Capelin in a changing environment

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Main findings from capelin research study 2018-2022

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Capelin (*Mallotus villosus*) in a changing environment

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THE IMPORTANCE OF CAPELIN IN THE ICELAND-EAST GREENLAND-JAN MAYEN (IEGJM) AREA

As a small pelagic forage fish, capelin (*Mallotus villosus*), is a keystone species in the Iceland-East Greenland-Jan Mayen (IEGJM) food web. It constitutes an important prey for many ecologically and commercially important demersal species, such as cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), saithe (*Pollachius virens*) (Pálsson & Bjornsson, 2011), as well as to marine mammals and seabirds (Linnebjerg et al., 2018). As a predator, it feeds on zooplankton and forms an important energy transfer pathway in the ecosystem (Astthorsson & Gislason, 1997). Thus, shifts in spatial distribution and varying abundance of capelin may have consequences for the overall structure and function of the food web in this region. In addition to this ecological importance, capelin also has considerable commercial, societal, and cultural importance. Capelin became prevalent in the Icelandic commercial fisheries in the 1960s after the collapse of the Atlantic herring stock. Landings in the early years were mostly utilized for fishmeal and fish oil, but with advances in capture and processing technology, an important market has since developed for frozen capelin, capelin roe and whole capelin with roe in Eastern Europe and Japan. In 2022, the value of capelin and capelin roe combined was approximately 48 million ISK (Statistics Iceland, 2023), second to cod on the list of Iceland's most commercially important fish species.

CHANGES IN STOCK ABUNDANCE AND DISTRIBUTION OVER TIME

The IEGJM capelin stock undertakes extensive seasonal migration from feeding areas in summer and autumn, located between Iceland, East Greenland, and Jan Mayen, to spawning grounds the following winter. The spawning migration path follows a clockwise route around Iceland, from the northern and eastern shelf break to the spawning grounds along the south and west coast. Capelin abundance and distribution, together with feeding and spawning migrations, have been studied in the last five decades through annual acoustic surveys, both in autumn and winter, conducted by the Icelandic Marine and Freshwater Research Institute (MFRI) (Vilhjálmsson, 2002; Vilhjálmsson & Carscadden, 2002). The Greenland Institute of Natural Resources (GINR) has participated in autumn surveys since 2018. Autumn surveys estimate the immature and mature stock components by the end of the feeding migration to issue an intermediate Total Allowable Catch (TAC) advice based on the biomass of the maturing capelin. Winter surveys estimate the fishable stock component during the spawning migration, whereupon a final TAC advice is issued.

Pronounced geographical shift in the distribution of capelin during autumn in the early 2000s was first highlighted by Vilhjalmsson (2007), who put forth a hypothesis of changes in feeding grounds from the northern shelf off Iceland and Iceland Sea to the shelf areas of East Greenland. This was later illustrated by Carscadden et al. (2013) (Figure 1). A delay in the arrival of capelin spawning migration to the shelf edge north of Iceland has also been observed in January (Singh et al., 2020).

Coinciding with this spatial shift around the early to mid-2000s, the stock size showed a declining trend, as evident from lower advised catch and subsequent landings (Figure 2, left), indicating lower stock productivity. The changes in stock distribution and low abundance led to the closure of the autumn and summer fishery in the early 2000s. No fishery was advised at the beginning of the fishing season for winters 2008/09, 2018/19 and 2019/20. Notably, in the years 2020 and 2021, recruitment increased again to levels prior to 2000 (resulting from the 2019 and 2020 year classes), and the 2009 year class estimate in autumn 2010 was also high. Furthermore, there was no fishery in the year 1982 and summer 1983. Despite the small spawning stock size, the year classes spawned during the moratorium had average abundance at age 1 and above average at spawning contributing to a catch of ~800-1300 kt in the fishing seasons of 1984/85–86/87. More than 50% of the catches of year class 1983 occurred in the season 1986/1987 (Figure 2).

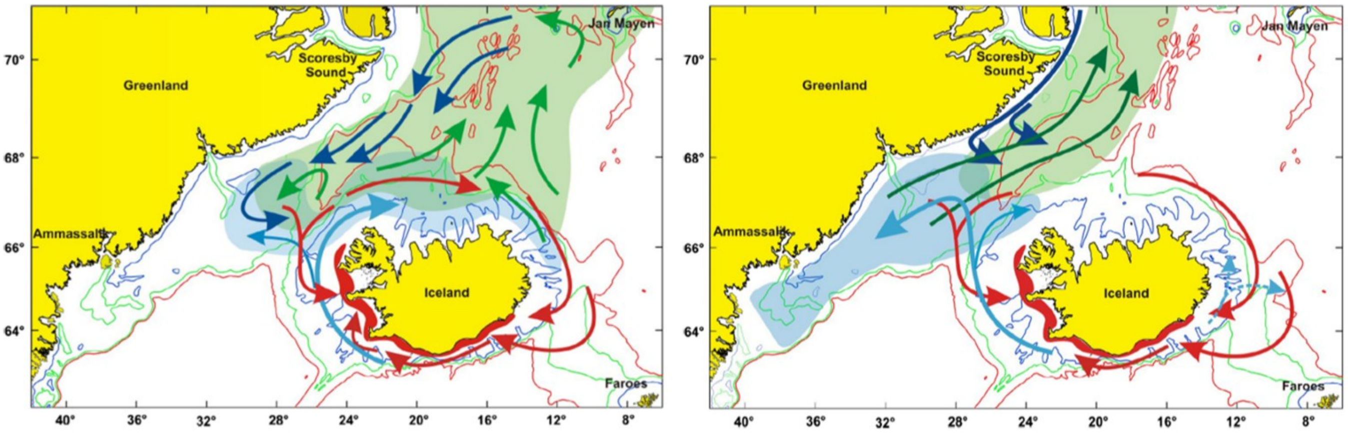

Figure 1. Map of the historical capelin distribution on the left and the recent distribution on the right. The red arrows delineate the spawning migration with the spawning area shaded in red. Light blue arrows denote larval drift and light blue areas show the distribution of juvenile capelin. The feeding area is shaded in green and green arrows show the feeding migration away from juvenile areas, with the return migration shown in blue (Illustration by Vilhjalmsson, 2007 & Carscadden et al. 2013).

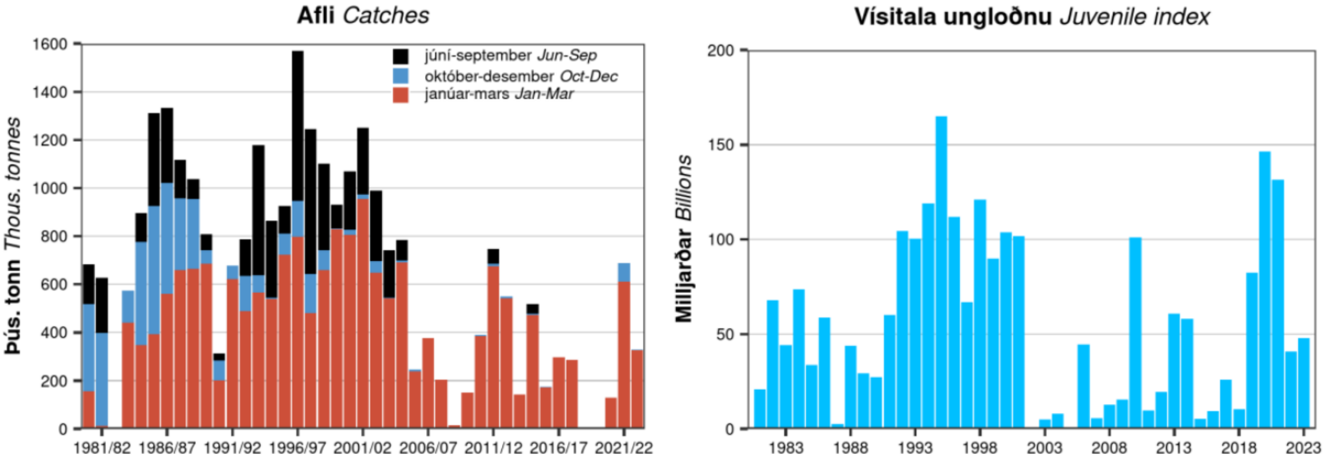

Figure 2. Trend of landed capelin catch by season (1980–2022) and estimated juvenile index from autumn by survey year (1981–2023).

EVIDENCE OF PERSISTENT CHANGES IN ENVIRONMENTAL CONDITIONS

Coinciding with the shift in capelin distribution, a weakening of the North Atlantic subpolar gyre was observed. This led to a reduction in the freshwater inflow into the North Atlantic region, impacting the thermohaline circulation and causing record high salinities (Hjálmar et al., 2005). A northward ocean heat transport also led to increasing sea temperature and receding sea-ice extent in the Nordic seas, with a significant increase in heat transport noted around 2001 (Tsubouchi et al., 2021). A temperature increase at the northern shelf of Iceland was evident around this time, with fluctuations in water mass circulation and mixing leading to variations in current strength and heat transport (Jónsson and Valdimarsson, 2012).

Previous studies considering the IEGJM capelin have postulated hydrographic variability as the primary cause of changes in abundance and distribution (Vilhjalmsson, 2007, Carscadden et al., 2013). It can be hypothesized that environmental changes observed north and northwest of Iceland contribute most to spatial distributional shifts in the capelin stock both in autumn and winter. To examine the changes in the underlying environmental drivers in this region, temperature and salinity can be used as indicators of change. Surface temperature and salinity data at 0.5 m depth were compiled from the E.U. Copernicus Marine Service (CMEMS) from 1993 to 2019 (http://marine.copernicus.eu/). An annual trend with monthly variations showed an average increase of 1.02°C in temperature and 0.27 PSU in salinity after 2002 in this region (Figure 3). Previous studies have also shown this increase in temperature using data from standard hydrography measurements along a single transect in the area. In 2003, a significant increase in heat transport was recorded (Jónsson & Valdimarsson, 2012a).

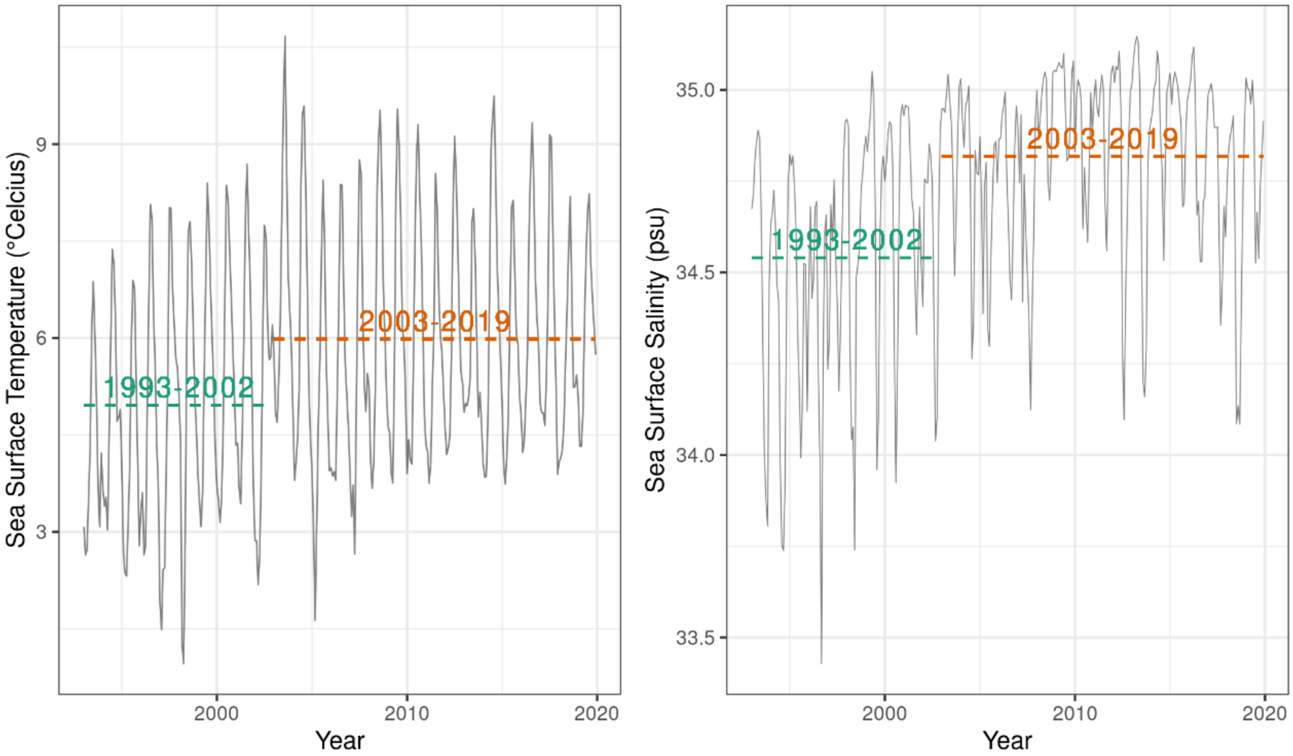

Figure 3. Monthly variations of temperature (A) and salinity (B) over the years 1993-2019 for areas north and northwest of Iceland (within 66°N and 68°N latitude and 25°E and 15°E longitude). The average (horizontal lines) temperature and salinity for periods before and after 2003 is shown to highlight the increase in temperature of 1.02 °C and salinity of 0.27 PSU.

THE INTERPLAY BETWEEN CAPELIN AND ENVIRONMENTAL CHANGE

The last extensive study in the habitat of capelin was conducted from 2006-2008 under the Iceland Sea Ecosystem project (Pálsson et al., 2012). The project was conducted to discern the ecosystem patterns in the Iceland Sea region and their connection to capelin's life history and aiming to understand the recently observed shift in capelin distribution. The northward displacement of 0-group capelin and a westward displacement of older capelin were attributed to changes in the physical environment in the Iceland Sea. The study included research on the taxonomic structure of zooplankton in the area (Gislason & Silva, 2012) and a trophic linkage study using stable isotopes with an emphasis on the role of capelin in the food web (Petursdottir et al., 2012).

After more than a decade, a new study was warranted to gain in-depth knowledge of how these large-scale distribution and abundance shifts have affected the different life history stages of capelin. In the past, descriptive trends have been used to relate capelin to environmental variability. Nowadays, the availability of global ocean model outputs makes high resolution analysis possible. Besides exposure to new physical conditions, the capelin presence in a new ecosystem can also affect predator-prey dynamics which has direct implications for the stock biomass and fishing opportunities. Furthermore, since the Iceland Sea Ecosystem project, data on the early life history stages of capelin has been scarce. Obtaining reliable estimates of the fishable component of the population is important to ensure maximum sustainable yield. A thorough examination of factors that can affect this biomass estimation from scientific surveys is therefore also crucial. Biomass estimation from acoustic surveys depends on a target strength-length relationship, and the one in use was established three decades ago. Consequently, the MFRI received funding for a five-year project (2017-2022) from the Ministry of Food, Agriculture & Fisheries to conduct research into investigating the above. The research focused on the following subject areas:

a. Long-term changes in the distribution and life history of capelin.
b. Capelin larval abundance and distribution around Iceland.
c. Contribution of potential spawning habitats by simulating larval dispersal.
d. Feeding ecology of capelin in its new feeding grounds.
e. Capelin distribution within East Greenland water masses during its feeding period.
f. Predator-prey dynamics after capelin distributional shifts.
g. Reliability of assigning maturity stages during stock assessment.
h. Effect of behavior and physiology of capelin on acoustic biomass estimation.

Additional survey time, tasks and sampling were added to routine MFRI surveys to obtain data for all studies included in the five-year project. The funding was also utilized to hire two scientists.

MAIN FINDINGS

The main findings for each subject area are summarized below. Detailed descriptions of methodology and results on each sub-topic within the subject area are presented in a collection of extended abstracts, referred to as papers henceforth. The papers (numbered 1–14) appear as chapters in this collection.

a. Long-term changes in distribution and life history of capelin

The migration route of capelin along the shelf break from the north and east of Iceland to spawning grounds located south and west of Iceland was investigated using catch data (logbook). By analyzing catches over two time periods encompassing more than two decades, slight changes were detected in the timing of the capelin migration. In recent years, the capelin spawning migration arrived later to the Icelandic shelf or in early January compared to earlier years when they had moved further southward along the migration route by January. This implies spatial distributional changes for the capelin stock in January, which can have consequences on predator-prey dynamics **(Paper 1)**.

To discern whether a relationship existed between the altered capelin distribution and the physical environment during autumn and winter, species distribution models were used to predict the presence and absence of capelin in pre-shift years (1993-2002) and post-shift years (2003-2019). These time periods were defined in accordance with environmental changes (Figure 3). The effects of temperature, salinity, current speed, net primary productivity, and bathymetry were tested. The predicted probability of occurrence from the models over these two periods demonstrates that changing environmental conditions have contributed to the modified distribution of the stock **(Paper 2)**.

A study of the life history traits of capelin over two decades showed that length-at-age, weight-at-age, body condition, and length-at-maturity increased over time, whereas age-at-maturity remained stable. Abundance and temperature were identified as key drivers of the observed life history trait changes. The observed negative relationship between abundance and length and weight indicates a density dependent effect where body size has potentially increased with decreased intra-specific competition. The smaller individuals prefer warmer conditions, while the larger individuals prefer colder conditions **(Paper 3)**.

b. Capelin larval abundance and distribution around Iceland

The capelin larval densities showed high interannual variability among the years studied (2017-2020). Larvae were present in various densities around Iceland, with the highest densities present in the south and west of Iceland, where most of the spawning takes place. As previously known, spawning occurs all around the Iceland shelf, as evident by the presence of newly hatched larvae in all sampled areas. The variability in larval densities is best explained by temperature. It is difficult to distinguish whether optimum temperature conditions lead to higher larval survival or whether the temperature effect is confounded because of the conditions at the spawning site. A more extensive dataset within areas is needed to examine this **(Paper 4)**.

c. Contribution of potential spawning habitats using simulated larval dispersal

The spawning events of capelin are difficult to measure as capelin are substrate spawners. A backtracking procedure combined with high resolution current data was used to trace larvae sampled in May 2018 from their sampling to hatching locations. An age-length relationship of larvae was used to determine larval age, which gave the number of days the larvae drifted with currents before being sampled. Further, the spawning dates were estimated using a relationship between temperature and incubation time from a cultivation experiment (**Paper 5**). Preliminary results show that larval dispersal in the west and north of Iceland is relatively localized for the samples taken in May 2018 **(Paper 6)**.

d. Feeding ecology of capelin at new feeding grounds

The diet of capelin was investigated in their new feeding area annually in autumn (September-October) from 2018 to 2021 and in winter (January and February) from 2018 to 2019. A high proportion of capelin stomachs contained food, both in autumn (84-99 %) and winter (64-77 %), suggesting active feeding during both seasons. Copepods and euphausiids were the most important prey groups in autumn, reflecting species composition of zooplankton in the feeding area. The findings from the study indicate that capelin is an opportunistic predator feeding according to prey availability. Interestingly, when a large year class entered the population in 2021, the stomach fullness of individuals was lower, affirming intra-specific competition for food **(Paper 7)**.

e. Capelin distribution in the east Greenland water masses during autumn feeding

The capelin migration takes place within the system of ocean currents in the Iceland-East Greenland-Jan Mayen area. During autumn, capelin is mainly present along the shelf and slope of East Greenland. Water masses characterized based on temperature and salinity along standard hydrography sections (70- and 72-degrees latitude) showed that capelin mostly preferred the warm nutrient rich Atlantic-origin Water (AW), which is known to be high in zooplankton abundance. They were also present in Polar Surface Water (PSW). The capelin schools move across water masses when conducting diel vertical migration. Preliminary results based on a small subset of data show a close correspondence between capelin and krill distribution, indicating that capelin follow their prey closely across environmental gradients **(Paper 8).**

f. Predator-prey dynamics after capelin distributional shifts

Capelin is an important prey item for cod on the Iceland shelf, and the predation from cod, haddock, and saithe is included in annual capelin stock assessments. Cod stomach content data analysis from the autumn groundfish survey revealed that capelin was consumed at higher levels in the past (1996-2001) compared to recent years (after 2001). This is consistent with the movement of capelin away from the north of Iceland to east Greenland around that time. During the winter groundfish survey (March), the stomach content is an indicator of the remaining biomass after the capelin fishery has concluded. This estimated index followed interannual variability observed in the capelin spawning stock biomass. The amount of capelin in cod stomachs in the March survey is not a good indicator of the amount of capelin available for cod in that season, nor the size of the fishable stock at the beginning of the season. Nonetheless, it can indicate the extent of predation over the years, which can be considered during stock assessment **(Paper 9)**.

In a separate study (not funded by this capelin research initiative), stable isotope analysis in combination with stomach content data analysis was used to confirm that harbour porpoise feeds on capelin as its main prey during March and April in Icelandic waters. This study corroborates findings from 30 years ago **(Paper 10)**.

At the new feeding grounds in autumn, cetaceans (marine mammals) were systematically counted during the capelin autumn surveys in 2017 and 2018 in a project funded jointly with the Greenland Institute of Natural Resources. The humpback whale (*Megaloptera novaanglea*) was the most common species in both years. A comparison of whale and capelin abundance showed that whales were found most frequently in areas where capelin were present. The two main species that overlapped most with capelin distribution were minke and humpback whales. The capelin abundance explained a certain amount of variation in whale abundance strongly suggesting predation on capelin by whales during this season **(Paper 11)**.

g. Reliability of assigning maturity stages during stock assessment

Reliable determination of maturity stages is important for estimating SSB. Currently, the assignment of maturity stages is based on visual inspection of whole gonads, which is a fast and inexpensive method. A more accurate method is microscopic examination, which is more expensive and time consuming. A comparison of the two methods showed low error rates overall for the macroscopic method, validating their use. The hardest length group to assign to a maturity stage was the 14-15 cm length group. When a large year class enters the population, density dependent effects can affect maturation, leading to small gonads and misidentification of maturity stages. In these instances, a precautionary approach should be applied when estimating the SSB **(Paper 12)**.

h. Effect of behavior and physiology of capelin on acoustic biomass estimation

The biomass of capelin is measured using echosounders. The movement, depth, and physiology of the fish (i.e., length, weight, body condition, swim bladder size, tilt, gonad status and fat index) can influence the strength of echoes returned from individual fish (target strength), affecting biomass estimations. An analysis of in-situ target strength shows that it varies with depth, fish length, swim bladder size, and potentially season. Continued technical development of instrumentation, additional data and analyses are required to make a reliable revision of the relationship of target strength with other factors **(Paper 13)**.

Capelin Cultivation Experiment

A capelin cultivation experiment has been ongoing at the MFRI experimental facility in Grindavík, which was out of this project's scope **(Paper 5).** The findings, however, have been relevant and were used to inform analyses on early life stages and larval drift modelling. Successful cultivation of capelin at all life stages now presents the opportunity to study the effects of environmental conditions on the larval development, growth, maturation, and survival of capelin. Data from such experiments can be utilized to comprehend the changes observed in the natural environment.

Capelin Stock Assessment Review

Scientific analyses on stock assessment and the level of the fishery it can sustain should be used on a regular basis to determine capelin stock conditions and provide science-based advice for fisheries management, such as catch quota allocations, e.g., total allowable catch (TAC). In 2022, a group of international scientists peer-reviewed the data, assessment methodology, and management strategy for the capelin stock. The panel decided that the assessment methodology will remain largely unchanged with three main exceptions:

- Autumn and winter survey data are combined for the final assessment. It was decided that instead of identical weighting, the autumn survey will get a weight of 1/3rd.
- The intermediate advice issued and based on the autumn survey should only be 2/3rd of the calculated advice value.
- The limit reference point for SSB (B_{lim}), which is used to set the final advice, was revised to 114 thousand tons (from 150 t.t.) based on recalculated values for the capelin SSB time series.

The harvest control rule, which is based on an escapement strategy, remains unchanged, i.e., the final TAC is advised with > 95% probability of SSB being greater than or equal to the B_{lim} at time of spawning. Detailed information and recommendations from the benchmark are presented in **Paper 14.**

Environmental DNA study

The general interest in nonlethal technology, such as environmental DNA (eDNA), has considerably increased in the last decade to monitor marine species exhibiting extensive migration patterns (Boussarie et al., 2018). As part of a separate research project, a study was conducted to assess the potential of using eDNA to infer the presence and abundance of capelin. The eDNA samples were collected during autumn MFRI surveys in 2019 and 2020. A positive correlation was observed between eDNA and capelin presence and abundance. The results showed that the targeted qPCR approach for the capelin gave relatively comparable results to the acoustic monitoring survey both for the distribution range and the horizontal quantification. Therefore, capelin eDNA concentrations can be used as a proxy for the presence/absence of capelin and for its abundance. The findings from this study have been published in a peer-reviewed journal (Pampoulie et al., 2023).

DISCUSSION & FUTURE PERSPECTIVES

Capelin ecology in IEGJM waters has undergone major changes at all life history stages in the last decades. Because they are small, highly migratory pelagic fish with a short life span (3-5 years), capelin are vulnerable to environmental changes (Vilhjálmsson, 2002). The current five-year research project partly fills our critical knowledge gap on the response of capelin to environmental changes during the last two decades.

The unpredictable abundance and distribution of capelin and its vulnerability to changing oceanic conditions can have direct implications for fisheries in the future and the food web dynamics for the IEGJM ecosystem. Through this research, we have established a statistical framework to describe the environmental niche of capelin and its potential responses to changing oceanic conditions during its juvenile and adult stages. Combined with high-resolution global ocean outputs, the species distribution models can be used to project capelin presence and absence into the future based on the various climate projection scenarios. In a similar manner, the abundance of capelin could be modelled for future projections.

Our knowledge of the life history response of capelin to this changing environment has also improved, where the effects of density-dependence are apparent during autumn. Intra-specific competition for resources can affect the growth and maturation of individuals when large year classes are entering the population. Therefore, in these years the biological characteristics, specifically the gonad maturity of the stock, should be closely examined to make a reliable distinction between immature and mature components of the stock.

Spawning events of capelin are challenging to detect. Here, a particle backtracking (drift) modelling framework provides a viable option to identify spawning locations and the timing of larval hatching based on larvae samples. For this study, only length data on larvae were used. However, analyses to determine larval ages (daily growth increments) are also underway, which can provide an updated age-length relationship. Also, the capelin otolith samples will be analyzed further for trace elements to distinguish differences in the natal origin of the larvae around the Iceland shelf. The subsequent step would be tracking adult capelin to their natal hatching grounds from trace-element analysis of the core area of their otoliths. This information can be used to validate and improve the drift model. The spatial and temporal differences in the growth of capelin larvae, together with estimated spawning locations, can be used to discern habitat-specific contributions to recruitment. Collectively, the study of spawning events and conditions in the early life stage can assist in gaining a better understanding of the recruitment variability observed for the IEGJM capelin stock. Further studies are also recommended to discern the abiotic and biotic environmental drivers of recruitment. In that context, the fact that the three largest year classes of IEGJM capelin since 2000 originate from years when there was no fishery allowed (i.e., a moratorium in 2009, 2019 and 2020) should be given attention.

This research also provides an updated insight into the predation of capelin during its spawning migration along the Iceland shelf. It was shown that the harbour porpoise feeds on capelin during its journey to the spawning grounds. Even though whales are known to be a major predator of capelin, at present, it is difficult to estimate the level of predation by whales during winter because the available data on whale sightings and systematical counting around Iceland does not correspond well in time and space with the capelin distribution. Nonetheless, predation by marine mammals should be given careful consideration as it can have implications for the biomass left behind for spawning. Along its new feeding grounds in autumn, a significant overlap between humpback and minke whales and capelin leads us to infer that capelin are also prey for whales during this season. To confirm this hypothesis, stable isotope analysis from selected whale samples is underway. Overall, these predator-prey dynamics pave the way forward for revising how predation should be considered after the distributional changes of capelin. Further research on this subject is needed, which couples with the recommendations set forth by the International Council for the Exploration of the Sea (ICES) capelin benchmark assessment group in 2022 (ICES 2023).

Recent data on the target strength of capelin is a crucial addition for future improvements in assessing and managing the capelin stock, given the changes observed in the life history of capelin over time. A combination of factors can affect the target strength measurements of capelin, such as fish length, body condition, swim bladder, depth of schools and season. Thus, an average value of the target strength-length relationship may result in imprecise estimates. An average value assumes that the catchability of the acoustic surveys is constant at 1. Preliminary analysis of this relationship based on data collected from this research indicates that the revised relationship will lead to a catchability below 1, making the biomass estimations from the survey precautionary. The importance of this research is recognized, and further studies are recommended as it directly impacts the maximum sustainable yield from the stock.

In conclusion, the knowledge gained from this five-year research project sheds light on the different life stages of capelin and its dependency on the surrounding environment. The multitude of data from all aspects of capelin monitoring and research, i.e., abundance, distribution, growth, recruitment, abiotic factors, and trophic linkages, can be used to develop models and methodology to describe the ecosystem of capelin and its response to abiotic and biotic drivers of change. The eventual goal is to be able to incorporate these data into larger ecosystem models that consider trophic interactions, such as Ecopath with Ecosim, and end-to-end models, such as Atlantis, which are currently under development for Icelandic waters.

This study leads us to make some recommendations for further avenues of research. The importance of the 0-group observations (larval stages) has been elucidated through this study. We recommend further data collection for the early life stages, which has considerable implications for recruitment success. Recommendations are also being made to verify anecdotal evidence of increased spawning of capelin in the northern region. For advancements in survey design and increasing precision of survey estimates, the use of autonomous systems, such as sail drones or gliders can be explored. These systems can be complementary and used to increase survey coverage and capture the patchy distribution of the capelin schools.

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1. Analyzing the route and timing of capelin migration over a quarter century using logbook data

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Abstract

The migration route of capelin along the shelf break from the north and east of Iceland to spawning grounds located south and west of Iceland was investigated using catch data. Fishing vessels usually follow the front of the capelin spawning migration as soon as it appears in fishable concentrations at the beginning of the year. This provides a good opportunity to assess the usefulness of the catch data to research changes in the migration path and timing of this species. The results show that the capelin fishery usually starts in early January along the north and east Icelandic shelf and gradually moves towards the southern spawning area in a clockwise manner. In addition, by analyzing catches over two time periods encompassing more than two decades together, we were able to detect slight changes in the timing of the capelin migration. In recent years, the capelin spawning migration arrived later to the Icelandic shelf compared to earlier years when the fishery started further south.

Keywords: migration route, catch, temporal change

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This extended abstract is based on:

Singh, W., Bárðarson, B., Jónsson, S.Þ., Elvarsson, E., Pampoulie, C. 2020. When logbooks show the path: Analyzing the route and timing of capelin (*Mallotus villosus*) migration over a quarter century using catch data. *Fisheries Research*, *230*, 105653. https://doi.org/10.1016/j.fishres.2020.105653

INTRODUCTION

The capelin fishery in Icelandic waters started in the 1960s, with Iceland, Greenland and Norway sharing the stock (Vilhjálmsson and Carscadden, 2002). The fishery has mainly been conducted by vessels from these nations and the Faroe Islands. For most of the period, Iceland has had the largest share of the fishery (~80% of the Total Allowable Catch (TAC)).

In general, the location of the fishery moves along the spawning migration route of the capelin, targeting the mature part of the stock (Carscadden et al., 2013). The winter fishery can start as early as the first week of January and typically proceeds until the beginning of March. However, the duration of the fisheries depends on the TAC issued, with a higher TAC resulting in an extended fishing season. The spatial patterns in the fishery correspond well to the front of the spawning migration of capelin, as described by previous annual scientific surveys (Carscadden et al., 2013; ICES, 2019). We therefore posit that the fishery closely follows the front of the migration. Thus, we used 26 years of logbook data to assess the timing and the migration path of capelin and examine if there have been changes.

MATERIALS & METHODS

Capelin catch data have been collected in a reliable manner from purse seiners and pelagic trawlers since 1993. These data were recorded by the fishermen in logbooks and were considered reliable because there was good correspondence between the recorded catches and the recorded landings. The data from the winter fishery on the amount of catch, location (latitude and longitude), and gear type from 1993-2018 were compiled. Only data from the Icelandic fleet were used for this study because this fleet had the least restriction on fishing areas. The Norwegian fleet, for example, is restricted to the area east and north of Iceland.

A visual preliminary exploration of the catch distribution plots by year showed a northwards movement starting in 2003, with larger amounts of catches recorded north of 66 °N. Therefore, the data were divided into two time periods, 1993–2002 and 2003–2018, to examine any distributional shifts in the fishery between them. A distribution of the catch intensities was plotted by month for the two time periods. To statistically examine the temporal shift in spatial patterns, the average weighted position of the catches or center of gravity was calculated for calendar weeks 1–12, representing January through March for each period and compared.

A principal component analysis (PCA) was conducted on each monthly subset to test whether catch distribution was different between the two periods. The data contained variables for the center of gravity latitude (clat) and longitude (clon) for each year *x* week combination (weeks 1–4 represented month 1, 5–8 month 2 and 9–12 month 3).

RESULTS

In January, the first month of the winter fishery, a visual comparison of capelin catch distribution showed a pronounced shift northward and an expansion in geographical area in recent years (2003–2018) compared to the earlier period (1993-2002; Figure 1). In March, capelin appeared to be migrating further northward along the west coast of Iceland, with some catches also recorded along the northern shelf of Iceland in recent years compared to the earlier period. For February, no significant difference in migration timing, location, and range was detected between the two periods.

A PCA applied to the estimated center of gravity of weekly catches by month and year showed that the catch distribution in January grouped separately for the two time periods, indicating a clear difference in the distribution of capelin fishery in earlier versus recent years (Figure 2). However, February and March catch distributions do not display any clear difference between the two time periods, indicating that the fishing locations during the middle and end of the fishing season have been consistent over the whole study period (Figure 1).

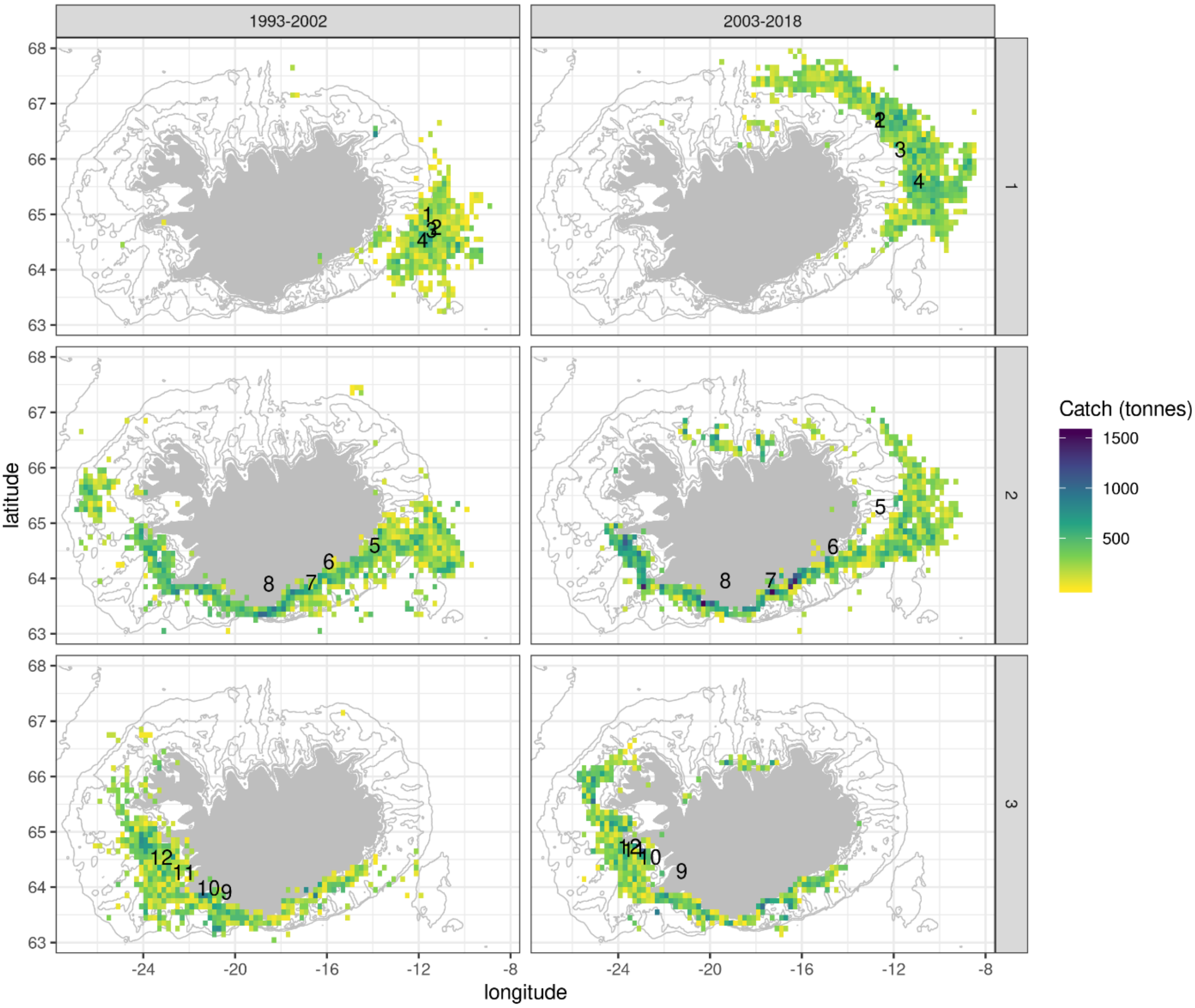

Figure 1. Distribution of catch intensities from the winter capelin fisheries separated by months (1–3, representing January – March) and two time periods (1993–2002 and 2003–2018). The position of the center of gravity of weekly catches is indicated by numbers corresponding to calendar weeks. Adapted from Singh et al. (2020).

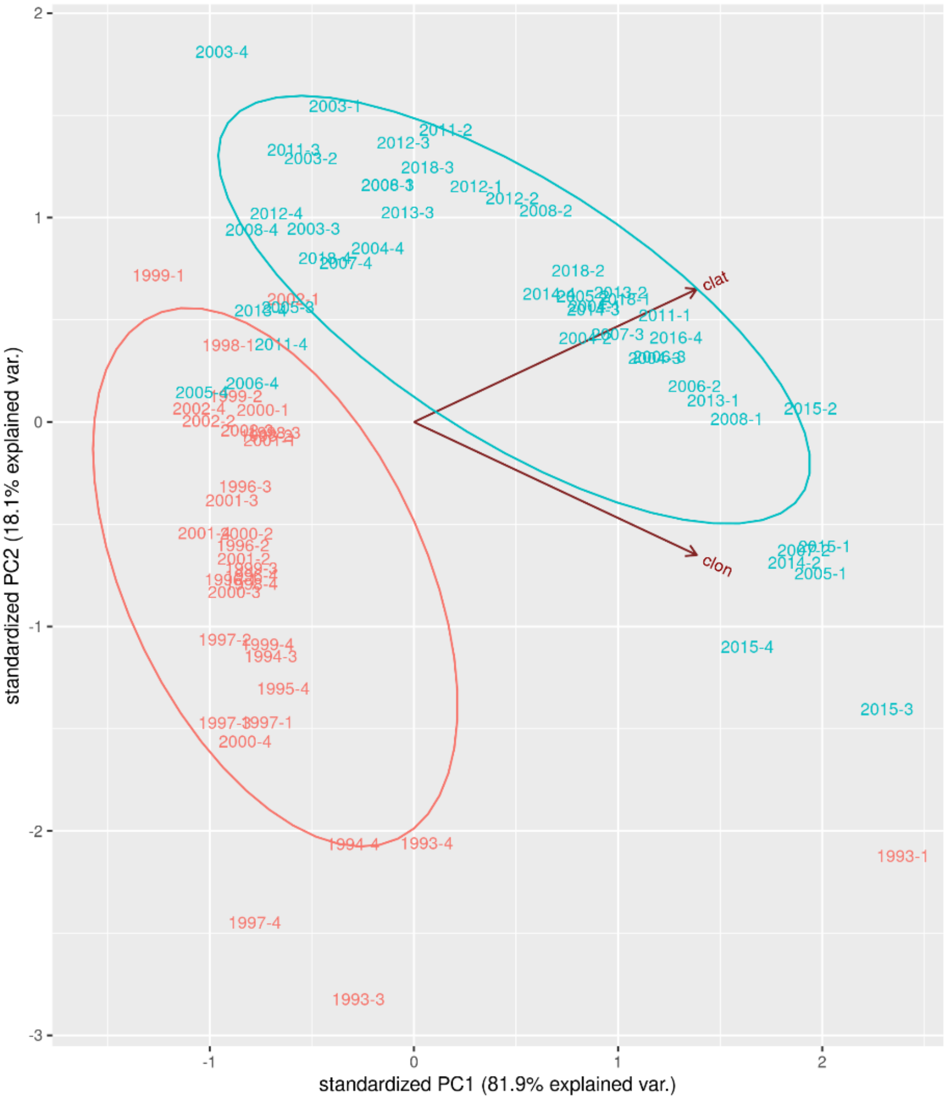

Figure 2. Principal Component Analysis of the center of gravity latitude (*clat*) and longitude (*clon*) of weekly catches per year for January. The lower ellipse indicates calendar weeks 1–4 of period 1993–2002, while the upper indicates calendar weeks 1–4 of period 2003–2018. Adapted from Singh et al. (2020).

DISCUSSION

Due to the specific behavior of the fisheries following the capelin stock, the logbook data were useful for assessing both the migration route and the migration timing of the capelin over a period spanning 26 years. Analysis of catches over this time revealed that the spatial locations of the catches have shifted in recent years (2003–2018) compared to earlier years (1993–2002). During the first month of the fishery in earlier years, the catches were further south compared to recent years. In recent years, during spawning migration, the capelin arrived later to the Icelandic shelf in the north, as evidenced by its presence in areas northeast of Iceland during weeks 1–4. Capelin was nonetheless still following the traditional migration path clockwise around the island and appeared to arrive at the spawning grounds at a similar time during both periods, in calendar weeks 6–7. All these results related to fishery data corroborated what has been shown during the last scientific surveys (ICES, 2019).

This spatial and temporal change in the location of fisheries can be used as an indicator of population distribution change and changed migration timing within this capelin stock. It is well-known that the distribution of both adult and juvenile capelin has been changing over the last two decades. A westward displacement was observed in the distribution during the feeding season in autumn during the late 1990s and early 2000s (Vilhjálmsson 2007; Carscadden et al., 2013). This general distributional shift towards the shelf of Greenland and further away from Iceland during autumn could potentially explain the observed delay in the arrival of capelin into Icelandic waters during the spawning season and, therefore, the observed changes in latitudes reported in the logbook data during weeks 1–4.

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HOW TO REFERENCE THE PAPER?

Singh, W., Bárðarson, B., Jónsson, S.Þ., Elvarsson, B., Pampoulie, C. (2023). Analyzing the route and timing of capelin migration over a quarter century using logbook data**.** In Singh, W., Ólafsdóttir, A.H., Jónsson, S.Þ. & Óskarsson, G.J. 2023 (Eds). *Capelin in a changing environment.* Haf- og vatnarannsóknir, HV 2023-43. (pp. 9-12)

2. Climate driven response of the Iceland-East Greenland-Jan Mayen capelin distribution

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Abstract

Climate change is altering the distribution of marine organisms worldwide. This may in turn affect the overall structure, functioning, and productivity of ecosystems. Pronounced shifts in distribution have been observed for capelin (*Mallotus villosus),* one of the ecologically and commercially important species in the Arctic. This study attempted to discern whether a relationship existed between the altered capelin distribution and the changing physical environmental conditions in the Iceland-East Greenland-Jan Mayen region using a multi-model approach. More specifically, three species distribution models were used to predict hindcasts (pre-shift years 1993-2002) and nowcasts (post-shift years 2003-2019) of capelin distribution based on relationships with temperature, salinity, current speed, net primary productivity, and bathymetry. The predicted probability of occurrence over these two time periods demonstrates that changing environmental conditions have contributed to the modified distribution of this stock. This study provides a solid statistical framework to describe the environmental niche of capelin and its potential responses to changing ocean climate.

Keywords: species distribution models, ocean climate, spatial shift, capelin, feeding distribution, spawning distribution

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INTRODUCTION

Climate change has been shown to profoundly alter the distribution of marine species worldwide (Basen et al., 2022; Champion et al., 2022). Notably, species have gradually moved towards higher latitudes in response to changing climatic conditions, such as rising sea surface temperatures, changes in salinity and receding ice cover (Champion et al., 2022). In the Iceland-East Greenland-Jan Mayen (IEGJM) region, spatial distributional shifts have been observed for capelin (*Mallotus villosus*), one of the ecologically and commercially important species. The distribution of capelin during its feeding season in summer and autumn shifted from the north of Iceland to the east coast of Greenland in the early 2000s (Carscadden et al., 2013a), signifying a pronounced and consistent geographic displacement ever since. Additionally, a delay has been observed in the arrival of the annual spawning migration of capelin into waters north of Iceland in January after 2003 (Singh et al., 2020). Previous studies considering the IEGJM capelin have postulated hydrographic variability as the primary cause of changes in distribution (Valdimarsson et al., 2012; Carscadden et al., 2013b). However, the underlying drivers of changes in capelin distribution and spawning migration timing are still unknown. In this study, we used multiple species distribution models (SDMs) to determine whether the observed shift in capelin distribution and migration timing can be related to the changes in the physical environment.

MATERIALS & METHODS

Data from the annual capelin acoustic surveys in autumn (September-November) and winter (January) were used to compile yearly georeferenced presence and absence data from 2000 to 2019. The capelin is measured down to 500 m. Areas of absence were delineated by the survey tracks along which capelin was not observed (Figure 1). Sea surface (0.5m) temperature, salinity, current speed, and net primary productivity (NPP) were obtained from the E.U. Copernicus Marine Service (CMEMS) (http://marine.copernicus.eu/). Bathymetry data was obtained from the National Oceanographic and Atmospheric Administration (Pante et al., 2022). All variables were averaged within 0.25° x 0.5° latitude and longitude to generate a spatial-temporal grid of capelin and physical environmental data to be used for model fitting and predictions.

A multi-model approach was used by fitting and comparing results across three SDMs: Generalized Additive Models (GAM) (Wood, 2017), Random Forest (RF) (Breiman, 2001) and Support Vector Machines (SVM) (Vapnik, 1999). The data was randomly divided into an 80% training data set on which the models were fitted. The model performance was then evaluated using the 20% test data set. For the predictive performance of the model, the mean area under the receiver operating characteristic curve (AUC) was used (Bradley, 1997). An AUC > 0.75 was set as a criterion for acceptable model performance and predictability. The predicted probability of occurrence was generated using the entire grid of environmental data within the 63°N and 75°N latitude and 38°W and 10°W longitude for winter and averaged across autumn months. A full model with all variables was used for predictions. For each season, predictions were generated separately for the pre-shift years (1993-2002) and the post-shift years (2003-2019) to examine whether the probability of occurrence from the models would reflect the observed shift in capelin distribution.

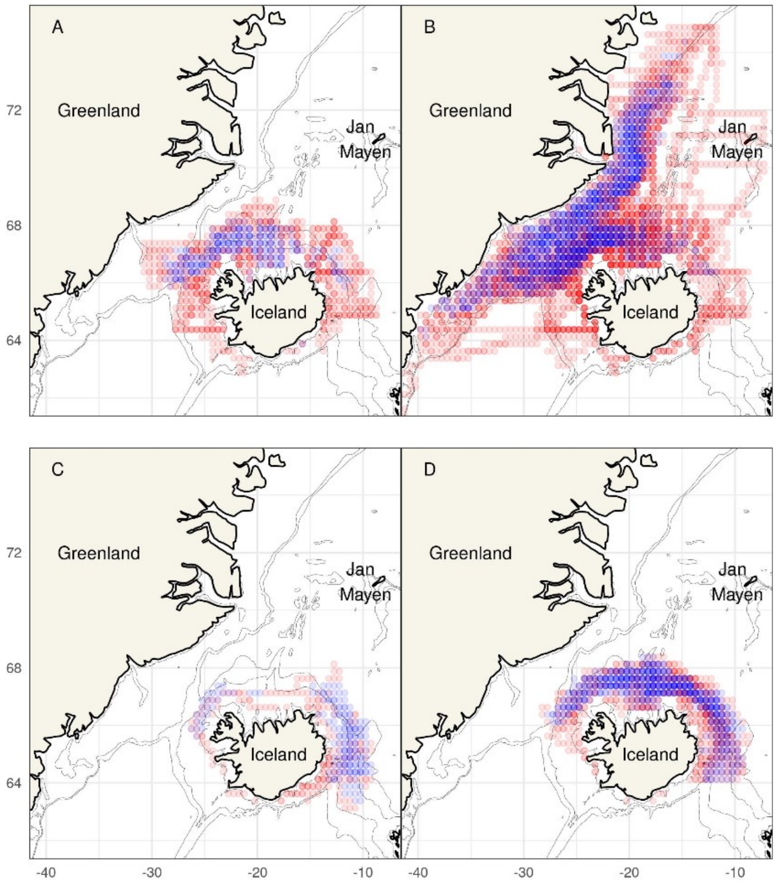

Figure 1. The study area showing the presence (blue) and absence (red) of capelin using the scientific acoustic survey data during autumn (September to November; late feeding season) for pre-shift years (A) and post-shift years (B) and during winter (January; beginning of spawning migration) pre-shift years (C) and post-shift years (D). Isobaths are shown at 100, 500 and 1000m.

RESULTS

For the autumn distribution, the RF (AUC = 0.85) and SVM (0.81) models performed better than GAM (0.75) in predicting the occurrence probabilities of capelin for the pre- and post-shift years and were able to discern the spatial shift in the distribution. Model predictions showed a higher probability of occurrence in the north of Iceland for the pre-shift years compared to the post-shift years when the occurrence probabilities were higher along the east coast of Greenland (Figure 2). Salinity, temperature, and NPP were influential variables, followed by current speed. The optimum temperature and salinity conditions for capelin presence were found between -1 to 4 °C and 32-33 PSU, showing a preference for colder, less saline waters. The probability of occurrence also coincided with areas of high current speed of 0.1 – 0.4 m/s with depths ranging from about 100 to 1000 m and in areas of high NPP.

For the winter distribution, the RF (AUC = 0.79) and SVM (0.75) model performance was better than GAM (0.7). Higher occurrence probabilities were predicted in the north of Iceland for the post-shift years for all models. The occurrence probabilities from the SVM model were higher in the south-eastern part of Iceland for the pre-shift years (Figure 3). A dome-shaped relationship was found with temperature, indicating a preference for a specific thermal range between 1- 4 °C. A positive relationship with salinity was found with the highest probabilities of occurrence between 34.5 and 35.5 PSU. A dome-shaped response with depth indicated that capelin schools are primarily found in association with the continental shelf edge around 500m depth during winter in high current speeds of 0.1 – 0.4 m/s and low NPP.

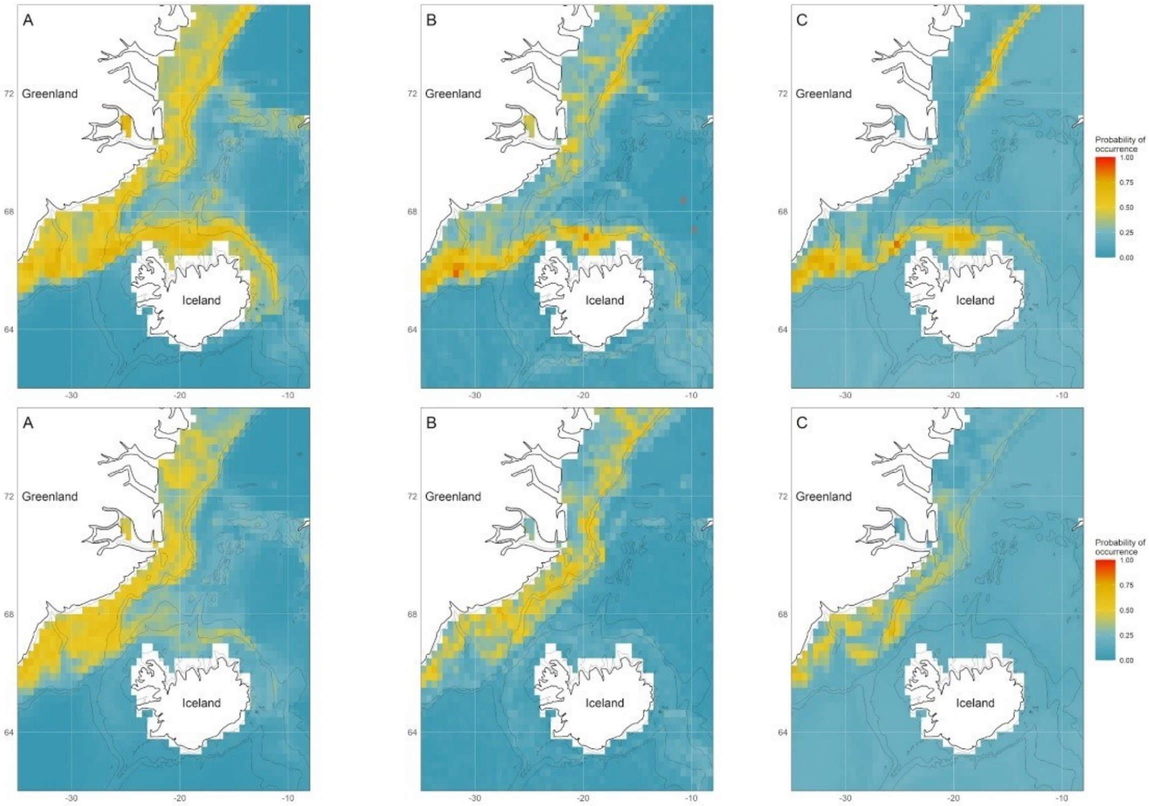

Figure 2. Predicted probability of occurrence of capelin during autumn (September – November) using GAM (A), RF (B), and SVM (C) for the pre-shift years (1993-2002; upper panel) and post-shift years (2003-2019; lower panel). All models were able to detect the spatial shift where the RF model had the best predictive performance. Isobaths are shown at 100, 500 and 1000m.

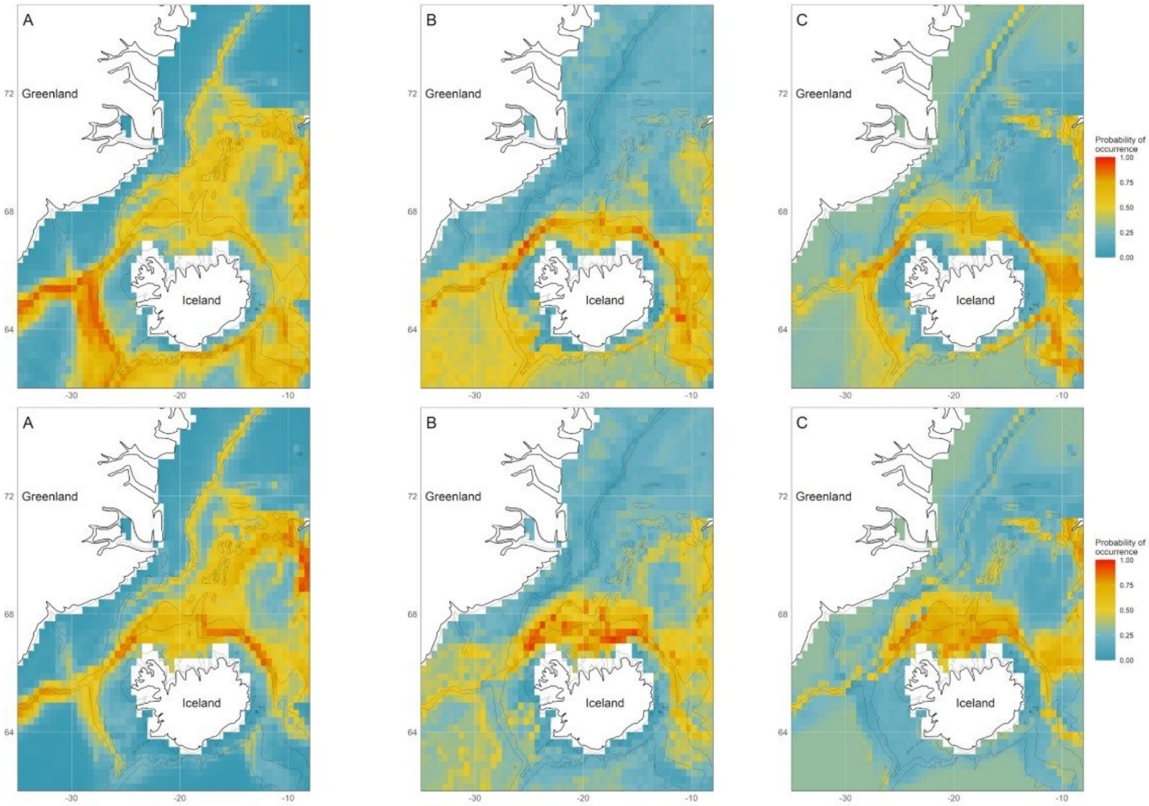

Figure 3. Predicted probability of occurrence of capelin during winter (January) using GAM (A), RF (B), and SVM (C) for the pre-shift years (1993-2002) (upper panel) and the post-shift years (2003-2019) (lower panel). The RF and SVM models were able to detect the delay observed in the arrival of capelin to the spawning grounds in later years. Isobaths are shown at 100, 500 and 1000m.

DISCUSSION

High-resolution data on environmental conditions and capelin presence was analyzed to identify the key drivers capable of explaining the spatial shifts observed in capelin distribution. The model predictions during the late feeding season in autumn for the pre- and post-shift years resemble the marked shifts delineated in Carscadden et al. (2013b). According to the combination of physical abiotic factors identified, suitable conditions existed in the north of Iceland and Denmark strait in the earlier period, but in concert with changing environmental conditions, this area seems to have become unsuitable for capelin feeding. The shift of the capelin stock away from this area is consistent with the exceptionally high salinity in the region because of the weakened sub-polar gyre around the early 2000s (Hjálmar et al., 2005). It is also consistent with the increased temperature in the region because of increased ocean heat transport in the early 2000s (Tsubouchi et al., 2021; Jónsson and Valdimarsson, 2012).

During spawning migration, capelin is known to follow the continental shelf edge north of Iceland (Olafsdottir and Rose, 2012). This observation is supported by our results showing that bathymetry was a prominent variable in explaining the presence and absence of capelin during January. Given that bathymetry does not vary, we postulate that the delay in the arrival of the capelin spawning migration in Icelandic waters in January, as delineated using logbook data (Singh et al., 2020), is primarily due to changes in temperature and salinity which were ranked as important variables in the SVM and RF models. Increased distance between the feeding and spawning area could also be a potential contributing factor.

Surface environmental measurements were considered sufficient in autumn because the surface layer represents a crucial part of capelin feeding habitat. In winter, the surface layer is representative of lower depths as the water column is homogenous to approximately where capelin is present. The multi-model approach used in this study has provided a solid statistical framework to describe the environmental niche of capelin in the IEGJM geographic range. With reliable climate forecast models, short to medium term projections using this approach can be generated of capelin distributions into the future. These projections can be highly useful in providing prior knowledge of any potential climate-induced geographical range shifts.

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3. Changes in life history traits of capelin consecutive to a spatial shift

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Abstract

It is well known that environmental conditions can alter life history traits of fish populations. Variability in life history traits of fish have long been used as a measure of population health and of its capability to adapt to changing conditions. Using data from the autumn capelin stock assessment surveys (2000-2021), we investigated changes in length- and weight-at-age, body condition, and age- and length-at-maturity of capelin over two decades. During the beginning of this period, the capelin distribution in autumn shifted from the north of Iceland to the east of Greenland. The results showed that length-at-age, weight-at-age, body condition, and length-at-maturity increased over time, whereas age-at-maturity remained stable. The effect of abundance, sea surface temperature and surface salinity on estimates of length and weight were assessed using a spatial-temporal GAM model. Abundance and temperature were identified as key drivers of the observed life history trait changes. The observed negative relationship between abundance and length and weight indicates a density-dependent effect where body size has potentially increased with decreased intra-specific competition. The smaller individuals prefer warmer conditions, while the larger individuals prefer colder conditions.

Keywords: life history traits, *Mallotus villosus*, condition, length-at-maturity, spatial temporal modelling

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INTRODUCTION

Life history traits (LHT) of fish comprise of measurements such as length- and weight-at-age, length- and age-at-maturation, and body condition. Spatial and temporal variation in LHT can be used to understand the response of fish populations to natural or anthropogenic changes in their environment (Beukhof et al., 2019). For example, large-scale geographic shifts can cause variations in LHT because of exposure to new physical environmental conditions and changes in food supply (Cardinale et al., 2002). Capelin has a short life span of 3-5 years and grows up to 20 cm in length, making it more prone to fluctuations in the physical environment (Perry et al., 2005) . The geographic shift in capelin from the north of Iceland to the shelf areas of east Greenland around 2000 is well-documented (Vilhjálmsson, 2007) and captured in the autumn scientific surveys where the survey area has been adapted over time in response to the observed distributional shift. Warming conditions have also been reported for Iceland-East Greenland-Jan Mayen region around this time (Tsubouchi et al., 2021). The effect of the distributional shift on capelin LHT was unknown. Therefore, biological data spanning two decades was used to understand the potential life history response of capelin to environmental conditions in their new habitat on the east Greenland shelf.

MATERIALS AND METHODS

Acoustic and biological samples from the annual autumn survey for the years 2000-2021 were used. During the surveys, a random sample of 100 capelin were sampled at each trawl station to collect data on the length, weight, age, sex, and maturity stage of each fish. The 4-year-old fish were removed from our analyses because of the low number of observations. Data from 2002 was also excluded because of missing age information. To make the samples representative of the population, they were weighted with abundance (Gjøsaeter, 2000). Based on an established target strength and length relationship for this capelin stock (Vilhjalmsson, 1994) and length data from the samples, the backscattering energy was converted to population abundance (numbers of fish) within a defined spatial grid of 0.25° x 0.5° latitude and longitude by year creating a spatial temporal time series. Because acoustic data were not available in a standardized format prior to 2000, the time series was limited to the years defined above.

First, overall long-term annual trends in length-at-age, weight-at-age, relative body condition (Kn), length-at-maturity (L50), and age-at-maturity (A50) were determined for both males and females. The L50 and A50, defined as size and age at which 50% of the sampled fish are mature, were used to examine long-term changes in maturation between sexes. These parameters represent a proxy for the reproductive potential of a stock as larger females produce larger eggs (Penton and Davoren, 2013) and subsequently larger larvae (Chambers and Leggett, 1996).

Second, the spatial-temporal time series of length and weight were divided into two time periods, 2000-2009 (Period 1, P1) and 2010-2021 (Period 2, P2). Since 2010, the monitoring surveys have shifted completely to the shelf areas of east Greenland. To evaluate whether any environmental fluctuations could potentially explain changes in length and weight within these two periods, we used two independent Generalized Additive Models (GAMs) (Wood, 2011). The explanatory variables tested were abundance, sea surface temperature and sea surface salinity. Due to confounding effects in the data introduced by the shift in the geographical distribution, which consequently influenced the timing of the survey and area coverage, the model formulation considered the response within each period separately. This creates an entirely separate relationship for each level of the period, enabling us to study the response of the traits for each period distinctly. Surface (0.5 m) temperature and salinity were obtained from the E.U. Copernicus Marine Service (CMEMS) (http://marine.copernicus.eu/).

RESULTS

There was an overall increase in both length- and weight-at-age for both sexes over time, especially for older ages ($p < 0.001$). The increase in length was steeper for males than females for age 2 (Figure 1 A, B). The increase in weight was steepest for age 2 males. For females, ages 2 and 3 showed a similar increase in weight for the whole time series (Figure 1 C, D).

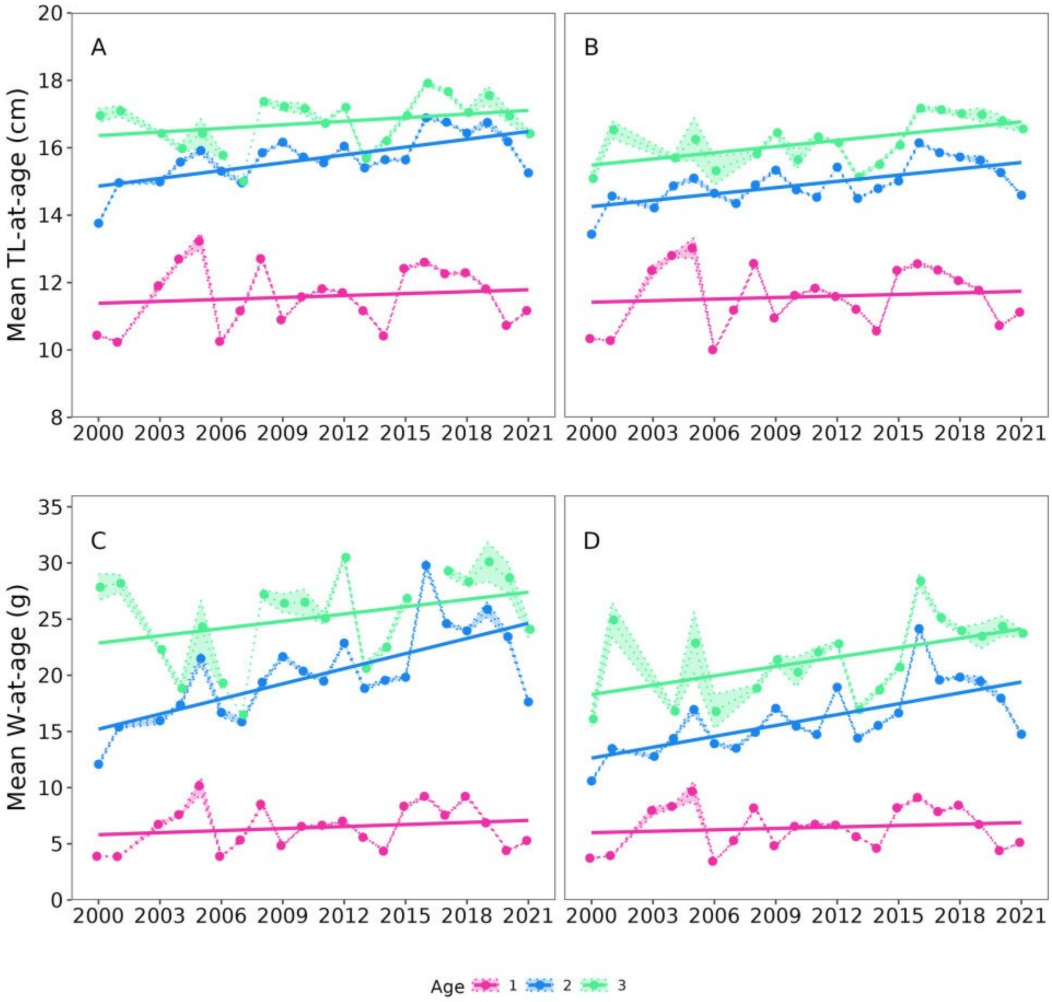

Figure 1. Long-term changes in the life history of capelin sampled during autumn from 2000 to 2021 showing yearly fluctuations and overall trend. Mean length-at-age (TL-at-age) for males (A) and females (B), and mean weight-at-age (W-at-age) for males (C) and females (D) are shown with a 95% confidence interval.

The relative condition of capelin was higher after 2009, with average values in general above 1 for both sexes in comparison to 2000-2009, when the values were mostly below 1 (Figure 2).

The L_{50} showed an overall increasing trend for both sexes ($p < 0.001$; Figure 3 A). In contrast, A_{50} was stable for both sexes over the time series (Figure 3 B). Estimating L_{50} and A_{50} was not possible in 2003 because of inadequate measurements of mature fish.

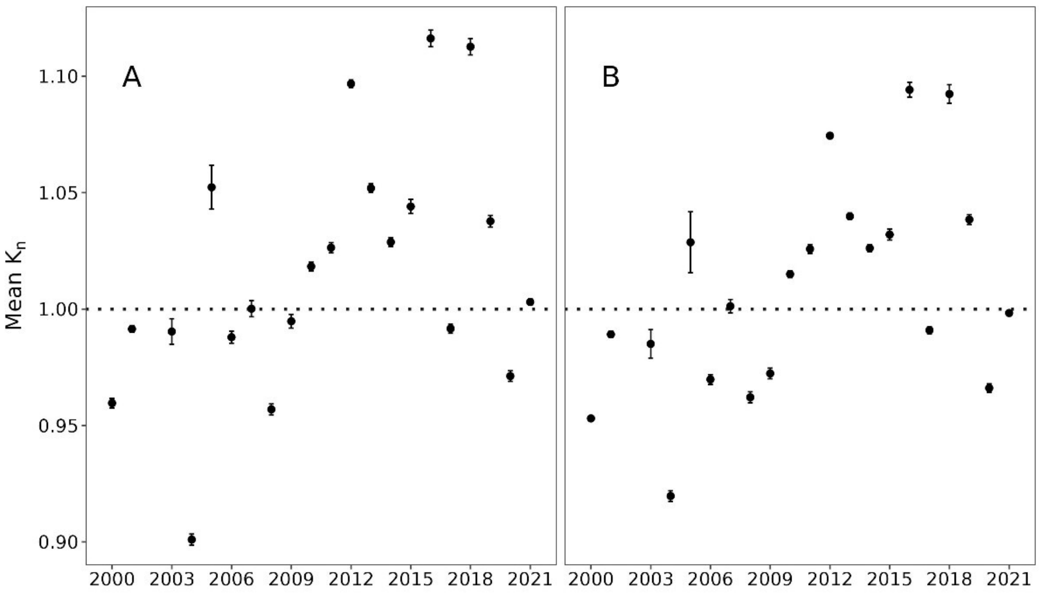

Figure 2. Long-term changes in mean relative condition for male (A) and female (B) capelin. Dashed line indicates the fish condition status (poor < 1 and good > 1).

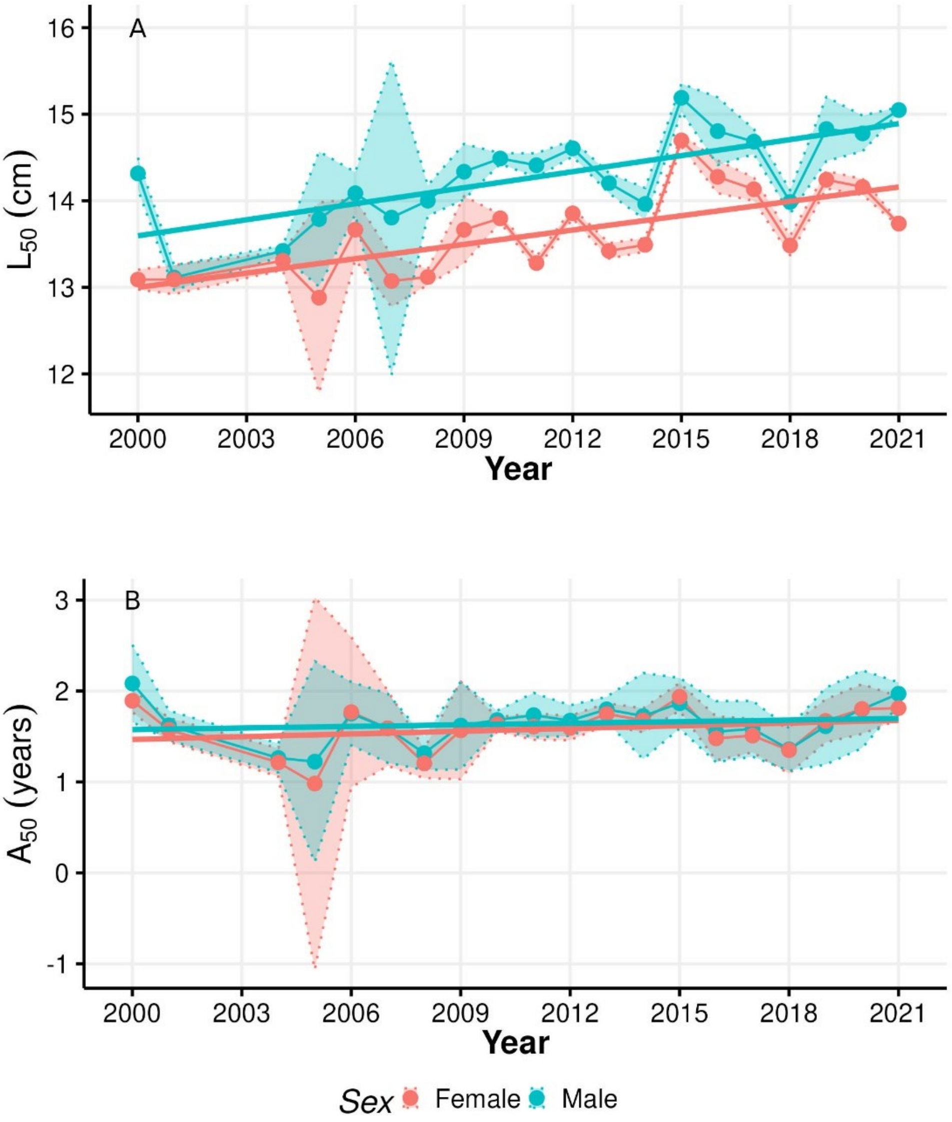

Figure 3. Long-term changes in length-at-maturity (L50) (A) and age-at-maturity (A50) (B) for males (blue) and females (red) with a 95% confidence interval. The CI is high for 2005-2007 because of a smaller sample size.

For the spatial-temporal GAM model, similar relationships between response and predictor variables were observed for both length and weight models (Figure 4). A negative relationship with abundance and temperature was observed for both periods, i.e., both length and weight increased when abundance and/or temperature decreased. Despite some significant relationships, the models explained a relatively low degree of deviance (27.8% for length and 28.2% for weight).

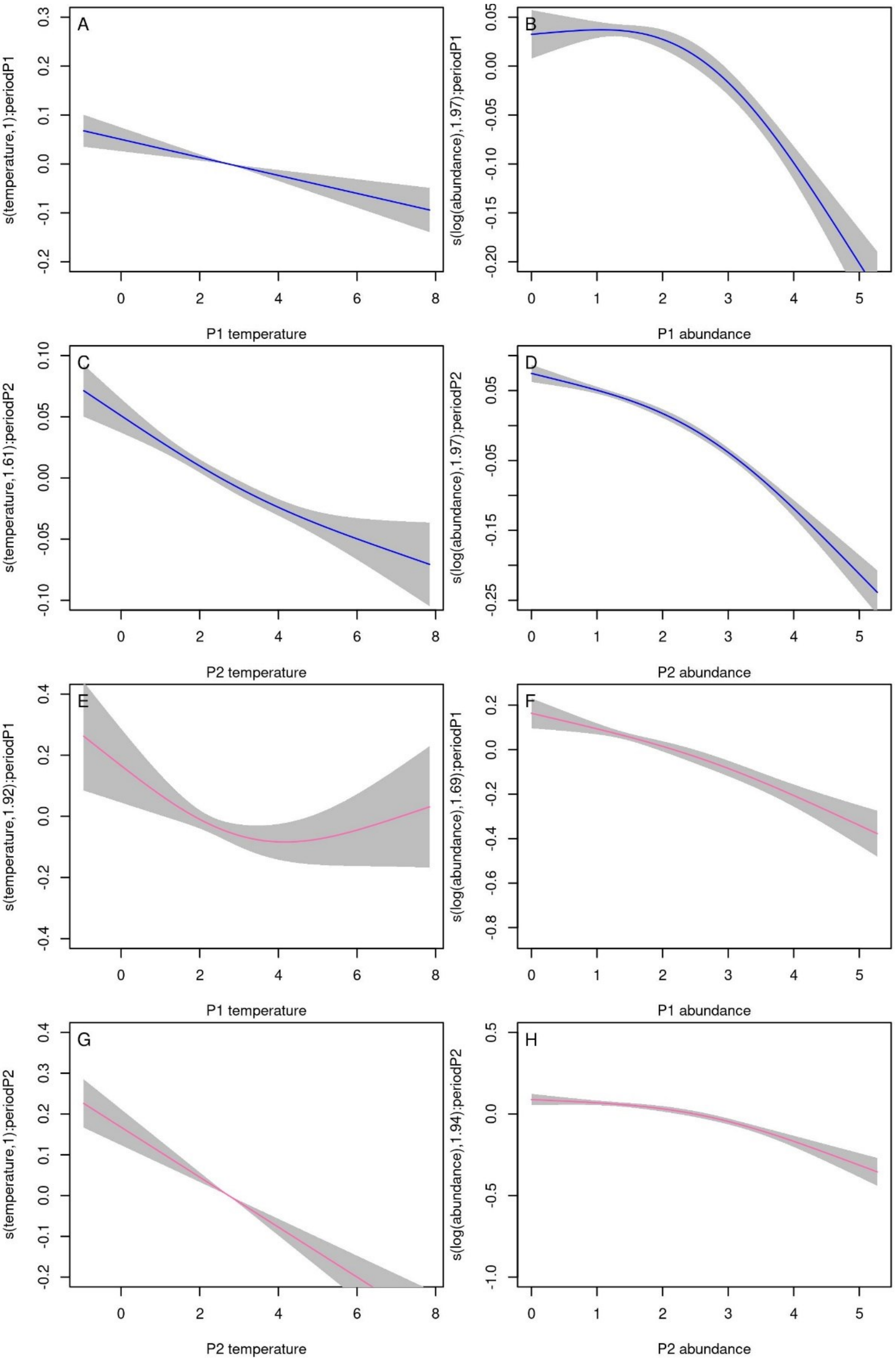

Figure 4. Response curves from the GAM length model (blue; A, B, C, D) and GAM weight model (pink; E, F, G, H) showing how the predicted length changes with the change in temperature and abundance for period 1 (P1: A, B) and period 2 (P2: C, D), and how the predicted weight changes with the change in temperature and abundance for period 1 (P1; E, F) and period 2 (P2; G, H).

DISCUSSION & CONCLUSION

This study demonstrates that the LHT of capelin has changed over the last two decades. An overall increase in length and weight was observed over the years, especially in older ages. Notably, body condition has also improved, implying an increase in the overall fitness of individuals during the study period. Since the early 2000s, the biomass of the capelin stock has generally been smaller than before, leading to lower total allowable catch and yield. While the reduction in biomass remains poorly understood, the increase in length and weight indicates a density-dependent effect where the size and condition of organisms have improved over the years because of less intra-specific competition and ample availability of food (Arranz et al., 2019). Typically, warmer temperatures are associated with faster growth (Rijn et al., 2017, Wang et. al., 2020). The negative relationship of length and weight with temperature for both periods indicates that smaller individuals are found in warmer conditions, which can facilitate faster growth. On the other hand, the larger, heavier individuals prefer colder conditions. This could be an adaptive behaviour to conserve energy before the onset of spawning migration in winter. The proxy of the reproductive potential of the stock also showed improvement with increasing L50. However, the environmental factors considered in this study only partially explained the variations observed in the length and weight of capelin. Further analysis is needed to consider the effect of other ecological factors, such as food availability and age- specific responses. By investigating changes in LHT, the adaptability of capelin to biotic and abiotic habitat changes can nevertheless be better understood.

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4. Effects of environment on distribution of capelin (*Mallotus villosus*) early life stages

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Abstract

Ecological factors, such as temperature, food, and suitable currents for the transportation of eggs and larvae to favorable nursery areas, can affect the survival of early fish life stages and can have implications for recruitment. Capelin is an important forage fish found in sub-Arctic and Arctic waters, with the Iceland-East Greenland-Jan Mayen stock spawning primarily off the south and southwest coast of Iceland. After hatching, larvae drift with currents to their nursery grounds north of Iceland and onto the East Greenland shelf. Our objective was to study the influence of environmental factors on the distribution, density, and growth of capelin larvae from year classes spawned in the years from 2017 to 2020 in Icelandic waters to enhance understanding of recruitment processes. Our results showed a high density of larvae south and west of Iceland in May and that warmer waters (> 6°C) had a negative effect on capelin larvae density. A weak positive relationship was evident between the density and chlorophyll-a levels. We observed that some large larvae (standard length > 30 mm) had reached the nursery areas in western and northern Iceland by May. However, we also found newly hatched larvae (< 10 mm) in all areas, especially in eastern Iceland.

Keywords: survival, early life stages, arctic fish, spawning grounds

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INTRODUCTION

Several factors have been found to impact recruitment success, such as environmental changes, stock size, prey availability, predation, and larvae transport (e.g., Carscadden et al. 2013, Endo et al. 2021, Gabellini et al. 2023, Gjøsæter et al. 2015). Overall, the interaction between spawning grounds and period, environmental conditions, and water masses play an important role in larval survival and drifting to nursery areas (Silve et al. 2023). Icelandic water masses are dominated by the cold and less saline East Greenland Current and East Icelandic Current in the north and warm and saline Atlantic water in the south (Vilhjálmsson 2002; Jónsson and Ólafsdóttir 2021).

Capelin (*Mallotus villosus*) is a key forage fish species in sub-Arctic and Arctic waters and is also of high commercial value (Carscadden et al. 2013). These small forage fish play an essential ecological role, connecting different trophic levels as they feed on secondary producers and are vital prey for predatory fish, whales, and marine birds (Vilhjálmsson 2002). Year class size is considered to be established during their first winter of life and recruited to the stock at age 1 (Vilhjálmsson 2002). During the last two decades, capelin year class size at recruitment (age 1) has been highly variable and ranging from 5–141 billion individuals (2002 and 2019 year-classes, respectively, ICES 2023). For the four-year classes included in the current study, larvae that hatched in 2017 to 2020, year class size at recruitment was 12, 83, 141, and 86 billion, respectively (ICES 2023).

Focusing on the importance of larval survival and drift to nursery areas, the objectives of this study were to: i) estimate interannual variation in the density and distribution of capelin larvae around Iceland from 2017 to 2020; ii) estimate the effect of *in situ* sea temperature and chlorophyll-a on larvae density and distribution; iii) and to analyze the larvae size distribution around Iceland.

MATERIALS AND METHODS

Capelin larvae were collected annually in May from 2017 to 2020 at haphazardly selected, fixed hydrographic stations and opportunistic sampling stations during MFRI surveys around the Iceland shelf (Table 1). Larvae were sampled using the Gulf 7 net (0-60m) with a flowmeter attached at the entrance of the net to measure the volume of filtered water. Capelin larval density was estimated by the number of larvae collected in each station divided by the filtered water volume (m^{-3}).

Temperature and salinity were recorded with depth (CTD) at all stations, and water samples were collected to measure the chlorophyll-a (Chl-a) levels at 0, 10, 20, 30, and 50m depth. We estimated the mean temperature from 0 to 60m depth and average of Chl-a (µg/l) for each station in all the layers combined. Larvae distribution was studied for five main areas, so-called Bormicon areas, using a suggested model to identify species interaction in Icelandic waters (Stefánsson and Pálsson, 1997)

A generalized additive model (GAM; R package mgcv [Wood, 2011]) was used to evaluate the effect of *in situ* environmental parameters (temperature and Chl-a) on the interannual density of capelin larvae. Chl-a was used as a proxy of food concentration in the area where capelin larvae were collected. Year was added as a partial effect so that each year could be evaluated independently.

Table 1. Number of stations using GULF 7 net among years and areas.

Year/Area	Southwest	Northwest	North	East	South
2017	7	22	17	32	19
2018	6	31	23	26	26
2019	5	34	20	25	21
2020	5	24	21	23	17

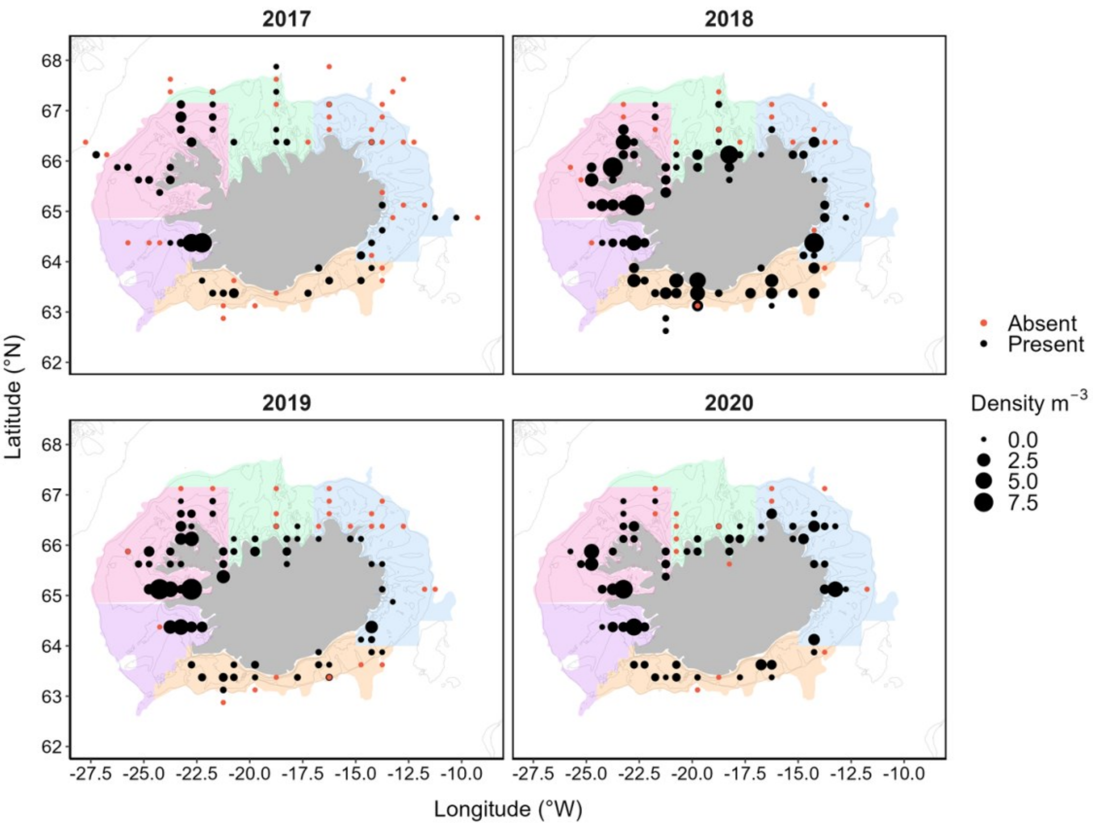

Figure 1. Spatio-temporal presence and density of capelin larvae around Iceland from 2017 to 2020. Stations without capelin larvae are also presented (red circle). Symbol size represents the larvae density. The Bormicon areas are also presented (southwest in purple, northwest in magenta, north in green, east in blue, and south in orange). Stations located outside the delimited areas were included in the nearest Bormicon area.

RESULTS

Larvae density and distribution varied interannually. Overall, the highest average density of capelin larvae was recorded in 2018 (mean = 1.08 ± standard deviation = 1.80 m^{-3}), followed by 2019 (0.79 ± 1.68 m^{-3}), 2020 (0.68 ± 1.28 m^{-3}), and 2017 (0.45 ± 1.42 m^{-3}), only including stations when capelin larvae were present. Differences in total density were also recorded among the areas within years ($p < 0.05$). The highest average density of larvae was recorded in the southwest in 2017 (3.65 ± 1.28 m^{-3}), south in 2018 (1.28 ± 1.33 m^{-3}), and again in the southwest area of Iceland in 2019 (2.39 ± 1.42 m^{-3}) and 2020 (1.64 ± 2.22 m^{-3}) (Figure 1).

The GAM explained 52.5% of the variance in larvae density. The density of larvae declined in waters warmer than 5-6°C for all years except 2020 ($p = 0.145$) and increased significantly as Chl-a concentration increased for 2017 but not in 2018 to 2020 ($p > 0.05$) (Figure 2).

The standard length of capelin larvae ranged from 4 to 62 mm, and the majority of samples (82%) were dominated by small larvae (< 20 mm). Larger larvae (> 20 mm) were collected mainly in the north and northeast and a few east of Iceland (Figure 3). A large amount of small (< 10 mm) and newly hatched larvae were recorded east of Iceland.

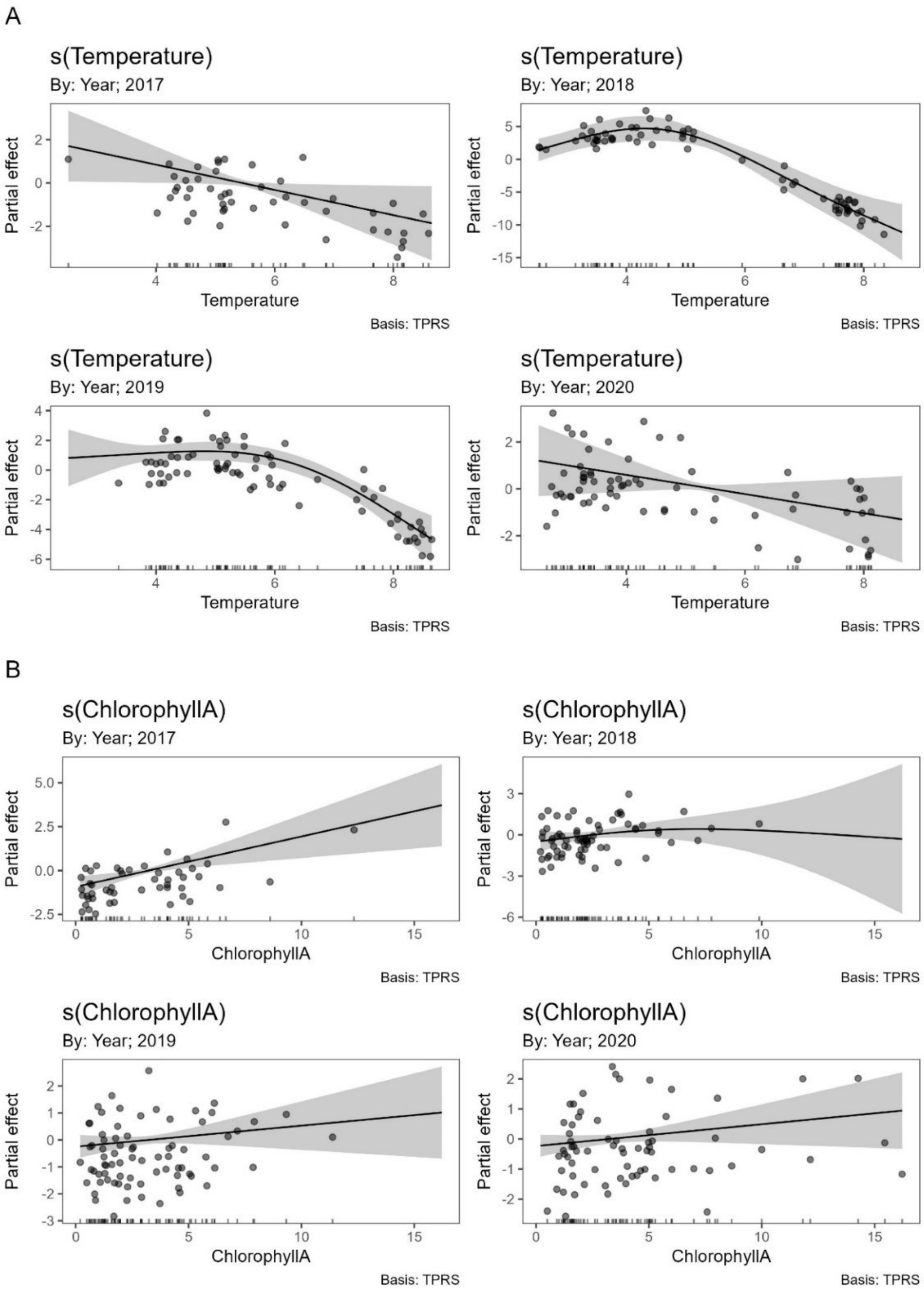

Figure 2. Effect of temperature (A) and chlorophyll-a levels (B) on the density of capelin larvae from 2017-2020 using a GAM.

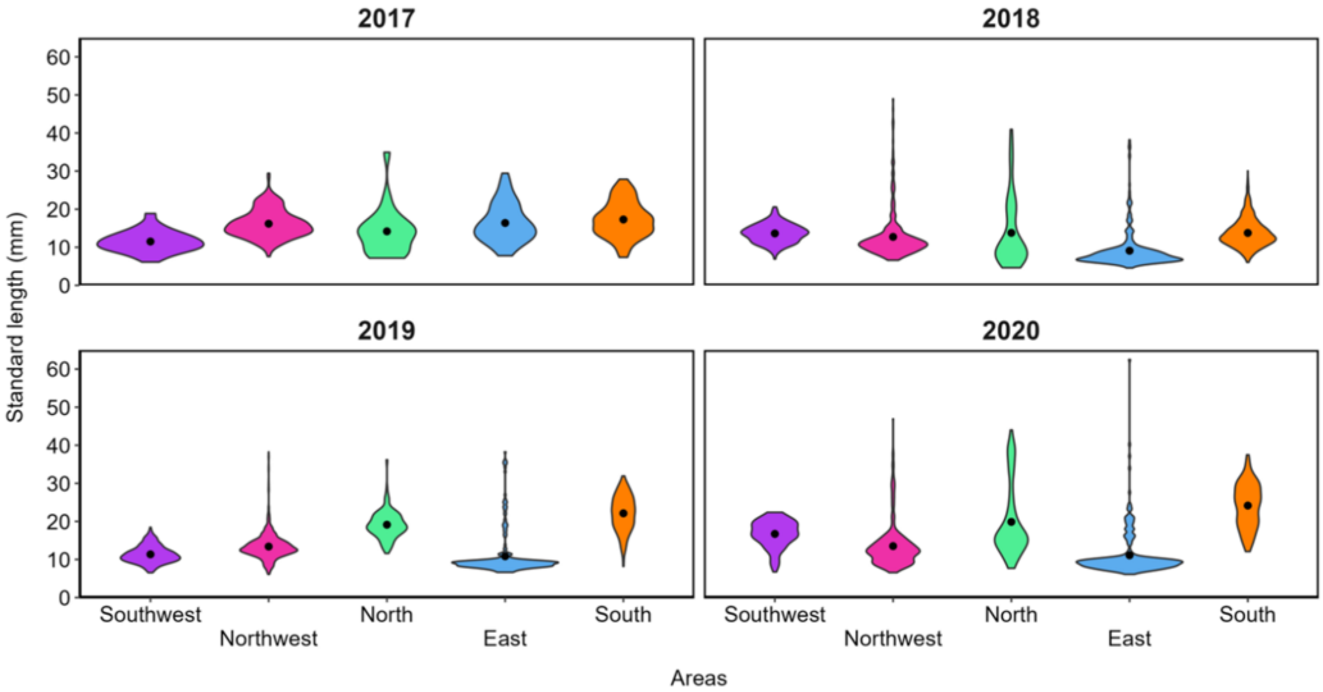

Figure 3. Capelin population length distribution per location (colored violin, a mix of a boxplot and density distribution) over the sampling years (2017-2020) as well as mean (black dots).

DISCUSSION & CONCLUSION

Our study showed an interannual variation in capelin larvae density in May between the four years (2017 to 2020). The south and southwest areas of the Iceland shelf are still the main spawning grounds (Vilhjálmsson 2002). We also found newly hatched larvae in all areas, especially in the south. According to Gunnarsson & Þórisson (2012 and references therein), capelin spawns all around the Iceland shelf. However, the larvae hatched to the north and east of Iceland have been considered to have little contribution to the population.

The negative correlation of capelin density with temperature indicates that temperatures above 6°C are above the optimum, but not prohibitive, for capelin larvae. It is unclear whether the higher temperature directly influences larval survival and thus density, or if capelin tends to select cooler spawning grounds, resulting in lower larval density due to lower spawning intensity at the nearby spawning grounds.

Recent drifting simulations (Jansen et al. 2021) showed that the spawning period (and subsequently hatching time) and location play a substantial role in the subsequent drift of the larvae. Larvae derived from west and northwest spawning grounds drifted westwards, while larvae from northern spawning grounds drifted eastwards. Position in the water column also impacted drift, with larvae located at the surface tending to drift more westwards in comparison with those within the mixed layer depth.

The selection of spawning grounds is complex. Adult capelin need to find suitable spawning areas to maximize the probability of offspring survival. However, migration around Iceland costs energy; thus, individual capelin can only migrate as far as their energy store will allow (McBride et al. 2015). Predation risk is also of concern; the further they migrate before spawning, the greater the risk of predation before they are able to spawn. As they are a shoaling species, the behavior of conspecifics may also influence the timing and location of spawning. Thus, selecting a spawning site relies on a suite of intrinsic and extrinsic factors.

Overall, newly hatched capelin larvae (< 10 mm) were found in all sampled areas on the Icelandic shelf, indicating that capelin is spawning all around Iceland. The location of spawning grounds may partially reflect the parental energy but is likely influenced by prevailing environmental conditions. The subsequent conditions experienced by the larvae after hatching appear to affect survival.

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5. Cultivation of capelin in the Aquaculture Research Station in Grindavík

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Abstract

In 2021, an experiment was conducted on the rearing of capelin larvae at the Aquaculture Research Station (ARS) in Grindavík. The objective of this experiment was to examine whether it was possible to rear capelin larvae under farming conditions and produce juveniles that could be used in laboratory studies. The cultivation methods, which were adapted from cod farming techniques, were found to be successful as we managed to rear and monitor the growth of the capelin from hatching to adulthood. In the experiment, the capelin, which were fed in moderate excess at stable 7°C, reached maturity as early as one year after hatching. After the first year, growth rates slowed down, and at the end of the experiment (681 days from hatching), the capelin were close to their estimated maximum length of 18.7 cm.

Keywords: capelin, cultivation, hatching, growth rate

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INTRODUCTION

Studies on captive capelin have a relatively long history, originating with the successful spawning of capelin in captivity in Russia in 1958 (Pozdnyakov, 1959). Since then, research on capelin has been conducted in laboratory settings and outdoor enclosures, covering a wide range of topics including development, spawning, growth (e.g. Friðgeirsson 1976; Moksness 1982; Christiansen et al., 2008).

These previous studies are, however, limited to the use of capelin of wild origin and have only been performed during egg- and larval stages, or with captive adults. This report presents the first successful cultivation of capelin from fertilization to adulthood in a land-based intensive aquaculture system.

MATERIALS AND METHODS

The experiment began on March 5th, 2021, when capelin eggs and sperm were collected from newly caught fish on board a commercial fishing vessel (Vikingur AK 100). Upon landing, the eggs were transported to the ARS, where the eggs were distributed over the bottom of a 3000-litre tank. The eggs hatched 30 days after fertilization on April 5th. In this first attempt, the number of newly hatched larvae was estimated to be 3000 – 5000 individuals.

The rearing of the capelin larvae was based on rearing methods previously used at the ARS for the rearing of Atlantic cod, with minor adjustments. In the initial stages of the rearing, live rotifers (*Brachionus rotundiformis*, 85 – 150 µm) were used as the first feed. Because capelin larvae are very small and have small mouths, it is crucial to start their feeding with small zooplankton. As the larvae grew, they were provided with larger rotifers (*Brachionus plicatilis*), followed by Artemia (*Artemia salina*), and eventually dry feed.

The capelin used in the experiment presented here were reared at a constant temperature (7°C) and always had ample access to food. The larvae were reared under simulated natural light conditions until day 255, but from that point until the end of the experiment on day 681, the capelin were reared under constant 24-hour daylight.

The average length of the experimental capelin was determined 34 times from hatching until day 681 through measurements of the total length of 5 to 35 randomly selected fish, except on the last day when all fish were measured. The sample sizes prior to the final measurement were intentionally kept at minimum due to the sensitivity of capelin to handling.

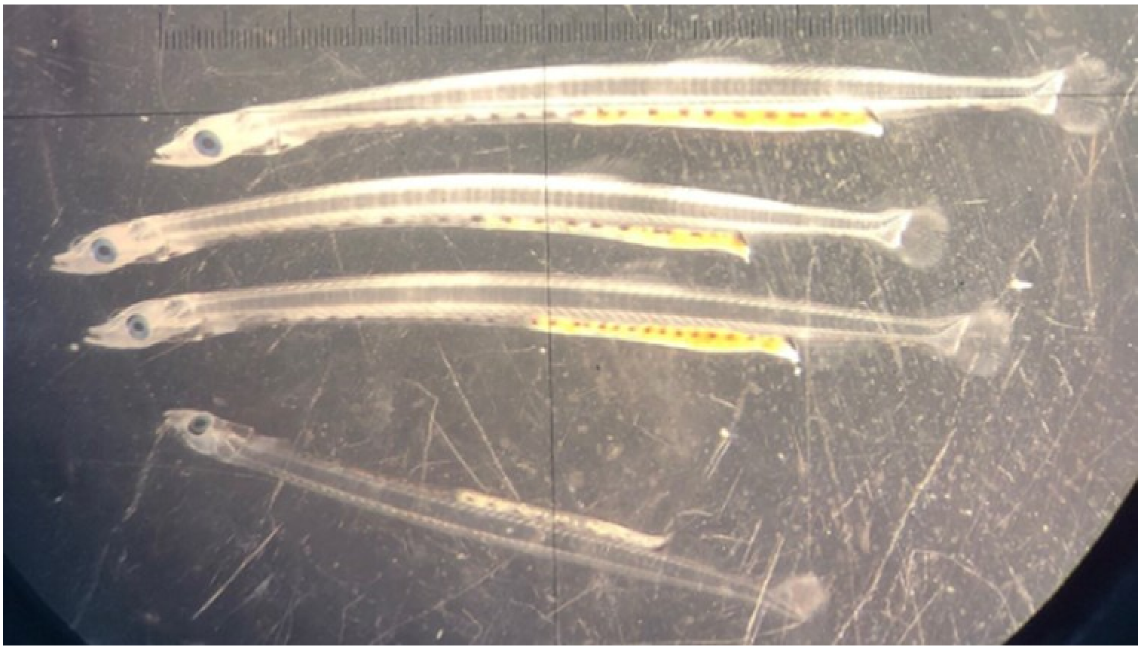

Figure 1. Capelin larvae 39 days from hatch. The three largest capelin larvae are around 21 mm in size, while the smallest one is 16 mm. The larger three feed on Artemia, whereas the smaller one does not handle such large prey and exclusively consumes rotifers.

RESULTS AND DISCUSSION

During the first year, the experimental capelin maintained a linear growth rate at 0.36 mm/day (Figure 2A), in line with the growth of wild capelin larvae in Icelandic waters (0.3 – 0.4 mm/day, Ólafsdóttir and Andersson, 2010). Since the experimental capelin were reared at a constant temperature and provided with a continuous and ample food supply, their growth rate, over the long term, was faster than in nature. When the capelin reached one year of age, their growth began to slow down (Figure 2B). Eventually, their maximum size was similar to that of wild Icelandic capelin (Figure 2C).

The rapid growth resulted in the first capelin reaching sexual maturity at just one year of age, which is two years ahead of wild capelin in Icelandic waters. In May 2022, the capelin's life cycle was closed when the first generation of experimental capelin larvae were hatched from eggs collected from the reared capelin.

Mortalities were recorded from day 255 until the end of the study. Overall, 62.4% of the capelin died in that period. The primary cause of death was attributed to handling procedures associated with fish measurements and transfers between tanks.

By successfully establishing capelin cultivation methods for all life stages, opportunities for research in its biology and ecology across its lifespan are now within reach.

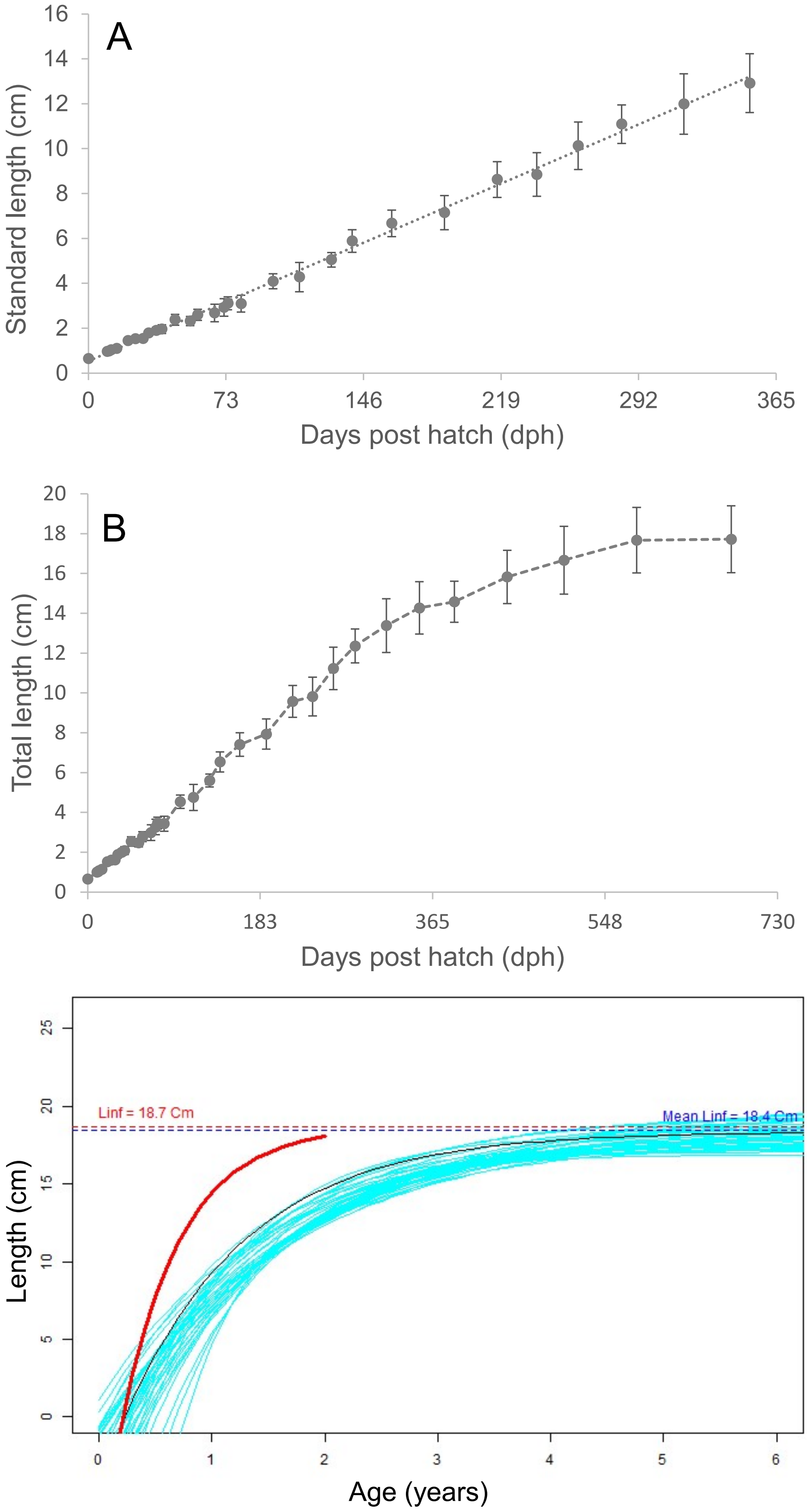

Figure 2. A) Mean length of the capelin larvae (± standard deviation) during the first year. B) Mean length during entire experimental period. C) Growth according to the von Bertalanffy growth model. The blue lines represent the growth of year classes from 1982 to 2019 in the Icelandic capelin stock based on data from the Marine and Freshwater Research Institute. The red line illustrates the growth trajectory of the capelin in the rearing experiment.

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6. A lagrangian particle-tracking approach to detecting capelin spawning event

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Abstract

Recruitment of pelagic fish stocks is considered to depend, among other factors, on ocean current variability as larvae drift from spawning grounds to suitable nursery areas with varying degrees of success. In the 2000s, both juvenile and adult capelin were distributed more to the west than before. This was possibly a result of changes in larval drift patterns and changes in spawning location. Changes in spawning location are difficult to analyze as capelin is a substrate spawner and thus hard to measure spawning activity. In this study, a backtracking procedure is developed to determine active spawning grounds using the high resolution ocean current model VIKING20. Larvae samples from 2018 were traced back to their point of origin with reverse Lagrangian particle tracking, whereby an age-length relationship was used to determine hatching locations along calculated trajectories. A relationship between temperature and incubation time was established with data from a hatching study. Subsequently, this information was used to determine spawning dates for simulated larvae based on the local bottom temperature at the identified hatching locations.

Keywords: spawning, drift, habitat, incubation, hatching

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INTRODUCTION

The spawning grounds of Iceland-East Greenland-Jan Mayen (IEGJM) capelin are primarily located in shallow waters no deeper than 150m off the south and west coasts of Iceland (Vilhjálmsson 2002), while spawning has also been known to occur in the north (Vilhjálmsson & Fridgeirsson 1976). After spawning, eggs adhere to bottom substrates (Friðgeirsson 1976) and undergo embryonic development. In the case of Newfoundland capelin (Pitt 1958), the hatching time is highly sensitive to temperature, with incubation time going as high as 55 days for 0°C and as low as 15 days for 12°C. In relation to IEGJM capelin, a study on the environmental features of spawning grounds south of Iceland (Thors 1981) recorded near-bottom temperatures ranging from 5-7°C. Water depth, substrate type, and current circulation were found to be critical factors in the selection of spawning grounds.

It has long been held that variability in drift during early life stages affects variability in recruitment (Hjort, 1914). In the early 2000s, the geographical distribution of the capelin stock, juveniles and maturing, shifted westward from the Iceland Sea and shelf areas northwest, north and northeast of Iceland to the East Greenland shelf (Vilhjálmsson, 2007; Carscadden et al., 2013). This was possibly a result of changes in drift patterns (Carscadden et. al. 2013), linking spawning habitats to nursery habitats on the East Greenland plateau. A recent study shows westward drift to be heavily influenced by spawning location (Jansen et al., 2021). Distribution of pre-spawning capelin based on maturity stage of catch samples taken during the spawning season shows a westward shift in spawning ground location occurring in the early 2000s (Figure 1). Most catches occurred in the south before 2003. After 2003, catches in the south dropped and increased in the northwest and southwest. A small but notable number of catches have occurred in the north. Thus, the observed shift in catches indicates changes in the spawning locations with increased spawning intensity, primarily in the west. The objective here is to develop a method for detecting capelin spawning events. It involves applying an ocean circulation model along with various biological parameters to trace observed larvae back to their spawning grounds and spawning date.

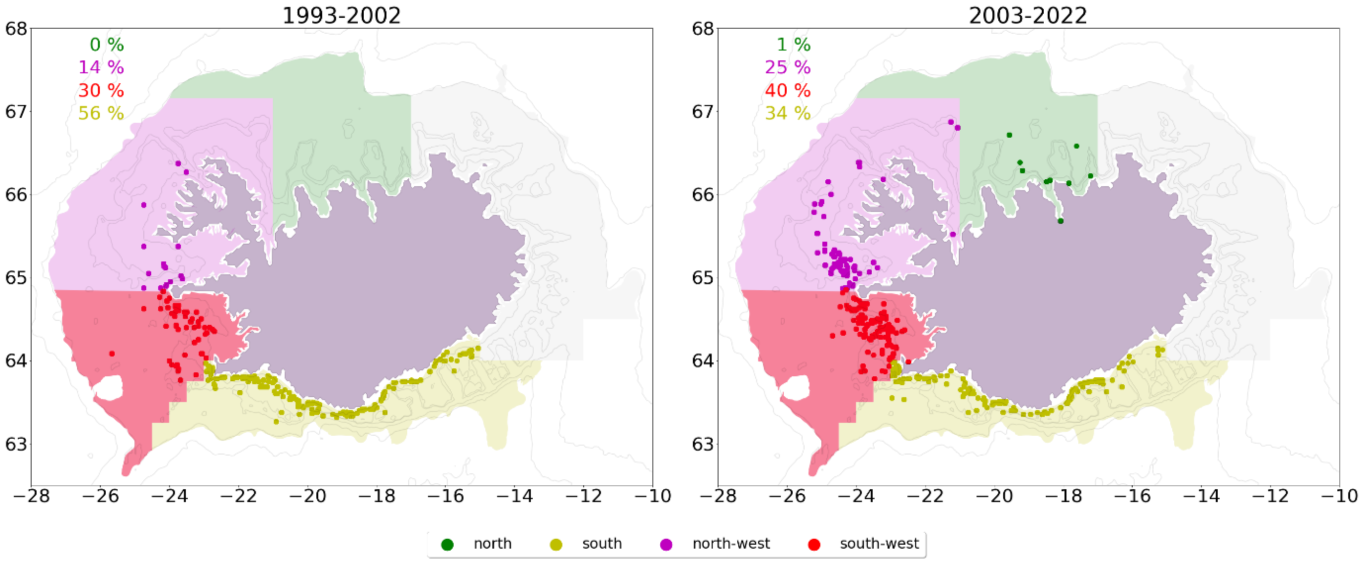

Figure 1. Pre-spawning capelin catches in different areas for time periods 1993-2002 on the left, and 2003-2022 shown on the right. The proportion of catches for each area are listed on the top left for each period.

MATERIALS AND METHODS

To determine the origin of sampled capelin larvae, Lagrangian particle tracking simulations were carried out using PARCELS “Probably A Really Computationally Efficient Lagrangian Simulator” (Delandmeter & Van Sebille, 2019). These simulations used the velocity field output from the ocean general circulation model VIKING20 (Böning et al., 2016), based on the NEMO ocean model (Madec et al., 2017). Using larvae length as a proxy for age in days, a backtracking procedure was implemented whereby particle trajectories are calculated backwards and reversed back to age 0 to find the place of hatching. The incubation time of each particle was then estimated with respect to local bottom temperature at determined hatching/spawning locations. With age and incubation times established, the time of spawning could be calculated.

Particle tracking simulations were based on larvae samples collected in MFRI research survey in May 2018 (**Paper 4** in this collection). Stations off the north and west coasts with a significantly high larvae count (>50) were considered. An age-length relationship was obtained using capelin larvae data collected in 2001 and 2002 (Olafsdottir and Anderson, 2010). A regression line with a confidence band was established using both years combined (Figure 2). A relationship between temperature and incubation time was established with data from a hatching study conducted in MFRI, Grindavík (Figure 3; **Paper 5** in this collection). Bottom temperatures close to the deduced hatching locations were used to estimate the incubation time of hatching particles.

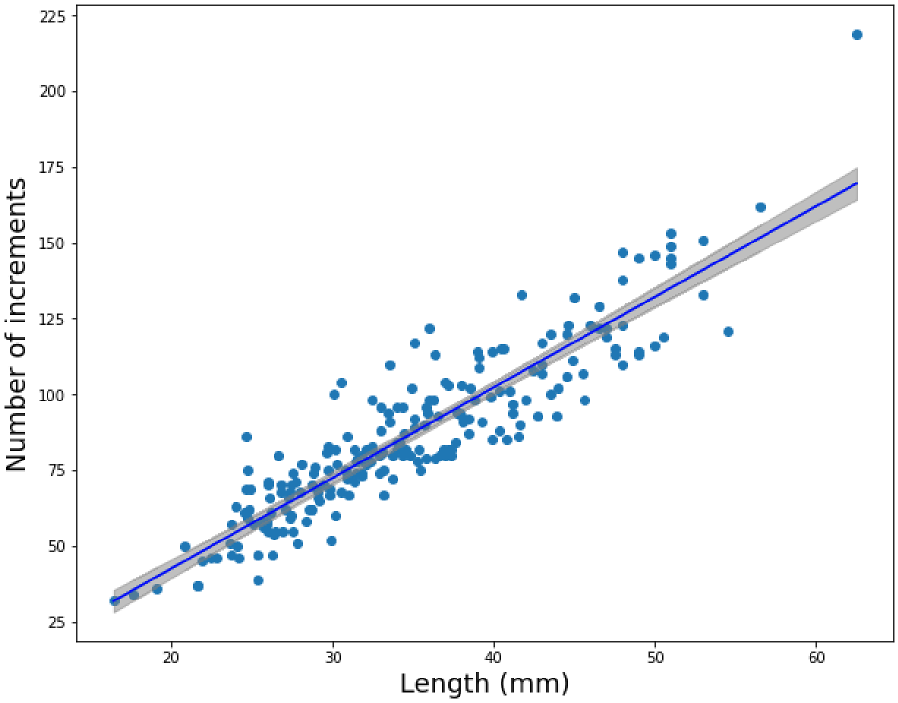

Figure 2. Linear age-length relationship with a 95% confidence band for capelin larvae collected 2001 and 2002 (Olafsdottir and Anderson, 2010). The number of increments refers to readings of daily otolith microstructure, used here as a proxy for age in days.

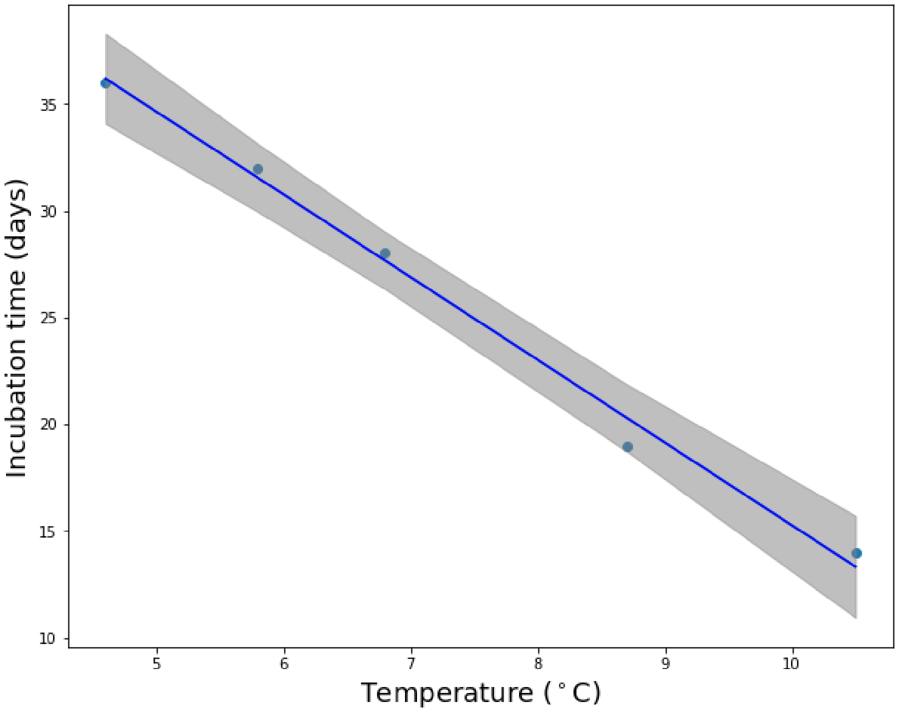

Figure 3. Linear temperature-incubation time relationship with 95% confidence band. Data from a hatching study conducted at MFRI Grindavík (**Paper 5** in this collection).

RESULTS

The spatial distribution of backtracking simulations for samples taken in the northern and western regions in May 2018 is presented in Figure 4. It shows estimated spawning/hatching sites of larvae, highlighting results from single stations (top) and overall density (bottom), signifying the likelihood of spawning/hatching events. Around 5% of particles were estimated to have hatched less than one day from the time of sampling. More than 99% of hatching/spawning locations fall within the 150m depth isobath. The distribution of estimated hatching and spawning times is shown in Figure 5. Spawning was estimated to have primarily occurred in the latter half of March. A marked increase in bottom temperature from VIKING20 was seen after 2003 (Figure 6).

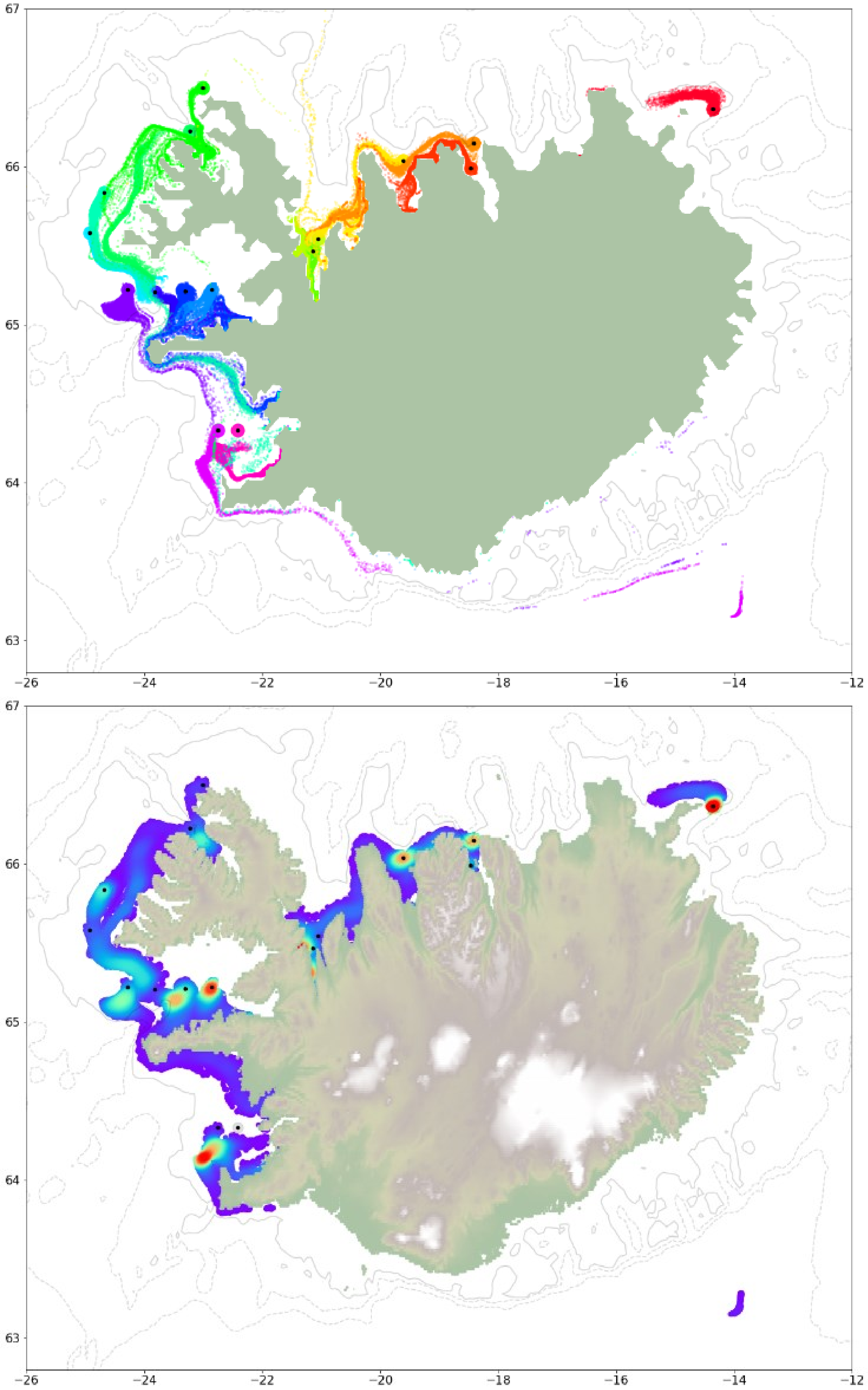

Figure 4. Backtracking results from northern and western sampling stations with high capelin larvae count (> 50), taken in May 2018. Stations are displayed as black dots. Upper panel: Estimated origin locations of particles, colored by station. Lower panel: Density of estimated origin locations, signifying likelihood of spawning/hatching events. Red indicates high density and blue indicates low.

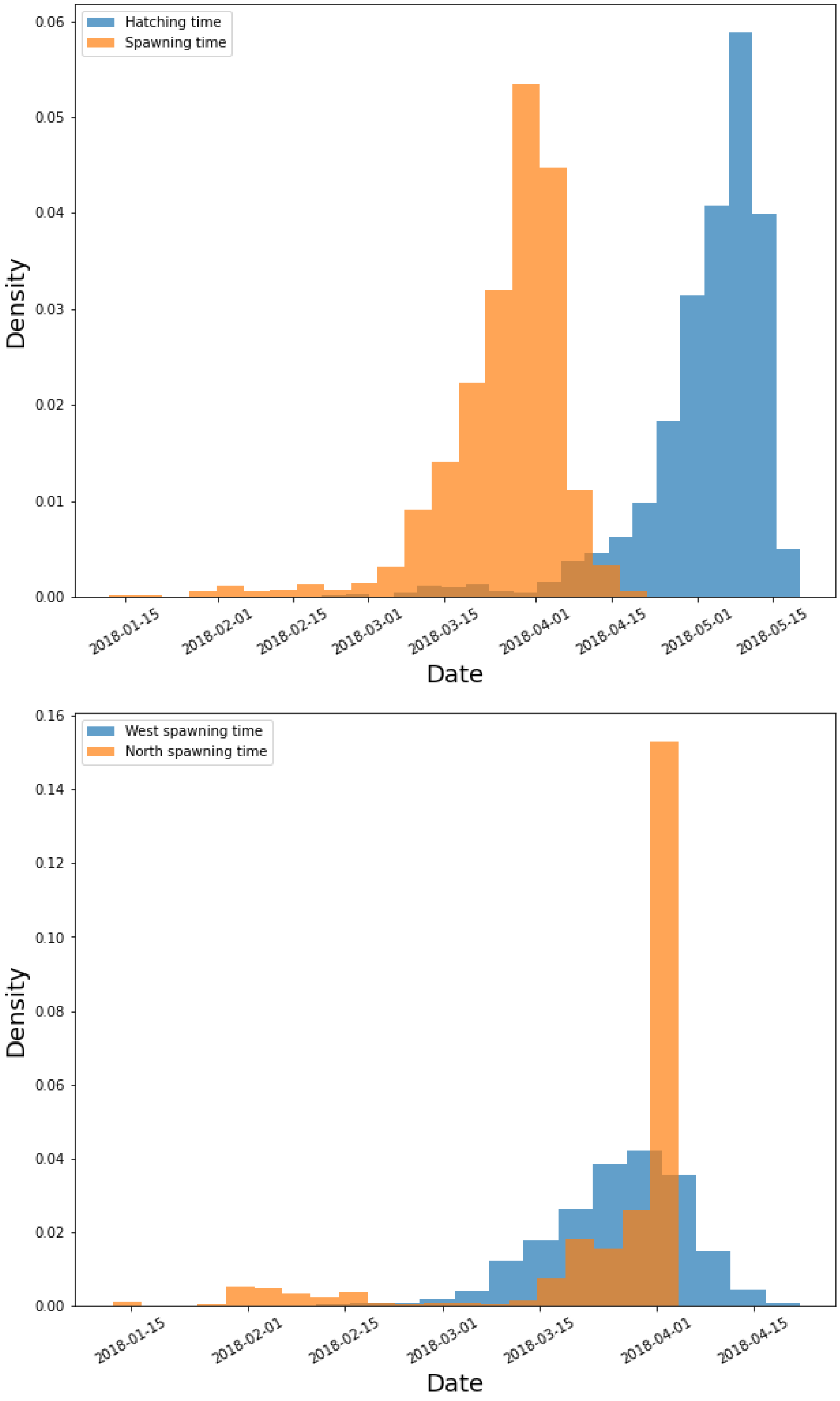

Figure 5. Above: Distribution of estimated hatching and spawning times of capelin from all spawning grounds. Below: Estimated spawning times in the north and western spawning grounds.

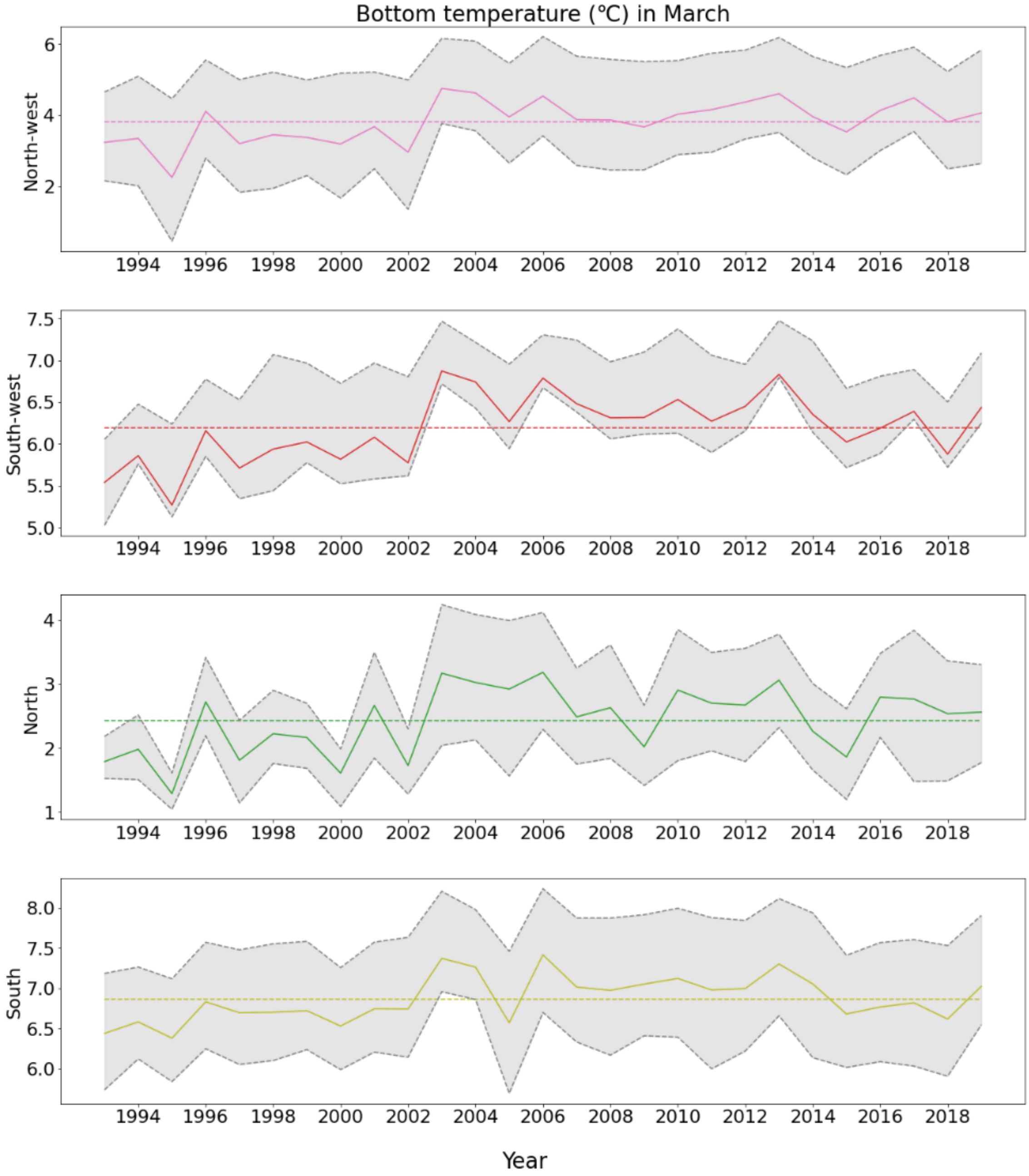

Figure 6. Icelandic shelf mean bottom temperatures in March of each year from 1993-2019 from VIKING20. The mean temperature of different areas is given by colored lines surrounded by grey quantile bands [20%, 80%]. Dashed horizontal lines show the mean temperature over the whole period. Note different temperature ranges on the y-axis between panels.

DISCUSSION & CONCLUSION

As capelin spawning is difficult to observe, the presented Lagrangian particle-tracking approach offers a viable alternative to estimate the location and timing of spawning events based on sampling of capelin larvae. Simulations based on capelin larvae sampled in May 2018 on the Iceland shelf indicated spawning events taking place on the shelf north and west of Iceland. The shift in catches (Figure 1) of pre-spawning capelin after 2003 coincides with increased bottom temperature (Figure 6). Thermal spawning conditions in the northwest became more favorable than before, assuming the observed near-bottom temperatures range of 5-7°C (Thors 1981) to be more suitable. In contrast, the mean bottom temperature in the south exceeds 7°C for some years after 2003, where catches of spawning capelin have decreased. It is to be expected that such a shift would lead to changes in connectivity as drift patterns are heavily influenced by spawning location (Jansen et al., 2021). Hence, the changes towards more spawning activity in the west and north after the early 2000s have implications for larvae drift and potential survival.

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7. Feeding ecology of capelin at new feeding grounds

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Abstract

Since the early 2000s, marked changes have been observed in the distribution of 0-group, juvenile, and adult capelin (*Mallotus villosus*) as their nursery and feeding areas shifted from the north of Iceland and Iceland Sea to East Greenland waters. This makes a comparison of their diet composition and prey availability in the new and earlier feeding grounds of interest. The diet of capelin was investigated in their new feeding area in autumn (September-October) from 2018–2021 and in winter (January and February) from 2018–2019. A high proportion of capelin stomachs contained food, both in autumn (77–99 %) and winter (60–64 %). Copepods and euphausiids were the most important prey groups in autumn, reflecting the species composition of zooplankton in the feeding area. The most important prey groups differed among years, from being euphausiids and copepods in 2018 to being euphausiids in 2020 and copepods in 2021. This indicates that capelin is an opportunistic predator preying according to the availability of zooplankton species in the feeding area. The percentage of larger prey items generally increased with the capelin length, as seen from species composition of stomach content (shift from copepods to euphausiids), and stable isotope analysis suggested this trend also held true for the longer term (weeks or months prior to sampling) with higher δ^{15}N values (i.e., higher trophic level) in larger capelin. The high density of capelin in 2020 and 2021 may have caused higher grazing pressure on zooplankton and could explain lower diet weight during those years. These results give valuable information for food web analysis and ecosystem modelling in the future.

Keywords: capelin, diet, trophic interactions, stomach content, stable isotopes

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INTRODUCTION

Capelin (*Mallotus villosus*) is an essential component of the Icelandic ecosystem, serving as a link between zooplankton and species at higher trophic levels (Sigurdsson & Astthorsson 1991, Astthorsson & Gislason 1997) and is an important component in the diet of many fish, marine mammals and sea birds (Magnússon & Pálsson 1989, Vilhjálmsson 1994)

To understand energy flows in marine ecosystems, knowledge of predator-prey relations is fundamental. Combining traditional stomach content analyses with stable isotope analysis (SIA) is a powerful tool, as stomach content analysis shows a snapshot of the "last meal," while SIA complements that and shows the integration of prey over a longer period (weeks to months, Fry et al. 1988, Divine et al. 2017). SIA of nitrogen provides information on species trophic position in the food web (Hobson et al. 1992).

The shifts in distribution of capelin since the early 2000s in their nursery and feeding areas from the north of Iceland and Iceland Sea to East Greenlandic waters (Vilhjálmsson 2007, Bárðarson et al. 2021) make a comparison of their diet composition between the new and old feeding grounds of relevance and interest. Information on trophic relationships in the pelagic ecosystem in their new feeding grounds is scarce (Pálsson et al. 2012 & Petursdottir et al. 2012). The aim of the present study was to analyze the feeding ecology of capelin in their new nursery and feeding areas along the east coast of Greenland in autumn, with a focus on the capelin stomach content, tissue samples, and food availability.

MATERIALS AND METHODS

Samples were collected along the east coast of Greenland in autumn and north of Iceland in winter (Figure 1, 3, 4 and Table 1). Capelin was sampled with pelagic trawls taken at locations with acoustical registrations. Stomachs and tissue samples from 10 randomly selected capelin were collected (Table 1) at each station. The prey was identified to species level or lowest classification possible, and their dry weight was obtained. Data from autumn 2019 could not be used as there were problems with the weighing scales. For each station, the mean Partial Fullness Index (PFI) was calculated to compare quantities of prey between different size capelin (Lilly & Fleming 1981).

The PFI of prey group *i* in predator *k* is given as:

$$PFI_{i,k} = \frac{S_{i,k}}{L_k^3} \times 10^4$$

Where S*i* is the weight (g) of prey species *i* found in the stomach of predator *k*, and L*k* is the length (cm) of predator *k*.

Further, the Total Fullness Index (TFI) was calculated for all stations (PFI summed for all prey).

To explore the importance of different diets in relation to the length of capelin, capelin were grouped into two size classes: <14 cm and ≥ 14, as 14 cm can be used as a knife-edge approximation of maturity (**Paper 13** this collection).

An analysis of naturally occurring stable isotopes of nitrogen ($\delta^{15}N = {}^{15}N/{}^{14}N$) was done on dried tissue samples of capelin after lipid extraction (Table 1).

To investigate capelin food availability, mesozooplankton were sampled with WP2 net (200 µm mesh size) from 0-50 m depth and 0-200 m depth (Table 1) and size-fractionated: <1000 µm and >1000µm. From the >1000µm samples, larger zooplankton groups were picked out to get information on the distribution of abundant macrozooplankton groups (i.e., euphausiids, amphipods and chaetognaths). All the fractions were dried for biomass estimates.

Table 1. Overview of samples analyzed for this study. Number of stations analyzed for zooplankton dry weight (dw), size range of analyzed capelin, number of stomachs analyzed and proportion with food (in parenthesis) and number of capelin (tissues) analyzed for stable nitrogen isotopes (SI).

			Zooplankton biomass (dw)		Capelin diet		
Year		Gear Month	WP2-net 0-50m N	0-200 N	Pelagic trawl Capelin size range (cm)	Stomachs N (%with food)	Tissues (for SI) N
2018	Autumn	7-23 September	101	100	7.5-19.0	318 (84)	218
	Winter	18-30 January	-	-	11.5-19.5	330 (64)	-
2019	Autumn	15 September-19 Oktober	93	86	10.1-18.8	175 (98)	156
	Winter	25 January-23 February	-	-	12.5-19.0	93 (60)	-
2020	Autumn	9-24 September	46	26	9.0-19.8	241 (77)	-
2021	Autumn	8-16 September	47	45	12.5-18.2	169 (99)	-

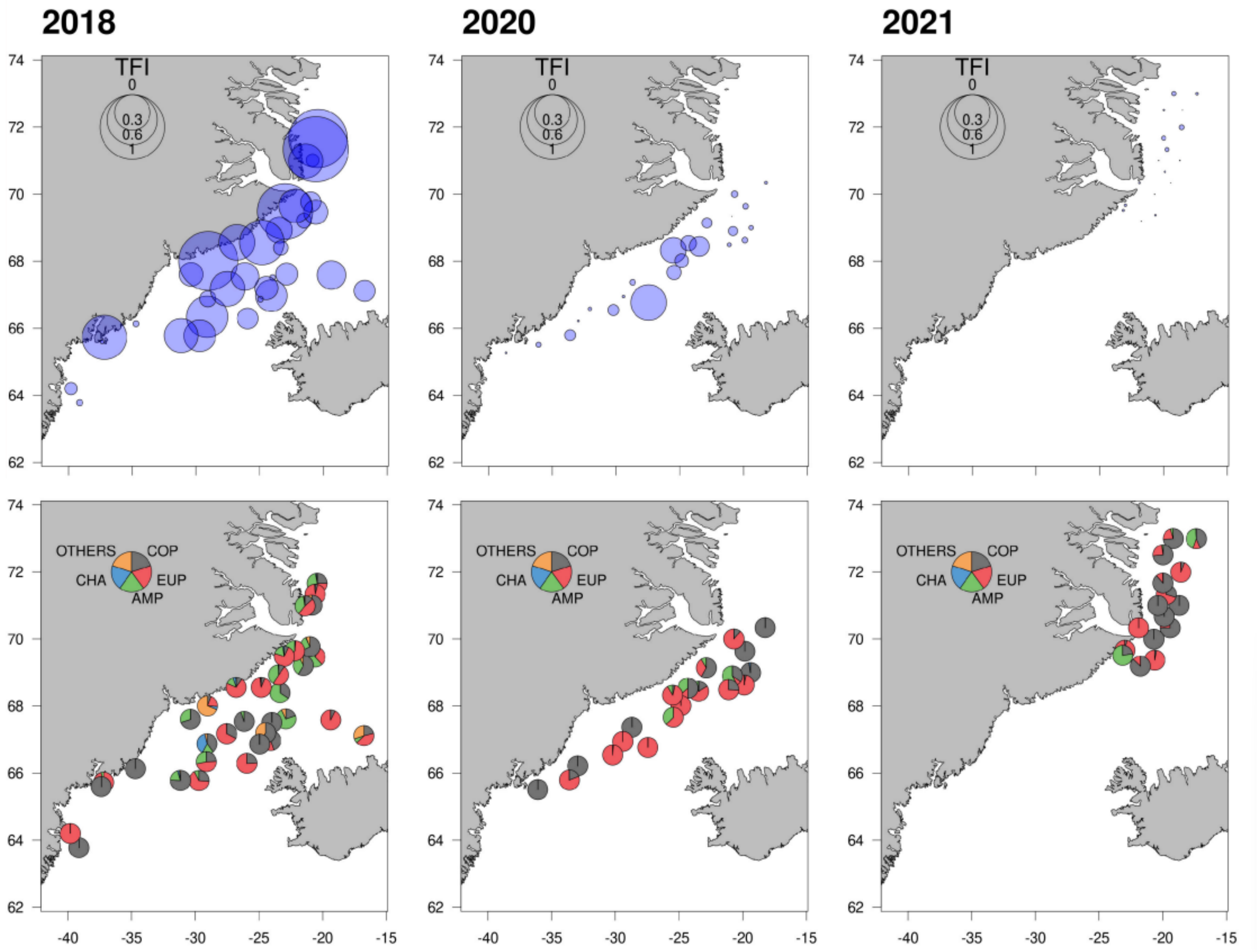

Figure 1. The Total Fullness Index (TFI: top panel) and Partial Fullness Index (PIF: bottom panel) for capelin at the different sampling locations in autumn 2018, 2020 and 2021. Copepods are gray, euphausiids red, amphipods are green, chaetognaths are blue and others are orange.

RESULTS

For the four-year study, stomach contents of 1326 capelin ranging in size from 7.5-19.8 cm were analyzed. A high percentage contained food, ranging from 60% to 99% for the sampling period (Table 1). In autumn, PFI indicated that copepods (mainly *Calanus* spp.) and euphausiids (mainly *Thysanoessa* spp.) were the most important groups (Figure 1). Copepods are dominant in the diet of smaller capelin (< 14 cm), whereas the importance of euphausiids increases in larger capelin (≥ 14cm, Figure 2). Furthermore, TFI was much higher in 2018 (mean 0.228) than in 2020 (mean 0.061) and 2021 (mean 0.019). In winter, TFI values from 2018 (mean 0.117) and 2019 (mean 0.109) showed that capelin were also feeding in that period (Figure 3). Copepods and euphausiids dominated their winter diet, but amphipods and chaetognaths contributed more than they did in autumn.

Mean stable isotope values of nitrogen ($\delta^{15}N$) in capelin < 14 cm were 10.39‰ in 2018 and 10.28‰ in 2019, while the mean values for capelin ≥ 14 cm were 10.88‰ in 2018 and 11.07‰ in 2019.

The estimated total mesozooplankton biomass (from 50-200 m) was higher in 2018 (mean 1.56 dw g m^{-2}) and 2019 (mean 1.60 dw g m^{-2}) than in 2020 (mean 1.14 dw g m^{-2}) and 2021 (mean 0.86 dw g m^{-2}, Figure 4). The <1000µm fraction reflects smaller copepods (mainly younger copepodite stages of *C. finmarchicus*), while >1000µm fraction reflects larger copepods (mainly larger stages of *C. finmarchicus* and *C. hyperboreus*). The biomass of euphausiids, amphipods and chaetognaths, which were picked out from the >1000µm fraction, is shown in Figure 5. Euphausiids are distributed in the whole study area, while amphipods and chaetognaths are more concentrated in the northern part.

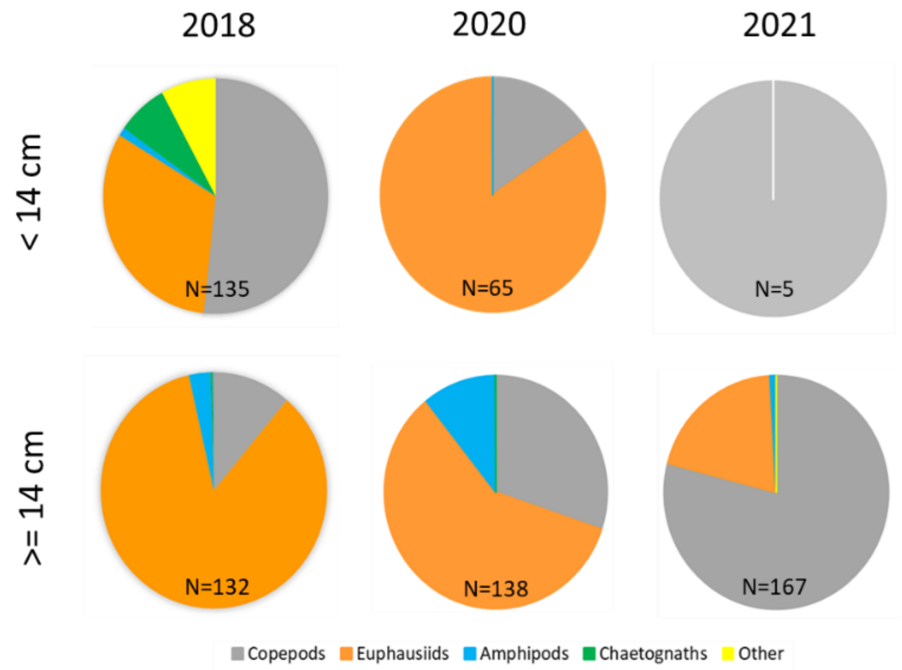

Figure 2. Diet composition (in groups) by mean dry weight of smaller capelin (< 14 cm) and larger capelin (≥ 14 cm) sampled in autumn 2018, 2020, and 2021.

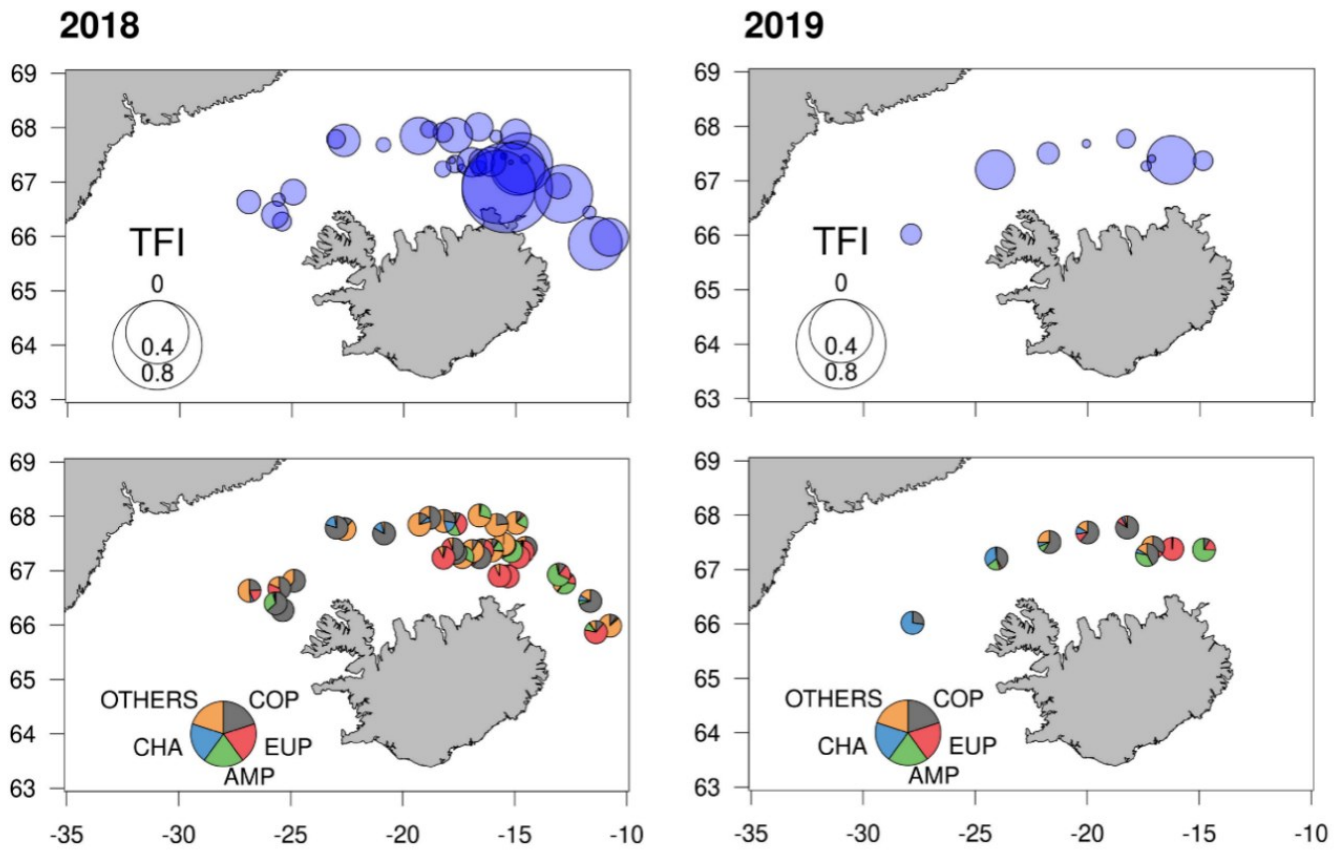

Figure 3. The Total Fullness Index (TFI: top panel) and Partial Fullness Index (PFI: bottom panel) for capelin at the different sampling locations in the winter 2018 and 2019. Copepods are gray, euphausiids red, amphipods are green, chaetognaths are blue and others are orange.

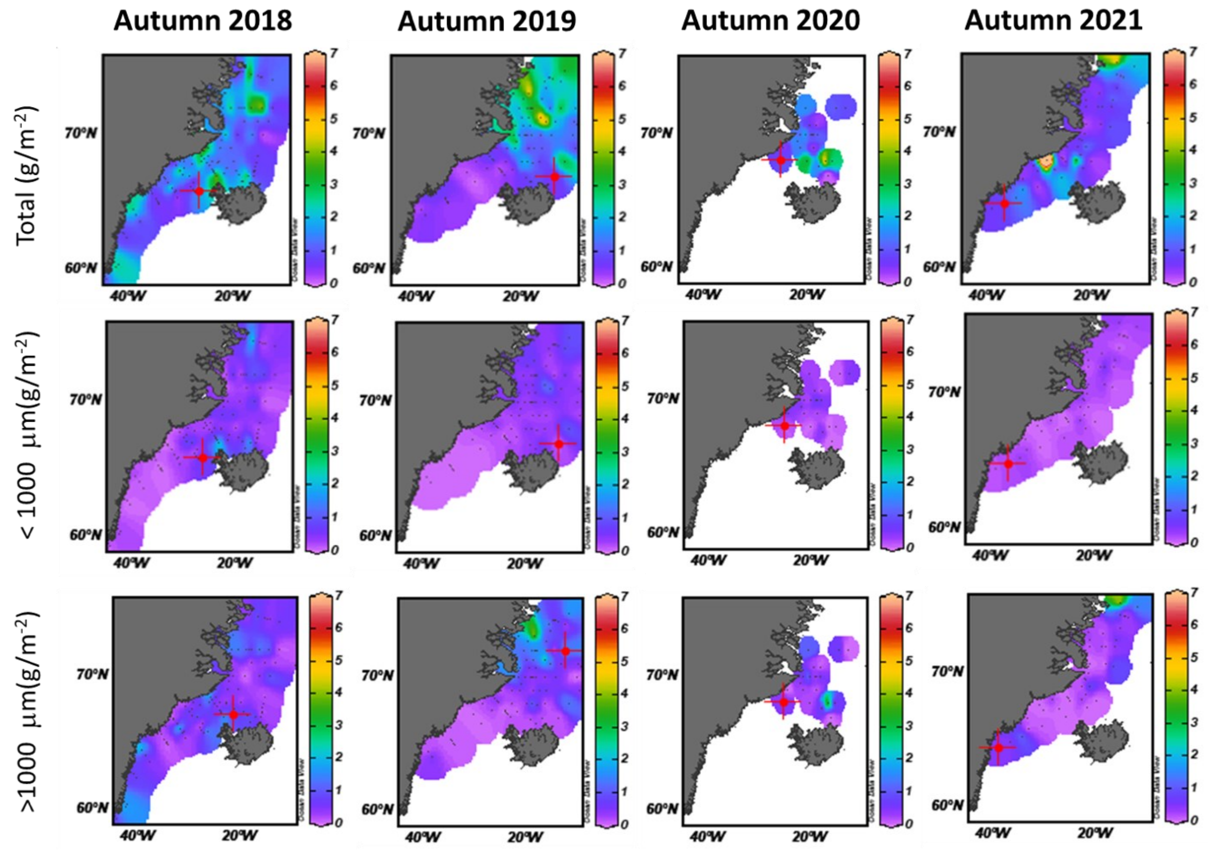

Figure 4. Mesozooplankton biomass: total (dw g m^{-2}, 50-200m; top panel), <1000mm (dw g m^{-2}, 50-200m; centere panel), >1000mm (dw g m^{-2}, 50-200m; bottom panel) during autumn 2018, 2019, 2020 and 2021.

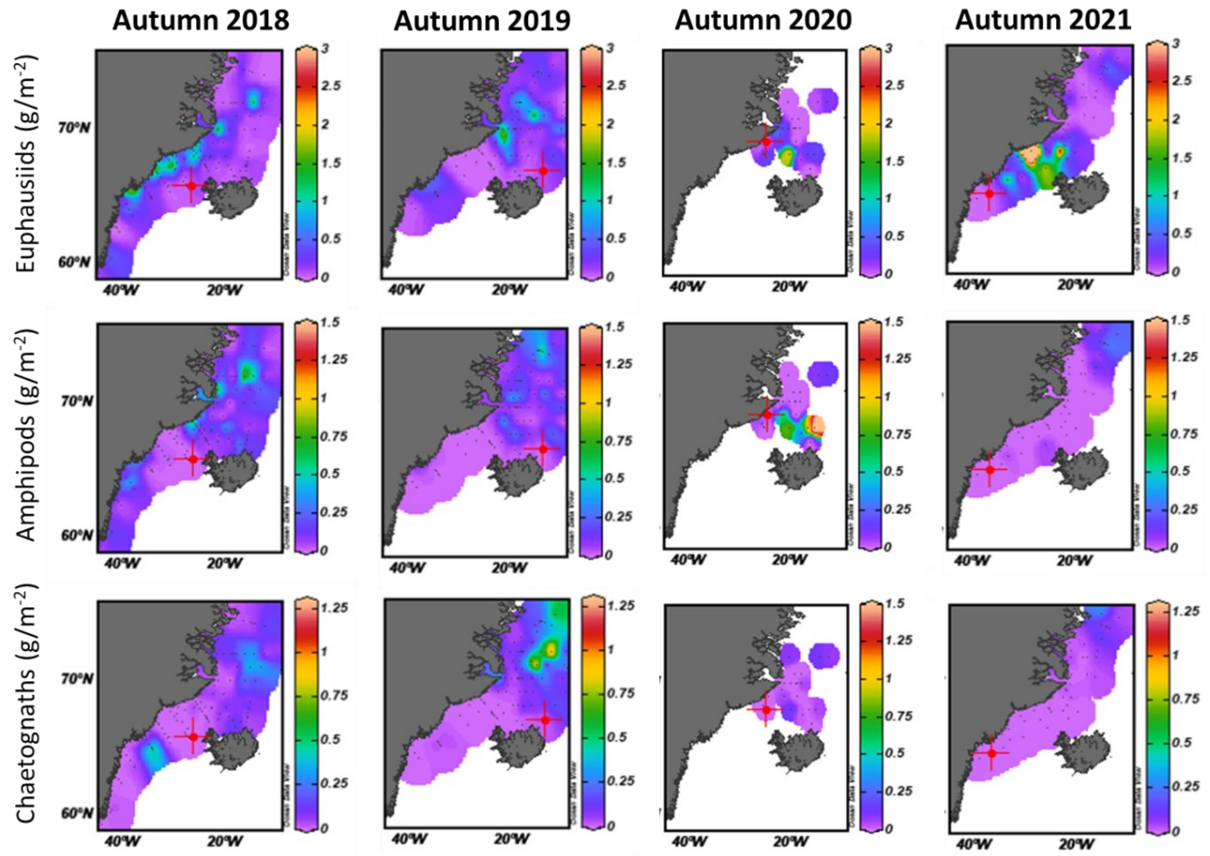

Figure 5. Biomass of euphausiids (dw g m^{-2}, 50-200m; top panel), amphipods (dw g m^{-2}, 50-200m; centre panel) and chaetognaths <1000mm (dw g m^{-2}, 50-200m; bottom panel) during autumn 2018, 2019, 2020 and 2021.

DISCUSSION

The analyses of the capelin stomachs sampled in the years 2018-2021 indicated high feeding activity both during autumn and winter. The proportion of stomachs containing food was similar to that observed in earlier studies on the feeding habits of capelin in the Iceland Sea during the main feeding period in summer (Astthorsson & Gislason 1997). Furthermore, the observed winter feeding now (60-64% of stomachs containing food) was more pronounced than in an earlier study (18% of stomachs containing food) by Sigurdsson and Astthorsson (1991).

Copepods (mainly *C. finmarchicus* and *C. hyperboreus*) and euphausiids (mainly *Thysanoessa* spp.) were the most important prey groups in the autumn, which reflects their biomass (dw g m^{-2}) in the area (Gislason & Silva 2012). The sampling locations for capelin differed among the years, so any comparisons need to account for that. Moreover, the capelin stomach content varied among locations within the years and seasons. In general, the pattern for all years was that euphausiids dominated in stomachs in the northern part of the study area and copepods in the southern part in 2018. Euphausiids dominated in stomach samples from the entire study area in 2020, and copepods contributed most to the diet in 2021. Together with the results on the zooplankton biomass, these findings support that capelin is an opportunistic predator, consuming the prey which is most abundant in their environment at any given time, which coincides with Astthorsson and Gislason (1997) results when investigating capelin summer feeding in the Iceland Sea in the early 1990s, the old feeding grounds.

The percentage of larger prey items generally increased with the capelin length, as seen from the species composition of stomach content (shift from copepods to euphausiids). SIA supported this trend in the longer term (weeks or months prior to sampling), with higher δ^{15}N values in larger capelin, as δ^{15}N values are enriched predictably in consumers relative to their prey (Hobson et al. 1995). The results are similar to those of studies on the diet of other capelin stocks. In the Barents Sea, capelin have a pronounced shift in the diet from copepods to euphausiids, correlating with changes in body size (Dalpadado & Mowbray 2013). In Newfoundland, copepods remained the most important prey (Dalpadado & Mowbray 2013), while in the Canadian Arctic, there is a shift from copepods to amphipods (Ogloff et al. 2020).

Both the zooplankton biomass and TFI, which reflects the capelin diet weight, were higher in autumn 2018 compared to 2020 and 2021. The capelin stock size was, on the contrary, higher in 2020 and 2021 than in 2018 (ICES 2023), which contributed most likely to higher grazing pressure on zooplankton in the area in 2020 and 2021. That could explain lower TFI these years and subsequently worse body condition of the capelin and slower growth as a result of density dependence (**Paper 3** of this collection).

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8. Capelin distribution in the east Greenland water masses during autumn feeding

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Abstract

Capelin migration routes are presumed to rely on currents and, hence, the combination of water masses in their habitat. Little is known about the vertical distribution of capelin with respect to the oceanic features at their present feeding location in autumn. Therefore, measurements on capelin distribution and selected hydrographic profiles from the 2019-2022 autumn surveys were used to visualize capelin's vertical and horizontal distribution in relation to water masses along the east Greenland shelf. Vertical profiles of two hydrographic sections, running from west to east and located at 70- and 72-degrees latitude, showed that two main water masses, classified based on temperature, salinity, and density values, were in the area. Capelin was present at both sections and both on and off the shelf with an inter-annual variability in horizontal distribution. Along these sections, potential temperature-salinity (T-S) diagrams for all years combined showed that capelin was present mainly in Atlantic-origin water but also in Polar Surface Water. During autumn, capelin is known to be actively feeding, and a close spatial overlap with krill was observed in two years (2019 and 2020). Capelin seems to move across water masses during its autumn feeding period, potentially following its prey or because of an innate diel vertical migration behaviour.

Keywords: water masses, Atlantic-origin water, Polar Surface Water, Polar Intermediate Water, krill-capelin overlap

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INTRODUCTION

The migration and distribution of capelin are linked to the intricate system of ocean currents in the Iceland-East Greenland-Jan Mayen (IEGJM) area and, thus, to the distribution of water masses in the region (Vilhjálmsson, 2002). In the early 2000s, capelin distribution in autumn shifted from the Iceland Sea towards the east Greenland shelf (Vilhjalmsson 2007; Carscadden et al., 2013). This shift has been attributed to changes in the physical environmental conditions in the Iceland Sea (**Paper 2** in this collection). During the summer and autumn seasons, capelin is actively feeding. Mature fish, primarily present in the northern part of the east Greenland shelf, mainly feed on euphausiids (krill), while immature fish, distributed in the southern part, mainly feed on copepods (**Paper 7** in this collection).

Along east Greenland, the east Greenland Current flows southward along the shelf and continental slope (Håvik et al., 2017). It is presumed that the return migration of capelin southwards from the feeding grounds in autumn utilizes this current (Vilhjálmsson, 2002). Little is known about the association of capelin with different water masses in this area. Therefore, this study aims to discern any such relationship descriptively. It is likely that capelin distribution at this time of year and in this location will be affected by prey availability, as they are still actively feeding (**Paper 7** in this collection). Thus, the spatial overlap between capelin and krill was also explored.

METHODS

Capelin and krill acoustic backscatter and hydrographic data were collected during annual autumn acoustic surveys conducted by the Marine and Freshwater Research Institute (MFRI) in September/October 2019-2022. For hydrographic sampling, a series of Conductivity, Temperature and Depth (CTDs) deployments were conducted down to 500 m or 10 m above the bottom when shallower than 500 m.

The potential temperature (ϑ) and salinity (S) values were then used to define water masses (Håvik et al., 2017; Rudels et al., 2002). Three water masses were defined: Atlantic-origin Water (AW) with $\vartheta > 0$ and $S > 34.4$, Polar Surface Water (PSW) with salinity $S < 34.4$ and comprises cold and warm components, Polar Intermediate Water (PIW), which is denser with $\vartheta < 0$ & $S > 34.4$ and has a potential density (σ) > 27.7.

First, hydrographic sections, which were repeated across years at 70- and 72-degrees latitude (Figure 1), were used to generate vertical profiles of temperature and salinity on which capelin backscatter was overlaid. This was used to visually identify the temperature and salinity gradients in which the capelin was present along the sections and within the water column.

Second, T-S diagrams delineating the three water masses were generated for the same hydrographic sections for all years combined. Capelin backscatter was overlaid on T-S diagrams to study potential spatial links visually.

Third, given that krill is capelin's main prey in this area (**Paper 7** in this collection), any spatial overlap of krill and capelin backscatter was visually examined for the whole survey area for 2019 and 2020.

RESULTS

Capelin was mainly located on the shelf and along the slope at the east Greenland shelf during the study period (Figure 1). A vertical profile of temperature and salinity with capelin distribution showed that capelin is present along a wide range of temperature and salinity values with some degree of inter-annual variability (Figure 2 and Figure 3). The diel vertical migration (Figure 6; **Paper 13** in this collection) is evident where capelin schools were present close to the bottom during the day in comparison with distribution closer to the surface during the night.

The survey area on the east Greenland shelf is dominated by AW. Along latitude 70 °N, capelin registrations were more frequent in AW compared to PSW with higher backscatter strength indicating the schools were denser (Figure 4, top panel). The presence of capelin in a warm envelope at a depth of 100–300m is another example of their presence in AW, seen in Figure 2. Some high capelin abundances were also present in PSW, where the observations of capelin were more scattered. Lower capelin abundance was registered at latitude 72 °N, compared to 70 °N, with capelin mostly concentrated in the AW (Figure 5). Krill was registered in most locations where capelin was present (Figure 5) but had a broader geographic distribution than capelin. A clear diel vertical migration overlap between capelin and krill was observed (Figure 6).

DISCUSSION AND CONCLUSION

Capelin seems to move across water masses during its autumn feeding period. During daylight hours, capelin was present further down in the water column and more in the warm envelope of AW than in PSW. At night, however, the distribution was scattered and mainly in PSW. The movement of capelin across these two water masses could be explained by capelin's innate diel vertical migration behavior (Figure 6; Mowbray, 2002).

The AW has a relatively high nutrient concentration because it renews much more efficiently in the surface layer by eddy diffusion than in the highly stratified PSW (Håvik et al., 2019). Due to high nutrient content, the layer is rich in zooplankton such as krill, thus a target area for capelin feeding. The PSW, on the other hand, is rich in large copepods (*Calanus hyperboreus*) (Gislason and Silva, 2012), which are also a preferred prey of capelin (Astthorsson and Gislason, 1997). The vertical movement of capelin could be driven by prey availability (Figure 6), where the weighted mean depth of capelin in the water column closely corresponds to the weighted mean depth of krill. This has also been observed in the past for the capelin stock in Newfoundland (Mowbray, 2002). Other factors, however, could also be at play, such as changes in the environment, particularly in the light intensity, as well as predator avoidance with the increased number of whale sightings in this region (**Paper 11** in this collection). Further analysis is required to better understand why capelin vertically migrates within the water column and the predator-prey dynamics in the area. Nonetheless, studying the spatial link between capelin distribution, its physical environment and prey provides an ecosystem-based perspective and can be used to discern the effects of changing environmental conditions on capelin dynamics.

Figure 1. The standard hydrographic sections along 70- and 72-degrees latitude. The stations on the eastern end were not sampled in all years.

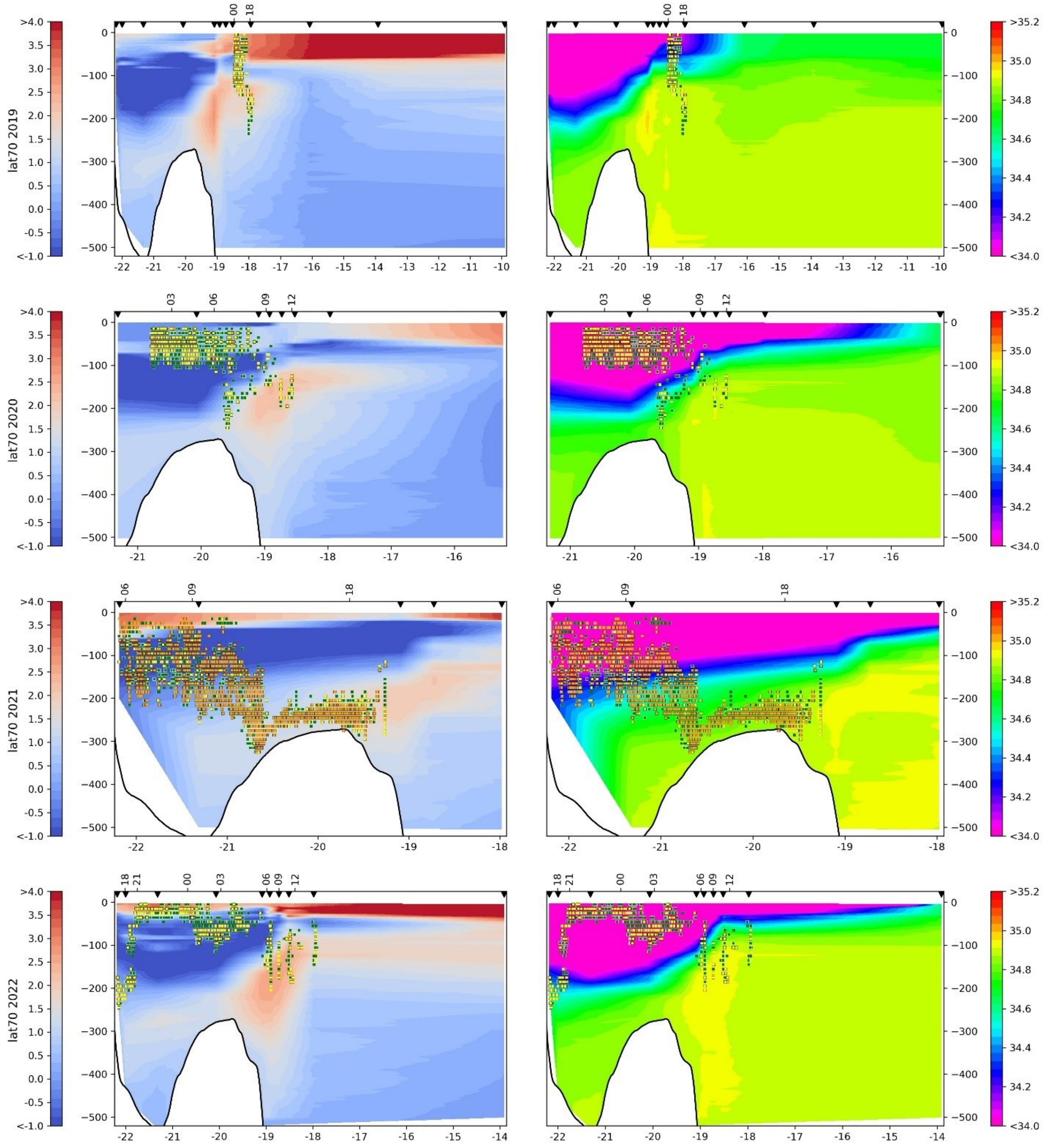

Figure 2. Temperature (left panel) and salinity (right panel) along the 70 °N section for the years 2019, 2020, 2021 and 2022, respectively. Overlaying is the distribution of capelin acoustic values (*nasc*) along the section (green: low (50th percentile of total *nasc* distribution), yellow: medium (50-75th percentile) and orange: high (> 75th percentile)). CTD locations are denoted by black triangles at the surface and the time of acoustic registrations is given above each panel. Note that the distance of the hydrographic section eastward from Greenland's shore is inconsistent because of irregular CTD sampling between years.

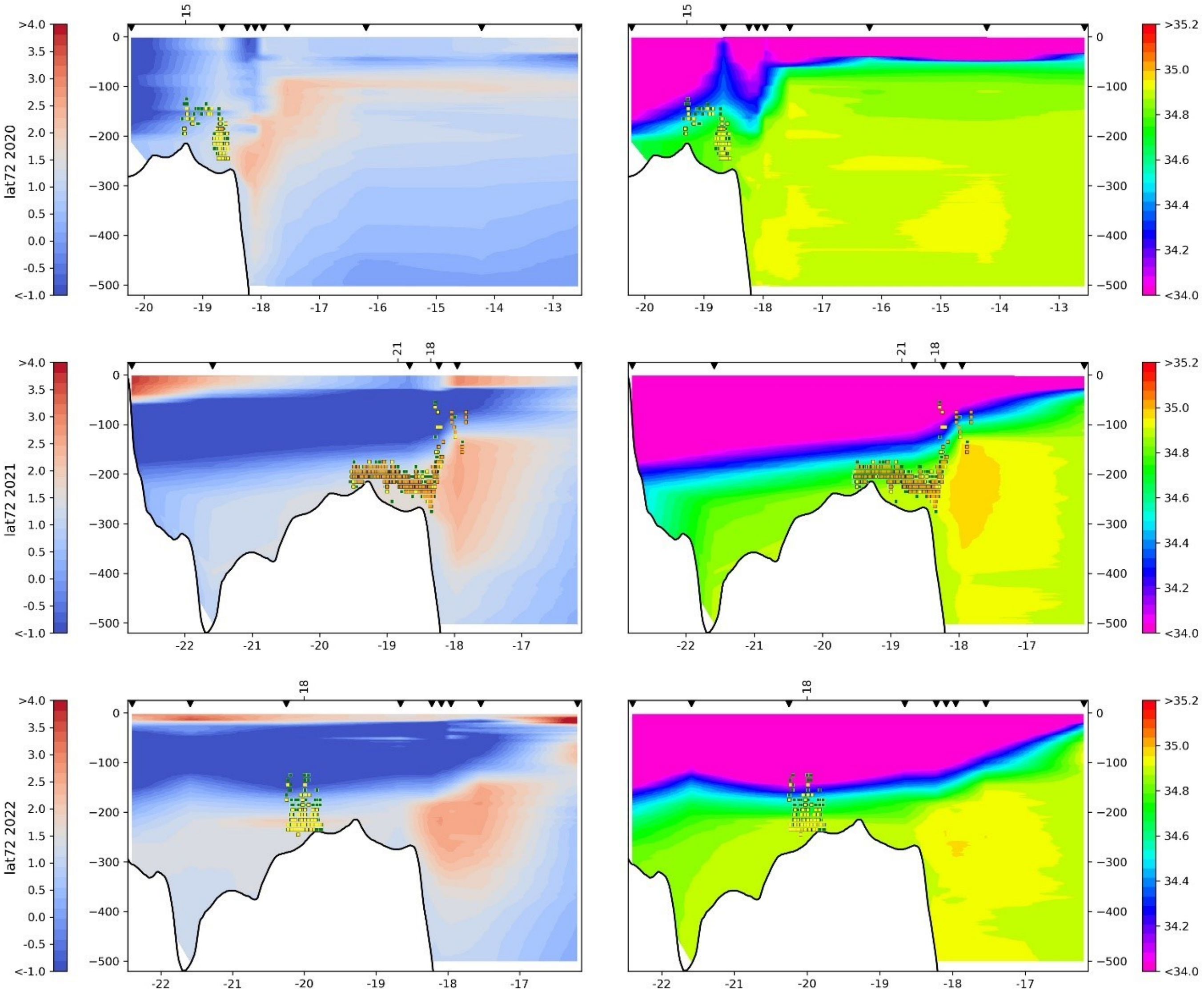

Figure 3. Temperature (left panel) and salinity (right panel) along the 72 °N section for the years 2020, 2021 and 2022, respectively. In 2019, no capelin was present on the section, hence not displayed. Overlaying is the distribution of capelin acoustic values (*nasc*) along the section (green: low (50th percentile of total *nasc* distribution), yellow: medium (50-75th percentile) and orange: high (> 75th percentile)). CTD locations are denoted by black triangles at the surface and the time of acoustic registrations is given above each panel. Note that the distance of the hydrographic section eastward from Greenland's shore is inconsistent because of irregular CTD sampling between years.

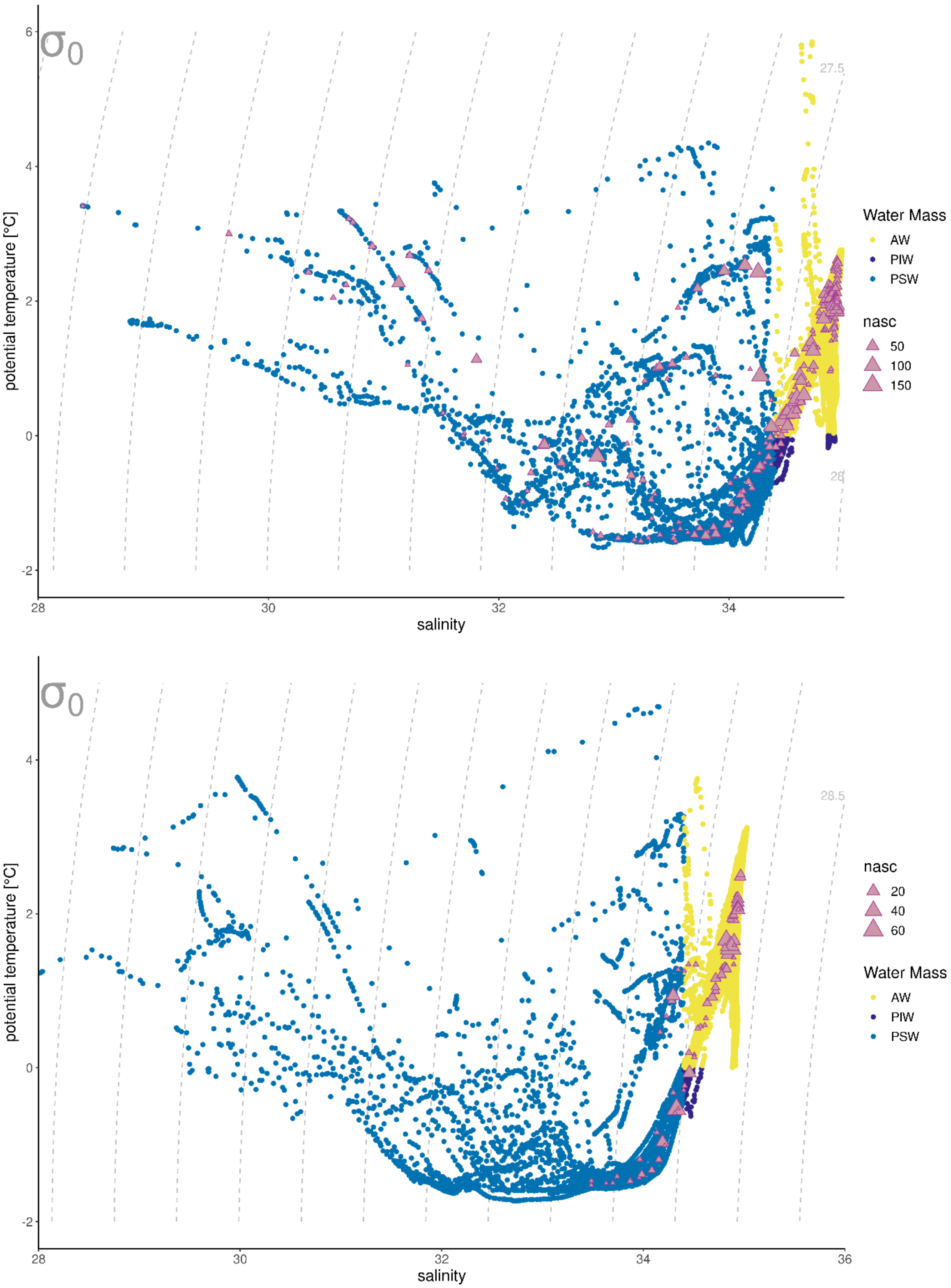

Figure 4. Temperature and salinity diagrams with capelin acoustic values (*nasc*) along the 70 °N (top panel) and 72 °N (bottom panel) hydrographic sections for the years 2019-2022. Points are color coded by the different water masses, and the potential density is marked by the dashed lines.

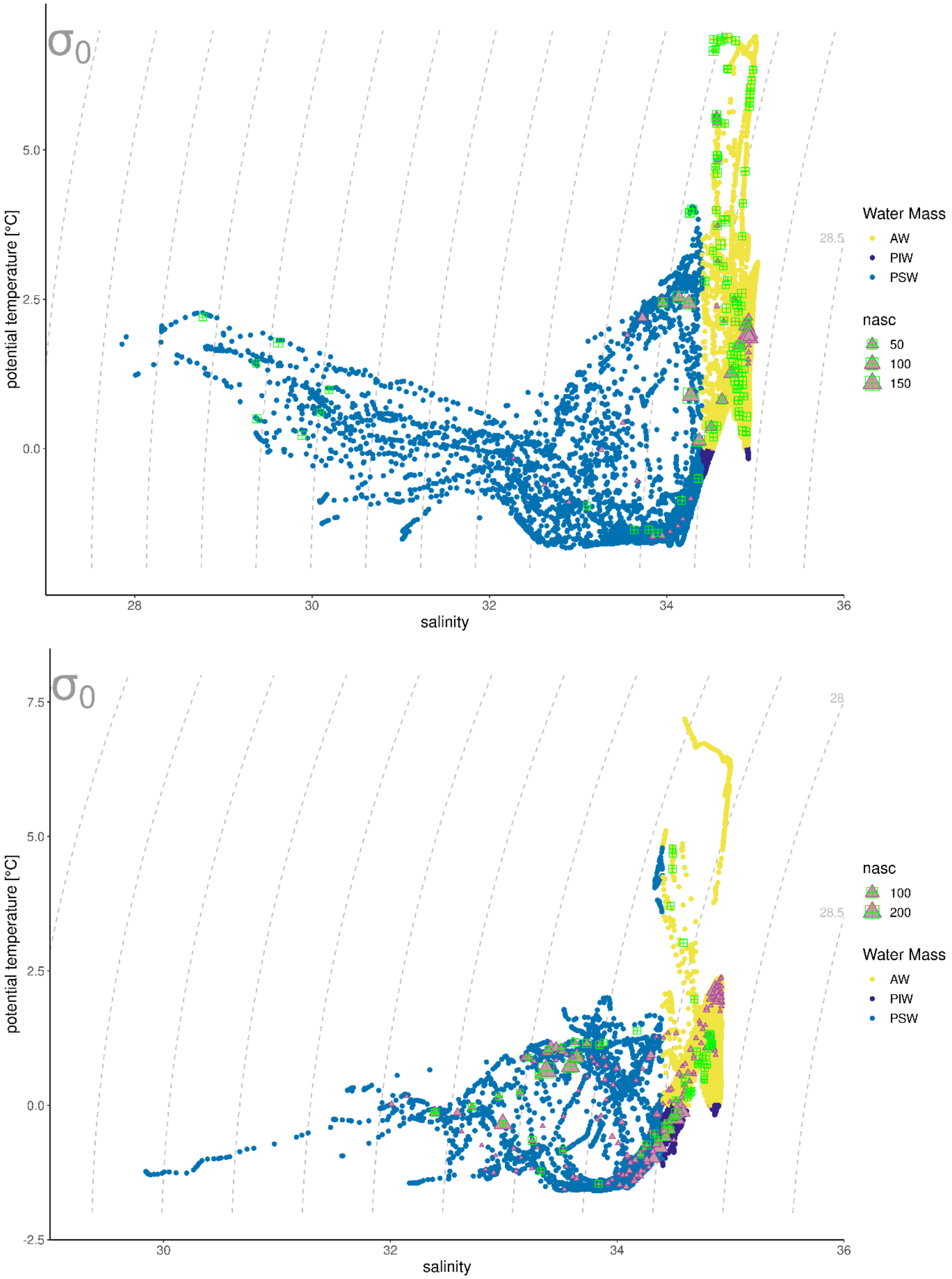

Figure 5. Temperature and salinity diagrams and acoustic values for capelin (nasc: pink triangles) and krill (nasc: green squares) across the whole survey area for years 2019 (top panel) and 2020 (bottom panel). Points are color coded by the different water masses, and the potential density is marked by the dashed lines.

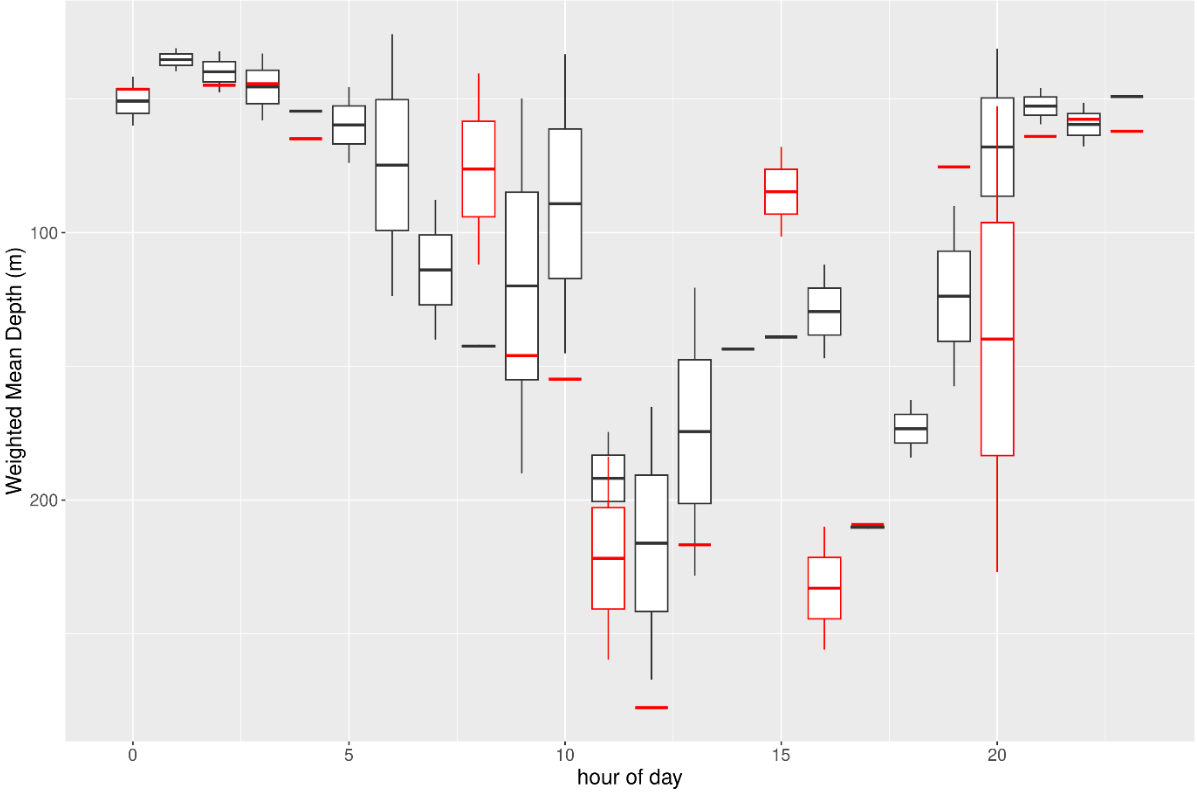

Figure 6. Boxplots showing the weighted mean depth (m) of capelin (black) and krill (red) by hour of day. Daylight hours are from 0800 to 2100.

ACKNOWLEDGEMENT

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9. The importance of capelin as prey for cod on the Iceland shelf

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Abstract

Capelin is an important prey species for demersal fish stocks on the Iceland shelf. In the two bottom trawl surveys conducted by MFRI, in October (SMH) and March (SMB), stomach content of selected fish species is analyzed. Here the focus is on the capelin content in cod stomachs. Estimates on capelin in cod stomachs from SMH during 1996-2023 indicate that overlap between cod and capelin is restricted to the edge of the shelf north of Iceland. In 2002-2004, there was a sharp decline in cod consumption of capelin, which coincided with more northerly distribution of the capelin stock and less spatial overlap￼. The amount of capelin in cod stomachs in SMB during 1993-2023 varied between years and represents the distribution of the capelin. SMB is conducted in March at a time when most of the capelin has arrived at the spawning grounds on the Icelandic shelf, and when the capelin fisheries is finished. Hence, the amount of capelin in cod stomachs in March indicates the amount of capelin left for spawning or the spawning stock biomass.

Keywords: cod, capelin, stomach content, diet, SMB, SMH

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INTRODUCTION

Capelin is an important prey species for demersal fish stocks on the Iceland shelf, specifically cod, Greenland halibut and saithe. Part of the sampling protocol in the two bottom trawl surveys conducted by MFRI in October (SMH) and March (SMB) (Figure 1 right) is to analyze the stomach content of selected fish species (Figure 1 left). The cod stomach time series is the longest and provides information on capelin distribution and abundance on the Iceland shelf annually since 1993 (SMB) and 1996 (SMH).

Annual predation on capelin by demersal fish has been estimated to range from 1000 to 1300 thousand tons (kt), and if marine mammals and seabirds are included, the range is from 3000 to 5000 kt (Vilhjálmsson 2002). The estimates for demersal fish predation are based on stomach samples and evacuation rate models (Pálsson and Björnsson 2009), while estimates for whale predation are best described as an educated guess. Cod, haddock, and saithe are the fish predators included in the model used to predict the spawning stock of capelin. Their annual predation of capelin is estimated at 900-1100 kt, of which around 250 kt are consumed from the main capelin spawning migration during a two-month period, January 15th to March 15th, when the maturing individuals migrate and spawn on the Iceland continental shelf. All those estimates are much higher than the estimated acoustic abundance of capelin, as demonstrated in Magnússon and Pálsson (1989). Obtaining updated estimate of predation and acoustic abundance is crucial in an attempt at explaining this discrepancy.

The maturing capelin are considered “winter food” for Icelandic cod (Magnússon and Pálsson 1989), as a large part of the capelin stock migrate northwards off the Icelandic shelf in early summer, consequently becoming inaccessible to cod. In October-November, the maturing capelin return to the Iceland shelf (Vilhjálmsson 2002). The spawning migration changed around 2000 when capelin began to return one to two months later to the Iceland shelf compared to previous decades (Carscadden et al. 2013). The time they are available as prey for cod is therefore shorter. Our objective is to examine the capelin abundance and distribution as represented by cod stomach samples obtained from SMB, SMH and commercial samples for the period 1993-2023.

METHODOLOGY

An annual index of the amount of capelin in cod stomachs on the Iceland shelf was estimated. The index is calculated as average stomach fullness, which is the weight of capelin in the stomach as a percentage of the predator’s bodyweight. Spatial distribution maps were generated yearly to visualize the patterns across time and space. Additionally, commercial samples can also be used for this type of analysis. Samples collected throughout the year by the crew of a commercial trawler, Páll Pálsson, from 2001-2017, were also used to calculate the average cod stomach fullness of capelin throughout the year.

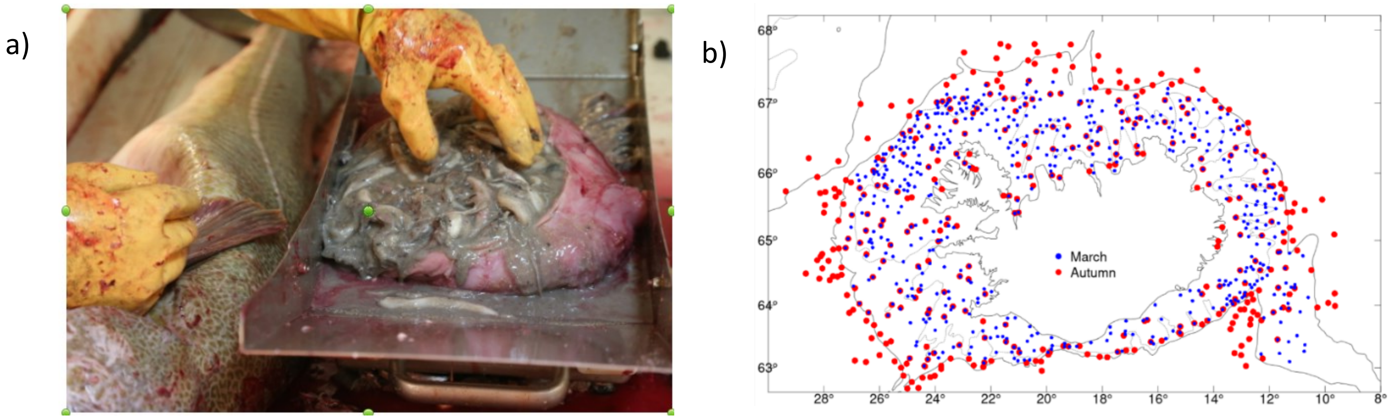

Figure 1. Cod stomach full of mature capelin from the MFRI bottom trawl survey in March (image by Höskuldur Björnsson) (left); Positions of bottom trawl stations in MFRI bottom trawl surveys in March (Spring) and October (Autumn) (right).

RESULTS AND DISCUSSION

Estimates based on capelin in cod stomachs from SMH (October) indicate that overlap between cod and capelin is restricted to the edge of the shelf north of Iceland (Figures 2 and 3 left). The survey began in 1996, and the results show that capelin consumption was higher in the early years, 1996-2001, compared to later years, from 2002 onwards (Figure 4). There was a sharp decline in cod consumption of capelin from 2002 to 2004, which coincided with changes in the distribution of the capelin stock. In those years, the feeding area of the capelin stock shifted from the Iceland Sea and shelf areas northwest, north, and northeast of Iceland to the East Greenland shelf (Carscadden et al. 2013).

The results on capelin content in cod stomachs in SMB (March) show considerable interannual variability in the distribution of the capelin (Figures 3 right and 6). SMB is conducted in March at a time when most of the capelin spawning on the Icelandic shelf has arrived at the spawning grounds. Most of the capelin fisheries are also finished by March. Hence, the amount of capelin in cod stomachs in March indicates the amount of capelin left for spawning after the fisheries have been conducted, or the spawning stock biomass (Figure 5).

The estimated spawning stock biomass of capelin has generally been high after a new management plan for capelin was introduced in 2016 (Figure 5, ICES 2023). This is to be expected, as the new plan is more precautionary than the old one. Since the estimate of the spawning stock has a high standard error, considerable variability in estimated stock spawning stock between years is not unexpected. The harvest control rule in place for capelin requires a certain amount to be left behind for spawning (escapement rule). Therefore, little correlation between stock size before and after fisheries is expected. Consequently, the amount of capelin in SMB is not a good indicator of the amount of capelin available for cod in that season, nor the size of the fishable stock at the beginning of the season.

The samples taken by the crew of the trawler Páll Pálsson from 2001-2017 show capelin in cod stomachs in all months (Figure 7). It is known that part of the mature capelin stock is often close to the Icelandic continental shelf during summer (Vilhjálmsson 1994, Pálsson 1985). These findings derived from commercial fishery targeting cod preying on capelin confirm the presence of capelin throughout the year deep off the Westfjords.

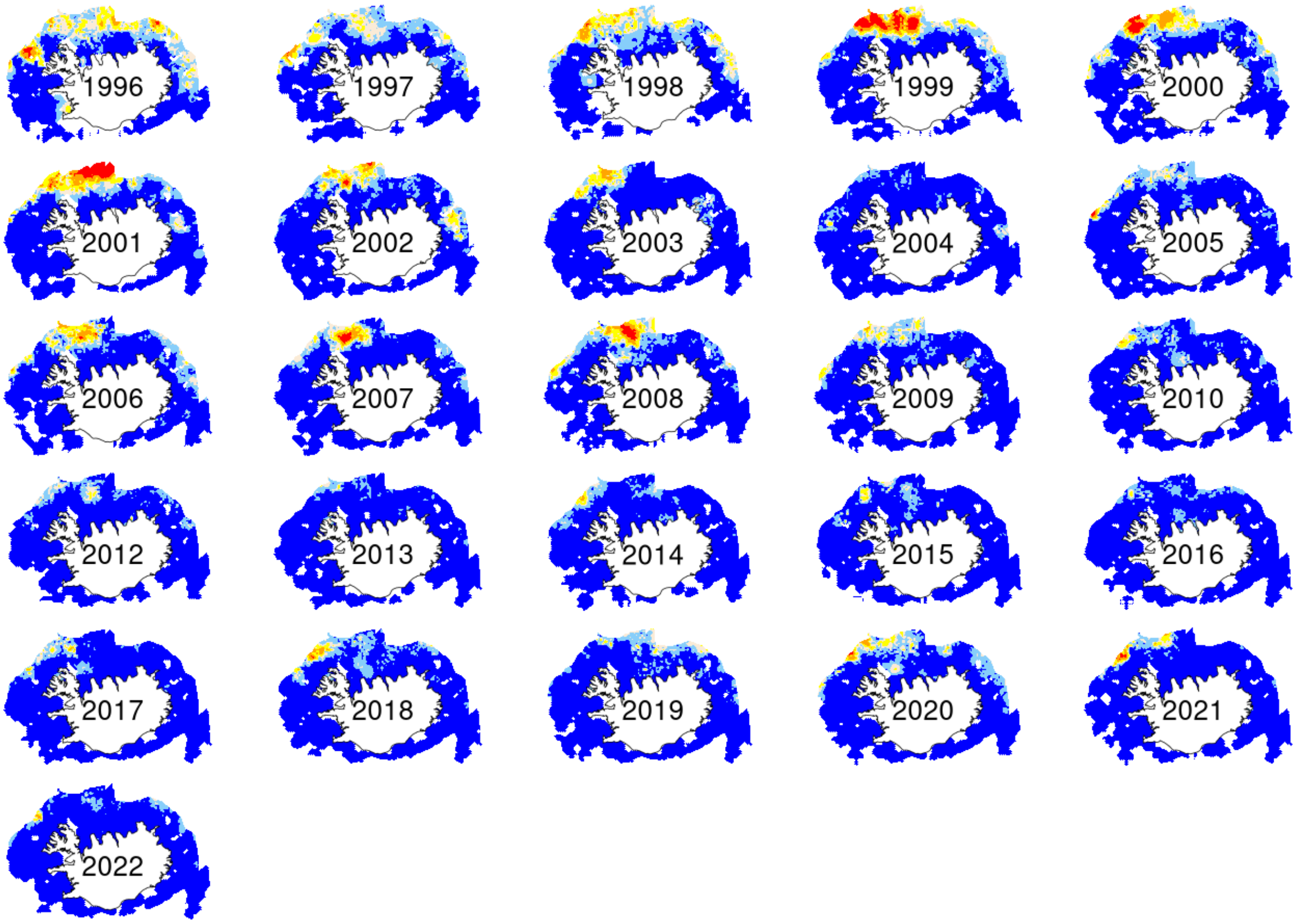

Figure 2. Capelin in cod stomachs in SMH is shown as a proportion of the predator's bodyweight from 1996 to 2022. The gradient indicates the value of the index going from zero (blue) to high (red).

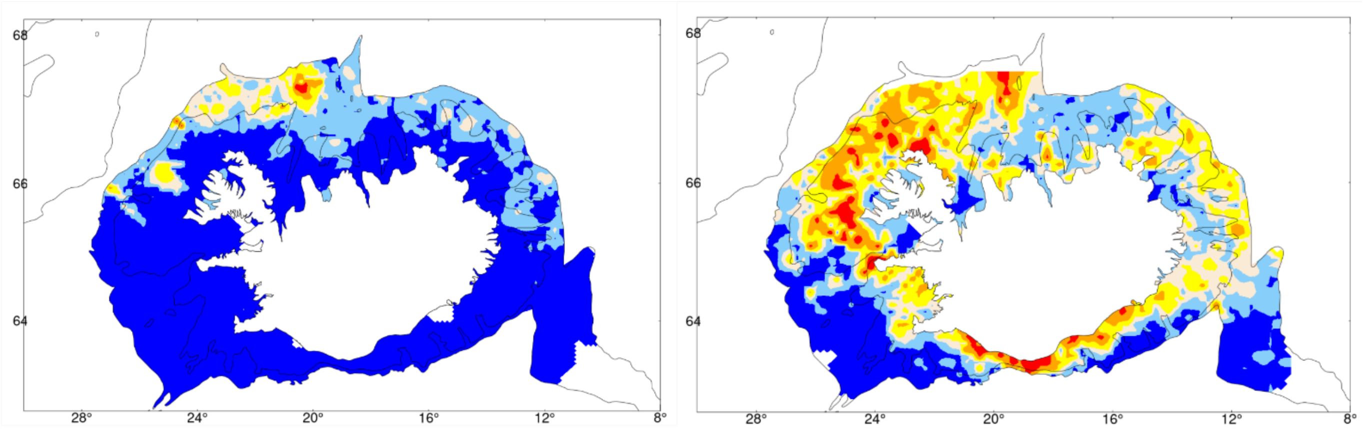

Figure 3. Average cod stomach fullness of capelin in the bottom trawl survey SMH in October from 1996-2022 (left); Average cod stomach fullness of capelin in the bottom trawl survey SMB in March from 1993-2023 (right). The gradient indicates the value of the index going from zero (blue) to high (red).

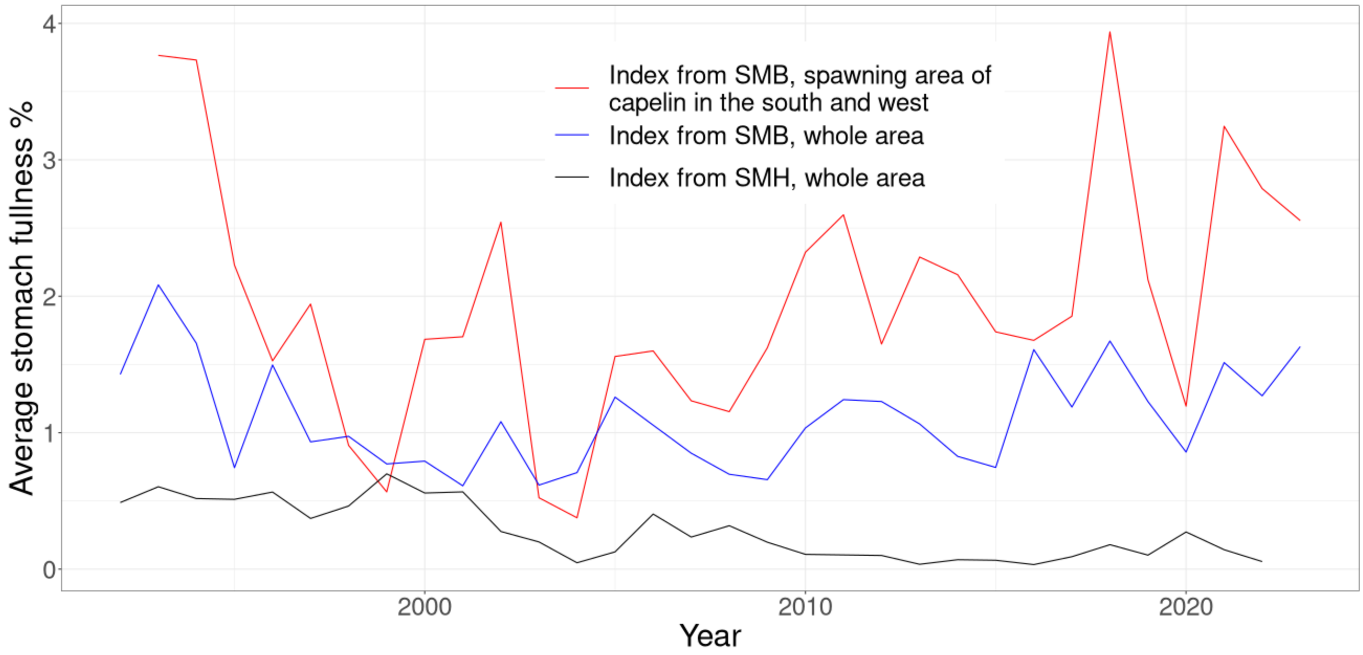

Figure 4. Index of capelin abundance shown as average stomach fullness of capelin in 40-100cm cod for years 1992-2023. The blue line is based on samples from the capelin spawning area south and west of Iceland.

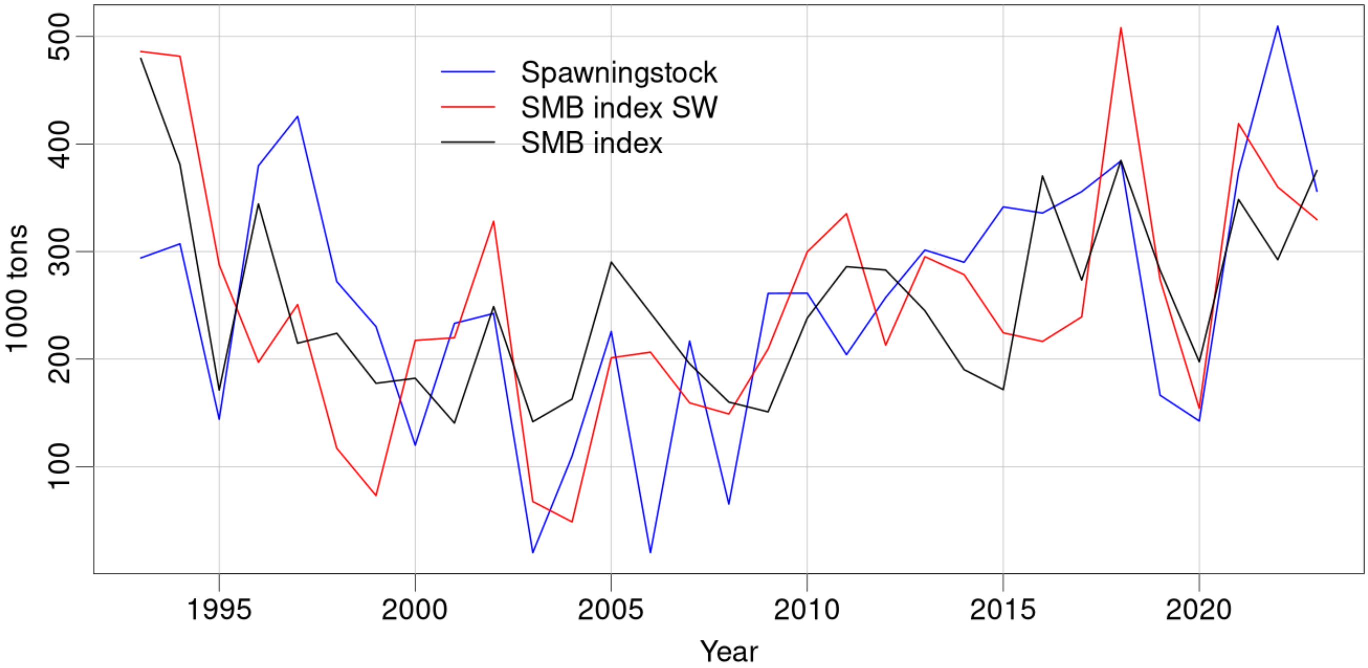

Figure 5. Capelin spawning stock biomass (SSB) (blue; ICES 2023), stomach fullness indices from SMB (black) and indices from SMB south-west (red). Stomach indices are the same as in Figure 4 but scaled to have the same mean as the SSB.

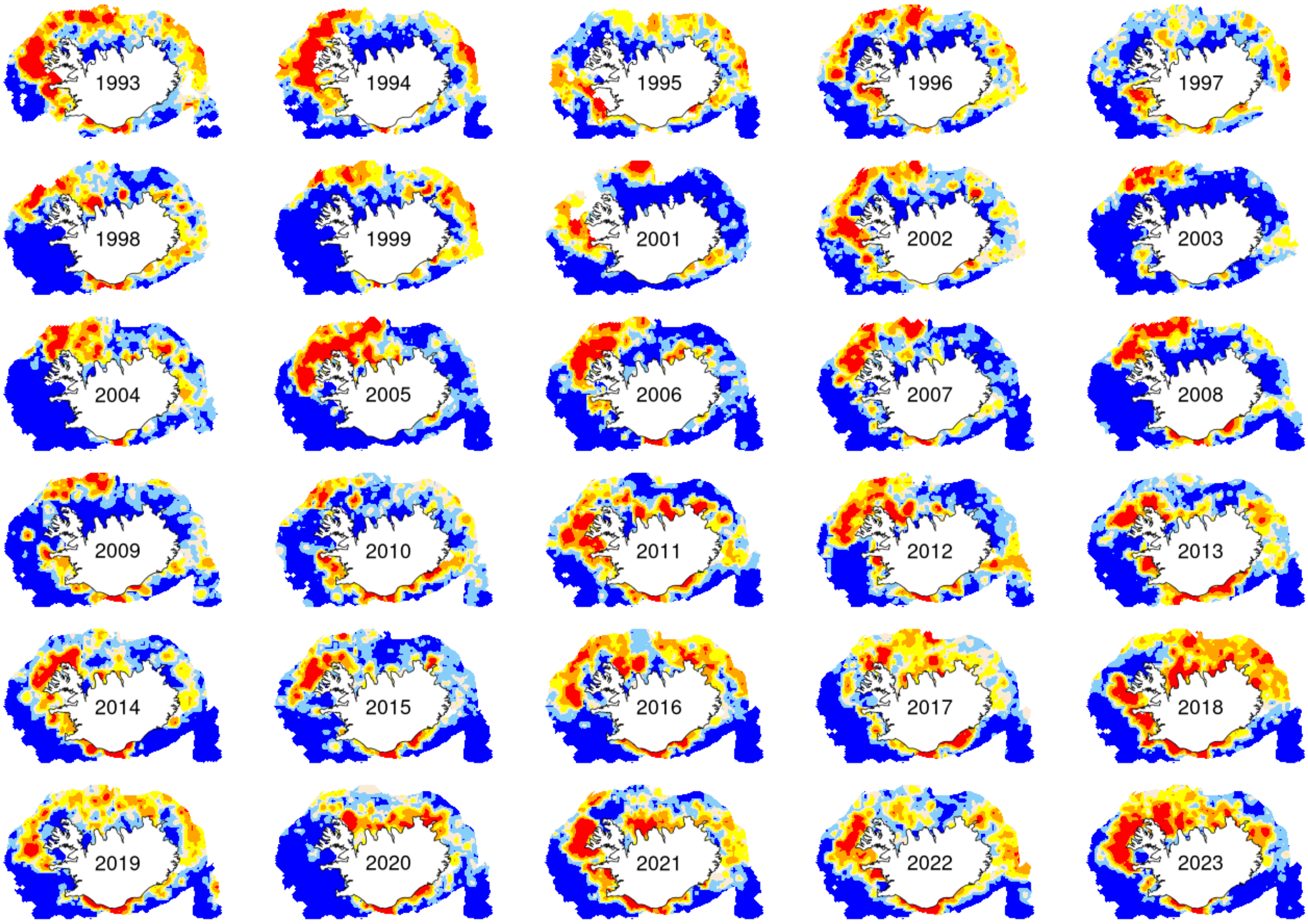

Figure 6. Capelin in the stomachs of cod in SMB is shown as a proportion of the predator's bodyweight. The gradient indicates the value of the index going from zero (blue) to high (red).

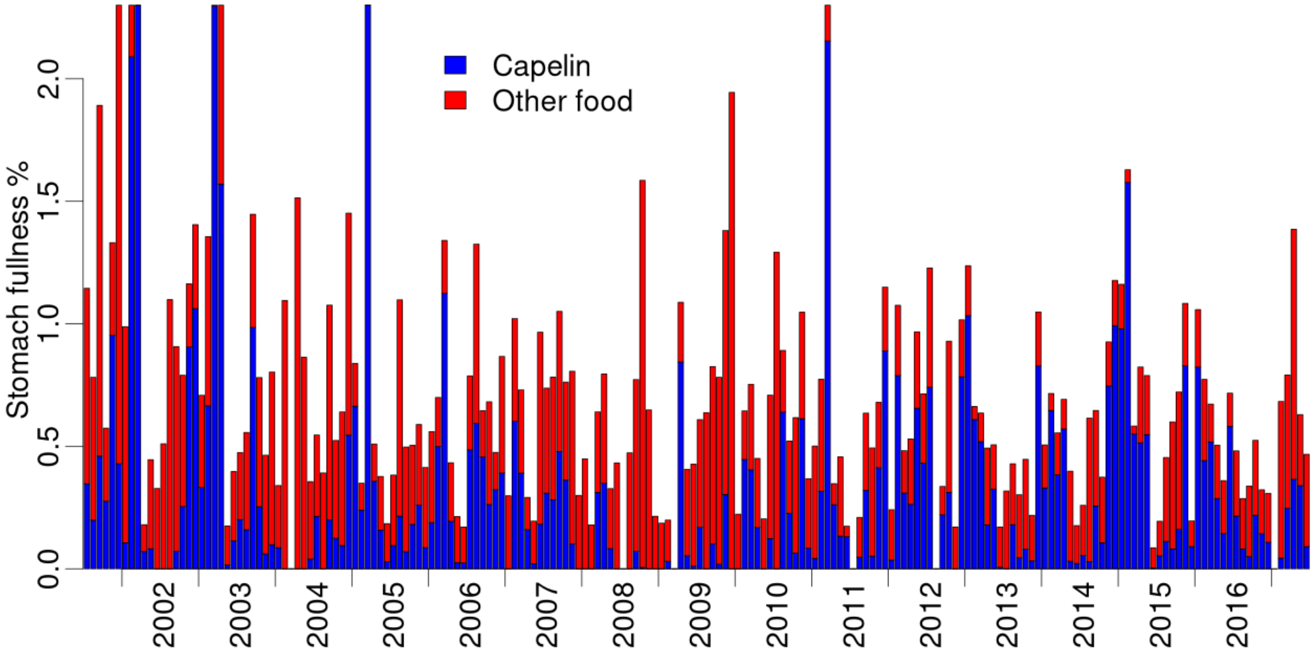

Figure 7. Capelin and other food based on samples by the crew of Páll Pálsson by month and year from 2001-2017.

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10. Capelin (*Mallotus villosus*) - harbor porpoise (*Phocoena phocoena*) - prey-predator relationship in Icelandic waters

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Abstract

In Icelandic waters, the diet of the harbour porpoise, a small marine mammal, has been studied using stomach content analysis of more than 1,000 bycaught individuals collected in 1991-1997. This analysis suggested that capelin was the predominant prey both in late winter and spring, while sandeel was dominant in the summer. However, this study was performed more than 30 years ago and there is a need to assess if harbour porpoise is still feeding mainly on capelin after the observed changes in capelin distribution and abundance. To answer this question, we used another method which can give rapid information about prey-predator relationships: stable isotopes of carbon (C) and nitrogen (N). The C and N isotope ratios in predator tissues reflect those of the environment and the prey ingested. This method was used on a subset of tissue samples collected during the months of March or April in the 1990s and 2010s. The results showed that harbour porpoise exhibited a rather small isotopic niche width, suggesting a stable diet composed of very few species (capelin, sandeel and gadoids). Bayesian mixing analysis of isotopes' data showed that capelin was still the main prey consumed by harbour porpoise during these months in Icelandic waters. Recent necropsies of bycaught individuals confirmed these results and showed that five out of seven stomachs collected in March/April were full of capelin. The two remaining ones were empty.

Keywords: stomach content, stable isotopes, diet composition, harbour porpoise, capelin.

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INTRODUCTION

The harbour porpoise (*Phocoena phocoena*) is a small cetacean measuring 1.5 to 1.7m, which reaches a maximum age of 24 years and is an important predator of pelagic fish. Its diet varies both seasonally and geographically and has been described to be mainly comprised of schooling fish such as sandeel (*Ammodytes marinus*), sprat (*Sprattus sprattus*), herring (*Clupea harengus*) and capelin (*Mallotus villosus*). In Icelandic waters, the annual consumption of pelagic fish by harbour porpoise has been estimated to reach 48,000 tons (Sigurjónsson & Víkingsson, 1997). The diet composition of harbour porpoise has been reported only recently and was based on analyses of stomach content performed on bycaught animals collected from 1991 to 1997 (Sigurjónsson & Víkingsson, 1997; Víkingsson et al., 2003). These analyses, performed on more than 1,000 bycaught individuals, suggested that capelin was the predominant prey both in late winter and spring, while sandeel was the dominant species in summer. However, this study was performed 30 years ago before the changes in capelin distribution and decrease in abundance (Carscadden et al., 2013). Therefore, there is a need to assess whether harbour porpoise has changed its diet in relation to the decrease of capelin abundance in Icelandic waters during late winter and spring (Carscadden et al., 2013; Singh et al., 2020). To answer this question, we used a stable isotope approach and examined the carbon (C) and nitrogen (N) stable isotope ratios in 29 harbour porpoises. If capelin remains an important prey for this species, the stable isotope ratios in harbour porpoise tissues should reflect those of the environment and capelin. Concurrently, we also collected and analyzed the stomach content of seven individuals bycaught in Faxaflói Bay in April 2020 for comparison with the stable isotope results.

MATERIALS AND METHODS

Harbour porpoise samples were collected from 1992 to 1998 (n=11) and 2011 to 2019 (n=33), but only 29 could be analyzed for stable isotope ratio (see Samarra et al., 2022 for explanation). Most samples were collected in the months of March or April, coinciding with the main coastal gillnet effort for cod (Figure 1). For the majority of individuals, the year of collection, sex and body length were recorded.

Methodologies for isotopes analyses and statistical models are described in Samarra et al. (2022).

In addition, preliminary stomach content analysis was performed on seven bycaught harbour porpoises caught in Faxaflói in April 2020.

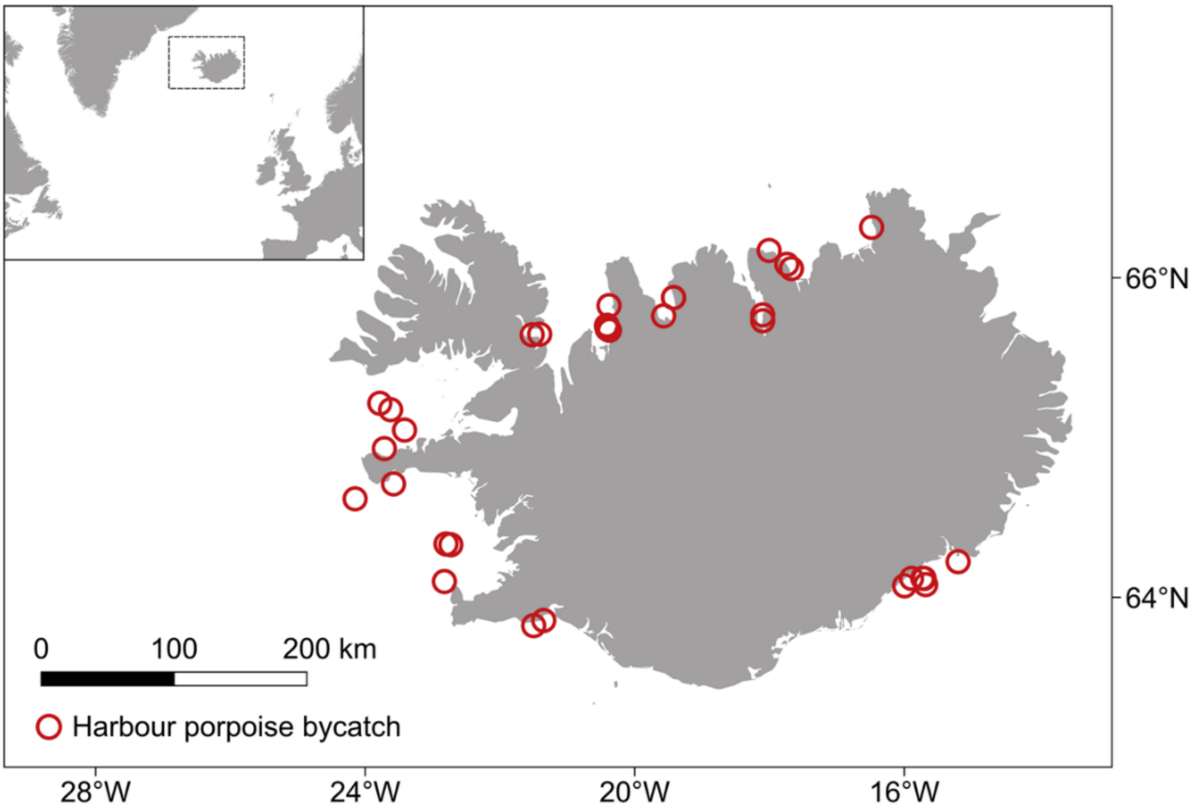
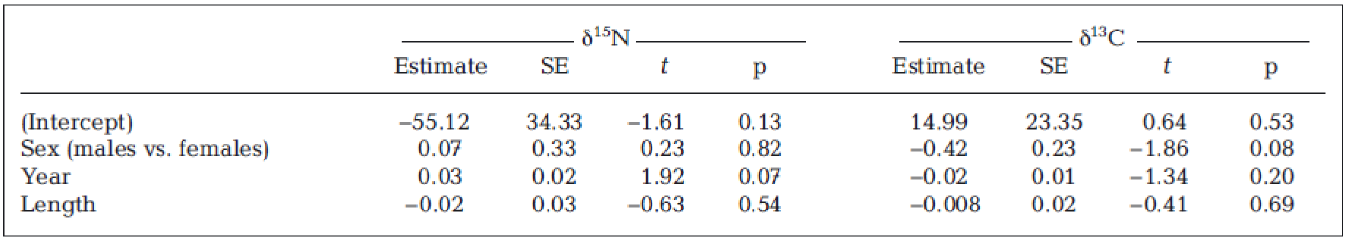


Figure 1. Sampling location of harbour porpoise (n = 29) for the isotope analysis collected from 1992 -2019.

RESULTS

Values of nitrogen isotope (δ^{15}N) for harbour porpoise muscle ranged between 11.35 and 14.57‰ (12.65 ± 0.74‰, n=29). Carbon isotope (δ^{13}C) values ranged between −20.37 and −17.64‰ (−19.19 ± 0.66‰, n=29). Both the δ^{15}N data (Shapiro-Wilks: *W*=0.97, p=0.64) and the δ^{13}C data (Shapiro-Wilks: *W*=0.98, p=0.84) followed a normal distribution. The Generalized Linear Model (GLM) revealed no significant difference in δ^{15}N values for sex, year or length (GLM, p>0.05, Table 1). Also, there were no significant effects on δ^{13}C values for any of these covariates (GLM, p>0.05, Table 1).

Table 1. Generalized Linear Model (GLM) testing for sex, year of sampling and length effect on isotopes values. SE: standard error; t, student t value; p, p value. Adapted from Samarra et al. (2022).



	$\delta^{15}N$				$\delta^{13}C$			
	Estimate	SE	*t*	p	Estimate	SE	*t*	p
(Intercept)	−55.12	34.33	−1.61	0.13	14.99	23.35	0.64	0.53
Sex (males vs. females)	0.07	0.33	0.23	0.82	−0.42	0.23	−1.86	0.08
Year	0.03	0.02	1.92	0.07	−0.02	0.01	−1.34	0.20
Length	−0.02	0.03	−0.63	0.54	−0.008	0.02	−0.41	0.69

A stable isotope Bayesian mixing model revealed that capelin was by far the most important prey source (94.60 ± 2.80%). In comparison, both gadoids (2.80 ± 1.50%) and sandeel (2.6 ± 2.2%) contributed very little to the diet composition of harbour porpoises (Figure 2).

Seven harbour porpoises, which were bycaught in April 2020 in Faxafloi Bay, were dissected in the Marine and Freshwater Research Institute in 2022, and stomachs were collected for diet analysis. Preliminary results showed that all stomachs but two contained a high amount of capelin skeleton and otoliths (Figure 3). Most of the otoliths were from capelin, and a few otoliths from haddock and sandeel were also retrieved (see Figure 3).

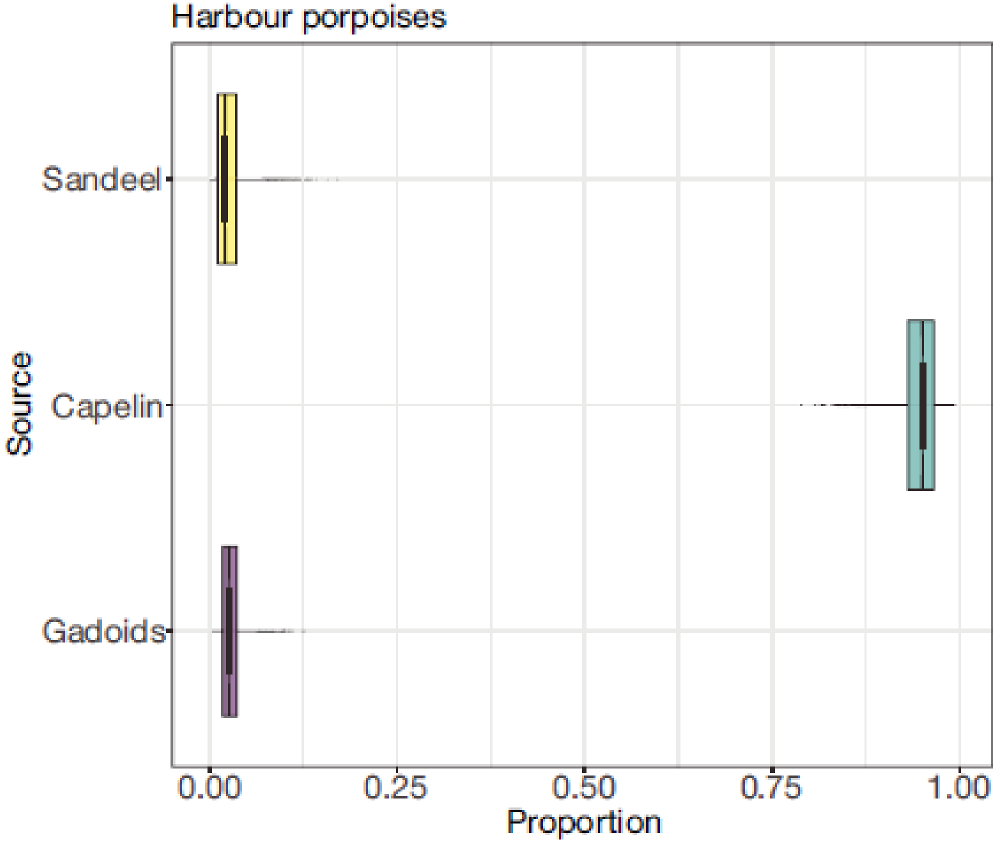


Figure 2. Bayesian mixing model estimates (mean, 25% and 75% percentiles) of diet composition for harbour porpoises *Phocoena phocoena*. Prey sources for gadoid species are grouped, which includes cod and haddock. Adapted from Samarra et al. (2022).

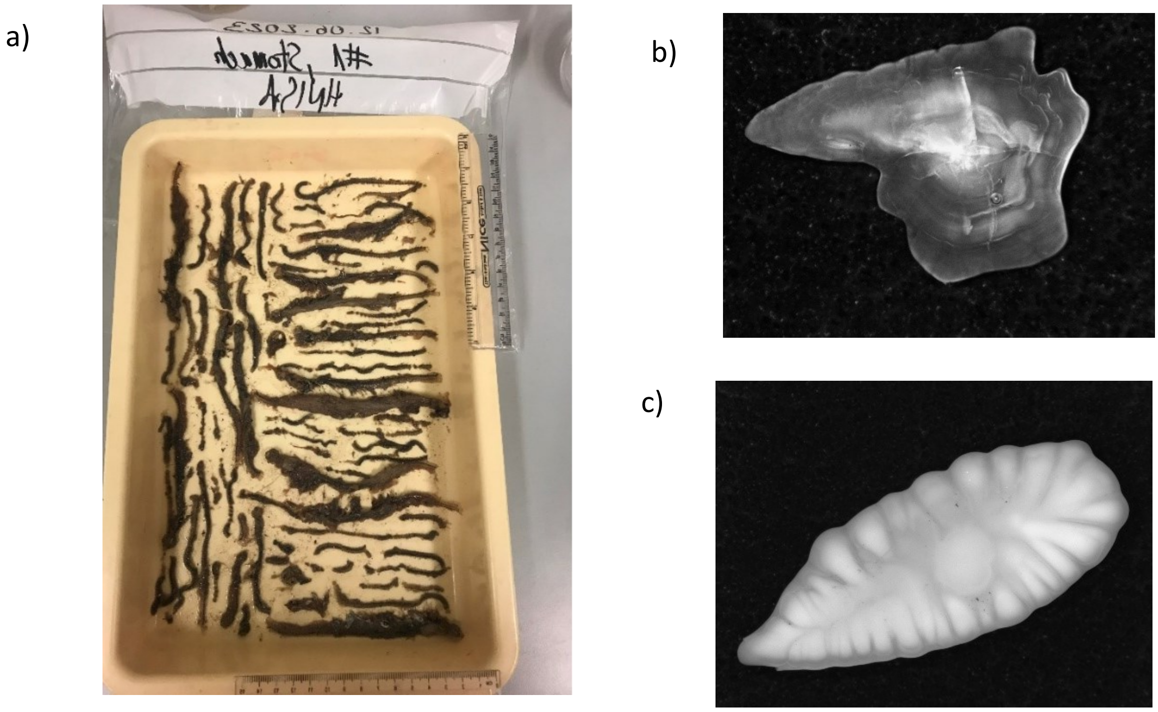


Figure 3. Samples collected in the stomach of Harbour porpoise: a) fish skeleton (capelin), b) capelin otolith, c) haddock otolith.

DISCUSSION & CONCLUSION

The objective of this study was to assess whether the harbour porpoise remains an important predator of capelin despite the observed decrease in the abundance of this pelagic fish (Carscadden et al., 2013). In a previous study, diet analyses of harbour porpoise were conducted on samples collected from 1991 to 1997 (Vikingsson et al., 2003). Hence, the diet of this species has not been studied for more than 30 years. As stomach content analyses are often difficult to perform and labor intensive, the present study used stable isotope analysis. The results revealed that the isotopic niche of harbour porpoises has a rather small width and that their diet is mainly composed of very few species during the months of March and April. The Bayesian mixing model analysis confirmed that capelin remains the most important prey source for harbour porpoise during this period of the year, even in the years 2011-2019, despite the changes in capelin's distribution and abundance. Samples for the isotope analysis have been collected from all around the country, suggesting that harbour porpoise could find capelin at this period of the year along the continental shelf of Iceland. The metabolic rate of harbour porpoise varies from 7.8 to 31.0 MJ per day, suggesting high food intake and assimilation rates (Rojano-Donãte et al., 2018). The stable isotope ratio analysis performed during the present study is expected to reflect food intake and assimilation from the last 7 to 30 days prior to the collection of samples (Rojano-Donãte et al., 2018). In conclusion, despite the long-term interval between the different studies performed (Vikingsson et al., 2003; Samarra et al., 2022) and the change in capelin distribution and abundance, the present study also confirms the dominance of capelin in the diet of harbour porpoise in March/April. Therefore, the harbour porpoise has not changed its diet in over 30 years and still relies heavily on the presence of capelin as a prey item.

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This study is dedicated to our colleague, mentor and friend, Gísli Víkingsson, who passed away last year.

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11. Whale abundance in relation to capelin abundance in east Greenland waters in autumn

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Abstract

Whales were systematically counted during the capelin autumn surveys in 2017 and 2018. The objective was to investigate whether any relationship existed between the abundance of identified functional groups of whales and capelin. A total of 205 whales of seven species were observed in 2017, while 1295 whales of eight species were observed in 2018. The most common species was the humpback whale (*Megaloptera novaanglea*) in both years. The species were divided into two functional groups: baleen and toothed whales. Whale and capelin abundance data were then compiled on a fine spatial grid (0.5° x 1° latitude and longitude) for statistical analysis. Whales of both functional groups were found at a higher frequency than expected where capelin was present, with the relationship being stronger for baleen whales. Further, a Generalized Additive Model (GAM) showed a weak (11% deviance explained) but significant relationship between capelin echo abundance and total whale abundance. When modelled separately for the two main species that overlapped with capelin, i.e. minke and humpback whales, this positive relationship was stronger (49% deviance explained for minke and 27% for humpback).

Keywords: whales, capelin, predation, ecological niche

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† Gísli Víkingsson passed away unexpectedly on the 18th of July 2022.

INTRODUCTION

In the waters between Iceland, East Greenland and Jan Mayen, capelin (*Mallotus villosus*) is one of the most important species in the ecosystem, as it is a vital source of prey for a wide variety of demersal fish, marine mammals, and seabirds. Despite this, relatively little is known about the interaction between whales and capelin, in particular, the relationship between humpback whales (*Megaloptera novaanglea*) and capelin (Heide-Jørgensen et al. 2022). Studies based on stomach contents of hunted animals have shown that fin whales (*Balaenoptera physalus*) and minke whales (*B. acutorostrata*) eat a considerable amount of capelin for parts of the year (Sigurjónsson and Víkingsson, 1997), and that humpback whales are commonly seen in association with capelin during the fishing season (Basran and Rasmussen, 2021). The population of humpback whales has increased substantially in recent years, from less than 2000 animals in 1987 to around 5000 animals in 2001 and up to more than 10,000 animals in 2015 (Pike et al. 2009, Pike et al. 2019). Given this increase, it was of interest to investigate the spatial overlap between humpback- and other whale species and capelin, particularly since the distribution of capelin has changed in recent years, where the summer distribution has changed from the north coast of Iceland to the east coast of Greenland (Vilhjálmsson 2007, Cascadden et al. 2013), and it appears that the presence of humpback whales in this general area has also increased in recent years (Heide-Jørgensen et al. 2022).

The objective of this study was to estimate the abundance of whales in capelin feeding grounds in autumn, when they are mainly present along the shelf area of east Greenland, and to explore the relationship between the abundance of functional whale groups and capelin echo abundance.

MATERIALS AND METHODS

Estimating capelin and whale abundance was done during the autumn surveys for capelin onboard three vessels. The research vessels Árni Friðriksson and Bjarni Sæmundsson were used in 2017, and in 2018, an additional commercial fishing vessel, EROS, was utilized. During the surveys, capelin was measured using calibrated echosounders on all three vessels.

Independent double platforms were used for the whale sightings on board Árni Friðriksson and Bjarni Sæmundsson, whereby the platforms were regarded to be completely independent of one another. Therefore, no communication related to sightings took place between the platforms. Observations onboard the EROS were made from two parallel observation stations situated above the bridge. These observation stations were in direct line with the vessel's two radars, and both observations were carried out from within the bridge ('single platform mode').

When weather conditions were suitable, or operationally when the ship's activities allowed, a minimum of two observers staffed each platform. Observers worked in teams and remained on the same platform. Binoculars were generally in use by at least one observer when sighting conditions allowed. Binoculars were frequently used for species ID and to estimate the radial distance using reticule readings from the horizon. Searching was usually abandoned in Beaufort Sea State (BSS) > 5 or when visibility from the vessel was 500 m or less (see further details in Pike et al. 2019). The observers strived to be on watch during all daylight hours when weather conditions were judged to be appropriate for surveying. The survey was carried out in 'passing mode' whereby the vessel did not deviate from the predesigned line transects to approach animals.

Sighting information had varying levels of certainty, but for the analysis, the most likely species was considered the right identification. The abundance (in numbers) of whales was estimated by species groups. The species were also divided into two functional groups: baleen and toothed whales. The capelin acoustic registration within defined spatial grids was divided by the area of the grid to obtain an estimate of echo abundance. Whale and capelin abundance data were then compiled on a fine spatial grid (0.5° x 1° latitude and longitude) for statistical analysis. The relationship between whale abundance and capelin echo abundance was explored. First, the proportion of whales found in "capelin squares" was contrasted with the proportion of squares where capelin was found, with the null hypothesis that whales would be found evenly regardless of capelin abundance using a one-proportion Z-test (prop.test). Second, a Generalized Additive Model (GAM) with family poisson and log-link, was fitted to the data using capelin echo abundance by square as a predictor for overall whale abundance. Subsequently, an alternative model was fitted using the abundance of only the two most common whales (minke and humpback) as the response variable. All statistical analysis was conducted in R v 4.0.3 (R Developmental Core Team 2021).

RESULTS

A total of 205 whales of seven species were observed in 2017, while 1295 whales of eight species were observed in 2018. The most common species of whale in both years was the humpback whale.

Whales were observed in 131 statistical squares (0.25 x 0.5-degree latitude and longitude) out of the 678 squares covered by the capelin surveys over the two years (Figure 1 top left). Baleen whales were found in more squares (Figure 1 top right, 121 squares) than toothed whales (Figure 1 bottom left, 30 squares). Capelin was observed in 73 out of the 678 squares covered, or around 11% of the squares covered. Whales were found significantly more often than expected in those 73 squares, with 47% of the whales observed found in squares where capelin were found ($X^2 = 2822$, $p < 0.0001$). This proportion was higher for baleen whales (39% found in "capelin squares") ($X^2 = 975$, $p < 0.0001$) than toothed whales (24% found in "capelin squares") ($X^2 = 142$, $p < 0.0001$). Humpback whales and minke whales mainly drove this, as 71% of the humpbacks ($X^2 = 1562$, $p < 0.0001$) and 69% of the minke whales ($X^2 = 158$, $p < 0.0001$) were found in "capelin squares" compared to 14% of the fin whales ($X^2 = 5$, $p = 0.02$) and none of the blue whales observed.

The relationship between capelin echo abundance and whale abundance was further explored with GAM. Overall, the capelin echo abundance explained 11% of the deviance in whale abundance ($p < 0.001$). However, this relationship was stronger when modelled separately for minke whales (49% of deviance explained) and humpbacks (27% of deviance explained).

Table 1. Species of whales observed in the study, and the proportion of them found in the statistical squares where capelin was found.

Species	Number observed	Proportion found in capelin squares
Humpback whale	427	71%
Minke whale	48	69%
Fin whale	592	14%
Blue whale	11	0%
Other/unidentified	235	36%
All baleen whales	**1313**	**38%**
White-beaked dolphin	245	42%
Long-finned pilot whale	560	16%
Sperm whale	19	37%
All toothed whales	**824**	**24%**

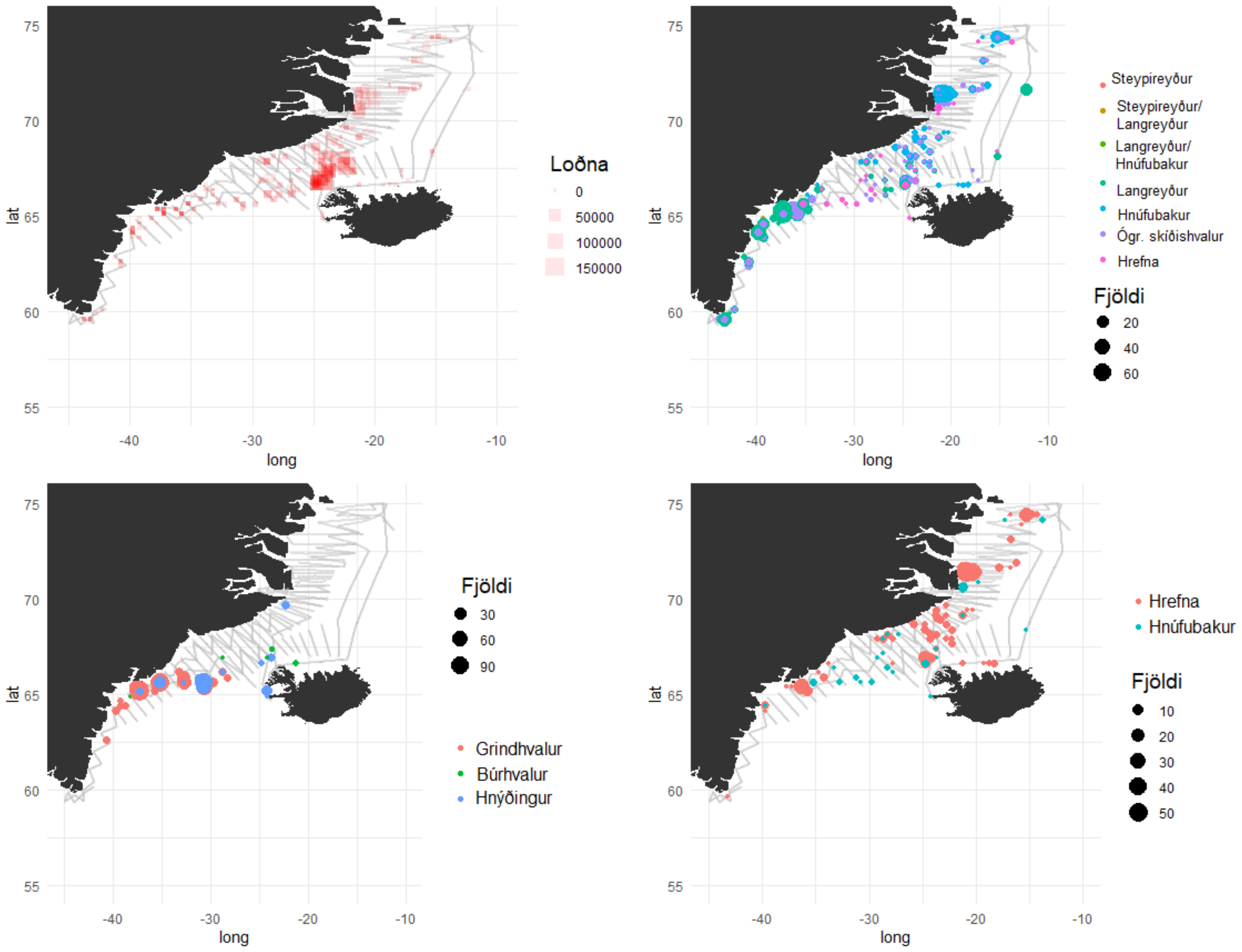

Figure 1. Maps showing capelin echo abundance (top left) and abundances of baleen whales (top right), toothed whales (bottom left), and humpback and minke whales (bottom right). Capelin survey tracks are shown in grey.

DISCUSSION & CONCLUSION

A definite spatial relationship between whale and capelin abundance was observed, as more whales were observed in squares where capelin was present. This relationship was stronger for species that are known or thought to eat capelin, in particular for the two most common baleen whales, humpbacks and minke whales, but also for white-beaked dolphins. The relationship was weaker for fin whales, but that is consistent with sampling from caught animals that have been observed to eat mainly krill.

The next steps are to link this analysis with stable isotope information from humpbacks that are being analyzed to confirm that they are, in fact, feeding on capelin. A recent study on white-beaked dolphins confirmed that they eat capelin but seem to prefer gadoids, while harbour porpoises seem to focus more on capelin (Samarra et al. 2022, **Paper 10** in this collection). Further information on the spatial overlap between humpback whales and capelin can be acquired from satellite tagging information, as 18 humpbacks were tagged in northern Iceland, Faxaflói and Ísafjarðardjúp in autumn and winter (October-February) in 2008-2015 (Figure 2). Some of the tagged animals, particularly those tagged in the north, seem to be moving towards the capelin grounds in the northwest, though this requires a more in-depth analysis.

In conclusion, considerable spatial overlap was observed between whale abundance and capelin echo abundance. This was strongest for species that are thought or known to feed on capelin.

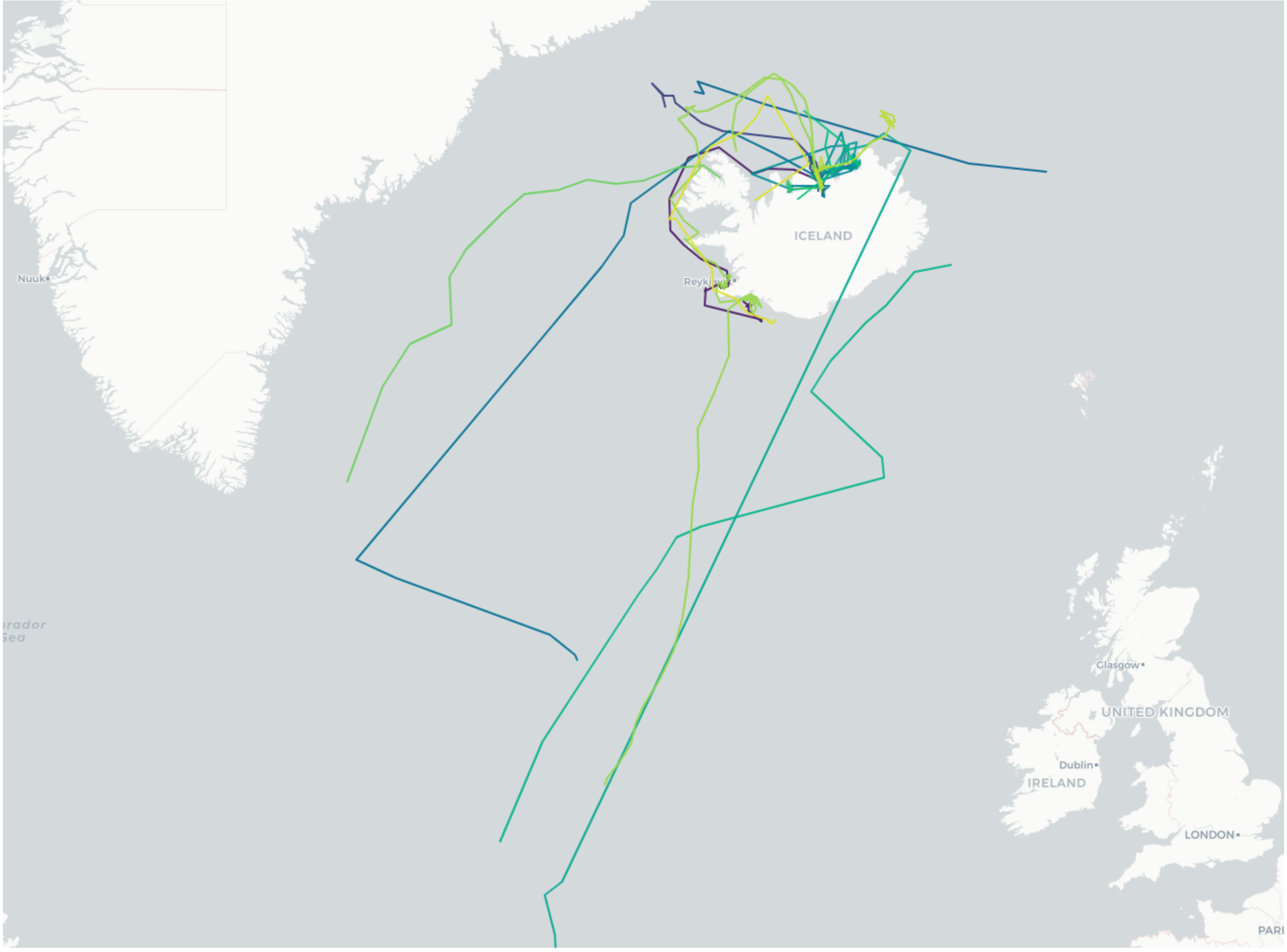

Figure 2. Tracks of 18 humpback whales tagged as part of this project with satellite tags. The animals were tagged in northern Iceland, Ísafjarðardjúp, Faxaflói, and eastern Iceland in 2008-2015 in autumn and winter (October-February).

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12. Verification of macroscopic maturity staging in Iceland-East Greenland-Jan Mayen capelin (*Mallotus villosus*)

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Abstract

Maturity determinations are essential when estimating spawning stock biomass in the assessment and management of commercial fish stocks. Spatial shift in feeding distribution of the Iceland-East Greenland-Jan Mayen (IEGJM) capelin stock in the early 2000s necessitated shifting their autumn stock assessment survey forward by approximately six weeks. This resulted in new challenges in identifying capelin maturity stage due to less developed gonads at that time. Capelin gonads from autumn surveys (2015–2018) were staged using both macroscopic and microscopic methods. The results showed that macroscopic and microscopic determinations were most often consistent for maturity stages I-III (>83% correctness), with stage III exhibiting the highest correspondence (88.2%). Statistical analysis did not reveal a significant difference between the two methods, supporting the continued use of the macroscopic method in stock assessment surveys. The overall survey maturity staging error rate was 17.4% in all stages (I-IV). Misclassifications in immature capelin being identified as mature and vice versa, resulted in a 1.3% overall underestimation of mature capelin. The 14-15 cm length group presented the most challenging interpretations, and the estimated length at first maturity (L_{50}) aligned with this length group for both staging methods. Additional histological sampling from this length group is recommended in future surveys for added certainty in maturity assessments.

Keywords: maturity, histology, maturity estimation, Iceland-East Greenland-Jan Mayen capelin, stock assessment

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INTRODUCTION

Traditionally, the determination of sexual maturity in fish research has been based on visual inspection (macroscopic) of whole gonads (West, 1990). Macroscopic maturity estimation can, however, be inaccurate since it is generally restricted to unclear and often subjective assessments of gonad size, shape or color that do not necessarily correspond with cellular development (Vitale et al., 2006; Costa, 2009). Despite its limitations, macroscopic staging remains the most frequently used approach for assigning maturity status since it is the fastest and least expensive method available. However, histological (microscopic) examination of gonad structures is considered the most accurate method (West, 1990). Histological staging provides information at a cellular level and a high degree of accuracy in distinguishing between immature and mature individuals (West, 1990; Vitale et al., 2006). The major drawback of the microscopic method is that it is labor and resource intensive.

Maturity stage information is crucial when estimating spawning stock biomass (SSB) of the IEGJM capelin stock. The capelin fishery focuses on the mature part of the stock. Therefore, it is important to accurately distinguish between immature and mature capelin during stock assessment surveys. Incorrect assignment of maturity stages during the autumn stock assessment survey can result in inaccurate SSB estimation in the subsequent assessment, which impacts the catch advice. Thus, the objective of this study was to examine the accuracy and reliability of macroscopic maturity assignment of capelin in autumn assessment surveys and to assess if improvements are required to the current macroscopic method through comparative analysis with the microscopic method.

MATERIALS AND METHODS

Gonads were sampled in stock assessment surveys during autumn 2015–2018. In total, 156 gonads were staged using macroscopic methods at sea prior to being preserved in a 4% buffered formaldehyde solution for microscopic analysis. The capelin maturity scale includes eight maturity stages (Forberg, 1982). Maturity stages I and II are immature and stages >II are mature. The current study focuses on stages I-IV as they dominate samples (98%) collected in autumn surveys.

The gonad histology was analyzed in a laboratory using a microscope. Specific histological characteristics were used to identify the maturity stage. For females, maturity stage identification was based on oocyte development, such as yolk accumulation and the formation of cortical alveoli, as described by Forberg (1982, 1983) (Figure 1). The microscopic criteria on maturity stages of male gonads represents the amount and growth of spermatogonia, spermatocytes and spermatozoa (Flynn and Burton, 2003) (Figure 2).

Percentage error in macroscopic determination was calculated based on deviations from the microscopic determination. The error distribution among maturity stages was analyzed by maturity stage and fish length. An independent t-test was used to test whether there was a significant difference between the two maturity staging methods. To examine if the accuracy in maturity staging varied with capelin length, we split the capelin into six length groups (table in Figure 3).

Length at sexual maturity was estimated and defined by the size at which 50% of the sampled fish was mature (L50). The data were fitted using a binomial logistic regression analysis (Magallanes, 2016).

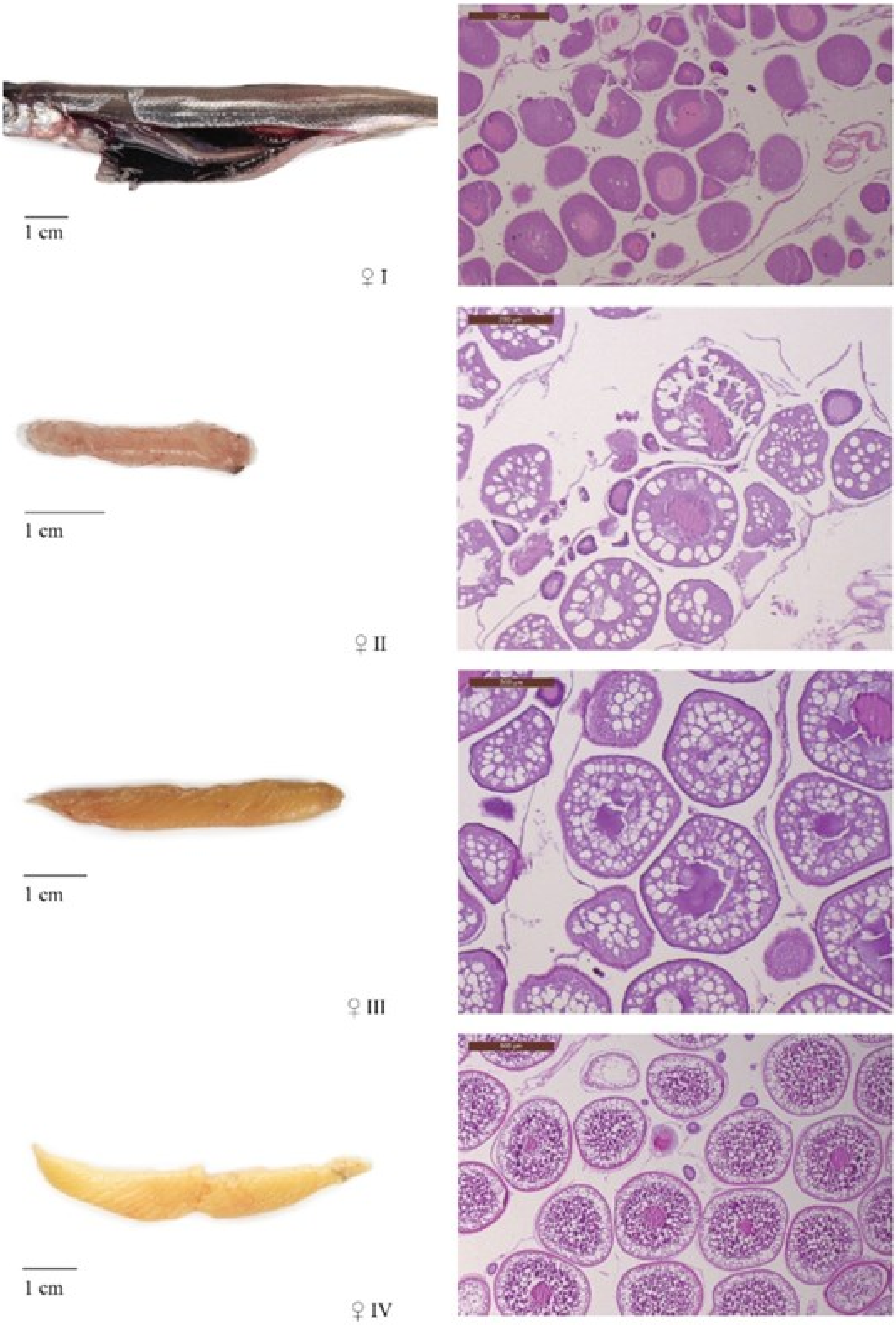


Figure 1. Macroscopic (left) and microscopic (right) images of capelin ovaries stages I-IV.

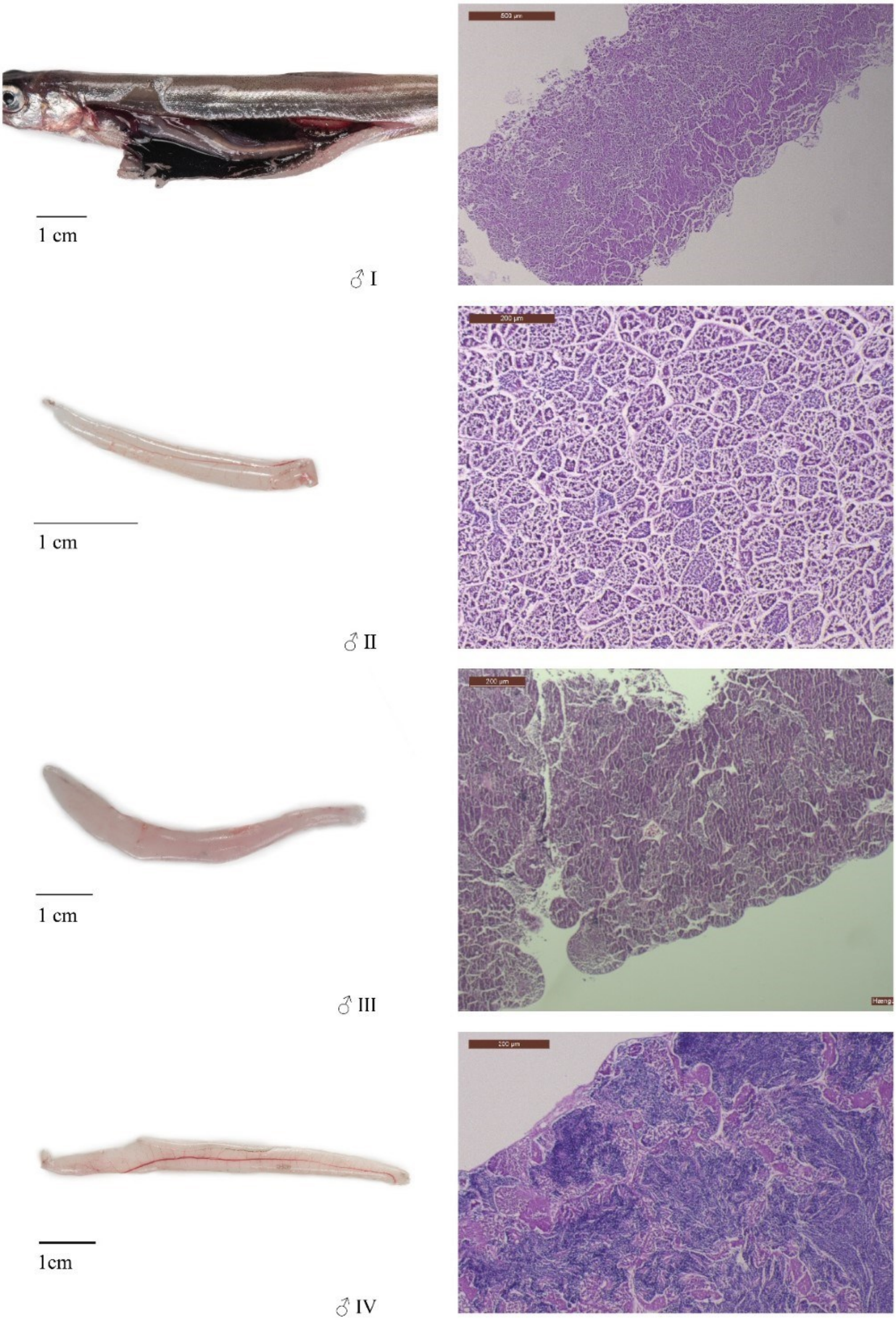


Figure 2. Macroscopic (left) and microscopic (right) images of capelin testes stages I-IV.

RESULTS

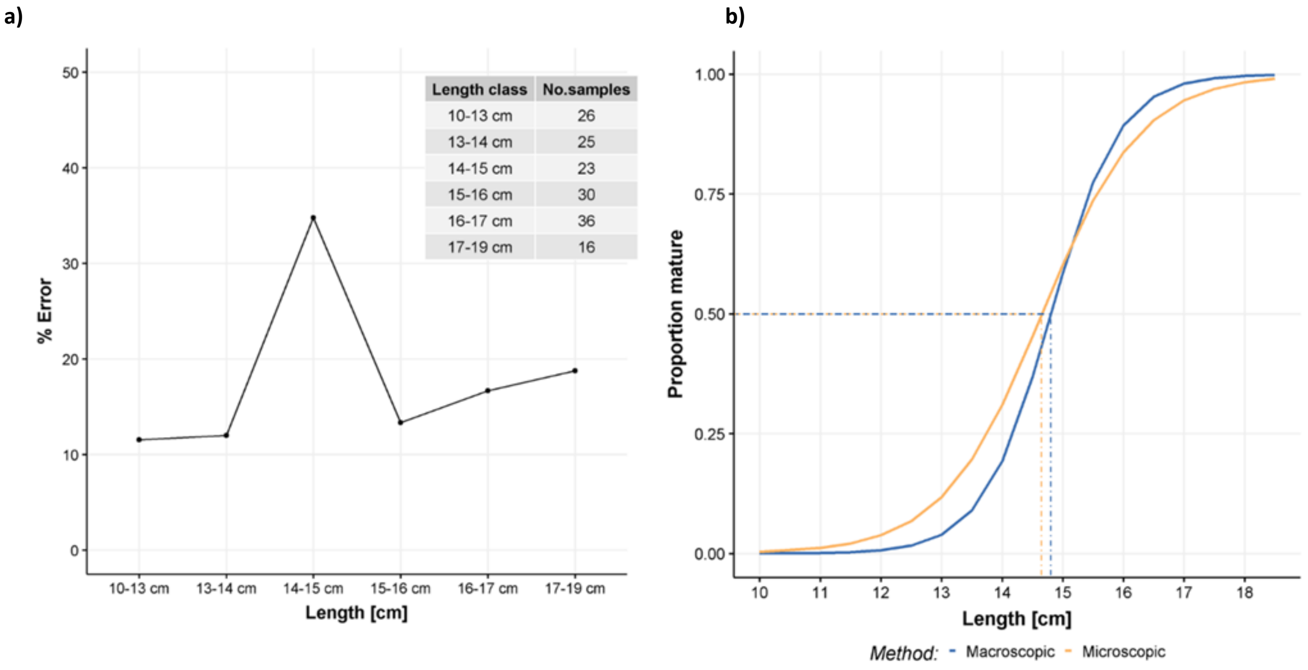
A comparison of macroscopic and microscopic determinations revealed that maturity stages I-III were most often (>83%) correctly identified (Table 1). The incidence of error in stages II and III was 16.3% and 11.8%, respectively. Stage III, the most frequent stage in the samples, exhibited the highest correspondence between micro – and macroscopic classifications (88.2%). It should be noted that the percentages for stage I and IV are based on a few individuals. The overall maturity staging error rate in autumn surveys was 17.4% (27 individual capelin were misidentified of the 156 used in the study). Of those, eight immature capelin were macroscopically identified as mature, and 10 mature capelin were considered immature (5.1% and 6.4%, respectively), leading to an underestimation of mature capelin by only 1.3%. The independent t-test revealed no difference between using the microscopic and macroscopic methods to distinguish between immature and mature capelin (t = 0.56, p = 0.57).

Compared to larger fish, the maturity stages of smaller fish (<14 cm) were more frequently correctly assigned macroscopically (Figure 3a). The length group with the highest maturity estimation error was 14 – 15 cm capelin.

Maturity ogives for microscopic and macroscopic analyses were similar (Figure 3b). The estimated length where 50% of the stock was mature (L50) was 14.8 cm for the macroscopic method and 14.7 cm for the microscopic method.

Table 1. Distribution of the macroscopic identification error for capelin gonads sampled in the autumn. Emboldened is the percentage of correspondence with microscopic maturity assignment. In brackets is the number of samples (n).

	Macroscopic identification (%)				
	Maturity stage				
Microscopic identification	**I**	**II**	**III**	**IV**	**Total % (n)**
I	**86.7** (13)	13.3 (2)	-	-	100 (15)
II	2.0 (1)	**83.6** (40)	16.3 (8)	-	100 (49)
III	-	11.8(10)	**88.2** (75)	-	100 (85)
IV	-	-	85.7 (6)	**14.3** (1)	100 (7)



Length class	No.samples
10-13 cm	26
13-14 cm	25
14-15 cm	23
15-16 cm	30
16-17 cm	36
17-19 cm	16

Figure 3. (a) Percentage error in macroscopic identification of capelin gonads by length class, where the table shows the number of samples in each length class. (b) Macroscopic (blue) and microscopic (yellow) maturity ogives of capelin as measured in autumn stock assessment surveys

DISCUSSION AND CONCLUSION

The most important finding of this research is the lack of significant difference in capelin maturity proportion estimates between the macroscopic and microscopic staging methods, a vital aspect for stock assessment and management. This supports the continued use of the macroscopic method in stock assessment surveys. However, in years with very large year classes coming into the stock, this might not be the case, as density-dependent effects can cause pelagic fish stocks to grow and mature at a slower rate (ICES, 2010; **Paper 3** in this collection). This research did not cover a period of large year classes entering the stock.

The observed overall maturity staging error rate of 17.4% highlights the importance of precise maturity assessment in capelin surveys. The misclassifications involved immature capelin being erroneously identified as mature and vice versa, leading to an overall underestimation of mature capelin by 1.3%.

By length class, the highest agreement between macroscopic and microscopic assessments occurred in smaller fish (<14 cm). Data from the 14-15 cm length group proved to be the most challenging to interpret and should be analyzed and interpreted with care. Moreover, the estimated length at first maturity, which was nearly identical for both methods, aligns with this same length group, underscoring its significance. As a precaution, we recommend that future autumn surveys include histological sampling from this length group for cases where the identification of maturity stages is considered uncertain.

When determining fish maturity stage, the most common sources of error in macroscopic analysis are related to the lack of standardization in the criteria used for maturity staging as well as poor interchange of criteria among observers (Vitale et al., 2006; McPherson et al., 2011). To reduce errors related to subjective maturity staging, more detailed classification criteria or a compilation of maturity stages (i.e., reduced number of maturity stages) are required.

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Bjarnason, S., Bárðason B, Óskarsson G.J, Egilsdóttir S. (2023). Verification of macroscopic maturity staging in Iceland-East Greenland-Jan Mayen capelin (*Mallotus villosus).* In W. Singh, A.H. Ólafsdóttir, S.Þ. Jónsson & G.J. Óskarsson (Eds.), *Capelin in a changing environment.* Haf- og vatnarannsóknir, HV 2023-43 (pp. 69-74)

13. The influence of vertical movement and physiology on capelin target strength

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Abstract

The biomass of capelin is measured using echosounders. Vertical movement and physiology of the fish (i.e., length, weight, body condition, swim bladder size, tilt, gonad status and fat index) can influence the strength of echoes returned from individual fish (target strength). This can consequently affect biomass estimation. The aim of this study was to evaluate how the target strength of capelin in the Iceland-East Greenland-Jan Mayen area is influenced by such factors. Acoustic and biological data collected during acoustic capelin assessment surveys between 2018 and 2022 were used to study capelin vertical movement behaviour during the late feeding season in the autumn and along their spawning migration during the winter. Capelin was found to undertake diel vertical migrations during both seasons, staying shallow (<100m) at night and moving to deeper waters (~200-250m) during the day. Mature fish tended to stay deeper during autumn (>150m) and shallower during winter (~100m). This can affect target strength measurements because of expansion or contraction of the swim bladder accompanying depth changes. Therefore, *in situ* target strength (TS) measurements were collected using a submersible echosounder deployed above capelin schools at varied depths. An analysis of these *in situ* measurements in relation to movement and physiology showed that the TS decreased with depth and was related to fish length and predicted swim bladder size. Additional data and analysis are required to make a reliable revision of the target strength-length relationship of capelin for this region.

Keywords: target strength, depth dependence, diel vertical migration, DVM

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INTRODUCTION

The acoustic assessment of capelin in the Iceland-East Greenland-Jan Mayen area follows echo-integration methods supported by biological samples (Vilhjálmsson, 1994). To convert acoustic backscatter (s_A) into fish abundance and biomass, an estimate of target strength (TS), which accounts for fish length, is needed (Simmonds and MacLennan, 2007). TS estimates applied for capelin vary between stocks in the North Atlantic and the Pacific (Dommasnes and Røttingen, 1985; Vilhjálmsson, 1994; Rose, 1998). In Iceland, the relationship is based on TS measurements from research carried out by the Norwegian Marine Research Institute more than 30 years ago on capelin scattering properties in the Barents Sea (Dommasnes and Røttingen, 1985; Vilhjálmsson, 1994). TS measurements must reflect capelin in their natural habitat (Jørgensen, 2004), as TS is influenced by the behaviour and physiology of the fish (i.e. fish length, swim bladder size, tilt, gonad status and fat index). The depth of the capelin in the water column can also significantly affect the TS (Jørgensen, 2004; Fässler et al., 2009). Therefore, the aim was to investigate 1) the movement and physiological properties of capelin schools with respect to depth and seasonal differences (autumn and winter) and 2) assess *in situ* TS measurements of individual capelin at different depths.

MATERIAL AND METHODS

For estimating the abundance of the capelin stock, the Marine and Freshwater Research Institute (MFRI) typically conducts two acoustic surveys, one in the autumn following the feeding period and another during the spawning migration in the winter. These involve large research vessels using calibrated acoustic echosounders and pelagic trawls for biological sampling (Vilhjalmsson, 1994; Vilhjálmsson and Carscadden, 2002).

Acoustic and biological data collected during the 2018-2022 surveys were analyzed for this research (Figure 1). For quantitative estimation on capelin diel vertical behaviour (DVM), the weighted mean depth of capelin backscatter by the hour of the day was estimated as it is hypothesized that TS declines with increasing depth. Also, variability in fish maturation, fat index, body condition, body weight and length with depth were studied. Additionally, in 2021 and 2022, a calibrated submersible echosounder equipped with a Wide Band Transceiver (WBT-TUBE) and two transducers (38 and 120kHz) was deployed. The instrument was positioned close to targeted capelin schools (~20m above the capelin) in three depth ranges: shallow, middle, and deep (Figure 1C), collecting single target data. TS data were collected with narrowband (continuous wave, CW at 38 and 120kHz) and broadband pulses (frequency modulated, FM, 35 to 45 and 90 to 170kHz, respectively). Single targets were automatically selected within >15-30m of the calibrated transducers central part of the beam (<3 degrees off-axis) (Ona, 1999; Jørgensen, 2004; Kubilius and Ona, 2012; Agersted et al., 2021).

Multiple regression analysis was used to test the effect of capelin physiology and depth on the *in situ* TS data. Effects tested were average fish length, weight, body condition factor and fat index of the capelin schools, pressure (i.e. depth of transducer) and estimated average swim bladder length (SBL) of capelin using a formula in Jørgensen (2004). The best model was selected based on the lowest Akaike information criterion (AIC) value.

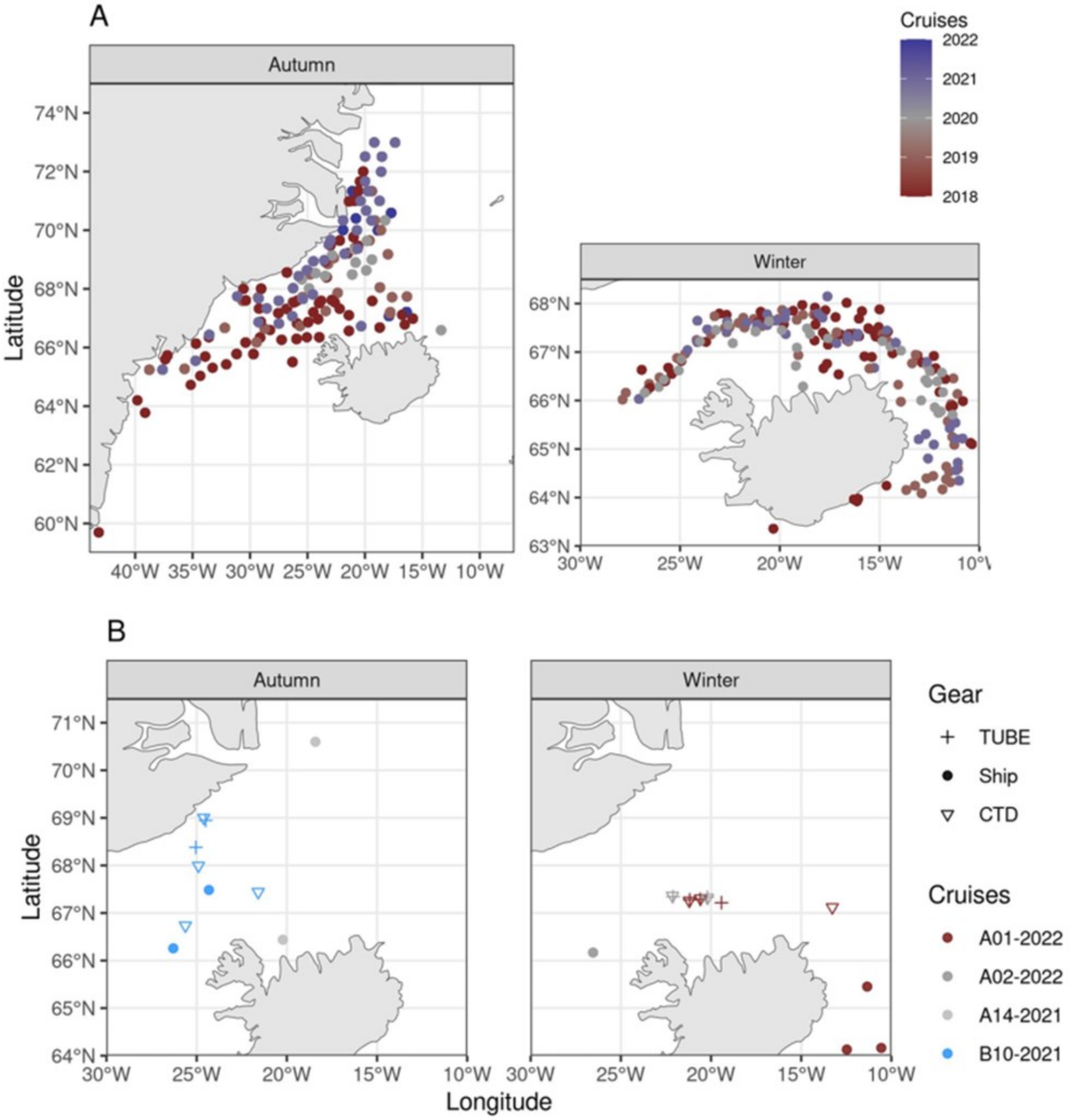

Figure 1. (A) The location of biological samples collected with pelagic trawl in autumn and winter during the 2018-2022 MFRI acoustic capelin assessment surveys. (B) The location of stations where *in situ* target strength measurements of capelin schools were conducted in autumn (A14-2021, B10-2021) and winter (A01-2022, A02-2022) are marked with different colours. The symbols indicate the type of gear used: WBT-TUBE (Tube), Hull-mounted acoustics (Ship) and Conductivity, Temperature and Depth - rosette (CTD).

RESULTS

Vertical movement and physiology of capelin between seasons

A combination of acoustical registrations and biological sampling showed that immature and mature capelin were found deeper (~150m) in autumn than in winter (~100m; Figure 2A). Fish length increased with depth during autumn, while in winter, larger individuals were generally found shallower (Figure 2B). Capelin displays DVM (Figure 2C), and this behaviour has been consistent over the years. However, DVM significantly differed between seasons (Nested Anova, $p<0.001$).

Capelin acoustic values were found to be variable by depth, hour of the day and season (Kruskal-Wallis-test, $p<0.001$). The highest variability of the acoustic values and generally least density was found >300m in both seasons (Figure 2D). Overall, ~36% of capelin acoustic backscatter was located at 100-200m, and 25% was deeper at >200m.

In situ TS measurements of capelin schools

The average TS of capelin decreased with depth but was found to be highly variable using both narrowband and broadband data (Figure 3). Fish length, predicted swim bladder size and depth of transducer were found to influence capelin's TS (Table 1).

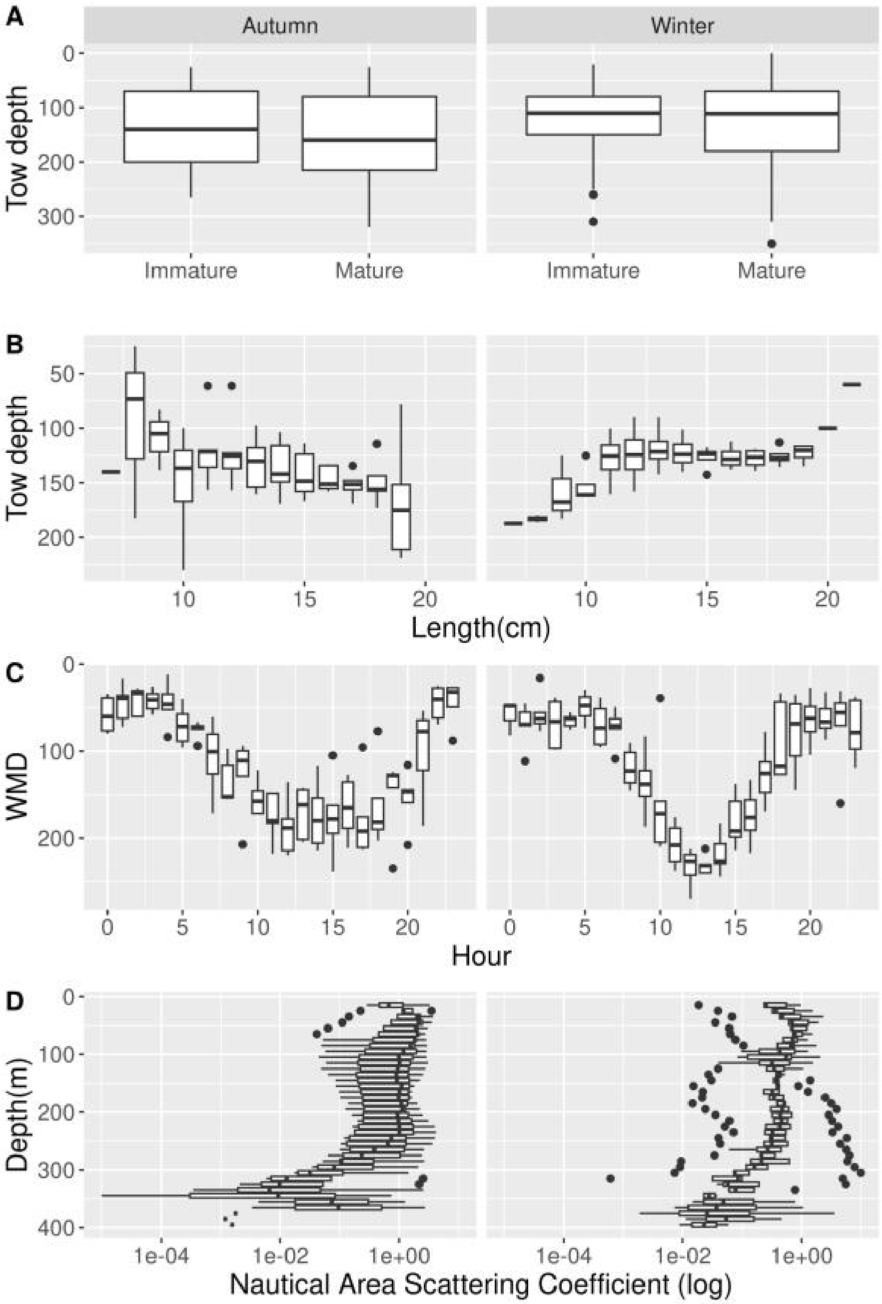

Figure 2. Capelin vertical movement and physiological differences between autumn and winter are illustrated using biological trawl samples and acoustic 38kHz data from 2018-2022 MFRI stock assessment surveys. Boxplots showing (A) depth distribution of immature and mature fish and (B) length by depth. (C) Diel variation in weighted mean depth (WMD, m) of capelin schools. (D) Boxplots showing the depth variability of capelin acoustic values (backscatter nautical area scattering coefficient, s_A, $m^2\ nmi^{-2}$).

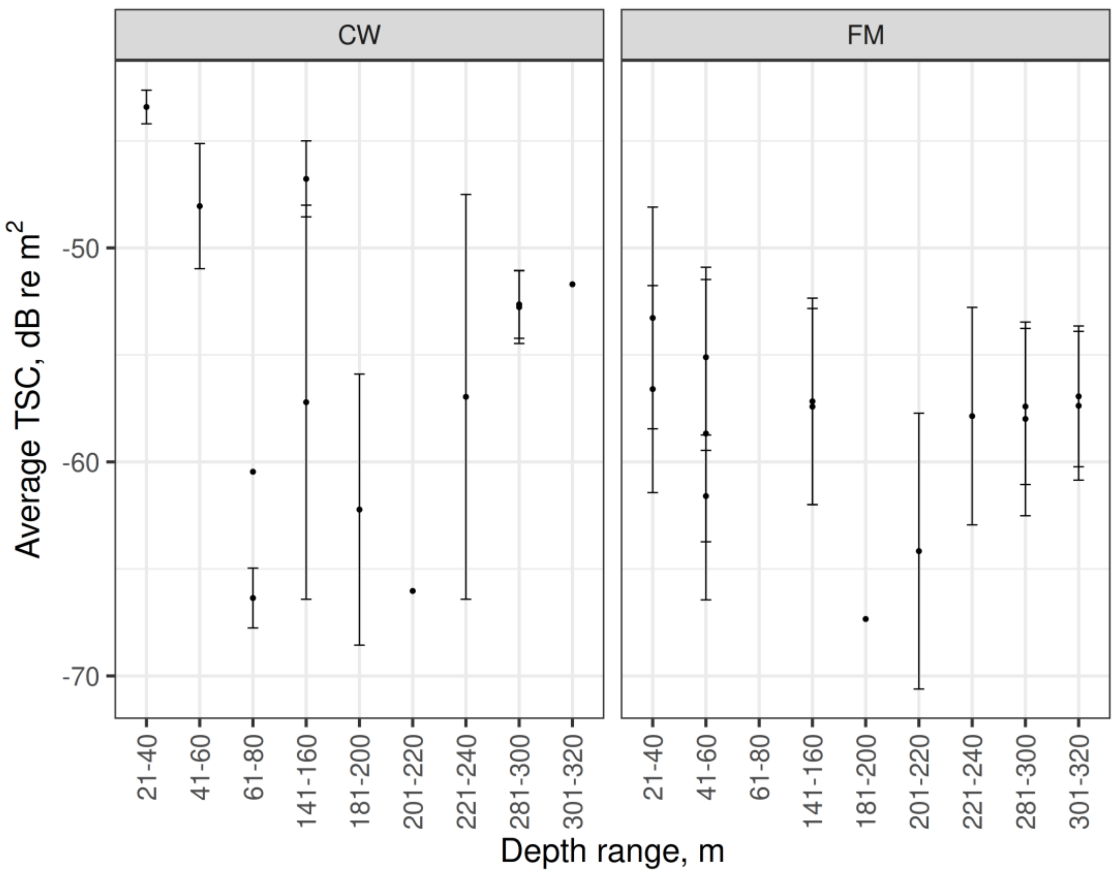

Figure 3. The average (dot) and standard deviation (whisker) of *in situ* TS beam Compensated (TSC, dB re m^2) of capelin for different depths (m) in narrowband (CW) and broadband (FM) acoustics modes of both WBT-TUBE and near-surface data from Hull-mounted acoustics. The total number of single targets (N=2059, >-70dB) automatically selected for both 38kHz calibrated transducers.

Table 1. The best multiple regression model, according to AIC, showing the effect of capelin physiology and depth/pressure on the *in situ* TSC (dB re m^2) broadband data (number of observations=20, R^2 = 0.833, R^2adjusted= 0.789, deviance=34.7). Effects tested were average fish length, weight, body condition factor and fat index of the capelin, pressure and estimated average swim bladder length (SBL) of capelin using a literature formula in Jørgensen (2004).

		TSC			
Predictors	*Estimates*	*CI*	*Statistic*	*p*	*df*
(Intercept)	-276.94	-379.34 – -174.54	-5.76	**<0.001**	15.00
Length [log10]	145.86	60.55 – 231.16	3.64	**0.002**	15.00
Body condition	28.24	-10.14 – 66.63	1.57	0.138	15.00
Pressure [log10]	15.16	9.37 – 20.96	5.58	**<0.001**	15.00
SBL [log10]	70.34	50.48 – 90.21	7.55	**<0.001**	15.00

DISCUSSION & CONCLUSION

Capelin performs diurnal vertical migration, migrating at night to shallow waters and having a deeper distribution during the day. During autumn, the capelin was deeper for a longer time during the day compared to winter. This could be due to a longer daylight regime as well as different vertical distribution of prey (Gislason and Silva, 2012).

The focus here was not to examine the reasons for the vertical migrations but its pattern, intensity and, thereby, the impacts it has on the acoustical properties of capelin. During descent, the contraction of the capelin swim bladder with corresponding increased pressure can introduce bias in the estimated biomass. The highest variability in the acoustic backscatter of capelin was found to be >300m, but it could be related to the scarce data found at these depths.

TS decreased with depth, likely influenced by swim bladder volume change with depth. The length and condition of fish were found to influence the TS of capelin. However, the current data is limited at depth and lacks correction for the swimming tilt of capelin (Gauthier and Horne, 2004).

In conclusion, the observed variation in the vertical distribution of capelin can introduce bias in the acoustic abundance measurements when ignoring depth dependency in acoustic backscatter properties. Furthermore, the backscatter properties were also shown to be influenced by biological variables that might have to be incorporated. Further data and work are needed to estimate capelin's TS-length relationship accurately.

ACKNOWLEDGEMENTS

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14. Benchmark assessment of the Iceland-East Greenland-Jan Mayen Capelin stock in 2022

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Abstract

The methodology and data behind the stock assessments and harvest control rules (HCR) are revised and improved regularly. This is done at benchmark assessment and management strategy evaluation workshops following extensive preparation work. Such a workshop took place in November 2022 within the International Council for the Exploration of the Sea (ICES) for the capelin stock in the Iceland-East Greenland-Jan Mayen area. Minor changes to the previous assessment procedure and HCR were suggested. The changes include limiting the weight given to the autumn survey acoustic measurements to 2/3rd in the intermediate advice and a maximum of 1/3rd in the final advice. Furthermore, based on the updated assessment method in 2015 assuming higher natural mortality, the capelin spawning stock biomass (SSB) and recruitment time series were recompiled for the period 1981-2015 resulting in a downward revision for most years. Based on the revised series of SSB and recruitment, the reference point for SSB (Blim) declined from 150 kt to 114 kt. The goal of the management plan remained unchanged, i.e., setting the final total allowable catch with >95% probability of SSB being greater than or equal to Blim at spawning time. The workshop concluded that the assessment approach represents the best available science following ICES procedures and considers the HCR precautionary.

Keywords: fisheries management. management plan. harvest control rule. ICES benchmark. capelin. predation model. stock assessment.

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INTRODUCTION

In November 2022, a benchmark workshop on capelin (*Mallotus villosus*) took place on behalf of the International Council for the Exploration of the Sea (ICES). The purpose of the benchmark (WKCAPELIN) was to review assessment methods and HCR of the Iceland-East Greenland-Jan Mayen (IEGJM) capelin stocks (ICES, 2023a). The goals were to evaluate the appropriateness of data and methods to determine stock status, the reference points and whether the current harvest control rule within the management plan is precautionary (ICES, 2023b).

The IEGJM capelin stock has been assessed annually by acoustic measurements in autumn and/or winter since 1980. On the basis of the last benchmark workshop in 2015 (ICES 2015), a new advice framework was adopted, which was founded on a stochastic approach, leaving 150 thousand tonnes for spawning with a 95% probability.

The current management plan, accepted by the coastal states in 2020, restricted the timing of the fishing season to begin on October 15th, thereby closing the summer fishery. The initial advice became irrelevant when the summer fishery closed and was therefore not reevaluated at WKCAPELIN.

To summarize the management plan, initial advice is set based on acoustic survey measurements of juveniles in the autumn, the year before advice year, with a very low probability of being higher than the estimated final advice. An intermediate advice is set on the basis of acoustic survey measurements of the fishable stock in the autumn, the same year as the advice, and as for the final advice following winter acoustic measurements, it will have >95% probability of SSB being greater than or equal to the limit reference point for spawning stock biomass (B_{lim}) at spawning time. The data and models used at each step of the process for intermediate and final advice were evaluated at the benchmark.

RESULTS

The acoustic surveys used to assess the stock size were evaluated. The process involved weighing the acoustic surveys in autumn and winter together in the assessment. This led to the conclusion that intermediate advice should only be $2^{nd}/3^{rd}$ of the calculated advice value from the autumn survey instead of 100%. Further, the autumn survey should have a maximum weight of 1/3rd in the final assessment. No such limit was in the assessment adopted by the 2015 benchmark. These changes were made as a precaution, mainly based on the recent (2021/2022) discrepancy between autumn and winter stock estimates (ICES 2023a).

It was also explored if uncertainty estimates (CV) derived from individual surveys should be used in the assessment or if a fixed value of 0.2 would be appropriate. Similarly, if a CV of 0.25 should be used for the intermediate assessment. Many surveys have high CV because of a patchy stock distribution, and this would lead to advice being too high if not accounted for (ICES 2009). Hence, the current methodology of using uncertainty estimates from individual surveys was accepted, while it was recognized that a floor on the CV of the final assessment might be needed.

The final assessment is based on a projection of the stock size from the 15th of January to the 15th of March using the predation model, where the proportional distribution of capelin migration and catches is projected in spatial and temporal steps, while predation from cod, haddock and saithe are considered. The advised catch corresponds to having a >95% probability of SSB being above Blim at spawning time. This approach is unchanged from what was decided at the 2015 benchmark assessment.

The only reference point needed for IEGJM capelin is Blim. Blim was set to 150 thousand tonnes in 2015 based on the average of the three lowest values of SSB, occurring in 1981, 1982 and 1990, which all led to average recruitment (ICES 2015). As a part of the 2022 benchmark, SSB estimates since 1981 were recalculated using the prediction model adopted in 2015 and revised acoustic survey indices from 2002–2006. The revised SSB estimates were lower than previous estimates for most years. After examining the recalculated stock-recruitment relationship with the revised SSB (Figure 1), it was considered appropriate to base Blim on the same three years as before. It resulted in a Blim of 114 thousand tonnes (Figure 1).

DISCUSSION & CONCLUSION

Following the 2022 benchmark results, the objective of the current management plan is to leave at least 114,000 t SSB for spawning with a 95% probability (escapement strategy). The TAC is advised in three steps:

1) *Initial TAC* for the coming fishing season is based on the autumn survey abundance estimate of immature capelin in relation to historical observations of recruitment and TAC.
2) *Intermediate TAC* is based on the biomass estimate of maturing capelin in the autumn survey. The TAC value is obtained by projecting the stock forwards with the predation model from September to March, but the intermediate advice only becomes $2^{nd}/3^{rd}$ of the calculated TAC value. Intermediate TAC will be available when the fishery opens on October 15th.
3) *Final TAC* is given in January/February based on the biomass estimate of maturing capelin from the weighted contribution of autumn and winter surveys, where the autumn survey can, at maximum, get 1/3 weighting.

The benchmark workshop in 2022 concluded that the assessment approach represents the best available science following ICES procedures and considered the HCR precautionary.

Reduction of B_{lim} from 150 kt to 114 kt will lead to approximately 36 kt increase in TAC varying slightly with different probability distributions within the stock assessments.

The main recommendations and future work to improve the assessment and management of the stock included: (a) Reevaluation of acoustic backscatter (TS) of capelin. These analyses are also a prerequisite for evaluating the importance of capelin in the ecosystem; (b) Further research on trophic interactions of capelin is needed both by adding further research linked to current surveys and by filling the temporal and spatial knowledge gaps between the annual surveys, e.g. during the main feeding during summer; (c) Predation rate and abundance of humpback whales should be investigated. The most crucial period is January – March after the final acoustic measurements, but predation estimates in summer and autumn are also important for improving the predation model for capelin and forecasting SSB; (d) Ongoing collaboration with stakeholders should be continued and further developed.

ICES approved the outcome of the benchmark with two caveats. First, correspondence work should be done to fully explore the combining of surveys in the assessment. Second, in the near future, the HCR should be tested with simulations in line with management strategy evaluation (MSE).

Some of the suggested improvements are already in progress at MFRI, others are being evaluated, and some will need extra funding.

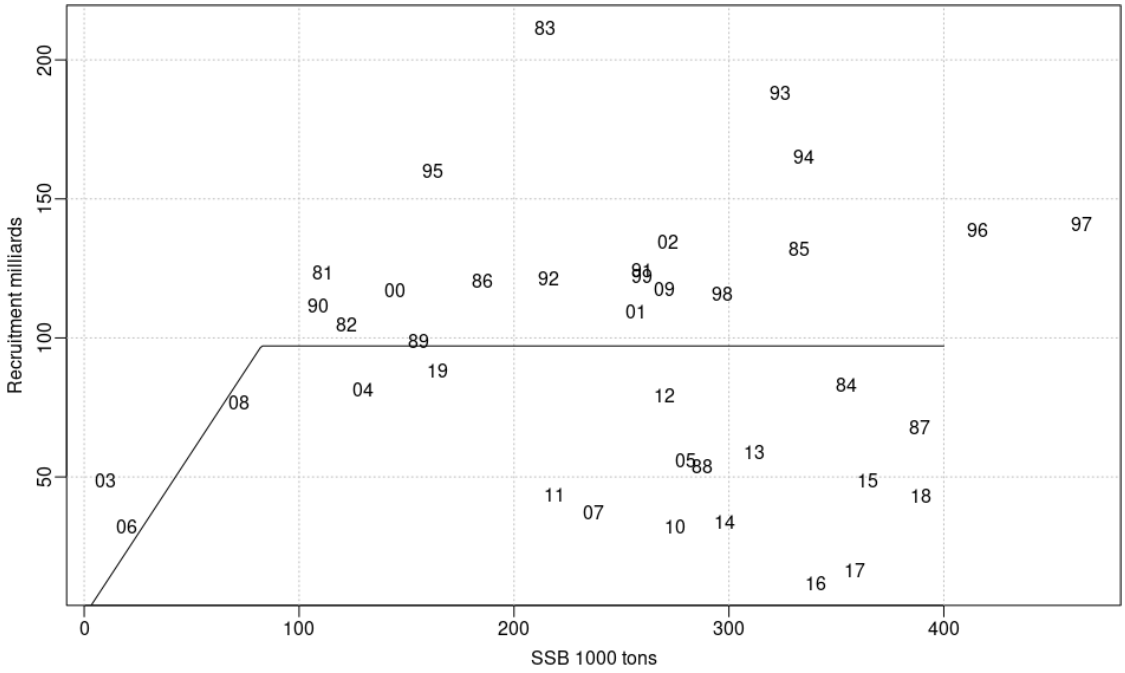

Figure 1. Back calculated number of 2 year old capelin. January the year before (vertical) vs the estimated spawning stock. Each year class indicated as two digit number (ICES, 2023a, 2023c). IEGJM capelin recruitment (number-at-age 1) as estimated from autumn acoustic measurements versus estimated spawning stock biomass (SSB). The year classes are indicated on the graph.

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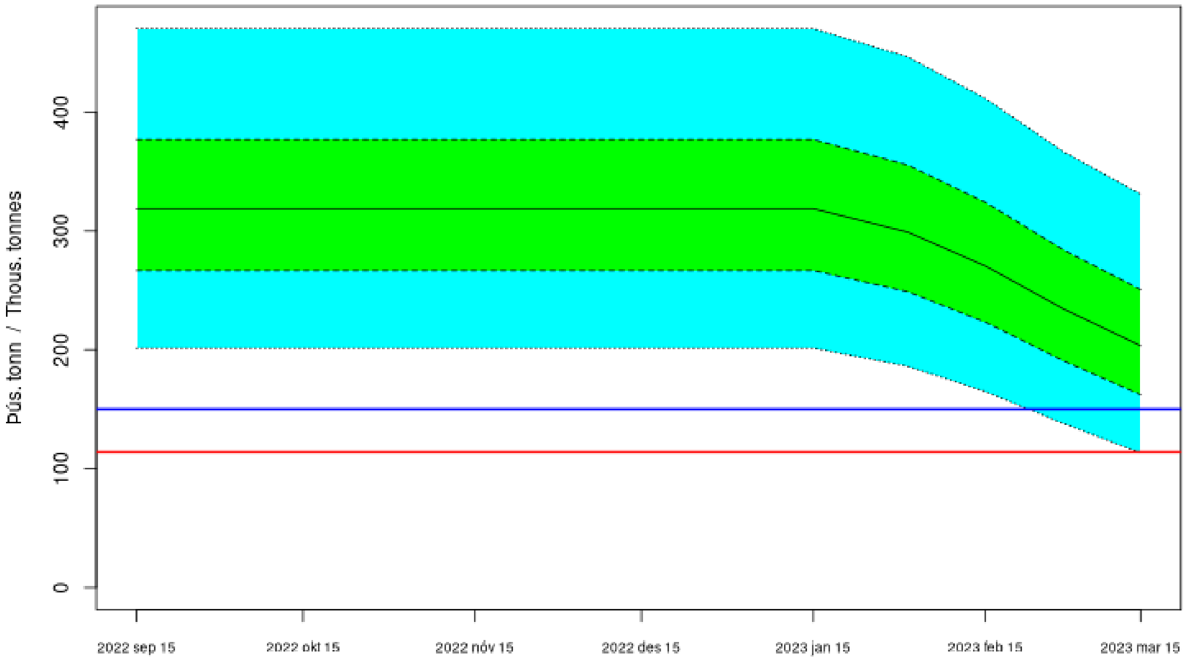

Figure 2. Example of predicted development of the spawning stock biomass with no catch based on the predation model. Projections are shown from acoustic measurement in autumn 2022 until the 15th of January 2023, when the predation model is started and runs until the 15th of March. The Blue line indicates B_{lim} = 150,000 tonnes from the previous HCR (ICES 2015), while the red line shows the current B_{lim} = 114,000 tonnes from the current HCR (ICES, 2023a, 2023c).

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