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Trophic interactions of meso- and macrozooplankton and fish in the Iceland Sea as evaluated by fatty acid and stable isotope analysis

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Abstract:

A trophic study was carried out in August of 2007 and 2008 on the pelagic ecosystem in the Subarctic Iceland Sea. Carbon and nitrogen stable isotopes and fatty acid biomarkers were used to study trophic linkages and the trophic ecology of the most important pelagic species in this ecosystem, with emphasis on capelin (*Mallotus villosus*). According to ^{15}N enrichment results, there are 3–4 trophic levels in this ecosystem excluding organisms of the microbial loop and birds and mammals. The primarily herbivorous copepod *Calanus hyperboreus* occupies the lowest trophic level of the animal species studied, and adult capelin and blue whiting (*Micromesistius poutassou*) occupy the highest level. *Calanus* spp. proved to be an important dietary component of most of the species studied, the euphausiid species *Thysanoessa inermis* and *T. longicaudata* being exceptions. The chaetognath *Eukrohnia hamata* is a pure carnivore, feeding heavily on *Calanus* spp., whereas most of the other zooplankton species studied practice an omnivorous–carnivorous feeding mode. The amphipod species *Themisto libellula* is important in the diet of adult capelin. Adult capelin and blue whiting share the same feeding habits and could therefore be competing for food.

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

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 production during a short period of time (Falk-Petersen *et al*., 1990; Thordardottir, 1994; Gislason and Astthorsson, 1998). Hence, marine pelagic animals in high-latitude ecosystems have adapted to a relatively short productive season by converting large amounts of excess food into stored 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 ground for several of the commercially important fish stocks in Iceland (Magnússon and Pálsson, 1989; Astthorsson and Gislason, 1997; Pálsson, 1997; Sólmundsson, 1997), the most abundant being capelin (*Mallotus villosus*), with an annual catch of about one million metric tons (Anon., 2005; Astthorsson *et al*., 2007). Capelin is an important component of the Icelandic ecosystem, serving as a link between zooplankton and species at higher trophic levels, and is essential to the diet of many species (Magnússon and Pálsson, 1989; Vilhjálmsson, 1994), e.g. Atlantic cod (*Gadus morhua*). Capelin is also important in transferring energy from the Iceland Sea (north of Iceland), where it feeds on lipid-rich zooplankton during summer, to the spawning grounds of capelin (south of Iceland; Vilhjálmsson, 1994; Astthorsson and Gislason, 1997; Astthorsson *et al*., 2007). In terms of biomass, copepods dominate the mesozooplankton community in the Iceland Sea, *Calanus finmarchicus* being the most abundant. Other common zooplankton species in the Iceland Sea are copepods (*Oithona* spp., *Pseudocalanus* spp., *Metridia longa*, and *C. hyperboreus*, the last two being mostly restricted to Arctic waters in the central and western part of the Iceland Sea), euphausiids (*Thysanoessa inermis*, *T. longicaudata*, and *Meganyctiphanes norvegica*), and amphipods (*Themisto abyssorum* and *T. libellula*, the latter found mainly in Arctic waters; Dalpadado *et al*., 1998; Gislason and Astthorsson, 1998; Gislason and Silva, 2012).

Knowledge of predator–prey relations is essential in understanding energy flows in marine ecosystems. Stable isotope analysis and fatty acid (FA) analysis are powerful and complementary tools to traditional stomach content analyses (Kharlamenko *et al*., 2001; Dahl *et al*., 2003; Petursdottir *et al*., 2008; Wold *et al*., 2011), because their patterns show an integration of prey over periods ranging from weeks to months (Fry, 1988; Rau *et al*., 1992; Dalsgaard *et al*., 2003). Additionally, the trophic position of a species can be deduced from stable isotope values, and FAs and alcohols may give more detailed information about diet.

The stable isotopes of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) are enriched, in a 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 $\delta^{13}C$. Hence, $\delta^{15}N$ values provide a good estimate of the trophic position of a species (Hobson and Welch, 1992; Dahl *et al*., 2003; Tamelander *et al*., 2006), and $\delta^{13}C$ values may provide information about carbon sources in the food chain and/or habitat, i.e. benthic vs. 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 FAs can be transferred relatively unchanged through trophic levels (Lee *et al*., 1971b; Graeve *et al*., 1994; Dalsgaard *et al*., 2003) and are referred to as fatty acid trophic markers (FATMs). Examples of known FATMs are 20:5n3, 16:1n7, and C16 polyunsaturated fatty acids (PUFAs) for diatoms; 22:6n3 and C18 PUFAs for dinoflagellates and *Phaeocystis*, and 20:1n9 and 22:1n11 mono-unsaturated fatty acids (MUFAs) for *Calanus* copepods (Table 1). To assist in the detection of relationships and patterns among FA profiles of different species, multivariate statistical analyses have been used (Grahl-Nielsen and Mjaavatten, 1991; Falk-Petersen *et al*., 2004).

Information on trophic relationships in the pelagic ecosystem of the Iceland Sea is scarce. Some data from stomach analyses on the diet of capelin are available (Sigurðsson and Astthorsson, 1991;

Astthorsson and Gislason, 1997), but there is no information on the food of organisms of lower trophic level (zooplankton). The aim of the present study was to investigate trophic relationships among some biomass-dominant mesozooplankters and the most abundant fish of the pelagic ecosystem of the Subarctic Iceland Sea north of Iceland, using stable isotope and fatty acid analyses. The study is part of an extensive ecological study of the Iceland Sea, the Iceland Sea Ecosystem Project, of tIceland's Marine Research Institute, with field activity lasting from 2006 to 2008. The overall objective of the project is to analyse the structure and function of the Iceland Sea ecosystem, with particular emphasis on the life history of capelin and changes during the past decade (Pálsson *et al*., 2012).

Material and methods

The Iceland Sea is demarcated by Iceland to the south, East Greenland to the west, and Jan Mayen to the northeast. Its maximum depth is about 2000 m. The main water mass in the western and central Iceland Sea consists of Arctic water carried by the East Greenland and East Icelandic currents, whereas the water in the northeast and southern parts is mainly of Atlantic origin (Figure 1; Blindheim and Østerhus, 2005, and references therein; Pálsson *et al*., 2012).

Abundant pelagic species in the Iceland Sea, as well as particulate organic matter (POM), were chosen as representative key elements of the pelagic foodweb in the central Iceland Sea, based on previous studies in the region (Dalpadado *et al*., 1998; Gislason and Asthorsson, 1998). Specimens were selected to minimize variation in size, and the size groups reflected the greatest abundance of every species in the respective catch (Table 2). The following species were chosen: the copepods *Calanus finmarchicus*, *C. hyperboreus*, *Metridia longa*, and *Paraeuchaeta glacialis*; the euphausiids *Thysanoessa inermis*, *T. longicaudata*, and *Meganyctiphanes norvegica*; the amphipods *Themisto libellula*, *T. abyssorum*, and *Gammarus wilkitzkii*; the chaetognath *Eukrohnia hamata*; and the fish capelin, Atlantic cod, *Melanogrammus aeglefinus* (Atlantic haddock), *Ammodytes marinus* (sandlance), and *Micromesistius poutassou* (blue whiting; Table 2).

Sampling

Samples were collected at 36 stations with various types of gear (multinet, Tucker trawl, pelagic trawl), mainly in the central and western parts of the Iceland Sea, during late summer of 2007 and 2008 (Figure 1, Table 2). In addition we present stable nitrogen isotope data for *C. hyperboreus* sampled in May 2007 to represent trophic level 2. For more details of sampling, see Anon. (2012).

Water samples for POM were collected from the ship's underway system, which has an intake 5 m deep. For the stable isotope analyses the water was filtered through pre-combusted (450°C, 4 h) Whatman GF/F glassfibre filters, and for FA analyses the filters were washed with chloroform:methanol 2:1 (v/v) solution before filtering. All species for FA and alcohol analyses were obtained by picking out a given number of individuals (Table 2) and storing them in a chloroform:methanol 2:1 (v/v) solution at −20°C, except for adult fish (capelin and blue whiting), which were frozen directly at −20°C. The frozen fish samples were also used for stable isotope analyses, and for those, samples containing a mixture of several species were frozen in plastic trays on the ship at −20°C, before the target species (zooplankton and juvenile fish) were subsequently sorted out in the laboratory (Table 2). The samples were then stored at −80°C prior to analysis.

Laboratory analyses

Stable isotope ratios were analysed at the Institute for Energy Technology (IFE), Kjeller, Norway. The samples were dried at 60–70°C to a constant weight and homogenized in a mortar using a glass pestle. According to protocols of the IFE (see Dahl *et al*., 2003), lipids were removed by Soxhlet extraction for 2 h using a solvent consisting of 93% dichloromethane (DCM) and 7% methanol, in order to reduce variability attributable to isotopically lighter lipid (Hobson and Welch, 1992). To remove traces of carbonates, the samples were rinsed with 2N HCl and dried at 80°C. Stable isotope 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 million (‰) 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 ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The standard for $\delta^{13}C$ is Pee Dee Belemnite (PDB: USGS 24), and for $\delta^{15}N$ it is atmospheric air (IAEA-N-1 and IAEA-N-2).

Lipid classes, fatty acids 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 subsample 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). 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°C 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 with known standards, and quantified using HPChemStation software (Hewlett-Packard).

Data analysis

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 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. hyperboreus* is primarily herbivorous in May (Søreide *et al*., 2008), for the present study it was assumed that it represented trophic level 2.

The relationship used for each individual sample of other trophic levels (Fisk *et al*., 2001) was $TL_{consumer} = 2 + (\delta^{15}N_{consumer} - \delta^{15}N_{C.hyperboreus})/3.8$, where $TL_{consumer}$ is the trophic level of an organism, $\delta^{15}N_{C.hyperboreus}$ is analytically determined as 5.6 ± 0.1 (mean ± s.e.), and 3.8 is the isotopic enrichment factor (Hobson and Welch, 1992; Hobson *et al*., 1995)

Most marine crustaceans store neutral lipid classes, triacylglycerols and/or wax esters in their lipid deposits. Wax esters consist of one fatty acid esterified to a long chain of fatty alcohol in an equimolar amount, and triacylglycerols contain three fatty acids connected to a glycerol molecule (Lee *et al*., 1971a; Sargent and Henderson, 1986).

The total neutral lipid fraction was analysed to determine the percentage weight composition of the FA methyl esters and the fatty alcohol acetates (the total FA methyl esters and fatty alcohol acetates made up 100%). In order 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 alkyls (from fatty alcohol acetates) and fatty acyls (from FA methyl esters) were averaged by molecular weight and were then referred to as moieties. For averaging, the % weight data for fatty alcohol acetate were converted to % mole data using molecular weight. The % mole data for fatty alcohol acetate were then converted to weight (g) of an individual alkyl unit. The same calculations were made for the % weight % data of FA methyl esters to obtain the weight (g) for an individual acyl unit. The sum of the weights (g) of individual alkyl and acyl units is then the average weight (g) of neutral lipid in the sample analysed. The neutral lipid in some species contained acyl and alkyl moieties that had the same chain length and number and positions of double bonds. In those cases, the acyl and alkyl moiety weights were summed and the new percentage data were calculated based on average molecular weights (Falk-Petersen *et al*., 2002).

Multivariate statistical analysis was performed on moiety compositional data. Samples with low quantities of moieties (<0.5%) were excluded from the analysis because the precision of their determination was too low. The remaining percentages were subjected to redundancy analysis (RDA) to analyse for trophic relationships among the study species. Species were used as explanatory variables, and moieties as response variables. To test for significant differences in moiety compositions among 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

There appeared to have been no significant differences between comparable samples or sampling stations during the two years of study. Hence, for this overall ecosystem trophic study, comparable samples (same species, similar size/developmental stage) were combined. Individual samples were used in the multivariate analyses, and in this study the focus was on late summer.

Stable isotopes

POM had the lowest $\delta^{13}C$ value (−25.5‰ mean value) followed by copepods, and the larvae of *M. villosus* and *A. marinus* had the highest value (−18.9‰, Figure 2). Stable nitrogen isotope ratios ($\delta^{15}N$) ranged from 4.9‰ for POM to 11.7‰ for adult *M. villosus* and *M. poutassou* (Figure 2).

As stated above *C. hyperboreus* from May were assigned to trophic level 2, with the lowest $\delta^{15}N$ value measured (5.6‰ mean value). The calculated trophic levels for the zooplankton species in August ranged from 2.4 (the copepod *M. longa* and the euphausiid *M. norvegica*) to 2.9 (the chaetognath *E. hamata*). The fish larvae occupied trophic levels between 3.1 (*G. morhua* and *M. villosus*) and 3.2 (*M. aeglefinus* and *A. marinus*), and adult fish (*M. villosus* and *M. poutassou*) occupied the highest trophic level at 3.6 (Figure 2).

Lipids

To follow energy transfer through the foodweb, FATMs were employed (Figure 3, Table 1). In all, 40 FAs and fatty alcohols were detected, 37 with levels >0.5% in at least one of the samples (Figure 3, Table 3).

The quantities of long-chained FATMs (moiety values), biosynthesized *de novo* in *Calanus* copepods (20:1n9 and 22:1n11), were recorded at high levels in all copepods, though at lower levels in *M. longa* and *P. glacialis* (15% and 35%, respectively) than in *C. finmarchicus* and *C. hyperboreus* (45−55%; Figure 3, Table 3). Generally, diatom FATMs (20:5n3 and C16PUFA) were in greater quantities in *Calanus* spp. and *M. longa* than the FATMs typical for dinoflagellates (22:6n3 and C18PUFA). *C. hyperboreus* had the highest levels of the *Calanus* FATMs.

Of the euphausiid species studied, *M. norvegica* had the highest quantity of *Calanus* FATMs (20%, Figure 3), and *T. inermis* and *T. longicaudata* had the least of all species studied (2% and 7%, respectively). Phytoplankton FATMs were at ~50% higher levels in *M. norvegica* than in other euphausiids. The mean levels of *Calanus* FATMs were high (~14−35%; Figure 3) in all amphipods. Phytoplankton FATMs were in considerably higher quantities in *Gammarus wilkitzkii* (38%) than in *T. abyssorum* and *T. libellula* (24%-32%), mainly because of the high values of diatom FATM 16:1n7 in *G. wilkitzkii* (21%), the highest value recorded in the study. The highest quantities of *Calanus* FATMs were in the chaetognath *E. hamata* (52%) if one excludes *C. hyperboreus* (55%; Figure 3). In *M. villosus*, values for *Calanus* FATMs increased with size, from larvae (4−7.5 cm) to adults (10−17 cm), with much higher mean values in adults (35%) than in larvae and juveniles (22%; Figure 3). *Ammodytes marinus*, *M. poutassou* and adult *M. villosus* had high values of these FATMs (~29−38%), but values were low in juvenile *M. aeglefinus*, *G. morhua*, and *M. villosus* (6−22%). Again, however, juvenile fish had high values of phytoplankton FATMs (~40−50%), mainly 20:5n3 and 22:6n3, compared with adult fish (26−30%).

Fatty alcohols

Fatty alcohols constituted 32−49% of the total weight of all moieties in copepods (Table 3). The euphausiid *T. inermis* yielded 25% fatty alcohols out of the total moieties, and no alcohols were observed in *T. longicaudata* and *M. norvegica*. Fatty alcohols were 12−27% of the total moieties in amphipods, but 46% in the chaetognath *E. hamata*. Fatty alcohols were in very low quantities in the larvae of *M. villosus*, *A. marinus*, and *G. morhua*, most likely associated with stomach contents (Table 3).

Trophic interaction

To examine trophic interactions of the pelagic species under investigation, RDA was applied to explore relationships in moiety composition (Figures 4, 5). Two analyses were carried out based on individual samples.

(i) Trophic relationships of all species sampled in August 2007 and 2008 (Figure 4). The species were significantly different in terms of moiety composition (Monte Carlo $F = 16.5$, $p = 0.002$). The first two axes explained 83% of the total variance in moiety composition. The main gradient along axis 1, which explained 65% of the variance, separated species with high levels of the *Calanus* FATMs in the left panel (e.g. *C. finmarchicus*, *C. hyperboreus, E. hamata*, *T. libellula*, and adult capelin) from species in the right panel that were almost depleted of these FATMs (e.g. *T. inermis* and *T. longicaudata*). The gradient along axis 2, explaining 18% of the variance, appears to distinguish fish larvae (lower panel) from the other species of larvae with higher quantities of phytoplankton FATMs 20:5n3 and 22:6n3.

(ii) Trophic relationships of adult capelin and its potential prey in August 2007 and 2008 were explored by RDA (Figure 5). Moiety composition was significantly different among species (Monte Carlo $F = 16.5$, $p = 0.002$). The first two axes explained 81% of the total variance. The main gradient along axis 1, explaining 70% of the variance, separated species with high levels of *Calanus* FATMs into the left panel (mainly *C. finmarchicus* and *C. hyperboreus*, *E. hamata*, and 4-cm *T. libellula*) from species with lesser quantities of those FATMs (e.g. some amphipods and euphausiids) in the right panel. The gradient along axis 2, explaining 11% of the variance, appears to distinguish species with more phytoplankton FATMs 20:5n3 and 22:6n3 (lower panel) from the rest. Adult capelin groups and 4-cm-long *T. libellula* had similar moiety composition.

Discussion

There was a typical late-summer situation in the pelagic ecosystem of the Iceland Sea during the present study, characterized by low nutrient and chlorophyll *a* concentration (Anon., 2007). The herbivores had utilized the phytoplankton production during the summer production season and converted part of the food into storage lipids (Falk-Petersen, 1981; Clarke, 1983; Hagen and Auel, 2001; Anon., 2007). Based on the high percentage of fatty alcohols in the total moieties (Table 3), we conclude that the copepods and chaetognaths we studied store wax esters (WEs) as their lipid deposit. Wax esters have been regarded as a long-term energy reserve, suitable for animals living in high latitude marine ecosystems. Euphausiids and amphipods store both WEs and triacylglycerols (TAGs), but TAGs are often regarded as short-term energy stores (Lee *et al.*, 1971a, 2006; Sargent and Henderson, 1986). Fish in the Iceland Sea store just TAGss, which is the case for most fish species (Falk-Petersen *et al.*, 1990).

According to the stable nitrogen isotope values ($\delta^{15}N$), there are between 3 and 4 trophic levels in the pelagic ecosystem of the Iceland Sea, excluding organisms of the microbial loop and birds and mammals, which were not included in the study. We allowed the primarily herbivorous copepod *C. hyperboreus* (in May) to represent trophic level 2 (Søreide *et al.*, 2008). In late summer, the copepod *M. longa* occupied trophic level 2.4, followed by the other zooplankton species, with adult capelin (*M. villosus*) and blue whiting (*M. poutassou*) occupying the highest trophic level (3.6). Compared with another high latitude pelagic ecosystem in the European Arctic, near Svalbaard, the number of trophic levels and the trophic level values of individual species were generally similar (Søreide *et al.*, 2006; Tamelander *et al.*, 2006).

C. hyperboreus occupies a higher trophic level in August (2.4) than in May (2.0), indicating a change in feeding strategy between those months. This species has been regarded as being primarily herbivorous in May (Søreide *et al.*, 2008), feeding intensively on phytoplankton. In August, when phytoplankton organisms are less abundant, *C. hyperboreus* shifts to a more omnivorous feeding habit, in line with studies of *C. hyperboreus* in the Arctic (Søreide *et al.*, 2008). Of the copepods in this study, *P. glacialis* belongs to the highest trophic level (3.1), the same as some fish larvae, indicating a carnivorous feeding

mode. The high levels of phytoplankton FATMs suggest grazing on phytoplankton during the bloom of the two copepods *M. longa* and *P. glacialis,* and the high levels of *Calanus* FATMs indicate feeding on *Calanus* spp. or on *Calanus* FATM associated with POM or detritus in other periods, typical for these omnivorous zooplankton species (Falk-Petersen *et al*., 1987).

The euphausiids *T. inermis* and *T. longicaudata* differ from the other species investigated in that they are almost depleted in *Calanus* FATMs, indicating that *Calanus* spp. constitute only a minor part of their diet. They occupy trophic levels 2.5−2.7, and we conclude that they are omnivorous−carnivorous, probably feeding extensively on small zooplankton. These values of trophic level are in line with those from other studies (Søreide *et al*., 2006; Tamelander *et al*., 2006). The omnivorous−carnivorous feeding mode of *T. inermis* contrasts with the results of the study of Falk-Petersen *et al*. (2000), who concluded that *T. inermis* is a true herbivore, although that conclusion was based only on lipid analyses whereas we also consider stable isotopes. *Meganyctiphanes norvegica* occupied the lowest trophic level of the euphausiids (2.4). In contrast to *T. inermis* and *T. longicaudata*, *Calanus* spp. are important in the diet of *M. norvegica* in the Iceland Sea, unlike *M. norvegica* studied south of Iceland, where other copepods are probably more important in the diet (Petursdottir *et al*., 2008). The rather high quantities of phytoplankton FATMs in *M. norvegica* also suggest feeding on phytoplankton, consistent 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* feed mainly on *Calanus* spp. *Gammarus wilkitzkii* had slightly lower trophic level values (2.4) than the other amphipods (2.7−2.9), however, suggesting that *G. wilkitzkii* also forage on phytoplankton. The species is a sympagic (ice-associated) species feeding on ice algae and calanoid copepods (Lønne and Gulliksen, 1991; Werner, 1997; Scott *et al*., 2001), but it has also been found in the open ocean in areas of ice-melt (Steele and Steele, 1974; Werner *et al*., 1999; Scott *et al*., 2001; Gislason and Silva, 2012), where it consumes mainly calanoid copepods. Moreover, *G. wilkitzkii* changes feeding strategy with size, from herbivorous to omnivorous−carnivorous (Scott *et al*., 2001). It is not common in the pelagic ecosystem of the Iceland Sea (Dalpadado *et al*., 1998; Gislason and Astthorsson, 1998). Nevertheless, it was found sporadically in great numbers in colder Arctic waters during this study. The FA composition of *G. wilkitzkii* in the Iceland Sea is comparable with that 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* most closely resembled the composition of *C. finmarchicus*. From this and the large quantities of *Calanus* FATMs, as well as the stable isotope results, we conclude that *E. hamata* forages mainly on *Calanus* spp. *Eukrohnia hamata* occupies a similar trophic level in the Arctic (Søreide *et al*. 2006), and Froneman *et al*. (1998) reported *Calanus* spp. to be an important component of its diet.

Fish larvae (cod, haddock, capelin, and sandeel) in the present study have similar trophic level values (3.2) and lipid moiety compositions too, suggesting comparable feeding habits, most likely feeding on herbivorous zooplankton which contain large quantities of the phytoplankton FATMs 20:5n3 and 22:6n3. This is in line with the results of studies on the food of young fish in Icelandic waters, where euphausiids and copepods such as *C. finmarchicus* and *Acartia* spp. are the major components of the diet of capelin and cod larvae (Pálsson, 1974). Capelin larvae from the Barents Sea have been reported as having a variety of prey in their stomachs, invertebrate eggs, bivalves, copepod eggs, nauplii, and copepodites from small copepods, and bryozoan larvae being particularly frequent (Pedersen and Fossheim, 2008). Further, phytoplankton and heterotrophic protists from the microbial loop are a part of the diet of capelin larvae in the pelagic ecosystem in coastal Newfoundland waters (Pepin and Dower, 2007). *Calanus* spp. form part of the diet of all developmental stages of capelin, but adults contain by far the largest quantity of *Calanus* FATMs, indicating that *Calanus* spp. and *Calanus* predators (e.g. euphausiids and amphipods) are extremely important in their diet. This conclusion is supported by the stable isotope analyses, and thefindings are in accord with observations from the Iceland Sea, Newfoundland, and the Barents Sea (Sigurðsson and Astthorsson,1991; Astthorsson and Gislason,1997; O´Driscoll *et al*.,2001; Orlova *et al*.,

2010) in which copepods, particularly *Calanus* and larger zooplankton species, were said to be major components of capelin diet. Interestingly, pelagic amphipods, especially larger *T. libellula*, and adult capelin have similar moiety composition, underscoring the importance of *T. libellula* in the diet of adult capelin in the Iceland Sea during August. Adult capelin in this study were caught mainly in the western part of the Iceland Sea, where *T. libellula* was the most abundant amphipod (Gislason and Silva, 2012). This high contribution of *T. libellula* in the diet of capelin could reflect the marked westward displacement of older capelin in the Iceland Sea in recent years (Vilhjálmsson, 2002; Pálsson *et al*., 2012) and therefore their different prey availability. The importance of amphipods in the diet of capelin appears to be greater in this study than previously reported for the Iceland Sea (Astthorsson and Gislason, 1997), but our results are consistent with those from a feeding study of capelin in Newfoundland waters, where hyperiid amphipods (*Themisto* spp.) were relatively important contributors to the diet of capelin (O´Driscoll *et al*., 2001). Hyperiid amphipods are also important in the diet of adult capelin in the eastern part of the Barents Sea, where they are abundant in the zooplankton community (Orlova *et al*., 2010). It is important, however, when comparing this with other studies, that the methods used here (FAs and stable isotopes) reflect the diet over a longer period than traditional stomach content analyses, which provide information only about the last meal.

Blue whiting in this study were caught in the northeastern part of the Iceland Sea and have only recently migrated in great numbers into Icelandic waters (Anon., 2007; Astthorsson *et al*., 2007). The present findings show that adult blue whiting and capelin share the same feeding habits, having the same trophic level values (3.6), almost identical $\delta^{13}C$ values, and similar lipid moiety composition. More-pronounced feeding migrations of blue whiting into the Iceland Sea could therefore result in these two species competing for food.

In summary, *Calanus* spp. are clearly key dietary components for higher trophic level organisms in the pelagic ecosystem of the Iceland Sea. However, there also exists a trophic pathway where *Calanus* spp. is unimportant, where energy is transferred via the two euphausiid species *T. inermis* and *T. longicaudata.* From the $\delta^{15}N$ levels found here, the conclusion is that most zooplankton species are omnivorous–carnivorous in late summer when phytoplankton abundance is low. Adult capelin and blue whiting occupy the highest trophic level (3.6) of the species studied, and they feed on *Calanus* spp. as well as larger zooplankton species such as euphausiids and amphipods. It is of note that the Arctic amphipod *T. libellula* is important in the diet of adult capelin in the Iceland Sea in August.

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Figure legends

Figure 1. Sampling stations in 2007 (circles) and 2008 (triangles), and circulation in the Iceland Sea, showing Atlantic Water in red, Polar Water in blue, and Arctic Water (a mixture of Polar and Atlantic Water) in green. EGC, East Greenland Current; NIIC, North Icelandic Irminger Current; EIC, East Icelandic Current. Figure courtesy Malin Daase, adapted after Blindheim and Østerhus (2005) and Hunegnaw *et al*. (2009).

Figure 2. Trophic relationships in the Iceland Sea in August of 2007 and 2008, showing stable isotopes of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) for all species. Values are means, and TL means trophic level. Abbreviations: Cf, *C. finmarchicus*; Ch, *C. hyperboreus*; Ml, *M. longa*; Pg, *P. glacialis*; Ti, *T. inermis*; Tlo, *T. longicaudata*; Mn, *M. norvegica*; Tl, *T. libellula*, Tl_1, 1 cm, Tl_4, 4 cm; Ta, *T. abyssorum*; Gw, *G. wilkitzkii*; Eh, *E. hamata*; Gm, *G. morhua*; Ma, *M. aeglefinus*; Mv, *M. villosus*, Mv_juv, larvae and juveniles, Mv_10, 10 cm, Mv_16, 16 cm, Mv_ad, adult (11–16 cm); Mp, *M. poutassou*; Am, *A. marinus*.

Figure 3. Fatty acid trophic markers relative to total fat (%).

Figure 4. Trophic relationships in the Iceland Sea in August of 2007 and 2008. Redundancy analysis (RDA) plot based on moiety values for all species. Symbols indicate mean values of the respective species. The species were applied as dummy variables (environmental variables) and moieties as response variables. The arrows point in the direction of the steepest increase in the respective moiety. The portion of unconstrained variance accounted for by each axis is shown. Abbreviations: see Figure 2 legend.

Figure 5. Trophic relationships of adult capelin (11 – 16 cm) and its potential prey in the Iceland Sea, 2007 and 2008. Redundancy analysis plot based on moiety (standardized FAs and fatty alcohols)

compositions of adult capelin and potential prey. Symbols show mean values of the respective species. The species were applied as dummy variables (environmental variables) and moieties as response variables. The arrows point in the direction of the steepest increase of the respective moiety. The portion of unconstrained variance accounted for by each axis is shown. Abbreviations: see Figure 2 legend.

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

FATM	**Taxa**
22:6n3 and C18 FFS	Dinoflagellates
18:4n3, 18:5n3, 18:2n6	*Phaeocystis pouchetti*
20:5n3, C16 FFS, 16:1n7	Diatoms
20:1n9, 22:1n11	*Calanus* copepods

Table 2. Summary of lipid samples (FA and fatty alcohol composition) and stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) analysed, showing the station number, gear, and depth of sampling, along with the number of replicates and animals per replica (in parenthesis; see footnote).

Species/group	Length/stage (cm)	Station	Gear	Depth (m)	Analysis		
					Lipids	$\delta^{13}C$	$\delta^{15}N$
POM and Copepoda							
POM		392	Water inlet	0–50	3(filter)	1(filter)	1(filter)
		731	Water inlet	5	2(filter)	1(filter)	1(filter)
Calanus finmarchicus	CV	309	Bongo	0–100	2(~10)	1(110)	1(110)
		392	WP2	0–50	3(~10)	1(100)	1(100)
		693	Multinet	0–600	3(~12)	1(120)	1(120)
		709	Multinet	0–400	3(12)	1(100)	1(100)
		344	Tucker	0–100	3(15)	3(100)	3(100)
		354	Tucker	0–100	3(15)	3(80)	3(80)
		505	WP2	0–100	2(15)	1(80)	1(80)
	Female	392	WP2	0–50	2(~10)	n.a.	n.a.
Calanus hyperboreus	CIV	420	Tucker	0–100	3(15)	3(100)	3(100)
	CV	309	Bongo	0–100	2(6)	n.a.	n.a.
		392	WP2	0–50	3(~5)	n.a.	n.a.
	Female	309	Bongo	0–100	3(5)	3(15)	3(15)
		392	WP2	0–50	3(~5)	3(15)	3(15)
		693	Multinet	0–600	3(10)	1(15)	1(15)
Metridia longa	Female	709	Multinet	0–400	3(12)	2(70)	2(70)
		391	WP2	0–100	3(15)	3(80)	3(80)
Paraeuchaeta glacialis	Female	710	Tucker	0–100	3(5)	3(20)	3(20)
Medusa							
Aglantha digitale	0.5	354	Tucker	0–100	n.a.	1(much)	1(much)
Euphausiacea							
Thysanoessa inermis	2.5	651	Tucker	0–100	3(3)	3(4)	3(4)
	2.5	364	Tucker	0–100	3(3)	3(1)	3(1)
Thysanoessa longicaudata	1–1.5	710	Tucker	0–100	3(10)	3(20)	3(20)
	0.65	354	Tucker	0–100	3(15)	3(40)	3(40)
Meganyctiphanes norvegica	3–3.5	710	Tucker	0–100	3(3)	3(5)	3(5)
	3–4	363	Pelagic trawl	17–20	3(3)	3(3)	3(3)
	4	490	Pelagic trawl	216–218	3(3)	3(3)	3(3)
Amphipoda							
Themisto libellula	1–1.5	710	Tucker	0–100	3(3)	3(20)	3(20)
	4–4.5	752	Pelagic trawl	0–200	3(3)	3(2)	3(2)
	3–4	363	Pelagic trawl	17–20	3(3)	3(3)	3(3)
	0.7	370	Tucker	0–100	3(3)	1(8)	1(8)
	3–4	420	Tucker	0–100	2(2)	3(1)	3(1)
	0.5–1.2	443	Tucker	0–100	3(3)	2(3)	2(3)

Themisto abyssorum	1.2–1.5	710	Tucker	0–100	3(3)	3(20)	3(20)
	0.35	385	Tucker	0–100	3(15)	3(45)	3(45)
Gammarus wilkitzkii	2.5	651	Tucker	0–100	3(1)	3(2)	3(2)
	4	396	Pelagic trawl	7–13	3(3)	3(3)	3(3)
Chaetognatha							
Eukrohnia hamata	3	693	Multinet	0–600	3(10)	3(15)	3(15)
	2.5–3	393	Tucker	0–100	3(10)	3(30)	3(30)
Pisces							
Mallotus villosus	4–5	652	Pelagic trawl	0–26	3(5)	3(5)	3(5)
	13-14.5	652	Pelagic trawl	0–26	2(1)	3(M)	3(M)
	6	706	Pelagic trawl	n.a.	3(3)	3(7)	3(7)
	14–15	738	Pelagic trawl	n.a.	3(1)	3(M)	3(M)
	15.5–16	748	Pelagic trawl	n.a.	3(1)	3(M)	3(M)
	13–14.5	757	Pelagic trawl	n.a.	3(1)	3(M)	3(M)
	14–16	758	Pelagic trawl	n.a.	3(1)	3(M)	3(M)
	6–7.5	767	Pelagic trawl	n.a.	3(3)	3(5)	3(5)
	5	369	Pelagic trawl	18–20	3(3)	3(M)	3(M)
	6	398	Pelagic trawl	15	3(2)	3(3M)	3(3M)
	10.5	414	Pelagic trawl	17–20	3(1)	3(M)	3(M)
	15–17	473	Pelagic trawl	270–300	3(1)	3(M)	3(M)
	5.5	498	Pelagic trawl	20–40	3(3)	3(2M)	3(2M)
	11–13	506	Pelagic trawl	70	3(1)	3(M)	3(M)
	15–16	506	Pelagic trawl	70	3(1)	3(M)	3(M)
Gadus morhua	5-5.5	704	Pelagic trawl	21	3(1)	3(1)	3(1)
	5.5	355	Pelagic trawl	15	3(1)	3(M)	3(M)
	6	493	Pelagic trawl	36–50	3(1)	3(M)	3(M)
	4.5	493	Pelagic trawl	36–50	3(1)	3(M)	3(M)
Melanogrammus aeglefinus	6.5–7.5	355	Pelagic trawl	15	3(1)	3(M)	3(M)
Ammodytes marinus	8.5	409	Pelagic trawl	50-100	3(5)	3(M)	3(M)
Micromesistius poutassou	30	721	Pelagic trawl	n.a.	3(1)	3(M)	3(M)

Note: where there is just a number in parenthesis, the whole animal was analysed, but M and L in parenthesis refer to muscle and liver, respectively.

Table 3. Fatty acid and fatty alcohol composition, and mass (%) of total fatty acids and alcohols of POM, zooplankton, and fish in August of 2007 and 2008 in the Iceland Sea.

Parameter	POM (*n* = 2)	*C. finmarchicus* V (*n* = 14)	*C.hyperboreus* IV (*n* = 3)	*C.hyberboreus* female (*n* = 3)	*M.longa* female (*n* = 6)	*P.glacialis* female (*n* = 3)	*T.inermis* 2.5 cm (*n* = 5)	*T.longicaudata* 0.65 cm (*n* = 3)	*T.longicaudata* 1–1.5 cm (*n* = 3)	*M.norvegica* 3–4 cm (*n* = 9)	*T.libellula* 0.7–1.5 cm (*n* = 9)	*T.libellula* 3–4.5 cm (*n* = 8)	*T.abyssorum* 0.35 cm (*n* = 3)	*T.abyssorum* 1.2–1.5 cm (*n* = 3)	*G.wilkitzkii* 2.5–4 cm (*n* = 6)	*E.hamata* 2.5–3 cm (*n* = 6)	*M.villosus* 4–7.5 cm (*n* = 18)	*M.villosus* 10.5 cm (*n* = 3)	*M.villosus* 11–17 cm (*n* = 20)	*G.morhua* 4–6 cm (*n* = 9)	*M.aeglefinus* 6.5–7.5 cm (*n* = 3)	*A.marinus* 8.5 cm (*n* = 3)	*M.poutassou* 30 cm (*n* = 3)
Fatty acids																							
14:0	10	17	8	5	2	1	3	22	6	7	6	5	5	4	5	3	8	9	8	6	4	8	4
16:0	12	9	5	4	3	1	18	11	35	16	12	11	12	10	11	2	13	12	13	14	12	12	14
16:1n9	2	1	1	1	2	1	1	1	0	0	1	0	1	0	0	1	0	0	0	0	1	0	0
16:1n7	5	10	10	9	16	25	10	7	9	9	5	10	4	9	23	10	9	8	9	9	4	6	6
16:1n5	1	1	1	0	0	1	1	1	1	1	1	0	1	0	0	1	1	1	0	1	0	1	0
16:3n4	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16:4n1	1	3	2	2	1	0	1	1	0	1	0	1	1	1	1	1	1	1	1	1	0	1	1
17:1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18:0	6	1	1	1	1	1	2	1	2	2	2	1	2	0	1	1	1	1	1	3	6	1	2
18:1n9	16	4	6	4	30	21	39	5	24	10	24	12	20	13	17	11	9	6	8	7	9	4	10
18:1n7	1	1	1	1	1	1	11	1	7	5	2	3	2	3	4	1	2	2	2	10	3	2	3
18:2n6	4	1	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18:3n6	4	1	0	2	1	0	0	0	0	0	3	0	0	0	1	0	0	0	0	0	0	0	1
18:3n3	2	1	1	1	2	1	1	2	1	1	2	1	1	1	1	1	1	1	1	1	2	1	1
18:4n3	8	9	8	3	6	3	3	13	1	3	7	7	4	5	3	8	6	4	4	4	5	5	2
18:5n3	0	0	1	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
20:1n11	1	1	1	2	1	1	0	1	0	1	1	4	2	4	1	2	0	1	1	1	1	1	1
20:1n9	5	7	9	20	7	14	1	5	5	12	5	13	10	12	6	15	9	14	15	7	4	14	14
20:1n7	0	1	2	2	0	0	0	2	0	1	0	1	1	2	1	1	0	0	1	0	1	0	1
20:2n6	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0
20:3n3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20:4n3	0	0	2	0	1	0	0	1	0	0	1	0	2	0	0	1	0	0	0	1	1	1	0
20:4n6	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0
20:5n3	7	14	9	14	12	6	6	11	2	11	10	10	13	11	11	13	14	8	6	16	20	9	9

22:0	0	0	0	2	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
22:1 n11	6	11	14	15	4	14	1	9	1	8	3	10	4	9	7	20	8	21	20	6	3	21	15
22:1n9	2	1	2	6	1	1	0	1	1	1	1	2	4	2	1	2	1	1	2	1	1	1	2
22:1n7	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22:5n6	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
22:5n3	0	0	1	0	0	0	0	1	0	1	0	0	1	0	0	1	0	1	0	1	1	1	0
22:6n3	6	3	5	4	7	5	1	3	1	8	12	7	10	11	4	4	13	7	5	12	19	9	12
Fatty alcohols																							
14:0	15	3	5	3	37	31	25	1			23	6	9	9	9	7	7			19		0	
16:0	25	9	11	4	30	14	61	10			28	9	16	10	11	11	12			41		7	
16:1n7	2	4	2	1	4	4	9	2			2	2	1	2	2	2	1			3		2	
18:1n9	2	3	2	0	1	1	0	4			1	1	1	1	2	2	5			3		4	
20:1n9	23	34	20	31	12	21	2	30			21	26	40	25	26	33	31			8		26	
22:1n11	28	43	55	51	12	25	3	49			22	48	23	42	42	40	39			25		61	
22:1n9	5	4	5	10	4	3	0	3			4	7	9	11	8	5	5			0		0	
22:1n11/20:1n9	1.2	1.3	2.7	1.6	1.0	1.2	1.7	1.7			1.1	1.8	0.6	1.7	1.6	1.2							
% fatty alcohol	28	46	49	45	32	39	25	50	1	0	19	24	27	15	12	46	9	0	0	3	0	7	1

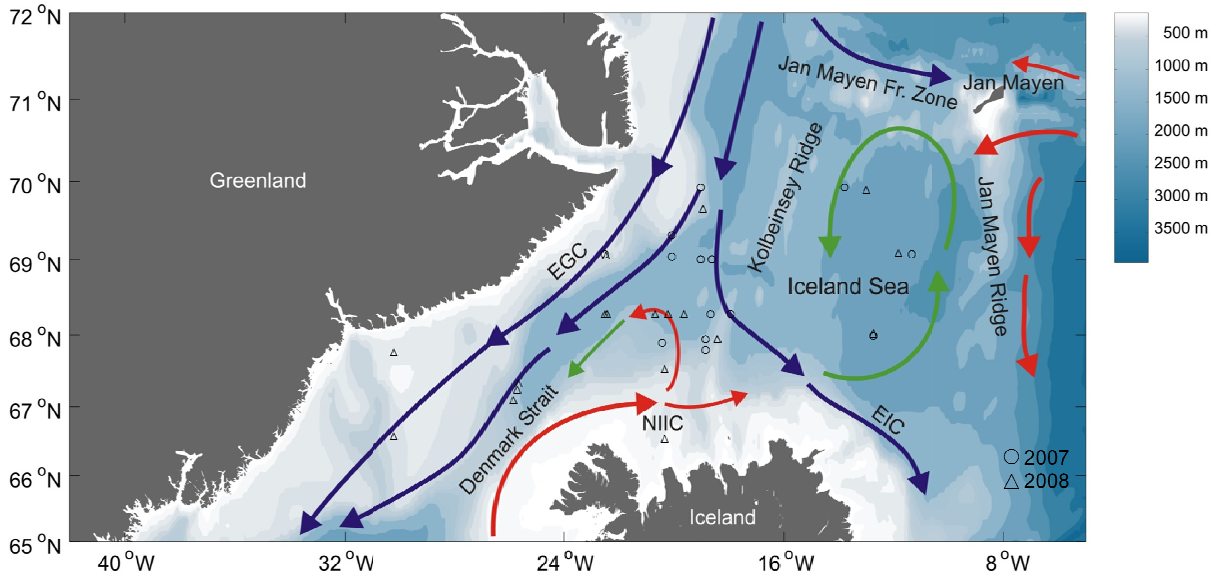


Figure 1.

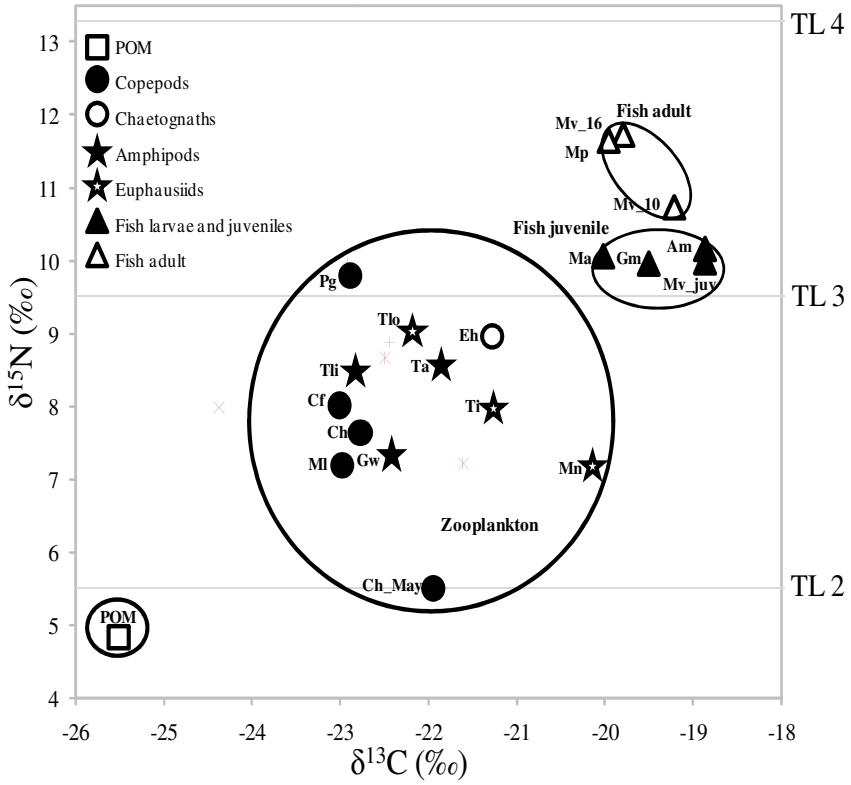


Figure 2.

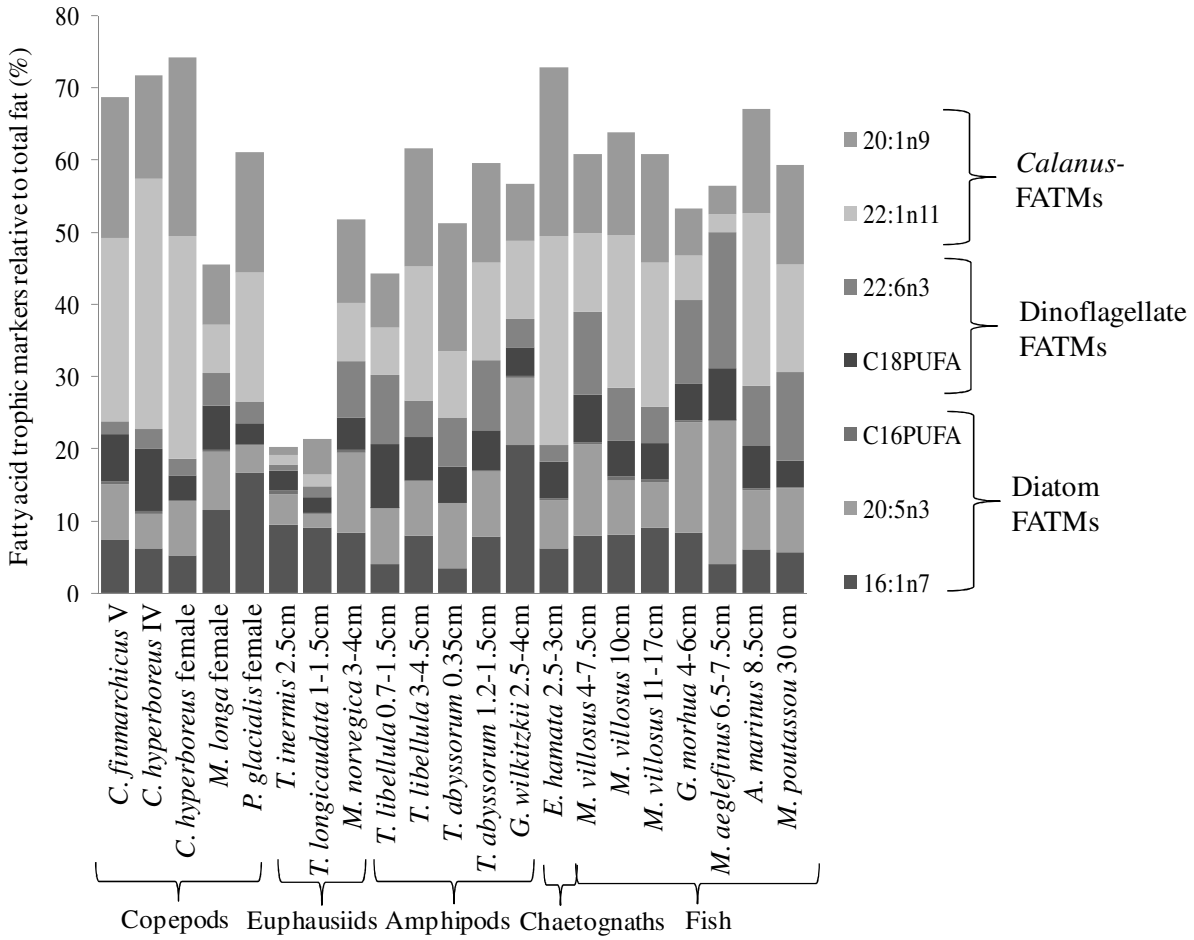
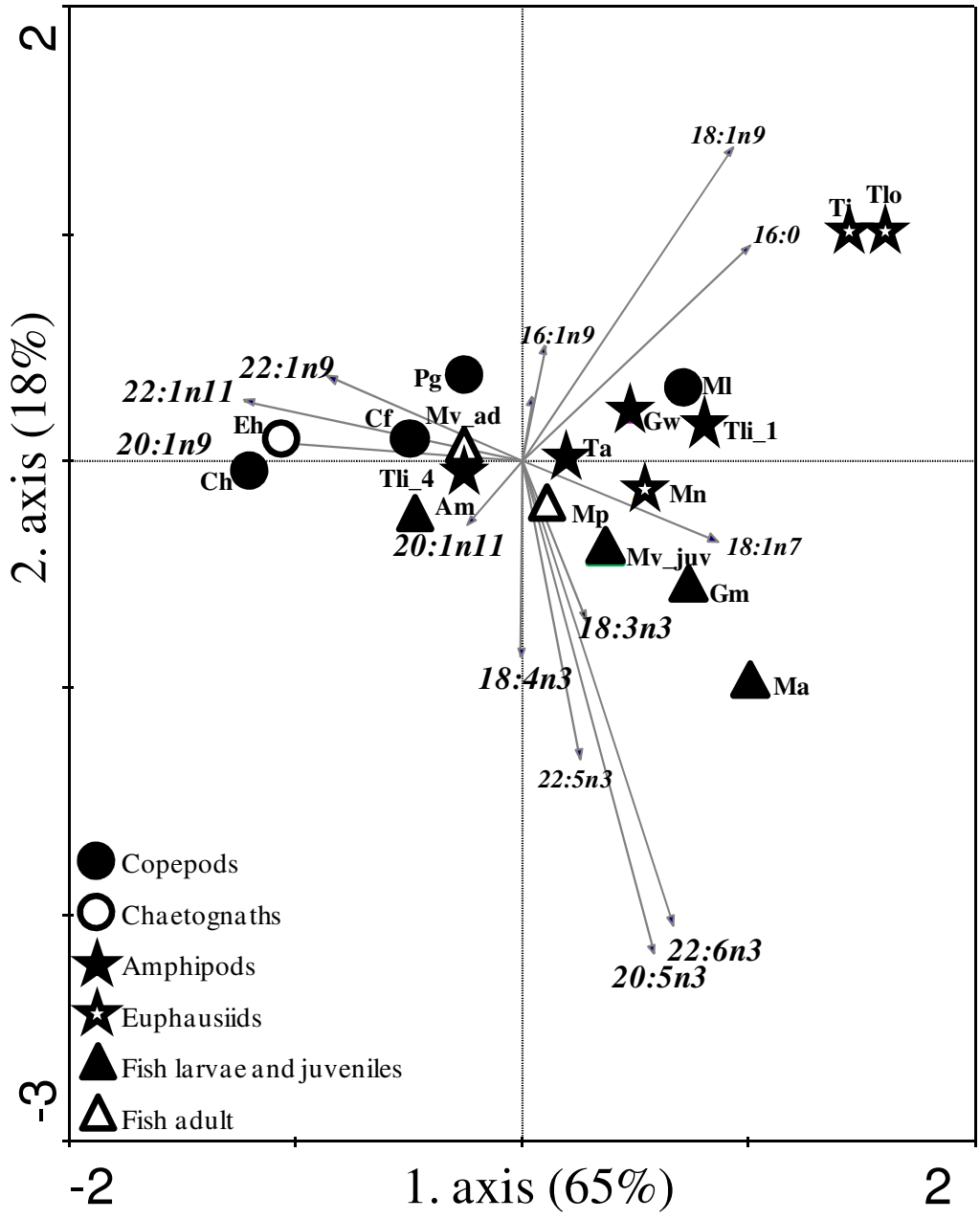

Fatty acid trophic markers relative to total fat (%)
80
70
60
50
40
30
20
10
0
20:1n9
22:1n11
Calanus-FATMs
22:6n3
C18PUFA
Dinoflagellate FATMs
C16PUFA
20:5n3
16:1n7
Diatom FATMs
C. finmarchicus V
C. hyperboreus IV
C. hyperboreus female
M. longa female
P. glacialis female
T. inermis 2.5cm
T. longicaudata 1-1.5cm
M. norvegica 3-4cm
T. libellula 0.7-1.5cm
T. libellula 3-4.5cm
T. abyssorum 0.35cm
T. abyssorum 1.2-1.5cm
G. wilkitzkii 2.5-4cm
E. hamata 2.5-3cm
M. villosus 4-7.5cm
M. villosus 10cm
M. villosus 11-17cm
G. morhua 4-6cm
M. aeglefinus 6.5-7.5cm
A. marinus 8.5cm
M. poutassou 30 cm
Copepods
Euphausiids
Amphipods
Chaetognaths
Fish

Figure 3.


2
2. axis (18%)
-3
-2
1. axis (65%)
2
18:1n9
16:0
Ti
Tlo
16:1n9
22:1n9
22:1n11
Pg
Ml
Cf
Mv_ad
Gw
Tli_1
Eh
20:1n9
Ta
Ch
Tli_4
Mn
Am
Mp
18:1n7
20:1n11
Mv_juv
Gm
18:3n3
18:4n3
Ma
22:5n3
22:6n3
20:5n3
Copepods
Chaetognaths
Amphipods
Euphausiids
Fish larvae and juveniles
Fish adult

1

Figure 4.

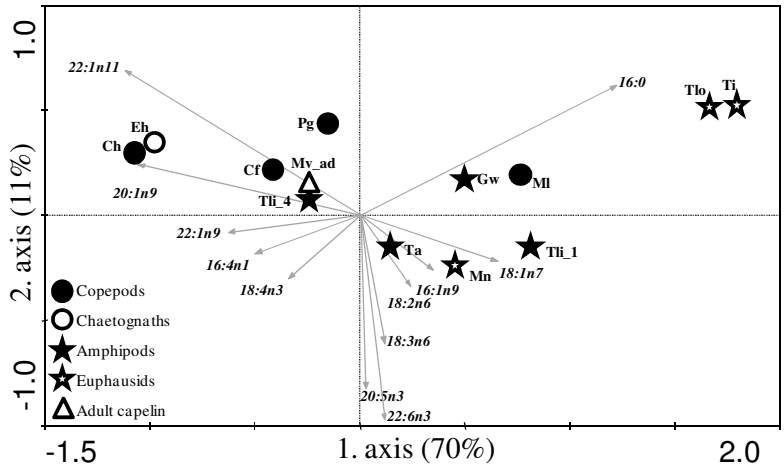

1.0
-1.0
2. axis (11%)
-1.5
1. axis (70%)
2.0
22:1n11
16:0
Tlo
Ti
Eh
Pg
Ch
Cf
Mv_ad
Gw
Ml
20:1n9
Tli_4
22:1n9
Ta
Tli_1
16:4n1
Mn
18:1n7
18:4n3
16:1n9
18:2n6
18:3n6
20:5n3
22:6n3
Copepods
Chaetognaths
Amphipods
Euphausids
Adult capelin

Figure 5.