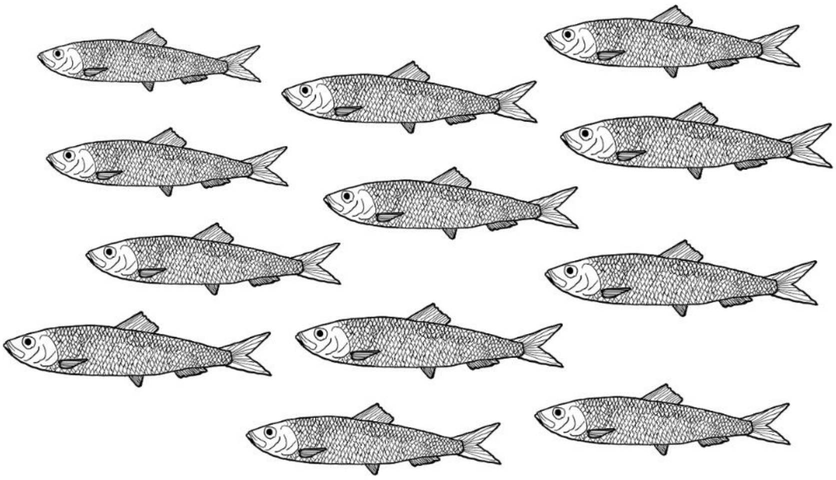
Spatial variability in life history traits of sprat (*Sprattus sprattus*) in Norwegian fjords suggests low mixing of adults between the fjords



Øydis Brendeland

Master of Science in Biology - Fisheries Biology and Management

June 2022

Supervisors:

Florian Berg, Institute of Marine Research

Arild Folkvord, Department of Biological Sciences, University of Bergen & Institute of Marine Research

Department of Biological Sciences, University of Bergen

Acknowledgments

First and foremost, I would like to thank my supervisors Florian Berg (IMR) and Arild Folkvord (UiB/IMR) for their knowledge and guidance with the writing of this thesis. They have helped me with understanding of both biological and statistical problems, in addition to answering all other questions I have come up with. Their help has been crucial in completing this thesis.

I would also like to thank Cecilie Kvamme for her helpful input on the interpretation on the results, Eilert Hermansen for his advice with the maturity data, and the rest of the Pelagic group at IMR for a friendly and helpful working environment. I am also grateful for the opportunity of participating on the coastal sprat cruise 2021 and would like to thank on that occasion cruise leader Cecilie, cruise participants, and the crew onboard RV "Kristine Bonnevie". I want to thank our seminar group, Florian, Arild, Tomine Grov Lekven, Daniel Stiti, and Karoline Hegdal, for interesting and useful discussions. A special thanks to Tomine for always being very generous with sharing her knowledge.

Lastly, thanks to the rest of my fellow study-friends for a great study period, and to friends and family for their love and support.

Abstract

Recent studies have shown almost no genetic variability of sprat (*Sprattus sprattus*) among Norwegian fjords. However, each fjord creates its own unique habitat, and local adaptations can thereby be expected. An annual coastal sprat cruise has been conducted between 1996-2021 by the Institute of Marine Research with the purpose of monitoring sprat in Nordfjord, Sognefjord, and Hardangerfjord. Investigation of the routinely sampled life history parameters are a cost-effective method supplementing genetic studies to gain insight into the potential population structure of sprat in the fjords. Life history traits are a phenotypic result of genotype and environmental factors. Therefore, it was attempted to consider the influential environmental factor temperature and determine the effect of density-dependence on growth.

Differences in life history traits between the fjords, specifically, in growth, length-at-age, length-at-maturity and condition were found. Most prominent results were found for lengths-at-age. The impact of temperature and effect of density-dependence on length of sprat showed differing results between ages and fjords. Shortest lengths-at-age were found in inner Hardangerfjord and Sognefjord, and an overall temporal decline in lengths-at-age were found in these fjords. Sprat in Sognefjord showed signs of density-dependent growth, while the models showed low goodness of fit in Hardangerfjord. Limited food availability, increasing temperatures, and consequently declining lengths-at-age and condition over time have also been seen in other sprat stocks throughout the species distribution. Nordfjord had an overall temporal increase in lengths-at-age, suggesting that the lower abundance found here is not sufficient to cause density-dependent growth.

The differing dynamics of life history traits among the fjords suggest that adult sprat mostly stay within its fjord and that potential mixing resulting in gene flow must then occur during the early life stages.

Table of Contents

1. Introduction

1.1. Fish ecology and life history theory

1.1.1. Fish ecology – influence of environmental factors

Studying ecology, we seek knowledge of the variation in species or populations' distributions and abundances, and how the physical environment affects these variations. In the marine habitat, some of the environmental factors of most significant influential importance for fish ecology are temperature, oxygen, and salinity. Survival is possible over a tolerance range of these factors, while active feeding, growth, and reproduction occur at a narrower optimal range (Payne et al. 2016). Fish are ectotherms and highly dependent on the temperature of the surrounding water. There is an optimal temperature for chemical processes and followingly metabolism (Neuheimer and Taggart 2007). Consequently, sea temperature influences the level of feeding, growth, and reproduction. The oxygen level influences the performance of fish, as with other animals, directly by limiting aerobic metabolism. Oxygen level and temperature also affect fish metabolism together; as oxygen has less solubility in warm water and the metabolic rate increase with temperature, a challenging environment is created (Svobodova 1993). Salinity is an important factor in determining osmotic regulation, and can also influence growth (Bœuf and Payan 2001). Most fish in the open ocean experience slight fluctuation in salinity. However, examples of significant variations in salinity are coastal areas with estuaries. An additional environmental factor that indirectly can influence fish ecology is light penetration. Light transmission is poor through water, and the penetration becomes less with the amount of dissolved organic matter. Many fish are visual predators with a demand for some level of light penetration (Cerri 1983). The highlighted environmental factors are among the most important driving forces in fish adaptation in life history traits.

1.1.2. Life history theory; key concepts and definitions

Life history theory is a branch of evolutionary ecology and explains how evolutionary forces drive organisms to optimize Darwinian fitness in response to the environment (Stearns 1992). The response is change in the features of an organism`s life cycle, in other words, its life history traits. Growth, survival, maturity, reproduction, and mortality are examples of life history traits, and these can differ vastly between species, populations, and individuals (Thorson et al. 2017).

A population's life history phenotype is determined by its genotype and its surrounding environment. Variation in the genotype enables selection of an optimal response to the environment. The term phenotypic plasticity refers to an organism's ability to adapt to the environment by letting different features be expressed in its phenotype based on its genotype (Via et al. 1995). The adaptation can be in terms of behaviour, morphology, or physiology (Price et al. 2003). Due to a populations' resources are limited, these factors are allocated. Trade-offs refer to an evolutionary change in one trait resulting in increasing fitness is linked to a trait resulting in decreasing fitness (Reznick 1985, Stearns 1989). Balancing life history traits involves many trade-offs. The dilemma of whether to reproduce or continue to grow is a classic trade-off example: contributing to the next generation's gene pool is the driving mechanism behind evolution, while reproduction is very energy consuming and generation of sufficient energy reserves takes time (Reznick 1985, Bernardo 1996). Reproduction at a small size can cause less offspring and decreased quality of eggs compared to reproduction at a larger size (Barneche et al. 2018). At the same time, later reproduction increases the probability of experiencing unfavourable environmental conditions in the future or being eaten by predators, (Reznick 1982) while being beneficial in terms of time and energy to grow to a larger size-at-age.

1.1.3. Growth and size-at-age

There are two types of growth considered in fisheries biology: population growth and individual growth. Population growth is of central interest in exploitation of renewable resources. However, individual growth is together with recruitment, the core input parameters when calculating the productivity of a stock. An additional reason underlying the importance of individual growth is its influence on survival and fecundity (Graeb et al. 2004, Hixon et al. 2014). Individual growth is a complex process determined by genotype and environmental conditions. Whereas growth is a process, individual size is the resulting state of this process (Enberg et al. 2012). Time-series data of size-at-age can be used in monitoring fish stocks, while differences between locations can provide information on stocks (Begg and Waldman 1999). A reduction in size-at-age over long-term data series has been observed for many stocks, and explanatory reasons are both evolutionary and phenotypic. Fishery-induced evolution, where selection forces favour smaller sizes, is an increasing concern (Edeline et al. 2007, Swain et al. 2007). Due to the complexity of growth, evolutionary selection processes can be challenging to determine and distinguish (Enberg et al. 2012). Before one can determine whether differences in size-at-age between years or locations are due to genetic differences, one must consider phenotypic plasticity by determining the environmental factors of influential importance.

The environmental conditions of most significant influential importance on growth are food availability and temperature (Weatherley et al. 1987, Frisk et al. 2015). Scarce food resources naturally limit growth. In addition, the composition of food resources has lately been given more attention. Many marine environments experience shifts in the state of the ecosystem, possibly due to climate change (Rocha et al. 2015). For example, this has been detected in the North Sea with a shift in the zooplankton community (Defriez et al. 2016), causing bottom-up cascading effects on the growth of forage fish preying on zooplankton (Clausen et al. 2018) and followingly a phenotypic reduction in size-at-age over time.

Density-dependence can indirectly influence populations through intraspecific competition for resources. Food availability is a common limiting factor; with increased density of individuals, availability of food per-capita decrease (Ward et al. 2006). Density dependence can thereby cause slower growth and a lower size-at-age. Shoaling species are especially susceptible to intraspecific competition (Krause et al. 1992), e. g. Norwegian spring-spawning herring have been proved to have density-dependent size-at-age (Stenevik et al. 2022).

Temperature has already been mentioned as a factor positively correlated with growth (up to a threshold) in ectotherms. At the same time, the “temperature-size rule” (TSR) states that individuals experiencing higher temperatures will reach smaller adult body sizes (Atkinson 1994). The mechanisms behind the rule are complex and not yet fully understood (Forster et al. 2011). Pauly and Kinne (2010) point at oxygen as a crucial factor; the consequences of warmer water are a decrease in oxygen solubility in combination with increase in anabolic oxygen demand. The large surface area to volume ratio enables smaller individuals to better balance demand and uptake of oxygen (Pauly and Kinne 2010). TSR, in combination with climate change, has thereby been identified as an underlying reason for the shift towards smaller size-at-age (Daufresne et al. 2009).

1.1.4. Length-weight relationships (LWRs) and condition

Investigating the length-weight relationship (LWR) and relative condition of a population can provide important insight to its ecology (Froese 2006). The environmental factors influencing the condition of the fish are similar to those determining growth, i.e., food availability and temperature, etc. LWRs are used to find the weight corresponding to a given length, while condition factors are used to determine the relative condition of the fish or population. Plotting observed LWR on a logarithmic scale and fitting a linear regression provide the parameters a (intercept) and b (slope). Growth according to cube law is termed isometric growth ($b=3$), but this is rarely the case in fish. Fish most often grow allometric, where positive-allometric growth is when they become "plumper" as they grow ($b > 3$), while negative-allometric growth is when they become slender with length ($b < 3$) (Tesch 1968). With use of the parameters estimated from LWR, one can determine the relative condition of a fish or population. Condition factors are a measure of the general well-being of the fish, assuming heavier fish for a given length are in better condition (Bagenal and Tesch 1978). Comparing relative condition factors between populations can thus give insight to the differences in ecology.

1.1.5. Length-at-maturity

Growth, size-at-age, and condition are all factors optimized to achieve the goal of an animal's life cycle, which is reproduction. Length at first maturity is under strong evolutionary selection pressure, and the earlier mentioned trade-off situation is illustrated. Maturation at a short length predicts an increased chance of contributing to the gene pool of the next generation, though the cost is lower fecundity as the energy investment is less (Wootton 1991). Early maturation can be a phenotypic advantage when adult survival is low. However, maturing at a larger size is often accompanied by slower growth and reaching a higher asymptotic length. Large size maturity can be an indication of better adult survival conditions, possibly due to less inter- or intra-specific competition, predation, fishing (Engelhard and Heino 2004, Lappalainen et al. 2016) or better food availability (Jonsson et al. 2013).

1.1.6. Life history strategies

Trade-offs limit evolution, but a variety of different strategies or combinations of life history traits seeking to optimize fitness have evolved. Different terms for these strategies have been described. MacArthur and Wilson (1967) implemented the terms r- and k-selection to describe biological characteristics that provide increased success for individuals in certain environments. R-selection is often favoured in unstable environments and is recognized by many small offspring, but with little energy investment in each. K-selection is on the other hand recognised by few offspring and more investment in each – a strategy often favoured in more stable environments (MacArthur and Wilson 1967). While MacArthur and Wilson implemented the general terms r- and k-selection for all animals, Winemiller and Rose (1997) categorized three endpoints of a triangular continuum of life history strategies among fish: equilibrium, periodic, and opportunistic. Their purpose was to predict populations' and species' responses to natural and anthropogenic disturbance. An equilibrium strategy is recognized by parental care, slow growth, late maturity, and few and large offspring. This accounts for many elasmobranchs (King and Mcfarlane 2003). A periodic strategy is recognized by late maturation to achieve a size sufficient for production of one large clutch of offspring spawned at an optimum time, in addition by a relatively long life span. Many demersal fish have a periodic strategy (King and Mcfarlane 2003). Lastly, an opportunistic strategy is recognised by small size, early maturation over an extended spawning season, and a short life span. The intrinsic rate of natural increase or turnover rate is thereby high. An unstable environment is often a driving force for this strategy, as the population can quickly recover with favourable environment after a disturbance. Several species of forage fish have an opportunistic strategy (King and Mcfarlane 2003).

The different strategies underline the variation and span of life history traits, and followingly the importance of studying life history traits to manage stocks sustainably. For example, an equilibrium strategy with slow growth and late maturity is vulnerable to overexploitation since recovering from low abundance requires several successive generations. This is contradictory to the opportunistic strategy where favourable conditions can result in abundant offspring despite low spawning biomass. Studying life history traits provides general insight into a stock's productivity and hence its ability to support fisheries (Thorson et al. 2017).

1.2.Biology and distribution of sprat

Species of forage fish, often small pelagic fish, play important ecological roles close to the base of the food chain by feeding on plankton and serving as prey for larger predators (Cury 2000). As mentioned, forage fish tend to have an opportunistic strategy, i.e., early maturation, relatively fast growth to a small asymptotic length, and a short life span (King and Mcfarlane 2003).

European sprat (*Sprattus sprattus*) is a species in the order clupeiformes, reaching up to 16 cm in length and 32 grams in weight (Coull et al. 1989). It is a shoaling pelagic species, which is reflected in its appearance with a streamlined body, silvery colour reflecting light, rather inflexible fins, and a forked tail fin. It is mostly found in the uppermost 150 meters of the water column. Sprat is a short-lived species reaching up to 5 years of age. Dependent on growth, it becomes mature within 1 or 2 years at 95-100 mm in length (Peck et al. 2012). Its distribution spans from Lofoten in Norway to Morocco and from the British Isles to the Baltic Sea. In addition, it is found in the northern Mediterranean and the Black Sea (Whitehead 1986). Sprat can adapt to very low salinity conditions, which for example can be seen in Landvikvannet, the Baltic Sea, and occasionally in coastal areas and fjords as a consequence of water runoff in spring and summer (Quintela et al. 2021). A turbid surface layer, which is a common characteristic of Norwegian fjords, function as a preferable feeding area and as refuge for predator avoidance for small pelagic fish (Giske et al. 1994). As a small pelagic species, sprat is ecologically important in its ecosystem; feeding on zooplankton and, in some registered occasions, phytoplankton (Falkenhaug and Dalpadado 2014); as prey for many predatory species (ICES 2018b); and as a competitor to other small pelagic species (Casini et al. 2011).

The strategy of sprat is opportunistic with batch spawning (Alheit 1989). Spawning over an extended period decreases the probability of mismatch with environmental conditions and increases the likelihood of succeeding with at least some offspring. Sprat has a high rate of intrinsic increase and can be highly productive when environmental conditions are favourable, while the recruitment can be almost zero if conditions are unfavourable. A single year-class can therefore lay the basis of the entire fishery (Kvamme 2020).

1.3. Management of sprat

1.3.1. Population structuring in relation to life history

In the marine habitat, the spatial structure of a species is often widespread. For example, many marine teleosts have a planktonic egg- and larval stage where they are dispersed passively with currents (e.g. van der Molen et al. (2007)), followed by an active adult stage where they migrate to preferable habitats (e.g. Vilhjálmsson (2002)). The distribution is restricted by intolerable environmental conditions or competition. Various abiotic and biotic factors are met throughout a species distribution, and populations adapting to the local environment may form. A population is defined as a group of relatively reproductively isolated individuals, either temporally and/or spatially separated from other individuals of the same species (Begg and Waldman 1999). The barriers separating populations can be physical, morphological, or behavioural. However, a range of types of populations exist dependent of the nature of the barrier – from closed populations to interacting subpopulations (Thomas and Kunin 1999). The term metapopulation describes several local populations with local adaptations that, to some extent, have their own internal dynamics, but where gene flow in between the local populations occurs to some degree (Kritzer and Sale 2004). When dividing an exploited species into stocks, i.e., manageable units, one seeks to divide in accordance with the underlying genetic structure, i.e., the populations, since life history traits, and consequentially its ability to supply fisheries, often differ between the populations. However, stock identification can be challenging since the population structure often can be viewed as several overlapping ranges rather than clear boundaries of separate populations. If homogeneity of life history traits is assumed for a stock that is not based on its actual genetic structure, the risk of overexploitation increases. For stock assessment purposes, insight into the population structure to ensure the correct proportions of the populations within an area is thereby important (Begg et al. 1999).

Studying genetics is important in determining evolutionary differences between stocks. However, in cases where only low levels of mixing occur, difficulties may arise concerning management applications (Begg et al. 1999). Since life history traits are phenotype measurements, they do not provide definite information on the genotype. However, indications of separation over an extended period of time for adult fish can be detected (Begg et al. 1999). For example, constant differences in lengths-at-age over years can indicate that the fish have been experiencing the same environment, likely because it has remained in its habitat. Distinguishing between genetic and environmental variation is though challenging, and interpretation of phylogenetic traits to population structure, must be seen in conjunction with influential environmental factors.

1.3.2. Sprat in Norwegian fjords

Three distinct genetic groups of sprat in the North Sea and its surrounding area have recently been identified and are managed accordingly: Norwegian fjords; the Northeast Atlantic region including the North Sea, Kattegat-Skagerrak, Celtic Sea, and Bay of Biscay; and the Baltic Sea (ICES 2018a, Quintela et al. 2020). The lack of detected genetic differences between the Norwegian fjords (except for some differentiation with sprat in Oslofjord and Landvikvannet) suggests spatial homogeneity in this region (Quintela et al. 2020, Quintela et al. 2021). However, the possibility of a low degree of genetic differences, i.e., population structure, could not be excluded (Quintela et al. 2020). Few studies have addressed the connectivity of sprat between Norwegian fjords. The exception is tagging studies attempted in 1960 in the Hardangerfjord, which revealed that sprat mostly stay within their respective fjords (Gundersen 1958, Devold et al. 1960, Gundersen 1961, 1963). The Norwegian Directorate of Fisheries manage sprat in Norwegian fjords with assessments and advice from the Institute of Marine Research (IMR), and quotas are set separately per fjord (Kvamme 2020). This is reasoned by the lack of knowledge of the connectivity of sprat between the fjords and, followingly, whether a fjord is capable of supplying another with recruits (Kvamme 2020). The rugged fjord coastline of Norway stretches from 58°N to 71°N – creating many unique marine habitats. As each fjord creates its own unique marine environment, optimum phenotypes and possibly genotype of sprat can thereby be expected to differ accordingly.

1.4. Objectives

This master thesis aims to compare life history traits of sprat between Norwegian fjords and to investigate the possible influence of environmental factors on the traits to gain insight into the potential population structure of the fjords. The study had the three following objectives:

1. Study the phenotypic variation of sprat in Norwegian fjords. Specifically, compare growth, length-at-age, length-at-maturity, and condition of sprat between Nordfjord, Sognefjord, and Hardangerfjord.
2. Detect possible variation in length-at-age and condition between time periods in the fjords.
3. Investigate whether the potential changes in length-at-age between fjords and periods are related to fluctuations in temperature and/or if the differences are related to density-dependence, represented by relative abundance estimates of sprat.

2. Material and methods

2.1 Biological data

Biological data of sprat, sampled from year 1996 to 2021, has been collected in the Norwegian fjords Nordfjord, Sognefjord, and inner and outer Hardangerfjord. Biological samples were collected during several scientific surveys conducted by the IMR. The majority of the sampling has been done during acoustic-trawl surveys with the purpose of monitoring coastal sprat. The survey has traditionally taken place from November to mid-December but was moved to July-August in 2019. A pelagic trawl (Harstad trawl) has been used to conduct opportunistic hauls based on acoustic registrations. The depth of trawling was decided based on the depth of the echo registrations (usually from the surface down to 150 meters), while trawling duration was based on the strength of the echo (usually around 20 minutes). Blind hauls, i.e., hauls without basis in acoustic registrations, were done occasionally during the night. At this time, sprat are often located near the water surface and are thereby within the blind zone of the echosounder a few meters below the surface. An additional reason for blind hauls is that sprat perform avoidance behaviour to the fishing vessel (Johnsen et al. 2020).

The catch procedure for the coastal sprat acoustic-trawl survey started with sorting the catch into species. In some cases, sprat catches consisted of two length groups and were separated into small (mainly 0-group) and larger fish (age 1 and older) to ensure representation of both. Thirty individuals were taken out for a representative individual subsample. For the sprat of the individual subsample, length and weight were measured, age was read from the otoliths, and sex and maturity stage (1-9) were determined according to “Håndbok for prøvetakning av fisk, krepsdyr og andre evertebrater” (Mjanger et al. 2019). Additionally, seventy individuals were taken out for a representative length/weight subsample. If less than 30 individuals were caught, all of them were fully sampled. The length was measured to the closest 0.5 cm below, while weight was sampled with 1 g precision. (Mjanger et al. 2019).

2.2 Study area

The study area was restricted to Nordfjord (NF), Sognefjord (SF), and inner and outer Hardangerfjord (HF) (Figure 1). The HF was divided at 59.82 °N between Huglo island and Sunde into outer and inner for most of the analyses due to differences in the topography of the parts. The outer part of the HF is more open, while the inner part is narrower. Common for the fjords is a typical seasonal cycle with freshwater runoff in the spring and summer due to snow and glacier-melting, and in autumn due to rainfall. The water is followingly colder and with lower salinity in the innermost parts of the fjord than in the main fjord (Rustad 1978, Asplin et al. 2014). A surface layer of low salinity creates an outgoing current, while a compensating current in the intermediate layer is directed the opposite way. In winter, the water is more homogenous vertically and less mixing occur.

Common determinants for water mixing in all oceanic systems is Coriolis effect and meteorological conditions. These factors are together with the geography of the fjord and the level of freshwater runoff, some of the most determining factors for interaction between water in the fjord and the coast outside. The depth of the sill and width of the fjord mouth are geographical features influencing the level of mixing. A shallow sill hinders free passage of water with the ocean outside (Stigebrandt 2001). Water circulation in the deepest parts of the fjord is largely determined by the density of the water outside the sill. The fjords of investigation are all relatively long fjords with several sills and basins, and water renewal occur more rare in the innermost basins (Johnsen et al. 2021).

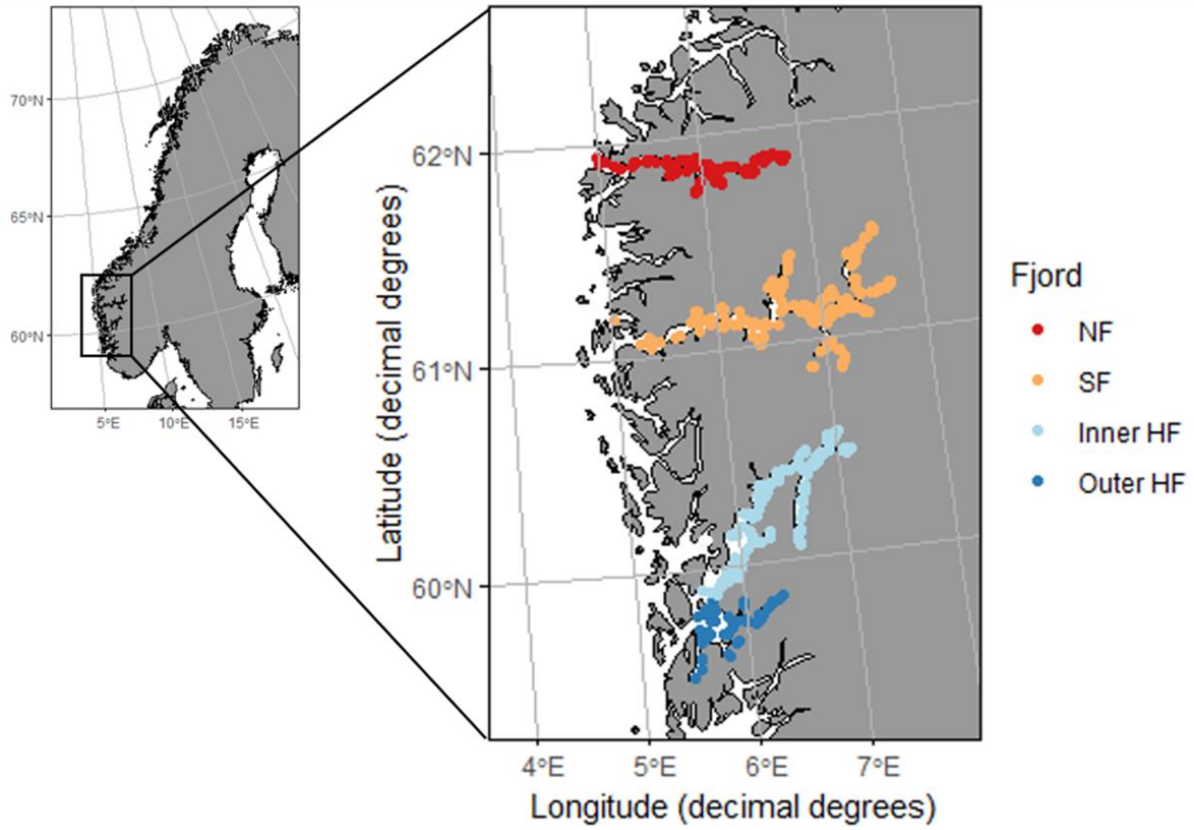


Figure 1: Stations where sprat have been sampled in the Norwegian fjords Nordfjord (NF), Sognefjord (SF), inner and outer Hardangerfjord (HF) during scientific surveys by IMR from 1996 to 2021.

The northernmost fjord of investigation is the 106 km long and 565 meters at its deepest NF. The fjord has a sill of 100–150-meter depth. The longest and deepest fjord in Norway is SF, with a length of 205 km and 1303 meters at its deepest. The sill is 100-200 meters deep. HF is a complex fjord consisting of a wide main fjord and several narrower fjord arms, reaching 180 km in length and a maximum depth of 852 m. The main sill separating the outer part from coastal waters is 150–200 meters deep, and the sill between the outer and inner part is at 140-meter depth (Holtedahl 1975).

2.3 Statistical analyses

R software was used for all statistical analyses and graphics (R Core Team 2021). Maps were made by use of the package ggOceanMaps (Vihtakari 2020). Unless otherwise specifically stated, data handling, figures, and statistical analyses were done with “RstoxData” (Umar et al. 2021), “FSA” (Ogle et al. 2021), “tidyverse” (Wickham et al. 2019), “emmeans” (Lenth 2021), and “RColorBrewer” (Neuwirth 2014). Prior to all analyses, data exploration was done according to the protocol by Zuur et al. (2010). The significance level used for all analyses was $p < 0.05$.

2.3.1. Estimating growth with Von Bertalanffy Growth Function (VBGF)

All data where length and age have been found were used to find the growth of sprat in NF, SF, and inner and outer HF (Table 1).

Table 1: Total number of age and length measured sprat sampled by the Institute of Marine Research (IMR) from the Norwegian fjords Nordfjord (NF), Sognefjord (SF), and inner and outer Hardangerfjord (HF) from 1996 to 2021.

	NF	SF	Inner HF	Outer HF
1996	167	148	323	
1997	250	457	693	249
1998	265	383	692	95
1999	96	360	163	
2000	125	293	114	
2001	48	35	116	50
2002	174	250	175	50
2005		187	114	119
2006	199	336	296	74
2007		248	171	95
2008	70	171	197	
2009			221	93
2015	356	492	381	110
2016	81	214	227	228
2017	54	178	266	27
2018	81	315	163	140
2019		30	203	117
2020		60	120	60
2021	78	572	463	118
Total	**2044**	**4729**	**5098**	**1625**

Von Bertalanffy Growth Function (VBGF) (Eqn. 1) was fitted to the data with use of the FSA package (Ogle et al. 2021).

$$\mathrm{L}_{\mathrm{age}} = \mathrm{L}_{\infty}\left(1 - e^{-k(age-t_0)}\right) \qquad \text{Eqn. 1}$$

Age is measured in years, L_{∞} is the asymptotic length, K is the curvature parameter, and t_0 is the theoretical age at zero length (Bertalanffy 1934). T_0 is expected to be negative and close to zero, but a common problem when estimating the parameter is the lack of observations in early life stages. The parameter should in these cases be interpreted with caution.

Spawning time for sprat is during spring and summer, peaking in May - June (Wahl and Alheit 1988). Since IMRs coastal sprat cruise have been conducted in November – December, most of the sprat are almost half a year old by this time. Therefore, it was assumed that the sprat has its birthday in end of May and age 1/12 were added for each month from May to the annual age, i.e., a fish for age 0 caught in November was assumed to be 6/12 year old.

2.3.2. Cumulative size distributions (CSDs): Comparing three time periods within fjords, and fjords within the time periods

IMRs coastal sprat cruise have taken place annually November – mid December in three periods: 1997-2002, 2005-2008, and 2015-2018, hereafter referred to as period 1, 2, and 3, respectively (Figure 2). For consistency reasons regarding the observations from the coastal sprat survey, only data from November – mid December (01/11 to 15/12) were included. In addition, only observations where age reading had been done were used (Table 2; Appendix 1.1 – 1.4).

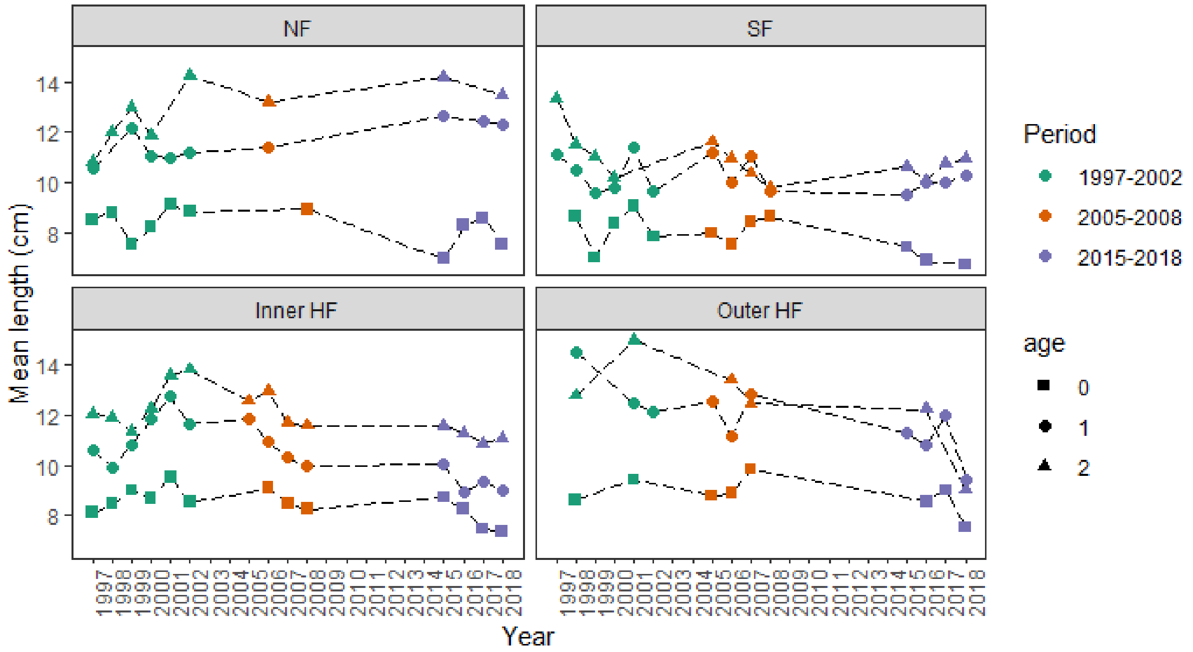


Figure 2: Mean length-at-age over the time-period 1997-2018 for the Norwegian western fjords Nordfjord (NF), Sognefjord (SF), and inner and outer Hardangerfjord (HF). There are two sampling gaps: from 2003-2004 and from 2009-2014. Three time periods of sampling can thereby be categorized: 1997-2002, 2005-2008, and 2015-2018.

Table 2: Total number of length-at-age observations of sprat sampled by IMR in the time of year interval 01/11 – 15/12, from the Norwegian fjords since 1997 until today. Three periods of sampling are defined in the time series.

Year	NF	SF	Inner HF	Outer HF	Total
1997	100	137	224		**461**
1998	75	29	196	95	**395**
1999	96	360	163		**619**
2000	125	293	114		**532**
2001	48	35	116	50	**249**
2002	174	250	175	50	**649**
2005		187	114	119	**420**
2006	199	336	296	74	**905**
2007		248	171	95	**514**
2008	70	171	197		**438**
2015	178	432	272	110	**992**
2016	81	126	180	124	**511**
2017	54	119	147	27	**347**
2018	81	255	163	82	**581**
Total	**1281**	**2978**	**2528**	**826**	**7613**

To investigate whether there are significant differences in length-at-age within the fjords between the three periods of sampling, cumulative size distribution (CSD) and Kolmogorov-Smirnov test were used. CSDs are advantageous for visualizing size distributions and revealing growth patterns of groups in different environments (Folkvord et al. 2009). The Kolmogorov-Smirnov test tells the probability of two sets of samples drawn from the same (but unknown) probability distribution (Kolmogorov 1933, Smirnov 1939). Function ks.test() within the R package "dgof" (Arnold and Emerson 2011) was used to perform the test:

$$\mathrm{D} = \mathrm{Maximum} \mid \mathrm{F}_{\mathrm{n1}}(\mathrm{X}) - \mathrm{F}_{\mathrm{n2}}(\mathrm{X})$$

Where D is the maximum absolute difference between the two cumulative distribution functions, n1 is length observations of fjord 1, and n2 is length observations from fjord 2.

2.3.3. Analysis of length-at-age over three time periods

Investigation of whether there has been a change in length-at-age over the three time periods and detecting whether the potential increase/decline in length have been similar for the fjords were done using multiple linear models for each age separately:

$$\mathrm{Length}_{\mathrm{ij}} = \beta_0 + \beta_1 \mathrm{Fjord}_{\mathrm{i}} + \beta_2 \mathrm{Period}_{\mathrm{j}} + \beta_3 \mathrm{Fjord{:}\,Period}_{\mathrm{ij}} + \varepsilon_{\mathrm{ij}}$$

Spatial clustering was found in the data as sampling was done further inside NF and SF in period 3 (Appendix 2.1). Since the sampling procedure involves trawling where acoustic registrations were seen on the echogram, it is most likely that sprat were distributed further inside the fjord in this time-period. Temporal clustering was also found as sampling was conducted later in the year in period 2 and 3 (Appendix 2.3). The influence of spatial and temporal clustering was assumed to be minor, however, potential effects were considered in the discussion.

2.3.4. Analysis of effect of temperature and relative abundance on length

Temperature measurements were done with CTD. CTD-stations within the dates 01/11-15/12 for each year in the fjords NF, SF, and HF were used in analyse of temperature and relative abundance effect on length (Table 3). Mean temperature of 5-, 10-, 15- and 25-meter depth and for each station within the year were used. This is the depth at which sprat is mostly located. Every fifth meter was used since CTD measurements was done in these intervals in some of the earliest years, and consistency is emphasized.

Table 3: Number of ctd-samples within the dates 01/11-15/12 for each year in the fjords Nordfjord (NF), Sognefjord (SF) and Hardangerfjord (HF).

Year	NF	SF	HF
1997	2		5
1998	2		4
1999	2		4
2000	2		4
2001	2		8
2002	2		4
2005		3	4
2006	2	2	4
2007	2		4
2008	2	1	4
2015	2	28	13
2016		8	8
2017	2	12	10
2018	2	9	10

Biomass of 0-year and 1+-year olds have been estimated by IMR (Kvamme 2020). Since biomass has been estimated for the entire HF, outer and inner HF were treated as one for this analysis. By adding the year classes together, total biomass was found for each fjord. With the use of the database "hoydedata", the surface area of NF, SF, and HF were estimated to be 462 km^2, 1109 km^2, and 1222 km^2, respectively (Statens Kartverk 2021). Relative abundance per area was estimated by dividing total biomass by the surface area of the fjord. Log transformed relative abundance estimates were used (Figure 3).

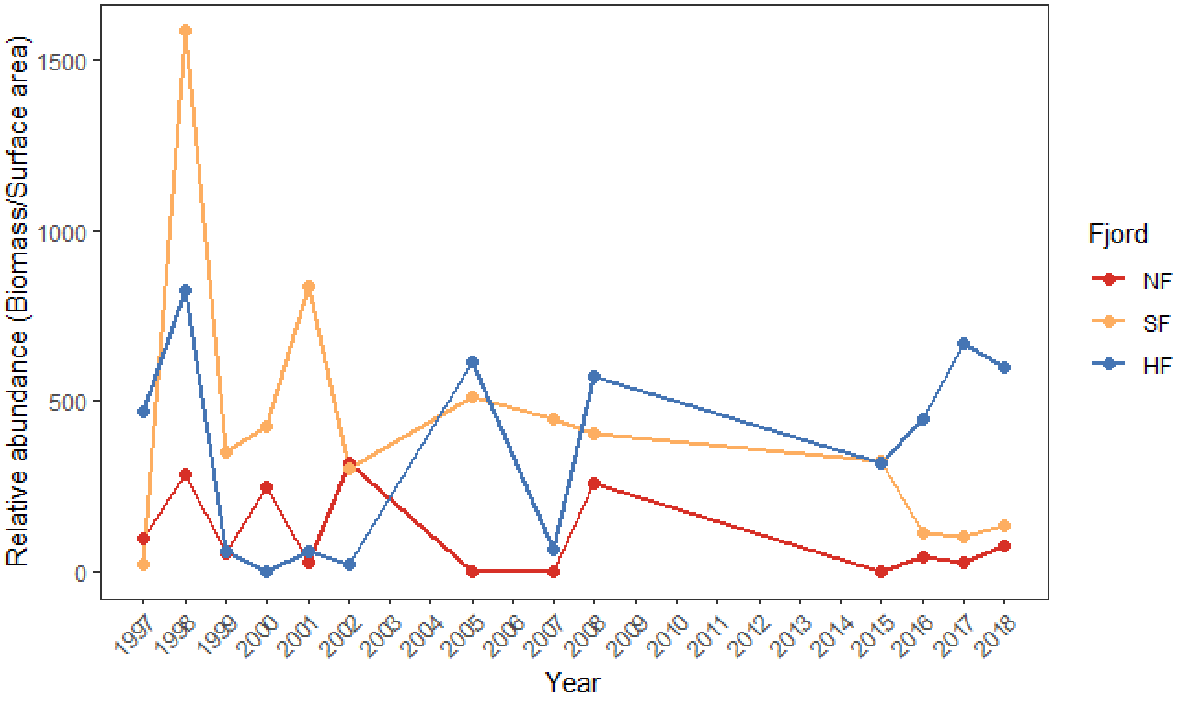


Figure 3: Relative abundance estimates over years in the Norwegian fjords Nordfjord (NF), Sognefjord (SF) and Hardangerfjord (HF). Total biomass has been estimated by IMR in November – mid December. Points show the biomass estimates used in the density-dependence analysis, while lines in between were added for visual purposes.

Linear mixed effect models were used to test if the length was related to temperature and/or abundance for each fjord and age:

$$\mathrm{Length}_{ij} = \beta_0 + \beta_1 \mathrm{Abundance}_i + \beta_2 \mathrm{Temperature}_j + \beta_3 \mathrm{Abundance{:}\,Temperature}_{ij} + \varepsilon_{ij}$$

In cases where the interaction was not significant, it was excluded.

2.3.5. Length-at-maturity

The R package sizeMat and function gonad_mature() with the Bayesian method was used in analyse of length-at-maturity (Torrejon-Magallanes 2020). Maturity stage 1-2 were categorized as immature, while 3-8 were categorized as mature (Mjanger et al. 2019). The length-at-maturity analysis was based on data from period 3, since maturity stage observations for mature and immature individuals were only available for period 3.

A group of individuals of age 2 and at 12-15 cm in length in NF raised concerns about the reliability of the maturity data as individuals within this group were characterised as “special stage” 1, 2, 3, and 8, while this group most allegedly are all mature (Figure 4). Special stage 1 is the immature juvenile phase; special stage 2 is immature, but sex can be determined; special stage 3 is maturing; while special stage 8 is resting. Sprats of age 2 at 12-15 cm are definitely not in the juvenile phase, while distinguishing between special stage 2 and 8 is challenging and has most likely been confounded (pers. Comm. Eilert Hermansen). On this basis, the immature age 2 observations in NF were all converted to be classified as mature. In addition, special stage 1 observations of age 2 and immature observations of age 3 were deleted.

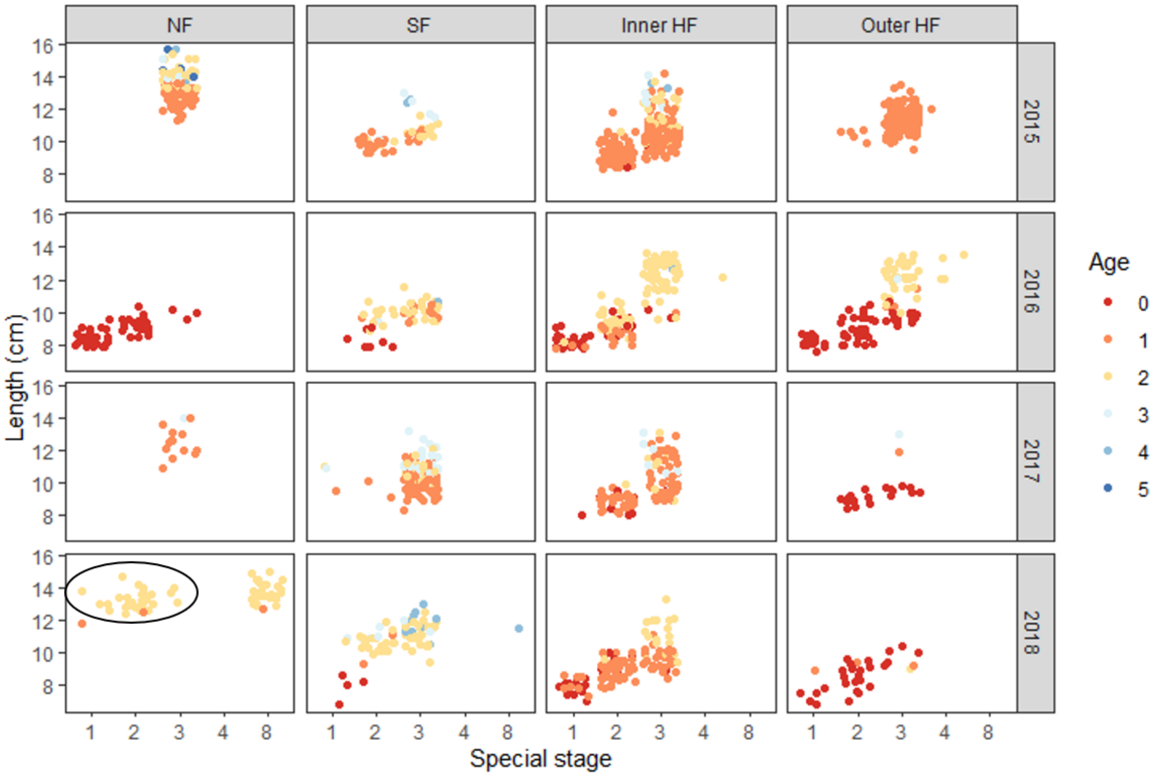


Figure 4: All maturity observations in the Norwegian fjords Nordfjord (NF), Sognefjord (SF), and inner and outer Hardangerfjord (HF) in the years 2015-2018 by length and age. Special stage 1 is the immature juvenile phase; special stage 2 is immature, but sex can be determined; special stage 3 and 4 is maturing; while special stage 8 is resting. Special stage 1 and 2 are classified as immature, while 3-8 as mature. The encircled immature age 2 observations in NF were all converted to mature for the estimation of length-at-maturity. In addition, the few cases of special stage 1 observations of age 2 and immature observations of age 3 were excluded from the analysis.

Some of the length-at-maturity graphs did not go through 0 and 100 percent mature. Length-observations where maturity stage was not determined was therefore used to force the graphs to be continuous (go from 0 to 100 percent mature); for each fjord, length-observations above maximum observed length of immature individuals was categorized as mature, while length-observations under minimum observed length of mature individuals were categorized as immature.

2.3.6. Analysis of condition

To analyse condition, mean LWR of all fjords was calculated. LWR are defined by Eqn. 2, and by logarithmic form in Eqn. 3 (Keys 1928):

$$W = aL^b \qquad \text{Eqn. 2}$$

$$\log W = \log a + b \log L \qquad \text{Eqn. 3}$$

where W is weight, L is length, a is the intercept, and b is the slope.

Equal numbers of randomly selected small, medium, and large observations per fjord and period were used to balance the relationship (Froese 2006). To compare condition between the fjords and periods, relative weight as percentage of mean weight (W_{rm}) was used:

$$W_{rm} = 100\ \frac{W}{a_m L^{b_m}} \qquad \text{Eqn. 4}$$

where W is weight, L is length, and a_m and b_m are derived from the mean LWR. ANOVA was used to test whether W_{rm} differed between the fjords and periods.

3. Results

3.1. Differences in growth between Norwegian fjords

Growth curves of sprat in the years 1996 – 2021 showed a higher asymptotic length for NF, and inner and outer HF ($L_\infty \approx 13$ cm) compared to SF ($L_\infty \approx 12$ cm) (Figure 5; Table 4; Appendix 3). The asymptotic length was reached at a slower rate ($K \approx 0.5$) in inner HF compared to NF and outer HF ($K \approx 0.9$ and $K \approx 1$, respectively).

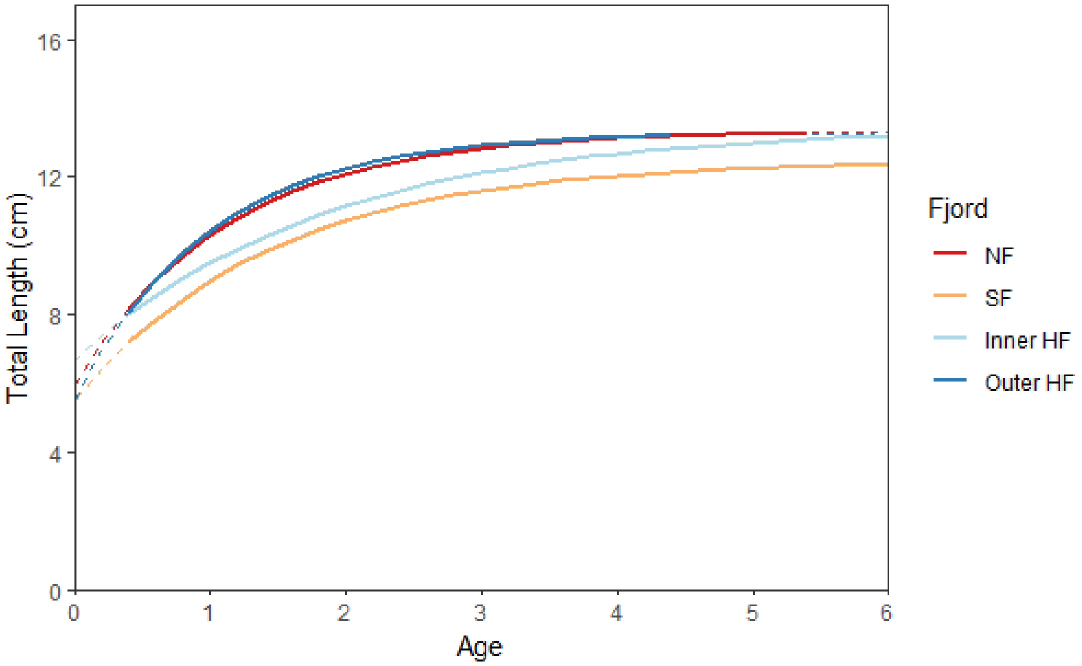


Figure 5: Von Bertalanffy growth curves fitted to length observations in the Norwegian fjords Nordfjord (NF), Sognefjord (SF), and inner and outer Hardangerfjord (HF) for the years 1996-2021. Spawning was assumed to be in the end of May (age = 0), and 1/12 age was added for each month (age 0.5 in the end of November). The solid lines are where observation of age have been made, while the dashed lines are a continuation of the fitted curve where observation of age has not been made.

Table 4: Parameters L_∞, K and t_0 estimated with VBGF for the Norwegian fjords Nordfjord (NF), Sognefjord (SF), and inner and outer Hardangerfjord (HF) for the years 1996-2021. Spawning was assumed to be in the end of May (age = 0), and 1/12 age was added for each month (age 0.5 in the end of November).

Fjord	L_∞	K	t_0
NF	13.336	0.893	-0.657
SF	12.474	0.691	-0.839
Inner HF	13.447	0.540	-1.268
Outer HF	13.293	1.001	-0.535

3.2. Differences in length-at-age between fjords

SF showed shorter cumulative size distributions for all ages and periods (Figure 6; Appendix 4.1). Inner HF and NF had a relatively similar cumulative size distribution, except for ages 1 and 2 for periods 2 and 3 where NF had larger sizes. Inner HF showed the largest size distribution for all ages and periods, except in period 3 for ages 1 and 2 and in period 2 for age 2 where NF had the largest sizes.

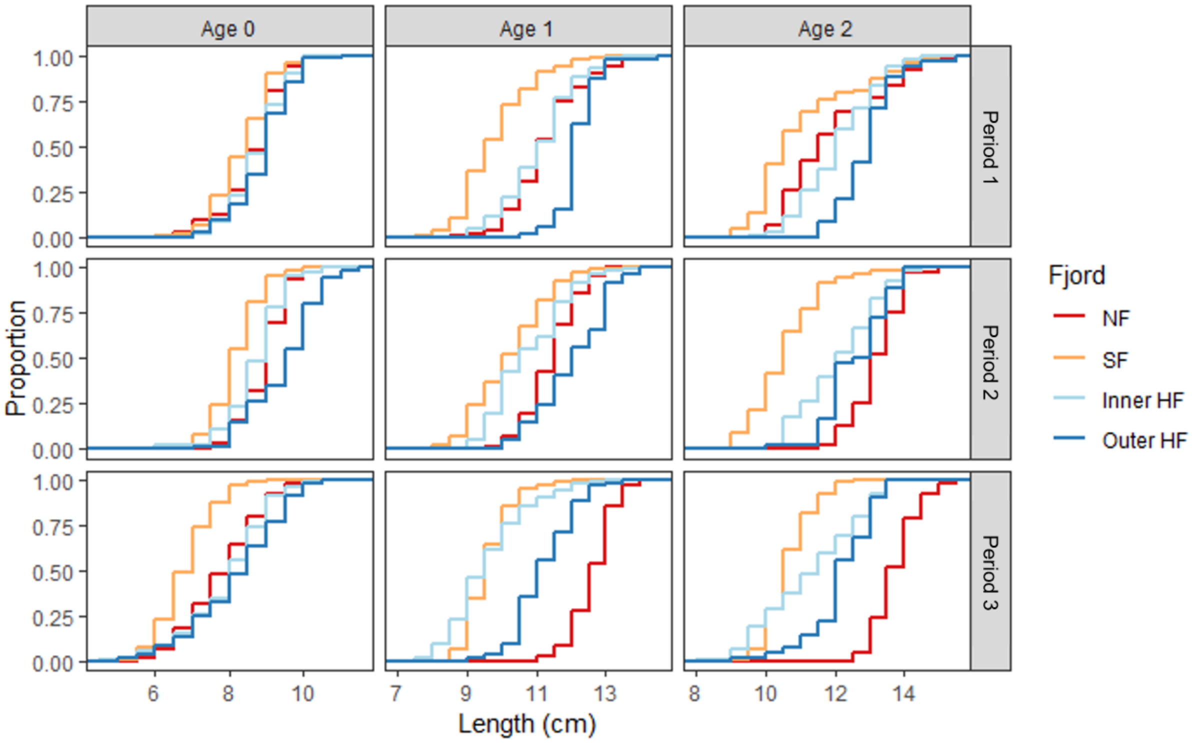


Figure 6: Cumulative size distributions (CSDs) of ages 0, 1 and 2 comparing the Norwegian fjords Nordfjord (NF), Sognefjord (SF), and inner and outer Hardangerfjord (HF) in the time periods 1997-2002 (Period 1), 2005-2008 (Period 2), and 2015-2018 (Period 3). Size is represented by length. SF shows the shortest size for all ages and periods, followed by inner HF and outer HF, respectively. NF show similar size as inner HF, except for age 1 and 2 in the last period, where size was largest among the fjords.

Considering differences in length-at-age between the fjords, SF showed the shortest length-at-age, followed by inner and outer HF, respectively (Figure 7; Appendix 5.2 – 5.7). NF showed similar lengths as inner HF, however, for age 2 in periods 2 and 3 and age 1 in period 3, length-at-age in NF were largest.

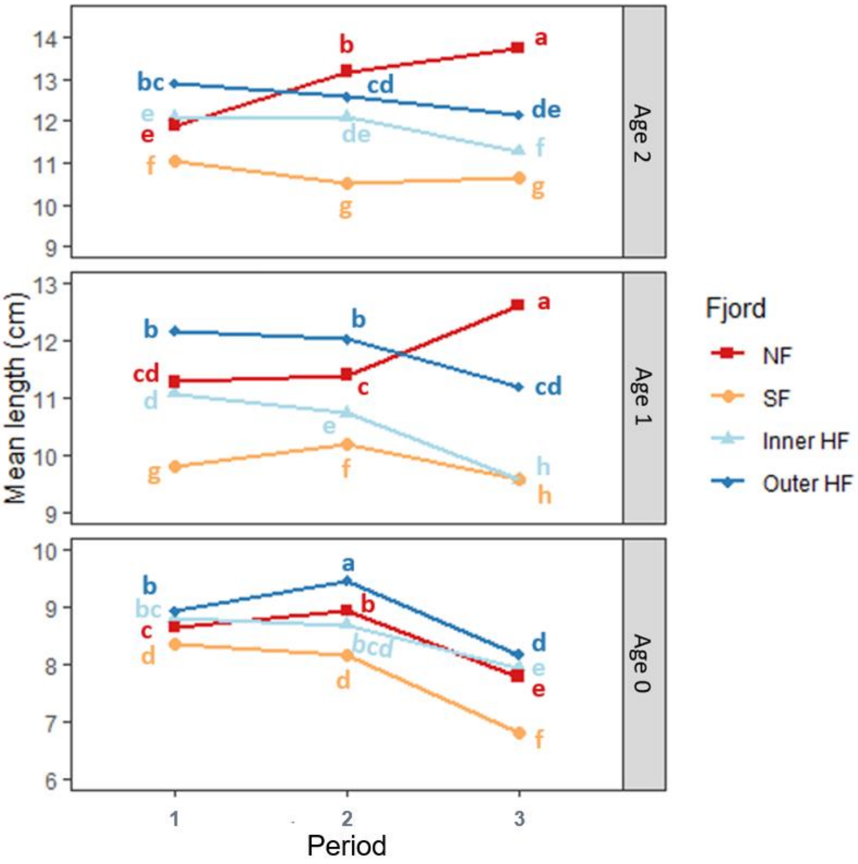


Figure 7: Mean length at age in the time periods 1997-2002 (Period 1), 2005-2008 (Period 2), and 2015-2018 (Period 3) for the Norwegian fjords Nordfjord (NF), Sognefjord (SF), and inner and outer Hardangerfjord (HF). The letters refer to homogenous groups, i.e., two points are statistically homogenous if they are marked with the same letter. The letters also refer to the order from largest to smallest group, meaning a is the largest group, b is the second largest, etc. The overall length-at-age decreased from the first to the last period for all ages and fjords, except for ages 1 and 2 in NF. Disregarding NF, sprat in outer HF was largest, followed by inner HF and NF, respectively.

3.3. Differences in length-at-age between time periods

Period 3 showed the shortest cumulative size distributions for all ages and fjords except for ages 1 and 2 in NF (Figure 8; Appendix 4.2). Periods 1 and 2 showed similar size distributions, except for age 2 in NF where period 1 had a much smaller size distribution.

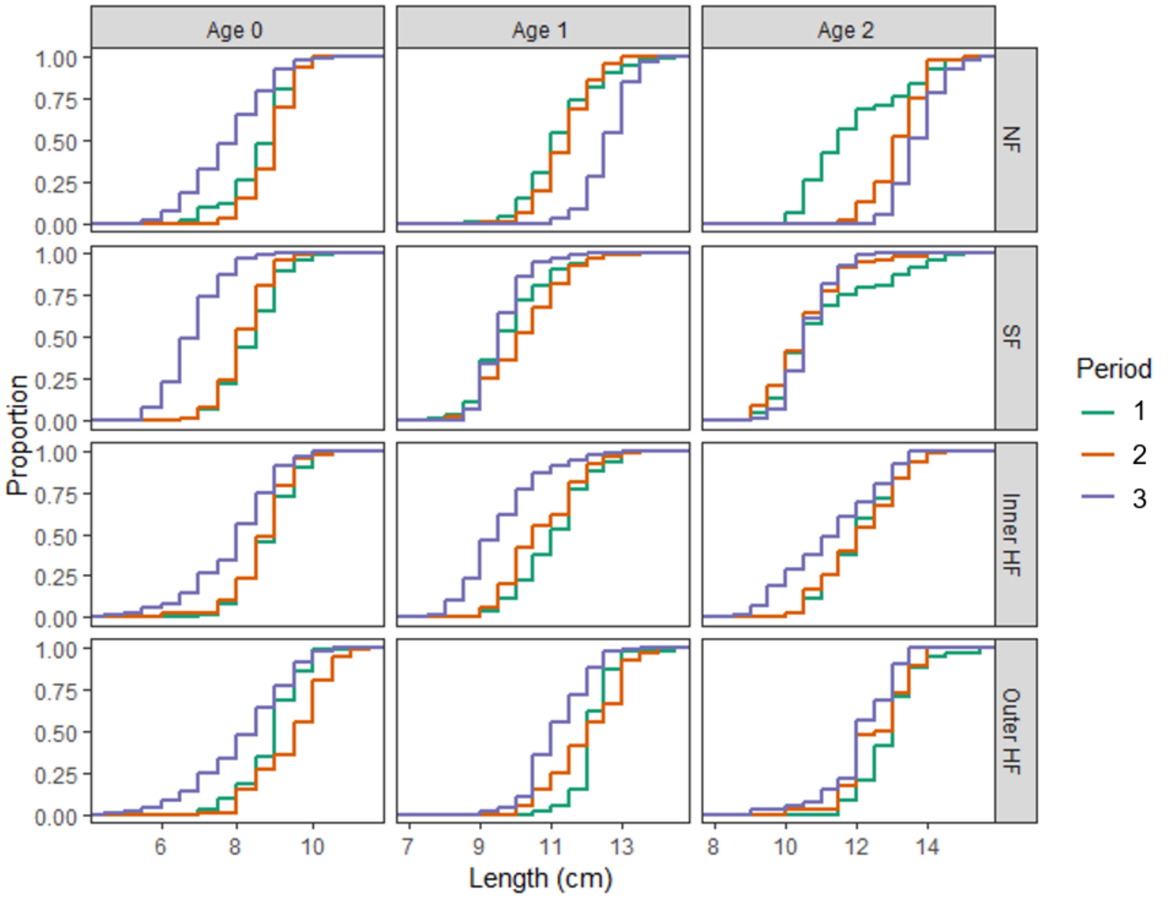


Figure 8: Cumulative size distributions (CSDs) of ages 0, 1, and 2 comparing the time periods 1997-2002 (Period 1), 2005-2008 (Period 2), and 2015-2018 (Period 3) in the Norwegian fjords Nordfjord (NF), Sognefjord (SF), inner and outer Hardangerfjord (HF). Size is represented by length. The period 3 shows the shortest sizes except for age 1 and 2 in NF. Period 1 and 2 show similar size distributions.

Considering differences in length-at-age between periods, a decrease was detected from period 1 to 3 for ages 0-2 in the fjords NF, SF, inner and outer HF, except in NF for ages 1 and 2 (Figure 7). Periods 1 and 2 showed similar length-at-age for most of the ages and fjords.

3.4. Temperature and relative abundance affect length-at-age

No interaction between relative abundance and temperature were found in SF and HF for ages 0 and 2, and the effect of these covariates varied with age and fjord. For age 0 in SF, the length decreased with temperature (P<0.001) (Table 8), while length increased with temperature for age 2 (P<0.001) (Table 10; Figure 9). Considering relative abundance, an increase was seen for age 0 in SF (P<0.001), while a decrease was seen for age 2 (P<0.001) (Figure 10). In HF, the models showed relatively low goodness of fit (age 0: R^2=0.11, age 2: R^2=0.02) (Table 11; Table 13).

An interaction term was included in the models for NF and for age 1 in SF and HF. The effect of temperature thereby depends on the level of relative abundance, and vice versa. For all ages in NF, length was largest at high abundance and high temperature (Table 5 – 7). For age 1 in SF, length was largest at low abundance and low temperature (Table 9). This was also the case for age 1 in HF, however, the effect was small, and the effect of temperature alone was insignificant (Table 12).

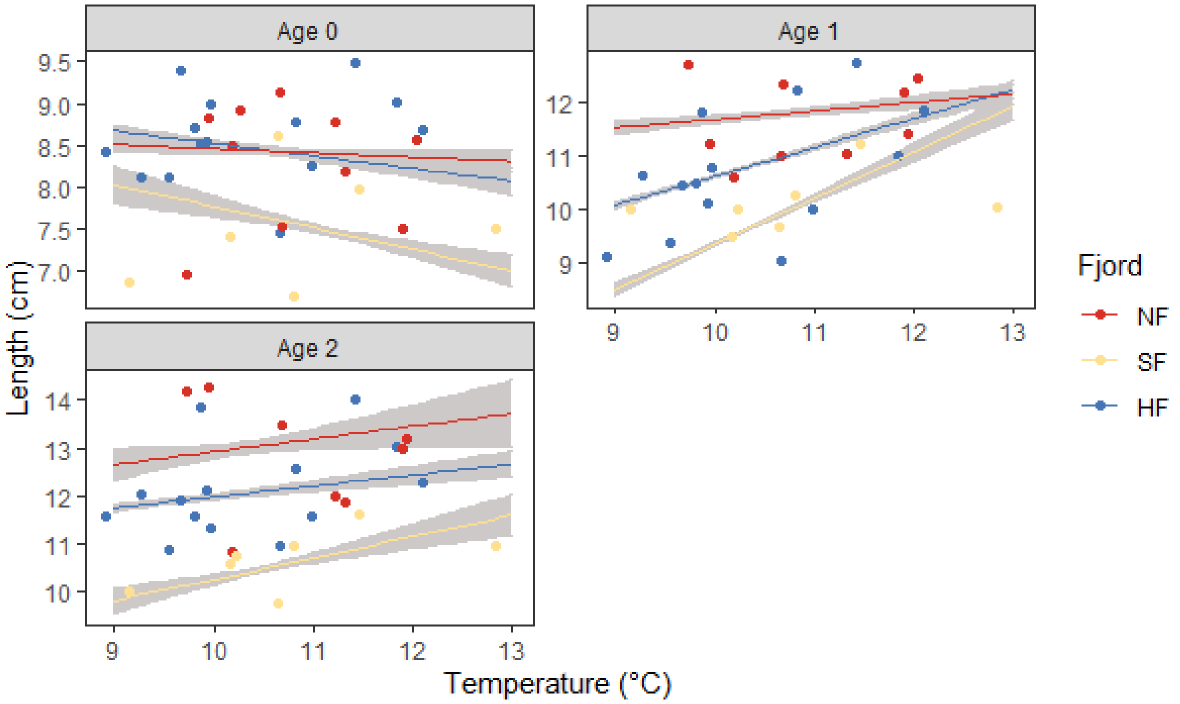


Figure 9: Predicted effect of temperature on length-at-age for the fjords Nordfjord (NF), Sognefjord (SF), and Hardangerfjord (HF) when log (biomass/surface area) was set to mean value. Ribbons are standard errors.

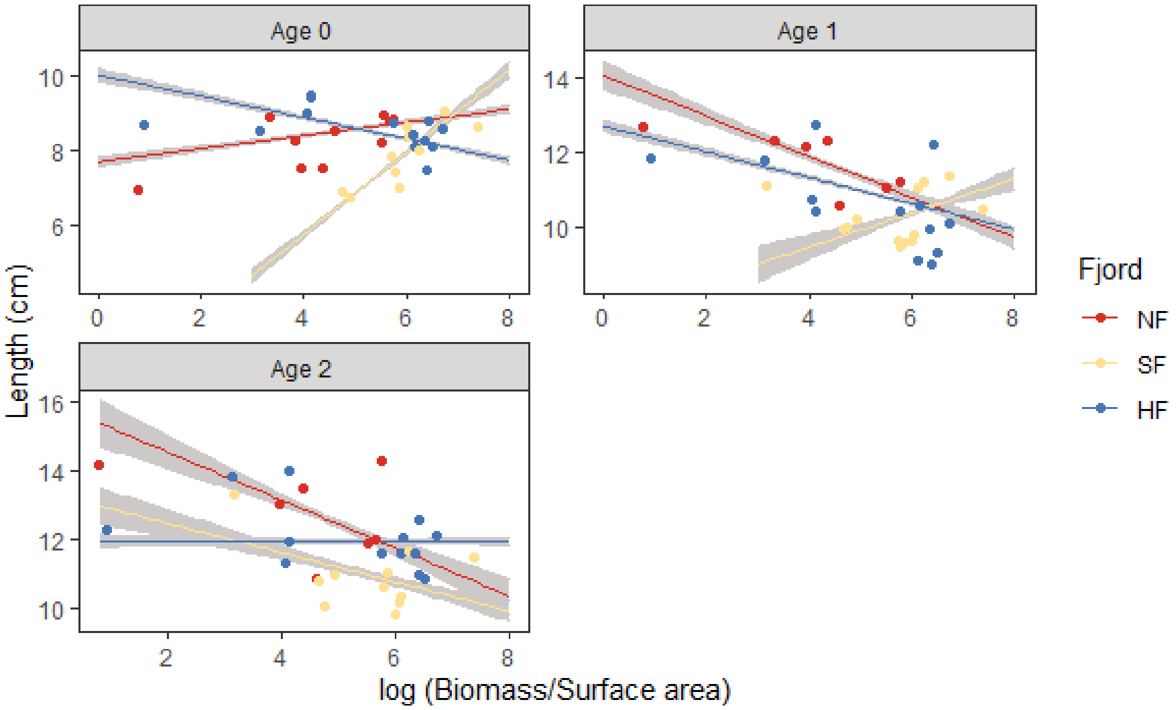


Figure 10: Predicted effect of relative abundance (log (Biomass/surface area)) on length-at-age for the fjords Nordfjord (NF), Sognefjord (SF), and Hardangerfjord (HF) when temperature is set to mean value. Ribbons are standard errors.

Table 5: Summary output from lm(Length ~ Abundance*Temperature) of age 0 in Nordfjord. Adjusted R^2 was estimated to 0.40.

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	-3.151	1.045	-3.014	<0.01
Abundance	2.915	0.259	11.228	<0.001
Temperature	1.014	0.104	9.733	<0.001
Abundance:Temperature	-0.256	0.025	-10.032	<0.001

Table 6: Summary output from lm(Length ~ Abundance*Temperature) of age 1 in Nordfjord. Adjusted R^2 was estimated to 0.36.

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	4.724	1.903	2.482	<0.05
Abundance	1.311	0.459	2.859	<0.01
Temperature	0.838	0.192	4.356	<0.001
Abundance:Temperature	-0.166	0.046	-3.621	<0.001

Table 7: Summary output from lm(Length ~ Abundance*Temperature) of age 2 in Nordfjord. Adjusted R^2 was estimated to 0.21.

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	-2.045	5.514	-0.371	0.711
Abundance	3.067	1.106	2.774	<0.01
Temperature	1.673	0.563	2.973	<0.01
Abundance:Temperature	-0.350	0.112	-3.117	<0.01

Table 8: Summary output from lm(Length ~ Abundance+Temperature) of age 0 in Sognefjord. Adjusted R^2 was estimated to 0.39.

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	3.590	0.478	7.503	<0.001
Abundance	1.109	0.076	14.617	<0.001
Temperature	-0.217	0.059	-3.697	<0.001

Table 9: Summary output from lm(Length ~ Abundance*Temperature) of age 1 in Sognefjord. Adjusted R^2 was estimated to 0.38.

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	66.983	6.441	10.398	<0.001
Abundance	-11.677	1.060	-11.018	<0.001
Temperature	-5.368	0.634	-8.466	<0.001
Abundance:Temperature	1.098	0.104	10.557	<0.001

Table 10: Summary output from lm(Length ~ Abundance+Temperature) of age 2 in Sognefjord. Adjusted R^2 was estimated to 0.18.

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	7.087	0.958	7.396	<0.001
Abundance	-0.425	0.108	-3.949	<0.001
Temperature	0.550	0.096	5.579	<0.001

Table 11: Summary output from lm(Length ~ Abundance+Temperature) of age 0 in Hardangerfjord. Adjusted R^2 was estimated to 0.11.

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	11.729	0.592	19.809	<0.001
Abundance	-0.287	0.029	-9.731	<0.001
Temperature	-0.168	0.050	-3.350	<0.001

Table 12: Summary output from lm(Length ~ Abundance*Temperature) of age 1 in Hardangerfjord. Adjusted R^2 was estimated to 0.16.

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	13.912	1.348	10.32	<0.001
Abundance	-1.601	0.239	-6.689	<0.001
Temperature	-0.116	0.131	-0.885	0.376
Abundance:Temperature	0.121	0.023	5.215	<0.001

Table 13: Summary output from lm(Length ~ Abundance+Temperature) of age 2 in Hardangerfjord. Adjusted R^2 was estimated to 0.02.

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	9.938	0.880	11.288	<0.001
Abundance	-0.001	0.039	-0.038	0.970
Temperature	0.202	0.073	2.764	<0.01

3.5. Differences in length-at-maturity between the fjords

Mature and immature observations in inner and outer HF show more overlapping compared to NF and SF (Figure 11). A second normal distribution can be visually detected in SF.

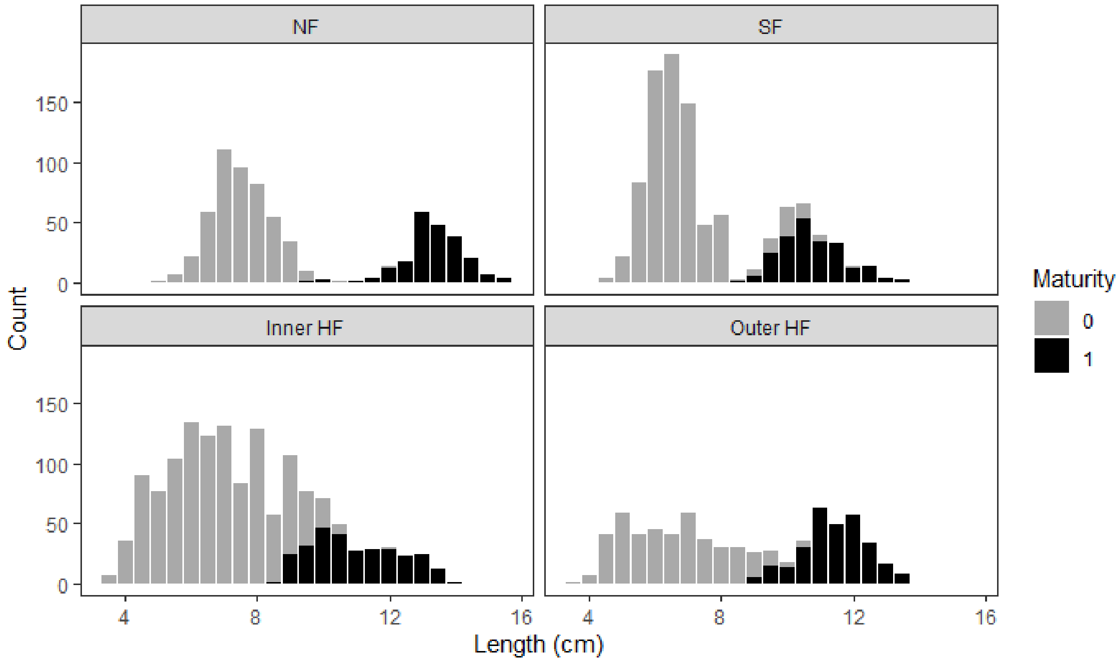


Figure 11: Number of immature and mature observations of sprat in the time period 2015-2018 in the Norwegian fjords Nordfjord (NF), Sognefjord (SF), and inner and outer Hardangerfjord (HF).

Length-at-maturity, represented by L_{50}, was at 10.6 cm for sprat in NF in period 3, while sprat in SF, and inner and outer HF mature at shorter lengths: 9.7, 9.7, and 9.5 cm, respectively (Figure 12; Table 20; Appendix 6).

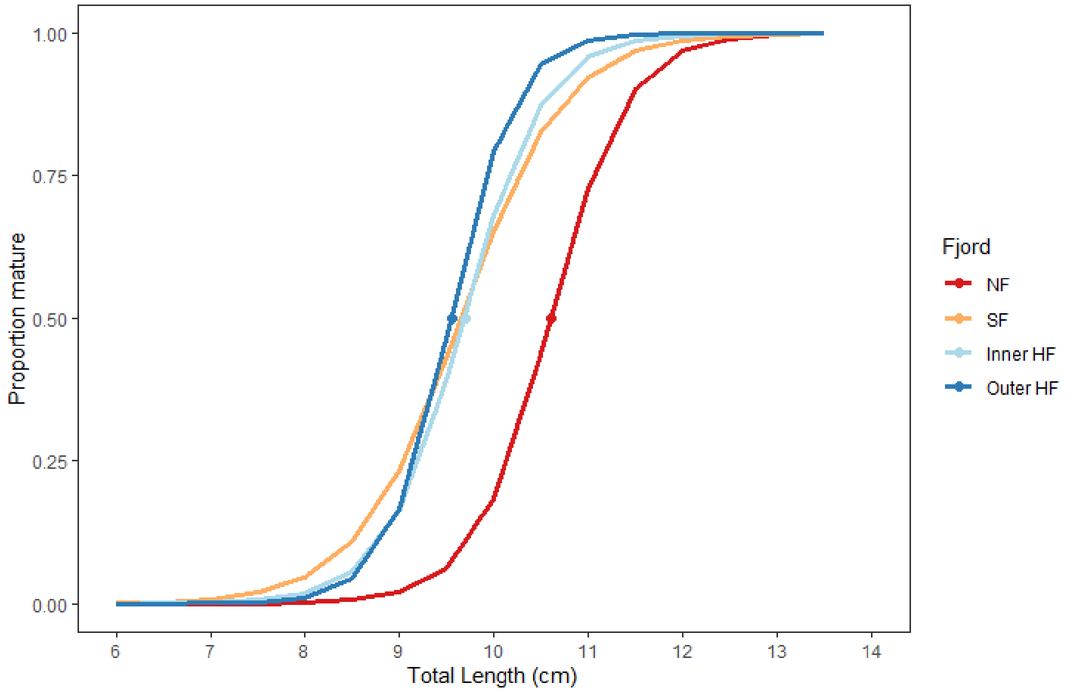


Figure 12: Estimated length at maturity of sprat in the Norwegian fjords Nordfjord (NF), Sognefjord (SF), and inner and outer Hardangerfjord (HF). Samples were taken November-December in years 2015-2018. The point resembles length at 50% maturity, which was estimated to be at 1 cm longer length in NF (L_{50} = 10.6) than in the three other fjords ($L_{50} \approx 9.6$).

Table 14: Estimated length at 50% maturity (L_{50}), confidence intervals, and R-squared (R^2) for sprat in the Norwegian fjords Nordfjord (NF), Sognefjord (SF), and inner and outer Hardangerfjord (HF). Samples were taken November-December in years 2015-2018.

	L_{50}	Confidence intervals	R^2
NF	10.6	10.2 – 11	0.98
SF	9.7	9.5 – 9.8	0.82
Inner HF	9.7	9.6 – 9.8	0.82
Outer HF	9.5	9.4 – 9.7	0.94

3.6. Differences in condition between the fjords

The mean a and b parameters were derived from the mean LWR, and were estimated to be 0.00601 and 3.03, respectively (Appendix 7.1). The difference in W_{rm} between the fjords varied with period (Figure 13; Appendix 7.2 and 7.3). In period 1, inner HF had significantly lower condition than NF and SF ($P<0.001$). In period 2, NF had the lowest condition ($P<0.05$ with SF; $P<0.01$ with outer HF; $P<0.001$ with outer HF), while SF had lower condition than outer HF ($P<0.001$). Inner HF had significantly lower condition than NF in period 3 ($P<0.01$). An overall decline in condition from period 1 to 3 is seen in all fjords ($P<0.001$).

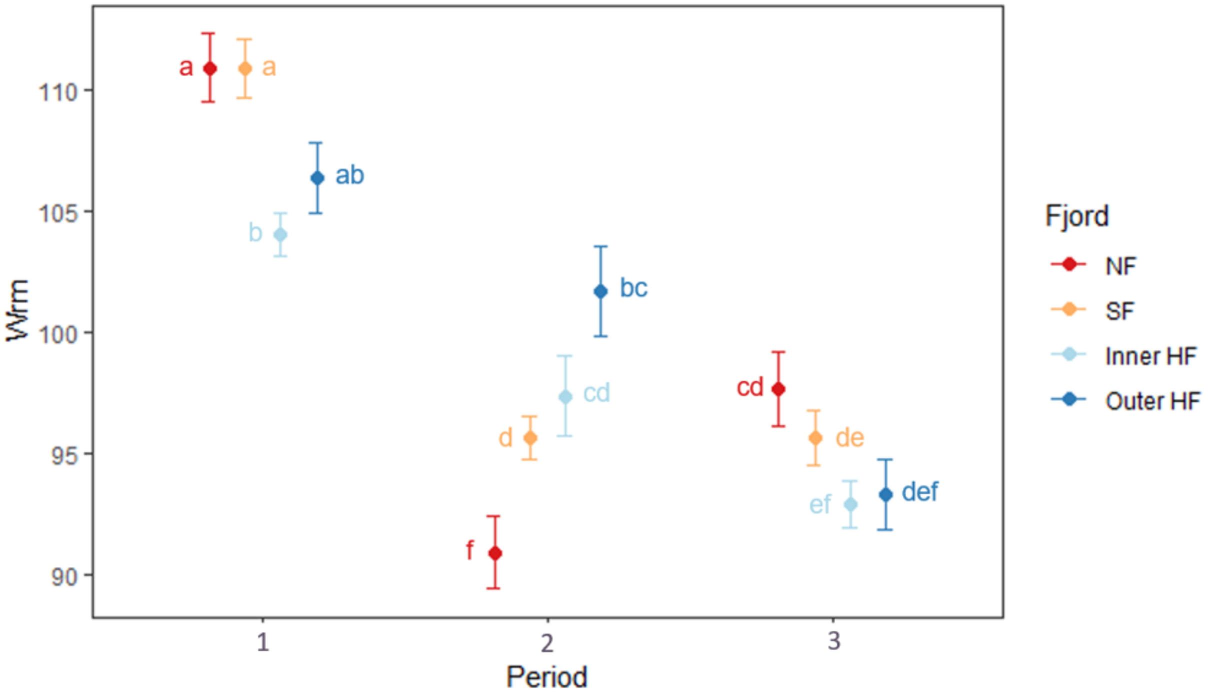


Figure 13: Mean and confidence intervals of relative weight as percentage of mean weight (W_{rm}) for the three time periods 1997-2002 (Period 1), 2005-2008 (Period 2), and 2015-2018 (Period 3) in the Norwegian fjords Nordfjord (NF), Sognefjord (SF), inner and outer Hardangerfjord (HF).

4. Discussion

This thesis compared life history traits, specifically, growth, length-at-age, length-at-maturity, and condition of sprat between Nordfjord, Sognefjord, and Hardangerfjord, to gain insight into the potential population structure of the fjords. Systematic differences in traits between the fjords were found, indicating that adult individuals mostly stay within their respective fjord. It was also tested whether environmental factors could explain some of the observed variation in length-at-age. The impact of temperature and the effect of density-dependence on sprat length showed differing results with fjord, suggesting unique characteristics in the fjords and followingly phenotypic response in the local sprat.

4.1. Differences in life history traits between the fjords

The current study showed that SF had shorter length-at-age, followed by inner and outer HF, respectively. Meanwhile, NF had similar length-at-age as inner HF, except for ages 1 and 2 in periods 2 and 3. Due to the geographic location of the fjords, possible exchange of sprat between the fjords is most likely between NF and SF or between SF and HF. The structural differences in length-at-age between SF and outer HF and between SF and NF suggest that the sprat most likely have been experiencing the same conditions within their respective fjords over a prolonged time and that the level of mixing between the fjords is low. This is especially evident for NF, as this fjord does not follow the same temporal pattern of declining lengths-at-age as SF and HF. The reason for the large sprat of ages 1 and 2 in period 3 in NF is either due to immigration of larger non-local sprat or due to local sprat experiencing favourable growth conditions. The smallest sprat was found in SF, and migration from this fjord to NF is therefore not likely.

The result from investigation of differences in length-at-maturity emphasize that sprat in NF differs in dynamics compared to the other fjords. Since sprat in NF reached a larger size in period 3, they also mature at a larger size. Maturation at a small size is related to reduced adult survival, and earlier studies have found increased exploitation to be the explanation for reduced length-at-maturity in herring (Engelhard and Heino 2004). It is difficult to determine whether changes in length-at-age and length-at-maturity are due to phenotypic plasticity or evolutionary responses (Engelhard and Heino 2004, Hunter et al. 2019). However, changes in growth and length-at-maturity in small pelagic fish are often thought to be due to plastic responses likely related to stock abundance and temperature (Hunter et al. 2019). This suggests that NF has a larger length-at-age and length-at-maturity in period 3 due to lower abundance and/or favourable temperature conditions.

SF, inner and outer HF showed a similar length-at-maturity while differing in length-at-age in the same period. This means that in inner HF and SF, some individuals waited an additional year (and thereby reached a larger length) before spawning, compared to outer HF. These results could indicate that sprat in SF and inner HF do not manage to grow to a sufficient size for maturation as fast as sprat in outer HF and NF. This is possibly due to less favourable growth conditions in terms of abundance and temperature in SF and inner HF compared to outer HF (Hunter et al. 2019).

Comparisons of conditions showed relatively similar factors between the fjords, but with some variations where a clear pattern is difficult to distinguish. Condition and growth are not always correlated (Sinovčić et al. 2008), and this seems to be the case in the current study. Condition is thought to mainly be affected by food availability in clupeoids (Brosset et al. 2015), and the results can thereby indicate similar feeding conditions between the fjords.

4.2. Temperature and density-dependence as explanatory variables for variation in length-at-age

A combination of external and internal factors is thought to determine the spatial and temporal heterogeneity of life history traits of sprat in the fjords. It was attempted to reveal the effect of temperature and density-dependence, which is considered important influential factors (Ward et al. 2006, Frisk et al. 2015, Hunter et al. 2019). The response of temperature and density-dependence on length-at-age were variable and dependent of fjord and age. Relationships of length-at-age and environmental variables are known to vary in their effect over time and locations due to growth being a complex process influenced by multiple selection forces (Drinkwater et al. 2013). Length-at-age increased with both temperature and relative abundance in NF, which can explain the larger length-at-maturity and length-at-age relative to the other fjords. The positive correlation between relative abundance and length in NF could be explained by relative abundance being collinear with favourable environmental conditions. NF has a lower relative abundance than the two other fjords of investigation, potentially causing the abundance not to be sufficiently high to cause density-dependence, but rather be a sign of higher survival and/or recruitment due to favourable environmental conditions. Apparent density independence has also been seen in earlier studies, and proposed explanations are that growth was rather driven by other environmental factors (Lorenzen and Enberg 2002). Even though sprat in NF were not proven to experience density-dependent growth, it does not exclude that they would have intra-specific density-dependent growth if abundance were sufficient. Sprat could also be contributing to just a small percentage of the pelagic fish of the fjord, but the potential effect of inter-specific density-dependence was not investigated. Inter-specific density-dependence has for example been found for sprat in the Baltic Sea competing with herring (Cardinale et al. 2002, Casini et al. 2006).

Length decreased with temperature for age 0 in HF and SF, while an increase was seen for age 2 in these fjords. SF age 2 and HF age 0 showed signs of density-dependent growth. However, temperature and relative abundance did not explain the variation in length-at-age in HF very well. This could be because the two different parts of the fjord, inner and outer HF, had to be merged. The parts differ in topography, where outer HF is much more open and connected to the cost, whereas the narrower inner HF with an additional sill separating it from the coast, is more isolated (Stigebrandt 2001). Looking at length-at-age alone in the fjord, sprat in outer HF was proven to be larger than in inner HF, indicating that sprat in these parts differ in their growth dynamics. Since the abundance of HF is relatively similar to the level in SF, density-dependent growth could likely also be the case here.

Analysis with density-dependence and temperature as explanatory variables provides insight into the fjord characteristics and followingly the causes for the phenotypic variation between the fjords. The results indicate that the low length-at-age in SF can, at least partly, be explained by the high abundance, while the larger length-at-age in NF can be explained by the low abundance. With differing growth and abundance dynamics, productivity and hence the fjords' ability to provide fisheries can be expected to differ. Separate quotas for each fjord should therefore continue to be set.

4.3. Differences in length-at-age and condition over time

A temporal decline in length-at-age and condition was detected in all fjords (except length of age 1 and 2 in NF). This is in accordance with investigations throughout the distribution of European sprat: a decline in condition of sprat has been seen in the Baltic Sea due to density-dependence and increased abundance (Cardinale et al. 2002, Casini et al. 2006); declines in length-at-age and condition have been observed in sprat and other clupeoids in the Mediterranean due to food limitations (Van Beveren et al. 2014, Brosset et al. 2017); and declining lengths-at-age have been found in sprat and other forage fish in the North Sea due to warmer temperatures (Baudron et al. 2014) and a shift in the plankton community both in terms of availability and composition (Defriez et al. 2016, Clausen et al. 2018). The explanations for the inter-annual variability in condition are mainly related to food availability, and this is highlighted as the reason for the decline in sprat condition in the Norwegian fjords. Falkenhaug and Dalpadado (2014) studied feeding ecology of sprat in HF and found its diet to be diverse and consisting of both zooplankton and phytoplankton, with copepods as the most important prey. The composition of the zooplankton community in western Norwegian fjords is found to be determined by both local production and by supplied advection from coastal waters (Salvanes et al. 1995). A similar shift in plankton community seen in the North Sea could also be the case in the relatively geographically close western Norwegian fjords, either through reduced local zooplankton production and/or less advected prey, with declining conditions as a result.

The decline in length-at-age could be explained by the same factors as the decline in condition, i.e., due to food limitations (Clausen et al. 2018), however, this makes it difficult to explain the increase in length at age 1 and 2 in NF. As growth is a complex process, multiple factors may interact, and the main driving force may be shifting (Drinkwater et al. 2013). The distinct overall temporal trend in NF suggests a different influential factor acting as a driving force for growth in NF. Other studies relate a decrease in length-at-age in temperate stocks to climate change (Baudron et al. 2014, Ikpewe et al. 2021) with TSR as reasoning. This has also been reported in the closely related herring (Claireaux et al. 2022, Smoliński and Berg 2022). Earlier studies have also suggested that the reported darkening of coastal waters can cause more challenging conditions for visual predation (Aksnes 2007, Aksnes et al. 2009). As sprat is a visual predator (Falkenhaug and Dalpadado 2014), this could be an additional explanation for the decline in length-at-age. Temporally declining lengths-at-age and conditions is a phenomenon seen in many small pelagic fish (reviewed in Peck et al. (2021)). Apart from the factors mentioned, Peck et al. (2021) point at impact of hypoxia and heatwaves as knowledge gaps in need of further research.

4.4. Limitations of this study

4.4.1. Mixing of early life stages

Due to sprat spawning in May-June while sampling was conducted in November – December, this study addresses mixing of sprat of approximately half a year old and above. Limitations to this study that aims to investigate mixing of sprat between fjords are thereby the potential mixing that may occur between spawning and until they are half a year old. Pelagic eggs and larvae of fish are to a large extent passively dispersed with water advection. Connectivity of coastal waters and basin water from fjords is largely determined by the topographic properties of the fjord (the depth of the sill and the length and width of the fjord) and variability in the wind regime (Aksnes et al. 1989). Advection of early life stages of fish is likely to occur occasionally with outgoing currents (Asplin et al. 1999). The Norwegian spring spawning herring (NSSH) spawns at the Norwegian coast, and larvae are dispersed with the Norwegian Coastal Current (NCC) up to the Barents Sea (Sætre et al. 2002). It can be expected that when the wind regime allows it, early life stages of sprat are driven out of the fjords and dispersed likewise with the NCC and end up in a different fjord (Asplin et al. 1999). With interannual variability in outgoing currents from the fjords, interannual variations in larval dispersal of sprat is consequently seemingly. Likewise, interannual variability in the distribution pattern of NSSH is common (Sætre et al. 2002). Since the current thesis suggests low mixing of adult sprat, while no genetic differences are found between the fjords (Quintela et al. 2020), the gene flow most likely occurs with dispersal of early life stages. The genetic isolation of sprat in each fjord would followingly be determined by the rate of outgoing currents.

4.4.2. CTD-data - a snapshot

The use of temperature data from CTD sampling conducted on the coastal sprat cruise only provides a snapshot of the temperature in the fjord regime. The sprat had experienced other temperatures than just the temperature measured when they were caught. This issue increase with age; where for example sprat of age 2 caught in November – December has experienced 2.5 years of temperature fluctuations. Despite this, significant increase in length-at-age with temperature was found for most fjords and ages, proposing that the measured temperature might have been representative for the fjord regime.

4.4.3. Cross-sectional study design

A limitation to the study is the gaps in the time series that limit the possibility of studying true cohorts from birth to death. These cohorts are therefore not followed over time in the length-at-age analysis. It is still suggested that the adult sprat perform low mixing between fjords due to prolonged exposure to the same habitat with the same conditions. The cross-sectional study design (using multiple periods, also referred to as cross-sectional study design (Wang and Cheng 2020)) adds uncertainty as there is a lack of knowledge of the length before and after sampling. However, as several cross-sections (the three periods) have been investigated, clear systematic differences can still be seen.

4.5. Potential sources of error

4.5.1. Spatial and temporal clustering

Spatial and temporal variability in sampling can cause false conclusions where potential significant differences between years in reality are caused by differences in where and when sampling was done. Growth of fish at low trophic levels has been documented to be less in inner parts of the fjord (Salvanes et al. 1995). Spatial clustering was detected in SF and NF with sampling further inside the fjord in period 3 compared to the earlier periods (Appendix 2.1). In NF, lengths at ages 1 and 2 increased in period 3, indicating that the spatial clustering did not affect the results. Lengths-at-age decreased in period 3 in SF, and concerns about whether the decline was due to spatial clustering could be made. However, since the sampling method was based on opportunistic hauls where sprat is recognized in the echogram, it is most likely that sprat was distributed further within the fjord in period 3 compared to the earlier periods. Interannual variability in the horizontal distribution of sprat has been detected in Norwegian fjords (Falkenhaug and Dalpadado 2014). In addition, overwintering further within the fjord is a common behaviour of sprat (Kaartvedt et al. 2009). The sampling in period 3 were conducted almost a month later than in period 1 (Appendix 2.3), and it is conceivable that the sprat have had time to migrate further within for overwintering in period 3. Sprat often inhabit innermost parts of a fjord, and migrations are conducted to inhabit more preferable conditions, for example in terms of predator avoidance or competition (Maes and Ollevier 2002, Kaartvedt et al. 2009). It is therefore likely that the sprat had shifted strategy and was distributed further within the fjord to achieve more favourable conditions, and that the decline in length-at-age in SF would have been the same or even more significant if they had been distributed equally in the periods.

Based on the sum of the listed arguments, it was assumed that the spatial clustering was due to interannual variation in distribution and that the effects were minor.

4.5.2. The reliability of the maturity-data

I am certain that some of the sprat were categorized with the wrong maturity stage. Since quite many samples were wrongly categorized, questions were raised concerning the reliability of the method and thereby whether the extent of the mistakes were more significant than what was dealt with here. However, the results are reasonable with logical explanations in accordance with the length-at-age analysis (see section 4.1.). They should nevertheless be confirmed, and further analyses should study histology samples of the gonads to do so.

4.5. Further investigations

The primary limitations to the current study are the mixing that potentially occurs in early life stages through dispersal with water currents. Some studies of current systems have been conducted in HF in particular (Asplin et al. 2014), while hydrodynamic models have been made for more general interpretations of fjord systems (Asplin et al. 1999). However, such studies lack from Nordfjord and Sognefjord, and future studies should aim at providing insight to current systems and planktonic dispersal in these fjords specifically. Hydrodynamic models (Asplin et al. 1999) could be used to indicate years where more connectivity between the fjords is possible.

The suggested explanations for the decline in length-at-age and condition, i.e., temperature increase due to climate change, regime shift in the zooplankton community, and darkening of coastal waters, should be investigated further and predictions should be assessed. Species distribution models can be used to predict spatial and temporal distribution with use of environmental data (Melo-Merino et al. 2020, Lindegren et al. 2022). Future monitoring of the spatial heterogeneity of life history traits is important both in terms of population structure and to detect potential interannual changes in the traits, especially considering the increasing concern of climate change and increased anthropogenic disturbance.

4.6. Conclusion

Investigation of life history traits is a cost-effective supplement to genetic studies investigating population structure due to the traits already being routinely sampled on the coastal sprat cruise. The current thesis has shown systematic differences in life history traits of sprat between the western Norwegian fjords, indicating low mixing of adult sprat between the fjords. Most prominent were differences in length-at-age, where outer HF showed largest lengths, followed by inner HF and SF, respectively. NF had similar lengths as inner HF except for ages 1 and 2 in period 3 where sprat of NF was largest of all fjords. Temperature and density-dependence were investigated as explanations for the spatial and temporal variability, and the results varied with age and fjord, indicating unique characteristics and dynamics of sprat in the specific fjords. Density-dependent growth was found in SF, but not in NF, suggesting this to be the main reason for the smaller length-at-age in SF compared to NF. The models showed low goodness of fit in HF, most likely since this fjord is diverse and sprat differs in growth dynamics between the inner and outer part. A temporal decline in length-at-age and condition were also found in all fjords (except length at age 1 and 2 in NF). Similar results for pelagic fish have been found by other researchers, where declining length-at-age and condition are caused by climate change resulting in a shift in the zooplankton community, in which sprat preys on, and increasing temperatures.

Despite no genetic differences found in earlier studies, this thesis suggests, based on differences in life history traits, that sprat in the Norwegian fjords to some extent are population structured. This can have consequences for management, and quotas should therefore continue to be set for each fjord.

5. References

Aksnes, D. 2007. Evidence for visual constraints in large marine fish stock. Limnology and Oceanography **52**:198-203.

Aksnes, D., J. Aure, S. Kaartvedt, T. Magnesen, and J. Richard. 1989. Significance of advection for the carrying capacities of fjord populations. Marine Ecology Progress Series **50**:263-274.

Aksnes, D., N. Dupont, A. Staby, Ø. Fiksen, S. Kaartvedt, and J. Aure. 2009. Coastal water darkening and implications for mesopelagic regime shifts in Norwegian fjords. Marine Ecology Progress Series **387**:39-49.

Alheit, J. 1989. Comparative spawning biology of anchovies, sardines, and sprats.

Arnold, T. A., and J. W. Emerson. 2011. Nonparametric Goodness-of-Fit Tests for Discrete Null Distributions. The R Journal **3**:34--39.

Asplin, L., I. A. Johnsen, A. D. Sandvik, J. Albretsen, V. Sundfjord, J. Aure, and K. K. Boxaspen. 2014. Dispersion of salmon lice in the Hardangerfjord. Marine Biology Research **10**:216-225.

Asplin, L., A. G. V. Salvanes, and J. B. Kristoffersen. 1999. Nonlocal wind-driven fjord-coast advection and its potential effect on plankton and fish recruitment. Fisheries Oceanography **8**:255-263.

Atkinson, D. 1994. Temperature and organism size-A biological law for ectotherms? Advances in Ecological Research 25: 1. Res. **25**.

Bagenal, T., and F. W. Tesch. 1978. Age and growth, In: Bagenal, T. (Ed.), Methods for assessment of fish production in fresh water, Handbook 3. Blackwell Scientific publications:101-136.

Barneche, D., D. R. Robertson, C. White, and D. Marshall. 2018. Fish reproductive-energy output increases disproportionately with body size. Science **360**:642-645.

Baudron, A. R., C. L. Needle, A. D. Rijnsdorp, and C. Tara Marshall. 2014. Warming temperatures and smaller body sizes: synchronous changes in growth of North Sea fishes. Global Change Biology **20**:1023-1031.

Begg, G., and J. Waldman. 1999. An holistic approach to fish stock identification. Fisheries Research **43**:35-44.

Begg, G. A., K. D. Friedland, and J. B. Pearce. 1999. Stock identification and its role in stock assessment and fisheries management: an overview. Fisheries Research **43**:1-8.

Bernardo, J. 1996. Maternal Effects in Animal Ecology1. American Zoologist **36**:83-105.

Bertalanffy, L. 1934. Untersuchungen über die Gesetzlichkeit des Wachstums. Wilhelm Roux' Archiv für Entwicklungsmechanik der Organismen **131**:613-652.

Bœuf, G., and P. Payan. 2001. How should salinity influence fish growth? Comparative Biochemistry and Physiology Part C: Toxicology & Pharmacology **130**:411-423.

Brosset, P., J.-M. Fromentin, E. Van Beveren, J. Lloret, V. Marques, G. Basilone, A. Bonanno, P. Carpi, F. Donato, V. Čikeš Keč, A. De Felice, R. Ferreri, D. Gašparević, A. Giráldez, A. Gücü, M. Iglesias, I. Leonori, I. Palomera, S. Somarakis, V. Tičina, P. Torres, A. Ventero, B. Zorica, F. Ménard, and C. Saraux. 2017. Spatio-temporal patterns and environmental controls of small pelagic fish body condition from contrasted Mediterranean areas. Progress in Oceanography **151**:149-162.

Brosset, P., F. Ménard, J. Fromentin, S. Bonhommeau, C. Ulses, J. Bourdeix, J. Bigot, E. Van Beveren, D. Roos, and C. Saraux. 2015. Influence of environmental variability and age on the body condition of small pelagic fish in the Gulf of Lions. Marine Ecology Progress Series **529**:219-231.

Cardinale, M., M. Casini, and F. Arrhenius. 2002. The influence of biotic and abiotic factors on the growth of sprat (*Sprattus sprattus*) in the Baltic Sea. Aquatic Living Resources **15**:273-281.

Casini, M., M. Cardinale, and J. Hjelm. 2006. Inter-annual variation in herring, *Clupea harengus*, and sprat, *Sprattus sprattus*, condition in the central Baltic Sea: what gives the tune? Oikos **112**:638-650.

Casini, M., G. Kornilovs, M. Cardinale, C. Möllmann, W. Grygiel, P. Jonsson, T. Raid, J. Flinkman, and V. Feldman. 2011. Spatial and temporal density dependence regulates the condition of central Baltic Sea clupeids: compelling evidence using an extensive international acoustic survey. Population Ecology **53**:511-523.

Cerri, R. D. 1983. The effect of light intensity on predator and prey behaviour in cyprinid fish: Factors that influence prey risk. Animal Behaviour **31**:736-742.

Claireaux, M., F. Zimmermann, B. Ernande, M. Heino, and K. Enberg. 2022. Environmental drivers of herring growth and how the perception shifts with time series length. Canadian Journal of Fisheries and Aquatic Sciences **0**:1-9.

Clausen, L. W., A. Rindorf, M. van Deurs, M. Dickey-Collas, and N. T. Hintzen. 2018. Shifts in North Sea forage fish productivity and potential fisheries yield. Journal of Applied Ecology **55**:1092-1101.

Coull, K. A., A. S. Jermyn, A. W. Newton, G. I. Henderson, and W. B. Hall. 1989. Length/Weight relationships for 88 fish species encouteres in the north- east Atlantic. Scottish Fisheries Research Report.

Cury, P. 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in “wasp-waist” ecosystems. ICES Journal of Marine Science **57**:603-618.

Daufresne, M., K. Lengfellner, and U. Sommer. 2009. Global warming benefits the small in aquatic ecosystems. Proceedings of the National Academy of Sciences **106**:12788-12793.

Defriez, E. J., L. W. Sheppard, P. C. Reid, and D. C. Reuman. 2016. Climate change-related regime shifts have altered spatial synchrony of plankton dynamics in the North Sea. Global Change Biology **22**:2069-2080.

Devold, F., P. T. Hognestad, O. Aasen, A. Revheim, T. Ellingsen, K. R. Gundersen, O. J. Østvedt, J. Eggvin, K. F. Wiborg, L. Midttun, and S. Olsen. 1960. Rapporter over tokter og undersøkelser trykt i Fiskets Gang i 1960. Havforskningsinstituttet.

Drinkwater, K., E. Colbourne, H. Loeng, S. Sundby, and T. Kristiansen. 2013. Comparison of the atmospheric forcing and oceanographic responses between the Labrador Sea and the Norwegian and Barents seas. Progress in Oceanography **114**:11-25.

Edeline, E., S. M. Carlson, L. C. Stige, I. J. Winfield, J. M. Fletcher, J. B. James, T. O. Haugen, L. A. Vøllestad, and N. C. Stenseth. 2007. Trait changes in a harvested population are driven by a dynamic tug-of-war between natural and harvest selection. Proceedings of the National Academy of Sciences **104**:15799-15804.

Enberg, K., C. Jørgensen, E. S. Dunlop, Ø. Varpe, D. S. Boukal, L. Baulier, S. Eliassen, and M. Heino. 2012. Fishing-induced evolution of growth: concepts, mechanisms and the empirical evidence. Marine Ecology **33**:1-25.

Engelhard, G., and M. Heino. 2004. Maturity changes in Norwegian spring-spawning herring *Clupea harengus*: compensatory or evolutionary responses? Marine Ecology Progress Series **272**:245-256.

Falkenhaug, T., and P. Dalpadado. 2014. Diet composition and food selectivity of sprat (*Sprattus sprattus*) in Hardangerfjord, Norway. Marine Biology Research **10**:203-215.

Folkvord, A., Ø. Fiksen, H. Høie, A. Johannessen, E. Otterlei, and K. Vollset. 2009. What can size distributions within cohorts tell us about ecological processes in fish larvae? Scientia Marina **73**:119-130.

Forster, J., A. G. Hirst, and D. Atkinson. 2011. How do organisms change size with changing temperature? The importance of reproductive method and ontogenetic timing. Functional Ecology **25**:1024-1031.

Frisk, C., K. H. Andersen, A. Temming, J. P. Herrmann, K. S. Madsen, and G. Kraus. 2015. Environmental effects on sprat (*Sprattus sprattus*) physiology and growth at the distribution frontier: A bioenergetic modelling approach. Ecological Modelling **299**:130-139.

Froese, R. 2006. Cube law, condition factor and weight-length relationships: history, meta-analysis and recommendations. Journal of Applied Ichthyology **22**:241-253.

Giske, J., D. Aksnes, and Ø. Fiksen. 1994. Visual predators, environmental variables and zooplankton mortality risk. Vie et Milieu **44**:1-9.

Graeb, B. D. S., J. M. Dettmers, D. H. Wahl, and C. E. Cáceres. 2004. Fish Size and Prey Availability Affect Growth, Survival, Prey Selection, and Foraging Behavior of Larval Yellow Perch. Transactions of the American Fisheries Society **133**:504-514.

Gundersen, K. R. 1958. Merkeforsøk på brisling 1958. Fiskeridirektøren.

Gundersen, K. R. 1961. Merkeforsøk på brisling i fjordene sør for Bergen i juni-september 1960. Havforskningsinstituttet.

Gundersen, K. R. 1963. Merkeforsøk på brisling i fjorder på Vestlandet 1961-1962. Havforskningsinstituttet.

Hixon, M. A., D. W. Johnson, and S. M. Sogard. 2014. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. ICES Journal of Marine Science **71**:2171-2185.

Holtedahl, H. 1975. The geology of the Hardangerfjord, West Norway. Norges geologiske undersøkelse 323.

Hunter, A., D. C. Speirs, and M. R. Heath. 2019. Population density and temperature correlate with long-term trends in somatic growth rates and maturation schedules of herring and sprat. PLoS One **14**:e0212176.

ICES. 2018a. Benchmark Workshop on Sprat (WKSPRAT 2018): 5–9 November 2018, ICES HQ, Copenhagen, Denmark. ICES.

ICES. 2018b. Interim report of the working group on multispecies assessment methods (WGSAM). San Sebastian, Spain.

Ikpewe, I. E., A. R. Baudron, A. Ponchon, and P. G. Fernandes. 2021. Bigger juveniles and smaller adults: Changes in fish size correlate with warming seas. Journal of Applied Ecology **58**:847-856.

Johnsen, E., A. Totland, and C. Kvamme. 2020. Measuring distribution and density of sprat in Årdalsfjorden with a kayak drone. Havforskningsinstituttet.

Johnsen, I. A., V. Husa, P. K. Hansen, and F. Vikebø. 2021. Utskiftning av bassengvatn i djupe terskelfjordar.

Jonsson, B., N. Jonsson, and A. G. Finstad. 2013. Effects of temperature and food quality on age and size at maturity in ectotherms: an experimental test with Atlantic salmon. The Journal of Animal Ecology **82**:201-210.

Keys, A. B. 1928. The Weight-Length Relation in Fishes. Proceedings of the National Academy of Sciences of the United States of America **14**:922-925.

King, J. R., and G. A. Mcfarlane. 2003. Marine fish life history strategies: applications to fishery management. Fisheries Management and Ecology **10**:249-264.

Kolmogorov, A. N. 1933. Sulla determinazione empirica di una legge di distribuzione. Giornale dell'Instituto Italiano degli Attuari.

Krause, J., D. Bumann, and D. Todt. 1992. Relationship between the position preference and nutritional state of individuals in schools of juvenile roach (*Rutilus rutilus*). Behavioral Ecology and Sociobiology **30**:177-180.

Kritzer, J. P., and P. F. Sale. 2004. Metapopulation ecology in the sea: from Levins' model to marine ecology and fisheries science. Fish and Fisheries **5**:131-140.

Kvamme, C. 2020. Kvoteråd: Kystbrisling i Hardangerfjorden, Sognefjorden, Nordfjord og Trondheimsfjorden. Havforskningsinstituttet.

Kaartvedt, S., A. Røstad, and T. Klevjer. 2009. Sprat *Sprattus sprattus* can exploit low oxygen waters for overwintering. Marine Ecology Progress Series **390**:237-249.

Lappalainen, A., L. Saks, M. Šuštar, O. Heikinheimo, K. Jürgens, E. Kokkonen, M. Kurkilahti, A. Verliin, and M. Vetemaa. 2016. Length at maturity as a potential indicator of fishing pressure effects on coastal pikeperch (*Sander lucioperca*) stocks in the northern Baltic Sea. Fisheries Research **174**:47-57.

Lenth, R. V. 2021. emmeans: Estimated Marginal Means, aka Least-Squares Means.

Lindegren, M., M. van Deurs, A. Maureaud, J. T. Thorson, and D. Bekkevold. 2022. A spatial statistical approach for identifying population structuring of marine fish species: European sprat as a case study. ICES Journal of Marine Science **79**:423-434.

Lorenzen, K., and K. Enberg. 2002. Density-Dependent Growth as a Key Mechanism in the Regulation of Fish Populations: Evidence from among-Population Comparisons. Proceedings: Biological Sciences **269**:49-54.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, N.J.

Maes, J., and F. Ollevier. 2002. Size structure and feeding dynamics in estuarine clupeoid fish schools: field evidence for the school trap hypothesis. Aquatic Living Resources **15**:211-216.

Melo-Merino, S. M., H. Reyes-Bonilla, and A. Lira-Noriega. 2020. Ecological niche models and species distribution models in marine environments: A literature review and spatial analysis of evidence. Ecological Modelling **415**:108837.

Mjanger, H., B. V. Svendsen, H. Senneset, Å. Fotland, S. Mehl, E. Fuglebakk, M. L. Gulbrandsen, and J. Diaz. 2019. Håndbok for prøvetaking av fisk, krepsdyr og andre evertebrater. Versjon 5.0 (SPD).

Neuheimer, A., and C. Taggart. 2007. The growing degree-day and fish size-at-age: The overlooked metric. Canadian Journal of Fisheries and Aquatic Sciences **64**:375-385.

Neuwirth, E. 2014. RColorBrewer: ColorBrewer Palettes.

Ogle, D. H., J. C. Doll, P. Wheeler, and A. Dinno. 2021. FSA: Fisheries Stock Analysis.

Pauly, D., and O. Kinne. 2010. Gasping Fish and Panting Squids: Oxygen. Temperature and the Growth of Water-Breathing Animals. Excellence in Ecology. Book 22 **22**.

Payne, N. L., J. A. Smith, D. E. Meulen, M. D. Taylor, Y. Y. Watanabe, A. Takahashi, T. A. Marzullo, C. A. Gray, G. Cadiou, and I. M. Suthers. 2016. Temperature dependence of fish performance in the wild: links with species biogeography and physiological thermal tolerance. Functional Ecology **30**:903-912.

Peck, M., H. Baumann, M. Bernreuther, C. Clemmesen, J.-P. Herrmann, H. Haslob, B. Huwer, P. Kanstinger, F. Koster, C. Petereit, A. Lemming, and R. Voss. 2012. The ecophysiology of *Sprattus sprattus* in the Baltic and North Seas. Progress in Oceanography **103**:42-57.

Peck, M. A., J. Alheit, A. Bertrand, I. A. Catalán, S. Garrido, M. Moyano, R. R. Rykaczewski, A. Takasuka, and C. D. van der Lingen. 2021. Small pelagic fish in the new millennium: A bottom-up view of global research effort. Progress in Oceanography **191**:102494.

Price, T. D., A. Qvarnström, and D. E. Irwin. 2003. The role of phenotypic plasticity in driving genetic evolution. Proceedings. Biological sciences **270**:1433-1440.

Quintela, M., R. B. Àlex, D. Bekkevold, C. Kvamme, F. Berg, E. Jansson, G. Dahle, F. Besnier, R. D. M. Nash, and K. A. Glover. 2021. Genetic response to human-induced habitat changes in the marine environment: A century of evolution of European sprat in Landvikvannet, Norway. Ecology and Evolution **11**:1691-1718.

Quintela, M., C. Kvamme, D. Bekkevold, R. D. M. Nash, E. Jansson, A. G. Sørvik, J. B. Taggart, Ø. Skaala, G. Dahle, and K. A. Glover. 2020. Genetic analysis redraws the management boundaries for the European sprat. Evolutionary Applications **13**:1906-1922.

R Core Team. 2021. R: A Language and Environment for Statistical Computing (version 4.1.2). R Foundation for Statistical Computing, Vienna, Austria.

Reznick, D. 1982. The Impact of Predation on Life History Evolution in Trinidadian Guppies: Genetic Basis of Observed Life History Patterns. Evolution **36**:1236-1250.

Reznick, D. 1985. Costs of Reproduction: An Evaluation of the Empirical Evidence. Oikos **44**:257-267.

Rocha, J., J. Yletyinen, R. Biggs, T. Blenckner, and G. Peterson. 2015. Marine regime shifts: drivers and impacts on ecosystems services. Philosophical Transactions of the Royal Society B: Biological Sciences **370**:20130273.

Rustad, D. 1978. Hydrographical observations from Sognefjorden (Western Norway). NTNU Vitenskapsmuseet.

Salvanes, A. G., D. A. G. Aksnes, J. H. FossÅ, and J. Giske. 1995. Simulated carrying capacities of fish in Norwegian fjords. Fisheries Oceanography **4**:17-32.

Sinovčić, G., V. Č. Keč, and B. Zorica. 2008. Population structure, size at maturity and condition of sardine, *Sardina pilchardus* (Walb., 1792), in the nursery ground of the eastern Adriatic Sea (Krka River Estuary, Croatia). Estuarine, Coastal and Shelf Science **76**:739-744.

Smirnov, N. V. 1939. Estimate of deviation between empirical distribution functions in two independent samples. Bull. Moscow Univ.

Smoliński, S., and F. Berg. 2022. Varying relationships between fish length and scale size under changing environmental conditions – Multidecadal perspective in Atlantic herring. Ecological Indicators **134**:108494.

Statens Kartverk. 2021. Creative Commons Navngivelse 4.0 international (CC BY 4.0). Statens Kartverk.

Stearns, S. C. 1989. Trade-Offs in Life-History Evolution. Functional Ecology **3**:259-268.

Stearns, S. C. 1992. The evolution of life histories / Stephen C. Stearns. Oxford University Press, Oxford ; New York.

Stenevik, E. K., S. Hølleland, K. Enberg, Å. Høines, A. Salthaug, A. Slotte, S. Vatnehol, and S. Aanes. 2022. Predicting density-dependent somatic growth in Norwegian spring-spawning herring. ICES Journal of Marine Science:fsac057.

Stigebrandt, A. 2001. FjordEnv – a water quality model for fjords and other inshore waters.

Svobodova, Z. 1993. Water quality and fish health.

Swain, D. P., A. F. Sinclair, and J. Mark Hanson. 2007. Evolutionary response to size-selective mortality in an exploited fish population. Proceedings of the Royal Society B: Biological Sciences **274**:1015-1022.

Sætre, R., R. Toresen, H. Søiland, and P. Fossum. 2002. The Norwegian spring-spawning herring - spawning, larval drift and larval retention. Sarsia **87**:167-178.

Tesch, F. W. 1968. Age and growth. In: Methods for assessment of fish production in fresh water. W.E. Ricker (Ed.). Blackwell Scientific publications:93-123.

Thomas, C. D., and W. E. Kunin. 1999. The spatial structure of populations. Journal of Animal Ecology **68**:647-657.

Thorson, J. T., S. B. Munch, J. M. Cope, and J. Gao. 2017. Predicting life history parameters for all fishes worldwide. Ecological Applications **27**:2262-2276.

Torrejon-Magallanes, J. 2020. sizeMat: Estimate Size at Sexual Maturity.

Umar, I., S. Vatnehol, A. J. Holmin, E. Fuglebakk, and E. Johnsen. 2021. RstoxData: Tools to Read and Manipulate Fisheries Data.

Van Beveren, E., S. Bonhommeau, J.-M. Fromentin, J.-L. Bigot, J.-H. Bourdeix, P. Brosset, D. Roos, and C. Saraux. 2014. Rapid changes in growth, condition, size and age of small pelagic fish in the Mediterranean. Marine Biology **161**:1809-1822.

van der Molen, J., S. I. Rogers, J. R. Ellis, C. J. Fox, and P. McCloghrie. 2007. Dispersal patterns of the eggs and larvae of spring-spawning fish in the Irish Sea, UK. Journal of Sea Research **58**:313-330.

Via, S., R. Gomulkiewicz, G. De Jong, S. M. Scheiner, C. D. Schlichting, and P. H. Van Tienderen. 1995. Adaptive phenotypic plasticity: consensus and controversy. Trends Ecol Evol **10**:212-217.

Vihtakari, M. 2020. ggOceanMaps: Plot Data on Oceanographic Maps using 'ggplot2'.

Vilhjálmsson, H. 2002. Capelin (*Mallotus villosus*) in the Iceland–East Greenland–Jan Mayen ecosystem. ICES Journal of Marine Science **59**:870-883.

Wahl, E. F., and J. Alheit. 1988. Changes in distribution and abundance of sprat eggs during spawning season.

Wang, X., and Z. Cheng. 2020. Cross-Sectional Studies. Chest **158**:S65-S71.

Ward, A. J. W., M. M. Webster, and P. J. B. Hart. 2006. Intraspecific food competition in fishes. Fish and Fisheries **7**:231-261.

Weatherley, A. H., H. S. Gill, and J. Casselman. 1987. The biology of fish growth.

Whitehead, P. J. P. 1986. Clupeidae. Fisheries of the North-eastern Atlantic and the Mediterranean Volume 1. UNESCO:268-281.

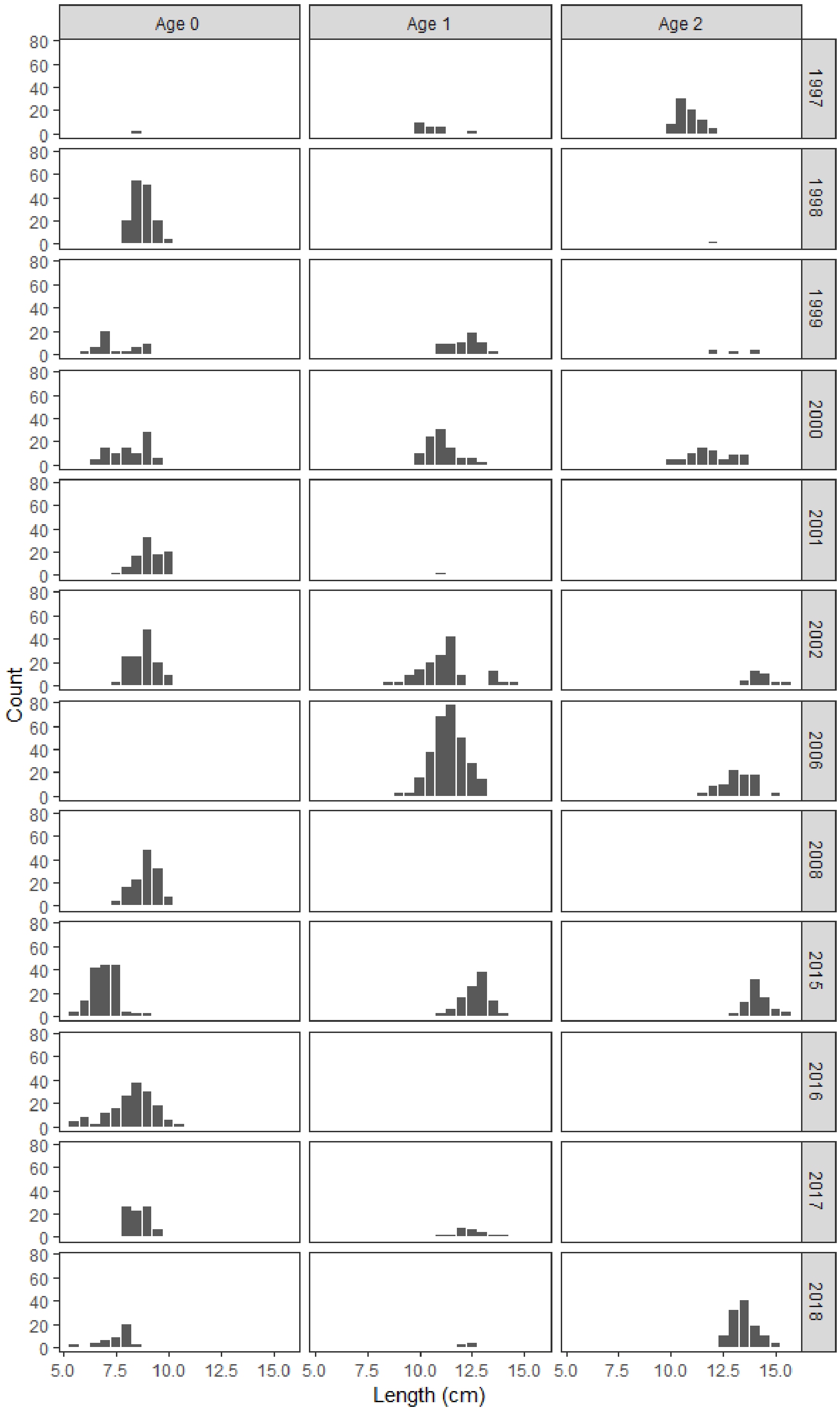
Wickham, H., M. Averick, J. Bryan, W. Chang, L. D. A. McGowan, R. François, G. Grolemund, A. H. a. L. Henry, J. H. a. M. Kuhn, T. L. Pedersen, E. Miller, S. M. Bache, K. Müller, J. Ooms, D. Robinson, D. P. Seidel, V. Spinu, K. Takahashi, D. Vaughan, C. Wilke, K. Woo, and H. Yutani. 2019. Welcome to the {tidyverse}. Journal of Open Source Software **4**:1686.

Wootton, R. J. 1991. Fish Ecology. Springer Netherlands, Dordrecht, NETHERLANDS, THE.

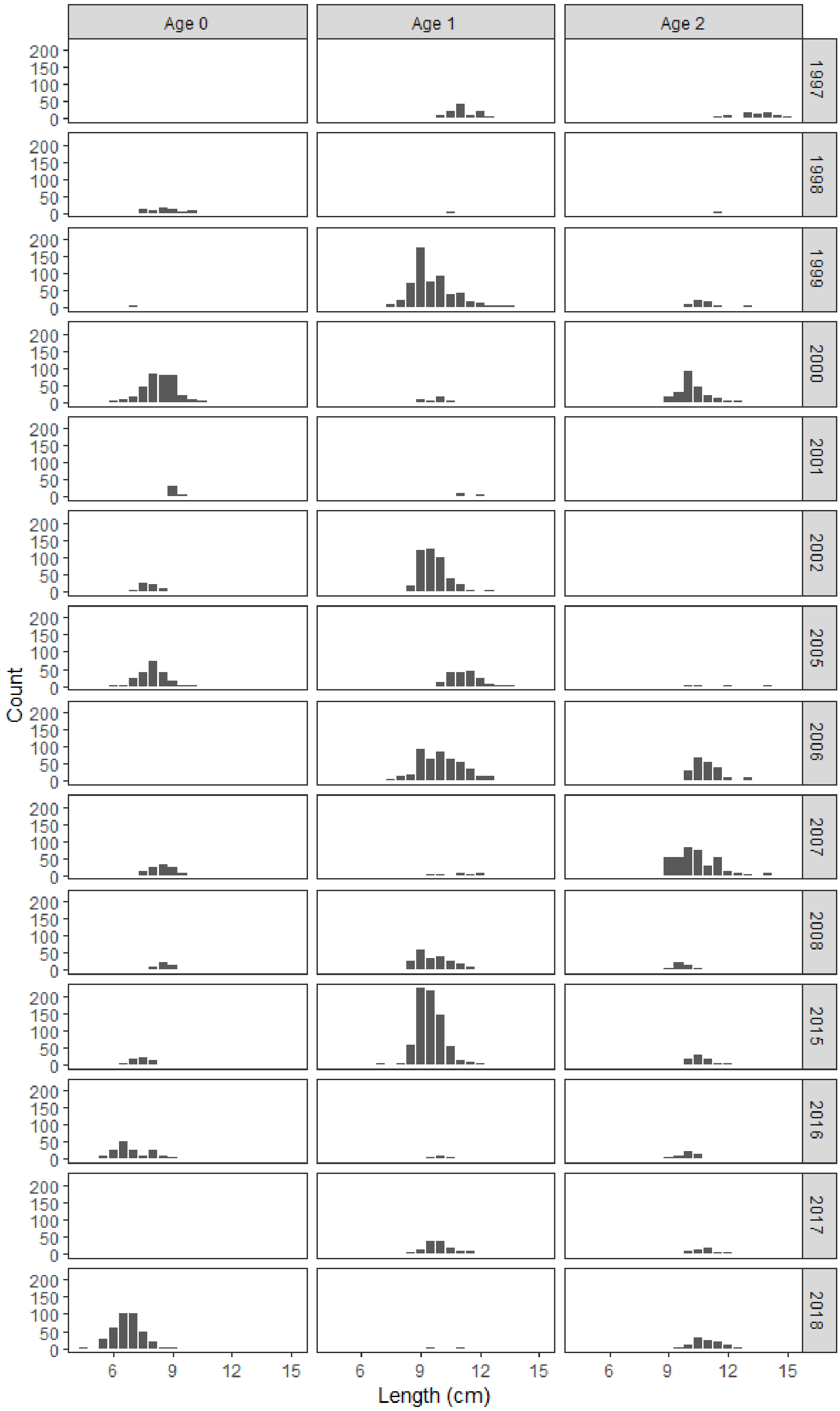
Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution **1**:3-14.

Appendices

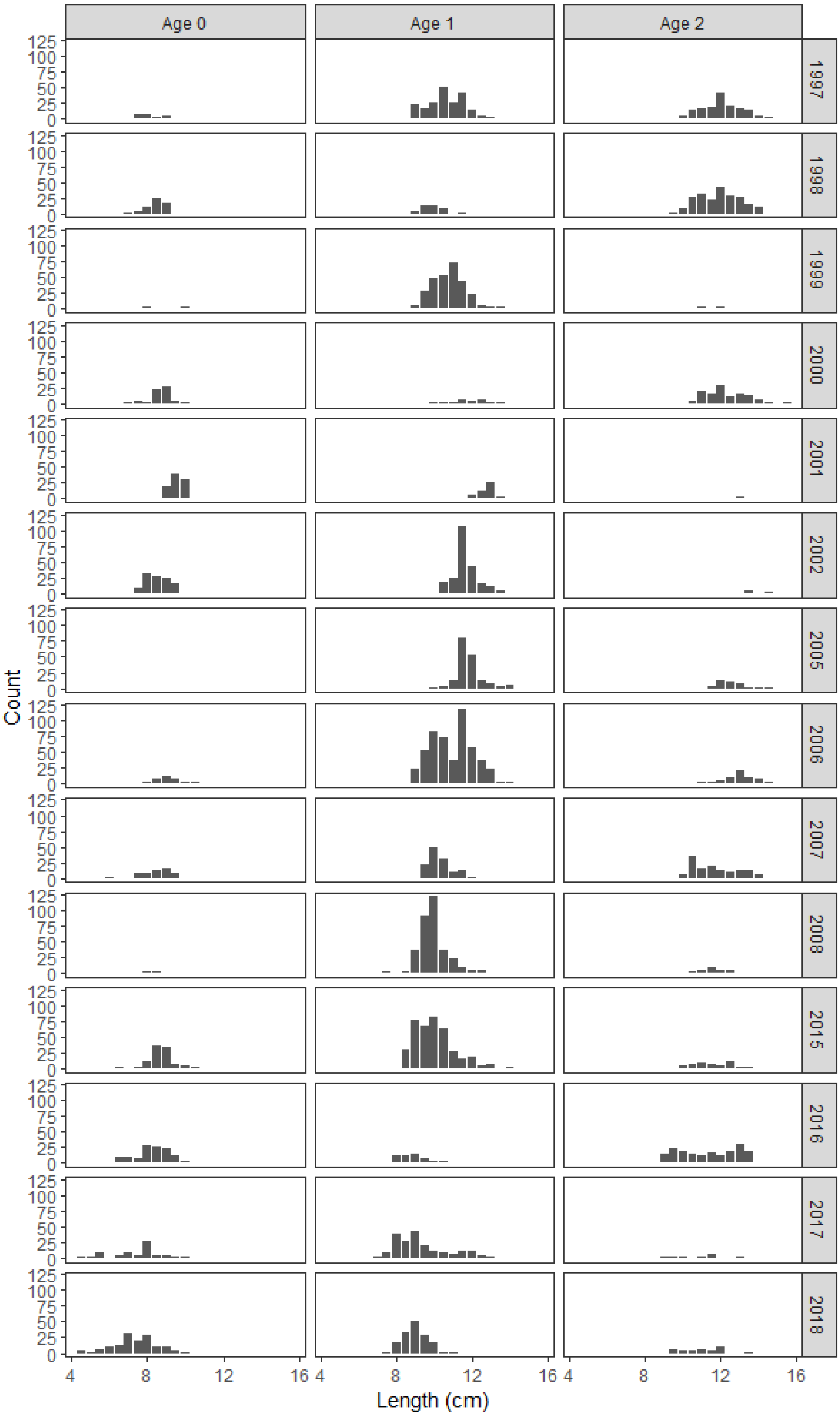
Appendix 1: Length distributions per age, year, and fjord



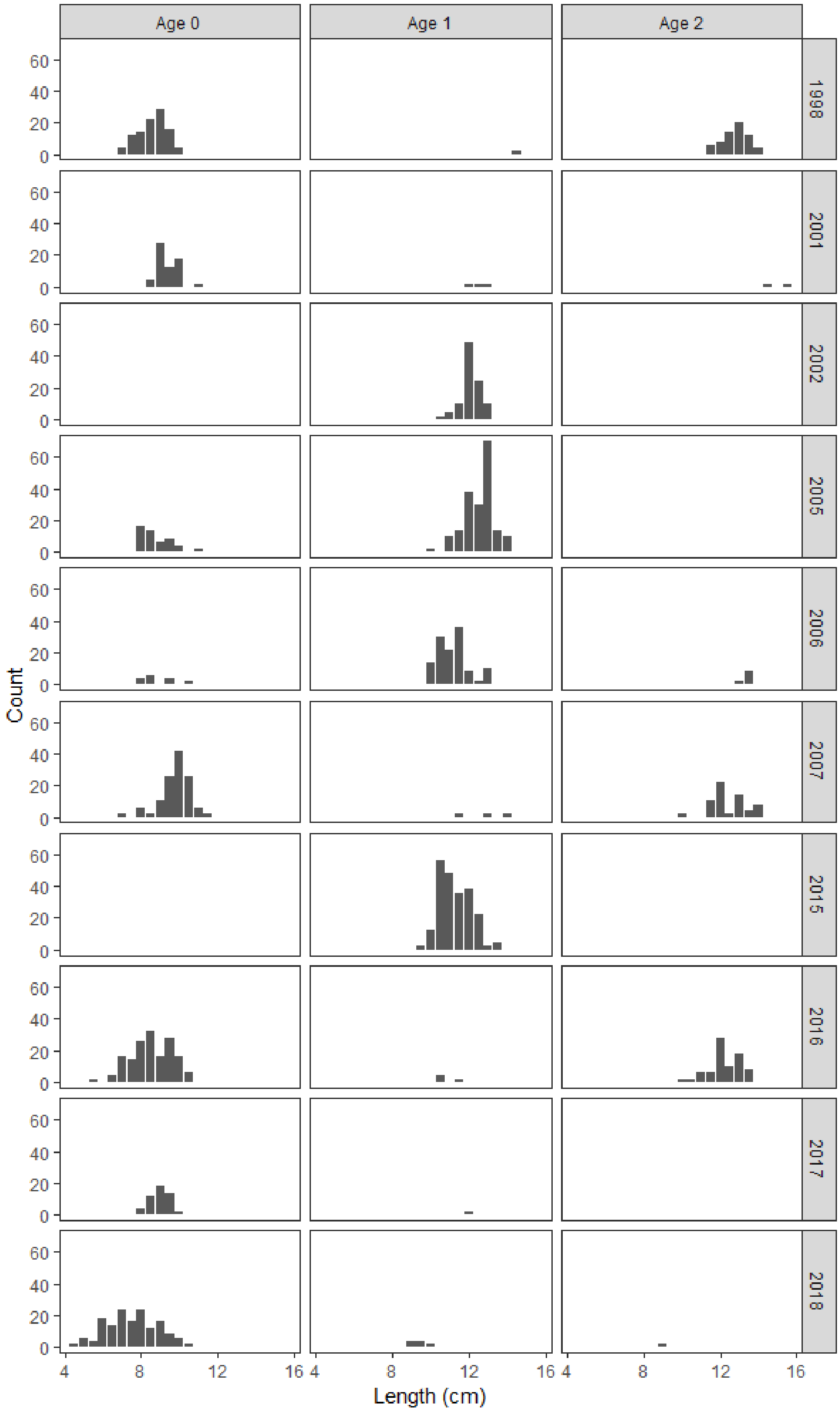
Appendix 1.1: Length distributions of sprat in Nordfjord per year and age



Appendix 1.2: Length distributions of sprat in Sognefjord per year and age

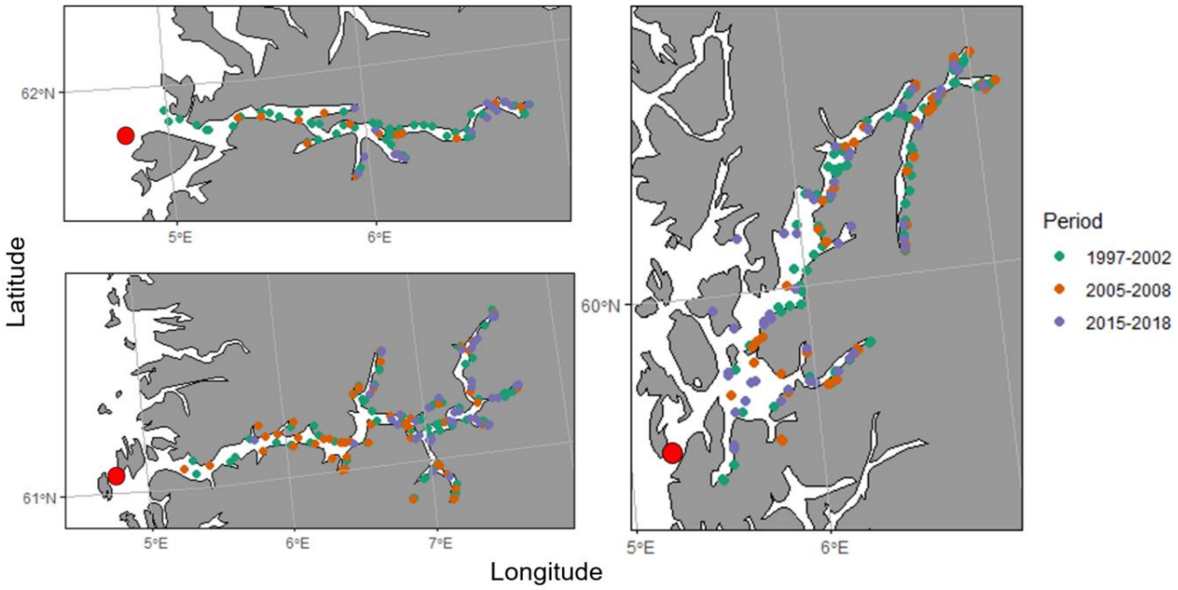


Appendix 1.3: Length distributions of sprat in inner part of Hardangerfjord per year and age

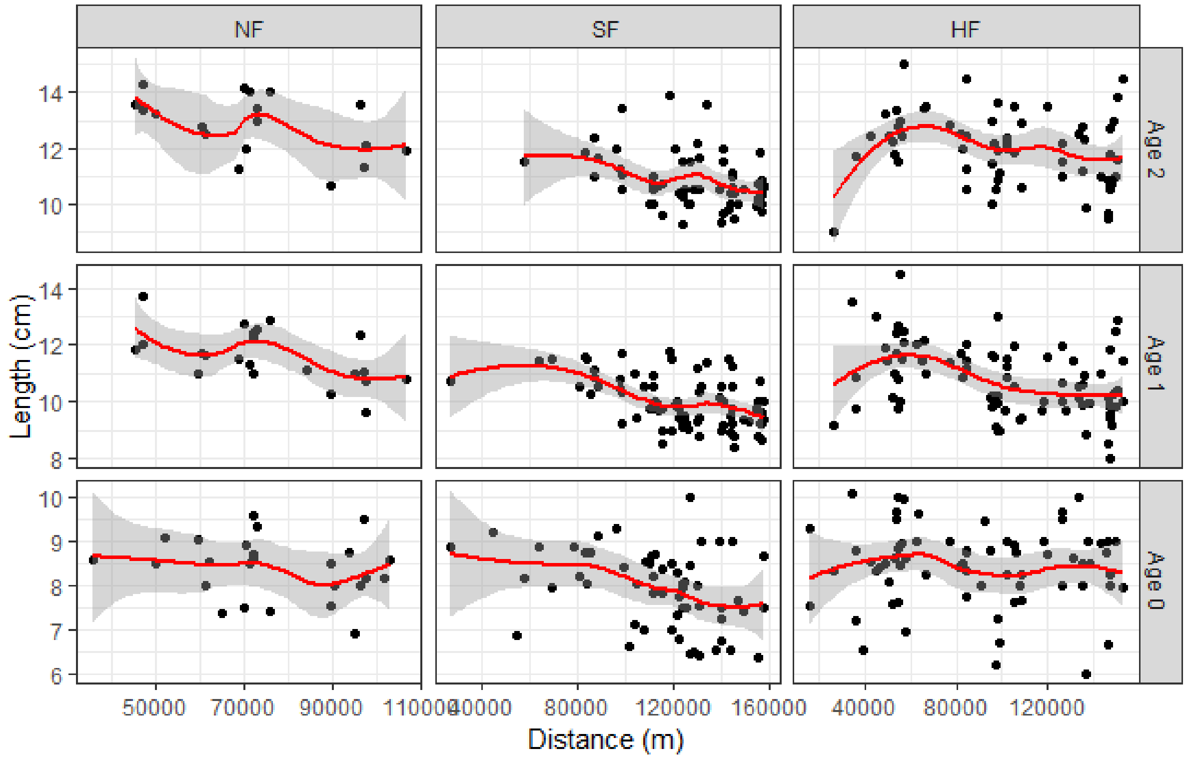


Appendix 1.4: Length distributions of sprat in outer part of Hardangerfjord per year and age

Appendix 2: Temporal and spatial clustering in between sampling periods



Appendix 2.1: Distribution of sampling locations for NF (upper left), SF (lower left) and HF (right) in the three time-periods 1997-2002, 2005-2008, and 2015-2018. The red doth is where distance from fjord mouth is measured from. Samling in period 2015-2018 were done further within the fjord in NF and SF than in earlier periods.



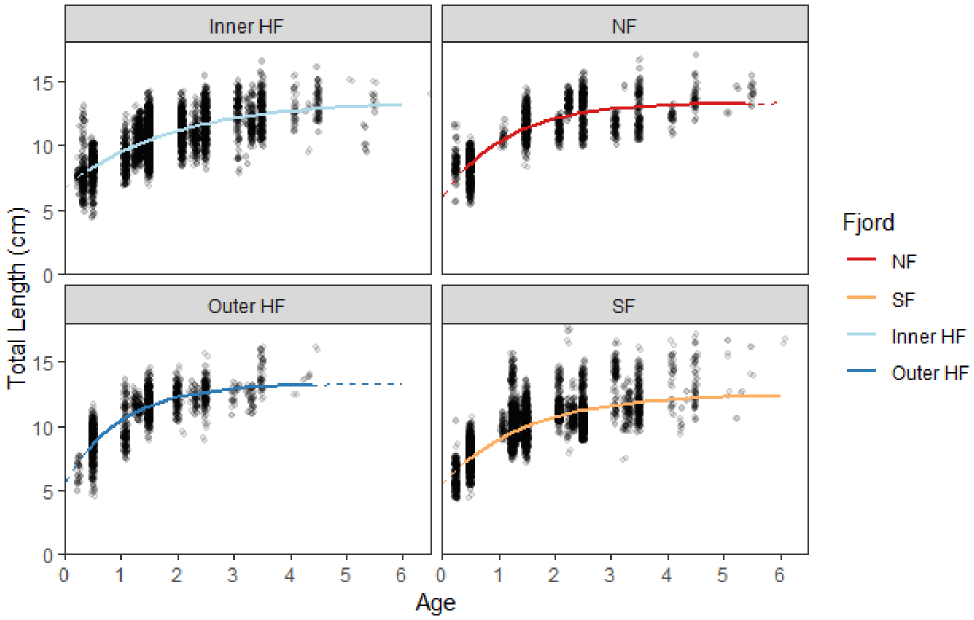
Appendix 2.2: Length distribution by distance from the fjord mouth for the fjords Nordfjord (NF), Sognefjord (SF) and Hardangerfjord (HF) by age 0, 1 and 2 in the periods 1997-2002, 2005-2008, and 2015-2018. The smoothed red line is the geom_smooth function with method=”loess” from the ggplot package. A decrease in length with distance from the fjord mouth

can in some cases be seen in SF and NF. This could affect the result of a declining length in SF over time from analyse of differences in length-at-age between time periods. However, the decline in length is thought to be due to temporal effects, and the spatial variation in sampling due to interannual spatial variability in overwintering.

Appendix 2.3: Dates of the coastal sprat cruise conducted by IMR. Sampling dates were almost a month later in period 3 (2015-2018) than in period 1 (1997-2002).

Year	Sampling dates
1997	11/09 - 11/15
1998	11/03 - 11/10
1999	11/11 - 11/17
2000	11/09 - 11/15
2001	11/09 - 11/16
2002	11/09 - 11/15
2005	11/11 - 11/16
2006	11/15 - 11/22
2007	11/13 - 11/19
2008	11/15 - 11/24
2015	12/05 - 12/14
2016	12/08 - 12/14
2017	11/26 - 12/05
2018	11/29 - 12/07

Appendix 3: Von Bertalanffy growth curves with observations



Appendix 3: Von Bertalanffy growth curves for the Norwegian fjords Nordfjord (NF), Sognefjord (SF), inner and outer Hardangerfjord (HF) with observations.

Appendix 4: Output of Kolmogorov-Smirnov tests

Appendix 4.1: Output of Kolmogorov-Smirnov tests comparing the fjords within the time periods

Period	Age	Fjords	D	P
1997-2002	0	NF - SF	0.187	<0.001
1997-2002	0	NF - Inner HF	0.080	0.141
1997-2002	0	NF - Outer HF	0.137	0.020
1997-2002	0	SF - Inner HF	0.211	<0.001
1997-2002	0	SF - Outer HF	0.312	<0.001
1997-2002	0	Inner HF - Outer HF	0.115	0.104
2005-2008	0	NF - SF	0.490	<0.001
2005-2008	0	NF - Inner HF	0.166	0.098
2005-2008	0	NF - Outer HF	0.385	<0.001
2005-2008	0	SF - Inner HF	0.324	<0.001
2005-2008	0	SF - Outer HF	0.608	<0.001
2005-2008	0	Inner HF - Outer HF	0.436	<0.001
2015-2018	0	NF - SF	0.420	<0.001
2015-2018	0	NF - Inner HF	0.135	<0.001
2015-2018	0	NF - Outer HF	0.169	<0.001
2015-2018	0	SF - Inner HF	0.531	<0.001
2015-2018	0	SF - Outer HF	0.542	<0.001
2015-2018	0	Inner HF - Outer HF	0.137	0.001
1997-2002	1	NF - SF	0.576	<0.001
1997-2002	1	NF - Inner HF	0.073	0.180
1997-2002	1	NF - Outer HF	0.593	<0.001
1997-2002	1	SF - Inner HF	0.503	<0.001
1997-2002	1	SF - Outer HF	0.855	<0.001
1997-2002	1	Inner HF - Outer HF	0.619	<0.001
2005-2008	1	NF - SF	0.484	<0.001
2005-2008	1	NF - Inner HF	0.355	<0.001
2005-2008	1	NF - Outer HF	0.301	<0.001
2005-2008	1	SF - Inner HF	0.198	<0.001
2005-2008	1	SF - Outer HF	0.571	<0.001
2005-2008	1	Inner HF - Outer HF	0.402	<0.001
2015-2018	1	NF - SF	0.949	<0.001
2015-2018	1	NF - Inner HF	0.874	<0.001
2015-2018	1	NF - Outer HF	0.626	<0.001
2015-2018	1	SF - Inner HF	0.159	<0.001
2015-2018	1	SF - Outer HF	0.759	<0.001
2015-2018	1	Inner HF - Outer HF	0.661	<0.001
1997-2002	2	NF - SF	0.333	<0.001
1997-2002	2	NF - Inner HF	0.195	<0.001
1997-2002	2	NF - Outer HF	0.483	<0.001
1997-2002	2	SF - Inner HF	0.468	<0.001
1997-2002	2	SF - Outer HF	0.692	<0.001
1997-2002	2	Inner HF - Outer HF	0.390	<0.001
2005-2008	2	NF - SF	0.894	<0.001
2005-2008	2	NF - Inner HF	0.419	<0.001
2005-2008	2	NF - Outer HF	0.347	<0.001
2005-2008	2	SF - Inner HF	0.518	<0.001
2005-2008	2	SF - Outer HF	0.752	<0.001
2005-2008	2	Inner HF - Outer HF	0.235	0.004

2015-2018	2	NF - SF	0.992	<0.001
2015-2018	2	NF - Inner HF	0.742	<0.001
2015-2018	2	NF - Outer HF	0.666	<0.001
2015-2018	2	SF - Inner HF	0.338	<0.001
2015-2018	2	SF - Outer HF	0.705	<0.001
2015-2018	2	Inner HF - Outer HF	0.379	<0.001

Appendix 4.2: Output of Kolmogorov-Smirnov tests comparing the time periods within the fjords.

Fjord	Age	Period	D	P
NF	0	1 - 2	0.155	0.014
NF	0	1 - 3	0.395	<0.001
NF	0	2 - 3	0.496	<0.001
NF	1	1 - 2	0.113	0.042
NF	1	1 - 3	0.655	<0.001
NF	1	2 - 3	0.601	<0.001
NF	2	1 - 2	0.564	<0.001
NF	2	1 - 3	0.689	<0.001
NF	2	2 - 3	0.288	<0.001
SF	0	1 - 2	0.159	<0.001
SF	0	1 - 3	0.672	<0.001
SF	0	1 - 3	0.661	<0.001
SF	1	1 - 2	0.197	<0.001
SF	1	1 - 3	0.137	<0.001
SF	1	2 - 3	0.333	<0.001
SF	2	1 - 2	0.162	<0.001
SF	2	1 - 3	0.198	<0.001
SF	2	2 - 3	0.146	<0.001
Inner HF	0	1 - 2	0.059	0.960
Inner HF	0	1 - 3	0.332	<0.001
Inner HF	0	2 - 3	0.329	<0.001
Inner HF	1	1 - 2	0.202	<0.001
Inner HF	1	1 - 3	0.542	<0.001
Inner HF	1	2 - 3	0.418	<0.001
Inner HF	2	1 - 2	0.061	0.567
Inner HF	2	1 - 3	0.264	<0.001
Inner HF	2	2 - 3	0.268	<0.001
Outer HF	0	1 - 2	0.332	<0.001
Outer HF	0	1 - 3	0.298	<0.001
Outer HF	0	2 - 3	0.422	<0.001
Outer HF	1	1 - 2	0.260	<0.001
Outer HF	1	1 - 3	0.563	<0.001
Outer HF	1	2 - 3	0.325	<0.001
Outer HF	2	1 - 2	0.266	0.014
Outer HF	2	1 - 3	0.355	<0.001
Outer HF	2	2 - 3	0.183	0.154

Appendix 5: Boxplots of length at age over three time periods

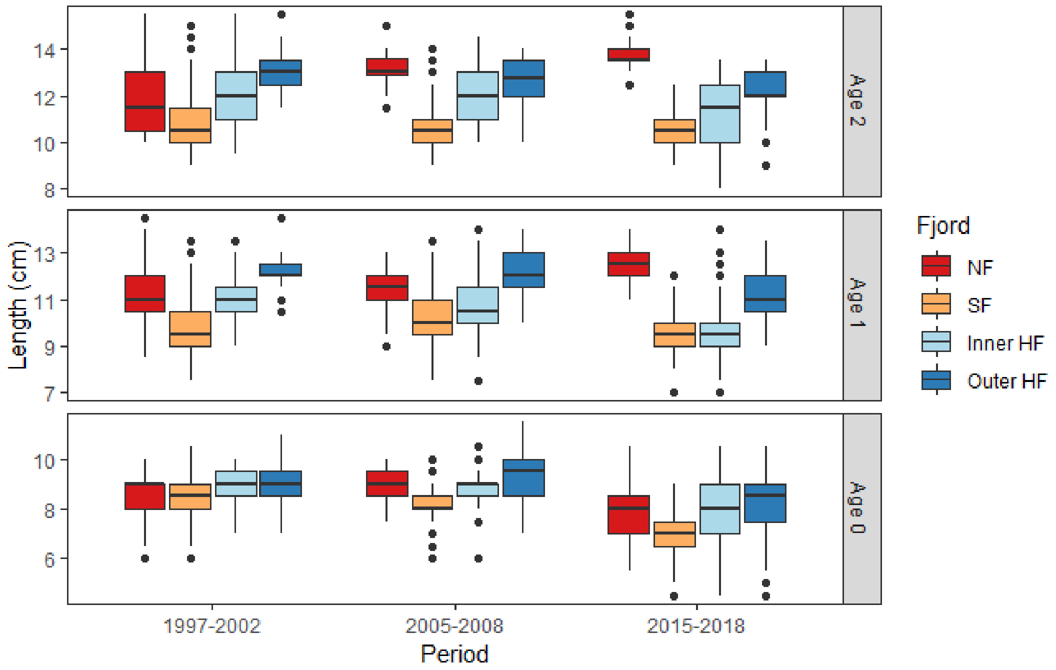


Figure 5.1: Boxplots of length-at-age in the Norwegian western fjords Nordfjord (NF), Sognefjord (SF), inner and outer Hardangerfjord (HF) in the three time-periods 1997-2002, 2005-2008, and 2015-2018 that illustrate the spread in the data.

Appendix 5.2: Output from posthoc-test with the emmeans package includes estimated mean (emmean), standard error (SE), degrees of freedom (df), lower and upper confidence levels of sprat of age 0 in the Norwegian fjords Nordfjord (NF), Sognefjord (SF), inner and outer Hardangerfjord (HF) in three time periods.

Fjord	**Period**	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**
NF	1997-2002	8.639	0.04	4068	8.561	8.718
SF	1997-2002	8.369	0.04	4068	8.29	8.447
Inner HF	1997-2002	8.795	0.048	4068	8.7	8.89
Outer HF	1997-2002	8.921	0.07	4068	8.783	9.059
NF	2005-2008	8.931	0.079	4068	8.776	9.086
SF	2005-2008	8.175	0.049	4068	8.08	8.271
Inner HF	2005-2008	8.691	0.093	4068	8.509	8.874
Outer HF	2005-2008	9.463	0.066	4068	9.334	9.592
NF	2015-2018	7.786	0.043	4068	7.702	7.871
SF	2015-2018	6.808	0.037	4068	6.735	6.881
Inner HF	2015-2018	7.944	0.044	4068	7.858	8.029
Outer HF	2015-2018	8.174	0.047	4068	8.081	8.267

Appendix 5.3: Output from posthoc-test with the emmeans package of Fjord*Period interactions comparing length of age 0 sprat. The Fjords are Nordfjord (NF), Sognefjord (SF), inner and outer Hardangerfjord (HF), and the three time periods are 1997-2002, 2005-2008, and 2015-2018.

Contrast	estimate	SE	df	t.ratio	p.value
(Inner HF 1997-2002) - (NF 1997-2002)	0.155	0.063	4068	2.468	0.361
(Inner HF 1997-2002) - (Outer HF 1997-2002)	-0.126	0.085	4068	-1.474	0.948
(Inner HF 1997-2002) - (SF 1997-2002)	0.426	0.063	4068	6.772	0
(Inner HF 1997-2002) - (Inner HF 2005-2008)	0.103	0.105	4068	0.986	0.998
(Inner HF 1997-2002) - (NF 2005-2008)	-0.136	0.093	4068	-1.467	0.949
(Inner HF 1997-2002) - (Outer HF 2005-2008)	-0.668	0.082	4068	-8.183	0
(Inner HF 1997-2002) - (SF 2005-2008)	0.619	0.069	4068	9.016	0
(Inner HF 1997-2002) - (Inner HF 2015-2018)	0.851	0.065	4068	13.054	0
(Inner HF 1997-2002) - (NF 2015-2018)	1.008	0.065	4068	15.578	0
(Inner HF 1997-2002) - (Outer HF 2015-2018)	0.621	0.068	4068	9.165	0
(Inner HF 1997-2002) - (SF 2015-2018)	1.987	0.061	4068	32.503	0
(NF 1997-2002) - (Outer HF 1997-2002)	-0.281	0.081	4068	-3.471	0.026
(NF 1997-2002) - (SF 1997-2002)	0.271	0.057	4068	4.764	0
(NF 1997-2002) - (Inner HF 2005-2008)	-0.052	0.101	4068	-0.514	1
(NF 1997-2002) - (NF 2005-2008)	-0.291	0.089	4068	-3.286	0.048
(NF 1997-2002) - (Outer HF 2005-2008)	-0.823	0.077	4068	-10.688	0
(NF 1997-2002) - (SF 2005-2008)	0.464	0.063	4068	7.346	0
(NF 1997-2002) - (Inner HF 2015-2018)	0.696	0.059	4068	11.724	0
(NF 1997-2002) - (NF 2015-2018)	0.853	0.059	4068	14.5	0
(NF 1997-2002) - (Outer HF 2015-2018)	0.465	0.062	4068	7.492	0
(NF 1997-2002) - (SF 2015-2018)	1.831	0.055	4068	33.397	0
(Outer HF 1997-2002) - (SF 1997-2002)	0.552	0.081	4068	6.815	0
(Outer HF 1997-2002) - (Inner HF 2005-2008)	0.229	0.117	4068	1.967	0.716
(Outer HF 1997-2002) - (NF 2005-2008)	-0.01	0.106	4068	-0.095	1
(Outer HF 1997-2002) - (Outer HF 2005-2008)	-0.542	0.096	4068	-5.631	0
(Outer HF 1997-2002) - (SF 2005-2008)	0.745	0.086	4068	8.71	0
(Outer HF 1997-2002) - (Inner HF 2015-2018)	0.977	0.083	4068	11.802	0
(Outer HF 1997-2002) - (NF 2015-2018)	1.134	0.082	4068	13.763	0
(Outer HF 1997-2002) - (Outer HF 2015-2018)	0.747	0.085	4068	8.805	0
(Outer HF 1997-2002) - (SF 2015-2018)	2.113	0.08	4068	26.534	0
(SF 1997-2002) - (Inner HF 2005-2008)	-0.323	0.101	4068	-3.19	0.064
(SF 1997-2002) - (NF 2005-2008)	-0.562	0.089	4068	-6.342	0
(SF 1997-2002) - (Outer HF 2005-2008)	-1.094	0.077	4068	-14.205	0
(SF 1997-2002) - (SF 2005-2008)	0.193	0.063	4068	3.057	0.093
(SF 1997-2002) - (Inner HF 2015-2018)	0.425	0.059	4068	7.159	0
(SF 1997-2002) - (NF 2015-2018)	0.582	0.059	4068	9.895	0
(SF 1997-2002) - (Outer HF 2015-2018)	0.194	0.062	4068	3.131	0.076
(SF 1997-2002) - (SF 2015-2018)	1.56	0.055	4068	28.456	0
(Inner HF 2005-2008) - (NF 2005-2008)	-0.239	0.122	4068	-1.962	0.72
(Inner HF 2005-2008) - (Outer HF 2005-2008)	-0.771	0.114	4068	-6.777	0
(Inner HF 2005-2008) - (SF 2005-2008)	0.516	0.105	4068	4.919	0
(Inner HF 2005-2008) - (Inner HF 2015-2018)	0.748	0.103	4068	7.284	0
(Inner HF 2005-2008) - (NF 2015-2018)	0.905	0.102	4068	8.842	0

(Inner HF 2005-2008) - (Outer HF 2015-2018)	0.517	0.104	4068	4.962	0
(Inner HF 2005-2008) - (SF 2015-2018)	1.883	0.1	4068	18.81	0
(NF 2005-2008) - (Outer HF 2005-2008)	-0.532	0.103	4068	-5.177	0
(NF 2005-2008) - (SF 2005-2008)	0.755	0.093	4068	8.137	0
(NF 2005-2008) - (Inner HF 2015-2018)	0.987	0.09	4068	10.935	0
(NF 2005-2008) - (NF 2015-2018)	1.144	0.09	4068	12.725	0
(NF 2005-2008) - (Outer HF 2015-2018)	0.757	0.092	4068	8.215	0
(NF 2005-2008) - (SF 2015-2018)	2.123	0.087	4068	24.294	0
(Outer HF 2005-2008) - (SF 2005-2008)	1.287	0.082	4068	15.738	0
(Outer HF 2005-2008) - (Inner HF 2015-2018)	1.519	0.079	4068	19.258	0
(Outer HF 2005-2008) - (NF 2015-2018)	1.676	0.078	4068	21.356	0
(Outer HF 2005-2008) - (Outer HF 2015-2018)	1.289	0.081	4068	15.912	0
(Outer HF 2005-2008) - (SF 2015-2018)	2.655	0.076	4068	35.139	0
(SF 2005-2008) - (Inner HF 2015-2018)	0.232	0.065	4068	3.543	0.02
(SF 2005-2008) - (NF 2015-2018)	0.389	0.065	4068	5.991	0
(SF 2005-2008) - (Outer HF 2015-2018)	0.001	0.068	4068	0.021	1
(SF 2005-2008) - (SF 2015-2018)	1.367	0.061	4068	22.288	0
(Inner HF 2015-2018) - (NF 2015-2018)	0.157	0.061	4068	2.569	0.298
(Inner HF 2015-2018) - (Outer HF 2015-2018)	-0.23	0.064	4068	-3.577	0.018
(Inner HF 2015-2018) - (SF 2015-2018)	1.135	0.057	4068	19.78	0
(NF 2015-2018) - (Outer HF 2015-2018)	-0.388	0.064	4068	-6.064	0
(NF 2015-2018) - (SF 2015-2018)	0.978	0.057	4068	17.199	0
(Outer HF 2015-2018) - (SF 2015-2018)	1.366	0.06	4068	22.663	0

Appendix 5.4: Output from posthoc-test with the emmeans package includes estimated mean (emmean), standard error (SE), degrees of freedom (df), lower and upper confidence levels of sprat of age 1 in the Norwegian fjords Nordfjord (NF), Sognefjord (SF), inner and outer Hardangerfjord (HF) in three time periods.

Fjord	**Period**	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**
NF	1997-2002	11.279	0.057	7044	11.167	11.39
SF	1997-2002	9.802	0.029	7044	9.744	9.86
Inner HF	1997-2002	11.077	0.035	7044	11.009	11.146
Outer HF	1997-2002	12.17	0.098	7044	11.978	12.361
NF	2005-2008	11.395	0.058	7044	11.281	11.51
SF	2005-2008	10.192	0.035	7044	10.124	10.26
Inner HF	2005-2008	10.739	0.03	7044	10.681	10.797
Outer HF	2005-2008	12.025	0.057	7044	11.914	12.136
NF	2015-2018	12.618	0.086	7044	12.449	12.787
SF	2015-2018	9.577	0.034	7044	9.51	9.644
Inner HF	2015-2018	9.572	0.036	7044	9.502	9.642
Outer HF	2015-2018	11.189	0.065	7044	11.061	11.317

Appendix 5.5: Output from posthoc-test with the emmeans package of Fjord*Period interactions comparing length of age 1 sprat. The Fjords are Nordfjord (NF), Sognefjord (SF), inner and outer Hardangerfjord (HF), and the three time periods are 1997-2002, 2005-2008, and 2015-2018.

contrast	**estimate**	**SE**	**df**	**t.ratio**	**p.value**
(Inner HF 1997-2002) - (NF 1997-2002)	-0.201	0.067	7044	-3.013	0.105
(Inner HF 1997-2002) - (Outer HF 1997-2002)	-1.092	0.104	7044	-10.526	0
(Inner HF 1997-2002) - (SF 1997-2002)	1.275	0.046	7044	27.913	0
(Inner HF 1997-2002) - (Inner HF 2005-2008)	0.338	0.046	7044	7.376	0
(Inner HF 1997-2002) - (NF 2005-2008)	-0.318	0.068	7044	-4.664	0
(Inner HF 1997-2002) - (Outer HF 2005-2008)	-0.948	0.067	7044	-14.247	0
(Inner HF 1997-2002) - (SF 2005-2008)	0.886	0.049	7044	17.989	0
(Inner HF 1997-2002) - (Inner HF 2015-2018)	1.505	0.05	7044	30.075	0
(Inner HF 1997-2002) - (NF 2015-2018)	-1.54	0.093	7044	-16.547	0
(Inner HF 1997-2002) - (Outer HF 2015-2018)	-0.112	0.074	7044	-1.508	0.939
(Inner HF 1997-2002) - (SF 2015-2018)	1.5	0.049	7044	30.708	0
(NF 1997-2002) - (Outer HF 1997-2002)	-0.891	0.113	7044	-7.879	0
(NF 1997-2002) - (SF 1997-2002)	1.477	0.064	7044	23.048	0
(NF 1997-2002) - (Inner HF 2005-2008)	0.54	0.064	7044	8.406	0
(NF 1997-2002) - (NF 2005-2008)	-0.116	0.082	7044	-1.427	0.959
(NF 1997-2002) - (Outer HF 2005-2008)	-0.746	0.08	7044	-9.299	0
(NF 1997-2002) - (SF 2005-2008)	1.087	0.067	7044	16.31	0
(NF 1997-2002) - (Inner HF 2015-2018)	1.707	0.067	7044	25.377	0
(NF 1997-2002) - (NF 2015-2018)	-1.339	0.103	7044	-12.954	0
(NF 1997-2002) - (Outer HF 2015-2018)	0.09	0.087	7044	1.037	0.997
(NF 1997-2002) - (SF 2015-2018)	1.702	0.066	7044	25.641	0
(Outer HF 1997-2002) - (SF 1997-2002)	2.368	0.102	7044	23.21	0
(Outer HF 1997-2002) - (Inner HF 2005-2008)	1.431	0.102	7044	14.013	0
(Outer HF 1997-2002) - (NF 2005-2008)	0.775	0.114	7044	6.803	0
(Outer HF 1997-2002) - (Outer HF 2005-2008)	0.144	0.113	7044	1.28	0.982
(Outer HF 1997-2002) - (SF 2005-2008)	1.978	0.104	7044	19.083	0
(Outer HF 1997-2002) - (Inner HF 2015-2018)	2.598	0.104	7044	24.968	0
(Outer HF 1997-2002) - (NF 2015-2018)	-0.448	0.13	7044	-3.437	0.029
(Outer HF 1997-2002) - (Outer HF 2015-2018)	0.981	0.117	7044	8.35	0
(Outer HF 1997-2002) - (SF 2015-2018)	2.593	0.103	7044	25.058	0
(SF 1997-2002) - (Inner HF 2005-2008)	-0.937	0.042	7044	-22.447	0
(SF 1997-2002) - (NF 2005-2008)	-1.593	0.065	7044	-24.351	0
(SF 1997-2002) - (Outer HF 2005-2008)	-2.223	0.064	7044	-34.873	0
(SF 1997-2002) - (SF 2005-2008)	-0.39	0.045	7044	-8.587	0
(SF 1997-2002) - (Inner HF 2015-2018)	0.23	0.046	7044	4.965	0
(SF 1997-2002) - (NF 2015-2018)	-2.816	0.091	7044	-30.902	0
(SF 1997-2002) - (Outer HF 2015-2018)	-1.387	0.072	7044	-19.396	0
(SF 1997-2002) - (SF 2015-2018)	0.225	0.045	7044	5	0
(Inner HF 2005-2008) - (NF 2005-2008)	-0.656	0.066	7044	-10.009	0
(Inner HF 2005-2008) - (Outer HF 2005-2008)	-1.286	0.064	7044	-20.134	0
(Inner HF 2005-2008) - (SF 2005-2008)	0.547	0.046	7044	12.003	0
(Inner HF 2005-2008) - (Inner HF 2015-2018)	1.167	0.046	7044	25.108	0
(Inner HF 2005-2008) - (NF 2015-2018)	-1.879	0.091	7044	-20.597	0

(Inner HF 2005-2008) - (Outer HF 2015-2018)	-0.45	0.072	7044	-6.282	0
(Inner HF 2005-2008) - (SF 2015-2018)	1.162	0.045	7044	25.714	0
(NF 2005-2008) - (Outer HF 2005-2008)	-0.63	0.081	7044	-7.744	0
(NF 2005-2008) - (SF 2005-2008)	1.203	0.068	7044	17.711	0
(NF 2005-2008) - (Inner HF 2015-2018)	1.823	0.069	7044	26.598	0
(NF 2005-2008) - (NF 2015-2018)	-1.222	0.104	7044	-11.732	0
(NF 2005-2008) - (Outer HF 2015-2018)	0.206	0.088	7044	2.355	0.438
(NF 2005-2008) - (SF 2015-2018)	1.818	0.068	7044	26.866	0
(Outer HF 2005-2008) - (SF 2005-2008)	1.833	0.066	7044	27.639	0
(Outer HF 2005-2008) - (Inner HF 2015-2018)	2.453	0.067	7044	36.644	0
(Outer HF 2005-2008) - (NF 2015-2018)	-0.592	0.103	7044	-5.742	0
(Outer HF 2005-2008) - (Outer HF 2015-2018)	0.836	0.086	7044	9.687	0
(Outer HF 2005-2008) - (SF 2015-2018)	2.448	0.066	7044	37.061	0
(SF 2005-2008) - (Inner HF 2015-2018)	0.62	0.05	7044	12.448	0
(SF 2005-2008) - (NF 2015-2018)	-2.426	0.093	7044	-26.101	0
(SF 2005-2008) - (Outer HF 2015-2018)	-0.997	0.074	7044	-13.508	0
(SF 2005-2008) - (SF 2015-2018)	0.615	0.049	7044	12.654	0
(Inner HF 2015-2018) - (NF 2015-2018)	-3.045	0.093	7044	-32.616	0
(Inner HF 2015-2018) - (Outer HF 2015-2018)	-1.617	0.074	7044	-21.741	0
(Inner HF 2015-2018) - (SF 2015-2018)	-0.005	0.049	7044	-0.098	1
(NF 2015-2018) - (Outer HF 2015-2018)	1.429	0.108	7044	13.213	0
(NF 2015-2018) - (SF 2015-2018)	3.041	0.093	7044	32.786	0
(Outer HF 2015-2018) - (SF 2015-2018)	1.612	0.074	7044	21.911	0

Appendix 5.6: Output from posthoc-test with the emmeans package includes estimated mean (emmean), standard error (SE), degrees of freedom (df), lower and upper confidence levels of sprat of age 2 in the Norwegian fjords Nordfjord (NF), Sognefjord (SF), inner and outer Hardangerfjord (HF) in three time periods

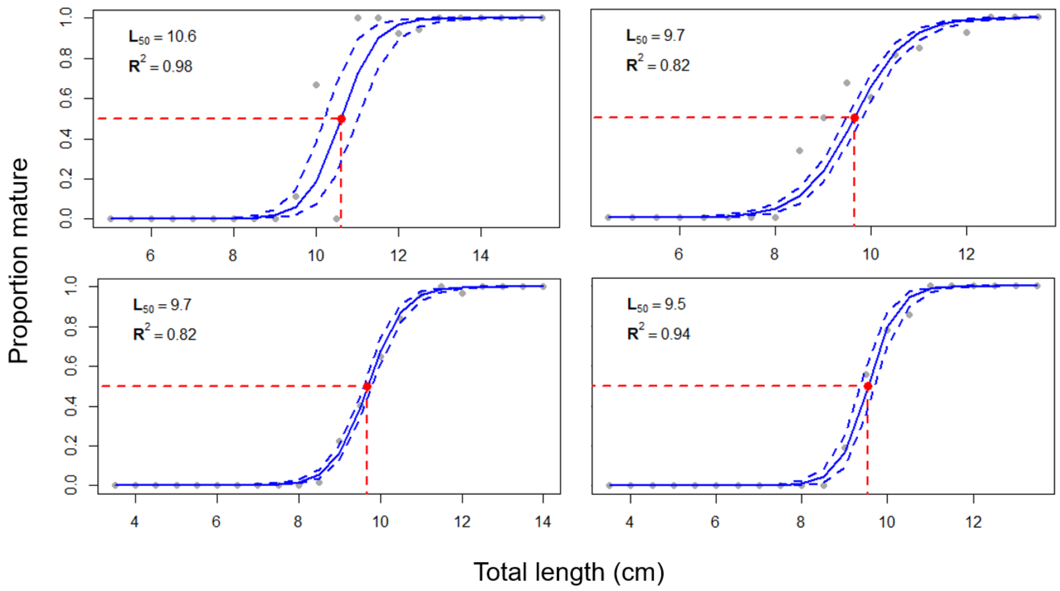
Fjord	**Period**	**emmean**	**SE**	**df**	**lower.CL**	**upper.CL**
NF	1997-2002	11.9	0.084	2958	11.736	12.064
SF	1997-2002	11.032	0.058	2958	10.918	11.147
Inner HF	1997-2002	12.084	0.05	2958	11.985	12.183
Outer HF	1997-2002	12.912	0.136	2958	12.644	13.179
NF	2005-2008	13.188	0.126	2958	12.941	13.434
SF	2005-2008	10.531	0.045	2958	10.444	10.619
Inner HF	2005-2008	12.094	0.071	2958	11.956	12.233
Outer HF	2005-2008	12.583	0.133	2958	12.323	12.843
NF	2015-2018	13.753	0.082	2958	13.591	13.914
SF	2015-2018	10.635	0.069	2958	10.5	10.771
Inner HF	2015-2018	11.277	0.068	2958	11.144	11.411
Outer HF	2015-2018	12.159	0.124	2958	11.915	12.402

Appendix 5.7: Output from posthoc-test with the emmeans package of Fjord*Period interactions comparing length of age 2 sprat. The Fjords are Nordfjord (NF), Sognefjord (SF), inner and outer Hardangerfjord (HF), and the three time periods are 1997-2002, 2005-2008, and 2015-2018.

Contrast	**estimate**	**SE**	**df**	**t.ratio**	**p.value**
(Inner HF 1997-2002) – (NF 1997-2002)	0.184	0.098	2958	1.882	0.771
(Inner HF 1997-2002) – (Outer HF 1997-2002)	-0.828	0.145	2958	-5.693	0
(Inner HF 1997-2002) – (SF 1997-2002)	1.052	0.077	2958	13.631	0
(Inner HF 1997-2002) – (Inner HF 2005-2008)	-0.01	0.087	2958	-0.121	1
(Inner HF 1997-2002) – (NF 2005-2008)	-1.104	0.135	2958	-8.146	0
(Inner HF 1997-2002) – (Outer HF 2005-2008)	-0.499	0.142	2958	-3.521	0.022
(Inner HF 1997-2002) – (SF 2005-2008)	1.553	0.067	2958	23.109	0
(Inner HF 1997-2002) – (Inner HF 2015-2018)	0.807	0.085	2958	9.54	0
(Inner HF 1997-2002) – (NF 2015-2018)	-1.669	0.097	2958	-17.272	0
(Inner HF 1997-2002) – (Outer HF 2015-2018)	-0.075	0.134	2958	-0.556	1
(Inner HF 1997-2002) – (SF 2015-2018)	1.449	0.085	2958	16.969	0
(NF 1997-2002) – (Outer HF 1997-2002)	-1.012	0.16	2958	-6.319	0
(NF 1997-2002) – (SF 1997-2002)	0.868	0.102	2958	8.487	0
(NF 1997-2002) – (Inner HF 2005-2008)	-0.194	0.11	2958	-1.775	0.832
(NF 1997-2002) – (NF 2005-2008)	-1.288	0.151	2958	-8.518	0
(NF 1997-2002) – (Outer HF 2005-2008)	-0.683	0.157	2958	-4.356	0.001
(NF 1997-2002) – (SF 2005-2008)	1.369	0.095	2958	14.416	0
(NF 1997-2002) – (Inner HF 2015-2018)	0.623	0.108	2958	5.769	0
(NF 1997-2002) – (NF 2015-2018)	-1.853	0.118	2958	-15.752	0
(NF 1997-2002) – (Outer HF 2015-2018)	-0.259	0.15	2958	-1.725	0.857
(NF 1997-2002) – (SF 2015-2018)	1.265	0.109	2958	11.648	0
(Outer HF 1997-2002) – (SF 1997-2002)	1.879	0.148	2958	12.662	0
(Outer HF 1997-2002) – (Inner HF 2005-2008)	0.817	0.154	2958	5.321	0
(Outer HF 1997-2002) – (NF 2005-2008)	-0.276	0.186	2958	-1.486	0.945
(Outer HF 1997-2002) – (Outer HF 2005-2008)	0.328	0.19	2958	1.727	0.856
(Outer HF 1997-2002) – (SF 2005-2008)	2.38	0.144	2958	16.588	0
(Outer HF 1997-2002) – (Inner HF 2015-2018)	1.634	0.152	2958	10.724	0
(Outer HF 1997-2002) – (NF 2015-2018)	-0.841	0.159	2958	-5.275	0
(Outer HF 1997-2002) – (Outer HF 2015-2018)	0.753	0.185	2958	4.082	0.003
(Outer HF 1997-2002) – (SF 2015-2018)	2.276	0.153	2958	14.892	0
(SF 1997-2002) – (Inner HF 2005-2008)	-1.062	0.092	2958	-11.587	0
(SF 1997-2002) – (NF 2005-2008)	-2.155	0.139	2958	-15.537	0
(SF 1997-2002) – (Outer HF 2005-2008)	-1.551	0.145	2958	-10.703	0
(SF 1997-2002) – (SF 2005-2008)	0.501	0.074	2958	6.817	0
(SF 1997-2002) – (Inner HF 2015-2018)	-0.245	0.09	2958	-2.732	0.211
(SF 1997-2002) – (NF 2015-2018)	-2.72	0.101	2958	-26.904	0
(SF 1997-2002) – (Outer HF 2015-2018)	-1.126	0.137	2958	-8.202	0
(SF 1997-2002) – (SF 2015-2018)	0.397	0.09	2958	4.391	0.001
(Inner HF 2005-2008) – (NF 2005-2008)	-1.093	0.144	2958	-7.579	0
(Inner HF 2005-2008) – (Outer HF 2005-2008)	-0.489	0.15	2958	-3.255	0.052
(Inner HF 2005-2008) – (SF 2005-2008)	1.563	0.083	2958	18.729	0
(Inner HF 2005-2008) – (Inner HF 2015-2018)	0.817	0.098	2958	8.339	0
(Inner HF 2005-2008) – (NF 2015-2018)	-1.658	0.109	2958	-15.274	0
(Inner HF 2005-2008) – (Outer HF 2015-2018)	-0.064	0.143	2958	-0.448	1
(Inner HF 2005-2008) – (SF 2015-2018)	1.459	0.099	2958	14.785	0
(NF 2005-2008) – (Outer HF 2005-2008)	0.604	0.183	2958	3.306	0.045
(NF 2005-2008) – (SF 2005-2008)	2.656	0.133	2958	19.908	0
(NF 2005-2008) – (Inner HF 2015-2018)	1.91	0.143	2958	13.362	0
(NF 2005-2008) – (NF 2015-2018)	-0.565	0.15	2958	-3.758	0.01
(NF 2005-2008) – (Outer HF 2015-2018)	1.029	0.177	2958	5.821	0
(NF 2005-2008) – (SF 2015-2018)	2.552	0.143	2958	17.792	0
(Outer HF 2005-2008) – (SF 2005-2008)	2.052	0.14	2958	14.672	0
(Outer HF 2005-2008) – (Inner HF 2015-2018)	1.306	0.149	2958	8.766	0
(Outer HF 2005-2008) – (NF 2015-2018)	-1.169	0.156	2958	-7.489	0

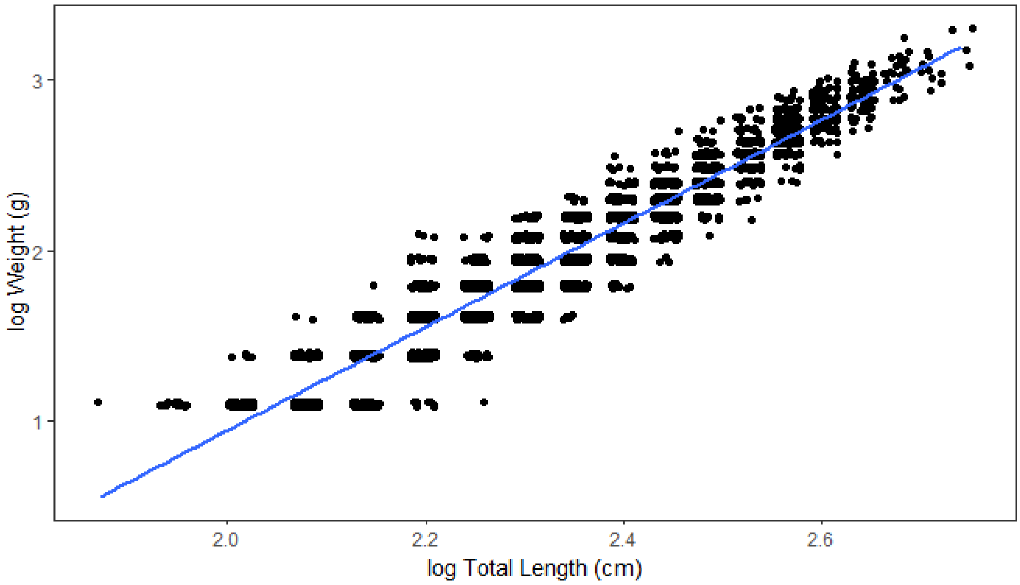
(Outer HF 2005-2008) – (Outer HF 2015-2018)	0.425	0.182	2958	2.338	0.449
(Outer HF 2005-2008) – (SF 2015-2018)	1.948	0.149	2958	13.035	0
(SF 2005-2008) – (Inner HF 2015-2018)	-0.746	0.081	2958	-9.182	0
(SF 2005-2008) – (NF 2015-2018)	-3.221	0.094	2958	-34.365	0
(SF 2005-2008) – (Outer HF 2015-2018)	-1.627	0.132	2958	-12.33	0
(SF 2005-2008) – (SF 2015-2018)	-0.104	0.082	2958	-1.267	0.983
(Inner HF 2015-2018) – (NF 2015-2018)	-2.475	0.107	2958	-23.161	0
(Inner HF 2015-2018) – (Outer HF 2015-2018)	-0.881	0.142	2958	-6.223	0
(Inner HF 2015-2018) – (SF 2015-2018)	0.642	0.097	2958	6.631	0
(NF 2015-2018) – (Outer HF 2015-2018)	1.594	0.149	2958	10.691	0
(NF 2015-2018) – (SF 2015-2018)	3.117	0.108	2958	28.993	0
(Outer HF 2015-2018) – (SF 2015-2018)	1.523	0.142	2958	10.72	0

Appendix 6: Length-at-maturity curves with observations



Appendix 6: Length-at-maturity observations and fitted curves (solid line) with confidence intervals (dotted line) for the fjords Nordfjord (NF) (upper left), Sognefjord (SF) (upper right), Inner (lower left) and Outer (lower right) Hardangerfjord (HF). Length at 50% maturity (L_{50}) were larger for NF than the three other fjords.

Appendix 7: Length-weight relationship and conditions



Appendix 7.1: Mean length-weight relationship for the fjords Nordfjord, Sognefjord, and inner and outer Hardangerfjord in the periods 1997-2002, 2005-2008, and 2015-2018. The slope (parameter b) was estimated to 3.03, and the intercept (parameter a) were estimated to be 0.00601.

Appendix 7.2: Output from posthoc-test with the emmeans package of Fjord*Period interactions comparing condition (relative weight as percentage of mean weight) of sprat. The Fjords are Nordfjord (NF), Sognefjord (SF), and inner and outer Hardangerfjord (HF), and the three time periods are 1997-2002, 2005-2008, and 2015-2018.

contrast	**estimate**	**SE**	**df**	**t.ratio**	**p.value**
(Inner HF 1997-2002) - (NF 1997-2002)	-6.902	0.96	3188	-7.19	<0.001
(Inner HF 1997-2002) - (Outer HF 1997-2002)	-2.354	1.392	3188	-1.691	0.873
(Inner HF 1997-2002) - (SF 1997-2002)	-6.875	0.78	3188	-8.812	<0.001
(Inner HF 1997-2002) - (Inner HF 2005-2008)	6.639	1.212	3188	5.477	<0.001
(Inner HF 1997-2002) - (NF 2005-2008)	13.111	1.299	3188	10.094	<0.001
(Inner HF 1997-2002) - (Outer HF 2005-2008)	2.322	1.348	3188	1.723	0.858
(Inner HF 1997-2002) - (SF 2005-2008)	8.379	0.802	3188	10.449	<0.001
(Inner HF 1997-2002) - (Inner HF 2015-2018)	11.082	0.864	3188	12.824	<0.001
(Inner HF 1997-2002) - (NF 2015-2018)	6.353	1.137	3188	5.587	<0.001
(Inner HF 1997-2002) - (Outer HF 2015-2018)	10.72	1.318	3188	8.137	<0.001
(Inner HF 1997-2002) - (SF 2015-2018)	8.363	0.938	3188	8.913	<0.001
(NF 1997-2002) - (Outer HF 1997-2002)	4.548	1.495	3188	3.042	0.097
(NF 1997-2002) - (SF 1997-2002)	0.027	0.952	3188	0.028	1
(NF 1997-2002) - (Inner HF 2005-2008)	13.541	1.329	3188	10.186	<0.001
(NF 1997-2002) - (NF 2005-2008)	20.013	1.409	3188	14.205	<0.001
(NF 1997-2002) - (Outer HF 2005-2008)	9.224	1.454	3188	6.345	<0.001
(NF 1997-2002) - (SF 2005-2008)	15.281	0.97	3188	15.755	<0.001
(NF 1997-2002) - (Inner HF 2015-2018)	17.984	1.022	3188	17.597	<0.001
(NF 1997-2002) - (NF 2015-2018)	13.255	1.261	3188	10.509	<0.001
(NF 1997-2002) - (Outer HF 2015-2018)	17.622	1.426	3188	12.357	<0.001
(NF 1997-2002) - (SF 2015-2018)	15.266	1.085	3188	14.064	<0.001
(Outer HF 1997-2002) - (SF 1997-2002)	-4.522	1.387	3188	-3.261	0.051
(Outer HF 1997-2002) - (Inner HF 2005-2008)	8.993	1.668	3188	5.39	<0.001

(Outer HF 1997-2002) - (NF 2005-2008)	15.465	1.732	3188	8.927	<0.001
(Outer HF 1997-2002) - (Outer HF 2005-2008)	4.675	1.769	3188	2.643	0.256
(Outer HF 1997-2002) - (SF 2005-2008)	10.732	1.399	3188	7.673	<0.001
(Outer HF 1997-2002) - (Inner HF 2015-2018)	13.436	1.435	3188	9.36	<0.001
(Outer HF 1997-2002) - (NF 2015-2018)	8.707	1.615	3188	5.393	<0.001
(Outer HF 1997-2002) - (Outer HF 2015-2018)	13.074	1.746	3188	7.487	<0.001
(Outer HF 1997-2002) - (SF 2015-2018)	10.717	1.481	3188	7.235	<0.001
(SF 1997-2002) - (Inner HF 2005-2008)	13.515	1.206	3188	11.205	<0.001
(SF 1997-2002) - (NF 2005-2008)	19.987	1.293	3188	15.455	<0.001
(SF 1997-2002) - (Outer HF 2005-2008)	9.197	1.342	3188	6.853	<0.001
(SF 1997-2002) - (SF 2005-2008)	15.254	0.792	3188	19.248	<0.001
(SF 1997-2002) - (Inner HF 2015-2018)	17.957	0.855	3188	20.991	<0.001
(SF 1997-2002) - (NF 2015-2018)	13.228	1.131	3188	11.701	<0.001
(SF 1997-2002) - (Outer HF 2015-2018)	17.596	1.312	3188	13.413	<0.001
(SF 1997-2002) - (SF 2015-2018)	15.239	0.93	3188	16.38	<0.001
(Inner HF 2005-2008) - (NF 2005-2008)	6.472	1.592	3188	4.066	<0.01
(Inner HF 2005-2008) - (Outer HF 2005-2008)	-4.317	1.631	3188	-2.646	0.254
(Inner HF 2005-2008) - (SF 2005-2008)	1.74	1.22	3188	1.426	0.959
(Inner HF 2005-2008) - (Inner HF 2015-2018)	4.443	1.262	3188	3.52	<0.05
(Inner HF 2005-2008) - (NF 2015-2018)	-0.286	1.463	3188	-0.196	1
(Inner HF 2005-2008) - (Outer HF 2015-2018)	4.081	1.607	3188	2.54	0.315
(Inner HF 2005-2008) - (SF 2015-2018)	1.724	1.314	3188	1.312	0.978
(NF 2005-2008) - (Outer HF 2005-2008)	-10.79	1.697	3188	-6.359	<0.001
(NF 2005-2008) - (SF 2005-2008)	-4.733	1.306	3188	-3.623	<0.05
(NF 2005-2008) - (Inner HF 2015-2018)	-2.029	1.345	3188	-1.508	0.939
(NF 2005-2008) - (NF 2015-2018)	-6.758	1.535	3188	-4.402	0.001
(NF 2005-2008) - (Outer HF 2015-2018)	-2.391	1.673	3188	-1.429	0.958
(NF 2005-2008) - (SF 2015-2018)	-4.748	1.394	3188	-3.405	0.033
(Outer HF 2005-2008) - (SF 2005-2008)	6.057	1.355	3188	4.471	<0.001
(Outer HF 2005-2008) - (Inner HF 2015-2018)	8.76	1.392	3188	6.291	<0.001
(Outer HF 2005-2008) - (NF 2015-2018)	4.031	1.576	3188	2.557	0.305
(Outer HF 2005-2008) - (Outer HF 2015-2018)	8.399	1.711	3188	4.908	<0.001
(Outer HF 2005-2008) - (SF 2015-2018)	6.042	1.44	3188	4.197	<0.01
(SF 2005-2008) - (Inner HF 2015-2018)	2.703	0.875	3188	3.089	0.085
(SF 2005-2008) - (NF 2015-2018)	-2.026	1.146	3188	-1.768	0.835
(SF 2005-2008) - (Outer HF 2015-2018)	2.342	1.325	3188	1.768	0.836
(SF 2005-2008) - (SF 2015-2018)	-0.015	0.949	3188	-0.016	1
(Inner HF 2015-2018) - (NF 2015-2018)	-4.729	1.19	3188	-3.974	<0.01
(Inner HF 2015-2018) - (Outer HF 2015-2018)	-0.362	1.363	3188	-0.265	1
(Inner HF 2015-2018) - (SF 2015-2018)	-2.718	1.002	3188	-2.714	0.22
(NF 2015-2018) - (Outer HF 2015-2018)	4.367	1.551	3188	2.816	0.174
(NF 2015-2018) - (SF 2015-2018)	2.01	1.245	3188	1.615	0.904
(Outer HF 2015-2018) - (SF 2015-2018)	-2.357	1.412	3188	-1.67	0.882

Appendix 7.3: Output from posthoc-test with the emmeans package includes estimated mean (emmean), standard error (SE), degrees of freedom (df), lower and upper confidence levels of condition (relative weight as percentage of mean weight) of sprat in the Norwegian fjords Nordfjord (NF), Sognefjord (SF), inner and outer Hardangerfjord (HF) in three time periods.

Fjord	Period	emmean	SE	df	lower.CL	upper.CL
Inner HF	1997-2002	104.048	0.558	3188	102.953	105.143
NF	1997-2002	110.95	0.781	3188	109.419	112.481
Outer HF	1997-2002	106.402	1.275	3188	103.902	108.901
SF	1997-2002	110.923	0.545	3188	109.855	111.992
Inner HF	2005-2008	97.409	1.076	3188	95.299	99.519
NF	2005-2008	90.937	1.173	3188	88.637	93.236
Outer HF	2005-2008	101.726	1.226	3188	99.322	104.131
SF	2005-2008	95.669	0.575	3188	94.541	96.798
Inner HF	2015-2018	92.966	0.659	3188	91.673	94.259
NF	2015-2018	97.695	0.991	3188	95.753	99.637
Outer HF	2015-2018	93.328	1.193	3188	90.988	95.667
SF	2015-2018	95.685	0.754	3188	94.206	97.163