Diet variation in Barents Sea haddock (*Melanogrammus aeglefinus*)

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Table of content

Abstract

Diet composition and feeding are crucial for assessing fish species ecological role, population dynamics, and overall ecosystem health. It provides insights into fish's functional role within the food web, and it contributes to their energy acquisition, overall survival, growth, and reproductive success. Barents Sea haddock (*Melanogrammus aeglefinus*) is an important commercial species in the Barents Sea, but there are few comprehensive studies and documentation on haddock stomach contents. This study aims to address this gap by utilizing haddock stomach data from 1984 to 2019, providing an overview of the haddock diet. Additionally, the year 2009 was studied in detail to explore the geographic variation diet composition and feeding success of Barents Sea haddock. To test for competition, the effect of density of haddock on the proportion of empty stomachs and the Total Fullness Index (TFI) was analyzed. For all years, the main prey categories found in haddock stomachs were Crustacea and Echinodermata. However, in 2009, the dominant prey category was Annelida. A significant difference was observed in the proportion of empty stomachs among the different areas in the Barents Sea, with the southwest having more empty stomachs compared to the southeast and northwest. The prey categories Annelida, Mollusca, and Crustacea were most found in the southeast, while Echinodermata was more prevalent in the northwest. As the size of haddock increased, the probability of empty stomachs decreased, with the southwest area having the highest probability. Additionally, larger haddock had a higher likelihood of containing Annelida, Mollusca, and others prey types in their stomachs. In the southeast area, there was a significant negative effect of haddock density on stomach fullness. My research contributes to a better understanding of haddock diet and address knowledge gaps about the Barents Sea haddock population where information on stomach content has been lacking. Improved knowledge of their diet is crucial for future management and conservation efforts.

Keywords: Barents Sea, haddock, diet, feeding, prey

1. Introduction

Consuming food is vital for all living organisms since it provides energy for survival, somatic growth, and reproduction. It also plays a crucial role in species interactions like predation and resource competition. Because of this, research on fish feeding ecology is essential for understanding trophic relationships, population and community dynamics, and system comparisons (Braga et al., 2012). To thoroughly explore diet composition and feeding ecology, analysis of stomach content is an important and universal method (Amundsen & Hernandez, 2019). Fish are particularly useful animals for nutritional research using stomach content analysis since they frequently have a well-defined stomach, can ingest large amounts of food, and typically swallow their prey whole. The study of data on stomach contents has been used in numerous publications that discuss various elements of the ecology of fish feeding. Understanding the choice of prey target and the fish's preferences for different types of prey are crucial objectives for fish dietary research. Quantifying the diet composition can help with several research issues and provide important information about fish behavior and their role in the ecosystem (Amundsen & Hernandez, 2019).

In addition to overall food availability and productivity, the diet is affected by the access to different prey, the quantity, and the suitability of those prey. Further, food intake can be affected by the density of their own species (intra-specific competition), or the competitors of other species (inter-specific competition) (Jones, 1983). Moreover, the fish's growth is impacted by the food quality and food availability (Holt et al., 2019). Most fish species' growth is indefinite and flexible and can be affected by several biotic and abiotic factors (Amundsen et al., 2007). Intraspecific competition is important in density dependence of somatic growth and other fish population characteristics, but density dependence in food consumption has not been well studied (Amundsen et al., 2007). In the regulation of many fish populations, density dependence growth in the recruit phase is a key process (Lorenzen & Enberg, 2002). The metabolic processes of ectothermic organisms like fish are strongly affected by the temperature (Baudron et al., 2011), and together with variation in prey availability, temperature influences biological characteristics like growth, which may regulate a stock's productivity (Rindorf et al., 2008; Holt et al., 2019).

Haddock (*Melanogrammus aeglefinus*) is the second-most important commercial species inhabiting the Barents Sea, after Barents Sea cod (*Gadus morhua*) (Devine & Heino, 2011), and one of the most abundant fish species in the Barents Sea (Russkikh & Dingsør, 2011).

The Northeast Arctic haddock (hereby called Barents Sea haddock) is the largest stock of haddock in the world. Year-class strength and density of Barents Sea haddock varies greatly (Figure 1), and haddock density may have an impact on growth rates (Korsbrekke, 1999). Competition among individuals for food access increased with density, which has an impact on how successfully they feed. For juvenile fish, including Barents Sea haddock, studies have shown a positive correlation between temperature, growth, and food availability (Bogstad et al., 2013).

Haddock is one of many demersal fish species that feed on the diverse benthos fauna in the Barents Sea and is classified as a benthos-eater (Dolgov et al., 2011; Eriksen et al., 2020). Jiang and Jørgensen (1996) argue that the haddock are generally believed to have difficulties catching big fast-moving pelagic prey due to their ventral mouth. Additionally, they used data from 1984-1991 to study the diet of haddock in the Barents Sea and found that haddock consumes a wide range of prey items, including seaweed and fish. Haddock’s primary diet consisted of echinoderms, molluscs, polychaetes, and crustaceans (Bergstad et al., 1987; Russkikh & Dingsør, 2011). However, as the haddock grows, fish starts to make up a larger percentage of their diet (Greenstreet et al., 1998; Russkikh & Dingsør, 2011). Tam et al. (2016) conducted an analysis of haddock diets across various ecosystems, while Schückel et al. (2010) studied the diet of haddock from the North Sea. Both studies revealed that benthic invertebrates predominated the diet of haddock.

The Barents Sea’s ecosystem is made up of a diverse, complex, and crucial component of benthic invertebrates that live at the seabed. Epibenthic organisms have a crucial ecological role by providing the benthic habitat substrate and structural hiding places for predators, and food for a range of fish and invertebrates at different stages of development (Jørgensen et al., 2014). This fauna component makes up more than 2500 different species from a diverse range of taxonomic groups (Eriksen et al., 2021). Crustaceans, molluscs and polychaetes make up more than half of the species in the bottom invertebrate in the Barents Sea (Anisimova et al., 2011). Although the distribution of benthos biomass fluctuates varies by years, it also has many consistent features. There is a depth-related zonation, with certain species dominating in shallow areas, while others are more prevalent in deeper regions. This vertical changes in species composition contributes to the diversity and structure of benthic communities. Furthermore, specific species or groups such as polychaetes, bivalves, and crustaceans contributing to the benthos biomass (Anisimova et al., 2011). Benthic organisms in the

Barents Sea also exhibit unique substrate preferences, where some prefer soft sediments, while others inhabit rocky or mixed substrates. Seasonal variations also have an impact on the diet and distribution of benthic organisms (Solan et al., 2020). Variables such as temperature, ice cover, and nutrient availability vary with the seasons and affect the abundance and distribution of benthic communities (Grebmeier & Barry, 1991).

The size of the Barents Sea haddock stock varied greatly between 1950 and 2008, and thereafter the total biomass has reached record high levels (Figure 1D) with recruitment of very large year classes (2005–2006) (Figure 1B), and reduction of fishing pressure (Figure 1C). Due to a decline in fishing mortality in the beginning of the century (Figure 1C), the stock started to increase, reaching a record high level (Figure 1D) in 2009, mainly due to the strong year classes.

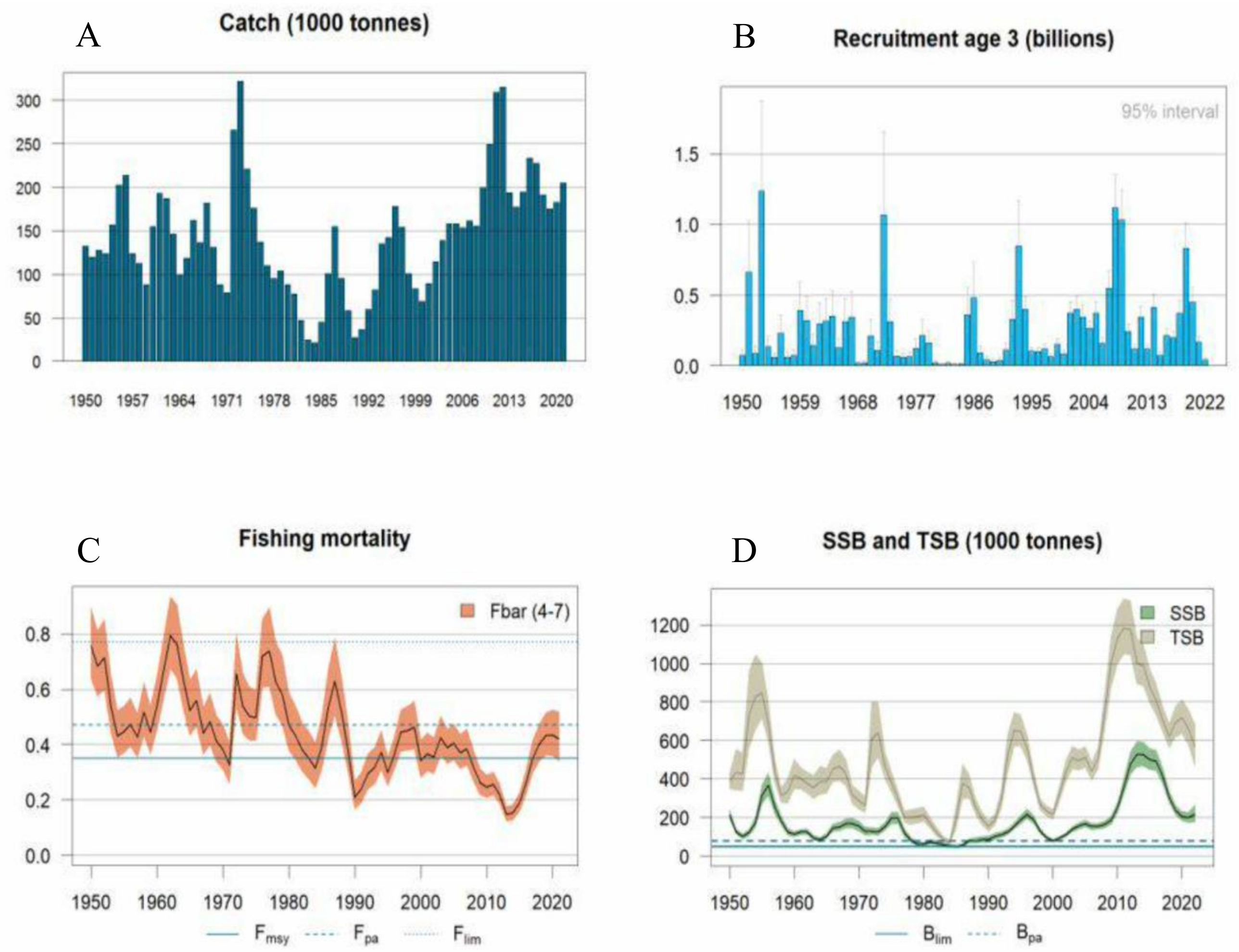

Figure 1 - Assessment results from the Joint Russian-Norwegian Working Group on Arctic Fisheries (JRN-AFWG 2022). A: catches in tonnes. B: recruitment at age 3 in billions. C: fishing mortality. D: the SSB and TSB. Recruitment in a fishery refers to when the fish are large enough to be caught. Spawning stock biomass, or SSB, is the sum of the weights of all the fish in the stock that are of sexual maturity. TSB stands for total stock biomass, which is the total biomass of the stock.

The diet of Barents Sea haddock has not been extensively studied since Jiang and Jørgensen (1996). Although diet data has been collected, analyzed in the laboratory, and thereafter stored in a database, the diet data has not been studied.

The aim of this thesis is two-fold. (1) First obtain an overview of the available haddock stomach data, including gear used, sampling protocol and when and where the data has been sampled. To achieve this, data from 1984 to 2019 were studied to gain an overview of the prey composition and feeding success of haddock. (2) Second, do an assessment of the following hypothesis for the year 2009: The haddock's diet varies geographically, similar to what is found for Barents Sea cod (Johannesen et al., 2012). Additionally, I expect that the diet composition and feeding success will change with individual haddock size. Further, it is argued that competition will affect the food consumption of haddock in the proportion of empty stomachs and Total Fullness Index (TFI). With increasing haddock density, I expect that TFI will decrease, while the proportion of empty stomachs will increase.

In this research, the main goal is to study the food composition and feeding success of haddock over an extended period, with a specific focus on the year 2009.

2. Material and methods

2.1 Study area

The Barents Sea has been the subject of scientific research for more than 100 years. The past 60 years, studies from collaborations between Norway, Institute of Marine Research (IMR) and Russia, Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO) has been conducted (Alekseev et al., 2011). The Barents Sea is an open Arcto-boreal ecosystem located at a high latitude, approximately between 70 and 80 degrees north of the polar circle (Figure 2). The depth ranges from 20 meters at the Spitsbergen Bank to approximately 500 meters near the Bear Island, and the average depth is 220 meters (Ozhigin et al., 2011). The Barents Sea's environment is affected by the entry of warm Atlantic water from the Norwegian Sea and coastal water (Bogstad et al., 2013). Depending on the impact of the Atlantic water, a substantial part of the northern and eastern Barents Sea may be covered in ice during the winter (Eriksen et al., 2021).

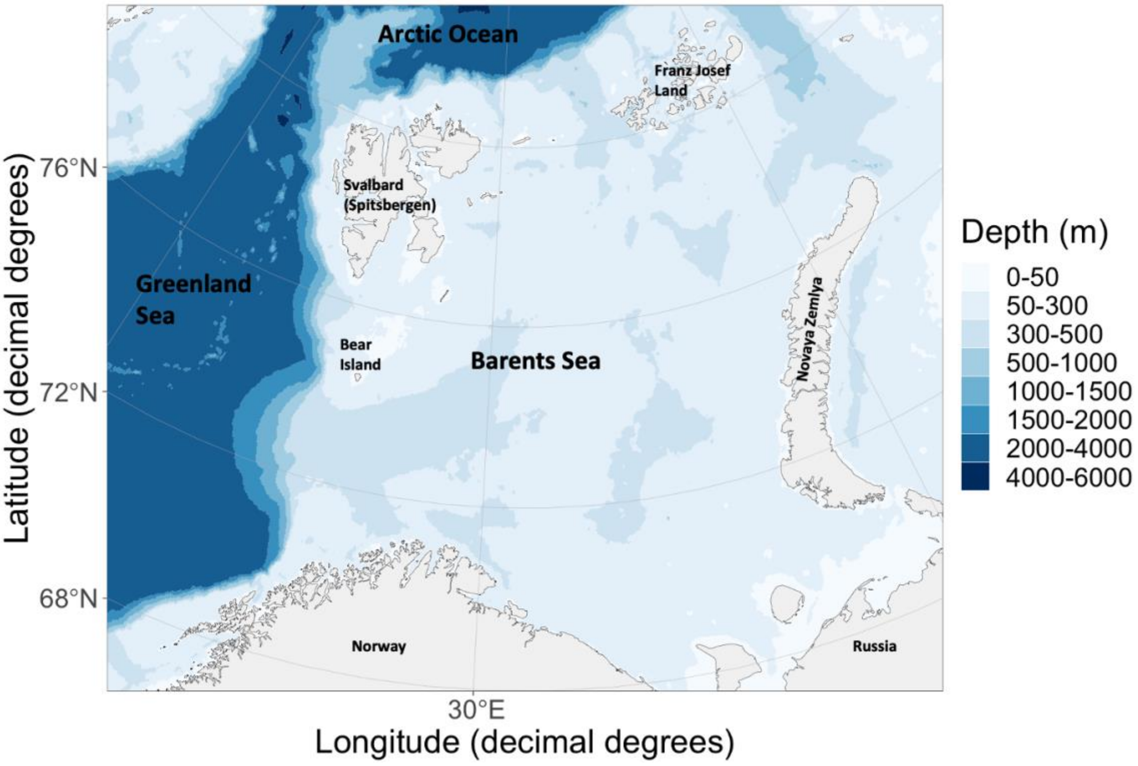

Figure 2 – A schematic overview of the study area in the Barents Sea, showing the locations of the various oceans as well as closest islands and countries. The depth contour of 500 m is used to delimit the Barents Sea.

The habitats of several important fish stocks, including haddock are found in the Barents Sea. Large fish stocks like cod, haddock, saithe (*Pollachius virens*), herring (*Clupea harengus*), and capelin (*Mallotus villosus*) are vital both as prey and as predators in the Norwegian and

Barents Sea (Olsen et al., 2009), and they have a significant role in the marine ecosystem, and in sustaining important fisheries.

2.2 Study species

Haddock is found in shelf seas in the North Atlantic Ocean. A distinct dark blotch above the pectoral fin and a black lateral line running along the haddock's white side make haddock easy to recognize. The Barents Sea haddock is the most northern stock of haddock, located in a region with climatic conditions and suboptimal temperatures (Russkikh & Dingsør, 2011). The stock primarily inhabits the Barents Sea throughout their lifespan (Bogstad et al., 2013). During its first year, the Barents Sea haddock undergoes a transition from a pelagic life-stage to a demersal life-stage (Russkikh & Dingsør, 2011). It reaches maturity at a length of 40 to 60 cm after four to seven years (Filin & Russkikh, 2019). Tagging experiments have revealed that the Barents Sea haddock stock is isolated, with small migrations outside of the region (Russkikh & Dingsør, 2011). The haddock spawns annually, and most spawning occurs between March and June. Their specific spawning grounds are not precisely known, but it is established that they spawn along the slope that extends from the continental shelf to the Norwegian Sea (Figure 3) (Devine & Heino, 2011). Adults start to feed intensively after spawning when they return to the Barents Sea (Figure 3).

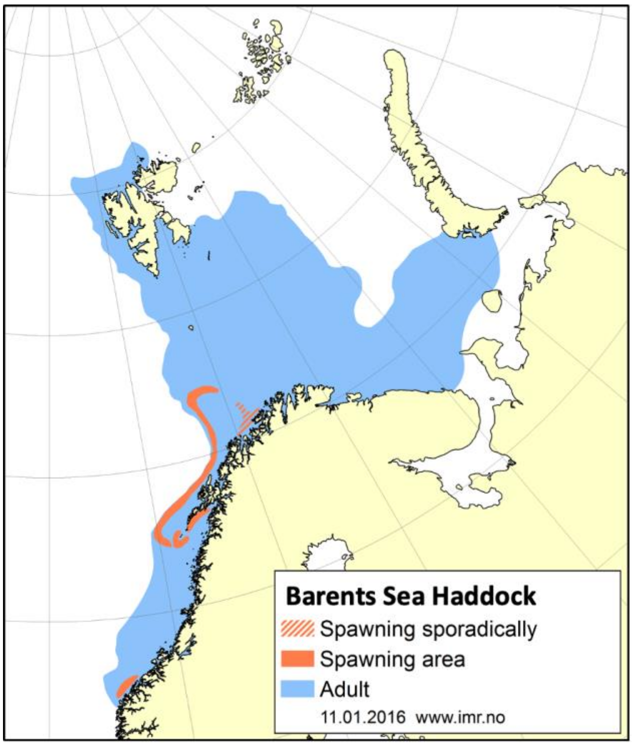

Figure 3 – Geographical distribution of Barents Sea haddock and the spawning area retrieved from the Institute of Marine Research.

2.3 Surveys in the Barents Sea

Since the 1960s, IMR has routinely collected data on several fish stocks in the Barents Sea every year. The research aims are to monitor and map the ocean's environmental conditions and investigate how the different fish stocks are developing over several years. Through various surveys conducted throughout all seasons, a wide variety of samples are collected.

The ecosystem survey is a series of surveys that started in 2004 and is conducted annually in the autumn, covering the whole Barents Sea (Eriksen et al., 2020; Prozorkevich & Van der Meeren, 2022). It is a collaboration with PINRO, and it is also IMR’s largest single survey (Alekseev et al., 2011). The primary objective of the studies was to map the distribution and abundance of the juvenile and adult stages of pelagic and demersal fish species such as haddock, as well as to collect data on hydrographic characteristics, zooplankton, benthos, seabirds, and marine mammals (Anon, 2009). It is usually comprised of three Norwegian and one to two Russian vessels that should simultaneously cover the whole Barents Sea.

2.4 Joint stomach database

The joint Norwegian-Russian stomach content database, a collaboration between IMR and PINRO, started in the middle of 1980s with studies on diet and food consumption of Barents Sea fish (Mehl & Yaragina, 1991). The objective of the study was to create multispecies models for the fish stocks in the Barents Sea, including detailed quantitative diet data and a stomach evacuation rate model to quantify stock interactions (Mehl & Yaragina, 1991). Since PINRO participation in the program in 1987, the two nations methods for sampling, laboratory analyses, and computer data registration were nearly identical (Mehl & Yaragina, 1991). Both nations have established identical stomach content databases protocols and exchange stomach data on a yearly basis. Fish stomach samples have been collected during several Norwegian surveys and on both Russian surveys and fishing vessels, using both bottom trawl and pelagic trawl.

Both IMR and PINRO sampled the contents of haddock’s stomachs from the start of the study, but IMR stopped doing routine sampling in 1991 because haddock only consumed a small number of commercially important prey species (Jiang & Jørgensen, 1996). The two nations have continued to routinely collect cod stomachs with standardized methods in order to estimate the natural mortality of cod, haddock, and capelin. Haddock diet data has been collected sporadically after 1991, whereas Russia continued to collect haddock stomach data.

In 2009 and 2015, Norway collected more haddock stomach data, and these data was exchanged between Norway and Russia.

2.5 Stomach content analysis

The stomachs were either analyzed just after the sorting of the trawl samples, or frozen and analyzed later in the laboratory. The same methods used for cod were used for analyzing the contents of haddock stomachs (Mehl & Yaragina, 1991). Each stomach was analyzed separately, and the total stomach content was extracted and weighed. When the content was identifiable, prey items were identified according to taxonomic level, and further degree of digestion and weighed was noted. Due to digestion, prey could often only be identified to genus, class, or family levels. If there were multiple individuals of the same species, they were all weighed together. Some prey could not be identified and was then labeled as "bony fish". The total number of identifiable prey per stomach was then counted (Mehl & Yaragina, 1991).

2.6 Stomach data 1984-2019

Data on haddock stomachs were retrieved from the IMR and PINRO databases and imported into R statistical software version 4.2.1 (R Core Team, 2021) and RStudio 2022.07.1+554. The database was provided in the “nydump” format which had S (predator and station) and P (prey) lines. The S lines included station and individual haddock information, while the P lines represented the prey data. These lines were merged, and the first step was to gain a better understanding of the raw data and create an overview by modifying the different datasets.

There were many different taxonomic levels of prey (Appendix Table 1), ranging from phylum to species in haddock stomachs during the years of 1984-2019. Since there were 370 different prey types recorded in the data set, all prey were grouped into five main taxonomically separate categories to describe diet composition and variation among the prey species: Annelida, Mollusca, Crustacea, Echinodermata, and Fish (Jiang & Jørgensen, 1996). The prey that didn't fit into one of these five categories were put in a category called “Others” (Jiang & Jørgensen, 1996). The category “unidentified” prey is not included in the six categories.

2.7 Data from the ecosystem survey in 2009

Diet data from the ecosystem survey 2009 was used to test for geographic and size variation in haddock diet and to test for density dependence in haddock feeding. This year is interesting because it contains two record-high year-classes, 2005 and 2006, being three and four years old. In 2009 the ecosystem survey lasted from August 7th to October 3rd (Anon, 2009). The sampling area for the survey included the area where the main part of the haddock population was distributed (Figure 3), and four vessels were used (Appendix Table 2). Haddock was collected in a large area, covering mainly in the southern part of the Barents Sea (Figure 4) (Anon, 2009).

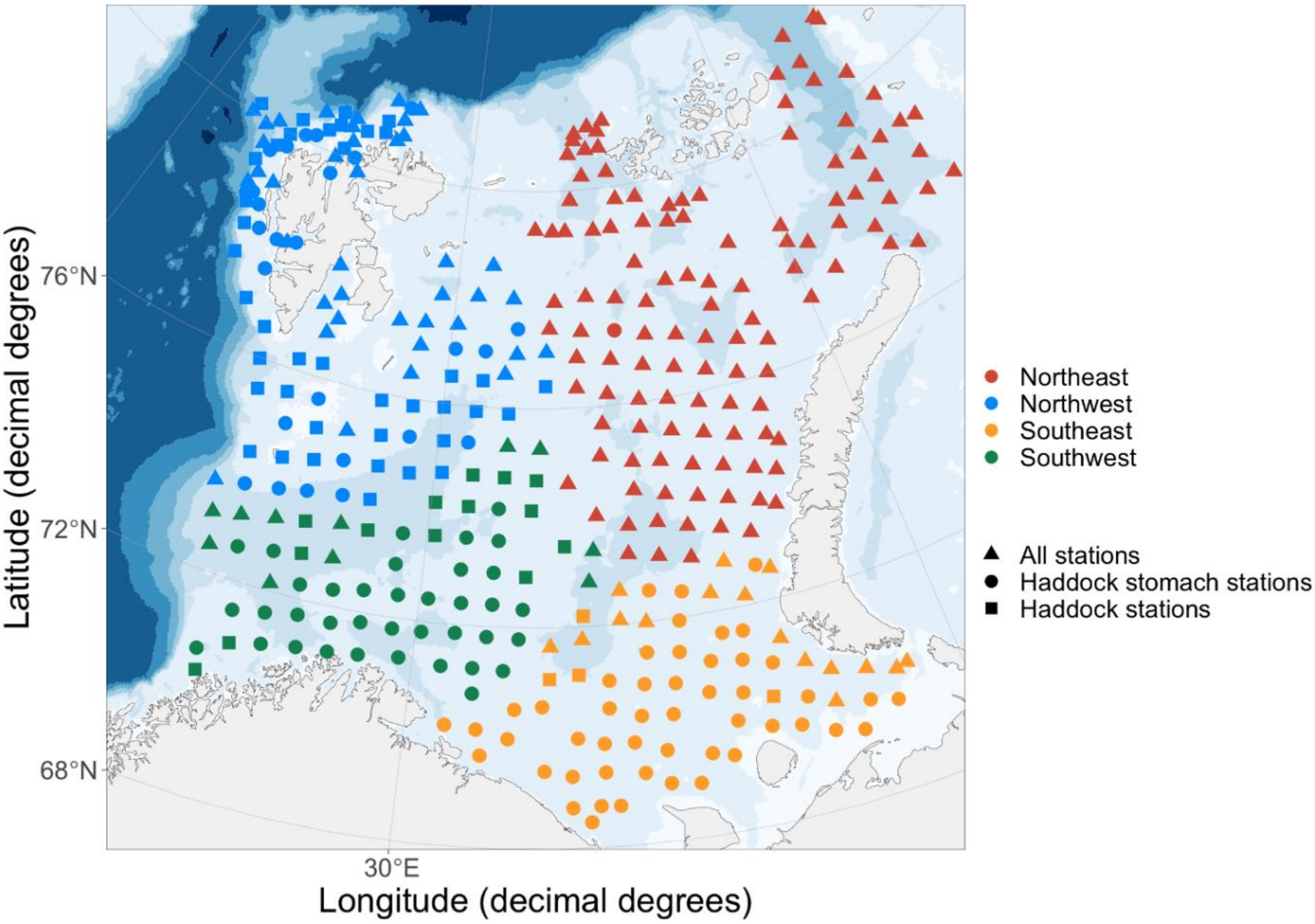

Figure 4 – A map of bottom trawl stations from the 2009 ecosystem survey in the Barents Sea. The areas which the data are divided into are represented by the various colors. The various shapes stand for bottom trawl stations triangles: without haddock, squares stations with haddock caught, and circles: haddock stomach sampling stations.

Of the 357 stations that were sampled during the ecosystem survey in 2009, 171 stations contained samples of haddock. The data analyzes are from 948 haddock stomachs collected from 113 stations (Table 1). The stations were divided into four separate areas to make it easier to work with the data, and the division is used throughout the data analyses (Figure 4).

The northeast area only had one stomach sample and was excluded from the analysis (Table 1).

Table 1 – Stations from the ecosystem survey from 2009 per area. The second column contains number of stations from the survey. The stations having haddock per area are shown in the third column, and the stations with haddock stomachs per area are shown in the fourth column.

Area	All stations	Stations with haddock	Stations with haddock stomachs
Northeast	121	1	1
Northwest	105	66	26
Southeast	69	53	49
Southwest	62	51	37
Total	**357**	**171**	**113**

The haddock sizes were divided into length groups, with each group representing a 5 cm length interval. However, the analysis excluded the 65 cm length group of haddock aged 10 because there was only one stomach available here (Figure 12).

2.7.1 Biological sampling of bottom trawl catches on board ecosystem survey 2009

Every vessel used a Campelen 1800 shrimp bottom trawl rigged with a rockhopper gear, to catch demersal fish. To get information about the door spread, trawl opening, and bottom contact, each trawl was rigged with sensors. The standard towing time for the vessel speed was 15 minutes at 3 knots (Anon, 2009). The mesh size was 16 to 22 mm at the cod end and 80 mm at the front. The vertical trawl opening was between 4 to 5 meters, and the horizontal opening was 20 meters.

The catches were sorted and weighed by species, and lengths of 100 different haddock were measured if possible. When there were more than 100 haddock in a catch, length measurements were taken from a representative subsample of the catch. One haddock per 5 cm length group was randomly selected for biological sample, including weight, sex, otoliths (otoliths were obtained to determine age) and maturity stage. Both Norway and Russia were expected to analyze one stomach for each group of 5 cm, but Russia analyzed more stomachs (Appendix Figure 1), and Norway did not sample stomach samples at every station (Figure 4). Because this information had previously not been noted by anyone, this was discovered after I studied the data more in detail.

2.7.2 Haddock density from ecosystem survey 2009

Haddock density (individuals per nautical miles squared) per 5 cm length groups was calculated using the program StoX (Johnsen et al., 2019; provided by supervisor). The program calculates the density from the raw data. While “Density” represents the density per length group on one station, the “Density Total” was calculated to sum the density of all length groups per stations.

2.7.3 Statistical analysis of the 2009 ecosystem survey data

The statistical analyses were chosen to test my predictions and determine whether there were any significant variations between the response and the predictor. The responses were TFI (Total Fullness Index), proportion of empty stomachs and proportion of different prey categories in the non-empty stomachs. TFI was defined as:

$$TFI = \frac{S}{(L)^3} \times 10^4$$

where S is the weight in grams of the total stomach content, and L is the haddock length in centimeters (Bogstad & Gjøsæter, 2001).

Logistic regression, which is a type of Generalized linear models (GLM) was used for the analysis of proportions, whereas linear regression was used for TFI (log transformed). Logistic regression and log transformation were used for the data analyzing due to the challenging data material (Appendix Figure 2), aiming to reduce or remove the skewness from the original data (Appendix Figure 3). Binary data for proportions were created by coding each empty stomach as either 0 (no empty stomach) or 1 (empty stomach) and for presence of prey categories coded as being 1 (prey present) or 0 (prey not present).

The analyzes were done in two steps. Firstly, the effects of geographical variation and haddock size on all response variables (TFI, proportion empty stomachs and proportion of prey categories) were tested. Secondly, the effect of density on TFI and proportion of empty stomachs was tested separately for each area.

Geographical variation was tested by including area (northwest, southwest and southeast) as a categorical variable, whereas haddock length was included as a continuous variable in additive models. Interactions were not considered due to the unequal number of samples in each area (Table 2, Appendix Figure 4). One-way ANOVA was used to test the significance of the area and haddock length.

To test for competitive effects on feeding success, TFI and empty stomachs were the response variables, while log transformed density and total density were the predictors. Additionally, haddock size was used as a co-variate if it was found to be significant in the analysis described above. The analyzes were done for each area separately since the southeast area had much more data than the northwest and southwest (Table 2, Appendix Figure 4).

All data plotting and statistical data analyses were performed using the R program, in particular the packages *tidyverse, ggplot2*, *ggOceanMaps, ggspatial, gridExtra* and *mgcv* (Appendix Table 3).

3. Results

This section provides an overview of the results from the haddock stomach data base using data from 1984 to 2019. Furthermore, it also presents an overview of the 2009 ecosystem survey results, which includes information about geographical variations, size differences and density effects in haddock's diet and feeding.

3.1 Overview of the haddock stomach data base

A total of 16 833 haddock stomachs were collected from the Barents Sea between 1984-2019 (Table 2, Appendix Table 4). Fish were from different parts of the Barents Sea with most samples along the coast of the southern Barents Sea (Appendix Figure 5).

Table 2 – The total number of haddock stomachs and the number of non-empty stomachs used in the analysis with number of stomachs per area in 2009.

Year	Haddock stomachs	Non-empty stomachs
1984-2019	16 833	12 583
2009	948	729
Northeast	1	0
Northwest	90	70
Southeast	620	516
Southwest	237	143

The stomachs of haddock have been sampled year around, with every month being represented in the collected data (Figure 5, Appendix Table 4). In the 1980s and 1990s, most of the sampling was done in February (Figure 5). The years between 1992 and 2008, were particularly low regarding the number of stomachs sampled. After 2008, the number of stomachs sampled was high in 2009 and 2015. The majority of the stomachs in 2015 were sampled in November and December by Russia (Figure 5, Appendix Figure 6).

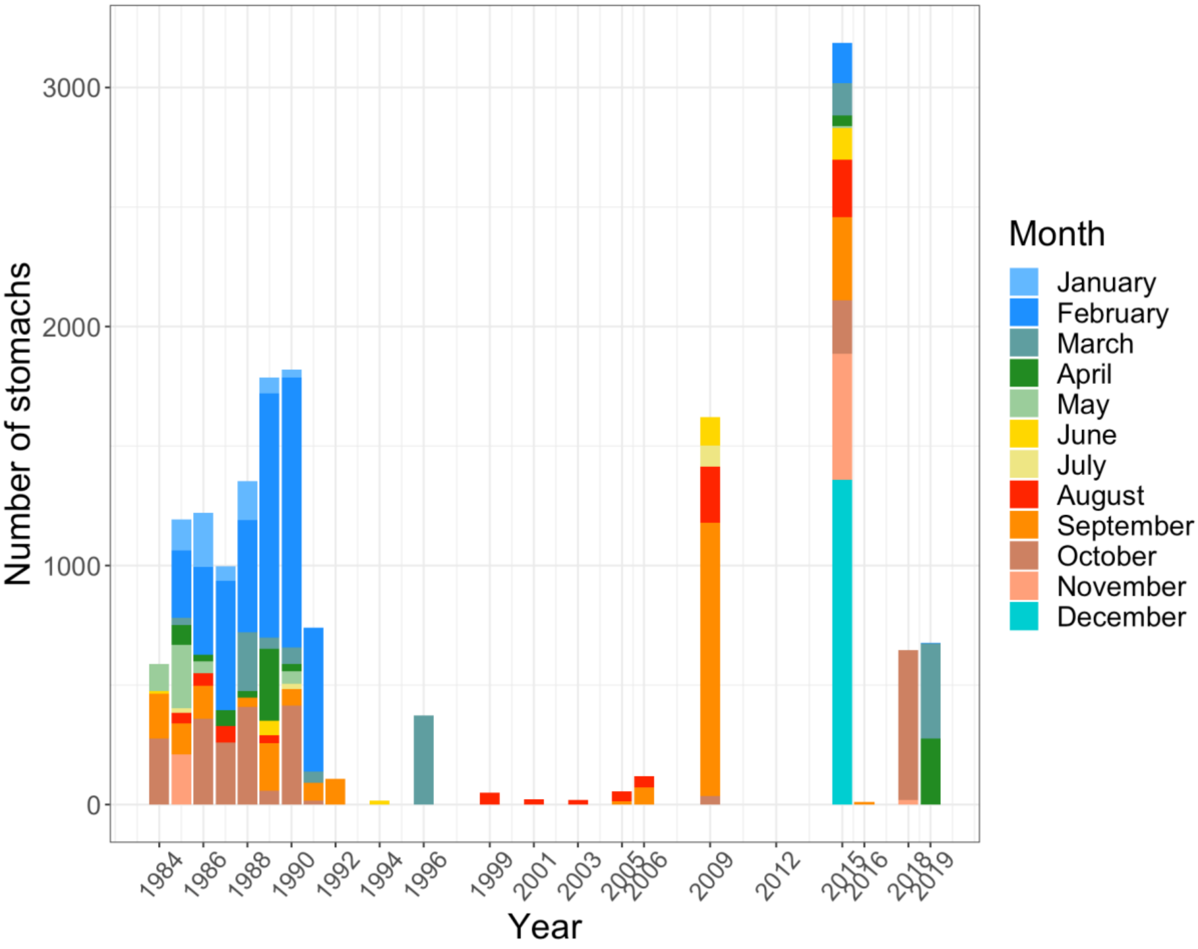

Figure 5 – An overview of all the stomach data, shared jointly by Norway and Russia, representing all the stomachs that were sampled over the years and over the four different months. The different months are represented by the colors shown to the right.

Overall stomachs were sampled from 1134 stations (Appendix Table 5), 1014 of the sampling was done by a bottom trawl while 108 stations were sampled by a pelagic trawl. The remaining 12 stations were collected by other gear (Appendix Figure 7). Most of the stomachs were from haddock between 20 cm and 24.9 cm (Appendix Figure 8). Only two haddock were larger than 80 cm, which belonged to the 14 and 16 age year-classes (Appendix Figure 9).

Norway carried out the majority of the haddock stomach sampling over the years (Appendix Figure 5), although Russia conducted most of the sampling in 2015. All samples from 2009 were done with bottom trawl (Appendix Figure 7), and most of the sampling this year was done by Norway (Appendix Figure 6). Most of the stations Norway sampled in 2015 were obtained using a pelagic trawl, which introduce difficulty comparing this year with other years (Appendix Figure 10).

Ages one and two were the most common ones, with 2917 and 3172 haddock in total, followed by three- and four-year old's (Appendix Figure 11). Of the total 16 833 haddock stomachs examined, 25% were found to be empty (Table 2). This percentage was lower for the larger haddock (Figure 6). Approximately 30-35% of the smallest haddock had empty stomachs, while for the largest haddock the percentage was only 16%.

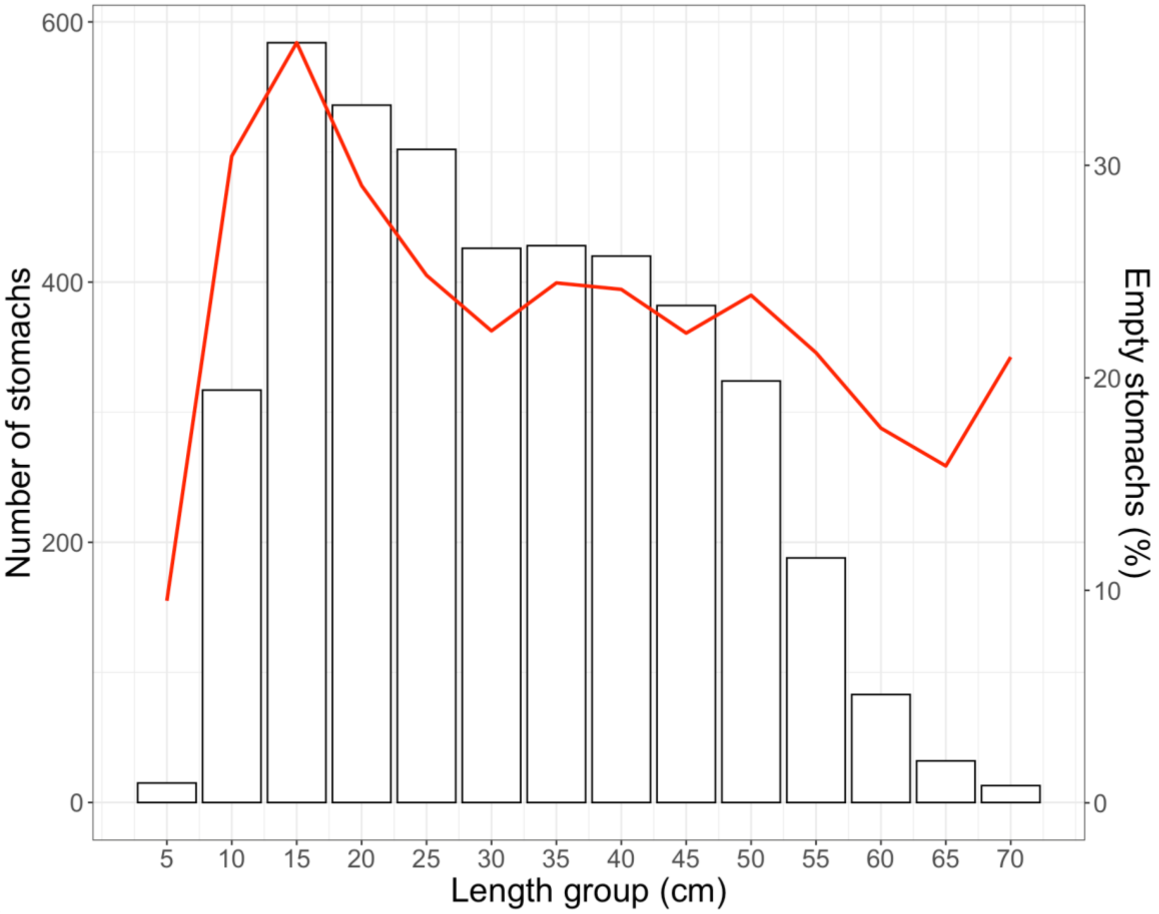

Figure 6 – Number of empty stomachs by 5 cm length group is shown by the bars on the left y-axis. The percentage of all the empty haddock stomachs by 5 cm length group is shown on the right y-axis. The estimated percentage of empty stomachs for each length group is shown by the red line.

Overall, 370 different prey types were recorded in the data set and grouped into six categories (Appendix Table 1). The category found most frequently in the stomachs is **Crustacea**, with 5067 occurrences and found in 40.3% of the stomachs, followed by **Echinodermata** with 4729 occurrences. **Annelida** and **Fish** were the two categories with the fewest registrations (2537 and 1164, respectively) (Figure 7).

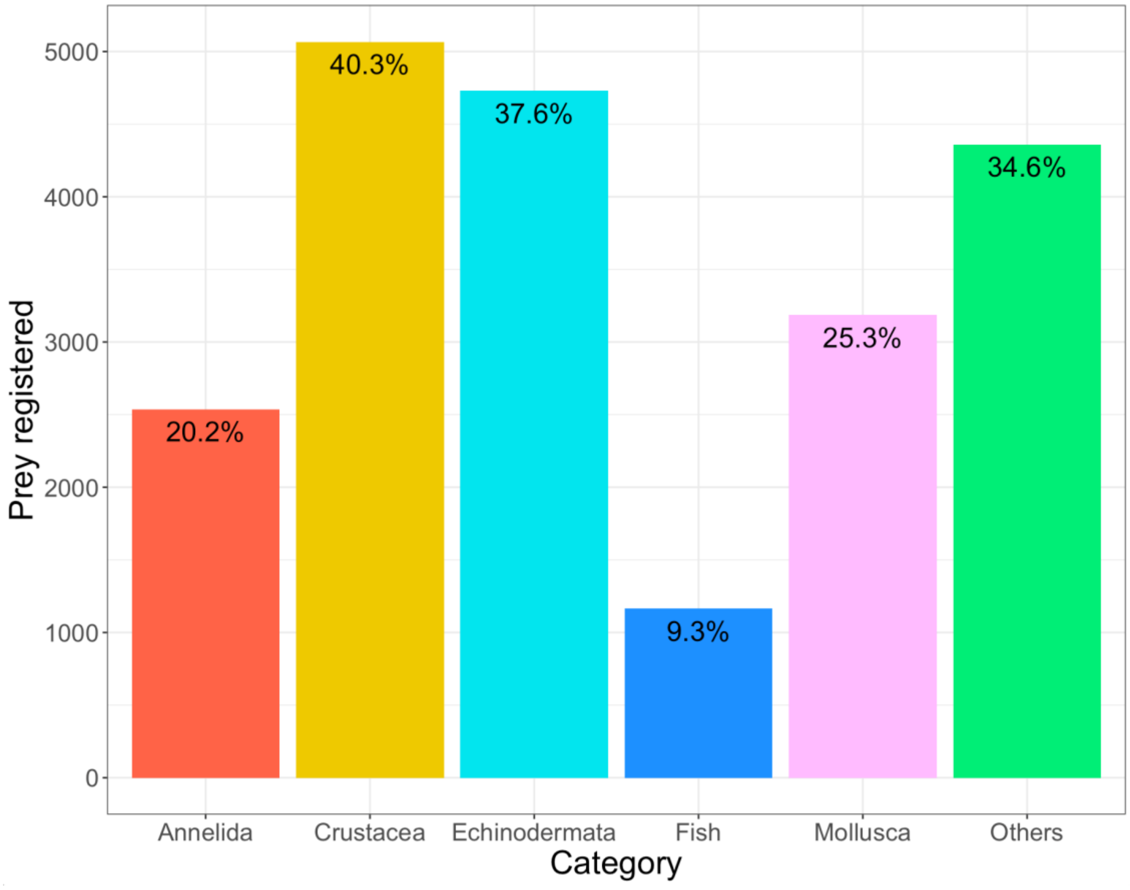

Figure 7 – The number of registrations of the prey categories, with the percentage of the stomach containing the prey out of the total number of stomachs with prey. The six separate categories are represented by the colors (Annelida = red, Crustacea = yellow, Echinodermata = turquoise, Fish = blue, Mollusca = pink and Others = green).

The group of brittle stars (Ophiuroidea Appendix Table 1) was the most dominant prey which belongs to **Echinodermata**. There were 2439 of these registered in all haddock stomachs. The class of polychaeta in the category **Annelida**, which was identified in 2068 stomachs, follows next. Under the Annelida category, the species *Galathowenia oculata* was identified 147 times, and was the most common prey of this category identified to species level.

Bivalvia, a class in the **Mollusca** category, had 1886 stomach registrations and was the most common prey in this category. *Cardium* was a dominant genus in the Mollusca category, accounting for 312 registrations. Out of these, *Cardium minimum* were observed in 147 stomachs. The Euphausiidae family (krill), registered 1258 times, was the most dominant prey in **Crustacea** category. Deep-sea shrimp (*Pandalus borealis*) was registered 216 times. The northern krill (*Meganyctiphanes norvegica*), which had 201 registrations, was another major species group in the same category.

The infraclass Teleostei (un-classified fish) which had 433 registrations, was the most common prey in the **Fish** category. The fish species capelin, which was recorded in 167 haddock stomachs, was the most dominant species in the Fish category. The phylum of Ctenophora, which was registered 467 times, was the most numerous prey in the **Others** prey category. The category of unknown prey was the most often registered prey overall. 2685 stomachs containing this prey category were recorded here, but they are not included in the six categories (Appendix Table 1).

The **Crustacea** category collected by the pelagic trawl had the highest percentage among both trawls (Figure 8). There were not big variations in percentage between the various prey categories for the bottom trawl. **Annelida** and **Echinodermata** categories, collected by the pelagic trawl had the least percentage overall. Most of the catch sampled by pelagic trawl, consisted of small haddock (Appendix Figure 12).

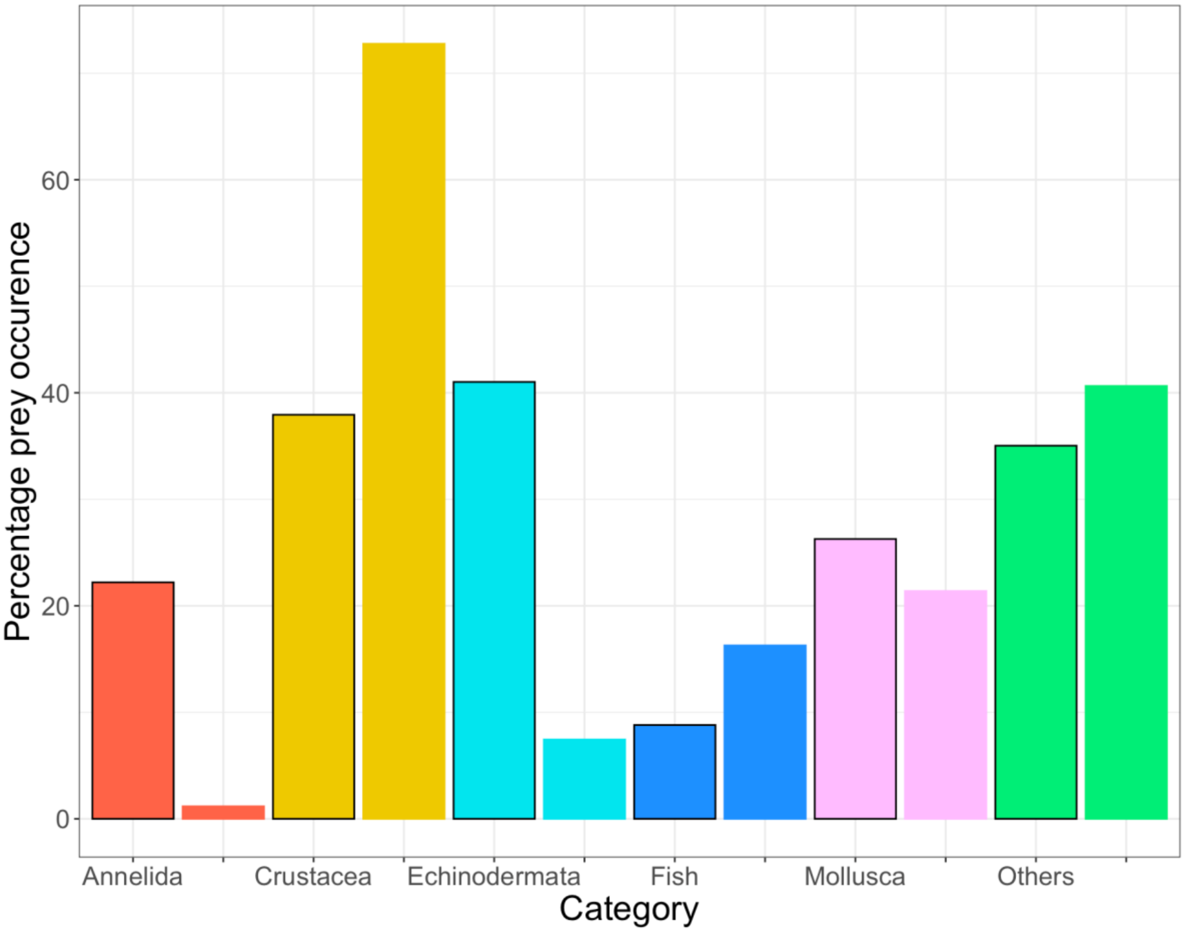

Figure 8 – The percentage of prey occurrence out of the total number of stomachs collected by pelagic- and bottom trawl (black frame). The six separate categories are represented by the colors (Annelida = red, Crustacea = yellow, Echinodermata = turquoise, Fish = blue, Mollusca = pink and Others = green).

The proportion of observing **Annelida**, **Echinodermata**, **Fish** and **Mollusca** in haddock stomachs increased with the size of the haddock. However, **Crustacea** and **Others** prey categories are more commonly found in smaller haddock (Figure 9). The percentage by weight varied less with haddock size (Figure 10) but showed a clear decline with size for **Crustacea** (Figure 10). Overall, **Fish** is the least important prey by occurrence, but one of the most important by weight (Figure 9 and 10).

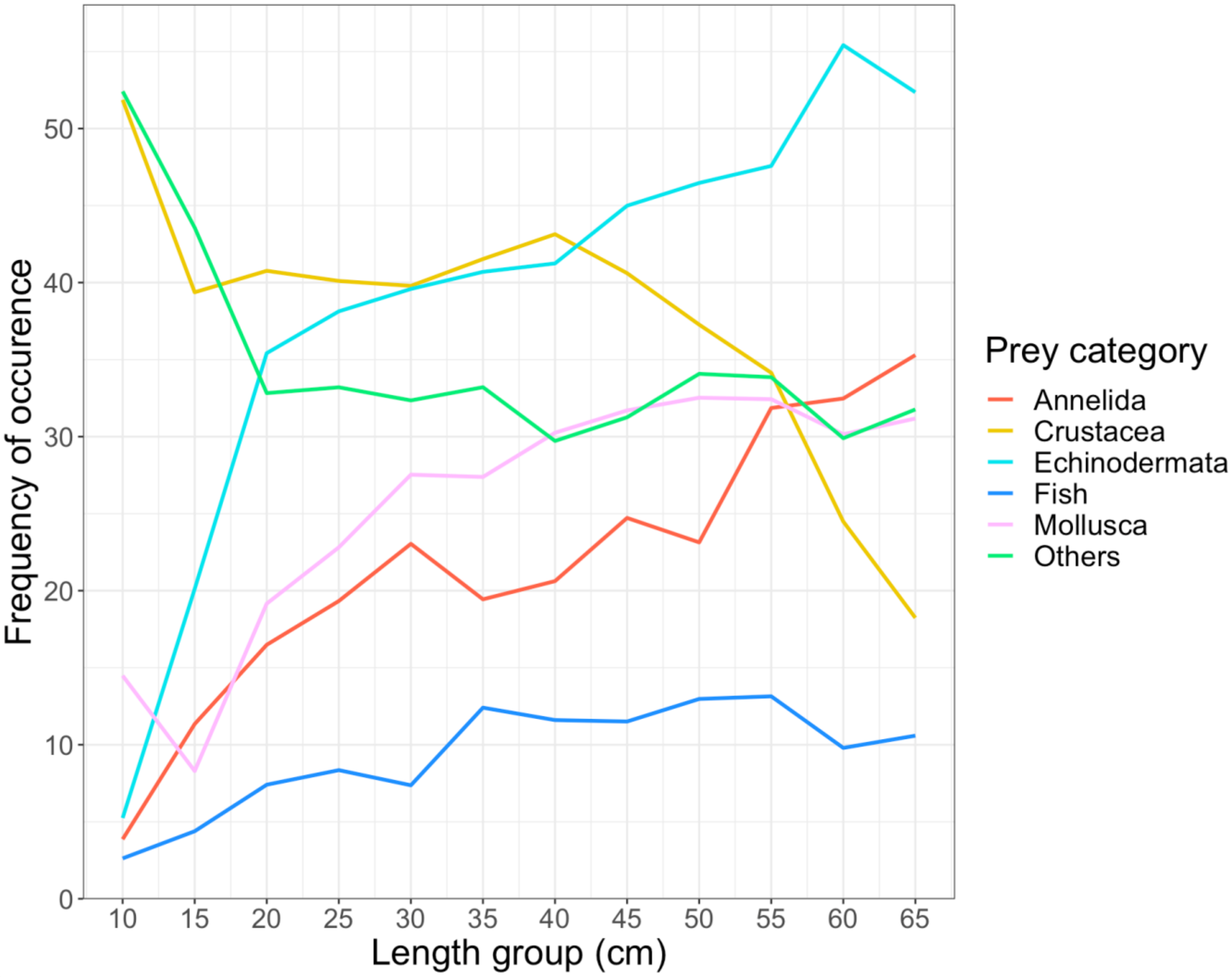

Figure 9 – The percentage of each category of prey occurrence for each haddock length group. The color of the lines represents the different prey categories. The y-axes display the frequency of prey in %, while the x-axes display the length group in cm. I excluded data on haddock length group < 10 cm and > 65 cm, leaving 12 377 non-empty haddock stomachs.

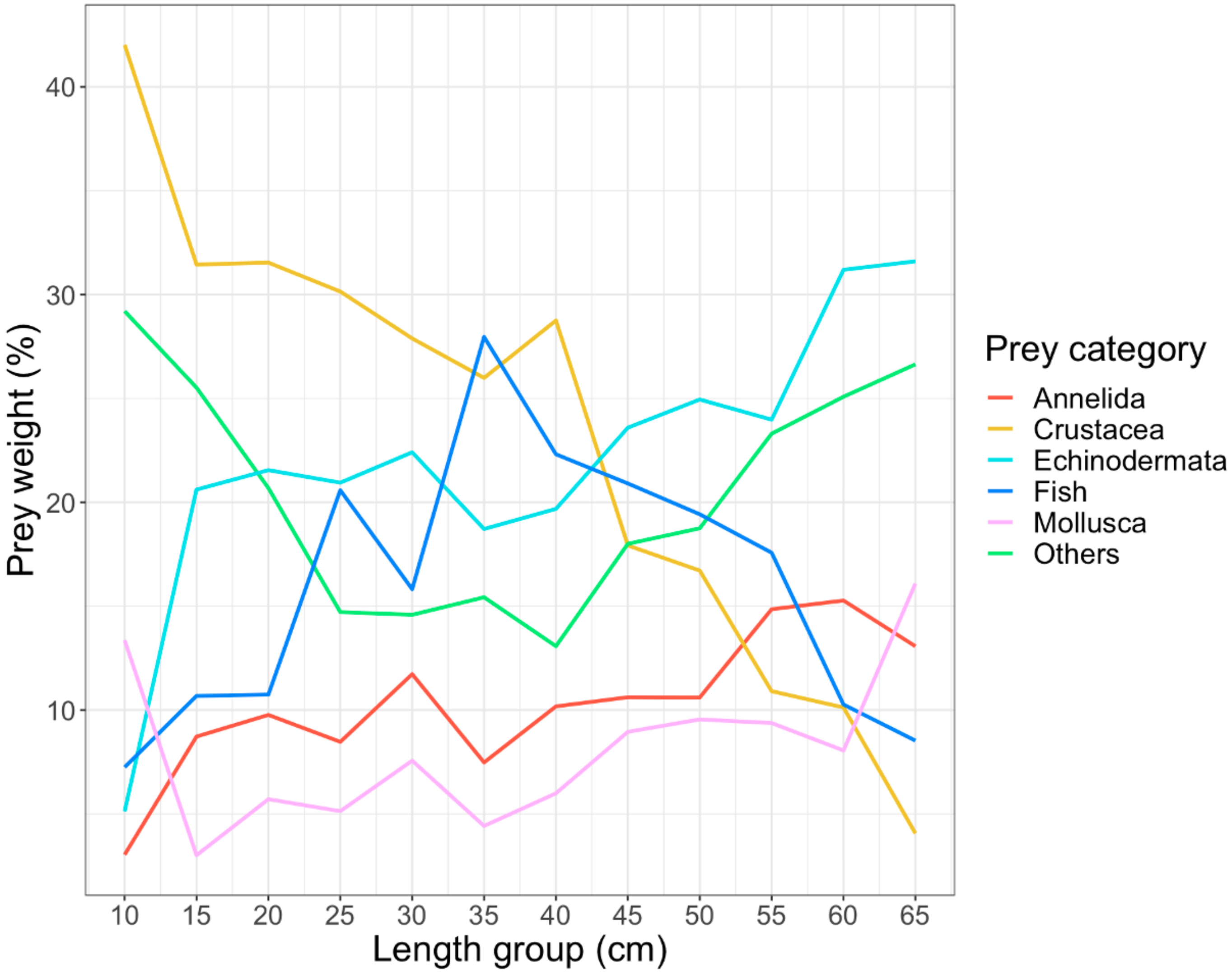

Figure 10 – The total weight percentage of each category for each haddock length group from the haddock stomachs of the whole dataset. Each line uses a different color to present different categories (Annelida = red, Crustacea = yellow, Others = green, Echinodermata = turquoise, Fish = blue and Mollusca = pink). I excluded data on haddock < 10 cm and > 65 cm, leaving 12 377 non-empty haddock stomachs.

3.2 Ecosystem survey 2009

3.2.1 Overview of the dataset

In 2009 from the ecosystem survey, 948 haddock stomachs (Table 2) were registered from 113 stations, all of them sampled by bottom trawls (Appendix Figure 7). Of these, 219 stomachs were empty (23.1%) (Table 2).

In the haddock stomachs, 59 unique prey were identified during the 2009 ecosystem survey. The prey category that was found in most stomachs, was **Annelida**, which was registered 274 times (Figure 11). **Mollusca** was registered 265 times, followed by **Crustacea** with 264 registrations. **Fish** and **Others** are registered the least, with 146- and 131 times (Figure 11).

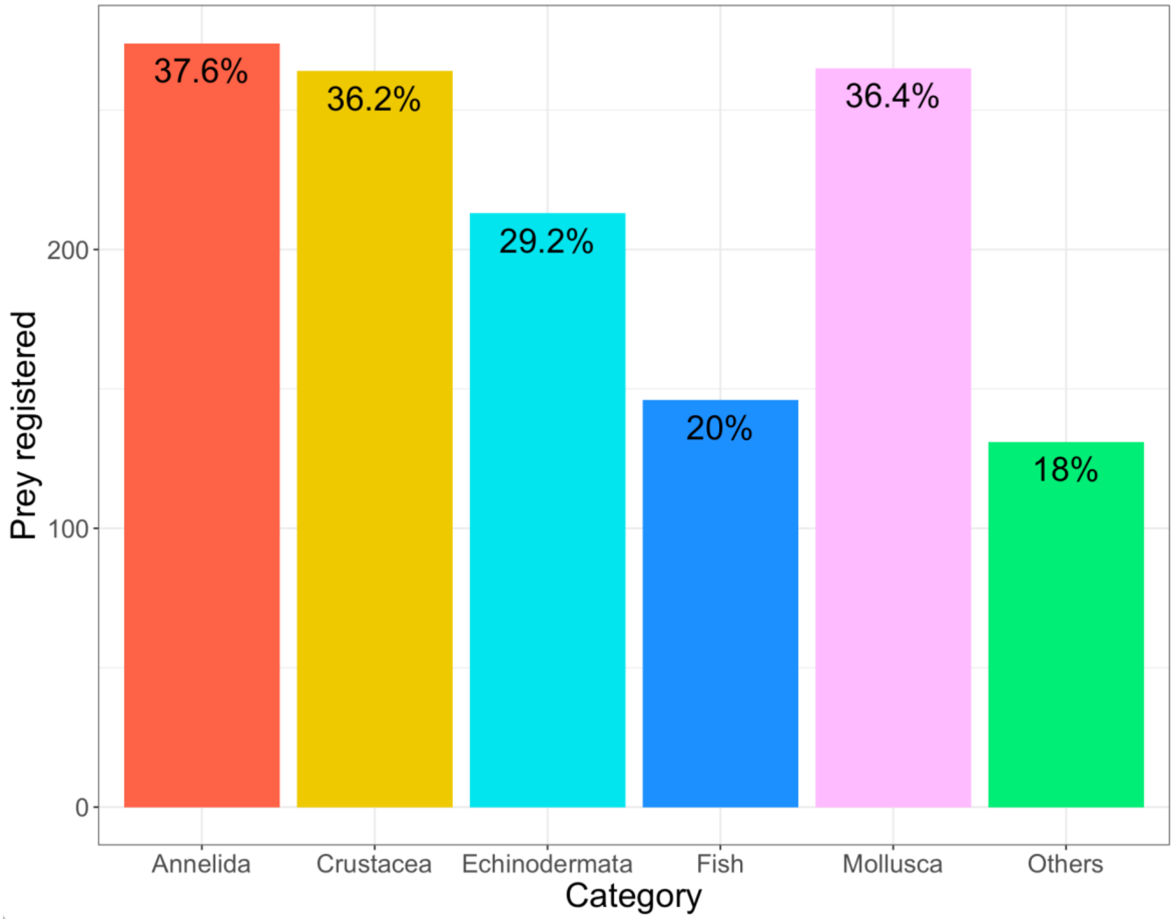

Figure 11 – The six prey categories with the number of registrations of the prey on the y-axis, showing the percentage of the prey registered out of the total number of non-empty stomachs, excluding the stomachs that are empty. The six separate categories are represented by the colors (Annelida = red, Crustacea = yellow, Echinodermata = turquoise, Fish = blue, Mollusca = pink and Others = green).

The most common prey was the class of bristle worms (Polychaeta, Appendix Table 1), which belongs to **Annelida** category. Out of all the haddock stomachs, this class had 397 registrations. The class of bivalves, with 387 registrations, has the second-highest number of prey, and this class belongs to **Mollusca** category. The group of brittle stars in the **Echinodermata** category, with 218 registrations, follows next.

The family Euphausiidae, or krill, had 137 registrations and was the most common prey in the **Crustacea** category. The Deep-sea shrimp, which they could identify in ten stomachs, was another major species group among Crustacea. The comb jellies had 123 registrations, making them the most often observed prey in the **Others** category (Appendix Table 1).

The Ammodytidae was the most common **Fish** prey and was found in 59 stomachs. The species capelin, which they could identify 22 times also made up an important species group among the Fish prey.

The age groups were between zero and ten, and most of the haddock was three- and four-year old, which were the two strong year classes from 2005 and 2006 (Figure 12). Almost 26% of all stomachs are from age group three, and nearly 30% of all stomachs from age group four. Haddock with lengths between 35- and 44.9 cm were the most common, accounting for around 20- and 18% of all sampled fish for stomach analysis (Figure 12).

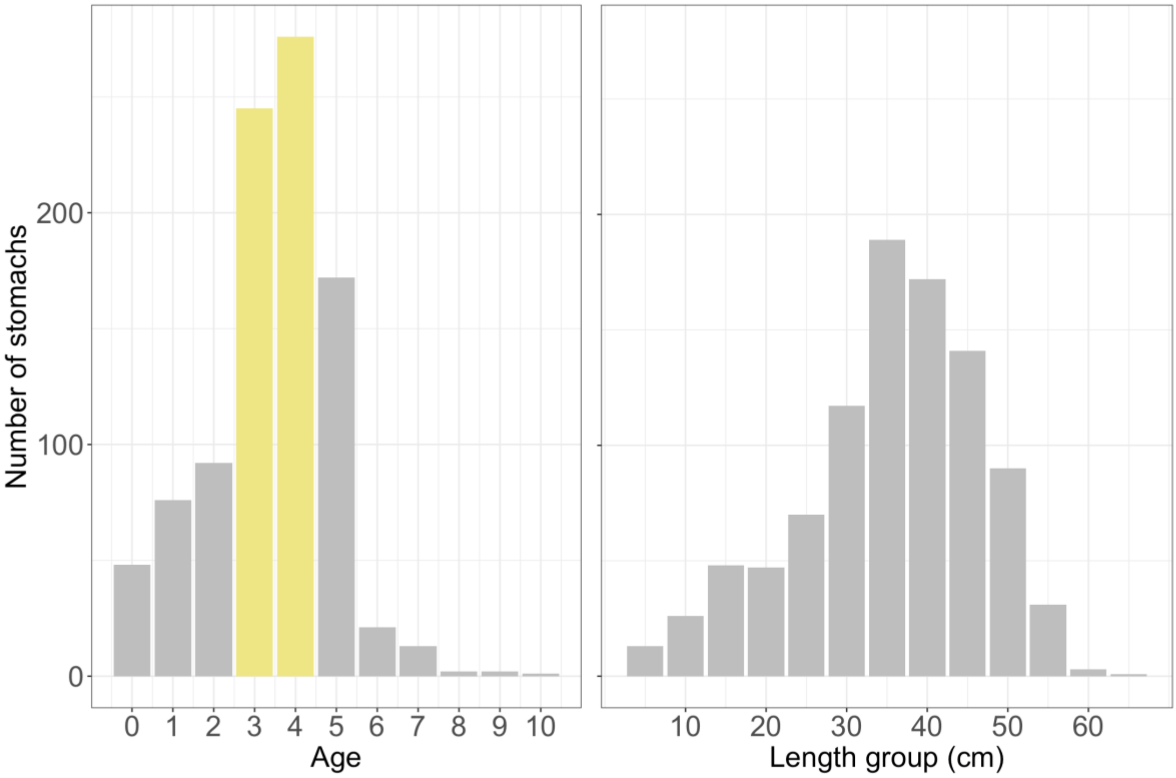

Figure 12 – Number of haddock stomachs in various age- and length-groups sampled in the 2009 ecosystem survey. Three- and four-year-old in the strong year classes are represented in yellow colors, while the others are represented in grey.

The average size of the three- and four-year-old, the most dominant ages in the data set, was 35.5 cm and 42 cm (Figure 13).

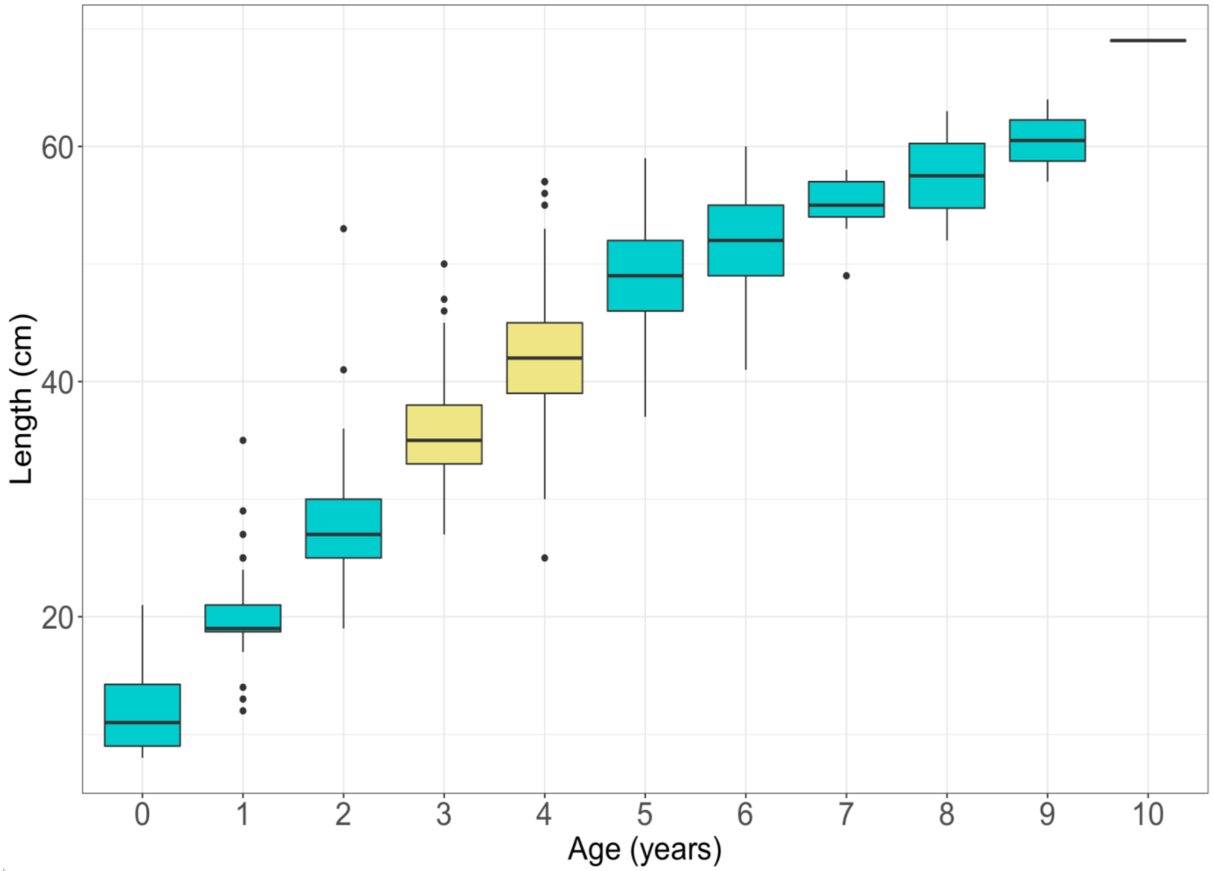

Figure 13 – Boxplots of haddock length (cm) by age for haddock with stomach samples. Every age group has multiple stomachs that are distributed according to length, but some groups have fewer stomachs than others.

3.2.2 Geographical variation in diet and feeding

There was only one station with one haddock stomach sampled in the northeast, this stomach was empty and excluded from further analysis (Figure 14).

The southwest had more empty stomachs than the other two areas (Figure 14). The percentage of empty stomachs in the southeast and northwest are almost similar (Table 2). The overall effect of area was significant (p-value < 0.05, Table 3).

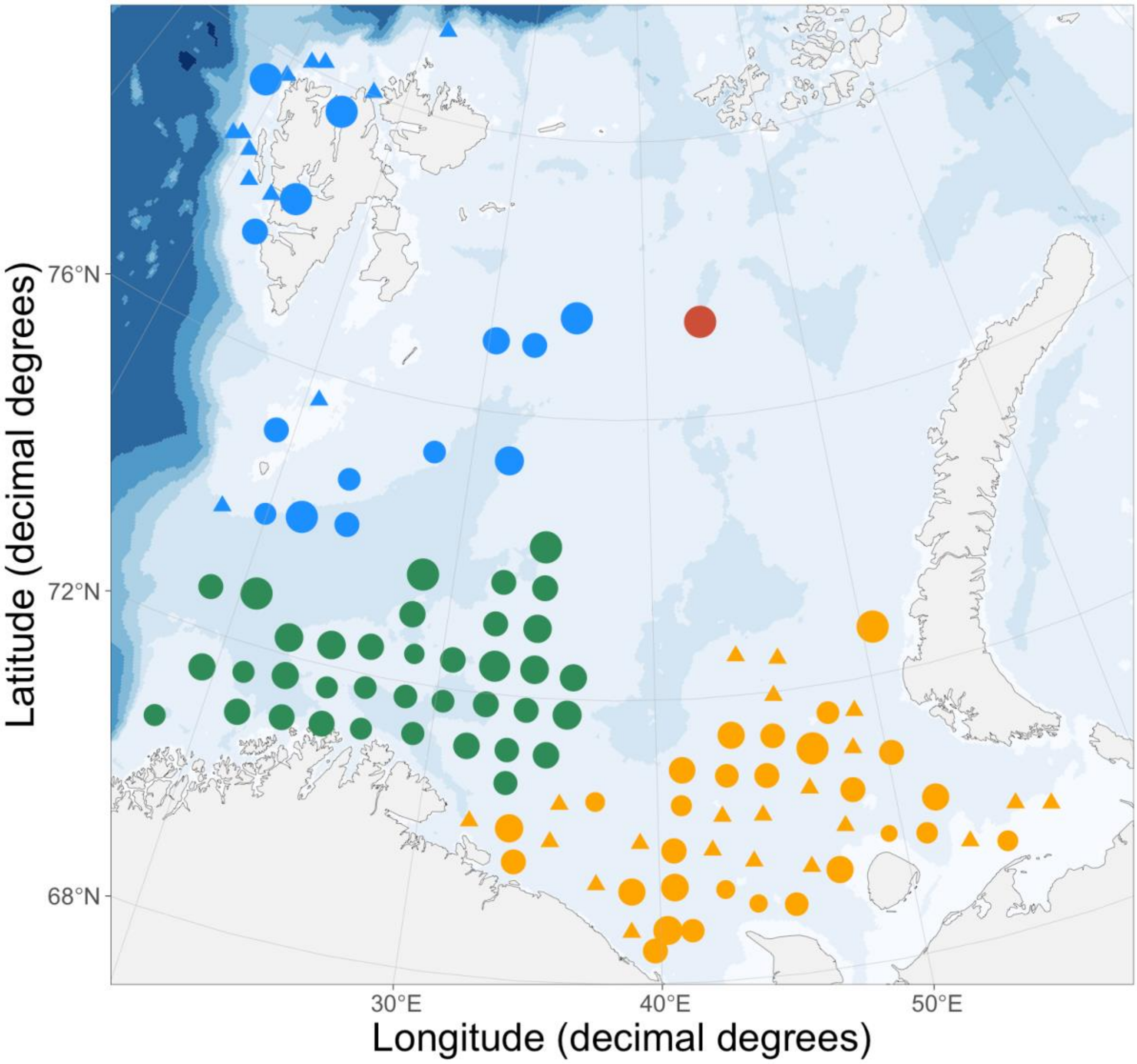

Figure 14 – A map of the Barents Sea showing stations with empty stomachs (shape = circle), including stations with non-empty stomachs (shape = triangle). A station may contain one or several haddock stomachs, and the size of the circles corresponds to the number of empty stomachs divided by the total number of stomachs at one station. There are no empty stomachs where triangles are present. The four different areas are marked with various colors (northeast = red, northwest = blue, southeast = yellow and southwest = dark-green).

Table 3 – Summary output of the one-way ANOVA test on the response variables TFI (log transformed, non-empty stomachs), empty stomachs, and the frequency of occurrence of various prey categories. Area was used as predictor variable. Data from ecosystem survey 2009. If there are three asterisks, the p-value is less than 0.001.

Test	Response	Predictor	P-value
ANOVA	Empty stomachs	Area	1.635e-12***
	TFI (log)	Area	6.862e-11***
	Annelida	Area	2.2e-16***
	Echinodermata	Area	1.036e-07***
	Mollusca	Area	0.001
	Others	Area	0.496
	Crustacea	Area	0.022
	Fish	Area	0.903

Haddock stomachs are less full in the southwest, than in the southeast and northwest (Figure 15). Geographical area has an impact on TFI (p-value < 0.05, Table 3, Appendix Table 6).

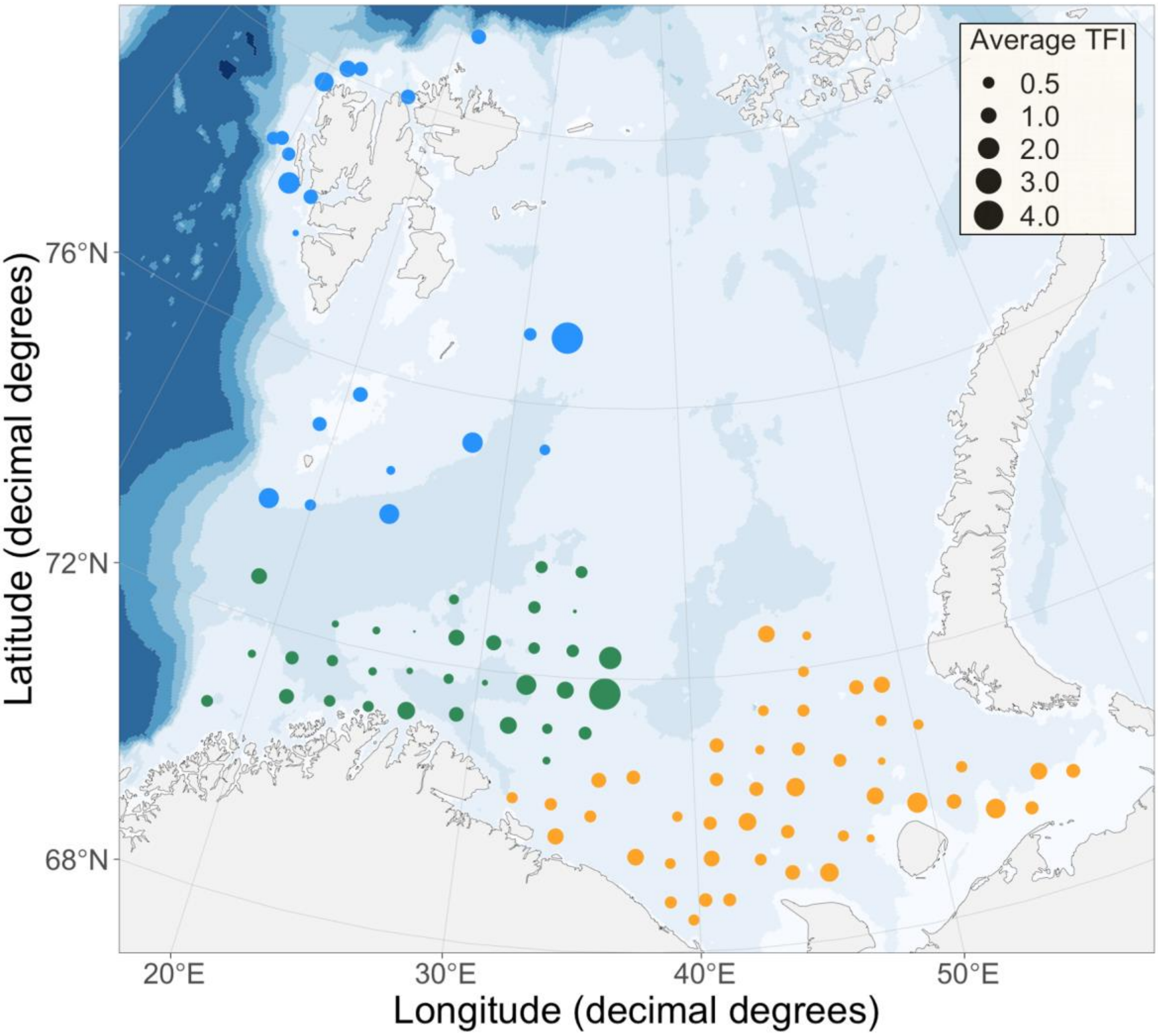

Figure 15 – The map of the Barents Sea shows the stations with haddock stomachs, where each station represents one circle with the average TFI. The circle gets larger the higher the average on one station. One station may have at least one stomach, but the number may vary. The colors represents the geographical areas (northwest = blue, southwest = green and southeast = orange). The empty stomachs are not included.

The results shown in Figure 16 show that **Echinodermata** has been consumed less in the southeast and more in the northwest, whereas haddock feed more on **Mollusca** and **Crustacea** in the southeast. The southeast is also where **Annelida** were most frequently eaten. We are unable to clearly determine any geographical variation from the maps in the two other prey categories (**Fish** and **Others**, Table 3). The area effect was significant for **Annelida**, **Echinodermata**, **Mollusca** and **Crustacea**, but not for the other two prey categories (Figure 16, Table 3).

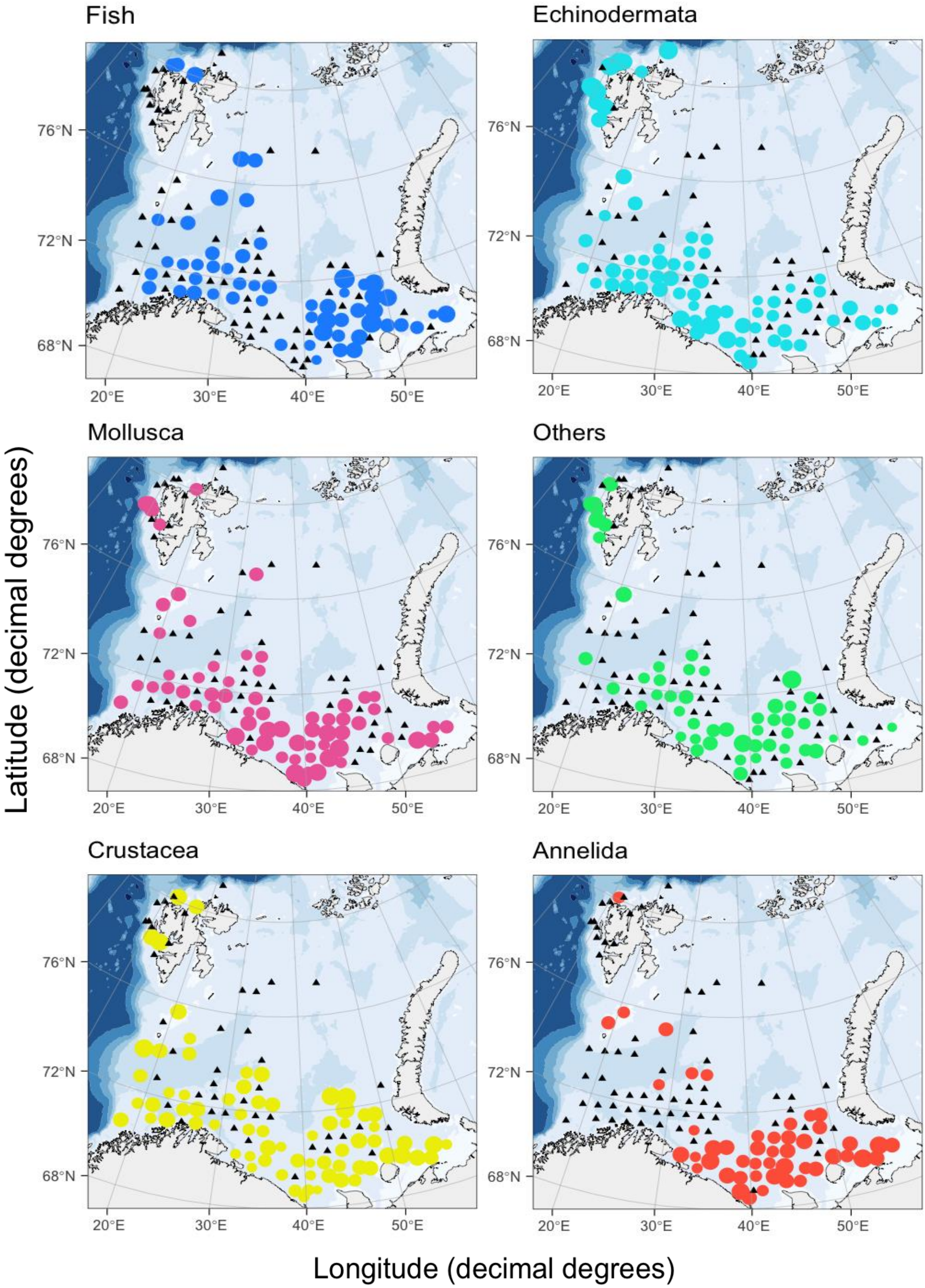

Figure 16 – Barents Sea maps from the 2009 ecosystem survey showing stations with all haddock stomachs. One map represents stations where haddock have consumed specific prey categories, which are represented as circles on the map, and geographic distribution of the prey categories. The size of the circles corresponds to the stomachs with the prey category recorded divided by the total number of stomachs at the station. All other haddock stomachs are represented as triangles, with either stations containing different prey or empty stomachs. Various colored circles (Fish = blue, Echinodermata = turquoise, Mollusca = pink, Others = green, Crustacea = yellow, and Annelida = red) are used to indicate the various categories.

3.2.3 Size differences in diet and feeding

The probability for empty stomachs declines with size and geographical area (Figure 17). The smallest haddock has the highest probability of having empty stomachs, nearly 60%, while the largest haddock, length group 50, had the lowest probability, less than 10%. Although there is a general decline in percentage across the length distribution, the size range of 50 to 55 shows a small increase due to low stomach numbers (Figure 12). Both size and geographical effects were significant (Table 3 and Table 4, Appendix Table 7).

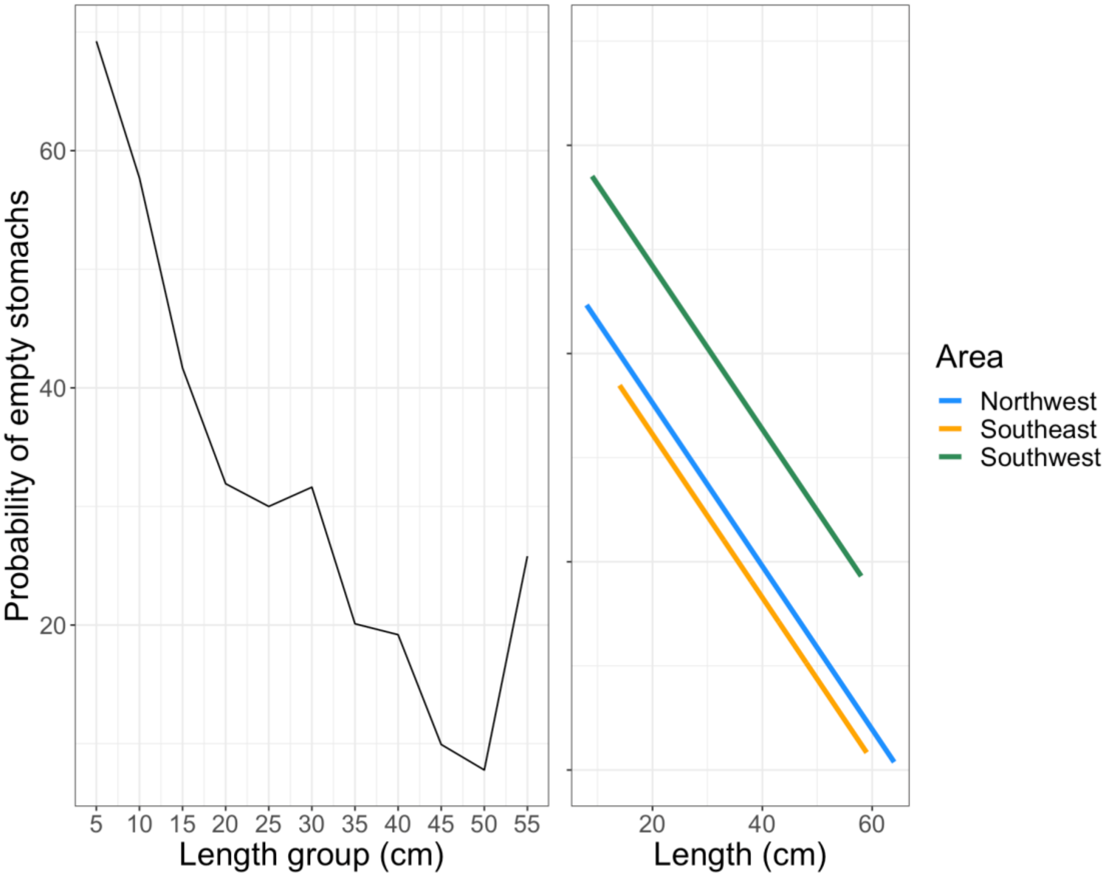

Figure 17 – The probability of empty haddock stomachs by length group. The estimated percentage of empty stomachs for each 5 cm length group is represented by the line in the left plot. The right plot displays predicted percentage of empty stomachs as a function of haddock length with area (northwest, southeast and southwest) as an additive effect.

Table 4 – Summary output of the one-way ANOVA test on the response variables TFI (log transformed, non-empty stomachs), empty stomachs, and the frequency of occurrence of various prey categories. Length was used as predictor variable. Data from ecosystem survey 2009. If there are three asterisks, the p-value is less than 0.001.

Test	Response	Predictor	P-value
ANOVA	Empty stomachs	Length	2.888e-10***
	TFI (log)	Length	0.176
	Annelida	Length	2.2e-16***
	Echinodermata	Length	0.701
	Mollusca	Length	8.068e-09***
	Others	Length	0.007
	Crustacea	Length	0.655
	Fish	Length	0.061

Across all length groups, the TFI is relatively stable (Figure 18). The TFI does not vary significantly with size (Table 4). Southeast is generally where they have the highest stomach fullness (Figure 18). The haddock stomachs in the southwest have significantly lower stomach fullness, than haddock in the southeast and northwest (p-value < 0.05, Table 5, Figure 18).

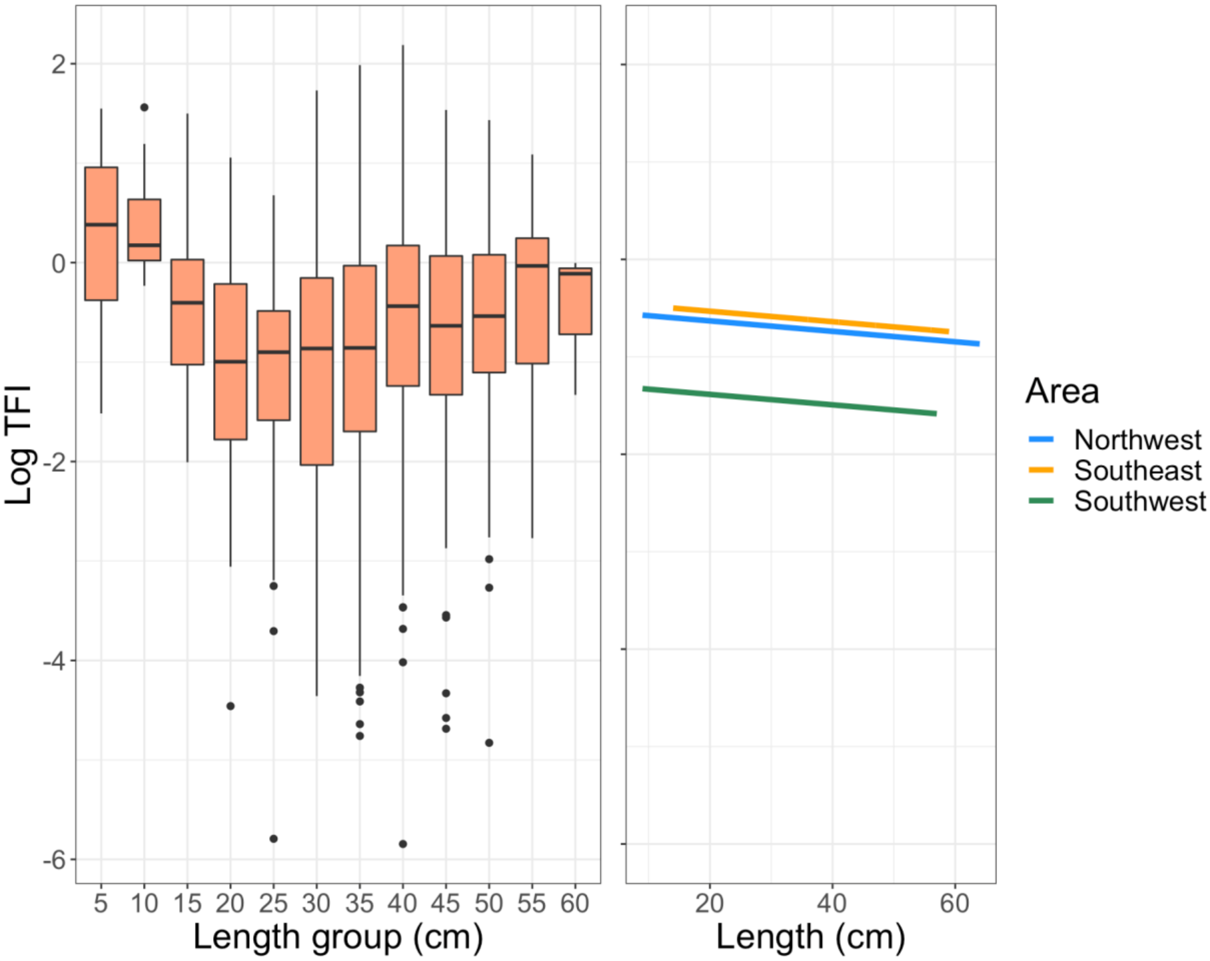

Figure 18 – Boxplot of the level of stomach fullness (TFI log transformed) of all 5 cm length groups (left plot). The right plot displays predicted probability of TFI as a function of haddock length with area (northwest, southeast and southwest) as an additive effect. The x-axes in this plot reflect all the haddock lengths, and the TFI is back transformed.

Figure 19 provides the predicted probability of each prey category by area and length. As haddock size increases, so does the probability of finding **Annelida, Mollusca** and **Others** in the stomachs (p-value < 0.05, Table 4, Figure 19). **Echinodermata, Fish** and **Crustacea**, the other three categories, show less variation with size (Table 5).

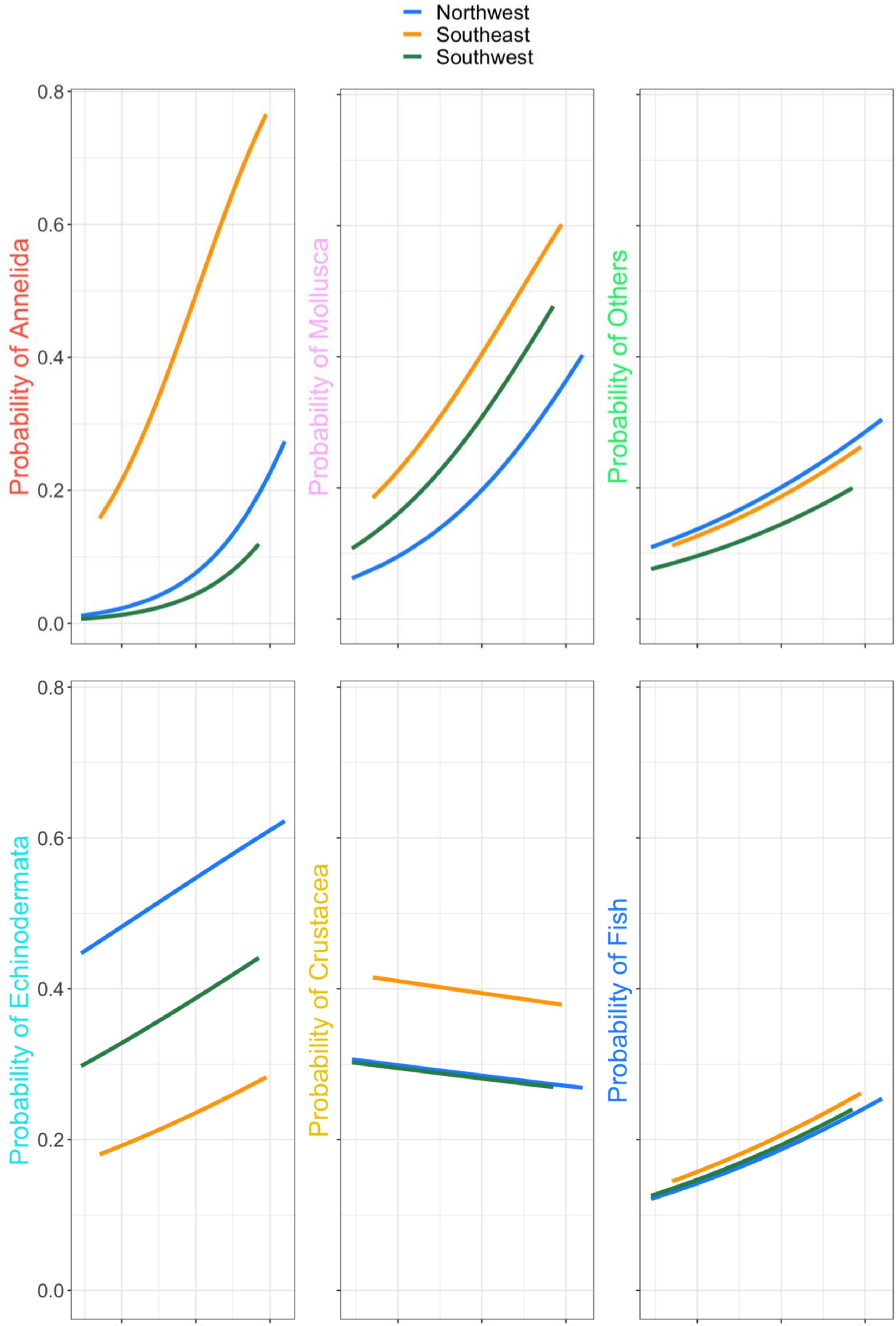

Figure 19 – Predicted probabilities of finding a prey in a haddock stomach (y-axis) modelled as a function of haddock length, and an additive effect of area (northwest, southeast and southwest).

Table 5 – The estimated coefficients for predictors geographic area, and haddock size on the response variables TFI (log transformed, non-empty stomachs), empty stomachs, and the frequency of occurrence of various prey categories. The coefficients are shown with standard error and upper and lower confidence limits (±1.96* SE).

Model	Response	Predictor	Estimate	Std. Err	Lower 95%	Upper 95%
Logistic regression (glm)	Empty stomachs	Northwest (Intercept)	0.510	0.062	0.387	0.631
		Southeast	-0.030	0.045	-0.119	0.059
		Southwest	0.132	0.050	0.033	0.230
		Length	-0.008	0.001	-0.010	-0.005
Linear (lm)	TFI (log)	Northwest (Intercept)	-0.524	0.234	-0.983	-0.065
		Southeast	0.099	0.156	-0.207	0.405
		Southwest	-0.754	0.181	-1.110	-0.399
		Length	-0.005	0.005	-0.015	0.004
Logistic regression (glm)	Annelida	Northwest (Intercept)	-5.044	0.654	-6.400	-3.824
		Southeast	2.478	0.447	1.679	3.460
		Southwest	-0.580	0.636	-1.876	0.677
		Length	0.064	0.011	0.047	0.085
	Echinodermata	Northwest (Intercept)	-0.330	0.409	-1.137	0.471
		Southeast	-1.365	0.263	-1.886	-0.852
		Southwest	-0.646	0.302	-1.242	-0.056
		Length	0.013	0.009	-0.004	0.030
	Mollusca	Northwest (Intercept)	-3.094	0.481	-4.069	-2.179
		Southeast	1.019	0.317	0.424	1.676
		Southwest	0.598	0.368	-0.107	1.345
		Length	0.042	0.009	0.025	0.060
	Others	Northwest (Intercept)	-2.303	0.525	-3.367	-1.304
		Southeast	-0.091	0.321	-0.695	0.572
		Southwest	-0.399	0.398	-1.178	0.395
		Length	0.023	0.011	0.003	0.044
	Crustacea	Northwest (Intercept)	-0.787	0.412	-1.608	0.010
		Southeast	0.491	0.280	-0.044	1.060
		Southwest	-0.018	0.328	-0.654	0.636
		Length	-0.003	0.008	-0.019	0.013
	Fish	Northwest (Intercept)	-2.127	0.504	-3.149	-1.167
		Southeast	0.120	0.327	-0.492	0.799
		Southwest	0.039	0.385	-0.702	0.817
		Length	0.016	0.010	-0.003	0.036

3.2.4 Effect of density on haddock feeding

The highest density levels can be found in the southeast, followed by the northwest, and then southwest (Figure 20). The most common length groups (Figure 12) show the highest density levels (Figure 20). In the southwest, we can observe that the density values decrease with increased haddock size.

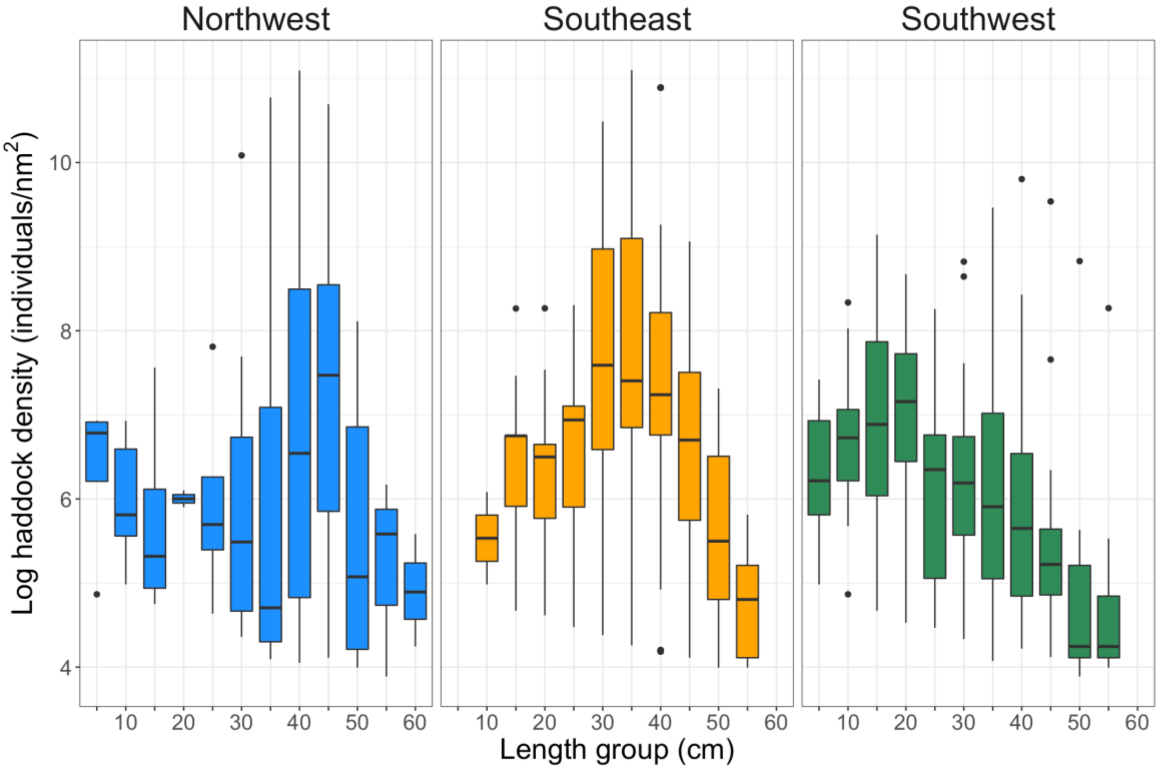

Figure 20 – Distribution of haddock density between the three areas according to haddock length groups. The boxplots display the various haddock density values, as well as the uncertainty distributed in the Barents Sea's northwest, southeast, and southwest. To obtain less skewed data, the density is log transformed.

The analysis of the effect of density on stomach fullness and proportion of empty stomachs were done separately for the three areas, due to the differences in sampling, length distribution and diet among the three areas. In the analysis of proportion empty stomachs, length was used as a co-variate (Appendix Table 7).

In terms of geographic distribution, southwest has the largest probability of having empty stomachs. There is no significant effect of density on proportion empty stomachs for the areas (Appendix Table 8).

There was a significant negative effect of haddock density in the same length group and station on stomach fullness in the southeast area (Figure 21, Table 6, Appendix Table 9). The density has no effect on TFI in the northwest and southwest (Table 6). The trend is not strong in this case, but it appears to be similar in northwest as it does in the southeast. There was also an effect of total haddock density by station on stomach fullness for southeast (Figure 21, Table 6, Appendix Table 10).

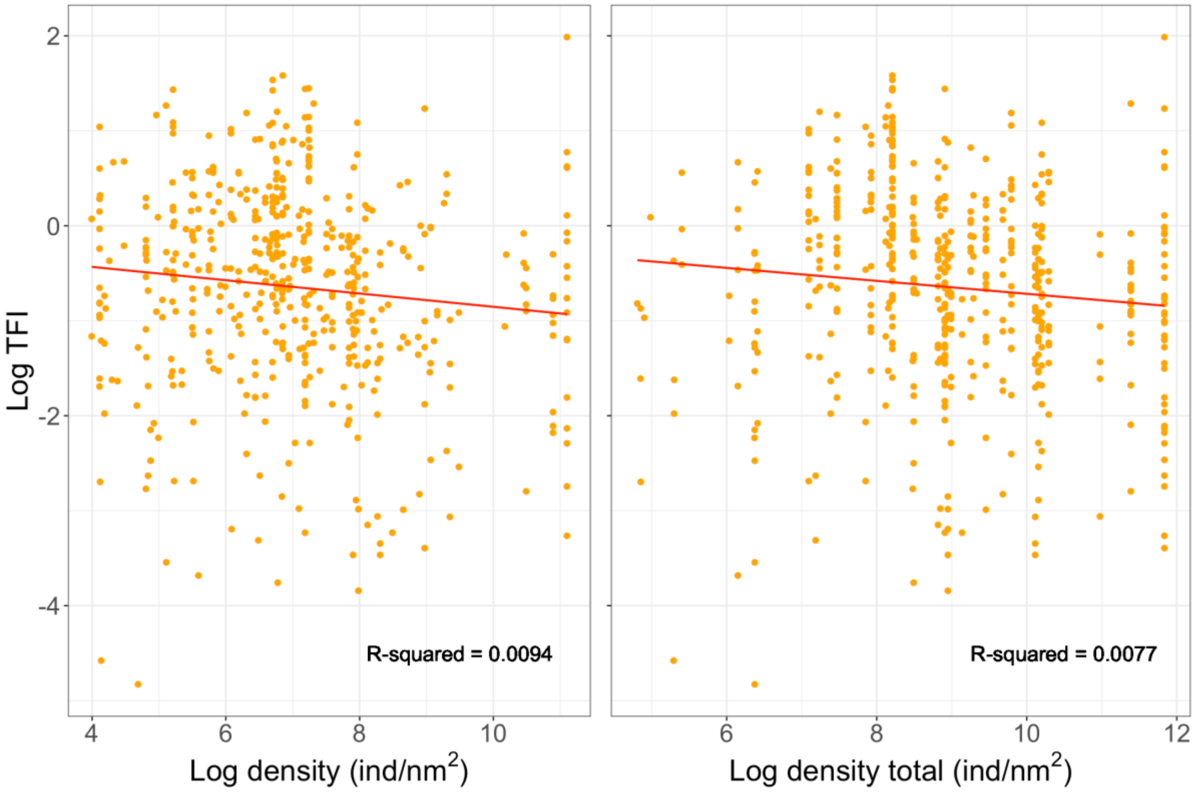

Figure 21 – The relationship between stomach fullness (log transformed TFI) and log haddock density in southeast area. Left: density by length group, and right: by total haddock density. Both x- and y-axes are log transformed. The points represent the stations specific densities, the red line predicted linear relationship between TFI and density. The quantity of variation that fits the model is shown by the R-squared.

Table 6 – The effect of density on TFI done separately for each area. Two sets of models were used for each area: one with density by station and length group (Density) and one by total density by station (Density Total).

Area	Coefficients	Estimate	Std. error	P-value
Southeast	Density (log)	-0.070	0.029	0.015
	Density total (log)	-0.068	0.031	0.026
Northwest	Density (log)	-0.067	0.091	0.466
	Density total (log))	-0.029	0.083	0.733
Southwest	Density (log)	0.079	0.099	0.426
	Density total (log)	-0.044	0.140	0.752

4. Discussion

In this section, I start by comparing the diet of haddock with other ecosystems and cod's diet. I also explore the variations in haddock caught using different gears and the challenges by comparing data from different years. Furthermore, I discuss the effects of area, size, and density based on the 2009 ecosystem survey data. Additionally, the limits of the stomach data and future research are discussed. Finally, I answer the study's objectives by providing a conclusion.

4.1 The haddock stomach database

4.1.1 Comparison with haddock diet from other ecosystems

Comparing the Barents Sea haddock diet between ocean areas could be interesting since it may differ among ecosystems. My research for all years (1984-2019) found that haddock ate mostly Crustacea and Echinodermata. These observations are in accordance with Tam et al. (2016), who observed that haddock in the northeast and northwest of the Atlantic Ocean (including the Barents Sea) had high food intakes of echinoderms. Even though Tam et al. (2016) studied haddock from various ecosystems, and since echinoderms were the main diet source, it is likely that this prey is an important food source for haddock across its distribution range.

In a paper that studied the feeding strategy and prey selection of haddock in the North Sea, found that echinoderms and polychaetes dominated the stomach content (Schückel et al., 2010), a find which align with my own research. The same paper found that the prey density in the field determined the prey selection. This suggests that haddock may have chosen polychaetes as a preferred prey due to high abundance of polychaetes in the North Sea.

Echinoderms are mainly made up of thick, calcareous exoskeletons that are digested slowly by most fish species and are lower in energy than other invertebrate species (Tam et al., 2016). This suggest that haddock may exhibit slower digestion rates for this prey, resulting in a longer retention time in their stomachs. Consequently, echinoderms are likely frequently observed and recorded in the stomach contents of haddock (Tam et al., 2016). Other prey that is digested more easily, like polychaetes, might be a main part of haddock's diet, but counted less often. A paper on diet of haddock and whiting (*Merlangius merlangus*) in the northeast of Scotland revealed that haddock tended to be benthivores, eating polychaetes, echinoderms and crustaceans (Greenstreet et al., 1998). This corresponds to what I have found that crustaceans and echinoderms are the primary components of haddock’s diet. It is possible that variations in the proportion of haddock’s diet are generally governed by changes in the availability of their preferred benthic prey. Based on this haddock choose prey that is easily accessible and consumable, confirming their preference of benthic food sources.

4.1.2 Haddock diet compared with cod diet in the Barents Sea

Given that both haddock and cod belong to the *Gadidae* family, have many similar characteristics and common features, and share the same environment (Dalpadado et al., 2009), it is reasonable to explore and compare their diets. The analysis of the complete dataset (1984-2019) revealed that haddock mostly ate Crustacea, primarily krill, and Echinodermata which were mainly brittle stars. A study of Barents Sea cod, which covered the years 1930 to 2018, discovered that teleost fish and crustaceans made up most of their diet (Townhill et al., 2021).

A study on cod diet in the Barents Sea from 1984 to 2016 found that fish was the most important food source (Holt et al., 2019), and the importance of fish increased as the cod grew. Their diet changed from containing krill, "other food" (mainly invertebrates, crustaceans, Polychaeta and Cephalopoda), and shrimps to one that was more fish-dominated (Holt et al., 2019). Additionally, seasonal variations were found as capelin dominated the winter diet, while cod, polar cod and other fish species were common in the summer and fall (Johannesen et al., 2015).

Dalpadado et al. (2009) studied 0-group haddock and cod in the Barents Sea in 2005 and 2006 found that both species exhibited a pelagic feeding behavior. The copepod *Calanus finmarchicus* and the krill *Thysanoessa inermis* were the main prey of both species. The main distribution, feeding areas and the 0-group's primary range overlapped, suggesting that the two species may compete for food (Dalpadado et al., 2009; Durant et al., 2020). The juvenile Barents Sea haddock (0–2-year old’s) consumes a lot of the same food as the juvenile cod. However, it appears that 0-group haddock prefer smaller and less mobile prey than 0-group cod (Dalpadado et al., 2009). In the Barents Sea, diet studies on cod at ages 0-, 1- and 2-year-old between 1984 and 2002 found that cod primarily consumed crustaceans, with krill and amphipods accounting for up to 70% of their diet. A shift in their diet from crustaceans to fish were observed from one to two years old. Capelin and other fish constituted most of the diet of 2-year-old cod (Dalpadado & Bogstad, 2004). The haddock’s diet is different from the cod’s diet as it consists more of benthic organisms and crustaceans than fish, although both fish species share much of the same diet as juveniles.

4.1.3 Diet differences between haddock caught in pelagic and bottom trawl

The pelagic zone closer to the surface is typically where small haddock are found, and there is other prey available here than near the seabed where the larger ones prefer to stay (Mahon & Neilson, 1987). Consequently, the diet of haddock caught by pelagic trawl is to differ from that of haddock caught using bottom trawl. Research from the Barents Sea in 2005 and 2006 observed that haddock in the zero-group had a clear pelagic feeding habit, and as haddock grew, their diet gradually changed from smaller copepods to larger prey such as krill and fish (Dalpadado et al., 2009). The consumption of crustaceans by small haddock caught using pelagic trawls aligns with my observations that show a small trend of increased Crustacea prey as haddock size decreased.

Haddock caught by bottom trawl appeared to have a wider variety of prey, which can be explained by that larger fish have a wider prey size range (Gill, 2003; Holt et al., 2019). Most haddock caught with the bottom trawl consumed Echinodermata, which makes sense given that brittle stars individuals are bottom dwellers on the seabed (Stöhr et al., 2012). I anticipated more contrast for the Mollusca category between the gears, but the lack of contrast could be due to the slower digestion of the Mollusca's hard shell (Esposito et al., 2022). The rates of digestion of different prey by the Atlantic cod were studied in the northwest Atlantic by Macdonald et al. (1982). They found that bivalves were digested more slowly than amphipods, which were digested more slowly than polychaetes, and that food items with high percentages of chitin or shell remained in stomachs longer (Macdonald et al., 1982). Chitin makes up 50–80% of the total volume of crustaceans (Tibbetts et al., 2004), which may also explain why they are registered so frequently.

4.1.4 Comparing periods and years

Since no one had previously analyzed the whole haddock stomach data set, the first step was to get an overview, organize the data, and determine whether the years were comparable. However, because sampling was done at different locations and seasons in the different years and periods, years and periods were not directly comparable. Furthermore, both gears and size distribution of sampled haddock differ between years. Not all the haddock on each station had their stomachs analyzed, and the number of stomachs analyzed differed between stations.

It would be interesting to determine whether haddock diets have changed since the study by Jiang and Jørgensen (1996) based on data from the 1980s when the haddock stock was smaller than it is now. Since this ended up not being an option, the plan was to compare the years 2009 and 2015 due to the huge data sampling these years. However, in 2015, Russia mainly sampled the eastern Barents Sea using a bottom trawl, and Norway primarily used a pelagic trawl to sample the stations this year. Since haddock is a demersal species, the bottom trawl is the most effective gear for catching haddock and whereas pelagic trawls mostly sample smaller haddock. It was therefore not informative to compare the data from these two years. I therefore concentrated on the dataset from the ecosystem survey in 2009 which had better documentation on haddock stomach samples.

4.2 Effects of area, haddock size and density on haddock diet from the ecosystem survey 2009

4.2.1 Geographical differences in diet

Geographical variation in prey distribution may cause geographical variation in the haddock's diet (Schückel et al., 2010). Haddock consumed considerably more Annelida than found in Jiang and Jørgensen (1996), and these prey were mostly registered in the southeast area of the Barents Sea, an area that was not covered well in the data set of Jiang and Jørgensen (1996). Russia has primary responsibility for sampling in the southeast and has generally sampled a lot more haddock stomachs per station (Appendix Figure 1). Therefore, there were more stomach samples here than in the other areas, so that the overall number of stomachs with Annelida was high this year. The reason why haddock feeds on Annelida in the southeast, might be that the southeast area simply just has more Annelida available, or that there was a lack of a better alternative prey there.

The phylum Annelida is extremely diverse, with organisms exhibiting a wide range of ecological preferences, long evolutionary histories, varied characteristics, and a vast variety of life strategies (Worsaae et al., 2021). Focusing on a particular genus of Annelida can make it simpler to extract meaningful biogeographic patterns, but in my research from 2009, the registered Annelida prey was only identified to polychaeta. Since most of the Annelida prey favor a sandy bottom, the southeast region's bottom will probably be softer than up in the north. A Russian paper that studied the bottom fauna in the Barents Sea between 1924 and 1935 found that the east and southeast region contained communities living on sandy sediments (Anisimova et al., 2011).

The prey categories Annelida, Mollusca, and Crustacea are consumed significantly more in the southeast. A paper that studied the distribution of benthic megafauna in the Barents Sea, sea stars, anemones, and snow crabs predominated on the banks and slopes in the southeast and southwest, along with filter feeders (sea cucumber and bivalves) (Jørgensen et al., 2014). These findings match my results regarding the predominance of the Mollusca category in haddock diet in the southeast. From the same study by Jørgensen et al. (2014), in the northwest and northeast, brittle stars were most frequently found mega-benthos using the bottom trawl. Most brittle stars are benthos dwellers on the seabed, buried in mud or hidden in crevices and holes in rock or coral (Stöhr et al., 2012). I found that the Echinodermata, mostly brittle star class, is the most common prey category in the northwest.

4.2.2 Fish size effects

For most fish species there are differences between the diets of large and small individuals. In the case of Barents Sea cod, it has been observed that larger individuals consume a higher quantity of fish in comparison to smaller cod individuals (Johannesen et al., 2015). In this regard, fish was the only prey category that I believed would be consumed more frequently as the haddock became larger. The prey category Fish didn’t have a significant effect in my results, but there was a small increasing trend with increasing haddock size. Schückel et al. (2010) found that fish prey had a less important part in the prey composition of haddock, and it did not dominate to the same degree as it did for whiting and cod. Following Greenstreet et al. (1998) who studied haddock in Scotland, fish constituted an important prey of haddock’s diet and this proportion increased as haddock size increased.

The prey categories Annelida, Mollusca, and Others had a significant increase in registration with increasing haddock size. Although there is no conclusive explanation for this, it is possible that individual types of prey could have been larger, and that small haddock struggle to consume this prey size. Research by Schückel et al. (2010) observed that larger body size allows larger fish to seek deeper into the sediment, allowing them to meet a wider variety of prey. This could imply that larger haddock may consume all prey sizes and that different sizes are represented in the categories of Annelida, Mollusca, and Others. Both Annelida and Mollusca are diverse phylum, and the Others category includes a wide variety of prey of various sizes. Larger fish typically exhibit a reduced feeding frequency (Vinson & Angradi, 2010). They don’t spend most of their energy searching for food, but rather more for reproduction (Van Leeuwen et al., 2008). In regard to these studies and my results, haddock's size seems to influence their preference for bottom-dwelling prey.

Small haddock had a higher likelihood of having empty stomachs, which can be attributed to several factors. Larger fish may find it easier to locate and consume food, benefiting a broader selection available with a wider ecological niche (Gill, 2003). In contrast, smaller fish may require more time and energy searching for food, and they also face higher natural mortality (Graeb et al., 2011). Predation risks are generally lower for larger fish than smaller fish (Salvanes & Braithwaite, 2005). The body size of both the predator and the prey is a crucial factor that is connected to the process of searching for food, specifically capture success and the dynamics of predation (Holt et al., 2019). Additionally, a variety of variables contribute to their feeding success as the fish grow, including increasing swimming ability, improved visual acuity and expanded gape size (Graeb et al., 2011; Holt et al., 2019). These characteristics of fish, a reduction of empty stomachs in larger haddock was as expected. The degree of prey digestion could also be a factor in this effect, and larger haddock may have more "leftovers" in their stomach which then is registered.

4.2.3 Effects of fish density

High local population density may affect the amount of food consumed, and ultimately impact growth rate (Rindorf et al., 2008). Regarding this, there might be objectives to find that the more haddock there are that compete for food, the less food there is in their stomachs. Food consumption and individual growth rates of Arctic charr in a lake in northern Norway were studied between 1980 and 1999 (Amundsen et al., 2007). The study revealed that the density dependence of individual growth and other population characteristics were affected by intraspecific competition for limited food resources.

My research showed the effect of haddock density on stomach fullness (TFI) in the southeast area, where more samples of haddock stomachs were taken, and the densities of 3- and 4-year old's haddock was high. Lower sample sizes and lower haddock densities might be the cause of why northwest and southwest don't have the same effect (Rindorf et al., 2008). It is difficult to explain all the variation in the TFI and the relationship between densities and TFI in the southeast is weak. There is an important variability in TFI that I was unable to explain using haddock density. The reason could be due to the skewed data, or to other unknown factors, that impacted haddock feeding apart from density.

The amount of food the haddock consumes might also vary due to competition between the cohorts (intercohort) and within cohorts (intracohort). In the southeast where there were high densities of three- and four-year-old’s, these year classes might compete with one another for food and with other cohorts, that is both smaller and larger. However, according to a report from the 1960s that studied the North Sea haddock, strong year classes caused intraspecific competition which was felt strongly by younger individuals or those of a similar age (Jones, 1983). Consequently, there is a chance that the strong year classes of three- and four-year-old haddock in the southeast caused this density dependent effect.

4.3 Limitations of stomach sampling

Stomach analyses is a challenging and time-consuming process that requires accuracy. Because Norway and Russia may have different procedures on determine the identification of the taxonomic prey, could affect my results. Additionally, since the stomach sampling only demonstrates a snapshot in time, the next day's content in the stomachs could be different (Eriksen et al., 2020). The degree of digestion may also make it difficult to identify the various prey. Also, due to differences in digestibility the stomach content may reflect both how often the prey is eaten but also how fast it is digested.

4.4 Future research

My research contributes to knowledge about the Barents Sea haddock’s diet, and there are few studies to compare against in the Barents Sea cod’s diet. Future studies should focus on the temporal and geographical dynamics of haddock diet and how it relates to variations in prey availability and haddock distribution. Studying this species' diet in the Barents Sea and other environments will increase our understanding of how diet ecology changes in ecosystems and climates. To study prey selectivity over time in the Barents Sea is crucial for understanding the importance of Crustacea, Annelida, and Echinodermata in the diet of haddock.

Studying the various mechanisms underlying potential effects of density dependence on food consumption and growth rates for haddock would also be interesting. This contributes to knowledge about factors that affect growth, including temperature, fish mortality, prey quantity, and fish density.

4.5 Conclusion

Haddock is a typical benthivores species and Echinodermata, Crustacea, and Annelida constitute the main diet. As the haddock get larger, they find food more easily by having more choices. Small haddock prefer to eat crustaceans and has higher proportion of empty stomach. In the southeast Barents Sea haddock favor eating Annelida, and further north they prefer eating Echinodermata. In 2009, when the haddock stock was high in population abundance, the haddock’s total stomach content decreased with increasing haddock density in the southeast.

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Appendices

Appendix Table 1 – Overview of all prey items recorded in the haddock stomachs, with the categories used in the analysis.

Prey category	Category	N prey	Mean prey weight	N 2009
Ochrophyta	Others			
Phaeophyta	Others	10	3.28	
Porifera	Others	3	1.13	
Calcarea	Others	2	0.09	
Foraminifera	Others	36	0.03	
Dicyemida	Others	1	13.77	1
Priapulida	Others	2	18.42	
Priapulopsis bicaudatus	Others	2	1.19	
Ectoprocta	Others	6	0.05	
Gymnolaemata	Others	11	0.32	
Cheilostomata	Others	6	0.02	
Ctenophora	Others	467	10.51	123
Nemertea	Others	145	6.56	20
Nematoda	Others	21	0.04	
Platyhelminthes	Others			
Trematoda	Others	25	0.02	
Cnidaria	Others	6	0.36	
Anthozoa	Others	212	8.98	7
Hormathia digitata	Others	9	4.06	
Adamsia palliata	Others	3	3.50	
Metridium senile	Others	18	1.81	
Hydrozoa	Others	57	0.76	
Scyphozoa	Others	12	24.80	2
Annelida	Annelida	103	4.56	18
Polychaeta	Annelida	2068	7.91	397
Aphrodita aculeata	Annelida	5	4.55	
Brada inhabilis	Annelida	1	1.42	
Echiura	Annelida	2	18.15	
Polynoidae	Annelida	3	0.17	
Phyllodocidae	Annelida	8	0.20	
Nereidae	Annelida	3	0.88	
Nephtyidae	Annelida	8	0.67	
Glyceridae	Annelida	10	0.91	
Onuphidae	Annelida	24	0.47	
Eunicidae	Annelida	29	0.14	
Lumbrineridae	Annelida	2	0.10	
Chaetopteridae	Annelida	1	1.10	
Spiochaetopterus typicus	Annelida	34	0.77	
Scalibregmatidae	Annelida	1	0.31	
Arenicolidae	Annelida	1	0.86	
Maldanidae	Annelida	14	0.51	
Oweniidae	Annelida	40	0.55	

Prey category	Category	N prey	Mean prey weight	N 2009
Galathowenia oculata	Annelida	147	0.41	
Pectinariidae	Annelida	91	1.74	
Terebellidae	Annelida	75	1.35	
Sabellidae	Annelida	5	0.20	
Serpulidae	Annelida	4	0.08	
Sipuncula	Annelida	35	3.03	
Phascolion strombi	Annelida	10	0.03	
Spiunculidae	Annelida	27	7.64	
Mollusca	Mollusca	1	2.42	1
Gastropoda	Mollusca	364	9.26	19
Solariella obscura	Mollusca	1	0.03	
Cylichna alba	Mollusca	3	0.07	
Clione limacine	Mollusca	12	0.51	
Patellidae	Mollusca	1	0.08	
Patina pellucida	Mollusca	1	0.02	
Trochidae	Mollusca	1	0.10	
Margaritidae	Mollusca			
Margarites	Mollusca	2	0.11	
Margarites groenlandicus	Mollusca	7	0.19	
Strombidae	Mollusca	8	0.004	
Cypraeidae	Mollusca	4	1.04	
Naticidae	Mollusca	2	0.23	
Cryptonatica affinis	Mollusca	3	0.16	
Euspira pallida	Mollusca	6	0.22	
Buccinidae	Mollusca	1	4.27	
Buccinum hydrophanum	Mollusca	1	0.72	
Volutopsius norwegicus	Mollusca	2	0.37	
Schaphandridae	Mollusca			
Schaphander	Mollusca	64	0.31	
Scaphander punctostriatus	Mollusca	1	0.90	
Scaphander lignarius	Mollusca	5	0.29	
Retusidae	Mollusca	2	3.13	
Limacinidae	Mollusca			
Limacina	Mollusca	57	0.10	
Limacina helicina	Mollusca	51	0.02	
Limacina retroversa	Mollusca	19	0.003	
Onchidorididae	Mollusca	1	0.39	
Dendronotidae	Mollusca	1	1.50	
Bivalvia	Mollusca	1886	3.94	387
Bathyarca glacialis	Mollusca	23	1.30	
Hiatella arctica	Mollusca	1	0.09	
Nuculidae	Mollusca	3	0.98	1
Ennucula	Mollusca	70	0.37	
Ennucula tenuis	Mollusca	20	0.14	
Nuculandidae	Mollusca	2	0.01	
Nuculana pernula	Mollusca	3	0.26	
Yoldiidae	Mollusca			
Yoldiella	Mollusca	302	0.12	2

Prey category	Category	N prey	Mean prey weight	N 2009
Yoldiella fraternal	Mollusca	1	0.23	
Yoldiella lucida	Mollusca	1	0.01	
Mytilidae	Mollusca	8	0.02	
Mytilus edulis	Mollusca	4	0.02	
Dacrydium vitreum	Mollusca	103	0.02	
Pectinidae	Mollusca	167	0.98	
Pandaridae	Mollusca			
Chlamys	Mollusca	10	0.18	
Chlamys islandica	Mollusca	2	7.18	
Chlamys tigerina	Mollusca	1	0.78	
Chlamys septemradiatus	Mollusca	24	0.12	
Propeamussiidae	Mollusca			
Arctinula	Mollusca	35	0.28	
Arctinula greenlandica	Mollusca	48	0.14	
Limidae	Mollusca	1	0.20	
Astartidae	Mollusca			
Astarte	Mollusca	39	0.44	
Astarte crenata	Mollusca	4	0.36	
Cardiidae	Mollusca	56	0.28	
Clinocardium ciliatum	Mollusca	11	0.62	
Serripes groenlandicus	Mollusca	1	7.58	1
Parvicardium minimum	Mollusca	1	0.39	
Cardium	Mollusca	312	0.21	
Cardium minimum	Mollusca	147	0.09	
Mactridae	Mollusca	2	0.22	
Spisula elliptica	Mollusca	1	0.32	
Tellinidae	Mollusca			
Macoma	Mollusca	29	1.53	
Clam macoma calcarean	Mollusca	34	5.26	
Veneridae	Mollusca	5	0.10	
Venus	Mollusca	1	0.16	
Myidae	Mollusca	23	1.92	
Mya arenaria	Mollusca	2	0.12	
Scaphopoda	Mollusca	249	2.10	12
Cephalopoda	Mollusca	22	30.68	
Ommastrephes sagittatus	Mollusca	2	4.13	
Polyplaophora	Mollusca	6	0.59	
Lepidopleurus asellus	Mollusca	3	0.14	
Echinodermata	Echinodermata	144	4.83	33
Asteroidea	Echinodermata	86	4.27	3
Asterias rubens	Echinodermata	1	0.20	
Ctenodiscus	Echinodermata	1	0.56	
Ctenodiscus crispatus	Echinodermata	70	4.32	
Solaster	Echinodermata	1	6.68	
Astropectinidae	Echinodermata	3	0.88	
Psilaster andromeda	Echinodermata	11	0.53	
Goniasteridae	Echinodermata	1	0.25	
Ceramaster granularis	Echinodermata	10	1.07	

Prey category	Category	N prey	Mean prey weight	N 2009
Ophiuroidea	Echinodermata	2439	1.55	72
Ophiacantha bidentata	Echinodermata	15	6.99	
Ophiopholis aculeata	Echinodermata	26	7.51	
Ophiolepididae	Echinodermata	349	5.97	
Ophiurida	Echinodermata	599	2.85	218
Ophiocten sericeum	Echinodermata	39	3.82	
Ophiura	Echinodermata	77	0.66	
Ophiura sarsi	Echinodermata	60	1.97	
Ophiura robusta	Echinodermata	1	0.02	
Holothuroidea	Echinodermata	262	19.46	20
Molpadia borealis	Echinodermata	1	4.72	
Psolidae	Echinodermata	2	0.90	
Psolus phantapus	Echinodermata	7	5.10	
Echinozoa	Echinodermata	244	1.02	
Echinoidea	Echinodermata	117	3.58	10
Echinocyamus pusillus	Echinodermata	1	0.03	
Brisaster fragilis	Echinodermata	1	0.20	
Strongylocentrotidae	Echinodermata	2	0.37	
Echinidae	Echinodermata	2	0.70	
Echinus acutus	Echinodermata	7	2.57	2
Strongylocentrotus	Echinodermata	2	0.02	
Echinoida	Echinodermata	11	6.17	
Spatangoida	Echinodermata	1	0.56	
Loveniidae	Echinodermata	3	0.97	
Crinoidea	Echinodermata	1	0.01	
Arthropoda	Crustacea			
Crustacea	Crustacea	738	2.05	20
Branchiopoda	Crustacea	20	6.47	
Copepoda	Crustacea	42	0.03	
Calanoida	Crustacea	64	0.04	
Centropages hamatus	Crustacea	1	0.0001	
Calanidae	Crustacea	1	0.08	
Calanus	Crustacea	29	0.79	1
Calanus hyperboreus	Crustacea	1	0.02	
Calanus finmarchicus	Crustacea	103	0.10	
Metridinidae	Crustacea			
Metridia	Crustacea	14	0.0007	
Metridia lucens	Crustacea	16	0.01	
Metridia longa	Crustacea	12	0.0005	
Pseudocalanidae	Crustacea	2	0.0001	
Tanaidacea	Crustacea	11	0.25	
Chelicerata	Crustacea			
Pycnogonida	Crustacea	25	5.45	
Gammarida	Crustacea			
Malacostraca	Crustacea	30	0.61	
Decapoda	Crustacea	21	0.38	
Sergestes arcticus	Crustacea	5	1.14	3
Brachyura	Crustacea	28	1.01	2

Prey category	Category	N prey	Mean prey weight	N 2009
Chionoecetes opilio	Crustacea	3	1.75	
Macropipus	Crustacea	2	0.15	
Hyas	Crustacea	11	2.07	1
Hyas coarctatus	Crustacea	3	0.62	
Hyas araneus	Crustacea	6	1.32	
Anomura	Crustacea	4	0.61	
Lithodes maja	Crustacea	1	0.81	
Paguridae	Crustacea	57	3.93	5
Pagurus	Crustacea	4	0.46	
Pagurus bernhardus	Crustacea	23	0.75	
Pagurus pubescens	Crustacea	20	4.29	
Galatheidae	Crustacea	152	3.62	8
Munididae	Crustacea			
Munida	Crustacea	48	1.37	
Munida sarsi	Crustacea	22	2.44	
Caridea	Crustacea	178	1.95	3
Spirontocaris liljeborgii	Crustacea	4	0.28	
Spirontocaris spinus	Crustacea	6	1.21	
Lebbeus Polaris	Crustacea	5	0.27	
Pasiphaeidae	Crustacea	2	2.01	
Pasiphaea	Crustacea	43	4.12	
Hyppolytidae	Crustacea	1	0.85	
Pandalidae	Crustacea	4	2.00	
Dichelopandalus bonnieri	Crustacea	1	6.98	
Pandalus	Crustacea	2	0.40	
Pandalus borealis	Crustacea	216	3.99	10
Pandalus montagui	Crustacea	2	0.21	
Pandalus propinquus	Crustacea	1	3.46	
Crangonidae	Crustacea	25	2.96	6
Crangon allmanni	Crustacea	2	0.33	
Sabinea septemcarinata	Crustacea	3	0.54	
Sabinea sarsii	Crustacea	1	0.34	
Pontophilus norvegicus	Crustacea	28	1.57	4
Euphausiacea	Crustacea	120	1.80	
Euphausiidae	Crustacea	1258	2.47	137
Meganyctiphanes norvegica	Crustacea	201	1.53	
Thysanoessa	Crustacea	36	8.75	
Thyasanoessa inermis	Crustacea	41	0.50	
Thyasanoessa longicaudata	Crustacea	20	0.002	
Amphipoda	Crustacea	785	1.10	4
Anonyx nugax	Crustacea	1	1.99	
Epimeria loricate	Crustacea	4	0.11	
Acanthonotozomatidae	Crustacea	1	0.36	
Ampeliscidae	Crustacea	1	0.05	
Ampelisca	Crustacea	6	0.10	
Calliopiidae	Crustacea	13	0.37	
Halirages fulvocinctus	Crustacea	1	0.06	
Corophiidae	Crustacea	2	0.17	

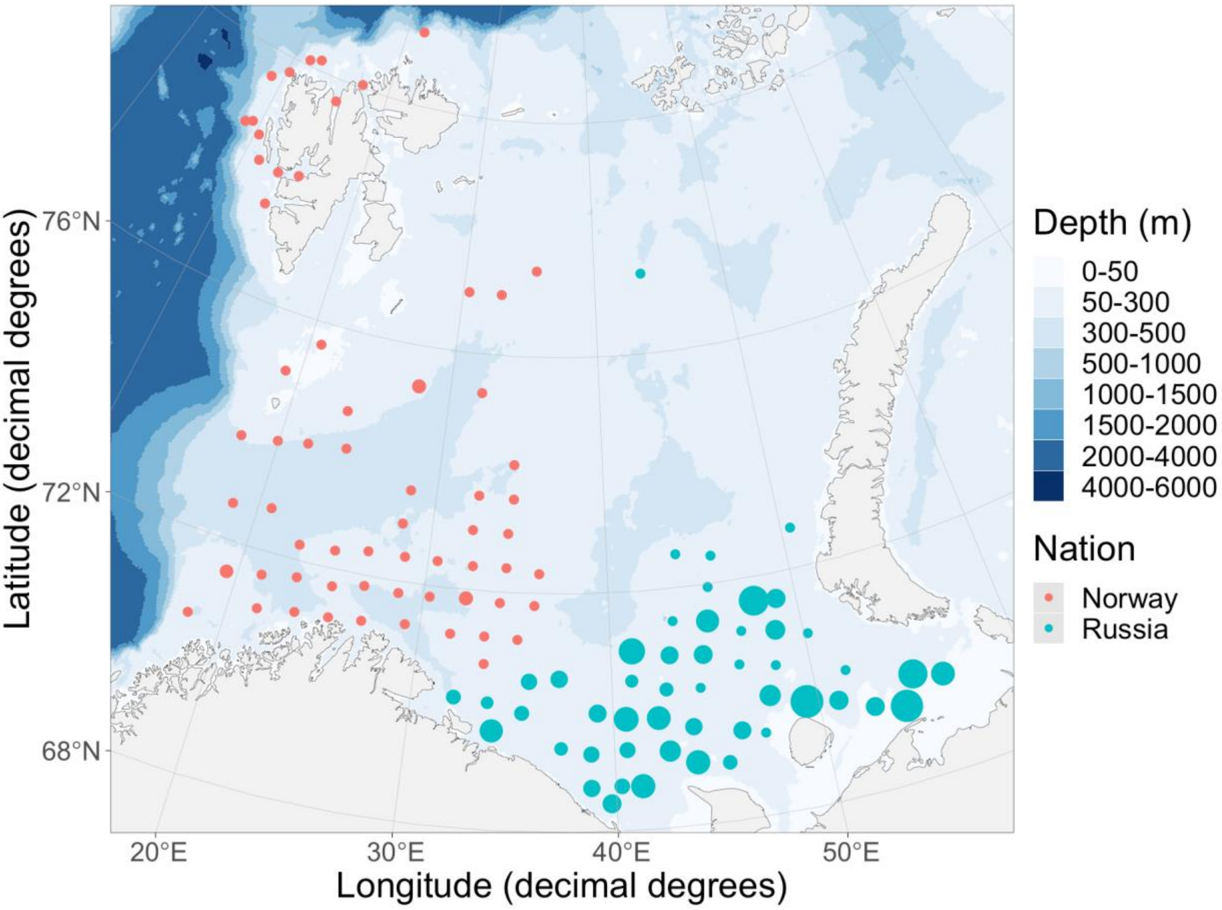
Prey category	Category	N prey	Mean prey weight	N 2009
Eusiridae	Crustacea	3	0.17	
Eusirus holmi	Crustacea	1	0.72	
Lysianassidae	Crustacea	17	0.28	
Stegocephalidae	Crustacea			
Stegocephalus	Crustacea	2	0.08	
Stegocephalus inflatus	Crustacea	7	0.46	
Gammaridea	Crustacea	535	2.08	132
Gammaridae	Crustacea	203	0.20	7
Gammarus	Crustacea	4	0.32	
Hyperiidea	Crustacea	3	1.12	
Hyperiidae	Crustacea	302	0.59	3
Themisto	Crustacea	65	5.31	1
Themisto abyssorum	Crustacea	19	0.02	
Caprellidea	Crustacea	2	0.24	
Isopoda	Crustacea	100	2.28	2
Aega psora	Crustacea	1	0.10	
Anthuridae	Crustacea	15	0.13	
Cirolanidae	Crustacea	19	0.20	
Arcturidae	Crustacea	1	0.04	
Idoteidae	Crustacea	4	0.94	
Munnopsidae	Crustacea	8	0.05	
Mysida	Crustacea			
Mysidae	Crustacea	11	0.08	
Cumacea	Crustacea	64	0.04	
Diastylis	Crustacea	23	0.37	
Leuconidae	Crustacea	1	0.11	
Leucon	Crustacea	4	0.55	
Chaetognatha	Others	16	0.37	2
Sagittidae	Others	13	15.62	
Parasagittal elegans	Others	1	0.0003	
Chordata	Others			
Copelata	Others	6	0.0005	
Ascidiacea	Others	37	9.66	
Thaliacea	Others	25	12.21	
Larvacea	Others	79	0.02	
Cephalochordata	Others	1	18.70	
Vertebrata	Fish			
Gnathostomata	Fish	2	0.03	
Osteichthyes	Fish	8	0.27	
Teleostei	Fish	433	4.97	56
Cryptacanthodidae	Fish	5	2.33	4
Clupeidae	Fish	3	53.63	
Clupea harengus	Fish	24	12.20	1
Osmmeridae	Fish			
Mallotus villosus	Fish	167	19.75	22
Argentinidae	Fish			
Argentina silus	Fish	3	6.63	
Sternoptychidae	Fish			

Prey category	Category	N prey	Mean prey weight	N 2009
Maurolicus muelleri	Fish	9	1.44	
Myctophidae	Fish			
Benthosema glaciale	Fish	20	2.88	
Zoarcidae	Fish			
Lycodes vahli	Fish	1	3.27	
Gasterosteidae	Fish			
Gasterosteus aculeatus	Fish	1	4.00	
Sebastidae	Fish			
Sebastes	Fish	115	4.16	
Sebastes marinus	Fish	1	2.58	
Sebastes mentella	Fish	4	9.95	
Cottidae	Fish	10	3.47	1
Artediellus atlanticus	Fish	4	6.08	1
Triglops	Fish	1	4.00	
Anarhichadidae	Fish			
Anarhichas minor	Fish	4	2.17	
Stichaeidae	Fish	1	4.10	
Leptoclinus maculatus	Fish	9	1.04	
Lumpenus	Fish	7	12.83	
Lumpenus lampretaeformis	Fish	16	1.84	
Ammodytidae	Fish	92	3.10	59
Ammodytes	Fish	19	3.49	9
Ammodytes marinus	Fish	1	7.00	
Pleuronectidae	Fish	4	2.91	
Glyptocephalus cynoglossus	Fish	1	0.65	
Hippoglossoides platessoides	Fish	22	2.84	4
Scorpaenidae	Fish	10	3.29	1
Agonidae	Fish	1	6.03	1
Gadidae	Fish	5	3.85	1
Boreogadus saida	Fish	10	2.76	7
Gadus morhua	Fish	26	15.60	10
Melanogrammus aeglefinus	Fish	11	26.91	2
Trisopterus minutus	Fish	1	6.01	
Trisopterus esmarkii	Fish	26	13.47	5
Gadiculus argenteus	Fish	4	11.31	
Micromesistius poutassou	Fish	13	23.29	
Other fish	Fish	1	0.001	
Unidentified		2685	1.03	30

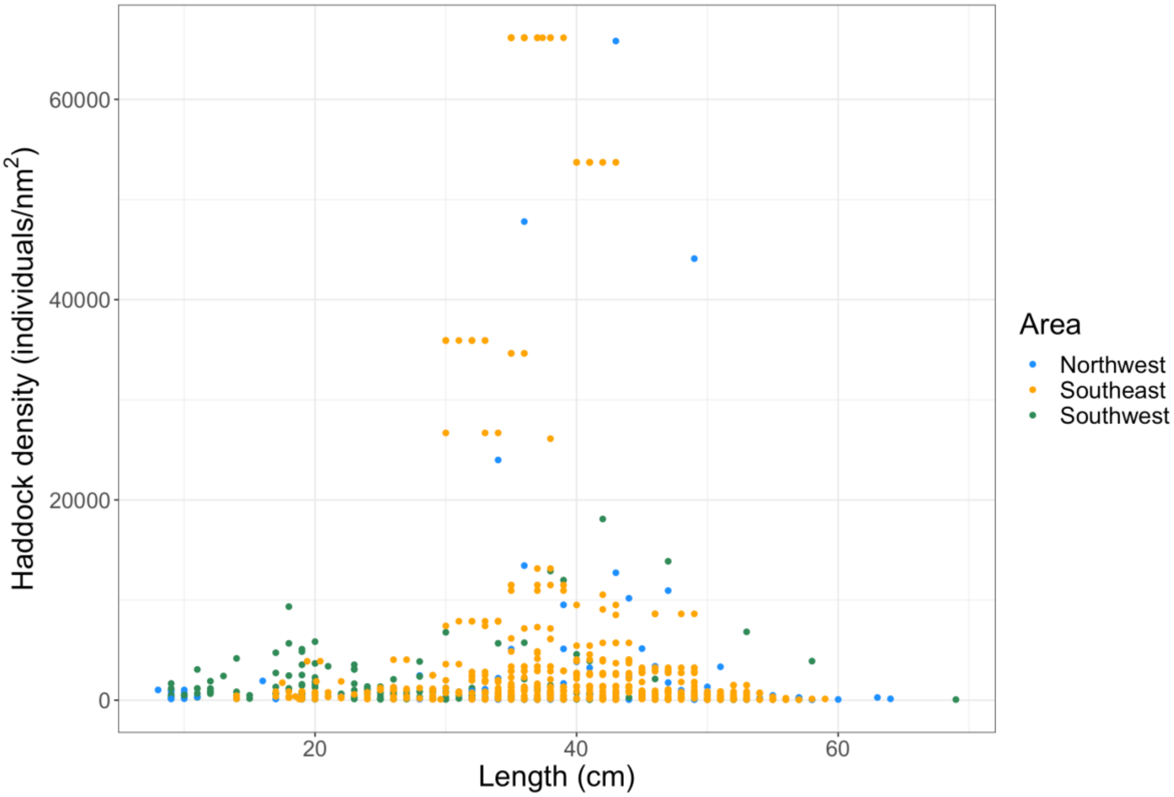
Appendix Table 2 – The four different vessels, sample stations and stomach samples from the 2009 ecosystem survey.

Vessel	Sampling stations	Haddock stomach sampled
RV. G.O. Sars	11	49
RV. Johan Hjort	36	224
RV. Helmer Hanssen	16	54
RV. Vilnius	50	621
Total	113	948

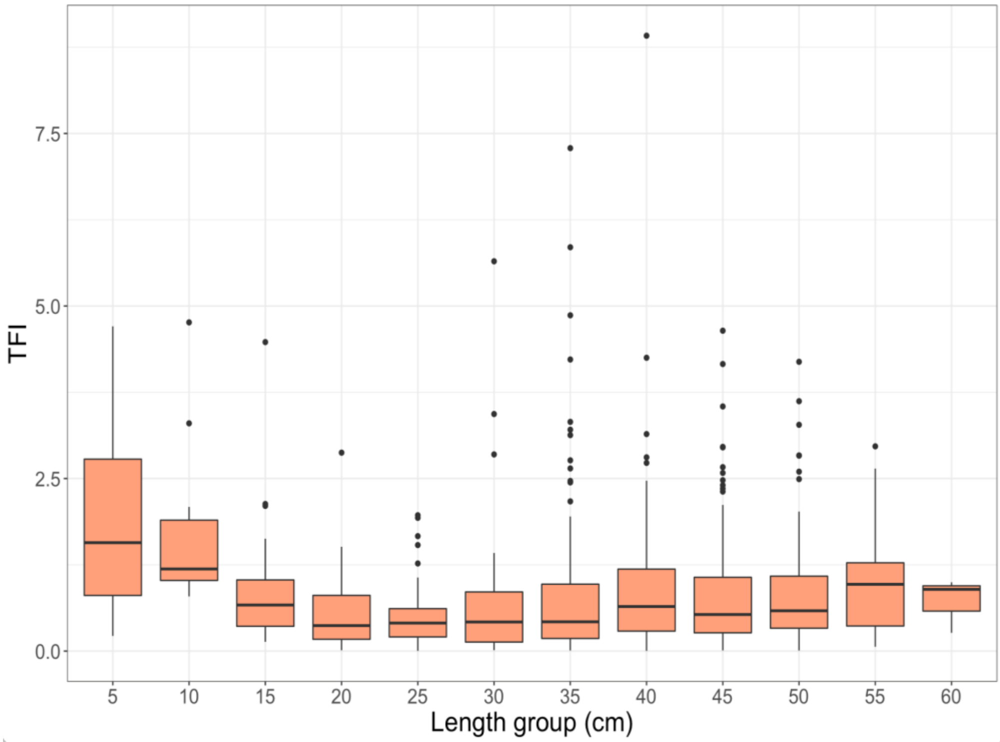
Appendix Figure 1 – A map of the Barents Sea showing all haddock stomach stations from the ecosystem survey 2009. The different colors show which stations Norway and Russia has sampled. The size of the circles corresponds to the main number of stomachs per length group. Almost all samples sampled by Norway has main length group 1.



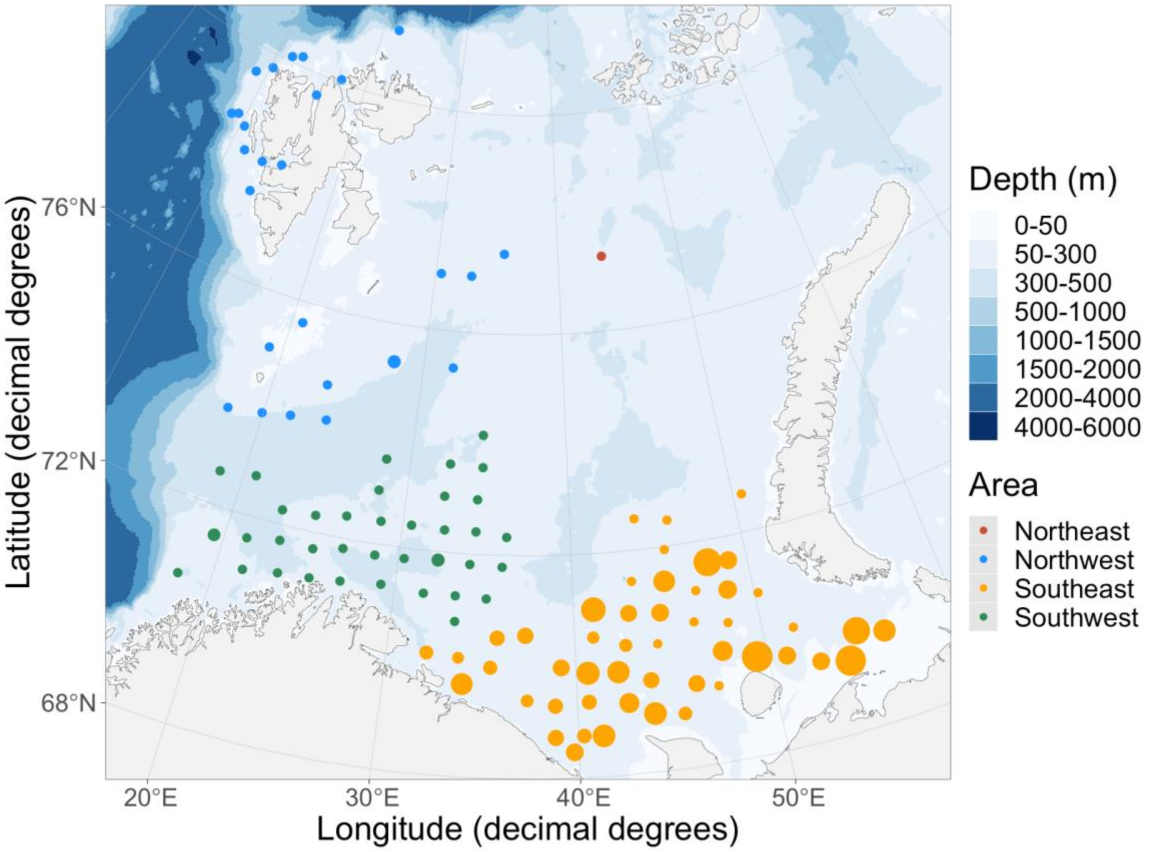
Appendix Figure 2 – The data from the 2009 ecosystem survey shows the distribution of haddock densities across different lengths for each area, indicating that the data is skewed.



Appendix Figure 3 – The level of total fullness index across all length groups, ecosystem survey 2009 data. The data is not log transformed.



Appendix Figure 4 – A map of the Barents Sea showing all haddock stomach stations from the ecosystem survey 2009. The different colors show the number of samples in each area. The size of the circles corresponds to the main number of stomachs per length group. Almost all samples sampled in northeast, northwest and southwest has main length group 1.



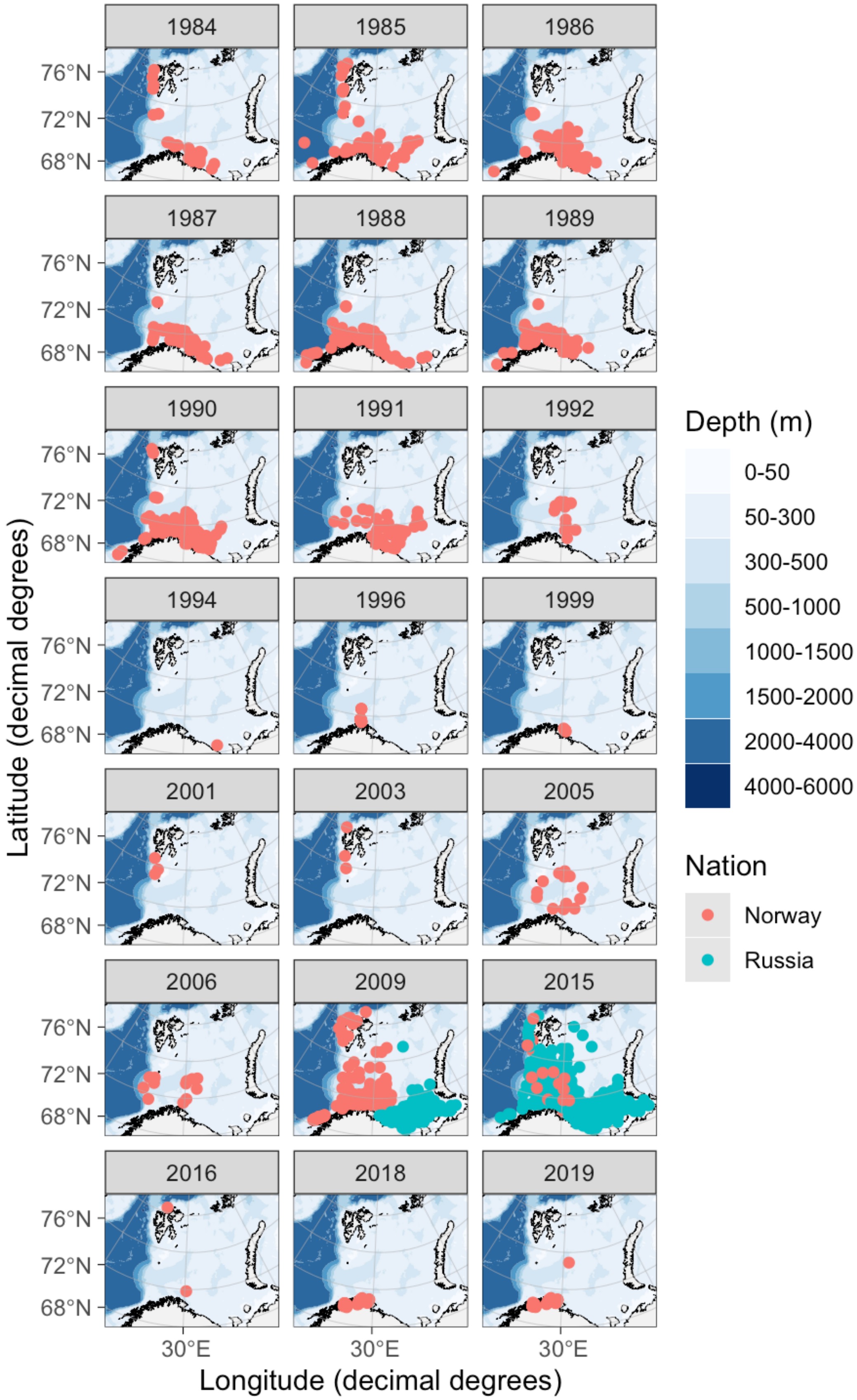
Appendix Table 3 – R packages used for the data plotting and statistical data analyses.

R Package	**Reference**
tidyverse	Wickham H, Averick M, Bryan J, Chang W, McGowan LD, François R, Grolemund G, Hayes A, Henry L, Hester J, Kuhn M, Pedersen TL, Miller E, Bache SM, Müller K, Ooms J, Robinson D, Seidel DP, Spinu V, Takahashi K, Vaughan D, Wilke C, Woo K, Yutani H (2019). "Welcome to the tidyverse." Journal of Open Source Software, 4(43), 1686.
ggplot2	Wickham, H. (2016). *Ggplot2: Elegant graphics for data analysis* (2nd ed.) [PDF]. Springer International Publishing.
ggOceanMaps	Vihtakari M (2022). _gg0ceanMaps: Plot Data on Oceanographic Maps using 'ggplot2'_. R package version 1.3.7, https://mikkovihtakari.github.io/gg0ceanMaps/.
ggspatial	Dewey Dunnington (2020). ggspatial: Spatial Data Framework for ggplot2. R package version 1.1.4. https://CRAN.R-project.org/package=ggspatial
gridExtra	Baptiste Auguie (2015). gridExtra: Miscellaneous Functions for "Grid" Graphics. R package version 2.0.0. http://CRAN.R-project.org/package=gridExtra
mgcv	Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. In *Journal of the Royal Statistical Society (B)* (Vol. 73, Issue 1, pp. 3–36).

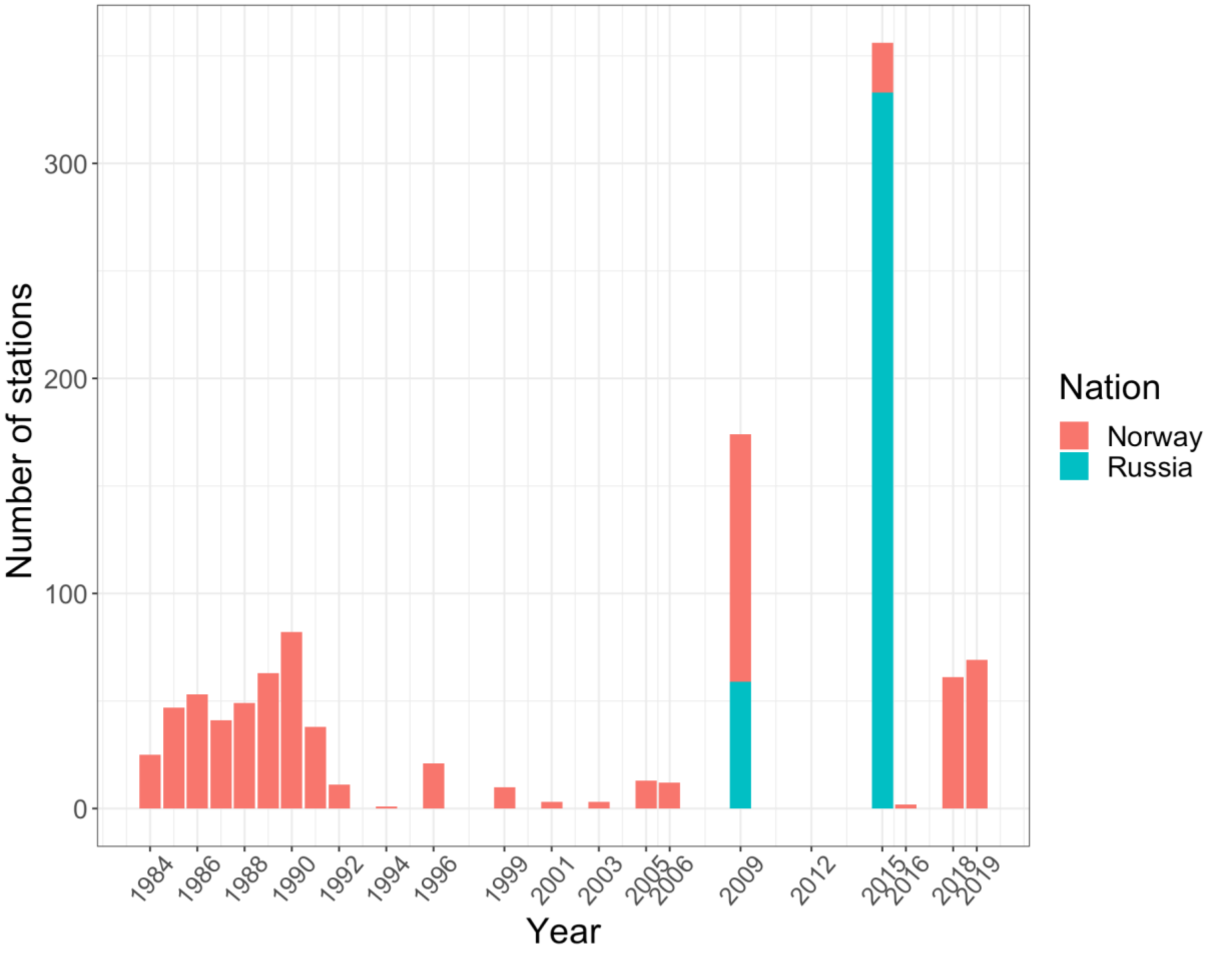
Appendix Table 4 – Number of haddock stomachs analyzed each month between 1984 and 2019.

Year/month	1	2	3	4	5	6	7	8	9	10	11	12	Total
1984					114	10			190	279			593
1985	132	282	30	84	265		18	45	129		215		1200
1986	226	368		26	51			53	138	361			1223
1987	62	541		67				69		260			999
1988	161	472	246	27					38	409			1353
1989	66	1023	45	302		60		34	200	59			1789
1990	34	1131	67	31	52		23		69	414			1821
1991		601	46						75	17			739
1992									110				110
1993													
1994						16							16
1995													
1996			373										373
1997													
1998													
1999								50					50
2000													
2001								21					21
2002													
2003								19					19
2004													
2005								65	28				93
2006								90	105				195
2007													
2008													
2009						118	89	240	1148	39			1634
2010													
2011													
2012													
2013													
2014													
2015		169	135	43	10	134		271	349	233	536	1387	3267
2016									11				11
2017													
2018										631	20		651
2019		2	399	275									676
Total													16833

Appendix Figure 5 – Maps of the Barents Sea showing all stations with haddock stomachs from 1984 to 2019. The colors represent which nation that have collected the samples.



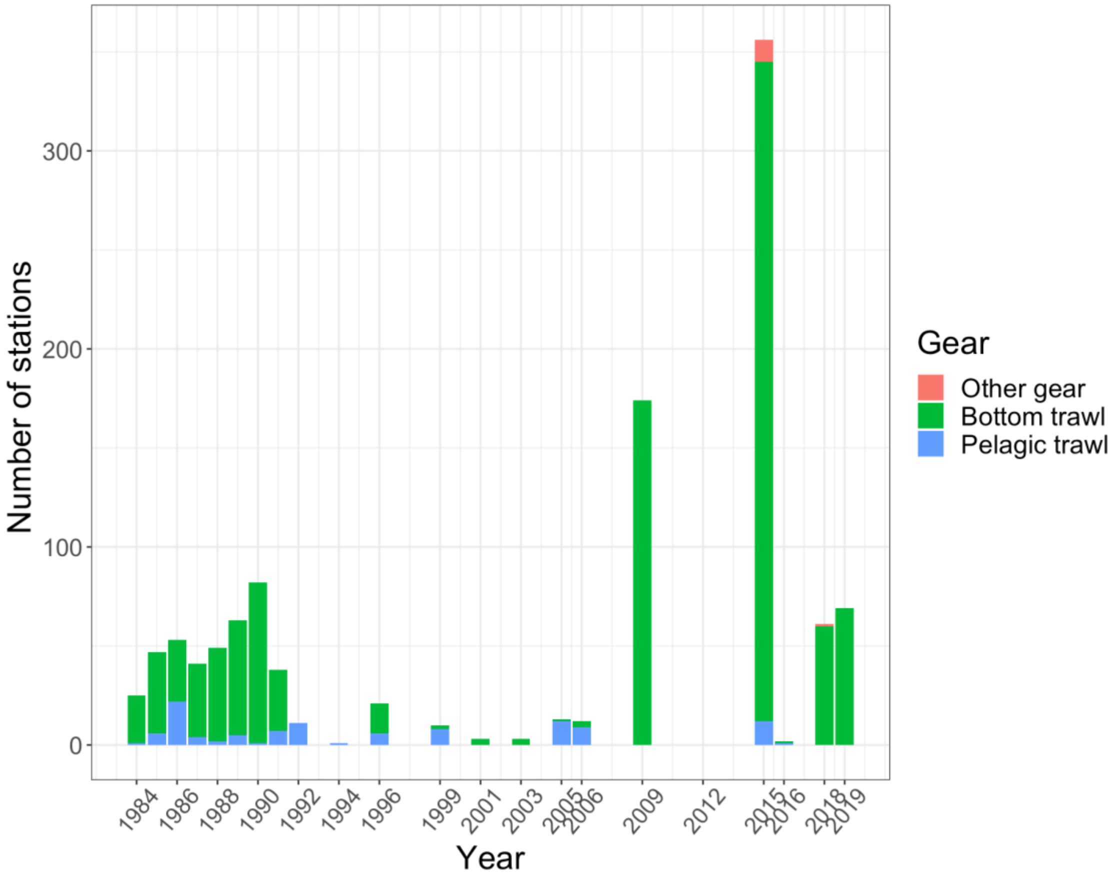
Appendix Figure 6 – Number of sampling station by year and nation (Norway = red and Russia = blue). Every station with haddock stomach samples per year between 1984 and 2019 is represented.



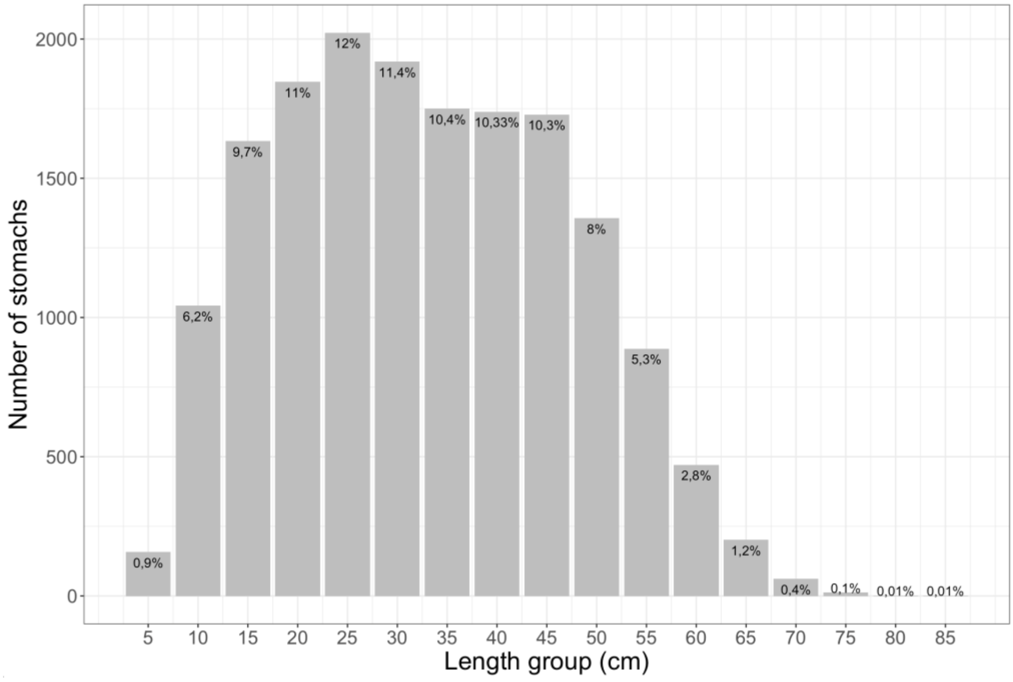
Appendix Table 5 – Number of sample stations each month between 1984 and 2019.

Year/month	1	2	3	4	5	6	7	8	9	10	11	12	Total
1984					9	1			6	9			25
1985	9	9	2	4	9		2	2	5		5		47
1986	8	23		1	2			2	5	12			53
1987	4	27		1				1		8			41
1988	7	20	7	1					2	12			49
1989	2	39	1	10		2		1	7	1			63
1990	1	57	1	2	3		2		3	13			82
1991		28	2						6	2			38
1992									11				11
1993													
1994						1							1
1995													
1996			21										21
1997													
1998													
1999								10					10
2000													
2001								3					3
2002													
2003								3					3
2004													
2005								8	5				13
2006								5	7				12
2007													
2008													
2009						18	20	35	97	4			174
2010													
2011													
2012													
2013													
2014													
2015		17	11	4	1	10		32	39	42	67	133	356
2016									2				2
2017													
2018										59	2		61
2019		1	40	28									69
Total													1134

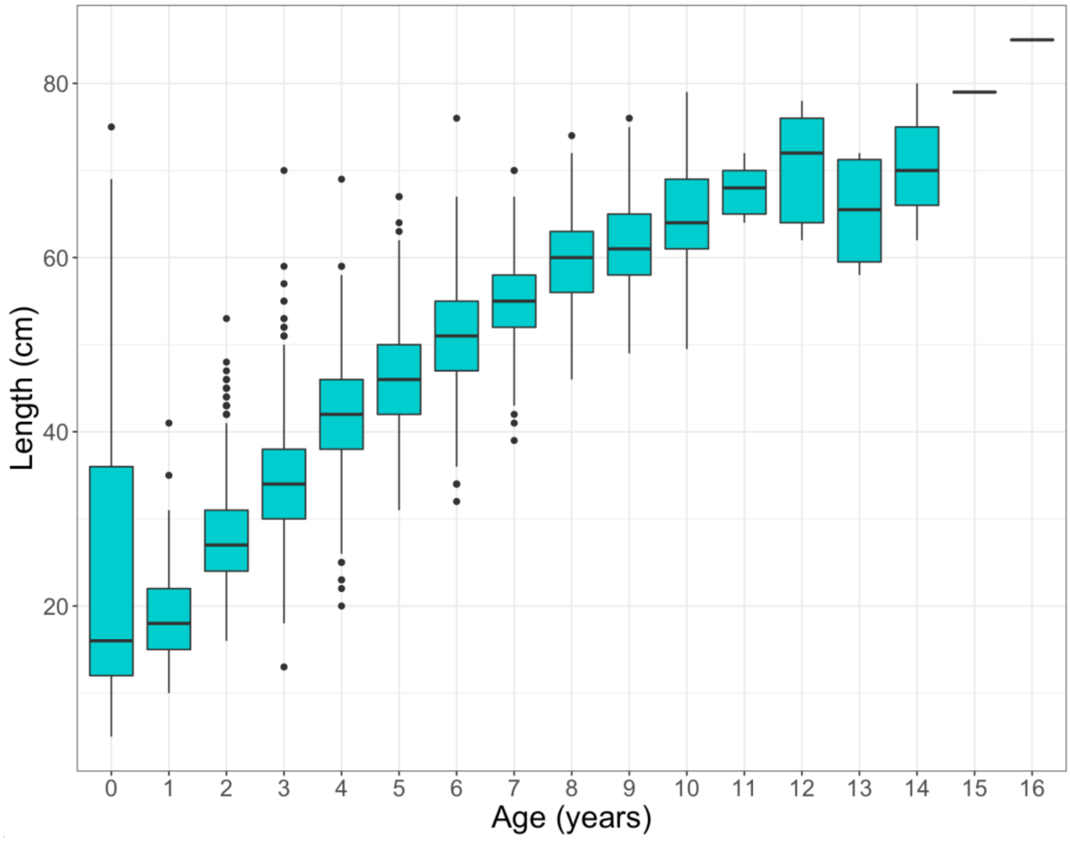
Appendix Figure 7 – Number of sampling station by year and gear used. Every haddock station per year between 1984 and 2019 are represented.



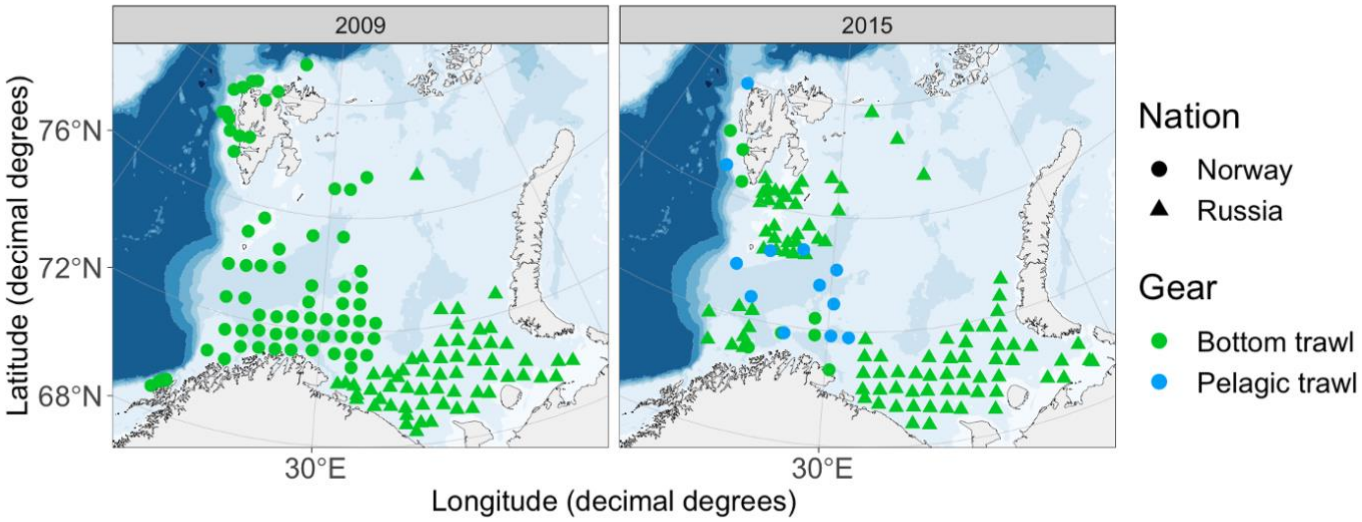
Appendix Figure 8 – Number and percentages of stomachs by 5 cm length group for all data 1984-2019.



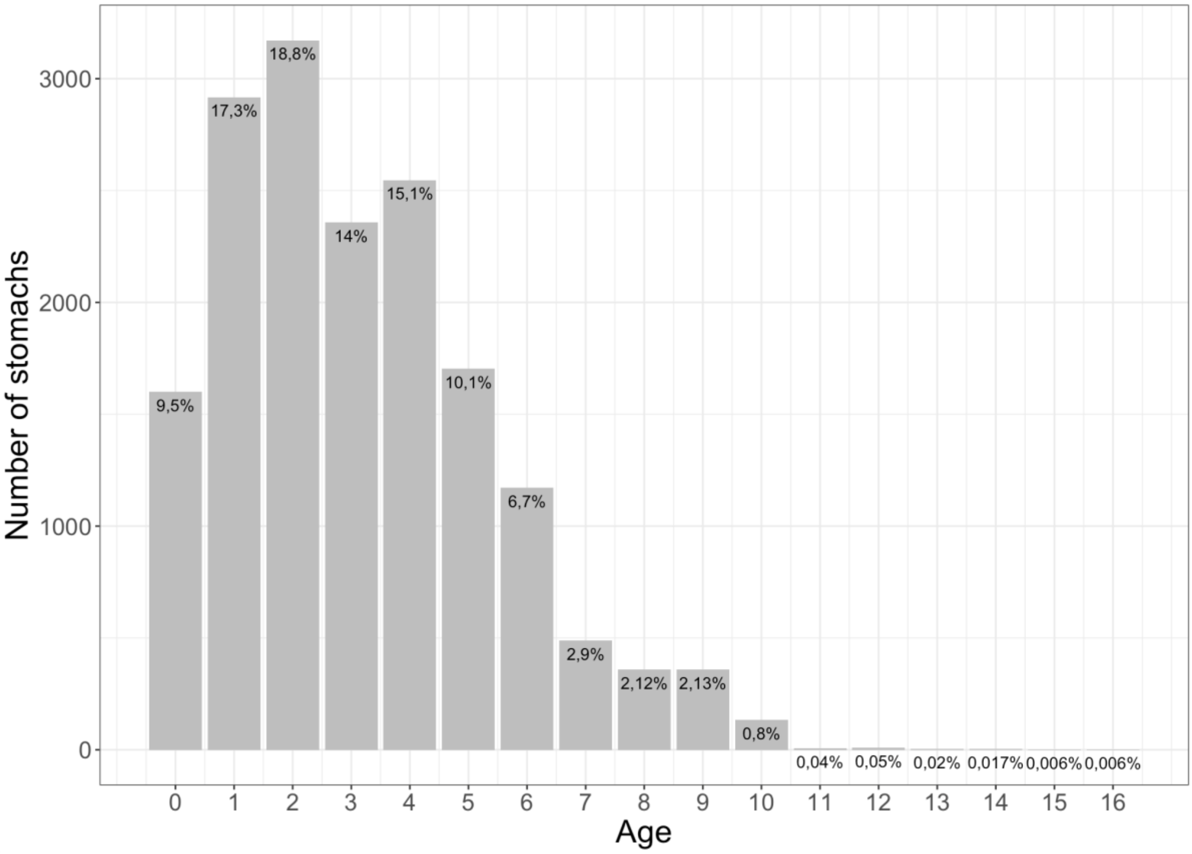
Appendix Figure 9 – The boxplot of age vs length for all data 1984-2019. Note that probably "0" as used for missing ages in the dataset.



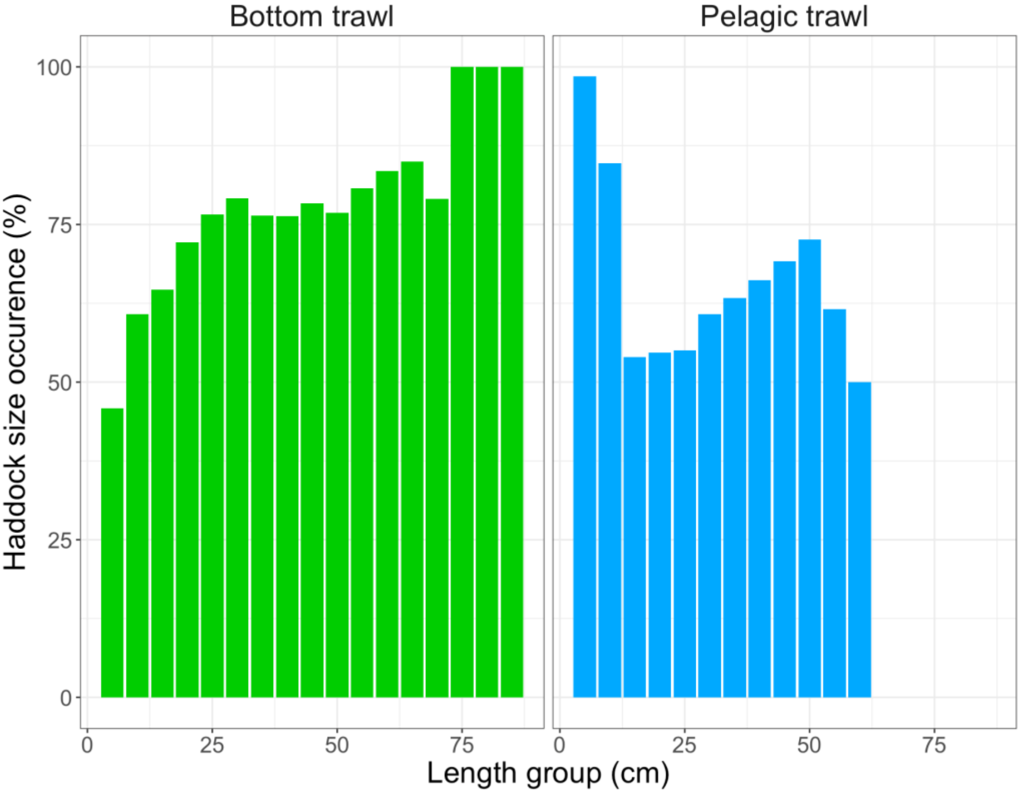
Appendix Figure 10 – Ecosystem survey stations from 2009 and 2015 with different shapes for nations and different colors for gears.



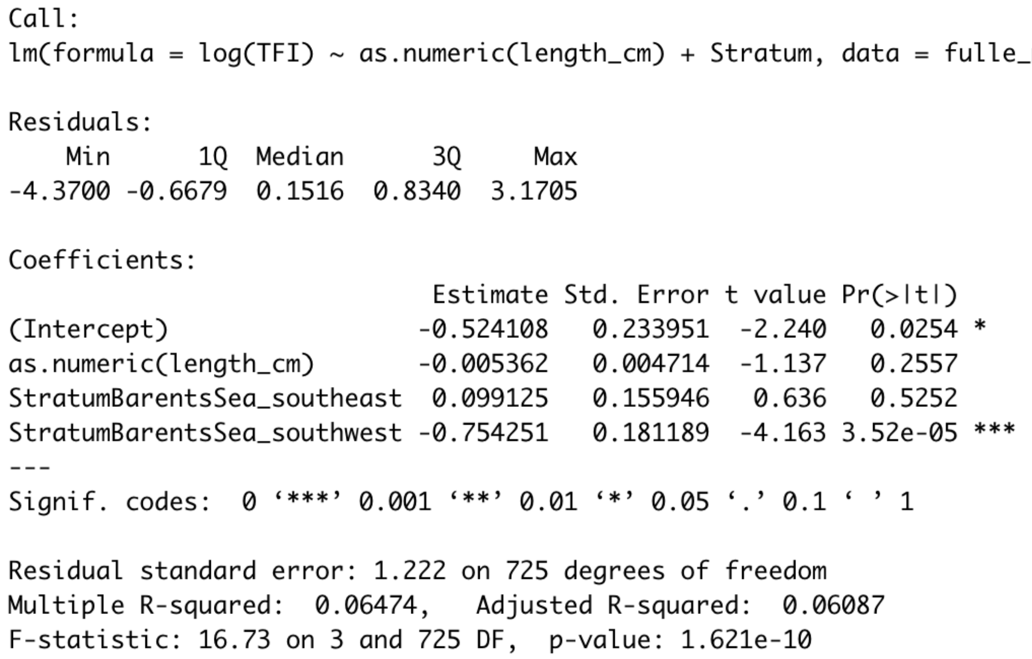
Appendix Figure 11 – Stomach samples by age group for all data 1984-2019.



Appendix Figure 12 – The percentage of haddock sizes collected by pelagic trawl and bottom trawl for all the data from 1984 to 2019.

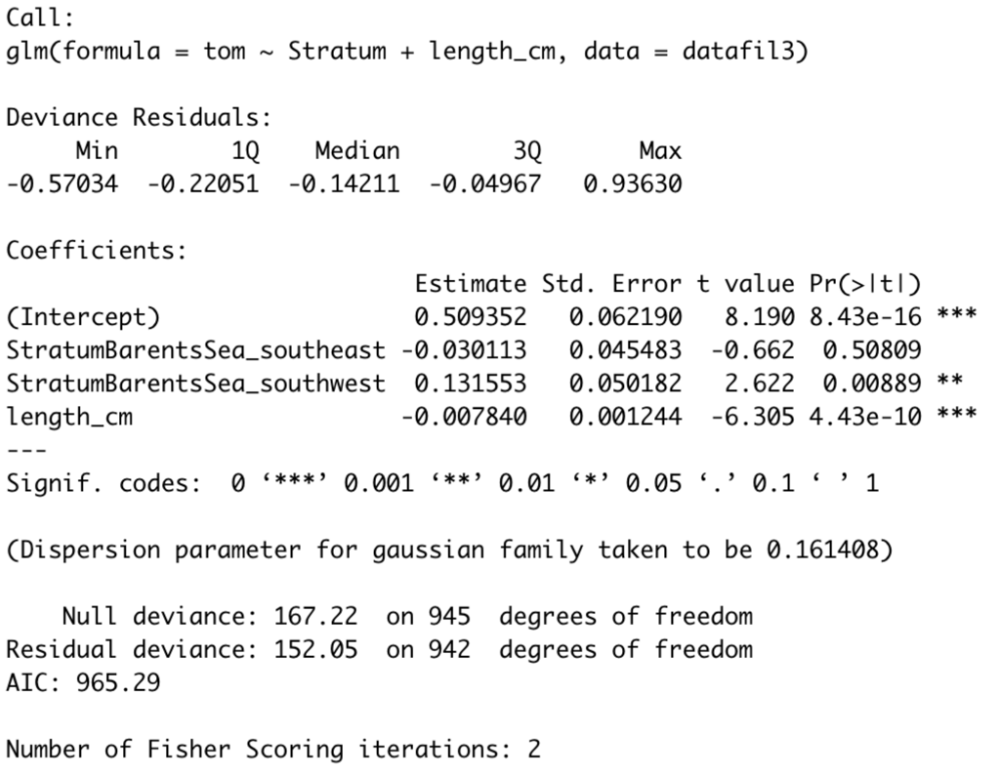


Appendix Table 6 – R-script and summary statistics for the linear regression on the response variable TFI (log transformed, non-empty stomachs). Some terms that I have used in the R-script: Stratum = Area and fulle_mager = non-empty stomachs.



```
Call:
lm(formula = log(TFI) ~ as.numeric(length_cm) + Stratum, data = fulle_mager)

Residuals:
    Min      1Q  Median      3Q     Max 
-4.3700 -0.6679  0.1516  0.8340  3.1705 

Coefficients:
                             Estimate Std. Error t value Pr(>|t|)    
(Intercept)                 -0.524108   0.233951  -2.240   0.0254 *  
as.numeric(length_cm)       -0.005362   0.004714  -1.137   0.2557    
StratumBarentsSea_southeast  0.099125   0.155946   0.636   0.5252    
StratumBarentsSea_southwest -0.754251   0.181189  -4.163 3.52e-05 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 1.222 on 725 degrees of freedom
Multiple R-squared:  0.06474,	Adjusted R-squared:  0.06087 
F-statistic: 16.73 on 3 and 725 DF,  p-value: 1.621e-10
```

Appendix Table 7 – R-script and summary statistics for the logistic regression on the response variable empty stomachs. Some terms that I have used in the R-script: Stratum = Area and tom = empty stomachs.

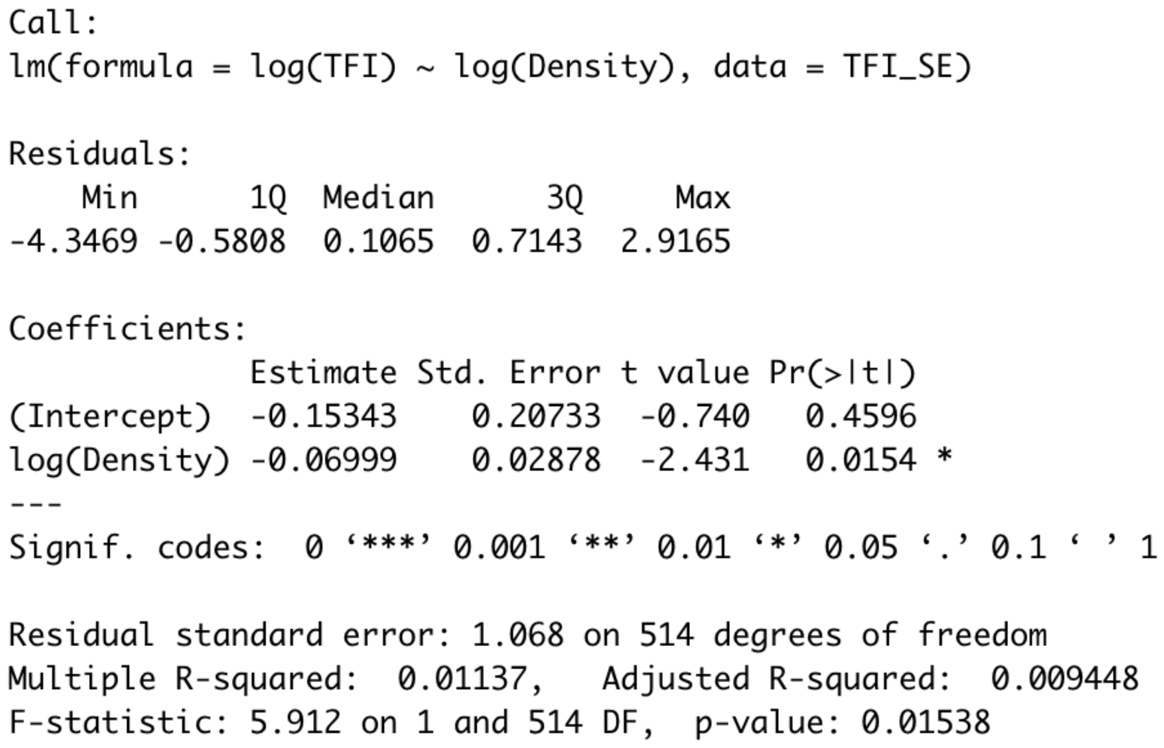


```
Call:
glm(formula = tom ~ Stratum + length_cm, data = datafil3)

Deviance Residuals: 
     Min        1Q    Median        3Q       Max  
-0.57034  -0.22051  -0.14211  -0.04967   0.93630  

Coefficients:
                             Estimate Std. Error t value Pr(>|t|)    
(Intercept)                  0.509352   0.062190   8.190 8.43e-16 ***
StratumBarentsSea_southeast -0.030113   0.045483  -0.662  0.50809    
StratumBarentsSea_southwest  0.131553   0.050182   2.622  0.00889 ** 
length_cm                   -0.007840   0.001244  -6.305 4.43e-10 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for gaussian family taken to be 0.161408)

    Null deviance: 167.22  on 945  degrees of freedom
Residual deviance: 152.05  on 942  degrees of freedom
AIC: 965.29

Number of Fisher Scoring iterations: 2
```

Appendix Table 8 – The effects of density on proportion empty stomachs done separately for each area. Haddock length is used as a co-variate in the analysis. Two sets of models were used for each area: one with density by station and length group (Density) and one by total density by station (Density Total). If there are three asterisks, the p-value is less than 0.001.

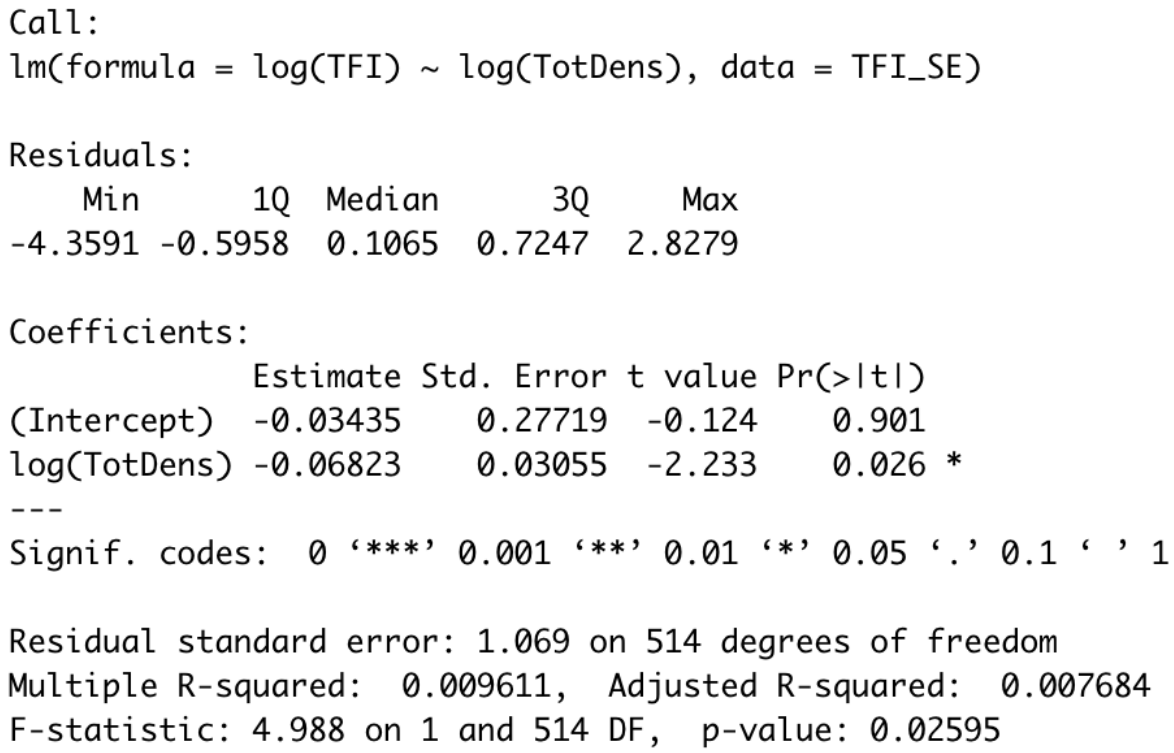
Area	Coefficients	Estimate	Std. error	P-value
Southeast	Length	-0.013	0.002	4.84e-15***
	Density (log)	-0.010	0.009	0.234
	Length	-0.013	0.002	3.91e-15***
	Density Total (log)	-0.012	0.009	0.188
Northwest	Length	-0.010	0.003	0.004
	Density (log)	-0.006	0.023	0.813
	Length	-0.009	0.003	0.006
	Density Total (log)	-0.014	0.021	0.517
Southwest	Length	-0.0009	0.003	0.743
	Density (log)	0.009	0.026	0.738
	Length	-0.0005	0.002	0.837
	Density Total (log)	-0.061	0.032	0.055

Appendix Table 9 – R-script and summary statistics of the effect of density on the response variable TFI (log transformed, non-empty stomachs) for southeast. One term that I have used in the R-script: TFI_SE = only southeast data.



```
Call:
lm(formula = log(TFI) ~ log(Density), data = TFI_SE)

Residuals:
    Min      1Q  Median      3Q     Max 
-4.3469 -0.5808  0.1065  0.7143  2.9165 

Coefficients:
             Estimate Std. Error t value Pr(>|t|)  
(Intercept)  -0.15343    0.20733  -0.740   0.4596  
log(Density) -0.06999    0.02878  -2.431   0.0154 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 1.068 on 514 degrees of freedom
Multiple R-squared:  0.01137,	Adjusted R-squared:  0.009448 
F-statistic: 5.912 on 1 and 514 DF,  p-value: 0.01538
```

Appendix Table 10 – R-script and summary statistics of the effect of total density on the response variable TFI (log transformed, non-empty stomachs) for southeast. One term that I have used in the R-script: TFI_SE = only southeast data.



```
Call:
lm(formula = log(TFI) ~ log(TotDens), data = TFI_SE)

Residuals:
    Min      1Q  Median      3Q     Max 
-4.3591 -0.5958  0.1065  0.7247  2.8279 

Coefficients:
             Estimate Std. Error t value Pr(>|t|)  
(Intercept)  -0.03435    0.27719  -0.124    0.901  
log(TotDens) -0.06823    0.03055  -2.233    0.026 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 1.069 on 514 degrees of freedom
Multiple R-squared:  0.009611,	Adjusted R-squared:  0.007684 
F-statistic: 4.988 on 1 and 514 DF,  p-value: 0.02595
```