

Does abundance of Northeast Arctic cod
Gadus morhua influence the schooling
dynamics of capelin *Mallotus villosus*?



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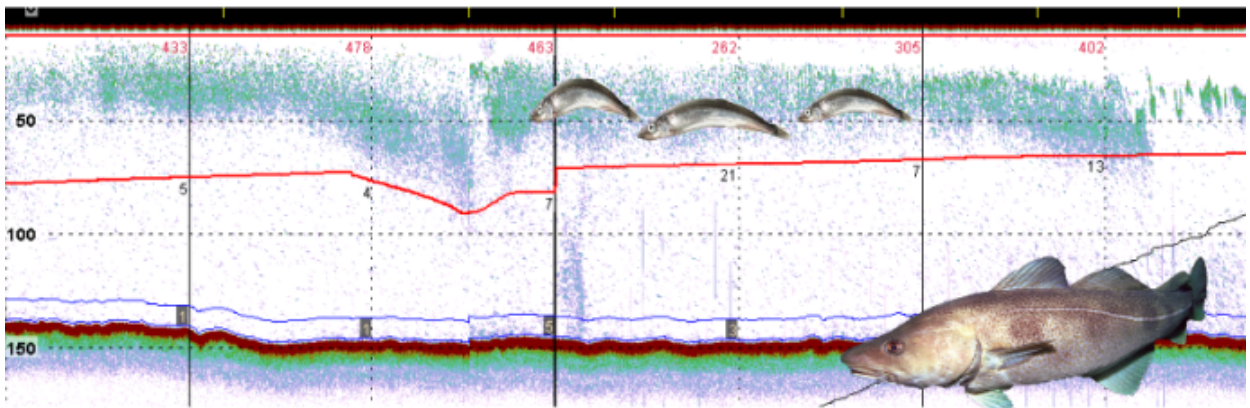
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Abstract

Cod *Gadus morhua* and capelin *Mallotus villosus* play an important ecological and commercial role in the Barents Sea. Capelin provide high lipid energy to many of its predators in the Barents Sea including cod, which is capelin's main predator. Exploring cod and capelin's interaction is instrumental when assessing the stocks and provides improved understanding about the Barents Sea Ecosystem. Studies concerning their interaction and overlap, have been conducted on a large scale, using survey data collected over the course of several years, but few studies have addressed their interaction on a finer scale.

Therefore, the main aim of this thesis was to assess small scale interactions by investigating whether abundance of cod affects capelin's schooling dynamics, namely *packing density* and *minimum distance to bottom*. To do this, one of the objectives of this study was to establish a method to enable the use of acoustic data to evaluate capelin school features.

Acoustic data was collected onboard the Barents Sea Ecosystem Survey in August/September, when cod and capelin have undergone migrations to the northern Barents Sea. The original interpretations of acoustic data were made on board by scientific personnel and I further examined the capelin school data using the program Large Scale Survey System (LSSS) and its multi-extension toolbox Korona, enabling for school detection.

Through sensitivity testing I found that the Korona school detection settings *acoustic threshold* in particular, but also *minimum school length*, strongly influenced the capelin school detection. I found a setting which was successful in detecting and delineating capelin schools and this setting can be utilized for future studies on capelin schooling dynamics, for instance using time-series data.

I found that abundance of cod had no direct impact on capelin's *packing density* and *minimum distance to bottom*. However, previous studies has demonstrated that light and bottom depth play an integral role in fish schooling dynamics and were therefore considered here. Testing a set of linear mixed models, the best model, showed that bottom depth and sun altitude contributed to significant variations in schooling dynamics. Packing density increased with increasing sun altitude and was higher at shallow banks, whereas minimum distance to bottom increased with increasing bottom depth and decreased with increasing sun altitude.

Although abundance of cod did not directly impact capelin's schooling dynamics, the results suggests that capelin's schooling dynamics is rooted in a trade-off between engaging in activities such as feeding and avoiding predators such as cod. The increase

in packing density along shallow banks during daytime suggests that capelin may have been responding to cod that are typically associated with shallow banks when feeding. The results from this study indicates that capelin adjusts their position in the water column to a depth where light gradients provide enough light to detect prey, but also avoid predation.

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1. Introduction

Northeast Arctic cod (*Gadus morhua*; hereafter cod) and Barents Sea capelin (*Mallotus villosus*; hereafter capelin) play an important commercial and ecological role in the Barents Sea (Gjørøseter, 1998; Sakshaug, 1997). Capelin provide a high energy rich (lipids) prey (Benoit et al., 2010; Hop and Gjørøseter, 2013) for fish, sea mammals and seabird predators, such as herring *Clupea harengus* (Hamre, 1994), harp seal *Pagophilus groenlandicus* (Dolgov, 2002), common guillemot *Uria aalge* and minke whale (*Balaenoptera acutorostrata*, as well as the most important predator on capelin, cod (Gjørøseter, 1998). In the Barents Sea, capelin is the main prey item for cod and studies have shown that cod's fitness and reproductive success is effected by capelin's population (Gjørøseter et al., 2009; Johannesen et al., 2012). Because capelin are semelparous (die after a single spawning event) and are vulnerable to predation by juvenile herring and cod, they have experienced dramatic fluctuations in their population size over the past decades (Gjørøseter and Bogstad, 1998; Gjørøseter et al., 2009). In periods with collapse in the capelin stock, serious cascade effects have been observed in the Barents Sea ecosystem. For example, during 1987, due to lack of food, thousands of hungry seals invaded the coastline and were caught in fishing gear, increased cannibalism was also recorded amongst cod in the 1980's and poor fitness and reproduction were observed amongst seabird populations such as kittiwakes and puffins, who have capelin as essential food (Hamre, 1994; Gjørøseter, 1998). These ripple effects caused by the capelin collapse after the 1980s have since been considered in fisheries management of capelin, in particular estimations on cod's predation of capelin (Gjørøseter et al., 2002).

When the Barents sea becomes increasingly ice-free, cod and capelin migrate northwards during the summer, reaching their maximum northernmost distribution in August/September (Bogstad et al., 2013; Fauchald et al., 2006). Capelin congregate to feed on concentrations of zooplankton along banks and shelves (Carscadden and Vilhjálmsson, 2002) and in turn, cod migrate to feed on organisms such as capelin. Large scale studies have previously been conducted, during this feeding season, using aggregated data to study cod and capelin's interaction and spatial overlap (Fall et al., 2018, 2021; Johannesen et al., 2012).

Schooling amongst fish has been investigated using theoretical explanations and models and observational studies (Aoki, 1984; Misund, 1993; Parrish et al., 2002; Pitcher, 1973; Vabø and Nøttestad, 1997), to understand the complex responses and internal behaviour

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of each individual and school as a whole. The consensus is that schooling behaviour is modulated by reproduction, migration and feeding, but tends to be largely regarded as an anti-predation response. Studies have shown that schooling fish can respond to predation by performing evasive tactics, such as shifting their position in the water column and minimizing their inter-distance to their neighbours by increasing packing density, to maximize their chances of survival. The level of reaction displayed may reflect the threat level detected (Helfman, 1989). In a study conducted off Newfoundland, Mowbray (2002), found that capelin demonstrated anti-predatory behaviour by increasing their distance to the bottom when cod density. Additionally, several studies have also shown that herring's packing density responds to predation (Rieucou et al., 2014; Vabø et al., 2002).

This thesis addresses cod and capelin's fine-scale predator/prey interaction. More specifically, it does this by investigating capelin school's *packing density* and *minimum distance to the bottom* (seafloor), as a response to the presence and abundance of cod. This will be done by analysing original raw acoustic data from a survey conducted in August/September when the two species overlap and interact. By using the post-processing system, Large Scale Survey System (LSSS), acoustic data can be utilized to determine what factors effect schooling dynamics.

1.1. The predator and the prey

1.1.1. Cod and capelin interaction

Prey and predator interaction are dependent on overlap and ultimately, proximity (Fall et al., 2018, 2021). Understanding cod and capelin interaction and overlap more thoroughly is essential in understanding how capelin schooling dynamics will respond to possible predation. During the months of August and September, cod are present in the northern ice-free areas and overlap to feed on pelagic fish such as polar cod *Boreogadus saida* and capelin. In a study conducted in early October, In the northern Barents Sea (West of the Great Bank), samples and acoustic measurements demonstrated that light was the main driver in affecting the spatial dynamics of cod, capelin and zooplankton (Skaret et al., 2020). Cod are both demersal and visual predators and rely on pelagic fish consumption. They must therefore expend energy moving vertically in the water column or wait patiently for capelin to approach closer to the sea bottom (Skaret et al., 2020).

Capelin's diel vertical migration pattern is generally determined by light intensity and can also be affected by the availability of zooplankton, temperature, bottom depth and predation (Mowbray, 2002). Capelin's school behaviour is rooted in a trade-off between avoiding predators, as well as feeding on zooplankton that are abundant during this time

of year. During daytime aggregations of krill submerge down into the water column, close to cod occupying the seafloor, in order to avoid predation from organisms such as capelin (Skaret et al., 2020). Here cod take advantage of vertically migrating capelin who descend into the depths after dawn commences, without expending significant energy (Skaret et al., 2020). Although cod are demersal fish, they can occasionally be found in the open water masses (Strand and Huse, 2007). As a possible anti-predatory response to predators such as cod, capelin's position themselves vertically at intermediate depths, away from the sea bottom, where light increasingly attenuates with depth, forming pelagic schools during daytime (Benoit et al., 2010; Mowbray, 2002).

Whilst cod may take advantage of prey density and optimal lighting, other environmental factors also affect this cod-capelin interaction, including bathymetric and topographical factors (Fall et al., 2021). Shallow bathymetry attracts plenty of fish and in the Barents Sea, cod consequently aggregate on the banks (Fall et al., 2018). Light penetrates to the sea floor in shallow shelves and the likelihood of detecting prey, for visual predators such as capelin and cod, increases. Currents carry zooplankton to shallower depths, where they are unable to descend into deeper, darker depths to avoid predation (Aarflot et al., 2019). When the zooplankton are trapped along these shallow banks, it provides a favorable feeding ground for capelin, who use light to detect prey. The capelin that aggregate to feed on zooplankton are consequently in closer proximity to cod and the shallow bank areas provide optimal feeding grounds for cod, who spend less energy foraging for pelagic fish (Skaret et al., 2020). Capelin density does not necessarily equate to an increase in cod predation, instead optimal lighting coupled with shallow depths, where capelin are more easily detected and vertically closer to the sea floor, can increase cod predation on capelin (Aarflot et al., 2020; Fall et al., 2021).

1.1.2. Using acoustics to tell a story

Interactions amongst predator and prey can be documented in many ways. Filming is often used to study and capture interactions that can provide informative stories about the dynamics between organisms. The ocean is vast and dark and to counter that, sound has been used to investigate and document what stirs beneath the ocean surface. Sound travels around 343 m/s on land and travels about 1500 m/s in water (Santucci et al., 2006). The application of sound waves, referred to as acoustics, have been used for many years to observe and monitor fish dynamics in an effective way as well as observe ecosystem interactions (Simmonds and MacLennan, 2007).

During hydro-acoustic surveys, several sound signals are sent out from the ship simultaneously. These sound signals are referred to as pings, which emit an echo when they come in contact with various objects in the sea. With the help of the same transducers that emitted the sound, the returning echoes are perceived as sound waves. The strength

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or weakness of an echo, and the time that it takes for a ping to be sent out, to when an echo is returned, tells us about the characteristics and position of the acoustic targets in the water column as well as characteristics and position of the depth of the sea floor. This information can be displayed as an echogram and further interpreted as biological components, such as plankton or fish. On board the Ecosystem survey, this acoustic technology is essential when estimating capelin abundance. These measurements have been further utilized in this thesis to extrapolate data associated to each individual capelin school's *packing density* and *minimum distance to bottom*

1.2. Schooling

Understanding how capelin schools respond to predation, means understanding a school's function and purpose. Existing literature demonstrates that schooling may provide hydrodynamic advantages (Weihs, 1973) and also happens when fish reproduce, migrate, feed or respond to predation (Pavlov and Kasumyan, 2000; Parrish et al., 2002; Pitcher, 1973). Definitions of schools differ, but the general consensus is that individuals within a school are mutually attracted to each other and exhibit coordination in movement and orientation, that benefit the individuals in a school (Pavlov and Kasumyan, 2000; Shaw, 1978). Schooling is in fact a social behaviour that is typically observed in aggregations of fish, some of whom spend their whole life in schools (Pitcher and Partridge, 1979). School behaviours and functions vary depending on species of fish, ontogeny, stimuli, feeding behaviour, detection of predation as well as other abiotic and biotic factors such as habitat and light (Pavlov and Kasumyan, 2000). Fish schools have developed ways of exchanging information within these formations which helps improve the fitness and survival of individuals. Maintaining flows of information can also signal to individual fish whether danger is looming nearby or if there is food available. In order to maximize the information input, fish within a school formation, position themselves at a particular distance to their neighbour (Parrish et al., 2002). Information is received through visual cues from the fish in their periphery as well as non-visual cues such as displacement of water (Pavlov and Kasumyan, 2000). Although the lateral side line of the fish may detect displacement in water (Partridge and Pitcher, 1980), the main cues are received through visual information (Partridge and Pitcher, 1980), making light an important component of school responses and formation (Misund, 1993; Pavlov and Kasumyan, 2000).

1.2.1. Schooling as an anti-predatory response

Schooling has been largely regarded as a response to risk of predation (Pitcher and Parrish, 1993). The capelin have larvae that are transparent and small in order to remain inconspicuous from potential predation (Fuiman and Magurran, 1994). How-

ever, as capelin grow in size and become more visible to predation, they must resort to other anti-predatory strategies, such as schooling (Pavlov and Kasumyan, 2000; Fuiman and Magurran, 1994; Ritz et al., 2011). When schooling fish forage, migrate or reproduce they can form large aggregations that may cause them to be more detectable to predation (Ritz, 1994). Yet, when migrating or reproducing in schools, a "safety in numbers" strategy provides more advantages than disadvantages for individual fish (Connell, 2000). When schools detect or respond to predation, they may respond in several ways and undergo various strategies by shifting shape and size (Misund, 1993; Pavlov and Kasumyan, 2000). The names of these given shapes and sizes vary, but schools may compress, reorganize, elongate, dive, surface and even form rings as a response to predation or food (Nottestad et al., 2002; Pavlov and Kasumyan, 2000). Capelin's response to predation can be detected by looking at schooling characteristics such as *packing density* and *vertical distribution*.

Packing density

Investigating capelin's schooling *packing density* in response to cod abundance, provides insight into how capelin respond to threat. The packing density of a school is altered as a response to external and internal drive and light is a significant external and visual cue (Misund, 1993; Partridge and Pitcher, 1980). Light also determines an individual's ability to form schools and to detect danger from predators (Shaw, 1978). It also provides an opportunity for visual predators to detect and capture their prey (Rickel and Genin, 2005). Moving in a tight knit school confers anti-predation advantages and incites effective information flow (Parrish et al., 2002). When predation is looming, it may cause schools to pack tighter and organize themselves strategically (Misund, 1993). This can be explained by the "selfish herd" model (Hamilton, 1971), which assumes that when individuals pack tighter to their neighbour, they selfishly reduce their risk of being attacked by a predator. Investing in anti-predatory behaviour is also energy costly and increasing packing density is not necessary if risk of predation is not detected. Packing density tends to be more loose during night and during feeding or reproduction (Fréon et al., 1996) when fish can invest in activities that increase their fitness. Fish are observed deeper in the water column during daylight, to avoid visual predators. These schools also tend to pack tighter during daytime, as an anti-predatory response (Fréon et al., 1996). Thus, packing density intensifies with increasing light, but is ultimately labile and fluctuates as a response to external and internal cues such as competition, feeding and predation.

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Minimum distance to bottom

Investigating capelin's vertical distribution (*minimum distance to bottom*) in the water column in relation to cod may provide insight into capelin school's response to predation. One of the most effective ways of avoiding predation is to simply limit encounters with predators, which means positioning themselves strategically to avoid proximity to predators. For many schooling fish, such as capelin, this entails avoiding light that can further expose them to visual predators. In such instances, school's vertical distribution is typically determined by a trade-off between enough light to detect prey as well as enough darkness to hide from visual predators (Pearre, 2003; Giske et al., 2013) referred to as the "light comfort zone" (Røstad et al., 2016). Thus, light is a proximate factor in determining the vertical distribution and proximity to bottom depth, for schooling fish. Vertical distribution adjustment based on light is exhibited with fish that perform diel vertical migration (DVM) as an anti-predatory tactic to avoid visual predators (Dalpadado and Mowbray, 2013). The onset of a more distinct day and night during spring and autumn, means the amplitude of vertical distribution increases (Geoffroy and Priou, 2020). However, during periods of midnight sun, the perpetual onset of light diminishes the benefits of undergoing DVM (Olsen et al., 2009). Alternatively, schooling becomes even more important, as an anti-predator response. Additionally, responding to danger is also relative to the threat level fish detect known as "threat sensitivity" (Helfman, 1989). Seghers (1981) distinguishes between the distance a school permits when the predator is spotted and the evasive response distance it creates when it reacts to predation. This tactful strategy is intended to avoid expending unnecessary energy towards response manoeuvres, such as evasive fast swimming, which require more energy than engaging in school behaviour, where the risk of predation decreases (Pavlov and Kasumyan, 2000). Depending on the direction of the predatory risk, fish may invest energy in moving away from the danger, by adjusting their vertical distribution in the water column. For schooling fish such as capelin, increasing vertical distribution to the seafloor, where cod reside, would thereby limit encounters.

1.3. What to expect

I will in my thesis, seek to examine how the abundance of cod aggregations impact capelin's fine-scale behaviour and schooling. This will be done by assessing acoustic raw data collected during a survey conducted in August- September, 2017 (Ecosystem Survey) in the Barents Sea.

Other studies have covered large spatial and geographical distribution and overlap of capelin and cod (Fall et al., 2018; Johannesen et al., 2012) yet few studies attempt to look at the small scale interaction between them. In particular, existing studies have not

examined how school behaviour and characteristics of capelin, in the Barents sea region, is affected by the local density of cod.

I will seek to examine how the schooling behaviour of capelin, represented by school *packing density* and school *minimum distance to bottom*, will be affected by density of cod. Based on the previous literature, it is expected that packing density will increase in response to abundance of cod. Minimum distance to bottom is also expected to increase as a response to increasing abundance of cod. Studies have demonstrated that light and bottom depth have an impact on schooling dynamics. Consequently, I will be considering these factors in my investigation.

1.3.1. Objectives

(a) I will establish a method using acoustic data to robustly assess the effect cod abundance has on capelin schooling dynamics.

Predictions

(b) I will assess the potential influence of cod abundance on capelin schooling dynamics by looking at number of cod, light and bottom depth.

- *P1*: Packing density increases with number of cod
- *P2*: Packing density increases with increasing light
- *P3*: Packing density increases with bottom depth
- *P4*: Minimum distance to bottom increases with number of cod
- *P5*: Minimum distance to bottom decreases with increasing light
- *P6*: Minimum distance to bottom increases with increasing bottom depth

2. Material & Methods

2.1. The Barents Sea ecosystem

2.1.1. Survey area description

The Barents Sea is a shallow shelf ecosystem, situated north of Norway and stretches east-west from Russia (Novaya Zemlya) to the Norwegian Sea (Sakshaug, 1997). The region extends from the Arctic ocean down to Norway and Russia (Ottersen et al., 2014). The sea is characterized by its influx of water masses originating from a cold Arctic current (northern parts), relatively warmer North Atlantic Current as well as the North Coastal Current (Loeng et al., 1997). The Polar front created along the east of the Norwegian Sea, form temperature and salinity gradients, where warm Atlantic water and cold Arctic water masses meet (Oziel et al., 2016). The Barents Sea ice cover varies seasonally and inter-annually, reaching a maximum around March/April and retreats to a minimum in September (Koenigk et al., 2009). Seasonal variation is prominent, in high-latitude environments affected by midnight sun during summer and polar nights in winter (Loeng, 1991). As the light returns in early March, melting ice causes vertical stabilization of water masses, to sustain a short period of phytoplankton production (Hegseth, 1998). Seasonal warming in the Atlantic water masses, sustains a longer pelagic phytoplankton production (Skjoldal, 1989) which provide zooplankton more time for grazing (Eriksen et al., 2018). The ecosystem is also dependant on zooplankton species that provide sustenance to several organisms such as capelin and polar cod (Orlova et al., 2009). In turn, the Barents Sea is an important feeding and nursery area supporting some of largest stocks of commercial fish such as cod, herring and haddock *Melanogrammus aeglefinus* as well as seabirds and mammals (Dalpadado et al., 2014; Sakshaug, 1997) that depend on the productivity of the Barents Sea.

2.1.2. Species description

Capelin

Capelin is silvery, pelagic schooling fish belonging to the smelt family Osmeridae (see Fig: 2.3), can attain a length of 21cm and live up to 6 years (Jourdain et al., 2021). They have a circumpolar distribution in the Arctic and Sub-Arctic region (Rose, 2005). Capelin exhibit high spawning mortality and spawning tends to peak in March-April (Gjørseter, 1998). Capelin conduct migration in large schools to spawn on shallow ocean shelves off the North-East coast of Norway in Troms, Finnmark and Russia (Gjørseter, 1998). In summer, capelin begin migrating towards the central and north of Barents Sea where they feed on zooplankton. The preference for copepod species (*Calanus.spp.*) decreases with capelin length, while adults feed on amphipods and varying amounts of euphausiid crustaceans (krill) such as *Meganyctiphanes norvegica* and *Thysanoessa inermis* (Dalpadado et al., 2002; Panasencko, 1981).

Cod

Northeast Arctic Cod belong to the family Gadidae (see Figure 2.4), can grow up to 1,5 meters and live more than 20 years (Kvamme and Bogstad, 2007). Northeast Arctic cod is the largest cod stock in the world (Rose, 2019) and lives mainly in the Barents Sea (Michalsen et al., 1998). Around the same time as the capelin spawning migration, cod travel thousands of kilometres in order to spawn in their native area (around Vesterålen/Lofoten), seeking favourable temperatures for spawning. Although cod are opportunist feeders, at an age of 3-4 years, their diet follows the availability of capelin (Nakken, 1994). Capelin is their main and preferred prey (Fall et al. 2018) and during summer, cod migrate to the Barents Sea to feed. Relatively high overlap between cod and capelin occur during winter and summer/early autumn (Fall et al., 2018), after which cod and capelin have conducted a large northbound feeding migration (Gjørseter, 1998) (see Figure 2.1 and 2.2), reaching their most northern distribution in August/September.

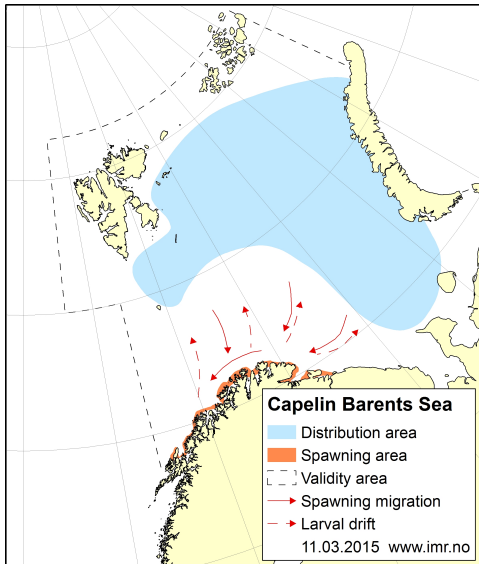


Figure 2.1.: This figure shows capelin distribution in Barents Sea. During spawning eggs are deposited on the ocean floor for about a month's time. The eggs later hatch and ascend to the upper layers where they drift with the strong Northeast-bound Norwegian Coastal Current and towards the Barents Sea. Maps by Horneland, Skulstad and Gjertsen/IMR.



Figure 2.3.: Pictured here is capelin. Photo by: Erling Svensen/IMR.

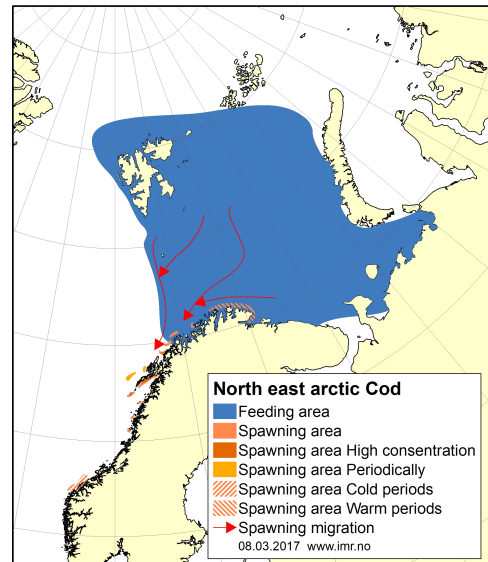


Figure 2.2.: This figure shows the cod distribution in Barents Sea. Cod spawn in waters with high salinity and their pelagic eggs and larvae drift with currents towards the north and east Norwegian coastline. It is a migratory species which swims from Barents Sea to the Norwegian coast for breeding.



Figure 2.4.: Pictured here is North-east Arctic cod. Photo by: Jan de Lange/IMR.

2.2. Survey and data collection

2.2.1. Survey design

In my thesis, I will assess data collected during "the Barents Sea Ecosystem Survey" (BESS) to determine whether abundance of cod impacts capelin school dynamics. The BESS was established in 2004 and runs from August-September collecting a range of data on the Barents Sea ecosystem, including synoptic data collection on cod and capelin during feeding season. It is a joint survey led by Norway and Russia, by the Institute of Marine Research (IMR) and the Knipovich Polar Institute of Marine Fisheries (PINRO), respectively.

The survey runs annually, using four to five ships, and its main objective is to collect a variety of data to monitor the status of the Barents Sea Ecosystem. In particular, it aims to collect data for the abundance estimate for the capelin stock assessment and quota advice, which can also be used for making general assessments about capelin abundance and distribution. Additionally, the data collected is used to assess key ecosystem interactions, such as the one between cod and capelin.

The sampling method for the BESS was standardized by specialists from IMR and PINRO to ensure consistent monitoring. The sampling stations are placed approximately 35 nautical miles (65km apart) within the grid design. During BESS, acoustic data are collected continuously along standard transects (Figure 2.5). To acquire more information about the adult capelin, additional acoustic transects were implemented in 2017, roughly 15 nautical miles (27 km) apart in the main capelin area.

2.2.2. Data collection

Acoustic data are consistently collected throughout the BESS survey. For each vessel utilized in the survey, the echo-sounder, Simrad EK-60/80- 18, 38, 120, 200 and 333 kHz split beam transducers sent out pings that essentially detected the sea floor and recorded fish echoes, such as capelin (Simrad EK-80 replaced Simrad EK60 in 2017/2018). Transducers were additionally mounted on drop keels to prevent bubble noise on both "Johan Hjort" and "G.O. Sars".

In order to monitor the pelagic and benthic communities, pelagic and demersal trawling are conducted at fixed positions in a regular grid on board all the ships. At each fixed station, the Campelen 1800 demersal trawl is towed around 15 minutes at 3 knots (kts) in order to collect demersal biological samples, such as cod samples. The demersal trawl has a 20mm mesh size in the cod end with a trawl sweep width of around 25 meters during towing and a height of up to 4.5 meters (see IMR-PINRO 2017 report: Prozorkevich and van der Meeren, 2008).

At each fixed station, a pelagic "Harstad" trawl is also used to collect pelagic samples

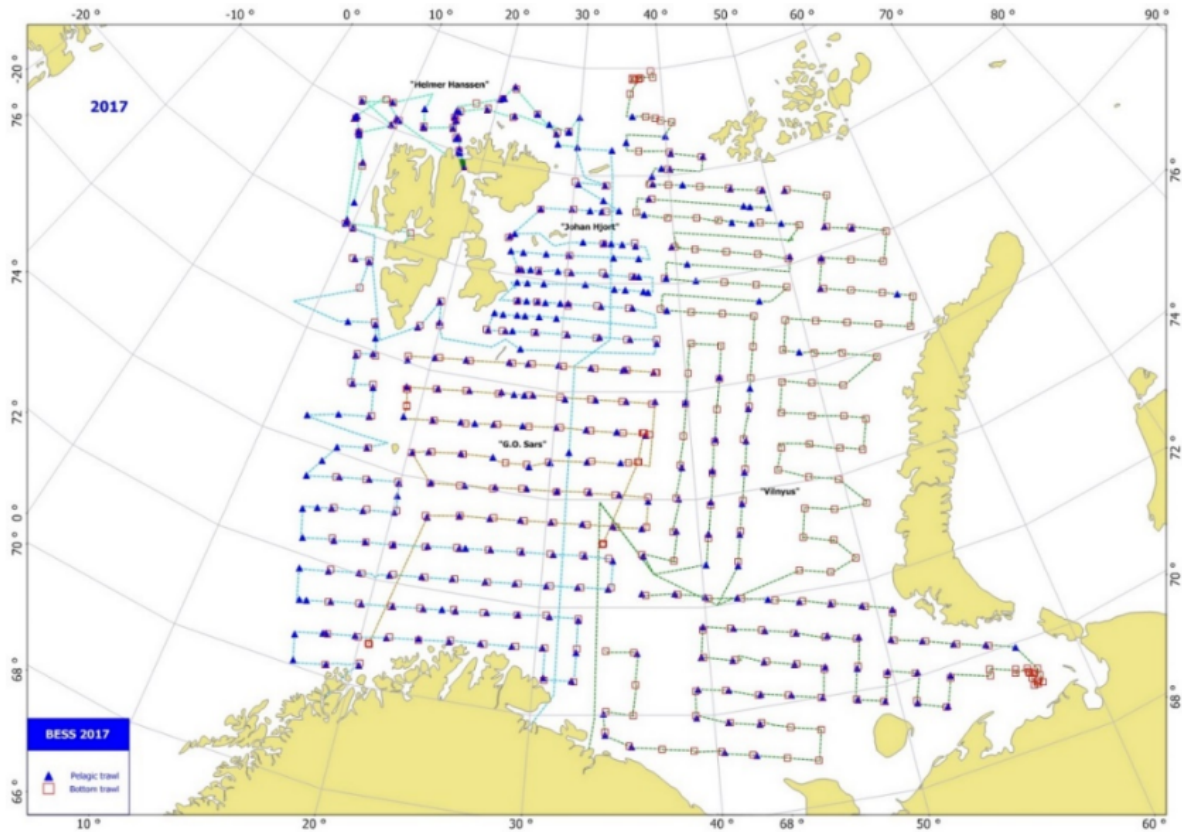


Figure 2.5.: Ecosystem survey, August–October 2017. Research vessel tracks and trawl stations for pelagic and bottom trawl stations (Eriksen et al., 2018).

of 0-group at three standard depths (0, 20 and 40 m). Also, when strong acoustic signals are recorded, additional pelagic trawling is conducted to support the acoustic readings and ensure high quality interpretation of acoustic data (see section below).

For each fixed station, the conductivity (salinity), temperature and depth (pressure) was also measured using a CTD.

For my analysis, BESS data from 2008–2018 were used to establish a method for capelin school detection and delineation (see section below). The method was further applied on selected BESS data from the year 2017 to investigate how abundance of cod would impact on capelin schooling dynamics.

2.3. Analysis of acoustic data

2.3.1. Onboard scrutiny of acoustic data

A key data input to this study was acoustic data collected during the BESS. The Norwegian and Russian vessels, that carry out the Barents Sea ecosystem survey, are equipped with the post-processing program, Large Scale Survey System (LSSS, www.marec.no) (Korneliussen et al., 2016). This is a package developed by MAREC to process large quantities of multi-frequency acoustic data (18 kHz to 364 kHz). The echosounder Simrad EK60/EK80 generate files on the .raw format, which are used by LSSS to carry out echo integration and the data is displayed in echograms for further data processing.

On board during BESS, the acoustic data displayed in LSSS are allocated to different groups, for instance target groups like capelin and herring and non-target groups like plankton. This is done by experienced scientific and instrument personnel. The allocation of acoustic data is often termed scrutiny of acoustic data and is done in conjunction with periodic trawling. In addition, general knowledge of echo characteristics of different targets like capelin schools, biology and back-scattering energy of species as well as physical/chemical data are used as background for the scrutiny. Distinguishing between species on the echogram can be difficult and there is always an element of subjectivity in the scrutiny. To reduce the uncertainty of the scrutiny, trawl samples are taken if the echogram is picking up strong echo recordings and supplementary biological samples are needed to resolve any ambiguity. Additionally, onboard the Norwegian vessels, it is common to use the information from different acoustic frequencies in order to improve to improve the quality of the scrutiny. In the typical distribution areas for capelin, the cruise leader normally has years of experience and has knowledge in recognizing capelin schools, which is crucial in the final analysis used for the capelin assessment.

In order to improve data quality, false echoes, echo contributions from the seabed as well as noise and bubbles are usually removed during pre-processing. Figure 2.6 below shows an example of the graphical user interface of LSSS where acoustic data are analysed.

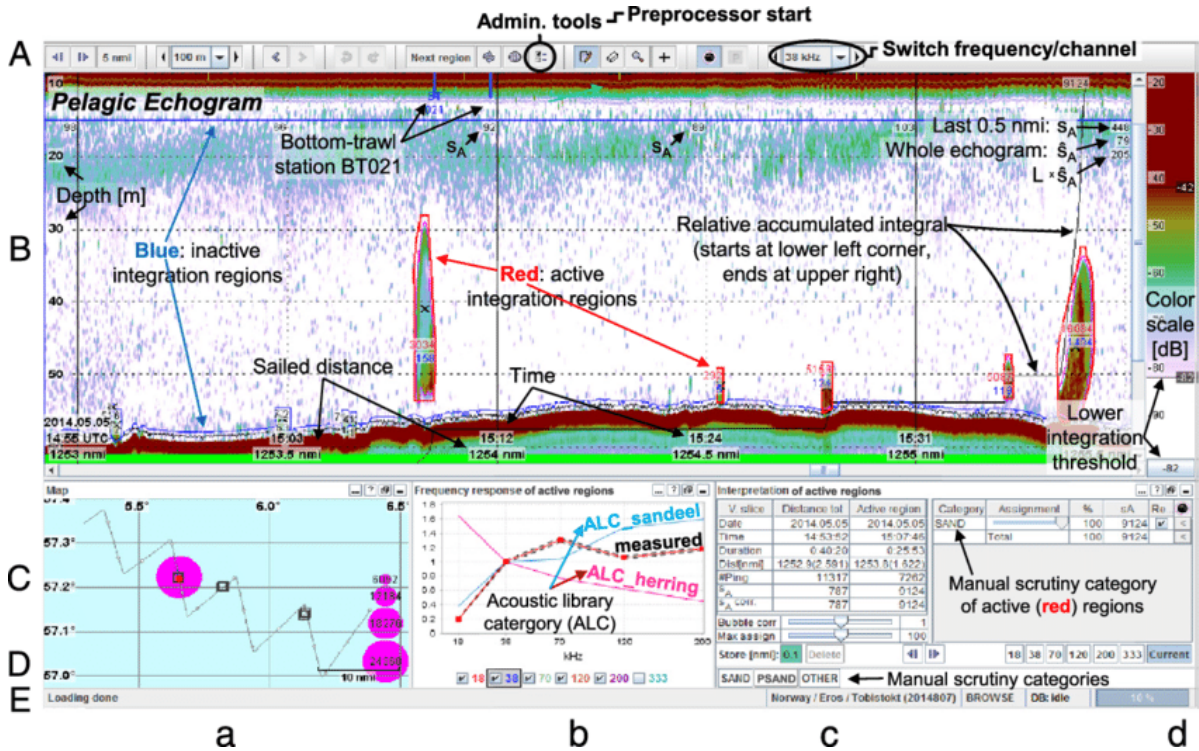


Figure 2.6.: Graphical user interface (GUI) of LSSS for interpreting backscatter data: The main window displays the pelagic view of the acoustic data at the frequency 38 kHz. To pinpoint where the acoustic information is recorded, the longitude, latitude and map of the ships track, is also displayed on LSSS. Additionally, the time is displayed at the bottom of the pelagic window together with the sailed distance, shown in nautical miles (nm). The toolbox allows the interpreter to correct the lower integration line as well as draw layer lines to separate acoustic returns. The back-scatterer regions encircled in red are being scrutinised and the windows in the bottom right corner display s_A values (see text for explanation) corresponding to the encircled regions. The colour scale on the right hand side displays the volume back-scattering strength (S_v) ($dBre1m^{-1}$). At 38 kHz, knowledge about the back-scattering response for specific groups of species aids in the post-processing and manual species allocation. The s_A values displayed on the right-hand corner of each block indicate the mean s_A value for last 0.5 nm , as well as the whole echogram. Figure is taken from: Korneliussen et al. 2016.

2.3.2. Quantification of acoustic backscatter

Integrated echo from echo sounders can be used for quantification in fisheries acoustics, and the scattering properties have special names, definitions and symbols (MacLennan, 2002).

The backscattering cross-section ($\sigma_{bs}; m^2$) is typically the smallest acoustic entity used and is normally derived from the echo of a single acoustic target (target strength or TS):

$$TS = 10 \log_{10}(\sigma_{bs}) \quad (2.1)$$

The volume backscattering coefficient ($s_v; m^{-1}$) can be derived from the (σ_{bs}) as:

$$s_v = (\sigma_{bs})/V \quad (2.2)$$

This quantity describes acoustic backscatter for a given volume (V), and the s_v on

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logarithmic form, the S_v (Mean volume backscattering strength) (MacLennan, 2002), is used to quantify and display acoustic backscatter on all the echograms scrutinised during BESS and echograms used in my study. In the present study I also use the volume backscattering coefficient as a proxy of schooling packing density (see later).

It is often relevant to integrate echo over an area and the s_a - Area backscattering coefficient (m^2m^{-2}) is defined as:

$$s_a = \int_{z_1}^{z_2} s_v dz \quad (2.3)$$

which is the volume backscattering coefficient (s_v) integrated between two depth layers, z_1 and z_2 in the water column. The s_a can be converted to s_A - Nautical area scattering coefficient m^2nm^{-2} as:

$$s_A = 4\pi (1852)^2 s_a \quad (2.4)$$

s_A is a standard quantification used in fisheries acoustics, for instance for abundance estimation of fish (MacLennan, 2002; Simmonds and MacLennan, 2007).

During BESS, after acoustic backscatter is assigned to available acoustic target categories in layers or boxes, the acoustic backscattering data are stored in an LSSS database as s_A values at a horizontal resolution of 1 nautical mile and a vertical resolution of 5 meters. The values are further stored at this resolution in reports, which are used for my analysis for this study.

2.3.3. Capelin school detection

In order to analyse capelin schooling dynamics using acoustic data, I applied the Korona-module in LSSS. Korona is LSSS' multi-frequency extension toolbox which I used to pre-process raw data files (Korneliussen et al., 2016). It was developed with the intention of analyzing echograms more time effectively as well as objectively. Korona provides standard modules that can be selected and altered. It is possible for the user to edit the settings and parameters within this modules, such as settings for detecting schools within a school detection module. Selected raw-files can be uploaded to Korona and further processed with the new settings. The post-processed files can then be viewed on the LSSS' pelagic echogram.

For my thesis, my selected modules and settings in Korona were used to detect capelin schools. BESS acoustic reports from LSSS containing the original interpretations from the years 2008-2018 were made available from IMR's database. To view the original interpretations made onboard the survey, EK60 raw-files, Korona-files and work-files were selected in the survey configuration window of LSSS. Transducer data, Korona processing setup, LSSS survey setup files and Export files were also made available in

order to set up a project and execute the school detection using Korona. It was then possible to edit the Korona configuration modules including school detection. A selection of Korona modules that were not necessary for school detection were removed and only modules that influenced school detection kept were edited. The available parameters in the Korona module "school detection" can be seen in Appendix A. The main parameters that were altered was frequency, minimum acoustic threshold for detection, blind zone depth, minimum length, area and thickness of schools. Korona traces a distinct pink line around the aggregations that correspond to schools detected, according to a given set of parameters.

2.4. Sensitivity testing to decide on a school detection setting

In order to explore how cod impact capelin school dynamics, it was essential to detect and delineate capelin schools in an efficient and representative manner. Therefore, a sensitivity test was conducted to evaluate how school detection in Korona was affected when changing some key parameter settings in the Korona school detection module including the acoustic threshold, minimum school length as well as blind zone depth.

I first reviewed the LSSS report files from the various BESS surveys which were carried out in the main capelin distribution area from 2008-2018 in conjunction with looking at the echograms and the original scrutiny that was available in the interpretation window in LSSS. In doing so, it was possible to distinguish where capelin schools had been found and select capelin schools for my sensitivity test, that were largely separated from other acoustic backscattering organisms.

It was clear that capelin schools aggregated in various shapes, forms and sizes (See Appendix A). Three main types of schools were observed that had different sizes, shapes and packing density. I observed both small and large schools in the water column. Additionally, I observed looser assemblages of fish scattered across the water column which was detected and formed during night-time. Their shape can be characterized as amorphous and the schools stretched horizontally. Since all these were capelin schools, but differed considerably in characteristics, it was imperative to find a single school detection setting that would detect these different capelin schools as effectively as possible. An overview of the different types of schools mentioned can be seen in Appendix A.

The first settings that was altered in the school detection module was minimum school detection threshold, which was altered to -60, -70 and -80 dB re 1 m^{-1} . The second setting that was altered was minimum school length which was changed to 5, 10 and 15 m . Both combination of settings were tested on the three different types of capelin schools for the same data-set. The output for each setting was compared by a) observing

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on the echogram how effective the setting was in detecting and delineating the capelin schools and b) comparing school features from the output for each of the settings. The exact same region on the echogram was used when testing the different settings. The following school output parameters were compared:

1. Mean Area of Schools (m^2)
2. School Height (m)
3. Packing Density (Median s_v (dB re 1 m^{-1}))
4. Nautical Area Scattering Coefficient (s_A (m^2nm^{-2}))
5. Number of objects (schools)

The mean s_A (m^2nm^{-2}), outlined in equation 2.4, is influenced first and foremost by packing density and size of the school. The average median of s_v ($4 \pi 1852^2 m^2/m^3$) were transformed to logarithmic domain for the presentation by using R script (See in Appendix C). The mean median S_v (dB re 1 m^{-1}) is based on the acoustic samples going into a given school (pixels on the echogram) and is a proxy for how densely packed a school is on average. The height (m) and mean area (m^2) of the schools, indicate the size of the schools detected using the settings. The number of objects detected indicate how many schools are detected using the given settings. Based on this information it was therefore possible to evaluate the performance of the Korona school detection settings in detecting and delineating capelin schools.

2.4.1. Impact of settings on capelin school detection

After testing the different acoustic thresholds and minimum school lengths on various types of schools, it was evident that these parameters had a significant impact on capelin school detection. When changing the threshold, Korona's ability to detect schools was drastically changed and this was evident on the echogram (See appendix A). When altering the setting to a threshold of -60 dB re 1 m^{-1} , Appendix A (Fig A.0.1), shows how little capelin school visible on the echogram which is traced by Korona. This is because only objects with a strong echo are detected when threshold is changed to -60 dB re 1 m^{-1} . Thus, number of schools detected with this setting was considerably lower compared to the other thresholds that were tested. When changing the threshold to -80 dB re 1 m^{-1} , many more schools are detected, also objects with a weak echo. Comparison with the original interpretation showed that the detected schools included backscatter s_A assigned not only to capelin, but other categories such as plankton mixed 0-group fish. The two thresholds, -60 and -80 dB re 1 m^{-1} , were therefore not optimal when selecting a setting that would effectively outline the capelin region. When viewing

-70 dB re 1 m^{-1} , the threshold outlined the capelin region more effectively, as well as not compromising too much of the capelin schools.

When changing the minimum school-length setting, differences in detection and delineation between the various settings were less evident than when comparing threshold settings. However, upon close observation there are clear differences. These differences became more evident when assessing looser assemblages of fish (fish veils). When setting the smallest minimum length to 5 m , very tiny parts of the assemblages were included in very high numbers. This was considered not to reflect the feature of loose assemblages in an ideal way going forward. It can be seen on the echogram images in Appendix A, (Fig A.0.10), the minimum length of 5 m traces a lot more of the smaller objects compared to the other two figures. Whereas the largest minimum length, 15 m , Appendix A (Fig A.0.12), excluded potential capelin schools assemblages.

Because the differences in school detection due to minimum length are difficult to detect with the naked eye, the exported parameters of detected schools (shown in Appendix A) was also instrumental in assessing output from the different settings of minimum school lengths. When comparing the export data, it is clear that a setting of 15 m detected far fewer schools. Whereas, a minimum distance of 5 m detected more. Thus, a compromise of minimum length 10 m was selected.

2.4.2. Golden setting

As outlined, deciding on a setting to use in the thesis would have an impact on the data I would further analyze. The golden setting was chosen based on critical analysis of echogram images and exported data. Although no setting was successful in detecting capelin schools perfectly, the golden setting decided was -70 dB re 1 m^{-1} and minimum length 10 m . To consolidate this, a former study looking at frequency-dependent acoustic back-scatter differentiating between juvenile pollock and capelin aggregations, (Wilson et al, 2004) found that -69 dB re 1 m^{-1} as a threshold for capelin, was optimal when discriminating between the two species. Essentially, the golden threshold selected would inevitably compromise some capelin school data. If the threshold is set too high (-60 dB re 1 m^{-1}), capelin schools are excluded. If it is too low (-80 dB re 1 m^{-1}), plankton and other objects with a weak echo are included. The default upper blind zone boundary (depth of blind zone below surface) was also an important component that needed to be considered. The default setting sometimes excluded capelin schools from school detection. The blind zone is evident on the echogram and is the area in front of the transducer that cannot detect an object (Simmonds and MacLennan, 2005). This is because the transducer cannot emit and receive sound at the same time. The default blind zone was marginally conservative and after close observation, the blind zone was moved up to 12 m , in order to include as many capelin schools as possible in

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school detection. The scrutiny of acoustic data during BESS is done at 38 kHz and I therefore selected only this frequency for the school detection. Below are the settings that I proceeded to use for my thesis for school detection (Table 2.1).

Table 2.1.: Table showing the default and new settings for Korona school detection

Settings	Default	New
Blind zone Depth (m)	15	12
Frequency (kHz)	All Channels	38
Threshold (dB re 1 m^{-1})	-65	-70
Minimum Length (m)	20	10
Minimum Thickness (m)	5	0
Minimum Area (m^2)	50	0

2.5. Selecting cod and capelin data

To effectively proceed testing how bottom depth, light and ultimately, abundance of cod affect the capelin school anti-predatory dynamics, I had to select a data-set to apply my settings to. Since cod was sampled using demersal trawls, the golden settings were eventually selected to detect capelin aggregations in areas where bottom trawling had also occurred.

In 2017 the overall capelin abundance was high, and therefore LSSS files from the 2017 Ecosystem Survey, was used in my thesis. I used data from the vessel Johan Hjort since this vessel covered the main capelin distribution. I then used the trawling station form to get specific details as to where and when bottom trawling took place. By noting the start and stop trawling time as well as the longitude and latitude from the demersal trawling form, it was possible to use the numerical window available in LSSS echogram to pinpoint the trawling regions. Additionally, the numerical window showed the vessel speed along the echogram. This information combined with trawling data allowed me to deduce, with certainty, where bottom trawling had taken place. The trawl stations where capelin schools were present were noted down before deciding to process the original LSSS files in Korona, using the golden settings I had decided on beforehand.

At the stations where capelin occurred, a feature on LSSS then allowed me to mark 1 *nmi* pre and post- trawling. The capelin schools detected in Korona were then converted to LSSS schools and exported. In total 26 files pertaining to the 26 stations, were exported from the 2017 survey and further analyzed. Cod density (individuals per nm^2) at the 26 stations were estimated using standard swept area methods applied in cod index calculation for cod stock assessment (Mehl et al., 2019) and was provided by my supervisors.

Figure 2.7 below shows the position of the 26 stations, used for further analysis. The data was taken in September from 05.09.2017 - 28.09.2017. The minimum and maximum latitude was 76.818° and 79.861° . The map also displays the topographic properties of the study area, showing continental shelves, depths and banks varying in depth.

2.6. Data analysis

It was decided, before conducting a statistical analysis that the following predictors would be used to build my model; number of cod, bottom depth, sun altitude and time of day categories (which is explained below). Data on cod abundance was collected by demersal trawling. The bottom depth data was attained by acoustic readings. Sun altitude served as a proxy for light and was calculated using the date, time, longitude and latitude for each observation. The two variables *packing density* and *minimum distance to bottom* were based on acoustic data and exported from LSSS and have previously been used

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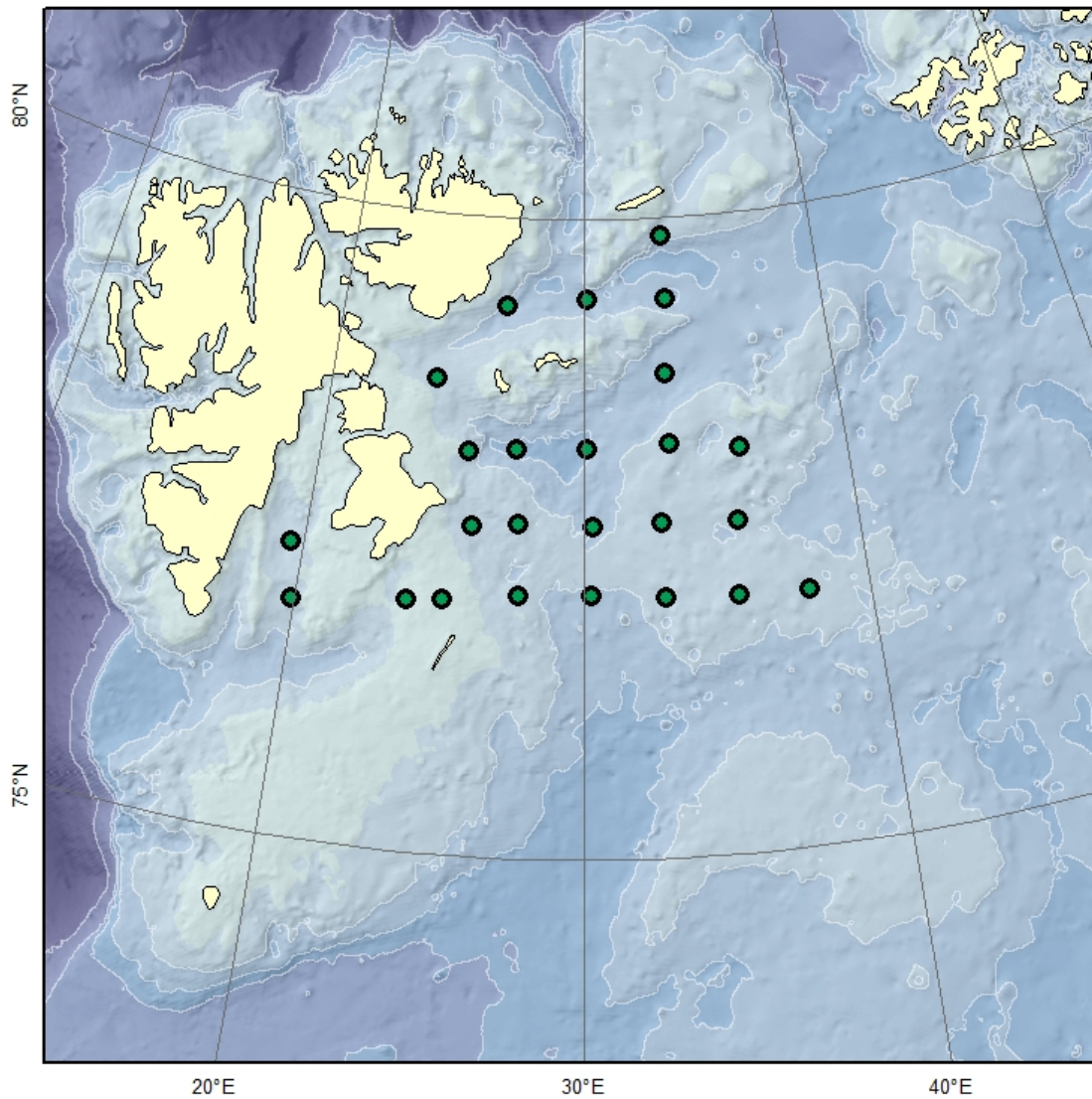


Figure 2.7.: Map of stations used for the analysis

in studies to quantify and describe anti-predation schooling responses. Additionally a random effect was added to the models: stations, which refers to the transect area where a block of observations was made. An overview of these variables can be seen in table 2.2.

Light as an independent variable

Because light was one of the variables I was interested in testing, sun altitude was calculated for each observation using the factors mentioned above. Sun altitude was also converted into categories, 'time of day'; daytime, twilight and night-time. Universally, there are three main phases of twilight, civil (sun altitude between 0 and -6°), nautical (-6 to -12°) and astronomical (-12 to -18°) occurring below the horizon. Considering the time of year (September) and high latitudinal area of study ($76.8 - 79.86^\circ$), civil twilight was applied to the sun altitude data (see script in Appendix C). Below in figure 2.8, is a representation of what time of the day the observations were made at the 26 stations.

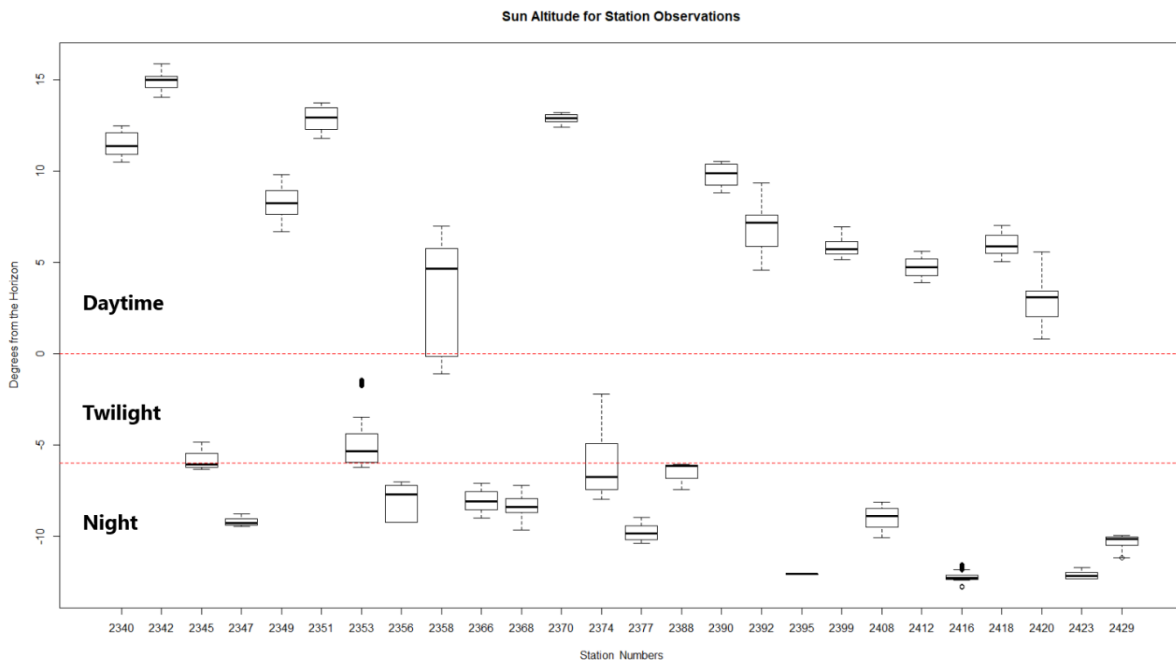


Figure 2.8.: Boxplots showing when each observation occurred during the day with sun altitude (shown in degrees ($^\circ$)) on the y-axis. Each boxplot represents the observations for each of the 26 stations. The ablines are shown as horizontal red lines. The upper line represents the horizon at 0° whereas the lower line represents the civil twilight delineation -6 to 0° . Daytime is when the sun is above the horizon and night is shown on the figure below -6° .

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Table 2.2.: Overview of the response and predictor variables. Response Variables: Packing Density (Logarithmic transformation of sv mean ($4 \pi 1852^2 m^2 / m^3$)) and capelin school minimum distance to bottom (m). Predictors: Bottom Depth = Depth at station (m). Sun Altitude = position of sun in relation to the horizon (radians). Cod Abundance = the logarithmic value of cod $\log(x+1)$ (nm^2). Time of Day= Night, Twilight and Daytime (converted from radians to degrees and then made to categories)

Responses	Predictors Included
Packing Density or Min Dist. to bottom	Cod
Packing Density or Min Dist. to bottom	Cod, Sun Alt.
Packing Density or Min Dist. to bottom	Cod, Sun alt., Bottom Depth
Packing Density or Min Dist. to bottom	Sun Alt.
Packing Density or Min Dist. to bottom	Sun Alt., Bottom Depth
Packing Density or Min Dist. to bottom	Cod, Time of Day
Packing Density or Min Dist. to bottom	Cod, Time of Day, Bottom Depth
Packing Density or Min Dist. to bottom	Time of Day
Packing Density or Min Dist. to bottom	Time of Day, Bottom Depth
Packing Density or Min Dist. to bottom	Bottom Depth
Packing Density or Min Dist. to bottom	Cod, Bottom Depth

2.6.1. Modelling the data

The variables were viewed as plots and histograms in order to observe their distribution and decide thereafter if transformation was necessary, in order to better fit a linear model (See Fig 3.1).

To test my predictions, assumptions of the linear model had to met. Firstly, the distribution of the response variables had to be normally distributed. The response variables *minimum distance to bottom* and the logarithmically transformed response variable, *packing density* were approximately normally distributed. A second assumption is multicollinearity which can be detected by testing if the explanatory variables are highly correlated (> 0.5), where the higher the correlation between independent variables, the greater the sampling error (Blalock, 1963). For my data correlation between the independent variables were below 0.5.

Another assumption is multivariate normality, which assumes that the residuals of the model are normally distributed, which was also approximately met. This is also shown by testing a model's homogeneity of residual variance, homoscedasticity (Goldfeld and Quandt, 1965) which can generally be done in two ways; graphically and through statistical tests. Because my data set exceeded 5000 observations, common tests such as Shapiro Wilk and Levene test would be futile. Therefore, normality of residuals was checked using the diagnostic plot, QQ-plots (See Appendix B. for QQ-plots). These plots were produced with every model to test for significant deviations of the residuals from the linearity of the model. Deviations, indicated that the model's residuals were not normally distributed. The linear model that was selected to test minimum distance to bottom deviated slightly (seen on the QQ-norm in Appendix B, Fig. B.0.3) and through testing, I found that residuals belonging to station 2395 caused the linearity of the model to stray. I proceeded to test the linearity of the model without station 2395 data and found that my model's residuals were approximately normally distributed. When comparing both model's (with and without data from station 2395) and their output, there were no significant differences that would deter me from using the best model for analysis. I therefore proceeded to use the model with data from station 2395 data to further investigate what factors effect minimum distance to bottom. The steps in this process can be seen in Appendix B.

My data set contained more than 5000 of capelin schools, each of them assigned to one of the 26 stations with information on cod abundance. Provided that the assumptions of a linear model were approximately met, stations were added to the models, as a random effect. By implementing station as a random effect, the assumption that observations are independent of each other, is also met. Station as a random effect was also implemented to avoid pseudo-replication which can provide optimistic outputs for p-values and standard error. By adding the random effect of the sampling blocks (which in this case, is

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stations) to the models, I could assess how much variance in the model was attributed to factors within the station or from the stations.

Furthermore, I tested all the possible combinations of predictor and response variables and selected the best statistical model based on minimisation of the AIC criterion (AIC: Akaike's An Information Criterion) to explain variation in each of my two dependent school variables: *packing density* and *minimum distance to bottom*. The Likelihood ratio test was conducted on models with similar small AIC values (<2 in AIC value)(Burnham, 1998) to select the model that represents the data adequately.

2.6.2. Statistical analysis

All data analyses were conducted in R, version 3.6.1 (R Core Team, <https://www.r-project.org/>), with Rstudio (RStudio version. 1.2.1335 (RStudio, Inc, Boston, MA, US) and the packages used for my study is outlined in Appendix C.1.

3. Results

3.1. Looking at the data

Upon observation of the final aggregated data, the 26 stations varied in *packing density*, *minimum distance to bottom*, *bottom depth*, *sun altitude* and *cod abundance*. The maximum number of cod caught at one of the stations was 7707.28 nm^2 and zero cod were found at 3 stations. The shallowest station had a mean depth of 47.20 m and deepest mean depth was 324.82 m . Sun altitude varied from a mean minimum of -0.21 (night) to mean maximum of 0.26 (day). Minimum distance to bottom of capelin schools varied from 23.55 m to maximum 249.43 m . And packing density went from mean minimum -66.63 to mean maximum -54.1 dB re 1 m^{-1} . The final aggregated data is presented in Appendix B, table B.5.

The distribution of the variables can be seen in figure 3.1. At first glance it is clear that cod and packing density (s_v mean) is skewed more heavily to the left hand side of the histogram. Minimum distance to bottom follows a satisfactory normal distribution. Additionally, sun altitude has negative values so a logarithmic transformation will produce NA values. I proceeded to transform cod and packing density logarithmically to assess its distribution. Because the logarithmic transformation of cod produced NA values and the cod $\log(x + 1)$ did not, the latter was used in the formulas when testing the various models. The remaining variables, bottom depth and sun altitude and minimum distance to bottom remained unchanged. The transformed distribution of cod abundance and packing density can be seen in figure 3.2.

3. Results

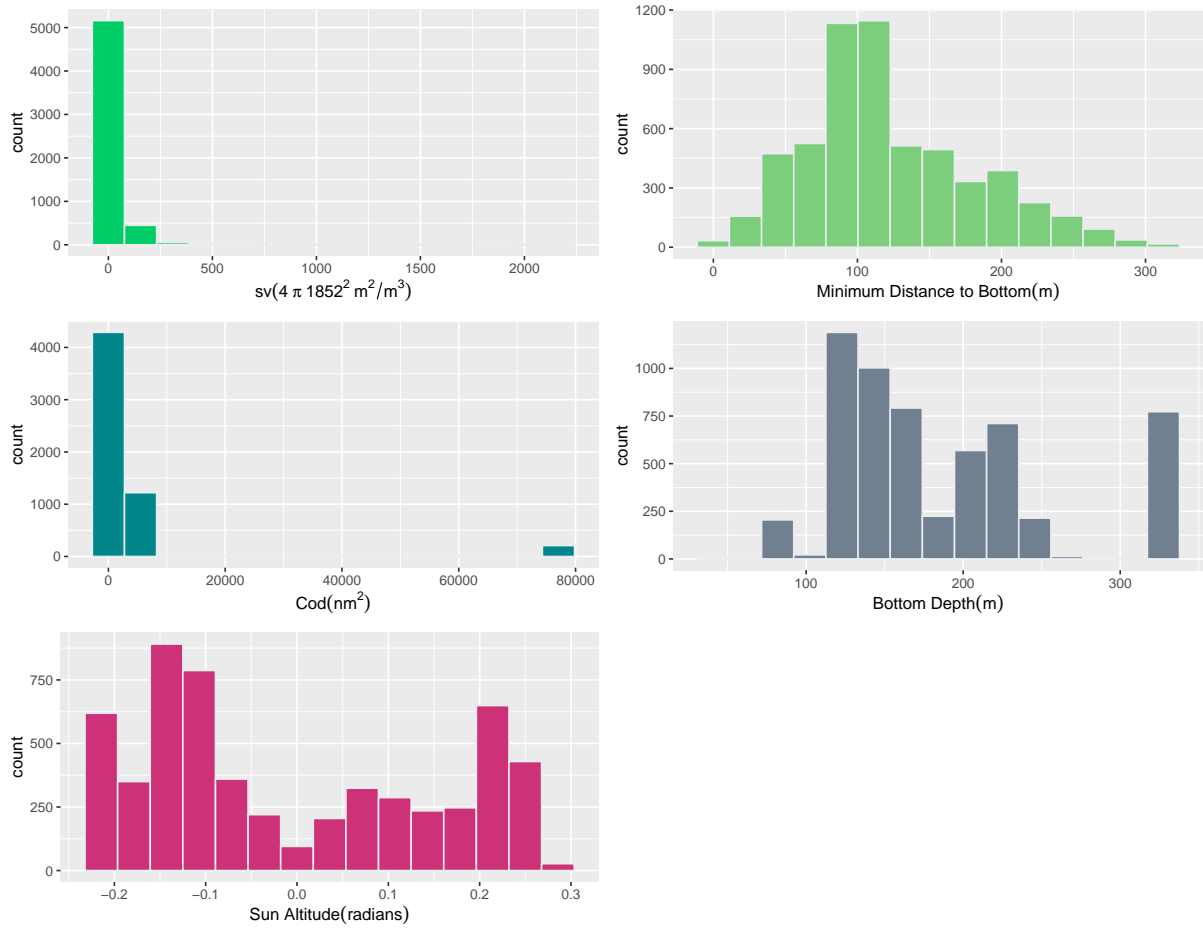


Figure 3.1.: Histogram showing distribution of variables

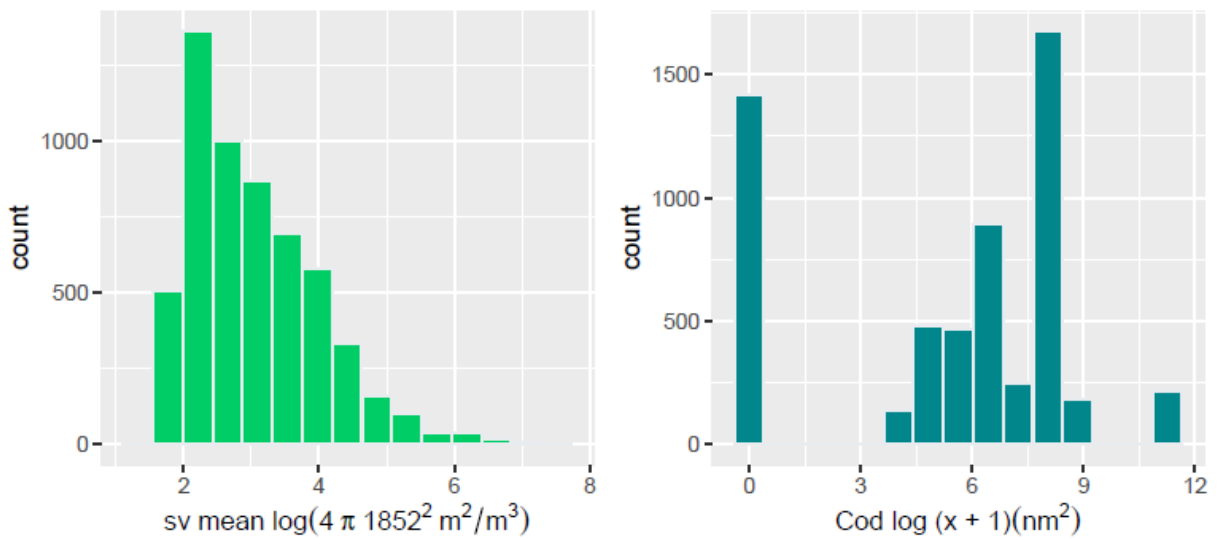


Figure 3.2.: Histogram showing distribution of transformed variable: $cod \log(x+1)$ and $sv \text{ mean } \log(4\pi 1852^2 m^2/m^3)$

3.2. Exploring what impacts capelin school dynamics

3.2.1. Choosing the best model to test packing density

Linear mixed models with a random effect was used to test what variables effect capelin's *packing density*. Below in table 3.1 an overview of the models that were tested can be seen. The table also provides an overview of which combination of predictor variables provided the lowest AIC values.

Table 3.1.: Overview of lmer models with their corresponding AIC value (lowest to highest AIC model shown). Response Variable = Packing Density (Logarithmic transformation of sv mean ($4 \pi 1852^2 m^2 / m^3$)). Predictor explanations: Bottom Depth = Depth measured at station in (m). Sun Altitude = position of sun in relation to the horizon (shown in radians). Cod = the logarithmic value of cod is used with $\log(x+1)$. Time of Day = Night, Twilight (civil) and Daytime (Made into categories using degrees)

Response	Predictors Included	AIC
Packing Density	Sun Alt., Bottom Depth	13771.36
Packing Density	Sun Alt.	13773.77
Packing Density	Cod, Sun alt., Bottom Depth	13776.56
Packing Density	Cod, Sun Alt.	13779.58
Packing Density	Time of Day, Bottom Depth	13809.96
Packing Density	Time of Day	13810.41
Packing Density	Bottom Depth	13813.09
Packing Density	Cod, Time of Day, Bottom Depth	13815.96
Packing Density	Cod, Time of Day	13816.54
Packing Density	Cod	13816.61
Packing Density	Cod, Bottom Depth	13819.41

The main output for the best linear mixed model is shown in table B.3 in Appendix B. The lowest AIC value was allocated to a model that did not include cod as a predictor, but only bottom depth and sun altitude. Cod showed very little significant effect on packing density ($p > 0.005$) in the other models. The best selected model showed that sun altitude and bottom depth were both very significant ($p.value < 0.005$) in affecting packing density. The model shows that when packing density increases, bottom depth decreases, as seen in figure 3.3. The model also shows that when sun altitude increases, packing density increases, seen in figure 3.4. Table B.4 in Appendix B, shows there is little difference in contribution to variance between and within the stations. The residual variance between schools is 0.63, more than residual variance between stations, which is 0.53.

3. Results

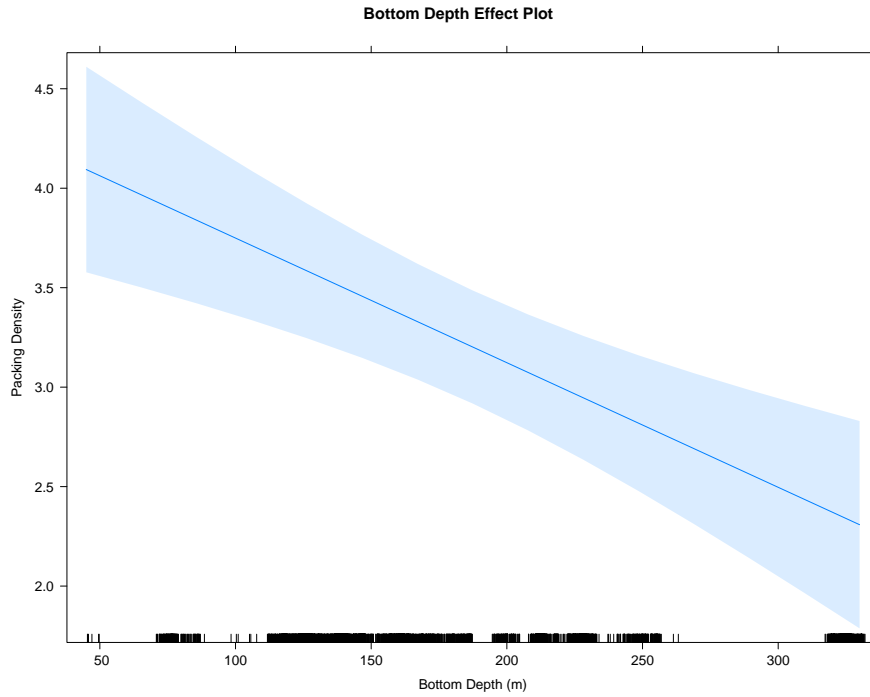


Figure 3.3.: Effect plots shows predicted values of the model outcome for certain values for the independent variables. Since the effect of the predictor, bottom depth, is being calculated here, sun altitude is being held constant. The plot shows that packing density (sv $4 \pi 1852^2 m^2 / m^3$) decreases with increasing bottom depth (m). The blue ribbon shows the range of the prediction intervals for my model.

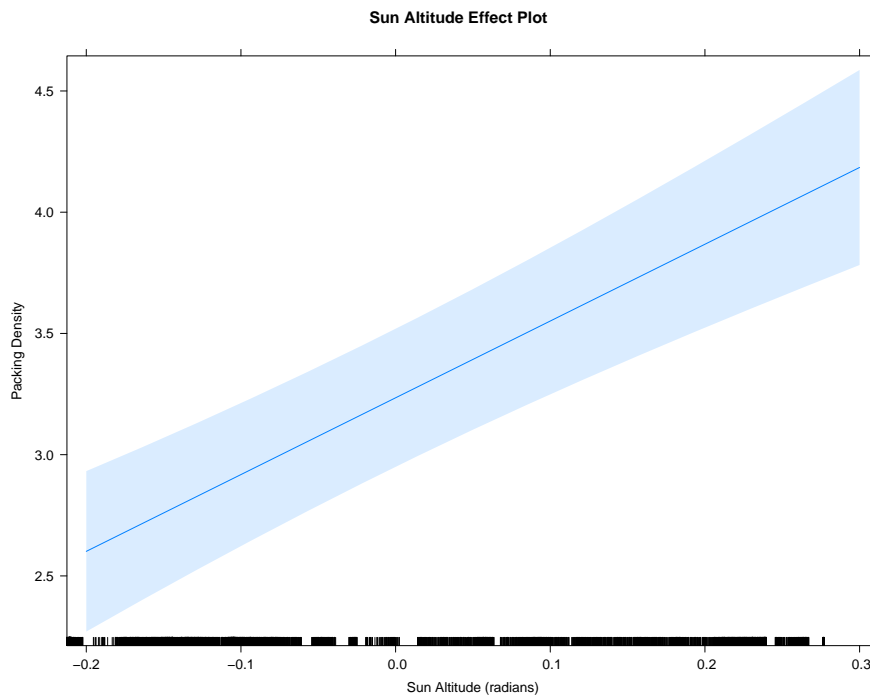


Figure 3.4.: Effect plot shows predicted values of the model outcome for certain values for the independent variables. The effect of sun altitude, is being calculated and bottom depth, is being held constant. The plot shows that packing density increases (sv $4 \pi 1852^2 m^2 / m^3$) with sun altitude (radians). The blue ribbon shows the range of the prediction intervals for my model.

3.2.2. Choosing the best model for minimum distance to bottom

Exploring what predictors would impact *minimum distance to bottom*, table 3.2 outlines which models were tested and which combination of predictor variables provided the lowest AIC.

Table 3.2.: Overview of lmer models with their corresponding AIC value (lowest to highest AIC model shown). Response Variable = Minimum distance to bottom (m). Predictor explanations: Bottom Depth = Depth measured at station in (m). Sun Altitude = position of sun in relation to the horizon (shown in radians). Cod = the logarithmic value of cod is used with $\log(x+1)$. Time of Day = Night, Twilight (civil) and Daytime (Made into categories using degrees)

Response	Predictors Included	AIC
Minimum Distance to Bottom	Cod, Sun alt., Bottom Depth	54527.18
Minimum Distance to Bottom	Sun Alt., Bottom Depth	54528.26
Minimum Distance to Bottom	Cod, Time of Day, Bottom Depth	54574.12
Minimum Distance to Bottom	Time of Day, Bottom Depth	54575.92
Minimum Distance to Bottom	Cod, Bottom Depth	54588.62
Minimum Distance to Bottom	Bottom Depth	54590.73
Minimum Distance to Bottom	Cod, Sun Alt.	54692.21
Minimum Distance to Bottom	Sun Alt.	54697.09
Minimum Distance to Bottom	Cod, Time of Day	54710.41
Minimum Distance to Bottom	Cod	54714.39
Minimum Distance to Bottom	Time of Day	54715.48

Table B.1 in Appendix B shows the main output for the best linear mixed models where minimum distance to bottom is the response variable. In this case, the lowest AIC value was allocated to a model that included cod as an explanatory variable. However, this model showed that cod had no significant impact on minimum distance to bottom ($p > 0.005$). Additionally, the two models with lowest AIC value differed with < 2 . Therefore a likelihood ratio test was used to compare the model with the lowest AIC value, which includes bottom depth, sun altitude and cod with the next lowest AIC value model that included bottom depth, sun altitude and cod abundance. The likelihood ratio test comparing the two models, showed that chisq had a significance over $\text{pr} > \text{chisq}$ of 0.53 for the first model and thus the model with the next lowest AIC value was selected. The script and steps can be seen in Appendix B.

The selected model, showed that sun altitude and bottom depth were both very significant ($p.\text{value} < 0.005$) in affecting minimum distance to bottom. The model also shows that when sun altitude increases, packing density increases, seen in 3.6. The model also shows that when bottom depth increases, minimum distance to bottom increases, seen in figure 3.5. Table B.2 in Appendix B shows there is little difference in contribution to variance between and within the stations. The residual variance between schools is 486.20 and the residual variance between stations is 786.40, meaning that most of the variances is contributed by the stations.

3. Results

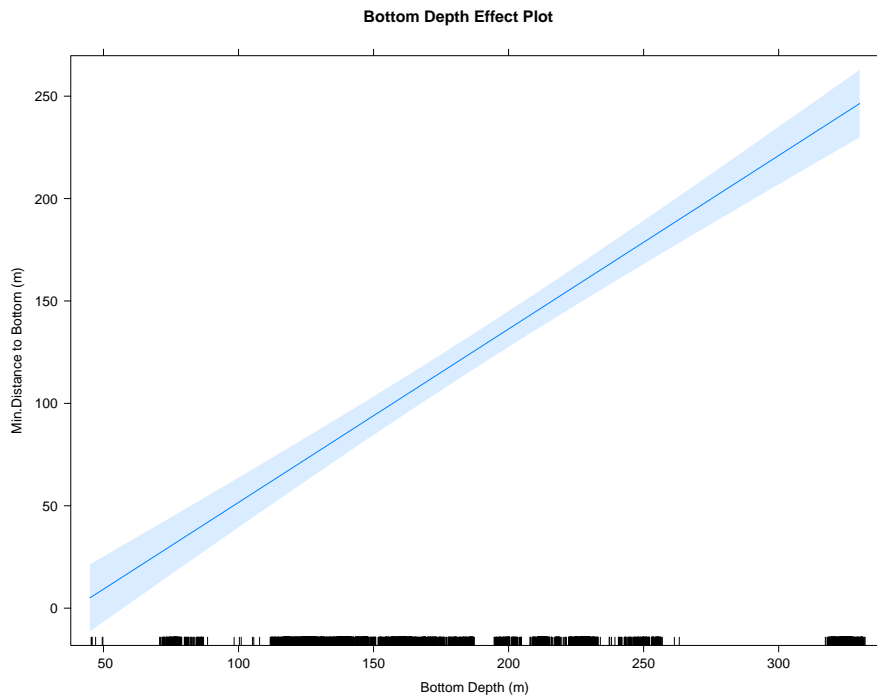


Figure 3.5.: Effect plot shows predicted values of the model outcome for certain values for the independent variables. Since only the effect of the predictor, bottom depth (m), is being calculated, sun altitude is being held constant. The plot shows that minimum distance to bottom (m) increases with increasing bottom depth. The blue ribbon shows the range of the prediction intervals for my model.

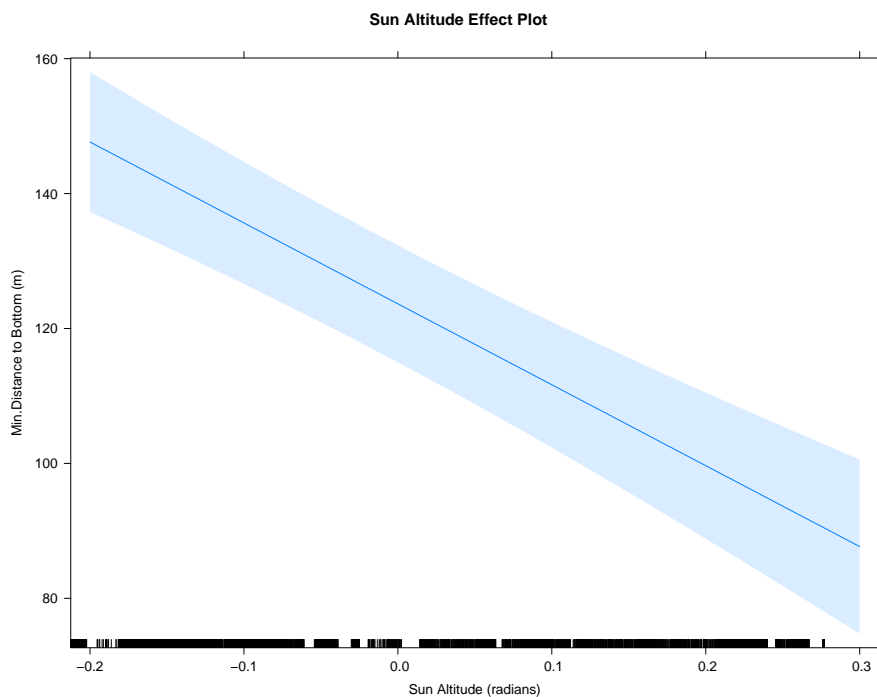


Figure 3.6.: Effect plot shows predicted values of the model outcome for certain values for the independent variables. Since only the effect of the predictor, sun altitude (radians), is being calculated, bottom depth is being held constant. The plot shows that minimum distance to bottom (m) decreases with increasing sun altitude. The blue ribbon shows the range of the prediction intervals for my model.

3.3. Summary of results

The results show that number of cod had little to no affect on the schooling dynamics; packing density and minimum distance to bottom. Light and bottom depth however did have an impact on these school dynamics.

- Packing density (sv mean $(4 \pi 1852^2 m^2 / m^3)$) increased when with decreasing bottom depth and increasing sun altitude.
- Minimum distance to bottom (m) decreased with increasing sun altitude and increased with increasing bottom depth.

Ultimately capelin schools packed tighter when bottom depth became shallower, especially when when the sun was situated higher in the sky (daytime). Additionally, minimum distance to bottom was not fixed to a depth and increased with increasing bottom depth. Minimum distance also decreased during daytime.

4. Discussion

This is the first study to directly investigate how capelin's schooling dynamics respond to the presence of cod in the Barents Sea. Large scale studies on cod-capelin interaction have examined the spatial association between the two, which is a prerequisite for predation to occur (Fall et al., 2018, 2021). Studies conducted in Newfoundland, Canada, have assessed how capelin's schooling behaviour responds to various predators, such as common murre *Uria aalge* and cod (Dalpadado and Mowbray, 2013; Mowbray, 2002; Crook and Davoren, 2014). Other studies on fish schooling behaviour have used theoretical models and experiments to study the effect of predation (Aoki, 1984; Pavlov and Kasumyan, 2000; Pitcher, 1973). Together, these studies have highlighted how light gradients, bottom depth, topography, the availability of prey, competition, temperature and predation play an essential role in determining predator and prey spatial interaction and behaviour.

In my study, I sought to determine whether cod, bottom depth and light influenced capelin's fine-scale school dynamics by analysing acoustic data collected throughout the BESS survey. By using the post-processing program, LSSS, it was possible to utilize the multi-extension toolbox, Korona, to detect capelin schools. My study demonstrates that although cod and capelin may overlap, capelin's *packing density* and *minimum distance to bottom*, which are two important aspects of schooling dynamics, were not affected by the abundance of cod. Light and bottom depth are also considered in this study and were both found to contribute significantly to changes in capelin's schooling dynamics. The study showed that the interplay between light and bottom depth are essential to consider in order to understand changes in capelin's schooling dynamics.

4.1. Establishing a method to assess cod-capelin interaction

One of the main objectives of this thesis was to establish a method that would enable me to utilize the acoustic data to assess the impact that the abundance of cod has on capelin schooling dynamics. My approach was to use a sensitivity test on different school detection settings and evaluate the result based on a combination of visual inspection of the echogram, comparison with the original scrutiny from the survey as well as comparing the exported school characteristics for the different settings. After testing the different acoustic thresholds and minimum school lengths on three different types of schools in Korona's school detection, it was evident that these school detection settings had a significant impact on capelin school detection.

Other studies which have used similar tests in order to discriminate between species from acoustic descriptors have also found that varying *acoustic threshold* and *minimum school length* can significantly impact the results. One study conducted in the Gulf of Alaska by Logerwell and Wilson, (2004) used frequency dependant acoustic backscatter to successfully distinguish between juvenile pollock and capelin and found the highest integration threshold distinguishing the two fish to be -69 dB. Another study on the South African continental shelf by Lawson et al., (2001) used both acoustic descriptors and ancillary information to distinguish between anchovy *Engraulis capensis*, sardine *Sardinops sagax* and round herring *Etrumeus whiteheadi* schools. This study found that changing the acoustic threshold from -65 dB to -60 dB had little effect on the ability to distinguish schools. However, their study found that their original minimum school length may have excluded additional school and that decreasing their length threshold would have detected more schools. In this study ancillary information such as latitude, longitude, sea temperature and bottom depth was included in identifying acoustic schools. The inclusion of this type of data, reportedly contributed to improving the accuracy of identifying the species significantly.

When using the golden settings with a minimum school length of 10 m and an acoustic threshold of -70 dB re 1 m^{-1} in my final analysis of the 2017 BESS data-set, I could observe on the echogram that the settings effectively outlined the capelin schools. This means that the exported data could successfully provide information about the capelin school dynamics such as *packing density* and *minimum distance to bottom*.

These settings can be adopted for future studies to learn more about how schools respond to changes in their environment using time series data. For improved school detection in a wider context, ancillary environmental information, such as the ones mentioned in the section above could help identify different types of schools, in particular in areas where capelin strongly interact with species having similar acoustic characteristics such as polar cod.

4.2. Changes in capelin school packing density

4.2.1. Cod's impact on capelin's school packing density

This investigation found that abundance of cod did not have a significant impact on *packing density* of capelin. This was unexpected, as the literature suggests that fish schools increase in packing density, as a response to predation, by reducing their inter-fish distance (Misund, 1993; Pavlov and Kasumyan, 2000). This result could be explained by several factors, as will be discussed below, including capelin's packing density reflecting feeding activity over predator avoidance, capelin's generally slow response behaviour to predation, capelin's response to threat being rooted in a fitness trade-off and/or the distance between capelin and cod being too far away to incite an anti-predatory response. Additionally, the results may have been affected by the sampling method and type of data-set used in this study.

Fluctuations in a school's packing density have been reported to reflect changes in conditions for feeding, reproduction and survival (Crook et al., 2014). Changes in packing density can be observed in pelagic fish which tend to dissociate for some time, when feeding (Pavlov and Kasumyan, 2000). This may have been the case for capelin schools, who in this period, are normally engaged in extensive feeding rituals, mainly on krill (Gjøsæter, 1998). Amongst fish that are highly motivated to feed, the attraction to neighbours is expected to diminish (Katz et al., 2011). Low packing densities in fish schools can also be explained by competition for prey. This is because hunger can motivate some fish to risk predation or incite more individualistic behaviour (Hensor et al., 2003; Sogard and Olla, 1997). Capelin schools with lower packing density (increased inter-distance) may thus be focusing their energy on activities such as feeding.

Capelin's generally slow response to predation may also explain why abundance of cod had no significant impact on school packing density. Capelin's reaction to an approaching vessel may provide insight into how capelin responds to predation. In a study conducted by Jørgensen et al., (2004), capelin demonstrate little or no vessel avoidance which suggests that capelin display a slow and non-reactive response to predation. Observations of capelin's sluggish response has been reported by Johansen, (2003) who suggests that capelin have a relatively slower swimming speed and less distinct schooling behaviour than herring. Although these anecdotal observations would need to be supported by further studies, they could explain the lack of response in capelin's school packing density to changing abundance of cod.

Furthermore, capelin's energy expenditure is rooted in survival and fitness and in order to engage in feeding activity, the response to predation is relative to the threat level detected (Lima and Dill, 1990). In my study, cod may have exhibited non-threatening behaviour and this could explain the lack of response in capelin's packing density. It

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may take several days for cod to digest their food in these cold waters (Temming and Herrmann, 2003), meaning that cod's satiation (gut limitation) could have been a factor in determining whether capelin detected a passiveness from cod. This could have caused capelin to spend less energy on schooling. Although capelin are cod's preferred prey, cod are also generalist predators and their diet include many other prey species (Holt et al., 2019) that could have been present at the time. A study conducted by Johannesen et al., (2016) during the winter and autumn 2003-2014, showed that cod's feeding diet was more diverse during the autumn than in the winter. While outside the scope of this thesis, it would be interesting to study stomach content from cod to properly test whether alternative prey in their stomachs was a factor that played a role in capelin's schooling response to cod.

My results on how capelin school behaviour was affected by cod abundance is dependant on my data-set that include 26 trawl stations from one year (2017). If this study had looked at data from another year or used a time-series data-set (from several years), capelin's packing density response to cod abundance may have been different. Furthermore, the data-set I used could have provided insufficient data to give a representative indication of capelin's response behaviour to cod abundance. In a future study, it would therefore have been interesting to see whether the inclusion of more data would have given different results that what I found here.

However, cod and capelin's overlap around August/September is prominent in the study area where my data was collected, and therefore provided an excellent opportunity to study cod-capelin interactions within a cod and capelin ecosystem.

The observed lack of response in capelin's packing density to changing cod abundance could also be caused my limitations in the use of demersal trawl data. When using demersal trawl data to assess cod's general distribution, there is an assumption that cod are associated with the seafloor throughout the day. However, a study conducted by Skaret et al., 2020, demonstrated that cod traversed 5-10 meters from the seafloor in the water column during daytime. There may similarly have been cod in the pelagic water column in my study that were not detected. More importantly, the fine scale distribution of cod was not recorded in my study. Since the cod abundance data is from trawl hauls covering a distance of 0.75 nautical miles, the actual local density of cod associated with each capelin school is unknown.

4.2.2. Light's effect on capelin's school packing density

This study demonstrates that light plays a more significant role in affecting capelin school's *packing density* than the number of cod itself. Studies have shown that fish use light as a visual cue to form schools (Partridge and Pitcher, 1980) and that pelagic schools form during daytime (Fréon et al., 1996). Therefore it was expected that increas-

4.2. Changes in capelin school packing density

ing light would increase capelin's schooling tendency and increase packing density. As discussed below, increased packing density as a response to light may occur both because fish can detect each other more easily, and because less attacks from visual predators occur during night-time which may cause fish to relax schooling and increase distance to neighbours (Brown and Magnavacca, 2003; Pavlov and Kasumyan, 2000).

Light is an important component influencing school responses and formation (Misund, 1993; Pavlov and Kasumyan, 2000) especially for capelin that are visual predators (Fall et al., 2021). Fish organize themselves by positioning themselves at a particular distance from their neighbour (Parrish et al., 2002). Although the lateral side line of the fish may detect displacement in water, visual information provides the main cues to form schools (Partridge and Pitcher, 1980). Light irradiance decreases with depth due to attenuation (Fiksen and Carlotti, 1998) and capelin's ability to detect cod and vice-versa are therefore sensitive to diffuse lighting and water clarity. This may play a role in affecting capelin's detection distance and threat detectability response. With increased light intensity, capelin's chances of not only detecting predation, but also responding to it, may explain why capelin's packing density increased with sun altitude.

Packing density increasing during daytime can also be explained by visual predators utilizing light to detect and hunt for their prey, presenting more of an imminent threat to fish. Pelagic schools tend to disperse during night time (Fréon et al., 1996) and although capelin school are less able to detect each other, a decrease in light means some visual predators are less of a threat to fish at night time. This may incite a less vigilant schooling behaviour and result in reduced packing density amongst capelin.

Although the best model from my study shows that light contributes significantly to changes in school packing density it is also worth mentioning that capelin have many predators (Hop and Gjørseter, 2013). These include organisms such as whales and seals in addition to cod (Gjørseter, 1998), which may attack from all angles. The packing density variation in capelin, detected in my study, might have been a response to other predators for which data were lacking. Hence, it is difficult to distinguish whether increased packing density during daytime is a result of schools forming more effectively, since individual capelin cannot see each other or whether it is a response to other forms of potential predation that are more distinguishable for capelin, with increased lighting.

Light is ultimately a proximate for schooling and as anti-predatory response to their environment, schooling can ensure survival for individual fish. During midnight sun (24-hour periods of sunlight), DVM stops for many species including polar cod *Boreogadus saida*, who undergo these movements to avoid predation. The lack of day and night triggers an increase in schooling, as an anti-predatory alternative to their environment. Although September in the Barents Sea does not experience midnight sun, in this study it is not surprising that increasing light conditions increased capelin's school packing

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density and consequently attribute advantages for capelin whose visual predators use the light to hunt for their prey.

4.2.3. Bottom depth's impact on capelin school packing density

In my study, *packing density* decreased with increasing bottom depth. School packing density is affected by factors such as food resources (Craig et al., 1982) and predation as well as light conditions. As light diminishes with depth, so does capelin's ability to detect each other and other predators. Therefore, packing density was expected to decrease with increasing depth as a combination of food resources, diminishing light and decreased predation overlap attribute to capelin's packing density diminishing. In deeper depths, capelin are able to distribute themselves in the water column. Capelin's increasing packing density with decreasing bottom depth, suggests that capelin schools observed in shallow banks may have displayed an anti-predatory behaviour by packing tighter, in particular because light penetrates to the seafloor and potentially exposes them to demersal visual predators. Capelin's distance to their predators also impacts their school packing density and be affected by demersal predators in closer proximity at shallow depths. The need to pack tightly in schools as an anti-predator strategy may not be so urgent for capelin in deeper areas where the vertical distance from cod to capelin is larger. Decreasing packing density with depth could therefore reflect capelin's schooling dynamics in response to a smaller vertical overlap with predators, where capelin could invest energy in feeding vs. investing in anti-predation behaviour, such as packing tighter.

The interplay between light and depth also play a role in capelin's packing density. At shallow depths, light can penetrate to the seafloor (Aarflot et al., 2020), providing optimal conditions for capelin to detect each other and form schools and thus pack tighter. Capelin are also more vulnerable to predation at shallow depths and their inability to seek refuge in the darkness, may cause the capelin to form denser schools as an anti-predation response. Capelin's packing density may have been affected by numerous factors that are associated with increasing depth, such as diminishing light, changes in temperature, oxygen levels as well as predation (some of which will be discussed below).

4.2.4. The interplay of factors that impacts capelin school packing density

Capelin's *packing density* increased at shallow depths along with increasing light. A multitude of factors impact fishing school packing density, such as inter- and intra-specific competition (Fernö et al., 1998) prey availability (Dalpadado and Mowbray, 2013), predation and temperature in addition to bottom depth and light (Misund, 1993). Although this study demonstrated that the number of cod did not impact packing density directly,

capelin's reaction to light and bottom depth might display an anti-predatory response that can be better understood by considering what factors impact packing density. By looking at the interplay between cod, light and bottom depth, it is possible to investigate what contributes to modulating packing density during capelin's diel cycle, around this time of year.

To understand why capelin aggregate in banks, and thereby expose themselves to predation, it is important to consider the hydrographical and bathymetrical factors that play a role in determining cod and capelin's overlap. In commercial fishing, banks and shallow depths attract fish (Fall et al., 2021). Foraging fish are dependant on advection of prey from deeper waters (Genin, 2004) and currents direct zooplankton towards the shallow shelves where light penetrates to the seafloor. This provides an opportunity for capelin to catch their prey more easily (Aarflot et al., 2020) as zooplankton are trapped and left more detectable to predators (Aarflot et al., 2019). Consequently, it also provides an optimal opportunity for cod to feed on capelin. Density of cod has been observed to be higher at shallow banks where cod adopt a sit- and pursue- feeding approach waiting for capelin to descend into the water column, without cod spending too much energy searching for food (Fall et al., 2018; Skaret et al., 2020). The aggregation of krill along the shallow banks entice capelin, and consequently cod, and therefore play a critical role in cod and capelin's overlap by forcing them into close proximity (Skaret et al., 2020). While outside the scope of this thesis, the impact of krill on capelin's schooling dynamic response would be an interesting factor to consider for future studies.

In a study conducted in Newfoundland, cod's consumption of capelin decreased with depth (Fahrig et al., 1993) and in the study conducted by (Fall et al., 2018) cod from the Barents Sea consumed most capelin on the banks, especially when capelin was in close proximity to the seafloor. Capelin's increasing packing density, at shallow banks during daytime, may exhibit capelin's threat sensitivity response to their environment. Additionally, capelin have many predators that may attack from all angles. On the banks, capelin are unable to migrate to a light level, where they can disperse or remain undetected. Therefore, capelin may be unable to distribute vertically in the water column as it may expose them to other predators in the water column. Packing tighter may therefore be one of the few anti-predatory responses left in their arsenal in order to maximize individual chances of survival and fitness.

In this study, packing density increased during daytime, which happens to be the time of the day where cod feed on capelin (Skaret et al., 2020). As a visual predator, the combination of light and capelin availability may in turn be beneficial to cod, that take advantage of the light to feed on capelin. This may have contributed to packing density increasing during daytime, as an anti-predatory response. Moreover, capelin may respond to cod when light gradients are optimal and provide visual cues for capelin to

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not only form schools, but also provide an optimal window for cod and capelin to detect each other. Thus, the interplay between light and bottom depth can explain capelin's schooling dynamic response to the presence of cod.

Furthermore, as bottom depth increased, the need for capelin to school, may also have decreased. For example, schooling as an anti-predator response to cod may not be necessary in deeper areas where the vertical distance from cod to capelin is larger. Cod are visual predators who use light to hunt their prey (Brawn, 1969) and although cod have light sensitive eyes (Anthony and Hawkins, 2009) as light diminishes rapidly in the water column, reduced consumption on capelin is expected (Fall et al., 2021). This was however not the case here since cod density were dispersed throughout 43-324 meters. Yet, studies have shown that bottom depth plays an important role in cod's feeding success. A potential factor limiting the interaction between cod and capelin in the deep is that cod's energy intake decreases with increasing depth (Johannesen et al., 2012). Ultimately, packing density may therefore have been affected by a combination of light and capelin's threat sensitivity to cod, who were possibly exhibiting non-threatening behaviour.

Increased packing density in shallow depths could reflect a cautious anti-predatory response, which is expected when a combination of predation, light and shallow depth exposes capelin to predation. Furthermore, decreasing packing density with increasing bottom depth could suggest that capelin did not detect immediate threats that would increase their packing density and instead spent energy investing in other forms of activity such as feeding.

4.3. Changes in capelin's minimum distance to bottom

4.3.1. Cod's impact on capelin's minimum distance to bottom

I found that capelin's *minimum distance to bottom* was not impacted by abundance of cod. This was unexpected since several studies have shown that fish schools exhibit an evasive response when attempting to escape from approaching predators (Rieucan et al., 2014; Vabø et al., 2002). This response is one of the more frequent responses to danger amongst animals (Jørgensen et al., 2004) and as a consequence, fish schools tend to adjust their vertical distribution in response to threat (Rieucan et al., 2014). In a study conducted off Newfoundland, Mowbray (2002), demonstrated that capelin schools shifted vertically in the water column away from the sea floor when cod density increased. Moving away from danger, is also a behaviour observed in herring schools (Pitcher et al., 1996), that also dive down into the water column as a response to a simulated predator (Rieucan et al., 2014) or an approaching vessel (Vabø et al., 2002). Cod are demersal fish which associate to the seafloor (Ottersen et al., 2014) and therefore capelin was ex-

4.3. Changes in capelin's minimum distance to bottom

pected to alter their distance from the seafloor when cod numbers increased. However, my results may have reflected capelin's modified response to different types of predation as well as balancing the risk of predation with the need to engage in feeding in order to maximize fitness.

Capelin may also be capable of assessing potential threats based on experience or other innate behaviour in evading predation ('risk allocation hypothesis') (Lima and Dill, 1990; Lima and Bednekoff, 1999), which could explain their lack of response to abundance of cod. In a study conducted off Newfoundland, common murrelets that dove into the water, tended to target individual fish as opposed to schools (Crook and Davoren, 2014). Additionally, capelin swam away from common murrelets exhibiting a more active foraging behaviour (attempted approaches) compared to murrelets with a more passive foraging behaviour (i.e search or travel). This suggests that capelin are capable of distinguishing between the two behaviours and spend energy on evading predation when necessary. Frequently being exposed to predation may also cause fish behaviour to be more effective in evading danger as result of increased experience with the predator (Wood and Hand, 1985). Energy being spent on anti-predatory behaviour, in this case evasiveness (increasing minimum distance to bottom) may be too costly. Energy may therefore be spent on other activities, such as foraging (Lima and Bednekoff, 1999), in particular if predators do not present an immediate threat. This could explain why capelin's vertical distribution did not change with changing abundance of cod.

Another possible explanation for why abundance of cod did not incite a response in capelin's minimum distance to bottom, is that capelin's evasive behaviour is modified as a response to changes in the environment. Interactions amongst fish are modified through experience, general environmental conditions, or by the number of prey and predator looming around (Crook and Davoren, 2014). In a study conducted by Clarke et al., (1967) jack mackerel *Trachurus symmetricus* tended to modify their response depending on the type of predator they interacted with. When attacked from above they dashed off as a unit whereas from below only certain individuals responded. A response similar to the one observed in jack mackerel could explain why the number of cod did not incite an evasive response amongst capelin schools. Capelin face potential threat from several predators (Gjøsæter, 1998) and so far, there is little literature that assesses capelin's evasive response to specific predators. Therefore, it would be interesting to investigate capelin's interactions with other predators.

Similar arguments made for cod's impact on capelin packing density could be made for minimum distance to bottom when it comes to how the selection of data for this study could affect the results (see above).

4.3.2. Light's impact on capelin's minimum distance to bottom

In this study, *minimum distance to bottom* decreased with increasing sun altitude. Capelin's distance to the seafloor is strongly affected by diel vertical migrations (DVM), (Dalpadado and Mowbray, 2013) meaning they tend to descend down during daytime and ascend upwards into the water column, by night (Skaret et al., 2020). Therefore, capelin's minimum distance to bottom was expected to decrease during daytime and increase during night, as shown in this study. The results display capelin's balance between engaging in feeding and reducing risk, by adjusting their position in the water column to depths where certain light gradients provide a balance between detecting prey and hiding from predators.

Capelin's vertical distribution in the water column is affected by the availability of prey and detection of predation which is significantly modulated by light gradients. In a study conducted by Skaret et al., (2020) just after the BESS in autumn pelagic fish such as capelin were found to avoid light intensities above $0.001\text{m}^{-2}\text{s}^{-1}\mu\text{mol}$ photons when traversing up and down the water column around dusk and dawn. This eludes to the idea that capelin associate to certain light gradients which can be referred to as the "light comfort zone" (LCZ) (Røstad et al., 2016). LCZ describes the position in the water column where aquatic organisms position themselves in a light gradient dark enough to remain conspicuous from visual predators and light enough to detect their own prey. Capelin's position in the water column and thus minimum distance to bottom is therefore modulated by light gradients that affect their migration up and down the water column during the day (DVM).

4.3.3. Bottom depth's impact on capelin's minimum distance to bottom

In this study, capelin's *minimum distance to bottom* increased with increasing bottom depth. It is expected that capelin select a habitat that provides optimal conditions with regards to factors such as light gradients (Dalpadado and Mowbray, 2013), presence of predators and prey (Mowbray, 2002) and temperature (Methven and Piatt, 1989) suggesting that capelin would not gain advantages from descending too far down into the water column. Therefore, the results in my study may reflect the different factors that determine capelin's vertical distribution in the water column as a trade-off between attaining energy and avoiding predation.

Capelin's minimum distance to bottom increasing with increasing bottom depth means that capelin's vertical distribution is not fixed relative to the bottom and reflects their response to prey, predation, light and temperature. Capelin may have been foraging on

zooplankton in the upper water column independent of the bottom depth, which could explain why capelin's distance to the bottom increased with increasing depth. Traversing further into the water columns could prove beneficial in avoiding predators from above. Conversely, capelin's distribution in this study could reflect an anti-predatory response to their predator, cod, residing on the seafloor. Also, traversing into deeper depths may be unnecessary for capelin if there is too little light and little prey. Their position is as mentioned, influenced by the light comfort zone and so by descending outside this light gradient may be futile and pose more risk than reward.

4.3.4. The interplay of factors that impacts capelin's minimum distance to bottom

Capelin's *minimum distance to bottom* increased with increasing bottom depth and decreased with increasing sun altitude. Generally, capelin's vertical distribution and position relative to the seafloor is a good example of their habitat selection (Mowbray, 2002). Their selection of habitat is modulated by a combination of temperature, prey, bottom depth, inter-intra-specific competition, and predation risk. Despite abundance of cod not having a significant effect on capelin's minimum distance to bottom, the interplay between light and bottom depth exhibit capelin's position in the water column as a balance between risk and reward.

In this study, minimum distance to bottom is strongly modulated by light. As mentioned, capelin's position in the water column exhibits an anti-predatory strategy that could be effective in avoiding predation from cod. Hence, probably as a response to light illuminating the upper water column during the day and making capelin more vulnerable to predation by visible predators, the capelin are closer to the seafloor during daytime. However, capelin schools examined here kept a minimum distance of 13 meters distance from the seafloor. This suggests that capelin's position in the water column is modulated by the LCZ and possible evasiveness from cod residing on the ocean floor.

Capelin's DVM behaviour means that cod feed on capelin during daytime, when capelin is closer to the ocean floor. Their proximity may play a role in determining capelin's evasive behaviour, which could have been exhibited along shallow banks, where abundance of cod is high and proximity to cod and capelin is close. If the capelin cannot disperse in the water column as a refuge, due to the potential threats from other predators, they may resort to increasing packing density instead, which was the case in my study

4.4. Conclusion

Based on the data provided by IMR, the abundance of cod did not contribute to significant changes in the two aspects of capelin schooling dynamics, that I chose to look at; packing density and minimum distance to bottom. However the best models showed that sun altitude and bottom depth played a significant role in altering *packing density* and *minimum distance to bottom*.

Capelin were found to invest their energy in packing tighter along shallow banks during daytime where cod reside in highest abundance. This suggests that the combination of cod abundance and proximity to cod affect capelin's school packing density, especially when light provides a visual cue to detect approaching predators and enables effective schooling. In particular, at shallow depths, capelin is unable to respond by moving vertically in the water column, thereby making packing density one of the few anti-predatory response's capelin is able to deploy. Minimum distance to bottom was a proxy for measuring capelin's evasive behaviour and response to cod, by increasing the vertical distance from the seafloor where cod reside. Minimum distance to bottom varied and capelin avoided close proximity to the seafloor when bottom depth increased, either because they were feeding in the upper water column and/or because deeper areas allowed capelin to distribute themselves vertically in the water column and avoid cod residing in the seafloor. The result that capelin increased minimum distance to bottom with increasing bottom depth suggests that capelin stay within an light comfort zone, where they avoid visual predators whilst having sufficient light for hunting.

There are several ways of assessing fish school dynamic interactions (experiments, filming, computer simulations, etc.) The use of acoustics in my study was advantageous because it covers vast spaces, provides data with high resolution and is a non-invasive approach to collecting data. By utilizing the data collected onboard the vessel and subsequently using school detection methods to extract data pertaining to biological characteristics, we can investigate how capelin respond to cod predation in the Barents Sea.

My findings suggest that capelin seek to improve feeding success whilst avoiding predation and that several factors impact capelin's schooling behaviour. Being able to understand capelin's adaptive behaviour to predation can provide insight into how capelin invest their energy and how they adapt to their environment. Very little is known about capelin and cod's fine-scale interaction and although cod follow capelin to the north of Barents Sea and migrate thousands of km, the study area (see Figure 2.7) where my data was collected, makes it possible to study cod and capelin's interaction on a small-scale. Although the combination of acoustic data and Korona school detection settings made it possible to study capelin school characteristics within a scale of hundreds of meters, cod abundance data from trawl hauls covered a larger scale of 0.75 nautical miles. Therefore,

it was not possible to know whether the schooling responses reflected immediate local pressure around the capelin schools. However, the data are on a smaller scale than what is usually applied in such studies, and this is the first study to use this methodology to study how cod abundance impacts capelin schooling dynamics. The approach is an important step in gathering information about predator/prey interactions provides data about capelin's response to their environment, which is rooted in maximizing fitness through activities such as feeding whilst avoiding predation.

As the ocean becomes warmer, it will have consequences for the Barents Sea marine life (Roderfeld et al., 2008; Skagseth et al., 2020) including predator-prey interactions. Modelling what factors impact capelin's schooling dynamics helps our general understanding of how capelin responds to predators. Studies from Canada have shown that prey availability and number of cod can affect the vertical distribution in capelin (Mowbray, 2002). Recording Barents Sea capelin's vertical distribution and schooling packing density over time can be helpful in determining how capelin are affected by environmental changes as a response to conditions that may take a longer time to recognize.

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Appendices

A. Data collected from the 2012- 2018 ecosystem cruise

In order to test the response different thresholds had on the schools that had been interpreted to capelin, the following thresholds were altered and tested on the three different types of schools; -60 -70 and -80 dB re 1 m^{-1} .

Examples of how different Thresholds detect capelin schools

The capelin schools were detected differently with different settings in the school detection algorithm:

Threshold (dB re 1 m^{-1}) remained the parameter that attributed to the most noticeable change in threshold as shown in the figures below.

Shown below is an example of how Korona detects and outlines schools differently depending on the threshold provided in the korona configuration setting "school detection". For each setting, the minimum length was set to 5 meters. Minimum thickness was set to 0. Additionally the blind zone remained at 12 m .

The different graphs show an evident difference in outlining. The schools that were outlined were converted from korona regions to LSSS schools for which features like length and packing density can be exported. Using the exported data, the table also shows how the different thresholds effects the mean length, height, area, s_A , s_V median as well as number of object (schools):

Table A.1.: Effect of varying Threshold dB re 1 m^{-1}

Variables	-60	-70	-80
Mean Area (m^2)	21.59	76.79	96.94
Mean Height (m)	1.35	1.65	1.39
Mean Length (m)	52.93	31.63	28.38
Mean s_V median (dB re 1 m^{-1})	-55.62	-64.24	-75.62
Mean s_A ($m^2 nm^{-2}$)	185.87	41.70	5.37
No. of schools	2464	9955	34109

A. Data collected from the 2012- 2018 ecosystem cruise

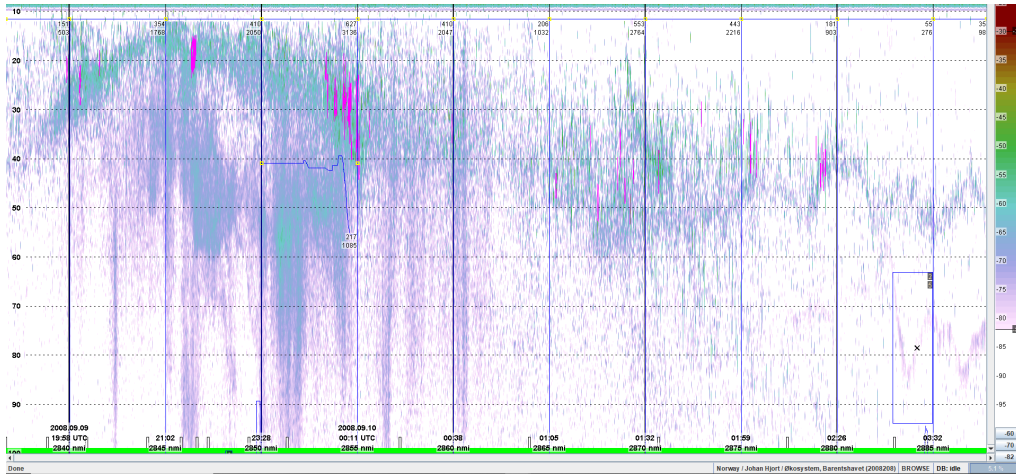


Figure A.0.1.: Echogram displaying a fish veil with the school detection setting being changed to a threshold of $-60 \text{ dB re } 1 \text{ m}^{-1}$.

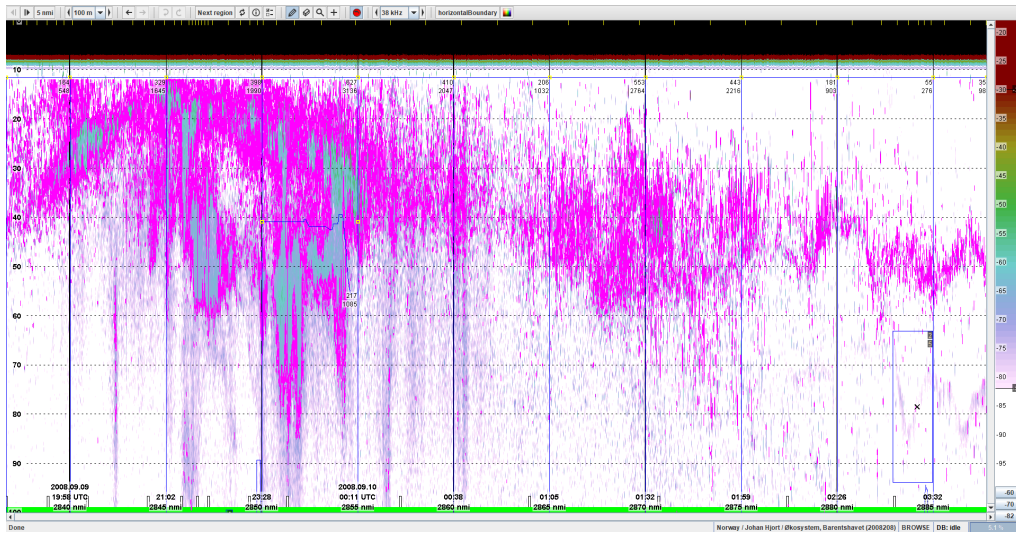


Figure A.0.2.: Echogram displaying a fish veil with the school detection setting being changed to a threshold of $-70 \text{ dB re } 1 \text{ m}^{-1}$.

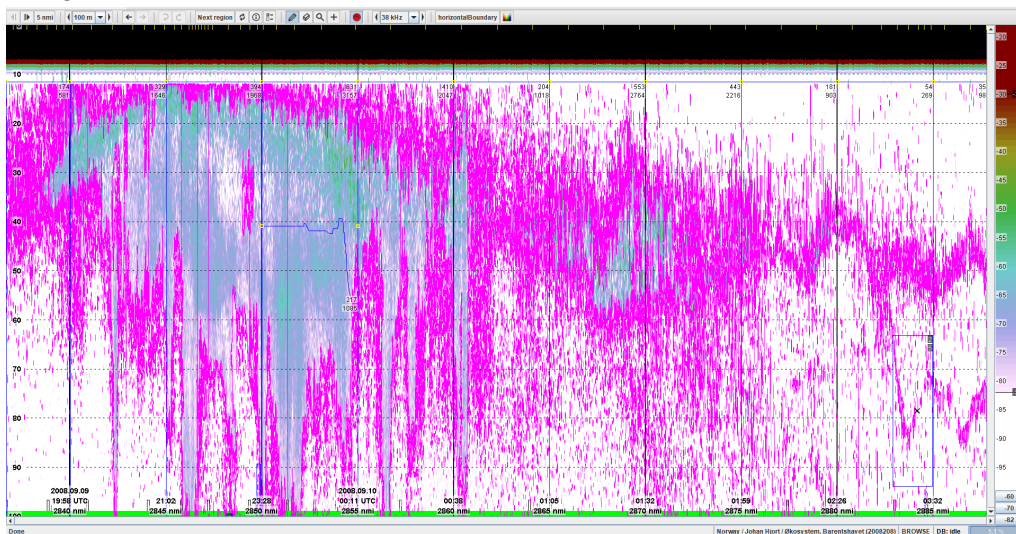


Figure A.0.3.: Echogram displaying a fish veil with the school detection setting being changed to a threshold of $-80 \text{ dB re } 1 \text{ m}^{-1}$.

A.0.1. How Length Affects Detection of Capelin Schools

Big, small and loose fish aggregations were also sensitive to changes in minimum length. Length was altered to 5, 10 and 15 meters. The following figures and tables illustrate how length affected the detection of capelin schools. This table compares the data exported for each of the minimum lengths: 5, 10 and 15 meters. Mean area, height, s_V median, s_A and number of schools were compared.

If the ship is cruising at a speed of 10 knots. There is around 5 meters distance between each ping, that is sent out from the vessel. Therefore, the minimum length for each setting increases subsequently with 5 meters. Settings were changed to 5, 10 and 15 meters.

Settings: Length

The following figures show how each setting outlines the small, big and fish veil schools (shown in this order).

A. Data collected from the 2012- 2018 ecosystem cruise

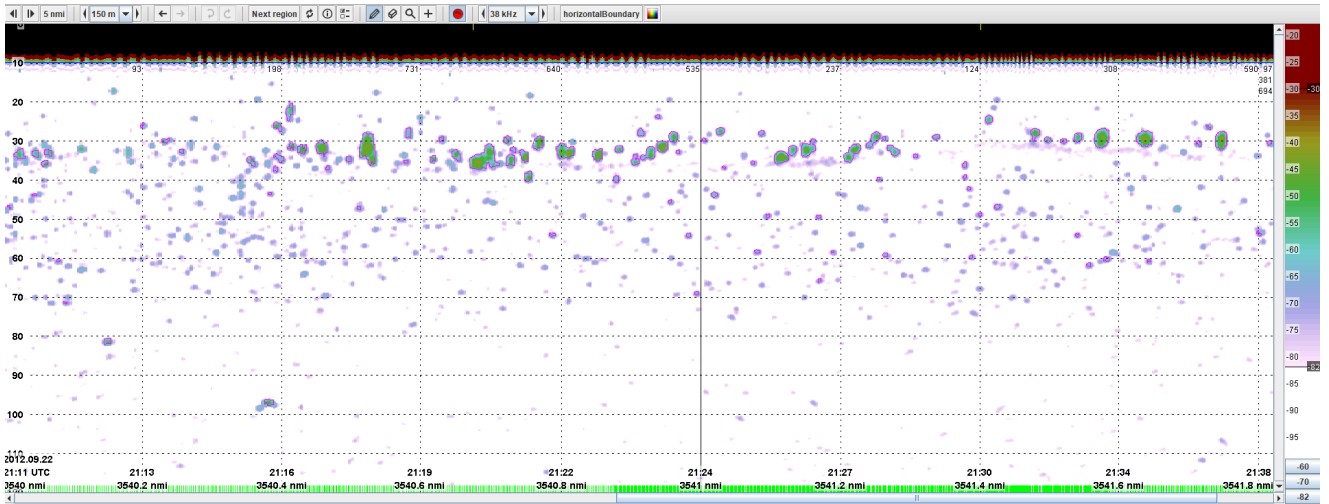


Figure A.0.4.: Echogram displaying small schools in the school detection settings with min. length = 5 m

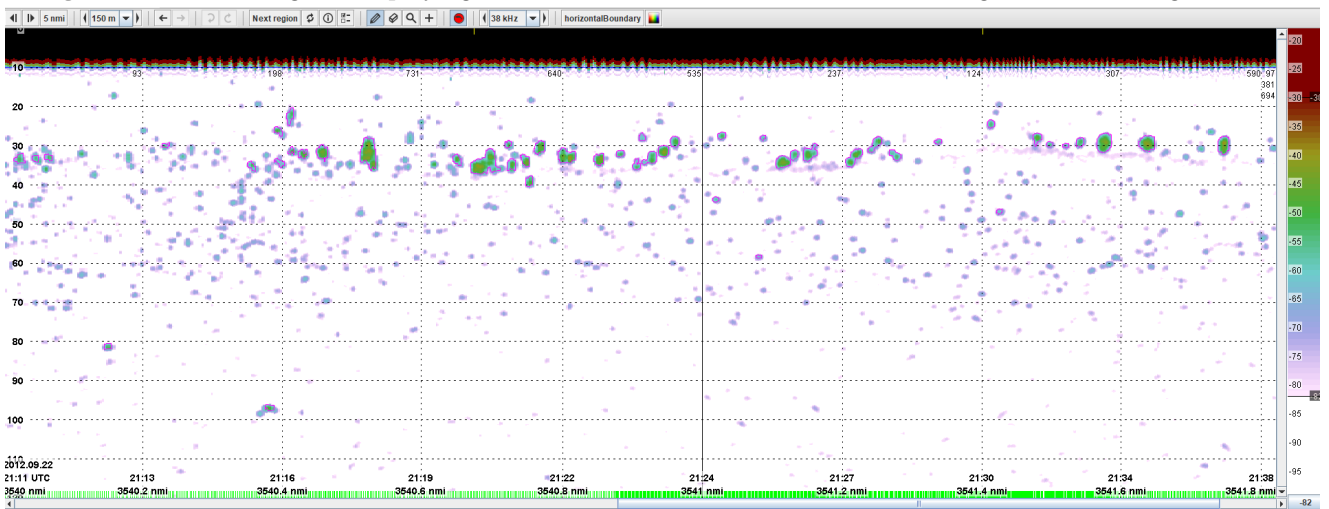


Figure A.0.5.: Echogram displaying small schools in the school detection settings with min. length = 10m

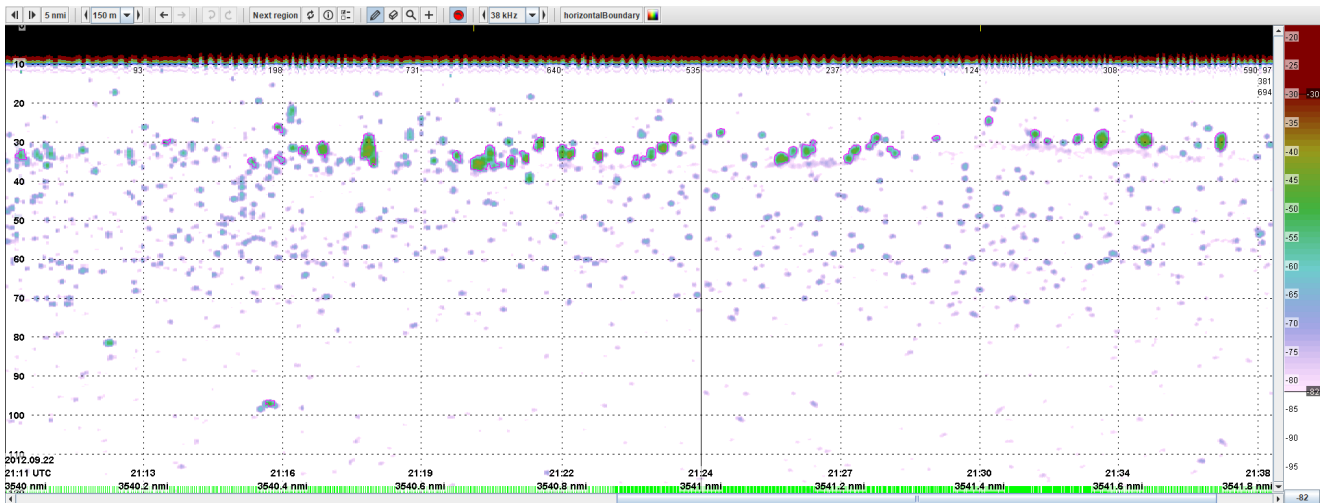


Figure A.0.6.: Echogram displaying small schools in the school detection settings with min. length= 15m

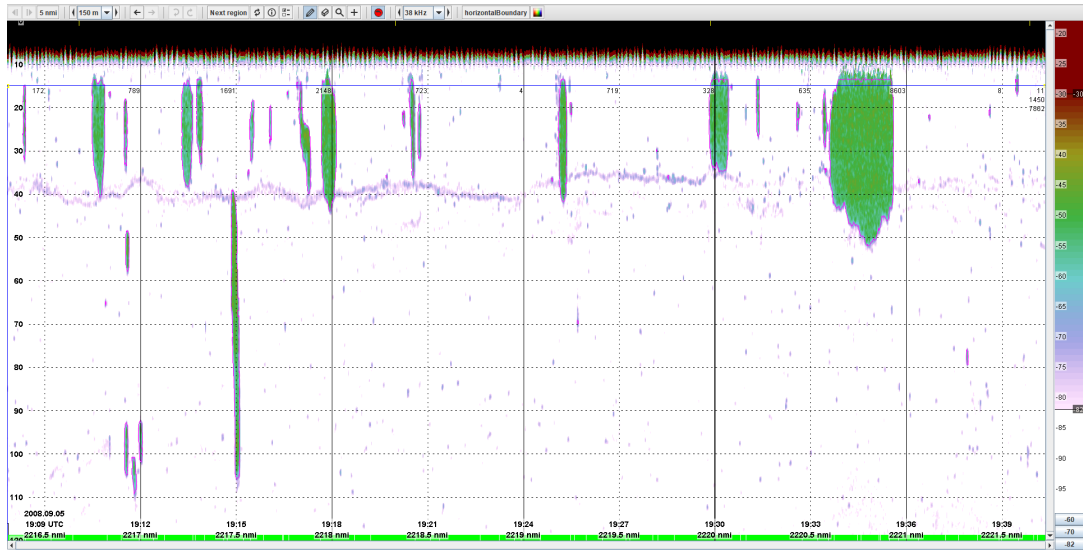


Figure A.0.7.: Echogram displaying big schools in the school detection setting with min. length= 5m

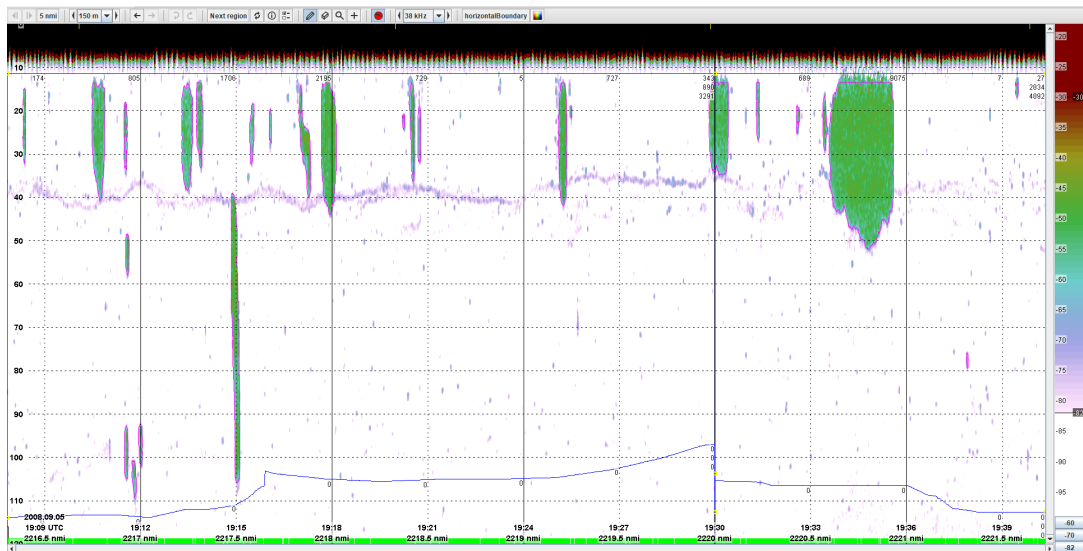


Figure A.0.8.: Echogram displaying big schools in the school detection setting with min. length= 10m

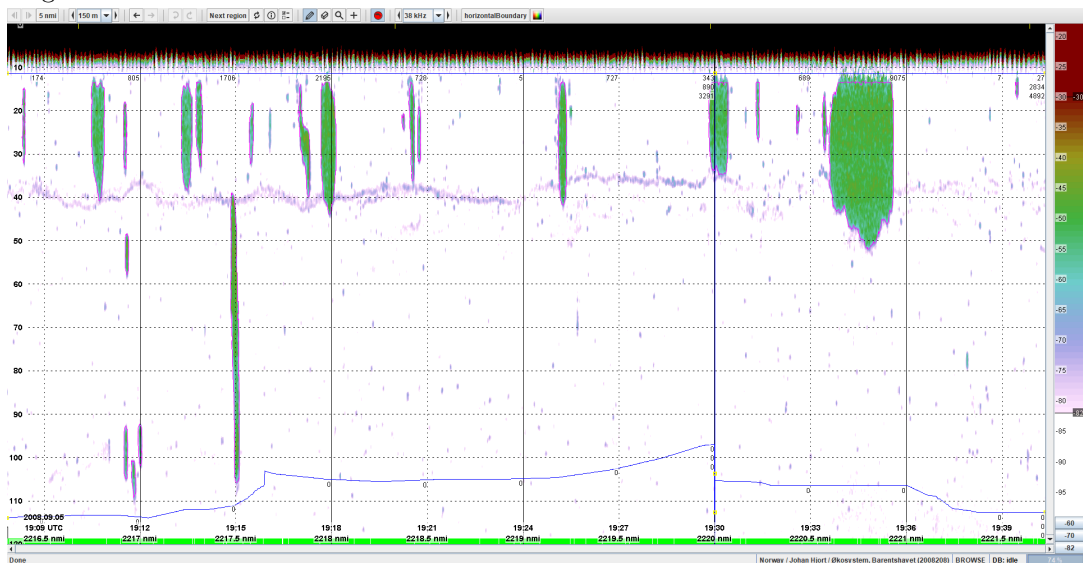


Figure A.0.9.: Echogram displaying big schools in the school detection setting with min. length=15m

A. Data collected from the 2012- 2018 ecosystem cruise

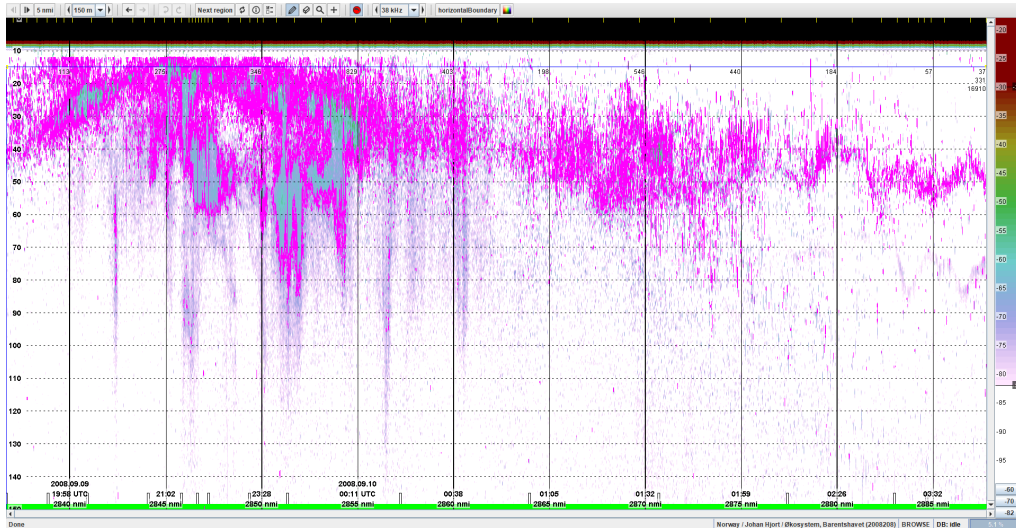


Figure A.0.10.: Echogram displaying fish veils in the school detection setting with min. length= 5m

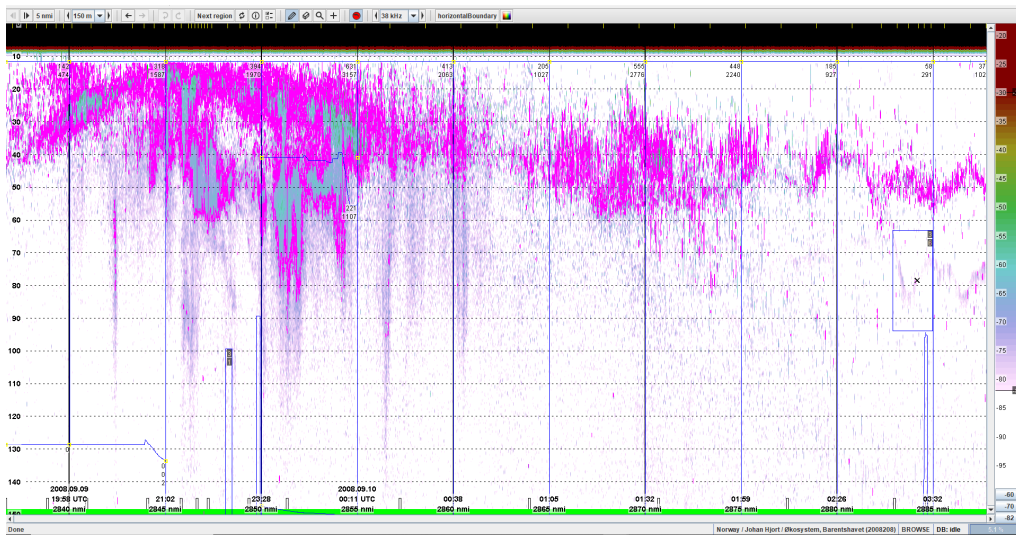


Figure A.0.11.: Echogram displaying fish veils in the school detection setting with min. length= 10m

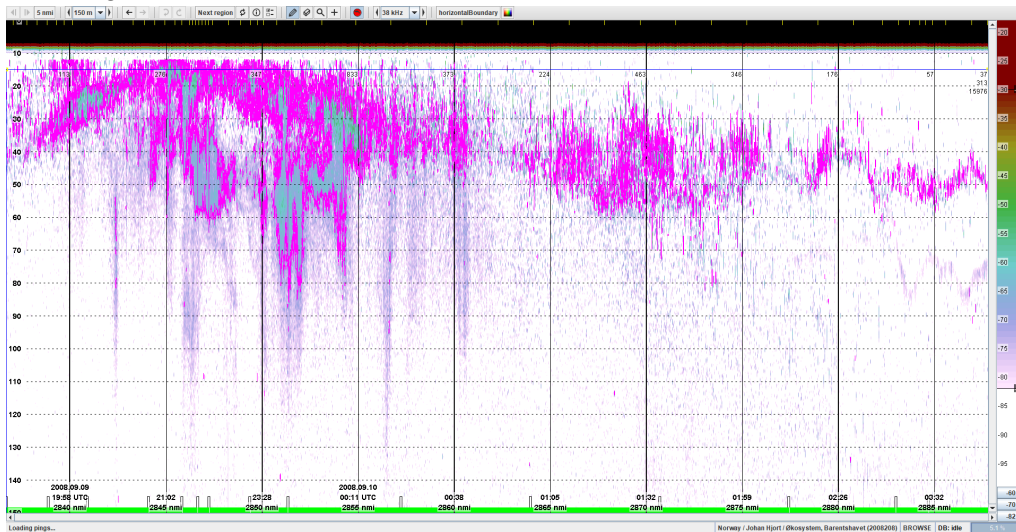


Figure A.0.12.: Echogram displaying fish veils in the school detection setting with min. length= 15m

A.0.2. Tables Comparing Minimum Length Settings

The tables show how each setting individually effects the mean area (m^2), height (m), length (m), (s_v) median, (s_A) and number of schools. As shown in the table the number of schools decreases with each setting.

Table A.2.: Small Schools, displaying school detection, minimum length = 5, 10, 15 m.

Settings	L= min.5m	L= min.10m	L= min.15m
Mean Area (m^2)	25.66	45.67	60.43
Mean Height (m)	1.36	2.10	2.56
Mean Length (m)	19.68	29.32	35.65
Mean s_v median (dB re 1 m^{-1})	-64.19	-61.80	-60.88
Mean s_A ($m^2 nm^{-2}$)	325.49	637.73	939.69
No. of schools	24	12	8

Table A.3.: Big Schools, displaying school detection, minimum length = 5, 10, 15 m.

Settings	L=min.5m	L= min.10m	L= min.15m
Mean Area (m^2)	512.65	993.12	1163.96
Mean Height (m)	5.47	9.84	11.15
Mean Length (m)	151.19	272.09	317.84
Mean s_v median (dB re 1 m^{-1})	-56.19	-54.25	-53.87
Mean s_A ($m^2 nm^{-2}$)	1021.42	1923.90	2241.15
No. of schools	86	46	39

Table A.4.: Fish Veil, displaying school detection, minimum length = 5, 10, 15 m.

Settings	L=min.5m	L= min.10m	L= min.15m
Mean Area (m^2)	76.79	146.63	220.87
Mean Height (m)	1.65	2.35	2.93
Mean Length (m)	31.63	54.48	77.04
Mean s_v median (dB re 1 m^{-1})	-64.24	-63.89	-63.61
Mean s_A ($m^2 nm^{-2}$)	41.70	57.08	73.78
No. of schools	9955	4915	3048

B. Output for results: LMM summary, QQ-norm plots, pearson residual plots

Finding the outlier

When testing how *packing density* responded to number of cod, as well as bottom depth and light, in the other models, the QQ-norm plots illustrated a seemingly straight linear model. However, when testing how cod, bottom depth and light effected minimum distance to bottom, a less then favourable normal distribution was displayed in the QQ-norm plot window. After testing which residuals stood out, it was clear that observations from station 2395 effected the QQ-norm plot distribution. Therefore I compared two models, where one model included the data from station 2395 and the other model excluded data from station 2395. The QQ-norm plot for the first model showed a more acceptable linear model that could be used to in my testing. I then compared the two models and their output values. I observed very few differences (See script and output in figure B.0.1 and figure B.0.2. Therefore, the original model including data from station 2395 could still be used to test minimum distance to bottom against cod, bottom depth and light.

B. Output for results: LMM summary, QQ-norm plots, pearson residual plots

```
d1 <- cod.capelin2[residuals(m8b) < -150, ] #testing for min dist
summary(d1)

d1 <- subset(cod.capelin2, serienr != 2395)

m8e<- lmer(minDistBottom ~ bottomDepth + sun_alt + (1|serienr), data=d1)
summary(m8e)
par(mfrow=c(2,2))
plot(m8e, main="m8e")
par(mfrow=c(1,1))
qqnorm(residuals(m8e), main="lmer(minDistBottom ~ bottomDepth + sun_alt + (1|serienr), data=d1)")
qqline(resid(m8e))
#library(car)

m8b<- lmer(minDistBottom ~ bottomDepth + sun_alt + (1|serienr), data=cod.capelin2)
summary(m8b)
par(mfrow=c(2,2))
plot(m8b, main="m8b")
par(mfrow=c(1,1))
qqnorm(residuals(m8b), main="lmer(minDistBottom ~ bottomDepth + sun_alt + (1|serienr), data=cod.capelin2)")
qqline(resid(m8b))
leveneTest(lmer(minDistBottom ~ torsknm2_log1 + bottomDepth.log + sun_alt + (1|serienr), data=cod.capelin2))

cbind(fixef(m8e), fixef(m8b))
cbind(coef(m8e), coef(m8b))
```

Figure B.0.1.: Shows the script where residuals below 150 (only station 2395 had residuals below) were removed from the original data set in order to test if the output or interpretation of the model changed.

```

      [,1]      [,2]
(Intercept) -40.3007794  4.018042293
bottomDepth  0.8872172 -0.005452746
timeofday2twilight -125.8644298  0.114392414
timeofday2day -40.3007794  0.388889683
```

Figure B.0.2.: Shows the output for the two models. The differences are relatively small.

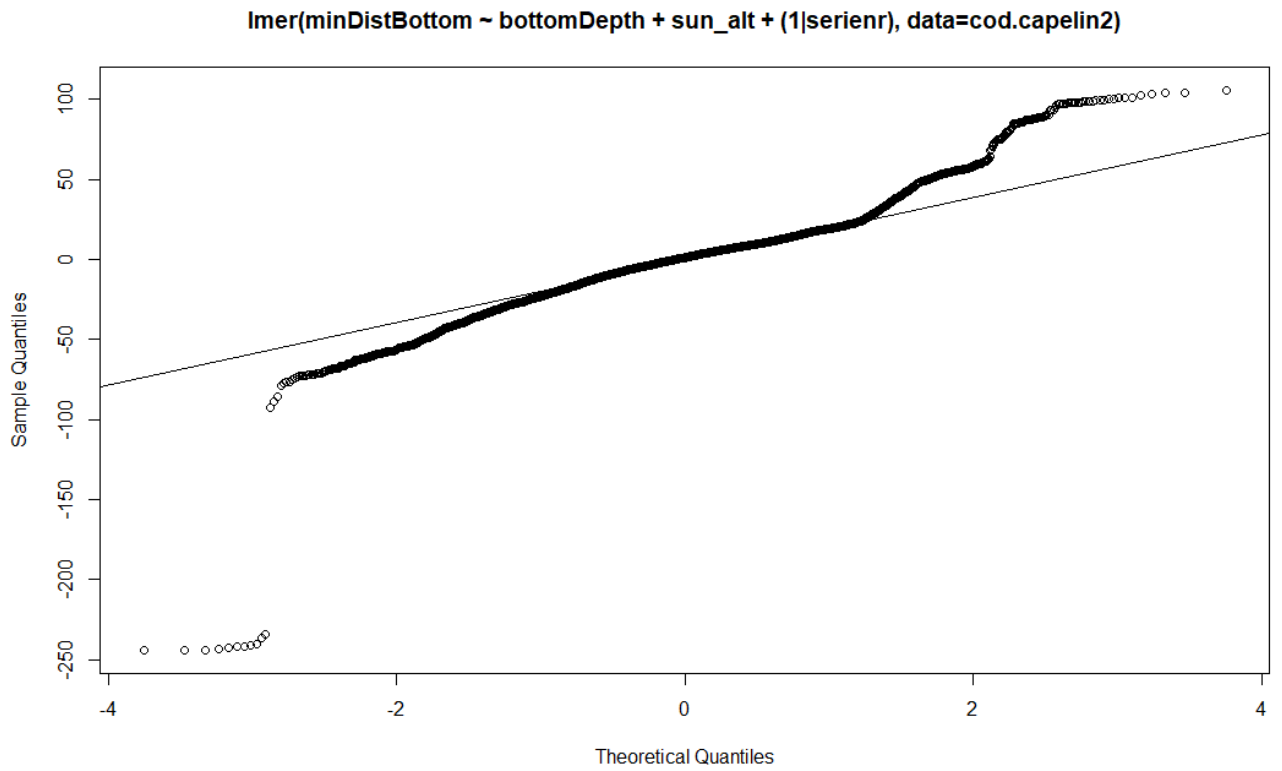


Figure B.0.3.: QQ-norm Plot Showing Model with Station 2395

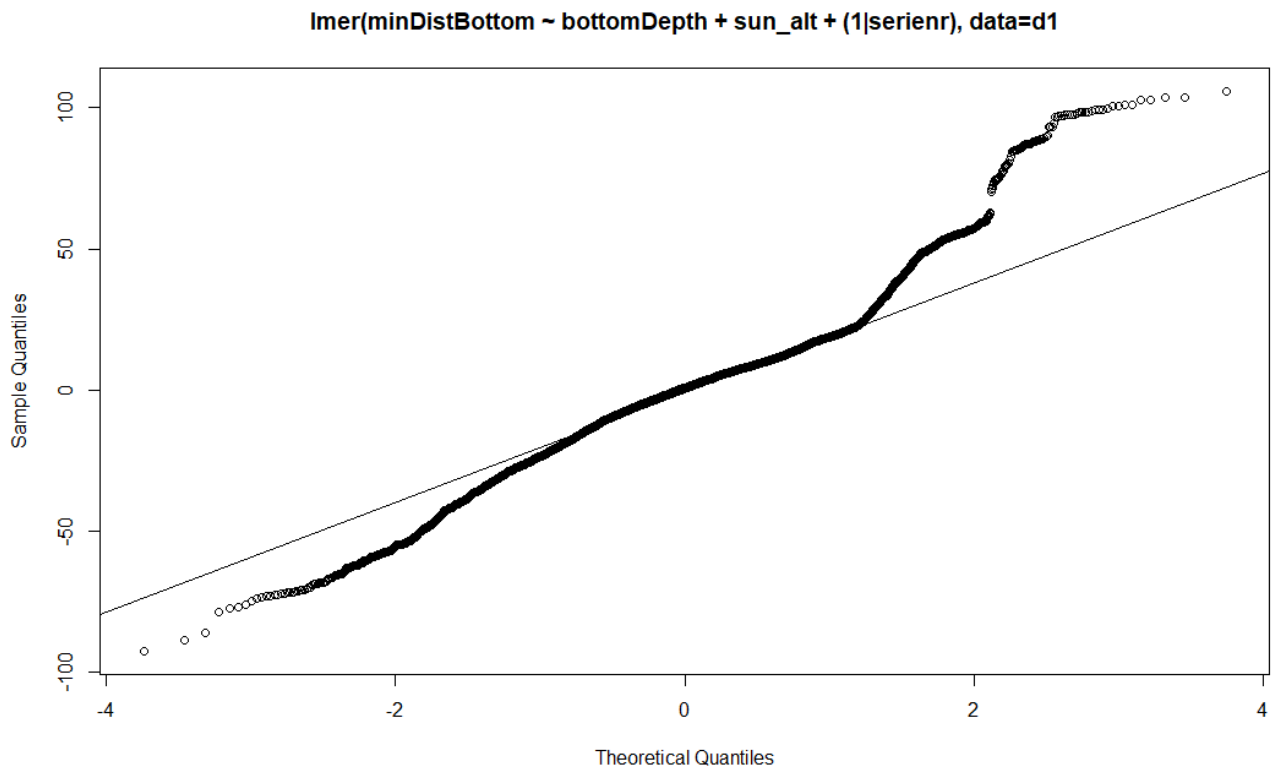


Figure B.0.4.: QQ-norm Plot Showing Model without Station 2395

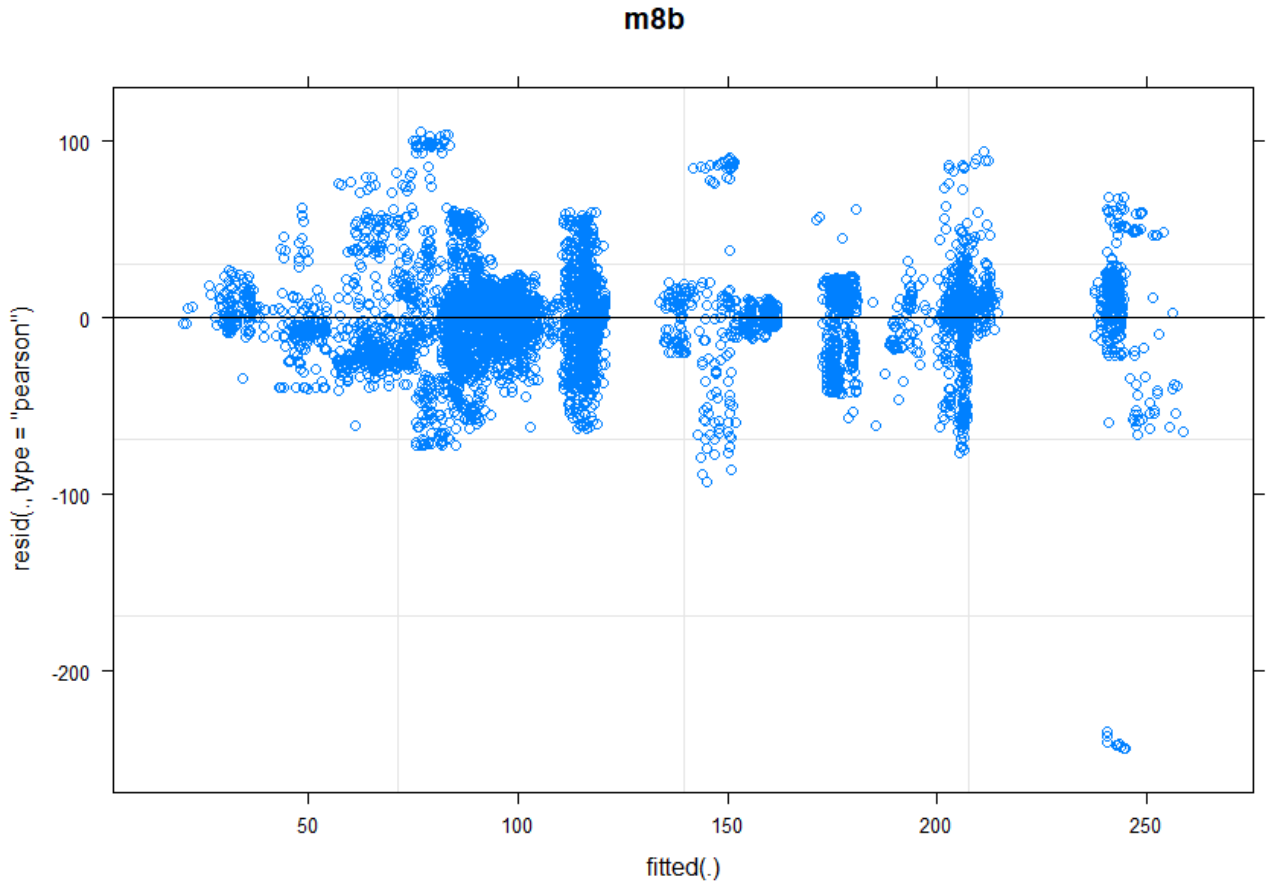


Figure B.0.5.: Pearson residual plot showing model with station 2395

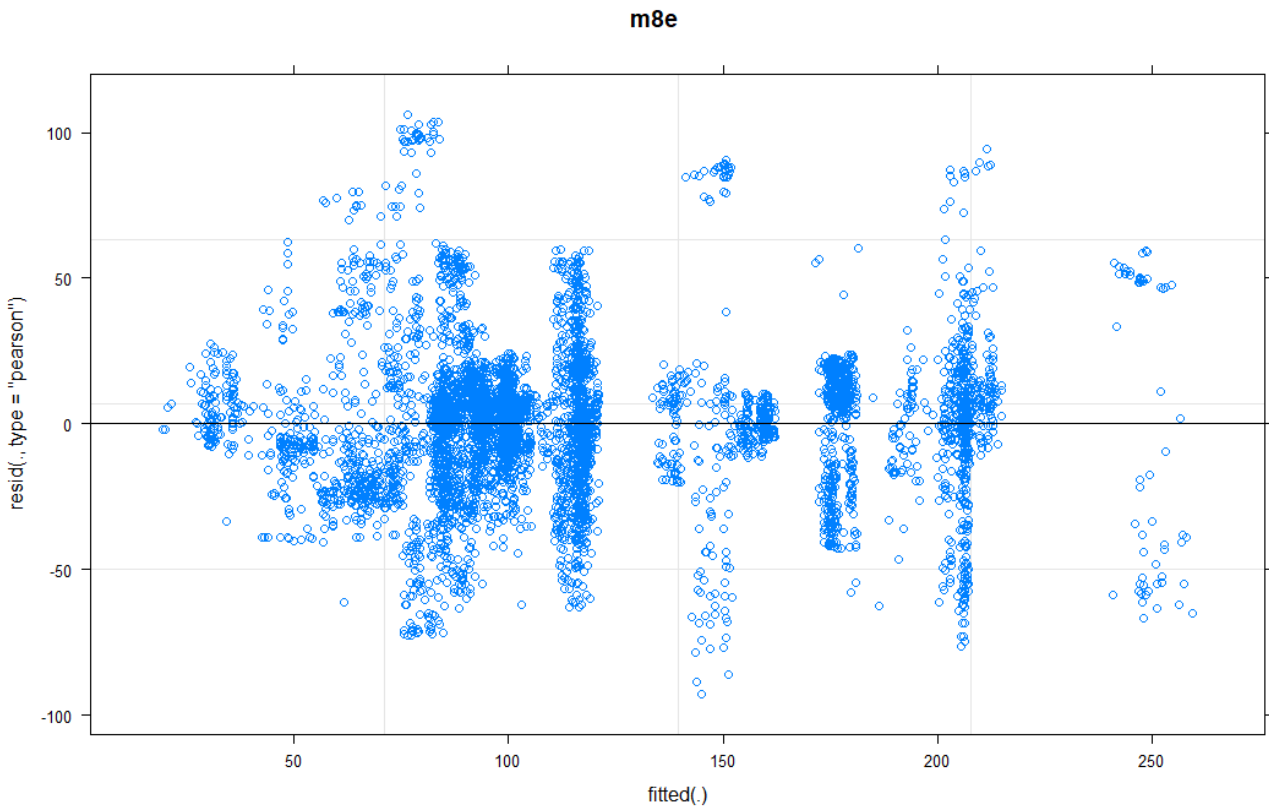


Figure B.0.6.: Pearson residual plot showing model without data from station 2395

B.0.1. Does Bottom Depth and Light Effect Minimum Distance in Capelin

This model was used to assess capelin's *minimum distance to bottom*. The output for the best model selected for this study, is shown below in table B.1 and table B.2.

Table B.1.: Output for `lmer(minDistBottom ~ bottomDepth + sunalt + (1|serienr), data = cod.capelin2)`

Fixed Effects	Estimate	SE	Lower CI	Upper CI	Pr(> t)
Intercept***	-34.004	10.368	-54.330	-13.680	5.80E-09
Sun Alt.***	-119.947	15.622	-150.570	-89.330	1.90E-04
Bottom Depth***	0.846	0.05	0.750	0.950	7.10E-03

Table B.2.: Random Effect for `lmer(minDistBottom ~ bottomDepth + sunalt + (1|serienr))`

Groups	Name	Variance	Std.Dev
Station	(Intercept)	486.200	22.05
Residual		786.4	28.04
Number of Obs.	5725	Groups:	station nr., 26

QQ-norm plot and pearson's residual graph for minimum distance model selected for this study, can be seen in the section above when comparing the two best models without residuals below 150 in figure B.0.3 and figure B.0.4. Pearson's residual graph is seen in figure B.0.5 and fig B.0.6.

B.0.2. Does bottom depth and light effect packing density in capelin

This is the output for the best model selected for this study. This model was used to assess capelin's *packing density*, shown in table B.1 and table B.4.

Table B.3.: Output for `lmer(svMean38log bottomDepth + sunalt + (1|serienr), data = cod.capelin2)`

Fixed Effects	Estimate	SE	Lower CI	Upper CI	Pr(> t)
Intercept ***	4.400	0.324	3.765	5.035	2.0E-16
Sun Alt.***	3.166	0.463	2.259	4.073	6.5E-11
Bottom Depth ***	-0.006	0.001	-0.008	-0.004	0.000171

Table B.4.: Random Effect for `lmer(svMean38log bottomDepth + sunalt + (1|serienr)`

Groups	Name	Variance	Standard Deviation
Station	(Intercept)	0.530	0.728
Residual		0.634	0.796
Number of Obs.	5725	Groups:	station nr., 26

The qq-norm plot and pearson's residual plot can be seen here in figure B.0.7 and figure B.0.8.

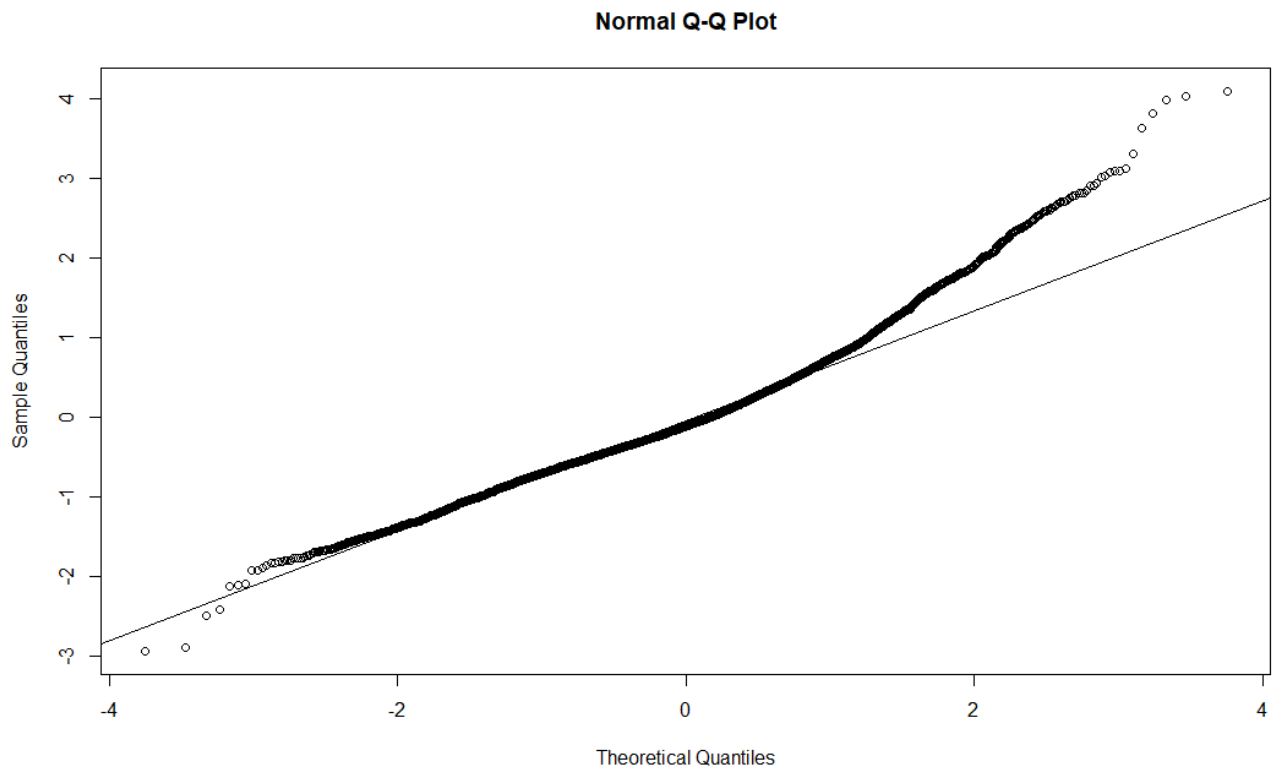


Figure B.0.7.: QQ-norm plot showing $\text{lmer}(\text{svMean}_{38}\log \text{bottomDepth} + \text{sun}_{alt} + (1|\text{serienr})$
 $\text{svMean}_{38}\log \sim \text{sun}_{alt} + \text{bottomDepth} + (1|\text{serienr}), \text{data}=\text{cod.capelin2}$

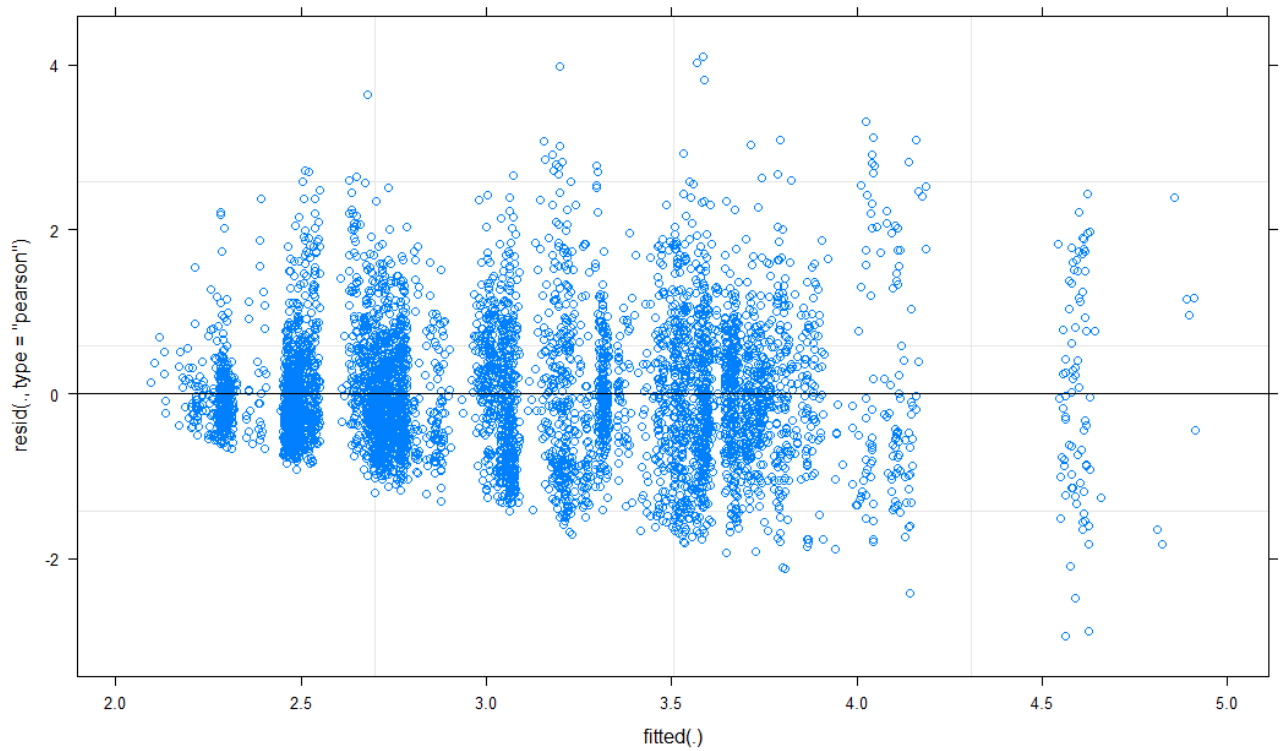


Figure B.0.8.: Pearson residual plot showing residual distribution for model: $\text{lmer}(\text{svMean}_{38}\log \text{bottomDepth} + \text{sun}_{alt} + (1|\text{serienr})$

B. Output for results: LMM summary, QQ-norm plots, pearson residual plots

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Table B.5.: Aggregated Overview of cod and capelin data from 26 Stations (3.s.f)

Station number	Area (m^2)	Bottom Depth (m)	Sv (dB re 1 m^{-1})	Cod (nm^{-2})	Min.distance (m)	Sun Alt (Radians)	Time of Day	Temperature (c°)
2340	31.43	164.14	-61.12	0	117.52	0.20	Day	-1.85
2342	50.33	157.85	-61.94	340.66	117.98	0.26	Day	-0.41
2345	43.47	178.92	-66.28	79.25	154.18	-0.10	Night	1.00
2347	17.72	116.56	-62.33	664.02	94.17	-0.16	Night	0.11
2349	21.41	160.46	-62.37	3851.35	87.35	0.14	Day	1.17
2351	42.35	227.53	-64.51	3394.39	115.29	0.22	Day	1.50
2353	131.63	131.09	-65.49	846.13	86.33	-0.09	Twilight	-1.17
2356	21.34	47.20	-60.28	58975.26	23.55	-0.14	Night	3.61
2358	48.75	77.56	-59.21	77072.28	39.65	0.06	Day/Twilight	3.61
2366	57.76	184.31	-60.09	521.43	159.67	-0.14	Night	-0.73
2368	43.46	138.52	-60.95	1246.25	65.36	-0.15	Night	1.08
2370	123.32	199.55	-62.44	2429.17	78.87	0.23	Day	-0.68
2374	100.09	124.48	-60.32	0	97.39	-0.10	Twilight	-1.61
2377	71.89	172.20	-56.27	153.13	138.20	-0.17	Night	-1.22
2388	61.72	100.53	-54.10	167.93	49.70	-0.11	Twilight	-1.13
2390	99.23	162.53	-60.98	7687.62	66.66	0.17	Day	0.65
2392	16.48	321.23	-66.55	2911.33	249.43	0.12	Day	-1.24
2395	17.78	324.79	-66.37	257.98	241.89	-0.21	Night	-1.42
2399	115.50	130.44	-61.54	159.72	50.01	0.10	Day	-1.22
2408	88.41	213.01	-63.16	2318.78	176.82	-0.16	Night	1.21
2412	62.47	250.09	-63.02	4169.15	147.71	0.08	Day	-0.46
2416	269.78	146.17	-65.50	132.33	98.97	-0.21	Night	-1.60
2418	53.23	255.53	-63.21	64.84	180.98	0.10	Day	-1.25
2420	43.59	324.82	-64.39	0	206.48	0.05	Day	-1.59
2423	563.02	249.53	-64.00	70.00	191.69	-0.21	Night	-1.35
2429	12.40	250.57	-66.63	1190.66	202.17	-0.18	Night	0.76

C. R scripts

C.0.1. Script for sun altitude

This script was used to convert time start of trawling per station to sun altitude and sun azimuth, using the `suncalc` package. The script also shows how sun altitude was further made into categories using by converting radians to degrees and splitting the categories into "Day", "Twilight" and "Night". As shown, civil twilight was used in this study as a definition of twilight.

```
#Converting datetime to date
cod.capelin$date<-as.POSIXct(cod.capelin$timeStart,format="%Y-%m-%dT%H:%M:%S")
cod.capelin$lat<-cod.capelin$latitudeStart
cod.capelin$lon<-cod.capelin$longitudeStart
sun<-getSunlightPosition(data=cod.capelin)

#Merge into dataframe
cod.capelin2<-cbind(cod.capelin,sun$altitude,sun$azimuth)
names(sun)[4] <- "sun_alt"
colnames(cod.capelin2)
names(cod.capelin2)[39]<- "sun_alt"

cod.capelin2$timeofday2<-cut(cod.capelin2$sun_alt, breaks= pi * c(-90, -6, 0, 90) /180, labels=c("night", "twilight", "day"))
```

Figure C.0.1.: Calculating Standard Error and Confidence Intervals

C.0.2. Script for Likelihood Ratio Test

This script was used to test two models with similar AIC values.

```
library("lmerTest")

m.a2 <- lmer(svMean_38log~ sun_alt + bottomDepth + (1|serienr), data=cod.capelin2)

m.a3 <- lmer(svMean_38log ~ sun_alt + bottomDepth + torsknm2_log1 + (1|serienr), data=cod.capelin2)

anova(m.a2, m.a3)

m.a2$deviance-m.a3$deviance
```

Figure C.0.2.: Likelihood ratio test to compare two models with similar AIC value

C.0.3. Script for json. to csv. conversion

This script was used to convert .json files to csv.files that could be used in R for further analysis.

C. R scripts

```
JH_476<-fromJSON("JH_476.json",simplifyDataFrame=TRUE, flatten = TRUE)
Schools<-JH_476$schools[,1:19]

density_38<-as.data.frame(matrix(ncol=length(JH_476$schools$channels[[2]][1,]),nrow=length(Schools[,1])))
for(i in 1:length(Schools[,1])){
  density_38[i,]<-JH_476$schools$channels[[i]][2,]
}

names(density_38)<-paste0(names(JH_476$schools$channels[[2]][2,]),'_38')
DATA<-cbind(Schools,density_38)
write.csv(DATA,'JH_2418.csv',row.names=FALSE)
```

Figure C.0.3.: Script used to convert .json files to csv.

C.0.4. Script to convert sv to Sv

This script was used to convert sv to Sv for visual presentation.

```
#Changing sv (m-1) to sV(db)
x<- cod.capelin2$svMean_38
cod.capelin2$sV_Mean<- 10*log10(x/(4*pi*(1852**2)))
```

Figure C.0.4.: Script used to convert .json files to csv.

C.0.5. Calculating standard error and confidence intervals

The upper and lower confidence interval (Lower and Upper CI, respectfully) and standard Error (SE) was calculated using the following method:

CI = Estimate +/- SE*1.96

SE = the standard error of model

1.96 = the standard constant approximation for a 95% CI

Figure C.0.5.: Calculating Standard Error and Confidence Intervals

R Packages

In my study, the following packages were used in R, see table C.1:

Table C.1.: Overview of packages in R used in this thesis

Name of Package	Purpose	Citation
<i>jsonlite</i>	convert j.son file from LSSS to "csv."file	(Ooms, 2014)
<i>effects</i>	Displays interactions for the statistical models, with the linear predictions.	(Fox and Weisberg, 2019)
<i>lme4</i>	Used to run linear mixed models (LMM) with random effect (lmer)	(Bates et al., 2015)
<i>lmerTest</i>	Provides a summary of lmer output (p-values etc.) as well as a summary	(Kuznetsova et al., 2017)
<i>AIC</i>	Generic function calculating Akaike's 'An Information Criterion' for one or several fitted model objects for which a log-likelihood value can be obtained,	(Sakamoto et al., 1986)
<i>suncalc</i>	Used to calculate sun altitude based on time and geographical position	(Benoit Thieurmel, 2019)
<i>ggOceanMaps</i>	Used to make map	(Vihtakari, 2021)
<i>ggplot2</i>	Used to make histograms of variables (distribution and transformation)	(Wickham, 2016)
<i>lmtest</i>	Used to run a likelihood ratio test between two models with similar AIC value	(Zeileis and Hothorn, 2002)
<i>R and R.Studio</i>	Data analyses and visualization of results conducted in this program	(R Core Team, 2020; RStudio Team, 2020)