



Juvenile mackerel (*Scomber scombrus*) along the Norwegian Coast:
distribution, condition and feeding ecology

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**Juvenile mackerel (*Scomber scombrus*) along the Norwegian Coast:
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Juvenile mackerel (*Scomber scombrus*) sampled during the Norwegian Spring Spawning
Herring post-larvae survey in 2018

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ABSTRACT

There has been a substantial increase in the stock size of North East Atlantic (NEA) mackerel (*Scomber scombrus*) during the last decade (2006-2016), coinciding with record high recruitment. This situation has resulted in a pronounced northward geographical expansion of mackerel in the North Atlantic, followed by an influx of juvenile mackerel into Norwegian waters. By using both scientific survey data and opportunistically submitted observations, this thesis aims at describing the geographic distribution and the weight-at-length of ~1-year old NEA mackerel in Norwegian waters during 2017 and 2018. The diet composition of juveniles was studied from the stomachs of sampled individuals from 2018 caught during the Norwegian Spring Spawning Herring (NSSH) post-larvae survey in June and the International Ecosystem Survey in the Nordic Seas (IESSNS) in July.

In 2017 and 2018 juvenile mackerel were caught between 56°N in the North Sea to the far north of the North Cape at 73°N, as well as in the Norwegian Sea. As far as we know, juvenile mackerel have never been observed this far north earlier in history. The juveniles were also present along the coast during all quarters of the year, from 58°N and northwards. The mean weight-at-length for juveniles from Norwegian waters was lower during winter and summer compared with the mean weight-at-length for juveniles from traditional nursery grounds in the North Sea. The individual length and the weight-at-length also varied with season and latitude along the Norwegian coast. Juveniles caught north of 63°N during winter were smaller and weighed significantly less than juveniles caught south in the study area, but had a significantly higher weight-at-length during the summer season than juveniles caught south of 63°N. These results suggest that individuals caught at more northern latitudes were able to consume enough prey to recover quickly during spring and summer, even though their condition during winter was lower than juveniles from the southern latitudes along the Norwegian coast.

Totally 78% of the 146 individuals sampled for dietary analysis had prey items in their stomachs (fullness degree 2-5), which confirmed that the juvenile mackerel were feeding during the summer season in Norwegian waters. Based upon the dietary analysis from individuals caught in June and July, the juvenile mackerel preyed on a wide number of prey groups and seemed to utilize both passive particulate feeding and active feeding to increase the intake of prey and be opportunistic when selecting prey. Appendicularians were the most abundant prey group, accounting for 31% of the dry stomach content weight. The copepod *Calanus finmarchicus* was found in approximately 1/3 of all stomachs but accounted only for 1.2% of the total dry weight. Although this was a low number considering *C. finmarchicus* is a preferred prey for juveniles in the nursery area, it was not unexpected as the density peak of *C. finmarchicus* likely was over at the time of sampling.

The findings in this thesis suggest that juvenile mackerel caught along the coast originated from spawnings in the southern parts of the Norwegian Sea, along the Norwegian coast, and north of 63°N. The opportunistic prey selection indicates that the juveniles feed on most types of available prey in the water column and are thus a potential competitor with other pelagic fish species that prey upon zooplankton, especially in coastal waters.

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1. INTRODUCTION

Fluctuations in the abundance and distribution of fish populations are natural processes regulated by internal and external factors over time (Mann and Lazier, 2006). The increase and decrease in the size of a population are direct effects of recruitment and mortality which are affected by numerous variables, including environmental variability, predation, resource availability and the competition for food within a habitat (Taylor and Taylor, 1977; Sinclair and Pech, 1996). Individuals in a growing population, which is approaching and exceeding the carrying capacity of the habitat, may thus be negatively affected by the reduction in available resources and by the declining quality of the habitat. This can force individuals within the population to migrate from the preferred habitat to less optimal areas with reduced suitability (MacCall, 1990), which in turn expands the spatial distribution of the population. However, a population cannot expand indefinitely. The outer limits for the possible area of distribution is often set by the temperature as all species have upper and lower physiological limits for thermal tolerance (Cossins and Bowler, 1987). The effects of declining availability of resources and the environmental constraints in the sea could thus affect the distribution of individuals in a growing population of a marine fish species that are dependent on patchily distributed and seasonally available planktonic blooms.

The North East Atlantic mackerel (*Scomber scombrus*) is an example of a fish species that feed on patchy and seasonally available resources and which population has expanded its distributional range in recent years (Nøttestad *et al.*, 2016a; Olafsdottir *et al.*, 2019). It is a temperate, pelagic, schooling species with an extensive migration between the feeding, overwintering and spawning areas (Nøttestad *et al.*, 1999; Iversen, 2002; Iversen, 2004; Trenkel *et al.*, 2014). During summer the Norwegian Sea and adjacent waters serve as the main feeding grounds. Here, the mackerel are predators on zooplankton and juvenile fish, competitors with other pelagic species, and prey for larger species (Iversen, 2004; Langøy *et al.*, 2012; Nøttestad *et al.*, 2016b; Bachiller *et al.*, 2018). As the summer season ends, the mackerel migrate to and aggregate in the North Sea (Reid *et al.*, 1997; Iversen, 2004) and west of the British Isles (ICES, 2018), before the different stock components migrate to the spawning grounds during winter along the European coastal shelf. The NEA mackerel stock is considered to consist of three spawning units which spawn successively beginning in the southern waters of Portugal and the Mediterranean Sea in late winter and early spring, whereas ending in the North Sea towards Skagerrak in early summer (Iversen, 2002; Iversen, 2004; Trenkel *et al.*, 2014; ICES, 2016). The temporal variation in spawning occurrence relates to the spatial distribution of the fish as the lower latitudinal stock component initiate spawning in late February, and as spring progresses, the spawning locations gradually shift northward with the spawning by the higher latitudinal stock units (Trenkel *et al.*, 2014; ICES, 2016; Brunel *et al.*, 2018).

In the most recent 10-15 years, the NEA mackerel stock has had a period of strong recruitment with 2002, 2006, 2010, 2011 and 2014 being notably favorable years (ICES, 2017). There are also indications that both the 2016- and the 2017-year classes are strong (Jansen, 2019). As a result, the spawning stock biomass (SSB), meaning the total biomass of all individuals capable of reproducing, has increased substantially. During this period, the population of NEA mackerel has also expanded its distribution in a northern and westward direction (Nøttestad *et al.*, 2016a). It is hypothesized that the expansion of the distribution area is caused by multiple factors, including the increase in SSB, increased resource competition between individuals, a change in the abundance and distribution of prey species, and a decline in the concentration of nutrients which limits the primary and secondary production in the feeding grounds (Utne *et al.*, 2012; Nøttestad *et al.*, 2016a; Pacariz *et al.*, 2016; Olafsdottir *et al.*, 2019). The mean size and weight of the adult mackerel during this period has also decreased (Olafsdottir *et al.*, 2016). The reduction in individual size has been hypothesised to be correlated with higher densities of mackerel, and is thus a likely result of increased competition with conspecifics and exploitative competition with other planktivorous species like herring (*Clupea harengus*) at the feeding grounds during summer (Olafsdottir *et al.*, 2016).

In addition to an expansion of the distribution, the primary spawning sites of the NEA mackerel are observed to have shifted in a poleward direction over the last 40 years (Reid, 2001; Hughes *et al.*, 2014; ICES, 2016). During these years the spawning activity west of the British Isles have been observed to decline in the south and increase in the north (Beare and Reid, 2002). ICES (2011) and Hughes *et al.* (2014) suggested that the change in spawning distribution was related to the increase in Sea Surface Temperature (SST). Within the last decade the spawning areas have reached the southwestern regions of the Norwegian Sea (Hughes *et al.*, 2014; ICES, 2016). There have also been an increasing number of sightings of fecund females along the Norwegian coast by both scientists and fishermen, indicating that the spawning adult mackerel are not vagrants in Norwegian waters, but distributed further north than they have been in the past (Peña *et al.*, 2012; Nøttestad *et al.*, 2018).

The increase in SSB, the expansion of the adult distribution, and the northward shift in spawning sites could alter the spatial distribution of immature mackerel (Nøttestad *et al.*, 2018). Spawning mackerel releases the small, buoyant eggs in the surface layers (Iversen, 2004). As the eggs hatch, the surface currents transport the larvae towards the nursery areas, where they grow and remain until they attain a reproductive age as 2- and 3- year olds (Uriarte *et al.*, 2001; Iversen, 2004). Juvenile mackerel become morphologically similar to the adult mackerel at an early age, and they have a high feeding intensity, a high growth rate, and a well-developed digestive system (Jansen, 2016). The core of the historical nursing grounds have been located from the Bay of Biscay in the south into the North Sea in the north, with the most important juvenile nursery areas in the present time distributed along the shelf around Ireland and Scotland, and in the North Sea (Jansen *et al.*, 2015).

Since 2010, 0- and 1-group mackerel have regularly been observed in Icelandic waters, a distribution of juvenile mackerel which is far west of the common nursery grounds (Astthorsson *et al.*, 2012). In this study, it was suggested that the shift in juvenile distribution was collectively influenced by the increasing SST, a lower plankton abundance in the Norwegian Sea, and better feeding conditions in Icelandic waters. Since 2012, 1-group juvenile mackerel have been observed in the Norwegian Sea during summer (Peña *et al.*, 2012), and within the past 5 years there has also been an increase in observations of 0-, 1-, and 2-group juvenile mackerel in the Norwegian Sea and along the entire Norwegian coast, from the far south at 58°N to the coast of Finnmark at 70°N (Nøttestad *et al.*, 2018). Since 2016, the Norwegian Institute of Marine Research (IMR) have caught juvenile mackerel more regularly, in increasing densities and at more northern latitudes for each year (Nøttestad *et al.*, 2018). Little is, however, known about the seasonal distribution of the mackerel juveniles in Norwegian waters and how far north along the coast their distribution has expanded the last few years.

How a more northern distribution affects the overall condition of the juveniles is not known. The fitness of the juvenile mackerel in Norwegian waters, compared with the juveniles from the common nursery grounds should depend on several factors. One important factor is the juveniles' ability to tolerate the variability in temperatures during winter and summer. Adult mackerel prefer temperatures between 8.0°C - 13.0°C, although they tolerate temperatures below this (Utne *et al.*, 2012; Olafsdottir *et al.*, 2019). It is thus probable that the optimal temperature for juvenile mackerel lies between these values. Survival also depends on their ability to survive predator attacks, both as larvae and metamorphosed juveniles. In addition, the juveniles need to locate suitable prey of the right size and energy density frequently enough to survive and grow.

At the first feeding stage, the mackerel larvae primarily feed on phytoplankton, copepod eggs and nauplii until they are big enough to feed on larger zooplankton (Conway *et al.*, 1999). During the post-larvae stage adult copepods, cladocerans and fish larvae become the main source of prey in the traditional nursery areas (Conway *et al.*, 1999). According to Trenkel *et al.* (2014) the feeding behaviour of the juveniles, as well as the diet, vary with time of day, size of the individual, and with geographical location. Their diet and feeding behaviour is also affected by the seasonal availability of zooplankton, as the zooplankton abundance in temporal waters follow the spring bloom of phytoplankton (Melle *et al.*, 2004), which also mean that the fitness of juveniles is likely to vary with season (Wilhelms, 2013). Depending on the prey type, the juveniles in the nursery areas are either selective particulate feeders or filter feeders, using the gill rakes to sieve potential prey items from the water (Trenkel *et al.*, 2014). The condition, diet, selectivity, and feeding behavior of juveniles in Norwegian waters has still not been studied. Ecologically, juvenile mackerel are potential competitors with other planktivorous pelagic species, as the 1-group, as well as the metamorphosed 0-group, are active predators on larger zooplankton and fish larvae in the traditional nursery areas (Conway *et al.*, 1999). That

could indicate that the influx of mackerel juveniles into Norwegian waters could have directly and indirectly regulatory effects on other fish populations if the juveniles feed on fish larvae and compete for the same sources of nutrients as other planktivore fish species. The increased presence of juvenile mackerel along the coast have raised concerns amongst fishermen regarding the possible consequences for the ecosystem and the commercially important stocks. This is because the effects of juveniles as competitors and predators on fish larvae could have a ripple effect on the abundance of other harvested species, and hence have an impact on the livelihood of coastal residents.

Due to their relatively short period as inhabitants in Norwegian waters little is known about the life of the juvenile mackerel that reside along the Norwegian coast. Their distribution, their diet, and general condition has until now not been studied. The main objective of this thesis was, therefore, to study and discuss the fundamental biological and ecological aspects concerning the life of 1-year old mackerel caught in Norwegian waters. The northwards shift in the distribution of juvenile mackerel is potentially the result of a change in the distribution of spawning adult individuals. If juveniles survive and thrive in Norwegian waters, a more northern distribution of juvenile mackerel might also have implications for the distribution of adult mackerel in the future. It is, therefore, important to increase the knowledge regarding the relative condition, the feeding preferences, and the ecological effects of the juveniles along the Norwegian coast.

During this study the distribution of one-year-old juvenile mackerel in Norwegian waters during 2017 and 2018 was mapped. The concerns of the industry and coastal residents regarding adequate data coverage of juvenile distribution throughout the year was met with opportunistic observations submitted on juvenile mackerel. Hence, both survey data from IMR and research independent data reported in have been used in order to study the temporal and spatial distribution of the juvenile mackerel. In addition to mapping the distribution, the weight-at-length for the registered juveniles was used to assess the relative condition of the 1-year-old mackerel during winter and summer compared to juveniles from more southern nursery areas. The assessment of the stomach fullness and diet analysis were conducted on sampled individuals from two research surveys in 2018 to study the diet and feeding preferences of the juveniles along the coast during summer. The results from this thesis concerning the distribution, reported observations, weight-at-length, and dietary preferences have been used to discuss the ecological role of the juveniles in Norwegian waters, and the possible effects of their presence on the coastal ecosystem.

2. MATERIALS AND METHODS

2.1 AVAILABLE DATA ON JUVENILE MACKEREL FROM NORWEGIAN WATERS

In this master thesis, three main sets of data have been used to examine juvenile mackerel distribution and diet. The first set consisted of data on juvenile mackerel sampled by the Institute of Marine research (IMR) in Norway and the Norwegian Coastal and High-seas Reference Fleet from 2017 and 2018. Juvenile mackerel are neither commercially targeted or the main focus of any specific research cruise. All the sampled one-group mackerel in 2017 and 2018 were, thus, caught as bycatch by various trawls used by the Reference Fleet and by IMR. The data on the juvenile mackerel included measurements of length and weight of individuals, geographical positions, date and time of capture. The dataset was a combination of data on aged and non-aged individuals. A large number of individuals had not been age determined, so the length distribution of the aged individuals was used to set a maximum length for individuals of age one for the winter (Q1) and summer (Q3) quartiles. The mackerel individuals in this study were determined to be one year of age if the length was equal to or less than the maximum length, set by the overlap in age distribution between one- and two-year old individuals, and if the juveniles were caught after January 1st, even if they most likely were spawned during summer and would be younger than 12 months of age. The scrutinized data was used to map the distribution of the sampled juveniles from 2017 and 2018, for each quartile, and to estimate the condition of the juveniles during winter and summer.

A smaller data set of submitted observations of juvenile mackerel by recreational fishermen and other members of the public was sampled with the use of an online registration form, customized specifically for this thesis. The form was made available through the IMR-home page (www.hi.no) (Appendix A). The purpose of sampling opportunistic observations of juvenile mackerel was to increase the number of observations of juvenile mackerel, and increase the spatial and temporal data coverage along the coast in areas and time periods without IMR surveys. The data retrieved from the submitted observations was used to map the distribution of mackerel juveniles along the coast and to examine how the juvenile mackerel was observed in these areas.

The third data set was collected with the purpose of increasing the number of observations of juvenile mackerel, assessing the stomach fullness, and to analyze the stomach content of 1-year-old mackerel caught in Norwegian waters. Individuals were caught during the Norwegian Spring Spawning Herring (NSSH) post-larvae cruise from June 5th to the 25th in 2018 and the International Ecosystem Summer Survey in the Nordic Seas (IESSNS)-survey from 4th of July to 6th of August in 2018. Individuals sampled during these two cruises for stomach content analysis were regarded as one year of age if body length was equal to, or less than, 25 cm. The juveniles were sampled with the Multpelt 832 pelagic trawl (ICES, 2013; Nøttestad *et al.*,

2016a) towed in the surface with a vertical opening of 30-35 m. During these two cruises juveniles were caught at trawl stations between 60°N and 70°N and as far west as 1.4°E (Figure 1). To minimize the digestion of stomach content after capture, the individuals were immediately frozen at sea as whole individuals and later stored in freezing facilities at the Institute of Marine Research (IMR) until biological sampling and the diet analyses of the individuals started in October 2018.

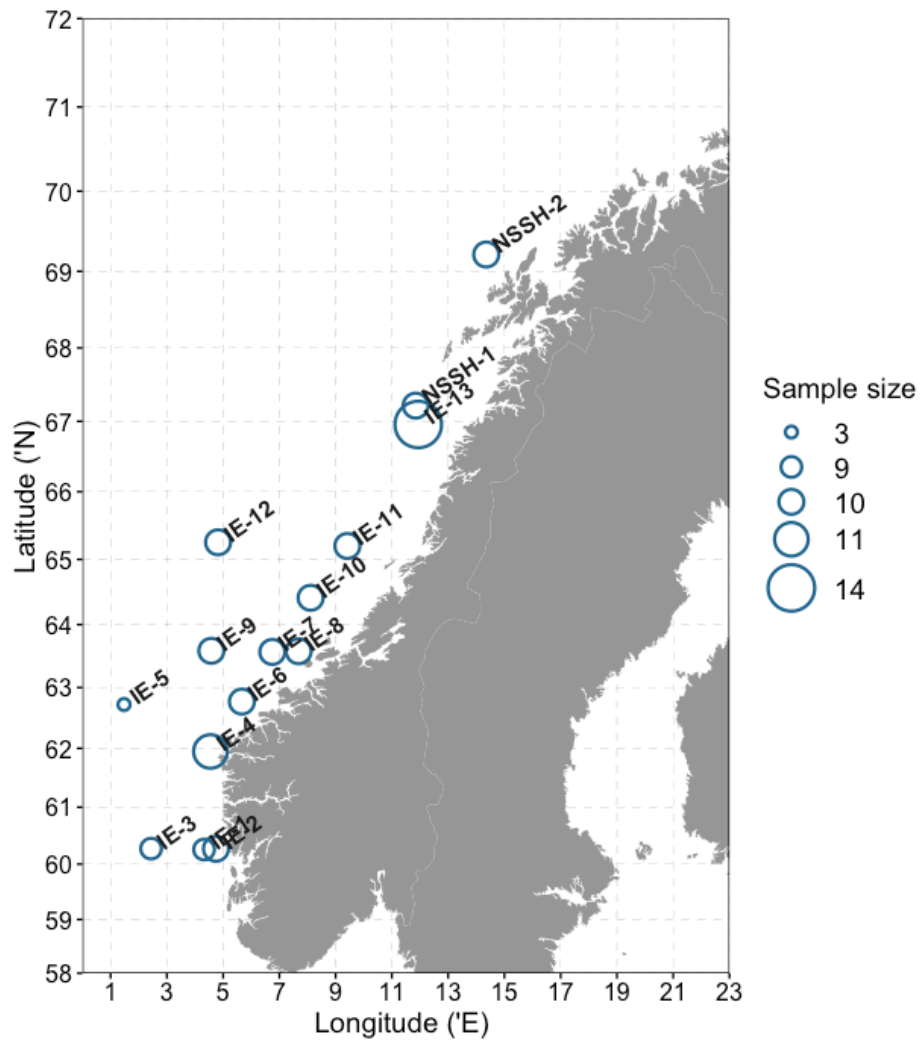


Figure 1: Trawl stations from the IESSNS survey and the NSSH post-larvae survey at which juvenile mackerel of lengths equal to or less than 25 cm were sampled for diet analysis. Station name was given based on the name of the survey and the latitude of station. IE-1-13 stations were from the IESSNS-survey, while NSSH-stations 1-2 were from the NSSH post-larvae survey.

2.1.1 AGE-AT-LENGTH DETERMINATION

The dataset on juvenile mackerel from the IMR-database used in this thesis consisted of a mix of aged and non-aged individuals caught during all four quartiles during 2017 and 2018. It was necessary to age determine the non-aged individuals to reduce the possibility of including two-year-old individuals in the dataset since mackerel mature between the age of two and three years old (Iversen, 2004). The length of aged individuals was therefore used to estimate the length distribution and the maximum length of one-year-old individuals. This was done by plotting the length frequency distribution of the aged one- and two-year old individuals, and visually identifying the overlap in size frequencies between the two age groups. The length of one-year old individuals was expected to increase during the year since juvenile mackerel grow during the feeding season in spring and summer. The increase in the maximum length over time for the one-year-olds was accounted for by plotting the size distribution of aged one- and two-year-old juveniles caught during winter and summer separately. The length frequency distributions of the aged one-year-old individuals were additionally used to determine the size of one-year-old individuals at northern ($>63^{\circ}\text{N}$) and southern (58°N - 63°N) latitudes in Norwegian waters and the North Sea during winter and summer. The non-aged juveniles in the dataset were, thus, determined to be one year of age based on the body length at capture, the season of capture, and the latitude at which they were caught at.

2.1.2 MAPPING OF JUVENILES FROM 2017 AND 2018 REGISTERED IN THE IMR-DATABASE

The available data on all juvenile mackerel were separated by year and by quartile. Geographic positions were used to plot the distribution of all registered individuals from Norwegian waters and the North Sea registered in the IMR database. The quartile observations (January-March, April-June, July-September, October-December) were used as a baseline for studying the distribution of the juvenile mackerel throughout 2017 and 2018, as well as discussing the possible seasonal distribution of juveniles along the coast in areas and periods without any registrations.

2.1.3 RESEARCH INDEPENDENT OBSERVATIONS FROM 2017 AND 2018

Observations of juvenile mackerel by the general public was reported in via an electronic form made available at the IMR website on December 12th, 2018. The form consisted of nine questions regarding where, when and how the juvenile mackerel was observed, the number of individuals and approximations of the sizes observed and whether the observer have graphical documentation of the observation (Appendix A). The submitted geographical information was

used to plot all the observations on a map. The positioning of the observations was most often “guesstimates” as all of the people who registered observations used local names of areas and/or bodies of water. All locations were, therefore, identified with the use of the search function in Google Maps (<https://www.google.com/maps>) and plottable coordinates were found by clicking the interactive map in the given area. People who submitted forms with a YES regarding documentation of the sighting were contacted by email with an optional request of sending the documentation. The data collected from these forms was neither included in any analysis or grouped with any of the data collected systematically during research surveys due to the uncertainties regarding the age and sizes of the observed juveniles and inconsistencies between the different submissions regarding the included data. The reported sightings could, for instance, include older mackerel (> 1 year) as several of the observations regarding length only were approximates, only mention year but not month, report accurate date and time but report in sightings of hundreds of tons of juvenile mackerel in a fjord and so on.

2.2 WEIGHT-AT-LENGTH FOR THE JUVENILE MACKEREL

2.2.1 CALCULATING THE INDIVIDUAL VARIATION BETWEEN THE WEIGHT-AT-LENGTH FOR NORWEGIAN JUVENILES AND THE ESTIMATED MEAN WEIGHT-AT-LENGTH FOR NORTH SEA JUVENILES

Many fish species, including the Northeast Atlantic mackerel (*Scomber scombrus*), grow isometrically. This means that throughout the life of an individual, all parts of the body grow at an approximately equal rate. The isometric growth makes it possible to predict the body weight of an individual after it has metamorphosed and become similar to an adult individual in the morphological traits. The expected weight-at-length can be derived by the use of the weight/length-relationship (WLR), and the estimated weight-at-length can be calculated with the use of the following equation (1);

$$(1) W = a \times L^b \text{ (Keys, 1928)}$$

where W is predicted body weight in grams, L is total length in centimeters, a is a species and population specific coefficient related to body shape and condition if $b \sim 3$, and b is a species and population specific exponent expressing the rate of weight change with length. The a - and b -coefficients for a specific species or a population are derived by plotting the \log_e of length L against the \log_e of the weight W for all sampled individuals from the specific population (Keys, 1928; Jennings *et al.*, 2013). The a -coefficient is the intercept from the logarithmic plot, while the b -coefficient is the slope. Equation (1) estimates the mean weight-at-length for individuals from a species, or a population, based upon individual body length.

The measured weights of individuals from a sample can be compared with the estimated mean weight-at-length derived from equation (1) for the same length frequencies. By doing so, it is possible to study the relative condition of individuals by assessing whether the sampled individuals weigh more or less than the estimated mean for the population the individuals are sampled from. It is also possible to compare the observed weight-at-length of individuals from another population with the estimated mean weight-at-length, to study whether there are significant differences in the weight-at-length between the two populations.

The a- and b-coefficients are derived from data on the species or population of interest, but can also become more specific by being derived from data on individuals caught during particular seasons or months. Hence, it is possible to estimate the mean weight of individuals from a specific population during a specific season during the year. This is useful when the species of interest is distributed at temporal latitudes and feed on seasonally available organisms because the fluctuations in the body weight during the year is likely to be correlated with the availability of food resources. This also means that the estimated mean weight-at-length can take the seasonal variability in food abundance into account since the mean weights of individuals of the same lengths from the same population, caught during different seasons, are not necessarily expected to be the same.

The relative condition of juvenile mackerel sampled by IMR was assessed by comparing the observed weights-at-length with the estimated mean weight-at-length for juveniles from the North Sea. Quartile specific a- and b- coefficients estimated from data on mackerel caught in the North Sea was retrieved from Wilhelms (2013) and are presented in Table 1 together with the number of juvenile individuals of mackerel from IMR sampled in 2017 and 2018, and per quartile. Since the a- and b-coefficients varied with quartile, it was implied that the estimated mean weight-at-length of the North Sea juveniles varied depending on the season (Appendix B), meaning that individuals caught during different times of the year could be of equal lengths and weigh the same, but would be expected to have different weights.

Table 1: The number of individuals in the used IMR-dataset per quartile and per year, the quartile specific a- and b- coefficients from Wilhelms (2013), the smallest body lengths in the dataset used by Wilhelms (2013) to estimate the a and b parameters. The two last columns list the shortest measured length of an individual in the IMR-data set, and the total number of individuals in the IMR data set that were smaller in length than the shortest length in the dataset used in Wilhelms (2013). Q2 and Q4 were not used for any analysis.

Quartile	Total (n)	2017	2018	a	b	Min. length	Min. measured	# below min. length
1	2644	1044	1600	0.0027	3.302	10.5 cm	14.5 cm	-
2	939	473	466	0.0024	3.308	16.5 cm	15.5 cm	35
3	3976	2440	1536	0.0043	3.210	7.5 cm	13 cm	-
4	756	595	161	0.0015	3.492	16.5 cm	14.5 cm	338

The calculation of the estimated mean weight-at-length was done by following three steps;

(1) The IMR-dataset was separated by quartiles. Then all recorded lengths from Q1 (winter) and Q3 (summer) (130 mm – 310 mm, separated by 5 mm intervals) were inserted into Equation (1) with the corresponding a- and b-coefficients to calculate the seasonal estimated weight-at-length. Thus, each observed length group in the dataset was given four different expected weights (Table 2), one per season.

To compare the weight-at-length for juveniles along the Norwegian coast with the mean weight-at-length for juveniles from the nursery areas, the individual variations between the mean estimated weight of North Sea juveniles and the recorded weights of juveniles from Norwegian waters, called residuals, were calculated. This was done to study whether the recorded juveniles weighed more or less than what is expected for juveniles of the same size from the traditional nursing grounds, and was calculated by the following two steps;

(2) The difference between the observed weight and the mean estimated weight for each individual was found by subtracting the mean estimated weight-at-length from the recorded weight. If the individual weighed less than the mean estimated weight, the residual was a negative number. If the individual weighed more than the mean estimated weight, the residual was a positive number (Table 2).

(3) Then, each residual was converted into a fraction of the expected weight, expressed as a number between -1 and 1 by dividing the difference between the observed and expected weight by the estimated weight. If each fraction in addition was multiplied by 100, they expressed the deviance between the recorded weight and the expected weight as a percentage (Table 2).

If an individual weighed less than the expected weight, the fraction and percentage was negative, and the relative juvenile condition was assumed to be lower than the mean condition for individuals of the same length from the North Sea. If an individual weighed more than what was expected, the fraction was positive and the relative condition of the juveniles was assumed to be higher than the mean condition of North Sea juveniles of the same length.

The last step (3) was needed to avoid long individuals having a larger impact on the results than short individuals. When converting the difference between recorded and expected weight from grams to fractions of the expected weight, the weight deviance was proportionally related to fish size.

Table 2 Table of the expected weights-at-length, the recorded weights, the deviance from the estimated weight (residuals), and the proportional deviance as fractions and percentages for four different individuals from the IMR dataset measuring 220 mm, one individual from each quartile.

Months	Quartile	Length (mm)	Weight (g)	Expected weight (g)	Weight deviance (g)	Proportional deviance	Percent deviance (%)
Jan - Mar	1	220	70	73,121	-3,121	-0,043	-4,3
Apr - Jun	2	220	79	66,213	12,787	0,193	19,3
Jul - Sep	3	220	102	87,628	14,372	0,164	16,4
Oct - Dec	4	220	76	73,086	2,914	0,040	4,0

2.2.2 PLOTTING THE INDIVIDUAL VARIATION TO ASSESS THE GENERAL CONDITION OF JUVENILES FROM NORWEGIAN WATERS

The registered length and weight data for the juvenile mackerel sampled by IMR during February (Q1) and July (Q3) of 2017 and 2018 were compared with the mean estimated weight-at-length found with equation (1) by inserting the coefficients from Wilhelms (2013) based on data on juveniles caught in traditional nursery areas in the North Sea and west of the British Isles. The length frequencies of juveniles from Norwegian waters and the northern parts of the North Sea caught were additionally plotted against latitude in order to study if the size of juveniles along the Norwegian coast varied with latitude and with the season.

In order to study the condition of the juveniles along the Norwegian coast the residuals, meaning the individual variations from the estimated mean weight-at-length, were assumed to give an indication of whether the condition of juveniles from Norwegian waters was poorer or better than the condition of their conspecifics in the North Sea. The residuals from the individuals caught in February and July were plotted against latitude and body length to examine whether the condition of the Norwegian juveniles varied with body length and with latitude and if there was a difference between individuals during winter and summer. If the residuals were negative, the relative juvenile condition was assumed to be poorer than the mean condition for individuals from the North Sea. If the residuals were positive, the relative condition of the juveniles was assumed to be better than the average condition of North Sea juveniles. The months used for comparisons between seasons, namely February and July, were chosen with the purpose of comparing juvenile condition during a season with little food (winter) and a season with food abundance (summer) to get an indication of habitat quality along the Norwegian coast throughout the year, and the available quantity of data.

2.3 DATA ANALYSIS AND STATISTICAL TESTS

Normality in the data was assessed by interpreting Q-Q plots of the length data and the Q-Q plots of the deviance from estimated mean weight (Appendix C). Parametric tests (simple linear regression (SLR) and analysis of covariates (ANCOVA)) were applied to the data to test for:

- (1) The effect of latitude on the body lengths of juvenile mackerel during winter and summer
- (2) A difference in the body lengths across latitudes, between the seasons
- (3) The effect of latitude on the deviance from estimated mean weight
- (4) The effect of body length on the deviance from estimated mean weight
- (5) A difference between the deviance from estimated mean weight during winter and summer

The tests assumed statistical significance if $p\text{-value} < 0.05$. The highest level of statistical significance was set to $p\text{-value} < 0.001$. In the circumstances when the SLM yielded a poor fit due to the distribution of the data, the data was grouped by two predictors and the statistical difference between the observed means of the predictor groups was tested by applying a Welch Two-Sample t-test. The two-sample t-test also assumed statistical significance if $p < 0.05$. All maps and plots were created by the use of the software R, version 3.4.1 (R Development Core Team, 2017) and R-studio, version 1.0.153 (RStudio Team, 2016) incorporating the packages named “ggplot2” (Wickham, 2016), “ggmaps” (Kahle and Wickham, 2013), and gridExtra” (Auguie, 2017).

2.4 WATER PROPERTIES AT SAMPLING STATIONS

Oceanographic measurements of water properties were made at all stations where juveniles were sampled for diet analysis. Measurements of conductivity, temperature and density used for this thesis were conducted at 10 m below the surface with a Seabird CTD on board all three vessels. Measurements of temperature and conductivity were used for calculating the salinity, and have been used with the purpose of studying the living conditions of the juvenile mackerel that were sampled for diet analysis.

2.5 BIOLOGICAL SAMPLING OF JUVENILES USED FOR DIET ANALYSIS

Biological sampling was done with the purpose of determining age, stomach fullness and feeding preferences of the individuals sampled during the NSSH post-larvae survey in June and the IESSNS survey in July of 2018. Sampling of length and weight, and removal of stomachs and otoliths were done at the fish laboratory at IMR in October 2018. The samples from each trawl station were defrosted separately in cold water and sampling of all data from one station

was completed before sampling of the next station begun. This was done to avoid mixing individuals from different trawl stations. Prior to the removal of stomach and otoliths, each individual was weighed and then measured for length from the anterior point of the head to the tip of the pinched tail as described in Mjanger et al. (2017). All stomachs were separated from the viscera and individually placed in a plastic bag labelled with the station name and the number of the individual. The stomachs were then stored in the freezer.

The sagittal pair of otoliths from each individual was sampled from all individuals, except from individual number 1 and 2 from trawl station 37428, which could not be retrieved due to unskilled scalpel usage or the disappearance of the otoliths into the cranial cavities. The success-rate of extracting the pair increased with the number of sampled individuals. The otoliths were prepared for age reading according to the standardized methods described in Mjanger *et al.* (2017) by removing the surrounding membrane prior to placing the otoliths in a dripping tray. The otoliths were then dried for 24 hours and then dripped with hardening, clear resin twice, with a drying period of 24 hours between each dripping. The embedding of the otoliths in resin is necessary for the fixation of the otoliths. Age of the individuals was determined by the presence/absence of winter rings, and the otoliths were read by research technician Stine Karlson from the Pelagic Fish Research Group at IMR.

2.6 DIET ANALYSIS OF THE JUVENILE MACKEREL

Stomach fullness and diet analyses provided information about whether the juvenile mackerel fed along the coast during summer, and whether they were selective by only feeding on specific prey items. Stomach sample analysis was conducted at the lab facilities at IMR under the supervision of Herdis Langøy Mørk. Stomach filling was determined prior to opening of the stomach according to the standardized methods mentioned in version 4.0 from Mjanger *et al.* (2017). The degree of fullness was determined by the following five categories;

- (1) Empty
- (2) Very little content, must be opened to differentiate between category 1 and 2
- (3) Some content, visible filling prior to opening of stomach
- (4) Stomach is full but not bursting
- (5) Bursting, content is visible through stomach lining which is thinly stretched

The stomachs of all 146 individuals were sampled. Each stomach with its content was individually worked through using a microscope to magnify the content, and a scalpel and thin tweezers to sort digested matter from less digested content. Stomachs were partially frozen when opened to simplify the opening process, reduce handling time, and to minimize mixing

of stomach lining fat into the stomach content. The content was sorted and labelled with a digestion grade between 1 and 5 described in Mjanger *et al.* (2017) as follows:

- (1) Undigested, countable
- (2) Digestion begun, species are identifiable and countable
- (3) Partially digested, species or group can be identified and be counted
- (4) Almost digested, only identifiable to prey group but cannot be counted
- (5) Completely digested in liquid form, can neither be identified to any taxonomic rank or counted

During the sorting, organisms were identified at species level when possible. Moderately digested organisms could most often only be identified at higher taxonomic ranks and not to species. In the stomachs where only one taxonomic group was found and sorted, the unidentifiable digested material was grouped according to this taxonomic rank. If undigested organisms from several taxonomic phyla were found within a stomach, the digested material was marked as a mix. When the stomach content consisted of multiple prey organisms from various taxonomic groups which were difficult to separate, handle, or count, the proportion of each prey group in the sample was estimated by subjective evaluation and labelled as a percentage of the total mix. To remove water weight from the samples, the sorted stomach content was put in separate pre-weighed aluminum cups with one species, taxonomic group, or digested mix in each, before being placed within a heating cabinet and dried at 70°C for a minimum of 24 hours (Mjanger *et al.*, 2017). When the content had dried sufficiently, each cup was individually weighed. The weight of the content was then found by subtracting the weight of the cup from the total weight. For the mixed content which could not be sorted, the estimated percentages were used to calculate how much each group weighed out of the total mix.

The smallest weight the scale used could detect was 0.0001 g. If organisms/parts were too few and/or too light to exceed the minimum weight after drying, the estimated weight of each organism/all parts were assessed based upon prey type, length, and the knowledge and experience of the technicians at IMR. It is not optimal to use the number of prey items for analysis due to the bad condition of certain prey groups at higher degrees of digestion, e.g. Appendicularians, which easily break apart when handled and are thus challenging to count accurately. The weight of the prey organisms was, therefore, the only parameter being used for further analysis.

3. RESULTS

3.1 AGING OF JUVENILE INDIVIDUALS

A total of 2330 mackerel individuals from 2017 and 2018 were determined to be 1 or 2 years old by research technicians at the Institute of Marine Research (IMR). One individual from June 2018 was removed from the dataset due to an unlikely length-at-age (360 mm at one year of age). Between the two years, a total of 668 one-year-old individuals and 56 two-year-old individuals were caught in 2017, while 649 and 957 individuals in 2018 were determined to be one and two years of age, respectively. The length frequencies of these individuals were used to determine the body lengths of 1-group mackerel caught in Norwegian waters and the northern North Sea.

Minimum length for the aged one-year-old individuals was 145 mm while maximum length was 310 mm. The shortest individual was caught in winter (1st quartile) while the longest was caught during fall (4th quartile). All one-year-old individuals of a length longer than 260 mm were caught in the third or fourth quartile, except for two individuals. Two-year-old individuals ranged between 195 and 345 mm. There was a clear overlap in length frequencies between the one- and two-year-old individuals from 245 to 310 mm (Figure 2). A total of nine two-year-olds in 2017 and 2018 were 240 mm or smaller.

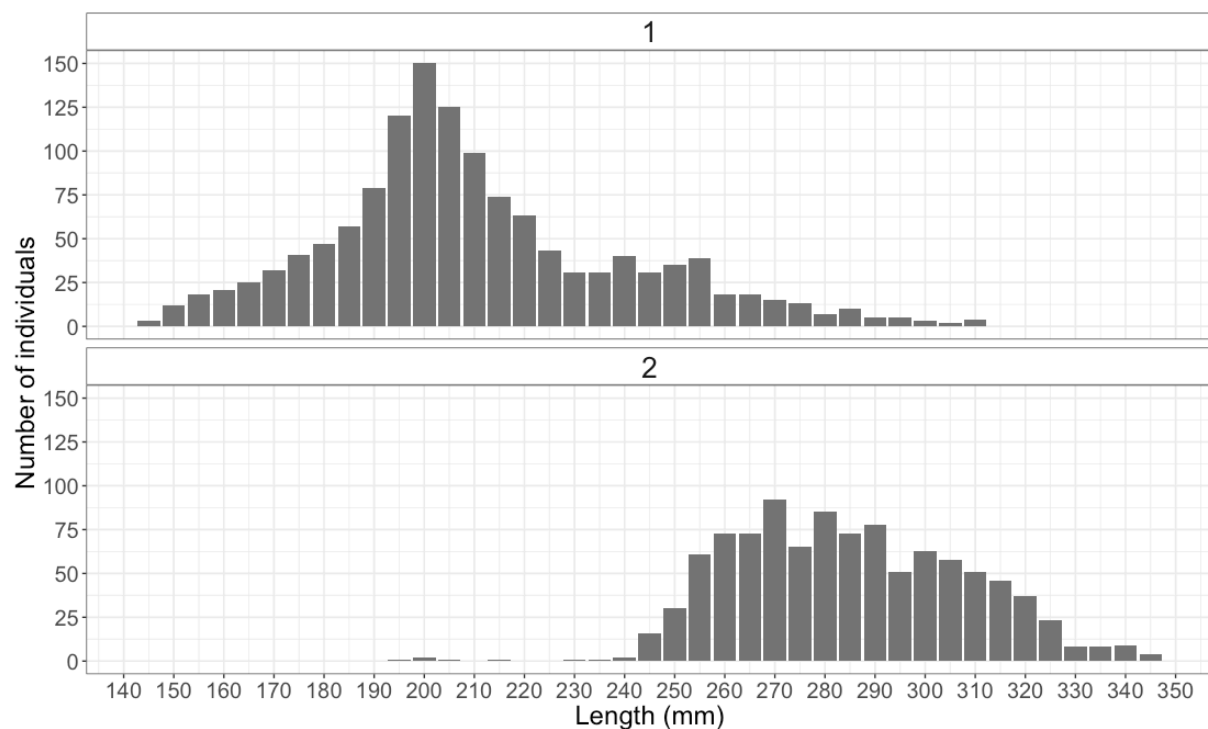


Figure 2. Body length (mm) frequencies of one- and two-year-old juveniles from 2017 and 2018. Plots are separated by the age (one and two years) of the individuals.

Then, age data from February and July was used to estimate the size of one-year-old individuals during the fasting period in the first quartile and the feeding season in the third quartile.

In February 2017 and 2018 a total of 749 individuals of the age one and two were caught and age determined. A total of 473 individuals were one year old while 276 individuals were two years old. One-year-old individuals ranged between 145 and 260 mm while two-year-old individuals ranged between 195 and 300 mm (Figure 3). Two one-year-old individuals were longer than 250 mm, with the longest individual measuring 260 mm. The overlap in length between the two age groups occurred between individuals with lengths between 240 and 245 mm (Figure 3). The maximum length of the non-aged one-year-old individuals caught in February was therefore assumed to be 240 mm.

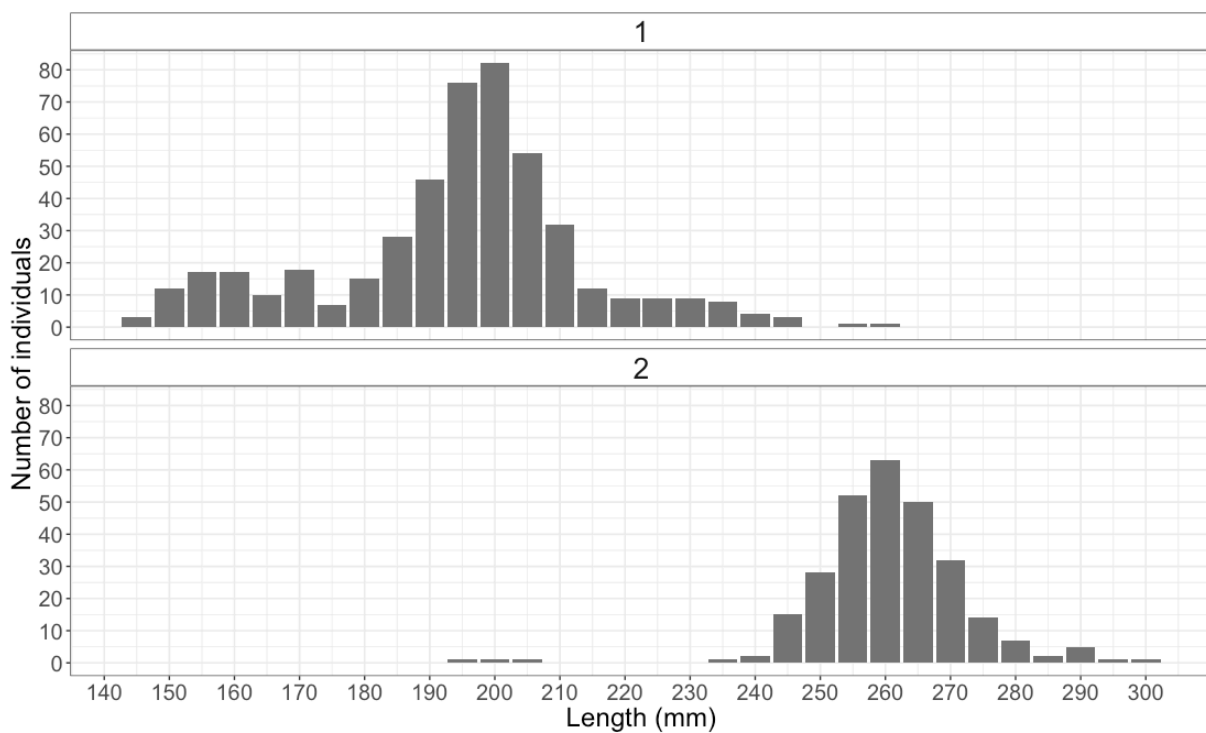


Figure 3. Body length (mm) frequencies for 1- and 2-year-old individuals caught in February of 2017 and 2018. Plots are separated by the age (one and two years) of the individuals.

In July of 2017 and 2018 a total of 592 individuals were determined to be two years of age, and 525 individuals were one year of age. One-year-old individuals ranged between 175 and 310 mm while two-year-old individuals ranged between 200 and 345 mm (Figure 4). The main size frequency overlap between individuals for one and two-year-old individuals occurred between 245 and 270 mm. The maximum size registered for a two-year-old individual was 345 mm, which was 45 mm longer than the longest two-year-old individual registered in February. Based upon the overlap between the two age groups the maximum length of one-year old individuals in July was assumed to be 255 mm.

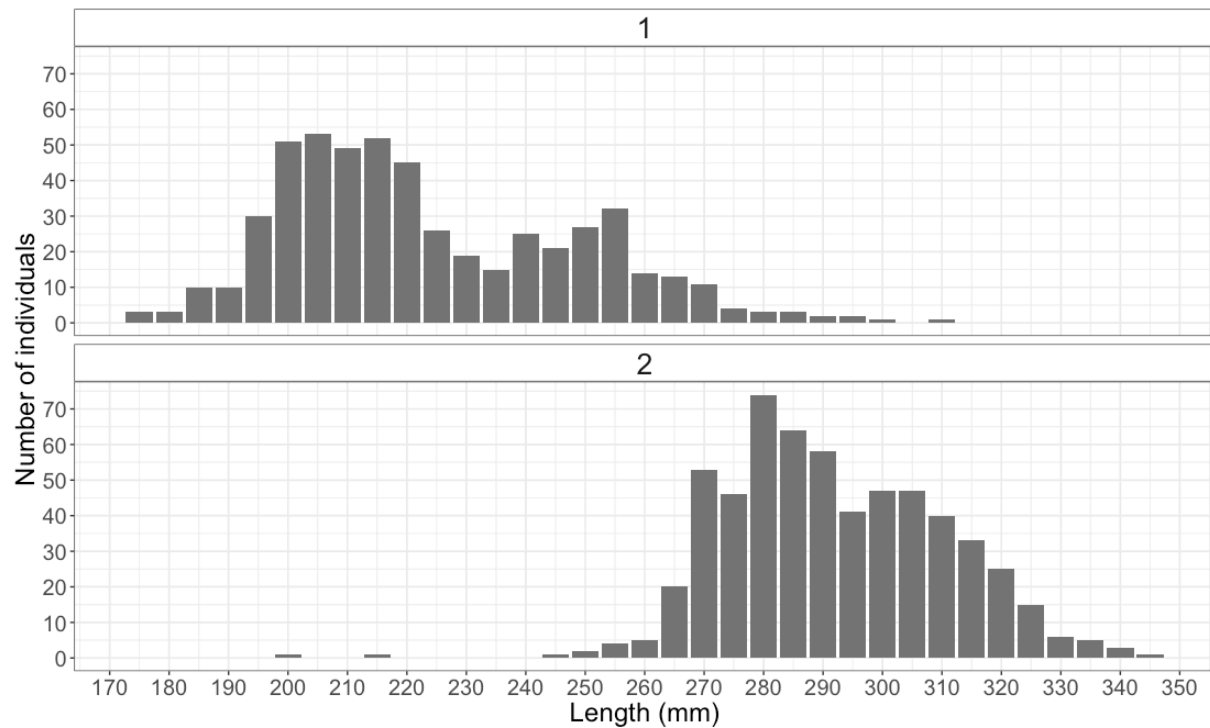


Figure 4. Body length frequencies for 1- and 2-year-old individuals caught in July of 2017 and 2018. Plots are separated by the age (one and two years) of the individuals.

The lengths of the aged individuals caught north of 58°N was plotted to examine if maximum length had to be adjusted when only juveniles caught north of the southernmost point in Norway was studied (Figure 5). By visual inspection, the maximum sizes for each month were determined to not differ significantly and was, therefore, not adjusted further.

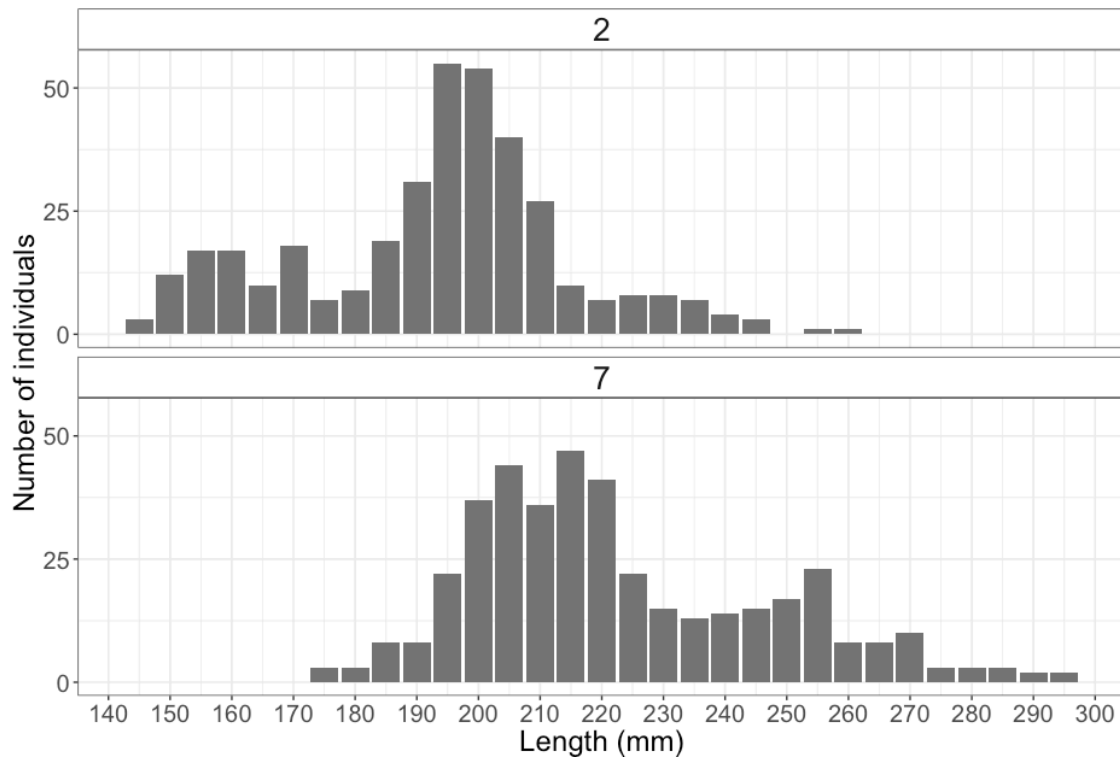


Figure 5. Body length frequencies of aged one-year-old juveniles caught at 58°N and northwards during February (top) and July (bottom) along the Norwegian coast.

The observed length frequencies of the aged individuals from winter and summer was plotted against latitudes in order to study whether latitude had an effect on the size of the juvenile individuals, and if there was a significant difference in condition between winter and summer which had to be adjusted for throughout the study. Individuals from February 2017 and 2018 were caught between 57°N and 68°N, and individuals from July 2017 and 2018 between 56°N and 68°N (Figure 6). Juveniles from July were caught more evenly across the latitudes than the juveniles from February.

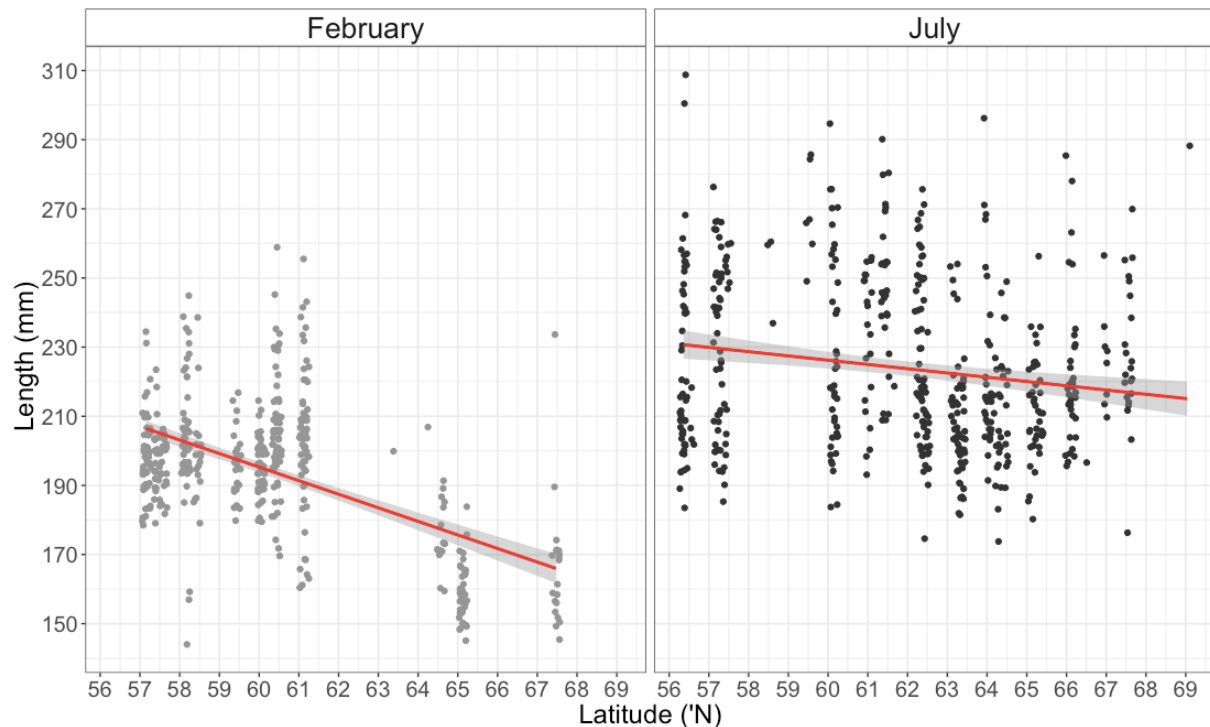


Figure 6. Length frequencies for one-year-old individuals from February and July of 2017 and 2018 with latitude. A regression line (red) including the confidence intervals (gray area) was applied to identify the general trend in the data. The plots are separated by month.

A Welch two-sample t-test was applied to test whether the mean length differed significantly between February and July. Age read individuals from February had a mean length of 194 ± 46 mm while July individuals had a mean length of 223 ± 45 mm, which was a significant difference (two-sample t-test: $p < 0.001$).

A linear regression model was applied to each month separately to test the effect of latitude on length. On average, the body length of individuals caught in February decreased by 4.2 mm per one degree increase in latitude, which was significant ($p < 0.001$). The individuals caught in July did on average decrease by 1.1 mm across the same distance, a reduction in length with latitude that also was statistically significant ($p < 0.001$). The output from the ANCOVA model, applied to compare whether the effect of the increase in latitude was significantly different between one-year-old individuals from February and July, stated that the reduction in body

length was significantly different between the two months ($p < 0.001$). This meant that the size of juveniles decreased significantly faster with latitude in February than in July.

Only two registered individuals north of 63°N were longer than 200 mm. The observed differences in the registered lengths of one-year-old individuals caught north and south of 63°N in February indicated that juveniles north of 63°N were smaller in size than the southern juveniles. The mean lengths south and north of 63°N were significantly different from each other (two-sample t-test: p -value < 0.001), as juveniles north of 63°N on average measured 164 ± 27 mm while juveniles south of 63°N measured 200 mm. Based upon the length frequencies observed in the dataset the maximum length of 240 ± 32 mm for February individuals was throughout this study, therefore, applied to all individuals caught south of 63°, while individuals north of 63°N were assumed to be one year old if they were 190 mm or shorter in total length.

There was less change in body size with latitude during July. Mean length for individuals did differ significantly north and south of 63°N (two sample t-test: p -value < 0.001), but since the mean length of the individuals caught north of 58°N along the Norwegian coast only differed by 7 mm ($< 58^\circ\text{N}$ -63°N: 219 mm, $> 63^\circ\text{N}$: 212 mm) and all length frequencies were observed across all latitudes, the assumed maximum length of 255 mm for non-aged one-year-old individuals was set to be equal at all latitudes in July.

3.2 MAPPING OF JUVENILE MACKEREL FROM IMR-RECORDINGS AND SUBMITTED OBSERVATIONS

The complete dataset on juvenile mackerel from the IMR-database consisted of registrations of individuals that were caught during all quartiles of 2017 and 2018 by IMR and the Norwegian coastal and oceanic reference fleet. The data set on observations submitted by the public via the IMR-form covered one observation from December of 2017, and registrations from all quartiles for 2018.

3.2.1 IMR AND REFERENCE FLEET-REGISTRATIONS OF JUVENILE MACKEREL

The combined number of aged one-year-old individuals and non-aged individuals assumed to be one year of age in the IMR-dataset was 8318, 1283 individuals were aged while 7035 were non-aged individuals. A total of 4552 of the individuals were caught at 291 trawl stations in 2017, and 3766 individuals at 289 trawl stations in 2018.

During the first quartile (Q1) a total of 2644 individuals were caught, 1044 individuals in 2017 and 1600 individuals in 2018. The northernmost catch of juvenile mackerel was taken in February at 70.1°N in both 2017 and 2018, while the southernmost catch of juvenile mackerel occurred at 57°N (Figure 7). North of 63°N a total of 288 juveniles were caught. There were no catches of juvenile mackerel in March both years.

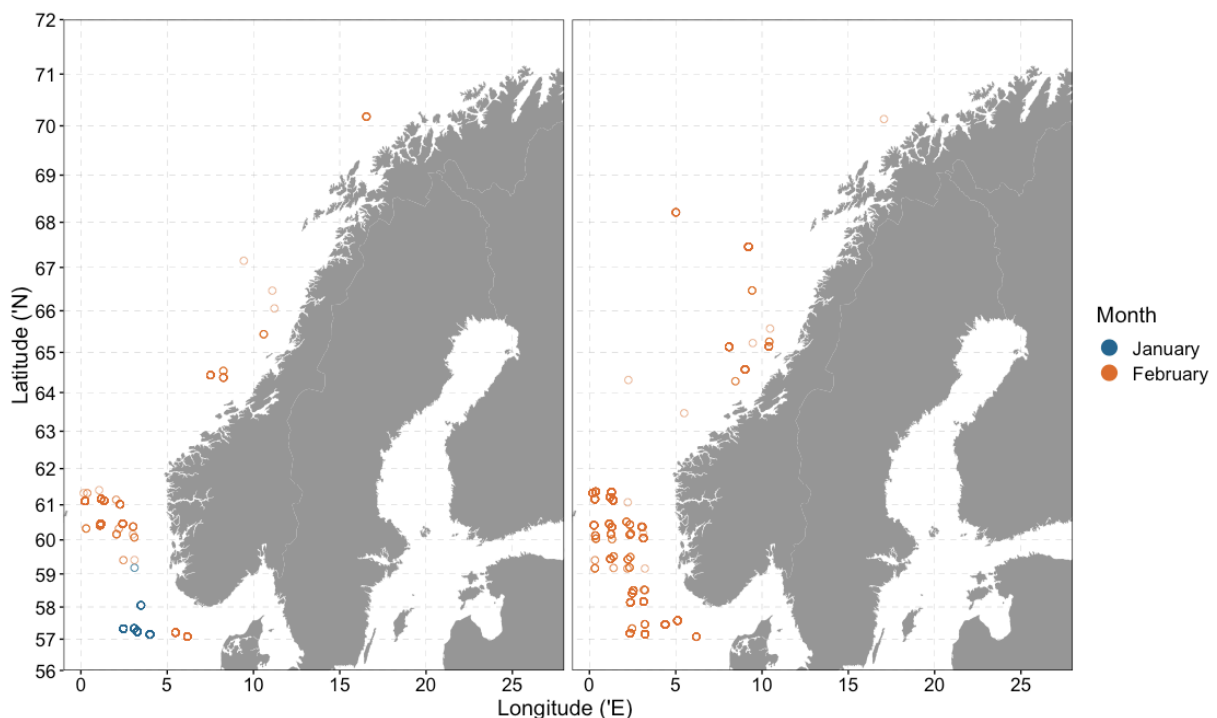


Figure 7. All trawl stations from the first quarter (Q1) in 2017 (left) and 2018 (right) at which juvenile mackerel of a size equal to, or less than, 190 mm ($> 63^{\circ}\text{N}$) and 240 mm ($< 63^{\circ}\text{N}$) were caught and registered in the IMR database. Point color marks capture month.

Juvenile mackerel (*Scomber scombrus*) along the Norwegian Coast

During the second quartile (Q2) a total of 939 individuals were caught, 473 individuals in 2017 and 466 individuals in 2018 (Figure 8). The registered catches of juvenile mackerel were more evenly distributed across latitudes in 2018 than in 2017. The westernmost catch of one year old mackerel during 2017 and 2018 occurred at approximately 0°E in May both years, while the northernmost catch was at 71°N in 2017.

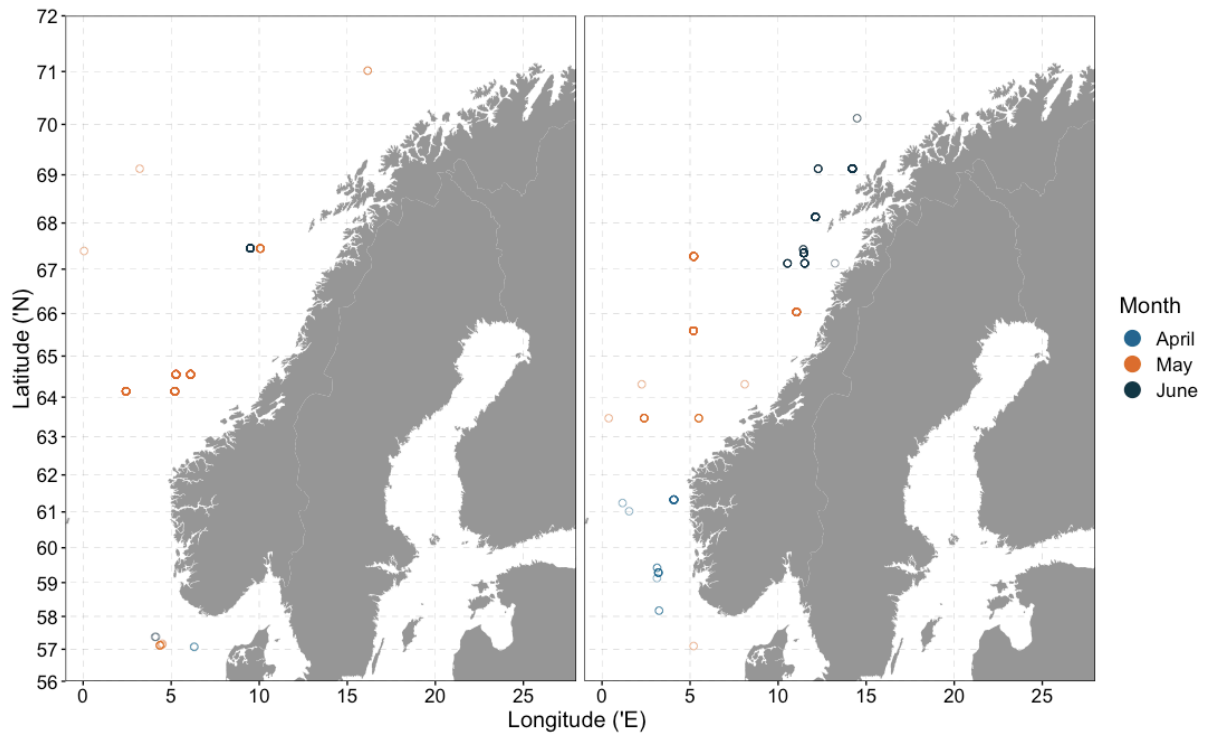


Figure 8. All trawl stations from the second quarter (Q2) in 2017 (left) and 2018 (right), at which juvenile mackerel of a size equal to, or less than, 255 mm were caught and registered in the IMR database. Point color marks capture month.

In the third quartile (Q3) the highest total number of juveniles was registered, with 2465 individuals caught in 2017, and 1537 in 2018. During July and August, the coverage of the IESSNS-cruise provided data on observations along most of the Norwegian coast (Figure 9). The northernmost registered juveniles across both years and all seasons were caught at 73.1°N in September of 2018 and measured 235 and 245 mm. A total of 217 individuals were registered north of 70°N in August and September of 2018. The largest one-year-old individual registered north of 70°N measured 250 mm and the smallest 200 mm.

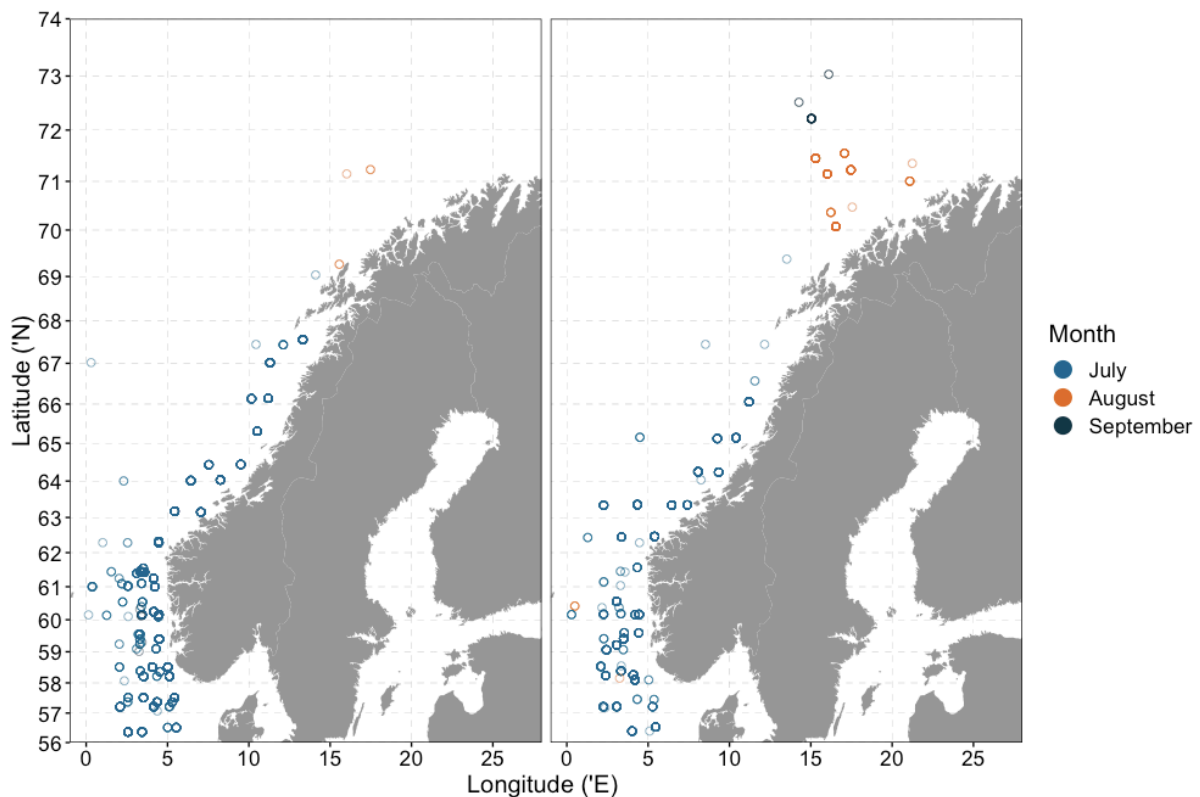


Figure 9. All trawl stations from quarter 3 (Q3) in 2017 (left) and 2018 (right), at which juvenile mackerel of a size equal to, or less than, 255 mm were caught and registered in the IMR database. Point color marks the capture month.

In the fourth quarter (Q4) a total of 756 individuals were registered, and only 45 of these were age read. A total of 570 individuals were caught in 2017 and 143 individuals in 2018 (Figure 10). The northernmost observation was at 62.2°N. Most observations were from Sognefjorden along the western coast at 61.5°N (figure 9). However, the distribution of juvenile mackerel in Q1 (Figure 7) and Q3 (Figure 9) during both years suggests that juvenile mackerel were present along the coast at higher latitudes than 63°N during fall and early winter.

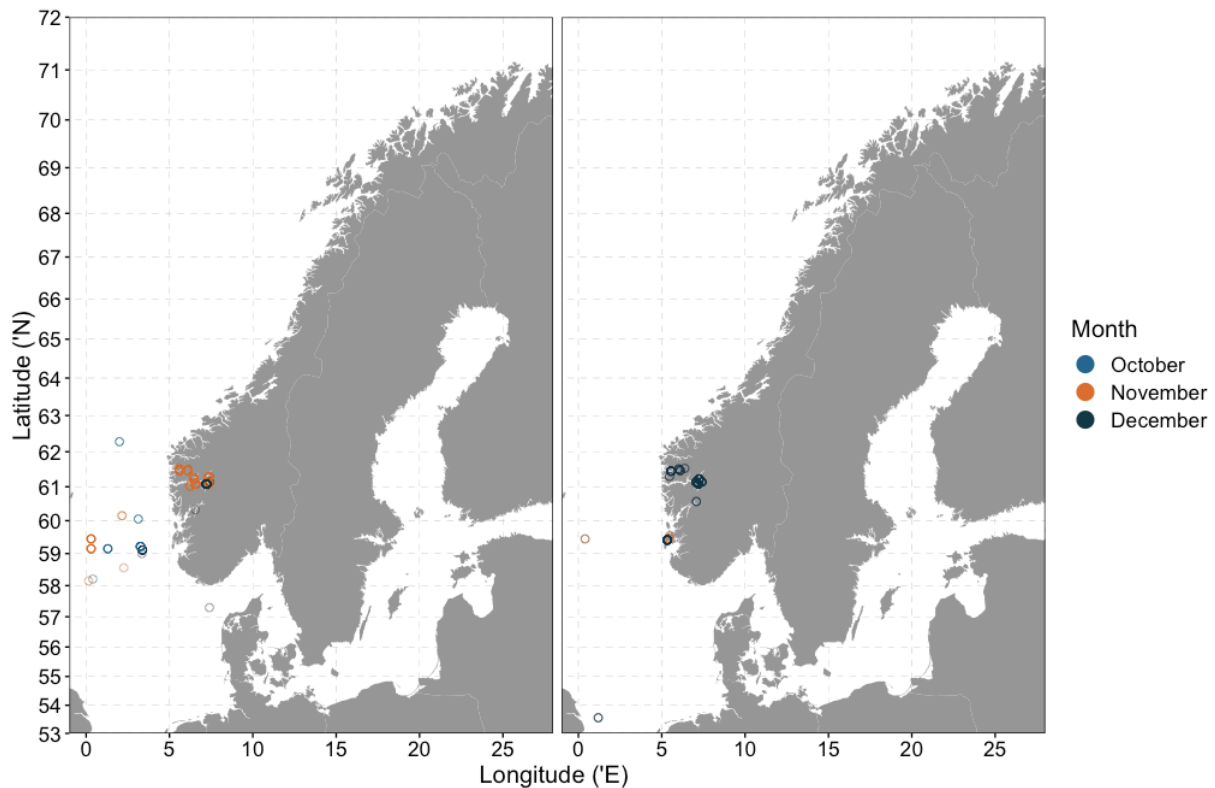


Figure 10. All trawl stations from quarter 4 (Q4) in 2017 (left) and 2018 (right), at which juvenile mackerel of a size equal to, or less than, 255 mm were caught and registered in the IMR database. Registrations are mostly within the western fjords. Point color marks capture month.

3.2.2 SUBMITTED OBSERVATIONS OF JUVENILE MACKEREL

A total of 20 observations were submitted with the registration form, altogether 19 for 2018 and 1 for 2017. The geographical range of the observations was spread from approximately 58°N to 69.2°N (Figure 11) meaning that individuals assumed to be juveniles were observed along the coast at all seasons by coastal residents. The juveniles were recorded in different ways. Of the 20 submitted observations, five were registrations of juvenile mackerel as prey, a total number of 10 observations were of juvenile mackerel as catch, two were acoustic observations, and three were visual observations.

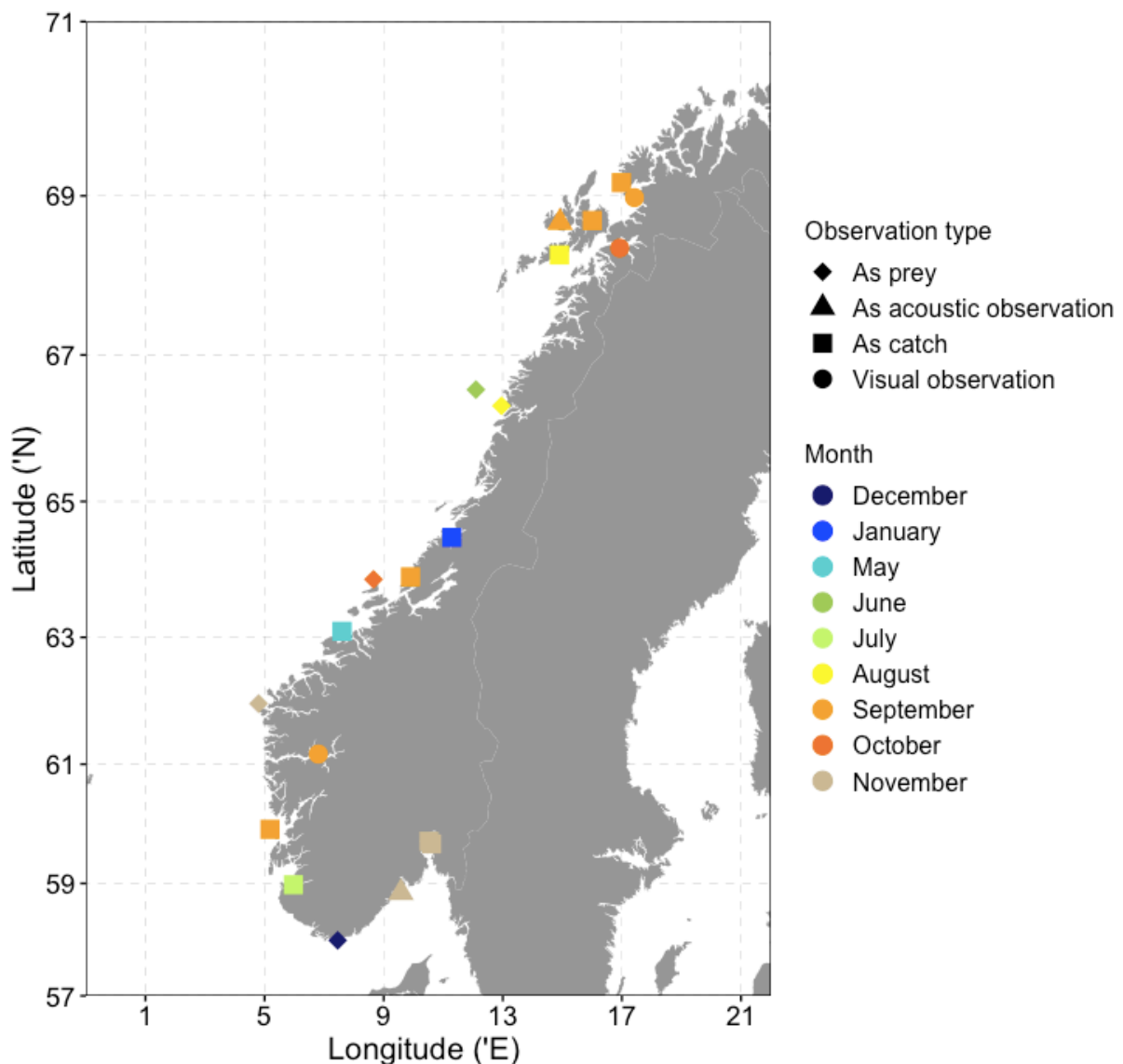


Figure 11. Observations by month and type. Color marks month and shape of point indicate type of observation. The only observation registered in December was also the only observation registered in 2017.

Juvenile mackerel (*Scomber scombrus*) along the Norwegian Coast

Juvenile mackerel occurred in the stomachs of five different fish species, namely saithe (*Pollachius virens*) (Figure 12), cod (*Gadus morhua*), pollack (*Pollachius pollachius*), ling (*Molva molva*), and angler fish (*Lophius piscatorius*). These observations were made between 58°N and 66°N.



Figure 12. Picture of juvenile mackerel (~10 cm) from the stomach of saithe caught in Stigfjorden at 66°N in August of 2018 (Photo: J.E. Martiniussen, photo used with permission). Due to the estimated size of the individuals and the registered time of year, the juveniles were assumed to be 0-group, meaning that they were spawned in spring/summer of 2018.

3.3 THE OBSERVED WEIGHT-AT-LENGTH OF JUVENILES ALONG THE NORWEGIAN COAST COMPARED WITH THE ESTIMATED MEAN WEIGHT-AT-LENGTH FOR NORTH SEA JUVENILES

The recorded weights of the juveniles caught by IMR and the reference fleet during winter (Q1) and summer (Q3) was plotted against the corresponding estimated mean weights for North Sea juveniles.

The observed weights for all length groups in Q1 followed the curvature of the estimated mean weight-at-lengths for North Sea individuals (Figure 13). However, the recorded mean weight for each length was somewhat lower than the estimated weight-at-length for all the length groups. An ANCOVA was applied to test whether there was a statistically significant difference between the predicted and recorded weights. The output from the model stated that there was a significant difference between the slope of the estimated mean weights and the recorded weights (p -value < 0.001). This meant that the individuals caught by IMR in Norwegian waters and the northern North Sea on average weighed less than the estimated weight for juveniles from the North Sea during February.

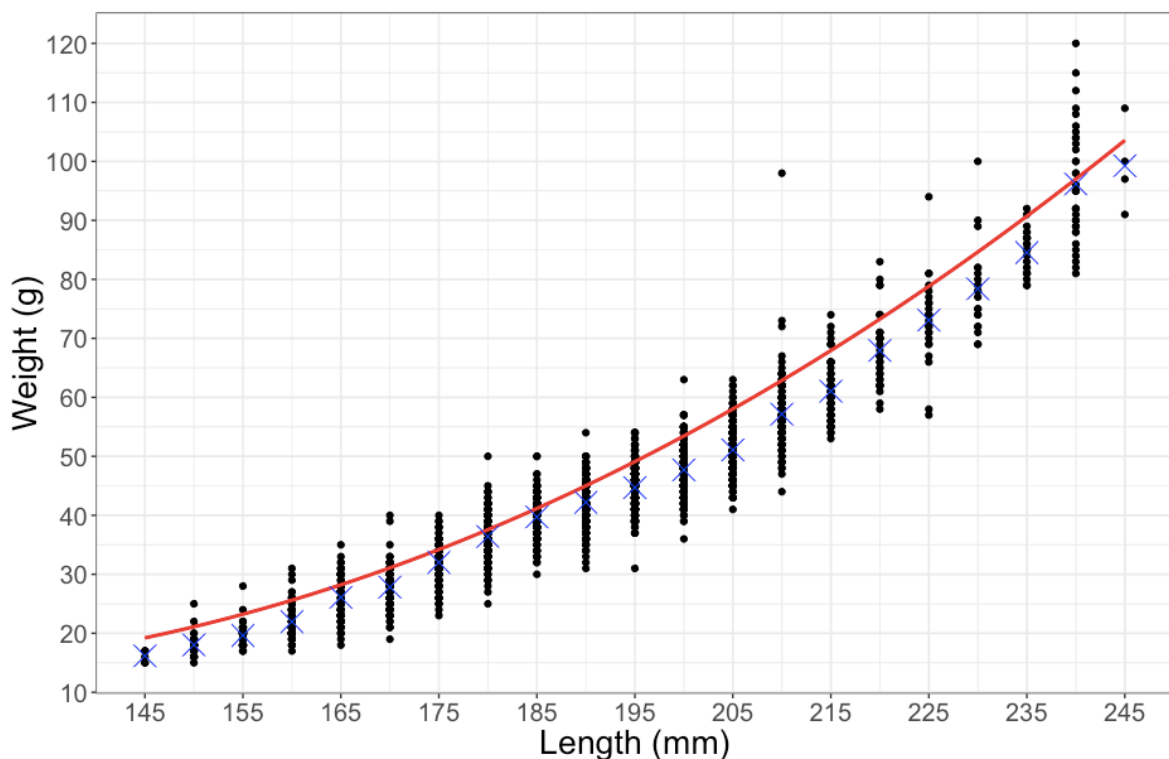


Figure 13. Plot of length and weight of all juvenile individuals from the IMR database from Q1 in 2017 (n=1044) and 2018 (n=1603). The mean weights for each length group are marked by blue crosses, and the predicted weight-at-length for mackerel is given as a red line.

The observed trend for the weight-at-length for individuals in Q3 was similar to the trend observed for individuals in Q1, as the juveniles caught by IMR in most cases had a lower mean weight than what was estimated for the North Sea juveniles. The most frequently observed length groups, from 170 to 255 mm, followed the curvature of the estimated weights (Figure 14). Although the juveniles were more similar to the estimated weight during Q3 than Q1, approximately ~94% of all the length group means were below the predicted weight.

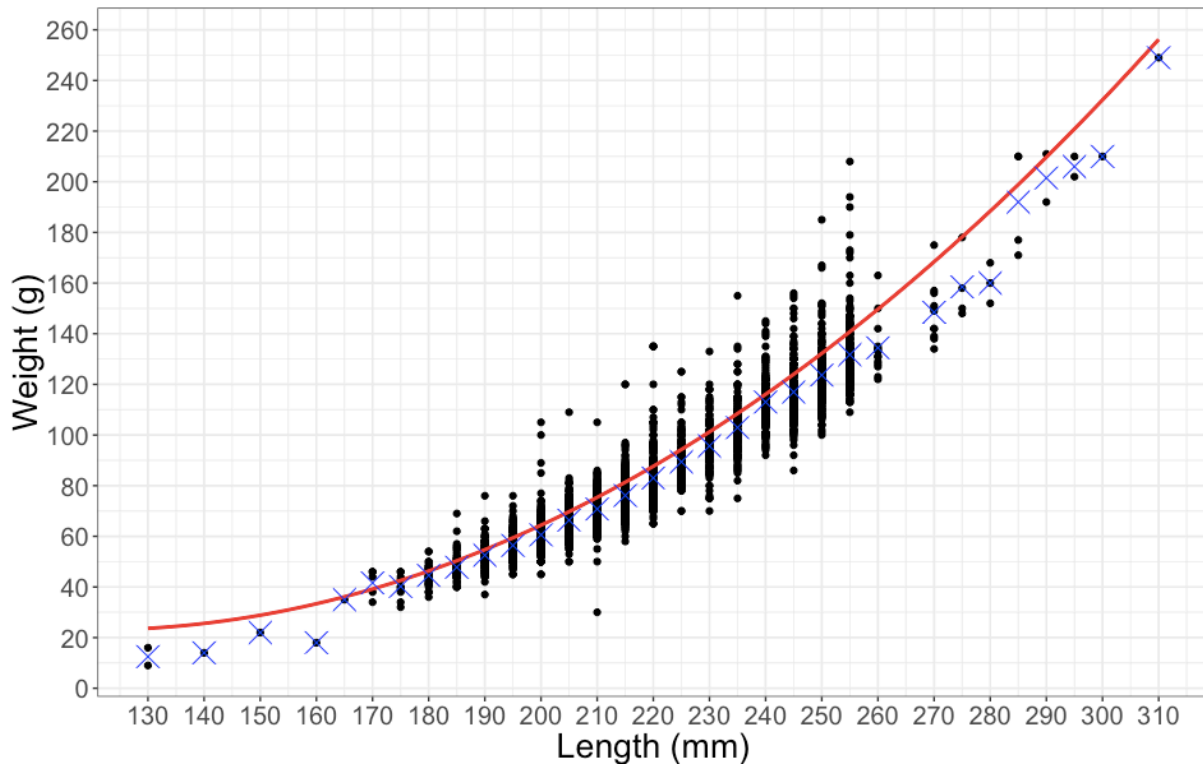


Figure 14. Plot of the length and weight of individuals from the IMR database from Q3 in 2017 (n=2440) and 2018 (n=1536), the mean weight for each length group marked by blue crosses, and the estimated weight-at-length for mackerel as a red line.

The ANCOVA model stated that there was a significant difference between the slope of the expected weights of the North Sea juveniles and the slope of the observed weights from the juveniles caught along the Norwegian coast and in the northern North Sea (p-value < 0.001). This meant that juveniles caught by IMR weighed significantly less than the estimated mean weight for North Sea juveniles.

In conclusion, 1-group mackerel from the Norwegian coast and the northern North Sea caught by IMR did on average weigh less than what was estimated for North Sea juveniles from Wilhelms (2013) during the same time of year caught in the nursery areas further south. During the summer months the differences between the predicted weights and recorded weights was less pronounced than during winter.

3.4 JUVENILE CONDITION DURING WINTER AND SUMMER

3.4.1 JUVENILE CONDITION DURING WINTER

The mean length of all one-year-old individuals in the IMR dataset from February was 193 ± 11 mm, and the general trend in the data showed that juveniles south of 63°N were larger than juveniles north of 63°N . The length of juveniles along the Norwegian coast from 58°N and northwards was on average 194 ± 19 mm. Preliminary analyses showed that there was not a linear relationship between all observed lengths and latitude in February due to the aggregation of the data at a few southern latitudes, and the number of data points in the northern latitudes. It was, therefore, not possible to run a linear regression model on the February data without separating the data into smaller datasets. The data was therefore divided into two latitude categories (South ($58^{\circ}\text{N} - 63^{\circ}\text{N}$)/ North of 63°N), and a two-sample t-test was used to test if the mean size of the individuals in the two groups differed significantly from each other. Mean length of individuals north of 63°N was 163 ± 9.9 mm while mean length for individuals south of 63°N was 200 ± 13 mm. There was a significant difference between the mean individual size north and south of 63°N , ($p\text{-value} < 0.001$) (Figure 15, top row). This meant that the mean length of individuals caught in February differed significantly between north and south and that the juveniles in the north were significantly smaller than juveniles in the south.

A linear model was applied to each latitude group separately. This was done to test if the size of juveniles north and south of 63°N along the coast was affected by latitude. The model stated that a change in latitude affected juvenile size significantly in the south but not in the north (South: $p\text{-value} < 0.001$, North: $p\text{-value} = 0.24$). This meant that the mean juvenile size in the south increased slightly with increasing latitude, while the body size of juveniles in the north did not differ with an increase in latitude.

Individuals north of 63°N had a lower maximum length than the southern individuals (North: 190, South: 240 mm). The dataset of the length groups in the south was, therefore, limited to only include the same observed length frequencies as in the north (Figure 15, bottom row). A two-sample t-test was applied to determine whether the mean of individuals in the south and the north differed significantly from each other when juveniles of the same sizes were compared to each other. The mean size of juveniles of the same size frequencies in the south and north was significantly different ($p\text{-value} < 0.001$). Mean length at the southern coast of Norway was 178 ± 6.1 mm and mean length north of 63°N was 163 ± 9.9 mm. The individuals were, thus, significantly shorter in the north than in the southern areas.

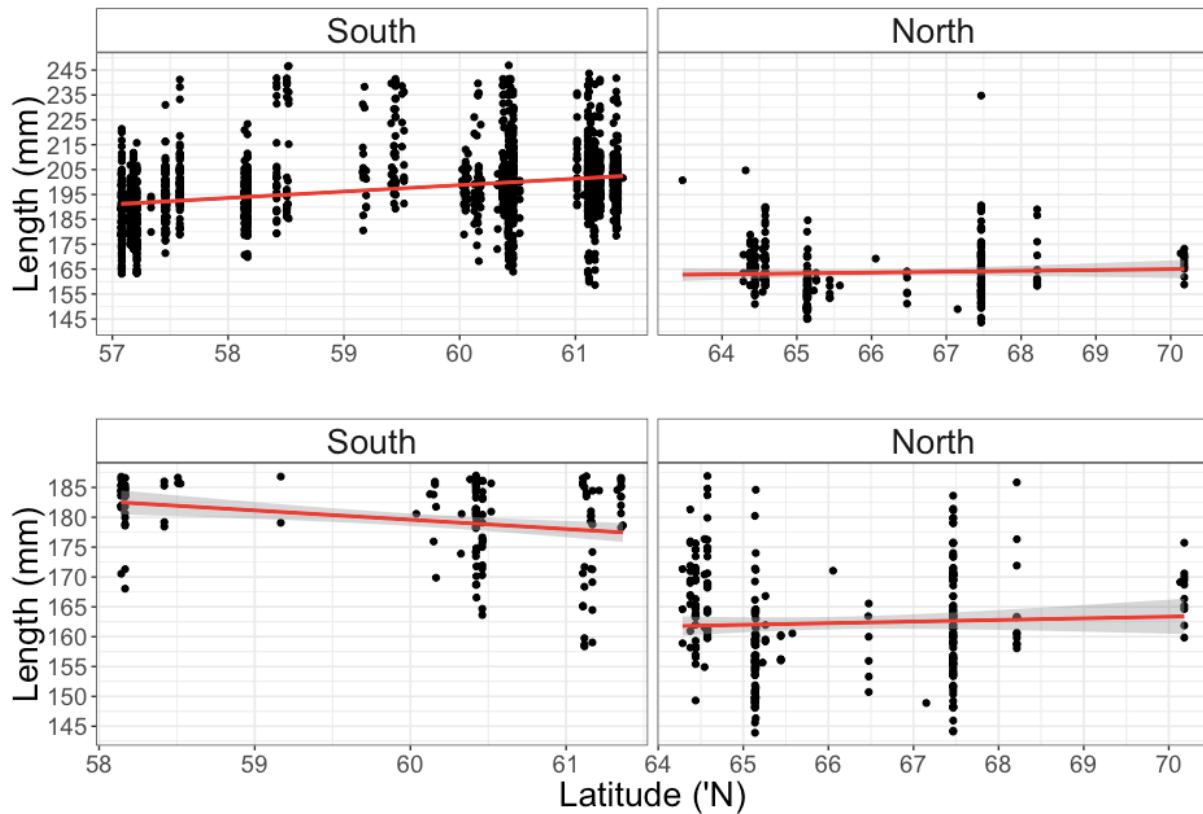


Figure 15. Plots of latitude and individual length (mm) for individuals, both age read and non-aged from the IMR-database from February 2017-2018. The top row of plots shows all measured lengths for individuals in the South (58°N - 63°N) and North (> 63°N). The bottom row of plots depicts the length of individuals in the South/North groups when the South group was limited to only include individuals equal to, or shorter than 190 mm. This was done to equal the length groups observed in the North. A regression line was included to highlight the general trend in the data. The plot points were jittered around the x-axis to reduce point overlapping. This slightly reduces latitude accuracy in the plot.

To examine whether the weight-at-length for juveniles in February varied depending on size and geographic position, the proportional residuals, meaning the individual variations between the estimated mean weight and the observed weight, were plotted against latitude and body length. The deviance from the expected weight was expressed as a positive or negative decimal number between -1 and 1, depending on whether the juveniles weighed less or more than the expected weight. Thus, if the proportional residuals between observed and expected weight were close to 0, the weight did not deviate considerably from the estimated mean weight for North Sea juveniles.

When plotting the proportional residuals from February with latitude it seemed like latitude affected the condition of juveniles during winter. As indicated by the regression line (Figure 16, top row) the trend in the data was that juveniles caught in the southern latitudes of Norwegian waters and in the northern North Sea (< 63°N) on average deviated less from the estimated North Sea mean than juveniles north of 63°N along the Norwegian coast. The deviation from the estimated mean weight became slightly reduced as the individuals became longer (Figure 16, bottom row).

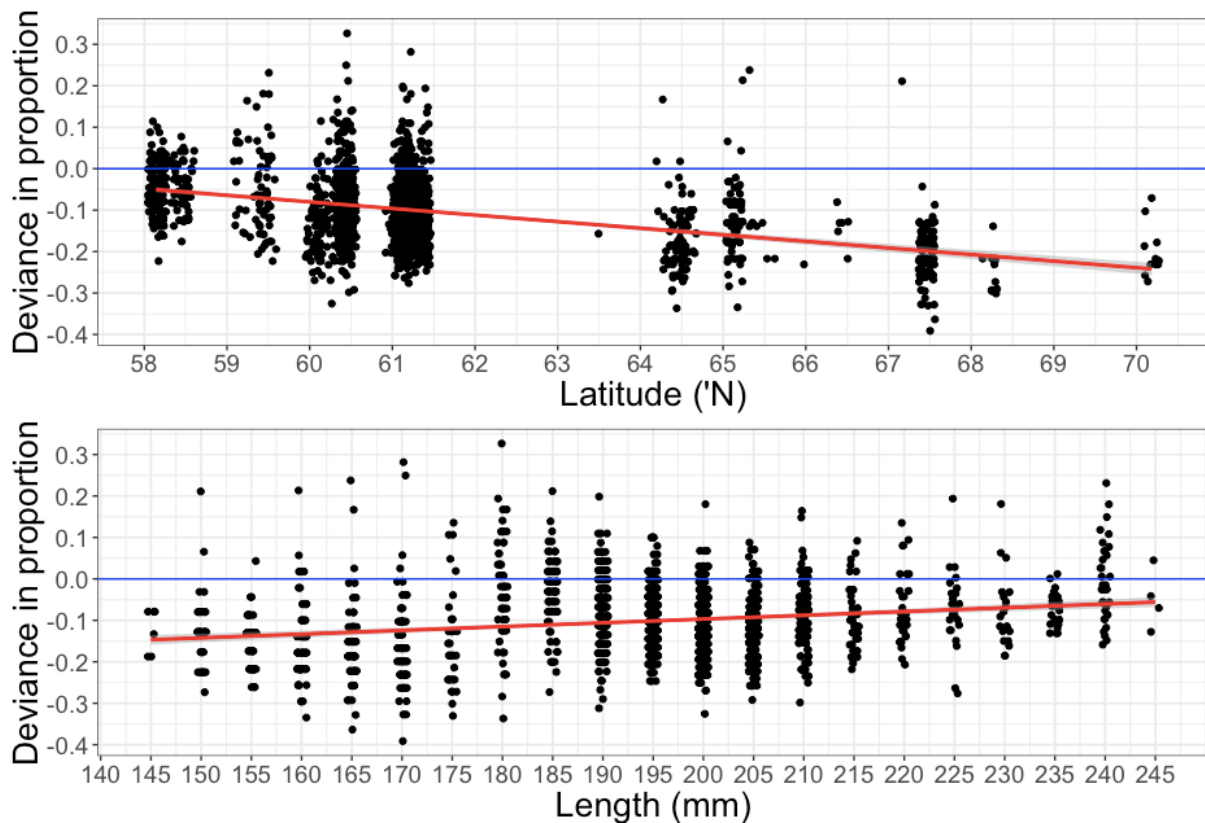


Figure 16. Latitude and proportional residuals (top), and body length and proportional residuals (bottom) from February of 2017 and 2018. The blue line shows the mean weight of the North Sea individuals, and the red line is the applied linear regression model. The plot points are jittered around the x-axis to reduce point overlapping. This reduced latitude and length accuracy in the plot.

The greatest observed individual deviances from the estimated weight were +32% and -39%. Juveniles deviated on average by -10 ± 8.9 % from the estimated mean weight-at-length for individuals from the North Sea during winter. The applied linear regression model stated that a change in latitude had a significant effect on the mean weight of individuals caught in February (p -value < 0.001). For each degree increase in latitude the mean weight decreased by -1.4%, thus, juveniles on average deviated more from the estimated weight farther north.

A linear regression model testing if the variation between observed and estimated mean weight was affected by the size of the individual stated that the effect on condition was significant (p -value < 0.001), meaning that smaller sized individuals on average deviated more from the estimated mean weight juveniles of a larger size (Figure 15, bottom). There was also a significant difference between the observed and estimated mean weights (ANCOVA: p -value < 0.001), meaning that the condition of juveniles of all lengths on average was lower than what is estimated for juveniles in the North Sea.

Since individuals north of 63°N were assumed to be 1-year-old if they were smaller or equal to 190 mm, while individuals south of 63°N along the coast were assumed to be longer (≤ 240 mm) and the juveniles in the northern latitudes on average had a lower condition than the

juveniles in the southern latitudes, the observed length frequencies north of 63°N were plotted with the corresponding length groups along the coast, south of 63°N, to compare the mean condition of juveniles of the same size at different latitudes (Figure 17).

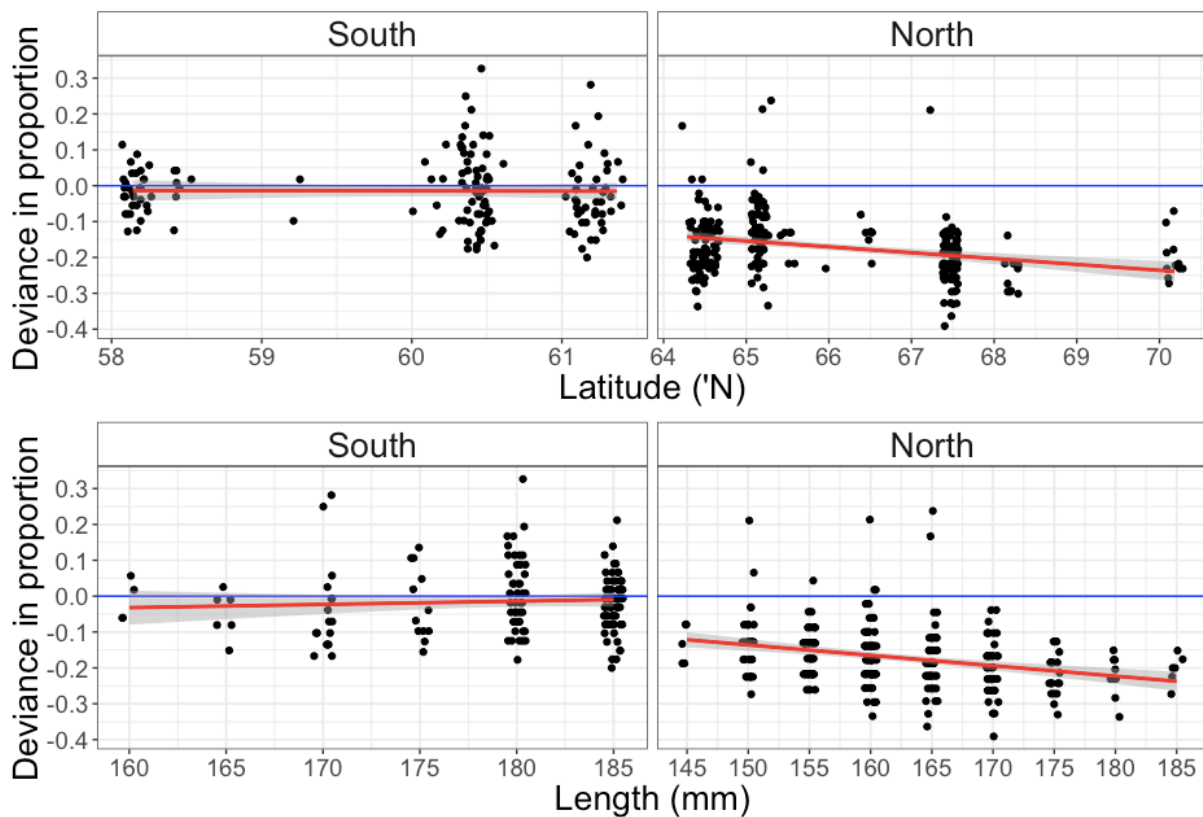


Figure 17. The individual variation from the mean for individuals smaller than 190 mm plotted against latitude °N (top) and length in mm (bottom), separated by latitude category south (58°N - 63°N) and north of 63°N. The blue line shows the estimated mean of the North Sea individuals, and the red line is the applied linear regression model. The plot points are jittered around the x-axis to reduce point overlapping. This reduces latitude accuracy in the plot.

The mean condition of juveniles north and south of 63°N were significantly different (two sample t-test: p -value < 0.001). Mean condition of small southern juveniles deviated by $-1.4 \pm 8\%$ from the North Sea mean while the mean weight of juveniles in the north deviated by $-17 \pm 8\%$. The increase in condition with latitude and length for juveniles south of 63°N was not statistically significant according to the LRM (Latitude; p -value = 0.2067, length; p -value = 0.5032). For juveniles north of 63°N the relative condition decreased with both increasing latitude and body length, and the effect of both latitude and length on body size was statistically significant (LRM: p -value < 0.001 ; body length, p -value < 0.001). This meant that in winter length and latitude had a significant effect on the condition of similar sized juveniles in the north, but not on juveniles in the south. This meant that the condition of the more northern juveniles decreased with increasing latitude and body length.

3.4.2 JUVENILE CONDITION DURING SUMMER

The same plottings of observed lengths with latitude and relative condition with latitude and body length were done based in on the data on juveniles from July during the same years. This was done to study whether the juveniles had grown, if the condition of the juveniles followed the same trend during summer as during winter, and if juveniles along the Norwegian coast were more or less similar to the estimated mean weight for the conspecifics the North Sea during summer.

Individuals caught north of 58°N in July had a mean length of 217 ± 17 mm. To test whether latitude had a significant effect on body length, a linear regression model was used. Juvenile body length was significantly affected by latitude (linear regression: p -value < 0.001), and the length decreased on average by 0.4 mm per degree increase in latitude (Figure 18). Since maximum length for juveniles was set to be the same for all latitudes and the linear regression model could be applied, the data was not split by latitude.

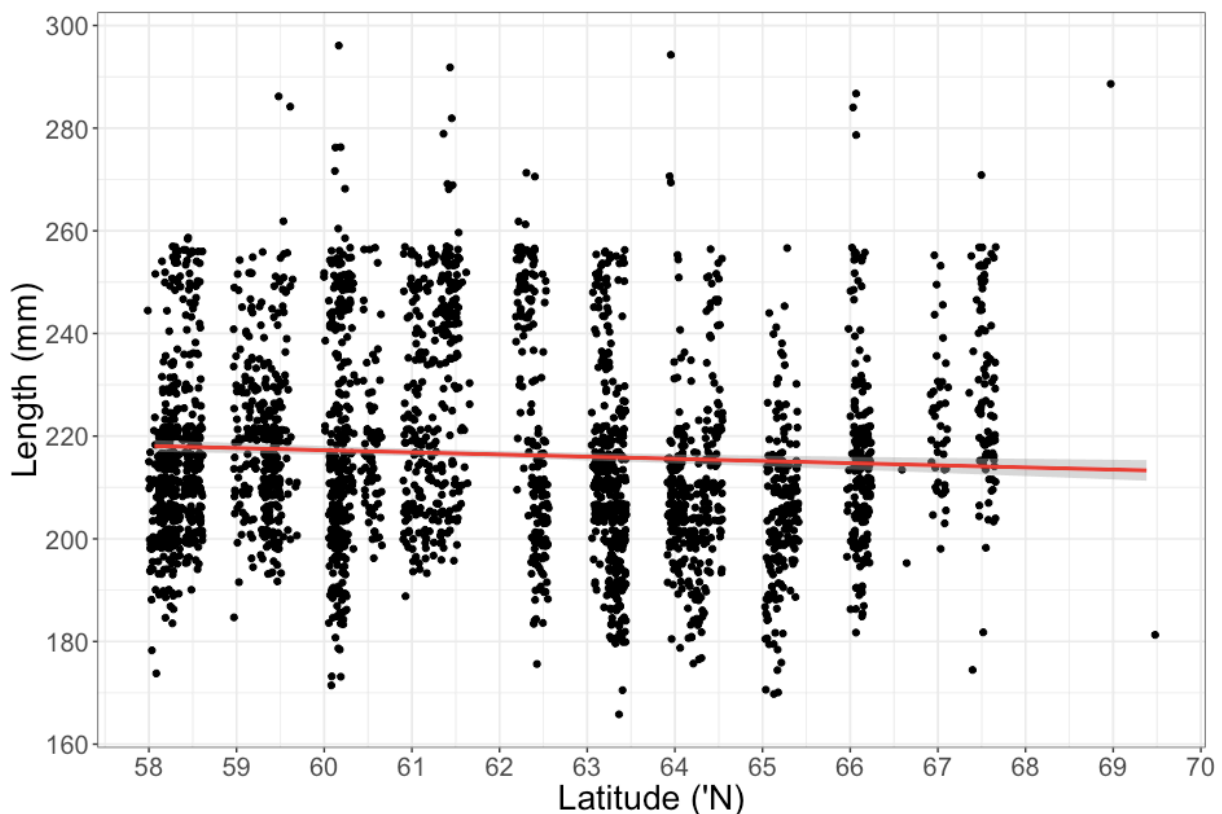


Figure 18. Latitude and individual length (mm) for all individuals, both age read and non-aged from the IMR-database from July 2017 and 2018 with an applied regression line (red). All observations exceeding maximum length (255 mm) were observations of age read individuals. The plot points were jittered around the x-axis to reduce point overlapping. This reduced latitude accuracy in the plot.

The individual variations from the North Sea mean weights were plotted against latitude and body length to study the difference from the estimated mean weight, which here was assumed to signify the condition of juveniles relative to their conspecifics in the North Sea. The mean weight of the individuals from July from 58°N and northwards was $-5 \pm 8.8\%$ lower than the mean estimated weight for individuals from July from the North Sea (Figure 19). If the juveniles were separated by latitude, individuals north of 63°N deviated by $-2.4 \pm 9.9\%$ from the North Sea individuals, while individuals south of 63°N deviated by $-7.3 \pm 8.7\%$. The greatest individual deviances from expected weight in percent were $+62\%$ and -60% . The output from the linear regression model stated that latitude had a significant effect on individuals caught in July (p-value < 0.001). Juveniles gained 0.8% body weight relative to the estimated mean weight per increase in latitude. This meant that for each increase in latitude degree the condition of July individuals increased, and the individual deviations from the North Sea mean was greater for individuals from the southern latitudes than from the higher latitudes.

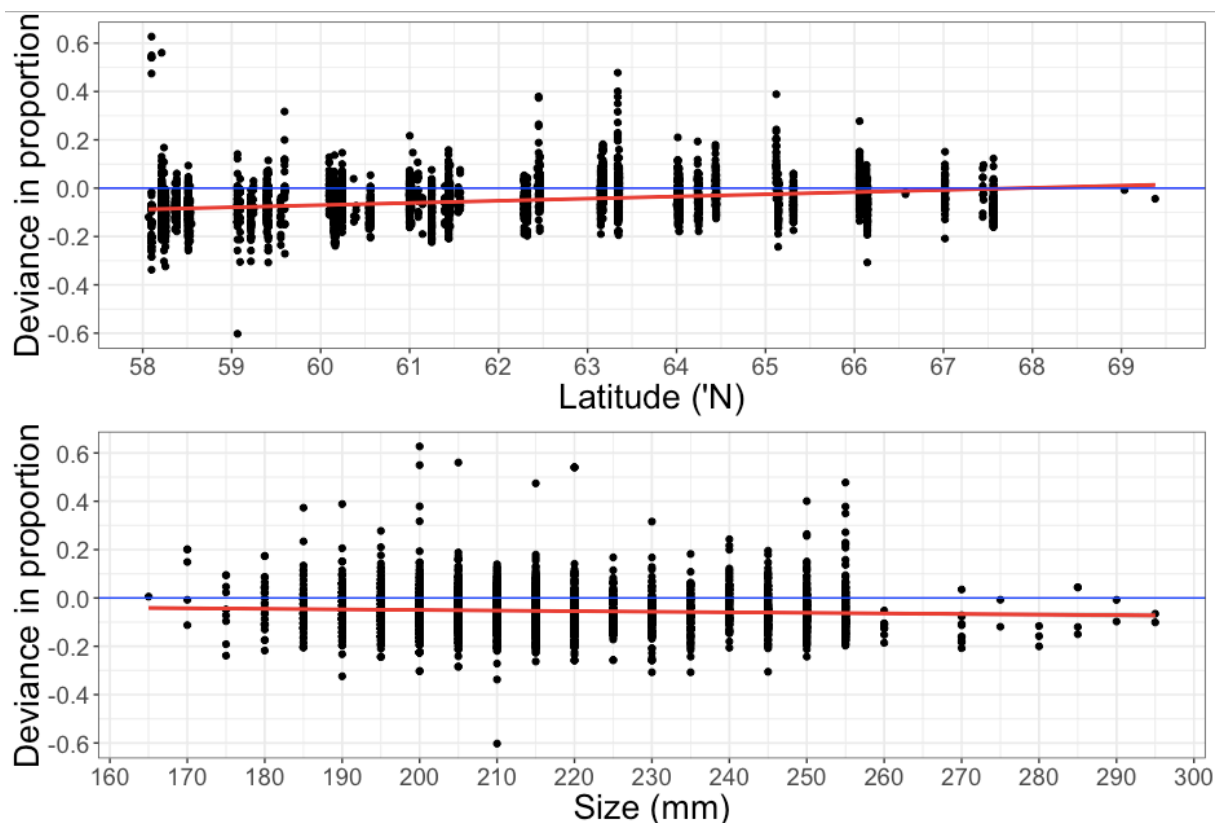


Figure 19. Latitude and proportional residuals (top), and body length and proportional residuals (bottom) from July of 2017 and 2018. The blue lines show the mean of the North Sea individuals, and the red lines are the applied linear regression model.

The change in condition with body length of juveniles was also studied to examine whether smaller individuals had significantly lower condition than larger individuals (Figure 19, bottom). The deviance with length from the North Sea mean was significant (ANCOVA; p-value < 0.001), which meant that the juveniles at Norwegian latitudes weighed significantly

less than was estimated for the corresponding sizes of juveniles from the North Sea. The output from the applied linear regression model determined that body length had a significant effect on the observed juvenile condition (p -value < 0.005). The slope of the regression line did on average, however, decline less than 0.1 mm with the increase in body length, which in practice meant little change in mean deviatin with increasing body length.

3.4.3 JUVENILE WINTER CONDITION COMPARED WITH JUVENILE SUMMER CONDITION

The juvenile size and condition in February were compared with size and condition in July to determine whether the relative condition differed between seasons. Since juvenile condition was expected to change with season, expressed by the change in a - and b -coefficients used for calculating relative condition, it was only possible to determine whether juveniles differed more or less from the expected mean weight for the North Sea juveniles during winter than during summer.

A two-sample t -test was applied to test whether there was a significant difference between the mean observed body length for juveniles along the coast during winter (194 ± 19 mm) and summer (216 ± 17 mm). The difference in mean length for individuals in February and July was significantly different (p -value < 0.001), which meant that juveniles along the coast on average were significantly larger during summer than winter.

A two-sample t -test was also applied to test if the mean observed variation from the estimated mean during winter and summer was statistically significant from each other. Mean condition differed significantly (p -value < 0.001), which implied that the juveniles caught during summer deviated less from the estimated mean weight-at-length, even when weight-at-length was expected to be higher during summer than winter (Appendix B).

The change in condition with individual length and latitude from February and July were tested against each other with two separate ANCOVA models to examine whether the effect of body size on condition, and the effect of latitude on condition, differed significantly with season. The change in condition with the change in latitude was also significant (p -value < 0.001), which meant that the observed change in condition with latitude also differed significantly between winter and summer. The p -value for interaction between body length and month was also significant (p -value < 0.001), meaning that the change in condition with body size during winter and summer were significantly different. This meant that the condition of juveniles during winter decreased faster with latitude and increased more with increasing body size.

3.5 THE DIET OF JUVENILE MACKEREL

A total of 146 individuals were sampled for dietary analysis. 126 individuals were caught at 12 trawl stations during the IESSNS-survey and an additional 20 individuals were caught at two trawl stations during the NSSH post-larvae survey. The sample sizes ranged between 3 and 14 individuals, and the most common number of individuals in the samples was 10.

All individuals used for stomach content analysis sampled during the NSSH post-larvae survey and the IESSNS-survey were determined to be one year old by the presence of one winter ring (first growth season in 2017) (Figure 20), except for the two individuals from which no otoliths could be retrieved. Since both individuals were 19 cm in length, they were assumed to be 1-group mackerel. Otoliths at the trawl station farthest north (69°N) caught in the middle of June had very little growth out from the winter ring, while most individuals from stations further south caught during the first weeks of July had otoliths with a clearly visible opaque growth zone.

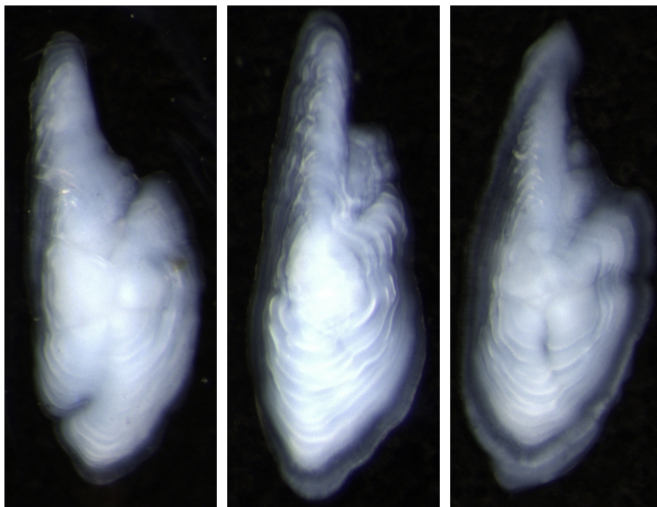


Figure 20. Left sagittal otoliths from 69°N in mid-June (left), 66°N in mid-July (middle), and 60°N in early July (right).

3.5.1 TEMPERATURE AND SALINITY AT SAMPLE STATIONS

The measured temperatures ranged between 5.2°C and 13.2°C and did on average decrease with increasing latitude. The highest measured temperature was measured at 60.2°N at station IE-3, while the lowest temperature was recorded at station IE-11 at 65.5°N (Figure 21, top figure). Salinity measurements ranged between 34.76 and 35.25 and generally followed the same trend as temperature with a decrease with increasing latitude (Figure 21, bottom figure). An error in the calibration of the CTD at IE-3 and NSSH-1 caused incorrect measurements of density, which resulted in the miscalculation of salinity at these stations.

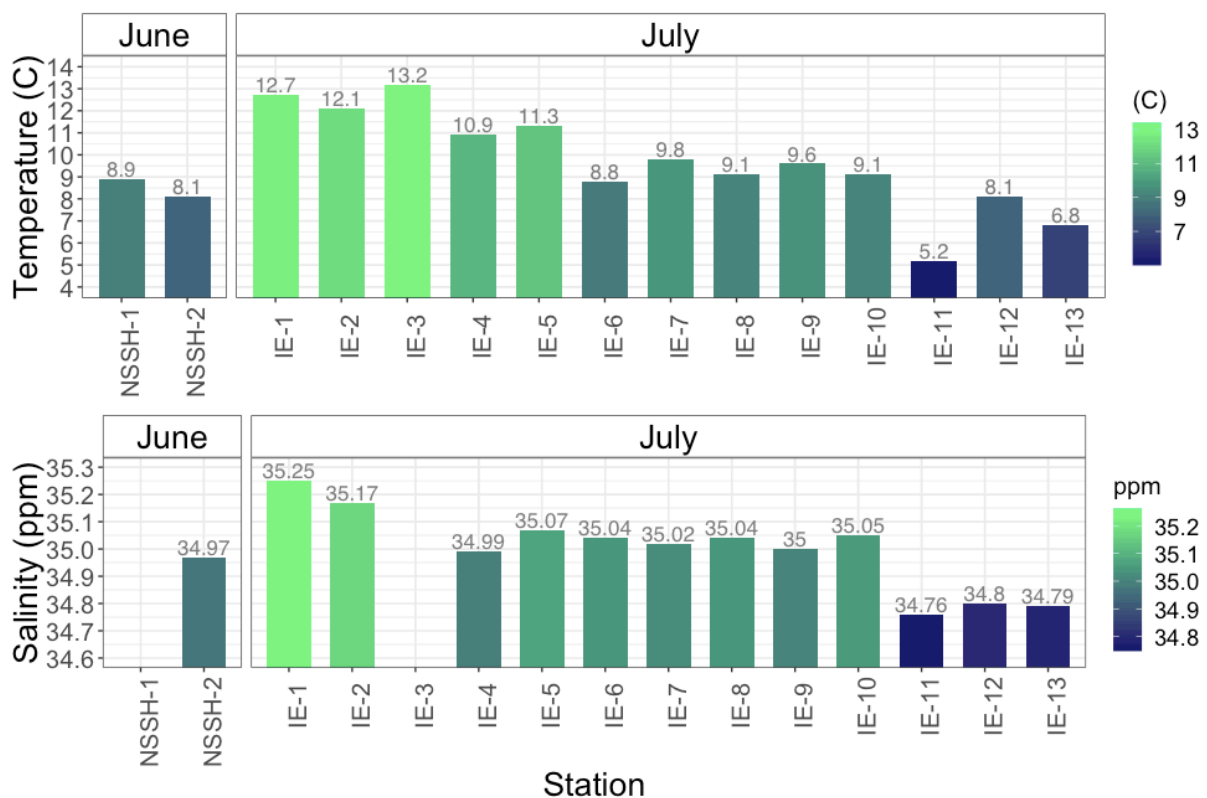


Figure 21. Measurements of temperature and salinity from the CTD at trawl stations where juveniles were caught for diet sampling. The two first stations, named NSSH-1-2 were sampled in June during the NSSH post-larvae cruise, while all other stations named IE-1-13 were sampled in July during the International Ecosystem Survey in the Nordic Seas (IESSNS). Order of the stations is by month, then by increasing latitude with locations mapped in figure 1 and figure 22.

3.5.2 STOMACH FULLNESS OF THE SAMPLED INDIVIDUALS

Altogether 78% (n=114) of the stomachs contained prey items, and the average stomach fullness degree was 2.6 ± 1.1 (some food content). Average degree of fullness of the individuals with prey items in the stomach was 3.0 ± 0.9 , and a total of 33 individuals had stomachs categorized as 4 (full, n=27) or 5 (bursting, n=6). Mean degree of stomach fullness did not seem to depend on latitude (Figure 22). Individuals from one station, IE-4, had an overall mean fullness degree of 1 (empty). The most common mean degree of fullness for the 15 stations was 3 (some content). The number of stomachs with content and the average degree of fullness suggested active feeding by the juveniles during the summer months.

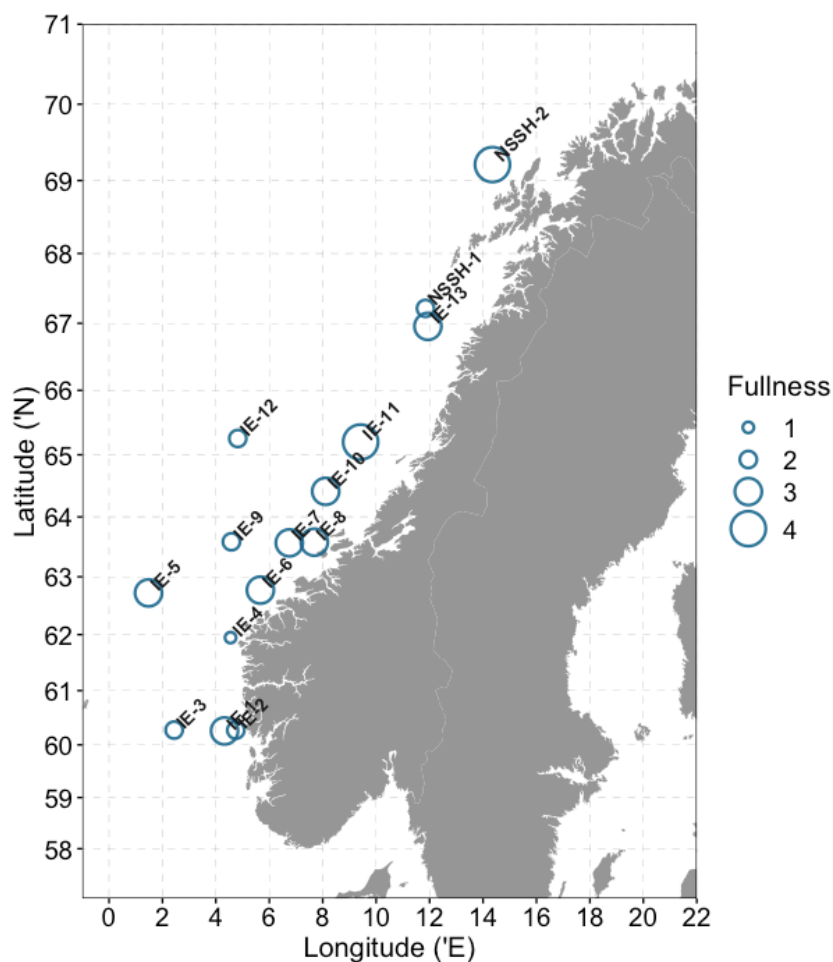


Figure 22. Overview of mean stomach filling from all individuals at each trawl station. The size of a circle indicates average filling degree. Points named IE-1-13 were from the International Ecosystem Survey in the Nordic Seas (IESSNS), and points named NSSH-1-2 were from the NSSH post-larvae survey. Calculated values of stomach fullness have been rounded to nearest whole number. Values with the decimal .5 or higher were rounded up.

3.5.3 DIET COMPOSITION OF THE SAMPLED INDIVIDUALS

The stomach content was analysed to study the prey composition of the juvenile mackerel, and to assess whether the juveniles were selective when feeding. Three main phyla were found in the stomachs, namely Chordata, Mollusca and the subphylum Crustacea. Of the 15 taxonomic ranks of prey identified, 12 belonged to various subgroups of crustaceans, two were within classes of chordata, and one prey group was identified as the mollusc genus *Limacina* sp. In addition to the 15 prey groups, prey items that could not be identified within the prey categories due to the degree of digestion were assigned to a “digested” category. The 15 + 1 prey groups have been grouped into 10 main categories, namely Amphipoda, Appendicularia, *Calanus finmarchicus*, Crustacea, Digested, Euphausiacea, *Limacina*, Other copepods, Other crustaceans, and Teleostei (Appendix D).

Prey items that could only be identified as crustacean organisms were sorted into the Crustacea category. The taxonomic groups Isopoda and Cladocera and larvae of crustaceans (zoea larvae, cirrus), which in most cases only were found as few numbers in few stomachs and accounted for less than one percent of the individual stomach content weight, were grouped together and labeled as Other crustaceans. The prey category “Other copepods” included digested copepods that could not be identified to species, as well as the two genus’ *Microcalanus* sp and *Pseudocalanus* sp. The identifiable copepods were not sorted by copepodite stages.

Appendicularians was the prey group that contributed the most to the total dry weight (31%) (Figure 23 and Figure 24). This prey group also occurred in 33% of all stomachs and at approximately 2/3 of all stations (Figure 23). The category that contributed the second most to the total dry weight was Digested prey (17.5%), and almost 25% of all stomachs contained some digested content. The two categories of copepods (Other copepods and *C. finmarchicus*) were the most common prey groups to find at the stations, and occurred in 2/3 and 1/3 of all stomachs, respectively (Figure 23 and Figure 24). Still, the total weight of *C. finmarchicus* only accounted for 1.2% of the total dry weight from all stomachs. The crustacean category was the third highest in station occurrence, and second highest in stomach occurrence. The three groups of Appendicularia, Other copepods, and Crustacea contributed each 10% or more each to the total dry weight, and accounted for ~72% of the dry weight. Fish larvae were present in stomachs of juveniles at two trawl stations, and contributed to 3.3% of the total stomach content weight (Figure 23).

Juvenile mackerel (*Scomber scombrus*) along the Norwegian Coast

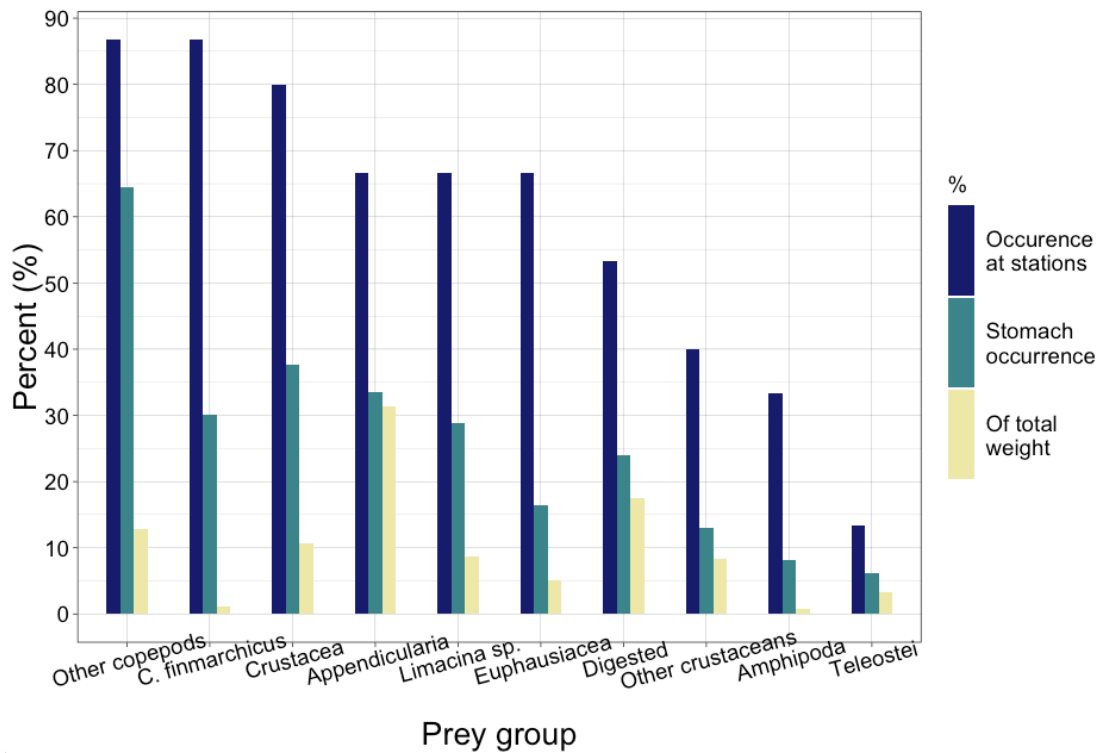


Figure 23. The occurrence of each prey group in percent at the trawl stations, number of individual stomachs each prey group occurred in as percent, and how much each prey group contributed in percent to the total dry weight from all 146 stomachs.

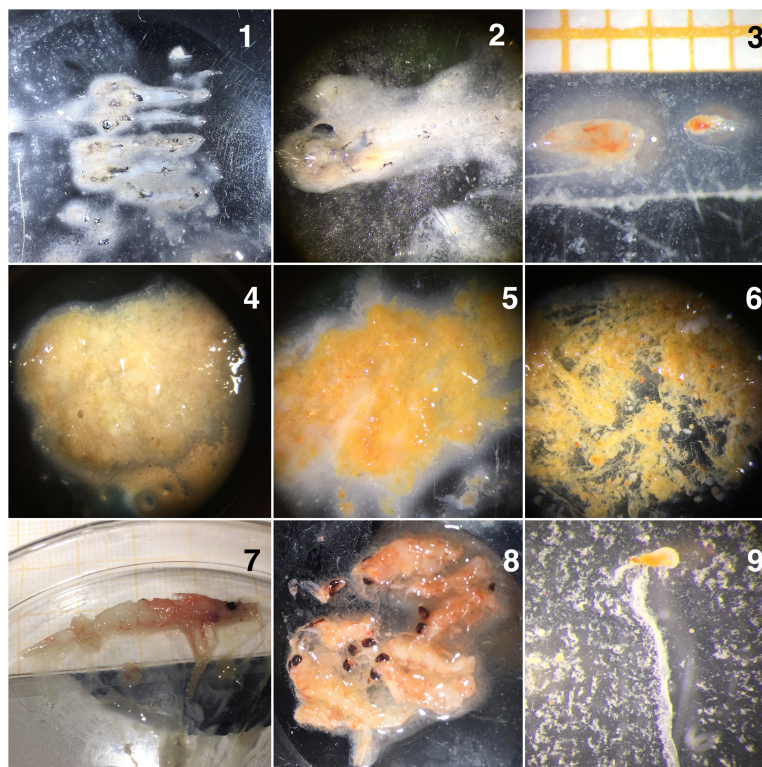


Figure 24. Images of recorded prey items. Fish larvae (1, 2), *C. finmarchicus* and *Microcalanus sp.* (3), digested prey (5, 6), mix of Appendicularia and copepods (6), Euphausiids (krill) (7, 8), and Appendicularia individ (9).

The stomach content composition of juveniles from the two samples taken during the NSSH-cruise in June differed from each other. The stomachs of juveniles caught at NSSH-1 mostly consisted of krill-remnants (Euphausiacea) and unidentifiable crustaceans. The northernmost station (NSSH-2, n=10) had the second highest total weight out of all the stations, and was dominated by crustaceans, digested stomach content and fish larvae (most likely herring larvae), but Amphipods, copepods and krill were also found (Figure 25). This was the only station out of the total 15 stations used for diet analysis where the juvenile mackerel had considerable quantities of fish larvae in the stomachs (~25%).

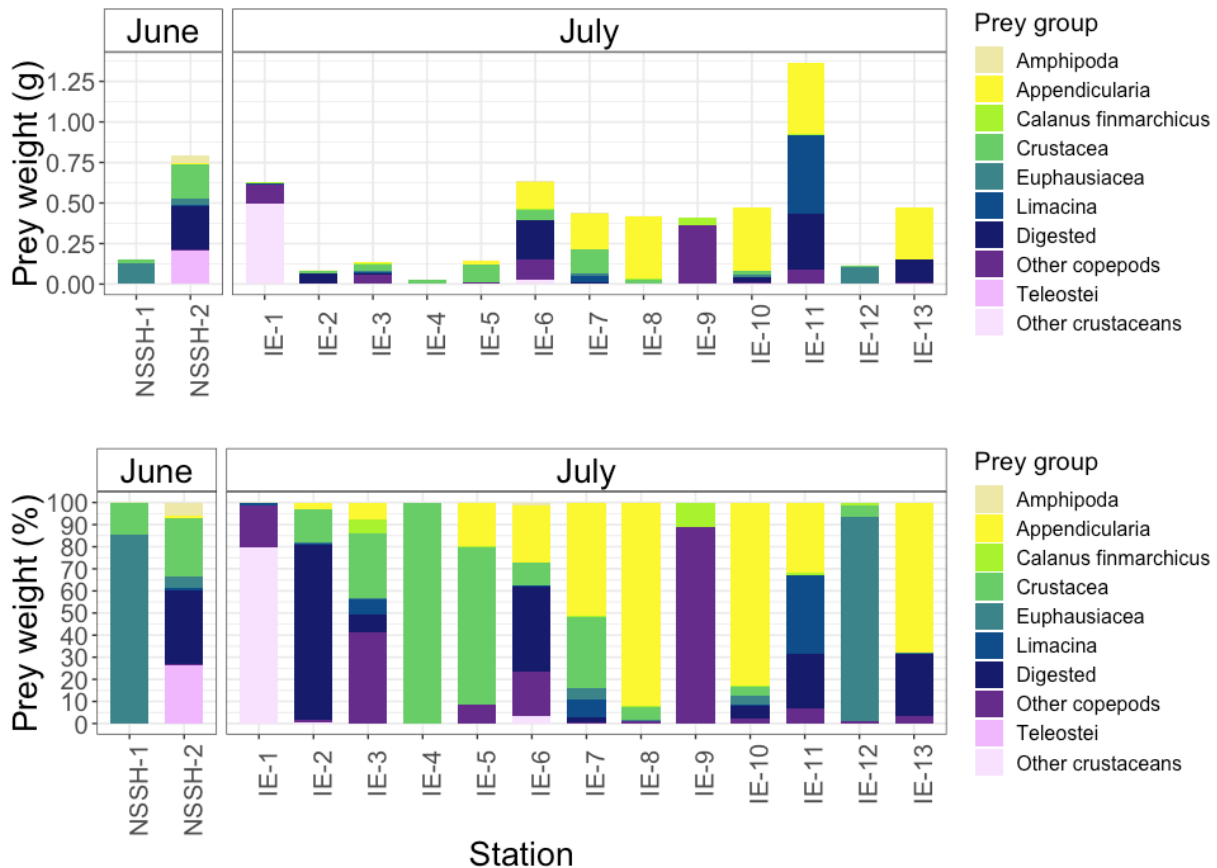


Figure 25 Diet composition at each station, separated by the month/cruise the individuals were sampled. The barplot on top shows content dry weight for all station in grams and the barplot on the bottom shows the prey content composition in percent. The two first stations, named NSSH-1-2 were sampled in June during the NSSH post-larvae survey, while all other stations named IE-1-13 were sampled in July during the International Ecosystem Survey in the Nordic Seas (IESSNS). Order of the stations is by month, then by increasing latitude with locations mapped in figure 1 and figure 22.

The stomachs from the IESSNS-survey during July were dominated by the presence of appendicularians and unidentified crustaceans (Figure 24). Appendicularians were not present in large quantities at the southernmost stations but contributed for the most part to 20% or more to the total stomach content weight at 7 stations north of 62°N (IE-5 and onward) (Figure 25, bottom row). Stomachs from IE-1 was dominated by Cladocerans (included in the group Other crustaceans), but this prey group was not found in the same quantities at any other stations.

Krill were mostly present in stomachs at more northern stations. Digested matter was found at multiple stations, scattered across all latitudes. The presence of very digested and less digested identifiable prey items in the same stomachs suggests that the juveniles feed continuously throughout the day, as well as feed whenever they locate prey of the right size. Prey items grouped together as Other copepods were found across multiple latitudes, and consisted for the most part of *Microcalanus* sp. in numbers, and non-identifiable/more digested copepods in weight (Appendix D). Identifiable individuals of *C. finmarchicus* was found in higher numbers at station IE-9, at 63.9°N than at any other station.

The number of individuals sampled at each station varied, meaning that the total stomach content weight at each station was not sampled from an equal number of individuals and weight per station is thus not comparable. Two of the three stations taken at night (2200 – 0600) were the third and fourth lowest in total stomach weight. No clear differences between the stomach weight at night and day was otherwise found. The presence of stomach content throughout the day/night cycle suggests active feeding at all hours of the day in the time of the year when the sun sets late or not at all. Generally, the diversity in prey selection and stomach content composition between each station suggests that the juvenile mackerel did not feed very selectively but had more of an *Eat-what-is-present* behavior.

4. DISCUSSION

The distribution of adult mackerel has expanded during the last decade (Nøttestad *et al.*, 2016a; Olafsdottir *et al.*, 2019), and the last few years an increasing number of juvenile mackerel have also been observed along the Norwegian coast (Nøttestad *et al.*, 2018). The northward distribution of juveniles into Norwegian waters, their weight-at-length along the coast, and their diet has to the best of my knowledge, not been studied prior to this study. My results show that juveniles were present along the Norwegian coast throughout 2017 and 2018, at least as far north at 70°N from winter through summer, indicating that the juvenile mackerel did not migrate from Norwegian waters during the fall and winter seasons but stayed throughout the year. Juveniles further north had a lower mean weight during winter than the conspecifics at more southern latitudes along the coast. But the mean weight-at-length of the northern juveniles increased significantly through spring and summer, and thus became more similar to the estimated weight of juveniles from the nursery areas than the juveniles at the southern latitudes from the Norwegian coast and the northern North Sea. Through diet analysis, a wide assortment of zooplankton groups, which to some extent varied with latitude, was found in the stomachs of juveniles caught along the coast. This demonstrate that juvenile mackerel along the coast fed on many types of zooplankton at all latitudes and were, thus, capable of locating and consuming prey during the summer season.

Several potential biases could affect the presented results. Firstly, there is a risk of including individuals of a younger or older age, when estimating age based on length frequencies of aged individuals. However, the potential errors of including juveniles of different ages are not substantial since the maximum lengths were set relatively conservatively, and the number of individuals would most likely only account for a small number in the data set. Since no quarterly surveys are covering the distribution of juvenile mackerel, and they are mostly regarded as bycatch along the coast, the full geographic distribution of juvenile mackerel throughout all quartiles, especially in Q4, may not have been adequately covered. It is, however, possible to assume that juveniles were present along the coast throughout all seasons of the year during 2017 and 2018, due to the observed distribution during adjacent quarters and by the information reported in through the IMR-questionnaires. The a- and b-coefficients for the North Sea individuals, used for a comparison between juveniles in Norwegian waters and juveniles from nursery areas, are based on survey data sampled between 1996 and 2008 (Wilhelms, 2013). Decadal variability in the weight-at-length for juveniles in the North Sea could, therefore, also affect the observed results from this study and be different from the present time. This was, however, the only source of a- and b-coefficients for juvenile individuals from the North Sea by quarters. The diet analysis of juvenile mackerel stomach content was only done on excess juveniles of the right sizes from trawl hauls during two IMR-cruises in June/July. To get more representative data on the juvenile feeding preferences in the future, the stomach content from

an increased number of juveniles caught from May through September would aid in answering what the juveniles preyed upon throughout the entire feeding season. Handling and analyzing digested stomach content is also an acquired skill that was challenging to become proficient in during a short amount of available time. This could be a source of potential error when the stomach content of the juveniles was handled and analyzed. When necessary, the results were cross-checked by Chief Engineer Herdis Mørk Langøy at IMR to limit potential errors.

4.1 THE HISTORIC DISTRIBUTION AND THE RECENT OBSERVED NORTHERN EXPANSION OF JUVENILE MACKEREL

THE DISTRIBUTION OF JUVENILES ALONG THE COAST

Juvenile NEA mackerel were distributed along most of the Norwegian coast and in Norwegian waters throughout 2017 and 2018. The described distribution extends far north of the traditional nursery grounds along the center of the European coastline (Jansen *et al.*, 2015). The distribution of juveniles during 2017 and 2018, is in accordance with the northward trend in juvenile distribution from 2014 to 2017 described in Nøttestad *et al.* (2018). Juveniles were found along the coast during all seasons, at 70°N or farther north during winter, spring and summer, and at a latitude 11° north of the northernmost observation in 2014 by Nøttestad *et al.* (2018). The number of caught individuals north of 70°N was higher in 2018 than in 2017, and the northernmost observation of juvenile mackerel was recorded at 73°N during early fall in 2018 which was 2°N north of the northernmost observation recorded in 2017. The registration of juvenile mackerel as far north as 73°N in September of 2018 is, to the best of my knowledge, the northernmost recorded observation of juvenile mackerel. The presented results could suggest that the number of juvenile individuals in the more northern latitudes has increased since 2016 (Nøttestad *et al.*, 2018), and that the juveniles were distributed further north in 2018 than in 2017. The observed pronounced northward distributional shift and the increase in juvenile density along the coast have taken place over a relatively short time period. Since 2016, sightings of juvenile mackerel as 0- and 1-group has been reported so far north as in Finnmark at 71°N (Nøttestad *et al.*, 2018). These observations were submitted by experienced fishermen and coastal residents who have never seen juvenile mackerel in the more northern latitudes along the coastline before. That the influx of young mackerel along most of the coast has taken place over a relatively short time is confirmed by data from the Norwegian Institute of Marine Research (IMR), as no juvenile mackerel were registered north of 62°N in Norwegian waters during winter or summer as recently as in 2014 (Nøttestad *et al.*, 2018).

POSSIBLE EXPLANATIONS FOR THE OBSERVED CHANGES IN THE DISTRIBUTION OF JUVENILES

A more northern juvenile mackerel distribution is likely caused by the increasing number of fecund adult mackerel residing and spawning in Norwegian waters, an anomaly in the adult distribution that has been observed during spring and summer since 2016 (Nøttestad *et al.*, 2018). A gradual northwards shift in the spawning distribution of NEA mackerel has also been observed during the past 40 years (Reid, 2001; Hughes *et al.*, 2014). However, the slower and more steady northwards shift in the spawning distribution described in these studies did not correspond with the pronounced and sudden influx of fecund females along the Norwegian coast and the northward expansion of the juvenile distribution occurring within the past three to four years.

The marked change in the distribution of juvenile mackerel along the coast is likely a result of a large adult mackerel stock and increasing sea surface temperatures (SST) that could have increased the potential habitat for the mackerel. The NEA mackerel stock has since 2007 increased in size and expanded its area of distribution in a northward and westward direction during the summer feeding season (Berge *et al.*, 2015; Nøttestad *et al.*, 2016a). During the same time the mean length and weight of adult individuals have decreased, an effect assumed to be caused by intensified resource competition between individuals due to the increase in stock size (Olafsdottir *et al.*, 2016). A large stock size, and the increased exploitation of the zooplankton biomass or the reduced primary production are likely factors that lead to overgrazing in waters where food availability previously has been abundant and thus result in local nutrient depletion. Therefore, the adult mackerel may have had to reduce the competition with conspecifics by migrating farther westward and northward during the feeding season into waters where mackerel previously not have been common in order to encounter sufficient amounts of prey.

The increasing SST during the last two decades is hypothesized to have expanded the potential habitat of adult mackerel, and thus facilitated a potential reduction of the density dependent effects caused by a larger mackerel stock (Olafsdottir *et al.*, 2019). Berge *et al.* (2015) hypothesized that the rising of sea temperatures in the North Atlantic has made it possible for adult mackerel to migrate as far as Isfjorden, located on Svalbard at 78°N. It is unlikely that adult mackerel would have migrated this far north without an incentive like increasing the feeding rate or reducing the competition with conspecifics. The increasing temperatures have also likely expanded the scope of the potential spawning areas (Bruge *et al.*, 2016), which are observed to have become realized spawning areas within the last couple of years as the stock has grown in size and the adult mackerel have expanded their area of distribution. Increasing temperatures along the coast would also expand the scope of potential mackerel nursery areas, and thus facilitate a more northward distribution of juveniles when adult mackerel spawn in more northern areas. Mackerel larvae and juveniles have been shown to be sensitive to the

surrounding temperatures (McManus *et al.*, 2018), meaning that the temperatures along the coast have to be within the tolerable limits throughout the year for the juveniles to survive and grow. The juveniles used for dietary analysis were caught at temperatures between 5°C and 13°C, which suggests that the juvenile mackerel, at least periodically, tolerate temperatures lower than the optimal temperatures reported for adult mackerel (Utne *et al.*, 2012; Olafsdottir *et al.*, 2019). In addition, my observation of juvenile mackerel as far north as 73°N in September of 2018, and above 70°N during winter (Q1) and spring (Q2), indicate that the surface temperatures at these latitudes at the time were tolerated by the juveniles. In the present study, the juvenile distribution throughout the year has not been studied in relation to the SST, but it is evident that the temperatures along the coast the past two years were adequate for the juvenile mackerel to be able to survive through all seasons.

THE CHANGE IN JUVENILE DISTRIBUTION IS LIKELY CAUSED BY A MORE NORTHERN SPAWNING DISTRIBUTION

The influx of juvenile mackerel along the Norwegian coast is likely a result of a more northern spawning distribution and not due to the drifting of eggs and larvae from the traditional nursery areas or migrating juveniles. If eggs and larvae were carried with the Norwegian Coastal Current northward from the traditional spawning areas and were able to survive, juvenile mackerel would most likely have been observed sporadically along the entire coast at an earlier point in time. In addition, preliminary egg simulations modelling the drift of spawned eggs and larvae showed that mackerel eggs released south of 64°N during spring and early summer (June) did not reach the archipelago of Vesterålen (68°N) or latitudes further north before the simulated larvae were 80 mm long (Nøttestad *et al.*, 2018). This means that there is a low probability of juveniles being carried northwards with the current from the spawning areas around the British Isles and the North Sea located south of 60°N to latitudes above 70°N. The migrating behavior of juvenile mackerel also reduces the probability of juveniles migrating northwards from the traditional nursery areas along the Norwegian coast. Juvenile mackerel do not migrate between spawning areas, summer feeding locations, and overwintering grounds until they have reached maturity (Uriarte *et al.*, 2001). A study of tagged juvenile mackerel between zero and two years of age found that the juveniles instead tended to remain close to the area at which they were first tagged (Uriarte *et al.*, 2001). The submitted observation of mackerel juveniles measuring ~10 cm found in the stomachs of saithe at 66°N (Figure 12) is also a strong indication of a shift in the spawning distribution of adult individuals, as it is highly unlikely that 0-group mackerel undergo migration from the spawning grounds in the North Sea. Hence, the available evidence strongly indicates the juveniles along the Norwegian coast were spawned at more northern locations than previously observed, and that the juveniles occupy waters within the egg- and larvae-drifting range of the new spawning sites.

The more northern distribution of juvenile mackerel indicates that the juveniles along the Norwegian coast have been spawned farther north, which also suggests that the spawning of parts of the adult mackerel stock occur at latitudes farther north than what has been described previously. Moreover, if juvenile mackerel spawned at northern latitudes along the coast undergo spawning migrations back to the same latitudes when they become mature adults, juvenile mackerel will likely continue to inhabit the Norwegian coastal waters in the upcoming years. If some mackerel spawn at more northern latitudes their migration route also has to deviate from the traditional migration route southwards to the traditional spawning locations. Jansen *et al.* (2015) hypothesized that the Norwegian coastal shelf in the future could be of increasing importance for spawning mackerel, most likely due to the rise in sea temperatures and the northward movement of the spawning areas. The more northern distribution of juvenile mackerel described in this thesis suggests that the assumptions by Jansen *et al.* (2015) are correct.

4.2 JUVENILE WEIGHT-AT-LENGTH IN NORWEGIAN WATERS

Body sizes of one-year-old juvenile individuals overlapped less with two-year-old juveniles during winter than summer, which makes them more difficult to age by the individual length as the calendar year progresses. The overlap in length frequency distribution with two-year-old individuals during summer is likely due to a higher growth rate of the one-year-old individuals relative to the older individuals, as the somatic growth of fish taper off with age (Jennings *et al.*, 2013), while younger fish grows at a faster rate. The results also show that the larger one-year-old juvenile individuals can reach the body lengths of two-year-old individuals during spring and early summer. Hence, one-year-old mackerel does feed and grow along the Norwegian coast during spring and summer. The results from the fullness analysis confirm this, as the stomachs of the sampled juveniles varied between all fullness degrees (1-5). Food was present in the stomachs at all latitudes, which confirms that the juveniles feed regardless of where they have been caught along the coast.

SEASONAL AND LATITUDINAL VARIABILITY

The mean weight of one-year-old juvenile mackerel from 2017 and 2018 caught along the Norwegian coast and in the northern North Sea was on average lower than the mean estimated weight of juveniles from the nursery areas in the North Sea during winter and summer. During winter, the differences were the largest and the juveniles on average weighed less and thus deviated more from the mean weight of juveniles in the nursery areas. Along the Norwegian coast, the body size of juveniles in the north decreased with increasing latitude and the juveniles north of 63°N during winter deviated more from the estimated weight than the juveniles south of 63°N. At the southern latitudes, the juveniles on average deviated by -1.4% from the estimated weight-at-length, meaning that the juveniles caught at the lower latitudes along the coastline were similar to the mean individual from the North Sea during winter. Juveniles in

the north deviated from the mean estimated weight by -17%, meaning that the average juvenile caught at northern latitudes along the Norwegian coast weighed 17% less than what was expected for the conspecifics of the same size from the nursery areas. These results suggest that the juveniles caught at the more southern latitudes during winter are more similar in body condition with the juveniles in the nearby nursery areas than they are to the juveniles in the north.

The observed differences between the nursery areas and the Norwegian juveniles, and the differences between juveniles from the southern and northern latitudes along the Norwegian coast, could be due to a delay in the spawning, as the mackerel spawn later at higher latitudes (Iversen, 2004). Adult mackerel spawn sequentially along the European coast, from February in the south to June and July in the north (Iversen, 2004; Trenkel *et al.*, 2014). The individuals from the Norwegian coast are thus likely to be spawned later than the juveniles that reside in the established nursery areas, and the juveniles north of 63°N are likely to be spawned after the juveniles south of 63°N. If this is the case, the size of juveniles at the end of the feeding season is likely to be negatively correlated with the spawning latitude as the juveniles farther north will be smaller since they start feeding later than their conspecifics farther south.

It is also reasonable to assume that the conditions along the Norwegian coast during winter become increasingly different with latitude, which also could aid in explaining why juveniles from Norwegian waters on average were slimmer than what was estimated for juveniles from the nursery areas, and why juveniles from the northern latitudes differed significantly from juveniles farther south. Decreasing availability of daylight during fall and winter affect the primary production in all temperate waters, leading to low abundances of zooplankton biomass in the water column (Melle *et al.*, 2004). The days are shorter in the higher latitudes, meaning that juveniles farther north experiences shorter days and thus have less time during the day to actively localize what little prey is available. The winter temperatures could also affect the juveniles physically, leading to a reduced metabolic rate and slower digestion and uptake of nutrients. Adult mackerel have been shown to increase their swimming speed when exposed to temperatures below the preferred minimum temperature (Olla *et al.*, 1976), but it is unknown whether this behavioral response occurs in juvenile mackerel or if the colder water makes the juvenile mackerel less active and thus reduces the energy consumption. Juveniles in the north, however, seems to be exposed to harsher conditions during the winter time. Still, they seem to be able to tolerate these conditions well enough to survive during winter as they were found above 70°N during winter, spring and summer.

During summer the differences between the observed mean weights of juveniles from Norwegian waters and the estimated mean weight for juvenile mackerel in the North Sea were less pronounced. This means that even though juveniles from the Norwegian coast on average weighed less during summer than what was estimated for the juveniles from the nursery areas, the Norwegian juveniles still increased their mean body weight during spring and early summer.

For juveniles along the coast, it was the juveniles north of 63°N that on average were more similar to the estimated mean weight-at-length for juveniles from the nursery during the summer. This meant that the trend observed during winter with decreasing deviance for the weight-at-length with latitude was reversed during summer. The juveniles in the north only deviated by -1% from the estimated mean weight, while juveniles in the southern latitudes along the coast average deviated by more than -7%. These results suggest that even if the spawning in the north might occur later which could shorten the feeding period and result in smaller body sizes of juveniles throughout fall and winter, and the environmental conditions in the north are likely to be more challenging, the environmental and nutritional conditions during spring and summer are favorable as the more northern juveniles were more similar to the estimated mean weight than both juveniles in southern latitudes along the coast, and juveniles in the northern North Sea. The pronounced growth of the northern juveniles could be a result of two circumstances, either higher food availability in the more northern latitudes or a possible prolonged feeding period throughout the day due to the increase in day length.

It is also possible that a temporal lag in the poleward succession of the zooplankton community between the southern latitudes and northern latitudes has an impact on the relative condition of the mackerel juveniles throughout spring and summer. The spring bloom of phytoplankton is initiated in the southern latitudes and propagates northwards as a response to the increase in day length, the rise and narrowing of the mixed layer, the warming of the surface waters, and accumulated concentration of nutrients (Mann and Lazier, 2006). The zooplankton community follows the poleward progression of the primary production, causing the abundances of zooplankton farther north to be higher at a later point during the spring and summer season than at more southern latitudes (Melle *et al.*, 2004). The northward progression of the primary and secondary production could cause the food availability to follow a successive pattern as there is likely to be higher food abundances in the south during spring, while food abundances in the north are likely to increase at a later point in time as spring progresses to summer (Melle *et al.*, 2004). This could mean that juveniles in the northern latitudes experience higher availability of nutrient rich prey at a later point during the season, and has an advantage as light availability is not limited during high summer at the more northern latitude which means that they can continuously feed on energy rich prey organisms throughout the day.

From the relative condition of individuals it seems like the weight-at-length for juveniles along the Norwegian coast is highly dependent on seasons, and that environmental conditions, spawning time, and food availability may affect the juveniles significantly. That juveniles north of 63°N are able to survive during winter, even when mean weight-at-length is more than 15% below the estimated mean weight for the conspecifics in the nursery areas show that the juveniles are capable of surviving through the winters along the Norwegian coast, as well as catch up and surpass the mean weight-at-length for juveniles in the southern parts of the coast. That they are capable of surviving through their first winter in Norwegian waters suggest that

a large number of juveniles found along the Norwegian coast and surrounding waters, especially in the more northern latitudes, occupy these waters throughout their first years. Juvenile mackerel are thus capable of tolerating the environmental conditions along the coast adequately enough to grow and potentially reach maturity.

4.3 THE DIET OF JUVENILE MACKEREL FROM THE NORWEGIAN COAST

DIET COMPOSITION

The identified prey groups found within the stomachs of the sampled juvenile mackerel strongly indicate that the juveniles caught along the Norwegian coast feed on the same prey sizes and prey groups as adult mackerel. Studies conducted on juveniles from the nursery areas have shown that the prey size and feeding frequency of juvenile mackerel increase with the individual size as the larvae undergo metamorphosis (Jansen, 2016), and that they in the nursery areas mostly feed on adult copepods, cladocerans and fish larvae (Conway et al., 1999). The precocious digestive system allows the juveniles to feed on prey items that also are preferred by adult mackerel (Prokopchuk&Sentyabov, 2006; Langøy et al., 2012; Jansen, 2016). Diet studies conducted on the stomach content of adult mackerel have shown that they have a high preference for calanoid copepods, especially *Calanus finmarchicus* (Langøy et al., 2012; Prokopchuk and Sentyabov, 2006). Other prey groups that are also commonly found are euphausiids, pteropod gastropods within the genus *Limacina* sp, tunicate species within the class Appendicularia, and pelagic amphipod species like *Themisto* sp. (Langøy et al., 2012). These prey groups were all found within the stomachs of the sampled juvenile mackerel. These findings demonstrate that the juveniles along the Norwegian coast as 1-year-old individuals does feed on the same prey groups as adult mackerel.

The types of prey found within the stomach of juveniles show that the juvenile mackerel are capable of feeding on various prey species that are assumed to require various amounts of digestion. The prey group that accounted for the highest amount of dry weight was appendicularia. These organisms are nutritious, slow swimming, gelatinous zooplankton without a carapace, which makes them easy to digest for the species that prey upon them (Purcell *et al.*, 2005). These plankton groups can thus be attractive prey to the juvenile mackerel as they are less likely to require the same time or energy to digest as prey species that are protected by an exoskeleton or shell such as the planktonic gastropod genus *Limacina* sp., which also was found within the stomachs of the sampled juveniles. These molluscs have a shell made of aragonite, a calciferous compound, which protects the soft tissue of the snail (Hickman Jr. *et al.*, 2014). The shell has to be digested by the species that prey upon them for the predator to be able to acquire the nutrients from the prey organism. The ratio between the time of digestion and the energy obtained per ingested prey is thus likely to be lower for these prey types relative to the gelatinous planktonic prey groups. If this is the case, it also means

that the shelled prey organisms have to be eaten in higher quantities to provide the same amount of energy as the more digestible prey types such as appendicularians. Larger crustacean organisms found within the juvenile stomachs, such as amphipods and euphausiids, have exoskeletons made of chitin, a polysaccharide similar to cellulose (Hickman Jr. *et al.*, 2014). The carapaces of these prey organisms also need to be digested for the juveniles to obtain the energy of the prey. Fish species that feed upon organisms with chitinous exoskeletons have specific enzymes within their gut that catalyze the dissolving of the chitin (Danulat, 1987; Seiderer *et al.*, 1987), and making the digestion process more time efficient. It is likely that mackerel have analogous enzymes in their digestive system as mackerel feed on numerous crustacean species and have to digest the prey efficiently due to their active behavior.

The presence of fish larvae in the stomachs of juveniles at two stations confirms that juvenile mackerel along the coast did prey on the larvae of fish, although only 6% of the sampled stomachs contained this type of prey and the dry weight only accounted for 3.3% of the total stomach content weight. The station at which fish larvae contributed significantly to the prey composition at the station was sampled during the NSSH (Norwegian Spring Spawning Herring) post-larvae cruise at 69°N. The purpose of this research cruise is to study the distribution of herring larvae and their predators, and the larvae found in the stomachs of the juveniles are thus assumed to be herring larvae. Adult mackerel have been found to feed opportunistically on herring larvae if their distribution have a temporal and spatial overlap (Skaret *et al.*, 2015). This could also be the case for juvenile mackerel as their distribution during spring and early summer along the Norwegian coast overlap with the distribution of herring larvae drifting northwards along the coast to the nursery areas (Dragesund *et al.*, 1997). The total weight of the larvae found within the studied stomachs does not signify that the predation on herring larvae by the juvenile mackerel is extensive and significant for the herring population. This, however, needs to be studied more extensively.

CALANUS FINMARCHICUS IN THE DIET

The occurrence of the calanoid copepod species *Calanus finmarchicus* in the stomachs of the studied juveniles was low when considering it is the most common and preferred prey of adult mackerel (Prokopchuk and Sentyabov, 2006; Langøy *et al.*, 2012; Bachiller *et al.*, 2016). One of the main reasons for adult mackerel sustaining the long migration to the summer feeding grounds in the Norwegian Sea and adjacent waters is the high densities of this copepod species (Prokopchuk and Sentyabov, 2006; Langøy *et al.*, 2012; Bachiller *et al.*, 2016). Generally, low numbers of *C. finmarchicus* was found in the stomachs of the sampled juveniles from the Norwegian coast which only accounted for 1.2% of the total stomach content weight. Even though *C. finmarchicus* was a small fraction of the examined content from the juvenile stomachs, one or more individuals were present in approximately 30% of the examined stomachs. These findings could either signify that there were low abundances of *C. finmarchicus* during the period and at the locations where the juveniles were caught, or that the

juvenile mackerel along the coast prefer other types of prey species. The latter explanation is very unlikely as juvenile mackerel in the nursery areas have high preferences for *C. finmarchicus*, and the survival of juveniles in these areas has been found to be linked with their abundance (Jansen, 2016). It is thus more likely that the first seasonal bloom of *C. finmarchicus* had occurred previous to the sampling of juveniles, while the onset of the second seasonal bloom occurred later in the season, resulting in lower abundances of this copepod species during late June through mid-July (Melle *et al.*, 2004). If a higher number of copepod individuals sorted into the general copepod group could have been identified down to species, it is likely that a higher number of *C. finmarchicus* would have been found, but not in such large quantities that it would have made *C. finmarchicus* the most dominant prey group of the juveniles or impacted the weight significantly. My findings strongly suggest that the juvenile mackerel caught along the Norwegian coast are capable of localizing other prey items of various sizes and species when the abundance of *C. finmarchicus* is low.

FEEDING BEHAVIOR

The content found in the stomachs of the individuals caught in June and July indicated that the individuals along the Norwegian coast, like the individuals in the nursery areas (Trenkel *et al.*, 2014), switch between passive filtering of plankton through the gill rakes and active feeding on larger types of prey. At the same time, it also appears like the juveniles are opportunistic when selecting prey, as there were many types of prey in the stomachs and the composition varied between all stations and across latitudes. The opportunistic prey selectivity is also observed for adult mackerel (Langøy *et al.*, 2012). The sizes of the prey found in the stomachs across all stations ranged between 1 mm (*Microcalanus sp.*) and 3-4 cm (krill and fish larvae). Of the 35 stomachs that were categorized as a 2 in fullness, meaning that the content was not noticeable until the stomachs were opened, 5 out of 7 only had one or more group of copepods in them. Small prey groups were thus present far more often than larger types of prey in the stomachs without much content. The presence of small prey within almost empty stomachs could indicate that the juveniles most of the time are passively filtering out prey organisms from the water while swimming, and switch to active particulate feeding when larger types of prey are present like adult mackerel have been observed to do (Bachiller and Irigoien, 2012). If the juveniles were more selective when feeding and only showed preferences for filtering organisms passively through the gill rakes, no large planktonic prey types would have been present in the stomachs. And if the juveniles were only selective towards larger prey types that have to be actively chased after, like fish larvae and euphausiids, these prey types would have been expected to contribute more to the total stomach content weight at the stations where these prey groups were found to be present in the stomachs. Based upon the stomach content it appears like the possibility of switching between feeding behavior, depending on prey concentrations, enables the juveniles to continuously feed on the smaller prey groups that are available in the water column, and if larger prey types emerge the juveniles can switch to more active feeding

behavior. By continuously feeding on smaller prey organisms when filtering passively, it is less likely that the energy reserves of the juveniles become depleted and that when the juveniles encounter larger prey organisms, they can feed on food items of a larger volume and with more energy per prey that is ingested. By altering their feeding behavior, the juveniles can conserve energy as they are less likely to deplete their energy reserves between each time they encounter larger prey organisms.

4.4 ECOLOGICAL ASPECTS OF THE SHIFT IN JUVENILE DISTRIBUTION

Although the ecological effects of the poleward expansion of juvenile mackerel distribution at this point are not fully known, it is possible that the local influx of juvenile mackerel in some areas could affect the coastal ecosystems. For instance, an increasing number of juvenile mackerel could, periodically, intensify the top-down control in local areas. Models have suggested that this occur in the Norwegian Sea, where multiple pelagic species feed on the sizable biomass of zooplankton during summer (Daewel *et al.*, 2014). The total biomass of juvenile mackerel in Norwegian waters is still yet to be estimated. Thus, it is not possible to determine the total energy requirements of the juveniles residing along the coast. It is, however, possible to assume that the juvenile mackerel are adept at locating prey and feeding at a high intensity since they are a fast swimming, schooling species. If the increasing numbers of juvenile mackerel along the coast do exert high predation pressure on the zooplankton community in local areas, it is possible that the planktonic biomass may be depleted faster than normal.

Local depletion of the plankton biomass could affect coastal species that feed on plankton. As has been shown in this thesis, juvenile mackerel from the Norwegian coast prey on species that adult mackerel also exploit during feeding season (Langøy *et al.*, 2012). However, during feeding season the adult mackerel migrate to the Norwegian Sea to feed, which likely reduces the competition between juveniles and adults during the summer. The relative condition of the juveniles may, however, be affected by competition between the juveniles as increased resource competition between juveniles from the nursery areas has been shown to reduce the individual body size (Jansen and Burns, 2015). Juvenile mackerel could also have the potential to affect the recruitment of other fish species, such as herring, which was found in the stomachs of juveniles in this study, if the distribution of juveniles and herring larvae overlap sufficiently in time and space. At this time, it is likely that the effects of the predation on herring larvae by juvenile mackerel along the Norwegian coast is not affecting the total herring population. It might, however, possibly affect the local recruitment to the herring population from localities along the coast if the predation rate becomes high.

The northward shift in juvenile distribution could also affect higher trophic levels. Both killer whales (*Orcinus orca*) and the bluefin tuna (*Thunnus thynnus*) have been studied in relation to

mackerel distribution (Nøttestad *et al.*, 2014; MacKenzie *et al.*, 2014). Mackerel have high fat content and are thus beneficial prey to these large, predatory species. The increased abundances of juveniles along the Norwegian coast are thus likely to be of nutritious value both to the predators that make frequent visits to the Norwegian coast during the year and to predators that inhabit coastal waters permanently. The reported observations of juveniles as prey to predatory species such as saithe (Figure 12), pollack, cod and angler fish provides evidence for this and the influx of juvenile mackerel along the coast can, therefore, potentially increase the prey availability for predatory species along the coast.

The ecological effects caused of the influx of juvenile mackerel in Norwegian waters have to be studied more extensively in the future if the juvenile mackerel continue to reside along the coast. If the distribution of the nursery areas continues to advance northwards, or an increasing number of adult mackerel make use of Norwegian waters as spawning areas, it is likely that the juvenile mackerel could impact local ecosystems along the coast as well as fjord ecosystems. To what extent the juvenile mackerel does, and potentially will, influence these ecosystems is still unclear. Mackerel as a species can play many roles in the ecosystem. It is a predatory species on zooplankton and as a schooling species, high food densities during the feeding season is likely required to sustain the population of juvenile mackerel until they begin the summer migration as adults. They are at the same time a potential source of valuable food for predators during the larval, juvenile, and adult phase. Thus, juvenile mackerel have the potential to regulate the zooplankton community in local areas, compete with other juveniles and planktivore species, while at the same time being prey for larger predatory species.

5. CONCLUDING REMARKS

The poleward expansion in the distribution of juvenile mackerel has happened subsequently of the increase in SSB and the expansion of the adult distribution. The influx of juvenile mackerel along the coast is, thus, likely a consequence of the broader and more poleward distribution of the older cohorts, which in turn has resulted in a northward shift in the spawning distribution. That the distribution of juvenile and adult mackerel gradually shifts northward could be an effect of warming surface temperatures which expands the potential habitat for temporal species. As a migrating species with a diverse planktonic diet, Atlantic mackerel can adapt and shift its distribution due to the growth of the stock and changes in the environment. While some species that are less adept at relocating to new areas or have lower tolerability for increasing temperatures might struggle in the future, Atlantic mackerel might continue to thrive at higher latitudes while spawning and inhabiting Norwegian waters during their first years.

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APPENDIX A

A: IMR-form for opportunistic submissions of observations of juvenile mackerel along the coast, published at the IMR homepage December 12th, 2018. Available at: <http://mform.imr.no/view.php?id=92689>



Observasjonsskjema for ungmakrell/pir

Navn

Fornavn Etternavn

E-post

Telefonnummer

Dato for observasjon/fangst

 / /

DD MM ÅÅÅÅ

Tidspunkt for observasjon/fangst

 :

HH MM

Hvor har ungmakrellen/piren blitt fanget/observert (posisjon/sted)?

Hvor mange ungmakrell/pir ble fanget/observert?

Ca. Lengde på ungmakrell/pir?

Hvordan ble ungmakrellen/piren observert?

- I fangst
 I mage som byttedyr
 På ekkolodd
 Visuell observasjon
 Annet

Er det første gang ungmakrell/pir har forekommet i dette området?

- Ja Nei

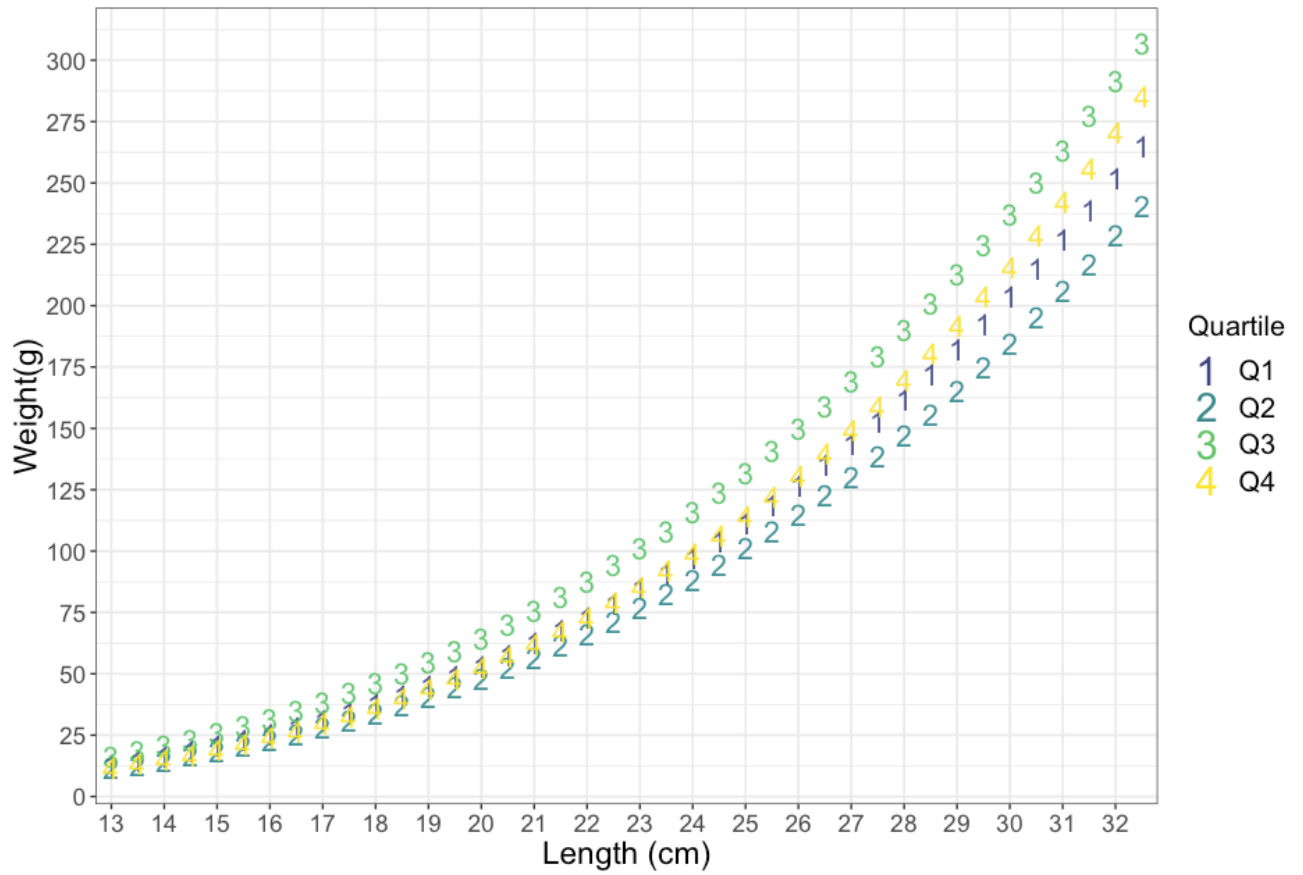
Hvis nei, når observerte du pir i området for første gang?

Dokumentasjon av ungmakrell/pir (bilde/film eller lignende)?

- Ja Nei

APPENDIX B

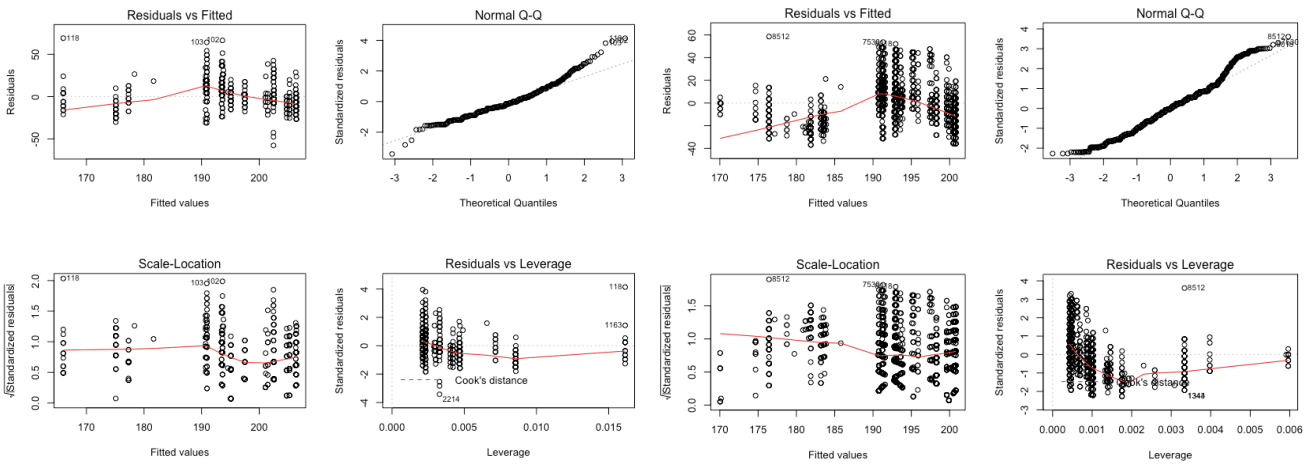
B: Expected weight-at-length for North-Sea juveniles at each quartile, calculated for all observed lengths in the dataset with the a- and b-coefficients retrieved from Wilhelms (2013).



APPENDIX C

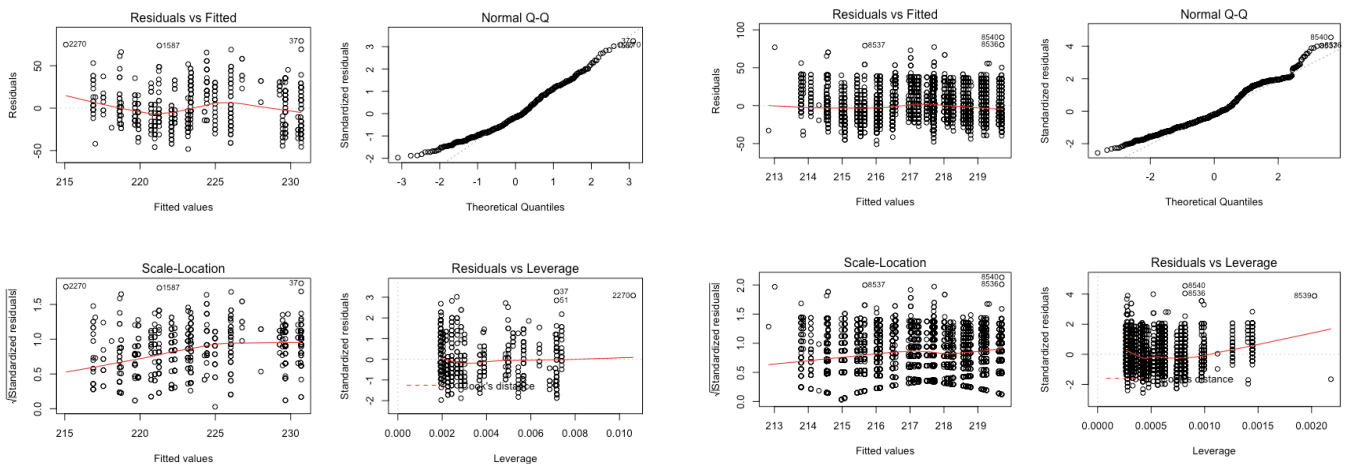
C: All diagnostics plots from the Linear Regression Model sorted by the parameters tested, and the month from which the data were sampled.

1: DIAGNOSTICS PLOTS FROM THE LRM - INDIVIDUAL LENGTH V.S LATITUDE



Aged individuals: February

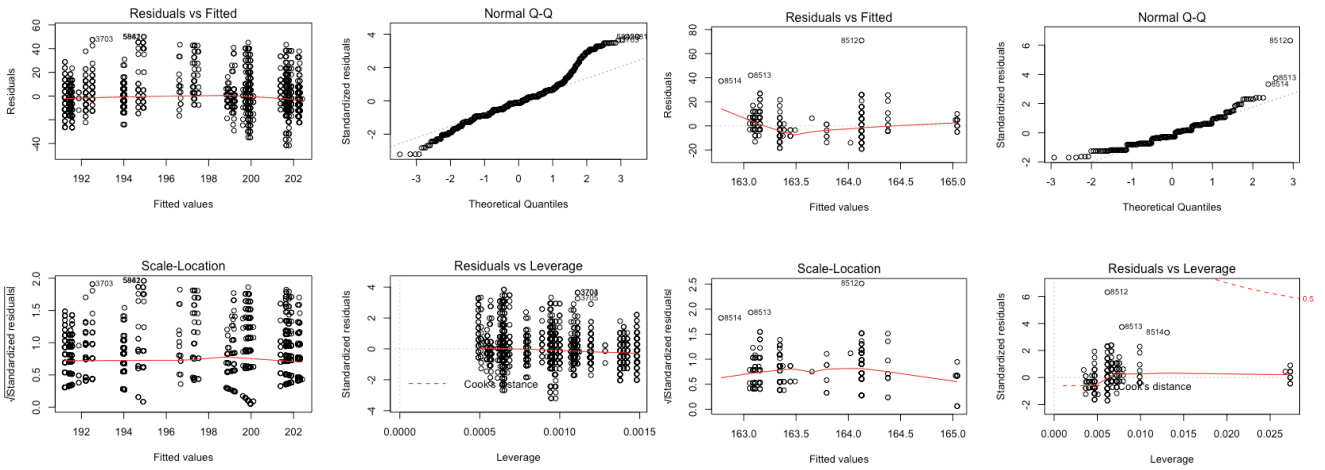
Individuals from February, $\geq 58^\circ\text{N}$



Aged individuals: July

Individuals from July, $\geq 58^\circ\text{N}$

Juvenile mackerel (*Scomber scombrus*) along the Norwegian Coast

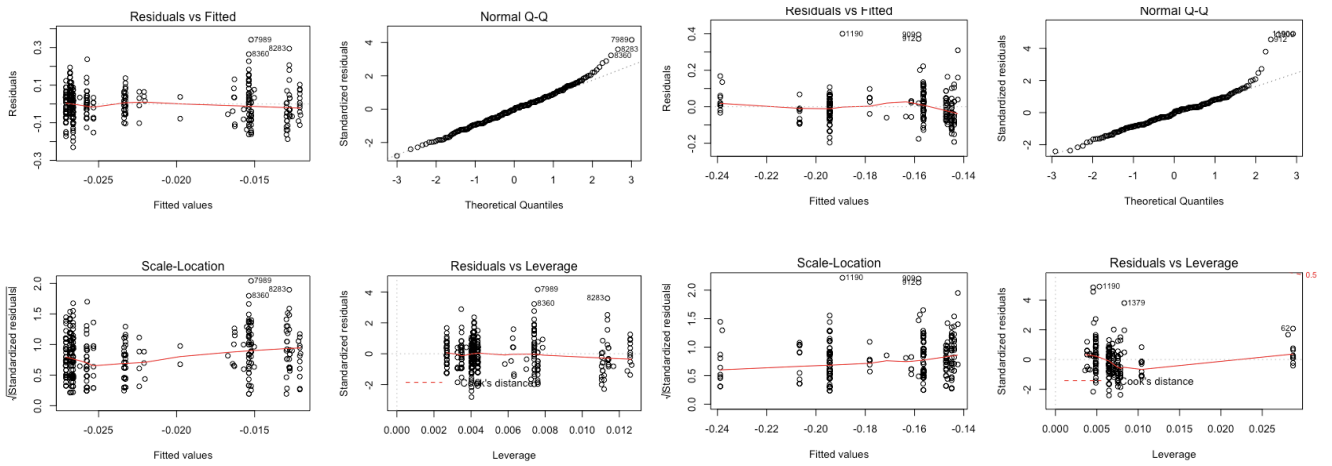


February: small individuals (58°N - 63°N)

February: small individuals (>63°N)

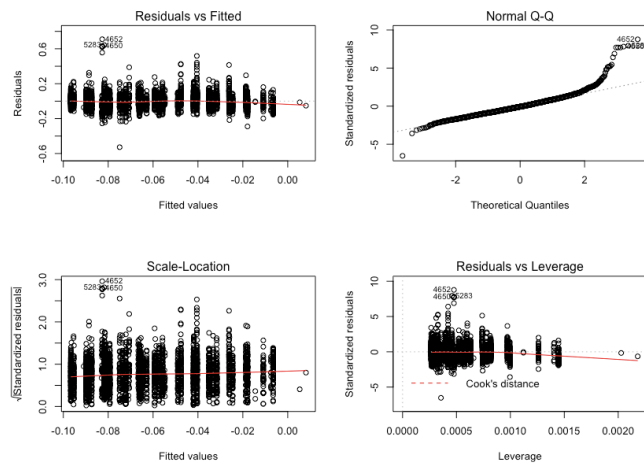
Juvenile mackerel (*Scomber scombrus*) along the Norwegian Coast

2: DIAGNOSTICS PLOTS FROM THE LRM- PROPORTIONAL DEVIANCE V.S LATITUDE



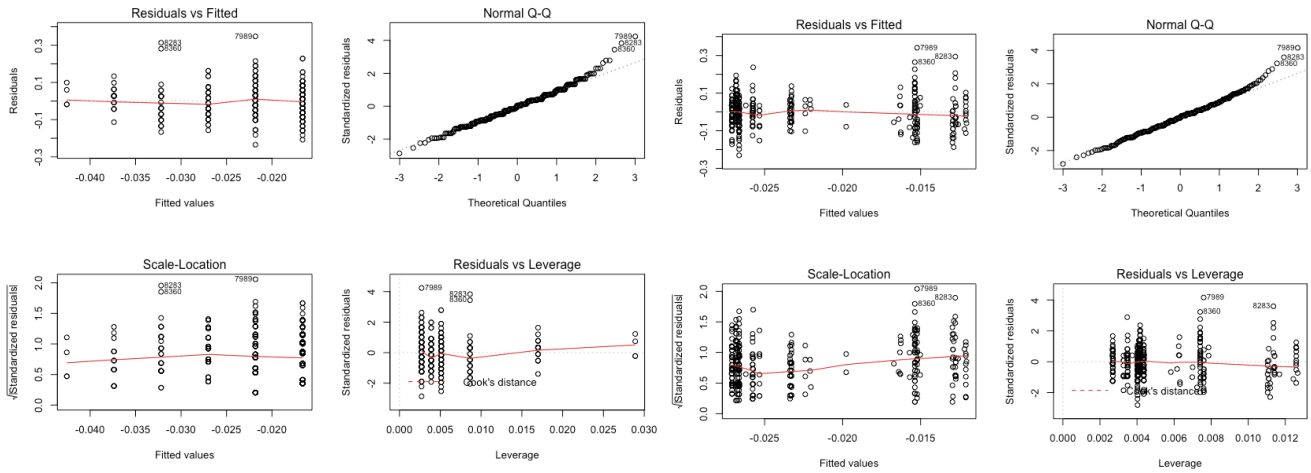
February: small individuals (58°-63°N)

February: small individuals (>63°N)



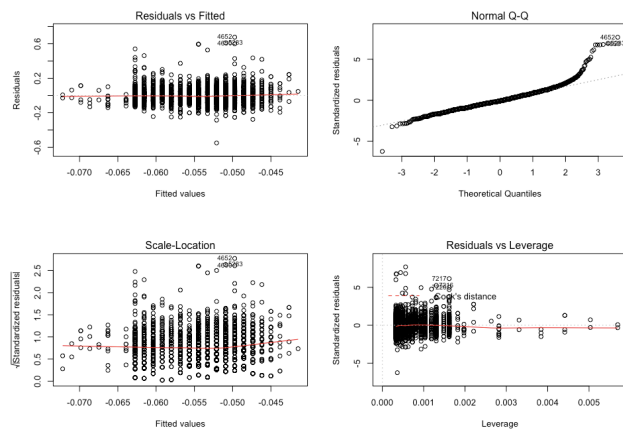
All individuals from July ($\geq 58^\circ\text{N}$)

3: DIAGNOSTICS PLOTS FROM THE LRM – PROPORTIONAL DEVIANCE V.S INDIVIDUAL LENGTH



February: small individuals (58°-63°N)

February: small individuals (>63°N)



All individuals from July (≥ 58°N)

APPENDIX D

D: Total dry weight (g) at each station, the percentwise partitioning of the total dry weight content at each trawl station, and prey group presence in number of stomachs at each trawl station. Grey adjacent columns mark the prey groups that were merged together into the three groups Amphipoda, Other Copepods, and Other Crustaceans.

Station	Weight type	Amphipoda	Themisto sp	Appendicularia	C. finmarchicus	Crustacea	Digested	Euphausiacea
NSSH-2 (10)	Weight (g)	0,0079	0,0376	0,00975	0,0008	0,20741	0,266785	0,0442
	% of dry weight at station	0,99558916	4,73850032	1,228733459	0,100819156	26,138626	33,62113	5,570258349
	# of stomachs with prey group	1	7	1	2	7	8	1
NSSH-1 (10)	Weight (g)	0	0	0	0,0002	0,0225	0	0,1315
	% of dry weight at station	0	0	0	0,129701686	14,59144	0	85,27885863
	# of stomachs with prey group							
IE-2 (10)	Weight (g)	0	0	0,00242	0	0,01244	0,06574	0,0007
	% of dry weight at station	0	0	2,924471299	0	15,033233	79,44411	0,84592145
	# of stomachs with prey group	0	0	1	0	5	6	1
IE-1 (9)	Weight (g)	0	0	0	0,0006	0	0	0
	% of dry weight at station	0	0	0	0,095938599	0	0	0
	# of stomachs with prey group	0	0	0	1	0	0	0
IE-3 (9)	Weight (g)	0	0	0,0106	0,0084	0,041215	0,01092	0,0006
	% of dry weight at station	0	0	7,656193572	6,067172264	29,76887	7,887324	0,433369447
	# of stomachs with prey group	0	0	1	6	4	1	2
IE-4 (11)	Weight (g)	0	0	0	0	0,0247	0	0
	% of dry weight at station	0	0	0	0	100	0	0
	# of stomachs with prey group	0	0	0	0	2	0	0
IE-5 (3)	Weight (g)	0,0002	0	0,028665	0,0006	0,10494	0	0,0001
	% of dry weight at station	0,13573125	0	19,45368171	0,407193756	71,218188	0	0,067865626
	# of stomachs with prey group	1	0	2	0	1	0	1
IE-12 (10)	Weight (g)	0	0	0	0,0014	0,0061	0	0,1033
	% of dry weight at station	0	0	0	1,249442213	5,4439982	0	92,19098617
	# of stomachs with prey group	0	0	0	2	2	0	4
IE-11 (10)	Weight (g)	0	0	0,43425	0,0107	0	0,342395	0
	% of dry weight at station	0	0	31,86337455	0,785119419	0	25,12345	0
	# of stomachs with prey group	0	0	5	7	0	4	0
IE-13(14)	Weight (g)	0	0	0,321465	0,0008	0,047195	0,13452	0,0022
	% of dry weight at station	0	0	61,60103478	0,153300757	9,0437865	25,77752	0,421577082
	# of stomachs with prey group	0	0	7	1	8	9	2
IE-6 (10)	Weight (g)	0,00692	0	0,165515	0,0012	0,01772	0,2434	0
	% of dry weight at station	1,17819321	0	28,18044063	0,204310961	3,0169919	41,44107	0
	# of stomachs with prey group	2	0	5	2	3	3	0
IE-8 (10)	Weight (g)	0,0003	0	0,38412	0,003	0,022935	0	0,0019
	% of dry weight at station	0,07186489	0	92,01581028	0,71864894	5,4940711	0	0,455144329
	# of stomachs with prey group	1	0	10	7	9	0	5
IE-7 (10)	Weight (g)	0,0004	0	0,22434	0,001	0,14248	0,01012	0,0205
	% of dry weight at station	0,09142857	0	51,27771429	0,228571429	32,566857	2,313143	4,685714286
	# of stomachs with prey group	1	0	10	3	10	1	5
IE-9(10)	Weight (g)	0	0	0	0,0469	0	0	0
	% of dry weight at station	0	0	0	11,33671743	0	0	0
	# of stomachs with prey group	0	0	0	6	0	0	0
IE-10(10)	Weight (g)	0	0	0,39554	0,001	0,020842	0,028443	0,019
	% of dry weight at station	0	0	83,04429981	0,209951711	4,3758136	5,971657	3,989082511
	# of stomachs with prey group	0	0	8	3	4	3	1

Juvenile mackerel (*Scomber scombrus*) along the Norwegian Coast

Station	Weight type	Limacina sp.	Copepoda	Microcalanus	Pseudocalanus	Teleostei	Cladocera	Isopoda	Zoea larvae	Cirrus
NSSH-2 (10)	Weight (g)	0,006485	0,0041	0	0	0,20847	0	0	0	0
	% of dry weight at station	0,81726528	0,5166982	0	0	26,2722117	0	0	0	0
	# of stomachs with prey group	1	5	0	0	8	0	0	0	0
NSSH-1 (10)	Weight (g)	0	0	0	0	0	0	0	0	0
	% of dry weight at station	0	0	0	0	0	0	0	0	0
	# of stomachs with prey group	0	0	0	0	0	0	0	0	0
IE-2 (10)	Weight (g)	0,0001	0,0009	0,0001	0	0	0,00015	0,0002	0	0
	% of dry weight at station	0,12084592	1,0876133	0,120845921	0	0	0,18126888	0,24169184	0	0
	# of stomachs with prey group	1	5	1	0	0	2	1	0	0
IE-1 (9)	Weight (g)	0,008584	0,115362	0,0026	0	0	0,498154	0	0,0001	0
	% of dry weight at station	1,37256156	18,446114	0,41573393	0	0	79,6536617	0	0,01598977	0
	# of stomachs with prey group	9	9	2	0	0	9	0	1	0
IE-3 (9)	Weight (g)	0,009665	0,0541	0,00295	0	0	0	0	0	0
	% of dry weight at station	6,98085952	39,075479	2,130733117	0	0	0	0	0	0
	# of stomachs with prey group	4	3	6	0	0	0	0	0	0
IE-4 (11)	Weight (g)	0	0	0	0	0	0	0	0	0
	% of dry weight at station	0	0	0	0	0	0	0	0	0
	# of stomachs with prey group	0	0	0	0	0	0	0	0	0
IE-5 (3)	Weight (g)	0	0,011695	0,001	0	0	0,00015	0	0	0
	% of dry weight at station	0	7,936885	0,678656261	0	0	0,10179844	0	0	0
	# of stomachs with prey group	0	2	1	0	1	2	0	0	0
IE-12 (10)	Weight (g)	0	0,00105	0	0	0,0002	NA	0	0	0
	% of dry weight at station	0	0,9370817	0	0	0,17849174	0	0	0	0
	# of stomachs with prey group	0	3	0	0	1	0	0	0	0
IE-11 (10)	Weight (g)	0,485497	0,090008	0	0	0	0	0	0	0
	% of dry weight at station	35,6236563	6,6043952	0	0	0	0	0	0	0
	# of stomachs with prey group	10	7	0	0	0	0	0	0	0
IE-13(14)	Weight (g)	0,00051	0,01281	0,00185	0	0	0,0002	0	0,0003	0
	% of dry weight at station	0,09772923	2,4547284	0,354508	0	0	0,03832519	0	0,05748778	0
	# of stomachs with prey group	2	7	9	0	0	4	0	1	0
IE-6 (10)	Weight (g)	0,0028	0,10836	0,018021	0	0	0,022205	0	0,0002	0,0009
	% of dry weight at station	0,47672558	18,44928	3,068239861	0	0	3,78060408	0	0,03405183	0,153233
	# of stomachs with prey group	4	8	10	0	0	6	0	1	3
IE-8 (10)	Weight (g)	0,0001	0,002995	0,001	0,0011	0	0	0	0	0
	% of dry weight at station	0,02395496	0,7174512	0,239549647	0,263504611	0	0	0	0	0
	# of stomachs with prey group	1	3	9	4	0	0	0	0	0
IE-7 (10)	Weight (g)	0,03706	0	0,0016	0	0	0	0	0	0
	% of dry weight at station	8,47085714	0	0,365714286	0	0	0	0	0	0
	# of stomachs with prey group	9	0	9	0	0	0	0	0	0
IE-9(10)	Weight (g)	0	0,3664	0,0004	0	0	0	0	0	0
	% of dry weight at station	0	88,566594	0,096688422	0	0	0	0	0	0
	# of stomachs with prey group	0	7	1	0	0	0	0	0	0
IE-10(10)	Weight (g)	0,00067	0,008355	0,00155	0,0004	0	0,0002	0	0,0003	0
	% of dry weight at station	0,14066765	1,7541465	0,325425152	0,083980684	0	0,04199034	0	0,06298551	0
	# of stomachs with prey group	2	6	7	2	0	2	0	1	0