



# Otolith elemental fingerprints reveal source–sink dynamics between two Greenland halibut nurseries in the St. Lawrence Estuary and Gulf

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**ABSTRACT:** In fisheries science, it is important to understand the population dynamics of commercial species and also their movements from the nursery to the population, especially for juvenile individuals, to avoid overfishing. To determine their migration patterns among nurseries, we collected juvenile Greenland halibut *Reinhardtius hippoglossoides* from 2 nurseries inside our study area, the Estuary and Gulf of St. Lawrence, in the summer of 2016. We measured the concentrations of chemical elements in their otoliths along a margin–core transect and used the margin elemental fingerprints of Mg, Mn, Sr, and Ba to infer migratory behaviour between 2 sample sites, the Estuary and North Anticosti nurseries. Using a random-forest analysis, we achieved an overall reclassification success of margin elemental fingerprints to their capture site of 77 %. Most fish sampled from both sample sites originated from the estuary (82.5 %), suggesting an important asymmetry in the source–sink dynamics between these nurseries. Juvenile Greenland halibut migrate towards the North Anticosti nursery at a smaller-than-expected size (approximately 26 cm) corresponding to 2.5–3 yr old fish. Despite sexual dimorphism in growth, sex does not affect migratory behaviour or timing of migration before sexual maturation. Our study highlights the recruitment dynamics of Greenland halibut and confirms the estuary as the main nursery in the St. Lawrence system.

**KEY WORDS:** Greenland halibut · *Reinhardtius hippoglossoides* · Microchemistry · Source–sink dynamics · LA-ICP-MS · Connectivity · Nurseries · St. Lawrence Estuary

## 1. INTRODUCTION

Estuaries play a key role for many fish and crustaceans as environments providing high food availability, favourable environmental conditions such as warm water and muddy ground, various and rich habitats providing protection against predation, and high turbidity (Beck et al. 2001, Able 2005, Secor & Rooker 2005). Juveniles of many marine fish species, such as Greenland halibut *Reinhardtius hippoglossoides*, commonly use estuarine nurseries to com-

plete their early life stages for stock recruitment, taking advantage of estuarine conditions and high connectivity between habitats (Beck et al. 2001, Sohn et al. 2010). Most estuaries are also currently subjected to high anthropic pressure stemming from intensive human activities that cause extreme environmental conditions, such as severe hypoxia in the Estuary of the Gulf of St. Lawrence (Courrat et al. 2009, Dupont-Prinet et al. 2013, Pillet et al. 2016). In fisheries management, determining the number and the extent of nursery grounds — along with their relative

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contribution to exploited stocks—is essential to assure sustainability (Gillanders et al. 2003, Nagelkerken et al. 2015).

During the late 1990s and early 2000s, systematic monitoring of Greenland halibut showed an increase in abundance, leading the species to become one of the most important commercially fished species of the northern Gulf of St. Lawrence fisheries (DFO 2019). Knowledge of Greenland halibut biology and ecology in the St. Lawrence remained relatively poor into the late 20th century. Our understanding of this species has since improved somewhat with several recent studies that investigated early-stage distribution (Ouellet et al. 2011), diet (Bernier & Chabot 2012), hypoxia tolerance (Ait Youcef et al. 2013, Dupont-Prinet et al. 2013), and the influence of sex and environmental conditions on growth (Ait Youcef et al. 2015, Ghinter et al. 2019, 2021). Nonetheless, information related to connectivity and population structure for the St. Lawrence Greenland halibut population remains scarce (Carrier et al. 2020, Bassi et al. 2023).

Fishery statistical data, sampling of commercial catches, and research surveys are commonly used to define the stock limits for marine species; however, these data do not provide information about the spatial connectivity of the different life history stages or the timing of movement between sites used by juvenile and adult populations (Gauthier et al. 2020). In a marine environment, investigating the connectivity between juvenile and adult populations and quantifying their contributions to different stocks can be difficult through conventional tagging techniques because of the small size of larvae and juveniles and the high mortality rate of early-stage individuals (Gillanders 2002). Over the last 20 yr, otolith chemistry has demonstrated its utility as a natural tag alternative to track fish movement from larval to adult stages (Kerr & Campana 2014). Otoliths are calcium carbonate structures located in the inner ear of fish. These structures grow continually by layer deposition at a rate closely related to fish somatic growth. Some trace elements (magnesium, strontium, barium) are permanently incorporated into the otolith matrix during its growth, influenced by ambient water concentrations at the time of deposition (Campana 1999). Identifying the chemical composition of the otolith, known as its elemental fingerprint, has allowed reconstructing migration patterns (Morissette et al. 2016), determining the connectivity between populations (Gibb et al. 2017), identifying juvenile sources and assessing stock structure (Lazartiques et al. 2016, Régnier et al. 2017, Wright et al.

2018, Rogers et al. 2019), quantifying migratory capacity (Morissette et al. 2021), and understanding fish life history (Schilling et al. 2018).

Greenland halibut, commonly named turbot, is a long-lived Pleuronectidae flatfish having a circumpolar distribution throughout the Northern Hemisphere. This fish also supports an important commercial fishery (Bowering & Brodie 1995, Brogan et al. 2021). Greenland halibut is characterized by a high dispersal potential because of its prolonged pelagic larval phase, which heightens connectivity between populations, thereby complicating the delineation of stocks (Ådlandsvik et al. 2004, Sohn et al. 2010, 2016, Stenberg et al. 2016). Greenland halibut is widely distributed in the Estuary and Gulf of the St. Lawrence River (EGSL). Large individuals are generally found in the EGSL main channel at depths ranging between 130 and 500 m, whereas juveniles are mostly concentrated in the estuary. The EGSL population demonstrates an important sexual dimorphism in growth, where 50% of females are mature at 44 cm compared with 50% maturity at 35 cm for males. Moreover, during their juvenile stage, females grow at a faster rate than males before sexual maturation (DFO 2017, Ghinter et al. 2019). Spawning occurs during the winter in the depths of the Laurentian Channel, southwest of Newfoundland, and eggs and larvae can drift up to 4 mo before settling in a nursery area (DFO 2019). Ait Youcef et al. (2013) identified the St. Lawrence Estuary as the main nursery, where juvenile Greenland halibut (1 and 2 yr old fish, <31 cm) are found at a high density. Recent genotyping and otolith microchemistry analyses of Greenland halibut confirm the St. Lawrence Estuary as the main nursery for the EGSL population (Carrier et al. 2020, Bassi et al. 2023). The area located north of Anticosti Island is currently considered as a second nursery in the EGSL; young and large post-larvae have been found in this region of the northern gulf (Ouellet et al. 2011, Ait Youcef et al. 2013, DFO 2019); however, the precise role of this area for Greenland halibut remains uncertain.

Here we used otolith chemistry to investigate the connectivity patterns of juvenile Greenland halibut between the nurseries in the St. Lawrence Estuary and the north of Anticosti Island. We aimed to identify the juvenile population dynamics of both areas and the relative contribution of each nursery to the EGSL Greenland halibut stocks. Our specific objectives were to (1) determine the migratory behaviour of captured Greenland halibut (either resident or migrant); (2) establish the timing of migration initiation; and (3) test the presence of sex-specific migra-

tion behaviour linked to the known growth sexual dimorphism.

## 2. MATERIALS AND METHODS

### 2.1. Collection of juvenile Greenland halibut

Greenland halibut were collected in the EGSL from the 2 putative nurseries: Estuary and North Anticosti (Fig. 1). A total of 200 juvenile Greenland halibut (100 individuals per nursery) were collected through bottom-trawl surveys conducted by Fisheries and Oceans Canada (DFO) from 21 to 31 August 2016. The sampling used an Alfredo III bottom otter trawl with a 140 mm mesh and a 30 mm mesh liner in the cod end. Halibut total length was measured on fresh specimens upon capture. Halibut heads were sectioned, labelled, and frozen on board. For Greenland halibut in the EGSL, Ait Youcef et al. (2015) identified 4 age classes for individuals smaller than 40 cm on the basis of a length-frequency distribution analysis: 1 yr old, 12–19 cm; 2 yr old, 22–29 cm; 3 yr old, 30–35 cm; and 4 yr old, 37–39 cm.

### 2.2. Otolith preparation

In the laboratory, we extracted both the left and right sagittal otoliths from each individual. After excising the otoliths, we removed any attached blood and organic tissues and then rinsed the otoliths 3 times in ultrapure water. The otoliths were then dried using Kimwipes and stored in acid-washed polypropylene vials until analysis. The otoliths were set in epoxy resin (Miapoxy 95 and Miapoxy 100) and sectioned in the transversal plane using a low-speed diamond-bladed saw (Isomet low speed, Buehler) to expose the core and growth annuli on the cross-section. Sections were sanded on both sides with different grades of aluminium oxide lapping films (3M Wetordry™ Polishing Paper #400, #1200, 5M, and 1M). All otolith sections were mounted on microscope petrographic slides using a thermoplastic glue (Crystalbond™509, AREMCO). We placed the otoliths randomly across the slides to avoid potential bias related to instrument drift. Each petrographic slide with mounted otoliths was then sonicated in ultrapure water for 5 min, triple rinsed in Super Q water, and then dried in a class-100 laminar flow hood for 24 h (Lazartigues et al. 2016).

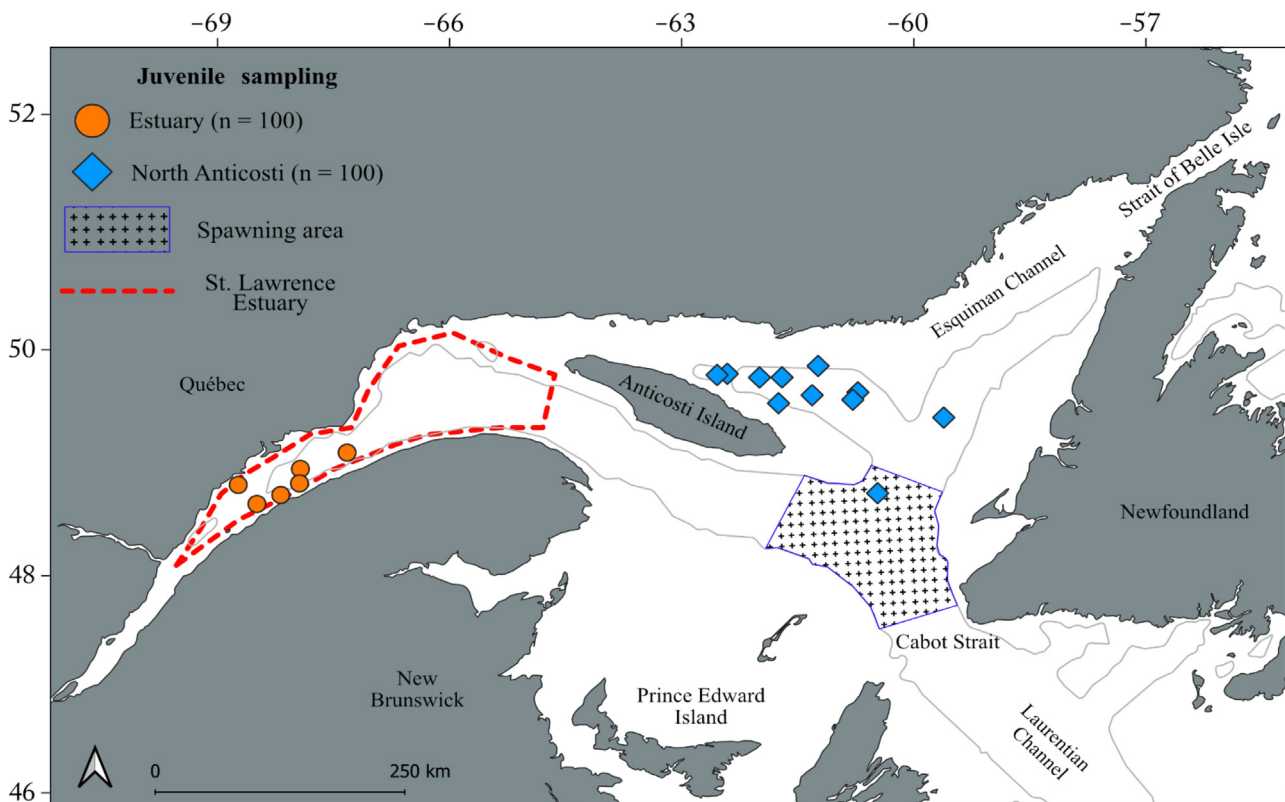


Fig. 1. Location of sampling nurseries for juvenile Greenland halibut *Reinhardtius hippoglossoides*; Estuary (orange circles), North Anticosti (blue diamonds). The map includes 200 m bathymetric curves (thin solid grey lines) and location (dashed red box) in the St. Lawrence Estuary where juveniles are commonly found (Ait Youcef et al. 2015)

### 2.3. Laser-ablation inductively coupled plasma mass spectrometry (LA-ICP-MS)

The LA-ICP-MS analysis was performed using a Resonetic Excimer 193 nm ArF laser coupled to an Agilent model 7900 ICP-MS in the LabMaTer facilities at the Université du Québec à Chicoutimi, Canada. Laser ablation was undertaken in transect mode along the entire otolith axis from the dorsal margin to the ventral margin passing through the otolith core. The laser beam diameter was set at 20  $\mu\text{m}$ , moving at a speed of 5  $\mu\text{m s}^{-1}$  at a frequency of 15 Hz and laser fluence of 5  $\text{J cm}^{-2}$ . The target elements were  $^7\text{Li}$ ,  $^{23}\text{Na}$ ,  $^{24}\text{Mg}$ ,  $^{25}\text{Mg}$ ,  $^{27}\text{Al}$ ,  $^{43}\text{Ca}$ ,  $^{44}\text{Ca}$ ,  $^{55}\text{Mn}$ ,  $^{64}\text{Zn}$ ,  $^{65}\text{Cu}$ ,  $^{66}\text{Zn}$ ,  $^{69}\text{Ga}$ ,  $^{85}\text{Rb}$ ,  $^{86}\text{Sr}$ ,  $^{87}\text{Sr}$ ,  $^{88}\text{Sr}$ ,  $^{136}\text{Ba}$ ,  $^{137}\text{Ba}$ ,  $^{138}\text{Ba}$ , and  $^{208}\text{Pb}$ . The calcium content was assumed to be 38.02% in each otolith (Campana 1999) and was used as the internal standard for calibration. Standard materials were ablated every 2 h (after approximately 8 samples) to correct for any temporal drift in the sensitivity of the mass spectrometer. Calibration was performed using NIST SRM 610 reference material (Chen et al. 2011) with reference working values ( $\pm$  uncertainties) obtained from the Geological and Environmental Reference Materials database ([http://georem.mpch-](http://georem.mpch-mainz.gwdg.de/)

[mainz.gwdg.de/](http://georem.mpch-mainz.gwdg.de/)). The US Geological Survey in Denver provided the MACS-3 working values ( $\pm$  uncertainties) for quality control (Ca 38.02%; [http://crustal.usgs.gov/geochemical\\_reference\\_standards/microanalytical\\_RM.html](http://crustal.usgs.gov/geochemical_reference_standards/microanalytical_RM.html)). The GP-4 reference material was also used for quality control. Aluminium counts ( $^{27}\text{Al}$ ) were monitored to certify the absence of contamination caused by the manipulation of otoliths.

To assess the validity of observed concentrations, we calculated the limit of detection (LOD) of the elements as 3 times the standard deviation (SD) of the gas blank divided by the sensitivity of the signal. Because of the asymmetric shape of Greenland halibut otoliths, we selected the longest path from the core towards the margin to increase the resolution of the elemental signal (Fig. 2). Along this transect, data were separated into 3 distinct zones: the post-core (first 10 laser points after the core, ca. 50  $\mu\text{m}$ ), the transect, and the margin (last 10 laser points, ca. 50  $\mu\text{m}$ ). The use of the post-core section avoids incorporating the elemental footprint associated with a pelagic larval phase potentially recorded in the otolith core. For all specimens, we assumed that post-core and margin elemental fingerprints represented the settlement habitat and the sampling site, respectively.

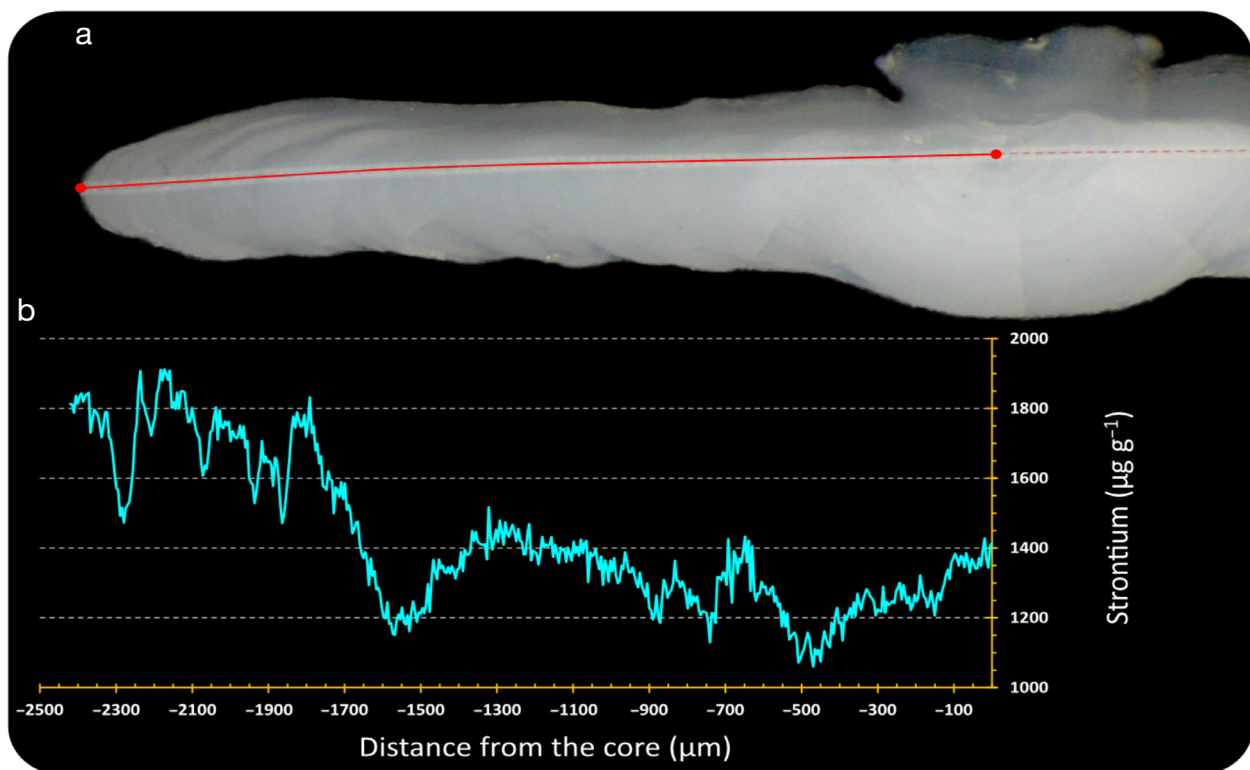


Fig. 2. (a) Illustration of an otolith cross-section showing the complete transect (red line) from the margin (left) to core (right) with (b) the corresponding LA-ICP-MS strontium elemental signal

## 2.4. Statistical methods

The otolith margin data of each nursery capture site were analysed by repeated-measure ANOVA (RM-ANOVA, function 'aov') performed in R software (R Core Team 2020, version 4.0.3). We used both capture sites (Estuary and North Anticosti) as a single factor and sample ID as a repeated factor to account for the non-independence of chemical signals within a specimen. The ability of the otolith elemental fingerprint of settled juveniles to discriminate nursery sampling locations was assessed using random-forest (RF) classification (Breiman 2001) in the 'RandomForest' R package v 4.6-14. Random forests are a combination of tree predictors, and the classification is based on consensus verdict of those multiple trees because a generalization error for forests converges to a limit when the number of trees in the forest becomes large (Breiman 2001). One of the main advantages of this machine-learning approach is the absence of an assumption of variable multinormality or distribution (Mercier et al. 2011), such as that observed in our study. A random-forest classification model was fitted using the elemental fingerprints from otolith margin data sets, representing 2000 points (1000 per nursery). The data set was randomly divided into a training (2/3 of the data) and test (1/3 of the data) set, the latter being used to assess the classification accuracy of each tree. We assessed the accuracy of the reclassification by the model using the function 'confusionMatrix' ('RandomForest' R package), which presents the average of 100 classification procedures for 1000 trees. Reconstruction of migratory history was made by RF classification of trace element values along the otolith transect (from margin to post-core) obtained for each individual.

The transect information was deduced by a successive classification of elemental fingerprints, denoised by the smoothing procedure following Morissette et al. (2021). The smoothing procedure was designed to be coherent with the geographical succession of nurseries occupied by juvenile Greenland halibut. Nurseries were transformed into numerical values: 1, Estuary; 2, North Anticosti. Successions of numerical classifications along each otolith transect (representing migration history) were smoothed with a Loess procedure ('stats' R package) using  $\alpha = 0.10$ , in order to remove occasional incorrect classifications by autocorrelations within the classification transect (smoothing of a given classification is correlated with the preceding values). Smoothed values were rounded to the nearest integer within the limits of the used numerical domain, 1 or 2, providing a smoothed numerical assignment. We also applied a second RF classification

model for estimating the hatching sites, using the mode values of classification for the post-core elemental fingerprints. Visual verification was performed on the transect classification to detect any aberrant transect pattern that could result in false post-core reclassification. We detected a single misclassified individual, which was then corrected.

Individual migratory movement was summarized by calculating an index termed 'migration behaviour', which provides information on the migratory behaviour and the migration direction of captured fish. The migration behaviour of juvenile halibut was calculated by subtracting the value of their capture site from their origin location. The capture site is known from the otolith margin, while the origin location was deduced by the RF classification from the post-core section of the otolith. This calculation provided a movement value ( $m$ ) for each individual. Thus, the  $m$ -value defined 3 behaviours: residency ( $m = 0$ ), upstream migration from North Anticosti towards the Estuary nursery ( $m = 1$ ), and downstream migration from the Estuary to the North Anticosti nursery ( $m = -1$ ). A migration index was also calculated as the mean of all values from the transect of every specimen to perform a double-check, combined with visual checking, to detect any aberrant behaviour. We analysed the migratory behaviours using a 1-way ANOVA as a function of capture site, while age class and sex were analysed using a 2-way ANOVA to assess the respective effects. Variables not satisfying normality assumptions were naturally log transformed (Quinn & Keough 2002), which is best suited for multivariate fingerprint analysis (Campana 2005). For the age class test, we removed 6 specimens of the 3 and 4 yr old classes from the analyses given their low numbers.

## 3. RESULTS

### 3.1. Sample composition, size, and age class

We analysed 200 right sagittae from juvenile halibut captured in the upper estuary and north of Anticosti Island inside the Anticosti Channel (Fig. 1). Captured fish averaged ( $\pm$ SD)  $24.2 \pm 4.37$  cm in total length and represented predominantly the 2 yr old ( $n = 159$ ) and 1 yr old classes ( $n = 35$ ). Four individuals were 3 yr old, and 2 were older than 4 yr (average length 44.6 and 54.8 cm, respectively). Individual age was based on the length-frequency function of Ait Youcef et al. (2015). Size at sexual maturity in 2016 was estimated at 41 cm for females and 33 cm for males in the EGSL. These

values have fluctuated since 1996, globally decreasing in males and females, but 2016 had the lowest values observed both for males and females (DFO 2019). Thus, 97% of our samples comprised juveniles aged between 1 and 2 yr. We observed significant differences in age (ANOVA,  $F_{1,198} = 15.38$ ,  $p < 0.001$ ) and length (ANOVA,  $F_{1,198} = 18.18$ ,  $p < 0.001$ ) between the nurseries. Greenland halibut captured in North Anticosti were significantly older and larger (average age 2 yr,  $25.4 \pm 4.1$  cm) than halibut captured in the estuary (average age 1.7 yr,  $22.91 \pm 4.31$  cm).

### 3.2. Spatial variability of nursery elemental fingerprints

Elemental concentrations below LOD were excluded from statistical analyses ( $^7\text{Li}$ ,  $^{59}\text{Co}$ ,  $^{60}\text{Ni}$ ,  $^{61}\text{Ni}$

$^{64}\text{Zn}$ ,  $^{65}\text{Cu}$ ,  $^{66}\text{Zn}$ ,  $^{69}\text{Ga}$ ,  $^{85}\text{Rb}$ , and  $^{208}\text{Pb}$ ). We used the 4 most informative trace elements ( $^{24}\text{Mg}$ ,  $^{55}\text{Mn}$ ,  $^{88}\text{Sr}$ , and  $^{138}\text{Ba}$ ) for subsequent analyses to build an elemental fingerprint. For simplification, no mass numbers are presented in the text (e.g.  $\text{Mg} = ^{24}\text{Mg}$ ). These selected elements have been successfully used in otolith chemistry studies in the St. Lawrence system and for demersal fish (Campana et al. 2007, Lazartigues et al. 2016, Bassi et al. 2023).

We recorded average concentrations and LODs for Mg (47.8 ppm, LOD = 0.2), Mn (12.1 ppm, LOD = 2.57), Sr (1532 ppm, LOD = 0.02), and Ba (1.29 ppm, LOD = 0.01). Elemental values of otolith margins differed significantly between capture nursery sites (Fig. 3). Mg (RM-ANOVA  $F_{1,198} = 11.88$ ,  $p < 0.001$ ) showed significant inter-nursery differences, whereas Mn (RM-ANOVA  $F_{1,198} = 1.689$ ,  $p = 0.195$ ), Sr (RM-ANOVA  $F_{1,198} = 0.026$ ,  $p = 0.873$ ), and Ba (RM-

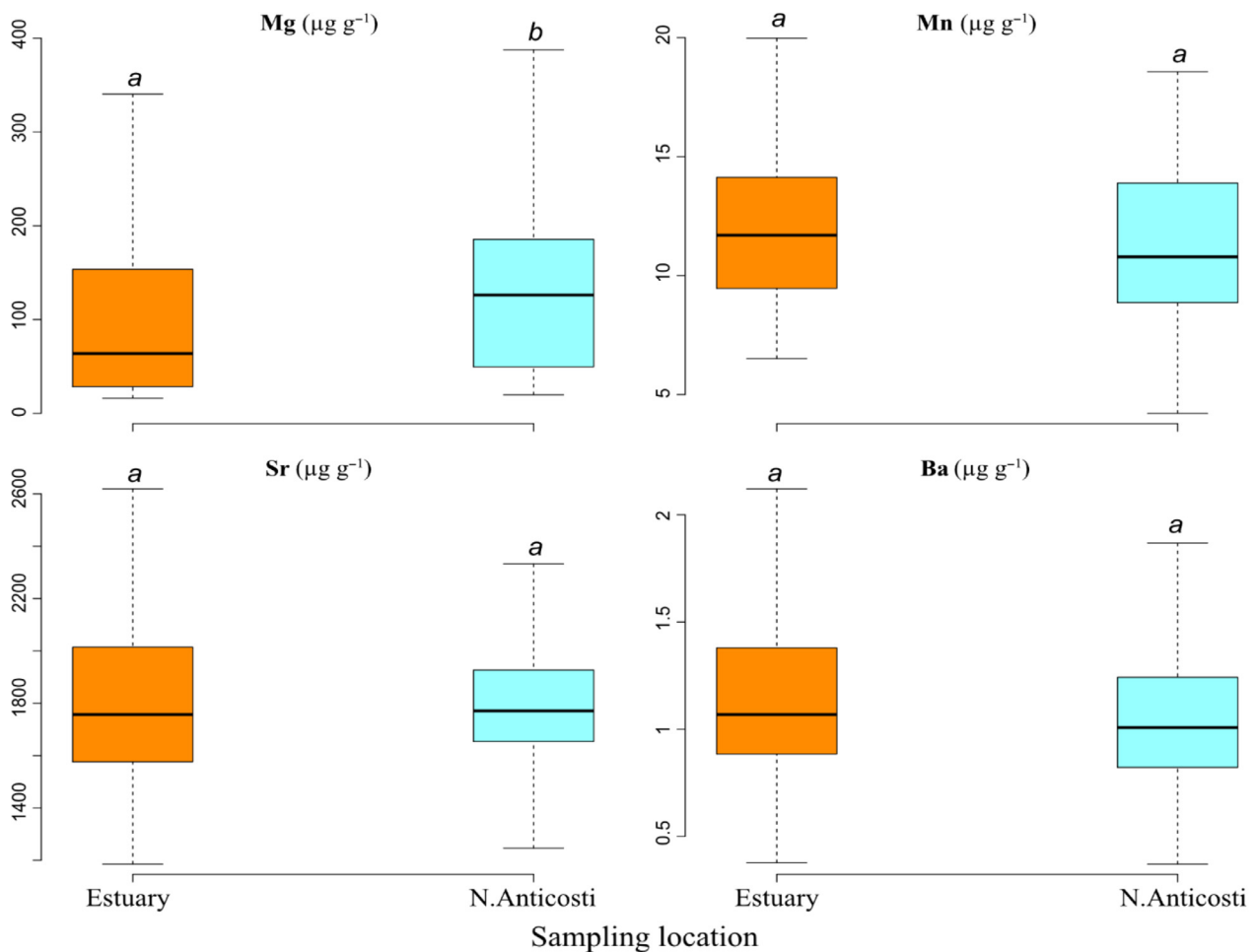


Fig. 3. Concentrations ( $\mu\text{g g}^{-1}$ ) of 4 elements (Mg, Mn, Sr, Ba) in the otolith margins of Greenland halibut juveniles collected at the Estuary and North Anticosti sites. For each element, concentrations with the same letter do not differ significantly (ANOVA, Tukey–Kramer HSD performed using the natural-log transformed variable). Bar: median; box: interquartile range (IQR); whiskers: max./min. within  $1.5 \times \text{IQR}$  above/below box

ANOVA  $F_{1,198} = 3.441$ ,  $p = 0.06$ ) did not differ significantly between sites. However, we used all 4 elements to create the classification model, despite an absence of significant differences between nurseries for Mn and Sr, as the inclusion of this pair of elements notably increased model accuracy (approximately 20% improvement). The random-forest model produced a classification accuracy of 76.6%, with a classification error rate slightly higher for the estuary (Table 1). Despite the few differences in elemental concentrations observed in RM-ANOVA, the random-forest model differentiated and accurately classified the nursery sites. Classification of the elemental signature of the otolith post-core revealed that 82.5% ( $n = 165$ ) of Greenland halibut originated in the estuary and the remainder (17.5%,  $n = 35$ ) from North Anticosti (Table 2).

### 3.3. Influence of capture site, sex, and age on migration behaviour

Migratory behaviour correlated with capture site (ANOVA,  $F_{1,198} = 333.1$ ,  $p << 0.001$ ); most juvenile Greenland halibut captured in the Estuary nursery were residents ( $m = 0$ ), whereas the North Anticosti nursery contained mostly downstream migrants ( $m = -1$ ).

Table 1. Confusion matrix for the random-forest classification model of Greenland halibut otolith margin chemistry. The table presents capture nurseries (rows), model classification (columns), and nursery classification errors. We used 10 margin points for 200 otoliths for total of 2000 points. Here, 1/3 of points ( $n = 672$ ) serve as classification and 2/3 ( $n = 1328$ ) as reference data

Nursery	Estuary	North Anticosti	% class. error
Estuary	250	90	26.5
North Anticosti	67	265	20.2

Migratory behaviour correlated with age class (ANOVA,  $F_{1,191} = 28.24$ ,  $p << 0.001$ ) but not sample sex (ANOVA,  $F_{1,191} = 1.56$ ,  $p < 0.213$ ). One year old halibut were mostly resident individuals (71%) with few migrants, whereas the 2 yr old class displayed a balanced proportion of residents (57%) and downstream migrants (42%) (Table 3). Thus, 1 yr old Greenland halibut were found mainly in the Estuary nursery, likely coming from local recruitment (Table 3). The 2 yr old class from the estuary was 97% resident, whereas the North Anticosti samples comprised mainly (74%) downstream migrants (Table 3). Downstream migrants had the largest average size of all the samples ( $25.95 \pm 4.4$  cm).

## 4. DISCUSSION

### 4.1. Source–sink dynamics and the key role of estuaries

Otolith chemistry illustrated the connectivity and the dynamics of juvenile populations of Greenland halibut in both EGSL nurseries. The random-forest classification model, based on Mg, Mn, Sr, and Ba, demonstrated the differences in the otolith margin

Table 2. Number of Greenland halibut classified with random forests to hatching sites (columns), as inferred from otolith post-core composition, and the actual capture site of the collected halibut (rows), indicating resident migratory behaviour (**bold** numbers,  $n = 117$ ), upstream migrants (upper right,  $n = 9$ ), and downstream migrants (lower left,  $n = 74$ )

Capture site	Hatching nursery (post-core elemental fingerprints)	
	Estuary	North Anticosti
Estuary	<b>91</b>	9
North Anticosti	74	<b>26</b>
Proportion (%)	82.5	17.5

Table 3. Summary of the migratory behaviour of juvenile Greenland halibut by their captured nursery, as detailed for each year class

Capture site	1 yr ( $n = 35$ )	2 yr ( $n = 159$ )	3 yr ( $n = 4$ )	$\geq 4$ yr ( $n = 2$ )	Total
Estuary total	29	69	1	1	100
Resident	22	67	1	1	91
Upstream	7	2	–	–	9
North Anticosti total	6	90	3	1	100
Resident	3	23	–	–	26
Downstream	3	67	3	1	74

elemental fingerprints between the Estuary and the North Anticosti nurseries. Otolith chemistry identified an important source–sink dynamic between the nurseries, and the post-core elemental fingerprint revealed that most individuals originated from the estuary, supporting a previous study (Ait Youcef et al. 2013).

Among the Estuary nursery samples, 91 were recruited locally and 9 originated from North Anticosti (upstream migrants). For the North Anticosti samples, we observed that 74 Greenland halibut originated from the Estuary, implying a downstream migration, whereas the last 26 individuals were recruited locally. This unbalance between migratory behaviour and fish origin suggests a source–sink dynamic in regional populations in which the Estuary nursery (the source) contributes disproportionately to recruitment in the North Anticosti area. In contrast, North Anticosti is a sink and contributes negligibly to recruitment. We observed that migrant specimens exhibited a lower average size than previous estimates and that sex did not drive the juvenile Greenland habitat migratory behaviour before maturation. The length and age class of resident and migrant individuals corroborated otolith chemistry, suggesting that migrants were the oldest (largest) specimens. We observed differences in length and the age class of individuals sampled in each nursery. Greenland halibut from the Estuary had a mean size of  $22.9 \pm 4.3$  cm, corresponding to younger 2 yr olds, and a high proportion (29%) of 1 yr old halibut. We found all to be residents, supporting the hypothesis that this species remains relatively sedentary for at least its first 2 yr (Ait Youcef et al. 2013). The North Anticosti sampling site was almost exclusively composed of individuals of the 2 yr age class having a mean size of  $25.4 \pm 4.1$  cm. A very low proportion (6%) of Greenland halibut captured at this site corresponded to the 1 yr old class. Most 2 yr old fish captured in the North Anticosti site originated from the Estuary nursery (67%). This percentage implies a downstream migration from the Estuary to North Anticosti nurseries during the second year of life. These downstream migrants had an average size of  $25.9 \pm 4.4$  cm, in contrast to previous estimates of migration patterns in this area that had 3 yr old Greenland halibut reaching 31 cm (Ait Youcef et al. 2013). Otolith chemistry suggests that migration can begin during their second year of life, earlier than the 3 yr as initially believed.

The local recruitment from the North Anticosti nursery, estimated at 26%, can be considered minor, as the estimated proportion is close to the classifica-

tion error of the random-forest model (23.5%). Furthermore, the 9 upstream migrants captured in the Estuary, mainly composed of 1 yr old halibut ( $n = 7$ ), likely represent a relatively rare behaviour or are an analytical artefact. We found that recruitment of juvenile Greenland halibut in the EGSL occurred almost exclusively in the Estuary nursery, whereas the North Anticosti area showed a low local recruitment and represented a site acting mainly as a shelter for individuals in the older 2 yr age class ( $>25$  cm).

The temporal variability in elemental composition observed in the otoliths of the specimens captured in 2016 must be considered, especially 2015 and 2014, as most specimens were aged 1 or 2 yr old. Unfortunately, no data exist in the studied regions to assess the temporal variability of the 2014–2015 period. We assumed that elemental fingerprints did not change drastically from year to year in the large and predictable ecosystem we studied. This is especially true for the elemental fingerprints observed in flatfish, living on the bottom between 220 and 300 m depth, where the water mass is not subject to strong disturbances or environmental variations, which was observed in other analogous systems. Accordingly, a 3 yr study by Tournois et al. (2013) showed the otolith fingerprints of sea bream *Sparus aurata* collected in 4 lagoons in the Mediterranean Sea remained sufficiently consistent between years to produce 80% of good classification when the data from the 3 years were pooled.

Another source of uncertainty could be the existence of additional and unknown sources (e.g. nurseries) of juveniles in the EGSL. In this case, the 2-source RF classification would result in the misclassification of individuals to 1 of the 2 sources from which they did not originate. However, evidence in the EGSL suggests that the presence of additional nurseries is highly unlikely. The annual stock monitoring performed by DFO targeting commercial species, including Greenland halibut, shows that juveniles are mainly and abundantly found in the estuary and more sporadically captured northeast of Anticosti Island (Gauthier et al. 2020) without any other notable high abundance of juveniles.

#### 4.2. Sexual dimorphism and maturity

Greenland halibut males reach sexual maturity earlier ( $L_{50}$ : 36 cm) than females ( $L_{50}$ : 44 cm) in the EGSL; although these values fluctuate from year to year, they have globally decreased since 1997 (DFO 2019). Thus, sexual growth dimorphism could pro-



duce differential nursery emigration with an initial migration by males. However, we found no correlation between the sex of individuals and migratory behaviour, thereby refuting the hypothesis that migratory activity begins earlier for males. Migration behaviour before sexual maturation was undifferentiated for both sexes but appears related to the length of individuals. As Greenland halibut have exhibited important sexual dimorphism in growth under laboratory conditions, with females growing at a faster rate than males before sexual maturation (Ghinter et al. 2019), we could infer that females migrate earlier in their development if this growth polymorphism is preserved under natural conditions. Our results support those of Albert (2003), who inferred that the fast-growing individuals left the nursery first. Further investigation should focus on the next age classes (3 and 4 yr old halibut) to explore whether sex has an impact on migratory behaviour after sexual maturation.

#### 4.3. Oceanographic circulation favours Greenland halibut settlement in the estuary

In the 2016 survey, the St. Lawrence Estuary was the quasi-exclusive source of recruitment for juvenile Greenland halibut. The biology of this species and physical oceanographic conditions could explain a preference for the estuary for early-stage settlement. Eggs and larvae of Greenland halibut are known to have a long period of drift in the water column before settlement (Jensen 1935, Smidt 1969). In the EGSL, spawning occurs between January and March in the deepest part of the Laurentian Channel, southwest of Newfoundland (Templeman 1973, Ouellet et al. 2011). The eggs of Greenland halibut are primarily mesopelagic, found at depths around 300 m, dispersed, and transported passively by currents from the spawning areas during approximately 30 d (depending on the water mass temperature). In the last days before hatching, their buoyancy changes radically and eggs rise through the water column (Ouellet et al. 2011). The pelagic larvae are primarily found in the surface layer (0–50 m), perfectly placed for first feeding on plankton prey and continuing their development. The complete development of Greenland halibut larvae in the EGSL requires up to 4 mo before they settle to the bottom of the nursery area and undergo their metamorphosis. When combined, the drift of the egg and larval stages extends over at least 5 mo in the EGSL. Ouellet et al. (2011) indicated that the westward bottom current produces

a limited displacement of the eggs, from 20 to 40 km over 30 d. Hence, hatching should occur relatively close to the spawning ground. Thus, the pelagic larvae are subjected to the surface circulation of the water masses and should be transported westward along the Laurentian Channel, according to the physical oceanographic conditions, towards the Anticosti Gyre and then to the estuary (Saucier et al. 2003, Galbraith et al. 2017). This current-driven mechanism could explain our results indicating that the estuary was the source of almost all juveniles sampled in both nurseries. To summarize, eggs and larvae are mechanically transported westward from the spawning area to the estuary, led by the dominant bottom and surface currents (Fig. 4). From the spawning area located in the deeper part of the Laurentian Channel (Fig. 4), it seems unlikely that most of the larvae in the surface layer can drift northward and reach the Anticosti Channel because of the orientation and dynamics of the currents (Galbraith et al. 2017). However, we do not exclude the possibility of finding larvae in the Anticosti Channel, some possibly trapped by small-scale hydrodynamic features or drifted in from other spawning areas.

#### 4.4. The estuary as the main nursery of the EGSL

Ait Youcef et al. (2015) reported that the density of juveniles (1 and 2 yr old individuals) in the estuary was considerably higher than in North Anticosti. Moreover, the spatial distribution of Greenland halibut of each age class during the 2016 survey corroborates these results (Gauthier et al. 2020). The spatial distribution in the EGSL is explicit; Greenland halibut were found mainly in the St. Lawrence Estuary, with the 2 yr age class being the most abundant (Gauthier et al. 2020). The presence of juveniles in North Anticosti is very sporadic relative to the estuary, supporting the hypothesis that most recruitment occurs in the estuary. The contribution of the North Anticosti nursery can vary between years, as observed from 1995 to 1999 and 2010 to 2014 when the concentration of 1 yr old halibut was greater in this area. These periods include the years of a stronger cohort observed in the EGSL (Gauthier et al. 2020). Another possibility is the potential contribution of larval sources from outside the EGSL. Bowering (1982) first proposed this idea; however, since the early 1990s, the EGSL population has been considered to be isolated from the Atlantic (Arthur & Albert 1993). A recent genetic study demonstrated that a contribution from the Newfoundland–Labrador stock

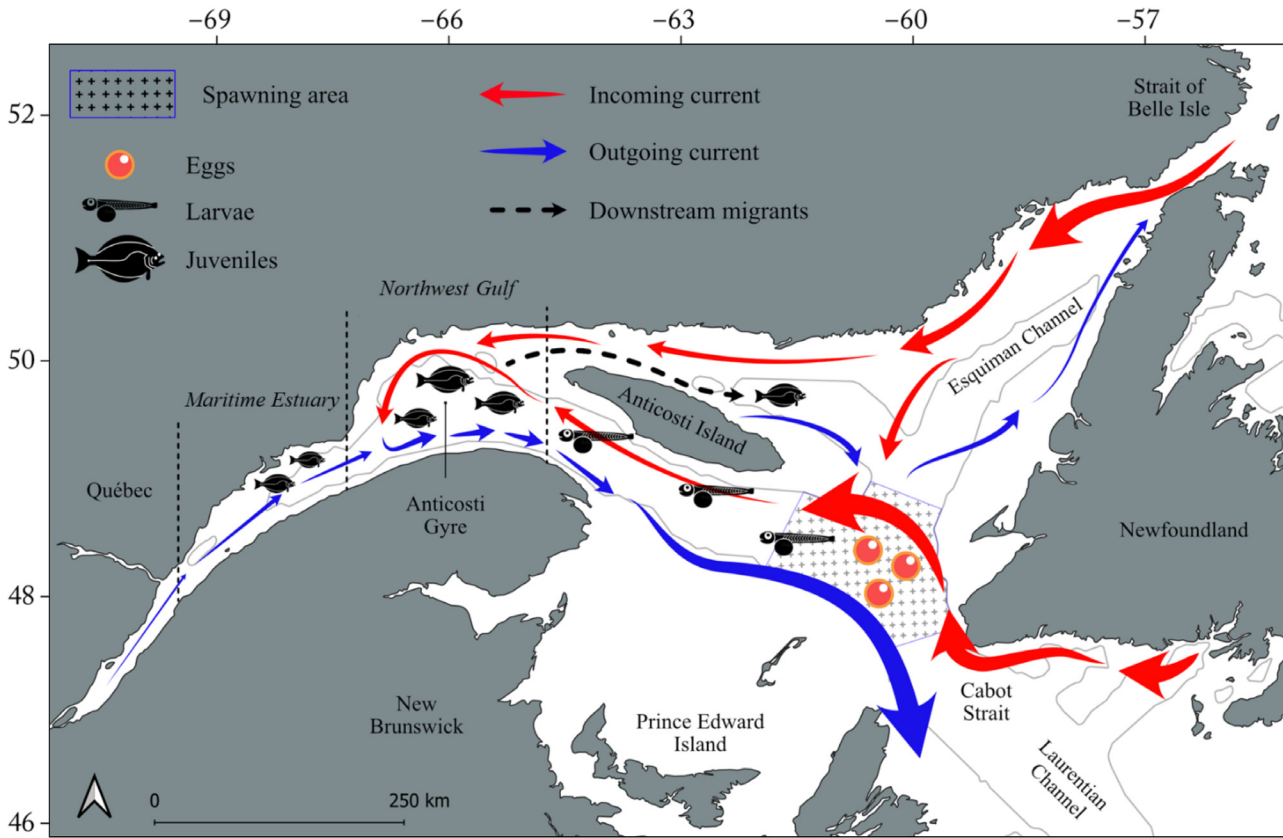


Fig. 4. Representation of Greenland halibut recruitment dynamics in the Estuary nursery, according to previous research and the results of this paper. Dominant surface currents (0–20 m) for the winter season 2016 are represented by the coloured arrows; arrow thickness represents current strength and arrow colour represents current flow direction (Galbraith et al. 2017)

can be significant, although highly variable between years (1–33%) (Carrier et al. 2020). During their extended pelagic phase, larvae drifting along the Labrador coast can enter via the Strait of Belle Isle and settle in the North Anticosti nursery (Wu et al. 2012, Galbraith et al. 2017). The Strait of Belle Isle has been reported to be a gateway towards the EGSL for several species, including redfish *Sebastes mentella* (Benestan et al. 2021), snow crab *Chionoecetes opilio* (Puebla et al. 2008), and capelin *Mallotus villosus* (Kenchington et al. 2015, H. Cayuela et al. preprint doi:10.1101/782201). The confirmation of a potential external source of larvae is critical to have an accurate understanding of the population dynamics of Greenland halibut in the EGSL.

#### 4.5. Concerns about future EGSL Greenland halibut populations

Being the main nursery for the EGSL stock, the St. Lawrence Estuary is a key area for Greenland halibut recruitment. This area is known to be very pro-

ductive; upwelling in the region favours biomass production and accumulation (Lavoie et al. 2008, Plourde & McQuinn 2010). Hence, forage species such as shrimp (*Pandalus borealis*), capelin, and various zooplankton species (euphausiids and hyperiids) are abundant and provide plenty of food for young developing Greenland halibut (Savenkoff 2012). Thus, 1 and 2 yr old juveniles appear to be fairly sedentary in the Estuary, taking advantage of estuarine conditions such as abundant food and protection from predators, before beginning migration by gradually moving to deeper water as they grow. Recently, however, environmental conditions of the EGSL have been changing because of a greater incursion of warmer, saltier, and less oxygenated water from the Gulf Stream through the Laurentian Channel relative to the cold water originating from the Labrador Current (Galbraith et al. 2019). This warm water flux has led to higher temperatures and oxygen depletion in the EGSL to the point that deepwater temperatures are commonly above average (Galbraith et al. 2019) and oxygen saturation has fallen to below 18% in the lower estuary since 2016 (Blais et al. 2018), a

level that is not sustainable for many species, including Atlantic cod *Gadus morhua*.

Greenland halibut are usually found at depths >150 m and thus frequently inhabit severely hypoxic areas (18–50% saturation). Ait Youcef et al. (2015) suggested a significant negative effect of low levels of saturation (below 25%) on the growth of Greenland halibut juveniles in the EGSL. Experimental estimates for a threshold of hypoxia tolerance are 15 and 11% for juveniles and adults, respectively; thus, juvenile Greenland halibut are less tolerant to low-oxygen conditions than adults (Dupont-Prinet et al. 2013). However, the observation of a greater number of juveniles in the deep waters of the estuary may suggest that the negative impacts are likely limited or largely compensated by other physical or biological characteristics, such as temperature, food abundance, food availability, and/or low predation. In the years following the study by Ait Youcef et al. (2015), dissolved oxygen in this area has dropped from 20 to 18% in 2018, 17% in 2019, and 15% in the most recent observations in the estuary. Over the next decade, changes in the environmental conditions of the EGSL deepwaters could significantly affect the abundance and distribution of many species, including Greenland halibut, which may be the most heavily impacted species under the combined impacts of warming and oxygen depletion because of the significant reduction (approx. 55%) of their optimal habitat (Stortini et al. 2017). Between 2011 and 2013, the EGSL saw the emergence of 3 massive redfish cohorts that could heighten the interspecific competition with the Greenland halibut for habitat and food resources, particularly for shrimp species as prey (Senay et al. 2019). Environmental changes observed in the EGSL may favour some species, such as redfish and lobsters, but may be unfavourable for others, such as northern shrimp and Greenland halibut.

Overall, the trace element record in the otoliths of juvenile Greenland halibut differentiated the 2 nurseries. Moreover, we found that Greenland halibut caught in each nursery shared the St. Lawrence Estuary as a common origin. Our results imply a nearly uniform downstream migration by juveniles caught in the North Anticosti area. This observation is the first evidence of an important source–sink dynamic between these 2 nurseries. Moreover, we observed that the migration of juveniles may begin at a smaller size than expected, approximately 26 cm (mean ca. 2.5 yr old), although migration appears to not be affected by the sex of individuals, at least before sexual maturation. The St. Lawrence Estuary plays a crucial role in Greenland halibut recruitment;

however, the EGSL system is undergoing profound changes that could involve direct consequences on stock viability, thereby affecting the economy of the Canadian provinces engaged in these commercial fisheries. Hence, it is urgent to develop a better understanding of these changes and their impacts on stocks and establish management approaches that favour sustainable exploitation of Greenland halibut.

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