Spatiotemporal variation in the density distribution of sprat (*Sprattus sprattus*) in Hardangerfjorden and Sognefjorden

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Table of Content

Symbols and definitions

TS	Target strength of one scatterer [dB re 1 m^2]
NASC/S_A	Nautical area scattering coefficient [m^2/nmi^2]
s_i	The altitude of the sun at the start of the *i*th nautical mile
ε_i	Error term
D	Amplitude of diel variation
α	Slope of the logistical curve, an indication of the diel migration speed
β	Midpoint of the logistical curve, where migration occurs

Abstract

Sprat (*Sprattus sprattus)* is a pelagic fish species of considerable importance for the Norwegian fjord ecosystems, especially in Sognefjorden and Hardangerfjorden. Coastal habitats like fjords are heavily impacted by human stressors such as aquaculture, hydropower, fishing, industry, and climate change. Therefore, there is a need to better understand how sprat is affected by these stressors regarding spatiotemporal distribution, behavioural changes, and abundance. During this thesis, the density structure of sprat, both horizontally and vertically, was investigated in two Norwegian fjords, Sognefjorden and Hardangerfjorden, to look for potential seasonal differences. The data were collected with research vessels using an echosounder (38 kHz) during an annual survey in the period 2015-2021, covering both summer and winter, though in different years. It appears as if most of the sprat density in Sognefjorden shifts further into each fjord arm during winter while staying further out in summer. However, this pattern did not appear for Hardangerfjorden. As for the vertical distribution, sprat perform diel vertical migration (DVM) and stay close to the surface at night and deeper during daytime, probably triggered by light intensity changes. During summer, sprat stay closer to the surface than during winter at night-time and performs a longer DVM. No size-dependent pattern was found when comparing horizontal and vertical distribution between small and large sprat. This master thesis shows that there is an effect of season and time of day on sprat's spatiotemporal distribution that might impact the abundance estimates from the surveys. Depending on the severity of human impact, the abundance of sprat might diminish further, ultimately affecting the entire fjord ecosystem.

Keywords: Sprat, acoustics, fjord arm, Sognefjorden, Hardangerfjorden, research vessel, seasonal, summer, winter, horizontal, diel vertical migration.

1 Introduction

The European sprat (*Sprattus sprattus*) is a small schooling clupeid species which inhabits the pelagic water masses (Limborg et al. 2009). Sprat usually gets no older than five years (Bailey 1980) and has a maximum length of 16 cm (Whitehead 1985). It has a wide range of distribution, inhabiting the Norwegian fjords, the Baltic Sea, Skagerrak-Kattegat, and the Bay of Biscay (Whitehead 1985, Glover et al. 2011, Quintela et al. 2020). Sprat is an important prey for several seabirds (Hansson et al. 2017), fish (Österblom et al. 2006, Mikkonen et al. 2011, Pachur and Horbowy 2013) and sea mammals (Lundström et al. 2010). Additionally, sprat feeds on zooplankton (Möllmann et al. 2004, Falkenhaug and Dalpadado 2014). Sprat, therefore, makes the transfer of energy possible from the lowest of the trophic levels to the highest in the marine food web, making it a so-called wasp-waist species (Fauchald et al. 2011). Given its energy transfer potential, sprat can be considered an ecosystem key species in the Norwegian fjord system, making it a species of considerable importance, especially for two of Norway's largest sprat fjords; Sognefjorden and Hardangerfjorden.

Regarding quotas, advice on sprat is split into two areas, the oceanic sprat (The North Sea and Skagerrak-Kattegat) and the coastal sprat (Norwegian coast and fjords) (Quintela et al. 2020). Whether or not this represents the true underlying biological unit is debated because recent studies using genetics show that sprat is distributed in many sub-populations and that genetic differences were lacking amongst fjord sprat populations, indicating a high level of gene flow between fjord populations (Quintela et al. 2020). Additionally, Glover et al. (2011) showed little connectivity between sprat populations in Norwegian fjords and those in the North Sea. Therefore, the fjord populations can be considered reproductively isolated from populations in the North Sea and Baltic Sea (Glover et al. 2011).

Sprat has also historically been a harvested fish species along the Norwegian coast, especially for the canning industry (Bakken 1973, Torstensen and Gjøsæter 1995). While sprat harvest is not as prominent as before, it is ongoing (ICES HQ 2021). Sales slips data from the Directorate of Fisheries shows that the harvest of sprat has drastically gone down since 1960 (Figure 1). While many factors could contribute to this, a reduction in sprat abundance could be a possible explanation. This reduction in sprat numbers could have consequences for other species in the Norwegian fjords relying on sprat as a main source of prey like the cod, whiting etc. (Kaartvedt et al. 2009), affecting their population abundance as well (Falkenhaug and Dalpadado 2014).

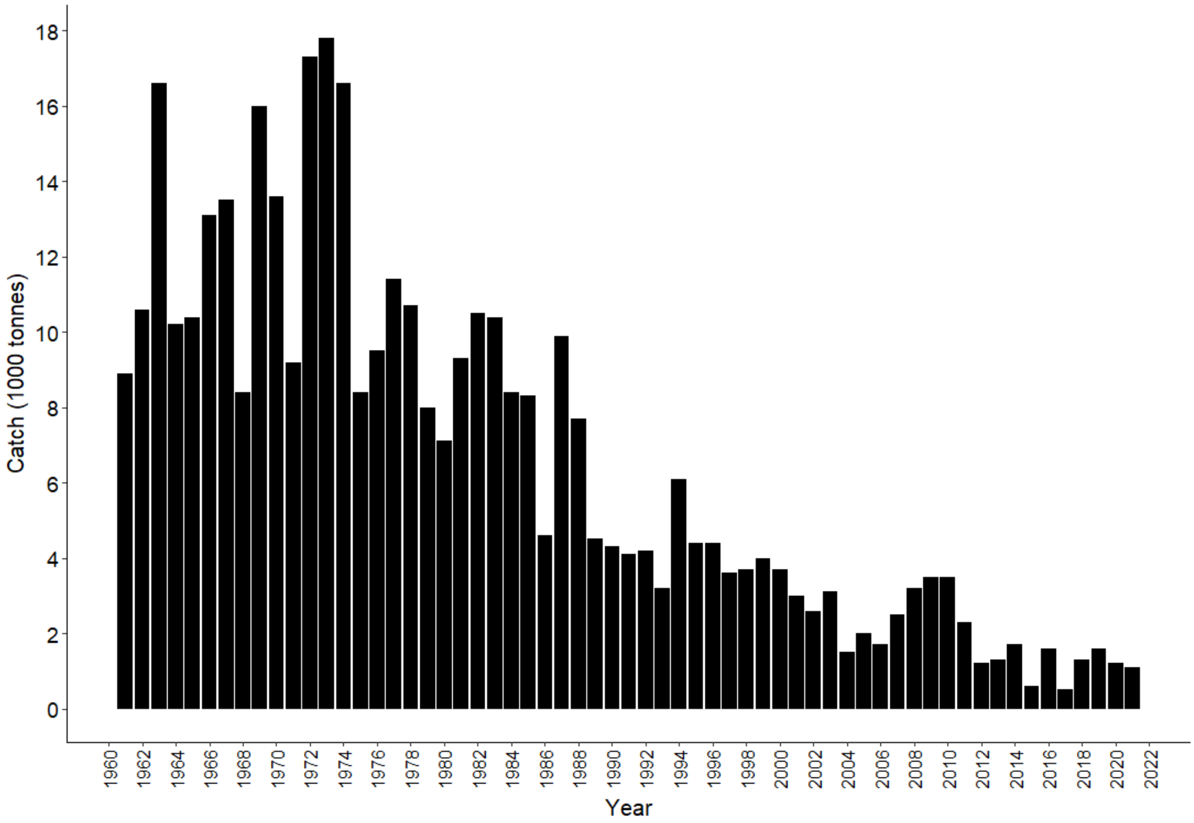


Figure 1 Annual catches of sprat from 1960-2021 from sale slips data from the Directorate of Fisheries.

Many factors affect species abundance, mainly since human activity heavily exploits coastal areas (Rick and Erlandson 2009). The Norwegian fjord is affected by direct and indirect human activities such as climate changes (Wernberg et al. 2021), hydropower and runoffs (Gracey and Verones 2016), fish farming (Tiller et al. 2012), fishing (Gullestad et al. 2013), industry activities (Azad et al. 2019), transport (Dalsøren et al. 2007), etc. These stressors may affect the hydrographical conditions (Sánchez Navarro et al. 2007), ecosystem processes (Hooper et al. 2005) and the food web (Bascompte et al. 2005, Essington et al. 2006) in the fjord ecosystems (Frigstad et al. 2020). Given all these possible human impacts, it is essential to monitor these changes and how our impacts affect the coastal and fjord ecosystems, especially for two of Norway's largest fjord systems and the most important sprat fjords Sognefjorden and Hardangerfjorden. These fjords also experience human impacts like littering and lost fishing gear (Buhl-Mortensen and Buhl-Mortensen 2014). Furthermore, Hardangerfjorden is also one of the largest areas for salmon farming in Norway; therefore, the ecosystem can be negatively affected by farm waste (Husa et al. 2014) and mercury pollution from the likes of aquaculture or hydropower plants (Azad et al. 2019).

The behaviour and distribution of sprat may be affected by changes in the hydrographical conditions of the fjords, and a better understanding of the natural behaviour is needed. Despite multiple studies on the spatiotemporal distribution of Norwegian fjord sprat in Oslofjorden (Solberg et al. 2012, Solberg and Kaartvedt 2014, Solberg et al. 2015, Solberg and Kaartvedt 2017, Kaartvedt et al. 2021), much is still unknown for sprat in Hardangerfjorden and Sognefjorden.

Sprat is a visual feeder (Solberg and Kaartvedt 2017), meaning that they need sufficient light to forage for prey (Voss et al. 2003). Multiple studies have shown that sprat in the Norwegian fjords and the Baltic Sea performs diel vertical migration (DVM) (Bernreuther et al. 2013, Solberg and Kaartvedt 2014, 2017). DVM is a widespread movement pattern for many marine organisms like plankton (Ohman 1990) and fish (Watanabe et al. 1999). There can be multiple reasons behind this change, like avoidance of predators (Ringelberg 1991), foraging for prey (Levy 1990), or optimizing bioenergetics (Wurtsbaugh and Neverman 1988). The aim of DVM can be to stay in a so-called antipredation window, meaning the most suited depth to hunt for prey while remaining as hidden from predators as possible (Scheuerell and Schindler 2003). The mirroring of plankton prey could mean that sprat in Sognefjorden and Hardangerfjorden also performs DVM or that they follow the light intensity levels, especially during feeding season when light intensity is more substantial. The schooling patterns of sprat might be different depending on the day or night situation. A study by Solberg and Kaartvedt (2017) in Bunnefjorden, Oslofjord showed that sprat was schooling at 50 m during the daytime, then dispersing to the surface about 4 min before sunset (Solberg and Kaartvedt 2017). Fish can implement different behavioural strategies, like schooling or shoaling, for survival purposes. Shoaling being a less structured aggregation of social groups in the same area, while schooling is the more well-ordered and synchronised movement of individuals in a group traveling in the same direction (Miller and Gerlai 2012).

This differing schooling pattern appears to be the same for other locations; while researching sprat in Lough Hyne (Ireland), Knudsen et al. (2009) found that sprat formed denser schools during the day and having the schools disperse during night-time when ascending to the surface. A study done by Falkenhaug and Dalpadado (2014) showed that sprat in Hardangerfjorden in Norway had *Microsetella norvegica* as the main prey of choice. In the Baltic Sea, *Temora longicornis*, and *Podon spp*. were the main preys (Bernreuther et al. 2013). Sprat can perform both selective feeding, which will require adequate light and filter-feeding, which does not have such requirements (Arrhenius 1996, Falkenhaug and Dalpadado 2014).

During overwintering, sprat in Oslofjorden inhabit deeper areas of the fjords, down to 150 m depth (Kaartvedt et al. 2009, Solberg et al. 2012). Interestingly, sprat can tolerate waters with low oxygen saturation (5-7 %) (Kaartvedt et al. 2009). This high tolerance proves beneficial in avoiding predators that cannot handle such low levels and allows for better survival. While investigating the diel vertical migration of overwintering sprat, Solberg and Kaartvedt (2017) showed that sprat were able to dive into severely hypoxic waters to feed on overwintering *Calanus spp* (Solberg and Kaartvedt 2017).

A study done in the Baltic Sea by Baumann et al. (2008) showed that *Acartia spp.* had its highest abundance during the summer months (June-July) when the surface water temp was above 12 °C. Arctica spp. is an important prey species for sprat (Baumann et al. 2008, Falkenhaug and Dalpadado 2014). Studies on the feeding ecology of sprat and herring in both the Baltic and the coast of Scotland show that they have higher feeding activity during spring, summer, and autumn than during winter (De Silva 1973, Möllmann et al. 2004). This difference in feeding behaviour could mean that sprat prefer areas further out in the fjord during summer/autumn due to a higher abundance of larger size zooplankton during these warmer seasons to optimize feeding (Falkenhaug and Dalpadado 2014). Reversely, a pattern might occur where sprat inhabits deeper areas of the fjord for protection while overwintering since feeding is not a significant priority. Optimal foraging theory (OFT) entails how an organism should act to maximise its energy intake (Stephens and Krebs 2019), meaning how and when an animal should feed to grow the fastest while reducing the chance of being eaten. To feed is a risk/reward choice the sprat must make. At the same time, it is potentially more food further out in the fjord (Falkenhaug and Dalpadado 2014) and further up in the water column (Lyse et al. 1998). These areas might also have the most predators (Hedger et al. 2011) and be the area where sprat is most easily spotted by predators (Solberg and Kaartvedt 2017). However, OFT also serves other purposes, such as increasing reproductive success (Brooker et al. 2013) and growing out of the size limitation of some predators (Cowan et al. 1996). Smaller sprat might take more risk to forage to grow enough to survive the coming winter, staying in more well-lit areas further up the water column, potentially having more predators (Biro et al. 2005). In contrast, larger sprat might favour predator avoidance and stay deeper (Solberg et al. 2015).

A common way to investigate a species' distribution, abundance and behaviour is acoustics (Simmonds 2003), which have been invaluable for fisheries stock assessment for decades (Koslow 2009). It is usually combined with trawling data for acoustic classification and to get the size and species composition of acoustic observations (Forebes.S.T and O.Nakk 1972, Reid and Simmonds 1993). Acoustic trawl surveys are usually done with vessels to investigate the geographical distribution of the target species. These vessels are equipped with an echosounder collecting acoustic data and a fishing gear, e.g., a trawl, making ground-truthing possible. During these acoustic surveys, echo sounders collect acoustic data that can be transformed to NASC (Nautical Area Scattering Coefficient), which means the echo energy pr 1 square nautical mile. By using this echosounder data, the spatio temporal distribution of sprat can be investigated, which can help in our understanding of its behaviour, and how it may be affected in the future if its continual exposure to human stressors. This furthering of knowledge is important not only for management purposes but also in aiding in preservation for the benefit of the ecosystem.

This thesis's main objective is to use acoustic data to investigate the horizontal and vertical distribution in the two important sprat fjords, Hardangerfjorden and Sognefjorden.

- Use NASC values of sprat to see whether there are any significant differences in density of sprat between seasons for each fjord arm. This analysis will see whether more abundance will relocate itself from the main fjord arm to the inner fjord arms during winter while remaining further out during summer.

- Investigate how the centre of gravity in sprat horizontal distribution within all fjord arms changes between seasons (summer vs winter). This analysis will test whether sprat will be in the inner part of the fjord arm during the winter season and further out during the summer season. Additionally, further analysis will be included focusing only on each fjord's main fjord to see where the sprat NASC values start to increase earlier in the fjord and reach a plateau earlier during summer than during winter regarding NASC. Finally, see whether the individual size of sprat determines its location within the fjord, using different size classes of sprat (above and including 7 cm vs under 7 cm) to test catch rates of different locations within each fjord. Here the goal will be to test the hypothesis that smaller sprat is more frequently caught further into the fjord, while larger induvial are more commonly caught further out.

- Look at how the sprat's location in the water column changes through the day and test how season (summer vs winter), solar altitude, and individual length (above and including 7 cm vs under 7 cm) affect sprat vertical position in the water column. These analyses will test the hypothesis that sprat stays deeper during the day and shallower during the night (performing diel vertical migration) and that solar altitude will affect the timing of this migration, therefore giving a seasonal difference. Furthermore, for the size class analyses, this will be to test the hypothesise that smaller individuals stay further up in the water column than larger individuals taking a higher risk to feed to ensure that they survive the winter season

2 Materials and Methods

2.1 Study area and period

The Institute of Marine Research (IMR) database provides all data used in this thesis. IMR conducted annual acoustic trawl surveys on the Norwegian fjord sprat populations in Norwegian fjords from 1975 until 2008 before reinstating the annual surveys in 2015.

This thesis will study data from 2015 to 2021 in Sognefjorden and Hardangerfjorden (Figure 2), which are the two fjords with the highest abundance of sprat. The annual surveys in 2015-2018 were carried out in late November and early December (Table 1). From 2019, the survey period was changed to the summer season (early June to early September) (see Table 1 for further details). This change was done to perform the survey before the fishing season began, removing some uncertainties regarding abundance in the fjord before harvest. The Research Vessel Haakon Mosby (HM) was used in 2015, and the Research Vessel Kristine Bonnevie (KB) in surveys thereafter (Table 1).

The surveys covered the entire fjords, including most smaller fjord arms. The fjords were separated into many strata, and the effort was allocated based on the area of the fjords. For each stratum, the survey design used the Rstox_surveyplanner (Holmin et al. 2019) to make a "zig-zag" route. The transects had a random starting position in each stratum that ensured an equal probability of coverage within a stratum (Harbitz 2019) (see appendix Figures 18-20). The vessel speed was about 8 knots mid-fjord but was reduced to a few knots before each turn when the vessel was close to the shore.

Figure 2 Map over study area of Norwegian fjords; Sognefjorden and Hardangerfjorden covered in the surveys from 2015-2021.

Table 1. IMR sprat surveys and data collected. HM refers to RV Haakon Mosby and KB RV Kristine Bonnevie. HF is short for Hardangerfjorden, and SF Sognefjorden.

Year	Survey number	Vessel	Start date	End date	Season	HF	SF
2015	2015625	HM	3.12	6.12	Winter	x	x
2016	2016624	KB	6.12	16.12	Winter	x	x
2017	2017623	KB	25.11	6.12	Winter	x	x
2018	2018625	KB	24.11	9.12	Winter	x	x
2019	2019620	KB	21.6	30.6	Summer	x	x
2020	2020618	KB	10.8	17.08	Summer	x	x
2021	2021619	KB	21.8	24.8	Summer	x	
2021	2021621	KB	26.8	7.9	Summer	x	x

2.2 Data collection

Acoustic data collection and processing

The acoustic data were recorded with SIMRAD EK60 (2015) (Andersen 2001) and SIMRAD EK80 (Demer et al. 2017) 38kHz calibrated split-beam echosounders along the transects. These echosounders consist of three main parts: a computer with the echosounder software for data storage and echosounder settings and a transceiver that transmits and receives an electrical signal through a cable that is connected to the transducer. The transducer on HM is mounted on the hull, and they are mounted on the drop keel on KB. For all the sprat surveys, the valid echo sounder recordings are from 8 m below the sea surface as the total blind zone consists of the transducer depth (~6 m) plus the 2 meters near field of the 38 kHz echosounder (SIMARD 2015). For all surveys, the ping rate, i.e., how frequent a sound pulse is sent from the transducer, was around 1 per second. Data from other echosounder frequencies (18 kHz, 70 kHz, 120 kHz, 200 kHz) were recorded during the surveys, but only 38 kHz data was used for the acoustic categorization and the analyses in this work. The echo sounders were calibrated using standard sphere calibration methods using metal spheres of known echo reflection strength (Foote 1987, Simmonds and MacLennan 2008).

During the surveys, the recorded echo sounder data were scrutinized using the post-processing LSSS (Korneliussen et al. 2016) software. The main aim was to identify and categorize the different acoustic backscatters observed in the water column. The backscatter is the energy received to the transducer reflected from objects with a different density than the water, e.g., the ocean floor, plankton, or fish. Sprat has a swim bladder filled with gas, which has a different density than the surrounding water. To quantify the acoustic energy received from the sprat, the following scrutinizing procedure has been used for all surveys:

Step 1: Define the upper interpretation depth (8 m)

Step 2: Define the bottom

Step 3: Remove non-biological backscatter such as vessel noise and false echo from the seabed (Korneliussen et al. 2016)

Step 4: Filtering away plankton and other weak targets by using thresholding (Figure 3).

Step 5: Once the plankton is removed by thresholding down the dB, the remaining targets are categorized into the most likely category based on the biological knowledge regarding the species of the people doing the scrutinizing process to separate what is most likely sprat and what is categorized as "other". The backscatter is attributed to different acoustic categories: "sprat", "herring", and "other". Sprat can also be confused with herring due to the similar echo values and ecology. The trawl sample could aid in the percentwise division between sprat and herring if trawling were performed in the same location as acoustic interpretation.

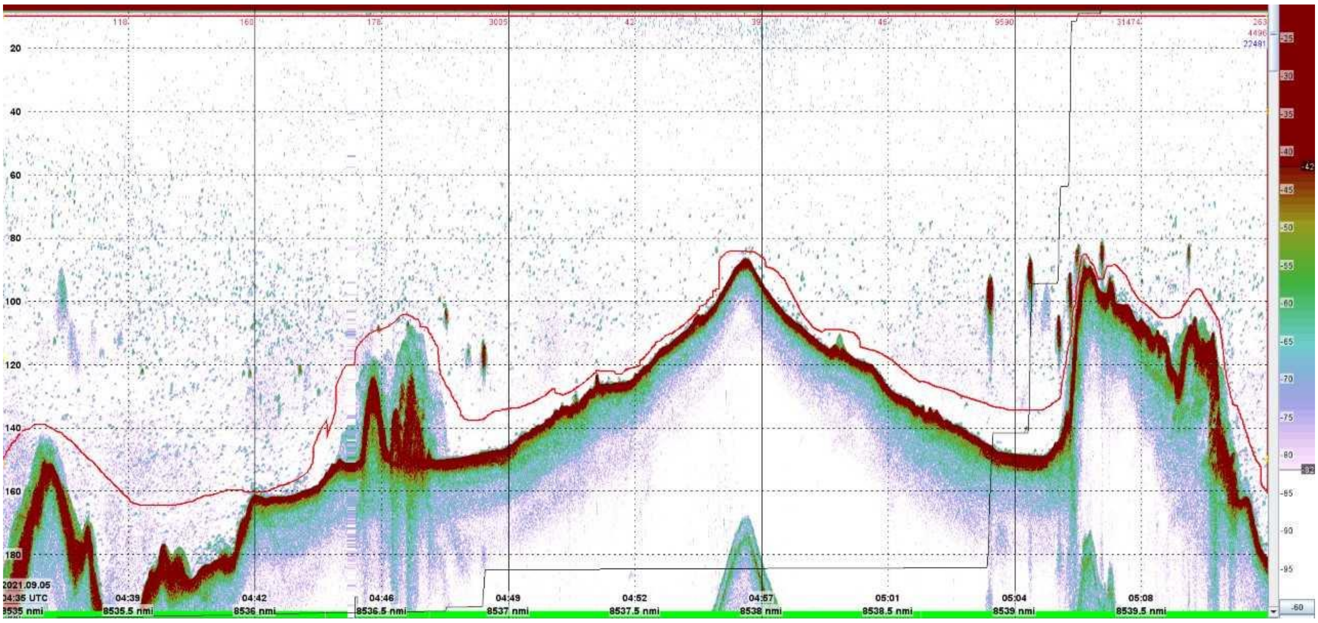
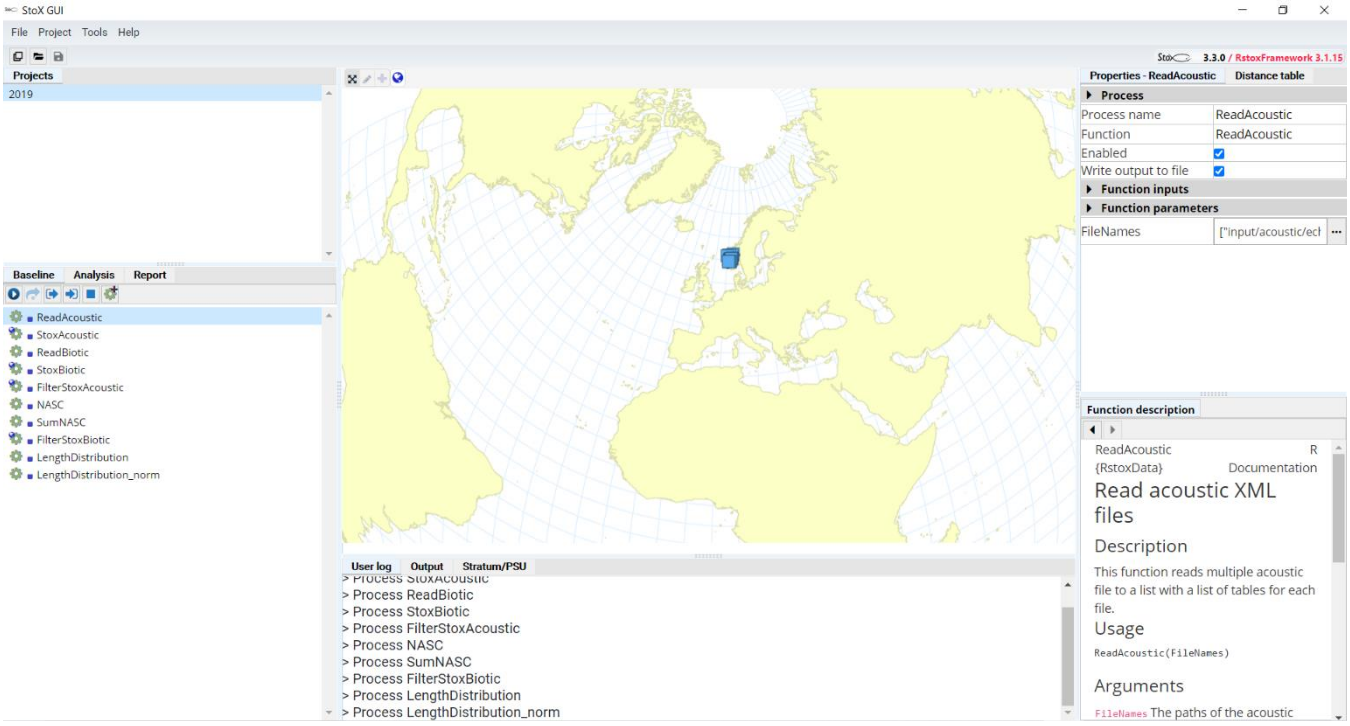


Figure 3 Screen duplicate of LSSS software from the sprat survey in Osafjorden, Hardangerfjorden 2021.

The acoustic density values were stored by acoustic category in Nautical Area Scattering Coefficient (NASC) units (Maclennan et al. 2002). NASC, also known as $S_{A,}$ is the total echo per area unit (1 nmi^2) (Maclennan et al. 2002, Simmonds and MacLennan 2008). This NASC data was stored in a database with a horizontal resolution of 0.1 nautical mile and a vertical mile and a vertical resolution of 10 m, referenced to the surface. The analyses of echo sounder data in this thesis are based on the reports of format LUF20.xml exported from this database named either biotic_ or echosounder_ with a corresponding cruise number, ship name, date, and file version. The acoustic and biotic data was downloaded from IMRs own database https://datasetexplorer.hi.no, choosing the corresponding survey number as seen in Table 1.

Once the data was downloaded, the acoustic and biotic files were prepared for statistical analyses by using the open-source software StoX 3.3.0 (Johnsen et al. 2019). Here the acoustic files are read in with "*ReadAcoustic*", then altered to have a better structure with "*StoxAcoustic*", and then sprat data was filtered out from the using the "*FilterStoxAcoustic*" for acoustic NASC (sprat = acoustic category "20"), the same with "*sumNASC*", which sum NASC data vertically. The biotic data are read in "*ReadBiotic*", then "*StoxBiotic*", and then filtering out biotic sprat data (sprat = "brisling/161789/126425/Sprattus sprattus") with "*FilterStoxBiotic*". To get length composition of sprat from the trawl hauls, the "*LengthDistribution*" function was used for sprat (Figure 4).



2019

- ReadAcoustic
- StoxAcoustic
- ReadBiotic
- StoxBiotic
- FilterStoxAcoustic
- NASC
- SumNASC
- FilterStoxBiotic
- LengthDistribution
- LengthDistribution_norm

Process

Process name	ReadAcoustic
Function	ReadAcoustic
Enabled	☑
Write output to file	☑

Function inputs

Function parameters

FileNames	["input/acoustic/ech

ReadAcoustic {RstoxData} R Documentation

Read acoustic XML files

Description

This function reads multiple acoustic file to a list with a list of tables for each file.

Usage

`ReadAcoustic(FileNames)`

Arguments

`FileNames` The paths of the acoustic

```
> Process StoxAcoustic
> Process ReadBiotic
> Process StoxBiotic
> Process FilterStoxAcoustic
> Process NASC
> Process SumNASC
> Process FilterStoxBiotic
> Process LengthDistribution
> Process LengthDistribution_norm
```

Figure 4 Screen duplication of Stox reading in the survey of 2019, including all steps performed to structure the data used for later analyses from the LUF_20 XML files

The data were imported to R (R Development Core Team,2022) by running the StoX projects using the "*runProject*" function from the R package RStoxFramework (https://github.com/StoXProject/RstoxFramework).

Biological data collection and on-board sampling for sprat and fish in general

Biological samples were collected by targeted trawl hauls (pelagic and bottom) and pelagic blind tows on the surface at dusk and night, mainly lasting for 30 minutes (Kvamme et al. 2010a). Trawl hauls were mainly pelagic (pelagic trawl: Harstad trawl 16x16 [8x8 on HM]) with some targeted bottom tows (bottom trawl: Campelen shrimp trawl). Thyborøn 125" Type 7A trawl doors [7.4 m^2, 1810 kg] were used for all tows. The trawls are equipped with Scanmar sensors that give information regarding e.g., trawl depth, trawl geometry, and fish entrance in the trawl opening.

The on-board sampling follows the procedure from IMR's handbook for sampling fish, crustations and other invertebrates (Mjanger et al. 2021). If the catch size is manageable, the full catch is sorted into species. A representative random subsample is taken if the entire catch is too large to be fully sorted and measured. The critical aspect here is to get a subsample reflecting the actual composition of the entire catch regarding species, length and weight (Mjanger et al. 2021).

From each trawl haul, 100 individuals of sprat were randomly chosen (if the catch was less than 100, fewer sprats were taken). Of these 100 individuals, 30 had their age, sex, maturity, and stomach fullness registered, while all 100 individuals were weighed (g) and length measured (total length down to the closest 0.5 cm).

2.3 Horizontal sprat density

For the spatial analyses, the data were grouped into the main Sognefjorden, the main Hardangerfjorden and several smaller fjords arms (Figures 5-6, Table 2). In the horizontal analyses, there are two different analyses. One analysis for all fjord arms, including the main fjord for both Sognefjorden and Hardangerfjorden, is referred to as all fjord arms analyses. While the second analysis only looks at the main fjord for each fjord (SOG and HAR), referred to as Main fjord arms analyses.

The reasoning behind analysing the main fjord in two different ways is because the main fjord is the area most consistently covered throughout the survey's years, therefore having a much better data foundation to conduct analyses. With this amount of data available, it is possible to perform a more thorough analysis than the rest of the smaller fjord arms.

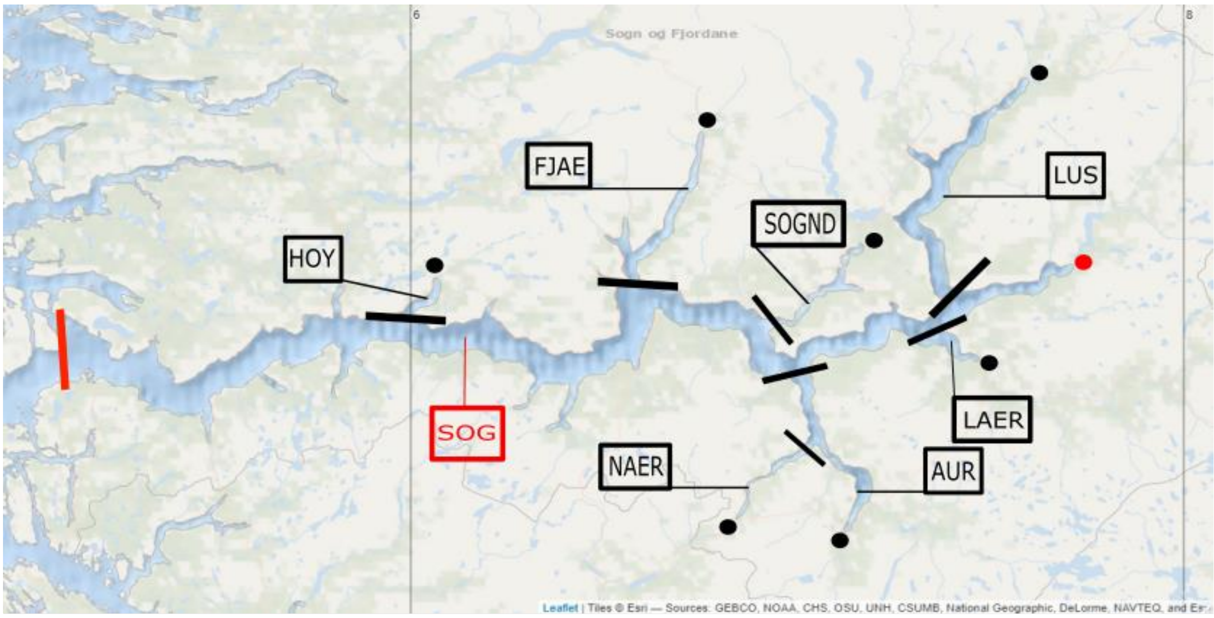


Figure 5 Sognefjorden fjord arms. Red indicates the main fjord; black is the side fjord arms. Dots are the innermost points of each fjord arm (points placed inland to show endpoint), and lines represent the outermost points of each fjord arm.

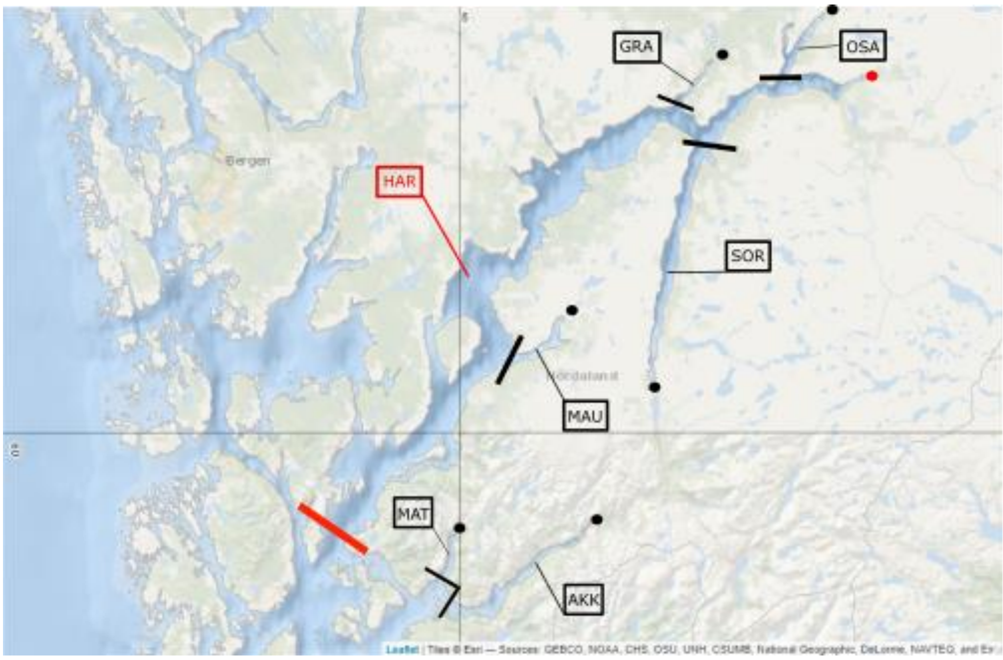


Figure 6 Hardangerfjorden fjord arms. Red indicates the main fjord; black is the side fjord arms. Dots are the innermost points of each fjord arm (points placed inland to show endpoint), and lines represent the outermost points of each fjord arm.

Table 2. Information regarding Sognefjorden and Hardangerfjorden, including manes and lengths of fjord arms.

Fjord	Fjord Arm	Name abbreviation	Fjord arm Length (km)
Sognefjorden	Main Sognefjorden	SOG	136.0
Sognefjorden	Høyangsfjorden	HOY	7.1
Sognefjorden	Fjærlandsfjorden	FJAE	25.4
Sognefjorden	Sogndalsfjorden	SOGND	13.5
Sognefjorden	Nærøyfjorden	NAER	16.2
Sognefjorden	Aurlandsfjorden	AUR	28.2
Sognefjorden	Lærdalsfjorden	LAER	7.9
Sognefjorden	Lustrafjorden	LUS	41.2
Hardangerfjorden	Main Hardangerfjorden	HAR	120.0
Hardangerfjorden	Åkrafjorden	AAK	26.1
Hardangerfjorden	Matersfjorden	MAT	8.2
Hardangerfjorden	Maurangsfjorden	MAU	11.7
Hardangerfjorden	Granvinsfjorden	GRA	7.6
Hardangerfjorden	Sørfjorden	SOR	37.8
Hardangerfjorden	Osafjorden	OSA	12.1

The latitude and longitude coordinates of the acoustic data were used to assign the log distances to each fjord arm (Table 2). To investigate the potential seasonal differences in the average density of sprat the mean NASC by fjord arm and by survey year was estimated as:

$$\overline{NASC_{(k,s)}} = \frac{\sum_{x=1}^{N} NASC_x}{N}$$

Here, the mean NASC for fjord "k" and survey year "s", the sum of all NASCs per log distance, was divided by the total amount of NASC observations (N) of that fjord arm. After which, the mean was log-transformed to suit the model assumptions of normal distribution better when implementing the t-test.

Statistics

For statistical analyses, the goal was to test whether this mean NASC differs between seasons for each fjord arm to investigate any potential seasonal patterns in how most of the sprat abundance locates itself split between the main and side fjord arms. Therefore, a simple t-test (Kim 2015) was implemented for each fjord arm separately, using the t-test function in the R package "stats".

Horizontal distribution analyses: all fjord arms analyses

To study possible seasonal changes in the distribution of density of sprat in the fjords, the centre of gravity in NASC along the main direction of the fjord arms was estimated by fjord arm and survey. First, the webpage geoplaner (https://www.geoplaner.de/) was used to find accurate coordinates for the innermost (dot in Figures 5-6) and outermost (line in Figures 5-6). The analyses did not include fjord arms not covered each year or with a low NASC (below 2% of the total NASC in Hardanger- or Sognefjorden, respectively). However, all fjord arms marked in Figures 5-6 are included in these analyses.

The length of each fjord arm was calculated using the R package "*geosphere*" by calculating the distance between the innermost and the outermost point. To make comparisons between fjord arms easier, the fjord arm distance was normalised to be between 0 and 1, where distance = 0 is at the innermost point, and distance = 1 is at the outermost point.

The centre of gravity (median) of these NASC values, meaning where most of the sprat abundance is located between each fjord arm's innermost and outmost point, was calculated (weighted by NASC) for each survey year (Friedland et al. 2021). This analysis will check for seasonal patterns in horizontal sprat distribution. Each NASC data point has a longitude and a latitude coordinate. The distance between each NASC data point and the innermost point of the fjord arm being investigated was calculated (in meters) using the function "*distm*" in the R package "geosphere" and then normalised by dividing by the total length of the fjord arm. This normalization gives every NASC value a normalized distance between 0 and 1, which refers to the distance from it and to the innermost point. The centre of gravity for NASC data was then calculated using the function "weighted. median" in the R package "*spatstat*", where NASC was used as a weight, meaning that the centre of gravity will skew towards the area with the highest NASC values. Depending on the number given, the result will show the centre of gravity in each fjord arm, between 0 and 1. The closer to 0 it gets, the further in the centre of gravity is located within that fjord arm for a given survey year. It is also worth noting that not all the fjord arms areas are entirely straight; therefore, some NASC datapoint may have a shorter distance towards the innermost point, given that the distance is calculated in a straight line.

Additionally, to look at the distribution of NASC values within each fjord arm by survey, NASC weighted percentiles were calculated. This calculation was done in the R package "*reldist*". The percentiles were then normalized, giving a number between 0 to 1.

Statistics:

A two-way ANOVA was used to investigate whether the centre of gravity in each fjord arm changed between seasons (summer and winter). The model has a continuous variable (centre of gravity) and two categorical predictors (season and fjord arm). The model was tested on the fjord arms in Hardangerfjorden and Sognefjorden separately.

Horizontal distribution analyses: main fjord arm analyses

The large-scale horizontal analysis investigates the same questions as the small-scale analyses, taking a different approach, focusing only on the main fjord arms (SOG and HAR, respectively, Figures 5-6). This analysis will investigate where the rise in NASC values occurs in the fjord, at what point a plateau is reached, and whether the season has any effect.

Each fjord (SOG and HAR) was divided into increments of 0.2 degrees longitude, starting from the outermost point of the fjord, and ending at the innermost point. A sum of all NASC vales per log distance was calculated within each increment. A cumulative sum of NASC was then calculated, summing the current and all previous increments' NASC sums. All increment NASC sum numbers were normalized between 0 and 1. The innermost point, where all NASC data has been accounted for, was set to 1, and the outermost point to 0. The same was done with fjord arm distance. This normalization was done for easier comparisons between surveys years,

$$Cumulative\ sum\ NASC\ = \sum_{i=1}^{n} x_i + x_{i-1} \dots x_{i-n}$$

Where *i* is the increment number, *X* is NASC at the corresponding *i*th increment. So, every increment is a sum of the current and all previous increments.

Statistics:

A two-sample Kolmogorov-Smirnov test was employed to compare the cumulative NASC distribution of sprat between years. The model was tested on Hardangerfjorden and Sognefjorden separately.

Comparing the horizontal distribution of small and large sprat

It was tested whether the horizontal distribution, meaning location in the fjord, differs between two length classes of sprat ($\geq$ 7 cm and < 7 cm). In the program Stox (Johnsen et al. 2019), catch data was normalized as if the trawling distance was 1 nautical mil, using the "*normalized*" and "*weight*" setting in the "*LengthDistribution*" function.

Both Hardangerfjorden and Sognefjorden were split into four areas: innermost, inner, intermediate, and outer (Figures 7-8), following a similar split as Falkenhaug and Dalpadado (2014). Horizontal distribution analyses by length class were done to check for differences between two size classes of sprat distributed within the fjord regarding horizontal positioning. The reasoning behind having the split here at 7 cm is that the average length of 0-year-old sprat is usually between 7.5 and 8 cm (Solberg et al. 2015). In contrast, they reach maturity at approximately 10 cm at about two years old (Glover et al. 2011, Peck et al. 2012). Therefore, by setting the bar slightly lower than the average, it is possibly safe to believe that all sprat included in the Under 7 cm category is 0-year-old sprat. The catch rates of the two size classes of sprat ($\geq$7cm and < 7cm) standardized to a towing distance of one nautical mile were summed up for all stations by area and by survey using a simple summing function:

$$Total\ Catch\ Rate_{x,y,i} = \sum Catch\ rates_{x,y,i}$$

To find the total catch rates (n/nmi) of the different size classes of sprat ($\geq$7cm and < 7cm) for a given position in the fjord (Innermost, Inner, Intermediate or outer), the sum of the catch rates (n/nmi) of all stations within that position “x”, for the given survey year “i”, for that size class “y” was calculated. This analysis was done separately in Hardangerfjorden and Sognefjorden.

Statistics:

A two-way ANOVA (Lopes et al. 2015) model was run for each size class separately for Hardangerfjorden and Sognefjorden. Log-transformed catch rates (continuous variable) were tested against the two categorical predictor variables, season and location.

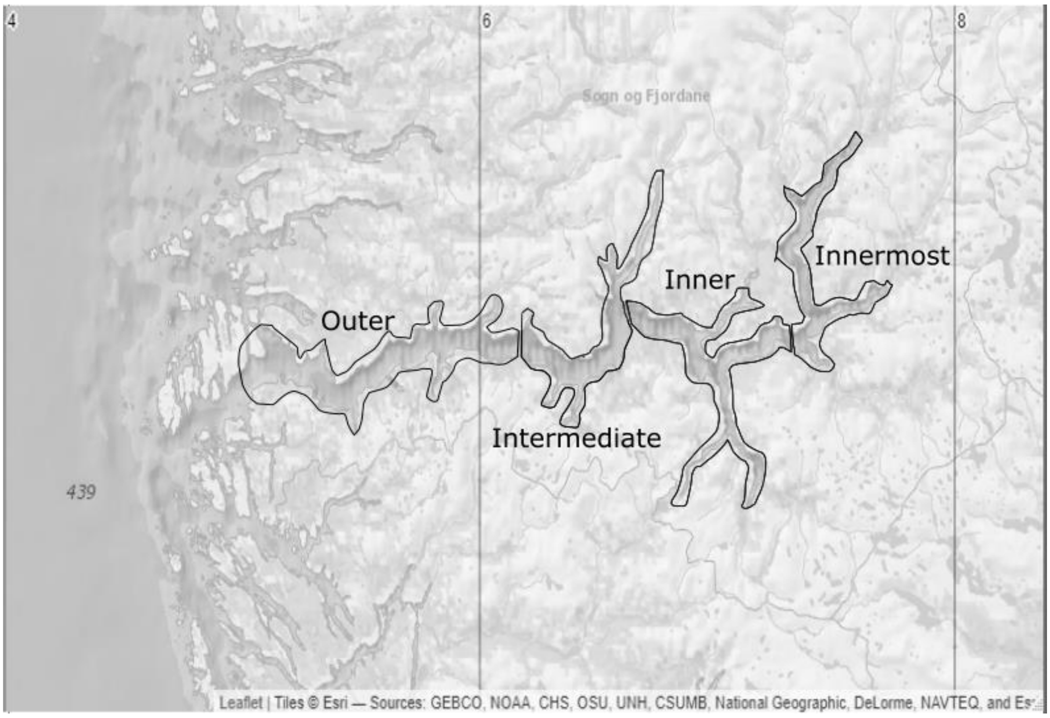


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Figure 7 Sognefjorden division for analyses of size class distribution.

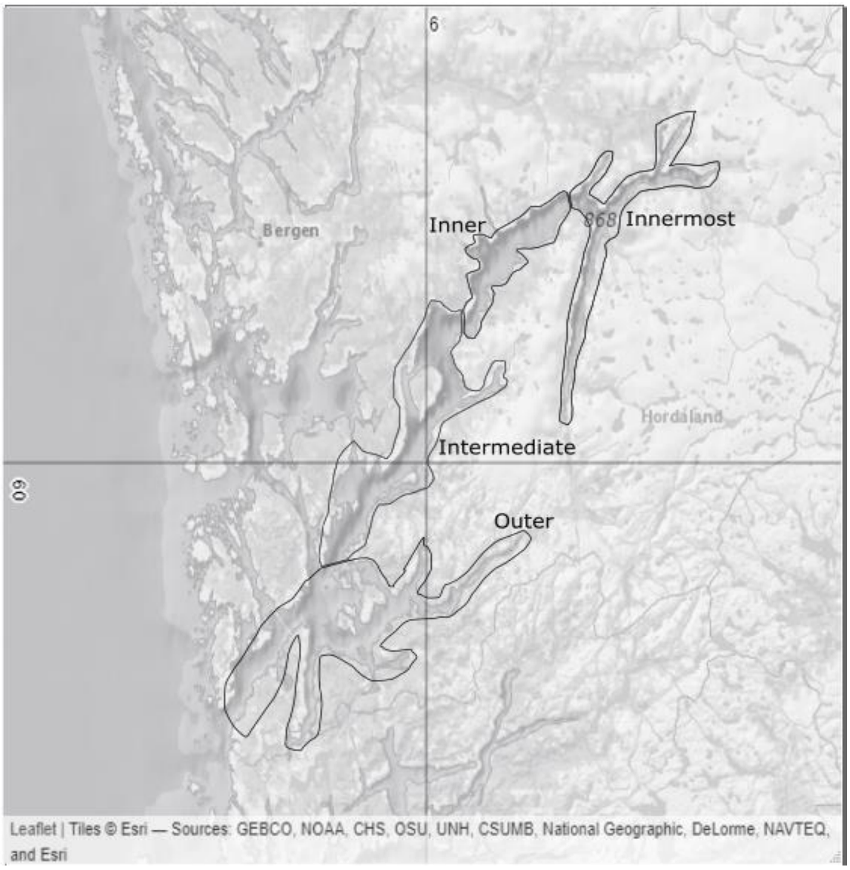

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Figure 8 Hardangerfjorden division for analyses of size class distribution

2.4 Vertical sprat density

Diel vertical distribution

To study the potential diel vertical migration of sprat, a vertical centre of gravity of NASC of sprat was defined by log distance *(j)*:

$$Weighted\ mean\ depth\_j\ = \frac{\sum_{i=1}^{n} NASC_i D_i}{\sum_{i=1}^{n} NASC_i}$$

Here, D_i is the depth at *i*th data sample corresponding *i*th NASC value. For each log distance, the solar altitude over the horizon in radians was estimated using time, date and position using the R package "*suncalc"* (Thieurmel and Elmarhraoui 2019). These values were converted to degrees.

The day and night difference in weighted mean depth (D) was estimated by modelling the diel oscillation a logistic function (Hjellvik et al. 2001, Johnsen and Godø 2007):

$$g\ (s) = \frac{De^{\alpha(s-\beta)}}{1 + e^{\alpha(s-\beta)}} - D$$

The day-night transition is represented as β and the speed of the transition as α. S_i is the sun's altitude at the start of the *i*th nautical mile. The data were stratified by fjord (Table 2) and survey year. This modelling is like the method used by Johnsen and Godø (2007) to estimate the day-night differences in weighted depth of blue whiting.

Figure 9 describes how the different parameters affect the shape of the function curve.

D is the difference between min and max weighted mean depth (amplitude of diel variation), and α is the slope of the logistical curve, which indicates the diel migration speed of the sprat. Finally, β indicates when the diel migration occurs by representing the midpoint of the logistical curve. These three parameters were estimated by minimizing the sum of squares by employing the "nls" function in the R package "stats". Initial values for α were set to 1, while β was set to be 15 for years referred to as the summer season. In contrast, the initial α was kept at 1 while β was changed to 0 for winter seasons. The reason for having different initial values of β here is because the model failed and gave numbers of diel depth difference, which would not be possible given the depth of the fjord.

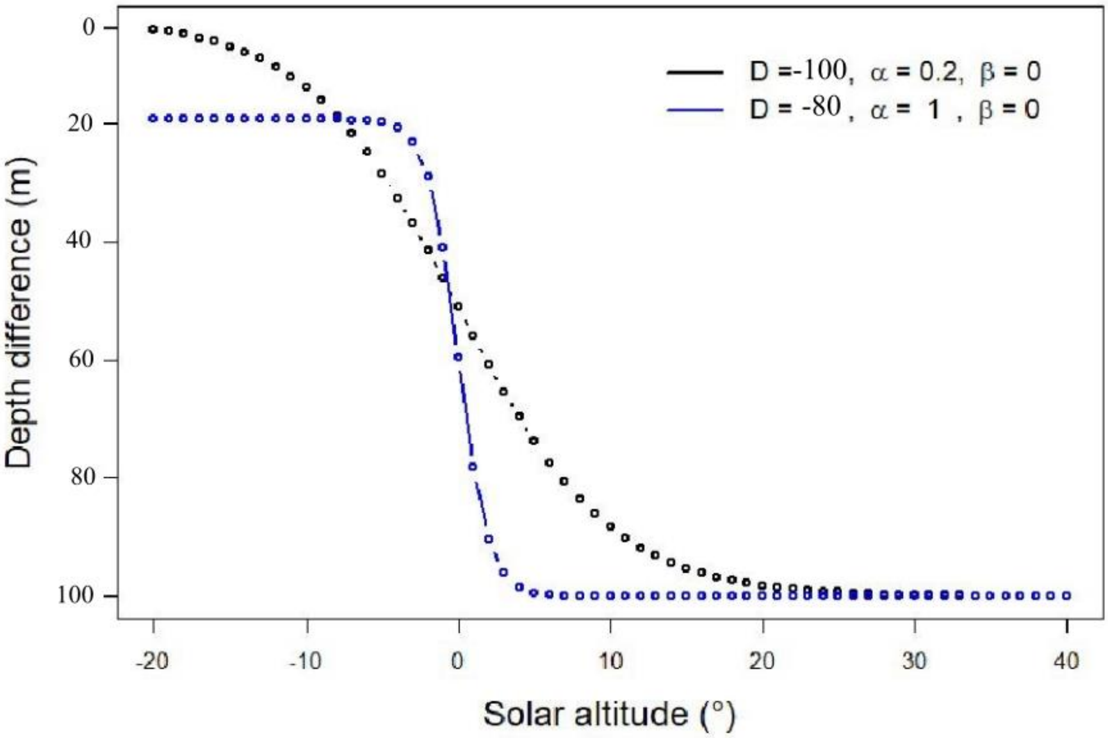

Figure 9 A schematic of g(s) explaining the difference between a steep curve (blue line, α = 1) and a slack curve (black line, α = 0.2). α is the slope of the curve, and β is the midpoint of the curve where the transition occurs. This Figure was adapted from (Komiyama 2021).

Comparing the vertical distribution of small and large sprat

It was tested whether the vertical distribution differs between two length classes of sprat (≥ 7 cm and < 7 cm). In the program Stox (Johnsen et al. 2019), catch data was normalized as if the trawling distance was one nautical mil, using the "*normalized*" and "*weight*" setting in the "*LengthDistribution*" function.

The two-size class's catch rates (n/nmi) were calculated by trawl station. The "*suncalc*" package (Thieurmel and Elmarhraoui 2019) in R was used to find the solar degree altitude when the trawl station was conducted, given in radians which were then converted to a degree. This analysis was to test where a size-dependent pattern existed and how solar degree and trawl haul depth had any effect. This analysis was done separately for Hardangerfjorden and Sognefjorden. All trawl stations are shown in appendix Figures A1.1 – A1.3.

Statistics:

A two-way ANOVA (Lopes et al. 2015) model was run for Hardangerfjorden and Sognefjorden separately, grouping by season and size lass. Catch rates (continuous variable) were tested against the two continuous predictor variables, depth and solar altitude degree.

3 Results

3.1 Horizontal density distribution

Average density distribution: Mean NASC analyses

In Sognefjorden, the average density distribution expressed as mean NASC is spread relatively evenly between the main fjord arm and the smaller, showing a similar spread between seasons (Figure 10). However, it does appear as if the average density is slightly lower in winter season than summer season. For Hardangerfjorden, the average density of sprat was markedly larger during summer season than during winter season in 6 out of 7 fjord arms (Figure 11). Furthermore, there were also signs of a higher average density in the innermost fjord arms than the main fjord arm when looking at the winter season. At the same time, it remained relatively constant when making the same comparison for summer season. The statistical analyses with a t-test did not find any significant differences in the average density when comparing summer and winter for each fjord arm given a *p-value* threshold of 0.05.

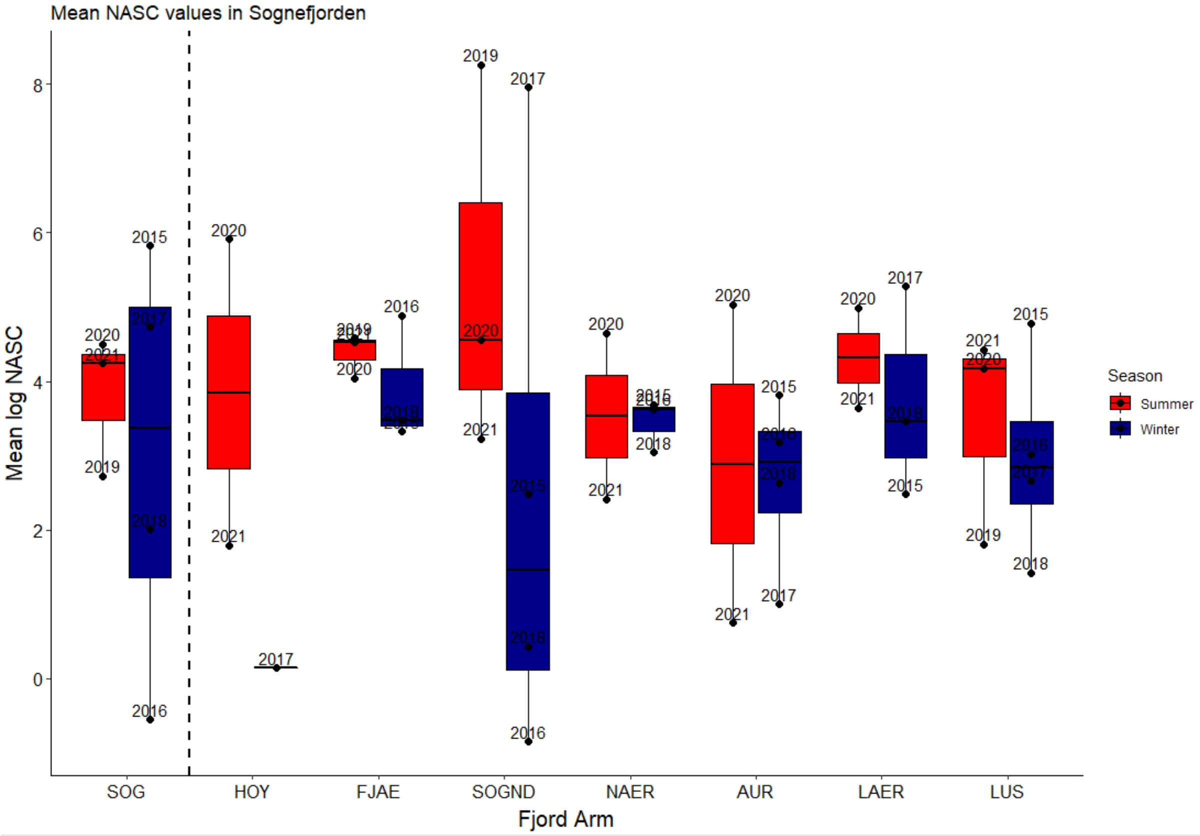

Figure 10 Mean NASC values for each season for each fjord arm in Sognefjorden. Mean NASC values are log-transformed, and each box contains the values for each survey within that season. (Summer = 2021, 2020, 2019, Winter = 2018, 2017,2016,2015). Fjord on the left side of the Dashed line is the main fjord arm for Sognefjorden. The Fjord arms on the right side of the dashed line are ordered from outermost to innermost, positioning in the fjord from left to right on the plot.

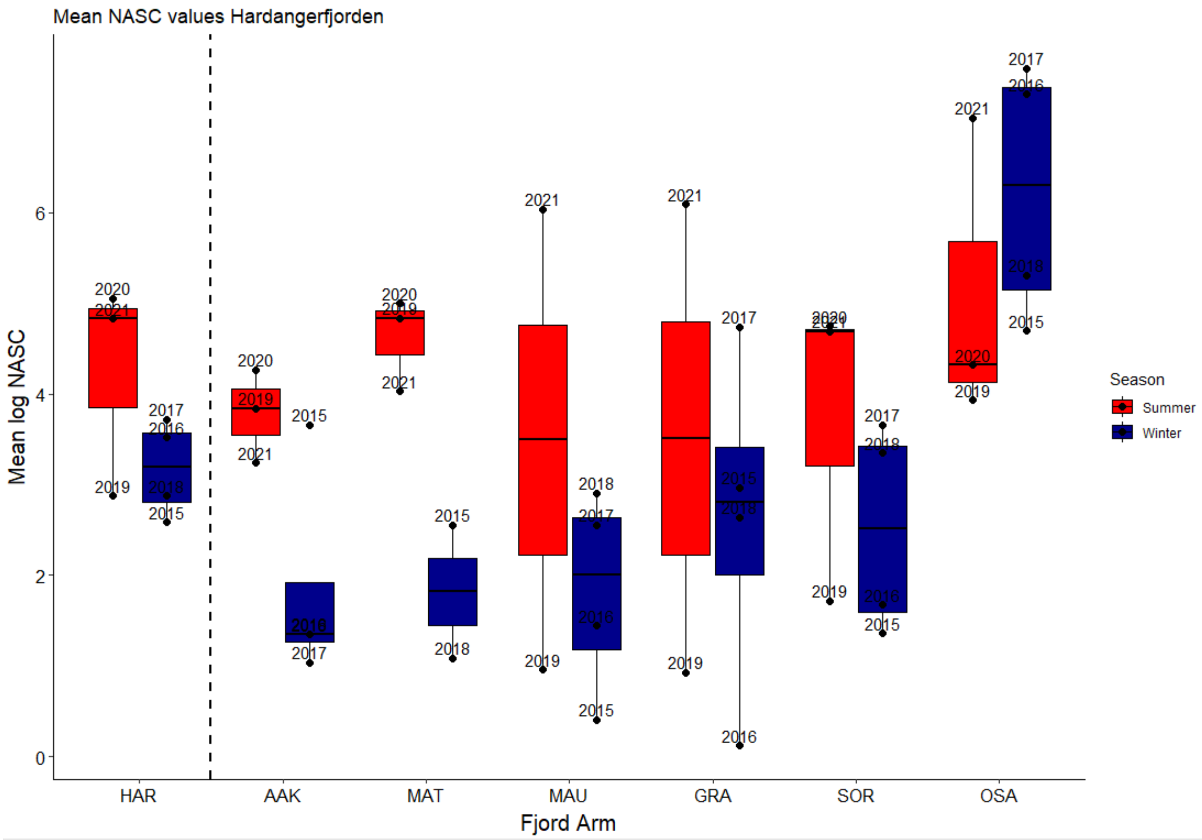

Figure 11 Mean NASC values for each season for each fjord arm in Hardangerfjorden. Mean NASC values are log-transformed, and each box contains the values for each survey within that season. (Summer = 2021, 2020, 2019, Winter = 2018, 2017,2016,2015). Fjord on the left side of the Dashed line is the main fjord arm for Hardangerfjorden. The Fjord arms on the right side of the dashed line are ordered from outermost to innermost, positioning in the fjord from left to right on the plot.

Table 3. Output from t.test of the different fjord arms, testing if Mean NASC differs between seasons. HOY shows NA value due to the lack of repeated measurements of this fjord arm.

Fjord	Fjord Arm	*p*-value
SF	SOG	0.53
SF	HOY	NA
SF	FJAE	0.66
SF	SOGND	0.70
SF	NAER	0.69
SF	AUR	0.59
SF	LAER	0.89
SF	LUS	0.75
HF	HAR	0.22
HF	AAK	0.09
HF	MAT	0.06
HF	MAU	0.51
HF	GRA	0.55
HF	SOR	0.24
HF	OSA	0.42

All fjord arms: centre of gravity analyses

For the centre of gravity in the sprat NASC distribution for each fjord arm, it appears that season does influence the centre of gravity in the fjord arms ($F_{7,1}$=8.7, ***p*=0.006**) for Sognefjorden, where it seems like the centre of gravity moves closer to the innermost point, meaning further into the fjord arm during winter while moving further out during summer season (Figure 12). However, it also gave a significant interaction between the fjord arm and season ($F_{7,1}$=2.5, ***p*=0.03**). When an interaction term is significant, one cannot interpret the main effect without considering this interaction. Unlike Sognefjorden, Hardangerfjorden did not follow the same pattern in the centre of gravity distribution pattern. Here, no significant difference was found regarding the centre of gravity when comparing seasons ($F_{6,1}$=0.14, *p*=0.71). The interaction term neither yielded a significant value ($F_{6,1}$=1.1, *p*=0.36).

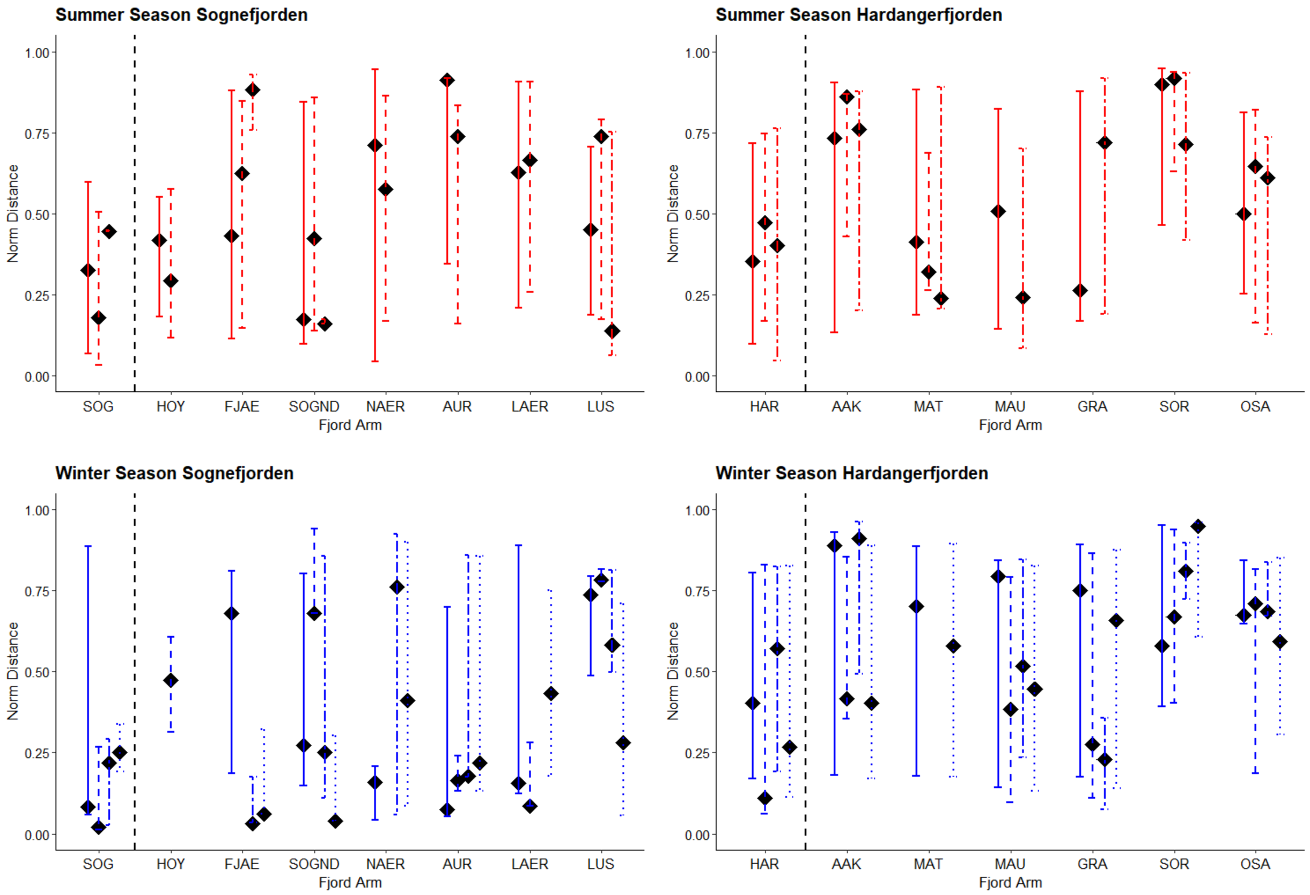

*Figure 12 (*Black diamond*) Weighted median distance (Centre of gravity) weighted on NASC for Sognefjorden and Hardangerfjorden during Summer (2021, 2020, 2019) and Winter season (2018, 2017, 2016, 2015). (Lines) Weighted percentile weighted on NASC showing (lower) 10% and (upper) 90 %. X- axis is the fjord, y- axis is normalized fjord arm distance where 0 is the innermost point, and 1 is the outer most point. Red = Feeding season, Blue = Overwintering season.*

Black dashed line separates main fjord from side fjord arms where main fjord is on the left side. Fjord arms on the right side of the black dashed line are ordered from left to right where left most is located furthest out in the fjord and the right most in the one furthest in the fjord

Red whole line = 2021, Red long dashed line = 2020, Red dash + dotted line = 2019.

Blue whole line = 2018, Blue long dashed line = 2017, Blue dash + dotted line = 2016, Blue short, dashed line = 2015.

Missing values; (NA = covered but not found), Not covered = No coverage of fjord arm))

Sognefjorden = 2019; HOY (NA), NAER(NA), AUR (NA), LAER(NA), 2018; HOY (Not covered), 2017; FJAE (NA), NAER (NA), 2016; HOY (Not covered), LAER (NA), 2015; HOY (NA)

Hardangerfjorden = 2020; MAU (Not covered), GRA(Not covered), 2017; MAT (NA), 2016; MAT (NA)

Main fjord arm: cumulative NASC analyses

To investigate the differences in the cumulative NASC distribution of sprat between season in the main fjord arm in both Sognefjorden and Hardangerfjorden, a two-sided Kolmogorov-Smirnov test was used.

This pattern shows that most sprat is probably located further in the main fjord arm during the winter than during the summer, given the earlier increase in NASC values during summer. By looking at how the cumulative curve changes throughout the fjord length, it appears as if the rise in NASC values happens earlier for most summer years than winter years (except for 2018, which is more like a summer year), and that a plateau in NASC value is reached sooner during summer than during winter. However, 2019 did appear to be quite different from the other summer years, most likely due to the very low NASC values of sprat that year (Figure 13). Furthermore, 2018 is also quite different from the rest of the winter years, making a significant difference between it and the years 2017,2016 and 2015, therefore having a more similar pattern to a summer year with an earlier rise in NASC values, meaning that sprat is located further out in the fjord here as well. This pattern shows that most sprat is probably located further in the main fjord arm during the winter than during the summer season.

The pattern of how sprat is distributed in the fjord appears to be slightly different for Hardangerfjorden. Both 2021 and 2020 were significantly different from 2018, 2017, and 2016, but not 2015. However, 2019 did not appear to be different from any winter year. Contrary to Sognefjorden, the rise in NASC value does not share the same pattern of an earlier rise in summer than in winter, and no earlier plateau reach was found. In the case of Hardangerfjorden, it appears as if there is a more similar distribution between seasons regarding how sprat is distributed within the main fjord arm.

The statistical analyses in Sognefjorden 2021 show that the NASC distribution is significantly different from 2018, 2017 and 2016. While 2020 is significantly different from 2017,2016 and very similar to 2018 (Table 4).

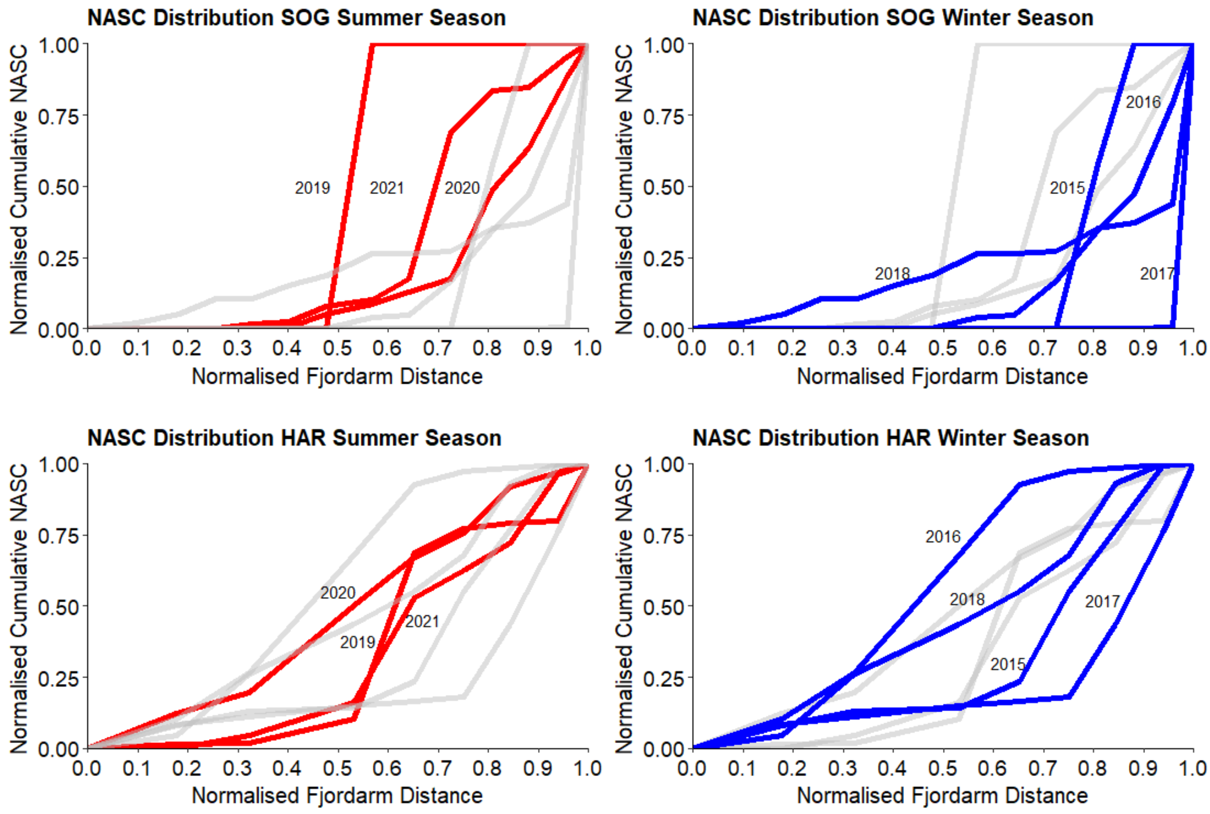

Figure 13 Lines represent cumulative NASC values throughout the fjord arm length. Red lines represent the summer season, while blue lines represent the winter season. Greyed out lines are the opposing season in each fjord. Both Fjord arm length and the cumulative NASC are normalized.

Table 4. Output from two-sided Kolmogorov-Smirnov test tests the cumulative NASC distribution between years for both the Main fjord in Sognefjorden (SF) and Hardangerfjorden (HF). D stands for distance and measures the maximum vertical distance between

Fjord	Year	Comparing year	D	*p*-value
SF	2021	2020	0.29	0.62
SF	2021	2019	0.71	**0.00**
SF	2021	2018	0.57	**0.02**
SF	2021	2017	0.64	**0.01**
SF	2021	2016	0.71	**0.00**
SF	2021	2015	0.43	0.15
SF	2020	2019	0.64	**0.01**
SF	2020	2018	0.50	0.06
SF	2020	2017	0.57	**0.02**
SF	2020	2016	0.64	**0.01**
SF	2020	2015	0.36	0.33
SF	2019	2018	0.93	**0.00**
SF	2019	2017	0.29	0.62
SF	2019	2016	0.29	0.62
SF	2019	2015	0.36	0.33
SF	2018	2017	0.79	**0.00**
SF	2018	2016	0.86	**0.00**
SF	2018	2015	0.57	**0.02**
SF	2017	2016	0.21	0.90
SF	2017	2015	0.21	0.90
SF	2016	2015	0.29	0.62
HF	2021	2020	0.44	0.34
HF	2021	2019	0.67	**0.04**
HF	2021	2018	0.67	**0.04**
HF	2021	2017	0.56	0.12
HF	2021	2016	0.67	**0.04**
HF	2021	2015	0.67	**0.04**
HF	2020	2019	0.78	**0.01**
HF	2020	2018	0.78	**0.01**
HF	2020	2017	0.67	**0.04**
HF	2020	2016	0.67	**0.04**
HF	2020	2015	0.67	**0.04**
HF	2019	2018	0.22	0.98
HF	2019	2017	0.33	0.70
HF	2019	2016	0.56	0.12
HF	2019	2015	0.33	0.70

HF	2018	2017	0.33	0.70
HF	2018	2016	0.56	0.12
HF	2018	2015	0.33	0.70
HF	2017	2016	0.44	0.34
HF	2017	2015	0.22	0.98
HF	2016	2015	0.22	0.98

Spatial differences between small and large sprat: Location analyses

For visual inspection, no clear pattern can be seen regarding positioning in the fjord and the catch numbers of the different size classes of sprat (Figure 14). While running the statistical analysis for the small sprat size class, no significant interaction was found between the catch rate numbers and positioning in the fjord (*p*=0.71). However, season was close but not significant (***p*=0.07**) in explaining the different catch rates of small sprat when setting the significance threshold to 0.05 (Table 5). As for larger sized sprat in Sognefjorden, no significant differences were found regarding the location in the fjord (*p*=0.17). Therefore, for both large and small-sized sprat, it does not appear as if there is a higher abundance for one location in the fjord over another

For Hardangerfjorden, no pattern was found for smaller sized sprat regarding positioning in the fjord. However, for the larger sprat in Hardangerfjorden, the size class and position became significant (***p*=0.01**). At the same time, season also yielded a significant result (***p*=0.02**), showing that larger-sized sprat's catch rates are different between summer and winter in Hardangerfjorden. A post hoc test using the Tukey HSD was implemented to investigate which position was significantly different. The innermost and the inner position were revealed to be significantly different (***p*=0.012**), showing that the catch rates of larges sized sprat are higher in the innermost location compared to the inner location.

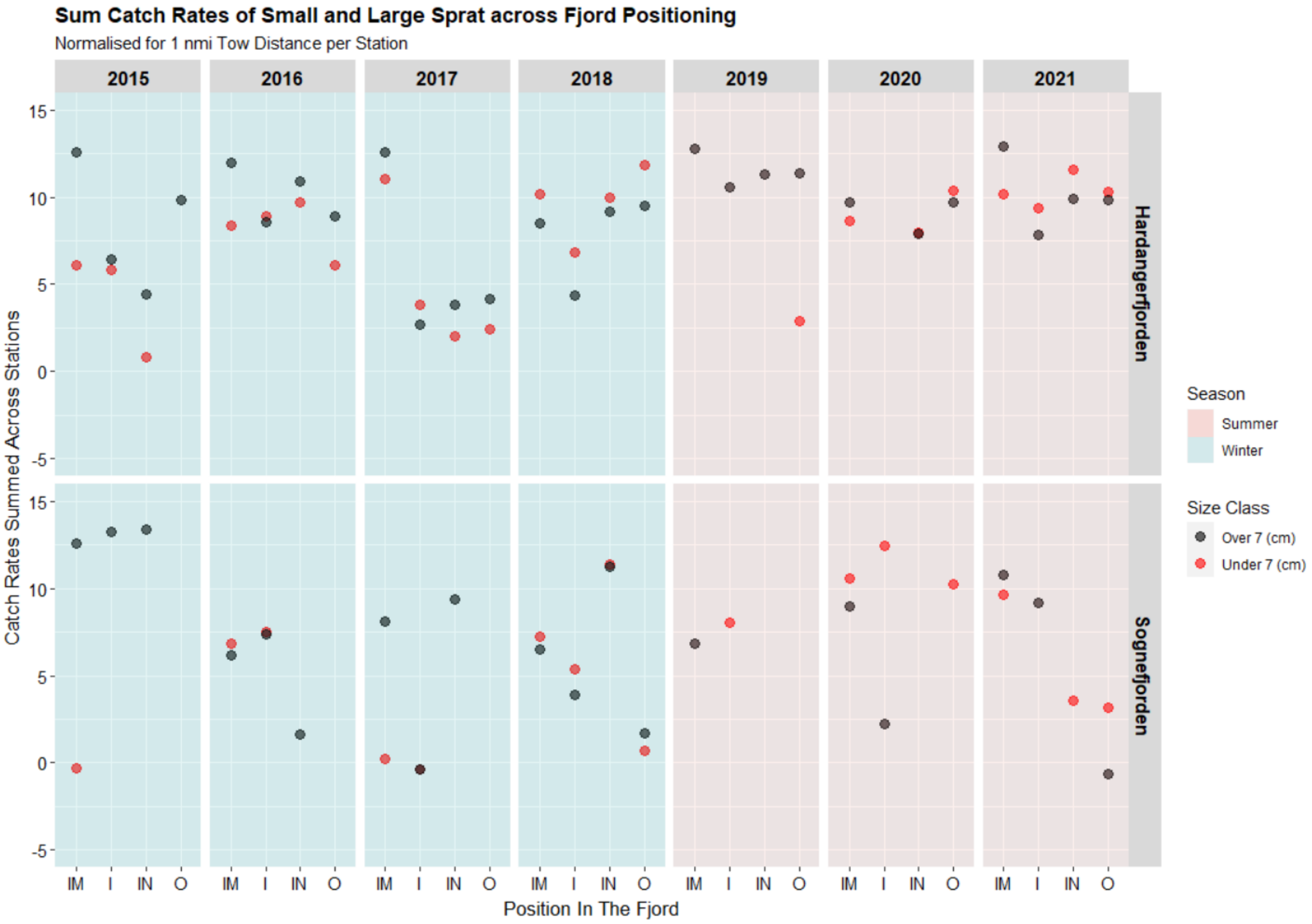

Figure 14 Summed Catch rates of different length classes of trawl stations normalised for 1 nmi tow distance for different horizontal positions in both Sognefjorden and Hardangerfjorden for all surveys. Position abbreviations: IM = Innermost, I = Inner, IN = Intermediate, O = Outer. The background coloration is indication what season the survey years are taken at (blue = Winter, red = Summer). The black dots are large size sprat (≥7 cm) and red dots are small size sprat (<7cm)

Table 5. The two-way ANOVA models compare catch rates of different size classes of sprat with season and location in the fjord and the interaction between season and location in the fjord.

Fjord	Size Class	Position *p* value	Season *p* value	Interaction *p* value
SF	< 7 cm	0.71	0.07	0.2
SF	≥7 cm	0.17	0.64	0.92
HF	< 7 cm	0.70	0.22	0.82
HF	≥7 cm	**0.01**	**0.02**	0.66

3.2 Vertical density distribution

Diel vertical migration analyses

All values, including α, β, μ, D, R^2, n and p-value, and local time at migration, can be seen in Table 6.

When looking at individual survey years, the most significant depth difference occurred in Sognefjorden in 2021, migrating from 26.9 (111.6 – 84.7) meters at night to 111 meters at day, having an 84 m depth difference according to the model. The average diel depth difference between seasons (D) in Sognefjorden showed that during summer seasons, the average was 53.3 m, while during the winter season, the average was 35.7 m. A similar pattern was true for Hardangerfjorden, where the diel depth difference was 41.9 m and 15.9 m, respectively, for the summer and winter season. This result shows that sprat performs a longer DVM during summer than during winter.

The average depth at night for the summer season in Sognefjorden was 15.5 meters, while the winter season was 38.8 meters. In Hardangerfjorden, the average night-time depth was 13.3 m and 25.6 m, respectively, for the summer and winter season. This pattern shows that sprat is closer to the surface at night during summer than during the winter season. For the average depth during the daytime, for summer seasons in Sognefjorden, the depth was 68.8 m, while for winter, the depth was 74.5 m. While for Hardangerfjorden, the average depth during daytime was 55 m in summer and 41.5 m in winter. This shows that Sognefjorden sprat is located further down the water column in winter during the daytime than in the summer season, while the opposite appears true for Hardangerfjorden.

When looking at the local time for when migration occurred during the summer season survey years, the migration ranges from 03:20 in the morning of late June 2019 in Sognefjorden to 06:30 in late July/early August 2021 in Sognefjorden. In contrast, the upward migration towards the surface in the evening ranges from 16:35 in the same survey in 2021 Sognefjorden to 19:40 in the 2019 survey in Sognefjorden. In comparison, the morning migration occurred from 06:50 in late November/early December of 2018 in Hardangerfjorden to 08:43 in early December of 2015. Comparative, the upward migration ranges from 14:10 in two survey years to about 15:55 in 2018 Hardangerfjorden

When comparing years in the summer season, the transition speed (α) was considerably slower during 2020 Sognefjorden (1) than during 2021 (0.37).

The model for 2016 in Hardangerfjorden did not have a significant *p*-value (p=0.32), meaning that this model could not explain the difference in the depth of sprat.

The little apparent sign of DVM during years labelled as winter season explains the relatively low R^2 value of many of the survey years. While the model with the highest R^2 value was 2019 Sognefjorden, this year contained very little NASC data and should probably not be fully trusted.

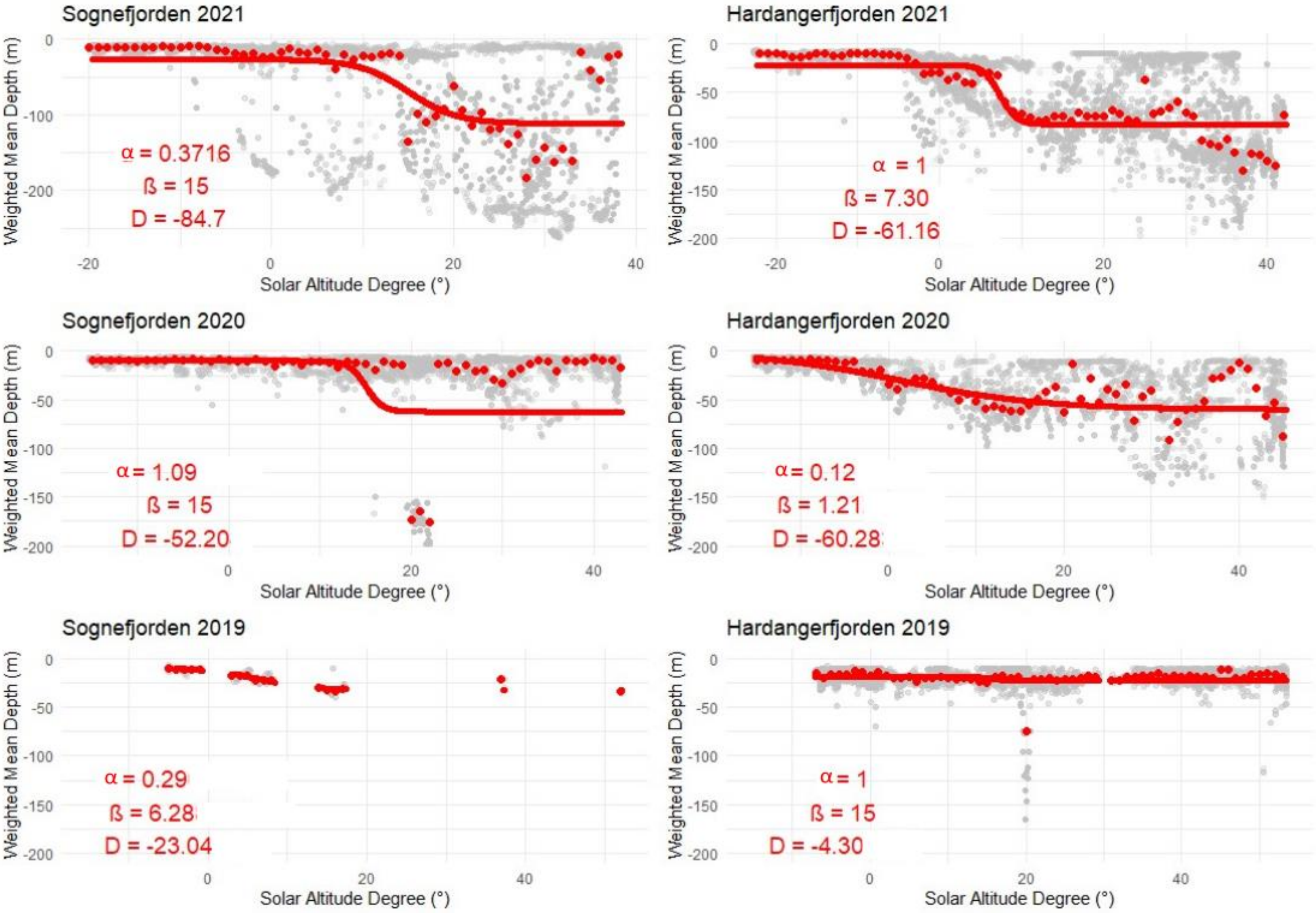

Figure 15 Vertical distribution of sprat in Sognefjorden and Hardangerfjorden in 2021, 2020 and 2019 overlayed with a fitted logistical model (red solid line). Weighted mean depth of sprat per log distance (grey points). Median of weighted mean depth per 1° of solar altitude (red dots)

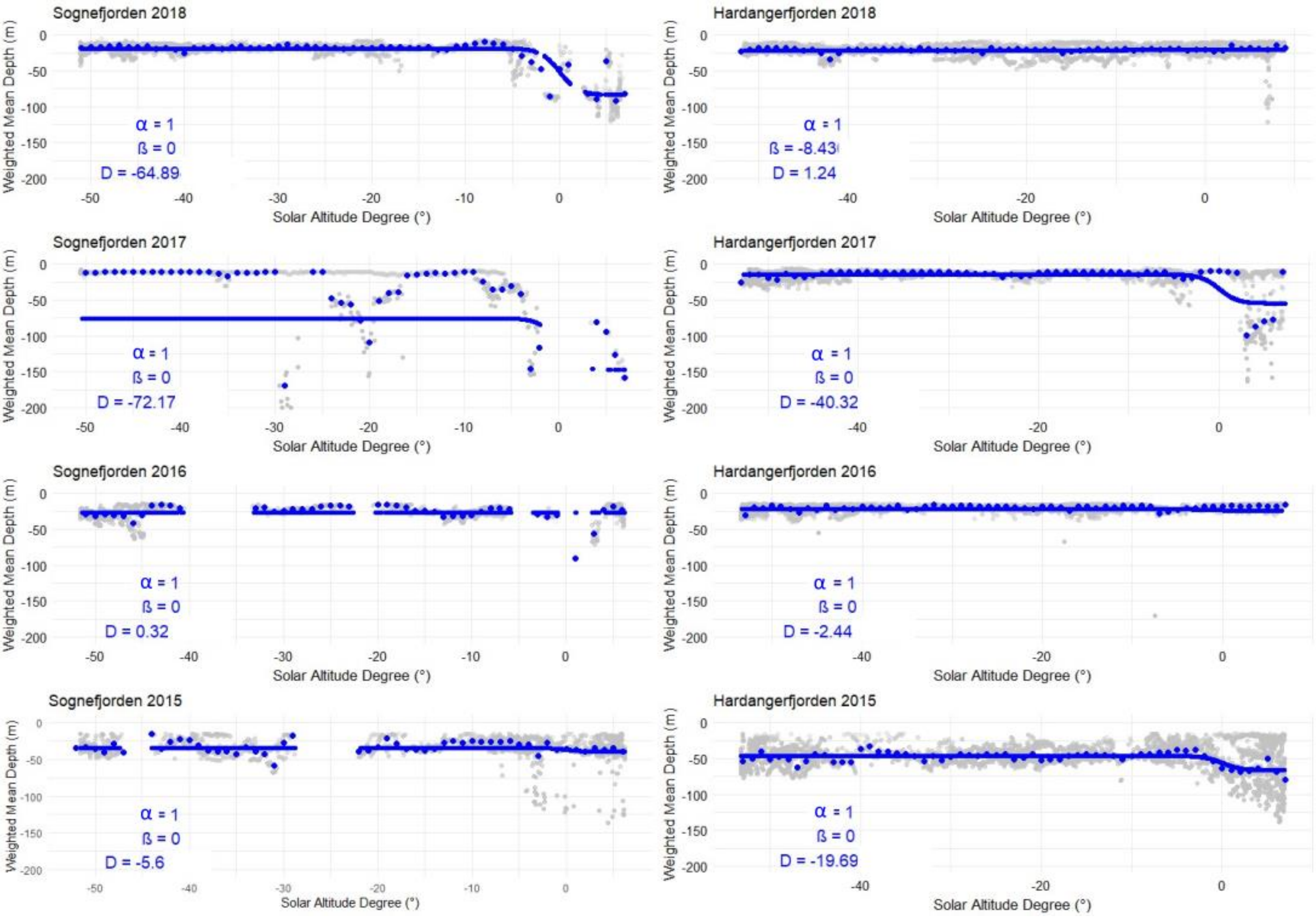

Figure 16 Vertical distribution of sprat in Sognefjorden and Hardangerfjorden in 2018, 2017, 2016 and 2015 overlayed with a fitted logistical model (blue solid line). Weighted mean depth of sprat per log distance (grey points). Median of weighted mean depth per 1° of solar altitude (blue dots)

Table 6. Parameter estimates of vertical distribution during dial variation of sprat in Sognefjorden (SF) and Hardangerfjorden (HF) during surveys from 2015 to 2021. S = summer season, W = winter season. *p*-values refer to the parameters D. n are the numbers of observations.

Year	Season	Fjord	α	β	D	μ	R^2	*p*-value	n	Local time at migration
2021	S	SF	0.37	15^{*}	-84.70	-111.64	0.28	**<0.05**	5604	06:30 /16:35
2021	S	HF	1^{*}	7.30	-61.16	-82.69	0.47	**<0.05**	6460	05:50/18:00
2020	S	SF	1.09	15^{*}	-52.20	-62.12	0.15	**<0.05**	5053	06:00/17:10
2020	S	HF	0.12	1.21	-60.28	-59.96	0.42	**<0.05**	4070	04:05/19:20
2019	S	SF	0.29	6.28	-23.04	-32.49	0.87	**<0.05**	4186	03:20/19:40
2019	S	HF	1^{*}	15^{*}	-4.30	-22.54	0.02	**<0.05**	4901	05:00/18:20
2018	W	SF	1^{*}	0^{*}	-64.89	-83.70	0.78	**<0.05**	4884	08:30/14:10
2018	W	HF	1^{*}	-8.43	1.24	-20.50	0.004	**<0.05**	4906	06:50/15:55
2017	W	SF	1^{*}	0^{*}	-72.17	-147.61	0.01	**<0.05**	3695	08:22/14:20
2017	W	HF	1^{*}	0^{*}	-40.32	-54.68	0.35	**<0.05**	4894	08:23/14:22
2016	W	SF	1^{*}	0^{*}	0.32	-26.92	0.0001	0.31	2656	08:40/14:08
2016	W	HF	1^{*}	0^{*}	-2.44	-24.81	0.001	**<0.05**	3258	08:45/14:10
2015	W	SF	1^{*}	0^{*}	-5.61	-39.64	0.02	**<0.05**	5024	08:42/14:15
2015	W	HF	1^{*}	0^{*}	-19.69	-66.15	0.17	**<0.05**	5381	08:43/14:20

*Model failed to converge and employed initial values

Spatial differences between small and large sprat; vertical analysis

By visual inspection of Figure 17, there is no clear pattern where the different size classes are caught regarding depth or solar altitude degree. The same holds true for the statistical analyses (Table 7), where neither depth nor solar degree became significant for the catch rates of the different size classes of sprat for both fjord and season.

Table 7. Two-way ANOVA outcome from comparing catch data of sprat to depth and solar altitude when grouping by length class, and season.

Fjord	Season	Size Class	Effect	F	*p*-value
SF	S	≥ 7 cm	Depth	0.04	0.95
SF	S	≥7 cm	Solar Degree	0.02	0.96
SF	S	≥7 cm	Interaction	0.00	0.98
SF	S	<7 cm	Depth	0.03	0.95
SF	S	<7 cm	Solar Degree	0.02	0.86
SF	S	<7 cm	Interaction	0.82	0.36
SF	W	≥7 cm	Depth	0.52	0.47
SF	W	≥7 cm	Solar Degree	0.27	0.60
SF	W	≥7 cm	Interaction	0.51	0.47
SF	W	<7 cm	Depth	0.00	1
SF	W	<7 cm	Solar Degree	0.00	0.97
SF	W	<7 cm	Interaction	0.00	0.97
HF	S	≥7 cm	Depth	0.54	0.46
HF	S	≥7 cm	Solar Degree	0.05	0.82
HF	S	≥7 cm	Interaction	0.24	0.62
HF	S	<7 cm	Depth	0.38	0.53
HF	S	<7 cm	Solar Degree	0.003	0.95
HF	S	<7 cm	Interaction	0.81	0.37
HF	W	≥7 cm	Depth	2.85	0.09
HF	W	≥7 cm	Solar Degree	0.55	0.45
HF	W	≥7 cm	Interaction	0.56	0.45
HF	W	<7 cm	Depth	0.06	0.8
HF	W	<7 cm	Solar Degree	0.54	0.46
HF	W	<7 cm	Interaction	0.00	0.99

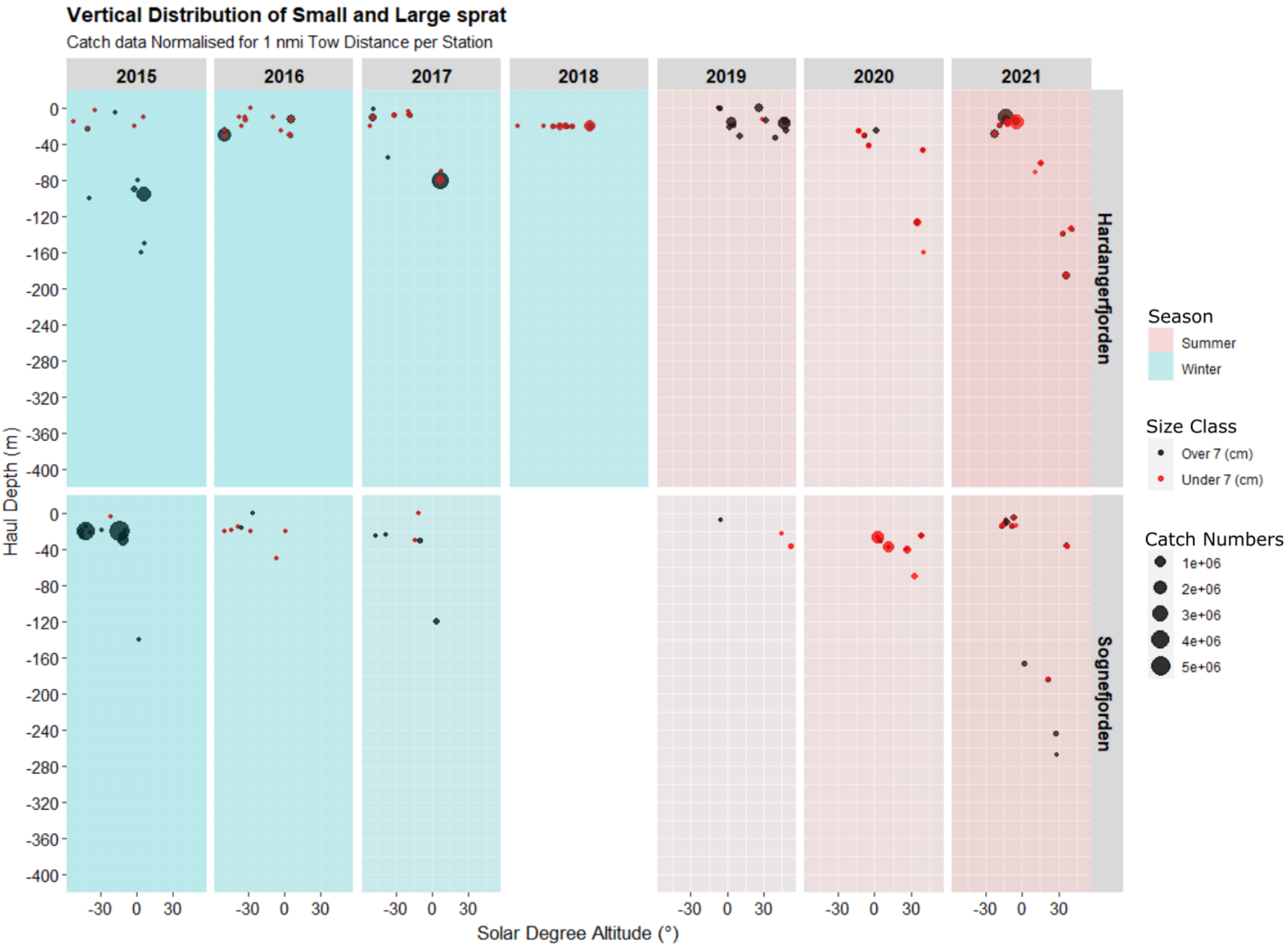

Figure 17 Catch data from sprat, including depth, Solar degree altitude and size class separation for Sognefjorden and Hardangerfjorden. 2018 Sognefjorden is removed due to lack of trawl depth data. Black dots are large size sprat (≥7 cm), and red dots are small size sprat (<7cm). Dot size increases with increasing catch numbers, and background colour indicates season, blue = winter and red = summer.

4 Discussion

Summary

In this thesis, multiple analyses have investigated the temporal and spatial variation in the vertical and horizontal density distribution of sprat (*Sprattus sprattus*) in Sognefjorden and Hardangerfjorden. Within the fjord arms, sprat stayed further into the fjord arms during the winter season while staying further out during the summer season, especially for Sognefjorden. However, the analyses for Hardangerfjorden did not show the same pattern in density distribution. Most fjord arms showed less sprat abundance during the winter season than during the summer season for both fjords. For the diel vertical migration (DVM) of sprat, the results show that sprat performs a larger DVM in the summer season than in the winter season while also being found closer to the surface at night during summer than in winter. When it comes to the depth during the daytime, the fjords varied, where they were deeper in summer for Hardangerfjorden, while winter was the season of deepest depth during daytime. Finally, Spatial differences between small and large sprat no clear differences were found between the two size classes regarding vertical distribution. While for the location analyses, only large sprat in Hardangerfjorden appeared to be more abundant in the innermost location compared to the inner location, while no other pattern could be found regarding catch rates of different size classes of sprat and location in the fjord.

While few studies have been done on the horizontal distribution of sprat in fjords, sprat might choose to move further into the fjord arm during winter to enter areas more suitable for predator avoidance (Giske et al. 1994). In the inner parts of the fjords, the surface layer is more turbid, which can decrease visibility, reducing visual predators' capability to locate prey (Falkenhaug and Dalpadado 2014). Therefore, the inner parts of the fjords can act as a refugee for sprat during winter, better protecting them from predators (Giske et al. 1994, Falkenhaug and Dalpadado 2014). Furthermore, sprat is a species which can tolerate both low salinity and low oxygen levels (Falkenhaug and Dalpadado 2014). This high tolerance can further explain their relocation, especially if their potential predators do not have an as strong tolerance for these abiotic factors (Kaartvedt et al. 2009). In their study on winter sprat in Norwegian fjords, Solberg et al. (2015) showed that most potential sprat predators inhabited waters depths with a fairly high oxygen content (~20-25%), which could support that sprat enter areas unreachable by their predators to survive the winter.

In Hardangerfjorden, a large part of the sprat abundance was found in the innermost fjord arm during winter, possibly for the same reasons. The horizontal distribution pattern of their prey species might explain why sprat inhabited areas further out in the fjord during summer. In Hardangerfjorden, Falkenhaug and Dalpadado (2014) found that the total fullness index (TFI), meaning how full their stomach was from prey consumption, was higher in the outer parts of the fjords while lowest in the inner and intermediate parts during the autumn of 2009. Combining this with the possible predator avoidance strategy during winter could explain the observed difference in sprat distribution between seasons. Another interesting observation was that the NASC abundances were generally lower during the winter than in the summer. This reduction could be explained by sprat, on average, inhabiting deeper waters during winter, compressing the swim bladder and therefore reducing target strength, as shown in herring (Fässler et al. 2009), or inhabiting areas unreachable to the RV like close to the shore (Johnsen et al. 2020). However, it could also mean that there is less abundance of sprat in the fjords during the winter season due to fishing efforts in late summer/early autumn or from predation.

Interestingly, no pattern was found regarding the horizontal distribution of small and large-sized sprat. While there are potential sources of errors which could cause some problems, this was somewhat unexpected. During the same study in Hardangerfjorden (2014), Falkenhaug and Dalpadado found that areas further out in the fjord have a higher proportion of larger sized zooplankton species. In contrast, smaller sized species dominated the inner part. This size pattern of prey species could create a similar pattern for sprat where the smaller individuals inhabited the inner areas to feed on appropriately sized prey while the larger sprat was to be found in the outer areas for the same reason. However, this did not appear to be the case, meaning that there could be other reasons than the size of their prey that determines where the different sprat sizes inhabit.

The vertical distribution analyses demonstrated that sprat performs DVM. This pattern was significant in most of the summer surveys and some of the winter surveys. This result coincides with studies performed on the diel spatial distribution of sprat in the Baltic Sea (Cardinale et al. 2003)and Bunnefjorden, Norway (Solberg et al. 2015). Interestingly, sprat remained closer to the surface at night during summer seasons than in winter. Therefore, because sprat is closer to the surface at night-time during summer, light alone is possibly not the only factor driving DVM. While there can be many reasons why a species chooses to perform DVM, the most likely cause of this dial shift in vertical positioning is mirroring the migration of their prey to optimise feeding (Mehner 2012). This movement pattern could also be the case for sprat since sprat need sufficient light for selective feeding, and there have been studies supporting the DVM of pelagic zooplankton (Hobbs et al. 2021). One reason why sprat might choose to inhabit depths closer to the surface could be because the majority of mesoplankton plankton inhabits the uppermost 30 m of the water column, as shown in a study performed in Masfjorden in 1985, Norway (Aksnes et al. 1989). Since sprat also can filter feed (Falkenhaug and Dalpadado 2014), it could also be to acquire appropriately sized food for filter-feeding rather than just being driven by light intensity, given that filter-feeding does not require light.

In winter, sprat performed a shorter DVM than in summer and remained closer to the surface for an extended period. The aim of this movement pattern could potentially be to enter areas with better oxygen conditions, as Kaartvedt et al. (2009) suggested. In winter, both the morning downward migration and the upward migration toward the surface occurred earlier than in summer. Thus, less time is spent in the deeper waters and more time in depth closer to the surface during winter than in the summer season.

It appears as if the relationship between solar altitude and vertical sprat distribution is stronger during summer than during winter, given the higher R^2 values in the summer season models. This difference could be explained by, e.g., prey movement mirroring. Given the higher importance of feeding and the higher abundance of available prey during summer than during winter (Falkenhaug and Dalpadado 2014), sprat will probably follow the prey more during summer and have a stronger DVM pattern. While in winter, zooplankton has been shown to overwinter at greater depths, which can be unavailable to sprat (Solberg et al. 2012).

It was surprising that no clear pattern was found between the size of the sprat and vertical distribution. A previous study by Solberg et al. (2015) in Bunnefjorden, Norway, did show that almost all sprat over 10 cm had empty stomachs during the 2005-2006 winter period while 0-year sprat still fed during winter, probably given the lack of stored up lipid reserves like the larger individuals have (Solberg et al. 2015). Given these differences, one could expect a difference in vertical distribution, smaller sprat taking more chances, and being higher up in the water with potentially more food. This thesis results could either mean that there is no clear difference in the vertical distribution of the two size classes or that the data or method chosen in this thesis were not adequate for detecting existing differences.

This thesis has focussed on seasonal differences in the spatiotemporal distribution of sprat. However, one should note that the surveys conducted are not occurring within the same year, meaning that summer and winter data are collected in different years. Interannual variation can thus potentially cause some of the differences observed in the results. Two surveys within the same year would be optimal for more informative comparisons. However, with the high financial cost of running these surveys, this will probably not be possible (Greene et al. 2014)

Thresholding is used to categorize the acoustic targets. This process removes plankton and, in combination with the knowledge of the cruise leader, sprat is most likely not misidentified as the likes of cod due to the different ecology, size and behaviour. However, there is a possibility that the NASC values categorized as sprat could be herring (*Clupea harengus*) because of their similar ecology and target strength (Johnsen et al. 2020).

Implementing "zig-zag" transects with a random starting point covers more of the fjord than a traditional parallel transect design. However, there are still issues regarding the traditional research vessels due to their limitations on how close to the shore they can come. These could be areas inhabited by sprat, and therefore, a complete picture of the actual distribution of sprat might not be possible (Johnsen et al. 2020). These limitations could explain why there is less abundance of sprat in winter than in the summer.

The trawl sampling was not designed for this type of analysis, as there is a lack of multiple trawl stations within the same area. Such a sampling design would be more appropriate for studying the vertical distribution of different size classes. An example of such a sampling design is 24 h stations where the same area is trawled multiple times per day within different depths (Kvamme et al. 2010b).

Clupeid fish, such as sprat, are sensitive to sounds (Hawkins and Popper 2014). Additionally, research vessels create radiated noise, which the fish can hear at a long distance if the frequency is within the range of what the fish can perceive, potentially altering its swimming behaviour (Engås et al. 1995). When fish like sprat are closer to the surface, this noise could lead to an avoidance reaction influencing the acoustic estimates (Vabø et al. 2002, Ona et al. 2007). A typical avoidance reaction in fish is diving (De Robertis and Handegard 2012). Research by Knudsen et al. (2009) in Lough Hyne (Ireland) did show that smaller schooling sprat near the surface during night-time dived in the presence of an approaching research vessel (Knudsen et al. 2009). Diving alters the tilt angle of the fish, which can have significant implications for acoustic survey biomass estimates (Vabø et al. 2002).

Anthropological impacts can have consequences for the future of coastal sprat stocks. An increase in water temperature is a known effect of climate change on marine ecosystems (Hoegh-Guldberg and Bruno 2010). Temperature changes can alter species distribution and survival, and even ocean circulation and the exchange between coastal and oceanic ecosystems (Doney et al. 2012). The influx from the North Sea and coastal waters is important for the exchange between fjord and oceanic ecosystems, e.g., by causing up- and downwelling (Nielsen and Andersen 2002). If this exchange is disturbed by e.g., climate change, it can alter the timing of nutrient upwelling, partially responsible for the bloom of plankton in the spring and summer seasons. Such alterations in ecological timing could lead to a mismatch between the plankton bloom and spawning events which can negatively impact the growth rate. If enough suitable food is not obtained, it could lead to a potential earlier death during winter (Van Ginderdeuren et al. 2013). Ultimately leading to a reduced abundance. Furthermore, a reduction in sprat abundance will have consequences for all species that rely on it as a source of prey, putting the entire fjord ecosystem at risk.

Human stressors can also alter water column light attenuation, which is critical for the ecosystem because of its significant impact on the primary production by regulating how far light can travel down the water column. Increased turbidity and dissolved matter from glacial melt water can alter euphotic depth (Mascarenhas et al. 2017) and possibly darken the fjord (Aksnes et al. 2009). Light intensity attenuation changes, in turn, can impact how fish migrates regarding DVM (Aksnes et al. 2004), especially sprat, given that it relies on its vision for feeding (Solberg and Kaartvedt 2017). Suppose Hardangerfjorden and Sognefjorden experience light attenuation changes. In that case, they may become less suitable for visual feeders like sprat and potentially better suited for jellyfish like *Periphylla periphylla*, which is numerous in Lurefjorden, Norway (Lalande et al. 2020).

Future surveys would be interesting to include day stations, meaning the RV remains in the same location for an extended period. Where acoustic measurements are combined, multiple trawl hauls are taken, covering more extensive parts of the water column in the same location, repeated several times throughout at least 24 h could give insight in e.g., size-related differences in behaviour. CTD data should also be collected to analyse whether abiotic factors like oxygen, temperature, and salinity affect the spatiotemporal sprat distribution. Furthermore, while time-consuming, further stomach content analyses would be valuable in mapping sprat's main preys (Falkenhaug and Dalpadado 2014). Such analyses could also look at how stomach fullness and content change with season and sprat size to understand sprat behaviour better and how it might change between seasons. Furthermore, while not financially possible, running these surveys twice a year to remove the possible temporal influence would improve the analyses of seasonal changes in the spatiotemporal distribution of sprat.

Finally, it would be fascinating to use tools that remove or reduce the potential errors of traditional research for acoustic surveys, like blind zones, avoidance behaviour, and the limitation of closeness to the shore. An example of such tools could be the kayak drone used in a study by IMR in 2020 (Johnsen et al. 2020) or sail drones (De Robertis et al. 2019). Blind zones of traditional research vessels are a potential issue for acoustic survey estimates, especially when the fish is near the surface. The blind zone (Totland et al. 2009) close to the surface layer (Aglen 1994) can affect acoustic estimates as the complete distribution might not be covered. Since sprat is located quite close to the surface, especially at night, this could be a potential issue when estimating abundance.

Given how spat distributed itself vertically, staying at a deeper depth during daytime reduces some of the RV's potential sources of errors. Combined with the fact that the sprat harvest begins in late summer/early autumn, the optimal time to perform sprat surveys in Sognefjorden and Hardangerfjorden would be during summer in the daytime to possibly acquire the most accurate abundance estimates.

Conclusions

In conclusion, this study aimed to improve our understanding of the spatiotemporal sprat distribution in two of our most important sprat fjords, Sognefjorden and Hardangerfjorden.

In winter, sprat appear to be closer to the inner part of the fjord arms while being further out during summer, at least for Sognefjorden. The abundance of sprat, i.e., NASC values, is lower in the winter than in summer. Diel vertical migration was observed in sprat, as they stayed closer to the surface at night and migrated to deeper depths during the day. Sprat also performed a longer DVM in summer than in winter. Additionally, the minimum mean depth at night was shallower in summer than in winter. However, no apparent size-related distribution pattern was detected, neither vertically nor horizontally.

Understanding the spatiotemporal distribution of a species is vital for optimizing the designs of our monitoring surveys used for giving catch advice, either for harvest in tonnes or when to implement a fishing stop. By increasing our knowledge, we can give better advice for future harvest and improve predictions of consequences of anthropological impacts, e.g., climate change. Understanding how sprat might be influenced is critical as sprat is considered a keystone species essential for keeping the Norwegian coastal ecosystem stable and healthy.

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Appendix

Appendix A

All transects (NASC) data and biological trawl stations

These maps were made with the R packages rnaturaleart and rnauralearthdata and ggspatial and are showing all NASC data as well as biological sampling stations for both fjords for all surveys.

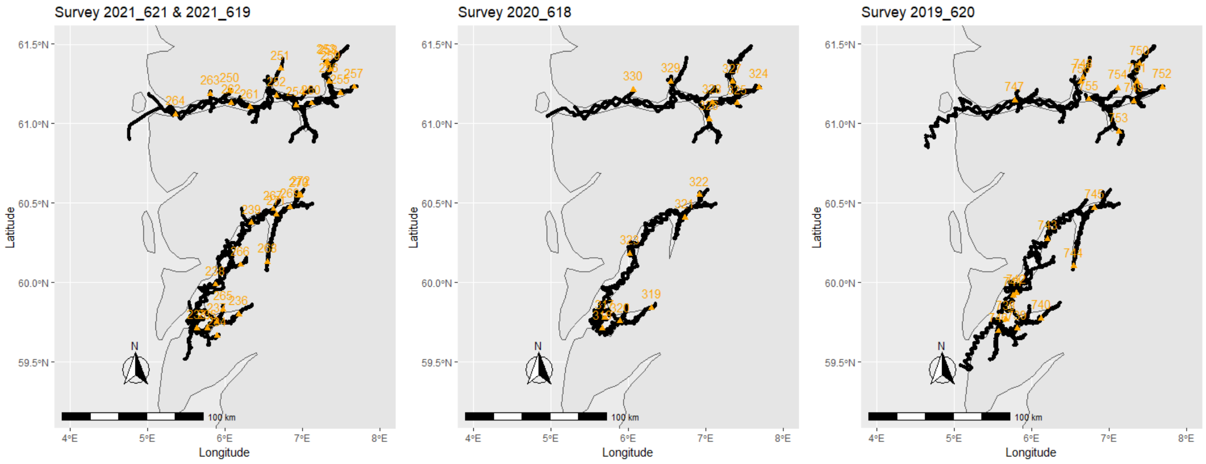

Figure A1.1 All NASC (black lines) data and biotic stations (orange triangles) for surveys in 2021, 2020, 2019 in Sognefjorden and Hardangerfjorden

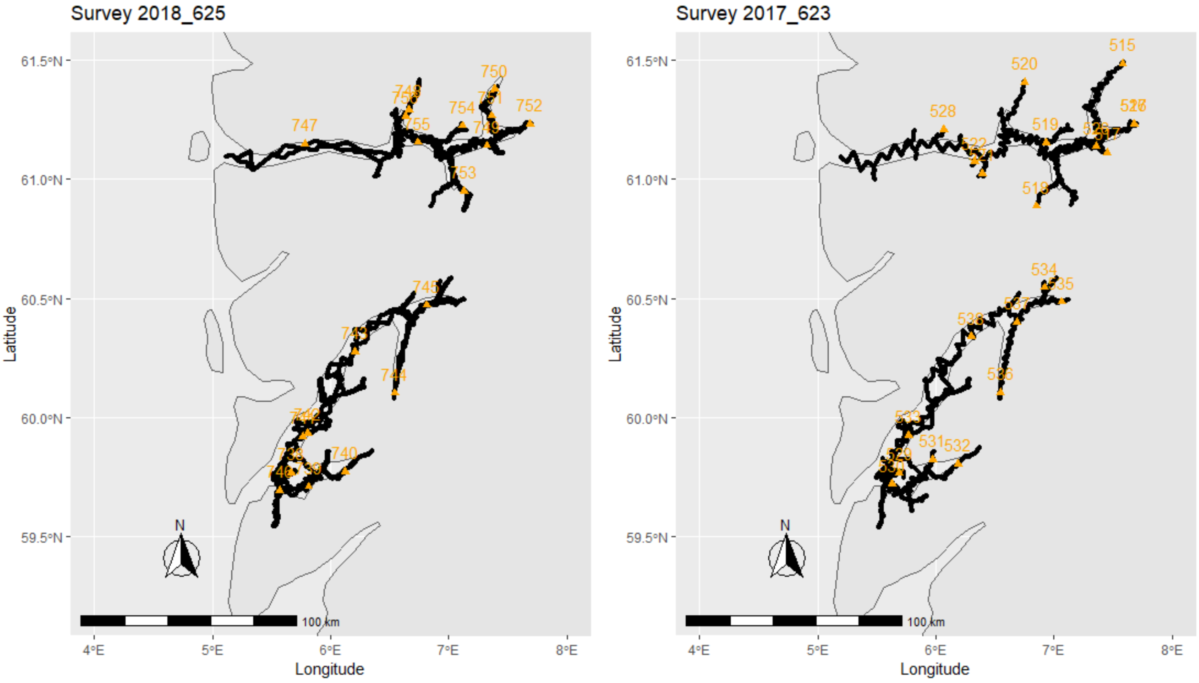

Figure A1.2 All NASC (black lines) data and biotic stations (orange triangles) for surveys in 2018, 2017 in Sognefjorden and Hardangerfjorden

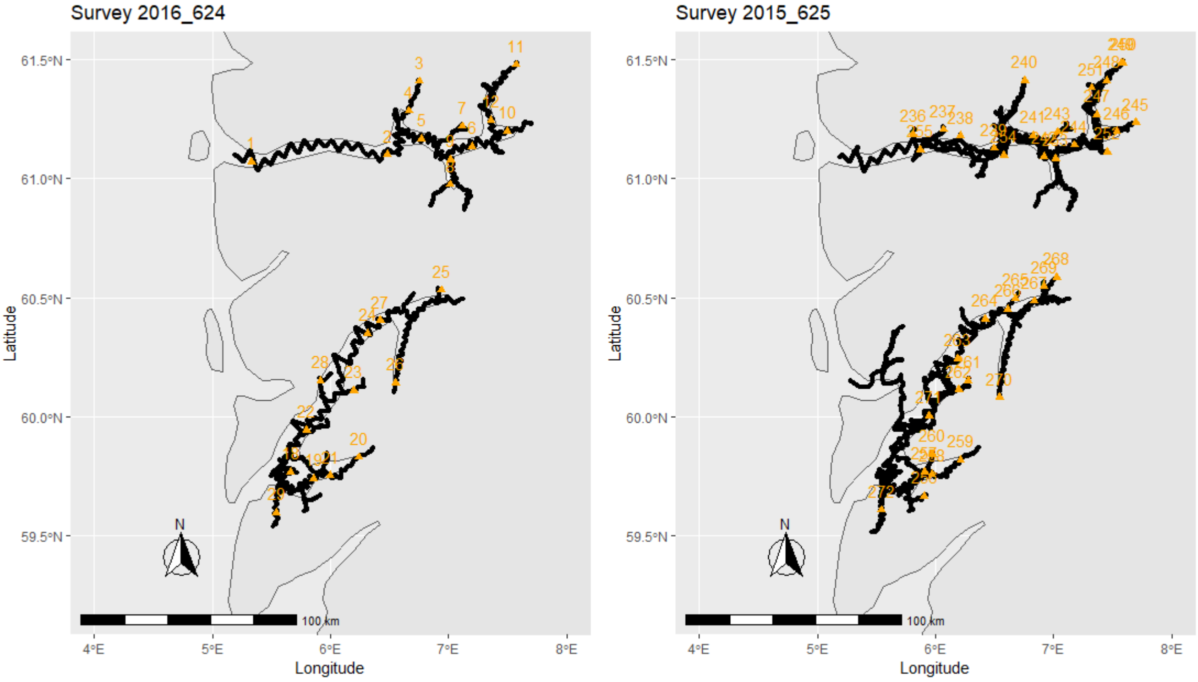

Figure A1.3 All NASC (black lines) data and biotic stations (orange triangles) for surveys in 2016, 2015 in Sognefjorden and Hardangerfjorden