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Trophic interactions and energy flow within the pelagic ecosystem in the Iceland Sea

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Abstract

A trophic study was carried out in August 2007 on the pelagic ecosystem in the sub-arctic Iceland Sea, north of Iceland, using carbon and nitrogen stable isotopes and fatty acid biomarkers. The aim was to study trophic linkages and positions of the most important pelagic species in this ecosystem with special emphasis on the trophic ecology of capelin. According to ^{15}N enrichment it is concluded that there are around 4 trophic levels in this pelagic ecosystem excluding bird and mammals, where the primarily herbivorous copepod *Calanus finmarchicus* occupies the lowest trophic level of the studied species and adults of capelin (*Mallotus villosus*) and blue whiting (*Micromesistius poutassou*) the highest. *Calanus* spp. proved to be important diet component (high amount of *Calanus* fatty acid trophic markers in the neutral lipid fraction), of most of the studied species. However the euphausiid species *Thysanoessa inermis* and *T. longicaudata* are exceptions as *Calanus* spp. are of minor importance in their diet. The chaetognath, *Eukrohnia hamata*, is a pure carnivore, feeding almost exclusively on *Calanus* spp., while most of the others zooplankton species studied practice omnivorous-carnivorous feeding mode. The capelin fatty acid profiles, indicate a shift in diet after metamorphosis when the capelin gets more mobile. The importance of *Calanus* spp. or *Calanus* derived diet increases with the size of capelin. Adults of capelin and blue whiting share the same feeding habits and could therefore be competing for food. Multivariate statistical methods were performed on fatty acid compositional data making it possible to detect relationships and patterns in the data. This study is a part of an ecological study in the Iceland Sea, with field work lasting from 2006-2008.

Keywords: trophic ecology, zooplankton, capelin, stable isotopes, fatty acids, Iceland Sea

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Introduction

High latitude marine ecosystems are characterized by extreme seasonality i.e. pronounced increase in light intensity during spring and summer and darker winter months, resulting in high primary and secondary productions during short period of time (Falk-Petersen, et al., 1990; Thordardottir, Th., 1994; Gislason and Astthorsson, 1998). Thus, marine pelagic animals in high latitude ecosystems have adapted to relatively short production season by converting large amount of excess food into storage lipids, making it possible for the animals to survive long periods of food scarcity (Falk-Petersen, 1981; Clarke, 1983; Hagen and Auel, 2001).

The Iceland Sea serves as a nursery or feeding grounds for several of the commercially important fish stocks in Iceland (Magnússon and Pálsson, 1989; Astthorsson and Gislason, 1997; Pálsson, 1997; Sólmundsson, 1997), e.g. the pelagic fish, capelin (*Mallotus villosus*) which annual catch is about one million ton (Anon, 2005; Astthorsson et al., 2007). The capelin is important component of the Icelandic ecosystem as a link between zooplankton and species at higher trophic levels, the capelin being essential in the diet of many species (Magnússon and Pálsson, 1989; Vilhjálmsson, 1994) e.g. the Atlantic cod (*Gadus morhua*). Further capelin is also important in transferring energy from the Iceland Sea (north of Iceland), were it has been feeding on lipid rich zooplankton during the summer, to the spawning grounds of capelin (south of Iceland, Vilhjálmsson, 1994; Astthorsson and Gislason, 1997; Astthorsson et al., 2007). Copepods dominate the zooplankton community in the Iceland Sea, thereof *Calanus finmarchicus* is the most abundant. Other common zooplankton species in the Iceland Sea are the copepods *Oithona* spp., *Pseudocalanus* spp. *Metridia longa* and *C. hyperboreus*, the latter two mostly restricted to the Arctic water in the center and western part of the Iceland Sea, the euphausiids *Thysanoessa inermis*, *T. longicaudata* and *Meganyctiphanes norvegica* and the amphipods *Themisto abyssorum* and *T. libellula*, the last named mainly found in the Arctic water (Astthorsson, et al., 1995; Dalpadado, et al., 1998; Gislason and Astthorsson, 1998).

Knowledge of predator-prey relations is essential in understanding trophic relationships and energy flows in marine ecosystems. Stable isotopes together with fatty acid (FA) analyses constitute a powerful and complementary tool to traditional stomach content analyses (Kharlamenko et al., 2001; Dahl et al., 2003; Petursdottir et al., 2008), as their patterns show an integration of prey over periods from weeks to months (Fry, 1988; Rau et al. 1992; Dalsgaard et al., 2003). Additionally, trophic position of the species can be deduced from stable isotopes values, while FAs and alcohols may give more detailed information about their diet.

The stable isotopes of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) are enriched, in predictable manner, in consumers relative to their prey (Minagawa and Wada, 1984; Hobson et al., 1995). The enrichment of $\delta^{15}N$ is more pronounced than of $\delta^{13}C$. Thus, $\delta^{15}N$ values provide good measure of trophic position of the species (Hobson and Welch, 1992; Dahl et al., 2003; Tamelander et al., 2006), while $\delta^{13}C$ values may give information about carbon source in the food chain and (or) habitat, i.e. benthic versus pelagic feeding (Peterson and Fry, 1987; Hecky and Hesslein, 1995; Peterson, 1999; Søreide, et al., 2006).

Lipids have been used as biomarkers in marine ecosystems to follow energy transfer and to study predator-prey relationships (Falk-Petersen et al., 1990; 2004; Dalsgaard et al., 2003). Primary producers and some zooplankton species can be characterized by their specific FA profiles. Some of these FAs can be transferred relatively unchanged through trophic levels (Lee, et al., 1971; Graeve et al., 1994; Dalsgaard, et al., 2003) and are referred to as fatty acid trophic markers (FATMs). Known FATMs are, for example, 20:5n3, 16:1n7 and C16 poly-unsaturated fatty acids (PUFAs) for diatoms; 22:6n3 and C18 PUFAs for dinoflagellates and *Phaeocystis* and 20:1n9 and 22:1n11 monounsaturated fatty acids (MUFAs) for *Calanus* copepods (Table 1). To assist with detecting relationships and patterns among FAs profiles of different species, Multivariate statistical analyses have been used (Grahl-Nielsen and Mjaavatten, 1991; Falk-Petersen, et al., 2004).

Table 1. Some known fatty acid trophic markers (FATMs) (Dalsgaard, et al., 2003).

FATM	Taxa
22:6(n-3) and C18PUFA	Dinoflagellates
18:4(n-3), 18:5(n-3), 18:2(n-6)	*Phaeocystis pouchetti*
20:5(n-3), C16PUFA, 16:1(n-7)	Diatoms
20:1(n-9), 22:1(n-11)	*Calanus* copepod

Information on the trophic relationships in the pelagic ecosystem in the Iceland Sea is scarce. Some data from stomach analyses exist on the diet of capelin (Sigurðsson and Astthorsson, 1991; Astthorsson and Gislason, 1997), but there is no previous information of the food of organisms of lower trophic levels (zooplankton). The aim of the present study was to study trophic relationships among some representative species of the pelagic ecosystem of the subarctic Iceland Sea, north of Iceland, using stable isotopes and fatty acids analyses. The study is a part of an extensive ecological study in the Iceland Sea, the Iceland Sea Ecosystem Project, of the Marine Research Institute, with field activity lasting from 2006-2008. The overall objective of that project is to analyze the structure and function of the Iceland Sea ecosystem, with particular emphasis on the life history of the capelin stock and recent changes during the last decade.

Materials and methods

The Iceland Sea is encircled by Iceland to the south, East Greenland to the west and Jan Mayen to the northeast, with a maximum depth around 2000 meters (Figure 1).The main water mass in the western and central Iceland Sea is Arctic water carried by the East Greenland and East Iceland currents while the water in the northeast and southern part is mainly of Atlantic origin (Blindheim and Østerhus, 2005 and references therein).

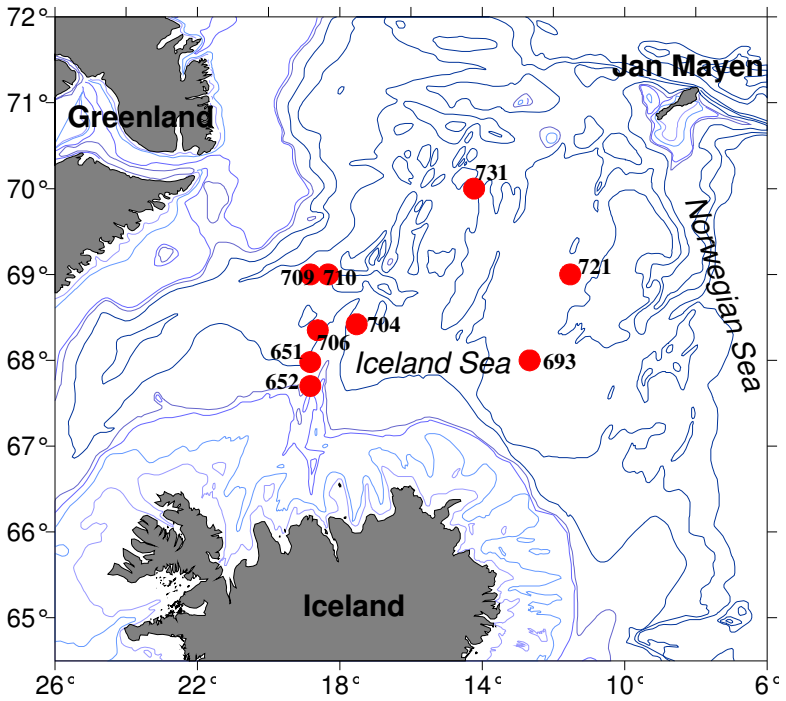

Figure 1. Station map for the August cruise in 2007.

Abundant pelagic species in the Iceland Sea as well as particulate organic matter (POM) were chosen as representative elements of the pelagic food web in the central Iceland Sea as based on previous studies on the pelagic ecosystem in the region (Astthorsson, et al., 1995; Dalpadado, et al., 1998; Gislason and Asthorsson, 1998). Specimens were selected so as to minimize variation in size, and the size groups reflected the highest abundance of every species in the respective catch (Table 3). The following species were chosen: the copepods *Calanus finmarchicus* (stage V), *Metridia longa* (female) and *Paraeuchaeta glacialis* (female); the euphausiids *Thysanoessa inermis* (~2.5 cm), *T. longicaudata* (~1.5 cm) and *Meganyctiphanes norvegica* (~3.5 cm); the amphipods *Themisto libellula* (~1.5 cm), *T. abyssorum* (~1.5 cm) and *Gammarus wilkitzkii* (~2.5 cm); the chaetognath *Eukrohnia hamata* (~3 cm); and the fish *Mallotus villosus* (larvae ~4 cm, juveniles ~7 cm and adults ~13 cm), *Gadus morhua* (juveniles 5 cm) and *Micromesistius poutassou* (adults ~30 cm, Table 3).

Table 2. Position and date of the stations sampled in Iceland Sea in August 2007.

Station	Lat (°N)	Long (°W)	Date
651	67°59´	18°50´	13 August
652	67°42´	18°50´	13 August
693	68°00´	12°40´	18 August
704	68°25´	17°32´	19 August
706	68°21´	18°37´	19 August
709	69°00´	18°50´	20 August
710	69°00´	18°20´	20 August
721	69°00´	11°32´	21 August
731	70°00´	14°14´	22 August

Table 3. Overview of samples for lipids (fatty acid and alcohol composition) and stable isotopes analyzed ($\delta^{13}C$, $\delta^{15}N$) as well as station number, depth of sampling and gear. The number of replicates analyzed and animals per replica (in brackets) are given.

Species/group	Length (cm)	Station no.	Gear	Depth (m)	Analyses		
					Lipids	$\delta^{13}C$	$\delta^{15}N$
POM		731	Water inlet	5	2(filter)	1(filter)	1(filter)
C. finmarchicus CV		709	Multinet	0-400	3(12)	1(100)	1(100)
M. longa female		709	Multinet	0-400	3(12)	2(70)	2(70)
P. glacialis female		710	Tucker trawl	0-100	3(5)	3(20)	3(20)
T. inermis	2.5	651	Tucker trawl	0-100	3(3)	3(4)	3(4)
T. longicaudata	1.5	710	Tucker trawl	0-100	3(10)	3(20)	3(20)
M. norvegica	3.5	710	Tucker trawl	0-100	3(3)	3(5)	3(5)
T. libellula	1.5	710	Tucker trawl	0-100	3(3)	3(20)	3(20)
T. abyssorum	1.5	710	Tucker trawl	0-100	3(3)	3(20)	3(20)
G. wilkitzkii	2.5	651	Tucker trawl	0-100	3(1)	3(2)	3(2)
E. hamata	3.0	693	Multinet	0-600	3(10)	3(15)	3(15)
M. villosus larvae	4.0	652	Pelagic trawl	0-26	3(5)	3(5)	3(5)
M. villosus juvenile	7.0	706	Pelagic trawl	n.a.	3(3)	3(5)	3(5)
M. villosus adult	13.0	652	Pelagic trawl	0-26	3(1)	3(1)[a]	3(1)[a]
G. morhua juvenile	5.0	704	Pelagic trawl	0-21	3(1)	3(1)	3(1)
M. poutassou adult	30.0	721	Pelagic trawl	n.a.	3(1)[a]	3(1)[a]	3(1)[a]

[a]Muscle tissue analysed (otherwise whole animals). n.a. = not available.

Sampling

Samples were collected at nine stations with various types of gear (Multinet, Tucker trawl, Pelagic trawl) in the central and eastern parts of the Iceland Sea in August 2007 (Tables 2 and 3, Figure 1). The net hauls were not quantitative in this study, only to sample the species.

Water samples for POM were collected from the ship´s underway system, which has an intake at 5 meters depth. For the stable isotope analyses the water was filtered through pre-combusted (450°C, 4h) Whatman GF/G glass fibre filters, while for fatty acid analyses the filters were washed with chloroform:methanol 2:1 (v/v) solution before filtering.

All the target species for fatty acid and alcohol analyses were obtained by picking out given number of individuals (Table 3) and storing them in chloroform:methanol 2:1 (v/v) solution at -20°C, except for the adult fish (*M. villosus* and *M. poutassou*) which were frozen directly at -20°C. The frozen fish samples were also used for stable isotopes analyses. For stable isotopes analyses bulk samples containing a mixture of several species were frozen in plastic trays at -20°C, and the target species (zooplankton and juvenile fish) were picked out later in the laboratory (Table 3). On shore, the samples were stored at -80°C prior to analyses.

Laboratory analyses

Stable isotopes ratios were analyzed 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 2h 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 2N HCl and dried at 80°C. Stable isotopes ratios ($\delta^{13}C$ and $\delta^{15}N$) of the residual material were analyzed 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 $\delta\ ^{15}N$ is atmospheric air (IAEA-N-1 and IAEA-N-2).

Lipid classes, fatty acids and fatty alcohols were analyzed 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 fatty acid 21:0 was added as an internal standard to both fractions and an acid-catalyzed transesterification was carried out with 1% sulphuric acid in methanol (Christie, 1982). The relative (%) compositions of fatty acid 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).

Data analyses

The fractionation factors 0.8‰ for $\delta^{13}C$ and 3.8‰ for $\delta^{15}N$ between trophic levels were used to help with interpreting the data. 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). As *C. finmarchicus* has been found to be primarily herbivorous (Harris, 1996; Søreide, et al., 2008) it was in the present study assumed that it represented trophic level 2.

The following relationship was used for each individual sample of other tropic levels (Fisk et al., 2001):

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

where $TL_{consumer}$ is the trophic level of an organism, $\delta^{15}N_{\textit{Calanus}}$ is analytically determined as 5.5 ± 0.1 (mean ± SE), and 3.8 is the isotopic enrichment factor (Hobson and Welch, 1992; Hobson et al., 1995)

The total neutral lipid fraction was analyzed to determine the weight % compositions of the fatty acid methyl esters and the fatty alcohol acetates. To be able to detect trophic relationships between species, neutral lipids (fatty acids 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 fatty acid 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 fatty acid methyl esters, the moieties of fatty alcohol acetates (with the same chain lengths, numbers and positions of double bonds as the moieties of fatty acid methyl esters) were combined in a known proportion of fatty alcohol acetates and fatty acid methyl esters in the neutral lipid, and new % data was 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 analyze for trophic relationships among the target species (Table 6, Figure 3). 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.

Results

Because of extremely low phytoplankton biomass in the Iceland Sea in August 2007 (Anon, 2007), around 20 liters of seawater had to be filtered for each sample of suspended POM, taking up to six hours of filtering. Thus, high risks of contaminations from small zooplankton species was likely to occur, which was then supported by the percentages of fatty alcohol of the total moieties in POM (27%). Therefore, POM was not used as a base of the food web in the trophic level calculations, nor was the fatty acid composition described.

Stable isotopes

POM had the lowest $\delta^{13}C$ value (-25.5‰, mean value) followed by the other copepods, while the larvae of *M. villosus* had the highest value (-18.1‰; Table 4, Figure 2).

Stable nitrogen isotope ratios ($\delta^{15}N$) ranged from 4.9‰ for POM to 11.6‰ for adult *M. poutassou* (Table 4, Figure 2).

The copepod *M .longa* occupied trophic level 2.3 followed by the euphausiid *M. norvegica*, the amphipods *G. wilkitzkii*, *T. libellula* and *T. abyssorum*, the euphausiid *T. longicaudata*, the juveniles of *M. villosus* and *G. morhua*, larvae of *M. villosus*, the copepod *P. glacialis*, adult *M. villosus*, whereas adult *M. poutassou* occupied the highest trophic level (3.6: Figure 2).

Table 4. Stable isotope ratios of carbon and nitrogen ($\delta^{13}C$, $\delta^{15}N$) from the target species in August 2007. Values are means ± SE. TL indicates trophic level calculated by the formula of Fisk et al. (2001).

	Number of samples	$\delta^{13}C$(‰)	$\delta^{15}N$(‰)	TL
Particulate organic matter (POM)	1	-25.5	4.9	
C. finmarchicus CV	1	-23.0	5.5	2
M. longa female	2	-23.4 ± 0.0	6.6 ± 0.6	2.3
P. glacialis female	3	-22.9 ± 0.1	10.0 ± 0.1	3.2
T. inermis	3	-20.2 ± 0.4	8.7 ± 0.1	2.8
T. longicaudata	3	-22.1 ± 0.1	9.0 ± 0.1	2.9
M. norvegica	3	-20.4 ± 0.2	7.5 ± 0.3	2.5
T. libellula	3	-22.8 ± 0.1	8.7 ± 0.2	2.9
T. abyssorum	3	-22.4 ± 0.1	8.9 ± 0.1	2.9
G. wilkitzkii	3	-22.8 ± 0.3	7.9 ± 0.6	2.6
E. hamata	3	-21.2 ± 0.1	8.9 ± 0.1	2.9
M. villosus larvae	3	-18.1 ± 0.2	9.9 ± 0.2	3.2
M. villosus juvenile	3	-19.4 ± 0.1	9.7 ± 0.1	3.1
M. villosus adult	3	-20.0 ± 0.1	11.4 ± 0.1	3.6
G. morhua juvenile	3	-19.1 ± 0.2	9.7 ± 0.4	3.1
M. poutassou adult	3	-20.0 ± 0.1	11.6 ± 0.1	3.6

Lipids

To follow energy transfer through the food web FATMs were employed (Table 1). A total of 41 FAs and fatty alcohols were detected, 32 of them with higher levels than 0.5% in at least one of the samples (Table 5).

Calanus finmarchicus. In the copepod *C. finmarchicus* the saturated fatty acids (SFAs) 14:0 and 16:0 occurred at high mean levels (16% and 9%, respectively, Table 5). The mono-unsaturated fatty acid (MUFA) 18:1n9 occurred at lower levels than in the other species (4%) and 18:1n7 was low as well (1%). The amounts of long-chained MUFAs, the FATMs typical for *Calanus* spp. were recorded at high levels with mean 9% for 20:1n9 and 12% for 22:1n11. Of the phytoplankton FATMs, the MUFA 16:1n7 was found in greatest amount (13%), while the 20:5n3 ranked second (11%), followed by 18:4n3 (6%) and 22:6n3 (2%). Fatty alcohols accounted for 43% of the total moieties of *C. finmarchicus*. The major fatty alcohols presented in the neutral lipid fraction were 22:1n11 (42%), 20:1n9 (37%), 16:0 (8%) and 16:1n7 (5%).

Table 5. Fatty acid (FA) and fatty alcohol (FAlc) composition (mass % of total FA and FAlc, respectively) of neutral lipids of the target species in August 2007.

	POM (n = 2)	*C. finmarchicus* (n = 3)	*M. longa* (n = 3)	*P. glacialis* (n = 3)	*T. inermis* (n = 3)	*T. longicaudata* (n = 3)	*M. norvegica* (n = 3)	*T. libellula* (n = 3)	*T. abyssorum* (n = 3)	*G. wilkitzkii* (n = 3)	*E. hamata* (n = 3)	*M. villosus* larvae (n = 3)	*M. villosus* juvenile (n = 3)	*M. villosus* adult (n = 3)	*G. morhua* juvenile (n = 3)	*M. poutassou* adult (n = 3)
FA																
14:0	9	16	3	1	3	6	7	6	4	5	2	5	10	8	4	4
16:0	11	9	4	1	18	34	16	12	9	11	2	13	13	14	16	13
16:1n9	2	1	2	1	1	0	0	0	0	0	1	1	0	0	0	0
16:1n7	5	13	15	24	10	9	6	9	9	20	9	8	10	9	7	5
16:1n5	1	1	0	1	0	1	0	1	0	0	1	0	0	0	0	0
16:3n4	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
16:4n1	1	2	1	0	1	0	1	0	1	1	1	1	1	1	1	1
18:0	5	1	2	1	2	2	3	1	0	1	0	2	1	1	4	2
18:1n9	15	4	24	20	38	23	11	18	12	16	7	6	13	7	19	10
18:1n7	1	1	1	1	11	7	4	2	2	4	1	3	2	2	6	3
18:2n6	4	1	3	2	2	1	1	2	1	2	1	3	2	1	2	1
18:3n6	4	1	2	0	0	0	0	1	0	1	1	0	0	0	0	1
18:3n3	2	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1
18:4n3	8	6	4	3	2	1	4	5	5	4	7	8	4	4	3	2
20:1n11	1	1	1	1	0	0	0	2	4	1	2	0	0	1	0	2
20:1n9	5	9	7	13	1	5	14	6	12	5	18	3	9	16	4	13
20:1n7	0	0	0	0	0	0	1	0	2	1	0	0	0	1	0	1
20:2n6	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
20:4n6	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
20:5n3	6	11	8	6	5	2	10	11	10	9	12	17	11	4	15	9
22:0	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0
22:1 n11	6	12	6	13	1	1	6	5	8	8	22	4	6	21	2	15
22:1n9	2	1	2	1	0	1	1	1	2	1	3	1	1	2	0	2
22:5n3	1	1	1	0	0	0	1	1	0	0	1	1	1	0	1	1
22:6n3	5	2	4	5	1	1	9	12	11	5	3	17	10	3	12	12
FAlc																
14:0	14	3	30	31	25			20	9	12	4	6	18		29	
16:0	24	8	22	14	61			27	10	12	8	10	18		49	
16:1n7	2	5	5	4	10			3	2	3	2	2	2		3	
18:1n9	2	2	1	1	0			1	1	2	2	20	1			
20:1n9	23	37	17	21	1			25	25	27	34	24	37		19	
22:1n11	28	42	20	25	2			21	42	37	44	32	20		1	
22:1n9	5	4	5	3	1			3	11	8	6	6	4			
%Falc	27	43	26	38	24	1	1	20	14	15	44	7	7	0	6	1

Values are means. All samples (excluding *M. poutassou*) are whole individuals whereas *M. poutassou* constitutes muscle samples. n = number of replicates.

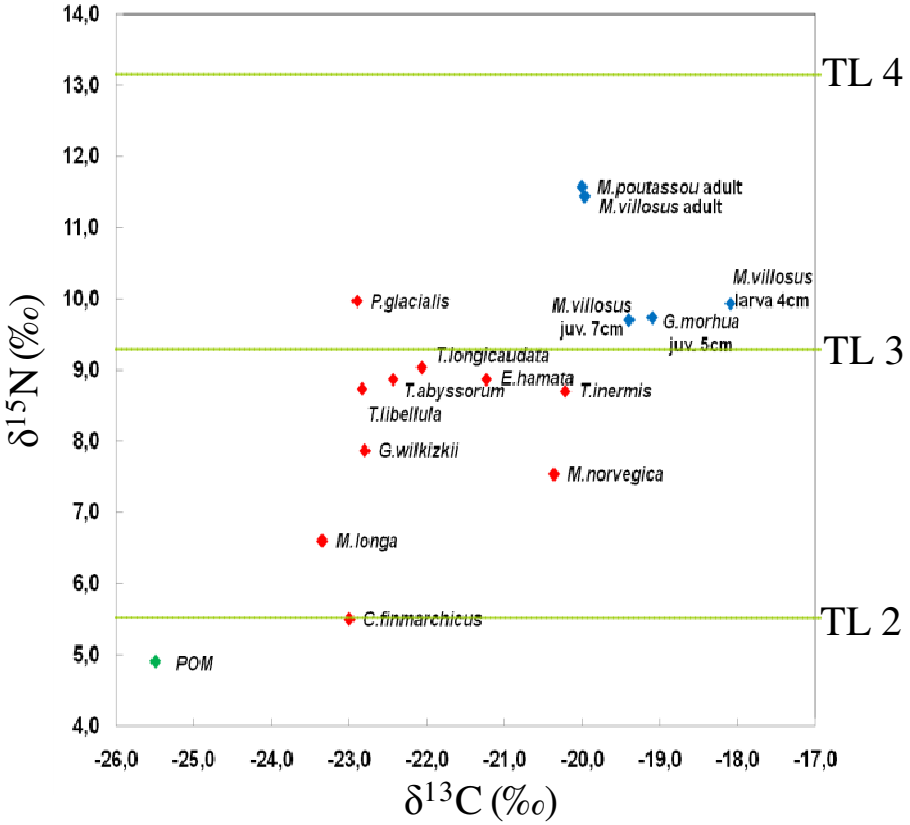

Figure 2. Scatter plot based on stable isotopes of nitrogen and carbon from POM and all the target species. Values are means and TL indicates trophic level. Green symbol: POM. Red symbols: Zooplankton. Blue symbols: Fish. For standard error see Table 4.

Metridia longa. In the copepod *M. longa* the SFAs 14:0 and 16:0, occurred at much lower levels than in *C. finmarchicus*, accounting for 3% and 4% of the total FAs (Table 5). By far the most dominant FA in *M. longa* was the MUFA 18:1n9 accounting for 24% of the total FAs. The *Calanus* spp. FATMs were recorded as 7% and 6% (20:1n9 and 22:1n11, respectively). The FA 16:1n7 had the highest levels of the phytoplankton FATMs (15%), followed by 20:5n3 (8%), 22:6n3 (4%) and 18:4n3 (4%). Fatty alcohols of the total moieties in *M. longa* accounted for 26%. The major fatty alcohols presented in the neutral lipid fraction were 14:0 (30%), 16:0 (22%), 22:1n11 (20%) and 20:1n9 (17%).

Paraeuchaeta glacialis. Of the copepods studied here *P. glacialis* had the lowest level of the SFAs 14:0 (1%) and 16:0 (1%, Table 5). The MUFA 18:1n9 occurred at high levels (20%) similar as in *M. longa* and the *Calanus* copepod FATMs were found in high amounts as well, accounting for 13% in both 20:1n9 and 22:1n11. The most abundant FA in *P. glacialis* was the phytoplankton FATM 16:1n7 (24%), at higher level than in the other species. The phytoplankton FATMs 20:5n3, 22:6n3 and 18:4n3 occurred at lower levels (6%, 5%, 3%, respectively). Fatty alcohols constituted 38% of the total moieties in *P. glacialis*. The major fatty alcohols presented in the neutral lipid fraction were 14:0 (31%), 22:1n11 (25%), 20:1n9 (21%) and 16:0 (14%).

Thysanoessa inermis. Very abundant FA in the neutral lipid fraction of the euphausiid *T. inermis* was the SFA 16:0, which occurred at mean levels of 18% (Table 5). The SFA 14:0 was recorded at lower levels (3%). By far the most dominant FA in *T. inermis* was the MUFA 18:1n9 accounting for 38% of the total FAs, at much higher level than in any of the other species. The MUFA 18:1n7 accounted for 11%. On the other hand very low amounts of the *Calanus* FATMs, 20:1n9 (1%) and 22:1n11 (1%) were recorded. High amount of the phyto-

plankton FATM 16:1n7 (10%) occurred, followed by 20:5n3 (5%), 18:4n3 (2%) and 22:6n3 (1%). Fatty alcohols of the total moieties in *T. inermis* were 24%. The major fatty alcohols presented in the neutral lipid were: 16:0 (61%), 14:0 (25%) and 16:1n7 (10%).

Thysanoessa longicaudata. The most abundant FA in the neutral lipid fraction of the euphausiid *T. longicaudata* was the SFA 16:0 (34%, Table 5). The SFA 14:0 (6%) occurred at lower levels. The MUFA 18:1n9 was recorded at high levels (23%) while the values for 18:1n7 were lower (7%). As in *T. inermis*, the mean levels for the *Calanus* FATMs 20:1n9 (5%) and 22:1n11 (1%) were low. Of the phytoplankton FATMs, 16:1n7 (9%) was recorded at high levels, followed by 20:5n3 (2%), 22:6n3 (1%) and 18:4n3 (1%). Fatty alcohols only accounted for 1% of the total moieties in *T. longicaudata*.

Meganyctiphanes norvegica. The mean levels of the SFA 16:0 were high in the euphausiid *M. norvegica* (16%) while the SFA 14:0 occurred at lower levels (7%, Table 5). The MUFA 18:1n9 accounted for 11%. The *Calanus* FATMs 20:1n9 (14%) and 22:1n11 (6%) were found in greater amount than in the other euphausiid species studied here. High amounts of the phytoplankton FATMs 20:5n3 (10%) and 22:6n3 (9%) occurred, followed by 16:1n7 (6%) and 18:4n3 (4%). Fatty alcohols of the total moieties in *M. norvegica* constituted only 1%.

Themisto libellula. In the amphipod *T. libellula,* the SFAs 14:0 and 16:0 occurred at mean levels of 6% and 12%, respectively (Table 5). The dominant FA was the MUFA 18:1n9 (18%). The *Calanus* copepod FATMs 20:1n9 and 22:1n9 accounted for 6% and 5%, respectively. High amounts of the phytoplankton FATMs 22:6n3 (12%), 20:5n3 (11%) and 16:1n7 (9%) were recorded. Fatty alcohols accounted for 20% of the total moieties in *T. libellula*. The major fatty alcohols presented in the neutral lipid fraction were 16:0 (27%), 20:1n9 (25%), 22:1n11 (21%) and 14:0 (20%).

Themisto abyssorum. The mean levels of the SFAs 14:0 and 16:0 in the amphipod *T. abyssorum* were 4% and 9%, respectively (Table 5). The MUFA 18:1n9 occurred at high levels (12%) as well as the *Calanus* FATMs 20:1n9 (12%) and 22:1n11 (8%). The phytoplankton FATMs 22:6n3 (11%), 20:5n3 (10%) and 16:1n7 (9%) were recorded at high levels. Fatty alcohols of the total moieties in *T. abyssorum* accounted for 14%. The major fatty alcohols presented in the neutral lipid were 20:1n11 (42%), 20:1n9 (25%), 22:1n9 (11%), 16:0 (10%) and 14:0 (9%).

Gammarus wilkitzkii. In the sympagic (ice-associated) amphipod species *G. wilkitzkii*, the SFAs 14:0 and 16:0 occurred at mean levels 5% and 11% respectively (Table 5). The mean level of the MUFA 18:1n9 (16%) was similar as in the other amphipods species, as well as the levels for *Calanus* FATMs 20:1n9 (5%) and 22:1n11 (8%). The most dominant FA in *G. wilkitzkii* was the phytoplankton FATM 16:1n7 (20%), with levels considerably higher than in the other amphipods. The phytoplankton FATMs 20:5n3 and 22:6n3 accounted for 9% and 5%, respectively. Fatty alcohols accounted for 15% of the total moieties in *G. wilkitzkii*. The major fatty alcohols were 20:1n11 (37%), 20:1n9 (27%), 14:0 (12%) and 16:0 (12%).

Eukrohnia hamata. The SFAs 14:0 (2%) and 16:0 (2%) occurred at low mean levels in the chaetognath *E. hamata* (Table 5). The MUFA 18:1n9 accounted for 7% while the *Calanus* FATMs 22:1n11 (22%), 20:1n9 (18%) occurred at higher levels than at the other species. The FA 20:5n3 (12%) had the highest level of the phytoplankton FATMs, followed by 16:1n7 (9%), 18:4n3 (7%) and 22:6n3 (3%). Fatty alcohols of the total moieties of *E. hamata* accounted for 44%. The major fatty alcohols presented in the neutral lipid fraction were 22:1n11 (44%), 20:1n9 (34%), 16:0 (8%) and 22:1n9 (6%).

Mallotus villosus. Larvae, juveniles and adults of the pelagic fish *M. villosus* were studied. The mean levels of the SFA 14:0 were 5%, 10% and 8% for the larva, juvenile and adult, respectively (Table 5). The mean levels of the SFA 16:0 were similar in all groups (~13%). The

mean levels of the MUFA 18:1n9 were 6%, 13% and 7% for the larvae, juveniles and adults, respectively. While, the values for the *Calanus* FATMs 20:1n9 (3%, 9% and 16%, respectively) and 22:1n11 (4%, 6% and 21%, respectively) increased with size, from larvae to adults, with much higher mean values in adults than in larvae and juveniles. Conversely, the phytoplankton FATMs 22:6n3 (17%, 10% and 3%, respectively) and 20:5n3 (17%, 11% and 4%, respectively) decreased with size (from larvae to adults), the larvae having noteworthy high levels. The levels of 16:1n7 were 8%, 10% and 9%, respectively and the levels of 18:4n3 were 8%, 4% and 4%, respectively (for the larvae, juveniles and adults, respectively). Fatty alcohols of the total moieties in *M. villosus* accounted for 7% in both larvae and juveniles, probably just from the stomach content, while no alcohols were found in the muscle of adult fish.

Gadus morhua. In the pelagic juveniles of the demersal fish *G. morhua*, the SFAs 14:0 and 16:0 occurred at mean levels 4% and 16%, respectively (Table 5). The MUFA 18:1n9 occurred at high levels (19%) while the *Calanus* FATMs 20:1n9 (4%) and 22:1n11 (2%) occurred at rather low levels, similar to those of *M. villosus* larvae. The phytoplankton FATMs 20:5n3 (15%) and 22:6n3 (12%) were recorded at high levels, followed by 16:1n7 (7%) and 18:4n3 (3%).Fatty alcohols of the total moieties in *G. morhua* constituted only 6%, most likely from the stomach content.

Micromesistius poutassou. In the pelagic fish *M. poutassou*, the SFAs 14:0 and 16:0 occurred at mean levels 4% and 13%, respectively (Table 5). The MUFA 18:1n9 accounted for 10% of the total moieties. The *Calanus* FATMs 20:1n9 and 22:1n11 were found in high amounts, accounting for 13% and 15% respectively. Of the phytoplankton FATMs, the 22:6n3 (12%) was recorded at high levels, followed by 20:5n3 (9%), 16:1n7 (5%) and 18:4n3 (2%). Fatty alcohols of the total moieties in *M. poutassou* constituted only 1%.

To examine trophic interactions of the pelagic species under investigation, RDA was applied to explore relationships in moieties compositions (Table 6, Figure 3). The target species were significantly different in moieties composition (Monte Carlo F = 16.5, P = 0.002) and 87.7% of the total variability in their compositions was explained by the species. The first two axes explained 76% of the total variance in the moieties composition.

The main gradient along axis 1, explaining 58% of the variance, separated species with high levels of the *Calanus* FATMs (*C. finmarchicus* and *E. hamata*) from species almost depleted in those FATMs (*T. inermis* and *T. longicaudata*). The gradient along axis 2, explaining 18% of the variance, appears to distinguish the larvae of *M. villosus* from the other species with a higher amount of the phytoplankton FATMs 20:5n3 and 22:6n3 in the larvae.

Discussion

A typical late-summer situation was in the pelagic ecosystem during this present study carried out in August 2007, characterized by shortage of nutrients, low concentrations of chlorophyll *a* and low amounts of zooplankton (Anon, 2007). Thus, the herbivores have used the primary production produced in the short summer production season and converted surfeit food into storage lipids (Falk-Petersen, 1981; Clarke, 1983; Hagen and Auel, 2001; Anon 2007).

According to stable nitrogen values ($\delta^{15}N$), there are between 3 and 4 trophic levels in the pelagic ecosystem of the Iceland Sea excluding birds and mammals which are not included in this study. We allowed for the primary herbivorous copepod *C. finmarchicus* to represent trophic level 2. The copepod *M. longa* occupied trophic level 2.3 followed by the other zooplankton species, and the adults of capelin (*M. villosus*), and blue whiting (*M. poutassou*) occupied the highest trophic level (3.6). Compared to another high latitude pelagic ecosystem in the European Arctic, near Svalbard, the number of trophic levels, and the trophic level values of individual species, were generally similar (Søreide, et al., 2006; Tamelander, et al., 2006).

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

	POM (n = 2)	*C. finmarchicus* (n = 3)	*M. longa* (n = 3)	*P. glacialis* (n = 3)	*T. inermis* (n = 3)	*T. longicaudata* (n = 3)	*M. norvegica* (n = 3)	*T. libellula* (n = 3)	*T. abyssorum* (n = 3)	*G. wilkitzkii* (n = 3)	*E. hamata* (n = 3)	*M. villosus* larvae (n = 3)	*M. villosus* juvenile (n = 3)	*M. villosus* adult (n = 3)	*G. morhua* juvenile (n = 3)	*M. poutassou* adult (n = 3)
14:0	11	10	11	13	8	6	7	8	5	6	3	5	10	9	5	4
16:0	16	9	9	6	29	34	16	15	9	12	5	14	15	14	19	13
16:1n9	2	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0
16:1n7	4	10	13	17	10	9	6	8	8	18	6	8	9	9	7	6
18:0	4	0	2	0	1	2	3	1	0	1	0	2	1	1	4	2
18:1n9	12	3	19	13	29	23	11	15	11	15	5	7	13	7	18	10
18:1n7	1	0	1	1	9	7	5	1	2	3	0	3	2	2	6	3
18:2n6	3	1	2	1	1	1	1	1	1	2	1	3	1	1	2	1
18:3n6	3	1	2	0	0	0	0	1	0	1	0	0	1	0	0	1
18:3n3	2	0	1	1	0	1	1	1	1	1	0	0	1	1	1	1
18:4n3	6	4	3	2	2	1	4	4	4	4	4	8	5	4	3	2
20:1n11	0	1	1	1	0	0	0	1	4	1	1	0	0	1	0	1
20:1n9	10	21	10	17	1	5	15	10	14	8	26	4	13	16	4	14
22:1n11	12	25	10	18	1	2	7	9	14	12	32	6	5	21	2	15
22:1n9	3	2	3	2	0	1	2	1	3	2	4	1	1	2	0	2
20:5n3	5	7	6	4	4	2	10	9	9	8	7	17	11	5	15	9
22:6n3	4	1	3	3	1	1	9	10	10	4	2	17	9	3	12	12
Minor comp.	2	3	3	2	2	2	4	3	4	3	3	4	4	3	3	4

Values are average percentages. n = number of replicates.

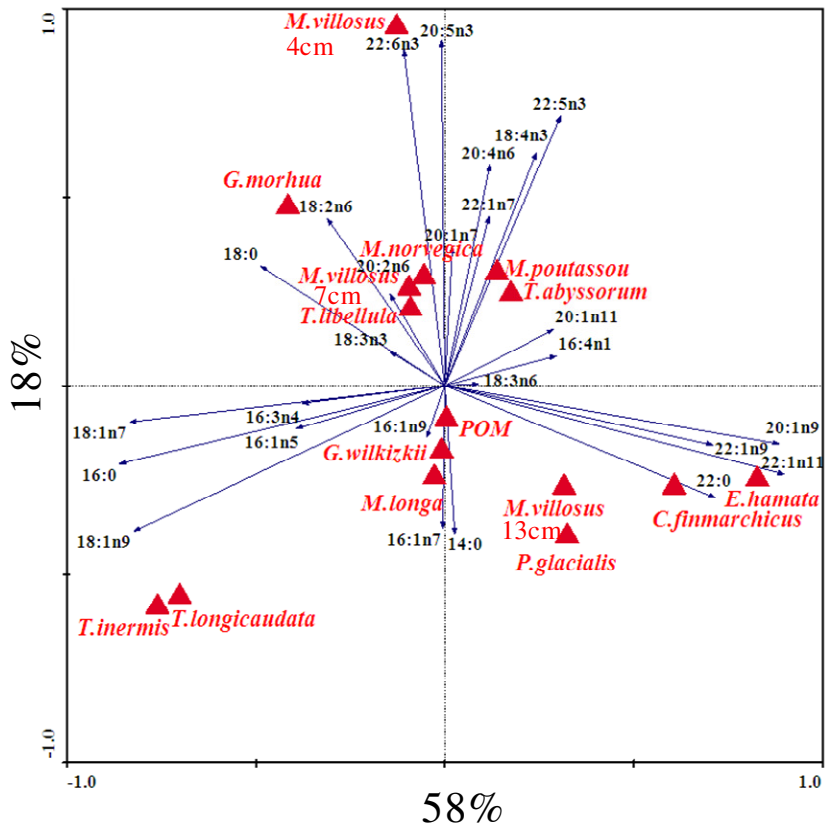

Figure 3. Redundancy analysis plot based on fatty acid values of POM and the target species. Triangles indicate mean values of the respective species. The species were applied as dummy variables (environmental variables) and fatty acids as response variables. The arrows point in the direction of steepest increase of the respective fatty acid. The fraction of unconstrained variance accounted for by each axis is given.

Calanus finmarchicus has been regarded as primarily herbivorous species (Harris, 1996; Søreide, et al., 2008), feeding intensively on phytoplankton during summer. Higher amounts of the diatom FATMs compare to the dinoflagellate FATMs indicate that *C. finmarchicus* grazed more on diatoms than dinoflagellates. Also, the considerably higher ratio of 18:1n7/18:1n9 in *C. finmarchicus* than in the other copepods reflect the mainly herbivorous feeding of *C. finmarchicus* and the more omnivorous-carnivorous diet of *M. longa* and *P. glacialis*. Thus the ratio of the 18:1n7/18:1n9 have been used as an indicator of trophic mode, i.e. low values pointing to a carnivorous-omnivorous diet (Dalsgaard et al., 2003 for review). This is also supported by the stable isotope results, showing that *M. longa* and *P. glacialis* occupy higher trophic levels (2.3, 3.2, respectively) than *C. finmarchicus* (2.0). This omnivorous-carnivorous feeding mode has been recorded for *M. longa* in Balsjord northern Norway as well (Falk-Petersen, 1990). The copepods *M. longa* and *P. glacialis* have rather high levels of *Calanus* FATMs, indicating feeding on *Calanus* spp. to some degree, but on the other hand high levels of the phytoplankton FATMs indicate some grazing on phytoplankton.

The euphausiids, *T. inermis* and *T. longicaudata* differ from the other species investigated in that they are almost depleted in the *Calanus* FATMs, indicating that *Calanus* spp. are only minor part of their diet. They occupy trophic level around 3, therefore we conclude that they are omnivorous-carnivorous, probably feeding heavily on small zooplankton. These trophic levels values are in line with other studies (Søreide, et al., 2006; Tamelander, et al., 2006). The omnivorous-carnivorous feeding mode of *T. inermis* is in contrast with the study of Falk-Petersen et al. (2000), where it is concluded that *T. inermis* is a true herbivore. However, their conclusion was only based on lipid analyses whereas we consider also the stable isotopes. *Meganyctiphanes norvegica* occupied the lowest trophic level of the euphausiids (2.5). *Calanus* spp. are important part of the diet of *M. norvegica* in the Iceland Sea, different from the *M. norvegica* studied south of Iceland (Petursdottir, et al., 2008). The rather high amount of the phytoplankton FATMs, also indicates phytoplankton feeding. This is in accordance with the results of other studies showing *M. norvegica* to be an omnivorous-carnivorous species (Mauchline and Fisher, 1969; Falk-Petersen, et al., 2000; Petursdottir, et al., 2008).

Based on their *Calanus* FATMs, the pelagic amphipods *T. libellula*, *T. abyssorum* and *G. wilkitzkii* are feeding to some degree on *Calanus* spp. *Gammarus wilkitzkii* had slightly lower trophic level values (2.6) than the other amphipods (2.9) studied here, suggesting that *G. wilkitzkii* forage also on phytoplankton. *Gammarus wilkitzkii* is a sympagic (ice-associated) species feeding on ice alga and calanoid copepods (Lønne and Gulliksen, 1991; Werner 1997; Scott, et al., 2001) but it has also been found in open ocean, where ice has melted (Steele and Steele, 1974; Werner et al., 1999; Scott, et al. 2001; this study), consuming mainly calanoid copepods. Moreover, *G. wilkitzkii* changes feeding strategy with size, from herbivorous to omnivorous-carnivorous (Scott, et al., 2001). *Gammarus wilkitzkii* is not a common species in the pelagic ecosystem in the Iceland Sea (Astthorsson, et al., 1995; Dalpadado, et al., 1998; Gislason and Astthorsson, 1998), nevertheless they were found sporadically in great numbers in the colder Arctic waters during this study. The fatty acid composition of *G. wilkitzkii* in the Iceland Sea is comparable of those of *G. wilkitzkii* in open waters in Kongsfjord in Svalbard (Scott, et al., 2001).

Of all the species studied, the moiety composition of the chaetognath *E. hamata* resembles the composition of *C. finmarchicus* the most. From this and the high amounts of the *Calanus* FATMs and with the stable isotopes results (e.g. trophic level 2.9) we conclude that *E. hamata* is mainly foraging on *Calanus* spp. *Eukrohnia hamata* was found to occupy similar trophic level in the Arctic (Søreide, et al. 2006). Also, Froneman et al. (1998) reported *Calanus* spp. to be an important component of their diet.

The cod and capelin larvae of the present study have similar trophic level values (~3) and like moieties compositions as well, suggesting comparable feeding habits, most likely feeding on herbivorous zooplankton. This is in line with the results on food of young fish in Icelandic waters, where euphausiids and copepods as *C. finmarchicus* and *Acartia* spp. were found to be the major components of the diet of capelin and cod larvae (Pálsson, 1974). Noteworthy, the capelin larvae (~4 cm) are more enriched in ^{13}C than the juveniles (~7 cm) and adults (~13 cm). These relatively high values could indicate that the larvae are feeding on a diet with higher $\delta^{13}C$ values than the adults. However, it may be more likely that the relatively high values may simply be due to the methods used, where whole individuals of larvae and juveniles were analyzed but muscle sample of the adults. Thus, bone collagen tissue is richer in ^{13}C than muscle tissue (Sholto-Douglas et al., 1991) and therefore the larvae may be more enriched than adults. On the other hand the much higher amounts of the phytoplankton originated fatty acids 20:5n3 and 22:6n3 in the larvae may indicate a shift in diet after metamorphosis (~4 cm) when the juveniles get more mobile. Phytoplankton and heterotrophic protists from the microbial loop have been shown to be a part of the diet of capelin larvae (Pepin and Dower, 2007), but these findings differ with stomach content analyses where small zooplankton species are mainly found in the stomachs. *Calanus* spp. is a part of the diet of all developmental stages of capelin, but adults have by far the highest amount of *Calanus* FATMs indicating that *Calanus* spp. and *Calanus* derived diet (through larger zooplankton species e.g. euphausiids) are an extremely important part of their diet. This is also supported by the stable isotope analyses. These findings are in accordance with observations in the Iceland Sea made by Sigurðsson and Astthorsson (1991) and Astthorsson and Gislason (1997), where *C. finmarchicus* and euphausiids were found to be the major components of the capelin diet.

The blue whiting in this study was caught in the north eastern part of the Iceland Sea and has just in recent years migrated in great amounts to the Icelandic waters (Anon, 2007; Astthorsson, et al., 2007). The present findings show that the pelagic fishes, blue whiting and capelin share the same feeding habits as adults i.e. have the same trophic levels values (3.6), almost identical $\delta^{13}C$ values and similar moieties composition. More pronounced feeding migrations of the blue whiting into the Iceland Sea could therefore result in that these two species would compete for food.

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