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Lower trophic level mixed fishery (LOTROMIX)

Implications for ecosystem and management

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Marine Coastal Development
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Abstract

There is an increasing interest in new marine resources for the production of aquaculture feed, to meet the increasing growth of the aquaculture industry. Marine species from lower trophic levels are a potential resource that could partly cover the increasing need for lipid and protein in aquaculture feed. The mesopelagic layer present a variety of species that is estimated to hold a vast biomass to harvest from, both globally and in the Norwegian Sea and fjords. Marine species at high latitudes are known for a high lipid content, with a potential for high concentrations of essential fatty acids and polyunsaturated fatty acids that are sought to incorporate into aquaculture feed.

The main objective of this present study was to quantify the species composition and assess the biomass distribution and production in the Norwegian Sea and fjords by trawling. The catch were further analysed, and the suitability catch from the mesopelagic layer would provide as a feed component was determined by analysing the total lipid content, and further assess the fatty acid and lipid class composition.

Catches from the mesopelagic layer showed high variation in densities of species at different season and location. With jellyfish and mesopelagic fish dominating the hauls conducted in the fjords, while krill and mesopelagic fish were dominating the hauls at sea. The mesopelagic fishes *Maurolicus muelleri* (Gmelin, 1789) and *Benthosema glaciale* (Reinhardt, 1837) had the highest lipid content of the analysed species from the mesopelagic layer, with mixed layer samples containing an average of 30.6 % lipid from dry weight, equivalent to 9.1 % lipid of wet weight. Placing a mixed catch from the mesopelagic layer between some of the pelagic fish species that are the main source of fishmeal and fish oil today in regards of lipid content. The highest lipid content was found in samples collected in the fjords during spring. The fatty acid composition of the catch contained favourable amounts of both PUFA and DHA+ EPA in all samples. With higher relative content found in smaller and leaner samples. The lipid class composition was satisfying, with the mixed layer samples containing well beneath the upper limit for the potentially limiting wax ester.

Sammendrag

Det er en økende interesse for nye marine fôrkilder til å produsere fôr til akvakultur, dette for å kunne møte den økende veksten av akvakulturindustrien. Marine arter fra lavere trofiske nivå er en potensiell kilde som kan bidra til fylle det økende behovet for protein og olje i akvakulturfôr. Det mesopelagiske laget presenterer en høy variasjon av arter som er estimert til å inneha enorme biomasser å høste fra både globalt, og i Norskehavet og fjordene. Marine arter ved høye breddegrader er kjent for et høyt innhold av lipid, som gir et potensiale for høye konsentrasjoner av essensielle fettsyrer, og flerumettede fettsyrer som er ønskelig å inkorporere i akvakulturfôr.

Formålet med denne studien var å kvantifisere artskomposisjonen og distribusjonen denne biomassen utgjør i Norskehavet og fjorder ved hjelp av trålhal. For deretter å evaluere fangstens egenskaper som fôrkomponent ved hjelp av analyser på totallipidinnhold og deretter fettsyre- og lipidklassekomposisjon.

Fangstdataene i denne studien, viste høy variasjon i tettheten av ulike arter ved ulike sesonger og lokasjoner. Maneter og mesopelagisk fisk var de dominerende komponentene i trålhal gjennomført i fjordene, mens krill og mesopelagisk fisk var de dominerende komponentene i havet. De mesopelagiske fiskene *Maurolicus muelleri* (Gmelin, 1789) og *Benthosema glaciale* (Reinhardt, 1837) innehadde det høyeste lipidinnholdet blant de analyserte artene, hvor samleprøver fra det mesopelagiske laget hadde et gjennomsnittlig lipidinnhold på 30.6 % fra tørrvekt, noe som tilsvarer 9.1 % lipid av våt vekt. Dette plasserer en samlet fangst fra det mesopeleagiske laget mellom pelagiske fiskearter som utgjør de viktigste kildene til produksjon av fiskemel- og olje i dagens produksjon med tanke på lipidinnhold. Det høyeste lipidinnholdet ble funnet i prøver innhentet om våren i fjordene. Fettsyrekomposisjonen av artene viste fordelaktig innhold av både flerumettede fettsyrer og DHA+EPA i alle prøver, med et relativt høyere innhold i prøver fra mindre og magrere individer. Lipidklassekomposisjonen viste seg å være tilfredsstillende, hvor samleprøvene hadde et innhold av den potensielt begrensende lipidklassen voks estere langt innenfor de øvre grenseverdiene. Hvilket tilsier at fangst fra det mesopelagiske laget kan utgjøre en komponent i fôr til laksefisk, og for et menneskelig konsum av produkter fra akvakulturindustrien.

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Abbreviations

ALA	α-linoleic acid, 18:3n-3
CH	Cholesterol
DHA	Docosahecaenoic acid, 22:6n-3
DPA	Docosapentaenoic acid, 22:5n-3
DVM	Diel vertical migration
DW	Dry weight
EFA	Essential fatty acid
EPA	Eicosapentaenoic acid, 20:5n-3
FA	Fatty acids
FFA	Free fatty acids
FAME	Fatty acid methyl esters
FAOH	Fatty acid alcohols
FATM	Fatty acid trophic marker
FFA	Free fatty acids
GC	Gas chromatography
HPTLC	High performance thin layer chromatography
IDVM	Inverse diel vertical migration
LC	Long chain
MUFA	Monounsaturated fatty acids
NF	Neutral lipids
PL	Phospholipids
PUFA	Polyunsaturated fatty acids
RPM	Revolutions per minute
SD	Standard deviation
SEM	Standard error of mean
SFA	Saturated fatty acids
TAG	Triacylglycerol
WE	Wax ester

1 Introduction

The aquaculture industry has increased steadily in biomass production since the 1980's, as shown in Figure 1.1 particularly since the end of the 1990's. The global aquaculture production of fish has increased from 55.7 mill tons in 2009, to 73.8 mill tons in 2014. Increasing from 31.1 % to 44.1 % of the total fish production in 5 years (FAO, 2016). Future predictions estimate that the aquaculture production will account for 93.6 million tons of fish, and will contribute with 62 % of the global supply of fish by 2030 (World Bank, 2013).

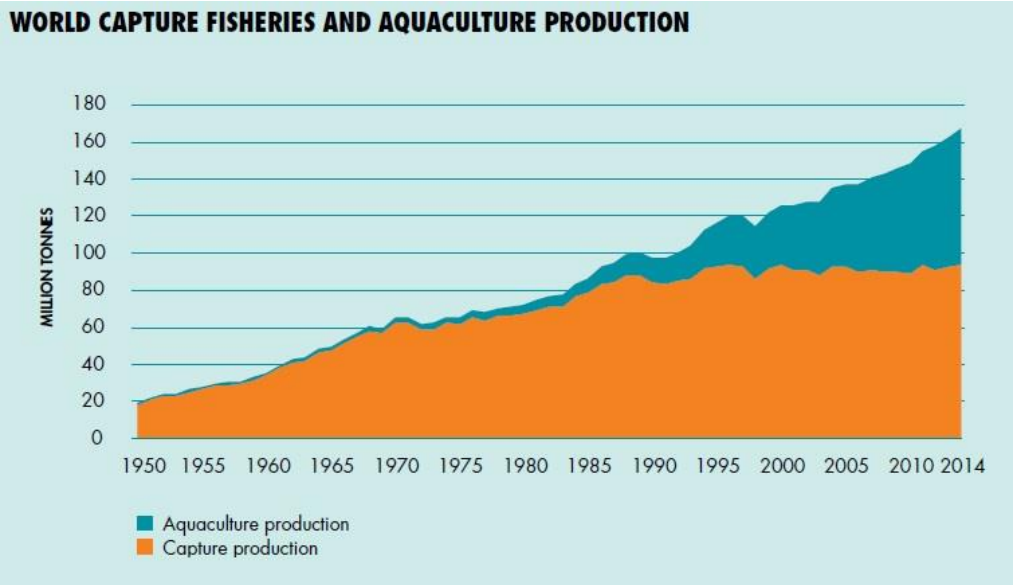


Figure 1.1. The growth in fisheries and aquaculture production up to 2014 (FAO, 2016).

In order to maintain this growth in a sustainable manner, several issues needs to be addressed. One major constraint is the availability of raw materials for feed (Tacon et al., 2011). The total capture from fisheries in 2015 contributed with 93.7 mill tons (FAO, 2017b) and has been stable since the late 1980's. The availability of fishmeal and fish oil rely on fisheries such as anchovy which are fully or over exploited today (FAO, 2017a). Therefore, the increase in marine resources to aquaculture feed has to be provided from other sources. This could be supported by fisheries on lower trophic level organisms such as krill, mesopelagic fish and copepods (Olsen et al., 2010). These species holds vast biomass, with an annual production often exceeding the standing biomass and can support a high annual harvest. The copepod *Calanus*. *sp* could present a possible catch where a total catch of 1 % of the annual production would yield 2-3.5 million tons for production of marine oils and protein (Torrissen et al., 2011).

Interest in harvest of organisms from lower trophic levels has "bloomed", and are now being considered as possible new sources for marine protein and lipids for use in aquaculture feeds. Today there is low levels of fisheries these organisms, due to only a few species can be regarded as economically and practically feasible at present time (Olsen et al., 2010). However, they present good sources of the essential fatty acids (EFAs) such as Eicosapentaenoic acid (EPA, 20:5n-3) and Docosahexaenoic acid (DHA, 22:6n-3), together with other omega-3 fatty acids that is both required and wanted in aquatic feed (Riediger et al., 2009).

The production of feed to the Norwegian aquaculture industry, that are heavily dominated by the production of Atlantic salmon (*Salmo salar)*, about 70% of the raw material comes from vegetable sources, while 30% comes from marine resources such as fishmeal and fish oil (Norges Sjømatråd, 2016) . With today's fisheries technology, parts of the favourable fatty acids have the possibility to be added into the vegetable raw material through genetic modification, creating genetically modified organisms (GMO) such as terrestrial plants (Miller et al., 2010). However, marine raw materials are still a necessity for the product to contain nutrients vital for human consumption (Rosenlund et al., 2010; Sargent et al., 1999b) .

Before a potential commercial fishery on lower trophic level species can be launched, we need to establish a scientific knowledge about the targeted ecosystem and assess the potential consequences posed by the harvest, in order to manage such a resource within a sustainable framework (Essington et al., 2006)

1.1 The mesopelagic layer

The general definition of the mesopelagic layer in the ocean is based on the depth, where the mesopelagic zone stretches from 200-1000 meters (Gjøsaeter et al., 1980). The mesopelagic layer, also named "the deep scattering layer" is inhabited by a high variety of species including krill, mesopelagic fish, zooplankton and squid as some of the major constituents (Dalpadado et al., 1998). Mesopelagic fish is one of the main components in terms of species in the mesopelagic layer and are virtually ubiquitous in the world's ocean, except for the Arctic ocean (Davison et al., 2015). The total biomass of mesopelagic fish is uncertain. Initial estimates were in the range of 1 billion tons (Gjøsaeter et al., 1980) while recent updates suggest a total biomass of up to 10 billion tons higher (Davison et al., 2015; Irigoien et al., 2014).

The biomass of mesopelagic fish in the Norwegian Sea has been estimated to 3.9 mill tons (Dalpadado et al., 1998), consisting mainly of *Benthosema glaciale* (Reinhardt, 1837) and *Maurolicus muelleri* (Gmelin, 1789). For the other major constituents of the mesopelagic layers such as krill (dominated by *Meganyctiphanes norvegica* (Sars, 1857)*)* and amphipods, the estimation was ~42 and ~29 million tons wet weight respectively (Skjoldal et al., 2004). In addition there are large quantities of the jellyfish *Periphylla periphylla* (Peron & Lesueur, 1809) (11 million tons), the squid *Gonatus* (8 million tons) and the pelagic shrimps *Sergestes*. *sp* and *Phasiphaea*. *sp* (1 million tons combined) (Skjoldal et al., 2004). The Institute of Marine Research (IMR) in Norway created an overview of the main species in the mesopelagic layer, describing the proportion of different animal groups based on their average wet weight (Figure 1.2). In this regard, jellyfish, krill and mesopelagic fish are also the dominating groups (Strand, 2017).

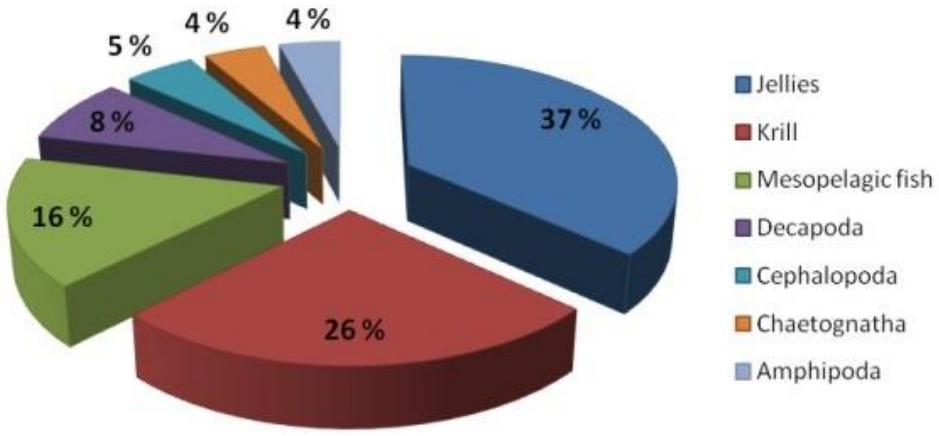


Figure 1.2. Mean wet weight of different animal groups from the mesopelagic community in the Norwegian Sea (Strand, 2017).

1.2 Food chain and vertical migration

Phytoplankton are the primary producers of the sea and makes the base of the food web in the oceans (Behrenfeld et al., 2006; Cloern et al., 2008). In the Norwegian Sea, there is a strong seasonal variation in phytoplankton production. In coastal waters the spring bloom occurs in April, while in the Atlantic water masses, the bloom begin in May (Rey, 2004). Some of the most prominent grazers of phytoplankton, which also represent an important link between the phytoplankton and higher trophic levels in the Norwegian Sea, are the mesozooplankton (Melle et al., 2014; Planque et al., 2000). *Calanus finmarchicus* (Gunnerus, 1770) dominates the zooplankton community in the Norwegian Sea where it constitutes the main source of energy

for higher trophic level animals (S. Falk-Petersen et al., 2009) and are regarded as a key species (Planque et al., 2000). The production of zooplankton is tightly affiliated with the blooms of phytoplankton (Broms et al., 2007; Diel et al., 1992; Niehoff et al., 2000). The species descend to great depths in the non-feeding season, and spend the winter months in diapause, before ascending to shallower depths when the spring bloom occurs (Berge et al., 2012).

A high variety of species performs diel vertical migrations (DVM), including copepods and the targeted species from the mesopelagic layer (Kaartvedt et al., 1988; Staby et al., 2011). With DVM, the organisms move upwards in the water column following the light intensity, reduction in light intensity in the upper levels trigger the organism towards the pelagic zone. When the light intensity again increase, the organism descends to deeper water (Lagergren et al., 2008; Lampert, 1989). Reasons for this migration pattern have been related to food abundancy and predation pressure among others. The feed abundancy in the deeper water levels are more scarce than in shallower water, while at the same time it holds a lower predation pressure. This movement can be viewed as a trade-off between feeding opportunities and risk of predation related to the changing light intensity (Dypvik et al., 2012b). Moreover, it represent an important factor by serving as a trophic link between zooplankton (Shreeve et al., 2009) and predators at higher trophic levels in the oceans (Hedd et al., 2009; Tsarin, 1997), in addition to the vertical flux of organic matter from the productive upper water levels, to the less productive deeper parts (Hernandez-Leon et al., 2010).

In some instances an opposite migration pattern emerges, described as inverse diel vertical migration (IDVM). In this case, the movement pattern becomes opposite and the organism move towards shallower water during daytime, and descends to deeper water during night time (Dypvik et al., 2012a). The IDVM pattern has been described for zooplankton, and could possibly be a defence mechanism against predators not performing diel vertical migration (NDVM) (Lagergren et al., 2008).

However, there are several factors, both biotic and abiotic that may affect the migration pattern, placement in the water column during night time and day time and vertical range. Such as developmental stage (Strand et al., 2002), season and ontogenetic variation relative to light intensity (Staby et al., 2011).

1.3 Lipids

To sustain the increased growth of aquaculture production, there is a need to incorporate new raw materials containing omega-3, essential fatty acids (EFAs) and protein to accommodate the need from both fish and human consumers of seafood.

1.3.1 Essential fatty acids and necessary nutrients in feed

Marine products are the main source for omega-3 and especially for the EFA in human consumption (Burri et al., 2012; Frøyland et al., 2011). These compounds are vital for human health and development. The recommended daily intake of DHA+EPA is ~250 mg (Skåre et al., 2014). As fish does not produce these fatty acids, they need to be added into the feed. Consequently, the fatty acid composition in the tissue of both salmonids and other aquaculture species tends to reflect that of their diet (Brown et al., 2010). These fatty acids are vital for the development of the fish and for the human consumers of fish. However, they are well as important for maintaining the fish health and welfare. Fish oil replaced with vegetable oils have proven to maintain the growth rate of the fish (Brown et al., 2010), however it alters the FA-composition of the tissue, resulting in reduced stress tolerance and resistance against diseases (Montero et al., 2010). Moreover, diets devoid of polyunsaturated fatty acids (PUFA) could reduce the percentages of DHA and EPA in the phospholipids (PL) thus limit growth and increase mortality in Atlantic salmon (Ruyter et al., 2000).

The species from the mesopelagic layer would present a possible new resource of EFAs and omega-3 fatty acids. Both mesopelagic fish, krill and copepods have been described as organisms with high lipid content (I.-B. Falk-Petersen, . et al., 1986; S. Falk-petersen et al., 1981; Lee, 1974). However, the quality, composition and usability of the caught species from the mesopelagic layer in Norwegian waters will probably vary between season and composition of the catch.

The lipid content will also most likely vary in relation to the species present in the catch. Species such as *B. glaciale* will contain wax ester (WE), while other species such as *M. muelleri* will contain solely triacylglycerol (TAG) as depot lipid (I.-B. Falk-Petersen, . et al., 1986), and leaner species such as *M. norvegica* can contain elevated levels of phospholipid (PL) (Albessard et al., 2001; Saether et al., 1986). WE could possibly cause implications for the quality of the lipid this catch would present. Studies have shown that WE inclusion levels exceeding 50% of the lipid content in the feed resulted in impaired lipid digestibility and

growth in salmon (Bogevik, 2011), and that the fatty alcohols present in WE oils accumulate in the intestine and cause discomfort in mammalians (Olsen et al., 2010). Phospholipids make up lesser amounts of the total lipid, especially in species with higher lipid content (I.-B. Falk-Petersen, . et al., 1986), while it constitute a higher relative percentage in leaner species, present as membrane lipid (Berg et al., 2002; Sargent et al., 1988). The cell membranes have been described as particularly rich in DHA and to some extent EPA (Sargent et al., 1999a). Phospholipids have however proven difficult to extract (Dumay et al., 2006), and are most likely a better source as fishmeal rather than fish oil when added into the feed. .

1.4 Management and suitability as feed resource

Before start-up of large-scale fisheries on species from lower trophic levels, it is necessary to portray the effects this can have for the marine ecosystem and possible amendments for the marine food web. Such shift of fisheries has the potential to alter the structure of food webs (Pauly et al., 1998), with mesopelagic fish proven to be an essential part of the diet to fish such as mackerel and salmon (Jacobsen et al., 1996; Walkrr et al., 1993). Mesopelagic fish and the other species in the mesopelagic layer also represent an important link between the epipelagic and deep-water food chain (Davison et al., 2015). Moreover, a fishery on this layer will contain several different species in addition to the mesopelagic fish. Species of pelagic shrimps, gelatinous plankton, jellyfish and squid that could provide possible sources of protein and lipid. There are however little information on their nutritional content, lipids and their suitability as a feed resource.

Guidelines regarding distribution, possible biomass and the nutritional content of the catch, with emphasis on season, time and geography would be beneficial for creating an efficient and successful fishery management.

1.5 Aim

The main goal of this project was to quantify the species composition, biomass distribution and production of the mesopelagic layer on a temporal and spatial scale in the Norwegian Sea, further analyse the quality of the catch for feed production.

1. Analyse the species composition of the deep scattering layer.
2. Document changes in composition over season and geographical areas.
3. Analyse the lipid content of the major constituents of the deep scattering layer.
4. Assess the quality of the catch with emphasis on the composition of the fatty acids and lipid classes.
5. Assess the suitability of the lipids from these species for feed production.

2 Materials and methods

The work was divided into two parts. One part consisted of trawling and the collection of samples. The second part consisted of lipid analysis that took place at NTNU SeaLab (Trondheim).

2.1 Trawling

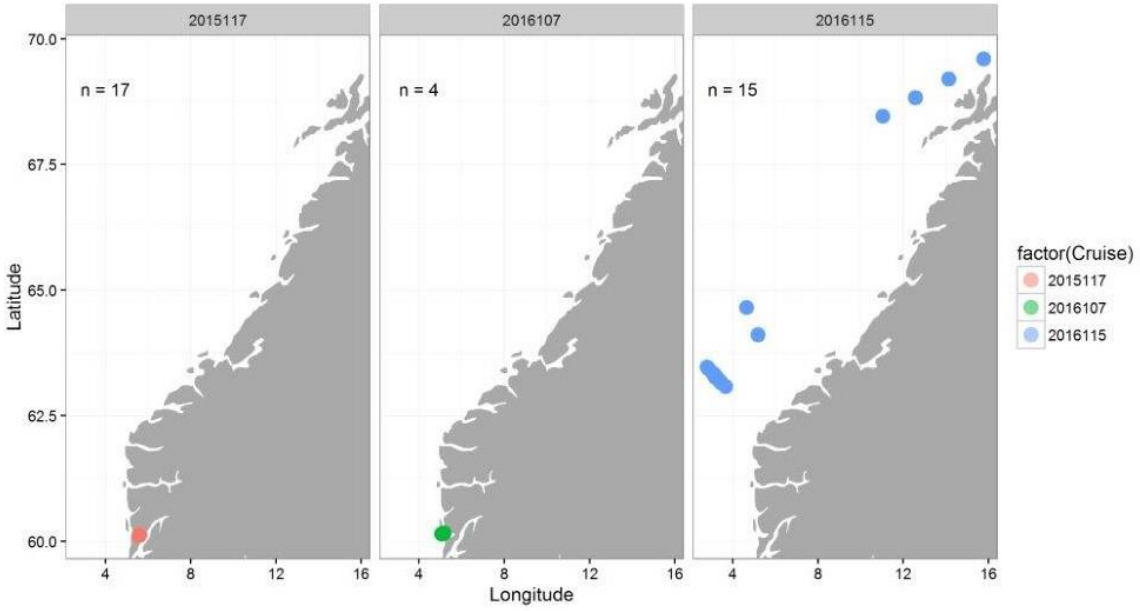


Figure 2.1. The trawl hauls conducted at the three expeditions. With autumn 2015 (red), spring 2016 (green) and autumn 2016 (blue), sampling spots described with markings. Latitude on the y-axis and longitude on the x-axis.

There were three different cruises to collect material, shown in Figure 2.1. The first cruise was conducted between November 15 and November 21 2015, in the inner fjords south of Bergen (Norway), using the research vessel G.O.Sars. There were a total of 37 trawl hauls using net sizes ranging from 10X10 meters to 4X4 meters, at different depths and time of day (Table A.1 Appendix I). 17 of these hauls were used for further analysis. The second expedition was performed between June 4 and June 6 2016, in the fjords outside of Bergen, using the research vessel G.O.Sars. During this period, there were nine trawl hauls, using the same net size at different depths and time of day (Table A.2 in Appendix I). Of these, 4 hauls were used for further analysis. The third expedition was performed between October 13 and October 26, 2016 off Tromsø (Norway), and in the open sea off Ålesund (Norway), using the research vessel G.O. Sars. 27 trawl hauls were performed, using the same net size, at different depths and time of day (Table A.3 Appendix I). 15 were used for further analysis.

2.2 Sampling

From each trawl haul, the total weight of the catch was measured, sampled and frozen for total haul nutrient composition. Then larger species such as *Periphylla periphylla* were removed and weighed separately. From the remaining mixture of smaller species, a subsample between 250-400 grams were collected and the different species were separated and length and weight was measured. For lipid analysis, species from the subsamples were collected with a size range described in Table 3.1. From the pooled samples, a representative part of the subsample were obtained. From larger animals such as *P. periphylla* the same size recommendations were considered when sampling. The same procedures were repeated at all samplings.

Table 2.1. Length groups and sampling sizes of the different target species.

Species	Small (mm)	Medium (mm)	Large (mm)
Benthosema glaciale	0-30	31-50	50<
Maurolicus muelleri	0-30	31-50	50<
Sergestes sp.	0-30	31-50	50<
Pasiphaea sp.	0-30	31-50	50<
Meganyctiphanes norvegica	0-20	21-30	30<
Periphylla periphylla	0-100 g	100-1000g	1000-3000g

2.3 Storage and transportation

In order to conserve samples and to avoid oxidation, smaller samples for lipid analysis were frozen in liquid nitrogen (N_2) and then stored in a -80°C freezer until landing. Larger samples, such as the pooled samples, were placed directly into the -80°C freezer. Transport of samples from Bergen to Trondheim were done in polystyrene containers with dry ice.

2.4 Lipid analyses

The lab work was conducted at the laboratories at NTNU SeaLab down at Brattørkaia in Trondheim. With help from SINTEF Ocean, the samples were freeze-dried prior to further processing. The freeze-dried samples were returned to -80°C at all times between handling to avoid oxidation. Before further analysis, the samples were homogenized by crushing them manually using a mortar, or a food processor.

2.4.1 Total lipid analyses

Total lipid was extracted from both single species and pooled samples. Samples of krill, shrimp and jellyfish were extracted by following the method of Bligh et al., (1959). Larger samples and samples of mesopelagic fish which were harder to homogenize were extracted following the method of Folch et al., (1957).

Weighed freeze-dried samples of krill, shrimp and jellyfish were homogenized in 0.8 ml distilled water, 2 ml of methanol and 1 ml chloroform for 1 min. 1 ml of chloroform was then added to the mixture and homogenized for another 20 seconds, and finally, 1 ml of distilled water was added to the mixture and homogenized for 20 seconds. The samples were mixed using a vortex mixer, before being centrifuged at 4000 rpm for 10 minutes at 5°C. Afterwards 0.5 ml of the lower phase was transferred to a previously weighed glass, evaporated under N_2 gas and placed in a desiccator over night. The next day these glass vials was weighed, and the total lipid content was calculated based on the weight of the glass. The remains of the lower phase was evaporated under N_2 gas and re-suspended in known amount of chloroform: Methanol (2:1 by volume) creating a 10 mg/ml lipid sample. Thereby the sample was transferred to a clean glass vial and sealed with a Teflon cap before being transferred to -80°C. Until used further.

Weighed freeze-dried samples of fish and pooled samples were moistened with a few drops of water before homogenized with 20x the volume of chloroform: Methanol (2:1 by volume) before being filtered through a filter paper (Whatman International Ltd., England) into a clean glass vial. The samples were then placed on ice to separate the phases. When separated completely, the bottom layer was transferred to a glass cylinder, and ¼ of the sample volume of KCL (88%) was added. Afterwards, 1 ml of the bottom layer was transferred to a clean previously weighed glass and evaporated under N_2 gas, before being placed in a desiccator over night. The next day these glass vials were weighed, and the total lipid content was calculated based on the weight of the glass. The remains of the lower phase was transferred to a glass vial, evaporated under N_2 gas and re-suspended in known amounts of chloroform: Methanol (2:1 by volume). Creating 10 mg/ml lipid samples that was put directly back to -80°C. Until used further.

2.4.2 High performance thin layer chromatography

Lipid class composition in the samples were done using the high performance thin-layer chromatography (HPTLC), as described in Olsen et al., (1989). HPTLC-plates (precoated silica

gel 60 plates, without fluorescent indicator (10*10 cm), Merck, Darmstadt) predeveloped to full length in hexane: Diethyl ether (1:1), dried and the upper 1 cm was scraped off. Thereby, the plates were activated at 110°C for 1 hour.

2 µl of the extracted lipid sample was applied to the plates as a 3 mm streak, using a Linomat IV (CAMAG, Muttenz, Switzerland) equipped with an N_2 spray unit and a Hamilton syringe (100µl). Standards (developed from lipid extraction from salmon white muscle, NTNU) containing known amounts of PL, CH & FFA and TAG were added in two bands. One 1 µl streak and one 3 µl. Lipid classes were separated by using the double development method, running the plates through two glass chambers (CAMAG Muttenz, Switzerland) containing two separate solvent systems and TLC saturation pads (SIGMA-ALDRICH, USA).

The plates were first developed to a distance of 4.5 cm from the origin using in methyl acetate: Isopropanol: Chloroform: Methanol: 0.25% KCL (25:25:25:10:9 by volume). The plates were dried using a hair drier and then placed in a desiccator over dry NaOH for 30 minutes. Afterwards, the plates were developed in hexane: Diethyl ether: Glacial acetic acid (80:20:2 by volume) to 8.8 cm from the origin. Developed plates were then dried using a hair drier, before being sprayed with a staining solution (3% cupric acetate in 8% phosphoric acid). The plates were dried under hot air followed by charring at 160ºC for 20 minutes (Olsen et al., 1989). The plates were analysed by photodensiometry in absorption mode at 370 nm using a Camag Scanner 3 with winCATS software (1.42), and the lipid classes were quantified against predeveloped calibration curves.

2.4.3 Gas chromatography

Fatty acid and fatty alcohol composition was analysed by gas liquid chromatography (GC). Fatty acid methyl ester of total lipid were produced as described by Christie (1989) with some modifications. In brief, 0.2 ml (10mg/ml in chloroform:methanol (2:1)) of the total lipid samples were evaporated and re-suspended with 0.5 ml C19:0 (0.18mg/ml) as internal standard (giving 10% of total lipid). Then 1 ml H_2SO_4 was added, flushed with nitrogen and sealed with a cap. The samples were then heated 50º overnight (16 hours) in a heating block (DB3D Techne Dri-block Bibby Scientific Limited, Staffordshire, UK). Afterwards, 2.5 ml of KCl (5% in distilled water) and 2.5 ml isooctane were added. The samples were mixed using a vortex mixer (Heidolph reax top) and centrifuged for 3 minutes on 3000 rpm at 5ºC to separate the phases (Hettich universal 32R). The top layer was then transferred into GC-vials (Teknolab) and sealed with aluminium seals w/Teflon (Teknolab) using a crimping tool. The samples were

then analysed with a gas chromatograph (GC) (Atosystem CL, Perkin Elmer, Waltham, MA), with Total Chrom Version 6.3.1 software. The GC was equipped with an auto-injector (1µl, inlet temperature 250ºC) and a flame ionization detector (FID, 280 ºC. The temperature program for the oven was as following; start up temperature 90ºC for 1 minute, with an temperature increase of 30ºC/min until 150 ºC, and finally raised to 225ºC and held for 7 minutes. The column used was a fused capillary column coated with a chemically bonded polyethylene glycol (CP-Wax 52CB, 25*0.25 mm) with helium as the carrier gas. Alongside the samples, external standards were applied, (68D (NuChecPrep), ECL (NuChecPrep) and 23:0 (NuChecPrep)) in order to identify undetected fatty acids based on their retention time.

2.4.4 Separation of samples containing Wax ester

Samples containing wax ester (WE) would also produce fatty alcohols (FAOH) with the methylation procedure described by Christie (1989), with the same modifications. The fatty alcohols were separated using a bond elut column (Supelclean LC-NH2, 3 mL Tubes) with the following procedure. The column was first conditioned using 4 ml isooctane. Then 0.6 ml of the methylated sample were run through the column, followed by 3 ml isooctane and 2 ml isooctane:ethyl acetate (9:1) that were collected in a test tube and sealed with a Teflon cap. The FAOH was eluted by adding 4 ml of chloroform that were collected in a test tube and sealed. All samples were evaporated to almost dryness under N_2 gas re-dissolved in 1 ml of isooctane and transferred to Teflon lined GC Vials (Teknolab). The samples were then analysed using the same GC with identical temperature program and external standards as previously described.

2.4.5 Equivalent Chain length

The main fatty acids were identified with reference to authentic standards. Unidentified fatty acids and fatty alcohols were identified using the equivalent chain length (ECL)-method described below.

Using a fixed condition GC, all fatty acids and alcohols naturally occurring in marine samples have been identified using GC-MS. The standards, saturated fatty acids were then used as basis for calculating the retention times for unknown fatty acids. This equation below gives an ECL-value that could be compared towards the ECL-library in order to identify unknown fatty acids/alcohols. In order to calculate the ECL-values, the values takes base in having known saturated fames on both sides of the unknown fatty acid/alcohol.

$$ECL_x = n\,\frac{logt_{R(x)} - logt_{R(z)}}{logt_{R(y)} - logt_{R(z)}} + Z$$

Equation 1. Equation used to find the ECL-values.

To identify the unknown fatty acid/alcohol (ECL_x) the following references needs to added into the equation.

n represents the difference in number of carbons between the two saturated FAMEs eluting on both sides of the unknown compound **x**. $\mathbf{t_R}$ equals the adjusted retention time to the unknown **x** and the two references **y** and **z**. With **z** representing the saturated FAME eluting prior to unknown, and **y** the saturated FAME after the unknown. **Z** represents the number of carbons in the saturated FAME prior to the unknown.

2.5 Calculations

$$\text{Weight of lipid} = (\text{weight of container} + \text{extracted lipid}) - (\text{weight of container})$$

Equation 2. Calculation of the weight of extracted lipid.

$$\text{Lipid content (\%)} = \left(\frac{\text{amount of lipid extracted (g)}}{\text{weight of original sample (g)}}\right) * 100$$

Equation 3. Calculation of total lipid content.

$$\text{Fatty acid content (\%)} = \left(\frac{\text{Area of fatty acid}}{\text{Sum of all areas of fatty acids}}\right) * 100$$

Equation 4. Calculation of the relative percentage of fatty acids from total lipid content.

Equation 5 and 6 shows how to convert lipid content found in dry weight (DW) to wet weight (WW), in a 100 g sample of DW with 30% lipid content. The content would equal to 70 g of DW without lipid. Membrane lipids would constitute 7 g and non-polar lipid 23 g, due to its water replacement capabilities. This would give a dry weight consisting of 77 g of lean tissue and 23 g of non-polar fat (TAG or WE). To calculate this into lipid content of the wet weight. Following two steps were followed.

$$(77\text{ g of lean tissue} * 4) + 23\text{ g of non polar lipid} = 331\text{ g of wet weight.}$$

Equation 5. Conversion of dry weight into wet weight.

In this sample of 331 g wet weight, the lipid content is 30 g (polar + non polar) giving following lipid content from wet weight

$$\left(\frac{30\text{ g lipid}}{331\text{ g wet weight}}\right) * 100 = 9.1\%\ of\ lipid\ from\ wet\ weight$$

Equation 6. Example of calculation of lipid content from wet weight.

2.6 Statistics

To test for normality a Shapiro-Wilk test was performed at significance level $P<0.05$, to test for equal variance between the measurements, a Brown- Forsythe test was performed with significance level at $P<0.05$.

The experimental data were tested for statistical significance by using one way ANOVA with Tukey's multiple comparison test, and Mann-Whitney rank sum test with differences considered significant at $P<0.05$. A regression analysis were also conducted, with significance level at $P<0.05$.

The statistical tests were conducted using Sigma plot 13.0 for Windows. Figures were made using Sigma plot 13.0 and RStudio, and tables were made in Excel 2013 and Word 2013 for Windows.

3 Results

3.1 Trawl compositions

The densities of the different species were quantified using the area covered by the trawls, and is reported as grams in wet weight pr. m^2 (ww m^2). The data in Figure 3.1 shows the average density of the eleven most prominent species from the three cruises. Regardless of location and season, *Periphylla periphylla* is the only with densities exceeding 10 g m^2. Other species, such as krill, mesopelagic fish and pelagic shrimps range between 1 to 5 g m^2.

To analyse the density of the species further, both geographical position (hauls from open sea and fjords) (Figure 3.2 a), and season (autumn and spring hauls) (Figure 3.2 b) were included as variables. *P. periphylla* had the highest density in the fjord samples (~20 g ww m^2), while *M. norvegica* has the highest density at sea (~7 g ww m^2). *P. periphylla, Sergestes. sp, M. muelleri* and *Aurelia auratia* dominated in fjord hauls, while *M. norvegica, Hymenodora. sp, Euchaeta. sp, Cyanea capillata, Chaetognatha. sp, Amphipoda. sp* and *B. glaciale* had highest densities in hauls at sea. *P. periphylla, B. glaciale, M. norvegica* and *Sergestes. sp* had highest densities in the autumn, while *M. muelleri, Cyanea capillata* and *Aurelia aurita* dominated in the spring.

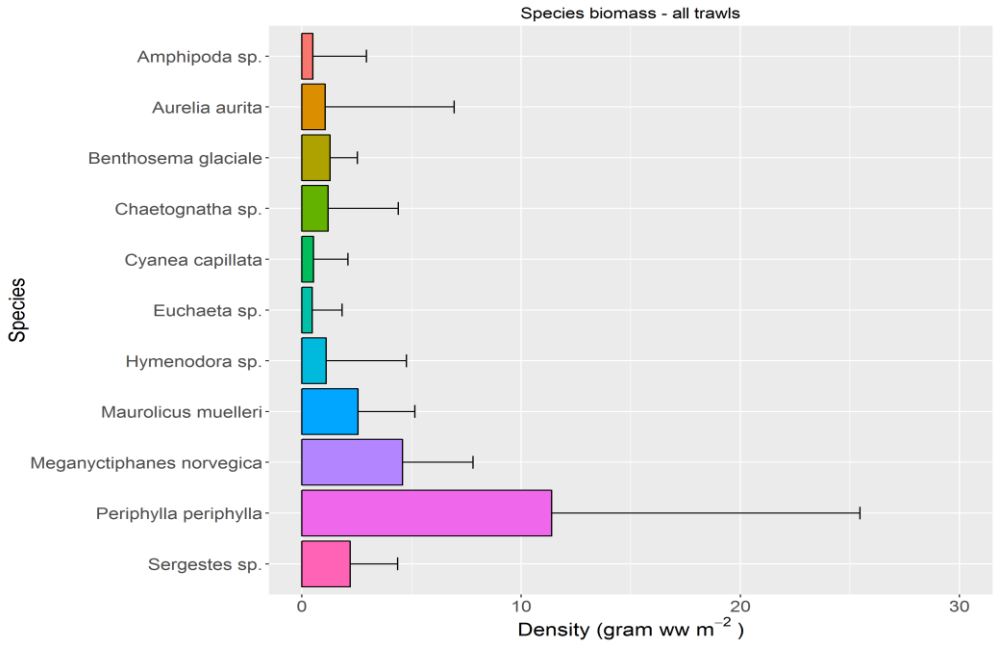


Figure 3.1. Average density of the eleven most prominent species from all included hauls (n=36) from the three cruises, given in grams of wet weight pr. m^2 for the surveyed area (+SEM).

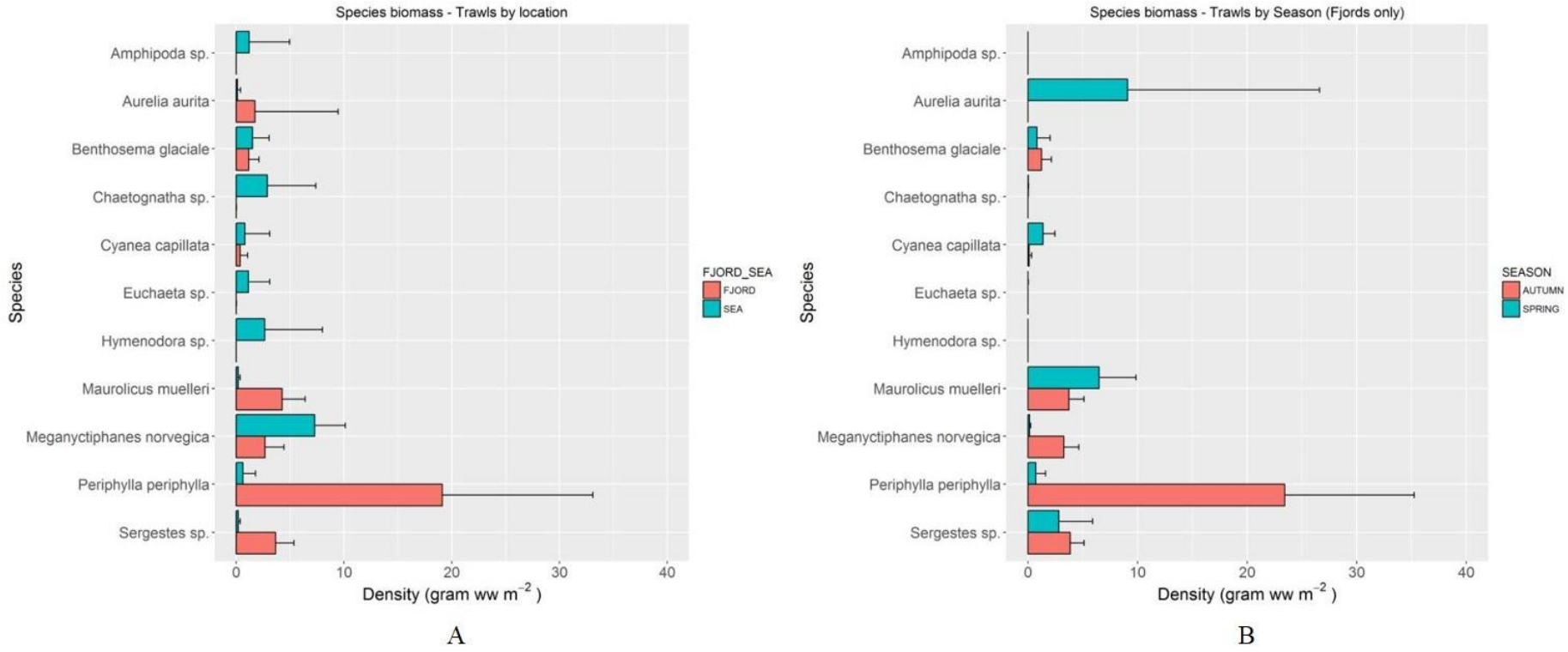


Figure 3.2. Density variation in trawls with emphasis on geography (A), and seasons (B). Density given in grams of wet weight pr. m^2 of sea in surveyed area (+SEM).

3.2 Variation of size at different depths

Hauls were made from both the mesopelagic layer (0-460 m) and the layer above (0-250 m) (Figure 3.3) and analysed for size distribution of the selected species. Although size appeared to vary with depth, the only significant difference was the predominance of larger speciemens of *B. glaciale* in the deeper hauls ($p<0.05$). The two types of pelagic shrimp (*Sergestes. sp, Pasiphaea. sp*) and *M. norvegica* had an opposite trend with the largest individuals being found in the shallower water masses. The results were however not significant. Figure 3.4 shows the vertical migration (VDM) pattern of species from the mesopelagic layer in the autumn, in both fjord (A) and sea (B) samples. The fjord sample show an inverse vertical migration (IDVM) pattern in the deepest layer where the species moved towards shallower depths during day time, while the top-layer performed the normal VDM pattern. At sea, the migration patterns were similar in both the top and bottom part of the mesopelagic layer, where the species moved towards the surface during night time, and descended to greater depths during day time.

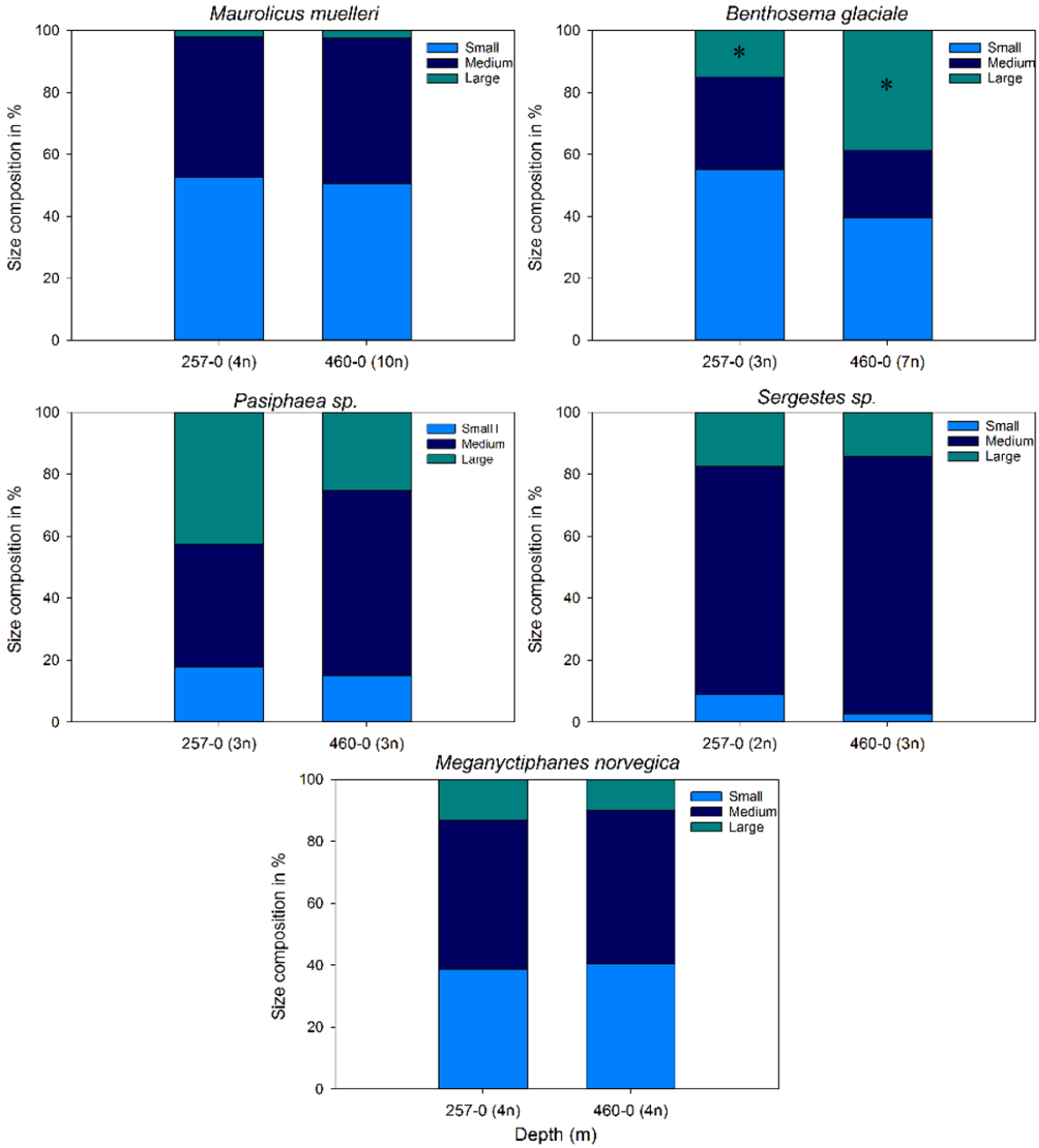
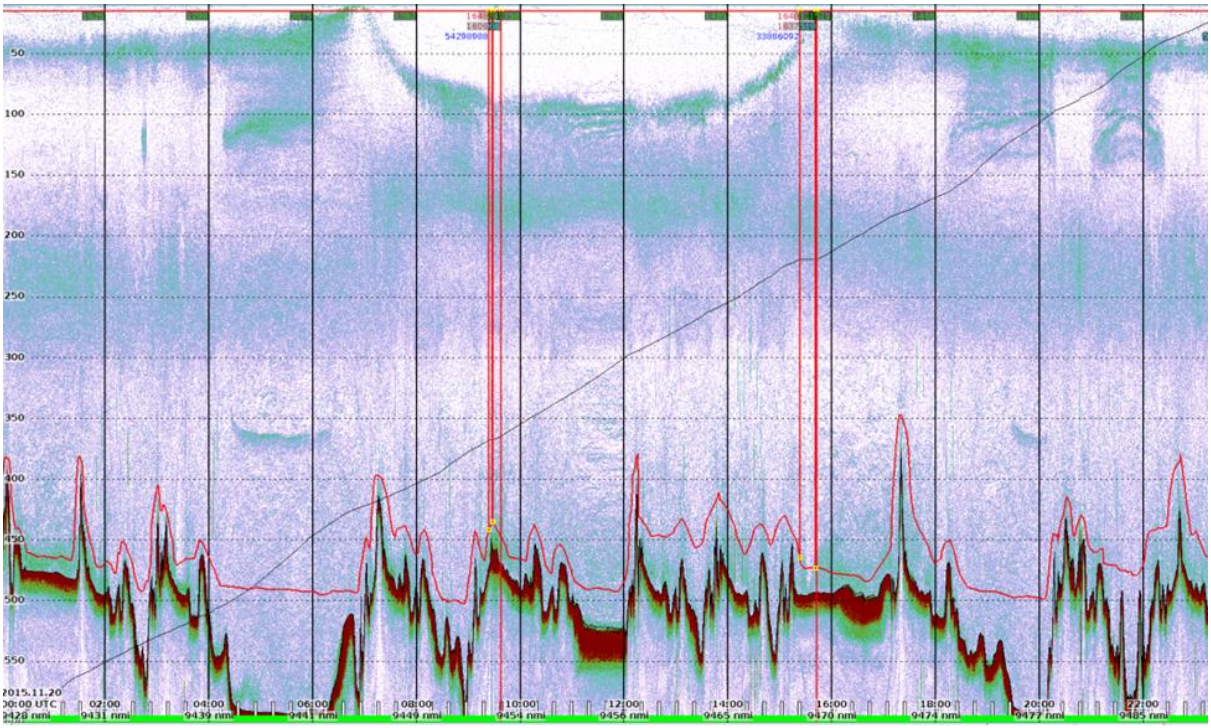
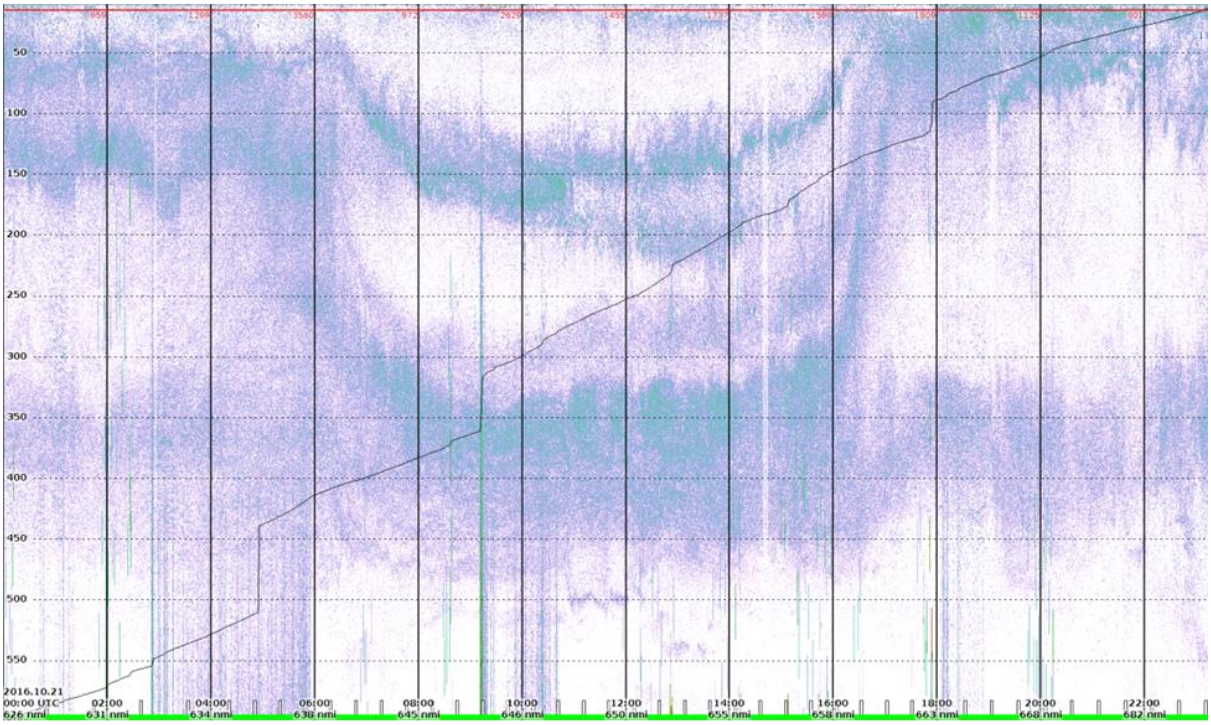


Figure 3.3. Size composition of *B. glaciale*, *M. muelleri*, *Pasiphaea*. Sp, *M. Norvegica* and *Sergestes*. Sp. at two different depths, from 0-257 m and 0-460 m in hauls conducted in the fjords in autumn. Significant differences within the size groups are indicated by the symbol (*).



A



B

Figure 3.4. Echograms created from Autumn 2015 cruise (A) and Autumn 2016 cruise (B). Depth on y-axis and timeline of the echograms on the x-axis.

3.3 Total lipid

3.3.1 General lipid content

Figure 3.5, shows the average total lipid content (percent of dry weight) from all samples of the same species in this report. The mesopelagic fish species, *B. glaciale* and *M. muelleri* contained the highest lipid level, averaging 40.2% and 42.0% respectively. The pooled hauls were also were relatively high in lipid, averaging 30.6% of the DW. The copepod *Calanus*. *sp* and *Sergestes*. *sp* had intermediate lipid levels (17.8 and 17.5% respectively) while the lowest lipid levels were found in jellyfish *C. capillata* (0.4%) , *P*. *periphylla* (4.6%) and pelagic shrimp *Pasiphae*. *sp* (7.7%).

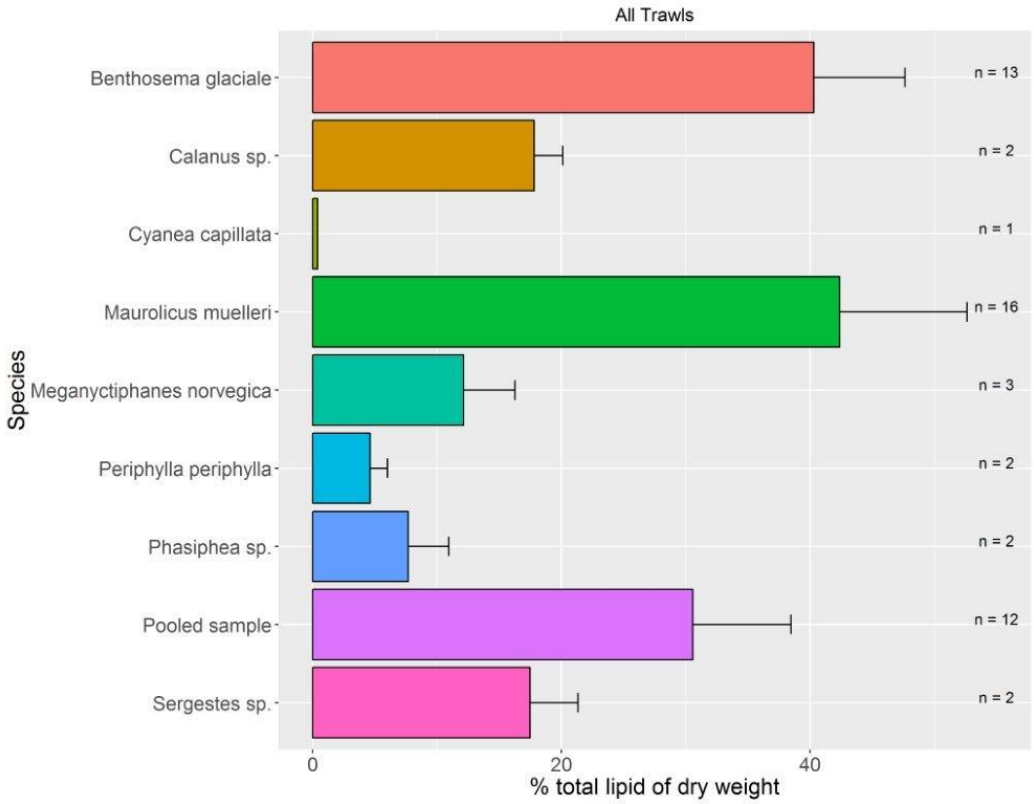


Figure 3.5. Average of the total lipid content from all samples taken of the same species. Given as percentage of the dry weight. Bars are ± SD.

3.3.2 Variation in total lipid regarding geography, seasons and size

Figure 3.6 shows the average lipid content in samples from the fjords compared to samples from the sea for *B. glaciale*, *M. muelleri* and mixed trawl hauls. For *B. glaciale* there were no significant differences between fjord and sea samples. For *M. muelleri* and the pooled samples there was a significantly higher lipid content in the fjord samples compared to samples from open sea ($p<0.05$). Figure 3.7 compares the average total lipid content in samples taken during autumn, compared to those from spring for *B. glaciale, M. muelleri* and pooled samples. All three groups had a clear trend towards higher lipid content in the spring, but the errors involved meant that these data were not statistically different.

Figure 3.8 presents the variation in total lipid content between different size groups of *B. glaciale* and *M. muelleri* as an average from all samples. In both cases, the smallest size group (0-30 mm) had a significantly lower lipid content compared to all the other size groups ($p<0.05$). For the larger size groups there were no significant differences.

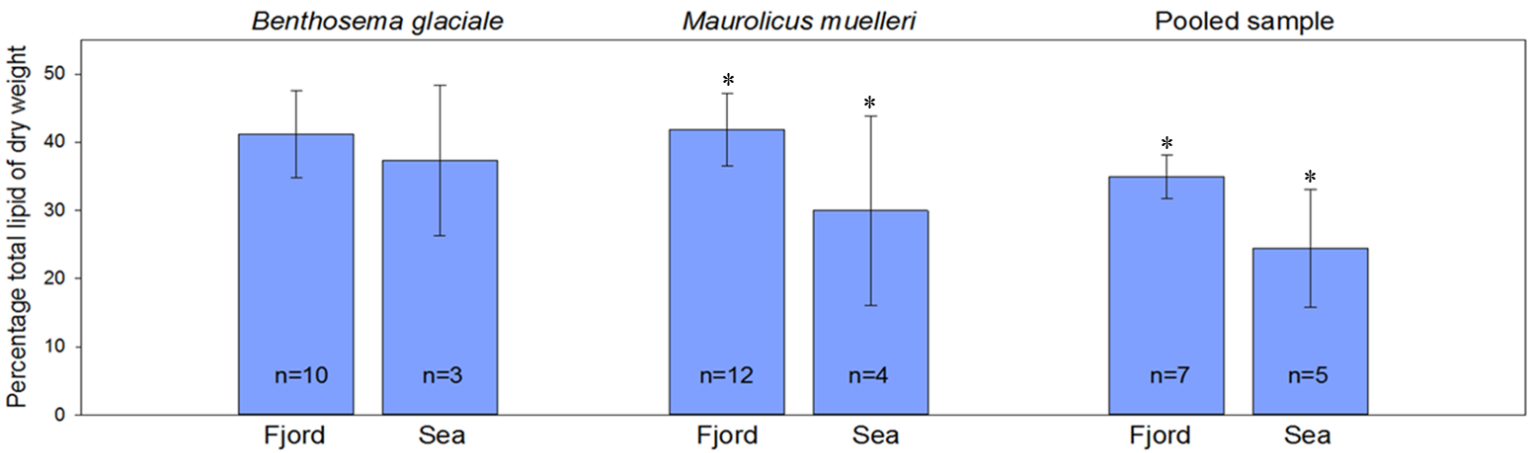


Figure 3.6. Comparison of total lipid content in samples collected in the fjords and at sea for *B. glaciale*, *M. muelleri* and pooled samples. Total lipid given as percentage of dry weight (±SD). Significant differences between fjord and sea within the species are indicated by the symbol (*).

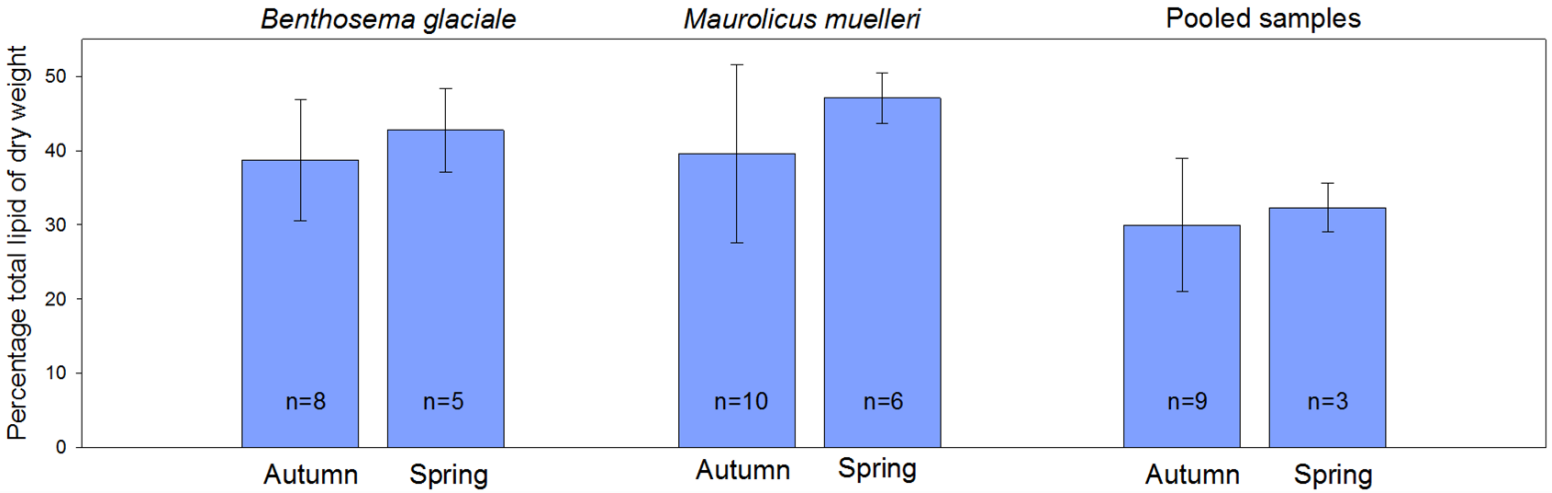


Figure 3.7. Comparison of total lipid collected at different seasons for *B. glaciale*, *M. muelleri* and pooled samples. Total lipid given as percentage of dry weight (±SD).

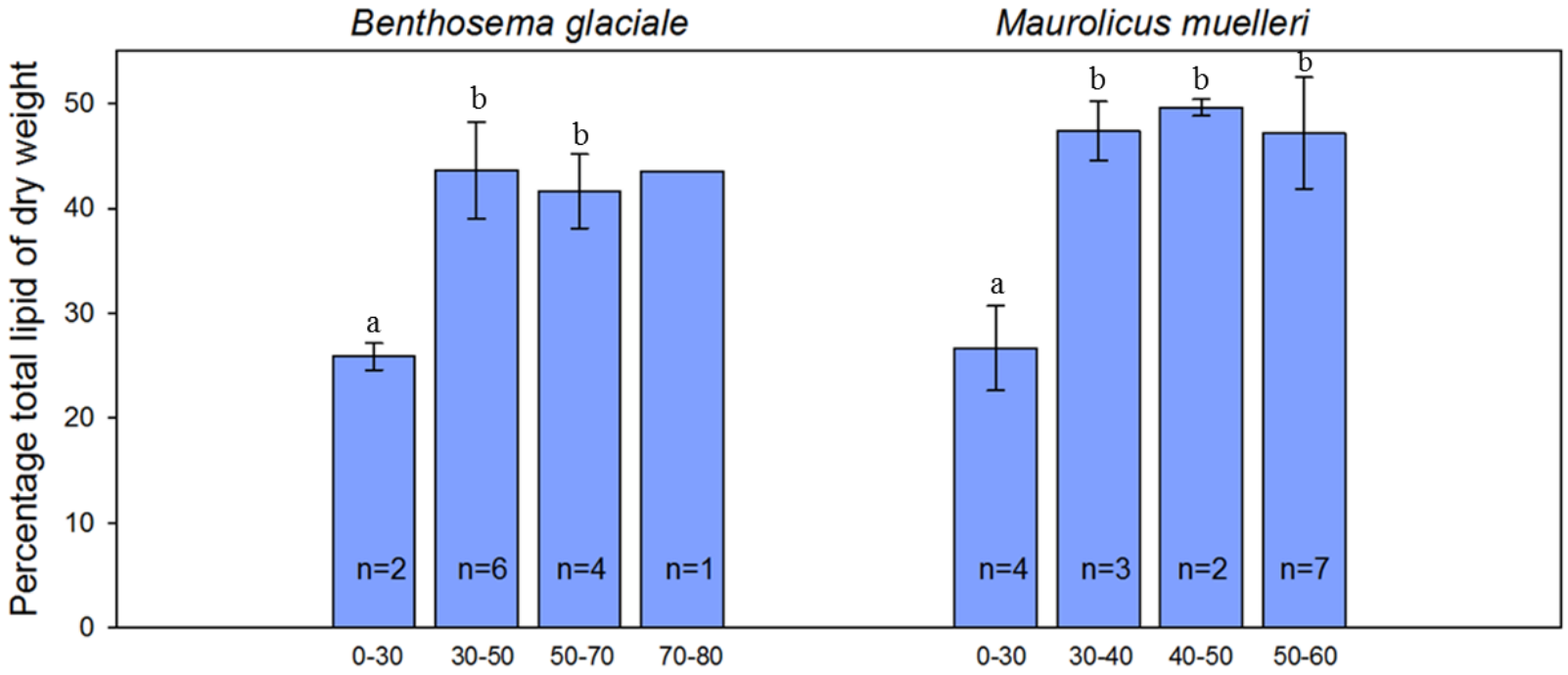


Figure 3.8. Variation in total lipid related to the size of *B. glaciale* and *M. muelleri*. Total lipid given as percentage of dry weight. Bars with ±SD. Significant differences between the size groups within the species are indicated by different letters.

3.4 Lipid class composition

Table 3.1. shows the composition of lipid classes in *B. glaciale, M. muelleri* and the pooled samples, as an average from all analysed samples. Both *B. glaciale* and the pooled samples contained relatively high levels of both wax esters and TAG while all samples of *M. muelleri* contained TAG as the only depot lipid. The pooled samples contained significantly higher amounts of phospholipids (PC, PE, PI and PS) compared to *B. glaciale* and *M. muelleri* ($p<0.05$).

Table 3.1. Composition of the different lipid classes for *B. glaciale*, pooled samples and *M. muelleri*. Lipid class given as percentage of the total lipid content (±SD).

Lipid class	***Benthosema glaciale***	***Maurolicus muelleri***	**Pooled samples**
	(12n)	**(11n)**	**(11n)**
CH & FFA (%)	1.2±0.25	2.3±0.44	1.8±0.51
PC (%)	4.9±1.23[a]	3.6±1.55[a]	8.4±3.96[b]
PE (%)	1.4±0.60[a]	1.4±0.54[a]	4.0±1.13[b]
PI (%)	0.4±0.33[a]	0.22±0.32[a]	1.2±0.45[b]
PS (%)	0.3±0.22[a]	0.29±0.33[a]	0.9±0.38[b]
TAG (%)	30.7±6.55[a]	91.3±2.38[b]	57.4±14.56[c]
WE (%)	61.1±5.95	nd.	26.3±15.56

Different letters indicate significant differences in the lipid classes between the species. No letter indicate no significant difference.

Season had only a marginal effect on the lipid class composition in the fjords (Table 3.2). The only significant difference observed ($p<0.05$) were elevated levels of TAG in *M. muelleri* in autumn compared to spring. There was also an interesting trend of an increase in TAG followed by a reduction of WE in *B. glaciale* and the pooled samples from autumn to spring. The geographical variations (Table 3.3), describe a trend with higher TAG content and lower WE content in the fjords compared to the sea in samples of *B. glaciale*. The same trend can be seen in the pooled samples. The TAG content in samples from the fjord are significantly higher compared to at sea ($p<0.05$), while no significant difference could be observed regarding the WE content.

Table 3.2. Comparison of lipid class composition between season in the fjord for *B. glaciale*, *M. muelleri* and pooled samples (±SD).

Seasons

	Benthosema glaciale		***Maurolicus muelleri***		**Pooled samples**	
Lipid class	**Autumn (4n)**	**Spring (5n)**	**Autumn (5n)**	**Spring (6n)**	**Autumn (3n)**	**Spring (3n)**
CH& FFA(%)	1.2±0.24	1.1±0.19	2.3±0.40	2.3±0.47	1.9±0.14	1.4±0.20
PC(%)	4.6±1.20	4.4±0.74	3.2±0.33	4.0±1.99	8.6±0.88	7.3±0.73
PE(%)	1.1±0.71	1.3±0.35	1.0±0.39	1.7±0.38	3.3±1.33	3.4±0.35
PI(%)	0.4±0.19	0.3±0.17	0.4±0.36	0.1±0.20	0.8±0.07	0.9±0.15
PS(%)	0.3±0.15	0.2±0.07	nd.	0.5±0.27	0.7±0.8	0.8±0.12
TAG(%)	28.8±5.09	33.8±6.67	93.7±1.29*	89.7±1.91*	63.8±3.90	71.5±2.89
WE(%)	63.8±2.81	58.8±7.56	nd.	nd.	21.0±2.83	14.6±2.58

Significant differences between the seasons are indicated by the symbol (*). No symbol indicates no significant difference. nd. implies not detected in the sample.

Table 3.3. Geographical variations in lipid class composition during the autumn for *B. glaciale* and pooled samples (±SD).

Fjord and Sea

	Benthosema glaciale		**Pooled samples**	
Lipid class	**Fjord (4n)**	**Sea (3n)**	**Fjord (3n)**	**Sea (5n)**
CH & FFA (%)	1.2±0.24	1.4±0.28	1.9±0.14	2.0±0.65
PC (%)	2.9±1.68	3.5±2.50	8.6±0.88	11.0±3.58
PE (%)	1.1±0.71	1.9±0.52	3.3±0.33	4.7±1.27
PI (%)	0.4±0.19	0.7±0.52	0.9±0.0.07	1.5±0.50
PS (%)	0.3±0.15	0.5±0.33	0.7±0.08	1.1±0.47
TAG (%)	28.8±5.09	28.2±7.06	63.8±3.90*	45.1±12.56*
WE (%)	65.45±5.63	63.8±7.39	21.0±2.83	34.6±18.52

Significant differences between the locations are indicated by the symbol (*). No symbol indicates no significant difference.

When data are split into size groups (Figure 3.9) it becomes evident that the relative relationship TAG/WE in *B. glaciale* show a similar trend as with the seasonal variation. Larger individuals contain more TAG than the smaller groups, while the WE content has an opposite trend. The smaller individuals also contain higher levels of PL compared to the larger groups. There were no evident patterns of size effects in *M. muelleri*

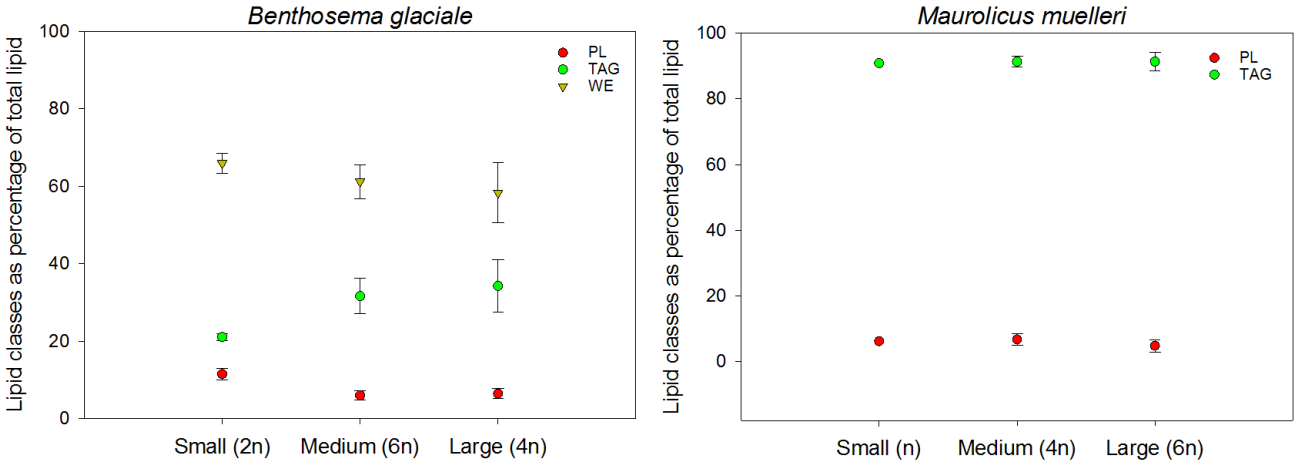


Figure 3.9. Lipid class composition for different size groups of *B. glaciale* (a) and *M. muelleri* (b). Lipid classes given as percentage of total lipid (±SD).

3.5 Variation in fatty acid content

3.5.1 Fatty acids

Table 3.4 shows the most predominant fatty acids (mol % total fatty acids) from all samples of *B. glaciale*, *M. muelleri* and mixed layer samples. Regardless of sample, the dominating fatty acids were 16:0, 18:1n9, 20:1n9 and 22:1n11 with a relative high content of both 20:5n3 and 22:6n3. The total PUFA content were high in all samples. There were only significant difference in 16:1n7 between *B. glaciale* and mixed layer samples. However, several significant differences was found between both *B. glaciale* and mixed layers samples compared to *M. muelleri*. Complete fatty acid profiles can be found in Appendix III (Table A.5).

Table 3.4. The most prominent fatty acids (mol % total fatty acids) within the different species given as an average of the total lipid from all samples (±SD). Different letters indicate significant differences between the fatty acids of the samples.

Fatty acid	*Benthosema glaciale (12n)*	*Maurolicus muelleri* (15n)	Pooled samples (11n)
14:0	4.8±0.90[a]	7.3±0.37[b]	5.0± 0.86[a]
16:0	6.5±1.32[a]	17.9±1.79[b]	11.3±3.26[a]
16:1n-7	10.4±1.95[a]	5.5±1.83[b]	7.0±1.70[b]
18:1n-9	23.2±3.76[a]	9.7±1.04[b]	15.6±6.04[a]
18:2n-6	1.7±0.31	1.5±0.20	1.6±0.11
18:3n-3	1.2±0.17	1.0±0.22	1.0±0.11
18:4n-3	2.7±0.72	2.3±1.02	2.3±0.51
20:1n-9	10.0±3.44	11.4±2.23	10.1±2.04
20:4n-6	0.4±0.12	0.1±0.09	0.4±0.17
20:5n-3	5.6±1.25[a]	3.5±1.23[b]	6.8±1.88[a]
22:1n11	13.1±4.37[a]	23.2±5.00[b]	15.6±4.82[a]
22:6n-3	9.7±3.14[a]	6.6±3.04[b]	10.3±3.00[a]
SAT	13.2±2.12[a]	27.9±2.29[b]	18.3±4.21[a]
MONO	59.6±5.90	54.0±7.22	53.3±7.13
PUFA	23.3±4.76[a]	15.5±5.38[b]	24.4±5.04[a]
n-3	20.2±4.73[a]	13.8±5.30[b]	22.2±4.94[a]
n-6	2.3±0.33	1.8±0.20	2.3±0.22
n3/n6	9.0±2.28	7.8±2.84	9.7±1.49

Different letters indicate significant differences between the fatty acids of the samples. No letter indicates no significant difference.

Table 3.5 shows the variation in the most prominent fatty acids (mol % total fatty acids) between season and geography for *B. glaciale*, *M. muelleri* and mixed layer samples. Season had no major effect on the fatty acids. The only difference noted the significantly higher level of 18:1n9 from fjord samples in *M. muelleri* when compared to those caught in open sea ($p<0.05$).

There were on the other hand major geographical variations in all three groups analysed. Sea samples did in general contain lower levels of 20:1n9 and 22:1n11 and more 20:5n3, 20:6n3 and total PUFA when compared to fjord samples. There were also some species differences. The content of 18:1n9 in *B. glaciale* and mixed layer samples were higher in samples from open sea, while they were lowered in *M. muelleri*. However, the only significant differences observed in the groups was lowered levels of 18:1n9 in *M. muelleri* at sea, and elevated levels of 20:5n3 combined with lowered levels of 22:1n11 in the mixed layer samples at sea ($p<0.05$).

Table 3.5. The most prominent fatty acids in TAG+ PL+FFA&CH of the different samples (% mol total fatty acids) as percentage of total lipid (±SD).

	B. glaciale			***M. muelleri***			**Pooled samples**		
Fatty acid % of TAG+ PL + FFA and CH	**Autumn Fjord (4n)**	**Spring Fjord (5n)**	**Autumn Sea (3n)**	**Autumn Fjord (5n)**	**Spring Fjord (6n)**	**Autumn Sea (4n)**	**Autumn Fjord (3n)**	**Spring Fjord (3n)**	**Autumn Sea (5n)**
14:0	5.2±0.91	5.1±0.37	3.6±0.29	6.9±0.18	7.5±0.20	7.4±0.57	5.1±0.05	5.9±0.39	4.3±0.67
16:0	6.4±0.86	6.2±.040	6.9±2.32	17.9±2.17	18.0±1.42	17.3±1.70	11.7±0.81	14.4±0.79	8.9±3.06
16:1n-7	9.3±2.02	11.9±1.42	9.4±0.42	3.9±0.26	7.4±1.04	4.1±0.38	5.7±0.13	7.2±0.35	7.9±2.07
18:1n-9	20.4±1.97	22.4±1.99	28.2±2.93	10.8±0.61[a]	9.0±0.71[b]	8.8±0.43[b]	13.4±0.15	10.1±1.76	21.1±4.97
18:3n-3	1.2±0.20	1.2±0.12	1.0±0.05	0.8±0.13[a]	2.0±0.08[a]	1.4±0.17[b]	1.0±0.04	1.1±0.03	1.0±0.12
18:4n-3	2.4±0.36	2.6±0.80	3.1±0.74	1.5±0.40	1.7±0.13	1.5±0.09	2.0±0.08	2.7±0.15	2.1±0.60
20:1n-9	10.6±2.10	11.5±2.69	6.9±3.9	12.1±1.47	11.8±1.36	8.7±2.82	12.4±0.43	11.3±0.45	9.6±2.34
20:5n-3	5.6±0.91	4.7±0.85	7.1±0.55	2.6±0.56	3.6±1.08	5.0±1.42	5.4±0.18[a]	6.0±0.41	8.5±1.71[b]
22:1n-11	14.6±2.79	15.1±2.48	7.7±4.17	25.9±4.29	22.9±4.29	18.6±4.37	18.6±0.36[a]	20.1±0.83	10.0±1.77[b]
22:6n-3	10.6±3.49	7.2±1.06	12.4±1.67	6.1±1.11	4.8±0.97	12.3±4.09	9.6±0.41	8.2±0.27	12.1±3.44
SAT	13.6±1.66	13.1±1.05	12.7±3.48	27.4±2.80	27.9±1.31	28.0±2.67	19.1±0.81	22.4±1.13	15.2±4.21
MONO	58.3±4.85	63.2±4.09	55.2±6.01	57.2±5.21	55.3±5.04	44.3±7.59	54.5±0.95	51.9±1.71	53.4±10.37
PUFA	24.1±4.77	20.1±2.93	27.7±2.98	13.1±2.48[a]	14.1±3.00	24.6±6.83[b]	21.6±0.76	21.9±0.74	27.5±6.10
n-3	21.0±4.74	16.8±2.48	24.8±2.84	11.5±2.42[a]	12.2±2.86	22.8±6.77[b]	19.8±0.69	19.4±0.71	25.3±5.97
n-6	2.4±0.51	2.3±0.18	2.1±0.09	1.6±0.09	1.9±0.14	1.7±0.20	2.1±0.05	2.2±0.07	2.5±0.16
n3/n6	9.2±1.95	7.2±1.08	11.6±1.30	7.2±1.29	6.4±1.05	13.1±3.94	9.6±0.17	9.0±0.39	10.1±2.07

Different letters indicate significant differences between the seasons and the locations at autumn within the species and the pooled samples. No letters indicate no significant difference.

3.5.2 Total lipid and size in relation to PUFA content

Figure 3.10 shows linear regressions for the relationship between lipid level and total PUFA content for the three groups studied. For both *M. muelleri* and the mixed layer the inverse relationship was clear and significant ($p<0.05$). This was not observed for *B. glaciale* ($p>0.05$) although there was a strong trend in the same direction.

Moreover, when PUFA content is related to size of the two mesopelagic fishes studied (Figure 3.11), it is clear that the PUFA content highest in small fish decreasing with size ($p<0.05$).

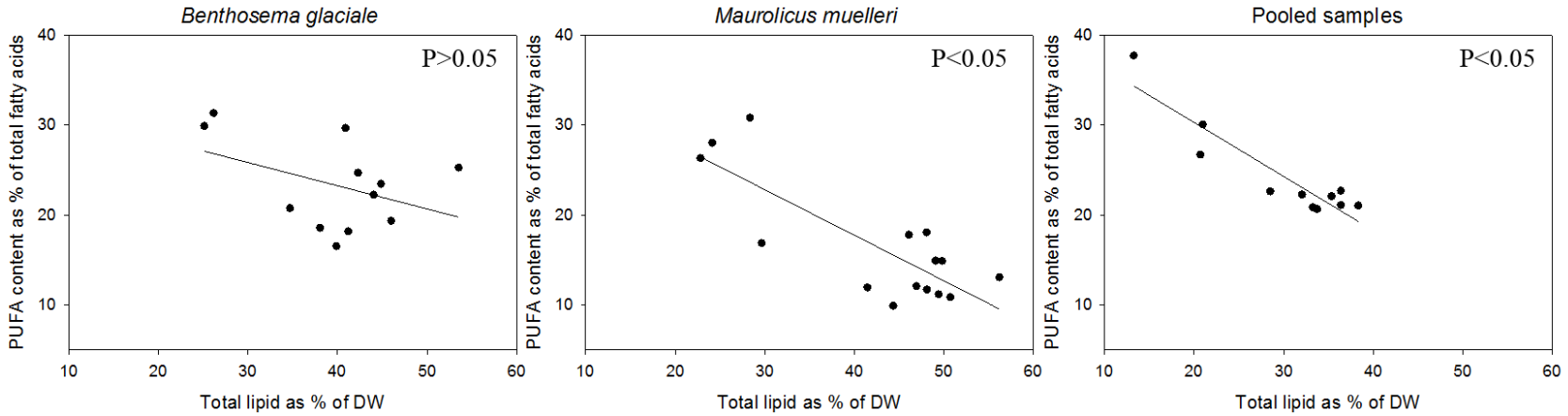


Figure 3.10. The relation between the total lipid (% of DW) and relative PUFA content from samples of B. glaciale, M. muelleri and pooled samples. Plots are made with linear regression, with corresponding p-values.

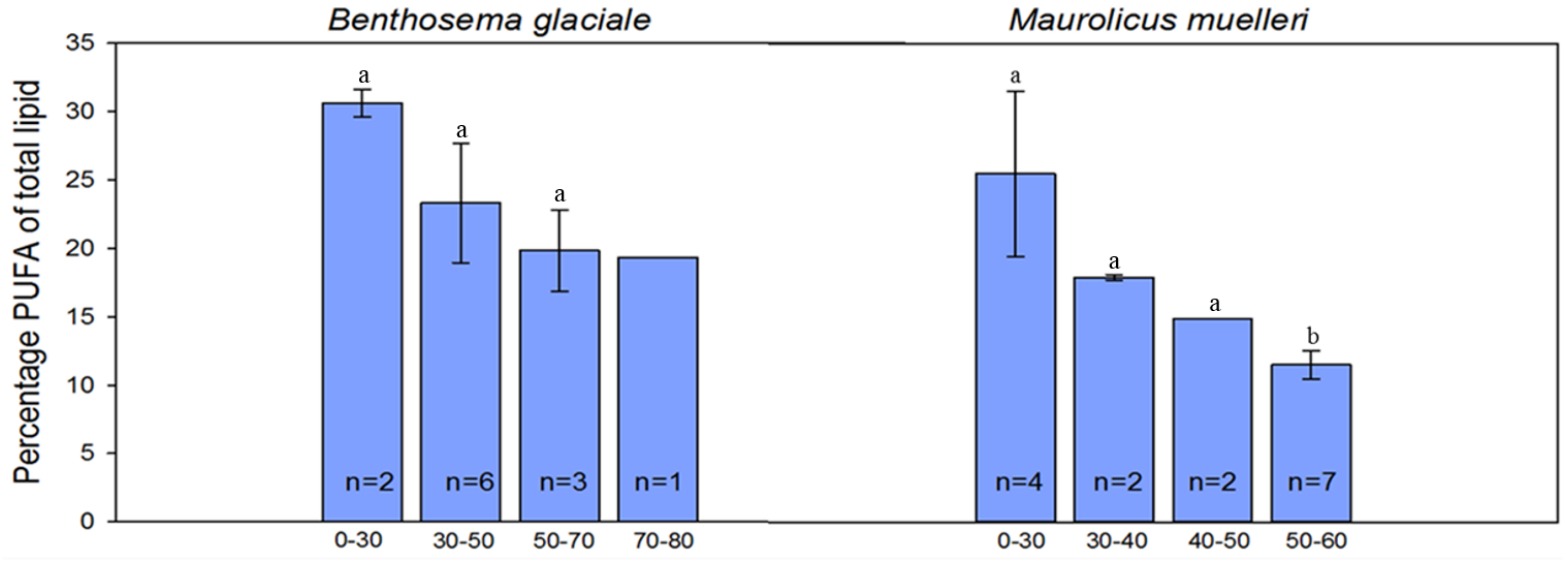


Figure 3.11. The relative amount of PUFA from total lipid content, related to different size groups of *B. glaciale* and *M. muelleri* (±SD). Significant differences are described with different letters.

3.5.3 Fatty alcohols

The most predominant fatty alcohols in samples of *B. glaciale* and mixed layer samples were the monounsaturated alcohols 16:1n7, 18:1n9, 20:1n9 and 22:1n11 accounting for approximately 80% of all fatty alcohols (Table 3.6). The pooled samples also contained traces of the saturated 14:0 and 16:0. Besides from this, the composition of pooled samples resembled that of *B. glaciale*.

Table 3.6. Relative percentage of the most prominent fatty alcohols present in *Benthosema* and pooled samples. Shown as an average with standard deviation.

Fatty alcohol	*Benthosema glaciale* (12n)	Pooled samples (6n)
14:0	nd.	1.2± 1.10
16:0	nd.	1.6± 2.16
16:1n7	9.9± 1.65	10.4± 2.35
18:1n9	36.7± 3.15	31.2± 4.96
18:1n7	3.1± 0.60	3.1 ±1.70
20:1n9	17.8± 3.88	16.2± 4.56
20:1n7	3.2±0.76	3.7 ±1.40
22:1n11	17.1 ±5.77	19.2 ±9.39

Comparisons of the most prominent fatty alcohols in both *B. glaciale* and pooled samples showed few differences in composition between seasons and geography in both samples (Table 3.7). The only significant differences was between the levels of 16:1n7 and 18:1n7 in *B. glaciale*, were both these fatty alcohols had elevated levels in samples at spring compared to autumn. No significant differences was detected in either *B. glaciale* or the pooled samples regarding location. However, trends show lower levels of 20:1n9 and 22:1n11 in both groups at sea.

Table 3.7. Fatty alcohol composition (± SD) of WE in *B. glaciale* and pooled samples at the different cruises, given as relative percentage of total lipid.

	B. glaciale			Pooled samples	
Fatty alcohol composition (%) of WE	**Autumn Fjord (4n)**	**Spring Fjord (5n)**	**Autumn Sea (3n)**	**Spring Fjord (3n)**	**Autumn Sea (3n)**
14:0	nd.	nd.	nd.	0.6±0.78	1.8±1.02
16:0	nd.	nd.	nd.	0.7±0.96	2.4±2.65
16:1n7	8.0±1.04	10.8±1.06	11.0±1.23	11.5±1.26	9.4±2.69
18:1n9	34.7±2.50	39.0±3.08	35.4±1.80	27.6±4.31	34.9±1.96
18:1n7	2.6±0.35	3.6±0.52	3.0±0.35	3.1±0.82	3.2±2.26
20:1n9	19.3±3.58	14.5±1.72	21.5±2.87	19.6±3.72	12.7±2.07
20:1n7	2.7±0.91	3.4±0.22	3.6±0.85	3.2±0.67	4.1±1.75
22:1n11	19.9±3.83	18.5±3.97	11.0±6.95	22.6±11.34	15.8±4.96

4 Discussion

The estimates of the global standing biomass of mesopelagic fish varies significantly, from 1 to 10 billion tons (Gjøsæter, 1981; Irigoien et al., 2014). As research progresses, better estimates are expected to emerge in the future. Research on the biomass of the mesopelagic layer in the Norwegian Sea has been performed, and the major constituents (krill, mesopelagic fish, pelagic shrimps, jellyfish and cephalopods) has been estimated to ~95 million tons (Dalpadado et al., 1998; Skjoldal et al., 2004). Due to a relatively large primary production in fjords and the coastal waters during spring (Rey, 2004) , it is likely a considerable biomass and production in these areas. These areas have not previously been targets for research activity. There is also a general lack of knowledge as to the nutrient composition of these layers, and how it changes with geography and seasons.

The main purpose of this thesis was to combine ecological data with lipid data for the major constituents of this layer. In this way, one could be able to give guidelines on management, and display the possibilities and expectations that could be directed towards fishery, in the mesopelagic layer.

4.1 Ecology

Density and abundance of the analysed species depend on parameters such as spawning, season and its natural habitat. The species analysed in this study are all native to the North Atlantic, where the food chain is highly dependent on the phytoplankton bloom and the following rise in food availability from copepods and other lower trophic level species (Broms et al., 2007; S. Falk-Petersen et al., 2009).

When comparing all trawl hauls, *P. periphylla* was found particularly abundant. However, the abundancy varied with season. This is contradictory to findings of Tiemann (2010), describing *P. periphylla* to have all developmental stages present at all seasons of the year, indicating a continuous release of gametes (Tiemann et al., 2010). However, seasonal variations have been suggested to be reasoned by natural fluctuation in the populations (Mills, 2001), or factors such as climate change (Brodeur et al., 1999) causing "blooms" of *P. periphylla* instead of an even distribution throughout the year. *P. periphylla* had also large changes in distributions with geography, as much higher densities were found in the fjords compared to at sea. This contrasts an earlier study describing *P. periphylla* as a deep oceanic species, with open ocean as the normal habitat (Fossa, 1992). However, other studies have also described vast densities of *P.*

periphylla in some fjords (Youngbluth et al., 2001), especially in fjord systems with low light intensity. This is known to favour non-visual predators, such as *P. periphylla* (Eiane et al., 1999). High turbidity in the fjords could have caused elevated densities of *P. periphylla* in this study.

The other species held a density of around 1-5 g ww m^2, where the density of krill exceeded those of mesopelagic fish, which again exceeds the density of the pelagic shrimp. This corresponds to studies by Dalpadado (1998) and Skjoldal (2004) estimating krill to be over ten times more abundant than mesopelagic fish (Dalpadado et al., 1998; Skjoldal et al., 2004) in the Norwegian Sea.

M. norvegica has a spawning season that begins in May where the spawning on both the Norwegian shelf and in the adjacent areas coincides with the spring bloom of phytoplankton and the consequent increase in abundance of copepods (Dalpadado, 2006). *M. norvergica* are described having wide distribution throughout the North Atlantic, in the region of the continental slope and in deep sea basins near the coast (Einarsson, 1945; Lass et al., 2001; Zhukova et al., 2009). The highest density of *M. norvegica* was found during autumn. This contradict previous reports where the spawning related schooling is expected to result in elevated abundances at spring (Cuzin-Roudy et al., 2004). A possible explanation could be that the fjord hauls during spring were more shallow compared to the fjord hauls at autumn. A study by Hirai et al., (2012) showed a higher predation pressure on *M. norvegica* in shallower water, which could cause *M. norvergica* to descend to greater depths during the fjord hauls. *M. norvegica* is also limited by temperature. The optimal range is from 2ºC to 15ºC. Their optimal range could have been exceeded and forced them to deeper water, or got them carried out with the ocean currents (Lindley, 1982; Papetti et al., 2005). Moreover, this species has been described to thrive at greater depths (Hirai et al., 2012), the shallower hauls within the fjords could explain the higher densities of *M. norvegica* in the sea, amplified by the fact that *M. norvegica* was almost non- existent in the spring hauls in the fjord, that would lower the total average from the fjords.

The spawning season for *M. muelleri* lasts from March to September in Norwegian waters (Lopes, 1979). Where the length of the spawning season decrease with higher latitudes (Kristoffersen et al., 1998), with the release of multiple batches during spawning season. *M. muelleri* is described as the dominant of the mesopelagic fish species in shallower waters (Goodson et al., 1995), and is generally considered a pelagic species in both inshore (I.-B. Falk-

Petersen, . et al., 1986) and offshore waters (Mauchline et al., 1983). The highest density of *M. muelleri* was found during spring, which fits well with the expected increased abundances during spawning season. The density of *M. muelleri* was higher in the fjord compared to sea. This correlates to earlier studies, stating M. *muelleri* to be the most abundant mesopelagic fish in some of the fjords (Gjøsæter, 1981), suggesting that the biomass of *M. muelleri* in the Norwegian Sea is likely to be several orders of magnitude lower than in the fjords (Kristoffersen et al., 1998).

B. glaciale is a batch spawner releasing at least five batches of eggs during the spawning period that lasts from June to July in the Northeast Atlantic (Gjøsæter, 1981). It is a widely distributed species in the deep areas of the North Atlantic and in several Norwegian fjords (Gjøsaeter et al., 1980). *B. glaciale* had slightly higher density during autumn compared to spring. The difference in seasonal abundancy could be due to the vertical distribution, with *B. glaciale* known to occupy the deeper water levels (Bagoien et al., 2001). The spring hauls could have been too shallow to provide a representative biomass of *B. glaciale* in the fjords. This is supproted by a study by Kristoffersen & Salvanes (2009) that noted *B. glaciale* to be almost non-existent in fjords shallower than 300 m, while having higher densities in deeper fjords (>300 m) (Kristoffersen et al., 2009). This could imply that some of the fjord hauls were too shallow. That also could have affected the distribution between fjord and sea, where the density in hauls from the sea are slightly higher compared to the fjords.

The composition of size and density of the species found in the mesopelagic layer will vary within the water column due to life strategy, DVM and season (Dypvik et al., 2012b; Giske et al., 1992; Lagergren et al., 2008). All the major constituents of the mesopelagic layer are known to have extensive diel vertical migration (Dalpadado, 2006; Dypvik et al., 2012b; Kaartvedt et al., 1988; Tarling et al., 2001; Vestheim et al., 2009). Smaller individuals would be expected to be higher in the water column due to their opportunistic life strategies, with higher investments in growth and development compared to larger individuals that invest more in reproduction (Kristoffersen et al., 2009). Smaller individuals of *M. muelleri* are known to perform DVM throughout the year while larger individuals perform this only during spring and summer (Prihartato et al., 2015) when they are rebuilding their energy reserves (Rosland et al., 1997). This pattern are also most likely applicable for the other species within the mesopelagic layer.

In this study *B. glaciale* was the only species describing a distribution pattern with higher abundancy of smaller individuals at shallower depth and higher abundancy of larger individuals deeper in the water column. *Sergestes. sp, Phasiphaea*. *sp* and *M. norvegica* described an opposite trend with higher densities of larger individuals at shallower depths. This could be due to the IDVM pattern observed in the echograms from these trawl hauls, that could have caused a larger proportion of larger animals closer to the surface compared to what a normal VDM pattern would. In addition to limited numbers of trawl hauls representative for the different depths. Thereby including hauls performed during both daytime and night time causing the species distribution to be affected by the DVM and IDVM pattern of the species.

4.2 Lipid

Marine pelagic ecosystems at high latitudes characteristically contain animals with large stores of lipid, with depot lipids accounting for ~90% of the total lipid (Benson et al., 1972; I.-B. Falk-Petersen, . et al., 1986). These stores are tightly related to the seasonality in primary production and distinct fluctuations in food supply (Kraft et al., 2015) alongside the reproduction cycle of the animals (Pedersen et al., 2001). With the energy stores fueling the reproductive processes in spring, and utilized for metabolic maintenance during the food-limited winter period. Accordingly Hagen (1996) showed that the energy reserves in krill and copepods to were highest in autumn, before reaching a minimum in early spring before the onset of substantial phytoplankton growth (Hagen et al., 1996a; Hagen et al., 1996b). For species inhabiting the Norwegian Sea and fjords this would imply a peak in lipid content in October/November, and lowest in April/May. Other studies have also shown this, where *B. glaciale* and *M. muelleri* have been described to inhabit more productive depths in the spring to rebuild their energy reserves (Dypvik et al., 2012b; Rosland et al., 1997).

Some variation in lipid content would be expected from the size composition of the species in the catch, due to selective feeding relative to the size of the species (Petursdottir et al., 2008). A study by Sameoto (1989) found *B. glaciale* to feed selectively on different species of the copepod *Calanus*, which could imply a different lipid intake from the diet. By feeding on different size groups of *Calanus. sp* containing different amounts of lipid and lipid class composition according to seasonal changes. The WE content drops in larger *Calanus. sp* from July to June, while the juvenile copepods have higher levels through the same cycle (Sargent et al., 1988). The different size groups of *B. glaciale* and the other consumers of *Calanus,* would thereby ingest feed with different lipid class composition and content.

4.3 Lipid variations

The highest lipid content in this study was found in B. *glaciale, M. muelleri* and the pooled samples, being the only samples with more than 30% lipid from DW. That is in line with the assumptions of species at high latitudes. The lipid content of *Sergestes*. sp, *Calanus sp, M. norvegica* and *P. periphylla* were all lower compared to earlier estimations of these species (S. Falk-petersen et al., 1981; Lee, 1974; Lucas, 2009). This could be due to smaller sample sizes and a different extraction method performed with these species. This could have caused lower lipid content compared to conducted analyses of *B. glaciale, M. muelleri* and the pooled samples.

Both the mesopelagic fishes and the pooled samples contained higher levels of lipid in the samples collected in spring compared to those collected in autumn. The spring cruise was conducted in June, which could imply that the species would have had time to rebuild their energy storage (Broms et al., 2007; Diel et al., 1992). During autumn the largest species would normally descend to greater depths to feed on the diapausing *Calanus* (Dypvik et al., 2012b), while the newly spawned individuals and immatures would dominate the upper water levels due to their opportunistic life strategy (Kristoffersen et al., 2009). This directly relates to the lipid content of the different size groups of *B. glaciale* and *M. muelleri*, where in both cases the smallest size groups contained significantly lower amounts of total lipid compared to the larger size groups. Higher abundancies of smaller individuals in the hauls during autumn would thereby lower the lipid content found in the autumn samples.

Larger individuals contained significantly higher amounts of lipid compared to the smallest size group (0-30 mm). *M. muelleri* is maturing at ~25 mm and *B. glaciale* at ~45 mm (Olsen et al., 2010). In both species, the smallest size group would consist of mainly juvenile individuals, while all the larger size groups would consist of mature individuals. The lipid content found in the different size groups correlates well to earlier studies, describing the difference in lipid content between juvenile and mature fish as a result of different life strategies (Kristoffersen et al., 2009). Juvenile individuals would have a diet consisting of prey with lower lipid levels (Sabates et al., 2000) and convert their energy into protein as they grow, while older fish would have a diet with higher levels of lipid and store the energy as lipids (Harris et al., 1986).
All analysed species described a trend with higher lipid content in samples from the fjord compared to at sea, with a significant difference found in both *M. muelleri* and the pooled samples. This is relates well to earlier studies, showing the growth rate of *B. glaciale* and *M.*

muelleri to be more rapid in the fjords compared to the sea (Kristoffersen et al., 2009). The lower growth rate at sea were not found to be related to higher reproduction investment, rather due to higher predation pressure by lower water turbidity in the sea (Kristoffersen et al., 1998). In addition could the feed abundancy in the fjords be higher, where the zooplankton does not possess the same possibilities to escape predation like in the sea (Bagoien et al., 2001).

4.4 Lipid class composition

The lipid class composition of the mesopelagic fish correspond well with earlier studies by I.-B- Falk-Petersen et al., (1986). She showed that *B. glaciale* was the only of the two fish species containing WE, and also characterized by containing WE and TAG as depot lipid, while *M. muelleri* contained solely TAG in all samples (I.-B. Falk-Petersen, . et al., 1986). The pooled samples contained significantly higher levels of PL compared to the mesopelagic fish species. This was possibly caused by the inclusion of krill, which stores PL as a metabolic reserve in addition to TAG (Albessard et al., 2001; Saether et al., 1986).

In samples of *B. glaciale,* there were elevated levels of TAG and lowered levels of WE in the spring. This corresponds well with theories suggesting that WE serves as a long time energy reserve, while TAG serve as the short time energy supplies (Lee et al., 2006; Olsen et al., 2010) for species predominantly inhabiting deeper water levels (Neighbors, 1988). Samples of *M. muelleri* also contained a significantly lowered depot lipids in the spring compared to autumn. The declining content of depot lipid correlates well with the spawning season of the mesopelagic fishes and the increased feed abundancy in the spring. Resulting in elevated lipid content in the short time storage of *B. glaciale*, indicating that both of the species have begun the rebuilding of their energy reserves. These findings are further enhanced by the findings in the pooled samples, describing the same trend as *B. glaciale*, implying that species containing both WE and TAG fills up their short time storage initially when rebuilding their energy reserves.

The variation between the fjord and sea with emphasis on lipid class composition had few differences. The only significant difference was elevated levels of TAG in the pooled samples in the fjords compared to the sea. The variation of TAG and WE was minimal in *B. glaciale*. This implies few differences in energy storage between individuals of the mesopelagic fish in the sea and the fjords. The elevated TAG levels in pooled samples from the fjord could be explained by a different species composition in the fjord and the sea. With *M. muelleri* rich in

TAG possibly dominating the fjord hauls, while *B. glaciale* rich in WE dominates the hauls conducted in the sea.

4.5 Fatty acid and fatty alcohol variation

The total average from all species shows the content of EFAs and PUFA to be relatively high in both *B. glaciale* and *M. muelleri*, with PUFA levels exceeded 20% and 15% of the total lipid content respectively. The same applied for the pooled samples, with PUFA levels exceeding 20% of the total lipid content. All of the samples contained high levels of especially 16:1n7 and DHA, implying the feeding on diatoms and dinoflagellates or animals feeding on these (S. Falk-Petersen et al., 2009; Olsen et al., 2010). Increased level of 18:1n9 indicates carnivorous feeding (Dalsgaard et al., 2003; Petursdottir et al., 2008) in addition to high levels of 20:1n9 and 22:1n11 that are considered good markers for copepod diets, or animals feeding on copepods (Olsen et al., 2010; Petursdottir et al., 2008). These fatty acids serves as fatty acid trophic markers (FATM), that gives a good indication about the trophic interactions and diet of the organisms in the food web.

The alcohols 16:1n7, 18:1n9, 20:1n9 and 22:1n11 were also the most prominent fatty alcohols in samples of *B. glaciale* and the pooled samples, which substantiates these findings. These findings are also consistent with an earlier study performed on *B. glaciale* (I.-B. Falk-Petersen, . et al., 1986) and suggest few other species in the samples.

The FA composition in *M. muelleri* are relatively similar between seasons and geography, with somewhat lower levels of 20:1n9 and 22:1n11 in samples from the sea. This could imply lower intake of copepods in this area. However, this also indicates a rather similar diet between the seasons and areas, with a diet dominated by copepods and euphasiids (Gjøsæter, 1981). The findings correlates well with an earlier study by Petursdottir et al., (2008), having a clear resemblances in the FA content of *M. muelleri* between open ocean and fjords.

The small differences in both FA and FAOH composition from *B. glaciale* between the seasons, indicate a rather similar diet throughout the year. There were significant differences in the FA composition between the two areas and minor differences in FAOH. There were higher levels of 18:1n9, while at the same time lower levels of 20:1n9 and 22:1n11, indicating an elevated carnivorous diet with less inclusion of copepods at sea. A similar pattern was observed in the pooled samples. This can indicate higher levels of carnivorous feeding performed by animals at sea, with lower inclusion levels of copepods in the diet, and higher inclusion levels of *B. glaciale* in the catch at sea compared to fjords.

The levels of EFAs showed similar patterns in all samples, with higher levels of EPA and DHA during the autumn compared to spring, and significantly higher levels at sea compared to the fjords. This relates well to the total lipid measurements conducted in this study, showing higher lipid content in the samples from the fjords during spring. This is due to the importance of EFAs as membrane compounds (Olsen et al., 2010), and their relatively high content in leaner samples compared to samples containing higher levels of lipid (Sargent et al., 1988). The EFA are not affected by the depletion of the energy reserves like other fatty acids and fatty alcohols that constitutes the depot lipids of the species. These findings are further enhanced by the PUFA content found in the samples, where all the species have higher PUFA content in the leaner samples. With the smallest size groups of *M. muelleri* and *B. glaciale* and the leaner samples of all species show significantly lower total lipid content combined with a significantly higher relative PUFA content. Indicating that the PUFA content of both lean and fattier samples will have a relatively high content of the favourable fatty acids.

4.6 Product suitability

To determine the suitability of using catch from the mesopelagic layer as a component in fish feed needs to be interpreted in several ways. One focus will be on catchability and ecological consequences. Another focus will be nutrient content and suitability as fish feed. As it is impossible to sort the harvested catch by species, the product for processing will be the content of the mesopelagic layer. This may affect the suitability of the catch.

One of the advantages with a fishery on the mesopelagic layers would be the vast biomass available to harvest. The pooled samples analysed in this study had a density that would result in a potential catch of 20 tons of ww. pr. km^2 in the sea, and 15 tons ww. pr. km^2 in the fjords (not including *P. periphylla*). These densities are too low to have a profitable fishery. However, these estimates does not take into account the significant trawl avoidance described by Kaartvedt et al., (2012) , and the schooling behaviour described for some of the species in this layer (Kaartvedt et al., 1998; Tarling et al., 2001) into account. Combined with the observed high densities from the echograms in this study, this would imply rather good possibilities for high density catches.

By looking at the Norwegian Sea isolated, a catch of only 1% of the standing biomass would yield 950 000 tons to be further processed into marine oils and meals. This is a significant contribution. In comparison, Peruvian anchovy, one of the most important fish species in the production of fish oil and fishmeal had a global capture of 3.1 million tons in 2014 (FAO,

2017a). In addition to the Peruvian anchovy, mackerel, blue whiting and sand eels are some of the main species constituting the global production of fishmeal and fish oil, with total landings of 29.5 million tons, providing 6.3 million tons of fishmeal and 950 000 tons of fish oil respectively. In the Norwegian fishery, capelin, blue whiting and sand eels among others constitute to a total landing of 1.1 million tons of fish, providing 203 000 tons of fishmeal and 47 500 tons of fish oil (Péron et al., 2010). When comparing the possible catch from the mesopelagic layer in the Norwegian Sea and total landings provided from the Norwegian fishery's, imply that it would be highly beneficial to harvest from the mesopelagic layer regarding the possible biomass to harvest from.

Due to rising prices of fish oil and fish meal, caused by reduced landings, in addition to increased human consumption of omega-3 oils, the amount of fishmeal and fish oil inclusion in aquaculture feeds has shown a downward trend (FAO, 2016; Tacon et al., 2009). This could imply that even if a fishery on the mesopelagic layer are less cost effective compared to pelagic fisheries, it would be able to compete with the prices.

The pooled samples contain roughly 30% lipid from the DW, this transfers into 9.1 % lipid from wet weight, placing it at the same level as the European anchovy and well beneath the content of blue whiting and European pilchard (Guil-Guerrero et al., 2011). The lipid content in the pooled samples from the mesopelagic layer would provide 91 kg pr. ton capture. This is somewhat lower compared to blue whiting and European anchovy (Guil-Guerrero et al., 2011) and somewhat higher compared to the described content in sardines (Luzia et al., 2003). From the 91 kg of lipid, ~76 kg would be present as neutral lipids (WE+TAG) possible to extract for fish oil, and ~14 kg present as PL that will go into fishmeal. Considering the EFAs and omega-3 such a catch would provide, there would be a total supply of ~19 kg EPA+ DHA and slightly higher levels of omega-3 and PUFA from every ton captured.

The amounts of lipids describes a catch that would provide large amounts of the sought lipids, and can be regarded as a possible vast contributor to the production of feed in aquaculture. The lipid class composition and digestibility a product from such fishery would present proved favourable. Where the upper levels of the possibly restricting WE was well beneath the recommendations for use in salmon feed and further human consumption of seafood (Bogevik, 2011; Olsen et al., 2010).

5 Conclusion

The most prominent species from the mesopelagic layer in the Norwegian Sea and fjords were *P. periphylla, M. norvegica, M. muelleri, B. glaciale, C. capillata, Chaetognatha. sp, Euchaeta. sp, Sergestes. sp, A. aurita*, *Hymenodora. sp,* and *Amphipoda. sp.*

There were observed differences in species distribution regarding both season and location of the trawls. *M. muelleri, P. periphylla* and *Sergestes. sp* dominated the species composition of the fjord hauls, while *M. norvegica* dominated the hauls at sea. Regarding season, *P. periphylla* and *M. norvegica* had elevated densities during autumn, while *M. muelleri* had higher densities during spring.

The highest lipid content of the species in the mesopelagic layer was found in *B. glaciale* and *M. muelleri*. A high lipid content was also found in the pooled samples taken from the mesopelagic layer. The highest lipid content was found during spring in the fjords. However, with a relative high lipid content found in the sea during autumn as well. Larger sized individuals of mesopelagic fish had significantly higher lipid content compared to smaller individuals, with a distinct shift in lipid storage observed after maturation.

The PUFA content from all samples was high on average, with the highest relative content of EFAs and PUFA found in smaller individuals and leaner samples. Describing a relatively high content of EFAs and PUFA in both leaner and fattier samples taken from the mesopelagic layer. The suitability as a feed component was good, with a beneficial lipid class composition for use in salmon feed and further human consumption of seafood.

The main challenge will be to provide large quantum of the catch that creates a sustainable fishery regarding both economy and management of the species. To ensure this, biomass estimates needs to be based on other methods than trawl hauls, which proved to be affected by the distribution of the species through the water column.

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Appendix I

Information about the conducted trawl hauls

Table A. 1 Information about the trawl hauls autumn 2015.

Trawl station	Start time	Finish time	Trawl size	Speed (knots)	From deep (m)	To deep (m)	Distance (m)	Latitude	Longitude
416	754	824	10x10	1.35	184	180	4324.2	60.120833	5.54716667
417	925	955	4x4	1.41	186	189	4684.1	60.121333	5.548
418	1408	1438	6x6	1.38	185	175	4380.5	60.120667	5.54683333
419	1617	1648	10x10	1.38	180	0	4385.5	60.119667	5.53675
420	2021	2052	4x4	1.35	223	0	4648.5	60.121	5.55008333
421	2250	2320	6x6	1.21	257	0	4364.7	60.12125	5.55
422	209	239	10x10	1.19	247	0	4223.4	60.120667	5.54633333
423	744	814	4x4	1.34	184	170	4239.0	60.121598	5.55393917
424	957	1027	6x6	1.25	192	170	3890.0	60.1215	5.5545
425	1631	1701	10x10	1.26	184	170	4001.5	60.119667	5.56283333
426	1910	1940	4x4	1.26	189	189	4448.1	60.121333	5.55625
427	2350	20	6x6	1.29	258	255	4743.5	60.119167	5.54666667
428	336	405	10x10	1.24	230	220	4479.8	60.1215	5.53308333

429	747	817	4x4	1.37	180	165	4332.3	60.122167	5.56633333
430	1200	1256	10x10	1.98	430	0	4214.9	60.118333	5.56666667
431	1508	1547	4x4	1.81	450	0	3395.5	60.113	5.57008333
432	2026	2118	6x6	1.94	460	0	3929.4	60.1185	5.55183333
433	2338	8	10x10	1.23	150	140	3689.5	60.118667	5.542
434	2040	2146	10x10	2.56	412	0	5083.9	60.118167	5.55116667
435	2320	10	4x4	2.17	440	0	4359.0	60.1185	5.55580833
436	100	154	6x6	2.27	440	0	4349.4	60.116333	5.54392333
437	252	346	10x10	2.1	420	0	4228.6	60.1155	5.54566667
438	714	754	4x4	1.79	435	0	3552.1	60.120583	5.57158333
439	1529	1609	6x6	1.84	441	0	3534.3	60.115167	5.543
440	1919	1949	10x10	1.37	30	40	2905.7	60.116333	5.54383333
441	2228	2258	10x10	1.36	250	240	5076.5	60.119667	5.54916667
442	139	230	4x4	2.36	450	0	4472.8	60.118	5.559
443	324	408	6x6	2.03	439	0	3836.7	60.113833	5.54566667
444	727	839	10x10	3.08	446	0	5362.8	60.115592	5.53979
445	1236	1307	10x10	1.24	105	95	3154.0	60.1175	5.5545
447	1732	1822	10x10	1.89	440	0	3221.5	60.116	5.55733333

448	2039	2128	4x4	2.34	450	0	3722.3	60.116333	5.53783333
449	2256	2343	6x6	1.91	450	0	4574.0	60.116	5.548
450	142	249	10x10	2.65	440	0	4076.0	60.116333	5.54766667
451	616	659	4x4	2.24	435	0	5049.3	60.118	5.55808333
453	955	1018	10x10	0.85	330	0	-	-	-

Table A. 2 Information about the trawl hauls spring 2016

Trawl station	Start time	Finish time	Trawl size	Speed (knots)	From deep (m)	To deep (m)	Latitude	Longitude
178	2242	2257	10x10	2.47	NA	NA	60.14905	4.5815
180	1605	1612	10x10	2.26	NA	NA	60.1485	5.058833
181	2307	8	10x10	2.33	500	0	60.151165	5.083833
182	113	136	10x10	2.18	100	0	60.152	5.0983334
183	2222	2252	10x10	2.7	30	30	60.170334	5.1588335
184	11	124	10x10	2.18	500	0	60.147	5.0511665
185	6	120	10x10	2.36	500	0	60.14517	5.0361667
186	955	1015	10x10	2.69	340	330	60.147167	5.066
187	1127	1147	10x10	2.71	420	390	60.1555	5.1021667
188	NA	NA	NA	NA	NA	NA	NA	NA
189	157	227	10x10	2.4	33	30	60.154	5.0893335

191	614	658	10x10	1.99	XX	XX	60.1635	5.158

Table A. 3 Information about the trawl hauls autumn 2016

Trawl station	Start time	Finish time	Trawl size	Speed (knots)	From deep (m)	To deep (m)	Latitude	Longitude
205	1912	2104	3561	2.28	1000	0	69.6065	15.765
206	0314	0452	3561	2	1030	0	69.20783	14.13
207	1000	1137	3561	2.06	1013	0	68.83566	12.560833
208	1625	1803	3561	2.13	1000	0	68.4635	11.021833
209	2047	2240	3561	2.33	1030	0	64.65683	4.6281
210	0320	0203	3561	2.03	1010	0	64.114334	5.1671667
211	746	922	3561	2.3	804	0	63.081165	3.6591666
212	1313	1433	3561	23.09	1016	0	63.2745	3.1658332
213	2347	0004	3561	2.63	350	0	63.2755	3.2078333
214	0155	0225	3561	2.73	82	0	63.276333	3.2188334
215	0650	844	3561	1.74	1006	0	63.3471	3.0417833
216	1201	1257	3561	1.94	353	0	63.286667	3.171
217	1322	1506	3561	2.07	360	0	63.261833	3.2345
218	1506	1607	3561	1.68	NA	NA	63.2895	3.1668334

219	1621	1800	3561	2.35	910	898	63.279835	3.1963334
220	1940	2010	3561	2.25	30	0	63.2815	3.1853333
221	1131	1206	3561	1.98	153	0	62.7925	4.6091666
222	0445	0620	3561	2.2	1002	0	63.437332	2.8400002
223	1547	1642	3561	2.62	350	0	63.265167	3.2233334
224	1721	1908	3561	3.02	1008	0	63.3165	3.1138334
225	0312	0436	3561	1.66	40	0	63.296333	3.1568334
226	1223	1313	3561	2.97	NA	NA	63.223667	3.3286667
227	1904	2111	3561	2.5	1015	0	63.4695	2.7798333
228	1042	1213	3548	2.6	964	0	63.161167	3.4423332
229	1250	1426	3561	2.37	990	0	63.211834	3.3285
231	1105	1150	3561	2.31	300	0	62.4165	6.4863334
232	1216	1246	3548	NA	300	0	62.4165	6.4968333

Appendix II

List of species gathered during the three cruises

Table A. 4 List of all gathered species during the three cruises

Type	Species	Found on trawl A15,S16,A16
Amphipod	Amphipoda 0	A15,S16,A16
Amphipod	Eusiridae 0	A16
Amphipod	Eusirus 0	A16
Amphipod	Liparis	A16
Cephalopod	Blekksprut	A16
Cephalopod	Cephalopoda 0	A16
Cephalopod	Clio 0	A16
Cephalopod	Decapoda 0	S16
Cephalopod	Gonatus 0	A16
Cephalopod	Grimpoteuthis 0	A16
Copepod	Euchaeta 0	A15
Copepod	Paraeuchaeta 0	S16,A16
Copepod	Paraeuchaeta barbata	A16
Fish	Arctozenus risso	A16
Fish	Argentina 0	S16
Fish	Argentina silus	S16
Fish	Coryphaenoides rupestris	A15,S16
Fish	Cyclopterus lumpus	S16
Fish	Etmopterus princeps	S16
Fish	Etmopterus spinax	S16
Fish	Eutrigla gurnardus	A16
Fish	Fisk	A16
Fish	Fiskeyngel	S16
Fish	Gadidae 0	S16,A16
Fish	Gadoidea	A15,S16
Fish	Gammarus 0	S16
Fish	Lophius piscatorius	A16
Fish	Micromesistius poutassou	A16
Fish	Nansenia 0	A16
Fish	Paralepididae 0	A16
Fish	Pollachius virens	A16
Fish	Schedophilus medusophagus	A16
Fish	Scomber scombrus	A16
Fish	Sebastes 0	A16
Fish	Stomiidae 0	A16
Fish	Teleostei 0	A15,S16,A16
Tunicate	Salpa 0	A16
Tunicate	Salpidae 0	A16
Crab	Liocarcinus 0	A16
Crab	Svømmekrabbe	A16
Krill	Boreomysis 0	A15,S16
Krill	Boreomysis arctica	A15,S16,A16
Krill	Euphausiacea 0	S16

Krill	Meganyctiphanes norvegica	A15,S16,A16
Krill	Nematobrachion boopis	A16
Krill	Nematoscelis 0	A15,S16
Krill	Nematoscelis megalops	S16,A16
Krill	Sergestes	A15,S16,A16
Krill	Sergestes 0	S16,A16
Krill	Sergestes arcticus	A16
krill	Thysanoessa inermis	S16
Krill	Thysanoessa raschii	S16
Mesopelagic fish	Argyropelecus hemigymnus	A16
Mesopelagic fish	Benthosema glaciale	A15,S16,A16
Mesopelagic fish	Gonostomatidae 0	A16
Mesopelagic fish	Lampanyctus 0	A16
Mesopelagic fish	Maurolicus muelleri	A15,16,A16
Mesopelagic fish	Myctophidae 0	A16
Mesopelagic fish	Notoscopelus kroeyeri 0	A16
Mesopelagic fish	Sternoptychidae 0	A16
Jellyfish	Aglantha digitalis	S16,A16
Jellyfish	Aurelia 0	A16
Jellyfish	Aurelia aurita	S16,A16
Jellyfish	Beroe 0	S16,A16
Jellyfish	Beroe cucumis	A16
Jellyfish	Bolinopsis infundibulum	A16
Jellyfish	Cnidaria 0	A15,S16,A16
Jellyfish	Ctenophora 0	A15,A16
Jellyfish	Cyanea 0	A15,S16,A16
Jellyfish	Cyanea capillata	A15,S16,A16
Jellyfish	Cyanea lamarcki	S16,A16
Jellyfish	Hydrozoa 0	S16,A16
Jellyfish	Octophialucium funerarium	S16
Jellyfish	Pelagia noctiluca	A16
Jellyfish	Periphylla periphylla	A15,S16,A16
Jellyfish	Pleurobrachia pileus	S16,A16
Jellyfish	Praya	A16
Jellyfish	Praya 0	A16
Jellyfish	Scyphozoa 0	A16
Jellyfish	Siphonophora 0	A15,S16,A16
Jellyfish	Staurophora mertensi	S16
Worm	Chaetognatha	S16,A16
Worm	Microstomidae 0	A16
Worm	Sagitta	S16
Worm	Sagitta 0	A16
Mysider	Mysida 0	S16,A16
Shrimp	Caridea 0	A15,S16,A16
Shrimp	Crangon 0	S16
Shrimp	Euphausia krohnii	A16
Shrimp	Hymenodora 0	A16
Shrimp	Pasiphaea 0	A15,S16,A16
Shrimp	Pasiphaea multidentata	A15
Crustacean	Crustacea 0	A15
Crustacean	Munida 0	S16

Snail	Clione limacina	A16
Snail	Cymbulia 0	A16
Snail	Cymbulia peronii	A16
Sponge	Cliona 0	A16
Myside	Mysida 0	S16,A16
Myside	Hyperia 0	S16,A16
Myside	Hyperiidae 0	A15,A16
Myside	Hyperoche medusarum	A16
Myside	Themisto compressa	A16
Myside	Themisto abyssorum	A15,S16,A16

Appendix III

Complete fatty acid profiles of *B. glaciale*, *M. muelleri* and pooled samples

Table A. 5 Complete fatty acid profiles of *B. glaciale*, *M. muelleri* and pooled samples. Fatty acids (% mol of total lipid) given as percentage of total lipid. Average of all samples (±SD).

Fatty acid	*Benthosema glaciale*	*Maurolicus muelleri*	Pooled samples
14:0	4.8±0.90	7.3±0.37	5.0±0.86
14:1n-5	0.2±0.03	0.3±0.03	0.2±0.09
15:0	0.2±0.04	0.6±0.12	0.4±0.09
16:0	6.5±1.32	17.9±1.79	11.3±3.26
16:1n-7	10.4±1.95	5.5±1.83	7.0±1.70
16:1n-5	0.3±0.03	0.3±0.05	0.5±0.35
16:1n-4	-	0.2±0.08	-
16:2n-4	0.4±0.09	-	-
17:0	0.1±0.07	0.3±0.12	0.2±0.07
16:3n4	0.2±0.09	-	0.2±0.15
16:4n3	-	0.0±0.06	0.1±0.04
16:4n1	0.3±0.29	-	0.3±0.20
18:0	1.5±0.43	1.8±0.43	1.4±0.17
18:1n-9	23.2±3.76	9.7±1.04	15.6±6.04
18:1n-7	0.7±0.83	1.7±0.27	2.4±0.65
18:1n5	0.3±0.05	0.3±0.04	0.4±0.15
18:2n-6	1.7±0.31	1.5±0.20	1.6±0.11
18:3n-4	-	0.2±0.06	-
18:3n-3	1.2±0.17	1.0±0.22	1.0±0.11
18:4n-3	2.7±0.72	2.3±1.02	2.3±0.51
18:4n-1	0.1±0.08	-	0.1±0.04
20:0	0.1±0.07	0.1±0.11	0.1±0.08
20:1n-11	-	0.3±0.53	11.0±2.04
20:1n-9	10.0±3.44	11.4±2.23	11.0±2.04
20:1n-7	-	0.2±0.00	0.4±0.19
20:2n-6	0.3±0.03	0.2±0.06	0.3±0.04
20:4n-6	0.4±0.12	0.1±0.09	0.4±0.17
20:3n-3	0.2±0.05	0.1±0.12	0.3±0.04
20:4n-3	1.0±0.14	0.4±0.12	0.7±0.08
20:5n-3	5.6±1.25	3.5±1.23	6.8±1.88
22:1n11	13.1±4.37	23.2±5.00	15.6±4.82
22:5n-3	-	-	0.6±0.04
22:6n-3	9.7±3.14	6.6±3.04	10.3±3.00
24:1	1.3±0.33	1.2±0.18	0.8±0.18
Unknown	3.8±0.69	2.5±0.97	3.5±0.66
SAT	13.2±2.12	27.9±2.29	18.3±4.21
MONO	59.6±5.90	54.0±7.22	53.3±7.13
PUFA	23.3±4.76	15.5±5.38	24.4±5.04
n-3	20.2±4.73	13.8±5.30	22.2±4.94
n-6	2.3±0.33	1.8±0.20	2.3±0.22
n3/n6	9.0±2.28	7.8±2.84	9.7±1.49

Appendix IV

Linear regression analysis

Table A 1 1. Regression analysis of Total lipid and relative PUFA content in *B. glaciale*, *M. muelleri* and pooled samples.

Relationship f= y_0+ax	**a**	**y0**	**r^2**	**P**	**Corrected P-value for the mean of the observations**
		Benthosema			
Total lipid % of DW vs PUFA content	-0.26±0.18	33.59±7.20	0.17	0.0009	0.1775
		Maurolicus			
Total lipid % of DW vs PUFA content	-0.51±0.10	38.04±4.45	0.66	<0.0001	0.0003
		Pooled samples			
Total lipid % of DW vs PUFA content	-0.60±0,08	42.31±2.61	0.84	<0.0001	<0.0001