagen unpubl. data). *H. glacialis* have no distinct spawning period but breed continuously throughout the year (Mauchline 1988). Accordingly, they depend on a continuous food supply, which again is in accordance with low seasonal fluctuations of somatic lipid stores.

Another major advantage of high lipid and wax ester levels may be their function as buoyancy aids. Among the dominant neutral lipid classes, wax esters provide the strongest uplift (Yayanos et al. 1978), which may be quite advantageous for the rather large and heavy *Hymenodora glacialis* in saving metabolic energy.

Fatty acids and fatty alcohols

FAs, which typically appear in specific prey organisms, can serve as suitable tracers or biomarkers for trophic interactions (e.g. Sargent & Whittle 1981, Graeve et al. 1994, Dalsgaard et al. 2003). In our samples the FA composition of *Meganyctiphanes norvegica* confirms their omnivorous but predominantly carnivorous feeding behaviour. On the one hand, the unsaturated FAs 20:1(n-9) and 22:1(n-11) contributes the highest shares to total FAs. These long-chain MUFAs are typical of wax esters originating from *Calanus* species (Kattner & Hagen 1995, Dalsgaard et al. 2003). Other FAs or the ratios between certain FAs such as 20:5(n-3) to 22:6(n-3) indicate omnivory with a strong tendency to carnivory as well (Ackman et al. 1970). On the other hand, the FAs 16:1(n-7) and 18:4(n-3) are typical for diatoms and dinoflagellates, respectively. In *M. norvegica* they are present at levels of only 5.0 and 0.7%. The ratio of 8:1 between 16:1(n-7) and 18:4(n-3) indicates a higher share of diatoms than dinoflagellates in the food (Stübing & Hagen 2003), although these phytoplankton markers may have been ingested with herbivorous calanid copepods.

The present study provides first information on the lipid and FA composition of *Hymenodora glacialis*. The highest share of 25% of total FA was contributed by 18:1(n-9), which may form a significant component of storage lipids (Stübing & Hagen 2003) and has been suggested as an indicator of carnivory (Falk-Petersen et al. 1990). The *Calanus* markers 20:1(n-9) and 22:1 (n-11) also showed high values of 13.7 and 11.6% TFAs, respectively, suggesting that *H. glacialis* feed on calanid copepods as a major food source. Accordingly, the fatty alcohols of *H. glacialis* were dominated by 20:1(n-9) and 22:1(n-11). These fatty alcohols certainly originate from ingested wax esters of calanid copepods, which are able to synthesize these monounsaturated lipid moieties de novo (Lee 1974, Kattner et al. 1989, Kattner & Graeve 1991, Lee et al. 2006). The FA 16:1(n-7) in *H. glacialis* indicates the presence of diatoms. Diatoms often dominate phytoplankton stock in the Greenland Sea. However, there is no indication that bathypelagic *H. glacialis* migrate into the euphotic zone to feed on phytoplankton (Mauchline 1988). Accordingly, this diatom marker may be incorporated in the lipids secondarily via ingested copepods. It is not clear whether detritus material that sinks as marine snow into deeper layers is a significant dietary component for *H. glacialis*. The presence of phytoplankton markers at depth was confirmed by Graeve et al. (1997), who found diatom markers in various benthic organisms from sub-arctic waters.

Digestive enzymes

Proteins are important metabolic energy sources in many crustaceans. This has been shown for both the Antarctic krill *Euphausia superba* and the northern krill *Meganyctiphanes norvegica* (Virtue et al. 1993, Saborowski et al. 2002, Stübing et al. 2003). In the present study, northern krill exhibited significantly higher proteolytic activities than the decapod *Hymenodora glacialis*. This indicates that *M. norvegica* is capable of utilizing alimentary proteins much more rapidly than *H. glacialis*, which might be a consequence of the higher metabolic energy demand and energy turnover in krill.

Northern krill performs diel vertical migrations, from ~100 m (in Scandinavian or Scottish fjords) to >800 m (in the Mediterranean) (Liljebladh & Thomasson 2001, Tarling et al. 2001). In sub-arctic waters, *Meganyctiphanes norvegica* is considered to be one of the most

important vertical migrators (Roe & Griffiths 1993). Acoustic Doppler current profiler records from the Greenland Sea showed backscattering layers ascending from 300 to 400 m depth at daytime to the surface at night (Heywood 1996). Extended and frequent vertical migration, however, is energy-demanding. In laboratory experiments northern krill increased respiration rates during extended swimming by 60% over routine metabolic rates (Saborowski 2004). Similar results were found in another euphausiid and some mysids (Torres & Childress 1983, Cowles & Childress 1988, Buskey 1998). Accordingly, elevated activities of digestive proteolytic enzymes are suitable to rapidly and efficiently utilize prey and, thus, to fuel the additional metabolic energy demands for vertical migration and the active life style in general.

Hymenodora glacialis specimens, in contrast, are considered sluggish bathypelagic non-migrators (Mauchline 1988). Therefore, they do not require additional metabolic energy for vertical migration and do not need to synthesize and maintain a vast amount of enzymes. Reduced catabolic rates due to low digestive enzyme activities can be compensated by prolonged gut retention. Many species of crustaceans and fishes, which ingest food of poor nutritive value, thus improve the assimilation of nutrients (Tirelli & Mayzaud 2005). We assume that this applies for *H. glacialis* as well (Teschke & Saborowski 2005). This suggestion is supported by the expression of different proteinase classes in both species.

Serine and cysteine proteinases, both representing endopeptidases with various specificities, belong to the dominant proteinase classes in crustaceans. There is some indication that the expression of serine and cysteine proteinases may be related to different systematic groups of crustaceans (Teschke & Saborowski 2005). For instance, serine proteinases prevail in the euphausiid *Euphausia superba*, while cysteine proteinases dominate in the caridean shrimps *Crangon crangon*, *C. allmani* and *Pandalus montagui*. Our results are in accordance with these findings: inhibitor assays confirmed that serine proteinases dominated in the euphausiid *M. norvegica*, while cysteine proteinases formed the major class in the caridean decapod *H. glacialis*. The physiological implication of expressing different proteinase classes is not yet clear. However, the different enzymes may act predominantly in different compartments of the midgut gland and the digestive tract (Teschke & Saborowski 2005).

Serine proteinases, representing trypsin- and chymotrypsin-like enzymes and brachyurins, have been identified in the digestive tract of many crustacean species. Maximum amounts were present in the stomach, where these enzymes accumulate (e.g. Saborow-ski et al. 2004). In the Antarctic krill *Euphausia superba*, proteolytic activity was more than 10 times higher in the stomach than in the midgut gland (Buchholz & Saborowski 1996). Accordingly, serine proteinases are synthesized in midgut gland cells, released into the lumen and accumulated in the stomach. There, these endopeptidases are able to rapidly hydrolyse alimentary proteins as soon as food is ingested. Hydrolysed peptides and amino acids are subsequently absorbed in the midgut gland. The strategy of protein utilization in *Meganyctiphanes norvegica* may follow rapid extraction of nutrients by high extracellular enzyme activities, fast gut passage and rapid ability to digest newly ingested food items.

Cysteine proteinases, e.g. cathepsin L-like enzymes, are thought to act also within the cells of the midgut gland (Hu & Leung 2004). Their more acidic activity profiles correspond better with the pH conditions in lysosomes. Therefore, it may be suggested that those crustaceans, which synthesize cysteine proteinases, retain these enzymes within the cell and thus perform a significant share of their digestion intracellularly (Hu & Leung 2007). In this way the amount of enzymes released into the stomach can be reduced, as well as the share of active enzymes in the midgut gland. Nevertheless, the catalytic potential is maintained, because the incorporated food items are retained in the digestive organs and longer exposed to enzymatic digestion. This strategy entails longer gut transit times and probably more complete digestion and resorption of nutrients. Simultaneously, the loss of enzymes via faeces is limited and thus the metabolic demand for enzyme synthesis is reduced. However, detailed histochemical investigations are needed to support this hypothesis.

CONCLUSIONS

Despite the unavoidable snapshot nature of the present study, the results revealed differences between the euphausiid *Meganyctiphanes norvegica* and the decapod *Hymenodora glacialis*. Both species exhibit very different ecophysiological traits of food utilization and energy storage, reflecting deviating life strategies. The northern krill *M. norvegica* tends to rely on a more continuous food supply in upper water layers, owing to its high mobility. Because of its high digestive enzyme activities, it is able to utilize scarcely appearing food more efficiently than *H. glacialis*. In contrast, the sluggish bathypelagic *H. glacialis* may better cope with longer periods of starvation, due to generally much larger lipid stores. They may contribute to neutral buoyancy and thus save additional metabolic energy which is otherwise spent for locomotion. Lipid analyses as well as enzyme measurements indicate that in *M. norvegica* protein catabolism may play a more important role, while in *H. glacialis* lipid catabolism seems to prevail.

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