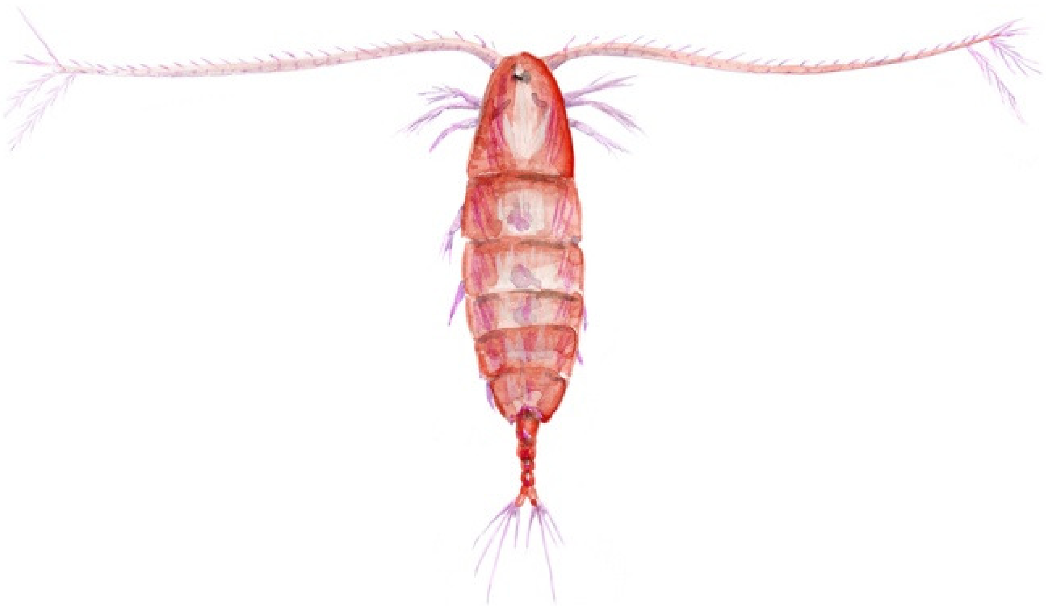
UNIVERSITY OF TROMSØ UIT

FACULTY OF BIOSCIENCES, FISHERIES AND ECONOMICS
DEPARTMENT OF ARCTIC AND MARINE BIOLOGY

Trophic relationships and the role of *Calanus* in the oceanic ecosystems south and north of Iceland



Hildur Pétursdóttir

A dissertation for the degree of Philosophiae Doctor
December 2012

Trophic relationships and the role of *Calanus* in the oceanic ecosystems south and north of Iceland

By Hildur Pétursdóttir

Department of Arctic and Marine Biology
Faculty of Bioscience, Fisheries and Economics

and

The Marine Research Institute in Iceland

Thesis for the degree Philosophiae Doctor
Tromsø 2012

Supervisors:

Professor Marit Reigstad
Department of Arctic and Marine Biology
Faculty of Bioscience, Fisheries and Economics
University of Tromsø
Norway

Professor Stig Falk-Petersen
Norwegian Polar Institute
Framsenteret, Tromsø
Norway

Dr. Astthor Gislason
Marine Research Institute in Iceland
Reykjavik
Iceland

Leader of the committee:

Associate Professor Else Nøst Hegseth
Department of Arctic and Marine Biology
Faculty of Bioscience, Fisheries and Economics
University of Tromsø
Norway

First opponent:

Associate Professor Ole Jørgen Lønne
The University Center in Svalbard
Svalbard
Norway

Second opponent:

Professor Patrick Mayzaud
Ville France sur Mer
University Pierre et Marie Curie, Paris
France

Acknowledgements

First and foremost I want to express my sincere gratitude to my supervisors Marit Reigstad, Stig Falk-Petersen and Astthor Gislason for their superior guidance, advice and support. Without their encouragement and motivation this synthesis would not have been possible. I want to thank Stig Falk-Petersen and Astthor Gislason for encouraging me to take on this PhD project. I am also grateful to Stig for giving me an opportunity to work at the Norwegian Polar Institute.

I want to thank my co-authors: Astthor Gislason, Stig Falk-Petersen, Haakon Hop and Jorundur Svavarsson (Paper I), Astthor Gislason and Stig Falk-Petersen (Papers II and III), Olafur Karvel Palsson, Hafsteinn G. Gudfinnsson, Astthor Gislason, Bjorn Gunnarsson, Solveig Rosa Olafsdottir, Sveinn Sveinbjornsson, Konrad Thorisson and Hedinn Valdimarsson (Paper IV) and Astthor Gislason, Olafur S. Astthorsson, Kristinn Gudmundsson and Hedinn Valdimarsson (Paper V). Their contribution was essential for this thesis.

I also would like to thank my friends in Tromsø, Anette Wold and Malin Daase for their friendship, encouragement and help through the study, e.g. Anette for guiding me through the administrative procedure of the PhD program and by commenting on the material and methods part of the thesis and Malin for drawing the nice maps of the study area.

I wish to give my special thanks to Janne Søreide for her constructive comments on an earlier draft of the synthesis and Olafur S. Astthorsson for his comments and inputs on a later version of the manuscript. Solveig Rosa Olafsdottir, Kristinn Gudmundsson and Olafur Karvel Palsson also gave me their helpful comments on parts of the manuscript. Further, I am thankful to the artist Jon Baldur Hlidberg for allowing me to use his drawing of *Calanus* copepod on the front page of the synthesis and my friend Anna Lara Masdottir for helping me with formatting the final synthesis.

My gratitude to the crews on the RVs *Árni Friðriksson*, *Bjarni Sæmundsson* and *G.O. Sars* as well as my co-workers at the Marine Research Institute in Iceland for assisting with the sampling and overall support during the study.

My heartful thanks go to my friends and family for their loving and unconditional support and friendship throughout this study.

Finally, I would sincerely like to thank Johann Sigurjonsson, the director of the Marine Research Institute in Iceland, for making it possible for me to take on this PhD.

This work was supported financially by the Marine Research Institute in Iceland and the international project MAR-ECO.

Table of Contents

Abstract

The waters south and north of Iceland vary greatly both oceanographically and biologically with the rather stable and warm Atlantic waters south and west of Iceland and the more variable and cold Arctic and sub-Arctic waters, north and east of Iceland. The aim of this study was to increase the knowledge on the role of *Calanus* copepods and trophic relations of the key components of the oceanic ecosystems south-west (over the Reykjanes Ridge; Papers I and II) and north (in the Iceland Sea; Papers III and IV) of Iceland. The trophic relationships and energy transfer to higher trophic levels were estimated by using fatty acid trophic markers, by comparing fatty acid profiles among species and by applying stable isotopes of carbon and nitrogen. The inter-annual variability in abundance and community composition of zooplankton on the shelves south and north of Iceland in relation to environmental condition in spring were also observed (Paper V). The energy rich *Calanus* species are key links between primary producers and higher trophic levels in the Icelandic waters. The *Calanus* species dominate the zooplankton biomass around Iceland and their markers (20:1n9 and 22:1n11) are found in high amount in animals at higher trophic levels (Papers I, III, IV and V). *Calanus finmarchicus* plays important role as a forage species in the Atlantic water south-west of Iceland while its high importance is replaced by the larger lipid rich *C. hyperboreus* in the Arctic and sub-Arctic waters north of Iceland (Papers I and III). Even though *Calanus* based food-web is the main driver in both areas, there exist a pathway where *Calanus* species are of less importance and the energy is channeled via euphausiids to higher trophic levels (Papers I, II and III). Around four trophic levels were observed in the two oceanic ecosystems where adult fish occupied the highest trophic levels. Over the Reykjanes Ridge vertically migrating mesopelagic fish, in pronounced deep-scattering layers, are actively bringing energy to deeper layers by feeding on *C. finmarchicus* in the upper layers (Paper I). In the Iceland Sea comparable deep-scattering layers were not observed. Epipelagic schools of capelin (*Mallotus villosus*) are important component of the pelagic ecosystem in the Iceland Sea (Paper IV). After feeding intensively in the Iceland Sea, they migrate and thus transfer the energy to adjacent ecosystems. The ecosystem around Iceland is extremely sensitive to climate variations. Increase in sea temperature has been related to shift in distribution and feeding migrations of capelin in the Iceland Sea with the result of diet switch of older capelin (Papers III and IV). The importance of the Arctic amphipod *Themisto libellula* in the diet of adult capelin increased in their new distribution area in the colder western part of the Iceland Sea (Paper III). A shift in distribution of species may thus influence the whole ecosystem structure and food web interactions in larger area. This study presents novel important knowledge on the food web structures and carbon flow in Icelandic waters (Papers I, II, III and IV).

List of papers

I. Petursdottir, H., Gislason, A., Falk-Petersen, S., Hop, H., and Svavarsson, J. 2008. Trophic interactions of the pelagic ecosystem over the Reykjanes Ridge as evaluated by fatty acid and stable isotope analyses. Deep-Sea Research II, 55: 83-93.

II. Petursdottir, H., Gislason, A., and Falk-Petersen, S. 2008. Lipid classes and fatty acid compositions of muscle, liver and skull oil in deep-sea redfish *Sebastes mentella* over the Reykjanes Ridge. Journal of Fish Biology, 73: 2485–2496.

III. Petursdottir, H., Falk-Petersen, S., and Gislason, A. 2012. Trophic interactions of meso- and macrozooplankton and fish in the Iceland Sea as evaluated by fatty acid and stable isotope analysis. ICES Journal of Marine Science, 69: 1277-1288.

IV. Pálsson, Ó.K., Gislason, A., Guðfinnsson, H.G., Gunnarsson, B., Ólafsdóttir, S.R., Petursdottir, H., Sveinbjörnsson, S., Thorisson, K., and Valdimarsson, H. 2012. Ecosystem structure in the Iceland Sea and recent changes to the capelin (*Mallotus villosus*) population. ICES Journal of Marine Science, 69: 1242-1254.

V. Gislason, A., Petursdottir, H., Astthorsson, O.S., Gudmundsson, K., and Valdimarsson, H. 2009. Inter-annual variability in abundance and community structure of zooplankton south and north of Iceland in relation to environmental conditions in spring 1990-2007. Journal of Plankton Research, 31: 541-551.

Papers I and II are part of an international ecological study, MAR-ECO (2003-2010), that explored the macrofauna along the northern Mid-Atlantic Ridge. Its main objective was to describe and understand the distribution, abundance and trophic relationships of organisms inhabiting the mid-ocean North Atlantic (Bergstad and Godø, 2003; Bergstad *et al.*, 2008).

Papers III and IV are part of the Iceland Sea Ecosystem Project (2006-2008), where the main objective was to increase our understanding of the Iceland Sea ecosystem, including linkages to the life history and the survival of capelin. The Iceland Sea Ecosystem Project is the Icelandic component of The Ecosystem Studies of Sub-Arctic Seas (ESSAS) which addresses how climate change affects marine ecosystems of the Sub-Arctic Seas and their sustainability.

Paper V is based on data from a long-term monitoring program on standard sections around Iceland in spring/early summer that has been carried out by the Marine Research Institute for more than 50 years with the main objective to monitor long-term changes in hydrography, nutrients and phytoplankton and zooplankton development around Iceland.

1. Introduction

Fisheries are the most important sector of the Icelandic economy and it is therefore important to understand the marine production, the ecosystems and energy transfer that are the basis for the large pelagic and benthic fisheries in Icelandic waters. The oceanic areas south-west and north of Iceland are different both oceanographically and biologically (Thordardottir, 1994; Gislason and Astthorsson, 2004; Ólafsdóttir, 2006). These areas serve as important feeding grounds for some ecologically and economically important fish species such as redfish (*Sebastes mentella*, south-west of Iceland) and capelin (*Mallotus villosus*, north of Iceland). This was a motivation to study the trophic interactions and energy transfer in the pelagic ecosystems of these two different areas.

Zooplankton are an important food component in the diet of most fish species in Icelandic waters at some stages of their life cycle, either being consumed directly as by capelin and herring (*Clupea harengus*) or indirectly as by demersal fish feeding on planktivorous fish, e.g. capelin is important in the diet of cod (*Gadus morhua*) and marine mammals (Magnusson and Pálsson, 1991; Magnusson and Magnusson, 1995; Astthorsson and Gislason, 1997; Óskarsson *et al*., 2012). Key zooplankton species, such as *Calanus* copepods and euphausiids, convert low energy sugars and protein in phytoplankton to high energy lipids and thus transferring energy directly from the primary producers to fish. Around Iceland, as in other high latitude ecosystems, marine pelagic animals have adapted to the relatively short and intense production season by converting large amounts of excess food into storage lipids, thus making it possible for them to survive long periods of food scarcity during winter (Falk-Petersen *et al*., 1990; Thordardottir, 1994).

The sea areas around Iceland constitute one of the most important fishing areas in the North Atlantic Ocean (Arnason, 1993) with a total annual catch of about 2 million tons (Astthorsson *et al*., 2007). The demersal fishery is much more important economically than the pelagic fishery. The most commercially important fish species in the demersal fisheries is cod followed by haddock (*Melanogrammus aeglefinus*), saithe (*Pollachius virens*), redfish (*Sebastes* sp.) and Greenland halibut (*Reinhardtius hippoglossoides*). During the last five decades, these five species have made up a total annual catch of 450.000 – 850.000 tons (Astthorsson *et al*., 2007). Since the late 1960s, capelin has been the economically most important pelagic fish stock, followed by herring. In recent years mackerel (*Scomber scombrus*) has increased in the Icelandic fisheries (Anon, 2011). The annual catch of capelin was around 1 million tons in 1990s – mid 2000s. Since 2003 there has been a drastic decrease in the capelin fishery as a consequence of decline in recruitment and stock size (Vilhjalmsson, 2002; Anon, 2011; Pálsson *et al.*, 2012).

The waters south and north off Iceland can be divided into two main hydrographic domains (Malmberg and Valdimarsson, 2003; Astthorsson *et al.*, 2007). The rather stable and warmer Atlantic water south and west of Iceland and the more variable and colder Arctic and sub-Arctic waters, north and east of Iceland, which to a variable degree are influenced by inflow of Atlantic water from the south. The highest fish diversity (species richness) is found in the warmer water southwest and west of Iceland, while the colder waters north and east of Iceland have lower diversity (based on long-term demersal ground fish survey; Stefansdottir *et al.*, 2010). By spawning in the Atlantic water south and southwest of Iceland and feeding in the waters north of Iceland (Astthorsson *et al.*, 1994, 2007) most of the economically important fish stocks utilize both these areas. As a consequence of climate variability during the 20th century, changes have been observed in abundance and distribution of many fish species in the Icelandic ecosystem (reviewed by Astthorsson *et al.*, 2007; Valdimarsson *et al.*, 2012). After the mid 1990s, warmer and more saline waters have been observed off the south and west shelves of Iceland than previously and temperature has increased by 1-2°C (Malmberg and Valdimarsson, 2003). These changes have also influenced the shelf areas north of Iceland. Southern species have extended their distribution area farther north, e.g. haddock, monkfish (*Lophius piscatorius*) and mackerel, while the Arctic capelin has retreated and changed its feeding migrations westward. Further, rare or new southern species have been observed more frequently (Valdimarsson *et al.*, 2005; Astthorsson and Palsson, 2006; Astthorsson *et al.*, 2007, 2010; Palsson, 2007, 2008, 2009, 2010; Solmundsson, 2010; Valdimarsson *et al.*, 2012). Primary production and zooplankton biomass north of Iceland is directly affected by climate variability, i.e. being higher in warmer years as a consequence of greater inflow of Atlantic water to the north (Astthorsson and Gislason, 1994, 1998; Astthorsson and Vilhjalmsson, 2002). Astthorsson and Gislason (1998) demonstrated that, higher annual phytoplankton production during warm years, were reflected in higher zooplankton biomass and capelin weight-at age.

Dietary studies of fish have been part of fisheries research in Iceland since investigations began (Faber, 1829; Sæmundsson, 1926; Friðriksson, 1944; Pálsson, 1983) with main emphasis on the ecologically important fish such as cod and herring. Apparent trophic interactions have for example been found between cod consumption and stock sizes of capelin and northern shrimp (Pálsson and Björnsson, 2011). Published results on the diet of pelagic fish are available (e.g. Sigurdsson and Astthorsson, 1991; Magnusson and Magnusson, 1995; Astthorsson and Gislason, 1997; Óskarsson *et al.*, 2012;) while there is limited information on the food of organism of lower trophic levels such as zooplankton. One of the aims of this study was to expand the traditional stomach content studies with the use of new techniques like stable isotope and fatty acid (FA) analyses that provide complementary information on the diet (Kharlamenko *et al.*, 2001; Dahl *et al.*, 2003; Wold *et al.*, 2011). Such investigations provide an integration of prey consumed over periods ranging from weeks to months (Fry, 1988; Rau *et al.*, 1992; Dalsgaard *et al.*, 2003). The trophic position of the species can be deduced from stable isotope values, and FAs and alcohols may give detailed information about their diet. This study achieved new important knowledge on the food web structures and carbon flow in Icelandic waters (Papers I, II, III and IV).

In the light of the high ecosystem sensitivity to climatic variations (Astthorsson *et al.*, 2007; Valdimarsson *et al.*, 2012) and the limited information on trophic relations in the Icelandic marine ecosystem, this study was initiated on, the role of *Calanus* and trophic relations, to increase our knowledge and understanding of the trophic structure of the key components of the pelagic ecosystem around Iceland. We focused on two hydrographically contrasting regions and their respective dominating meso- and macrozooplankton (in terms of biomass) and fish species. One of the areas was the oceanic ecosystem over the Reykjanes Ridge, southwest of Iceland where redfish is commercially important fish species (Papers I and II). The other area was the Iceland Sea, north of Iceland, where capelin is a dominant fish species (Papers III and IV). In addition we studied long-term changes of zooplankton communities south and north of Iceland (Paper V) to elucidate if the zooplankton communities had changed in recent years as a consequence of the observed climate warming.

2. Objectives

The overall objective of this thesis is to describe the trophic interactions and energy flow from zooplankton to pelagic fish in two contrasting oceanic areas i.e. the relatively warm Atlantic waters southwest of Iceland and the cold Arctic waters north of Iceland.

Specific aims were:

1. To describe the main trophic structure and the role of *Calanus* in the pelagic ecosystems over the Reykjanes Ridge southwest off Iceland and in the Iceland Sea north off Iceland using fatty acid and stable isotope analyses (Papers I, II, III, IV and V)

2. To study the variability in zooplankton community structure south and north of Iceland (Papers IV and V)

3. To describe the recent changes in capelin abundance and distribution, and in their diet preferences (Papers III and IV)

3. The abiotic and biotic environment

3.1 Bottom-topography, currents and water masses

Iceland rests at the junction of two large submarine ridges, the Mid-Atlantic Ridge and the Greenland-Scotland Ridge (Figure 1). The complicated bottom topography of ridges is believed to have a pronounced effect on the flow of currents, both deep water and near surface, and therefore also on the distribution of biological production (Astthorsson *et al.*, 1983; Stefánsson and Ólafsson, 1991; Søiland *et al.*, 2008). The Mid-Atlantic Ridge nearly splits the entire Atlantic Ocean floor from south to north. A part of the Mid-Atlantic Ridge, the Reykjanes Ridge reaches Iceland from southwest. The Mid-Atlantic Ridge then extends north of Iceland as the Kolbeinsey Ridge and divides the Iceland Sea into two parts (west and east; Figure 1). The Reykjanes Ridge delimitates the Irminger Sea southwest of Iceland from

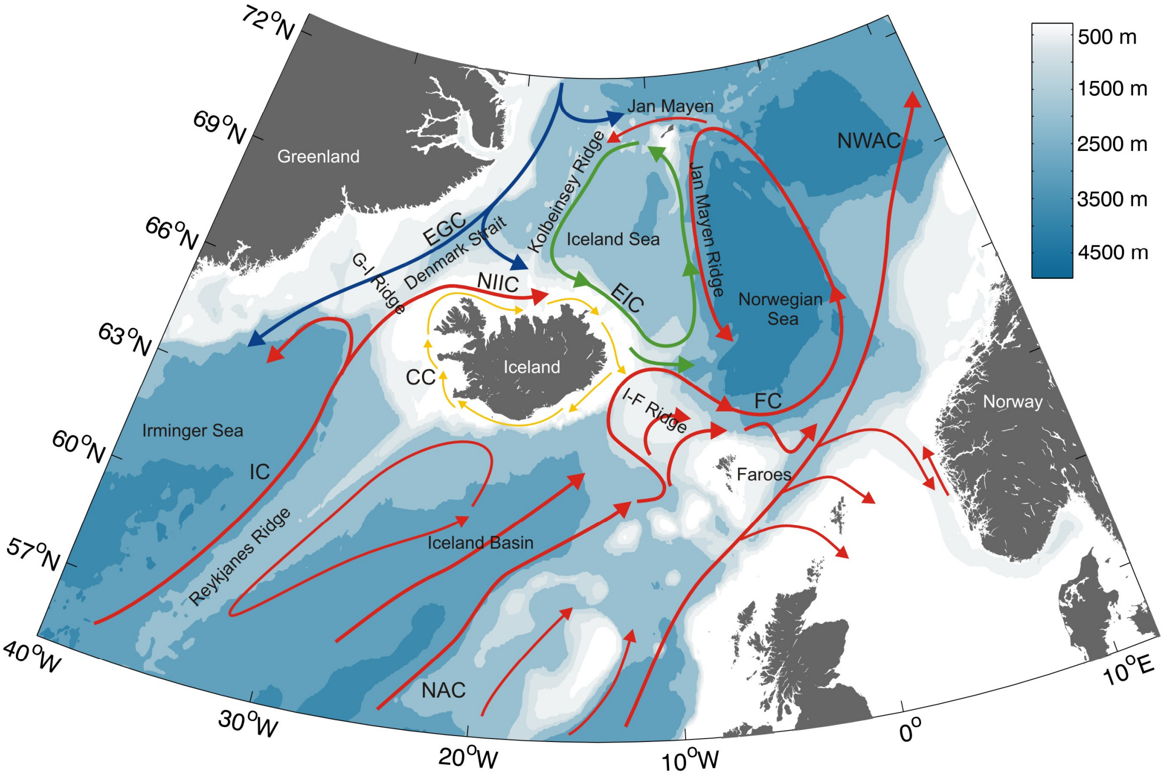


Figure 1. Topography and circulation around Iceland. North Atlantic Current (NAC), Irminger Current (IC), North Icelandic Irminger Current (NIIC), Faroe Current and Norwegian Atlantic Current (NWAC); East Greenland Current (EGC); East Iceland Current (EIC); Icelandic Costal Current (CC); Greenland Iceland Ridge (G-I Ridge); Iceland Faroe Ridge (I-F Ridge). Figure courtesy of Malin Daase, adapted after Hansen and Østerhus, 2000.

the Iceland Basin south and southeast of Iceland. The Iceland-Jan Mayen Ridge stretches from Jan Mayen in north to the Iceland-Faroe Ridge, and separates the Iceland Sea from the Norwegian Sea. The Iceland Sea is bounded by Greenland to the west, the Denmark Strait and the continental shelf break north of Iceland to the south and by Jan Mayen and the Jan Mayen Fracture Zone to the north.

The Greenland-Scotland Ridge is of importance in dividing the oceanic area around Iceland into two main hydrographic domains, the relatively warm Atlantic water south and west of Iceland and the cold Arctic or sub-Arctic water, north and east of Iceland (Stefánsson, 1962).

The warm (5-12°C) and saline (>35.2) Atlantic water south of Iceland reaches the south coast as the Irminger Current that flows westwards along the south coast of Iceland and northward along the west coast (Figure 1). When reaching the Greenland-Iceland Ridge most of this water turns west towards Greenland while a small branch continues northwards to the north Icelandic shelf area. Continuing eastward the current is called North Icelandic Irminger Current (Stefánsson, 1962; Valdimarsson and Malmberg, 1999; Malmberg and Valdimarsson, 2003). Profound variations in hydrographic conditions have been observed north of Iceland, reflecting the variable inflow of Atlantic water to the area (Valdimarsson *et al.*, 2012). From the north, cold ($t<0$°C) and less saline ($S<34.5$) water, originating in the Arctic Ocean, is transported with the East-Greenland Current southwards along the continental slope of East-Greenland (Stefánsson, 1962; Hansen and Østerhus, 2000). When reaching the Iceland Sea, large part of it continues through the Denmark Strait, while a part of the current turns southeast in the Iceland Sea where it mixes with the Atlantic water of the North Icelandic Irminger Current (Figure 1). The East-Icelandic Current flowing south-eastward, north-east of Iceland, carries Arctic Water which is a mixture of Atlantic water (form the North Icelandic Irminger Current with some inflow from Jan Mayen) and Polar water (from the East-Greenland Current). Deep cold overflow waters are transported southward over the ridges northwest and southeast of Iceland out of the Nordic Seas (Perkins *et al.*, 1998; Jonsson and Valdimarsson, 2004). Close to the land the Coastal Current carries low salinity water partly derived from fresh water run-off clockwise around Iceland.

3.2 Nutrients

The concentrations of nitrate, phosphate and silicate are considerately higher in the Atlantic water south and west of Iceland compared to the Arctic waters north and east of Iceland (Stefánsson and Ólafsson, 1991; Ólafsdóttir, 2006). The winter concentrations have been estimated as 14 and 12 µM for nitrate, 0.9 and 0.8 µM for phosphate and 7 and c. 5.5 µM for silicate, in the Atlantic and Arctic waters, respectively (Ólafsdóttir, 2006, 2012). Nutrient concentrations decline in spring when the conditions for phytoplankton growth have become favorable with increased light intensity and stratification in the surface waters. The coastal waters usually become stratified earlier than offshore waters because of mixture of freshwater runoff causing lower salinity. Stratification occurs later in spring farther from the shore, as it is primarily caused by warming of the surface waters by solar radiation. Due to enrichment of silicate from runoff (Stefánsson and Ólafsson, 1991) the growth of diatoms is prolonged in shallow waters (Ólafsson *et al.*, 2008). Vertical mixing in the high salinity Atlantic water south and west of Iceland is more pronounced than in the Arctic water north of Iceland, due to differences in salinity and wind. Consequently renewal of nutrients to the surface layer is more efficient in the south. The Atlantic water, carried with the Irminger Current to the north Icelandic shelf, is therefore an important source of nutrients north of Iceland.

3.3 Primary production and phytoplankton

The total annual primary production within the Icelandic economic zone has been estimated to be c.160 $gCm^{-2}yr^{-1}$ (Thordardottir, 1994). In general, the average annual primary production is higher in the waters south of Iceland c.150-400 $gCm^{-2}yr^{-1}$ than north of Iceland c.100-200 $gCm^{-2}yr^{-1}$ (Thordardottir, 1994). The main reason for this variability is the stronger stratification of the surface layers in the northern area due to the admixture of low salinity Polar and Arctic Water to the surface layers and therefore limited renewal of nutrients from deeper layers (Thordardottir, 1976, 1994; Stefánsson and Ólafsson, 1991; Gudmundsson, 1998). There is generally a strong phytoplankton bloom in the spring and sometimes another smaller bloom in the autumn (Gudmundsson, 1998). The spring phytoplankton bloom starts in late March or early April and culminates in May, but this varies both inter-annually and regionally depending on variable hydrographic conditions (Gudmundsson, 1998; Gudmundsson *et al.*, 2009; Zhai *et al.*, 2012). Diatoms (*Thalassiosira* spp. and *Chaetoceros* spp.) dominate the spring bloom (Thordardottir and Gudmundsson, 1998) both in the north and south while the prymnesiophyte *Phaeocystis pouchetii* may be abundant in the north. The composition of the autumn bloom, if present, is a mixture of dinoflagellates, small flagellates and diatoms (Thordardottir, 1994).

3.4 Zooplankton

In spring, zooplankton biomass in the upper 50 m of the water column in the waters around Iceland varies from 2-4 g dw m^{-2} (Gislason, 2002) with the highest biomass generally being observed in the southern and western shelf waters (*Calanus finmarchicus*) and in the oceanic waters north and northeast where larger Arctic zooplankton species tend to dominate (*C. hyperboreus*). Relatively high biomass is also observed in offshore waters of the Irminger and Norwegian Seas. In general, total zooplankton biomass and abundance are low during the winters with peaks during the summer, in late May on the shelf, but later in the oceanic areas (Hallgrimsson, 1954; Astthorsson and Gislason, 1992; Gislason *et al.*, 1994; Gislason and Astthorsson, 1995, 1996, 1998; Gislason and Silva, 2012).

As in most other marine systems, copepods numerically dominate the mesozooplankton in Icelandic shelf waters (Astthorsson *et al.*, 1983; Gislason and Astthorsson, 1995, 1998, 2000; Gislason, 2002) and *C. finmarchicus* is by far the most abundant species (60-80%). Gislason and Astthorsson (2004) revealed 4 different mesozooplankton communities in 4 different areas during spring mainly reflecting different hydrography. In the coastal water south and west of Iceland, cirripede larvae were by far the most abundant group, followed by *C. finmarchicus* and euphausiid larvae, while in the northern coastal water, *C. finmarchicus*, euphausiid larvae and larvaceans were most abundant. In the offshore waters south of the island, *C. finmarchicus*, *Oithona* spp. and echinoderm larvae were most abundant, whereas in the offshore area north of Iceland *C. finmarchicus*, *Oithona* spp. and the Arctic *C. hyperboreus* were most abundant.

4. Material and methods

4.1 The study of trophic relationships

Trophic relationships describe the feeding interactions among species within a food web. They reflect how energy is transferred from lower to higher trophic levels, where primary producers are at the first trophic level. Organisms within a trophic web can also be defined according to their feeding mode. Ecological efficiencies of energy transfer from one trophic level to another range from 2% to 24% in marine systems (Lindemann, 1942), usually around 20% from primary producers to primary consumers and around 10% between higher trophic levels.

Comprehensive knowledge of trophic interactions within the pelagic ecosystem is essential in order to understand the dynamics of a system, and how its different components, including commercially harvestable species, may vary under different environmental conditions.

Various methods have been used to study trophic interactions in marine ecosystems. The most traditional one has been stomach content analyses. Below is a list of some of the methods used today:

- Stomach content analyses (this study as reference data)
- Direct observations in the field
- Analysis of faecal remains (hard parts)
- Gut fluorescence analyses, for herbivorous zooplankton
- Serological analyses
- Molecular genetics
- Mitochondrial and nuclear DNA markers
- Analysis of stable isotope markers (this study)
- Analysis of fatty acid markers and signatures (this study)

In this study stable isotopes and fatty acid were used in order to describe the trophic relationships in marine pelagic ecosystems around Iceland. Combined with available knowledge about stomach contents, ecology of the species and the use of multivariate statistical analyses, the stable isotopes and fatty acid analyses can be an efficient tool in food web studies, as they reflect dietary assimilation over longer time periods than the more traditional stomach content analyses (Papers I, II, III and IV).

4.2 Stable isotope markers

Analyses of naturally occurring stable isotopes of carbon ($\delta^{13}C={}^{13}C/{}^{12}C$) and nitrogen ($\delta^{15}N={}^{15}N/{}^{14}N$) are commonly applied to determine food web structure and carbon sources in marine ecosystems (Hobson *et al.*, 1995; Post, 2002; Wold *et al.*, 2011). A stepwise enrichment of $\delta^{13}C$ and $\delta^{15}N$ generally occurs between trophic levels in the food web because of preferential excretion and respiration of the lighter isotopes (DeNiro and Epstein, 1978, 1981; Minagawa and Wada, 1984; Wada *et al.* 1987; Hobson and Welch, 1992; Hobson *et al.*, 1995; Post, 2002). Stable nitrogen isotopes provide information on trophic position in the food web (Hobson and Welch, 1992; Dahl *et al.*, 2003; Tamelander *et al.*, 2006) while stable carbon isotopes may provide information about the carbon source (Peterson and Fry, 1987; Peterson, 1999; Post, 2002; Søreide *et al.*, 2006).

There are several challenges when using stable isotope techniques in trophic studies such as:

- Finding the appropriate baseline in the food web
- Obtaining a pure sample of the first trophic level is difficult as it is problematic to separate live autotrophic phytoplankton from detritus and heterotrophic microplankton. Therefore particulate organic matter (POM) is often used as a representative of the first trophic level. Another option is to use organisms at trophic level 2 as the baseline (Papers I, III and IV)
- Choose an appropriate enrichment factor
- Limited knowledge of the time it takes for the isotope composition of consumer tissue to reach equilibrium with the prey tissue (i.e. turnover time)

In the present study, the ratios between heavy and light stable isotopes of carbon and nitrogen (${}^{13}C/{}^{12}C$ and ${}^{15}N/{}^{14}N$ respectively) were analyzed (Papers I, III and IV). Prior to the analyses the lipids were extracted from the samples in order to reduce variability due to isotopically lighter lipids (Hobson and Welch, 1992), since lipids are depleted in ${}^{13}C$ relative to proteins and carbohydrates (van Dongen *et al.*, 2002). For determining tropic levels (TL) the method described by Fisk *et al.* (2001) was used, with trophic level 2 used as baseline. In Paper I it was assumed that *Calanus finmarchicus* from summer samples represented trophic level 2 while in Papers III and IV spring samples of *C. hyperboreus* were used as a representative of trophic level 2. The following relationship was used for each individual sample of other tropic levels:

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

where TL_{consumer} is the trophic level of an organism, $\delta\,^{15}N_{Calanus}$ is analytically determined as 3.5‰ in paper I and 5.6‰ in paper III and IV, and F is the isotopic enrichment factor (3.8, Hobson and Welch, 1992; Hobson *et al*., 1995).

4.3 Fatty acid trophic markers and signatures

Fatty acid trophic markers (FATMs), which are fatty acids that are transferred relatively unchanged through the food chain, have been used in several studies in marine ecosystems to follow energy transfer and to study predator-prey relationships (Falk-Petersen *et al*., 1990, 2000, 2002, 2004; Dalsgaard *et al*., 2003). Primary producers and some herbivores biosynthesize most of the fatty acids and can thus be characterized by their specific fatty acid profiles. While organisms at higher trophic levels have limited ability to synthesize and modify fatty acids, and their fatty acid composition may reflect that of their prey. Generally, only plants are able to synthesize the essential polyunsaturated fatty acids (n3 and n6; Sargent and Henderson, 1986), and some of these essential fatty acids are transferred relatively unchanged through trophic levels (Lee *et al*., 1971; Graeve *et al*., 1994; Daalsgard *et al*., 2003). In addition to providing information about potential prey (by comparing fatty acid signatures between prey and predator species), FATMs provide knowledge about the origin of the food web. Diatoms are known to have relatively high amounts of 20:5n3, 16:1n7 and C16 polyunsaturated fatty acids (PUFAs), whereas elevated amounts of 22:6n3 and C18 PUFAs area characteristic for dinoflagellates and *Phaeocystis* (Dalsgaard *et al*., 2003). *Calanus* species are unique as they biosynthesize *de novo* large amounts of C20 and C22, long-chain, high energy, monounsaturated fatty acids fatty acids and alcohols (Table 1; Dalsgaard *et al*., 2003, for review). All these fatty acids are regarded as good trophic markers, i.e. are transferred relatively unmodified into neutral lipids of consumers.

There are several uncertainties involved when using these methods to study trophic interactions among species such as:

- The turnover times of the fatty acids can be species-specific and are often related to the metabolic conditions and reproductive status of the animals (Dalsgaard *et al.*, 2003; Graeve *et al.*, 2005)
- Some essential fatty acids such as 20:5n3 and 22:6n3 may become more elevated at higher trophic levels than at lower levels since they might be selectively retained (Graeve *et al.*, 2005)
- When the diet of the consumer constitutes a mixture of prey with similar fatty acid profiles the interpretation becomes more challenging

However, this method has been proven to be useful in trophic studies and combined with stable isotopes analyses it becomes more powerful. Nevertheless, the results must be interpreted with care and with their limitations in mind.

In the present study FATMs and fatty acid profiles were used to study trophic interactions in the pelagic food webs over the Reykjanes Ridge (Papers I and II) and in the Iceland Sea (Paper III). The multivariate statistical method Redundancy analyses were more further used to compare the fatty acid profiles of the species which commonly contain 30-40 different fatty acids.

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

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

5. Results and discussion

5.1 Trophic interactions and the role of *Calanus* species in the ecosystem

5.1.1 Reykjanes Ridge

Area and main species

The area over the Reykjanes Ridge and in the Irminger Sea, serves as nursery and feeding grounds for the commercially important redfish (*Sebastes mentella*). The stock size of the deep-sea stock is c. 500.000 tons (ICES, 2012). This area is characterized by more or less continuous deep-scattering layers, made by a mixture of organisms such as mesopelagic fish, shrimps, euphausiids, cephalopods and medusae as well as the redfish (Magnusson, 1996; Heger *et al*., 2008; Hoisa *et al*., 2008; Opdal *et al*., 2008; Pierrot-Bults, 2008; Sutton *et al*., 2008). The region is also an important feeding area for several baleen whale species during summer where zooplankton and small fish is important in their diet (Sigurjónsson and Víkingsson, 1998).

The recent interest in conducting a commercial fishery for the unexploited fish community over the Reykjanes Ridge and in the Irminger Sea, was an important motivation to study the trophic interactions of zooplankton and fish in this oceanic area (Papers I and II). Magnusson (1995) studied the food of redfish in the Irminger Sea, while only very limited information is available on the feeding of the non-exploited fish species in the area. Thus, to enable a better management of the ecosystem, more knowledge on species interactions is important. Recent comprehensive studies on the epi- (0-200 m), meso- (200-1000 m) and bathypelagic (1000-4000 m) ecosystems over the northern Mid-Atlantic Ridge (MAR-ECO; Papers I and II) have investigated abundance and distribution patterns of phytoplankton, meso- and macrozooplankton (Gaard *et al*., 2008; Gislason *et al*., 2008; Gudfinnsson *et al*., 2008; Heger *et al*., 2008; Pierrot-Bults, 2008; Hoisa *et al*., 2008) and nekton (Opdal *et al*., 2008; Sutton *et al*., 2008).

Deep-scattering layers were first described in 1948 (Barham, 1948) and have since been observed in various oceans around the world (Tont, 1976; Magnusson, 1996). Opdal *et al.* (2008) observed deep-scattering layers over the entire northern Mid-Atlantic Ridge in June-July 2004, which were usually layered meso- and bathypelagic to 3000 m. Mesopelagic fish were the most important constituent of these layers (Sutton *et al*., 2008). In all, 44 mesopelagic fish species from 23 families were identified by Sutton and Sigurdsson (2008) in the deep-scattering layers, where lanternfish (Myctophidae), pearlsides (Sternoptychidae), barracudinas (Paralepididae), dragonfish (Stofmiidae) and deep-sea smelts (Microstomatidae) were in highest abundance. The dominating lanthernfish, have a circumglobal distribution (Catul *et al.*, 2011). Most mesopelagic species ascend into the epipelagic zone during the night and descent after sunset to their daytime depths (Salvanes and Kristoffersen, 2001; Catul *et al.*, 2011). Species like *Maurolicus muelleri*, *Benthosema glaciale*, *Notoscopelus kroyeri* and *N. bolini* migrate to the surface at dusk and descent at dawn, others like *Scopelogadus beanii*, *Serrivomer beanie* and *M. microlepis* exhibit no diel migration and remain at depth (Opdal *et al.*, 2008). The diely migrating species are thought to perform these migrations to avoid predation and to follow their zooplankton prey, which also conduct diel vertical migrations to feed in the upper layers (Gliwicz, 1986; Kaartvedt *et al.*, 1996). Thus extensive biomass is actively transported between the surface and the deep ocean. Therefore, knowledge of their trophic interactions is essential for a better understanding of the functioning of the pelagic ecosystem.

The most important meso- and macrozooplankton species in the oceanic area over the Reykjanes Ridge and in the Irminger Sea are the copepods *Calanus finmarchicus, Oithona* spp., *Oncaea* spp. and *Pareuchaeta norvegica*, the euphausiids *Thysanoessa longicaudata* and *Meganyctiphanes norvegica,* the chaetognaths *Eukrohnia hamata* and *Sagitta elegans* and the shrimp *Sergestes arcticus* (Bainbridge and Corlett, 1968; Gislason, 2003; Gaard *et al.*, 2008; Letessier *et al.*, 2011, 2012). During winter the main distribution of *C. finmarchicus* is in deeper waters with significant parts of the stock staying deeper than the deep-scattering layers with a limited overlap between *C. finmarchicus* and its potential predators during the overwintering period resulting in very low winter mortality rates (Anderson *et al.*, 2005; Gislason *et al.*, 2007). Even though *C. hyperboreus* is not in high numbers it is known to be an important part of the zooplankton biomass in the Irminger Sea during winter and spring (Gislason, 2003).

Trophic structure

During the present investigation four trophic levels were identified in the pelagic ecosystem over the Reykjanes Ridge in mid-June (Paper I), about one month after the vernal phytoplankton bloom (Petursdottir *et al.*, 2010; Gaard *et al.*, 2008). Of the studied species the

C. finmarchicus occupied the lowest trophic level (TL=2.0) and the mesopelagic redfish the highest (TL=4.2).

The copepods mainly occurred in the upper part of the water column (0-100 m), where food in form of phytoplankton was located in highest abundance. Still, some of the most abundant species in terms of numbers, such as *Microcalanus*, *Pleuromamma*, *Oncea* and partly *Oithona*, were mainly located below the phytoplankton layer and were thus probably feeding on particles other than algae (Gaard *et al.*, 2008).

Maurolicus muelleri were found to prey heavily on *C. finmarchicus* which is indicated by their similar moiety composition (Figure 2) as well as the high amounts of *Calanus* FATMs (Figure 3; Paper I).

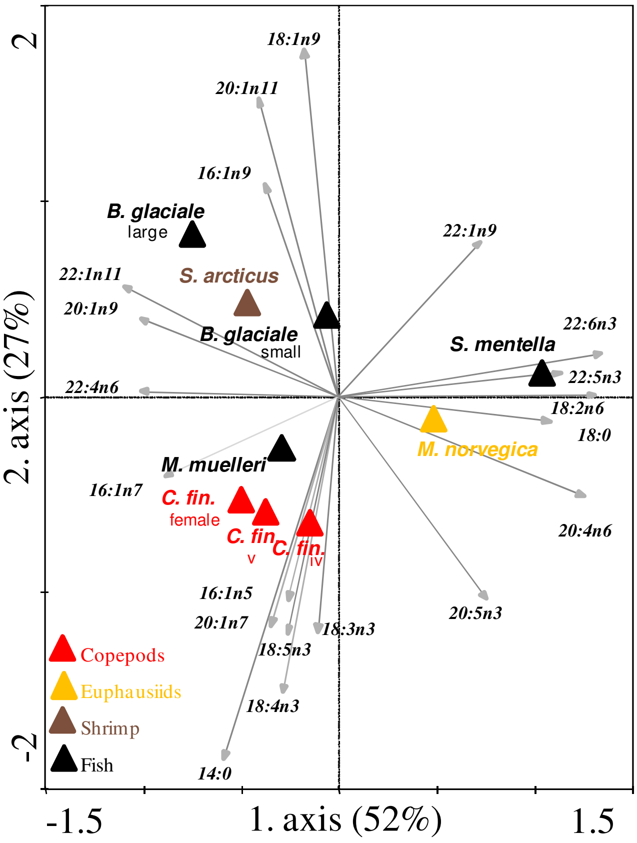


Figure 2. Trophic relationships over the Reykjanes Ridge in June 2004. Redundancy analysis (RDA) plot based on moiety values for all species. Triangles indicate mean values of the respective species. The species were applied as dummy variables (environmental variables) and moieties as response variables. The arrows point in the direction of steepest increase of the respective moiety. The fraction of unconstrained variance accounted for by each axis is given. Modified after Petursdottir *et al.*, 2008 (Paper I).

The whole population of *C. finmarchicus* was restricted to the uppermost layer (Gaard *et al.*, 2008) while *M. muelleri* were sampled at 500 m depth, indicating that *M. muelleri* were migrating to the epipelagic zone in order to feed on *C. finmarchicus* (Paper I). Earlier studies have also found calanoid copepods to be a considerable part of the diet of *M. muelleri* (Mauchline and Gordon, 1983; Gorelova and Krasilnikova, 1990). The *M. muelleri* dominated the 0-200 m depth stratum in the study area, at least during the day (Opdal *et al.*, 2008; Sutton *et al.*, 2008) while the lanternfish *B. glaciale* dominated both in numbers and biomass in deeper epipelagic and mesopelagic zones. Based on acoustic records and abundance of fish from trawl, Opdal *et al.* (2008) suggested that the *M. muelleri* were migrating vertically within the epi- and upper mesopelagic which is in line with our results.

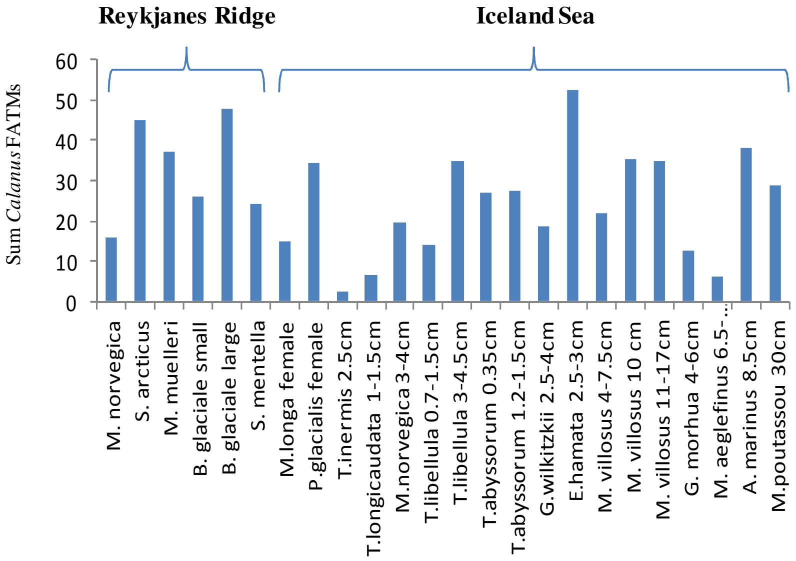


Figure 3. Sum of *Calanus* moieties (relative amounts) of the studied species over the Reykjanes Ridge and in the Iceland Sea (Papers I and III).

Both size groups of *B. glaciale* contained high levels of *Calanus* FATMs indicating the importance of *Calanus* in their diet (Figure 3; Paper I). We suggest that the larger *B. glacialis* is feeding selectively on the larger deeper living *C. hyperboreus* which were mainly distributed at 800-1000 m depth in June (Gaard *et al.*, 2008), as the ratio between their fatty alcohols 22:1n11 and 20:1n9 was around two which is the same value as reported by Scott *et al.* (2002) for *C. hyperboreus* (Table 2). The smaller *B. glaciale*, however, were feeding on *C. finmarchicus* in the surface layers (Paper I) with the ratio between their fatty alcohols 22:1n11 and 20:1n9 around 1 as is reported for *C. finmarchicus* (Scott *et al.*, 2002). The smaller size group of *B. glaciale* was sampled at 500 m depth, in the same depth stratum as *M. muelleri*, while the larger one was sampled at 900 m depth (Paper I). In the Davis Strait, Sameoto (1989) found *B. glaciale* to feed selectively on the older stages of *C. finmarchicus* and *C. hyperboreus*. Similar to *M. muelleri*, the lanternfish *B. glaciale* migrated vertically between the epipelagic and mesopelagic zones (Opdal *et al.*, 2008) as is reflected by the feeding preferences of the smaller *B. glaciale* and *M. muelleri* in this study.

As with the small mesopelagic fish, *Calanus* species were important in the diet of the shrimp *S. arcticus,* as supported by the relatively high amounts of the *Calanus* FATMs (Figure 3; Paper I). Further, the ratio between the fatty alcohols 22:1n11 and 20:1n9 may indicate that *S. arcticus* were also feeding on the deep living *C. hyperboreus* (Table 2; Paper I).

Table 2. The ratio between the fatty alcohols 22:1n11 and 20:1n9 in the species studied that store wax esters as their lipid stores. Reported in mid-June over the Reykjanes Ridge (Paper I) and in late August in the Iceland Sea (Paper III) and values reported by Scott *et al.*, 2002.

	Reykjanes Ridge (Paper I)				Iceland Sea (Paper III)										Scott et al. 2002	
	C. finmarchicus CV	*S. arcticus*	*B. glaciale* small	*B. glaciale* large	*C. finmarchicus* CV	*C. hyperboreus* CIV	*M. longa* female	*P. glacialis* female	*T. inermis* 2.5 cm	*T. libellula* 0.7-1.5 cm	*T. libellula* 3-4.5 cm	*T. abyssorum* 0.35 cm	*G. wilkitzkii* 2.5-4 cm	*E. hamata* 2.5-3 cm	*C. finmarchicus* CV	*C. hyperboreus* CV
FAlc 22:1n11/20:1n9	1.3	2.2	1.5	2.1	1.3	2.7	1.0	1.2	1.5	1.0	1.8	0.6	1.7	1.7	1.0	2.0

Sergestes arcticus had also higher of δ^{13}C levels than the other species in this study with similar trophic position (Figure 2 in Paper I), that may indicate a more benthic input in the diet of *S. arcticus* than of the other species studied (McConnaughey and McRoy, 1979; Tamelander *et al.*, 2006). Benthic organisms have actually been found in the stomach of *S. arcticus* on the slope of Porcupine Seabight, in the northern northeast Atlantic (Hargreaves, 1984; Paper I). The recent study by Letessier *et al.* (2012) from the Charlie-Gibbs fracture zone confirms these findings. As stated above, *S. arcticus* is found in high abundance over the Reykjanes Ridge (Letessier *et al.*, 2012). The species undertakes extensive diel vertical migrations and has been recorded as both a meso- and a bathypelagic species (Omori, 1974; Koukouras *et al.*, 2000).

Unlike for the previously mentioned species, *Calanus* spp. was not important in the diet of the euphausiid *M. norvegica*, indicated by their low amounts of *Calanus* FATMs (Figure 3; Paper I). *Meganyctiphanes norvegica* was found to occupy trophic level 2.9 (Figure 2 in Paper I) with relatively high amount of 18:1n9 indicating a carnivorous feeding mode (Dalsgaard *et al.*, 2003) in June. Euphausiids use filter-feeding to obtain food and are capable of switching from herbivorous to carnivorous feeding depending on food availability (Mauchline and Fisher, 1969). The euphausiid *M. norvegica* is abundant over the Reykjanes Ridge (Einarsson, 1945; Saunders *et al.*, 2007; Letessier *et al.*, 2011, 2012). Over the Reykjanes Ridge, the euphausiids are mainly located in the 0-300 m depth stratum (Letessier *et al.*, 2011) but their presence at greater depth is not uncommon as they are capable of extensive diel vertical migrations (e.g. Kaartvedt *et al.*, 2002).

The redfish occupied the highest trophic level of the studied species (Figure 2 in Paper I). They were sampled at around 800-900 m depth by the present study and were identified as being postspawners of the deep-sea stock (Paper II). The relatively low amount of *Calanus* FATMs distinguished the redfish from the small mesopelagic fish species studied, indicating that *Calanus* species were not as important in the diet of redfish as in the other species (Paper I). The moiety composition of *M. norvegica* resembled the redfish composition (Figure 2), indicating that euphausiids, or organisms with similar moiety and trophic position were important in their diet. Euphausiids have been observed to be one of the main food of redfish over the Reykjanes Ridge as well as chaetognaths and amphipods, while small mesopelagic fish are less important (Magnusson and Magnusson, 1995).

Another factor distinguishing the redfish from the other species studied is their very high levels of the phytoplankton originated FATMs 22:6n3 (Figure 2; Papers I and II). The high values of 22:6n3 and 20:5n3 as well, are in agreement with known values in some long-lived, meso/bentho pelagic species studied in the waters around Iceland and Norway, e.g. the gadoids blue ling (*Molva dyperigia*), four-beard rockling (*Rhinonemus cimbrius*), torsk (*Brosme brosme*), cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*; Sigurgisladottir & Palmadottir, 1993; Lie *et al.*, 1994). Also in the deep Mediterranean waters i.e mora (*Mora moro*; Rossano *et al.*, 2005). Similarly Budge *et al.* (2002) studying fatty acid compositions of 28 species of fish and invertebrates on the Scotian Shelf, Georges Bank and in the Gulf of St. Lawrence found *Sebastes* sp. to group with gadoids, which suggests that they share similar feeding strategies (Budge *et al*., 2002). In our study, the *Calanus* FATMs were found in higher amounts in *S. mentella* than in the long-lived species mentioned above, indicating that *S. mentella* feeds to some degree closer to the base of the food web than the previously mentioned long-lived meso/bentho pelagic species (Paper II). Sarà *et al*. (2009) used stable isotopes (carbon and nitrogen) to identify the main sources of organic matter for the most abundant demersal fish captured by benthic gear southwest of Iceland. Their results support our findings that *Sebastes* sp. occupied a position between the pelagic and benthic realms.

In summary, there are around four trophic levels in the pelagic ecosystem over the Reykjanes Ridge during summer, with deep-living redfish occupying the highest trophic level and the primarily herbivorous copepod *C. finmarchicus* occupying the lowest trophic level. Two main trophic pathways were observed (Figure 4). One *Calanus*-based, including the small oceanic mesopelagic fish species like *M. muelleri* and *B. glacialis* and the shrimp *S. arcticus*. In the other trophic route, *Calanus* species are of less importance and the euphausiid *M. norvegica* is the most important food source for the redfish. The small vertically migrating mesopelagic fish, *M. muelleri* and *B. glaciale* (smaller specimens) feed on *C. finmarchicus*, which is distributed in the surface layers. Thus these fish actively bring energy to the deeper layers. The larger *B. glaciale* and the shrimp *S. arcticus* feed on the larger deeper-living *C. hyperboreus*. In contrast to the true pelagic species studied, the shrimp seems to alternate between pelagic and benthic feeding habits and thus constitutes an important “player” in the biological pump (Figure 4).

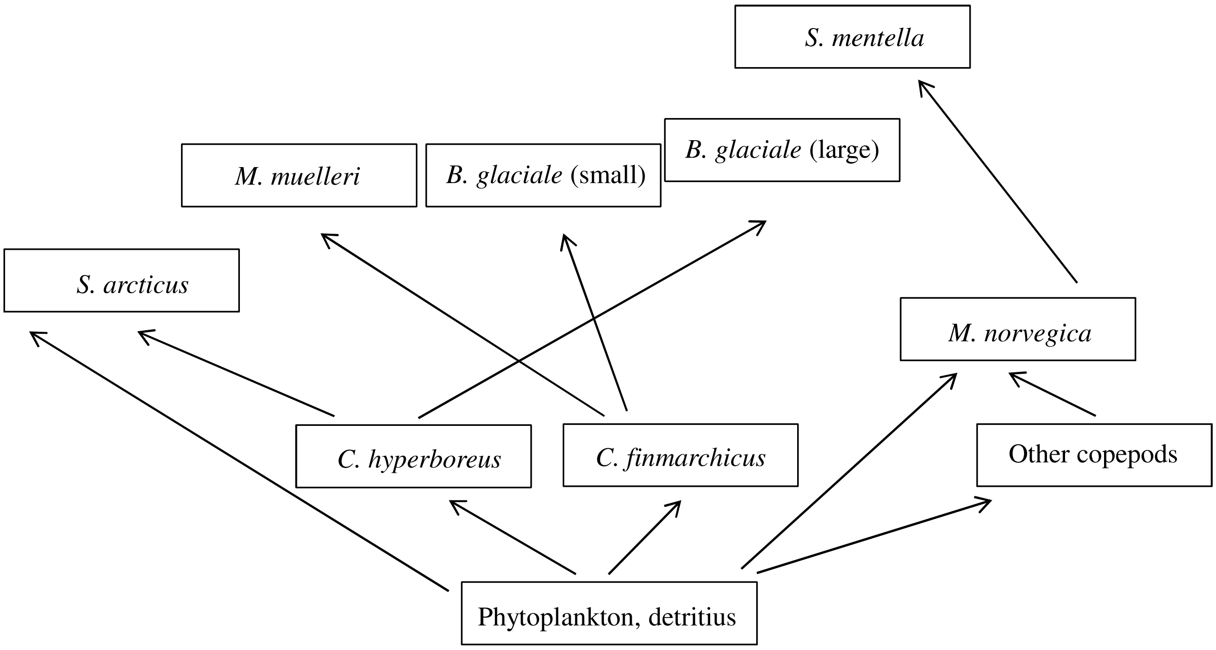


Figure 4. Schematic of the food-web over the Reykjanes Ridge based on Paper I.

5.1.2 Iceland Sea

Area and main species

The shelf area north of Iceland is important as a nursery ground for several of the commercially important fish stocks in Icelandic waters. The pelagic fish fauna in the Iceland Sea was dominated by a few species, and consisted primarily of capelin (*Mallotus villosus*) and high number of larval fish species, i.e. 0-group cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*), and low numbers of blue whiting (*Micromesistius poutassou*) and herring (*Clupea harengus*) in terms of species occurrence (Paper IV). The recent changes in the distribution of capelin in the nursery and feeding area in the Iceland Sea, motivated us to study this region more extensively (Papers III and IV).

The zooplankton fauna was characterized by few species (Paper IV). Of the macrozooplankton, the amphipod *Themisto abyssorum* was by far the most abundant species in the Iceland Sea, followed by the euphausiids *Thysanoessa longicaudata*, the amphipod *T. libellula* and the euphausiids *T. inermis* and *Meganyctiphanes norvegica* (Gislason and Silva, 2012). Copepods dominated the mesozooplankton in the Iceland Sea. *Calanus hyperboreus*, followed by *C. finmarchicus*, *Metridia longa*, *Pseudocalanus* spp., *Oithona* spp. and *Pareuchaeta glacialis* dominated the biomass throughout the year making up c. 95% of the total copepod biomass (Gislason and Silva, 2012; Paper IV). Euphausiids are important in the energy transfer to higher trophic levels. They are for example important in the diet of many fish species, seabirds and seals (Sigurdsson and Astthorsson, 1991; Astthorsson and Gislason, 1997; Falk-Petersen *et al*., 2009; Orlova *et al*., 2010).

In the Iceland Sea, the spring bloom takes place in late May, followed by a post-bloom period in June-July, probably fuelled by regenerated nutrients (Paper IV). Throughout the winter, the main distribution of mesozooplankton is in the deeper, colder layers. In May the population had ascended to the surface layers and resided there until they descended to deeper layers in July-August to overwinter (Gislason and Silva, 2012). The zooplankton abundance peaked in late summer, July-August, and is mainly concentrated in the upper 50-100 meters (Gislason and Silva, 2012; Paper IV). Gislason and Silva (2012) identified three main mesozooplankton communities in the Iceland Sea during late summer, an Atlantic community in the east characterized by high amounts of *C. finmarchicus* and *Pseudocalanus* spp. an Arctic community in north were *C. hyperboreus* and *C. glacialis* were in high numbers and costal community at lower latitudes in the southern part of the Iceland Sea, with *Temora longicornis* and *Acartia* spp. in relatively large numbers.

It should be noted that in the Iceland Sea the main sampling took place in the epipelagic zone while southwest of Iceland, over the Reykjanes Ridge, both the epi- and mesopelagic zones were studied. However, comparable deep-scattering layers were not observed during the Iceland Sea study (Ólafur K. Pálsson, pers. comm.) as seen over the Reykjanes Ridge.

Trophic structure

In late summer, four trophic levels were identified in the pelagic ecosystem of the Iceland Sea (Figure 2 in Paper III). The trophic levels of the zooplankton species ranged from 2.4 for the copepod *M. longa* to 3.1 for the larger copepod *P. glacialis*. The fish juveniles occupied a slightly higher trophic level (c. 3.2) than the zooplankton and adult fish the highest (3.6). This trophic level structure is comparable to the high latitude pelagic ecosystem near Svalbard (Søreide *et al*., 2006; Tamelander *et al*., 2006).

We used stable nitrogen isotope data for the primarily herbivorous copepod *C. hyperboreus* sampled in spring 2007 to represent the baseline for trophic level 2 (Papers III and IV). In late summer, the copepod *C. hyperboreus* had changed its feeding strategy from being primarily herbivorous in May (TL=2.0; Søreide *et al.*, 2008) to more omnivorous feeding (TL=2.4) when phytoplankton was less abundant (Figure 2 in Paper III). *Metridia longa* belongs to the lowest trophic level of the studied copepods in late summer. High levels of phytoplankton FATMs as well as *Calanus* FATMs in *M. longa* indicate feeding on phytoplankton as well as on *Calanus* spp. or *Calanus* FATMs associated with POM or detritus, reflecting its omnivorous feeding strategy. This is in an agreement with the findings of Falk-Petersen *et al.* (1987) in the Barents Sea. In contrast, *P. glacialis* seem to be a pure carnivore, occupying trophic level 3.1 with twice as high levels of *Calanus* FATMs as *M. longa* (Figure 3; Paper III).

The euphausiids in Iceland Sea were omnivorous in late summer, and occupied trophic levels between 2.4 and 2.7 (Figure 2 in Paper III). The omnivorous feeding of *T. longicaudata* and *M. norvegica* in the Iceland Sea is in an agreement with studies from nearby areas (Mauchline and Fisher, 1969; Falk-Petersen 2002; Dalpadado *et al.*, 2008). Our findings of an omnivorous feeding behavior of *T. inermis* contrasts some of the earlier studies in the Arctic, which found *T. inermis* to be a true herbivore (Falk-Petersen *et al.*, 2000; Dalpadado *et al.*, 2008). The stable isotope values of *T. inermis* in Iceland Sea indicate omnivorous feeding behavior in late summer when the phytoplankton biomass is low (Paper III). *Calanus* species are an important part in the diet of *M. norvegica* (high levels of *Calanus* FATMs; Figure 3) while *Calanus* species constitute only a minor part of the diet of the more abundant euphausiids *T. inermis* and *T. longicaudata* which were almost depleted in *Calanus* FATMs (Paper III). For these smaller euphausiids, other smaller zooplankton species are probably more important in the diet.

The amphipods *T. libellula* and *T. abyssorum* are carnivorous, occupying trophic levels between 2.7 and 2.9 (Figure 2 in Paper III). They have well developed maxillipeds that they use to capture their prey. Based on their high amounts of *Calanus* FATMs, *Calanus* species appeared to be their major food source (Figure 3; Paper III). This is in an agreement with earlier studies on lipid biomarkers and stomach content, suggesting that copepods are the major food source for adult *T. libellula* (Auel *et al.*, 2002; Dalsgaard *et al.*, 2003; Dalpadado *et al.*, 2008). The sympagic (ice-associated) amphipod species, *Gammarus wilkitzkii* was only found in the westernmost Arctic region of the Iceland Sea (Gislason and Silva, 2012) and in our study to occupying the lowest trophic level of the amphipods (Figure 2 in Paper III). That suggests grazing on phytoplankton in addition predation on *Calanus*. As in our study, *G. wilkitzkii* has previously been found in open ocean were ice has melted and then mainly feeding on calanoid copepods (Steele and Steele, 1974; Werner *et al.*, 1999; Scott *et al.*, 2001). The fatty acid composition of *G. wilkitzkii* in the present study resembles that of *G. wilkitzkii* in open waters in Kongsfjord in Svalbard (Scott *et al.*, 2001). These amphipods show clear ontogeny shift in the diet from herbi-, omnivorous as juveniles to more carnivorous feedings as adults (Scott *et al.*, 2001; Noyon *et al.*, 2012).

Based on the similar moiety composition of the chaetognath *Eukrohnia hamata* and the *Calanus* species (Figure 5) and their stable isotope composition (Figure 2 in Paper III) we suggested *E. hamata* to be foraging mainly on *Calanus* species in the Iceland Sea (Paper III), which is in agreement to the study by Froneman *et al.* (1998) in the southern ocean (Marion Island) who found *Calanus* species to be important prey. Chaetognaths are active predators, feeding for example on copepods, fish larva and other chaetognaths. They are widely distributed in the Iceland Sea (Gislason and Silva, 2012).

We studied the juveniles of cod, haddock, capelin and sandeel (*Ammodytes marinus*) which were mainly distributed in the shelf areas north and northwest of Iceland (Paper IV). The fatty acid composition of the fish juveniles was different from the other groups as they had relatively higher amounts of the phytoplankton originated FATMs 20:5n3 and 22:6n3 than the other groups (Figure 5; Paper III). This was particularly evident for the gadoids haddock and cod, which also had relatively low amounts of the *Calanus* FATMs compared to the other species (Figure 3) suggesting that *Calanus* species were not as important in the diet of cod and haddock juveniles as they were for capelin and sandeel (Paper III). The juveniles occupied similar trophic level (c. 3.2; Figure 2 in Paper III), pointing to comparable feeding habits, probably feeding on herbivorous zooplankton containing high amounts of 20:5n3 and 22:6n3, such as young herbivorous euphausiids. This is in an agreement with the studies of the food of young fish in Icelandic waters based on stomach content analyses, where young euphausiids and copepods such as *C. finmarchicus* and *Acartia* spp. were found to be the major components of the diet of capelin and cod larvae (Pálsson, 1974) and a study from the Barents Sea were *C. finmarchicus* and the *T. inermis* were the main prey of 0-group cod and haddock (Dalpadado *et al.*, 2009).

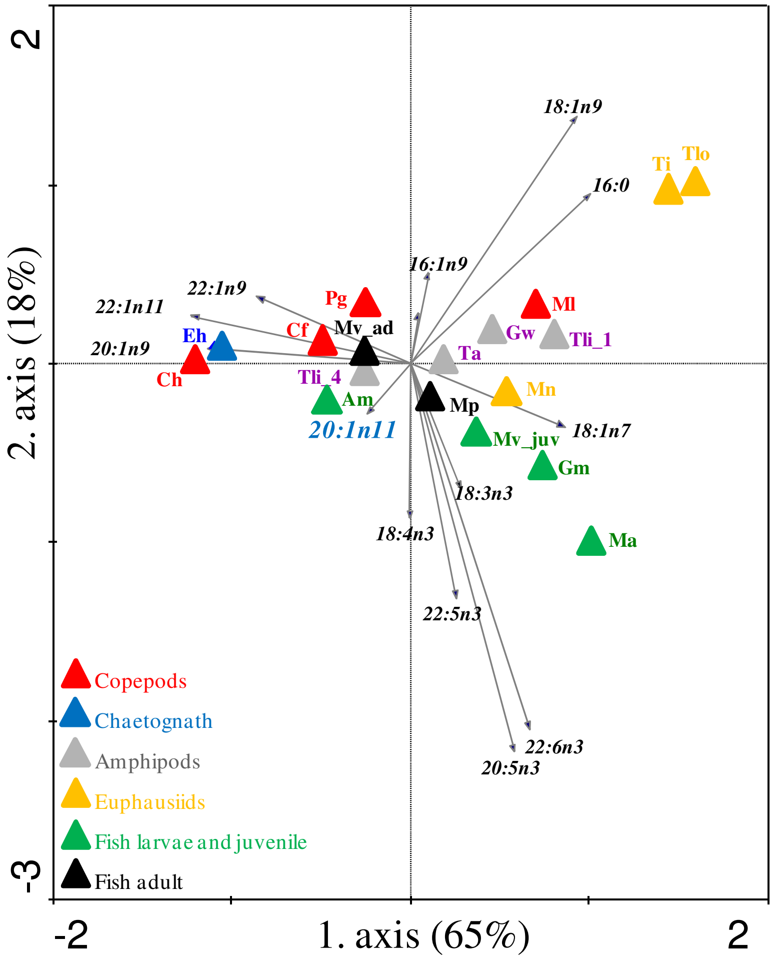


Figure 5. Trophic relationships in the Iceland Sea in August 2007 and 2008. Redundancy analysis (RDA) plot based on moiety values for all species. Triangles indicate mean values of the respective species. The species were applied as dummy variables (environmental variables) and moieties as response variables. The arrows point in the direction of steepest increase of the respective moiety. The fraction of unconstrained variance accounted for by each axis is given. Abbrevations: 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 juvenile, Mv_10: 10 cm, Mv_16: 16 cm, Mv_ad: adult (11-16 cm); Mp: *M. poutassou*; Am: *A. marinus*. Modified after Petursdottir *et al*., 2012 (Paper III).

The importance of *Calanus* species as a food source for capelin increases with increasing size (increasing amount of *Calanus* FATMs; Figure 3; Paper III). This finding is in agreement with earlier stomach content analyses of capelin in the Iceland Sea (Astthorsson and Gislason, 1997). Prey selection by capelin is related to fish size (Astthorsson and Gislason, 1997; Gjøsæter *et al*., 2002; Orlova *et al*., 2009). The adult capelin (2-3 years) and blue whiting occupy the highest trophic level (3.6) of the studied species (Figure 2 in Paper III; Paper IV). *Calanus* species and *Calanus* predators (e.g. euphausiids and amphipods) are their major food source which is supported by their high amounts of *Calanus* FATMs as well as their relatively enriched stable isotope compositions (Figure 2 in Paper III). This is in line with the stomach content analyses from the concurrent sampling in the Iceland Sea (Pálsson *et al*., 2012) as well as diet studies from the Barents Sea and Newfoundland waters (O´Driscoll *et al*., 2001; Orlova *et al*., 2010) where copepods, particularly *Calanus* and larger zooplankton species, were found to be major components of the capelin diet.

Blue whiting was found in low numbers and was mainly distributed in the central and eastern Iceland Sea (Paper IV), where influences from warmer Atlantic water were apparent. Our results indicate that blue whiting and capelin share the same feeding habits, having almost identical stable isotope values and similar lipid moiety composition (Figure 5; Figure 2 in Paper III). Pronounced feeding migrations of blue whiting into the Iceland Sea could therefore result in these two species competing for food. However, they prefer different water temperatures and because of the observed westward displacement of capelin into colder Polar waters as a result of increased temperature in the Iceland Sea in recent years (Paper IV), an overlap in their distribution and competition for food is unlikely.

To conclude, there were around four trophic levels identified in the pelagic ecosystem of the Iceland Sea in late summer with the adult capelin and blue whiting occupying the highest trophic level and the copepod *M. longa* occupying the lowest (Figure 6). The pelagic ecosystem was mainly *Calanus* based, where both the Atlantic *C. finmarchicus* and the larger Arctic *C. hyperboreus* were important as an energy source for animals at higher trophic levels. However, the abundant euphausiids *T. longicaudata* and *T. inermis* were not closely linked to the *Calanus* based food web. Euphausiids and amphipods as well as *Calanus* species were found to be important in transferring energy to higher predators like capelin and blue whiting (Figure 6).

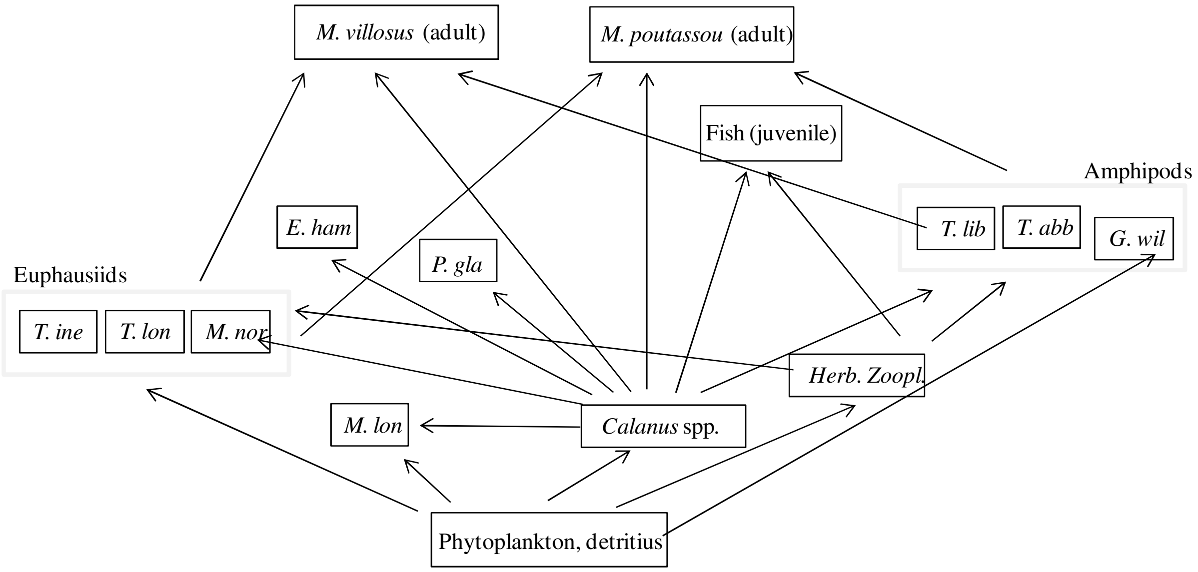


Figure 6. Schematic of the food-web in the Iceland Sea based on Paper III.

5.1.3 Comparison between the oceanic systems south and north of Iceland

As reviewed before, the waters south and north of Iceland differ both oceanographically and biologically (Papers I, II, III, IV and V). The warmer Atlantic waters south and west of Iceland, have higher concentration of nutrients, higher phytoplankton and zooplankton biomass as well as higher diversity of fish than the waters north of Iceland. Different zooplankton and fish communities have been observed in these two areas with higher numbers of Arctic and lipid rich zooplankton species in the north.

Development of Calanus *population during sampling time*

The stable carbon isotopes are more enriched in the Reykjanes Ridge food web than in the Iceland Sea food web, while the reverse is true for stable nitrogen isotopes (Figure 7; Papers I and III). The observed differences in the stable isotopes values in these two ecosystems partly reflect differences in seasonal plankton development (Søreide *et al*., 2008) which at the time of investigation was more advanced in the Iceland Sea. The sampling over the Reykjanes Ridge took place c. 1 month after the spring bloom while in the Iceland Sea it took place more than 2 months after the vernal bloom.

The higher relative amounts of wax esters in *C. finmarchicus* in the Iceland Sea than over the Reykjanes Ridge (Papers I and III) also reflect a slightly later sampling in the season in the former region. *Calanus finmarchicus* accumulates wax esters during the relatively short feeding season to prepare for overwintering at depth (Sargent and Henderson, 1986; Lee *et al*., 2006). Over the Reykjanes Ridge in June the copepodite stage V had c. 36% of total moieties consisting of fatty alcohols indicating around 70% wax ester levels, while copepodite stage V in the Iceland Sea in August were recorded with c. 46% of total moieties as fatty alcohols which means that wax ester levels were around 92%. Thus, as with the different stable isotope baselines, the higher levels of wax ester in *C. finmarchicus* in the Iceland Sea than over the Reykjanes Ridge indicate more advanced seasonal development in the Iceland Sea. These high wax esters values of *C. finmarchicus* in the Iceland Sea suggest that the population is ready for overwintering.

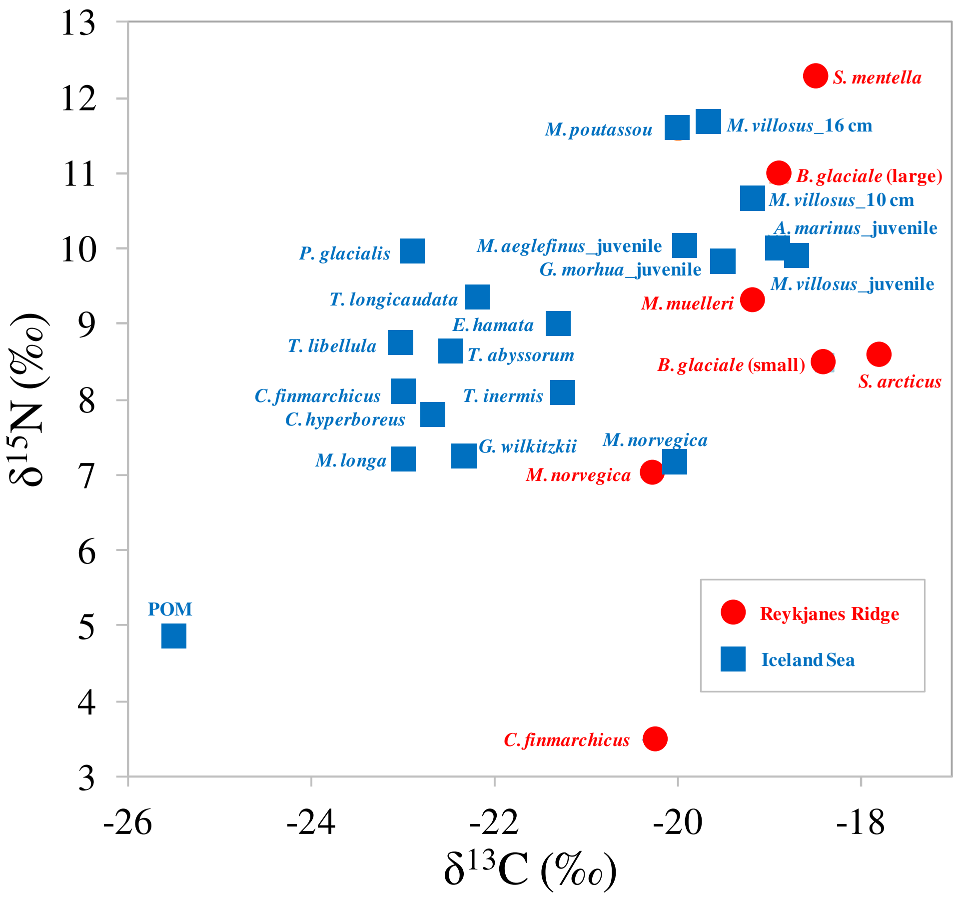


Figure 7. Trophic relationships over the Reykjanes Ridge (June 2004) and in the Iceland Sea (August 2007 and 2008). Stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) of all the species studied.

The importance of Calanus *species in the ecosystem*

The high biomass of *Calanus* species in Icelandic waters (Papers IV and V) makes them a key link between primary producers and higher trophic levels and therefore extremely important in energy transfer through the ecosystem. The importance of the energy rich *Calanus* species as food for higher predators is further supported by the high amounts of the *Calanus* moieties in most of the species that were investigated (Figure 3; Papers I, II and III). These long-chain high energy fatty acids and alcohols (20:1 and 22:1) are only synthesized by *Calanus* species (Sargent and Henderson, 1986) and are therefore easily traced through the ecosystem. In the present study *Calanus* species have been proven to be important in the diet of other mesozooplankton species (Paper III), macrozooplankton (Papers I and III) and epi-, meso- and bathypelagic fish (Papers I, II and III) in the pelagic ecosystem of Icelandic waters during summer.

The *Calanus* species, *C. finmarchicus* and *C. hyperboreus*, can be distinguished in autumn on the basis of their different fatty alcohol ratio of 22:1n11 relative to 20:1n9 in their wax esters (Table 2; Scott *et al.*, 2002), being around 1 for *C. finmarchicus* and around 2 for *C. hyperboreus* in the Arctic. In the Reykjanes Ridge area, in June, two of the mesopelagic species, the shrimp *Sergestes arcticus* and the lanternfish *Benthosema glaciale* (larger specimens), showed indication of large input of *C. hyperboreus* (Table 2; Paper I) and these species were found at similar depth range over the Reykjanes Ridge in June (Gaard *et al.*, 2008; Paper I). In the Iceland Sea in late summer, most of the studied species had alcohol ratios that suggested *C. finmarchicus* to be the most important *Calanus* prey. However, the larger specimens of the amphipods *Themisto libellula*, *T. abyssorum* and *Gammarus wilkitzkii* had ratios suggesting substantial proportion of *C. hyperboreus* in their diet in addition to *C. finmarchicus* (Table 2; Paper III). These findings are in agreement with the main distribution patterns of *C. finmarchicus* and *C. hyperboreus* in the Iceland Sea in August (Gislason and Silva, 2012; Papers III and IV) where *C. hyperboreus* were in highest abundance in the relatively cold waters in the west and northwest part of Iceland Sea. Most of the *C. hyperboreus* population in the Iceland Sea, however, had by August already descended to deeper layers (c. 800-1000 m; Gislason and Silva, 2012), and were therefore out of reach for the pelagic species studied. The seasonal migration to deep water appeared to start one month earlier for *C. hyperboreus* (July) than *C. finmarchicus* (August), the latter being still in the upper layers in this study (Gislason and Silva, 2012). In spite of the importance of *C.*

finmarchicus as prey in the Iceland Sea in August, the larger and more lipid rich *C. hyperboreus* was most likely far more important as food in this pelagic ecosystem earlier in summer when the population had shallower depth distribution. Contrary, the smaller *C. finmarchicus* is more important as a food source over the Reykjanes Ridge. Thus, reflecting the much lower abundance of *C. hyperboreus* in the south. It is relevant here that in general, copepodite stage V of *C. hyperboreus* has approximately 25 times higher energy than the smaller *C. finmarchicus* (Falk-Petersen *et al.*, 2009).

Trophic structure of the two ecosystems

The pelagic ecosystems over the Reykjanes Ridge and in the Iceland Sea have around 4 trophic levels (birds and mammals excluded). The adults of capelin (*Mallotus villosus*) and blue whiting (*Micromesistius poutassou*) in the Iceland Sea occupy trophic level around 3.6 while the deeper-living redfish (*Sebastes mentella*) had slightly higher trophic level (4.2) over the Reykjanes Ridge. The small mesopelagic fish over the Reykjanes Ridge and the juvenile fish in the Iceland Sea, occupy similar trophic positions and copepods and small zooplankton constitute the major part of their diet (Figures 4 and 6). Although *Calanus* is the main driver in both systems there exists a pathway where *Calanus* species are of less importance, and where the main energy is channeled from the primary producers through the euphausiid species, *Thysanoessa inermis* and *T. longicaudata* in the north and through *Meganyctiphanes norvegica* in the south, to species that are located higher in the food web.

In the Iceland Sea, capelin is the main fish species in the pelagic ecosystem, while they are absent over the Reykjanes Ridge. This large fish population feed on the lipid rich zooplankton in the Iceland Sea and transfers the huge amount of energy during the return migrations to adjacent sea areas. Over the Reykjanes Ridge, the mesopelagic lanternfish dominate the deep-scattering layers (Opdal *et al.*, 2008) but in the Iceland Sea comparable scattering layers were not observed during present study (Ólafur K. Pálsson, pers. comm.). Most of the mesopelagic species in these deep-scattering layers exhibit diel vertical migration and feed in the upper layer during the night (like *Maurolicus muelleri* and small *B. glaciale* in this study) and descend at dawn and thus actively bring energy to the deeper layers.

5.2 Long-term changes in zooplankton community composition

As was reviewed in the Introduction, shifts in distribution and abundance of many fish species have been observed and may be a result of increased temperature. This pattern is also evident for zooplankton abundance and community composition in the North Atlantic (Planque and Froementin, 1996; Reid and Beaugrand, 2002; Beaugrand, 2003; Pershing *et al.*, 2004; Hays *et al.*, 2005; Valdes *et al.*, 2007), where obvious shifts of warm water zooplankton species to the north and a retreat of the cold water species to more northerly, colder areas, have been observed (Beaugrand *et al.*, 2002; Beaugrand, 2005). The aim of Paper V was to study the zooplankton communities south and north of Iceland and to cast light on if similar changes in zooplankton abundance and distribution have been taking place in the waters around Iceland. Paper V uses samples from 1990-2007 on two transects representing different hydrographic domains around Iceland, one in the south called Selvogsbanki transect (Atlantic water) and the other in the north, called Siglunes transect (sub-Arctic water).

5.2.1 Zooplankton communities south and north of Iceland

Principal component analysis revealed clear differences in zooplankton composition between the south and north of Iceland mainly determined by hydrographic conditions i.e. higher temperature and salinity south of Iceland (Figure 4A in Paper V). *Calanus finmarchicus* and *Oithona* spp. were dominant in both areas whereas the most important species in distinguishing between the different communities were *Podon leuckarti*, cirripedes, bivalves, polychaetes and *Centropages hamatus* in the warmer southern area (relatively higher amounts in the south compared to the north) and *C. hyperboreus* in the colder northern area (relatively higher amounts in the north compared to the south; Figure 4B in Paper V). These zooplankton community characteristics are in agreement with earlier studies who have found *C. finmarchicus* to be dominant in Icelandic waters, with coastal species being more common in the south and Arctic species in the north (Jespersen, 1940; Gislason and Astthorsson, 2004). The abundance of zooplankton is considerably higher in the south compared to the north (long-term mean; Paper V), which is in line with previous observations from Gislason (2002) who found mean annual biomass of *C. finmarchicus* in the surface layers to be more than two times higher in south than north.

5.2.2 *Inter-annual variations in zooplankton community composition and possible effects of global warming*

In spite of general warming of surface water south of Iceland no unidirectional trends in the zooplankton community composition were observed i.e. the results did not indicate that certain zooplankton communities were being replaced by others as a result of increasing temperature during 1990-2007 (Paper V). These results appear to contrast the findings of Beaugrand *et al.* (2002) for the north Atlantic. However, Beaugrand *et al.* (2002) analysed a longer time series (1960-1997) and observed distinctive change in the zooplankton community in the mid to late 1980s which was before our time series started. As our time series was mainly taken after the recent warming had taken place that may have influenced our finding of no obvious shifts of zooplankton communities during 1990-2007 in the Icelandic waters.

Still, clear inter-annual variations in zooplankton community composition were evident both south and north of Iceland (Paper V) and several environmental variables were tested to estimate their contribution to the inter-annual variability. Salinity and used N, i.e. decline in nitrate from winter to period of sampling (spring), contributed significantly to the observed inter-annual variability in the zooplankton community composition in the south while only temperature was significant to the inter-annual variability in the north (Paper V). The inter-annual variability in zooplankton composition south of Iceland is thus related to freshwater runoff from rivers (low salinity), and relatively high phytoplankton growth i.e. high used N (Gudmundsson, 1998). In years with low salinity and high levels of used N, relatively high numbers of coastal species were detected. The waters in the northern area are characterized by more extensive hydrographic fluctuations reflecting the inflow of Atlantic water from the south which can vary greatly between years (Stefánsson, 1962; Stefánsson and Gudmundsson, 1969; Ólafsson, 1999). The studies by Astthorsson and Gislason (1995, 1998) showed that the zooplankton biomass was almost two times higher in warm years than in cold years. This observation was linked to increased primary production in warm years providing better feeding conditions for the zooplankton, advection of zooplankton into the area from the south and faster temperature-dependent growth of zooplankton. In line with this, Paper V reported the relative abundance of juvenile stages of *C. finmarchicus* and euphausiids as higher in warm years while the abundance of amphipods and *C. hyperboreus* were relatively higher in cold years (Figure 8; Paper V).

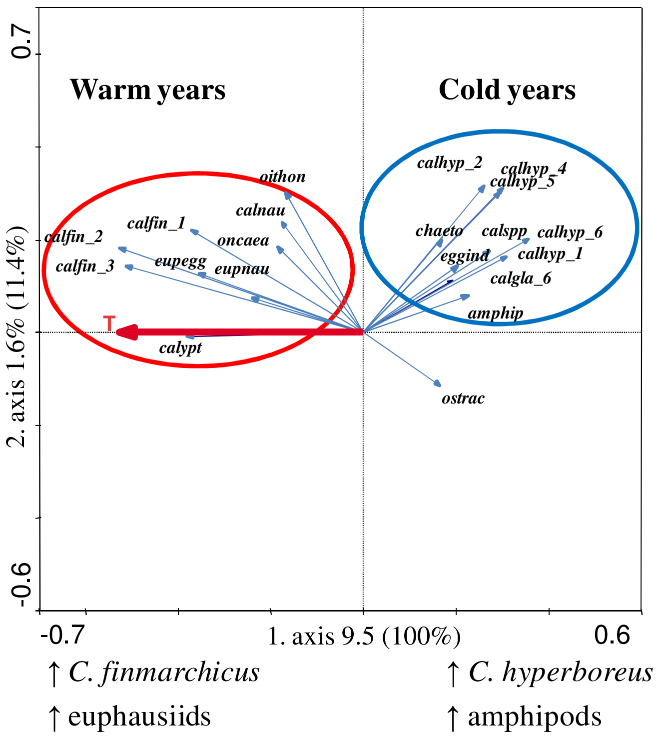


Figure 8. RDA plot of zooplankton species (thin arrows) and environmental variable T: Temperature (the only one which tested significant) for Siglunes transect (north of Iceland). Modified after Gislason *et al*., 2009 (Paper V). For details: See text for figure 6B in Paper V.

Furevik *et al*. (2002) predicts further warming of the Nordic Seas. In light of our results (Figure 8; Paper V), a potential scenario of the effect of global warming in Icelandic waters may be more favorable conditions for *C. finmarchicus* and euphausiids and less favorable conditions for the larger cold water species *C. hyperboreus* and amphipods. These results agree with the investigation by Dalpadado *et al*. (2012) who studied long-term trends in zooplankton groups in the Barents Sea in relation to climatic variability. Reflecting an increase in temperature the biomass of euphausiids has increased and Arctic zooplankton has declined such as *C. hyperboreus*, *C. glacialis* and amphipods (Dalpadado *et al*., 2012). A model study by Slagstad *et al*. (2011) for the Barents Sea also predicts that the Arctic copepods *C. hyperboreus* and *C. glacialis* will decline during warming while the Atlantic *C. finmarchicus* will have more favorable conditions. Dalpadado *et al*. (2012) further predict that Atlantic 0-group fish and cod and the sub-Arctic capelin will benefit from the warming in the Barents Sea (i.e. good feeding conditions). Contrary, the Arctic fish species such as polar cod (*Boreogadus saida*) might be affected negatively. Thus, the different responses by different species to increases in temperature could therefore have a considerable impact on ecosystem structure and food web interactions around Iceland.

5.3 Recent changes in the capelin population and its diet

Observations in the Iceland Sea during 2006, 2007 and 2008 confirmed the earlier observed northward displacement of 0-group and westward displacement of older capelin (*Mallotus villosus*; Figure 9 and 10; Pálsson *et al.*, 2012; Paper IV). Since the late 1990s, marked changes have been observed in the distribution of 0-group, juvenile, and adult capelin in their nursery and feeding areas in the Iceland Sea (Figure 9 and 10; Vilhjalmsson, 2002). This has been followed by a drastic decline in recruitment and stock size (Anon, 2011; Pálsson *et al.*, 2012; Paper IV). These observed changes in the capelin distribution are suggested to be a consequence of a warming in the Iceland Sea (0.5-1°C) in recent years (Vilhjalmsson, 2002; Anon, 2011; Paper IV). Dramatic fluctuations in the capelin population in the Barents Sea have also been reported and linked with changes in climatic conditions, predation, inter- and intraspecific competition for food and fishing pressure in complex interactions (Orlova *et al.*, 2010 and references therein). During the 1980s - 1990s the distribution and migration pattern of the Icelandic capelin seemed relatively stable and predictable (Figure 9; Vilhjalmsson, 1994). The spawning usually took place in March on their main spawning grounds in the warm Atlantic water south and southwest off Iceland. The larvae drifted with the surface currents to their nursery areas, west and north of Iceland, were the immature stock fed. During June to September the oldest and largest capelins took on more extensive feeding migrations to the north, into the Arctic waters of the Iceland Sea, probably to utilize a progressing seasonal food availability to optimize growth conditions, before the return migration to their spawning grounds in winter (Figure 9). As stated previously, capelin is therefore important in transferring energy from the Iceland Sea, where it feeds on the lipid rich zooplankton, to the Icelandic shelf ecosystem where it gathers until spawning south of Iceland (Figure 9, 10; Vilhjálmsson, 1994; Astthorsson and Gislason, 1997; Astthorsson *et al.*, 2007). Comparison of the feeding of capelin on the new and earlier feeding grounds is therefore of interest (Paper III).

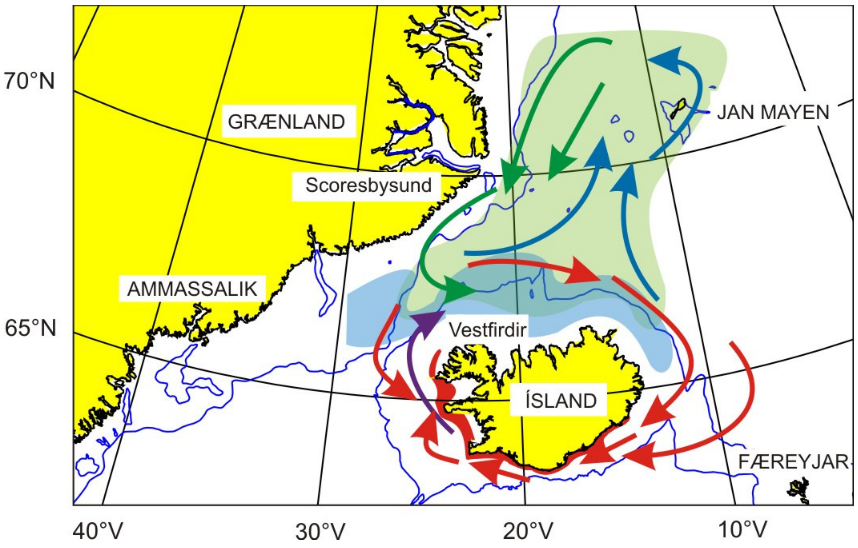


Figure 9. Main patterns in distribution and migration of capelin until the turn of the last century. Light blue: Nursery area. Green: Feeding grounds of adult capelin. Blue arrows indicate feeding migrations and green arrows autumn returning migrations towards Iceland waters. Red: Spawning migrations and areas. Violet arrows: 0-group drift. Figure from Pálsson *et al*., 2012.

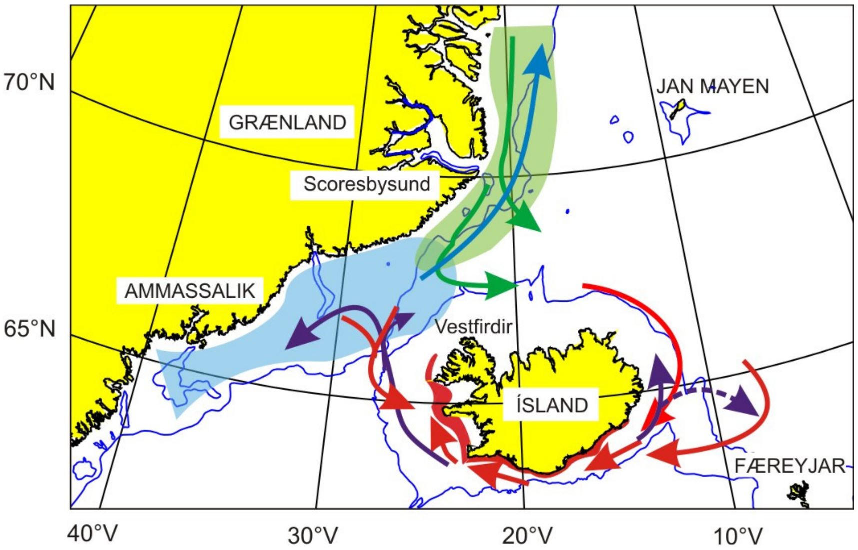


Figure 10. A hypothesis for changed patterns of distribution and migration of capelin in recent years (Pálsson *et al*., 2012). Blue: Nursery area. Green: Feeding grounds of adult capelin. Spring and summer feeding migrations are indicated by blue arrows, but autumn returning migrations by green arrows. Red: Spawning migrations (arrows) and main spawning areas. Violet arrows: 0-group drift. Figure from Pálsson *et al*., 2012.

As stated earlier *Calanus* species, euphausiids and amphipods were important in the diet of adult capelin in late summer 2007 and 2008 in their new distribution area (Paper III). Further, it is noteworthy, that the arctic amphipod, *Themisto libellula* is important food source for adult capelin in the western Iceland Sea (Figure 5). The higher contribution of amphipods in the diet of capelin is in contrast to earlier investigations in their former feeding area where *Calanus* species and euphausiids were the major part of their diet and amphipods were of minor importance (Sigurdsson and Astthorsson, 1991; Astthorsson and Gislason, 1997). We hypothesize that these findings reflect the recent changes in the feeding area of capelin, with the capelin now feeding in the relatively colder waters of the East Greenland Sea and the Denmark Strait (Figure 10; Paper III), where *T. libellula* is probably advected in great amounts with the East-Greenland Current from the Greenland Sea (Gislason and Silva, 2012). The marked changes in food composition in the recent study compared to earlier ones could therefore be a result of the geographic displacement of capelin and thus different prey availability. The greater importance of amphipods in the diet of capelin is also supported by the stomach content analyses carried out concurrently with the sampling for fatty acids and stable isotopes (Pálsson *et al.*, 2012). Lack of proper time series of zooplankton in the Iceland Sea render us unable to evaluate changes in the zooplankton community. We do however suggest amphipods to be high quality food for adult capelin, as suggested by Orlova *et al.* (2010) who found the fat content of capelin to be higher in the north east Barents Sea where proportion of hyperiid amphipods was higher. Thus, we believe that the increased length and growth of 1 year old capelin in recent years (Pálsson *et al.*, 2012) could be linked to the high contributions of hyperiid amphipods in their diet.

The Arctic pelagic amphipod *T. libellula* has a broad distribution and is found in high abundance in the Arctic (Dunbar, 1957; Dalpadado *et al.*, 2001; Dalpadado, 2002), where it is important in transferring energy from the copepods to higher trophic level. *Themisto libellula* exist in relatively high numbers in the Iceland Sea, but are as stated above mainly distributed in the western part where they are probably transported with the East-Greenland current (Gislason and Silva, 2012). *Themisto libellula* is important in the adjacent waters of the Iceland Sea, being key species in the Norwegian Sea ecosystem, where it contributes highly to the zooplankton biomass and are important prey for a number of predators (Skjoldal *et al.*, 2004). It is also of importance as prey for seals, especially ringed seals (*Phoca hispida*) and harp seals (*P. groenlandica*) in Greenland waters (Haug *et al.*, 2004) and in the Barents Sea

(Nilssen *et al.*, 1995; Wathne *et al.*, 2000). The schools of capelin in their new feeding areas (Paper IV), in the western part of the Iceland Sea, could therefore have considerable impact on the *T. libellula* population. Increased competition amongst organisms feeding on *T. libellula* may influence the ecosystem structure and growth for the other species in this area.

Capelin is an important component of the Icelandic ecosystem and crucial in the diet of many demersal fish, seabirds and mammals (e.g. Magnusson and Palsson, 1991; Vilhjalmsson, 1994). It is for example the most important food source for the commercially important cod (*Gadus morhua*; Pálsson and Björnsson, 2011). Further enforcing the importance of capelin in the Icelandic ecosystem is the clear relationship between weight at age of cod and the biomass of capelin i.e. lower capelin biomass is reflected in decreased weight of cod (Vilhjalmsson, 1997; Astthorsson and Vilhjalmsson, 2002; Pálsson and Björnsson, 2011). The prevailing decline in the stock size of capelin and changed distribution could therefore have dramatic consequences also for higher trophic levels in their previous distribution area.

Pálsson *et al.* (2012) hypothesized that the changed drift pattern of 0-group capelin from the southern part of the Iceland Sea into new and possibly less favorable nursery areas in East Greenland continental shelf waters and the reduced capelin recruitment in recent years might be traced to the larval phase of capelin on the Icelandic shelf (spawning area, onset of the spawning, hatching and larval drift). It is difficult to interpret about the declined recruitment due to limited information about the larval phase of capelin on the Icelandic shelf. Still, we suggest that the quality of food in the new distribution area is similar to that in the old feeding area as the life history traits of 1-3 year old capelin i.e. growth, feeding and fat content have been without a trend over the last three decades, except for increased growth of 1 year old capelin as discussed earlier (Pálsson *et al.*, 2012). There is therefore a need for further studies to investigate the larval feeding, growth and survival during first months of their life history of capelin on the Icelandic shelf.

6. Conclusions

The difference in zooplankton community compositions on the shelf south and north of Iceland are mainly influenced by Atlantic and Arctic water masses. The smaller *Calanus finmarchicus* dominated the biomass (Papers IV and V) and was abundant in both areas while higher abundance of the larger, lipid rich copepod *C. hyperboreus* in the north was important in distinguishing between different zooplankton communities in the two areas (Paper V).
Calanus based food web is an important driver for the pelagic ecosystem in Icelandic waters. High levels of *Calanus* markers (20:1n9 and 22:1n11) in most of the species signifies the importance of *Calanus* copepods as an energy pool for higher trophic levels (Papers I, II and III). *Calanus finmarchicus* is of higher trophic importance in the south than north whereas the opposite is true for *C. hyperboreus* (Papers I and III).

Although *Calanus* is the main driver in both areas there exists a trophic pathway were *Calanus* species are of less importance. There the energy is transferred via the euphausiid *Meganyctiphanes norvegica* to the redfish *Sebastes mentella* over the Reykjanes Ridge and through the euphausiids *Thysanoessa inermis* and *T. longicaudata* to higher trophic levels in the Iceland Sea (Papers I and III).

About four trophic levels were observed in the two oceanic ecosystems studied. In both regions, the adult pelagic fish occupied the highest trophic level, capelin (*Mallotus villosus*) and blue whiting (*Micromesistius poutassou*) in the Iceland Sea and redfish over the Reykjanes Ridge. In early summer, herbivorous copepods occupied the lowest trophic levels. In late summer in the Iceland Sea most of the zooplankton species are either omnivorous or strictly carnivorous (Papers I, III and IV).

Above the Reykjanes Ridge vertically migrating mesopelagic fish create a trophic structure that links primary production and the primary grazer *C. finmarchicus* in the upper layer, to predatory mesopelagic fish in the food web in the deep-scattering layers. This vertically migrating behavior contributes to an active energy transport from the upper layers to the deeper ones. The key players in this active transport of energy to deeper layers are the mesopelagic fish, *Maurolicus muelleri* and *Benthosema glaciale* (smaller specimens) which feed on *C. finmarchicus*, which is distributed in the surface layers while the larger *B. glaciale* and the shrimp *Sergestes arcticus* feed on the larger deeper-living *C. hyperboreus*. The shrimp seems to alternate between pelagic and benthic feeding habits. The deep-living redfish occupies a position between the pelagic and benthic realms as well (Papers I and II).

A moderate increase of sea temperature (0.5–1°C) in the Iceland Sea has resulted in a westward displacement of older capelin (2-3 years) and northward displacement of 0-group capelin (Paper IV). This resulted in a diet switch by the older capelin, with increased importance of the Arctic amphipod *Themisto libellula* in the diet and less importance of *Calanus* species (Paper III). That suggests that the capelin is able to utilize the most abundant and available food source. The food quality in the new distribution area is believed to be at least as good as in the earlier distribution area. The greatly reduced recruitment and decreased stock size of capelin in 2005-2009 may be due to unfavorable conditions in their larval phase on the Icelandic shelf. The competition for food in the new distribution region may impact existing groups feeding on *T. libellula*, and predators on capelin in the previous distribution region may be affected. Such a distributional shift could therefore have a considerable impact on ecosystem structure and food web interactions in a larger area.

Predicted warming in the Nordic Seas may affect the zooplankton community composition north of Iceland. The abundance of the Atlantic species *C. finmarchicus* and euphausiids is likely to increase whereas the Arctic species *C. hyperboreus* and amphipods are expected to decrease. Different responses by different species to increases in temperature may influence the community and trophic structure around Iceland. Northern species might retreat as has already been seen with capelin and southern species extend their distribution area toward north.

7. References

Anderson, C.I.H., Brierley, A.S., and Armstrong, F. 2005. Spatio-temporal variability in the distribution of epi- and meso-pelagic acoustic backscatter in the Irminger Sea, North Atlantic, with implications for predation on *Calanus finmarchicus*. Marine Biology, 146: 1177-1188.

Anon, 2011. Nytjasofnar sjávar 2011/2012, aflahorfur fiskveiðiárið 2012/2013 (State of Marine Stocks in Icelandic Waters 2011/2012, Prospect for the Quota Year 2012/2013). Marine Research in Iceland, 163: 186 pp.

Arnason, R. 1993. Ocean fisheries management: recent international developments. Marine Policy, 334-339.

Astthorsson, O.S., and Gislason, A. 1992. Investigations on the ecology of the zooplankton community in Isafjord-deep, northwest Iceland. Sarsia, 77: 225-236.

Astthorsson, O.S., and Gislason, A. 1994. Dýrasvif i hafinu vid Ísland (Zooplankton in Icelandic waters). *In* Íslendingar, hafið og auðlindir þess. (Icelandairs, the sea and its resources), pp 89-106. Ed. by U. Stefánsson. Vísindafélag Íslendinga (Societas scientarium Islandica), Reykjavík (in Icelandic).

Astthorsson, O.S., and Gislason, A. 1995. Long-term changes in zooplankton biomass in Icelandic waters in spring. ICES Journal of Marine Science, 52: 657-668.

Astthorsson, O.S., and Gislason, A. 1997. On the food of capelin in the subarctic waters north of Iceland. Sarsia, 82: 81-86.

Astthorsson, O.S., and Gislason, A. 1998. Environmental conditions, zooplankton and capelin in the waters north of Iceland. ICES Journal of Marine Science, 55: 808-810.

Astthorsson, O.S., Gislason, A., and Gudmundsdottir, A. 1994. Distribution, abundance, and length of pelagic juvenile cod in Icelandic waters in relation to environmental conditions. ICES Marine Science Symposia, 198: 529-541

Astthorsson, O.S., Gislason, A., and Jonsson, S. 2007. Climate variability and the Icelandic marine ecosystem. Deep-Sea Research II, 54: 2456-2477.

Astthorsson, O.S., Hallgrímsson, I., and Jónsson, G.S. 1983. Variations in zooplankton densities in Icelandic waters in spring during the years 1961-1982. Rit Fiskideildar, 7: 73-113 (in Icelandic).

Astthorsson, O.S., and Palsson, J. 2006. New fish records and records of rare southern fish species in Icelandic waters in the warm period 1996-2005. ICES Document CM 2006/C:20. 22 pp.

Astthorsson, O.S., Sigurdsson, Th., and Sveinbjornsson, S. 2010. Mackerel in Icelandic waters. Hafrannsóknir, 152: 25-32 (in Icelandic with English summary).

Astthorsson, O.S., and Vilhjalmsson, H., 2002. Iceland shelf LME: decadal assessment and resource sustainability. In: Sherman, K., Skjoldal, H.R. (Eds.), Large Marine Ecosystems of the North Atlantic. Elsevier, Amsterdam, pp. 219-243.

Auel, H., Harjes, M., da Rocha, R., Stubing, D., and Hagen, W. 2002. Lipid biomarkers indicate different ecological niches and trophic relationships of the Arctic hyperiid amphipods *Themisto abyssorum* and *T. libellula*. Polar Biology, 25: 374-383.

Bainbridge, V., and Corlett, J. 1968. The zooplankton of the NORWESTLANDT surveys. International Commission for the Northwest Atlantic Fisheries (ICNAF) Special Publication, 7: 101-122.

Barham, E.G. 1948. Siphonophores and the deep scattering layer. Science, 140: 826-828.

Beaugrand, G. 2003. Long-term changes in copepod abundance and diversity in the north-east Atlantic in relation to fluctuations in hydroclimatic environment. Fisheries Oceanography, 12: 270-283.

Beaugrand, G. 2005. Monitoring Pelagic ecosystems using plankton indicators. ICES Journal of Marine Science, 62: 333-338.

Beaugrand, G., Reid, P.C., Ibanez, F. *et al*. 2002. Reorganization of North Atlantic marine copepod biodiversisty and climate. Science, 296: 1692-1694.

Bergstad, O.A., Falkenhaug, T., Astthorsson, O.S., Byrkjedal, I., Gebruk, A.V., Piatkowski, U., Priede, I.G., Santos, R.S., Vecchione, M., Lorance, P., and Gordon, J.D.M. 2008. Towards improved understanding of the diversity and abundance patterns of the mid-ocean ridge macro and megafauna. Deep-Sea Research II, 55: 1-5.

Bergstad, O.A., and Godø, O.R. 2003. The pilot project "Patterns and processes of the ecosystems of the northern Mid-Atlantic": aims, strategy and status. Oceanologica Acta 25: 219-226.

Budge, S. M., Iverson, S. J., Bowen, W. D., and Ackman R. G. 2002. Among- and within-species variability in fatty acid signatures of marine fish and invertebrates on the Scotian Shelf, Georges Bank, and southern Gulf of St. Lawrence. Canadian Journal of Fisheries and Aquatic Sciences, 59: 886-898.

Catul, V., Gauns, M., and Karuppasamy, P.K. 2011. A review on mesopelagic fishes belonging to family Myctophidae. Reviews in Fish Biology and Fisheries, 21: 339-354.

Dahl, T.M., Falk-Petersen, S., Gabrielsen, G.W., Sargent, J.R., Hop, H., and Millar, R.-M. 2003. Lipids and stable isotopes in common eider, black-legged kittiwake and northern fulmar: a trophic study from an Arctic fjord. Marine Ecology Progress Series, 256: 257-269.

Dalpadado, P. 2002. Inter-specific variations in distribution, abundance and possible life-cycle patterns of *Themisto* spp. (Amphipoda) in the Barents Sea. Polar Biology, 25: 656-666.

Dalpadado, P., Bogstad, B., Eriksen, E., and Rey, L. 2009. Distribution and diet of 0-group cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) in the Barents Sea in relation to food availability and temperature. Polar Biology, 32: 1583-1596.

Dalpadado, P., Borkner, N., Bogstad, B., and Mehl, S. 2001. Distribution of *Themisto* (Amphipoda) spp. in the Barents Sea and predator-prey interactions. ICES Journal of Marine Science, 58: 876-895.

Dalpadado, P., Ingvaldsen, R.B., Stige, L.C., Bogstad, B., Knutsen, T., Ottersen, G., and Ellertsen, B. 2012. Climate effects on Barents Sea ecosystem dynamics. ICES Journal of Marine Science, 69: 1303-1316.

Dalpadado, P., Yamaguchi, A., Ellertsen, B., and Johannessen, S. 2008. Trophic interactions of macro-zooplankton (krill and amphipods) in the Marginal Ice Zone of the Barents Sea. Deep-Sea Research II, 55: 2266-2274.

Dalsgaard, J., St John, M., Kattner, G., Muller-Navarra, D., and Hagen, W., 2003. Fatty acid trophic markers in the pelagic marine environment. Advances in Marine Biology, 46: 225-340.

DeNiro, M.J., and Epstein, S. 1978. Influence of diet on distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta, 42: 495-506.

DeNiro, M.J., and Epstein, S. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. Geochimica et Cosmochimica Acta, 45: 341-351.

Dunbar, M.J. 1957. The determinants of production in Northern Seas: A study of the biology of *Themisto libellula* (Mandt.). Canadian Journal Research, 35: 797-819.

Einarsson, H. 1945. Euphausiacea I. Northern Atlantic species. Dana report, 27: 1-185. (Doctoral thesis)

Faber, F. 1829. Naturgeschichte der Fische Islands. Druck und Verlag Heinrich Ludwig Brönner. Frankfurt am Main. 204 pp. (in German).

Falk-Petersen, S., Dahl, T.M., Scott, C.L., Sargent, J.R., Gulliksen, B., Kwasniewski, S., Hop, H., and Millar, R.M. 2002. Lipid biomarkers and trophic linkages between ctenophores and copepods in Svalbard waters. Marine Ecology Progress Series, 227: 187-198.

Falk-Petersen, S., Hagen, W., Kattner, G., Clarke, A., and Sargent, J. 2000. Lipids, trophic relationships, and biodiversity in Arctic and Antarctic krill. Canadian Journal of Fisheries and Aquatic Sciences, 57: 178-191.

Falk-Petersen, S., Haug, T., Nilssen, K.T., Wold, A., and Dahl, T.M. 2004. Lipids and trophic linkages in harp seal (*Phoca groenlandica*) from the eastern Barents Sea. Polar Research, 23: 43-50.

Falk-Petersen, S., Haug, T., Hop, H., Nilssen, K.T., and Wold, A. 2009. Transfer of lipids from plankton to blubber of harp and hooded seals off East Greenland. Deep-Sea Research II, 56: 2080-2086.

Falk-Petersen, S., Hopkins, C.C.E., and Sargent, J.R. 1990. Trophic relationships in the pelagic, arctic food web. In: Barnes, M. and Gibson, R.N. (Eds.), Trophic relationships in the marine environment. Aberdeen University Press, Aberdeen, pp. 315-333.

Falk-Petersen, S., Sargent, J.R., and Tande, K. 1987. Food pathways and life strategy in relation to the lipid composition of sub-Arctic zooplankton. Polar Biology, 8: 115-120.

Fisk, A.T., Hobson, K.A., and Norstrom, R.J. 2001. Influence of chemical and biological factors on trophic transfer of persistent organic pollutants in the Northwater Polynya marine food web. Environmental Science and Technology, 35: 732-738.

Friðriksson, Á. 1944. Norðurlandssíldin (The herring of the north coast of Iceland). Rit Fiskideildar (Journal of the Marine Research Institute), 1-339.

Froneman, P.W., Pakhomov, E.A., Perissinotto, R., and Meaton, V. 1998. Feeding and predation impact of two chaetognath species, *Eukrohnia hamata* and *Sagitta gazellae*, in the vicinity of Marion Island (southern ocean). Marine Biology, 131: 95-101.

Fry, B., 1988. Food web structure on Georges Bank from stable C, N, and S isotopic compositions. Limnology and Oceanography, 33: 1182-1190.

Furevik, T., Drange, H., and Sorteberg, A. 2002. Anticipated changes in the Nordic Seas marine climate: Scenarios for 2020, 2050 and 2080. Fisken og Havet 4/2002: 1-13.

Gaard, E., Gislason, A., Falkenhaug, T., Søiland, H., Musaeva, E., Vereshchaka, A., and Vinogradov, G. 2008. Horizontal and vertical copepod distribution and abundance on the Mid-Atlantic Ridge in June 2004. Deep-Sea Research II, 55: 59-71.

Gislason, A. 2002. Ecology of zooplankton in Icelandic waters with special reference to *Calanus finmarchicus*. Dr. Philos Thesis, Faculty of Mathematics and Nature Sciences, Section for Marine Zoology and Marine Chemistry, University of Oslo, Norway. 70 pp.

Gislason, A. 2003. Life-cycle strategies and seasonal migrations of oceanic copepods in the Irminger Sea. Hydrobiologia, 503: 195-209.

Gislason, A., and Astthorsson, O.S. 1995. Seasonal cycle of zooplankton southwest of Iceland. Journal of Plankton Research, 17: 1959-1976.

Gislason, A. and Astthorsson, O.S., 1996. Seasonal development of *Calanus finmarchicus* along and inshore-offshore gradient southwest of Iceland. Ophelia, 44: 71-84.

Gislason, A. and Astthorsson, O.S., 1998. Seasonal variations in biomass, abundance and composition of zooplankton in the subarctic waters north of Iceland. Polar Biology 20: 85-94.

Gislason, A., and Astthorsson, O.S. 2000. Winter distribution, ontogenetic migration and rates of egg production of *Calanus finmarchicus* southwest of Iceland. ICES Journal of Marine Science, 57: 1727-1739.

Gislason, A., and Astthorsson, O.S. 2004. Distribution patterns of zooplankton around Iceland in spring. Sarsia, 20: 85-94.

Gislason, A., Astthorsson, O.S., and Gudfinnsson, H. 1994. Phytoplankton, *Calanus finmarchicus*, and fish eggs southwest of Iceland 1990-1992. ICES Marine Science Symposia, 198: 423-430.

Gislason, A., Eiane, K., and Reynisson, P. 2007. Vertical distribution and mortality of *Calanus finmarchicus* during overwintering in oceanic waters southwest of Iceland. Marine Biology, 150: 1253-1263.

Gislason, A., Gaard, E., Debes, H., and Falkenhaug, T. 2008. Abundance, feeding and reproduction of *Calanus finmarchicus* in the Irminger Sea and on the northern Mid-Atlantic Ridge in June. Deep-Sea Research II, 55: 72-82.

Gislason, A., and Silva, T. 2012. Abundance, composition and development of zooplankton in the Subarctic Iceland Sea in 2006, 2007 and 2008. ICES Journal of Marine Science, 69: 1263-1276.

Gjøsæter, H., Dalpadado, P., and Hassel, A. 2002. Growth of Barents Sea capelin (*Mallotus villosus*) in relation to zooplankton abundance. ICES Journal of Marine Science, 59: 959-967.

Gliwicz, M.Z. 1986. Predation and the evolution of vertical migration in zooplankton. Nature, 320: 746-748.

Gorelova, T.A., and Krasilnikova, N.A. 1990. On the diet of *Maurolicus muelleri* in the vicinity of Seamounts Discovery, Nasca, and Mt. Africana. Journal of Ichthyology, 30: 42-52.

Graeve, M., Hagen, W., and Kattner, G. 1994. Diet-induced changes in the fatty acid composition of Arctic herbivorous copepods: experimental evidence of trophic markers. Journal of Experimental Marine Biology and Ecology, 182: 97-110.

Graeve, M., Albers, C., and Kattner, G. 2005. Assimilation and biosynthesis of lipids in Arctic *Calanus* species based on 13C feeding experiments with a diatom. Journal of Experimental Marine Biology and Ecology, 317: 109-125.

Gudfinnsson, H.G., Debes, H., Falkenhaug, T., Gaard, E., Gislason, A., Petursdottir, H., Sigurdsson, Th., Stupnikova, A., and Valdimarsson, H. 2008. Abundance and productivity of the pelagic ecosystem along a transect across the northern Mid Atlantic Ridge in June 2003. ICES CM 2008/C:13.

Gudmundsson, K. 1998. Long-term variations in phytoplankton productivity during spring in Icelandic waters. ICES Journal of Marine Science, 55: 635-643.

Gudmundsson, K., Heath, M.R., and Clark, E.D. 2009. Average seasonal changes in chlorophyll a in Icelandic waters. ICES Journal of Marine Science, 66: 2133-2140.

Hallgrimsson, I. 1954. Noen bemerkinger om Faxaflois hydrografi og zooplankton bestand I 1948 (Aspects of the hydrography and zooplankton of Faxafloi Bay during 1948). M.Sc. Dissertation, University of Oslo, Norway, 87 pp. (in Norwegian).

Hansen, B., and Østerhus, S. 2000. North Atlantic – Nordic Seas exchanges. Progress in Oceanography, 45: 109-208.

Hargreaves, P.M. 1984. The distribution of decapoda (Crustacea) in the open ocean and near-bottom over an adjacent slope in the northern northeast Atlantic ocean during autumn 1979. Journal of the Marine Biological Association of the United Kingdom, 64: 829-857.

Haug, T., Nilssen, K.T. and Lindblom, L. 2004. Feeding habits of harp and hooded seals in drift ice waters along the east coast of Greenland in summer and winter. Polar Research, 23: 35-42.

Hays, G.C., Richardson, A.J., and Robinson, C. 2005. Trends in Ecology & Evolution, 20: 337-344.

Heger, A., Ieno, E.N., King, N.J., Morris, K.J., Bagley, P.M., and Priede, I.G. 2008. Deep-sea pelagic bioluminescence over the Mid-Atlantic Ridge. Deep-Sea Research II, 55: 126-136.

Hobson, K.A., and Welch, H.E. 1992. Determination of trophic relationships within a high arctic marine food web using $\delta^{13}C$ and $\delta\ ^{15}N$ analysis. Marine Ecology Progress Series, 84: 9-18.

Hobson, K.A., Ambrose, Jr. W.G., and Renaud, P.E. 1995. Sources of primary production, benthic-pelagic coupling, and trophic relationships within the Northeast Water Polynya: Insights from $\delta^{13}C$ and $\delta\ ^{15}N$ analysis. Marine Ecology Progress Series, 128: 1-10.

Hosia, A., Stemmann, L., and Youngbluth, M. 2008. Distribution of net-collected planktonic cnidarians along northern Mid-Atlantic Ridge and their associations with the main water masses. Deep-Sea Research II, 55: 106-118.

ICES, 2012. Report of the North-Western Working Group. Advisory Committee on Fisheries Management. Available at: http://www.ices.dk/workinggroups/ViewWorkingGroup.aspx?ID=30

Jespersen, P. 1940. Investigations on the quantity and distribution of zooplankton in Icelandic waters. Medr Kommn Havunders (Ser. Plankton), 3: 1-77.

Jonsson, S., and Valdimarsson, H. 2004. A new path for the Demark Strait overflow water from the Iceland Sea to Denmark Strait. Geophysical Research Letters, 31: Lo3305.

Kaartvedt, S., Larsen, T., Hjelmseth, K., and Onsrud, M.S.R. 2002. Is the omnivorous krill *Meganyctiphanes norvegica* primarily a selectively feeding carnivore? Marine Ecology Progress Series, 228: 193-204.

Kaartvedt, S., Melle, W., Knutsen, T., and Skjoldal, H.R. 1996. Vertical distribution of fish and krill beneath water of varying optical properties. Marine Ecology Progress Series, 136: 51-58.

Kharlamenko, V.I., Kiyashko, S.I., Imbs, A.B., and Vyshkvartzev, D.I. 2001. Identification of food sources of invertebrates from the seagrass *Zostera marina* community using carbon and sulphur stable isotope ratio and fatty acid analyses. Marine Ecology Progress Series, 220: 103-117.

Koukouras, A., Doulgeraki, S., and Kitsos, M.S. 2000. Notes on the vertical distribution of pelagic shrimps (Decapoda, Natantia) in the Aegean Sea. Crustaceana, 73: 979-993.

Lee, R.F., Hagen, W., and Kattner, G., 2006. Lipid storage in marine zooplankton. Marine Ecology Progress Series, 307: 273-306.

Lee, R.F., Nevenzel, J.C. and Paffenhöfer, G.A. 1971. Importance of wax esters and other lipids in marine food chain: phytoplankton and copepods. Marine Biology, 9: 99-108.

Letessier, T.B., Falkenhaug, T., Debes, H., Bergstad, O.A., and Brierley, A.S. 2011. Abundance patterns and species assemblages of euphausiids associated with the Mid-Atlantic Ridge, North Atlantic. Journal of Plankton Research: 0: 1-16.

Letessier, T.B., Pond, D.W., McGill, R.A.R., Reid, W.D.K., and Brierley, A.S. 2012. Trophic interaction of invertebrate zooplankton on either side of the Charlie Gibbs Fracture Zone/Subpolar Front of the Mid-Atlantic Ridge. Journal of Marine Systems, 94: 174-184.

Lie, Ø., Lied, E., Maage, A., Njaa, L. R., and Sanders, K. 1994. Nutrient content in fish and shellfish. Fiskeridirektoratets Skrifter, Serie Ernæring, 6: 83-105.

Lindemann, R.L. 1942. The Trophic-Dynamic Aspect of Ecology. Ecology, 23: 399-417.

Magnusson, J. 1996. The deep scattering layers in the Irminger Sea. Journal of Fish Biology, 49: 182-191.

Magnusson, J., and Magnusson, J. V. 1995. Oceanic redfish (*Sebastes mentella*) in the Irminger Sea and adjacent waters. Scientia Marina, 59: 241-254.

Magnusson, K., and Palsson, O.K. 1991. Predator-prey interactions of cod and capelin in Icelandic waters. ICES Marine Science Symposia, 193: 153-170.

Malmberg, S. A., and Valdimarsson, H. 2003. Hydrographic conditions in Icelandic waters, 1990-2000. In: Turrell, S., Lavin, A., Drinkwater, K.F., St. John, M., Watson, J. (Eds.). Hydrographical Variability in the ICES Area, 1990-1999. ICES Marine Science Symposia, 219: 50-60.

Mauchline, J., and Fisher, L.R. 1969. The biology of euphausiids. Advances in Marine Biology, 7: 1-421.

Mauchline, J., and Gordon, J.D.M. 1983. Diets of clupeoid, stomiatoid and salmonoid fish of the Rockall Trough, northeastern Atlantic Ocean. Marine Biology, 77: 67-78.

McConnaughey, T., and McRoy, C.P. 1979. Food-web structure and the fractionation of carbon isotopes in the Bering Sea. Marine Biology, 53: 257-262.

Minagawa, M., and Wada, E. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between δ^{15}N and animal age. Geochimica et Cosmochimica Acta, 48: 1135-1140.

Nilssen, K.T., Haug, T., Potelov, V., and Timoshenko, Y.K. 1995. Feeding habits of harp seals (*Phoca groenlandica*) during early summer and autumn in the northern Barents Sea. Polar Biology, 15: 485-493.

Noyon, M., Narcy, F., Gasparini, S., and Mayzaud, P. 2012. Ontogenic variations in fatty acid and alcohol composition of the pelagic amphipod *Themisto libellula* in Kongsfjorden (Svalbard). Marine Biology, 159: 805-816.

O´Driscoll, R.L., Parsons, M.J.D., and Rose G.A., 2001. Feeding of capelin (*Mallotus villosus*) in Newfoundland waters. Sarsia, 86: 165-176

Omori, M. 1974. The biology of pelagic shrimps in the ocean. Advances in Marine Biology, 12: 233-324.

Opdal., A.F., Godø, O.R., Bergstad, O.A., and Fiksen, Ø. 2008. Distribution, identity, and possible processes sustaining meso- and bathypelagic scattering layers on the northern Mid-Atlantic Ridge. Deep-Sea Research II, 55: 45-58.

Orlova, E.L., Dolgov, A.V., Rudneva, G.B., Oganin, I.A., and Konstantinova, L.L. 2009. Trophic relations of capelin *Mallotus villous* and polar cod *Boreogadus saida* in the Barents Sea as a factor of impact on the ecosystem. Deep-Sea Research II, 56: 2054-2067.

Orlova, E.L., Rudneva, G.B., Renaud, P.E., Einae, K., Savinov, V., and Yurko, A.S. 2010. Climate impacts on feeding and condition of capelin *Mallotus villosus* in the Barents Sea: evidence and mechanisms from a 30 year data set. Aquatic Biology, 10: 105-118.

Ólafsdóttir, S. R. 2006. Styrkur næringarefna í hafinu umhverfis Ísland (Nutrient concentration in Icelandic waters). Hafrannsoknstofnunin Fjolrit, 122. 24 pp. (in Icelandic with English summary).

Ólafsdóttir, S. R. 2012. Svæðatengdur styrkur og nýting næringarefna í Íslandshafi / Regional distribution and uptake of nutrients in the Iceland Sea. Marine Research in Iceland, 164: 30-44. (in Icelandic with English summary).

Ólafsson, J. 1999. Connection between oceanic conditions off N-Iceland, Lake Mývatn temperature, regional wind direction variability and the North Atlantic Oscillation. Rit Fiskideildar, 16: 41-57.

Ólafsson, J., and Ólafsdóttir, S.R. 2003. Tímaraðir í mælingum á ólífrænu kolefni í sjó. Fjölrit Hafrannsóknastofnunarinnar, 96.

Ólafsson, J., Ólafsdóttir, S.R., and Briem, J. 2008. Vatnsföll og vistkerfi strandsjávar. Náttúrufræðingurinn, 76: 95-108.

Óskarsson, G.J., Sveinbjörnsson, S., Gudmundsdottir, A., and Sigurdsson, Th. 2012. Ecological impacts on recent extension of feeding migrations of NE-Atlantic mackerel into the ecosystem around Iceland. ICES CM 2012/M:03, 25pp.

Palsson, J. 2007. Sjaldgæfir fiskar á Íslandsmiðum 2006 (Rare fishes in Icelandic waters 2006). Ægir, 100: 12-14 (in Icelandic).

Palsson, J. 2008. Sjaldgæfir fiskar á Íslandsmiðum 2007 (Rare fishes in Icelandic waters 2007). Ægir, 101: 104-107 (in Icelandic).

Palsson, J. 2009. Sjaldgæfir fiskar á Íslandsmiðum 2008 (Rare fishes in Icelandic waters 2008). Ægir, 102: 22-23 (in Icelandic).

Palsson, J. 2010. Sjaldgæfir fiskar á Íslandsmiðum 2019 (Rare fishes in Icelandic waters 2009). Ægir, 103: 12-13 (in Icelandic).

Pálsson, Ó.K. 1974. Investigation on the food of young fish (0-group) in Icelandic waters. (In Icelandic, English summary). Náttúrufræðingurinn, 44: 1-21.

Pálsson, Ó.K. 1983. The feeding habit of demersal fish species in Icelandic waters. Rit Fiskideildar, 7(1). 60 pp.

Pálsson, Ó.K. and Björnsson, H. 2011. Long-term changes in trophic patterns of Iceland cod and linkages to main prey stock sizes. ICES Journal of Marine Science, 68: 1488-1499.

Pálsson, Ó.K., Sveinbjörnsson, S., Valdimarsson, H., Gislason, A., and Vilhjálmsson, H. 2012. Lífshættir loðnu í Íslandshafi / Capelin life-history traits in the Iceland Sea. Marine Research in Iceland, 164: 119-132.

Perkins, H., Hopkins, T., Malmberg, S.A., Poulain, P.-M., and Warn-Varnas, A. 1998. Oceanographic conditions east of Iceland. Journal of Geophysical Research, 103 (C10): 21531-21542.

Pershing, A.J., Greene, C.H., Planque, B. *et al.* 2004. The influences of climate variability on North Atlantic zooplankton populations. In Stenseth, N.C., Ottersen, G., Hurrel, J.W. *et al.* (eds). Marine Ecosystem and Climate Variation, The North Atlantic, A Comparative Perspective. Oxford University Press, USA. pp. 59-69.

Peterson, B.J. 1999. Stable isotopes as tracers of organic matter input and transfer in benthic food webs: A review. Acta Oecologica, 20: 479-487.

Peterson, B.J., and Fry, B. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics, 18: 293-230.

Petursdottir, H., Falk-Petersen, S., Hop, H., and Gislason, A. 2010. *Calanus finmarchicus* along the northern Mid-Atlantic Ridge: variation in fatty acid and alcohol profiles and stable isotope values, δ^{15}N and δ^{13}C.

Pierrot-Bults, A.C. 2008. A short note on the biogeographic patterns of the Chaetognatha fauna in the North Atlantic. Deep-Sea Research II, 55: 137-141.

Planque, B., and Fromentin, M. 1996. *Calanus* and environment in the eastern North Atlantic. Spatial and temporal patterns of *C. finmarchicus* and *C. helgolandicus*. Marine Ecology Progress Series, 134: 101-109.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. Ecology, 83: 703-718

Rau, G.H., Ainley, D.G., Bengtson, J.L., Torres, J.J., and Hopkins, T.L. 1992. $^{15}N/^{14}N$ and $^{13}C/^{12}C$ in Weddell Sea birds, seals, and fish: implications for diet and trophic structure. Marine Ecology Progress Series, 84: 1-8.

Reid, P.C., and Beaugrand, G. 2002. Interregional biological responses in the North Atlantic to hydrometerological forcing. In Sherman, K. and Skjoldal, H.R. (eds), Large Marine Ecosystems of the North Atlantic. Changing Stages and Sustainability. Elsevier Science, Amsterdam, pp. 27-48.

Rossano, R., Caggiano, M. A., Mastrangelo, L., Lauro, R. Di., Ungaro, N., Ettorre, M., and Riccio, P. 2005. Proteins, fatty acids and nutritional value in the muscle of the fish species *Mora moro* (Risso, 1810). Molecular Nutrition & Food Research, 49: 926-931.

Salvanes, A.G., and Kristoffersen, J.B. 2001. Mesopelagic fishes. In: Steele, J. (Ed). Encyclopedia of ocean science, 3rd edn. Academic Press, London, pp. 1711-1717.

Sameoto, D. 1989. Feeding ecology of the lantern fish *Benthosema glaciale* in a subarctic region. Polar Biology, 9: 169-178.

Sarà, G., De Pirro, M., Sprovieri, M., Rumolo, P., Halldórsson, H.P., and Svavarsson, J. 2009. Carbon and nitrogen stable isotopic incentory of the most abundant demersal fish captured by benthic gears in southwestern Iceland (North Atlantic). Helgoland Marine Research, 63: 309-315.

Sargent, J.R., Henderson, R.J., 1986. Lipids: In: Corner, E.D.S., O´Hara, S.C.M. (Eds.), The Biological Chemistry of Marine Copepods. Clarendon Press, Oxford, pp. 59-108.

Saunders, R.A., Ingvarsdottir, A., Rasmussen, J., *et al.* 2007. Regional variation in distribution pattern, population structure and growth rates of *Meganyctiphanes norvegica* and *Thysanoessa longicaudata* in the Irminger Sea, North Atlantic. Progress in Oceanography, 72: 313-342.

Scott, C.L., Falk-Petersen, S., Gulliksen, B., Lønne, O.J., and Sargent, R. 2001. Lipid indicators of the diet of sympagic amphipod *Gammarus wilkitzkii* in the Marginal Ice Zone and in open waters of Svalbard (Arctic). Polar Biology, 24: 572-576.

Scott, C.L., Kwasniewski, S., Falk-Petersen, S., and Sargent, J.R. 2002. Species differences, origins and functions of fatty alcohols and fatty acids in the wax esters and phospholipids of *Calanus hyperboreus*, *C. glacialis* and *C. finmarchicus* from Arctic waters. Marine Ecology Progress Series, 235: 127-134.

Sigurdsson, Th., and Astthorsson, O.S. 1991. Aspect of the feeding of capelin (*Mallotus villosus*) during autumn and early winter in the waters north of Iceland. ICES C.M. 1991/H 49. 16 pp.

Sigurgisladottir, S., and Palmadottir, H. 1993. Fatty acid composition of thirty-five Icelandic fish species. Journal of the American Oil Chemist Society, 70: 1081-1087.

Sigurjónsson, J., and Víkingsson, G. 1998. Seasonal abundance of and estimated food composition by cetaceans in Icelandic and adjacent waters. Journal of Northwest Atlantic Fishery Science, 22: 271-287.

Skjoldal, H.R., Dalpadado, P., and Dommasnes, A. 2004. Food webs and trophic interactions. In: Skjoldal, H.R. (ed). The Norwegian Sea ecosystem. Tapir Academic Press, Trondheim, pp 447-506.

Slagstad, D., Ellingsen, I.H., and Wassmann, P. 2011. Evaluating primary and secondary production in an Arctic Ocean void of summer ice: an experimental simulation approach. Progress in Oceanography, 90: 117-131.

Solmundsson, J., Jonsson, E., and Bjornsson, H. 2010. Monkfish at Iceland: environmental effects on the stock and connections to other areas. Marine Research in Iceland, 152: 33-38 (in Icelandic with English summary).

Steele, D.H., and Steele, V.J. 1974. The biology of *Gammarus* (Crustacea, Amphipoda) in the north-western Atlantic. VIII. Geographic distribution of the northern species. Canadian Journal of Zoology, 52: 1115-1120.

Stefansdottir, L., Solmundsson, J., Marteinsdottir, G., Kristinsson, K., and Jonasson, J.P. 2010. Groundfish species diversity and assemblage structure in Icelandic waters during recent years of warming. Fisheries and Oceanography, 19:1, 42-62.

Stefánsson, U. 1962. North Icelandic waters. Rit Fiskideildar, 3: 1-269.

Stefánsson, U., and Gudmundsson, G. 1969. Hydrographic conditions off the northeast coast of Iceland in relation to meteorological factors. Tellus, 21: 245-258.

Stefánsson, U., and Ólafsson, J. 1991. Nutrients and fertility of Icelandic waters. Rit Fiskideildar, 12: 1-56.

Sutton, T.T., Porteiro, F.M., Heino, M., Byrkjedal, I., Langhelle, G., Anderson, C.I.H., Horne, J., Søiland, H., Falkenhaug, T., Godø, O.R., and Bergstad, O.A. 2008. Vertical structure, biomass and topographic association of deep-pelagic fishes in relation to a mid-ocean ridge system. Deep-Sea Research II, 55: 161-184.

Sutton, T., and Sigurdsson, Th. 2008. Vertical and horizontal distribution of mesopelagic fishes along a transect across the northern Mid-Atlantic Ridge. ICES CM/2008/C:16. 12 pp.

Søiland, H., Budgell, W.P., and Knutsen, Ø. 2008. The physical oceanographic conditions along the Mid-Atlantic Ridge north of the Azores in June-July 2004. Deep-Sea Research II, 55: 29-44.

Søreide, J.E., Falk-Petersen, S., Hegseth, E.N., Hop, H., Carroll, M.L., Hobson, K.A., and Blachowiak-Samolyk, K. 2008. Seasonal feeding strategies of *Calanus* in the high-Arctic Svalbard region. Deep-Sea Research II, 55: 2225-2244.

Søreide, J.E., Hop, H., Carroll, M.L., Falk-Petersen, S., and Hegseth, E.N. 2006. Seasonal food web structures and sympagic-pelagic coupling in the European Arctic revealed by stable isotopes and a two-source food web model. Progress in Oceanography, 71: 59-87.

Sæmundsson, B. 1926. Fiskarnir (The Fishes of Iceland). Bókaverslun Sigfúsar Eymundssonar, Reykjavík. 583 pp. (in Icelandic).

Tamelander, T., Renaud, P.E., Hop, H., Carroll, M.L., Ambrose, Jr. W.G., and Hobson, K.A. 2006. Trophic relationships and pelagic-benthic coupling during summer in the Barents Sea Marginal Ice Zone, revealed by stable carbon and nitrogen isotope measurements. Marine Ecology Progress Series, 310: 33-46.

Thordardottir, Th. 1976. The spring primary production in Icelandic waters 1970-1975. ICES CM 1976/L: 31, 37 pp.

Thordardottir, Th. 1994. Plöntusvif og frumframleiðni í sjónum við Ísland. (Phytoplankton and primary production in Icelandic waters. In Icelandic). *In* Íslendingar, hafið og auðlindir þess. (Icelandairs, the sea and its resources), pp 65-88. Ed. by U. Stefánsson. Vísindafélag Íslendinga (Societas scientarium Islandica), Reykjavík (in Icelandic).

Thordardottir, Th., and Gudmundsson, K. 1998. Plöntusvif. (Phytoplankton. In Icelandic). Námsgagnastofnun og Hafrannsóknastofnunin, Reykjavík. 12 pp.

Tont, S.A. 1976. Deep scattering layers: patterns in the pacific. California Cooperative Oceanic Fisheries Investigations, Reports, 18: 112-117.

Valdes, L., López-Urrutia, A., and Cabal, J. *et al.* 2007. A decade of sampling in the Bay of Biscay: what are the zooplankton time series telling us? Progress in Oceanography, 74: 98-114.

Valdimarsson, H., Astthorsson, O.S., and Palsson, J. 2012. Hydrographic variability in Icelandic waters during recent decades and related changes in distribution of some fish species. ICES Journal of Marine Science, 69: 816-825.

Valdimarsson, H., Bjornsson, H., and Gudmundsson, K. 2005. Climatic variability in Icelandic waters and effects on marine biota. Hafrannsoknastofnunin Fjolrit, 116: 23-28 (in Icelandic with English summary).

Valdimarsson, H., and Malmberg, S.A. 1999. Near-surface circulation in Icelandic waters derived from satellite tracked drifters. Rit Fiskideildar, 16: 23-39.

van Dongen, B.E., Schouten, S., and Sinninghe Damsté, J.S. 2002. Carbon isotope variability in monosaccharides and lipids of aquatic algae and terrestrial plants. Marine Ecology Progress Series, 232: 83-92.

Vilhjalmsson, H. 1994. The Icelandic capelin stock. Capelin (*Mallotus villosus*) in the Iceland-East Greenland-Jan Mayen ecosystem. Rit Fiskideildar, 13. 281 pp.

Vilhjalmsson, H. 1997. Interaction between capelin (*Mallotus villosus*) and other species and the significance of such interactions for the management and harvesting of marine ecosystems in the northern North Atlantic. Rit Fiskideildar, 15: 33-60.

Vilhjalmsson, H. 2002. Capelin (*Mallotus villosus*) in the Iceland-East Greenland-Jan Mayen ecosystem. ICES Journal of Marine Science, 59:870-883.

Wada, E., Terazaki, M., Kabaya, Y., and Nemoto, T. 1987. ^{15}N and ^{13}C abundances in the Antarctic Ocean with emphasis on the biogeochemical structure of the food web. Deep-Sea Research Part A-Oceanographic Research Papers, 34: 829-841.

Wathne, J.A., Haug, T. and Lydersen, C. 2000. Prey preference and niche overlap of ringed seals *Phoca hispida* and harp seals *P. groenlandica* in the Barents Sea. Marine Ecology Progress Series, 194: 233-239.

Werner, I., Auel, H., Garrity, C., and Hagen, W. 1999. Pelagic occurrence of the sympagic amphipod *Gammarus wilkitzkii* in ice-free waters of the Greenland Sea - dead end or part of life-cycle? Polar Biology, 22: 56-60.

Wold, A., Jæger, I., Hop, H., Gabrielsen, G.W. and Falk-Petersen, S. 2011. Arctic seabird food chains explored by fatty acid composition and stable isotopes in Kongsfjorden, Svalbard. Polar Biology, 34: 1147-1155.

Zhai, Li., Gudmundsson, K., Miller, P., Peng, W., Gudfinnsson, H., Debes, H., Hátún, H., White III, G.N., Walls, R.H., Sathyendranath, S., and Platt, T. 2012. Phytoplankton phenology and production around Iceland and Faroes. Continental Shelf Research, 37: 15-25.

Paper I

Paper II

Paper III

Paper IV

Paper V

UNIVERSITY OF TROMSØ

ISBN xxx-xx-xxxx-xxx-x