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Using food web structure based on stable nitrogen and carbon isotopes to investigate pelagic-benthic coupling in different areas of the Barents Sea

by

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“Tänk när du en gång en tanke tänker,
tänk på den som ännu ingen tanke tänkt,
och när du nu din tanke tänker,
tänk på vad du tänker,
så din tanke inte bliver tanklös tänkt."

Abstract

Pelagic-benthic coupling is generally assumed to be tighter on Arctic shelves than in lower latitudes, due to for example pronounced seasonal cycles of sunlight and primary production and a potential mismatch between the bloom and its pelagic consumers. Pelagic-benthic coupling is also often stronger in shallower areas compared to deeper areas, due to the shorter distance between the productive, euphotic zone and the benthic realm. Recent studies have investigated this relationship between the pelagic and benthic communities and found stable isotope ratios to be depleted in areas where the coupling is tight and enriched where coupling is weaker. This study compares the pelagic-benthic coupling in the NE Fram Strait and SW Barents Sea and on the continental shelf relative to the continental slope, via the use of stable nitrogen and carbon isotopes. The approach was to study those contrasting regimes, both at the level of select species and at that of feeding guilds. Niche metrics were calculated to describe and compare trophic structure between the different areas. Contrary to the expectations, however, no differences in isotopic enrichment between the NE Fram Strait and the SW Barents Sea or between the continental shelf and the continental slope were observed. Pelagic feeding guilds were depleted in ^{15}N and ^{13}C compared to benthopelagic and benthic feeding guilds. The similarities observed between the NE Fram Strait and SW Barents sea may be attributed to substantial advection of Atlantic Water, with its associated biota, in the West Spitsbergen Current, which would cause the two areas to have the same water mass characteristics. The similarities observed between the continental shelf and to the continental slope sea may be attributed to deep vertical mixing in the study area.

Keywords: Pelagic-benthic coupling, stable isotope analysis, trophic ecology and benthic food webs

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Abbreviations

Bcarni	**B**enthic **Carni**vores
BDetri	**B**enthic **Detri**vores
BPomni	**B**entho-**P**elagic **omni**vores
BSusp	**B**enthic **Susp**ension feeders
CD	**C**entroid **D**istance
MNND	**M**ean of **N**earest **N**eighbour **D**istance
PCarni	**P**elagic **Carni**vores
Pomni	**P**elagic **Omni**vores
RC	**R**ange **C**arbon
RN	**R**ange **N**itrogen
SDNND	**S**tandard **D**eviation of **N**earest **N**eighbour **D**istance
TA	**T**otal **A**area
WSC	**W**est **S**pitsbergen **C**urrent

Abbreviations

Bath	*Bathyarca glacialis*
Chla	*Chlamys islandica*
Col hol	*Colus holboelli*
Col pub	*Colus pubescens*
Col sab	*Colus sabini*
Col spp	*Colus* spp.
Cte	*Ctenodisus crispatus*
Gon	*Gonatus fabricii*
Leb	*Lebbeus polaris*
Meg	*Meganyctiphanes norvegica*
Molp	*Molpadia borealis*
Oph	*Ophiura sarsi*
Pan	*Pandalus borealis*
Pas	*Pasiphaea*
Pon	*Pontohophilus norvegicus*
Sab sar	*Sabinea sarsi*
Sab sep	*Sabinea septemcarinata*
Sab spp	*Sabinea* spp.
The lib	*Themisto libellula*
Str spp	*Strongylecentrotus* spp.
The ab	*Themisto abyssorum*
The lib	*Themisto libellula*
The sp	*Themisto* sp.
The spp	*Themisto* spp.
Thys	*Thysanoessa inermis*

Chapter 1

Introduction

1.1 The importance of benthic communities in food webs

Food webs describe the exchange of matter, such as carbon, nitrogen and various nutrients among organisms within an ecosystem [Krumins et al., 2013]. Knowledge about food web structure and trophic links, such as food web length, the relative trophic positions of species, niche space and primary carbon sources can help us understand pathways of energy transfer. This knowledge can also help to predict the relative stability of systems and their susceptibility to changes, either abiotic or biotic [Renaud et al., 2011].

On Arctic shelves, benthic communities are particularly important parts of the food web, given that the benthic biomass is much higher and a larger proportion of carbon is cycling through the benthos than in lower latitudes [Grebmeier and McRoy, 1989; Høpner Petersen and Curtis, 1980]. In other words, the pelagic-benthic coupling is assumed to be tight on Arctic shelves [Renaud et al., 2008]. Benthic communities directly serve as food for several commercial fishes, mammals and invertebrates [Lovvorn et al., 2005; Lowry et al., 2004; Planque et al., 2014]. They also serve other functions in the ecosystem, such as contributing to carbon cycling, remineralization and secondary production [Grebmeier, 2012; Grebmeier and McRoy, 1989; Renaud et al., 2006]. Some taxonomic groups such as polychaetes, crustaceans, molluscs and echinoderms are particularly important in the redistribution and remineralization of organic carbon that falls out to the seafloor [Grebmeier, 2012; Piepenburg et al., 1995].

Given these important roles of Arctic shelf benthic communities the focus of this study is on the benthic food web. Of the many different taxa that use benthic communities as feeding grounds, several are commercial species [Lovvorn et al., 2005; Lowry et al., 2004; Planque et al., 2014]. The species chosen for investigation in this study are almost all important prey for commercial fish species in the Barents Sea [Planque et al., 2014]. In addition, I included a few key pelagic species to contrast their trophic roles to those of the benthic taxa. Investigations of benthic ecosystems and food webs are also especially valuable for long term monitoring since many benthic taxa often are relatively long lived and immobile, compared to pelagic taxa [Beuchel and Gulliksen, 2008] and thus integrate water column processes and changes over time.

1.2 Pelagic-benthic coupling

The terms pelagic-benthic coupling or benthic-pelagic coupling refer to the relationship between the pelagic realm and the benthic realm in aquatic systems and the exchange of solute, particulate and gaseous fluxes between the two systems [Griffiths et al., 2017]. These fluxes are mediated by biological, physical and chemical processes [Griffiths et al., 2017]. The predominant direction of the transfer is indicated by the ordering of the words: benthic-pelagic coupling refers to when the predominant direction of transfer is from the benthic system to the pelagic, and pelagic-benthic refers to when the predominant direction of transfer is out of the pelagic system towards the benthic [Renaud et al., 2008]. In this present study the direction of interest is out of the pelagic system into the benthic, thus the term pelagic-benthic coupling is used consistently. Tight pelagic-benthic coupling refers to when the sinking matter undergo little reworking while sinking through the water column,a and is relatively little degraded when reaching the seafloor. In contrast, weak pelagic-benthic coupling refers to when the sinking matter undergo substantial reworking in the water column, and is degraded when reaching the seabed.

1.3 Approach to studying food webs: Stable isotopes as trophic markers

1.3.1 Concept of stable isotope use in food web studies

In polar ecosystems where long term sampling of food web components may be close to impossible, due to sea ice and darkness during winter, stable isotope analysis can shed light on sources of primary production and trophic links in the food web since these biomarkers provide time-integrated averages of assimilated food [Hobson and Welch; Rau et al., 1992]. In addition, direct observations of feeding are often impractical in the marine realm, and thus one has to rely on indirect methods, such as analysis of stomach or feces, fatty acids, or stable isotope analysis. The basic idea of stable carbon and nitrogen isotope analysis is that “You are what you eat”, or “You are what you assimilate” [Middelburg, 2014]. Stable isotope analysis tracks the integrated assimilation of organic matter within an isotopic turnover window [Harrigan et al., 1989; Hobson and Welch] , i.e. the period over which the isotopic signature reflects the species’ assimilated diet.

In order to track assimilated organic matter over time, tissues with a low turnover rate, such as muscles or body walls should be used [McTigue and Dunton, 2013]. The turnover window in Arctic benthic invertebrates is not extensively studied, but appears to be in the order of around a month: Kaufman et al. [2008] estimated the isotopic turnover to be approximately 20 days in Arctic amphipods, while McMahon et al. [2006] estimated the isotopic turnover to be approximately 28 days in the muscle tissue of Arctic bivalves. Hence this method tracks assimilation over a longer time than stomach or feces analyses, and in contrast to these approaches reveals information about food assimilation and not just recent food ingestion [Hobson and Welch; McTigue and Dunton, 2013].

In organic substances we find naturally different abundances of isotopes of the same elements and it is the ratio of these that is investigated during a stable isotope analysis. The ratios of nitrogen and carbon isotopes, ^{15}N:^{14}N and ^{13}C:^{12}C, are the most commonly used isotopic ratios in food web studies [Post, 2002] and these ratios are investigated in this study. Nitrogen isotope ratios can be used to estimate the trophic positions of consumers relative to their diet [Minagawa and Wada, 1984], since the heavier isotope of nitrogen is accumulated through the food chain. Due to kinetic fractionation, the lighter isotope is preferentially excreted and the tissues become enriched in relation to the diet [Peterson and Fry, 1987]. The magnitude of the fractionation in each trophic step may vary due to type of excretion, diet, the tissue analyzed, the taxon and the environment, but is often assumed to be around 3.4 ‰ [Post, 2002].

The fractionation, or enrichment, of carbon in each trophic step is usually low, 0–1‰ [Peterson and Fry, 1987; Post, 2002], and hence carbon sources at the base of the food web can be assessed from the δ^{13}C-values of the consumers. To assess the food web baseline, the potential sources should have distinct carbon signatures [Søreide et al., 2006a] and these sources should be sampled within the time periods over which a consumer's isotopic signature reflects its diet and assimilation time. The δ^{13}C-values of plants vary due to isotopic differences in their inorganic carbon substrate and also depending on what photosynthetic pathway (C3 or C4) they use [Smith and Epstein, 1970]. Isotopic fractionation associated with carbon fixation may vary due to differences in CO_2-availability during photosynthesis and the algae may also discriminate between isotopes when fixing carbon. In aquatic plants this discrimination is related to the thickness of the diffusive boundary layer, which controls the rate of $CO_2 - HCO_3^-$ diffusion. The diffusive boundary layer may vary in thickness among species or depending on position in the water column [France, 1995]. These differences in δ^{13}C-values among primary producers and the small enrichment in each trophic step is what makes it possible to discriminate different base lines for food web via stable isotope analysis. According to the principle "You are what you eat" the isotopic ratio of the primary producers is then reflected in the consumers' tissues [Middelburg, 2014].

There are differences in biochemical and isotopic composition between tissues and different tissues can have a range of turnover times, and thus mirror assimilation from different time aspects [Middelburg, 2014]. This will be a challenge if small organisms are analyzed and the whole organism or several organisms have to be pooled for analysis, as the tissues can have different signatures relative to each other [Søreide and Nygård, 2012]. For exaple lipids often have depleted δ^{13}C-values and carbonates have enriched δ^{13}C-values, compared to e g muscle tissue.

1.3.2 Trophic niche space and Layman metrics

In addition to giving information on food web carbon sources and estimating trophic levels stable isotope data can help to picture more general patterns in food web structure, using the relative positions and spacing of target groups in δ^{15}N:δ^{13}C isotopic niche space or along a temporal or spatial gradient. A common way to present results from a stable isotope analysis is in δ^{15}N:δ^{13}C-biplots with taxa plotted as their mean stable isotope signatures, which is done in this study. Interpretations of the positions of the taxa, or of entire communities or populations, reveal valuable information as their positions relative to each other, but not as absolute values. The use of δ^{15}N:δ^{13}C-biplots and some relatively simple geometric calculations of the target group's relative positions within the bi-plot may give insight into the use of trophic niche space in an ecosystem [Layman et al., 2007].

Hutchinson [1957] defined the ecological niche as an n-dimensional hypervolume in a n-dimensional space with resources and environmental conditions as its axes. The realized trophic niche is then the hypervolume bounded by the subset of dimensions related to trophic resources and trophic resource use. As stable isotope analysis investigates the assimilation of trophic resources it is a suitable tool for depicting the trophic niche dynamics of an ecosystem as an isotopic niche. It is important to remember however, that the isotopic niche is a proxy, and not an actual depiction of the trophic niche, as its axes are not the actual resource use. [Cucherousset and Villéger, 2015].

Layman et al. [2007] described six community-wide trophic niche metrics, which can shed light on important aspects of trophic structures. The metrics are: δ^{15}N-range (RN), δ^{13}C-range (RC), total area (TA), mean distance to centroid (CD), mean nearest neighbour distance (MNND) and standard deviation of nearest neighbour distance (SDNND). These metrics and how to calculate them are further described in the chapter 2.3.1. Via the use of these metrics trophic complexity and its multiple dimensions can be simplified to continuous variables, that can be used for comparison across ecosystems and communities or across time periods, space, depth or other parameters. Since the δ^{15}N- and δ^{13}C-values are simultaneously analyzed some patterns may be uncovered, that would not have been uncovered if each variable was analyzed alone. Also in cases where not enough information is available to establish a baseline and estimate trophic positions or to quantify carbon sources, the metrics mentioned above still allow for quantification of food web structures and comparisons between different ecosystems [Layman and Post, 2008].

1.4 Study area

The Barents Sea (figures 1.1 and 1.2) is the largest Arctic inflow shelf [Carmack and Wassmann, 2006] and as such, the interplay of inflowing Atlantic Water and resident Arctic Water shapes its ecosystems and food webs. There are various definitions of the boundaries of the Barents Sea. Jakobsen and Ozhigin [2011] defined the continental break west of Spitsbergen and Norway as the western boundary, the shelf break north of Svalbard and Franz Joseph land as the northern boundary, the coast of Norway and Russia as the southern boundary and a line drawn from Franz Josef Land to the northern tip of Novaya Zemlya towards the mainland as the eastern boundary. This definition will be used thoughout this study.

The average depth of the Barents Sea is 230 meters and the deepest point in the western end of the Bear Island Trough is 500 meters [Sakshaug, 1997], making it one of the deepest Arctic shelves. Even though the Barents Sea is a shelf sea it consists of several troughs and basins, separated by shallow bank areas. The troughs run through the western continental shelf break and from the central Barents Sea to the north. The shelf drops off across an often steep slope towards the Norwegian Sea in the west, and towards the Arctic Basin north of Svalbard (figures 1.1 and 1.2), [Jakobsen and Ozhigin, 2011].

The western troughs allow warm and saline Atlantic Water to flow into the Barents Sea. The Atlantic Water splits into two branches, one going north-east along the Novaya Zemlya coast and then towards the Arctic Ocean and one that goes north along the west and north west coast of Svalbard, in the eastern Fram Strait. The latter is the West Spitsbergen Current (WSC) [Loeng, 1991] (figures 1.1 and 1.2). In the Fram Strait, the WSC subducts under Arctic Surface Water, which has low temperature and salinity. This keeps the water masses north west of Svalbard mainly Atlantic at depths down to 500m [Rudels et al., 2000]. Cold Arctic Water enters the Barents Sea between Spitsbergen and Franz-Josef Land and through the trough between Franz-Josef Land and Novaya Zemlya [Loeng, 1991]. Arctic Water also enters along the east coast of Svalbard and along the southern coast of Novaya Zemlya. Some of the Arctic Water that enters along the east coast of Spitsbergen goes back up along the western coast and affects the West Spitsbergen Water [Cottier et al., 2005].

Resulting from the above described circulation, the Barents Sea and Fram Strait system consist of three main water masses: Atlantic Water, Arctic Water and Coastal Water. The Atlantic Water has a salinity higher than 34.8 [Loeng, 1991] and it has temperatures ranging from 3.5 to 6.5°C, depending both on seasonal and inter-annual variations. Temperature and salinity decrease as the Atlantic Water is advected north [Boyd and D'Asaro, 1994]. The Coastal Water has temperatures in the same range as the Atlantic Water, but the salinity is lower <34.7 [Loeng, 1991]. The Arctic Water is cold, <0°C, and has a salinity ranging from 34.4 and 34.7 [Loeng, 1991]. The polar front separates the Arctic and Atlantic Waters (figures 1.1 and 1.2). In the warm season, the sea ice melts and produces a surface layer of melt water with low salinity that rest on top of the Arctic Water in the northern areas of the Barents Sea [Jakobsen and Ozhigin, 2011].

1.5 Pelagic-benthic coupling in the NE Fram Strait and SW Barents Sea

The Barents Sea and the Fram Strait are situated at a high latitudes and thus experiences extreme seasonal variations in light conditions with polar day and polar night [Berge et al., 2015]. Sunlight is necessary for most primary production and thus primary production exhibits a peak in spring, or early summer, and a low in winter [Leu et al., 2011]. During the winter, when no light is available and no primary production takes place, the water column tends to be mixed due to cooling, ice formation and winter storms. This mixing brings up abundant nutrient from the depths [Loeng, 1991]. In spring, the sun returns and the temperatures increase and hence the sea ice, where it is present such as in the northern Barents Sea, starts to melt. Due to the winter mixing of the water column there are abundant nutrients and as soon as there is enough sunlight the bloom starts [Sakshaug, 1997]. The melting sea ice, where is is present, creates a prominent halocline, which keep the nutrients in the euphotic zone and prevents them from being renewed from depth as the bloom progresses. Primary production along the marginal ice zone can thus be very high, but is of short duration, and as the ice edge retracts north though-out the warm season an intense bloom can be seen following the ice edge [Sakshaug, 1997]. This 30-50 kilometers wide phytoplankton bloom zone is known as the ice edge effect and is observed in all seasonally ice-covered polar seas, and was first suggested by [Gran et al., 1931].

Where sea ice is present, as in the northern Barents Sea, an ice-algae-spring bloom may occur before the pelagic phytoplankton spring bloom, as the ice melts and sufficient sunlight can penetrate the ice to reach the ice algae [Falk-Petersen et al., 1998; Leu et al., 2011]. Once melting out of the ice, the ice algae often aggregate and thus have a high sinking velocity and are degraded relatively little as they reach the seabed. Hence, they may be an important food source for benthos living in seasonally ice covered areas and contribute to a tighter pelagic-benthic coupling in these areas with their high sinking rate [Renaud et al., 2007]. In the southern areas of the Barents Sea, where sea ice is absent, the water columns is only stratified due to warming temperatures as the sun returns, and not due to differences in salinity as the ice melts. The thermocline develops slower, is much weaker and deeper than the halocline along the ice edge.

Due to the weaker pycnocline nutrients and primary producers show lower concentrations and are not kept entirely in the euphotic zone, and the concentrations of both are lower than along the marginal ice zone. But, thanks to the weaker stratification nutrients can be replenished throughout the season and the bloom lasts longer than in the more stratified northern waters [Slagstad and Wassmann, 1996; Wassmann et al., 1999].

The timing of the spring bloom affects the match, or mismatch, between herbivorous zooplankton production and grazing and maximum primary production [Wassmann et al., 1996]. When the bloom is more episodic and has a shorter duration, as in the northern seasonally ice covered area, there is more often a mismatch and the zooplankton cannot control the bloom. A larger proportion of the bloom is then deposited to the seafloor, where it supports a thriving benthic community [Wassmann et al., 1996]. Typically the highest vertical carbon fluxes are recorded in spring, before balance between production and consumption is achieved [Olli et al., 2002]. This pattern is pronounced along the marginal ice zone, where the bloom is intense and of short duration. Hence, phytoplankton blooms in newly opened waters often result in high vertical export of fresh organic matter and tight pelagic-benthic coupling in seasonally ice covered waters [Tamelander et al., 2006]. When the bloom is less epsiodic, as in the southern Barents Sea, the probability of match between primary production and zooplankton production is much larger. Hence, the zooplankton are to a larger extent able to control the primary production, and a larger proportion of the primary production is grazed in the water column and less is settling to the seafloor and the benthic fauna [Båmstedt et al., 1991].

With this in mind, it is easily understandable why it has been suggested that Arctic shelves have a stronger pelagic-benthic coupling than areas in warmer seas in several studies [Ambrose and Renaud, 1995; Grebmeier and Barry, 1991; Hobson et al., 1995; Petersen and Curtis, 1980; Piepenburg, 2005]. As a result, warmer systems have been suggested to have a higher carbon flow through the pelagic realm and colder systems through the benthic realm. This study will investigate differences in pelagic-benthic coupling in the SW Barents Sea and NE Fram Strait by means of stable isotope analysis. The pelagic-benthic coupling is expected to be stronger in the NE Fram Strait the in the SW Barents sea (figure 1.1), and this is expected to be reflected in depleted stable isotope ratios in the NE Fram Strait compared to SW Barents sea, due to a more reworked food supply for the benthos where the pelagic-benthic coupling is weaker.

The inflow and mixing of cold Arctic water and warm Atlantic water and not the least the inter-annually and seasonally variable ice cover makes the Barents Sea very sensitive to climate change. Via changes in the large scale thermohaline circulation a warming climate is expected to influence the inflow of warm Atlantic water to the Barents Sea and subsequently affect the duration and extent of the ice cover [Polyakov et al., 2017]. Today Arctic marine areas are warming twice as fast as the global average [Hoegh-Guldberg and Bruno, 2010] and as a consequence, the Arctic is

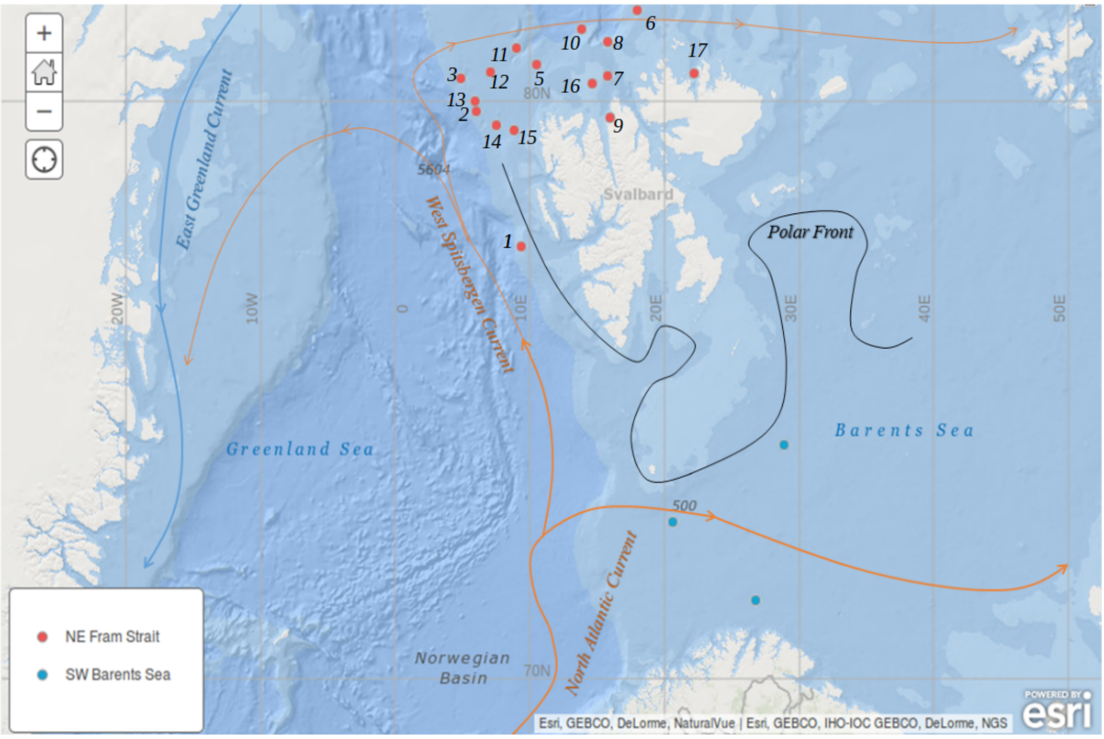

FIGURE 1.1: Map of the Barents Sea. Stations in the NE Fram Strait sampling area are red, and stations in the SW Barents Sea sampling area are blue. Atlantic, warm currents are marked in red, and Arctic, cold currents are marked in blue. Thinner lines indicate where the currents subduct the surface water. The approximate position of the Polar Front is indicated by the black line.

facing unprecedented challenges associated with climate change. Sea ice, timing and magnitude of primary production and species distribution are only examples of what may be affected.

A warming climate will have severe impacts on the organic matter flux to the seafloor, especially in the Arctic [Grebmeier et al., 2006], since a warming climate may affect the seasonality and duration of the bloom, matching of the bloom and its consumers, the magnitude and species composition of the bloom, and hence the subsequent vertical transport to the seafloor. A climate warming induced shift from an ice influenced, stratified, very seasonal, tightly coupled and benthic dominated ecosystem to an ice free, less stratified, less seasonal, less tightly coupled and more pelagic oriented system can be expected from future warming and reduction in sea ice cover [Kiyko and Pogrebov, 1997; Wassmann, 2006]. Since the benthic invertebrate fauna plays such an important role in nutrient regeneration and biogeochemical cycles and as important prey for many top predators on Arctic shelves [Grebmeier and McRoy, 1989; Grebmeier et al., 2015; Lovvorn et al., 2005; Lowry et al., 2004], altered pelagic-benthic coupling may have far reaching consequences throughout the ecosystem [Grebmeier et al., 2015]. Thus it is important to understand the coupling between pelagic and benthic systems thoroughly.

1.6 Pelagic-benthic coupling along a depth gradient from the shelf, to the shelf break and slope

Benthic ecosystems, deeper than the euphotic zone, rely on settling particles from the euphotic zone, such as algal matter, fecal matter, carcasses etc., that reach the seafloor either as vertical particle flux or as particles transported along the continental slope [Klages et al., 2001]. This reliance on surface production imposes depth related constraints on food availability and quality reaching the seabed since organic material is consumed and reworked as it settles through the water column [Mintenbeck et al., 2007; Roy et al., 2014].

Depending on the particle size and shape and water depth, it may take up to several weeks before the descending particulate organic matter (POM) reaches the seabed. As the particles settle towards the seabed they are reworked by zooplankton, or by microbial processes [De La Rocha and Passow, 2007; Klages et al., 2001]. This reworking, or remineralization, has been shown to increase the carbon [Dunton et al., 1989; Hobson et al., 1995; McConnaughey and McRoy, 1979] and nitrogen stable isotope ratios [Iken et al., 2010; Mintenbeck et al., 2007]. This change in isotopic ratios may be used to investigate to what extent the benthic ecosystem is coupled to the pelagic [Hobson et al., 1995; Iken et al., 2001; Mintenbeck et al., 2007]. In a more tightly coupled ecosystem, such as many shallow Arctic shelves [Carmack and Wassmann, 2006; Iken et al., 2010], the benthic community receives relatively fresh organic matter and thus depleted stable isotope ratios can be expected. On the contrary, in a less tightly coupled system, as can often be found in deeper areas [Bell et al., 2016; Iken et al., 2001], enriched isotopic values can be expected.

This study will investigate the hypothesis that the continental slope is less coupled to the pelagic than the continental shelf, since it is deeper and retrieves less fresh organic matter, which is which is expected to be reflected in enriched stable isotope ratios. The continental shelf is assumed to be more tightly coupled to the pelagic system, retrieve more fresh organic matter, which is expected to be reflected in depleted stable isotope ratios (figure 1.2).

1.7 Feeding strategy comparison

In order to understand how organic matter is passed through the food web it is helpful to investigate and understand the functional roles of groups of animals, relative to their feeding mode. A functional group includes all taxa who use and affect the environment in comparable ways [Pearson, 2001]. Pearson [2001] made an extensive overview of functional groups in soft-sediment marine benthos, and developed the trophic group concept further by dividing the five broad groups traditionally recognized in benthos into sub-groups. Feeding guilds are groups

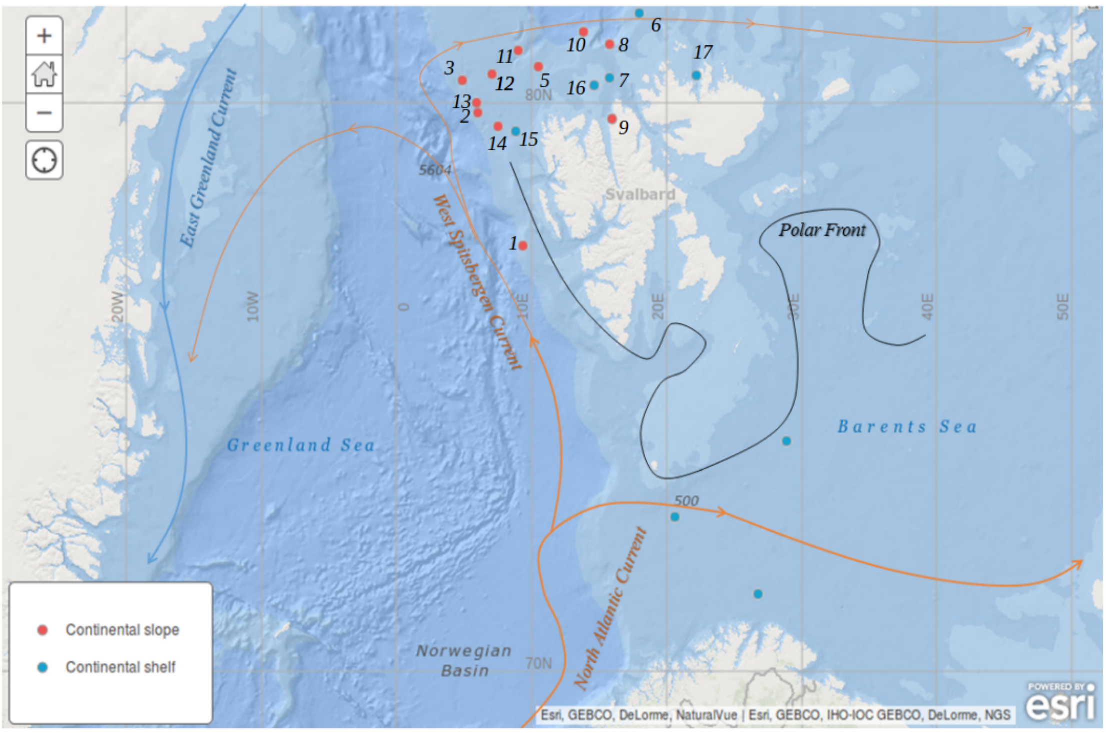

FIGURE 1.2: Map of the Barents Sea. Stations in the continental slope sampling area are red, and stations in the continental shelf sampling area are blue. Atlantic, warm currents are marked in red, and Arctic, cold currents are marked in blue. Thinner lines indicate where the currents subduct the surface water. The approximate position of the Polar Front is indicated by the black line.

of taxa solely based on modes of exploitation of resources [Fauchald and Jumars, 1979; Root, 1967]. Since this study is mainly focusing on trophic ecology, and not other aspects of functional ecology, organisms are divided in to trophic groups or feeding guilds. Pelagic taxa, were grouped into pelagic omnivores (Pomni) and pelagic carnivores (Pcarni) based on diet-literature. Benthic taxa were grouped into the five broad groups recognized by Pearson [2001]; herbivores (Bherb), suspension feeders (Bsusp), detrivores, (Bdetri) and carnivores (Bcarni), based on diet-literature. Benthopelagic taxa were assigned to the feeding guild benthopelagic omnivores (BPomni). For references and grouping of taxa, see table 1.1.

The trophic responses and plasticity of these groups along gradients, such as depth or latitude, may help in understanding changes in food supply due to environmental constraints, that may shape the benthic community [Bergmann et al., 2009]. For example benthic suspension feeders and benthic detrivores feed on particles of different size [Mintenbeck et al., 2007], benthic detrivores and carnivores may change between a predatory, detrivory or omnivory feeding behaviour, depending on the food supply available [Bergmann et al., 2009]. Likewise benthic organisms can be expected to switch to fresher resources when these are abundant, such as in the post bloom season.

The pelagic amphipods *Themisto* spp. and krill species *Thysanoessa inermis* and *Meganyctiphanes norvegica* were assigned to the feeding guild pelagic omnivores in this study [Auel et al., 2002; Falk-Petersen et al.; McClatchie, 1985; Noyon et al., 2009]. Since they are highly motile taxa that can migrate vertically to feed in the whole water column they are expected to have access to fresher material than the obligate benthic groups and have less enriched isotope ratios.

The cephalopod *Gonatus fabricii* is the only pelagic carnivore in this study [Roper et al., 2010; Zumholz and Frandsen, 2006] and since they also are highly motile animals they are expected to feed on fresh carbon in the water column and have depleted $\delta^{13}C$-values relative to benthic taxa. Since they are carnivores [Roper et al., 2010; Zumholz and Frandsen, 2006] they are expected to be enriched in ^{15}N compared to pelagic omnivores.

Benthic suspension feeders consume organic matter suspended in the water column just above the seafloor. They can either be active filter feeders with powerful filtering mechanisms, such as bivalves, or passive with structures capturing particles passing by in the water current, such as hydrozoans [Gili and Coma, 1998]. In this present study the bivalves *Bathyarca glacialis* and *Chlamys islandica* were included to represent this group [Gaillard et al., 2015; Habbestad, 2012]. The benthic suspension feeders are expected to have more enriched carbon isotope ratios than the truly pelagic taxa in the same trophic level, since they cannot undergo vertical migrations to feed on fresher material higher up in the water column. They are not necessarily expected to be more very much more enriched in ^{15}N than the pelagic omnivores since they feed on lower trophic levels

The decapods *Pandalus borealis*, *Pasiphaea* spp. and *Lebbeus polaris* comprise the feeding guild benthopelagic omnivores [Birkely and Gulliksen, 2003; WoRMS, 2017] in this study. They are all motile species that can migrate into the water column to feed on material of more pelagic origin, but studies have shown how *P. borealis* adapt to a more benthic feeding behaviour with increasing size and age [Hopkins et al., 1993; Nilssen et al., 1986]. The benthopelagic omnivores are expected to feed on higher trophic levels than benthic suspension feeders.

The echinoderms *Ophiura sarsii*, *Strongylocentrotus* spp., *Ctenodiscus crispatus* and *Molpadia borealis* were assigned to the feeding guild benthic detrivores. They all have different feeding mechanisms, but they have in common that they feed in the sediments on reworked and degraded organic matter [Amaro et al., 2010; Barnes, 1982; Billett, 1991; Gilkinson et al., 1988; Harris et al., 2009; Shick et al., 1981]

The gastropods *Colus* spp., and the decapods *Sabinea* spp., *Pontophilus norvegicus* and *Sclerocrangon ferox* were assigned to the feeding guild benthic carnivores. These taxa have an omnivorous, predatory and scavenging feeding behaviour [Birkely and Gulliksen, 2003; Graham, 1988; WoRMS, 2017] and are thus expected to be at the highest trophic level of the taxa included in this study. These taxa all have heavy exoskeletons and cannot do extended vertical migration. Hence they are expected to rely on organic matter of benthic origin.

Isotopic enrichment at the slope and along a latitudinal gradient is expected to be stronger in groups consisting of obligate benthic taxa, such as benthic suspension feeders, benthic detrivores, and benthic carnivores, who cannot do vertical migrations into the water column to feed on fresher organic matter. This enrichment is also expected to be stronger in carnivorous and scavenging groups, which feed on benthic organisms. Benthopelagic and pelagic taxa, in contrast, are able to complement their diet with pelagic resources, as documented for Arctic fishes in the Beaufort Sea [Stasko et al., 2016], and are expected to show less of an enrichment with decreasing latitude and increasing depth.

TABLE 1.1: All invertebrate taxa included in this study. Y=yes, N=no, Pomni=Pelagic omvivores, BPomni=Benthopelagic omnivores, Busp=Benthic suspension feeders, Bdetri=Benthic detrivores and Bcarni=Benthic carnivores. Species names and taxonomic classification in is according to the World Register of Marine Species [WoRMS, 2017].

Phylum	**Class**	**Order**	**Species**	**Tissue**	**Acidified**	**F. guild**	**Reference**
Arthropoda	Malacostraca	Amphipoda	*Themisto abyssorum*	whole animal	Y	Pomni	[Auel et al., 2002] [Noyon et al., 2009]
Arthropoda	Malacostraca	Amphipoda	*Themisto libellula*	whole animal	Y	Pomni	[Auel et al., 2002] [Noyon et al., 2009]
Arthropoda	Malacostraca	Decapoda	*Lebbeus polaris*	muscle	N	BPomni	[Birkely and Gulliksen, 2003]
Arthropoda	Malacostraca	Decapoda	*Pandalus borealis*	muscle	N	BPomni	[Hopkins et al., 1993] [Nilssen et al., 1986]
Arthropoda	Malacostraca	Decapoda	*Pasiphaea* spp.	muscle	N	Bcarni	[WoRMS, 2017]
Arthropoda	Malacostraca	Decapoda	*Pontophilus norvegicus*	muscle	N	Bcarni	[WoRMS, 2017]
Arthropoda	Malacostraca	Decapoda	*Sabinea sarsi*	muscle	N	Bcarni	[Birkely and Gulliksen, 2003]
Arthropoda	Malacostraca	Decapoda	*Sabinea septemcarinata*	muscle	N	Bcarni	[Birkely and Gulliksen, 2003]
Arthropoda	Malacostraca	Decapoda	*Sclerocrangon ferox*	muscle	N	Bcarni	[Birkely and Gulliksen, 2003]
Arthropoda	Malacostraca	Euphausiacea	*Meganyctiphanes norvegica*	whole animal	N	Pomni	[Agersted and Nielsen, 2016] [McClatchie, 1985]
Arthropoda	Malacostraca	Euphausiacea	*Thysanoessa inermis*	whole animal	Y	Pomni	[Falk-Petersen et al.] [Petursdottir et al., 2012]
Echinodermata	Asteroidea	Paxillosida	*Ctenodiscus crispatus*	tube feet	Y	Bdetri	[Shick et al., 1981]
Echinodermata	Echinoidea	Echinoida	*Strongylocentrotus* spp.	tissue around mouth	Y	Bdetri	[Gilkinson et al., 1988]
Echinodermata	Holothuroidea	Molpadiida	*Molpadia borealis*	body wall	Y	Bdetri	[Amaro et al., 2010] [Barnes, 1982] [Billett, 1991]
Echinodermata	Ophiuroidea	Ophiurida	*Ophiura sarsii*	central disc	Y	Bdetri	[Harris et al., 2009]
Mollusca	Bivalvia	Arcida	*Bathyarca glacialis*	muscle	Y	Bsusp	[Gaillard et al., 2015]
Mollusca	Bivalvia	Pectinida	*Chlamys islandica*	muscle	N	Bsusp	[Habbestad, 2012]
Mollusca	Cephalophoda	Teuthida	*Gonatus fabricii*	muscle	N	Bcarni	[Roper et al., 2010] [Zumholz and Frandsen, 2006]
Mollusca	Gastropoda	Neogastropoda	*Colus holboelli*	muscle	N	Bcarni	[Graham, 1988]
Mollusca	Gastropoda	Neogastropoda	*Colus sabini*	muscle	N	Bcarni	[Graham, 1988]

1.8 Objectives

This study aims to describe and compare the food web structure of primarily the benthic and benthopelagic community in the Barents Sea via the use of stable isotope analysis of nitrogen and carbon. First, food web structure in the NE Fram Strait and SW Barents will be compared, then food web structure will be analyzed between the continental shelf and slope. The below hypotheses for which the background is described in chapters 1.5, 1.6 and 1.7 were tested.

Hypothesis 1: Pelagic-benthic coupling is tighter in the NE Fram Strait than in the SW Barents Sea, and this will be reflected in more depleted stable isotope ratios in the NE Fram Strait than in the SW Barents sea.

Hypothesis 2: Pelagic-benthic coupling is tighter on the continental shelf than on the continental slope and this will be reflected in more depleted stable isotope ratios on the continental shelf than on the continental slope.

Hypothesis 3: a) Obligate benthic feeding guilds are enriched compared to pelagic and benthopelagic feeding guilds. b) Obligate benthic feedings guilds also have stronger isotopic enrichment with increasing depth and decreasing latitude than pelagic and benthopelagic feeding guilds.

Chapter 2

Material and methods

2.1 Field sampling and at sea processing

To investigate food web structure, marine invertebrates were sampled during the TIBIA (Trophic Interactions in the Barents Sea) cruise in the SW Barents Sea in 21015 (27 May- 6 June 2015) on board R/V G.O Sars, and during the SI ARCTIC (Strategic Initiative Arctic) cruise in 2016 (2 September - 16 September) north of Svalbard in NE Fram Strait, on board R/V Helmer Hansen. Samples were taken between latitude 71.78°N to 74.88°N and longitude 20.65°E to 28.87°E in the southern sampling area and latitude 78.03°N to 81.04°N and longitude 5.03°E to 17.94°E in the northern sampling area (figures 1.1 and 1.2 and table 2.1). The depth range in the northern area was from 47m to 1198m and from 150m to 367m in the southern sampling area, A total of 20 different benthic, benthopelagic and pelagic invertebrate taxa were sampled (table 1.1).

During all cruises the following equipment was used at the sampled stations: Macroplankton trawl for zooplankton (mesh size 3mm), such as *Meganyctiphanes norvegica*, *Thysanoessa inermis* and *Themisto* spp., and a Campelen 1800 trawl (4 m vertical and 15 m horizontal trawl opening), triangular scrape and beam trawl for benthic taxa. The trawl distance for the beam trawl was 5000 meters, 800-1500 meters for the Campelen trawl and 1000-4000 meters for the pelagic trawls. The catch was sorted on board and species were identified to the lowest possible taxon by Lis Lindal Jørgensen at the Institute of Marine Research (IMR). The goal was to collect dominant macro zooplankton and epibenthic invertebrate species in replicates of three per station and species. This goal could not be achieved everywhere, due to small catches of some taxa. The samples were frozen in separate bags per taxon and station, and stored at -20 °C until further processing. When there was time, tissue samples were dissected out and frozen in separate bags and stored at -20 °C.

TABLE 2.1: Station information. Serial nr.: Station number referred to by research vehicle, R/V Go Sars in 2015 and R/V Helmer Hanssen in 2016, Y: Year 16 = 2016 and 15 = 2015, Lat: Latitude (°N), Long: Longitude (°E), ID: Station number referred to in figures 1.1 and 1.2, D: bottom depth in meters, Gear: Ctr = Campelen trawl, Ptr = Pelagic trawl, Btr = Beam trawl and Trscr = Triangular scrape

Serial nr.	**Year**	**Lat.**	**Long.**	**ID**	**D**	**Area**	**Area**	**Gear**
2002	16	78.08	9.33	1	620	NE Fram Strait	Slope	Ptr
2004	16	78.03	9.43	1	501	NE Fram Strait	Slope	Ctr
2005	16	78.09	9.36	1	546	NE Fram Strait	Slope	Ptr
2006	16	79.88	5.99	2	975	NE Fram Strait	Slope	Ptr
2007	16	80.32	4.86	2	814	NE Fram Strait	Slope	Ptr
2008	16	80.25	5.03	2	818	NE Fram Strait	Slope e	Ctr
2015	16	80.44	10.42	3	612	NE Fram Strait	Slope	Ptr
2016	16	80.42	10.73	3	616	NE Fram Strait	Slope	Ctr
2021	16	81.04	17.94	4	350	NE Fram Strait	Shelf	Ctr
2026	16	80.73	15.78	5	849	NE Fram Strait	Slope	Ptr
2027	16	80.75	16.11	5	882	NE Fram Strait	Slope	Ctr
2032	16	80.68	15.43	5	463	NE Fram Strait	Shelf	Ctr
2036	16	80.46	16.19	5	356	NE Fram Strait	Shelf	Ptr
2037	16	80.51	16.06	5	339	NE Fram Strait	Shelf	Ctr
2042	16	80.27	16.31	5	326	NE Fram Strait	Shelf	Ctr
2046	16	79.96	17.68	6	399	NE Fram Strait	Slope	Ptr
2047	16	80.03	17.45	6	399	NE Fram Strait	Slope	Ctr
2052	16	79.71	18.33	6	414	NE Fram Strait	Slope	Ctr
2053	16	80.84	13.99	7	1198	NE Fram Strait	Slope	Ptr
2054	16	80.84	13.77	7	1297	NE Fram Strait	Slope	Btr
2062	16	80.62	9.24	8	1069	NE Fram Strait	Slope	Ptr
2063	16	80.62	8.76	8	920	NE Fram Strait	Slope	Ctr
2067	16	80.35	7.12	9	630	NE Fram Strait	Slope	Ctr
2069	16	80.22	5.88	10	662	NE Fram Strait	Slope	Ctr
2073	16	79.85	6.05	10	987	NE Fram Strait	Slope	Ctr
2077	16	79.71	7.67	11	750	NE Fram Strait	Slope	Ptr
2078	16	79.72	7.45	11	788	NE Fram Strait	Slope	Ctr
2079	16	79.66	8.77	12	450	NE Fram Strait	Slope	Ptr
2080	16	79.63	8.93	12	401	NE Fram Strait	Slope	Ctr
1577	16	80.21	14.63	13	47	NE Fram Strait	Shelf	Trscr
1587	16	80.34	22.26	14	145	NE Fram Strait	Shelf	Ptr
1593	16	80.37	22.08	14	263	NE Fram Strait	Shelf	Ctr
2616	15	71.78	26.79	15	331	SW Barents Sea	Shelf	Ctr
2633	15	72.28	26.65	15	262	SW Barents Sea	Shelf	Ctr
72004	15	73.41	20.65	16	265	SW Barents Sea	Shelf	Ptr
72005	15	73.41	20.65	16	265	SW Barents Sea	Shelf	Ctr
72022	15	74.88	28.87	17	367	SW Barents Sea	Shelf	Ctr
72023	15	74.88	28.87	17	330	SW Barents Sea	Shelf	Ctr

2.2 Lab processing and stable isotope analysis

In the laboratory at UiT – The Arctic University of Norway in Tromsø, organisms were dissected to sample tissues with high complex protein content and mass-dominant tissues, which were dried at 60°C to constant mass and ground using a pestle and mortar. For larger specimens, such as large shrimps and mollusks, muscle tissue was used, for echinoderms soft tissue, such as body wall or tube feet, was sampled and for smaller organisms such as amphipods, the whole organism was used and sometimes several organisms were pooled. To see which tissues that were used in each taxa, see table 1.1 in chapter 1.

Samples containing calcium carbonate, such as echinoderms and amphipods, were acidified in 1M HCl drop by drop until bubbling ceased to dissolve the inorganic carbonates and were then dried and ground again [Bell et al., 2016]. The removal of carbonates may affect the nitrogen values [Søreide et al., 2006b] thus the samples where split in two before acidification, of which the one used for carbon isotope analysis was acidified and the one for nitrogen analysis was not. To see which taxa that were acidified, see table 1.1 in chapter 1. Lipids were not extracted, although they can confound stable carbon isotope analysis [Søreide et al., 2006b], since benthic organisms generally are low in lipids [Graeve et al., 1997].

The dried and ground samples were transferred to plastic vials and sent to Elemtex Ltd in Cornwall for mass spectrometry. Approximately 0.3 mg of the dried homogenized tissues were measured on a Thermo EA 1110 elemental analyzer linked to a Europa Scientific 2020 stable isotope ratio mass spectrometer. Isotopic ratios were calculated using laboratory references of Vienna Pee Dee Belemnite and gaseous N_2. The standard deviation for the measurements for δ^{13}C was maximum 0.12‰ and maximum 0.25‰ for δ^{15}N.

2.3 Stable isotopes as trophic markers

The conventional notation used to represent each isotopic value is the δ-notation, expressing each ratio of the sample ^{15}N:^{14}N and ^{13}C:^{12}C to the ratio of the reference material in parts per thousand (‰). The δ-values were calculated according to the formula below.

$$\delta\mathrm{X} = [\mathrm{R}_{sample}/R_{standard}) - 1]x * 1000$$

$$\mathrm{X} = \text{Nitrogen or Carbon, } \mathrm{R} = {}^{15}\mathrm{N}:{}^{14}\mathrm{N} \text{ or } {}^{13}\mathrm{C}:{}^{12}\mathrm{C}$$

The more positive the δX-value is, the more enriched, or heavy the material analyzed is. Since $R_{sample} : R_{standard}$ is always <1 for carbon the δ^{13}C-value is always negative.

2.3.1 Trophic niche space and Layman metrics

Layman et al. [2007] described six community-wide metrics, which can illuminate important aspects of trophic structures. The first four metrics in the list below measure the total extent of spacing within the δ^{15}N:δ^{13}C:-bi-plot space, and put in other words they are community wide measures of trophic diversity. The last two metrics mirror the relative position of taxa to each other within a defined niche space [Layman et al., 2007]. By performing this relatively simple calculations, overall trophic complexity is expressed by continuous one- or two-dimensional variables that can be compared across spatial or temporal scales to investigate and compare ecosystems.

1) The δ^{15}N-range (RN) is the difference between the two most extreme δ^{15}N-values, i.e. the most enriched and the most depleted values, and is one representation of vertical structure in a food web. The RN is calculated after the formula:

$$RN = \delta^{15}\mathrm{N}_{max} - \delta^{15}\mathrm{N}_{min}$$

In general a larger RN indicates a longer food chain and can be used as a proxy for food chain length.

2) The δ^{13}C-range (RC) is the difference between the two most extreme δ^{13}C-values, i. e. the most enriched and the most depleted values. The RC is calculated after the formula:

$$\mathrm{RC} = \delta^{13}\mathrm{C}_{max} - \delta^{13}\mathrm{C}_{min}$$

A larger RC is expected where there are multiple basal resources with varying δ^{13}C-values.

3) The total area (TA) depicts the convex hull area enclosed by all taxa in a δ^{13}C:δ^{15}N-bi-plot space and reflects the total amount of niche space occupied and is hence a proxy for the total extent of trophic diversity within the food web under investigation. The area of the convex hull is calculated according to the formula:

$$TA = [(\delta^{13}\mathrm{C}_1 + \delta^{13}\mathrm{C}_2)(\delta^{15}\mathrm{N}_1 - \delta^{15}\mathrm{N}_2) + (\delta^{13}\mathrm{C}_2 + \delta^{13}\mathrm{C}_3)(\delta^{15}\mathrm{N}_2 - \delta^{15}\mathrm{N}_3) + \ldots + (\delta^{13}\mathrm{C}_n + \delta^{13}\mathrm{C}_{n+1})(\delta^{15}\mathrm{N}_n - \delta^{15}\mathrm{N}_{n+1})]/2$$

where n is the number of vertices in the polygon.

Since the convex hull is drawn around the most extreme points the TA is highly influenced by extreme values on both the x- and y-axes and tends to grow bigger as the sample size grows bigger. This metric does not reflect distribution of data, which is done by the three following metrics.

4) The mean distance to the centroid (CD) is the arithmetic mean of the Euclidean distances of each taxon to the δ^{13}C:δ^{15}N-centroid; the arithmetic mean of the δ^{15}N- and δ^{13}C-values in the whole community or food web. This point minimizes the sum of squared Euclidean distances between itself and each point in the set.

The Euclidian distance between two points (p_1, p_2) in a two-dimensional space, in this case the δ^{13}C:δ^{15}N-space, is calculated according to the formula:

$$d(p_1, p_2) = \sqrt{[(\delta^{13}C_1 - \delta^{13}C_2)^2 + (\delta^{15}\mathrm{N}_1 - \delta^{15}\mathrm{N}_2)^2]}$$

The CD gives an estimate of the average degree of trophic diversity, or separation, within a food web, and is more robust to outliers than TA. Nevertheless this metric is also a function of the degree of taxa spacing.

5) The mean nearest neighbour distance (MNND) is the mean of the Euclidean distances of each taxon to the nearest neighbor in the δ^{13}C:δ^{15}N-bi-plot space and provides a measure of the overall density of taxa packing. In a food web with a large proportion of taxa having similar trophic ecologies the MNND will be smaller than in a food web having a smaller proportion of taxa with similar trophic ecologies. Put in other words, the more divergent the taxa are in terms of trophic niche in a food web, the larger value the MNND will take, and the more convergent the taxa are in their trophic niches, the larger the value of MMND will be. A food web with a small MNND (large trophic) overlap has a larger trophic redundancy than a food web with a large MNND (low trophic overlap). In a food web with large trophic overlap the removal of one species is less likely to lead to a vacant niche, since most likely other species will fill this vacant niche; i.e. the resilience to changes is high. The MNND is sensitive to differences in sample size.

6) The standard deviation of nearest neighbour distance (SDNND) provides a measure of the evenness of species packing in δ^{13}C:δ^{15}N-bi-plot space. Low values of SDNND indicate a more even distribution of trophic niches. The SDNND is less sensitive to differences in sample size in MNND.

These metrics and the graphical representation of communities in δ^{15}N:δ^{13}C-biplots will give us insight in isotopic trophic niche widths, the taxa's isotopic redundancy, the isotopic trophic diversity and community structure.

2.4 Data analysis

To compare pelagic-benthic coupling in the NE Fram Strait and the SW Barents Sea food webs, stations were grouped into ‘NE Fram Strait‘ and ‘SW Barents Sea‘, by geographic location (figure 1.1 and table 2.1). In all comparisons between the northern and southern area two subsets of data were used, comprising only taxa that occurs in both the northern and southern sampling areas and only samples from the same depth range (≤ 350m, see figure A.1 for distribution of depth in the NE Fram Strait and the SW Barents Sea sampling areas). To compare pelagic-benthic coupling between the continental shelf and slope stations were grouped into ’shelf’ and ’slope’ (figure 1.2 and table 2.1). The shelf was distinguished from the slope at a depth of 350m [Jakobsen and Ozhigin, 2011]. Again subsets of the total dataset were used, but this time only taxa that occurred on both the shelf and the slope were used. Hence, the north-south comparison and the shelf-slope comparison consist of slightly different subsets of taxa. Species within the same genus, such as *Colus holboelli, Colus pubescens* and *Colus sabini*, *Sabinea sarsi* and *Sabinea septemcarinata* and *Themisto abyssorom* and *Themisto libellula* were grouped into *Colus* spp., *Sabinea* spp. and *Themisto* spp., since the sample sizes were small for each individual species and for being able to compare the genuses between the sampling areas.

Normality was assessed using Q-Q-plots [Wilk and Gnanadesikan, 1968] and Shapiro-Wilks-normality-tests [Shapiro and Wilk, 1965]. When the populations compared were non-normally, distributed homogeneity of variances was tested using a Levene’s test [Levene et al., 1960], since the variance-F-test is non-robust against violence of the assumption of normality. When the populations were normally distributed homogeneity of variances was tested using using a variance-F-test. The isotopic values in the northern and southern study area, and on the shelf and the slope, were compared using Welch’s t-tests when the assumptions of normality and homogeneity of variances were met, [Welch, 1947], and by non-parametric Wilcoxon-rank-sum-tests when the assumptions were violated [Fay and Proschan, 2010; Mann and Whitney, 1947; Wilcoxon, 1945]. The significance level in all tests was 0.05. Both the Wilcoxon-rank-sum-test and the Welch’s t-test assume independence of data. Replicates of the same taxa from the same station cannot be considered as independent data points, so to obtain independence the mean of replicates per taxon and station were used in all statistical analyses. Since these mean values were used in all statistical comparisons they were also plotted in all scatterplots and boxplots.

The Wilcoxon-rank-sum-test is a non-parametric test of the null hypothesis that the probability of one randomly selected value from one population will be greater or less than another randomly selected value from another population is equal [Mann and Whitney, 1947; Wilcoxon, 1945]. As the name implies, the Wilcoxon-rank-sum-test rank the observations in each population and a test statistic is calculated from this ranking [Zar, 1999]. For details of formulas and calculations see Zar [1999], page 147. The Wilcoxon-rank-sum-test does not assume normality and can be used to test if two independent samples are selected from populations with the same distribution. The Wilcoxon-rank-sum-test tests for shifts in one distribution relative to the other, i.e. if the distributions are symmetric and have the same shapes, any significant difference is then a difference in central tendency [Fagerland and Sandvik, 2009; Voraprateep, 2013]. Hence, if the observations are independent and the distributions are symmetric and have equal distributional shapes, the Wilcoxon-rank-sum-test can be considered the non-parametric equivalent of the t-test, since the mean and median are equivalents in a symmetric distribution [Fagerland and Sandvik, 2009]. If the distributions are asymmetric, but have the same distributional shapes, the Wilcoxon-rank-sum-test tests for differences in location, and if the distributions are asymmetric and have different distributional shapes the Wilcoxon-rank-sum-test tests for differences in distributional shapes rather than differences in central tendency [Fagerland and Sandvik, 2009]. These underlying assumptions of symmetry and distributional shapes imply that significant test results may be achieved even when the populations in comparison do have close to the same mean. In other words, the Wilcoxon-rank-sum-test is non-robust against the assumption of symmetry and if the assumption on symmetry is violated the Wilcoxon-rank-sum-test has a high type I error rate (the false rejection of a true null-hypothesis) [Fagerland and Sandvik, 2009]. This is important to know, and consider, when interpreting test results, not to just interpret a significant p-value as a difference in central tendency between the poulations being compared. Thus all distributions were plotted in histograms before testing, and the histograms were investigated extra thoroughly in cases were the null-hypothesis was rejected.

Based on the groupings mentioned above (NE Fram Strait versus SW Barents Sea and continental shelf versus continental slope), isotopic niche size metrics were calculated and compared between the groups, based on Layman et al. [2007]. The data were plotted as the mean per taxon and station in scatterplots, with error bars indicating the standard deviations of the means. The data were also plotted in boxplots. The top and the bottom of the boxplots are the 25th and 75th percentiles and the band inside the box is the 50th percentile, the median. The whiskers extend to the most extreme data point, which is no more than 1.5 times the length of the box away from the box. Points outside the whiskers may indicate presence of outliers. All statistical analyses were carried out in R, R version 3.0.2 (2013-09-25) – "Frisbee Sailing", apart from calculations of Layman metrics, which were carried out in R version 3.2.5 (2016-04-14)–"Very, Very Secure Dishes", using the package SIBER [Jackson et al., 2011]. The thesis was written in ©2017ShareLaTeX, and the thesis.cls file was based on 'ECSthesis.cls', created by Steve R. Gunn, modified by Sunil Patel. Maps where done in the online version of ArcGis, by Esri.

Chapter 3

Results

3.1 Overview

A visual investigation of the results (figure 3.1, ,3.2, 3.3, 3.4 and 3.5) shows a partitioning of the data, both along the x-axis, the carbon range, and y-axis, the nitrogen range. Along the y-axis, the clustering into two groups is not as obvious and the data seem to be in more of a continuum. A closer look at figure 3.1 shows pelagic taxa in the left cluster, and benthic and benthopelagic taxa in the right (see table 1.1 in chapter 1 for grouping of taxa into pelagic and benthopelagic/benthic taxa).

In the entire data set mean δ^{15}N-values ranged from 7.7 ‰ (±0.7 ‰) for the amphipod *Themisto libellula*. to 13.9‰ (±0.6‰) for the decapod *Sabinea sarsii* and mean δ^{13}C-values ranged from -25.4‰ (±1.1 ‰) for *T.libellula* to -16.9‰ (±0.5‰) for the decapod *Sclerocrangon ferox*. The RN was 5.8‰ and the RC was 8.4‰ (table A.1 and A.2 and figure 3.1).

In the entire data set the standard deviation of the mean in δ^{15}N-values was largest for the holothuroidean *Molpadia borealis* (1.8‰) and smallest for the decapods *Pasiphaea* spp. (0.4‰) and the standard deviation of the mean in δ^{13}C-values was largest for the asteroid *Ctenodiscus crispatus* (1.5‰) and smallest for the bivalve *Chlamys islandica* (0.3‰) (table A.1 and A.2 and figure 3.1).

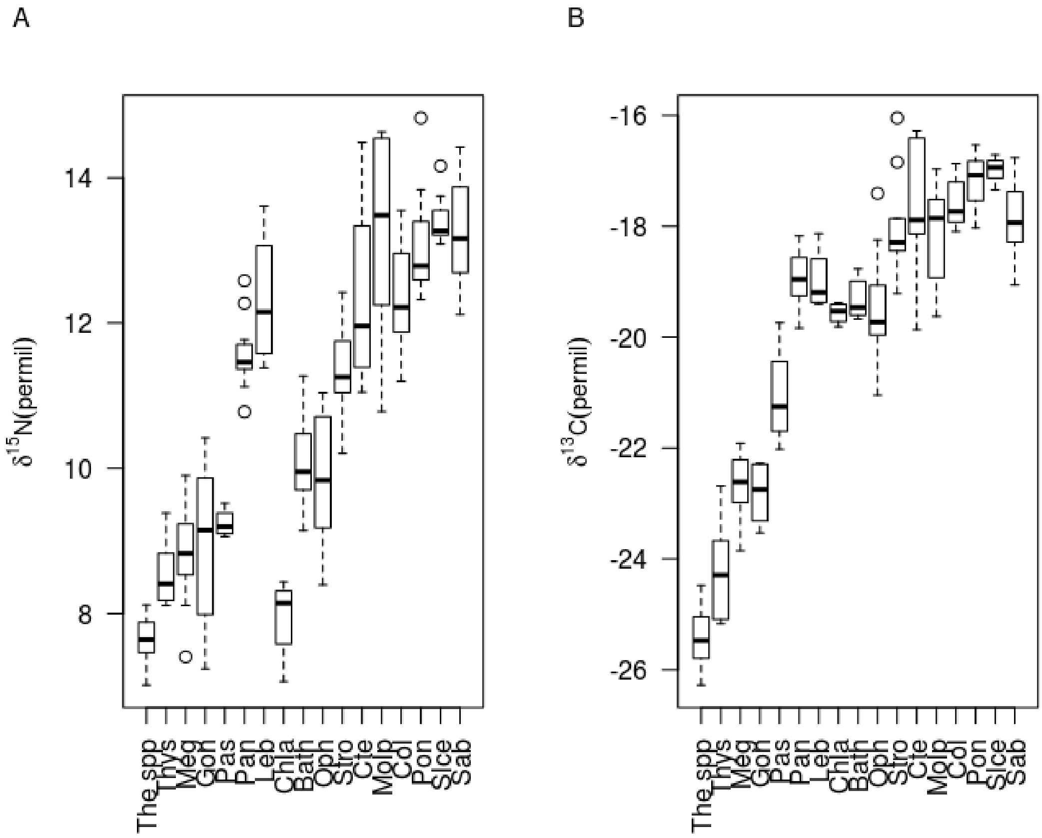

Figure 3.1: Boxplots of δ^{15}N- and δ^{13}C-values in 17 invertebrate taxa from the complete dataset. The key to the abbreviations for the taxa is found on page IX. A definition of the features in the plots is found in section 2.4 in chapter 2. A) Boxplots of δ^{15}N-values in all 17 invertebrate taxa in all sampling areas combined. B) Boxplots of δ^{13}C-values in all 17 invertebrate taxa in all sampling areas combined.

3.2 Hypothesis 1: Pelagic-benthic coupling is tighter in the NE Fram Strait than in the SW Barents Sea

Convex hull analysis of isotopic signatures showed an almost complete overlap within the NE Fram Strait and SW Barents Sea (figure 3.2). Niche metrics largely reflected this overlap: the TA for the NE Fram Strait area was 25.6 and the TA or the SW Barents Sea area was 20.8. In the NE Fram Strait area, CD was 2.7, the MNND was 0.8 and the SDNND was 0.8. In the SW Barents Sea area the CD was was 2.8, and MNND 0.7 and the SDNND 0.4 (table 3.1).

In the NE Fram Strait sampling area, mean δ^{15}N-values ranged from 7.5‰ (±0.3 ‰) for *Themisto* sp. to 13.6 ‰ (±1.8‰) for *M. borealis* and 13.6‰ (±0.8‰) for *Sabinea* spp.. Mean δ^{13}C-values ranged from -25.4‰ (±0.6‰) for *Themisto* sp. to -16.6‰ (±0.4 ‰) for the decapod *Pontophilus norvegicus*. The RN was 6.1‰ and the RC was 8.9‰ (table A.3, A.4 and 3.1and figure 3.3).

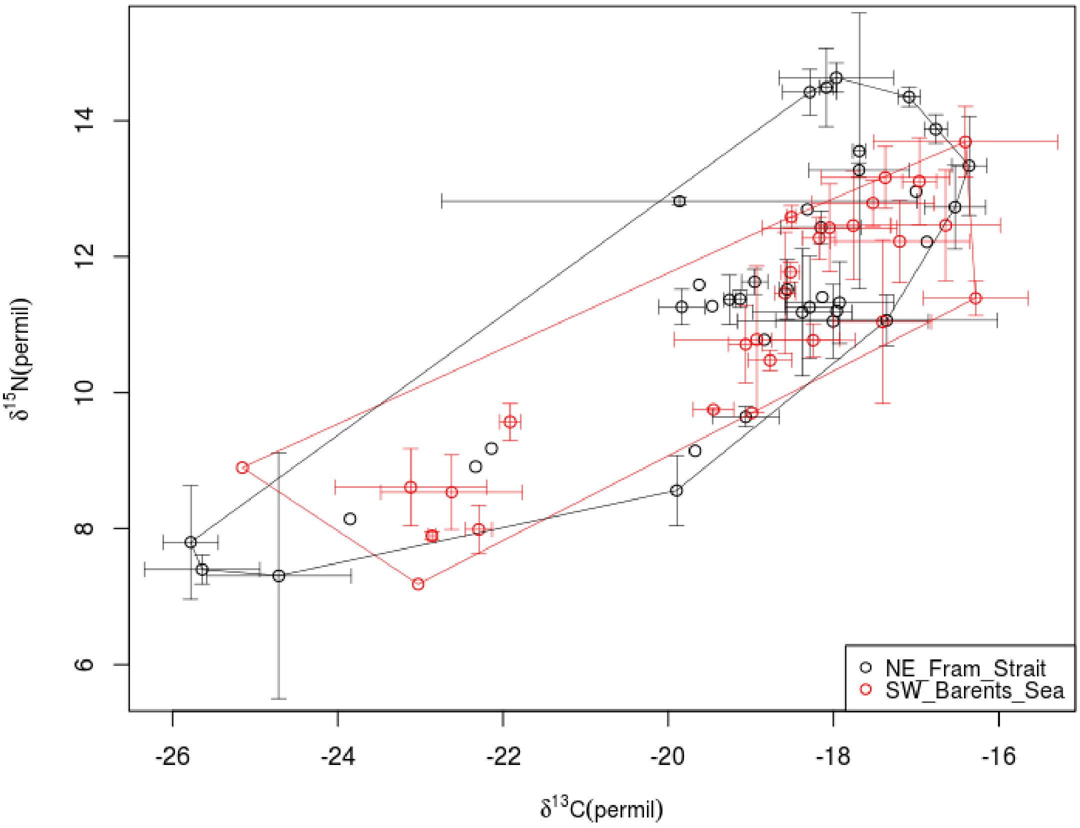

FIGURE 3.2: δ^{15}N:δ^{13}C-biplot of taxa occurring in both the NE Fram Strait and the SW Barents Sea sampling areas, and within the same depth range, ($\leq$ 350). Samples from the NE Fram Strait sampling area (n=38) are black and samples from the SW Barents Sea sampling area (n=28) are red. Convex hulls are shown for both areas. Each point represents the mean per taxa and station. The error bars show the standard deviations of the means.

TABLE 3.1: Layman metrics for the NE Fram Strait and SW Barents Sea sampling areas

	NE Fram Strait	**SW Barents Sea**
TA	25.6	20.8
CD	2.7	2.8
MNND	0.8	0.7
SDNND	0.8	0.4
RN (‰)	6.1	5.2
RC (‰)	8.9	6.6

In the SW Barents Sea sampling area mean δ^{15}N-values ranged from 8.0 ‰ (±0.4 ‰) for the cephalopod *Gonatus fabricii* and 8.0‰ (±0.9‰) for *Themisto* sp. to 13.2 ‰ (±0.5 ‰) for *Sabinea* spp.. Mean δ^{13}C-values ranged from -23.5‰ (±1.3‰) for *Themisto* sp. to -16.9‰ (±1.0 ‰) for *C. crispatus*. The RN was 5.2‰ and the RC was 6.6‰ (tables A.5, A.6 and 3.1 and figure 3.3).

In the NE Fram Strait area the largest standard deviation of the mean in δ^{15}N-values was found in *M. borealis* (1.8‰) and the smallest in the decapod *Pandalus borealis* (0.3‰) and *Themisto* sp. (0.3‰). For the δ^{13}C-values the largest standard deviation was found in *C. crispatus* (1.5‰)

and the smallest in the euphausiid *Meganyctiphanes norvegica* (0.1‰). In the SW Barents Sea area the largest standard deviation of the mean in δ^{15}N-values was found in *C. crispatus* and *M. borealis* (1.1‰) and the smallest in *G. fabricii* (0.4‰). For the δ^{13}C-values the largest standard deviation was found in *Themisto* sp. (1.3‰) and the smallest in *G. fabricii* (0.2‰) (tables A.3, A.4, A.5 and A.6 and figure 3.3).

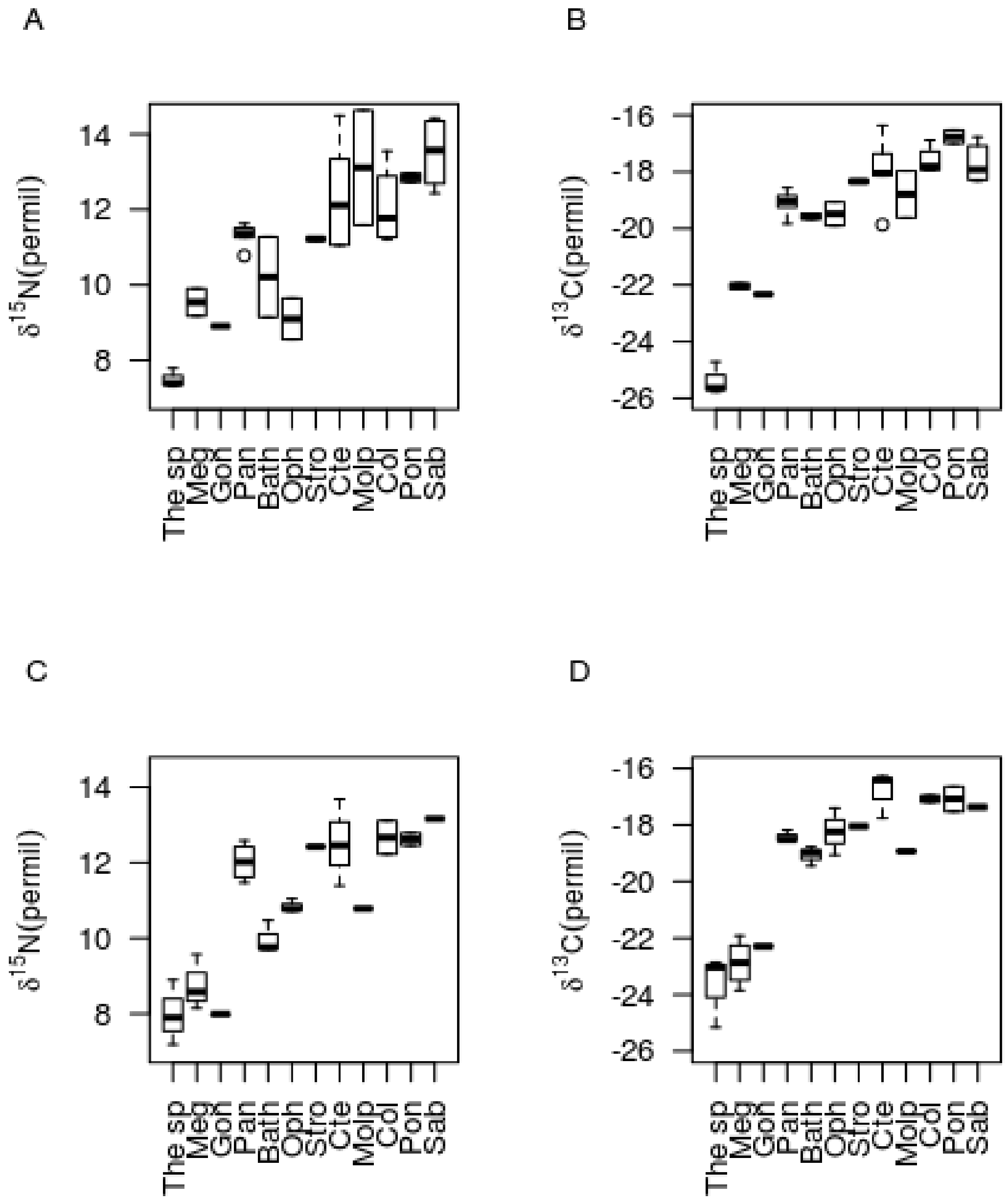

FIGURE 3.3: Boxplots of δ^{15}N- and δ^{13}C-values in 12 invertebrate taxa sampled in both NE Fram Strait and SW Barents Sea, and within the same depth range, ≤350m. The key to the abbreviations for the taxa is found on page IX. A definition of the features in the plots is found in section 2.4 in chapter 2. A) δ^{15}N-values from the NE Fram Strait. B) δ^{13}C-values from the NE Fram Strait. C) δ^{15}N-values from the SW Barents Sea. D) δ^{13}C-values from the SW Barents Sea.

No significant difference in nitrogen isotope values between the NE Fram Strait (mean = 11.4 ±1.9‰) and SW Barents Sea (mean = 10.8 ±1.8‰) areas was detected (T_{60} = 1.4, p-value>0.05, Welch's t-test). Similarly carbon isotopes did not vary significantly between the two areas either, mean$_{NE\ Fram\ Strait}$ = -19.0 ±2.4 ‰ and mean$_{SW\ Barents\ Sea}$ = -19.0 ±2. 9‰, (W = 542, p-value>0.05, Wilcoxon-rank-sum-test)

3.3 Hypothesis 2: Pelagic-benthic coupling is tighter on the continental shelf than on the continental slope

The scatterplot for the continental shelf sampling area and continental slope sampling area showed an almost complete overlap of values within the two areas (figure 3.4). Convex hulls and niche metrics largely reflected the overlap: the TA was 39.0, the CD was 3.0 , the MNND was 0.8 and the SDNND was 0.1 for shelf areas. In the slope area the TA was 33.8 the CD was was 2.8, and MNND 0.8 and the SDNND 0.4 (table 3.2).

TABLE 3.2: Layman metrics for the continental shelf and slope

	Continental shelf (≤350 m)	**Continental slope (>350 m)**
TA	39.0	33.8
CD	3.0	2.8
MNND	0.8	0.8
SDNND	0.1	0.4
RN (‰)	5.7	5.9
RC (‰)	7.7	8.0

On the shelf (<350m) mean δ^{15}N-values ranged from 7.7 ‰ (±0.6 ‰) for *C. islandica* to 13.5 ‰ (±0.8‰) for *Sabinea* spp. and mean δ^{13}C-values ranged from -24.5‰ (±1.3‰) for *Themisto* spp. to -17.1 ‰ (±0.7‰) for *P. norvegicus* and -17.1 ‰ (±1.0‰) for *C. crispatus* (tables A.7, A.8 and figure 3.5). The RN was 5.7‰ and the RC was 7.7‰ (table 3.2).

On the slope the mean δ^{15}N-values ranged from 7.7 ‰ (±0.6 ‰) for *Themisto* spp. to 13.6 ‰ (±1.6 ‰) for *M. borealis* and the mean δ^{13}C-values ranged from -25.4‰ (±1.2‰) for *Themisto* spp. to -17.4‰ (±0.7‰) for *P. norvegicus* The RN was 5.9‰ and the RC was 8.0‰. (tables A.9 and A.10 and figure 3.5).

On the shelf the standard deviation of the mean in δ^{15}N was smallest for *G. fabricii* (0.4‰) and largest for *M. borealis* (2.0‰) and smallest for *G. fabricii* (0.2‰) and largest *Themisto* spp. (1.3 ‰) in δ^{13}C. On the slope the standard deviation of the mean in δ^{15}N was smallest for *P. borealis* (0.3 ‰) and largest for *M. borealis* (1.6‰) and smallest for *P. borealis* (0.2‰) and largest for *C. crispatus* (1.8 in δ^{13}C (tables A.7, A.8, A.9 and A.10 and figure 3.5)

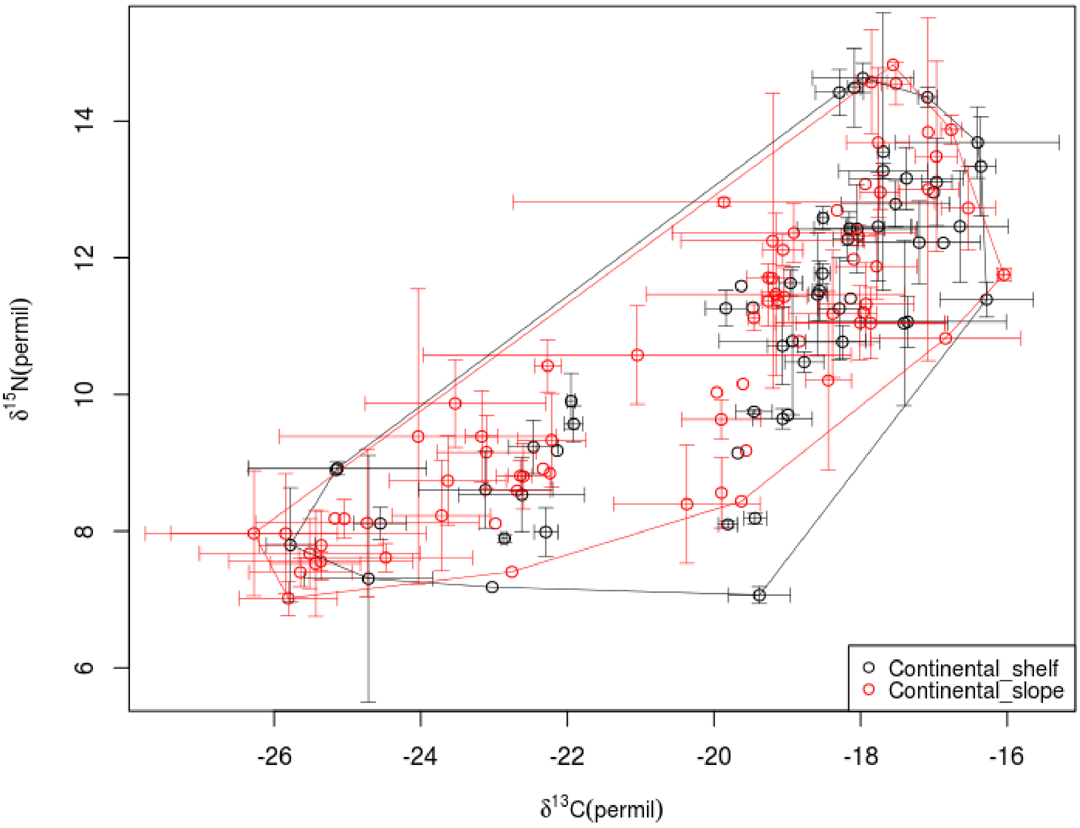

FIGURE 3.4: δ^{15}N:δ^{13}C-biplot of taxa occurring both on the continental shelf and slope sampling areas. Samples from the shelf sampling area (n=57) are black and samples from the slope sampling area (n=71) are red. Convex hull are shown for both areas. Each point represents the mean of replicates per taxon and station. The error bars show the standard deviations of the means.

No significant difference in nitrogen isotope ratios was observed between the continental shelf (mean = 10.9 ± 2.1‰) and slope (mean = 10.4 ± 2.1‰) (W = 2301, p-value>0.05, Wilcoxon-rank-sum-test). The carbon isotope ratios for the shelf (mean = -19.5 ± 2.6 ‰) and carbon isotope ratios for the slope (mean -20.6 ± 3.0 -19.6‰) did differ significantly from each other (W = 2504, p-value<0.05, Wilcoxon-rank-sum-test).

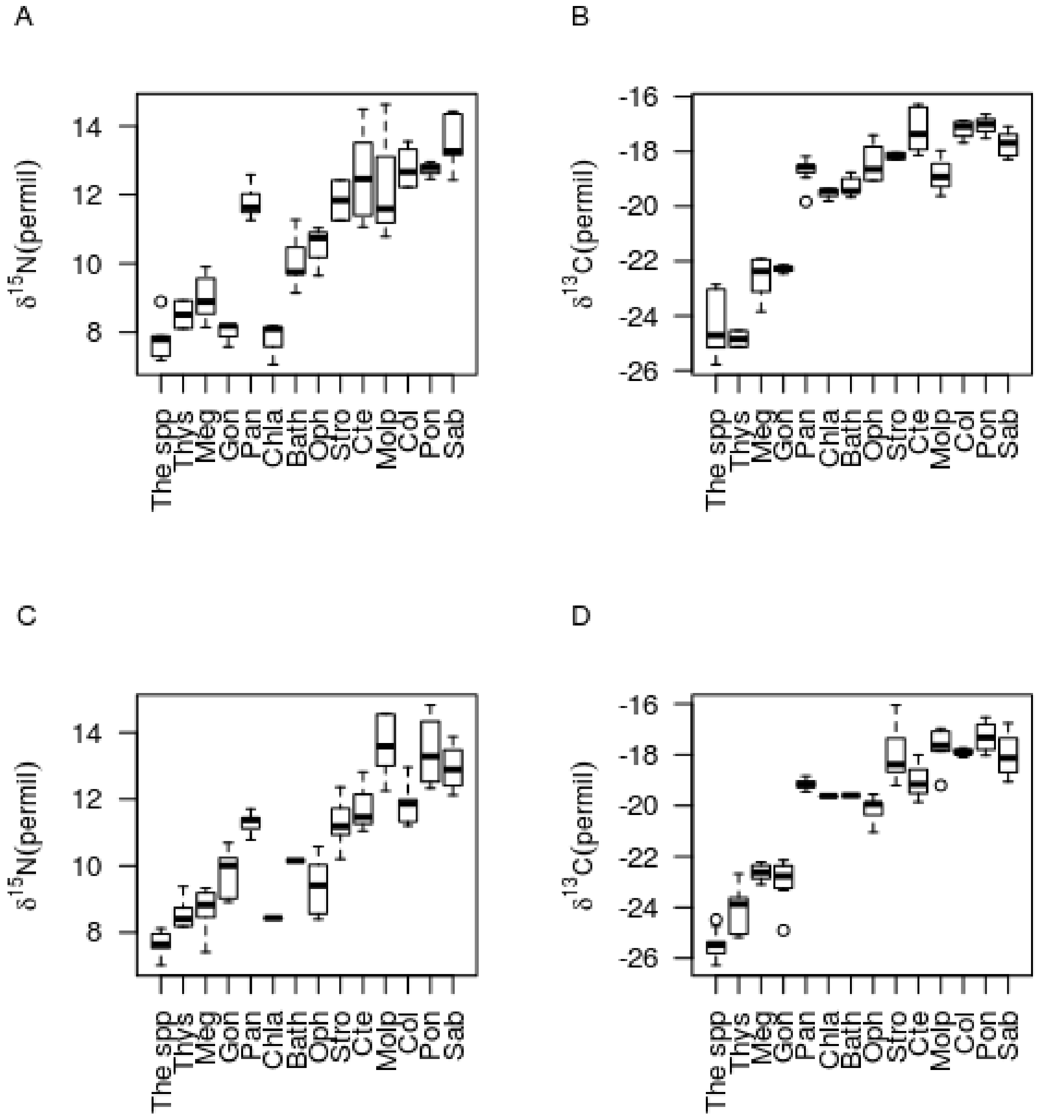

Figure 3.5: Boxplots of δ^{15}N- and δ^{13}C-values in for 14 invertebrate taxa sampled both on the continental shelf and continental slope. The key to the abbreviations for the taxa is found on page IX. A definition of the features in the plots is found in section 2.4 in chapter 2. A) δ^{15}N-values from the continental shelf. B) δ^{13}C-values from the continental shelf. C) δ^{15}N-values from the continental slope. D) δ^{13}C-values from the continental slope

3.4 Hypothesis 3: Obligate benthic feeding guilds are enriched compared to pelagic and benthopelagic feeding guilds and have stronger isotopic enrichment with increasing depth and decreasing latitude.

3.4.1 Hypothesis 3a: Obligate benthic feeding guilds have stronger isotopic enrichment than pelagic and benthopelagic feeding guilds.

Pelagic omnivores were the most depleted in both heavy nitrogen and carbon and benthic carnivores were the most enriched in both heavy nitrogen and carbon (figures 3.6 and 3.7 and tables A.11 and A.12).

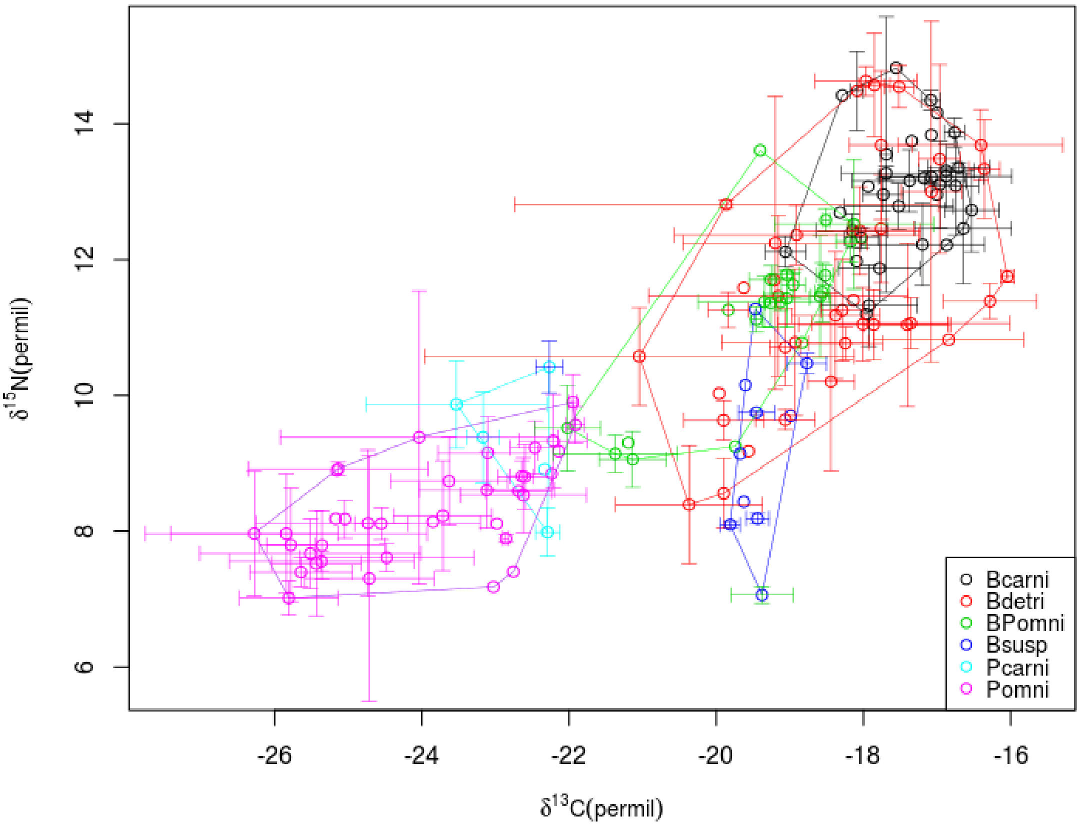

FIGURE 3.6: δ^{15}N:δ^{13}C-biplot of feeding guilds from all sampling areas. Convex hull are shown for each feeding guild. Each point represents the mean of replicates per taxon and station in the given feeding guild. The error bars show the standard deviations of the means. Pomni = Pelagic omnivores, BPomn = Benthopelagic omnivores, Bsusp = Benthic suspension feeder, Bdetri = Benthic detrivores and Bcarni = Benthic carnivores.

In δ^{13}C the data are clearly divided into two clusters; one consisting of the two pelagic feeding guilds (mean=-23.8‰ ±1.4‰) and one consisting of the benthopelagic/benthic feeding guilds (mean=-18.4‰ ±1.2‰) (figures 3.6 and 3.7). When these two groups were compared they were significantly different (W=4324, p-value<0.05, Wilcoxon-rank-sum-test).

In δ^{15}N the same partitioning as in δ^{13}C can be seen, but the pelagic and benthopelagic/benthic feeding guilds are not as separated as for the carbon isotope ratios (figures 3.6 and 3.7). When the pelagic feeding guilds (mean=8.4‰ ±0.8‰) were compared to benthopelagic/benthic feeding guilds (mean=11.7‰ ±1.7‰) they were significantly different (W=4107, p-value<0.05, Wilcoxon-rank-sum-test).

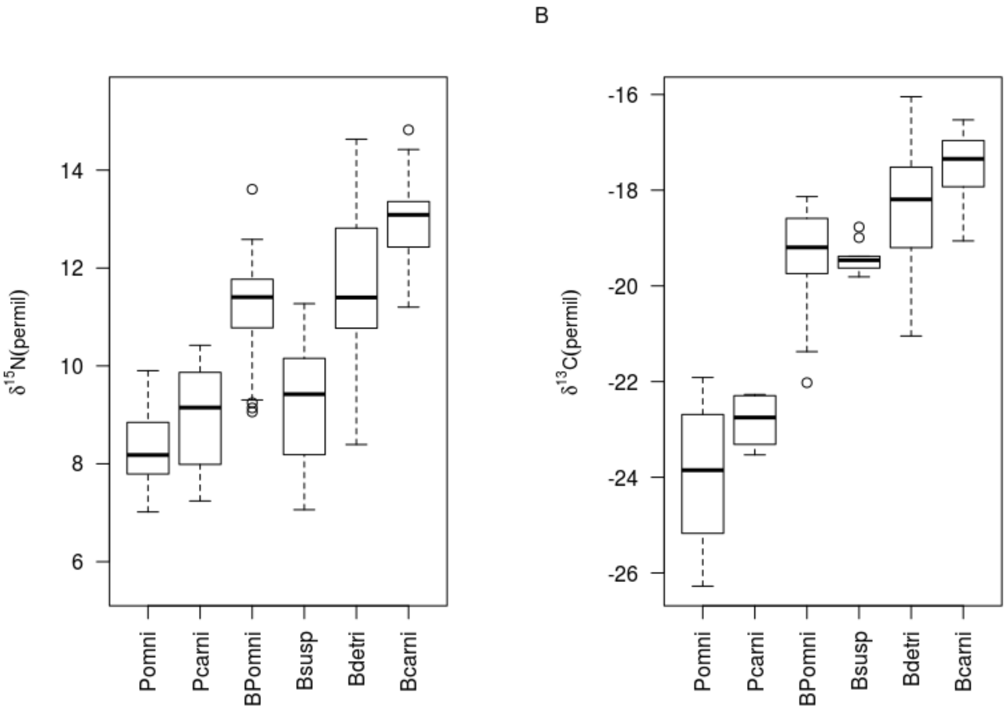

FIGURE 3.7: Boxplots of δ^{15}N- and δ^{13}C-values in 6 feeding guilds from the complete dataset. Pomni = Pelagic omnivores, BPomn = Benthopelagic omnivores, Bsusp = Benthic suspension feeder, Bdetri = Benthic detrivores and Bcarni = Benthic carnivores. A definition of the features in the plots is found in section 2.4 in chapter 2. A) Boxplots of δ^{15}N-values in 6 feeding guilds from the complete dataset. B) Boxplots of δ^{13}C-values in 6 feeding guilds from the complete dataset.

3.4.2 Hypothesis 3b: Obligate benthic feedings guilds have stronger isotopic enrichment with increasing depth and decreasing latitude than pelagic and benthopelagic feeding guilds.

The datasets were too small, and the distributions varied to much for any statistical comparisons between the NE Fram Strait and SW Barents sea sampling areas regarding feeding guilds, for others than pelagic omnivores, benthic detrivores and benthic carnivores. None of them differed significantly (tables 3.3 and 3.4). The remaining feeding guilds were compared visually by using tables A.13, A.14, A.15 and A.16 and figure 3.8. These comparisons did not reveal any obvious differences between feeding guilds in the NE Fram Strait and SW Barents Sea areas, in either δ^{15}N-values or δ^{13}C-values.

TABLE 3.3: Results for Wilcoxon-rank-sum-test for δ^{15}N-values from the NE Fram Strait and SW Barents Sea

Feeding guild	**Mean**$_{NE\ Fram\ Strait}$ **± sd (‰)**	**Mean**$_{SW\ Barents\ Sea}$ **± sd (‰)**	**W**	**p-value**
Pomni	8.3 ± 1.2.	8.4 ± 0.8	16	>0.05
Bdetri	11.8 ± 1.8	11.7 ± 1.1	56	>0.05
Bpred	12.9 ± 1.0	12.8 ± 0.8	54	>0.05

TABLE 3.4: Results for Wilcoxon-rank-sum-test for δ^{13}C-values from the NE Fram Strait and SW Barents Sea

Feeding guild	**Mean**$_{NE\ Fram\ Strait}$ **± sd (‰)**	**Mean**$_{SW\ Barents\ Sea}$ **± sd (‰)**	**W**	**p-value**
Pomni	-24.0 ± 1.9	-22.2 ± 1.0	13	>0.05
Bdetri	-18.4 ± 1.0	-17.8 ± 1.0	32	>0.05
Bpred	-17.5 ± 0.6	-17.1 ± 0.3	19	>0.05

Between the continental shelf and continental slope pelagic omnivores, benthopelagic omnivores, benthic detrivores and benthic predators were compared statistically. None of them differed significantly, see tables 3.5 and 3.6 for test results and mean values. The remaining feeding guilds had too different distributions or too small sample sizes for statistical comparisons (tables A.17, A.18, A.19 and A.20), but they were investigated visually (figure 3.9 and tables A.17, A.18, A.19 and A.20). No differences between the shelf and slope areas could be revealed, apart from in pelagic carnivores in δ^{15}N . However, this feeding guild only contains one species and the sample sizes are too small for any solid conclusions to be based on this visual difference.

TABLE 3.5: Results for Wilcoxon-rank-sum-test for δ^{15}N-values from the continental shelf and slope

Feeding guild	**Mean**$_{shelf \leq 350m}$ **± sd (‰)**	**Mean**$_{slope > 350m}$ **± sd (‰)**	**W**	**p-value**
Pomni	8.4 ± 0.	8.3 ± 0,7	132	>0.05
BPomni	11.8 ± 0.5	11.3 ± 0.3	7	>0.05
Bdetri	11.9 ± 1.4	11.5 ± 1.8	152	>0.05
Bpred	13.1 ± 0.7	12.7 ± 1.0	54	>0.05

TABLE 3.6: Results for Wilcoxon-rank-sum-test for δ^{13}C-values from the continental shelf and slope

Feeding guild	**Mean**$_{shelf \leq 350m}$ **± sd (‰)**	**Mean**$_{slope > 350m}$ **± sd (‰)**	**W**	**p-value**
Pomni	-23.0 ± 1.3	-24.2 ± 1.4	116	>0.05
BPomni	-18.7 ± 0.5	-19.2 ± 0.2	7	>0.05
Bdetri	-17.9 ± 1.0	-18.6 ± 1.3	122	>0.05
Bpred	-17.4 ± 0.5	-17.6 ± 0.7	49	>0.05

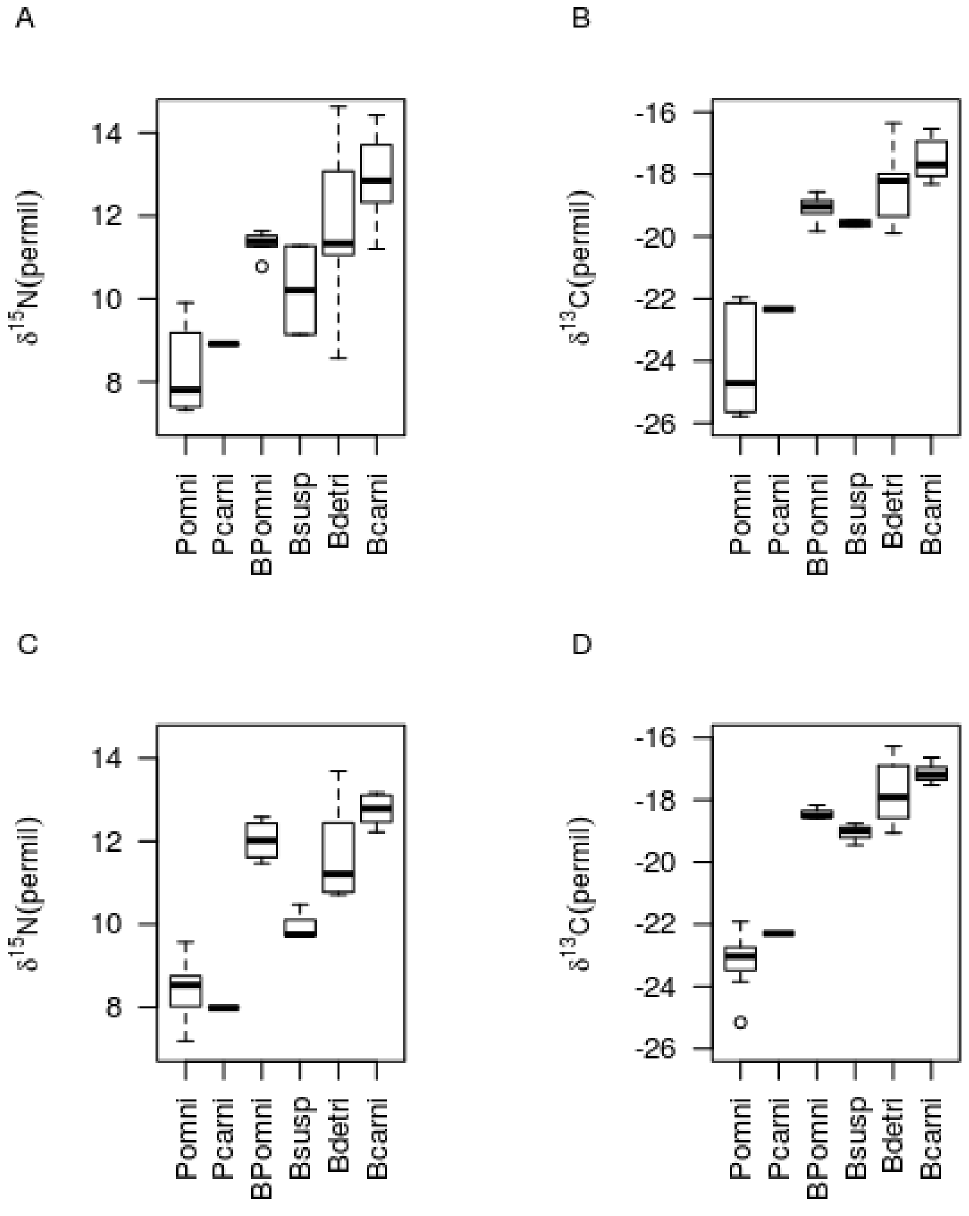

Figure 3.8: Boxplots of δ^{15}N- and δ^{13}C-values in 6 feeding guilds sampled in both NE Fram Strait and SW Barents Sea and within the same depth range, ≤350m. Pomni = Pelagic omnivores, BPomn = Benthopelagic omnivores, Bsusp = Benthic suspension feeder, Bdetri = Benthic detrivores and Bcarni = Benthic carnivores. A definition of the features in the plots is found in section 2.4 in chapter 2. A) δ^{15}N-values from the NE Fram Strait. B) δ^{13}C-values from the NE Fram Strait. C) δ^{15}N-values from the SW Barents Sea. D) δ^{13}C-values from the SW Barents Sea.

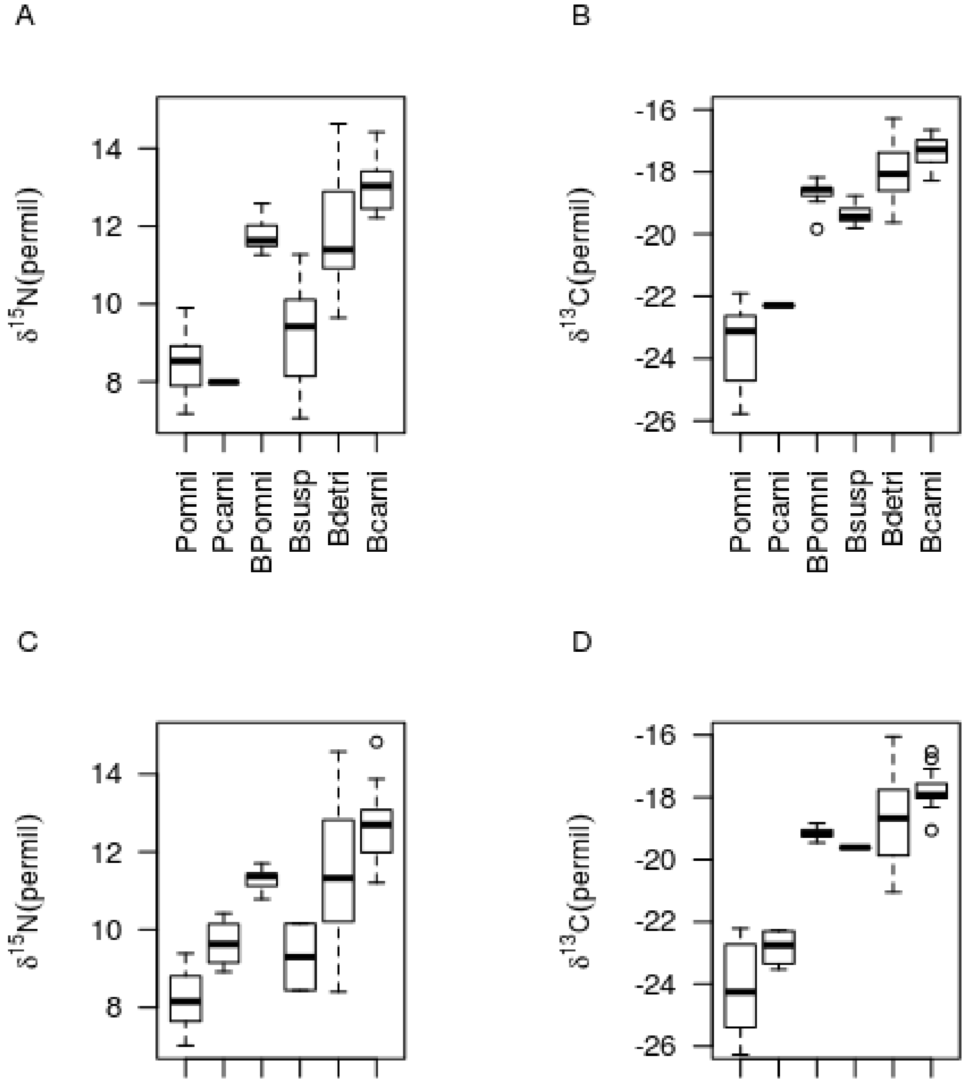

Figure 3.9: Boxplots of δ^{15}N- and δ^{13}C-values in 6 feeding guilds sampled both on the continental shelf and slope. Pomni = Pelagic omnivores, BPomn = Benthopelagic omnivores, Bsusp = Benthic suspension feeder, Bdetri = Benthic detrivores and Bcarni = Benthic carnivores. A definition of the features in the plots is found in section 2.4 in chapter 2. A) δ^{15}N-values from the continental shelf. B) δ^{13}C-values from the continental shelf. C) δ^{15}N-values from the continental slope. D) δ^{13}C-values from the continental slope.

Chapter 4

Discussion

4.1 Hypothesis 1: Pelagic-benthic coupling is tighter in the NE Fram Strait than in the SW Barents Sea

Tighter pelagic-benthic coupling was expected in the NE Fram Strait than in the SW Barents Sea, and this was expected to be reflected in depleted stable isotope ratios in the benthic communities in the north compared to the south. No such difference was observed. Instead a similar partitioning of the data into two distinct clusters of pelagic versus benthopelagic/benthic taxa was observed both in the northern and southern areas. This pattern may indicate a similar decoupling between benthic and pelagic communities in both the NE Fram Strait and the SW Barents Sea. Layman metrics were similar between the NE Fram Strait and the SW Barents Sea (table 3.1).

4.1.1 Advection of Atlantic Water in the West Spitsbergen Current

When entering the Barents Sea the North Atlantic Current splits up in two branches [Loeng, 1991]. The West Spitsbergen Current (WSC) branch flows along the continental slope west of Svalbard, and towards the Yermak Plateau, north of Svalbard [Rudels et al., 2000] (figures 1.1 and 1.2). It transports Atlantic Water towards the Arctic Ocean, and thus influences the biological and physical properties along the Fram Strait and in the Arctic Ocean [Piechura and Walczowski, 2009; Willis et al., 2006]. This advection of warm Atlantic Water and its associated biota [Willis et al., 2006], including larvae of benthic invertebrates, might explain the similarities in food web structure found between the northern and southern sampling areas. Even though the WSC is observed to loose temperature and salinity downstream, it still has an Atlantic Water signature when entering the Arctic Ocean [Boyd and D'Asaro, 1994]. Rudels et al. [2000] showed that the Atlantic Water layer subducts a thin layer of Polar Melt Water, and extends down to between 500m depth, below which there is deep water with low temperature and high salinity. This depth range of the Atlantic layer indicates that most of my samples were taken in the Atlantic Water assemblage, even if they were taken at high latitudes. Tamelander et al. [2006] suggested that northern areas dominated by Atlantic Water may receive more of their organic matter as degraded material than areas dominated by Arctic Water because of the advected inputs and more pelagic dominance in Atlantic Water masses. Feeding on reworked material by the benthic community would enrich its stable isotope ratios [Hobson et al., 1995; Mintenbeck et al., 2007].Tamelander et al. [2006] observed a disparity in δ^{13}C-values between pelagic and benthic taxa in areas dominated by Atlantic Water, and suggested this disparity to be attributed to weaker pelagic-benthic coupling in Atlantic-Water-dominated areas. Iken et al. [2010] showed how there may be substantial differences in isotopic composition and pelagic-benthic coupling in different water masses; also across very short distances; in their study of the communities in the different water masses the southern Chukchi Sea. All these observations may support the theory that the similarities of isotopic values observed in this present study, across large distances and several degrees of latitude, could be attributed to the dominance of Atlantic Water in both areas. This is further supported by the findings of Carroll and Ambrose [2012], who observed stronger pelagic grazing in areas dominated by Atlantic Water on the northern Svalbard Shelf and greater benthic consumption in areas dominated by Arctic Water on the northern Svalbard Shelf. Since the areas sampled in my study both were dominated by Atlantic Water, pelagic dominance, with subsequent release of reworked material to the benthos could then be expected, both in the NE Fram Strait and SW Barents Sea sampling areas. This is also supported by my data, where a disparity in δ^{15}N-values, and especially δ^{13}C-values, between pelagic and benthopelagic/benthic taxa is observed in both sampling areas. This disparity may indicate reworking of organic matter in the pelagic realms, and a weaker pelagic-benthic coupling, as observed by Carroll and Ambrose [2012] and [Tamelander et al., 2006] in areas dominated by Atlantic Water.

The warm Atlantic Water carried in the WSC meets the sea ice along the marginal ice zone north of Svalbard, and consequently contributes to melting of the sea ice. The presence of Atlantic Water and Melt Water in the NE Fram Strait is confirmed by CTD-profiles from the cruise [Ingvaldsen et al., 2017]. The decoupling in δ^{15}N-values and especially δ^{13}C-values between the pelagic and the benthopelagic/benthic taxa seen in all plots, implies that the ice edge bloom might not have been supplied as fresh food for the benthos, since the benthos seemed to rely on enriched, reworked organic matter in both the northern and southern area investigated. It is also possible that sampling took place too long after the ice edge bloom for detecting any signal of it via stable isotope analysis of tissues of the benthic organisms. Whether the ice-edge bloom was non-significant, or if it was consumed in pelagic zone is not possible to conclude from these data, but a substantial northward advection of zooplankton in the WSC [Willis et al., 2006] could increase the grazing pressure on the ice edge bloom. Willis et al. [2006] showed that there was a strong correlation between water mass advection and changes in zooplankton communities in the Kongsfjord, Svalbard and noted how the WSC transported more boreal zooplankton into the Kongsfjord from the beginning of July to the beginning of September in 2002. The same tendency was observed during the SI Arctic cruise during the first two weeks in September, where species that have their center of distribution further south were observed even in the northernmost stations [Ingvaldsen et al., 2017]. For example the northern krill *Meganyctiphanes norvegica*, and the temperate Atlantic krill *Nematoscelis megalops* were both observed north of Svalbard and over deeper waters north of the shelf break [Ingvaldsen et al., 2017]. The presence of these species indicate advection of zooplankton in the WSC, and advection of these zooplankton in the WSC could potentially enhance grazing pressure in the pelagic. This advection of zooplankton in the WSC could provide an explanation for the observed decoupling between benthic and pelagic taxa.

4.1.2 Possible contributions of ice algae

In the offshore Arctic, two main sources of primary production, phytoplankton and ice algae, fuel pelagic and benthic communities [Søreide et al., 2006a; Tamelander et al., 2006]. The northernmost stations in the present study were located along the ice edge on the Yermak Plateau, so ice was certainly present at stations in the northern sampling area. At 80°north the ice algal bloom is estimated to start in February or March, peak in May or June and end in June or July [Leu et al., 2011; Syvertsen, 1991]. Ice algae have been found to contribute significantly to benthic food webs in the Arctic Ocean [Gosselin et al., 1997; Kohlbach et al., 2016], but their importance seem to depend on how extensive the sea ice algal bloom is. Nøst Hegseth [1998] estimated ice algae to contribute to roughly 20% of the primary production in the northern Barents Sea, while Gosselin et al. [1997] estimated ice algae to contribute to on average 57% of total primary production in the multi year ice pack of the Arctic Ocean basins. The stations on the Yermak Plateau were all located along the marginal ice zone, but due to to large transport of Atlantic Water in the WSC along the shelf break west and north-west of Svalbard, the food web in this area appears to be highly influenced by Atlantic Water [Loeng, 1991; Rudels et al., 2000]. Moreover, the stations were in first year ice [Ingvaldsen et al., 2017], were the proportional importance of ice algae is less than in multi year ice [Gosselin et al., 1997]. In addition Tamelander et al. [2008] concluded that the main bulk of organic matter transported to the seafloor in Barents Sea originates from pelagic primary production, even though ice algae may episodically contribute to inputs of fresh organic matter. The proportional contribution of ice algae is therefore more likely to be closer to what Nøst Hegseth [1998] observed in the northern Barents Sea than what Gosselin et al. [1997] observed in the Arctic Ocean. If ice algae only contribute to a small part of the total primary production, they would also be harder to detect via stable isotope analysis, especially when sampling in September, after the pelagic phytoplankton bloom have settled to seafloor. Roy et al. [2014] also discussed how ice algae not were expected to contribute to the carbon pool in the sediment, when sampling in late summer or early fall.

4.2 Hypothesis 2: Pelagic-benthic coupling is tighter on the continental shelf than on the continental shelf break and slope

Tighter pelagic-benthic coupling was expected on the continental shelf than on the slope, and this was expected to be reflected in depleted isotopic ratios in the benthic communities on the shelf compared to slope. My hypothesis was based on observations of isotopic enrichment of both δ^{15}N-values and δ^{13}C-values in particulate organic matter (POM) with depth in several high latitude studies [Dunton et al., 1989; Hobson et al., 1995; McConnaughey and McRoy, 1979; Mintenbeck et al., 2007; Roy et al., 2014]. This enrichment of POM with water depth is mainly caused by fractionation during bacterial remineralization and zooplankton scavenging, resulting in release of ^{14}N and ^{12}C and subsequent enrichment of POM [Checkley and Miller, 1989; Macko and Estep, 1984].

Contrary to this hypothesis, no significant difference in nitrogen stable isotope ratios was found between the shelf and slope, but carbon stable isotope ratios in the two areas differed significantly. A closer investigation of the distributions of the δ^{13}C-ratios for the continental shelf and slope in histograms (figure A.5), suggests the significance to be attributed to differences in distribution shapes rather than differences in central tendency, as the Wilcoxon-rank-sum is sensitive to differences in distribution shapes and symmetry for the populations being compared, and has a high type I error rate when these assumptions are violated [Fagerland and Sandvik, 2009; Voraprateep, 2013]. Especially since the means with their standard deviations overlap for the two areas, the significant difference does not seem to be attributed to differences in central tendency, but rather to differences in distributional shapes (mean_{shelf} = -19.5 ± 2.6‰ and mean_{slope} = -20.6 ± 3.0‰). Also, the Layman metrics in table 3.2 show no difference in food web structure between shelf and slope, which further indicates a similar food web structure between the two areas.

The similarities of food web structure observed between the continental shelf and slope in this study may be attributed to one or several of- to some degree mutually exclusive and contradictory - factors, such as a high grazing pressure by zooplankton advected in the WSC and retention in the upper water column, advection of Atlantic water in the WSC or substantial mixing of the water column . All these factors are discussed in the following paragraphs and are evaluated in light of their likelihood of explaining the present results.

4.2.1 Retention of organic matter in the upper water column

Primary and secondary production in the euphotic zone are essential for life in the deeper realms, where the benthic communities investigated in this study live. Processes in the water column, such as consumption and microbial activity control the quality and quantity of organic matter that is transferred to the benthic community and the proportion that is retained in the water column [Reigstad et al., 2008; Tamelander et al., 2009]. Most retention takes place in the upper water column in the Barents Sea [Olli et al., 2002; Reigstad et al., 2008; Wassmann et al., 2003]

More specifically, Reigstad et al. [2008] showed how the most active retention filter of carbon flux is in the upper 200m, in the northern Barents Sea, east of Svalbard. These authors defined the upper 30-60m as a vertical hotspot, or the most active part of the water column, where most of the retention and heterotrophic grazing take place. Most of the continental shelf stations (depth<350m) in this present study were at depth greater than 200m, so it could be argued that a large fraction of the organic matter was retained in the water column above the shelf benthos samples and the material reaching the shelf seafloor was already degraded and isotopically enriched.

Wassmann et al. [2003] noted that the vertical flux peaked at the compensation point (the depth where primary production equals community respiration rate), and then decreased below this point. These authors further noted how the downward flux of organic matter follows a power function, eventually reaching a vertical asymptote (see fig 1 in Wassmann et al. [2003]). The similarity in stable isotope ratios between the continental shelf and slope in the present study could possibly indicate that the attenuation of the vertical flux has approached its asymptote already at depths less than 350 m. If so, the vertical flux would not attenuate much more when being vertically advected towards greater depths than the continental shelf. Consequently, with minimal additional degradation the organic matter would not enrich farther isotopically when being transported to depth greater than where it reaches this asymptote. This situation could be a plausible reason to why no difference in isotopic enrichment of benthic taxa was observed between the relatively deep continental shelf and continental slope in this study.

4.2.2 Effect of fecal pellets and zooplankton grazing on the downward flux

A discussed previously there is advection of zooplankton in the WSC [Willis et al., 2006], and indices for this was also observed during the data sampling for the present study, where zooplankton having their centre of distribution further south were observed at high latitudes north of Svalbard. The larger advected species, such as *Calanus finmarchicus*, may stimulate the downward flux of organic matter [Komar et al., 1981; Turner, 2015] by producing fast sinking fecal pellets, which may have have contributed to homogenization of stable isotope ratios at shelf and slope stations. Sinking velocities of up to 800m d^{-1} have been recorded for fecal pellets [Cadée et al., 1992]. The high sinking velocity implies that these fecal pellets constitute an important food source for benthic communities at greater depths, where slower sinking particles hardly make their way [Mintenbeck et al., 2007]. Several studies have found fecal pellets to be important in the vertical flux of organic matter [Bathmann et al., 1991; Cavan et al., 2015; Miquel et al., 2015; Nöthig and von Bodungen, 1989]. The fast-sinking fecal pellets of mesozooplankton (>200 µm) are usually enriched in ^{15}N over primary producers to some degree [Checkley Jr and Entzeroth, 1985], but still represent a relatively undegraded food source for the benthos [Iken et al., 2010] especially at greater depths. The fecal pellets can provide a less degraded food source than the ungrazed food items would have when reaching greater depths, had they been sinking on their own [Mintenbeck et al., 2007], thanks to their high sinking velocity.

Microzooplankton (20-200m protists), in contrast, may contribute to more recycling and retention of organic matter in the water column, as they consume and fragment organic matter [Wassmann et al., 2003]. Microbial processes are mediated by fragmentation of larger particles, making them more easily accessible for microbes and giving them a longer residence time in the water column due to their smaller size and slower sinking velocity after fragmentation [Turner, 2015]. The small fecal pellets of microzooplankton sink very slowly and may be more reworked and degraded while sinking, and may be retained in the water column and never reach the seafloor [Wassmann et al., 2003].

Consequently zooplankton abundance may either enhance or suppress the vertical export of organic matter, depending on the composition of the zooplankton community. The similar food web structures observed on the shelf and the slope in this study and the prominent activity of the biological retention filter in the upper 200m of the water column discussed above [Reigstad et al., 2008; Wassmann et al., 2003], could indicate that the organic matter is already attenuated and degraded as it reaches the seafloor of continental shelf. Studies have shown that most fecal pellets produced in the epipelagic zone never sink very far below it, but rather are recycled by the activities of other zooplankton [Turner, 2015]. If the zooplankton attenuates the downward flux of organic matter through ingestion and fragmentation into smaller pieces with a longer residence time in the water column, these processes mostly takes place in the upper 200m of the water column [Reigstad et al., 2008; Wassmann et al., 2003], suggesting that the zooplankton would affect the seafloor of the deeper part of the shelf and the slope in a similar way.

Alternatively, it could be argued that advection of zooplankton in the WSC, and production of fast sinking fecal pellets contributes to effective transport of fresh organic matter out of the euphotic zone, and efficient transport to the benthos, again with similar consequences, both on the continental shelf and slope. If the transport is efficient enough, the organic matter will not be much more degraded when it reaches the slope than when it reaches the shelf and this could potentially explain the similarities in food web structure observed in this study. Size-fractionated stable isotope analysis of the organic matter available for the benthos at different depths could have contributed to clarifying the proportional importance of fecal pellets as a food source for the benthos.

4.2.3 Mixing of the water column in the West Spitsbergen Current

Mixing of the water column is an important factor affecting the sinking velocity of particles, and their subsequent time to degrade and isotopically enrich in the water column. The slope west of Svalbard, where many of the stations in this study were situated, is very steep [Hanzlick, 1983], which promotes vertical mixing [Rippeth et al., 2015] . Rippeth et al. [2015] showed how the rate of dissipation of turbulent kinetic energy, which directly affects vertical mixing, was enhanced by a factor of 100 over the continental slope regions, compared to the central Arctic Ocean. The greatest increase was found on the slope north of Svalbard, and the dissipation rates observed were enough to drive significant turbulent mixing [Rippeth et al., 2015], which in turn could enhance the downward flux of organic matter. Steele and Morison [1993] observed similar patterns for the same area and Padman and Dillon [1991] observed similar trends on the Yermak Plateau. Efficient vertical mixing can be expected along the shelf close to the shelf break, along the shelf break and on the upper part of the slope, down to the depth of the core of the WSC (Arild Sundfjord, NP, personal communication 2017-10-22, and [Hanzlick, 1983]). Saloranta and Haugan [2004] also discussed how the current speed and topographic steering in the WSC increased towards the shelf break and upper part of the slope; where the slope samples in the present study were taken.

The discussion above on turbulent mixing along bathymetric features such as the shelf break and the upper slope together with the discussion by Reigstad et al. [2008] and Wassmann et al. [2003] on substantial retention of organic matter in the upper 200m by biological processes may explain the similarities in food web structure observed between the shelf and the slope in the this study. According to Reigstad et al. [2008] and Wassmann et al. [2003] the organic matter may already be reworked and attenuated by the biological retention filter in the upper water column before reaching the seafloor at the shelf, and according to the discussion on turbulent mixing along bathymetric features by e g Rippeth et al. [2015] suggest that the already degraded organic matter is effectively mixed along the shelf break and slope. Turbulent vertical mixing enhances the downward flux of organic matter [Olli et al., 2002]. With enhanced downward flux the qualitative and quantitative differences in organic matter reaching the benthos in shelf and slope locations would be reduced even if the difference in depth range investigated is considerable.

4.3 Hypothesis 3: Obligate benthic feeding guilds are enriched compared to pelagic and benthopelagic feeding guilds and have stronger isotopic enrichment with increasing depth and decreasing latitude.

This study sampled five feeding guilds, of which three were obligate benthic, one benthopelagic, and two pelagic (table 1.1). Pelagic omnivores were the most depleted feeding guild in terms of both δ^{15}N-values and δ^{13}C-values, followed by pelagic carnivores, benthic suspension feeders, benthopelagic omnivores, benthic detrivores and benthic carnivores. Pelagic and benthopelagic taxa were expected to be less enriched isotopically and less affected by increased reworking of the organic matter by pelagic processes with increasing depth and decreasing latitude. This expectation was based on these groups' ability to undertake vertical migrations, or live higher up in the water column, and feed on fresher material there. This would tie them more closely to the less isotopically enriched and fresher pelagic production. The benthic taxa, which cannot undertake vertical migrations, have to rely on benthic prey or reworked organic matter reaching the seafloor (Hypothesis 3a). This organic matter reaching the seafloor was expected to be more enriched with increasing depth and decreasing latitude. Thus, I hypothesized that the benthic feeding guilds would have more enriched stable isotope ratios, and be more affected by increased reworking of the organic matter by pelagic processes with increasing depth and decreasing latitude than the pelagic feeding guilds (Hypothesis 3b).

Indeed were the pelagic feeding guilds depleted compared to the benthic feeding guilds, especially in ^{13}C, but not compared to the benthopelagic feeders (figures 3.6 and 3.7). Further, the anticipated stronger isotopic enrichment with depth and latitude in benthic versus pelagic and benthopelagic feeding guilds was not confirmed. The rejection of hypothesis 3b is in harmony with the rejections of the two former hypotheses, 1 and 2 regarding latitude and depth (sections 4.1 and 4.2), and the hypotheses are by no means independent of each other.

The data suggested some interesting trends, with a partitioning between pelagic and benthopelagic/benthic feeding guilds, but not between pelagic/benthopelagic and benthic as expected. The partitioning of the data was most obvious for δ^{13}C-values, but it was also significant for δ^{15}N-values (figures 3.1 and 3.7). In the comparison of the pelagic feeding guilds to the benthopelagic/benthic the assumption of symmetry was not met (figures A.6 and A.7). When these assumptions are not met the Wilcoxon-rank-sum-test has a higher type I error rate [Fagerland and Sandvik, 2009]. A type I error is an incorrect rejection of a true null hypothesis. Contrary to when the shelf and slope were compared in chapter 3.3, the means with their standard deviations did not overlap when comparing benthopelagic/benthic and pelagic feeding guilds. Hence it may be less likely that the significance is attributed to a type I error.

One important factor that should be taken into account, when discussing the separation of pelagic and benthopelagic/benthic feeding guilds, is that no samples were lipid extracted before isotope analysis. Lipids have depleted δ^{13}C-values [Post et al., 2007] and the krill species *M. norvegica* and *Thysanoessa inermis* and the amphipods *Themisto* spp. and are all known to be lipid rich [Søreide et al., 2006b]. Significant positive correlations (p-value<0.05) between δ^{13}C-values and C:N-ratios were observed for *T. inermis* ($\text{mean}_{C:N}$=4.9 ± 1.1 and $\text{range}_{C:N}$=[2.8,10.4] and *Themisto* spp. ($\text{mean}_{C:N}$=5.0 ± 1.1 and $\text{range}_{C:N}$=[2.9,7.5]) (figure A.12). For *M. norvegica* ($\text{mean}_{C:N}$=3.6 ± 0.5 and $\text{range}_{C:N}$=[2.5,5.8]) only muscle tissue was analyzed and the δ^{13}C-values were not significantly correlated to the C:N-ratio. This implies that δ^{13}C-values may be biased by lipid content for *T. inermis* and *Themisto* spp., and perhaps be underestimated. Still, with δ^{13}C-values in the range of what was observed for *M.norvegica* for *T.inermis* and *Themisto* spp. there is a considerable gap in δ^{13}C-values between pelagic taxa versus benthopelagic and benthic taxa. The difference in δ^{15}N-values between pelagic taxa and benthopelagic/benthic is also significant, however, and this is unbiased by lipid content.

The partitioning of data into two clusters in figures 3.1, 3.3, 3.5, 3.7, 3.8 and 3.9 indicates reliance on reworked and isotopically enriched benthic material for benthopelagic as well as benthic taxa. This may suggest that the benthopelagic taxa sampled here do not undertake vertical migrations to feed in the pelagic realm, but stay near the bottom and rather rely on reworked and possibly resuspended benthic food particles. Depleted δ^{13}C- and δ^{15}N-values in pelagic groups may indicate a stronger reliance on fresher pelagic food sources. Similar patterns were observed by Hobson et al. [1995] in the NE Water Polynya and by Hobson et al. [2002] in the North Water Polynya off Greenland. Hobson et al. [1995, 2002] observed how consumers relying on pelagic primary production had depleted δ^{13}C-values compared to consumers relying heavily on benthic resources. Also Iken et al. [2001] observed a similar pattern, with pelagic taxa being depleted in ^{15}N compared to benthic taxa, on the Porcupine Abyssal Plain. These authors concluded that highly motile taxa were decoupled from the benthic food wed based on sedimented recycled organic matter and instead feed in the pelagic on fresher material. This interpretation also matches well with more motile, pelagic taxa having depleted δ^{13}C- and δ^{15}N-values, since they may do vertical migrations and feed on fresher material higher up in the water column, and more benthic, less motile taxa having more enriched δ^{13}C- and δ^{15}N-values in this study.

4.3.1 Trophic positions of feeding guilds and taxa within them

My results are largely within the range of stable isotope literature data for benthic taxa in Arctic areas. The literature ranges were rather wide, though, documenting that isotopic ratios for the same taxa may vary widely both spatially and temporarily. Isotope values found in other Arctic studies were from the Chukchi Sea [Iken et al., 2010], Bering Sea [Lovvorn et al., 2005], Beaufort Sea [Bell et al., 2016], Barents Sea [Nilsen et al., 2008; Søreide et al., 2006a; Tamelander et al., 2006], NE Water Polynya off NE Greenland [Hobson et al., 1995], North Water Polynya off NW Greenland [Hobson et al., 2002] and a Greenland fjord [Agersted et al., 2014]. The isotopic ratios from the present study were mostly in the lower part of the range of literature values regarding nitrogen, and well within the ranges regarding carbon.

The pelagic omnivores *Themisto* spp., *T. inermis* and *M. norvegica* were expected to be feeding in the pelagic and to have depleted δ^{15}N-values and δ^{13}C-values, which this study confirms. Petursdottir et al. [2012] have suggested an omnivorous-carnivorous feeding style for the krill *T. inermis* based on stable isotope studies and Huenerlage et al. [2015] have suggested a predominantly herbivorous feeding strategy for *T. inermis* based stable isotope and fatty acids analysis. Others [Agersted and Nielsen, 2016; Agersted et al., 2014; Falk-Petersen et al.] have described both krill species *T. inermis* and *M. norvegica* as omnivorous, but *M. norvegica* as having a more carnivorous feeding strategy. [Agersted and Nielsen, 2016] found *T. inermis* to graze only on items <10m and *M. norvegica* to graze on items > 10m and *M. norvegica* to have a higher grazing rate on copepods than on diatoms. Auel et al. [2002] observed *Themisto libellula* to predate on the herbivorous copepods *Calanus* spp. and *Themisto abyssorum* to have a higher trophic level than *T. libellula* and predate on omnivorous and carnivorous prey. My data showed the most depleted stable isotope ratios for *Themisto* spp., followed by *T. inermis* and *M. norvegica* (figure 3.1), which is partly contradictory to the literature suggesting a more herbivorous feeding strategy for *T. inermis*. *M. norvegica* had the most enriched values of the three, suggesting a more carnivorous feeding style, which matches the literature. When comparing the pelagic omnivores it has to be remembered that no samples were lipid extracted and that both *Themisto* spp. *T. inermis* had δ^{13}C-values significantly correlated to the C:N-ratio (figure A.12 and thus might have δ^{13}C-values biased by lipid content. The fact that the δ^{13}C-values are within the literature range makes the lipid content less of a concern.

In this study only one taxon was assigned to the feeding guild pelagic carnivores, the squid *Gonatus fabricii*. *G. fabricii* was expected to have a more carnivorous feeding strategy and thus be more enriched than the pelagic omnivores, especially in ^{15}N, but less enriched in ^{13}C than the benthic feeding guilds, since *G. fabricii* was expected to feed in the pelagic. *G. fabricii* showed a large variance in δ^{15}N-values, and the mean was surprisingly low considering that *G. fabricii* is described as a predator on fish [Roper et al., 2010]. Zumholz and Frandsen [2006] described how *G. fabricii* ascend into to the water column during night to feed on pelagic prey, hence *G. fabricii* was expected to have less enriched stable isotope ratios than obligate benthic taxa. Roper et al. [2010] described how fish become gradually more and more important in the diet of *G. fabrcii* as they grow larger than 25mm. Juveniles smaller than 25 mm feed on a range of zooplankton prey including chaetognaths, copepods, euphausids and pelagic amphipods [Roper et al., 2010]. *G. fabricii* included in my study were comparatively small (>30mm and <70mm, max size 300 mm [Roper et al., 2010]). If the prey preference in *G. fabricii* is size-dependent as Roper et al. [2010] suggest the small sizes of *G. fabricii* sampled might explain the relatively depleted nitrogen values, similar to the krill *M. norvegica*. The relatively large variance observed in δ^{15}N-values may also be attributed to the size dependent feeding behaviour described by Roper et al. [2010].

Benthopelagic omnivores were expected to have depleted stable isotope ratios compared to obligate benthic feeding guilds. The benthopelagic feeding guild was represented by the shrimps *Pandalus borealis*, *Lebbeus polaris* and *Pasiphaea* spp., which are all are highly motile. The isotope ration found in this study were within the range of literature values [Nilsen et al., 2008] for *P.borealis*, but in the lower range considering δ^{15}N-values. Benthopelagic omnivores were expected to be depleted in ^{15}N and ^{13}C compared to benthic feeding guilds, but the data did not confirm this. Instead, the stable isotope ratios where similar to what was observed for obligate benthic feeding guilds (figure 3.7). Hopkins et al. [1993] and Nilssen et al. [1986], observed a size dependent feeding behaviour for *P. borealis*, with larger individuals (corresponding to females in this protandrous hermaphrodite) relying more on benthic resources and smaller individuals (corresponding to males) relying more on pelagic production. Almost all benthopelagic omnivores in this study were large, and caught in a benthic trawl, apart from a few *Pasiphaea* spp., of which a few individuals were small and caught in a pelagic trawl. *Pasiphaea* spp. had the most depleted δ^{13}C-values of the benthopelagic omnivores, some were almost in the range of pelagic omnivores, and perhaps these small individuals were feeding on fresher, more depleted prey.

Benthic suspension feeders were expected to have enriched stable isotope ratios compared to pelagic and benthopelagic omnivores. My results indicated this in δ^{13}C, but not in δ^{15}N. The depleted mean δ^{15}N-values found for benthic suspension feeders indicate that they presumably feed on lower trophic levels, as suggested by Orejas et al. [2000]. Filter feeding bivalves such as *Chlamys islandica* are often used as a baseline when conducting stable isotope analyses [Kharlamenko et al., 2013; Nadon and Himmelman, 2010; Nerot et al., 2012]. The range of δ^{15}N-values observed in this study however, is substantial, perhaps indicating trophic plasticity and obtaining of food from various trophic levels, especially during periods of starvation when food is limited [Cresson et al., 2016]. More likely, however, is that the only two taxa assigned to this feeding guild,*C. islandica* and *Bathyarca glacialis* exploit different resources, and thus cause a large range δ^{15}N-values. Figure 3.1 shows only a small variance within each taxon, but clearly different δ^{15}N-values for the two bivalves, with *B. glacialis* being more enriched than *C. islandica*.

Iken et al. [2001] showed how benthic suspension feeders may feed on resuspended organic matter, which would give them nitrogen and carbon isotope ratios close to those of benthic detrivores. Resuspension of organic matter may explain the enriched δ^{15}N-values observed for *B. glacialis*, and the enriched δ^{13}C-values observed for both *C. islandica* and *B. glacialis*. The disparity between the δ^{15}N- and δ^{13}C-values observed for *C. islandica* cannot be easily explained solely from the data in this study. The sample size for *C. islandica* is low (n=4), hence it is hard to know if the values observed are extremes or if they are representative for the species in the area. The δ^{15}N-values observed for *C. islandica* were definitely in the lower range when being compared to the literature, while the δ^{13}C-values were within the range of the literature [Nilsen et al., 2008; Tamelander et al., 2006]. δ^{13}C-values similar to pelagic omnivores were observed for *C. islandica* by Tamelander et al. [2006], and they interpreted the depleted δ^{13}C-values in the filter feeding bivalve to indicate how fresh phytodetritus reaching the seafloor is immediately exploited by filter feeders. The same pattern was shown by Dunton et al. [1989] and Hobson et al. [1995]. In contrast, in the present study quite enriched δ^{13}C-values were observed for benthic suspension feeders, which might indicate feeding on resuspended material as suggested by Iken et al. [2001]. Roy et al. [2014] also discussed how microbial activity has been observed to actually deplete δ^{15}N-values of organic matter [Macko and Estep, 1984] and how this microbial alteration could explain some extreme δ^{15}N-values. In this case, if microbial alteration have depleted δ^{15}N, this could provide an explanation for the depleted δ^{15}N-values observed for *C. islandica* even if the bivalve feed on reworked and resuspended material.

The restricted access to fresh food causes many benthic communities to be detrital-based [Bergmann et al., 2009]. Detrital-based benthic food webs often contain consumers with a high degree of feeding plasticity [North et al., 2014; Sweeting et al., 2005]. This is reflected by the large ranges in my results, especially nitrogen isotope ratios, for the benthic detrivores, which may imply that they feed on wide range of resources. The benthic detrivores were expected to have enriched stable nitrogen and carbon isotope ratios compared to pelagic and benthopelagic feeding guilds, which the results in this study confirmed.

Ophiura sarsii had the most depleted values, for both δ^{15}N and δ^{13}C among the benthic detrivores. The depleted values and large variance in δ^{15}N-values for *O. sarsii*, could perhaps be attributed to the species' generalistic feeding behaviour [Harris et al., 2009]. These authors found *O. sarsii* to feed on 31 different taxa, but mainly on arthropods, such as amphipods. Hessler and Jumars [1974] suggested *O. sarsii* to be a facultative scavenger. All these observations would put *O. sarsii* in a carnivorous or scavenging feeding guild, rather than detrivorous, which could explain the δ^{13}C-values observed in this study, but they do certainly not explain the depleted δ^{15}N-values. The depleted δ^{15}N-values observed may be explained by how microbial activity sometimes have been observed to actually deplete δ^{15}N of organic matter [Macko and Estep, 1984; Roy et al., 2014], at least if *O. sarsii* is scavenging in dead organisms. Feeding on motile pelagic taxa, as observed by Harris et al. [2009], can explain the depleted δ^{15}N-values observed, since this would cause less reliance on benthic nitrogen and carbon. Regardless of the cause, *O. sarsii* had carbon and nitrogen isotope ratios within the literature range [Bell et al., 2016; Hobson et al., 1995, 2002; Iken et al., 2010; Lovvorn et al., 2005; Nilsen et al., 2008; Tamelander et al., 2006] but in the lower part of the range considering δ^{15}N and the range for δ^{13}C found in literature was very wide. In conclusion, a huge range in mean δ^{13}C, [-19.0, ‰ ,-11.3 ‰], have been observed for *O. sarsii* in a number of studies in the Arctic [Bell et al., 2016; Hobson et al., 1995, 2002; Iken et al., 2010; Lovvorn et al., 2005; Nilsen et al., 2008; Tamelander et al., 2006], which may indicate a very plastic omnivorous feeding strategy and adaption to seasonal food limitation. So even if the δ^{15}N-values seem very low when compared to diet studies of *O. sarsii*, results within the same range found in other stable isotope analyses. This may indicate that the stomach contentstudies yielded atypical snap shots rather than long term integrated diet habits that stable isotopes reveal.

Strongylocentrotus spp. are described as grazers and where there are no fresh primary producers to graze on, such as in greater depths it grazes on various benthic fauna including barnacles, hydrozoans, bryozoans and foraminifera [Gilkinson et al., 1988]. The sampled stations were too deep even for low-light adapted coralline red algae which are grazed in other shelf areas [Gilkinson et al., 1988]. The δ^{15}N-values indicate feeding on reworked material, and the rather enriched δ^{13}C-values indicate reliance on benthic carbon. This might indicate grazing on reworked benthic detritus. *Strongylocentrotus* spp. were depleted in ^{15}N compared to the other benthic detrivores and carnivores, apart from *O. sarsii*. This may indicate feeding on less reworked material, and perhaps the grazing feeding mechanism make *Strongylocentrotus* spp. feed more superficial than the burrowing *Ctenodiscus crispatus* [Shick et al., 1981] and *Molpadia borealis* [Barnes, 1982]. Stable isotopes ratios observed in this study were within the range compared to literature values [Iken et al., 2010].

Ctenodiscus crispatus, the mud star, is described as a non selective deposit feeder that burrows into the sediments and ingest bulk sediments to get food [Shick et al., 1981]. Since *C. crispatus* consumes reworked benthic material it would be expected to show enriched isotope ratios, which this study confirms. The quite large variance found, especially in δ^{15}N-values can be explained by its non-selective feeding behaviour [Shick et al., 1981]. *C. crispatus* was within the ranges of other isotope studies regarding both nitrogen and carbon isotope ratios [Bell et al., 2016; Nilsen et al., 2008; Tamelander et al., 2006].

The values observed for *Molpadia borealis* in this study were below the range found in the literature [Bell et al., 2016] of nitrogen isotope ratios, but within the range of carbon isotope ratios [Bell et al., 2016]. The wide range of values also suggest non-selective feeding. *M. borealis* burrows into the sediments and feeds on the organic matter that is to be found there [Barnes, 1982; Billett, 1991], hence *M. borealis* was expected to have enriched stable isotope ratios. The carbon and nitrogen isotope ratios observed in this study support this conclusion and indicate reliance on benthic organic matter rather than pelagic. *Molpadia* spp. have body shapes adapted for a burrowing lifestyle and tentacles adapted for shoveling sediments into their mouth [Barnes, 1982]. In addition enzymatic activity in the gut content of *Molpadia blakei* have been observed to indicate capability of breaking down bacterial membranes, and the enteric bacteria of *M. blakei* can break down refractory material [Roberts et al., 2001]. These adaptions enable *M. blakei* to exploit refractory organic matter of low nutritional quality often encountered in the sediments, also outside of peak bloom season, and in this way they can feed without investing to much energy all year round [Iken et al., 2001]. The enriched δ^{15}N-values observed for *M. borealis* in this study imply that they have a similar feeding strategy to *M. blakei*, and hence are well adapted to life in an environment strongly influenced by seasonal inputs of organic matter and periods of low organic matter in the dark season during winter.

In conclusion, the spread of especially δ^{15}N-values for the detrivores is most likely attributed to different feeding strategies among the detrivores, with the enriched *C. crispatus* and *M. borealis* burrowing into the sediments and feeding less selectively, on subsurface material, which is more degraded and hence isotopically enriched. Conversely, the comparatively more depleted values measured for *O. sarsii* and *Strongylocentrotus* spp. could be attributed to more selective feeding on top of the sediments, on newly deposited, fresher and thus isotopically depleted, organic matter. The large variance may also indicate individual specialization and intraspecific differences in food preferences.

The benthic carnivores consist of a group of taxa described as carnivores and scavengers [Birkely and Gulliksen, 2003; Graham, 1988; WoRMS, 2017]. They were expected to have the most enriched stable isotope ratios as they feed on already enriched deposit feeding organisms and hence are the end-consumers of the benthic food web. The shrimps *Pontophilus norvegicus, Sclerocrangon ferox* and *Sabinea* spp. do all have heavily armoured exoskeleton, and in contrast the laterally-compressed swimming benthopelagic taxa they are dorso-ventrally compressed and not adapted to extensive swimming or vertical migrations. The gastropods *Colus* spp. are also obligate benthic species with a heavy exoskeleton. Hence they are expected to rely on organic matter of benthic origin. It has been observed how primarily carnivorous taxa may feed more opportunistically on detritus when food is scarce [Bergmann et al., 2009; Gontikaki et al., 2011]. The overlap in stable isotope ratio between carnivorous taxa and detrivorous taxa may indicate an omnivorous feeding strategy by the carnivorous taxa, where they partly share food resources with the benthic detrivores when food is scarce.

4.3.2 Opportunistic feeding strategies

Some taxa show plasticity in their feeding mode, depending on the period of their life-cycle or presence or absence of resources. Besides food limitation in deeper waters [Bergmann et al., 2009], benthic organisms in high latitudes also experience periods of starvation in the dark time when production in the water column is low, and photosynthetic primary production is absent [Berge et al., 2015]. Benthic organisms in high latitudes can be expected to switch to fresher resources when these are abundant, such as in post bloom season . When access to food is limited, consumers have to rely on a more generalistic feeding strategy and expand their feeding preferences to avoid starving [Bergmann et al., 2009]. Bergmann et al. [2009] also discussed of an increasing degree of omnivory with depth was a plausible explanation to why δ^{15}N-values did not change with depth in benthic carnivores. Gontikaki et al. [2011] observed overlapping diets in benthic detrivores and carnivores and suggested this to be due to omnivorous feeding strategies by benthic carnivores with increasing depth and food limitation in the Faeroe-Shetland Channel. The present study confirms the above findings in that the nitrogen and carbon isotope ratios have overlapping values for benthic carnivores and detrivores, both in the NE Fram Strait and SW Barents Sea areas, and in the continental shelf and slope sampling areas. Sweeting et al. [2005] suggested how large within-population variability indicates omnivory. The variance in the present study barely changed from NE Fram Strait to SW Barents Sea from shelf to slope for the benthic carnivores in the present study. This together with an overlap between detrivores and carnivores may indicate an omnivorous feeding strategy for benthic carnivores in all areas sampled, which in turn possibly may indicate shortage of food in all areas sampled. Investigating this plasticity, either at the taxon or at feeding guild levels, may provide understanding of the influence of changing conditions along vertical or latitudinal gradients on the benthic community. Nevertheless, the data set is rather small for individual feeding guilds, but this is something that could be investigated closer with a larger data material.

4.3.3 Responses in feeding guilds to increasing water depth

Benthic feeding guilds have shown varying trends in their isotopic values with increasing depth [Bergmann et al., 2009; Mintenbeck et al., 2007]. For example Bergmann et al. [2009] observed increasing δ^{15}N-values for suspension feeders, decreasing δ^{15}N-values for detrivores, and no trend for benthic carnivores/scavengers with increasing depth in HAUSGARTEN in Fram Strait. Mintenbeck et al. [2007] also observed enrichment of δ^{15}N-values in suspension feeders with increasing depth in the high Antarctic Weddell Sea and barely detectable effect of depth on δ^{15}N-values in benthic detrivores. These authors argued that the enrichment of δ^{15}N-values with increasing depth observed in suspension feeder could be attributed to their preferential feeding on small suspended particles, which have a longer residence time in the water column. Further Mintenbeck et al. [2007] and Roy et al. [2014] argued that the organic matter integrated in the sediment, on which the benthic detrivores feed, in contrast to suspended organic matter, mainly consist of large fast sinking particles. Mintenbeck et al. [2007] argued that enrichment in fast sinking, large-sized POM is negligible, and to how these fast sinking particles might have almost the same δ^{15}N-value swhen deposited at the seafloor as in the euphotic zone. Finally these authors argued that the barely detectable increase in δ^{15}N-values observed in benthic detrivores was attributed to their non-selective feeding on various particle sizes and ability to feed on large, fast-sinking particles, which would mask increases in δ^{15}N-values due to depth. For benthic detrivores and benthic carnivores, no increase in stable isotope ratios was observed, in trend with the results from Mintenbeck et al. [2007] and Bergmann et al. [2009]. Unfortunately, in this study, the sample size for suspension feeders on the slope was too small (n=2) in this study for a comparison between shelf and slope regarding this feeding guild. Referring to Mintenbeck et al. [2007] and their discussion on particle size and sinking velocity, isotopic enrichment is perhaps only to be expected in benthic suspension feeders, due to their preferential feeding on small suspended particles. Looking at the small sample size for benthic suspension feeders on the slope and the significantly larger sample sizes for the other feeding guilds (tables A.19 and A.20), which according to findings of Mintenbeck et al. [2007]. and Bergmann et al. [2009] are supposed to how less enrichment with depth it perhaps not so striking that no significant differences were observed between the shelf and the slope in the present study.

4.4 Reflections

4.4.1 Sampling regime

Looking back, a couple of key improvements and adjustments in the sampling regime would have improved this study. The most obvious were are the lack of baselines and the relatively few stations sampled in the southern area. The southern area was also sampled one year in advance of the northern area, and stable isotope ratios are know to vary in both space and time [Iken et al., 2010; Tamelander et al., 2006] so this has to taken into consideration while interpreting results.

Pelagic omnivores were sampled as a baseline for trophic calculations, but limited knowledge of the dataset for the SW Barents Sea sampling area caused taxa with limited abundances in the south being sampled in the north. Baselines for the north and the south were then not comparable due to different sample sizes and different taxa sampled. Without a baseline trophic levels could not be calculated. Nevertheless, transformation of δ^{15}N-values into trophic levels require solid a priori information, such as spatially and temporal accurate estimates of carbon sources and fractionation factors. If this a priori information is of poor quality or non-existent, trophic level-transformations may not be accurate, and the trophic structure may be better depicted by relative stable isotope ratios of taxa or feeding guilds. In this study, I therefore discussed trophic position of species relative to each other, but did not calculate trophic levels.

Samples in the northern sampling area were taken in September, whereas samples in the southern sampling area were taken in May and June. Kaufman et al. [2008] estimated the isotopic turnover to be approximately 20 days in arctic amphipods, while McMahon et al. [2006] estimated the isotopic turnover to be approximately 28 days in Arctic bivalves. With a turnover time of 20-28 days samples taken in May and June mainly represent a prebloom state and the samples taken in September a postbloom state. If there was an ice-bloom prior to the phytoplankton bloom, this would not be reflected in the stable isotope values achieved from sampling in September with turnover time ranging from 20-28 days. While these turnover studies suggest ice algal inputs may have been missed in the present study, seasonal trends in isotope signatures are apparently not that pronounced in Arctic benthos, as the variability is integrated in the tissues of long lived organisms[Dunton et al., 1989; McGovern, 2016; Mintenbeck et al., 2007; Søreide et al., 2013]. More specifically Kędra et al. [2012] compared isotope values in benthic samples taken March to August and May to July in Kongsfjord and found a lack of a strong seasonal shift in benthic food web structure. The authors concluded that omnivorous feeding strategies together with detrital food resources dampen the effects of the seasonal primary production at high latitudes. These findings indicate that sampling at different times of the year when comparing different areas probably is of minor importance. Mintenbeck et al. [2007] also discussed how short-term variability is integrated in the tissues of long living organisms. While I cannot exclude that an ice-algal signature may have occurred earlier in the year, these findings indicate that sampling at different times of the year when comparing different areas probably is of minor importance.

There were many more stations in the NE Fram Strait sampling area, than in the SW Barents Sea sampling area (figure 1.1), which makes the sample sizes unbalanced when comparing north and south. However, when only taxa occurring both in the NE Fram Strait and SW Barents Sea, within the same depth range ($\leq$ 350m), were used for the comparison the sample sizes did not differ so much ($n_{NE\ Fram\ Strait}$=38 and $n_{SW\ Barents\ Sea}$=28).

At the taxon level large sample sizes could not be achieved, and there are not replicates for each taxon at each station. Some taxa only occur at a few stations and not in replicates, while some taxa occur at more stations and in replicates. Without replicates it is hard to know if the values achieved are extreme or in the normal range and the variance cannot be assessed. To reduce this problem, taxa were only included in the final analysis of this study if they were present at a minimum of three stations. In some cases species in the same genus were combined, such as for example *Colus* spp.. When the data were subset into north and south within the same depth range or shelf and slope, not all taxa were represented at multiple stations any longer. This is especially the case for the southern subset and the shelf subset, where many taxa were present only at one station. Where only one individual was present, spatial variance can not be assessed, and it is also hard to know if the values achieved were representative for the area under investigation or not. As a whole, however, the data sets had large enough sample sizes when making comparisons between the northern and southern communities, or the shelf and slope communities. Using subsets with comparable taxa and depth, balanced sample sizes were also achieved and statistical comparisons were therefore done at the whole community or for feeding guilds, but not at taxon levels.

4.4.2 Data analysis

Convex hulls may be biased by sample size, and tend to increase as sample size increases [Jackson et al., 2011]. Bayesian ellipses [Jackson et al., 2011] are more robust against differences in sample size and may represent the community better than convex hulls [Jackson et al., 2011]. When only using taxa that were sampled in both the NE Fram Strait and the SW Barents Sea or both on the continental shelf and slope, the sample sizes in this study were rather balanced ($n_{NE\ Fram\ Strait}$=38, $n_{SW\ Barents\ Sea}$=28, n_{shelf}=57 and n_{slope}=71), so the convex hulls would not be so biased by sample size. Further, Bayesian ellipse based approaches are based on normal distribution theory [Jackson et al., 2011; Swanson et al., 2015], and very few sample sets in this study were normally distributed. Therefore, with rather balanced sample sizes and lack of normality I concluded that use of convex hull is advantageous compared to the use of Bayesian ellipses in this case. Further, Cucherousset and Villéger [2015] discussed how it is unlikely observe normality among taxa within a communities, since there often is a limited number of taxa sampled. Thus, these authors concluded that convex hull analysis may provide more accurate results when analyzing overlap between groups of taxa.

4.4.3 Stable isotope analysis

Stable isotope analysis is good tool for studying food webs, but as already mentioned in the introduction there are several drawbacks with the technique. Taxa with very different anatomy were analyzed in this study, and due to this different tissues were analyzed for different taxa. In cases with small individuals, such as for amphipods, whole individuals had to be used and several individuals were pooled to get enough material for analysis. When whole individuals are used for analysis there is no way of knowing if the results are biased by differences in composition between different tissues or not. Compound-specific stable isotope analysis analysis has proven to be the most reliable when comparing different taxa [Budge and Parrish, 1998], but it is very costly and is not always a possible choice.

Lipids are depleted in ^{13}C compared to carbohydrates and proteins [Søreide et al., 2006b]. Therefore, the δ^{13}C-values may be underestimated in lipid rich organisms and this may lead to misleading conclusions regarding the carbon sources [Post, 2002]. To avoid this lipids may be removed prior to stable isotope analysis, but this removal may in turn remove some nitrogenous compounds and deplete δ^{15}N-values [Søreide et al., 2006b]. These authors found nitrogen in their lipid removal extract, suggesting that lipid removal may also remove some proteins and amino acids and should only be done if considered necessary, or on split samples. Furthermore Søreide et al. [2006b] concluded that δ^{15}N-values and δ^{13}C-values of samples with low lipid content are highly comparable regardless of pretreatment, further suggesting that lipid removal is unnecessary if lipid content is low. Studies have shown that benthic organisms are often low in lipid content [Graeve et al., 1997]. Iken et al. [2010] compared isotope ratios before and after lipid removal in individuals of benthic and plankton taxa found that lipids were not affecting δ^{13}C-values in benthic organisms, making lipid removal of these organisms unnecessary. Furthermore, in most cases tissues with slow turnover time and low lipid content were selected (see chapter 2). Only for *Themisto* spp., *Thysanoessa inermis* and a few very small individuals of *M. norvegica* whole organisms were analyzed. Some individual *T. inermis* had a large lipid sac, and these were removed prior to stable isotope analysis. Nevertheless both, *Themisto* spp. and *Thysanoessa inermis* had δ^{13}C-values significantly correlated to the C:N ratio (figure A.12). This is very important to consider when discussing whether the benthic communities are coupled to the pelagic communities or not, based on a difference in δ^{13}C-values. *M. norvegica* did not have δ^{13}C-values significantly correlated to the C:N-ratio, but still had δ^{13}C-values considerably depleted compared to the benthic taxa, which support the conclusion of the benthic taxa being isotopically enriched compared to the pelagic.

4.5 Conclusions

This study documents continuity of trophic structure within northward flowing Atlantic water across several degrees of latitude. This study also shows that previously documented enrichment with depth is not a universal phenomenon, but probably modulated strongly by water mass processes, such as turbulence and vertical mixing. Future studies might focus on identifying the region of transition between Atlantic type versus Arctic type food web. Future studies could also include measurements of hydrography and circulation in the sampling design in addition to trophic biomarkers, to illuminate how oceanographic processes affect the pelagic-benthic coupling. In harmony with the two observations above, no differences in isotopic enrichment were observed for the feeding guilds between the areas sampled. Finally this study confirms the separation of pelagic and benthic trophic pathways observed in earlier studies. This may imply that the anticipated shift in proportion of production retained in surface waters and exported will affect pelagic and benthic taxa in different ways. To get a comprehensive understanding of the key processes in trophic ecology a multi-method approach, combining stable isotope analysis with fatty acid analysis or gut content analysis would be very helpful.

This study highlights how oceanographic processes, such as lateral advection of water masses and vertical mixing, may shape pelagic-benthic coupling and benthic communities, both in shallow areas and at greater depths and across several degrees of latitude. A future study that compare Atlantic Water dominated areas with Arctic Water dominated areas may unravel to what extent water mass properties affect the pelagic-benthic coupling. A future study that compare areas with little vertical mixing with areas with substantial vertical mixing may shed light on to what extent vertical mixing affects the pelagic-benthic coupling.

Appendix A

TABLE A.1: δ^{15}N-values for all invertebrate taxa analyzed in all sampling areas. The integer **n** refers to the number of replicates per taxon and station.

Taxa	**Min (‰)**	**Max (‰)**	**Range (‰)**	**Mean ± sd (‰)**	**n**
Bathyarca glacialis	9.1	11.3	2.1	10.1±0.6	6
Chlamys islandica	7.0	8.4	1.5	7.8±0.6	4
Colus pubescens	12.5	13.8	1.3	13.1±0.6	1
Colus sabini	10.7	15.0	4.3	12.2±1.0	6
Colus holboelli	11.7	12.2	0.4	11.9±0.2	1
Colus spp.	10.7	15.0	4.3	12.4±1.1	8
Ctenodiscus crispatus	10.4	14.9	4.5	12.2±1.3	10
Gonatus fabricii	7.6	10.7	3.1	9.3±1.0	5
Lebbeus polaris	11.0	13.6	2.6	12.1±0.9	4
Meganyctiphanes norvegica	7.4	10.4	3.0	9.0±0.7	14
Molpadia borealis	9.8	15.5	5.7	13.2±1.8	9
Ophiura sarsii	7.6	12.5	5.0	10.0 ±1.1	11
Pandalus borealis	10.8	12.8	2.0	11.6±0.5	13
Pasiphaea spp.	8.7	10.1	1.4	9.2±0.4	5
Pontophilus norvegicus	7.2	14.8	7.6	12.8±0.8	7
Sabinea septemcarinata	12.0	14.8	2.8	13.1 ±0.8	6
Sabinea sarsii	12.7	14.5	1.8	13.9±0.6	3
Sabinea spp.	12.0	14.8	2.8	13.5±0.8	9
Sclerocrangon ferox	12.3	14.2	1.9	13.3±0.4	8
Strongylocentrotus spp.	9.3	13.1	3.9	11.5±0.9	9
Themisto libellula	6.0	8.9	2.9	7.7±0.7	9
Themisto abyssorum	7.9	9.1	1.3	8.0±0.7	2
Themisto spp.	6.0	9.1	3.1	7.7±0.7	11
Thysanoessa inermis	7.5	12.5	5.0	8.6±1.1	8

Table A.2: δ^{13}C-values for all invertebrate taxa analyzed in all sampling areas. The integer **n** refers to the number of replicates per taxon and station.

Taxa	**Min (‰)**	**Max (‰)**	**Range (‰)**	**Mean ± sd (‰)**	**n**
Bathyarca glacialis	-19.7	-18.6	1.1	-19.2±0.4	6
Chlamys islandica	-19.9	-19.0	0.9	-19.5±0.3	4
Colus pubescens	-17.1	-16.7	0.4	-17.0±0.2	1
Colus sabini	-18.9	-16.9	2.0	-17.8±0.5	6
Colus holboelli	-18.2	-16.0	2.3	-17.0±0.9	1
Colus spp.	-18.9	-16.0	2.9	-17.3±0.7	8
Ctenodiscus crispatus	-21.9	-15.3	6.6	-17.7±1.5	10
Gonatus fabricii	-24.9	-22.1	2.8	-22.8±0.8	5
Lebbeus polaris	-20.3	-16.9	3.5	-18.9±0.9	4
Meganyctiphanes norvegica	-23.9	-21.7	2.1	-22.6±0.6	14
Molpadia borealis	-20.3	-16.7	3.6	-18.0±1.0	9
Ophiura sarsii	-23.1	-16.7	6.4	-19.1±1.4	11
Pandalus borealis	-20.1	-18.0	2.1	-18.9±0.5	13
Pasiphaea spp.	-22.3	-19.7	2.6	-21.3±0.8	5
Pontophilus norvegicus	-23.0	-16.0	7.1	-17.2±07	7
Sabinea septemcarinata	-19.3	-16.5	2.7	-18.0±0.7	6
Sabinea sarsii	-18.3	-16.6	1.7	-17.1±0.6	3
Sabinea spp.	-19.3	-16.5	2.7	-17.6±0.7	9
Sclerocrangon ferox	-17.9	-16.1	1.8	-16.9±0.5	8
Strongylocentrotus spp.	-20.3	-16.0	4.3	-18.0±1.1	9
Themisto libellula	-27.3	-23.0	4.3	-25.4±1.1	9
Themisto abyssorum	-25.2	-22.8	2.3	-23.5±1.1	2
Themisto spp.	-25.2	-22.0	3.2	24.4±1.1	11
Thysanoessa inermis	-26.0	-21.7	4.3	-24.0 ± 1.2	8

Table A.3: δ^{15}N-values from the NE Fram Strait sampling area, for 12 invertebrate taxa common to the NE Fram Strait and SW Barents Sea sampling areas, and from depths ≤350m. The integer **n** refers to the number of replicates per taxon and station.

Taxa	**Min (‰)**	**Max (‰)**	**Range (‰)**	**Mean ± sd (‰)**	**n**
Bathyarca glacialis	9.1	11.3	2.2	10.2 ± 1.5	2
Colus spp.	10.7	15.0	4.3	12.0 ± 1.3	4
Ctenodiscus crispatus	10.4	14.9	4.5	12.1 ± 1.4	6
Gonatus fabricii	8.9	8.9	0.0	8.9	1
Meganyctiphanes norvegica	9.2	10.4	1.2	9.7 ± 0.5	2
Molpadia borealis	11.6	14.8	3.2	13.6 ± 1.8	2
Ophiura sarsii	8.2	9.8	1.6	9.2 ± 0.7	2
Pandalus borealis	10.8	12.0	1.2	11.4 ± 0.3	6
Pontophilus norvegicus	12.0	13.2	1.2	12.8 ± 0.5	2
Sabinea spp.	12.2	14.8	2.6	13.6 ± 0.8	6
Strongylocentrotus spp.	10.5	12.0	1.5	11.2 ± 0.7	2
Themisto sp.	6.0	8.6	2.6	7.5 ± 0.3	3

TABLE A.4: δ^{13}C-values from the NE Fram Strait sampling area for 12 invertebrate taxa common to the NE Fram Strait and SW Barents Sea sampling areas, and from depths $\leq 350m$. The integer **n** refers to the number of replicates per taxon and station.

Taxa	**Min (‰)**	**Max (‰)**	**Range (‰)**	**Mean ± sd (‰)**	**n**
Bathyarca glacialis	-19.7	-19.5	0.2	-19.6 ± 0.1	2
Colus spp.	-16.9	-18.9	2.0	-17.7 ± 0.6	4
Ctenodiscus crispatus	-21.9	-15.6	6.3	-17.9 ± 1.5	6
Gonatus fabricii	-22.3	-22.3	0.0	-22.3	1
Meganyctiphanes norvegica	-22.1	-21.9	0.2	-22.0 ± 0.1	2
Molpadia borealis	-19.6	-17.3	2.3	-18.4 ± 1.0	2
Ophiura sarsii	-19.9	-18.0	1.9	-19.3 ± 0.5	2
Pandalus borealis	-20.1	-18.5	1.6	-19.1 ± 0.4	6
Pontophilus norvegicus	-17.0	-16.3	0.7	-16.6 ± 0.4	2
Sabinea spp.	-18.7	-16.6	2.1	-17.6 ± 0.7	6
Strongylocentrotus sp	-18.8	-18.0	0.8	-18.3 ± 0.4	2
Themisto sp.	-26.1	-24.1	2.0	-25.4 ± 0.6	3

TABLE A.5: δ^{15}N-values from the SW Barents Sea sampling area, for 12 invertebrate taxa common to the NE Fram Strait and SW Barents Sea sampling areas, and from depths $\leq 350m$. The integer **n** refers to the number of replicates per taxon and station.

Taxa	**Min (‰)**	**Max (‰)**	**Range (‰)**	**Mean ± sd (‰)**	**n**
Bathyarca glacialis	9.7	10.6	0.9	10.1 ± 0.4	3
Colus spp.	11.3	13.8	2.5	12.6 ± 0.7	2
Ctenodiscus crispatus	11.2	14.1	2.9	12.7 ± 1.1	3
Gonatus fabricii	7.6	8.2	0.6	8.0 ± 0.4	1
Meganyctiphanes norvegica	8.1	9.8	1.7	8.9 ± 0.7	4
Molpadia borealis	10.1	12.0	1.9	10.8 ± 1.1	1
Ophiura sarsii	10.3	12.5	2.2	10.9 ± 0.8	3
Pandalus borealis	10.8	12.8	2.0	12.0 ± 06	4
Pontophilus norvegicus	11.9	13.4	1.5	12.6 ±0.6	2
Sabinea spp.	12.6	13.5	0.9	13.2 ± 0.5	1
Strongylocentrotus spp.	11.9	13.1	1.2	12.4 ± 0.6	1
Themisto sp.	7.2	8.9	1.7	8.0 ± 0.9	3

Table A.6: δ^{13}C-values from the SW Barents Sea sampling area, for 12 invertebrate taxa common to the NE Fram Strait and SW Barents Sea sampling areas, and from depths $\leq 350m$. The integer **n** refers to the number of replicates per taxon and station.

Taxa	**Min (‰)**	**Max (‰)**	**Range (‰)**	**Mean ± sd (‰)**	**n**
Bathyarca glacialis	-19.7	-18.6	1.1	-19.1 ± 0.4	3
Colus spp.	-17.8	-16.0	1.8	-17.1 ± 0.6	2
Ctenodiscus crispatus	-18.3	-15.3	3.0	-16.9 ± 1.0	3
Gonatus fabricii	-22.5	-22.1	0.4	-22.3 ± 0.2	1
Meganyctiphanes norvegica	-23.9	-21.7	2.2	-22.6 ± 0.9	4
Molpadia borealis	-19.6	-17.8	1.8	-18.9 ± 1.0	1
Ophiura sarsii	-19.2	-16.7	2.5	-18.1 ± 0.9	3
Pandalus borealis	-18.7	-18.0	0.7	-18.4 ± 0.2	4
Pontophilus norvegicus	-18.0	-16.0	2.0	-17.1 ± 0.8	2
Sabinea spp.	-18.1	-16.5	1.6	-17.4 ± 0.8	1
Strongylocentrotus spp.	-19.0	-17.5	1.5	-18.0 ± 0.8	1
Themisto sp.	-25.1	-22.9	2.2	-23.5 ± 1.3	3

Table A.7: δ^{15}N-values from the continental shelf sampling area, in 14 invertebrate taxa common to the continental shelf and slope. The integer **n** refers to the number of replicates per taxon and station.

Taxa	**Min (‰)**	**Max (‰)**	**Range (‰)**	**Mean ± sd (‰)**	**n**
Bathyarca glacialis	9.1	11.3	2.1	10.1 ± 0.6	5
Chlamys islandica	7.0	8.2	1.2	7.7± 0.6	3
Colus spp.	11.7	15.0	3.3	12.8± 1.0	4
Ctenodiscus crispatus	10.6	14.9	4.4	12.5 ± 1.3	7
Gonatus fabricii	7.6	8.2	0.6	8.0 ± 0.4	1
Meganyctiphanes norvegica	8.1	10.4	2.2	9.1 ± 0.7	6
Molpadia borealis	10.1	14.8	4.6	12.2 ± 2.0	3
Ophiura sarsii	9.3	11.5	2.2	10.6 ± 0.9	4
Pandalus borealis	10.8	12.5	1.7	11.8 ± 0.6	7
Pontophilus norvegicus	12.1	13.4	1.3	12.7 ± 0.5	3
Sabinea spp.	12.2	14.8	2.6	13.5 ± 0.8	5
Strongylocentrotus spp.	10.6	13.1	2.6	11.8 ± 0.9	2
Themisto spp.	6.0	8.9	2.9	7.8 ± 0.9	5
Thysanoessa inermis	8.0	9.0	1.0	8.5 ± 0.5	2

Table A.8: δ^{13}C-values from the continental shelf sampling area, in 14 invertebrate taxa common to the continental shelf and slope. The integer **n** refers to the number of replicates per taxon and station.

Taxa	**Min (‰)**	**Max (‰)**	**Range (‰)**	**Mean ± sd (‰)**	**n**
Bathyarca glacialis	-19.7	-18.6	1.1	-19.2 ± 0.4	5
Chlamys islandica	-19.9	-19.0	0.9	-19.5 ± 0.3	3
Colus spp.	-17.8	-16.0	1.8	-17.2 ± 0.6	4
Ctenodiscus crispatus	-19.1	-15.3	3.8	-17.1 ± 1.0	7
Gonatus fabricii	-22.5	-22.1	0.3	-22.3 ± 0.2	1
Meganyctiphanes norvegica	-23.8	-21.7	2.0	-22.4 ± 0.8	6
Molpadia borealis	-19.6	-17.3	2.3	-18.6 ± 1.0	3
Ophiura sarsii	-19.4	-16.7	2.7	-18.3 ± 0.9	4
Pandalus borealis	-20.1	-18.0	2.1	-18.7 ± 0.5	7
Pontophilus norvegicus	-18.0	-16.0	2.0	-17.1 ± 0.7	3
Sabinea spp.	-18.4	-16.5	1.9	-17.7 ± 0.6	5
Strongylocentrotus spp.	-19.0	-17.5	1.5	-18.2 ± 0.6	2
Themisto spp.	-25.8	-22.9	2.9	-24.5 ± 1.3	5
Thysanoessa inermis	-26.0	-24.3	1.7	-24.8 ± 0.8	2

Table A.9: δ^{15}N-values from the continental slope sampling area, from 14 invertebrate taxa common to the continental shelf and slope. The integer **n** refers to the number of replicates per taxon and station.

Taxa	**Min (‰)**	**Max (‰)**	**Range (‰)**	**Mean ± sd (‰)**	**n**
Bathyarca glacialis	10.2	10.2	0.0	10.2	1
Chlamys islandica	8.4	8.4	0.0	8.4	1
Colus spp.	10.7	13.1	2.4	11.9 ± 0.8	5
Ctenodiscus crispatus	10.4	12.9	2.5	11.6 ± 1.0	3
Gonatus fabricii	8.9	10.7	1.8	9.8 ± 0.7	4
Meganyctiphanes norvegica	7.4	10.1	2.7	8.9 ± 0.6	8
Molpadia borealis	9.8	15.4	5.7	13.6 ± 1.6	6
Ophiura sarsii	7.5	10.1	2.5	9.3 ± 1.0	6
Pandalus borealis	10.8	11.9	1.1	11.4 ± 0.3	6
Pontophilus norvegicus	12.0	14.8	2.8	12.9 ± 0.9	4
Sabinea spp.	12.0	14.0	2.0	13.0 ± 0.8	4
Strongylocentrotus spp.	10.5	12.7	2.2	11.3 ± 0.9	7
Themisto spp.	7.0	9.0	2.0	7.7 ± 0.6	10
Thysanosessa inermis	7.7	12.5	4.7	8.7 ± 1.2	6

Table A.10: δ^{13}C-values from the continental slope sampling area, in 14 invertebrate taxa common to the continental shelf and slope. The integer **n** refers to the number of replicates per taxon and station.

Taxa	**Min (‰)**	**Max (‰)**	**Range (‰)**	**Mean ± sd (‰)**	**n**
Bathyarca glacialis	-19.6	-19.6	0.0	-19.6	1
Chlamys islandica	-19.6	-19.6	0.0	-19.6	1
Colus spp.	-18.9	-17.2	1.8	-17.9 ± 0.4	5
Ctenodiscus crispatus	-21.9	-16.7	5.2	-18.9 ± 1.8	3
Gonatus fabricii	-24.9	-22.1	2.8	-23.0 ± 0.9	4
Meganyctiphanes norvegica	-23.7	-21.7	1.9	-22.6 ± 0.5	8
Molpadia borealis	-20.4	-16.7	3.6	-17.7 ± 0.9	6
Ophiura sarsii	-23.1	-19.2	3.9	-20.2 ± 1.2	6
Pandalus borealis	-19.5	-18.8	0.7	-19.2 ± 0.2	6
Pontophilus norvegicus	-18.3	-16.3	2.1	-17.4 ± 0.7	4
Sabinea spp.	-19.3	-16.6	2.6	-17.9 ± 1.1	4
Strongylocentrotus spp.	-20.3	-16.0	4.3	-17.9 ±1 .3	7
Themisto spp.	-27.3	-23.0	4.3	-25.4± 1.2	10
Thysanoessa inermis	-25.9	-21.7	4.3	-23.8 ± 1.2	6

Table A.11: δ^{15}N-values for 6 feeding guilds analyzed in all sampling areas. The integer **n** refers to the number of replicates per feeding guild and station.

Feeding guild	**Min (‰)**	**Max (‰)**	**Range (‰)**	**Mean ± sd (‰)**	**n**
Pelagic omnivores	7.0	9.9	2.9	8.3 ± 0.7	37
Pelagic carnivores	7.2	10.4	3.2	9.0 ± 1.2	6
Benthopelagic omnivores	9.1	13.6	4.5	11.2 ± 1.2	22
Benthic suspension feeders	7.1	11.3	4.2	9.2 ± 1.3	10
Benthic detrivores	8.4	14.6	6.2	11.3 ± 1.6	38
Benthic carnivores	11.2	14.8	3.6	13 ± 0.8	33

Table A.12: δ^{13}C-values for 6 feeding guilds analyzed in all sampling areas. The integer **n** refers to the number of replicates per feeding guild and station.

Feeding guild	**Min (‰)**	**Max (‰)**	**Range (‰)**	**Mean ± sd (‰)**	**n**
Pelagic omnivores	-26.3	-21.0	5.3	-24.0 ± 1.4	37
Pelagic carnivores	-23.5	-22.3	1.2	-22.8 ± 0.6	6
Benthopelagic omnivores	- 22.0	-18.1	3.9	-19.4 ± 1.1	22
Benthic suspension feeders	-19.8	-18.8	1.0	-19.4 ± 0.5	10
Benthic detrivores	-21.0	-16.0	5.0	- 18.3 ± 1.2	38
Benthic carnivores	-19.1	-16.5	2.6	- 17.4 ± 0.5	33

Table A.13: delta^{15}N-values for 6 feeding guilds analyzed in the NE Fram Strait sampling area. The integer **n** refers to the number of replicates per feeding guild and station.

Feeding guild	**Min (‰)**	**Max (‰)**	**Range (‰)**	**Mean ± sd (‰)**	**n**
Pelagic omnivores	7.3	9.9	2.6	8.3 ± 1.2	5
Pelagic carnivores	8.9	8.9	0.0	8.9	1
Benthopelagic omnivores	10.8	11.6	0.8	11.3 ± 0.3	6
Benthic suspension feeders	9.1	11.3	2.2	10.2 ± 1.5	2
Benthic detrivores	8.6	14.6	6.0	11.6 ± 1.8	12
Benthic carnivores	11.2	14.3	3.1	12.9 ± 1.0	12

Table A.14: δ^{13}C-values for 6 feeding guilds analyzed in the NE Fram Strait sampling area. The integer **n** refers to the number of replicates per feeding guild and station.

Feeding guild	**Min (‰)**	**Max (‰)**	**Range (‰)**	**Mean ± sd (‰)**	**n**
Pelagic omnivores	-25.8	-21.9	3.9	-24 ± 1.9	5
Pelagic carnivores	-22.3	-22.3	0.0	-22.3	1
Benthopelagic omnivores	-19.8	-18.6	1.2	-19.1 ± 0.4	6
Benthic suspension feeders	-19.7	-19.5	0.2	-19.6 ± 0.1	2
Benthic detrivores	-19.9	-16.4	3.5	- 18.1± 1.0	12
Benthic carnivores	-18.3	-16.5	1.8	-17.5 ± 0.6	12

Table A.15: δ^{15}N-values for 6 feeding guilds analyzed in the SW Barents Sea sampling area. The integer **n** refers to the number of replicates per feeding guild and station.

Feeding guild	**Min (‰)**	**Max (‰)**	**Range (‰)**	**Mean ± sd (‰)**	**n**
Pelagic omnivores	7.2	9.6	2.4	8.4 ± 0.8	7
Pelagic carnivores	7.6	8.2	0.6	8.0 ± 0.4	1
Benthopelagic omnivores	11.5	12.6	1.1	12±0.5	4
Benthic suspension feeders	9.7	10.5	0.8	10 ± 0.4	3
Benthic detrivores	10.7	13.7	2.8	11.7 ± 1.1	8
Benthic carnivores	12.2	13.2	1.0	12.7 ± 0.4	5

Table A.16: δ^{13}C for 6 feeding guilds analyzed in the SW Barents Sea sampling area. The integer **n** refers to the number of replicates per feeding guild and station.

Feeding guild	**Min (‰)**	**Max (‰)**	**Range (‰)**	**Mean ± sd (‰)**	**n**
Pelagic omnivores	-25.1	-21.9	3.2	-23.2 ± 1.0	7
Pelagic carnivores	-22.5	-22.1	0.4	-22.3 ± 0.2	1
Benthopelagic omnivores	-18.6	-18.5	0.1	-18.4 ± 0.2	4
Benthic suspension feeders	-19.5	-18.8	0.7	-19.1 ± 0.3	3
Benthic detrivores	-19.1	-16.3	2.8	- 17.8± 1.0	8
Benthic carnivores	-17.5	-17.3	0.2	-17.1 ± 0.3	5

Table A.17: δ^{15}N-values for 6 feeding guilds analyzed in the continental shelf sampling area. The integer **n** refers to the number of replicates per feeding guild and station.

Feeding guild	**Min (‰)**	**Max (‰)**	**Range (‰)**	**Mean ± sd (‰)**	n
Pelagic omnivores	7.2	9.9	2.7	8.4 ± 0.8	13
Pelagic carnivores	7.6	8.2	0.6	8.0 ± 0.4	1
Benthopelagic omnivores	11.3	12.6	1.3	11.8 ± 0.4	7
Benthic suspension feeders	7.1	11.3	4.2	9.2 ± 1.4	8
Benthic detrivores	9.6	14.6	5.00	11.9 ± 1.4	16
Benthic carnivores	12.2	14.1	2.2	13.1 ± 0.7	12

Table A.18: δ^{13}C-values for 6 feeding guilds analyzed in the continental shelf sampling area. The integer **n** refers to the number of replicates per feeding guild and station.

Feeding guild	**Min (‰)**	**Max (‰)**	**Range (‰)**	**Mean ± sd (‰)**	**n**
Pelagic omnivores	-25.8	-21.9	2.7	-23.0 ± 1.3	13
Pelagic carnivores	-22.5	-22.1	0.4	-22.3 ± 0.2	1
Benthopelagic omnivores	-19.8	-18.2	1.3	-18.7 ± m0.5	7
Benthic suspension feeders	-19.8	-18.8	4.2	-19.4 ± 0.3	8
Benthic detrivores	-19.6	-16.3	5.00	-17.9 ± 1.0	16
Benthic carnivores	-18.3	-16.6	2.2	-17.4 ± 0.5	12

Table A.19: δ^{15}N-values for 6 feeding guilds analyzed in the continental slope sampling area. The integer **n** refers to the number of replicates per feeding guild and station.

Feeding guild	**Min (‰)**	**Max (‰)**	**Range (‰)**	**Mean ± sd (‰)**	**n**
Pelagic omnivores	7.0	9.4	2.4	8.3 ± 0.7	24
Pelagic carnivores	8.9	10.4	1.5	9.6 ± 0.6	4
Benthopelagic omnivores	10.8	11.7	0.9	11.3 ± 0.3	6
Benthic suspension feeder	8.4	10.2	1.8	9.3 ± 1.2	2
Benthic detrivores	8.4	14.6	5.00	11.5 ± 1.8	22
Benthic carnivores	11.2	14.8	3.6	12.7 ± 1.0	13

Table A.20: δ^{13}C-values for 6 feeding guilds analyzed in the continental slope sampling area. The integer **n** refers to number of replicates per feeding guild and station.

Feeding guild	**Min (‰)**	**Max (‰)**	**Range (‰)**	**Mean ± sd (‰)**	**n**
Pelagic omnivores	-26.3	-22.1	2.4	-24.2 ± 1.4	24
Pelagic carnivores	-23.5	-22.3	1.5	-22.8 ± 0.6	4
Benthopelagic omnivores	-19.5	-18.8	0.9	-19.2 ± 0.2	6
Benthic suspension feeder	-19.6	-19.6	0.03	-19.6 ± 0.02	2
Benthic detrivores	-21.0	-16.0	4.0	-18.6 ± 1.3	22
Benthic carnivores	-18.0	-17.6	3.6	-17.6 ± 0.7	13

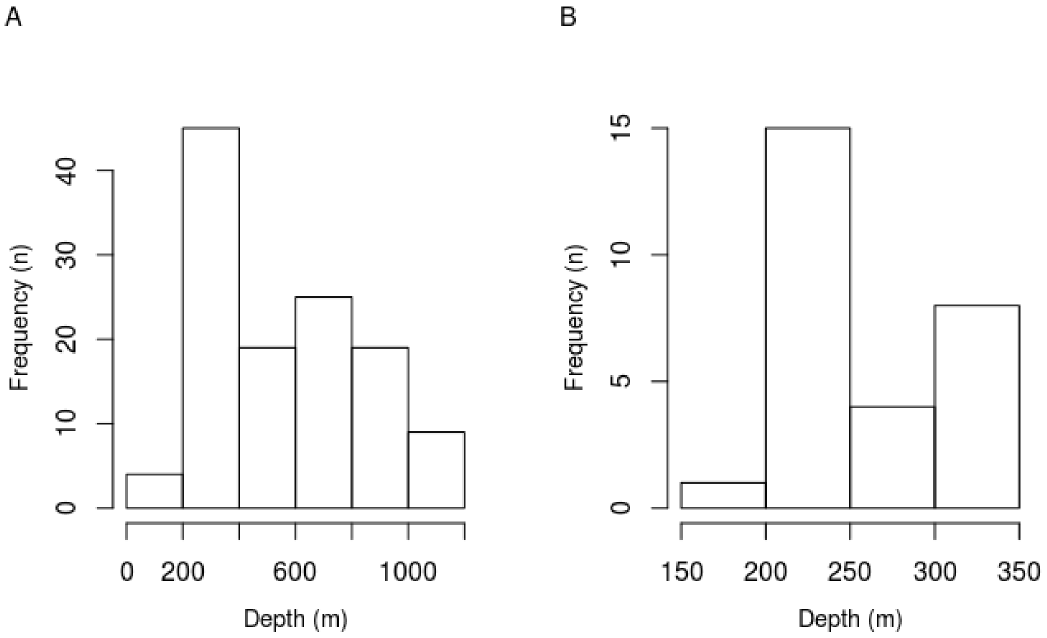

Figure A.1: A) Frequency histogram of depth for samples from the NE Fram Strait. B) Frequency histogram of depth for samples from the SW Barents Sea.

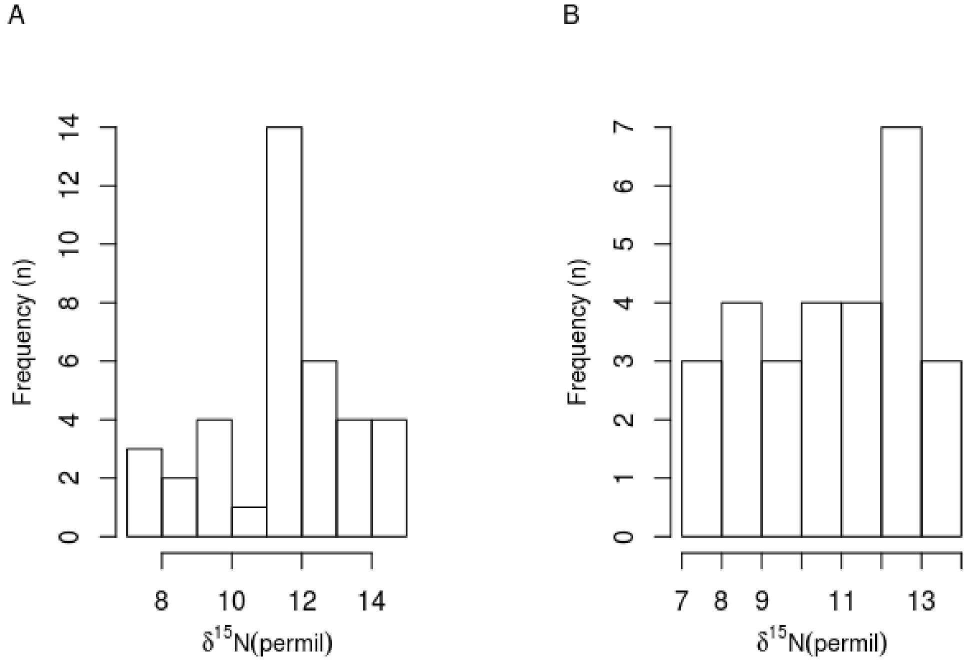

FIGURE A.2: A) Frequency histograms for δ^{15}N-values from the NE Fram Strait. B) Frequency histograms for δ^{15}N-values from the SW Barents Sea.

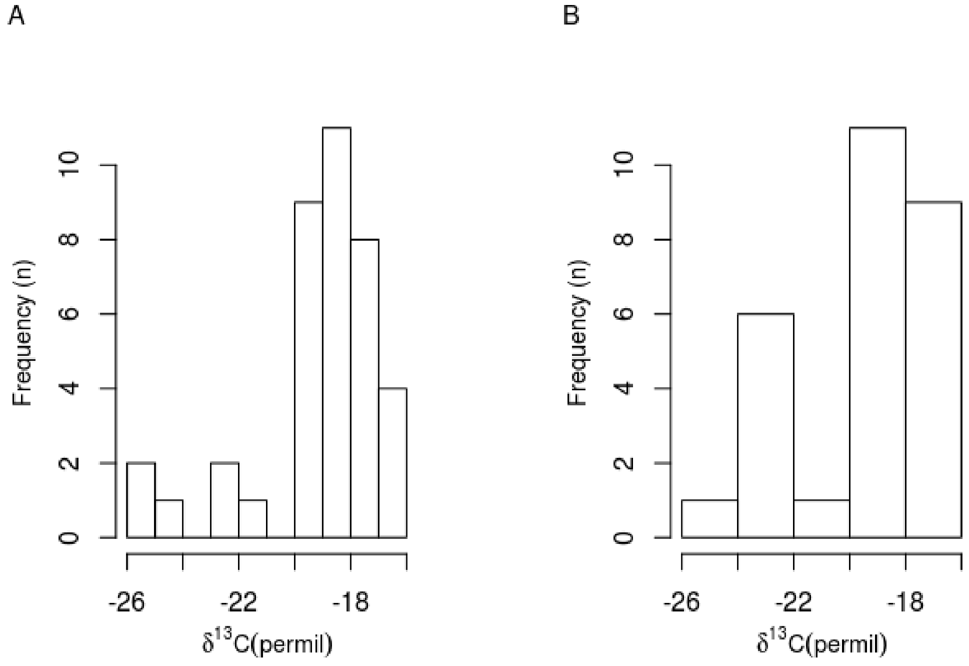

FIGURE A.3: A) Frequency histogram for δ^{13}C-values from the NE Fram Strait. B) Frequency histogram for δ^{13}C-values from the SW Barents Sea.

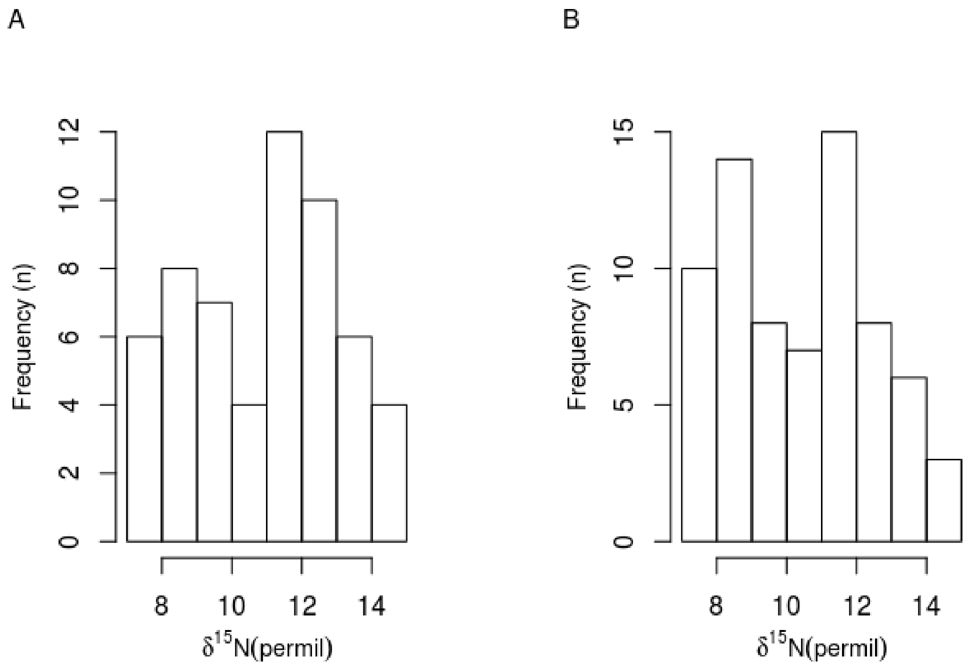

FIGURE A.4: A) Frequency histogram for δ^{15}N-values from the continental shelf. B) Frequency histogram for δ^{15}N-values from the continental slope.

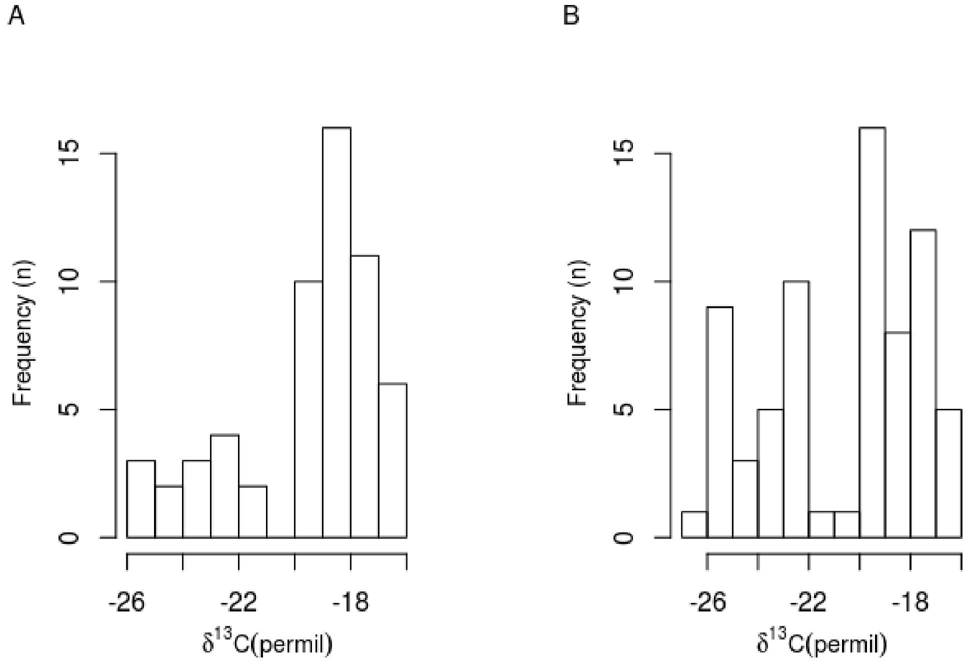

FIGURE A.5: A) Frequency histogram for δ^{13}C-values from the continental shelf B) Frequency histogram for δ^{13}C-values from the continental slope.

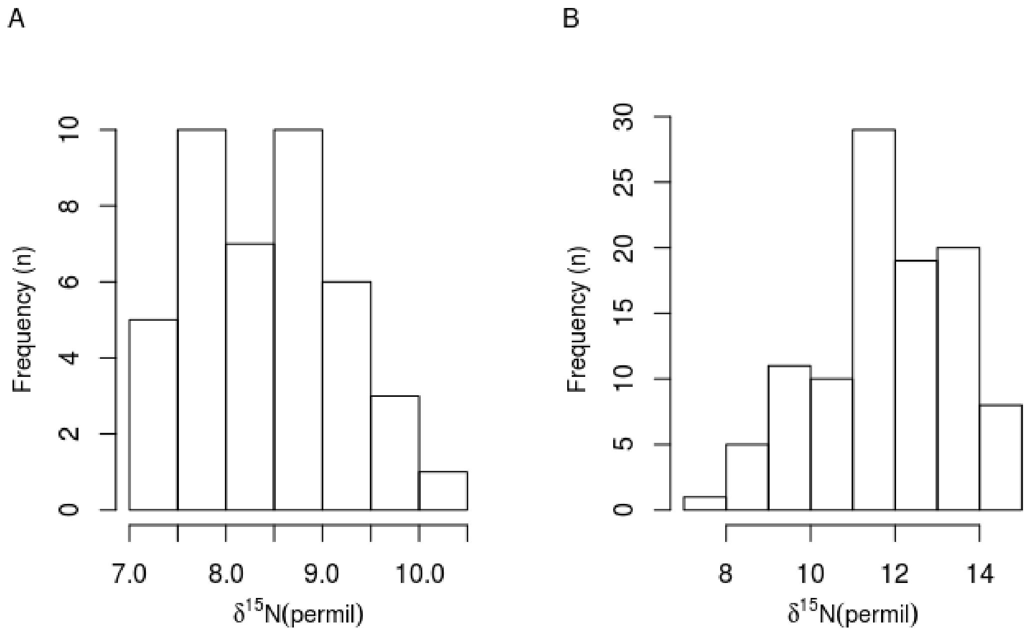

Figure A.6: Frequency histograms for δ^{15}N-values in pelagic and benthopelagic/benthic feeding guilds. A) Frequency histograms for δ^{15}N-values in pelagic feeding guilds. B) Frequency histograms for δ^{15}N-values in benthopelagic/benthic feeding guilds.

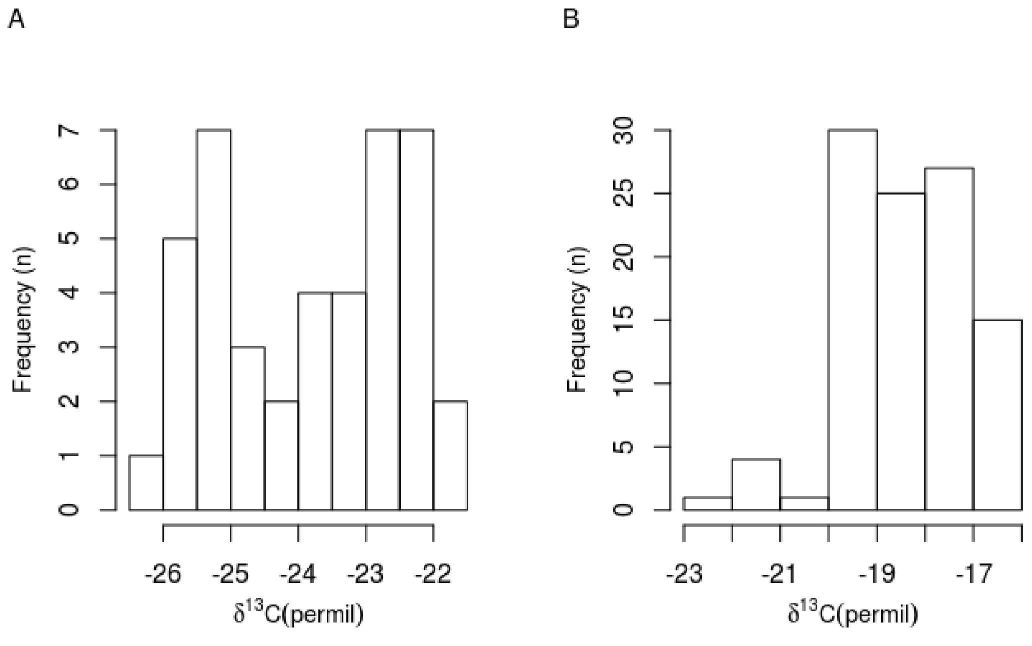

Figure A.7: Frequency histograms for δ^{13}C-values in pelagic and benthopelagic/benthic feeding guilds. A) Frequency histograms for δ^{13}C-values in pelagic feeding guilds. B) Frequency histograms for δ^{13}C-values benthopelagic/benthic feeding guilds.

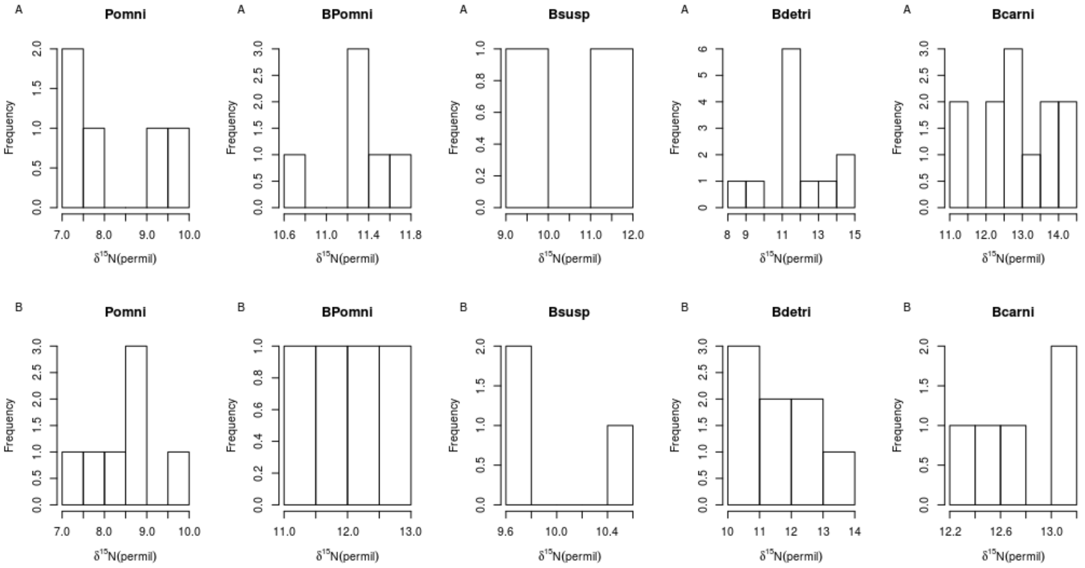

FIGURE A.8: Frequency histograms for δ^{15}N-values in feeding guilds from the NE Fram Strait and SW Barents Sea. Pelagic omnivores were excluded since n=1. A) Frequency histograms for δ^{15}N-values in feeding guilds from the NE Fram Strait. B) Frequency histograms for δ^{15}N-values in feeding guilds from the SW Barents Sea

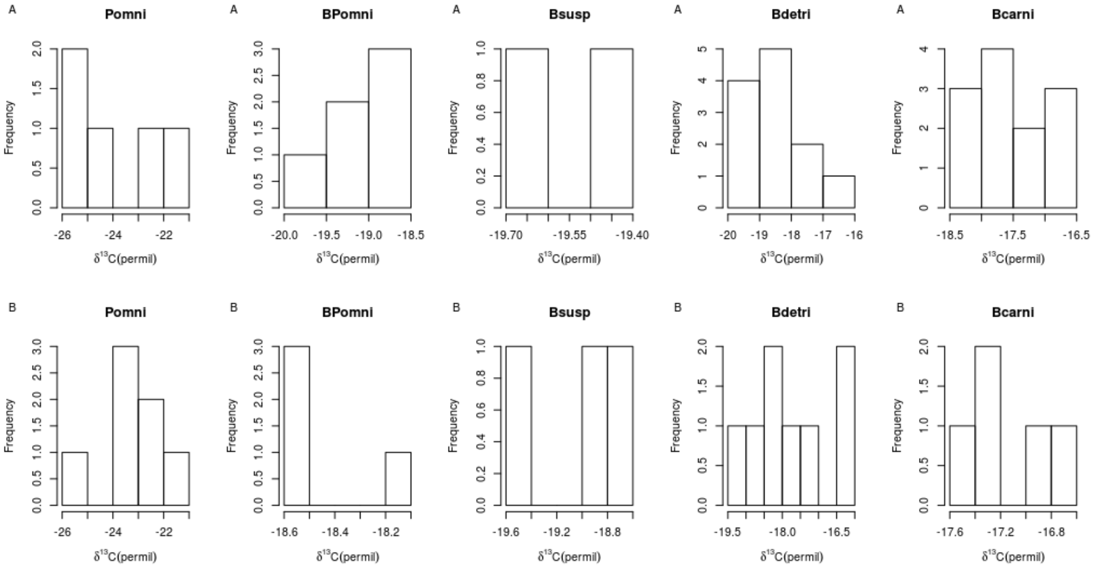

FIGURE A.9: Frequency histograms for δ^{13}C-values in feeding guilds from the NE Fram Strait and SW Barents Sea. Pelagic omnivores were excluded since n=1. A) Frequency histograms for δ^{13}C-values in feeding guilds from the NE Fram Strait. B) Frequency histograms forδ^{13}C-values in feeding guilds from the SW Barents Sea.

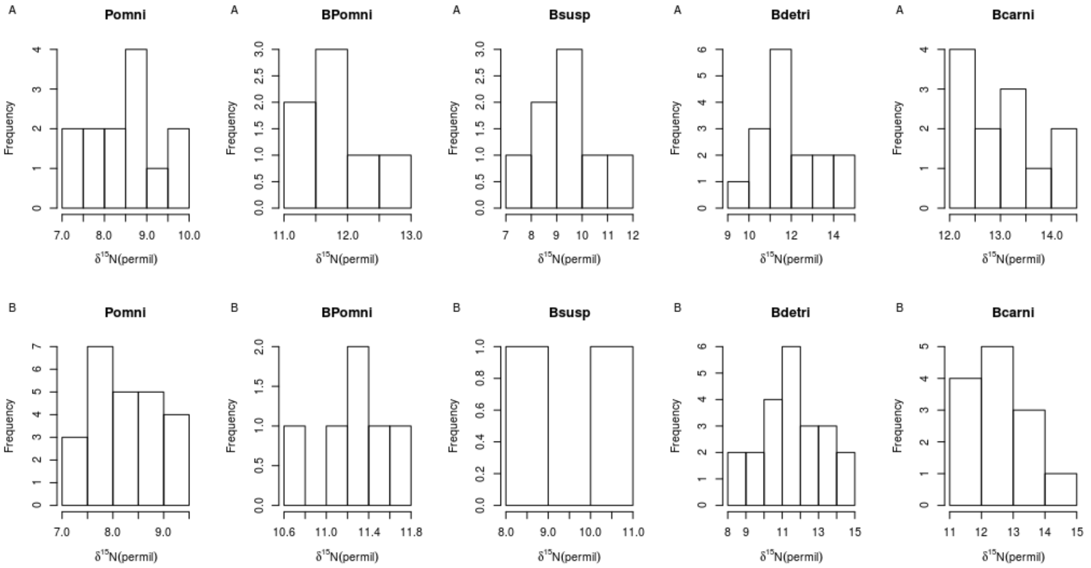

FIGURE A.10: Frequency histograms for δ^{15}N-values in feeding guilds from the continental shelf and slope. Pelagic omnivores were excluded since n=1. A) Frequency histograms for δ^{15}N-values in feeding guilds from the continental shelf. B) Frequency histograms for δ^{15}N-values in feeding guilds from the continental slope.

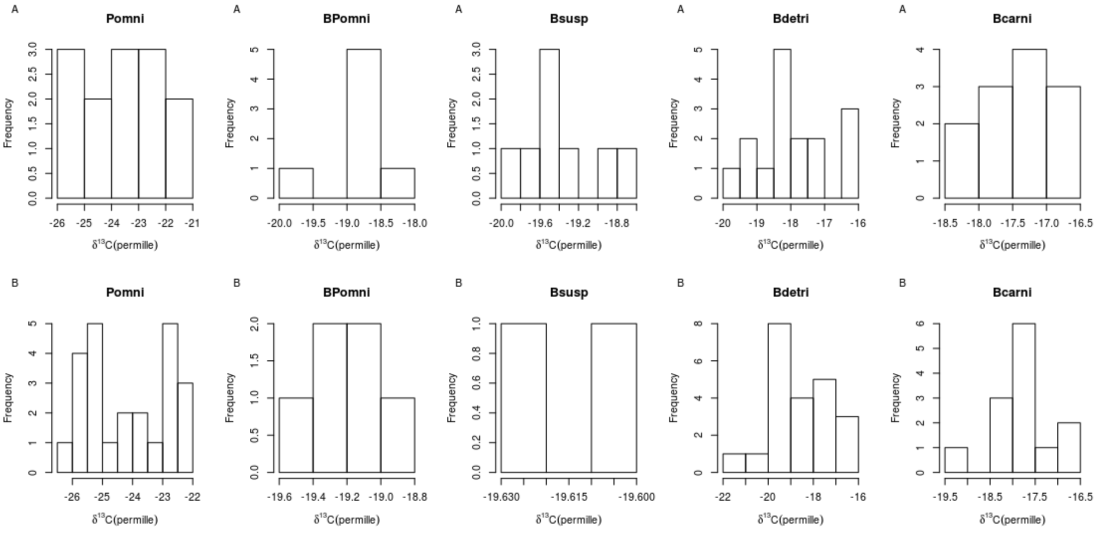

FIGURE A.11: Frequency histograms for δ^{13}C-values in feeding guilds from the continental shelf and slope. Pelagic omnivores were excluded since n=1. A) Frequency histograms for δ^{13}C-values in feeding guilds from the continental shelf. B) Frequency histograms for δ^{13}C-values in feeding guilds from the continental slope.

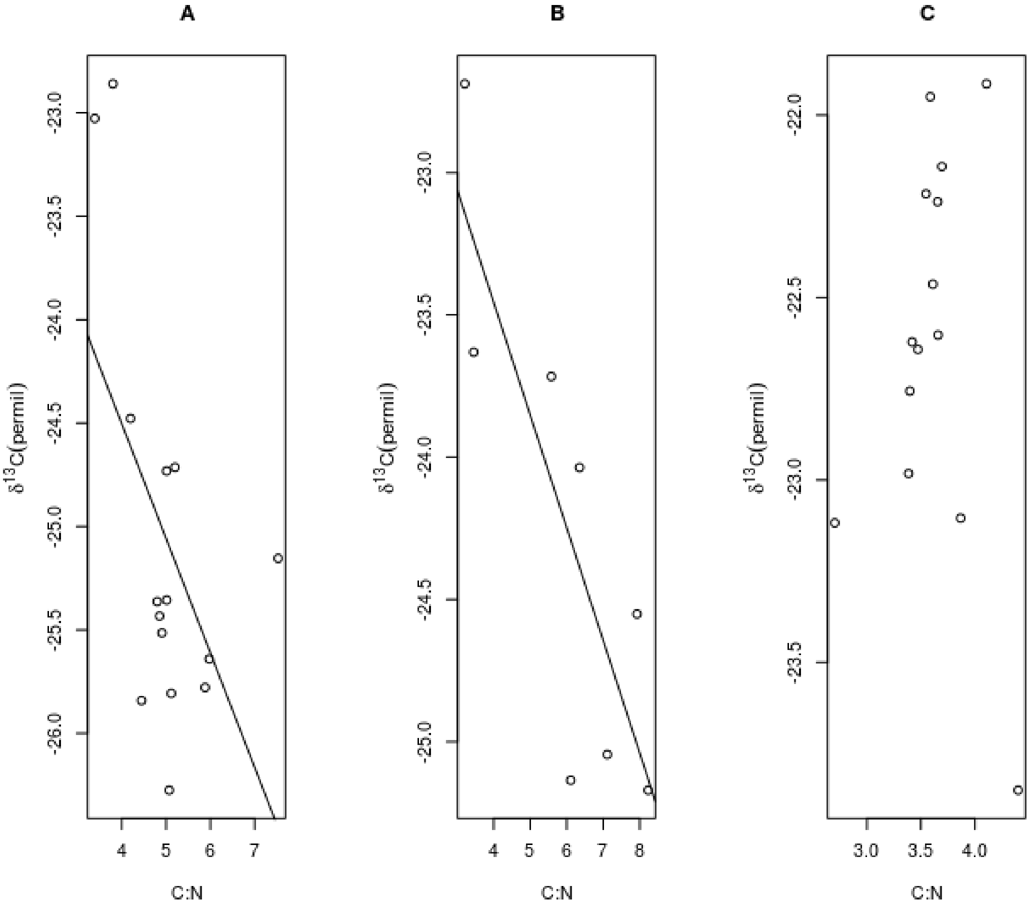

FIGURE A.12: A) Correlation of δ^{13}C-values and C:N-ratios for *Themisto* spp, $F_{1,13}$=5.5, R^2=0.3, $p\text{-value}<0.05$. B) Correlation of δ^{13}C-values for *Thysanoessa inermis*, $F_{1,6}$=13.8, R^2=0.7, $p\text{-value}<0.05$. C) Correlation of δ^{13}C-values for *Meganyctiphanes norvegica*, $F_{1,12}$=0.05, $p\text{-value}>0.05$

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