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BRIEF COMMUNICATION

A first glimpse of larval ecology of halibut species in the Gulf of St. Lawrence, Canada

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Abstract

Knowledge of the larval ecology of winter-spawning fish from the Estuary and Gulf of St. Lawrence, Canada, remains scarce due to the seasonal ice cover that prevents ichthyoplankton sampling using conventional methods. Two winter-spawning species, Atlantic halibut (AH, *Hippoglossus hippoglossus*) and Greenland halibut (GH, *Reinhardtius hippoglossoides*), support the most important groundfish fisheries of this area. In March 2020, the authors captured 10 halibut larvae ranging in size from 5 to 14 mm during an opportunistic survey in the GSL onboard an icebreaking vessel. Of these, eight were AH and two GH. Judging by their very small size, the larvae were only a few days old, suggesting that the spawning grounds are close to the capture sites. This effort constitutes a first step in validating the putative spawning areas for these two important GSL stocks. This knowledge is important for the conservation and sustainable management of these fisheries.

KEYWORDS
Atlantic halibut, Greenland halibut, larval distribution, larval ecology, spawning ground, winter ecology

Atlantic halibut (AH), *Hippoglossus hippoglossus*, and Greenland halibut (GH), *Reinhardtius hippoglossoides*, support the two most important groundfish fisheries in Atlantic Canada, representing 53% of overall groundfish landing value for the region in 2020 (DFO, 2022). The two flatfish species are characterized by discrete stocks in the Estuary and Gulf of St. Lawrence (EGSL) (DFO, 2021; Gauthier *et al*., 2021). Despite their high commercial importance, larval ecology remains poorly resolved for both species (Dominguez-Petit *et al*., 2013; Duffy-Anderson *et al*., 2013; Shackell *et al*., 2022), and most of the knowledge on early life stages comes from laboratory studies (AH: Blaxter *et al*., 1983; Dominguez-Petit *et al*., 2013; Jonassen *et al*., 1999; Mangor-Jensen *et al*., 1997; Pittman *et al*., 1990; GH: Stene *et al*., 1998; Stickney & Liu, 1993). In fact, only about 60 larvae captured at sea have been reported for AH over the whole species distribution (Bergstad & Gordon, 1993; Haug, 1990; Van Der Meeren *et al*., 2013). And although more observations exist for wild GH larvae, with several hundred larvae captured throughout the species range (*e.g*., preflexion, flexion and postflexion stages), observations of young preflexion larvae are scarce and account for less than 100 in the literature (Duffy-Anderson *et al*., 2013; Ouellet *et al*., 2011; Simonsen *et al*., 2006; Sohn *et al*., 2010), including 50 individuals in a specific sector of the EGSL (Ouellet *et al*., 2011). This black box corresponding to a critical life stage needs to be investigated to understand natural larval mortality and its drivers and shed light on processes regulating recruitment.

In the EGSL, both halibut species reproduce in winter. Relying on the observation of spawning increases from geolocated pop-up satellite archival tag data, Gatti *et al*. (2020) revealed peak spawning activity in AH throughout the deep channels of the EGSL in February. Although telemetry data are not available to infer on spawning area of GH, historical occurrences of larvae in the EGSL summarized by Ouellet *et al*. (2011) point to a spawning area corresponding to the junction of the Laurentian and Esquiman channels, with peak spawning also occurring in February or in early March.

At hatching, larvae measure *c*. 6–7 mm in both species (Dominguez-Petit *et al*., 2013; Duffy-Anderson *et al*., 2013; Haug, 1990).

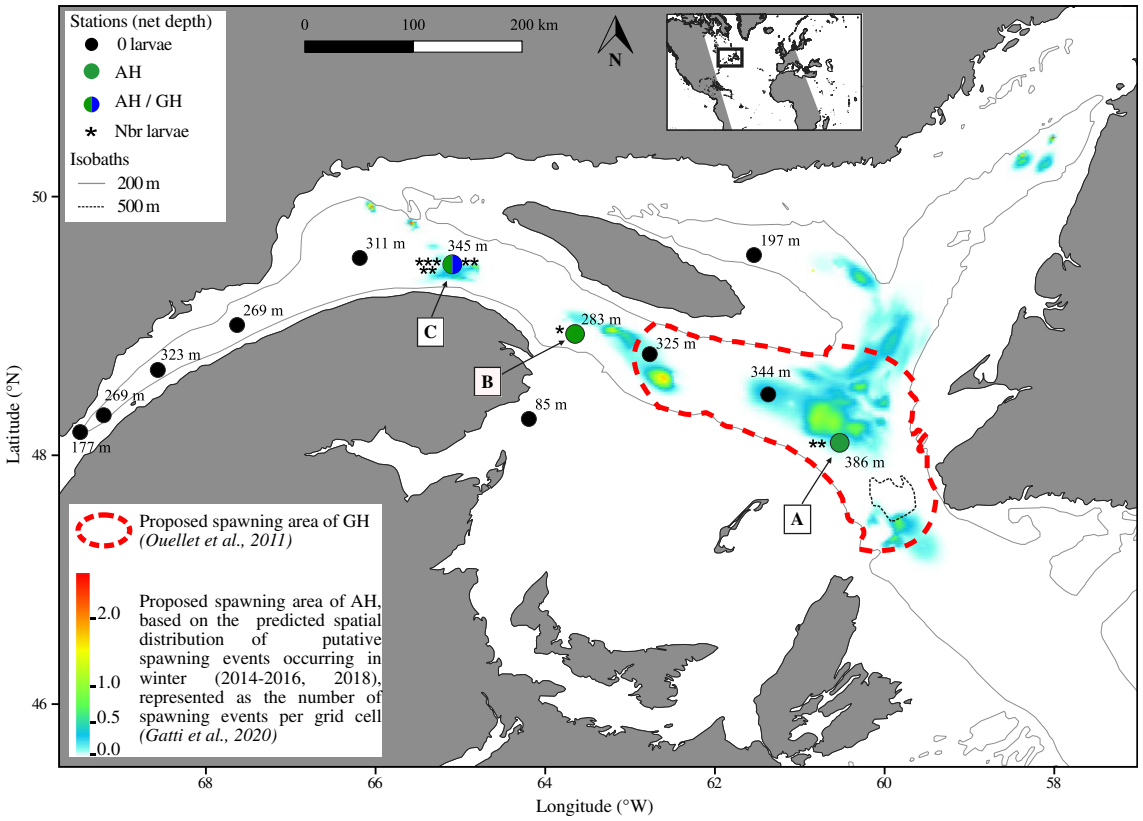

FIGURE 1 Map of winter ichthyoplankton stations sampled onboard the CCGS *Amundsen*. Larvae were captured at stations A, B and C; the species and numbers are indicated. The spawning areas proposed by Gatti *et al.* (2020) for Atlantic halibut (AH) and Ouellet *et al.* (2011) for Greenland halibut (GH) are also shown

The larvae are then bilateral, and as their yolk reserves become depleted and they initiate exogenous feeding, they show positive phototaxis (Karlsen, 2001; Naas & Mangor-Jensen, 1990) and gradually rise towards the upper 100–200 m of the water column to feed on zooplankton (Haug, 1990; Ouellet *et al.*, 2011; Simonsen *et al.*, 2006). They passively drift with ocean currents and gradually reach the nursery areas (Albert *et al.*, 2001; Bowering & Nedreaas, 2001; Ouellet *et al.*, 2011; Riget & Boje, 1988; Sohn *et al.*, 2010). Compared to the majority of boreal marine fishes, this drifting phase is relatively long in halibut species, lasting 4–6 months in GH according to observations in the natural environment (Ouellet *et al.*, 2011; Sohn *et al.*, 2010). Based on laboratory studies, Einarsdóttir *et al.* (2006) estimated that the duration of this phase would be 800 degree-days for AH, which would amount to 4–6 months for temperatures between 4 and 6°C.

In the EGSL, the spatial distribution and connectivity between spawning and potential nursery locations during halibut ontogeny remain unknown. Obtaining this information is critical because early life drift patterns can affect settlement success, larval survival, recruitment strength and population structure (Sohn *et al.*, 2010; Van der Veer *et al.*, 1998, 2000). In the present study, the authors relied on an opportunistic winter survey in the EGSL in March 2020 onboard a Canadian Coast Guard icebreaker to target larval halibut for the first time during the larval drift season. From this first glimpse of larval halibut under the seasonal ice cover, they discuss potential spawning areas and larval drift patterns of halibut larvae in the EGSL.

Sampling took place in March 2020 aboard the CCGS *Amundsen* icebreaker during the "Odyssée Saint-Laurent" winter survey. One objective of this oceanographic survey was to characterize the winter zooplankton and ichthyoplankton communities in the EGSL. During the survey, 12 stations were sampled using a ring net (Ø = 1 m, mesh-size 333 µm; Figure 1) towed in an oblique pattern; vessel speed was *c.* 2 kt to maintain a constant cable angle between 45° and 60°. The nets were lowered and raised at a winch speed of 45 and 30 m min^{-1}, respectively and maintained for 1 min at their maximum depth, *i.e.*, *c.* 15 m above the seabed. Except for one shallow station in the southern GSL (depth: 85 m), water depths at the different stations in the Laurentian and Anticosti channels ranged from 177 to 386 m (average: 293 ± 63 m). Sampling durations varied from 12 to 33 min (average: 22 ± 06 min), and filtered water volumes varied from 188 to 471 m^3 (average: 329 ± 91 m^3).

Sorted fresh fish larvae were photographed under a stereomicroscope, body width (BW; measured from the anus to the top of the back, excluding fins) and standard length (SL; from the lower jaw to the end of notochord, excluding caudal fin) were immediately measured given that larvae may shrink after death. One larva was damaged (no head) for which no standard length could be measured. Larvae were then stored in RNAlater at −20°C.

TABLE 1 Sequences of primers used to amplify the cytochrome oxidase I (*COI*) gene from mtDNA

Primer	5′–3′ sequence
FishCOI-F	AAY CAY AAA GAY ATY GGY ACC CT
FishCOI-R	TAN ACT TCN GGR TGN CCR ZZG AAY CA

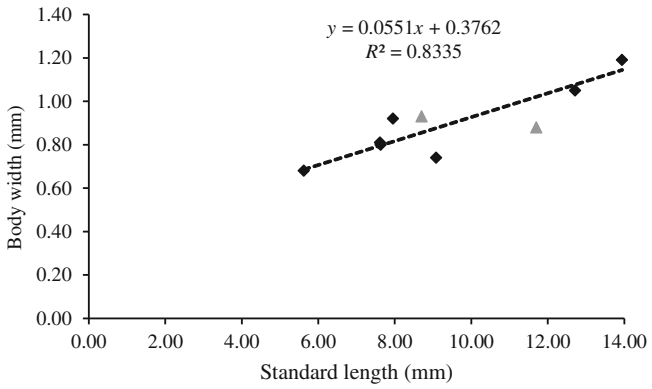

FIGURE 2 Linear regression of the standard length of the Atlantic halibut (AH) larvae as a function of their body width. Only AH larvae were used to establish the regression equation; Greenland halibut (GH) larvae are shown for comparison only. The damaged AH larva was not included in this analysis. ◆ AH, ▲ GH

Macroscopic identification of these species was not possible due to the lack of knowledge of the morphological characteristics of the early life stages; thus, specimens were identified using genetic barcoding (Hebert *et al*., 2003).

DNA from each larva was extracted using a DNeasy blood and tissue kit (Qiagen, Inc., Mississauga, Ontorio, Canada). DNA purity, quality, concentration and 260/280 absorbance ratio were determined using SYBR Safe DNA Gel Stain 2% agarose gel electrophoresis (ChemiDoc XRS+ system, Biorad, CA, USA) and spectrophotometry (NanoVue Plus, GE Healthcare, Pittsburgh, PA, USA). A region of 658 bp of the mitochondrial cytochrome oxidase I (COI) gene was amplified with the -FishCOI-F and FishCOI-R primers (Table 1). The PCR for each sample consisted of 6.25 µl of AccuStart reagent (commercial ready-to-use kit, which includes Taq polymerase, deoxynucleotide triphosphate and $MgCl_2$), 3.25 µl of H_2O, 0.5 µl of each primer and 2 µl of DNA, for a final reaction volume of 12.5 µl. The following sequence was used for amplification: 1 min at 94°C, then 35 cycles of the series 30 s at 94°C/30 s at 55°C/45 s at 72°C and finally 5 min at 72°C.

The PCR products were then sequenced using the Sanger method on the genomic analysis platform of IBIS (Institute of Integrative and Systems Biology) at Laval University with an ABI Prism 3100 automated sequencer (Applied Biosystems, Waltham, MA, USA).

The obtained sequences were edited using Geneious software and compared to the reference sequences available in the BOLD database using the BOLD Identification System (http://www.boldsystems.org/index.php/IDS_OpenIdEngine) or GenBank's Basic Local Alignment Search Tool (BLAST) (https://www.ncbi.nlm.nih.gov/genbank).

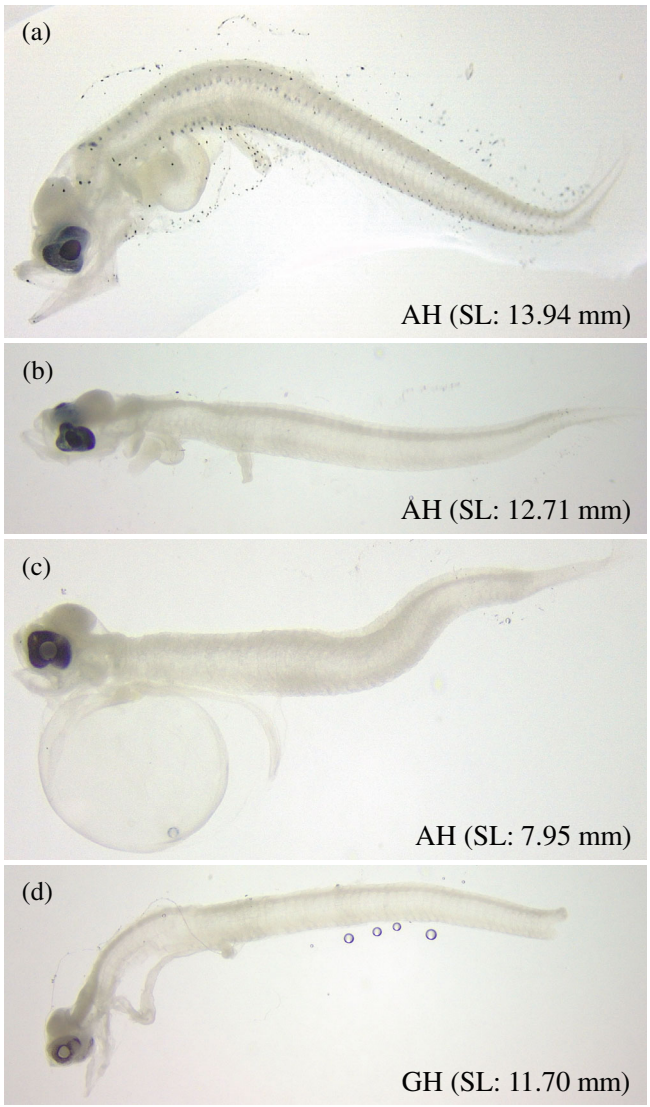

FIGURE 3 Stereomicroscopic images of Atlantic halibut (AH; a, b, c) and Greenland halibut (GH; d) larvae

A sequence was considered correctly assigned to a species when the similarity was greater than or equal to 99%.

Ten halibut larvae were captured during the mission, ranging in size from 5.62 to 13.94 mm SL and 0.59 to 1.19 mm BW. Larvae were captured at 3 of the 12 survey stations, all of which were in the Laurentian Channel (Figure 1). One station was near Cabot Strait (station A) and the other two further upstream, north of the Gaspé Peninsula (stations B and C).

Of these 10 larvae, 8 were identified as AH and 2 as GH. AH larvae were present at all three stations (A, B and C), whereas GH was found only at station C.

AH larvae ranged from 5.62 to 13.94 mm SL (Figure 2). The two larvae captured near Cabot Strait (station A) were the largest (SL: 12.71 and 13.94 mm; BW: 1.05 and 1.19 mm), whereas larvae from stations north of Gaspé Peninsula (B and C) were smaller (SL: 5.62–9.08 mm; BW: 0.68 and 0.92 mm). The two GH larvae measured 8.7 and 11.7 mm SL, with 0.88 and 0.93 mm BW, respectively (Figure 2).

TABLE 2 Information relative to capture stations (A: 48° 05′ 29″ N, 60° 32′ 22″ W; B: 48° 56′ 47″ N, 63° 39′ 29″ W; C: 49° 28′ 34″ N, 65° 04′ 56″ W), morphology and development stage of the larvae

Station	Date (d/m/y)	Station depth (m)	Sampling depth (m)	Species	SL (mm)	BW (mm)	Larval stage	Larval characteristics
A	9 March 2020	448	386	AH	12.71	1.05	Exogenous feeding	Yolk absent, eyes fully pigmented, mouth opened, some black melanophores along the body
A	9 March 2020	448	386	AH	13.94	1.19	Exogenous feeding	Yolk absent, eyes fully pigmented, mouth opened, black melanophores along the body
B	11 March 2020	323	283	AH	7.95	0.92	Yolk sac	Yolk present, eyes pigmented, mouth closed, no body pigmentation
C	12 March 2020	369	345	GH	8.7	0.93	Yolk sac	Yolk absent, eyes lightly pigmented, mouth closed, no body pigmentation
C	12 March 2020	369	345	AH	5.62	0.68	Yolk sac	Yolk absent, eyes lightly pigmented, mouth closed, no body pigmentation
C	12 March 2020	369	345	AH	NA	0.59	Yolk sac	Head missing, yolk absent, no body pigmentation
C	12 March 2020	369	345	AH	9.08	0.74	Yolk sac	Yolk absent, eyes lightly pigmented, mouth closed, no body pigmentation
C	12 March 2020	369	345	GH	11.7	0.88	Yolk sac	Yolk absent, eyes pigmented, mouth opened, no body pigmentation
C	12 March 2020	369	345	AH	7.61	0.81	Yolk sac	Yolk absent, eyes lightly pigmented, mouth closed, no body pigmentation
C	12 March 2020	369	345	AH	7.63	0.8	Yolk sac	Yolk absent, eyes lightly pigmented, mouth closed, no body pigmentation

Abbreviations: BW, body width; SL, standard length.

This study reports the first mention of AH larvae captured in the EGSL, and they are the smallest wild-caught larvae that have been reported in the scientific literature for this species. Among the 60 larvae captured in the wild that have been described, the smallest was 9.1 mm long (Bergstad & Gordon, 1993). In the present study, five larvae were below this length, the smallest being 5.62 mm long.

The larvae captured at stations B and C were close to – or even below – hatching sizes estimated from laboratory studies (6–7 mm; Haug, 1990), which indicates that they should be just a few days old. The authors noted the presence of a yolk sac on a larva of *c*. 8 mm (Figure 3c), whereas it was absent in the rest of the larvae (*e.g.*, Figure 3a,b,d). Yolk sacs may have been damaged during capture: studies under controlled conditions have shown that yolk resorption occurs at the age of 50 days at temperatures ranging between 5.0 and 6.0°C, which corresponds to a larval size ranging between 11.5 and 13 mm (Blaxter *et al*., 1983; Pittman *et al*., 1990). Nonetheless, these larvae may also have reached the stage of exogenous feeding. The two larvae captured at station A were larger than those sampled at stations B and C. According to laboratory studies conducted at 6.0°C, larvae exceeding 12.5 mm approach or exceed the age of 50 days post-hatch (Haug, 1990; Karlsen, 1998; Pittman *et al*., 1987). At this size, larvae have a functional mouth, the yolk sac is resorbed and exogenous feeding has already been initiated (Harboe & Mangor-Jensen, 1998; Haug, 1990). These two larvae from station A also presented weak pigmentation on their body (Table 2; Figure 3a). These characteristics indicate that these two larvae have absorbed their yolk reserves and started their exogenous feeding (Table 2). Based on larval-stage classifications from Haug (1990) and Duffy-Anderson *et al*. (2013) for AH and GH, respectively, the authors consider that larvae captured at stations B and C were at the yolk-sac stage given their morphological characteristics (Table 2) whereas the two larvae captured at station A should be at the exogenous feeding stage. Even though AH larval density was low and heterogeneous, the presence of these post-hatch larvae in the Laurentian Channel is in agreement and supports the estimated spawning area by Gatti *et al*. (2020) from electronic tagging.

It should be noted that the surface (0–75 m) water temperature in March is below 0°C in the EGSL, and temperatures above 4.0°C, which are favourable to larval AH survival, are found only below 200 m depth (Galbraith *et al*., 2021). North of the Gaspé Peninsula,

eggs released at depth (>200 m) experience temperatures varying between 4.5 and 5.5°C depending on the location, whereas the deeper waters at Cabot Strait (station A) are warmer, between 5.5 and 6.5°C. Although it is not possible to draw conclusions with the few larvae captured here, the difference in size between the individuals at stations A and B/C may reflect differences in embryonic and larval development rate under this gradient of temperature conditions, despite identical reproductive peaks in February (Gatti *et al*., 2020). The temperature stratification of the water column in March and the very young age of the larvae strongly suggest that all the larvae from stations B and C were captured at depth, whereas the two larger larvae from station A had probably started their gradual ascent in the water column to feed on prey. Later in the spring, warming surface water, melting sea ice and continental runoff lead to the formation of a warm surface layer under which the cold waters of the previous winter are isolated and then form the cold intermediate layer. This layer is located between 50 and 100 m in depth, with temperatures between 0 and 1°C, whereas the surface layer (≤50 m) gradually warms to temperatures near 6°C (Galbraith *et al*., 2021). Larvae must thus eventually cross the cold layer to feed and develop in the warmer surface waters, but the timing of this vertical migration is unknown.

GH larvae are hypothesized to follow the same pattern as previously described for AH larvae at stations B and C; that is, the eggs are released at depths (>200 m) where they incubate at temperatures between 4.5 and 5.5°C. Subsequently, as their yolk reserves are depleted, the larvae migrate to feed in the surface water layer at a size of *c*. 15–16 mm (Ouellet *et al*., 2011; Sohn *et al*., 2010). During fish surveys carried out in May and June from 2005 to 2009, Ouellet *et al*. (2011) captured 50 GH late larvae (*c*. 14–31 mm) in the upper 150 m of the EGSL. These larvae were larger and more developed than those captured in the present study and had already completed their vertical migration in the water column. These authors hypothesized that the main spawning area is located in the portion of the Laurentian Channel facing southwest Newfoundland (Figure 1). Given the location of larvae captured in their study, the authors speculate that at least a part of the spawning occurs more widely across the Laurentian Channel.

The authors report rare captures of AH and GH larvae in the EGSL. The difficulty in capturing these very young larvae is largely due to the complex logistics of working in this area during winter. The very small size of the larvae confirms local reproduction in the EGSL, and the thermal stratification of the water column in March confirms spawning at depth, at temperatures sufficient for embryonic development. The effects of temperature on larval development remain largely unknown, which constitutes a major knowledge gap for estimating age and growth from size, and facilitate larval ecological studies in nature. Given the typical low larval halibut densities previously reported (Ouellet *et al*., 2011) and observed in the present study, follow-up studies on the ecology of halibut larvae in the EGSL will require higher sampling effort, which will allow us to further our knowledge on larva distribution, as well as obtain new information on diet composition, growth rate patterns and other recruitment-relevant variables over the distribution of these two stocks.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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