Master of Science in Biology – Fisheries Biology and Management

Otolith growth of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the Norwegian fjords

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Abstract

Small pelagic fish play an important role in the ecosystem and are an important economical resource. The two most abundant pelagic fish in the Norwegian fjords are herring and sprat. It is documented that offshore herring and sprat are genetically different from coastal populations. For sprat, there is to this day not found any genetic difference in sprat between the fjords. And the connectivity between the fjords is still not known. By applying otolith microstructure, it is possible to investigate early growth in sprat and herring. Daily increments set in the otoliths are usually directly correlated with somatic growth, and otolith microstructure is therefore a powerful tool when looking at early growth. It is hypothesised that early otolith growth between the fjords and between species show different otolith growth patterns. This study shows some small variation between year class 2021 and 2020 in Hardangerfjorden, and non-significant difference in otolith growth between the year classes in Sognefjorden. In addition, otolith growth between the fjords were compered, individually for both specie, showed a significant difference with the same growth pattern in the different fjords. When otolith growth between the species were compared it showed different otolith growth trends, indicating that they grow at different rates. Given the small difference between the year classes, but larger difference between the fjords, one could assume that mixing between the fjords are low.

Keywords: Herring (*Clupea harengus*), sprat (*Sprattus sprattus*), otolith microstructure

Contents

1.Introduction

1.1 Small pelagic fish

Small pelagic fish play an important role in the marine ecosystem, as well as an important economical resource. Stocks of small pelagic fish typically have short lifespans with fast reproduction. Abundance of these species can fluctuate under variable environmental conditions, as well as with high fishing pressure, which can result in changes in the ecosystem (Kaiser, 2011). Small pelagic fish prey on plankton and is in itself an important food resource for many top predators (Kaiser, 2011). Therefore, small pelagic fish are a crucial link between primary producers and predators higher up in the food chain, conducting energy from lower to upper tropical levels (Pikitch et al., 2012). This is called a bottom-up control in the ecosystem, where top predators are dependent on the level of lower producers to survive (Smith & Smith, 2015). Small pelagic fish have been harvested by humans for centuries. Millions of tonnes of small pelagic fish are harvested every year, making it an important part of the economy (FAO, 2015). Small pelagic fish are harvested for direct human consumption as well as for global food security by being critical in fishmeal production, and fish oil used in agriculture and aqua culture feed (FAO, 2016). As an example of a small pelagic fish, Norwegian spring spawning herring (*Clupea harengus*) represents the most abundant fish stock in the North Atlantic (Bjørndal & Gordon, 2000) and over 600 000 tonnes was harvested in 2021 (Havforskningsinstituttet, 2021b).

1.2 Pelagic fish in Norwegian coastal waters

Two species from the Clupeidae family, European sprat (*Sprattus sprats*) and Atlantic herring (*Clupea harengus*), are the two most abundant pelagic species in the Norwegian fjords. In the Norwegian fjords the European sprat (hereafter referred to as sprat) and Atlantic herring (hereafter referred to as herring) can be found in the pelagic environment down to 150 m depth (Moen, 2020). Both species perform diurnal vertical migrations, where they move towards the surface at dusk (Nilsson et al., 2003). Previously studies have found that sprat spawn locally in the fjords (Torstensen, 1984), while Norwegian spring spawning (NSS) herrings have a spawning migration from Tromsø in north and down to Karmøy (Havforskningsinstituttet, 2019).

Recent studies have documented a genetic difference between sprat and herring individuals offshore in the North Sea compared to coastal individuals (Han, Jamsandekar, Pettersson, Su, Fuentes-Pardo, Davis, Bekkevold, Berg, Casini, et al., 2020; Quintela et al., 2020). At current status, it is documented that there are no clear genetic difference for sprat between the different fjords (Quintela et al., 2020). And research on migration patterns for sprat in the fjords have not found any result that sprat in the fjords migrate to the North Sea or Skagerrak (Bakken, 1973). And the connectivity between the fjords for sprat is not known. Given the genetic data, it is known that there must be some exchange of sprat individuals between the fjords. However, this could be a small exchange in egg, larvae, or fish, which is all that is needed to obtain this genetic flow for sprat between the fjords. For herring on the other hand, there are clear differences between local populations in the different fjords (Lie et al., 1978). They are also genetically different from offshore individuals and migratory herring (Han, Jamsandekar, Pettersson, Su, Fuentes-Pardo, Davis, Bekkevold, Berg, Cassini, et al., 2020). However, some of the juvenile Norwegian spring spawning herring might use the fjords as nursery area and are then mixing with local populations of herring. Herring has demersal eggs which means that herring lay their eggs at the bottom of the sea, while sprat have pelagic eggs which drifts around in the pelagic environment (Moen, 2020). This gives sprat eggs a couple of weeks to drift with the currents compared to herring during the earliest stages. Knowledge about connectivity between the fjords can provide important information that can be used in management.

There are restrictions and regulations when it comes to fishing sprat and herring in the Norwegian fjords. Management of sprat in the Norwegian fjords are decided after yearly advice from Institute of Marine Research (Havforskningsinstituttet, 2021a). The quotas for sprat are given after calculations performed after yearly surveys, and it is given one quota for each of the fjords; Hardangerfjorden, Sognefjorden, Nordfjorden and Trondheimsfjorden (Havforskningsinstituttet, 2021a). Herring quota in Norway are managed and assessed by the International Council for the Exploration of the Sea (ICES), with the exception of Trondheimsfjorden (Havforskningsinstituttet, 2021a). Local populations of herring are considered as Norwegian spring spawning herring even though it is known that they are genetically different. Ideally for the fishermen, there would be given one overall quota for all the fjords combined for sprat, instead of one quota per fjord. One quota would do the fishing more efficient and easier for the fishermen. They could save time fishing their quota in one of two of the fjords instead of using time travelling between all the fjords. It might also be easier for them fishing in the larger fjords compared to the smaller once, like Nordfjorden. The request for one overall quota was given to the Institute of Marine Research in 2018 (Havforskningsinstituttet, 2021a). The problem with one quota for the fjords combined is that the connectivity between the fjords is still debated, therefore there is not enough information about the migrations of sprat between the fjords to provide one overall quota (Havforskningsinstituttet, 2021a). All that can be said with certainty is that there is some migration between the fjords to obtain the genetic results. Meaning that if the quota is given for the fjords combined, there is not a guaranty that fjords with non or less fishing will provide sprat to the fjords that are heavily fished. The consequence of one overall quota if the fjords are actually distinct could be that sprat in some fjords is overfished and disappears, while no or little fishing in other fjords. Therefore, it is important to know more about the connectivity between the fjords.

1.3 Norwegian fjords

Along the Norwegian coastline there are numerous fjords, each with their own unique ecosystems that nurture marine life. These fjords are the result from the last ice age when glaciers shaped the land mass (Pettersen, 1884). Fjords are characteristically long, narrow, deep, and with mountains on the side. Usually fjords have a sill at the entrance, separating deep-water in the fjords from deep-water in the open ocean (Kaiser, 2011). With a sill at the fjord entrance, the exchange of water is limited to the depth of the sill, where deep water rarely is exchanged (Kaiser, 2011). All fjords are unique, with different environmental factors effecting the marine life within. An upper brackish water layer with lower salinity is created due to fresh water running down the mountains (Kaiser, 2011). The amount of freshwater from the mountain's determinate how much brackish water it is, and for how long.

The Norwegian coast is dominated by two water masses, the Atlantic water and coastal water. As an extension of the warm Gulf Stream the Atlantic current provides a warm current along the Norwegian coast. The Norwegian coastal current goes from south to north along the coast and the main movement of the current is in the upper layer (Sætre & Ljøen, 1972). The coastal current is less saline water compared to the Atlantic current, given that the coastal waters consist of the brackish water from the fjords. Mixing of the coastal current and the Atlantic current along the coast is an intense mixing both vertically and lateral (Sætre & Ljøen, 1972). Less saline coastal water mix with the more saline Atlantic water and reduce the density difference along the coast. The differences is less in the northern part of the Norwegian coast when the currents have mixed for the longest (Sætre & Ljøen, 1972). Including salinity and temperature, other factors affecting the life of fish in the fjords are density of food (mostly plankton for sprat and herring), population density (competition for food) and predators (Smith & Smith, 2015). Previously studies have found these factors to affect time at first maturation, growth, and otolith growth (Baumann, Gröhsler, et al., 2006; Folkvord & Johannessen, 2004; Grauman & Yula, 1989). These environmental factors can vary from year to year, but also from season to season. Each fjord has an ecosystem that consist of differences in environmental factor.

1.3.1 Studied fjords

Stretching over a distance of 205 km with a maximum depth of 1308 m, Sognefjorden is the longest and deepest fjord in Norway (Manzetti & Stenersen, 2010). The fjord contains six main fjord branches, with several smaller fjord branches. The second largest fjord in Norway is Hardangerfjorden, which is 183 km long and have a maximum depth of 820 m. The fjord spreads into several fjord branches and are surrounded by mountains with steep slopes inward of the fjord. It is strongly influenced by freshwater from the mountains and Folgefonna glacier (Husa et al., 2014). Nordfjorden is the fifth longest fjord in Norway and is 106 km long. The maximum depth of Nordfjorden is 565 m, and the fjord has several fjord branches. On the south side of Nordfjorden there are several glaciers. Fjords as ecosystems are important and sensitive habitats which are easily disturbed by humans.

1.4 Otoliths

Otoliths are a frequently used tool in many types of studies on teleost fish. Otoliths are hard, calcified structures that contain information about age and growth, on both daily and annual level (Campana & Thorrold, 2001). Otoliths are located in the inner ear of teleost fishes, and their function for the fish is related to balance and hearing (Rodriguez Mendoza, 2006). Otoliths are composed by mostly calcium carbonate ($CaCO_3$), in addition to some minor elements that reflects the environment (Rodriguez Mendoza, 2006). The material from the otolith will not be reabsorbed if it first has been deposited (Rodriguez Mendoza, 2006). Starting with a core, the otoliths grow continuously around throughout the fish's life, creating a record of the fish's growth and its surroundings like trace elements from the surrounding environment, water temperature and food resources (Rodriguez Mendoza, 2006).

There are three pairs of otoliths: asteriscus, lapillus and sagitta, where sagitta is the largest one (Campana & National Research Council, 2004), and the one used in most studies, including this thesis. Otoliths (sagittal otolith, hereafter called only otolith) form a sequence of opaque and translucent zones departing the core (which is the center of the otolith) and out towards the edge, reflecting respectively fastest and slowest periods of growth throughout the year (Aps et al., 1991). The increments are made due to environmental changes in the different seasons throughout a year (Campana, 2016). Ageing fish by counting these zones (hereafter called increments), is a technique developed over 100 years ago (Campana & Stevenson, 1992) and are otoliths most known feature. Counting of the increments is usually performed by using a microscope.

Otolith shape is species specific, with varying sizes and growth patterns (Campana, 2016; Tuset et al., 2006). For the two species used in this thesis, herring otoliths have a longer rostrum than sprat, while sprat otoliths are rounder (Figure 1).

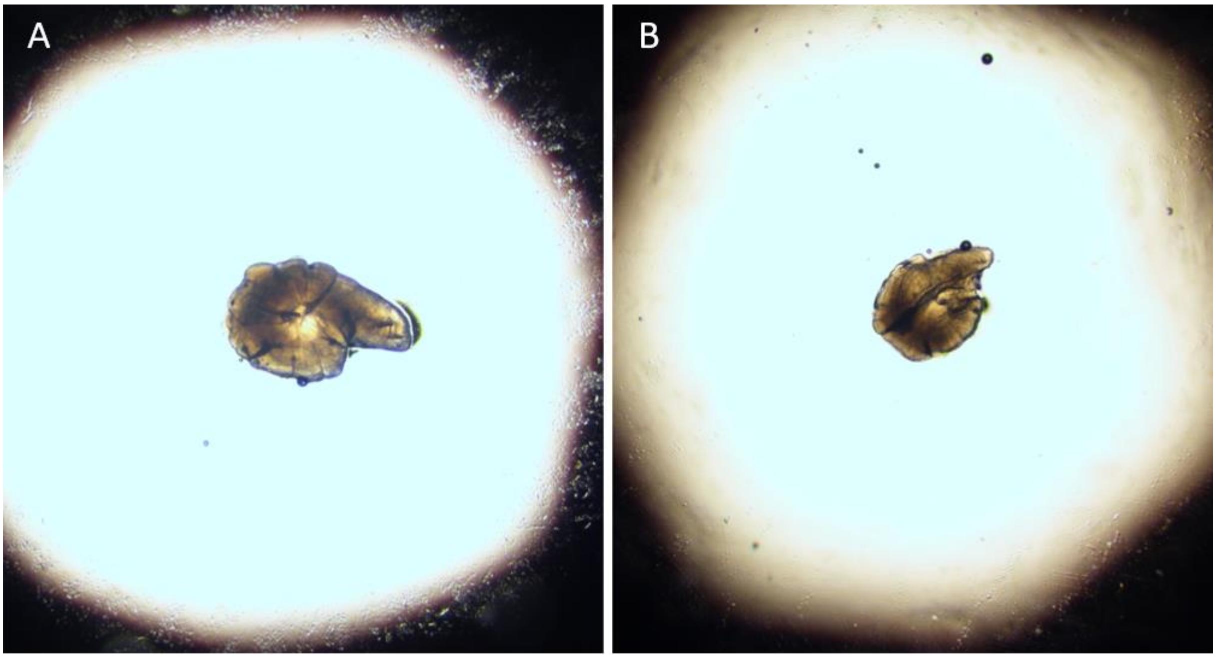

Figure 1: Overview of otolith shape of herring (A) and sprat (B), pictures taken with a magnification of 2.5 x. Both otoliths are from fish at age 0 from Sognefjorden, with a fish length of 6.0 cm for herring and 5.5 cm for sprat.

Counting annual increments is a useful technique for fish older than a year, while are not useful in estimation of age for individuals that have not formed the first annual increments. In the 1970's Pannella (1971 and 1974) conducted studies where it was observed approximately 360 fine increments between the annual increments. These results were found by looking at otolith microstructure in fish from temperate waters, as well as tropical fish. The increments were thought to be formed daily in the otoliths (Pannella, 1971; Pannella, 1974). The technique started to be used by other scientists, who tested this on freshwater fish and other saltwater species. They concluded that these species also formed daily increments in the otoliths (Barkman, 1978; Taubert & Coble, 1977).

Since the 1970's, the technique of grinding or polishing the otoliths to look at the microstructure has become an important tool in many studies. In a study investigating otolith microstructure in spring and autumn spawning herring it was found that increment width could separate fish from the two different spawning seasons, where spring spawning herring had the larger increment width at a given distance from the core (Moksness & Fossum, 1991). Otolith microstructure analysis are also frequently used in growth studies because it can be used to investigate early growth rate for fish by looking at increment width, which is usually directly correlated with daily somatic growth (Black et al., 2019; Moksness, 1989). Daily increments are assumed to be formed over 24 hours and can be seperated when looking in the microscope by seeing one dark and one ligher increment (Thresher et al., 1995). Daily growth is reflected by increment width, where larger increments indicate fast growth and smaller increments indicate slow growth (Moksness, 1989). The first increments formed in the otoliths are difficult to separate since they are small and might not be set daily, but after 20 µm from the core the increments are assumed to be daily (Geffen, 1982, Campana et al. 1987). The surrounding environment is affecting the otolith growth, temperature is one example (Folkvord & Johannessen, 2004). Food availability is another factor affecting otolith growth (Fablet et al., 2011).

1.5 Knowledge gap

Fjords as ecosystems are underrepresented in studies, even though they are the source of tonnes of harvested fish every year here in Norway. Few studies have focused on sprat and herring in the Norwegian fjords. There is an abundance of literature on herring in Europe, while less on sprat. A previously conducted study (Peck et al., 2021) documented that a relatively high proportion of research on small pelagic fish on a global scale are conducted in the Baltic Sea.

There is a shorter distance between the North Sea and the fjords, compared to the distance between the fjords. Still, there is a significant genetic difference between sprat and herring population for offshore and inshore individuals. While there is no significant genetic difference between the fjords for sprat (Quintela et al., 2020). And clear differences between local herring populations between the fjords. Therefore, it is interesting to investigate if there is a difference in early growth for the Norwegian coast sprat and herring populations within and between the fjords. Differences, or no differences, in early growth for sprat and herring can provide some information about the connectivity between the fjords.

1.6 Aim of study

The aim of this thesis is to increase the knowledge on herring and sprat otolith growth within and between the Norwegian fjords. Herring and sprat were sampled in the Norwegian fjords; Nordfjord, Sognefjorden, Hardangerfjorden at the end of August and start of September 2021. With otolith microstructure analysis it is possible to investigate the daily growth rates for both species, and also compare growth between species. Both sprat and herring are pelagic species, that live together in the fjords, and they therefore experience the same environment, with variations between the fjords. They are both schooling pelagic fish species that feed on approximately the same types of food organisms. And when using a pelagic trawl within one fjord, one might catch both herring and sprat in one haul, indicating that they live together or close to each other. These reasons are good reasons for why it is possible to compare growth rate found by looking at otolith microstructure for herring and sprat.

I hypothesize that the growth between year classes is stable, and that otolith growth between the fjords contain small differences since each fjord have unique ecosystem. I also hypothesize that the otolith growth between the species will be different from each other.

The main objectives for this thesis:

- Investigate if there is a difference in growth between the year classes of sprat and herring.
- Investigate if there is a difference in growth of herring between the fjords.
- Investigate if there is a difference in growth of sprat between the fjords.
- Investigate if there is a difference in growth between herring and sprat

2. Materials and method

2.1 Study area and sample collection

Materials used in this study were collected by the Institute of Marine Research (IMR) on board of the research vessel “Kristine Bonnevie” during the acoustic survey “Brislingtoktet” in 2021. The survey was divided into two time periods, from the 21st of August until 24th of August and 26th of August until 7th of September (Table 1). Herring and sprat were sampled in three fjords along the Norwegian coastline, Nordfjord, Hardangerfjorden and Sognefjorden (Figure 2; Table 1). Samples were collected using a pelagic trawl (Harstad trawl). Location of trawl hauls were decided based on registration of herring and/or sprat schools with use of a sonar and acoustics. Additionally, one random trawl haul was taken each night without use of sonar or acoustics to investigate if herring and/or spart made vertically movements.

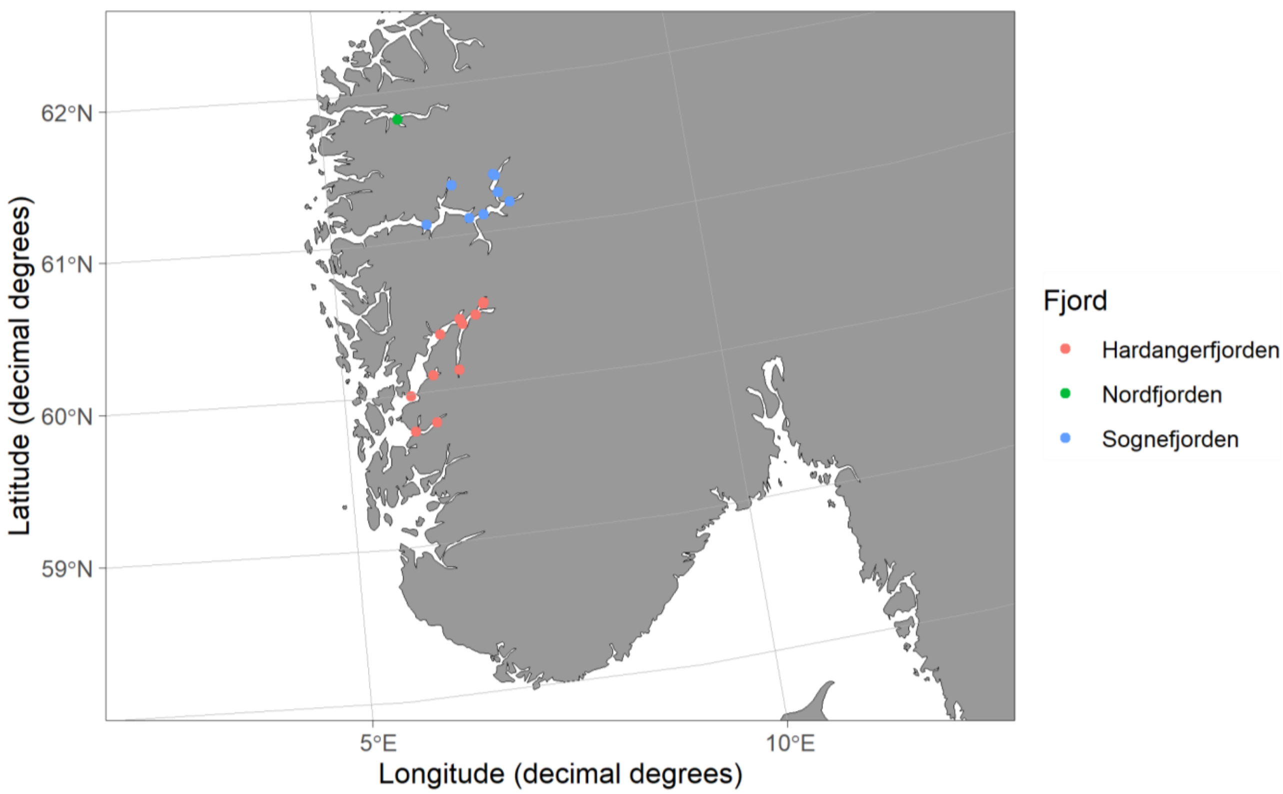

Figure 2: Map over all sampling stations in Nordfjorden, Sognefjorden and Hardangerfjorden.

Table 1: Sample inventory, with total number of sprat and herring sampled, and number used in this study from each station.

Serial number:	Date	Fjord	Sprat sampled (Otoliths analysed)	Herring sampled (Otoliths analysed)
22556	22.08.2021	Hardangerfjorden	170	46 (17)
22558	23.08.2021	Hardangerfjorden	56	49 (16)
22560	27.08.2021	Nordfjord	212 (36)	100 (16)
22563	28.08.2021	Sognefjorden	13 (12)	0
22564	29.08.2021	Sognefjorden	186 (35)	3 (3)
22566	29.08.2021	Sognefjorden	116	58 (20)
22567	30.08.2021	Sognefjorden	120 (18)	120 (14)
22568	30.08.2021	Sognefjorden	120 (18)	1
22569	31.08.2021	Sognefjorden	220 (36)	1
22571	01.09.2021	Sognefjorden	150 (22)	63 (27)
22572	01.09.2021	Sognefjorden	170 (34)	0
22573	02.08.2021	Sognefjorden	120 (17)	3
22574	02.09.2021	Sognefjorden	120 (19)	1
22578	03.09.2021	Hardangerfjorden	140 (33)	0
22579	04.09.2021	Hardangerfjorden	294 (39)	44 (22)
22580	04.09.2021	Hardangerfjorden	170 (34)	57 (12)
22581	04.08.2021	Hardangerfjorden	108 (18)	100 (18)
22582	04.09.2021	Hardangerfjorden	120 (19)	5
22583	05.09.2021	Hardangerfjorden	131 (16)	4
22584	05.09.2021	Hardangerfjorden	220	81 (14)

2.2 Sample procedure

Once the sample were on the table, the fish were sorted by species first. Distinguishing features that separate small/juvenile herring and sprat include the sprats sharply toothed keel on the belly, while herring do not have these. The dorsal coloration is greyer for sprat, while bluer for herring. One can also look at the positions of dorsal and pelvic fins, for sprat the pelvic fin is in front of the dorsal fin, while herring has the pelvic fin placed under the dorsal fin (Moen, 2020).

Subsamples of herring and sprat were taken when the sample included more than 100 individuals of each species. For all herring and sprat, weight (in grams, with one decimal) and total length (to the nearest 0.5 centimetres below) was measured (Figure 3). A fish-ID number was given to each fish for tracking information. Sex was determined visually for the first individuals in each subsample. Subsamples of sprat and herring were divided in three:

- Subsample 1: Up to 100 larger individuals (one year old and older) were randomly selected from the sample. Individual 1-30 were subject to full sampling (length, weight, sex, stomach fullness and otoliths). For the rest (individual 31-100) only length and weight were measured. These individuals were sampled after subsample 2 was collected.

- Subsample 2: 20 larger individuals were randomly selected from the sample. Length and weight were measured. Both otoliths were collected, one loose otolith placed in a Nunc tray, and one otolith mounted for reading. The 20 loose otoliths in Nunc trays are used in this study from the larger fish. This subsample was taken after the first 30 fish of subsample 1.
- Subsample 3: 100 smaller individuals (mainly 0-group, maybe some at age 1) were randomly selected from the sample. Individual 1-10 was taken full sample off (length, weight, sex, stomach fullness and otoliths). For individuals 11-30 two loose otoliths placed in Nunc trays and is the ones used in this study for the smaller individuals. For the rest of the fish in the subsample (individual 31-100), length and weight were registered.

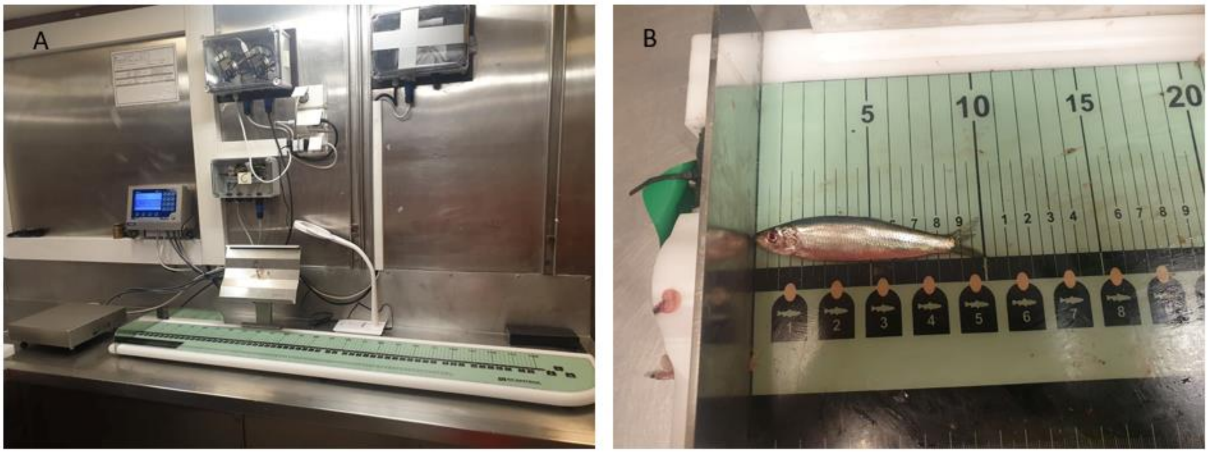

Figure 3: Procedure at the wet lab on board Kristine Bonnevie. Fish weight was measured first and then length measured (A). Herring measured to the nearest 0.5 cm below (B)

2.3 Otolith microstructure analysis

Otoliths were grinded to analyse microstructure near the core of the otolith. Microscope slides were marked with fish species, year, subsample, serial number, and individual fish-ID number. The microscope slides were then placed on a hotplate (Stuart Scientific hotplate SH2) and heated up enough to melt a drop of thermoplastic glue (Crystalbond 509) in the middle of the microscope slide (Figure 4A). One otolith for each fish was placed on the warm melted thermoplastic glue with the sulcus side facing down. Microscope slides were then placed on the worktable until cooled.

Otoliths were then grinded on a Saphir 330E grinding machine with sandpaper (P1200/1400 and P2500), until the core (nuclei) was visible (Figure 4B). Microscope slides were held with the otolith horizontal down on the sandpaper. Level of grinding was managed through regulating the rotation speed, time of grinding and the coarseness of the sandpaper. Otolith microstructures were checked under a Leica DMLB light with a magnification of mainly 40x (used for increment measurements) and sometimes 20x, with a Nikon camera DS-Fi2 attached to both microscope and computer (Figure 4C). NIS Elements program was used for photographing otoliths. An overview photo was taken of each otolith before the grinding process. To avoid destroying otoliths with over-polishing, there were taken several photos during the grinding process. Digital calibration images were taken and checked every other day at the lab.

Figure 4: Process of otoliths for microstructure analysis. Otoliths glued on marked microscope slides with help from a hotplate and crystal bond (A), grinding machine with sandpaper (P2500) (B), and microscope with camera attached to a computer for visualization and for photographing microstructure (C).

Digital images of otolith microstructure were analysed with Caliper function in Image Pro-Plus® version 7.0 (Media Cybernetics, USA). Increments were measured from the core to the edge of the otolith in the direction with clearest increments. Increments were marked automatically by the Caliper function of ImagePro. Every annotation was checked manually, and additional increments were added, or false annotations removed if needed. Daily increments with a distance of 20 µm from the core and up to a distance of at least 160 µm from the core, and further when possible. This was done for both sprat (Figure 5A) and herring (Figure 5B). Increments with a distance less than 20 µm from the core represent early development and are not easily separated (Campana et al., 1987; Geffen, 1982). If the core of the otolith was impossible to visualize, that otolith was omitted from this study. In this study a total of 385 sprat and 179 herring otoliths were grinded and analysed.

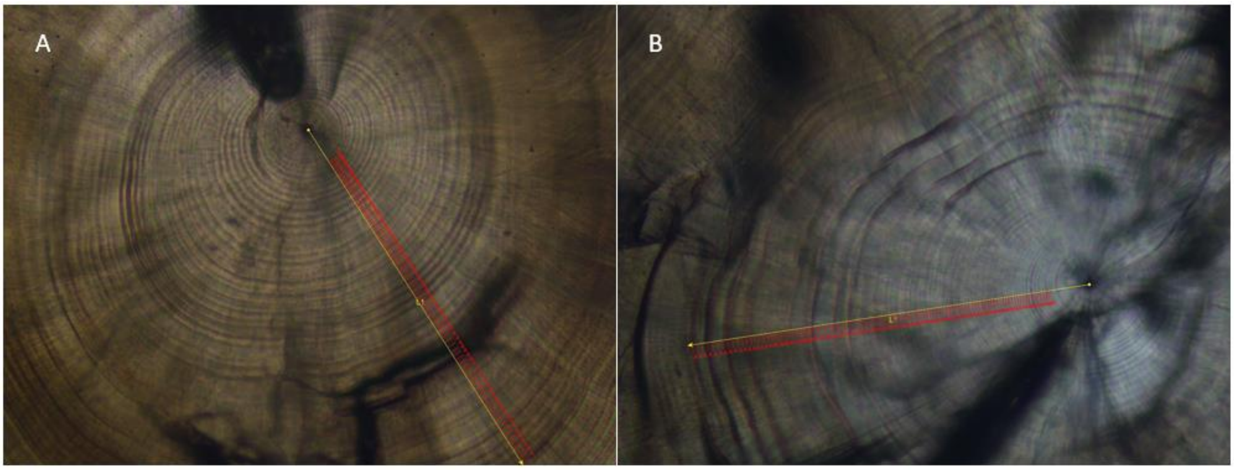

Figure 5: Otolith microstructure marked in Image Pro, sprat (A) and herring (B)

2.4 Statistical analysis

All data were analysed in R, version 4.1.0 (R Core Team, 2021). Map of study area with all sampling stations (Figure 2) was made with the R package *ggOceanMap* (Mikko Vihtakari, 2022). All figures were made with the *ggplot2* package within the package *tidyverse* (Wickham, 2019). For complete list of R packages used in this thesis see Appendix B: R packages used. For all analysis 0.05 was used as a statistically significant threshold, with the null hypothesis that there is no significant difference.

For individuals where the age had not been determined by otolith readings, age was determined by looking at length distribution when possible (see results section 3.1). Using the age of individuals and catch year (2021), the corresponding year class of individuals was estimated. Individuals without an assigned year class were excluded from the analysis (number excluded; sprats = 21, herring = 2).

All fjords have been included in the figure, but due to only one sampling station with herring and sprat in Nordfjord this fjord was excluded from all statistical analysis. Therefore, statistical analyses were performed for Hardangerfjorden and Sognefjorden only. The same accounts for different year classes, where only the 2021 and 2020 year classes were present for both species in both fjords. Other year classes were excluded from statistical analysis to avoid bias due to large differences in sampling size.

To model increment width, as a proxy for otolith growth, for different year classes a normal distributed linear mixed effect model (lme) was used. All linear mixed effect models were made with the package *nlme* (Bates, Maechler, Bolker, & Walker, 2015). Only increments between 40 – 140 µm from the core for herring and 40 – 150 µm for sprat, were used in the statistical analysis because they were showing a linear increase within this range. The general structure of all models included increment width and distance from the core as continuous response and predictor variable, respectively, as a proxy for otolith growth. Additional predictor variables have been added. To incorporate dependency among observations of the same individuals, individual was used as random effect in all models. An analysis of covariance (ANCOVA) of the lme model were performed for the model selection. For the model selection, a full model with all interaction terms was estimated and non-significant terms were discarded until the final model only included significant variables and interaction terms. All finally selected models were inspected using Q-Q plots and residuals were investigated.

The first model was estimated to investigate if otolith growth varied between *year classes*. The full model (Equation 1) was applied to each *fjord* and *species* separately. As additional predictor variable *year class* (categorical) was added to the general structure of the model. Based on the results from this model (see result section 3.2), it was decided to combine year classes 0 and 1 in both fjords for further analysis.

Equation 1:

$$\begin{aligned} Increment\_width &= \alpha + \beta_1 * Distance\_from\_core + \beta_2 * Year\_class + \beta_3 \\ &* Distance\_from\_core * Year\_class \end{aligned}$$

To investigate the difference between *fjords*, they were added as categorical predictor variable to the general model structure (Equation 2). This model was used separately for sprat and herring.

Equation 2:

$$\begin{aligned} Increment\ width &= \alpha + \beta_1 * Distance\_from\_core + \beta_2 * Fjord + \beta_3 \\ &* Distance\_from\_core * Fjord \end{aligned}$$

To investigate the difference between *species*, *species* were added as categorical predictor variable to the general model structure (Equation 3). This model was used separately for Hardangerfjorden and Sognefjorden.

Equation 3:

$$\begin{aligned} Increment\_width &= \alpha + \beta_1 * Distance\_from\_core + \beta_2 * Species + \beta_3 \\ &* Distance\_from\_core * Species \end{aligned}$$

3. Results

3.1 Length and age distribution

3.1.1 Sprat

Sprat sampled for this study had a length distribution from 3 cm to 14.5 cm (Figure 6A). Year class 2021 (age 0) and 2020 (age 1) were the dominant year classes, while there were few individuals in the year classes 2019 (age 2), 2018 (age 3), 2017 (age 4) and 2016 (age 5). For sprat that have not been aged it was possible to divide them into year classes by looking at their length distribution. All fish with a size of 7 cm or below belonged to year class 2021 (Figure 6A). However, when sprat was above 7 cm, there was an overlap in length for the different year classes, which made it difficult to assign year classes based on length alone. Based on this, sprat individuals <7 cm was assigned to year class 2021 and included in analysis. Sprat >7 cm was excluded (N = 21, Figure 6B) since it would be to many assumptions when assigning year class at the individual level. Since there are so few individuals in the year class 2017 and 2016, they will be excluded from figures and analysis.

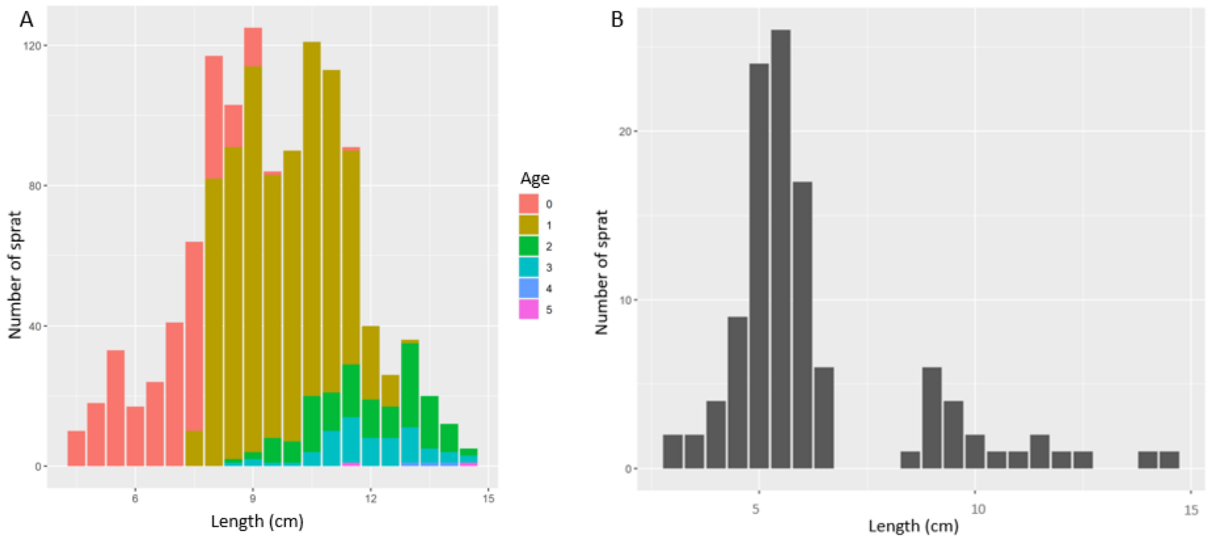

Figure 6: Length distribution in meter for sprat that have been assigned a year class based on the number of annual rings in the otolith (A). Length distribution for sprat not aged (B).

3.1.2 Herring

Herring sampled for this study had a length distribution from 5 cm to 21 cm. Year class 2021 and 2020 were dominant, while there were few individuals of year class 2019 (Figure 7A). For herring that have not been aged by counting annual growth rings, it was possible to assign them a year class based on their length distribution. By looking at the length distribution for individuals that have been aged, herring <12 cm were assigned to year class 2021 (Figure 7A), while herring >=14 cm and <=15 cm belong solely to year class 2020. And these two different year classes were included in the analysis. Leaving 2 individuals without year class, which are therefore excluded from following figures and analysis (Figure 7B). In addition, there are so few individuals (N = 4) of year class 2019 that they are excluded from the analysis.

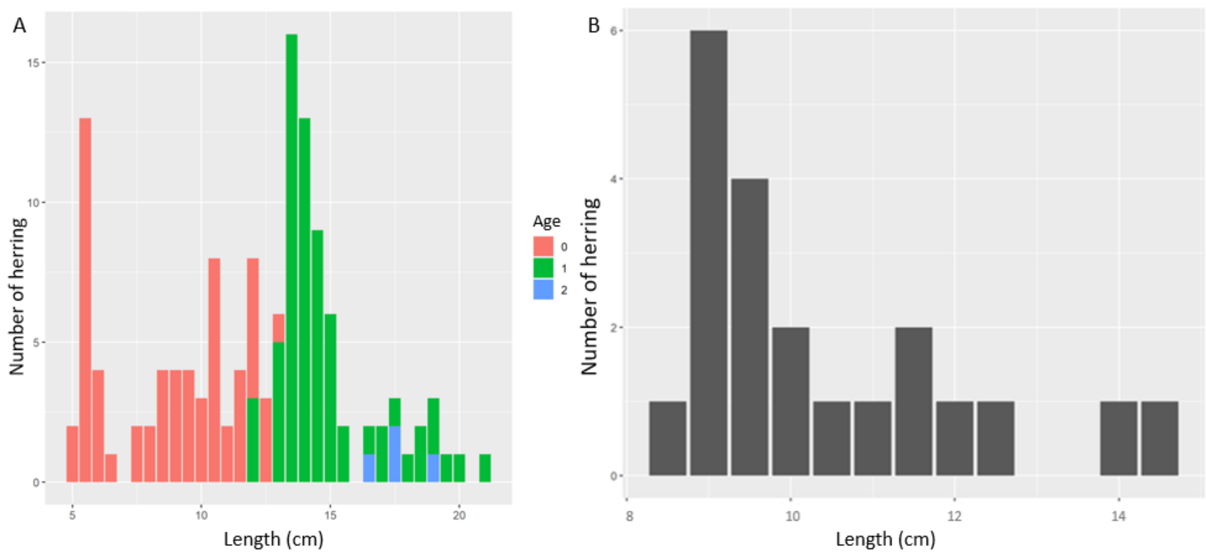

Figure 7: Length distribution in meter for herring that have been assigned a year class based on the number of annual rings in the otolith (A). Length distribution for herring not aged (B).

3.2 Compare early growth between year classes

For both species, the general trend within the measured interval 30 µm – 190 µm from the core, was that increment width increased with increasing distance from the core (Figure 8). The general trend for sprat was linear increase in increment width throughout the measured interval (Figure 8A), while in herring there was a linear increase until 140 µm from the core before the increase in increment width started to flatten out (Figure 8B).

For sprat in Hardangerfjorden there was a significant difference between the year classes 2021 and 2020 (Figure 8A; $p<0.01$). While the 2020 year class started with larger increments near the core, the increase in daily increment width was lower compared to the year class of 2021 (see Appendix C: Model outputs; Table C1 and Table C2). For Sognefjorden, there was no significant difference between the two year classes ($p>0.05$).

For herring in Hardangerfjorden there was a significant difference between the year classes 2021 and 2020 (Figure 8B; $p<0.05$). While the year class 2021 starts with larger increment width near the core, the increase in daily increment width was lower compared to the year class 2020 (see Appendix C: Model outputs; Table C4 and Table C5). For Sognefjorden, there was no significant differences between the two year classes ($p>0.05$).

For both species, the data of the two year classes were combined for following analysis for Sognefjorden as well as for Hardangerfjorden despite the significance. This was done because the actual differences in otolith growth were only minor.

For groups with few individuals (Table 1, mainly older individuals), the increasing trend was not as stable as for other groups and the increment width varied up and down along the distance from the core (Figure 8). However, there might be a tendency that individuals from other year classes had a slightly lower daily otolith growth for both species and between fjords.

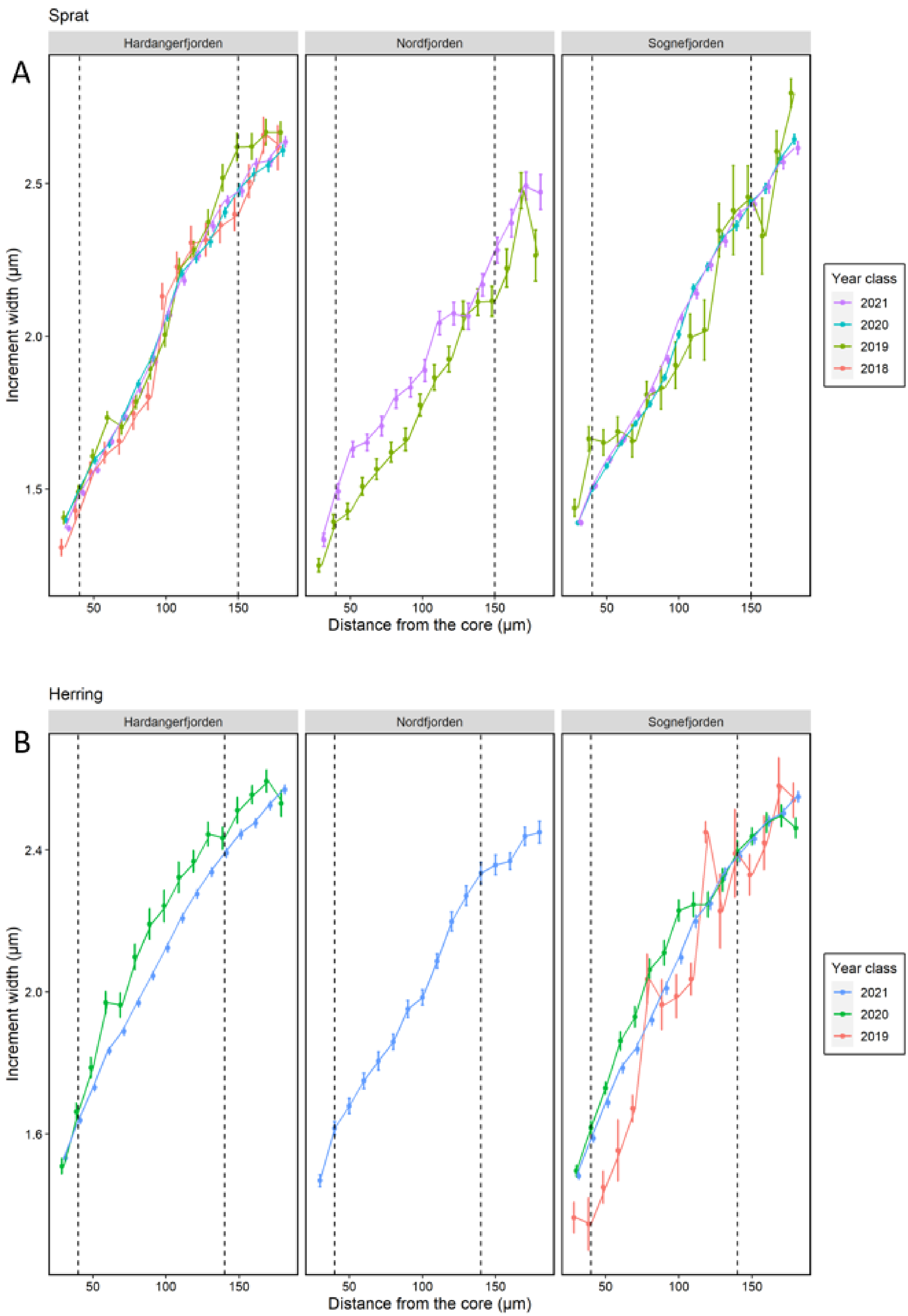

Figure 8: Mean width for each 10 µm from the core over increasing distance from the core for sprat (A) and herring (B). Showing the different year classes divided by fjords. The interval within the dashed lines illustrates the interval included in the analysis, and error bars showing standard error. Mean increment width for all year classes is made at the same distance from the core but are shifted some to show the data more clearly.

3.3 Early growth between fjords

Increment width near the core was larger in Sognefjorden than Hardangerfjorden for sprat (Figure 9A; $p<0.01$), but smaller for herring (Figure 9B; $p<0.05$). The increase in increment width was larger in Sognefjorden for sprat and Hardangerfjorden for herring, respectively (see Appendix C: Model outputs; Table C3 and Table C6). In Nordfjorden the increment widths were visually smaller at a given distance from the core compared to Hardangerfjorden and Sognefjorden, for both herring and sprat.

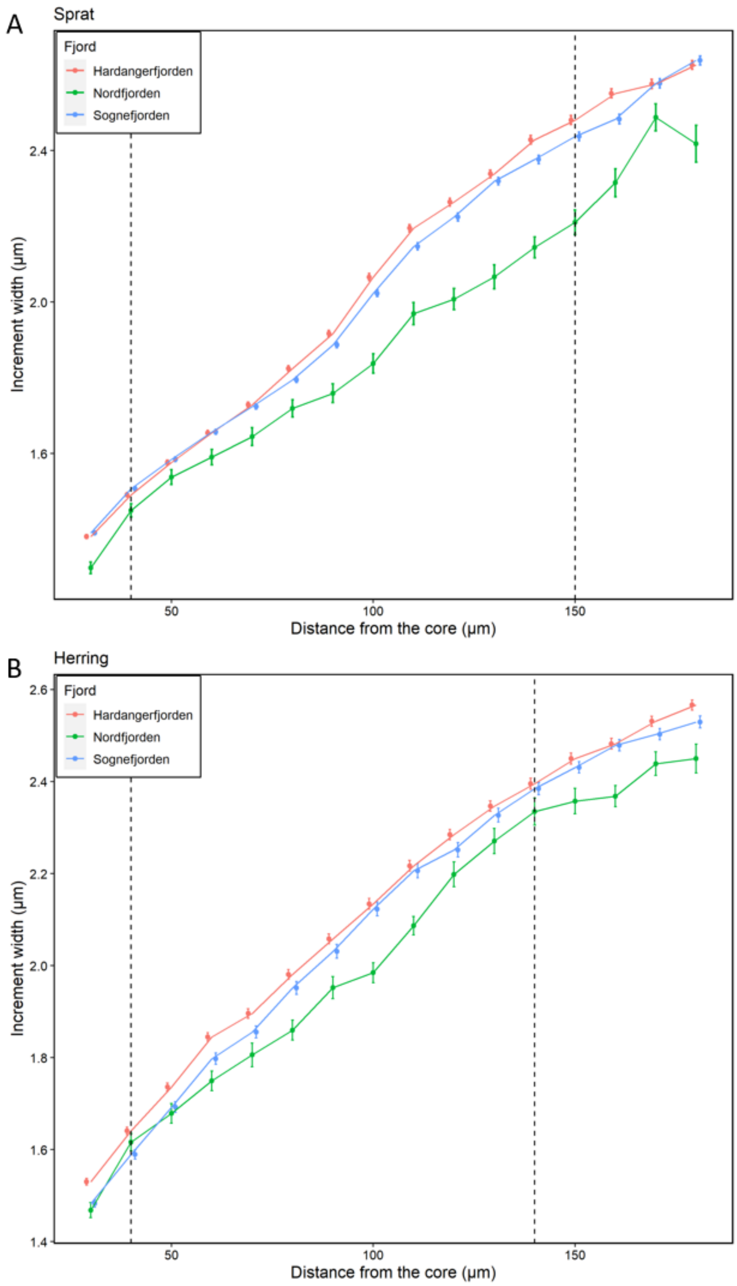

Figure 9: Mean width between increments over increasing distance from the core for sprat (A) and herring (B) in the different fjords. The interval within the dashed lines illustrates the interval included in the analysis, and the error bars show standard error. Mean increment width for all fjords is made for the same distance from the core but are shifted some to show the data more clearly.

3.4 Compare early growth in herring and sprat

In both fjords there was a significant difference between the herring and sprat (Figure 10; p<0.01). While herring starts with larger increment width near the core in both fjords, the increase in daily increment width was lower compared to sprat (see Appendix C: Model outputs; Table C7 and Table C8). In Nordfjorden, a similar trend was visually observed.

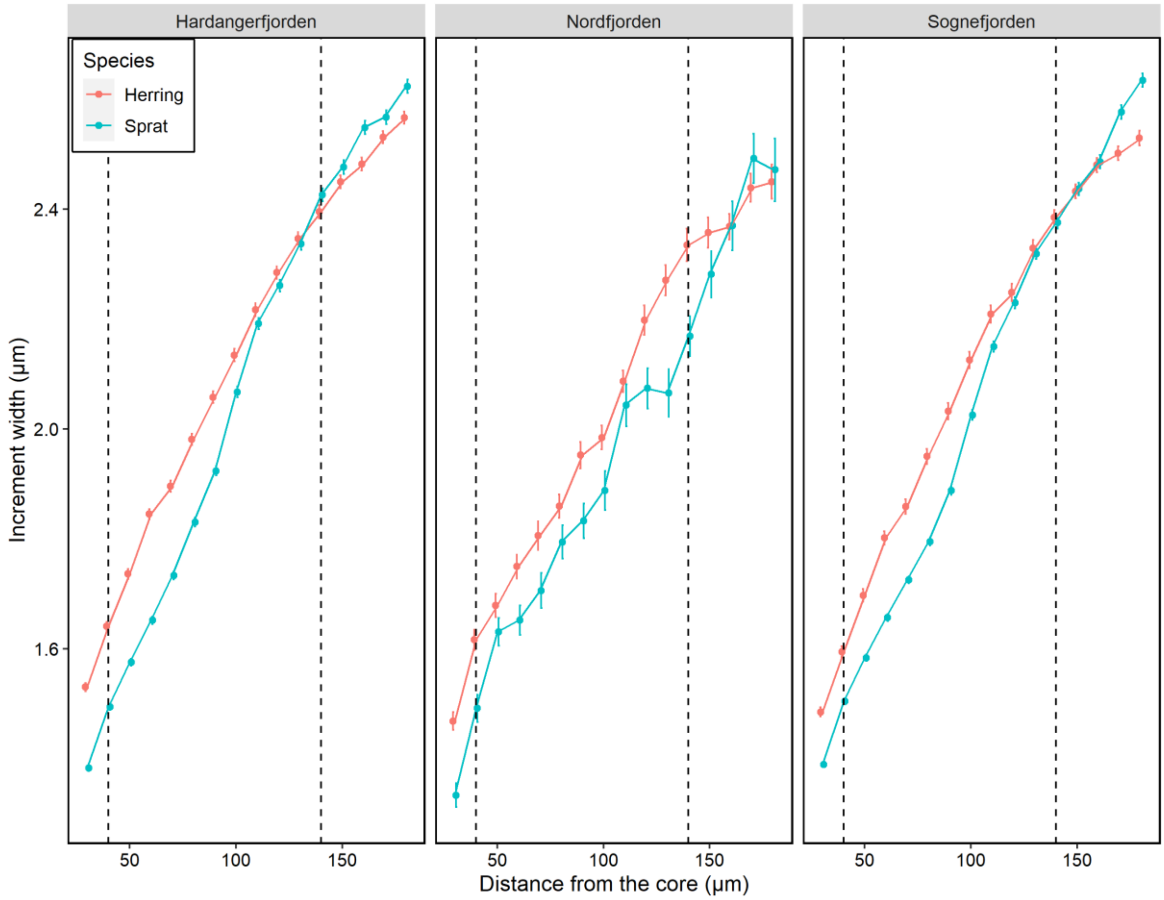

Figure 10: Mean width between increments over increasing distance from the core for sprat and herring Sognefjorden and Hardangerfjorden. The interval within the dashed lines (40 µm– 140 µm) illustrate the interval which is included in analysis. Error bars show standard error. Mean increment width for all fjords is made for the same distance from the core but are shifted some to show the data more clearly.

4. Discussion

The result showed that for both species there was a significant otolith growth difference between year class 2021 and 2020 in Hardangerfjorden, while no significant otolith growth differences in Sognefjorden. Both species revealed significant different otolith growth trends between Hardangerfjorden and Sognefjorden, where the increment width was larger in Hardangerfjorden. In addition, the result showed significant difference in otolith growth between sprat and herring in the fjords.

4.1 Discussion of ecological implications

Larvae and early otolith microstructure growth can be influenced by the environment the fish experiences after hatching. Therefore, small variation in otolith microstructure growth can be expected as a natural effect of variability in the environment which the fish larvae encounter after hatching. This was documented for Sognefjorden in this study, some small differences were visible but non-significant, while in Hardangerfjorden the differences were significant. The increment width for both year classes of sprat in Hardangerfjorden start with about the same increment width, which can indicate that sprat in Hardangerfjorden hatch at the same size. When increment width within the same species is similar at the same distance from the core it would indicate that fish have a similar length, since otolith microstructure is directly correlated with somatic growth (Moksness, 1989). The same pattern can be seen in Sognefjorden, and for herring between the different year classes in both fjords. Similar increment width near the core could also mean that they hatched in the same season. Sprat have one long spawning season which peaks between May and June. Herring on the other hand have different populations with different spawning seasons. It is documented that spring spawning herring have larger increment width at a given distance from the core compared to autumn spawning herring (Berg et al., 2020; Moksness & Fossum, 1991). The larger differences between the year classes in this study were seen later in the larvae stage, indicating that there are some factors after hatching that the fish experience which affect the otolith growth.

Previously it has been documented that the two main factors affecting otolith growth are temperature (Folkvord & Johannessen, 2004) and food availability (Fablet et al., 2011; Folkvord et al., 2000). In Hardangerfjorden sprat year class 2021 have a faster growth than yar class 2020, while for herring the faster otolith growth for the year classes is the opposite. The two pelagic species live in the same environment and since the trends for year classes in Hardangerfjorden is indistinguishable, the differences are most likely not linked to temperature or any other abiotic factors. However, it is documented that sprat and herring prey mostly on the same food (Blaxter & Hunter, 1982; Russell, 1976). Sprat and herring have an interspecific competition about the food, which might be the limiting factor explaining the differences between the year classes and why the species have faster otolith growth for different year classes.

On the other hand, the differences between the two year classes in Hardangerfjorden are extremely small for both species, and the two year classes do not show an indistinguishable growth trend. A previously study (Husebø et al., 2005) have investigated otolith microstructure growth between year classes of spring spawning herring in Norway, this study did not find any significant difference in otolith growth between the year classes of herring. Given the small differences between year class 2021 and 2020 in Hardangerfjorden and that there have not been found differences between year classes before, it was decided to combine the data for two year class for the following analysis.

When it comes to difference in otolith growth between the fjords it was hypothesized that there would be a difference in otolith growth, because each fjord has a unique ecosystem, consisting of different environmental factors. It is documented that abiotic factors like temperature, salinity and oxygen content of the water are factors influencing otolith growth for sprat and herring at larvae stage (Baumann, Gröhsler, et al., 2006; Folkvord & Johannessen, 2004; Grauman & Yula, 1989). Comparison of otolith growth between Hardangerfjorden and Sognefjorden show a significant difference. Increment width within both species, for all fjords, starts at the approximately same increment width. Meaning that factors in the environment encountered by newly hatched sprat and herring affect the otolith growth. Small differences in otolith growth between year classes and larger differences in otolith growth between the fjords indicates that it is environmental factors causing these differences, which is documented to affect otolith growth (Folkvord et al., 2000). Both species show the same trend within the fjords, with largest otolith growth in Hardangerfjorden and smallest in Nordfjorden.

Nordfjord show the same trend for both species, the increment width is smaller compared to the two other fjords. Considering that less sprat and herring were caught in Nordfjorden, and the small increment width, it might indicate that Nordfjorden is not the most favorable for the two pelagic species. Sprat and herring in Nordfjorden might have a different life strategi. This thesis finds smallest otolith growth in Nordfjorden, while it has previously been demonstrated that length at age 0 were smallest in Sognefjorden (Havforskningsinstituttet, 2021a). However, one problem with looking at length at age studies is that this study focuses on the first few months of growth, and growth pattern after the measured distance is unknown.

It has been found that both sprat and herring spawn locally in the fjords (Lie et al., 1978; Torstensen, 1984), and since the fjords show different otolith growth patterns it might indicate that, at least for the first part of the fish's life, sprat and herring remains in the fjord where they hatched. A previous study in migration of sprat between four different areas in the Baltic Sea have been investigated, which concluded that, except for some expected larvae drift, sprat remained in that area where they hatched (Baumann, Gröhsler, et al., 2006). Given that there is genetic similarity between the fjords for sprat, it is known that there must be some migration or drift of eggs or larvae with the Norwegian coastal current, therefore, some individuals might drift between the fjords, but the main part of the spawned fish seems to stay in the same fjord. The pelagic eggs of sprat hatch after a week (Moen, 2020), and have one week of possible drifting between the fjords before they hatch. Herrings demersal eggs lay on the bottom of the sea hatch after 2-3 weeks (Moen, 2020), and after hatching the larvae swims and drifts to the pelagic environment. Therefore, sprat have a couple of possible drifting before the herring larvae enters the pelagic environment. If drift of sprat eggs occurs before they hatch and not after, that could explain the connectivity between the fjords, as well as the differences in otolith growth due to different environment in the fjords. Drift and/or migration of herring would occur after the herring larvae enters the pelagic environment with costal currents. A previous study suggested that early hatching and/or fast drift of herring is important for larval survival (Slotte et al., 2019). Given the difference in growth between the fjords, the data could not be combined for the following analysis.

Given that both sprat and herring are small pelagic fish in the fjords, swim in shoals which overlap between the species and that they prey on approximately the same food, one could expect to find similar otolith growth between the species. Despite the similarities between the species, this thesis documented otolith growth at larvae stage between sprat and herring, which show two different growth trends. Herring starts with a larger daily increment width compared to sprat. One explanation for this is that herring larvae hatch after 2-3 weeks at 8-10 mm length (Moen, 2020; Russell, 1976), while sprat larvae hatch after 1 week with a length of 3.0-3.6 mm (Moen, 2020; Russell, 1976).

The otolith growth starts to flatten out for herring which is also seen for spring spawning herring in a previously study on otolith microstructure (Berg et al., 2020), while this trend is not seen for sprat. Given the spawning time and the growth interval investigated in this study, it is reasonable to assume that there should still be enough prey available. In addition, if the growth flattens out due to restricted food, then sprat would show the same trend in the growth. Otolith growth for sprat does not flatten out, but continuous to grow. A previously study on two species of *Ceratoscopelus* (Osteichthes: Myctophidae) found a reduction in otolith growth rate when the fish reached a length of 5 cm (Linkowski et al., 1993). Which could be a reason for why the otolith growth for herring is starting to flatten out, while sprat might have a reduction in otolith growth at a later stage than what is measured in this thesis. Another possible explanation for the different trends in otolith growth is that sprat and herring have different life span. Most sprat is mature at age 1 (Moen, 2020), while most herring become mature at age 2-3 years (Moen, 2020). Herring can reach a length of up to 50 cm, in comparison can sprat reach a length of 20 cm. Therefore, herring have a larger length growth to obtain which can be the reason for why the otolith microstructure growth for herring starts to slow at the end of larvae stage. Sprat on the other hand depends on the growth in its first year to become mature at age 1.

4.2 Discussion of the methods

The use of otolith microstructure analysis in this study have successfully visualized larvae otolith microstructure growth between year classes, fjords, and the two studied species. Otoliths were grinded to reveal the otolith microstructure, which were photographed and analyzed. Reading the microstructure can be challenging, and in most studies the otoliths are read by two persons. In this study, the first images were checked by two persons to reduce reader bias, and then the rest of the otoliths were read once. One of two otoliths was analyzed for each of the individuals. Photographs of otolith microstructure were documented and stored so that they could be read again if there was any doubt about increment width. The otolith microstructure analysis has a delicate grinding process. Otoliths used in this study are small and fragile, and are easily broken, both when handling them with a tweezer and by grinding too much. When the reader was insecure about the otolith microstructure and found it too difficult to analyze, that otolith was omitted from the study. Unclear microstructure detected on some parts of the otolith can be caused by too little or too much grinding. Some of the otoliths in this study had some parts where the growth zones were difficult to determine. There was some variability in the opacity and translucent zone of the otoliths, which can be explained by factors affecting otolith growth. The two main factors affecting otolith growth are temperature and food availability (Folkvord et al., 1997; Folkvord & Johannessen, 2004; Fablet et al., 2011)

When conducting otolith growth studies in laboratories, with fish reared in aquariums, the exact age in days is known. Making it possible to back calculate the number of days in increments, marking only those that represent one day of growth. However, this is not possible when the fish are captured in the fjords, which is a limitation of this study. For the first few days the increment width is small, making it difficult to separate the increments and they might not represent daily growth, while after the first 20 µm from the core the increment is assumed daily (Campana et al., 1987; Geffen, 1982). Therefore, measurements registered in this study started at 20 µm and up to a minimum of 160 µm. Determination and marking of increment are a demanding job and daily growth zones are not always easily separated. Therefore, increment width and distance from the core is used in this study, instead of number of increments. When looking at the distance from the core for each increment, that distance will be the same even if one increment is skipped or one extra marked. If one increment is skipped or one false increment is marked it will only create a small difference on the total dataset.

Light microscope used to analyze otoliths in this study have a theoretical resolution limit of 0.3 µm, but in reality, this limit is probably higher. Therefore, the visibility of otolith microstructure might be limited by the resolution of the light microscope and small growth zones might not always be detected (Campana et al., 1987). The differences in otolith microstructure growth in this study are so small that with the limitations of the light microscope, there might not be a difference. At least not one that is possible to detect with a light microscope. The sampling size included in the analysis are large, therefore there is a chance that even small differences can become significant when using statistical analysis.

The method used for otolith microstructure analysis in this study have been successfully used in a number of growth studies (Baumann, Gröhsler, et al., 2006; Baumann, Hinrichsen, et al., 2006), as the microstructure can be directly correlated to somatic growth (Moksness, 1989). The otolith microstructure analysis is also used for other types of studies, for example to separate different spawning populations of herring (Berg et al., 2020; Moksness & Fossum, 1991), and is used in the Baltic Sea to separate populations (Baumann, Gröhsler, et al., 2006). Analysis of otolith microstructure are therefore considered a powerful tool when investigating growth and comparing differences in growth.

4.3 Future studies

Otolith microstructure is used in various types of studies and can give valuable information about the history of the lives of fish. There are a several different abiotic and biotic factors that affect the formation of otolith microstructure. Ideally, when looking at otolith microstructure there would also be available data on factors like salinity, prey density and temperature measured at the time period of interest in the otoliths. For this study, otolith growth in larvae stage is in focus, meaning that temperature measurements taken in September are not represented for the temperature at larval growth. Including all this sampling demands a lot of effort by sampling but can give more accurate information.

Spawning season for sprat in the Norwegian fjords has been documented by back calculating daily growth zones (Torstensen, 1998). In the future it would be interesting to investigate if the spawning season is different in the inner and outer part of the longest/largest fjords and research the early growth to look for differences, since it is found that spawning take place within the fjords (Torstensen, 1998). It has been found that older individuals spawn earlier in the season compared to younger individuals. Therefore, it would be interesting to back calculate spawning time and investigate if there is a difference in early otolith growth between fish spawned early and late in the spawning season.

Previous studies have found that there is a difference in otolith growth between spring and autumn spawning herring (Berg et al., 2020). Therefore, it might be worth considering the two different spawning seasons and dividing the spawning season in analyses. Combining genetics studies and otolith microstructure of herring, or use the increment width to determinate which spawning season each individual belongs to would reduce small errors in the dataset if some autumn spawning herring were included (Berg et al., 2020).

4.4 Conclusions

The small differences between year class 2021 and 2020 in Hardangerfjorden can be explained by interspecific competition between sprat and herring, given the fact that they prey on mostly the same food. It could also be due to normal variations in the biological data set since no significant otolith growth was detected in Sognefjorden. The difference in otolith growth between fish from different fjords show similar trends for both species. Given the small difference between the year classes, but larger difference between the fjords, one could assume that mixing between the fjords are low. For management of sprat this means that it is not enough connectivity between the fjords to give one quota for the fjords combined. Except for some eggs, larvae, or fish drift between the fjords, which is proven to exist given that there are no significant genetic differences between the fjords for sprat. The difference in otolith growth between sprat and herring indicate differences in their life cycle despite the similarity of the two species. For instance, herrings hatch with a longer length, compared to sprat.

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Appendix:

Appendix A: Increment width for sprat and herring divided by age and fjords

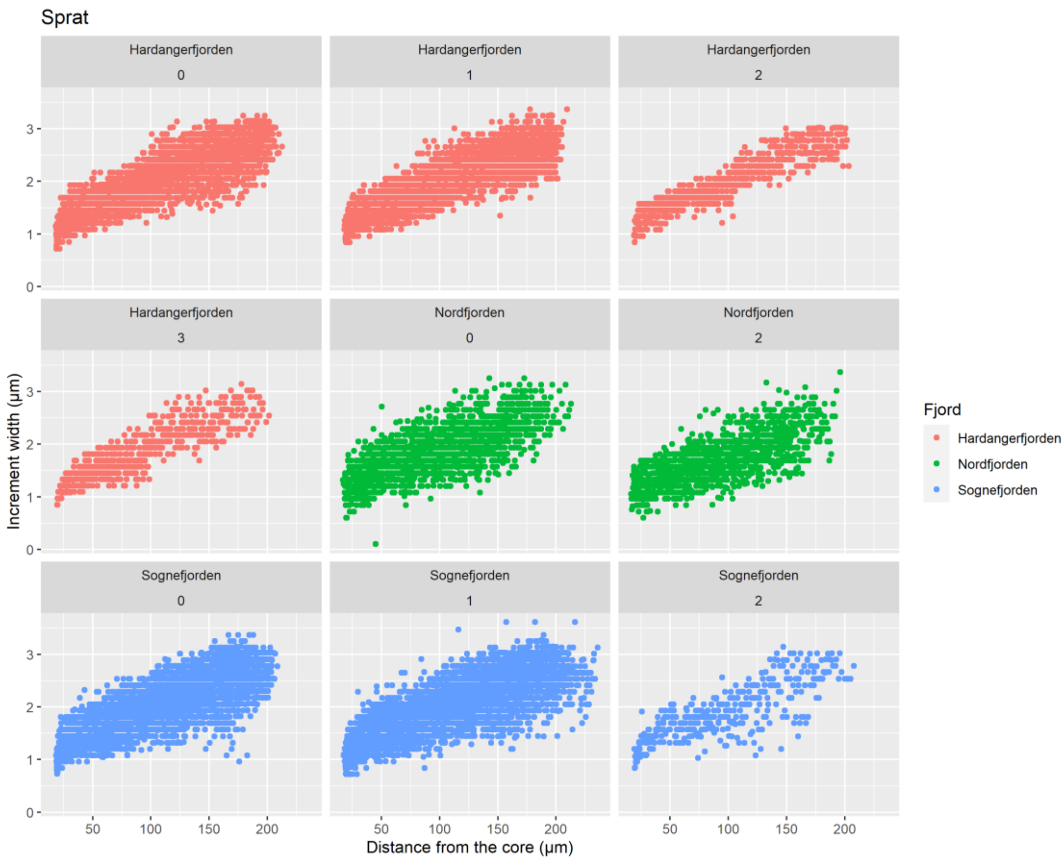

Figure A1: Increment width for all individuals of sprat within the different age groups and fjords.

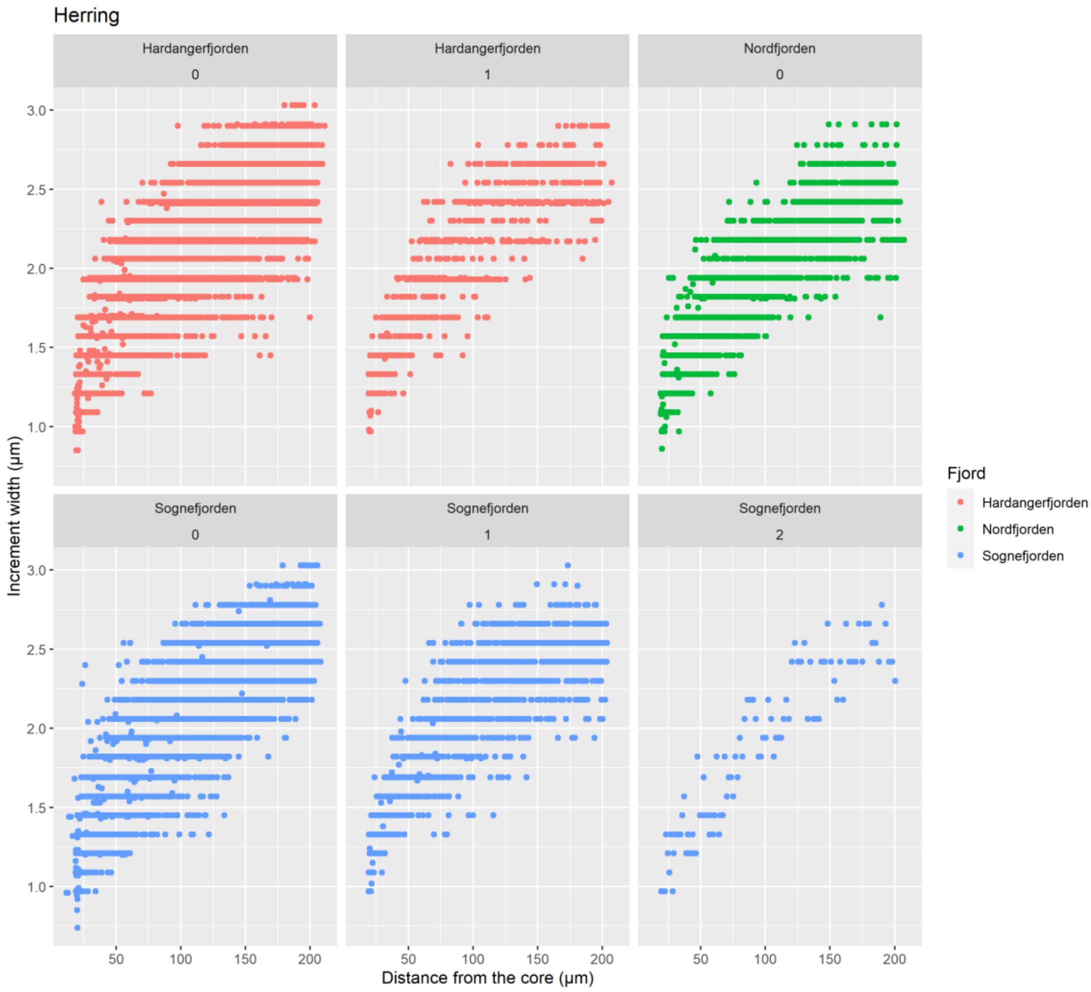

Figure A2: Increment width for all individuals of herring within the different age groups and fjords.

Appendix B: R packages used

- Tidyverse (Wickham, 2017)
- ggOceanMaps (Mikko Vihtakari 2022)
- ggspatial
- nlme
- readxl
- RstoxData
- smoothr
- stars

Appendix C: Model outputs

Table C1: model output for sprat in Sognefjorden when comparing otolith growth between year class 2021 and 2020 (Equation 1). Dist_CORE is an abbreviation for distance from the core.

	Value	Std.Error	DF	t-value	p-value
Intercept	1.0675538	0.009508373	11329	112.2751	0.0000
Dist_CORE	0.0091509	0.000067432	11329	135.7056	0.0000

Table C2: model output for sprat in Hardangerfjorden when comparing otolith growth between year class 2021 and 2020 (Equation 1). Dist_CORE is an abbreviation for distance from the core. Age1 is year class 2020.

	Value	Std.Error	DF	t-value	p-value
Intercept	1.0134283	0.013235252	7759	76.57039	0.0000
Dist_CORE	0.0099262	0.000097925	7759	101.36462	0.0000
Age1	0.0524022	0.020111259	134	2.60561	0.0102
Dist_CORE:age1	-0.0005415	0.000148788	7759	-3.63910	0.0003

Table C3: model output for sprat when comparing difference in otolith growth between Hardangerfjorden and Sognefjorden (Equation 2). Dist_CORE is an abbreviation for distance from the core.

	Value	Std.Error	DF	t-value	p-value
Intercept	1.0361282	0.010858578	19089	95.42025	0.0000
Dist_CORE	0.0096918	0.000078335	19089	123.72137	0.0000
FjordSognefjorden	0.0314160	0.014118392	331	2.22518	0.0267
Dist_CORE:FjordSognefjorden	-0.0005410	0.000101771	19089	-5.31565	0.0000

Table C4: model output for herring in Sognefjorden when comparing otolith growth between year class 2021 and 2020 (Equation 1). Dist_CORE is an abbreviation for distance from the core.

	Value	Std.Error	DF	t-value	p-value
Intercept	1.2625806	0.022032475	3141	57.30544	0.0000
Dist_CORE	0.0081433	0.000115931	3141	70.24247	0.0000

Table C5: model output for herring in Hardangerfjorden when comparing otolith growth between year class 2021 and 2020 (Equation 1). Dist_CORE is an abbreviation for distance from the core. Age1 is year class 2020.

	Value	Std.Error	DF	t-value	p-value
Intercept	1.3130459	0.01553513	4899	84.52110	0.0000
Dist_CORE	0.0077782	0.00009777	4899	79.55730	0.0000
Age1	0.0277865	0.05169874	97	0.53747	0.5922
Dist_CORE:age1	0.0007658	0.00032829	4899	2.33254	0.0197

Table C6: model output for herring when comparing differences in otolith growth between Hardangerfjorden an Sognefjorden (Equation 2). Dist_CORE is an abbreviation for distance from the core.

	Value	Std.Error	DF	t-value	p-value
Intercept	1.3157502	0.016067370	8041	81.88958	0.0000
Dist_CORE	0.0078462	0.000093062	8041	84.31170	0.0000
FjordSognefjorden	-0.0532827	0.025734176	160	-2.07050	0.0400
Dist_CORE:FjordSognefjorden	0.0002974	0.000149137	8041	1.99438	0.0461

Table C7: model output for when comparing otolith growth for sprat and herring in Sognefjorden (Equation 3). Dist_CORE is an abbreviation for distance from the core.

	Value	Std.Error	DF	t-value	p-value
Intercept	1.2783522	0.017254590	13651	74.08766	0.0000
Dist_CORE	0.0081408	0.000132302	13651	61.53197	0.0000
SpeciesSprat	-0.2211169	0.019185447	13651	-11.52524	0.0000
Dist_CORE:SpeciesSprat	0.0010712	0.000151041	13651	7.09212	0.0000

Table C8: model output for when comparing otolith growth for sprat and herring in Hardangerfjorden (Equation 3). Dist_CORE is an abbreviation for distance from the core.

	Value	Std.Error	DF	t-value	p-value
Intercept	1.3155713	0.013483697	12101	97.56756	0.0000
Dist_CORE	0.0078454	0.000096587	12101	81.22586	0.0000
SpeciesSprat	-0.2829691	0.017610013	233	-16.06865	0.0000
Dist_CORE:SpeciesSprat	0.0019010	0.000125596	12101	15.13555	0.0000