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Trophic interactions of the pelagic ecosystem over the Reykjanes Ridge as evaluated by fatty acid and stable isotope analyses

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Abstract

Trophic relationships of the important oceanic crustacean species *Calanus finmarchicus*, *Meganyctiphanes norvegica* and *Sergestes arcticus*, as well as the mesopelagic fishes *Maurolicus muelleri*, *Benthosema glaciale* and *Sebastes mentella*, were investigated over the Reykjanes Ridge in June 2003 and in June 2004. Measurements were performed of length, wet weight, dry weight, total lipid, lipid class, fatty acid and fatty alcohol profiles and stable isotopes ($\delta^{13}C$ and $\delta^{15}N$). High amounts of the *Calanus* lipid markers, 20:1(n-9) and 22:1(n-11) in these species confirm the importance of *Calanus* spp. in this ecosystem. Comparisons of fatty acid/alcohol profiles by multivariate analysis revealed two main trophic pathways over the Reykjanes Ridge. In one pathway, *Calanus* spp. was an important part of the diet for the small mesopelagic fish species *M. muelleri* and *B. glaciale* and the shrimp *S. arcticus*, whereas in the other pathway, the euphausiid *M. norvegica* was the dominant food for the redfish *S. mentella*, and *Calanus* spp. were of less importance. *M. muelleri* and the smaller *B. glaciale* feed on *C. finmarchicus*, whereas the larger *B. glaciale* and *S. arcticus* select the larger, deeper-living *C. hyperboreus*. All investigated species are true pelagic species except for the shrimp *S. arcticus*, which seems to have a benthic feeding habit as well. The $\delta^{15}N$ levels show that of the species investigated, *C. finmarchicus* occupies the lowest trophic level (2.0) and the redfish, *S. mentella*, the highest (4.2). All the species were lipid rich, typical for subarctic pelagic ecosystem. *Calanus finmarchicus*, *S. arcticus* and *B. glaciale* store wax esters as their lipid stores, while *M. norvegica*, *M. muelleri* and *S. mentella* store triacylglycerols.

Keywords: Zooplankton; Mesopelagic fish; Stable isotopes; Fatty acids; Lipids; Trophic interactions; Reykjanes Ridge

1. Introduction

The biological productivity of the northern part of the Mid-Atlantic Ridge (Reykjanes Ridge) and nearby areas (Irminger Sea and Iceland Basin), which form a part of the offshore North Atlantic Ocean, is considered to be very high (Gjøsæter and Kawaguchi, 1980; Magnusson, 1996). More or less continuous deep-scattering layers exist in the area (mostly at 300–800 m depth) consisting of a great variety of organisms, including a large stock size of the commercially important pelagic redfish, *Sebastes mentella* (Travin, 1951) (Magnusson, 1996; Anonymous, 1999; Sigurdsson et al., 2002; Anderson et al., 2005; Gislason et al., 2007). Abundant taxa in these layers are, for example, fishes belonging to the family of Myctophidae and various species of shrimps, euphausiids, cephalopods and medusae (Magnusson, 1996).

Zooplankton (mainly copepods) is a very important part of the diet of small mesopelagic oceanic fish (Mauchline and Gordon, 1983; Roe and Badcock, 1984; Sameoto, 1988). The redfish also mainly feeds on zooplankton, of which euphausiids, chaetognaths, amphipods and gastropods are most important. Myctophids also form a part of their diet, although in much smaller quantities than the zooplankton (Magnusson and Magnusson, 1995).

Stable isotopes together with fatty acid (FA) analysis constitute an efficient tool in food web studies (Kharlamenko et al., 2001; Dahl et al., 2003), as their patterns reflect dietary intake/assimilation over longer time periods

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than the more traditional stomach content analyses (Fry, 1988; Rau et al., 1992; Dalsgaard et al., 2003). The stable isotope ratios of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$ values) in consumer proteins, and FA signature in consumer lipids reflect those of their prey. Stable isotopes give rough information about trophic position of the species while from FAs and alcohols the food they actually have been eating can be deduced. A stepwise enrichment of $\delta^{13}C$ and $\delta^{15}N$ values generally occurs between trophic levels because of preferential excretion and respiration of the lighter isotopes (Minagawa and Wada, 1984; Hobson et al., 1995). Stable nitrogen values have been used to estimate trophic levels (Hobson and Welch, 1992; Dahl et al., 2003; Tamelander et al., 2006), whereas carbon values provide information about the carbon source (Peterson and Fry, 1987; Peterson, 1999; Søreide et al., 2006).

Fatty acid trophic markers (FATMs) have been used in marine ecosystems to follow energy transfer and to study predator–prey relationships (Falk-Petersen et al., 1990, 2004; Dalsgaard et al., 2003). The concept of FATM is based on observations of FA patterns, characteristic for specific taxa of primary producers and some zooplankters, with the pattern being transferred relatively unchanged trough food chains (Lee et al., 1971b; Dalsgaard et al., 2003). Well known FATMs are, for example, 20:5(n-3) for diatoms; 22:6(n-3) and C18 polyunsaturated fatty acids (PUFAs) for dinoflagellates and 20:1(n-9) and 22:1(n-11) monounsaturated fatty acids (MUFAs) for *Calanus* copepods (Dalsgaard et al., 2003).

Information on trophic relationships in the pelagic ecosystem over the Reykjanes Ridge is scarce. Limited data from stomach analyses exist on the diet of redfish (Magnusson and Magnusson, 1995), but there is no previous information on the feeding of small mesopelagic oceanic fish stocks in the area nor of organisms of lower trophic levels (zooplankton).

The overall objective of this study was to determine the trophic relationships among some important species of the pelagic ecosystem over the Reykjanes Ridge using lipids (FA and alcohol compositions) and stable isotopes ($\delta^{13}C$ and $\delta^{15}N$). The target species were the copepod *Calanus finmarchicus* (Gunnerus, 1765), the euphausiid *Meganyctiphanes norvegica* (M. Sars, 1857), the bathypelagic shrimp *Sergestes arcticus* (Krøyer, 1855), the small mesopelagic fishes, pearlsides *Maurolicus muelleri* (Gmelin, 1788) and glacier lanternfish *Benthosema glaciale* (Reinhardt, 1837), and the redfish *S. mentella*. These species are the dominant components of the ecosystem and represent different trophic positions in the food chain (Magnusson, 1996; Gislason, 2003).

2. Materials and methods

2.1. Sampling

Samples were collected at three stations with various types of gear on the northern part of the Reykjanes Ridge in June 2003 and June 2004 (Table 1, Fig. 1). The stations were within approximately 60–100 nm from each other and are regarded here as belonging to the same study area. Further details on sampling methods in June 2004 by the R.V. *G.O. Sars* are given in Wenneck et al. (2008).

Samples for FA and fatty alcohol analyses were obtained by picking out individuals of the target species and storing them in chloroform:methanol 2:1 (v/v) solution at −80 °C (*C. finmarchicus*, *M. norvegica*, *S. arcticus*), or freezing them directly at −80 °C (*B. glaciale*, *M. muelleri*) or at −20 °C (*S. mentella*) (Table 2). These frozen fish amples also were used for stable isotopes analyses. Bulk samples containing a mixture of several species were frozen in plastic trays at −80 °C, and the cructaceans *C. finmarchicus*, *M. norvegica* and *S. arcticus* were picked out later in the laboratory for stable isotopes analyses (Table 2). The samples were stored for 6 months prior to analyses. Due to the rather high storage temperature of *S. mentella*, prior to FA and fatty alcohol analyses, some oxidation of the lipids may have taken place. However, fish with minimum deterioration were chosen for analyses (i.e. with fresh colour, etc.). Furthermore, since the muscle tissue is protected from the external oxygen and little variation appeared in FA profiles among the samples, we used these samples in further analyses in this study. In this contest, it may further be noted that Joensen and Grahl-Nielsen (2001) in their study of FA composition of different *Sebastes* species considered internal organs as being in less danger of deterioration than for instance gills.

Table 1
Activity on the stations at the Reykjanes Ridge

Station	Cruise	Position		Date	Gear	Lipids	Stable isotopes
		Lat (°N)	Long (°W)				
4	*Árni Friðriksson* 2003	60°25′	28°40′	21.6 2003	Multinet		X
2	*G.O. Sars* 2004	59°58′	25°53′	10.6 2004	Krill trawl	X	
4	*G.O. Sars* 2004	60°13′	28°14′	11.6 2004	Multinet, krill-, åkratrawls	X	X
184	*Árni Friðriksson* 2004	61°23′	28°28′	15.6 2004	Gloria 1024	X	X

Samples were taken for lipids and stable isotopes ($\delta^{13}C$, $\delta^{15}N$) from several species.

2.2. Laboratory analyses

Specimens were selected to minimize variation in size, and the size groups reflected the highest abundance of every species in the respective catch. The following groups were chosen: copepodid stages CIV and CV and adult females for *C. finmarchicus*, the size group 35–41 mm for *M. norvegica*, 55–65 mm for *S. arcticus*, 48–56 mm for *M. muelleri*, 30–42 mm and 60–66 mm for respectively smaller and larger size groups of *B. glaciale*, and 31–33 cm for *S. mentella*. The length of *M. norvegica* and *S. arcticus* was measured from the tip of rostrum to the end of telson and standard length of the fish species was measured.

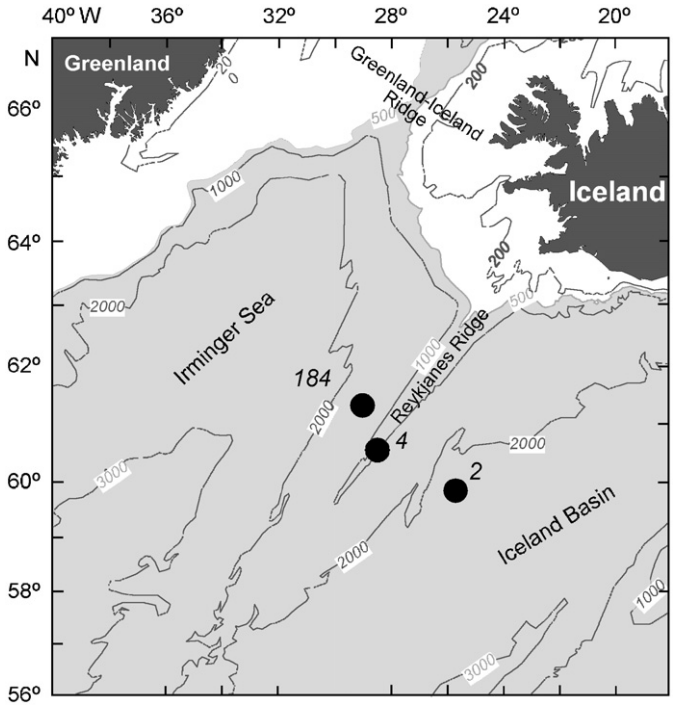

Fig. 1. Map of the study area, showing the sampling stations over the Reykjanes Ridge. Station 4 was sampled on R.V. *G.O. Sars* in June 2004 and on R.V. *Árni Friðriksson* in June 2003. Station 2 was sampled on R.V. *G.O. Sars* in June 2004, and station 184 was sampled on R.V. *Árni Friðriksson* in June 2004 (Table 1).

Stable isotopes ratios were analysed at the Institute for Energy Technology (IFE), Kjeller, Norway. The samples were dried at 60–70 °C to constant weight and homogenized in a mortar using a glass pestle. According to protocols of the IFE (see, e.g., Dahl et al., 2003), lipids were removed by Soxhlet extraction for 2 h by using a solvent consisting of 93% dichloromethane (DCM) and 7% methanol, in order to reduce variability due to isotopically lighter lipid (Hobson and Welch, 1992). To remove traces of carbonates; The samples were acid-rinsed with 2 N HCl and dried at 80 °C. Stable isotopes ratios ($\delta^{13}C$ and $\delta^{15}N$) of the residual material were analysed on a Micromass Optima, Isotope Ratio Mass Spectrometer and expressed as per mill (‰) enrichment relative to international standards according to the relationship:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000,$$

where X (‰) is ^{13}C or ^{15}N and R is the corresponding ratios of $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Standard for $\delta^{13}C$ is Pee Dee Belemnite (PDB: USGS 24) and for δ ^{15}N is atmospheric air (IAEA-n-1 and IAEA-n-2).

For wet weight determination, defrosted samples were weighed on a calibrated scale (accuracy = 0.01 mg). For dry weight determination, the samples were dried at 60–70 °C to constant weight. The total lipid was extracted from the dried samples following the procedure by Folch et al. (1957) and weighed.

Lipid classes, FAs and fatty alcohols were analysed at UNILAB, Tromsø, Norway. The samples were homogenized in chloroform:methanol 2:1 (v/v), and total lipid was extracted and weighed. A sub-sample of the extract was separated into a polar and a neutral lipid fraction, using solid bond extraction–fractionation as described by Kaluzny et al. (1985). A known amount of the FA 21:0 was added as an internal standard to both fractions and an

Table 2
Overview of samples for lipids (fatty acid and alcohol composition) and stable isotope analyses ($\delta^{13}C$, $\delta^{15}N$) as well as total lipid weight (TLW), wet weight (WW) and dry weight (DW)

Species	Station no.	Depth (m)	Analyses					
			Lipids	$\delta^{13}C$	$\delta^{15}N$	TLW	WW	DW
Calanus finmarchicus CIV	4	0–1000	3(10)	3(80)	3(80)			
Calanus finmarchicus CV	4	0–1000	3(10)	3(80)	3(80)			
Calanus finmarchicus female	4	0–1000	3(10)	3(50)	3(50)			
Meganyctiphanes norvegica	2	0–200	2(3)					
Meganyctiphanes norvegica	4	0–350		3(4)	3(4)			
Sergestes arcticus	4	0–200	3(1)	3(1)[a]	3(1)[a]	3(1)	3(1)	3(1)
Maurolicus muelleri	2	500	3(1)	3(1)[a]	3(1)[a]	3(1)	3(1)	3(1)
Benthosema glaciale (small)	2	500	3(1)	3(1)[a]	3(1)[a]	3(1)	3(1)	3(1)
Benthosema glaciale (large)	2	900	3(1)	3(1)[a]	3(1)[a]	3(1)	3(1)	3(1)
Sebastes mentella	184	786–900	3(1)[a]	3(1)[a]	3(1)[a]			

Station number, depth of sampling, the number of replicates analysed and animals per replica (in brackets) are given.
[a]Muscle tissue analysed (otherwise whole animals).

acid-catalysed transesterification was carried out with 1% sulphuric acid in methanol (Christie, 1982). The relative (%) compositions of FA methyl esters and fatty alcohol acetates were determined on an Agilent 6890 N gas chromatograph, equipped with a fused silica, wall-coated capillary column with an Agilent 7683 injector and flame ionization detection. Hydrogen was used as the carrier gas with an oven thermal gradient from an initial 60 to 150 °C at 30 °C min^{-1}, and then to a final temperature of 230 °C at 1.5 °C min^{-1}. Individual components were identified by comparing them to known standards, and were quantified using HPChemStation software (Hewlett-Packard).

2.3. Data analyses

To assist with the interpretation of the $\delta^{13}C$ and $\delta^{15}N$ values, the fractionation factors 0.8‰ for $\delta^{13}C$ and 3.8‰ for $\delta^{15}N$ were used between trophic levels. Previous trophic studies have applied fractionation factors between 0.4‰ and 1‰ for $\delta^{13}C$ (DeNiro and Epstein, 1978; Post, 2002) and between 3‰ and 4‰ for $\delta^{15}N$ (DeNiro and Epstein, 1981; Minagawa and Wada, 1984; Hobson and Welch, 1992).

It was assumed that *C. finmarchicus* represented trophic level 2 (i.e., primary herbivore). The following relationship was used for each individual sample of other tropic levels (Fisk et al., 2001):

$$TL_{consumer} = 2 + (\delta^{15}N_{consumer} - \delta^{15}N_{Calanus})/3.8,$$

where $TL_{consumer}$ is the trophic level of an organism, $\delta^{15}N_{Calanus}$ is analytically determined as 3.5 ± 0.1 (mean ± SE), and 3.8 is the isotopic enrichment factor (Hobson and Welch, 1992; Hobson et al., 1995).

The Shapiro–Wilk's test was used to test for normality of the data. As both isotopes $\delta^{13}C$ and $\delta^{15}N$ data were normally distributed, the univariate statistical test analysis of variance (ANOVA) was conducted to analyse for differences in stable isotopes ratios among species, followed by the Tukey's honestly significant difference test (HDS). Individual samples (n) were used in all analyses.

The total neutral lipid fraction was analysed to determine the weight percentage compositions of the FA methyl esters and the fatty alcohol acetates. To be able to detect trophic relationships between species, neutral lipids (FAs and fatty alcohols) need to be treated as one and the same (Falk-Petersen et al., 2002). Given fatty alkyl (from fatty alcohol acetates) and fatty acyl (from FA methyl esters) were averaged by molecular weight. The term moiety was used for processed data. When the neutral lipid in a given species contained both fatty alcohol acetates and FA methyl esters, the moieties of fatty alcohol acetates (with the same chain lengths, numbers and positions of double bonds as the moieties of FA methyl esters) were combined in a known proportion of fatty alcohol acetates and FA methyl esters in the neutral lipid, and new percentage data were calculated.

Multivariate statistical analysis was performed on moiety compositional data. Samples with low amounts of moieties (<0.5%) were excluded from the analysis because the precision of their determination was too low. The remaining percentage was subjected to redundancy analysis (RDA) to analyse for trophic relationships among the target species. Species were used as explanatory variables, and the moieties as response variables. To test for significant differences in moieties compositions of the species, a Monte Carlo test with 999 permutations was applied. This multivariate statistical analysis was performed in CANOCO 4.5 for Windows®. Individual samples (n) were used in the analysis, but in the tables only mean values are presented (Tables 5, 6).

3. Results

3.1. Stable isotopes

C. finmarchicus had the lowest $\delta^{13}C$ value (−20.3‰), while the shrimp *S. arcticus* had the highest value (−17.8‰; Fig. 2). Stable carbon isotope ratios ($\delta^{13}C$) differed significantly among species (ANOVA $F_{5,16} = 16.65$, $p < 0.001$; Fig. 2). The pelagic crustaceans *C. finmarchicus* and *M. norvegica* did not differ, and both had significantly lower $\delta^{13}C$ values (Tukey's HSD, $p < 0.05$) than *S. arcticus*, *B. glaciale* (both size groups combined) and *S. mentella* (Table 3), whereas *S. arcticus* had a significantly higher mean $\delta^{13}C$ value than *M. muelleri* (Table 3).

Stable nitrogen isotope ratios ($\delta^{15}N$) ranged from 3.5‰ (mean value) for *C. finmarchicus* to 12.3‰ for *S. mentella* (Fig. 2). Stable nitrogen isotope ratios ($\delta^{15}N$) differed significantly among species (ANOVA $F_{5,16} = 23.23$, $p < 0.001$; Fig. 2). *C. finmarchicus* had a significantly lower mean $\delta^{15}N$ value (Tukey's HSD, $p < 0.05$) than all the other

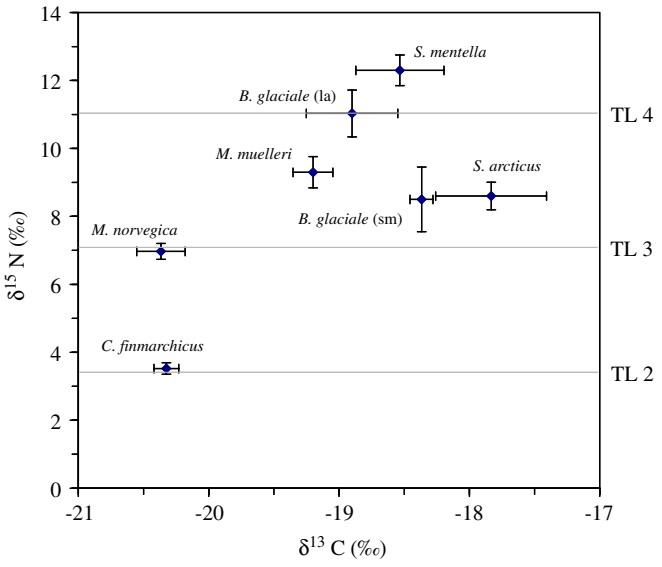

Fig. 2. Stable isotopes of nitrogen and carbon from *Calanus finmarchicus*, *Meganyctiphanes norvegica*, *Sergestes arcticus*, *Maurolicus muelleri*, *Benthosema glaciale* (two size groups, sm = small and la = large) and *Sebastes mentella* from station 4. Values are mean ± SE and TL indicates trophic level.

Table 3
Tukey's HSD test between species differences in $\delta^{13}C$ and $\delta^{15}N$

Species	$\delta^{13}C$						$\delta^{15}N$					
	C. finmarchicus	*M. norvegica*	*S. arcticus*	*M. muelleri*	*B. glaciale*	*S. mentella*	*C. finmarchicus*	*M. norvegica*	*S. arcticus*	*M. muelleri*	*B. glaciale*	*S. mentella*
C. finmarchicus												
M. norvegica	ns						*					
S. arcticus	*	*					*	ns				
M. muelleri	ns	ns	*				*	ns	ns			
B. glaciale	*	*	ns	ns			*	*	ns	ns		
S. mentella	*	*	ns	ns	ns		*	*	*	ns	ns	

* = $p<0.05$; ns = $p>0.05$.

species (Table 3). *M. norvegica* had a significantly lower $\delta^{15}N$ values than *B. glaciale* and *S. mentella*, whereas *S. mentella* had a significantly higher $\delta^{15}N$ values than *S. arcticus* (Table 3).

The krill *M. norvegica* occupied trophic level 2.9 followed by the shrimp *S. arcticus* (3.3), the small mesopelagic fish species *M. muelleri* (3.5) and *B. glaciale* (3.3 and 4.0, smaller and larger fish, respectively), whereas the redfish occupied the highest trophic level (4.3; Fig. 2).

3.2. Lipids

In *S. arcticus*, total lipid accounted for about 20% of the dry weight (Table 4). In *B. glaciale*, the ratio increased with increasing size from ~24% in small (30–42 mm) fish to ~28% in large (60–66 mm) fish, while *M. muelleri* had the highest ratio (~29%).

FATMs were used to follow energy transfer through the food web. A total of 51 FAs and fatty alcohols were detected, 43 of them with higher levels than 0.5% in at least one of the samples accounting for 98.4–99.9% of the total amount (Table 5).

3.2.1. *Calanus finmarchicus*

The major FA in all stages was the saturated fatty acid (SFA) 14:0, ranging from 15.3% in copepodid CIV to 20.0% in adult females (Table 5). The portion of FA 16:0 was also rather high (7.8–9.7%). The MUFA 18:1(n-9) was recorded at rather low levels in *C. finmarchicus* (3.7–5.4%) compared to most of the other species. The amount of the long-chained MUFAs, the FATMs typical for *Calanus* spp., increased with developmental stage: 20:1(n-9) from 2.4% to 4.8% and 22:1(n-11) from 4.8 to 7.0%.

The PUFA 20:5(n-3), which is generally considered to be a diatom FATM, had rather high values and increased from 7.4% in CIV to 12.3% in CV of *C. finmarchicus* and accounted for 11.4% in adult females (Table 5). The diatom FATM 16:1(n-7) increased from 3.3% in CIV, 6.3% in CV to 12.2% in adult females, where it was the second most abundant of all FAs. On the other hand, the diatom FATM 16:4(n-1) had much lower values and decreased with increasing stage from 7.6% in CIV to 2.2% in adult females.

The dinoflagellate FATMs 22:6(n-3) and C18 PUFAs decreased from CIV to females (from 3.9% to 1.2% and 22.2% to 6.7%, respectively), whereas 18:4(n-3) was the second and third most important FA in CIV and CV (13.4% and 11.3%, respectively) (Table 5).

In *C. finmarchicus*, the percentage of fatty alcohols of total moieties increased with increasing stages (Table 5). The values ranged from 28.5% in CIV to more than 35% in CV, and adult females. The major fatty alcohols recorded in all stages were, in decreasing order: 22:1(n-11), 20:1(n-9), 16:0 and 16:1(n-7). The sum of 20:1(n-9) and 22:1(n-11) increased from CIV (60.6%) to CV and adult females (~72%).

Table 4
Length, wet weight (WW), dry weight (DW), total lipid weight (TLW) and weight ratios (%) in *S. arcticus*, *M. muelleri* and two size groups of *B. glaciale* from stations 2 and 4, 2004

	n	Length (mm)	WW (g)	DW (g)	TLW (g)	TLW/DW (%)
Sergestes arcticus	3	58.3±1.7	0.72±0.05	0.20±0.01	0.04±0.00	19.6
Maurolicus muelleri	3	51.3±1.3	1.10±0.10	0.31±0.04	0.09±0.02	29.1
Benthosema glaciale (small)	3	38.3±2.7	0.58±0.12	0.15±0.03	0.03±0.01	23.5
Benthosema glaciale (large)	3	61.3±2.9	2.18±0.20	0.55±0.03	0.15±0.01	27.8

Values are means±SE. *n* = number of replicates.

Table 5
Fatty acid (FA) and fatty alcohol (FAlc) composition (mass % of total FA and FAlc, respectively) of neutral lipids of the target species from the study area (stations 2, 4 and 184) in June 2004

	C. finmarchicus			*M. norvegica* (*n* = 2)	*S. arcticus* (*n* = 3)	*M. muelleri* (*n* = 3)	*B. glaciale*		*S. mentella* (*n* = 6)
	CIV (*n* = 3)	CV (*n* = 3)	Adult female (*n* = 3)				Small (*n* = 3)	Large (*n* = 3)	
FA									
14:0	15.3±0.4	19.4±0.7	20.0±0.8	8.6±0.2	2.9±0.4	8.6±0.4	5.9±0.3	4.7±0.7	2.5±0.5
14:1	0.9±0.1	0.3±0.1	0.3±0.1	0.7±0.1	0.1±0.0	0.1±0.0	0.0±0.0	0.3±0.2	0.1±0.0
16:0	7.8±0.2	8.4±0.1	9.7±0.2	18.2±0.8	4.9±0.4	13.1±0.0	3.6±0.1	2.3±0.5	14.0±1.3
16:1(n-9)	0.2±0.0	0.2±0.0	0.3±0.0	0.3±0.1	0.5±0.0	0.2±0.0	0.7±0.2	0.6±0.3	0.4±0.0
16:1(n-7)	3.3±0.3	6.3±0.5	12.2±0.5	6.0±0.1	5.4±0.4	8.2±0.3	13.5±0.1	9.3±0.8	3.2±0.4
16:1(n-5)	1.1±0.0	0.7±0.0	0.6±0.1	0.3±0.0	0.3±0.0	0.2±0.0	0.4±0.2	0.2±0.0	0.3±0.0
16:3(n-4)	0.2±0.0	0.7±0.1	0.6±0.1	0.3±0.0	0.3±0.0	0.5±0.0	1.0±0.0	0.3±0.1	0.2±0.1
16:4(n-l)	7.6±1.3	3.5±0.5	2.2±0.2	1.2±0.4	5.3±1.2	2.7±0.1	2.8±0.2	1.3±0.0	1.2±0.1
18:0	2.2±0.1	0.7±0.3	1.2±0.1	3.4±0.4	1.1±0.1	1.6±0.0	1.5±0.0	1.2±0.2	3.5±0.2
18:1(n-9)	5.4±0.1	3.7±0.1	4.5±0.4	11.8±0.6	14.5±0.3	5.5±0.6	18.0±1.6	23.4±4.8	8.9±0.8
18:1(n-7)	0.3±0.0	0.3±0.0	0.6±0.0	7.0±0.5	4.3±0.5	1.8±0.1	1.7±0.1	1.8±0.5	2.2±0.1
18:2(n-6)	1.4±0.1	1.0±0.1	1.1±0.1	1.2±0.0	1.3±0.0	1.1±0.0	1.0±0.1	1.0±0.2	1.6±0.1
18:3(n-3)	4.2±1.5	1.1±0.1	1.5±0.6	0.5±0.1	0.5±0.0	0.4±0.0	0.4±0.1	0.6±0.2	0.5±0.1
18:4(n-3)	13.4±0.4	11.3±1.2	3.0±0.2	1.6±0.2	1.2±0.0	1.4±0.1	1.8±0.1	0.8±0.2	1.0±0.3
18:5(n-3)	3.2±0.7	1.2±0.4	1.1±0.6	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.0±0.0	0.1±0.0
20:1(n-11)	0.6±0.0	0.9±0.1	1.3±0.1	1.0±0.1	4.7±0.1	1.3±0.1	1.5±0.6	5.2±1.1	1.2±0.2
20:1(n-9)	2.4±0.1	3.7±0.3	4.8±0.2	7.3±1.1	15.1±1.1	13.3±0.3	6.1±0.2	14.5±3.2	8.2±1.7
20:1(n-7)	1.7±0.1	1.3±0.0	1.7±0.8	1.2±0.2	0.6±0.1	0.2±0.0	0.2±0.0	0.6±0.1	0.3±0.1
20:4(n-6)	0.9±0.0	0.9±0.1	1.1±0.0	0.6±0.1	0.4±0.0	0.5±0.0	0.8±0.0	0.2±0.0	2.2±0.4
20:4(n-3)	1.5±0.2	1.3±0.0	1.4±0.2	0.8±0.1	1.2±0.1	0.5±0.0	1.1±0.1	1.0±0.0	0.6±0.1
20:5(n-3)	7.4±0.4	12.3±1.0	11.4±1.7	9.1±0.6	6.6±0.9	8.5±0.7	12.0±0.8	1.0±0.6	8.4±0.9
22:1(n-11)	4.8±0.3	6.7±0.2	7.0±0.2	5.0±0.4	14.9±0.9	21.4±0.4	8.4±0.4	17.3±3.4	9.5±2.4
22:1(n-9)	0.8±0.1	0.6±0.1	0.7±0.1	1.1±0.3	1.0±0.1	0.0±0.0	0.7±0.1	1.5±0.4	1.3±0.2
22:1(n-7)	0.0±0.0	0.1±0.1	0.2±0.0	0.1±0.0	0.2±0.0	0.1±0.0	0.2±0.0	0.5±0.2	0.1±0.0
22:4(n-6)	1.3±0.0	2.5±0.3	2.2±0.3	0.1±0.0	2.3±0.2	0.0±0.0	1.3±0.2	2.6±0.1	0.1±0.0
22:5(n-6)	0.0±0.0	0.2±0.0	0.5±0.0	0.3±0.0	0.1±0.0	0.5±0.0	0.4±0.0	0.4±0.1	0.2±0.1
22:5(n-3)	0.3±0.0	0.6±0.1	0.7±0.0	0.9±0.0	0.5±0.1	0.9±0.0	0.9±0.0	0.1±0.0	1.3±0.1
22:6(n-3)	3.9±0.1	3.2±0.3	1.2±0.0	6.9±1.1	4.3±0.6	3.7±0.1	5.7±1.0	0.9±0.3	23.2±3.5
Minor components	7.7	6.2	6.3	4.6	5.8	3.7	8.3	6.4	3.8
22:1(n-11)/ 20:1(n-9)	2.0	1.8	1.5	0.7	1.0	1.6	1.4	1.2	1.2
FAlc									
16:0	18.0±0.4	15.0±0.4	14.5±0.9		25.3±4.6		36.4±1.0	26.1±5.0	
16:1(n-7)	15.0±1.2	8.3±1.4	10.1±0.4		4.3±0.6		6.5±0.2	2.2±0.5	
18:1(n-9)	5.3±0.2	4.1±0.1	3.4±0.5		9.7±1.8		18.3±2.7	15.4±2.9	
20:1(n-9)	25.6±1.1	32.6±1.3	33.9±0.4		19.1±1.4		15.4±0.6	18.0±2.1	
22:1(n-11)	35.0±1.0	39.5±1.8	37.7±1.0		41.6±4.8		23.1±1.0	37.8±6.3	
22:1(n-9)	1.2±0.2	0.6±0.6	0.5±0.5		0.0±0.0		0.3±0.3	0.5±0.5	
22:1(n-11)/ 20:1(n-9)	1.4	1.2	1.1		2.2		1.5	2.1	
% of FAlc of total moieties	28.5	35.8	36.2	0.5	32.0	0.5	34.5	35.7	0.6

Values are means±SE. All samples (excluding *S. mentella*) are whole individuals whereas *S. mentella* constitutes muscle samples. *n* = number of replicates.

3.2.2. Meganyctiphanes norvegica

The most abundant FA in the neutral lipid fraction of *M. norvegica* was the SFA 16:0, which occurred at mean levels of 18.2% (Table 5). The SFA 14:0 was recorded at lower levels (8.6%). The MUFA 18:1(n-9) was recorded at high levels (mean 11.8%), while 18:1(n-7) had lower levels (mean 7.0%). Moderate amounts of the *Calanus* FATMs, the MUFAs 20:1(n-9) and 22:1(n-11) occurred at mean levels of 7.3% and 5.0%, respectively. The FA 20:5(n-3) had the highest level of the phytoplankton FATMs (mean 9.1%), followed by 22:6(n-3) (mean 6.9%), 16:1(n-7) (mean 6.0%), C18 PUFA (mean 3.3%) and 16:4(n-1) (mean 1.2%). Fatty alcohols only accounted for 0.5% of the total moieties in *M. norvegica*.

3.2.3. Sergestes arcticus

In the decapod *S. arcticus*, the SFAs 14:0 and 16:0 occurred at much lower levels than in *M. norvegica*, accounting for 2.9% and 4.9% of the total FAs (Table 5). The MUFA 18:1(n-9) occurred at high levels (mean 14.5%), while 18:1(n-7) occurred at much lower levels (mean 4.3%). The dominant FAs in *S. arcticus* were the *Calanus* FATMs, 20:1(n-9) (mean 15.1%) and 22:1(n-11) (mean 14.9%). The phytoplankton FATMs recorded were in decreasing order: 20:5(n-3) (mean 6.6%), 16:1(n-7) (mean 5.4%), 16:4(n-1) (mean 5.3%), 22:6(n-3) (mean 4.3%) and C18 PUFA (mean 3.0%). Fatty alcohols constituted 32.0% of the total moieties in *S. arcticus*. The major fatty alcohols presented in the neutral lipid fraction were 22:1(n-11) (41.6%), 16:0 (25.3%) and 20:1(n-9) (19.1%).

3.2.4. Maurolicus muelleri

In the mesopelagic fish species *M. muelleri*, the SFAs 14:0 and 16:0 occurred at mean levels of 8.6% and 13.1%, respectively (Table 5). The MUFAs 18:1(n-9) (5.5%) and 18:1(n-7) (1.8%) occurred at lower levels than in the other species (not including *C. finmarchicus*), whereas the *Calanus* FATM 22:1(n-11) was found in the greatest amount accounting for 21.4% of the total FAs, followed by the other *Calanus* copepod FATM 20:1(n-9), which accounted for 13.3%. Of the phytoplankton FATMs, 20:5(n-3) was recorded at high levels with mean 8.5%, followed by 16:1(n-7) (mean 8.2%), 22:6(n-3) (mean 3.7%), 16:4(n-1) (mean 2.7%) and C18 PUFAs (mean 2.9%). Fatty alcohols only accounted for 0.5% of the total moieties in *M. muelleri*.

3.2.5. Benthosema glaciale

The mean levels of the SFAs 14:0 and 16:0 in both size groups of the myctophid *B. glaciale* were similar (Table 5). For FA 14:0, the mean levels were 5.9% and 4.7% for the smaller and larger fish, respectively, whereas FA 16:0 in the smaller and larger fish was 3.6% and 2.3%, respectively. The difference between the two size groups of *B. glaciale* was mainly due to much higher amounts of the *Calanus* FATMs in the larger fish, 20:1(n-9) (6.1% and 14.5%, in small and large fish, respectively) and 22:1(n-11) (8.4% and 17.3%, in small and large fish, respectively) and the higher amount in the large size group of the MUFA 18:1(n-9) (18.0% in the smaller fish and 23.4% in the larger fish). In contrast, the mean levels of the phytoplankton FATMs were much higher in the smaller size group than in the larger size group: 16:1(n-7) (13.5 and 9.3%, respectively), 20:5(n-3) (12% and 1.0%, respectively) and 22:6(n-3) (5.7 and 0.9%, respectively). Fatty alcohols of the total moieties in *B. glaciale* were approximately 35% in both size groups. The major fatty alcohols presented in the neutral lipid were for smaller and larger fish, respectively: 16:0 (36.4 and 26.1%), 18:1(n-9) (18.3 and 15.4%), 20:1(n-9) (15.4 and 18.0%) and 22:1(n-11) (23.1 and 37.8%).

3.2.6. Sebastes mentella

The SFA 16:0 occurred at high mean levels (14.0%) in the redfish, *S. mentella*, while 14:0 and 18:0 were recorded at much lower levels, 2.5% and 3.5%, respectively (Table 5). The MUFA 18:1(n-9) occurred at moderate levels (mean 8.9%), but similar amounts of the *Calanus* FATMs 20:1(n-9) (8.2%) and 22:1(n-11) (9.5%) were recorded. By far the most dominant FA in *S. mentella* was the dinoflagellates FATM 22:6(n-3) accounting for about 23.2% of the total FAs, at a much higher level than any of the other species. High amounts of the phytoplankton FATM 20:5(n-3) (8.4%) occurred , followed by 16:1 (n-7) (3.2%) and C18 PUFAs (3.2%). In total, PUFA phytoplankton FATMs together with 16:1(n-7) diatoms FATM accounted for about 40%. Fatty alcohols of the total moieties in *S. mentella* constituted only 0.6%.

3.2.7. Trophic interactions

RDA was applied to explore the similarities in the moieties composition of the pelagic species under investigation (Table 6, Fig. 3). The target species were significantly different in moieties composition (Monte Carlo $F = 16.5$, $p = 0.002$) and 87.8% of the total variability in their compositions was explained by the species. The first two axes explained 79% of the total variance in the moieties composition.

The main gradient along axis 1 divided the species into two groups, based on similarities, where *S. mentella* and *M. norvegica* made up one group and *C. finmarchicus*, *S. arcticus*, *M. muelleri* and *B. glaciale* made up another group (Fig. 3). The moieties 22:6(n-3), 20:1(n-9) and 22:1(n-11) were the main distinguishing factors in those groups. *S. mentella* and *M. norvegica* had relatively high amounts of the FA 22:6(n-3) and low amounts of the *Calanus* FATMs 20:1(n-9) and 22:1(n-11) compared to the other species. The gradient along axis 2 was from the herbivorous *C. finmarchicus* to carnivorous species with a higher amount of the FA 18:1(n-9).

4. Discussion

The importance of *Calanus* spp. in the pelagic ecosystem over the Reykjanes Ridge is enforced by the high amount

Table 6
Moiety compositions (relative amounts) of the studied species

Moiety	*C. finmarchicus*			*M. norvegica* ($n = 2$)	*S. arcticus* ($n = 3$)	*M. muelleri* ($n = 3$)	*B. glaciale*		*S. mentella* ($n = 6$)
	CIV ($n = 3$)	CV ($n = 3$)	Female ($n = 3$)				Small ($n = 3$)	Large ($n = 3$)	
14:0	12	13	14	9	2	9	4	3	3
14:1	1	0	0	1	0	0	0	0	0
16:0	11	11	12	19	11	14	15	10	13
16:1(n-7)	7	7	12	6	5	8	12	7	4
16:3(n-4)	0	0	0	0	0	1	1	0	0
16:4(n-l)	6	2	2	1	4	3	2	1	1
18:0	2	0	1	4	1	2	1	1	3
18:1(n-9)	6	4	4	12	13	6	19	22	9
18:1(n-7)	0	0	0	7	3	2	1	1	2
18:2(n-6)	1	1	1	1	1	1	1	1	2
18:3(n-3)	3	1	1	0	0	0	0	0	0
18:4(n-3)	10	8	2	2	1	1	1	1	1
18:5(n-3)	2	1	1	0	0	0	0	0	0
20:1(n-11)	0	1	1	1	3	1	1	4	1
20:1(n-9)	9	14	15	8	17	14	10	17	10
20:1(n-7)	1	1	1	1	0	0	0	0	0
20:4(n-6)	1	1	1	1	0	1	1	0	2
20:4(n-3)	1	1	1	1	1	1	1	0	1
20:5(n-3)	6	9	8	9	5	9	9	1	8
22:0	0	0	0	1	1	1	0	0	0
22:1(n-ll)	14	19	18	5	24	22	14	26	12
22:1(n-9)	1	1	1	1	1	0	1	1	1
22:4(n-6)	1	2	1	0	2	0	1	1	0
22:5(n-6)	0	0	0	0	0	0	0	0	0
22:5(n-3)	0	0	1	1	0	1	1	0	1
22:6(n-3)	3	2	1	7	3	4	4	1	23
Minor comp.	1	1	1	1	1	1	1	1	1

Values are average percentages. n = number of replicates.

of *Calanus* FATMs moieties in all investigated species in this study, ranging from 15% in *Meganyctiphanes norvegica* to 48% in the larger size group of *Benthosema glaciale*. This is in accordance with previous studies that have found *Calanus finmarchicus* to be the most important copepod in the area in terms of biomass (Gislason, 2003; Gaard et al., 2008).

In the present study, the FA 18:1(n-9) was found in high amounts in *M. norvegica*, indicating carnivorous feeding (Falk-Petersen et al., 2000; Dalsgaard et al., 2003). This is in accordance with the results of other studies showing *M. norvegica* to be an omnivorous/carnivorous species that performs dial vertical migrations (Mauchline and Fisher, 1969; Kaartvedt et al., 1988). The relatively low amount of *Calanus* FATMs in *M. norvegica* shows that *Calanus* spp. is not a very important part of its diet. The stable isotope $\delta^{13}C$ values of *M. norvegica* were almost the same as those of *C. finmarchicus*, further suggesting that *Calanus* did not constitute the main diet of *M. norvegica*. According to the present study, *M. norvegica* occupies trophic level 2.9, indicating that phytoplankton is not a dominant part of their diet either. This is in line with other studies where *M. norvegica* is found to have a flexible omnivorous feeding strategy, feeding on copepods during winter and on phytoplankton during the spring bloom (Sargent and Falk-Petersen, 1981). Our samples were collected about 1 month after the vernal plankton bloom (Gaard et al., 2008).

The shrimp *S. arcticus* is a bathypelagic species with a wide range of vertical distribution (Mauchline and Gordon, 1991; Koukouras et al., 2000). It is known to have a rather deep distribution in the water column and to undertake dial vertical migrations (Kaartvedt et al., 1988; Mauchline and Gordon, 1991).

S. arcticus had relatively high amounts of the *Calanus* FATMs, indicating the importance of *Calanus* spp. in its diet. The relative amounts of *Calanus* FATMs in *S. arcticus* were actually much higher than those found in the *C. finmarchicus* studied here. The ratio between the fatty alcohols 22:1(n-11) and 20:1(n-9) was around 1 in *C. finmarchicus* in contrast to approximately 2 in *S. arcticus*. This is the same value as reported by Scott et al. (2002) for *Calanus hyperboreus*, indicating that *S. arcticus* feeds on the larger, deeper-living *C. hyperboreus* during winter and spring. *C. hyperboreus* is a species that is known to be an important part of the zooplankton biomass

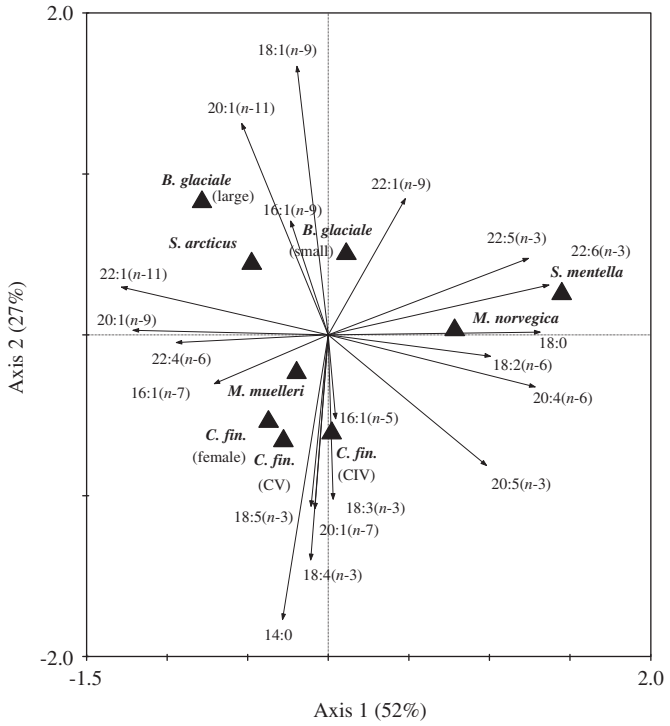

Fig. 3. Redundancy analysis (RDA) plot based on mean moiety values of differnt individuals of *Calanus finmarchcius* (copepodid stage CIV, CV and female), *Meganyctiphanes norvegica*, *Sergestes arcticus*, *Maurolicus muelleri*, *Benthosema glaciale* (two size groups) and *Sebastes mentella*. Triangles indicate mean values of the respective species. The species were applied as dummy variables (environmental variables) and fatty acids as response variables. The fraction of unconstrained variance accounted for by each axis is given in bracket.

in the Irminger Sea during winter and spring (Gislason, 2003), and it was also found in deep water samples from the Mid-Atlantic Ridge by Gaard et al. (2008).

Additionally, if it is assumed that benthic organisms and carcasses have higher levels of $\delta^{13}C$ than pelagic animals (McConnaughey and McRoy, 1979; Tamelander et al., 2006), the high $\delta^{13}C$ levels in *S. arcticus* in this study, compared to the other species at similar trophic level, may indicate a more benthic input to the diet of *S. arcticus*. This is in line with the results on the feeding of *S. arcticus* on the continental slope of the Bay of Biscay (Lagardere, 1975), where it is known to have a scavenging feeding strategy feeding both in the surface water (evening) and near the bottom (afternoon). In the Bay of Biscay, copepods are the most important part of their diet, but fish carcasses are also important during winter (Lagardere, 1975). On the slope of Porcupine Seabight, in the northern northeast Atlantic, benthic organisms have been found in the stomach of *S. arcticus* (Hargreaves, 1984). It can also be noted that on the slope of the Porcupine Seabight and of the Rockall Trough, which may be considered as somewhat comparable bathymetric features as an oceanic ridge, *S. arcticus* stay deeper than in the adjacent oceanic water column (Hargreaves, 1984; Mauchline and Gordon, 1991).

M. muelleri is a small oceanic mesopelagic fish that is found at depths between 10 and 400 m during the day, with some migration at dusk to the upper 100 m (Badcock, 1984). Their distribution is shallower than the distribution of *B. glaciale,* the other small oceanic mesopelagic fish of the present study (Bagøien et al., 2001). *M. muelleri* had high amounts of *Calanus* FATMs. The moiety composition is more related to the *C. finmarchicus* studied here than the moiety composition of the other species of the present study. This indicates that *M. muelleri* preys more heavily on *C. finmarchicus* than *B. glaciale* and *S. arcticus*. It is a selective feeder on planktonic organism, mainly including copepods and euphausiids (Gjøsæter, 1981; Badcock, 1984). Calanoid copepods are a big part of their diet (Mauchline and Gordon, 1983; Gorelova and Krasilnikova, 1990). The FA composition of *M. muelleri* on the Reykjanes Ridge resembled that of *M. muelleri* in Northern Norway (Falk-Petersen et al., 1986), indicating similar diets in the two areas.

B. glaciale performs dial vertical migrations similarly to *M. muelleri* (Bagøien et al., 2001). The smaller size group of *B. glaciale* had a much lower relative amount of *Calanus* FATMs than the larger specimens of the same species. The smaller ones had concentrations similar to those of *C. finmarchicus*, whereas the larger ones resembled *C. hyperboreus* with fatty alcohol ratios of 22:1(n-11) and 20:1(n-9) around two (Falk-Petersen et al., 1987; Scott et al., 2002). This difference might indicate selective feeding by the smaller *B. glaciale* on *C. finmarchicus* and the larger *B. glaciale* on *C. hyperboreus*. In this context, it is noteworthy that Sameoto (1989) found *B. glaciale* in Davis Strait to feed selectively on the older stages of *C. finmarchicus* and *C. hyperboreus*.

The redfish *S. mentella* differs from the other species investigated in that they have extremely high levels of the dinoflagellate FATM 22:6(n-3), which is found in high amounts in polar lipids and is essential to membrane structures. The relatively low values of *Calanus* FATMs in redfish indicate that *Calanus* spp. or *Calanus*-derived diet is not an important part of the diet of *S. mentella*. The moieties composition of *S. mentella* is quite similar to the euphausiid *M. norvegica*, which indicates that *S. mentella* preys heavily on euphausiids or organisms with similar moieties composition. This is also supported by the results of the stable isotope analyses. These findings are in accordance with observations made by Magnusson and Magnusson (1995), where euphausiids were found to be one of the major components of the *S. mentella* diet together with chaetognaths and amphipods. *M. norvegica* accounted for ~50% of the total prey volume of redfish in the northwest Atlantic (Pikanowski et al., 1999). The relatively low importance of *Calanus* spp. as food for *S. mentella* is noteworthy in light of their general abundance in the area (Gislason, 2003; Gaard et al., 2008), but the prey size of *Calanus* was likely too small for the size class of *S. mentella* in our study. While the adult redfish thus seem to be feeding mainly on euphausiids, the

redfish larvae are known to feed almost exclusively on eggs and young developmental stages of *C. finmarchicus* (Bainbridge and McKay, 1968; Runge and DeLafontaine, 1996).

The discussion above for *S. mentella* is based on analyses of lipids from muscle tissues alone. However, as *S. mentella* is known also to store lipids in the skull and liver, these tissues were also analysed. Despite some differences compared to the muscle tissue (mainly in lower levels of 22:6(n-3)), when projected in the multivariate analysis, the same pattern was observed for all tissues (data not shown).

The zooplankton and fish species analysed in this study are all lipid-rich species typical for high-latitude pelagic ecosystems (Falk-Petersen et al., 2007). Based on the percentage of fatty alcohols of the total moieties, it is concluded that *C. finmarchicus*, *S. arcticus* and *B. glaciale* store wax esters as their lipid stores, while *M. norvegica*, *M. muelleri* and *S. mentella* store triacylglycerol. Wax esters have been regarded as a long-term energy reserve, while triacylglycerols are often regarded as a short-term energy deposit (Lee et al., 1971a, 2006; Sargent and Henderson, 1986).

Based on our general knowledge of the ecosystem over the Reykjanes Ridge, the biology of the studied species, lipid biomarkers, multivariate analyses and results from stable isotopes analyses, we conclude that *Calanus* spp. are very important in the pelagic ecosystem over the Reykjanes Ridge as food (energy) for organisms at higher trophic levels. We suggest that there are two trophic pathways over the Reykjanes Ridge: one where *Calanus* spp. are an important part of the diet, for i.e. the small oceanic mesopelagic fish species *M. muelleri* and *B. glaciale* and the shrimp *S. arcticus*, and another where the euphausiid *M. norvegica* is the dominant food for the redfish *S. mentella* and *Calanus* spp. are of less importance.

Furthermore, we deduce that *M. muelleri* and the smaller *B. glaciale* feed on *C. finmarchicus* and the larger *B. glaciale* and *S. arcticus* select the larger, deeper living *Calanus* species, *C. hyperboreus*. Finally, we conclude that all the investigated species are true pelagic species with respect to their feeding habits, except for the shrimp *S. arcticus* which seems to alternate between pelagic and benthic feeding habits.

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