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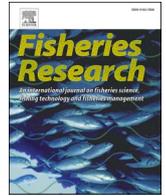
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Lifetime residency of capelin (*Mallotus villosus*) in West Greenland revealed by temporal patterns in otolith microchemistry

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ABSTRACT

Capelin (*Mallotus villosus*) is a marine fish species that spawns along the shorelines of Greenlandic fjords during late spring/early summer, but its migration patterns from hatching to spawning are largely unknown. This prohibits optimal fisheries advice and management of the stock. In this study, we examine spatial population structure through the lifetime of capelin in West Greenland using otolith microchemistry of 421 individual fish, caught while spawning at 16 different localities. In order to investigate the life-time residency of each fish, otolith core-to-edge measurements of Ba, Li, and Pb concentrations are classified to either of two West Greenland regions (north/south of ~68° N). Classifications suggest that West Greenland capelin reside mostly within one region throughout their life. Secondly, examination of Pb profiles indicate local residency on a smaller geographical scale. Otolith Pb levels, which most likely reflect bioavailable Pb derived from local geological and anthropogenic sources, vary between localities, but are found to be largely consistent throughout otolith chronologies of individual fish. Fish from neighboring localities are in some cases found to have contrasting otolith Pb levels, which suggests the existence of locally segregated populations with little or no connectivity. Significant Pb increases are observed towards the otolith edge, which indicates relatively high Pb exposure during the spawning period, where the fish enter shallow waters. These findings are in stark contrast to what is seen in other North Atlantic capelin stocks, such as those spawning in the Barents Sea, around Iceland and off East Canada, which exhibit long-distance migrations between spawning, feeding and overwintering areas. The information presented here has implications for West Greenland capelin stock management, which should be fitted within a high spatial resolution framework that takes locally segregated populations into account to avoid local collapses.

1. Introduction

Sustainable management of fish stocks relies on information on their spatial distribution throughout the year. Whereas some fish remain relatively stationary, others perform migrations to gain advantages in terms of foraging, survival and/or reproductive opportunities (Grubbs and Kraus, 2019). Knowledge on spatial structure and connectivity between different populations is key to successfully managing fisheries. Different approaches must be considered for populations that remain isolated within a confined area, as opposed to those that migrate and mix with other populations. For example, stocks consisting of smaller,

segregated management units may require individual management of each unit.

Capelin (*Mallotus villosus*) is a small pelagic fish from the smelt family that is known to migrate long distances. It is widely distributed in northern parts of the Pacific and Atlantic oceans (Præbel et al., 2008), where it is targeted by large-scale commercial fisheries (Carscadden et al., 2013). In the North Atlantic, three major populations are found: a Barents Sea population, an Iceland population (including Iceland Sea, Greenland Sea, and Denmark Strait), and a Canadian population off the coast of Newfoundland and Labrador. These stocks migrate several hundred (sometimes thousands) of kilometers annually between

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spawning, feeding, and overwintering habitats (e.g., the nursery area of capelin that spawn around Iceland is in East Greenland) (Carscadden et al., 2013). Decades of monitoring of these stocks have shown changes in stock distributions as a response to changing sea temperatures and stock sizes (Gjøsaeter et al., 1998; Jansen et al., 2016), emphasizing the need for continuous monitoring. In these stocks, spawning takes place during spring at depths ranging from surface waters to 100 m (Carscadden et al., 2013). Semelparity is widespread (Christiansen et al., 2008).

In West Greenland, capelin typically spawn in shallow water in the fjords and along the outer coast. Males are most likely semelparous, and therefore die after spawning, whereas females may survive and can potentially spawn during multiple seasons (see Friis-Rodel and Kanneworff, 2002, for a review on capelin in Greenland waters). Whereas migrations by the Barents Sea, Iceland and Canadian populations are well documented, little is known about the spatial dynamics of capelin populations in West Greenland, but West Greenland capelin are assumed to be less migratory than the previously mentioned stocks (Friis-Rodel and Kanneworff, 2002). Studies have shown capelin from West Greenland to be genetically distinguishable from North Atlantic stocks, such as Canadian (Cayuela et al., 2020) and the Northeast Atlantic populations (Präbel et al., 2008). On a local scale, an isozyme study has found genetic differences between capelin from three different locations in central West Greenland, suggesting the existence of fjord-specific, isolated populations with limited inter-connectivity and gene flow (Sørensen and Simonsen, 1988). However, further studies are needed to support these results. A lack of knowledge about population structure has long been a hindrance for sustainable and optimal fisheries advice and management of capelin in Greenland. Importantly, it is unknown to what extent different spawning segments along the coast are connected. This prevents governing authorities from deciding at which resolution the stock should be managed. Presently, no large-scale commercial fishery of capelin takes place in West Greenland, although the fishing industry actively seeks this by arranging experimental fisheries (DFFL, 2020; Pers. Comm. Anders Bjørn Larsen, Directorate for Fisheries (APNN), Government of Greenland. 7 April 2020).

In this study, we investigate capelin migration and population connectivity by utilizing natural chemical signatures (tags) stored in otoliths as indicators of the physicochemical environment the fish have experienced. Otoliths are chemically inert, metabolically stable, carbonate structures that are found pairwise in the inner ear of teleost fish, where they serve as indicators of, e.g., balance, direction and sound detection. They are typically composed of ~96 wt. % calcium carbonate (CaCO₃), usually aragonite, ~3 wt. % organic matrix and <1 wt. % minor and trace elements. They grow incrementally and chronologically during the entire lifespan of the fish, during which specific trace elements are incorporated either as substitutes for calcium, in interstitial spaces in the crystalline structure, or as part of an organic matrix. Element accumulation is regulated by environmental factors, e.g., water chemistry, temperature, and food availability, as well as physiological factors, e.g., growth, maturity stage, and maternal influence (e.g., Campana, 1999; Elsdon and Gillanders, 2002; Hüsey et al., 2020; Izzo et al., 2016; Kerr and Campana, 2014; Sturrock et al., 2015). Spatial and temporal variation amongst these factors may lead to distinct chemical signals that allow for differentiation of fish with separate space-time life histories (see e.g., Elsdon et al., 2008). However, in strictly marine settings, this can be challenging due to low spatial chemical variability and a lack of spatial boundaries (Sturrock et al., 2012).

Spatial discrimination of fish populations on the basis of environmentally induced chemical tags in otoliths is the most common application of otolith microchemistry. Applications of spatial discrimination include stock discrimination (e.g., Ferguson et al., 2011; Heidemann et al., 2012; Moreira et al., 2018), spatial segregation of nursery areas (e.g., Bouchard et al., 2015; Bradbury et al., 2011; Hamer et al., 2003; Rooker et al., 2001), identification of spatial chemical variation (e.g., Hamer and Jenkins, 2007; Izzo et al., 2016) and tracking fish movement

(for reviews, see e.g., Elsdon et al., 2008; Elsdon and Gillanders, 2003; Sturrock et al., 2012). The current study is a continuation of Fink-Jensen et al. (2021), which utilized capelin otolith chemistry to identify and characterize two chemically distinct marine regions in West Greenland (north/south of ~68°N). Chemical disparity was demonstrated primarily by concentrations of Li, Ba, and Pb in otolith edges, representing different chemical environments during time of catch. Here, we examine concentrations of the three elements in the entire chronology of the same samples. On a larger spatial scale, capelin lifetime residency is investigated by classification of time-resolved chemical data between the two regional tags identified in Fink-Jensen et al. (2021). On a finer spatial scale, we use otolith Pb as a spatial tracer. Several studies have shown positive correlation between Pb in otoliths and ambient water (e.g., Friedrich and Halden, 2010; Hansson et al., 2020; Ranaldi and Gagnon, 2008; Selleslagh et al., 2016; Søndergaard et al., 2015). Here, we examine if temporal and spatial differences in otolith Pb can be tied to environmental variability in bioavailable Pb from geological and/or anthropogenic sources, and use inter-locality differences to investigate connectivity between fish from different areas.

The aim of this study is to provide information on the spatial structure of capelin in West Greenland. We hypothesize that lifetime residency of individual fish can be inferred by comparing otolith chemical signatures between their lifespan and otolith edges, with edge signatures representing region of capture. Using this approach, we aim to identify the extent of movement and connectivity between capelin from different areas, and evaluate if spatially segregated management units exist. We thereby aim to provide knowledge on stock structure that may be applied to management of the stock.

2. Materials and Methods

2.1. Sample selection and preparation

Capelin spawning in shallow waters were caught in 2017 from 16 localities situated along Greenland's west coast (Fig. 1; Table 1), spanning from north-western Upernavik to Tasiusaq in south. Sampling sites were selected to broadly represent the west coast, with extended focus on the Ummannaq fjord. Sample collection techniques are described in Fink-Jensen et al. (2021). After catch, the samples were kept cold (<5 °C) for a few hours until freezing at -18 to -40 °C. Once defrosted, the following characteristics were noted: sex, total weight to nearest 0.1 g, and lengths with pinched tail (nearest millimetre rounded down) (Hansen et al., 2018). Sagittal otolith pairs were removed and stored in sealed polyester trays.

Ages were determined following the procedure outlined in Røttingen and Alvarez (2011) by counting of annual growth rings in the otoliths while they were submersed in water. This was done using a stereomicroscope (LeicaMZ6) at 3.2 μm pixel⁻¹ magnification under reflected light (Fig. 2). In general, incremental winter- and summer rings were well contrasted and distinguishable, and ~80% of the samples were aged with confidence. For the remaining samples, some summer and winter increments could not be clearly identified, and these samples were therefore omitted from the study. Ages ranged from 2 to 6 years, with 3 and 4-year-olds being most abundant. ANOVA ("aov" function, "stats" package (R Core Team, 2020)) of age vs. elemental concentrations revealed that concentrations of each analyzed element differed significantly among age classes. To avoid age-related bias, only 4-year-olds were selected for the study. One otolith from each of up to 34 fish was selected from each locality (Table 1) based on the following criteria: Sex (seeking a 50/50 male/female ratio) and otolith structural integrity (i.e., avoiding cracks and vaterite crystallization), resulting in a total sample size of 421 otoliths. The otoliths were embedded individually in epoxy resin and polished along the sagittal plane to expose a continuous core-edge surface. For many of the samples, a general lack of markers for core exposure, combined with a miniscule core size (~20 μ diameter), led to uncertainty as to whether the core had been correctly located.

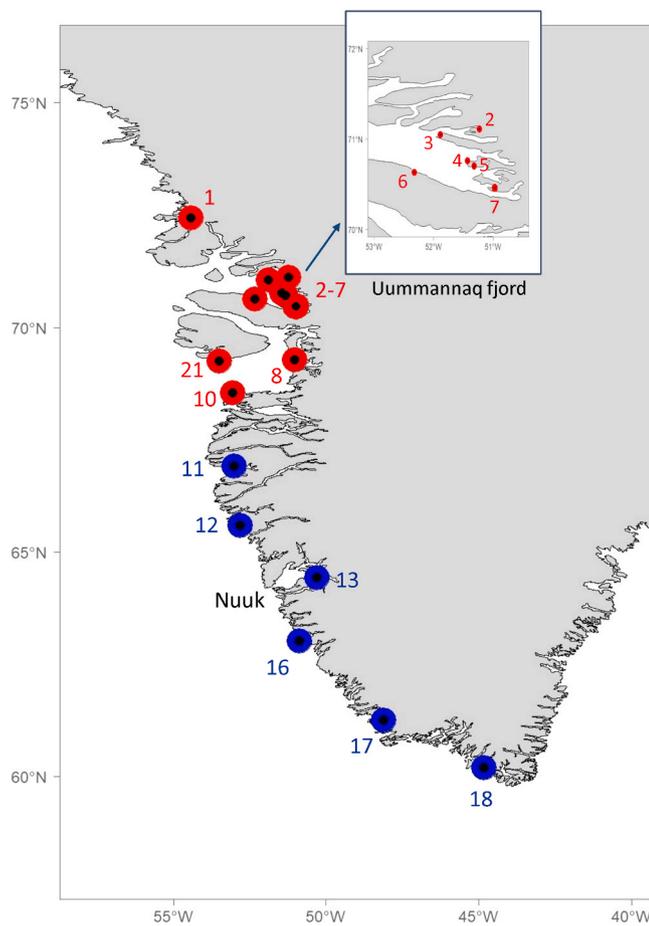


Fig. 1. Map of southwest Greenland with markings (circles) of sample localities. Marking colors indicate locality groups 1-NW (red) and 2-SW (blue). The Uummannaq fjord system is highlighted due to high locality density. Locality names are as follows: 1: Upernavik, 2: Maarmorilik, 3: Ukkusissat, 4: Anoritup Nua, 5: Qaqugdługssuit Syd, 6: Qajanguit, 7: Marrait, 8: Illulisat, 10: Aasiaat, 11: Sisimiut, 12: Manitsoq, 13: Kapisillit, 16: Fiskenaesset, 17: Ivittut/Arsuk, 18: Tasiusaq, 21: Qeqertarsuaq. For interpretation of the references to color, the reader is referred to the web version of this article.

Therefore, less emphasis was put on measurements of supposed core concentrations. Polished epoxy mounts were cleansed with ethanol wipes, and placed in an ultrasonic bath for 40 min, first 20 min in

Milli-Q H₂O, followed by 20 min in pure ethanol.

In order to investigate annual variations in the microchemistry over the entire otolith chronology, annual growth intervals were determined by identifying otolith core, annual winter rings (ring centers) and edge along the analyzed core-to-edge transects (Fig. 2), using ImageJ software, v.1.52d.

2.2. LA-ICP-MS of otoliths

The embedded otoliths were subjected to trace element analysis using Laser Ablation Inductively Coupled Plasma Mass Spectrometry (LA-ICP-MS), conducting core to edge transects analyses on the exposed otolith surface following the general routine described by Serre et al. (2018). Positions of LA-ICP-MS transects were determined by lines drawn from core to edge, perpendicular to growth increments observed on reflected light optical photos, which were imported as overlay images into the laser ablation software. Lines were placed to avoid cracks and scratches in the otolith surface (Fig. 2).

All LA-ICP-MS analyses were performed at Geological Survey of Greenland and Denmark (GEUS) using a Thermo Finnigan Element 2

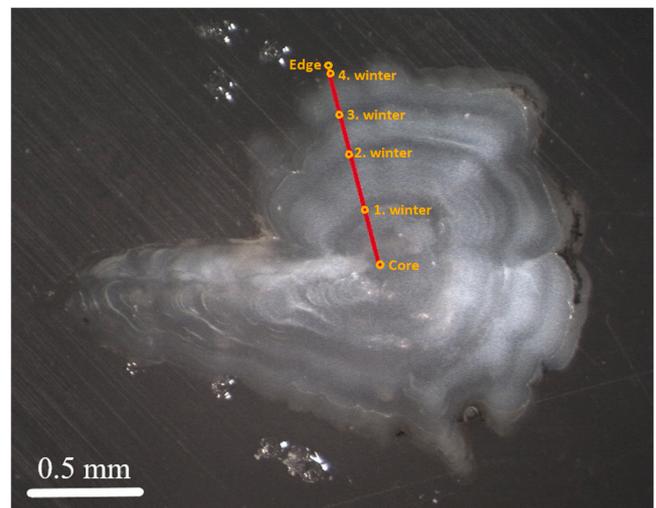


Fig. 2. Sagittal plane cross-section of a capelin otolith sample after embedding and polishing. The red line marks the core-edge transect along which LA-ICP-MS analysis was performed. Orange rings mark otolith sections: core, center of winter rings and edge. For interpretation of the references to color, the reader is referred to the web version of this article.

Table 1

Overview of sample localities. “M/F” is the total number of sampled males/females, respectively. Locality groups 1-NW and 2-SW are defined in Fink-Jensen et al. (2021), based on otolith edge chemistry. All fish are 4-year-olds caught in 2017.

Locality groups	Locality ID	Locality Name	Lat	Lon	M/F	Mean length (mm)	Mean weight (g)
1-NW	1	Upernavik	72.438	-54.415	11/4	152.39	25.34
1-NW	2	Maarmorilik	71.111	-51.232	20/14	155.97	26.59
1-NW	3	Ukkusissat	71.050	-51.889	21/7	161.06	28.15
1-NW	4	Anoritup Nua	70.759	-51.434	22/6	163.38	30.16
1-NW	5	Qaqugdługssuit Syd	70.704	-51.320	31/0	165.76	33.95
1-NW	6	Qajanguit	70.633	-52.323	28/3	160.97	29.22
1-NW	7	Marrait	70.458	-50.979	18/8	141.29	23.73
1-NW	8	Illulisat	69.279	-51.025	2/29	156.86	26.57
1-NW	10	Aasiaat	68.540	-53.063	24/8	162.69	27.26
1-NW	21	Qeqertarsuaq	69.250	-53.500	23/0	168.48	36.98
2-SW	11	Sisimiut	66.905	-53.007	18/6	141.84	18.71
2-SW	12	Manitsoq	65.590	-52.809	13/11	134.85	14.14
2-SW	13	Kapisillit	64.429	-50.303	20/2	138.04	16.61
2-SW	16	Fiskenaesset	63.015	-50.878	8/4	126.71	11.16
2-SW	17	Ivittut/Arsuk	61.253	-48.100	30/1	132.06	12.86
2-SW	18	Tasiusaq	60.196	-44.822	17/12	133.77	15.51

magnetic sector field ICP-MS coupled to a NWR 213 solid state Nd:YAG laser ablation system from Elemental Lasers. The LA-ICP-MS measurements were carried out using a laser beam spot size of 25 μm , a repetition rate of 10 Hz, and a nominal laser fluency of 8–9 J/cm^2 . During analysis, the mass spectrometer measured signal intensities of the isotopes ^7Li , ^{137}Ba and ^{208}Pb every 2.80 s at a 3 $\mu\text{m s}^{-1}$ scan speed along the transects. The ICP-MS signal-to-noise ratios were optimized under dry plasma conditions for the entire isotopic mass range (i.e., ^7Li to ^{208}Pb) through continuous laser ablation of the NIST 612 artificial glass standard (Jochum et al., 2011), opting for maximum isotopic sensitivity under the lowest possible element-oxide production levels (monitored by the $^{254}\text{UO}_2/^{238}\text{U}$ ratio). Instrumental mass drift was monitored and corrected for by using a standard-sample-standard bracketing protocol throughout all otolith analysis sequences. The LA-ICP-MS analytical protocol is described in detail in Fink-Jensen et al. (2021).

Unfortunately, limits of detection (LOD) for the utilized LA-ICP-MS instrument could not be obtained. For Li and Ba, secondary standards BHVO-2 and NIST614 yielded concentrations in line with preferred values in the literature. For Li (NIST614) and Ba (BHVO-2), these values were largely below otolith concentrations. For Pb, the same standards averaged concentrations of 2 ± 0.3 ppm and 2.3 ± 0.2 ppm, respectively, also in line with preferred values in the literature. However, most of the otolith Pb concentrations presented here were below 1 ppm. For quantitative comparison, Pb concentrations of six whole-otolith samples from the Uummannaq Fjord were estimated by solution-based ICP-MS (PerkinElmer TotalQuant), yielding bulk concentrations ranging from 0.59 to 1.44 ppm, i.e., slightly higher than the general level obtained by LA-ICP-MS. Using the same analytical setup and ICP-MS instrument model, Friedrich and Halden (2010, 2011) reported Pb detection limits of 0.01 and 0.07, respectively, which are below the majority of our measurements. We therefore argue that the Pb concentrations presented in this study are broadly representative of actual concentrations, and may be used for relative comparisons.

2.3. Data processing

The statistical analysis in this study followed the general analysis protocol for microchemistry-based stock identification outlined in Campana (2005) and Kerr and Campana (2014). All data analysis was carried out in the statistical software “R” (R Core Team, 2020).

For Li and Pb we observed negative ppm values (Li: 399/49774, Pb: 6160/49774 of total measurements), likely because some concentrations were lower than the measurement error due to background “noise” during LA-ICP-MS analysis. As concentrations cannot be negative, all negative values were set to zero. For Li and Ba, statistical outliers, which were assumed to be derived from instrumental errors, were detected and removed through two steps: 1) Extreme outliers, defined as measurements that exceeded mean fish concentrations multiplied by an element-specific factor (Li: 10, Ba: 20), were removed (Li: 2/49774, Ba: 2/49774 of total measurements). Element-specific factors were determined by visual inspection of element distribution plots, 2) Outliers, defined as measurements with values exceeding mean ± 4 standard deviations, were removed (Li: 225/49772, Ba: 310/49772 of total measurements). Extreme Pb values were also detected, mostly in singular (i.e., not adjacent) measurements. During the LA-ICP-MS analysis, continuous measurements were registered for every 8.4 μm of analyzed otolith surface, with each measurement reflecting the average concentration measured since the prior measurement. With a beam radius of 12.5 μm , adjacent measurements therefore overlapped. It was therefore deemed that actual extreme observations should be detectable in consecutive measurements, and that singular extreme Pb values were mostly caused by instrumental error. Such statistical outliers of Pb were identified by a running mean algorithm (“rollapply” function, “zoo” package, Zeileis and Grothendieck (2005)), where each measurement was compared to the mean of spatially adjacent measurements (two on each side). Individual measurements higher than this mean $\times 10$ were considered

instrumental errors and were removed (1005/49774 of total measurements).

A central part of the study was the classification of whole otolith multivariate data to the two regional tags defined in Fink-Jensen et al. (2021) based on otolith edge data. Edge chemistry included the capelin spawning period and thereby chemical fingerprints from the spawning/catch site, allowing us to relate otolith chemistry to geography. Due to difficulties in assessing the timespan covered by intervals in the otolith chronology, two different definitions of “edge” measurements and their mean values were used: “Edge5”, using the five measurements closest to the otolith margin (outermost- 54.5–62.9 μm of the analytical transect), and “Edge2”, using the outermost two measurements (20.9–29.3 μm). To accommodate parametric assumptions, edge concentrations of each element were transformed by the procedure used in Fink-Jensen et al. (2021): 1) + 1 and log transformations, 2) Box-Cox power transformation (lambda parameters: Li $\hat{0}$.39, Ba $\hat{0}$.06, Pb $\hat{0}$.26) (“boxcox” function, “MASS” package, Venables and Ripley (2002)) based on the relationship between element concentration vs. locality and sex (boxcox(Pb ~ Sex + StationID). Normal distributions of edge data were assessed by distribution histograms (“ggplot” function, “ggplot2” package, Wickham (2016)) and Q-Q plots. After data transformations, edge concentrations of each element were found to be normally distributed. For classification analysis, whole otolith data were transformed equivalently, i.e., first by + 1 and log-transformation, and subsequently by the same values used for Box Cox transformation of edge data, allowing for comparison of edge and whole otolith data. Henceforward, “*” will be used to denote transformed data, i.e., transformed concentrations = “concentrations*”, transformed ppm = “ppm*”. Assessment of whole otolith concentrations* found that none of the three elements had normally distributed data. Homogeneity of Variances was tested by Bartlett Test (“bartlett.test” function, “stats” package, R Core Team (2019)), and was found to be unequal for all three elements in both edge and whole otolith data. Therefore, where deemed necessary, parametric tests were accompanied by non-parametric tests.

In Fink-Jensen et al. (2021), significant relationship between element concentrations* and sex were detected for Ba, but not for Li and Pb. These effects were assumed to be constant throughout life. Consequently, in the present study, all Ba concentrations* were corrected for sex effect by subtracting the parameter estimate (Ba: -0.0085) calculated in Fink-Jensen et al. (2021) of the effect of males relative to females from concentrations* of males, thereby normalizing all concentrations* to females. Possible correlation between fish size and otolith chemistry was examined by visual inspection of fish length vs. concentration diagrams for each element on a locality basis, following the procedure suggested by Kerr and Campana (2014). No considerable unidirectional trends were detected across localities for any of the three elements (Fig. A1). Furthermore, Fink-Jensen et al. (2021) found considerable collinearity between fish size and locality, potentially leading to artificial inflation of regression model coefficients. Consequently, element concentrations were not corrected for length effect and size was not used as a variable in statistical models.

For comparisons of Pb concentrations* at different localities, mean ppm* values were calculated for each fish ($n = 421$) in order to accommodate parametric assumptions of the regression models used. For comparison of Pb concentrations* in different otolith sections, individual measurements were divided into core, edge, and middle sections, and averaged for each section on a fish-to-fish basis ($n = 368$). “Core” measurements were defined as the single innermost measurement of each otolith, based on a general otolith core size of 20 μm and a LA-ICP-MS beam size of 25 μm . “Edge” measurements were defined as either Edge2 or Edge5 measurements. “Middle” measurements were defined as all other (non-“Core”, non-“Edge”) measurements.

2.4. Data analysis

Measurements of element concentrations, following the otolith

chronology from core to edge, were presented as time-resolved element profiles using the “ggplot” function (“ggplot2” package, Wickham, 2016). In Fink-Jensen et al. (2021), the two chemically distinct signature groups, 1-NW and 2-SW, were identified by linear discriminant analysis (LDA) of measurements from capelin otolith edges, which were represented by the five measurements closest to the otolith margin, as in the present study. Group 1-NW included northern localities 1–8, 10, and 21, whereas group 2-SW included southern localities 11–13 and 16–18 (Fig. 1; Table 1). In that study, Li, Ba, and Pb were identified as the primary elements responsible for discrimination of the two groups. Therefore, in the present study, a LDA (“lda” function, “MASS” package (Venables and Ripley, 2002)) model based on Edge5 means of Li, Ba, and Pb was fitted to define group signatures, following the routine described in Fink-Jensen et al. (2021). LDA assumes that data are normally distributed and have equal covariance for every group. However, even if these assumptions are not met, LDA can still be used for dimensionality reduction and classification (Li et al., 2006). Subsequently, each individual, multivariate (Li, Ba, Pb) measurement from the full chronology was predicted to either group by best fits based on the LDA model (“predict” function, “stats” package, R Core Team, 2020). Time-resolved group classifications were presented using “plot” function (“graphics” package, R Core Team (2020)).

Statistical differences in Pb concentrations* between localities were examined by a generalized linear mixed model (GLMM) of the relationship between Pb concentration* and locality, with individual fish as a random effect (glmmTMB(Pb ~ StationID + (1|FishID)) (“glmmTMB” function, “glmmTMB” package, Brooks et al., 2017). For the alternative hypothesis, p-values below 0.05 indicated that the effect of a given locality differed significantly from the model intercept (here set to locality 21 “Qeqertarsuaq”). Model residuals were tested using DHARMA residual diagnostics (“testResiduals” function, “DHARMA” package, Hartig, 2020), and were found to be normally distributed (One-Sample Kolmogorov-Smirnov Test: $D = 0.06$, $p = 0.08$), with no considerable

over/underdispersion (DHARMA nonparametric dispersion test: $p = 0.928$) and no significance of outliers (DHARMA bootstrapped outlier test: $p = 1$). Differences between Pb concentrations* in core vs. middle, and edge vs. middle were tested for individual localities on a fish-to-fish basis. Due to the non-parametric nature of the data, this was done by Welch One Sample T-test (“t.test” function, “stats” package, R Core Team, 2020) accompanied by the non-parametric one-sample Wilcoxon Rank Sum Test (“wilcox.test” function, “stats” package, R Core Team, 2020). Here, p-values below 0.05 indicated that Pb means in the tested otolith sections were significantly different. For localities 10, 11, and 12, untransformed otolith Pb concentrations were compared to Pb abundances in the neighboring continental geology. Here, stream sediment data from The Greenland Mineral Resources Portal (www.greenmin.gi; Steenfelt, 2001) was used to represent general geological Pb abundances. The stream sediment samples were collected in 1992–1993 and Pb content was determined by X-ray Fluorescence Spectrometry (XRF) (for full sampling details, see Steenfelt, 2001, 1999).

3. Results

3.1. Element distributions

Elemental profiles of non-transformed mean concentrations at each locality over time showed temporal patterns for each element (Fig. 3). At age 0, Li concentrations were similar at most localities, except for localities 11 and 18, where concentrations were higher and lower, respectively. For the remaining life span, the two locality groups showed contrasting Li patterns. Variations between concentrations in summer and winter otolith growth zones were observed in Group 1-NW with peaks at, or shortly after, formation of the center of each winter ring. In Group 2-SW, Li concentrations generally showed less temporal variation and a lack of seasonality patterns, apart from elevated concentrations around the first winter ring in 5 out of 6 localities.

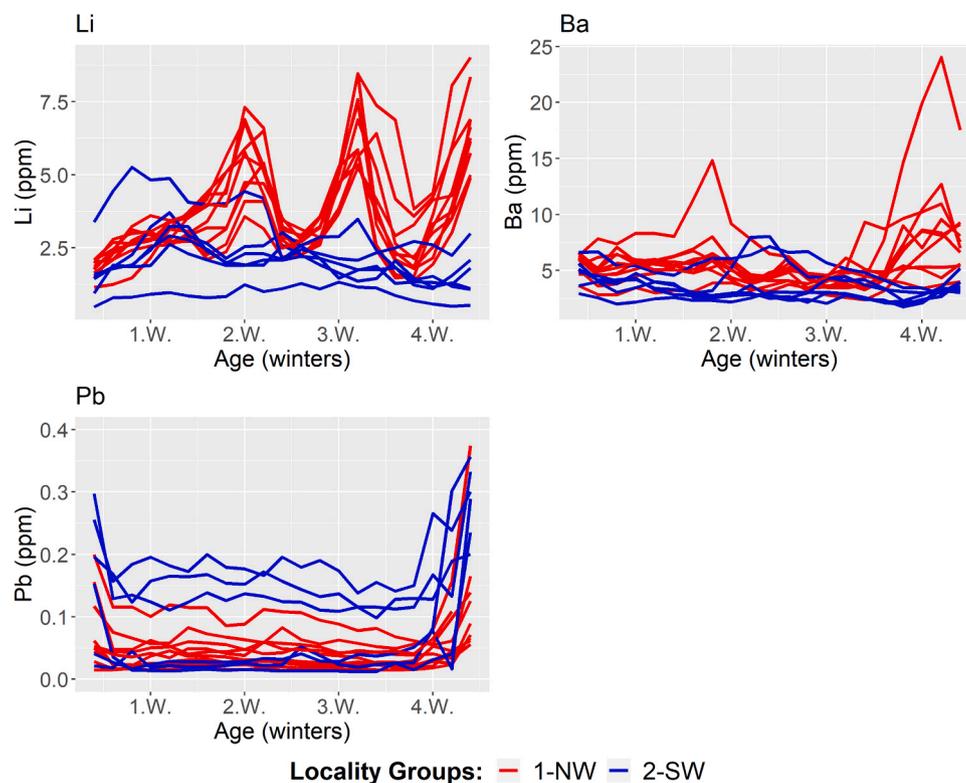


Fig. 3. Elemental profiles of Li, Ba, and Pb concentrations (ppm) in core-to-edge otolith profiles. Lines represent mean concentrations at each locality. Age (x-axis), corresponding to otolith chronology, is measured in winter rings. Concentrations have been averaged for every 0.2 year. For interpretation of the references to color in the figure legend, the reader is referred to the web version of this article.

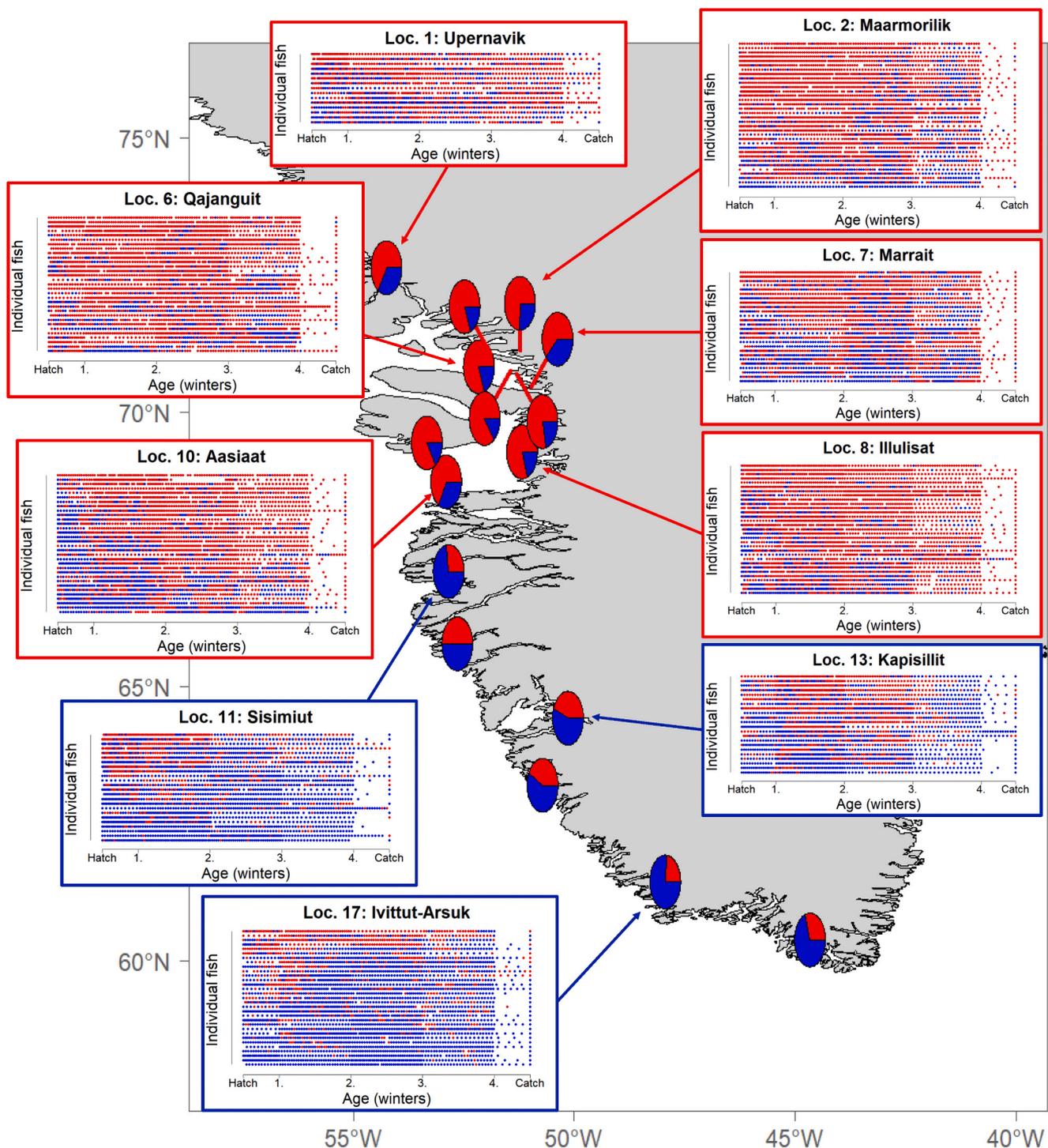


Fig. 4. Map of group classifications at 9 representative sample localities (all localities are presented in Fig. A.3.). Pies (circles) mark locality positions and indicate mean classifications to locality groups 1-NW (red) and 2-SW (blue). Classification profiles (boxes) show classifications of time-resolved, multivariate measurements to either group 1-NW (red) or 2-SW (blue). Each horizontal line of dots represents one fish. Individual fish are ordered along the y-axis by their total classification percentage to either group 1-NW (top of y-axis) or 2-SW (bottom of y-axis). Age (x-axis), corresponding to otolith chronology, is measured in winter rings. Bold red lines from some pies indicate their exact geographic location. For interpretation of the references to color, the reader is referred to the web version of this article.

Ba concentrations were slightly higher in Group 1-NW than in 2-SW. Minor temporal variations were observed at many Group 1-NW localities, as mean Ba concentrations were found to peak in the latter part of age 1 and 2 intervals, as well as just after the center of age 4 winter rings. This trend was most pronounced at localities 1–7.

Pb concentrations differed between localities, but were found to be relatively constant over time, except for visible increases towards the

edge at most localities, and towards the core at some localities (see Section 3.3 for Pb tests).

3.2. Group classifications

The Li-Ba-Pb-based LDA model, based on Edge5 data, successfully classified individuals to groups based on their signatures (Fig. A2).

Model classification successes for assigning fish to groups were high: 97% for group 1-NW and 92% for group 2-SW. This indicated two well-defined, chemically distinct groups.

The LDA model was used to predict individual time-resolved measurements to either locality group 1-NW or 2-SW (Figs. A3, 4). Overall classification of group 1-NW measurements to group 1-NW was 76%, with mean locality classifications ranging from 61% at locality 7, to 85% at localities 4 and 21 (Table 2). Overall group 2-SW to group 2-SW classification was 64%, ranging from 50% at locality 12, to 75% at locality 17. For both groups, mean classifications to respective catch groups were highest at age 4 (1-NW to 1-NW: 89%; 2-SW to 2-SW: 86%) (Table 3).

Time-resolved mean classifications for each locality illustrated a general tendency of fish being classified primarily to their catch region, although considerable overlap between the two locality groups was observed (Fig. 5). For group 1-NW, classifications varied with season, as group 1-NW to 1-NW classifications generally peaked in or just after winter rings. In both groups, mean classifications showed increasing classification to group 2-SW towards the otolith core.

3.3. Spatial and chronological Pb variations

The GLMM model of Pb concentrations* by locality indicated significantly higher concentrations* at localities 1, 7, 11, 13, and 17 than at other localities (Table 4). At locality 11 (Sisimiut), concentrations* were significantly higher than at neighboring localities 10 (Aasiaat) and 12 (Manitsoq) (Table 4, Fig. 6a & 7), and mean concentrations* of individual fish ranged from 0.406 to 0.704 ppm* at locality 11, compared to 0.172–0.342 ppm* and 0.149–0.445 ppm* at localities 10 and 12, respectively. In fact, only one fish from locality 12, and none from locality 10, was found to have a higher mean Pb concentration* than any fish from locality 11. By comparison, stream sediment samples from the general area surrounding locality 11 were found to have higher and more extreme Pb concentrations (ranging from 0 to 100 ppm) than areas surrounding localities 10 (0–20 ppm) and 12 (0–40 ppm) (Fig. 7).

In Uummannaq Fjord (localities 2–7), otolith Pb levels were markedly higher at locality 7 (Marrait) than at the other five localities (Fig. 6b). In the southern part of the fjord, mean Pb levels increased towards the inner fjord, in locality order 6, 4, 5, 7 (Figs. 1, 6b). Pb profiles of individual fish showed increasing Pb concentrations towards the otolith margin for a substantial number of fish, whereas increases towards the otolith core were observed for only a few fish (Fig. 6c, A4). One fish from locality 2, FishID 45, exhibited elevated Pb levels throughout most of its chronology relative to other fish caught at this site.

Edge2 and Edge5 mean Pb concentrations* were found to be significantly higher than middle concentrations* at 12 of 16 localities and 11 of 16 localities, respectively (Table 5, A.1), with relative differences of 39.7% and 17.6% higher edge than middle ppm* , respectively.

Table 2
Mean classifications (%) of time-resolved measurements at individual localities between locality groups 1-NW and 2-SW.

Locality group	Locality ID	Classification to group 1 (%)	Classification to group 2 (%)
1-NW	1	66	34
1-NW	2	75	25
1-NW	3	82	18
1-NW	4	85	15
1-NW	5	78	22
1-NW	6	81	19
1-NW	7	61	39
1-NW	8	80	20
1-NW	10	68	33
1-NW	21	85	15

Table 3

Mean classifications (%) of time-resolved measurements at different ages between locality groups 1-NW and 2-SW.

Locality group	Age	Classification to group 1 (%)	Classification to group 2 (%)
1-NW	0	70	30
1-NW	1	80	20
1-NW	2	76	24
1-NW	3	76	24
1-NW	4	89	11
2-SW	0	36	64
2-SW	1	38	62
2-SW	2	38	62
2-SW	3	24	76
2-SW	4	14	86

The highest relative edge-mid differences were found at localities 2 (Edge2: 74.7%, Edge5: 37.1%) and 18 (Edge2: 81.0%, Edge5: 41.9%). For all localities, Pb means and relative differences were higher in Edge2 than Edge5. Core mean Pb concentrations* were significantly higher than middle means at just 2 of 16 localities (Table A.2). On average, core concentrations* were 9.8% higher than middle concentrations* . The highest relative core-mid differences were found at the same localities that also showed the highest edge increases: Localities 2 (36.5% higher ppm* in core) and 18 (34.3% higher ppm* in core).

4. Discussion

4.1. Group classifications

The first part of the data analysis examines large scale spatial patterns through the lives of individual capelin by comparing multivariate chemical profiles obtained from core-to-edge otolith transects. Individual chronological measurements are classified to either of the chemical tags (groups 1-NW or 2-SW) defined by otolith edge data. Time-resolved classification profiles suggests that most fish spend the majority of their life in the region where they were eventually caught. The mean classification of all group 1-NW localities to group 1-NW is 76%, whereas the mean classification of all 2-SW localities to group 2-SW is 64%.

The classifications indicate that movement amongst West Greenland capelin is more limited than the stocks that spawn in the Barents Sea, around Iceland and off East Canada, and perhaps behaviorally similar to other inshore stocks, such as in the Balsfjord, Norway (Friis-Rodel and Kanneworff, 2002, and references herein). Long-distance migrations by capelin are typically monitored by acoustic surveys and catch data (Carscadden et al., 2013; Gjøsaeter et al., 2002; ICES, 2019a, 2019b), but no such data are collected for capelin in Greenland (T. Jansen, personal communication, February 2021). In recent years, several studies have used otolith chemistry for spatial discrimination amongst stocks in East Canada. Unlike the present study, these studies generally do not include a temporal aspect, but use regional tags derived from otoliths of larvae and/or juveniles to determine natal origins of adults and recruitment contributions of different spawning and nursery areas to the greater adult population (Davoren et al., 2015; Lazartigues et al., 2016; Loeppky et al., 2018; Tripp et al., 2020). Davoren and Halden (2014) included a temporal aspect, as they compared otolith microchemistry of capelin from two different Newfoundland regions at different age stages. The study did not find significant differences between regional signatures, but did identify habitat-specific differences between signatures in beach vs. deep-water spawners within each region. This exemplifies that environmental chemical variability is not necessarily related to distance, but can be governed by a multitude of local factors. Using otolith chemistry to track fish movement in marine environments is often complicated by temporal variability in the environment, e.g., seasonal or inter-annual changes in water characteristics, resulting in spatial signatures changing over time. In marine environments, low spatial

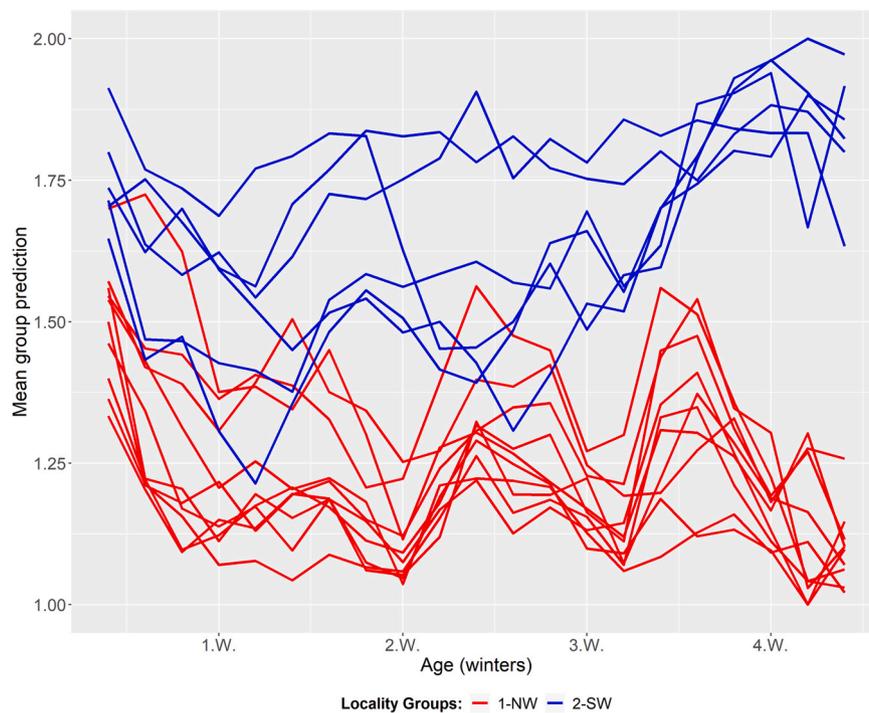


Fig. 5. Time-resolved mean group classifications. Lines represent mean classifications between groups 1-NW and 2-SW for separate localities. Age (x-axis), corresponding to otolith chronology, is measured in winter rings. For interpretation of the references to color in the figure legend, the reader is referred to the web version of this article.

Table 4

Results of generalized linear mixed model (GLMM) of Pb concentrations* as a function of locality. Also listed are locality mean Pb concentrations* and ranges of mean fish Pb concentrations* at each locality. Sign. (significance) codes for p-values are: **** = 0–0.001; *** = 0.001–0.01; * = 0.01–0.05; † = 0.05–0.1.

Locality ID	Estimate	Std. Error	z value	Pr (> z)	Significance Code	Locality mean Pb (ppm*)	Mean fish Pb range (ppm*)
(Intercept) 21	0.386	0.013	29.553	< 0.001	***	0.388	0.276–0.478
1	0.070	0.021	3.352	< 0.001	***	0.456	0.390–0.506
2	-0.027	0.017	-1.622	0.105		0.357	0.225–0.785
3	-0.041	0.018	-2.334	< 0.05	*	0.343	0.169–0.528
4	-0.064	0.018	-3.654	< 0.001	***	0.323	0.231–0.440
5	0.025	0.017	1.452	0.147		0.410	0.296–0.489
6	-0.109	0.017	-6.321	< 0.001	***	0.279	0.207–0.467
7	0.114	0.018	6.361	< 0.001	***	0.499	0.416–0.589
8	-0.058	0.017	-3.361	< 0.001	***	0.328	0.210–0.516
10	-0.097	0.017	-5.685	< 0.001	***	0.289	0.172–0.342
11	0.172	0.018	9.445	< 0.001	***	0.558	0.406–0.704
12	-0.106	0.018	-5.82	< 0.001	***	0.280	0.149–0.445
13	0.211	0.019	11.317	< 0.001	***	0.597	0.533–0.674
16	-0.063	0.022	-2.81	< 0.01	**	0.324	0.252–0.557
17	0.135	0.017	7.821	< 0.001	***	0.521	0.303–0.729
18	-0.127	0.017	-7.254	< 0.001	***	0.258	0.149–0.356

chemical variability may further complicate the ability to distinguish spatial signatures reliably (Elsdon et al., 2008; Kerr and Campana, 2014). As a consequence, very few studies have attempted to backtrack fish movement in marine environments by otolith microchemistry (Sturrock et al., 2012). Similarly to the present study, Mercier et al. (2012) used multi-element, time-resolved profiles to predict lifetime residency and migration of 12 individual gilthead sea breams (*Sparus aurata*) between four habitats in a lagoon system in the Gulf of Lion (NW Mediterranean). However, unlike the present study, spatial tags were characterized at different life stages in order to avoid temporal variations in environmental chemistry to negatively influence classification accuracy.

In the present study, classifications rely on distinct differences in Li, Ba, and Pb concentrations between groups 1-NW and 2-SW, and the ability to compare the regional tags identified in Fink-Jensen et al. (2021) to the lifetime chronological record investigated in the present

study. Otolith Ba and Li are routinely used as environmental proxies in studies of spatial variability, as their otolith concentrations are related primarily to their concentrations in the ambient water (Grammer et al., 2017; Hüsey et al., 2020; Reis-Santos et al., 2013; Sturrock et al., 2012). Our results show that the time-resolved measurements are classified primarily to the tag of their catch region. However, most fish exhibit classifications to both groups. Classifications vary between fish caught at the same locality, indicating different space-time life histories. Curiously, there are multiple instances of single or few measurements classified to the one tag being mixed in between multiple, consecutive measurements classified to the other tag. This would indicate movement between the regions in relatively short timespans. Furthermore, singular non-catch group classifications are found in otolith edges, even for fish caught far from the boundary between the two regions, e.g., at 17-Iviit-tut/Arsuk and 18-Tasiusaq. For these classifications to be correct, these fish would have travelled more than 2000 km in a relatively short time

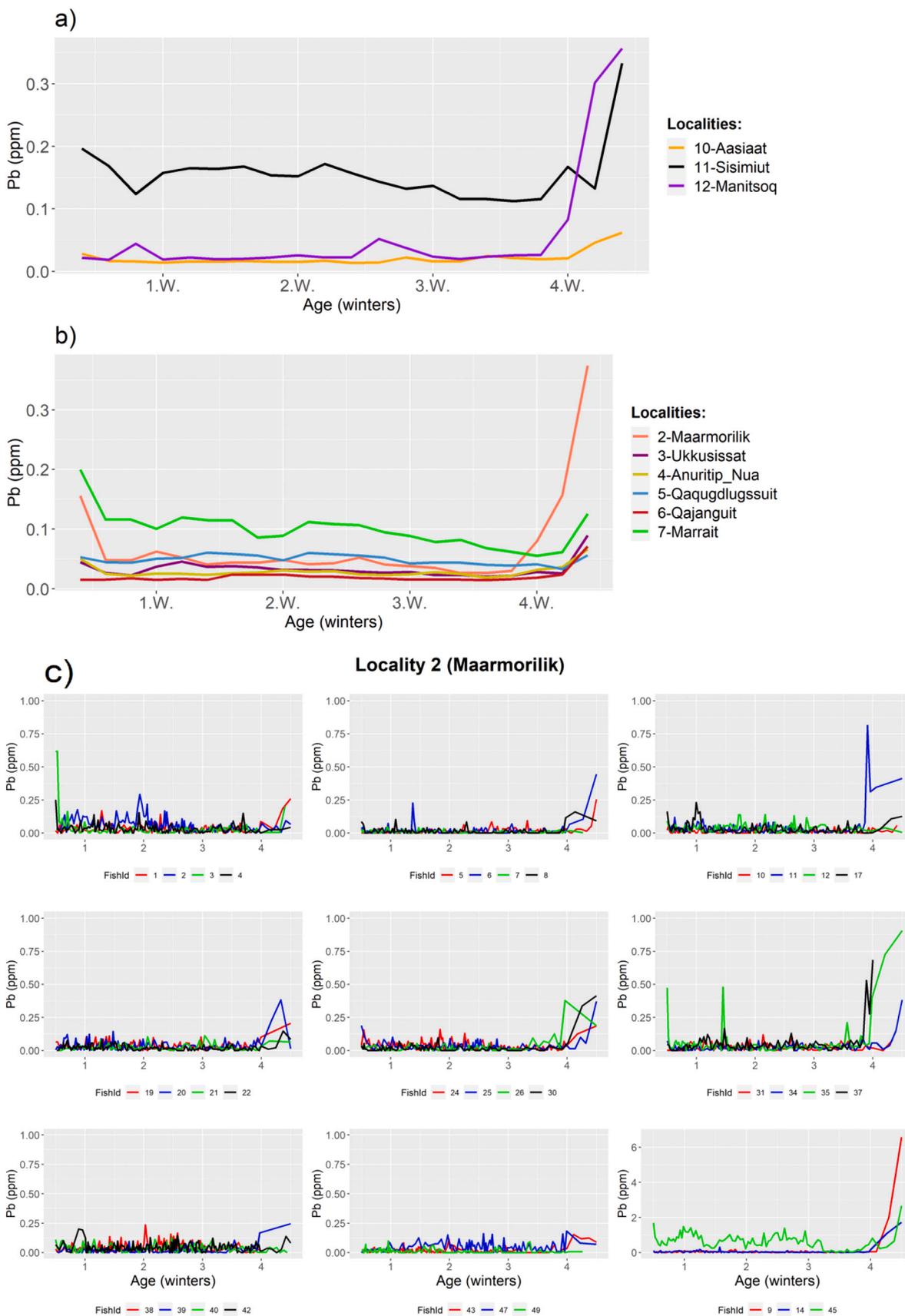


Fig. 6. Time-resolved Pb concentrations (non-transformed) from a) three adjacent localities on the central west coast of Greenland (mean concentrations), b) 6 localities in the Uummanaq Fjord (mean concentrations), c) individual fish from locality 2 (Maarmorilik). Note the different y-axis limit in the lower right plot in c). Age (x-axis), corresponding to otolith chronology, is measured in winter rings. In a) and b), concentrations have been averaged for every 0.2 year. For interpretation of the references to color in figure legends, the reader is referred to the web version of this article.

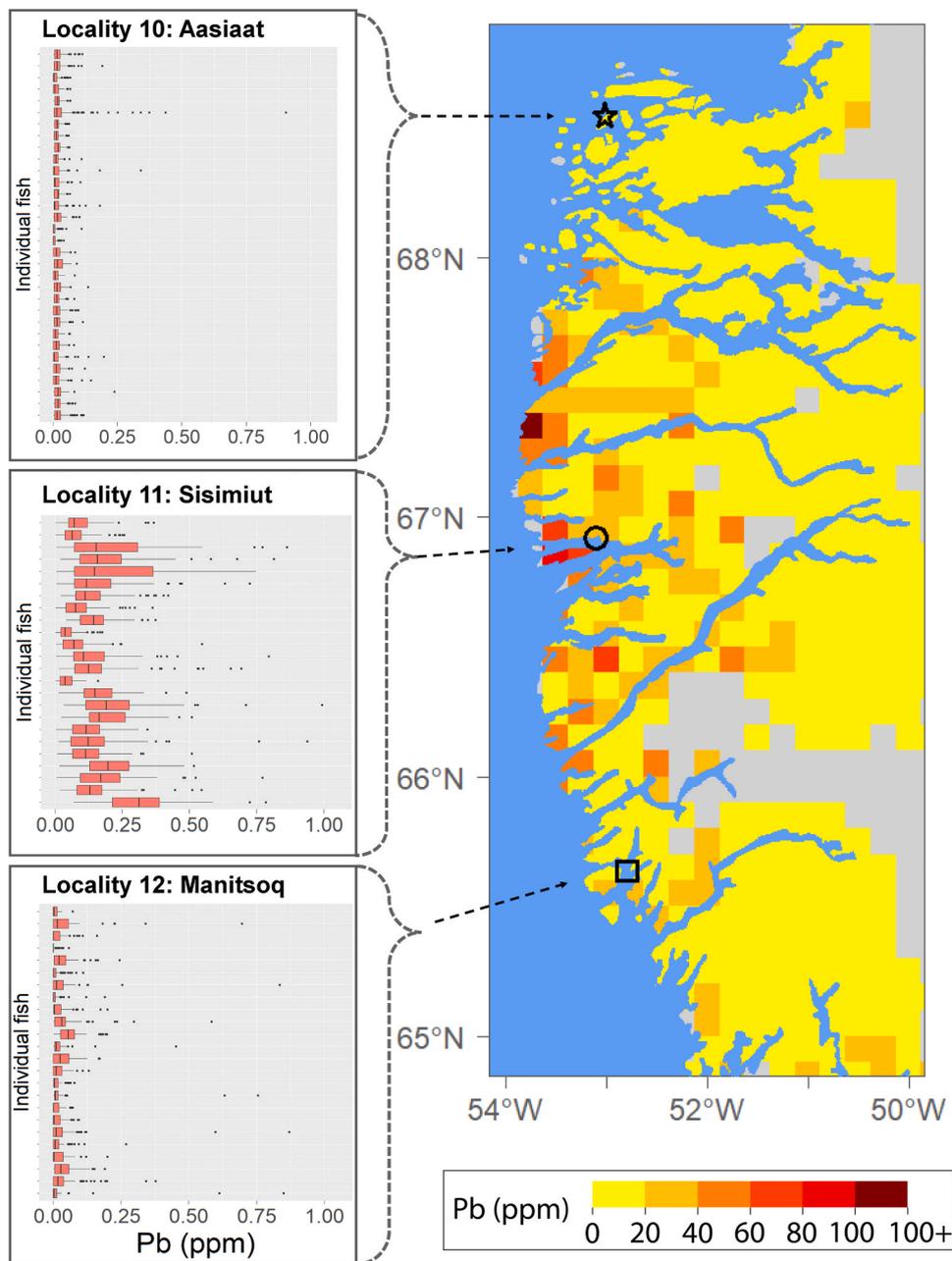


Fig. 7. Comparison between Pb concentrations in otoliths and stream sediments. Left: Boxplots of each locality show the range of Pb concentrations in individual fish (salmon colored, horizontal boxplots) from localities 10, 11, and 12. Right: A map of a section of the West Greenland coastline that includes localities 10, 11, and 12. It shows Pb concentrations in stream sediments. The map is divided in quadrants, which are colored according to mean Pb concentrations in the quadrants (see scale below the map). Capelin sample localities are marked with black symbols: star = 10 (Aasiaat), circle = 11 (Sisimiut), square = 12 (Manitsaq). For interpretation of the references to color in the figure legend, the reader is referred to the web version of this article.

span (e.g., a few weeks) just prior to being caught. This is not possible and such classifications are therefore considered to be misclassifications, highlighting a limitation to the model. In the following section, factors that can lead to such misclassifications are discussed.

Classification percentages to catch groups (1-NW to 1-NW, and 2-SW to 2-SW) are highest at age 4. As this age section includes the edge data used to characterize regional tags, a high classification success is to be expected. In the preceding chronology, however, catch group classification percentages are lower, indicating differences between chemistry in the edge and the preceding record. This can primarily be attributed to the observed temporal variability in otolith Li concentrations, particularly for group 1-NW localities. Such variability likely reflects differences in ambient Li exposure over time, and could result from regional or more local movement, but may just as well reflect local seasonal variations in Li bioavailability within the fjords. During summer, freshwater and sediment influx from glaciers and rivers are considerably higher than during the winter, and water chemistry may therefore vary

markedly (Delaney and Adhikari, 2020; Fink-Jensen et al., 2021; Fries, 2018; Hasholt et al., 2018; Koppes and Montgomery, 2009). Seasonal chemical variations have previously been detected in fish otoliths from Greenlandic fjords, such as Sr and Mn variations detected in otoliths from sculpin (*Myoxocephalus scorpius*, a stationary fish species) (Søndergaard et al., 2015), and Sr variations detected in otoliths from Greenland cod (*Gadus ogac*) (Hansson et al., 2020).

Our results exemplify the challenge of using tags derived from a fixed point in time to track lifetime movement in environments where physicochemical conditions change over time (Cook, 2011; Elsdon et al., 2008). Comparative studies of water and otolith chemistry in in-shore and off-shore environments at different times of the year can perhaps clarify whether the observed Li variations are related to seasonal variability within delimited areas, e.g., fjords, or are the consequence of migration between chemically diverse environments.

Table 5

Comparison of mean Edge2 concentrations* to mean middle concentrations* for each locality. T-test (Welch One Sample T-test and Wilcoxon test (one-sample Wilcoxon Rank Sum Test) were performed on average Pb concentrations* of individual fish (n = 368). Sign. (significance) codes for p-values are: *** = 0–0.001; ** = 0.001–0.01; * = 0.01–0.05; . = 0.05–0.1.

Locality	Mean Pb, Edge2 (ppm*)	Mean Pb, mid (ppm*)	Mean Edge increase (%)	t-test (p)	Wilcoxon (p)	Sign. Code
1	0.557	0.453	22.7	< 0.01	< 0.01	**
2	0.616	0.353	74.7	< 0.001	< 0.001	***
3	0.484	0.340	42.2	< 0.001	< 0.001	***
4	0.419	0.322	30.3	< 0.01	< 0.01	*
5	0.441	0.410	7.5	0.274	0.143	
6	0.400	0.277	44.6	< 0.001	< 0.001	***
7	0.510	0.499	2.1	0.607	0.474	
8	0.484	0.326	48.3	< 0.001	< 0.001	***
10	0.411	0.287	43.3	< 0.001	< 0.001	***
21	0.661	0.384	72.4	< 0.001	< 0.001	***
11	0.673	0.556	21.1	< 0.001	< 0.001	***
12	0.476	0.277	72.0	< 0.05	0.1819	
13	0.697	0.595	17.2	< 0.001	< 0.001	***
16	0.478	0.322	48.7	< 0.05	< 0.05	*
17	0.559	0.520	7.6	< 0.05	0.091	
18	0.460	0.254	81.0	< 0.05	< 0.05	*

4.2. Otolith Pb as a tracer of spatial residency

The second approach to unravelling the spatial structure of capelin in West Greenland is based on otolith Pb. The presented results indicate relationships between Pb concentrations in the otoliths and the environment that may provide information about capelin spatial dynamics. As mentioned previously, there is some concern regarding the quantitative accuracy of the Pb data, but we argue that the employed methodology can resolve qualitative Pb variations, even below 1 ppm, as demonstrated by Friedrich and Halden (2011, 2010). The measurement error around true means is assumed to be random and the same for all measurements, and the Pb data can therefore likely be used for comparative relationships. We also argue that setting negative Pb values to zero was a conservative approach. Negative Pb values were more common at localities with generally lower Pb levels. A consequence of setting negative values to zero was therefore a reduction of the difference between Pb values at localities with relatively low vs. high Pb concentrations, thereby minimizing locality differences.

In the present study, we have examined possible relationships between Pb in the otoliths and environmental exposure to Pb in an attempt to utilize otolith Pb as a spatial marker. Pb may be susceptible to physiological fractionation in fish, with studies indicating influences related to age (Köck et al., 1996) and body weight (Geffen et al., 1998). However, otolith Pb has primarily been used to trace anthropogenic contamination, and has in several studies been shown to correlate positively with Pb levels in ambient water (Friedrich and Halden, 2010; Hansson et al., 2020; Ranaldi and Gagnon, 2008; Selleslagh et al., 2016; Søndergaard et al., 2015). Otolith Pb therefore appears to have a legitimate role as proxy for exposure to Pb from the environment. In Arctic oceans, Pb may have anthropogenic and/or geological origins (Gobeil et al., 2001; Søndergaard et al., 2020). Geologically derived Pb enters the marine realm through weathering of continental rocks, as sediments are transported by wind, rivers, glaciers, or coastal erosion (Maccali et al., 2012). Pb content in both bottom sediments and the water column is therefore influenced by factors such as proximity to the coast, Pb concentrations in neighboring continental rocks, and sedimentation rate (Elberling et al., 2002; Rainbow, 1995).

Our results indicate relationships between otolith Pb and environmental exposure. Fish caught at localities 1 (Upernavik), 7 (Marrait), 11 (Sisimiut), 13 (Kapisillit), and 17 (Ivittut/Arsuk) have significantly higher mean otolith Pb than at their neighboring localities. At locality 17

(Ivittut/Arsuk), elevated otolith Pb can most likely be attributed to the presence of a nearby former cryolite mine, which to this day still pollutes the Arsuk Fjord with Pb and Zn from waste rock (Bach et al., 2014; Søndergaard et al., 2020). At neighboring localities 16 (Fiskenaeset) and 18 (Tasiusaq), otolith Pb levels are significantly lower, indicating spatial separation between populations on a scale of 250–300 km. At localities 1, 7, and 13, high otolith Pb levels are unlikely to have an anthropogenic origin. However, these localities are situated deep in fjord systems, where a higher degree of adjacent coastline may lead to increased sedimentation and bioavailability of Pb. Localities 1 and 7 are furthermore located near major glaciers, which are considerable sources of sedimentation. This is supported by a decreasing otolith Pb gradient along localities 7, 5, 4 and 6, which corresponds with distance to the glacier, as well as a decrease in adjacent coastline. Pb profiles of individual fish from these localities indicate that these are general trends that are not tied to a few fish. As Pb levels are relatively constant throughout the lifespan of the fish, we therefore suggest that all or most of the fish caught at these localities have resided locally throughout their lives, separated from populations at neighboring localities. Here, spatial separation between populations may be as little as 15–50 km. At locality 11 (Sisimiut), mean otolith Pb levels are higher than at neighboring localities 10 and 12, corresponding with Pb concentrations in the surrounding geology, as demonstrated by stream sediment Pb data. In fact, the Sisimiut region is the only larger region in our study area where stream sediment Pb levels above 50 ppm are found consistently. Again, this indicates spatial separation between populations on a scale of 150–300 km. Overall, these results suggest that capelin dynamics may be limited to in-fjord movements, and that West Greenland capelin are much less migratory than stocks that spawn in the Barents Sea, around Iceland and off East Canada.

4.2.1. Pb in otolith edges

Pb levels in the analyzed otoliths are generally found to be constant over time. However, at many localities, concentrations are found to be significantly higher in otolith edges than in the preceding chronology. This is unlikely to originate from the analytical procedure, e.g., variations in laser ablation intensity or measuring capability, as similar increases were not observed for Ba or Li. Pb concentrations in the embedding epoxy were generally found to be lower than in the otoliths, and contamination at the otolith surface was considered to be negligible. It can be argued that the edge increases are caused by physiological circumstances, as increased consumption during periods of maturation may lead to increased concentrations of Pb and other metals in fish tissues, particularly in liver and muscles (Marijić and Raspor, 2010; Monsefrad et al., 2012). However, no literature could be found on this having an effect on otolith Pb. Cook (2011), found increasing otolith Pb concentrations during spawning season of the garibaldi (*Hypsypops rubicundus*), but did not relate this to physiology. We therefore submit that the most likely origin of the observed edge Pb increases is connected to increased environmental exposure. In oceans, Pb accumulates in bottom sediments, and its bioavailability in the water column therefore typically increases towards the seabed (Hansson et al., 2020; Webb et al., 2020). As the capelin enter shallow water to spawn in bottom sediments, Pb exposure is likely higher, which may have resulted in increased edge concentrations. Conversely, this also implies that the capelin reside mostly at deeper water in their preceding lifespan.

For localities in the Uummannaq Fjord (localities 2–7), the highest edge increase is found at locality 2 (Maarmorilik). The fish from this locality were caught less than 2.5 km from the former Black Angel lead-zinc mine in a confined body of relatively shallow waters. The mine has an extensive pollution history (Søndergaard et al., 2020), and elevated Pb levels have been detected in otoliths from sculpin (*Myoxocephalus scorpius*), a stationary fish species, in a gradient that increases towards the mining area (Hansson et al., 2020; Søndergaard et al., 2015). The particularly strong increases in edge Pb in capelin otoliths from this locality can likely be linked to the pollution, demonstrating the use of

otolith Pb as an environmental and spatial marker.

4.2.2. Pb in otolith cores

Otolith cores represent early life stages (pre-hatch and larval), and may therefore reflect conditions in the shallow water spawning grounds, similarly to otolith edges. However, core concentrations do not mirror the elevated Pb levels found in otolith edges. Although many localities exhibit increasing Pb towards the core, at only two localities, 2 and 18, are these increases significant. Furthermore, at locality 2, high core concentrations appear to be connected to just a few fish. There may be several reasons why significantly higher Pb concentrations are not found in the core. First of all, capelin fry typically drift off-shore with ocean currents shortly after hatching (Carscadden et al., 2013). The few fish that do exhibit elevated Pb in their core may initially have “avoided” drifting and resided near the coast for an extended period. Perhaps more importantly, the results are challenged by the difficulties associated with locating cores during sample preparation. It is likely that many supposed core measurements are “off the mark”. Therefore, we do not wish to put too much emphasis on these results. Microchemistry in the core may also be affected by ontogenetic changes in otolith biomineralization (Hüssy et al., 2020) and maternal overprinting (Loeppky et al., 2018; Sturrock et al., 2015), which further challenges interpretations.

5. Conclusions

Our results indicate that spatial structure amongst the investigated NW Greenland capelin is limited to intra-fjord movements or possibly migrations between inshore and adjacent offshore areas. On a large geographical scale, time-resolved classifications suggest little or no movement between northwest and southwest Greenland. On a smaller geographical scale, Pb is found useful as a spatial tracer, despite minor concerns about instrumental accuracy of the Pb data. Two localities (11 and 17) have consistently higher otolith Pb than at neighboring localities, indicating spatial separation between populations on a scale of 150–300 km. In one of the largest fjords, Uummanaq Fjord, which can be regarded as a large $\sim 100 \times 150$ km bay with smaller branches (Fig. 1), migrations appear to be limited to certain parts. Here, four closely spaced localities exhibit different otolith Pb concentrations, indicating spatial separation on an even smaller scale of 15–50 km. Migrations between fjords and offshore areas cannot be ruled out in all areas, but Pb profiles indicate that the capelin do not travel up or down along the coast. Furthermore, we suggest that increasing Pb concentrations towards otolith edges are related to spawning in shallow waters, where Pb exposure may be higher due to proximity to geological and/or anthropogenic Pb sources. This also implies that capelin primarily reside at deeper waters, most likely in or just outside the fjords. Future research should map the elemental profiles of hydrographical environments in and out of fjords to allow for further investigations of capelin movement. In conclusion, our results indicate that capelin fjord populations in West Greenland are substantially less migratory than the stocks that spawn in the Barents Sea, around Iceland and off East Canada. A fishery for capelin in West Greenland should therefore be managed in high spatial resolution to avoid local collapses.

CRedit authorship contribution statement

Peter Fink-Jensen: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Karin Hüssy:** Conceptualization, Methodology, Resources, Writing – review & editing, Supervision, Project Administration, Funding acquisition. **Teunis Janzen:** Conceptualization, Methodology, Formal analysis, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Tonny Bernt Thomsen:** Methodology, Investigation, Resources, Writing – review & editing. **Simon Hansen Serre:** Methodology, Formal analysis, Investigation, Writing – review & editing. **Jens**

Søndergaard: Conceptualization, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.fishres.2021.106172](https://doi.org/10.1016/j.fishres.2021.106172).

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