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Multi-year stability of spatial patterns in capelin otolith-edge chemical fingerprints in the Gulf of St. Lawrence, Canada

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ABSTRACT

In the Gulf of St. Lawrence (GSL, Canada), the population structure and dynamics of capelin (*Mallotus villosus*), an abundant small pelagic forage fish, remain poorly understood, limiting the implementation of reliable stock assessment. Otolith-edge elemental signatures were analysed to identify regions with statically distinct element signatures and evaluate the potential of otolith chemistry as a tool for tracking capelin movements and life history events in the GSL. A total of 679 individuals were collected between 2022 and 2024, and their otolith elemental composition was analysed using Laser Ablation Inductively Coupled Plasma Mass Spectrometry (LA-ICP-MS). Seven elements (lithium, boron, magnesium, potassium, zinc, strontium, and barium) were retained for discriminating among three regions: Estuary, South and Strait of Belle Isle (SBI). Quadratic discriminant analysis (QDA) assigned individuals to their region of origin with reallocation success rates of 64.3 % for the Estuary, 60.0 % for the South, and 80.5 % for the SBI. A sensitivity analysis confirmed the robustness of the results and indicated a negligible effect of individual length. Although some interannual variability was detected over the three-year period, spatial differences consistently exceeded temporal variation. Spatial differences in elemental signatures likely reflect underlying oceanographic drivers, such as water temperature and salinity, which influence otolith-edge chemistry. These results indicate that otolith-edge elemental fingerprints can provide significant discrimination among regions, supporting their potential use in studies of capelin movement and spatial population structure. Such information may ultimately contribute to improved stock assessment and management in the GSL.

1. Introduction

Understanding population structure and connectivity is essential for effective fisheries management (e.g., Fontoura et al., 2022; Gebremedhin et al., 2021; Kerr et al., 2017). Stock assessment models often assume that fish populations are closed and homogeneous (Secor, 2014), ignoring the potential spatial complexity and connectivity among

subpopulations (Hilborn and Ovando, 2014; Randon et al., 2021). This may result in unbiased or unreliable stock assessment (Archambault et al., 2016; Cadrin, 2020; Spies et al., 2015) and increase the risk of over-exploitation or local depletion (Singh et al., 2025; Wilson et al., 2023), as spatial structure and metapopulation dynamics influence population resilience and responses to both exploitation and environmental change. In Canadian fisheries, the population structure and connectivity of

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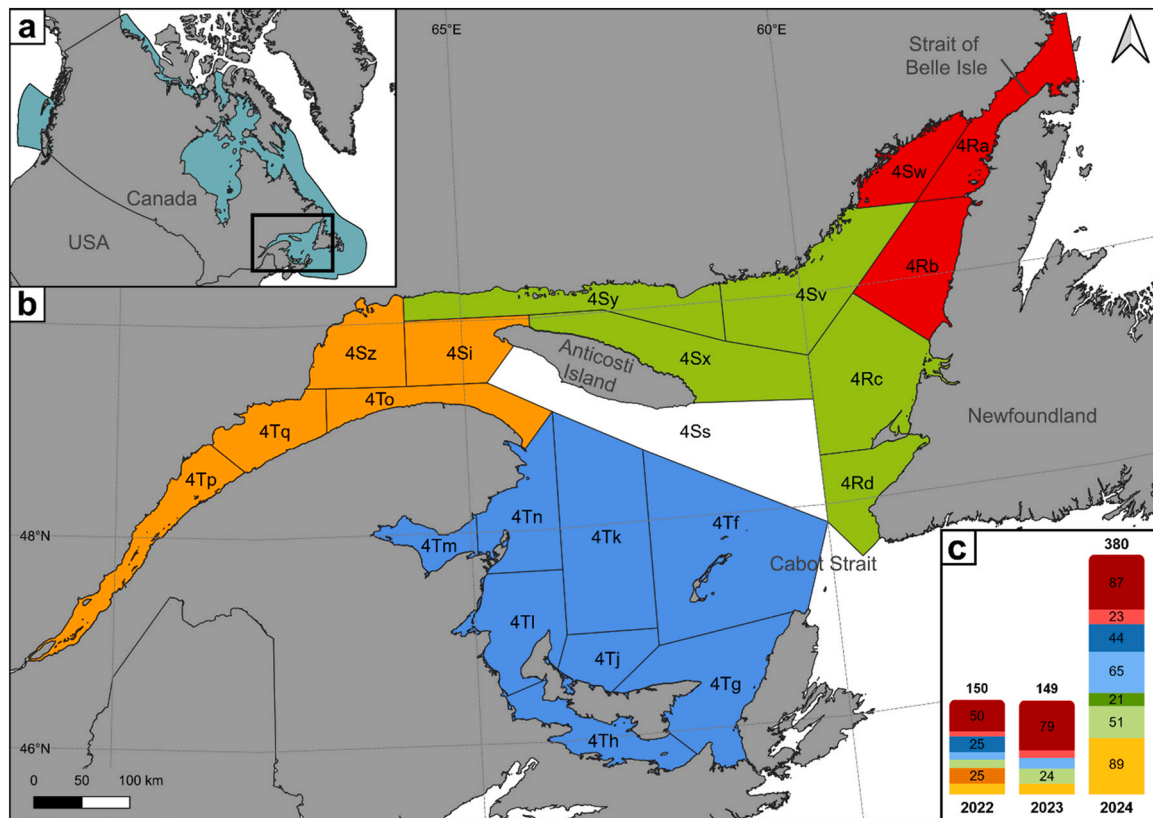


Fig. 1. Maps showing (a) the schematic distribution of capelin across Canada's three oceans (adapted from Jac et al. (2025)), (b) the study area with NAFO subdivisions and regions identified in the clustering analysis, and (c) a stacked bar chart displaying the number of individuals sampled per year and region. Colours represent regions as follows: orange for the Estuary, green for the North, blue for the South, and red for the Strait of Belle Isle. In the stacked bar chart, light shades represent samples from DFO multi-species bottom trawl surveys, while dark shades correspond to commercial fishery samples. Sample sizes are labelled when exceeding 20 individuals.

several forage fish stocks remain poorly characterised (Boldt et al., 2022; Jac et al., 2025), despite their economic importance and the central role they play in marine food webs (Cury et al., 2011; Konar et al., 2019; Ruzicka et al., 2024).

Capelin (*Mallotus villosus* (O. F. Müller, 1776)) is one of the most abundant forage fish in Canadian waters, with exploited stocks distributed around eastern Newfoundland and Labrador, as well as the Estuary and the Gulf of St. Lawrence (hereafter referred to as the GSL). Most ecological knowledge about capelin in Canada comes from the Newfoundland stock (Jac et al., 2025), where its importance as key prey to the Northern Atlantic cod stock has prompted extensive research into its reproduction (e.g., Murphy et al., 2021; Tripp et al., 2020), population dynamics and environmental drivers of abundance (Tripp and Davoren, 2025). In contrast, the GSL stock have received much less scientific attention due to a lesser perceived importance to the fisheries ecosystem (Boudreau et al., 2023; Brown, 2002; Jac et al., 2025). However, ecosystem modelling has identified capelin as a key species in the GSL ecosystem, so shedding light on its population structure is crucial to develop an ecosystem-based approach to fishery management for the region (Savenkoff et al., 2004).

Otolith elemental analysis is a powerful tool for resolving fish stock structure and connectivity, as it integrates spatially distinct environmental signatures experienced by individuals throughout their life history, providing substantial potential for investigating capelin population structure and connectivity (Jac et al., 2025). Moreover, the GSL complex hydrography, shaped by freshwater inputs, shelf currents, and episodic intrusions of deep Atlantic water (Galbraith et al., 2025), creates spatially heterogeneous environmental conditions that offer strong contrasts for the application of otolith chemistry. Otoliths are metabolically inert structures, incorporating trace elements from seawater

and preserving a chronological record of environmental exposure (Campana, 1999). The core reflects natal origin, while the edge represents conditions at or near the time and place of capture. The effectiveness of this method relies on the presence of spatially distinct physical and/or chemical conditions that generate unique otolith trace element signatures. When these differences remain stable over time, they allow for robust discrimination of population structure and movement patterns (e.g., Elsdon et al., 2008; Kerr and Campana, 2014). This method has been successfully applied to capelin populations along Newfoundland's east coast (e.g., Loeppky and Davoren, 2018; Tripp et al., 2020; Tripp and Davoren, 2025), and recently in Greenland waters (Fink-Jensen et al., 2022, 2021). Within the GSL, elemental fingerprints have been used at a smaller spatial scale to identify natal origins of capelin within the Estuary (Lazartigues et al., 2016), as well as for other adult forage fish species (Couillard et al., 2022).

Extended marine systems, such as the GSL, present challenges for otolith chemistry as water mixing and elemental fractionation can obscure spatial signals (Sturrock et al., 2012; Trueman et al., 2012). This study aims to (1) delineate regions with similar capelin otolith-edge elemental fingerprints, (2) identify the optimal combination of elements for discriminating among regions, and (3) evaluate the temporal stability of these chemical zones. Ultimately, the study seeks to establish regional elemental fingerprints that can serve as a chemical baseline for future research on the spatial structure and connectivity of capelin populations. It can be hypothesised that hydrographic variability across the GSL generates spatially distinct elemental signatures in capelin otoliths, which can serve as a baseline to study natal origins and reconstruct individuals' ontogenetic movements.

Table 1

Clustering results for both regions and NAFO sub-divisions, with the number of capelins sampled per year for each sub-division as well as the type of survey: commercial fishery samples and DFO multi-species bottom trawl surveys. Cells shaded in grey indicate sub-divisions and years where no capelin were captured.

	Commercial fishery			DFO bottom trawl		
	2022	2023	2024	2022	2023	2024
Estuary						
4Si					3	27
4Sz				5		30
4To	12				13	11
4Tp	13			7		11
4Tq				5	1	10
Total	25	0	0	16	17	89
North						
4Rc						10
4Rd				5	6	6
4Sv					1	
4Sx				4	8	25
4Sy			21	4	9	10
Total	0	0	21	13	24	51
South						
4Tf					2	6
4Tg			4	3	2	6
4Th						6
4Tj				2	3	6
4Tk				2	3	12
4Tl					2	9
4Tm				3	2	9
4Tn	25		40	2	3	11
Total	25	0	44	12	17	65
SBI						
4Ra	13	60	49		6	23
4Rb	12			8	6	
4Sw	25	19	38			
Total	50	79	87	8	12	23

2. Materials and methods

2.1. Study area and sample collection

The GSL is a semi-enclosed sea receiving primary water input from the Gulf Stream via Cabot Strait and, to a lesser extent, the Labrador Current through the Strait of Belle Isle (El-Sabh, 1976; Galbraith et al., 2025; White and Johns, 1997; Fig. 1). In summer, the GSL exhibits a three-layered thermal structure: a warm surface layer, a cold intermediate layer (50–120 m), and a deeper, slightly warmer Atlantic-derived layer (Galbraith et al., 2025). Capelin, a cold-water species, is primarily associated with the intermediate layer, whose horizontal and vertical extend varies regionally (Chamberland et al., 2022).

From 2022–2024, a total of 679 capelin were collected throughout the GSL, their total length (TL) measured, and sex was determined by external examination or gonad observation when necessary. These individuals originated from two primary sources (Fig. 1; Table 1). The first was the commercial fishery, sampled between May and July through Fisheries and Oceans Canada's (DFO) commercial port sampling program, which coincide with the capelin reproductive period in this area (Boudreau et al., 2023). Commercial capelin in the GSL is harvested in coastal waters using a variety of nearshore gears, including pound nets, baited traps, and purse seines. Spatial information was therefore limited to Northwest Atlantic Fisheries Organisation (NAFO) subdivisions reported by fishers, with most samples originating from 4Ra, 4Sw, and 4Tn (Table 1). Commercial samples consisted predominantly of larger individuals, ranging from 10.5 to 19 cm (TL). The second source consisted of DFO's annual multi-species bottom trawl surveys, conducted in the

northern and southern GSL during August and September, corresponding to the post-reproductive period (Chamberland et al., 2022). These surveys are performed using a standardised stern otter trawl, providing consistent sampling gear and tow characteristics across years and regions. Survey samples offered broader and more precise spatial coverage throughout the GSL and included exact sampling coordinates. Individuals collected during these surveys ranged from 7.5 to 17.0 cm (TL).

Although sampling differed between the commercial fishery and scientific surveys in terms of gear type, depth of capture, and sampling period, these differences do not influence the objectives or interpretation of the study. The analyses focus solely on otolith elemental chemistry, which reflects environmental exposure rather than capture conditions. Sampling during two periods of the summer (May–July and August–September) allows for the characterisation of the elemental signature along the entire summer season (Galbraith et al., 2025). Moreover, to avoid biases from gear-specific catch composition, individuals are selected using a random stratified design balancing among (i) sources, (ii) NAFO subdivision (Fig. 1; Table 1), (iii) fish length (Fig. S1), and (iv) sex. Therefore 679 capelin otoliths – 150 in 2022, 149 in 2023 and 380 in 2024 – have been analysed (Fig. 1; Table 1). These individuals were composed of 354 females, 247 males and 37 of undetermined sex.

2.2. Otolith preparation and elemental analysis

Sagittal otoliths were extracted using acid-cleaned tweezers and were cleaned of organic matter and rinsed three times with ultrapure

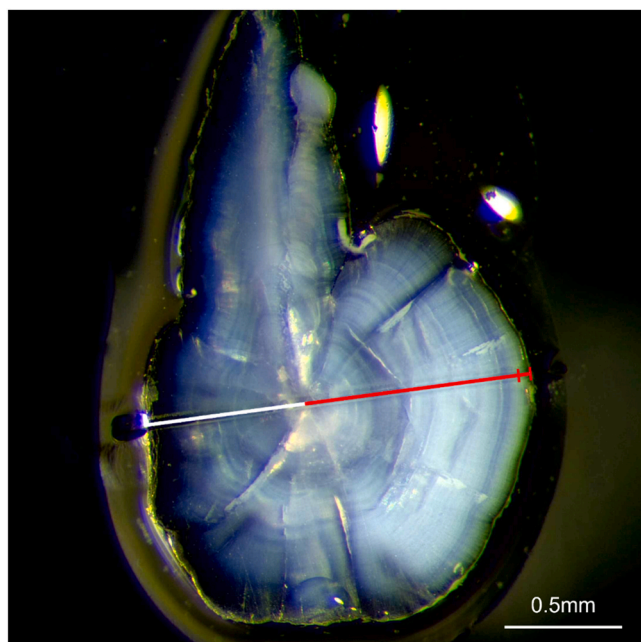


Fig. 2. Photo of a sanded capelin otolith submerged in water following LA-ICP-MS analysis. The long white line represents the ablation transect performed during the procedure, with the red segment indicating the portion extending from the otolith core to the outer edge. The two short perpendicular red lines delineate the 40 µm edge region used to extract chemical signatures reflecting environmental and physiological conditions during a maximum of 2–3 months preceding capture.

water. Both otoliths were preserved, but only the right sagitta was used for analysis. They were then stored in acid-washed Eppendorf tubes and dried under a laminar flow hood for 24 h. Otoliths mounted on microscope slides with thermoplastic glue, and then ground and polished using a sequence of abrasive papers (1200 µm, 5 µm, and 1 µm), applying circular and figure-eight motions. This two-dimensional polishing approach has been successfully applied for capelin and allows reliable exposure of the ventral edge for chemical transects (e.g.,

Lazartigues et al., 2016, 2014). Polishing progress was monitored with a compound microscope to ensure even surface flatness and clear visualisation of the edge. Polished otoliths were transferred to petrographic slides and photographed (Fig. 2).

Laser Ablation-Inductively Coupled Plasma-Mass Spectrometry (LA-ICP-MS) was performed at LabMaTer (Université du Québec à Chicoutimi, Canada) using a Resolution M-50 Excimer 193 nm laser coupled to an Agilent 7900x quadrupole ICP-MS. Linear transects were ablated along the ventral edge of each otolith (Fig. 2). A laser fluence of 5 J·cm⁻², repetition rate of 25 Hz, beam of 44 µm diameter, and scan speed of 5 µm·s⁻¹ were used. The relatively large beam diameter was selected to optimise material removal and signal stability in juvenile and adult capelin otoliths, thereby reducing limits of detection (Lazartigues et al., 2014). Given that capelin otoliths are 15–20 µm in diameter at hatching, a 44 µm beam integrates signal over only a few days of early life and does not compromise temporal resolution at the life-stage targeted here. Data were collected at an acquisition rate of 4 measurements per second for all selected isotopes (integration time 0.252 s), providing sufficiently dense sampling along each transect. Multiple replicates transect were therefore unnecessary, as analytical replication occurred at sub-second resolution, and biological replication was ensured by the large number of individuals analysed. Ablated aerosols were transported using an argon-helium carrier gas mixture with added nitrogen. Each transect was preceded by a 30-second gas blank measurement. During LA-ICP-MS ablation, the otoliths were only in contact with the laser beam, eliminating any additional contamination risk.

A total of 38 isotopes were measured: ⁷Li, ¹¹B, ²³Na, ²⁴Mg, ²⁵Mg, ²⁷Al, ²⁹Si, ³¹P, ³⁴S, ³⁹K, ⁴²Ca, ⁴³Ca, ⁴⁴Ca, ⁵⁵Mn, ⁵⁶Fe, ⁵⁷Fe, ⁵⁹Co, ⁶⁰Ni, ⁶¹Ni, ⁶³Cu, ⁶⁴Zn, ⁶⁵Cu, ⁶⁶Zn, ⁶⁹Ga, ⁸⁵Rb, ⁸⁶Sr, ⁸⁷Sr, ⁸⁸Sr, ¹¹¹Cd, ¹¹⁴Cd, ¹¹⁸Sn, ¹¹⁹Sn, ¹²⁰Sn, ¹³⁶Ba, ¹³⁷Ba, ¹³⁸Ba, ²⁰²Hg, and ²⁰⁸Pb. Certified reference materials (NIST SRM-610/612; USGS GSE-1, GP4-A, MACS-3) were analysed at the start, end, and after every seven otoliths to ensure calibration accuracy. Accuracy and precision were evaluated by comparing measured element/Ca ratios to published reference values (USGS; Weis et al., 2022), and all standards performed within acceptable ranges (see Table S1). Data reduction was performed using the “Iolite” package (Paton et al., 2011) in Igor Pro. Calcium (⁴⁴Ca) was used as an internal standard (38.02 % of otolith mass; Campana, 1999), with calibration based on NIST SRM-610. Only otoliths with stable calcium

Table 2

Summary of pre-processing steps applied to capelin otolith elemental data before statistical analyses. Cells shaded in grey indicate cases where no elements were removed during the pre-processing step.

Description	Elements removed	Number of elements
Original dataset		38
Step 1 Keep only last 40 µm of the transect		
Step 2 Replace values below detection with LOD/2		
Step 3 Remove outliers > 3 SD (outliers)		
Step 4 Average values per element (along the last 40 µm)		
Step 5 Remove elements/isotopes based on analytical issues	²⁹ Si, ⁴³ Ca, ⁴⁴ Ca, ³¹ P, ⁶³ Cu, ⁶⁵ Cu, ²⁷ Al, ⁸⁵ Rb, ²⁰² Hg	29
Step 6 Remove elements/isotopes correlated with LA-ICP-MS analysis time	⁵⁷ Fe, ⁶¹ Ni	27
Step 7 Remove elements/isotopes showing interactions with others	²⁴ Mg, ⁶⁹ Ga, ⁵⁶ Fe, ⁵⁹ Co, ³⁴ S, ⁷⁵ As,	21
Step 8 Keep only the isotope per element most frequent in the data set	²⁶ Mg, ⁶⁶ Zn, ⁸⁶ Sr, ⁸⁷ Sr, ¹³⁶ Ba, ¹³⁷ Ba	15
Step 9 Remove elements with >50% of values < LOD/2	⁶⁰ Ni, ⁷⁹ Br, ¹¹⁴ Cd, ¹²⁰ Sn, ²⁰⁸ Pb	10
Step 10 Calculate ratios using ⁴² Ca		
Step 11 Remove ⁴² Ca post-ratio calculation	⁴² Ca	9
Step 12 Apply log(x+1) transformation to all the element required (B, Na, Mg, Mn, and Zn)		
Step 13 Assess effect of fish length and sex		
Clean dataset		9

profiles were retained for analysis. Trace element concentrations were expressed in parts per million (ppm). Element concentration limits of detection (LOD) were calculated as $3 \times \text{SD}$ of the gas blank divided by analyte sensitivity (Lazartigues et al., 2014). This methodology follows the same protocol previously applied to capelin (Lazartigues et al., 2016) and other fish species in the GSL (e.g., Coussau et al., 2023; Gauthier et al., 2024) and ensures consistency and comparability across studies. All pre-processing steps implemented before statistical analyses are described in Table 2.

2.3. Data cleaning and transformation

To characterise the elemental signature of the capture site, only the outermost 40 μm of each otolith was used (Fig. 2). This section has been widely applied in studies of capelin otolith-edge elemental fingerprints (Davoren and Halden, 2014; Fink-Jensen et al., 2021). Although species-specific otolith growth rates for capelin in the GSL are not available, comparisons with studies from other regions suggest that this section represents a maximum of 2–3 months of growth (Fink-Jensen et al., 2021). Values below the LOD were replaced with $\text{LOD}/2$, and outliers ($>\pm 3 \text{ SD}$) were removed. To confirm that this section accurately reflects the environmental conditions at the capture site, elemental signatures were examined to ensure no abrupt fluctuations occurred. Finally, the values were averaged to produce a single representative value per element, corresponding to the elemental fingerprint of the capture site.

Of the 38 isotopes measured, element selection was based on three main criteria (Table 2; step 5–9): (1, steps 5–6) order of measurement in LA-ICP-MS: elements measured at the beginning or end of an acquisition can be affected by memory effects or signal drift, and such elements were excluded; (2, step 7) analytical interference and standard availability: elements with known interferences, lack of suitable reference materials, or limited analytical reliability were removed; and (3, step 8–9) isotopic abundance: only isotopes with sufficiently high natural abundance were retained to ensure accurate and precise measurements. Additionally, aluminium and silicon were measured solely as indicators of potential contamination and were therefore removed from the final elemental list. Aluminium tracked contributions from polishing sandpaper (Al_2O_3), while silicon checked for contact with the histology blade or slide. No contamination was detected in any sample. Following these procedures, the final dataset included nine elements: ^7Li , ^{11}B , ^{23}Na , ^{25}Mg , ^{39}K , ^{55}Mn , ^{64}Zn , ^{88}Sr , and ^{138}Ba . For simplicity, isotopic numbers are omitted in subsequent sections. Elemental concentrations were expressed as ratio to calcium. Non-normally distributed elements (Li, B, Na, Mg, Mn, and Zn) were then $\log_{10}(x + 1)$ transformed to meet parametric assumptions.

2.4. Effects of capelin length and sex on element concentrations

Variations in otolith-edge elemental composition may be confounded by differences in capelin length or sex (e.g., Fink-Jensen et al., 2021). To account for these potential confounding effects, the relationships between capelin length, sex, and selected trace elements at the edge were assessed (Table 2, step 13). First, collinearity between length and sex was evaluated using Variance Inflation Factors (VIF; “vif” function, “car” package (Fox and Weisberg, 2019). Following Zuur et al. (2010), VIF values > 3 were considered indicative of potential multicollinearity. For all elements, VIF values for both length and sex were low (<1.16), indicating negligible collinearity.

The effect of length and sex on elemental concentrations was then tested using a multivariate analysis of variance (MANOVA). Sex had no significant effect, whereas capelin length significantly influenced the concentrations of most elements (B, Na, Mg, Mn, Zn, Sr, and Ba; Table S2). For these elements, concentrations (C_i) were adjusted to account for variation in individual fish (i) length. The adjusted concentration (Cadji) for each individual was calculated using the slope (s) of

the linear relationship between elemental concentration and capelin length (L_i), relative to the mean length ($\bar{L}$), as follows:

$$\text{Cadji} = C_i - s * (L_i - \bar{L})$$

This adjustment ensured that observed elemental differences reflected environmental variation rather than length-related effects.

2.5. Defining chemical regions and regional chemical characteristics

To delineate regions with similar capelin otolith-edge elemental fingerprints, spatially constrained hierarchical clustering was conducted on data pooled across all years. Two complementary approaches were implemented: (1) a fine-scale clustering using the precise coordinates of individuals collected during the DFO bottom trawl survey (2) a broader-scale clustering of the full dataset based on NAFO sub-divisions. In both cases, the Ward2 agglomerative method (Kaufman and Rousseeuw, 1990; Legendre and Legendre, 2012) was used with an optimised spatial constraint parameter ($\alpha = 0.4$), implemented in the R package *ClustGeo* (Chavent et al., 2018). Ward2 was selected because it minimises within-cluster variance and is well suited for identifying compact, homogeneous groups when combining spatial and multivariate information. Sensitivity tests using alternative linkage methods (e.g., single, complete, average) yielded less consistent or interpretable results. Cluster solutions ranging from two to ten groups were explored, and the clustering results obtained using the full dataset were compared with those derived from scientific survey data alone. The approach that best reflected the dataset's structure and spatial coverage was retained for subsequent analyses.

To assess whether otolith-edge elemental signatures could reliably reassign individual capelin to their respective capture regions, the statistical classification framework described by Mercier et al. (2012) was applied. Two multivariate classification models—Linear Discriminant Analysis (LDA) and Quadratic Discriminant Analysis (QDA)—were compared to identify the model and combination of elemental variables that best distinguishes chemically distinct areas within the GSL. Model performance was assessed over 1000 iterations using a stratified cross-validation procedure, in which 75 % of individuals were randomly selected for model training and the remaining 25 % used for validation. Spatial structure in otolith-edge chemistry was further visualised using t-distributed Stochastic Neighbour Embedding (t-SNE), and radar plots were generated to display mean standardised concentrations for each element by region. Statistical significance of spatial (between regions) and temporal (between years within each region) variation in elemental fingerprints was tested using MANOVA and ANOVA. Finally, the classification accuracy of the best-performing model and element combination was evaluated through reallocation procedures using the same cross-validation framework as before.

To evaluate the influence of fish length on regional discrimination, the full clustering and classification workflow was repeated using unadjusted elemental concentrations (C_i).

3. Results

3.1. Spatial delineation and temporal stability of otolith-edge elemental regions

Cluster analysis based on the concentrations of nine elements (Li, B, Na, Mg, K, Mn, Zn, Sr, and Ba) identified four distinct regions within the GSL: (1) the St. Lawrence Estuary, with 148 individuals; (2) the northern GSL, the smallest cluster, with 109 individuals; (3) the southern GSL, the largest cluster in geographic extent, with 163 individuals; and (4) the Strait of Belle Isle (hereafter SBI), the largest cluster in terms of sample size, with 259 individuals (Fig. 1; Table 1). Most fish assigned to the SBI were collected from NAFO (Northwest Atlantic Fisheries Organisation) 4RA subdivision ($n = 151$), which largely shaped the chemical patterns

Table 3
Classification accuracies (maximum, mean with 95 % confidence intervals, and minimum) for assigning capelin otolith edge samples to their capture regions (Estuary, North, South, and Strait of Belle Isle), using the best-performing discriminant analysis and optimal combination of elements, following the procedure of Mercier et al. (2012).

Classification method	Best combination of elements	Max accuracy	Mean accuracy	Min accuracy
LDA	Li, B ^a Mg, K, Zn, Sr, Ba	0.63	0.54 ± 0.03	0.45
QDA	Li, B ^a Mg, K, Zn, Sr, Ba	0.67	0.57 ± 0.02	0.49

observed patterns for this region.

Temporal stability of this regional structure was supported by several complementary analyses. First, restricting the dataset to spatiotemporally balanced scientific survey samples yielded cluster solutions that were consistent with those obtained from the full dataset. Second, year-specific analyses conducted independently for each of the three sampling years reproduced the same number of regions and comparable spatial configurations. Although interannual variability in elemental concentrations was observed, temporal effects were weaker than spatial

effects, indicating that the regional chemical structure was stable across the spring–summer season and among years.

The magnitude of regional chemical differences was sufficient to support individual-level classification. Among the classification approaches evaluated, quadratic discriminant analysis (QDA) provided the highest performance, achieving an overall reallocation accuracy of 67 % when assigning capelin otolith-edge chemistry to their capture regions in the GSL. The optimal multielement signature included Li, B, Mg, K, Zn, Sr, and Ba (Table 3).

Together, these results demonstrate that otolith-edge elemental signatures are spatially structured across the GSL, with individuals captured in close geographical proximity exhibiting similar chemical signatures. The robustness of this pattern across time, as well as its strength, indicates that this delineation is ecologically meaningful. Subsequent analyses focus on these defined regions to explore their ecological and biological significance.

3.2. Regional elemental differentiation and interannual variability

Elemental concentration profiles based on Li, B, Mg, K, Zn, Sr, and Ba revealed clear and consistent spatial patterns among regions (Fig. 3; Table S3). The SBI was the most chemically distinct region,

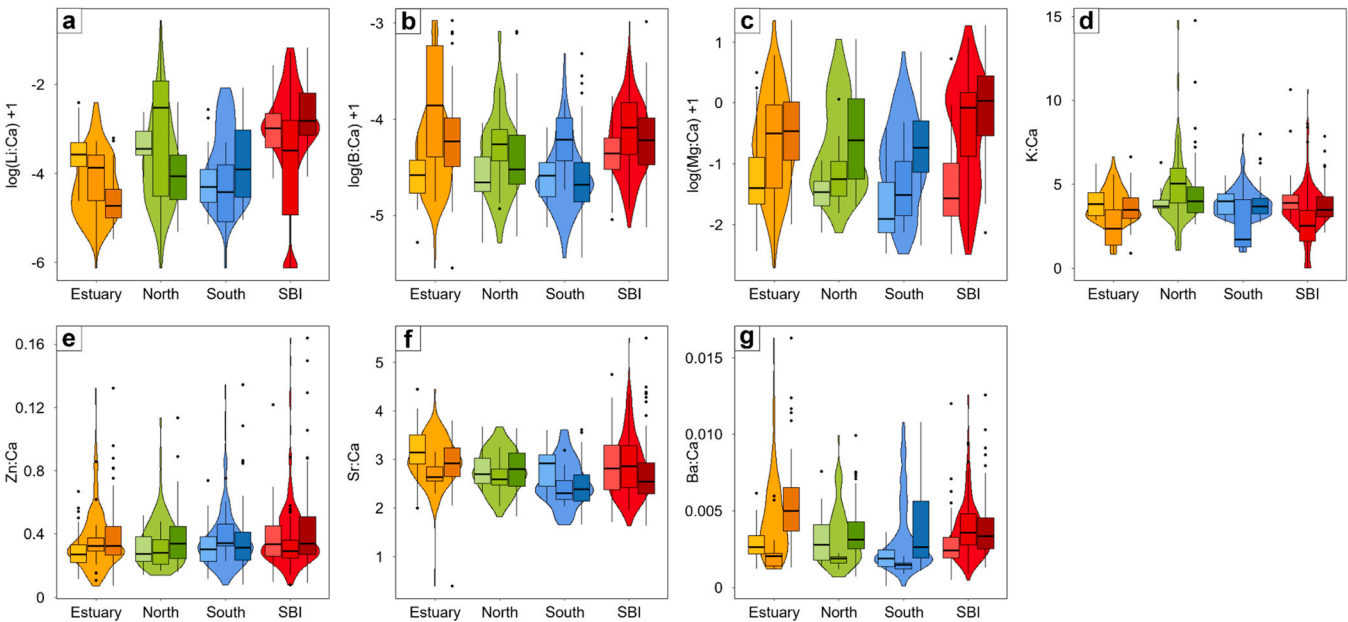


Fig. 3. Boxplots illustrating spatial (x-axis) and temporal (boxplots; from 2022 to 2024) variability in elemental concentrations across defined regions of the Gulf of St. Lawrence, based on the elemental combination that maximized habitat assignment accuracy: (a) lithium (Li), (b) boron (B), (c) magnesium (Mg), (d) potassium (K), (e) zinc (Zn), (f) strontium (Sr), and (g) barium (Ba). Background violin-boxplots show the overall yearly distribution of elemental concentrations for each region. Colours represent regions as follows: orange for the Estuary, green for the North, blue for the South, and red for the Strait of Belle Isle.

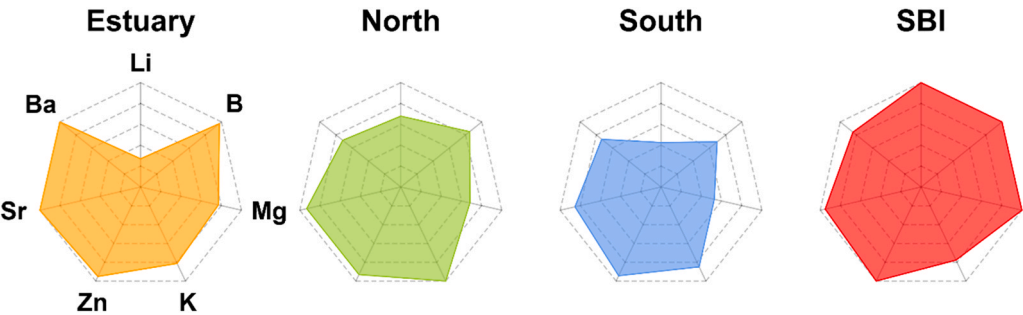


Fig. 4. Radar plot comparing the elemental fingerprints of the defined regions in the Gulf of St. Lawrence, based on the elemental combination that maximized habitat assignment accuracy (Li, B, Mg, K, Zn, Sr, and Ba).

Table 4

Results of multivariate and univariate analyses assessing spatial and temporal variation in elemental concentrations of capelin otolith edges from four regions of the Gulf of St. Lawrence (Estuary, North, South, and Strait of Belle Isle) between 2022 and 2024 with a (a) Multivariate analysis (MANOVA) testing the effect of Region and Year on the combined concentrations of Li, B, Mg, K, Zn, Sr, and Ba. Pillai's Trace, degrees of freedom (df), F-values, and p-values are reported and a (b) Univariate analyses (ANOVA) testing each element separately for the effects of Region and Year. Analyses were performed using the elemental combination that maximized habitat assignment accuracy. Significance levels are indicated as: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

a				
Factor	Pillai Trace	df	F	p-value
Region	0.47	3	17.38	***
Year	0.33	1	46.38	***
b				
Element	Factor	Mean square	F	p-value
Li	Region	45.49	47.49	***
	Year	0.67	0.70	
B	Region	4.65	29.63	***
	Year	1.70	10.82	**
Mg	Region	10.43	20.96	***
	Year	125.21	251.75	***
K	Region	25.70	13.86	***
	Year	0.14	0.07	
Zn	Region	2.49e-04	0.76	
	Year	4.42e-03	13.42	***
Sr	Region	5.18	19.26	***
	Year	5.62	20.88	***
Ba	Region	4.48e-05	11.05	***
	Year	3.13e-04	77.15	***

characterised by elevated Li and Mg concentrations. The St. Lawrence Estuary exhibited the highest Ba concentrations, whereas the northern GSL was distinguished by relatively high K levels. The southern GSL displayed comparatively low Li concentrations. Zinc concentrations were relatively similar among regions but contributed to differentiation between the Estuary and the SBI. Boron and strontium showed elevated concentrations in both the Estuary and the SBI compared to the northern and southern GSL, following broadly similar spatial gradients (Fig. 4).

Temporal variability in otolith-edge elemental signatures was observed across the three sampling years, particularly for Mg, Zn, and Ba (Fig. 3; Table S3). Interannual variability was most pronounced in the Estuary. Despite these fluctuations, MANOVA indicated that spatial differences among regions explained a greater proportion of the total variance than temporal differences within regions (Table 4), further supporting the temporal robustness of the regional chemical structure.

QDA applied to pooled data from all years yielded region-specific reallocation success rates of 47.6 % for the Estuary, 21.9 % for the northern GSL, 60.0 % for the southern GSL, and 80.5 % for the SBI (Fig. 5a, b). Due to mixed and weakly assignable chemical signatures, individuals from the northern GSL were excluded from subsequent focused analyses. Restricting classification to the Estuary, southern GSL, and SBI substantially improved performance, with reallocation success rates of 64.3 %, 60.0 %, and 80.5 %, respectively, and low misallocation rates (Fig. 5c, d), indicating strong and consistent chemical differentiation among these regions.

Capelin sampled across the four regions encompassed a broad range of body lengths (7.5–20.0 cm), capturing much of the population-level size variability (Fig. S1). Length distributions were broadly similar among the Estuary, northern GSL, and southern GSL, whereas samples from the SBI consistently included the largest individuals (>17.5 cm). Repeating the full clustering and classification workflow using unadjusted elemental concentrations produced nearly identical spatial patterns and classification results (Fig. S2), confirming that the delineation of chemical regions was robust to potential length-related effects.

4. Discussion

This study demonstrates spatial differentiation and temporal stability in otolith-edge elemental fingerprints of capelin across the GSL. Sampling was conducted for two summer periods (May–July and August–September), allowing for the characterisation of elemental signatures across the entire summer season (Galbraith et al., 2025). Potential differences in otolith-edge chemistry, which could arise from variations in metabolic rates, physiological condition, or local environmental exposure during summer, did not affect classification performance. Although the SBI included slightly larger capelin (Fig. S1), reflecting the predominance of commercial fishery samples, significant differences in classification success among sources were not detected. Furthermore, repeating analyses using uncorrected elemental concentrations produced the same spatial clusters and nearly identical reallocation patterns (Fig. S2), indicating that fish length did not influence cluster structure or individual assignments. Overall, this dataset provides a reliable chemical baseline for the summer season, although these signatures may not fully capture variability outside this seasonal window.

4.1. Chemically distinct regions within the Gulf of St. Lawrence

In this study, the otolith-edge of 679 capelin shown a clear regional differentiation chemical signature across the GSL, likely driven by environmental heterogeneity. Seven elements (Li, B, Mg, K, Zn, Sr, and Ba) contributed to this differentiation, all of which have been widely used in previous studies of capelin and other marine fishes in the GSL and comparable systems (Table 5). This consistency supports both the robustness of the element selection protocol (Table 2; Table S1) and the comparability of the present results with earlier work. In particular, Sr, Ba, and Mg have repeatedly proven informative for resolving natal origin and movement patterns within the GSL (Couillard et al., 2022; Coussau et al., 2023; Gauthier et al., 2025, 2024).

The SBI region displayed the most pronounced chemical distinctiveness, with a high rate of reallocation (72.7 %). As the main area for commercial fishing, these elemental signatures provide a practical tool to determine the origin of harvested fish, assess stock mixing, and inform region-specific management strategies. Otolith-edge elemental signatures from individuals in that area were markedly different from those of other regions, indicating that water masses in the SBI possess unique physicochemical properties. This region is characterised by relatively shallow depths (<100 m), an expansive continental shelf, and elevated surface salinities (Blais et al., 2024). The SBI is strongly influenced by inflows of cold, saline waters from the Labrador Shelf, which partially enter the GSL at that point (Shaw and Galbraith, 2023). The limited freshwater input and sustained influence of Labrador Sea water likely imparts a stable and distinctive hydrographic identity to the SBI (Blais et al., 2024; Galbraith et al., 2025), which is reflected in the elemental composition of capelin otolith-edge from this region.

Distinct, albeit less sharply delineated, chemical signatures were also found in capelin from the Estuary and the southern GSL. The relatively lower degree of chemical separation between these regions likely reflects stronger hydrodynamic connectivity, driven by the southward advection of estuarine surface waters into the southern GSL (El-Sabh, 1976; Galbraith et al., 2025). This persistent exchange of surface water may promote chemical mixing and reduce regional differentiation in otolith element signatures. The Estuary is strongly influenced by the freshwater discharge from the St. Lawrence River, as well as by seasonal freshwater inputs from melting sea ice, with extensive ice coverage occurring during winter months (Galbraith et al., 2025). The southern GSL maintains a distinct hydrographic profile, shaped by a shallow shelf system (Koutitonsky and Bugden, 1991). It experiences significant seasonal contrasts, ranging from ice coverage in winter to some of the warmest surface waters in the GSL during summer (Galbraith et al., 2025). These factors likely contribute to the establishment of a

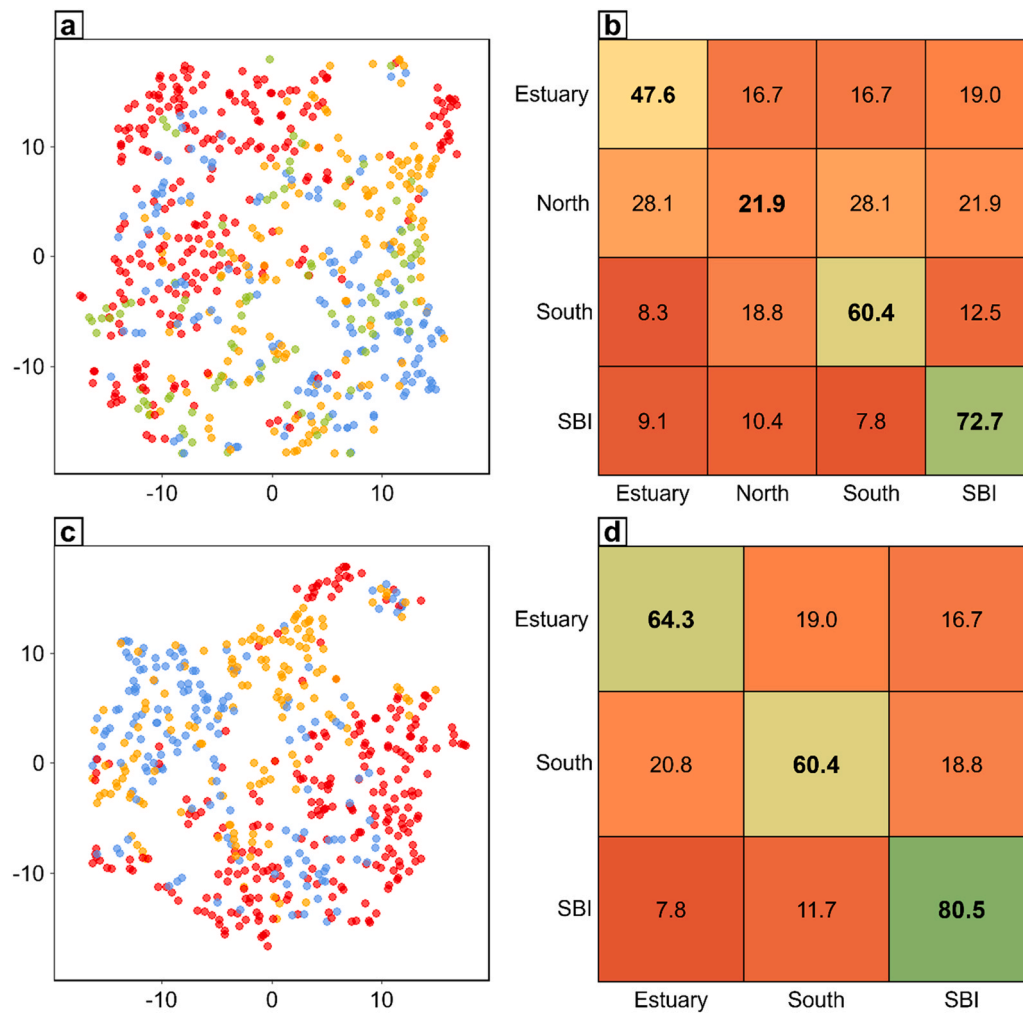


Fig. 5. Chemical differentiation and reallocation rates of capelin based on optimal elemental combinations (Li, B, Mg, K, Zn, Sr and Ba) from the otolith edge. Panels (a–b) show results for 4 regions (Estuary, North, South, and Strait of Belle Isle; overall reallocation rate = 57 %), while panels (c–d) show results for 3 regions (Estuary, South, and Strait of Belle Isle; overall reallocation rate = 72 %). Chemical differentiation is visualized using (a–c) t-distributed Stochastic Neighbour Embedding (t-SNE) plots in which each point represents an individual and colours represent regions as follows: orange for the Estuary, green for the North, blue for the South, and red for the Strait of Belle Isle. Reallocation performance is shown using (b–d) confusion matrices from quadratic discriminant analysis. Diagonal cells indicate correct assignments, while off-diagonal cells indicate misassignments. Colour intensity reflects assignment probability, from green (100 %) to red (0 %).

recognisable, though variable, chemical signature.

In contrast, capelin from the northern GSL were more difficult to reallocate based on otolith-edge chemistry. This region is influenced by multiple overlapping water masses, including freshwater inputs from the Estuary, Atlantic inflows through the Cabot Strait, and the intrusion of cold, saline water from the SBI (Blais et al., 2024; Galbraith et al., 2025; Shaw and Galbraith, 2023). Consequently, the northern GSL likely functions as a hydrographic transition zone, with a mixed environmental identity that reduces the clarity of spatially discrete chemical baselines. The challenge of defining a distinct elemental signature in this area may have been further compounded by the relatively limited sample availability, which could have affected the ability to detect finer-scale spatial patterns. Future studies incorporating greater sampling density in this region may improve classification accuracy.

4.2. Temporal stability of otolith-edge elemental signatures

Temporal variability in otolith-edge elemental signatures is a well-recognised challenge, as fluctuations over time can obscure spatial patterns and potentially lead to misinterpretations of habitat use and movement (Gillanders, 2002). Such variability occurs at both interannual and seasonal scales (Reis-Santos et al., 2012) and results from a

complex interplay of extrinsic environmental factors and intrinsic physiological processes that influence element uptake and incorporation into otoliths (Barnes and Gillanders, 2013; Hüsey et al., 2020; Miller and Hurst, 2020).

Among environmental drivers of temporal variability, temperature and salinity are particularly important as they affect both water chemistry and the metabolic activity of the fish (Barnes and Gillanders, 2013; Elsdon and Gillanders, 2004). These parameters are especially relevant for capelin, given their diel vertical migration behaviour, ascending into the upper water column at night and descending during the day (Jac et al., 2025). Capelin may thus be exposed to a mosaic of hydrographic conditions, potentially influencing otolith elemental incorporation (Elsdon et al., 2008; Reis-Santos et al., 2012). Nonetheless, capelin sampled from 2022 to 2024 were reallocated to their region of origin with high accuracy. Reclassification success rates were comparable to those reported in other studies conducted in the GSL (Bassi et al., 2023; Coussau et al., 2023; Gauthier et al., 2024) and aligned with findings from capelin research in eastern Newfoundland, where persistent regional differences in otolith chemistry have also been reported over time (Davoren et al., 2015; Loepky et al., 2018; Tripp and Davoren, 2025).

These results indicate that spatial differences in otolith-edge

Table 5

Chronological overview of otolith chemistry studies on capelin worldwide and other marine fish species in the Gulf of St. Lawrence.

Capelin worldwide				
Study	Area	Life stage	Analysis	Elements analyzed
This study	GSL	Juveniles/adults	Edge	Li, B, Mg, K, Zn, Sr, Ba
Tripp and Davoren, (2025)	Newfoundland	Embryonic	Complete	Sr, Ba
Fink-Jensen et al. (2022)	Greenland	Adults	Transect	Li, Ba, Pb
Tripp et al., 2022	Newfoundland	Embryonic	Complete	Mg, Mn, Sr, Ba
Fink-Jensen et al. (2021)	Greenland	Adults	Edge	Li, Mg, Al, Si, P, K, Ti, Mn, Cu, Zn, Rb, Sr, Ba, Pb
Tripp et al. (2020)	Notre Dame Bay	Larvae	Complete	Mg, Mn, Zn, Sr, Ba
Loeppky and Davoren, (2018)	Notre Dame Bay	Embryonic	Complete	Mg, Mn, Sr, Ba
Loeppky et al. (2018)	Middle Cove Beach	Embryonic	Complete	Mg, Mn, Sr, Ba
Maxner et al., 2016	Notre Dame Bay	Adults	Core	Sr, Ba
Lazartigues et al., (2016)	Fjord of Sagueny	Larvae	Complete	B, Na, Mg, K, Mn, Fe, Sr, Ba
Davoren et al. (2015)	Notre Dame Bay	Larvae	Complete	Mg, Mn, Sr, Ba
Davoren and Halden, (2014)	Newfoundland	Adults	Transect	Sr, Ba
Other species in the GSL				
Study	Species	Life stage	Analysis	Elements analyzed
Gauthier et al. (2025)	<i>H. hippoglossus</i>	Juveniles/adults	Core	Mg, Sr, Ba
Gauthier et al. (2024)	<i>H. hippoglossus</i>	Juveniles/adults	Transect	Mg, Sr, Ba
Coussau et al. (2023)	<i>S. mentella</i>	Juveniles/adults	Edge	Li, Na, Sr, Ba
Bassi et al. (2023)	<i>H. hippoglossus</i>	Juveniles/adults	Core	Mg, Sr, Ba
Couillard et al. (2022)	<i>C. harengus</i>	Juveniles/adults	Core	Mg, Sr, Ba
Stanley et al., 2016	<i>G. morhua</i>	Juveniles	Complete	Mg, Mn, Sr, Ba
Campana et al., 2007	<i>Sebastes</i> sp.	Juveniles/adults	Complete	Li, Na, Mg, K, Sr, Cd, Ba

chemistry outweighed the influence of interannual environmental variability, highlighting the temporal robustness of elemental fingerprints and supporting their use as indicators of regional population structure and connectivity in capelin.

4.3. Environmental drivers of capelin otolith-edge elemental variation

Element incorporation into otoliths is influenced by both environmental and physiological factors (Hüssy et al., 2020; Izzo et al., 2016; Sturrock et al., 2015). While physiological processes, such as growth, metabolic rate, and reproductive state, can affect element deposition, especially for elements associated with the organic matrix of otoliths (Hüssy et al., 2020; Walther et al., 2017), their influence is limited. The consistent spatial differences observed here suggest that the chemical contrasts primarily reflect environmental heterogeneity rather than individual physiology.

The GSL is characterised by pronounced gradients in freshwater input, salinity, temperature, and water-mass composition, driven by the discharge of the St. Lawrence River, seasonal ice melt, and complex circulation patterns linking estuarine, shelf, and Labrador-influenced

waters (Galbraith et al., 2025). These gradients provide plausible mechanistic drivers for the observed elemental structuring. Elevated Ba concentrations in capelin from the Estuary are consistent with strong riverine influence, as Ba predominantly occurs in dissolved form in freshwater and becomes increasingly particle-bound in saline environments (Hüssy et al., 2020; Turner et al., 1981). In contrast, Sr concentrations are typically low in freshwater and higher and relatively stable in marine waters (Walther and Limburg, 2012; (Avigliano, 2022; Hüssy et al., 2020; Walther and Limburg, 2012), making Sr a robust tracer of salinity gradients and water-mass origin across the estuarine–Gulf continuum.

Mg concentrations are known to respond to temperature and local biogeochemical conditions (Hüssy et al., 2020; Sturrock et al., 2015), both of which vary substantially across the GSL as a function of shelf depth, stratification, and seasonal circulation (Galbraith et al., 2025). Zn, while exhibiting weaker large-scale spatial structuring, may integrate finer-scale variability linked to productivity, biological activity, and localised water chemistry (Hüssy et al., 2020; Izzo et al., 2016). For several of these elements, including Sr, Ba, Li, Mn, and Zn, up to 80–90 % of otolith concentrations are thought to reflect ambient water conditions (Avigliano, 2022; Hüssy et al., 2020; Kerr and Campana, 2014; Sturrock et al., 2012), reinforcing their utility as environmental tracers.

Together, these region-specific physical and chemical gradients in the GSL likely underpin the spatial differentiation observed in capelin otolith-edge elemental signatures and explain the classification success achieved when assigning individuals to their capture regions.

5. Outlook

The regional chemical baselines established here show that otolith microchemistry can reliably distinguish capelin from different areas of the GSL, with particularly strong resolution for the SBI region. Building on these baselines, a key next step is to analyse otolith cores and full core-to-edge transects, which could reveal early-life habitat use, identify natal or spawning environments, and quantify the contributions of different spawning areas to the adult population (e.g., Fink-Jensen et al., 2022, 2021; Tripp and Davoren, 2025). Integrating otolith microchemistry with transect-based movement reconstructions offers a promising way to refine our understanding of connectivity and life-history strategies (Jac et al., 2025). While developed for capelin, this approach and the regional baselines presented here could also be applied to other forage species in the GSL, supporting broader ecosystem-based assessments of pelagic fish dynamics.

CRedit authorship contribution statement

Romarc Jac: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Lola Coussau:** Writing – review & editing, Validation, Formal analysis, Data curation. **Elisabeth van Beveren:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Mathieu Boudreau:** Writing – review & editing, Validation, Methodology. **Oliver Le Pape:** Writing – review & editing, Validation, Supervision, Methodology, Funding acquisition, Conceptualization. **Dominique Robert:** Writing – review & editing, Validation, Supervision, Methodology, Funding acquisition, Conceptualization. **Pablo Brosset:** Writing – review & editing, Validation, Supervision, Methodology, Funding acquisition, Conceptualization. **Pascal Sirois:** Writing – review & editing, Validation, Supervision, Methodology, Funding acquisition, Conceptualization.

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.2026.107671](https://doi.org/10.1016/j.fishres.2026.107671).

Data availability

Data will be made available on request.

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