Spatiotemporal variation in the growth and size distributions of lesser sandeel (*Ammodytes marinus*) in the north-eastern North Sea

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Spring 2023

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Acknowledgements

Ever since I was a kid, I've been curious about nature's processes and the elementary aspects of the world we live in. My initial interest in physics quickly manifested itself into something else, something biological. This interest in biology stems from a childhood filled with hikes and fishing trips, largely due to my parents and their own interest in nature and the outdoors. Therefore, I think they deserve the first and largest gratitude.

At the time of my bachelor's, I didn't know if I wanted to study marine or terrestrial biology. The only thing I knew was that I was having fun studying all the different topics covering different aspects of the biological world. About a year leading up to the application for the masters, I decided that this is what I wanted to do, and I made every effort to see it through.

Now, five years after my journey in biology started, I'm about to finish my master thesis in marine biology. For this, I would like to thank my supervisors Espen Johnsen and Maria Tenningen from the Institute of Marine Research who gave me this opportunity. I am incredibly grateful for the help they have given me.

I would also like to thank Richard Telford for his invaluable help in the R-Club, Sander Digre who helped me make sense of both logical and illogical problems, and finally my partner Mimi for her continuous support.

Abstract

The lesser sandeel (*Ammodytes marinus*) is a key constituent of the North Sea ecosystem and prey for a variety of predators such as larger fish, seabirds, and marine mammals. Historically, the sandeel fishery has been one of the largest fisheries in the North Sea, and annual landings have increased significantly since its start in the 1950s, occasionally reaching above 1 million tons.

While spatial differences in growth of sandeels have been investigated previously, this work is an investigation into spatial differences specific to the Norwegian Exclusive Economic Zone (NEEZ) and the sandeel management areas therein. A cross-examination of commercial fishery data and scientific survey data was conducted to check for differences in length selectivity. No considerable differences were found, resulting in an integration of biological sandeel data from both commercial and scientific sources representing a novel approach that allows for comprehensive investigations of sandeel growth in NEEZ.

Length at age was found to be lowest for sandeels in the southernmost area, possibly due to higher fishing pressure and poor connectivity. Fulton's condition factor at age was found to differ spatially in one or more age groups, but there were no clear spatial patterns. Differences in length at age between the management areas became larger over time, possibly pointing to a demographic disconnect. Reduction in length was observed late in the season, indicating a spatial difference in the timing of overwintering. Sandeel weight increased two- to three-fold during the fishing season, meaning that the number of fish needed to fill the quota may potentially double or triple during the fishing season.

Keywords: Sandeel, length, condition, weight, spatiotemporal variation, North Sea

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1. Introduction

The mid-trophic interaction between zooplankton and forage fish is an integral link in marine food webs (Cury *et al.*, 2000; Bakun, 2006; Davison *et al.*, 2013). Forage fish serve a crucial role in the marine food web as consumer of zooplankton (Hill, Daly and Brodeur, 2015) and as prey for larger fish, seabirds, and marine mammals (Furness, 1990; Wanless, Harris and Greenstreet, 1998; Bull *et al.*, 2004). Forage fish consume mostly zooplankton, which are seasonal prey, and thus exhibit seasonal growth patterns and variable populations dynamics (Bergstad, Høines and Jørgensen, 2002; Lindegren *et al.*, 2013; Rindorf *et al.*, 2016; Albo-Puigserver *et al.*, 2017). Most marine fish species are habitat-dependent (Shaffer, 2004; Holland *et al.*, 2005; Thedinga, Johnson and Mortensen, 2006), limiting their distribution and introducing additional considerations when managing a fishery. Regional growth patterns can occur for the same species of forage fish, a result of varying food availability or competition due to spatial differences in distribution of prey. This can in turn lead to regional variation in abundance which can affect other species by bottom-up control (Frederiksen, Furness and Wanless, 2007; Engelhard *et al.*, 2013). Because of forage fish's essential role in the ecosystem and their variable dynamics, understanding their interactions with the environment is crucial when developing managerial strategies designed to explain and predict stock dynamics.

1.1 Trophic significance of the sandeel

The sandeel belongs to the family Ammodytes, a group of small, oblong forage fish found in many parts of the world. In the North Sea there are five species of Ammodytes (Johnsen *et al.*, 2021), the lesser sandeel (*Ammodytes marinus*) being the most common. The lesser sandeel (hereafter sandeel) is one of the most abundant fish species in the North Sea. It feeds on zooplankton and is preyed upon by other, larger fish, seabirds, and marine mammals (Furness, 1990; Wanless, Harris and Greenstreet, 1998). Commercially important species like haddock, saithe, whiting, cod, and mackerel are common predators of the lesser sandeel (Daan *et al.*, 1990). This makes the sandeel an important trophic link in the food web and a key species in the North Sea ecosystem. This has caused a concern that heavy fishing pressure on sandeels may threaten both marine and terrestrial predators due to reduced food availability (Monaghan, 1992; Wanless, Harris and Greenstreet, 1998; Daunt *et al.*, 2008). In a study on the spatial comparison between sandeels and the common guillemot (Wright and Begg, 1997), sandeel distribution was considered an important influence on the distribution of guillemots during the breeding season.

In addition to prey availability, prey quality affects the condition of predators because of a lower energy yield. Condition is a proxy for healthiness, a measure of weight versus length (Jones, Petrell and Pauly, 1999). Low energy values of fish have been proposed as a possible cause for major seabird breeding failure (Wanless *et al.*, 2005). Zooplankton is integral to the sandeel's diet (Arnott and Ruxton, 2002; Frederiksen *et al.*, 2006; van der Kooij, Scott and Mackinson, 2008), meaning that the predominant factor deciding sandeel condition likely is zooplankton availability (van Deurs *et al.*, 2009). This means that reduction in sandeel condition, for example by trophic mismatches of hatching sandeel larvae and zooplankton, may cause trophic cascades through entire ecosystems (Frederiksen *et al.*, 2006). Sandeels also exhibit variability in year-class strength (Wright and Bailey, 1996), an important aspect considered when estimating future spawning stocks and quotas.

1.2 Sandeel life history

During a short planktivorous feeding season, the sandeel forms schools to feed on zooplankton shortly after sunrise and bury in sand at sundown (Freeman, Mackinson and Flatt, 2004; Johnsen *et al.*, 2017). The feeding period for one-year-olds and older sandeels lasts from approximately March to July, and from April to November for individuals of age zero (Johnsen *et al.*, 2021). Sandeels are regarded as capital breeders (Boulcott and Wright, 2008), which means that they breed when reaching a certain energy threshold (Jönsson, 1997; Stephens, 2009), using stored energy at the end of their dormant phase. The sandeel stays buried in the seabed during winter, from July-August to February-March, and spawn in December-January (Webb and Macer, 1968; Bergstad, Hoines and Krüger-Johnsen, 2001; van Deurs *et al.*, 2010; Sundby *et al.*, 2017; Johnsen *et al.*, 2021).

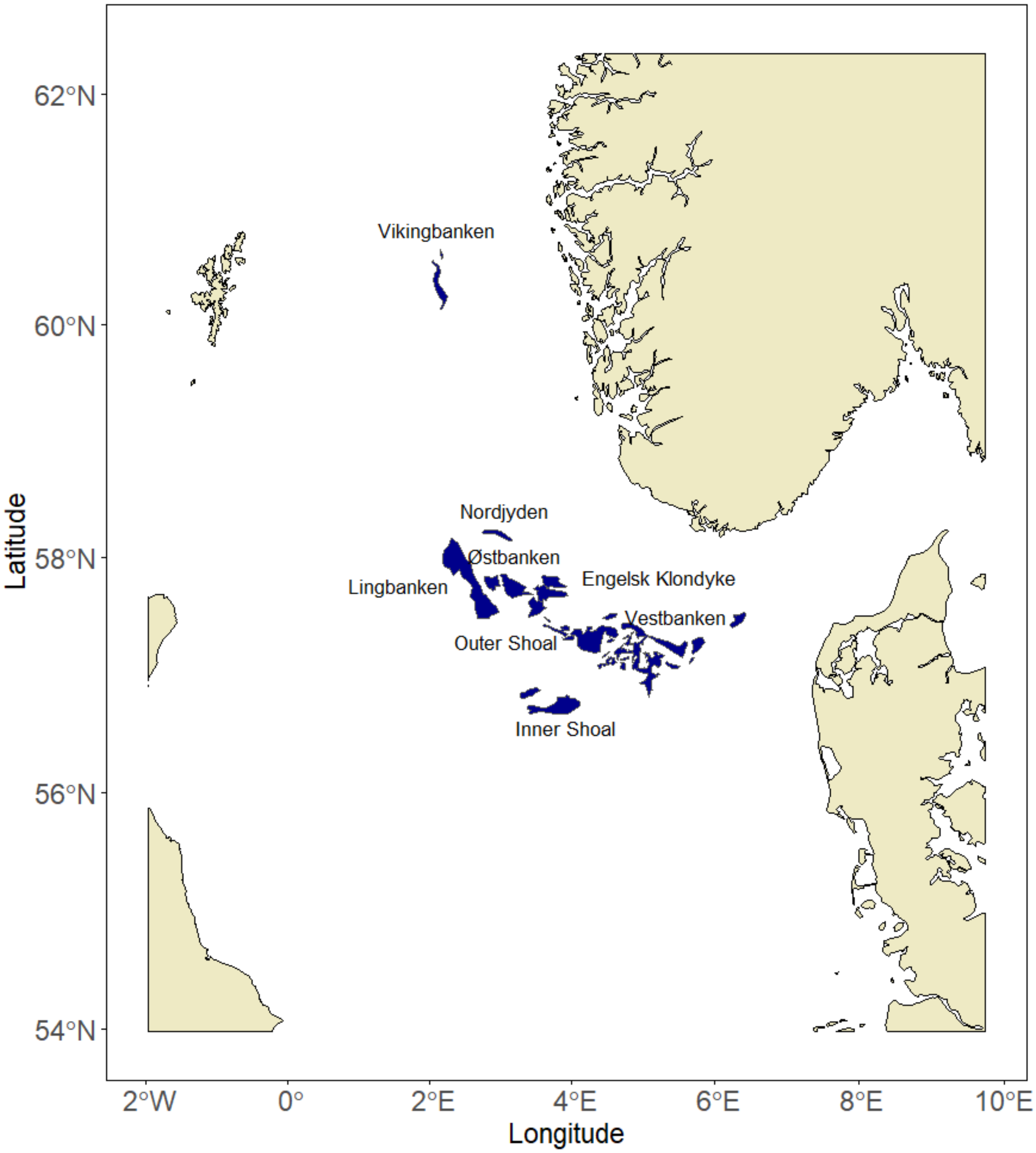
The sandeel is distributed in patches throughout the North Sea due to its behavior of burying into the sand (Wright, Jensen and Tuck, 2000; Holland *et al.*, 2005). Sandeels spawn where they live, and eggs stick to the sand grains until hatching (Wright and Bailey, 1996), therefore spawning grounds are also fishing grounds. Hatching occurs during February-March, and the pelagic larvae drift before settling in late June (Wright and Bailey, 1996; Johnsen *et al.*, 2021). Hatching time and duration vary with ocean temperature, giving rise to variations in hatching time dependent on local conditions (Wright and Bailey, 1996; Régnier, Gibb and Wright, 2018). After hatching, the larvae are distributed throughout the water column (Conway, Coombs and Smith, 1997).

Post settlement movement of sandeel is suggested to be low between grounds (Kunzlik, Gauld and Hutcheon, 1986; Jensen *et al.*, 2011). The potential for sandeel larvae to move post-hatching is dependent on their ability to eat before the entire egg yolk is consumed (Yamashita and Aoyama, 1986), making it possible to save energy reserves for when growth conditions are poor. Whether larvae move to specific depths to minimize drift away from the spawning grounds is unclear, though the return of sandeel to natal habitats is suggested to happen by active homing (Johannessen and Johnsen, 2015).

1.3 The sandeel fishery and management

Historically, the sandeel fishery has been one of the largest fisheries in the North Sea, and annual landings have increased significantly since its start in the 1950s, occasionally reaching above 1 million tons (ICES, 2021). In the early 2000's, a decline in sandeel stocks in the North Sea were observed, particularly in the Norwegian Exclusive Economic Zone (NEEZ) (ICES, 2010). The quotas given for sandeels concerned the entirety of the North Sea, allowing high fishing pressure without taking into account local differences in stock size. This was especially alarming considering the particularly low stocks in Norwegian waters, which led to the Institute of Marine Research (IMR) giving additional advice on quotas to prevent high local fishing pressure in NEEZ. From this, an acoustic trawling survey program was initiated in 2005 with the goal of mapping the spatial distribution and stock development of sandeels in NEEZ (Johnsen, Pedersen and Ona, 2009). By 2011, this program had contributed to the development and implementation of an area-based management model which is still in use today (ICES, 2010; Johnsen *et al.*, 2021). One particular finding showed that a collection of sandeel fishing grounds (Vestbanken) had consistently higher recruitment (Johannessen and Johnsen, 2015). The reason for this turned out to be natural rock structures protecting the smaller habitats from the oversized fishing gear. The other sandeel habitats consist of larger unprotected regions, consequently exhibiting poorer recruitment. This indicated that locally protected spawning stocks increase the likelihood of better local recruitment, substantiating the benefit of an area-based management model.

The management areas created have since been modified in 2014, 2017, and 2020 (Johnsen *et al.*, 2021; Johnsen, 2022). Since 2020, there have been five main areas (1-5) encompassing the sandeel fishing grounds, which in this thesis have been dubbed A-E for clarity (Figure 1; Johnsen *et al.*, 2021). Management area A consists of Inner Shoal, management area B consists of Outer Shoal, management area C consists of Vestbanken, management area D consists of Nordgyden, Lingbanken, Østbanken and English Klondyke (Figure 1). Management area E consists of Vikingbanken, but very little biological data have been collected from this area as the biomass of sandeels has been critically low since the end of the 1990's (Johnsen *et al.*, 2021; ICES, 2010). To prevent fishing of lean individuals, the fishery opens on the 15th of April. To prevent fishing of juveniles settling in late June, the fishery closes June 23rd (Johnsen *et al.* 2021; Johnsen, 2023).


Vikingbanken
Nordjyden
Østbanken
Engelsk Klondyke
Lingbanken
Vestbanken
Outer Shoal
Inner Shoal
62°N
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58°N
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Longitude

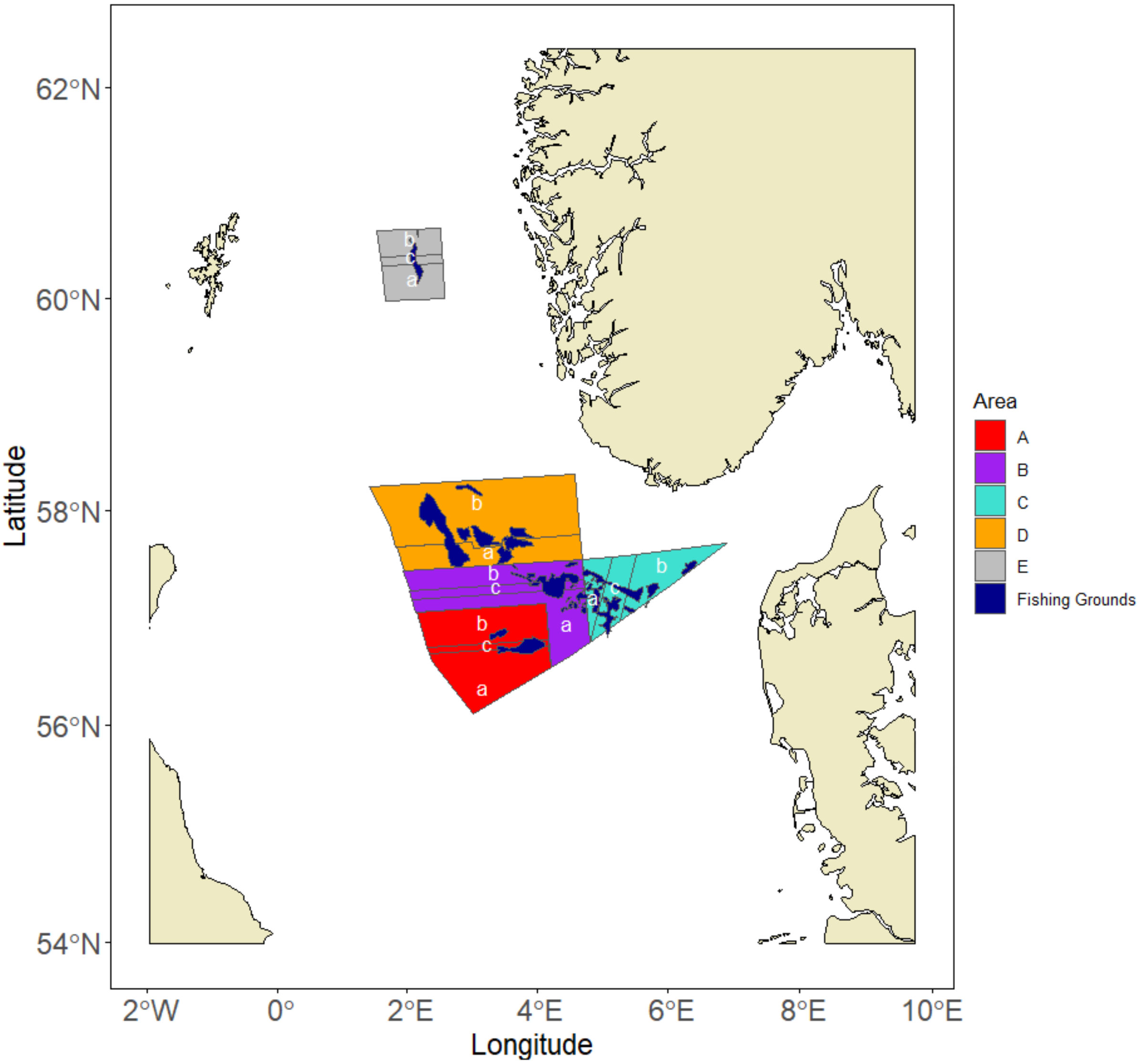


Figure 1 *Maps of the sandeel fishing grounds (top) and sandeel management areas (bottom) in the Norwegian Economic Exclusive Zone. Management areas A, B, C and E consist of sub-areas a, b and c, and management area D consists of sub-areas a and b.*

A common quota is given for areas A-D, and a separate quota is given for area E (Table 1). In any opened main management area, either its sub-area “a” or “b” is to stay closed for the entirety of the fishing season. This is done to ensure that a part of the local sandeel stock survives, even if all fishing is concentrated in only one area. In February, a preliminary stock assessment is carried out and a provisional quota is given, deciding in which area and sub-area fishing is allowed (Table 1). During April-May, acoustic trawl surveys are carried out to give updated information on sandeels of age one and older, from which a final advised quota is given (Table 1; Johnsen, 2023).

Table 1 *Preliminary and final advised quotas, and landings for areas (1-4) and sub-areas (a-d) in the Norwegian Economic Exclusive Zone in the North Sea from 2010-2023* (Johnsen, 2023). *Area 5 (Vikingbanken) has been closed for fishing during this entire period. Management areas A-D are here shown as 1-4, and their spatial boundaries have changed since 2010.*

	Preliminary advice		**Final advice**		
Year	**Advised quota (tons)**	**Open sub-areas**	**Advised quota (tons)**	**Open sub-areas**	**Landings (tons)**
2010	20 000	1b, 2b, 3b	50 000	1b, 2b, 3b	50 471
2011	60 000	1a, 2a, 3a	90 000	1a, 2a, 3a	88 424
2012	40 000	1b, 2b, 3b	40 000	1b, 2b, 3b	40 889
2013	20 000	3a	20 000	3a	9 052
2014	15 000	3b, 3c	90 000	2a, 3b, 3c, 4b	82 499
2015	100 000	2b, 3b, 3a	100 000	1b, 2b, 3a, 3b, 4a	100 858
2016	40 000	1b, 2a, 3a, 3b	40 000	1b, 2a, 3a, 3b, 4a	40 836
2017	50 000	1b, 1c, 2b, 2c, 3c, 3b, 4a	120 000	1b, 1c, 2b, 2c, 3c, 3b, 4a	119 975
2018	70 000	1b, 1c, 2a, 2c, 3a, 3b, 4b	70 000	1b, 1c, 2a, 2c, 3a, 3b, 4b	69 531
2019	55 000	1b, 1c, 2b, 2c, 3b, 3c, 4a	125 000	1b, 1c, 2b, 2c, 3b, 3c, 4a	123 958
2020	70 000	1a, 1c, 2b, 2c,3b,3c, 4a	250 000	1a, 1c, 2b, 2c,3b,3c, 4a	234 754
2021	110 000	1b,1c, 2a, 2c, 3a, 3c, 4b	145 000	1b,1c, 2a, 2c, 3a, 3c, 4b	146 442
2022	60 000	1a,1c, 2b, 2c, 3b, 3c, 4a	95 000	1a, 1c, 2b, 2c, 3b, 3c	81 676
2023	60 000	1b, 1c, 2a, 2c, 3a,3c			

1.4 Spatial variation

In a study on the mixing between sandeel habitats (Wright *et al.*, 2019), year-class strength varied among habitats across the North Sea, indicating limited mixing and thereby vulnerability to fishing pressure. In another study from the North Sea (Jensen *et al.*, 2011), they found that mixing was too low to eliminate differences in length distributions between sandeel fishing grounds down to 5 km. However, within fishing grounds, mixing was sufficient to eliminate differences in length distributions at scales up to 28 km. This may suggest that mixing is facilitated by the continuous access to a suitable habitat, and likewise that potential mixing over stretches of space lacking suitable habitat is reduced. Since the distance from Inner Shoal in area A is the furthest from any other fishing grounds (Figure 1), different demographics may arise. Further research on the spatial and temporal differences in length of sandeels between fishing grounds in NEEZ of the North Sea can help to make informed inferences about the degree of mixing and connectivity between them.

The sandeel exhibits strong seasonal variation in growth (Hislop, Harris and Smith, 1991; Bergstad, Høines and Jørgensen, 2002; Rindorf *et al.*, 2016), dictated by availability and fat-content of zooplankton (Danielsen, Hedeholm and Grønkjær, 2016). Individual growth in length is nonetheless expected to increase throughout the season due to the nature of organisms growing larger. Interestingly, a reduction in mean length at age of sandeels in the North Sea has been recorded in the latter half of the year (Bergstad, Høines and Jørgensen, 2002). These observations are consistent with reports on the timing of overwintering (Bergstad, Hoines and Krüger-Johnsen, 2001), and are suggested to be the cause of behavioral changes in which larger individuals bury earlier, rather than caused by mortality (Reeves, 1994). It is also of interest to investigate whether a reduction in mean length can be observed within the temporal boundaries of the sandeel fishery season (April 15th – June 23rd), as observed by Rindorf *et al.* (2016). In the case of spatial differences in the timing of overwintering, indicated by reduction in mean length, area-specific temporal boundaries may be beneficial in terms of fishing when abundance and mean weight is highest.

The division of management areas within NEEZ was originally motivated by avoiding overfishing and depletion of sandeels in any sub-area. This approach was rather hastily implemented, but arguably with good reason given the stock situation in NEEZ in the early 2000’s. While this approach continues to be effective at protecting local sandeel stocks in Norwegian waters from depletion, the model can be improved with further knowledge on the spatial and temporal distribution of sandeels. The degree of connectivity plays a large role in predicting future stock dynamics, especially when there is strong variability in recruitment (Johnsen *et al.*, 2021). As mentioned, naturally protected habitats (Vestbanken) led to higher recruitment. This suggests that protecting habitats, especially those of greater connectivity, can lead to overall higher recruitment success over large regions. Disconnected stocks imply increased vulnerability to overfishing or poor recruitment, and possibly slower recovery rates. Knowing if connectivity is poor or not, can thereby also affect area-specific management.

Within NEEZ there are multiple sandeel habitats (Sundby *et al.*, 2017; Johnsen *et al.*, 2021), which are interchangeable with spawning grounds and fishing grounds due to demersal eggs sticking to the seabed until hatching. Because of the sandeels' dependence on this specific type of habitat, distribution may be limited beyond grounds, and spatial patterns in growth may vary between grounds. By exploring the spatial differences in length, weight, and condition at age of sandeels, more accurate inferences can be made about the level of connectivity between fishing grounds, how they differ in growth patterns, and to what extent to treat the stock as either a single population or multiple. At one extreme, frequent migration between all sandeel habitats implies that there is a single, large population with a demographic structure that can be different from that of multiple isolated populations. Multiple isolated populations can imply separate demographic structures, each varying in its ability to deal with fishing pressure.

1.5 Aim and objectives

The aim of this thesis is to investigate length, weight, and condition at age of sandeel belonging to the four management areas in the southern NEEZ (Johnsen *et al.*, 2021). The goal is to determine (1) whether there are spatial differences in length and condition at age between areas A-D, (2) whether differences in length at age persist over time, giving an indication of connectivity, (3) whether reduction in length at age occurs late in the fishing season as reported by Rindorf *et al.* (2016), indicating earlier overwintering behavior of larger individuals, and (4) whether the fishery should open later in the season in order to let the sandeel gain more weight and thereby decrease the number of individuals needed to fulfill quotas. In order to discuss these results in relation to the management of the Norwegian sandeel fishery, the areas used in the analyses are those currently defined and managed (Johnsen *et al.*, 2021).

2. Materials and Methods

2.1 Sampling of biological data

Both commercial and scientific data used in this thesis were gathered in the period 2007-2022 from April-June and followed the same sampling procedure. This combination of biological sandeel data from both commercial and scientific sources represents a novel approach, allowing for a comprehensive understanding of sandeel growth in NEEZ. The fishing activity varied considerably from 2007 to 2009 in NEEZ due to different spatial and temporal closures. In 2007, the fishing period was initially from April 1st to May 4th where stock size was estimated based on CPUE (catch per unit effort) (ICES, 2007). This led to fishery closure from May 5th to May 15th pending TAC (Total Allowable Catch) advice from ICES (International Council for the Exploration of the Sea). Fishing then resumed May 16th and closed June 23rd in Engelsk Klondyke, Østbanken, Lingbanken, Nordgyden and Vikingbanken (see Figure 1) due to fulfillment of the TAC. In 2008, the fishing period was initially April 1st to May 3rd and the commercial data were used to estimate the stock size based on CPUE, leading to fishery closure from May 4th to May 8th pending TAC advice from ICES. The fishing period resumed May 9th and closed June 3rd in Østbanken, Lingbanken, Nordgyden and Vikingbanken (see Figure 1) prior to meeting the limit of the TAC. Five vessels were fishing from June 2nd till June 8th in Østbanken, Lingbanken and Nordgyden (see Figure 1), but no fish was landed. In 2009 there was a fishing moratorium on sandeels in NEEZ. The location from which commercial sandeel samples originate after 2010 is dependent on the advised quotas for specific sub-areas (Table 1). As for the scientific sandeel samples, sampling has been carried out in sub-areas defined in the sandeel management plan. The commercial and scientific data was gathered using various trawls and other gears (Table 2; Mjanger *et al.*, 2022).

In both commercial and scientific biological sampling of sandeel, length and weight were taken from 100 individuals. Age was sampled from the 25 first of those 100 individuals. The length measurements of sandeel in the data were recorded as total length of either 0.5 cm or 1 cm intervals. To make the individual length measurements consistent over time, all individual total lengths were rounded down to the nearest cm using the *floor-function* (R Core Team, 2021).

2.2 Biological data

The datafiles used in this work were downloaded from two different data sources stored at IMR. The NMDbiotic database, which is only available for internal users at IMR through the IMR web application (https://datasetexplorer.hi.no/apps/datasetexplorer/v2/navigation) was used to download all the data from scientific surveys and commercial catches from 2015 to 2022 as NMDbiotic.xml files (https://www.imr.no/formats/nmdbiotic/v3.1/bioticv3_1_en.html). In addition, all commercial biological data before 2015 were taken from an old data file structure stored on an IMR server as these years are not yet available in the web application database. These data were converted to the NMDbiotic.xml file format using the IMR "bioticeditor" software.

The xml data file follows a hierarchical format consisting of 11 tables: *missions*, *mission*, *fishstation*, *catchsample*, *individual*, *prey*, *agedetermination*, *preylengthfrequencytable*, *copepoddevstagefrequencytable*, *tag*, *metadata*. The RstoxData package (Umar *et al.* 2021) was used to read the xml-data files, and the *fishstation*, *catchsample*, *individual*, *agedetermination* tables were merged to make one combined data file that included all the relevant information to be used in this thesis (see Table A1 for the variables kept). The data file provided information to know if the data was collected from a scientific survey or the commercial fishery. By using the variable "Gear" containing gear-codes, five different types of gear were defined; commercial gear, scientific bottom trawl, scientific pelagic trawl, scientific sandeel dredge and scientific sandeel grab (Table 2).

Norwegian trawlers use echosounders to identify sandeel schools prior to trawling. The commercial sandeel fishery is carried out with trawls of small mesh size (≤16 mm) equipped with metal chain footropes which only allow trawling on smooth, sandy bottom substrate (Casey *and Dörner*, 2011). For the first time in 2022, Norwegian trawlers fished in the pelagic zone where footropes were 10-20 m above the seabed (Pers.comm. Espen Johnsen, 2023). This was done to avoid bycatch of bottom dwelling species such as haddock and whiting. The scientific bottom trawls have been carried out with a Campelen 1800 shrimp trawl with a small meshed sandeel cod-end. The Harstad pelagic trawl was originally a 16x16 fathom Capelin trawl with 5 mm mesh size in the cod-end, which is used to catch schools of fish in the pelagic zone and near the surface (Johnsen, Pedersen and Ona, 2009). The sandeel dredge is a modified scallop dredge with a hood, identical to the Danish dredge (Johnsen and Harbitz, 2013). Dredge width was 1 m, and mesh size 5 mm. Dredge towing duration was 10 minutes, and speed was 2 knots.

Table 2 Number of individuals that were length measured (# length) and aged (# age), the number of stations (# stations) belonging to the gear groups (Commercial gear, Scientific bottom trawl, Scientific pelagic trawl, Scientific sandeel dredge, and Scientific sandeel grab), and the associated gear names and gear codes (see Mjanger *et al.*, 2022). Gear names in bold are those used in chapter 2.3.

Gear group	Gear name	Gear code	# length	# age	# stations
Commercial gear	**Bunntrål**	3100	30 499	7696	363
	Industritrål	3130	7728	2354	141
	Tobistrål	3131	20886	4165	277
	Tobistrål	3172	2654	145	16
	Andre tråler	3400	1175	425	12
	Semipelagisk trål	3410	1620	1167	23
	Semipelagisk trål	3411	4211	1868	52
	Semipelagisk trål	3412	8786	3965	100
	Flytetrål	3500	4952	1310	60
	Åkratrål	3532	50	0	1
Scientific bottom trawl	**Shrimp trawl**	3270	31293	9561	269
	Shrimp trawl	3271	99	30	1
Scientific pelagic trawl	**Flytetrål**	3500	99	25	1
	Harstadtrål	3513	222	46	6
Scientific sandeel grab	Grab	4202	2031	110	60
Scientific sandeel dredge	Dansk slede	4401	18992	6366	413

2.3 Comparison of length selectivity between commercial and scientific gears

Both the commercial and scientific gears use very small mesh sizes in the cod-end, and there is therefore no reason to believe that there are differences in the length-selectivity between the gears. However, to test this assumption, the length-selectivity of commercial and scientific gears were compared. This was done to check whether the different gears could be combined when analyzing spatiotemporal variability in sandeel growth. All scientific trawls (Table 2) in this thesis are assumed to represent the population equally, which is also assumed for the acoustic sandeel surveys (Johnsen, 2021). There was therefore no need for grouping types of scientific gear, for example bottom trawl and pelagic trawl prior to comparison. The gears used in the comparison are those in bold (Table 2). The commercial gears are also grouped under one category due to uncertainty regarding the gear codes being used by fishing vessels (Directorate of Fisheries, 2010). The length-selectivity of sandeel samples taken from commercial and scientific gears close in space and time were compared (Figure 2). Firstly, the data was grouped by survey year to distinguish between annual catches. Secondly, data was grouped in space by creating polygons around each station and extracting each adjacent station within a spatial threshold. This grouping in space was done using the *sf-package* (Pebesma, 2018). *St_as_sf* was used to transform the coordinate system and create all the points (stations), and *st_buffer* was used to generate the radius determining which of the adjacent points are included. *St_join* was then used to create the polygons with all the stations that were within 15 km of the center of each polygon. Different radiuses were tested, but 15 km was chosen for the polygons because it returned enough stations for comparison.

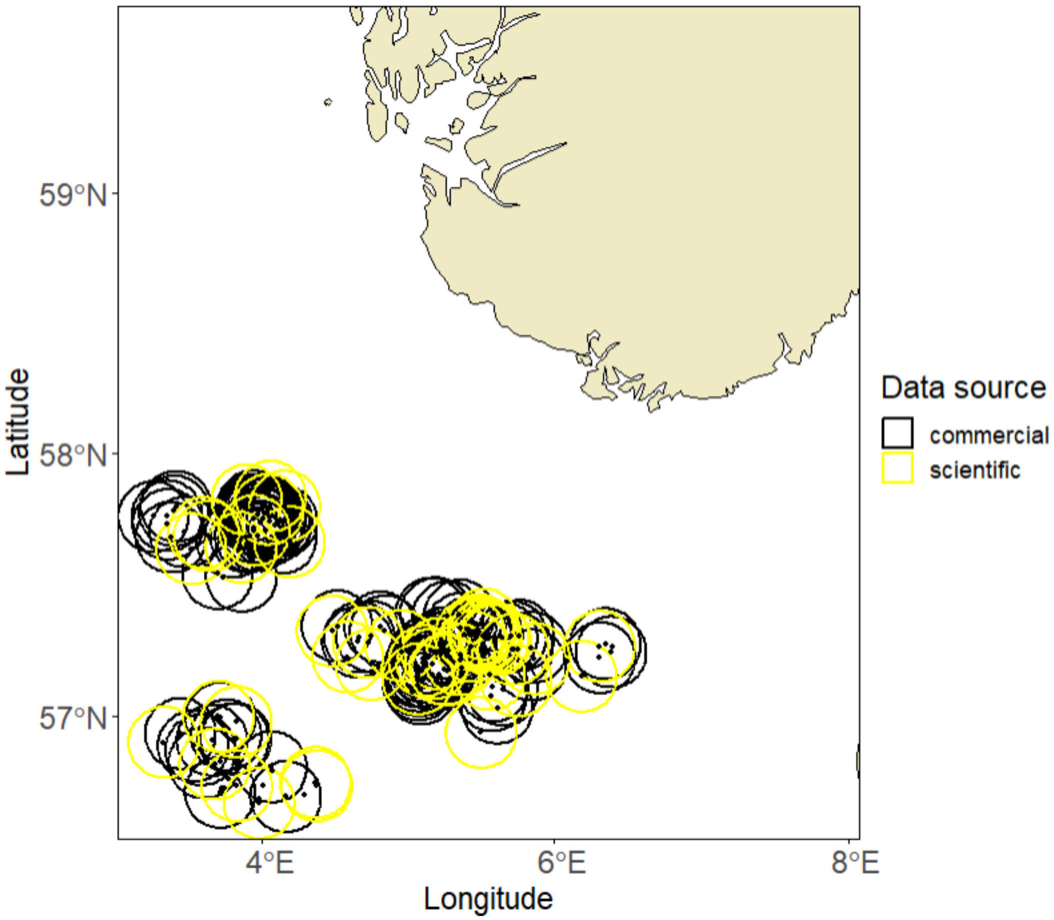


Figure 2 *A visual representation of the polygonal grouping of data used in the comparison of length distribution for commercial and scientific gear in 2007, 2008, 2015-2019, 2021 and 2022 (Table 3). Polygons have a radius of 15 km. Each black dot represents one unique observation of each station. The color of the polygon represents its data source.*

Each unique station in the data represents a polygon with a radius of 15 km (Figure 2). *Slice_head()* was used to create a polygon of the first observation of each station. All data points within each polygon were compared based on two additional criteria: (1) a minimum of three unique hauls from commercial data and two unique hauls from scientific data, (2) an interval of two weeks. Since there is a higher number of commercial data, the scientific data was assigned a less rigid criterium. A visual inspection of the relative length distribution in each polygon was done (Figure 3). In addition, a statistical comparison of length frequencies was carried out using the package *fishmethods* (Nelson, 2022) to compare length distributions, giving p-values for each survey year used in the analysis (Figure A1). The function used was *clus.lf()*, which compares length frequencies from simple random cluster sampling. The function contains the arguments *group*, *len*, *haul*, *number*. These arguments correspond to mission type, length measurements, serial number, respectively. Additionally, *binsize*, and *resamples* were defined as the length distribution interval, and the number of randomizations, respectively. *Binsize* was set to 1 and *resamples* was set to 200.

Table 3 *Number of individuals used in the comparison of length distribution for commercial and scientific gears. All survey years that met the criteria of spatial and temporal filtering are shown along with their respective data source (Commercial and Scientific), the total number of commercial stations (# stations_com), scientific stations (# stations_sci), and polygon IDs. Many polygons are produced due to the overlapping of stations.*

Survey year	Commercial	Scientific	# stations_com	# stations_sci	# polygon IDs
2007	11187	3450	4	3	33
2008	15953	4525	3	3	53
2015	3956	2442	11	8	27
2016	8374	3739	13	7	61
2017	2400	950	13	6	16
2018	7736	2084	29	9	39
2019	3426	1444	19	8	25
2021	62461	8051	41	7	87
2022	145	70	5	2	1

The comparison of length distribution of sandeel catches from commercial and scientific gears showed only a few instances where length distributions were significantly different between gears (Figure A1). It is important to note that the length distributions for commercial and scientific gears are not expected to always be the same because there can exist large variations in sandeel populations over short distances and time periods.

2.4 Variation in sandeel length, weight, and condition

All spatial and temporal analyses carried out in this thesis use all available biological data without grouping by gear. Because the focus of this thesis is on spatial variation within NEEZ and its management areas (see Figure 1), coordinates of the observations were appropriately grouped to overlap the current defined areas (A-D). This was done by using a shapefile of the areas in NEEZ provided by IMR, and the function *st_filter* from the *sf* package (Pebesma, 2018). For the purposes of describing spatial and temporal variation in demographics, this new grouping is more useful as the results may be tied to the ongoing fishery and management in these exact areas, or alternatively slightly different area-definitions in the future.

For the analyses that were done across year-classes, the data was filtered to contain ages 1-4 (Table 4) as few observations of individuals older than age four exist. As a result, year-classes 2009, 2014, 2016 and 2018 had the highest number of samples representing individual age (Table 4). These year-classes are hereafter abbreviated C09, C14, C16 and C18 respectively. The weeks used in the analyses were 17 and 18 because they had the largest number of observations. This was done to account for seasonal differences, which are strong in sandeels (Bergstad, Høines and Jørgensen, 2002).

Table 4 *Number of individuals in age groups and areas used in the analyses on year-classes. The data is from weeks 17 and 18.*

Year-class	Area	Age 1	Age 2	Age 3	Age 4
C09	A	49	286	188	11
	B	164	569	422	49
	C	184	149	43	18
	D	107	92	46	0
C14	A	302	332	65	6
	B	321	146	38	11
	C	314	165	18	14
	D	7	26	37	26
C16	A	257	427	232	78
	B	256	193	70	33
	C	651	324	184	68
	D	57	202	273	69
C18	A	217	51	13	12
	B	105	28	30	52
	C	113	99	80	44
	D	255	52	151	12

The first objective of this thesis was to examine the spatial variation in length and condition at age between management areas A-D. This was done separately for length and condition. For length at age, a nonlinear least squares regression model containing the von Bertalanffy growth function was fitted to the length and age data using the *nls()* function from base R (R Core Team, 2021), as shown below:

$$Eq.(1.1) \rightarrow \mathrm{length} \sim \mathrm{L\_inf} - (\mathrm{L\_inf} - \mathrm{L0}) * \exp(-\mathrm{K} * \mathrm{age})$$

$$Eq.(1.2) \rightarrow \mathrm{length} \sim \mathrm{L\_inf[Area]} - (\mathrm{L\_inf[Area]} - \mathrm{L0[Area]}) * \exp(-\mathrm{K[Area]} * \mathrm{age})$$

Where *L_inf* is the asymptotic length, *K* is the asymptotic growth rate, *Area* is management areas A-D, and *exp* is the exponential component (^). The age variable consisted of all available ages (1-10) because this gave the most accurate estimates of the described parameters used in the model. Two models were created based on this formula. The simplest model (Eq. 1.1) predicted length as a function of age. The other model (Eq. 1.2) predicted length as a function of age and management area. A graphical representation of the two growth models is shown (Figure 4), and residuals are shown for Eq. 1.2 (Figure A2). This model gives estimates of three parameters: asymptotic length ($L\infty$) given in cm, length at age zero (L_0) given in cm, and asymptotic growth rate (K) given as the inverse of time (time^{-1}) (Table 5).

To determine whether there was spatial variation in condition, separate linear regressions were fitted to condition as a function of age and area, one for each year-class (C09, C14, C16, and C18). The following formula was used in the *lm()* function in base R (R Core Team, 2021):

$$Eq. (1.3) \rightarrow \text{condition} \sim \text{factor(age)} \; * \; \text{area}$$

$$Condition = \frac{W}{L^3}$$

Where condition is the product of dividing individual weight (W, g) by total length (L, cm) cubed, known as Fulton's condition factor (Jones, Petrell and Pauly, 1999). Age represents the factor variable of ages 1-4, and area is a factor variable consisting of management areas A-D. Additionally, analysis of variance (ANOVA) was performed on the linear model (Eq. 1.3) for each year-class (Figure A3).

To determine whether initial differences in length persisted within year-classes, length was initially modelled linearly as a function of age and management area to check for differences between areas as the sandeels grew larger. Secondly, the correlation between the mean length of one- and two-year-old sandeels was found, giving an indication of the initial spatial differences between sandeels of age one compared to age two. This was repeated between one- and four-year-old sandeels. Whether spatial differences in length at age persisted could then be deduced by looking at the change in correlation from sandeels at ages 1 and 2 compared to sandeels at ages 1 and 4. Decreased correlation was assumed to indicate larger spatial differences in length at age, while increased correlation was assumed to indicate smaller spatial differences in length at age. Optimally, this would be favorable to do on an individual level, but that would require recapture of the individuals, therefore mean length is used. Whether changes persist may give an indication of whether there is a flux of individuals between the management areas. For the linear model, the following formula was used in the *lm()* function from base R (R Core Team, 2021):

$$Eq. (2) \rightarrow \text{length} \sim \text{factor(age)} * \text{area}$$

Where the age variable consists of ages 1-4 and area consists of areas A-D. Separate analyses were done on each year-class. Additionally, analysis of variance (ANOVA) was performed on the linear model (Eq. 2) for each year-class (Table A4).

The third objective was to determine whether there was a reduction on length at age late in the season, as reported in the latter half of the year by Bergstad, Høines and Jørgensen (2002), and late in the fishing season by Rindorf *et al.*, (2016). Weeks analyzed are therefore 20-25. Since length is a parameter that increases for individuals throughout the season, a decrease in length-at-age is likely due to reduced availability of the fish in the water column. In turn, this is likely due to a behavioral change in which larger individuals of sandeels bury earlier than smaller ones. This analysis was done using the following formula in the *lm()* function from base R (R Core Team, 2021):

$$Eq.(3) \rightarrow \text{length} \sim \text{factor(age)} * \text{week} * \text{area}$$

Age is a factor, thus giving separate interactions for each age instead of an average for all ages. The week variable is continuous and consists of weeks 20-25, age is a factor variable consisting of ages 1-4, and area consists of areas A-D. The rationale was to check whether the slope was negative late in the season, indicating a reduction in length at age. Individual length and age samples from the scientific sandeel dredge were not used here because this gear caught sandeels where they were buried, thus defeating the purpose of utilizing decrease in length as an indication of overwintering behavior.

The fourth objective was to determine whether the fishery should open earlier based on seasonal variation in weight. Since Total Allowable Catch (TAC) is given in weight (tons), the number of sandeels harvested depends on the individual weight. Harvesting at an optimal time is therefore crucial to avoid catching unnecessarily many individuals and increasing the fishing mortality. To get an idea of the potential seasonal differences in weight at age, weight was modelled with a second-degree polynomial regression. A third-degree polynomial was avoided due to very little explanatory difference in the response variable and to decrease the complexity of the model. This was done using the *lm()* and the *poly()* functions from base R (R Core Team, 2021):

$$Eq.(4) \rightarrow \text{weight} \sim \text{poly(age, 2)} \; * \; \text{area}$$

Where the age variable is a factor representing ages 1-4, and area represents areas A-D. The data used was from all survey years (2007-2022).

When producing the figures for each model, raw data is presented using *geom_jitter()*, spreading out the observations along the x and y axes. “Position = position_jitterdodge” is also used to place the area observations next to each other. “Position = position_dodge” is used in the boxplots.

3. Results

3.1 Comparison of length selectivity of fishing gears

A graphical representation of the length selectivity shows that commercial and scientific fishing gears are mostly the same (Figure 3). The scientific gears sometimes catch larger sandeels than the commercial gears (e.g., survey years 2015 and 2016). The statistical analysis performed with simple cluster sampling also indicates similar selectivity (Figure A1).

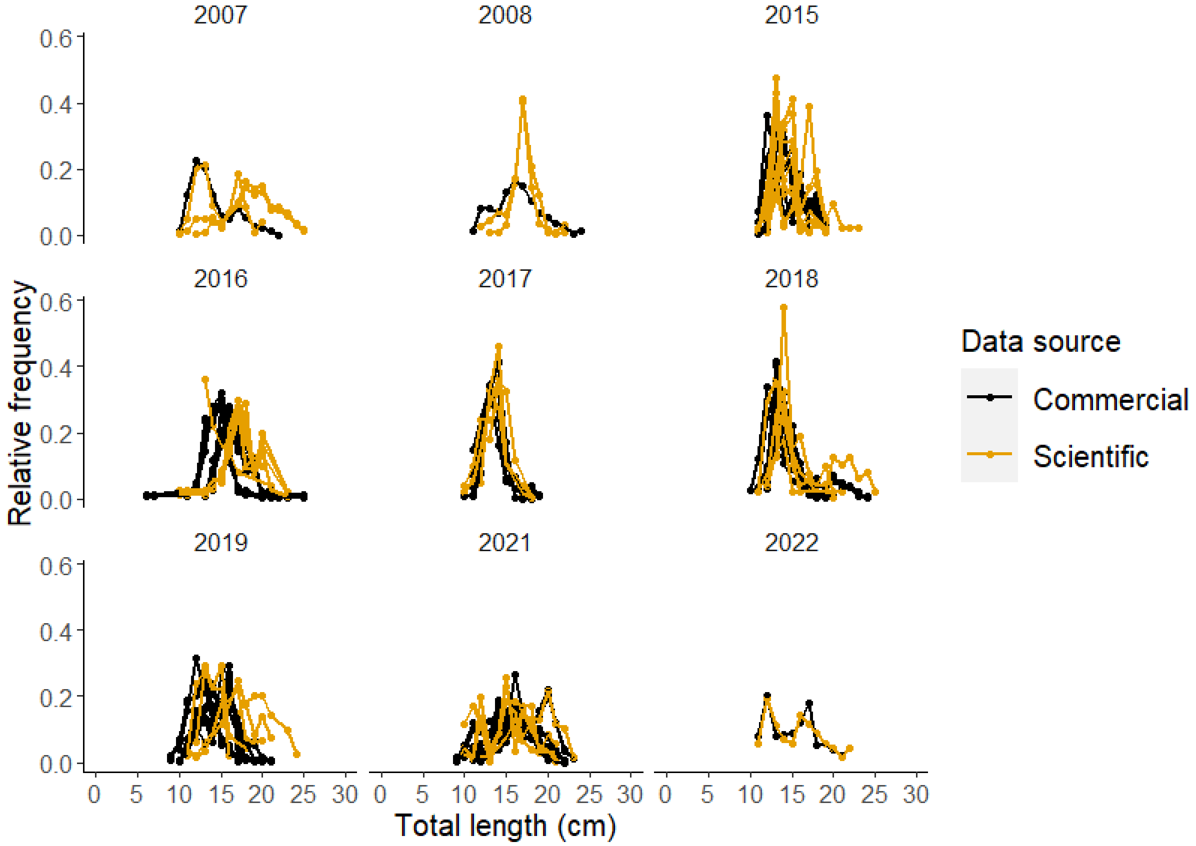


Figure 3 *Relative length distribution of sandeel caught by commercial gear (black lines) and scientific gear (orange lines). Each pair of lines represents one polygon ID.*

3.2 Spatial variation in length and condition at age

Sandeels had relatively similar length at age in areas B-D, but they were shortest at age in area A (Figure 4). The rate (K) at which sandeels grew toward their maximum length was considerably higher in area B compared to any other area (Table 5). The rate at which sandeels in area D grew toward their maximum length was somewhat lower compared to the other areas, while also exhibiting the highest maximum length (Table 5). Asymptotic length and length at age zero was highest in area D. Analysis of variance indicated that the model considering area (see Eq. 1.2) was significantly better at explaining variation in length at age ($p < 0.001$) compared to Eq 1.1, indicating spatial difference in growth (Table A2).

Table 5 *Estimates of asymptotic length ($L\infty$), length at age zero (L_0) and the asymptotic growth rate (K) in areas A-D from the von Bertalanffy growth function. Estimates from Eq 1.1 are included on the bottom.*

Parameter	Estimate	P-value
$L\infty A$ (cm)	23.3	< 0.001
$L\infty B$ (cm)	23.2	< 0.001
$L\infty C$ (cm)	25.2	< 0.001
$L\infty D$ (cm)	26.4	< 0.001
L_0A (cm)	9.54	< 0.001
L_0B (cm)	8.06	< 0.001
L_0C (cm)	8.71	< 0.001
L_0D (cm)	10.1	< 0.001
K_A ($time^{-1}$)	0.231	< 0.001
K_B ($time^{-1}$)	0.342	< 0.001
K_C ($time^{-1}$)	0.279	< 0.001
K_D ($time^{-1}$)	0.199	< 0.001
$L\infty$(Eq. 1.1) (cm)	24.8	< 0.001
L_0(Eq. 1.1) (cm)	9.07	< 0.001
K(Eq. 1.1) ($time^{-1}$)	0.254	< 0.001

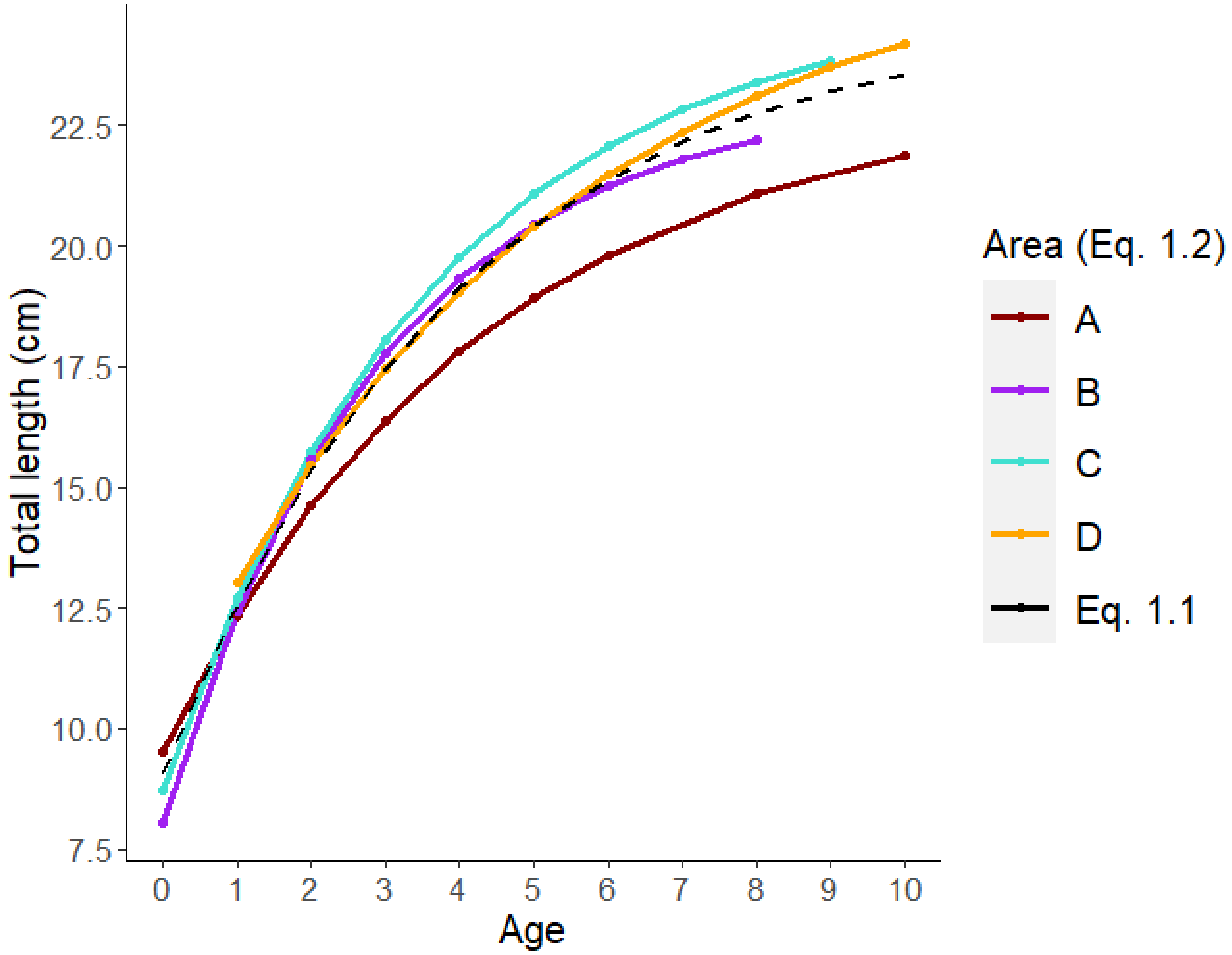


Figure 4 *Predicted total length at age of sandeels by the von Bartalanffy growth function. The dashed black line (Eq. 1.1) represents the model without area as a predictor variable. The colored lines (Eq. 1.2) represent the model with area as a predictor variable. Data is from weeks 17 and 18 and all survey years.*

Fulton's condition factor was similar for sandeels across areas (Figure 5). There were no obvious or marked trends in spatial difference for any area. However, the condition factor was significantly associated with age ($p < 0.001$), management area ($p < 0.001$), and the interaction between age and area ($p < 0.001$) in all year-classes (Table A3), indicating a difference in condition between areas A-D in one or more age groups. Residuals are shown in Appendix 6.3 (Figure A3).

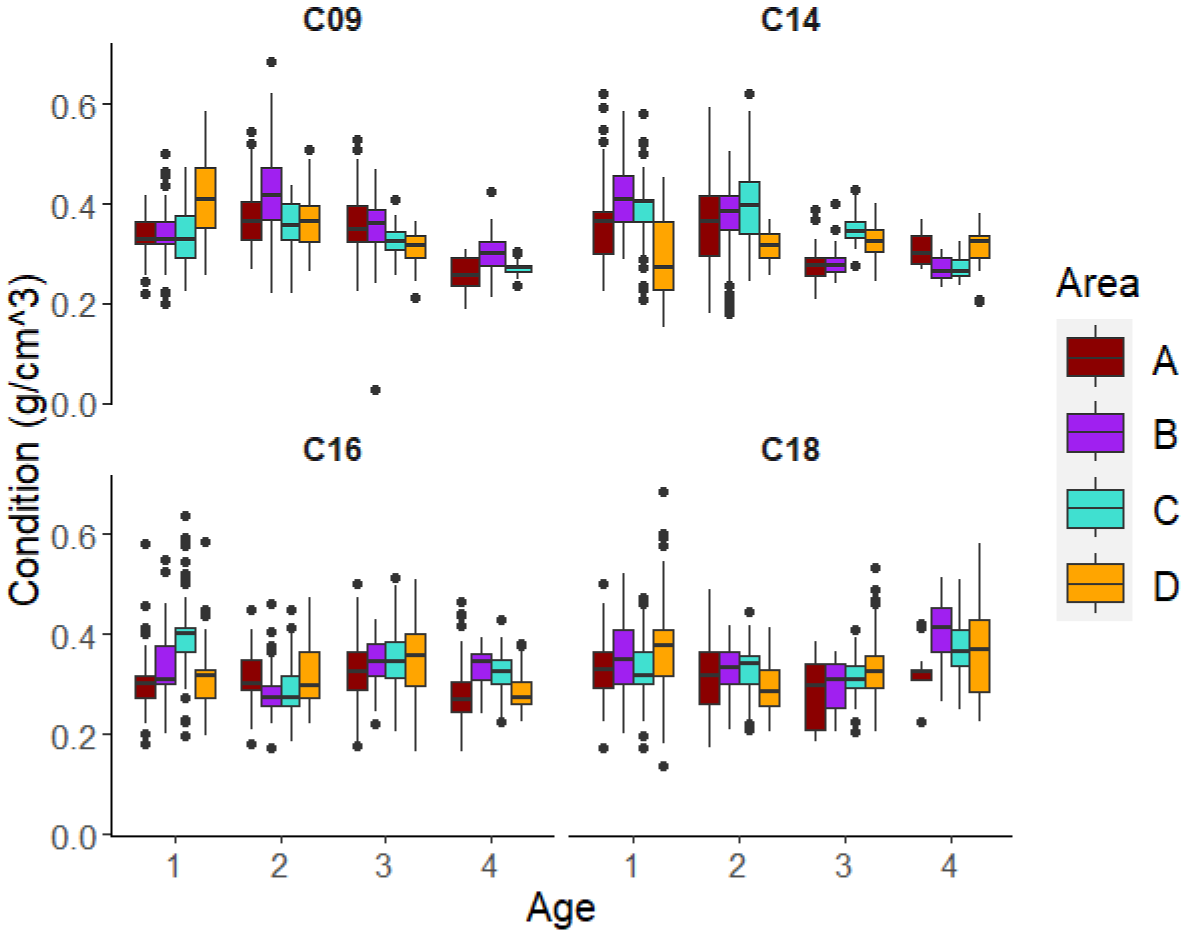


Figure 5 *Fulton's condition factor of sandeels at ages 1-4 in areas A-D, and year-classes C09, C14, C16, and C18. Data is from weeks 17 and 18. "position = position_dodge()" is used to place boxes of the same age next to each other. Black dots above and below the boxes are outliers.*

3.3 Changes in length at age over time

Sandeels in area A were consistently shorter in all year-classes compared to any other area (Figure 6). Length was significantly associated with age ($p < 0.001$), area ($p < 0.001$), and the interaction between age and area ($p < 0.001$) in all year-classes (Table A4). A significant interaction between age and area indicates that length at age of sandeels varies depending on which management area it is from. Residuals are shown in Appendix 6.3 (Figure A4).

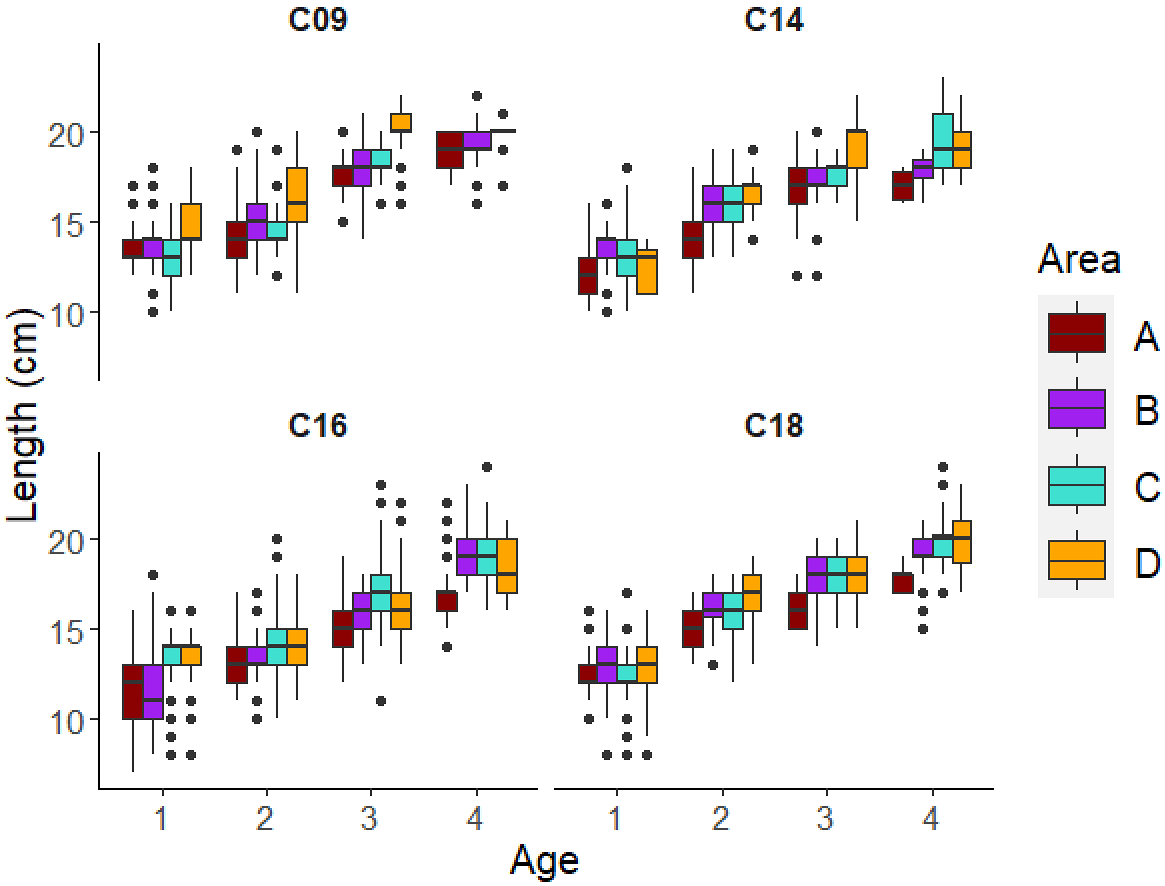
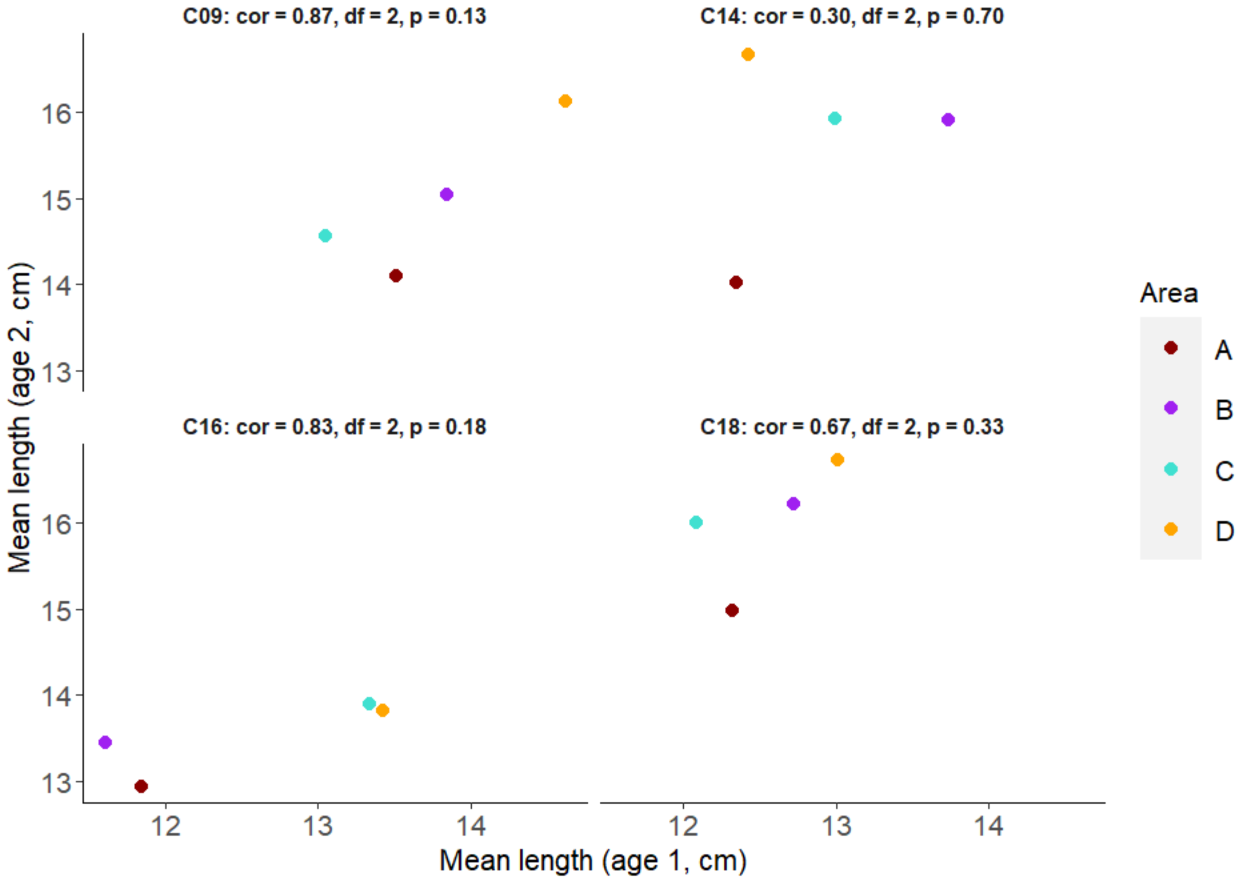


Figure 6 *Total length of sandeels as a function of the interaction between age and area for year-classes C09, C14, C16, and C18. Data is from weeks 17 and 18. "position = position_dodge()" is used to place boxes from the same age group next to each other. Black dots above and below the boxes are outliers.*

The correlation between the mean length of sandeels at ages 1 and 2 was higher than between sandeels at ages 1 and 4 (Figure 7). High correlation between the mean length of sandeels at ages 1 and 2 suggests that the initial difference in length between areas persist from age 1 to age 2. The correlation between length of sandeels at age 1 compared to age 4 varied more. The lower correlation observed between mean lengths at ages 1 and 4 suggests that initial differences in length become greater by the time the sandeels become 4 years old.


C09: cor = 0.87, df = 2, p = 0.13
C14: cor = 0.30, df = 2, p = 0.70
C16: cor = 0.83, df = 2, p = 0.18
C18: cor = 0.67, df = 2, p = 0.33
Mean length (age 2, cm)
13
14
15
16
12
13
14
Mean length (age 1, cm)
Area
A
B
C
D

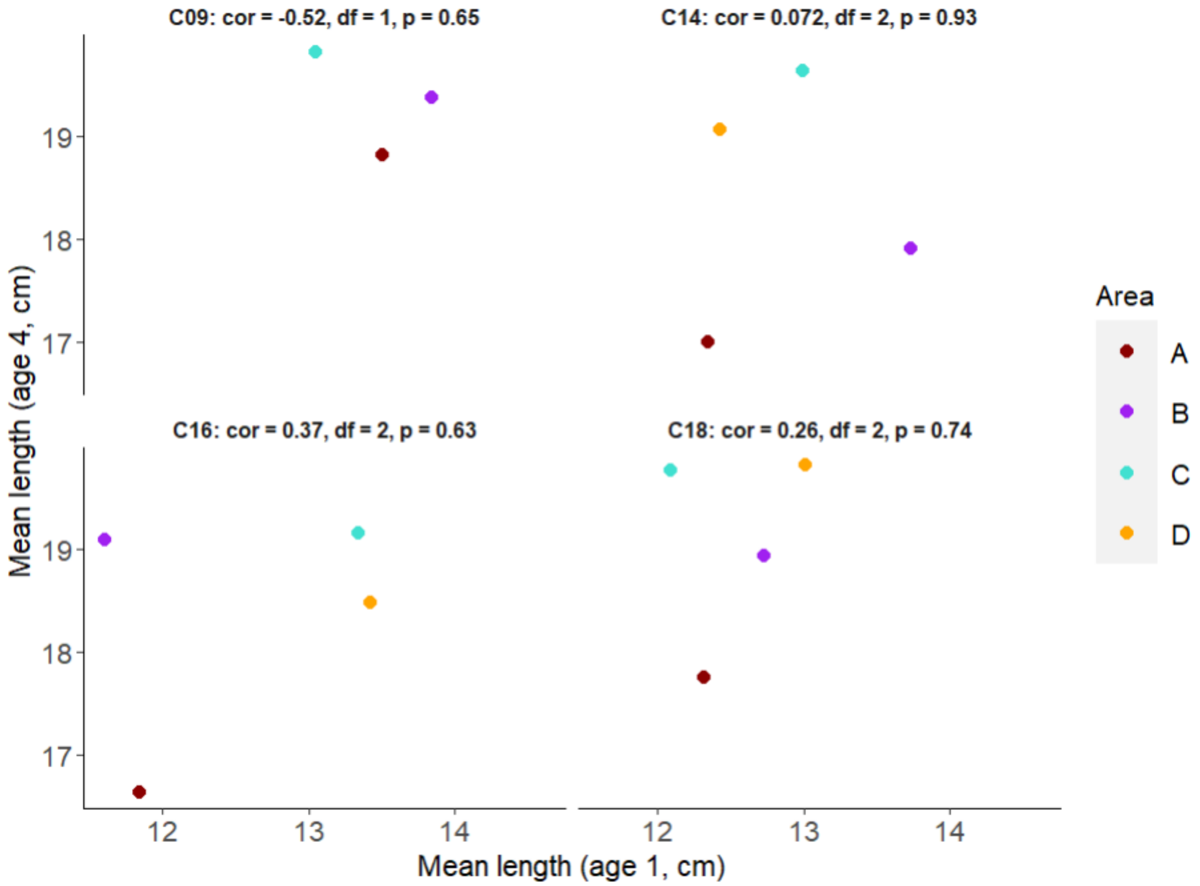


Figure 7 *Correlation between the mean length of sandeels at ages 1 and 2 (top) and ages 1 and 4 (bottom). Correlations are done for each year-class. The data is from weeks 17 and 18.*

3.4 Length reduction late in the season

Two-, three- and four-year-old sandeels from area A, two-year-old sandeels from area B and D, and three-year-old sandeels from area D decreased in length from weeks 20 to 25 (Figure 8). The estimated interactive effect between sandeel age and week is either positive or negative, indicating an increase or decrease in length respectively (Table 6). The effect was least prominent for one-year-old sandeels (Figure 8), indicated by the somewhat constant length at age. All variables and interactions were significant (Table A5) and explained 67% ($R^2 = 0.671$) of the variation in length. Residuals are shown in Appendix 6.3 (Figure A5).

Table 6 *Estimates of the added interactive effect of age and week (Age:Week) on length for ages 1-4 of sandeels in areas A-D, and associated p-values indicating the significance of difference compared to area A. Data covers week 20-25 and is from all available survey years (2007-2022). Asterisk (*) represents significance.*

Age	**Area**	**Age:Week**	**P-value**
1	A	0.09	0.030*
	B	0.13	0.007*
	C	0.035	0.48
	D	-0.073	0.18
2	A	-0.45	< 0.001*
	B	-0.45	0.987
	C	+0.06	< 0.001*
	D	-0.28	0.229
3	A	-0.71	< 0.001*
	B	+0.04	< 0.001*
	C	+0.39	< 0.001*
	D	-0.16	< 0.001*
4	A	-0.73	< 0.001*
	B	+0.11	< 0.001*
	C	+0.18	< 0.001*
	D	+0.11	< 0.001*

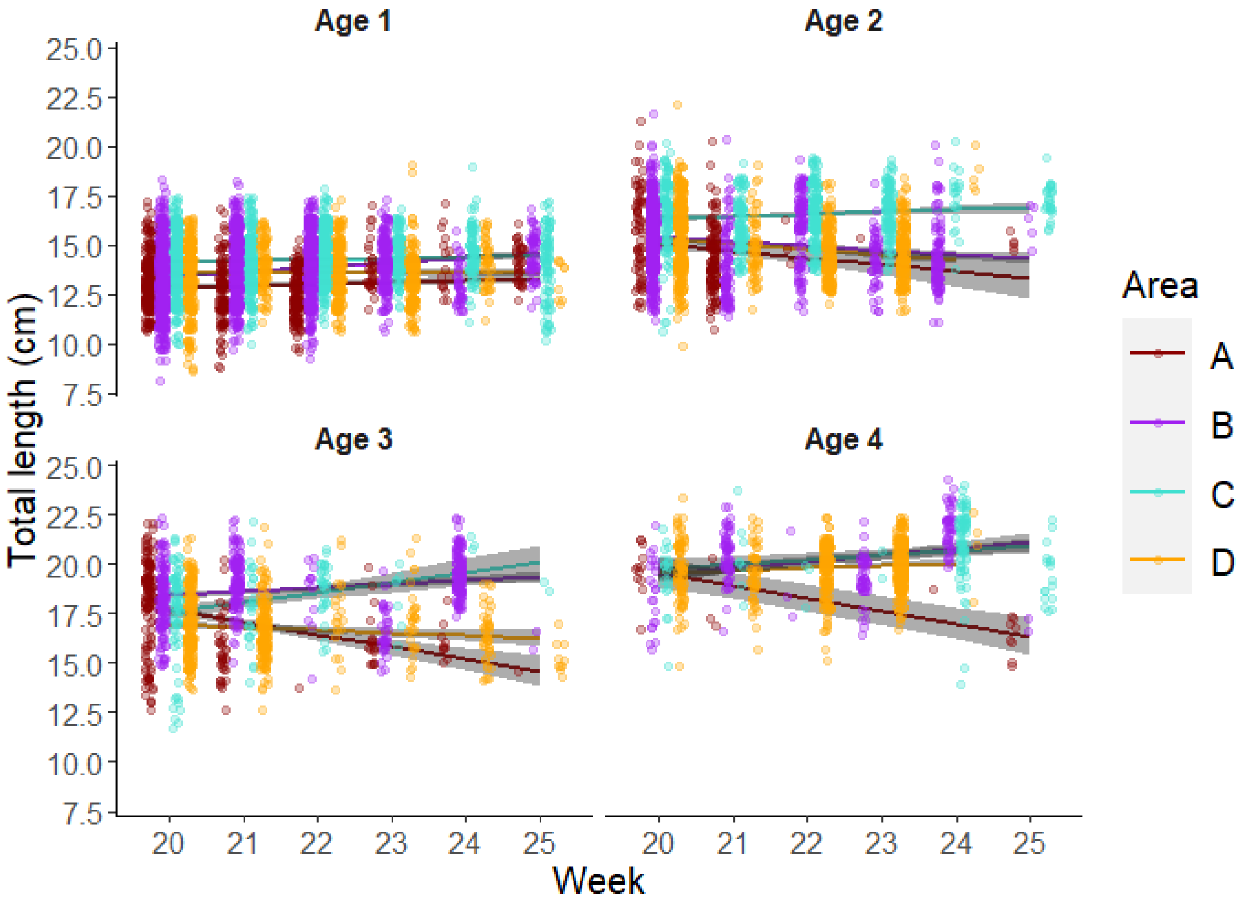


***Figure 8** Predicted length at age one (top left), age two (top right), age three (bottom left), and age four (bottom right) of sandeel in areas A-D in weeks 20-25 from a linear regression model including a confidence interval of 95% (shaded area). Data is from all available survey years (2007-2022). "Geom_jitter()" is used to spread out the observations on the x and y axes. "position = position_jitterdodge()" is also used to place samples from areas A-D next to each other for increased clarity.*

3.5 Seasonal variation in individual weight

The individual weight of sandeels was the highest in area C and increased throughout the season for all age groups (Figure 9). The increase is about three-fold for one-year-old sandeels, and about two-fold for two-, three-, and four-year-old sandeels. In area A, the weight of three- and four-year-old sandeels peaked markedly around week 21, a two-fold increase from the initial weight of about 10 g in weeks 15-16. All variables and their interactions were significant (Table A6) and explained 62% ($R^2 = 0.617$) of the variation in weight (see Eq. 4). Residuals are shown in Appendix 6.3 (Figure A6).

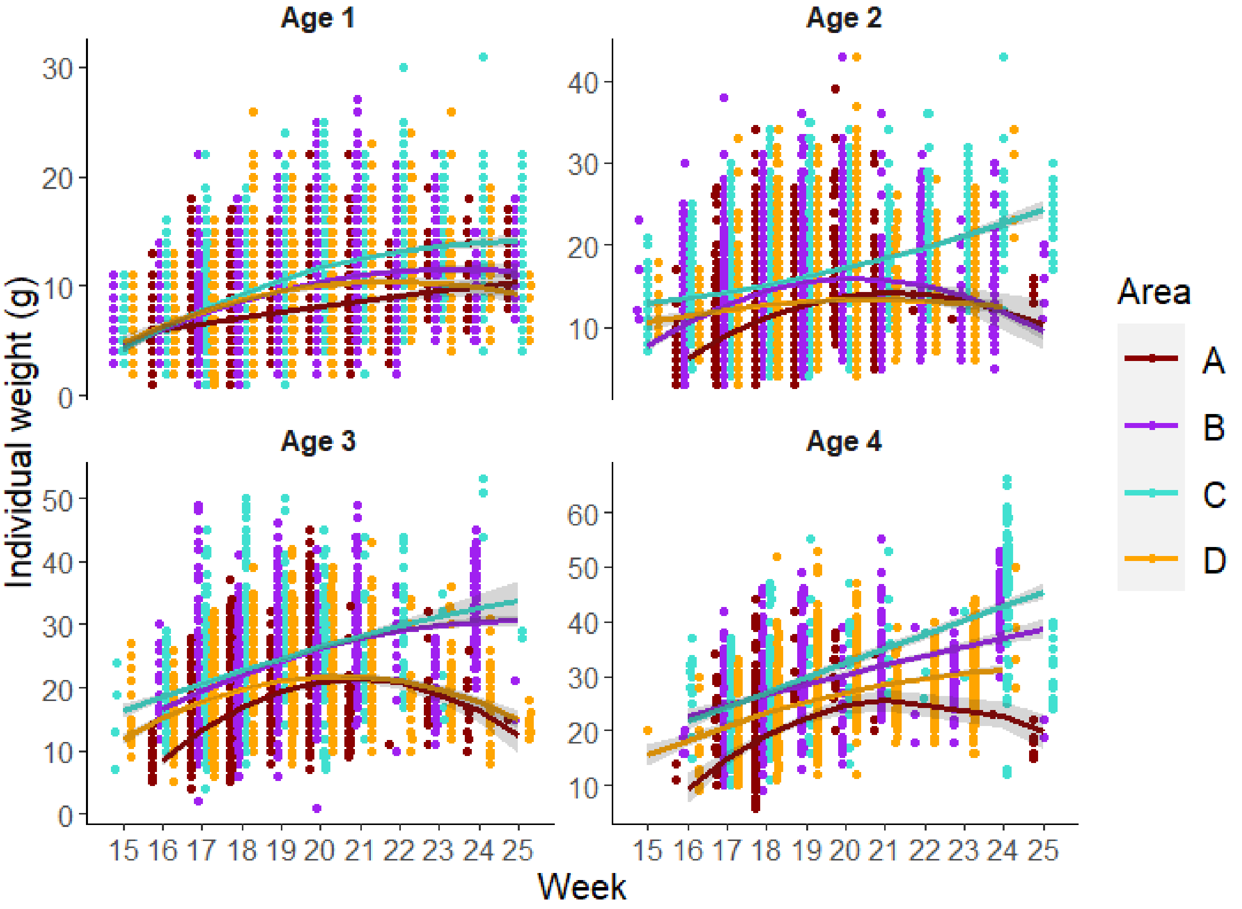


Figure 9 *Predicted individual weight at age one (top left), age two (top right), age three (bottom left) and age four (bottom right) as function of week (15-25) and area (A-D). Data is from all survey years (2007-2022). The shaded area represents the 95% confidence interval of the fitted third-degree polynomial regression (lines) for each area. "Geom_jitter()" is used to spread out the observations on the x and y axes. "Position = jitterdodge" is also used to place samples from areas A-D next to each other for increased clarity. Y-axis scales are adapting to the data presented.*

4. Discussion

Spatial differences in growth of the sandeel have been reported previously in the North Sea (Webb and Macer, 1968; Bergstad, Høines and Jørgensen, 2002; Wanless *et al.*, 2004), as well as an elaborate study on regional variation between fishing grounds (Rindorf *et al.*, 2016). The range at which mixing of individuals occurs has also been investigated (Jensen *et al.*, 2011) - suggesting that mixing is stronger within grounds than between grounds. The rationale for the area-based management system implemented in NEEZ in 2010 is based on evidence that sub-populations of sandeels are demographically disconnected over short distances (Johannessen and Johnsen, 2015). Sandeels in areas consisting of fewer fishing grounds further apart are therefore likely to benefit more from this area-based management plan because each sub-population may be more susceptible to fishing pressure. On the other hand, in areas where fishing grounds are close to each other, higher connectivity may alleviate the stress of fishing and contribute to a faster recovery of the targeted population or populations. This thesis provides additional insight into the spatial variation in growth of sandeel between the current management areas in NEEZ.

This study shows that length at age was lowest for sandeels in the southernmost area (A), consistent with the findings of Bergstad, Høines and Jørgensen (2002). It also coincides with the demographic disconnect over short distances reported by Johannessen and Johnsen (2015). Fulton's condition factor at age was found to differ spatially in one or more age groups, but there were no clear spatial patterns. The correlation between the mean length of one- and four-year-old sandeels was considerably lower than that between one- and two-year-old sandeels, suggesting that length-differences of sandeels become larger between areas over time, indicating low connectivity. Length at age was found to decrease in the end of the season for sandeels of ages 2-4, similar to the decrease in length of ages 1-2 reported by Rindorf *et al.* (2016), in the arguably disconnected fishing grounds of Berwick Bank. The most considerable reduction in length at the end of the season was observed for sandeels in area A, encapsulating the southernmost fishing ground which is relatively far from the neighboring fishing grounds. Sandeel weight increased two- three-fold during the fishing season, and sandeels in area C gained weight consistently throughout the season in all age groups. Sandeels of ages 2-4 in area A peaked in weight at around week 21.

4.1 Comparison of length selectivity of fishing gears

The results from the random cluster sampling, based on annual, weekly, and spatial grouping criteria, indicate high similarity between commercial and scientific length selectivity (Figure A1). This was expected because the mesh is small in both commercial and scientific gears. It was also advantageous because it gave many biological samples in space and time. An assumption made when comparing the gears was that of exchangeability. Only one group of commercial gear was compared to another group of scientific gear, both of which varied in the type of gear (e.g., bottom trawl, pelagic trawl). For scientific gears, interchangeability was assumed because this is what is done in practice, the gears are assumed to represent the population equally (Johnsen, 2022). The commercial gears were assumed interchangeable due to the uncertainty around the exact type of gear used by the fishing vessels (Directorate of Fisheries, 2010).

The scientific gears are found to sometimes catch larger fish (e.g., 2015 & 2016). The cause of this may be due to that commercial vessels are targeting areas of high acoustic density when trawling for sandeels, thus catching fish independently of size. Another explanation could be that smaller scientific trawls are able to reach parts of the sandeel habitats that are less exposed to fishing, which ultimately inhabits older and larger sandeels. Natural rock structures in Vestbanken are thought to be the cause of increased annual recruitment due to reduced fishing pressure because of the inaccessibility of the larger commercial fishing gears (Johannessen and Johnsen, 2015).

4.2 Spatial variations in length and condition at age

Sandeels in the southernmost area (A) were the shortest at age. The length growth of sandeel in areas B-D was similar, though it diverged when approaching the asymptotic length. Asymptotic length and length at age zero was highest in the Northwestern-most fishing grounds (D), corresponding to the findings of Rindorf *et al.* (2016). Higher length at age zero may imply potential for increased recruitment due to increased survivability of larger sandeels. Investigation into spatial differences in growth of sandeels (Johannessen and Johnsen, 2015) suggest that protective rock structures gave rise to consistently high recruitment annually in Vestbanken, corresponding to area C in this thesis. The protective rock structures may serve as protection from trawls and thereby sandeels maintain larger length at age due to less fishing pressure (Neuheimer and Taggart, 2010). This may partly explain the relatively high length at age observed for sandeels in area C. The comparatively low length at age in area A may by the same token be explained by higher fishing pressure due to more exposed fishing grounds, and possibly by lower recruitment and recovery rates as a result of poor connectivity. Speculatively, larger individuals may emigrate North, while smaller individuals migrate to area A from the south, leading to decreased mean length at age.

Spatial differences in condition were indicated in one or more age groups of sandeel. However, post-hoc exploration of area-specific differences was not conducted due to the lack of any marked spatial pattern. There are both ecological implications and fishery-management implications tied to spatial differences in condition at age of sandeels. Ecologically, the sandeel is important as an energy source of both marine fish, mammals, and seabirds (Furness, 1990; Wanless, Harris and Greenstreet, 1998). Spatial differences in the energy values of sandeels may therefore have area-dependent effects on predators that consume the sandeel. An example is seabirds (Wanless *et al.*, 2005), where shortages of sandeel and consequently lower energy values of an alternative food source is thought to have caused major breeding failure. The fishery wants individuals of high condition because this yields the highest profit. Thus, in the case of spatiotemporal differences in condition, the fishery might need to adapt different strategies depending on area and time of the year.

4.3 Changes in length at age over time

The observed consistently different length at age of sandeels in area A may be partly explained by weak demographic connectivity due to relatively large distances (~100km) to adjacent sandeel fishing grounds (Jensen *et al.*, 2011; Johannessen and Johnsen, 2015). Jensen et al (2011) suggests that mixing within fishing grounds eliminates differences over greater distances than between fishing grounds. Specifically, they found that mixing was sufficient to eliminate differences in length distribution up to 28 km within fishing grounds. Between fishing grounds, however, mixing eliminated differences in length distribution up to only 5 km. Kunzlik, Gauld and Hutcheons (1986) also suggests little movement of sandeels between grounds. The lack of intermediate sandeel habitat grounds close to area A may drastically reduce the range at which the sandeel can distribute because of their strong dependence on this specific type of habitat (Wright, Jensen and Tuck, 2000; Holland *et al.*, 2005), leading to localized growth conditions. The correlation between the mean lengths of one- and four-year-old sandeels was lower than the correlation between one- and two-year-olds, indicating that initial differences in length became larger. This implies that there may be weak connectivity and consequently a low flux of individuals between the management areas. Hypothetically, increased correlation by age four would mean that the lengths became more similar, pointing to an exchange of individuals between the management areas. Length-at-age can be affected by several factors, for example environmental conditions, fishing pressure, and competition. Fishing pressure may cause length-at-age and maturity-at-age to decrease (Olsen *et al.*, 2004; Neuheimer and Taggart, 2010; Lappalainen *et al.*, 2016). Furthermore, reduced connectivity to other fishing grounds may increase the recovery time of the population following intensive fishing, emphasizing the need to understand the spatial variation in growth and connectivity.

Seasonal fluctuation in food availability is emphasized as an important factor leading to seasonal growth patterns in sandeels (Bergstad, Høines and Jørgensen, 2002; Gurkan *et al.*, 2012). Since zooplankton is important to their diet (Arnott and Ruxton, 2002; Frederiksen *et al.*, 2006; van der Kooij, Scott and Mackinson, 2008), and their temporal match with zooplankton availability is found as important for early survival (Wright and Bailey, 1996; Arnott and Ruxton, 2002; Régnier, Gibb and Wright, 2017), sandeel populations are controlled by bottom-up mechanisms (Frederiksen, Furness and Wanless, 2007), thus supporting of the existence of a major driver having a large influence on the growth across the entire region. The way the spatial difference in length at age increases with age coincides with the idea that local conditions promote growth differently, where differences initially are small because of the effect of regional food availability on growth, indicated by the higher correlation between sandeels of ages one and two. These differences are small at age one but become increasingly prominent over time, hence the correlation decreases with sandeels of older ages. If spatial differences increase, indicated by lower correlation, there is arguably a lower flux of individuals between the areas, which may result in difference demographics over time.

An assumption made when using proximity of adjacent fishing grounds to explain the difference in length-at-age is that the fishing grounds used in the analysis are equivalent to and comprise all sandeel habitats in the region. It is also important to note that differences in length-at-age between two given areas are not necessarily due to a lack of migration. At the same time, similar length-at-age is not necessarily due to migration, but can be a combination of identical recruitment, growth and mortality patterns across multiple areas independently, in addition to a lack of migration, as suggested by Jensen *et al* (2011).

4.4 Reduction in length at age late in the season

The most considerable reduction in length during the season was observed for sandeels at ages 2-4 in area A. Sandeels in area B and D showed a similar decrease in length at age two. The onset of overwintering depends on individual lipid reserves, condition, and length (Bergstad, Høines and Jørgensen, 2002; Wanless *et al.*, 2004; van Deurs, Hartvig and Steffensen, 2011). The cause of this is suggested to be linked to the ability to stay buried for longer periods, based on the potential to store energy (Boulcott and Wright, 2008). Since length naturally increases during the feeding season, decreases in length may reasonably be assumed to happen due to the sandeel avoiding the fishing gear, more specifically the trawl because of its use in the water column. Hence, the likely explanation is overwintering behavior of larger sandeel, consequently decreasing the mean length of the age group in question. This has been observed in the latter half of the year (Bergstad, Høines and Jørgensen, 2002), during a period where sandeels are known to start or already have started overwintering behavior (Bergstad, Hoines and Krüger-Johnsen, 2001; van Deurs *et al.*, 2010). Length reduction of sandeels late in the fishing season (weeks 20-25) has also been observed (Rindorf *et al.*, 2016). The temporal period investigated in this thesis may be too early to detect a reduction in length at age across all areas, as is expected eventually. This may imply that the onset of overwintering occurs earlier in area A. Further studies concentrated around this crucial period of the sandeels life history, and possibly later in the year, may therefore be useful.

There are both ecological and managerial implications linked to the sandeels behavior of overwintering. Sandeel is a very important constituent of the marine ecosystem, their link in the trophic chain facilitates the transfer of energy between trophic levels by consuming zooplankton

(Hill, Daly and Brodeur, 2015) and being consumed by larger fish, sea birds, and marine mammals (Furness, 1990; Wanless, Harris and Greenstreet, 1998; Bull *et al.*, 2004). This means that area-specific timing of sandeel emergence may also affect the dynamics of other species dependent on the sandeel. For the fishery, overwintering behavior first and foremost results in having to fish sandeel in a specific seasonal window due to varying availability. If overwintering behavior differs in management areas A-D, the optimal seasonal window for fishing might then differ between areas. Currently, the start of the fishing season is set to 15th of April to avoid fishing lean individuals, while 23rd of June is the end to avoid fishing fry, independent of area (Johnsen *et al.*, 2021). Different times of emergence may influence when the season should start, and timing of burying may influence when it should close. Based on the length reduction observed in this thesis, implying reduced availability of larger sandeels, area A could arguably be closed for fishing earlier than the other areas to avoid selective fishing of the smaller individuals that still is available in the water column. However, due to fry settling in lane June (Johnsen *et al.*, 2021) extending the fishing season beyond its current limit may not be favorable even though there seems to be discrepancies in the timing of overwintering.

4.5 Seasonal variation in weight at age

Growth of sandeel is highly seasonal (Bergstad, Høines and Jørgensen, 2002), and this study shows that sandeel weight may increase two- to three-fold during the fishing season. Sandeels of ages 2-4 in area A peaked in weight at around week 21. In area C, sandeels of all ages gained weight throughout the season, increasing as much as three-fold in weight at age one, and two-fold at ages three and four. Hence, twice as many individuals may be required to fulfill the quota in these areas early in the season compared to late- or mid-season. However, it is important to strike a balance, as opening the season too late could result in more intense fishing pressure over a shorter period. Furthermore, these results imply that the energy values of sandeels as prey to predators varies considerably throughout the season and between areas. The breeding success of the Kittiwake has been linked to sandeel recruitment (Frederiksen *et al.*, 2005). Thus, predators in area A may be more sensitive to changes in sandeel abundance compared to predators in area C where sandeels weigh more at all ages. This emphasizes the area-specific ecosystem impacts that may arise from varying sandeel quality and abundance.

4.6 Limitations of the study

Clustered sampling of the data may have impacted the analyses done in this work. It violates the assumption of independence among observations, which is an assumption in many statistical analyses. Clustered sampling can lead to biased estimates because observations within each cluster (haul/station) tend to be more similar to each other than to other clusters.

There is thought to exist considerable annual variation in growth of sandeels due to the influence of bottom-up control (Frederiksen *et al.*, 2006) and the importance of a trophic match (Régnier, Gibb and Wright, 2017). One example is the 2017 year-class (Figure A7), which reportedly is weak (Johnsen *et al.*, 2021). When conducting the analysis of growth using the von Bertalanffy growth model, the year-class variable was not considered because of too few individual age samples (0-10) for each year-class. Similarly, annual variation was not considered when investigating length reduction late in the season and seasonal variation in length. The potential problem with this is that growth conditions from year to year may give a skewed representation of the growth between age groups. However, the observed lower length at age in area A (Eq. 1.2) is supported by the analysis of length conducted on year-classes (Eq. 2).

4.7 Further research

Further research could be directed towards the comparatively low growth observed in management area A. It would be interesting to link spatiotemporal variation in growth to diet analysis or simply stomach fullness. Since the sandeels diet consists largely of zooplankton, stomach fullness could be used as a proxy for food availability, and thus as an explanatory variable for spatiotemporal variation in growth.

There exists much evidence for the importance of a temporal match between hatching and food availability on the condition of forage fish (Wright and Bailey, 1996; Arnott and Ruxton, 2002; Régnier, Gibb and Wright, 2017). While these studies have found that food availability is important for survival immediately after hatching and that year-class strength is established during early larval development, less is known about the recovery of weak year-classes in the sandeel management areas and whether low condition in in a young year-class determines its future condition. It could therefore be interesting to investigate whether sandeels in one management area react differently following a year of poor growth, compared to sandeels in another area. This information could be used to assess year-class strength, which is used when estimating future spawning stocks and quotas.

4.8 Conclusion

Spatial differences in growth of the sandeel have been reported previously in the North Sea (Webb and Macer, 1968; Bergstad, Høines and Jørgensen, 2002; Wanless *et al.*, 2004), as well as an elaborate study on regional variation between fishing grounds (Rindorf *et al.*, 2016). However, the combination of both commercial and scientific sources used in this thesis encompasses a vast amount of biological sandeel data and represents a novel approach to investigating sandeel growth in NEEZ. Sandeel grew slower in management area A, possibly due to higher fishing pressure and weaker connectivity to neighboring fishing grounds. The high length at age observed in area C may be explained by protective rock structures reducing fishing pressure, leading to higher length at age. Asymptotic length was highest in the Northwestern-most fishing grounds (D), corresponding to previous findings. Fulton's condition factor varied with sandeel age and area, but there were no clear spatial patterns. Initial spatial differences in length of one-year-old sandeels became greater by age four, suggesting that the flux of individuals between the management areas in NEEZ is low, thus substantiating the importance of an area-based management model. Length at age was found to decrease for sandeels of ages 2-4 in the southernmost area (A), suggesting an early onset of overwintering. For the fishery, this could imply area-specific variation in availability of sandeels late in the season. Weight at age increased considerably during the fishing season. Spatiotemporal differences resulted in two- and three-fold increases in weight, meaning that the number of fish required to fulfill a quota may vary substantially during the fishing season. This might also affect other species of fish, sea birds or marine mammals that may rely on sandeel as prey.

5. References

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6. Appendices

Table A1 *Variables kept when extracting relevant data from the hierarchical (Data level) xml file format.*

Data level	Mission	Fishstation	Catchsample	Individual	Agedetermination
Variables	Startyear	Serialnumber	Aphia	Individualweight	Age
		Station	Scientificname	Length	
		Stationstartdate			
		Latitudestart			
		Longitudestart			
		Gear			

6.1 Comparison of length selectivity of fishing gears

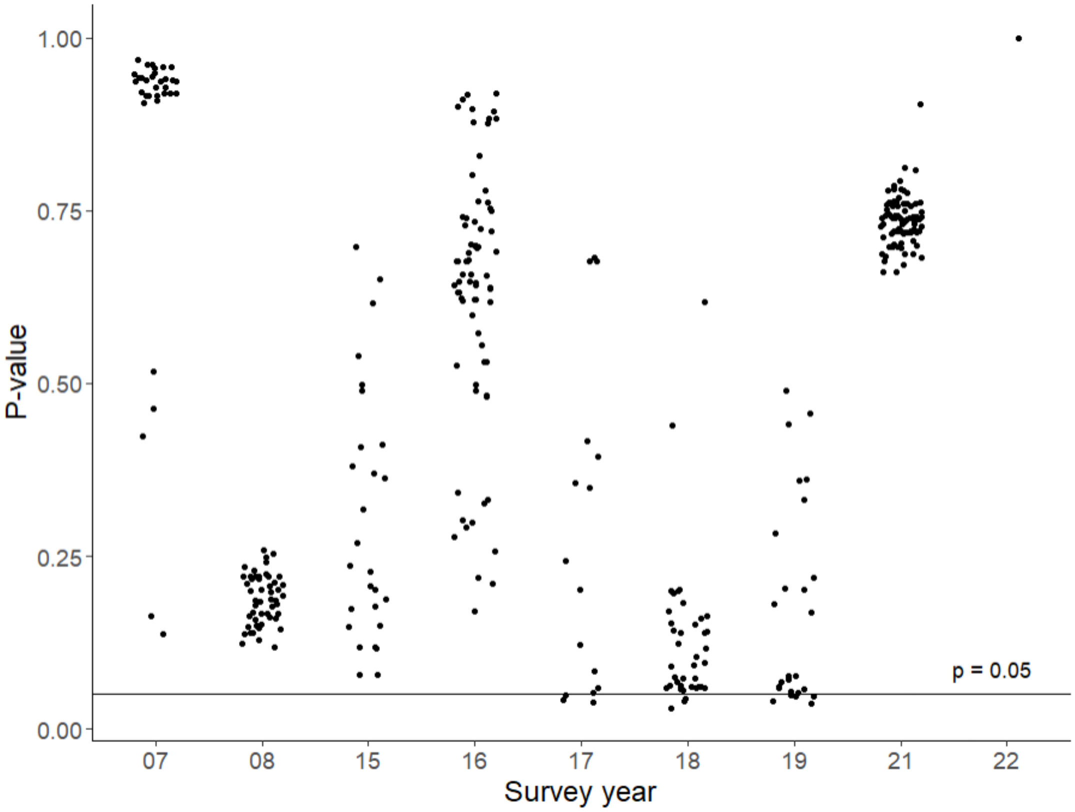

Figure A1 *Results from a statistical comparison of length selectivity of commercial and scientific gears from simple random cluster sampling from each survey year. The horizontal line represents a p-value of 0.05, indicating the threshold of a significant difference in length distribution of commercial and scientific gears. "Geom_jitter()" is used to spread data points horizontally.*

6.2 Model results

Table A2 *Analysis of variance between Eq. 1.1 and Eq. 1.2. Degrees of freedom (Df), F-value and P-value are given for each variable and interaction.*

Equation	Df	F-value	P-value
1.1	-	-	-
1.2	9	79.50	<0.001

Table A3 *Analysis of variance on Fulton's condition factor as a function of age and management area (see Eq. 1.3). Degrees of freedom (Df), F-value and P-value are given for each variable and interaction.*

Year-class	Variable	Df	F-value	P-value
C09	Age	3	169.4	<0.001
	Area	3	59.54	<0.001
	Age:Area	8	38.75	<0.001
C14	Age	3	121.4	<0.001
	Area	3	50.83	<0.001
	Age:Area	9	13.85	<0.001
C16	Age	3	235.4	<0.001
	Area	3	102.1	<0.001
	Age:Area	9	59.33	<0.001
C18	Age	3	41.20	<0.001
	Area	3	15.59	<0.001
	Age:Area	9	6.025	<0.001

Table A4 *Analysis of variance on total length as a function of age and management area (see Eq. 2). Degrees of freedom (Df), F-value and P-value are given for each variable and interaction.*

Year-class	Variable	Df	F-value	P-value
C09	Age	3	1570	<0.001
	Area	3	121.4	<0.001
	Age:Area	8	10.20	<0.001
C14	Age	3	996.6	<0.001
	Area	3	201.5	<0.001
	Age:Area	9	14.28	<0.001
C16	Age	3	1612	<0.001
	Area	3	222.3	<0.001
	Age:Area	9	16.27	<0.001
C18	Age	3	1730	<0.001
	Area	3	29.23	<0.001
	Age:Area	9	7.986	<0.001

Table A5 *Analysis of variance on length as a function of week, age, and area (see Eq. 3). Degrees of freedom (Df), F-value and P-value are given for each variable and interaction.*

Variable/interaction	**Df**	**F-value**	**P-value**
Factor(Age)	3	6826	<0.001
Area	3	315.6	<0.001
Week	1	37.71	<0.001
Factor(Age):Area	9	47.53	<0.001
Factor(Age):Week	3	39.70	<0.001
Area:Week	3	26.31	<0.001
Age:Area:Week	9	17.21	<0.001
Residuals	10872	-	-

Table A6 *Analysis of variance from a second-degree polynomial model (Eq. 4) predicting weight as a function of week, age, and area. Degrees of freedom (Df), F-value and P-value are given for each variable and interaction.*

Variable/interaction	**Df**	**F-value**	**P-value**
Poly(week, 2)	2	3257	<0.001
Age	3	1495e+1	<0.001
Area	3	1088	<0.001
Poly(week, 2):Age	6	185.2	<0.001
Poly(week, 2):Area	6	96.39	<0.001
Age:Area	9	119.3	<0.001
Poly(week, 2):Age:Area	18	31.96	<0.001
Residuals	35956	-	-

6.3 Model residuals

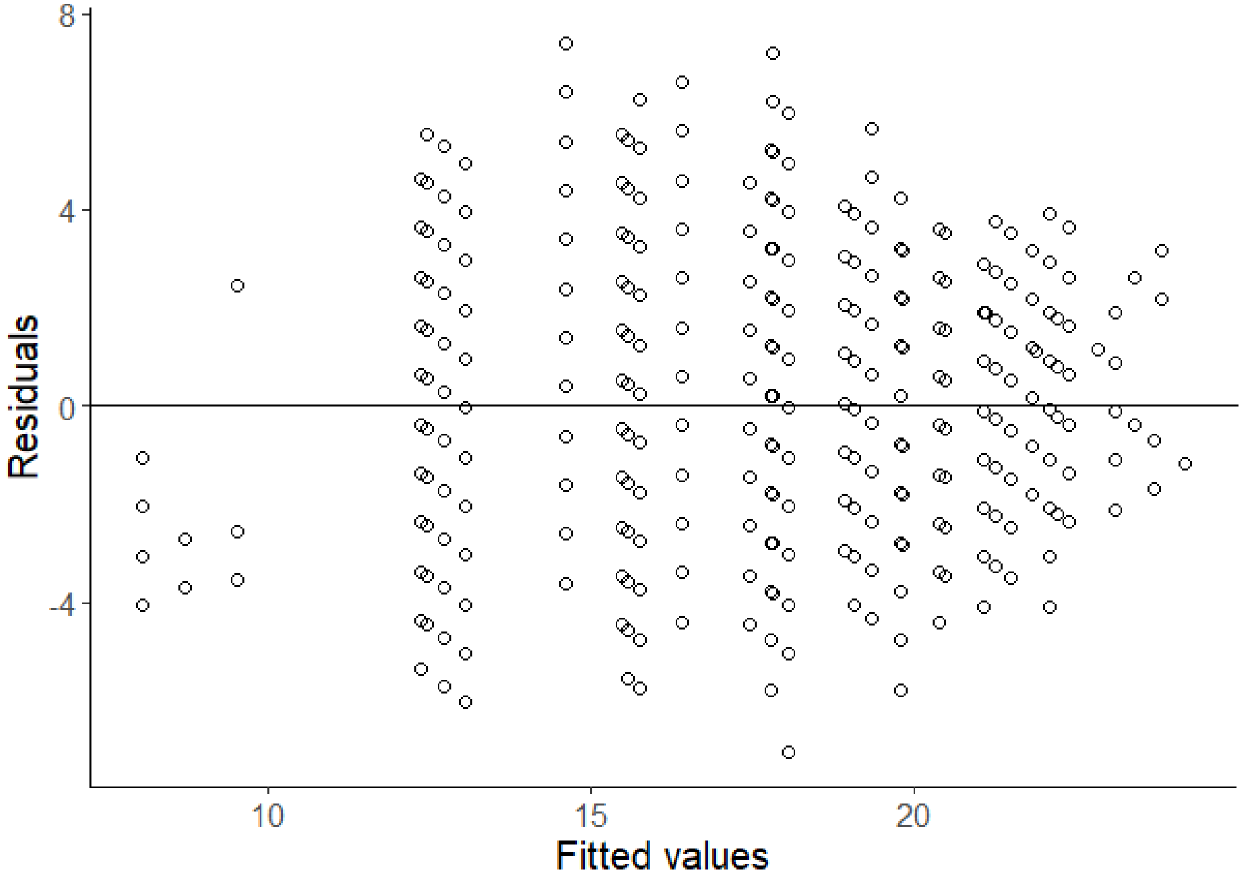

Figure A2 *Fitted values versus residuals from a von Bertalanffy growth function (see Eq. 1.2) predicting length as a function of age and area.*

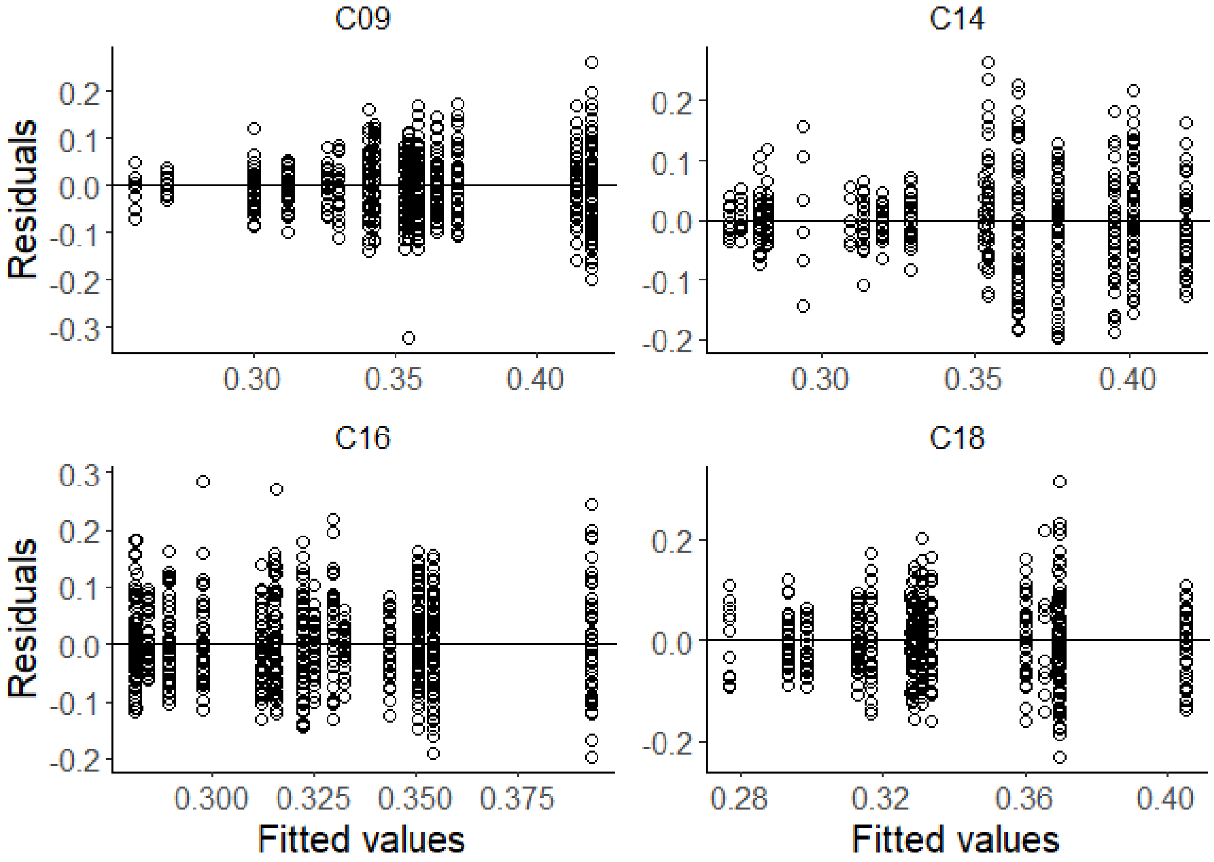

Figure A3 *Fitted values versus residuals from a linear regression model (see Eq. 1.3) predicting Fulton's condition factor as a function of age and area in year-classes C09, C14, C16, and C18.*

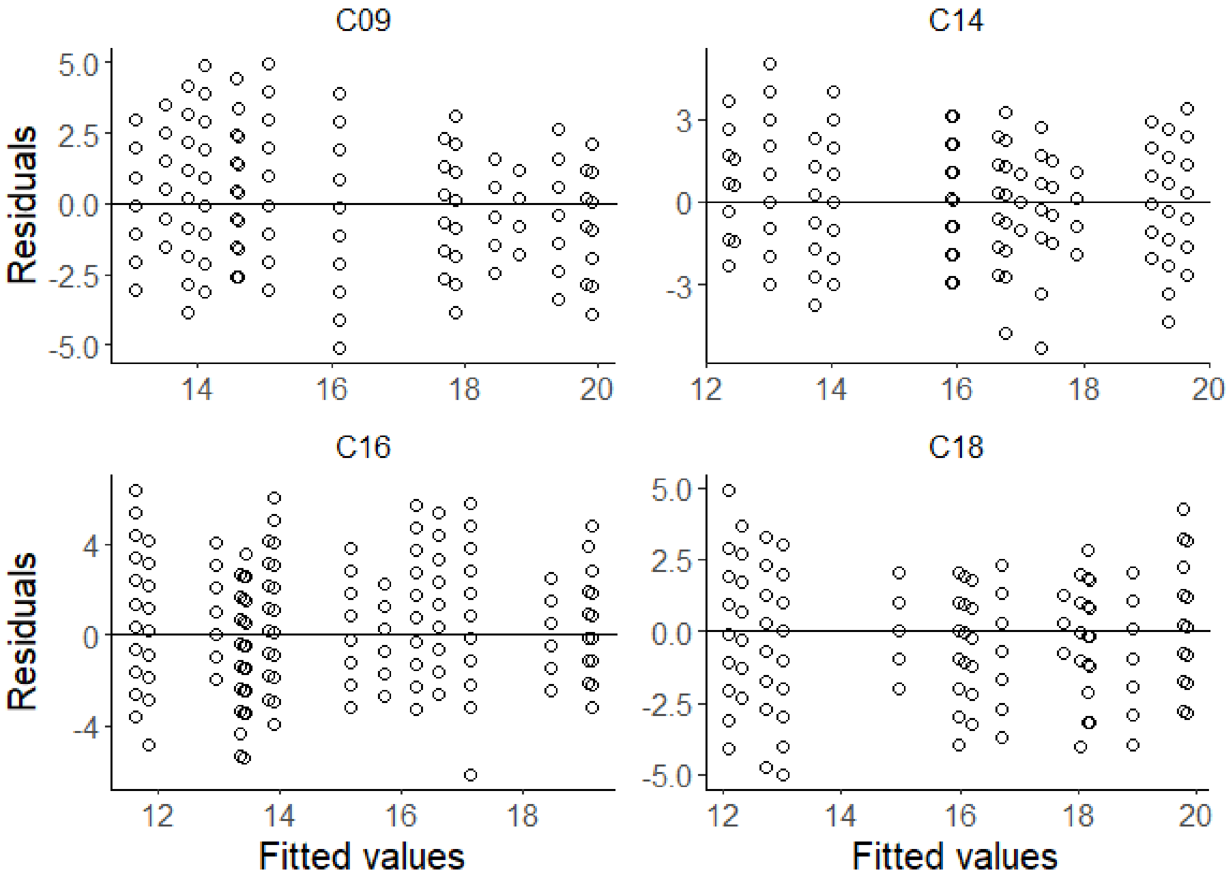

Figure A4 *Fitted values versus residuals from a linear regression model (see Eq. 2) predicting length as a function of age and area in year-classes C09, C14, C16, and C18.*

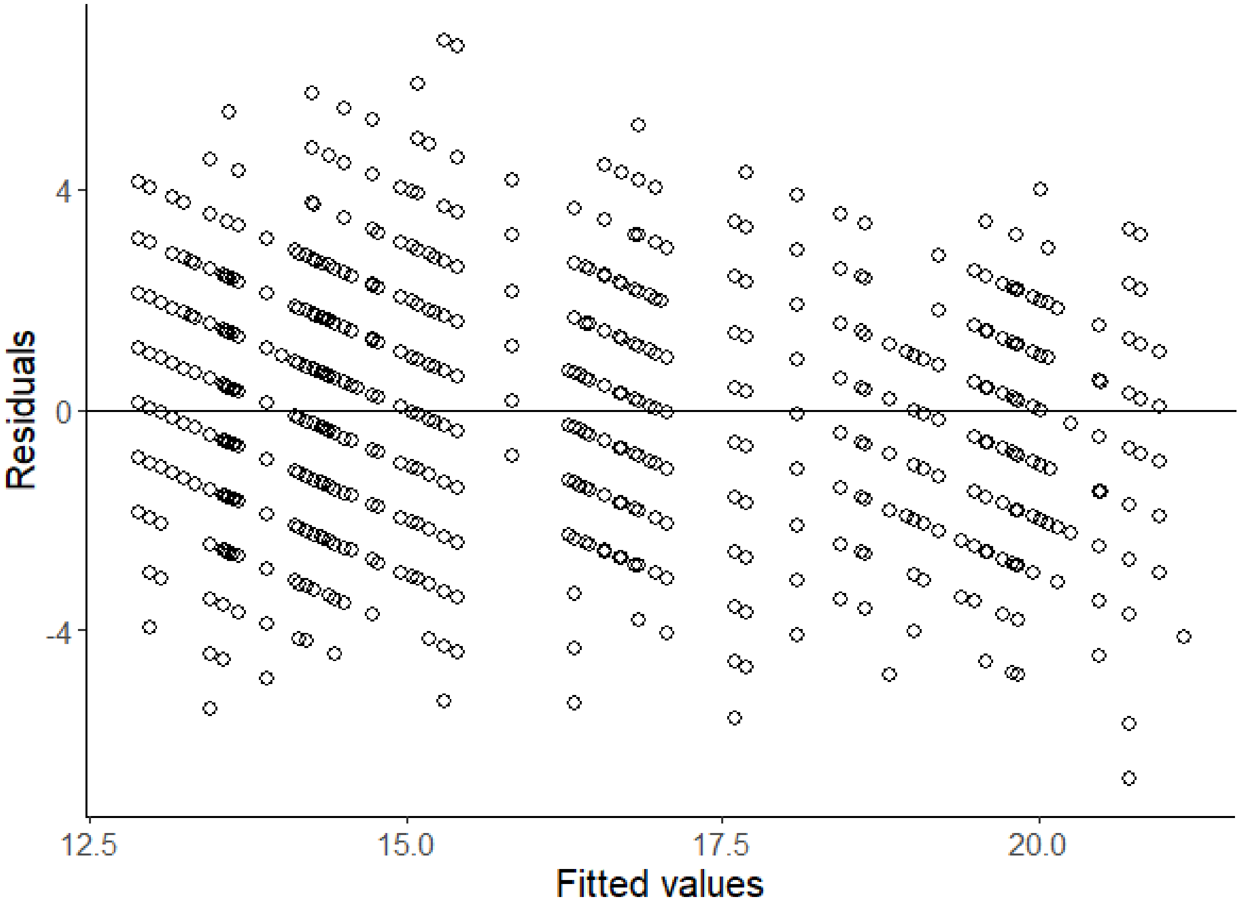

Figure A5 *Fitted values versus residuals from a linear regression model (see Eq. 3) predicting length as a function of week, age, and area.*

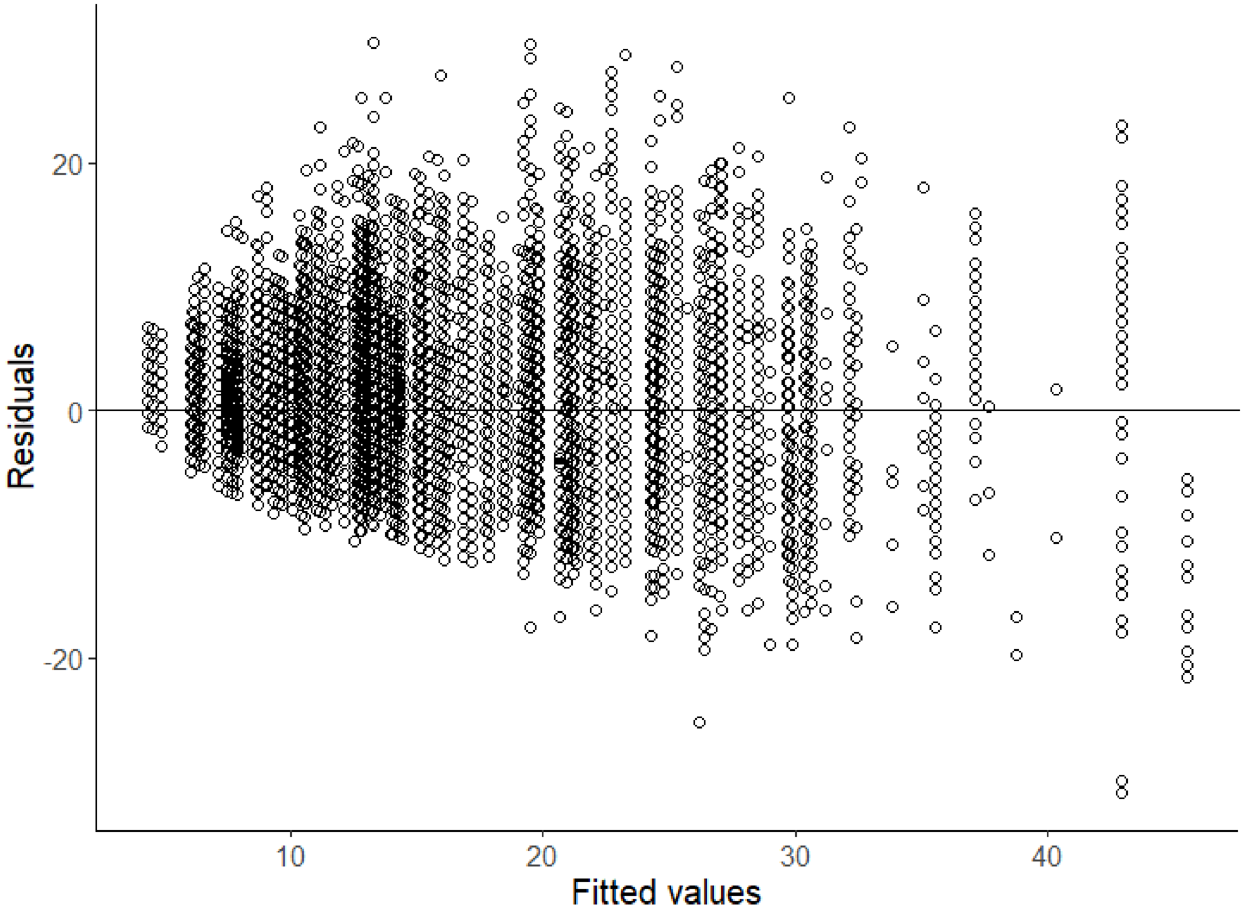

Figure A6 *Fitted values versus residuals from a second-degree polynomial model (see Eq. 4) predicting weight as a function of week, age, and area.*

6.4 Supplementary figures

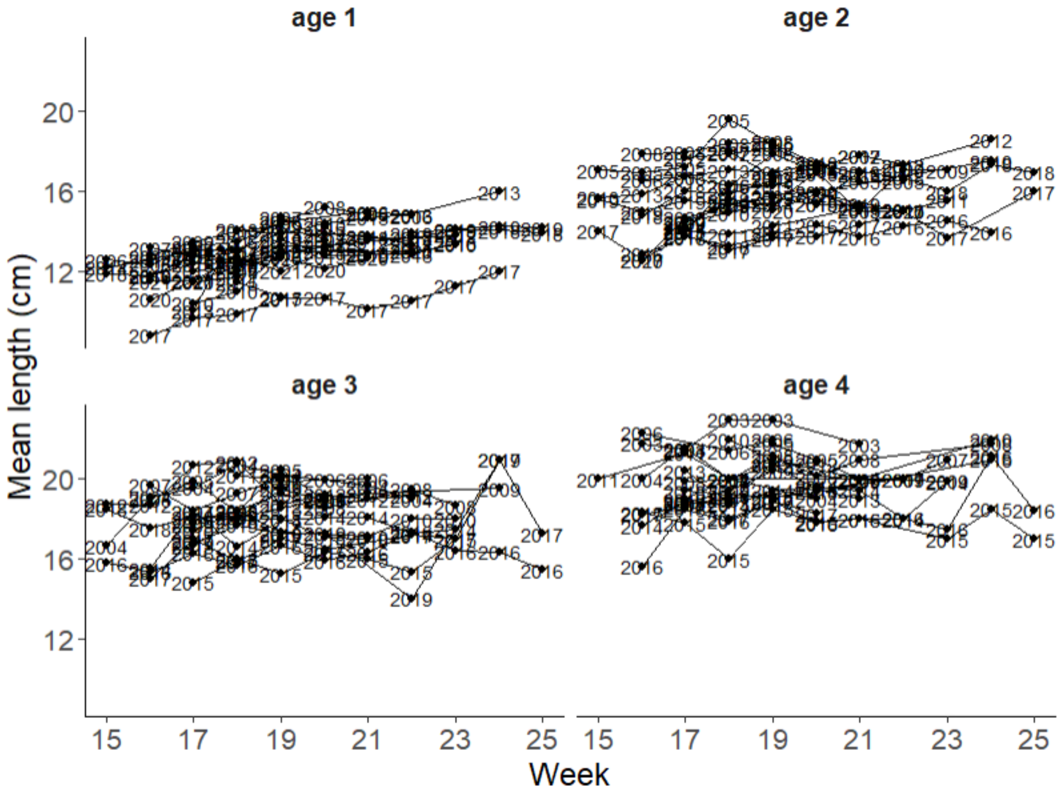

Figure A7 *Mean length of sandeels at ages 1-4 in weeks 15-25. Lines and corresponding numbers represent year-classes.*