Eelpouts diet in the Barents Sea: variation between species, areas, fish length and sex

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June 2019

University of Bergen, Department of Biological Sciences

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Abstract

The eelpout family is one of the most common fish families in the Barents Sea. Despite the diversity and wide distribution, we have little information about their ecology, feeding preferences and interaction with other fish. In the Barents Sea, regular monitoring of fish diet started in 1960 and was mainly focused on commercially important fish, while the diet and interactions of other fish were studied sporadically. In 2015, a large-scale stomach sampling program called "Year of the stomachs" was carried out. In total, 27.657 stomachs from 67 fish species, including six species of eelpouts, were collected during the joint Norwegian-Russian ecosystem survey (BESS). The study focuses on eelpouts diet in the Barents Sea: variation between species, areas, fish length and sex. This study is based on 280 stomachs of eelpouts and information of fish length and sex supplemented with habitat data, such as geographical position, sediment type and bottom water temperature. The eelpouts had a diet of great variety. Worms, crustaceans and hyperiids were common prey for both the boreal gracile eelpout and the arctic pale eelpout, but they do not overlap geographically. The pale, arctic and longear eelpout overlapped geographically and partly in the diet. Hyperiids formed an important part of the diet of these three arctic species. The pale eelpout was also found to prey on *M. norvegica* which have not before been observed in the northern Barents Sea. The greater eelpout differed the most from the other eelpouts, and preyed mainly on echinoderms. These results on the eelpout diet in 2015 didn't show great changes from earlier findings. However, this study presents important information about temporal and spatial distribution of eelpouts and their prey, that was missing in previous studies, and supplement earlier findings with new prey types, and thus gives an important contribution to mapping of the eelpouts' diet in the Barents Sea. This is a limited, but important data set that gives better insight to eelpout feeding ecology, trophic interactions and diet similarity.

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#lektorlove

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1 Introduction

Eelpouts belong to the family Zoarcidae, which contains about 308 species of perciform fish (Mecklenburg *et al.*, 2018). The Barents Sea includes 18 species of the family Zoarcidae, which frequently occur (Karamushko, 2008; Dolgov, Johannesen and Høynes, 2011; Mecklenburg *et al.*, 2018). Despite wide distribution and species diversity, there have been few studies of the Zoarcid's ecology and feeding, with a few rare exceptions (Balanov *et al.*, 2006). Monitoring surveys have been focused mainly on commercially important species, but since the ecosystem survey started, more knowledge about non-commercial species distribution and abundance has been available. In addition to lack of focus on eelpouts, there are challenges with species identification, due to great morphological, intraspecific variation (Møller and Jørgensen, 2000). Møller and Jørgensen (2000) studied distribution and abundance of eelpouts in the waters of West Greenland based on surveys from 1992 to 1998. The lack of knowledge on this subject was demonstrated during the study by revealing 11 new species found in the West Greenland and Canadian waters (Møller and Jørgensen, 2000).

The eelpouts have long slender bodies with dorsal and anal fins that ends with the caudal fin. The colour pattern, including the number and shapes of dark bands and saddles, and the configuration of the lateral lines of the body of the Lycodes are some of the most useful characters for species identification. The Lycodes are one of the most phenotypically plastic genera of the Zoarcidae family, and multiple species exist as polymorphic populations (Mecklenburg *et al.*, 2018). Eelpouts are mesobenthic and common in shelf seas and the continental slope in the Northern hemisphere (Dolgov, Johannesen and Høynes, 2011), and live in contact with seabed. They may be digging into the ground (Dolgov et al., 2011; Mecklenburg, 2016) or plow the bottom in search of food (Mecklenburg *et al.*, 2018). They preferred muddy and soft sediment (Wienerroither *et al.*, 2011). The eelpouts are recorded at depths between 1 – 3,580 m (Mecklenburg *et al.*, 2018) and prefer temperatures close to 0 - 1°C (Dolgov, 2016; Mecklenburg *et al.*, 2018). Earlier studies have shown that eelpouts prey on benthos organisms (crustaceans, polychaetes, and molluscs) in the Barents Sea and other areas (Andriyashev, 1954; Albert, 1993; von Dorrien, 1993; Mecklenburg *et al.*, 2018)

The Barents Sea is located entirely in the north of the Arctic Circle and surrounds the Arctic Ocean with its shallow shelf. The geographical boundaries in the North follows the continental break west of Norway and Spitsbergen, to the shelf break, the north of Svalbard. These boundaries separate the Barents Sea from the Norwegian and Greenland seas. In the east, the Barents Sea is defined by the line from Franz Joseph Land to the northern tip of Novaya Zemlya, which separates it from the Kara Sea. The southern boundary is made up by the coast of Norway and Russia (Ozhigin *et al.*, 2011). The ecosystem monitoring contributed to change focus from single species (mainly commercial) to the ecosystem level, including non-commercial species, where fish interaction is a keystone to understand ecosystem functioning (Dolgov, Johannesen, & Høynes, 2011). Since the joint Norwegian-Russian Barents Sea ecosystem survey (BESS) started in 2004, the number of species described and recorded has increased.

During the BESS more than 200 species of fish from 66 families have been registered in the Barents Sea. The most common families are eelpouts (Zoarcidae), snailfish (Liparidae), codfish (Gadidae), sculpins (Cottidae), skates (Rajidae), Flatfish (Pleuronectidae) and rockling (Lotidae, Dolgov, Johannesen and Høynes, 2011). Andriyashev & Chernova (as described in (Dolgov, Johannesen and Høynes, 2011) classified the Barents Sea species into seven zoogeographical groups based on the species main distribution area: Arctic, mainly arctic, acto-boreal, mainly boreal, boreal, south boreal, widely distributed. Most (24) eelpouts species are found living in the Arctic region, while only five eelpout species are mainly boreal. During the BESS 13 eelpouts are commonly found (Prozorkevich and Sunnanå, 2016, 2017; Prozorkevich, Johansen and van der Meeren, 2018) two of which are mainly boreal, that is, they have the species characteristics of boreal waters but are common also in the boundary regions of the Arctic. The other eelpouts that are found are arctic species, they are continuously distributed and reproducing in Arctic waters and not, or only rarely or infrequently found in adjacent cold-temperature (boreal) waters (Dolgov, Johannesen and Høynes, 2011; Mecklenburg *et al.*, 2018)

In 2015, named "year of the stomach", the Institute of Marine Research (IMR, Norway) and Polar Branch of Russian Federal Research Institute of Fisheries and Oceanography (PINRO, Russia) conducted a large-scale stomach sampling program of fish caught on several cruises. In total, 27.657 stomachs (mainly commercial) from 67 species were collected and analysed by experienced technicians and scientists. This large-scale sampling program gave basis for new and additional knowledge of spatial and seasonal variability in diets of the Barents Sea fish. Through statistical analyses, collected fish were divided into three main groups for feeding pattern; fish-eaters, fish feeding on worm-like benthic invertebrates and fish feeding on crustaceans (Eriksen *et al.*, 2019). Eelpouts were collected during the BESS with the full coverage of the Barents Sea. 11 eelpouts species were identified to species level, these dominated by four species; Gracile eelpout *Lycodes gracilis*, Pale eelpout *Lycodes pallidus,* Threespot eelpout *Lycodes rossi* and Arctic eelpout *Lycodes reticulatus* (Prokhorova, Wienerroither and Malkov, 2016).

Data of eelpout stomachs, from 280 individuals, were collected during the Barents Sea ecosystem survey (BESS) in August - September 2015, and supplemented with habitat data, such as geographical position, sediment types, bottom water temperature. Fish diet will be analysed in relation their habitat. Statistical analyses (correlation analyses, cluster analyses, and principal components analyses) will be used to analysed species diet and to identify feeding pattern. The main aims of this thesis will be to answer the following questions:

- What is the diet of the Barents Sea eelpouts (Zoarcinae)?
- How does the diet vary between species, length groups, sexes and areas?
- What are the habitats of eelpouts and how does it influence their diet?

2 Material and methods

2.1 Data sampling

2.1.1 Survey

The Barents Sea ecosystem survey (BESS) has been carried out as a cooperation between IMR and PINRO every year in the period August – September since 2004. The BESS follows the status and changes of the ecosystem in the Barents Sea by monitoring of hydrography and marine organisms in the area (Eriksen *et al.*, 2017; ICES, 2018). The survey covered the ice-free Barents Sea and stomachs were collected on Norwegian and Russian research vessels (Figure 1). Eelpout stomachs were collected during the BESS in 2015 between 13th August and 9th of October. Stomach samples were taken by bottom trawl “Campelen 1800” with 15 m horizontal and 4 m vertical opening (Prokhorova, Wienerroither and Malkov, 2016; Eriksen *et al.*, 2019).

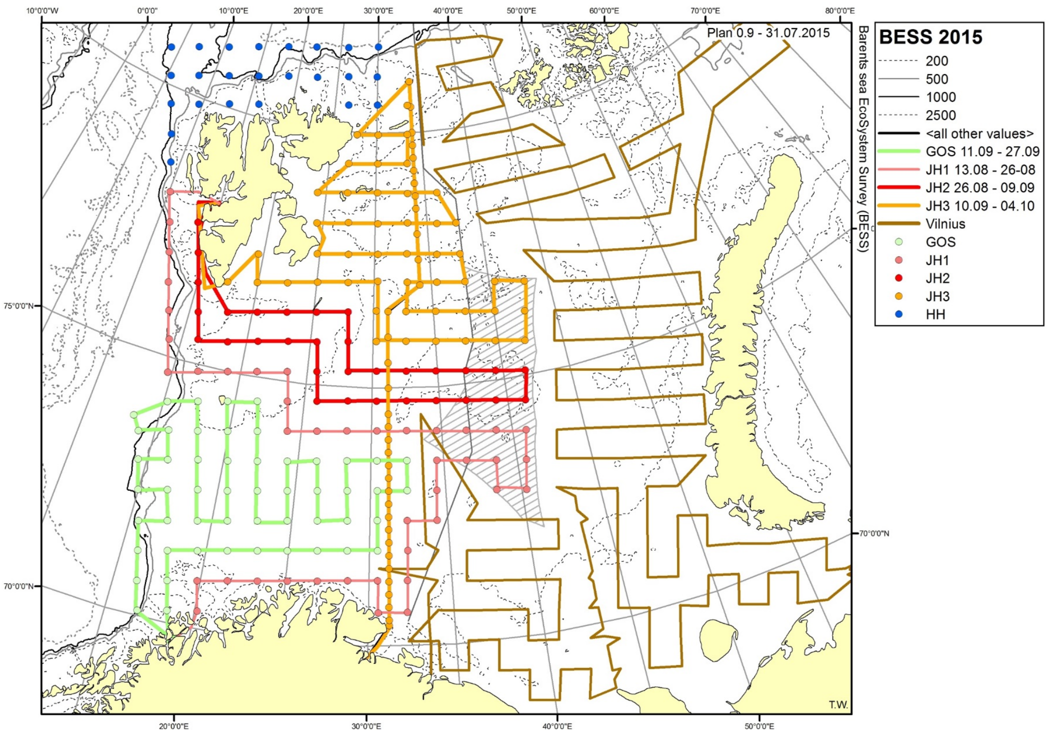

Figure 1. Overview of survey area during the ecosystem survey 2015, carried out by Norwegian vessels (G.O. Sars, Johan Hjort, Vilnius and Helmer Hanssen). Map were taken from the BESS report (https://www.imr.no/filarkiv/2016/11/imr-pinro_1-2016_18.10.pdf/nb-no)

During the survey, biological data of fish were collected: fish length (to the nearest millimetre) and weight (to the nearest gram) were measured and sex recorded. In addition, environmental data (bottom water temperature and salinity) were also recorded. Temperature and salinity were measured by CTD and temperature close to the bottom was used here (Prozorkevich and Sunnanå, 2016). To study eelpouts habitat, the sediment map (taken from NGU.no) was used, where the sediment types were categorized into groups of sediment by definition, classified by grain size composition (Table 1)

Table 1. There were 8 sediment types recorded in the study. Codes of lower numbers categorises finer sediments while larger number represent coarser and rocky sediments. Detailed description is found at; https://www.ngu.no/Mareano/Grainsize.html

Sediment name	Classification code
Mud	20
Sandy mud	40
Muddy sand	80
Gravelly sandy mud	115
Gravelly muddy sand	120
Gravelly sand	130
Muddy sandy gravel	150
Gravel, cobbles and boulders	175

2.2 Species studied

Greater eelpout (*Lycodes esmarkii*), mainly boreal species, are known to be distributed in the area that stretches from the western and northern Barents Sea, to Iceland and Greenland, and in the western North Atlantic (Mecklenburg, 2018).

Figure 2: Greater eelpout (*Lycodes esmarkii*). Photo: Thomas de Lange Wenneck

Its lengths has reached 102 cm off Iceland, and 75 cm in the Barents Sea and by the coast off Norway. Their main habitat is waters of high salinity, temperatures between -0.4 to 5.6°C (usually above 0°C) and at soft substrate of 143 – 1,090 meters depth. Age analysis of otoliths from fish of the Barents Sea indicates that the greater eelpout has a maximum age of 12 years (Mecklenburg, 2018).

Gracile eelpout (*L. gracilis*), mainly boreal species, are known to be distributed in the Eastern Atlantic from Greenland and Iceland to Kattegat, and in the southern parts of the Barents Sea and to the north of Svalbard (Mecklenburg, 2018).

Figure 3: Gracile eelpout (*Lycodes gracilis*). Photo: Thomas de Lange Wenneck

Its length has reached 56 cm, but does typically not exceed 30 – 35 cm. Its main habitat is at temperatures between -0.6 - 7.3 °C at muddy bottom of 50 – 540 meters depth. Age analysis by otoliths indicates that the maximum age is 7 years (Mecklenburg, 2018). The gracile eelpout was previously called Vahl's eelpout (due to the earlier consideration of being a subspecies of *L. vahlii*), and might sometimes appear by that name due to historical consistency. Gracile eelpout is a relatively new name recommended in 2013 to avoid confusion with *L. vahlii* (Mecklenburg, 2018).

Pale eelpout (*L. pallidus*), arctic species, are known to be nearly circumpolar. It is found all over the Barents Sea (Mecklenburg, 2018).

Figure 4: Pale eelpout (*Lycodes pallidus*). Photo: Thomas de Lange Wenneck

Its length seems to reach about 30 cm and the maximum length recorded has reached 38 cm by reports in the Barents Sea, but still needs verification. Its main habitats are at temperatures of -1.8 - 3.7°C at muddy substrate of 11-750 m. There is no data on age (Mecklenburg, 2018). The pale eelpout (*L. pallidus*) has recently been separated from scalebelly eelpout (*L. squamiventer*), as a result, earlier descriptions have combined characteristics of the two species (Møller, 2001; Mecklenburg *et al.*, 2018), More taxonomic work is needed due to uncertainties about the pale eelpout species, which does not appear as a monophyletic group thus multiple species seems to be in the synonymy of *L. pallidus* (Mecklenburg, 2018).

Arctic eelpout (*Lycodes reticulatus*), arctic species, are known to be distributed along the coast of Canada from the Hudson strait in the south to Robeson Channel in the north, western and eastern part of Greenland and in most parts (except the south) of the Barents Sea (Mecklenburg, 2018).

Figure 5: Arctic eelpout (*Lycodes reticulatus*). Photo: Thomas de Lange Wenneck

The length of the Arctic eelpout is recorded to be up to 61 - 65 cm in the Barents Sea. Its main habitats are at temperatures below or slightly above zero at soft substrate bottom of 6 – 930 m depth, but are typically found on the outer shelf and upper slopes at 100 – 380 m. By otolith studies the maximum age has been indicated to reach 10 years (Mecklenburg, 2018). The arctic eelpout (*L. reticulatus*) and the threespot eelpout (*L. rossi*) might be difficult to differentiate and it has been questioned whether they are two distinct species (Andriyashev, 1954; von Dorrien, 1993; Mecklenburg *et al.*, 2018). More taxonomic work is needed, but if there is found to be only one valid species, the *L. reticulatus* is the name of priority (Mecklenburg, 2018).

Threespot eelpout (*L. rossi*), arctic species, are known to be distributed along the northern coast of Alaska to Dease Strait in the east, in Greenland Sea and in most of the Barents Sea area (Mecklenburg, 2018).

Figure 6: Threespot eelpout (*Lycodes rossi*). Photo: Thomas de Lange Wenneck

The length of the threespot eelpout are reported to usually reach up to 31 cm, but it has also been recorded at 38 cm. They are usually found by bottom temperatures below zero, and salinity of at least 34. By otolith studies the maximum age has been indicated to reach 9 years (Mecklenburg, 2018). Some question whether the arctic eelpout (*L. reticulatus*) and the threespot eelpout (*L. rossi*) are distinct species. Some researches based on barcoding have found some molecular genetic differences which indicated two good species (Mecklenburg, 2018), and they will therefore until further notice be treated as two valid species.

Longear eelpout (*Lycodes seminudus*), arctic species, are known to be nearly circumpolar and it is found in the northern and central Barents Sea (Mecklenburg, 2018).

Figure 7: Longear eelpout (*Lycodes seminudus*). Photo: Thomas de Lange Wenneck

The length of the longear eelpout is reported to reach 57 cm. During otolith studies the maximum age has been indicated to reach 8 years. They are associated with bottom temperatures below zero or slightly above, but they are registered in temperatures ranging from -1.7 - 4.9°C. Their main bottom habitat are soft and muddy at depths of 50 - 1400 m (usually found deeper than 200 m), but they are also found at bottoms with mixed mud and gravel (Mecklenburg, 2018).

2.3 Stomach analysis

During the BESS, stomach content was sampled for up to 10 selected individuals of each species, representing the length distribution in the catch. In total, 280 eelpout stomachs were collected. The processing of stomachs was different for large and smaller fish. Larger fish were analysed on board, while the smaller (less than 10 – 12 cm) were frozen and sent to laboratories for processing. The stomach content was analysed, and prey items were identified to species, if possible.

The stomachs contained a wide range of prey types that had a wide range of taxonomic ranking, from phylum to species, which were combined into 15 larger groups: copepods, euphausiids, hyperiids, cephalopods, gelatinous plankton, small demersal crustaceans (SD_crustacea), large demersal crustaceans (LD_crustacea), Crustacea_mix, other plankton, fish, echinoderms, worms, molluscs, other food and digested food (Eriksen *et al.*, 2019). Here, only the groups which were found in the diet were used.

2.4 Data treatment

To identify variation in diet with length, the eelpouts were divided into different length groups depending on their length. The length groups ranged from 4 cm to 60 cm. For the smallest fish the interval of 2 cm was used (4.0-6.0, 6.1-8.0, 8.1-10.0, 10.1-12.0, 12.1-14.0, 14.1-16.0, 16.1-18.0, 18.1-20.0), for medium sized fish intervals of 5 cm were used (20.1-25.0, 25.1-30.0, 30.1-35.0, 35.1-40.0), and for larger fish 10 cm intervals (40.1-50.0, 50.1-60.0). Species diet composition is presented by bar graphs for these length groups. Size classes without data were excluded from the bar graphs.

Prey composition (if dividing to prey types were possible) were presented as percentage of the stomach content weight. The diet proportion based on prey types were calculated to percentage of weight (%W) as standard indicator by:

$$\%W = \frac{W_i}{W_{tot}} \times 100$$

W_i the wet weight of each prey group in the stomach, W_{tot} is the total wet weight of the stomach content. The frequency of occurrence (%F) of each prey category in the stomach contents was calculated by:

$$\%F = \frac{F_i}{F_{tot}} \times 100$$

F_i is the number of stomachs where at least one individual of a specific prey group are present, and F_{tot} is the total amount of stomachs with content.

To present the diet composition data for the six species of lycodes, Microsoft Excel for Mac (version 16.23) were used. Pie charts and post charts were used to show the total diet of each species, sex and length groups by showing proportions (by mean percentage) of each prey group found in the stomach. Here, proportion of each prey group in each stomach is taken into account. To illustrate the habitat of the eelpout species, abiotic factors (such as temperature and sediment size) were presented as post charts. The individuals with empty stomachs or missing recordings of environmental factors were excluded from the data before analyses. For every graph presenting percentage ratio, the number of individuals are stated as a value of N.

Sampling effort was presented by mapping the geographical position of the eelpout samples and ggplot2 and marmap package in RStudio (version 1.1.419) was used for this purpose. The gplot2 package was also used to make boxplot to present body length and thermal habitat for each species.

2.4.1 Statistical tests – RStudio

A binomial test was performed to investigate whether the distribution between sexes were equally distributed assuming 50% of each sex. The binomial test was only used for species with N > 50.

binom.test (x, n, p = 0.5)

Two samples t.tests were used for testing the similarities between average length between species and sex. The null-hypotheses are "the average length of males and females are equal". For $p < 0.05$, the null-hypotheses are rejected in favour of the alternative hypothesis: "the average length of males and females are unequal". T.tests were only performed for populations of N > 30.

t.test (Predictor~respons, data = x.csv)

2.4.2 Multivariate analysis: Cluster analysis and Principal Components Analysis - PCA

Hierarchical clustering was performed to identify similar diet preferences between species. The species diet was clustered by an algorithm by unweighted pair group average (UPGMA) with Euclidean similarity index (Hammer, Harper and Ryan, 2001). The clusters joined the most similar species by the composition of their diet and presented it as a dendrogram.

Principal component analysis (PCA) was run to investigate diet preferences of six species of eelpouts (*L. gracilis*, *L. esmarkii*, *L. pallidus*, *L. reticulatus*, *L. rossi*, and *L. seminudus*) with combination of environmental habitat (sediment, bottom temperature and salinity, and geographic position indicated by longitude and latitude). The PCA was used to investigate variance by a linear combination of the variables, and a reduction of dimensions, to present the components which explain most of the total variance (Hammer, Harper and Ryan, 2001). Fish observations with missing environmental data were excluded, leaving 210 fish observations in the multivariate analyse. The environmental data was continuous variables categorised in bottom temperature, bottom salinity and sediment size together with the geographical position given by latitude and longitude. All the data was standardized; by $\frac{(x-mean)}{stdev}$ before analysis. The Multivariate analysis was conducted in PAST (version 13.4).

3 Results

3.1 Sampling effort

In 2015 during the Barents Sea ecosystem survey (BESS), 280 stomachs from six species of eelpouts: greater eelpout (*L. esmarkii*, 12), gracile eelpout (*L. gracilis*, 148), pale eelpout (*L. pallidus*, 39), arctic eelpout (*L. reticulatus*, 34), threespot eelpout (*L. rossi*, 42), and longear eelpout (*L. seminudus*, 5) – were collected and analysed (Table 2). The spatial distribution of the eelpouts varied between species. The gracile eelpout, a mainly boreal species, had a wide distribution range from the northern coast of Norway and Russia to the south of Svalbard. Arctic (*L. pallidus, L. reticulatus, L. rossi* and *L. seminudus*) and mainly boreal (*L. esmarkii*) species were most abundant in the northern Barents Sea: west and east of Svalbard (Figure 8).

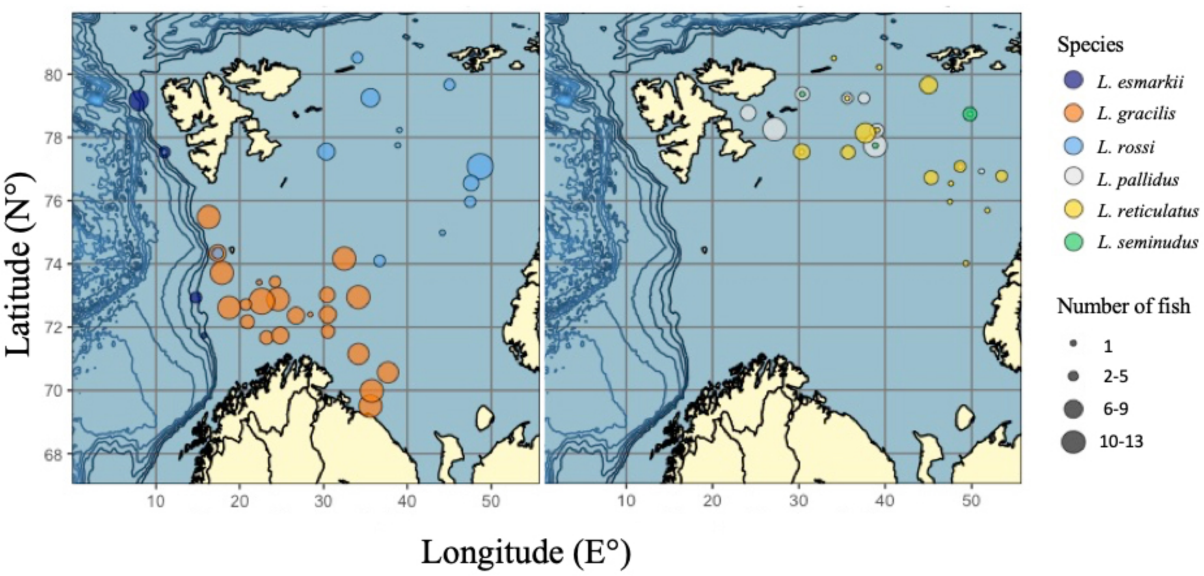

Figure 8. The number of fish (Left part: *L. esmarkii*, *L. gracilis* and *L. rossi*. Right part: *L. pallidus*, *L. reticulatus* and *L. seminudus*.), taken at trawl stations during the Barents Sea ecosystem survey.

The number of empty stomachs varied between species, in total there were 110. The arctic eelpout had the biggest percentage of empty stomachs of 62%, while the greater eelpout had the lowest of 8% (Table 1). Stomachs with content varied in number from the gracile eelpout with 104 stomachs to the longear eelpout with 4. The proportion of females were bigger than males (binom.test; $p < 0.05$). Average length between males and females was quite similar (t.test $p > 0.05$) except for *L. reticulatus* where the average male length was larger than females (t.test $p < 0.05$, Table 2). There were only a few fish smaller than 10 cm which were considered juveniles.

Table 2. Overview of collected stomach sampling, number of stomachs (N) with (N_{food}) and without food (N_{emty}), the minimum (L_{min}), maximum (L_{max}) and average ($L_{average}$) fish lengths (L, in cm) and sex are given.

Species	N	N_{emty}	N_{food}	L_{min}	L_{max}	$L_{average}$	Males		Female		Juvenile	
							N	L	N	L	N	L
Lycodes esmarkii	12	1	11	17.5	55.0	31.3	6	30.1	6	32.5	0	0
Lycodes gracilis	148	44	104	8.0	31.5	19.0	59	18.6	88	19.3	1	8.0
Lycodes pallidus	39	25	14	7.5	21.0	14.1	17	14.0	21	14.5	1	7.5
Lycodes reticulatus	34	21	13	5.5	40.5	20.2	14	25.1	18	17.9	2	7.6
Lycodes rossi	42	18	24	9.0	28.5	14.6	19	14.2	21	15.5	2	9.2
Lycodes seminudus	5	1	4	10.5	24.3	17.1	3	15.0	2	20.1	0	0
Total	**280**	**110**	**170**	**5.5**	**55.0**	**19.4**	**118**	**19.5**	**156**	**20.0**	**6**	**8.1**

Length of the eelpouts varied between species, and the greater eelpout was significantly larger than the other species (t.test $p < 0.05$), while pale eelpout and threespot eelpout were smallest (Figure 9).

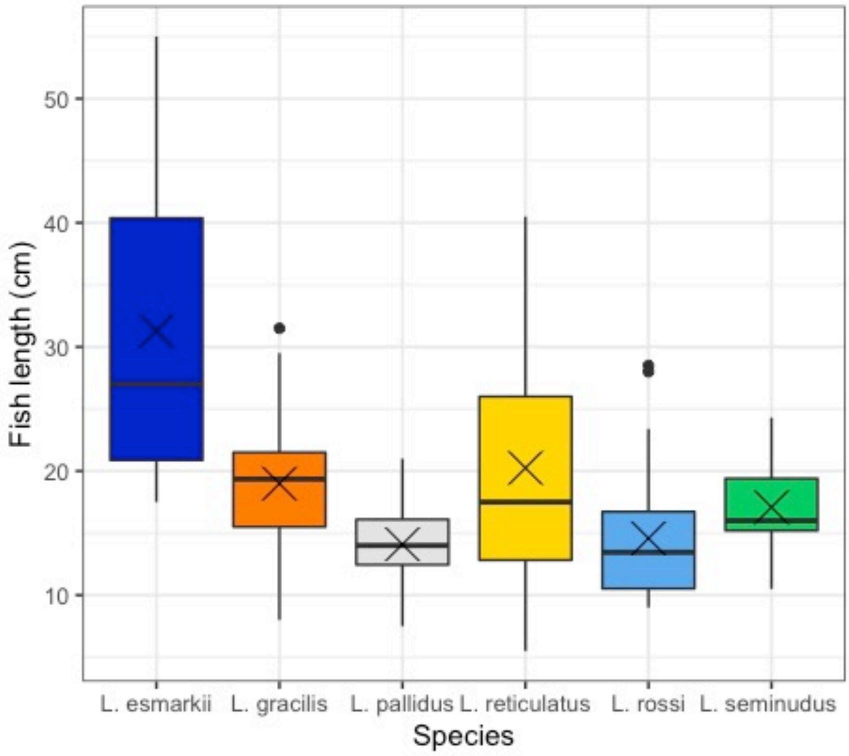

Figure 9. Fish length (cm) of six eelpouts species. Number of fish pr. species can be found in table 1. The boxplot includes the mean value (presented as X), median, outliers, maximum- and minimum value. The central rectangle includes the values between the first quartile to the third quartile.

3.2 Species diet

Below, the dietary findings are presented for all six eelpout species. These findings are ordered by species and presented by sex and length group. Information on weight percentage (%W) and the frequency of occurrence (%F) of each prey group in the stomach content of all species is presented in the appendix (A-III).

3.2.1 Greater eelpout, *L. esmarkii*

The greater eelpout was taken in the western Barents Sea (Figure 2). In total, 12 stomachs were sampled where one of them was empty. Females and males were equally represented in the sampling (Table 2).

The diet of the greater eelpot was dominated by echinoderms. The other prey items belonging to molluscs, worms, large demersal Crustacea were also recorded (Figure 10). Echinoderms were represented by *Ophiura sarsi*, *Ophicantha bidentate*, *Ophiocten sericeum*, ophiuroidea, mollusca by Gastropoda, *Arctinula greenlandica* and Pectinidae, worms by Polychaeta, and large demersal crustaceans by *Pandalus borealis*. Only an average 8 % of stomach content were difficult to identify and was registered as digested food.

There was little difference in diet between females and males. The diet were dominated by echnioderms for both females and males. The differing diet composition for females were mollusca and digested food, while males consumed worms and large demersal Crustacea (Figure 10AB).

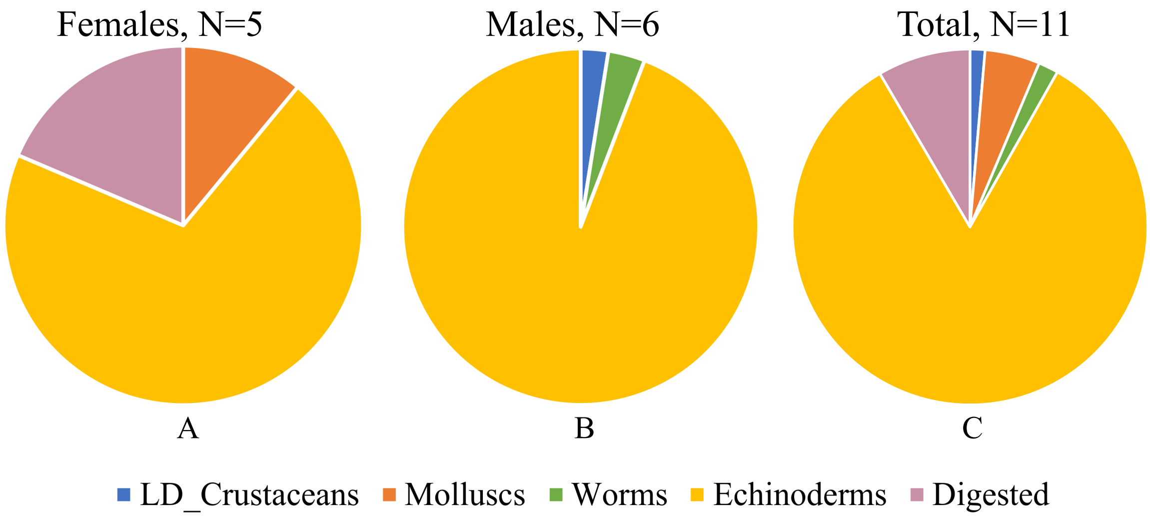

Figure 10. Percentage of prey group in *L.esmarkii* stomachs, for females (A), males (B) and total (C). N represents the number of stomachs with food.

The greater eelpout of all sizes preyed on echnioderms, but their proportion in the diet varied. Fish shorter than 35 cm preyed on echniodems only, while larger fish also preyed on other organisms such as molluscs, worms and large demersal Crustacea (Figure 11).

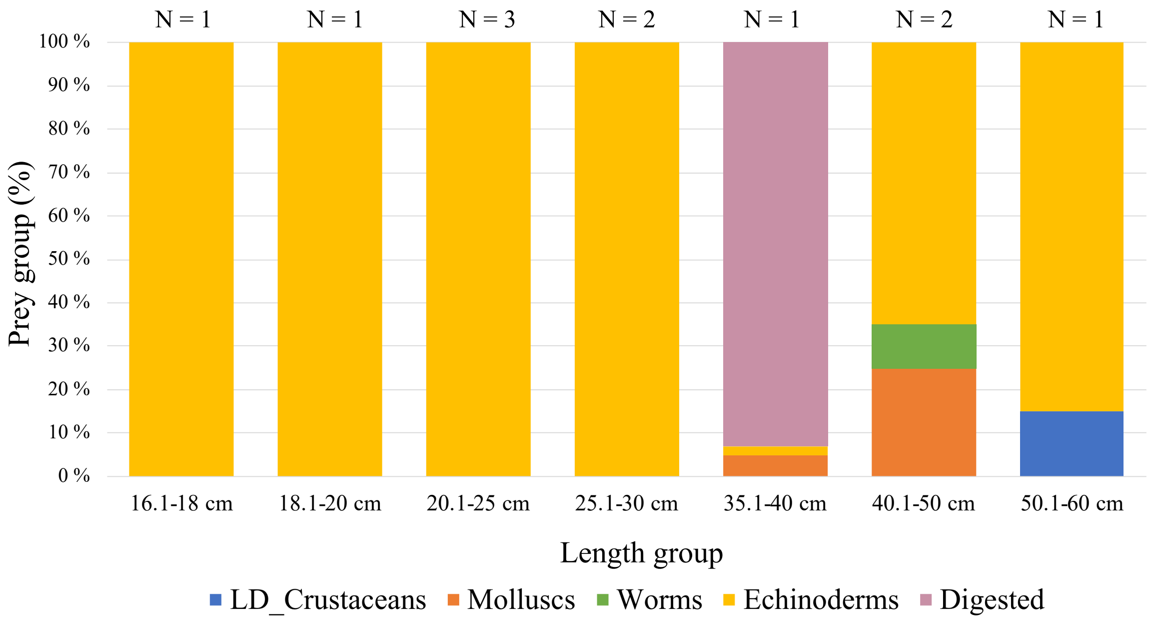

Figure 11. Percentage of prey groups in stomach per length group for *L. esmarkii*. N represents the number of stomachs with food. Size groups without fish with stomach content are not included.

3.2.2 Gracile eelpout, *L. gracilis*

The gracile eelpout was taken in the western and centeral Barents Sea (Figure 2). In total, 148 stomachs were sampled of *L. gracilis,* where 44 (30%) was empty. There was collected more females (88) than males (59, bin.test, $p < 0.05$), and one juveline. The length of the gracile eelpout ranged from 8 cm to 31.5 cm with an average length of 20.3 cm. Females (19.3 cm) and males (18.7 cm) had quite similar average length (t.test, $p > 0.05$) and the juvenile was 8 cm long (Table 2).

The diet of the gracile eelpout had a great variety. Worms, echnioderms and molluscs were the most common prey groups of *L. gracilis*. Other prey groups recorded in the stomachs were small demersal Crustacea, euphausiids, hyperiids, large demersal Crustacea, Crustacea mix, other plankton, fish, other and some digested food (Figure 12). Worms were represented by Polychaeta, echinoderms by Ophiuroidea, hyperiids by Amphipoda, mollusca by Bivalvia and Arctinula, small demersal Crustacea by Gammaridea, euphausiids by *Meganyctiphanes norvegica*, large demersal Crustacea by *Pandalus borealis* and *Saduria sabini*, fish (osteichthyes, including pleuronectiformes) and others (Foraminiferida).

The diet of females and males was quite similar, and dominated by three prey groups (worms, echinoderms and molluscs, Figure 12 AB). Their stomach samples also contained small demersal Crustacea, hyperiids, fish, large demersal crustaceans, diegsted food and other food groups. Juveline gracile eelpout comsumed other plankton (Chaetognatha) only.

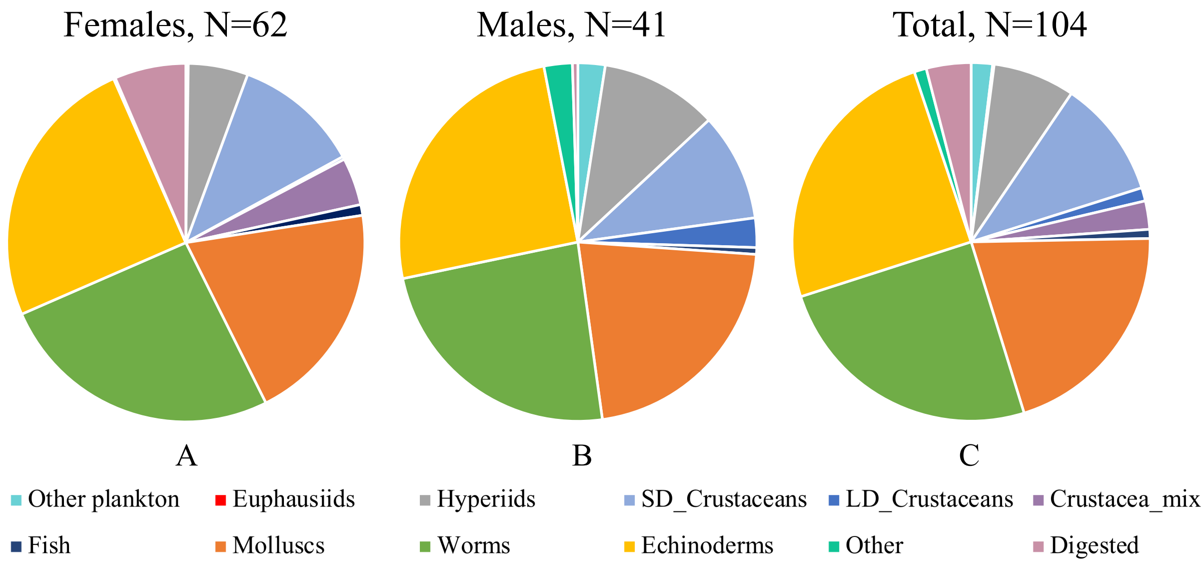

Figure 12. Percentage of prey group in *L. gracilis* stomachs, for females (A), males (B) and total (C). N represents the number of stomachs with content. The juvenile diet are not included.

The three dominating prey groups, echinoderms, worms and molluscs, were common in the fish diet, but the composition of these groups varied between size groups (Figure 13). The diet of fish below 12 cm was dominated by other plankton (Chaetognata). Echnioderms dominated most of the fish diet of all length groups, however their proportion decreased with incresed fish length. Only one stomach was collected from the largest length group which contained hyperiids and echnioderms. Worm's proportions in fish diet increased with fish length up to 40% (18-20 cm) and decreased with further increasing of fish length. The contribution of Mollusca to fish diet was about 20% and was highest for fish of 16-18 cm long. Other prey groups contributed less than 20%.

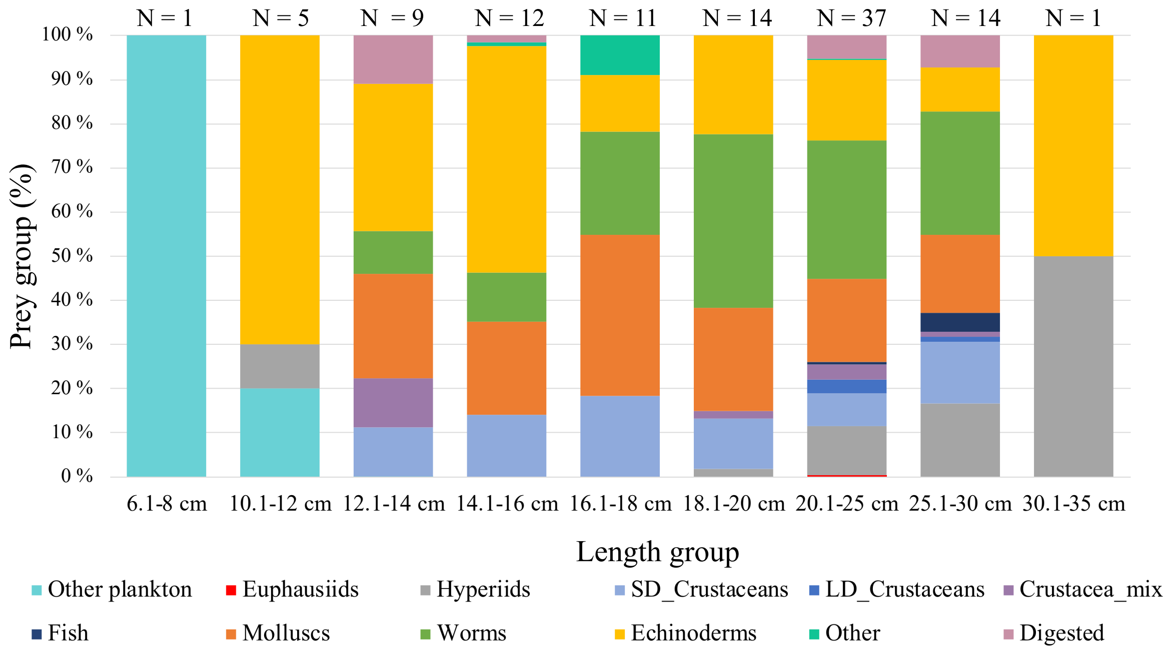

Figure 13. Percentage of prey group in stomachs per length group for L. gracilis. N represents the number of stomachs with content.

3.2.3 Pale eelpout, *L. pallidus*

The pale eelpout was tanken in the northern Barents Sea. There were collected 39 stomachs of pale eelpouts where 25 of them (64%) were empty. The sampling contained 21 females, 17 males and one juvenile. The average length of males and females was quite similar (t.test, $p > 0.05$, Table 2).

The composition of the diet of the pale eelpout was made up of several prey groups. Hyperiids was the most common prey group. Other recorded prey groups were worms, crustaceans, euphausiids, other, echinoderms and some digested food (Figure 14). Hyperiids were represented by *Parathemisto libellula*, worms by Polychaeta, echinoderms by Ophiuroidea, euphausiids by *Meganyctiphanes norvegica*.

There were some dietary differences between males and females, although hyperiids contributed a big part of their diet. Both female and male diet contained Crustacea and digested food. Some prey groups were found in male samples only, there among these were echinoderms, worms and other. Euphausiids were registered in one female sample only (Figure 14 AB). Each of the female eelpouts preyed on different types of Crustacea (Figure 14 A).

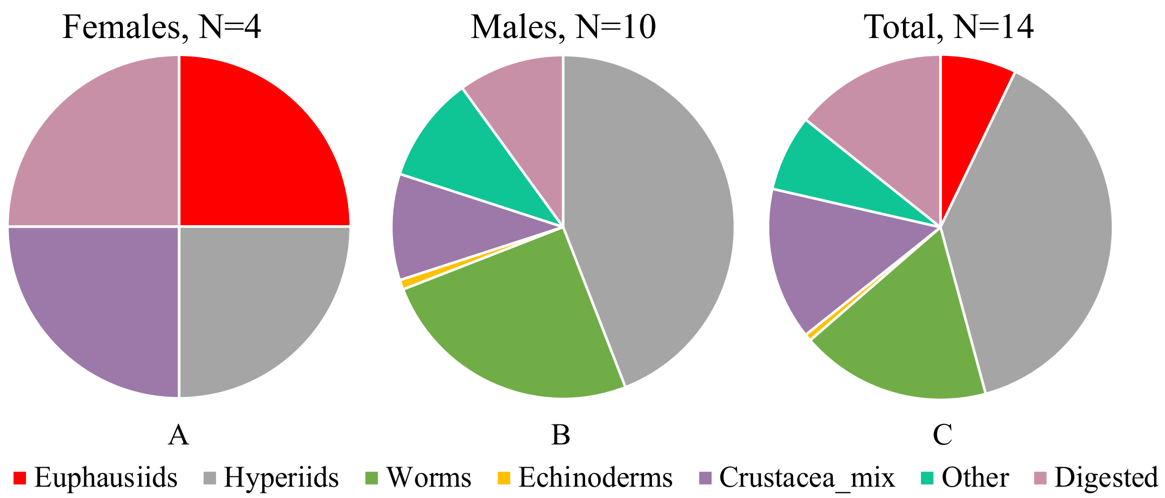

Figure 14. Percentage of prey group in *Lycodes pallidus* stomachs, for females (A), males (B) and total (C). N represents the number of stomachs with content.

Eelpouts of 8-10 cm and 18-20 cm preyed on worms only. The prey diversity was greater in the three middle length groups (10 – 16 cm), which also were the most abundant groups. Hyperiids made up the biggest part of the composition of the diet in these three groups, followed by digested food, euphausiids and other. The rest of the observed preys contributed less than 20% of the total composition in the length groups (Figure 15). Food items were difficult to identify in the stomach of the smallest eelpout and were categorised as digested food.

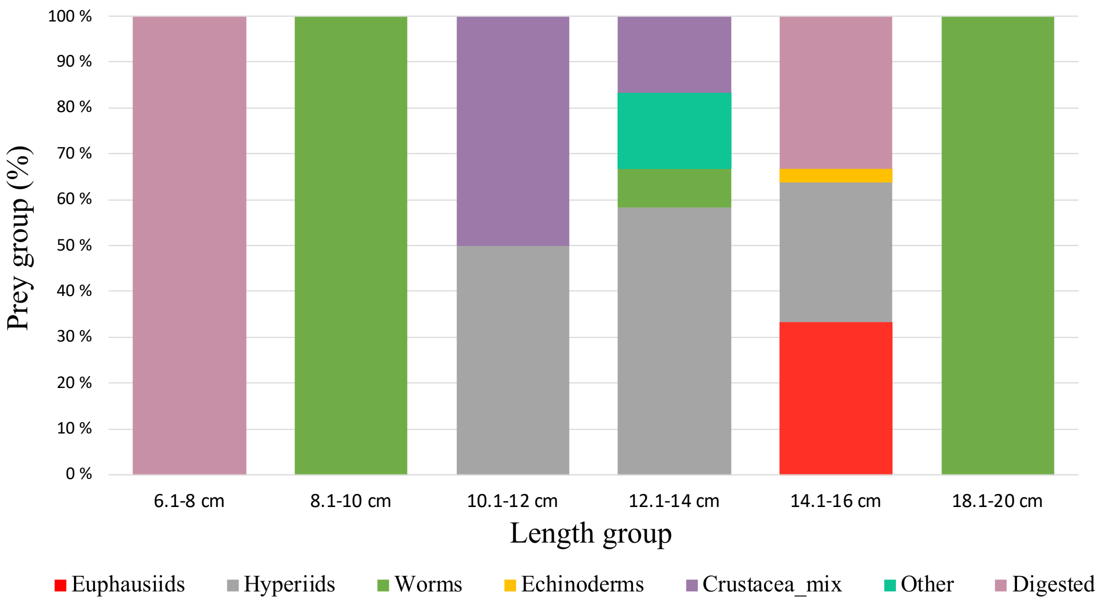

Figure 15. Percentage of prey in stomachs per length group for *L. pallidus*. N represents the number of stomachs with content.

3.2.4 Arctic eelpout, *L. reticulatus*

Stomach samples of the actic eelpout were taken in the northern Barents Sea. In total, 34 stomach samples were collected of the arctic eelpout, where 21 (62%) was empty. There were collected 18 stomachs from females, 14 from males and two stomachs of juveniles. The length of the arctic eelpout ranged from 5.5 cm to 40 cm with an average length of 20.3 cm. The male avragde length (25.1) was significantly larger than females length (17.9, t.tes, $p < 0.05$, Table 2).

The diet of the arctic eelpout contained several prey groups. Worms and fish were the most common prey. The stomachs also contained hyperiids, Crustacea mix, small dermersal Crustacea, cephalopoda and digested food (Figure 16). Worms were represented by Polychaeta, fish by *Mallotus villousus*, *Liparis fabricii* and Agonidae, Hyperiids by *Parathemisto libellula* and small demersal Crustacea by Gammaridae.

There were some differences in diet of males and females. Fish, hyperiids, worms and Crustacea mix were observed in the diet of both females and males, while the contribution varied between sexes. Worms dominated males diet but their contribution was low in female diet. Cephalopoda and small demersal Crustacea were presented in the male diet only (Figure 16 BC). The two juveniles had eaten worms only.

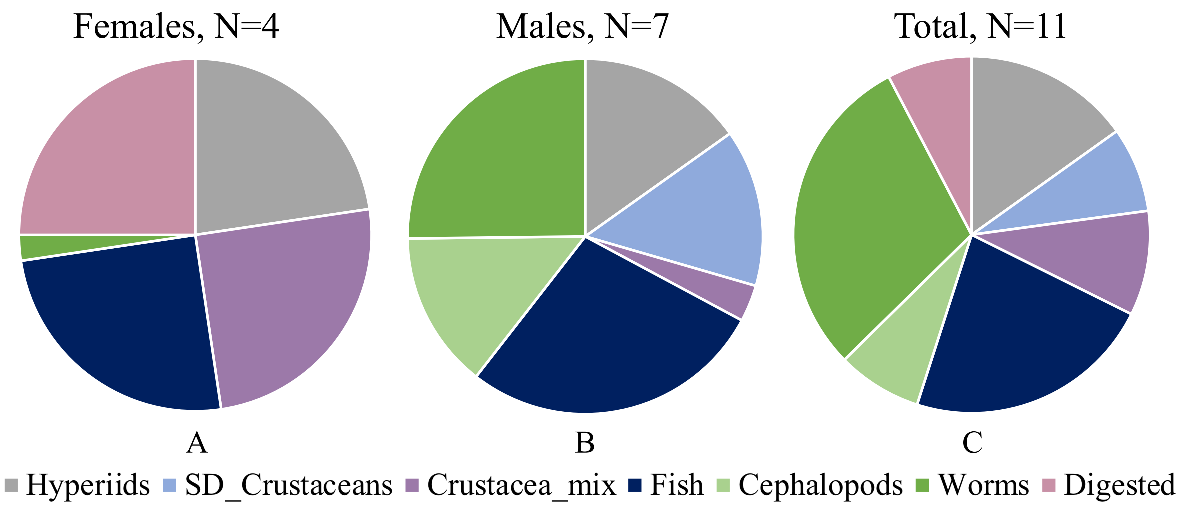

Figure 16. Percentage of prey group in *L. reticulatus* stomachs, for females (A), for males (B) and total (C). N represents the number of stomachs with content. Juveniles not included

The smalles fish of 4–12 cm had mainly been eating worms and some mix of Crustacae. Fish of 12-14 cm and 16-18 cm had been eating hyperiids (Figure 17). Arctic eelpouts of 16 - 35 cm preyed on fish, while the largest arctic eelpout (40-50 cm) had preyed on Cephalopoda only.

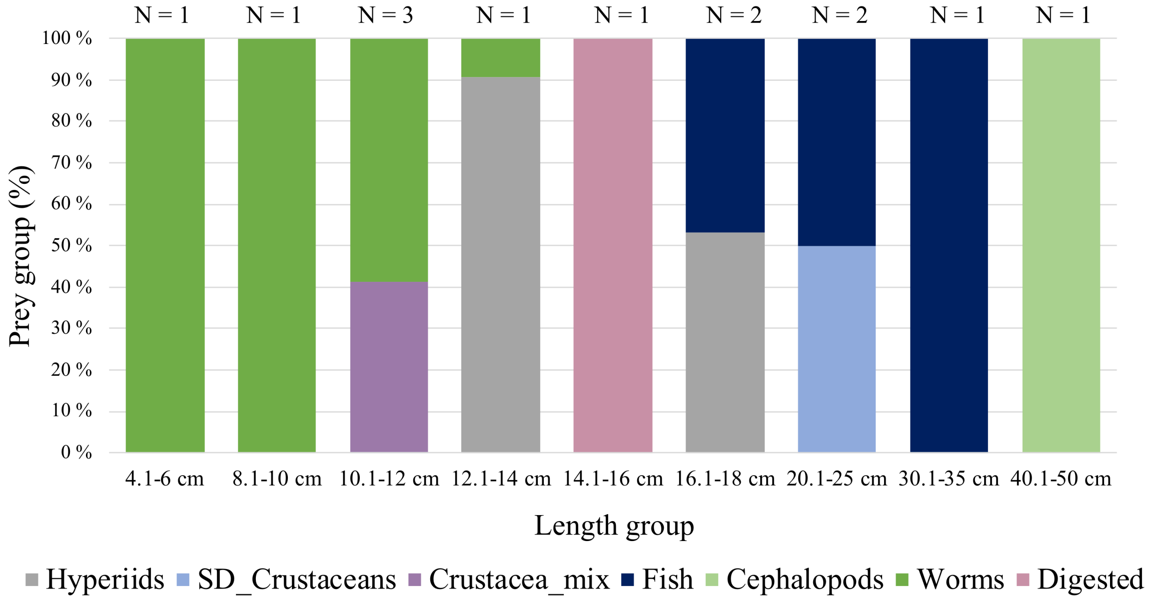

Figure 17. Percentage of prey in stomachs per length group for *L. reticulatus*. N represents the number of stomachs with content.

3.2.5 Threespot eelpout, *L. rossi*

Stomachs of the threespot eelpot were taken in the northern Barents Sea (Figure 2). There were collected 42 stomachs from the threespot eeplout, where 18 (43%) stomachs were empty. In total, there were collected more females than males, and two juveniles. The male average length (15.0) was quite similar to the females length (20.1, t.test, $p > 0.05$, Table 2).

The diet of threespot eelpout consisted of multiple prey types. Worms dominated the diet composition. Other prey groups recorded in the stomachs were Mollusca, Hyperiidea, small demersal Crustacea, Crustacea mix, Echinodermata and some digested food (Figure 18). Worms were presented by Polychaeta and Nephtyidae, Mollusca by *Bathyarca gracialis* and *Yoldia hyperborean*, small demersal Crustacea by Gammaridea, Hyperiidea by *Parathemisto libellula* and Echinodermata by Ophiurida.

Worms dominated in both female and male diet. Some prey groups were found only in female samples such as Crustacea mix and echinoderms, while hyperiids were presented in male samples only (Figure 18 AB). The juvenile consumed worms only.

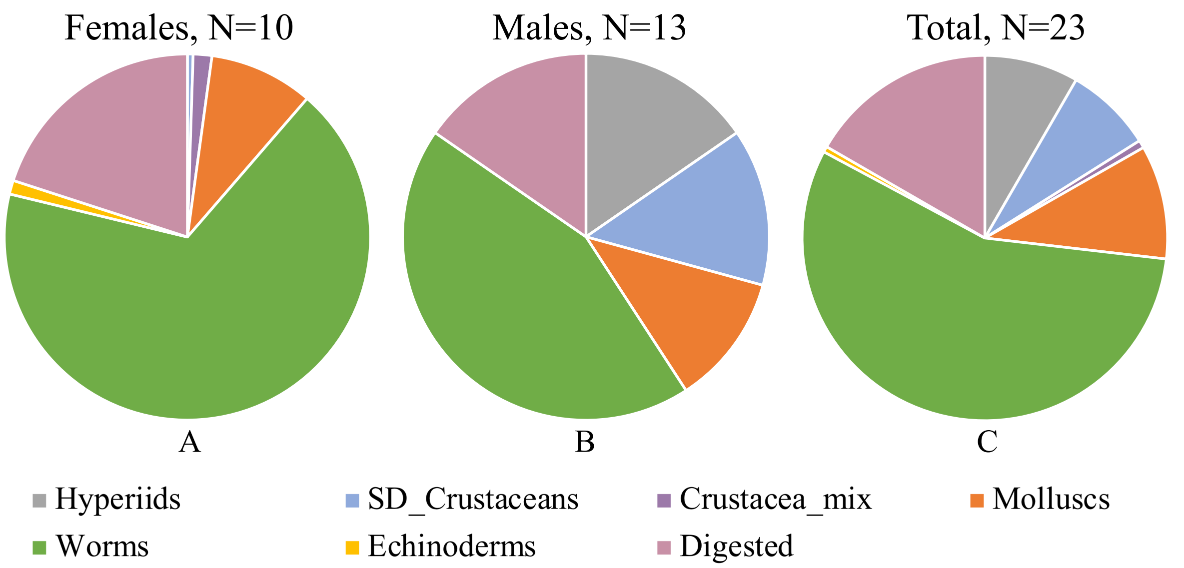

Figure 18. Percentage of prey group in *L. rossi* stomachs, for females (A), males (B) and total (C). N represents the number of stomachs with content. Juveniles is not included.

Worms were found in stomachs of fish of all length groups (Figure 19). The prey diversity was greatest in most abundant length group (10 – 12 cm) and was composed of five types of prey (worms, SD_Crustaceans, molluscs, hyperiids and echinoderms), while threespot eelpout of 25 – 30 cm preyed on worms only (Figure 20).

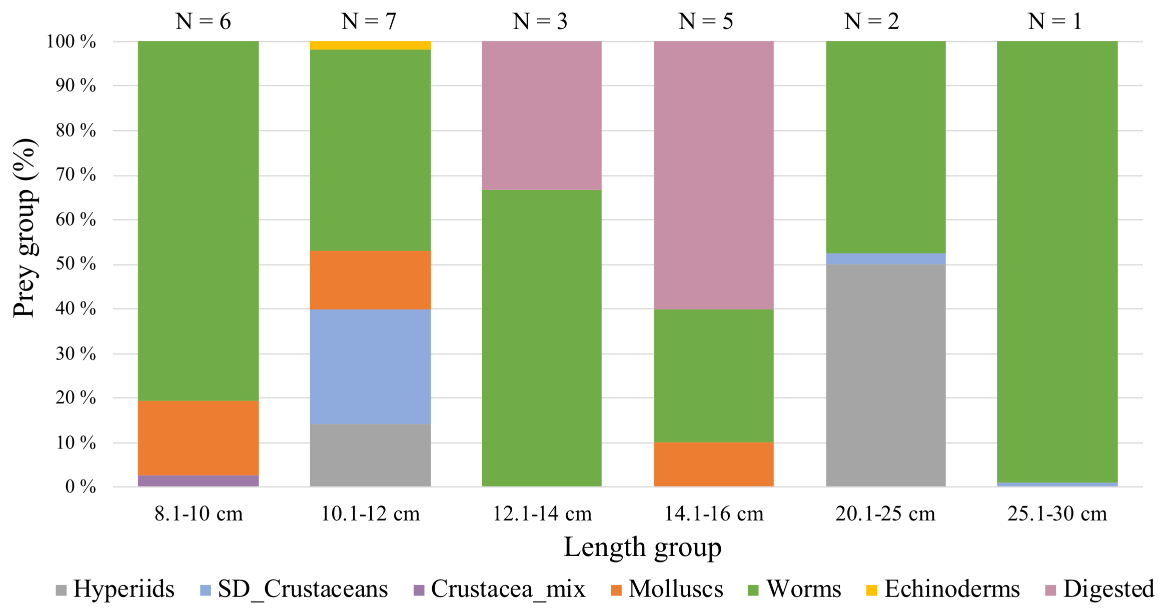

Figure 20. Percentage of prey in stomachs per length group for *L. rossi*. N represents the number of stomachs with content.

3.2.6 Longear eelpout, *L. seminudus*

Stomach samples of the longear eelpout were taken in the northern Barents Sea. There were collected only 5 stomachs of the longear eelpout, where 1 of the stomachs were empty. The diet of the longear eelpout are presented in Table 3.

Table 3. Description of the diet of the *L. seminudus*, N = 4

Sex	Fish length group	Stomach content	Prey group species
Female	14 – 16 cm	Hyperiids	*Parathemisto libellula*
	20 – 25 cm	Digested food	Digested
Male	14 – 16 cm	Digested food	Digested
	20 – 25 cm	Fish	*Liparis fabricii*

3.3 Eelpout diet composition

The cluster analysis was performed with 170 stomachs from six species and thirteen prey groups (digested food included). The cluster analysis is shown in firgure 21 (lower part) and the mean diet composition for all species is shown in percentage in figure 21 (upper part). The gracile eelpout (*L. garcilis*) and threespot eelpout (*L. rossi*) were clustered together based on their diet composition which was dominated of worms, mollusca, small demersal Crustacea and hyperiids, but the proportion of these preys varied between species (Figure 21, Table 4). The next cluster consited of the pale eelpout (*L. pallidus*) and arctic eelpout (*L. reticulatus*) whose preyed on worms, Crustacea mix and hyperiids. The diet of the longear eelpout (*L. seminudus)* and the greater eelpout (*L. esmarkii*) were different from the other clusters as well as each other. The longear eelpout preyed on fish and hyperiids, while greater eelpout preyed on echinoderms mainly. Digested food was observed in stomachs of all species, but the proportion varied between species.

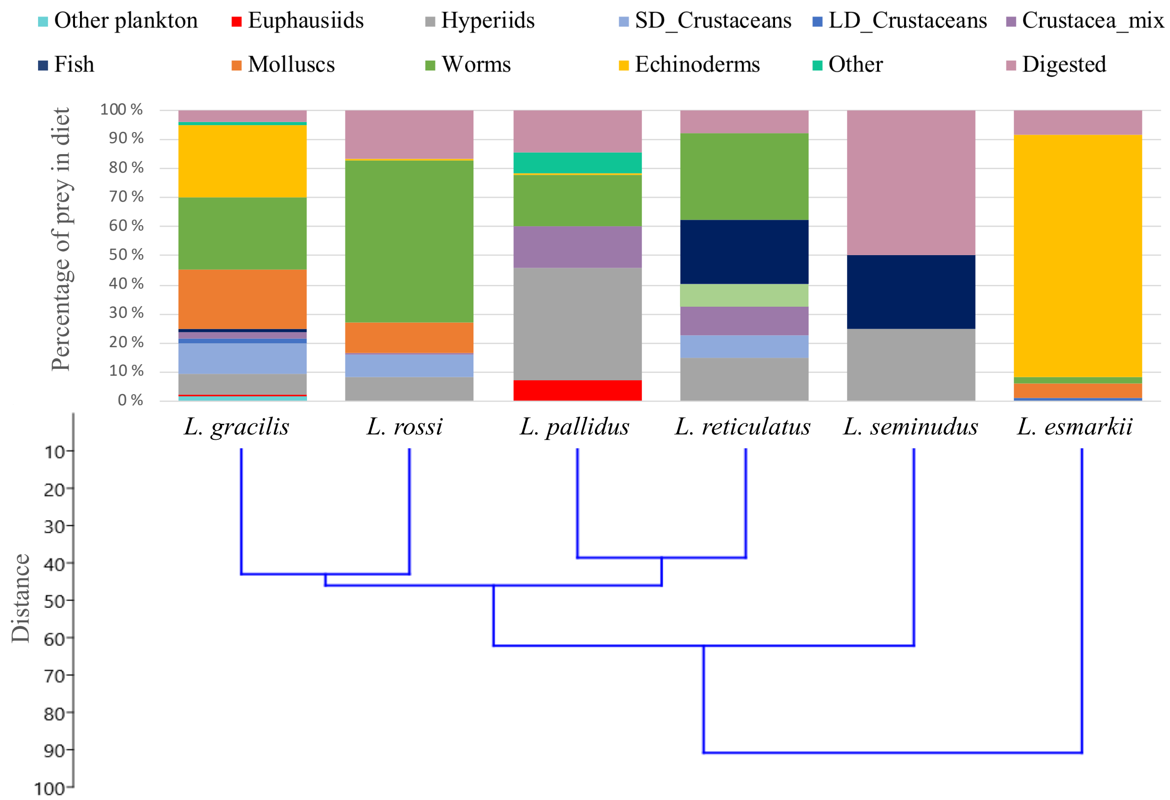

Figure 21. Diet composition for six eelpout species shown in the upper panel as average % wet weight of each prey group relative to the total stomach content of each individual fish. Clustering (unconstrained) of the six eelpout species based on diet composition are shown in the lower panel, and the sequence of species in upper panel has been arranged according to the outcome of the cluster analysis.

Table 4. Clusters of lycode species based on diet composition from stomach analysis. Results from cluster analysis of mean weight of stomach content of 13 prey categories (see Figure 21).

Cluster	Eelpout species	Main prey groups (species)
1.	Gracile eelpout (*L. gracilis*)	Worms (Polychaeta) Mollusca (Bivalvia, Arctinula) Small demersal Crustacea (Gammaridea) Hyperiids (Amphipoda) Echinoderms (Ophiuroidea)
	Threespot eelpout (*L. rossi*)	Worms (Polychaeta and Nephtyidae) Mollusca (*Bathyarca gracialis* and *Yoldia hyperborean*) Small demersal Crustacea (Gammaridea) Hyperiids (*Parathemisto libellula*).
2.	Pale eelpout (*L. pallidus*)	Worms (Polychaeta) Hyperiids (*Parathemisto libellula*) Euphausiids (*Meganyctiphanes norvegica*) Echinoderms (Ophiuroidea)
	Arctic eelpout (*L. reticulatus*)	Worms (Polychaeta) Hyperiids (*Parathemisto libellula*) Small demersal Crustacea (Gammaridea) Fish (*Mallotus villosus, Liparis fabricii,* Agonidae)
3.	Longear eelpout (*L. seminudus*)	Fish (*Liparis fabricii*) Hyperiids (*Parathemisto libellula*)
4.	Greater eelpout (*L. esmarkii*)	Echinoderms (*Ophiura sarsi, Ophicantha bidentate, Ophiocten sericeum*, Ophiuroidea) Worms (Polychaeta) Large demersal Crustacea (*Pandalus borealis*) Mollusca (Gastropoda, *Arctinula greenlandica*, Pectinidae)

3.4 Habitat

3.4.1 Bottom habitat

Sediment type could also be characterised by particle size which increased from "mud" to "gravel, stone and block". The eelpouts were observed at 8 types of sediment. Most of the eelpouts were found on muddy bottom (mud, gravely sandy mud and sandy mud), while *L. esmarkii* were found on sandy bottom (Figure 22).

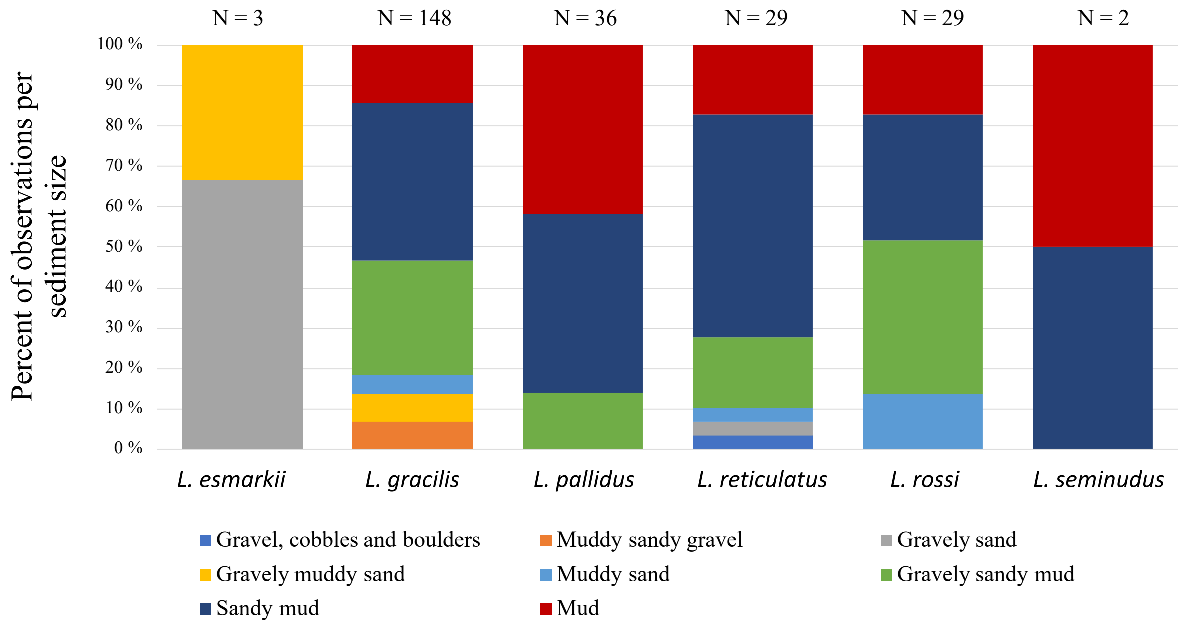

Figure 22. Bottom habitat (shown by sediment type) for six eelpout species. For more information of sediment type and grain size taken from table 1.

3.4.2 Thermal habitat

The eelpout species were collected at stations with bottom temperatures ranging from -1°C to 6°C. Most of the eelpouts were present in waters with temperature interval of 0 °C to 1°C. The gracile eelpout was diverging from the other species, and was most abundant with warmer bottom temperatures of 3 - 6 °C (Figure 23). In the appendix (A-I) extended information is presented about the number of fish collected per station, and its corresponding temperature measurement.

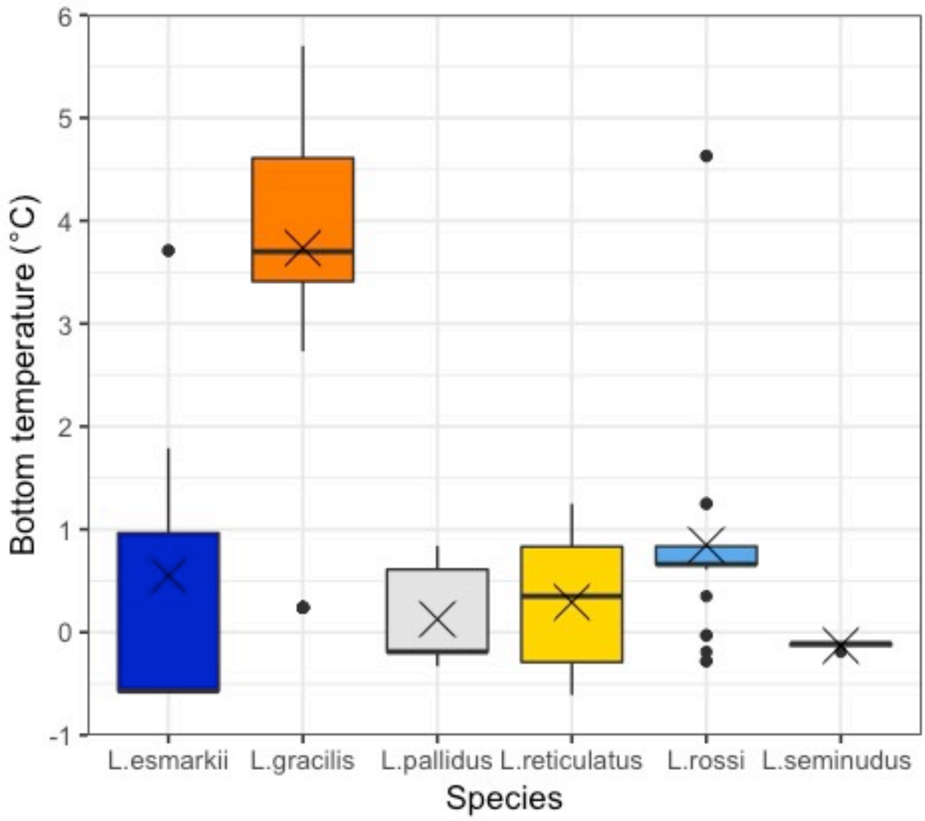

Figure 23. Thermal habitat for six eelpout species (bottom temperature, °C). Number of fish samples, where bottom temperatures were recorded: *L. esmarkii* (N = 12), *L. gracilis* (N = 138), *L. pallidus* (N = 26), *L. reticulatus* (N = 28), *L. rossi* (N = 35), *L. seminudus* (N = 4). The boxplot includes the mean value (presented as X), median, outliers, maximum- and minimum value of all registered fish. The central rectangle includes the values between the first quartile to the third quartile.

3.4.3 Environmental factors – PCA analysis

PCA analysis performed on the data of six eelpout species and their habitat (sediment, bottom temperature and salinity, and geographic position indicated by longitude and latitude). PC1 indicated boreal species (gracile eelpout (*L. gracilis*) and greater eelpout (*L. esmarkii*)) were associated with higher bottom temperature and salinity, and larger sediment particle size, while arctic species (pale eelpout (*L. pallidus*), arctic eelpout (*L. reticulatus*), threespot eelpout (*L. rossi*) and longear eelpout (*L. seminudus*)) were associated with lower temperatures and salinity. PC 2 indicated larger sediment particles with higher latitude, and higher temperature in westers part of the sampling area. PC 1 and PC 2 together explained 75.6% of the total variance of the eelpouts distribution relative to measured environmental variables (Figure 24). The precise correlation values are presented in Appendix (A-II).

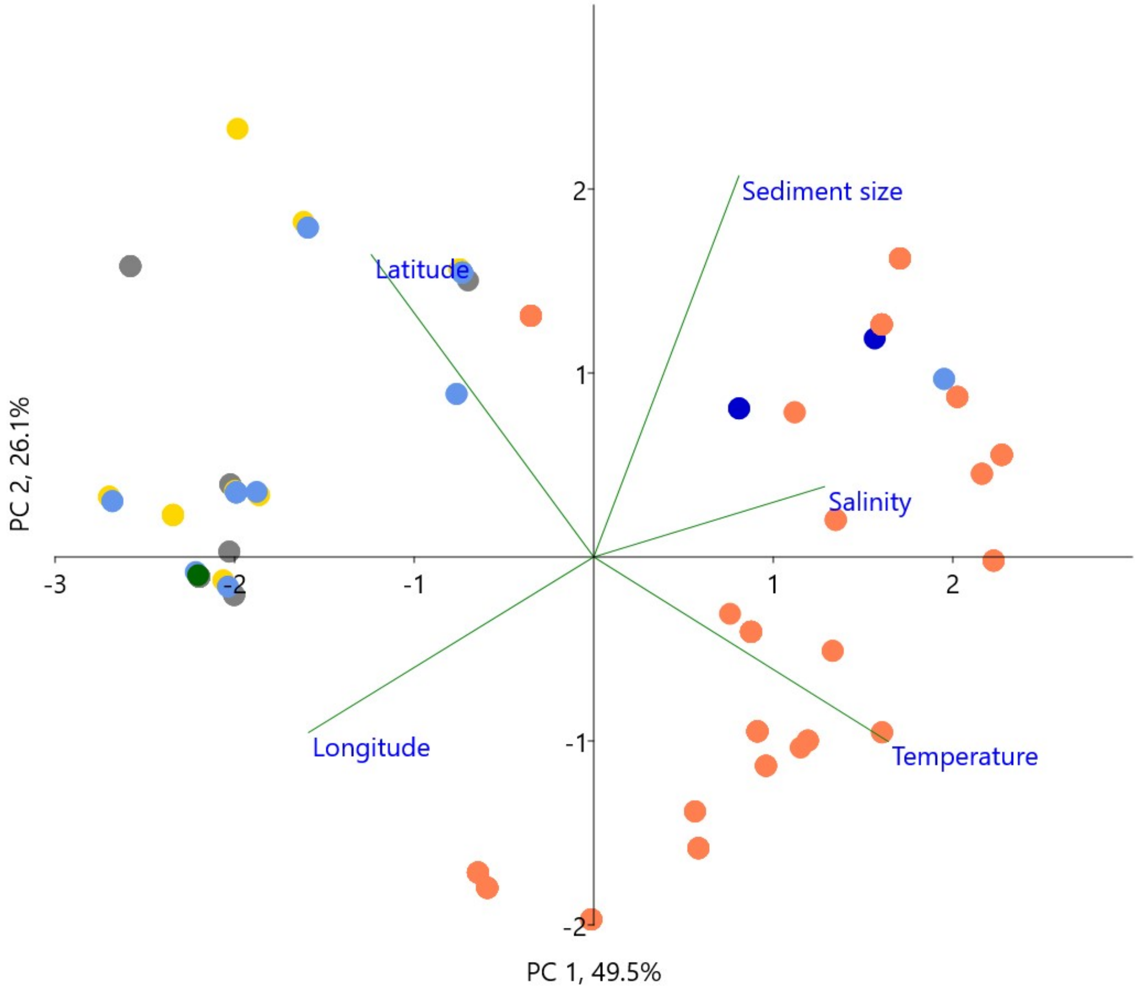

Figure 24. Results from PCA analysis of eelpouts (six species shown by different colour: orange - *L. gracilis*, dark blue – *L. esmarkii*, grey – *L. pallidus*, yellow – *L. reticulatus*, light blue – *L. rossi*, green – *L. seminudus*) and habitat (sediment, bottom temperature and salinity, and geographic position indicated by longitude and latitude). PC 1 and PC 2 together explained 75.6% of the total variance.

4 Discussion

The eelpouts are common fish families in the Barents Sea, still we have little information about their ecology, feeding preferences and interaction with other fish (Balanov *et al.*, 2006). The large-scale sampling program, during the “2015 - year of the stomach”, gave a basis for new and additional knowledge of spatial and seasonal variability in the diets of the Barents Sea fish, including the eelpouts (Eriksen *et al.*, 2019). This study has contributed to detailed descriptions of the eelpouts diet variation between species, area, fish length and sex. The eelpouts had a diet of great variety. Some earlier studies of eelpouts diet have been performed (Andriyashev, 1954; Albert, 1993; von Dorrien, 1993) and in the 1990s to the early 2000s (summarized by Dolgov, 2016).

Since 1980 the Barents Sea has experienced large changes: water temperature has increased and 2016 was one of the warmest years recorded. Areas covered by Atlantic water (>3 °C) and mixed water (0 – 3 °C) masses increased, while areas covered by arctic water (<0 °C) decreased and was lowest in 2016. The Barents Sea had a strong reduction of its ice, during the last two decades (ICES, 2018). Therefore, this study is important to be able to investigate if changes in environmental conditions influenced the diet of fish, especially in the northern Barents Sea, where most rapid changes occurred (ICES, 2018).

This study focused on eelpouts diet in the western, central and northern Barents Sea during August-September 2015, and how their diet varied between species, fish length groups, sexes, and habitats. Two eelpouts species (gracile and greater eelpout) in this study are mainly-boreal species and distruibuted in the western and central Barents Sea, while the other species (Pale, arctic threespot and longear eelpout) are arctic species and distributed in the northern Barents Sea.

4.1 Diet of eelpout species

This study has presented the diet of the greater eelpout (*L. esmarkii*), gathered along the continental slope in the western Barents Sea. The diet of the greater eelpout was largely dominated by echinoderms (*Ophiura sarsi*, *Ophicantha bidentate*, *Ophiocten sericeum* and other). The greater eelpouts also consumed molluscs, worms and *Pandalus borealis*, but to a lesser degree. Dolgov (2016) noted that information about the Barents Sea greater eelpouts is very limited. Since 1991 it has been reported that greater eelpouts have preyed on different benthos organisms, but mainly on Ophiuroidea (77.5%), however no information on sampling location or season were given (Dolgov, 2016). In studies of the early 1900s in the Norwegian Sea, the greater eelpouts were observed consuming echinoderms and small and large crustaceans (Collett, 1905, cited in Dolgov, 2016). This study is in aggreemnt with earlier studies about greater eelpouts food preferences and suplemented with additional food items.

The gracile eelpout (*L. gracilis*) was collected in the central and western Barents Sea. In total 148 stomachs were collected and one third was empty. The diet of the gracile eelpout was diverse and dominated by worms (Polychaeta), echinoderms (Ophiuroidea) and molluscs (Bivalvia and Arctinula). The gracile eelpout had also consumed small and large Crustacea and fish. Several studies showed that the diet of the gracile eelpout were diverse. Andriashev (1954) mentioned that gracile eelpouts consumed Polychaeta, small demersal Crustacea and Mollusca. Studies in the Norwegian deep during 1984-1987 showed that Crustacea, Mollusca (Bivalvia) and Ophiurida were the most common prey (Albert, 1993). During the sampling program performed by PINRO (1993-2010) there were collected 597 stomachs of gracile eelpouts, and 81 % of them were empty (Dolgov, 2016). The gracile eelpouts preyed on 15 taxa, but mainly on molluscs (Bivalvia), worms (Polychaeta), Ophiuroidea and Gammaridae based on previous sampling programs (Dolgov, 2016). The information of the gracile eelpout diet in this study stated that the prey types worms, echinoderms and molluscs made up the majority, and are consistent with earlier findings.

The pale eelpouts (*L. pallidus*) were collected in the northern Barents Sea, and of 39 stomachs only 14 contained food. The most common prey of the pale eelpout was hyperiids (only *P. libellula* was identified to species level). Other prey presented in the diet were worms (Polychaeta), euphausiids (*M. norvegica*) and echinoderms (Ophiuroidea). Since 2004, *M. norvegica* were commonly found in the western and central areas, their distribution extended eastwards in recent years (Eriksen *et al.*, 2016), but were not reported in the area east of Svalbard in the northern Barents Sea (Eriksen *et al*., 2016, Prozorkevich and Sunnanå, 2016, 2017; Prozorkevich, and van der Meeren, 2018). Most likely, that the pale eelpouts utilized a new boreal food resources that redistributed due to increased area of Atlantic water. Dolgov (2016) noted that information about the Barents Sea pale eelpouts are very limited to some observations in 1930s, where they consumed mainly Polychaeta, Mollusca, Ophiuroidea and in lesser degree on fish and Gammaridae. During 1999-2008 there were collected 112 stomachs where 70% of them were empty, and pale eelpouts preyed mainly on Ophiuroidea (47%), Gammaridae and polychaeta (Dolgov, 2016). The information of the pale eelpout diet in this study provides additional information to the earlier findings. Dolgov (2016) stated that Ophiuroidea was the dominating prey group, while in this study Ophiuroidea was only present in a small decree in the content of one stomach. Hyperiids were shown to be the dominating group of this study, while it only provided 2.9% of the diet of earlier findings (Dolgov, 2016). These results indicated that hyperiids, especially of boreal *M. norvegica*, have become a more important part of the pale eelpouts diet than previously stated.

The arctic eelpouts (*L. reticulatus*), collected in the northern Barents Sea, are presented by totally 34 stomachs (21 empty) in this study. The diet of the arctic eelpout was dominated by Polychaeta and larger eelpouts (>16 cm) and preyed also on fish such as *Mallotus villousus*, *Liparis fabricii* and Agonidae. Hyperiidea, Gammaridea and Cephalopoda were also found in the stomachs, but in a smaller degree. During 1994-2010 there was collected 426 stomachs where 24 % were empty. Dolgov (2016) reported that arctic eelpouts consumed different types of benthic organisms (such as Polychaeta and Gammaridea), including fish such as Cottidae and polar cod. These results provides supplementary observations that Polycheta, Hyperiidea and fish are a frequently part of the arctic eelpots diet. Arctic eelpouts collected in the studies performed in the Barents Sea, late June to late July 1991, stated that Polychaeta made out the biggest part of the diet, followed by Amphipoda and fish (von Dorrien, 1993). However, both arctic and threespot eelpouts were categorized under the *L. reticulatus* species name in this study (von Dorrien, 1993), which might have caused the results to represent a mixture of the two species. All of the the stated prey types observed in the actic eelpout diet of this study are earlier confirmed prey types of the species (Dorrien, 1993; Dolgov, 2016).

The threespot eelpots (*L. rossi*), collected in the northern Barents Sea, were presented by 42 stomachs where 18 of them were empty. The diet of the threespot eelpout was largely dominated by worms presented by polychaeta and nephtyidae. The threespot eelpout had also consumed Mollusca, Gammaridea, Hyperiidea and Ophiurida, but in smaller amounts. Andriashev (1954) mentioned that threespot eelpouts consumed Amphipoda, Polychaeta, and Mollusca. During the period 1993-2010 there were collected 100 stomachs of that threespot eelpouts, and 86 % of them were empty (Dolgov, 2016). Their diet consisted mainly of polychaeta (64% of frequency of occurrence). The results of this study supported earlier studies regarding food preferences and give additional information about other prey such as hyperiids and echinoderms.

The longear eelpouts (*L. seminudus*), collected in the northern Barents Sea, are presented by only five stomachs (1 empty). The stomach content of two fish only were identified to species level, *P. libellula* (hyperiids) and *Liparis fabricii* (fish). During the period 1994-2010, PINRO collected 186 stomachs, and 56 % of them were empty (Dolgov, 2016). The longear eelpout preyed mainly on fish (polar cod, capelin, bigeye sculpin and other), Gammaridea, and Polychaeta (Dolgov, 2016). The information given in this study is limited and supported previously studies.

Here, diets of eelpouts species were presented, and compared with earlier findings. Sampling effort varied between species and thus provided supplementary information of different value, however, this study showed that the eelpouts diet didn't changed significantly from previous periods and thus indicated no negative implications yet due to their preferred prey vanishing as a result of increasing temperatures. New information of the diet composition of the eelpouts were presented, including new types of prey, such as boreal *M. norvegica*, which have not been observed before in the northern Barents Sea. This indicated that the pale eelpouts most likely could utilise new food resources, due to the extension of Atlantic water masses.

4.2 Diet variation between length groups and sex

The body length of ellpouts varied between species. Studies by Scharf, Juanes and Rountree (2000) found correlation between prey size compared to predator size and that prey size may range from about 10% to more than 50% of the predator size. In this study, the pale eelpout and threespot eelpout were the smallest of the six eelpouts species, with an avarage length of 14 cm. The largest eelpout was the greater eelpout with an avarage length of 31 cm, while the other species were close to 20 cm in length. The body length of ellpouts varied also within species as well.

This study also indicated that small individuals preyed generally on smaller prey than larger. Smaller gracile eelpouts preyed on chaetognaths, while larger preyed on molluscs, echinoderms and hyperiids. Smaller arctic eelpouts preyed on worms, while larger preyed on fish. Smaller longear eelpouts preyed on hyperiids, while the larger preyed on fish. For some species sampling effort were small, therefore this is only an indication of change in diet with length. It is common for several fish species that the size of the comsumed prey are generally increases with the size of the predator. In addition, its been found that the maximum prey size increases with the larger predators, while the minimum prey size might be relatively constant, causing a asymetric distribution between predator size and prey size. This asymetric distribution makes fish of multiple sizes compete for food, which might seem to give the bigger predators a competitive adventage due to their abillity to eat the big prey, without competitions from smaller predators (Scharf, Juanes and Rountree, 2000). Therefore, measures of prey size have been used to represent the trophic niche of a species (Scharf, Juanes and Rountree, 2000), and can be important for further investigation of the eelpouts niche and the trophic relations in the Barents Sea.

There was no great difference in diet between sexes in this study. The small variation between sex may be due to the small difference in length between males and female. In this study, the arctic eelpout was the only species which showed a significant difference in length between sexes. The males were larger than the females of the arctic eelpout, however there was only a small difference in diet.

Interspecific competition

Dietary overlap is one of the common factors causing interspecific competition (Smith and Smith, 2015). The gracile eelpouts diet overlapped with the diet of the other eelpouts, however gracile eelpout did not overlap with them geographically, and therefore does not compete with them for food. In contrast, threespot, pale and arctic eelpouts are distributed in the northern Barents Sea and therefore overlapping both geographically and dietary with each other. These species were also of similar size, which could indicate that they are competing for similar types of prey items (including Polychaeta and *Parathemisto libellula*). Still, due to the great variety in diet, the strength of competition might be reduced. Pale eelpouts were also found consuming new boreal food sources such as *M. norvegica,* and with decreasing or redistribution of common prey could most likely adapt better to changing conditions.

Longear eelpout overlapped geographically with other arctic species in the northern Barents Sea (Figure 2). The longear eelpout diet overlapped mainly with arctic eelpouts which also consumed fish and hyperiids. The sampling effort were limited to two individuals, which were collected at different areas. Each of the longer eelpouts preyed on different organisms which could indicate different prey availability in these areas or that they prefer different types of prey.

4.3 Eelpouts habitat and how it influences their diet

The diet of the greater eelpout differed most from the diet of other eelpouts, most likely due to their geographic distribution and bottom habitat. Distribution of greater eelpout and gracile eelpout varied from the other species. Greater eelpout where distributed along the continental slope in the western Barents Sea on "gravely sand" and "gravely muddy sand" bottom and at low temperatures (mostly below 1°C). The gracile eelpouts were distributed in the central and western Barents Sea, over multiple sediment types and the warmest temperature interval of approximately 3 – 6 °C. The gracilis eelpouts diet preferences was wider that other eelpouts most likely due to different distribution and access to food. Arctic eelpouts (pale, arctic, threespot and longear eelpout), distributed in the northern Barents Sea, by generally the same sediment types and temperatures (-0.5 – 1.5 °C).

This study showed that eelpout distribution is limited to the central area (gracile eelpout), northern area (pale, arctic and threespot eelpout), and the continental shelf slope (greater eelpout) of the Barents Sea. This geographically distribution also indicates limitation in habitats (thermal, sediment and other). In addition, the eel-shaped body, which is not ideal for long migrations (Aune *et al.*, 2018), also limits the eelpouts geographical range or migrating behaviour. In contrast, the North East Atlantic cod (*Gadus morhua*) which is a boreal migrating species, spawn along the northern part of the Norwegian coast and undertake feeding migrations to the northern Barents Sea. Cod diet variates and they prey on different types of food (Yaragina, Aglen and Sokolov, 2011). In addition, cod is a highly mobile species which adapt better to changes in environmental conditions, such as ongoing warming, than stationary species which are limited to a specific habitat (Kortsch *et al.*, 2015). At different rates, caused by unequal sensitivity to environmental change, spreading capability, and capability to utilize new recourses, species will change their distribution and abundance at different amounts (Fossheim *et al.*, 2015). Fish diet is one of the important indicators of a fish species' ability to adapt to environmental changes. Combined with information about species abundance and distribution, this information are fundamental to get an understanding of the trophic structures in the Barents Sea (Dolgov *et al.*, 2011).

The boreal food web contains a greater number of trophic generalists than the arctic: the number of food web links pr. species are about 40% higher for the boreal areas compared to the arctic area (Kortsch *et al.*, 2015). Depending on the species position in the food web, species with fewer interactions might also have large structural impact. In Kortsch et al. (2015) the gracile eelpout (*Lycodes gracilis*) were categorized as a taxa of few trophic interactions, but possessed an important connecting role between benthic and pelagic modules, due to their position in the network (Kortsch *et al.*, 2015).

This study showed that eelpout diet in 2015 was generally similar to the diet described earlier (from periods with lower temperature conditions and larger ice-covered areas, Dolgov, 2016). Thus, domination of preferred prey items in the eelpouts diet in 2015 indicated no dramatic changes in prey distribution and prey availability. However, extended distribution ranges of boreal species in the arctic part of the Barents Sea (borealization, Fossheim et al., 2015), could lead to strengthened food competition between arctic and boreal species (Kortsch *et al.*, 2015), and therefore further investigations of eelpouts diet are important to monitor changes.

4.4 Methodological challenges

In this study 280 eelpouts were sampled and analysed, and 170 stomachs contained food. Eelpouts are common species in the Barents Sea, but sampling effort are lower than other common species such as cod, haddock and redfish. Sampling effort in this study was limited, however it was the first time IMR collected eelpouts stomachs over a larger area. For some species, number of stomachs were low, and caused results that most likely are uncertain. Still, this information can be used as additional information to other studies. For further investigation of eelpouts diet more evenly distributed sampling (temporal and spatial) should be performed. This study gives an insight to the eelpout diet during autumn and can be used in comparison to other seasons with later studies. Sampling in the arctic part of the Barents Sea could be challenging in other seasons due to ice coverage.

In addition to low sampling effort of some species, several prey items were not identified to species level. Some prey items are digested faster than other, which makes identification more difficult for some prey species, and can limit our understanding of trophic interaction between species in the Barents Sea. In this study, most of the samples were processed on board right after the catch was sorted. Stomach contents were processed when stomach were fresh, which secured better species identification. However, time limitation on board could lead to higher taxa level of diet identification. In contrast, on lab the technicians could use the time they needed for species identification of stomach content, but further digestion of samples before freezing, and freezing reduced the quality of stomach content. New genetic methods (e.g. barcoding) can make the species identification of fish diet more accurate and can be helpful when morphological criteria for species identifications are not sufficient (Valentini, Pompanon and Taberlet, 2009), and reduce human impact (errors and limitations).

In this study, prey items were categorized to prey groups based on earlier studies (Eriksen *et al.*, 2019) which influenced diet precision, but gives general patterns of fish diet. In addition, the percentage of prey items could make a distorted picture of prey importance because hundreds of krill, and one fish in stomach content gives the same importance of prey. To avoid misinterpretation of diet, also the weight of different prey species should also be taken into account in additions to prey occurrence, shown by percentage. However, this study based on samples processed on board had difficulties obtaining the correct weight for small prey items, and therefore occurrence might give more unbiased information of the diet.

Despite of some methodological challenges, this study gives important contribution to mapping of the eelpouts diet and trophic interactions in the Barents Sea.

5 Conclusions

The study focussed on eelpouts diet in the Barents Sea: variation between species, areas, fish length and sex and based dietary and biological information from 280 eelpouts from six species, which were supplemented with habitat data, such as geographical position, sediment types and bottom water temperature. The study showed that eelpouts had a diet of great variety. The boreal gracile eelpout and the arctic threespot eelpout overlapped dietary (preyed mainly on worms, molluscs and hyperiids), but not geographically and were therefore not competing for food resources. The pale, arctic and longear eelpout overlapped geographically and partly dietary (pale and arctic: hyperiids and worms, while arctic and longear: hyperiids and fish), however, these species have a diverse diet and thus could reduce the strength of the food competition. The eelpout diet in 2015 didn't show great changes from previous findings and thus indicated the species' ability to adapt to environmental changes such as ongoing warming in the Barents Sea. The pale eelpout was found to have consumed *M. norvegica*. This finding might be an indication that the pale eelpout is able to utilise new food resources caused by an extended area of Atlantic waters and boreal species in the arctic parts of the Barents Sea. Due to the eelpouts position as a link between the benthic and pelagic communities in the food web network this needs to be further investigated. This study has contributed to detailed descriptions of the eelpouts dietary variation between species, area, fish length and sex.

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APPENDIX

A – I Temperature and number of fish caught pr. trawl

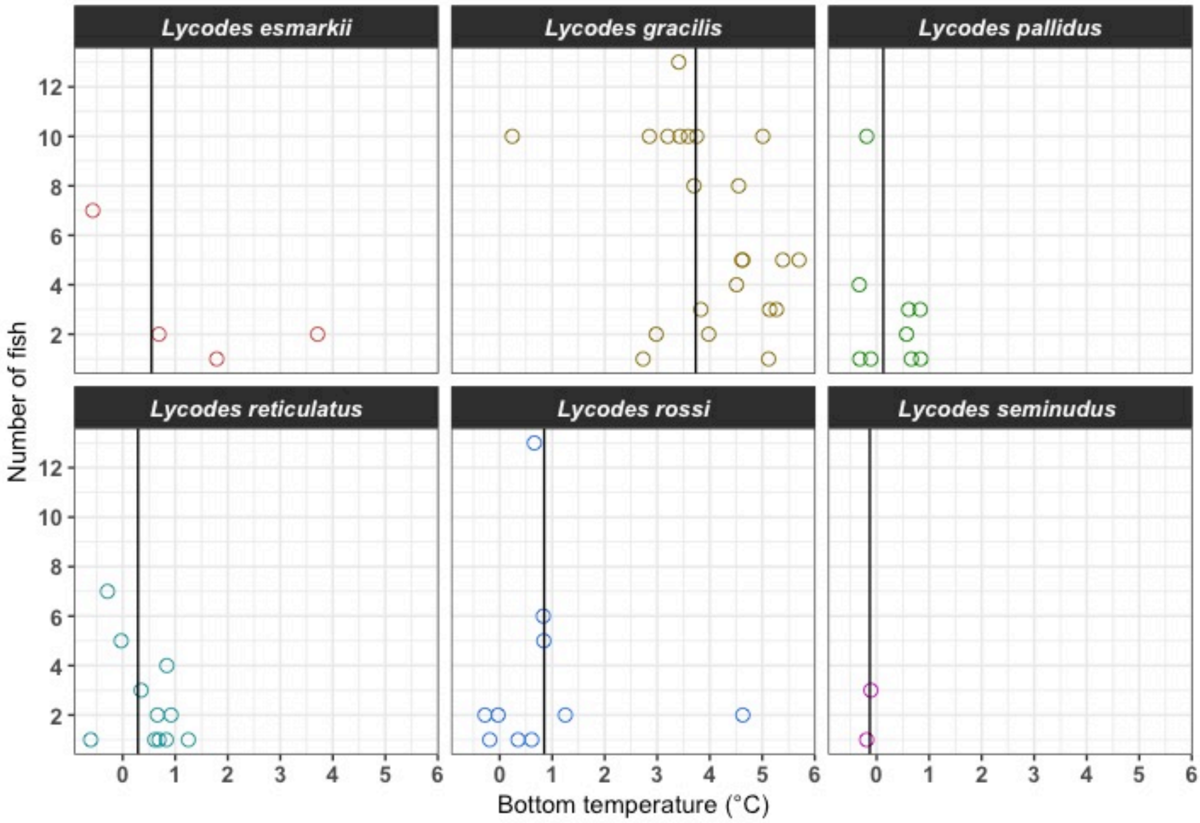

Figure A-2. Thermal habitat of six eelpout species. Number of fish registered with the same temperature were caught on the same trawl. The black line represents the weighted mean, which take the number of fish pr. trawl into account. Fish with no registered temperature were excluded from the figure. Trawls without associated bottom temperature measurement are not included.

A – II Correlation between habitat variables

Table A-II. Correlation between habitat variables. Left part shows Pearson's correlations coefficient (r), right part shows p – value.

	Latitude	**Longitude**	**Temperature**	**Salinity**	**Sediment size**
Latitude		0.000	0.000	0.008	0.359
Longitude	0.295		0.000	0.000	0.000
Temperature	-0.717	-0.557		0.000	0.241
Salinity	-0.184	-0.480	0.454		0.004
Sediment size	0.064	-0.555	0.081	0.200	

A – III Mean stomach content by weight and occurrence

Table A-III. Stomach contents of six eelpout species. %W (percent weight) and %F (frequency of occurrence of each prey category among stomachs with content) are stated for each species. The numbers are rounded to the nearest integer.

	Greater eelpout (*Lycodes esmarkii*)		Gracile eelpout (*Lycodes gracilis*)		Pale eelpout (*Lycodes pallidus*)		Arcitc eelpout (*Lycodes reticulatus*)		Threespot eelpout (*Lycodes rossi*)		Longear eelpout (*Lycodes seminudus*)	
Prey category	**%W**	**%F**	**%W**	**%F**	**%W**	**%F**	**%W**	**%F**	**%W**	**%F**	**%W**	**%F**
Other plankton	---	---	0	3	---	---	---	---	---	---	---	---
Euphausiids	---	---	1	1	16	7	---	---	---	---	---	---
Hyperiids	---	---	8	12	57	43	2	23	5	8	16	25
SD_Crustaceans	---	---	16	34	---	---	5	8	2	17	---	---
LD_Crustaceans	3	9	1	3	---	---	---	---	---	---	---	---
Crustacea_mix	---	---	2	5	2	14	0	23	0	4	---	---
Cephalopods	---	---	---	---	---	---	18	8	---	---	---	---
Fish	---	---	2	2	---	---	74	23	---	---	75	25
Molluscs	3	18	18	45	---	---	---	---	2	17	---	---
Worms	3	9	32	48	17	21	0	38	89	67	---	---
Echinoderms	87	100	20	48	1	7	---	---	0	4	---	---
Other	---	---	1	3	6	7	---	---	---	---	---	---
Digested	4	9	0	5	1	14	0	8	3	17	9	50
Number of stomachs with food	11		104		14		13		24		4	
Number of empty stomachs	1		44		25		21		18		1	
Number of stations	4		23		11		15		13		3	